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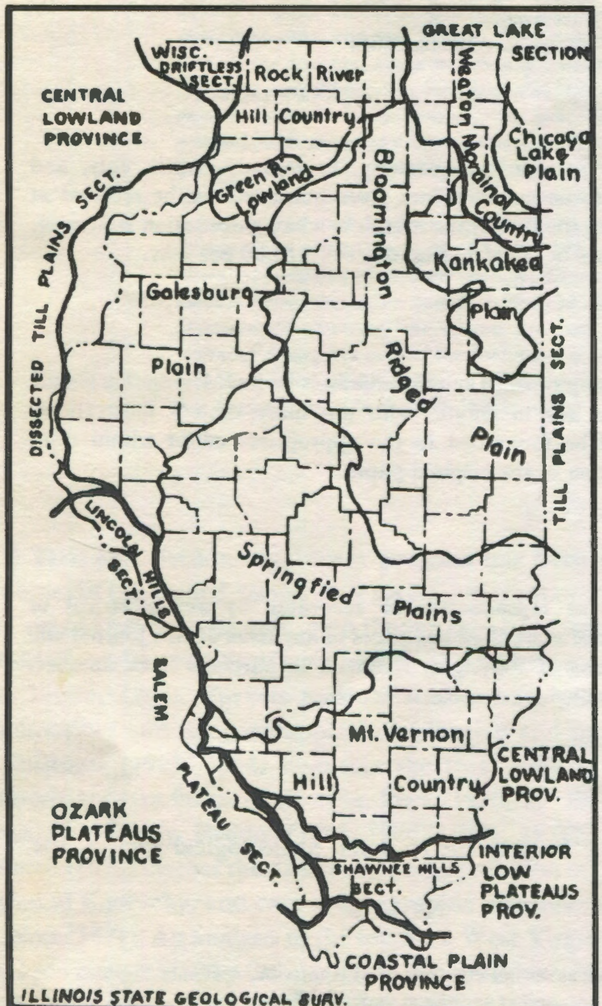

PHYSIOGRAPHIC DIVISIONS OF ILLINOIS

NATIONAL SPELEOLOGICAL SOCIETY

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Contents

Cover Illustration: Physiographic divisions map of Illinois (see Peck and Lewis, p. 40). The Illinoisan glacial drift lobe nearly reaches the head of the Mississippi Embayment of coastal plain sediments. Ozark Plateau faunas occur to the west, in Missouri and Arkansas; Interior Low Plateau faunas occur to the east, in Kentucky, Tennessee, and adjoining states. The glacial history of the Midwest has strongly influenced the development, preservation, and human accessibility of caves, as well as of cave faunas.

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Zoogeography and Evolution of the Subterranean Invertebrate Faunas of Illinois and Southeastern Missouri

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ABSTRACT

Some 215 species of invertebrates, excluding accidentals and parasites, are known to occur in cave and groundwater habitats in Illinois [excluding the Driftless Area] and adjacent Missouri counties bordering the Mississippi River. Fourty-three of these species are troglobites or phreatobites, of which 24 are aquatic and 19 are terrestrial.

This troglobite-phreatobite category includes three flatworms, three snails, one copepod, eight aquatic isopods, nine amphipods, two pseudoscorpions, one spider, five millipeds, four collembolans, three diplurans, and four beetles. The terrestrial species have generally smaller distributional ranges than do the aquatics. Some members of the cave community are pre-Pleistocene relicts, and some may represent early-Pleistocene invasions of subterranean habitats. Most of the fauna has been derived from eastern (Appalachian) sources. Because Illinois and nearby Missouri caves were probably uninhabitable (because of the nearness of glacial ice) during the Illinoian glacial maximum, the local fauna represents a post-Illinoian (early Sangamonian) occupation of the caves. Warm-dry middle Sangamonian climates caused the genetic isolation of some pre-adapted epigean invertebrate populations in caves, and some of these survived to become cave-adapted troglobites. At its maximum, Wisconsinan glacial ice came to within 100 miles of part of the cave area. Cool-moist Wisconsinan climatic conditions allowed the overland dispersal of terrestrial troglobites through deep moss and litter carpets, and the subterranean-interstitial dispersal of most aquatic troglobites. Through this Wisconsinan dispersal, the species attained much of their modern distribution. Recent climatic warming-drying has caused the limitation of these species to their present day cave and groundwater localities. Interstitial distribution of phreatobites northward along major valleys into glacial drift plains has been extensive in the post-Wisconsinan.

INTRODUCTION

IN THE past decade, significant progress has been made in achieving an understanding of the cave invertebrate faunas of the United States. As a result, older summaries, such as that of Nicholas (1960a), are now highly out of date and are of historical use only, even though they have served as valuable stimuli for additional research. Contributions to a modern understanding of cave ecology and evolution are now available (*e.g.*: Barr, 1967a, 1968; Culver, 1976; Poulson and White, 1969). Various regional studies have greatly improved our knowledge of species composition of cave communities and the geographical distribution and dynamics of these species. In the following, we cite only a few.

Holsinger (1963, 1964) discusses the troglobitic fauna of Virginia, and Holsinger and Peck (1971) cover the invertebrate cave fauna of Georgia. Peck (1970, 1973b) covers the cave faunas of Florida and of northwestern volcanic caves, respectively. Reddell (1965, 1966, 1970a, 1970b) lists the invertebrate faunas of Texas caves, and Mitchell and Reddell (1971) discuss the distribution and evolution of this fauna. Black (1971) treats Oklahoma. The Mammoth Cave region of Kentucky, and cave zoögeographic provinces and ecology, are summarized by Barr (1967b) and by Barr and Kuehne (1971). An analysis of the southern West Virginia cave fauna, in the light of the theory of island biogeography, has been contributed by Culver (1971) and by Culver, Holsinger, and Baroody (1974). A more comprehensive treatment of the cave invertebrates of West Virginia was recently completed (Holsinger, Baroody, and Culver, 1976).

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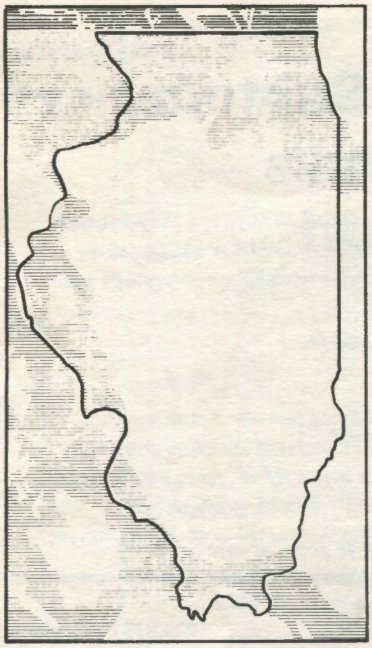

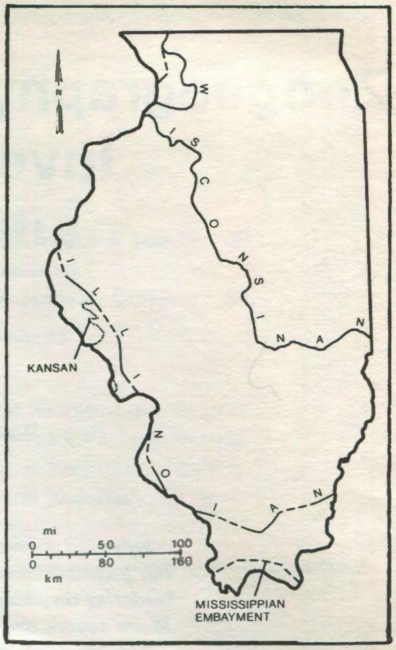

Figure 1. Limestone and dolomite bedrock regions of Illinois and parts of adjacent states. Cave and spring sites are most common in these rocks (compiled mostly from Bretz, 1939; Bretz and Harris, 1961; and Vineyard and Feder, 1974).

Figure 2. Physiographic regions of Illinois (from Bier, 1956).

Figure 3. Illinois, with the northward limits of the Eocene Mississippian embayment of the Gulf Coast, and the southward limits of the late Pleistocene Illinoian and Wisconsinan glacial ice sheets (from Flint, *et al.*, 1959; Frye and Willman, 1973; and Leighton and Brophy, 1961).

Although scattered records exist in the literature on invertebrate taxonomy, no analytical summaries are available on the species composition and distribution of invertebrate cave faunas of Indiana, Illinois, or Missouri, in spite of the early listings of Missouri cave fauna given by Hubricht (1950) and by Nicholas (1960b). Craig (1975a, 1977) has completed a study of the cave faunas of the limited region to be flooded by the Meramec River dam in Missouri and has reviewed all previous cave faunal reports for Missouri, in general (1975b). Lewis (in preparation) is conducting a study of the invertebrate fauna of eastern Indiana and has given a list of the invertebrate fauna of Mystery and other caves in the Cinque Hommes Valley of Perry County, Missouri (Lewis, 1974). Peck and Christiansen (in preparation) are conducting a study of the invertebrate cave fauna of the "Driftless Area" of Iowa, Illinois, Wisconsin, and Minnesota.

We present this study of the distribution of the subterranean invertebrate faunas of glaciated and southern unglaciated Illinois and of adjacent southeastern Missouri counties bordering the Mississippi River as a contribution towards a comprehensive understanding of the North American cave faunas. The study is based on extensive field work by us, on a complete literature review, on the study of specimens in available museum collections, and on contributions from the records and collections of all active invertebrate taxonomists and zoölogists studying cave faunas of Illinois and Missouri. We have excluded the "Driftless Area" of Jo Daviess and Carroll counties in Northwestern Illinois, since it is a distinct faunal region in its own right.

We wish to dedicate this paper to Mr. Leslie Hubricht, of Meridian, Mississippi, in recognition of his contributions to American cave biology, in general, and for his historically important and extensive collections in caves in Illinois and Missouri, upon which so many of the early systematic studies were based.

REGIONAL PHYSIOGRAPHY AND GEOLOGY

The caves of the region under study, in Illinois and adjacent Missouri, are formed in Paleozoic limestones ranging from Ordovician to Mississippian in age. Most of the limestones occurring at the surface in Illinois lie along the western and southern edges of the state and, hence, caves are generally found only at these edges (Fig. 1). Large areas of limestone and dolomite occur in northeastern Illinois, but any caves that may have existed here have been destroyed or filled by repeated glaciation. Most of central Illinois (the Illinois Basin) is covered by Pennsylvanian shale, sandstone, and coal deposits.

The limestones of the extreme southern edge of the state are in a local region of uplift called the Shawnee Hills (Fig. 2), an area of sandstone capped hills and limestone floored valleys with considerable topographic relief. Complex faulting and differential uplift is prevalent in the eastern Shawnee Hills, in the fluorspar mining district of Pope and Hardin counties (Bastin, 1931; Weller, Grogan, and Tippie, 1952). The Shawnee Hills are a northwestward continuation of the Pennyroyal Plateau and Chester (Dripping Springs) Escarpment Section of the Interior Low Plateaus of the Mammoth Cave region of Kentucky. The most southerly of the Pleistocene glaciations in Illinois, the Illinoian, only reached the northern flank of the Shawnee Hills (Fig. 3).

The rest of the limestone study area, in both Illinois and Missouri, has been placed in the Ozark Plateau Province, on the northeastern flank of the Ozark Uplift (McCracken, 1971). It is generally characterized by flat-bedded limestones with extensive karst (Fig. 2). This province can be divided into two sections. The northern, containing Calhoun, Pike and Adams counties, Illinois, is called the Lincoln Hills Section and of this, Calhoun County is a "mini-Driftless Area," having experienced no glaciation. Along both sides of the Mississippi River, south of St. Louis, is the Salem Plateau. Karst topography is widely developed on it. In Illinois, much of this karst was overriden by the Kansan and Illinoian ice sheets (Flint, Colton, *et al.*, 1959) and is now mantled by their drift sheets. Post-Illinoian erosion has exhumed some of the extensive sinkhole plains in Monroe and St. Clair counties, Illinois, and has removed fill from the caves, especially near the Mississippi River where the gradient is greatest between the upland drift plain surface and the river. Away from the river, much of the karst is still buried.

In Missouri, the limestones vary from gently dipping Ordovician rocks with deep, narrow, joint controlled caves in the St. Louis vicinity

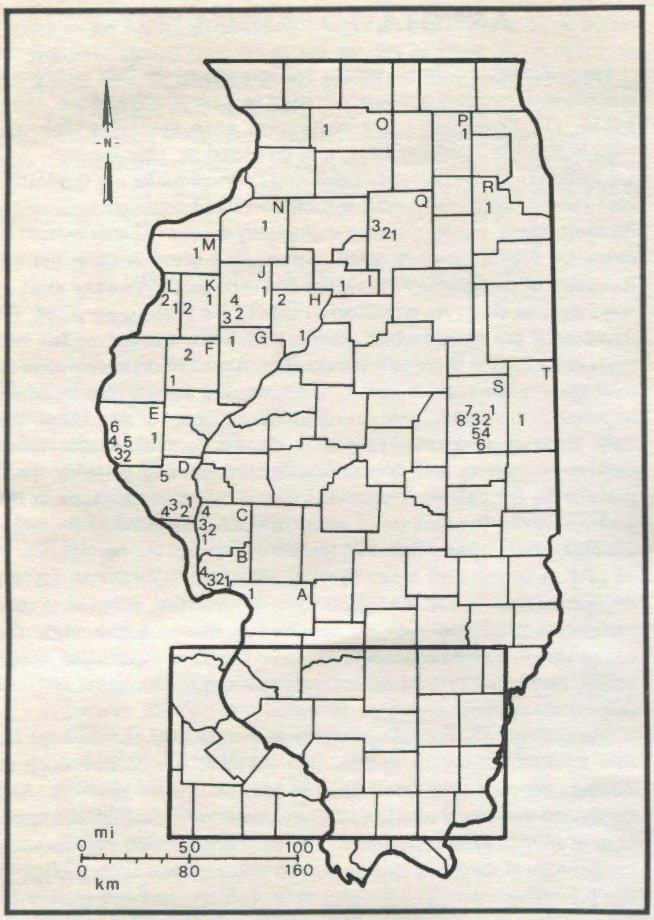

Figure 4. Field collection localities of subterranean fauna in Illinois (see Figure 5 for map of inset area of southern Illinois and adjacent Missouri). *A—Madison County*. 1, cave 1 mi N. Alton. *B—Jersey County*. 1, Chautauqua Spring. 2, spring near Grafton. 3, spring, Père Marquette State Park. 4, Brainerd (Grafton) Cave. 5, small seep (location unknown). *C—Greene County*. 1, spring 3 mi N. Elred. 2, Old Settlers Spring, 4 mi S. Hillview. 3, spring 2.5 mi S. Hillview. 4, small roadside caves 4 mi N. Hillview. *D—Pike County*. 1, small spring, near Pearl. 2, Lost Creek Cave. 3, Twin Culvert Cave. 4, spring 5 mi W. Pearl. 5, Croxville Cave. *E—Adams County*. 1, Large House Spring. 2, Burton Cave. 3, pumpwell S. Quincy. 4, Peters Spring, Quincy. 5, Cole Spring, Quincy. 6, spring 4 mi SSW Ursa. *F—McDonough County*. 1, drain 3 mi S. Colmar. 2, drain 4.8 mi N. Macomb. *G—Fulton County* 1, drain 1 mi S Avon. *H—Peoria County*. 1, Rocky Glen, Peoria. 2, drain 1.5 mi E. Laura. *I—Marshall County*. 1, spring run near Lacon. *J—Knox County*.1, drain 1.5 mi SE Williamsfield. 2, well near Abingdon. 3, drain 3.1 mi N. St. Augustine. 4, drain 2 mi N. Abingdon. *K—Warren County*. 1, drain 1 mi SE Cameron. 2, drain 5.2 mi E. Biggsville. *L—Henderson County*. 1, drain 3 mi W. Biggsville. 2, Goose Hollow Cave. *M—Mercer County*. 1, Sherrard. *N—Henry County*. 1, Atkinson. *O—Ogle County*. 1, White Pines State Park. *P—Kane County*. 1, spring stream at Elgin. *Q—LaSalle County*. 1, Blackball Mine. 2, spring in Spring Dell. 3, well on Engelhaupt Farm, N. Peru. 4, drain outlet. *R—Will County*. 1, well, Joliet. *S—Champaign County*. 1, drainage ditch 1 mi N. Mayview. 2, Urbana: N. Crystal Lake in sinkhole; Urbana: old well. 3, Champaign: ditches; old well; open well. 4, drain tile 1 mi S. Urbana. 5, S. of Champaign. 6, Savoy. 7, Kaskaskia River, 1 mi E. Bondville. 8, Seymour. *T—Vermillion County*. 1, drain 1 mi W. Fairmont. Literature and old collection sites whose exact locations are not known to us are not shown on this or the following map.

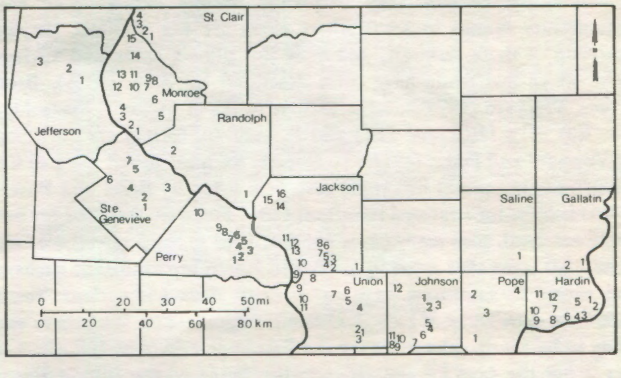

Figure 5. Field collection localities of subterranean fauna in the Shawnee Hills and Salem Plateaus of southern Illinois and three adjacent counties in Missouri (inset from Figure 4). **Illinois**. *Gallatin County*. 1, spring at Saline Wells. 2, sandstone spring in Oxlot Cave, Pounds Hollow. *Hardin County*. 1, spring near Lamb, 2, Brown's Hole. 3, Cave-in-Rock. 4, small cave W. Cave-in-Rock. 5, unnamed cave N. Cave-in-Rock. 6, Round Spring. 7, Griffith Cave. 8, Layoff Cave. 9, Cave Spring Cave. 10, Jacksons Sandstone Cave and seeps. 11, Kaskaskia Exp. Forest Spring. 12, small spring N. Illinois Iron Furnace. *Saline County*. 1, Equality Cave. *Pope County*. 1, Dixon Springs. 2, Bell Smith Springs. 3, Frieze Cave. 4, spring near Herod. *Johnson County*. 1, Jug Spring Cave. 2, Casey Spring. 3, Will Thomas Spring Cave. 4, Firestone Creek Cave. 5, Firestone Creek Spring. 6, Teal Cave. 7, Belknap Cave. 8, Masons Cave No. 1. 9, Masons Cave No. 2. 10, Thapsus Cave. 11, Persimmon Pit. 12, sandstone spring at Ferne Clyffe. *Union County*. 1. Roaring Spring. 2, Cricket Cave. 3, Sensemeyer Cave. 4, Saratoga Cave. 5, Rich's Cave. 6. Guthrie Cave. 7, Union Point Cave. 8, Cave Spring Cave. 9, seep 2.5 mi NE Aldridge. 10, Elm Spring. 11, Triple Spring. *Jackson County*. 1, Giant City caves and seeps. 2, spring 1 at Hickman Cave. 3, spring 2 at Hickman Cave. 4, Hickman Cave. 5, Cave No. 1. 6, Mt. Pleasant Spring. 7, Bat Cave. 8, spring SW. Pomona. 9, Devil's Backbone Cave. 10, Clear Spring. 11, Happy Hollow Spring. 12, Fountain Bluff spring 1. 13, Fountain Bluff spring 2. 14, Ava Cave. 15, Degognia Cave. 16, sandstone seep near Degognia. *Randolph County*. 1, Ebenezer Church Spring, 5 mi NE Rockwood. 2, Allied Chemical Quarry Spring, Prairie du Rocher. *Monroe County*. 1, Fults Creek Cave. 2, Saltpeter Cave. 3, small cave 1 mi S. Fountain Gap. 4, Spring 1 mi N. Fountain Gap. 5, Fogelpole Cave. 6, Illinois Caverns. 7, small cave near Wartburg. 8, Fruth's Spider Cave. 9, Dry Run Cave. 10, Madonnaville Cave. 11, Pautler Cave. 12, seep near Valmeyer. 13, Horsethief Cave. 14, Camp Vandeventer Cave. 15, Terry Spring Cave. *St. Clair County*. 1, Stemmler Cave. 2, swales 1 mi S. Falling Spring. 3, Falling Spring Cave. 4, small spring near Falling Spring. **Missouri**. *Perry County*. 1, Slope Cave. 2, Mystery Cave. 3, Garbage Hole Cave. 4, Lost and Found Cave. 5, Running Bull Cave. 6, Mertz Cave. 7, Klump Cave. 8, Berome Moore Cave. 9, Tom Moore Cave. 10, cave N. Perryville Airport. 11, Mecker Cave (location unknown). *Ste. Geneviève County*. 1, Batty's Cave. 2, Buddy's Cave. 3, spring 1.5 mi S. Ste. Geneviève. 4, Gegg Cave. 5, Kohm's Cave. 6, Pickle Springs. 7, Sims' Cave. *Jefferson County*. 1. Friedmans Cave. 2, cave S. Antonia. 3, Pleasant Valley Cave.

(Brod, 1964; Oesch, 1967), to younger and more flat lying Mississippian limestones to the south in Ste. Geneviève, and Cape Girardeau Counties, and back to Ordovician limestone and dolomite in Perry County, where stream passage caves are more prevalent. The Ste. Geneviève fault system is a prominent east-west structural zone subdividing the region (McCracken, 1971). Topographic relief is more pronounced near St. Louis, while Perry County, away from the trench of the Mississippi River, is typified by a gently undulating karst erosional surface of little relief. Relief in the region varies from about 100 to 130m along the Mississippi River to about 300m at the crest of the Shawnee Hills. These Missouri landscapes have not been covered by glacial ice, but the glacial margins in Nebraskan, Kansan, and Illinoian times lay near them. The southern margins of these limestone areas are bounded by the Gulf Coastal Plain. More detailed topographic, physiographic, and speleological discussions can be found in references cited above and in other regional works on these subjects (such as Bier, 1956; Fenneman, 1938; Hunt, 1974; and Thornbury, 1965).

Cave and groundwater temperatures average from about 10°C in the northern to 14°C in the southern parts of the study area. Cave and cave stream temperatures have wider seasonal fluctuations than do those of less open groundwater wells, springs, and seeps.

FIELD STUDY

Our cave-directed field work has been thorough in terms of time spent on the project and the number of sites personally visited. Emphasis was placed on Illinois. In all cases where possible, we attempted to verify published locality records. Peck was involved in Missouri and Illinois cave faunal field studies from 1966 to 1968 and made 76 visits to 43 caves and 13 springs in the region reported on in this study. Lewis conducted field studies in Illinois and Missouri from 1972 to the present, and made some 175 collecting visits to 66 caves and springs (figs. 4 and 5). We include springs, seeps, drain tiles, and wells in this study, because they frequently contain subterranean and groundwater faunas in areas where caves are not available for the sampling of these habitats. Many of the Illinois caves and springs surveyed in this study have been described by Bretz (1956), Brod (1964), Vineyard (1973), and in various issues of Missouri Speleology (*i.e.* 7(3), 8(1), 11(3), and 12 (1 and 2). Missouri springs are described by Vineyard and Feder (1974). In Illinois, we have visited most of the biologically important limestone cave sites listed by Bretz and Harris (1961) (except for Brainerd [Grafton] Cave, which we searched for but could not find), plus many caves not described in these references. We found that some sites listed by Bretz and Harris are sandstone shelters and, except for sandstone seeps and springs, these and various "fossil caves" are usually not of biological-habitat significance. We believe our study to be nearly exhaustive for the limestone region of Illinois, but this is not the case for the groundwater fauna in the Illinois Basin region or for Missouri, where many faunal locality records undoubtedly remain to be made.

Most previous faunal studies in this geographic region were concerned with taxonomic studies of specific groups. These will be cited in the following list, with the appropriate species. Additional and related faunal studies are some discussing inhabitants of Missouri springs (Pflieger, 1974), aquatic malacostracan crustaceans in Illinois (Page, 1974), cave fishes in Illinois and adjacent regions (Poulson, 1963; Weise, 1957; Woods and Inger, 1957), cave-inhabiting salamanders (Hutchinson, 1956), and vertebrate bone deposits (Parmalee, 1967; Oesch, 1967; and included references).

Our collecting efforts have been as extensive as possible. We have neither consciously favored nor neglected any particular taxon over any others in search efforts in either terrestrial or aquatic environments. In addition to direct searching we have used Berlese funnels, baits, and baited traps (Peck 1973a, 1975a, and Newton and Peck, 1975), and have repeatedly visited and searched large cave systems.

