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IRVINGTONIAN *MICROTUS, PEDOMYS,* AND *PITYMYS* (MAMMALIA, RODENTIA, CRICETIDAE) FROM TROUT CAVE NO. 2, WEST VIRGINIA

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ABSTRACT

Microtus paroperarius Hibbard, 1944, *Pedomys llanensis* Hibbard, 1944, and *Pitymys cumberlandensis* Van der Meulen, 1978 are identified in the Irvingtonian Trout Cave No. 2 fauna from Trout Cave, Pendleton County, West Virginia. Identifications are based on typological and biometric analyses of first lower molars. Dental morphology of *Pedomys llanensis* from this locality is intermediate between *Allophaiomys guildayi* from Cumberland Cave and *P. llanensis* from Cudahy and Conard Fissure. The *M. paroperarius* population has slightly higher mean values for biometric measures of anteroconid complexity than do most other samples of this species. *Pitymys cumberlandensis* from Trout 2 does not differ significantly from samples of this species from Cumberland Cave and Hanover Quarry Fissure, the only other known occurrences. Biochronologic correlations indicate an Irvingtonian II microtine age (from 900 to 400 ± 25 ka) for the Trout 2 fauna. Comparisons of first lower molars of *Pedomys llanensis* suggest that the fauna is older than the Cudahy fauna (that is, older than 610 ka) and younger than the undated fauna of Cumberland Cave, Maryland.

INTRODUCTION

Many Pleistocene fossil localities occur in the caves, fissures, and sinkholes of the Appalachian Mountains (see Kurtén and Anderson, 1980). Most of these sites contain Rancholabrean faunas from the latest Pleistocene, however. The list of Irvingtonian (early-mid Pleistocene) faunal localities in the Appalachian region includes only: Port Kennedy Cave, Pennsylvania (Cope, 1871, 1899; Hibbard, 1955); Cumberland Cave, Maryland (Gidley and Gazin, 1933, 1938; Van der Meulen, 1978); Hanover Quarry No. 1 Fissure, Pennsylvania (Guilday *et al.,* 1984; Guilday, unpublished ms., 1982*b*); Hamilton Cave, West Virginia (Repenning and Grady, 1988); and two localities in Trout Cave, West Virginia—Trout Cave Entrance (Guilday, 1967) and Trout Cave No. 2. A brief history of paleontological work in Trout Cave is provided below.

This paper describes the three most common and biochronologically useful vole species from Trout 2, *Microtus paroperarius, Pedomys llanensis,* and *Pitymys cumberlandensis.* These three species are reported to occur together at only one other locality, Conard Fissure, Arkansas (Brown, 1908; Graham, 1972; Van der Meulen, 1978). However, the probable ancestor of *Pedomys llanensis, Allophaiomys guildayi,* occurs with *M. paroperarius* and *Pitymys cumberlandensis* at two other Appalachian sites, Cumberland Cave and Hanover Quarry Fissure. Comparisons of Trout 2 fossils with material from these and other sites are presented in the systematic accounts. A study, by the author, of the complete mammalian fauna from Trout 2 is in progress.

History of Investigation at Trout Cave

In 1966, Harold Hamilton, Research Associate, The Carnegie Museum of Natural History, found isolated molars of *Ochotona* and *Neofiber* near the entrance

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to Trout Cave. This locality, referred to as Trout Cave in previous references (such as Kurtén and Anderson, 1980), is here referred to as Trout Cave Entrance to distinguish it from Trout 2. Guilday (1967) reported the entrance locality and provided a preliminary faunal list. Many extant species, presently confined to the Canadian Boreal Zone, were found in the upper portion of the 3.6 m deep, stratified deposit. Irvingtonian forms, including *Ondatra annectens, Peromyscus cumberlandensis, Parahodomys,* and *Pleisiothomomys potomacensis,* were recovered from the lower levels. Zakrzewski (1975) described a new vole species, *Atopomys salvelinus,* from the site.

In 1980, Fred Holmes, a local caver, discovered the molar of an extinct peccary at the Trout 2 locality. Initial investigation, under the direction of Frederick Grady (Smithsonian Institution), revealed a diverse fossil assemblage that includes many taxa found in the lower portion of Trout Cave Entrance (Grady, 1981, 1984). Holman (1982) described the herpetofauna of Trout 2 and considered it to be late Kansan in age and generally similar to the herpetofauna of Cumberland Cave, Maryland. The Carnegie Museum of Natural History (CM) made several excavations from 1983 to 1985 under the direction of Allen McCrady and Anthony Barnosky. The fossil material was washed and picked at the museum's New Paris, Pennsylvania, field-processing facility and the resultant bone concentrate was placed in the CM Section of Vertebrate Paleontology, Pittsburgh.

Locality Description

Trout Cave, described by Davies (1958), is located in Pendleton County, east central West Virginia (38°36′14″N, 79°22′10″W, Circleville Quad, USGS 15′ series), about 5 km south of Franklin, West Virginia, on US Highway 220. It occurs in the Coeymans-New Scotland Limestones of the Devonian Helderberg Group. Trout Cave lies within a few hundred meters of Hamilton Cave, another Irvingtonian faunal locality (see Repenning and Grady, 1988).

The Trout 2 locality is situated about 200 m into the cave in a low-ceilinged chamber that is approximately 3 m below the level of the main gallery and connected to it by a narrow chimney. Detailed locality information and maps are on file at CM. The deposit is several square meters in area but only about 0.75 m deep. Most of the fossils were recovered from one horizon, roughly the middle third of the deposit. Fossils were less densely distributed through the upper third of the deposit. No fossils were recovered from the more compact clay beneath the fossiliferous layer. The matrix of the upper, fossil-bearing layers is red-brown clay and silt, very loose and dry.

Before excavation, the floor of the site was divided into five horizontal sections, each being 1 m long (measured parallel to the long axis of the chamber) and as wide as the chamber, approximately 2 m (Fig. 1). The material from each grid was kept separate. The majority of the deposit was excavated without regard to vertical position, with the exception of an alcove to the right of the main chamber that was excavated with stratigraphic as well as horizontal control.

METHODS AND TERMINOLOGY

Fossil material from Meter 0–1 and Meter 4–5 was first compared to ascertain whether there were differences in the fauna that could be related to horizontal position at the site. No faunal differences were discerned. Hence, fossils are described without reference to their horizontal position, although this information is retained in the CM catalog.

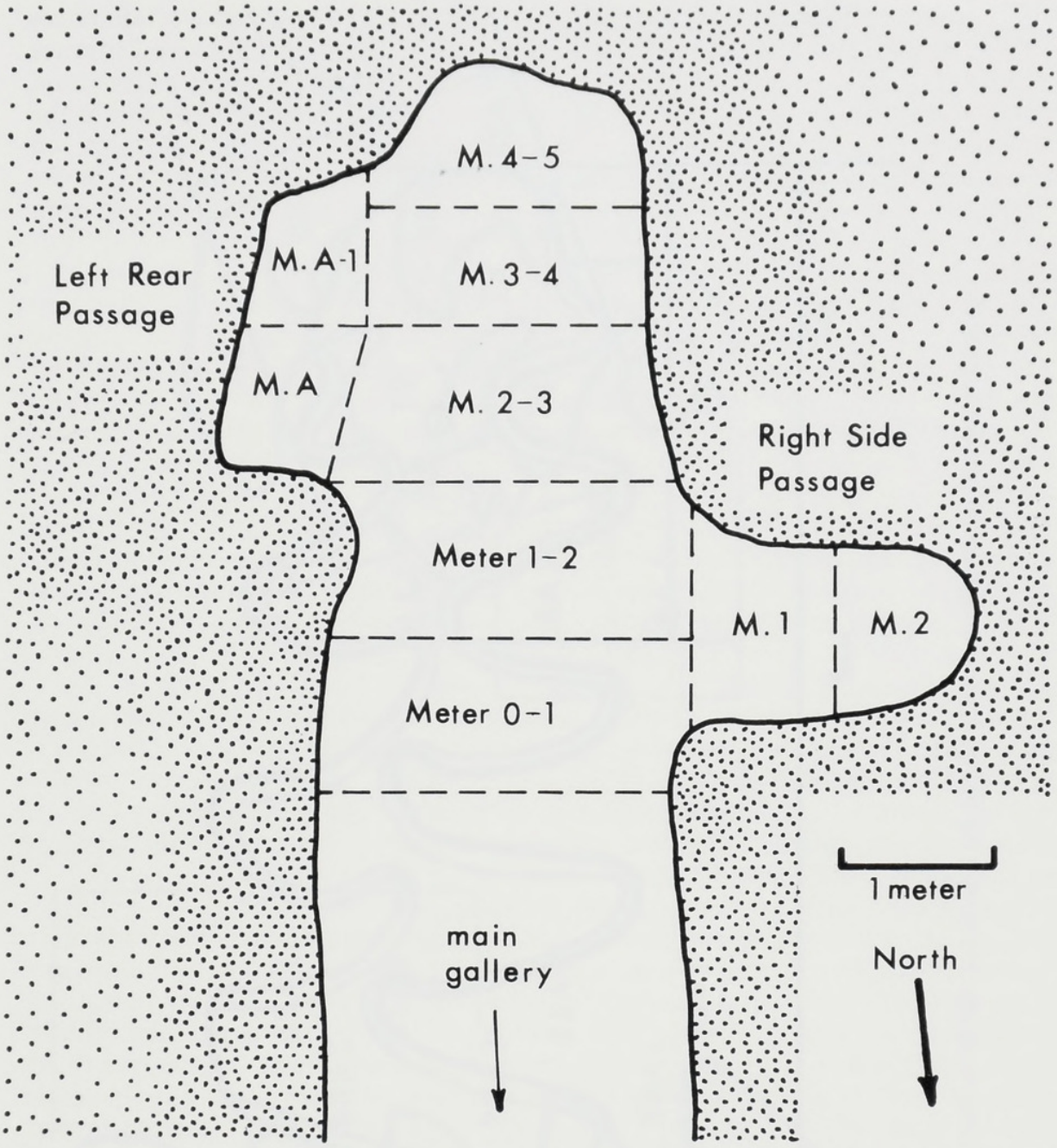

Fig. 1.—Excavation plan of Trout Cave No. 2 locality, Trout Cave, West Virginia. Note "Meters" (abbreviated "M.") are not necessarily one meter in length or width.

Measurements were taken on CM's BIOQUANT digitizing system, which projects images of the teeth onto a computer monitor through a video camera attached to a Wild M8 microscope set at 25× magnification.

The morphometric parameters, a, b, c, L, W, and w′ (Fig. 2) and the ratios derived from these are consistent with those described by Van der Meulen (1973, 1978). Angle T4, Angle T4–T5, and Angle BRA3, which quantify selected components of the m1 occlusal surface, are illustrated in Fig. 9 and described following the systematic account of *Pitymys cumberlandensis.*

Molar terminology is shown in Fig. 3. Lower molar terminology is that of Van der Meulen (1973, 1978). Triangles of upper molars are numbered consecutively,

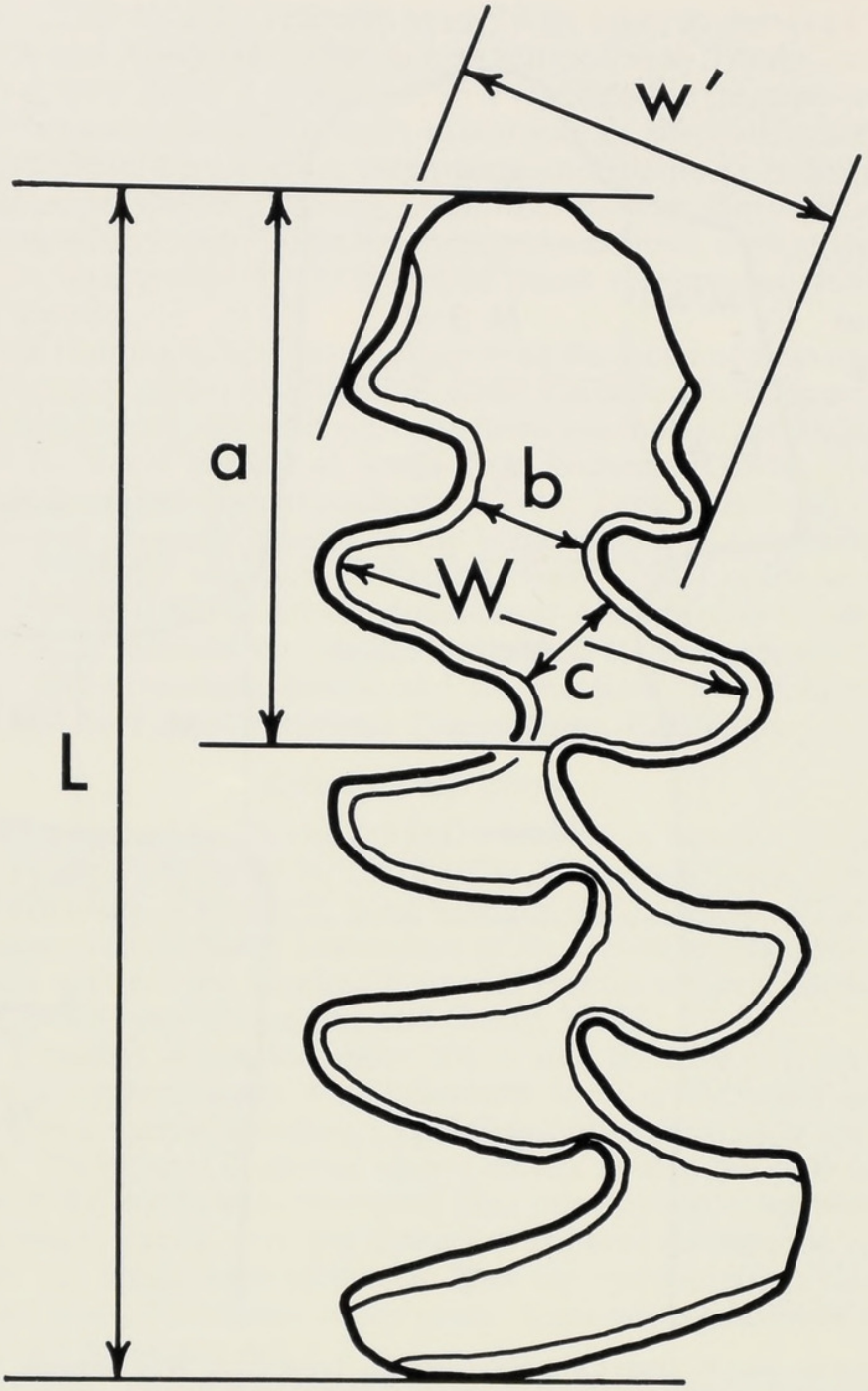

Fig. 2.—Occlusal surface of a right *Pedomys* m1 illustrating the measurements. A/L = 100 a/L; W'/W = 100 w'/W; B/W = 100 b/W; and C/W = 100 c/W, as in Van der Meulen (1973, 1978).

unlike Van der Meulen's system, in which homologous triangles are given the same serial numbers.

