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NORTH AMERICAN TROGLOBITIC SALAMANDERS

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JANUARY 1971

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BIOLOGY ISSUE

John E. Cooper and Thomas L. Poulson, Guest Editors

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North American Troglobitic Salamanders: Some Aspects of Modification in Cave Habitats, with Special Reference to *Gyrinophilus palleucus*

By Ronald A. Brandon*

ABSTRACT

Seven of the eight known species of troglobitic salamanders are found in North America. Of these seven, all closely related within the family Plethodontidae, only *Typhlotriton spelaeus* normally undergoes metamorphosis. There is ample evidence that the others, *Eurycea troglodytes*, *Gyrinophilus palleucus*, *Haideotriton wallacei*, *Typhlomolge rathbuni*, *Typhlomolge tridentifera*, and probably *Eurycea latitans*, are paedogenetic and reproduce while retaining larval body morphology. Of the last six, only *G. palleucus* is known to undergo major metamorphic change readily in response to experimentally administered thyroxin. The more highly specialized species tend to have more rigid control of paedogenesis, increased numbers of teeth, fewer trunk vertebrae, more reduced eyes, more reduced integumentary pigmentation, broader heads, flatter snouts, and more elongate and attenuate limbs. All of these features, except number of trunk vertebrae, are considered selectively advantageous to salamanders living under cave conditions; they probably evolved in response to food requirements and food availability and result in more efficient energy utilization by the population. Probable mechanisms in the evolution of these features are general neontenic trends and allometric growth changes. The number of trunk vertebrae seems related not to degree of specialization to cave habitats, but rather to the ancestry of the species.

Gyrinophilus palleucus, in several ways, seems to be the least specialized troglobitic salamander. It responds readily to thyroxin, its eyes are not greatly reduced, members of some populations are quite heavily pigmented, and in most regards it is similar to larvae of the epigean species *Gyrinophilus porphyriticus*. It is highly variable geographically, and has a range which is on the periphery of that of *G. porphyriticus*, from which species it may have arisen under changing climatic conditions of the Pleistocene.

INTRODUCTION

Of the more than 300 known species of salamanders, arranged in eight families

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(Brame, 1967), only eight species are troglobites (*sensu* Barr, 1960). These are obligative cave-dwellers and can complete their life cycles only in caves. Larvae of one species, *Typhlotriton spelaeus*, can be found in springs and spring-fed surface streams in

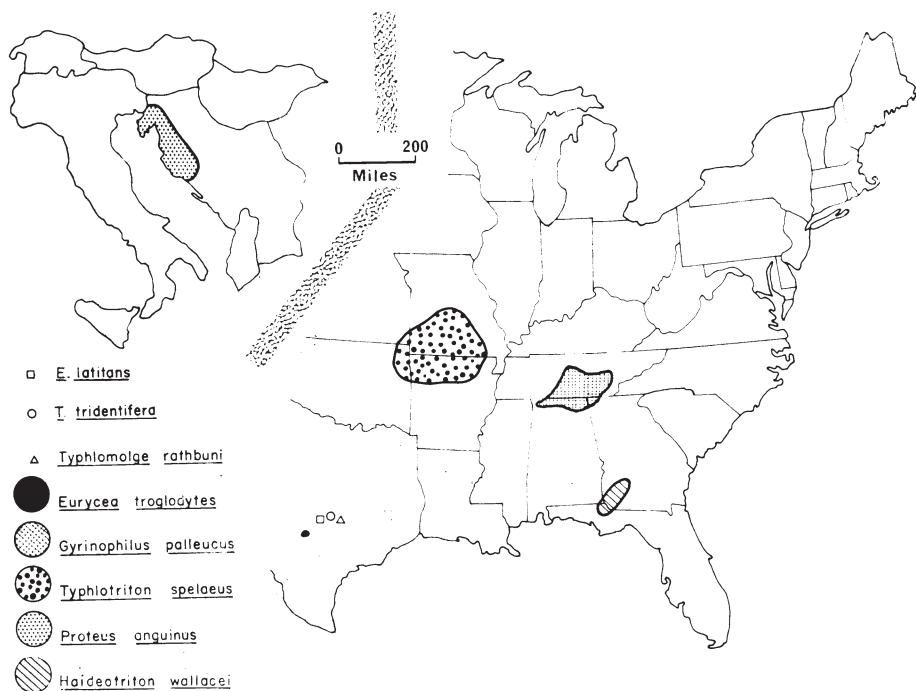


Figure 1. Distribution of troglobitic salamanders.

the vicinity of caves (and for this reason is not considered a troglobite by Vandel, 1964, or Poulson, 1964), but there is no evidence that they can transform outside of caves, and adults have not been found outside of caves. Except in rare instances when they may be washed out in flood waters, individuals of the other troglobitic species are never found in epigeal situations.

