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Brimleyana, the Journal of the North Carolina State Museum of Natural Sciences, will appear at irregular intervals in consecutively numbered issues. Contents will emphasize zoology of the southeastern United States, especially North Carolina and adjacent areas. Geographic coverage will be limited to Alabama, Delaware, Florida, Georgia, Kentucky, Louisiana, Maryland, Mississippi, North Carolina, South Carolina, Tennessee, Virginia, and West Virginia.

Subject matter will focus on taxonomy and systematics, ecology, zoogeography, evolution, and behavior. Subdiscipline areas will include general invertebrate zoology, ichthyology, herpetology, ornithology, mammalogy, and paleontology. Papers will stress the results of original empirical field studies, but synthesizing reviews and papers of significant historical interest to southeastern zoology will be included.

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The Invertebrate Cave Fauna of Virginia and a Part of Eastern Tennessee: Zoogeography and Ecology

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ABSTRACT.— Collections of macroscopic invertebrate animals and ecological data were made from approximately 500 caves in the Appalachian Valley and Ridge province of Virginia and eastern Tennessee from 1961 to 1980. The study area comprised 26 counties in western Virginia and all or parts of seven counties in northeastern Tennessee. Approximately 335 species of invertebrates were recorded from the caves, including 140 troglobites (obligatory cavernicoles) and 61 troglophiles (facultative cavernicoles). The troglobites are numerically distributed as follows: flatworms (5), oligochaetes (3), snails (3), amphipods (20), isopods (15), pseudoscorpions (15), mites (2), spiders (8), centipedes (1), millipeds (9), collembolans (4), diplurans (6), and beetles (49). Basic ecological characteristics of cave species are considered, including habitats, trophic relationships, life histories, and species interactions.

Seven regional cave faunas, which coincide with major drainage basins, are recognized: (1) Shenandoah, (2) James, (3) Roanoke, (4) New, (5) Holston, (6) Clinch, and (7) Powell. Drainage basins that contain extensive exposures of cavernous limestone, such as the Clinch and Powell, have a greater diversity of cave-limited species than those with limited exposures of limestone. There is a strong linear relationship between cave species density and cave density, and an "area effect" exists among the endemic terrestrial troglobites. Aquatic troglobites are apparently derived both indirectly through ancestral lineages living in subterranean water prior to the present generation of caves and directly from surface ancestors. Terrestrial troglobites are apparently derived from preadapted surface ancestors living on cool, moist forest floors in the Appalachian Mountains. Invasion and colonization of caves by terrestrial organisms might have occurred in response to changing climates during the Pleistocene. Many troglobites are highly localized endemics that are restricted to only one or a few caves, whereas others have much broader ranges.

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Areas in the Appalachians of western Virginia and eastern Tennessee underlain by carbonate rocks contain numerous caves inhabited by an interesting diversity of cavernicolous organisms. The caves in these areas have been investigated extensively for many years, resulting in the accumulation of a significant body of information on many important aspects of biology, geology, and hydrology. Biologists have long been interested in the cave faunas of the Appalachian region. Probably one of the first biologists to visit caves in Virginia was E. D. Cope, who collected beetles and millipeds from caves in Giles and Montgomery counties (see Horn 1868, Cope 1869). A. S. Packard (1881, 1888) visited four caves in Virginia in 1874 and 1880 and collected specimens from Grand Caverns (then called Weyers Cave) and Fountain Cave (mistakenly called Madisons Cave by Packard) in Augusta County, Endless Caverns (then called New Market Cave) in Rockingham County, and Luray Caverns in Page County (see also Emerton 1875, Ryder 1881).

After a long lull, caves in the study area were visited in the 1920s and early 1930s by American biologists H. S. Barber (1928) and J. M. Valentine (1931, 1932) and by European biologists C. Bolivar and René Jeannel (see Berland 1931, Bolivar and Jeannel 1931, Chopard 1931, Jeannel 1931). In the late 1930s and early 1940s, specimens were collected from caves in the area by Kenneth Dearolf (1953; see also Loomis 1939), Leslie Hubricht (1943), J. P. E. Morrison (1949), and others (see Fowler 1942, 1943, 1944, 1946). In 1946, the French biologist Henri Henrot visited 11 caves in Virginia and four in northeastern Tennessee. He collected many specimens, some of which were subsequently described as new species (see Henrot 1949, Jeannel 1949, Vandel 1950, Bresson 1955). Bruno Condé, another French biologist, visited several caves in Virginia in 1956 (see Chappuis 1957). In 1958, T. C. Barr, Jr., visited 24 caves in Tennessee and 37 in Virginia and made many important biological collections (Barr 1959). The present study was initiated in 1961, when J. R. Holsinger began a detailed survey of the Virginia-West Virginia cave fauna (see Holsinger 1962, 1963a, 1963b, 1964). The survey was joined later by D. C. Culver, and in the early 1970s it was extended to include parts of eastern Tennessee. During our field work, which extended through 1980, collections of biological specimens and ecological observations were made in approximately 500 caves in Virginia and northeastern Tennessee.

In the present paper, we have prepared an annotated listing of all invertebrate species from caves in the study area (defined below), using the data collected during our field work and supplemented by information from the literature. We have also discussed observations on the ecology of cavernicolous species and presented a detailed zoogeographical analysis of the cave-limited fauna of the study area. Prevailing hypotheses on the ecology and zoogeography of invertebrate cave faunas are critically examined and tested against our data in an attempt to gain a better understanding of the factors that have influenced the present distribution of cave organisms in the study area. Because there have been very few detailed studies on the ecology or zoogeography of an entire regional cave fauna, this study should provide some interesting new insights in these areas.

The results of the present study will also complement previously published data on cave faunas of other areas in the eastern United States and will considerably update the data in earlier papers on the cave faunas of Tennessee by Barr (1961) and Virginia by Holsinger (1963a, 1964). The cave faunas of North America have been sampled extensively in recent years and, as a result, are becoming well documented. In the eastern United States, regional cave faunas have been analyzed to one extent or another in papers by Krekeler and Williams (1966) on Indiana, Barr (1967a) on Kentucky, Peck (1970) on Florida, Franz and Slifer (1971) on Maryland, Holsinger and Peck (1971) on Georgia, Holsinger (1976) on Pennsylvania, Holsinger et al. (1976) on West Virginia, Peck and Lewis (1978) on Illinois, and Hobbs (1981) and Hobbs and Flynn (1981) on Ohio.

THE STUDY AREA

As shown in Figure 1, the study area encompasses the 26 counties in western Virginia that contain cavernous limestones, and a part of eastern Tennessee. The Tennessee portion includes all of the lower Powell Valley (parts of Campbell, Claiborne, Hancock, and Union counties); that part of the Clinch Valley extending from the state line southwest to the confluence of the Clinch and Powell rivers (most of Hancock and Union counties and parts of Campbell, Grainger, and Hawkins counties); and the northern periphery of Hawkins and Sullivan counties, which lies just south of the state line in the Holston Valley. The study area covers parts of seven major drainage basins (Fig. 2), detailed discussions of which are included later under "Zoogeography."

GEOGRAPHIC AND GEOLOGIC RELATIONSHIPS

Excluding the limestone region of Florida, the major cave and karst areas of the eastern United States, east of Mississippi River, are developed in Paleozoic limestones of the Appalachian Valley and Ridge (or simply "Appalachian Valley"), Appalachian Plateau (or Alleghany Plateau of some authors), and Interior Low Plateaus physiographic provinces (see Fig. 3). Although the Appalachian Valley and Ridge and Appalachian Plateau provinces are usually assigned to a major physiographic division called the Appalachian Highlands, and the Interior Low Plateaus province is assigned to the Interior Plains division (see

Hunt 1967), the Interior Low Plateaus is sometimes referred to as "Appalachian" in the broad sense, because it is closely allied biologically and geologically with parts of the Appalachian Highlands. References in this paper to the "greater Appalachian region" include the Interior Low Plateaus.

For all intents and purposes, the study area as defined above lies within the Appalachian Valley and Ridge province. Only its western periphery in southwestern Virginia and east Tennessee encroaches on the eastern margin of the Appalachian Plateau, where cavernous limestones crop out along the flanks of Cumberland and Stone mountains. The Appalachian Valley is underlain by folded and faulted bedrock that varies in geological age from Lower Cambrian to Upper Mississippian, about half of which is limestone and dolomite. The total number of caves recorded from the study area through 1980 was 2611, including 2377 in Virginia and 234 in east Tennessee.

Limestones in the Appalachian Valley and Ridge province are exposed on valley floors and along the sides of low ridges and are generally restricted to long, linear strike belts. As a result, the principal orientation of most cave passages is along the regional strike (NE-SW), trending parallel to the valleys and ridges in which the caves occur. Strike-oriented belts of cavernous limestone are generally relatively narrow and separated from each other by intervening parallel exposures of non-carbonate, clastic rocks such as sandstones, shales, and quartzites. Karst topography is generally common on most limestone terranes but is usually much more prominent in valleys floored by broad exposures of Middle Cambrian and Middle Ordovician limestones (Holsinger 1975) (see Fig. 4). The overall drainage pattern is trellised, and, with the exception of a segment of the New River that flows north, most major streams flow roughly parallel to the strike (see Fig. 2).

South and southwest of the study area, the cave region of the Appalachian Valley and Ridge extends through eastern Tennessee into northwestern Georgia and northeastern Alabama. North and west of the study area, it extends through eastern West Virginia, west-central Maryland and across south-central Pennsylvania. The Appalachian Plateau is capped with resistant, non-carbonate clastics of Pennsylvanian age, but in several places, especially on its eastern and western sides, cavernous limestones are exposed. On the eastern side significant exposures of limestones occur in eastern New York (Helderberg Plateau), southwestern Pennsylvania, western Maryland, parts of eastern West Virginia, southeastern Kentucky (Pine Mountain), east-central Tennessee (Grassy Cove, Lookout, and Sequatchie valleys), northwestern Georgia (Lookout Valley), and northeastern Alabama (Lookout, Sequatchie, and Wills valleys). Barr (1981a) appropriately termed some of these disjunct limestone areas "karst islands" to call attention to their

Fig. 1. Outline map of the study area in western Virginia and northeastern Tennessee, showing counties and county seats.

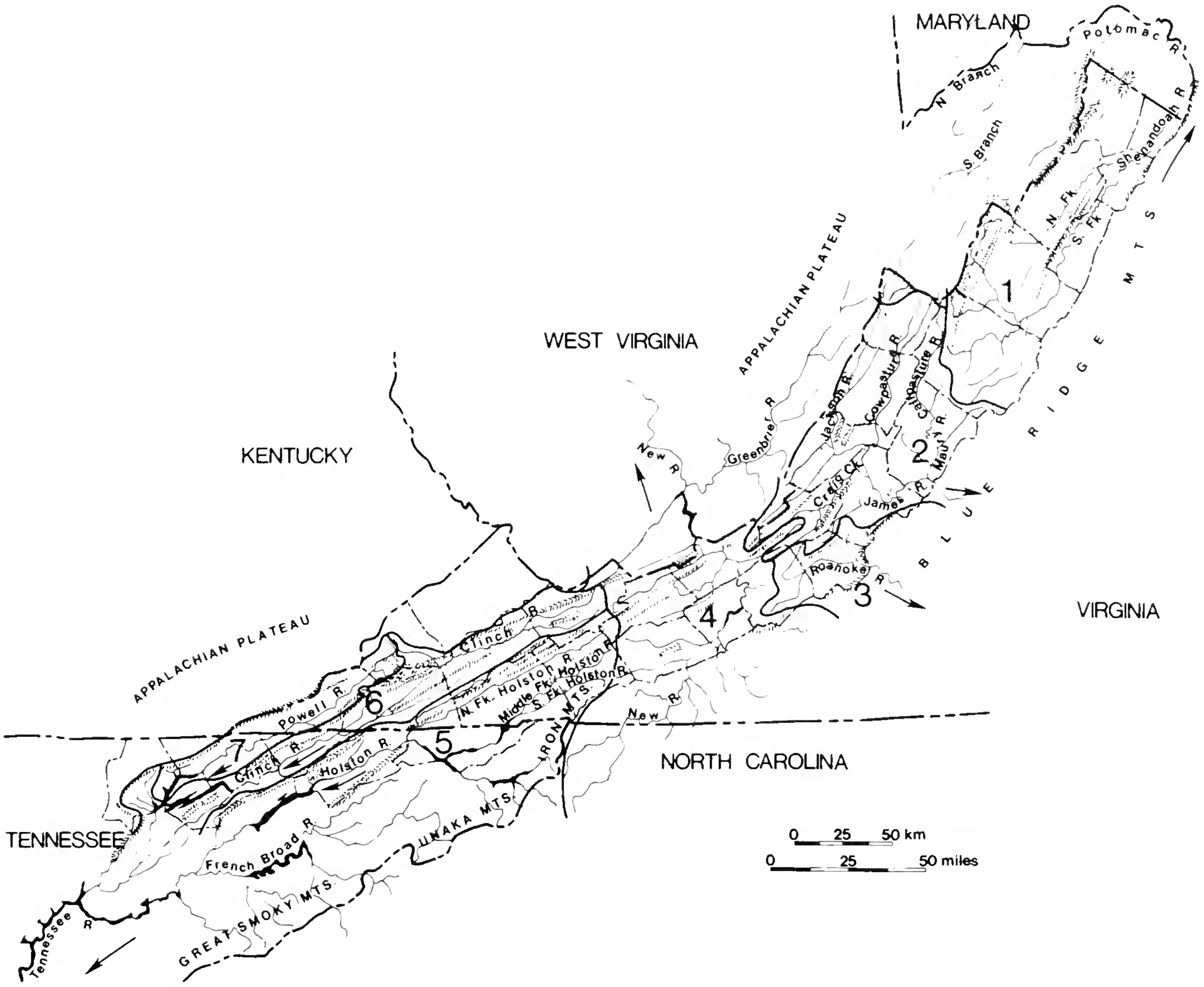


Fig. 2. Map of the study area showing major drainage basins as follows: 1, Shenandoah; 2, James; 3, Roanoke; 4, New; 5, Holston; 6, Clinch; 7, Powell. Arrows indicate direction of drainage. Principal mountains and ridges indicated by hachuring.

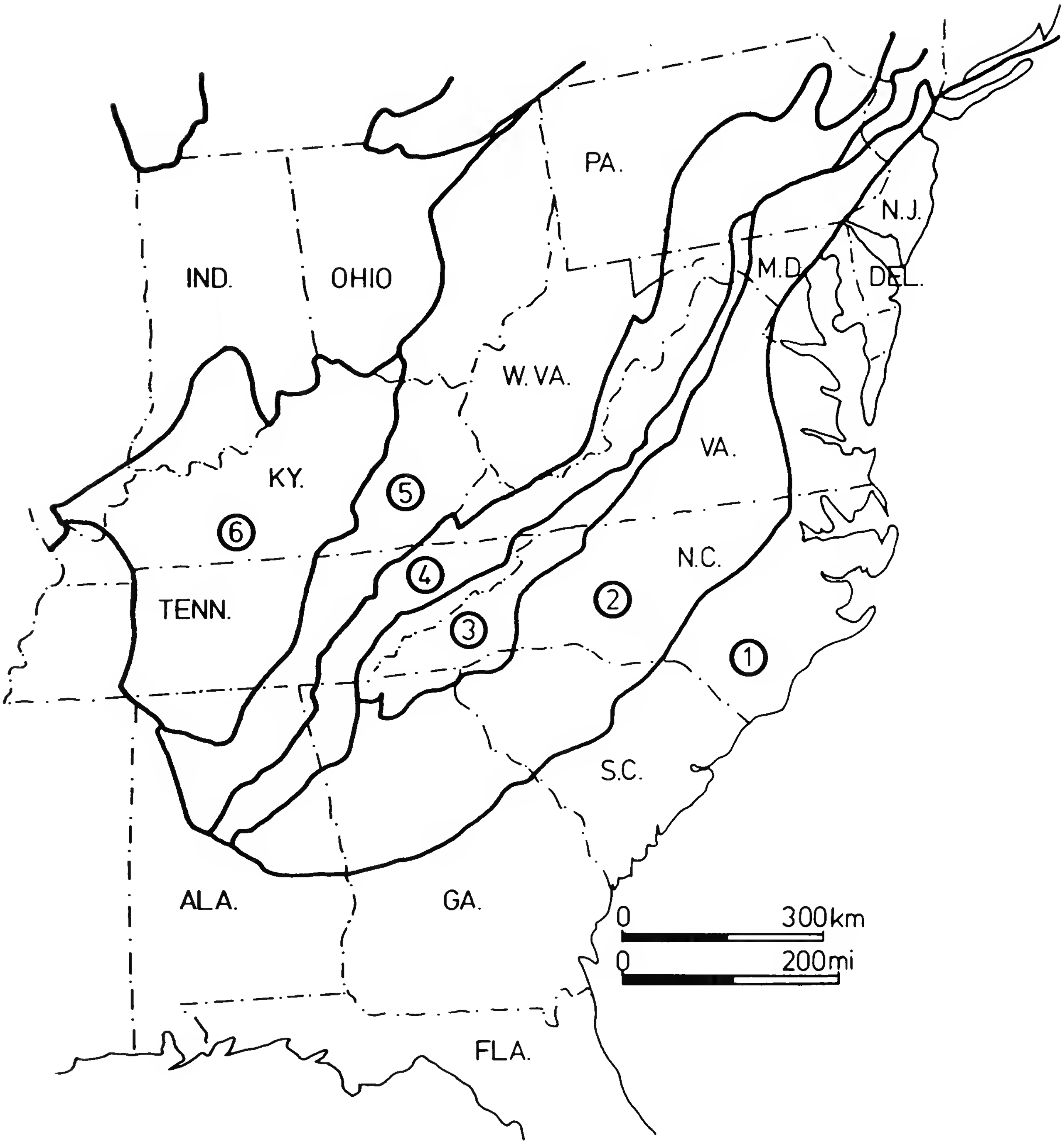


Fig. 3. Part of the eastern United States showing major physiographic provinces as follows: 1, Coastal Plain; 2, Piedmont; 3, Blue Ridge; 4, Appalachian Valley and Ridge (= Appalachian Valley); 5, Appalachian Plateau; 6, Interior Low Plateaus.

geographic isolation. Although these karst areas are situated within the Appalachian Plateau proper, they are geographically close and geologically similar to belts of cavernous limestone on the western side of the Appalachian Valley.

In Alabama, Kentucky, and Tennessee, where the Appalachian Plateau is known locally as the Cumberland Plateau, cavernous limestones of Mississippian age are exposed along the highly dissected western margin of the Plateau in all three states. Cavernous areas on the western side of the plateau, unlike those on the eastern side, are closely allied with those of the adjoining Eastern Highland Rim of the Interior Low Plateaus.

A few caves are also recorded from the Blue Ridge province south and southeast of the study area in the higher mountains of southeastern Tennessee (Barr 1961) and in western North Carolina (Cato Holler, Jr., pers. comm.). With the exception of those in Blount County, Tenn., however, most of these caves consist of fissure passages in non-carbonate rocks.

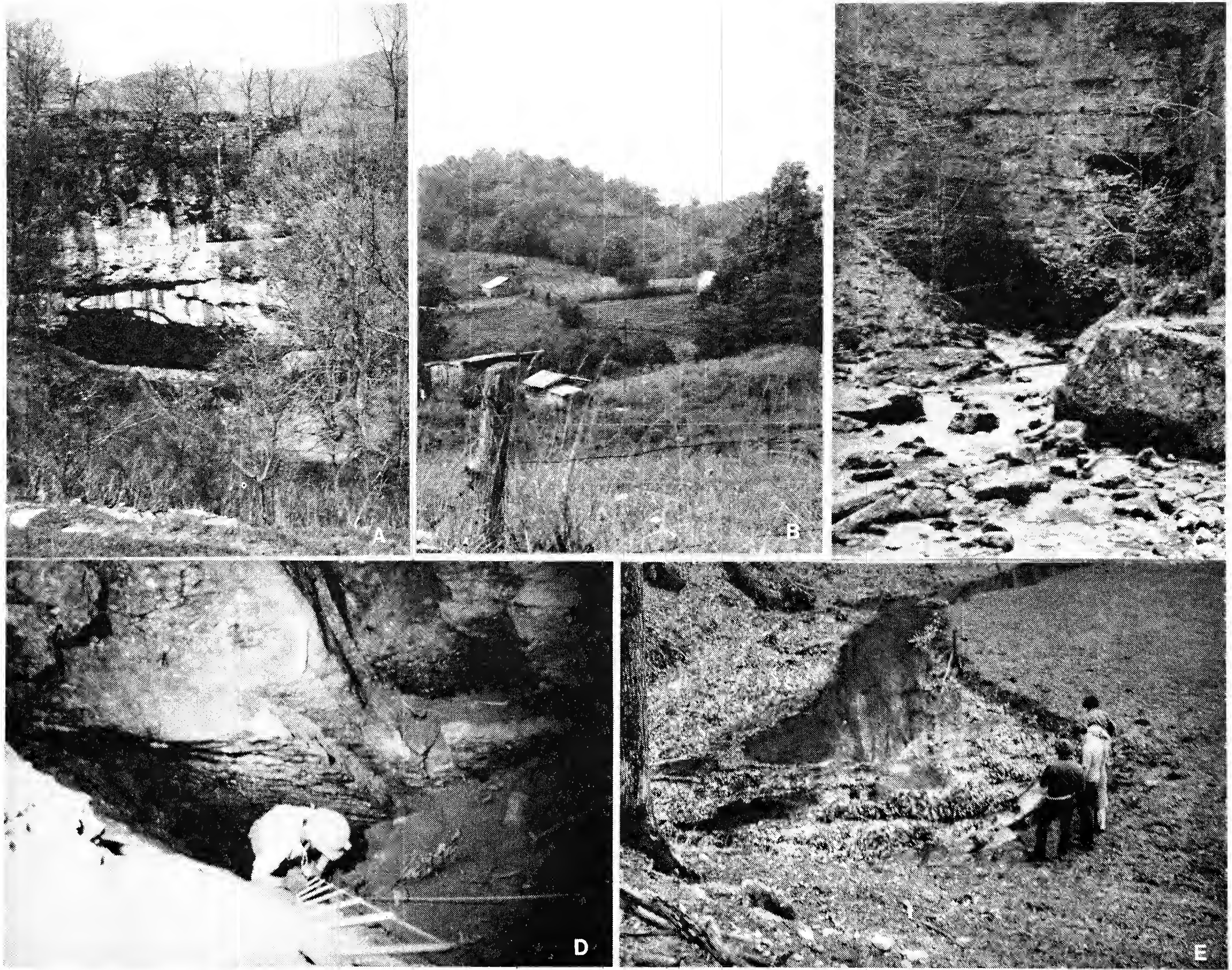
FAUNISTIC RELATIONSHIPS

For the most part, the cave-limited faunas of the Appalachian Valley and karst islands on the eastern side of the Appalachian Plateau differ significantly from those of the Interior Low Plateaus and western margin of the Cumberland Plateau. Since many genera with troglobites (see definition under "Methods") are shared by these two major cave regions, this difference is considerably greater on the species level. However, differences in the cave faunas of the two regions are less pronounced in southern Tennessee, northeastern Alabama, and northwestern Georgia, where only short distances separate cave areas in the Appalachian Valley, Cumberland Plateau, and Eastern Highland Rim. Farther north in Kentucky and Virginia-West Virginia, where the distance between the cave areas of the Interior Low Plateaus-Cumberland Plateau and Appalachian Valley-eastern Appalachian Plateau is much greater (see Fig. 3), the faunas are more different.

The ranges of a number of troglobitic species in the study area extend into adjoining cave areas on the north, south, and west. However, to the north the number of troglobitic species decreases significantly in Maryland and Pennsylvania, where the cave-limited fauna is very sparse (see Franz and Slifer 1971, Holsinger 1976). Even farther north, in the glaciated cave area of New York, the only known troglobite is the amphipod crustacean *Stygobromus allegheniensis* (Holsinger 1967a, 1978).

West of the study area in the adjoining cave areas of eastern West Virginia, the cave-limited fauna is comparable in diversity to that in western Virginia, and there is a strong taxonomic affinity among many troglobitic species throughout much of the two-state area (cf., Holsinger et al. 1976). There is also a strong affinity between certain cave-limited species in the study area and those of Pine Mountain, a karst island in the Appalachian Plateau about 16 km northwest of the study area in southeastern Kentucky and northwestern Campbell County, Tenn.

Much of the cave-limited fauna in the Appalachian Valley of eastern Tennessee south and southwest of the study area has not been documented in the same detail as that of areas north and west of the study area. But those observations and literature records that are


A
B
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available (cited under "Review of the Fauna" elsewhere this paper) suggest a close taxonomic affinity between troglobites of this area and those of the southern part of the study area. For example, troglobitic species from the Clinch drainage basin south of the confluence of the Clinch and Powell rivers are closely related to, or in some cases the same as, species from that part of the Clinch basin included in the study area. In contrast to the Clinch basin, the cave-limited fauna of the adjoining Holston drainage basin in northeastern Tennessee is generally much less diverse, apparently reflecting the same relationship we have noted elsewhere in this paper (see "Zoogeography") between the cave faunas of these two basins farther north in the study area.

In comparison with northeastern Tennessee (principally the Clinch, Holston, and Powell basins), the Appalachian Valley of southeastern Tennessee between Kingston in Roane County and the Georgia-Tennessee state line near Chattanooga contains fewer and generally smaller caves (see Barr 1961, Matthews 1971), and the cave-limited fauna is poorly known. The cave-limited fauna of the Appalachian Valley and eastern margin of the Appalachian Plateau south of Chattanooga in northwestern Georgia has been documented in detail, however (see Holsinger and Peck 1971). This fauna is diverse and shares affinities with that of both the Appalachian Valley farther north and the Cumberland Plateau and Eastern Highland Rim in adjacent northern Alabama and south-central Tennessee.

CAVE VERTEBRATES

The present study is limited to invertebrates, but some pertinent observations are included on the ecology of the plethodontid salamander *Gyrinophilus porphyriticus* (Green), a species that our research has shown to be a major predator in certain cave-stream communities in southwestern Virginia and eastern Tennessee (see "Ecology" elsewhere this paper). Although there are no bona fide troglobitic vertebrates recorded from the study area, certain populations of *G. porphyriticus* in caves of the Clinch and Powell valleys are apparently cave-limited and dominated by large, pale larvae. The systematics of these populations warrants further detailed study. Elsewhere in the Appalachian Valley, just west and south of the study area, several populations of *Gyrinophilus* are considered troglobitic and include *G. subterraneus* Besharse and

Fig. 4. Karst features in the study area: A, entrance to Hugh Young Cave in large sinkhole, Tazewell County; B, sinkhole topography on Middle Cambrian limestone in the Clinch Valley, Scott County; C, Maiden Spring, a large resurgence in the Ward Cove karst, Tazewell County; D, vertical entrance to Stegers Fissure, Augusta County (courtesy of K. E. Wark and D. G. Whall); E, sinks of Meadow Creek near Looney, Craig County.

Holsinger (1977) from General Davis Cave in Greenbrier County, W.Va., and *G. palleucus* McCrady (*sensu lato*) from several caves and a temporary spring in Knox, McMinn, and Roane counties, Tenn. (see Brandon 1965, Simmons 1975).

Troglobitic fishes of the family Amblyopsidae occur on the western margin of the Cumberland Plateau and in the Interior Low Plateaus and Ozark Plateaus, but are absent from the Appalachian Valley and eastern side of the Appalachian Plateau except for the documented occurrence of *Typhlichthys subterraneus* Girard in Lookout and Wills valleys in northeastern Alabama and northwestern Georgia (see Cooper and Iles 1971).

METHODS

Field Work

During the course of our investigation (1961-1980), 450 caves in Virginia and 53 in eastern Tennessee were explored for biological specimens. In addition, biological data were obtained from the literature or from other biologists on approximately 38 caves in Virginia and 9 in Tennessee not visited by us during the field work. As of 1980, these totals represented approximately 21% of the recorded caves in the study area. Caves were visited in all counties in the study area except Clarke County in northwestern Virginia, which has only four insignificant caves reported (see Douglas 1964, Holsinger 1975). Virtually all caves considered "large" (see Holsinger 1975) were checked at least once, and some of the most complex ones, especially in the Clinch and Powell valleys, were visited on several separate occasions. In addition to the field work in Virginia and east Tennessee, biological data were collected concurrently from 152 caves in adjacent West Virginia, but the results of this part of the study have been published separately (see Holsinger et al. 1976).

In most of the caves investigated, sampling for specimens was done in all potential habitats, including banks of damp clay and silt, decomposing organic detritus (e.g., wood, leaves, guano), damp flowstone and dripstone, pools fed by drips and seeps, and streams (see Fig. 5). With the exception of specimens obtained from pit-fall traps used for a short time in four Lee County caves during the summer of 1975, in a special study by T. C. Kane, and the occasional use of cheese and shrimp baits on an experimental basis, trapping, baiting, Berlese, and phreatic pumping techniques were not employed in collecting. A majority of records in this report are based on collections made directly from the substrate, aided only by small brushes or syringes.

Collecting efforts were focused principally on troglobites and troglophiles, but selective collections were also made of trogloxenes and accidentals in order to document their occurrence. Non-cave habitats,

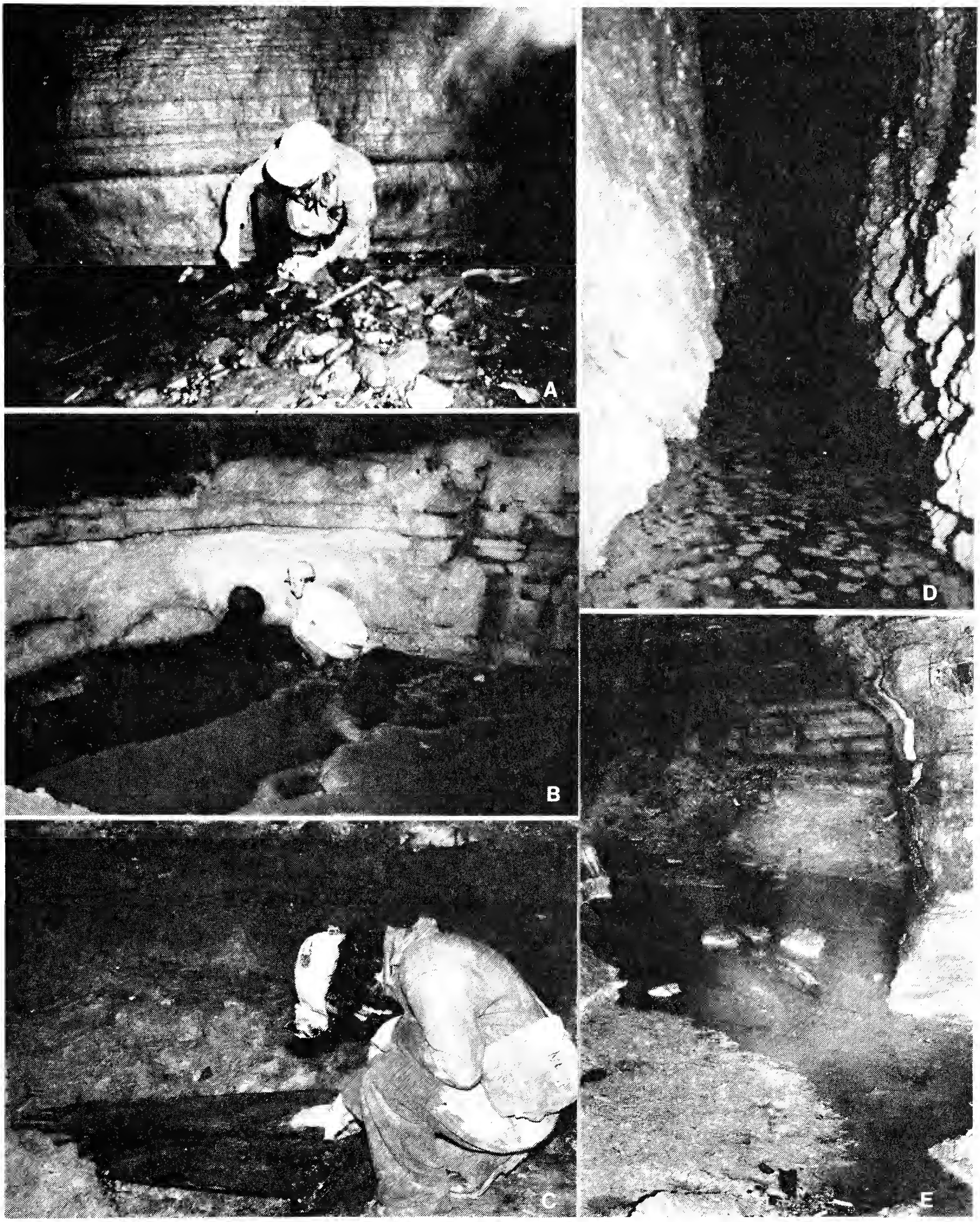

Fig. 5. Cave habitats in the study are: A, stream in Gallohan Cave No. 1, Lee County (courtesy of D. E. Wapinski); B, rimstone pools in Sweet Potato Cave, Lee County; C, decomposing wood in English Cave, Claiborne County; D, East Lake in Madisons Saltpetre Cave, Augusta County; E, mud-bottom drip pool in Molly Wagle Cave, Lee County.

such as springs and seeps, were sampled occasionally in order to obtain specimens for comparison with those taken from nearby caves.

The species covered in this study are essentially macroscopic forms (i.e., generally larger than 1 mm). Microscopic forms ($\leq$ 1 mm) that are sometimes reported from cave waters (e.g., protozoans, rotifers; see Gittleson and Hoover 1970) or from the interstices of sand and gravel substrates beneath cave streams (e.g., tiny oligochaeates, copepods, ostracods) have not been included. Some preliminary studies, however, on polluted pools in Banners Corner Cave in Russell County (see Holsinger 1966) and the interstitial habitat beneath a stream in Buis Saltpetre Cave in Claiborne County (unpubl. data) indicate a potential richness of subterranean microscopic organisms that would be profitable to investigate in a future study.

Although our study does not cover all of the Clinch Valley in Tennessee (Fig. 2), some pertinent data on the distribution of species recorded from caves just southwest of the study area in Anderson County are included. These data add significant details to the picture of the geographic distribution of species or species groups whose ranges extend into parts of the Clinch basin outside the study area. Moreover, except for a few major caves in Hawkins and Sullivan counties, which lie just south of the Tennessee-Virginia border, our survey does not cover the Holston Valley in eastern Tennessee (see Fig. 1, 2).

DEFINITION OF TERMS

Cavernicoles are usually classified ecologically according to their level of adaptation and degree of restriction to the cave environment. The commonly accepted system, which is used throughout this paper, is defined as follows (see also Barr 1963, 1968). (1) *Troglobites* are obligatory species, which are restricted to caves or similar habitats. Morphological modifications (specializations) called troglomorphisms usually distinguish troglobites and may include, among other things, loss or rudimentation of eyes and pigment, and attenuation of the body, appendages, or sensory hairs. (2) *Troglophiles* are facultative species, which are able to complete their life cycle within a cave but may also occur in ecologically suitable habitats outside caves. (3) *Trogloxenes* are species habitually found in caves or similar cool, dark habitats outside caves, but they must return periodically to the surface or at least to the entrance zone of a cave for food. Some species, however, such as certain cave crickets, may be trogloxenic under one set of circumstances and troglophilic under another (see Barr 1963). (4) *Accidentals* are species that wander, fall, or are washed into caves and generally exist there temporarily.

Many small aquatic invertebrates (e.g., flatworms, crustaceans) simultaneously inhabit both caves and subterranean groundwater habitats outside of caves and even outside of karst areas and are sometimes called *phreatobites* (see Holsinger 1967a, Barr 1968) or *stygobionts*. Because some of these species occur in shallow groundwater (i.e., vadose water) above the zone of permanent saturation (i.e., phreatic water), the less restrictive designation *stygobiont*, now commonly used by European workers, is probably preferable to *phreatobite*. Some examples of non-cave habitats occupied by stygobionts include springs, wells, the interstitial media of small gravels either beneath a stream (= hyporheic or nappes fluviales) or beside a stream (= parafluvial or nappes phréatiques), small seeps or their outflow above the water table (= hypotelminorheic or nappes perchées), and outlets of drain tiles placed beneath cultivated fields with poor natural drainage (for further details see Henry 1978, Holsinger 1978, Culver 1982).

Edaphobites are obligatory deep-soil species that occasionally occur in caves. Although frequently blind and weakly pigmented, edaphobites are usually distinguished from true troglobites by the absence of other troglomorphisms. This distinction is often a subtle one, however, and is best made between species in a carefully studied group. *Endogean* is used in a rather broad sense to designate species living in deep ground-litter or soil (i.e., endogean species) or the habitat type itself (i.e., endogean habitat).

CAVE NOMENCLATURE

Locations and descriptions of most of the caves cited herein have been published by Barr (1961) and Matthews (1971) for Tennessee and by Douglas (1964) and Holsinger (1975) for Virginia, or are on file with the Tennessee Cave Survey or the Virginia Speleological Survey. Most cave names are now standardized for both states, but a few are listed in the biological literature under different names and tend to be confusing. In the following list the currently accepted, standardized name is followed by the former name in parentheses: Banners Corner Cave (Big Spring Cave), Russell County; Battlefield Crystal Cave (Crystal Cave), Shenandoah County; Caney Sinks Cave (Sinks Cave), Hancock County; Cudjos Cavern (King Solomons Cave in part), Lee County; Endless Caverns (New Market or Zirkles Cave), Rockingham County; Fred Bulls Cave (Mark Smiths Cave), Montgomery County; Giant Caverns (Hopkins Cave), Giles County; Gilley Cave (Elys or Shalers Cave), Lee County [refers to Ely Cave on p. 294 in Douglas (1964), not Ely Cave on p. 306]; Grand Caverns (Weyers Cave), Augusta County; and Wills Cave (Fraleys Cave), Washington County.

It should also be noted that we have retained the original name for Buck Hill Cave (Rockbridge County), which was recently commercialized under the name Caverns of Natural Bridge. Cassell Farm Cave No. 1 and 2 in Tazewell County are two separate caves located very close together (see Holsinger 1975), but they are frequently not differentiated as two caves in the older literature. In citing records from the literature where it was not clear which cave was intended, we have listed the locality as Cassell Farm Cave(s).

The following caves have been listed in the biological literature but are unknown to either state's cave survey by the name given (see also indication in "Review of the Fauna"): Big Stony Cave, Giles County; Cave No. 1 and No. 3, Pennington Gap, Lee County; Coopers (or Parkeys) Cave, Hancock County; Field Cave, Russell County (apparently not the Fields Cave in Holsinger 1975:240); Hammers Cave, Campbell County (possibly same as Big Hollow Cave); Mushroom Cave, Page County (possibly same as Ruffners Cave No. 1); Newman Ridge Cave, Hancock County (could be any one of several caves in Newman Ridge near Sneedville, Tenn.); Old Hollins Road Cave, Roanoke County: Old Joe's Cave near Wingina, Buckingham County (not in study area): Sikes Cave, Russell County (apparently not the same as Sykes Cave in Holsinger 1975:259); and Water Cave (presumably in the Shenandoah Valley).

REVIEW OF THE FAUNA

Approximately 335 species of invertebrate animals, representing some 90 families and 173 genera, have been recorded from caves in the study area. An exact number is meaningless, of course, because many species are incompletely known taxonomically and some groups have been collected more intensively than others. Of the known species, 42% are troglobites (some questionable pending further study); 18% are troglophiles; 14% are trogloxenes; and the remaining 26% are marginal trogloxenes and accidentals. The numerical distribution of troglobitic and troglophilic species by taxonomic order (or subclass for arachnids) is given in Table 1. Of the 140 troglobitic species, 42 are aquatic and 98 are terrestrial.

In the following list the higher taxa (phyla, classes, orders) are arranged in generally accepted phylogenetic sequence. The lower taxa (families, genera, species) are listed alphabetically within their respective taxonomic groups. Species are arranged in species groups (under genera) where usage of these groups is well established in the recent literature. Some of the troglobites listed are only provisionally recognized or just now in the process of being described (i.e., description in manuscript or in press) and are therefore designated by upper case letters (viz., sp. A, sp. B, etc.) under their respective genera or species groups. The abbreviations TB, TP, TX, and AC designate troglobite, troglophile, trogloxene, and accidental, respectively. However, as noted in the lists, the ecological status of some species is questionable or provisional, and

Table 1. Frequency distribution by order or subclass of troglobites and troglophiles in the study area.

Order or Subclass [1]	No. of Troglobites [2]	No. of Troglophiles [2]
Alloeocoela (flatworms)	1	-
Tricladida (flatworms)	4	2
Lumbriculida (oligochaetes)	3	-
Mesogastropoda (snails)	2	2
Stylommatophora (snails)	1	2
Amphipoda (amphipods)	20	1
Isopoda (isopods)	15	3
Decapoda (crayfishes)	-	1
Pseudoscorpiones (pseudoscorpions)	15	2
Acari (mites)	2	3
Opiliones (harvestmen)	-	2
Araneae (spiders)	8	9
Lithobiomorpha (centipedes)	1	-
Spirostreptida (millipeds)	-	1
Chordeumatida (millipeds)	9	7
Julida (millipeds)	-	1
Collembola (springtails)	4	8
Diplura (bristletails)	6	-
Orthoptera (crickets)	-	1
Coleoptera (beetles)	49	13
Diptera (flies)	-	3
Total number of species	140	61

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[1] The arachnid groups Pseudoscorpiones, Acari, Opiliones, and Araneae are considered subclasses by some workers (see Krantz 1970) and orders by others (see Barnes 1980).

[2] Includes several species whoes ecological status is presently unclear (see text).

clarification must await additional information on ecology, systematics, or both.

All known cave records within the study area are listed alphabetically by county for each species. Type localities for troglobites are indicated in parentheses following the cave name when these localities occur in the study area. Quotation marks and a reference (in parentheses) to the author who used the name indicate cave localities taken from the literature and unknown to either the Virginia Speleological Survey or the Tennessee Cave Survey by the name published. Many of the troglobites listed are endemic to the study area and, unless indicated otherwise in the preliminary discussions or under “Comments,” the caves listed include all known locality records. A question mark after a cave name indicates a questionable species record. Additional data on the geographic distribution or taxonomy of a species are sometimes given under "Comments," following the list of cave records.

PHYLUM PLATYHELMINTHES

Among the free-living flatworms (class Turbellaria) found in Virginia and east Tennessee caves are alloeocoels and tricladids. The former are restricted to a single, curious species also recorded from single caves in Kentucky and West Virginia; it is the only alloeocoel reported from caves (Carpenter 1970a, Holsinger et al. 1976). The other flatworms are planarians in the genera *Sphalloplana* and *Phagocata*.

Cavernicolous flatworms are generally encountered in drip or stream-fed pools or on the flat surface of rocks in small streams; population numbers fluctuate greatly. Outside the study area, *Sphalloplana chandleri* is recorded from springs in Davidson County, Tenn., and Floyd County, Ind. (Kenk 1977), and is apparently a relatively widespread stygobiont. In contrast, the troglobites *Sphalloplana consimilis* (Fig. 13E) and *S. virginiana* have narrowly delimited ranges (Fig. 6) and are known only from the caves listed below (see Hyman 1945, Kenk 1977). The presence of *Sphalloplana percoeca* in northeastern Tennessee is highly questionable. In redescribing this species, Kenk (1977) listed many localities in Alabama, Kentucky, and Tennessee and indicated that the range might possibly extend into West Virginia and Georgia. He also pointed out that some of these records, especially those from Tennessee, need verification.

Phagocata gracilis is recorded from numerous localities (viz., caves, springs, headwaters of small streams) in the eastern and east-central United States (Kenk 1970). Although *Phagocata subterranea* (Hyman 1937) was previously reported from Banners Corner Cave by Holsinger (1963a, 1964, 1966), it is apparently a subterranean ecophenotype of *P. gracilis* and is therefore now considered a synonym of this species by Kenk (1970). *Phagocata morgani*, common in the subterranean groundwaters of the Ward Cove karst in Tazewell County, is recorded from many springs, small streams, and caves in eastern North America (Carpenter 1970b).

Order Alloeocoela

Family Prorhynchidae

Geocentrophora cavernicola Carpenter (TB?)

Virginia.—Tazewell Co.: Fallen Rock Cave.

Geocentrophora sp.

Virginia.—Lee Co.: Cliff Cave.

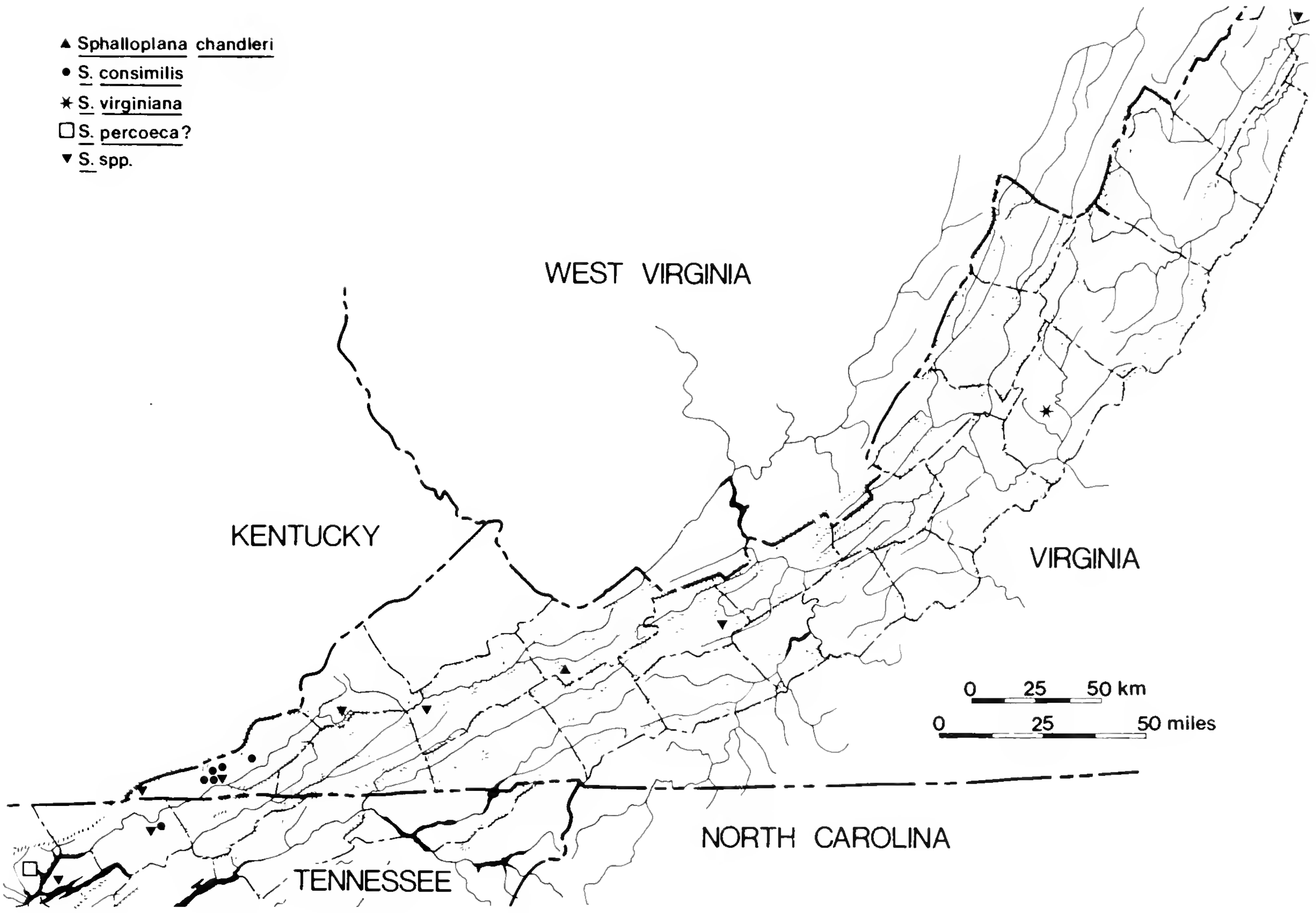

Fig. 6. Distribution of troglobitic planarians (*Sphalloplana*) in the study area.

Order Tricladida

Family Kenkiidae

Sphalloplana (*Speophila*) *chandleri* Kenk (TB?)
Virginia.—Tazewell Co.: Fallen Rock Cave.

Sphalloplana (*Sphalloplana*) *consimilis* Kenk (TB)
Tennessee.—Claiborne Co.: Buis Saltpetre Cave.
Virginia.—Lee Co.: Bowling, Cope, Gallohan No. 1 (type locality), Gregorys and McClure caves.

Sphalloplana (*Sphalloplana*) *percoeca* (?) (Packard) (TB)
Tennessee.—Campbell Co.: Meredith Cave.

Sphalloplana (*Speophila*) *virginiana* Hyman (TB)
Virginia.—Rockbridge Co.: Showalters Cave (type locality).
Comments. Previous records from Bland and Lee counties (Holsinger 1963b, 1964) are invalid in light of subsequent revisionary studies by Kenk (1977).

Sphalloplana spp.
Tennessee.—Claiborne Co.: Chadwells Cave. Union Co.: Oaks Cave.

Virginia.—Bland Co.: Newberry-Bane Cave. Frederick Co.: Ogdens Cave. Lee Co.: Cliff and Smiths Milk caves. Russell Co.: Banners Corner Cave. Wise Co.: Rocky Hollow Cave.

Comments.—These records are based on juveniles or poorly preserved specimens of which specific determinations could not be made.

Family Planariidae

Phagocata gracilis (Haldeman) (TP or TX)

Virginia.—Russell Co.: Banners Corner Cave.

Phagocata morgani (Stevens and Boring) (TP or TX)

Virginia.—Giles Co.: Starnes Cave. Tazewell Co.: Fallen Rock and Hugh Young caves.

PHYLUM ANNELIDA

All segmented worms recorded from caves in Virginia and east Tennessee are in the class Oligochaeta and belong to the orders Branchiobdellida, Haplotaxida, Lumbriculida, and Tubificida. The records given in the list below are based on either literature references (e.g., Gates 1959) or selective collecting and by no means represent an exhaustive survey.

The branchiobdellids occur as epizoites on freshwater crustaceans, and all species recorded from caves in the study area were taken on the troglophilic crayfish *Cambarus bartonii s. lat.* (see Holt 1973). The occurrence of these species in Appalachian caves is probably largely accidental, inasmuch as they are generally widespread in epigean habitats and are transported into caves secondarily by their crayfish hosts.

The haplotaxids include several species of terrestrial and semi-terrestrial "earthworms" that are probably initially introduced into caves in mud or silt washed underground by flooding or filtration. However, many of these species probably exist in caves as trogloxenes, or even as troglophiles, under certain conditions. All of the haplotaxids listed below are also reported from caves elsewhere in the eastern United States (see Gates 1959, Franz and Slifer 1971, Cook 1975, Holsinger et al. 1976, Peck and Lewis 1978).

Of greater interest zoogeographically are the "thread-like" lumbriculid worms, of which all three species found to date are apparently troglobites with narrowly defined ranges. These worms have been collected from the gravel substrate of small streams, but only after diligent searching. In comparison with Europe, the North American cavernicolous lumbriculid fauna is very poorly known (Cook 1975).

Although they have been observed in several study-area caves, tubificid worms remain poorly known to date. An undetermined genus and species of the family Enchytraeidae has been collected from the stream in Fallen Rock Cave in Tazewell County, and *Tubifex tubifex*

Müller (Tubificidae) has been observed in Banners Corner Cave, Russell County, in pools polluted by sewage (see Holsinger 1966).

Order Branchiobdellida

Family Branchiobdellidae

Ankyrodrilus legacus Holt (AC)
Tennessee.—Hancock Co.: Fairmont School Cave.
Virginia.—Tazewell Co.: Fallen Rock Cave.
Bdellodrilus illuminatus (Moore) (AC)
Tennessee.—Hancock Co.: Cantwell Valley Cave.
Cambarincola fallax Hoffman (TX or AC)
Tennessee.—Hancock Co.: Cantwell Valley and Fairmont School caves.
Virginia.—Scott Co.: McDavids Cave. Tazewell Co.: Fallen Rock Cave.
Cambarincola philadephicus (Leidy) (TX or AC)
Tennessee.—Hancock Co.: Fairmont School Cave.
Virginia.—Tazewell Co.: Wagoners Cave.
Cambarincola sp.
Tennessee.—Sullivan Co.: Bristol Caverns.
Oedipodrilus macbaini (Holt) (AC)
Tennessee.—Sullivan Co.: Bristol Caverns.
Xironodrilus formosus Ellis (AC)
Tennessee.—Sullivan Co.: Bristol Caverns.
Xironogiton instabilis (Moore) (AC)
Virginia.—Tazewell Co.: Wagoners Cave.

Order Haplotaxida

Family Lumbricidae

Allolobophora chlorotica (Savigny) (TX)
Virginia.—Rockbridge Co.: Showalters Cave.
Allolobophora turgida Eisen (TX)
Virginia.—Rockbridge Co.: Showalters and Tolleys caves.
Bimastos tumidus (Eisen) (TX)
Tennessee.—Claiborne Co.: English Cave.
Virginia.—Lee Co.: Gilley Cave. Russell Co.: "Field Cave" (Gates, 1959:80).
Dendrobaena rubida (Savigny) (TX)
Tennessee.—Claiborne Co.: English Cave.
Virginia.—Lee Co.: Cudjos Cavern. Russell Co.: Jessie Cave.
Eisenia rosea (Savigny) (TX)
Virginia.—Giles Co.: Clover Hollow and Tawneys caves.
Eiseniella tetraedra (Savigny) (TX)
Virginia.—Russell Co.: Banners Corner Cave. Tazewell Co.: Fallen Rock Cave.

Octolasium lacteum (Oerley) (TX)
Virginia.—Bland Co.: Newberry-Bane Cave. Scott Co.: Grigsby Cave.

Order Lumbriculida

Family Lumbriculidae
Spelaedrilus multiporus Cook (TB)
Virginia.—Russell Co.: Smiths Cave (type locality).
Stylodrilus (*Bythonomus*) *beattiei* Cook (TB)
Virginia.—Tazewell Co.: Steeles Cave.
Comments.—Also recorded from three caves in southern West Virginia (Cook 1975).
Genus (?) species (?)
Virginia.—Lee Co.: McClure and Spangler caves.
Comments.—These populations represent an undescribed, troglobitic species (D. G. Cook, pers. comm.)

PHYLUM MOLLUSCA

Both aquatic and terrestrial snails (class Gastropoda) have been collected from caves in Virginia and eastern Tennessee, but the former are far more common in subterranean habitats than are the latter. Aside from several species of *Goniobasis*, which are sometimes abundant in karst springs and occasionally penetrate some distance into cave streams, aquatic cave snails of the Appalachians are members of the family Hydrobiidae, and most apparently belong to the genus *Fontigens* (Fig. 13D). Cavernicolous hydrobiids commonly inhabit the undersides of flat rocks in small streams with relatively constant flow.

Owing to the fact that the taxonomy of the cave and spring hydrobiids is based largely on shell morphology (see Hubricht 1976), which is often highly variable, identities of some of the species listed below are, in our opinion, questionable. There are a number of peculiarities that are perplexing about the geographic distribution (Fig. 7) and ecology of these species. For example, *Fontigens aldrichi* has been recorded from caves and springs in the Ozarks and Appalachians and is represented in both regions by eyed, pigmented populations living principally in springs, and by eyeless, unpigmented populations living principally in caves (Hubricht 1976, Peck and Lewis 1978). Another species, *F. orolibas*, although resticted to the Appalachians, has been identified from eyed, pigmented populations living in springs in the Blue Ridge Mountains and from blind, unpigmented populations living in caves in karst valleys to the west (see Hubricht 1957, 1976). Similarly, blind, white snails from caves in the Powell Valley of southwestern Virginia have been tentatively assigned by Hubricht (1976) to

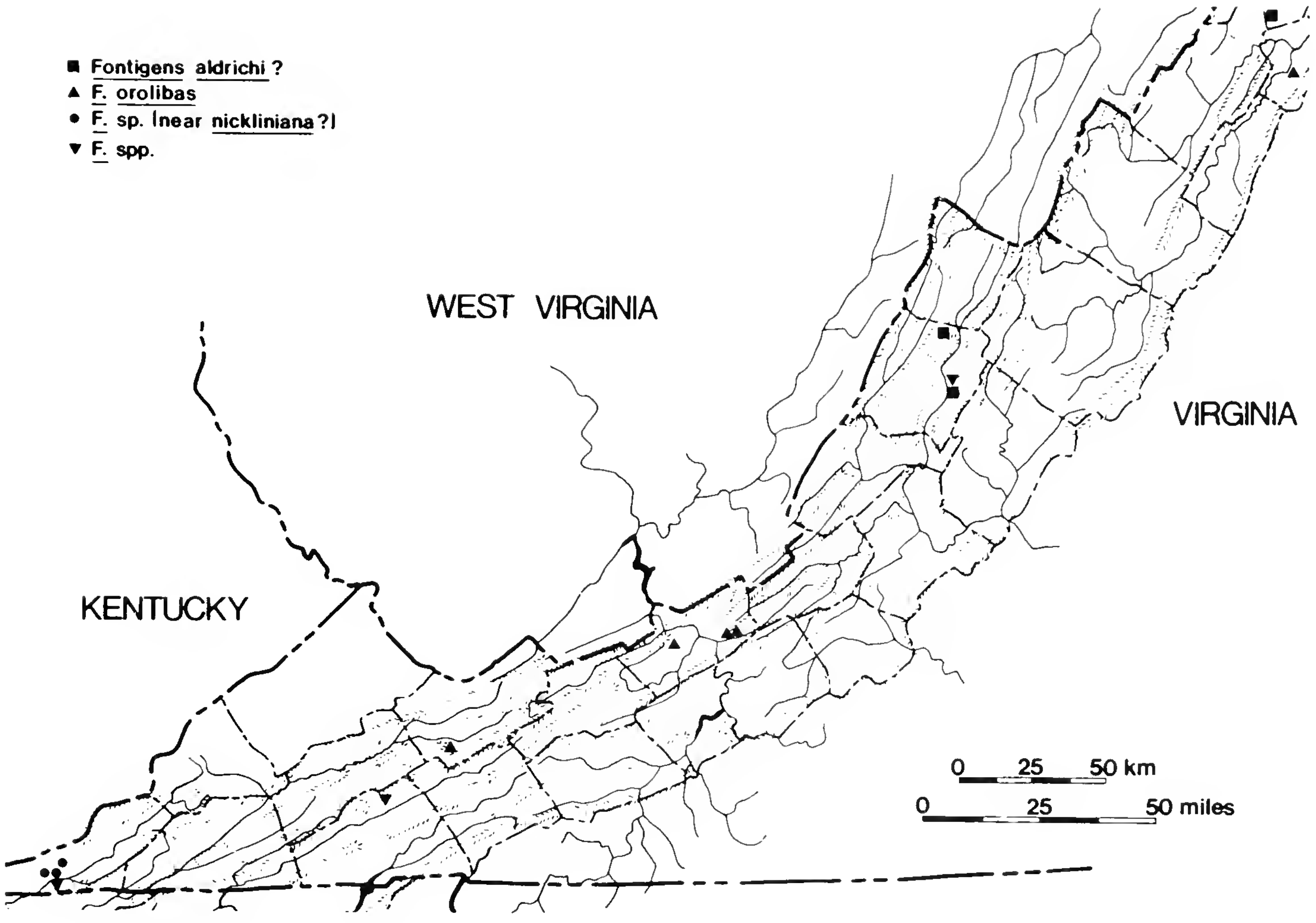

Fig. 7. Distribution of aquatic cavernicolous snails (*Fontigens*) in the study area. Spring localities for *F. orolibas* in the Blue Ridge Mountains not shown.

F. nickliniana, an epigean species previously recorded from a number of localities in the eastern United States. However, the recent study of a population in Unthanks Cave, utilizing internal anatomy in combination with shell morphology, suggests that one or more undescribed troglobitic species inhabit caves of the Powell Valley (R. Hershler and F. G. Thompson, in litt.). Another population in need of additional taxonomic study and clarification is one from Skyline Caverns tentatively identified by Morrison (1949, pers. comm.) as an undescribed species of the European subterranean genus *Lartetia*. Morrison (1949, pers. comm.) has taken a different view from that of Hubricht and believes that *Fontigens* in the Appalachians represents a complex of closely similar genera composed collectively of many well-isolated troglobites. Unfortunately, his observations are mostly unpublished and thus unavailable for biogeographic analysis.

Terrestrial cave snails were usually collected from damp, rotting wood; only a few populations were noted. Seven species in three families have been recorded to date. *Helicodiscus notius specus* (Helicodiscidae), a “somewhat degenerate form” (see Barr 1967a) of the widespread, primarily epigean *H. notius* (Hubricht 1962) was originally described from Burnet Cave in Barren County, Ky., and has since been identified from Bristol Caverns in east Tennessee by Hubricht (in litt.). *Helicodiscus inermis*, recorded from two caves in west-central Virginia, is also reported from caves in Alabama, Georgia, and Tennessee, and from surface localilties elsewhere in the eastern and southern United States (see Hubricht 1964, 1985; Holsinger and Peck 1971).