In discussions of enamel thickness, I follow Martin (1987), who used the term "positive differentiation" to describe molars in which enamel is thicker on concave than on convex sides of triangles. The term "undifferentiated" describes molars that show little or no appreciable difference in thickness of anterior and posterior enamel edges.

Abbreviations are as follows: AC, anterior cap; ACC, anteroconid complex; AL, anterior loop; BRA, buccal reentrant angle; BSA, buccal salient angle; CM,

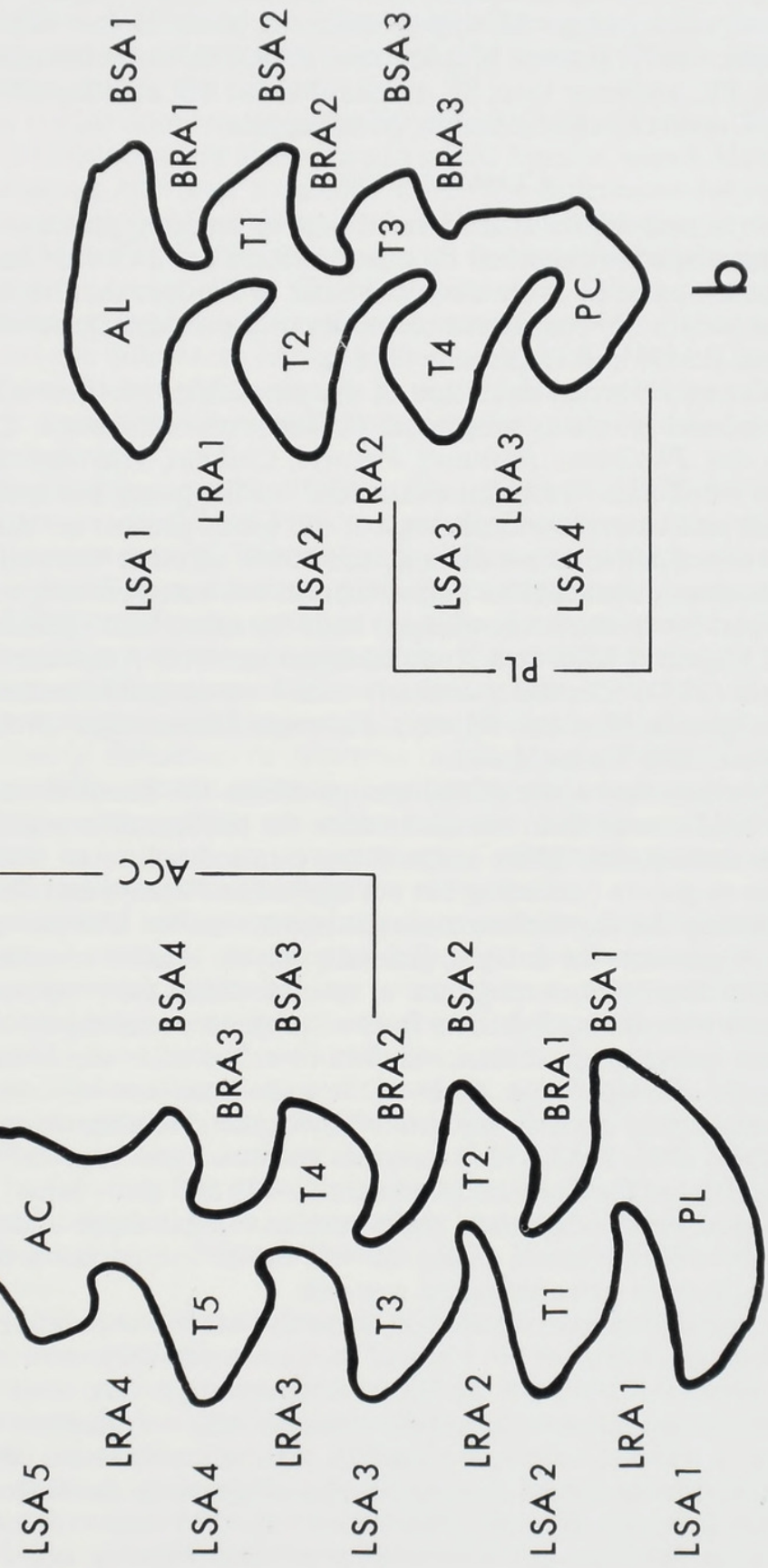

Fig. 3.—Outlines of right m1 (a) and left M3 (b) of *Microtus* illustrating dental terminology.

The Carnegie Museum of Natural History, Pittsburgh; ka, thousand years before present; L, antero-posterior molar length; LOC, locality; LRA, lingual reentrant angle; LSA, lingual salient angle; M, upper molar; m, lower molar; Ma, million years before present; n or N, number of specimens; PARAM, biometric parameter; PC, posterior cap; PL, posterior loop; SE, standard error; SD, standard deviation; T, triangle; UM, University of Minnesota, Minneapolis.

CLASSIFICATION

Pedomys, Pitymys, and *Microtus* are treated here as separate genera. *Microtus* is restricted to those species classified by many authors as *Microtus* (*Microtus*). *Pedomys* is not assumed to be more closely related to *Pitymys* than to *Microtus* or *vice versa.* The genera are considered to belong to the subfamily Arvicolinae, as used by Kretzoi (1969) and Repenning (1987).

Miller (1896) favored a broad definition of the genus *Microtus* that subsumed these previously named genera as subgenera: *Eothenomys, Anteliomys, Lagurus, Alticola, Hyperacrius, Phaiomys, Pedomys, Pitymys, Chilotus, Microtus, Arvicola,* and *Neofiber.* He listed nine "essential characters" of the genus but noted that, although the skull and external morphology of the genus present no diagnostic characters, members of *Microtus* are distinguished from all other voles simply by the presence of rootless molars. Miller's classification was based entirely on extant species; nonetheless, it was the acknowledged basis for many later classifications, including that of Hinton (1926). In a study confined to North American species, Hall and Cockrum (1953) adopted a similarly broad version of *Microtus,* which recognized the subgenera *Microtus, Pitymys, Pedomys, Herpetomys, Orthriomys, Aulacomys, Chilotus,* and *Stenocranius.*

The possibility exists that some of the groups within the broad definition of *Microtus* should be divorced from the taxon once the phylogenetic relationships of the group are understood. Many authors have raised a limited number of Miller's subgenera to genera (including but not limited to *Pitymys* and *Pedomys*), explicitly or implicitly leaving the remaining subgenera under *Microtus* pending further research. Arguments for doing so generally rely on relative morphological and/or biochemical similarity, noting that: a) species within the proposed genus share certain traits which distinguish them from all subgenera retained in *Microtus*; and b) this greater morphologic distance should be reflected in classification by a higher-level taxonomic separation. Some of the traits examined in comparative studies undertaken to help uncover microtine phylogenetic relationships include karyotypes (Matthey, 1952, 1955, 1957), enzymes and nonezymatic proteins (Graf, 1982), the morphology of the baculum (Anderson, 1960) and glans penis (Hooper and Hart, 1962), and suites of physical traits such as cranial shape and number of mammae (Miller 1896; Hinton, 1926), as well as the comparisons of dental morphology ubiquitous in paleontological research.

Unfortunately, the classifications based on these and other comparative studies disagree on the arrangement of all but a few of the genera and subgenera involved (see Anderson, 1985, for a review of *Microtus* taxonomy). But, even if such classifications were in agreement, the result would be only a systematic ranking of relative similarity. How closely such a ranking represents the actual phylogeny is another question, best answered through studies of precisely dated fossil populations, which are uncommon in the Pleistocene record of vole evolution. The biostratigraphic evidence does not demonstrate whether *Pitymys* and *Pedomys* diverged from the ancestry of *M. arvalis* (type species of *Microtus*) before or after

many other vole lineages often subsumed under *Microtus.* As Carleton and Musser (1984:321) noted, "To date, any treatment intermediate to an inclusive or exclusive definition of *Microtus* has been unsatisfactory and will continue to be until the species and all subgenera are revised and more is known about phylogenetic relationships among the clusters."

Hinton (1926) adopted an exclusive definition of *Microtus.* He elevated all of Miller's (1896) subgenera to genera and raised *Neodon,* which Miller synonymized in the subgenus *Microtus,* to generic rank. The differences between these classifications are mainly hierarchical in that Hinton acknowledged the essential correctness of Miller's classification and, with few exceptions, changed only the rank of taxa, not the composition. However, because it elevates the subgenera of *Microtus* while leaving other microtines as ranked by Miller, Hinton's classification emphasizes the differences between the members of *Microtus* (*sensu* Miller). Although it would have been simple to reunite these voles by erecting a new supergeneric taxon that subsumed all species previously included in *Microtus,* Hinton did not do so.

The classification used here follows that of Hinton (1926) in that *Pitymys* and *Pedomys* are removed from *Microtus,* not as special cases but, instead, along with many other vole groups. This course is chosen partly because it increases clarity through reduced nomenclature. Also, this arrangement leaves room under the restricted *Microtus* for the eventual erection of subgenera with which to organize the many species remaining in that genus. If the reader prefers to regard *Pedomys* and *Pitymys* as subgenera of *Microtus* (*sensu lato,* including *Allophaiomys*), the transition is made easily because only the hierarchy is affected. Admittedly, the more inclusive definition of *Microtus* (as in Martin, 1987) better portrays the similarity of the voles in question (considering the usual scope of genera). Nonetheless, I'm convinced that use of the inclusive definition of *Microtus* eventually would force us to adopt an unwieldy set of subgeneric taxonomic categories to describe the multiramous phylogenies of the voles.

The second and perhaps more important problem faced in classifying the voles from Trout 2 concerns the proposed *Pitymys* group and its taxonomic status. Specialists have long noted that true voles can be segregated into two groups based on m1 morphology—one group composed of those species in which triangles anterior to T3 are apposed and confluent and the other group in which triangles anterior to T3 are alternating and closed, or nearly closed. The first group, the *Pitymys* group, generally includes Old and New World *Pitymys, Pedomys, Neodon,* and *Tyrrhenicola.* Some authors also include *Phaiomys* and *Allophaiomys* in the group. The fact that it is possible to construct a *Pitymys* group in which membership is determined by m1 morphology and supported by other selected traits is not disputed here. What is questioned is the conclusion that this group is monophyletic.

Miller (1896) noted the similarities of tooth pattern between *Pitymys, Pedomys,* and *Phaiomys,* especially the latter two. He did not place these subgenera into a distinct category, however. Instead, he maintained their separation as subgenera of *Microtus* on the basis of other morphologic traits. Miller held that *Neodon* was not worthy of even subgeneric distinction and placed *Neodon sikkimensis* of previous authors under *Microtus* (*Microtus*). Miller (1896:65) did not discuss *Neodon*'s m1 morphology, however, noting only features of M1 and M2.

Later, Miller (1912) raised *Pitymys* to generic rank but left other subgenera with similar m1's within *Microtus,* with the result of further increasing the taxonomic

distance between *Pitymys* on one hand, and *Pedomys, Phaiomys,* and *Neodon,* on the other. However, Miller's (1912) work focused on living European species and, thus, he had little cause to reconsider his views on the latter three taxa.

