



Speciation in Cave Faunas

Thomas C. Barr, Jr.; John R. Holsinger

Annual Review of Ecology and Systematics, Vol. 16. (1985), pp. 313-337.

Stable URL:

<http://links.jstor.org/sici?sici=0066-4162%281985%2916%3C313%3ASICF%3E2.0.CO%3B2-K>

Annual Review of Ecology and Systematics is currently published by Annual Reviews.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/annrevs.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

SPECIATION IN CAVE FAUNAS

Thomas C. Barr, Jr.

School of Biological Sciences, University of Kentucky, Lexington, Kentucky 40506

John R. Holsinger

Department of Biological Sciences, Old Dominion University, Norfolk, Virginia 23508

INTRODUCTION

Speciation in obligate cave faunas typically follows patterns reminiscent of faunas of other discontinuous habitats, such as islands, mountaintops, or desert springs (6, 95). Where cave systems are separated by frequent extrinsic barriers, as in the Appalachian Valley and Ridge province (i.e. the Appalachian Valley) of the eastern United States, many endemic species with small geographic ranges may occur (13, 74), but in terranes with extensive exposures of undisturbed cavernous limestones, as in the Mississippian plateaus farther west, fewer and more widely ranging cave species exist per unit area of exposed karst (4, 6).

Cave speciation studies have not yet been integrated with the growing body of theory of island biogeography (92, 137), in part because progress in taxonomy of cave species has traditionally lagged behind that of most island species, but also because the degree to which various caves and cave systems are isolated from each other has not always been clear (18, 48, 49, 51, 52). Other factors to be considered in comparing caves with islands include (a) dependence of cave communities on allochthonous, epigeal food sources (20); (b) dispersal of many aquatic and some small, terrestrial obligate cavernicoles widely through subterranean spaces in nonlimestone regions; and (c) separation (or not) of caves by extrinsic barriers to gene flow (and possible circularity of reasoning in determining this) (4, 6, 10, 13).

The physical environment in both temperate zone and tropical caves and its implications for cave speciation have been reasonably well described (6, 20, 77). Remote from entrances, deep portions of caves are dark, with fairly

constant temperature, relative humidity often near saturation, and an extremely low rate of evaporation (20). Seasonal climatic changes, however—primarily through influx of colder, drier winter air or flooding from surface streams that flow underground into caves—may be profound (20, 118). Some tropical caves in regions of wide daily temperature fluctuations may experience the “winter effect” every 24 hours (77).

Most caves are in limestone, but faunistically significant caves in gypsum karst or lava tubes are also known (77, 115, 118). Distribution of cave regions in the conterminous United States is shown in Figure 1. The most important regions in terms of major faunas of cave-obligate species are: (a) the Appalachian Valley (AV); (b) the Interior Low Plateaus, which include the western (MP-I) and eastern (MP-II) Mississippian plateaus on either side of the Cincinnati arch, as well as the Bluegrass and Central Basin regions along the axis of the arch; (c) the Greenbrier Valley of West Virginia (MP-III), (d) the Ozark Plateaus; (e) the lime sink karst of the Florida highlands; (f) the Edwards Plateau; and (g) a series of disjunct caves in central California. Other cave areas of lesser biological interest are also indicated in Figure 1.

Classification of Cavernicoles

Any animal living in a cave can be defined as a cavernicole. *Troglobites*, which are obligate cavernicoles, are the focus of this review. Many troglobites are descendants of *troglophiles*, facultative cave inhabitants able to live in or outside caves (6). *Trogloxenes* are regular cave inhabitants that return periodically to the surface for food; bats and cave-cricket are examples (in some European usage troglloxenes are equivalent to accidentals; see discussion in 6). Some cavernicoles may simultaneously be edaphobites—obligate inhabitants of deep soil—or phreatobites—obligate inhabitants of groundwater systems both in calcareous and noncalcareous terranes (6). It is now common practice, especially among European biologists, to use the term *stygobiont* for obligate subterranean species that inhabit one or more kinds of hypogean biotopes saturated with groundwater (74). Because many groups of troglobites include species with widely varying degrees of morphological modifications associated with cave life, Christiansen (39) suggested the term *trogloform* for the more highly modified forms. Problems with terms in cavernicole classification arise primarily through a shift in emphasis from ecological (troglobite) to evolutionary (trogloform) status, or because a “cave” is a comparatively large subterranean opening accessible to man; most troglobites are small and not necessarily confined to large caves penetrable by man (6).

Taxonomic Distribution of Troglobites

Major taxonomic groups of animals with numerous troglobitic species include turbellarians, gastropods, millipedes, spiders, pseudoscorpions, opilionids,

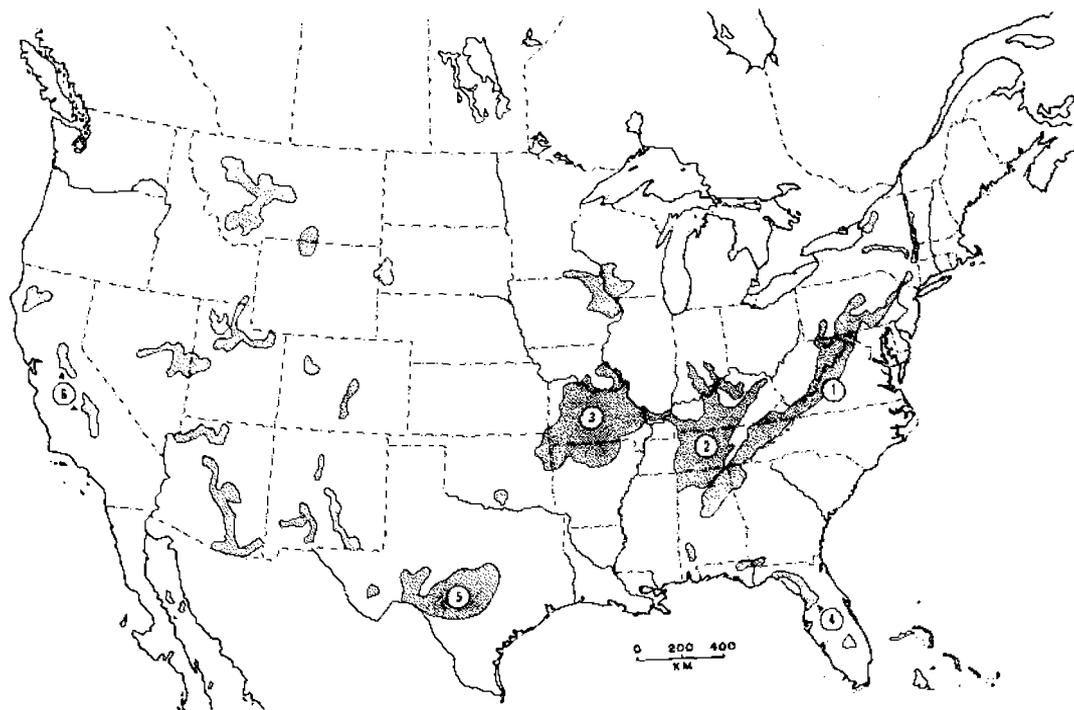


Figure 1 Map of the conterminous United States shows distribution of major limestone cave areas. Regions with high diversity of troglobites are indicated as follows: 1. Appalachian Valley and eastern margin of the Allegheny Plateau; 2. Interior Low Plateaus including Mississippian plateaus, Bluegrass, and Central Basin; 3. Ozark Plateaus; 4. Florida lime sink region; 5. Edwards Plateau; 6. Sierra Nevada. Lava cave areas not shown; the most important ones are in Hawaii, Washington, Oregon, California, and Idaho. In North America outside the United States numerous limestone caves occur in central and southern Mexico and the West Indies.

isopods, amphipods, decapods, collembolans, diplurans, beetles (Carabidae, Leiodidae, Pselaphidae), fishes, and salamanders (6, 124, 136). Preadaptation of ancestors of troglobites to microhabitats such as cool, moist, forest floor humus, dark swamps, or mouths of springs has been emphasized by many authors (see 6 and cited references). The relict status of many troglobites and their preponderance in temperate zone caves has similarly received much attention (6 and cited references; also 81, 136), but tropical and subtropical caves—particularly in the Nearctic region—are yielding more and more newly discovered troglobites (14, 15, 77, 124). Our discussion of speciation patterns in different taxonomic groups is necessarily eclectic; it focuses especially on better studied groups with large numbers of species and emphasizes the eastern North American fauna. Although we have not treated the rich Mexican cave fauna in depth, we draw attention to the extremely valuable and detailed review by Reddell (124). Different examples and different perspectives on cave speciation are offered in the recent review by Sbordoni (125).

ISOLATION AND DISPERSAL

There are two classes of extrinsic barriers to dispersal of terrestrial troglobites: fluvial barriers and stratigraphic barriers (16). Large rivers are almost always barriers to terrestrial troglobites but not to aquatic ones. Troglobitic carabid beetles can apparently maintain gene flow across smaller streams by means of flooding, flotation, and reentry processes (16, 21). A close correlation exists between the barrier or nonbarrier status of a smaller stream in a karst region and the stage of its fluviomorphic cycle as measured by meander frequency. In the eastern United States (MP-I, MP-II) the stream becomes an effective barrier when its meander frequency falls below approximately 1.0/km. Beetles flooded out of a cave on one side of a stream are less likely to succeed in entering cave systems on the other side if there are infrequent meanders and thus fewer limestone bluffs on the outside of the meanders with cracks and crevices leading into cave systems (16).