In the Polygyridae, *Mesodon appressus* is recorded from Flannery Cave in Scott County, and this species, in its broadest sense, is also reported from caves in Kentucky and Tennessee by Barr (1961, 1967a) and Hubricht (1964). *Glyphyalinia specus* (Zonitidae), a white, apparently blind species unknown outside caves and possibly a troglobite, is recorded from Bristol Caverns in Sullivan County and also from caves in Alabama, Georgia, Kentucky, middle Tennessee, and possibly West Virginia (see Hubricht 1965, 1985; Barr 1967a; Holsinger and Peck 1971; Holsinger et al. 1976). Another zonitid, *Zonitoides arboreus*, probably a troglophile, is recorded from one cave in the study area and from many other caves in the east-central and southeastern United States (see Hubricht 1964, Holsinger and Peck 1971, Peck and Lewis 1978).

Order Mesogastropoda

Family Pleuroceridae

Goniobasis clavaeformis (Lea) (TX or AC)

Tennessee.—Hancock Co.: Cantwell Valley Cave.

Goniobasis simplex (Say) (TX)

Virginia.—Lee Co.: Surgener and Young-Fugate caves. Scott Co.: Alley and McDavids caves.

Goniobasis sp.

Virginia.—Scott Co.: Speers Ferry Cave.

Family Hydrobiidae

Fontigens aldrichi (Call and Beecher) (?) (TP?)

Virginia.—Bath Co.: Blowing and Butler-Sinking Creek caves. Frederick Co.: Ogdens Cave.

Comments.—In or near the study area this species is also recorded from springs in Highland Co., Va., and Washington Co., Md. (see Hubricht 1976).

Fontigens orolibas Hubricht (TP)

Virginia.—Giles Co.: Smokehole, Starnes, and Tawneys caves. Tazewell Co.: Hugh Young Cave. Warren Co.: Skyline Caverns.

Fontigens sp. (near *nickliniana*?) (TB?)

Virginia.—Lee Co.: Gallohan No. 1, Smiths Milk, and Spangler caves.

Fontigens spp.

Virginia.—Bath Co.: Witheros Cave. Lee Co.: Unthanks Cave. Washington Co.: Perkins Cave.

Lartetia (?) sp. (TB)
Virginia.—Warren Co.: Skyline Caverns.

Order Stylommatophora

Family Helicodiscidae
Helicodiscus inermis Baker (TP or TX)
Virginia.—Augusta Co.: Grand Caverns. Bath Co.: Dunns Cave.
Helicodiscus notius specus Hubricht (TP or TX)
Tennessee.—Sullivan Co.: Bristol Caverns.

Family Polygyridae
Mesodon appressus (Say) (TX?)
Virginia.—Scott Co.: Flannery Cave.
Mesodon normalis (Pilsbry) (AC?)
Tennessee.—Claiborne Co.: English Cave.
Polygyra albolabris Say (AC?)
Virginia.—Shenandoah Co.: Shenandoah Caverns.

Family Zonitidae
Glyphyalinia specus Hubricht (TB?)
Tennessee.—Sullivan Co.: Bristol Caverns.
Zonitoides arboreus (Say) (TP?)
Virginia.—Rockingham Co.: Endless Caverns.

PHYLUM ARTHROPODA: SUBPHYLUM CRUSTACEA

A significant number of the species recorded from caves in Virginia and eastern Tennessee are crustaceans and include copepods, amphipods, isopods, crayfishes, and possibly ostracods. The vast majority, however, are amphipods and isopods, both of which are frequently well represented in aquatic cave communities.

Class Copepoda

Cave copepods are very poorly known from the study area and only a single species has been recorded to date. However, as pointed out earlier, no attempt was made to sample microscopic cave faunas, and the lack of data on tiny crustaceans such as copepods and ostracods is to be expected.

Order Cyclopoida

Family Cyclopidae
Cyclops vernalis Fischer (TX)
Virginia.—Tazewell Co.: Hugh Young Cave.
Comments.—Extremely variable and widespread species sometimes recorded from caves (e.g., in Georgia, Kentucky, New Mexico, Texas) (see Barr 1967a, Reddell 1965, Barr and Reddell 1967, Holsinger and Peck 1971).

Class Ostracoda

Hobbs (1975) alluded to the presence of the ectocommensal ostracod *Phymocythere phyma* (Hobbs and Walton) (Entocytheridae) in Virginia and West Virginia caves but gave no specific records. Because a principal host of this species is *Cambarus bartonii*, a crayfish found in caves of the study area (see below), the occurrence of this ostracod in Virginia and east Tennessee caves should be expected. However, to our knowledge there are no published records.

Class Malacostraca

Malacostracan crustaceans are represented in study-area caves by three orders: Amphipoda (2 families, 3 genera, 21 species), Isopoda (6 families, 10 genera, 23 species), and Decapoda (1 family, 1 genus, 2 species).

Order Amphipoda

Amphipods are common faunal components of cave waters where they are usually found among gravels or under small rocks in streams, on the organically enriched mud substrate of pools fed by drips and/or seeps, and rarely in deep phreatic lakes. A total of 21 species, all in the suborder Gammaridea, have been recorded, of which 20 are of troglobitic facies and known only from groundwater biotopes. The troglobitic species belong to the genera *Stygobromus*, *Bactrurus*, and *Crangonyx*, all in the family Crangonyctidae; the single troglophile, *Gammarus minus*, is in the family Gammaridae.

A majority of the species (18) have been assigned to *Stygobromus*, a large, exclusively subterranean genus that is distributed throughout a large part of North America (Holsinger 1977, 1978, 1986a, 1986b). Most species of *Stygobromus* from the study area have narrowly circumscribed ranges (Fig. 8, 9), and many are local endemics; three are known only from their type localities. Only four species listed below occur outside the study area, and none extends beyond this area for a great distance. The most common and widespread species is *S. mackini*, which is distributed from Monroe County in southern West Virginia (New River drainage) southwestward to Roane County in eastern Tennessee (Tennessee River drainage) (Holsinger 1978).

Bactrurus is represented by a single, undescribed (provisionally recognized) species that is recorded to date from only three caves in the Powell Valley (Fig. 8). This is one of five or six undescribed species in the genus (Holsinger 1986b) and the first to be found in the Appalachian Valley. Three described species are reported from caves and other groundwater biotopes in the eastern and central United States (see Holsinger 1972, 1986a, 1986b).

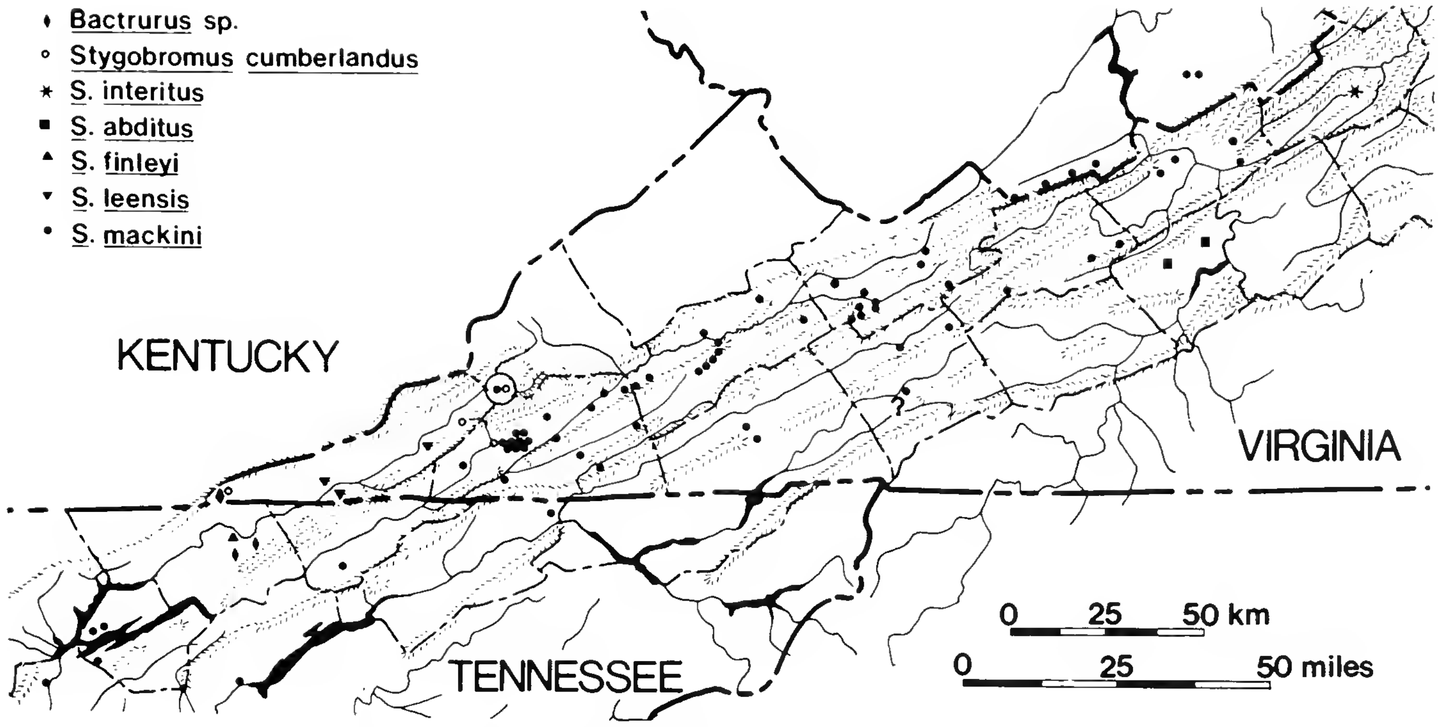

Fig. 8. Distribution of troglobitic amphipods (*Bactrurus* and *Stygobromus*) in the study area. All localities for *S. mackini* (including those in Anderson and Grainger counties, Tenn., and Mercer and Monroe counties, W.Va.) shown except Berry Cave, Roane County, Tenn. Two symbols in a circle indicate two species from the same cave.

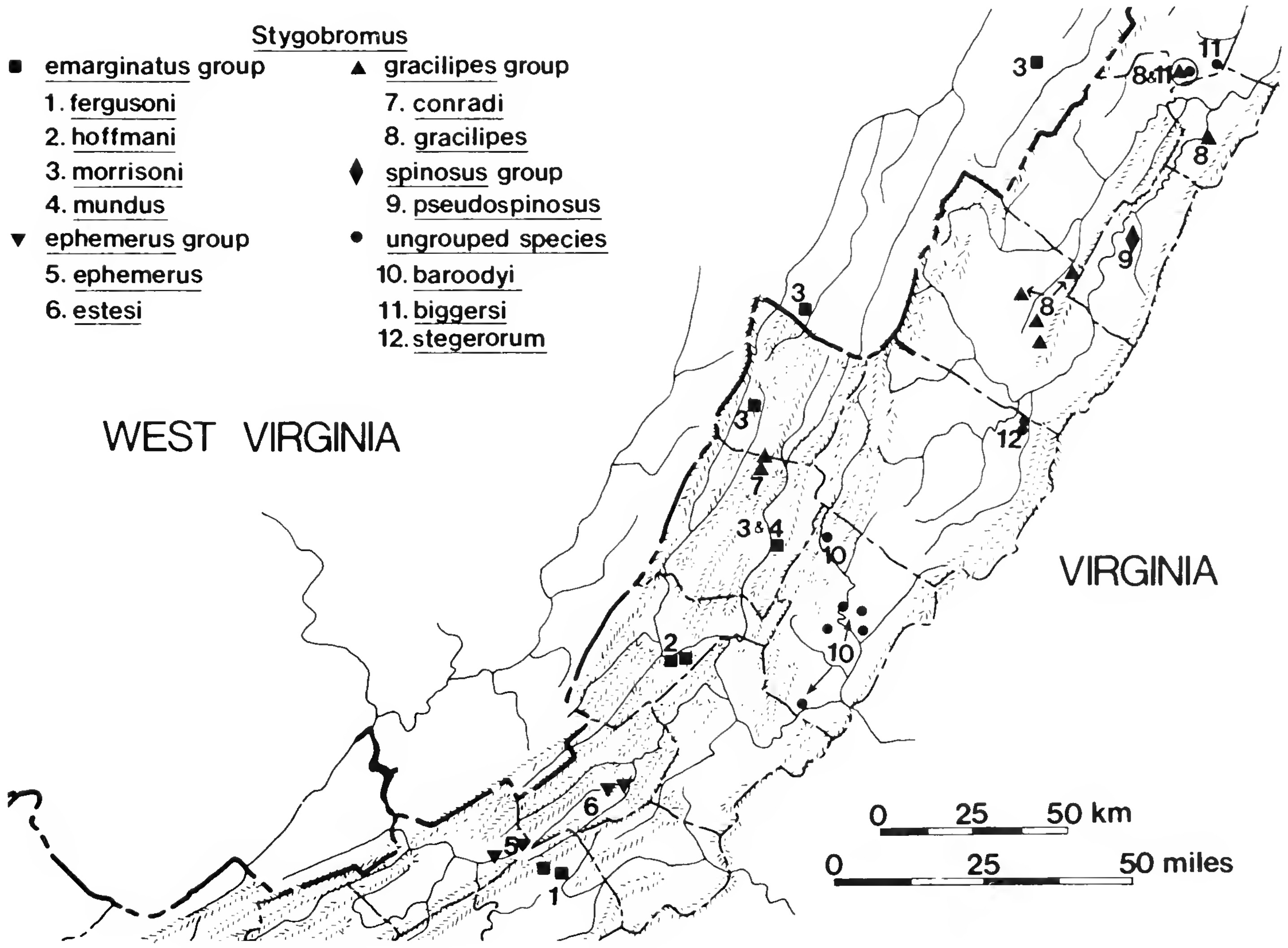

Fig. 9. Distribution of troglobitic amphipods (*Stygobromus*) in the study area. Single localities for *S. morrisoni* in Hardy and Pendleton counties, W.Va., also shown. Two symbols in a circle indicate two species from the same cave.

Crangonyx antennatus is recorded from numerous caves in the Powell Valley and the middle and lower parts of the Clinch Valley (Fig. 10, 13B). It is the most common and, after *Stygobromus mackini*, most widespread troglobitic amphipod in Virginia and eastern Tennessee. Its range, which needs further evaluation in view of morphological variation, extends south of the study area through eastern Tennessee into northwestern Georgia and northern Alabama and then westward to south-central Tennessee (see Holsinger 1969a, 1972, 1986a, 1986b). In addition to caves, *C. antennatus* has been collected occasionally from surface springs or seeps, including Spout Spring in Lee County (Holsinger 1969a).

Gammarus minus is recorded from caves, springs, and small spring-fed streams, principally in karst regions of the eastern and east-central United States (see Holsinger and Culver 1970; Holsinger 1969a, 1972; Stock 1986). In the study area this species is abundant only in caves of the Ward Cove karst area (upper Clinch drainage) in Tazewell County (Fig. 10). Here a majority of the populations have developed a troglomorphic facies referred to as Form I in an earlier paper (Holsinger and Culver 1970). Within the study area, *G. minus* is more widespread in springs than in caves and is recorded from the former habitat in the Tennessee counties of Claiborne, Hancock, and Sullivan, and the Virginia counties of Alleghany, Bath, Botetourt, Craig, Frederick, Lee, Montgomery, Pulaski, Russell, Scott, Shenandoah, Tazewell, Washington, and Wythe.

Family Crangonyctidae
Bactrurus sp. (TB)
Tennessee.—Claiborne Co.: Kings Saltpetre and Saur Kraut caves.
Virginia.—Lee Co.: Cumberland Gap Saltpetre Cave.
Crangonyx antennatus Packard (TB)
Tennessee.—Campbell Co.: Meredith Cave. Claiborne Co.: Buis Saltpetre, Chadwells, English, Hauser Spring, John Lard, Kings Saltpetre, and Station Creek caves. Grainger Co.: Horseshoe Cave. Hancock Co.: Cantwell Valley, Fairmont School, and Subers caves. Hawkins Co.: Pearson Cave. Sullivan Co.: Morrills Cave. Union Co.: Oaks, Wolf, and Wrights caves.
Virginia.—Lee Co.: Baileys, Bowling, Cave Springs, Cedar Hill, Chances, Combs No. 1, Cope, Crouse, Cudjos (Cavern), Cumberland Gap Saltpetre, Frazier, Gallohan No. 1 and 2, Garretts, Gibson-Frazier, Gilliam, Glen Olingers, Golf Course No. 1 and 2, Gregorys, Jones Saltpetre, Knapper, Lesters, Litton No. 1, Lucy Beatty, McClure, Minors Saltpetre, Molly Wagle, Mount Moriah Pit, Olinger, Roadside No. 1, Seal, Slemp, Smiths Milk, Spangler, Sweet Potato, Taylor Pit, Thompson, Thompson

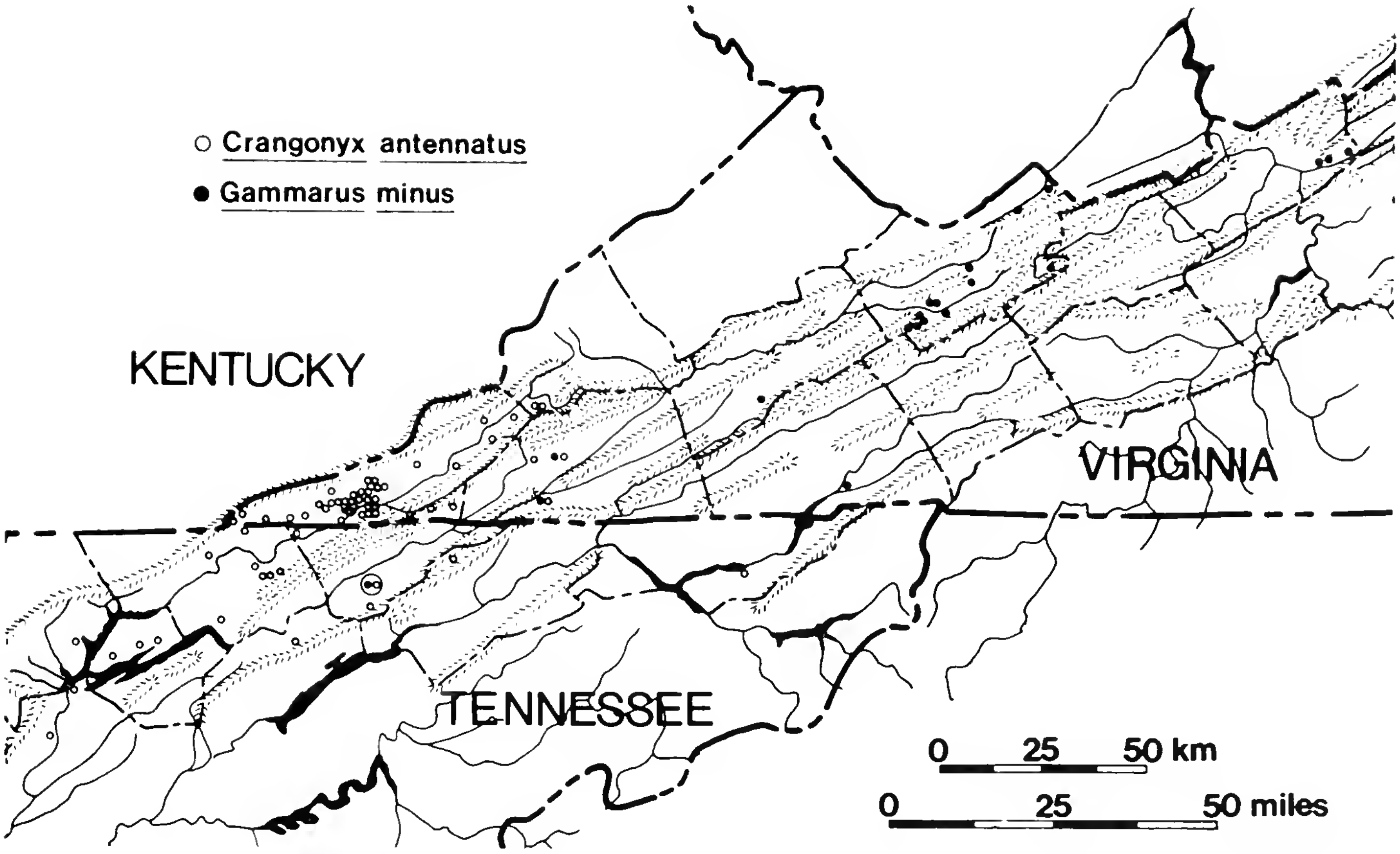

Fig. 10. Distribution of cavernicolous amphipods (*Crangonyx* and *Gammarus*) in the study area. Only cave localities shown for *G. minus*. Anderson County, Tenn., records for *C. antennatus* also indicated. Two symbols in a circle indicate two species from the same cave.

Cedar, Unthanks, Watsons No. 1, and Young-Fugate caves. Scott Co.: McDavids, Speers Ferry, and Spurlock caves. Wise Co.: Wildcat Cavern and Wildcat Saltpetre Cave.

Stygobromus (species listed by group as indicated)

cumberlandus group

Stygobromus cumberlandus Holsinger (TB)

Virginia.—Lee Co.: Baileys and Cliff caves. Wise Co.: Wildcat Saltpetre Cave (type locality).

Comments.—Also recorded from a well at Duffield in Scott County (Holsinger 1978).

Stygobromus interitus Holsinger (TB)

Virginia.—Craig Co.: New Castle Murder Hole Cave (type locality).

emarginatus group

Stygobromus fergusoni Holsinger (TB)

Virginia.—Montgomery Co.: Old Mill and Slussers Chapel (type locality) caves.

Stygobromus hoffmani Holsinger (TB)

Virginia.—Alleghany Co.: Lowmoor (type locality) and Mc Elwee caves.

Stygobromus morrisoni (Holsinger) (TB)

Virginia.—Bath Co.: Witheros Cave (type locality). Highland Co.: Corbett Cave.

Comments.—Also recorded from single caves in Hardy and Pendleton counties, W. Va. (Holsinger 1978).

Stygobromus mundus (Holsinger) (TB)

Virginia.—Bath Co.: Witheros Cave (type locality).

Comments.—Also recorded from a tributary to the Cowpasture River in Alleghany County (see Holsinger 1967a, 1978).

ephemerus group

Stygobromus ephemerus (Holsinger) (TB)

Virginia.—Giles Co.: Canoe and Tawneys (type locality) caves.

Stygobromus estesi (Holsinger) (TB)

Virginia.—Craig Co.: New Castle Murder Hole and Rufe Caldwell (type locality) caves.

gracilipes group

Stygobromus conradi (Holsinger) (TB)

Virginia.—Bath Co.: Breathing (type locality) and Butler-Sinking Creek caves.

Stygobromus gracilipes (Holsinger) (TB)

Virginia.—Frederick Co.: Ogdens Cave. Rockingham Co.: Deer Hole, Endless (Caverns), Massanutten (Caverns), and Three-D Maze caves. Warren Co.: Skyline Caverns (type locality).

Comments.—Also recorded from caves just north of the study area in Washington Co., Md.; Franklin Co., Pa.; and Berkeley and Jefferson counties, W. Va. (Holsinger 1967a, 1978).

mackini group

Stygobromus abditus Holsinger (TB)

Virginia.—Pulaski Co.: James (type locality) and Sam Bells caves.

Stygobromus finleyi Holsinger (TB)

Tennessee.—Claiborne Co.: English Cave (type locality).

Stygobromus leensis Holsinger (TB)

Virginia.—Lee Co.: Gallohan No. 2, Litton No. 1 (type locality), and Skull caves.

Stygobromus mackini Hubricht (TB)

Tennessee.—Hancock Co.: Cantwell Valley Cave. Hawkins Co.: Sensabaugh Saltpetre Cave. Union Co.: Lost Creek, Oaks, and Ridenour Pit caves.

Virginia.—Giles Co.: Ballards, Starnes, and Tawneys caves. Russell Co.: Banners Corner, Bundys No. 2, Burns, Grays, Jessie, Johnson, Munsey, Porgie Bundys, "Sikes" (Hubricht 1943:697; type locality), and Smith Drop caves. Scott Co.: Blair-Collins, Blowing Hole, Deep Spring, Flannery, Greears Sweet Potato, Grigsby, Hill, Jack, Jackson, Kerns Smoke-Hole, McDavids, McNew, Moccasin Valley, Natural Tunnel (Cavern), Pond, Spurlock, Taylor No. 1, Winding Stair, and Wolfe caves. Smyth Co.: Buchanan Saltpetre, McMullin (?), and Tilson Saltpetre caves. Tazewell Co.: Cauliflower, Chimney Rock, Crocketts, Fallen Rock, Glenwood Church, Hugh Young, Lost Mill No. 1, Steeles, and Ward Cove caves. Washington Co.: Singleton Cave. Wise Co.: Wildcat Saltpetre Cave.

Comments.—Also recorded from caves in Anderson, Grainger, and Roane counties, Tenn., and Mercer and Monroe counties, W. Va., and occasionally from small springs or seeps in Giles, Tazewell, and Washington counties, Va. (see Holsinger 1978).

spinosus group

Stygobromus pseudospinosus Holsinger (TB)

Virginia.—Page Co.: Luray Caverns (type locality).

Ungrouped Species

Stygobromus baroodyi Holsinger (TB)

Virginia.—Rockbridge Co.: Bathers (type locality), Bell, Billy Williams, Buck Hill, Grahams, and Showalter caves.

Stygobromus biggersi Holsinger (TB)

Virginia.—Frederick Co.: Johns and Ogdens (type locality) caves.

Comments.—Also recorded from caves just north of the study area in Washington Co., Md., Franklin Co., Pa., and Jefferson Co., W. Va. (Holsinger 1978).

Stygobromus stegerorum Holsinger (TB)

Virginia.—Augusta Co.: Madisons Saltpetre (type locality) and Stegers Fissure caves.

Stygobromus spp.

Tennessee.—Campbell Co.: Norris Dam Cave.

Virginia.—Craig Co.: New Castle Murder Hole Cave. Washington Co.: Neals Cave.

Comments.—These populations may represent several undescribed species, all probably in the *mackini* group.

Family Gammaridae

Gammarus minus Say (TP)

Tennessee.—Hancock Co.: Cantwell Valley Cave.

Virginia.—Giles Co.: Canoe, Smokehole, and Tawneys caves. Russell Co.: Smiths Cave. Scott Co.: Alley and Wolfe caves. Tazewell Co.: Bowens, Cauliflower, Crocketts, Fallen Rock, Gillespie Water, Hugh Young, Lawson, Lost Mill No. 1 and 3, Quarry, Rosenbaums Water, and Wagoners caves. Washington Co.: Hookers Rock Cave.

Order Isopoda

Isopods are represented in the regional cave fauna by three suborders: Asellota, Flabellifera, and Oniscoida. All asellotids from caves in Virginia and eastern Tennessee are in the large, Holarctic, freshwater family Asellidae. Flabelliferans are represented by a single, unique member of the predominantly marine family Cirolanidae. Oniscoids are terrestrial and are represented by the families Armadillidiidae, Ligiidae, Oniscidae, and Trichoniscidae.

Cavernicolous asellids are usually associated with the gravel or rock substrate of small streams or the mud-bottom substrate of drip/seep pools. Some species apparently prefer riffle zones, whereas others are sometimes seen in large concentrations on flowstone surfaces covered by thin films of moving water (see Culver 1973a, Estes and Holsinger 1982). Two genera, *Caecidotea* and *Lirceus*, occur in study-area caves. The former is represented by 11 species, 9 of which are troglobites; the latter is represented by two species (both troglobites) and possibly several undescribed (non-troglobitic) ones as well (see Henry et al. 1986).

Although several troglobitic species of *Caecidotea* have relatively wide ranges, their distributions generally correspond rather closely to drainage basins (Fig. 11, 12). Some of the wide-ranging species, such as *C. richardsonae*, *C. recurvata*, and *C. pricei*, have also been collected occasionally from subterranean waters outside caves (e.g., seeps, wells). Five species, viz., *C. holsingeri*, *C. incurva*, *C. recurvata* (Fig. 13C), *C. richardsonae*, and *C. pricei*, have ranges that extend beyond the study area, whereas *C. bowmani*, *C. henroti*, and the undescribed species from Cliff Cave (Lee County) are local endemics with very restricted ranges. Of particular interest here is *C. bowmani*, at present known only from a drain-tile habitat in Rockbridge County (see Lewis 1980). Although this species is not recorded from a cave *per se*, it is of troglobitic facies and, with careful searching, will possibly be found in caves. Because of this we have listed it as a troglobite. Moreover, careful reevaluation of collections from caves in the James River basin previously assigned to *C. vandeli* by Fleming (1972) may very well result in their reassignment to *C. bowmani*.

Because taxonomic studies of *Caecidotea* have placed almost complete emphasis on the morphology of the male second pleopod and tended toward the "lumping" of species, a careful reevaluation of the systematics of the Appalachian cave species is warranted. In support of this view is the recent research by J. J. Lewis (in progress) on the systematics of subterranean *Caecidotea* of the east-central United States, which has revealed additional new species from material previously assigned to described taxa. Based on geographic distribution and ecology, we suspect that *C. richardsonae*, for example, can; with careful

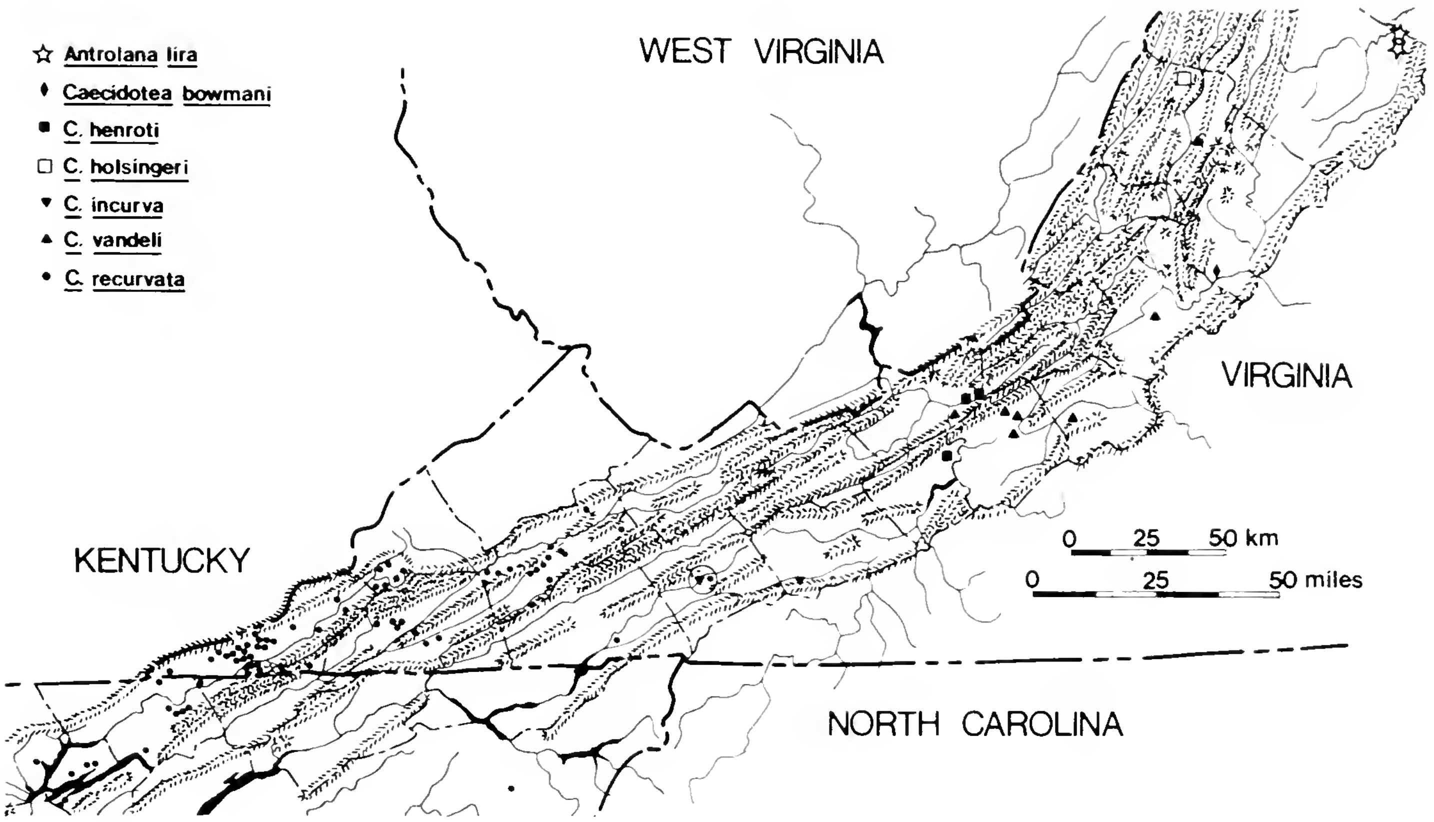

Fig. 11. Distribution of aquatic troglobitic isopods (*Antrolana* and *Caecidotea*) in the study area. All localities for *C. recurvata* (including a single cave in Washington County, Tenn.) shown except spring in Knox County, Tenn. Two symbols in a circle indicate two species from the same cave.

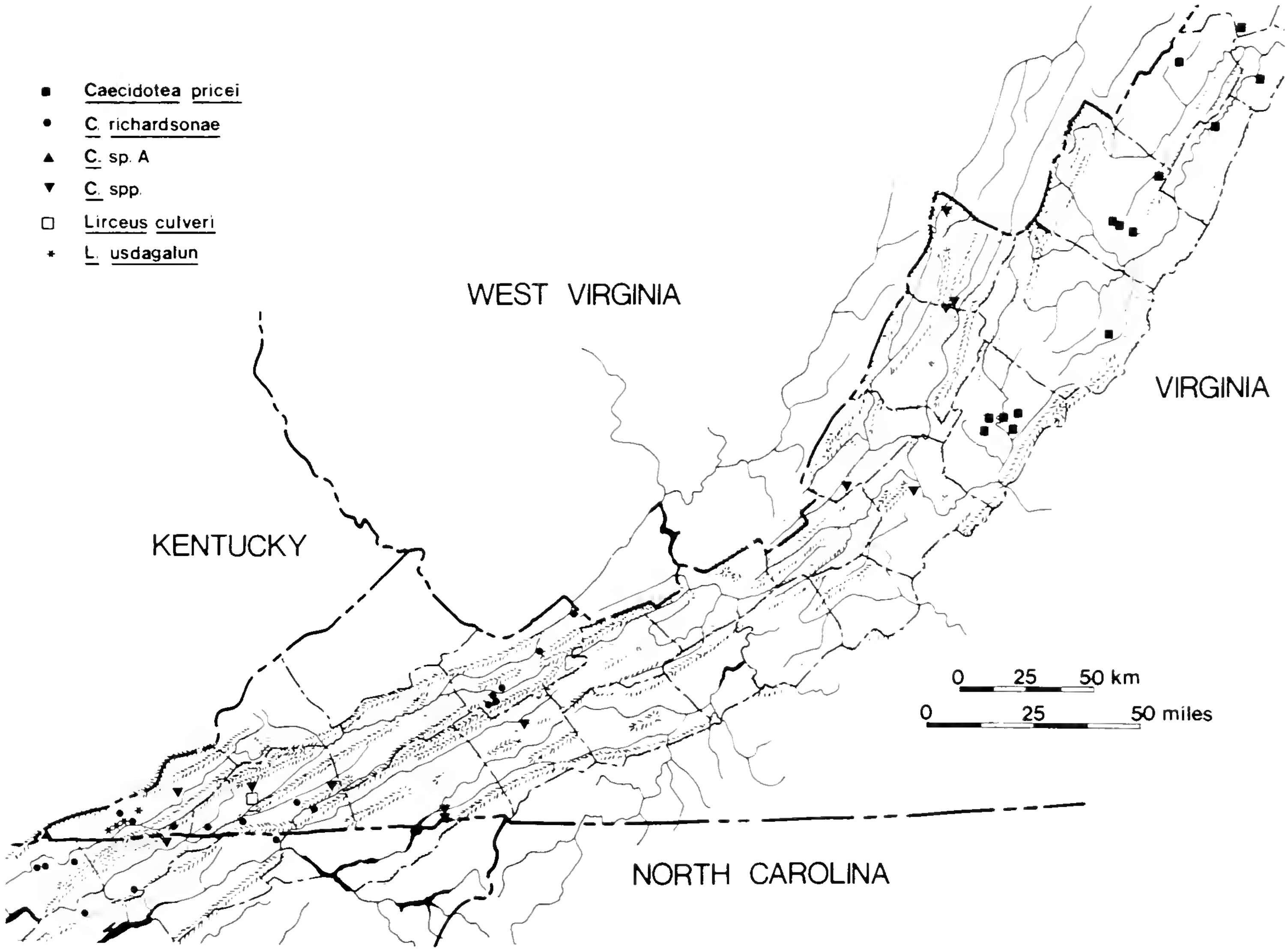

Fig. 12. Distribution of aquatic troglobitic isopods (*Caecidotea* and *Lirceus*) in the study area.

taxonomic analysis, be shown to be a complex of closely related species. This may also be true of other species, such as *C. holsingeri* and *C. pricei*.

In addition to the troglobitic species of *Caecidotea*, *C. intermedia* and *C. r. racovitzai* are both unknown from caves except for the records cited below from Tazewell and Smyth counties and a record for the former from southern Illinois (see Lisowski 1979). *Caecidotea intermedia* is relatively common in the east-central United States and southeastern Canada, whereas *C. r. racovitzai* is relatively common in southeastern Canada but sparsely distributed in the east-central and northeastern United States (Williams 1970, Fleming 1972). The Virginia cave populations warrant further study, especially since they are geographically and ecologically isolated from other localities documented for their respective species.

Lirceus is commonly found in springs and occasionally in caves in eastern North America, but only two troglobitic species have been recognized to date. Both of these occur in southwestern Virginia, where their respective ranges (Fig. 12) are greatly delimited as indicated in the list below. At least one undescribed troglophile inhabits caves and springs in the Ward Cove karst area of Tazewell County where several large populations composed of very pale individuals with tiny eyes have been noted.

The sole member of the family Cirolanidae in the Appalachians is *Antrolana lira,* an unusual monotypic form that is restricted to an isolated groundwater aquifer in Cave Hill in Augusta County (Fig. 11, 13A). This species inhabits lakes of deep phreatic water in two caves (Bowman 1964, Collins and Holsinger 1981, Botosaneanu et al. 1986). It is the only freshwater cirolanid in North America north of Texas, Mexico, and the West Indies, and is therefore of great interest zoogeographically.

Of the four families of oniscoid isopods, only the Trichoniscidae contains troglobites. The remainder contain epigean species, some of which, however, are commonly associated with cave habitats. *Armadillidium vulgare* (family Armadillidiidae), one of the so-called "pill bugs" is a common, widespread epigean species sometimes found under damp wood in the entrance zone of caves. This species has been collected from a few Virginia caves.

Ligiidae is represented in study-area caves by *Ligidium elrodii*, a species sometimes abundant on wet organic detritus flushed into caves by flooding. It is recorded from epigean localities in the eastern United States and southern Canada (Schultz 1970). In addition to the cave records cited below for Virginia and east Tennessee, it is recorded from caves in northern Arkansas, southern Illinois, northwestern Georgia, and southern West Virginia (Schultz 1970, Holsinger and Peck 1971,

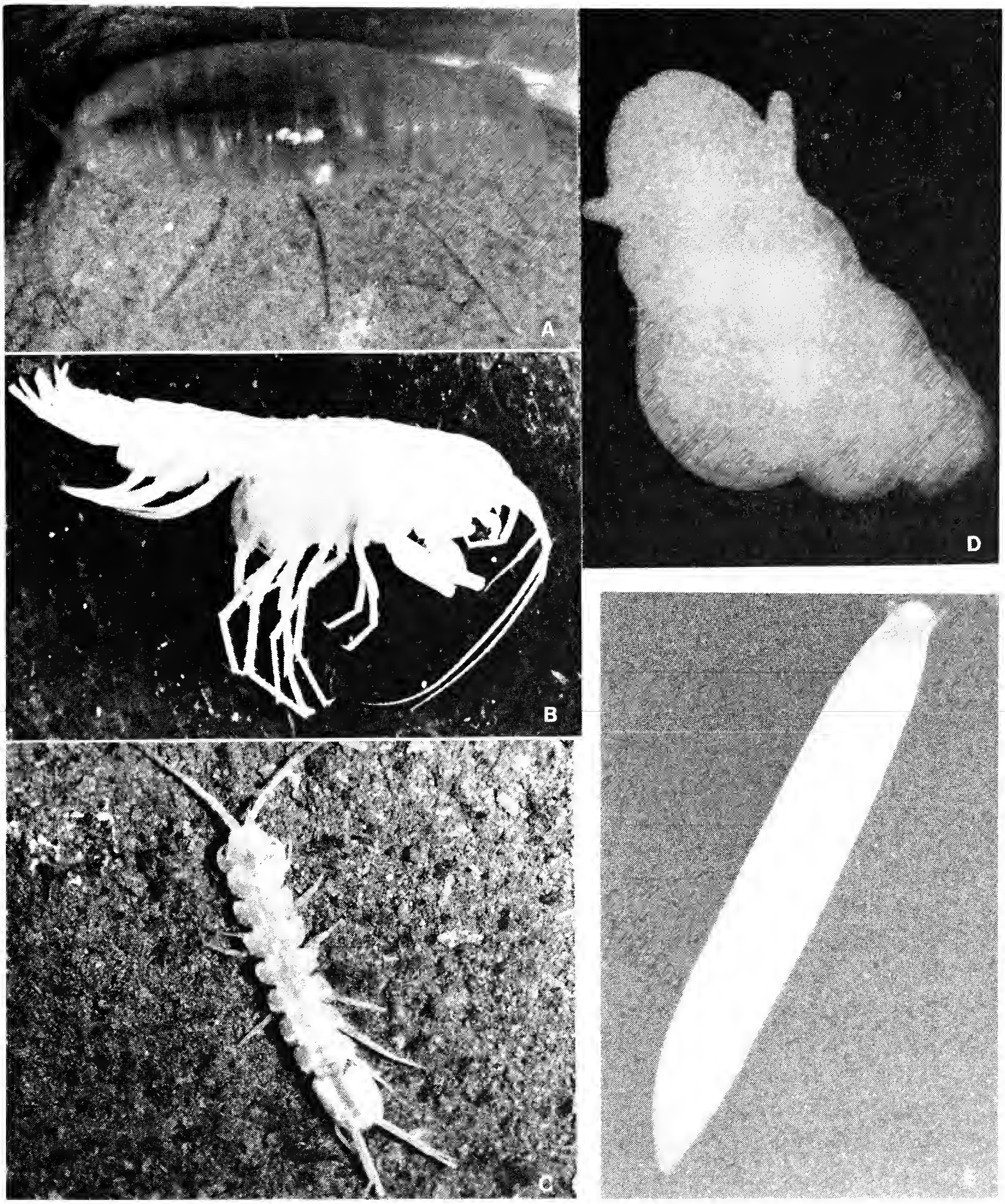

Fig. 13. Aquatic troglobites from the study area (approximate body lengths in parentheses): A, isopod, *Antrolana lira* (16 mm); B, amphipod, *Crangonyx antennatus* (14 mm); C, isopod, *Caecidotea recurvata* (15 mm); D, snail, *Fontigens* sp. (3 mm); E, planarian, *Sphalloplana comsimilis* (14 mm).

Holsinger et al. 1976, McDaniel and Smith 1976, Peck and Lewis 1978). Five subspecies have been designated by Schultz (1970), of which three—*leensis*, *scottensis*, and *hancockensis*—occur in southwestern Virginia and northeastern Tennessee.

Cylisticus convexus (family Oniscidae), a common epigean species throughout the United States, has been found in a few Virginia caves and is also reported from caves elsewhere in the southeastern and south-central parts of the country (see Schultz 1970, Franz and Slifer 1971, Holsinger and Peck 1971, Peck and Lewis 1978, Hobbs and Flynn 1981).

Cavernicolous trichoniscid isopods are usually found on damp to wet, decomposing wood. Six species in four genera are recorded from caves in the study area. Three of these species are troglobites (Fig. 14): *Amerigoniscus henroti* (Fig. 31E) from caves in central Lee County (Holsinger 1967b, Vandel 1977), *A. paynei* from caves in the Clinch Valley of eastern Tennessee (Muchmore 1970a), and *Miktoniscus r. racovitzai* from caves in the James and Shenandoah river drainage basins (Vandel 1965a).

Vandel (1977) considered *A. paynei* Muchmore (1970a) synonymous with *A. nicholasi*, a species described earlier by Vandel (1965a) from Columbia Caverns in middle Tennessee just west of Nashville in Dickson County. In our opinion, however, the small morphological differences between this population and those from eastern Tennessee noted by Muchmore (1970a), combined with the rather wide geographic separation of the populations, provides a good reason for the recognition of two separate species.

Outside the study area, *Miktoniscus r. racovitzai* is reported from Slacks Cave in Scott County, Ky., by Vandel (1965a); and a second subspecies, *M. r. oklahomensis*, was designated by Vandel for a single cave population in Murray County, Oklahoma. The systematic status of these populations is questionable, in view of their disjunct distributions, and should be carefully reevaluated.

The non-troglobitic trichoniscids include: *Haplophthalmus danicus*, recorded from caves and epigean localities throughout a large part of North America and also found in Europe (see Vandel 1965a, Holsinger et al. 1976); *Miktoniscus medcofi* (synonym = *M. alabamensis* Muchmore; see Muchmore 1964, Schultz 1976), recorded from many caves in the southeastern United States; and *Trichoniscus pusillus*, a common epigean species occasionally found in caves (see Holsinger et al. 1976).

Suborder Asellota

Family Asellidae

Caecidotea (species listed by groups as indicated)

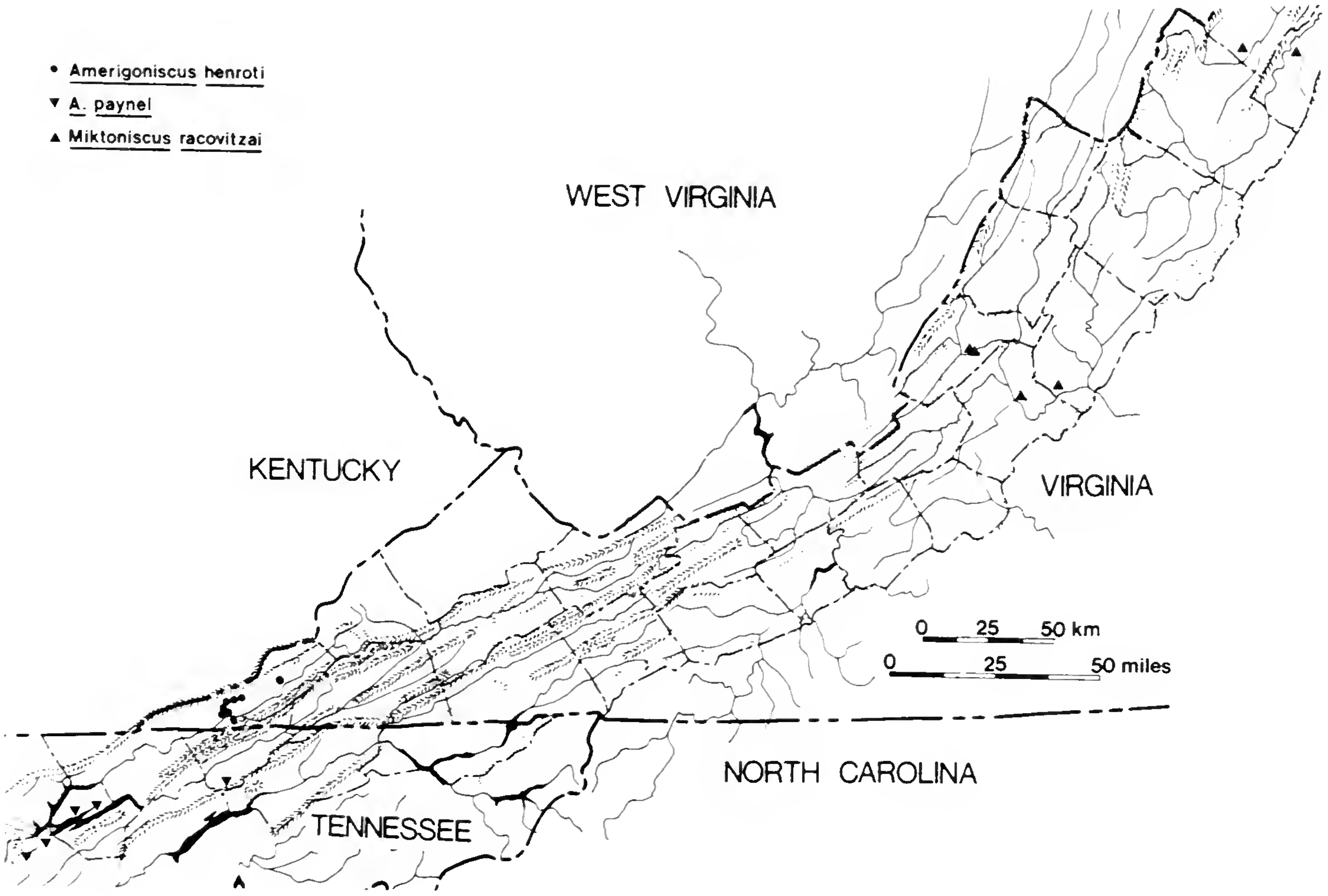

Fig. 14. Distribution of terrestrial troglobitic isopods (*Amerigonicus* and *Miktoniscus*) in the study area. Localities for *A. paynei* in Anderson County, Tenn., also shown.

cannula group

Caecidotea bowmani Lewis (TB)

Virginia.—Rockbridge Co.: drain tile near Natural Bridge (type locality).

Caecidotea henroti (Bresson) (TB)

Virginia.—Giles Co.: Smokehole (type locality) and Tawneys caves. Pulaski Co.: James Cave.

Caecidotea holsingeri (Steeves) (TB)

Virginia.—Bath Co.: Butler-Sinking Creek Cave.

Comments.—Recorded from numerous caves in West Virginia (Greenbrier, Monroe, Pocahontas, and Randolph counties) and from one cave in Garrett Co., Md. (Steeves 1963a, 1969; Holsinger et al. 1976; Lewis 1980).

Caecidotea incurva (Steeves and Holsinger) (TB)

Virginia.-Smyth Co.: McMullin Cave. Wythe Co.: Groseclose Cave No. 1.

Comments.—Also recorded from single caves in Blount and Roane counties, Tenn. (Steeves and Holsinger 1968).

Caecidotea vandeli (Bresson) (TB)

Virginia.—Bath Co.: Blowing Cave. Botetourt Co.: Brough Cave

No. 2. Giles Co.: New River Cave. Montgomery Co.: Erhart (type locality), Old Mill, and Slussers Chapel caves. Roanoke Co.: Goodwins Cave (?).

stygia group

Caecidotea recurvata (Steeves) (TB)

Tennessee.—Campbell Co.: Meredith Cave. Claiborne Co.: Buis Saltpetre, Chadwells, English, Hauser Spring, Kings Saltpetre, and Station Creek caves. Hancock Co.: Subers Cave. Union Co.: Coppock, Lost Creek, Ridenour Pit, Wolf, and Wright caves.

Virginia.—Lee Co.: Baileys, Bowling, Cave Springs, Combs No. 1, Cope, Crouse, Fisher, Gallohan No. 1 and 2, Gilliam, Golf Course No. 1 and 2, Kinzer Hollow, Litton No. 1, McClure, Minors Saltpetre, Molly Wagle, Roadside No. 1, Seal, Skull, Smiths Milk, Spangler, Sweet Potato, Taylor Pit, T-Bone, Thompson Cedar, Unthanks (type locality), and Young-Fugate caves. Russell Co.: Banners Corner, Breeding, Bundys Pearl, Burns, Daugherty, Grays, Indian, Jessie, Johnson, Munsey, Porgie Bundys, Seven Springs, Smiths, and "Sikes" (Hubricht 1943:697) caves. Scott Co.: Blair-Collins, Coley No. 2, Flannery, Jack. McDavids, Spurlock, and Taylor No. 1 caves. Smyth Co.: McMullin Cave. Washington Co.: Brass Kettle Hole Cave, Wise Co.: Hairy Hole, Kelly, Little Kennedy, Parsons, Rocky Hollow, and Wildcat Saltpetre caves.

Comments.—Also recorded from a spring in Knox County (see Fleming 1972) and a cave in Washington County, both in eastern Tennessee. "*Asellus forcipitus* n. sp." recorded from English Cave by Dearolf (1953), was never described in the literature and should be regarded as a *nomen nudum*.

Caecidotea richardsonae Hay (TB)

Tennessee.—Claiborne Co.: Buis Saltpetre, Cline, and Holt caves. Grainger Co.: Horseshoe Cave. Hancock Co.: Fairmont School Cave. Hawkins Co.: Sensabaugh Saltpetre Cave.

Virginia.—Lee Co.: Gregory, Olinger, and Smiths Milk caves. Scott Co.: Blair-Collins, Horton, Moccasin Valley, and Wolfe caves. Tazewell Co.: Bowens, Fallen Rock, Hugh Young, Lost Mill No. 3, Rosenbaums Water, and Stonley caves.

Comments.—Also reported from caves and occasionally wells in central and northeastern Alabama, northwestern Georgia, and south-central Tennessee (Steeves 1963b, 1969; Fleming 1972).

Ungrouped Species

Caecidotea intermedia (Forbes) (AC?)

Virginia.—Smyth Co.: Interstate-81 Cave.

Caecidotea racovitzai racovitzai Williams (TX?)

Virginia.—Tazewell Co.: Lawson and Quarry caves.

Caecidotea pricei Levi (TB)

Virginia.—Augusta Co.: Barterbrook Spring Cave. Frederick Co.: Ogdens Cave. Page Co.: Will Mauck Cave. Rockbridge Co.: Bathers, Bell, Billy Williams, Showalters, and Tolleys caves. Rockingham Co.: Endless Caverns. Shenandoah Co.: Flemings Cave. Warren Co.: Skyline Caverns. Also: "Water Cave, Va." (Dearolf 1953:227).

Comments.—Outside the study area, this species is recorded from groundwater habitats (mostly caves) in central Maryland, southern Pennsylvania, and eastern West Virginia (Holsinger and Steeves 1971, Franz and Slifer 1971, Holsinger 1976, Holsinger et al. 1976). Within the study area, it is also recorded from three small springs or seeps in Rockingham County and one spring in Rockbridge County (see Holsinger and Steeves 1971).

Asellus condei, described by Chappuis (1957) from Ogdens Cave, is considered a synonym of *C. pricei* (see Holsinger and Steeves 1971, Fleming 1973).

Caecidotea sp. A (TB)

Virginia.—Lee Co.: Cliff Cave.

Comments.—Fleming (1972) listed this population as belonging to *Caecidotea scrupulosa* Williams, but subsequent examination indicates that it represents an undescribed troglobitic species.

Caecidotea spp. (TB)

Tennessee.—Hancock Co.: Panther Creek Cave. Union Co.: Oaks Cave.

Virginia.—Alleghany Co.: Paxtons Cave. Botetourt Co.: Eagle Rock Cave. Highland Co.: Aqua, Better Forgotten, and Roaring Springs caves. Lee Co.: Gilley Cave. Scott Co.: Grigsby and Pond caves. Smyth Co.: Buchanan Saltpetre Cave. Washington Co.: Neals and Reeds No. 1 caves.

Comments.—Collections from the caves listed above lacked males, therefore precluding specific determinations.

Lirceus culveri Estes and Holsinger (TB)

Virginia.—Scott Co.: McDavids Cave (type locality).

Lirceus usdagalun Holsinger and Bowman (TB)

Virginia.—Lee Co.: Gallohan No. 1 (type locality), Gallohan No. 2, Surgener, and Thompson Cedar caves.

Lirceus spp.

Tennessee.—Claiborne Co.: Billingsley and Lower Coonsies Creek caves. Hancock Co.: Lawsons Cave No. 3.

Virginia.—Lee Co.: Baileys, Olinger, and Young-Fugate caves. Rockbridge Co.: Tolleys Cave. Scott Co.: Alley, Wolfe, Coley No. 2, and Speers Ferry caves. Tazewell Co.: Fallen Rock, Gillespie Water, and Hugh Young caves. Washington Co.: Singleton Cave.

Comments.—Several species, some apparently undescribed, are represented in these collections; none appears to be of troglobitic facies (see Holsinger and Bowman 1973).

Suborder Flabellifera

Family Cirolanidae

Antrolana lira Bowman (TB)

Virginia.—Augusta Co.: Madisons Saltpetre (type locality) and Stegers Fissure caves.

Suborder Oniscoidea

Family Armadillidiidae

Armadillidium vulgare (Latreille) (TX or AC)

Virginia.—Alleghany Co.: Lowmoor Cave. Augusta Co.: Madisons Saltpetre Cave. Bath Co.: Roy Lyle Cave. Page Co.: Foltz Cave No. 1. Rockbridge Co.: Doll House and Tolleys caves.

Family Ligiidae

Ligidium elrodii (*s. lat.*) (Packard) (TB)

Tennessee.—Claiborne Co.: Lower Coonsies Creek Cave. Hancock Co.: Cantwell Valley Cave. Sullivan Co.: Bristol Caverns.

Virginia.—Lee Co.: Bowling and Waltons caves. Scott Co.: Coley Cave No. 2.

Ligidium sp.

Virginia.—Craig Co.: New Castle Murder Hole Cave. Lee Co.: Carter Cave.

Comments.—These populations are probably *L. elrodii*, but the lack of males precludes specific determination.

Family Oniscidae

Cylisticus convexus (De Greer) (TX)

Virginia.—Botetourt Co.: Thomas Cave. Roanoke Co.: Dixie Caverns. Smyth Co.: Stones No. 2 and Sugar Grove No. 10 caves.

Family Trichoniscidae

Amerigoniscus henroti Vandel (TB)

Virginia.—Lee Co.: Cope, Gallohan No. 1, Gilley (type locality), Kinzer Hollow, Smiths Milk, Spangler, Sweet Potato, and Unthanks caves.

Amerigoniscus paynei (Muchmore) (TB)

Tennessee.—Hancock Co.: Fairmont School Cave. Union Co.: Lost Creek and Wolf caves.

Comments.—This species is also recorded from Hill and Offutts (type locality) caves just south of the study area in Anderson County and may also inhabit Melton Hill Cave No. 1 in Roane County, Tenn. (see Muchmore 1970a).

Haplophthalmus danicus Budde-Lund (TP or TX)

Virginia.—Lee Co.: Ruths Cave. Page Co.: Luray Caverns. Pulaski Co.: James Cave. Roanoke Co.: Goodwins Cave. Rockbridge Co.: Showalters Cave. Rockingham Co.: Massanutten Caverns. Russell Co.: Banners Corner Cave. Tazewell Co.: Wagoners Cave.

Miktoniscus medcofi (Van Name) (TP or TX)

Virginia.—Alleghany Co.: Lowmoor Cave. Giles Co.: Smokehole Cave. Rockbridge Co.: Buck Hill Cave.

Miktoniscus racovitzai racovitzai Vandel (TB)

Virginia.—Alleghany Co.: Island Ford and Lowmoor caves. Botetourt Co.: Peery Saltpetre Cave. Page Co.: Luray Caverns (type locality). Rockbridge Co.: Buck Hill Cave. Shenandoah Co.: Shenandoah Caverns.

Miktoniscus spp.

Tennessee.—Campbell Co.: Norris Dam Cave. Sullivan Co.: Bristol Caverns.

Virginia.—Washington Co.: Hall Bottom Cave No. 1.

Comments.—These populations may be referable to *M. medcofi* after further study.

Trichoniscus pusillus Brandt (TX)

Virginia.—Augusta Co.: Staunton Quarry Cave (?). Lee Co.: Cudjos Cavern. Tazewell Co.: Wagoners Cave. Washington Co.: Hall Bottom Cave No. 1.

Order Decapoda

The only decapod crustaceans recorded from caves in Virginia and eastern Tennessee are crayfishes of the family Astacidae. Two species of the genus *Cambarus* are known: *C. bartonii* (*s. lat.*) and *C. dubius* (see also Hobbs et al. 1977, Holthuis 1986). The former is common throughout much of the eastern United States (see Hobbs 1972, 1974) and is often found in caves of the Appalachian region, where it is probably a troglophile. The latter, recorded only once from a cave in the study area, is apparently an accidental, inasmuch as it is normally found in burrows and not caves (Hobbs 1974). In caves *C. bartonii* is usually found in streams or stream pools. Individuals or whole populations may sometimes be quite pale, probably reflecting ecophenotypic rather than genetic changes (see Hobbs and Barr 1960). In addition to the caves listed below, there are many sight records for *C. bartonii*, especially from caves in the Powell and Clinch valleys where relatively large populations were sometimes observed in streams. According to Hobbs (1972, 1974) at least two subspecies inhabit caves of the study area: *C. b. cavatus* Hay in the upper Tennessee River drainage of southwestern Virginia and eastern Tennessee, and *C. b. bartonii* (Fabricius) elsewhere. The systematic status of *C. b. cavatus*, however, is unclear and in need of further evaluation (H. H. Hobbs, Jr., pers. comm.).