In contrast to Miller's view, Hinton (1926:54) posited that, among voles, "the possession by m1 of three closed triangles only, on the one hand, or of four or more on the other, has been a distinction of generic importance since Pliocene times at least." Hinton explicitly placed genera with only three closed triangles into a *Pitymys* group, which included: *Pitymys, Neodon, Pedomys, Orthriomys, Herpetomys,* and *Tyrrhenicola.* Although he did not erect a formal taxon for this group, it is clear from his discussion that he considered the genera within it to share a close phylogenetic relationship distinct from the *Microtus* group.

The content of Hinton's *Pitymys* group is equivalent to the broad conception of *Pitymys* proposed by Ellerman and Morrison-Scott (1951) and advocated in various forms by Barnosky and Rasmussen (1988), Hibbard *et al.* (1978), Martin (1974), and Zakrzewski (1985). Repenning (1983) and Repenning and Grady (1988) restricted *Pitymys* to include mainly or only North American species but retained the *Pitymys* group as a taxon in the form of the tribe Pitymyini. Species included in the *Pitymys* group differ somewhat from author to author but it is agreed that membership in the genus, or tribe, is determined on the basis of m1 morphology, and that these dental traits reflect a distinct phylogenetic history for the group.

Hinton's division of the voles into the *Microtus* and *Pitymys* groups was tied to his view that both groups descended from an early, undiscovered form of *Phenacomys.* Hinton (1926:50–54) pointed out that, among the various species of *Phenacomys,* the number of closed m1 triangles ranges from three to seven. Therefore, he argued, *Phenacomys* exhibits the morphological variety expected in the common ancestor of both the *Microtus* and *Pitymys* groups.

Fossil discoveries since the publication of Hinton's monograph indicate that the *Allophaiomys deucalion-pliocaenicus* lineage, not *Phenacomys,* is ancestral to *Microtus* and Old World "*Pitymys*" (Chaline, 1966, 1972, 1974; Kretzoi, 1969; Van der Meulen, 1973). *Allophaiomys* is also the most likely ancestor of *Pedomys* (Van der Meulen, 1978), a view supported by the findings from Trout 2. In addition, Repenning and Grady (1988) recently reported evidence of transitional morphotypes linking *Pitymys pinetorum* with *Allophaiomys pliocaenicus* and concluded that the former species is another descendant of *Allophaiomys.*

As an ancestor to both *Microtus* and *Pitymys* group voles, *A. pliocaenicus* cannot be the common ancestor of a discrete *Pitymys*-group taxon. Van der Meulen (1978) indicated that the *Pitymys* group is polyphyletic when he excluded Eurasian "*Pitymys*" from his restricted North American *Pitymys.* Repenning (1983) presented further evidence that the *Pitymys* group is polyphyletic; but, by erecting the tribe Pitymyini, he also implied that the included lineages share a common ancestor not shared by voles in the sister tribe, Microtini—unless, of course, Pitymyini is a polyphyletic taxon.

Comparative studies have tended to produce equivocal results concerning *Pitymys*-group relationships. For example, Matthey (1955) found 62 chromosomes (2N) in both *Pitymys pinetorum* and Eurasian "*P.*" *duodecimcostatus* and concluded that this indicates a close relationship between the two species. For comparison, *Pedomys ochrogaster,* which is considered to be closer than any Eurasian species to *Pitymys pinetorum* (Chaline and Graf, 1988; Repenning, 1983), has 54

chromosomes, as does "*Pitymys*" *subterraneus,* while two other Eurasian species, "*P.*" *fatioi* and "*P.*" *multiplex,* have 48 (Matthey, 1955, 1957).

In a paper on the morphology of the glans penis, Hooper and Hart (1962) noted that *Pedomys ochrogaster* shares affinities with *Pitymys pinetorum* on one hand and with *Microtus californicus* on the other. They considered the similarities between *P. ochrogaster* and *M. californicus* to be so striking as to indicate that the species could be offshoots of the same minor phylogenetic branch. Nonetheless, they concluded that *Pedomys ochrogaster* should be included in *Pitymys* while *Microtus californicus* should remain within *Microtus.*

Biochemical evidence reported by Chaline and Graf (1988), based on a study by Graf (1982), does not support a *Pitymys*-group taxon. Graf's genetic differentiation dendrogram shows *Pitymys pinetorum* to be nearest to *Microtus californicus.* In addition, the branch composed of these two species is no closer, biochemically, to *Pedomys ochrogaster* than to *Microtus montanus.* The results of Graf's analysis can be viewed as evidence that North American *Pitymys* and *Pedomys* are more closely related to Nearctic *Microtus* than to Palearctic "*Pitymys.*" Until it is shown that *Pitymys, Pedomys,* and the remainder of the *Pitymys* group share a common ancestor not shared by *Microtus,* little can be gained by assuming that the *Pitymys* group is a monophyletic taxon or by combining the members into a single genus or tribe that implies the same thing.

Given that taxa are best defined by phylogeny, as advocated by Ghiselin (1966, 1984) and Rowe (1987), consider the usefulness of a taxon defined as *Allophaiomys pliocaenicus* and its descendants. The complete list of membership in this group remains to be determined, largely because of a problematic lack of temporal control at many of the early-mid Pleistocene localities where apparently transitional populations are found. Nonetheless, the taxon, which probably includes most of the true voles, including *Microtus, Pitymys,* and *Pedomys,* promises to be large. Given a classification such as Hinton's (1926), in which *Pitymys, Pedomys,* and other groups often subsumed under *Microtus* are made genera, the taxon defined by *Allophaiomys* and its descendants must be given supergeneric status, perhaps a subtribe. To formally erect such a taxon would go well beyond the scope of this paper; however, the assumption that this group exists as a phylogenetic, and therefore taxonomic, reality underlies much of the foregoing discussion.

SYSTEMATICS

Microtus Schrank, 1798

Microtus paroperarius Hibbard, 1944

(Fig. 4)

Material.—20 isolated m1's (CM 49900–49919); 10 isolated M2's (CM 60731); 13 isolated M3's (CM 60052–60064). See Table 1 for measurements.

Diagnosis.—A species of *Microtus* with m1 with T1–T4 closed and alternating; with T5 confluent with AC in at least 80 percent of the population, differing from species of *Microtus* with T5 closed; and with BSA4 and LSA5 present.

Description.—In addition to the diagnostic characteristics, m1's from Trout 2 assigned to this species have thin, positively differentiated enamel and generally sharp salient angles, although the shape of BSA4 and LSA5 is variable, ranging from rounded to sharply acute. Seventeen percent (3/18) exhibit

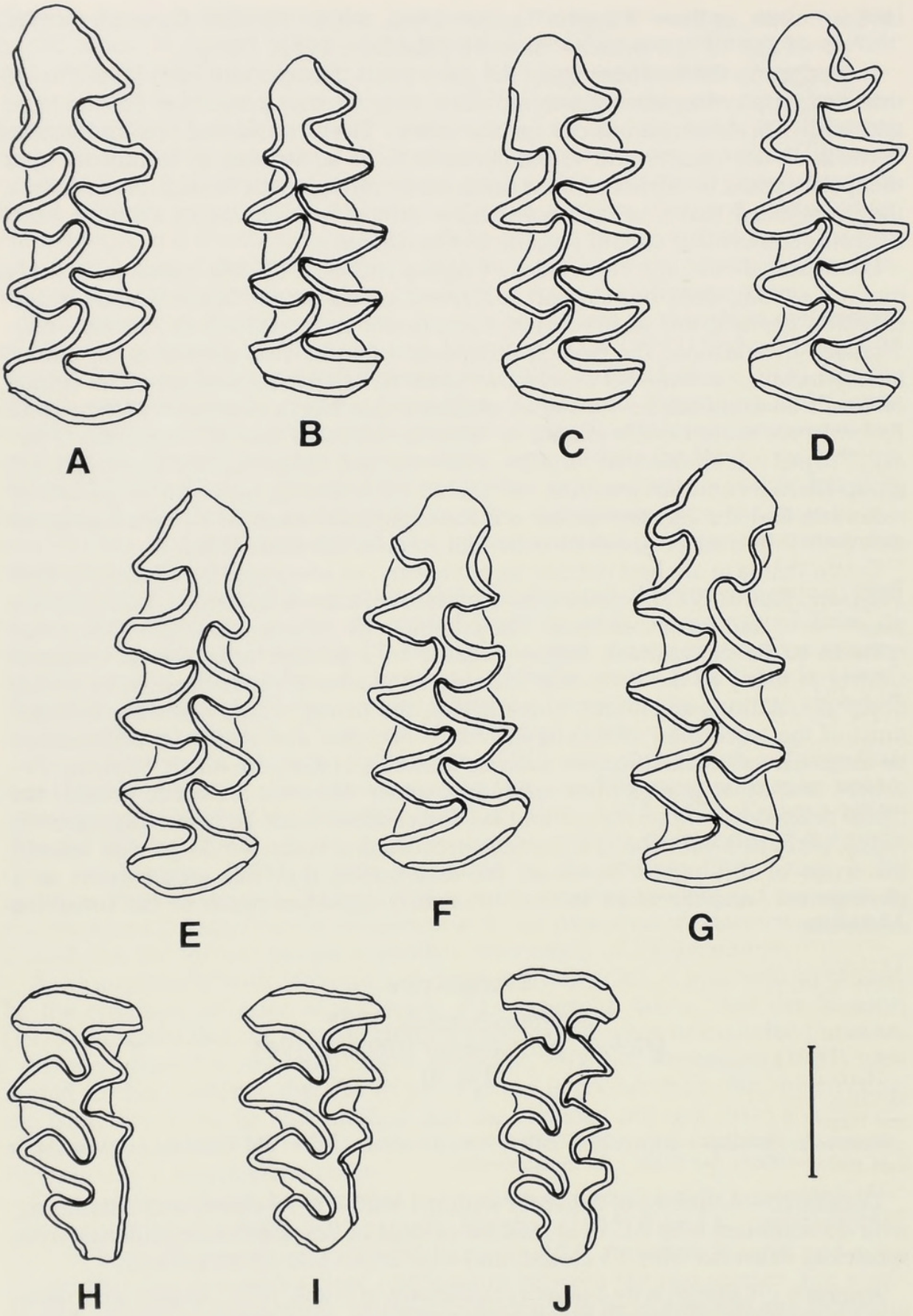

Fig. 4.—*Microtus paroperarius* from Trout Cave No. 2, West Virginia. A–D) left m1's, CM 49903, CM 49911, CM 49905, and CM 49908; E–G) right m1's, CM 49900, CM 49901, CM 49913; H–J) left M3's, CM 60052, CM 60055, CM 60053. Bar equals 1 mm.

Table 1.—*Measurement and ratio data for m1's of* Microtus paroperarius *(n = 17) from Trout Cave No. 2, West Virginia.*

Mean ± SE	SD	Range	Param.
2.89 ± 0.06	0.25	2.51–3.39	L
49.2 ± 0.5	2.0	45.5–52.2	A/L
86.0 ± 1.7	7.0	75.5–100.6	W'/W
16.1 ± 1.4	5.7	5.9–25.2	B/W
2.5 ± 0.5	2.0	0–5.8	C/W

five closed triangles, formed by greater intrusion of BRA3. Thirty-nine percent contain cementum in BRA4 and 28% contain cementum in LRA5.

M3's assigned to *Microtus paroperarius* consist of an anterior loop followed by three triangles and a "complex" PL (that is, one with well developed LSA3 and LRA3 and with LSA4 varying from incipient to well developed). All M3's contain cementum in LRA3. Seventy-seven percent (10/13) contain cementum in BRA3. All M3's exhibit closure between T2 and T3 (T3 and T4 of Van der Meulen, 1978). Thirty-eight percent (5/13) are closed between T1 and T2. One exceptional M3 (CM 60053, Fig. 4J) exhibited much greater development of the posterior salient angles and contained cementum in LRA4 as well as LRA3 and BRA3.

Ten M2's were segregated from a sample of 77 microtine M2's from Level 0–1 and assigned to *M. paroperarius*. They are distinguished from the remaining M2's by their larger size (mean L = 1.89 mm, SD = 0.11, n = 10), sharper salient angles, and by the presence of cementum in the inflection posterior to T2 that corresponds to location of a second lingual reentrant. None of the M2's from Trout 2, including those assigned to *M. paroperarius,* exhibited a fifth dentine field, or "*pennsylvanicus* loop."

The Trout 2 material was compared directly with *M. paroperarius* from Cumberland Cave, Maryland (79 m1's, CM 20412; 80 m1's, CM 30277; and 89 M3's, CM 30277), Cudahy Ash Mine, Kansas (3 m1's, CM 7477–CM 7479) and Hanover Quarry Fissure, Pennsylvania (3 m1's, CM 41415, CM 41416, CM 41424) and with descriptions and figures provided by Hibbard (1944) and Paulson (1961). Morphometric data are listed on Table 2. There is no doubt as to the assignment; however, there are several differences between the Trout 2 population and samples from other sites.

