

MICROTUS XANTHOGNATHUS AND SYNAPTOMYS BOREALIS IN THE LATE PLEISTOCENE OF SOUTHERN INDIANA

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INTRODUCTION

Arvicoline rodents and shrews are often abundant in Late Pleistocene faunal deposits, where they usually display a greater species diversity than in modern faunas (Graham, 1976). Because the arvicoline rodents and shrews recovered from Late Pleistocene sites are, for the most part, living today, knowledge of their modern habitats and environmental tolerances suggest possible habitats and environments during deposition. The extralimital occurrence of *Phenacomys* cf. *P. intermedius* (heather vole) and *Clethrionomys gapperi* (southern red-backed vole) (Richards, 1986) supported pollen spectra that indicated boreal woodlands in southern Indiana during the Late Pleistocene. The recovery of two fossil arvicolines (*Microtus xanthognathus*, yellow-cheeked vole, and *Synaptomys borealis*, the northern bog lemming) from stratified deposits for the first time in Indiana provides new information on biotic community transition in the Late Pleistocene and Early Holocene of Indiana.

Today, *Microtus xanthognathus* occurs in east-central Alaska eastward to the Northwest Territories and south through central Alberta, northern Saskatchewan, and northern Manitoba (Hall, 1981; Figure 1). This large vole is local in occurrence and undergoes extreme fluctuation in population size (Guilday, Martin, and McCrady, 1964; Guilday, Parmalee, and Hamilton, 1977). Feeding primarily on horsetails, lichens, and grasses, the yellow-checked vole occurs in well-drained upland woods and in moist valleys; it constructs runways from its burrow to sphagnum bogs (Banfield, 1974; Guilday, Parmalee, and Hamilton, 1977; Wolff and Lidicker, 1980). It prefers at least partially forested habitat with a thick humus or bryophyte cover (Wolff and Lidicker, 1980). Guilday, *et al.* (1977) related that "a thin boreal forest dominated by spruce and jackpine with a ground covering of heaths and sphagnum would accommodate this vole," and that it apparently did not occur in grasslands.

Microtus xanthognathus molars are readily recognized by their large size, an occlusal pattern like that of *M. pennsylvanicus*, and a distinctive absence of cement in the third lateral reentrant of M3 (Guilday, 1982; Guilday and Bender, 1960; Guilday, Parmalee, and Hamilton, 1977; Hallberg, *et al.*, 1974; Rhodes, 1984; Semken, 1984). Fossils have been reported from at least 20 Late Pleistocene localities and one Holocene locality in 13 other States (Figure 1). The fossils recovered from Megenity Peccary Cave, Indiana, occurred 2132 km (1325 miles) south of the nearest living population in Manitoba.

Today, *Synaptomys borealis* occurs throughout much of Canada and Alaska with its range extending south into Washington, Idaho, Montana, Minnesota,

Maine, and New Hampshire (Hall, 1981; Figure 2). It occupies the boreal forest region, occurring primarily in sphagnum/spruce bogs but also in thick, mossy spruce woods, wet subalpine meadows, and alpine tundra (Banfield, 1974). Lower molars of *Synaptomys borealis* are separated from those of *S. cooperi* (southern bog lemming) by the lack of labial triangles (Semken, 1984). Upper molars of the two species are very similar. *Synaptomys borealis* fossils are known from at least 21 Late (and one Middle) Pleistocene localities in 11 other States (Figure 2).

DESCRIPTIVE PALEOZOLOGY

Vertebrate nomenclature used in this report follows Banks, *et al.* (1987). Abbreviations used are as follows: L, R, left, right; M1, M2, M3, m1, m2, m3, upper and lower molars one through three, respectively; MNI, minimum number of individuals; BP, Before Present (AD 1950).

One Indiana Late Pleistocene locality (Megenity Peccary Cave) produced fossils of both *Microtus xanthognathus* and *Synaptomys borealis* while work at a second locality (Prairie Creek Site) produced only *M. xanthognathus*.

LOCALITY 1.

Location. Megenity Peccary Cave (Taswell Quad.), Crawford County, Indiana.