Only one troglobitic salamander, the proteid *Proteus anguinus* Laurenti, 1768, is known in the Old World. It occurs in karst regions along the eastern Adriatic coast, in Trieste and Yugoslavia (Figure 1). The remaining seven troglobitic species are all found in eastern United States; they are *Typhlomolge rathbuni* Stejneger, 1896; *Typhlomolge tridentifera* (Mitchell and Reddell, 1965); *Eurycea latitans* Smith and Potter, 1946; and *Eurycea troglodytes* Baker, 1957, all in the Edwards Plateau of Texas; *Haideotriton wallacei* Carr, 1939, in the Daugherty Plain of southwestern Georgia

and adjacent Florida; *Typhlotriton spelaeus* Stejneger, 1892, in the ozarkian Springfield and Salem plateaus; and *Gyrinophilus pallescens* McCrady, 1954, in Tennessee, northern Alabama, and northwestern Georgia. These seven species are all placed in the family Plethodontidae, the largest (containing about 180 species in 24 genera) and most diverse salamander family. The family Plethodontidae is thought to be indigenous to the Appalachian Mountains of eastern North America (Dunn, 1926; Wake, 1966), and, except for two species of *Hydromantes* in southern Europe, it is presently restricted to the New World. The only salamanders known to have invaded the tropics south of the equator are members of this family (the genus *Bolitoglossa* in South America).

Of all the troglobitic salamanders, only *Typhlotriton spelaeus* undergoes the complete metamorphosis common to the life cycles of most salamanders. In all other troglobitic species sexual maturity, mating,

and deposition of eggs apparently occur while the adult retains larval morphology. Natural metamorphosis does not occur and they are paedogenetic. Different amounts of metamorphic change can be induced experimentally in these salamanders, ranging from nearly complete metamorphosis in *G. paleucus* to only a very few metamorphic changes in *H. wallacei*. The paedogenetic adults of North American troglobitic salamanders are definitely of plethodontid larval morphology. They lack lungs (as do all members of this family and certain stream-dwelling members of three other families), have no ypsiloid cartilage, have three gill slits, and generally resemble plethodontid larvae externally. The paedogenetic species of *Eurycea* and *Gyrinophilus* closely resemble larvae of epigeal members of the same genera. *Typhlomolge rathbuni*, *T. tridentifera* and *Haideotriton wallacei* are more similar in structure to larvae of *Gyrinophilus*, *Pseudotriton*, *Eurycea* and *Typhlotriton* than to those of other plethodontids. Thus, not only are all North American troglobitic salamanders placed in the same family, but within the family they group closely and are probably closely related (cf. Wake, 1966).

CHARACTERISTICS
OF TROGLOBITIC SALAMANDERS

The striking convergence of morphology, eye reduction, and depigmentation in many

troglobitic invertebrates and in troglobitic fishes is also evident among the troglobitic salamanders. Similarly convergent, but more cryptic, features of physiology and ecology certainly exist, but have barely been investigated in troglobitic salamanders (cf. Poulson, 1964). There is a general trend toward more rigidly controlled paedogenesis, increased number of teeth, reduced number of trunk vertebrae, reduced eyes, reduced body pigmentation, broadening of the head and flattening of the snout, and elongation and attenuation of the limbs. The remainder of this paper deals in detail only with the North American species (Table 1).

Paedogenesis

Data indicating the paedogenetic nature of some of the troglobitic salamanders are circumstantial only, and perhaps the question of whether they are actually paedogenetic should be renewed and reviewed briefly here. Misinterpretations have occurred in the past when paedogenesis was assumed but not documented. *Gyrinophilus lutescens* (see Rafinesque, 1832; Mittleman, 1942; Brandon, 1966a) and *Typhlotriton nereus* (see Bishop, 1944; Brandon, 1966b) are good examples. *T. nereus*, described as a paedogenetic species, was based on larval, immature specimens of *T. spelaeus*. The name *G. lutescens*, as used by Mittleman for a paedogenetic species, was applied to immature larvae of *G. porphyriticus*.

TABLE 1. Sample of specimens examined, and known maximum snout-vent length of each species (in this, and subsequent tables and figures, all measurements are in mm).

Species	Maximum Known Body Length	Size Range of Specimens Examined	Number of Specimens Examined
<i>Typhlomolge rathbuni</i>	76	28-60	44
<i>Typhlomolge tridentifera</i>	37	19-34	20
<i>Haideotriton wallacei</i>	44	13-35	25
<i>Eurycea troglodytes</i>	40	22-40	13
<i>Eurycea latitans</i>	53	39-46	2
Larval <i>Typhlotriton spelaeus</i>	56	13-56	hundreds
<i>Gyrinophilus p. gulolineatus</i>	136	66-136	11
<i>Gyrinophilus p. necturoides</i>	105	48-105	19
<i>Gyrinophilus p. paleucus</i>	100	47-94	20

Following is a summary of information, some from the literature and some original, indicating paedogenesis in troglobitic salamanders found in North America.