Family Astacidae

Cambarus (*Cambarus*) *bartonii* (s. lat.) (Fabricius) (TP)

Tennessee.—Hancock Co.: Cantwell Valley and Fairmont School caves.

Virginia.—Alleghany Co.: Paxtons and Wares caves. Augusta Co.: Barterbrook Spring Cave. Bath Co.: Roy Lyle Cave. Highland Co.: Aqua Cave. Lee Co.: Crouse Cave. Rockbridge Co.: Billy Williams Cave. Russell Co.: Quillens Field Cave. Scott Co.: Johnson, McDavids, Riggs Chapel, and Wolfe caves. Smyth Co.: Atwells Tunnel Cave. Tazewell Co.: Fallen Rock, Stonely, and Wagoners Cave. Warren Co.: Skyline Caverns. Washington Co.: Hall Bottom Cave No. 1.

Cambarus (*Jugicambarus*) *dubius* Faxon (AC)

Virginia.—Russell Co.: Jessie Cave.

Cambarus sp.

Virginia.—Montgomery Co.: Fred Bull Cave. Tazewell Co.: Steeles Cave.

PHYLUM ARTHROPODA: SUBPHYLUM CHELICERATA

All cavernicolous chelicerates are in the class Arachnida, and in the study area they include pseudoscorpions, acarines (mites and ticks), harvestmen, and spiders. A considerable number of arachnids are troglobites, especially spiders and pseudoscorpions.

Subclass Pseudoscorpiones

Although represented by a significant number of species, pseudoscorpions are generally very rare in a given cave, and a majority of the species are known only from a few individuals. Cavernicolous pseudoscorpions are usually found in damp places, frequently under rocks or small pieces of wood. In caves of Virginia and eastern Tennessee, they are represented by four families, six genera, and 15 described species. Two species are provisionally recognized but remain undescribed to date. Most species are troglobitic.

The family Chthoniidae contains the majority of cave species, and all of these are troglobites in the study area. *Kleptochthonius* (subgenus *Chamberlinochthonius*) includes 10 species (2 undescribed) (see Malcolm and Chamberlin 1961; Muchmore 1970b, 1974, 1976a), all of which are rare, extremely localized endemics (Fig. 15) that are morphologically strongly modified for cave existence (Fig. 19E). Only one species, *K. affinis*, has been recorded from more than a single cave to date. All but two species of *Kleptochthonius* from the study area occur in caves of the upper Tennessee drainage in southwestern Virginia and eastern Tennessee. Five species from this area (viz., *K. affinis*, *K. binoculatus*, *K. gertschi*, *K. proximosetus*, and *K. regulus*) are very closely allied morphologically and were placed in a *proximosetus* group by Muchmore (1976a). Other chthoniids include two species of *Apochthonius* (see Muchmore 1963, 1967) and one species of *Mundochthonius* (see Benedict and Malcolm 1974), all highly localized in distribution (Fig. 15).

The families Neobisiidae and Syarinidae also include troglobites—*Microcreagris valentinei* in the former and *Chitrella superba* in the latter. Both species are known only from single caves (Fig. 15) and are quite rare (Chamberlin 1962, Muchmore 1973). *Chitrella cavicola*, a troglophile or trogloxene recorded from Endless Caverns in Rockingham County, is also reported from several epigean localities in northern Virginia and a cave in Berkeley County, W.Va. (Muchmore 1973, Holsinger et al. 1976).

The family Chernetidae is represented by a single species, *Hesperochernes mirabilis* (formerly in *Pseudozaona*, see Muchmore

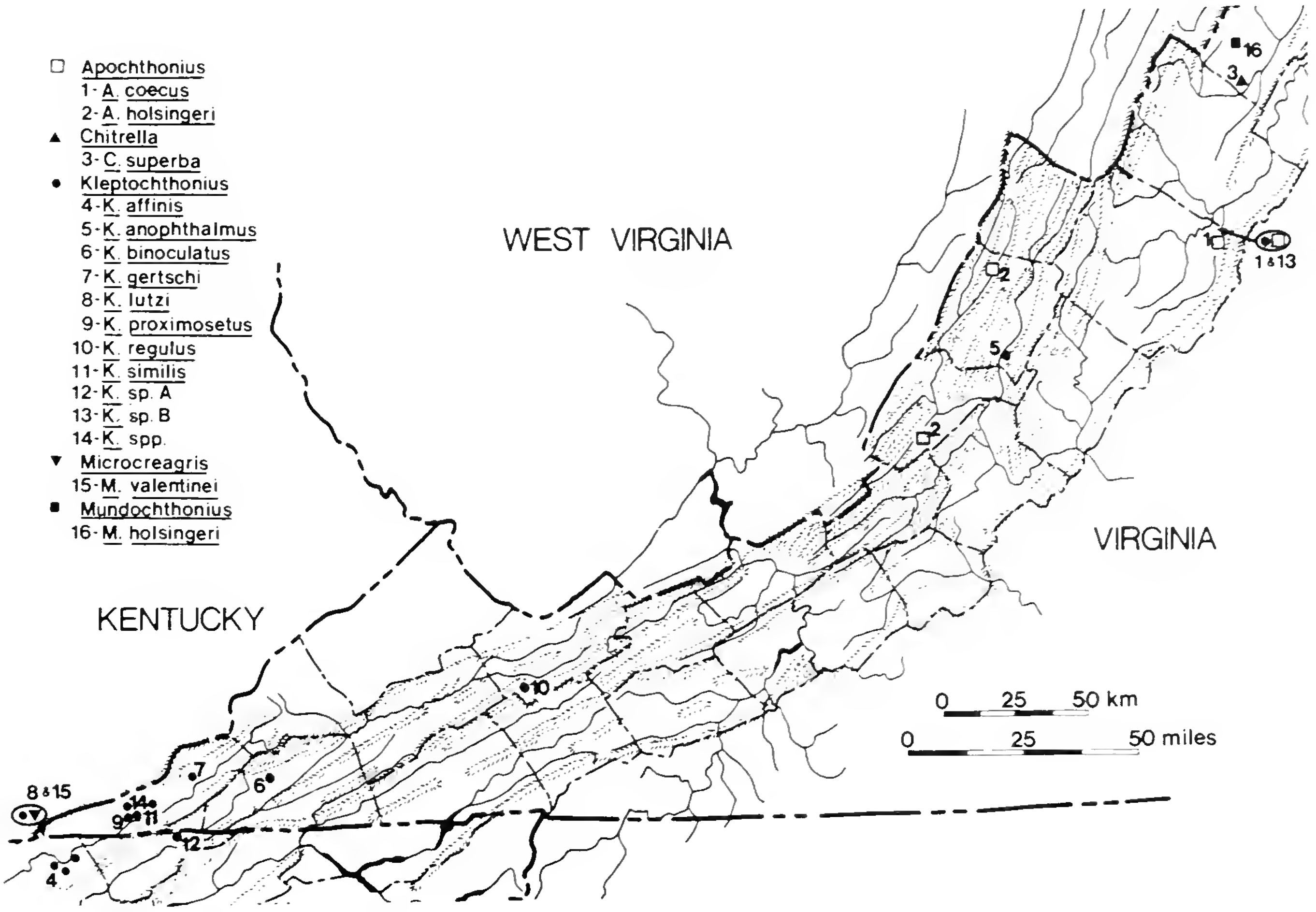

Fig. 15. Distribution of troglobitic pseudoscorpions (*Apochthonius*, *Chitrella*, *Kleptochthonius*, *Microcreagris*, and *Mundochthonius*) in the study area. Two symbols in a circle indicate two species from the same cave.

1981), reported from a cave at Pennington Gap (possibly Gilley Cave). This species is also recorded from several caves in south-central Kentucky (Hoff 1958, Barr 1967a), and, although never recorded outside caves, it is probably not a troglobite (see Chamberlin and Malcolm 1960, Barr 1967a).

Family Chernetidae

Hesperochernes mirabilis (Banks) (TP?)

Virginia.—Lee Co.: "Cave at Pennington Gap" (Banks 1895:4).

Hesperochernes spp.

Virginia.—Bath Co.: Cave Run Pit Cave. Giles Co.: Smokehole Cave. Highland Co.: Van Devanters Cave.

Family Chthoniidae

Apochthonius coecus (Packard) (TB)

Virginia.—Augusta Co.: Grand Caverns (type locality) and Madisons Saltpetre Cave.

Apochthonius holsingeri Muchmore (TB)

Virginia.—Alleghany Co.: Blue Springs Cave (?). Bath Co.: Cave Run Pit Cave (type locality).

Comments.—The single specimen from Blue Springs Cave is a tritonymph, and determination is tentative pending further study (Muchmore 1976b).

Apochthonius sp.

Virginia.—Giles Co.: Harris Cave.

Kleptochthonius (*Chamberlinochthonius*) *affinis* Muchmore (TB)

Tennessee.—Claiborne Co.: Chadwells (type locality), English and Jennings caves.

Kleptochthonius (*C.*) *anophthalmus* Muchmore (TB)

Virginia.—Bath Co.: Porters Cave (type locality).

Kleptochthonius (*C.*) *binoculatus* Muchmore (TB)

Virginia.—Scott Co.: Hill Cave (type locality).

Kleptochthonius (*C.*) *gertschi* Malcolm and Chamberlin (TB)

Virginia.—Lee Co.: Gilley Cave (type locality).

Kleptochthonius (*C.*) *lutzi* Malcolm and Chamberlin (TB)

Virginia.—Lee Co.: Cudjos Cavern (type locality).

Kleptochthonius (*C.*) *proximosetus* Muchmore (TB)

Virginia.—Lee Co.: Gallohan Cave No. 1 (type locality).

Kleptochthonius (*C.*) *regulus* Muchmore (TB)

Virginia.—Tazewell Co.: Fallen Rock Cave (type locality).

Kleptochthonius (*C.*) *similis* Muchmore (TB)

Virginia.—Lee Co.: Sweet Potato Cave (type locality).

Kleptochthonius (*C.*) sp. A (TB)

Tennessee.—Hancock Co.: Panther Creek Cave.

Comments.—This population represents an undescribed species (W. B. Muchmore, in litt.).

Kleptochthonius (*C.*) sp. B (TB)
Virginia.—Augusta Co.: Madisons Saltpetre Cave.
Comments.—This population represents an undescribed species (see Muchmore 1970b).

Kleptochthonius (*C.*) spp.
Virginia.—Lee Co.: Elys Moonshine and Molly Wagle caves.
Comments.—Specimens from these caves are juveniles (deutonymphs or tritonymphs), therefore precluding specific determination.

Mundochthonius holsingeri Benedict and Malcolm (TB)
Virginia.—Shenandoah Co.: Helsley Cave (type locality).

Family Neobisiidae

Microcreagris valentinei Chamberlin (TB)
Virginia.—Lee Co.: Cudjos Cavern (type locality).

Family Syarinidae

Chitrella cavicola (Packard) (TP or TX)
Virginia.—Rockingham Co.: Endless Caverns (type locality).

Chitrella superba Muchmore (TB)
Virginia.—Shenandoah Co.: Maddens Cave (type locality).

Subclass Acari

Although ticks (Ixodida) are occasionally transported into caves by bats or pack rats, most cavernicolous acarines are mites. Several families of mites have been recorded from caves in Virginia and east Tennessee, including Laelapidae and Parasitidae in the order Parasitiformes and Eupodidae and Rhagidiidae in the order Acariformes (see Holsinger 1965a). Aside from Rhagidiidae, however, the taxonomy and ecology of cave-associated mites is very poorly known. Rhagidiid mites are relatively common in caves, and to date four genera and five species have been recorded from the study area (Fig. 16). In caves these mites are usually found in mesic areas beneath rocks or decomposing organic detritus. The family is primarily edaphic; although many species are reported from caves in the Northern Hemisphere, only a few appear to be bona fide troglobites (Zacharda 1980). The possession of troglomorphisms and restriction to caves are criteria used by Zacharda (1980) and Zacharda and Elliott (1981) to distinguish troglobites from troglophiles and trogloxenes. In the Virginia-east Tennessee cave-mite fauna, two species are possibly troglobitic, whereas three are probably troglophilic.

The most common cave mite in Virginia is *Robustocheles hilli* (Fig. 19c), an apparent troglophile, which is also recorded from many caves in the eastern and western United States (Zacharda 1985) and from epigean habitats in Alaska and northern Canada (Zacharda 1980, Zacharda and Elliott 1981). *Poecilophysis weyerensis* (formerly *Rhagidia weyerensis*) was originally described from Grand Caverns by Packard

(1888) and thought to be a troglobite. It was redescribed by Holsinger (1965b) and subsequently reported from caves in Missouri, New Mexico, and Mexico by Elliott and Strandtmann (1971). Zacharda (1980) listed this species from Long Cave in Edmonson County, Ky. (synonym = *Rhagidia cavernarum*) and from epigean localities (scree and moist ground litter) in Czechoslovakia, but questioned the records given by Elliott and Strandtmann (1971). Zacharda (1985) gave additional cave records for this species in the study area (see list below) and also recorded it from a cave in Monroe County, Tenn.

Three other species of rhagidiid mites have been identified from caves in the Virginia-east Tennessee area by Zacharda (1985). Two of these, *Foveacheles paralleloseta* and *Rhagidia varia*, are probably troglobites since they possess some troglomorphisms and are known only from caves. The third species, *Poecilophysis extraneostella*, although known only from caves at present, is not troglomorphic and is probably a troglophile that eventually will be found outside caves.

Linopodes sp. (possibly *motatorius*; see Holsinger 1965a), a member of the family Eupodidae, was noted occasionally in study-area caves, but specimens were not collected.

Order Parasitiformes

Suborder Ixodida

Family Ixodidae
  Ixodes cookei Pakcard (AC)
    Virginia.—Giles Co.: Harris Cave.

Suborder Gamasida

Family Laelapidae
  Androlaelaps sp.
    Virginia.—Shenandoah Co.: Shenandoah Wild Cave.
  Hypoaspis sp.
    Virginia.—Shenandoah Co.: Shenandoah Wild Cave.

Family Parasitidae
  Eugamasus sp.
    Virginia.—Russell Co.: Banners Corner Cave.
  Pergamasus sp.
    Virginia.—Russell Co.: Banners Corner Cave.

Unidentified gamasid mites are recorded as follows:
  Tennessee.—Anderson Co.: Hill Cave. Union Co.: Lost Creek Cave.
  Virginia.—Rockbridge Co.: Showalters Cave. Tazewell Co.: Fallen Rock and Wagoners caves.

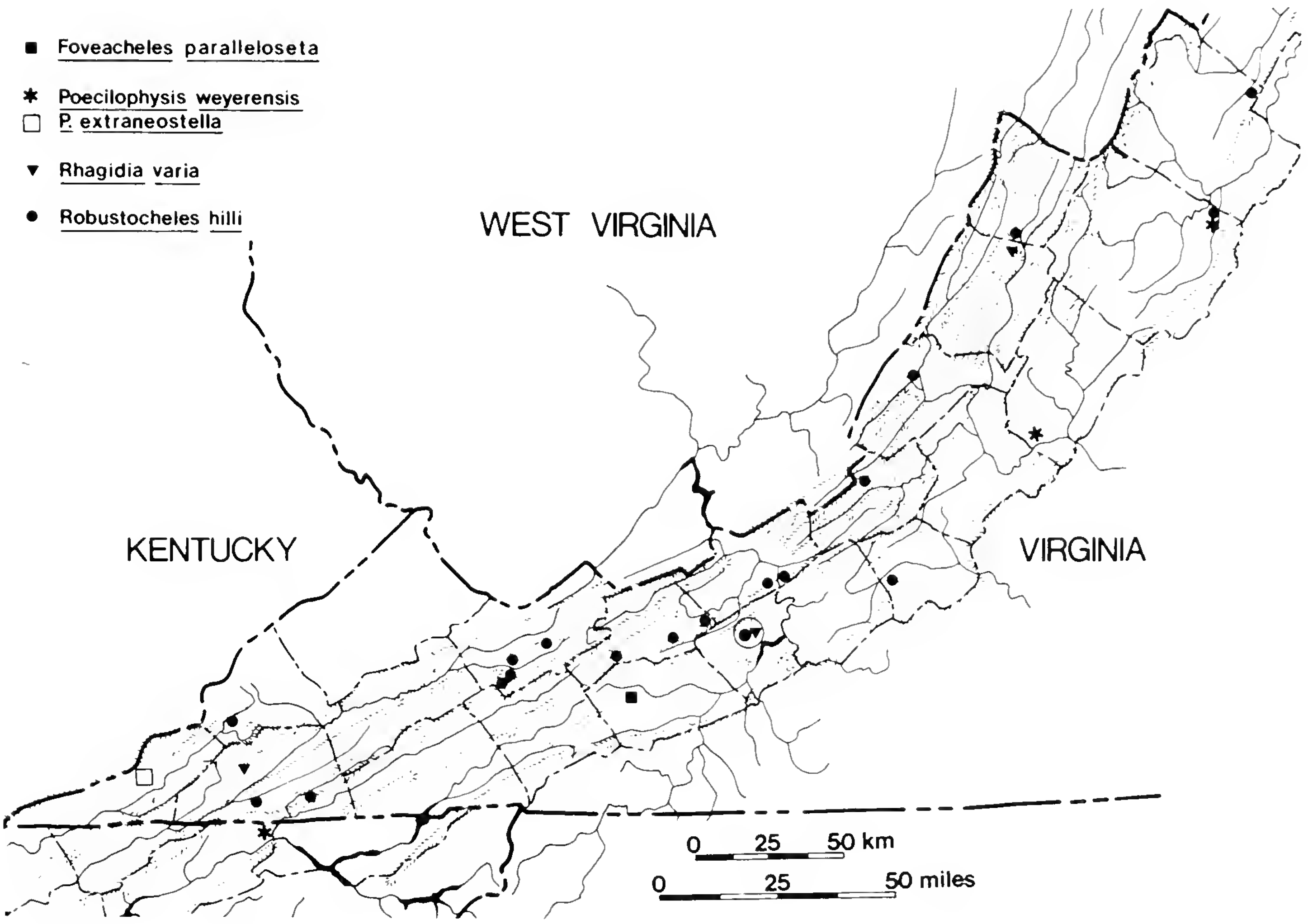

Fig. 16. Distribution of cavernicolous mites (*Foveacheles*, *Poecilophysis*, *Rhagidia*, and *Robustocheles*) in the study area. Two symbols in a circle indicate two species from the same cave.

Order Acariformes

Family Rhagidiidae

Foveacheles paralleloseta Zacharda (TB?)

Virginia.—Wythe Co.: Sam Six Cave.

Poecilophysis extraneostella Zacharda (TP)

Virginia.—Lee Co.: Bowling Cave.

Comments.—Also recorded from Steeles Cave, Monroe County, W.Va.

Poecilophysis weyerensis (Packard) (TP)

Tennessee.—Hawkins Co.: Sensabaugh Saltpetre Cave.

Virginia.—Augusta Co.: Grand Caverns (type locality). Rockbridge Co.: Buck Hill Cave.

Rhagidia varia Zacharda (TB?)

Virginia.—Bath Co.: Butler-Sinking Creek Cave. Pulaski Co.: Sam Bells Cave. Scott Co.: Hill Cave.

Comments.—Also recorded from single caves in Greenbrier and Pocahontas counties, W.Va.

Robustocheles hilli (Strandtmann) (TP)

Tennessee.—Hawkins Co.: Pearson Cave.

Virginia.—Alleghany Co.: Rumbolds Cave. Augusta Co.: Madisons Saltpetre Cave. Bland Co.: Banes Spring, Hamilton, and Repass Saltpetre caves. Craig Co.: Loneys Cave. Giles Co.: New River and Straleys No. 1 caves, Highland Co.: Aqua Cave. Pulaski Co.: Sam Bells Cave. Roanoke Co.: Goodwins Cave. Rockingham Co.: Endless Caverns. Scott Co.: Lane and Moccasin Valley caves. Tazewell Co.: Crocketts, Fallen Rock, Gillespie Water, and Gully caves. Wise Co.: Kelly Cave.

Undetermined rhagidiid mites:

Tennessee.—Claiborne Co.: Tazewell Saltpetre Cave.

Virginia.—Augusta Co.: Staunton Quarry Cave. Lee Co.: Waltons Cave. Montgomery Co.: Vickers Road Cave. Scott Co.: Greears Sweet Potato and Taylor No. 1 caves. Smyth Co.: Tilson Saltpetre Cave.

Subclass Opiliones

Except for *Leiobunum* (Phalangiidae), a sporadically common threshold trogloxene, opilionids (also called phalangids or harvestmen) are not common in the caves of Virginia and east Tennessee. Only a few species are recorded, and none is a troglobite. Probably the most interesting species with respect to cave association is *Erebomaster acanthina* (Erebomastridae), a troglophile found in several caves in the Shenandoah Valley (Fig. 19B). This species is also recorded from caves in Maryland (under *Phalangodes acanthina* by Franz and Slifer 1971) and West Virginia (under *Phalangodes flavescens weyerensis* by Holsinger et al. 1976), and from epigean localities in the Piedmont and Blue Ridge Mountains of North Carolina and Virginia (see Goodnight and Goodnight 1942, Briggs 1969). Packard (1888) described *Phalangodes flavescens* var. *weyerensis* from Grand Caverns, and Hadži (1935) later described *Cladonychium corii* from Endless Caverns. Both the "variety" *weyerensis* and *C. corii* are now considered synonyms of *Erebomaster acanthina*, which was redescribed in detail by Briggs (1969, in litt.).

Erebomaster acanthina may be a troglobite *in statu nascendi*, inasmuch as several populations appear to be cave limited and consist of individuals with reduced eyes and pigment. Both adults and juveniles of this species have been observed many times on damp, rotting wood in Endless Caverns and Madisons Saltpetre Cave.

The range of *Phalangodes laciniosa* (Phalangodidae), also a troglophile, extends to the southern end of the study area, where it has been found once in Norris Dam Cave in Campbell County. To the south and southwest this species is recorded from caves in northern Alabama, northern Florida, northwestern Georgia, and other parts of Tennessee, and occasionally from epigean localities in the same general region (Goodnight and Goodnight 1960, Barr 1961, Peck 1970, Holsinger and Peck 1971).

Crosbycus goodnighti (Nemastomatidae) is reported from Fountain Cave in Augusta County. According to W. A. Shear (in litt.), the description and figure of this species by Roewer (1951) apply to the juvenile of a European nemastomatid, and the identity of this taxon is therefore questionable.

Family Erebomastridae
  Erebomaster acanthina (Crosby and Bishop) (TP)
    Virginia.—Augusta Co.: Fountain, Grand (Caverns), and Madisons Saltpetre caves. Frederick Co.: Ogdens Cave. Rockingham Co.: Endless Caverns.
  Erebomaster (?) spp.
    Virginia.—Alleghany Co.: Paxtons Cave. Bath Co.: Roy Lyle Cave. Bland Co.: Newberry-Bane Cave.

Family Nemastomatidae
  Crosbycus (?) *goodnighti* (?) Roewer
    Virginia.—Augusta Co.: Fountain Cave.

Family Phalangiidae
  Leiobunum bicolor (?) (Wood) (TX)
    Comments.—One or more species of *Leiobunum* were seen sporadically in caves of the study area, but no attempt was made to collect them systematically.

Family Phalangodidae
  Phalangodes (*Bishopella*) *laciniosa* Crosby and Bishop (TP)
    Tennessee.—Campbell Co.: Norris Dam Cave.

Subclass Araneae

The cave spider fauna of Virginia and east Tennessee is quite diverse and comprises 13 families, 31 genera, and approximately 38 species. However, about one-third of the species recorded are accidentals or only marginal trogloxenes and contribute very little to the fauna of most caves. The remaining species are divided roughly equally between trogloxenes/trogophiles and troglobites. As noted in the list below, most of the trogloxenic and trogophilic spiders associated with caves in the study area are also recorded from caves in other parts of the eastern and southeastern United States as well as from epigean localities. Many species are associated with ground litter and similar habitats at the surface. In caves, spiders occupy a number of microhabitats and are often found around decomposing wood, in the damp recesses of passage walls and ceilings, and sometimes beneath rocks near the banks of streams.

Troglobitic spiders in the study area, as well as in most of the eastern United States, belong to the families Linyphiidae and Nesticidae. Five species of linyphiids have been recorded, all of which are presumably troglobitic but have wide ranges (Fig. 17) and occur outside of the Virginia-Tennessee cave region. *Anthrobia monmouthia* has been found in several Virginia caves and is also recorded from caves in south-central Kentucky, middle Tennessee, and southern West Virginia (Barr 1961, 1967a; Holsinger et al. 1976). The Appalachian Valley populations of Virginia and West Virginia may represent one or more subspecies and are in need of further study. In the study area *Bathyphantes weyeri* is known only from Grand Caverns but is also recorded from caves in Arkansas, Kentucky, Pennsylvania, West Virginia, and Wisconsin (Ivie 1969). According to W. J. Gertsch (unpublished data) this species was collected once from an epigean habitat. *Islandiana muma*, an extremely rare and poorly known species, was described from Buck Hill Cave in Rockbridge County but is also reported from a single cave in Colbert County, Ala. (Ivie 1965).

The most common, widespread linyphiid spider in Virginia and Tennessee is *Phanetta subterranea*. It is also common in caves throughout the eastern United States and ranges from Pennsylvania south to Georgia and Alabama and west to Illinois and Missouri. *Porrhomma cavernicolum* is also widespread in caves of the study area but is generally not as common as *P. subterranea*. It is recorded from caves throughout much of the central and eastern United States and ranges from Pennsylvania south to Georgia and west to Missouri and Oklahoma. Linyphiids have the widest ranges of any troglobites in North America, leading to the speculation that these are morphological species, each representing several separate gene pools (Barr 1967a, Holsinger et al. 1976).

With the exception of *Eidmannella pallida* (formerly *Nesticus pallidus*), a troglophile or trogloxene relatively common in caves throughout much of the United States and Mexico, cavernicolous spiders of the family Nesticidae in the study area have relatively restricted distributions (Fig. 18). Those that are not troglobites are represented by populations primarily limited to caves. The most common and widespread nesticid in the Appalachian region is *Nesticus carteri*, a troglophile that is sometimes quite abundant in caves of the Powell Valley (Fig. 19D). It is recorded from numerous caves and a few epigean localities (ground detritus) in southern Indiana, eastern Kentucky, eastern Tennessee, southwestern Virginia, and southeastern West Virginia (Gertsch 1984). In or near the study area this species has been collected from ground detritus in Dickenson County, Va., and Mercer County, W.Va. The type locality of *N. carteri* is Bat Cave (Carter Caves State Park), Carter County, Ky., and not Mammoth Cave as erroneously reported by Nicholas (1960) and Holsinger (1963a).

The other species of *Nesticus* from the study area have more closely circumscribed ranges and are largely restricted to areas east of the

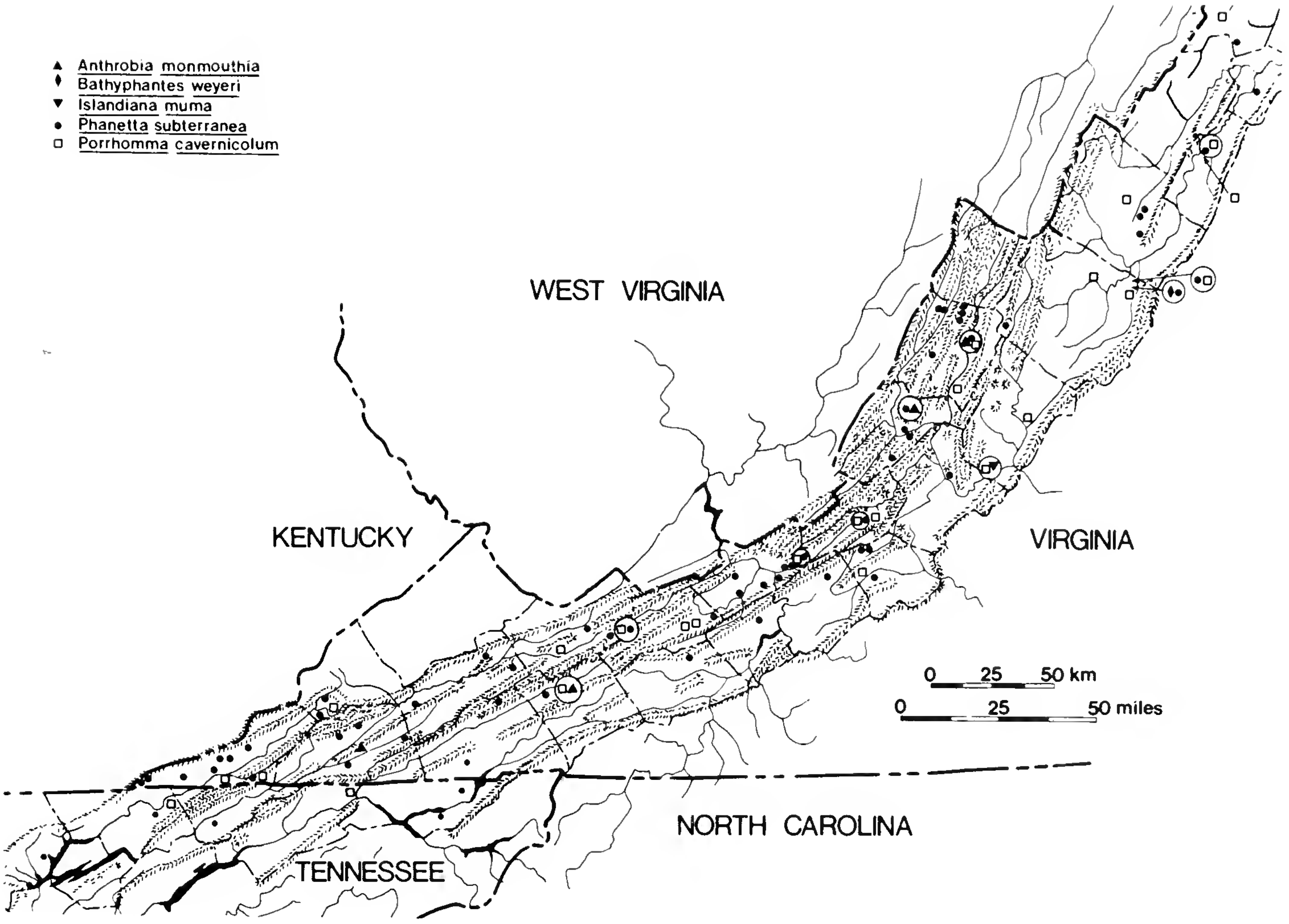

Fig. 17. Distribution of troglobitic spiders (*Anthrobia*, *Bathyphantes*, *Islandiana*, *Phanetta*, and *Porrhomma*) in the study area. Two or more symbols in a circle indicate two or more species from the same cave.

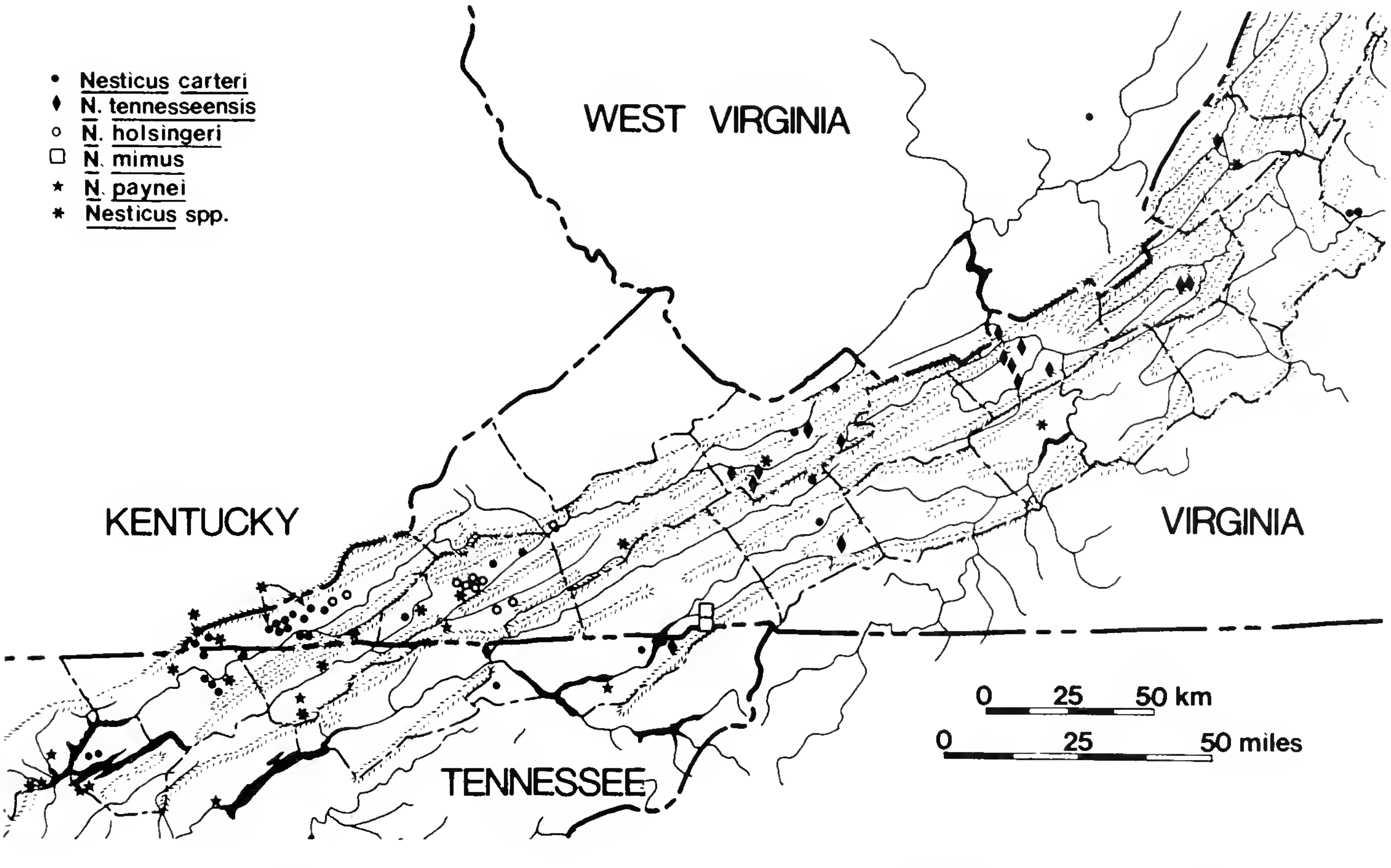

Fig. 18. Distribution of cavernicolous spiders (*Nesticus*) in the study area. Single cave localities for *N. carteri* in Greenbrier County, W.Va., and *N. tennesseensis* in Grainger County, Tenn., also shown. Epigean localities for *N. carteri* and *N. tennesseensis* not shown.

Appalachian Plateau. These four species are closely allied morphologically and are assigned to the *tennesseensis* group by Gertsch (1984). The most widespread member of this suite is *N. tennesseensis*, a probable troglobite with variation in both eye-pigment reduction and elongation of the legs. Its range extends from Highland County, Va., southwestward to Roane County, Tenn. In addition to the localities listed below, it is recorded from single caves in Grainger and Roane counties, Tenn., and from ground detritus (epigean) at single localities in Raleigh County, W.Va., and Giles and Highland counties, Va. (Gertsch 1984). The remaining three species were recently described by Gertsch (1984) and inhabit caves in the upper Tennessee drainage in southwestern Virginia and eastern Tennessee. *Nesticus holsingeri*, a probable troglobite with reduced eyes, is known only from caves in Lee and Scott counties. *Nesticus mimus* is recorded from two caves in Washington County and also from epigean habitats at higher elevations in Burke and Watauga counties in nearby North Carolina. *Nesticus paynei* has fully developed eyes but is at present unknown outside caves. This species is also recorded from caves just south of the study area in Anderson, Carter, and Knox counties, Tenn.

Probably the most conspicuous cave spider in the Virginia-east Tennessee area is the orb weaver *Meta menardi* (Argiopidae), a trogloxene or troglophile frequently seen near cave entrances. This species is widespread in caves of the eastern United States and is also found in western Europe. Sight records are numerous from the study area, but no attempt was made to collect it systematically.

Family Agelenidae

Calymmaria cavicola (Banks) (TP or TX)

Virginia.—Tazewell Co.: Steeles Cave.

Comments.—Also recorded from caves in Alabama, Georgia, Illinois, Kentucky, Tennessee, and West Virginia (Barr 1967a, Holsinger and Peck 1971, Holsinger et al. 1976, Peck and Lewis 1978); widespread in epigean localities.

Cicurina pallida Keyserling (TP or TX)

Virginia.—Augusta Co.: Fountain, Glade, and Madisons Saltpetre caves. Shenandoah Co.: Hensleys Cave.

Comments.—Also recorded from caves in Illinois and West Virginia (Holsinger et al. 1976, Peck and Lewis 1978); widespread in the eastern United States.

Circurina sp.

Virginia.—Rockbridge Co.: Tolleys Cave.

Family Anyphaenidae

Anyphaena sp. (AC)

Virginia.—Roanoke Co.: "Old Hollins Road Cave" (L. M. Ferguson, in litt.).

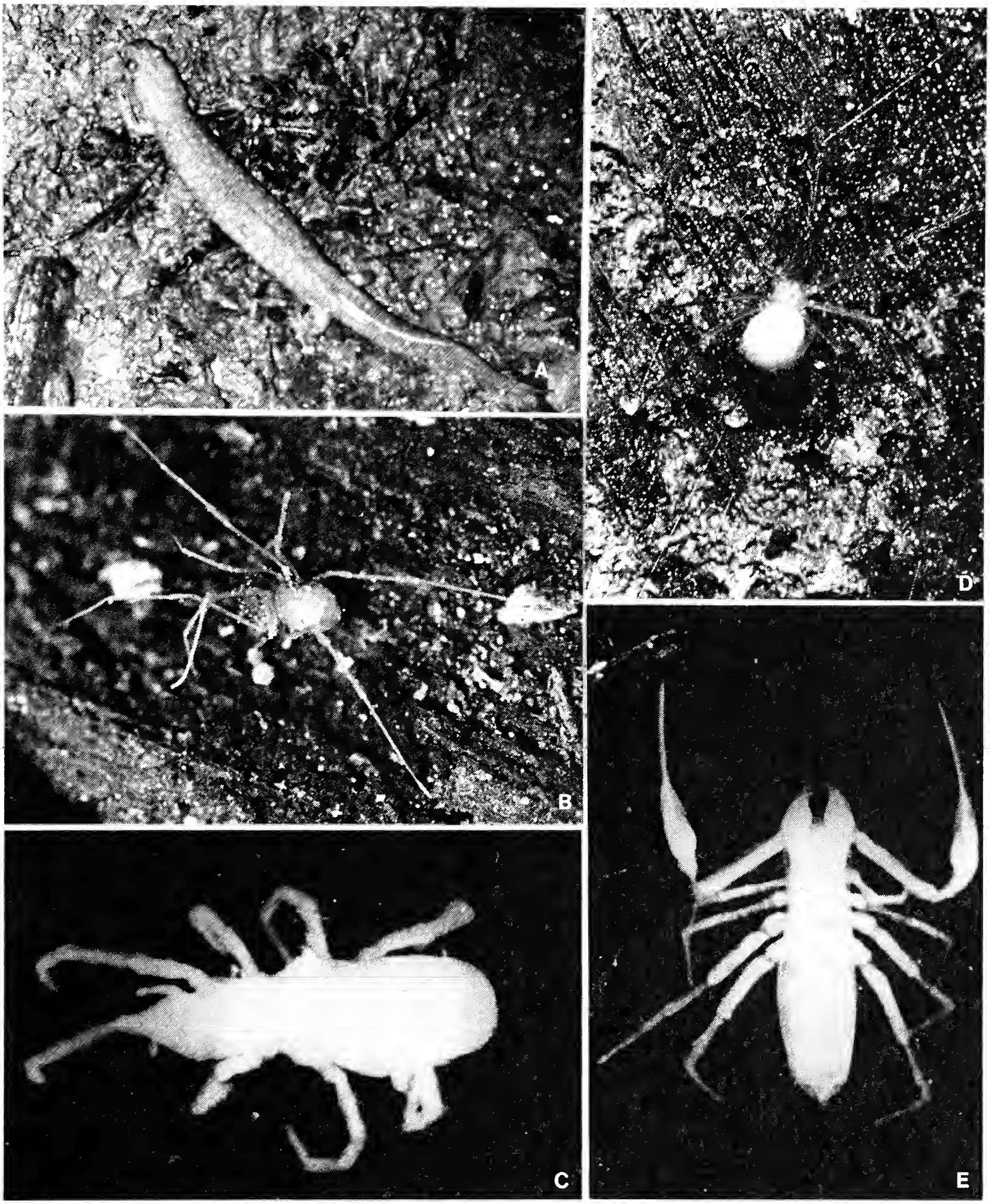

Fig. 19. Terrestrial cavernicoles from the study area (approximate body lengths in parentheses): A, salamander (adult), *Gyrinophilus porphyriticus* (13 cm); B, opilionid, *Erebomaster acathina* (3 mm); C, mite, *Robustocheles hilli* (1 mm); D, spider, *Nesticus carteri* (4 mm); E, pseudoscorpion, *Kleptochthonius* sp. (2 mm).

Aysha sp. (AC)
Virginia.—Roanoke Co.: Newmans Cave.

Family Argiopidae

Araniella displicata (Hentz) (AC)
Virginia.—Roanoke Co.: Newmans Cave.

Leucauge venusta Walckenaer (AC)
Virginia.—Craig Co.: Rufe Caldwell Cave.

Mangora placida Hentz (AC)
Virginia.—Rockbridge Co.: Bell Cave.

Meta menardi (Latreille) (TP or TX)
Comments.—Common throughout the study area; specific records not documented.

Family Clubionidae

Liocranoides unicolor Keyserling (TP or TX)
Virginia.—Washington Co.: Hall Bottom Cave No. 1.
Comments.—Common in caves in northern Alabama, northwestern Georgia, and south-central Tennessee (Barr 1961, Holsinger and Peck 1971).

Liocranoides sp. (TX?)
Virginia.—Washington Co.: Neals Cave.
Comments.—This population probably represents an undescribed species (W. J. Gertsch, in litt.).

Family Ctenizidae

Antrodiaetus unicolor (Hentz) (AC)
Virginia.—Tazewell Co.: Hugh Young Cave.

Family Dictynidae

Lathys sp. (AC)
Virginia.—Tazewell Co.: Cassell Farm Cave(s).

Family Linyphiidae

Anthrobia monmouthia Tellkampf (TB)
Virginia.—Alleghany Co.: Wares Cave. Bath Co.: Clarks Cave. Scott Co.: Harris Pit Cave. Smyth Co.: Buchanan Saltpetre Cave.

Bathyphantes (*Bathyphantes*) *albiventris* (Banks) (TX or AC)
Virginia.—Lee Co.: Bowling Cave.
Comments.—Reported from epigean localities in the eastern and northeastern United States (Ivie 1969) and from one cave in Illinois (Peck and Lewis 1978).

Bathyphantes (*Weyerphantes*) *weyeri* (Emerton) (TB?)
Virginia.—Augusta Co.: Grand Caverns (type locality).

Centromerus cornupalpis (Pickard-Cambridge) (TX?)
Virginia.—Montgomery Co.: Erharts Cave.

Comments.—Also recorded from caves in Illinois and Missouri (see Peck and Lewis 1978).

Centromerus latidens (Emerton) (TP or TX)

Virginia.—Lee Co.: Sweet Potato Cave. Shenandoah Co.: Shenandoah Wild Cave.

Comments.—Widespread in the central and eastern United States; recorded from caves in Florida, Illinois, Kentucky, Missouri, Oklahoma, and possibly Texas (Reddell 1965, Barr 1967a, Peck 1970, Black 1971, Craig 1977, Peck and Lewis 1978).

Centromerus spp.

Tennessee.—Sullivan Co.: Bristol Caverns.

Virginia.—Alleghany Co.: Second Dam and Wares caves. Tazewell Co.: Lost Mill No. 1 and Steeles caves.

Frontinella communis Hentz (AC)

Virginia.—Rockbridge Co.: Showalters Cave.

Islandiana muma Ivie (TB)

Virginia.—Rockbridge Co.: Buck Hill Cave (type locality)

Islandiana (?) sp.

Virginia.—Montgomery Co.: Vickers Road Cave.

Linyphia marginata Koch (TX?)

Virginia.—Roanoke Co.: "Old Hollins Road Cave" (L. M. Ferguson, in litt.).

Comments.—Also recorded from a few caves in Missouri, Oklahoma, and West Virginia (Black 1971, Holsinger et al. 1976, Craig 1977).

Meioneta sp. (TX or AC)

Tennessee.—Claiborne Co.: Lower Coonsies Creek Cave.

Microneta sp. (TX or AC)

Virginia.—Alleghany Co.: Wares Cave.

Oreonetides sp. (AC)

Virginia.—Tazewell Co.: Rosenbaums Water Cave.

Phanetta subterranea (Emerton) (TB)

Tennessee.—Campbell Co.: Meredith and Norris Dam caves. Claiborne Co.: English and Keck No. 1 caves. Hancock Co.: Cantwell Valley Cave. Sullivan Co.: Bristol Caverns and Morrill Cave.

Virginia.—Alleghany Co.: Blue Springs, Island Ford, Lowmoor, and Wares caves. Augusta Co.: Fountain and Madisons Saltpetre caves. Bath Co.: Boundless, Breathing, Butler-Sinking Creek, Cave Run Pit, Clarks, Dunns, and Starr Chapel caves. Bland Co.: Hamilton Cave. Botetourt Co.: Peery Saltpetre and Thomas caves. Craig Co.: Rufe Caldwell Cave. Frederick Co.: Ogdens Cave. Giles Co.: Clover Hollow, Harris, New River, Smokehole, Starnes, Straleys No. 1, and Tawneys caves. Lee Co.: Bowling, Cudjos (Cavern), Cumberland Gap Saltpetre, Gibson-Frazier, Lucy Beatty, Molly Wagle, Olinger and Spangler caves. Montgomery Co.: Slussers Chapel Cave. Page Co.: Luray Caverns. Pulaski Co.: Sam Bells Cave. Roanoke Co.: Goodwins, Hodges No. 1, and Millers Cove caves. Rockingham Co.: Deer Hole, Massanutten (Caverns), and Stephens caves. Russell Co.: Banners Corner, Jessie, and Porgie Bundys caves. Scott Co.: Grigsby, Herron No. 1, Hill, and Kerns No. 1 caves. Smyth Co.: Beaver Creek Cave. Tazewell Co.: Cassell Farm, Lawson, and Steeles caves. Warren Co.: Skyline Caverns. Washington Co.: Hall Bottom No. 1 and Perkins caves. Wise Co.: Kelly and Wildcat Saltpetre caves. Wythe Co.: Picketts Cave.

Porrhomma cavernicolum (Keyserling) (TB)

Tennessee.—Claiborne Co.: Jennings Cave. Hawkins Co.: Sensabaugh Saltpetre Cave.

Virginia.—Augusta Co.: Fountain, Glade, and Madisons Saltpetre caves. Bath Co.: Clarks, Crossroads, Porters, and Witheros caves. Bland Co.: Coon and Banes Spring caves. Craig Co.: New Castle Murder Hole and Rufe Caldwell caves. Frederick Co.: Beans Cave. Giles Co.: Clover Hollow Cave. Lee Co.: Fisher and Unthanks caves. Page Co.: Luray Caverns and Ruffners Cave No. 1. Roanoke Co.: Dixie Caverns. Rockbridge Co.: Bell and Buck Hill caves. Rockingham Co.: Three-D Maze Cave. Smyth Co.: Buchanan Saltpetre Cave. Tazewell Co.: Gully and Lawson caves. Wise Co.: Parsons Cave.

Sciastes sp. (AC)

Virginia.—Lee Co.: Young-Fugate Cave.

Family Lycosidae

Lycosa rabida Walckenaer (AC)

Virginia.—Giles Co.: Tawneys Cave.

Comments.—Also reported from single caves in Oklahoma (Black 1971) and Texas (Reddell 1965).

Pirata sp. (AC)

Virginia.—Lee Co.: Bowling Cave.

Family Nesticidae

Eidmannella pallida (Emerton) (TP or TX)

Virginia.—Alleghany Co.: Walking Cave. Augusta Co.: Fountain, Glade and Grand (Caverns) caves. Giles Co.: New River Cave. Lee Co.: Cattle, Gallohan No. 1, Glen Olingers, and Smiths Milk caves. Page Co.: Luray Caverns and Ruffners Cave No. 1. Rockbridge Co.: Tolleys Cave. Rockingham Co.: Massanutten Caverns and Steam Hole Cave. Scott Co.: Ellington and Harris Pit caves. Washington Co.: Hall Bottom No. 1 and Perkins caves.

Nesticus carteri Emerton (TP)

Tennessee.—Claiborne Co.: Chadwells, English, Keck No. 1, and Tom Balls caves. Hancock Co.: Subers Cave. Sullivan Co.: Bristol Caverns. Union Co.: Lost Creek and Oaks caves.

Virginia.—Lee Co.: Cope, Cudjos (Cavern), Frazier, Gilliam, Kinzer Hollow, McClure, Molly Wagle, Roadside No. 1, Sheep, Skull, Skylight, Sweet Potato, Taylor Pit, and Thompson caves. Rockbridge Co.: Buck Hill and Doll House caves. Scott Co.: Blowing Hole, Greears Sweet Potato, and Kerns No. 1 caves. Smyth Co.: Atwells Tunnel and Stones No. 2 caves. Tazewell Co.: Quarry and Wagoners caves.

Nesticus holsingeri Gertsch (TB)

Virginia.—Lee Co.: Bowling and Gibson No. 1 caves. Scott Co.: Alley, Blair-Collins, Coley No. 2, Jackson, McDavids, Pond (type locality), and Taylor No. 1 caves. Wise Co.: Burtons Cave.

Nesticus mimus Gertsch (TP)

Virginia.—Washington Co.: Fritz Breathing and Shiloh School (type locality) caves.

Nesticus paynei Gertsch (TB?)

Tennessee.—Campbell Co.: "Hammers" (Gertsch 1984:28) and Norris Dam caves. Hancock Co.: Cantwell Valley Cave. Sullivan Co.: Morrills Cave. Union Co.: Coppock and Ridenour Pit caves.

Virginia.—Scott Co.: Wolfe Cave.

Nesticus tennesseensis (Petrunkevitch) (TB?)

Tennessee.—Hawkins Co.: Sensabaugh Saltpetre Cave. Sullivan Co.: Potters Cave.

Virginia.—Alleghany Co.: Rumbolds Cave. Craig Co.: Fish Hatchery and Walkthrough caves. Giles Co.: Ballards, Giant (Caverns), Glenlyn, Harris, Starnes, and Straleys No. 1 caves. Smyth Co.: Sugar Grove Cave No. 10. Tazewell Co.: Cassell Farm, Chimney Rock, Fallen Rock, Hugh Young, and Steeles caves.

Nesticus spp.

Tennessee.—Campbell Co.: Easterly Cave. Claiborne Co.: John Lard and Lower Coonsies Creek caves. Hancock Co.: Fairmont School and Lawsons No. 3 caves.

Virginia.—Alleghany Co.: Island Ford Cave. Lee Co.: Ely, Fisher, Indian, Spangler, and Young-Fugate caves. Pulaski Co.: Fifty-Foot Hell Cave. Russell Co.: Smiths Cave. Scott Co.: Flannery and Sparks caves. Tazewell Co.: Lost Mill Cave No. 1.

Comments.—Specimens from these caves are juveniles, therefore precluding specific determination.

Family Pholcidae

Pholcus phalangioides Fuesslin (TX)

Virginia.—Page Co.: Luray Caverns.

Comments.—Also reported from caves in Tennessee (Barr 1961).

Family Tetragnathidae

Tetragnatha sp. (AC)

Virginia.—Smyth Co.: Stones Cave No. 2.

Family Theridiidae

Achaearanea tepidariorum (Kock) (TP or TX)

Virginia.—Augusta Co.: Barterbrook Spring, Fountain, Grand (Caverns), and Madisons Saltpetre caves. Page Co.: Will Mauck Cave. Rockbridge Co.: Bell and Showalters caves.

Comments.—Recorded from caves throughout a large part of the southeastern and south-central United States (see Black 1971, Franz and Slifer 1971, Holsinger and Peck 1971, Holsinger et al. 1976, Craig 1977, Peck and Lewis 1978).

Family Thomisidae

Misumenops celer Hentz (AC)

Virginia.—Bath Co.: Porters Cave.

PHYLUM ARTHROPODA: SUBPHYLUM UNIRAMIA

Among the uniramians, the classes Diplopoda (millipeds) and Insecta are very well represented in the cave fauna of Virginia and east Tennessee; many troglobites and troglophiles are recorded in each group. Of significantly less importance in the regional cave fauna is the class Chilopoda (centipedes), species of which are seldom found in caves. Only one such species is a possible troglobite. Representatives of the classes Pauropoda and Symphyla are extremely rare in caves, and only a single cave record for each group is noted from the study area. Both pauropods and symphylans are rare, cryptic organisms that live in soil and leaf mold, and their occurrence in caves is probably accidental.

Class Pauropoda

Genus (?) species (?)

Virginia.—Roanoke Co.: McVitty Cave.

Class Symphyla

Scutigerella sp. (AC)

Virginia.—Lee Co.: Molly Wagle Cave.

Class Chilopoda

Cave records for centipedes are very sparse, and all species but one are recorded from single caves and are probably accidentals. *Nampabius turbator* (Lithobiidae), however, is recorded from two caves in Alleghany County and possesses reduced eyes and pigment (see Crabill 1952).

Although to our knowledge this species has not been found outside caves to date, its status as a troglobite is uncertain.

Order Geophilomorpha

Family Chilenophilidae

Arctogeophilus umbracticus (McNeill) (AC)

Virginia.—Scott Co.: Coley Cave No. 2. Shenandoah Co.: Pingleys Cave.

Order Lithobiomorpha

Family Ethypoliidae

Bothropolys multidentatus (Newport) (AC)

Virginia.—Rockbridge Co.: Tolleys Cave.

Family Lithobiidae

Nampabius parienus Chamberlin (TX or AC)

Virginia.—Smyth Co.: Atwells Tunnel Cave.

Nampabius turbator Crabill (TB?)

Virginia.—Alleghany Co.: Island Ford and Lowmoor (type locality) caves.

Nampabius sp.

Virginia.—Montgomery Co.: Erharts Cave.

Order Scolopendromorpha

Family Cryptopidae

Cryptops hortensis Leach (AC)

Virginia.—Lee Co.: Ruths Cave.

Crytops hyalinus Say (AC)

Virginia.—Tazewell Co. Gully Cave.

Scolopocryptops sexpinosus (Say) (AC)

Tennessee.—Claiborne Co.: English Cave.

Theatops posticus (Say) (AC)

Virginia.—Frederick Co.: Ogdens Cave.

Class Diplopoda

Millipeds are among the most common cavernicoles in Virginia and east Tennessee and are well represented by a diverse taxonomic assemblage consisting of 5 orders, 9 families, 12 genera, and 24 described species. Probably about one-half of the species collected from caves are undescribed at present. Approximately 25% of the species (including both described and undescribed forms) are troglobites. Cavernicolous millipeds are usually found in damp to wet areas associated with decomposing organic matter (e.g., wood, guano, carcasses)

Clearly the most significant order with respect to the diversity of cavernicolous species and their affinity for the cave environment is the Chordeumatida. All of the trogolobitic millipeds in the study area are included in this group, which is represented by the families Cleidogonidae, Conotylidae, Striariidae, and Trichopetalidae. The most widespread genus in caves of the study area is *Pseudotremia* (Cleidogonidae); it is found in all major drainage basins except the Shenandoah (Fig. 20, 21). In study-area caves the genus is represented by 12 described and approximately 20 undescribed species. Two species, *P. nodosa* (Fig. 31D) and *P. cavernarum*, have greatly reduced eyes (ocelli) and are either unpigmented or only lightly so. Both are clearly troglobitic (see Loomis 1939, Hoffman 1958, Shear 1972). Three other species—*P. deprehendor*, *P. tuberculata*, and *P. valga*—although known only from caves at present, are generally pigmented, possess relatively well-developed ocelli, and are questionable troglobites. The remaining species (described) have been found in both cave and epigean habitats and are apparently troglophiles.

Pseudotremia nodosa, originally described from English Cave in Claiborne County, has been recorded from many caves in the Powell Valley and, along with morphologically closely allied populations in the adjacent Clinch Valley, may represent a complex of closely similar (sibling ?) species (W. A. Shear, in litt.). This species, or complex, is the most troglomorphic member of the genus in the Virginia-east Tennessee area. Another species complex in the upper Tennessee basin is represented by *P. fracta* (*s. lat.*) and *P. cocytus.* Although Shear (1972) described *P. cottus* from cave and epigean habitats in Anderson, Blount, Knox, Roane, and Sevier counties, Tenn., Hoffman (1981) pointed out that *P. fracta* is actually the objective senior synonym of the species and therefore should take nomenclatural priority. Hoffman (1981) further divided *P. fracta* into four subspecies: *P. f. fracta*, *P. f. paynei*, *P. f. ingens*, and *P. f. nantahala*. The records listed below for *P. fracta* (*s. lat.*) are based on material determined by W. A. Shear as *P. cottus*, but in light of Hoffman's recent study, they probably should be assigned to *P. f. paynei.*

Pseudotremia hobbsi is the most common species of the genus in west-central Virginia, where it is recorded from a number of caves and a few epigean localities in the upper James and Roanoke basins; it is also found in southern West Virginia (Hoffman 1950, Shear 1972, Holsinger et. al. 1976).

As indicated in the list below, many species of *Pseudotremia* remain undescribed. In addition, numerous collections are undetermined, primarily because they lack mature males. Further, detailed taxonomic study of the genus is clearly needed to resolve species complexes and elucidate distributional patterns.

Three troglobitic species of *Trichopetalum* (Trichopetalidae), formerly assigned to *Zygonopus* by Causey (1960a) but reassigned to the present genus by Shear (1972), occupy caves from the New River

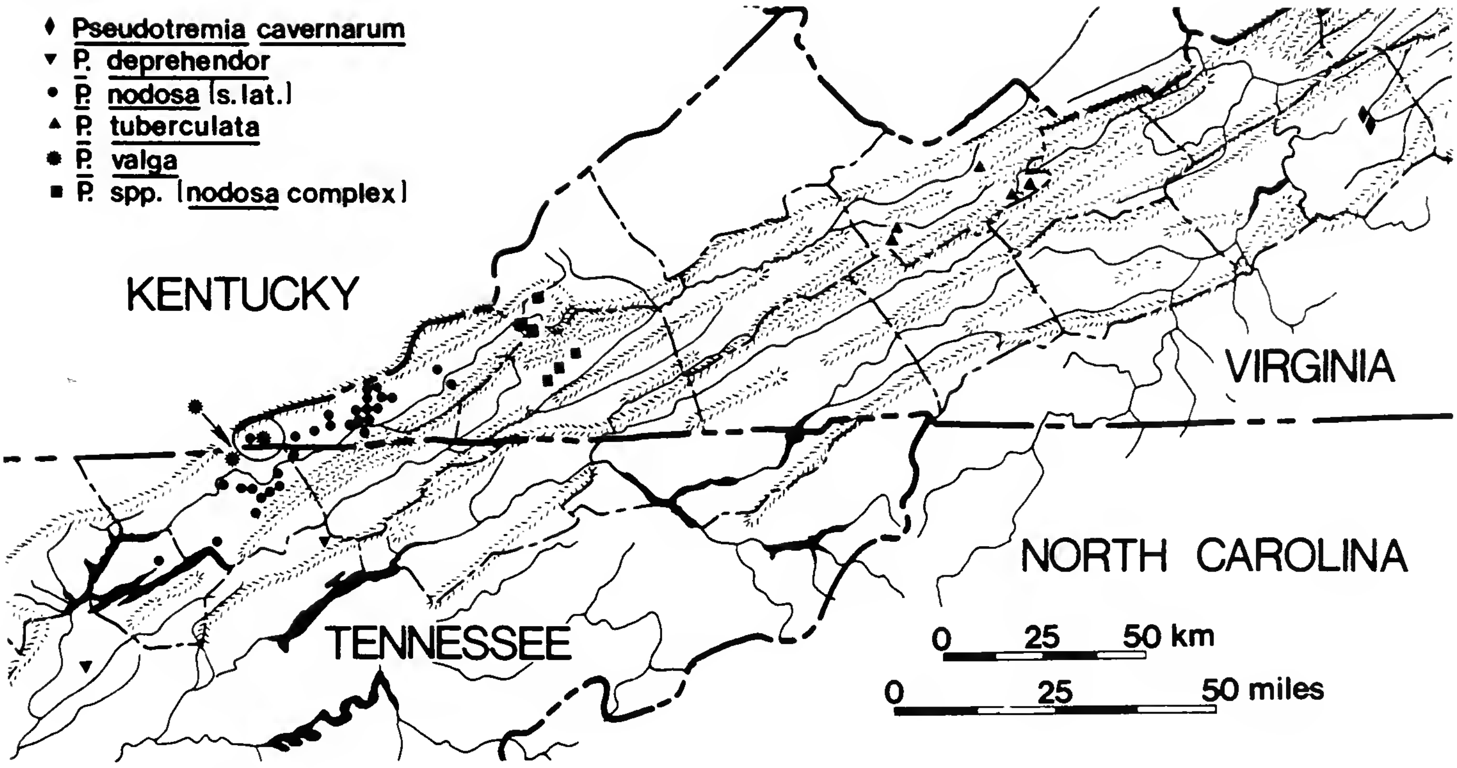

Fig. 20. Distribution of troglobitic millipeds (*Pseudotremia*) in the study area. Single locality for *P. deprehendor* in Anderson County, Tenn., also shown. Two symbols in a circle indicate two species from the same cave.