Stratigraphic barriers exist when noncaverniferous strata (shales, sandstones) are interposed between cavernous (limestone) beds. These barriers may occur along the margins of the Interior Low Plateaus but are far more frequent in the heavily folded and faulted Appalachian Valley (AV) (2, 4, 6, 13, 16, 74). The most extensive areas of continuous karst without extrinsic barriers are in the two Mississippian plateaus (MP-I, MP-II) that flank the Cincinnati arch, and in a much smaller but similar area along the Greenbrier River valley in eastern West Virginia (MP-III). More diverse communities of troglobites have evolved in MP areas than in the AV, a phenomenon attributed to greater dispersal potential for troglobites in MP limestones (4, 6, 16). Different troglobitic species that colonized different caves at different times in the past

can eventually come together through subterranean dispersal into the same cave systems (4, 74). Secular fluctuations in populations of predators such as trechine carabids are less pronounced where the troglobite community offers alternative prey species; larger species are more frequent in MP areas because the more diverse community offers a larger set of mosaic elements from which a predator may "choose" in establishing its niche (4, 79).

Stratigraphic barriers that are highly significant in dispersal of certain terrestrial troglobites (e.g. beetles) may have little effect on terrestrial arthropods that can disperse through "microcaverns"—interstitial spaces around roots of trees, between rocks in the beds of wet-weather streamlets, or between rocks in soil at the bedrock-mantle interface (*milieu superficiel*). Juberthie and his colleagues (83) have trapped a number of terrestrial troglobites from the *milieu superficiel* in fractured, noncalcareous rocks in France, but the significance of this dispersal route in caves of the eastern United States has not been demonstrated (16).

The wide distributions of many aquatic stygobionts and the occurrence of several species in wells, seeps, or springs in noncalcareous terranes is a clear indication that such species are rarely limited by stratigraphic barriers that are effective against dispersal of terrestrial troglobites. As a rule, fluvial barriers would be expected to have a minimal effect on aquatic troglobites. However, the blind cavefish *Amblyopsis spelaea* does not occur north of East Fork of White River near Bedford, Indiana, an extrinsic barrier that also divides mutually exclusive ranges of several trechine beetles (16). Troglobitic crayfishes of the genus *Orconectes* are confined to MP areas, with the exception of two Central Basin populations; and the ranges of *O. inermis* and *O. pellucidus* (63) are separated by the Hart County Ridge, a stratigraphic barrier.

PATTERNS OF TROGLOBITE SPECIATION

Because aquatic troglobites are typically not confined to isolated cave systems in contiguous karst, as many terrestrial troglobites are, we consider speciation of terrestrial and aquatic troglobites separately. While solutional networks below the water table may be continuous over wide areas, cavities above the water table are subject to collapse, silt deposition, and blockage by sinkhole feed, and thus the cavities are discontinuous.

Speciation in Terrestrial Troglobites

In numbers of species trechine carabid beetles are the most abundant and most widely represented group of terrestrial troglobites in the eastern United States and are also abundant in caves of France, Spain, Italy, Yugoslavia, Japan, Korea, New Zealand, and northeastern Mexico (14, 16, 80). In the eastern United States approximately 240 species are assigned to *Pseudanopthalmus*

and one to five species each to *Neaphaenops*, *Nelsonites*, *Ameroduvallius*, *Darlingtonia*, and *Xenotrechus*. *Neaphaenops* and *Nelsonites* are paraphyletic to *Pseudanophthalmus* (1–3, 11, 12, 13, 16, 17, 19); *Darlingtonia* and *Ameroduvallius* are closely related to each other but not to other North American trechine genera (7, 135); and *Xenotrechus* is allied to the eastern European *Chaetoduvallius* by nine synapomorphic characters (19). The *Pseudanophthalmus* group of genera belongs to the “*Trechoblemus* series” (80, 82), but *Trechoblemus* is a predominantly Eurasian genus of winged, oculate trechines with a single species known from North America, *T. westcotti* in the Willamette valley of Oregon (7). No obvious ancestors of the cave genera exist in eastern North America, with the possible exception of *Lasiotrechus discus*, which is believed to have been introduced (7, 80). Mexican cave trechines, on the other hand, are derived from the primarily epigeal genus *Paratrechus*, which is so similar that assignment of certain cave species to *Mexaphaenops*, *Chiapadytes*, or *Paratrechus* is arbitrary. Nevertheless, pigmented, oculate species of *Paratrechus* do not occur in northeastern Mexico where troglobitic species of *Mexaphaenops/Paratrechus* are prevalent in the caves; the distributions of troglobitic and epigeal species of the lineage are thus mutually exclusive (14).

Such distribution patterns imply that troglobitic species are relicts of formerly widespread epigeal faunas (81). In western Europe and eastern Asia many species of edaphobitic trechines exist with rudimentary eyes and reduced melanin pigment (80), but in the United States only one edaphobitic trechine is known, *Pseudanophthalmus sylvaticus*, from the mountains of eastern West Virginia (5); it is closely similar to species of the *grandis* group in nearby caves of MP-III.

The model of cave trechine speciation developed by Barr (4–6, 13, 16) relies heavily on the founder principle and the genetic revolution (95). Two stages are envisioned—an initial one in which epigeal ancestors became edaphobites, and a second stage in which these edaphobites became widespread in eastern forests during glacial maxima, then were progressively restricted to caves with the onset of warmer, drier interglacials. Distributions of closely similar allopatric species suggest that several regional ancestors may have independently colonized a number of isolated cave systems in which descendant populations diverged (2, 13, 16). However, the often minimal morphological divergence between such isolates and the indexes of genetic-similarity between them (84; T. C. Kane & T. C. Barr, in preparation) indicate that in several cases something less than a “genetic revolution” characterized their divergence (16, 17). The existence of isolating mechanisms between morphologically very similar species is well established in MP karst regions by frequent sympatry and parapatry.

The gradual warming and drying of regional climates during glacial retreat presumably led to a similarly gradual isolation of trechine populations in

cooler, wetter cave systems. Although divergence of these populations, once isolated by inimical epigeal climate (4), might appear rapid on a geological time scale (see 120), it was probably no more rapid than the divergence of Hawaiian *Drosophila* species studied by Throckmorton (134). About 14 isolates of the Cumberland Plateau endemic *Trechus cumberlandus* are known from Kentucky and Tennessee; the species is closely similar to 5 mountain species around the margins of the Asheville basin, North Carolina, and is probably a Wisconsinan relict (11). These isolates are at present confined to deep, moist, wooded ravines ("coves"), sinkholes, and caves, possibly repeating the restriction of range postulated for ancestors of cave trechine in the same area (16). At least one case of cave trechine speciation by the dumbbell model (31) was probably initiated by the early Kansan development of the "new" Ohio River (123), dividing an early Pleistocene population that then gave rise to the sister species *P. tenuis* (Indiana) and *P. barberi* (Kentucky) in MP-I (16, 82). Similarly, the new Ohio may have split an ancestral population that gave rise to the descendant sister species *P. barri* (Indiana) and *P. troglodytes* (Kentucky) near Louisville (89). Dispersal and maintenance of gene flow across a youthful stream with a high meander frequency may in time be succeeded by divergence as the stream matures and becomes a barrier; the Baren River near Bowling Green, Kentucky, divides the ranges of the closely similar *Pseudanophthalmus menetriesi* and *P. transfluvialis* (17).

Trechines in caves in the Mississippian plateaus (MP) of Indiana, Kentucky, Tennessee, and eastern West Virginia enjoy much greater dispersal potential than species confined to caves of narrow, linear strike valleys in the Appalachian Valley (AV). In the MP areas, sympatry is much more common (to a maximum of six trechine species in the Mammoth Cave system), modal body size is greater, population densities are consistently higher (attributed to alternative prey sources in the more complex MP troglobite communities), geographic ranges are more extensive, and there are fewer species per unit area of exposed karst (4, 6, 13, 16, 74). MP species consequently offer more opportunities for study of cave speciation than do species occupying isolated AV limestone valleys or local karst islands (small patches of exposed limestone) in the interior of the Allegheny Plateau (13, 16). Higher population densities permit sampling for electrophoretic analyses in the MP but not in the AV, where no two sufficiently abundant, morphologically similar populations are known to exist. Frequent sympatry among MP species allows development of a "yardstick" of morphological difference between species (96) that can be applied to isolates in the AV or in karst islands.

Sampling of trechine populations is easier in the MP because of the high cave density and high population density there. Consider the hypothetical case of two slightly but consistently distinct morphotaxa collected from different caves 25–30 km apart. Because of high cave density found in the MPs, sufficient

geographically intermediate caves usually can be sampled to determine the interaction, if any, between these two morphotaxa. When this is done, one of five possible outcomes is realized: (a) clinal gradation, (b) hybridization, (c) parapatry, (d) sympatry, or (e) strict allopatry (both morphotaxa are absent from intermediate caves). All five outcomes have been observed in MP caves in the eastern United States, but clinal variation, hybridization, and parapatry are unknown in the AV (16). Different approaches to taxonomy of MP and AV trechines are indicated. In MP areas we must do widespread sampling to locate and observe what happens at the interface (if any) between morphotaxa, while in the AV we must pay special attention to details of geologic structure and stratigraphy, from which the existence of extrinsic barriers may be inferred; at the same time we need to employ the "yardstick" of difference developed from study of sympatric and parapatric MP species (13, 16).

Distributional patterns similar to those of eastern trechines appear in troglobitic species of the agonine carabid genus *Rhadine*. The genus is primarily western in distribution, with only 2 species known east of the Mississippi River but more than 60 in the west. All troglobites in *Rhadine* are assigned to the presumably monophyletic *subterranea* group, which includes 11 species (5 supposedly polyphyletic) in the eastern Edwards Plateau in Texas and 2 species in Nuevo Leon (8, 15). Three or four pairs of the Texas species are sympatric in certain caves, and both fluvial and stratigraphic barriers appear to be determinants of species range (8:28).

Troglobitic species of *Ptomaphagus* beetles (Leiodidae) include 1 species in the Mammoth Cave region, Kentucky; 2 allopatric species in the Central Basin in Tennessee; and 15 species from MP-II in northeast Alabama and adjacent Georgia and Tennessee (82, 116, 120). Some of the Alabama species are differentiated by quite minor morphological characters and exhibit parapatric ranges. The ranges closely approximate those of component species of the *loedingi* series of *Pseudanophthalmus*, which are endemic to the same area (T. C. Barr, unpublished). In laboratory crosses Peck (119) demonstrated a reproductive barrier between closely similar morphotaxa of *Ptomaphagus*; compared to intrapopulational crosses, the crosses between morphologically distinct populations exhibited drastic F_1 reductions in viability of larvae and longevity of adults, and the F_1 hybrids were virtually sterile.