Gyrinophilus pallescens.—Courtship, laid eggs, and newly hatched young have not been reported. Lazell & Brandon (1962) reported a male whose cloaca held a spermatophore. Dent & Kirby-Smith (1963) found that males of *G. p. pallescens* begin to produce sperm when they are 70 to 84 mm long (snout to vent), and that a female 100 mm long contained large (3.2 mm diameter) ovarian eggs. The testes of three male *G. p. gulolineatus* bore black pigment (Brandon, 1965b), a sign of sexual maturity in *G. porphyriticus* and many other plethodontids. These data, plus the nature of their response to metamorphic agents (Dent, et al., 1955; Dent & Kirby-Smith, 1963) make it clear that *G. pallescens* is normally neotenic, even though specimens readily and consistently undergo much metamorphic change in response to thyroxin experimentally administered.

Haideotriton wallacei.—Courtship and laid eggs have not been observed. The holotype, the largest specimen known (44 mm snout to vent) is a gravid female as Carr's (1939) photographs clearly show. It was preserved late in May. Valentine (1964) measured its ovarian eggs at 2 to 2.2 mm in diameter; these are probably nearly full size judging by size of mature eggs in other salamanders of comparable size—e.g., 2.5 to 3 mm in *Eurycea bislineata* (Bishop, 1941). I have examined the reproductive organs of 14 specimens ranging in snout-vent length from 13 to 28 mm. On the basis of their relatively undifferentiated gonads and reproductive tracts all are considered immature. Response of several subadults to treatment with thyroxin in Dundee's experiments (1962) (only slight metamorphic changes in the integument, loss of the coronoid bone in the lower jaw, and resultant death within 25 days) strongly suggests that *H. wallacei* does not transform in nature and will not under experimental conditions.

Typhlomolge rathbuni.—Courtship has not been observed nor have laid eggs been

described. Stejneger (1896, p. 620) commented that one living female specimen “. . . expelled three eggs after being caught . . .”, and that the body of another female contained large eggs. Dunn (1926) examined a female specimen whose spermatheca was packed with sperm. Both of Emerson's (1905) specimens were females, and her figures (fig. D & E on p. 69) and her textual description show that one was mature. Its oviducts were enlarged and convoluted, and its ovaries contained large (1.5 mm diameter), yolked ova. Enlarged and convoluted oviducts indicate sexual maturity in *Plethodon cinereus* (Saylor, 1966) and in several species of *Desmognathus* (Organ, 1961), and probably in *T. rathbuni* as well. I have examined the reproductive organs of 19 female specimens ranging from 33 to 60 mm snout to vent. Oviducts were enlarged and convoluted in the two largest specimens (58 & 60 mm), and these specimens contained yolked ovarian eggs 0.7 to 0.9 mm in diameter. In five specimens, considered immature (39, 42, 45, 45, 51 mm) the oviducts were small, straight, and medially placed; ovaries contained only small (0.2 to 0.4 mm diameter), unyolked ova. The gonads of two smaller specimens (33 & 37 mm) were not sufficiently differentiated for determination of sex by gross examination. Sexual maturity probably occurs at 40 to 50 mm snout-vent length in female *T. rathbuni*. This compares with an estimate of 40 mm for males based on testicular lobulation.

Humphrey (1922) showed, in *Desmognathus fuscus*, that a positive correlation exists between number of testicular lobes and age of mature males. The manner in which the spermatogenic wave passes through the testis causes a progressive increase in number of lobes throughout the life of the male. Organ (1961) used the number of lobes to recognize year classes of several species of *Desmognathus*, and a similar relationship between number of lobes and specimen length has been observed in some other salamanders: for example, in *Phaeognathus hubrichti* by Brandon (1965a)

and *Typhlotriton spelaeus* and others included below.

The number of lobes in males of *T. rathbuni* ranged from none to four in seven specimens examined, and relates well to specimen length (Figure 2). It is probable that individuals with 3 or 4 lobes have produced sperm 4 to 7 times previously (see Organ, 1961, for method of estimating). In sexually mature *T. rathbuni* the testicular lobes are finely reticulated with melanophores and interlobular portions of the testes and the vasa deferentia are solid black. Black pigment on these structures indicates sexual maturity in many other plethodontid salamanders and certainly does in *T. rathbuni* as well.