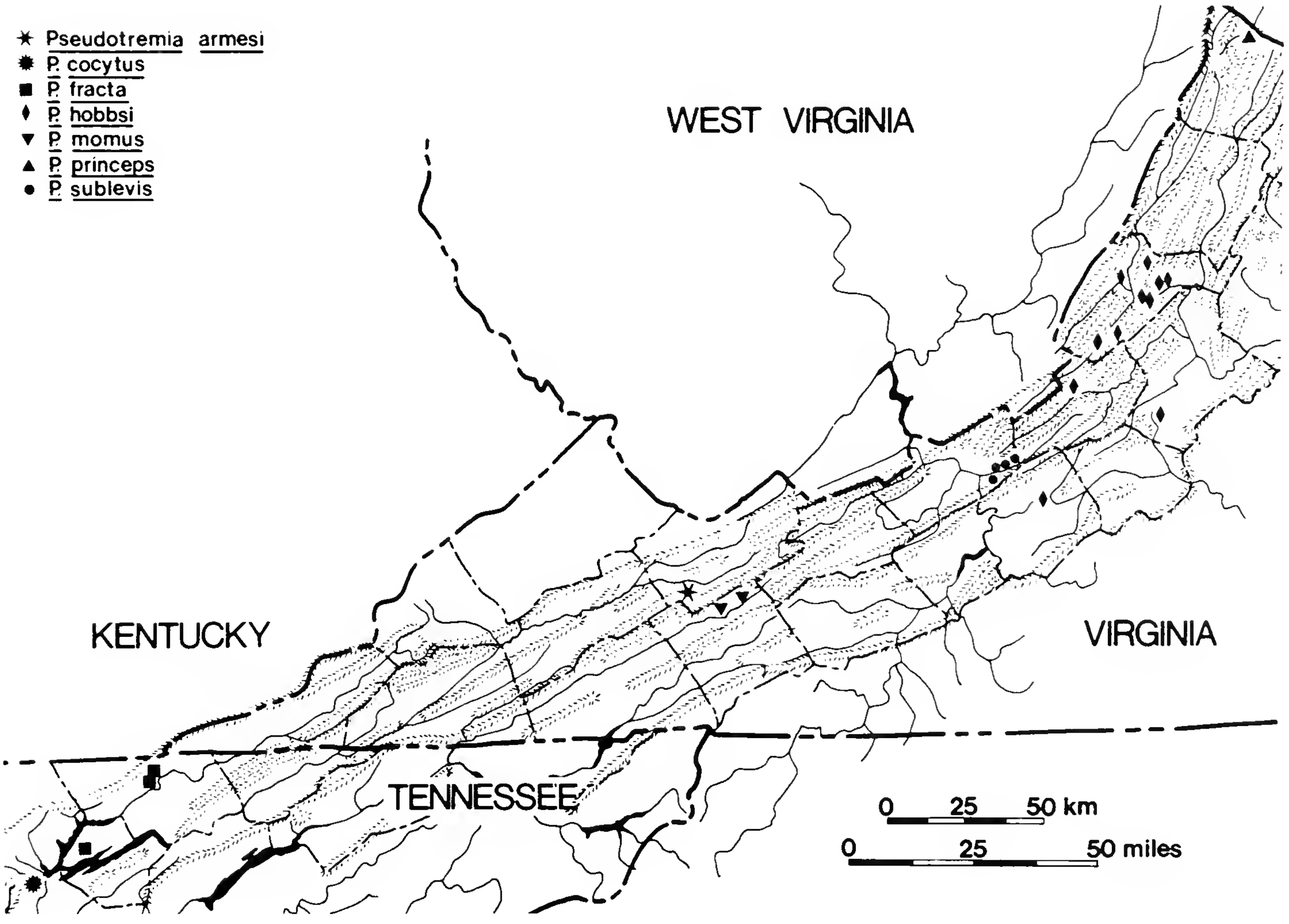

Fig. 21. Distribution of troglophilic millipeds (*Pseudotremia*) in the study area.

basin northeastward to the Shenandoah Valley (Fig. 22). The genus has never been found in caves of the upper Tennessee basin. Troglobitic species of *Trichopetalum* are usually much smaller than those of *Pseudotremia*, and all individuals lack ocelli and pigment.

Trichopetalum whitei inhabits caves of the Shenandoah Valley and is also recorded from caves in adjacent Grant and Pendleton counties, W.Va. (see Holsinger et al. 1976). *Trichopetalum weyeriensis* ranges generally south and west of *T. whitei* and is also recorded from caves in Greenbrier, Monroe, Pendleton, and Pocahontas counties, W.Va. (see Holsinger et al. 1976). *Trichopetalum packardi* occurs to the southwest of *T. weyeriensis* and is common in caves of the New River drainage; it is also recorded from caves in Greenbrier, Mercer, and Monroe counties, W.Va. (Holsinger et al. 1976).

On the basis of collections made in the early 1960s, N. B. Causey (in litt.) concluded that some populations of *T. weyeriensis* showed evidence of intergradation with both *T. packardi* and *T. whitei* in different parts of West Virginia. Based on these observations, Causey (1963) suggested that the three species are subspecies of a single, rather widespread species and not three distinct species as she had indicated earlier (Causey 1960a). In our judgment, this situation is far from being as clear-cut as Causey suggested and cannot be properly resolved until all collections from the Virginia-West Virginia cave region (many of which have been made since 1963) have been carefully examined and analyzed in detail.

Other chordeumatids recorded from caves in the study area include *Conotyla venetia* (Conotylidae), a possible trogloxene reported from one cave and two epigean localities in Alleghany County (see Shear 1971); and one or more species of *Striaria* (Striariidae), of which *S. columbiana* is a possible trogloxene known primarily from epigean habitats in northwestern Virginia, adjacent Maryland, and the District of Columbia (Chamberlin and Hoffman 1958). One population of *Striaria* from Madisons Saltpetre Cave in Augusta County appears to be troglomorphic and may represent an undescribed species, but additional study is needed to determine its status vis-à-vis *S. columbiana* and other species in the genus (W. A. Shear, in litt.).

In the order Julida, *Ophyiulus pilosus* (Julidae), an introduction from Europe and a probable troglophile, is rather widespread and occasionally abundant in Virginia caves. It is also recorded from caves in Maryland, Ohio, and West Virginia (see Franz and Slifer 1971, Holsinger et al. 1976, Hobbs and Flynn 1981). The order Polydesmida is poorly represented in study-area caves, and only a few records are known. *Brachydesmus superus* (Polydesmidae), either a trogloxene or accidental, is common in Europe and in cultivated areas of the United States; it is recorded from single caves in Virginia and West Virginia

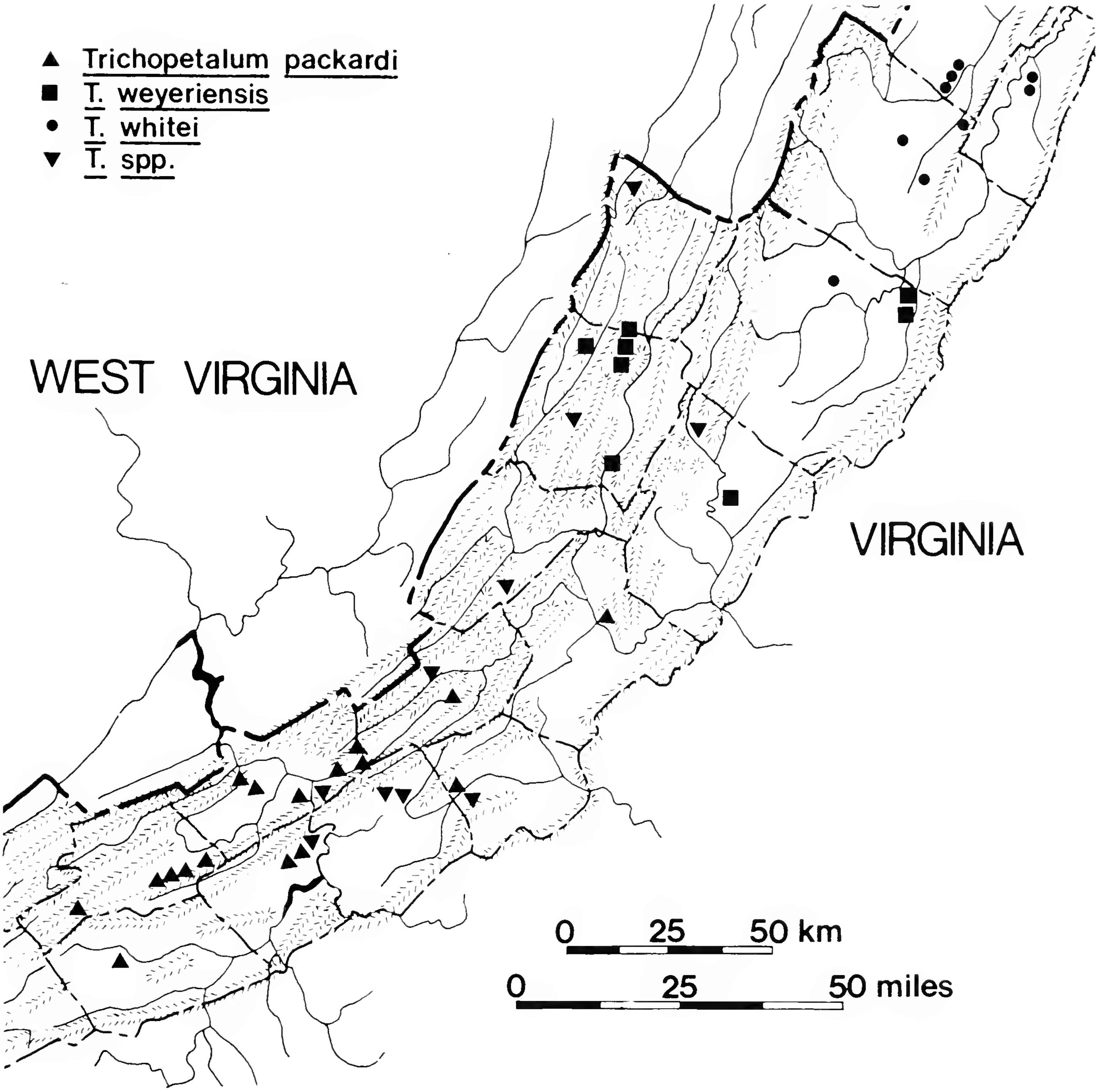

Fig. 22. Distribution of troglobitic millipeds (*Trichopetalum*) in the study area.

(see Holsinger et al. 1976). Another polydesmid, *Scytonotus granulatus*, probably a trogloxene, is recorded from a single cave in Virginia and from caves in Maryland, Ohio, and Pennsylvania (Franz and Slifer 1971, Holsinger 1976, Hobbs and Flynn 1981); it is widespread over most of the eastern half of the United States (Chamberlin and Hoffman 1958).

The order Spirostreptida is represented by two species of *Cambala* (Cambalidae). *Cambala minor*, a troglophile, is widespread in the southeastern and east-central United States (Shelley 1979) and has been collected from caves in Virginia and eight other states within its range (see Loomis 1943, Shear 1969, Holsinger and Peck 1971, Black 1971, Craig 1975, Holsinger et al. 1976, Peck and Lewis 1978, Hobbs and

Flynn 1981). *Cambala annulata*, a probable trogloxene, ranges over a large part of the southeastern United States (Shelley 1979) and is recorded from a few caves in Florida, Georgia, Alabama, and Virginia (see Holsinger and Peck 1971). *Abacion magnum* (Caspiopetalidae), the only representative of the order Callipodida in study-area caves, is a trogloxene recorded from several caves in southwestern Virginia and northwestern Georgia (see Holsinger and Peck 1971).

Order Polydesmida

Family Polydesmidae

Brachydesmus superus Latzel (TX or AC)

Virginia.—Tazewell Co.: Lawson Cave.

Pseudopolydesmus sp.

Virginia.—Russell Co.: Dickenson Cave.

Polydesmus angustus Latzel (AC)

Virginia.—Page Co.: Ruffners Cave No. 1.

Scytonotus granulatus (Say) (TX?)

Virginia.—Rockbridge Co.: Billy Williams Cave.

Order Spirostreptida

Family Cambalidae

Cambala annulata (Say) (TX?)

Virginia.—Giles Co.: New River Cave. Page Co.: Luray Caverns (?) Smyth Co.: Sugar Grove Cave No. 10.

Cambala minor Bollman (TP)

Virginia.—Alleghany Co.: Mc Elwee Cave. Augusta Co.:, Glade Cave. Bath Co.: Clarks Cave. Washington Co.: Wills Cave.

Cambala sp.

Virginia.—Augusta Co.: Fountain and Madisons Saltpetre caves. Giles Co.: Spruce Run Mountain Cave. Roanoke Co.: Millers Cove Cave.

Order Callipodia

Family Caspiopetalidae

Abacion magnum (Loomis) (TX)

Virginia.—Lee Co.: Cumberland Gap Saltpetre Cave. Russell Co.: Dickenson Cave. Tazewell Co.: Lost Mill Cave No. 3.

Order Chordeumatida

Family Cleidogonidae

Pseudotremia (species listed by group as indicated)

eburnea group

Pseudotremia nodosa (*s. lat.*) Loomis (TB)

Tennessee.—Claiborne Co.: Buis Saltpetre, Chadwells, Clines, English (type locality), Hauser Spring, Keck No. 1, Lower

Coonsies Creek, Saur Kraut, and Tazewell Saltpetre caves. Hancock Co.: Subers Cave. Union Co.: Wolf Cave.

Virginia.—Lee Co.: Cedar Hill, Cope, Crouse, Gallohan No. 1 and 2, Gibson-Frazier, Gilley, Jones Saltpetre, Knapper, Litton No. 1, Lucy Beatty, Molly Wagle, Smith, Spangler, Surgener, Sweet Potato, Thompson Cedar, Unthanks, and Young-Fugate caves.

Pseudotremia sp. (*nodsa* complex) (TB)

Virginia.—Scott Co.: Flannery, Kerns No. 1, and McDavids caves. Wise Co: Kelly, Wildcat (Cavern) and Wildcat Saltpetre caves.

fracta group

Pseudotremia cocytus Shear (TP)

Tennessee.—Campbell Co.: Norris Dam Cave.

Comments.—Also recorded from two caves and a wooded hillside (epigean) just south of the study area in Anderson County, Tenn. (see Shear 1972).

Pseudotremia fracta (*s. lat.*) Chamberlin (TP)

Tennessee.—Claiborne Co.: Bug Hole No. 1 and John Lard caves. Union Co.: Lost Creek Cave.

hobbsi group

Pseudotremia cavernarum Cope (TB)

Virginia.—Montgomery Co.: Daves and Erhart (type locality) caves.

Pseudotremia deprehendor Shear (TB?)

Tennessee.—Grainger Co.: Cedar Springs Cave.

Comments.—Also recorded from Feathers Cave (type locality) just south of the study area in Anderson County, Tenn. (see Shear 1972).

Pseudotremia hobbsi Hoffman (TP)

Virginia.—Alleghany Co.: Arritt Mill Tunnel, Blue Springs, Chestnut Ridge (type locality), Island Ford, Lowmoor, Rumbolds, Second Dam, and Wares caves. Botetourt Co.: Henderson No. 1 and Thomas caves. Craig Co.: Shires Saltpetre Cave. Montgomery Co.: Slussers Chapel Cave.

Pseudotremia princeps Loomis (TP)

Virginia.—Highland Co.: Van Devanters Cave.

Comments.—Also recorded from several caves and one epigean locality just north and west of the study area in Pendleton County, W.Va. (see Shear 1972, Holsinger et al. 1976).

Pseudotremia sublevis Loomis (TP)

Virginia.—Giles Co.: "Big Stony" (Cope 1869), Clover Hollow, Smokehole, Spruce Run Mountain, and Tawneys (type locality) caves.

Comments.—Also recorded from several epigean localities in the Giles-Montgomery county area (see Loomis 1944, Shear 1972).

spira group

Pseudotremia valga Loomis (TB?)

Tennessee.—Claiborne Co.: Station Creek Cave.

Virginia.—Lee Co.: Cudjos Cavern (type locality) and Young-Fugate Cave.

tuberculata group

Pseudotremia armesi (*s. lat.*) Shear (TP)

Virginia.—Tazewell Co.: Fallen Rock Cave.

Comments.—Also recorded from two caves and one epigean locality just west of the study area in Mercer County, W.Va. (Shear 1972, Holsinger et al. 1976).

Pseudotremia momus Shear (TP)

Virginia.—Smyth Co.: Atwells Tunnel and Spence (type locality) caves.

Comments.—Also recorded from an epigean habitat on the crest of Big Walker Mountain near the Wythe-Bland county line (Shear 1972.

Pseudotremia tuberculata (s. lat.) Loomis (TB?)

Virginia.—Tazewell Co.: Bowens, Cassell Farm (type locality), Fallen Rock, Lawson, and Stonley caves.

Undescribed and undetermined species

Pseudotremia n. spp. (TB and TP)

In addition to several undescribed probable species in the *nodosa* complex listed above, the following cave populations have been tentatively recognized as undescribed species by either W. A. Shear or R. L. Hoffman (in litt.). All need further study and are not counted in our numerical analyses.

1. Ballards Cave, Giles County.
2. Banners Corner and Dickenson caves, Russell County.
3. Blowing Cave, Bath County.
4. Buchanan Saltpetre Cave, Smyth County.
5. Carter Cave, Lee County.
6. Cave School Water Cave, Wythe County.
7. Coley Cave No. 2, Scott County.
8. Crossroads and Porters caves, Bath County.
9. Cumberland Gap Saltpetre Cave, Lee County.
10. Elys Moonshine and Sweet Potato caves, Lee County.
11. Fisher Cave, Lee County.
12. Greears Sweet Potato and Kerns No. 1 caves, Scott County.
13. Little Kennedy Cave, Wise County.
14. Moccasin Valley Cave, Scott County.
15. New Castle Murder Hole and Rufe Caldwell caves, Craig County (two species).
16. Pearson Cave, Hawkins County.

17. Smiths Cave, Russell County; Hugh Young and Steeles caves, Tazewell County.
18. Starnes Cave, Giles County.
19. Wares Cave, Alleghany County.

Pseudotremia spp.

Tennessee.—Campbell Co.: Easterly, Meredith, and Panther No. 1 caves. Claiborne Co.: Buis Saltpetre and Kings Saltpetre caves. Grainger Co.: Horseshoe Cave. Hancock Co.: Cantwell Valley, Fairmont School, and Panther Creek caves. Hawkins Co.: Pearson and Sensabaugh Saltpetre caves. Sullivan Co.: Morrill and Potters caves. Union Co.: Lost Creek and Oaks caves.

Virginia.—Alleghany Co.: Rumbolds, Walking, and Wares caves. Bath Co.: Clarks and Dunns caves. Bland Co.: Repass Saltpetre Cave. Craig Co.: Loneys Cave. Giles Co.: Canoe, Giant (Caverns), New River, and Starnes caves. Highland Co.: Roaring Springs Cave. Lee Co.: Bowling, Cattle, Davis, Ely, Frazier, Gibson No. 1, Gilley, Gregory, Indian, Kinzer Hollow, McClure, Roadside No. 1, Ruths, Seals Pit, Skylight, and Smiths Milk caves. Montgomery Co.: Fred Bulls Cave. Roanoke Co.: Hodges No. 1 and Millers Cove caves. Russell Co.: Jessie, Johnson, and Porgie Bundy caves. Rockbridge Co.: Doll House Cave. Scott Co.: Alley, Blair-Collins, Blowing Hole, Bolling, Cox Ram Pump, Cox Ridge, Grigsby, Harris Pit, Herron No. 1, Hill, Hortons, Jack, Jackson, Lane, Obeys Creek, Pond, Natural Tunnel (Cavern), Quillen No. 1, Spurlock, Taylor No. 1, Winding Stair, and Wolfe caves. Smyth Co.: Tilson Saltpetre Cave. Tazewell Co.: Barnes Dry, Gillespie Water, Gully, Lawson, Lost Mill No. 3, Rosebaums Water, and Wagoners caves. Washington Co.: Neals and Perkins caves. Wise Co.: Parsons and Rocky Hollow caves. Wythe Co.: Pickett Cave.

Comments.—These records are based primarily on collections containing juveniles and females, of which specific determinations could not be made.

Family Conotylidae

Conotyla venetia Hoffman (TX?)

Virginia.—Alleghany Co.: Paxtons Cave.

Family Striariidae

Striaria columbiana Cook (TX?)

Virginia.—Warren Co.: Allens Cave.

Striaria sp. A. (TB?)

Virginia.—Augusta Co.: Madisons Saltpetre Cave.

Striaria sp.

Virginia.—Page Co.: Will Mauck Cave. Shenandoah Co.: Hensleys Cave.

Family Trichopetalidae

Trichopetalum packardi (*s. lat.*) (Causey) (TB)

Virginia.—Bland Co.: Coon, Hamilton, Newberry-Bane, and Repass Saltpetre caves. Botetourt Co.: Peery Saltpetre Cave. Craig Co.: Rufe Caldwell Cave. Giles Co.: Canoe, Clover Hollow, Giant (Caverns), Starnes, Straleys No. 1, and Tawneys caves. Pulaski Co.: Fifty-Foot Hell and Sam Bells caves. Roanoke Co.: Dixie Caverns. Wythe Co.: Sam Six Cave.

Trichopetalum weyeriensis (*s. lat.*) (Causey) (TB)

Virginia.—Augusta Co.: Grand Caverns (type locality) and Madisons Saltpetre Cave. Bath Co.: Boundless, Breathing, Butler-Sinking Creek, Porters, and Starr Chapel caves. Rockbridge Co.: Billy Williams Cave.

Trichopetalum whitei (*s. lat.*) (Ryder) (TB)

Virginia.—Augusta Co.: Glade Cave. Page Co.: Luray Caverns (type locality) and Ruffners Cave No. 1. Rockingham Co.: Endless (Caverns), Stevens, and Three-D Maze caves. Shenandoah Co.: Maddens, Shenandoah (Caverns), and Shenandoah Wild caves.

Trichopetalum spp.

Virginia.—Alleghany Co.: Blue Spring Cave. Bath Co.: Dunns Cave. Bland Co.: Banes Spring Cave. Craig Co.: Loneys Cave. Giles Co.: New River Cave. Highland Co.: Roaring Springs Cave. Montgomery Co.: Old Mill and Slussers Chapel caves. Pulaski Co.: James Cave. Roanoke Co.: Goodwins Cave. Rockbridge Co.: Grahams Cave.

Comments.—These records are based primarily on juveniles and females, for which specific determinations could not be made.

Order Julida

Family Julidae

Ophyiulus pilosus (Newport) (TP or TX)

Tennessee.—Hawkins Co.: Sensabaugh Saltpetre Cave.

Virginia.—Alleghany Co.: Wares Cave. Giles Co.: Ballards Cave. Lee Co.: Carter Cave. Montgomery Co.: Erharts Cave. Page Co.: Ruffners and Will Mauck caves. Rockbridge Co.: Tolleys Cave. Rockingham Co.: Melrose Cave. Russell Co.: Banners Corner and Dickenson caves. Washington Co.: Hall Bottom Cave No. 1.

Family Parajulidae

Ptyoiulus sp.

Virginia.—Tazewell Co.: Gully Cave.

Class Insecta

Insects, along with crustaceans, spiders, and millipeds, are the most common animals in the caves of Virginia and east Tennessee. At least 11 orders have been documented from study-area caves, but a majority of the cavernicoles are in the orders Collembola, Diplura, Orthoptera, Coleoptera, and Diptera. Many troglobites are noted among the collembolans, diplurans, and coleopterans.

Only a few scattered records exist for representatives of other insect orders, none of which is commonly found in caves of the study area. These include the: mayfly order Ephemeroptera; moth and butterfly order Lepidoptera (e.g., *Scoliopteryx libatrix*); scorpion fly order Mecoptera (e.g., family Bittacidae); stonefly order Plecoptera (e.g., *Leuctra decepta*); caddis fly order Trichoptera (e.g., *Hydropsyche deprevata*, *H. betteni*, and *Ochrotrichia*); and bristletail order Thysanura (e.g., *Machiloides*).

Order Collembola

Colembolans or springtails are common and often abundant in caves where they are frequently seen in and around damp, decaying organic material. In the study area the order is represented by 5 families, 9 genera, and 26 described species. Three or four species are troglobites, eight or nine are troglophiles, and the remainder are trogloxenes and accidentals

Of the five families, Entomobryidae is clearly the most significant in terms of abundance and diversity. *Pseudosinella* is represented by seven described species from caves in the Virginia-east Tennessee area (Fig. 23, 24) and two, *P. hirsuta* and *P. orba*, are troglobites. Outside the area, the former species is recorded from numerous caves in northern Alabama, northwestern Georgia, central Kentucky, and middle Tennessee, and from one epigean locality on Pine Mountain in Campbell County, Tenn. (Christiansen and Bellinger 1980c). The latter species has a much narrower range and is restricted to the study area and adjacent Mercer County in southern West Virginia (see Holsinger et al. 1976). The other species of this genus reported from study-area caves are troglophiles and trogloxenes that range over much of the southeastern United States.

The genus *Sinella* is representd in study-area caves by four species, one of which, *S. hoffmani* (see Wray 1952), is considered a troglobite (Fig. 23, 24). This species is also recorded from nine counties in eastern West Virginia (Holsinger et al. 1976) and one in Pennsylvania (K. A. Christiansen, in litt.). It has been collected three times from surface habitats, twice in North Carolina and once in West Virginia (Christiansen and Bellinger 1980c), but the identity of the North Carolina specimens is questionable (Christiansen 1982). The lone record of this species from Tazewell County in the Clinch drainage basin is also questionable. The other species of *Sinella* noted from study-area caves are troglophiles and trogloxenes and have wide ranges outside Virginia and eastern Tennessee (see Christiansen 1960a).

Probably the most common and widespread cavernicolous collembolan in the study area is *Tomocerus bidentatus* (Fig. 31A), a lightly pigmented troglophile with small eyes that is also recorded from epigean and cave habitats in the eastern United States and from two caves in California (Christiansen 1964a, Christiansen and Bellinger 1980c). *Tomocerus flavescens*, also a troglophile (or trogloxene?), is recorded from caves in many parts of the United States (Christiansen 1964a, Christiansen and Bellinger 1980c), but it is much less common than *T. bidentatus* in the study area (Fig. 25).

The second most significant family in the regional cave collembolan fauna is Sminthuridae, represented by six species in the genus *Arrhopalites* (Fig. 24). Most of these species are troglophiles and trogloxenes and are recorded from a large part of the United States (see Christiansen and Bellinger 1981). *Arrhopalites clarus*, however, is at present known only from caves and is apparently troglobitic despite its broad distribution, which includes localities in Arkansas, Missouri, Virginia, and West Virginia (see Christiansen 1982). The most common species of the genus in regional caves is *A. pygmaeus*, a troglophile uncommon in epigean habitats but recorded from caves throughout a large part of the southeastern and south-central United States (Christiansen 1964a, Christiansen and Bellinger 1981). *Arrhopalites ferrugineus* (Packard), reported earlier from caves in Virginia by Holsinger (1963a), is considered a synonym of this species by Christiansen (1966).

In other families, *Folsomia candida* (Isotomidae), a probable troglophile, is recorded from a few caves in Virginia as well as from caves over a wide area of the United States (Christiansen and Bellinger 1980b). The families Hypogastruridae and Onychiuridae are represented in study-area caves by several trogloxene or accidental species, which, with the exception of *Onychiurus ramosus*, are based on single cave records. *Onychiurus ramosus* is recorded from several caves in Virginia and one in northeastern Utah (see Peck 1981a); otherwise it is widespread in epigean habitats over much of the United States (Christiansen and Bellinger 1980b).

Family Entomobryidae

Entomobrya socia Bören (TX or AC)

Virginia.—Giles Co.: New River Cave.

Pseudosinella aera Christiansen and Bellinger (TP or TX)

Virginia.—Shenandoah Co.: "Cave" (Christiansen and Bellinger 1980c:966).

Comments.—Also recorded from caves in Illinois, Kentucky, Missouri, Tennessee, and Texas (Christiansen and Bellinger 1980c).

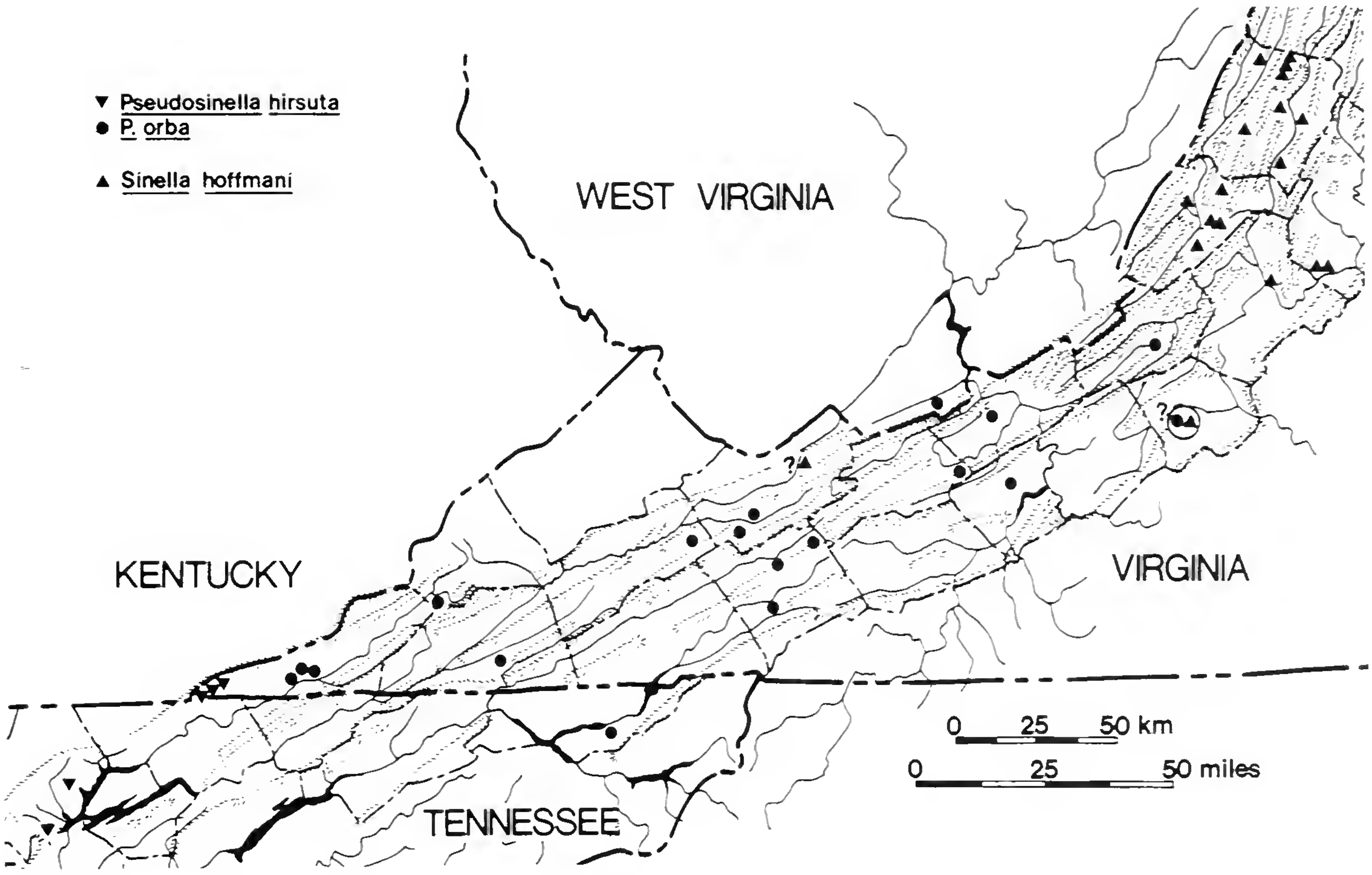

Fig. 23. Distribution of troglobitic collembolans (*Pseudosinella* and *Sinella*) in the study area. Single locality for *P. orba* in Mercer County, W.Va., also shown. Two symbols in a circle indicate two species from the same cave.

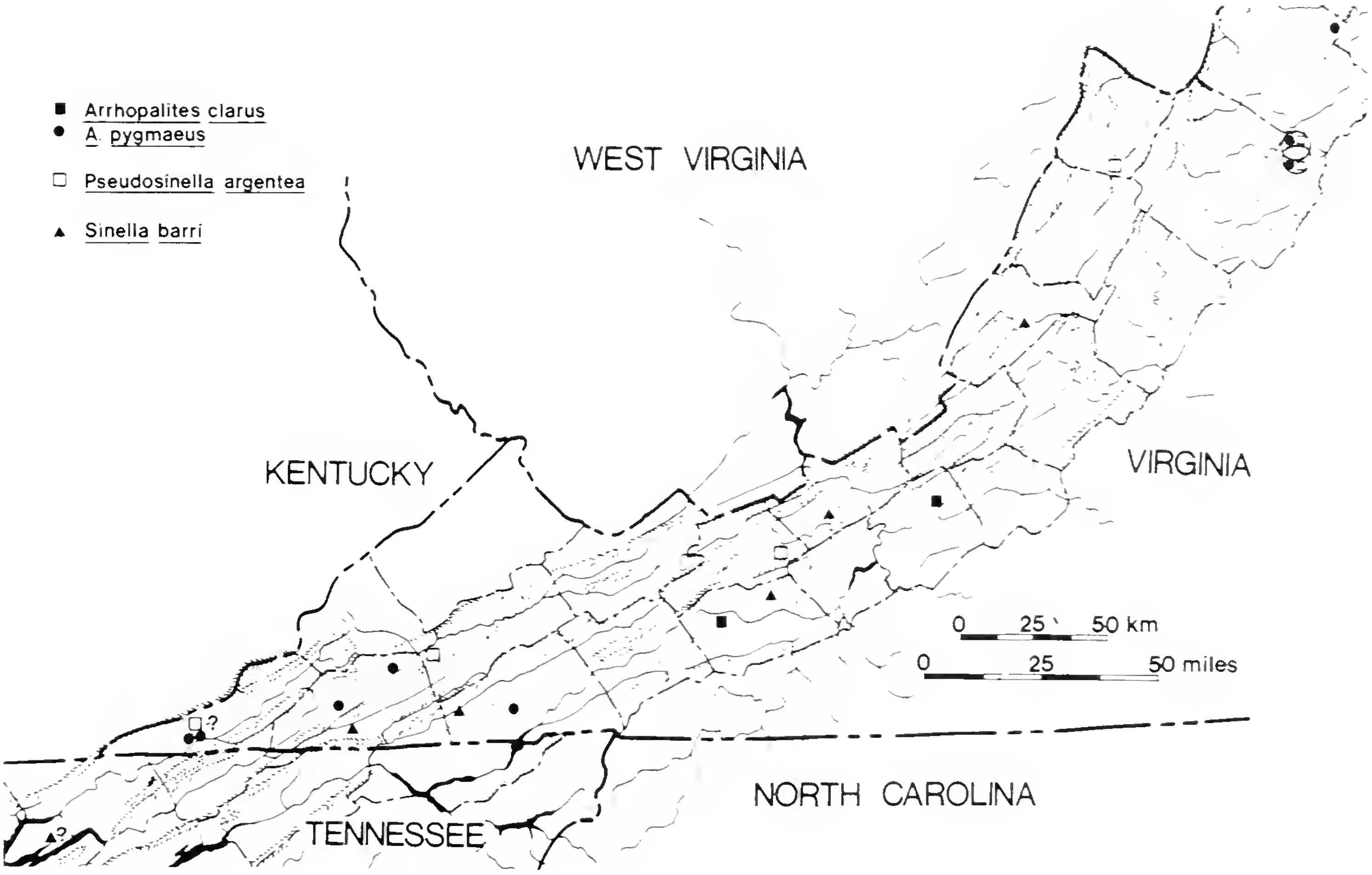

Fig. 24. Distribution of cavernicolous collembolans (*Arrhopalites*, *Pseudosinella*, and *Sinella*) in the study area. Two symbols in a circle indicate two species from the same cave.

Pseudosinella alba (Packard) (TX)
Virginia.—Shenandoah Co.: Shenandoah Wild Cave.
Comments.—Widely distributed in United States; recorded from a few caves (Christiansen and Bellinger 1980c).

Pseudosinella argentea Folsom (TP)
Virginia.—Augusta Co.: Grand Caverns and Madisons Saltpetre Cave. Bland Co.: Newberry-Bane Cave. Highland Co.: Marshall Cave. Lee Co.: Kinzer Hollow Cave (?). Russell Co.: Fraleys Cave.
Comments.—Also recorded from caves in Arkansas, Illinois, Kentucky, Missouri, and Tennessee (Christiansen and Bellinger 1980c).

Pseudosinella collina Wray (TP or TX)
Virginia.—Giles Co.: New River Cave. Pulaski Co.: Sam Bells Cave.
Comments.—Also recorded from caves in Alabama, Kentucky, and Tennessee (Christiansen and Bellinger 1980c). All North American records for *P. duodecimpuncata* Denis probably should be referred to this species (Christiansen and Bellinger 1980c).

Pseudosinella hirsuta (Delamare) (TB)
Tennessee.—Campbell Co.: Easterly and Meredith caves.
Virginia.—Lee Co.: Cliff, Cudjos (Cavern), and Skylight caves.

Pseudosinella orba Christiansen (TB)
Tennessee.—Sullivan Co.: Morrill Cave (type locality).
Virginia.—Bland Co.: Hamilton Cave. Craig Co.: Rufe Caldwell Cave. Giles Co.: Starnes Cave. Lee Co.: Gallohan No. 1, Smith, and Sweet Potato caves. Pulaski Co.: Sam Bells Cave. Roanoke Co.: Goodwins Cave (?). Russell Co.: Porgie Bundys Cave. Scott Co.: Blair-Collins Cave. Smyth Co.: Buchanan Saltpetre, Interstate-81, and Tilson Saltpetre caves. Tazewell Co.: Fallen Rock and Gully caves. Wise Co.: Wildcat Saltpetre Cave.

Pseudosinella sexoculata Schött (TX)
Virginia.—Shenandoah Co.: Battlefield Crystal Cave.
Comments.—Distributed over much of the United States; also recorded from caves in Iowa, Kentucky, and New Mexico (Christiansen 1960a,b; Christiansen and Bellinger 1980c).

Pseudosinella spp.
Tennessee.—Hawkins Co.: Pearson Cave.
Virginia.—Tazewell Co.: Cassell Farm and Lawson caves. Washington Co.: Fritz Breathing Cave.
Comments.—Both the Pearson Cave and Fritz Breathing Cave populations probably represent undescribed species (K. A. Christiansen, in litt.).

Sinella barri Christiansen (TP)
Tennessee.—Union Co.: Wolfe Cave (?).

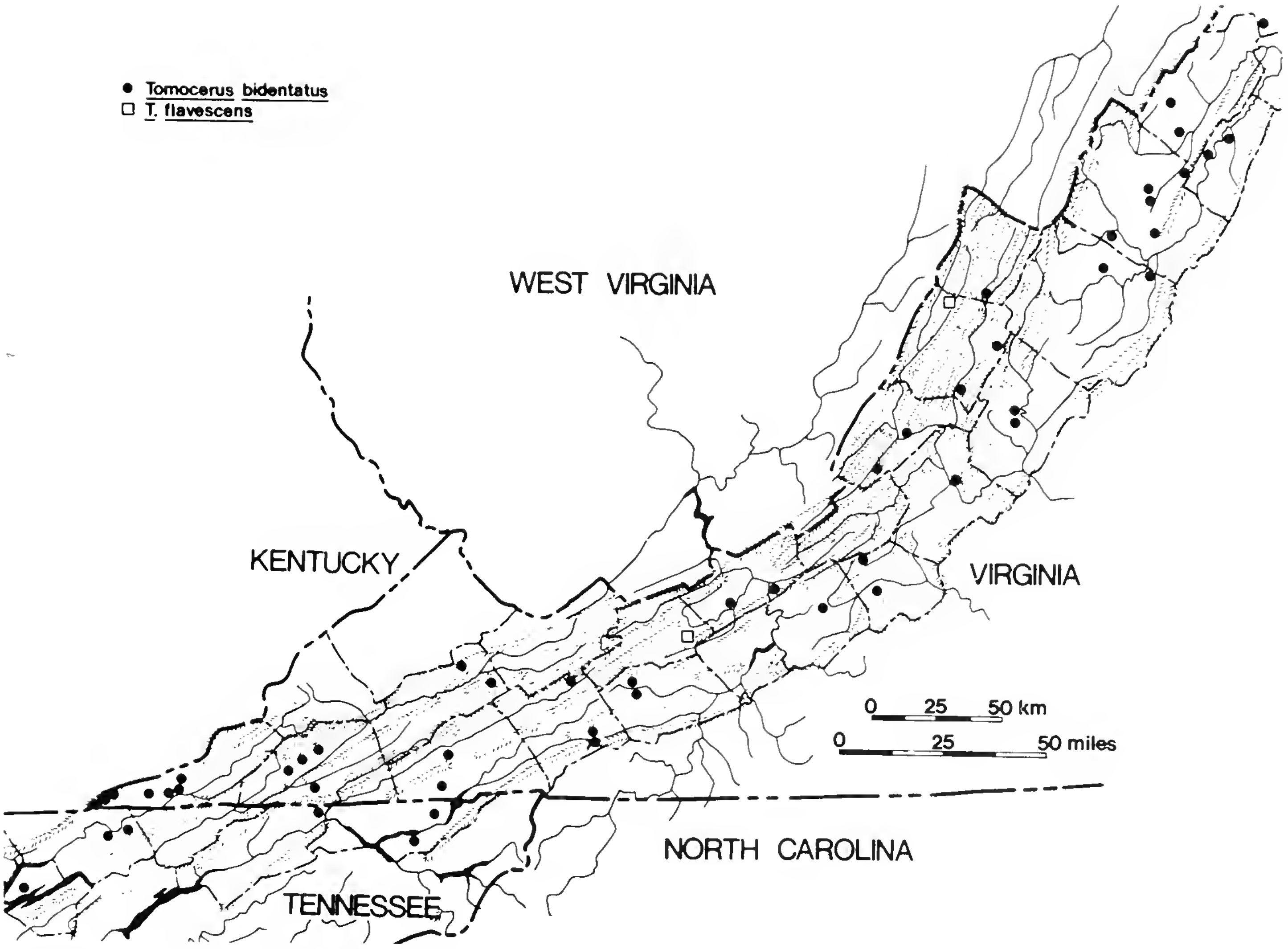

Fig. 25. Distribution of troglophilic collembolans (*Tomocerus*) in the study area.

Virginia.—Alleghany Co.: Island Ford Cave. Giles Co.: Parsells Cave. Scott Co.: Herron Cave No. 1. Washington Co.: Vickers Cave. Wythe Co.: Picketts Cave.

Comments.—Also recorded from caves in Arkansas, Illinois, Kentucky, Missouri, and Tennessee (Christiansen and Bellinger 1980c).

Sinella caeca Schött (TX)

Virginia.—Frederick Co.: Ogdens Cave. Page Co.: Luray Caverns. Pulaski Co.: James Cave. Rockbridge Co.: Showalters Cave. Shenandoah Co.: Shenandoah Caverns.

Comments.—Reported from epigean localities throughout most of the United States; also recorded from caves in Iowa, Kentucky, Missouri, Texas, and Wisconsin (Christiansen and Bellinger 1980c).

Sinella curviseta Brook (TX or AC)

Virginia.—Montgomery Co.: Erharts Cave.

Comments.—Reported from epigean localities over much of the United States; also recorded from a cave in Kentucky (Bonet 1934, Christiansen and Bellinger 1980c).

Sinella hoffmani Wray (TB)

Virginia.—Alleghany Co.: Blue Spring, Island Ford, Lowmoor (type locality), Rumbolds, and Wares caves. Bath Co.: Boundless, Breathing, Butler-Sinking Creek, Crossroads, Dunns, Porters, Starr Chapel, and Witheros caves. Botetourt Co.: Peery Saltpetre Cave. Roanoke Co.: Goodwins Cave. Rockbridge Co.: Buck Hill and Doll House caves. Tazewell Co.: Stonley Cave (?).

Tomocerus bidentatus Folsom (TP)

Tennessee.—Claiborne Co.: English and Lower Coonsies Creek caves. Hawkins Co.: Sensabaugh Saltpetre Cave. Sullivan Co.: Bristol Caverns and Morrill Cave. Union Co.: Lost Creek Cave.

Virginia.—Alleghany Co.: Island Ford and Paxtons caves. Augusta Co.: Glade and Madisons Saltpetre caves. Bath Co.: Roy Lyle and Porters caves. Botetourt Co.: Peery Saltpetre Cave. Frederick Co.: Ogdens Cave. Giles Co.: Harris and New River caves. Highland Co.: Marshalls Cave. Lee Co.: Cudjos (Cavern), Cumberland Gap Saltpetre, Gallohan No. 1, Kinzer Hollow, Lucy Beatty, Skylight, and Sweet Potato caves. Montgomery Co.: Erharts Cave. Page Co.: Foltz Cave No. 1 and Luray Caverns. Roanoke Co.: Goodwins and Hodges No. 1 caves. Rockbridge Co.: Showalters and Tolley caves. Rockingham Co.: Church Mountain, Massanutten (Caverns), Melrose (Caverns), Round Hill, Steam Hole, and Stephens caves. Russell Co.: Jessie and Porgie Bundys caves. Scott Co.: Bolling, Hill, Kerns No. 1, and Lane caves. Shenandoah Co.: Helsley and Shenandoah Wild caves. Smyth Co.: Atwells Tunnel, Roberts, and Sugar Grove No. 10 caves. Washington Co.: Hall Bottom No. 1 and Singleton caves. Wythe Co.: Cave School Water and Sam Six caves.

Tomocerus flavescens (Tullberg) (TP or TX)

Virginia.—Bath Co.: Cave Run Pit Cave. Bland Co.: Banes Spring Cave.

Family Hypogastruridae

Hypogastrura denticulata (Bagnall) (TX)

Virginia.—Giles Co.: Tawneys Cave.

Comments.—Widespread species complex, occasionally found in caves (see Christiansen and Bellinger 1980a).

Neanura barberi (Handschin) (TX?)

Virginia.—Augusta Co.: Madisons Saltpetre Cave.

Comments.—Recorded from epigean localities in the eastern and midwestern United States; occasionally found in caves (Christiansen and Bellinger 1980a).

Family Isotomidae

Folsomia candida Willem (TP)

Tennessee.—Campbell Co.: Meredith Cave.

Virginia.—Augusta Co.: Madisons Saltpetre Cave. Pulaski Co.:

Fifty-Foot Hell Cave. Roanoke Co.: Goodwins Cave. Wise Co.: Wildcat Saltpetre Cave.

Folsomia sp.

Tennessee.—Claiborne Co.: English Cave.

Virginia.—Rockbridge Co.: Showalters Cave.

Family Onychiuridae

Onychiurus magninus Wray (AC)

Virginia.—Roanoke Co.: Goodwins Cave.

Onychiurus ramosus Folsom (TX)

Virginia.—Lee Co.: Sweet Potato Cave. Russell Co.: Bundy Cave No. 2. Wise Co.: Kelly and Wildcat Saltpetre caves.

Onychiurus reus Christiansen and Bellinger (TX or AC)

Virginia.—Warren Co.: Baldwin Hill Cave(s).

Comments.—Recorded from several epigean localities in the eastern United States and a cave in Kentucky (Christiansen and Bellinger 1980b).

Family Sminthuridae

Arrhopalites benitus (Folsom) (TX)

Virginia.—Alleghany Co.: Island Ford Cave. Bath Co.: Breathing Cave.

Comments.—Also recorded from a cave in Greenbrier County, W.Va. (Holsinger et al. 1976).

Arrhopalites caecus (Tullberg) (TX)

Virginia.—Rockbridge Co.: Showalters Cave.

Comments.—Also recorded from caves in Iowa, Minnesota, and South Dakota (Christiansen and Bellinger 1981).

Arrhopalites clarus Christiansen (TB?)

Virginia.—Montgomery Co.: Old Mill Cave. Wythe Co.: Sam Six Cave.

Arrhopalites hirtus Christiansen (TP or TX)

Virginia.—Lee Co.: Gallohan Cave No. 1.

Comments.—Also recorded from caves in Illinois, Iowa, Kentucky, and Wisconsin (Christiansen and Bellinger 1981).

Arrhopalites pygmaeus (Wankel) (TP)

Tennessee.—Claiborne Co.: Station Creek Cave.

Virginia.—Augusta Co.: Grand Caverns and Madisons Saltpetre Cave. Lee Co.: Smith and Sweet Potato caves. Rockingham Co.: Endless Caverns, Scott Co.: Flannery and Greears Sweet Potato caves. Washington Co.: Wills Cave.

Arrhopalites whiteside Jacot (TX)

Virginia.—Alleghany Co.: Island Ford and Lowmoor caves.

Arrhopalites sp.

Virginia.—Russell Co.: Porgie Bundys Cave.

Order Diplura

Cavernicolous diplurans (Fig. 31C) are represented in the study area by a single genus, *Litocampa* (Campodeidae), and six species. Only one of the species has been described; the remainder were recognized in a thesis and a dissertation by Ferguson (1974, 1981a), but descriptions have not been published to date and formal names are not available. All species of *Litocampa* (formerly a subgenus of *Plusiocampa*) in North America are troglobites (Ferguson 1981b). The range of *Litocampa* in the study area is restricted to the New and Tennessee drainage basins (Fig. 26). Cavernicolous diplurans are generally found on damp mud or silt banks near streams and occasionally on damp to wet surfaces elsewhere. They are sometimes locally abundant on organically enriched silt but otherwise usually uncommon in a given cave.

Litocampa cookei inhabits caves of the Powell Valley and parts of the adjacent Clinch Valley. The species is also recorded from caves in south-central Kentucky and middle Tennessee, where it is common and fairly widespread (Ferguson 1974). The other species are endemic to the Appalachian Valley and eastern side of the Appalachian Plateau and, with two exceptions, are known only from caves in the study area. *Litocampa* sp. A and D have very restricted ranges; the former is found only in caves of the Ward Cove karst in Tazewell County, and the latter is known only from a single cave in Hancock County. In comparison, *L.* sp. B, C, and E have wider ranges as indicated by the records cited below.

Litocampa sp. B is recorded from caves in the New River basin (southeast of Walker and Gap mountains) and parts of the Holston basin. In addition to three caves in Scott County, *L.* sp. C has been found in Angel Cave on Pine Mountain, just west of the study area in Letcher County, Ky. (Ferguson 1981a). *Litocampa* sp. E has a moderately extensive range that covers parts of the New, Holston, and Clinch basins and includes one cave just outside the study area in Mercer County, W.Va. (Ferguson 1974, Holsinger et al. 1976).

Family Campodeidae

Litocampa cookei (Packard) (TB)

Tenneessee.—Campbell Co.: Meredith and Norris Dam caves. Claiborne Co.: Tazewell Saltpetre Cave. Hancock Co.: Panther Creek and Subers caves.

Virginia.—Lee Co.: Gallohan No. 1, Molly Wagle, Sweet Potato, and Young-Fugate caves. Scott Co.: Spurlock Cave. Wise Co.: Little Kennedy, Parsons, and Rocky Hollow caves.

Litocampa sp. A (L. M. Ferguson, in ms.) (TB)

Virginia.—Tazewell Co.: Bowens, Fallen Rock (type locality), Gillespie Water, and Lost Mill No. 1 and 3 caves.

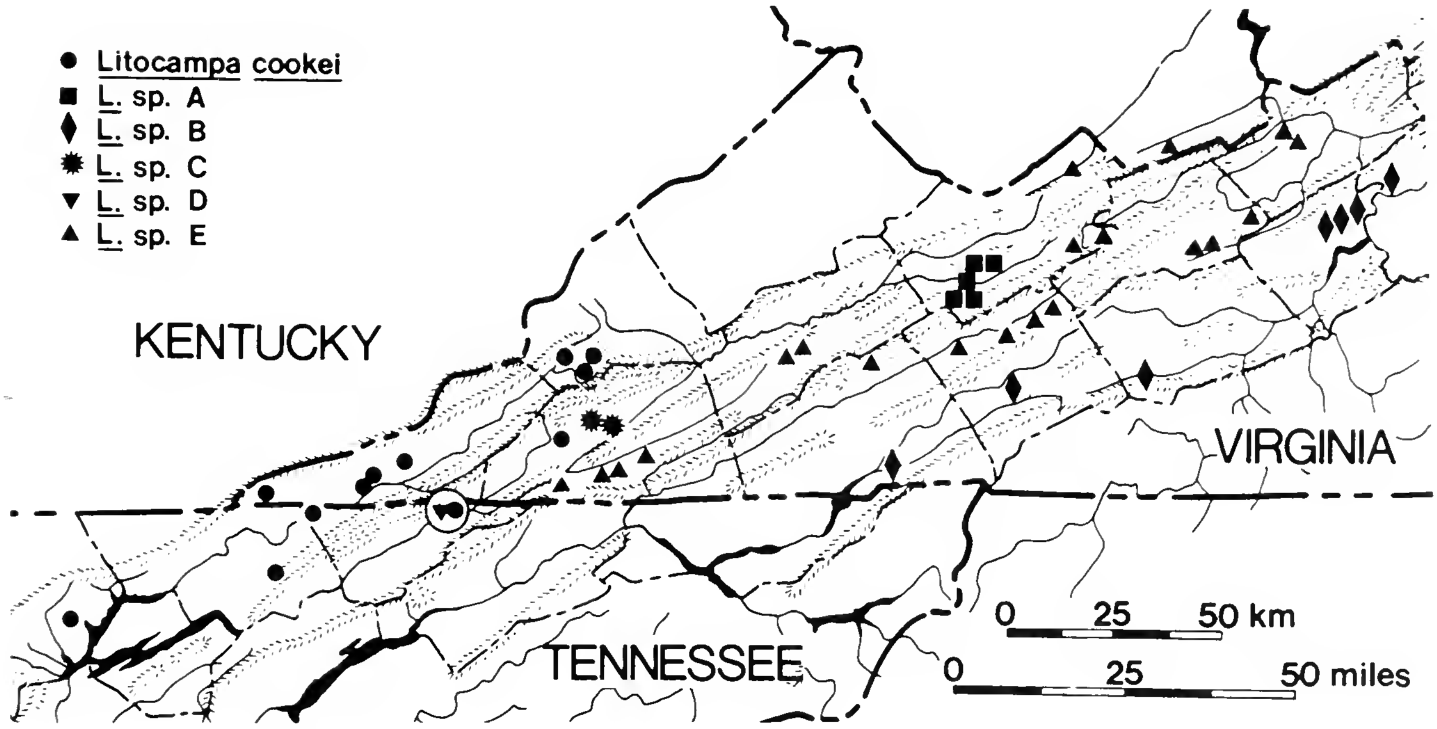

Fig. 26. Distribution of troglobitic diplurans (*Litocampa*) in the study area.

Litocampa sp. B (L. M. Ferguson, in ms.) (TB)
Virginia.—Montgomery Co.: Vickers Road Cave. Pulaski Co.: Fifty-Foot Hell, James, and Sam Bells caves. Smyth Co.: Interstate-81 Cave. Washington Co.: Brass Kettle Hole Cave. Wythe Co.: Speedwell Cave No. 1 (type locality).

Litocampa sp. C (L. M. Ferguson, in ms.) (TB)
Virginia.—Scott Co.: Hill, McDavids (type locality), and Queens caves.

Litocampa sp. D (L. M. Ferguson, in ms.) (TB)
Tennessee.—Hancock Co.: Panther Creek Cave (type locality).

Litocampa sp. E (L. M. Ferguson, in ms.) (TB)
Virginia.—Bland Co.: Coon, Hamilton, and Newberry-Bane caves. Giles Co.: Giant Caverns and Starnes Cave (type locality). Russell Co.: Bundys No. 2 and Grays caves. Scott Co.: Blair-Collins, Coley No. 2, Lane, and Wolfe caves. Smyth Co.: Beaver Creek, Buchanan Saltpetre, Hancock, and Tilson Saltpetre caves. Tazewell Co.: Cassell Farm, Lawson, and Wagoners caves. Washington Co.: Perkins Cave.

Order Orthoptera

Cave crickets (Rhaphidophoridae) are common in caves of Virginia and east Tennessee, where they are represented by two genera and at least five species. *Ceuthophilus* is yellowish-brown with black bands on the abdomen, is usually seen near entrances, and rarely, if ever, penetrates caves for an appreciable distance. Three species have been reported from study-area caves, but *C. gracilipes*, a threshold trogloxene, is the most common and widespread. The range of this species extends from the Ozarks eastward throughout much of the Appalachian region and includes numerous caves (Hubbell 1936, Holsinger and Peck 1971, Peck and Lewis 1978). No attempt has been made to collect *Ceuthophilus* systematically from caves in Virginia and east Tennessee; thus its occurrence in study-area caves is more common than indicated by the few records cited below.

In comparison with *Ceuthophilus*, *Euhadenoecus*, the other genus found in regional caves, is light brown in color, lacks conspicuous banding, and has a more slender body with longer legs. *Euhadenoecus puteanus*, a threshold trogloxene like *C. gracilipes,* is widely distributed throughout much of the Appalachian region and a part of the Interior Low Plateaus. It is recorded from numerous caves and epigean localities, many of these in Virginia and east Tennessee (see Hubbell and Norton 1978). *Euhadenoecus fragilis*, in contrast to *E. puteanus*, is a habitual trogloxene, or a troglophile under some circumstances. It is lightly pigmented, has attenuated legs (Fig. 32B), and is closely associated with the cave environment. It breeds in caves and commonly occurs far from entrance zones. The range of this species (Fig. 27) extends from Bath County, Va., and southern Randolph County, W.Va., southwestward to Claiborne County, Tenn., and includes Pine Mountain in southeastern Kentucky; the majority of locality records are from caves (see Hubbell and Norton 1978). Although common in the Clinch and Powell valleys, it is to date unrecorded from the Holston Valley. In addition to the localities listed below, we have made many unrecorded sightings of *E. fragilis* in southwestern Virginia caves.

Family Rhaphidophoridae

Ceuthophilus brevipes Scudder (TX)

Virginia.—Botetourt Co.: Thomas Cave. Giles Co.: Tawneys Cave. Roanoke Co.: Hodges Cave No. 1. Tazewell Co.: Cassell Farm and Little Gully caves.

Ceuthophilus gracilipes gracilipes (Haldeman) (TX)

Virginia.—Botetourt Co.: Henderson Cave No. 1. Giles Co.: Tawneys Cave. Highland Co.: Hamilton Cave. Lee Co.: Waltons Cave. Montgomery Co.: Fred Bulls Cave. Roanoke Co.: McVitty, Millers Cove, and New Dixie caves. Rockbridge Co.: Doll House Cave. Rockingham Co.: Massanutten Caverns. Scott Co.: Queens and Speers Ferry caves. Tazewell Co.: Cassell Farm and Little Gully caves.

Comments.—Also recorded from "Old Joe's Cave," east of the Blue Ridge Mountains in Buckingham County, Va. (see Hubbell 1936).