Pselaphid beetles in North American caves include three groups of cavernicoles: (a) several species (*Batrisodes*, *Batriasymmodes*, *Bythinopsis*) lacking pronounced troglomorphic features but nevertheless known only from caves; (b) a small number of species, eyeless and with elongated appendages (*Speleobama*, *Texamaurops*, *Arianops*), that have discrete geographic ranges limited to one cave or a group of closely approximate caves; and (c) 12 minute (1.5–2.0 mm), eyeless species, each known from only one or two caves (*Speleochus*) (9, 22, 113, 114; T. C. Barr & H. R. Steeves, in preparation).

Speleobama vana (the genus is monotypic) is an exceptionally rare relict from a single Alabama cave, and *Texamaurops reddelli* (related to *Batrisesodes*) is known from a few caves in the Edwards Plateau (9, 22, 113). *Arianops*, the sole North American representative of the tribe Amauropsini, is a relict group all of whose species are edaphobites or troglobites; five species of the *cavernensis* group occur in caves of Virginia, Tennessee, and Alabama and are probably troglobites (9). Although *Batriasymmodes quisnamus* occupies a much larger range than most cave trechines (and perhaps includes several recently and independently isolated populations), the great majority of cave pselaphids have much smaller ranges than trechines; this is perhaps attributable to smaller body size and lower vagility (113, 114).

Minimal geographic ranges in both the AV and MPs are characteristic of troglobitic pseudoscorpions of the eastern United States, which include 55–60 troglobitic species assigned to 11 genera. About 75% of these belong to the Chthoniidae and the remainder to *Microcreagris* (Neobisiidae, 9–10 species) and *Chitrella* (Syarinidae, 4 species) (34, 93, 94, 100–110). Of *Kleptochthonius*, 30 troglobitic species have been described, including 9 from the AV, 7 from MP-I, 10 from MP-II, 3 from MP-III, and 1 from the Central Basin in Tennessee. Of these species, 23 are known from only one cave, 5 from two caves, and only 2 from three or more caves. Twenty-nine species are assigned to the exclusively cavernicolous subgenus *Chamberlinochthonius*; the only case of sympatry of *Kleptochthonius* species involves *K. (C.) tantalus* and *K. (s.str.) magnus* in Dry Cave, near Sewanee, Tennessee (102). However, *K. lutzi* and *Microcreagris valentinei* coexist in Cudjos Cave, Virginia (34, 94), and both *Chitrella regina* and *K. henroti* are recorded from the Higginbotham caves in MP-III (107).

Except for *K. henroti*, known from 10 MP-III caves (101, 105, 108), troglobitic pseudoscorpions of the eastern United States appear to exist in highly localized populations of low density. Distinct species may occur in different caves only a kilometer or two apart (94, 100, 108). *Kleptochthonius* species prevail in the heartland of the eastern cave region, and caves around the periphery—in Illinois, Indiana, Virginia, West Virginia, north Alabama, and adjacent Tennessee and Georgia—harbor species of *Mundochthonius* (103), *Apochthonius* (110), *Aphrastochthonius* (106), *Tyrannochthonius*, and *Microcreagris* (104). Most genus-name categories (except *Chamberlinochthonius*) include a number of noncave species, the taxonomy of which is less well-known than that of the cave species. Unlike carabid and leiodid beetles, cave pseudoscorpions have a low vagility that restricts them, like the tiny *Speleocheus* pselaphids, to very limited geographic ranges, whether or not contiguous karst offers the possibility of subterranean dispersal.

Millipedes are widely distributed in North American caves. In the east two genera best suited for detailed speciation studies are *Pseudotremia* (Cleidogoni-

dae) and *Scoterpes* (Trichopetalidae). The phylogenetic relationships and zoogeography of the two closely related families to which these genera belong were discussed in detail by Shear (126); both had a Mesozoic origin in the Mexican highlands; the trichopetalids became a boreal element in the eastern fauna, and the cleidogonids an austral element. *Pseudotremia*, the most primitive genus of cleidogonids, numbers 35 described species in the Appalachian region, including 16 troglobites (10 known only from one cave each), 15 troglophiles, and only 4 species not yet known from caves (65, 126). Probably a number of undescribed species exist—immatures occur widely in cave systems from which named species are not recorded. Shear (126) suggests that the exclusively troglobitic genus *Scoterpes*, in need of taxonomic study, may contain as many as 30 species from caves of the Interior Low Plateaus and Ozark Plateaus. Compared with cave trechines, *Pseudotremia* species seem to have much smaller geographic ranges; only *P. indianae* (MP-I), *P. acheron* (MP-II), and *P. fulgida* (MP-III) have ranges of roughly comparable extent. Smaller millipede ranges may be at least in part an artifact of insufficient collecting. No two congeneric species of millipede troglobites are known to be sympatric in eastern caves; however, species of *Scoterpes* and *Pseudotremia* coexist, and the troglobite *P. fulgida* and the troglophile *P. hobbsi* occur in some of the same MP-III caves. Comparisons of range size and dispersal ability in *Scoterpes* species are not possible until the taxonomy becomes much better known.

Spiders of the family Nesticidae include both troglophilic and troglobitic species (59a). *Nesticus* species are concentrated in three areas—the Appalachian region, California, and Mexico. Appalachian species include widely ranging troglophiles such as *N. carteri* (KY, TN, WV, VA), highly troglomorphic species (*N. stygius*, TN; *N. barri*, TN/AL), and species that are apparent troglobites but less troglomorphic than *N. stygius* or *N. barri* (*N. holsingeri*, VA). Existence of related species (*N. crosbyi*, *N. bishopi*, both NC) in mountain microhabitats suggests preadaptation of the lineage to the cool, moist microhabitats of caves. *Eidmannella* includes 6 species, of which the troglophilic *E. pallida* ranges from Massachusetts, Wisconsin, and Oregon to Panama and the West Indies. In central Texas, however, there are 5 troglobitic species of *Eidmannella*, apparently descendants of a single ancestor that colonized separate caves as a troglophile; regional climatic drying led to extinction of epigeal populations, after which cave populations were extrinsically isolated and diverged (59a).

In the eastern United States there are no troglobitic cave-cricket (Rhabdophoridae), but the five troglaxene species of the *subterraneus* group of *Hadenocetus* are restricted to areas of high cave density (10) found only in the MPs; these have ranges that resemble those of widely distributed troglobites. All five species are highly significant in MP-I and MP-II cave food webs,

contributing guano for detritivores and eggs for carabid beetle predators (10, 16, 20, 78). *Hadenoeus subterraneus* is confined to part of MP-I in Kentucky, and the other four species of the *subterraneus* group are parapatric in MP-II from northeast Kentucky through Tennessee to northeast Alabama (78). Discontinuous MP-II karst in northeast Kentucky has led to geographic parthenogenesis in *H. cumberlandicus* (60, 78, 90). Sexual and parthenogenetic populations are sharply separated by the Red River valley in Powell County, Kentucky, where the two sorts of populations are 12 km apart; all populations to the northeast along the edge of the Cumberland Plateau are parthenogenetic, while all populations to the southwest are bisexual (T. C. Barr, unpublished).

The extent to which some terrestrial troglobites disperse through "microcaverns" in the eastern United States has not been fully investigated. Certainly some of the species of *Litocampa* (Diplura: Campodeidae) studied by Ferguson (57) have geographic distributions transcending the boundaries of contiguous karst. Four troglotitic linyphiid spiders—*Phanetta subterranea*, *Porhomma cavernicolum*, *Anthrobia monmouthia*, and *Bathyphantes weyeri*—are quite widely distributed in the eastern United States, yet they would appear to have very low vagility because of their minute size (74). The ubiquitous *P. subterranea* is known from every cave region in the east, a distribution suggesting two explanations: (a) it is very successful at penetrating microcaverns, or (b) it consists of many local populations that represent independent colonizations of a widely distributed ancestor now extinct at the surface. If the first explanation is true, then it is surprising that the species has not been encountered in edaphobitic microhabitats. If the second is true, then *P. subterranea* must be a quite recent cave colonist in the early stage of becoming a troglobite. *Anthrobia monmouthia* exists in at least four disjunct populations in MP-I (Kentucky), the Central Basin (Tennessee), MP-II (Tennessee), and AV/MP-III (Virginia and West Virginia). The other two linyphiids cited have similarly puzzling distributions exhibiting marked disjunction. Although an explanation of the distribution in campodeids and linyphiids must await detailed intraspecific analysis of variation, Christiansen & Culver (43, 44) have produced strong evidence that, for a similar situation in cave collembolans, favors alternative *b*.

The collembolan fauna of eastern caves has been well described by Christiansen (35–37, 40, 42), who demonstrated convergence and parallelism in cave-dependent characters in the Entomobryinae (38–41). Elongation of the unguis and empodial appendage is a troglomorphic character that enables collembolans to walk on the surface tension film of cave pools instead of being trapped by it. Other troglomorphic features include elongated antennae and legs, a flattened outermost antennal segment, a "humped" thorax from larger furcular muscles, and increased body size. Highly troglomorphic collembolans inhabit open spaces in cave chambers, instead of small interstices of ancestral microhabitats in leaf litter and humus, and so more readily escape predation by

trechines or pseudoscorpions with their longer jumps. The more highly troglomorphic species are clustered in the heartland of eastern caves, as are the majority of trechine, *Kleptochthonius*, and *Pseudotremia* species. Some of these species exhibit comparatively discrete ranges (in contrast to more widely distributed cave collembolans with fewer troglomorphic modifications)—*Pseudosinella gisini* (MP-III), *P. spinosa* (MP-II and Central Basin), *P. christianseni* (MP-II), some species of *Sinella*, and *Arrhopalites altus* (36, 37, 42). However, most of the species cited have larger ranges than trechine species, and some include remote, disjunct populations.