Mean antero-posterior length of m1's of *M. paroperarius* from Trout 2 is 2.89 mm. This is near the upper end of the range of means reported for this species, but well below the maximum. Mean lengths that have been reported include 2.96 mm from Cudahy (Paulson, 1961), 2.80 from Hall Ash (Eshelman and Hager, 1984), 2.79 mm from Sunbrite Ash Mine (Van der Meulen, 1978), 2.74 mm from Cumberland Cave (Van der Meulen, 1978), and 2.61 mm from Porcupine Cave, Colorado (Barnosky and Rasmussen, 1988). The largest reported m1's of *M. paroperarius,* with lengths up to 3.6 mm, are from the Alamosa fauna (Rogers *et al.,* 1985).

Seventeen percent (3/18) of m1's from Trout 2 exhibit closure of T5. The remainder have only T1–T4 closed. Of the samples of m1's of *M. paroperarius* reported, 20% from the Cudahy fauna (Paulson, 1961); 8–9% (n = 59) from Sunbrite Ash Mine (Van der Meulen, 1978); 2.5% (n = 152) from Cumberland Cave (Van der Meulen, 1978); and none of the specimens (n = 9) from Hall Ash (Eshelman and Hager, 1984) exhibit closure of five triangles. Apparently, the Trout 2 population is near the higher end of the range of variation for this trait.

Thirty-nine percent of m1's from Trout 2 contained cementum in BRA4. Of m1's from other localities, over 50% of those from Cudahy (Paulson, 1961), 20% of those from Hall Ash (Eshelman and Hager, 1984), and only 10% of those from Cumberland Cave (Van der Meulen, 1978) contain cementum in BRA4. In this trait also, the Trout 2 population is nearer the higher end of the range of variation.

The mean A/L ratio of m1's from Trout 2 was greater, and the mean B/W ratio was less, than means obtained by Van der Meulen (1978) from samples from Cumberland Cave, Sunbrite Ash Mine, and Conard Fissure (see Table 2). These differences both suggest that the Trout 2 *M. paroperarius* population exhibits greater relative development of the ACC.

Discussion.—If the evolution of *M. paroperarius* included a trend toward greater m1 ACC complexity, the Trout 2 population is an advanced form of this species (based on comparisons of T5 closure, BRA4 cementum, and A/L and B/W ratios). However, the assumption regarding the polarity of this trait is based only on

Table 2.—*Measurement and ratio data for* Microtus paroperarius *m1's from four localities, including Trout Cave No. 2 (T2). Data from Cumberland Cave (CC), Sunbrite Ash Mine (SA), and Conard Fissure (CF) from Van der Meulen (1978: table 3).*

Loc.	N	Mean ± SE	SD	Range	Param.
T2	17	49.2 ± 0.5	2.0	46–52	A/L
CC	60	48.5 ± 0.23	1.76	45–54	
SA	46	48.2 ± 0.28	1.92	43–52	
CF	5	48.0 ± 0.71	1.58	46–50	
T2	17	16.1 ± 1.4	5.7	6–25	B/W
CC	66	19.2 ± 0.83	6.73	≤5–36	
SA	51	17.5 ± 1.02	7.29	≤5–35	
CF	3	17.3 ± 1.45	2.52	15–20	

general trends among microtines, not on evidence particular to this species. Also, the observed differences are slight, about equal to the range of individual variation reported within modern species of *Microtus*.

Repenning and Grady (1988) note progressive evolution of the M3 from simple to complex in *M. paroperarius*. All M3's from Trout 2 assigned to this species are complex, which might indicate that the Trout 2 population is relatively advanced in that regard.

Authors disagree regarding the dental traits, if any, that distinguish *M. paroperarius* from the extant species *M. oeconomus*. Repenning and Grady (1988:15) stated that the two species differ in that the m1 of *M. paroperarius* usually has a less inflated AC with less prominent LSA5 and LRA5. In contrast, Paulson (1961: 144) stated that *M. paroperarius* from the type locality shows greater development of the ACC with an LRA5 that " is almost always present and is deeper and better developed than in *M. oeconomus*" and with a BRA4 that contains cementum in over half of the specimens. Van der Meulen (1978:123) stated that m1's of the two taxa cannot be distinguished and that their dental morphologies differ only in that T1 and T2 of M3 are more often confluent in *M. paroperarius*. The degree of development of BSA4 might differentiate m1's of the two forms. BSA4 is reported to be extremely rare in m1's of *M. oeconomus* (Morlan, 1984), whereas this angle is present in all m1's of *M. paroperarius* from Trout 2 and in nearly all specimens from other localities examined by the author. This difference was relied upon for the present study with the understanding that further comparative work is needed.

Large samples of *Microtus paroperarius* are known from localities in southwestern Kansas, including the Cudahy and Sunbrite ash mines (Hibbard, 1944; Paulson, 1961); Conard Fissure, Arkansas (Graham, 1972); Cumberland Cave, Maryland (Van der Meulen, 1978); and Hansen Bluff, Colorado (Rogers *et al.*, 1985; Repenning, 1987). Other localities where this species has been found include Wellsch Valley, Saskatchewan (Stalker and Churcher, 1982); Porcupine Cave,

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Fig. 5.—*Pedomys llanensis* from Trout Cave No. 2, West Virginia. A–G) left m1's, CM 49920, CM 49941, CM 49928, CM 49950, CM 49925, CM 49922, CM 49957; H–J) right m1's, CM 49933, CM 49961, CM 49945; K) left M3, CM 60090; L, M) right M3's, CM 60086, CM 60088. Bar equals 1 mm.

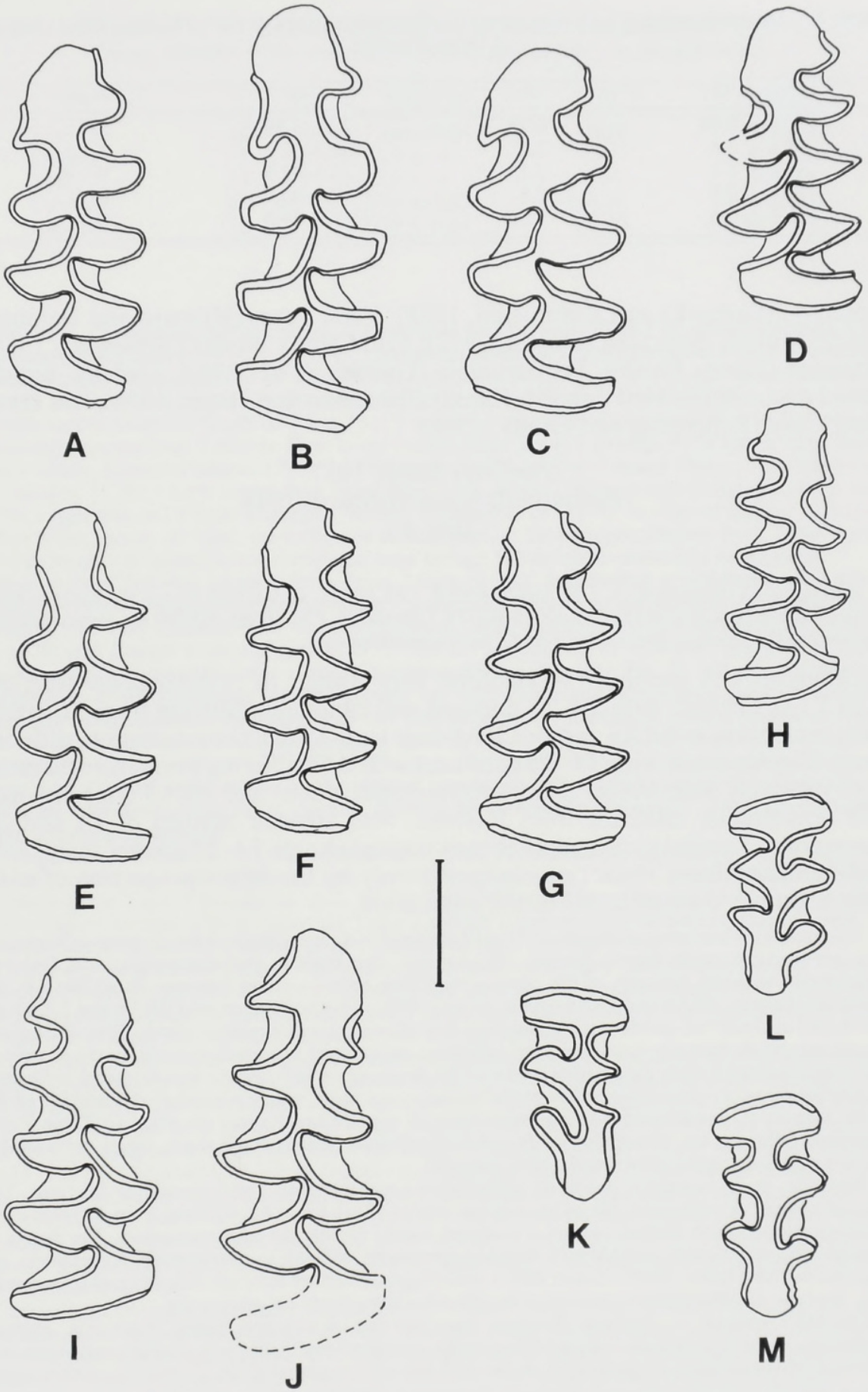
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Table 3.—*Measurement and ratio data for m1's of* Pedomys llanensis *(n = 44) from Trout Cave No. 2, West Virginia.*

Mean ± SE	SD	Range	Param.
3.18 ± 0.04	0.28	2.51–3.59	L
47.2 ± 0.4	2.5	39.5–52.1	A/L
84.8 ± 1.1	7.1	73.7–98.5	W′/W
19.8 ± 0.9	5.6	9.9–30.6	B/W
21.0 ± 0.6	4.0	13.3–29.0	C/W

Colorado (Barnosky and Rasmussen, 1988); Vera, Texas (Hibbard and Dalquest, 1966); Mullen, Nebraska (Martin, 1972); Little Sioux, Iowa (Zakrzewski, 1985); Hanover Quarry Fissure, Pennsylvania (Guilday *et al.*, 1984; Guilday, unpublished ms., 1982*b*); Hall Ash Pit, Kansas (Eshelman and Hager, 1984); and Hamilton Cave (Repenning and Grady, 1988).

Pedomys Baird, 1857
Pedomys llanensis Hibbard, 1944
(Fig. 5)

Material.—58 isolated m1's (CM 49920-49968, CM 60033, CM 60038 [8 m1's]). Eight isolated M3's (CM 60070, CM 60075, CM 60078–60079, CM 60086, CM 60088–60090) are also tentatively assigned to this species. See Tables 3 and 7 for measurements.

Diagnosis.—A species of Arvicolinae very similar to *P. ochrogaster* with m1 with T1–T3 closed; with T4–T5 apposed and confluent, differing from *Microtus*; with cementum in BRA4 and/or LRA5 in at least 25% of the population, differing from *Allophaiomys*; with T4–T5 confluent with AC, differing from *M. meadensis*; with relatively wide buccal reentrants (see description) and BRA3 typically open and semicircular, differing from *Pitymys*; with anterior borders of T4 and T5 more nearly parallel to one another than normal (Angle T4–T5 greater than 140°). Differentiated from *Pedomys ochrogaster* only by the larger proportion of m1's with a simple, crescentic AC in the population.

Description.—First lower molars from Trout 2 assigned to this species show a wide range of variation. The anterior cap varies from a simple, *Allophaiomys*-like knob to one matching typical *Pedomys ochrogaster,* with the majority of the population falling between either extreme. In addition to the traits listed above, BSA4 and LSA5 appear in over 90% of the population and BRA4 and LRA5 are developed in about two-thirds of the population. Buccal reentrants are relatively wide. First and second buccal reentrants typically have an abrupt inflection, as opposed to a gradual curve, in the enamel of the posterior border while the anterior border of the reentrants is less concave than is typical in *Pitymys cumberlandensis.* General orientation of the triangles was more nearly normal to the midline of the tooth than in *P. cumberlandensis* (measurements of triangle orientation are listed in Table 7 and discussed following the description of *P. cumberlandensis*). Salient angle shape varies considerably but the angles are more often angular than rounded.

Typically, molar enamel is positively differentiated and relatively thin, resembling *Microtus.* The thinner enamel extends along the entire convex border of m1 triangles, differing from *Pitymys cumberlandensis,* in which thinner enamel is confined mainly to near the reentrant apices. The degree of enamel differentiation is variable and, in many specimens, difficult to characterize. Nonetheless, for specimens with enamel differentiation that is unambiguously either *llanensis*-like or *cumberlandensis*-like, the type of differentiation concurs with identifications based on other traits.