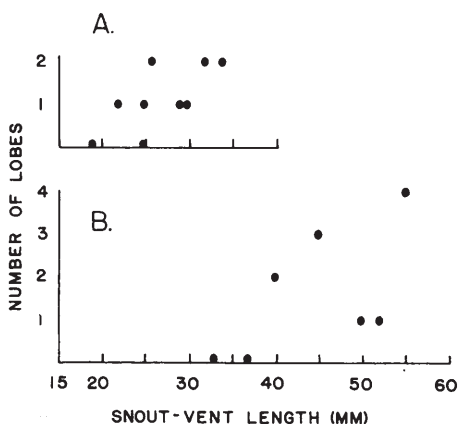


Figure 2. Correlation between snout-vent length and number of testicular lobes in *Typhlomolge tridentifera* (A) and *Typhlomolge rathbuni* (B).

Typhlomolge tridentifera.—Courtship and laid eggs are unknown. Most specimens in the type-series were identified to sex by Mitchell & Reddell (1965) but no criteria for recognizing mature individuals were given. I have examined reproductive organs of 18 specimens: eight males, nine females, and one undetermined juvenile. The number of testicular lobes ranges from none to two in specimens 22 to 34 mm long (Figure 2). Lobes of the two-lobe males were heavily reticulated with black pigment and the vasa deferentia and interlobular spaces of

the testes were black. Cloacal lips were swollen conspicuously and appeared to be glandular on the two largest males, were less distinctly swollen on two males, and were not swollen at all on three. I would judge the 34, 32, 30, and 26-mm males to be adult and sexually active. The 29-mm male looked adult but sexually inactive, one 25-mm male and the 22-mm one seemed to be approaching maturity, and another 25-mm male looked immature. Sexual maturity, therefore, seems to be reached in males 22 to 25 mm long. Females also appear to mature at about 25 mm. Immature females (20, 22, 23, 25 mm long) had small, medially placed oviducts and tiny (0.15 to 0.2 mm diameter), unyolked ovarian ova. Females with enlarged and convoluted oviducts were 27, 28 (3), and 30 mm long, and two of these contained enlarging (0.6 to 1.5 mm diameter), yolked ovarian ova.

Eurycea latitans.—Courtship and laid eggs are unknown, and extremely little information of any kind is available on this species. The maximum known snout-vent length is about 53 mm (Brown, 1967). Smith & Potter (1946) included some information on reproductive structures in their description of this species. For example, they mentioned (p. 107) that two of their female specimens under 53 mm snout-vent “. . . possess very large eggs presumably nearly ready to be laid”, and that “The males, regardless of date of collection, are rather well marked by the swollen glandular area about the anus.” Brown (1967) noted that a swollen glandular vent is a feature of mature males. It should be pointed out that the holotype, USNM 123594, identified originally as an adult male, actually is a female whose oviducts are slightly enlarged and whose ovaries contain numerous small (0.5 mm diameter) ova. The specimen listed by Smith and Potter (1946) as TCWC 1195, a paratype and the only additional specimen which I have been able to borrow for examination, is a mature male whose darkly pigmented testes are composed of one large and one small lobe each.

Eurycea troglodytes.—Nothing is reported about courtship or laid eggs. Known speci-

mens range from 23 to 40 mm snout-vent. Baker (1957) identified the 38-mm holotype as a sexually mature female, apparently on the basis of its folded cloacal walls. He did not comment on the size at sexual maturity or criteria for determining maturity; the body cavities of neither the holotype nor twelve paratypes which I have seen had been opened. I have examined the reproductive organs of the holotype (a female) and 6 paratypes (3 males, 3 females). Preservation of internal organs is poor, but all specimens over 23 mm snout-vent appear mature. Four of the females (32 to 40 mm) have straight, medially placed, slightly enlarged oviducts and numerous small (0.2 to 0.6 mm diameter) ovarian ova. The poor preservation makes it impossible to determine if the largest ova are yolked; the specimens appear mature but sexually inactive. The males (32 to 39 mm long) all have black vasa deferentia and darkly reticulated testes. The number of testicular lobes ranges from 1 to 3. All of the males, thus, are sexually mature. Sexual maturity probably occurs at around 25 to 30 mm snout-vent in this species.

In summary, there is ample evidence of sexually mature, branchiate individuals of all of the North American troglobitic salamanders except *Typhlotriton spelaeus* and *Eurycea latitans*. Indications are that the latter actually is paedogenetic as well.

In all instances in the family Plethodontidae, paedogenesis is correlated with ecological restriction to cave or spring habitats. The only non-cavernicolous paedogenetic plethodontids are *Eurycea tynerensis* and some populations of *E. multiplicata* which inhabit springs and spring-fed streams along the southwestern edge of the Ozark Plateau, and several more species of *Eurycea* (*E. nana*, *E. neotenes*, *E. pterophila*) in springs along the Balcones Escarpment in Texas. All other paedogenetic plethodontids are troglobites, and all of the troglobites, except *T. spelaeus*, are paedogenetic. It should be pointed out that paedogenesis and neoteny do occur in other salamander families, but in them (with the exception of *Proteus anguinus* in the family Proteidae) is not

correlated with dwelling in spring and cave habitats.