ANNOTATED FAUNAL LIST

Cave-inhabiting animals usually fall into one of the four ecological-evolutionary categories commonly used in cave biology (Barr, 1963, 1968). (1) *Troglobites* are obligatory cave species which are morphologically specialized for, and restricted to, cave habitats, and are unable to live in non-cave habitats. (2) *Troglophiles* are facultative cave species, which frequently inhabit caves and complete their entire life cycles there, but may occupy ecologically similar habitats outside of caves. (3) *Trogloxenes* are species which often occur in caves but are incapable of completing their entire life cycle in caves. They must at some time or times leave the cave, usually for feeding purposes. (4) *Accidentals* are species which accidentally wash, wander, or fall into caves and can exist there only temporarily. Although these may serve as food sources for regular cave inhabitants, the accidentals are of no importance in distributional or evolutionary analyses of cave fauna. We have listed most species judged to be accidentals (but excluded herbivores such as leaf hoppers), even though this category could potentially, through time, come to embrace much of the fauna in the area containing the cave (such as the invertebrates listed by Parmalee 1967). In many cases, it is still too early to judge the relative degree of cave association of many species. We think it better to include the species than to lose the information. By so doing, patterns of cave association that are not yet apparent may emerge through the compilation of additional data (as was found for cantharid beetle larvae, Peck, 1975b), and the category to which the species is assigned may be changed.

The ecological term *endogean* or *edaphobite* may also be used for cave animals. These are species that normally live in soil, such as earthworms, and their occurrence in caves is usually sporadic. And finally, *phreatobite* is used to describe animals which inhabit the upper layer of ground waters (Holsinger, 1969b). These species, with the same morphological modifications as troglobites, are found more often in slowly moving interstitial ground water habitats and can usually be sampled only at temporary springs, seeps, wells, etc. These species are often scarce or absent in the more open ground waters present in caves.

Many of the species found in the following list are still inadequately known in their distribution outside Illinois and in their ecology; their assignment to one of the above ecological-evolutionary categories should be considered tentative and subject to readjustment when additional information is available. The following abbreviations, placed after the organisms' names, have been employed: TB = troglobite; TP = troglophile; TX = trogloxene, ED = edaphobite; PB = phreatobite; AC = accidental.

Some of the taxa found in this list are still poorly known and, therefore, could not be determined to species. Other forms, such as planarians and diplurans, are currently being studied and specific names are not yet available. Still other material represents undescribed species, for which names and descriptions have not been published. Because of these reasons, this list should be regarded as subject to later refinement. However, considering the number of sites sampled, the data given in this list are believed to form a nearly complete picture of the invertebrate fauna of the caves and of the subterranean ground waters of the region.

Because of space limitations, we do not give supporting data for species records presented here, such as date of collection, collector's name, or collection containing the specimens. Records not found in the references listed for each species should generally be assumed to be new records made by us or provided by the specialists adknowledged at the end of the paper. Many (but not all) well, spring, and seep records for groundwater crustaceans from the Illinois Basin came from the collections of the Illinois Natural History Survey, Urbana, and from the unpublished data of J.R. Holsinger.

Published cave names which do not agree with present usage are placed in parentheses following the currently accepted cave names.

Where species names and names of higher taxa do not correspond to those given in some of the older literature, it is because we have used names based on more recent revisional studies. Where more recent studies have shown older literature locality records to be based on inaccurate identifications, we have not listed the erroneous localities.

The higher taxa have been listed in generally accepted phylogenetic sequence. Genera within families, and species within genera have been listed in alphabetical order. Localities are listed alphabetically by state, by county within the state, and by cave, spring, well site, etc., within the county.

PHYLUM PLATYHELMINTHES
Class Turbellaria
ORDER TRICLADIDA

Family Kenkiidae

Macrocotyla lewisi Kenk, TB

Missouri. Perry County: Mystery Cave (type locality), Tom Moore, and Lost and Found caves. The species was recently described (Kenk, 1975), and a second species, *M. glandulosa*, redescribed from Devil's Icebox Cave, Boone County, Missouri. The only other species in the genus is a West Virginia troglobite.

Sphalloplana hubrichti (Hyman), TB

Illinois. Jackson County: Happy Hollow Spring. Monroe County: Coonrod, Fults Creek, and Fogelpole caves, and Illinois (Morrison's, Mammoth of Illinois, Eckert's Burkesville) Caverns. St. Clair County: Stemmler (Oerter) Cave. Union County: Rich's Cave. **Missouri**. Jefferson County: unspecified springs. Ste. Geneviève County: Kohm's Cave. Records of unidentifiable material that are probably this species are: **Illinois**. Monroe County: Dry Run Cave. Union County: Cricket Cave. Both Illinois Caverns and Kohm's Cave have been given as the type locality (Hyman, 1945; Kenk, 1972, 1977).

Sphalloplana evaginata Kenk, TB

Missouri. Perry County: Klump, Garbage Hole, Crevice and Berome Moore caves (Kenk, 1977).

Family Planariidae

Phagocata gracilis (Haldeman), TP

Illinois. Hardin County: Spring near Lamb. Jackson County: Fountain Bluff Spring Nos. 1 and 2. Johnson County: Casey Spring, Jug Spring and Will Thomas Spring caves. Monroe County: Fults Creek and Horsethief caves. Union County: Elm Spring, and Guthrie and Rich's caves. **Missouri**. Perry County: Lost and Found, Mertz, Mystery, Running Bull, and Tom Moore caves. Some populations of this species are blind and/or unpigmented. It is distributed from Missouri to Pennsylvania and Virginia; in southern Illinois and Missouri it is common in most springs and many caves (Jenio, 1972; Kenk, 1970, 1972).

Family Rhyncodemidae

Microplana atrocyaneus (Walton), TP?

Hubricht (1950) reports this terrestrial flatworm species, formerly in the genus *Geodesmus*, from Mecker Cave, Perry County, and from River Cave, Camden County, **Missouri**.

PHYLUM ANNELIDA
Class Clitellata
ORDER OLIGOCHAETA*

Family Acanthrodrilidae

Diplocardia singularis Ude, ED

Illinois. Union County: Guthrie Cave.

Diplocardia verruscosa Ude, ED

Missouri. Ste. Geneviève County: Kohm's Cave.

Diplocardia sp., ED

Illinois. Hardin County: Brown's Hole. Monroe County: Camp Vandeventer Cave. Pike County: Lost Creek Cave. **Missouri**. Perry County: Mertz and Mystery caves. The genus occurs only in the U.S. and Mexico. Since the genus is presently in a state of taxonomic confusion it is difficult to determine if these records represent the above or other species (Gates, 1959).

Family Komarekionidae

Komarekiona eatoni Gates, ED

Illinois. Hardin County: Brown's Hole. This is the first Illinois record for the species (Gates, 1974).

Family Lumbricidae

Allolobophora trapezoides (Duges), ED

Illinois. Hardin County: Cave north of Cave-in-Rock. Johnson County: Mason Cave No. 1. The species is also known from caves in Arkansas, Kentucky, Tennessee, and West Virginia (Gates, 1959) and is distributed over much of North America (Gates, 1972a). Undetermined material of this genus that may be this or other species is from Brown's Hole, Hardin County, and Will Thomas Spring Cave, Johnson County, **Illinois**, and from Mystery Cave, Perry County, **Missouri**.

Bimastos heimburgeri Smith, ED

Illinois. Hardin County: Brown's Hole.

Bimastos longicinctus Smith and Gittens, ED

Illinois. Hardin County: Brown's Hole.

Bimastos tumidus (Eisen), ED

Missouri. Perry County: Mystery Cave. The species is also known from caves in Virginia and Tennessee (Gates, 1959).

Dendrobaena rubida (Savigny), ED

Illinois. Hardin County: Brown's Hole, Layoff Cave and cave north of Cave-in-Rock. Johnson County: Will Thomas Spring Cave. Monroe County: Illinois Caverns. **Missouri**. Perry County: Mertz Cave. Ste. Geneviève County: Kohm's Cave. This species is also reported from caves elsewhere in Missouri and from four other states (Gates, 1959).

Eisenoides carolinensis (Michaelsen), ED

Illinois. Hardin County: Brown's Hole. This is a new state record for the species, which is widespread in much of the eastern United States (Gates, 1972b).

Lumbricus rubellus Hoffmeister, ED

Illinois. Hardin County: Griffith Cave. Johnson County: Will Thomas Spring Cave.

Octolasion tyrtaeum (Savigny), ED

Illinois. Hardin County: Layoff Cave.

ORDER HIRUDINEA

Family Erpobdellidae

Dina (Mooreobdella) microstoma (Moore), TP?

Missouri. Perry County: Mystery Cave. We have also seen leeches in Kohm's Cave, Ste. Geneviève County, and Hubricht (1950) reports leeches from Ozark caves. The above species is widespread in Mystery Cave and is probably a troglophile, since its main food is crustaceans and aquatic insects (Klemm, 1972).

PHYLUM MOLLUSCA
Class Gastropoda
ORDER PULMONATA

Family Physidae

Physa halei Lea, TP or TB?

Illinois. Monroe County: Camp Vandeventer (Ice) and Fogelpole caves, and Illinois (Morrison's) Caverns. **Missouri**. Perry County: Berome Moore, Mertz, Mystery, and Running Bull caves, and also in caves in Pulaski and Christian Counties.

* It should be noted that of all fauna found in caves, earthworms have distributions most affected by man. Native American species probably did not migrate north to any significant extent into glaciated regions. Earthworms in these regions are usually European species that have been introduced by man (Gates, 1976a, 1976b, and references).

Hubricht (1941) found the Illinois populations to be small and with greatly reduced pigmentation. We (SBP) have also noted the depigmentation and believe it worthy of additional, perhaps electrophoretic, study (Laing, Carmody, Peck, 1976a).
~~phoretic, study (Laing, Carmody, Peck, 1976a).~~

ORDER CTENOBRANCHIATA

Family Hydrobiidae

Amnicola stygia Hubricht, TB

Missouri. Perry County: Berome Moore and Tom Moore caves. The species is known only from these two localities (Hubricht, 1971).

Amnicola
~~*Fontigens*~~ *proserpina* (Hubricht), TB

Missouri. Jefferson County: Rice's Cave. Ste. Geneviève County: Saltpeter Cave. St. Louis County: drain outlet of spring, Osage Hills golf course, Kirkwood; large spring on Glencoe Creek. These are the only known localities for this species, originally placed in the genus *Amnicola* (Hubricht, 1940, 1942). still there?

Fontigens antroecetes (Hubricht), TB

Illinois. St. Clair County: Stemmler Cave (type locality). **Missouri**. Perry County: Berome Moore, Tom Moore, Klump, Mertz, and Mystery caves. St. Louis County: Cliff Cave. As the species is now understood, these are the only known localities. It was originally placed in the genus *Amnicola*, as a subscpecies of *Amnicola aldrichi*, with which some of the early records have been confused. *Fontigens aldrichi* (Call and Beecher), itself also previously in *Amnicola*, occurs in springs in St. Louis and Jefferson counties, and in springs or caves in more western Missouri counties (Butler, Carter, Crawford, Dent, Franklin, Osage, Phelps, Pulaski, Reynolds, Shannon, St. Francois, Washington, and Wayne). Eyed and pigmented forms of this latter species live on gravel in springs and blind and white forms on gravel in cave streams. The eyed form is usually not found in a spring with the blind form in the cave behind it, but in two cases (one at Piquet Cave, Phelps County), the blind form was abundant in the cave but not the spring on one visit and several years later the blind form had moved out of the cave into the spring, being rare in the cave and common in the spring (Craig, 1975, 1977; Hubricht, 1940, 1941, 1942, and *in litt.*). This form variation suggests an interesting research problem on their ecology and population genetics (see Holsinger and Culver, 1970; Laing, Carmody, and Peck, 1976a).

ORDER STYLOMMATOPHORA

Family Polygyridae

Mesodon inflectus (Say), TP

Illinois. Hardin County: Layoff Cave. **Missouri**. Ste. Geneviève County: Kohm's Cave. The species is also known from caves in Kentucky and Alabama (Hubricht, 1964).

Triodopsis fosteri (F. C. Baker), TP?

Illinois. Union County: Cricket Cave.

Triodopsis vulgatus (Pilsbry), TP?

Illinois. Union County: Guthrie Cave.

Family Zonitidae

Hawaiia miniscula (Binney), TX

Missouri. Perry County: Mystery Cave.

Zonitoides arboreus (Say), TP/TX

Illinois. Johnson County: Firestone Creek Cave. **Missouri**. Perry County: Mystery Cave. The species is spread through much of the eastern United States and is often associated with caves (Hubricht, 1964, 1968).

Class Pelycypoda

ORDER HETERONDONTA

Family Sphaeriidae

Musculium transversum (Say), TP

Missouri. Perry County: Berome Moore Cave. Hubricht (1941) reports an undetermined species of this genus to be a reproducing population in Illinois Caverns, Monroe County.

PHYLUM ARTHROPODA

Class Crustacea

ORDER CYCLOPOIDA

Family Cyclopidae

Cyclops clandestinus Yeatman, PB?

Illinois. Vermillion County: a drain tile. **Missouri**. St. Charles County: Dingledine Cave (J.R. Holsinger, unpubl. data). The species is otherwise known only from Big Mouth Cave, Grundy County, Tennessee (Yeatman, 1964).

ORDER ISOPODA

Family Asellidae

Caecidotea sp. no. 1, TB

Illinois. Union County: Cricket, Roaring Spring, and Sensemeyer caves. The species, from Cricket Cave, was erroneously reported (Fleming, 1972) as *A. alabamensis*, which occurs in Alabama, but not in Kentucky, and Tennessee (Fleming, 1972; Steeves, 1963a, 1963b; Lewis and Bowman, in prep.). Much recent discussion has been published on the subject of the correct name for this genus. Henry and Magniez (1970) split the eastern asellids (excluding *Lirceus*) into *Conasellus* and *Pseudobaicalasellus*. Fleming (1973) discussed this and his proposal was rejected by Bowman (1975), who pointed out the priority that the name *Caecidotea* has over *Conasellus*. We use *Caecidotea* in the sense of Bowman, recognizing that the genus contains epigean as well as troglobitic species.

Caecidotea sp. no. 2, TB

Illinois. Johnson County: unnamed cave at White Hill.

Caecidotea sp. no. 3, TB

Illinois. Pope County: Stream from pumphouse at Dixon Springs State Park.

Caecidotea antricola (Creaser), TB

Missouri. Perry County: Crevice, Grapevine, Klump, Lost and Found, Mystery, and Tom Moore caves. The species is also known from caves in Crawford, Green, Phelps, and Wright Counties, Missouri and from Kentucky and Arkansas (Fleming, 1972; Steeves, 1966; Craig, 1975b).

Caecidotea brevicauda (Forbes), TP

Illinois. Calhoun County: McNabb Hollow Cave. Hardin County: Cave Spring Cave, spring near Lamb, and Round Spring. Jackson County: Ava and Degognia Cave, and Cave No. 1, springs no. 1 and no. 2 across from Hickman Cave, sandstone seep near Degognia, sandstone seep 1.5 mi SW Pomona, and Mt. Pleasant Spring. Jersey County: spring near Grafton. Johnson County: Firestone Creek Cave and Spring. Monroe County: Camp Vandeventer, Fogelpole, Fruth's Spider, Horsethief, Madonnaville, Pautler, and Terry Spring (Long Slash) caves and Illinois (Morrison's) Caverns. Pike County: Lost Creek Cave. Pope County: Bell Smith Springs. Randolph County: Spring at Allied Chemical Quarry in Prairie du Rocher, spring 2 mi NE Rockwood. St. Clair County: Falling Spring and Stemmler caves. Union County: Cave Spring, Saratoga, and Union Point caves. **Missouri**. Perry County: Mertz and Mystery caves and cave 2 mi N Perryville airport. Ste. Geneviève County: Spring 1.5 mi south of Ste. Geneviève, on road. This species is also known from caves elsewhere in Missouri, Arkansas, and Tennessee (Mackin and Hubricht, 1938; Fleming, 1972; Williams, 1970; Craig, 1977) and we believe it to be present in almost all suitable habitats. Cave populations of the species tend to become depigmented.

Caecidotea kendeighi (Steeves and Seidenberg), PB

Illinois. Champaign County: Drainage ditch 3 mi N Mayview (Steeves and Seidenberg, 1971). The species is probably common throughout the Illinois Basin.

Caecidotea packardi Mackin and Hubricht, TB

Illinois. Adams County: Burton Cave, pumpwell south of Quincy. Monroe County: Fogelpole, Fruth's Spider, Fults Creek, Horsethief, Pautler, Terry Spring caves and Illinois (Morrison's) Caverns (type locality). Pike County: Croxville Cave. St. Clair County: Falling Spring Cave, small cave 2 mi N Fountain Gap, and Stemmler Cave. This species is known only from Illinois (Mackin and Hubricht, 1940; Fleming, 1972).

Caecidotea spatulata (Mackin and Hubricht), TP or TX

This vestigially-eyed species is known from swales 1 mi S of Falling Spring, St. Clair County (type locality) and also occurs in glaciated **Illinois** in Smith Park Cave, Carroll County, and in a spring in Weldon Springs State Park, Dewitt County, as well as in epigean sites in St. Louis and Boone Counties, **Missouri** (Mackin and Hubricht, 1940; Fleming, 1972). A Maryland record is probably a misidentification (Hubricht, pers. comm.).

Caecidotea stygia Packard, TB - PB

Illinois. Hardin County: Cave Spring, Griffith, and Layoff caves. The species is also known from caves in Indiana, Kentucky, Ohio, and Tennessee (Fleming, 1972). Earlier reports of this species from Pennsylvania and Virginia are in error (J. Holsinger and L. Hubricht, pers. comm.) and we doubt the Monroe County records of "wells" of Steeves (1963), and the Missouri records of Fleming (1972).

Caecidotea tridentata Hungerford, TB or PB?

headwater drainage surface stream in Champaign Co, Illinois (Dexter, 1954).

Illinois. LaSalle County: drain outlet. L. Hubricht (in litt.) has frequently found the species at drain outlets in the prairies of Iowa, Illinois and Indiana (specimens in USNM). The species is also known from caves in Arkansas, Kansas, Missouri, and Oklahoma (Fleming, 1972).

Caecidotea spp., TB

Illinois. Adams County: Quincy cave, Coe Spring, and Peter's Spring. Calhoun County: Madison Creek Cave. Champaign County: Seymour, Savoy, and Kaskaskia River (1 mi E Bondville) ditches in Champaign, open well at 107 E Bell Fountain Ave. (Champaign), south of Champaign, Urbana, end of drain tile 1 mi S Urbana, and in sinkhole near Crystal Lake (Urbana). Henry County: Atkinson. Johnson County: Teal Cave. Mercer County: Sherrard. Monroe County: Dry Run Cave. Ogle County: White Pines State Park. Peoria County: Peoria, Rocky Glen. Will County: drilled well at Joliet. County localities unknown: Grand Avenue Cave, Valley City, "from udders of cow"! All of these records represent populations of eyeless and depigmented isopods. Most of the records for non-cave sites are from the Illinois Natural History Survey collections. These records are probably the species already listed and at least some of the Champaign County records are undoubtedly of *C. kendeighi*. The other records show the ability of eyeless *Caecidotea* to re-invade areas of Illinoian and Wisconsinan glaciation, by intersitial dispersal, where limestones are absent.

Lirceus fontinalis Rafinesque, TX

Illinois. Hardin County: Round Spring. Monroe County: Illinois Caverns (Hubricht and Mackin, 1949).

Family Armadillidiidae

Armadillidium vulgare (Latreille), TX

Illinois. Hardin County: Cave-in-Rock Cave. **Missouri**. Perry County: Mystery Cave. This introduced species is in several states. It is usually found only near cave entrances, but is reproducing in Cave-in-Rock in the back room (Schultz, 1970).

Family Ligiidae

Ligidium elrodii elrodii (Packard), TP

Illinois. Hardin County: Brown's Hole and Layoff caves. Johnson County: Will Thomas Spring Cave. Union County: Cave Spring Cave (Dry Entrance). This species, formerly considered *L. longicaudatum*, is fairly abundant in organic debris across the eastern United States and is commonly in caves within its range. Several cave populations have been recognized as subspecifically distinct (Schultz, 1970).

Family Porcellionidae

Cyclisticus convexus (DeGeer), TP?

Illinois. Adams County: Burton Cave. Hardin County: Cave-in-Rock Cave. This widespread introduced species is found in caves in several states (Schultz, 1970).

Family Trichoniscidae

Miktoniscus sp., probably *medcofi* Van Name, TP

Illinois. Hardin County: Brown's Hole. The species is known from several caves and from many forested sites in the eastern U.S. (Vandel, 1965; Muchmore, 1957, 1964; Schultz, 1976).

ORDER AMPHIPODA

Family Crangonyctidae*

Bactrurus brachycaudus Hubricht and Mackin, TB

Illinois. Calhoun County: Orchard Spring at Hardin. Green County: Spring 2.5 mi S Hillview, spring 3 mi N Eldred. Jackson County: Giant City seeps. Johnson County: Belknap and Firestone Creek caves. Monroe County: Camp Vandeventer, Fogelpole, Fults Creek and Terry Spring caves, small cave near Wartburg, seep near Valmeyer, and Illinois (Morrison's) Caverns. St. Clair County; Stemmler's Cave and small spring near Falling Spring. Pike County: Croxville and Twin Culvert caves, and a small spring near Pearl. Union County: seep 2.5 mi NE Aldridge. **Missouri**. Perry County: Mystery and Tom Moore caves. Ste. Geneviève County: Kohm's Cave. St. Louis County: walled spring on Keider Creek 0.6 mi NW Fern Glen (type locality). This species (limited to Illinois and Missouri), the following species, and *B. hubrichti* from Kansas, Oklahoma, and western Missouri, are the only described members of the genus (Holsinger, 1972; Hubricht and Mackin, 1940; Hubricht, 1943; Craig, 1977).

Bactrurus mucronatus (Forbes), PB

Illinois. Champaign County: drain, drainage ditch, and old well in Champaign. Fulton County: drain 1.4 mi S Avon. Henderson County: drain 3 mi E. Biggsville. Knox County: drains 3.1 mi S St. Augustine, 2 mi N. Abingdon, and 1.5 mi SE Williamsfield. LaSalle County: drain on Engelhaupt farm N of Peru. McDonough County: drains 4.8 mi N Macomb and 3 mi S Colmar. McLean County: well at Normal (type locality). Peoria County: drain 1.5 mi E Laura. Saline County: Equality (Cave Hill) Cave. Vermillion County: drain 1 mi W Fairmont. Warren County: drains 2 mi SE Cameron and 5.2 mi E Biggsville. This eyeless interstitial species has been taken in only the one above cave in the region under consideration, but this population has been sampled at least four times in the past 20 years, and was present in 1976. The species is also known from many localities, few of which are caves, in Iowa, Indiana, Ohio, and Michigan, (Holsinger, 1972; Hubricht, 1943). A closely related species or subspecies occurs in caves in southern Missouri and northern Arkansas (Holsinger, 1972).

Crangonyx forbesi Hubricht and Mackin, TP

Illinois. Calhoun County: Orchard Spring at Hardin. Gallatin County: seeps near Salt Spring. Hardin County: spring near Lamb. Jackson County: Cave No. 1, Fountain Bluff spring No. 1 and No. 2, Giant City seeps, Happy Hollow Spring, sandstone seep near Degognia, Hickman Cave, and spring no. 1 and no. 2 across from Hickman Cave. Jersey County: spring near Grafton. Johnson County: Firestone Creek Cave. Monroe County: Camp

*The North American amphipod genera *Bactrurus, Crangonyx, Stygobromus* (including *Apocrangonyx* and *Stygonectes*) and *Synurella* were recently assigned to the family Crangonyctidae by Bousfield (1973) and by Holsinger (in press). They were formerly considered to be Gammaridae.

Vandeventer, Dry Run, Fogelpole, Fruth's Spider, Horsethief, Pautler, Terry Spring, and Wilde's (identity unknown) caves, and Illinois (Morrison's) Caverns. Pike County: Lost Creek Cave. Randolph County: spring 2 mi NE Rockwood. St. Clair County: Stemmler Cave. **Missouri**. Ste. Geneviève County. Kohm's Cave and spring on road 1.5 mi S Ste. Genevieve. Perry County: Garbage Hole, Mystery, and Tom Moore caves. St. Louis County: drain outlet, Osage Hills Golf Course, Kirkwood (type locality). A possible subspecies occurs in Indiana, Ohio, and Kentucky (Holsinger, 1972). Other populations previously assigned to *C. forbesi*, from southern Missouri, Arkansas, and Oklahoma (Bousfield, 1958; Hubricht and Mackin, 1940; Hubricht, 1943) are probably an undescribed species (Holsinger, 1972).