Materials. *Microtus xanthognathus*: 32 partial skulls; 32L, 34R dentaries; 34L, 34R M1; 35L, 35R M2; 38L, 35R M3; 33L, 34R m1; 33L, 34R m2; and 32L, 35R m3 (MNI = 38; Figure 3). *Synaptomys borealis*: 5L, 8R dentaries; 11L, 11R m1; 13L, 11R m2; and 12L, 11R m3 (MNI = 13). Postcranial material of both species has been recovered but not separated.

Occurrence. The materials were recovered from a laminated clay bank in the "Microfauna Room", entered by a 4.9 m drop, 44.2 m from the present entrance. *Microtus xanthognathus* and *Synaptomys borealis* both occurred in Units C and D (respectively 30-40 and 40-50 cm below the surface).

Important associations. Extralimital species: *Sorex arcticus* (arctic shrew), *Clethrionomys gapperi*, and *Phenacomys* cf. *P. intermedius*.

Comments. Excavation units (0.5 m²) were separated at ca 10 cm intervals along natural bedding planes. Most units produced extensive microfaunas dominated by ranid frogs. Units A (uppermost) and B included arvicolines and shrews that reside in Indiana today (*Microtus pinetorum/ochrogaster*, the pine/prairie vole, *Sorex cinereus*, masked shrew, and *Blarina brevicauda*, the short-tailed shrew). Unit C contained the same resident taxa as well as *Microtus pennsylvanicus* (meadow vole), *Synaptomys cooperi*, and *Sorex fumeus* (smoky shrew). Extralimital species included *Clethrionomys gapperi* and *Sorex arcticus*. *Synaptomys borealis* and especially *Microtus xanthognathus* were most abundant. A 20.04 gm sample of selected *M. xanthognathus* limb bones and vertebrae (supplemented with some *M. pennsylvanicus* elements) from Unit C produced an AMS radiocarbon age of 14,125 ± 140 BP (Beta-31905; ETH-5525). Unit D was also dominated by *Synaptomys borealis* and *Microtus xanthognathus*. *Phenacomys* cf. *P. intermedius* was the only other extralimital species, and *Microtus pennsylvanicus*, *Synaptomys cooperi*, and *Sorex cinereus* were the resident species. Sparsely sampled unit E produced only *Microtus pennsylvanicus* and *Synaptomys* sp. Megenity Peccary