The M3's assigned to *Pedomys llanensis* have two buccal and two lingual reentrants, all with cementum. Generally, shallow folds are found on the posterior loop in the place of additional reentrants; but these folds are absent on some M3's. A few teeth have an incipient LRA3. T1 and T2 are alternating, rather than directly apposed, and LRA1 is moderately deep and curves posteriorly as it approaches

Table 4.—*Comparison of m1 antero-posterior length of* Pedomys llanensis *from Trout 2, Conard Fissure, Cudahy, Vera, and Kanopolis local faunas (see text for references).*

Loc.	N	Mean ± SE	SD	Range
Trout 2	44	3.18 ± 0.04	0.28	2.51–3.59
Cudahy	3	2.9 ± —	—	2.8–3.0
Vera	33	2.8 ± —	—	2.6–3.1
Conard	47	2.74 ± 0.03	0.18	2.32–3.26
Kanopolis	12	2.74 ± 0.04	0.20	2.61–2.92

the midline. The result is partial closure of the dentine field between T1 and T2, which contrasts with the complete confluence of T1–T2 in *Pitymys cumberlandensis.* M3 enamel is characterized by positive differentiation. The assignment of Trout 2 M3's to either *P. llanensis* or *Pitymys cumberlandensis* remains tentative; this problem is discussed further in the section on *P. cumberlandensis.*

Mean antero-posterior length of Trout 2 m1's is greater than that of any population of *P. llanensis* previously reported (see Table 4). First lower molars from Trout 2 average 9.4% longer than those from Cudahy, Kansas (Paulson, 1961); 16.5% longer than those from Conard Fissure, Arkansas (Van der Meulen, 1978); 13.4% longer than those from Vera, Texas (Hibbard and Dalquest, 1966); and 15.8% longer than m1's from Kanopolis, Kansas (Hibbard *et al.,* 1978). In view of the size variation within living species of voles, the difference in this measure between populations from Trout 2 and the type locality (Cudahy) is not considered large enough to warrant erection of a new species.

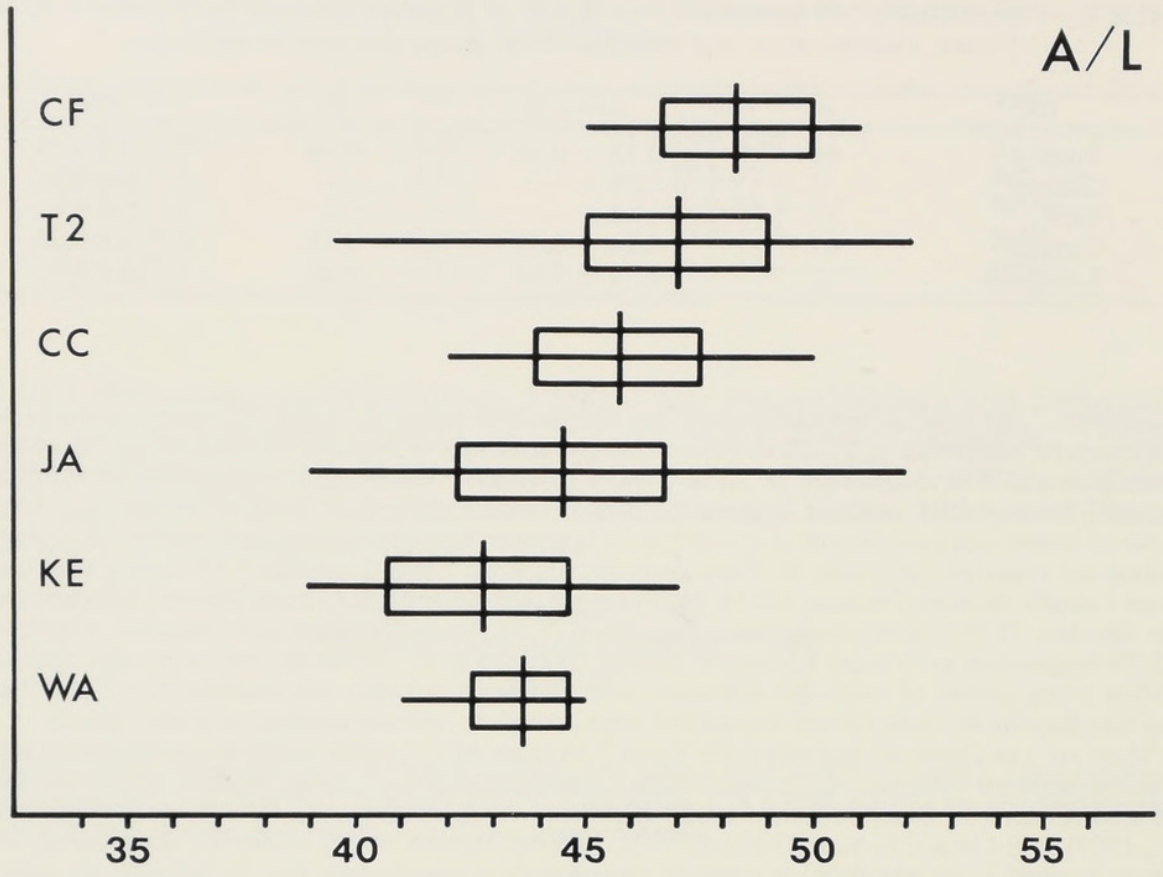
Most m1's of *Pedomys llanensis* from Trout 2 have an ACC pattern that is morphologically intermediate between *Allophaiomys guildayi* from Cumberland Cave (Van der Meulen, 1978) and more advanced *Pedomys llanensis* from Cudahy (Hibbard, 1944; Paulson, 1961), Kanopolis (Hibbard *et al.,* 1978), and Conard Fissure (Graham, 1972; Van der Meulen, 1978). However, the material from Trout 2 spans a remarkably wide range of morphologic variation (see Fig. 5). Initially, an attempt was made to divide the sample into two groups, one with a simpler *Allophaiomys*-like ACC and the other with a more complex, *Pedomys*-like ACC. This attempt was abandoned when it became obvious that the bulk of the sample was intermediate between the two types and that there was a complete continuum from one extreme to the other. The Trout 2 material was assigned to *Pedomys llanensis* rather than *Allophaiomys guildayi* on the basis of population-wide statistics based on measurements and single-trait surveys that, taken together, describe the complexity of the ACC. These are discussed in the following paragraphs.

Comparison of biometric values and ratios between the Trout 2 sample and *Pedomys llanensis* from Conard Fissure (measured by Van der Meulen, 1978) indicates that the ACC is less developed among members of the Trout 2 population. A/L, W'/W, and C/W are all lower for the Trout 2 sample and B/W is higher. In each of these ratios the Trout 2 sample is intermediate between Conard Fissure *P. llanensis* and *Allophaiomys guildayi* from Cumberland Cave (see Fig. 6 and 7).

First lower molars from Trout 2 were compared directly with four *P. llanensis* m1's from Conard Fissure, Arkansas (CM 41860). The Conard Fissure teeth matched many Trout 2 m1's in overall morphology and in point-by-point comparisons. Population-wide differences were discerned only upon comparison of biometric statistics obtained from a larger sample.

The material from Trout 2 assigned to *Pedomys llanensis* was first suspected to be *Allophaiomys guildayi* (=*Microtus* [*Pedomys*] *guildayi* Van der Meulen, 1978). It was compared to the holotype (CM 20333), paratypes (CM 20412), and a large sample (n = 180) of *A. guildayi* from Cumberland Cave. *A. pliocaenicus* from Java Local Fauna, South Dakota (CM 24693, 5 m1's), was also examined, as was material assigned to *A.* cf. *guildayi* from Hanover Quarry Fissure, Pennsylvania (CM 41409–41411, 3 m1's; CM 41420, 45 m1's). Guilday (unpublished ms., 1982*b*) regarded the material from Hanover Quarry to be slightly less advanced than *A. guildayi* from the type locality, but not as primitive as *A. pliocaenicus,* based on ml ACC development. Comparative studies made in the course of Trout 2 research fully support this conclusion. The Hanover Quarry material is referred to here as *A. guildayi* with the understanding that a diagnostic boundary separating *A. pliocaenicus* from *A. guildayi* is not yet clearly established.

Comparison revealed that many individual m1's from Trout 2 and Cumberland Cave are not separable on the basis of morphology; however, taken as a whole, the population from Trout 2 evidences slightly greater development of the ACC than is typical for *A. guildayi.* Measurements showed that, in addition to greater mean length, Trout 2 m1's have higher mean values for A/L, W'/W, and C/W, and a lower mean B/W ratio than *A. guildayi* (as measured by Van der Meulen, 1978). Both samples


A/L
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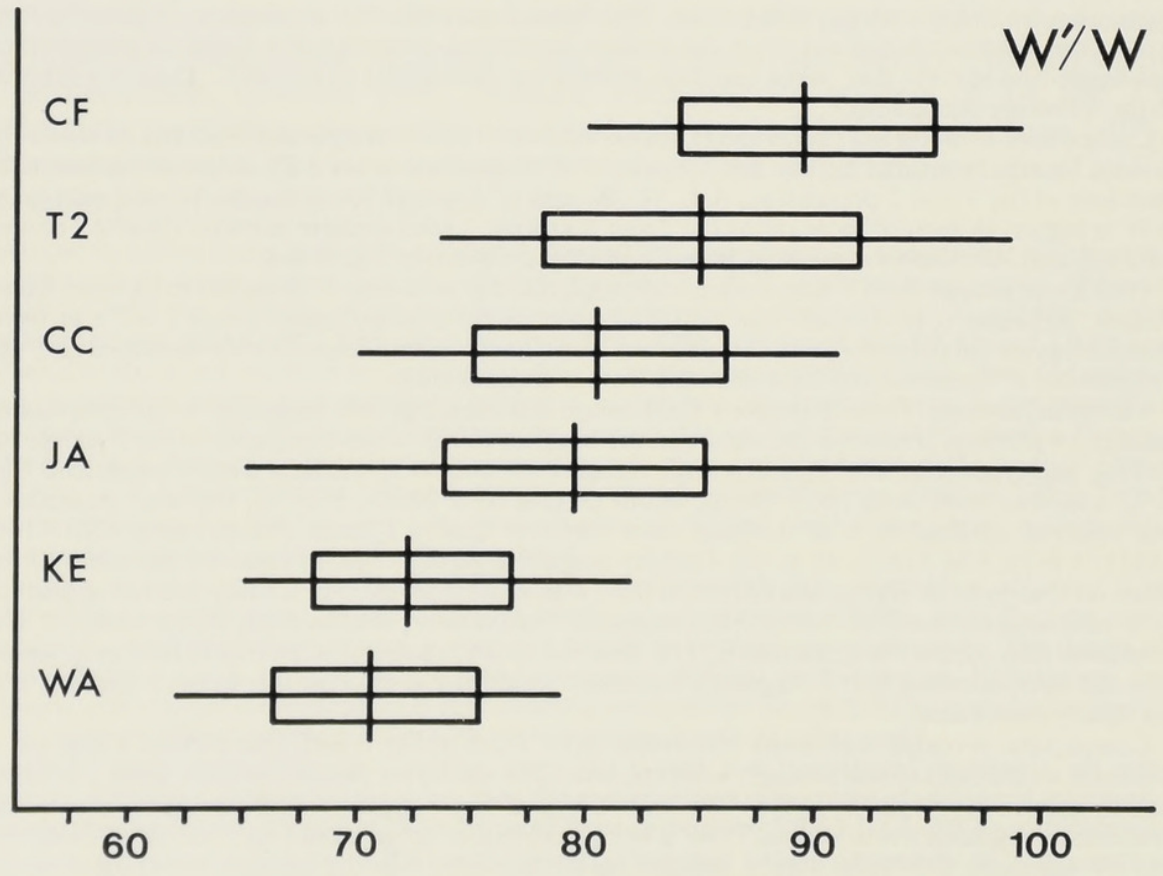
W′/W
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100

are characterized by wide ranges of variation and there is a great deal of overlap in the ranges (see Fig. 6 and 7).

Over 90% of the m1's from Trout 2 exhibited some development of BSA4 and LSA5, ranging from a small but sharp turn in the enamel anterior to BRA3 and LRA4 up to complete development of T6 and T7 with cement in BRA4 and LRA5. By comparison, only 64% (n = 148) of *A. guildayi* m1's from Cumberland Cave (samples CM 20413 and CM 20416) and only 50% (n = 40) of those from Hanover Quarry (CM 41420) exhibited equivalent development of these angles. In addition, 66% of m1's from Trout 2 show at least incipient development of BRA4 and LRA5, whereas less than 8% of *A. guildayi* from both Cumberland Cave and Hanover Quarry have these same reentrants.

Discussion.—Van der Meulen (1978) recognized that *Allophaiomys guildayi* was the most probable ancestor of *Pedomys llanensis* and suggested that those two species formed the central portion of an evolutionary lineage from *A. pliocaenicus* (=*A.* sp. of Van der Meulen) to *P. ochrogaster.* Repenning (1983) noted that the largest morphologic gap in the record of that lineage was between *A. guildayi* and then known samples of *P. llanensis.* He viewed this gap as the practical diagnostic boundary between *Allophaiomys* and *Pedomys* and, accordingly, placed *Microtus* (*Pedomys*) *guildayi* of Van der Meulen under *Allophaiomys.*

Martin (1987) proposed a more precise definition of the necessarily artificial border between these two genera (his subgenera). Noting that neither *Allophaiomys pliocaenicus* nor *A. guildayi* exhibit cementum in BRA4 or LRA5 of m1, he suggested that the diagnostic line between *Allophaiomys* and *Pedomys* be drawn where at least 25% of the sample m1's contain cementum in one or both of BRA4 and LRA5.

Pedomys llanensis from Trout 2 has cementum in BRA4 and/or LRA5 in approximately 25% of the population. In one sample, 18% (8/44) had cementum in BRA4 and 25% (11/44) had cementum in LRA5. By this measure, the Trout 2 population is the least advanced form of *Pedomys* that has been reported.