Crangonyx sp., (*gracilis* group), TP or TX

Illinois. Adams County: Large House Spring. Jackson County: sandstone seep in Giant City State Park. *Crangonyx gracilis s. str.* is probably limited to the Great Lakes drainage (Holsinger, 1972), and other records such as these possibly represent undescribed species and/or subspecies (Bousfield, 1958; Hubricht and Mackin, 1940; Hubricht, 1943). The *gracilis* group appears to be a species complex which needs considerable study (J. Holsinger, in litt.).

Crangonyx sp., (*packardi* group), TB

Illinois. Hardin County: Griffith, Layoff, and Cave Spring caves, and a spring N of Illinois Iron Furnace. Johnson County: Firestone Creek Cave and Spring, and an unnamed cave at White Hill. Pike County: Croxville Cave. Saline County: Equality Cave. Union County: Cricket (Wet), and Sensemeyer caves. A complex of this and other closely related species occurs in caves and other subterranean habitats in southern Indiana, many parts of Kentucky, eastern Kansas, and southern Ohio (Holsinger, 1972, in litt.).

Stygobromus lucifugus (Hay) TB or PB

Illinois. Knox County: Well near Abingdon. This species, formerly placed in the genus *Apocrangonyx*, is known only from the original collection and may likely be a synonym of *S. subtilis* (Holsinger, 1969a).

Stygobromus heteropodus (Hubricht), PB

Missouri. Ste. Geneviève County: Pickle Spring (type locality). The species is known only from this locality, but the genus is widespread and contains many Appalachian cave species (Holsinger, 1969a, 1972; Hubricht, 1943; Karaman, 1974).

Stygobromus subtilis (Hubricht), TB or PB

Illinois. Adams County: Burton Cave. Monroe County: Saltpeter Cave (Cave on Bluff), Bat (Toothless) Cave (type locality), and sandstone seep near Bat Cave Sink. Jackson County: Pomona, and Giant City seeps. Jersey County: small seep. Union County: small sandstone seep. **Missouri**. Ste. Geneviève County: Batty's Cave. This species, formerly placed in the genus *Apocrangonyx*, seems commonly to be associated with the exsurgence of subterranean waters at sandstone seeps. At Giant City, it is found only in the springtime when ground waters are "high." It occurs here with the much scarcer amphipod *Bactrurus brachycaudus*. We (JL) have found a reproducing population only in the rear room of the type locality (Bat Cave). This leads us to think that cave collections are more or less accidental, and that the species normally reproduces in interstitial ground waters, (Hubricht, 1943; Holsinger, 1969a, and in press; Karaman, 1974).

Stygobromus sp. 1, TB or PB

Illinois. Hardin County: Jackson's Sandstone Cave. This undescribed species is known only from two specimens taken in a seep in this 30 ft sandstone cave.

Stygobromus sp. 2, TB or PB

Illinois. Pope County: Dixon Springs.

Synurella dentata (Hubricht), TX?

Illinois. Johnson County: Firestone Creek Cave and Spring. Pope County: Spring near Herod. Tentatively determined material comes from a spring on the road N of Illinois Iron Furnace, Hardin County, and from Belknap Cave, Johnson County. The species mostly inhabits springs and spring fed streams from SE Indiana and southern Ohio, south to Kentucky and northcentral Tennessee. It is previously unrecorded from Illinois (Holsinger, 1972).

Family Gammaridae

Gammarus acherondytes (Hubricht and Mackin), TB

Illinois. Monroe County. Fogelpole, Fruth's Spider, Pautler caves, and Illinois (Morrison's) Caverns (type locality). St. Clair County: Stemmler Cave. The species is limited to these Illinois caves, where it occurs with the more common *G. troglophilus* (Hubricht and Mackin, 1940; Holsinger, 1972).

Gammarus minus Say, TP

Illinois. Adams County: Spring 4 mi SSW Ursa and Burton Spring near Quincy. Calhoun County: McNabb Hollow Cave Spring and Orchard Spring at Hardin. Hardin County: spring in Kaskaskia Experimental Forest. Jackson County: Clear Spring in Shawnee National Forest, and Degognia Cave and seep near Degognia. Jersey County: Chautauqua Spring and spring in Père Marquette State Park. Johnson County: Will Thomas Spring Cave. Pike County: Croxville Cave Spring, and spring 5 mi W Pearl. Randolph County: Allied Chemical Quarry Spring at Prairie du Rocher. St. Clair County: Falling Spring. Union County: spring near Cricket Cave, and Roaring and Elm springs. The species is widespread over much of the limestone region of the unglaciated eastern United States, and is commonly found in cave springs. Cole (1970a, 1970b) studied geographic variation in the species and called most of the above listed populations "post-Kansan." He has proposed the subspecific name *pinicollis* for non-cave Union County, Illinois and Ste. Geneviève County, Missouri populations (see Bousfield, 1958; Ciniglio and Payne, 1977; Holsinger, 1969a, 1972; Holsinger and Culver, 1970; and Jenio, 1972).

Gammarus pseudolimnaeus Bousfield, TX

Illinois. Adams County: Spring 4 mi SW Ursa, and Burton Spring. Brown County: Siloam Springs. Calhoun County: Orchard Spring at Hardin. Gallatin County: sandstone seep at Pounds Hollow. Greene County: Old Settler's Spring, 4 mi S Millview. Hardin County: Cave Spring Cave and Round Springs. Jackson County: Cave No. 1 and Hickman Cave, Fountain Bluff sandstone seep springs no. 1 and no. 2, Happy Hollow Spring, and sandstone seep near Degognia. Jersey County: Chautauqua Spring. Johnson County: Casey Spring. LaSalle County: spring in Spring Dell. Monroe County: spring 2 mi N Fountain Gap. Randolph County: spring at Allied Chemical Quarry at Prairie du Rocher and spring 2 mi NE Rockwood. St. Clair County: Falling Spring. Union County: spring near Cricket (Wet) Cave, and Elm, Roaring, and Triple springs. The species is also known from caves and springs in NE Iowa, Missouri, and Arkansas. It ranges from Ontario and New York westward through Michigan and Wisconsin down to the Ozarks, Kentucky, and Tennessee (Ciniglio and Payne, 1977; Holsinger, 1972). It occurs with *G. troglophilus* in Illinois caves. The Illinois records of *G. limnaeus* of Hubricht and Mackin (1940) and Hubricht (1943) belong here (Bousfield, 1958).

Gammarus troglophilus (Hubricht and Mackin), TP

Illinois. Calhoun County: Madison Creek and McNabb Hollow caves. Jackson County: Ava, Cave No. 1, Degognia, and Hickman caves and springs no. 1 and no. 2 at Hickman Cave, spring at Clear Spring Picnic Area, and Mt. Pleasant Spring. Johnson County: Jug Spring Cave. Monroe County: Cave 2 mi N Fountain Gap, and Camp Vandeventer (Ice), Dry Run, Fogelpole, Fruth's Spider, Fults Creek, Horsethief, Madonnaville, Pautler, Terry (Long Slash), and Wilde's (2 mi E Columbia, but identity unknown) caves, and Illinois (Morrison's, Eckert's, Burkesville) Caverns (type locality). St. Clair County: Falling Spring and Stemmler caves. Union County: At spring and dry entrances of Cave Spring Cave, and Cricket, Guthrie, Rich's, Saratoga, and Sensemeyer caves, and Elm and Triple springs. **Missouri**. Perry County: Mystery and Running Bull caves and cave 2 mi N Perryville airport on road. Ste. Geneviève County: Kohm's Cave. The species is also known from other Illinois counties, from caves in Jefferson and St. Louis counties, Missouri, and from other non-cave habitats in eastern Missouri and southwestern Tennessee. It occurs with *G. minus*, *G. acherondytes*, and/or *G. pseudolimnaeus* (Bousfield, 1958; Holsinger, 1972; Hubricht and Mackin, 1940; Hubricht, 1943; Ciniglio and Payne, 1977).

ORDER DECAPODA

Family Astacidae

Cambarus laevis Faxon, TP

Illinois. Hardin County: Cave Spring Cave.

Cambarus ornatus Rhoades, TP

Illinois. Hardin County: Layoff Cave. This is a reproducing population. The species was previously known only from Kentucky (Hobbs, 1974).

Cambarus tenebrosus Hay (?), TP

Illinois. Hardin County: Griffith Cave, 1 juvenile female.

Cambarus sp., probably *diogenes* section, TP

Illinois. Pike County: Lost Creek Cave, 1 female.

Cambarus (?) sp., TP

Missouri. Perry County: Tom Moore Cave. Ste. Geneviève County: Kohm's Cave. These are both sight records.

Class Arachnida

ORDER PSEUDOSCORPIONIDA

Family Chthoniidae

Apochthonius mysterius Muchmore, TB

Missouri. Perry County: This species was taken in a pitfall trap and is similar to *A. typhlus* (TB) and *A. colecampi* (TP) from caves in Stone and Benton counties respectively (Muchmore, 1967, 1976; Craig, 1977).

Apochthonius sp., TP or TB

Illinois. Hardin County: Brown's Hole. Other species in the genus have been described from caves in Missouri, Arkansas, West Virginia, Indiana, and Virginia (Muchmore, 1967; Muchmore and Benedict, 1976).

Mundochthonius cavernicolus Muchmore, TB

Illinois. Monroe County: Saltpeter Cave. This is the only troglobite in this large genus (Hoff, 1958; Muchmore, 1968).

ORDER ACARINA

Family Acaridae

Caloglyphus sp., TP?

Missouri. Perry County: Mystery Cave.

Family Cunaxidae

Cunaxa sp., TP?

Missouri. Perry County: Mystery Cave.

Family Eupodidae

Linopodes sp., TP

Illinois. Monroe County: Illinois Caverns.

Family Galumnidae

Galumna sp., TP

Illinois. Monroe County: Illinois Caverns

Family Laelapidae

Hypoaspis, nr. *angusta* Karg, TP

Illinois. Monroe County: Illinois Caverns.

Hypoaspis nr. *subterranea* (Willmann), TP

Illinois. Monroe County: Illinois Caverns.

Hypoaspis sp. 3, TP

Illinois. Monroe County: Illinois Caverns.

Stratiolaelaps sp., TP?

Missouri. Perry County: Mystery Cave.

Undetermined genus and species, TP?

Missouri. Perry County: Mystery Cave.

Family Phthiracaridae

Steganacarus sp., TP

Illinois. Monroe County: Illinois Caverns.

Family Rhagidiidae

Rhagidia sp., TP?

Illinois. Monroe County: Saltpeter Cave. Two species in this genus are known from Ozark Caves (Elliott and Strandtman, 1971; Craig, 1977).

Family Uropodidae

Discourella, nr. *dubiosa* (Schweizer), TP

Illinois. Monroe County: Illinois Caverns.

Family Veigaiaidae

Genus and species undetermined, TP

Illinois. Monroe County: Illinois Caverns.

ORDER PHALANGIDA

Family Cosmetidae

Vonones sp., AC

Illinois. Johnson County: Firestone Creek Cave.

Family Ischyropsalidae

Sabacon sp., TX

Illinois. Johnson County: Jug Spring Cave, in entrance. This is probably a record of *S. cavicolens* (Packard), a species widespread in the eastern U.S., but only occasionally associated with caves (Shear, 1975).

ORDER ARANEAE

Family Agelenidae

Calymmaria cavicola (Banks), TP

Illinois. Hardin County: Layoff Cave. Johnson County: Teal Cave. This widespread species was previously unknown in Illinois.

Circurina cavealis Crosby and Bishop, TP

Illinois. Monroe County: Saltpeter Cave. This widespread species is known from caves in Missouri and Arkansas as well as more eastern states (Bishop and Crosby, 1926; Chamberlin and Ivie, 1940; Craig, 1977).

Circurina pallida Keyserling, TP

Illinois. Adams County: Burton Cave. Jackson County: Bat Cave. Union County: Cave Spring Cave, both entrances. This is a widespread eastern species.

Coras lamellosus (Keyserling), TP

Illinois. Jackson County: Degognia Cave. An undetermined species in this genus occurs in Jug Spring Cave, Johnson County. The species also occurs in Missouri caves (Craig, 1977).

Family Araneidae

Meta menardi (Latreille), TP

Illinois. Hardin County: Griffith Cave. Monroe County: Illinois Caverns. Jackson County: Bat Cave, Cave No. 1, Degognia, and Giant City Sandstone caves. Johnson County: Will Thomas Spring, and Mason No. 1 and No. 2 caves. Saline County: Equality Cave. Union County: Cave Spring, Guthrie, Rich's, Saratoga, and Sensemeyer caves. **Missouri**. Perry County: Mystery, and Lost and Found caves. This is a widespread species in caves and cave-like habitats in the eastern United States.

Family Dictynidae

Dictyna sp., AC

Illinois. Pope County: Frieze Cave, from stomach of *Eurycea lucifuga* salamander.

Family Gnaphosidae

Zelotes sp., TX

Illinois. Union County: Cave Spring Cave, dry entrance.

Family Linyphiidae

Bathyphantes albiventris (Banks), TP

Illinois. Johnson County: Jug Spring Cave.

Bathyphantes pallidus (Banks), TP

Illinois. Johnson County: Firestone Creek Cave. **Missouri**. Ste. Geneviève County. Kohm's Cave. This species, also occuring in other Missouri caves (Craig, 1977), is one of the most common species in the genus, living under epigean trash and objects on moist ground (Ivie, 1969).

Centromerus cornupalpis (O. P. Cambridge), TP

Illinois. Hardin County: Layoff Cave. The species occurs in Missouri caves (Craig, 1977).

Centromerus latidens (Emerton), TP

Illinois. Jackson County: Degognia Cave. Johnson County: Firestone Creek Cave. Hardin County: unnamed cave N Cave-in-Rock. **Missouri**. Jefferson County: Pleasant Valley Cave. The species is widespread in the eastern United States, and occasionally occurs in caves (Van Helsdingen, 1973; Craig, 1977).

Eperigone antraea (Crosby), TP

Illinois. Union County: Sensemeyer Cave.

Eperigone eschatologica Crosby, TP

Illinois. Hardin County: Cave-In-Rock Cave.

Eperigone maculata Banks, TP

Missouri. Ste. Geneviève County: Buddy's and Kohm's caves.

Islandiana sp., TP

Missouri. Ste. Geneviève County: Kohm's Cave. This is an undescribed species. Other cave species live in Texas, Kentucky, West Virginia, and Alabama (Ivie, 1965).

Phanetta subterranea (Emerton), TB

Illinois. Hardin County: Cave Spring Cave. Jackson County: Devils Backbone Cave. Johnson County: Firestone Creek, and Will Thomas Spring caves. Monroe County: Camp Vandeventer, Fults Creek, Horsethief, and Terry Spring caves, and Illinois Caverns. Saline County: Equality Cave. Union County: Sensemeyer Cave. **Missouri**. Ste. Geneviève County: Kohm's Cave. Perry County: Lost and Found Cave. The species is widespread in the eastern United States, but is known only from caves. It was previously unknown from Illinois and Missouri.

Porrhoma sp., TP

Illinois. Monroe County: Dry Run Cave.

Family Lycosidae

Pardosa sp., AC

Illinois. Hardin County: Cave-in-Rock Cave. **Missouri**. Perry County: Mystery Cave, immatures.

Pirata sp., AC

Illinois. Jackson County: Ava Cave, 2 immatures. The genus is also in Missouri caves (Craig, 1977).

Schizocosa ocreata Hentz, TX

Illinois. Monroe County: Illinois Caverns, 1 male. The genus is also in Missouri caves (Craig, 1977).

Trochosa avara Keyserling, AC

Illinois. Monroe County: Camp Vandeventer Cave, 1 male.

Family Nesticidae

Nesticus pallidus Emerton, TP

Illinois. Hardin County: Cave-in-Rock, Cave Spring, and Layoff caves. This is a widespread species often associated with caves.

Family Pholcidae

Pholcus phalangoides Fuesslin, TX

Illinois. Hardin County: Cave-in-Rock Cave. Madison County: Cave 1 mi NW Alton.

Family Pisauridae

Dolomedes vittatus Walckenaer, TX

Illinois. Johnson County: Will Thomas Spring Cave.

Dolomedes sp., TX

Illinois. Johnson County: unnamed cave at White Hill. Union County: Cobden Cave.

Family Salticidae

Metaphidippus exiguus (Banks), AC

Illinois. Hardin County: Cave-in-Rock Cave.

Family Symphytognathidae

Maymena ambita (Barrows), TP

Illinois. Monroe County: Saltpeter Cave. The species is otherwise known from caves and dark habitats in Tennessee, Alabama, and Kentucky (Gertsch, 1960).

Family Theridiidae

Archaeranea tepidariorum (Koch), TX

Illinois. Hardin County: Cave-in-Rock, cave near Cave-in-Rock, and Layoff caves.

Steatoda triangulosa (Walckenaer), AC

Illinois. Hardin County: Cave-in-Rock Cave.

Class Chilopoda

ORDER LITHOBIOMORPHA

Family Lithobiidae

Nadabius sp., TP?

Illinois. Hardin County: Layoff Cave. Monroe County: Saltpeter Cave. This is possibly an undescribed species.

Nadabius amales Chamberlin, TP?

Missouri. Ste. Geneviève County: Buddy's Cave.

Undetermined genus and species.

Illinois. Johnson County: Firestone Creek Cave.

ORDER SCUTIGEROMORPHA

Family Scutigeridae

Scutigera sp., probably *coleoptrata* (Linnaeus), TX

Illinois. Hardin County: Cave-in-Rock and deepest part of Layoff Cave.

Class Diplopoda

ORDER POLYDESMIDA

Family Xystodesmidae

Semionellus placidus (?) (Wood), TP?

Illinois. Union County: Rich's Cave. Causey (1952) reports "a larva of the genus," but since the genus is monotypic, this is the most likely species. This is the most southern record for an otherwise northern and montane species (Hoffman, 1969).

Family Nearctodesmidae

Ergodesmus remingtoni (Hoffman), TB

Illinois. Adams County: Burton Cave. Jersey County: Brainard Cave (type locality). Monroe County: Pautler Cave. Pike County: Lost Creek and Twin Culvert caves. The species formerly in the genus *Ectopodesmus*, was previously known only from the type locality. The only other species in the genus occur in the Pacific Northwest (Shear, 1969), and Jalisco, Mexico. (Hoffman, 1975).

Family Polydesmidae

Pseudopolydesmus pinetorum (Bollman), TP

Illinois. Johnson County: Will Thomas Spring Cave.

Pseudopolydesmus sp., TP

Illinois. Calhoun County: McNabb Hollow Cave. Jackson County: Ava Cave. Hardin County: cave north of Cave-in-Rock. These records are all based on females or immatures.

Family Trichopolydesmidae

Antriadesmus sp., TB?

Illinois. Monroe County: Pautler Cave, immatures. Only troglobitic species occur in this genus, thought previously to be limited to Kentucky and Tennessee, but we have observed them farther west, in Missouri (Tumbling Creek Cave, Taney Co.) (Shear 1969, 1972b).

ORDER CHORDEUMIDA

Family Cleidogonidae

Cleidogona unita Causey, TP

Illinois. Hardin County: Brown's Hole. Johnson County: Will Thomas Spring Cave. The species occurs in epigean habitats in Illinois and Kentucky (Shear, 1972a).

Pseudotremia sp., TB

Illinois. Hardin County: Cave Spring Cave. This undescribed species is the only known Illinois population of this large Appalachian genus with several troglobitic species (Shear, 1969, 1972a).

Family Conotylidae

Austrotyla specus (Loomis), TP

Illinois. Henderson County: Goose Hollow Cave. Jackson County: Ava Cave. Madison County: cave 1 mi NW Alton, in gut of *Eurycea longicauda* salamander. Monroe County: Camp Vandeventer, Dry Run, and Horsethief caves, and Illinois Caverns. St. Clair County: Stemmler Cave. Saline County: Equality Cave. Union County: Saratoga and Sensemeyer caves. **Missouri**. Perry County: Berome Moore, Klump, Mertz, Mystery, and Slope caves. Ste. Geneviève County: Batty's, Buddy's, Gegg, and Kohm's caves. The species, originally described in the genus *Conotyla*, also occurs in caves in Franklin, Jefferson (Rice Cave; type locality), and St. Louis counties, and is known from cave and epigean habitats in northern Illinois, Wisconsin, and possibly Minnesota. Other species in the genus are western, ranging down the Rocky Mountains from Alberta to Chihuahua (Causey, 1960a, 1960b, 1961; Craig, 1977; Shear, 1969, 1971, 1972a).

Family Trichopetalidae

Scoterpes sp, TB

Illinois. Monroe County: Illinois Caverns? **Missouri**. Jefferson and Franklin counties: unspecified sites. *S. dendropus* Loomis occurs in SW Missouri caves. Illinois localities are indicated by Shear for the genus but we do not know of specific sites. One might be Illinois Caverns, Monroe County, judging from an old M. W. Sanderson record. The genus is entirely troglobitic, with most species in the Appalachians (Causey, 1960a, 1960b, Hubricht, 1950; Shear, 1972a).

Family Tingupidae

Tingupa pallida Loomis, TP

Illinois. Jackson County: Ava Cave. Johnson County: Teal and Will Thomas Spring caves. Pike County: Twin Culvert cave. **Missouri**. Jefferson County: Rankin Cave (unknown to us). The species is known from caves in 13 Missouri counties and is reported from leaf litter at Collinsville, Illinois, but this may be an error (Shear, pers. comm.). All other species in this genus occur in the mountains of the western U.S. (Causey, 1951, 1960b; Shear, 1969, 1972a; Craig, 1977).

ORDER JULIDA

Family Nemasomatidae

Zosteractis interminata Loomis, TB

Illinois. Pike County: Lost Creek Cave. **Missouri**. St. Louis County: South Rankin Cave (type locality). Ste. Geneviève County: Cellar Cave. (Causey, 1960a, 1960b; Shear, 1969).

ORDER SPIROBOLIDA

Family Spirobolidae

Narceus sp. AC

Illinois. Johnson County: Will Thomas Spring Cave.

ORDER SPIROSTREPTIDA

Family Cambalidae

Cambala minor (Bollman), TP

Illinois. Monroe County: Saltpeter Cave. Hardin County: Layoff Cave. Union County: Union Point Cave. The species (or species complex) is widespread in the southeastern U.S.

ORDER CALLIPODIDA

Family Schizopetalidae

Abacion sp., AC

Illinois. Pike County: Croxville (spring entrance) and Twin Culvert caves.

Class Insecta

ORDER COLLEMBOLA

Family Entomobryidae

Lepidocyrtus sp., TX

Illinois. Hardin County: Cave-in-Rock and cave north of Cave-in-Rock. Pope County: Frieze Cave. The species is found in cave entrances.

Pseudosinella sp. 1, *argentea* complex, TB

Illinois. Hardin County: Brown's Hole and Cave Spring Cave. Monroe County: Saltpeter Cave. **Missouri**. Perry County: Mystery Cave. The group is known from caves in other parts of Missouri and in other states (Christiansen, 1960a; Craig, 1977).

Pseudosinella sp. 2, TB?

Illinois. Johnson County: Firestone Creek Cave. This is an undescribed species.

Sinella cavernarum (Packard), TP

Illinois. Hardin County: Brown's Hole and Cave Spring Cave. Johnson County: Firestone Creek Cave. Saline County: Equality (Cave Hill) Cave. This is a widespread species, often found in caves in the central eastern United States (Christiansen, 1960b).

Sinella auita Christiansen, TP

Illinois. Johnson County: Firestone Creek Cave. The species also occurs in Kentucky caves (Christiansen, 1960b).

Entomobrya intermedia Brook, AC

Illinois. Hardin County: Cave-in-Rock.

Family Hypogastruridae

Hypogastrura sp., *denticulata* complex, TP

Illinois. Johnson County: Firestone Creek and Will Thomas Spring caves. **Missouri**. Perry County: Mystery Cave.

Hypogastrura matura Folsom, AC/TX

Illinois. Hardin County: cave north of Cave-in-Rock. **Missouri**. Perry County: Mystery Cave.

Hypogastrura notha (MacNamara), AC

Illinois. Hardin County: cave north of Cave-in-Rock.

Hypogastrura sp., TP?

Missouri. Perry County: Klump and Mertz caves. The species is undescribed.

Schafferia (*Typhlogastrura*) sp., TP?/TB

Illinois. Johnson County: Firestone Creek Cave. This is tentatively an undescribed species, based on one immature specimen.

Family Isotomidae

Folsomia candida Willem, TP

Illinois. Jackson County: Cave No. 1. Monroe County: Illinois Caverns (Mammoth Cave of Illinois). Union County: Cricket Cave. **Missouri**. Perry County: Mystery Cave. Ste. Geneviève County: Gegg Cave.

Folsomia elongata MacGillivray, AC

Illinois. Hardin County: Layoff Cave.

Folsomia nivalis (Packard), AC

Illinois. Pope County: Frieze Cave.

Folsomia prima Mills, AC

Illinois. Hardin County: cave north of Cave-in-Rock.

Folsomia sp. M, TX?