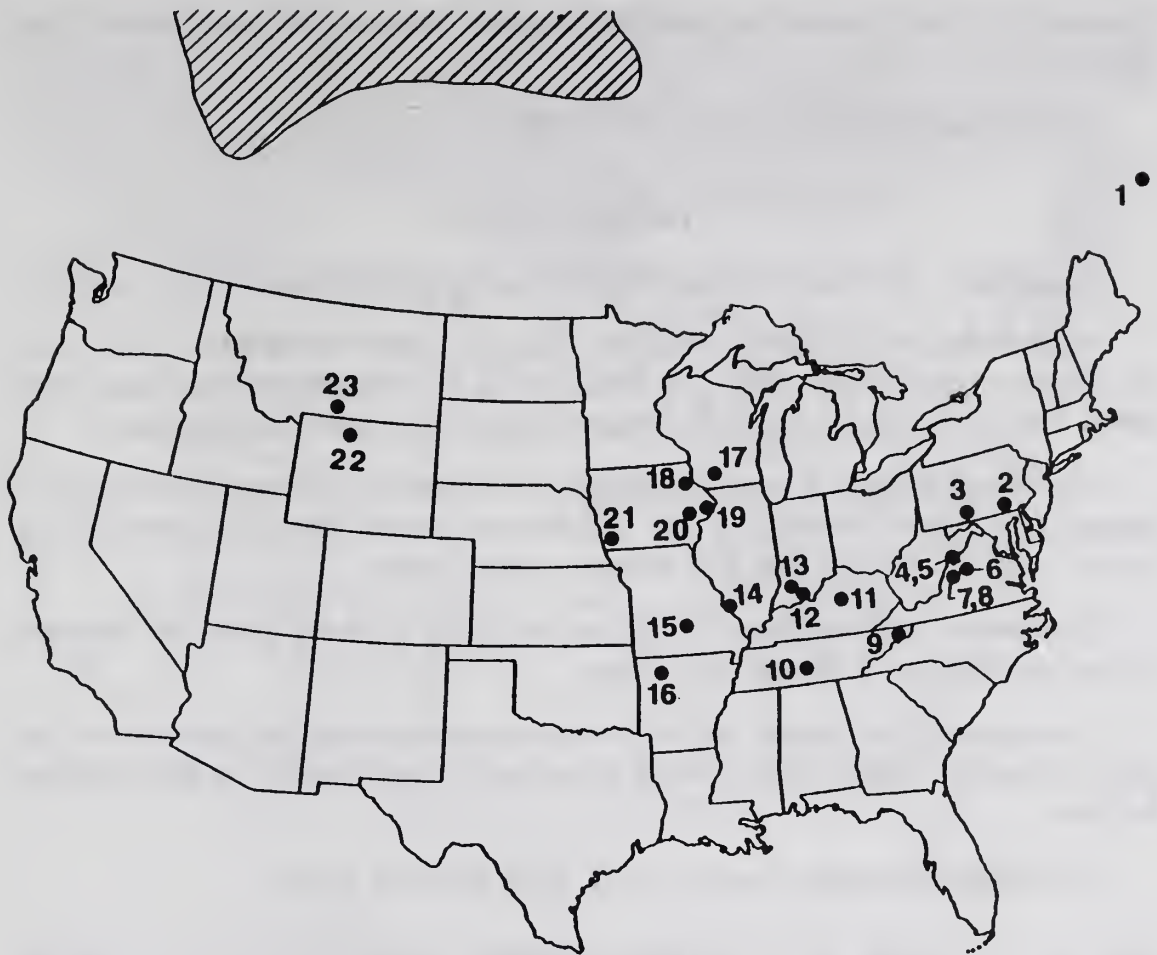


FIGURE 1. Late Pleistocene extralimital occurrence of *Microtus xanthognathus*. Southern part of the modern range (hatched) after Hall (1981). 1. St. Elzear Cave, Quebec, Canada (Lasalle, 1984). 2. Bootlegger Sink, York County, Pennsylvania (Guilday, Hamilton, and McCrady, 1966). 3. New Paris No. 4, Bedford County, Pennsylvania (Guilday and Bender, 1960; Guilday, Martin, and McCrady, 1964). 4. Eagle (Eagle Rock) Cave, Pendleton County, West Virginia (Guilday, 1971; Guilday and Hamilton, 1973). 5. New Trout Cave, Pendleton County, West Virginia (Grady, 1984; Grady and Garton, 1981). 6. Natural Chimneys, Augusta County, Virginia (Guilday, 1962; Guilday and Bender, 1960). 7. Clark's Cave, Bath County, Virginia (Guilday, Parmalee, and Hamilton, 1977). 8. Back Creek Cave No. 2, Bath County, Virginia (Guilday, Parmalee, and Hamilton, 1977). 9. Baker Bluff Cave, Sullivan County, Tennessee (Guilday, Hamilton, Anderson, and Parmalee, 1978). 10. Cheek Bend Cave, Maury County, Tennessee (Parmalee and Klippel 1981a, b). 11. Welsh Cave, Woodford County, Kentucky (Guilday, Hamilton, and McCrady, 1971). 12. Megenity Peccary Cave, Crawford County, Indiana (this report). 13. Prairie Creek Site, Daviess County, Indiana (this report). 14. Meyer Cave, Monroe County, Illinois (Parmalee, 1967). 15. Bat Cave, Pulaski County, Missouri (Hawksley, Reynolds, and Foley, 1973). 16. Peccary Cave, Newton County, Arkansas (Hallberg, Semken, and Davis, 1974; Semken, 1984). 17. Moscow Fissure, Iowa County, Wisconsin (Foley, 1984). 18. Elkader 1.f., Clayton County, Iowa (Graham and Mead, 1987; Woodman, 1982). 19. Eagle Point 1.f., Clinton County, Iowa (Rosenberg, 1983). 20. Conklin Quarry, Johnson County, Iowa (Baker, *et al.*, 1986). 21. Waubonsie 1.f., Mills County, Iowa (Hallberg, Semken, and Davis, 1974; Rhodes, 1984; Rhodes and Semken, 1986). 22. Prospects Shelter, Bighorn County, Wyoming (Walker, 1987). 23. False Cougar Cave, Carbon County, Montana (Holocene; Graham, Wilson, and Graham, 1987).