Pseudosinella hirsuta occurs over much of MP-I, MP-II, and the Central Basin; a few populations are also known from caves of Pine Mountain (eastern Kentucky and Tennessee) and part of the AV. It is moderately troglomorphic but highly variable geographically. Christiansen & Culver (43) argued that *hirsuta* is a morphospecies consisting of a complex of genetically discontinuous populations that evolved *hirsuta* characteristics independently in at least four different cave systems. Genetic discontinuity was inferred from morphological evidence, and dispersal in *hirsuta* was thought to occur primarily via underground routes. However, *P. hirsuta* has more recently been found in a cave in Pine Mountain, Tennessee, as well as under rocks in a wooded ravine on the sandstone-capped summit of the mountain; microcavern dispersal is at least possible in *hirsuta* whether it occurs frequently or not (T. C. Barr, unpublished). Christiansen & Culver (43) contended that the biological species concept was inapplicable to *P. hirsuta*; the entire complex is the "functional evolutionary unit."

Extending their analysis to *Pseudosinella violenta*, a troglophile, the same authors (44) examined surface and cave populations from central Texas, concluding that surface populations reflect dispersal from both northern and southern parts of the range of this widespread midwestern species. The surface populations have invaded Texas caves several times. Surface and cave populations are "presently quite distinct over most of their region of overlap," and secondary contact between the two has sometimes led to character displacement. The scenario for cave speciation in collembolans may thus begin with multiple invasions of a troglophile similar to *P. violenta*, followed by gradual reduction of gene flow between cave and epigeal populations. After extinction of epigeal populations occurs, the cave isolates acquire troglomorphic features at different rates and may disperse outward either through solutional openings in the limestone or via microcaverns; *P. hirsuta* perhaps represents this stage. In the final stage, further cave adaptation takes place, which leads to highly advanced troglomorphs with smaller, discrete geographic ranges.

Speciation in Aquatic Troglobites

The taxonomically diverse, widespread stygobiont amphipod fauna provides excellent examples of speciation in small troglobitic crustaceans. Both the

Crangonyctidae and Hadziidae are well represented in North America but probably colonized hypogean environments at different times under markedly different conditions. Crangonyctids are exclusively freshwater organisms without close taxonomic relationship to any known marine forms. They are believed to represent a very old group that originated in Laurasia prior to the separation of North America and Eurasia in the Jurassic period (69, 72, 73). Three genera of this family—*Crangonyx*, *Stygobromus*, and *Bactrurus*—contain troglobitic North American species; the first has both epigean and hypogean species, and the other two are composed exclusively of stygobionts.

To date (literature search concluded February, 1985) 99 species of *Stygobromus* have been described (97 from North America and 2 from Eurasia), and at least 50 more species have been recognized provisionally (73; J. R. Holsinger, in preparation). The genus is widespread, but the majority of its species are from eastern caves (66, 67, 69, 73). Of 118 species (25 undescribed), 83 are found primarily in caves (karst species) and 35 are known only from groundwater habitats exclusive of caves (nonkarst species) (69; J. R. Holsinger, in preparation). Although 20 of the karst species are also recorded from noncave habitats, they are more frequently found in caves. In a detailed analysis of *Stygobromus* from Appalachian caves, it was determined that approximately 21 species were collected exclusively from pools in inactive vadose zones, and 9 species were collected primarily from streams in active vadose zones. Several species occurred in both pools and streams, and one came from a deep phreatic lake (69). However, cave pools in the inactive vadose zone are rarely primary habitats for organisms (50) and are apparently populated at random by amphipods that move into them via drips and seeps from small tubes and crevices (51, 69). These observations led to the conclusion that caves originally were and now continue to be invaded and colonized by a pervasive stygobiont amphipod fauna that enters caves from surrounding groundwater habitats (69). The same observations also suggest that a moderately high degree of dispersal takes place within caves, between caves, and between karst areas through shallow groundwaters in nonkarst terranes.

Because epigean species of *Stygobromus* are unknown, and there is no trace of an ancestral fauna living in surface waters, it has been suggested that present-day karst species were derived from stygobiont ancestors already established in the hypogean realm (74). This theory assumes that *Stygobromus* is a very old stygobiont group. Evidence in its favor is the broad geographic distribution of the genus, combined with its ecological and taxonomic diversity (73), and the occurrence of some species in caves far north of the southern limits of glaciation, where they presumably survived one or more Pleistocene glacial periods in deep groundwater refugia (70, 71, 73).

Speciation in *Stygobromus* is probably the result in part of the dispersal of organisms from one kind of groundwater habitat to another, followed by isolation of founder populations when previously occupied habitats were de-

stroyed by lowering water tables, erosion, siltation, or other geomorphic processes. In karst areas where new generations of caves are actively forming beneath old ones, vertical migration of amphipods probably occurs in response to availability of newly developing habitats. In all major karst regions in the eastern United States, there are one or two widespread species of *Stygobromus* and several closely related species with much smaller ranges. The species with more limited distributions typically occur just beyond the outer margins of the ranges of the widespread species. This sort of pattern, seen at least twice in the Appalachians (*emarginatus* and allies; *mackini* and allies), once in the Interior Low Plateaus (*exilis* and allies), and once in the Ozarks (*onondagaensis* and allies), suggests that those species with narrowly circumscribed ranges have arisen as peripheral isolates by allopatric speciation.

Crangonyx occurs in both North America and Europe, but 18 of 21 described species are found in North America (68, 72). In the eastern United States 5 species are troglobitic and inhabit caves primarily in karst areas of the Appalachians, the Interior Low Plateaus, and the lime sink region of Florida (72, 73). Of other species, 2 are troglaphiles, 1 in Florida and 1 in the Ozarks. *Crangonyx* has probably been represented in subterranean waters for a much shorter time than has *Stygobromus*. Troglobitic species of *Crangonyx* appear to be less specialized morphologically for a subterranean existence than those of *Stygobromus*; with the exception of the rather aberrant *C. hobbsi* from Florida, they are apparently closely allied to epigean congeners (73). This close taxonomic relationship and the comparatively broad ranges of troglobitic species, especially *antennatus* in southwest Virginia and east Tennessee and *packardi* in southern Indiana and central Kentucky, indicate relatively recent invasions of subterranean waters in karst areas by widespread epigean ancestors. Further evidence of the probable "youth" of the troglobites is the presence of vestigial eyes in some populations of at least 3 of the 5 species (74).

The biology of one troglobitic *Crangonyx* species has been studied rather extensively, and the results provide some insight into incipient microevolutionary processes that may be operating in small, semi-isolated cave populations. *Crangonyx antennatus* is common in both mud-bottom drip pools and small gravel-bottom streams in caves of the Powell Valley in southwest Virginia (74). In a series of studies, small but consistent differences in behavior, ecology, and morphology were found to exist between populations living in these two habitats (53–55). Six populations from the same area, three from pools and three from streams, were analyzed electrophoretically; they revealed a high degree of polymorphism among populations and a tendency for stream and pool populations to cluster distinct from one another (51, 56). Powell River separates the most distinct population from the other five. Although other observations suggest cave-to-cave dispersal in this species (69, 74), the work of Dickson and his colleagues indicates at least some degree of habitat selection by *C. antennatus* and suggests its differentiation into microgeographic races (54).

Hadziid amphipods (73) include 16 genera with a circumtropical distribution. The weckeliid group, a distinct subset of 9 stygobiont genera from southern North America, is of particular zoogeographic interest because it is composed of species evolved from marine/brackish water ancestors. In northern Mexico and south-central Texas, stranding of preadapted ancestral weckeliids in new freshwater habitats occurred when shallow marine waters receded from these areas in Late Cretaceous and Eocene times. High generic diversity of weckeliids (4 monotypic genera) in the Edwards aquifer may be the result of both lineage diversification prior to stranding and subsequent divergence (75). The 2 monotypic genera from Cuban and Puerto Rican caves probably originated during emergence of these islands in the late Oligocene (western Cuba) and middle or late Miocene (Puerto Rico). One genus (2 species) of weckeliids from caves of the Yucatan peninsula probably originated during the late Tertiary.

The 12 stygobiont species of *Metaniphargus* in the West Indies are hypothesized to have originated from marine ancestors by stranding during emergence of Antillean islands in the middle Tertiary (73, 127). With 2 troglobitic species from anchialine caves in the Bahamas and Turks and Caicos Islands, *Bahadzia* may have originated from a preadapted marine ancestor by direct dispersal rather than through stranding, because the Bahamas chain has a geological history of submergence rather than emergence. Isolation of these 2 species in caves on separate islands probably resulted from development of deep marine channels at several places in the Bahamas (76).

Troglobitic isopods in the freshwater Asellidae and predominantly marine Cirolanidae also show contrasting patterns of distribution and speciation. Asellids are an ancient Holarctic group probably already established in freshwater prior to breakup of Laurasia (24, 74, 91). Five genera and 88 species are recognized from North America, 58 of which are found in subterranean waters (91). *Caecidotea*, the largest genus, contains 69 described species, 53 of which are stygobionts (91). Although the hypogean species are widespread in collective distribution, the majority are from caves in eastern United States, especially the Appalachians, Interior Low Plateaus, and Ozarks. Lewis (91) placed the troglobites in 6 species groups, only 1 of which contains epigeal species; this suggests that epigeal ancestors of many troglobites are now extinct. *Caecidotea* includes both very localized and widely distributed species. Lewis (91) attributed the wider ranges of species in the Interior Low Plateaus and Ozarks to an earlier, widespread distribution of epigeal ancestors; subsequent dispersal through subterranean waters was either secondary or unimportant. Alternatively, dispersal through shallow groundwater habitats in noncalcareous rocks between karst areas could account for wide distributions (74).