The m1 of the Trout 2 population of *P. llanensis* represents the morphological and, perhaps, evolutionary link between *A. guildayi* and more typical *P. llanensis.* This is not to say that the Trout 2 fauna is necessarily younger than the fauna from Cumberland Cave (type locality of *A. guildayi*). The differences between these populations are of the scale observed between contemporaneous subspecies of modern voles. One drawback of the classification used here (as opposed to one in which *Allophaiomys* and *Pedomys* are subsumed under *Microtus*) is that the close relationship between *A. guildayi* and *P. llanensis* is obscured by a generic-level taxonomic leap. Nevertheless, any division of an evolutionary lineage is artificial—the system used here merely increases the prominence of the division, not its artificiality.

Although it has been stated that *P. llanensis* differs from *P. ochrogaster* by the lesser development of the ACC on m1 (Van der Meulen, 1978), a thorough comparison of the two forms has not been published, to my knowledge. In view of the lack of diagnostic features separating these species and the wide range of variation generally ascribed to *P. ochrogaster,* such a comparison might show that

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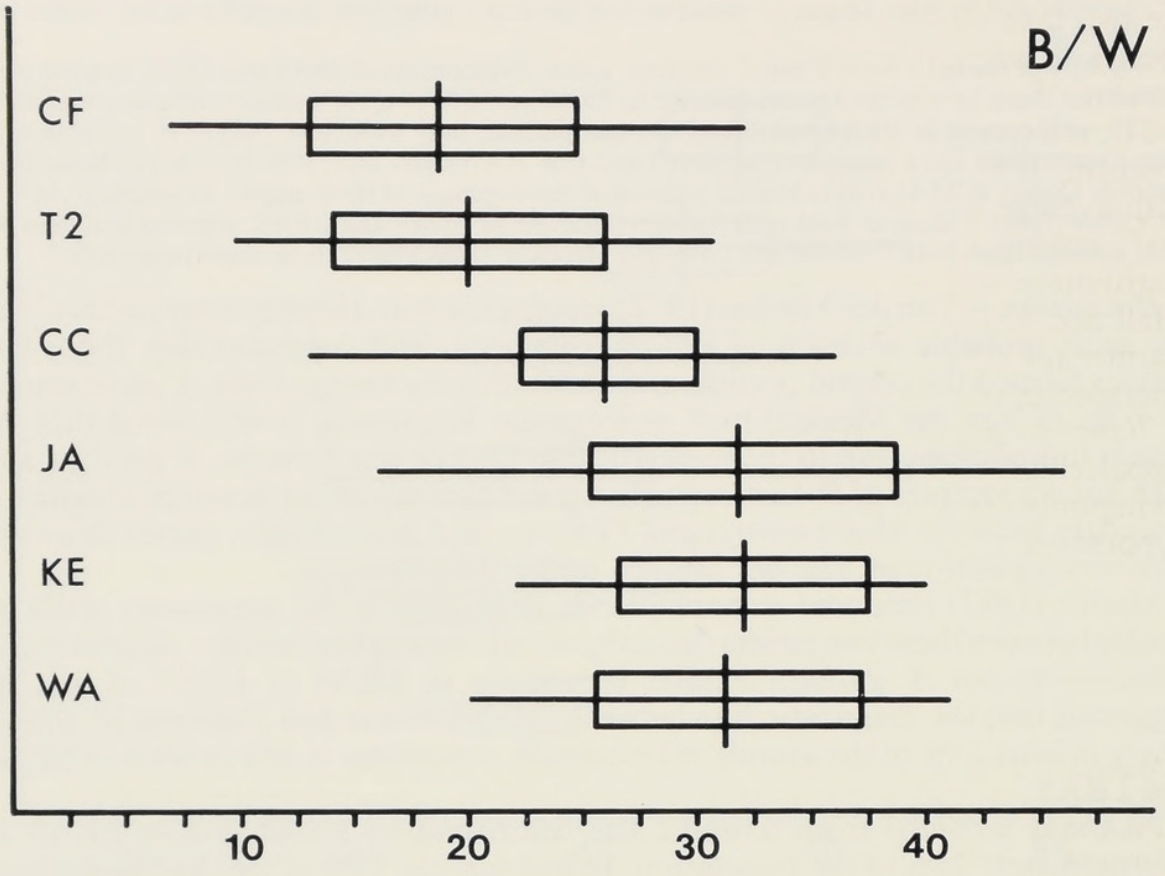
Fig. 6.—Box plots of m1 A/L and W'/W ratios for populations of *Allophaiomys pliocaenicus* from Wathena (WA), Kentuck (KE), and Java (JA) local faunas; *A. guildayi* from Cumberland Cave (CC); and *Pedomys llanensis* from Trout 2 (T2) and Conard Fissure (CF). See Fig. 2 for explanation of measurements. Data for *A. pliocaenicus* from Martin (1989, Table 5) and Van der Meulen (1978, Table 2). *A. guildayi* and Conard Fissure *P. llanensis* data from Van der Meulen (1978, Table 2).


B/W
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T2
CC
JA
KE
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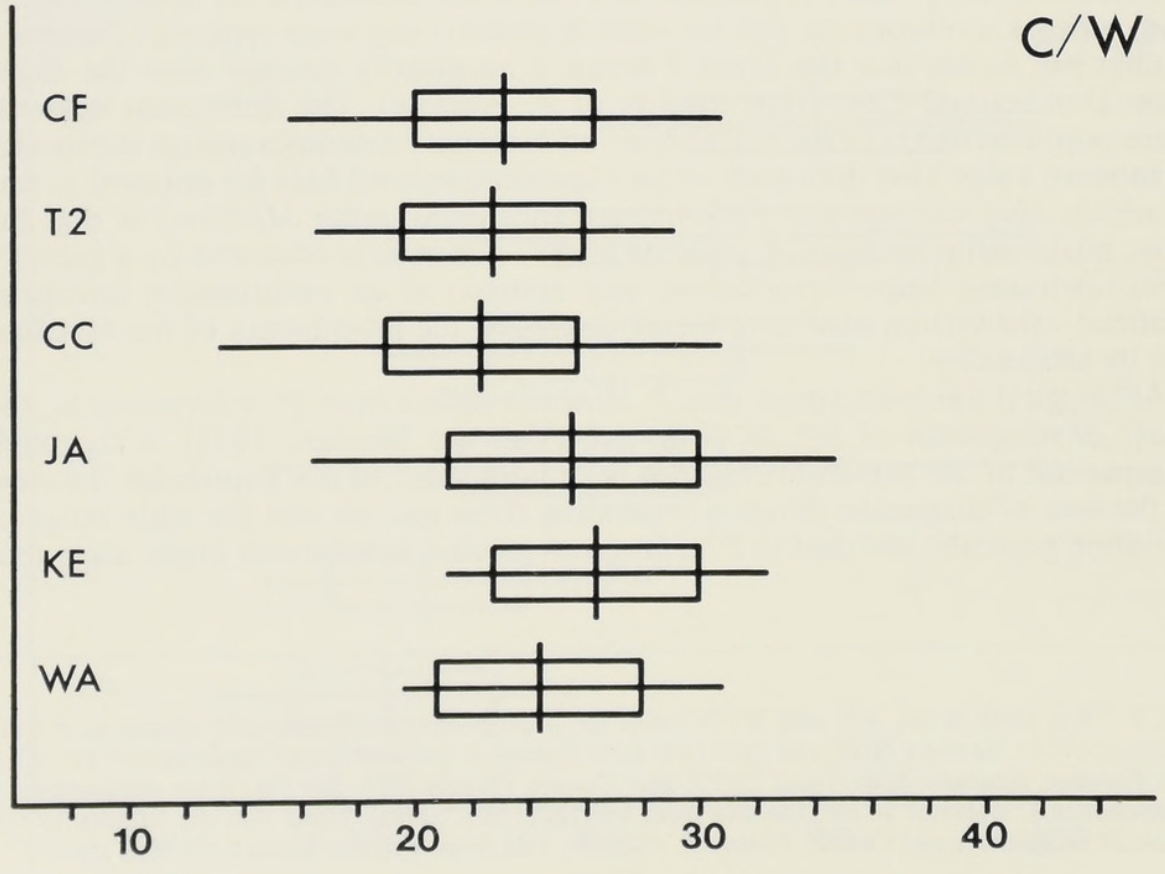
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the two taxa are conspecific. I have not examined enough populations of either species to support or reject such a revision, so *P. llanensis* is retained for the present.

The relatively large size of *P. llanensis* m1's from Trout 2 poses an interesting problem. It is not known whether climatic conditions were directly correlated with average size (as in Bergmann's Rule) for either *P. llanensis* or *A. guildayi.* In *P. ochrogaster,* the smallest subspecies, *P. o. minor,* has the most northerly distribution and the largest subspecies, *P. o. ludovicianus,* is the most southern (Hall and Kelson, 1959). Perhaps the Trout 2 population dates from a time of warmer (or otherwise more favorable) climate. Alternatively, perhaps a lack of interspecific competition from larger vole species "allowed" a marginal or isolated *P. llanensis* population to evolve larger body size during that time in the mid-Appalachian region. Comparison of the complete Trout 2 fauna with similar Irvingtonian faunas might help support or contradict these and other speculative hypotheses.

Pitymys McMurtrie, 1831
Pitymys cumberlandensis Van der Meulen, 1978
(Fig. 8)

Material.—247 isolated m1's (CM 49969–49999, CM 60000–60024, CM 60025 [49 m1's], CM 60026 [42 m1's], CM 60027 [41 m1's], CM 60028 [43 m1's], CM 60029 [5 m1's], CM 60030 [6 m1's], CM 60032 [5 m1's]). See Tables 5 and 7 for measurements.

Fourteen isolated M3's (CM 60068, CM 60069, CM 60071–CM 60074, CM 60077, CM 60080–CM 60085, CM 60087) are tentatively assigned to this species.

Diagnosis.—A species of Arvicolinae similar to *Pitymys pinetorum* with m1 with T1–T3 closed; with T4–T5 apposed and confluent, differing from *Microtus*; with narrow reentrants that trend anteriorly as they approach the midline of the tooth, differing from *Pedomys*; with anterior borders of T4 and T5 more nearly normal than parallel (mean Angle T4–T5 less than 135°), differing from *Pedomys llanensis*; with very shallow BRA4 and LRA5; with a narrow but open dentine field between T5 and AC; and with an unreduced M3 with T1–T2 broadly confluent.

Description.—First lower molars assigned to *Pitymys cumberlandensis* from Trout 2 conform closely to Van der Meulen's (1978:126) original diagnosis and description. Like specimens from the type locality, *P. cumberlandensis* molars from Trout 2 typically exhibit relatively thick enamel that thins only near the reentrant apices, more-or-less rounded salient angles, and narrow, curving reentrants. The shape of the reentrants, especially the buccal ones, was found to be one of the most reliable traits distinguishing *P. cumberlandensis* from *Pedomys llanensis* in the fauna (see discussion below). BSA4 and LSA5 are only weakly developed—of 70 m1's from Trout 2, only one was found with cementum in BRA4. Similarly, two of 67 m1's from the type locality contained cementum in this angle (Van der Meulen, 1978:127).

Comparison of biometric values obtained from m1's of *P. cumberlandensis* from Trout 2 and Cumberland Cave shows the populations to be very similar in all regards (Table 6). The strong resemblance between the two samples contrasts with the noteworthy differences that separate, re-

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Fig. 7.—Box plots of m1 B/W and C/W ratios for populations of *Allophaiomys pliocaenicus* from Wathena (WA), Kentuck (KE), and Java (JA) local faunas; *A. guildayi* from Cumberland Cave; and *Pedomys llanensis* from Trout 2 (T2) and Conard Fissure (CF). See Fig. 6 for further information.