Paedogenesis is probably of adaptive value to troglobitic salamanders and certainly is not merely a phenotypic response to cave climatic conditions. In some way the rather elaborate changes which take place in the usual pattern of salamander metamorphosis are avoided. *P. anguinus* has an active thyroid gland, but its tissues do not respond to thyroxin (Schreiber, 1933). *H. wallacei* and *T. rathbuni* respond only slightly to large experimental doses of thyroxin, even though their thyroid follicles secrete and release hormone (Dundee, 1957, 1962; Gorbman, 1957); the treatment usually is fatal. *G. pallescens* readily undergoes almost complete metamorphosis during thyroxin treatment, but the thyroid gland normally maintains a low level of activity (Dent and Kirby-Smith, 1963). No metamorphosed individual of *G. pallescens* has ever been found in nature, but a few have transformed "spontaneously" in the laboratory (Dent & Kirby-Smith, 1963). Since at least three paedogenetic species of *Eurycea* (*E. tynerensis*, *E. nana*, and *E. neotenes*) are known to undergo metamorphic changes after thyroxin treatment (Kezer, 1952; Potter & Rabb, 1959), it is likely that *E. troglodytes* and *E. latitans* may give similar responses when tested. Dundee and Gorbman (1960) have shown that *E. tynerensis* is paedogenetic probably due to a low level of thyroxin synthesis.

There seem to be at least two different mechanisms resulting in paedogenesis in troglobitic salamanders: (1) loss of target tissue sensitivity, and (2) low production of thyroxin. Paedogenesis seems to have survival value regardless of the mechanism by which it is obtained. In more specialized troglobites resistance to metamorphosis is more rigidly controlled; *i. e.*, environmental variables and experimental treatments will not induce a successful metamorphosis. *G. pallescens*, a relatively unspecialized troglobite morphologically, does not "resist" environmentally or experimentally induced metamorphosis, although metamorphosis in nature seems to be extremely rare if it occurs at all.

Adults of *Typhlotriton spelaeus* have no paedogenetic features, with the possible exception of a delayed metamorphosis of the premaxillary bone (Wake, 1966). Accordingly, Vandel (1964) and Poulson (1964) do not consider *T. spelaeus* a troglobite at all since, in addition, its larvae are sometimes common in surface waters. Barr (1963) and Brandon, on the other hand, do consider *T. spelaeus* a troglobite. Adult *T. spelaeus* are restricted ecologically to cave habitats, and apparently can complete their life cycle only there. In addition they are distinguished morphologically by reduced body pigmentation and reduced eyes. A recurrent idea in the literature (*e. g.*, Noble, 1927; Mittleman, 1950; Conant, 1958; Vandel, 1964) is that larvae of *T. spelaeus* live primarily in cave entrances and surface streams and that as metamorphosis approaches they retreat into caves. Actually, there is no evidence that this is the usual sequence of events, or that significant numbers of surface-dwelling larvae actually do return to caves. It is probable that subsequent generations are produced mainly by larvae that never leave the caves at all, and that rather high mortality prevails among epigeal larvae. Such large numbers of larvae in above-ground situations, however, does suggest that epigeal dispersion may be important in this species. *T. spelaeus* has the largest geographic range of any troglobitic salamander and yet varies little geographically.

Avoidance of metamorphosis in troglobitic salamanders is probably related to food requirements and food availability. Most available food items deep within caves are aquatic, either aquatic cavernicolous invertebrates or organisms washed in from outside. Even transformed *T. spelaeus*, which are essentially terrestrial, can feed heavily on aquatic animals (Smith, 1948). Food in caves is usually scarce (Poulson, 1964). Avoidance of metamorphosis greatly reduces the energy requirements of the individual and of the population. In addition, neuro-masts typically degenerate when larval plethodontid salamanders transform. These sense organs are sensitive to water move-

ments, and would be important in nonvisual feeding behavior. As Poulson has also pointed out, it is likely that some apparently neotenic features are really secondary, allometric effects of selection for lower developmental and growth rates in response to food scarcity.

Number of Teeth

Tooth counts most commonly made on salamander larvae are of those on the premaxillary, prevomerine (vomerine of some authors), and pterygoid (palatine or palatopterygoid of some authors) bones. Data on number of teeth on the lower jaw (on the dentary and coronoid bones) have seldom been given, and I have not counted these either. Seldom are counts of samples throughout the size range of a species given in the literature. Statements of average tooth numbers are seldom comparable because of ontogenetic changes in number. Counts of premaxillary teeth from *T. tridentifera* of known body size, however, are given by Mitchell & Reddel (1965).