Only a small number of cirolanid isopods live in fresh water, and nearly all of them are troglobites; North American stygobiont cirolanids include 12 genera and 23 species, the majority of which are reported from cave lakes. Species

from Bermuda, the Bahamas, and Aruba occur in anchialine waters; the remainder inhabit freshwater habitats in Texas, Virginia, Mexico, and several West Indian islands (26–28, 74, 112). Except for species in the Bahamas, probably derived from marine ancestors by direct dispersal, most cirolanids appear to have originated by stranding during regression of marine embayments or through uplifting (25, 26, 32, 45, 46, 111, 112, 136). The origin of *Antrolana lira*, known from a single cave system in Virginia, is more difficult to explain; it occurs far inland from any marine embayment since the Paleozoic (26). Holsinger & Culver (74) advanced the hypothesis that it is an old relict that migrated inland following a marine origin some 100 km to the east in a Late Cretaceous or early Tertiary embayment of the Atlantic coastal plain.

Troglobitic planarians in the United States include 1 or a few species of *Phagocata*, but most belong to the Kenkiidae, with 17 species in *Sphalloplana* and 4 in *Kenkia* (85, 87, 88). All kenkiids are stygobionts, 13 from caves, 4 from caves, springs, and/or wells, and 4 from groundwater habitats outside cave areas (85–88). Cave species are known from the Appalachians, Interior Low Plateaus, Ozarks, Edwards Plateau, Sierra Nevada, and a single lava tube cave in Oregon. Ranges of most species are small and rather local, but *Sphalloplana chandleri* is known from disjunct populations in springs in southern Indiana and central Tennessee and a cave in southwest Virginia (87). Separate invasions of groundwater habitats by widespread epigeic ancestors is the most likely speciation pattern in troglobitic planarians, and the wide range of *S. chandleri* and its occurrence in both springs and a cave may illustrate an early stage in the range fragmentation of putative ancestors of local endemics, which led to allopatric isolates.

Most troglobitic shrimps in North America belong to the Atyidae and the Palaemonidae, the origin and geographic distribution of which were discussed in detail by Hobbs et al (64) and Reddell (124). *Palaemonias ganteri* (Mammoth Cave system) and *P. alabamae* (north Alabama) are local, sister species of cave atyids found about 280 km apart. They are probably thermophilic relicts derived by independent cave invasions of a common ancestor (6, 64). *Palaemonetes cummingsi* (north Florida) and *P. antrorum* and *P. holthuisi* (Edwards Plateau) are survivors of eastern and western segments, respectively, of an epigeic ancestral stock divided by an epeiric sea in the Late Cretaceous and early Tertiary periods. Pre-Pleistocene colonizations of subterranean habitats by both stocks were postulated by Strenth (129) and Hobbs et al (64).

The largest troglobites in caves of the United States are crayfishes, fishes, and salamanders. Troglobitic crayfishes are represented in eastern caves by species of *Cambarus*, *Procambarus*, *Orconectes*, and the remarkable *Troglocambarus maclanei* (61–64). They occur in MP-I, MP-II, the Ozark Plateaus, and in Florida. We discuss two groups, the troglobitic *Orconectes* and the Florida *Procambarus*, that exhibit a striking difference in distribution patterns.

Four allopatric troglobitic *Orconectes* species were recognized by Hobbs & Barr (63)—*O. inermis* in MP-I north of the Hart County ridge (Indiana, Kentucky); *O. pellucidus* in MP-I south of the same barrier (Kentucky, Tennessee); *O. australis* in MP-II from southern Kentucky to north Alabama; and *O. incomptus* in the eastern edge of the Central Basin of Tennessee. These authors postulated separate invasions of the Green, Cumberland, and preglacial Teays river systems by a common ancestor related to *O. limosus*, which subsequently went through substantial dispersal via subterranean routes in the MPs. The surface ancestor became extinct in late Pliocene or early Pleistocene time when the low-gradient streams in which it lived were transformed into rapidly flowing ones with steeper gradients. Divergence of northern and southern geographic races of *inermis* and *australis* and perhaps stratigraphic isolation of *incomptus* from *australis* probably occurred in mid- to late-Pleistocene time. A recently discovered population at Central Basin level in Coffee County, Tennessee, is typical *O. a. australis* and presumably represents a colonization in Recent time (H. H. Hobbs, Jr. & T. C. Barr, unpublished).

Ten troglobitic *Procambarus* species are known from Florida, all but *P. milleri* (Dade County) in 16 counties in the northern lime sink region (58, 59). With the addition of one species each of *Cambarus* and *Troglocambarus*, more troglobitic crayfish species exist in Florida than in any other cave region in North America (59, 64). Of the 10 species of *Procambarus*, 8 belong to subgenus *Ortmannicus* (the "pictus group"), 2 species belong to different subgenera, and *Troglocambarus* is probably derived from the *pictus* group. Two species complexes in the *pictus* group are believed to have been derived from a single epigeal progenitor by multiple invasions at different times and places: species of the *lucifugus* complex adapted to food-rich caves, and species of the *pallidus* complex and *Troglocambarus maclanei* adapted to areas of low food input (59). *Troglocambarus maclanei*, the most widely distributed troglobitic crayfish in Florida, coexists with several of the more localized *Procambarus* species. Concentration of troglobites in the part of Florida that was not submerged by Pleistocene seas [*P. milleri* in the south is presumed to be a recent cavernicole (59)] suggests survival of troglobite ancestors in large freshwater springs surrounded by areas in which the groundwater was brackish (61, 64)].

The cave, spring, and swamp fishes of the family Amblyopsidae include four genera and six species (47, 122, 138). *Chologaster cornutus* inhabits swamps of the southern Atlantic coastal plain, and *C. agassizi* lives in springs, sinkhole ponds, and caves in the Interior Low Plateaus. *Typhlichthys subterraneus*, *Amblyopsis spelaea*, *A. rosae*, and *Speoplatyrhinus poulsoni* are troglobites restricted to the Interior Low Plateaus and Ozark Plateaus. By far the widest range among the troglobites is exhibited by *T. subterraneus*, which occurs from southern Kentucky, central Tennessee, north Alabama to northern Arkansas,

southern Missouri, and northeast Oklahoma, certainly the most widely distributed troglobite in North America, with the possible exception of the linyphiid spider *Phanetta subterranea*. The huge range of *T. subterraneus* suggests that it is a morphospecies composed of several local biological species separated by extrinsic dispersal barriers. Swofford et al (133) reported a mean genetic similarity (*I*) of only 0.679 for 13 populations of the species, in contrast to 1.00 for 3 populations of *A. spelaea* and 0.854 for 2 populations of *A. rosae*. *Amblyopsis spelaea* occupies caves of MP-I from the East Fork of White River in southern Indiana south to the Mammoth Cave system in Kentucky, while *A. rosae* is restricted to the Springfield plain in southwest Missouri. *Speoplatyrhinus poulsoni* is known from a single cave in northwest Alabama.

Among troglobitic amblyopsids the degree of morphological, behavioral, and physiological specialization to cave existence varies inversely with range size. *Typhlichthys*, the least specialized, has the broadest range, while *Speoplatyrhinus*, the most highly specialized, has the smallest (47, 122). Degree of eye and pigment loss (regressive characters), possibly an indication of length of time of isolation in caves, parallels a progression of sensory and metabolic adaptations to low food supply (122).

Troglobitic plethodontid salamanders in North America include: *Haideotriton wallacei* from south Georgia and adjacent Florida; four or five taxa of *Gyrinophilus* from Alabama, Tennessee, and West Virginia; *Typhlotriton spelaeus* from the southwest Ozark Plateau; and two species of *Typhlomolge* and two or more species of *Eurycea* from the Edwards Plateau of Texas (23, 33, 97, 130). Only *G. subterraneus* and *T. spelaeus* undergo metamorphosis; the other species are neotenic. In *Typhlotriton*, the pigmented, oculate larvae occur as troglonexes near cave entrances; metamorphosed adults, however, are bona fide troglobites with reduced pigment and small eye rudiments covered with a fold of skin (6, 29, 128).

Neotenic salamanders in Edwards Plateau caves show a graded series of cave-adapted populations, ranging from epigean, spring-dwelling forms with unmodified morphology to highly troglomorphic species (98, 99, 121, 131, 132). Excluding *Eurycea nana*, this series consists of *E. neotenes*, a relatively widespread species commonly found in springs and occasionally in sinkhole systems and caves; *E. tridentifera*, a troglobitic species restricted to caves in Bexar, Comal, and Kendall counties; and *Typhlomolge robusta* and *T. rathbuni*, two highly modified troglobites from subterranean waters near San Marcos, Texas. According to Sweet (132), populations of *E. neotenes* (including *trogloodytes* and *latitans*, both previously described as full species) in different springs and caves show different degrees of morphological adaptation to cave life and a certain degree of parallelism. Potter & Sweet (121) suggested that *Typhlomolge* is a distinct lineage whose ancestor(s) invaded and colonized subterranean waters of the Edwards aquifer along the Balcones fault zone at an

earlier time than invasion of caves by *Eurycea* elsewhere on the Plateau. Advanced troglomorphy in *Typhlomolge* may also indicate that it is an older troglobite than the less specialized *Eurycea* species (99).

Origin of neoteny in the Texas cave salamanders seems a significant factor in the evolution of troglobitic salamander species (29, 130, 131). Both springs and caves furnished refugia for salamander populations as the central Texas climate became progressively drier. Absence of suitable habitats other than springs and caves led to selection for neoteny, probably enhanced by episodic droughts that eliminated surface streams and most springs (132). Gradual and progressive drying of regional climates, however, is an unsatisfactory explanation for the origin of neoteny in eastern salamanders. Bruce (30) suggested that neoteny appeared in the southeastern troglobitic species of *Gyrinophilus* (*G. pallaucus* and related taxa) as a selective response to food scarcity; adults of the epigeal *G. porphyriticus* are specialist feeders on other species of salamanders, which are absent in caves colonized by *G. pallaucus* and its relatives (see also 51).