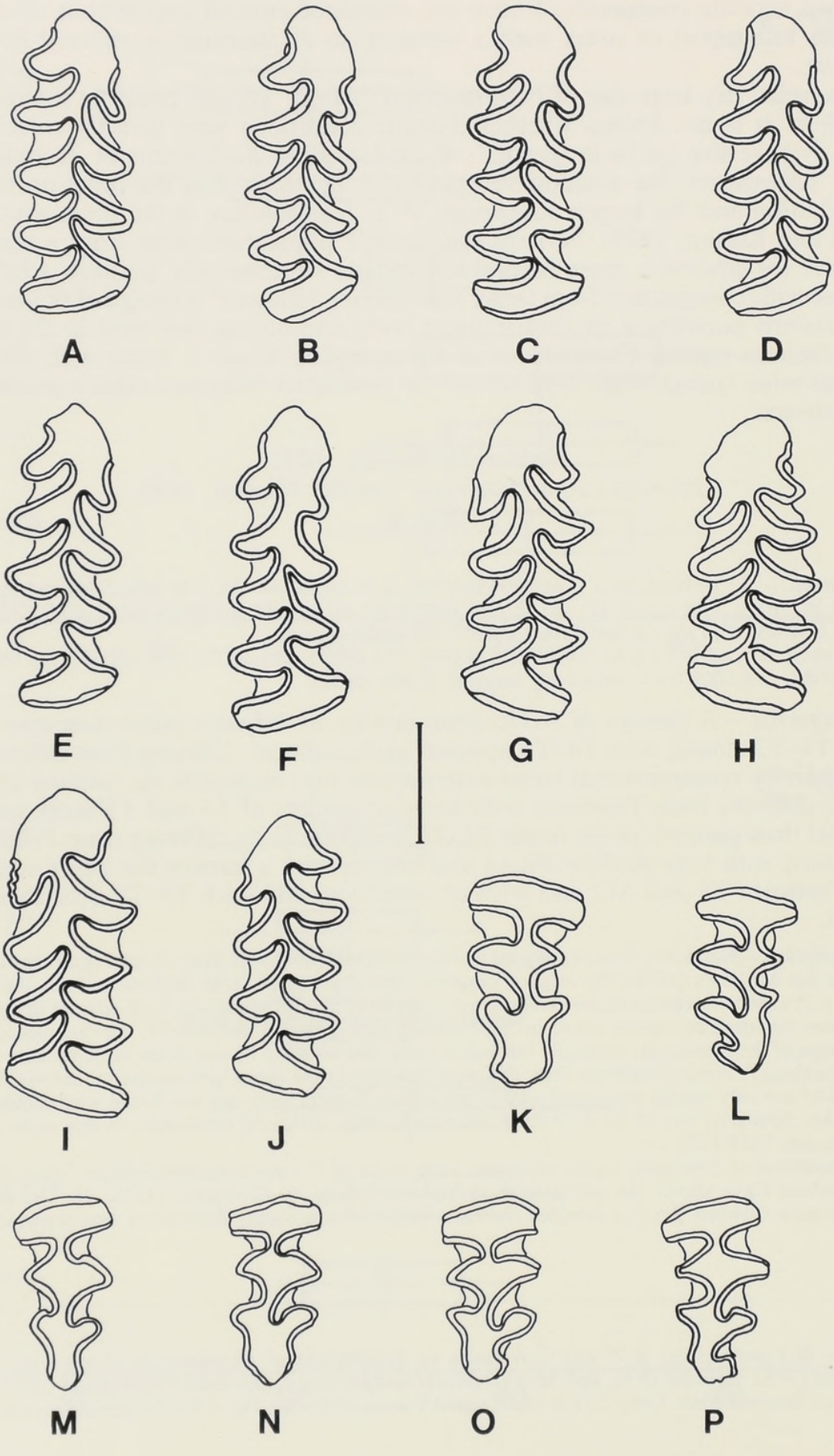
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Table 5.—*Measurement and ratio data for m1's of* Pitymys cumberlandensis *(n = 44) from Trout Cave No. 2, West Virginia.*

Mean ± SE	SD	Range	Param.
2.62 ± 0.02	0.13	2.36–2.92	L
47.5 ± 0.4	2.4	42.2–53.1	A/L
91.5 ± 0.7	4.5	79.0–101.2	W'/W
14.1 ± 0.6	3.7	7.3–24.0	B/W
15.4 ± 0.6	4.3	8.5–26.0	C/W

spectively, *M. paroperarius* and *P. llanensis* of Trout 2 from *M. paroperarius* and *A. guildayi* of Cumberland Cave.

Van der Meulen's (1978) "morphotype b" M3, which he regarded as *Pitymys cumberlandensis,* is characterized by: a) largely undifferentiated enamel; b) two buccal and two lingual reentrants filled with cementum; and c) broadly confluent, apposed triangles T1 and T2 (T2 and T3 of Van der Meulen). Based on this description and on a comparison with specimens from Cumberland Cave (batch samples CM 30278 and CM 20416), 14 M3's from Trout 2 were tentatively assigned to *P. cumberlandensis* out of a group of 25 M3's thought to be either *Pitymys* or *Pedomys.* (*Microtus* M3's were distinguished on the basis of their larger size, greater relative development of the PL, and more complete separation of T1–T3.) The specific assignment is tentative for several reasons. Firstly, I question the value of T1–T2 confluence as a diagnostic character. Guilday (1982*a*) has shown that this trait is highly variable within species of *Microtus* and the same appears to be the case in closely related genera. *P. cumberlandensis* and *Pedomys llanensis* from Trout 2 vary widely in this trait and a considerable number of specimens would remain unidentified if this were the sole basis for diagnosis. Secondly, extensive acid erosion of occlusal surfaces hinders assessment of enamel differentiation for a large proportion of M3's from Trout 2.

Of M3's assigned to *Pitymys cumberlandensis,* five (CM 60077, CM 60082, CM 60083, CM 60085, and CM 60087) have a complex posterior loop, defined by the presence of LSA4 and LRA3 with cementum (for example, see Fig. 8L, O, and P). Although the degree of complexity marks these M3's as different from modern members of the genus, each has relatively thick enamel that typically thins only near reentrant apices, T1–T2 confluent, and rounded salient angle apices. In all respects other than the complex posterior loop, these M3's most nearly resemble typical *P. cumberlandensis* from the type locality. Among the remaining M3's, posterior loops vary from simple, as in typical *Pitymys,* through incipiently complex, lacking only LRA3 cementum. Roughly half of the M3's were typically "simple."

Discussion.—Other than Trout Cave No. 2, *Pitymys cumberlandensis* is reported from Cumberland Cave (type locality) and Hanover Quarry Fissure (Guilday *et al.,* 1984; Guilday, unpublished ms., 1982*b*). Van der Meulen (1978:126) also assigned several molars from Conard Fissure, Arkansas, to this species. The Conard Fissure teeth were not examined for this report. Comparison of m1's from the remaining three localities indicates that the species exhibits a narrower range of morphological variation than observed among either *Pedomys llanensis* from Trout 2 or *Allophaiomys guildayi* from Cumberland Cave. *P. cumberlandensis* m1's from these three sites also show less variability than that observed between samples of *Pitymys pinetorum* from the central Appalachians (based on examination of specimens from CM Section of Mammals). Although this apparently

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Fig. 8.—*Pitymys cumberlandensis* from Trout Cave No. 2, West Virginia. A–F) right m1's, CM 49981, CM 49997, CM 60000, CM 60013, CM 49978, CM 60015; G–J) left m1's, CM 49973, CM 60018, CM 49974, CM 49969; K, L) left M3's, CM 60068, CM 60077; M–P) CM 60081, CM 60069, CM 60082, CM 60083. Bar equals 1 mm.

Table 6.—*Measurement and ratio data for m1's of* Pitymys cumberlandensis *from Trout Cave No. 2 (T2) and Cumberland Cave (CC). Data for Cumberland Cave from Van der Meulen (1978).*

Loc.	N	Mean ± SE	SD	Range	Param.
T2	44	2.62 ± 0.02	0.13	2.36–2.92	L
CC	45	2.54 ± 0.02	0.15	2.28–2.87	
T2	44	47.5 ± 0.40	2.4	42–53	A/L
CC	45	48.2 ± 0.36	2.4	44–53	
T2	44	91.5 ± 0.7	4.5	79–101	W'/W
CC	42	92.6 ± 0.63	4.1	84–102	
T2	44	14.1 ± 0.6	3.7	7–24	B/W
CC	42	16.2 ± 0.82	5.3	6–27	
T2	44	15.4 ± 0.6	4.3	8.5–26	C/W
CC	42	15.1 ± 0.79	5.1	6–32	

characteristic uniformity might be a significant finding in itself, comparison of these *P. cumberlandensis* populations did not provide additional insight regarding the evolutionary history of the species.

Van der Meulen (1978: fig. 5) demonstrated that m1's of *P. cumberlandensis* and *A. guildayi* are separable into two distinct groups based on the relationship between b and w'. He also reported that m1's of these species could be distinguished on the basis of salient and reentrant angle shape and enamel thickness and that, although no adequate standardized measurements of these characteristics were found, the morphologies were distinct enough to leave virtually no teeth undetermined. My examination of *P. cumberlandensis* and *A. guildayi* from Cumberland Cave confirm that there is no morphological continuum between the two species at that locality. Furthermore, although *Pedomys llanensis* has a more developed m1 ACC than *A. guildayi,* m1's of *P. llanensis* and *Pitymys cumberlandensis* from Trout 2 were readily separable using those traits that distinguish *A. guildayi* from *P. cumberlandensis.*

Van der Meulen (1978) felt that *P. cumberlandensis* was the ancestor of *P. pinetorum* (type species of *Pitymys*). This conclusion, combined with his view that *P. cumberlandensis* could not have descended from *Allophaiomys,* led him to exclude *Pitymys* from his otherwise broad concept of *Microtus.* However, the ancestry of *P. pinetorum* and the phylogenetic position of *P. cumberlandensis* remain open to interpretation. In Martin's (1987: fig. 4) cladogram, the two species are widely separated on the basis of enamel differentiation. On the other hand, Repenning (1983:477, 481) cited Van der Meulen's (1978) work as evidence that *P. pinetorum* is a descendant of *Allophaiomys,* perhaps by way of a transition from *A. guildayi* through *Pitymys cumberlandensis.* Descent of *P. cumberlandensis* from *A. guildayi* is contrary to the conclusion that no close phylogenetic relationship exists between the two species, based on their relatively distinct m1 morphologies (as noted above); however, descent of *P. pinetorum* from the *Allophaiomys-Pedomys* lineage might not require a connection through *Pitymys cumberlandensis.* Repenning and Grady (1988) asserted that *P. pinetorum* is a descendant of *A. pliocaenicus,* based on a sample of *Pitymys hibbardi* from Hamilton Cave that reportedly shows a complete transition between ancestral *A. pliocaenicus* and *Pedomys ochrogaster* and *Pitymys pinetorum.* A comparison of *P.*

Table 7.—*Comparison of Angle T4, Angle T4–T5, and Angle BRA3 measures for* Pitymys cumberlandensis *and* Pedomys llanensis *from Trout Cave No. 2, West Virginia. Sample size for both species is 44. All measurements are in degrees (see text and Fig. 9 for explanations).*

Species	Mean ± SE	SD	Range	Param.
P. cumberlandensis	56.42 ± 0.63	4.21	45–70	Angle T4
P. llanensis	67.80 ± 0.93	6.16	55–82	
P. cumberlandensis	123.85 ± 2.54	8.81	109–140	Angle T4–T5
P. llanensis	148.32 ± 2.14	6.52	139–161	
P. cumberlandensis	42.73 ± 1.80	8.83	25–75	Angle BRA 3
P. llanensis	71.85 ± 4.69	22.01	45–115	

hibbardi from Hamilton Cave with *P. cumberlandensis* might provide evidence regarding the phylogenies of both species.

If *P. cumberlandensis* is not part of the lineage ancestral to *P. pinetorum,* then it does not belong in *Pitymys* (*sensu stricto*). Nonetheless, *P. cumberlandensis* is left in its original genus for the present until the phylogeny of both this species and *P. pinetorum* are better understood.

Measuring Shape Differences

Although m1's of *Pitymys cumberlandensis* and *Pedomys llanensis* are similar, they are separable on the basis of reentrant angle shape and orientation, and orientation of the triangles relative to the midline of the tooth, as noted in the species descriptions. In an attempt to quantify these observed differences, several biometric parameters were defined, measured, and compared for samples of both species. The results are offered here in hopes that these parameters might prove useful for separating other species of *Pitymys*-like morphology.

First lower molars of *Pitymys cumberlandensis* and *Pedomys llanensis* from Trout 2 differed in the angle of orientation between the buccal triangles and the midline of the tooth. This is especially evident in comparison of T4's (compare Fig. 5 and 8). The angle is smaller among individuals of *P. cumberlandensis* and more nearly approaches perpendicular among individuals of *P. llanensis.* For measurement, Angle T4 was defined as the angle between a line parallel to a portion of the anterior edge of T4 and the midline of the tooth (see Fig. 9). The entire length of the anterior edge of T4 was not used because of the difficulty of estimating a line over that curve. Instead, a line was projected through the middle portion of the anterior edge, excluding (approximately) the first 10% and the final 40% of the length along the curve connecting the apex of BSA3 to the innermost point of BRA3. Using these criteria, the mean Angle T4 of *Pitymys cumberlandensis* is 56.4° (n = 44) and the mean Angle T4 of *Pedomys llanensis* is 67.8° (n = 44) (see Table 7).