I have counted teeth on a series of specimens of each troglobitic species, except *E. latitans*, using a binocular microscope at 15-20x, on specimens whose jaws were cut to reveal the entire roof of the mouth. Data on larval *T. spelaeus* can be found elsewhere (Brandon, 1966b), as can some information on *T. tridentifera* (Mitchell & Reddel, 1965), *E. latitans* (Smith & Potter, 1946), and *H. wallacei* (Valentine, 1964).

In each species examined, except *G. palleucus*, there is a distinct ontogenetic increase in number of premaxillary teeth (Figures 3 and 4). *T. rathbuni* and *H. wallacei* have the most and larval *T. spelaeus* and *E. latitans* have the fewest. Data on the latter, however, are available from only two specimens. *G. palleucus*, at all sizes, has more than larvae of its epigeal congener *G. porphyriticus*. *T. tridentifera* and *E. troglodytes* have an intermediate number and do not differ from each other.

The number of prevomerine teeth increases distinctly with ontogeny in *H. wallacei*, *T. tridentifera* and larval *T. spelaeus*, slightly in *G. palleucus*, but not in *T. rathbuni* or *E. troglodytes* (Figures 5 and 6).

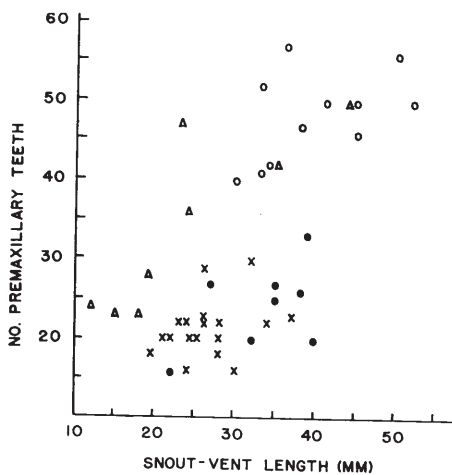


Figure 3. Number of premaxillary teeth versus snout-vent length in *Haideotriton wallacei* (triangles), *Typhlomolge rathbuni* (open circles), *Typhlomolge tridentifera* (X) and *Eurycea troglodytes* (solid circles).

The number is reported to be low in *E. latitans* (Smith & Potter, 1946). Among larger specimens, *H. wallacei*, *T. rathbuni* and *T. tridentifera* have the most prevomerine teeth, whereas *E. troglodytes*, *E. latitans* and *G. palleucus* have fewer, although data are not comparable because of the difference in ontogenetic increase. Again, *G. palleucus* generally has more than larvae of its relative *G. porphyriticus*.

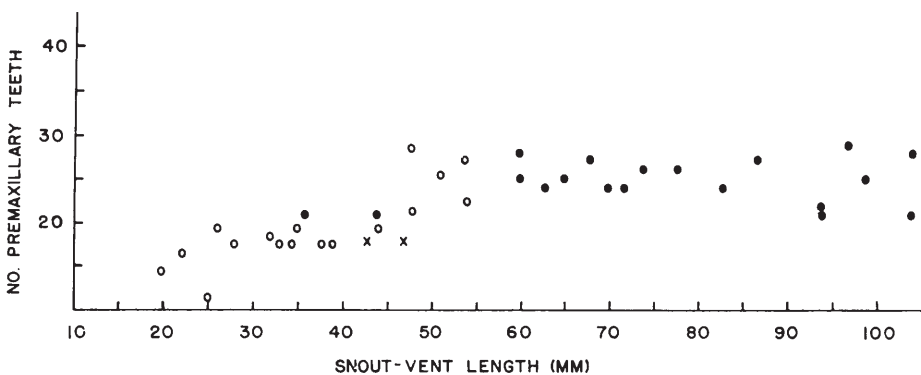


Figure 4. Number of premaxillary teeth versus snout-vent length in larval *Typhlotriton spelaeus* (open circles), *Eurycea latitans* (X), and *Gyrinophilus palleucus* (solid circles).

An ontogenetic change from a broadly elongate patch of pterygoid teeth to fewer teeth arranged in a single row occurs about half-way through larval life in *T. spelaeus* (Brandon, 1966b), perhaps in *E. troglodytes*, and in at least two epigeal species of *Eurycea* (*E. lucifuga* and *E. multiplicata*). Even in the smallest specimens of the other troglobites examined, these teeth were arranged in a single row, as they were in larval *G. porphyriticus*. Interestingly, *H. wallacei* has generally fewer pterygoid teeth than all other species examined, except large, larval *T. spelaeus* and larval *G. porphyriticus* (Figures 7 and 8). Of those species with these teeth in a single row throughout ontogeny, *T. rathbuni* has the most, followed by *T. tridentifera*, *E. troglodytes* and *E. latitans*, *G. palleucus*, and *H. wallacei*.