Ceuthophilus pallidipes Walker (TX)

Virginia.—Bland Co.: Hamilton Cave. Highland Co.: Better Forgotton Cave. Lee Co.: Waltons Cave. Roanoke Co.: Hodges

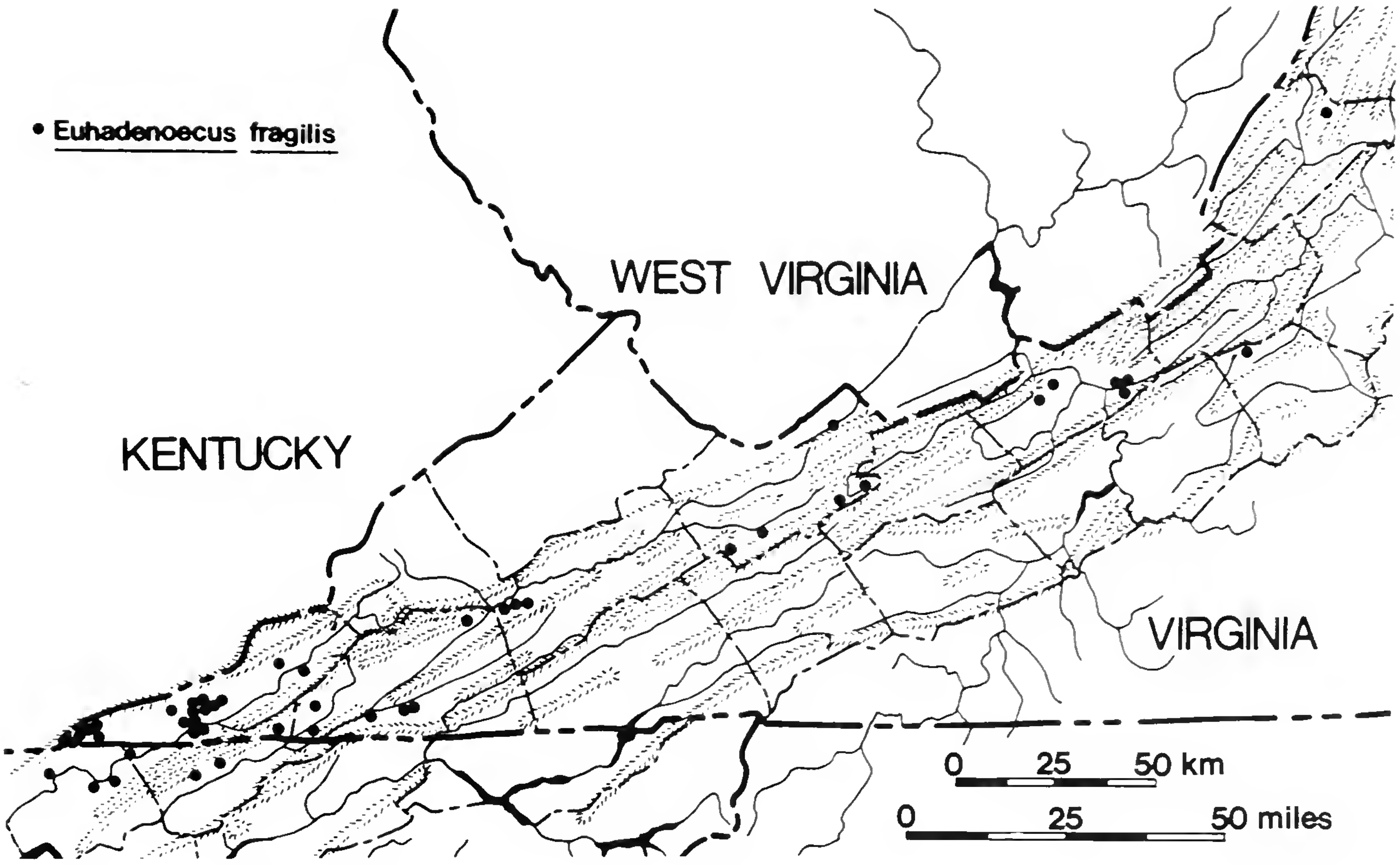

Fig. 27. Distribution of troglophilic crickets (*Euhadenoecus*) in the study area.

Cave No. 1. Rockbridge Co.: Tolleys Cave. Scott Co.: Queens Cave.

Euhadenocecus fragilis Hubbell (TP or TX)

Tennessee.—Claiborne Co.: Bug Hole No. 1, English, and Saur Kraut caves. Hancock Co.: Newmans Ridge (Hubbell and Norton 1978:43), Caney Sinks, and Subers caves.

Virginia.—Alleghany Co.: Wares Cave. Giles Co.: Ballards, Links, Smokehole, Starnes, and Tawneys (type locality) caves. Lee Co.: Cattle, Cliff, Crouse, Cumberland Gap Saltpetre, Gibson No. 2, Gibson-Frazier, Gilley, Indian, Kinzer Holow, Molly Wagle, Roadside No. 1, Smiths Milk, Spangler, Sweet Potato, Thompson Cedar, Unthanks, Waltons, and Young-Fugate caves; also "small caves," Pennington Gap (Hubbell and Norton 1978:43). Roanoke Co.: Millers Cove Cave. Russell Co.: Banners Corner, Indian, and Seven Springs caves. Scott Co.: Blowing Hole, Coley No. 1 and 2, Hortons, Queens, and Speers Ferry caves. Tazewell Co.: Cassell Farm, Glenwood Church, Lawson, Spider, and Wagoners caves.

Euhadenoecus puteanus (Scudder) (TX)

Tennessee.—Claiborne Co.: Yoakum Cave. Sullivan Co.: Bristol (Caverns), Morrill, and Potters caves.

Virginia.—Alleghany Co.: Lowmoor and Wares caves. Giles Co.: New River Cave. Highland Co.: Better Forgotten and Van Devanters caves. Lee Co.: Gilley Cave (not Billeys Cave or Baileys Cave as listed by Hubbell and Norton 1978:31). Roanoke

Co.: Dixie Caverns and McVitty Cave. Rockbridge Co.: Doll House Cave. Rockingham Co.: "cave" (see Hubbell and Norton 1978:31). Russell Co.: Seven Springs Cave. Smyth Co.: Atwells Tunnel and Stones No. 2 caves. Tazewell Co.: Cassell Farm Cave(s). Washington Co.: Hookers Rock Cave.

Euhadenoecus spp.

Virginia.—Bath Co.: Roy Lyle Cave. Giles Co.: Clover Hollow Cave. Highland Co.: Better Forgotten Cave. Rockbridge Co.: Billy Williams and Tolleys caves. Rockingham Co.: Gay Hill and Three-D Maze caves. Russell Co.: Johnson Dry Cave.

Order Coleoptera

Beetles constitute the most diverse group of insects in study-area caves, where they are represented by 8 families, 36 genera, and more than 75 species. Biospeleologically, the most important families are Cantharidae, Carabidae, Leiodidae, Pselaphidae, and Staphylinidae. Representatives of Cryptophagidae (*Cryptophagus* sp.), Dytiscidae (*Hydroporus wickhami*), and Scarabaeidae (*Ataenuis spretulus* and *Aphodius rufipes*) were also noted, but only as occasional accidentals.

Most of the cavernicolous beetles in the study area belong to the Carabidae and the large, predominantly troglobitic genus *Pseudanophthalmus*. Forty-seven species of this genus have been recognized, 36 of which have been described to date (see Barber 1928; Jeannel 1928, 1931, 1949; Valentine 1931, 1932, 1945, 1948; Barr 1960a, 1965, 1981a, 1985). Many closely related species inhabit caves in adjacent areas (e.g., West Virginia, eastern Kentucky, southeastern Tennessee). Most of the species are locally endemic; 26 are known only from a single cave and 13 from a small cluster of caves (Fig. 28, 29, 30). However, a few, like *P. delicatus* (Fig. 32A) and *P. hoffmani*, have significantly wider ranges with linear extents of approximately 50 and 75 km, respectively. Of the 11 species groups currently recognized from the region by Barr (1981a), only two are endemic to the study area. The other nine contain species that also occur outside the area. Both the *engelhardti* and the *hirsutus* groups include species that occur relatively far from the study area in southeastern Tennessee, northwestern Georgia, and northern Alabama (see Barr 1981a). One member of the *engelhardti* group, *P. wallacei*, occurs just south of the study area in Anderson County, however. The *gracilis*, *grandis*, *hubbardi*, and *pusio* groups contain species that inhabit caves just west of the study area is eastern West Virginia. Four of the five species assigned to the *hypolithos* group by Barr (1981a) occur in caves on the northwest side of Pine Mountain in southeastern Kentucky, also just west of the study area. The *jonesi* group also contains species that occupy caves in Pine Mountain, one in southeastern Kentucky and one in Campbell County, Tenn. Another species of this group is found

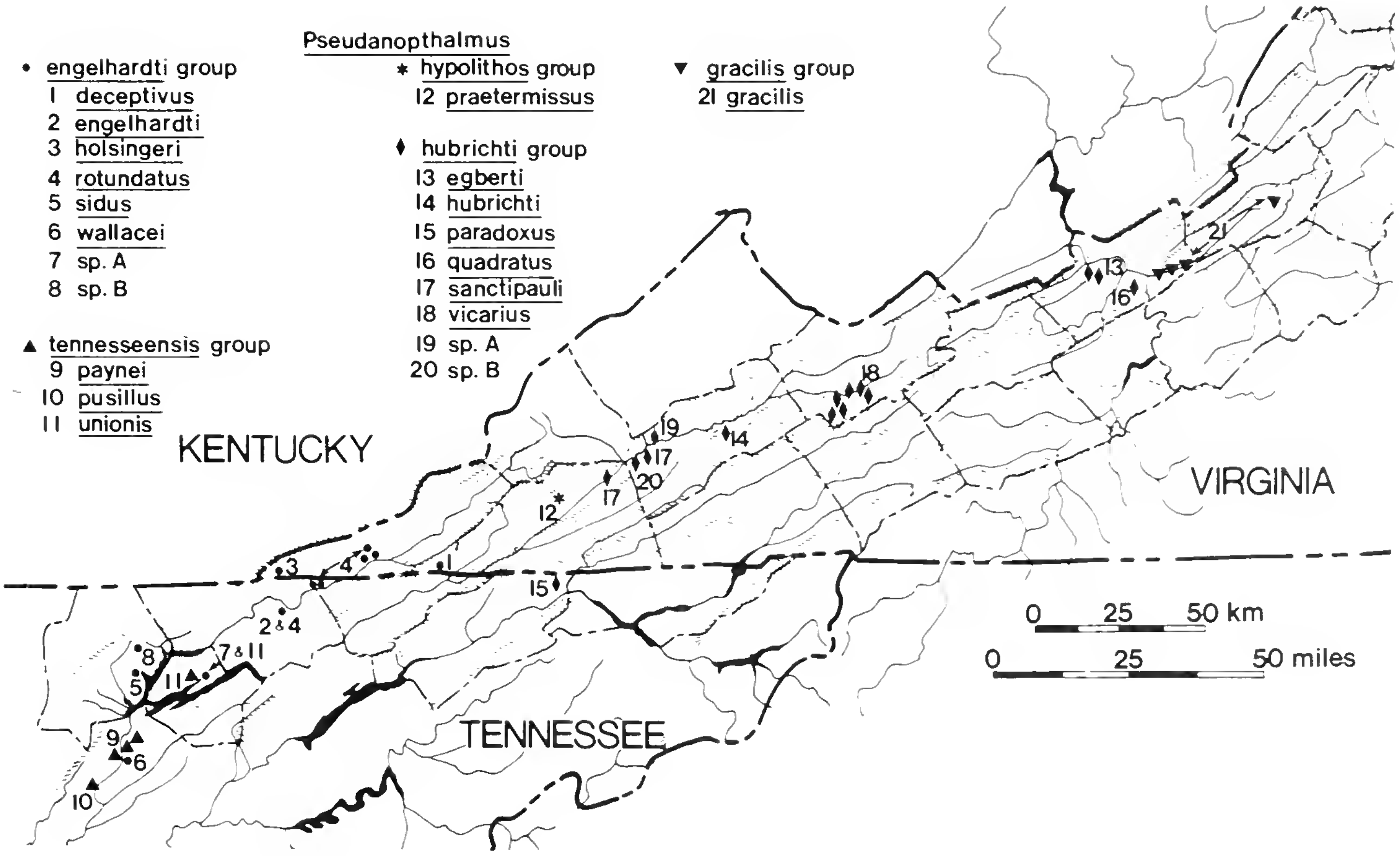

Fig. 28. Distribution of troglobitic beetles (*Pseudanophthalmus*) in the study area. Localities for three species just south of the study area in Anderson County, Tenn., also shown.

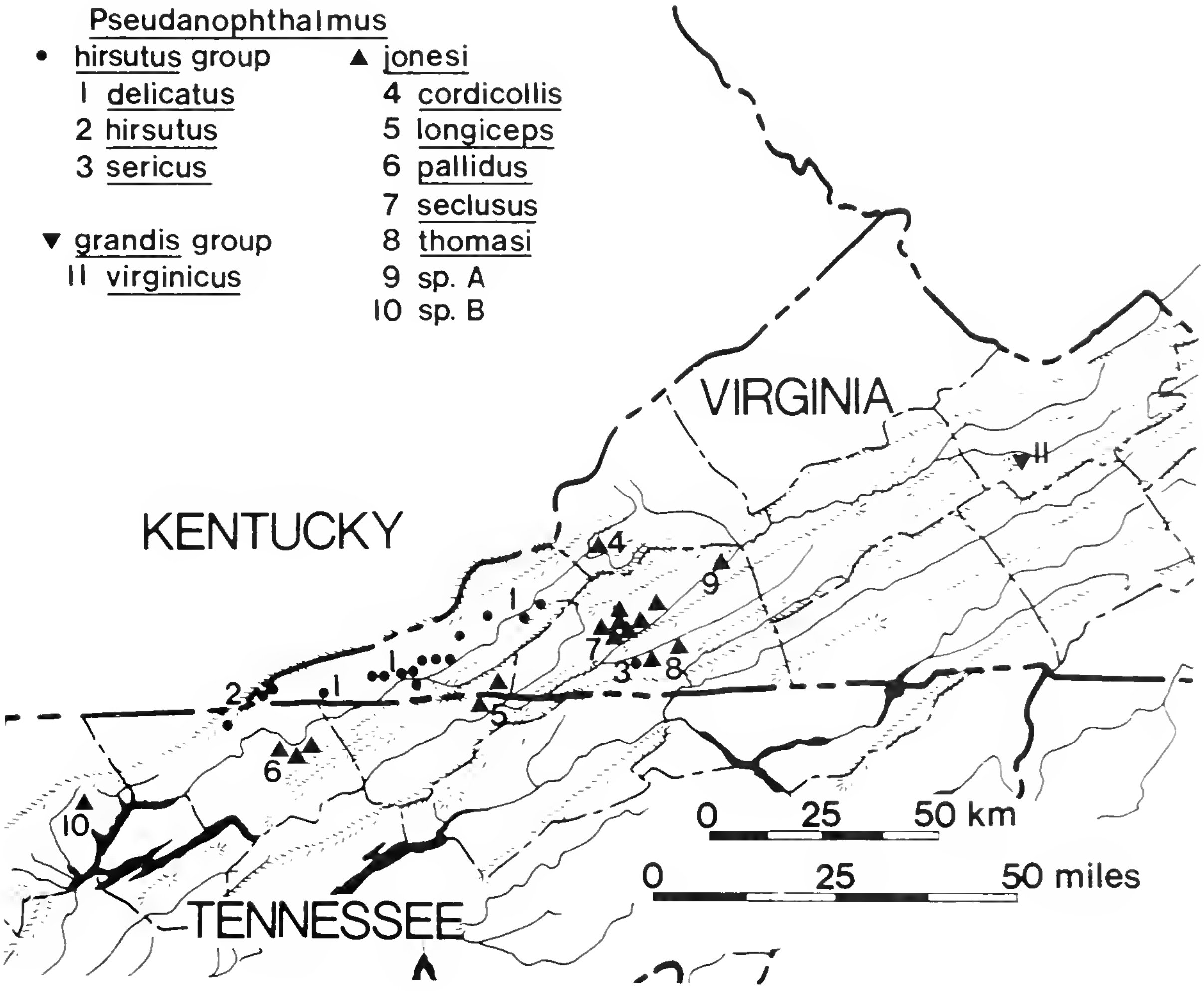

Fig. 29. Distribution of troglobitic beetles (*Peudanophthalmus*) in the study area.

in Grassy Cove, a karst island in the Cumberland Plateau some 80 km southwest of the study area (see Barr 1981a). Three of the four species of the *tennesseensis* group are recorded from caves just south of the study area in Anderson, Knox, and Roane counties (viz., *P. paynei*, *P. pusillus*, and *P. tennesseensis*).

Although some species of *Pseudanophthalmus* may be sporadically abundant in a given cave, most are quite rare; and several species, such as those of the *hubbardi* group in the Shenandoah Valley, are known only from a few specimens collected over a period of many years. Cavernicolous carabids, especially *Pseudanophthalmus*, are typically found in damp to wet areas under rocks or around organic detritus.

The non-troglobitic carabids from regional caves include species of *Atranus*, *Bembidion*, *Patrobus*, *Platynus*, *Rhadine*, *Stenolophus*, and *Trechus*. Perhaps the most common of these is *Platynus tenuicollis*, a troglophile recorded from caves in the eastern United States, the Ozarks, and Texas (Peck and Lewis 1978). *Agonum* (*Platynus*) *reflexum*, reported from caves in the eastern United States by Barr (1964), is now considered a synonym of *P. tenuicollis* (T. C. Barr, Jr., in litt.). *Bembidion* and *Atranus* may also be occasionally abundant. Both *B. lacunarium* and *B. wingatei* are recorded from Virginia caves; the former is common in caves in the central and eastern United States (Peck and Lewis 1978); the latter is reported from caves in eastern Kentucky, Pennsylvania, and West Virginia (Barr 1964, Holsinger et al. 1976). *Atranus pubescens*, a troglophile recorded from caves in the central and eastern United States (see Peck and Lewis 1978), is known from several Virginia caves. *Rhadine caudata*, a fairly widespread troglophile in caves in Alabama, Georgia, and Tennessee (Barr 1960b, 1964; Holsinger and Peck 1971), was reported from a single cave in Virginia by Bolivar and Jeannel (1931). *Trechus hydropicus canus*, probably a trogloxene, is recorded from a single cave in Lee County but is more common in surface localities at higher elevations in eastern Kentucky and southwestern Virginia (Barr 1979).

Cavernicolous pselaphid and leiodid beetles are poorly represented in the study area in contrast to parts of the Cumberland Plateau and Interior Low Plateaus where they are more diverse and represented by numerous troglobites (Park 1960, Peck 1973). Only two troglobitic pselaphids are known from the study area: *Arianops jeanneli* and *Batriasymmodes greeveri* (Fig. 30). Both species are very rare, local endemics (see Park 1956, 1965; Barr 1974, 1987). The former has been found only once, despite several diligent searches in the type locality. These species may be edaphobites and not troglobites, but this remains to be determined. Other pselaphids include *Batriasymmodes monstrosus*, probably accidental, for which Poor Farm Cave in Lee County is the only documented cave record to date for this widespread epigean species

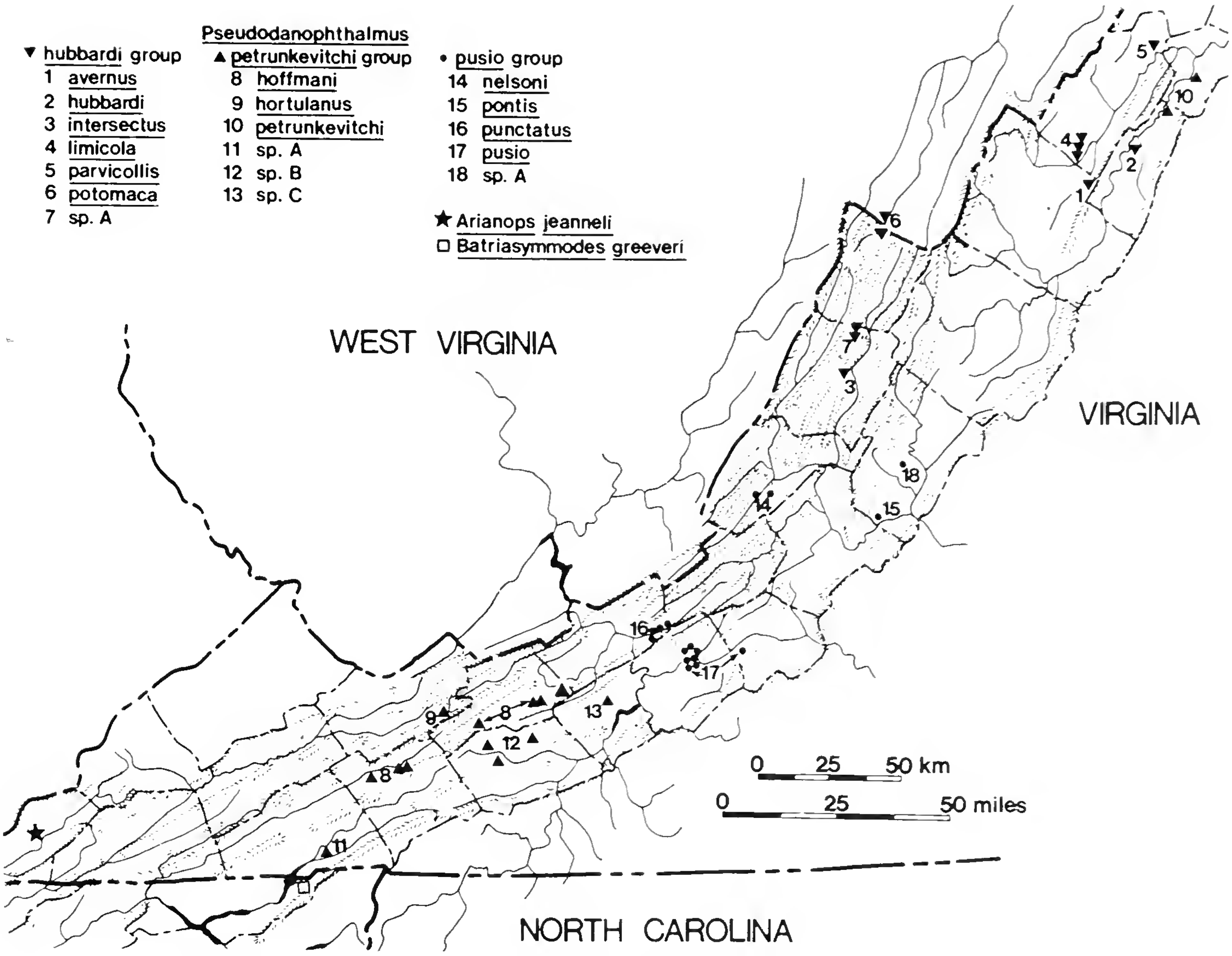

Fig. 30. Distribution of troglobitic beetles (*Arianops*, *Batriasymmodes*, and *Pseudanophthalmus*) in the study area. Single locality for *P. potomaca* in Pendleton County, W.Va., also shown.

(see Park 1965, Barr 1987), and *Batrisodes globosus*, a trogloxene widespread in eastern North America and recorded from single caves in Alabama, Georgia, and Virginia (Holsinger and Peck 1971). *Prionochaeta opaca*, a trogloxenic leiodid, is recorded from a single cave in Virginia but is widespread in eastern North America and reported from caves elsewhere in the southeastern United States (Peck 1977).

Most of the cavernicolous staphylinid beetles are in three subfamilies—Aleocharinae, Omaliinae, and Staphylininae. Although fairly common and sometimes moderately abundant in caves, none is a troglobite. The systematics of the aleocharines, previously poorly known, is being revised by J. Klimaszewski and S. B. Peck (Klimaszewski 1984, Klimaszewski and Peck 1986). *Aleochara lucifuga* appears to be the most frequently seen member of the subfamily in regional caves, but *Aloconota insecta* and *Atheta annexa* are also relatively common and widespread. Outside the study area, all of these aleocharines are found in a number of cave areas in the southeastern United States.

The omaliine *Brathinus nitidus* (sometimes placed in the family Brathinidae) is widespread in eastern North America and reported from caves in several states (Peck 1975a).

Several troglophilic species in the genus *Quedius* (Staphylininae) inhabit regional caves. Both *Q. erythrogaster* and *Q. spelaeus* are recorded from a number of Virginia caves, are found over much of North America, and are common in caves elsewhere in the eastern United States (Smetana 1971, Holsinger and Peck 1971, Peck and Lewis 1978). *Quedius mesomelinus* is found in caves much less frequently, although its distribution is Holarctic (Smetana 1971).

The family Cantharidae is represented in study-area caves by *Cantharis*, a genus with one or more undetermined trogloxenic species. In Virginia and east Tennessee, as well as elsewhere in eastern North America, only larvae have been found in caves (see Peck 1975b).

Family Cantharidae
  Cantharis sp. (TX)
    Tennessee.—Claiborne Co.: English Cave.
    Virginia.—Pulaski Co.: Sam Bells Cave. Scott. Co.: Greears Sweet Potato Cave. Washington Co.: Brass Kettle Hole Cave.

Family Carabidae
  Atranus pubescens (Dejean) (TP)
    Virginia.—Scott Co.: Coley Cave No. 2. Washington Co.: Hall Bottom Cave No. 1.
  Bembidion (*Peryphus*) *lacunarium* (Zimmermann) (TP)
    Virginia.—Smyth Co.: Atwells Tunnel and Stones No. 2 caves.
  Bembidion (*Amerizus*) *wingatei* (Bland) (TP)
    Virginia.—Alleghany Co : Wares Cave. Tazewell Co.: Lawson Cave.
  Patrobus longicornis (Say) (TX)
    Virginia.—Scott Co.: Coley No. 2 and Sparks caves.
    Comments.—Also recorded from caves in Alabama, Illinois, Kentucky, and Missouri (Barr 1964, Peck and Lewis 1978).
  Platynus tenuicollis (LeConte) (TP)
    Tennessee.—Claiborne Co.: Bug Hole Cave No. 1.
    Virginia.—Giles Co.: Ballards Cave. Montgomery Co.: Old Mill Cave. Rockbridge Co.: Tolleys Cave. Russell Co.: Banners Corner Cave. Smyth Co.: Atwells Tunnel Cave. Washington Co.: Hall Bottom Cave No. 1.

  Pseudanophthalmus (species listed by group as indicated)

engelhardti group

  Pseudanophthalmus deceptivus Barr (TB)
    Virginia.—Lee Co.: Fisher Cave (type locality).
  Pseudanophthalmus engelhardti (Barber) (TB)
    Tennessee.—Claiborne Co.: English Cave (type locality).
  Pseudanophthalmus holsingeri Barr (TB)
    Virginia.—Lee Co.: Young-Fugate Cave (type locality).

Pseudanophthalmus rotundatus Valentine (TB)
Tennessee.—Claiborne Co.: English Cave (type locality). Hancock Co.: "Coopers" (Jeannel 1949:82) and Subers caves.
Virginia.—Lee Co.: Elys Moonshine, Smith, and Sweet Potato caves.

Pseudanophthalmus sidus Barr (TB)
Tennessee.—Campbell Co.: Meredith Cave (type locality).

Pseudanophthalmus sp. A (T. C. Barr, Jr., in ms.) (TB)
Tennessee.—Union Co.: Wolf Cave.

Pseudanophthalmus sp. B (T. C. Barr, Jr., in ms.) (TB)
Tennessee.—Campbell Co.: Valley View Cave.

gracilis group

Pseudanophthalmus gracilis Valentine (TB)
Virginia.—Craig Co.: Rufe Caldwell Cave. Giles Co.: Clover Hollow, Smokehole, and Tawneys (type locality) caves.

grandis group

Pseudanophthalmus virginicus Barr (TB)
Virginia.—Tazewell Co.: Hugh Young Cave (type locality).
Comments.—This species was originally the type species of the genus *Aphanotrechus* but is now assigned to *Pseudanophthalmus* (see Barr 1960a, 1981a).

hirsutus group

Pseudanophthalmus delicatus Valentine (TB)
Virginia.—Lee Co.: Baileys, Bowling, Cattle, Gallohan No. 1, Garrett, Gilley (type locality), Jones Saltpetre, Molly Wagle, Poor Farm, Seal Pit, Smith, Spangler, and Unthanks caves.

Pseudanophthalmus hirsutus Valentine (TB)
Tennessee.—Claiborne Co.: Powell Mountain Cave.
Virginia.—Lee Co.: Cudjos Caverns (type locality) and Cumberland Gap Saltpetre Cave.

Pseudanophthalmus sericus Barr (TB)
Virginia.—Scott Co.: Lane Cave (type locality).

hubbardi group

Pseudanophthalmus avernus (Valentine) (TB)
Virginia.—Rockingham Co.: Endless Caverns (type locality).

Pseudanophthalmus hubbardi (Barber) (TB)
Virginia.—Page Co.: Luray Caverns (type locality).

Pseudanophthalmus intersectus Barr (TB)
Virginia.—Bath Co.: Crossroads Cave (type locality).

Pseudanophthalmus limicola (Jeannel) (TB)
Virginia.—Shenandoah Co.: Maddens (type locality), Shenandoah (Caverns), and Shenandoah Wild caves.

Pseudanophthalmus parvicollis (Jeannel) (TB)
Virginia.—Shenandoah Co.: Battlefield Crystal Cave (type locality).

Pseudanophthalmus potomaca Valentine (TB)
Virginia.—Highland Co.: Van Devanter Cave.
Comments.—Also recorded from Kenny Simmons Cave (type locality) in adjoining Pendleton County, W.Va.

Pseudanophthalmus sp. A (T. C. Barr, Jr., in ms.) (TB)
Virginia.—Bath Co.: Breathing and Butler-Sinking Creek caves.

hubrichti group

Pseudanophthalmus egberti Barr (TB)
Virginia.—Giles Co.: Giant Caverns and Starnes Cave (type locality).

Pseudanophthalmus hubrichti Valentine (TB)
Virginia.—Russell Co.: Daughtery Cave (type locality).

Pseudanophthalmus paradoxus Barr (TB)
Tennessee.—Hawkins Co.: Sensabaugh Saltpetre Cave (type locality).

Pseudanophthalmus quadratus Barr (TB)
Virginia.—Giles Co.: Straleys Cave No. 1 (type locality).

Pseudanophthalmus sanctipauli Barr (TB)
Virginia.—Russell Co.: Banners Corner Cave (type locality). Scott Co.: Greears Sweet Potato Cave.

Pseudanophthalmus vicarius Barr (TB)
Virginia.—Tazewell Co.: Bowens, Cauliflower, Fallen Rock, Gully, Hugh Young (type locality), and Lost Mill No. 3 caves.

Pseudanophthalmus sp. A (T. C. Barr, Jr., in ms.) (TB)
Virginia.—Russell Co.: Banner Cave.

Pseudanophthalmus sp. B (T. C. Barr, Jr., in ms.) (TB)
Virginia.—Russell Co.: Indian Cave.

hypolithos group

Pseudanophthalmus praetermissus Barr (TB)
Virginia.—Scott Co.: Kerns Cave No. 1 (type locality).

jonesi group

Pseudanophthalmus cordicollis Barr (TB)
Virginia.—Wise Co.: Little Kennedy Cave (type locality).

Pseudanophthalmus longiceps Barr (TB)
Tennessee.—Hancock Co.: Panther Creek Cave.
Virginia.—Lee Co.: Fisher Cave (type locality).

Pseudanophthalmus pallidus Barr (TB)
Tennessee.—Claiborne Co.: Buis Saltpetre, Chadwells (type locality), and English caves.

Pseudanophthalmus seclusus Barr (TB)
Virginia.—Scott Co.: Alley, Cox Ram Pump, Flannery (type locality), Hill, Kerns No. 1, McDavids, and Pond caves.

Pseudanophthalmus thomasi Barr (TB)
Virginia.—Scott Co.: Blair-Collins (type locality) and Coley No. 2 caves.
Pseudanophthalmus sp. A (T. C. Barr, Jr., in ms.) (TB)
Virginia.—Scott Co.: Greears Sweet Potato Cave.
Pseudanophthalmus sp. B (T. C. Barr, Jr., in ms.) (TB)
Tennessee.—Campbell Co.: Valley View Cave.

petrunkevitchi group

Pseudanophthalmus hoffmani Barr (TB)
Virginia.—Bland Co.: Coon, Hamilton, Newberry-Bane, and Repass Saltpetre caves. Smyth Co.: Beaver Creek, Buchanan Saltpetre (type locality), and Marble caves.
Pseudanophthalmus hortulanus Barr (TB)
Virginia.—Tazewell Co.: Cassell Farm Cave No. 2 (type locality).
Pseudanophthalmus petrunkevitchi Valentine (TB)
Virginia.—Page Co.: Woods Cave. Warren Co.: Skyline Caverns (type locality).
Pseudanophthalmus sp. A (T. C. Barr, Jr., in ms.) (TB)
Virginia.—Washington Co.: Brass Kettle Hole Cave.
Pseudanophthalmus sp. B (T. C. Barr, Jr., in ms.) (TB)
Virginia.—Wythe Co.: Cave School Water, Pickett, and Sam Six caves.
Pseudanophthalmus sp. C (T. C. Barr, Jr., in ms.) (TB)
Virginia.—Pulaski Co.: Sam Bells Cave.

pusio group

Pseudanophthalmus nelsoni Barr (TB)
Virginia.—Alleghany Co.: Arritt Mill Tunnel (type locality) and Blue Springs (?) caves.
Pseudanophthalmus pontis Barr (TB)
Virginia.—Rockbridge Co.: Buck Hill Cave (type locality).
Pseudanophthalmus punctatus Valentine (TB)
Virginia.—Giles Co.: Clover Hollow, Smokehole, Spruce Run Mountain, and Tawneys (type locality) caves.
Pseudanophthalmus pusio (Horn) (TB)
Virginia.—Montgomery Co.: Agnew, Aunt Nellies, Erhart (type locality), Fred Bulls, Old Mill, Slussers Chapel, and Thorn Hill caves. Roanoke Co.: Goodwins Cave.
Pseudanophthalmus sp. A (T. C. Barr, Jr., in ms.) (TB)
Virginia.—Rockbridge Co.: Showalters Cave.

tennesseensis group

Pseudanophthalmus unionis Barr (TB)
Tennessee.—Union Co.: Wolf (type locality) and Wright caves.

Rhadine caudata (LeConte) (TP)
Virginia.—Roanoke Co.: Dixie Caverns.

Stenolophus ochropezus (Say) (TX)
Virginia.—Scott Co.: Coley Cave No. 2.
Trechus (*Trechus*) *hydropicus canus* Barr (TX)
Virginia.—Lee Co.: Bowling Cave.

Other Carabidae

Other species occasionally collected from study-area caves, where they probably occurred as accidentals, include: *Bradycellus* sp., *Harpalus compar*, *Platynus decens*, *P. extensicollis*, *P. gratiosus*, *P. punctiforme*, *P. retractus*, *Pterostichus lucublandus*, and *Tachys* (*Tachyura*) sp.

Family Leiodidae
Catops sp.
Virginia.—Giles Co.: Spruce Run Mountain Cave.
Nemadus horni (?) Hatch (TX?)
Virginia.—Lee Co.: Gilley and Sweet Potato caves.
Prionochaeta opaca Say (TX)
Virginia.—Smyth Co.: Stones Cave No. 2.

Family Pselaphidae
Arianops jeanneli Park (TB)
Virginia.—Lee Co.: Gilley Cave (type locality).
Batriasymmodes greeveri Park (TB)
Tennessee.—Sullivan Co.: Potters Cave (type locality).
Batriasymmodes monstrosus (LeConte) (AC)
Virginia.—Lee Co.: Poor Farm Cave.
Batrisodes globosus (LeConte) (TX)
Virginia.—Lee Co.: Sweet Potato Cave.

Family Staphylinidae
Aleochara lucifuga (Casey) (TP)
Tennessee.—Claiborne Co.: English Cave.
Virginia.—Bland Co.: Hamilton Cave. Frederick Co.: Ogdens Cave. Lee Co.: Elys Moonshine, Gilley, Lucy Beatty, Smith, and Sweet Potato caves. Page Co.: "Mushroom Cave" (Klimaszewski 1984:93). Roanoke Co.: Goodwins Cave. Russell Co.: Dickenson Cave. Smyth Co.: Roberts and Sugar Grove No. 10 caves. Tazewell Co.: Cassell Farm Cave(s). Wise Co.: Wildcat Saltpetre Cave. Wythe Co.: Sam Six Cave.
Aloconota insecta (Thomson) (TP)
Virginia.—Botetourt Co.: Thomas Cave. Lee Co.: Bowling Cave. Page Co.: Ruffners Cave No. 1. Roanoke Co.: Hodges Cave No. 1. Rockingham Co.: Endless Caverns. Russell Co.: Banners Corner Cave. Tazewell Co.: Fallen Rock and Gully caves. Washington Co.: Hall Bottom Cave No. 1.

Atheta annexa Casey (TP)

Virginia.—Giles Co.: Giant Caverns. Montgomery Co.: Old Mill Cave. Roanoke Co.: Goodwins Cave. Shenandoah Co.: Battlefield Crystal Cave. Smyth Co.: Stones Cave No. 2.

Atheta troglophila Klimaszewski and Peck (TP)

Virginia.—Lee Co.: Lucy Beatty, Smith, and Young-Fugate caves.

Aleocharinae (undetermined genus and species)

Virginia.—Augusta Co.: Glade Cave.

Brathinus nitidus LeConte (TP or TX)

Virginia.—Lee Co.: Bowling Cave. Russell Co.: Banners Corner Cave. Scott Co.: Coley No. 2 and Flannery caves.

Quedius (*Microsaurus*) *erythrogaster* Mannerheim (TP)

Virginia.—Bath Co.: Porters and Roy Lyle caves. Giles Co.: Giant (Caverns), Harris and Straleys No. 1 caves. Highland Co.: Marshalls Cave. Lee Co.: "Cave No. 1 and No. 3, Pennington Gap" (Smetana, 1971:85), and Indian Cave. Rockbridge Co.: Doll House Cave. Rockingham Co.: Melrose Cave. Scott Co.: Sounding Cave. Shenandoah Co.: Hensleys and Shenandoah Wild caves. Smyth Co.: Buchanan Saltpetre Cave.

Quedius (*Microsaurus*) *mesomelinus* (Marsham) (TP or TX)

Virginia.—Pulaski Co.: Sam Bells Cave.

Quedius (*Microsaurus*) *spelaeus* Horn (TP)

Virginia.—Bath Co.: Cave Run Pit and Crossroads caves. Frederick Co.: Ogdens Cave. Giles Co.: Tawneys Cave. Pulaski Co.: Fifty-Foot Hell Cave. Rockingham Co.: Three-D Maze Cave.

Quedius sp.

Virginia.—Augusta Co.: Grand Caverns and Madisons Saltpetre Cave. Lee Co.: Young-Fugate Cave. Page Co.: Luray Caverns. Rockingham Co.: Massanutten Caverns. Warren Co.: Skyline Caverns.

Other Staphylinidae

Nine other genera, based largely on single records and presumably including mostly accidental species, are recorded from study-area caves as follows: *Cratarea*, *Emplenota*, *Erichsonius*, *Homaeotarsus*, *Lathrobium*, *Lesteva* (probably *L. pallipes* LeConte, a common trogloxene), *Megalinus*, *Philonthus*, and *Trichophya* (probably *T. pilicornis* Gyllenhal).

Order Diptera

With the possible exception of one species, there are no troglobitic dipterans (flies) in the study area. Several species are relatively common in caves, however, and sometimes make an important contribution to the cavernicolous fauna. At least six families are found in regional caves with some degree of regularity: Heleomyzidae, Mycetophilidae, Phoridae, Psychodidae, Sciaridae, and Sphaeroceridae. In addition, seven other families are sporadically observed, usually in entrance zones; but they rarely, if ever, contribute significantly to the fauna of a given cave. These are Calliphoridae, Chironomidae, Culicidae, Dolichopodidae, Empidae, Streblidae (e.g., *Trichobius*, an ectoparasite of bats), and Tipulidae. Although no attempt was made to systematically collect dipterans from caves, a few collections were made selectively to establish the identity of the most common species.

The fly most frequently seen in regional caves was *Amoebalaria defessa* (Heleomyzidae), a troglophile or trogloxene common in caves throughout much of the eastern United States (see Gill 1962, Peck and Lewis 1978) (Fig. 31B). Two other heleomyzids, *Aecothea* (probably *A. specus* Aldrich) and *Heleomyza brachyptera* (Loew), were observed occasionally , but specific cave records are unavailable. Heleomyzids are generally found on damp walls and ceilings, sometimes in large numbers and usually not far from entrance zones (see also Busacca 1975).

Also relatively common in study-area caves are *Megaselia cavernicola* (Phoridae), a troglophile widespread in the east-central and eastern United States (see Borgmeier 1965), and members of the Sphaeroceridae, of which several species are often found in caves of the United States (see Curran 1965, Stone et al. 1965, Marshall 1985). Although the sphaerocerid *Spelobia tenebrarum* is recorded from only two caves in Lee County, it probably inhabits many other caves in the study area. This species is recorded from numerous caves in the eastern United States and has been listed as a troglophile or trogloxene under the name *Leptocera tenebrarum* by a number of workers (viz., Barr 1967a, Holsinger and Peck 1971, Holsinger et al. 1976, Peck and Lewis 1978). However, in a recent study of cavernicolous sphaerocerids, Marshall and Peck (1984, 1985) suggest that it may be a troglobite. Both *Megaselia* and *Spelobia* are associated with decaying organic material (e.g., vegetal matter, feces, and carcasses) in caves.

Both larvae and adults of fungus gnats (families Sciaridae and Mycetophilidae) are recorded from regional caves. Sciarids are usually found in and around damp, rotting vegetal debris. Mycetophilid larvae are sometimes luminescent and build silken webs on dung and damp clay and under rocks. Peck and Russell (1976) identified the mycetophilid *Macrocera nobilis* Johnson from many caves in the southeastern United States, but none of these records is from the study area. Although *M. nobilis* should occur in study-area caves on the basis of its geographic distribution, most of the larvae seen to date have been smaller than those of this species and probably represent other genera.

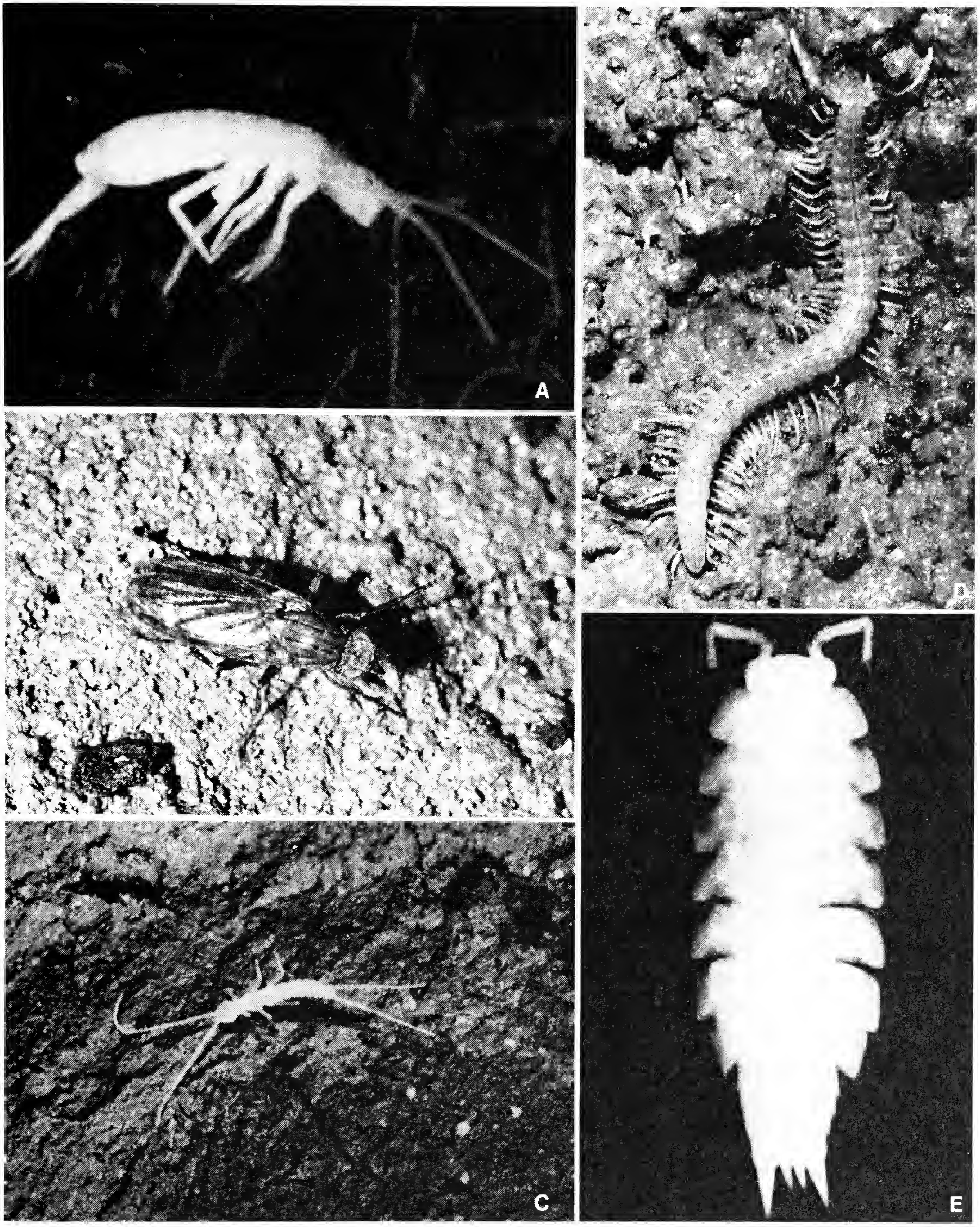

Fig. 31. Terrestrial cavernicoles from the study area (approximate body lengths in parentheses): A, collembolan, *Tomocerus bidentatus* (3 mm); B, fly, *Amoebalaria defessa* (6 mm); C, dipluran, *Litocampa* sp. (7 mm) (courtesy of L. M. Ferguson); D, milliped, *Pseudotremia nodosa* (15 mm); E, terrestrial isopod, *Amerigoniscus henroti* (6 mm).

Family Heleomyzidae

Amoebalaria defessa (Osten-Sacken) (TP or TX)

Tennessee.—Claiborne Co.: Buis Saltpetre and Keck No. 1 caves. Grainger Co.: Horseshoe Cave. Hancock Co.: Subers Cave.

Virginia.—Bland Co.: Hamilton Cave. Craig Co.: Carpers and Rufe Caldwell caves. Frederick Co.: Ogdens Cave. Giles Co.: Ballards Cave. Lee Co.: Gallohan No. 1, Olinger, Roadside No. 1, and Young-Fugate caves. Montgomery Co.: Vickers Road Cave. Pulaski Co.: Fifty-Foot Hell Cave. Rockbridge Co.: Showalters Cave. Rockingham Co.: Massanutten Caverns. Russell Co.: Banners Corner and Campbells Spring caves. Scott Co.: Blair-Collins and Hill caves. Smyth Co.: Tilson Saltpetre Cave. Tazewell Co.: Fallen Rock, Hugh Young, and Steeles caves.

Family Mycetophilidae

Genus (?) species (?)

Tennessee.—Claiborne Co.: Jennings Cave.

Virginia.—Bath Co.: Porters Cave. Lee Co.: Cumberland Gap Saltpetre Cave. Rockbridge Co.: Doll House Cave.

Family Phoridae

Megaselia cavernicola (Brues) (TP)

Virginia.—Lee Co.: Gallohan No. 1, Molly Wagle, Smith, and Sweet Potato caves. Page Co.: Luray Caverns. Smyth Co.: Tilson Saltpetre Cave. Tazewell Co.: Lawson Cave.

Family Psychodidae

Psychoda sp.

Virginia.—Lee Co.: Sweet Potato Cave.

Family Sciaridae

Bradysia luravi (Johannsen) (TX or AC)

Virginia.—Page Co.: Luray Caverns.

Bradysia sp.

Virginia.—Lee Co.: Gallohan No. 1, Molly Wagle, Smith, and Sweet Potato caves. Smyth Co.: Tilson Saltpetre Cave.

Pnyxia scabiei (Hopkins) (AC)

Virginia.—Page Co.: Luray Caverns.

Sciara (?) sp.

Tennessee.—Claiborne Co.: English Cave.

Virginia.—Tazewell Co.: Lawson Cave.

Family Sphaeroceridae

Leptocera pararoralis (?) Duda (TX?)

Virginia.—Lee Co.: Gallohan No. 1 and Sweet Potato caves.

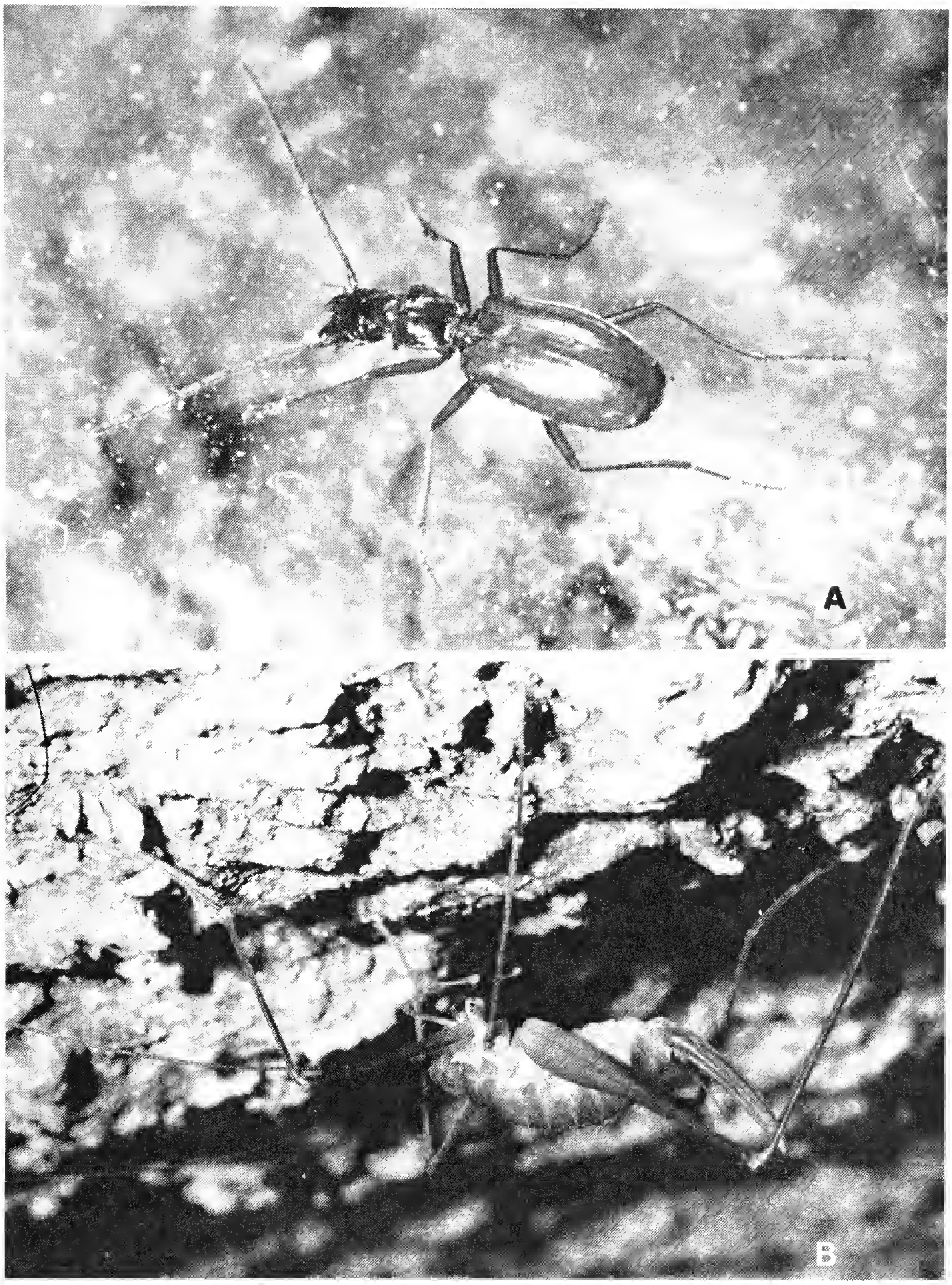

Fig. 32. Terrestrial cavernicoles from the study area (approximate body lengths in parentheses): A, beetle, *Pseudanophthalmus delicatus* (4 mm); B, cricket, *Euhadenoecus fragilis* (15 mm).

Spelobia semioculata (Richards) (TX?)
  Virginia.—Lee Co.: Smith Cave. Shenandoah Co.: Maddens Cave.
Spelobia tenebrarum (Aldrich) (TP?)
  Virginia.—Lee Co.: Molly Wagle and Sweet Potato caves.
Spelobia (?) spp.
  Virginia.—Page Co.: Luray Caverns. Shenandoah Co.: Shenandoah Caverns. Smyth Co.: Tilson Saltpetre Cave.

ECOLOGY

SOURCES OF FOOD

Aside from darkness, the most striking feature of most caves is the scarcity of food. Except for a few chemosynthetic autotrophic bacteria that use iron and sulfur as an electron donor, primary producers are absent. Thus, in a general sense, cave communities are decomposer communities. Allochthonous food is brought in by both biological and physical agents in different amounts, continuously or in pulses, and in different spatial configurations. These differences affect the kind of species present, so that it is useful to review them.

In the terrestrial biotope, there are at least five major sources of food: (1) bat guano, (2) cave cricket eggs and guano, (3) microorganisms, (4) mammalian feces and dead animals, and (5) plant detritus left by flooding. A few caves harbor large bat colonies with large guano concentrations beneath the roosting sites. In this case food is abundant, and the fauna feeding on guano is quite different from the rest of the cave fauna (Harris 1970). Caves with large bat populations are rare in Virginia and east Tennessee and have not been studied with respect to their invertebrate communities. Small piles of bat guano rarely seem to have any macroscopic fauna. Perhaps this is because no species are present that are physiologically equipped to digest bat guano.

A major source of food input comes from the cave crickets in the genus *Euhadenoecus*. These crickets regularly leave the cave at night and feed "opportunistically and omnivorously as a scavenger" (Hubbell and Norton 1978), eating the vast majority of their food outside the cave. The females oviposit inside the cave, usually in sandy substrates. In parts of the Edwards Plateau of Texas and the Interior Low Plateaus of Kentucky, cave-cricket eggs are the major dietary item for some species of beetles. This fascinating interaction has been extensively studied (Culver 1982) because the cricket-beetle interaction comes close to being a naturally isolated predator-prey pair. This facilitates study of morphological, behavioral, and demographic characteristics because selective pressures are relatively simple and clear-cut. We have found no evidence that cricket eggs form a major part of the diet of any beetles in Virginia and east-Tennessee caves. We suspect that this interaction is absent because sandy substrates are rare in Appalachian Valley caves and *Euhadenoecus* species oviposit in substrates difficult for beetles to excavate. Cricket guano, on the other hand, is an important food source. Some of the most diverse terrestrial communities occur in areas where cricket guano is spattered on walls and floors. We suspect that in many caves it is a major source of food, either directly, or indirectly by serving as a substrate for microflora.

Microorganisms occur on a variety of substrates, including wood, dung, and plant detritus. At least part of the diet of many terrestrial cave invertebrates is microorganisms (see below). The richest sources of microorganisms are dung near entrances and decaying arthropod remains in aphotic passages (Dickson and Kirk 1976). Fungi are more concentrated and patchily distributed than bacteria, and fungi are also a more important food source, perhaps because they are concentrated.

Besides serving as a substrate for microfungi, dung and dead animals are important food in their own right and attract a wide variety of invertebrates. Peck (1973) has also used human dung as a very effective bait for cave invertebrates.

Plant detritus may also be an important food source. A layer of mud and finely divided leaves, often rich in oligochaetes, is deposited in many caves by slowly receding floodwaters. Such areas often have a rich fauna. In caves subject to severe, rapid flooding, piles of twigs and leaves are left behind. On these resource patches is a relatively distinct fauna that will be described below.

Food in streams is almost entirely allochthonous in origin. Stream detritus is usually divided into coarse particulate organic matter (CPOM > 1 mm) and fine particulate organic matter ($0.0005 \text{ mm} < \text{FPOM} < 1$ mm) (Cummins and Klug 1979). By convention, organic matter smaller than 0.0005 mm is considered dissolved (DOM). CPOM is a substrate for microorganisms.

RESOURCE LEVELS

Although there is a great deal of indirect evidence of food scarcity in caves, there have been few direct measurements of resource levels in caves. Many of the physiological and morphological changes associated with isolation in caves (reviewed by Culver 1982) make sense only in the context of a relatively stable, food-poor environment. It is obvious to anyone visiting a cave that at least the standing crop of resources is very low indeed.

Dickson and Kirk (1976) have provided direct evidence from Old Mill Cave in Montgomery County. They found that, for the most part, resource levels were lower in the cave than in forest soil, but there are exceptions. Dung in the entrance and mud floors with chitin remains had high plate counts. Thus food is scarce and very patchy. Dickson and Kirk (1976) also found that fungi are correlated with abundance of the terrestrial macrofauna whereas bacteria are not. This may help explain why wet passages have more fauna than dry passages, where fungi are relatively uncommon.

There remains the question of how much food is actually available to cave animals. The best comparative study is that of Peck and Richardson (1976), who compared stomach contents of the "cave salamander" *Eurycea lucifuga* Rafinesque from entrance and dark zones of caves in Tennessee and Alabama. Salamanders collected at the

Table 2. Fauna associated with discrete habitats with abundant resources—dung, wood, and plant detritus. Troglobites indicated by an asterisk.

Cave	Location	Habitat	Fauna	
Smiths Cave	Russell Co.	Dung	Collembola:	*Tomocerus* sp.
			Diptera:	*Spelobia* (?) sp.
			Chordeumatida:	*Pseudotremia* sp.
Smith Cave	Lee Co.	Dung	Chordeumatida:	*Pseudotremia nodosa**
				Pseudotremia sp.
Tilson Saltpetre Cave	Smyth Co.	Plant detritus	Diptera:	*Bradysia* sp.
				Spelobia (?) sp.
				Megaselia cavernicola
			Collembola:	*Pseudosinella orba**
			Acari:	Rhagidiidae
			Coleoptera:	Staphylinidae
			Diplura:	*Litocampa* sp. E*
			Chordeumatida:	*Pseudotremia* sp.
Lower Coonsies Creek Cave	Claiborne Co.	Plant detritus	Araneae:	*Nesticus* sp.
			Coleoptera:	*Platynus* sp.
				Staphylinidae
			Diptera:	*Megaselia* sp.
			Collembola:	*Tomocerus bidentatus*
			Isopoda:	*Ligidium elrodii*
			Chordeumatida:	*Pseudotremia nodosa**
Hill Cave	Scott Co.	Wood	Collembola:	*Tomcerus bidentatus*
			Araneae:	*Phanetta subterranea**
			Pseudoscorpiones:	*Kleptochthonius binoculatus**

Wolf Cave	Union Co.	Wood	Collembola:	*Sinella barri*
			Chordeumatida:	*Pseudotremia nodosa**
			Isopoda:	*Amerigoniscus paynei**
			Coleoptera:	*Pseudanophthalmus* sp. A*
				*Pseudanophthalmus unionis**
English Cave	Claiborne Co.	Wood	Chordeumatida:	*Pseudotremia nodosa**
			Aranea:	*Nesticus carteri*
			Coleoptera:	*Pseudanophthalmus engelhardti**
				*Pseudanophthalmus rotundatus**
Kinzer Hollow Cave	Lee Co.	Wood	Isopoda:	*Amerigoniscus henroti**
Cattle Cave	Lee Co.	Wood	Diptera:	*Megaselia* sp.
			Chordeumatida:	*Pseudotremia* sp.
			Araneae:	*Nesticus* sp.
			Coleoptera:	*Pseudanophthalmus delicatus**

entrance, where one would expect food to be more abundant, had 19.6 prey items with a volume of 0.14 ml per stomach. By contrast salamanders from dark zones had only 3.4 prey items with a volume of 0.05 ml per stomach.

DIETS

Our knowledge of the diet of cavernicoles is woefully inadequate. While food webs are not available for most communities (see Cohen 1978) and most published food webs are fanciful, the problem is particularly acute for cave communities. Packard (1888) pointed out nearly a century ago, that "cave animals, even the carnivorous species, take remarkably little food." Contemporary ecological theory predicts that a species faced with scarce resources should increase the range of foods taken. That is, one would expect little specificity in diet. One obvious fact about cave animals is that even their surface relatives tend to be omnivorous.

Many terrestrial cavernicoles feed directly on dead and decaying organic matter and associated microorganisms. Except for crickets, millipeds are usually the most abundant terrestial cavernicoles. Millipeds are frequently found on dead and decaying organic matter, and they often ingest rotting wood (Shear 1969). Other invertebrates that feed directly on dead and decaying organic matter include staphylinid beetles, isopods, and dipterans. Collembolans apparently concentrate on microfungi (Christiansen 1964b).