Illinois. Hardin County: Brown's Hole, in entrance.

Isotoma andrei Mills, TX

Illinois. Pope County: Frieze Cave.

Isotoma gelida Folsom, TX

Illinois. Hardin County: Cave-in-Rock.

Isotoma trispinata MacGillivray, TX

Illinois. Union County: Cave Spring Cave.

Isotoma viridis Bourlet, TX

Missouri. Perry County: Mystery and Mertz caves.

Isotoma (Desoria) notabilis Schafter, TP

Illinois. LaSalle County: Blackball Mine. **Missouri**. Perry County: Mystery and Slope caves. The species is a Holarctic troglophile.

Isotoma (Desoria) sp., TP

Illinois. Hardin County: Cave-in-Rock. Jackson County: Degognia and Devil's Backbone caves. Pope County: Frieze Cave. **Missouri**. Perry County: Mystery Cave.

Family Neanuridae

Neanura persimilis Mills, AC

Illinois. Hardin County: cave north of Cave-in-Rock.

Neanura pseudoquadrioculata (Stach), AC

Illinois. Hardin County: cave north of Cave-in-Rock.

Pseudachorutes saxatilis MacNamara, AC

Illinois. Hardin County: cave north of Cave-in-Rock. Jackson County: Devil's Backbone Cave.

Pseudachorutes sp. G, AC

Illinois. Pope County: Frieze Cave.

Family Onychiuridae

Onychiurus sp., TX/TP

Illinois. Johnson County: Teal Cave. Union County: Cave Spring Cave.

Onychiurus sp. C, TP

Illinois. Hardin County: Brown's Hole. This is an undescribed species, also known from six Kentucky caves (Christiansen, pers. comm.).

Tullbergia clavata Mills, TP

Illinois. Hardin County: cave north of Cave-in-Rock.

Family Sminthuridae

Arrhopalites clarus Christiansen, TB

Missouri. Perry County: Mystery Cave. This species occurs in other caves to the west in Missouri and in Arkansas (Christiansen, 1966).

Arrhopalites hirtus Christiansen, TP

Illinois. Pike County: Twin Culvert Cave. This species is recorded from caves in Iowa, and Wisconsin, and from a drain tile in Illinois. An epigean records exists for Ohio, and three doubtful records exist for Oregon, California, and Utah (Christiansen, 1966).

Arrhopalites pygmaeus Wankel, TP

Illinois. Hardin County: Brown's Hole and Layoff Cave. Johnson County: Firestone Creek and Will Thomas Spring caves. **Missouri**. Perry County: Mystery Cave. The species is widespread in the epigean of the eastern U.S. It occurs in caves in Arkansas, Tennessee, Virginia, Alabama, and commonly in western Missouri (Christiansen, 1966; Craig, 1977).

Arrhopalites whitesidei Jacot, TP

Illinois. Monroe County: Saltpeter Cave. This widespread epigean species occurs across the continent, and in caves in Wisconsin, Iowa, Alabama, Indiana, and western Missouri. (Christiansen, 1966).

Ptenothrix atra Linnaeus, TX

Illinois. Johnson County: Firestone Creek Cave.

Sminthurides sp. 1, TX

Illinois. Hardin County: Brown's Hole, Cave-in-Rock. Pope County: Frieze Cave. The first record (at least) represents an undescribed species.

Sminthurides malmgreni Tullberg, TX

Illinois. Hardin County: Cave-in-Rock.

Family Tomoceridae

Tomocerus bidentatus Folsom, TP

Illinois. Pope County: Frieze Cave. Union County: Sensemeyer Cave. This is a widespread cave and epigean species (Christiansen, 1964).

Tomocerus flavescens (Tullberg), TP

Illinois. Adams County: Burton Cave. Hardin County: Cave-in-Rock and Brown's Hole. Jackson County: Cave No. 1, Devil's Backbone Cave. Johnson County: Teal Cave. Monroe County: Camp Vandeventer Cave and Illinois Caverns. St. Clair County: Stemmler and Falling Spring caves. **Missouri**. Perry County: Berome Moore Cave. Ste. Geneviève County: Buddy's Cave. Christiansen (1964) notes that the species is spread across the continent and is known from caves in 14 states.

Tomocerus missus Mills, TB

Illinois. Jersey County: Brainard (Grafton) Cave (type locality). Monroe County: Illinois Caverns (Eckert's Cave). **Missouri**. Jefferson County: Fox Cave. Perry County: Berome Moore Cave. Ste. Geneviève County: Kohm's Cave. The species is also known from a cave in Kentucky. Christiansen (1964) speculates that this distinctive species, sometimes placed in the genus or subgenus *Tritomurus*, is the last survivor of an otherwise extinct species group, and that its relict affinities are with European species (pers. comm.).

ORDER DIPLURA

Family Campodeidae

Eumesocampa sp., TB

Illinois. Monroe County: Camp Vandeventer, Horsethief, and Madonnaville caves. Pike County: Lost Creek and Twin Culvert caves. Union County: Sensemeyer Cave. **Missouri**. Jefferson County: cave south of Antonia. Perry County: Berome Moore and Mystery caves. Ste. Geneviève County: Buddy's, Batty's, and Kohm's caves. The closest relative to this undescribed species occurs in epigean sites in Colorado.

Haplocampa sp., TB

Illinois. Monroe County: Illinois Caverns. The species is otherwise known only from caves in Crawford and Washington counties, Missouri. The genus contains cavernicolous species in California and Washington, and epigean species in California, Montana, Oregon, Washington, and Alberta (Craig, 1977).

Metriocampa (Tricampa) sp., TB

Illinois. Adams County: Burton Cave. Hardin County: Brown's Hole. Saline County: Equality Cave. This undescribed species is closest to *M. remingtoni*, known only from epigean sites in Colorado.

Family Japygidae

Undetermined genus and species, AC

Illinois. Jackson County: Degognia Cave, in entrance leaf litter.

ORDER THYSANURA

Family Machilidae

Machilus (?) sp., TX

Illinois. Hardin County: Layoff, Griffith, and Jackson Sandstone caves. These are common on rock outcrops at cave entrances and may enter caves in the winter.

ORDER ORTHOPTERA

Family Gryllacrididae

Ceuthophilus elegans Hubbell, TX

Illinois. Johnson County: Firestone Creek Cave. Monroe County: Fogelpole Cave and Illinois Caverns. Union County: Rich's Cave. **Missouri**. Perry County: Berome Moore and Mystery caves. Ste. Geneviève County: Buddy's and Sims' caves. The species also occurs in epigean sites in Iowa, Wisconsin, and Indiana (Hubbell, 1936).

Ceuthophilus gracilipes (Haldeman), TX

Illinois. Hardin County: Cave Spring and Layoff caves. Pope County: Frieze Cave. Saline County: Equality Cave. Union County: Guthrie Cave. The species occurs in Illinois only in the south, and is spread from Missouri eastward through much of eastern U.S. It is a frequent inhabitant of caves (Hubbell, 1936, and MS).

Ceuthophilus seclusus Scudder, TX

Illinois. Monroe County: Fruth's Spider Cave. The species has also been taken outside of Fogelpole and Burton caves, Illinois, and is known from or near caves in Missouri and Oklahoma, and from epigean sites in these states and in Arkansas, Iowa, and Indiana (Hubbell, 1936).

Ceuthophilus williamsoni Hubbell, TX

Illinois. Adams County: Burton Cave?. Calhoun County: Madison Creek and McNabb Hollow caves. Henderson County: Goose Hollow Cave. Hardin County: Layoff Cave?. Jackson County: Ava Cave. Johnson County: Will Thomas Spring Cave. Pike County: Lost Creek and Twin Culvert caves. Saline County: Equality Cave. Union County: Saratoga and Guthrie caves. The species also occurs in Iowa and in caves in Missouri (Hubbell, 1936; Craig, 1977). At Burton Cave, *C. divergens* Scudder and *C. seclusus* Scudder have been taken in the forest.

Ceuthophilus sp., TX

Illinois. Hardin County: Brown's Hole. Jackson County: Cave No. 1 and Giant City Cave. Johnson County: Mason No. 1 and No. 2, Jug Spring, Thapsis, Persimmon Pit, Firestone Creek and Teal caves. Union County: Guthrie Cave. These populations are represented by immature specimens which cannot be determined.

Tachycines asynamorous Adelung, TX

Illinois. Hardin County: Cave-in-Rock. This introduced asiatic species, usually associated with buildings (Rehn, 1944), is now known to be established in the above natural environment as well as in natural sites in Alabama and Georgia. The species of *Ceuthophilus* formerly in Cave-in-Rock seem to have been displaced from the cave by this cricket. *C. gracilipes* (Haldeman), *C. latens* Scudder and *C. williamsoni* Hubbell are known from epigean sites in Cave-in-Rock State Park.

ORDER COLEOPTERA

Family Carabidae

Agonum extensicolle Say, AC

Missouri. Perry County: Mystery Cave.

Anisodactylus opaculus (LeConte), AC

Missouri. Perry County: Mystery Cave.

Atranus pubescens (DeJean), TP

Illinois. Hardin County: Cave-in-Rock and Layoff Cave. Johnson County: Will Thomas Spring Cave. Monroe County: Illinois Caverns. **Missouri**. Perry County: Mystery Cave. This species is widespread in eastern North America (Lindroth, 1961-1969) and is found in caves in eastern U.S., the Ozarks, and Texas (Barr, 1964a).

Bembidion lacunarium Zimmermann, TP

Illinois. Adams County: Burton Cave. Hardin County: Cave-in-Rock. Monroe County: Horsethief Cave. This species is spread through much of eastern U.S. (Lindroth, 1961-1969) and is common in caves in the east, the Ozarks, and Texas (Barr, 1964a).

Bembidion texanum Chaudoir, TP

Illinois. Jackson County: Ava Cave. Hardin County: Cave-in-Rock. Monroe County: Camp Vandeventer, Horsethief, and Fogelpole caves. Union County: Saratoga Cave. **Missouri**. Perry County: Mystery Cave. The species is spread over much of eastern U.S. (Lindroth, 1961-1969) and occurs in caves at least in Oklahoma (Black, 1971) and Texas (Reddell, 1966).

Bembidion (Amerizus) wingatei Bland, TP

Illinois. Adams County: Burton Cave. This reproducing population has been sampled many times over a span of some 20 years. The species is distributed over much of the northern half of eastern U.S. and Canada (Lindroth, 1961-1969). It is known from caves in NE Kentucky, NW Virginia, West Virginia, and Pennsylvania (Barr, 1964a, and in litt.).

Bembidion (Furcacampa) sp., AC

Illinois. Hardin County: Cave Spring Cave.

Brachinus fumans Fabricius, AC

Missouri. Perry County: Mystery Cave.

Chalaenius aestivus (Say), AC

Illinois. Hardin County: Cave-in-Rock.

Evarthrus sodalis colossus Leconte, AC

Illinois. Monroe County: Illinois Caverns.

Evarthrus fucatus Freitag, AC

Illinois. Hardin County: Brown's Hole.

Galerita bicolor Crury, AC

Missouri. Perry County: Mystery Cave.

Harpalus fulgens Csiki, AC

Missouri. Perry County: Mystery Cave.

Paratachys sp., *corruscus* complex, AC

Missouri. Perry County: Mystery Cave.

Patrobus longicornis Say, TX?

Illinois. Monroe County: Fogelpole Cave. **Missouri**. Perry County: Mystery Cave. The species is also known as a TX or AC in caves in Alabama and Kentucky (Barr, in litt.).

Platynus tenuicollis (LeConte), TP

Illinois. Hardin County: Cave Spring Cave. Jackson County: Ava Cave. Johnson County: Will Thomas Spring Cave. Monroe County: Dry Run, Fogelpole and Horsethief caves, and Illinois Caverns. **Missouri**. Jefferson County: Pleasant Valley Cave. Perry County: Mystery Cave. St. Charles County: Dingledine Cave. Ste. Geneviève County: Kohm's and Sims' caves. This widespread species, sometimes called *Agonum tenuicolle*, is often found in caves in eastern U.S., the Ozarks, and Texas (Barr, 1964a; Lindroth, 1961-1969; Craig, 1977).

Pseudanophthalmus illinoisensis Barr and Peck, TB

Illinois. Hardin County: Cave Spring Cave (type locality). The species is known only from this cave (Barr and Peck, 1965). The closest relative is *P. barberi* in caves in Meade Co., Kentucky. The genus is widespread in caves in nine eastern Appalachian states and is known from one epigean West Virginia locality (Barr, 1967c, 1969). It also occurs in endogean habitats in the Carpathians and Transylvanian Alps and has been known there as the genus *Duvaliopsis* (Barr, 1964b).

Pterostichus (Euferonia) coracinus Say, AC

Illinois. Monroe County: Illinois Caverns.

Rhadine larvalis LeConte, TX?

Illinois. St. Clair County: Falling Spring Cave. This is the third known specimen and locality record for the species. The others were from the vicinity of St. Louis and from "central Illinois". The species is most closely related to *Rhadine jonesi*, a troglophile known only from a cave in southern Alabama. (Barr, 1960).

Stenolophus ochropezus (Say), TX

Missouri. Perry County: Klump Cave.

Tachyura incurva (Say), AC

Illinois. Monroe County: Fogelpole Cave.

Tachys sp., AC

Illinois. Hardin County: Cave-in-Rock.

Xenotrechus condei Barr and Krekeler, TB

Missouri. Jefferson County: Friedman's and Pleasant Valley caves.

Xenotrechus denticollis Barr and Krekeler, TB

Missouri. Ste. Geneviève County: Kohm's and Sims' caves. The genus is known by only this and the above species. Its closest relative is *Chaetoduvalius* of the Transylvanian Alps (Barr and Krekeler, 1967).

Family Histeridae

Hister sp., AC

Illinois. Johnson County: Firestone Creek Cave.

Family Leiodidae

Catops gratiosus Blanchard, TP

Illinois. Hardin County: Cave-in-Rock. Saline County: Equality

Cave. The species is widespread in North America and is frequently found in eastern caves.

Ptomaphagus nicholasi Barr, TB

Illinois. Monroe County: Fogelpole Cave (type locality). Extensive searching and trapping in the type locality and other western Illinois caves has not found this species a second time (Peck, 1973a). It is very similar to *P. hirtus* of the Mammoth Cave area of Kentucky, and the possibility exists that the species is based on erroneously labeled material from Kentucky.

Ptomaphagus cavernicola Schwarz, TP

Missouri. Jefferson County: Pleasant Valley Cave. This species occurs frequently in caves in the Ozarks and in Texas, sporadically in caves in Iowa, Alabama, Florida and Mexico, and is absent in caves in Illinois (Peck, 1973a). Only one epigean record is known for the species.

Family Pselaphidae

Batrisodes rossi Park, TP

Illinois. Johnson County: Teal Cave, in pitfall trap in rear of cave. This is the second collection of the species, which was previously known only from Illinois leaf litter.

Family Staphylinidae

Atheta sp. no. 1, TP

Illinois. Hardin County: Brown's Hole. Johnson County: Firestone Creek and Teal caves. **Missouri**. Perry County: Mystery Cave.

Atheta sp. no. 3, TP

Illinois. Hardin County: Cave-in-Rock, cave north of Cave-in-Rock, and Brown's Hole. **Missouri**. Perry County: Mystery Cave.

Atheta sp., undetermined, TP

Illinois. Hardin County: Cave Spring and Griffiths caves. Jackson County: Ava Cave. Monroe County: Camp Vandeventer, Fogelpole, Horsethief, and Saltpeter caves, and Illinois Caverns. Pike County: Lost Creek Cave. Saline County: Equality Cave.

Deinopsis sp., AC

Illinois. Hardin County: Brown's Hole.

Emplenota lucifuga Casey, TP

Illinois. Adams County: Burton Cave. Johnson County: Teal Cave. The species is a frequent inhabitant of caves in southeastern U.S., especially along gravel streamsides.

Erichsonius nanus Horn, TX?

Illinois. Hardin County: Brown's Hole.

Geodromicus brunneus (Say), TX?

Illinois. Hardin County. Layoff Cave.

Homoeotarsus bicolor (Gravenhorst), AC

Illinois. Hardin County: Cave-in-Rock.

Homoeotarsus (*Gastrolobium*) sp., AC

Illinois. Monroe County: Fogelpole Cave.

Lesteva pallipes LeConte, TP

Illinois. Hardin County: Brown's Hole, Layoff Cave, and cave north of Cave-in-Rock. Johnson County: Jug Spring and Belknap caves. Pope County: Frieze Cave.

Myllaena sp., AC

Illinois. Hardin County: Brown's Hole. Pope County: Frieze Cave.

Neobisnius paederoides LeConte, AC

Illinois. Hardin County: cave north of Cave-in-Rock.

Neobisnius sp., AC

Missouri. Perry County: Mystery Cave.

Oxytelus exiggus Erichson, AC

Illinois. Monroe County: Illinois Caverns.

Philonthus micropthalmus Horn, AC?

Illinois. Hardin County: Brown's Hole.

Philonthus sp., AC?

Illinois. Hardin County: Cave-in-Rock. Johnson County: Belknap Cave.

Quedius erythrogaster Mannerheim, TP

Illinois. Adams County: Burton Cave. Calhoun County: McNabb Hollow Cave. Hardin County: Cave-in-Rock. Jersey County: Brainerd Cave. Johnson County: Firestone Creek, Teal, and Will Thomas Spring caves. Monroe County: Camp Vandeventer, Horsethief, Fogelpole, and Saltpeter caves, and Illinois Caverns. Pike County: Twin Culvert and Lost Creek (Pearl) caves. The species is transcontinental and common in caves, where it is frequently found on animal dung (Smetana, 1971).

Quedius fulgidus (Fabricius), TP

Illinois. Adams County: Burton Cave. Hardin County: Cave-in-Rock. Union County: Cricket and Sensemeyer caves. This introduced European species is widely spread over much of North America and is often found in caves (Smetana, 1971).

Quedius spelaeus Horn, TP

Illinois. Monroe County: Illinois Caverns. Pike County: Lost Creek Cave. The species is transcontinental, but most commonly occurs in caves in the northeastern quarter of the U.S. (Smetana, 1971).

Quedius sp., TP

Illinois. Henderson County: Goose Hollow Cave. Monroe County: Fruth's Spider Cave. These collections cannot be determined but undoubtedly belong to the above species.

Rimulincola divalis Sanderson, TP

Illinois. Monroe County: Horsethief Cave. Pike County: Lost Creek Cave. The genus contains only this species, which otherwise occurs only in the Ozark region (Craig, 1975a). These are the first Illinois records. The closest known relative, with which it may be congeneric, occurs in southern Asia (M.W. Sanderson, J.M. Campbell, pers. comm.).

Rugilus dentatus (Say), AC

Missouri. Perry County: Mystery Cave.

Scopaeus sp., AC

Illinois. Monroe County: Horsethief Cave.

Stenus alacer Casey, AC

Missouri. Perry County: Klump Cave.

Tachyporus maculipennis LeConte, AC

Illinois. Hardin County: Cave-in-Rock.

Aleocharinae, genus and species undetermined, AC

Missouri. Perry County: Slope Cave.

Omaliinae, genus and species undetermined, AC

Illinois. Monroe County: Camp Vandeventer Cave.

Family Cryptophagidae

Cryptophagus valens Casey, AC

Illinois. Johnson County: Teal Cave.

Family Cucujidae

Cathartus sp., AC

Illinois. Hardin County: Cave-in-Rock, in debris at damp wall.

ORDER LEPIDOPTERA

Family Noctuidae

Scoliopteryx libatrix (Linnaeus), TX

Illinois. Hardin County: Layoff and Jackson's Sandstone caves. Jackson County: Giant City Cave. Johnson County: Mason No. 1 and Will Thomas Spring caves. Union County: Guthrie Cave. The species is worldwide in distribution, and common in caves, which it seems to use as overwintering sites.

ORDER DIPTERA

Family Trichoceridae

Trichocera regelationis (Linnaeus), TX

Illinois. Hardin County: Griffith Cave.

Trichocera sp., TX

Illinois. Pike County: Twin Culvert Cave.

Family Tipulidae

Dactylolabis montana (Osten Sacken), TP

Missouri. Perry County: Mystery Cave.

Gnophomyia tristissima (Osten Sacken), TX

Illinois. Monroe County: Illinois Caverns.

Undetermined genus and species, TX

Illinois. Pike County: Twin Culvert Cave.

Family Psychodidae

Undetermined genera and species, TP?

Illinois. Calhoun County: McNabb Hollow Cave. Johnson County: Will Thomas Spring Cave. Pike County: Lost Creek Cave. St. Clair County: Falling Spring Cave.

Family Culicidae

Anopheles punctipennis (Say), TX

Illinois. Calhoun County: McNabb Hollow Cave. Pike County: Twin Culvert Cave. Saline County: Equality Cave. This species frequently overwinters in caves. Only a small fraction of the mosquitoes known from Illinois are known to be associated with caves. (see Ross and Horsfall, 1965).

Culex pipiens Linnaeus, TX

Illinois. Calhoun County: McNabb Hollow Cave. Henderson County: Goose Hollow Cave. Monroe County: Illinois Caverns, Saltpeter and Terry Spring caves. Pike County: Twin Culvert Cave. This species frequently overwinters in caves.

Culex sp., TX

Illinois. Henderson County: Goose Hollow Cave. Monroe County: Saltpeter and Terry Spring caves. Saline County: Equality Cave.

Family Chironomidae

Conchapelopia sp., TX?

Missouri. Perry County: Berome Moore Cave.

Orthocladius sp., TX

Illinois. Hardin County: Cave-in-Rock, larvae.

Trichocladius sp., TX

Illinois. Hardin County: Brown's Hole, larvae.

Family Mycetophilidae

Exechia sp. 6, TX

Illinois. Union County: Sensemeyer Cave.

Exechia sp., TX

Illinois. Jackson County: Cave No. 1.

Orfelia sp., TX

Illinois. Hardin County: Brown's Hole. Johnson County: Firestone Creek Cave. Saline County: Equality Cave. Union County: Cricket Cave.

Rymosia triangularis Shaw, TX

Illinois. Jackson County: Cave No. 1.

Rymosia sp. A, TX

Illinois. Saline county: Equality Cave.

Rymosia sp., TX

Illinois. Pope County: Frieze Cave.

Undetermined genus and species, TX

Illinois. Hardin County: Layoff Cave.

Family Sciaridae

Bradysia sp., TP

Illinois. Hardin County: Brown's Hole.

Corynoptera sp., TX

Illinois. Pope County: Frieze Cave.

Corynoptera sp., near *subtrivialis* (Pettey), TX

Illinois. Hardin County: Layoff Cave.

Lycoriella sp., TX

Illinois. Johnson County: Teal Cave. **Missouri**. Perry County: Mystery Cave.

Undetermined genera and species, TP

Illinois. Adams County: Burton Cave. Hardin County: Cave Spring Cave. Henderson County: Goose Hollow Cave. Monroe County: Illinois Caverns and Fogelpole Cave. St. Clair County: Falling Spring Cave.

Family Scatopsidae

Scatopse notata (LeConte), TX

Illinois. Hardin County: Cave-in-Rock.

Family Cecidomyidae

Undetermined genus and species. AC

Illinois. St. Clair County: Falling Spring Cave.

Family Phoridae

Megaselia cavernicola (Brues), TP

Illinois. Adams County: Burton Cave. Calhoun County: McNabb Hollow Cave. Hardin County: Cave-in-Rock and Brown's Hole. Johnson County: Firestone Creek and Teal caves, unnamed cave at White Hill. Monroe County: Fogelpole and Horsethief caves and Illinois Caverns. Union County: Guthrie Cave. The species is widespread in eastern U.S., in caves and epigean localities (Borgmeier, 1965).

Family Sphaeroceridae

Leptocera tenebrarum Aldrich, TP

Illinois. Johnson County: Teal Cave.

Leptocera sp., TP

Illinois. Adams County: Burton Cave. Calhoun County: McNabb Hollow Cave. Hardin County: Cave-in-Rock, Brown's Hole, Layoff and Cave Spring caves. Henderson County: Goose Hollow Cave. Jackson County: Cave No. 1. Johnson County: Jug Spring, Firestone Creek and Belknap caves. Monroe County: Camp Vandeventer, Fogelpole and Horsethief caves, and Illinois Caverns. Pope County: Frieze Cave. Saline County: Equality Cave. St. Clair County: Falling Spring and Stemmler caves. Union County: Cricket, Saratoga, and Sensemeyer caves. The genus is common in caves, where the larvae are probably scavengers.

Family Heleomyzidae

Aecothea specus (Aldrich), TX

Illinois. Adams County: Burton Cave. Johnson County: Jug Spring Cave. Monroe County: Illinois Caverns. Pope County: Frieze Cave. St. Clair County: Falling Spring Cave. Union County: Cricket and Sensemeyer caves. The species ranges over much of the United States and is common in caves (Gill, 1962).