The correlation between increased numbers of teeth and specialization to cave habitats has been pointed out previously (Baker, 1957), at least for paedogenetic forms inhabiting the Edwards Plateau in Texas. The increased numbers of premaxillary and prevomerine teeth in more specialized troglobites is probably correlated with increased efficiency in catching and holding prey in an environment where the population density of prey organisms is low.

Reduction of Eyes

The detailed histological structure of the eyes of several of the troglobitic salamanders

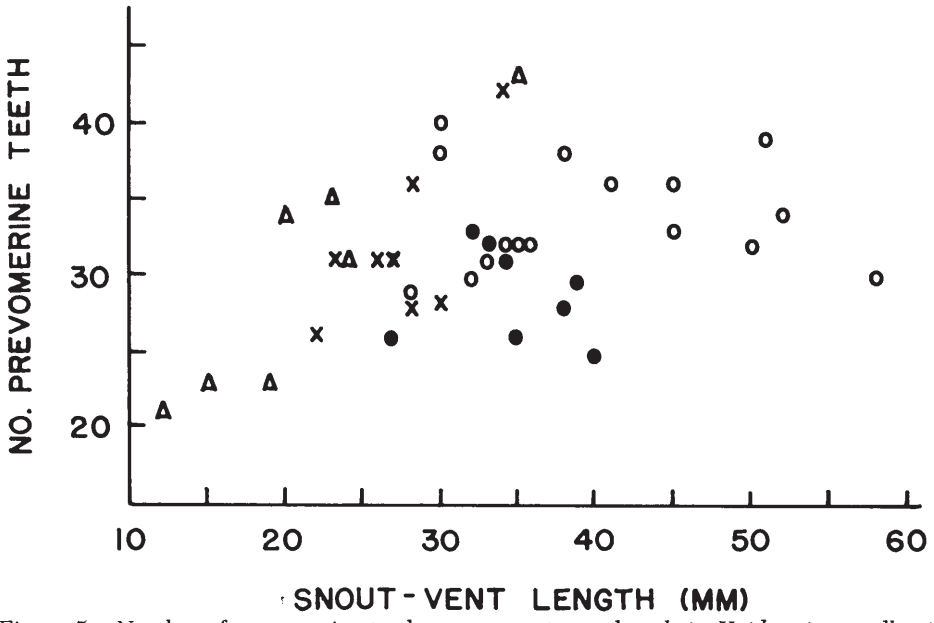


Figure 5. Number of prevomerine teeth versus snout-vent length in *Haideotriton wallacei* (triangles), *Typhlomolge rathbuni* (open circles), *Typhlomolge tridentifera* (X), and *Eurycea troglodytes* (solid circles).

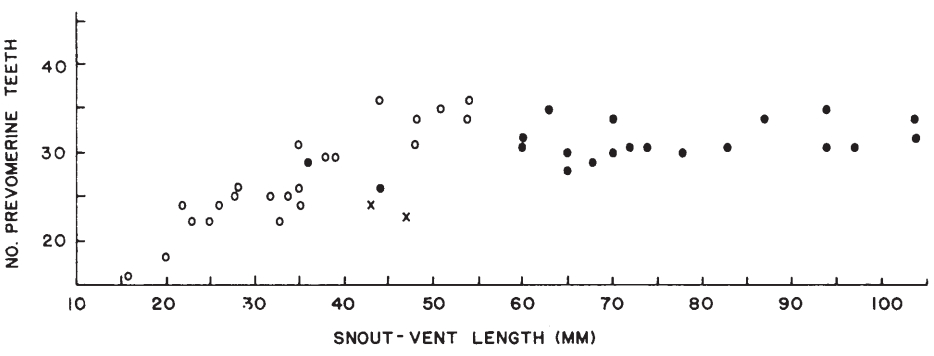


Figure 6. Number of prevomerine teeth versus snout-vent length in larval *Typhlotriton spelaeus* (open circles), *Eurycea latitans* (X), and *Gyrinophilus palleucus* (solid circles).

has been investigated: e. g., of *T. rathbuni* (Eigenmann, 1900), *T. spelaeus* (Eigenmann & Denny, 1900; Alt, 1910; Stone, 1964), *G. palleucus* (Lazell & Brandon, 1962; Dent & Kirby-Smith, 1963), and *H. wallacei* (Brandon, 1968). For other species only general comments or information on gross eye size are available. For example,

Baker (1957) included information on eye diameter in series of *E. latitans*, *E. troglodytes* and *T. rathbuni* of known body length, and showed a progressive decrease in eye size through this series. Mitchell & Reddell (1965) listed eye diameters of several specimens of *T. tridentifera* of known body lengths and noted that about one-half of the