Cave is still under excavation, with all material repositied at the Indiana State Museum.

Published record. Richards (1988, 1993).

LOCALITY 2.

Location. Prairie Creek Site (Washington Quad.), Daviess County, Indiana.

Materials. *Microtus xanthognathus*. (Zone D, Late Pleistocene): 2L M1, lacking anterior loops (Units 2460 and 2462); and L M3, lacking anterior loop (Unit 2460). Some postcranial material is questionably referred to this species.

Occurrence. Zone D represents alluvial redeposition of bones and sediments flushed from a Late Pleistocene lake bed that had accumulated at approximately 14,010 \pm 140 B.P. (DIC-234; P.J. Munson, pers. comm.).

Important associations. An extensive fauna is under study by Munson, Parmalee, Holman, Richards, and others.

Comments. The present *Microtus xanthognathus* material, and most of the fauna, is on file at the Glenn A. Black Laboratory of Archaeology in Bloomington, Indiana.

Published Records. Tomak (1975, 1982; Richard, 1993).

DISCUSSION

Microtus xanthognathus, *Synaptomys borealis*, *Phenacomys intermedius*, and *Sorex arcticus* are characteristic northern elements of early post-Wisconsinan cave faunas in the central and southern Appalachians (e.g., Bootlegger Sink and New Paris No. 4, Pennsylvania; Eagle Cave, West Virginia; Clark's Cave and Natural Chimneys, Virginia; Baker Bluff Cave and Robinson Cave, Tennessee; and Welsh Cave, Kentucky; Guilday and Hamilton, 1973). Other cave faunas outside the Appalachian region (e.g., Bat Cave and Crankshaft Cave, Missouri; and Peccary Cave, Arkansas) have also produced various suites of northern extralimital species, similarly tempered by Late Pleistocene environmental gradients that relocate progressively fewer boreal taxa toward the south (Guilday, Hamilton, Anderson and Parmalee, 1978) and presumably more distant in all directions from the Appalachians. The arvicoline and shrew taxa identified from the Microfauna Room of Megenity Peccary Cave display the strong boreal affinities of those recovered from central and southern Appalachian Late Pleistocene faunas. Other taxa that frequently occur in Appalachian Late Pleistocene faunas, but have not been recovered in Indiana, include *Microtus chrotorrhinus* (rock vole), *Dicrostonyx hudsonius* (Labrador collared lemming), and *Sorex palustris* (northern water shrew).

Most Late Pleistocene faunas in the eastern U.S. also include taxa indicative of open areas (e.g., *Geomys bursarius*, plains pocket gopher, *Spermophilus tridecemlineatus*, the thirteen-lined ground squirrel, and *Microtus pennsylvanicus*). These faunas usually include species that co-inhabited a region at the time of deposition, but that occupy segregated ranges today (e.g., *Microtus xanthognathus* and *Blarina brevicauda* in the Megenity Peccary Cave paleofauna). These seem-

