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SYMPOSIUM: Speciation and Raciation in Cavernicoles[1]

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Introduction

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Vast areas of the United States are underlain by caverniferous limestone. Conservatively estimated, there are at least 10,000 accessible caves in these limestone areas, with a collective total length of penetrable passages of fully 1,000 miles. Many caves, especially in (1) the Appalachian Valley and Plateau, (2) the Interior Low Plateaus, (3) the lime sink region of northern Florida, (4) the Ozark Plateau, and (5) the Edwards Plateau of Texas, are richly populated by animal life which, until recently, has received scant

[1] Presented at the 1959 Annual Meeting of the American Association for the Advancement of Science, December 28 sponsored by the National Speleological Society and the Society of Systematic Zoology. Arranged by Thomas C. Barr, Jr.

attention from American zoologists. Although the first obligatory cavernicoles from the United States were described in 1842 (DeKay) and 1844 (Tellkampf), cave faunas generated little interest until the explorations of A. S. Packard (compiled and summarized in 1888). North American cave vertebrates were surveyed by Eigenmann in 1909, but most invertebrates have been neglected. As late as 1931 Bolívar and Jeannel could write:

> . . . les naturalistes américaines n'ont enterpris aucune étude sérieuse de la faune de l'immense domaine souterraine qui s'offre à leurs investigations. On chercherait en vain dans les collections des Musées un seul cavernicole dont la capture date du XX^e siècle!

As the contributions of this symposium amply demonstrate, this situation no longer exists.

Obligatory cavernicoles exhibit an unusually striking correlation between structural modification and their peculiar environment, providing a ready source of material well suited for investigations in community dynamics, comparative physiology and ethology, evolution, and zoogeography. Such investigations presuppose a body of taxonomic information which, for most of the United States, has heretofore been wholly inadequate. Extensive collecting during the past decade and critical work by a number of specialists have resulted in rapid advances — principally, though not wholly, taxonomic in nature — in American biospeleology. Reviews of these advances in eight different groups of cavernicoles are brought together in the present symposium.[1]

The classification of cavernicoles, perhaps unfamiliar to American readers, employed by most of the contributors is that of Schiödte (1849) and Schiner (1853), modified and popularized in Europe by Racovitza (1907). *Troglobites* are animals found only in caves, except by accident (e.g., being washed out of caves by flooding of underground streams), and are so modified that they are unable to live outside of caves and associated solutional cavities. Examples are discussed by each symposium author. *Troglophiles* are animals found frequently in caves, reproducing there and completing their life cycles underground, but having no rudimentations restricting them to a cave existence. *Trogloxenes* are animals often found in caves, but not completing their whole life cycle underground. The best known examples are bats and cave crickets. The term *accidental* is usually applied to stray visitors, occurring fortuitously and fleetingly within caves. It should not be confused with *threshold trogloxene*, an expression properly reserved for a member of the array of animals habitually frequenting the twilight zone of caves.

The immediate problems facing biospeleology in the United

[1] The following paper is not available for publication at this time: T. L. Poulson: "The sequential development of cave adaptation in the Amblyopsidae." In addition, the paper delivered by C. H. Krekeler has been published elsewhere (see References, page 8).

States are those of discovering, collecting, and describing the troglobitic species. The present status of troglobite taxonomy can be ascertained by examination of the checklist prepared by Brother G. Nicholas and appended to this symposium. Approximately two hundred fifty species have been described. The greatest numbers of species are found in the Coleoptera (97), Amphipoda (34), Diplopoda (34), and Isopoda (24). The greatest numbers of individuals include these groups, plus the Collembola and Araneae.

Problems in the systematics of cavernicole turbellarians, crayfishes, millipedes, collembolans, rhadiniform carabids, pselaphids, pseudoscorpions, and opilionids are discussed in the papers which follow. Despite this wide coverage, at least nine troglobite groups of major importance are not represented in the symposium contributions.

(1) *Snails.* Undoubted troglobites occur in the families Amnicolidae and Pleuroceridae. One species of *Carychium* (Carychiidae) is an abundant terrestrial troglobite in the Mammoth Cave region. A number of species (some undescribed) of *Helicodiscus* (Endodontidae) and *Retinella* (Zonitidae) from Tennessee and Kentucky are troglophiles or troglobites.