Amoebaleria defessa (Osten Sacken), TX

Illinois. Hardin County: Layoff Cave. Johnson County: Jug Spring Cave. Monroe County: Illinois Caverns and Saltpeter Cave. Saline County: Equality Cave. Union County: Guthrie, Cricket, Sensemeyer and Saratoga caves. **Missouri**. Perry County: Mystery and other caves. The species occurs through much of the northern part of eastern U.S. and is common in caves (Gill, 1962; Busacca, 1975; Craig, 1977). All the flies listed in this family are considered trogloxenes, because convincing evidence has not been gathered or presented to show that the flies reproduce and complete their full life cycles in caves. It seems that they use caves most, in the fall and winter, as hibernation sites (Busacca, 1975).

Amoebaleria sackeni Garrett, TX

Illinois. Saline County: Equality Cave. The species is widespread in the more northerly part of eastern U.S. and is common in caves (Gill, 1962). This species can be separated from the preceding mainly on the characters of the male genitalia. Steyskal (1967) provided other characters to separate the species, but after studying a series from Equality Cave, he decided (1968) that the names apply to extremes of variation within one species. However, my own (SBP) examination of our collections have led me to think that two species are actually present, and not one variable species.

Heleomyza brachypterna (Loew), TX

Illinois. Monroe County: Horsethief (in gut of *Eurycea lucifuga* salamander), Saltpeter, and Terry Spring (in gut of *Plethodon glutinosus* salamander) caves. Saline County: Equality Cave. Union County: Saratoga, Cricket, and Sensemeyer caves. The species is spread over much of North America and is most frequent in caves in the winter (Gill, 1962; Busacca, 1975; Craig, 1977).

Family Muscidae

Fannia sp., AC

Illinois. Hardin County: Cave-in-Rock.

Family Calliphoridae

Caliphora vicina, AC

Illinois. Hardin County: Cave-in-Rock.

FAUNAL REGIONS

Regional and local cave faunal units can be based on a synthesis of the geographic ranges of cave-limited species. These ranges are controlled by the species' dispersal abilities and by factors which affect it, such as local structural geology, drainage, and past climatic events. All of these have affected local cave faunas through the opening or closing of past and present avenues of dispersal.

An extension of the scheme used by Barr (1967b), Holsinger and Peck (1971) and Holsinger, *et al.* (1976) is here suggested for the region we are considering. It is applicable to adjoining areas, also.

I. Ozark Plateaus Province Faunas.
   - A. Springfield Plateau Regional Fauna—The southwestern Ozark region of Missouri extending south into northwestern Arkansas and northeastern Oklahoma. This is composed of several smaller faunal units.
   - B. Salem Plateau Regional Fauna
     1. Central Missouri Fauna—The Ozarks of south central Missouri, west of the St. François Mountains, extending from the Missouri River south to north-central Arkansas.
     2. Eastern Missouri Fauna—Composed of the counties of eastern Missouri, bordering the Mississippi River, and east of the intrusive dome of the St. Francois Mountains. Franklin, Crawford, and Washington counties are a major zone of overlap of this fauna with that of the Central Missouri area.
        - a. St. Louis-Ste. Geneviève County Fauna—composed of St. Louis, Jefferson, and Ste. Genevieve counties, north of the Ste. Geneviève fault, which now acts as a barrier to subterranean dispersal through limestones.
        - b. Perry County Fauna—located entirely within Perry County, south of the Ste. Geneviève fault, and predominantly along Cinques Hommes Creek (containing some of the longest caves of Missouri, with over 50 miles of surveyed passages among four large systems on either side of the valley).
     3. Western Illinois Fauna—predominantly in Monroe, St. Clair, and Randolph counties, but including a northward extension along the Mississippi River into the Lincoln Hills areas of Adams, Pike, Calhoun, and Jersey counties. There is only one distinct local fauna, the Monroe County Fauna.

II. Interior Low Plateaus Province
   - A. The Pennyroyal Fauna (of Barr, 1967b)
     - 1-4. Pennyroyal faunal regions of Indiana and Kentucky
     - 5. Shawnee Hills Fauna—a physiographic and geological continuation of the Hopkinsville region of the Pennyroyal of western Kentucky. The Ohio River is a barrier between the Hopkinsville and Shawnee Hills faunas. Included are Gallatin, Saline, Hardin, Pope, Johnson, Union, and Jackson counties, Illinois. The western edges of the last two counties are usually considered to be part of the Salem Plateau (along with Perry and Cape Girardeau counties, Missouri), but their faunal affinities are with the eastern parts of the Shawnee Hills, proper.
   - B. The other regions given by Barr (1967b)

III. Dissected Till Plains Province Faunas—This is the region of glacial drift, mostly overlying Pennsylvanian strata of the Illinois Basin. Caves as such are absent. The subterranean fauna is composed solely of phreatobitic crustaceans occupying the Galesburg Plain and the Bloomington Ridged Plain. The Springfield Plain and the Mt. Vernon Hill Country sections seem not to be commonly occupied by phreatobites. These species usually range east through Indiana to Ohio, west to Kansas, and northwest to Iowa, probably through northeastern Missouri (which is poorly collected).

IV. Driftless Area Regional Fauna—This is the largely drift-free portion of the upper Mississippi Valley in Iowa, Illinois, Wisconsin, and Minnesota (to be covered by Peck and Christiansen, in prep.).

GEOGRAPHIC RANGES OF THE TROGLOBITES AND PHREATOBITES

Some 215 species of invertebrates recorded in this paper have an ecological association with caves (accidentals are excluded). Of these, 43 are troglobites or phreatobites. These represent 20% of the total cave invertebrate fauna. There is a small predominance of aquatic species over the terrestrial, 11% aquatic to 9% terrestrial. Based on their geographic ranges, and as controlled by regional geology, physiography, and past events of dispersal and isolation, these species can be separated into the several faunal regions already indicated. We will examine these by first considering the species with small ranges, and then those with progressively larger ranges.

There are eight species found only in eastern Missouri, in the Salem Plateau region, that do not enter Illinois. These species occur only in the area that lies north of the Ste. Geneviève fault (St. Louis to Ste. Geneviève counties). They are the snail *Fontigens proserpina*, the amphipod *Stygobromus heteropodus*, and the two carabid beetles *Xenotrechus condei* and *X. denticollis*. The species that occur only in the area south of the Ste. Geneviève Fault (and exclusively in the caves of the Cinque Hommes Valley of Perry County), are the planarians *Macrocotyla lewisi* and *Sphalloplana evaginata*, the snail *Amnicola stygia*, and the pseudoscorpion *Apochthonius mysterius*. Most of these species are highly localized, being known from only one cave system.

There are 18 species that occur only in Illinois. Two of these, the isopod *Caecidotea kendeighi* and the amphipod *Stygobromus lucifugus*, occur only in the Illinois Basin. Six species occur only in the Salem Plateau region, with its Lincoln Hills extension northward to Adams County. These are the isopod *Caecidotea packardi*, the amphipod *Gammarus acherondytes*, the pseudoscorpion *Mundochthonius cavernicolous*, the millipeds *Ergodesmus remingtoni* and *Antriadesmus* sp., and the catopid beetle *Ptomaphagus nicholasi*. With the marginal exception of *Gammarus acherondytes*, all the troglobites of the Monroe County section of the Salem Plateau are rare and occur in different (but not especially isolated) caves. To illustrate this point, three caves within 10 km of each other in flatbedded, continuous limestones have different troglobites not known from other caves despite intensive searching: Saltpeter Cave (*M. cavernicolous*, known from 2 specimens), Fogelpole Cave (*P. nicholasi*, questionably known from 5 specimens), and Pautler Cave (*Antriadesmus* sp.).

Eight species (mostly undescribed) are restricted to the Shawnee Hills. They are three species of *Caecidotea* isopods, two species of *Stygobromus* amphipods, the milliped *Pseudotremia* sp., the collembola *Pseudosinella* sp. 2, and the carabid beetle *Pseudanophthalmus illinoisenis*. As presently understood, two Illinois endemics, the amphipod *Crangonyx* sp. and the dipluran *Metriocampa* sp., occur in both the Shawnee Hills and the Salem Plateau sections. The endemic animals of the Shawnee Hills area are concentrated in caves in Hardin County, and these are taxa characteristic of caves to the east on the Pennyroyal Plateau of Kentucky (*Stygobromus, Pseudotremia, Pseudanophthalmus*, and *Caecidotea stygia*). Pope and Johnson counties in the central Shawnee Hills act as a mixing ground between the faunas of the eastern Interior Low Plateaus and those of the western Ozark Plateaus. Perhaps the complex geological structure of the hills (such as fault systems, or Hick's Dome) or various biological interactions have prevented these more eastern groups from dispersing into or surviving in the western Shawnee Hills.

There are nine species that occur on both sides of the Mississippi

River. Five of these occur in the Salem Plateau region. They are the planarian *Sphalloplana hubrichti,* the snail *Fontigens antroecetes*, the millipeds *Scoterpes* sp. and *Zosteractis interminata*, and the dipluran *Haplocampa* sp. The snail and *Scoterpes* extend westward beyond the limits of this study. Three species range through the Salem Plateau of Missouri and Illinois and into the Shawnee Hills. These are the amphipod *Bactrurus brachycaudus*, the collembolan *Pseudosinella* sp. 1 (in the *argentea* complex), and the dipluran *Eumesocampa*. The amphipod *Stygobromus subtilis* completes this series. It occurs in these regions, plus the Illinois Basin.

Nine species have ranges that go far beyond the geographic limits of this study. Species that range widely into the eastern United States are: *Cyclops clandestinus*, from the Illinois Basin to Tennessee; *Caecidotea stygia*, from the Shawnee Hills to Indiana, Ohio, Kentucky and Tennessee; the spider *Phanetta subterranea*, which ranges through much of the Appalachian cave region; and the collembolan *Tomocerus missus*, ranging from Missouri and Illinois to Kentucky. Species that occur in part of our study area and which range both to the east and west are: *Caecidotea antricola*, from the Salem Plateau of Missouri to Arkansas, and to Kentucky (but this last [Fleming, 1972] may not be a valid record and the species is unknown from Illinois); *Caecidotea tridentata*, from the Illinois Basin to Indiana, Iowa, Kansas, and Arkansas; and *Bactrurus mucronatus*, from the Illinois Basin to Iowa, Indiana, Michigan, and Ohio, with a disjunct Shawnee Hills population. *Arrhopalites clarus* has a wide range in eastern and central Missouri but is unknown from Illinois.

GEOGRAPHIC RANGES OF THE TROGLOPHILES AND TROGLOXENES

In contrast to the above discussed troglobites, the troglophiles and trogloxenes (including edaphobites) account for about 80% of the species in the caves. Because they do not have an obligate relationship with caves, they do not present any general regional patterns of endemism or of similarly overlapping ranges. Many of the species are wide ranging, and in the extreme they may occur in caves from Texas or Mexico, through the Ozarks, and on eastward into the Appalachians. Most of the troglophiles and trogloxenes, however, have ranges only from the Ozarks to the Appalachians.

FAUNAL ORIGIN, DISPERSAL, ISOLATION, AND EVOLUTION

Introduction

Only a detailed knowledge of the geological, topographic, climatic, and vegetational history of central and eastern United States during the Tertiary and Quaternary will permit a meaningful interpretation of the taxonomic and distributional data already presented on the Illinois and Missouri cave faunas. The present faunal patterns are the result of phenomena of faunal differentiation that vary in age from Pleistocene to Early Tertiary. The correct correlation of these phenomena with environmental events of increasing age is necessary for an understanding of the historic processes which caused the distributional patterns observed today.

Faunal Source Areas. The general affinities of the troglobite-phreatobite fauna, with regards to the site of its origin, are with the Appalachian fauna. The Ozarks themselves have not been an important primary site of evolutionary innovation and specialization forming cave-limited taxa above the species level. The troglobites and phreatobites are thus predominantly in genera that are widespread throughout the cave regions of the eastern U.S. Nevertheless the Ozarks do have some genera (troglobites, phreatobites, and troglophiles) that are regional endemics or distributional relicts. These would include *Macrocotyla, Bactrurus, Xenotrechus, Rimulincola, Ectopodesmus*, and *Zosteractis*. Thus, although there are some regional replacements by locally endemic taxa, the Missouri-Illinois cave fauna, above the species level, is generally of the same sort that is found through the cave regions of the unglaciated eastern U.S.

After the Appalachians, the next most important regional link of this fauna is the Rocky Mountains and the Pacific Northwest. This is recorded by taxa with disjunct ranges, their nearest phylogenetic relatives being in these western regions. Examples are the millipeds *Ergodesmus, Austrotyla*, and *Tingupa*, and the diplurans *Metriocampa* and *Eumesocampa*. These, in addition to the European affinities of *Xenotrechus* and *Tomocerus missus*, and the Asian affinities of *Rimulincola*, must all be considered as relicts of formerly wide-ranging ancestral groups which experienced extinction in intervening regions.

The cause of the faunal poverty of the Ozarks, when compared to the rich Appalachian fauna, lies not in the amount of time available for the evolution of endemics, for both are old mountains, but in their relative areas and amount of topographic relief. The Appalachians occupy a much larger area. They also have greater vertical relief, so that more stratified climatic conditions exist within a local area. They thus present a greater variety of environments and support a larger and more diverse biota in more life zones. They have also been a better site for the development and persistent local survival of endemics in past times of climatic fluctuation and biotic range adjustments. These adjustments required colonization only by the local movement of migrants up and down, not over large horizontal distances. This is important in accounting for the comparative lack of Ozark endemics in general and in the cave faunas in particular. Most terrestrial cave taxa originated from preadapted ancestors living in the deep litter of cool, moist montane forests (Barr, 1968). The low-lying Ozarks were incapable of supporting such forests and their litter fauna through the periods of time needed for the development of a large and regionally distinct litter fauna. Without a large and preadapted terrestrial litter fauna, Ozark caves then had few locally derived terrestrial arthropods that were able to successfully occupy them. As a result, and because of the past dispersal difficulties of such a fauna coming from the east or elsewhere to the Ozarks, the Ozark caves now have few terrestrial troglobite species.

Pre-Pleistocene faunal connections. The few regional endemic genera undoubtedly mark events of Tertiary range connections and fragmentations. Examples are the carabid beetles *Xenotrechus*, the staphylinid *Rimulincola*, the collembolan *Tomocerus missus*, the millipeds *Tingupa, Austrotyla*, and *Ergodesmus*, and the diplurans *Eumesocampa* and *Metriocampa*. These and other soil-dwelling arthropods such as other millipeds and some spiders have disjunct generic distributions in the Ozarks and the Rockies, or in the Pacific Northwest, or in temperate Eurasia (Shear, 1972a; p. 273). Such distributions are in many cases remnants of former and more continuous ones when Teritary forests lay at mid-latitudes across the North American continent and were connected with Eurasia across what is now the Bering Straits (Hopkins, 1967). Mid- and late-Tertiary cooling and drying (Axelrod, 1958; Axelrod and Bailey, 1969; Dorf, 1970) fragmented these forests through the creation of the Great Plains grasslands after the uplift of the Rocky Mountains. The increasing aridity of the Miocene and Pliocene divided the arthropod ranges through the elimination of the Plains forests and the extinction of geographically intermediate arthropod populations. Hoffman (1969) recognizes such old faunal connections in millipeds and from them forms two categories: an ancient Holartic group, and a Tertiary Neartic endemic group. Although there is disagreement, these forests and arthropod distributional ranges were most likely not continuous between the Ozarks and the western mountains at any time during the Pleistocene, because the presence of the Rocky Mountains and their persistent rain shadow seemingly has not allowed the re-establishment of a broad and continuously forested corridor across the mid-continent.

Early Pleistocene connections. After their separation from western forested regions, the Ozarks could maintain faunal contact through the forests eastward to the Appalachians. Dispersal then was probably easier than now for organisms of low dispersal ability (non-flying soil and forest litter inhabitants) because river systems probably presented a less formidable set of barriers. The ancient Ohio River, between Kentucky and Illinois, was smaller in pre-Kansan times, since much of the drainage of the present Ohio headwaters was carried to the north through central Ohio, Indiana, and Illinois by the ancient Teays River, before emptying into the ancient Mississippi (Teller, 1973, and references). The ancient Mississippi River was smaller north of St. Louis before the Illinoian glaciation, since more of its present headwaters drained northwards, and it flowed east and south through central Illinois. Thus, the Lincoln Hills of Illinois and Missouri were less separated than now. The ancient Mississippi River between Illinois and Missouri, below the confluence of the Missouri and Illinois rivers, however, must have been a significant barrier to flightless terrestrial organisms much of the time.

However, all this only sets the stage for the development of the zoögeographic picture of the cave fauna as it is today, and these earlier details are obscure because of the massive influence on the region of the Illinoian glaciation and an undoubted but less drastic effect of later glacials and interglacials.

The model of a Taxon Cycle in cave faunas. Without an understanding of the dynamic picture of past changes in climates and in the expanding and contracting nature of the geographic extent of habitats and their inhabitants, it would be difficult to understand the biological and genetic pressures that resulted in the invasion, evolution, and extinction of faunas in caves. With an understanding of this dynamic past and a consideration of species ranges, range fragmentations, and patterns of endemicity, we can reconstruct a "taxon cycle" (see Rickleffs, 1973, pp. 582-585, and references) to explain the present day cave faunas of Illinois and eastern Missouri.

The goal, then, is to identify the similarities or patterns that exist within the cave faunas (which for our purposes can be judged to be similar to island faunas), to relate these to the stages in the taxon cycle, and then to associate these to known events in a geological time frame.

The detailed documentation provided in the following reconstruction and discussion is to show the validity and magnitude of past climatic-biotic fluctuations and movements in the eastern and central United States. This is necessary to give strength to the fundamental hypothesis upon which the model is based; that at least the present day *terrestrial* cave faunas of temperate continental regions are mostly composed of species that are adapted to cool-moist-dark environments, and that these species are predominantly (if not entirely) descendants of earlier species that occupied forested environments with these characteristics in the deep litter and moss carpets. Such forests and arthropods are now generally limited to higher elevations in the Appalachian Mountains. The paleoclimatic and paleobotanic record documents the intermittent presence and absence of such forests (and as a consequence their preadapted faunas) in areas where the descendant cave fauna now exists.

We emphasize the terrestrial biota in the following synthesis of the taxon cycle model with past climates and evolutionary-dispersal events. We do not understand the aquatic biota as well as the terrestrial, and thus do not care to here attempt a hypothesis on the details of their history. Barr (1968) and Culver (1976) have briefly considered some of the effects of Pleistocene events on the aquatic fauna of caves.

The following reconstruction of late Pleistocene events and climates and their biotic effects is based on summaries in the following references: Bergstrom, 1968; Cushing and Wright, 1967; Dort and Jones, 1970; Flint, 1971; Frey, 1965; Frye and Willman, 1973; Leighton and Brophy, 1971; Martin and Mehringer, 1965; Ross, 1965; Turekian, 1971; Whitehead, 1965; and Wright, 1971. The following scenario is proposed as the hypothetical model that best explains the details of the present fauna in the light of past events. The time stratigraphic units are based on classical North America Pleistocene nomenclature, but it should be pointed out that, because of the flood of information that has become available in the past ten years, one should be cautious in accepting too firmly a framework that unites these classical names based on continental deposits with paleotemperature and geochronological units which are mostly based on oceanic sediment studies (Emiliani, 1971). This oceanic sediment record does, however, roughly correspond to the continental record recovered from isotope analysis of cave deposits (Harmon, Thompson, Schwarz, and Ford, 1975). The taxon cycle model has already been used (but not by this name) to achieve an evolutionary understanding of the development of North American cave faunas by Barr (1967a, 1968, 1973), Culver (1976), and Peck (1973a, 1977).

Illinoian Glaciation. We can begin the development of the story with the Illinoian glaciation, lasting from about 180,000 to 130,000 years B.P. (dates here and following from Broecker and Van Donk, 1970; and Shackleton and Opdyke, 1973). There were at least three major periods of ice advance, with significant interstadial recessions during this glaciation. At its maximum extent, the ice undoubtedly drastically affected the subterranean environment of Illinois and eastern Missouri. Even the caves that were not overridden by the ice would have been so affected by periglacial phenomena that they were probably uninhabitable; periglacially frozen ground may have prevented water from percolating into the caves, cave temperatures were very cold if not sub-freezing, there was a lowered input of organic matter as a food source from the local (tundra-like) vegetation, and most importantly, there were vast quantities of glacial meltwater which flooded and scoured cave systems. Consequently, any cave fauna already existing in the study area probably could not have survived in the region, and either retreated southwest to the Ozarks proper, or to the southeast, or became extinct.

Sangamon Interglacial. Interglacial climates in the central U.S. have been largely temperate, and at times somewhat warmer and drier than at present. Consequently, the caves became available for faunal re-colonization after the ice had retreated. Regional conditions became more warm and moist, and forests and their associated faunas returned. This would have been early in the Sangamon interglacial, which in its entirety lasted from 125,000 to 80,000 years BP. The biota was from the south, where it had been displaced during the preceding glacial. Much of what we now generally call an Appalachian fauna may have used at least some part of the Coastal Plain as a refugium. The Plain in the Mississippian Embayment Region could easily have been occupied on both sides of the Mississippi River during the Illinoian glaciation, because the river was less of a dispersal barrier to flightless litter arthropods as lower sea levels formed better drained conditions with fewer or narrower barriers of wetlands or floodplain swamps along the river, and because of the decreased volume of the river itself from the comparatively decreased runoff from an advancing ice mass. Other refugia that became biotic source areas were the Ozarks to the southwest, the middle and southern Appalachians, and the Interior Low Plateaus to the southeast. In these last regions, a cave and groundwater fauna undoubtedly already existed.

Thus, as the Sangamon began, the study region was re-occupied by the generally northward migration of a fauna from the glacial refugia of the forested plains, plateaus, and highlands. Some of the migrant terrestrial litter fauna had already been troglophilous in the Ozarks or Interior Plateaus, but there is no compelling evidence to suggest that any of this fauna was already troglobitic there, although such overland movements of troglobites were probably possible at that time and may help to account for such extreme present day relicts as *Tomocerus missus* and *Xenotrechus*. On the other hand, the ground water fauna moving into the region already contained species highly adapted to subterranean life.

The early Sangamon was the significant time of cave colonization because the immigrant terrestrial species that could live in the cool, dark, and moist conditions of caves found them and occupied them as troglophiles. At this time, these populations maintained genetic contact with epigean populations of the same species. But, as the Sangamon continued and the regional climate became drier and warmer, epigean conditions deteriorated with respect to the survival of the epigean populations that required cool and moist habitats. In response to the climatic change, oak-hickory forests moved east to southern Indiana (Kapp and Goodring, 1964). The Don Valley site near Toronto also suggests a climate a few degrees warmer than that at present (Flint, 1971; p. 553). Many epigean arthropod populations undoubtedly became locally extinct as whole species ranges shifted in the direction of movement of the required habitat. The remaining populations of troglophilic species were thus restricted to the caves, alone.

This break of gene flow with their epigean fellows resulted in genetic isolation. The populations that were able to survive genetic isolation could then experience the different set of selective pressures (see Barr, 1968; and Peck, 1973a; p.44) that the caves presented, and could adapt to them. This was the time and these were the conditions of origin and isolation of most if not all of what would become the regional terrestrial troglobites. The same events also precipitated the isolation and adaptation of at least some of the aquatics, through the restriction of aquatic habitats to subterranean waters. Even though an analysis of Pleistocene insect fossils gives little evidence for insect speciation in the resulting time span (Coope, 1970), the severe selective pressures of caves are undoubtedly an exception to this generalization and have caused much speciation in the populations limited to them.

Wisconsinan Glaciation. With the climatic deterioration that signaled the arrival of the Wisconsinan glaciation (from 80,000 to 10,000 years B.P.), the troglophiles that had now become troglobites had a new glacial survival crisis, but also new dispersal opportunities. The Wisconsinan glaciation was composed of many advances and retreats, and thus many cool episodes were separated by warmer intervals of varying duration. At its maximum extent, the Wisconsinan ice lay as close as 160 km to the cave area of Monroe County, Illinois. The survival of the cave fauna in a condition as rich as it is today indicates that there was little or no extinction or displacement and that severe periglacial conditions did not exist in the cave region. Lindroth (1970) investigated the climate of refugia at glacial margins and found them to be mild and with an appreciable biota, but these are coastal and not continental interior situations. The exact nature of the local climate in southern Illinois and eastern Missouri at the time of Wisconsinan maximum is not known. Watts (1970, 1975) documented extensive changes in vegetational composition in and near a cave region of the Cumberland Plateau, in the southern Appalachians of Georgia, during full glacial conditions. Closer to our region, Mehringer, Schmeger, *et al.* (1968) documented local forests containing spruce and larch from sediment cores from Boney Spring in southwestern Missouri. From the same region, a more detailed study (King, 1973) has shown that the western Ozarks were covered by open pine-parkland from at least 40,000 years BP until the start of the full glacial stadial 20,000 to 25,000 years BP and then by boreal spruce until at least 13,500 years BP. Deciduous elements and the present oak-hickory forest developed after the decline of the spruce. Mammals that are presently boreal left remains in local caves (Oesch, 1967; Parmalee, Oesch, and Guilday, 1969; Parmalee, 1967, 1968). Flint (1971; p. 510) places spruce forest along the Mississippi River during a Wisconsinan maximum.