Carnivores are also very catholic in their diets. Around cave entrances the orbweb-building spider *Meta menardi* is often common; it captures a variety of flying insects, especially Diptera. Cantharid beetle larvae may also be important predators in entrances (Peck 1975b). In the dark zones, nesticid and linyphiid spiders construct several small sheet webs in which they capture a variety of walking invertebrates. Other web-builders are likely to be in the study area—the larvae of the fungus gnat *Macrocera nobilis* (Peck and Russell 1976). These larvae build webs in which they catch mostly other dipterans, but they also feed on dead organic matter while constructing their webs (Peck and Russell 1976). Trechine beetles, which are often common in caves in the Interior Low Plateaus, are generally uncommon in Virginia and east Tennessee. In common with the small species of *Pseudanopthalmus* in the Interior Low Plateaus, species of this genus in the study area probably eat collembolans, small oligochaetes in the mud, diplurans, and small diplopods (Barr 1968, Keith 1975, McKinney 1975). Even less is known about other invertebrate predators, such as opilionids, pseudoscorpions, and rhagidiid mites; but they probably feed mainly on Collembola, spider eggs, and small spiders. Finally, the salamanders, *Eurycea lucifuga* and *Gyrinophilus prophyriticus* eat a wide range of invertebrates.

Most cavernicoles in streams feed directly on detritus and its associated microorganisms. The epigean amphipod *Gammarus pseudolimnaeus* Bousfield is a facultative shredder (Cummins and Klug 1979), preferring CPOM, but also using FPOM and DOM. Cave-stream amphipods are probably similar in this regard. No direct information on isopods is available, but Estes (1978) suggests that *Lirceus usdagalun* tends to eat CPOM whereas *Caecidotea recurvata* tends to eat DOM. On the basis of their size, crayfish are probably shredders, and snails and lumbriculid worms probably ingest DOM.

The diet of cave flatworms is more problematical than that of crustaceans. Mitchell (1974) has demonstrated that Texas cave flatworms (*Sphalloplana* sp.) eat injured and moribund amphipods and crickets. Holsinger (1966), on the other hand, suggested that flatworms eat tubificid worms. The greatest concentrations of flatworms that we have observed in cave streams have been in stream pools with no amphipods or isopods. We suspect that flatworms feed on small oligochaetes and perhaps on microorganisms.

The primary stream predator is larval *Gyrinophilus porphyriticus*. These salamander larvae are voracious feeders on amphipods and isopods (Culver 1973b, 1985) and appear to be exclusively predaceous. They are generally limited to caves with high densities of amphipods and isopods.

The amphipods and isopods occurring in drip pools and in deep phreatic lakes ingest the organically rich mud. Guts of animals from these habitats are often filled with mud, as can be seen in the photograph of the cirolanid isopod *Antrolana lira* (Fig. 13A). Dickson (1975) shows that abundance of *Crangonyx antennatus* in pools is correlated with abundance of microfungi. A tentative food web for pool habitats in Banners Corner Cave is shown in Figure 33, based on Holsinger's (1966) study.

HABITATS

Because of the scarcity and patchiness of resources, terrestrial cavernicoles are often concentrated on discrete patches of dung, wood, and plant detritus. Examples of the fauna found in these habitats are listed in Table 2. The most interesting pattern that emerges from Table 2 is that the frequency of troglobites is lowest on dung (20%), slightly higher on patches of plant detritus (28%), and much higher on wood (76%). The difference between wood and the other habitats is highly significant ($G = 9.44$ $P > 0.99$). As Poulson (1978) pointed out, resources with high caloric value and low residence time, such as dung, should have a high frequency of vagile troglophiles with relatively high reproductive rates, compared with long-lasting resources having low caloric value, such as wood.

Cavernicoles also are found in habitats that are less discrete, where resources are more or less homogeneously distributed over a larger area. The most notable example of this is mud banks, which are often near streams. The faunas from three such habitats are listed in Table 3. In Fallen Rock Cave, a layer of finely divided detritus rich in oligochaetes was present, and in the other two caves there were spatterings of cricket guano. In all three caves there was a high proportion of troglobites, ranging from 50% in Tazewell Saltpetre Cave to 73% in Gallohan Cave No. 1. In these situations, low resource density probably puts troglophiles at a disadvantage.

Most cave streams have an alternating riffle-pool structure (shallows and deeps) that is characteristic of stony-bottomed streams in general. Most stream-dwelling cavernicoles prefer riffles for several reasons. First, water in riffles is well oxygenated. Second, riffles serve as traps for leaf litter, thus increasing availability of food resources. Species characteristic of riffles are the isopods *Caecidotea* and *Lirceus*, the amphipod *Crangonyx antennatus*, and the snails *Fontigens*. There is a finer division of the riffle habitat. In general, small individuals tend to be under small rocks, which are deep in the riffle. In a study of two caves in southwestern Virginia, Estes (1978) found that the small *Crangonyx antennatus* was under small rocks and gravels, but the larger *Lirceus usdagalun* and *Caecidotea recurvata* tended to be under large rocks and gravels.

A few species are concentrated in steam pools. Flatworms seem to be more common in pools, where they glide along the surface of the water, than in riffles; but no quantitative data exist on this point. Larval *Gyrinophilus prophyriticus* are concentrated in pools, where it is relatively easy for them to detect prey movements (Culver 1975).

Drip pools are the habitat of most species of *Stygobromus*, although occasionally some (especially *Stygobromus mackini*) are found in streams (Holsinger 1978). *Crangonyx antennatus* also occurs in pools (Dickson 1977a), where it frequently constructs shallow burrows, apparently to avoid desiccation during droughts (Holsinger and Dickson 1977). Burrowing behavior may be widespread in *Stygobromus* as well, but this point has not been investigated.

LIFE HISTORIES

Relatively little work has been done on life histories of cavernicoles in the study area. Nonetheless, because of the importance of the subject, a brief overview of the problem will be presented. A more comprehensive treatment is given by Culver (1982). In general three sorts of comparisons have been made. First, cavernicoles have been compared with epigean species (Ginet 1960, Rouch 1968). While comparisons have not always been made with phyletically similar species, these comparisons usually show striking differences between cave and epigean species. Second, cavernicoles of different ages in caves have been compared. Age in caves

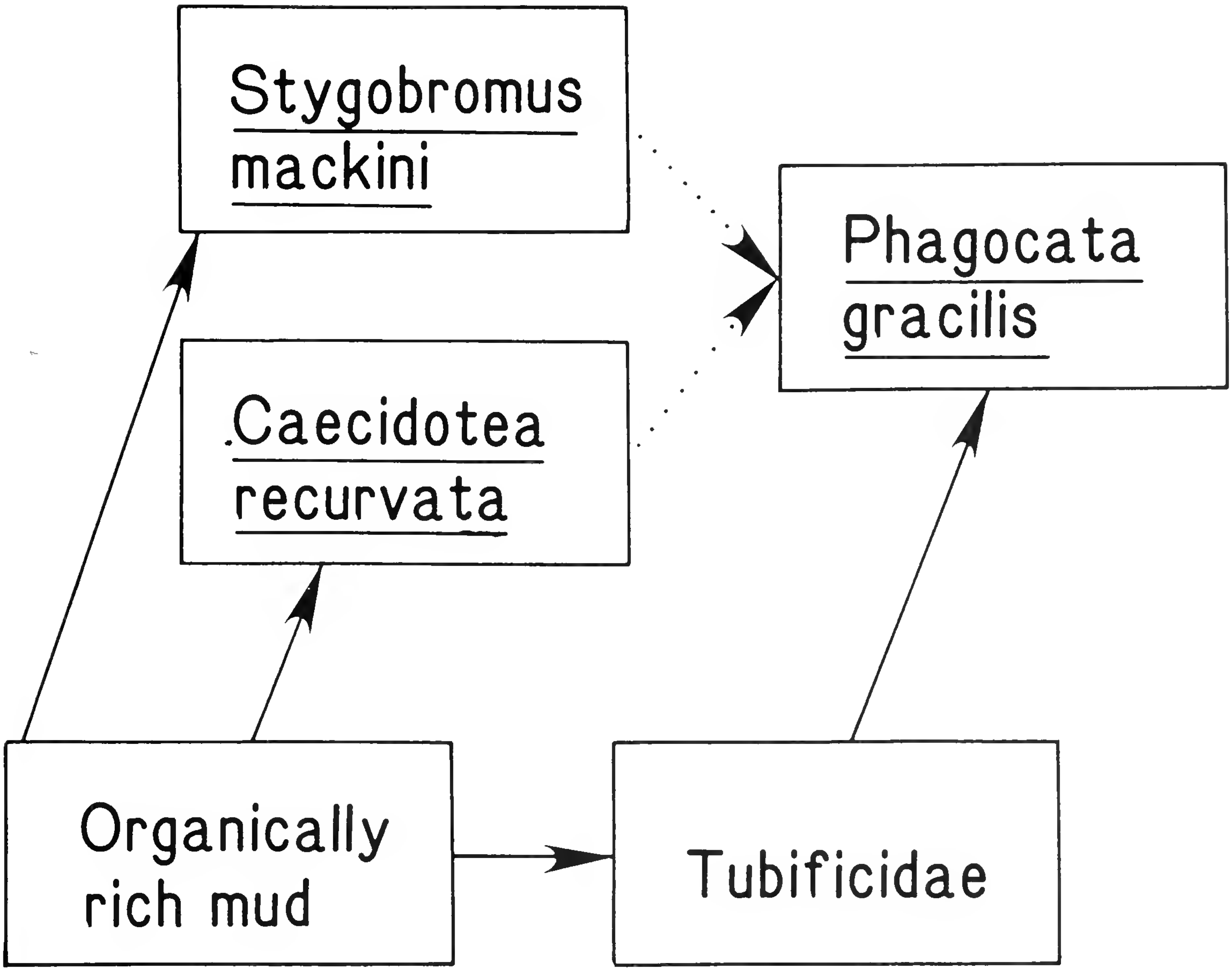

Fig. 33. Food web for Banners Corner Cave, Russell County, Va. The dotted lines indicate feeding by flatworms on injured and moribund amphipods and isopods.

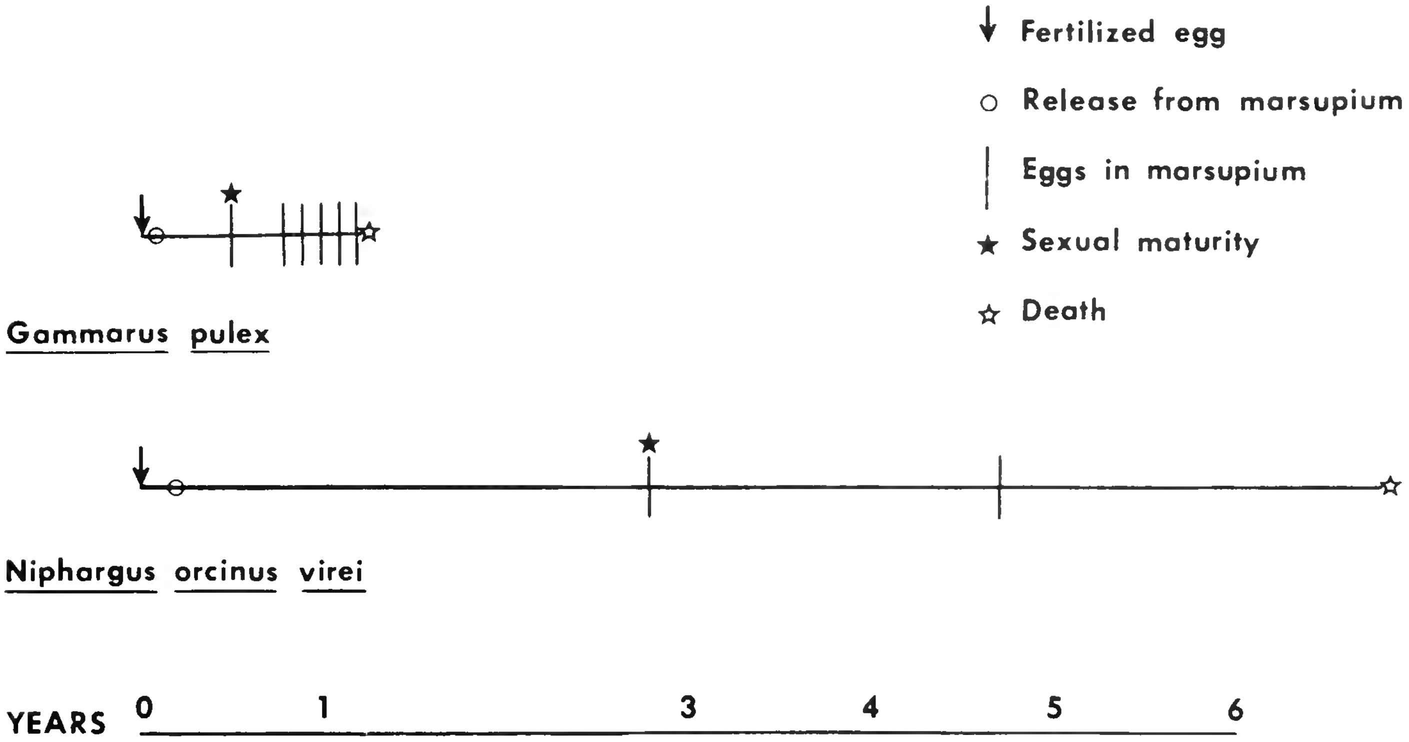

Fig. 34. Life history comparison of the troglobitic amphipod *Niphargus orcinus virei* with the epigean amphipod *Gammarus pulex*. Modified from Ginet (1960).

Table 3. Fauna associated with diffuse food supplies. Troglobites indicated by an asterisk.

Cave	Location	Habitat	Fauna	
Fallen Rock Cave	Tazewell Co.	Mud with finely divided detritus	Coleoptera:	*Staphylinidae*
				*Pseudanophthalmus vicarius**
			Collembola:	*Pseudosinella orba**
			Diplura:	*Litocampa* sp. A*
			Chordeumatida:	*Pseudotremia armesi*
Gallohan Cave No. 1	Lee Co.	Mud with cricket guano	Arcari:	Rhagidiidae
			Araneae:	*Nesticus carteri*
				*Phanetta subterranea**
			Pseudoscorpiones:	*Kleptochthonius proximosetus**
			Isopoda:	*Amerigoniscus henroti**
			Chordeumatida:	*Pseudotremia nodosa**
				Pseudotremia sp.
			Diplura:	*Litocampa cookei**
			Collembola:	*Pseudosinella orba**
				Arrhopalites hirtus
				Tomocerus bidentatus
Tazewell Saltpetre Cave	Claiborne Co.	Mud with cricket guano	Chordeumatida:	*Pseudotremia nodosa**
			Arcari:	Rhagidiidae
			Diptera:	*Spelobia* (?) sp.
			Araneae:	*Nesticus carteri*

is usually measured by the level of regressive evolution (Poulson 1963). Third, cavernicoles in different cave habitats have been compared (Dickson and Holsinger 1981, Estes 1978).

Selection for delayed reproduction, increased longevity, and the like is frequently called K-selection. Recent models (reviewed by Charlesworth 1980) show that there is no simple dichotomy between r-selection and K-selection, but the following characteristics are likely to be selected for in at least some cavernicoles:

1. Delayed maturity
2. Increased longevity
3. Fewer clutches
4. Smaller clutch size
5. Larger eggs
6. Low percentage of mature females ovigerous
7. Sex ratio skewed toward females

Examples of each of these characteristics will be discussed, but their generality will not.

Ginet's (1960) study of the amphipod *Niphargus orcinus virei* Chevreux illustrates the first three characteristics (Fig. 34). Compared with *Gammarus duebeni* Lilljeborg, *N. orcinus virei* takes four times longer to mature, lives five times longer, and has only two broods (as opposed to seven). The most striking example of increased longevity is the crayfish *Orconectes australis australis* (Rhoades), which lives a minimum of 40 years (Cooper 1975). The amphipod *Crangonyx antennatus*, which is common in many Virginia and Tennessee caves, lives at least 6 years in the laboratory. Life spans of terrestrial animals are apparently shorter. Peck (1975c) found that the leiodid beetle *Ptomaphagus hirtus* Tellkampf lived an average of 2 years.

Rouch (1968), in a comprehensive study of cave harpacticoid copepods in France, found that cavernicolous species had fewer eggs per unit size of female and that egg diameters were larger than was the case for low-altitude epigean species. High-altitude epigean harpacticoids, like cavernicolus species, also had fewer eggs with larger diameters when compared with low-altitude epigean species.

Many populations of cavernicoles have low percentages of ovigerous females and mature females. One very clear case is Dickson's data (Dickson and Holsinger 1981) on *Crangonyx antennatus* from two caves in Lee County, Va. (Fig. 35). These data raise some interesting evolutionary questions. If ovigerous females are genetically different from non-ovigerous females, then those genotypes should increase, resulting in higher frequencies of ovigery. Low ovigery may be maintained by strong intraspecific competition, with little genetic basis, which allows only an occasional female to take in enough food to reproduce. Alternatively, low rates of ovigery may be maintained by group selection, with populations with excessively high reproductive rates becoming extinct.

Apparently in response to low population densities, some aquatic species have evolved to the point where males are quite rare. We suspect that this is accompanied by some form of parthenogenesis (Culver and Holsinger 1969), but the genetics have not been studied. The isopod *Lirceus usdagalun* has a sex ratio favoring females by at least three to one (Estes 1978); and in the amphipod *Crangonyx antennatus*, male frequency is positively correlated with density (Dickson and Holsinger 1981). However, male rarity is most strikingly developed in the amphipod genus *Stygobromus*. Cave populations usually have sex ratios of the order of 10 females to every male (Culver and Holsinger 1969).

POPULATION SIZE AND STABILITY

For populations undergoing K-selection, increased efficiency, reduced clutch size, and the like should result in an increase in the carrying capacity, and thus increase population size. The best comparative data are from Poulson's (1963) study of the amblyopsid fishes in caves in the Interior Low Plateaus. There is an unambiguous increase in population size with increasing morphological adaptation. Considering life-history characteristics, however, *Amblyopsis spelaea* De Kay would be expected to have a high population size because its growth rate is low. In a less comprehensive study of the isopods *Lirceus usdagalun* and *Caecidotea recurvata*, Culver (1976) found that *L. usdagalun* had a lower carrying capacity than did the more specialized *C. recurvata*.

However, there is considerable doubt that those species with the longest evolutionary history in caves have the largest population sizes. Although actual population sizes are determined by interspecific interactions as well as carrying capacity, the intensity of these interactions should also be under evolutionary control. Culver (1976) showed that the intensity of competition between any pair of species declined through evolutionary time but that success in competition did not increase. Thus, the troglophilic amphipod *Gammarus minus* (Form I) is much more common than the troglobitic amphipod *Stygobromus mackini* and the isopod *Caecidotea richardsonae* in the caves of the Ward Cove karst in Tazewell County. In the milliped genus *Pseudotremia,* troglophiles can be as abundant as troglobites. Comparatively more specialized millipeds in the genus *Trichopetalum* are always less common than those in *Pseudotremia*. Many troglobites, such as pseudoscorpions, are always rare. These observations suggest that rarity *per se* is advantageous, since the population avoids increases that lead to crashes and extinction. The most likely mechanism for evolution of rarity is group selection. This conclusion is supported by the fact that population extinctions are known to occur (Culver 1970).

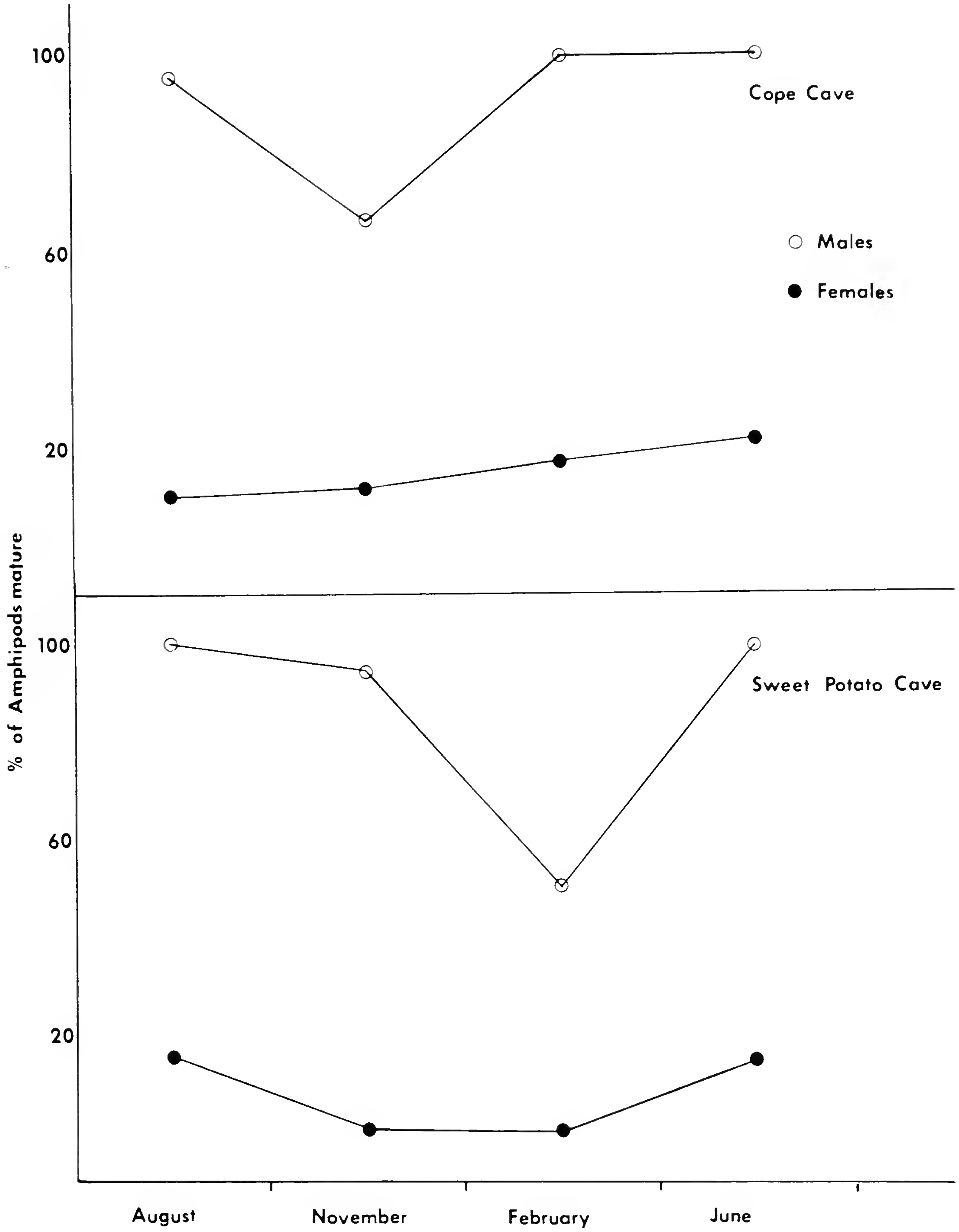

Fig. 35. Frequency of males that are mature and frequency of females that are mature for *Crangonyx antennatus*. From Dickson and Holsinger (1981).

INTERSPECIFIC INTERACTIONS—GENERAL

Compared with other ecological problems, interspecific interactions among cavernicoles have received considerable attention. Cave communities offer several advantages to the student of species interactions. First, cave environments and population sizes are relatively stable compared with most epigean populations. Thus cave communities correspond more closely to the assumptions of ecological models than do most communities. Second, the number of species is so small that all interactions can be studied. Third, because there are many caves with very similar environmental conditions, there are many replicates as well as many "natural experiments" where species composition is different. The main disadvantage of cave communities is the long generation time of species, which makes the study of long-term dynamics difficult.

MUTUALISM

No free-living mutualists have been reported from caves. Mutualistic gut endosymbionts may be important, but they have not been studied. Two ectosymbionts on crayfish are known, branchiodbellid worms and entocytherid ostracods, both of which occur in the study area. Hobbs (1975) has studied ostracod symbionts in Indiana caves, and his work shows that cave crayfish may be convenient systems for the study of symbiosis. The ecosymbiotic entocytherids attach to the exoskeleton of crayfish and feed on microorganisms and detritus that accumulate on the host exoskeleton.

The troglobitic crayfish *Orconectes inermis* Cope has several advantages for further study. First, more than 90% of the ostracods on *Orconectes inermis inermis* belonged to one species, *Sagittocythere barri* (Hart and Hobbs), which in turn was rarely found on other crayfish in Hobbs' study area. Thus it is essentially a two-species system. Second, the ectosymbionts are common. More than half of the *O. inermis* populations had ostracods. The average number of *S. barri* per crayfish was 17.2 (Hobbs 1975). One of Hobbs' most interesting findings was that there was a significant increase in the number of ostracods with increasing length of the crayfish carapace. Thus the crayfish are like islands that are colonized by ostracods.

PREDATION

While predation appears to be more frequent in the terrestrial fauna than in the aquatic fauna, there have been no ecological or behavioral studies of terrestrial predators in the study area. One aquatic predator, larval *Gyrinophilus porphyriticus*, has been extensively studied (Culver 1973b, 1975, 1985). This work is summarized below.

Gyrinophilus porphyriticus larvae form significant populations in stream pools in several caves in the Powell Valley of Claiborne and Lee counties. Their prey are amphipods and isopods. None of the larvae reacted to dead amphipods and isopods, but when a live amphipod or isopod was put in the water, the larva would raise itself on its front legs and usually its hind legs as well. It then remained motionless until the prey came within 2 to 4 cm of its snout. Then, with rapid sucking action, the salamander ate the prey item. Larvae will also attack the ends of small brushes moved slowly through the water, indicating that mechano-reception is the primary method of prey detection.

The behavior of the larvae toward prey is remarkably uncomplicated. The functional response is linear over a wide range of prey densities (Fig. 36), a wider range than is normally encountered in the field. This linearity is apparently due to the very short handling time and the larvae's prodigious appetites. One larva ate eight *Caecidotea recurvata* in 30 minutes in the laboratory.

Although *G. prophyriticus* attempts to capture any *Caecidotea recurvata* or *Crangonyx antennatus* that comes close to its snout, it is about three times as successful at capturing *C. recurvata,* apparently because *C. antennatus* often avoids predation by swimming out of range. Actual predation rates also depend on the fraction of the population accessible to predators. Because nearly all *G. porphyriticus* larvae are in pools rather than riffles, and relatively still water aids prey detection, individuals in riffles and on flowstone are inaccessible to predators. In McClure Cave in Lee County, it was found that the actual predation rates (proportional to success rate times the proportion accessible to predation) did not significantly differ between the two species (Culver 1975). This is probably coincidental, but it does facilitate modeling the system. Using standard competition and predation equations, which is justified in part by the linear functional response, it was predicted that both the density and frequency of *C. antennatus* should increase. Even though it is preyed upon, the reduction in density of its competitor *C. recurvata* more than compensates for predation losses. Field data confirmed these predictions. Frequency of *C. antennatus* increased from 0.09 away from larvae, to 0.44 in the immedidate vicinity of larvae.

Salamander predation also resulted in habitat shifts of the prey. With salamanders nearby, a greater frequency of both prey species was found in riffle and flowstone "refuges." Consequently, when salamanders first invade a cave, a greater frequency of the prey population is available. Potential predation rates are nearly double those at equilibrium. Thus, invasion should be easy, but the establishment of a reproducing population should be difficult. This prediction is also confirmed by the data. Most "populations" are fewer than five individuals.

COMPETITION

Competition is the most extensively studied and probably the most important interaction in caves. Barr (1967b) and McKinney (1975) have found it to be important in cave beetles, and Cooper (1975) discussed the importance of competition among cave crayfish. The most extensive study of competition has concerned peracarid crustacean communities in southwest Virginia and east Tennessee caves (Culver 1973a, 1976, 1981, 1982; Dickson 1976, 1977a; Dickson and Holsinger 1981; Estes 1978; Estes and Holsinger 1982). Various combinations of three species are present: *Cacidotea recurvata, Crangonyx antennatus,* and *Lirceus usdagalun.*

The basis for competition is that, in the stream, amphipods and isopods need a place to avoid the brunt of the current and a place to feed on detritus washed into the cave. Because riffles are food-rich and well oxygenated, amphipods and isopods congregate there, even though high current velocities increase the risk of being washed out. Although many stones in a riffle are unoccupied (Culver 1973a), amphipods and isopods frequently meet because of jostling about by the current and directed movement toward food. When two individuals meet, one is almost invariably washed downstream. Some of these individuals die; all are removed from the riffle.

Since washout is the basis of competition, it was possible to derive a formula for measuring the competition coefficients and to measure washout in an artificial stream in the laboratory. Competition coefficients (αij) for all pairs of the three species studied were as follows:

$$\begin{array}{rc} & \begin{array}{ccc} \textit{C.a.} & \textit{C.r.} & \textit{L.u.} \end{array} \\ \begin{array}{r} \textit{Crangonyx antennatus} \\ \textit{Caecidotea recurvata} \\ \textit{Lirceus usdagalun} \end{array} & \left[\begin{array}{ccc} 1 & 0.99 & 1.32 \\ 0.32 & 1 & 1.29 \\ 1.16 & 0.49 & 1 \end{array}\right] \end{array}$$

If these are adequate measures of competition and our reasoning above has been correct, then the greater the competition, the greater the microhabitat separation. *Crangonyx antennatus* and *L. usdagalun,* which show the strongest competition, barely coexist in the same cave; *C. recurvata* and *L. usdagalun* occupy different riffles; and *C. antennatus* and *C. recurvata* occupy different-sized rocks in the same riffle.

Estes (1978) has closely examined microhabitat niche differences among the three species and determined that *L. usdagalun* was almost always found in current with a velocity/depth ratio greater than 0.67, whereas the other two species were found over a greater range of current velocities. In addition, relative densities on different rock sizes varied (Table 4). The large *C. recurvata* was under large rocks, and the small *C. antennatus* was in gravel. *Lirceus usdagalun* was on an intermediate substrate.

There is evidence that the intensity of competition between a pair of species declines through evolutionary time. Culver (1976) showed

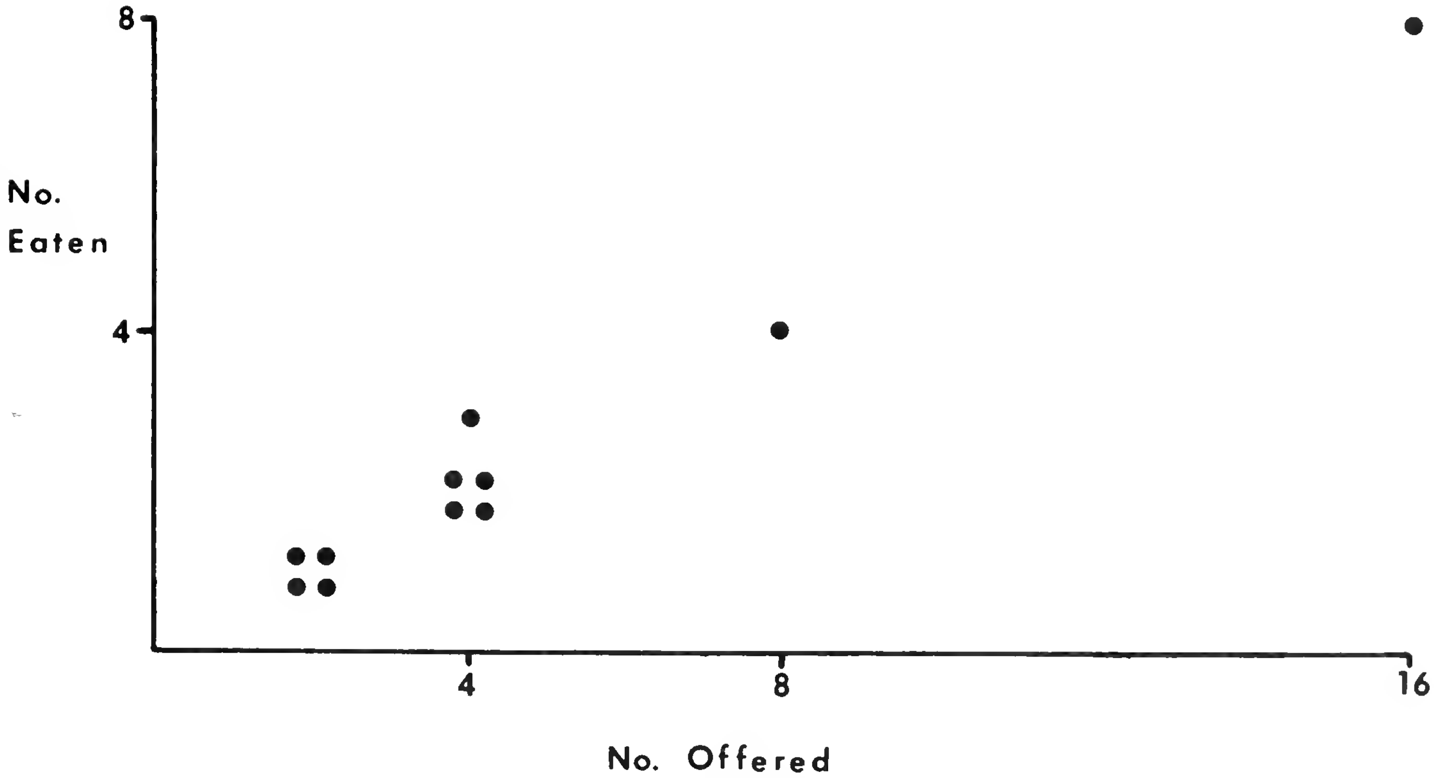

Fig. 36. Functional response of *Gyrinophilus porphyriticus* larva to *Caecidotea recurvata*.

Table 4. Occurrence of *Caecidotea recurvata*, *Lirceus usdagalun*, and *Crangonyx antennatus* under stones and gravel in areas of strong current in Gallohan Cave No. 1 (modified from Estes 1978). The first number is the mean $0.09_m{}^2$ and the second is the relative density with the highest density for each species given a value of 100. Actual stone sizes were not given.

	Habitat			
Species/Individuals	Large Stones	Medium Stones	Small Stones	Gravel
C. recurvata 53	1.0(28)	3.63(100)	1.69(47)	2.67(74)
L. usdagalun 412	7.5(28)	21.75(82)	26.62(100)	16.67(63)
C. antennatus 13	0.0(0)	0.50(38)	0.62(47)	1.33(100)

that relative age of the interaction (as measured by the amount of regressive evolution and speciation) and competition where negatively correlated for Virginia and West Virginia peracarid crustacean communities.

SPECIES PACKING AND SPECIES DIVERSITY

For most of the best-studied communities, species diversity is limited by competitive interactions. Culver (1976) showed that competition theory predicts a maximum of three species. Three-species communities in the Greenbrier Valley in West Virginia and in the Powell

Valley in Virginia were resistant to invasion, but two-species communities often were not. In the Powell Valley, *L. usdagalun* successfully invaded a *C. recurvata* - *C. antennatus* community in Gallohan No. 2. On the other hand, *L. usdagalun* in Thompson Cedar Cave is resistant to invasion by *L. recurvata,* which is limited to a small section of stream near the entrance. Both of these events are in agreement with the theory.

Salamander predators can have a large effect on species diversity. In McClure Cave, relative density of *C. antennatus* increases near *G. porphyriticus* larvae, primarily because its competitor *C. recurvata* is also preyed upon. Refugia ensure the persistence of both prey. In Sweet Potato Cave, *G. porphyriticus* eliminates *C. recurvata* from rimstone pools, but *C. antennatus* escapes predation by burrowing (Holsinger and Dickson 1977). In pools without salamander larvae, both prey species persist.

Flooding has a major impact on both aquatic and terrestrial fauna. Caves where water slowly recedes following regular flooding often have a very rich terrestrial fauna as a result of the detritus left by receding waters. Although no quantitative data are available, caves that have much detritus often have a diverse fauna (Table 3). On the other hand, caves that flood have a depauperate aquatic fauna. In a study of caves of the Greenbrier Valley in West Virginia, Culver (1970) found that caves that flood have 0.5 amphipod and isopod species ($s = 0.7$, $n = 13$), while caves that do not flood have 2.3 species ($s = 1.1$, $n = 15$).

Finally, the island-like nature of caves has two important effects (Culver 1976). First, the mean number of peracarid crustaceans is less than the predicted three due to continuing extinctions. Second, the regional faunal diversity is enhanced because patchiness allows coexistence of competitors.

ZOOGEOGRAPHY

Drainage Basins and Regional Cave Faunas

The Appalachian Valley and Ridge in Virginia and northeastern Tennessee is drained by seven major river systems or drainage basins as indicated in Figure 2. Because each basin is well defined geographically and contains topographically confined karst areas with a unique assemblage of endemic cave species, we have chosen to treat them as regional cave faunal units for the purpose of analyzing and discussing zoogeographical relationships. Although some of the divides and interfluves that separate these basins contain carbonate rocks (limestone and dolomite) as indicated below, as a rule the major part of each basin is enclosed by clastic rocks. The faunal units, which correspond to drainage basins of the same name, are: (1) Shenandoah, (2) James, (3) Roanoke, (4) New, (5) Holston, (6) Clinch, and (7) Powell. A very small cavernous area in northern Highland County drained by the South

Branch of the Potomac River actually constitutes an eighth drainage basin but has been excluded from our analysis because of its insignificant size in the study area. The cave fauna of this basin was discussed previously by Holsinger et al. (1976).

In the companion study on the cave invertebrates of West Virginia (Holsinger et al. 1976), we also divided that area into cave faunal units that corresponded to major drainage basins and discussed zoogeographical relationships in a context similar to that of the present paper. Somewhat similar, but broader, faunal units than those recognized in the Virginias and northeastern Tennessee were distinguished for the regional cave faunas of the Interior Low Plateaus by Barr (1967a), northwestern Georgia by Holsinger and Peck (1971), and Illinois-southeastern Missouri by Peck and Lewis (1978).

A list of the cave-limited species has been compiled for each basin or faunal unit (Tables 5-11). Although these lists are restricted primarily to troglobites, we have included a few select troglophiles that our observations indicate are commonly represented by cave-restricted populations.

1. *Shenandoah Basin.*—This faunal unit includes that part of the study area drained by the Shenandoah River and its tributaries and covers approximately 8328 km^2 (Fig. 2). It is defined by the Blue Ridge Mountains on the east, North and Shenandoah mountains on the west, the Virginia-West Virginia state line on the north, and a drainage divide (composed partly of carbonate rock) with the James River basin on the south. Outside the study area, the basin continues for a short distance through the extreme northeastern corner of West Virginia to a point where the Shenandoah River joins the Potomac River at Harpers Ferry.

The regional terrain is generally rolling and is significantly punctuated only by Massanutten Mountain, a prominent ridge that partly divides the basin into two valleys for about half of its length. A total of 396 caves are recorded from the basin in the study area; a majority are small, and only a few are of major extent. Although the area contains a fairly extensive exposure of carbonate rock (Cambrian to Devonian), much of it is dolomite and calcareous shale. As a result, the potential for extensive cave development has been greatly limited. The regional cavernicolous fauna contains 25 cave-limited species; 23 are troglobites, and 14 are endemic to the basin (Table 5).

2. *James Basin.*—In the study area this faunal unit includes all of that part of west-central Virginia drained by the James River and its tributaries and covers approximately 7745 km^2 (Fig. 2). It is defined by the Blue Ridge Mountains on the east, Allegheny and Peters mountains on the west, drainage divides (with carbonate rocks) with the upper Potomac drainage system (i.e., South Branch and Shenandoah rivers) on the north, and drainage divides (also with carbonate rocks) with the

New and Roanoke rivers on the south. The regional terrain varies considerably from one part of the basin to another. In the western two-thirds it is relatively rugged and characterized by numerous prominent ridges and narrow valleys, whereas in the eastern third it is of lower relief and generally rolling.

A total of 431 caves are recorded, including some of the largest in the study area. There are significant exposures of Silurian and Devonian limestones in the western part of the basin, where caves are often extensive but frequently localized in isolated belts of limestone that crop out along the flanks of ridges and in valley floors. Limestones and dolomites of Cambrian and Ordovician age predominate in the eastern part of the basin, where caves are less extensive but relatively numerous. The regional cavernicolous fauna is composed of 32 cave-limited species; 31 are troglobites, and 16 are endemic to the basin (Table 6).

3. *Roanoke Basin.*—This faunal unit is the smallest in the study area and covers only approximately 1073 km^2 (Fig. 2). It is drained by the Roanoke River and its tributaries and is defined by the Blue Ridge Mountains on the east and south, Brush and Catawba mountains in part on the north, and a drainage divide (with carbonate rock) with the New River on the west. Although the regional terrain varies considerably, most of the karst topography is moderately rolling and developed on valley floors and low hills. Ninety-one caves are recorded, and all of them are developed in Cambrian and Ordovician limestones and dolomites. Because of the extensive exposures of dolomite, most of the caves are small, although several large ones are excavated in Ordovician limestone in the valley of the North Fork of the Roanoke River. The regional cavernicolous fauna consists of only 10 cave-limited species, all trogobites; three species are endemic to the basin (Table 7).

4. *New Basin.*—This faunal unit encompasses that part of the study area drained by the New River and its tributaries and covers approximately 4087 km^2 (Fig. 2). Unlike other major rivers in the study area, New River flows generally northward and cuts across the regional strike instead of flowing parallel to it. The basin is defined by the Iron Mountains and by Poplar Camp and Macks mountains on the south, complex drainage divides with the Roanoke and James rivers composed of several ridges of prominent relief on the east, Peters and East River mountains and Big Stone Ridge on the north, and complex drainage divides (partly composed of carbonate rocks) with the Holston and Clinch rivers on the west. The regional terrain is heterogeneous and characterized in general by both broad and narrow valleys and a number of prominent ridges.

A total of 419 caves are recorded, a significant number of which are extensive. Both caves and karst terranes occur in many parts of the basin but are especially well developed in large valleys on opposite sides of Cloyds and Brush mountains, along the western side of Big Walker

Table 5. List of cave-limited species (see text for definition) in the Shenandoah basin regional fauna. Species listed in same sequence as in text (cf., "Review of the Fauna"). * = endemic species. TB = troglobite or probable troglobite.

AQUATIC SPECIES
Fontigens orolibas
**Lartetia* sp. (TB)
Stygobromus gracilipes (TB)
**S. pseudospinosus* (TB)
S. biggersi (TB)
**S. stegerorum* (TB)
Caecidotea pricei (TB)
**Antrolana lira* (TB)

TERRESTRIAL SPECIES
Miktoniscus racovitzai (TB)
**Apochthonius coecus* (TB)
**Kleptochthonius* sp. B (TB)
**Mundochthonius holsingeri* (TB)

TERRESTRIAL SPECIES (continued)
**Chitrella superba* (TB)
Erebomaster acanthina
Bathyphantes weyeri (TB)
Phanetta subterranea (TB)
Porrhomma cavernicolum (TB)
**Striaria* sp. (TB)
Trichopetalum weyeriensis (TB)
T. whitei (TB)
**Pseudanophthalmus avernus* (TB)
**P. hubbardi* (TB)
**P. limicola* (TB)
**P. parvicollis* (TB)
**P. petrunkevitchi* (TB)

Summary: Total species = 25 (8 aquatic, 17 terrestrial); endemics = 14.

Table 6. List of cave-limited species (see text for definition) in the James basin regional fauna. Species listed in same sequence as in text (cf., "Review of the Fauna"). * = endemic species. TB = troglobite or probable troglobite.

AQUATIC SPECIES
**Sphalloplana virginiana* (TB)
**Stygobromus interitus* (TB)
**S. hoffmani* (TB)
S. morrisoni (TB)
**S. mundus* (TB)
**S. estesi* (TB)
**S. conradi* (TB)
**S. baroodyi* (TB)
**Caecidotea bowmani* (TB)
C. holsingeri (TB)
C. vandeli (TB)
C. pricei (TB)

TERRESTRIAL SPECIES
Miktoniscus racovitzai (TB)
**Apochthonius holsingeri* (TB)
**Kleptochthonius anophthalmus* (TB)

TERRESTRIAL SPECIES (continued)
Rhagidia varia (TB)
Anthrobia monmouthia (TB)
Islandiana muma (TB)
Phanetta subterranea (TB)
Porrhomma cavernicolum (TB)
Nesticus tennesseensis (TB)
**Nampabius turbator* (TB)
Trichopetalum packardi (TB)
T. weyeriensis (TB)
Sinella hoffmani (TB)
Euhadenoecus fragilis
Pseudanophthalmus gracilis (TB)
**Pseudanophthalmus intersectus* (TB)
**P.* sp. A (*hubbardi* group) (TB)
**P. nelsoni* (TB)
**P. pontis* (TB)
**P.* sp, A (*pusio* group) (TB)

Summary: Total species = 32 (12 aquatic, 20 terrestrial); endemics = 16.

Mountain and in Burkes Garden. The carbonate rocks are predominantly limestones and dolomites of Cambrian and Ordovician age, although a limited exposure of Mississippian limestone crops out in the extreme northwestern part of the basin. The New River also drains several karst areas in adjacent West Virginia, and the cave fauna of these areas was discussed in some detail in a previous paper (Holsinger et al. 1976). The regional cavernicolous fauna includes 29 cave-limited species; 26 are troglobites, and 10 are endemic to the basin (Table 8).

5. *Holston Basin.*—That part of the Holston basin in the study area lies almost entirely in Virginia and extends only a few kilometers into Tennessee (Fig. 2). It is drained by three major tributaries of the Holston River and covers approximately 3690 km^2. This faunal unit is defined by the Iron Mountains on the southeast, the drainage divide with the New River on the east, and Clinch Mountain and Moccasin Ridge on the north and northwest. Outside the study area, the basin continues southwestward through eastern Tennessee to the vicinity of Knoxville, where the Holston River joins the French Broad River to form the Tennessee River. The regional terrain varies from moderately rugged in areas drained by the North Fork to moderately rolling in the southern two-thirds of the basin drained by the Middle and South forks of the Holston River. The basin is bisected in part by Walker Mountain, which trends southwest and forms a prominent interfluve between the North Fork and Middle Fork.

Although most of the exposed carbonates are limestones and dolomites of Cambrian and Ordovician age, limited outcrops of Silurian-Devonian and Mississippian limestones occur in parts of Scott and Washington counties. A total of 308 caves are recorded, and a number of them are large. However, much of the carbonate rock exposed in the southern part of the basin is dolomite and has limited the development of extensive caves. The regional cavernicolous fauna is composed of 19 cave-limited species; 18 are troglobites, and only three are endemic to the basin (Table 9).

6. *Clinch Basin.*—Most of this basin lies within the study area and is drained by the Clinch River and its tributaries (Fig. 2). It is defined by the short drainage divide with New River on the northeast, the eastern margin of the Appalachian Plateau and Powell Mountain on the north and west, and Clinch Mountain on the south except for a short stretch in Russell and Scott counties where Big Moccasin Creek flows north of Clinch Mountain before turning south to join the North Fork of the Holston River south of Gate City, Va. As defined in the present study, this faunal unit ends in Campbell County and in the vicinity of Norris Dam about 10 km south of where the Clinch River is joined by the Powell River; it covers approximately 4048 km^2. Beyond the study area, however, the basin extends southwestward for approximately 60

Table 7. List of cave-limited species (see text for definition) in the Roanoke Drainage basin regional fauna. Species listed in same sequence as in text (cf., "Review of the Fauna"). * = endemic species. TB = troglobite or probable troglobite.

AQUATIC SPECIES	TERRESTRIAL SPECIES
**Stygobromus fergusoni* (TB)	*Phanetta subterranea* (TB)
Caecidotea vandeli (TB)	*Porrhomma cavernicolum* (TB)
	**Pseudotremia cavernarum* (TB)
	Trichopetalum packardi (TB)
	Pseudosinella orba (TB)
	Sinella hoffmani (TB)
	Arrhopalites clarus (TB)
	**Pseudanophthalmus pusio* (TB)

Summary: Total species = 10 (2 aquatic, 8 terrestrial); endemics = 3.

Table 8. List of cave-limited species (see text for definition) in the New basin regional fauna. Species listed in same sequence as in text (cf., "Review of the Fauna"). * = endemic species. TB = troglobite or probable troglobite.

AQUATIC SPECIES	TERRESTRIAL SPECIES (continued)
Fontigens orolibas	*Pseudotremia tuberculata* (TB)
**Stygobromus ephemerus* (TB)	*Trichopetalum packardi* (TB)
**S. abditus* (TB)	*Pseudosinella orba* (TB)
S. mackini (TB)	*Arrhopalites clarus* (TB)
**Caecidotea henroti* (TB)	*Litocampa* sp. B (TB)
C. incurva (TB)	*L.* sp. E (TB)
C. vandeli (TB)	*Euhadenoecus fragilis*
C. richardsonae (TB)	*Pseudanophthalmus gracilis* (TB)
TERRESTRIAL SPECIES	**P. egberti* (TB)
**Foveacheles paralleloseta* (TB)	**P. quadratus* (TB)
Rhagidia varia (TB)	*P. hoffmani* (TB)
Phanetta subterranea (TB)	**P. hortulanus* (TB)
Porrhomma cavernicolum (TB)	**P.* sp. B (*petrunkevitchi* group) (TB)
Nesticus carteri	**P.* sp. C (*petrunkevitchi* group) (TB)
Nesticus tennesseensis (TB)	**P. punctatus* (TB)

Summary: Total species = 29 (8 aquatic, 21 terrestrial); endemics = 10.

Table 9. List of cave-limited species (see text for definition) in the Holston basin regional fauna. Species listed in same sequence as in text (cf., "Review of the Fauna"). * = endemic species. TB = troglobite or probable troglobite.

AQUATIC SPECIES
Crangonyx antennatus (TB)
Stygobromus mackini (TB)
Caecidotea incurva (TB)
C. recurvata (TB)
C. richardsonae (TB)
TERRESTRIAL SPECIES
Glyphyalinia specus (TB)
Anthrobia monmouthia (TB)
Phanetta subterranea (TB)
Porrhomma cavernicolum (TB)

TERRESTRIAL SPECIES (continued)
Nesticus carteri
N. tennesseensis (TB)
N. paynei (TB)
Pseudosinella orba (TB)
Litocampa sp. B (TB)
L. sp. E (TB)
**Pseudanophthalmus paradoxus* (TB)
P. hoffmani (TB)
**P.* sp. A (*petrunkevitchi* group) (TB)
**Batriasymmodes greeveri* (TB)

Summary: Total species = 19 (5 aquatic, 14 terrestrial); endemics = 3.

km to the vicinity of Kingston in Roane County, Tenn., where the Clinch River joins the Tennessee River. The regional terrain is highly variable but is generally rugged and characterized by prominent ridges and relatively narrow valleys. However, in several places, especially in the northeastern half, broad coves with karsted limestone floors are formed between mountains, two good examples being Ward Cove in Tazewell County and Rye Cove in Scott County.

Numerous belts of carbonate rock, ranging in age from Cambrian to Mississippian, are exposed in the basin. A total of 537 caves are recorded, many of which are extensive and most of which are excavated in Cambrian, Ordovician, and Mississippian limestones. The regional cavernicolous fauna contains 51 cave-limited species; 47 are troglobites, and 24 are endemic to the basin (Table 10).

7. *Powell Basin.*—This basin lies completely within the study area and is drained by the Powell River and its tributaries (Fig. 2). It covers approximately 2278 km^2 and is defined by the eastern margin of the Appalachian Plateau on the northeast, north, and west, and by Powell Mountain on the south except in Claiborne and Union counties where the interfluve with the Clinch drainage is Wallen Ridge and a series of low, dolomitic ridges that extend across the Central Peninsula between the arms of Norris Lake. The Powell basin is essentially one large valley with generally rolling terrain of moderately low relief. However, Wallen Ridge on the eastern side of the Valley is a topographic feature.

Extensive exposures of Cambrian, Ordovician, and Mississippian limestones and dolomites occur throughout the basin. The middle of the valley is floored by several broad belts of Ordovician limestone, whereas a significant belt of Mississippian limestone crops out along the front of

Table 10. List of cave-limited species (see text for definition) in the Clinch basin regional fauna. Species listed in same sequence as in text (cf., "Review of the Fauna"). * = endemic species. TB = troglobite or probable troglobite.

AQUATIC SPECIES

Geocentrophora cavernicola (TB)
Sphalloplana chandleri (TB)
*_Spelaedrilus multiporus_ (TB)
Stylodrilus beattiei (TB)
Fontigens orolibas
Crangonyx antennatus (TB)
Stygobromus cumberlandus (TB)
Stygobromus mackini (TB)
Gammarus minus (Form I)
Caecidotea recurvata (TB)
C. richardsonae (TB)
*_Lirceus culveri_ (TB)

TERRESTRIAL SPECIES

*_Amerigoniscus paynei_ (TB)
*_Kleptochthonius binoculatus_ (TB)
*_K. regulus_ (TB)
*_K._ sp. A (TB)
Rhagidia varia (TB)
Anthrobia monmouthia (TB)
Phanetta subterranea (TB)
Porrhomma cavernicolum (TB)
Nesticus carteri
N. tennesseensis (TB)
N. holsingeri (TB)
N. paynei (TB)
Pseudotremia nodosa (TB)

TERRESTRIAL SPECIES (continued)

Pseudotremia tuberculata (TB)
*_P. deprehendor_ (TB)
Pseudosinella orba (TB)
P. hirsuta (TB)
Sinella hoffmani (TB)
Litocampa cookei (TB)
*_L._ sp. A (TB)
_L._ sp. C (TB)
*_L._ sp. D (TB)
_L._ sp. E (TB)
Euhadenoecus fragilis
*_Pseudanophthalmus deceptivus_ (TB)
*_P._ sp. A (_engelhardti_ group) (TB)
*_P. vicarius_ (TB)
*_P. sericus_ (TB)
*_P. hubrichti_ (TB)
*_P. sanctipauli_ (TB)
*_P._ sp. A (_hubrichti_ group) (TB)
*_P._ sp. B (_hubrichti_ group) (TB)
*_P. praetermissus_ (TB)
*_P. longiceps_ (TB)
*_P. seclusus_ (TB)
*_P. thomasi_ (TB)
*_P._ sp. A (_jonesi_ group) (TB)
*_P. unionis_ (TB)
*_P. virginicus_ (TB)

Summary: Total species = 51 (12 aquatic, 39 terrestrial); endemics = 24.

the Appalachian Plateau on the western side of the valley. A total of 394 caves are recorded, many of which are extensive and among the largest in the study area. Karst terrane is especially well developed, and the center of the valley, from Jonesville, Va., to Tazewell, Tenn., is the largest continuous karst corridor in the study area. The regional cavernicolous fauna contains 44 cave-limited species; 41 are troglobites, and 27 are endemic to the basin (Table 11).

PATTERNS OF DISTRIBUTION

We have recognized three general types of distributional patterns exhibited by cave-limited species of the study area. Ranges may be (1) very widespread, (2) trans-Appalachian, or (3) Appalachian Valley. Most of the species exhibit the Appalachian Valley pattern, whereas only 13 are trans-Appalachian. Four are very widespread.

The four very widespread species are the linyphiid spiders *Bathyphantes weyeri, Phanetta subterranea,* and *Porrhomma cavernicolum,* and the collembolan *Arrhopalites clarus.* The spiders are recorded from caves throughout much of the eastern United States and apparently show little morphological variation (W. J. Gertsch, in litt.). The range of *A. clarus,* on the other hand, is disjunct, with cave populations restricted to the Ozark region and the Appalachians (Christiansen 1982).

Trans-Appalachian species are recorded from caves on both sides of the Appalachian Plateau—in the Appalachian Valley and Ridge and eastern margin of the Appalachian Plateau on the east and Interior Low Plateaus and western margin of the Appalachian Plateau on the west. The taxonomic status of many of these species is unclear, and, as a result, their geographic distributions are questionable and in need of further study. The 13 trans-Appalachian species are the flatworms *Geocentrophora cavernicola, Sphalloplana chandleri,* and *S. percoeca*; the terrestrial snail *Glyphyalinia specus*; the amphipod *Crangonyx antennatus*; the aquatic isopod *Caecidotea richardsonae*; the terrestrial isopod *Miktoniscus racovitzai*; the pseudoscorpion *Hesperochernes mirabilis*, the spiders *Anthrobia monmouthia, Islandiana muma*, and *Nesticus carteri*; the collembolan *Pseudosinella hirsuta*; and the dipluran *Litocampa cookei.*

Appalachian Valley species are limited to the Appalachian Valley and Ridge province and closely associated karst islands on the eastern side of the Appalachian Plateau. There are basically two categories of Appalachian Valley species with respect to range: (a) species usually with moderately extensive ranges that inhabit caves in two or more of the faunal units in the study area and sometimes occur outside the study area, and (b) species known only from a single faunal unit in the study area. Species in the first category are the lumbriculid worm *Stylodrilus beattiei*; the aquatic snail *Fontigens orolibas* (*s. lat.*); the amphipods *Gammarus minus* (Form I), *Stygobromus biggersi, S. cumberlandus, S. gracilipes, S. mackini,* and *S. morrisoni*; the aquatic isopods *Caecidotea incurva, C. holsingeri, C. pricei, C. recurvata,* and *C. vandeli*; the mite *Rhagidia varia*; the phalangid *Erebomaster acanthina*; the spiders *Nesticus tennesseensis*, *N. holsingeri*, and *N. paynei*; the millipeds *Pseudotremia nodosa, P. tuberculata, Trichopetalum packardi, T. weyeriensis,* and *T. whitei*; the collembolans *Pseudosinella orba* and *Sinella hoffmani*; the diplurans *Litocampa* spp. B, C, and E; the cricket *Euhadenoecus fragilis*; and the beetles *Pseudanophthalmus gracilis* and *P. hoffmani.*

The second category comprises 97 species, or 66% of the 146 cave-limited species in the study area. Except for the beetle *Pseudanophthalmus potomaca* (northern Highland County and southern Pendleton County, W.Va.), these species are indicated by an asterisk in the lists

Table 11. List of cave-limited species (see text for definition) in the Powell basin regional fauna. Species listed in same sequence as in text (cf., "Review of the Fauna"). * = endemic species. TB = troglobite or probable troglobite.

AQUATIC SPECIES

Sphalloplana consimilis (TB)
S. percoeca (?) (TB)
**Lumbriculid* (sp.) (TB)
**Fontigens* sp. (TB)
**Bactrurus* sp. (TB)
Crangonyx antennatus (TB)
Stygobromus cumberlandus (TB)
**S. finleyi* (TB)
**S. leensis* (TB)
S. mackini (TB)
Caecidotea recurvata (TB)
C. richardsonae (TB)
**C.* sp. A (TB)
**Lirceus usdagalun* (TB)

TERRESTRIAL SPECIES

**Amerigonsicus henroti* (TB)
**Kleptochthonius affinis* (TB)
**K. gertschi* (TB)
**K. lutzi* (TB)
**K. proximosetus* (TB)
**K. similis* (TB)
**Microcreagris valentinei* (TB)
Hesperochernes mirabilis

TERRESTRIAL SPECIES (continued)

Phanetta subterranea (TB)
Porrhomma cavernicolum (TB)
Nesticus carteri
N. holsingeri (TB)
N. paynei (TB)
**Pseudotremia valga* (TB)
P. nodosa (TB)
Pseudosinella hirsuta (TB)
P. orba (TB)
Litocampa cookei (TB)
Euhadenoecus fragilis
**Pseudanophthalmus engelhardti* (TB)
**P. holsingeri* (TB)
**P. rotundatus* (TB)
**P. sidus* (TB)
**P.* sp. B (*engelhardti* group) (TB)
**P. delicatus* (TB)
**P. hirsutus* (TB)
**P. cordicollis* (TB)
**P. pallidus* (TB)
**P.* sp. B (*jonesi* group) (TB)
**Arianops jeanneli* (TB)

Summary: Total species = 44 (14 aquatic, 30 terrestrial); endemics = 27.

given in Tables 5 through 11 and need not be enumerated here. They are distributed numerically by taxon as follows: flatworms (2), lumbriculid worms (2), aquatic snails (2), amphipods (14), aquatic isopods (6), terrestrial isopods (2), pseudoscorpions (15), mites (1), centipedes (1), millipeds (4), diplurans (2), and beetles (46). An analysis of the ranges of these species indicates that 53 are recorded from single caves, 15 from two or rarely three caves within 5 km of each other, and 29 from two or more (usually more) caves located some distance apart. The percent of endemic species in each basin is: Shenandoah (0.56), James (0.50), Roanoke (0.30), New (0.34), Holston (0.16), Clinch (0.47), and Powell (0.61).

These data give a clear picture of the degree of endemism among cave-limited species in the study area. The highest percentage of regional faunal endemics is found among the beetles (principally *Pseudanophthalmus*) and pseudoscorpions (principally *Kleptochthonius*), where, in both taxa, almost all species are restricted to a single faunal unit, and a majority of species in both groups are single-cave isolates. There is also a high percentage of regional faunal endemics among lumbriculid worms, snails, amphipods, and isopods; and more than half of the species in each of these groups are recorded from a single faunal unit. On the whole, comparatively fewer endemics are noted among flatworms, mites, millipeds, and diplurans; and no endemics are recorded for spiders and collembolans.