(2) *Isopods* (Asellidae) and (3) *amphipods* (Gammaridae) can be found in almost any cave stream in the major caverniferous areas. The species of the latter are somewhat better known at present because of the work of Hubricht and Mackin (1940) and Hubricht (1943). The cave asellids demand considerable further investigation. Three trichoniscid (terrestrial), one ligiid (aquatic), and one cirolanid (aquatic) isopods have been described.

(4) *Spiders.* Most troglobite species of araneids in the United States belong to the families Linyphiidae and Nesticidae. Troglophiles and trogloxenes of other families are locally very abundant. A comprehensive study of North American cave spiders is being undertaken by Dr. W. J. Gertsch (pers. comm.), Department of Insects and Spiders, American Museum of Natural History.

(5) Five species of *Plusiocampa* (Campodeidae, Diplura) have been described from caves in the United States (Condé 1949). They occur in all of the major limestone areas.

(6) *Trechine beetles* (Carabidae). This large and significant group of troglobites is perhaps better known than any of the others, principally because of the work of J. Manson Valentine (1931, 1932, 1937, 1945, 1948, 1952). Jeannel (1949) revised the species known at that time, and additional genera and species have been added by Valentine (1952), Krekeler (1958), and Barr (1959a, 1959b, 1960a, 1960b). The largest genus, *Pseudanophthalmus,* is known from the Interior Low Plateaus and Appalachian Valley and Plateau in the eastern United States, from Pennsylvania to Georgia, and west to Indiana, Tennessee, and Kentucky. More than half of the described taxa are known from a single cave.

(7) The cavernicole beetles of the subgenus *Adelops* (*Ptomaphagus,* Catopidae) were revised by Jeannel (1949) and one species was added by Barr (1958). Eight troglobite and one troglophile species (*P. cavernicola* Schwarz) have been described. The troglobite species are most abundant in

northern Alabama and southern Tennessee, with one species each in central Tennessee and central Kentucky.

(8) *Amblyopsid fishes.* Three eyeless species are recognized in a revision of this family by Woods and Inger (1957). They are restricted to the Interior Low Plateaus and part of the Ozark Plateau.

(9) *Plethodontid salamanders.* The genera *Typhlotriton* and *Typhlomolge* have been known for more than sixty years. *Haideotriton wallacei* Carr was described in 1939. Of considerable interest are the recent discoveries of *Gyrinophilus palleucus* (McCrady 1954) and *Eurycea troglodytes* (Baker 1957). Whether *Typhlotriton nereus* Bishop or the various subspecies of *Eurycea neotenes* Bishop and Wright are to be considered troglobites or troglophiles seems debatable. The status of *Gyrinophilus lutescens* (Rafinesque) certainly cannot be satisfactorily determined without further study.

Little attention has been devoted to the ostracods, copepods, and other small aquatic crustaceans of the subterranean waters of the United States (Klie 1931; Chappuis 1931 and 1933). Among major groups of terrestrial cavernicoles, the abundant and diversified Acarina, at least some representatives of which occur in nearly every cave, have been almost wholly neglected.

Geographic isolation as a major factor in cavernicole speciation was stressed by nearly all the symposium contributors. Few other biotopes exhibit in so salient a manner the influence of extrinsic barriers to genetic continuity. The most spectacular cases of intense troglobite speciation are found among the beetles and the millipedes. Of 98 described species and subspecies of troglobite carabids, 54 are known only from a single cave. Twenty-eight are known from as many as 5 caves. Only 7 are known from 10 or more caves. Park (this symposium) gives similar data for the pselaphids. Similar estimates for cave millipedes are not yet possible. However, Causey (this symposium; pers. comm.) believes that the intensity of cave endemism in the millipede genus *Pseudotremia* (Cleidogonidae) approaches that of *Pseudanophthalmus* (Carabidae). The systematic picture emerging from study of such groups strongly suggests a dominant role for genetic drift, but the possibility of varying selection pressures in different cave systems has not been investigated.