In the only mid-Wisconsinan (interstadial) sites that have been investigated in Illinois, Grüger (1972a, 1972b) interprets the vegetation of southern Illinois as prairie with oak-hickory groves. Northern Illinois, he felt, contained pine and spruce forest with a few deciduous trees. This interpretation shows a warmer and/or drier climate than existed in western Missouri during the mid-Wisconsinan. Wayne (1967) interpreted the distribution of fossil snails to suggest that the 5°C mean annual isotherm and the north edge of the mixed conifer and hardwood forest probably lay about 200 km south of the ice margin during the Wisconsinan maximum. The arthropod (especially beetle) faunal changes that accompanied these vegetational changes are best known for western Europe (Coope, 1967; 1970) but studies now appearing document the faunal changes at North American sites (Askworth, Clayton, and Bickley, 1972).

In what we will assume to be cold and wet (through reduced evapotranspiration, even if there also was reduced precipitation) boreal forests that lay south of the Wisconsinan ice, conditions were favorable for the above ground survival and movement of troglobites through the deep, dark, cold, and wet mats of moss and deep litter that presumably blanketed the forest floors (Barr, 1973). By overland movement through these epigean habitats, some terrestrial troglobites acquired their present ranges through or over areas that do not have continuous limestone available for subterranean dispersal. Such a means of range expansion was probably utilized by all the species that occur in more than one small faunal area. Terrestrial and aquatic species of troglobites that originated in Missouri moved across the shrunken Mississippi river into Monroe County, Illinois, and moved northwards into the Lincoln Hills section, along with the terrestrial and aquatic troglobites that originated in the Monroe fauna. In this same way the carabid beetle ancestral to *Pseudanophthalmus illinoisenis* and *P. barberi* entered Illinois from Kentucky and (or) Indiana. The catopid beetle ancestral to *Ptomaphagus hirtus* and *P. nicholasi* (if it is a valid species record) made an even more incredible overland journey from the Mammoth Cave region of Kentucky to Monroe County, Illinois (see Laing, *et al.* 1976b). Other animals, such as the collembolans *Pseudosinella* and *Tomocerus missus* and the millipeds *Pseudotremia* and *Scoterpes* traveled the same route from Kentucky and/or Indiana into Illinois, and some went on to Missouri.

That there was faunal exchange across the Mississippi River, shrunken in size because of its diminished headwater supply, is witnessed by the aquatic and terrestrial species that occur on both sides of it today. The aquatic species (the snail *Fontigens antroecetes*, the planarian *Sphalloplana hubrichti*, and the amphipod *Apocrangonyx*) may have crossed under the river in subfluvial channels (the bedrock channel at that time did not contain 46m of fill as it now does near St. Louis), but we think it more likely that they moved through large interstitial pores or cavities in riverine sediments. (We doubt the possibility of modern gene flow through subfluvial channels under the Mississippi.) They may have been aided in interstitial dispersal as the river's main channel changed its course from one side of the valley to the other. Just as for terrestrials, there was also aquatic faunal exchange to the east and southeast across the shrunken Ohio River, either, as is more likely, from Kentucky to Indiana and then to Illinois, or, as is less likely, directly from Kentucky to Illinois. Such opportunities for Wisconsinan dispersal were probably not successfully used by species with limited ranges, such as those that are found today in only a few caves in a small area.

The aquatic troglobites and phreatobites that today range over a wide region (Fig. 6) probably began dispersing in Wisconsinan time. They have used interstitial dispersal to distribute themselves northwards (to the northeast and northwest) under both the Illinoian and the Wisconsinan glacial drift plains during post-Wisconsinan time. In Illinois at least, most of the records of phreatobites are near major stream valleys, where the animals could have interstitially migrated through gravels and other coarse streamside sediments. A large fauna is known to live in such sites (Stanford and Gaufin, 1974). We should not expect interstitial dispersal to be as likely through the fine-grained sediments blanketing the upland drift plains, with their reduced drainage gradient and perhaps less oxygenated subsurface waters. The absence of a phreatobitic fauna (Fig. 6) from the Springfield Plain and the Mount Vernon Hill Country (Fig. 2) is probably caused by relatively high groundwater acidity resulting from oxidation of sulfides in underlying Carboniferous rocks.

The widespread phreatobite *Bactrurus mucronatus* is known only from one cave, this at the southern end of its range, on the north flank of the Shawnee Hills. This population may have existed since the species range was pushed south in the Wisconsinan. The rest of the present range would then have resulted from post-Wisconsinan northwards dispersal.

The only clear example of the Wisconsinan splitting of the range of a species through the extinction of geographically intermediate populations is that of the loss of the cave fish *Typhlicthys subterraneus*

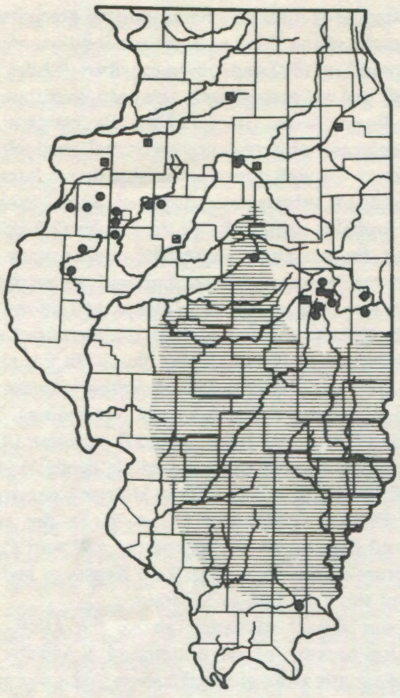

Figure 6. Distribution of phreatobitic crustaceans in groundwaters of Illinoian and Wisconsinan glacial drift in the Galesburg and Bloomington Ridged plains of the Illinois Basin. Shaded area is underlain by Pennsylvanian Mattoon, Bend, and Modesto formations. The crustaceans live largely in groundwaters over Pennsylvanian Spoon and Carbondale formations. Symbols: diamond, *Cyclops clandestinus*; open squares, *Apocrangonyx lucifugus*; closed circles, *Bactrurus mucronatus* (the only cave record on the map is for this species in the southern tip of the state); and closed squares, various species of *Caecidotea*.

from our study area of Missouri and Illinois. It survives to the east and southeast in Indiana and Kentucky and to the west in central Missouri. If this range split dated from the earlier Illinoian, we would expect more differences to be evident between the populations but this is not the situation found by Woods and Inger (1957). Using this line of reasoning, the latest time of separation of the fish genus *Amblyopsis* into an east and west population followed their elimination from Illinois during the Illinoisan glaciation. The evolution of the then two widely disjunct populations into two separate species of *Amblyopsis* has been since then and was probably reinforced if not initiated by the Sangamon interglacial.

The Recent. The climatic warming following the retreat of the Wisconsinan glacier (the past 18,000 years) has caused the isolation of all populations of troglobites and the formation of species that though still poorly differentiated morphologically, are real biological species because of their extrinsic reproductive isolation. *Pseudanophthalmus illinoisensis, Ptomaphagus nicholasi* and *Pseudotremia* sp. are examples. The spider *Phanetta subterranea* has retreated into caves over an immense geographic area, and no remnant surface populations are known.

Climatic warming has caused the (at least partial) cave-isolation of some troglophiles as well. The milliped *Tingupa pallida*, known from many caves, is known from only one epigean site. The best example is the milliped *Austrotyla specus*, which is now confined to caves in the southern part of its range, but occurs in epigean sites to the north. The milliped *Semionellus placidus*, otherwise northern and montane, has a cave record as its most southern-low elevation population. Other examples of similar patterns of ranges with northern epigean and southern cave populations undoubtedly occur but adequate information is not available on the epigean distribution of most troglophiles to detail this phenomenon. Ross (1965) gives details of ranges of many aquatic insects that have an "Ozark-plus-boreal" distribution, resulting from the Ozark survival of populations that remain there because they could find appropriately cool sites (coldwater springs). An excellent example of this type of range is that of the cave fungus gnat *Macrocera nobilis* (Peck and Russell, 1976).

The xerothermic (also called the altithermal or hypsithermal) warm-dry period of the Recent (from 8000 to 4000 years BP) saw the eastward extension of the prairies as a peninsula into the deciduous forests, as far east as Ohio (Wright, 1968). It has been important in shaping the present distributional patterns of some grassland vertebrates (Smith, 1957; 1965) and epigean invertebrates (Frey, 1965; Ross, 1970), but it is not reflected in cave invertebrate distributions. If anything, this period of climates which were warmer and drier than those at present, as indicated by many pollen studies (King, 1976) would have given the last final boost to the complete or partial cave isolation of today's troglobites and troglophiles and the establishment of their modern distributions.

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The Pleistocene Mammalian Fauna of Harrodsburg Crevice, Monroe County, Indiana

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ABSTRACT

Harrodsburg Crevice is a collapsed, filled-in cave in the unglaciated, hilly, karst region of south-central Indiana. The mammalian faunal remains described were recovered from floor deposits of this former cave and include extinct Pleistocene species of the genera Canis, Smilodon, Panthera, Equus, *and* Platygonus, *as well as several extant species no longer present in the region.*

INTRODUCTION

THE VERTEBRATE remains which form the basis of this study were recovered from the basal portions of a filled vertical limestone crevice or fissure. At the time of deposition, it was probably a moderately large, more or less horizontal cave. The fissure deposit, which was exposed and partially removed during construction of "new" Indiana State Route 37, is located 6 mi south of Bloomington, Monroe County, Indiana (SE¼, NE½, SE¼, SE¼, SE¼ of Sec. 17, T7N, R1W, Clear Creek 7½-minute quadrangle).

The fissure is near the top of an east-facing slope approximately 715 ft asl and overlooks the head of a small, unnamed tributary of Little Clear Creek. Local minimum elevation is 490 ft at Salt Creek, some 1.5 mi southeast of the fissure; local maximum elevation is 950 ft on a hill 3.5 mi to the southwest. The topography in the immediate vicinity of Harrodsburg Crevice consists of rolling upland dissected by several small streams with steep-walled valleys and relatively narrow floodplains.

Modern vegetation is classified as Western Mesophytic. Beech (*Fagus*), maple (*Acer*), oak (*Quercus*), and hickory (*Carya*) comprise approximately 80% of the forest species (Lindsey, *et al.*, 1965; Petty and Jackson, 1966). Average annual precipitation for the area is 43 in, and mean annual temperature is 55° F (U.S. Dept. Commerce, 1974). The nearest source of permanent water, other than springs, is Little Clear Creek, about one-half mile to the east. The area is drained by the Ohio River system, via Clear Creek, Salt Creek, White River, and the Wabash River.

Geology of the Region

The physiographic region in which Harrodsburg Crevice is located is the Mitchell Plain (Malott, 1922), a moderately dissected peneplain formed on westward-dipping Mississippian limestones, specifically the Harrodsburg, Salem, St. Louis, Ste. Geneviève, and Paoli formations. The latter three are very susceptible to solution, and the Mitchell Plain exhibits some of the best karst topography in the world. Fissures, sinkholes, and extensive cave systems are common features of the area and, except for the larger and more deeply entrenched streams, most drainage is subterranean (Powell, 1961).

The Mitchell Plain, plus the highly dissected Crawford Uplands region to the west and the highly dissected Norman Uplands to the east, form a northward-extending "tongue" of unglaciated highlands in south-central Indiana. Lobes of the Illinoian Glacier extended along both the western and eastern boundaries of these highlands, passing within 20 mi of Harrodsburg Crevice on each side and terminating, to the southwest and southeast, at a latitude some 75 mi to the south. During the Wisconsinan maximum, the ice front again advanced to near the northern tip of this area and to within 27 mi of Harrodsburg Crevice (Wayne, 1961).

Description of the Crevice

Harrodsburg Crevice is exposed in cross-section on the vertical face of a road cut, on the east side of new Indiana Route 37. Prior to highway construction, the crevice had been filled and no indication of its presence existed on the surface. The filled cavity which contained the faunal materials was formed at the intersection of two solutionally enlarged joint planes within the Salem Limestone. The cavity presently extends vertically from the interface of this limestone with the overlying red, highly acidic, limestone-derived "terra rosa" (about 6 ft above the top of the bone deposit) to an undetermined depth below the surface of the road-cut (Fig.1).

It is not possible to determine with certainty the characteristics of the fissure at the time the bones were deposited because (1) it was partially destroyed by highway construction and subsequent erosion, (2) considerable filling and other natural forms of alteration occurred after the bones were deposited, and (3) the deposit has not been completely excavated. However, it is unlikely that the fissure acted as a natural trap. It would appear that it served primarily as a den or shelter, particularly for large carnivores and perhaps peccaries. Bone accumulation resulted from animals that died during natural habitation of the site, from portions of kills which were carried into it, and possibly from the contents of deposited feces.

Originally, the fissure probably was a subterranean cavity, with the ceiling a short distance below the bedrock-terra rosa interface. During this time, when the cavity was probably not open to the surface, a sizeable deposit of vertically banded, reddish flowstone (Fig. 1"b" formed along the north and northeast sides of a large triangular block of limestone (Fig. 1"a") which, presumably, rests upon an earlier floor of this cavity. Subsequently, an opening to the surface developed somewhere within the fissure system; its location is unknown and probably it cannot be ascertained now, but the most reasonable guess would place it some 25 to 50 ft southeast of the cavity where the main fissure intersects the east-facing slope.

With an opening to the surface, the cave could have been used as a den or habitation site by a variety of animals. It would have been possible for them to make their way from the entrance (wherever it was) along one of the open fissures to the "room" formed by the intersection of the two fissures; they could have then occupied the relatively flat surface formed by the large limestone block and its attached mass of flowstone (Fig. 1"a"-1"b"). Bones of animals that died a natural death (weak or abandoned young; sick, injured, or aged adults), kills carried into the den, and fecal material accumulated in a wide crevice at the north edge of the room. These faunal remains were included in a matrix consisting of clay-like sediment and limestone detritus (derived from the walls and ceiling of the cave). They formed a sloping, talus-like deposit (Fig. 1"c") adjacent to the north edge of the large limestone block and attached mass of flowstone.

During or after this stage of deposition in the cave, a layer of grey travertine began forming on the top of the bone deposit. Eventually, it capped and solidly cemented the uppermost one foot, with decreasing amounts of travertine formation but considerable mineralization of bones extending to a depth of at least four ft below the top of the main bone-bearing deposits. The mineralization that occurred at this time protected the faunal materials from decay which would probably have resulted from their subsequent contact with acidic terra rosa (discussed below); the travertine cap also appears to have sealed the deposit against "contamination" by later faunal materials.

The final depositional episode resulted from the ceiling breaking through to the base of the overlying terra rosa which, presumably through solifluction, then filled the cavity (Fig. 1"d"). After the cavity was filled, a number of geode-like formations colloquially referred to as "cornstones" (crusty shells of carbonate cemented soils) formed along the interface of the fissure and the terra rosa fill above the bone-bearing deposits.

FIELDWORK AND METHODS

Discovery, Excavation, and Laboratory Work

The Harrodsburg Crevice deposits were discovered in September, 1974, by Richard L. Powell, then with the Indiana State Geological Survey, who collected a small sample of the exposed bones. These were taken to the Ethnozoological Laboratory, Department of Anthropology, Indiana University, and brought to the attention of William R. Adams and P. J. Munson. The mineralized condition of much of the bone and the recognition of teeth of peccary, dire wolf, and a large feline made the potential importance of this deposit obvious. Munson subsequently visited the location and found the deposit to consist of a partially exposed, undisturbed mass of bone embedded in a beige clay-limestone, detritus-travertine matrix. In addition, there was a sizeable talus slope of mixed bones and matrix which had been disturbed since its exposure during highway construction by erosion, slumping, and the activities of amateur fossil collectors (who had dug into the deposit in the course of collecting shark teeth and other Mississippian fossils from the adjacent limestone exposures). All of the disturbed material, which consisted of approximately 20 cu ft of bones and bone fragments, beige sediment, and travertine-cemented blocks of bone, limestone chunks, and sediment, was removed at this time and transported to the Glenn A. Black Laboratory of Archaeology, Indiana University, for further processing.

Within a few days of this collecting trip, the Black Laboratory was contacted by Mr. and Mrs. Ray E. Fitzpatrick, who reported that several weeks previously they had found some "fossilized" remains of large animals in a crevice south of Bloomington. Their materials were also from Harrodsburg Crevice and these specimens, consisting of about 50 isolated teeth, foot bones, and bone fragments, were kindly donated. The Fitzpatricks also had the names and address of other persons who had materials from this deposit, namely Mr. Harry M. Smith and his two sons, Michael and Mark. The Smiths were contacted and found to possess numerous teeth, bones, and bone fragments (including two paired jaws of peccary which were the most complete of any of the *Platygonus* cranial material recovered), plus approximately 5 cf of deposit matrix containing an abundance of small specimens. These materials were kindly made available to us on permanent loan. Subsequently, Miss Diana L. Seider brought to the Glenn A. Black Laboratory several blocks of travertine containing bones and teeth which had been removed from this deposit. This material was also donated.

The final collecting trip to the deposit was made by Munson in late October, 1974, and excavations were undertaken in undisturbed portions of the deposit. This investigation revealed large quantities of bones, many of them often partially articulated. Most of these, however, were greatly fractured ("checked") *in situ* and, furthermore, most were embedded in a moist, clay-like, tacky matrix or were cemented by travertine either to each other or to limestone detritus. Consequently, it became obvious that to avoid damage during recovery more sophisticated and time-consuming techniques were required. Since neither time nor resources were immediately available, excavation of the undisturbed portion of the deposit was discontinued after about two cubic ft had been removed. The remaining parts were buried beneath a layer of limestone slabs and loose soil in an attempt to

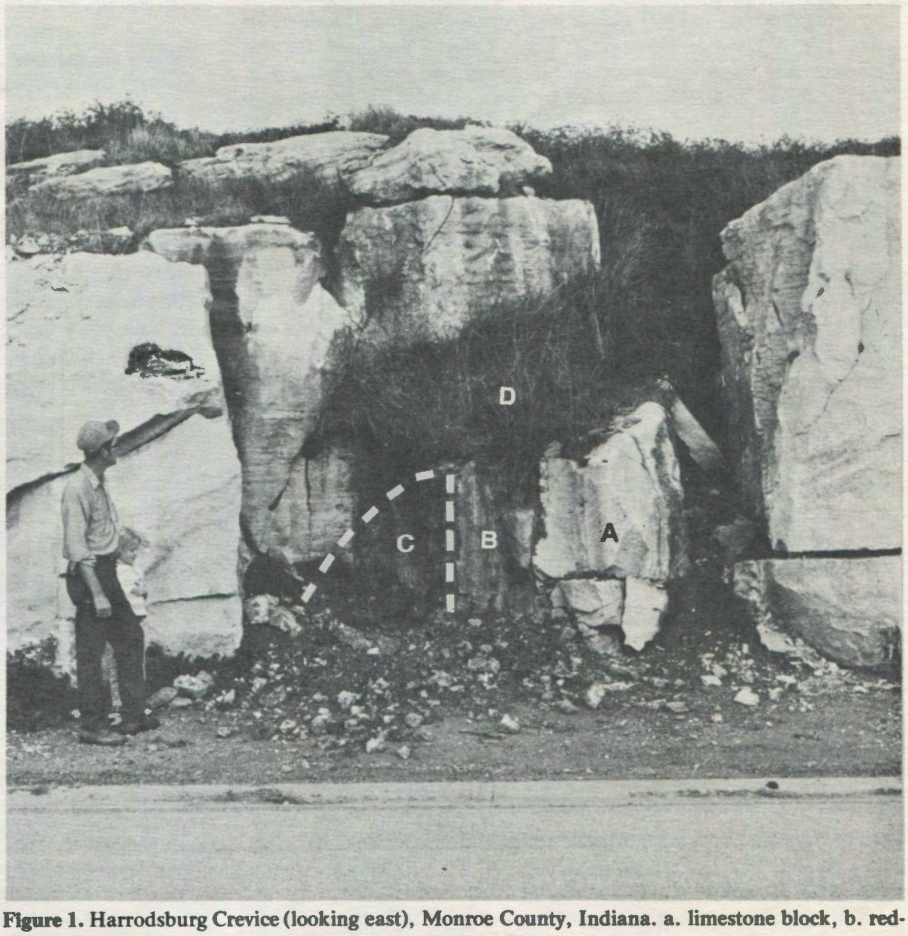

Figure 1. Harrodsburg Crevice (looking east), Monroe County, Indiana. a. limestone block, b. reddish flowstone, c. bone-bearing deposit, d. terra rosa fill.

protect and preserve the deposit. This endeavor failed, however. Sometime during the summer of 1975, persons unknown removed all of the bone-bearing matrix above the level of the highway, about 10 cubic ft. An undetermined quantity (possibly a considerable amount) of undisturbed bone-bearing deposit still remains, however, extending downward in the crevice below the level of the road-cut.

Initial processing of the material was carried out at the Glenn A. Black Laboratory. Bones and teeth already isolated from their matrix were simply washed. The smaller specimens contained in the approx. 27 cubic ft of matrix which were returned to the Laboratory presented greater problems, however. The bulk of the matrix was a tenacious beige "clay" which, in its original moist state, proved impossible to separate from the contained bones and teeth. It was discovered, however, that it could be removed by the following steps. The material was slowly dried, then soaked for a minimum of five hours in a water-detergent solution. When reduced to a semi-fluid state, it was poured onto window screen (about 1 mm mesh) and gently rinsed with a garden hose. Most of the sediment would go into suspension and wash off, reducing the bulk of the mixed matrix-bone sample by about 80% and leaving a "residue" of small bones and teeth, bone fragments, and small pieces of rock and travertine. However, a thin film of clay still remained on the material which was impossible to remove by additional rinsing and which would make sorting difficult. Consequently, the mixed material was thoroughly dried once more, again soaked in detergent, and then rerinsed. When dried again this loose mixture of small faunal specimens and pieces of limestone and travertine was sent to the senior author for sorting.

Another sizeable portion of the matrix consisted of specimens embedded in solid blocks of travertine or travertine-cemented masses of limestone detritus and clay that would not wash. These masses of material were sent to the senior author who was able to recover some additional bone and teeth by further soaking (weak acetic acid—commercial vinegar) and/or mechanical chipping. Considerable time was involved in restoration; Duco Cement was used for this purpose. The faunal remains were then sorted into major groups (*e.g.* canids, felids, mustelids), followed by species determinations through comparisons with reference specimens in the collections of the Zoöarchaeology Section, Department of Anthropology, University of Tennessee, Knoxville, and Section of Vertebrate Fossils, Carnegie Museum of Natural History, Pittsburgh. Mammals identified from Harrodsburg Crevice are listed in Table 1.

Soil Analyses

Two "soil" samples, one from the bone-bearing deposit and the other from the red clay fill above it, were analyzed for particle size and heavy minerals by the Indiana State Geological Survey, through the courtesy of Henry H. Gray, whose comments are paraphrased below:

The red fill is 77.3% clay-sized particles, 18.9% silt, and 3.1% sand. Virtually all of the heavy minerals are opaque and probably represent some form of limonite. The high clay content, the red color, and the composition of the heavy minerals are typical of the subsurface, limestone-derived terra rosa of the Mitchell Plain; this portion of the fill undoubtedly resulted from overlying terra rosa washing or slumping into the crevice.

The beige sediment which comprises the bulk of the matrix of the bone-bearing deposit is quite different in terms of particle size: 26.6% silt, and 11.2% sand. Heavy minerals, however, are similar, with almost all being opaque and probably representing some form of limonite. Analysis for the presence of loess in this sample was inconclusive but on the basis of the high silt content and the color it is possible that there is some loess mixture. The overall impression is that this material is rather typical of cave sediments in this area and represents sediments which have been washed in from the external surface.

Radiocarbon Analysis

Through the courtesy of the Illinois State Geological Survey, Urbana, Illinois, a radiocarbon analysis was obtained on a sample of bone from the Harrodsburg Crevice deposit. An effort was made to select "large" pieces, *i.e.* fragments or sections of bone felt to be mostly those of *Platygonus*, with possibly some pieces of *Canis dirus, Ursus* and/or *Panthera onca*—the larger mammals represented in the deposit. The result of the analysis (ISGS-424) was a date of 25,050 ± 660 BP radiocarbon years. This date is based on the bone-apatite fraction; the analyst was unable to extract enough collagen for a date on that fraction. If this date is reliable, at least some of the Harrodsburg Crevice fauna inhabited this region and their remains were deposited during the Farmdalian Substage, an interval of major glacial withdrawal, of the Wisconsinan Stage, but several of the component species suggest an earlier age.