SUMMARY

Although caves are inherently discontinuous habitats, and the multiplicity of troglobite species reflects such discontinuity, speciation patterns differ in various taxonomic groups because the organisms themselves differ both in vagility and in their ability (or lack of ability) to disperse through nonkarst terranes via microcaverns or groundwater networks. For groups of species confined to contiguous karst, greater dispersal potential in the Mississippian plateaus leads to more extensive geographic ranges and higher frequency of sympatry, in contrast to the patterns seen in patchy karst of the Appalachian Valley.

Nevertheless, the broad tapestry of cave speciation is crisscrossed by several common threads. Many examples suggest multiple cave invasions by one or a few widely distributed epigeal ancestors. After initial cave colonization, gene flow between cave systems is greatly reduced by various mechanisms that include: 1. Postglacial climates becoming warmer and drier, and thus inimical to ancestors preadapted to cool, wet microhabitats; 2. drainage changing, by such means as (a) conversion of the preglacial Ohio River from a small, presumably nonbarrier stream to a large river that was an effective barrier to terrestrial troglobites, (b) gradual evolution of a youthful stream with many meanders (no barrier) into a mature stream with low meander frequency (barrier), or (c) simple erosion that divides a karst area into isolated segments by cutting down into underlying noncavernous strata; and 3. area effect, or isolation by distance, possibly providing an adequate explanation for intense speciation among troglobites of low vagility.

The process of speciation in caves is viewed by most authors as a gradual and

continuing one; examples have been cited of groups of populations in various stages of cave colonization and subsequent divergence, speciation (acquisition of isolating mechanisms), and postspeciation evolution of troglomorphic characters. Several authors assume that advanced troglomorphy implies long residence in caves, a hypothesis perhaps deserving critical investigation. The stranding of marine ancestors of troglobites in freshwater interstitial and cave microhabitats during marine regressions is a rather different mechanism of troglobite origin, but it does share the element of geographic isolation present in all of the other mechanisms previously cited.

ACKNOWLEDGMENTS

Kenneth A. Christiansen, David C. Culver, and Samuel S. Sweet read and provided helpful comments on the manuscript of this paper.

We thank L. Villa-Lobos for assistance with the figure, compilation of some of the references, and for reading an earlier draft of the manuscript. Assistance with drafting the figure was provided by the Center for Instructional Development at Old Dominion University. The late Thomas J. M. Schopf is largely responsible for goading the authors to produce this paper; we regret very much that he could not read and criticize it. This paper was supported in part by NSF grants DEB-8202339 to T. C. Barr and DEB-8206716 to J. R. Holsinger.

Literature Cited

1. Barr, T. C. 1962. The *robustus* group in the genus *Pseudanopthalmus* (Coleoptera: Carabidae: Trechini). *Coleopt. Bull.* 16:109-18
2. Barr, T. C. 1965. The *Pseudanopthalmus* of the Appalachian valley (Coleoptera: Carabidae). *Am. Midl. Nat.* 73:41-72
3. Barr, T. C. 1966-1967. Cave Carabidae (Coleoptera) of Mammoth Cave. *Psyche* 73:284-87; 74:24-26
4. Barr, T. C. 1967. Observations on the ecology of caves. *Am. Nat.* 101:475-92
5. Barr, T. C. 1967. A new *Pseudanopthalmus* from an epigeal environment in West Virginia (Coleoptera: Carabidae). *Psyche* 74:166-72
6. Barr, T. C. 1968. Cave ecology and the evolution of troglobites. *Evol. Biol.* 2:35-102
7. Barr, T. C. 1972. *Trechoblemus* in North America, with a key to North American genera of Trechinae (Coleoptera: Carabidae). *Psyche* 78:140-49
8. Barr, T. C. 1974. Revision of *Rhadine* LeConte (Coleoptera, Carabidae). I. The *subterranea* group. *Am. Mus. Novit.* 2539. 30 pp.
9. Barr, T. C. 1974. The eyeless beetles of the genus *Arianops* Brendel (Coleoptera, Pselaphidae). *Am. Mus. Nat. Hist. Bull.* 154:1-51
10. Barr, T. C. 1979. The taxonomy, distribution, and affinities of *Neaphaenops*, with notes on associated species of *Pseudanopthalmus* (Coleoptera, Carabidae). *Amer. Mus. Novit.* 2682. 20 pp.
11. Barr, T. C. 1979. Revision of Appalachian *Trechus* (Coleoptera: Carabidae). *Brimleyana*, No. 2:29-75
12. Barr, T. C. 1980. New species groups of *Pseudanopthalmus* from the Central Basin of Tennessee (Coleoptera: Carabidae: Trechinae). *Brimleyana*, No. 3:85-96
13. Barr, T. C. 1981. *Pseudanopthalmus* from Appalachian caves (Coleoptera: Carabidae): the *engelhardti* complex. *Brimleyana*, No. 5:37-94
14. Barr, T. C. 1982. The trechine beetles of the *Paratrechus* series in Mexico and Central America, with special reference to the cave species (Coleoptera: Carabidae: Trechinae). *Assoc. Mex. Cave Stud. Bull. No. 8*, and *Tex. Mem. Mus. Bull. No. 28*, pp. 193-236
15. Barr, T. C. 1982. The cavernicolous anachomenine beetles of Mexico (Cole-

- optera: Carabidae: Agonini) *Assoc. Mex. Cave Stud. Bull. No. 8*, and *Tex. Mem. Mus. Bull. No. 28*:161-92
16. Barr, T. C. 1985. Pattern and process in speciation of trechine beetles in eastern North America (Coleoptera: Carabidae: Trechinae). In *Taxonomy, Phylogeny, and Zoogeography of Beetles and Ants (Series Entomologia 33)*, ed. G. E. Ball, pp. 350-407. Dordrecht, The Netherlands: Junk
 17. Barr, T. C. 1985. New trechine beetles from the Appalachian region (Coleoptera: Carabidae). *Brimleyana* No. 11:119-32
 18. Barr, T. C., Crowley, P. H. 1981. Do cave carabid beetles really show character displacement in body size? *Am. Nat.* 117:363-71
 19. Barr, T. C., Krekeler, C. H. 1967. *Xenotrechus*, a new genus of cave trechines from Missouri (Coleoptera: Carabidae). *Ann. Entomol. Soc. Am.* 60:1322-25
 20. Barr, T. C., Kuehne, R. A. 1971. Ecological studies in the Mammoth Cave system of Kentucky. II. The ecosystem. *Ann. Speleol.* 26:47-96
 21. Barr, T. C., Peck, S. B. 1965. Occurrence of a troglotic *Pseudanophthalmus* outside a cave (Coleoptera: Carabidae). *Am. Midl. Nat.* 73:73-74
 22. Barr, T. C., Steeves, H. R. 1963. *Texamaurops*, a new genus of pselaphids from caves in central Texas (Coleoptera: Pselaphidae). *Coleopt. Bull.* 17:117-20
 23. Besharse, J. C., Holsinger, J. R. 1977. *Gyrinophilus subterraneus*, a new troglotic salamander from southern West Virginia. *Copeia* 1977:624-34
 24. Birstein, Y. A. 1964. Freshwater isopods (Asellota). *Fauna of USSR, Crustacea* 7:1-148. Transl. Israel Prog. Sci. Transl. Smithsonian Inst., Washington, DC
 25. Botosaneanu, L., Stock, J. H. 1979. *Arubolana imula* n. gen., n. sp., the first hypogean cirolanid isopod crustacean found in the Lesser Antilles. *Bijdr. Dierkd.* 49:227-33
 26. Bowman, T. E. 1964. *Antrolana lira*, a new genus and species of troglotic cirolanid isopod crustacean from springs in eastern United States. *Proc. Biol. Soc. Wash.* 80:131-40
 27. Bowman, T. E. 1981. *Specirolana pubens* and *S. endeca*, new troglotic isopod crustaceans from Mexico (Flabellifera: Cirolanidae). *Assoc. Mex. Cave Stud. Bull. No. 8*, and *Tex. Mem. Mus. Bull. No. 28*:13-23
 28. Bowman, T. E., Iliffe, T. M. 1983. *Bermudalana aruboides*, a new genus and species of troglotic Isopoda (Cirolanidae) from marine caves on Bermuda. *Proc. Biol. Soc. Wash.* 196:291-300
 29. Brandon, R. A. 1971. North American troglotic salamanders: some aspects of modification in cave habitats, with special reference to *Gyrinophilus paleucus*. *Nat. Speleol. Soc. Bull.* 23:1-21
 30. Bruce, R. C. 1979. Evolution of paedomorphosis in salamanders of the genus *Gyrinophilus*. *Evolution* 33:998-1000
 31. Bush, G. L. 1975. Modes of animal speciation. *Ann. Rev. Ecol. Syst.* 6:339-64
 32. Carpenter, J. H. 1981. *Bahalana geracei* n. gen., n. sp., a troglotic marine cirolanid isopod from Lighthouse Cave, San Salvador Island, Bahamas. *Bijdr. Dierkd.* 51:259-67
 33. Carr, A. F. 1939. *Haideotriton wallacei*, a new subterranean salamander from Georgia. *Occas. Pap. Boston Soc. Nat. Hist.* 8:333-36
 34. Chamberlin, J. C. 1962. New and little-known false scorpions, principally from caves, belonging to the families Chthoniidae and Neobisiidae (Arachnida, Chelonethida). *Am. Mus. Nat. Hist. Bull.* 123:299-352
 35. Christiansen, K. A. 1960. A preliminary survey of the knowledge of North American cave Collembola. *Am. Midl. Nat.* 64:39-44
 36. Christiansen, K. A. 1960. The genus *Pseudosinella* (Collembola, Entomobryidae) in caves of the United States. *Psyche* 67:1-25
 37. Christiansen, K. A. 1960. The genus *Sinella* Brook (Collembola: Entomobryidae) in Nearctic caves. *Ann. Entomol. Soc. Am.* 53:481-91
 38. Christiansen, K. A. 1961. Convergence and parallelism in cave Entomobryinae. *Evolution* 15:288-301
 39. Christiansen, K. A. 1962. Proposition pour la classification des arimaux cavernicoles. *Spelunca Mem.* 2:76-78
 40. Christiansen, K. A. 1964. A revision of the Nearctic members of the genus *Tomocerus* (Collembola: Entomobryidae). *Rev. Ecol. Biol. du Sol.* 1:639-78
 41. Christiansen, K. A. 1965. Behavior and form in the evolution of cave Collembola. *Evolution* 19:529-537
 42. Christiansen, K. A. 1966. The genus *Arrhopalites* in the United States and Canada. *Int. J. Speleol.* 2:43-73
 43. Christiansen, K. A., Culver, D. C. 1968. Geographical variation and evolution in *Pseudosinella hirsuta*. *Evolution* 22:237-55
 44. Christiansen, K. A., Culver, D. C. 1969. Geographical variation and evolution in