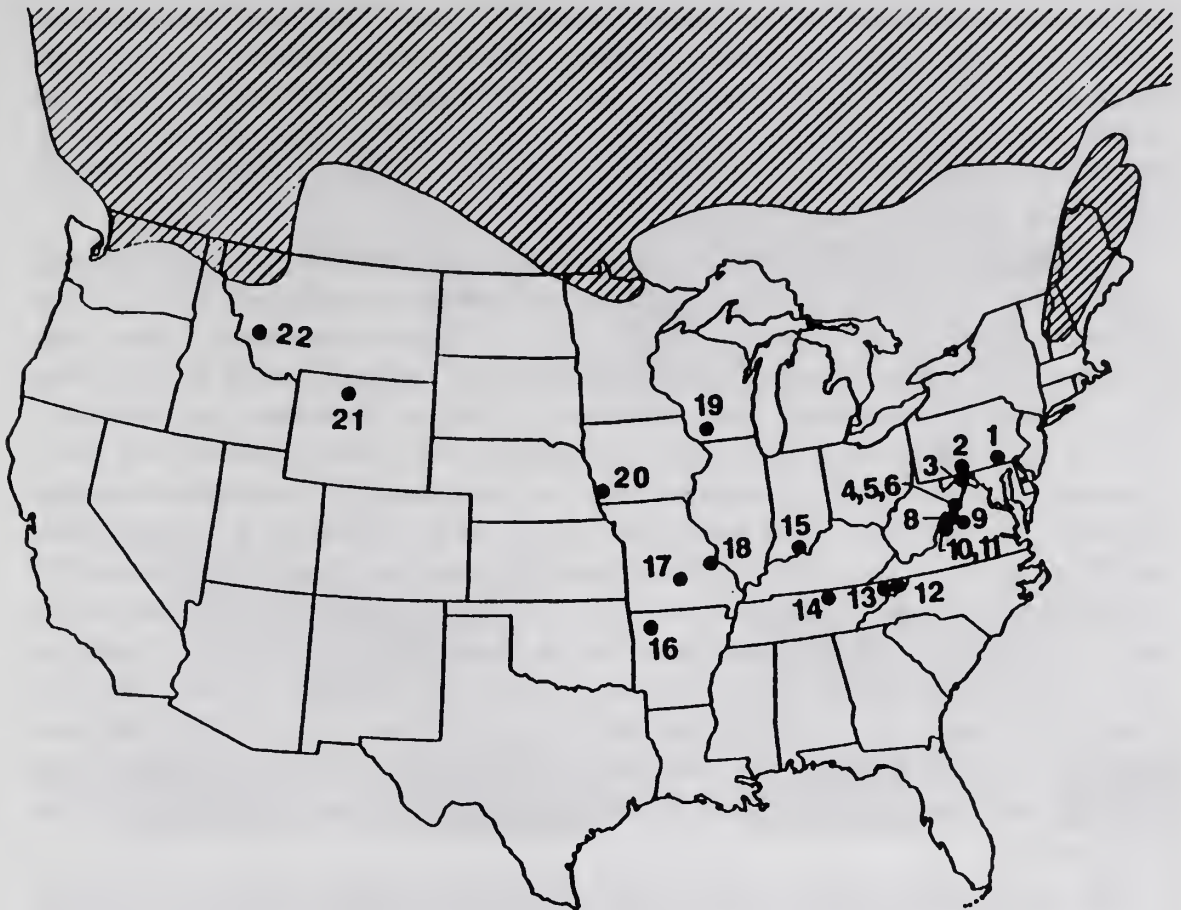


FIGURE 2. Late Pleistocene extralimital occurrence of *Synaptomys borealis*. Southern part of the modern range (hatched) after Hall (1981). 1. Bootlegger Sink, York County, Pennsylvania (Guilday, Hamilton, and McCrady, 1966). 2. New Paris No. 4, Bedford County, Pennsylvania (Guilday, Martin, and McCrady, 1964). 3. Cumberland Cave, Allegany County, Maryland (Middle Pleistocene; Gidley and Gazin, 1938; Kurten and Anderson, 1980). 4. Eagle (Eagle Rock) Cave, Pendleton County, West Virginia (Guilday and Hamilton, 1973). 5. Hoffman School Cave, Pendleton County, West Virginia (Guilday and Hamilton, 1978). 6. Mandy Walters Cave, Pendleton County, West Virginia (Guilday and Hamilton, 1978). 7. NOT SHOWN ON MAP: Bowden Cave, county not available, West Virginia (Guilday, Parmalee, and Hamilton, 1977). 8. Straight Canyon Fissure, Highland County, Virginia (Jones, *et al.*, 1984). 9. Natural Chimneys, Augusta County, Virginia (Guilday, 1962). 10. Clark's Cave, Bath County, Virginia (Guilday, Parmalee, and Hamilton, 1977). 11. Back Creek Cave No. 2, Bath County, Virginia (Guilday, Parmalee, and Hamilton, 1977). 12. Guy Wilson Cave, Sullivan County, Tennessee (Corgan, 1976; Guilday, Hamilton, and Parmalee, 1975). 13. Baker Bluff Cave, Sullivan County, Tennessee (Guilday, Hamilton, Anderson, and Parmalee, 1978). 14. Robinson Cave, Overton County, Tennessee (Guilday, Hamilton, and McCrady, 1969). 15. Megenity Peccary Cave, Crawford County, Indiana (this report). 16. Peccary Cave, Newton County, Arkansas (Semken, 1984). 17. Bat Cave, Pulaski County, Missouri (Hawksley, Reynolds, and Foley, 1973). 18. Crankshaft Cave, Jefferson County, Missouri (Parmalee, Oesch, and Guilday, 1969). 19. Moscow Fissure, Iowa County, Wisconsin (Foley, 1984). 20. Craigmile 1.f., Mills County, Iowa (Rhodes, 1984; Rhodes and Semken, 1986). 21. Prospects Shelter, Bighorn County, Wyoming (Walker, 1987). 22. Morse Creek #1, Granite County, Montana (Graham, Wilson, and Graham, 1987).