TABLE 1. Mammals identified from Harrodsburg Crevice, Indiana

Species	No. of pieces	Minimum No. of individuals
TALPIDAE		
Parascalops breweri (Bachman), Hairy-tailed Mole	3	1
SCIURIDAE		
Marmota monax (Linnaeus), Woodchuck	1	1
CRICETIDAE		
Neotoma cf. *floridana* (Ord), Wood Rat	68	12
Microtus (*Pedomys*) cf. *ochrogaster* (Wagner), Prairie Vole	6	5
Microtus Schrank, Vole	10	—
Synaptomys cooperi Baird, Southern Bog Lemming	4	2
GEOMYIDAE		
Geomys cf. *bursarius* (Shaw), Plains Pocket Gopher	18	3
LEPORIDAE		
Sylvilagus sp. and/or *Lepus* sp., Cottontail?, Snowshoe Hare?	148	8
CANIDAE		
Canis cf. *dirus* Leidy, Dire Wolf	59	6
Canis spp., Dire Wolf?, Indet. Wolf Species?	335	6
Canis sp.: *C.* cf. *latrans* Say, Coyote?	2	2
Urocyon cinereoargenteus (Schreber),	15	4
Urocyon?, *Vulpes*?, Fox sp.	12	2
URSIDAE		
Ursus cf. *americanus* Pallas, Black Bear	48	5
MUSTELIDAE		
Mustela Linnaeus, Weasel sp.	1	1
Mephitis mephitis (Schreber), Striped Skunk	22	5
Spilogale cf. *putorius* (Linnaeus), Spotted Skunk	1	1
FELIDAE		
Lynx cf. *rufus* (Schreber), Bobcat	31	3
Smilodon cf. *floridanus* (Leidy), Sabertooth Cat	1	1
Panthera onca augusta (Leidy), Jaguar	22	2
EQUIDAE		
Equus cf. *complicatus* Leidy, Horse	1	1
TAYASSUIDAE		
Platygonus cf. *cumberlandensis* Gidley, Peccary	420	10
CERVIDAE		
Odocoileus cf. *virginianus* (Zimmermann), White-tailed Deer	2	1

ACCOUNTS OF SPECIES

The vertebrate fauna from Harrodsburg Crevice, with the exception of six carapace fragments of what appears to be box turtle, *Terrapene* sp., consisted entirely of mammals. Problems involving recovery of the remains and their general crushed and fragmented condition, compounded by their fusion into the breccia, have been discussed. In spite of these difficulties, careful sorting of the rock and soil matrix yielded minute bone pieces and such small items as isolated microtine teeth. It was felt, therefore, that the absence of remains of "expected" animals, such as bats and soricids, and the recovery of so few small rodent elements was not due to oversight in processing the matrix or from natural destruction. Rather, it was a reflection of the former presence or absence of these forms at the cave site.

Because of the fragmentary condition of the vertebrate material, only a small percentage of the several thousand pieces recovered could be identified. A total of 20 species of mammals, representing a minimum of about 85 individuals (a conservative number), were identified. Five of these species represent extinct Pleistocene forms, one or possibly two species (*Ursus, Spilogale*) have been extirpated in Indiana in historic times, and two species (*Neotoma, Geomys*) no longer occur within at least a 50 mi radius of Harrodsburg Crevice. Therefore, only about half of the mammals identified from this deposit still inhabit the general vicinity of the site.

The collection of faunal remains from Harrodsburg Crevice is presently housed in the Zooarchaeology Section, Department of Anthropology, University of Tennessee, Knoxville.

CLASS MAMMALIA

ORDER INSECTIVORA

Family Talpidae

Parascalops breweri (Bachman)—Hairy-tailed Mole

Material: Paired humeri, right radius. MNI (Minimum Number of Individuals): 1.

Remarks: There is some uncertainty as to whether or not the hairy-tailed mole is a recent inhabitant of Indiana. Lyon (1936) includes it in his *Mammals of Indiana* only on the basis of the hypothetical lists presented by Evermann and Butler (1894) and by Hahn (1909); two extant specimens in the Indiana University collections were labeled as having come from Bloomington. Mumford (1966) makes no mention of it, and Hall and Kelson (1959) apparently did not accept these hypothetical Indiana records, because their distribution map (Vol. 1, p. 71) includes east Tennessee, eastern Kentucky and central Ohio as the western limits of its range.

Parmalee, Oesch, and Guilday (1969) identified 63 elements (MNI-15) of *P. breweri* in an extensive Pleistocene faunal deposit recovered from Crankshaft Cave, Jefferson County, Missouri. They suggested that the former geographic range of this mole probably extended westward across the northern edge of Lake Superior and southward along the Mississippi River. The Harrodsburg Crevice record definitely establishes the former occurrence of the hairy-tailed mole in south-central Indiana, but how widespread it was in the State or how far westward its range may have extended in late-Pleistocene times south of the Great Lakes remains uncertain.

ORDER RODENTIA

Family Sciuridae

Marmota monax (Linnaeus)—Woodchuck

Material: Distal ⅓ upper left incisor. MNI: 1.

Remarks: This rodent is common throughout Indiana today. Remains of woodchuck are often found in abundance in cave and rock shelter sites, so it is surprising that bones of this burrowing species were not more numerous in the deposit.

Family Cricetidae

Neotoma cf. *floridana* (Ord)—Wood Rat

Material: 1 skull (embedded in travertine), 66 isolated molars, distal ½ humerus. MNI: 12.

Remarks: Lyon (1936) states that "Cave Rats [wood rats] are found in Indiana in small limestone caves or crevices in the cliffs along the Ohio River or its tributaries in Harrison County, and probably adjoining counties." The recovery of approximately 70 remains, mostly isolated molars, of *Neotoma floridana* in the Harrodsburg Crevice deposit establishes a former (late Pleistocene?) population of this rat approximately 100 mi north of its present restricted range in Indiana. Elements of the wood rat have been reported from caves in Missouri (Parmalee and Jacobson, 1959; Parmalee, 1967) which are situated considerably north of the animal's present range. It has been suggested that extreme periods of climatic fluctuation during the late Wisconsinan glaciation exterminated these northern populations and that the animal failed to re-establish itself in these former locales.

Based on the Harrodsburg Crevice record, a similar situation may have taken place in Indiana. The southernmost portion of the Wisconsinan glacial boundary lies immediately north of Monroe County, and glacial advances would have brought boreal conditions here. There appears to have been a contig-

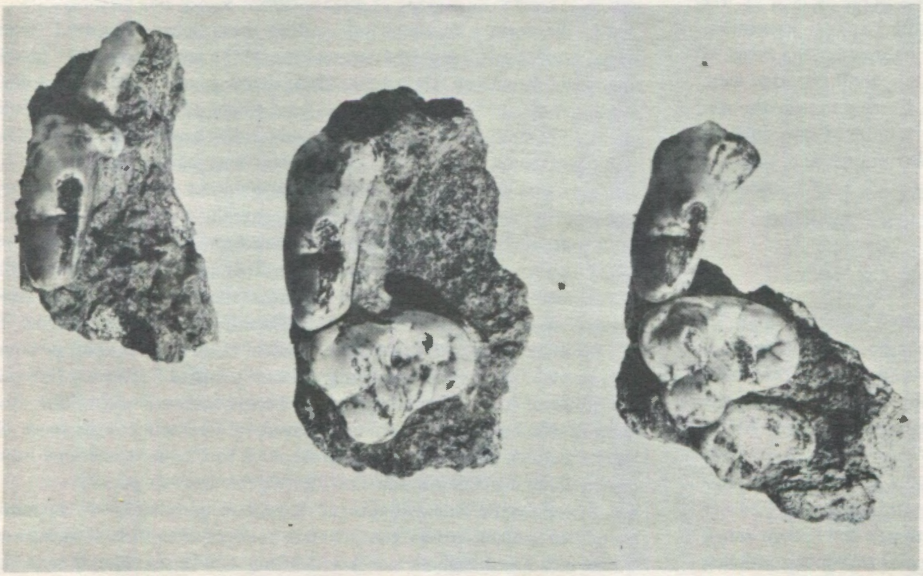

Figure 2. Partial right maxillae of *Canis* cf. *dirus* with premolars/molars embedded in travertine, from Harrodsburg Crevice, Monroe County, Indiana.

uous population of wood rats from the Harrodsburg Crevice locale to the Ohio River bluffs; the numerous caves and escarpments between these two points would have provided suitable habitat. The discovery of wood rat nests and/or remains in five Monroe County caves and in caves in all counties between Monroe and Ohio River (Richards, 1972) tend to bear this out.

Microtus (*Pedomys*) cf. *ochrogaster* (Wagner)—Prairie Vole
Material: 4 right, 2 left lower M_1's. MNI: 5.

Microtus sp.—Vole
Material: 10 isolated fragmentary cheek teeth.
Remarks: All lower first molars had a crown pattern consisting of a posterior crescent, three alternating triangles and an anterior dentine field consisting of confluent triangles 4 and 5 broadly confluent to the anterior trefoil. The enamel is relatively thinner on the posterior walls of the salient angles than on the anterior. The 3rd buccal and 4th lingual re-entrants are broadly open and relatively shallow. The 4th buccal and 5th lingual re-entrants vary from barely suggested without cementum in two specimens, shallow but pronounced with cementum in the 4th buccal re-entrant in three specimens, and extremely well developed with cementum in both the 4th buccal and 5th lingual re-entrants in one specimen. They were compared directly with modern specimens of *M. ochrogaster* from Illinois and referred dentitions of Irvingtonian *M. llanensis* from the Conard Fissure, Arkansas. They appear to resemble *M. ochrogaster* most closely. The two species, however, are believed to be on the same phyletic line in a slow conservative progression in M^1 morphology, so that a positive identification of these few specimens is tentative. As a series, they appear to be more advanced than *M. llanensis* and, on that basis, the Harrodsburg local fauna postdates the Conard Fissure local fauna.

Because of their small size and shallow burrowing activities, voles and lemmings could have easily traversed small vertical cracks or fissures which may have remained open for some time before the main deposit was sealed permanently.

Synaptomys cooperi Baird—Southern Bog Lemming
Material: 1 right M^2, 1 left M_3, 2 upper incisor fragments. MNI: 2.
Remarks: Specimens of the southern bog lemming have been collected in both northern and southern Indiana counties, including Monroe County (Lyon, 1936), but populations, although sometimes dense, are often localized. This bog lemming may inhabit relatively dry upland prairie areas as well as wet lowlands comprised of sedges and other herbaceous vegetation. It is, therefore, difficult to imply local habitat on the basis of remains of only two individuals. Although small cricetids were poorly represented in the Harrodsburg Crevice fauna, the absence of remains of any typically northern boreal forms such as the northern bog lemming (*S. borealis*) suggests a possibly warmer interstadial period during the period of crevice fill and/or occupation.

Family Geomyidae

Geomys cf. *bursarius* (Shaw)—Plains Pocket Gopher
Material: 8 isolated cheek teeth, 10 isolated incisors. MNI: 3.
Remarks: Lyon (1936) records the plains pocket gopher from Newton, Jasper, and Tippecanoe counties in northwestern Indiana. Kirkpatrick and Conaway (1948) mention sight records of "gopher activity" in Warren and Benton counties. All of these counties are north or west of the Wabash River. Identification of the Harrodsburg Crevice specimens is necessarily tentative. Assuming that the individuals represented are *Geomys busarius*, this Monroe County record extends the known range of these fossorial rodents approximately 100 mi south-southeast of their present range in Indiana. The occurrence of pocket gophers in the unglaciated or "knob" area of south-central Indiana is noteworthy in light of their typical habitat in the Midwest, one consisting of flat or gently rolling grassland. Their former presence at or in the vicinity of Harrodsburg Crevice is indicative of an open, short grass prairie.

ORDER LAGOMORPHA

Family Leporidae

Sylvilagus and/or *Lepus*—Cottontail? and/or Snowshoe Hare?
Material: 98 isolated molars; 30 isolated incisors; fragments of 4 jaws, 2 maxillae, 2 ulnae, 5 humeri, 4 tibiae, 2 calcanea, 1 astragalus. MNI: 8.
Remarks: None of the lagomorph remains from Harrodsburg Crevice was specifically diagnostic. Although the former occurrence of snowshoe hare (*Lepus americanus*) at the northern edge of the unglaciated region of south-central Indiana is possible, the absence of any identified boreal species from the deposit suggests that the possibility of snowshoe hare in the Harrodsburg local fauna is minimal. The eastern cottontail (*Sylvilagus floridanus*) is a common mammal throughout the State. Since the lagomorph remains occur with those of grassland or short grass prairie forms, such as the prairie vole and pocket gopher, a greater probability exists that the recovered rabbit remains are *Sylvilagus* rather than *Lepus americanus*.

ORDER CARNIVORA

Family Canidae

Canis cf. *dirus* Leidy—Dire Wolf
Material: Four maxillae sections embedded in travertine: (1) right P^4, M^1; (2) right $P^{3\text{-}4}$; (3) right P^4, $M^{1\text{-}2}$; (4) left M^1 (Fig. 2). Isolated teeth including 5 canines; 2 left, 3 right I_3's; 6 left, 1 right P^1's; 1 left P^2; 2 right, 1 left P^3's; 2 right, 1 left P_3's; 4 right P^4's; 4 left, 1 right P_4's; 6 left, 2 right M_1's; 1 left, 2 right M^1's; 1 left, 2 right M_2's; 2 left, 3 right M^2's. 1 left astragalus, proximal (semi-lunar notch) section right ulna, proximal section left humerus. MNI: 6.

Canis sp.: *C. dirus*? Indet. *Canis*—Dire Wolf? Indet. Wolf sp.?
Material: 10 scapholunar, 6 cuboid, 6 navicular, 5 unciform, 4 trapezium, 7 cuneiform, 1 left calcaneum, 2 patellae, and sections (majority of elements/teeth broken) of 51 metatarsals/metacarpals, 58 phalanx I, 57 phalanx II, 49 phalanx III, 2 calcanea, 3 astragali, 4 proximal humeri, 2 proximal scapulae, 4 distal/4 proximal ulnae, 2 proximal femora, 2 proximal/2 distal tibiae, 1 proximal/2 distal radii, 15 canines, 14 incisors, 15 premolars (1-3), 7 molars. MNI: 6.
Remarks: Remains of wolves have been reported from numerous Late Pleistocene cave and rock shelter sites in the Midwest (*e.g.* Galbreath, 1964; Guilday, *et al.*, 1971; Hawksley, *et al.*, 1973), and elsewhere from Rancho La Brea in California to Cumberland Cave, Maryland (Gidley and Gazin, 1938). The common extinct species of the late Pleistocene was the dire wolf, *Canis dirus*, a canid osteologically similar to the contemporary gray wolf but characterized by generally heavier limb elements and larger and more massive dentition. The type specimen of dire wolf, *Canis* (= *Aenocyon*) *dirus* (Leidy), a right maxilla section with $P^{2\text{-}4}$, M^2, was found at the mouth of Pigeon Creek below Evansville, Vanderburg County, Indiana. It occurred in association with remains of Pleistocene forms such as *Megalonyx* and *Tapirus* and represented the only find of *C. dirus* in Indiana prior to the Harrodsburg Crevice specimens. Bones of the dire wolf have also been encountered in association with those of extinct peccaries (*Platygonus*), and this large canid may have been a major predator of these herbivores.

Specific determination of the *Canis* material from Harrodsburg Crevice was complicated because of a lack of complete skull and limb elements which might have provided diagnostic

TABLE 2. Tooth measurements (mm) of *Canis* cf. *dirus* from Harrodsburg Crevice specimens compared with those from 4 Missouri caves, Welsh Cave, Kentucky and Guy Wilson Cave, Tennessee.

Measurement	Harrodsburg, Indiana N	O.R.	$\overline{X}$	Missouri caves (Hawksley, *et al.*, 1973) $\overline{X}$	Guy Wilson Cave, Sullivan Co., Tenn. (Unpub. record) (1 specimen)	Welsh Cave, Ky. (Guilday, *et al.* 1971) CM 12625
P^3, length	5	15.8-18.9	17.4	18.7	17.7	18.3
P^3, width	5	6.3-8.7	7.3	8.5	7.3	8.3
P^4, length	6	26.3-29.3	28.0	32.1	30.0	30.8
P^4, width	4	12.7-15.3	13.7	13.5	13.6	16.2-15.4 (14.2-14.1)
M^1, length	5	18.6-19.0	18.8	19.9	18.7	20.6
M^1, width	4	24.8-25.6	25.3	25.9	24.7	27.3
M^2, length	7	10.0-11.9	10.7	11.5	10.7	10.9
M^2, width	7	13.4-17.2	15.5	16.1	16.1	15.5
P_1, length	7	8.1-9.2	8.5	7.2	8.0	—
P_1, width	7	4.9-5.6	5.2	—	5.5	—
P_3, length	2	14.7.15.4	15.1	16.6	18.0	—
P_3, width	2	6.9-7.0	7.0	—	8.3	—
P_4, length	1	17.5	—	19.4	19.9	19.6
P_4, width	1	8.2	—	—	10.3	9.9
M_1, length	2	31.9-34.0	33.0	35.9	39.0	36.8
M_1, width	5	11.5-13.2	12.3	14.2	14.5	13.5
M_2, length	2	12.9-13.5	13.2	14.4	—	—
M_2, width	2	9.0-9.9	9.5	11.2	—	—

measurements. Consequently, the identification of some of the canid material as *C. dirus* is based primarily on measurements of isolated teeth from at least six individuals (Table 2). It may be noted that the Means ($\bar{x}$) for the Harrodsburg Crevice premolars and molars tend to be slightly less than those computed for specimens of *C. dirus* from Missouri, Tennessee, and Kentucky.

Nine partial skulls and 17 complete or partial lower jaws, plus a few isolated limb and foot elements of wolves recovered in Cumberland Cave, Maryland, were described by Gidley and Gazin (1938) as *Canis armbrusteri*. Gidley and Gazin (1938) pointed out slight variation in cusp patterns which they felt distinguishes this species from the "more robust" *C. dirus*. Hawksley, *et al.* (1973), after reviewing a large sample of *C. dirus* material (177 elements; MNI: 6) from Bat Cave and other sites in Missouri, concluded that dire wolves—taking into account size differences between males and females—from Missouri are consistently larger than those from Rancho La Brea and other locales in the West (Texas) and South (Arkansas). The massive size of several carnassials and other molar teeth in the Harrodsburg Crevice sample are equal to those of the Guy Wilson Cave individual (unpublished Sullivan Co., Tenn., record; Univ. Tenn. Coll., Knoxville) and some of the Missouri specimens of *C. dirus*. On the other hand some teeth and postcranial elements (fragments of limb bones, metapodials, carpals) are equal in size to those of the modern gray wolf (*Canis lupus*). Length/width measurements of five right M^1's of wolves from Harrodsburg Crevice have been plotted with those of three Pleistocene wolf "species" and *C. lupus* (Fig. 3). The M^1's from the Harrodsburg Crevice sample fall well above the Mean of *C. lupus*, but within its upper limits; they agree with *C. armbrusteri* and the one Rancho La Brea specimen of *C. dirus* plotted, but below other eastern *C. dirus*. On the basis of dentition, the dire wolf is represented in the Harrodsburg Crevice assemblage, but another, somewhat smaller Pleistocene wolf may also be represented.

Canis sp.: *C. latrans* Say—Coyote?

Material: 1 right M^2, 1 partial left M^1. MNI: 2.

Remarks: Two teeth, a portion (hypocone/protocone/metaconule) of a left M^1 and a complete right M^2 approximate closely the size and general cusp pattern of *Canis latrans*. Both the gray wolf and coyote were once found throughout most of Indiana; the wolf is now extirpated in the state, although the coyote still occurs in varying numbers, mostly in the unglaciated regions. Lyon (1936) mentions that "A few bones referable to Coyote have been found in Boone County [central Indiana] in association with remains of a mammoth. Hay (1912) thinks the animal in question lived after the passing of the last glacial ice." These two molars (two individuals) from the Harrodsburg Crevice deposit were the only canid remains which could be referred to as *C.* cf. *latrans* with any degree of certainty.

cf. *Urocyon cinereoargenteus* (Schreber)—Gray Fox

Material: 1 right maxilla, embedded in travertine, containing M^1, M^2. Isolated teeth including 1 right, 1 left P^4; 3 right, 2 left M^1's; 1 right, 1 left M_1; 2 right M^2's; 2 right, 1 left M_2's. MNI: 4.

Urocyon?, *Vulpes*?—Fox

Material: 1 cuboid, fragmented sections of 2 distal tibiae, 2 distal radii, 1 distal and 1 proximal humerus, 1 distal femur, 1 astragalus, 2 innominates, 1 atlas. MNI: 2.

Remarks: The gray fox has been reported from every county in Indiana and in timbered areas it is fairly numerous. Isolated fourth premolars and molars from the deposit compared closely in size and cusp pattern with a series of seven modern specimens of *U. cinereoargenteus* from Illinois and Tennessee (Table 3), especially with those of a large adult male from Illinois. Post-

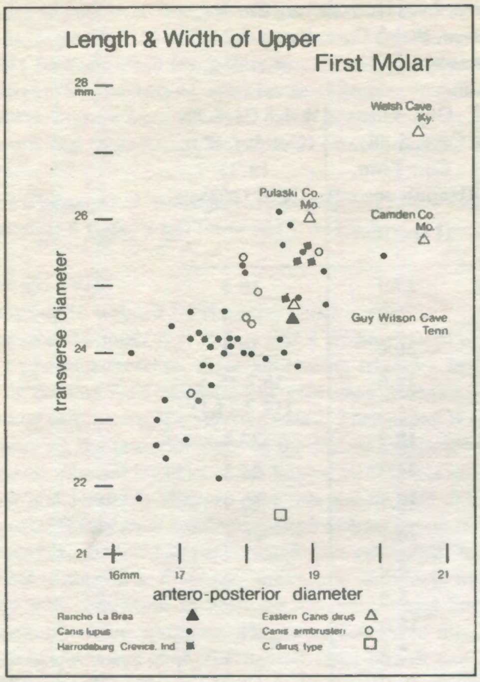

Figure 3. Length/width of upper first molar *Canis armbrusteri* (pre-Wisconsinan), from Gidley and Gazin, 1938. *C. dirus* (Wisconsinan): Rancho La Brea, California, CM3995; Welsh Cave, Kentucky, CM 12625; Pulaski and Camden counties, Missouri, Hawksley, *et al.*, 1963. *C. dirus* Leidy, Type, Pigeon Creek, Indiana, ANS 11614, from Merriam, 1938. *C.* cf. *dirus*, Harrodsburg Crevice, Indiana. *C. lupus* (modern), from Young and Goldman, 1944.

cranial elements, on the other hand, were too fragmentary for identification.

Family Ursidae

Ursus cf. *americanus* Pallas—Black Bear

Material: Isolated teeth including 1 right, 1 left C; 1 left M^1; 2 left, 1 right M^2's; 2 left, 2 right M_1's; 4 left, 3 right M_2's; 1 right M_3. 1 navicular plus sections of a distal right radius, 1 right proximal humerus (lateral tuberosity), 1 right calcaneum, 3 carpals, 8 phalanx I, 4 phalanx II, 6 phalanx III, 5 distal phalanx, MNI: 5.

Remarks: Approximately 50 elements, primarily isolated teeth and foot bones were determined as *Ursus*. Lengths and widths of molars are presented in Table 4. Cusp patterns of the Harrodsburg Crevice ursids are similar to those of the modern black bear and all of the individuals represented are well within the size range of *U. americanus*, based on tooth measurements. Judging by the lack of cusp wear, at least four of the bears were probably young adults.

Family Mustelidae

Mustela Linnaeus, ? species—Weasel

Material: 1 incomplete lower right jaw. MNI: 1.

Remarks: Although this partial jaw is within the size range of the long-tailed weasel, *Mustela frenata*, the only weasel known to occur in the vicinity of Harrodsburg Crevice today, the loss of teeth and its fragmentary condition makes species identification impossible.

Mephitis mephitis (Schreber)—Striped Skunk

Material: 2 right, 1 left proximal ulnae. Isolated teeth including 2 P^2's; 1 right, 1 left P^3; 5 left, 2 right M^1; 1 right, 1 left M_1; 6 M_2's. MNI: 5.

TABLE 3. Dentition measurements of *Urocyon* cf. *cinereoargenteus* from Harrodsburg Crevice, Indiana compared with specimens from Illinois and Tennessee (UTK Anthropology Dept. Coll.)