Although the cave-limited fauna contains many highly localized endemics, there are a number of species—especially the few, select troglophiles, troglobitic spiders, and collembolans, and some of the troglobitic amphipods, isopods, millipeds, and diplurans—that have relatively extensive ranges within the study area and are apparently good dispersers. These species are found in two or more of the seven faunal units, and at least two species, the highly vagile spiders *Phanetta subterranea* and *Porrhomma cavernicolum*, occur in all seven.

The extent to which drainage basins or faunal units share cave-limited species is indicated by the data compiled in Table 12. Theoretically, dispersal between basins could take place by some of the more vagile troglobites through caves and solution channels developed in parts of drainage divides and interfluves composed of carbonate rock, and through endogean habitats (e.g., deep ground litter and shallow underground compartments) and groundwater habitats (e.g., interstitial, hypotelminorheic) outside karst areas. At least three of the troglophiles we have included in the cave-limited fauna (*Euhadenoecus fragilis*, *Erebomaster acanthina*, and *Nesticus carteri*) should be able to undergo limited dispersal through ecologically suitable epigean habitats. The frequency of species exchange between basins would be influenced by proximity of the basins as well as by the geological structure and geographic extent of drainage divides. The farther removed two basins are from each other, the fewer species they would be expected to share, and, by the same analogy, the closer they are, the more species they would be expected to share. Moreover, long common divides or interfluves, especially those containing carbonate rock, would be expected to facilitate more dispersal than do short divides or divides composed entirely of non-carbonate, clastic rock.

Our data (Table 12) strongly support these assumptions and indicate clearly that, with few exceptions, adjacent basins have more species in common than far removed ones, and, furthermore, that basins on opposite sides of divides or interfluves containing carbonate rock generally share more species than those separated by divides composed entirely of non-carbonate rock.

DIVERSITY-AREA RELATIONSHIPS

In the course of the present investigation it became increasingly obvious that some drainage basins in the study area had signifi-

Table 12. Number of cave-limited species shared by drainage basins. Data based on species listed in Tables 5 through 11.

Drainage Basin	Shenandoah	James	Roanoke	New	Holston	Clinch	Powell
Shenandoah	-	5	2	3	2	3	2
James	5	-	5	8	4	7	3
Roanoke	2	5	-	6	3	4	3
New	3	8	6	-	11	10	7
Holston	2	4	3	11	-	10	9
Clinch	3	7	4	10	10	-	15
Powell	2	3	3	7	9	15	-

cantly more cave-limited species and ecologically more complex cave communities than others, and, that with few exceptions, cave species diversity and ecological complexity increased in those areas with large numbers of caves and extensive karst development. To gain a better understanding of this apparent relationship and to translate it into quantitative terms, we compiled the data shown in Table 13. As these data indicate, there are major differences among the seven drainage basins with respect to area, number of cave-limited species, and number of recorded caves. In order to demonstrate the relationship between these variables concisely, we calculated both species density and cave density per unit of area for each basin (Table 13). We then plotted these values and found a strong linear relationship between species density and cave density in the different basins (Fig. 37). There is a progressive increase in density of species per unit of area from the Shenandoah basin, with the lowest cave density, to the Powell basin, with the highest cave density. The slope of the regression line in Figure 37 is highly significant ($b = 0.13$, $p < .001$) and 92% of the variation can be explained by variation in cave density.

Cave density alone probably does not determine the number of cave-limited species in a given area or basin. Other factors, which are more difficult to quantify, but probably equally important in determining the species diversity of a faunal unit, include both the amount and continuity of exposed, cavernous limestone and the degree of karst development. Cave density, however, which can be easily calculated for an area where the caves are well documented, is an excellent indication of the extent of cavernous limestone and also often reflects the extent of karst development.

Table 13. Summary of data used in determining species-density/cave-density relationship.

Drainage Basin	Area (km^2)	No. of Cave-limited Species[1]	No. of Recorded Caves[2]	Density/km^2 of Cave-limited Species	Density/km^2 of Recorded Caves
Shenandoah	8328	25	396	0.30×10^{-2}	4.8×10^{-2}
James	7745	32	431	0.41×10^{-2}	5.6×10^{-2}
Roanoke	1073	10	91	0.93×10^{-2}	8.5×10^{-2}
New	4087	29	419	0.71×10^{-2}	10.3×10^{-2}
Holston	3690	19	308	0.51×10^{-2}	8.3×10^{-2}
Clinch	4048	51	537	1.26×10^{-2}	13.3×10^{-2}
Powell	2278	44	394	1.93×10^{-2}	17.3×10^{-2}

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[1] Based on species listed in Tables 5 through 11.

[2] Includes all caves recorded from the study area through 1980.

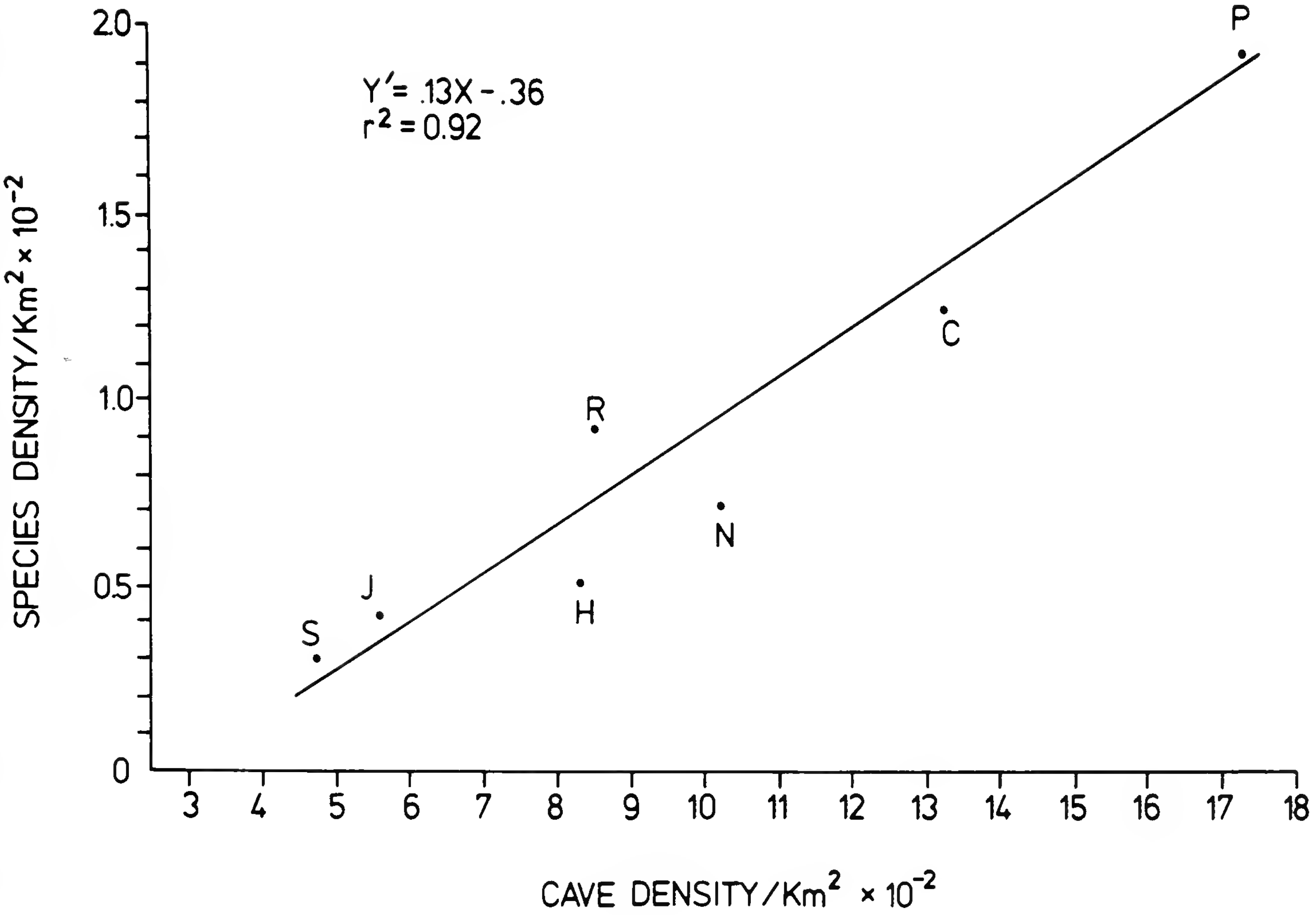

Fig. 37. Relationship of species density to cave density in the seven drainage basins of the study area. Regression line calculated by least squares method. Drainage basins: S = Shenandoah; J = James; R = Roanoke; N = New; H = Holston; C = Clinch; P = Powell.

The geological structure of an area, then, appears to play a significant role in determining the diversity of cave species. There are apparently several complex, interrelated reasons for this. First, large areas of continuously exposed, cavernous limestone would increase the opportunities for invasion of subterranean habitats by surface ancestors of cavernicoles; expand the potential for dispersal by hypogean species following cave colonization; increase potential habitat space in the form of cave passages and solution channels, thus allowing additional colonizations and, subsequently, the development of complex communities as the number of species increased; and increase the accessibility of caves to trogloxenes and troglophiles, which periodically introduce food underground. Second, well-developed karst terranes, characterized in the Appalachians by numerous sinkholes, blind valleys, sinking streams, bare limestone outcrops, and springs, would provide accessible avenues for the invasion of subterranean habitats by surface ancestors, greatly facilitate the movement of organic nutrients into subterranean channels, and increase the hydrological complexity of subterranean groundwater systems.

Regional terrains and the potential for cave and karst development in the seven drainage basins have already been characterized briefly, and our assumption that geological structure directly affects cave species diversity and ecological complexity appears to be supported by the differences noted. Clearly, those basins with limited, discontinuous exposures of cavernous limestone and restricted karst terranes, such as the Shenandoah, James, and Holston, have significantly fewer cave-limited species per unit of area than those basins with extensive, continuous exposures of cavernous limestone and well-developed karst terranes, such as the Clinch and Powell. Those basins intermediate in these geological parameters, the Roanoke and New, fall somewhere between the two extremes of species diversity. Direct field observations tend to reinforce our assumption, namely that, by and large, we found more species and larger populations in the caves of the Clinch and Powell basins than anywhere else in the study area.

The numbers of genera and families represented in the cave fauna of a basin should provide a further indication of taxonomic diversity and ecological complexity. In order to check this, we compiled the numbers of genera and families with cave-limited species in the seven drainage basins of the study area (Table 14). As the data indicate, the numbers of both genera and families are highest for the Clinch and Powell basins, again emphasizing that the greatest faunistic diversity occurs in areas with the most extensive, continuous exposure of cavernous limestone.

Barr (1967b, 1968) compared the cave systems of the Appalachian Valley and Ridge province with those of the Mississippian limestone plateaus in the Interior Low Plateaus region (i.e., Mitchell Plain in southern Indiana, Pennyroyal Plateau in Kentucky, and the Cumberland Plateau margin in Kentucky, central Tennessee, and northern Alabama) and concluded that they were ecologically very different. Ecological differences were attributed to differences in geological structure. The Paleozoic limestones (Cambrian to Mississippian) of the Appalachian Valley and Ridge are faulted and folded and exposed in long, linear anticlinal valleys that are separated by synclinal ridges of clastic rocks. In comparison, the Mississippian limestones of the Interior Low Plateaus are relatively undisturbed and exposed over broad areas. Because of this, dispersal of troglobites in the Appalachian Valley and Ridge would be restricted, whereas dispersal would be enhanced in the Mississippian plateaus. This comparison was based primarily on troglobitic trechine beetles (especially *Pseudanophthalmus*), which are represented by many species in both regions. But as Barr (1967b, 1968) has pointed out, the implications apparently apply to many other groups of cavernicoles as well. On a broad scale, the troglobitic fauna of the Mississippian plateau is more diverse than that of the Appalachian Valley.

Although our comparison of drainage basins in the study area of Virginia and northeastern Tennessee focused on relatively small cave

Table 14. Frequency distribution by drainage basin of genera and families with cave-limited species.

Drainage Basin	Number of Genera	Number of Families
Shenandoah	17	12
James	17	13
Roanoke	10	8
New	15	13
Holston	11	9
Clinch	23	17
Powell	21	17

regions within a single physiographic province and considered trechine beetles as well as all other groups of cave-limited species, our findings are essentially the same as those of Barr. The results of both of these studies corroborate the hypothesis that in a geographic region where climatic conditions are historically similar, areas with extensive, continuous exposures of cavernous limestone will harbor more diverse troglobite faunas than areas with limited, discontinuous exposures of limestone.

The data from two other studies, both on Appalachian cave faunas, also tend to corroborate this hypothesis. In a study of the invertebrate cave fauna of West Virginia (Holsinger et al. 1976), we documented a significantly richer troglobitic fauna in the Greenbrier Valley than in any other limestone region of that state. Like the Clinch and Powell valleys in Virginia, the Greenbrier Valley contains extensive, continuous exposures of cavernous limestone and a well-developed karst terrane; cave density is very high. In other major cave regions of West Virginia (e.g., the Monongahela and Potomac basins), where limestone exposures and karst terranes are more restricted and cave density is lower, the troglobitic faunas are correspondingly less diverse. In the other study, the troglobitic fauna of Pennsylvania was compared on a broad, regional scale with that of the Virginias (Holsinger 1976). In Pennsylvania, limestone areas are mostly very narrowly delimited, and caves are typically very small. The troglobitic fauna is exceedingly sparse (only 15 species) and contains largely aquatic species, some of which are stygobionts. In contrast, the troglobitic fauna of the Virginias, where cavernous limestone areas are generally much more extensive, is significantly richer. Although, admittedly, the proximity of the cave region of Pennsylvania to Pleistocene glaciation probably has had something to do with its impoverished troglobitic fauna (Holsinger 1976), the effect of geological structure has probably been of equal or greater significance (Holsinger 1976).

KARST AREAS AS ISLANDS

Several authors (e.g., Barr 1968, Culver et al. 1973) have explored the potential analogy between caves and islands. Of special interest is whether the number of species in a cave or a karst region is determined by an equilibrium of immigration and extinction rates when applied to individual caves or parts of caves. The time scale is ecological in the sense that populations rather than species are becoming extinct. Crawford (1981) and Culver (1982) have critically reviewed the validity of the cave-island analogy in ecological time. On a larger geographic scale, the number of species in a karst region may be determined by a balance between the rate of isolation of species in caves and the rate of extinction of cave species. The time scale for this process is evolutionary rather than ecological.

As Simberloff (1976) points out, there has been an uncritical acceptance of island biogeography theory, and attempts to test the hypothesis are few. The best tests of the hypothesis involve direct observations of immigrations and extinctions, but such verification is clearly not possible for evolutionary time scales. Therefore we must fall back on an analysis of area effect. It is often assumed that there is a one-to-one correspondence between island biogeography theory and a value of z in the following equation:

$$S = CA^z \qquad (1)$$

where S is species numbers, A is area, and C and z are fitted constants. Although processes other than an equilibrium between immigration and extinction can result in a z-value near 0.26 (Connor and McCoy 1979), the validity of the equilibrium model does not require a z-value of 0.26 (Culver 1982).

Analysis of area effect can provide some useful clues about the processes that determine species numbers. First, the absence of an area effect would indicate that area was incorrectly measured or that some other variable and some other process is more important. For example, terrestrial cave species numbers might be determined by availability of suitable epigean ancestors for which elevation might be more important than area. Second, if the island analogy holds, then equation (1), sometimes called the power function, should be a better fit than the untransformed linear model:

$$S = C + zA \qquad (2)$$

Equation (2) represents a model for area effect where species numbers are controlled by passive sampling from the species pool (Connor and McCoy 1979), and does not involve a balance between immigration and extinction. Third, if the power function is the best fit, then the larger the exponent z, the longer the time required to reach equilibrium (Culver et al. 1973). A large z-value indicates that it is unlikely the system is in equilibrium. What follows is a preliminary analysis, with extensive analysis in preparation by the authors.

The basic units of analysis are the seven drainage basins defined above. Area was estimated in three ways, each with somewhat different biological interpretations and with its share of technical problems. The first measurement is the total area of the drainage basin. While relatively accurate, the measurement combines karst and non-karst areas. If most terrestrial cave species occur in shallow underground compartments (Juberthie and Delay 1981, and see elsewhere this paper) in karst and non-karst areas as well as caves, and if most aquatic cave species occur in interstitial habitats as well as caves (Henry 1978, and elsewhere this paper), then total area of the drainage basin is the appropriate measurement of area. The second measurement is that of the area underlain by soluble carbonate rock in each drainage basin. This should measure the area in which caves potentially occur. The measurement itself was obtained by finding the percentage of limestone on a series of randomly chosen USGS topographic quadrangles, according to Douglas's (1964) mapping of exposed carbonate rock. The problem is that not all of the exposed carbonates are equally likely to have caves, because, as shown by Douglas, they include both limestone and dolomite, and the latter usually has significantly fewer and smaller caves depending on its composition (see Holsinger 1975). The third measurement estimates the area underlain by caves by the total number of caves for each drainage basin. This measurement avoids the problem of differential cave development in different limestone strata, but adds the problem that the number of known caves is correlated with sampling intensity.

We have limited our analysis to terrestrial troglobites that are endemic to a particular drainage basin for several reasons. First and most important, the terrestrial troglobite endemics are assumed to be a relatively homogeneous group with respect to their time of isolation in caves. This allows us to formulate and test the following hypothesis that terrestrial species were isolated in caves during the series of Pleistocene interglacials (immigrations) with extinctions also occurring. If the endemic terrestrial fauna is a more or less perfect record of these events, then the power series model should be a better fit than the linear model, and the exponent z of equation (1) should be around 0.26. Alternative hypotheses of special interest are three. If the number of endemic terrestrial troglobites reflects sampling intensity, then the linear model should provide a better fit. If a significant proportion of the terrestrial species arose not directly from epigean ancestors, but from subterranean colonization by other troglobites, then species numbers should depend on the amount of fragmentation of the limestone. Finally, if significant extinctions have occurred since the Pleistocene, the coefficient of area effect z, will be much greater than 0.26.

The second reason for limiting analysis to terrestrial troglobites endemic to a basin is that non-endemic terrestrial species either can move between basins, unlike the endemics, or are actually several unrecognized sibling species. In any case, they complicate interpretation of the results. The third reason for limiting the analysis is that aquatic troglobites frequently inhabit caves and interstitial or non-cave karstic waters simultaneously.

The lists of basin endemic terrestrial species are given in Tables 5 through 11, and various area measurements for the drainage basins are given in Table 15. The primary basis for choosing between regression models is whether the residuals after regression show any systematic pattern (see Sugihara 1981). However, the residuals of neither equation (1) nor equation (2) show any systematic bias, which is not surprising given the small number of points. A secondary criterion, how much of the variance in the dependent variable is explained by the independent variable, can be used to tentatively decide between alternatives (see Connor and McCoy 1979).

The results are given in Table 16, and given the small number of data points, the results are remarkably consistent. For both the log and linear models, number of caves (or log of the number of caves) explained more of the variance than either drainage area or limestone area. The log model consistently gave a better fit than the linear model. Finally, the best fit was provided by the log model using number of caves as the independent variable, with $C = 0.007$ and $z = 1.20$. The large z-value indicates extinctions have been occurring since the Pleistocene, but that the basic island analogy holds. The lack of significant correlation between the log of species and a measure of limestone fragmentation, namely percent of area covered by limestone, indicates that speciation resulting from underground movement is unimportant. Finally, we must stress the tentative nature of our conclusions, especially because correlations among independent variables have not been thoroughly explored.

ORIGIN, EVOLUTION, AND DISPERSAL

Because there are fundamental differences between aquatic and terrestrial cave species with respect to modes of origin, habitats, and dispersal, we will discuss them under separate headings.

Aquatic Species.—Basically two different patterns have been noted for aquatic troglobites in the study area with regard to their origin. It should be noted that these patterns are perceived as general trends only and are not intended to be rigid categories. The first pattern is exemplified by species that appear to have evolved directly from preadapted epigean ancestors. Morphological and physiological changes have developed concurrently with colonization of subterranean waters. These species belong to genera that are simultaneously represented by eyed, pigmented surface species, some of which are not far removed taxonomically (or genetically?) from subterranean forms. Taxa fitting this pattern are hydrobiid snails (*Fontigens*), some crangonyctid amphipods (*Crangonyx*), and asellid isopods (*Caecidotea* and *Lirceus*).

Table 15. Summary of data on area used in regression analysis.

Drainage Basin	Area(km^2)	% Limestone	Limestone Area(km^2)	Number of Caves*
Shenandoah	8328	46	3847	396
James	7745	38	2943	431
Roanoke	1073	36	386	91
New	4087	33	1349	419
Holston	3690	62	2288	308
Clinch	4048	55	2210	537
Powell	2278	43	981	394

*Includes all caves recorded from the study area through 1980.

Table 16. Comparison of regression equations using data in Tables 5 through 11 and Table 15. Abbreviations for independent variables: DA = drainage area; LA = limestone area; NC = Number of caves. Endemic terrestrial species (dependent variable) is abbreviated ET.

Dependent Variable	Independent Variable	Percent Variance Explained	P
ET	DA	0.0	N.S.
ET	LA	0.6	N.S.
ET	NC	52.0	>0.95
ln ET	ln DA	17.3	N.S.
ln ET	ln LA	17.7	N.S.
ln ET	ln NC	63.9	>0.95

The second pattern is exemplified by species that do not appear to have evolved directly from epigean ancestors but instead were probably derived through lineages from ancestors already living in subterranean groundwater habitats. These species have no known surface congeners and belong to phylogenetically very old groups. Taxa corresponding to this pattern are crangonyctid amphipods (*Bactrurus* and *Stygobromus*), cirolanid isopods (*Antrolana*), and possibly planarians (*Sphalloplana*).

Alloeocoelid and lumbriculid worms are still too poorly known taxonomically and ecologically in North American subterranean waters to identify them with either of the two patterns (see Carpenter 1970a, Cook 1977). Common troglophiles, such as *Phagocata* spp., *Fontigens orolibas, Gammarus minus,* and *Cambarus bartonii,* are found in both epigean and hypogean waters, and the cave populations probably represent recent invasions of subterranean habitats. However, as indicated below, *F. orolibas* and *G. minus* (Form I) could be special cases.

It is difficult to speculate on a time of origin for aquatic troglobites. Factors that might have been responsible for invasion and colonization of subterranean waters by putative ancestors undoubtedly revolve around a complex of interacting, interrelated biological and geological processes (see also Barr and Holsinger 1985). Changes in stream gradients and flow patterns and diversion of surface streams into underground channels by subterranean stream piracy in karst areas have been suggested as possible factors (Barr 1968, Holsinger et al. 1976, Culver 1982). All of these geological processes have continued over millions of years of erosional history in the Appalachians (see Hack 1969), and none is easily identifiable with a given time period. If combined biological and geological-area cladograms can be developed for some of the taxa and areas in question, they might prove useful in approximating vicariant events that led to the isolation of ancestral populations in groundwater habitats.

One intuitively obvious avenue for the underground invasion of aquatic organisms in karst areas would be through springs whose waters are the continuation to the surface of cave streams. Many aquatic trogloxenes and troglophiles (viz., species of *Phagocata*, *Fontigens*, *Goniobasis*, *Gammarus*, *Lirceus*, and *Cambarus*) inhabit both springs and cave streams, and populations are occasionally continuous from a spring well upstream into an adjoining cave. Moreover, some troglobitic species (viz., in *Fontigens*, *Crangonyx*, *Caecidotea*, and *Lirceus*) are closely allied taxonomically with congeneric epigean species living in surface springs, suggesting close genetic affinities between surface and cave forms. The geographic isolation of a population in an underground stream could occur if the spring fed by this stream was eliminated by erosion or lowering of base level.

The origin of troglobitic planarians of the genus *Sphalloplana* is somewhat obscure. Of the four species in the study area, two—*S. consimilis* and *S. virginiana*—are isolated in widely separated karst areas and have been assigned to different subgenera (see Kenk 1977). The taxonomic position of *S. percoeca* is unclear as mentioned earlier, and its range may extend far outside the study area. *Sphalloplana chanderli*, which is widespread but known only from three disjunct localities, is probably a "morphological" species. Except for one species with eyes and dark pigmentation from a spring in central Japan (see Mitchell 1968), the anatomy of which has not been studied (Kenk 1977), all other members of *Sphalloplana* are eyeless, unpigmented forms restricted to subterranean groundwater habitats, and most of them inhabit caves in North America (Kenk 1977, Kawakatsu and Mitchell 1981).

Despite unresolved taxonomic problems in the genus *Fontigens*, it is obvious from similarities in shell structure that the eyeless, unpigmented cave populations are closely allied morphologically with the eyed, pigmented spring populations; the former probably evolved directly from the latter. Spring populations of the *Fontigens orolibas* "complex" in the Blue Ridge Mountains are presumably physically well isolated from cave populations in the Appalachian Valley at present, and because there is no evidence for much dispersal mobility in these tiny snails, we must assume that this isolation has prevailed for a long period of time. Presumably, however, at one time in the past these populations were more or less contiguous.

The isopod family Asellidae is probably a very ancient freshwater group dating back perhaps to the Mesozoic (Birstein 1964). There are many genera and numerous subterranean species. Some of the troglobitic species of *Caecidotea* undoubtedly have been in subterranean groundwaters for a long period of time, but based on the fact that there are a number of epigean species in the genus, of which some are apparently not far removed taxonomically from hypogean species, we suspect that the majority of troglobitic species have evolved directly from surface ancestors. The genus also contains a small number of troglophiles or trogloxenes, and some of the stygobionts from the east-central United States sometimes have vestigial eyes and light pigmentation (Lewis and Bowman 1981). In the Greenbrier Valley of West Virginia just west of the study area, *Caecidotea scrupulosa* (Williams), a typical epigean species outside karst areas, has apparently recently invaded caves. and populations show varying degrees of eye and pigment loss, sometimes corresponding to the distance these animals live inside caves (Steeves 1969).

The occurrence in subterranean waters of *Lirceus* is probably more recent than that of *Caecidotea*, inasmuch as species of the former are much less common in caves and only two of the 15 described species in this genus are troglobites. These two troglobites, which are closely related sister species that occupy very delimited ranges in different karst areas on opposite sides of Powell Mountain in southwestern Virginia, do not appear highly specialized morphologically for a cave existence or far removed traxonomically from epigean congeners (Holsinger and Bowman 1973, Estes and Holsinger 1976). In the Ward Cove karst of Tazewell County, an undescribed species of *Lirceus* with tiny eyes inhabits several cave streams and their combined resurgence at Maiden Spring. Specimens from the spring population are pigmented, whereas those from the caves are not.

Following colonization of subterranean waters, asellid isopods can apparently disperse over relatively broad areas through groundwater habitats outside of caves and even karst areas. Of the 11 troglobites in the study area, six are found in more than one drainage basin, and only four are known from a single karst area. *Caecidotea pricei* for example, although usually found in caves, has been collected several times in the

Shenandoah Valley from small springs and seeps in alluvium underlain by Martinsburg shale (Holsinger and Steeves 1971). The relatively long range of this species, i.e., Rockbridge County, Va., northeastward to southeastern Pennsylvania, can probably be attributed to its ecological flexibility to live in both interstitial and hypotelminorheic habitats between karst areas. Several other troglobitic isopods in the study area have also been collected from non-cave groundwater habitats.

The occurrence of the cirolanid isopod *Antrolana lira* in a single, isolated subterranean groundwater aquifer in the Shenandoah Valley is one of the most intriguing zoogeographic problems in North American biospeleology. This unique, monotypic form is the only subterranean freshwater cirolanid isopod found in North America north of Texas, Mexico, and the West Indies, and is probably a very old relict. The family Cirolanidae is predominantly marine and only a small number of species live in freshwater, all of which, except for two poorly known forms from Africa and one from Cuba, are eyeless, unpigmented species obligatory to subterranean groundwaters. A total of 17 species in 10 genera have been described to date from subterranean waters in the Western Hemisphere, and several additional forms from the Bahamas, Grand Cayman Island, and Haiti are being described. Other genera and species have been reported from groundwater habitats in southern Europe and the Mediterranean region.

With the notable exception of *A. lira*, troglobitic cirolanids live in areas that are either presently near coastal marine zones or were exposed to shallow marine transgressions in the Cretaceous or Tertiary. Because a majority of the cirolanids are marine and the troglobitic species live either in close proximity to the sea or in old marine embayment areas, many workers have hypothesized that the subterranean freshwater species were derived directly from marine ancestors during the recession of seawater from limestone regions (Bowman 1964, Vandel 1965b, Cole and Minckley 1966, Carpenter 1981, Contreras-Balderas and Purata-Velarde 1982, and others). The presence of troglobitic cirolanids in the saline water of a small cave on San Salvador Island in the Bahamas (see Carpenter 1981) and in the brackish water of a limestone tunnel on the island of Aruba (see Botosaneanu and Stock 1979) offers additional support for this hypothesis. Since these troglobitic cirolanids live in brackish or saline water, they may well represent ecological transition stages in the evolution of subterranean freshwater forms from preadapted marine ancestors (Carpenter 1981).

If the prevailing hypothesis for the origin of troglobitic cirolanids is applied to *A. lira*, then this species would have to be regarded as the derivative of an ancient lineage dating back to the Paleozoic, when what is now the Appalachian Valley was last subjected to marine transgressions (Collins and Holsinger 1981). The evidence, however, argues strongly against a Paleozoic origin. Although the oldest known isopods are recorded from fossils of Pennsylvanian age, these early forms were phreatoicideans and not flabelliferans (Schram 1974, 1977). Based on fossil evidence, flabelliferan isopods did not appear until the Triassic (Schram 1974). Furthermore, the Appalachians did not develop into their present form until periods of extensive uplifting, folding, and faulting occurred in late Paleozoic and early Mesozoic times. "Stable" groundwater habitats almost certainly could not have existed in this region until post-Triassic times.

It appears more probable that freshwater cirolanids ancestral to *A. lira* were derived from marine forms in the Late Cretaceous or early Tertiary when marine embayments existed on the coastal plain of Virginia approximately 100 km east of the Appalachian Valley. Their invasion of freshwater habitats would have been followed by their migration west into karst areas west of the Blue Ridge. Bowman (1964) has also suggested the possibility of an origin along the Atlantic coast with subsequent dispersal to the west. But he pointed out that this mode of origin would have required a freshwater epigean progenitor, in contrast to other troglobitic cirolanids, which are believed to have descended directly from marine ancestors.

Whether its ancestral stock was epigean or hypogean cannot be determined, but in view of the evidence given above, it is doubtful that *A. lira* was derived directly from a marine ancestor. It should be noted further that, despite the extreme rarity of epigean freshwater cirolanids, at least one bona fide freshwater species, *Saharolana seurati* Monod, is recorded from a spring basin in southern Tunisia (see Monod 1930, Vandel 1965b). The reduced eyes and association with a groundwater outlet of this species suggest that it is preadapted to a subterranean existence. A similar stage may have occurred during the evolutionary history of *A. lira*.

The troglobitic amphipod fauna has probably originated directly both from epigean ancestors (e.g., *Crangonyx*) and from ancestral lineages already living in subterranean waters (e.g., *Bactrurus* and *Stygobromus*). The family Crangonyctidae, which contains all of the troglobitic amphipods in the study area, is widespread over the Holarctic region and, like Asellidae, is presumably an ancient freshwater group dating back to the Mesozoic (Holsinger 1977, 1978, 1986a, 1986b).

With the exception of one species from Florida and two or three from Europe, troglobitic species of *Crangonyx* are not far removed taxonomically from surface congeners and do not appear to be as highly specialized for a subterranean existence as species of *Bactrurus* and *Stygobromus* (see Holsinger 1969a, 1977; Culver 1976; Dickson and Holsinger 1981). Of the 22 described species in the genus, eight are troglobitic (or phreatobitic) and two are troglophilic. Most of the troglobites in North America, including *C. antennatus* from the study area, are represented by some populations with vestigial eyes, but the presence or absence of eyes may vary both within and between populations.

Recent studies by Dickson (1976, 1977a, 1977b, 1979) and Dickson and Holsinger (1981) on the ecology of *C. antennatus* in Lee County, where the species is very common in caves, have revealed what are apparently two microgeographic races corresponding to habitat types. One race is found in mud-bottom drip pools, and the other in small gravel-bottom streams. Dickson has found small differences in behavior, ecology, and morphology between the races. In addition to ecological studies, six populations from the same area were genetically analyzed by electrophoresis (Dickson et al. 1979), but allozyme allele frequencies were determined at only two polymorphic loci. This study revealed a high degree of allele frequency heterogeneity among the populations and indicated a tendency for stream and pool amphipods to cluster in populations distinct from one another (see Table 1 in Dickson et al. 1979).

Despite some apparent isolation between the two habitat types and the microgeographic heterogeneity among populations, additional observations on *C. antennatus* indicate that at least a limited amount of dispersal can occur between cave populations. One of us (Holsinger 1969a, 1978) has shown that this species may also inhabit perched groundwater above cave passages and occasionally enter caves from this habitat in dripping vadose water. The ecological flexibility of *C. antennatus* that allows it to inhabit simultaneously several different types of subterranean groundwater habitats undoubtedly accounts in part for its large range, which extends far southwest of the study area. The fact that *C. antennatus* does not appear to be far removed taxonomically from surface congeners and is not a highly specialized troglobite indicates to us that it has evolved directly from an epigean ancestor in fairly recent times.

In contrast to *Crangonyx*, *Bactrurus* and *Stygobromus* are exclusively subterranean groups in which all known species are eyeless and unpigmented, and apparently highly specialized stygobionts. Species of these genera inhabit a wide variety of groundwater biotopes: cave streams, pools and phreatic lakes; interstitial media; small springs and seeps; wells; drain tiles; and, rarely, even Pleistocene relict lakes. Some species are restricted primarily to caves *per se*, where they are often associated with small streams; others simultaneously inhabit caves (usually drip or seep pools) and groundwater habitats outside caves; and even others inhabit groundwater habitats outside karst areas and are never found in caves (Holsinger 1967a, 1969b, 1972, 1977, 1978; Culver 1982). Although *Bactrurus* and *Stygobromus* are apparently closely allied morphologically, the latter has a much wider geographic distribution and contains many more species (Holsinger 1977).

Bactrurus and *Stygobromus* are exclusively of subterranean facies and occupy virtually every conceivable type of groundwater habitat. Moreover, *Stygobromus* occurs throughout a large part of North America north of Mexico and is represented by numerous species (more than 160 counting undescribed forms). These facts strongly imply that these amphipods are very old stygobionts that have inhabited groundwaters for a long period of time. The invasion of cave waters, especially small drip and seep pools, appears to be a dynamic, ongoing process that has occurred in the past and is continuing at present (Holsinger 1978, Culver 1982). The original colonization of subterranean groundwaters by various crangonyctid amphipods probably occurred long before the present generation of cave habitats was available (Culver 1982). Our observations (Holsinger 1978, Culver 1982) indicate that cave drip-pools are not usually the primary habitats of many small species of *Stygobromus*. These cave habitats are only secondary or marginal biotopes that are periodically populated by animals from interstitial groundwaters outside caves *per se*. Some good examples in the study area of small species recorded only from drip/seep pools include *S. cumberlandus*, *S. ephemerus*, *S. estesi*, *S. finleyi*, *S. hoffmani*, *S. leensis*, and *S. pseudospinosus*. Other species in the study area appear to be permanent members of the cavernicole fauna and include *S. baroodyi*, *S. conradi*, *S. gracilipes*, *S. mackini*, *S. morrisoni*, and *Bactrurus* sp. These species are usually comparatively large in size and inhabit small streams, although some, especially *S. mackini*, are commonly found in drip pools as well. One cavernicolous species in the study area, *S. stegerorum*, is unique, however. It is known only from deep lakes of phreatic water in two caves in Cave Hill in Augusta County, where it is associated with the cirolanid isopod *Antrolana lira*.

Another amphipod, *Gammarus minus* (Gammaridae), although not considered a troglobite, is of considerable interest. In the Appalachian Valley this species is apparently represented by three morphological forms (see Holsinger and Culver 1970). Form III has relatively short antennae, well-developed eyes, and dark pigmentation; it inhabits surface springs throughout the range of the species. Form II has relatively long antennae, slightly reduced eyes, and weak pigmentation (variable); it inhabits caves over a broad geographic area. Form I has relatively long antennae, greatly reduced eyes, and weak pigmentation; it is known only from caves in the Ward Cove karst of Tazewell County, Va., and the Great Savannah karst of Greenbrier County, W.Va. These two areas are situated in different drainage basins and are separated geographically by a distance of 122 km and several prominent mountains. Form II occurs in many caves in the Virginias but is rarely as common as Form I in a given cave. These two forms are never found together in the same cave, although they sometimes inhabit caves no more than 5 to 10 km apart.

In a previous study (Holsinger and Culver 1970), in which the morphological variation of this species was carefully analyzed, we concluded that the three forms probably represented different ecophenotypes of a single, highly variable species. However, we were unable to give a satisfactory explanation for the presence of Form I in only two isolated karst areas, except to suggest that it might represent a convergent ecotype that occurs only under special environmental conditions in the presence of proper genetic variants. Both of these karst areas are similar in that they contain large, integrated subterranean drainage systems. On the other hand, Form II populations are also sometimes found in caves that are components of extensive subterranean drainage systems and, in some instances, not far removed geographically from caves with Form I populations.

Genetic studies on *G. minus*, principally in the Greenbrier Valley of West Virginia, by Hetrick (1975), Hetrick and Gooch (1981), and Gooch and Hetrick (1979), in which allozyme allele frequencies were determined at three polymorphic loci, tend to support the ecophenotype concept. The results of these studies indicate that there is generally a greater genetic distance between populations of the same ecophenotype in different geographic areas than between populations of different ecophenotypes in the same small, defined geographic area, and that most of the sharper discontinuities coincide closely with potential barriers to dispersal, such as streams, stream and karst drainage divides, and stratigraphic changes.

Whether the troglomorphic populations in Ward Cove and the Great Savannah are already incipient troglobitic species, are on their way to becoming separate species, or simply represent the extreme expression of a highly plastic phenotype is debatable and cannot be resolved on the basis of the information presently available. Further study is clearly needed.

Terrestrial Species.—The origin of terrestrial troglobites has perhaps been more direct and has involved fewer variables than that of aquatic troglobites. Most workers agree that the troglobitic terrestrial fauna of the north temperate region (viz., North America, Europe, and Japan) has been derived from preadapted, epigean ancestors that occupied moss, ground litter, and deep-soil habitats of humid forest floors (see Vandel 1965b, Barr 1968, Peck and Lewis 1978, Peck 1981b, Culver 1982, Barr and Holsinger 1985). Moreover, the invasion and colonization of caves by terrestrial invertebrates has probably been, and still is, an ongoing process, involving the dynamics of taxon cycles and pulses (see also Peck 1980, 1981b). With few exceptions, all terrestrial troglobites in the study area belong to higher taxa that are simultaneously well represented by cryptozoic, epigean species living in the cool, moist litter microhabitats of montane forests of the Appalachians. Furthermore, the greater Appalachian region, because of its rich diversity of both habitats and biota, has been suggested as the site of origin for much of the ancestral stock of the terrestrial troglobite fauna of the entire eastern United States (Peck and Lewis 1978).

The widely accepted model for the origin of terrestrial troglobites in temperate regions of the Northern Hemisphere is based on climatic fluctuations in the Pleistocene (Barr 1967a, 1968, 1973, 1985; Poulson and White 1969; Peck 1981b; Culver 1982). According to this hypothesis, during periods of glacial maxima, the cold, moist areas lying south of glaciation, such as the southern Appalachians, would have provided a suitable environment for the extensive distribution of a cryophilic endogean fauna. Both caves and ecologically suitable surface habitats would have been colonized by this fauna. During interglacial periods, when the regional climate became warmer and drier, many elements of this fauna would have become extinct at the surface, especially at low elevations, but other elements would have survived in caves and at high elevations in cool-mesic forests. The extinction of surface populations at low elevations during interglacials would have resulted in the genetic isolation of founder populations in caves, because migration and gene exchange between epigean and hypogean populations would have been eliminated in many karst areas. Ultimately this series of events would have led to the evolution of troglobitic species, depending on the length of time of physical isolation underground and whether or not certain populations subsequently reinvaded suitable surface habitats during succeeding glacial advances (c.f., the taxon cycle of Peck 1980). Eventually, however, isolation was completed for many cave populations. Since the onset of the Pleistocene, there has probably been a sequence of invasions and colonizations of caves by preadapted, troglophile ancestors and concomitant extirpations of closely related epigean populations. The detailed evolutionary history of any troglobitic group, however, must be relatively complex, because, as Peck (1980) suggests, many groups have probably passed through a taxon cycle that first involved isolation of populations in caves, followed by expansion into epigean habitats and, then, ultimately by isolation again in caves during a succeeding interglacial.

One of us (Culver 1982) recently reviewed the evidence in favor of the Pleistocene climatic-effect paradigm and concluded that, although indirect, the evidence supporting the hypothesis was strong. Nonetheless, this hypothesis has recently been questioned by several workers. Based on studies of the newly discovered troglobitic fauna of Hawaiian lava caves, Howarth (1980, 1981) suggested that troglobitic organisms have evolved, in the tropical Hawaiian Islands at least, through adaptive shifts of preadapted ancestors into newly opened niches and not by isolation of troglophilic ancestors during climatic shifts in the Pleistocene. Although Howarth's theory is based on data from Hawaiian lava tubes, which are generally much younger geologically and contain a significantly different food supply than limestone caves in temperate regions, he believes that his theory can be extended to explain to a large extent the evolution of terrestrial troglobites in temperate regions, where, as he points out, a complex geological history and glaciations have obscured the early history and obfuscated the previous distribution and evolution of troglobites. In Hawaii, cave populations may be larger than those of their surface relatives because the colonizable subterranean habitat is much larger in area than the rain forest or new lava substrate habitats on the surface (Howarth 1980). Howarth also suggests that an analogous situation may exist in limestone karst areas as well, but the data from our present study neither confirm nor refute this.

In her research on cave spiders in the temperate region of southern Europe, Deeleman-Reinhold (1981) concluded that physical properties of the subterranean environment and the present areal climate have been the principal factors in the evolution of the high diversity of troglobitic species in the southwestern Yugoslavian karst. Her conclusion also raises a serious question about the effect of past climates on the evolution of terrestrial troglobites, specifically in temperate karst areas.

One of the arguments made in the past in support of the Pleistocene climatic-effect theory was that terrestrial troglobites are far more abundant in the temperate zone than in the tropics (Barr 1968). It was previously assumed that terrestrial troglobites were extremely rare in tropical areas (see Vandel 1965b, Barr 1968, Mitchell 1969), but the recent discovery of rich terrestrial troglobitic faunas in Hawaii (Howarth 1972), Jamaica (Peck 1975d), and the lowlands of Mexico and Central America (Reddell 1981) has proven otherwise. Because the effects of climatic fluctuations in the Pleistocene were probably different at low elevations in the tropics than in temperate zones, the Pleistocene climatic-effect model is questionable for areas outside temperate karst regions and high elevations in the tropics; thus, other explanations for the origin of terrestrial troglobites in the lowland tropics may be warranted. One such explanation is Howarth's adaptive-shift hypothesis, discussed above.

The adaptive-shift theory is attractive because it can be applied to all parts of the world. Therefore, it eliminates the need for different paradigms for different regions and is applicable to both terrestrial and aquatic troglobites. It is not necessarily an allopatric model, however, but infers a kind of parapatric speciation in which new troglobitic species can arise in the absence of complete physical isolation between epigean ancestral populations and hypogean founder populations.

Barr (1965, 1967a, 1967c, 1968, 1973, 1981a, 1985), on the other hand, based on his studies on the geographic distribution and ecology of troglobitic trechine beetles, has made a convincing case for the Pleistocene climatic-effect model. Barr (1967b, 1968) has also made a strong argument for the allopatric speciation process in the evolution of troglobites and has suggested that after isolation of a founder population in a cave or series of interconnected caves, following the extinction of epigean ancestors, the newly isolated cave colony will pass through a period of lowered genetic variability (genetic bottleneck). Moreover, if the colony survives, an extensive genetic reorganization will result in a reconstructed epigenotype, the end point of which is a well-adapted troglobite. Genetic studies by Sbordoni et al. (1981) on cave crickets in southern Europe tend to support the bottleneck effect in the evolution of cave species, but the degree to which an epigenotype is reconstructed in the evolution of a troglobite remains unclear. It is entirely possible, however, that genetic differences between troglobites and epigean congeners have been overstressed, despite the prominent regressive features that develop almost universally in highly specialized cavernicoles.

It is beyond the scope of this paper to debate the pros and cons of allopatric versus parapatric speciation. But it should be pointed out that, whereas allopatric speciation is still favored over parapatric speciation for most groups of organisms, a rather strong case has been made for parapatric speciation (*sensu* Bush 1975, Endler 1977) in some groups under certain conditions, and it cannot be ruled out as a possible mode of evolution for some troglobites.

Trechine beetles of the genus *Pseudanophthalmus* are taxonomically the most numerous and thoroughly studied terrestrial troglobites in the study area and therefore provide good data for zoogeographic analyses. According to Barr (1981a, 1981b), ancestors of troglobitic species presently living in caves of both the Appalachian Valley and Ridge and the Interior Low Plateaus probably originated in upland forests of the Appalachian Plateau and spread out under periglacial climates. Caves were colonized at the beginning of interglacial periods. The ancestors were probably edaphobites already strongly preadapted for a cave existence. An earlier hypothesis by Jeannel (1949) suggested that ancestors spread out from an interglacial refugium in the Unaka Mountains along the Tennessee-North Carolina border, but Barr has made a more convincing case for an Appalachian Plateau center of distribution. Barr's theory is based principally on dissimilarities of species on opposite sides of the Appalachian Plateau, the increased richness of species closer to the plateau front in the Appalachian Valley, and the occurrence of a single edaphobitic species (*Pseudanophthalmus sylvaticus*) in the Plateau and not in the Unakas. The Unaka hypothesis was not discarded altogether by Barr, however, since, as he points out, distributions of the *engelhardti* and *petrunkevitchi* groups are not incompatible with an origin in the higher mountains on the eastern side of the Appalachian Valley.

The presence of vestigial eyes in some species of *Pseudanophthalmus* viz., members of the *petrunkevitchi* group and *P. vicarius*) suggests a fairly recent invasion of caves by some species (Barr 1965) if the degree of eye reduction is a crude measure of the length of time a species has lived in a cave. On the other hand, the level of intrageneric diversity and the occurrence of many distinct species groups suggest the possibility that *Pseudanophthalmus* is much older than the Pleistocene (see Barr 1981a). Given this background, one might postulate that the colonization of caves by species of *Pseudanophthalmus* has taken place over a long period of time through a succession of independent invasions. The occurrence of many distinct species groups, some of which broadly overlap geographically in southwestern Virginia and eastern Tennessee, suggests several independent colonizations of caves by ancestral stocks. How closely these colonizations might have coincided with the beginning of Pleistocene interglacials is difficult to determine, however.

The presence of *P. sylvaticus* in a non-cave habitat is of zoogeographic interest because this species is the only non-troglobitic *Pseudanophthalmus* recorded from North America. Barr (1967c, 1969) believes it is probably a periglacial relict that survived in the ecologically suitable habitat of a cold mountain forest during one of the interglacials when many of its congeners either were extirpated on the surface by a progressively warmer and drier climate or survived by colonizing caves at low elevations. *Pseudanophthalmus sylvaticus* was collected and described by Barr (1967c) from an endogean habitat in the Yew Mountains, approximately 36 km west of the study area on the eastern margin of the Appalachian Plateau in Pocahontas County, W.Va. This species, which has rudimentation of both eyes and pigment, is an edaphobite, presumably closely similar to putative preadapted ancestors of troglobitic members of the genus. It is not far removed taxonomically from some of the present cave forms living in limestone areas just to the east.

Although Barr (1967c) suggested that the discovery of *P. sylvaticus* supports the Pleistocene climatic-effect theory, we believe that it could also support Howarth's adaptive-shift theory. For example, if preadapted species of *Pseudanophthalmus* colonized caves in response to newly opened niches, it is unlikely that all members of the genus would have gone underground. Those left behind on the surface could have persisted in ecologically suitable habitats like that of *P. sylvaticus* in the Yew Mountains. In reality, neither hypothesis is falsified by the discovery of *P. sylvaticus*, since both predict the occurrence of preadapted epigean congeners in groups with troglobitic species.

With the exception of *P. nelsoni*, for which there is an apparent identity problem (see Barr 1965:45), the ranges of all species of *Pseudanophthalmus* in the study area are restricted to continuous exposures of cavernous limestone. As already pointed out, most of the species are known from single caves or small clusters of caves, although a few, like *P. delicatus*, *P. gracilis*, *P. hoffmani*, and *P. rotundatus*, have significantly larger ranges. Closely delimited ranges that coincide with continuous exposures of limestone strongly suggest that the dispersal of these beetles is limited to caves, solution channels, and other openings in carbonate bedrock. The two troglobitic pselaphid beetles from the study area also have highly restricted ranges, and each is known only from a single cave. These species were probably derived directly from edaphobitic ancestors in relatively recent times. Epigean congeners live in damp, deciduous-forest floors or in deep soil; in the genus *Arianops*, both epigean and hypogean species are eyeless (see Park 1960, 1965; Barr 1974).

Troglobitic pseudoscorpions, like troglobitic trechine and pselaphid beetles, also have narrowly circumscribed ranges, and most are known only from single cave localities. Subterranean dispersal is apparently highly restricted and limited to continuous belts of cavernous limestone. Chamberlin and Malcolm (1960) concluded that the pseudoscorpion cave fauna is derived from epigean (endogean) forms in the same general geographic area. The highly localized distribution of the cavernicolous species tends to support their conclusion.

Muchmore (1981) has pointed out that all of the troglobitic species of *Kleptochthonius* (29 described species in the subgenus *Chamberlinochthonius*) are restricted to the southeastern cave region in Kentucky, Tennessee, Virginia, West Virginia, and southern Indiana, and that troglobitic species in other chthoniid genera (viz., *Apochthonius* and *Mundochthonius* in the study area) occur on the periphery of the range of cavernicolous *Kleptochthonius* with little or no overlap. This suggests the possibility of competitive exclusion of other cavernicolous pseudoscorpions by the strongly troglomorphic species of *Kleptochthonius*. The range of *Kleptochthonius* (*Chamberlinochthonius*), like that of *Pseudanophthalmus*, forms a trans-Appalachian distributional track, extending from the Interior Low Plateaus on the west to the Appalachian Valley and Ridge on the east. By comparison, troglobitic species of *Apochthonius* and *Microcreagris* are very widely scattered (Muchmore 1981), but troglobitic *Chitrella* and *Mundochthonius* are rare and represented by only a few species (Malcolm and Chamberlin 1960, Muchmore 1973, Benedict and Malcolm 1974).

With few exceptions, the ranges of other troglobitic arthropods (e.g., isopods, mites, spiders, millipeds, collembolans, and diplurans) in the study area do not show the same high degrees of restriction to isolated, continuous belts of limestone as do those of beetles and pseudoscorpions. Populations of many of these species are found in caves developed in discontinuous exposures of limestone physically separated by clastic rocks. Assuming, however, that some gene exchange takes place between cave populations of the same species in different karst areas, then limited dispersal through areas composed of non-calcareous rock must occur.

Recent discoveries of troglobites in non-calcareous caves and artificial mine adits in Japan by Uêno (1977) and in shallow underground compartments in Europe by Juberthie and Delay (1981) indicate how subterranean dispersal may occur outside caves *per se*. Uêno found troglobitic beetles, isopods, millipeds, and spiders in natural cavities and artificial mines excavated in fissured, non-calcareous rocks in Japan. In the Alps, Pyrenees, and Carpathians, Juberthie and his colleagues discovered troglobitic beetles, millipeds, isopods, and spiders in a distinct habitat type they named the shallow underground compartment (S.U.C.). Most of these species had been recorded previously from nearby caves. According to Juberthie and Delay (1981), the S.U.C. exists under the last layer of soil in mountainous areas and consists of cracks and fissures in the mantle rock. These cracks and fissures are in turn connected to caves and/or deep cracks that represent the deep underground compartment. In non-limestone areas, the S.U.C. was usually identified in schists; in limestone areas it was commonly associated with screes or talus.

The observations by Uêno (1977) and Juberthie and Delay (1981) are good evidence that many troglobites inhabit shallow fissures and crevices near the surface in non-cavernous areas. Although not yet specifically identified, similar conditions probably exist in the Appalachians. We do have good evidence, however, that some terrestrial troglobites in the study area occur outside caves and are therefore able to move between caves situated in different exposures of limestone. Both spiders (*Nesticus tennesseensis*) and collembolans (*Pseudosinella hirsuta* and *Sinella hoffmani*) have been collected from deep ground-litter habitats in forested areas on mountainsides outside limestone terranes (Barr 1967c, Christiansen and Bellinger 1980c, Gertsch 1984, and elsewhere this paper). It will not be surprising if other troglobitic species are eventually found in similar habitats, either in deep ground litter or under conditions analogous to those described by Uêno (1977) and Juberthie and Delay (1981).

Of the three troglobitic trichoniscid isopods in the Virginia-east Tennessee area, *Miktoniscus racovitzai* is fairly widely distributed, whereas *Amerigoniscus henroti* and *A. paynei* have relatively limited ranges. The range of *A. henroti* is restricted to caves in a continuous exposure of cavernous limestone in the Powell Valley of Lee County (see Holsinger 1967b). In the adjacent Clinch Valley, *A. paynei*, a probable sister species, inhabits caves that are developed in several separate exposures of limestone.

Miktoniscus racovitzai (*s. lat.*), the only eyeless, troglobitic member of its genus, is closely allied morphologically with epigean congeners in the eastern United States (see Vandel 1950). It is probably a relatively recent derivative of a widespread, preadapted troglophile ancestor. In comparison, *Amerigoniscus* comprises 10 eyeless, unpigmented species, of which nine are troglobites and seven are recorded from single localities. The widespread, highly disjunct distribution of the species in this genus (viz., three from northwestern Georgia, one from south-central Oklahoma, two from Oregon, one from middle Tennessee, one from northwestern Texas, and two from the study area; see Vandel 1965a and 1977, Schultz 1982), combined with the fact that all are of troglobitic facies, suggests that members of this genus are old, isolated, subterranean relicts of a formerly widespread surface fauna. With the exception of *A. rothi* (Vandel) from an endogean habitat (under rocks and moss in a dense forest; see Vandel 1953) in Curry County, Oregon, no other epigean congener is known.

Recent studies by Zacharda (1980, 1985) indicate that a majority of the cavernicolous rhagidiid mites in the North American and European faunas are troglophiles and that only a few species have well-developed troglomorphisms and are restricted to caves. Because the family Rhagidiidae is predominantly edaphic and some of the edaphobites occur in caves, it is reasonable to assume that the troglobites are relatively recent derivatives of soil-dwelling forms. Of the two species considered troglobitic in the study area, one (*Foveacheles paralleloseta*) is known only from a single cave, whereas the other (*Rhagidia viria*) has a much broader distribution and is recorded from caves in several drainage basins.

None of the eight spiders considered troglobitic in the study area has a range that is limited to a single, continuous exposure of limestone. As already mentioned, the ranges of the troglobitic linyphiid spiders are among the most extensive of all troglobites in North America. Several explanations for these broad ranges have been suggested (Holsinger 1963a, Barr 1967a, Holsinger et al. 1976, and elsewhere this paper), but until the genetics of the species are studied, nothing definitive can be said. However, the presence of eyes (although variable) and some pigment in many populations, combined with the wide ranges, strongly indicates that these species are recently evolved troglobites.

Compared with linyphiids, nesticid spiders have much smaller ranges. Troglobitic nesticids show varying levels of eye and pigment reduction and appendage attenuation. Gertsch (1984) has pointed out that *Nesticus tennesseensis* has more reduced eyes, lighter pigmentation, and longer legs in the southern part of its range than in the northern part. In addition, this species has been collected occasionally from deep ground litter outside caves in the northern part of its range. Of the three troglobitic nesticids in the study area, *Nesticus holsingeri* has the most reduced eyes and pigmentation and also the most limited range. Reductions in eye structure, pigment, and geographic distribution may be positively correlated with a relatively advanced level of cave specialization.

In the eastern United States *Nesticus* is represented by 24 species that inhabit both caves and the rich ground litter of mesic forest floors, largely in the southern Appalachian region (Gertsch 1984). Troglobitic nesticids have apparently evolved from troglophilic ancestors as the latter became progressively more restricted to caves. The moderately widespread troglophile *Nesticus carteri* may very well be a good example of a troglobite *in statu nascendi* in a portion of its range, inasmuch as it is represented by numerous cavernicole populations, some of which are large and feed and reproduce in caves.

Millipeds constitute one of the most significant groups of cavernicoles in the eastern United States, but unfortunately they remain one of the most underworked taxonomically. Probably more than 50% of the species known from caves are undescribed, which makes zoogeographic analysis difficult. The genus *Pseudotremia* is represented by many species that inhabit both caves and epigean habitats in parts of the Appalachian Valley, Appalachian Plateau, and Interior Low Plateaus. The range of the genus forms a distributional track across the Appalachian Plateau similar to that of *Pseudanophthalmus* and *Kleptochthonius* (*Chamberlinochthonius*). Of the 34 species of *Pseudotremia* recognized by Shear (1972), 15 are obvious troglobites, 7 are questionable troglobites, 8 are troglophiles, and 4 are apparently strictly epigean. Ranges of both the troglobites and the troglophiles are generally localized; but without further taxonomic refinements, it cannot be determined how closely the geographic distributions of troglobites coincide with isolated exposures of limestone.

In the study area, the most highly specialized troglobitic pseudotrimiids are in the *nodosa* complex, a group of closely allied species that are unpigmented and have greatly reduced eyes (ca. 10-11 ocelli per eye). They are common in caves in the Clinch and Powell valleys. Presumably, colonization of caves by members of this complex predates that of the less specialized troglobites, which are pigmented and have more ocelli. In caves of the Clinch and Powell valleys, it is not uncommon to find both pigmented and unpigmented species in the same cave, but the latter (species of the *P. nodosa* complex) are usually more abundant and often occur at greater distances from cave entrances.

The milliped genus *Trichopetalum* has a much broader geographic distribution and fewer species (ca. 15) than *Pseudotremia* (see Shear 1972). Troglobites are unpigmented and completely eyeless. *Scoterpes* is closely related to *Trichopetalum* and contains perhaps 30 troglobitic species (many undescribed) that inhabit caves to the south and west of the study area in Alabama, Georgia, Illinois, Kentucky, Missouri, and Tennessee (Causey 1960b; Shear 1969, 1972). *Trichopetalum* contains five troglobites and three troglophiles. Four of the troglobites occur in the Appalachians of Virginia and West Virginia, and one is known from northern Alabama (Causey 1960a, Shear 1972). The troglophiles occur in Alabama, Kentucky, Maryland, and Oklahoma (see Causey 1967, 1969; Shear 1972), and all species possess eyes and pigment.

The three species of *Trichopetalum* in the study area are apparently very closely related genetically, as suggested by the possibility of hybridization between some of the populations (see Causey 1963 and elsewhere this paper). This possibility, combined with the contiguous distribution and closely similar morphologies of the species, suggests a relatively recent common ancestor, possibly involving a moderately widespread humicolous epigean form that invaded caves over parts of western Virginia and eastern West Virginia. A fourth species, *T. krekeleri* (Causey), from caves in Randolph and Tucker counties, W.Va., is distinct, but it was probably derived from the same ancestor.

A majority of the North American troglobitic collembolans are in the Entomobryinae genera *Pseudosinella* and *Sinella*. Three troglobites (viz., *P. hirsuta*, *P. orba,* and *S. hoffmani*) and a number of troglophiles/trogloxenes occur in the study area. In two recent papers on the zoogeography of eastern North American cave collembolans, Christiansen (1981, 1982) assigned caves in the Appalachian Valley and Interior Low Plateaus region to a category he called "heartland caves." Two other categories in the eastern United States were designated "glaciated area caves" and "non-glaciated non-heartland caves." As might be expected, the most highly specialized troglobitic collembolans (based on degree of troglomorphy) generally occur in heartland caves. In an earlier paper, Christiansen (1961) recognized two types of characteristics in cave species: cave-dependent and cave-independent characters. Using cave-dependent characters as a basis to measure evolutionary changes leading to an increase in troglomorphy, he devised a seven-step evolutionary scale for the cave Entomobryinae, with step 7 representing the highest level of adaptation. On this scale, *Pseudosinella hirsuta* was considered to be in step 5; *P. orba* and *Sinella hoffmani* were in step 6.

Troglobitic collembolans in the study area have relatively extensive ranges, and none is restricted to caves in a single exposure of limestone. Troglobites, however, have much more compact ranges than troglophiles.

In the Entomobryinae, Christiansen (1981, 1982) postulated several evolutionary lineages for each genus. In *Sinella*, *S. hoffmani* is placed in a lineage with the troglophile *S. barri*. In *Pseudosinella*, *P. hirsuta*, *P. orba*, and *P. argentea* (a troglophile) are each placed in a separate lineage.