The orientation of T4 has been recognized as a trait distinguishing *Pitymys pinetorum* from *Pedomys ochrogaster.* Martin (1974) reported that the anterior edge of T4 is approximately normal to the midline of the tooth in *P. ochrogaster,* whereas the T4 angle is nearly always 50° or less in specimens of *Pitymys pinetorum.* He stated that this trait can be used to discriminate between the two species with about 90% reliability (Martin, 1987:272). A comparison of this angle (estimated) on 40 recent specimens (80 m1's) of *Pedomys ochrogaster* and *Pitymys*

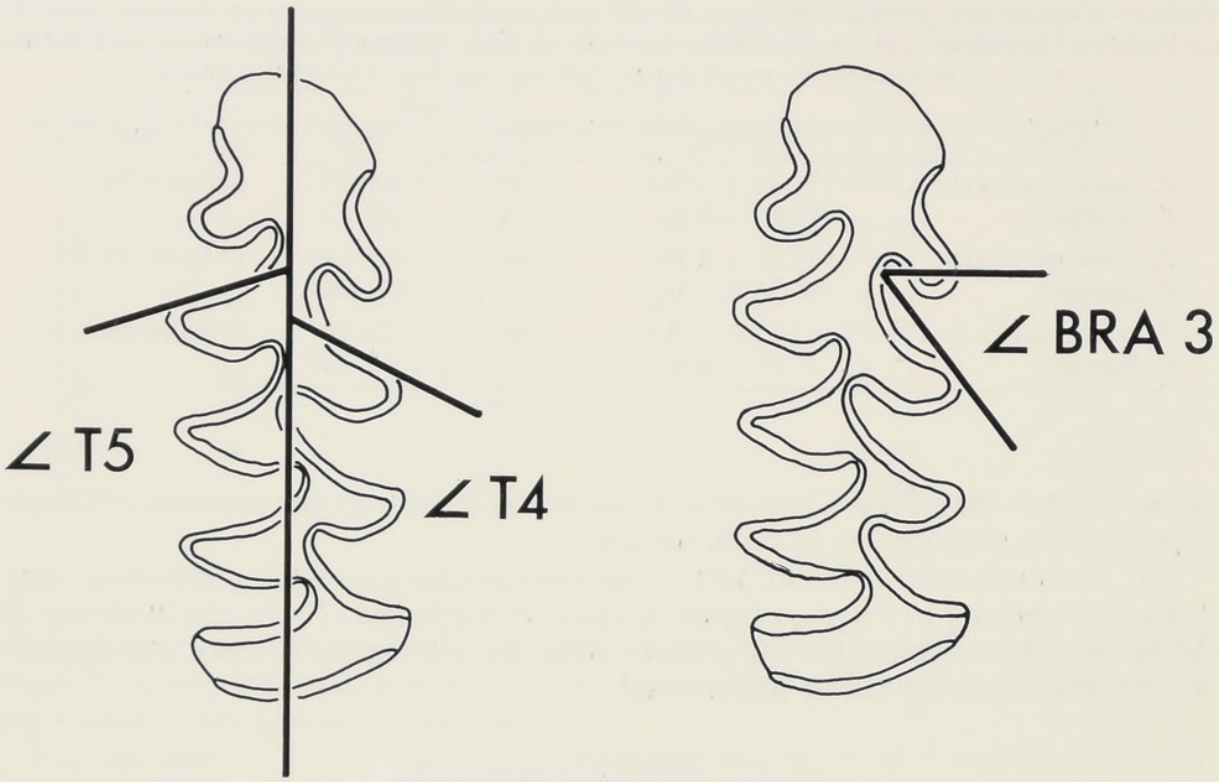

Fig. 9.—Occlusal surface of typical *Pitymys cumberlandensis* right m1 showing Angle T4, Angle T5, and Angle BRA3 measurements.

pinetorum from the CM Section of Mammals did not contradict Martin's assertion.

The orientation of T4 relative to T5 probably is a more meaningful measure of shape than the orientation of T4 relative to the midline. In order to quantify the spatial relationship between these triangles, Angle T5 was defined and measured in essentially the same manner as Angle T4 (Fig. 9) and the measured value was added to the Angle T4 value for each tooth, producing Angle T4–T5. Because the same midline is used in measuring both angles, Angle T4–T5 relates the orientation of the anterior edge of T4 directly to the anterior edge of T5 and removes the ill-defined midline from consideration. This has the advantage of eliminating one possible source of error—the tendency to locate the midline of the tooth differently in different species and individuals.

The mean Angle T4–T5 for *P. cumberlandensis* is 123.85° (n = 44) whereas the mean for *P. llanensis* is 148.32° (n = 44). Although the range of Angle T4–T5 is large, especially for *P. cumberlandensis,* there is almost no overlap between the ranges of the two species (see Table 7).

As noted in the species descriptions, buccal reentrant shape also differs between the two species. BRAs of *Pedomys llanensis* are typically wider and the bend of the posterior face is more often expressed as a single distinct angle, in contrast to the gradual curve of the posterior edge that is typical in *Pitymys cumberlandensis* (compare Fig. 5 and 8). Differences are most distinct when comparing the third BRA. BRA3s of *Pedomys llanensis* are typically wide and semi-circular, whereas BRA3s of *Pitymys cumberlandensis* abruptly narrow and turn to "point" anteriorly as they approach the midline of the tooth. This difference is related to the greater convex development of the posterior edge of BSA4 in *P. cumberlandensis.*

Although interspecific differences in BRA3 shape are apparent to the eye, finding a useful quantitative measure of this trait proved difficult. Attempts to measure BRA3 shape by tracing the reentrant's outline and calculating various shape factors were inconclusive. Angle BRA3 is an abstraction of the reentrant's shape that relates the antero-medial segment of the reentrant to the adjacent salient angles. The angle is defined by a vertex, located at the anteriormost point along that portion of BRA3 nearest the midline of the tooth, and two rays, one passing through the point of BSA3 furthest from the midline, the other through the point of BSA4 furthest from the midline (Fig. 9). Angle BRA3 was measured and compared for samples (n = 44 each) of *Pitymys* and *Pedomys* from Trout 2 (Table 7). The mean Angle BRA3 for *Pitymys cumberlandensis* was 42.73° while the mean for *Pedomys llanensis* was 71.85°. Range, SE, and SD values were particularly high for the sample of *P. llanensis*. This is an accurate reflection of the wide range of ACC morphologies seen in this species.

BIOSTRATIGRAPHIC CORRELATIONS

No radiometrically datable tephra, flowstone, or other material is associated with the deposit at the Trout 2 locality. Paleomagnetic samples, collected at the site, are currently being measured and evaluated.

Of the faunas that include one or more of the species of *Microtus, Pedomys,* and *Pitymys* described from Trout 2, the Cudahy, Vera, Wellsch Valley, and Alamosa faunas are known to be associated with radiometric or paleomagnetic dates. *Microtus paroperarius* and *Pedomys llanensis* are members of both the Cudahy and Vera faunas. *M. paroperarius* is a member of the Wellsch Valley and Alamosa faunas. *Pitymys cumberlandensis* is not known from any localities with external age control.

At the several localities of the Cudahy fauna and at the Vera locality, fossils were recovered from deposits directly beneath the 610,000-year-old Pearlette Type "O" ash (Dalquest, 1977; Hibbard, 1944; Hibbard and Dalquest, 1966; Paulson, 1961). The sediments containing the Cudahy fauna are normally magnetized and are considered to be younger than the Matuyama-Brunhes reversal (Lindsay *et al.,* 1975). Radiometric and paleomagnetic data therefore bracket the Cudahy fauna between 610 and 740 ka.

The fossils of the Wellsch Valley fauna are found beneath a tephra layer which has been given ages of 17.0 and 0.69 Ma (Westgate *et al.,* 1978), but the older of these two dates is reported to be in error due to contamination (Westgate and Garton, 1981). Electron spin resonance dating of tooth enamel from this locality gave dates of about 280 ± 35 ka, but these dates might be too young due to a late introduction of uranium into the teeth (Zymela *et al.,* 1988). The paleomagnetic record of the site shows several reversals. The lowermost, normally polarized unit might date from the Olduvai Normal Subchron, between 1.87 and 1.67 Ma (Barendregt, 1984; Churcher, 1984; Foster and Stalker, 1976; Repenning, 1987). The paleomagnetic evidence, supported by the presence of several Blancan taxa in the fauna, indicates this is the earliest known appearance of *M. paroperarius.*

The Alamosa faunal succession occurs in strata that encompass both the 740,000-year-old Bishop Ash and the Matuyama-Brunhes boundary. The faunal succession is interpreted to span the period from 840 to less than 700 ka (Repenning, 1983; Rogers *et al.,* 1985).

Localities that yield all three of the vole species (or their close relatives) that are present at Trout 2—*M. paroperarius, Pitymys cumberlandensis,* and either

Pedomys llanensis or *Allophaiomys guildayi*—are not well dated. They include Conard Fissure (Graham, 1972), Cumberland Cave (Van der Meulen, 1978), and Hanover Quarry Fissure (Guilday *et al.,* 1984). Each of these faunas falls within the Irvingtonian Land-Mammal Age, based on biostratigraphic correlations. Repenning (1987) further refined the age assignments of the Cumberland Cave and Conard Fissure faunas by placing them in the Irvingtonian II microtine age, which dates from about 900 to 400 ± 25 ka. The Trout 2 fauna similarly is considered of Irvingtonian II age, based on the presence of *M. paroperarius* and *P. cumberlandensis,* absence of modern *Microtus,* and the obviously primitive m1 morphology of *P. llanensis.*

The m1 morphology of *P. llanensis* might provide evidence that the Trout 2 fauna is older than faunas with more typical *P. llanensis* (such as Cudahy), but younger than the Cumberland Cave and Hanover Quarry Fissure faunas, which contain *A. guildayi.* However, the wide range of individual variation in populations of the *Pedomys* lineage and the lack of nonbiostratigraphic means of correlation combine to make this a highly speculative conclusion.

Conclusions

Based on the three species described here, the Trout 2 fauna is an Irvingtonian assemblage, most probably from the Irvingtonian II biochron (as defined by Repenning, 1987). Based on the odontology of *P. llanensis,* the Trout 2 fauna might be slightly older than the Cudahy and Vera faunas (which date between 740 and 610 ka) and the undated Conard Fissure fauna and slightly younger than the undated Cumberland Cave and Hanover Quarry Fissure faunas. But correlations based on *Allophaiomys-Pedomys* evolution require corroboration from other elements of the complete Trout 2 fauna.

M. paroperarius from Trout 2 shows relatively high values for biometric measures of ACC complexity in m1, indicating that the population is relatively advanced (assuming the species evolved toward greater m1 complexity). Whether the Trout 2 population is more recent than populations of this species that have a simpler ACC cannot be surmised because geographic rather than temporal variation might account for the differences.

First lower molars of *Pedomys llanensis* from Trout 2 are morphologically intermediate between typical *A. guildayi* and typical *P. llanensis.* Therefore, the Trout 2 population supports Van der Meulen's (1978) conclusion that *P. llanensis* is a direct descendant of *A. guildayi.* If the compared, overlapping, transitional populations of the proposed lineage are arranged from least to most advanced, this list results: 1) *A. guildayi* from Hanover Quarry Fissure; 2) *A. guildayi* from Cumberland Cave; 3) *P. llanensis* from Trout 2; and 4) *P. llanensis* from Conard Fissure. Unfortunately, no nonbiochronologic means of correlation is known to be associated with these faunas. Lacking an independent temporal control, problems regarding the validity of the proposed lineage and the speed and mode of its evolution remain unresolved.

The wide and overlapping ranges of individual variation that characterize populations of the *Allophaiomys-Pedomys* lineage should be considered when very small samples are being assigned to a particular species.

Recovery of *P. llanensis* in eastern West Virginia extends the geographic range of the species more than 1000 km eastward from the previous easternmost occurrence, Conard Fissure, Arkansas. Trout Cave also is outside the historic range of the presumed descendant of *P. llanensis, P. ochrogaster* (Hall and Kelson, 1959).

This might indicate differing habitat preferences for *P. llanensis* and *P. ochrogaster* and/or it may indicate that a substantially different environment (as perceived by voles) prevailed in the central Appalachians during the accumulation of the Trout 2 fauna.

The ancestry of *P. cumberlandensis* remains unknown. *P. cumberlandensis* m1 morphology, which shows a comparatively narrow range of variation, does not overlap with that of either *A. guildayi* or *P. llanensis.* There is no reason, other than confluence of T4–T5 and roughly equivalent grades of ACC development, to presume that *P. cumberlandensis* is closely related to those two species. Several details of m1 morphology argue against a close relationship between the species.

Comparisons of Trout 2 material with other samples of *P. cumberlandensis* neither support nor contradict the presumed ancestral-descendant relationship between this species and *P. pinetorum.* If *P. pinetorum* shares a relatively recent common ancestor with *Pedomys ochrogaster,* as suggested by several authors, then *Pitymys cumberlandensis* is not likely to have been part of that lineage and should be removed from *Pitymys* (*sensu stricto*).

The growing likelihood of an evolutionary lineage from *Allophaiomys pliocaenicus* to *Pedomys ochrogaster* and the unresolved ancestry of *Pitymys pinetorum* have ramifications for a significant amount of fossil material from the Great Plains and eastern North America. Involved are species of *Allophaiomys, Pedomys,* and *Pitymys* that are acknowledged to be generally similar, widely variable, and notoriously difficult to separate. Biometric measures, such as those developed by Van der Meulen (1973), have proven to be valuable diagnostic aids. The Angle T4, T4–T5, and BRA3 parameters, used here on *Pitymys cumberlandensis* and *Pedomys llanensis,* are potentially useful additions to the list of biometric measurements. More thorough tests of these parameters should be conducted with population samples of modern *Pedomys ochrogaster* and *Pitymys pinetorum,* which can be separated on the basis of nondental traits. If shown to be of general diagnostic value, these tools could be applied to fossil populations to help decipher the uncertain phylogenetic relationship between *Pitymys* and *Pedomys.*

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