	Harrodsburg Crevice			Modern Gray Fox; 7 Specimens, Ill. and Tenn.		
Measurement	N	O.R.	$\bar{X}$	N	O.R.	$\bar{X}$
M^1, length	4	8.8-10.2	9.6	14	8.5-9.9	8.9
M^1, width	4	11.8-12.7	12.3	14	10.1-12.3	11.4
M^2, length	1	6.5	—	14	5.5-7.3	6.0
M^2, width	1	9.2	—	14	7.6-10.4	8.5
M_2, length	3	7.4-7.6	7.5	14	6.7-8.1	7.0
M_2, width	3	5.4-6.2	5.8	14	5.0-5.8	5.2

TABLE 4. Dentition measurements of *Ursus* cf. *americanus* from Harrodsburg Crevice, Indiana compared with specimens from Tennessee (Coll. UTK, Forestry/Wildl. Mgt. Dept.)

	Harrodsburg Crevice			Modern Black Bears 6 males, East Tennessee		
Measurement	N	O.R.	$\bar{X}$	N	O.R.	$\bar{X}$
M^1, length	1	17.7	—	6	17.5-20.4	19.0
M^1, width	1	13.2	—	6	13.7-14.7	14.1
M_1, length	4	18.3-19.1	18.63	6	18.4-20.4	19.4
M_1, width	4	8.3-8.9	8.60	6	9.3-10.5	9.7
M_2, length	5	18.0-20.0	19.10	6	20.5-22.7	21.3
M_2, width	5	10.5-11.6	11.34	6	11.9-14.1	12.9
M_3, length	1	14.4	—	6	14.9-17.2	16.2
M_3, width	1	11.0	—	6	11.6-13.5	12.4

Remarks: The striped skunk has been recorded from every county in Indiana (Lyon 1936) and, in the less populated regions, it is common in both farm land and forested areas. Of the three species of mustelids represented in the deposit, remains of the striped skunk were the most numerous (about 22) and represented at least five individuals. Skunks, because of their awkward gait and ground-foraging habits, have a propensity for blundering into open wells, excavations, and cave fissures as evidenced by the abundance of their remains in numerous cave faunal assemblages (*e.g.* Parmalee, 1967).

Spilogale cf. *putorius* (Linnaeus)—Spotted Skunk

Material: Distal end of a left humerus. MNI: 1.

Remarks: There is apparently no evidence for the presence of spotted skunk in Indiana during historic times. The former occurrence of this mustelid is based on osteological remains from caves located in the southern and south-central regions of the state. Richards (1972) records elements of *Spilogale* from cave sites in Monroe, Lawrence, and Harrison counties ("knob" area) and comments that it had "...an ancient northerly distribution, much as *Neotoma*. This *Neotoma-Ursus-Erethizon-Spilogale* component commonly occurs together, and can be used locally to recognize a prehistoric fauna." Although only a single element of the spotted skunk was recovered in the Harrodsburg Crevice deposit, it does establish this mustelid as a member of probably the earliest known Pleistocene faunal assemblage in Indiana.

Family Felidae

Lynx cf. *rufus* (Schreber)—Bobcat

Material: Incomplete lower left jaw with C, P_{3-4}, M_1; section of lower right jaw with M_1. 1 scapholunar, 2 navicular, 1 digit I, 2 phalanx II, 2 metacarpal I, 3 distal phalanx. Isolated teeth including 2 left P^4's; 2 left, 1 right P_4's; 2 right, 1 left M_1's. Fragmented sections of 1 left calcaneum, 1 right astragalus, distal end (medial condyle) right femur, right innominate (acetabulum/ilium), proximal right scapula, proximal diaphysis right radius, proximal diaphysis and distal end left ulna, 2 metatarsals. MNI: 3.

Remarks: Lyon (1936) states that "There are no entirely satisfactory records of the occurrence of the Canada Lynx in Indiana, none based on specimens or even measurements of killed animals." Some of the early State records for Canada lynx may be due to confusing common names (wildcat, bobcat, Bay-lynx, Catamount). However, statements by some of the early naturalists traveling through northern and central Indiana make specific mention of the Canada lynx and, on the basis of these accounts, Lyon (1936) concludes that "It seems reasonable to assume that some of these numerous reports must truly refer to the Canada Lynx,..." Hall and Kelson (1959) accept a reported specimen from Knox County (southwestern Indiana) as a marginal record for *Lynx canadensis* and include all of Indiana except the southernmost border as part of its former range.

Three or possibly four Canada lynx and/or bobcats are represented in the Harrodsburg Crevice deposit by approximately 30 elements. Both cats are inhabitants of densely forested areas, although the Canada lynx is found today primarily in the northern boreal coniferous forests. Major changes took place in plant communities bordering and for some distance south of the ice sheets (Engle, 1975), but the extent and durations of these changes in the unglaciated regions of Indiana are unknown. The periodic establishment of boreal communities in these periglacial areas has been established by the recovery of remains of environmentally diagnostic small mammals in late Pleistocene cave deposits (*e.g.* Guilday, 1963; Guilday and Parmalee, 1972). However, the former occurrence of larger, strictly boreal species such as the Canada lynx in periglacial areas in the Midwest has not been established. Although the *Lynx* remains from Harrodsburg Crevice could conceivably be those of *L. canadensis*, the uncertainty of its former presence in Indiana, the absence of other boreal forms in the deposit, and the former occurrence of the bobcat throughout the region suggests the remains are probably those of *L. rufus*.

Smilodon cf. *floridanus* (Leidy)—Sabertooth Cat

Material: Partial left lower jaw with deciduous M_4. MNI: 1.

Remarks: Sabertooth cats are best known from the quantity of remains recovered from the tar pits at Rancho La Brea, California. In the Midwest, isolated elements have been reported from two localities, one in Missouri (Crevice Cave: Oesch, 1969) and one in Arkansas (Conard Fissure: Brown, 1908). Until the recent discovery of an adult specimen in Nashville, Tennessee (First American Bank Site: Guilday, 1977), the only known locales of *Smilodon* east of the Mississippi River were those from Florida (Kurtén, 1965) and Port Kennedy Cave, Pa. (Cope, 1899). The recovery of a lower right jaw fragment of Sabertooth Cat containing a fully erupted but unworn deciduous M_4 from Harrodsburg Crevice is especially noteworthy. This is the first record of *Smilodon* from Indiana, and it extends considerably the known range of sabertooth cats in eastern North America. Harrodsburg Crevice is approximately 200 mi northeast of Crevice Cave (Perry County, Missouri) and 200 mi north of the First American Bank site, Nashville, Tennessee.

Merriam and Stock (1932) provide tooth measurements of seven juvenile individuals of *Smilodon* from Rancho La Brea; the Observed Range of the deciduous M_4 length-width was 16.3-19.4 mm x 6.5-8.9 mm. The Harrodsburg Crevice specimen measured 17.1 mm x 7.0 mm, well within the range of *Smilodon floridanus*. Kurtén (1965) found that the size of *Smilodon* gradually increased during the Middle and Late Pleistocene but, unfortunately, on the basis of only one deciduous molar from the Harrodsburg Crevice no information can be derived relative to the actual size of adults which once occupied this region of south-central Indiana.

Panthera onca augusta (Leidy)—Jaguar

Material: Incomplete lower right jaw with C, P_4 and M_1; isolated right P_4. MNI: 2.

Remarks: Guilday and McGinnis (1972) summarized the finds of jaguar remains from cave sites in east-central North America. They agree with the view expressed by Simpson (1941) and Kurtén (1965) that this Pleistocene jaguar was "... an extinct, especially robust, subspecies of the modern jaguar, *Panthera onca*." Seven of the 10 specimens considered by Guilday and McGinnis (1972) were recovered in Central and East Tennessee caves and were probably a part of the late Pleistocene faunal assemblage of that region. The two most northeastern locales from which remains of these extinct jaguars were recovered are Port Kennedy Cave, Pennsylvania and Cumberland Cave, Maryland, both of which are probably pre-Wisconsinan in age. "An age range of 35,000 years BP to 10,000 years BP is tentatively suggested for the Tennessee jaguars" (Guilday and McGinnis, 1972).

At least two adult individuals were represented in the Harrodsburg Crevice fauna, one on the basis of an isolated unworn right P_4 and the other on a partial right jaw containing the canine, P_4 and M_1 (Fig. 4). In addition, an abraded right proximal humerus section, two cuboids, 16 2nd and 3rd digits and several carpals are also referred to *P. o. augusta*. Measurements of the teeth of these two individuals are presented in Table 5 and are compared with those recorded by Guilday and McGinnis (1972) for four Tennessee jaguars. Except for a slightly shorter P_4 length, which may simply be individual variation, the Indiana jaguars are comparable in size, based on these four teeth measurements, to the four specimens from Tennessee. Recovery of *P. o. augusta* remains from the Harrodsburg Crevice deposit represents the first record of this Pleistocene felid for Indiana and establishes its former occurrence in the Midwest some 200 mi north-northwest of the Cumberland Plateau in Tennessee.

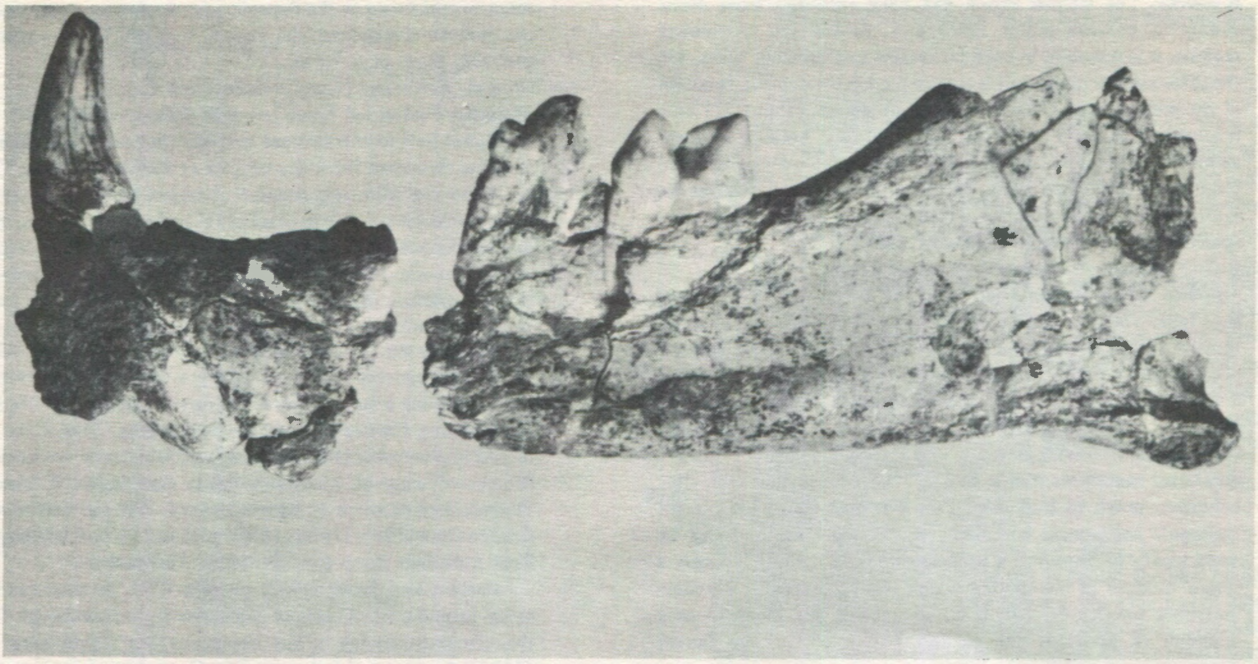

Figure 4. Lingual view of lower jaw of *Panthera onca augusta* with $\overline{C}$, P_4, M_1, Harrodsburg Crevice, Indiana.

TABLE 5. Tooth measurements (mm) of *Panthera onca augusta* from Harrodsburg Crevice, Indiana compared with those from three Tennessee caves.

Measurement	Indiana (Harrodsburg Crevice) Isolated Right P_4	Right Jaw w/C,P_4,M_1	Tennessee (Guilday & McGinnis 1972) Caves* CH-1	LA-1	LA-2	BBC
C, ant.-post. diameter		22.2	26.0	18.9	20.3	20.8
C, transverse diameter		~ 14.6	22.0	17.1	15.8	15.0
P_4, length	20.4	~ 20.0	24.7	—	21.9	21.9
P_4, width	10.7	~ 10.2	12.4	—	10.4	10.1
M_1, length		23.6	24.6	22.0	21.0	19.8
M_1, width		11.6	12.7	11.8	11.8	—

*CH-1: Craighead Caverns; LA-1&2: Little Airplane Cave; BBC: Big Bone Cave

ORDER PERISSODACTYLA

Family Equidae

Equus sp.: *Equus* cf. *complicatus* Leidy—Horse

Material: Isolated left P^3. MNI: 1.

Remarks: A horse was represented in the Harrodsburg Crevice fauna by a left P^3. This tooth was identified by Dr. William D. Turnbull, Curator, Fossil Mammals, Field Museum of Natural History, Chicago, as *Equus* cf. *complicatus*. Hay (1923) records a last cervical vertebra of *Equus* recovered near Evansville, Vanderburg County, which was tentatively identified by Leidy as *E. complicatus*; Lyon (1931) refers to another find of Pleistocene horse (2 molars) from La Porte County in northwestern Indiana. Martin and Guilday (1967) comment that numerous species of fossil horses have been described from the late Pleistocene of North America and that their remains are among the most common of Pleistocene fossils. However, deposits containing numerous remains of horse have been found primarily in western North America; although sites containing bones of *Equus* east of the Great Plains are not uncommon, the number of elements at each is small (*e.g.* Missouri sites, Mehl, 1962; Cumberland Cave, Gidley and Gazin, 1938; Wythe Co., Va., Guilday, 1962). This situation may reflect either fewer individuals in the forested regions of eastern North America or the physical restrictions limiting caves as entrapment and repository locales.

ORDER ARTIODACTYLA

Family Tayassuidae

Platygonus cf. *cumberlandensis* Gidley—Peccary

Material: Postcranial elements, most of which are incomplete or fragmentary: 1 right, 1 left scapula; 3 distal, 3 proximal humeri, 2 left proximal ulnae/radii; 1 left distal tibia; 2 innominates; 2 patellae; 2 left calcanea, 1 astragalus; 2 right distal fibulae; 14 metacarpals/metatarsals; 12 carpals; 8 tarsals; 26 phalanges. Teeth, skull/jaw elements (adults): 1 skull frontal section; 2 jaw condyles; partial paired jaws, left with P_2-M_1, M_3, right with P_3-M_3; isolated teeth including 22 premolars and 60 molars in addition to about 175 cheeck teeth fragments; 16 incisors; 26 canines. Teeth, skull/jaw elements (juveniles): left maxilla with P^3-M^2; left jaw with P_3-M_1; 34 isolated cheek teeth. MNI: 6 juveniles, 4 adults.

TABLE 6. Dentition measurements (mm) of *Platygonus* cf. *cumberlandensis* from Harrodsburg Crevice, Indiana and Cumberland Cave, Maryland

Measurement	Harrodsburg Crevice N	O.R.	$\bar{X}$	Cumberland Cave U.S.N.M. No. 8146	U.S.N.M. No. 8200
Permanent Dentition					
P^3, length	1	13.4	—	11.7	11
P^3, width	1	14.4	—	13.5	13.3
P^4, length	2	12.6-12.9	12.8	11.7	11.6
P^4, width	2	14.1-14.5	14.3	14.3	14
M^1, length	3	17.2-17.4	17.4	15.2	12.6
M^1, width	3	14.4-14.8	14.6	15	16
M^2, length	6	17.0-21.9	20.4	19.6	18
M^2, width	6	16.0-20.8	18.3	18	16
M^3, length	4	23.5-26.0	24.5	24.5	20.6
M^3, width	7	18.8-22.2	20.5	18.2	17
P_2, length	1	10.5	—	9.5	10
P_2, width	1	7.3	—	8	7.5
P_3, length	3	12.1-13.4	12.8	12.8	11.6
P_3, width	3	9.6-10.6	10.0	10	9
P_4, length	4	12.5-14.9	14.0	12.8	11.6
P_4, width	4	10.9-12.5	11.6	11.7	11.5
M_1, length	2	17.5-17.8	17.7	14	12.6
M_1, width	2	13.5-13.8	13.7	13	11.8
M_2, length	2	20.0-20.4	20.2	20	18
M_2, width	2	15.8-15.9	15.9	15.5	14
M_3, length	5	26.4-28.4	27.4	25.5	22.8
M_3, width	6	16.1-17.6	16.9	16	15
Deciduous Dentition					
P_4, length	3	11.9-12.2	12.0		
P_4, width	3	7.6-8.6	8.0		
M_1, length	1	21.1	—		
M_1, width	1	10.0	—		

Remarks: Approximately 425 teeth and bone sections of an extinct peccary *Platygonus* were recovered from the Harrodsburg deposit. Numerous carpals, a few tarsals and distal phalanges, and about 80 premolars and molars were removed intact (or were restorable), but no cranial elements or limb bones were complete enough to be measured. Specific identification is based, therefore, on the measurements of teeth presented in Table 6; dentition size compares closely with *P. cumberlandensis* from Cumberland Cave, Maryland (Gidley and Gazin, 1938).

Both *P. compressus* and *P. vetus* have been recorded from the Indiana Pleistocene. Lyon (1936), in referring to a specimen (portion of a left ramus) of *P. compressus* from Wabash County originally identified by Cope, states: "Hay (1912) failed to find the specimen. He reported what appeared to be photographs of this specimen and a part of an upper jaw in the collection of Earlham University." Remains of *P. vetus*, consisting of one complete and one partial upper right molar, were found in Rock Cliff quarry in Lawrence County. Guilday, Hamilton, and McCrady (1971) point out that there were, apparently, only two species in the Appalachian area, ". . . the smaller Wisconsinan and post-Wisconsinan form, *Platygonus compressus* Le Conte, comprising approximately 90% of the reported finds, and the larger *Platygonus cumberlandensis* (probably including *P. intermedius* and *P. vetus*). Judging from the accompanying fauna, *P. cumberlandensis* is pre-Wisconsinan and probably Illinoian in age."

Both juvenile and adult peccaries are represented in the Harrodsburg Crevice faunal assemblage. The question arises as to whether these animals used the cave for shelter or farrowing, or if they were prey species brought into the cave by carnivores such as dire wolf, jaguar, and sabertooth cat. The isolated or fragmentary condition of the majority of remains in this deposit offers little evidence of the method(s) of accumulation.

Family Cervidae

Odocoileus cf. *virginianus* (Zimmermann)—White-tailed Deer

Material: 1 right radial carpel, 1 left intermediate carpal. MNI: 1.

Remarks: Only two elements of a cervid were found in the deposit. These were carpals of a deer and, on the basis of the modern species of *Odocoileus* in Indiana, are tentatively identified as white-tailed deer.

DISCUSSION AND SUMMARY

The Harrodsburg Crevice faunal materials were found in a physically homogeneous deposit sealed by a thick deposit of travertine; it is assumed, therefore, that the animals represented were more or less contemporaries. At least 20 mammalian species were identified, five of which are extinct and an additional five of which are either extirpated in Indiana or no longer occur within the vicinity of the site. There are some apparent discrepancies in local habitat type, however, resulting from the presence of species inhabiting open, short grass areas (pocket gopher, prairie vole) as well as those generally associated with brushy or forested regions (bobcat, gray fox). However, an open prairie area bordering the wooded bluff of a creek would, for example, bring species with such diverse habitat requirements into close contact.

The absence of soricids from the crevice and the paucity of small rodents, often the best indicators of past habitat and climatic change, is unusual for a deposit of this type. Also, the severe breakage of nearly all bones and most of the teeth prevented a positive determination of several ecologically critical forms represented in the faunal sample. The non-extinct forms identified from the assemblage, however, are today found in habitats which are as warm as the area presently enjoys (woodchuck, pocket gopher, gray fox) or warmer (wood rat, spotted skunk); there is a complete absence of species presently confined to northern or boreal biomes.

The interpretation of relatively warm climatic conditions during the period of faunal deposition is also suggested by the geological nature of the deposit. The limestone detritus is superficially corroded, with rounded edges, and is thus indicative of corrosion-solution processes (as opposed to thermoclastic fracture); such processes are "only possible in temperate or warm climate with considerable precipitation" (Schmid, 1963). Furthermore, travertine formation occurs most rapidly under warm-moist conditions and little if any is formed under extremely cold and/or dry conditions (Butzer, 1971).

Although the Harrodsburg Crevice locale was south of the Wisconsinan ice-front, conditions in the area during the Woodfordian Stadial appear to have been quite cool. Wayne (1967) estimates the mean annual temperature to have been 32°F during the Woodfordian maximum (ca. 20,000 BP). Two pollen cores taken within 10 mi of Harrodsburg Crevice and apparently dating to this period are dominated by pollen of tundra-spruce parkland species (Engle, 1975). On the basis of recent investigations of macro-fossil plant materials from near Washington, Indiana, spruce-fir appear to have continued to be dominant as late as 14,010 ± 275 BP (DIC-234) at a latitude 22 mi south of Harrodsburg Crevice (Munson, unpublished data). Spruce still heavily dominated the arboreal pollen of Sunbeam Prairie Bog near the Indiana-Ohio border, at a latitude only 55 mi to the north, as late as 11,700 ± 250 BP (L-550c, Kapp and Gooding 1964a).

Since climatic conditions during the Woodfordian Stadial of the Wisconsinan were generally cool in this area, and since geological indications from Harrodsburg Crevice and the faunal complex correlate with relatively warm conditions, the age of the assemblage appears to be pre-Woodfordian. The radiocarbon age determination of 25,050 ± 660 PF, on the face of it, would seem to place the period of accumulation of the Harrodsburg Crevice fauna prior to the Woodfordian Stadial, at some point during the preceding Farmdalian Interstadial. This interstadial is considered to have an interval of substantial glacial withdrawal and, presumably, corresponding warming conditions (Frye, Willman, and Black 1965). It would have resulted in a biota different from that of the preceding (Altonian) and following (Woodfordian) glacial stades.

The question that arises, however, despite the seeming "fit" of these various lines of evidence, is whether conditions were sufficiently warm during the Farmdalian to support the faunal composition represented at Harrodsburg Crevice? Other lines of evidence suggest that they were not. Geological and palynological studies in southeastern Indiana, only 50 mi to the east and about the same latitude as Harrodsburg Crevice, indicate that all of the Wisconsinan interstadials were of short duration, did not have a succession to mesophytic forest, and were appreciably cooler than the present (Kapp and Gooding 1964b). In Illinois, Farmdalian "sediments and fauna indicate cool moist conditions" (Frye, Willman, and Black, 1965). The arboreal pollen of the Canton site in west-central Illinois (Voss, 1939), now considered to be a Farmdalian deposit (Kapp and Gooding, 1964b), is heavily dominated by spruce, fir, pine, and hemlock. A mid-Wisconsinan interstadial pollen spectrum from western Missouri indicates an open pine-parkland environment. The spectrum has some similarities with that of the modern pollen rain of southern Manitoba (King, 1973). Insect remains from deposits near Cleveland, Ohio, radiocarbon dated about 24,000 BP, suggest an environment cooler than at present, much like that of the modern northern timberline (Coope, 1968).

If a Farmdalian Interstadial correlation is rejected, or at least seriously questioned, on the basis of these data, an earlier and warmer-drier period is suggested. Consensus of opinion is that the Illinoian/Wisconsinan Interglacial (Sangamonian) is the only period in the "recent" past when conditions in the Midwest were as warm and dry as, or warmer and drier than, the Holocene (Kapp and Gooding, 1964b; Whitehead, 1965).

A Sangamonian temporal placement would not only agree with indications of drier, short grass prairie conditions (pocket gopher, prairie vole) and warmer conditions (wood rat, spotted skunk), but would also account for the presence of the large peccary, *Platygonus cumberlandensis*, which has previously been found only in Illinoian deposits. The presence of jaguars and sabertoothed cat does not detract from this position, since they range in time throughout the Pleistocene. Finds of the large Pleistocene dire wolf, however, have heretofore generally been considered late Wisconsinan in age.

Whatever the temporal placement of the assemblage (Wisconsinan, Sangamonian, or Illinoian), the presence of sabertooth cat and jaguar remains in the Harrodsburg Crevice deposit represent the first records of these Pleistocene felids from Indiana. A former established population of an extinct wolf and large peccary in a section of the unglaciated "Knobs" region of south-central Indiana is evident from the number of their remains recovered.

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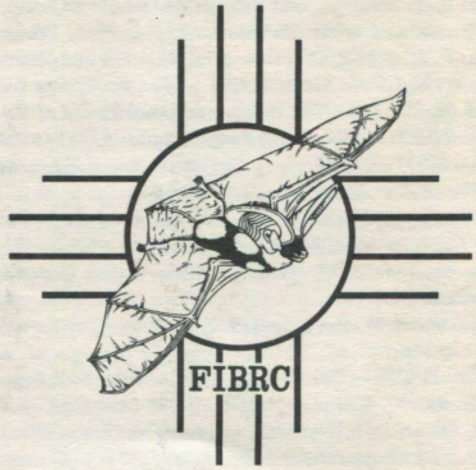

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