To account for the extensive range of *P. hirsuta* (parts of Alabama, Georgia, Kentucky, Tennessee, and Virginia), Christiansen and Culver (1968) and Christiansen (1982) postulated a process they termed "parallel speciation," which was envisioned as having resulted from the invasion of caves by an ancestor over a wide geographic area, followed by independent parallel development of the same morphology in separate, physically isolated lineages. The end products would resemble each other so precisely in behavior, morphology, and ecology that they could be called the same species. According to this interpretation, *P. hirsuta* would have to be regarded as a complex of several biological (sibling?) species. Populations in the study area, although apparently morphologically indistinguishable from those farther west in Kentucky and middle Tennessee, are probably genetically distinct. Christiansen (1982) interprets the rather wide and discontinuous range of *S. hoffmani* as either the result of parallel speciation or representative of the vestiges of a previously continuous range. However, both *P. hirsuta* and *S. hoffmani* have been found outside caves on rare occasions, and the possibility that their wide ranges have resulted in part from dispersal between karst areas through shallow underground compartments or similar endogean habitats cannot be dismissed.

According to Christiansen (1982), the evolution of *P. orba,* which has a more limited geographic distribution than either *P. hirsuta* or *S. hoffmani,* has probably resulted from the single invasion of caves by a putative ancestor and subsequent subsurface dispersal to the present limits of its range. In the genus *Arrhopalites,* Christiansen (1982) suggests that the troglomorphic *A clarus,* recorded from caves in both the Ozarks and the Appalachian Valley, might be the product of parallel speciation at least twice from a common, widespread ancestor.

The dipluran genus *Litocampa* contains 32 species worldwide; a majority (20) inhabit caves in the United States, and all are troglobites (Ferguson 1981a, 1981b). The wide geographic distribution of the genus (viz., parts of Africa, Europe, and North and South America), combined with retention of certain characters judged to be primitive for the order, has led Ferguson (1981a, 1981b) to suggest that its origin may predate the breakup of the supercontinent Pangaea in the Mesozoic. The absence of epigean congeners anywhere in North America suggests that troglobitic species of *Litocampa* are probably relatively old cavernicoles. Moreover, based on the richness of species and number of endemics in the southern Appalachian region, Ferguson has suggested this area as a probable center of distribution for species of *Litocampa* in the United States. Of the 20 species currently recognized from the United States, 17 occur in the greater Appalachian region, and their combined ranges form a distributional track from the Interior Low Plateaus to the Appalachian Valley and Ridge (see Ferguson 1981a: Fig. 43).

Of the six species of *Litocampa* in the study area, only two have narrowly circumscribed ranges that coincide with isolated exposures of limestone. The other species have wider ranges, although all except *L. cookei,* whose range extends as far west as central Kentucky and middle Tennessee, have relatively localized ranges confined to the study area or its periphery. The extensive distribution of *L. cookei,* the largest of any troglobitic dipluran in North America, is puzzling. Its distribution is not contiguous, however, but occurs in five disjunct clusters (Ferguson 1981a: Fig. 43). Ferguson (1981a) has studied the morphology of this species in detail and has concluded that it may represent a complex of allopatric sibling species.

Two final points should be made with respect to the origin of terrestrial troglobites. (1) The geographic distributions of four genera—viz., *Kleptochthonius* (*Chamberlinochthonius*), *Litocampa, Pseudanophthalmus,* and *Pseudotremia*—represented collectively by numerous troglobites in the study area are nearly congruent and together form a strong generalized distributional track that extends across the Appalachian Plateau. The importance of generalized tracks in biogeographic analysis has been reviewed by Wiley (1981). Such tracks may be used to estimate the range of ancestral species in monophyletic groups with similar distributions.

The possibility suggested by Barr (1981a) that ancestors of troglobitic species of *Pseudanophthalmus* originated in the forest floors of the Appalachian Plateau in late Cenozoic times, with subsequent thrusts into limestone areas on either side, was discussed above. The coincident distributions of *Kleptochthonius* (*Chamberlinochthonius*), *Litocampa,* and *Pseudotremia* suggest a similar place of origin and center of distribution for ancestors of troglobites in these groups as well. Shear (1972) alluded to the possibility that *Pseudotremia* originated in the southern Appalachian Mountains through evolution from a proto-*Pseudotremia* stock in the Cenozoic. Similarly, Ferguson (1981a) suggested that the southern Appalachians might have been the center of distribution for North American species of *Litocampa.* The generalized track formed by these taxa tends to support these ideas and points to the central and southern parts of the Appalachian Plateau as an important geographic center for the distribution of ancestors of terrestrial troglobites in the Appalachian Valley, Interior Low Plateaus, and limestone areas on the eastern and western sides of the Appalachian Plateau.

(2) Some common caves species in the study area, such as the spider *Meta menardi,* the cricket *Euhadenoecus fragilis,* and the dipterans *Amoebalaria defessa* and *Megaselia cavernicola,* are apparently well adapted in their present roles as troglophiles or (habitual) trogloxenes and show no evidence of evolving into troglobites. Other troglophiles, however, such as the harvestman *Erebomaster acanthina,* the spider *Nesticus carteri,* and certain species of the milliped *Pseudotremia,* show good evidence of becoming bona fide troglobites, and, as such, they are probably troglobites *in statu nascendi.*

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LITERATURE CITED

Banks, N. 1895. Notes on the Pseudoscorpionida. J. N.Y. Entomol. Soc. 3:1-13.

Barber, Henry S. 1928. Two new cave beetles related to *Anophthalmus pusio* Horn. J. Wash. Acad. Sci. 18:195-196.

Barnes, Robert D. 1980. Invertebrate Zoology. W. B. Saunders, Philadelphia.

Barr, Thomas C., Jr. 1959. Speciation and distribution of cavernicolous invertebrates in the eastern United States. Yr. Bk. Am. Phil. Soc. (1959):229-230.

Barr, Thomas C., Jr. 1960a. A new genus of cave beetle (Carabidae: Trechini) from southwestern Virginia, with a key to the genera of Trechini of North America north of Mexico. Coleopt. Bull. 14:65-70.

Barr, Thomas C., Jr. 1960b. The cavernicolous beetles of the subgenus *Rhadine,* genus *Agonum* (Coleoptera: Carabidae). Am. Midl. Nat. 64:45-65.

Barr, Thomas C., Jr. 1961. Caves of Tennessee. Tenn. Div. Geol. Bull. 64, Nashville.

Barr, Thomas C., Jr. 1963. Ecological classification of cavernicoles. Cave Notes 5:9-12.

Barr, Thomas C., Jr. 1964. Non-troglobitic Carabidae (Coleoptera) from caves in the United States. Coleopt. Bull. 18:1-4.

Barr, Thomas C., Jr. 1965. The *Pseudanophthalmus* of the Appalachian Valley (Coleoptera: Carabidae). Am. Midl. Nat. 73:41-72.

Barr, Thomas C., Jr. 1967a. Ecological studies in the Mammoth Cave system of Kentucky. I. The biota. Int. J. Speleol. 3:147-203.

Barr, Thomas C., Jr. 1967b. Observations on the ecology of caves. Am. Nat. 101:475-492.

Barr, Thomas C., Jr. 1967c. A new *Pseudanophthalmus* from an epigean environment in West Virginia (Coleoptera: Carabidae). Psyche 74:166-172.

Barr, Thomas C., Jr. 1968. Cave ecology and the evolution of troglobites. Evol. Biol. 2:35-102.

Barr, Thomas C., Jr. 1969. Evolution of the Carabidae (Coleoptera) in the southern Appalachians. Pages 67-92 *in* The Distributional History of the Biota of the Southern Appalachians, Part I: Invertebrates, P. C. Holt, editor. Res. Div. Mongr. 1, Virginia Polytech. Inst. and State Univ., Blacksburg.

Barr, Thomas C., Jr. 1973. Refugees of the Ice Age. Nat. Hist. 82:26-35,72-73.

Barr, Thomas C., Jr. 1974. The eyeless beetles of the genus *Arianops* Brendel (Coleoptera, Pselaphidae). Bull. Am. Mus. Nat. Hist. 154:3-51.

Barr, Thomas C., Jr. 1979. Revision of Appalachian *Trechus* (Coleoptera: Carabidae). Brimleyana 2:29-75.

Barr, Thomas C., Jr. 1981a. *Pseudanophthalmus* from Appalachian caves (Coleoptera: Carabidae): the *engelhardti* complex. Brimleyana 5:37-94.

Barr, Thomas C., Jr. 1981b. The cavernicolous carabid beetles of North America. Proc. Eighth Int. Cong. Speleol., Bowling Green, Ky. 1:343-344.

Barr, Thomas C., Jr. 1985. Pattern and process in speciation of trechine beetles in eastern North America (Coleoptera: Carabidae: Trechinae). Pages 350-407 *in* Taxonomy, Phylogeny and Zoogeography of Beetles and Ants (Series Entomologia 33), G. E. Ball, editor. Junk, Dordrecht, The Netherlands.

Barr, Thomas C., Jr. 1987. *Batriasymmodes* from caves in the Virginias (Coleoptera: Pselaphidae). Brimleyana 13:21-23.

Barr, Thomas C., Jr., and J. R. Reddell. 1967. The arthropod cave fauna of the Carlsbad Caverns region, New Mexico. Southwestern Nat. 12:253-274.

Barr, Thomas C., Jr., and J. R. Holsinger. 1985. Speciation in cave faunas. Ann. Rev. Ecol. Syst. 16:313-337.

Benedict, Ellen M., and D. R. Malcolm. 1974. A new cavernicolous species of *Mundochthonius* from the eastern United States (Pseudoscorpionida: Chthoniidae). J. Arachnol. 2:1-4.

Berland, Lucien. 1931. Campagne spéléologique de C. Bolivar et R. Jeannel dans l'Amérique du Nord (1928). 7. Arachnides Araneides. Arch. Zool. Exp. Gen. 71:383-387.

Besharse, Joseph C., and J. R. Holsinger. 1977. *Gyrinophilus subterraneus,* a new troglobitic salamander from southern West Virginia. Copeia (1977):624-634.

Birstein, Y. A. 1964. Freshwater isopods (Asellota). Fauna of U.S.S.R., Crustacea 7:1-148. (English trans. by Israel Prog. for Sci. Trans., publ. by Smithsonian Inst., Washington, D.C.).

Black, Jeffrey H. 1971. The cave life of Oklahoma: a preliminary study (excluding Chiroptera). Oklahoma Underground 4:2-53.

Bolivar, C., and R. Jeannel. 1931. Campagne spéléologique de C. Bolivar et R. Jeannel dans l'Amérique du Nord (1928). 1. Énumération des grottes visitées. Arch. Zool. Exp. Gen. 71:294-316.

Bonet, M. F. 1934. Campagne spéléologique de C. Bolivar et R. Jeannel dans l'Amérique du Nord. 10. Collemboles. Arch. Zool. Exp. Gen. 76:361-377.

Borgmeier, T. 1965. Revision of North American phorid flies. Part III. The species of the genus *Megaselia,* subgenus *Megaselia* (Diptera, Phoridae). Studia Entomol. 8:1-60.

Botosaneanu, Lazare, N. Bruce, and J. Notenboom. 1986. Isopoda: Cirolanidae. 412-422 *in* Stygofauna Mundi, L. Botosaneanu, editor. Brill/Backhuys, Leiden, The Netherlands.

Botosaneanu, Lazare, and J. H. Stock. 1979. *Arubolana imula* n. gen., n. sp., the first hypogean cirolanid isopod crustacean found in the Lesser Antilles. Bejdragen tot de Dierkunde 49:227-233.

Bowman, Thomas E. 1964. *Antrolana lira,* a new genus and species of troglobitic isopod from Madison Cave, Virginia. Int. J. Speleol. 1:229-236.

Brandon, Ronald A. 1965. A new race of the neotenic salamander *Gyrinophilus palleucus.* Copeia (1965):346-352.

Bresson, Janine. 1955. Aselles de sources et de grottes d'Eurasie et d'Amérique du Nord. Arch. Zool. Exp. Gen. 92:45-77.

Briggs, Thomas S. 1969. A new holarctic family of laniatorid phalangids (Opiliones). Pan-Pacific Entomol. 45:35-50.

Busacca, John. 1975. Distribution and biology of *Amoebalaria defessa* (Osten Sacken) and *Heleomyza brachyptera* (Loew) (Diptera: Heleomyzidae) in an Indiana cave. Bull. Nat. Speleol. Soc. 37:5-8.

Bush, Guy L. 1975. Modes of animal speciation. Ann. Rev. Ecol. Syst. 6:339-364.

Carpenter, Jerry H. 1970a. *Geocentrophora cavernicola* n. sp. (Turbellaria, Alloeocoela)—first cave alloeocoel. Trans. Am. Micros. Soc. 89:124-133.

Carpenter, Jerry H. 1970b. Systematics and ecology of cave planarians of the United States. Ph.D. dissert., Univ. Kentucky, Lexington.

Carpenter, Jerry H. 1981. *Bahalana geracei* n. gen., n. sp., a troglobitic cirolanid isopod from Lighthouse Cave, San Salvador Island, Bahamas. Bejdragen tot de Dierkunde 51:259:267.

Causey, Nell B. 1960a. The troglobitic milliped genus *Zygonopus* (Chordeumida, Conotylidae, Trichopetalinae). J. N.Y. Entomol. Soc. 68:69-80.

Causey, Nell B. 1960b. Speciation in North American millipeds. Am. Midl. Nat. 64:116-122.

Causey, Nell B. 1963. *Mexiterpes sabinus,* new genus and new species, a Mexican troglobite (Diplopoda: Trichopetalidae). Psyche 70:235-239.

Causey, Nell B. 1967. *Trichopetalum subterraneum,* new species from Kentucky, new records and a key to the genus (Diplopoda; Chordeumida; Trichopetalidae). Proc. Biol. Soc. Wash. 80:117-122.

Causey, Nell B. 1969. New trichopetalid (Chordeumidea: Chodeumida) millipeds from caves in North and Central America. Proc. Louisiana Acad. Sci. 32:43-49.

Chamberlin, Joseph C. 1962. New and little-known false scorpions, principally from caves, belonging to the families Chthoniidae and Neobisiidae (Arachnida, Chelonethida). Bull. Am. Mus. Nat. Hist. 123:299-352.

Chamberlin, Joseph C., and D. R. Malcolm. 1960. The occurrence of false scorpions in caves with special reference to cavernicolous adaptation of cave species in North America. Am. Midl. Nat. 64:105-115.

Chamberlin, Ralph V., and R. L. Hoffman. 1958. Checklist of the millipeds of North America. Bull. U.S. Nat. Mus. 212:1-236.

Chappuis, P. A. 1957. Un asellide nouveau de l'Amérique du Nord. Notes Biospéol. 12:37-43.

Charlesworth, Brian. 1980. Evolution in age-structured populations. Cambridge Univ. Press, Cambridge.

Chopard, L. 1931. Campagne spéléologique de C. Bolivar et R. Jeannel dans l'Amérique du Nord (1928). 8. Insectes Orthoptères. Arch. Zool. Exp. Gen. 71:389-401.

Christiansen, Kenneth A. 1960a. The genus *Sinella* Brook (Collembola: Entomobryidae) in nearctic caves. Ann. Entomol. Soc. Am. 53:481-491.

Christiansen, Kenneth A. 1960b. The genus *Pseudosinella* (Collembola, Entomobryidae) in caves of the United States. Psyche 67:1-25.

Christiansen, Kenneth A. 1961. Convergence and parallelism in cave Entomobryinae. Evolution 15:288-301.

Christiansen, Kenneth A. 1964a. A revision of the nearctic members of the genus *Tomocerus* (Collembola: Entomobryidae). Rev. Ecol. Biol. Sol 1:639-678.

Christiansen, Kenneth A. 1964b. Bionomics of Collembola. Ann. Rev. Entomol. 9:147-178.

Christiansen, Kenneth A. 1966. The genus *Arrhopalites* in the United States and Canada. Int. J. Speleol. 2:43-73.

Christiansen, Kenneth A. 1981. The zoogeography of eastern North American cave Collembola. Proc. Eighth Int. Speleol., Bowling Green, Ky. 2:618-622.

Christiansen, Kenneth A. 1982. Zoogeography of cave Collembola east of the Great Plains. Bull. Nat. Speleol. Soc. 44:32-41.

Christiansen, Kenneth A., and P. Bellinger. 1980a. The Collembola of North America North of the Rio Grande. Part 1. Introduction, General, Families Poduridae and Hypogastruridae. Grinnell College, Grinnell, Ia.

Christiansen, Kenneth A., and P. Bellinger. 1980b. The Collembola of North America North of the Rio Grande. Part 2. Families Onychiuridae and Isotomidae. Grinnell College, Grinnell, Ia.

Christiansen, Kenneth A., and P. Bellinger. 1980c. The Collembola of North America North of the Rio Grande. Part 3. Family Entomobryidae. Grinnell College, Grinnell, Ia.

Christiansen, Kenneth A., and P. Bellinger. 1981. The Collembola of North America North of the Rio Grande. Part 4. Families Neelidae and Sminthuridae (glossary, bibliography, index). Grinnel College, Grinnell, Ia.

Christiansen, Kenneth A., and D. C. Culver. 1968. Geographical variation and evolution in *Pseudosinella hirsuta*. Evolution 22:237-255.

Cohen, Joel E. 1978. Food Webs and Niche Space. Princeton Univ. Press, Princeton, N.J.

Cole, Gerald A., and W. L. Minckley. 1966. *Speocirolana thermydronis,* a new species of cirolanid isopod crustacean from central Coahuila, Mexico. Tulane Stud. Zool. 13:17-22.

Collins, T. Lynn, and J. R. Holsinger. 1981. Population ecology of the troglobitic isopod crustacean *Antrolana lira* Bowman (Cirolanidae). Proc. Eighth Int. Cong. Speleology, Bowling Green, Ky. 1:129-132.

Connor, Edward F., and E. D. McCoy. 1979. The statistics and biology of the species-area relationship. Am. Nat. 113:791-833.

Contreras-Balderas, Salvador, and D. C. Purata-Velarde. 1982. *Speocirolana guerrae* sp. nov., cirolanido troglobio anoptalmo de la Cueva de la Chorrera, Linares, Nuevo Leon, Mexico (Crustacea: Isopoda). Texas Mem. Mus. Bull. 28:1-12.

Cook, David G. 1975. Cave-dwelling aquatic Oligochaeta (Annelida) from the eastern United States. Trans. Am. Micros. Soc. 94:24-37.

Cooper, John E. 1975. Ecological and behavioral studies in Shelta Cave, Alabama, with emphasis on decapod crustaceans. Ph.D. dissert., Univ. Kentucky, Lexington.

Cooper, John E., and A. Iles. 1971. The southern cavefish, *Typhlichthys subterraneus,* at the southwestern periphery of its range. Bull. Nat. Speleol. Soc. 33:45-49.

Cope, Edward D. 1869. Synopsis of the extinct Mammalia of the cave formations of the United States with observations on some Myriapoda found in and near same. Proc. Am. Phil. Soc. 11:171-192.

Crabill, Ralph E., Jr. 1952. New cavernicolous *Nampabius* with a key to its northeastern American congeners (Chilopoda, Lithobiidae). Entomol. News 63:203-206.

Craig, John L. 1975. A checklist of the invertebrate species recorded from Missouri subterranean habitats. Missouri Speleol. 15:1-10.

Craig, John L. 1977. Invertebrate faunas of caves to be inundated by the Meramec Park Lake in eastern Missouri. Bull. Nat. Speleol. Soc. 39:80-89.

Crawford, Rodney L. 1981. A critique of the analogy between caves and islands. Proc. Eighth Int. Cong. Speleol., Bowling Green, Ky. 1:295-297.

Culver, David C. 1970. Analysis of simple cave communities. I. Caves as islands. Evolution 24:463-474.

Culver, David C. 1973a. Competition in spatially heterogeneous systems: an analysis of simple cave communities. Ecology 54:102-110.

Culver, David C. 1973b. Feeding behavior of the salamander *Gyrinophilus porphyriticus* in caves. Int. J. Speleol. 5:369-377.

Culver, David C. 1975. The interaction of competition and predation in cave stream communities. Int. J. Speleol. 7:229-245.

Culver, David C. 1976. The evolution of aquatic cave communities. Am. Nat. 110:945-957.

Culver, David C. 1981. Some implications of competition for cave stream communities. Int. J. Speleol. 11:49-62.

Culver, David C. 1982. Cave Life: Evolution and Ecology. Harvard Univ. Press, Cambridge.

Culver, David C. 1985. Trophic relationships in aquatic cave environments. Stygologia 1:43-53.

Culver, David C., and J. R. Holsinger. 1969. Preliminary observations on sex ratios in the subterranean amphipod genus *Stygonectes* (Gammaridae). Am. Midl. Nat. 82:631-633.

Culver, David C., J. R. Holsinger, and R. A. Baroody. 1973. Toward a predictive cave biogeography: the Greenbrier Valley as a case study. Evolution 27:689-695.

Cummins, Kenneth W., and M. J. Klug. 1979. Feeding ecology of stream invertebrates. Ann. Rev. Ecol. Syst. 10:147-172.

Curran, Charles H. 1965. The Families and Genera of North American Diptera. Henry Tripp Publ., Woodhaven, N.Y.

Dearolf, Kenneth. 1953. The invertebrates of 75 caves in the United States. Proc. Penn. Acad. Sci. 27:225-241.

Deeleman-Reinhold, Christa L. 1981. Remarks on origin and distribution of troglobitic spiders. Proc. Eighth Int. Cong. Speleol., Bowling Green, Ky. 1:305-308.

Dickson, Gary W. 1975. A preliminary study of heterotrophic microorganisms as factors in substrate of troglobitic invertebrates. Bull. Nat. Speleol. Soc. 37:89-93.

Dickson, Gary W. 1976. Variation in the ecology, morphology and behavior of the troglobitic amphipod crustacean *Crangonyx antennatus* Packard (Crangonychidae) from different habitats. M.S. thesis, Old Dominion Univ., Norfolk.

Dickson, Gary W. 1977a. Variation among populations of the troglobitic amphipod crustacean *Crangonyx antennatus* Packard living in different habitats. I. Morphology. Int. J. Speleol. 9:43-58.

Dickson, Gary W. 1977b. Behavioral adaptation of the troglobitic amphipod crustacean *Crangonyx antennatus* to stream habitats. Hydrobiologia 56:17-20.

Dickson, Gary W. 1979. The importance of cave mud sediments in food preference, growth and mortality of the troglobitic crustacean *Crangonyx antennatus* Packard (Crangonyctidae). Crustaceana 36:129-140.

Dickson, Gary W., and J. R. Holsinger. 1981. Variation among populations of the troglobitic amphipod crustacean *Crangonyx antennatus* Packard (Crangonyctidae) living in different habitats. III. Population dynamics and stability. Int. J. Speleol. 11:33-48.

Dickson, Gary W., and P. W. Kirk. 1976. Distribution of heterotrophic microorganisms in relation to detritivores in Virginia caves (with supplemental bibliography on cave mycology and microbiology). Pages 205-226 *in* The Distributional History of the Biota of the Southern Appalachians, Part IV: Algae and Fungi, B. C. Parker and M. K. Roane, editors. Univ. Press Virginia, Charlottesville.

Dickson, Gary W., J. C. Patton, J. R. Holsinger, and J. C. Avise. 1979. Genetic variation in cave-dwelling and deep-sea organisms, with emphasis on *Crangonyx antennatus* (Crustacea: Amphipoda) in Virginia. Brimleyana 2:119-130.

Douglas, Henry H. 1964. Caves of Virginia. Va. Cave Survey, Falls Church.

Elliott, William R., and R. W. Strandtmann. 1971. New locality records for *Rhagidia* from Mexican and American caves. J. Kansas Entomol. Soc. 44:468-475.

Emerton, J. H. 1875. Notes on spiders from caves in Kentucky, Virginia, and Indiana. Am. Nat. 9:278-281.

Endler, John A. 1977. Geographic Variation, Speciation, and Clines. Princeton Univ. Press, Princeton, N.J.

Estes, James A. 1978. The comparative ecology of two populations of the troglobitic isopod crustacean *Lirceus usdagalun* (Asesllidae). M.S. thesis, Old Dominion Univ., Norfolk.

Estes, James A., and J. R. Holsinger. 1976. A second troglobitic species of the genus *Lirceus* (Isopoda, Asellidae) from southwestern Virginia. Proc. Biol. Soc. Wash. 89:481-490.

Estes, James A., and J. R. Holsinger. 1982. A comparison of the structure of two populations of the troglobitic isopod crustacean *Lirceus usdagalun* (Asellidae). Polskie Arch. Hydrobiol. 29:453-461.

Ferguson, Lynn M. 1974. Taxonomy, distribution, and evolution of cavernicolous campodeids in Virginia (Diplura: Campodeidae). M.S. thesis, Virginia Polytech. Inst. and State Univ., Blacksburg.

Ferguson, Lynn M. 1981a. Systematics, evolution, and zoogeography of the cavernicolous campodeids of the genus *Litocampa* (Diplura: Campodeidae) in the United States. Ph.D. dissert. Virginia Polytech. Inst. and State Univ., Blacksburg.

Ferguson, Lynn M. 1981b. Cave Diplura of the United States. Proc. Eighth Int. Cong. Speleol., Bowling Green, Ky. 1:11-12.

Fleming, Lawrence E. 1972. The evolution of the eastern North American isopods of the genus *Asellus* (Crustacea: Asellidae). Part I. Int. J. Speleol. 4:221-256.

Fleming, Lawrence E. 1973. The evolution of the eastern North American isopods of the genus *Asellus* (Crustacea: Asellidae). Part II. Int. J. Speleol, 5:283-310.

Fowler, James A. 1942. Cave fauna. Bull. Nat. Speleol. Soc. 4:11-12.

Fowler, James A. 1943. Cave fauna. Bull. Nat. Speleol. Soc. 5:37-40.

Fowler, James A. 1944. Report of the work of the committee on cave fauna. Bull Nat. Speleol. Soc. 6:55-57.

Fowler, James A. 1946. Report of the committee on fauna. Bull. Nat. Speleol. Soc. 8:79-81.

Franz, Richard, and D. Slifer. 1971. Caves of Maryland. Maryland Geol. Survey Educ. Ser. No. 3, Baltimore, Md.

Gates, Gordon E. 1959. Earthworms of North American caves. Bull. Nat. Speleol. Soc. 21:77-84.

Gertsch, Willis J. 1984. The spider family Nesticidae (Araneae) in North America, Central America, and the West Indies. Texas Mem. Mus. Bull. 31:1-91.

Gill, Gordon D. 1962. The heleomyzid flies of America north of Mexico (Diptera: Heleomyzidae). Proc. U.S. Nat. Mus. 113:495-603.

Ginet, René. 1960. Écologie, ēthologie, et biologie de *Niphargus* (Amphipodes Gammarides hypoges). Ann. Spēlēol. 15:1-254.

Gittleson, Stephen M., and R. L. Hoover. 1970. Protozoa of underground waters in caves. Ann. Spéléol. 25:91-106.

Gooch, James L., and W. W. Hetrick. 1979. The relation of genetic structure to environmental structure: *Gammarus minus* in a karst area. Evolution 33:192-206.

Goodnight, Clarence J., and M. L. Goodnight. 1942. New Phalangodidae (Phalangida) from the United States. Am. Mus. Novitates 1188:1-18.

Goodnight, Clarence L., and M. L. Goodnight. 1960. Speciation among cave opilionids of the United States. Am. Midl. Nat. 64:34-38.

Hack, John T. 1969. The area, its geology: Cenozoic development of the southern Appalachians. Pages 1-17 *in* The Distributional History of the Biota of the Southern Appalachians, Part I: Invertebrates, P. C. Holt, editor. Res. Div. Monogr. 1, Virginia Polytech. Inst. and State Univ., Blacksburg.

Hadži, Jovan. 1935. Ein eigentumlicher neuer Höhlen-Opilionid aus Nord-Amerika, *Cladonychium corii* g.n. sp.n. Biol. Gen. 11:49-72.

Harris, J. A. 1970. Bat-guano cave environment. Science 169:1342-1343.

Henrot, Henri. 1949. Les coléoptères cavernicoles de la région des Appalaches. Liste des grottes explorées. Notes Biospéol., fasc. 4, Publ. Mus. Hist. Nat., Paris 12:17-35.

Henry, Jean-Paul. 1978. Observations sur les peuplements de Crustacés Aselloides des milieux souterrains. Bull. Soc. Zool. France 103:491-497.

Henry, Jean-Paul, J. J. Lewis, and G. Magniez. 1986. Isopoda: Asellota: Asellidea, Gnathostenetroidea, Stenetroidea. Pages 434-464 *in* Stygofauna Mundi, L. Botosaneanu, editor. Brill/Backhuys, Leiden, The Netherlands.

Hetrick, Steven W. 1975. Genetic studies of cave and spring populations of the freshwater amphipod *Gammarus minus* Say. M.S. thesis, Old Dominion Univ., Norfolk, Va.

Hetrick, Steven W., and J. L. Gooch. 1981. Genetic differentiation in populations of the freshwater amphipod *Gammarus minus* in a karst area. Int. J. Speleol. 11:7-13.

Hobbs, Horton H., Jr. 1972. Crayfishes (Astacidae) of North and Middle America. EPA Water Pollution Control Res. Ser., Iden. Manual No. 9, U.S. Gov. Printing Off., Washington, D.C.

Hobbs, Horton H., Jr. 1974. A checklist of the North and Middle American crayfishes (Decapoda: Astacidae and Cambaridae). Smithsonian Contrib. Zool. 166:1-161.

Hobbs, Horton H., Jr., and T. C. Barr, Jr. 1960. The origins and affinities of the troglobitic crayfishes of North America (Decapoda, Astacidae). Am. Midl. Nat. 64:12-33.

Hobbs, Horton H., Jr., H. H. Hobbs, III, and M. A. Daniel. 1977. A review of the troglobitic decapod crustaceans of the Americas. Smithsonian Contrib. Zool. 244:1-183.

Hobbs, Horton H., III. 1975. Distribution of Indiana cavernicolous crayfishes and their ectocommensal ostracods. Int. J. Speleol. 7:273-302.

Hobbs, Horton H., III. 1981. The cavernicolous fauna of Ohio. Part I: preliminary report. Proc. Eighth Int. Cong. Speleol., Bowling Green, Ky. 2:444-447.

Hobbs, Horton H., III, and M. F. Flynn. 1981. The cave fauna of Ohio. Pholeos (Wittenberg Univ. Speleol. Soc. Publ.) 1:7-14.

Hoff, C. Clayton. 1958. List of the pseudoscorpions of North America north of Mexico. Am. Mus. Novitates 1875:1-50.

Hoffman, Richard L. 1950. A preliminary list of the cleidogonid millipeds, with descriptions of a new genus from Guatemala and a new species from Virginia. J. Wash. Acad. Sci. 40:87-92.

Hoffman, Richard L. 1958. On the identity of *Pseudotremia cavernarum* Cope, a poorly known American chordeumid diplopod. Proc. Biol. Soc. Wash. 71:113-118.

Hoffman, Richard L. 1981. On the taxonomic status, distribution and subspecies of the milliped *Pseudotremia fracta* (Chamberlin) (Chordeumatida: Cleidogonidae). Brimleyana 5:135-144.

Holsinger, John R. 1962. Progress of the biological survey of Virginia caves. Nat. Speleol. Soc. News 20:100-102.

Holsinger, John R. 1963a. Annotated checklist of the macroscopic troglobites of Virginia with notes on their geographic distribution. Bull. Nat. Speleol. Soc. 25:23-26.

Holsinger, John R. 1963b. Studies on the ecology and geographic distribution of macroscopic cavernicolous invertebrates of the central Appalachians. M.S. thesis, James Madison Univ., Harrisonburg, Va.

Holsinger, John R. 1964. The biology of Virginia caves. Pages 57-74 *in* Caves of Virginia, by H. H. Douglas. Virginia Cave Survey, Falls Church.

Holsinger, John R. 1965a. Free living mites (Acarina) in caves of the eastern United States. Bull. Nat. Speleol. Soc. 27:47-54.

Holsinger, John R. 1965b. Redescriptions of two poorly known species of cavernicolous rhagidiid mites (Acarina: Trombidiformes) from Virginia and Kentucky. Acarologia 7:654-662.

Holsinger, John R. 1966. A preliminary study of the effects of organic pollution of Banners Corner Cave, Virginia. Int. J. Speleol. 2:75-89.

Holsinger, John R. 1967a. Systematics, speciation, and distribution of the subterranean amphipod genus *Stygonectes* (Gammaridae). Bull. U.S. Nat. Mus. 259:1-176.

Holsinger, John R. 1967b. New data on the range of the trichoniscid isopod, *Caucasonethes henroti*. J. Tenn. Acad. Sci. 42:15.

Holsinger, John R. 1969a. Biogeography of the freshwater amphipod crustaceans (Gammaridae) of the central and southern Appalachians. Pages 19-50 *in* The Distributional History of the biota of the Southern Appalachians, Part I: Invertebrates, P.C. Holt, editor. Res. Div. Monogr. 1, Virginia Polytech. Inst. and State Univ., Blacksburg.

Holsinger, John R. 1969b. The systematics of the North American subterranean amphipod genus *Apocrangonyx* (Gammaridae), with remarks on ecology and zoogeography. Am. Midl. Nat. 81:1-28.

Holsinger, John R. 1972. The Freshwater Amphipod Crustaceans (Gammaridae) of North America. EPA Water Pollution Control Res. Ser., Iden. Manual No. 5. U.S. Gov. Printing Off. Washington, D.C.

Holsinger, John R. 1975. Descriptions of Virginia Caves. Va. Div. Mineral Res., Bull. 81, Charlottesville.

Holsinger, John R. 1976. The cave fauna of Pennsylvania. Pages 72-87 *in* Geology and Biology of Pennsylvania Caves, W. B. White, editor. Pa. Geol. Survey Gen. Geol. Rep., 4th Ser. Vol. 66, Harrisburg.

Holsinger, John R. 1977. A review of the systematics of the Holarctic amphipod family Crangonyctidae. Crustaceana (supplement) 4:244-281.

Holsinger, John R. 1978. Systematics of the subterranean amphipod genus *Stygobromus* (Crangonyctidae), part II: Species of the eastern United States. Smithsonian Contrib. Zool. 266:1-144.

Holsinger, John R. 1986a. Holarctic crangonyctid amphipods. Pages 535-549 *in* Stygofauna Mundi, L. Botosaneanu, editor. Brill/Backhuys, Leiden, The Netherlands.

Holsinger, John R. 1986b. Zoogeographic patterns of North American subterranean amphipod crustaceans. Pages 85-106 *in* Crustacean Issues 4. Crustacean Biogeography, R. H. Gore and K. L. Heck, editors. Balkema, Rotterdam, The Netherlands.

Holsinger, John R., R. A. Baroody, and D. C. Culver. 1976. The Invertebrate Cave Fauna of West Virginia. W.Va. Speleol. Survey Bull. 7:1-82.

Holsinger, John R., and T. E. Bowman. 1973. A new troglobitic isopod of the genus *Lirceus* (Asellidae) from southwestern Virginia, with notes on its ecology and additional cave records for the genus in the Appalachians. Int. J. Speleol. 5:261-271.

Holsinger, John R., and D. C. Culver. 1970. Morphological variation in *Gammarus minus* Say (Amphipoda, Gammaridae) with emphasis on subterranean forms. Postilla 146:1-24.

Holsinger, John R., and G. W. Dickson. 1977. Burrowing as a means of survival in the troglobitic amphipod crustacean *Crangonyx antennatus* Packard (Crangonyctidae). Hydrobiologia 54:195-199.

Holsinger, John R., and S. B. Peck. 1971. The invertebrate cave fauna of Georgia. Bull. Nat. Speleol. Soc. 33:23-44.

Holsinger, John R., and H. R. Steeves, III. 1971. A new species of subterranean isopod crustacean (Asellidae) with remarks on distribution of other isopods of the region. Proc. Biol. Soc. Wash. 84:189-200.

Holt, Perry D. 1973. Branchiobdellids (Annelida: Clitellata) from some eastern North American caves, with descriptions on new species of the genus *Cambarincola*. Int. J. Speleol. 5:219-255.

Holthuis, Lipke B. 1986. Decapoda. Pages 589-615 *in* Stygofauna Mundi, L. Botosaneanu, editor. Brill/Backhuys, Leiden, The Netherlands.

Horn, George H. 1868. Catalogue of Coleoptera from south-west Virginia. Trans. Am. Entomol. Soc. 2:123-128.

Howarth, Francis G. 1972. Cavernicoles in lava tubes on the island of Hawaii. Science 175:325-326.

Howarth, Francis G. 1980. The zoogeography of specialized cave animals: a bioclimatic model. Evolution 34:394-406.

Howarth, Francis G. 1981. Non-relictual terrestrial troglobites in the tropical Hawaiian caves. Proc. Eighth Int. Cong. Speleol., Bowling Green, Ky. 2:539-541.

Hubbell, Theodore H. 1936. A monographic revision of the genus *Ceuthophilus* (Orthoptera, Gryllacrididae, Rhaphidophorinae). Univ. Florida Publ., Biol. Ser. 2:1-551.

Hubbell, Theodore H., and R. M. Norton. 1978. The systematics and biology of the cave-crickets of the North American tribe Hadenoicini (Orthoptera: Saltatoria: Ensifera: Rhaphidophoridae: Dolichopodinae). Misc. Publ. Mus. Zool. Univ. Mich. 156:1-124.

Hubricht, Leslie. 1943. Studies on the Nearctic freshwater Amphipoda, III. Notes on the freshwater Amphipoda of eastern United States, with description of ten new species. Am. Midl. Nat. 29:683-712.

Hubricht, Leslie. 1957. New species of *Fontigens* from Shenandoah National Park. Nautilus 71:9-10.

Hubricht, Leslie. 1962. New species of *Helicodiscus* from the eastern United States. Nautilus 75:102-107.

Hubricht, Leslie. 1964. Land snails from the caves of Kentucky, Tennessee, and Alabama. Bull. Nat. Speleol. Soc. 26:33-36.

Hubricht, Leslie. 1965. Four new land snails from the southeastern United States. Nautilus 79:4-7.

Hubricht, Leslie. 1976. The genus *Fontigens* from Appalachian caves (Hydrobidae: Mesogastropoda). Nautilus 90:86-88.

Hubricht, Leslie. 1985. The distributions of the native land mollusks of the eastern United States. Fieldiana (Zool., New Ser.) 24:1-191.

Hunt, Charles B. 1967. Physiography of the United States. W. H. Freeman and Co., San Francisco.

Hyman, Libby H. 1937. Studies on the morphology, taxonomy, and distribution of North American triclad Turbellaria, VIII: Some cave planarians of the United States. Trans. Am. Micros. Soc. 56:457-477.

Hyman, Libby H. 1945. North American triclad Turbellaria. XI. New, chiefly cavernicolous, planarians. Am. Midl. Nat. 34:475-484.

Ivie, Wilton. 1965. The spiders of the genus *Islandia* (Linyphiidae, Erigoninae). Am. Mus. Nat. Hist. Novitates 2221:1-25.

Ivie, Wilton. 1969. North American spiders of the genus *Bathyphantes* (Araneae: Linyphiidae). Am. Mus. Nat. Hist. Novitates 2364:1-70.

Jeannel, René. 1928. Monographie des Trechinae. III. Les Trechini cavernicoles. Soc. Entomol. France 35:123-139.

Jeannel, René. 1931. Campagne spéléologique de C. Bolivar et R. Jeannel dans l'Amérique du Nord (1928). 9. Insectes coléoptères et revision des Trechinae de l'Amérique du Nord. Arch. Zool. Exp. Gen. 71:403-499.

Jeannel, René. 1949. Les coléoptères cavernicoles de la région des Appalaches. Etude systematique. Notes Biospeleol., fasc. 4, Publ. Mus. Hist. Nat., Paris 12:37-104.

Juberthie, Christian, and B. Delay. 1981. Ecological and biological implications of a "superficial underground compartment." Proc. Eighth Int. Cong. Speleol., Bowling Green, Ky. 1:203-205.

Kawakatsu, Masahari, and R. W. Mitchell. 1981. Redescription of *Kenkia rhynchida,* a troglobitic planarian from Oregon, and a redescription of the family Kenkiidae and its genera (Turbellaria, Tricladida, Paludicoles). Annot. Zool. Japaneses 54:125-141.

Keith, James H. 1975. Seasonal changes in a population of *Pseudanophthalmus tenuis* (Coleoptera, Carabidae) in Murray Spring Cave, Indiana: a preliminary report. Int. J. Speleol. 7:33-44.

Kenk, Roman. 1970. Freshwater triclads (Turbellaria) of North America. IV. The polypharyngeal species of *Phagocata*. Smithsonian Contrib. Zool. 80:1-17.

Kenk, Roman. 1977. Freshwater triclads (Turbellaria) of North America. IX. The genus *Sphalloplana*. Smithsonian Contrib. Zool. 246:1-38.

Klimaszewski, Jan. 1984. A revision of the genus *Aleochara* Gravenhorst of America north of Mexico (Coleoptera: Staphylinidae, Aleocharinae). Mem. Entomol. Soc. Canada 129:1-211.

Klimaszewski, Jan, and S. B. Peck. 1986. A review of the cavernicolous Staphylinidae (Coleoptera) of eastern North America: Part I. Aleocharinae. Questiones Entomologicae 22:51-113.

Krantz, G. W. 1970. A Manual of Acarology. Oregon State Univ. Bookstores, Corvallis.

Krekeler, Carl H., and E. C. Williams, Jr. 1966. Cave fauna. Pages 390-400 *in* Natural Features of Indiana, A. L. Lindsey, editor. Ind. Acad. Sci., Ind. State Lib., Indianapolis.

Lewis, Julian J. 1980. A comparison of *Pseudobaicalasellus* and *Caecidotea,* with a description of *Caecidotea bowmani*, n. sp. (Crustacea: Isopoda: Asellidae). Proc. Biol. Soc. Wash. 93:314-326.

Lewis, Julian J., and T. E. Bowman. 1981. The subterranean asellids (*Caecidotea*) of Illinois (Crustacea: Isopoda: Asellidae). Smithsonian Contrib. Zool. 335:1-66.

Lisowski, Edward A. 1979. Variations in body color and eye pigmentation of *Asellus brevicauda* Forbes (Isopoda: Asellidae) in a southern Illinois cave stream. Bull. Nat. Speleol. Soc. 41:11-14.

Loomis, Harold F. 1939. The millipeds collected in Appalachian caves by Mr. Kenneth Dearolf. Bull. Mus. Comp. Zool. 86:165-193.

Loomis, Harold F. 1943. New cave and epigean millipeds. Bull. Mus. Comp. Zool. 92:373-410.

Loomis, Harold F. 1944. Millipeds principally collected by Professor V. E. Shelford in the eastern and southeastern states. Psyche 51:166-177.

Malcolm, David R., and J. C. Chamberlin. 1960. The pseudoscorpion genus *Chitrella* (Chelonethida, Syarinidae). Am. Mus. Novitates 1989:1-19.

Malcolm, David R., and J. C. Chamberlin. 1961. The pseudoscorpion genus *Kleptochthonius* Chamberlin (Chelonethida, Cnthoniidae). Am. Mus. Nat. Hist. Novitates 2063:1-35.

Marshall, S. A. 1985. A revision of the genus *Spelobia* Spuler (Diptera: Sphaeroceridae) in North America and Mexico. Trans. Am. Entomol. Soc. 111:1-101.

Marshall, S. A., and S. B. Peck. 1984. Distribution of cave-dwelling Sphaeroceridae (Diptera) of eastern North America. Proc. Entomol. Soc. Ontario 115:37-41.

Marshall, S. A., and S. B. Peck. 1985. The origin and relationships of *Spelobia tenebrarum* (Aldrich), a troglobitic, eastern North American, sphaerocerid fly. Can. Entomol. 117:1013-1015.

Matthews, Larry E. 1971. Descriptions of Tennessee Caves. Tenn. Div. Geol. Bull. 69, Nashville.

McDaniel, V. Rick, and K. L. Smith. 1976. Cave fauna of Arkansas: selected invertebrate taxa. Proc. Ark. Acad. Sci. 30:57-60.

McKinney, Thomas. 1975. Studies on the niche separation in two carabid cave beetles. Int. J. Speleol. 7:65-78.

Mitchell, Robert W. 1968. New species of *Sphalloplana* (Turbellaria; Paludicola) from the caves of Texas and a reexamination of the genus *Speophila* and the family Kenkiidae. Ann. Spéléol. 23:597-620.

Mitchell, Robert W. 1969. A comparison of temperate and tropical cave communities. Southwestern Nat. 14:73-88.

Mitchell, Robert W. 1974. The cave-adapted flatworms of Texas; systematics, natural history, and responses to light and temperature. Pages 402-430 *in* Biology of the Turbellaria, N. W. Riser and M. P. Morse, editors. McGraw-Hill, New York.

Monod, Th. 1930. Contribution a l'édude des "Cirolanidae." Ann. Sci. Nat. Zool. (10th ser.) 13:129-183.

Morrison, Joseph P. E. 1949. The cave snails of eastern North America. Am. Malacol. Union, News Bull. and Ann. Rep. (1949):13-15.

Muchmore, William B. 1963. Redescription of some cavernicolous pseudoscorpions (Arachnida, Chelonethida) in the collection of the Museum of Comparative Zoology. Breviora 188:1-16.

Muchmore, William B. 1964. New terrestrial isopods of the genus *Miktoniscus* from eastern United States (Crustacea: Isopods: Oniscoidea). Ohio J. Sci. 64:51-57.

Muchmore, William B. 1967. New cave pseudoscorpions of the genus *Apochthonius* (Arachnida, Chelonethida). Ohio J. Sci. 76:89-95.

Muchmore, William B. 1970a. A new troglobitic trichoniscid isopod of the genus *Caucasonethes*. J. Tenn. Acad. Sci. 45:27-28.

Muchmore, William B. 1970b. New cavernicolous *Kleptochthonius* spp. from Virginia (Arachnida, Pseudoscorpionida, Chthoniidae). Entomol. News 81:210-212.

Muchmore, William B. 1973. The genus *Chitrella* in America (Pseudoscorpionida, Syarinidae). J. N.Y. Entomol. Soc. 81:183-192.

Muchmore, William B. 1974. New cavernicolous species of *Kleptochthonius* from Virginia and West Virginia (Pseudoscorpionida, Chthoniidae). Entomol. News 85:81-84.

Muchmore, William B. 1976a. New cavernicolous species of *Kleptochthonius* and recognition of a new species group within the genus (Pseudoscorpionida: Chthoniidae). Entomol. News 87:211-217.

Muchmore, William B. 1976b. New species of *Apochthonius,* mainly from caves in central and eastern United States (Pseudoscorpionida, Chthoniidae). Proc. Biol. Soc. Wash. 89:67-80.

Muchmore, William B. 1981. Cavernicolous pseudoscorpions in North and Middle America. Proc. Eighth Int. Cong. Speleol., Bowling Green, Ky. 1:381-384.

Nicholas, Bro. George. 1960. Checklist of the troglobitic organisms of the United States. Am. Midl. Nat. 64:123-160.

Packard, Alphonse S. 1881. Fauna of Luray and New Market Caves, Virginia. Am. Nat. 15:231-232.

Packard, Alphonse S. 1888. The cave fauna of North America with remarks on the anatomy of the brain and origin of the blind species. Mem. Nat. Acad. Sci. 4(1)1-156.

Park, Orlando. 1956. New or little known species of pselaphid beetles from southeastern United States. J. Tenn. Acad. Sci. 33:39-74.

Park, Orlando. 1960. Cavernicolous pselaphid beetles of the United States. Am. Midl. Nat. 64:66-104.

Park, Orlando. 1965. Revision of the genus *Batriasymmodes* (Coleoptera: Pselaphidae). Trans. Am. Micros. Soc. 84:184-201.

Peck, Stewart B. 1970. The terrestrial arthropod fauna of Florida caves. Florida Entomol. 53:203-207.

Peck, Stewart B. 1973. A systematic revision and the evolutionary biology of the *Ptomaphagus* (*Adelops*) beetles of North America (Coleoptera; Leiodidae; Catopinae), with emphasis on cave inhabiting species. Bull. Mus. Comp. Zool. 145:29-162.

Peck, Stewart B. 1975a. A review of the distribution and habitats of North American *Brathinus* (Coleoptera; Staphylinidae; Omaliinae). Psyche 82:59-66.

Peck, Stewart B. 1975b. Cantharid beetle larvae in American caves. Bull. Nat. Speleol. Soc. 37:77-78.

Peck, Stewart B. 1975c. The life cycle of a Kentucky cave beetle, *Ptomaphagus hirtus* (Coleoptera; Leiodidae; Catopinae). Int. J. Speleol. 7:7-17.

Peck, Stewart B. 1975d. The invertebrate fauna of tropical American caves, part III: Jamaica, an introduction. Int. J. Speleol. 7:303-326.

Peck, Stewart B. 1977. A review of the distribution and biology of the small carrion beetle *Prionochaeta opaca* of North America (Coleoptera; Leiodidae; Catopinae). Psyche 83:299-307.

Peck, Stewart B. 1980. Climatic change and the evolution of cave invertebrates in the Grand Canyon, Arizona. Bull. Nat. Speleol. Soc. 42:53-60.

Peck, Stewart B. 1981a. The invertebrate fauna of the caves of the Uinta Mountains, northeastern Utah. Great Basin Nat. 41:207-212.

Peck, Stewart B. 1981b. The geological, geographical, and environmental setting of cave faunal evolution. Proc. Eighth Int. Cong. Speleol., Bowling Green, Ky. 2:501-502.

Peck, Stewart B., and J. J. Lewis. 1978. Zoogeography and evolution of the subterranean invertebrate faunas of Illinois and southeastern Missouri. Bull. Nat. Speleol. Soc. 40:39-63.

Peck, Stewart B., and B. L. Richardson. 1976. Feeding ecology of the salamander *Eurycea lucifuga* in the entrance, twilight, and dark zones of caves. Ann. Spéléol. 31:175-182.

Peck, Stewart B., and D. R. Russell. 1976. Life history of the fungus gnat *Macrocera nobilis* in American caves (Diptera: Mycetophilidae). Can. Entomol. 108:1235-1241.

Poulson, Thomas L. 1963. Cave adaptation in amblyopsid fishes. Am. Midl. Nat. 70:257-290.

Poulson, Thomas L. 1978. Community organization. Pages 41-45 *in* Cave Research Foundation 1978 Annual Report, S. G. Wells, editor. Yellow Springs, Ohio.

Poulson, Thomas L., and W. B. White. 1969. The cave environment. Science 165:971-981.

Reddell, James R. 1965. A checklist of the cave fauna of Texas. I. The Invertebrata (exclusive of Insecta). Texas J. Sci. 17:143-187.

Reddell, James R. 1981. A review of the cavernicole fauna of Mexico, Guatemala, and Belize. Texas Mem. Mus. Bull. 27:1-327.

Roewer, C. F. 1951. Über Nemastomatiden. Senckenbergiana 32:95-153.

Rouch, Raymond. 1968. Contribution à la connaissance des harpacticides hypogés (Crustaces - Copepodes). Ann. Spéléol. 23:5-167.

Ryder, J. A. 1881. List of the North American species of myriapods belonging to the family of the Lysiopetalidae, with a description of a blind form from Luray Cave, Virginia. Proc. U.S. Nat. Mus. 3:524-529.

Sbordoni, Valarrio, G. Allegrucci, A. Caccone, D. Cesaroni, M. Cobolli Sbordoni, and E. DeMatthaeis. 1981. Genetic variability and divergence in cave populations of *Troglophilus cavicola* and *T. andreinii* (Orthoptera, Rhaphidophoridae). Evolution 35:226-233.

Schram, Frederick R. 1974. Paleozoic Peracarida of North America. Fieldiana: Geol. 33:95-124.

Schram, Frederick R. 1977. Paleozoogeography of Late Paleozoic and Triassic Malacostsraca. Syst. Zool. 26:367-379.

Schultz, George A. 1970. Descriptions of new subspecies of *Ligidium elrodii* (Packard) comb. nov. with notes on other isopod crustaceans from caves in North America (Oniscoidea). Am. Midl. Nat. 84:36-45.

Schultz, George A. 1976. *Miktoniscus halophilus* Blake, *M. medcofi* (Van Name) and *M. morganensis* n. comb., reconsidered with notes on New World species of the genus (Crustacea, Isopoda, Trichoniscidae). Am. Midl. Nat. 95:28-41.

Schultz, George A. 1982. *Amerigoniscus malheurensis,* new species, from a cave in western [sic] Oregon (Crustacea: Isopoda: Trichoniscidae). Proc. Biol. Soc. Wash. 95:89-92.

Shear, William A. 1969. A synopsis of the cave millipeds of the United States, with an illustrated key to genera. Psyche 76:126-143.

Shear, William A. 1971. The milliped family Conotylidae in North America with a description of the new family Adritylidae (Diplopoda: Chordeumida). Bull. Mus. Comp. Zool. 141:55-98.

Shear, William A. 1972. Studies in the milliped order Chordeumida (Diplopoda): a revision of the family Cleidogonidae and a reclassification of the order Chordeumida in the New World. Bull. Mus. Comp. Zool. 144:151-352.

Shelley, Rowland M. 1979. A synopsis of the milliped genus *Cambala,* with a description of *C. minor* Bollman (Spirostreptida: Cambalidae). Proc. Biol. Soc. Wash. 92:551-571.

Simberloff, Daniel S. 1976. Species turnover and equilibrium biogeography. Science 194:572-578.

Simmons, Douglas D. 1975. The evolutionary ecology of *Gyrinophilus palleucus.* M.S. thesis, Univ. Florida, Gainesville.

Smetana, Aleš. 1971. Revision of the tribe Quediini of America north of Mexico (Coleoptera: Staphylinidae). Mem. Entomol. Soc. Canada 79:1-303.

Steeves, Harrison R., III. 1963a. Two new troglobitic asellids from West Virginia. Am. Midl. Nat. 70:462-465.

Steeves, Harrison R., III. 1963b. The troglobitic asellids of the United States: the *stygius* group. Am. Midl. Nat. 69:470-481.

Steeves, Harrison R., III. 1969. The origin and affinities of the troglobitic asellids of the southern Appalachians. Pages 51-65 *in* The Distributional History of the Biota of the Southern Appalachians, Part I: Invertebrates, P. C. Holt, editor. Res. Div. Monogr. 1, Virginia. Polytech. Inst., Blacksburg.

Steeves, Harrison R., III, and J. R. Holsinger. 1968. Biology of three new species of troglobitic asellids from Tennessee. Am. Midl. Nat. 80:75-83.

Stock, Jan H. 1986. Amphipoda: Gammarid grouping (Gammaridae s. str. sensu Bousfield). Pages 497-503 *in* Stygofauna Mundi, L. Botosaneanu, editor. Brill/Backhuys, Leiden, The Netherlands.

Stone, A., C. W. Sabrosky, W. W. Wirth, R. H. Foote, and J. R. Coulson. 1965. A catalogue of the Diptera of America north of Mexico. U.S. Dept. Agric., Agric. Res. Serv. Agric. Handbook No. 276, Washington.

Sugihara, George. 1981. $S=CA^z$, $z=1/4$: a reply to Connor and McCoy. Am. Nat. 117:790-793.

Uéno, Shun-Ichi. 1977. The biospeleological importance of non-calcareous caves. Proc. Seventh Int. Cong. Speleol., Sheffield, England, pp. 407-408.

Valentine, J. Manson. 1931. New cavernicole Carabidae of the subfamily Trechinae Jeannel. J. Elisha Mitchell Sci. Soc. 46:247-258.

Valentine, J. Manson. 1932. A classification of the genus *Pseudanophthalmus* Jeannel (fam. Carabidae) with descriptions of new species and notes on distribution. J. Elisha Mitchell Sci. Soc. 53:93-100.

Valentine, J. Manson. 1945. Speciation and raciation in *Pseudanophthalmus* (cavernicolous Carabidae). Trans. Conn. Acad. Arts Sci. 36:631-672.

Valentine, J. Manson. 1948. New anophthalmid beetles from the Appalachian region. Geol. Survey Ala. Mus. Pap. 27:1-20.

Vandel, Albert. 1950. Campagne spéléologique de Bolivar et R. Jeannel dans l'Amérique du Nord (1928). Isopodes terrestres recueillis par C. Bolivar et R. Jeannel (1928) et le Dr. Henrot (1946). Arch. Zool. Exp. Gen. 87:183-210.

Vandel, Albert. 1953. A new terrestrial isopod from Oregon, *Caucasonethes rothi* n. sp. Pacific Sci. 7:175-178.

Vandel, Albert. 1965a. Les Trichoniscidae cavernicoles (Isopoda terrestria; Crustacea) de l'Amérique du Nord. Ann. Spéléol. 20:347-389.

Vandel, Albert. 1965b. Biospeleology. Pergamon Press, London.

Vandel, Albert. 1977. Les espèces appartenant au genre *Amerigoniscus* Vandel, 1950 (Crustacés, Isopodes, Oniscoides). Bull. Soc. Hist. Nat. Toulouse 113:303-310.

Wiley, E. O. 1981. Phylogenetics. John Wiley and Sons, New York.

Williams, W. D. 1970. A revision of North American epigean species of *Asellus* (Crustacea: Isopoda). Smithsonian Contrib. Zool. 49:1-80.

Wray, David L. 1952. Some new North American Collembola. Bull. Brooklyn Entomol. Soc. 47:95-106.

Zacharda, Miloslav. 1980. Soil mites of the family Rhagidiidae (Actinedida: Eupodoidea). Morphology, systematics, and ecology. Acta Univ. Carolinae Biologica (1978):489-785.

Zacharda, Miloslav. 1985. New Rhagidiidae (Arcarina: Prostigmata) from caves of the U.S.A. Věst. Čs. Společ. Zool. 49:67-80.

Zacharda, Miloslav, and W. R. Elliott. 1981. Holarctic cave mites of the family Rhagidiidae (Actinedida: Eupodoidea). Proc. Eighth Int. Congr. Speleol., Bowling Green, Ky. 2:604-607.

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NEW EDITOR

Frank J. Radovsky, Curator of Research and Collections at the North Carolina State Museum of Natural Sciences, has been named Editor of *Brimleyana,* effective 15 January 1988. Eloise F. Potter, who has been Acting Editor of the journal since the resignation of John E. Cooper, will continue in that capacity through the publication of *Brimleyana* No. 15 and will serve as Managing Editor under Dr. Radovsky.

During the transition period, Radovsky will conclude his editorship of the *Journal of Medical Entomology,* which is published by the Entomological Society of America. In December 1987 he was named to a 5-year term on the Editorial Board of that journal. He has served as an Associate Editor of the *Annual Review of Entomology* for 10 years, and he was recently appointed to another 5-year term. Radovsky is on the Executive Committee of the Acarological Society of America, and he formerly served on the Board of Directors of the Association of Systematics Collections (1982-1985) and as Executive Secretary of the International Congress of Acarology (1971-1978).

Prior to coming to the North Carolina State Museum of Natural Sciences, Radovsky was on the staff of the Bishop Museum in Honolulu, Hawaii (1969-1986), where he was Assistant Director (1977-1985) and holder of the L. A. Bishop Distinguished Chair of Zoology (1984-1986). From 1986 to 1987, he was Visiting Professor of Entomology at Oregon State University, Corvallis.

Radovsky received an A.B. degree in Zoology from the University of Colorado, Boulder, and M.S. and Ph.D. degrees in Parasitology from the University of California, Berkeley. His current research interests include the systematics and ecology of mites, ticks, and fleas.

DATE OF MAILING

Brimleyana No. 13 was mailed on 16 July 1987.

ENDANGERED, THREATENED, AND RARE FAUNA OF NORTH CAROLINA
PART I.
A RE-EVALUATION OF THE MAMMALS
Edited by Mary Kay Clark

This book is a report prepared by a committee appointed in 1985 by the North Carolina State Museum of Natural Sciences to re-evaluate the list of mammals presented in *Endangered and Threatened Plants and Animals of North Carolina* (John E. Cooper, Sarah S. Robinson, and John B. Funderburg, editors. N.C. State Mus. Nat. Hist., Raleigh, 1977), which is now out of print. Committee members were Mary Kay Clark, David A. Adams, William F. Adams, Carl W. Betsill, John B. Funderburg, Roger A. Powell, Wm. David Webster, and Peter D. Weigl. The report treats 21 species listed in the following status categories: Endangered (5), Threatened (1), Vulnerable (6), and Undetermined (9). Most species accounts discuss the animal's physical characteristics, range, habitat, life history and ecology, special significance, and status (including the rationale for the evaluation and recommendations for protection) and provide a range map and an illustration of the animal's external characters. Ruth Brunstetter and Renaldo Kuhler illustrated the book. An introductory section contributed by Ms. Clark discusses the changes in status that occurred in the decade between 1975 and 1985. It also mentions efforts to protect marine mammals and includes a checklist of the cetaceans known from North Carolina.

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