- Pseudosinella violenta* (Folsom). *Evolution* 23:602-21
45. Cole, G. A., Minckley, W. L. 1966. *Speocirrolana therymydronis*, a new species of cirrolanid isopod crustacean from central Coahuila, Mexico. *Tulane Stud. Zool.* 13:17-22
 46. Contreras-Balderas, S., Purata-Velarde, D. C. 1981. *Speocirrolana guerrai* sp. nov., cirrolanido troglobio anoptalmo de la Cueva de la Chorrera, Linares, Nuevo Leon, México (Crustacea: Isopoda). *Assoc. Mex. Cave Stud. Bull. No. 8*, and *Tex. Mem. Mus. Bull. No. 28*. pp. 1-12
 47. Cooper, J. E., Kuehne, R. A. 1974. *Speoplatyrhinus poulsoni*, a new genus and species of subterranean fish from Alabama. *Copeia* 1974:486-93
 48. Culver, D. C. 1970. Analysis of simple cave communities. I. Caves as islands. *Evolution* 24:463-74
 49. Culver, D. C. 1971. Caves as archipelagoes. *Nat. Speleol. Soc. Bull.* 33:97-100
 50. Culver, D. C. 1981. Some implications of competition for cave stream communities. *Int. J. Speleol.* 11:49-62
 51. Culver, D. C. 1982. *Cave Life: Evolution and Ecology*. Cambridge: Harvard Univ. Press. 189 pp.
 52. Culver, D. C., Holsinger, J. R., Baroody, R. A. 1973. Toward a predictive cave biogeography: the Greenbrier Valley as a case study. *Evolution* 27:689-95
 53. Dickson, G. W. 1977. Behavioral adaptation of the troglotic amphipod crustacean *Crangonyx antennatus* to stream habitats. *Hydrobiologia* 56:17-20
 54. Dickson, G. W. 1977. Variation among populations of the troglotic amphipod crustacean *Crangonyx antennatus* Packard living in different habitats. I. Morphology. *Int. J. Speleol.* 9:43-58
 55. Dickson, G. W., Holsinger, J. R. 1981. Variation among populations of the troglotic amphipod crustacean *Crangonyx antennatus* (Crangonyctidae) living in different habitats. III. Population dynamics and stability. *Int. J. Speleol.* 11:33-48
 56. Dickson, G. W., Patton, J. C., Holsinger, J. R., Avise, J. C. 1979. Genetic variation in cave dwelling and deep sea organisms with emphasis on *Crangonyx antennatus* (Crustacea: Amphipoda) in Virginia. *Brimleyana* (2):119-30
 57. Ferguson, L. M. 1981. Systematics, evolution, and zoogeography of the cavernicolous campodeids of the genus *Litocampa* (Diplura: Campodeidae) in the United States. PhD thesis. Va. Polytechnic Inst. & State Univ. 372 pp.
 58. Franz, R., Hobbs, H. H. Jr. 1983. *Procambarus (Ortmannicus) leitheuseri*, new species, another troglotic crayfish (Decapoda: Cambaridae) from peninsular Florida. *Proc. Biol. Soc. Wash.* 96:323-32
 59. Franz, R., Lee, D. D. 1982. Distribution and evolution of Florida's troglotic crayfishes. *Bull. Fl. State Mus., Biol. Ser.* 28:53-78
 - 59a. Gertsch, W. J. 1984. The spider family Nesticidae (Araneae) in North America, Central America, and the West Indies. *Tex. Mem. Mus. Bull.* 31. 91 pp.
 60. Glesener, R. R., Tiltman, D. 1978. Sexuality and the components of environmental uncertainty: clues from geographic parthenogenesis in terrestrial animals. *Am. Nat.* 112:659-73
 61. Hobbs, H. H. Jr. 1942. The crayfishes of Florida. *Univ. Fla. Publ., Biol. Sci. Ser.* 3(2) 179 pp.
 62. Hobbs, H. H. Jr., Barr, T. C. 1960. The origins and affinities of the troglotic crayfishes of North America (Decapoda, Astacidae). I. The genus *Cambarus*. *Am. Midl. Nat.* 64:12-33
 63. Hobbs, H. H. Jr., Barr, T. C. 1972. Origins and affinities of the troglotic crayfishes of North America (Decapoda: Astacidae). II. Genus *Orconectes*. *Smithson. Contrib. Zool.* 105:1-84
 64. Hobbs, H. H. Jr., Hobbs, H. H. III, Daniel, M. A. 1977. A review of the troglotic decapod crustaceans of the Americas. *Smithson. Contrib. Zool.* 244:1-177
 65. Hoffman, R. L. 1981. On the taxonomic status, distribution, and subspecies of the milliped *Pseudotremia fracta* (Chamberlin) (Chordeumatida: Cleidogonidae). *Brimleyana*, No. 5:135-144
 66. Holsinger, J. R. 1967. Systematics, speciation, and distribution of the subterranean amphipod genus *Stygonectes* (Gammaridae). *Bull. US Nat. Mus.* 259:1-176
 67. Holsinger, J. R. 1974. Systematics of the subterranean amphipod genus *Stygobromus* (Gammaridae). I. Species of the western United States. *Smithson. Contrib. Zool.* 160:1-62
 68. Holsinger, J. R. 1977. A review of the systematics of the Holarctic amphipod family Crangonyctidae. *Crustaceana Suppl.* 4:244-77
 69. Holsinger, J. R. 1978. Systematics of the subterranean amphipod genus *Stygobromus* (Crangonyctidae). II. Species of the eastern United States. *Smithson. Contrib. Zool.* 266:1-144
 70. Holsinger, J. R. 1980. *Stygobromus canadensis*, a new subterranean amphi-

- pod crustacean (Crangonyctidae) from Canada, with remarks on Wisconsin refugia. *Can. J. Zool.* 58:290-97
71. Holsinger, J. R. 1981. *Stygobromus canadensis*, a troglobitic amphipod crustacean from Castleguard Cave, with remarks on the concept of cave glacial refugia. *Proc. 8th Int. Congr. Speleol.* 1:93-95
 72. Holsinger, J. R. 1985. Holarctic crangonyctid amphipods. In *Stygofauna Mundi*, ed. L. Botosaneanu, Leiden: Brill. In press
 73. Holsinger, J. R. 1985. Zoogeographic patterns of North American subterranean amphipod crustaceans. In *Crustacean Issues 4: Crustacean Biogeography*, ed. F. R. Schram. Rotterdam: Balkema. In press
 74. Holsinger, J. R., Culver, D. C. 1985. The invertebrate cave fauna of Virginia and a part of eastern Tennessee: zoogeography and ecology. *Brimleyana* (12): In press
 75. Holsinger, J. R., Longley, G. 1980. The subterranean amphipod fauna of an artesian well in Texas. *Smithson. Contrib. Zool.* 308:1-62
 76. Holsinger, J. R., Yager, J. 1985. A new genus and two new species of subterranean amphipod crustaceans (Hadziidae) from the Bahamas and Caicos Islands. *Bijdr. Dierkd.* 55: In press
 77. Howarth, F. G. 1980. The zoogeography of specialized cave animals: a bioclimatic model. *Evolution* 34:394-406
 78. Hubbell, T. H., Norton, R. M. 1978. The systematics and biology of the cave-crickets of the North American tribe Hadenocini (Orthoptera Saltatoria: Ensifera: Rhaphidophoridae: Dolichopodiinae). *Misc. Publ. Mus. Zool., Univ. Mich.*, No. 156:1-124
 79. Hutchinson, G. E., MacArthur, R. H. 1959. A theoretical ecological model of size distribution among species of animals. *Am. Nat.* 93:117-25
 80. Jeannel, R. 1926-1930. Monographie des-Trechinae. Morphologie comparée et distribution d'un groupe de Coléoptères. *L'Abeille* 32:221-550; 33:1-592; 34:59-122; 35:1-808
 81. Jeannel, R. 1943. *Les fossiles vivants des cavernes*. Paris: Gallimard. 321 pp.
 82. Jeannel, R. 1949. Les coléoptères cavernicoles de la région des Appalaches. Etude systématique. *Notes Biospéol.* 4, *Publ. Mus. Nat. Hist. Paris*, No. 12:37-104
 83. Juberthie, C., Delay, B., Bouillon, M. 1980. Extension du milieu souterrain en zone non-calcaire: description d'un nouveau milieu et de son peuplement par les Coléoptères troglobies. *Mém. Biospéol.* 7:19-52
 84. Kane, T. C. 1982. Genetic patterns and population structure in cave animals. In *Environmental Adaptation and Evolution: A Theoretical and Empirical Approach*, ed. D. Mossakowski, D. Roth, pp. 131-49. Stuttgart: Fischer Verlag
 85. Kawakatsu, M., Mitchell, R. W. 1981. Redescription of *Kenkia rhynchida*, a troglobitic planarian from Oregon, and a reconsideration of the family Kenkiidae and its genera (Turbellaria, Tricladida, Paludicola). *Annot. Zool. Jpn.* 54:125-41
 86. Kenk, R. 1974. Fresh-water triclads (Turbellaria) of North America. VII. The genus *Macrocoxya*. *Trans. Am. Microsc. Soc.* 94:324-39
 87. Kenk, R. 1977. Freshwater triclads (Turbellaria) of North America. IX. The genus *Sphalloplana*. *Smithson. Contrib. Zool.* 246:1-38
 88. Kenk, R. 1984. Freshwater triclads (Turbellaria) of North America. XV. Two new subterranean species from the Appalachian region. *Proc. Biol. Soc. Wash.* 97:209-16
 89. Kröckler, C. H. 1973. Cave beetles of the genus *Pseudanophthalmus* (Coleoptera, Carabidae) from the Kentucky Bluegrass and vicinity. *Fieldiana, Zool.* 62:35-83
 90. Lamb, R. Y., Willey, R. B. 1975. The first parthenogenetic populations of Orthoptera Saltatoria to be reported from North America. *Ann. Entomol. Soc. Am.* 68:721-22
 91. Lewis, J. I. 1984. *The systematics, zoogeography, and life history of the troglobitic isopods of the Interior Plateaus of the eastern United States*. PhD thesis. Univ. Louisville. 278 pp.
 92. MacArthur, R. H., Wilson, E. O. 1967. *The Theory of Island Biogeography*. Princeton, NJ: Princeton Univ. Press. 203 pp.
 93. Malcolm, D. R., Chamberlin, J. C. 1960. The pseudoscorpion genus *Chirella* (Chelonethida, Syariniidae). *Am. Mus. Novit.* 1989. 19 pp.
 94. Malcolm, D. R., Chamberlin, J. C. 1961. The pseudoscorpion genus *Kleptochthonius* Chamberlin (Chelonethida, Chthoniidae). *Am. Mus. Novit.* 2063. 35 pp.
 95. Mayr, E. 1963. *Animal Species and Evolution*. Cambridge: Harvard Univ. Press. 797 pp.
 96. Mayr, E. 1969. *Principles of Systematic Zoology*. New York: McGraw-Hill. 428 pp.
 97. McCrady, E. 1954. A new species of