ingly anomalous associations of taxa are thought to have been structured by more equable Late Pleistocene climates (climates with reduced seasonal temperature extremes) that allowed individual taxa to reorganize their distribution according to their own tolerances along changing environmental gradients, producing unique biotic communities (Graham, 1976, 1985a, 1985b; Graham and Mead, 1987; King and Graham, 1981).

Guilday (1971) and Guilday, Parmalee, and Hamilton (1977) suggested that *Microtus xanthognathus* is a good indicator of parklands composed of thin, open coniferous forest. Hallberg, *et al.* (1974) found the same boreal associations with *M. xanthognathus* at Peccary Cave, Arkansas that Guilday did at Appalachian sites, but they also recovered more temperate fauna (e.g., *Sciurus niger*, fox squirrel, and *Microtus pinetorum*) suggesting higher winter temperatures and some deciduous vegetation. They contended that the presence of *M. xanthognathus* was indicative of conditions more analogous to the open parklands of the southern boreal forest than the northern boreal forest-tundra transition. The presence of temperate deciduous woodland taxa (e.g., *Blarina brevicauda* and *Synaptomys cooperi*) associated with *M. xanthognathus* at Megenity Peccary Cave suggests a good analogy with the southern boreal forest/parkland, when boreal and temperate forest taxa were reorganized into unique communities. Though *M. xanthognathus* occupies the northern boreal forest today, it may not have inhabited a clearly analogous environment in the reorganized communities of the Late Pleistocene.

Microtus xanthognathus has not been reported from sites older than Wisconsinan age (Guilday, Parmalee, and Hamilton, 1977). Associated radiocarbon dates include $11,300 \pm 1,000$ BP (New Paris No. 4, Pennsylvania), $12,950 \pm 550$ BP (Welsh Cave, Kentucky), $14,010 \pm 140$ B.P. (Prairie Creek, Indiana), $14,125 \pm 140$ B.P. (Megenity Peccary Cave, Indiana), and $19,100 \pm 850$ BP to $10,560 \pm 220$ BP (Baker Bluff Cave, Tennessee) (Graham and Mead, 1987). According to the concept of shifting environmental gradients produced by the advance and recession of Wisconsinan ice, *M. xanthognathus* should have populated southern localities later and abandoned them earlier than it did in more northern Appalachian regions. More dates associated with key strata are needed before it will be possible to define and map population movement of any species during the Quaternary. *Microtus xanthognathus* was one of the first boreal voles to disappear from the mid-Appalachian mammalian fauna, as early post-Wisconsinan warming allowed closed-canopy forests (Guilday and Hamilton, 1978; Guilday, Parmalee, and Hamilton, 1977).

Today, *Synaptomys borealis* inhabits the boreal forest region, and *S. cooperi* inhabits the mixed forest to the south; the two are nearly allopatric, with a narrow area of sympatry in portions of southeastern Manitoba, southwestern Ontario, northwestern Minnesota, eastern Quebec, Maine, and New Hampshire (Hall, 1981). Both species are found in the same deposits in many Late Pleistocene localities as far south as Peccary Cave, Arkansas; this fossil association suggests that environmental conditions during their deposition may have been similar to those in their area of sympatry today (Guilday, Martin, and McCrady, 1964). *Synaptomys cooperi* replaced *S. borealis* in the central Appalachians around 11,000 BP (Guilday, Parmalee, and Hamilton, 1977). Both species coexisted during the deposition of Units C and D at Megenity Peccary Cave, but neither was recorded in succeeding Units B and A.