By no means are all troglobites narrowly restricted in geographic distribution. On the contrary, there extends a spectrum of range size from the "one-cave-one-taxon" extreme to whole cave systems, groups of adjacent systems, physiographic provinces, and virtually the entire unglaciated Paleozoic limestone portion of the eastern United States. Even the cave carabids include a few surprisingly vagile species. *Neaphaenops tellkampfi* abounds in the Mammoth Cave district of west-central Kentucky and extends (with minor racial variations) northward to the Ohio River (Jeannel 1949) and southward to the Tennessee border (Barr 1959a). *Darlingtonea kentuckensis* — another large, cursorial species with similar habits — occurs in large numbers from Rockcastle County, Kentucky, southwestward along the ragged margin of the Cumberland Plateau into northern Tennessee.[2] *Pseudanophthalmus tiresias* is a small, usually secretive species whose range is coextensive with the Central Basin of Tennessee, though local populations are subject to considerable geographic (supposedly subspecific) variation (Barr 1959a). Among the pselaphid beetles, two cavernicole species of *Batriasymmodes* (*spelaeus* and *quisnamus*) have such wide distributions that Park (this symposium) characterized them as "bothersome" because of the difficulty of explaining their subterranean dispersal by the usual means. In *Batriasymmodes,* however, the remarkably complex male genitalia provide virtual assurance of gene exchange throughout the known ranges of the species.

The more common aquatic troglobites have consistently more extensive ranges than most terrestrial troglobites, possibly because subterranean watercourses are less likely to be destroyed by erosion and collapse or blocked by silting and dripstone deposition, and probably because dispersal occurs beneath the water table under certain circumstances. The kenkiid planarian *Sphalloplana alabamensis* is known from the Cumberland Plateau of northern Alabama, northward into the Central Basin, Cumberland Plateau, and Appalachian Valley of Tennessee, in caves of the Cumberland and Tennessee River drainages (L. H. Hyman, pers. comm.). The amphipod *Stygobromus exilis,* described by Hubricht (1943) from the Mammoth Cave district, extends southward through central Tennessee into northern Alabama (L. Hubricht, pers. comm.). The eyeless crayfish *Orconectes pellucidus* is known from the Mitchell plain in southern Indiana, the western Pennyroyal Plateau of Kentucky, and the Cumberland Plateau of Kentucky, Tennessee, and Alabama. Five subspecies are recognized (Hobbs and Barr, in preparation). *Typhlichthys subterraneus,* the cave blindfish, is known from scattered colonies across central Kentucky and Tennessee to Missouri, Oklahoma, and northern Alabama (Woods and Inger 1957).

The most unusual and puzzling troglobite distributions, however, are those of the linyphiid cave spiders *Willibaldia cavernicola* (Missouri, Arkansas, Alabama, Georgia), *Bathyphantes weyeri* (Virginia, Kentucky), *Anthrobia monmouthia* (Kentucky, Tennessee, West Virginia), and *Phanetta subterranea* (Pennsylvania west to Indiana and south to Virginia, Tennessee, and Alabama).[3] It seems doubtful that such extensive ranges can be explained by dispersal through caves and solution crevices, yet none of these species is known from an epigean collection.

It is significant that six of the ten symposium participants mention the occurrence of related species in the same drainage system. That such a correlation should exist is quite probable in a limestone

[2] Collected January, 1959, in Copperas Saltpeter Cave, Clinton Co., Ky., and Sells Cave, Fentress Co., Tenn. (T.C.B.); data from unpublished records.

[3] Distributions based on material collected by the writer and determined by W. J. Gertsch.

terrain, where subterranean erosions proceeds concomitantly with surface erosion, and many cave streams are demonstrable tributaries of surface streams. Dispersal of a troglobite species is thus believed to be facilitated by a ramifying network of solutional openings beneath the slopes of valleys occupied by surface streams (cf. Barr 1959a and this symposium; Park, this symposium). Yet so many serious anomalies arise when this concept is hard-pressed (most commonly the occurence of one or two related species across a divide near the headwaters of an adjacent drainage system) that its pattern value may be critically questioned.