- Gyrinophilus* (Plethodontidae) from Tennessee caves. *Copeia* 1954:200-206
98. Mitchell, R. W., Reddell, J. R. 1965. *Eurycea tridentifera*, a new species of troglotic salamander from Texas and a reclassification of *Typhlomolge rathbuni*. *Tex. J. Sci.* 17:12-27
 99. Mitchell, R. W., Smith, R. E. 1972. Some aspects of the osteology and evolution of the neotenic spring and cave salamanders (*Eurycea*, Plethodontidae) of central Texas. *Tex. J. Sci.* 23:343-62
 100. Muchmore, W. B. 1963. Redescription of some cavernicolous pseudoscorpions (Arachnida, Chelonethida) in the collection of the Museum of Comparative Zoology. *Breviora* 188. 16 pp.
 101. Muchmore, W. B. 1965. North American cave pseudoscorpions of the genus *Kleptochthonius*, subgenus *Chamberlinochthonius* (Chelonethida, Chthoniidae). *Am. Mus. Novit.* 2234. 27 pp.
 102. Muchmore, W. B. 1966. Two new species of *Kleptochthonius* (Arachnida, Chelonethida) from a cave in Tennessee. *J. Tenn. Acad. Sci.* 41:68-69
 103. Muchmore, W. B. 1968. A cavernicolous species of the pseudoscorpion genus *Mundochthonius* (Arachnida, Chelonethida, Chthoniidae). *Trans. Am. Microsc. Soc.* 87:110-12
 104. Muchmore, W. B. 1969. New species and records of cavernicolous pseudoscorpions of the genus *Microcreagris* (Arachnida, Chelonethida, Neobisiidae, Ideobisiinae). *Am. Mus. Novit.* 2392. 21 pp.
 105. Muchmore, W. B. 1970. New cavernicolous *Kleptochthonius* species from Virginia (Arachnida, Pseudoscorpionida, Chthoniidae). *Entomol. News* 8:210-12
 106. Muchmore, W. B. 1972. The unique, cave-restricted genus *Aphrastochthonius* (Pseudoscorpionida, Chthoniidae). *Proc. Biol. Soc. Wash.* 85:433-44
 107. Muchmore, W. B. 1973. The genus *Chitrella* in America (Pseudoscorpionida, Syarinidae). *J. NY Entomol. Soc.* 81: 183-92
 108. Muchmore, W. B. 1974. New cavernicolous species of *Kleptochthonius* from Virginia and West Virginia (Pseudoscorpionida, Chthoniidae). *Entomol. News* 85:81-84
 109. Muchmore, W. B. 1976. New cavernicolous species of *Kleptochthonius* and recognition of a new species group within the genus (Pseudoscorpionida, Chthoniidae). *Entomol. News* 87:211-17
 110. Muchmore, W. B. 1976. New species of *Apochthonius*, mainly from caves in central and eastern United States (Pseudoscorpionida, Chthoniidae). *Proc. Biol. Soc. Wash.* 89:67-79
 111. Notenboom, J. 1981. Some new hypogean cirolanid isopod crustaceans from Haiti and Mayaguana (Bahamas). *Bijdr. Dierkd.* 51:313-31
 112. Notenboom, J. 1984. *Arubolana parvioculata* n. sp. (Isopoda, Cirolanidae) from the interstitial of an intermittent river in Jamaica, with notes on *A. aruboides* (Bowman and Iliffe). *Bijdr. Dierkd.* 54:51-65
 113. Park, O. 1960. Cavernicolous pselaphid beetles of the United States. *Am. Midl. Nat.* 64:66-104
 114. Park, O. 1965. Revision of the genus *Batriasymmodes* (Coleoptera: Pselaphidae). *Trans. Am. Microsc. Soc.* 84:184-201
 115. Peck, S. B. 1973. A review of the invertebrate fauna of volcanic caves in western North America. *Nat. Speleol. Soc. Bull.* 35:99-107
 116. Peck, S. 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., Harv. Univ.* 145:29-162
 117. Peck, S. B. 1976. The effect of cave entrances on the distribution of cave-inhabiting terrestrial arthropods. *Int. J. Speleol.* 8:309-21
 118. Peck, S. B. 1982. Invertebrate faunas and zoogeographic significance of lava tube caves of Arizona and New Mexico. *Great Basin Nat.* 42:405-12
 119. Peck, S. B. 1983. Experimental hybridizations between populations of cavernicolous *Ptomaphagus* beetles (Coleoptera: Leiodidae: Cholevinae). *Can. Entomol.* 115:445-52
 120. Peck, S. B. 1984. The distribution and evolution of cavernicolous *Ptomaphagus* beetles in the southeastern United States (Coleoptera; Leiodidae; Cholevinae) with new species and records. *Can. J. Zool.* 62:730-40
 121. Potter, F. E., Sweet, S. S. 1981. Generic boundaries in Texas cave salamanders and a redescription of *Typhlomolge robusta* (Amphibia: Plethodontidae). *Copeia* 1981:64-75
 122. Poulson, T. C. Cave adaptation in amblyopsid fishes. *Am. Midl. Nat.* 70: 257-90
 123. Powell, R. L. 1970. Geology of the falls of the Ohio River. *Ind. Dept. Cons., Geol. Surv. Circ.* 10. 45 pp.
 124. Reddell, J. R. 1981. A review of the cavernicole fauna of Mexico, Guatemala, and Belize. *Tex. Mem. Mus. Bull.* 27 327 pp.
 125. Sbordoni, V. 1982. Advances in speciation of cave animals. In *Mechanisms of*

- Speciation*, ed. C. Barrigozzi, pp. 219-40. New York: Liss
126. Shear, W. 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., Harv. Univ.* 144:151-352
 127. Stock, J. H. 1977. The taxonomy and zoogeography of the hadziid Amphipoda, with emphasis on the West Indian taxa. *Stud. Fauna Curaçao* 55:1-130
 128. Stone, L. S. 1964. The structure and visual function of the eye of larval and adult cave salamanders, *Typhlotriton spe-laeus*. *J. Exp. Zool.* 156:201-28
 129. Strenth, N. E. 1976. A review of the systematics and zoogeography of the freshwater species of *Palaemonetes* Heller of North America (Crustacea: Decapoda). *Smithson. Contrib. Zool.* 228:1-27
 130. Sweet, S. S. 1977. Natural metamorphosis in *Eurycea neotenes* and the generic allocation of the Texas *Eurycea* (Amphibia: Plethodontidae). *Herpetologica* 33:364-75
 131. Sweet, S. S. 1982. A distributional analysis of epigeal populations of *Eurycea neotenes* in central Texas, with comments on the origin of troglolithic populations. *Herpetologica* 38:430-44
 132. Sweet, S. S. 1984. Secondary contact and hybridization in the Texas cave salamanders *Eurycea neotenes* and *E. tridentifera*. *Copeia* 1984:428-41
 133. Swofford, D. L., Branson, B. A., Sievert, G. A. 1980. Genetic differentiation of cavefish populations. *Isozyme Bull.* 13:109-10
 134. Throckmorton, L. H. 1977. *Drosophila* systematics and biochemical evolution. *Ann. Rev. Ecol. Syst.* 8:235-54
 135. Valentine, J. M. 1952. New genera of anophthalmid beetles from Cumberland caves (Carabidae: Trechinae). *Geol. Surv. Alabama, Mus. Pap.* 34:1-41
 136. Vandel, A. 1964. *Biospéologie: La Biologie des Animaux Cavernicoles*. Paris: Gauthier-Villars. 619 pp.
 137. Williamson, M. H. 1981. *Island Populations*. Oxford Univ. Press. 286 pp.
 138. Woods, L. P., Inger, R. R. 1957. The cave, spring, and swamp fishes of the family Amblyopsidae of central and eastern United States. *Am. Midl. Nat.* 58:232-256