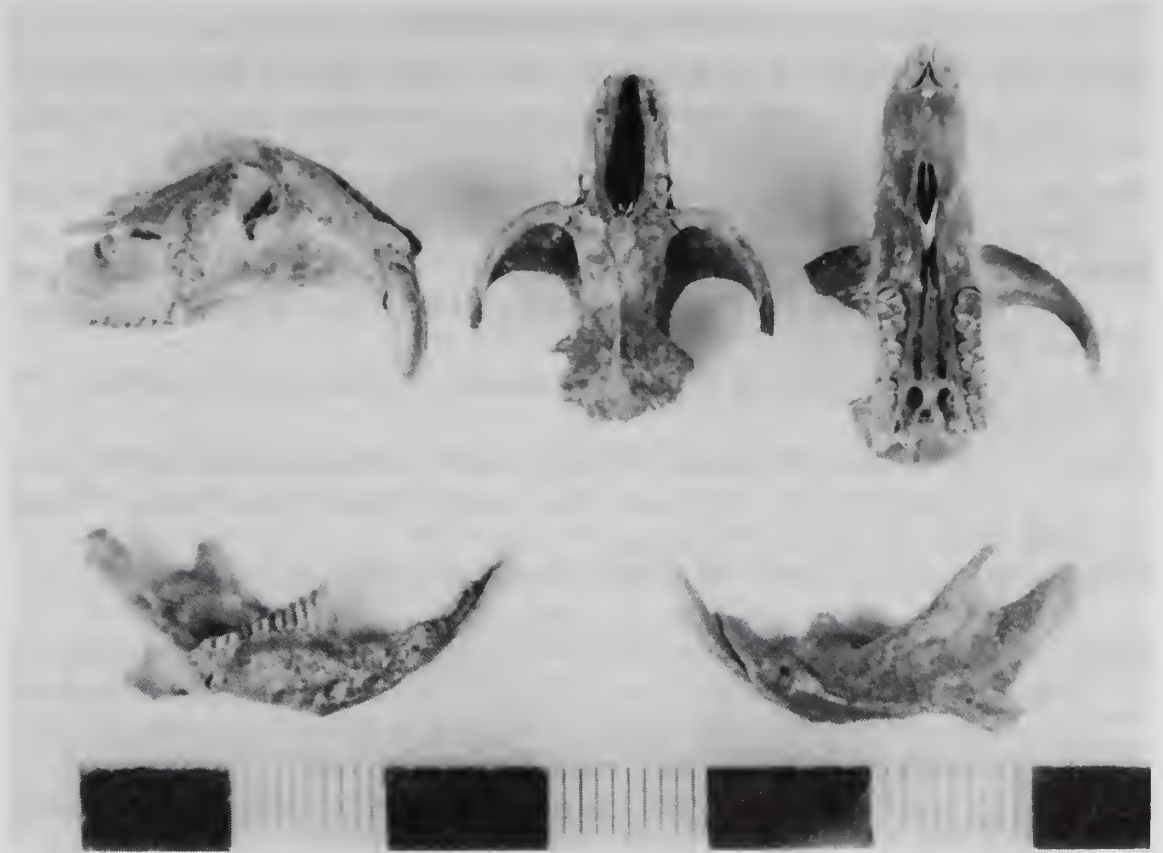


FIGURE 3. Three fragmented crania and two L dentaries of *Microtus xanthognathus* from unit C, Microfauna Room, Megenity Peccary Cave, Indiana. Scale in mm and cm.

The extralimital taxa from Units C and D of Megenity Peccary Cave (*Microtus xanthognathus*, *Synaptomys borealis*, *Phenacomys* cf. *P. intermedius*, *Clethrionomys gapperi*, and *Sorex arcticus*) are found together today in central and northern Alberta east to Manitoba. Other species recovered from those units (*Blarina brevicauda* and *Synaptomys cooperi*) presently occupy more temperate areas. Units C and D accumulated with taxa that do not co-exist today, suggesting deposition in an environment that has no modern analog. Units C and D appear to have formed in a thin, spruce-dominated woodland that included some temperate elements existing in a cool, moist, more equable climate (i.e., reduced temperature extremes). Units A and B were apparently deposited after postglacial warming and migration north of deciduous forests.

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