Although surface and subterranean erosion can and do take place in a limestone terrain simultaneously, they may not proceed at the same rate (Piper 1932), and surface and subterranean divides may not necessarily coincide. Furthermore, a large part of underground erosion is believed to take place beneath the water table (Bretz 1942). Terrestrial troglobites are distributed via the abandoned channels of ancient underground systems, the boundaries of which can conceivably overlap those of surface drainage basins. By a combination of overlap and underground stream piracy, hypothetical mechanisms can be elaborated by which a continuous system of solutional openings can extend completely through a limestone ridge separating two surface drainage basins. Ridges of insoluble clastic rocks, on the other hand, are very effective barriers. For example, the upper Elk River valley and the headwaters of Battle Creek are separated by the thick sandstones of the Cumberland Plateaus, which is less than three miles wide near Monteagle, Tennessee. On the west side of the Plateau (Elk drainage) the crayfish *Orconectes pellucidus australis* (Rhoades) and the cave fish *Typhlichthys subterraneus* Girard are abundant. In the Battle Creek valley caves years of exploration have never revealed *Typhlichthys.* Troglobitic crayfishes, though abundant, are not *Orconectes* but *Cambarus hamulatus* Cope and Packard (Hobbs and Barr, this symposium). Trechine carabids (*Pseudanophthalmus intermedius* Val., *P. lodingi humeralis* Val.) occur west of the Plateau, but a prolonged search for them in Battle Creek valley has been unproductive. When a limestone barrier is involved, the situation may be quite different. In the southeastern corner of the Central Basin of Tennessee, the valleys of the Elk and Duck Rivers are separated by Elk Ridge, composed of Ordovician limestone and capped with loose shale and chert. *Pseudanophthalmus tiresias tullahoma* Barr and an undescribed species of the millipede genus *Scoterpes* (det. by Nell B. Causey) occur in Duck valley caves in Coffee County and also in Elk valley caves in Bedford and Moore Counties. A distance of 12 to 15 miles intervenes.

Not only geomorphology but stratigraphy and geologic structure determine subterranean avenues of dispersal, and the student of cavernicole distribution can ill afford to ignore the contributions of these fields. Unfortunately for zoologists the investigation of cave origin and groundwater flow in limestone terrains is yet in its infancy For further details the reader is referred to the germinal works of Cvijič (1918), Martel (1921), Davis (1931), Piper (1932), and Bretz (1942), and to the reviews of Warwick (1953), Thornbury (1954), and Barr (1954, 1960c).

The contributions of biospeleology to the study of geographic isolation and its effect on speciation are considerable, yet the foregoing observations suggest that the vagility of different animals and the variable, usually incompletely known extent of different cave systems must be taken into account in individual cases. Furthermore, it must be understood that any provisional conclusions or generalizations are (in most instances) predicated upon patently inadequate data. It may be unequivocally stated that more collections are needed in each group of troglobites now known from the United States. We need more specimens of most of the described species in order to determine the ranges of morphological variation. We need to know with considerable precision the geographic distribution of each taxon, requiring collections from as many caves as possible. *A priori* notions of the degree of isolation in individual caves must be abandoned, and taxonomic interpretation must rest on morphological and, where incontrovertible, geological evidence. Finally, it seems quite probable that a substantial number of the extant species of cavernicoles have not yet been collected. This extrapolation is justified in two ways: (1) repeated visits to biologically rather well-known caves have resulted in the discovery of rare, previously unknown species; and (2) there are still many cave areas in the United States which have never been thoroughly investigated by an experienced biospeleologist.

As stated near the beginning of this discussion, American biospeleology has not fully emerged from the stage of discovery and description of cavernicole species. The application of cave studies to basic ecological problems must be delayed until at least the preliminary foundation has been laid by taxonomy. To further such groundwork this symposium has been arranged. The following collection of papers might more properly be designated a "progress report" than a symposium. If, however, it serves as a spur to further investigation and, for a time, as an introduction to the study of North American cavernicole speciation, then its goal will have been achieved.

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