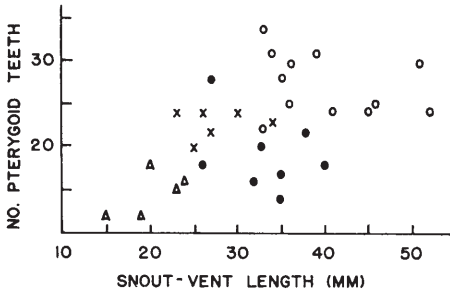


Figure 7. Number of pterygoid teeth versus snout-vent length in *Haideotriton wallacei* (triangles), *Typhlomolge rathbuni* (open circles), *Typhlomolge tridentifera* (X), and *Eurycea troglodytes* (solid circles).

eyes lacked lenses; they further noted that in a series of *E. troglodytes* all had lenses.

Eye reduction involves both decrease in eye size and histological simplification. Among those species living in the Edwards Plateau of Texas, the progression from largest to smallest eyes runs from *E. latitans* to *E. troglodytes* to *T. tridentifera* to *T. rathbuni*, but the progression of histological degeneration and maximum eye degeneration in this series are not known.

The eyes of *G. palleucus* are small and comparable in size to those of *E. troglodytes*. Although smaller than those of *G. porphyriticus* of comparable body length,

they apparently are functional under lighted conditions (Besharse and Brandon, unpublished) and are not degenerate histologically (Lazell and Brandon, 1962; Dent and Kirby-Smith, 1963).

Ontogeny of eye structure in *T. spelaeus* represents a special case since the eyes may be functional in larvae which live under lighted conditions in springs and spring runs, but are not functional in the strictly cavernicolous adults. The differing selective pressures on larvae and adults, therefore, have resulted in larval eyes which are relatively large, histologically complete and, in all but the largest larvae, perceptive. During and after metamorphosis tissue degeneration sufficient to cause blindness occurs (Stone, 1964), but the adult eyes still are not as degenerate as those of *T. rathbuni*, *H. wallacei* or *P. anguinus*. Stone's (1964) observation that some large larvae with histologically normal eyes behaved as though they were blind suggests that the initiation of blindness may be extraoptic. Eye degeneration at metamorphosis in *T. spelaeus* includes changes in the ganglionic and bacillary layers, loss of the outer plexiform layer, atrophy of the optic nerve, recession of the eyeball, and fusion of the eyelids over the eye with accompanying invasion of the cornea by integumentary cells.

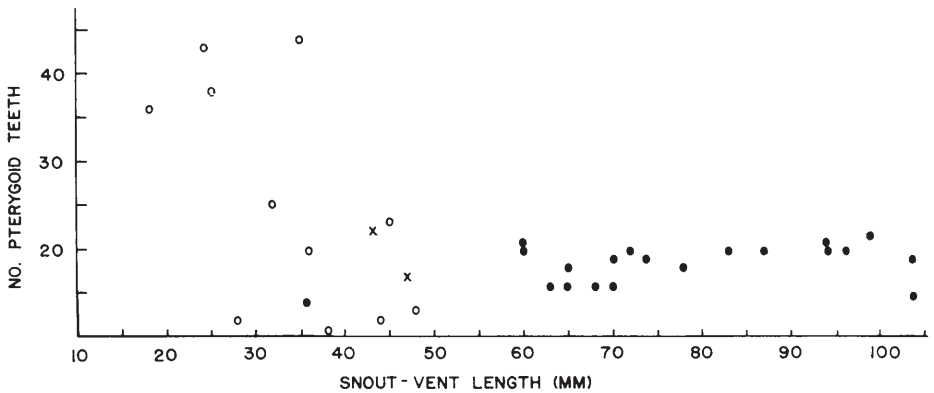


Figure 8. Number of pterygoid teeth versus snout-vent length in larval *Typhlotriton spelaeus* (open circles), *Eurycea latitans* (X), and *Gyrinophilus palleucus* (solid circles).

Histological studies of the tremendously reduced eyes of *P. anguinus*, *T. rathbuni* and *H. wallacei* suggest arrested development of the secondary optic vesicle followed, possibly, by some degeneration (Schlampp, 1892; Hawes, 1946; Brandon, 1968). These three species seem to differ somewhat in degree of differentiation prior to arrest, but ontogenetic changes in eye structure have been studied well only in *P. anguinus*. Of these three species *H. wallacei* has the smallest, most compact, least differentiated eyes (Brandon, 1968), and *P. anguinus* the largest and most highly differentiated. The eyes in these salamanders certainly are incapable of image perception and probably are not particularly sensitive to light intensity either (see Hawes, 1946; Pylka & Warren, 1958). Comparative examinations of embryonic and young larval eyes to determine the maximum extent of eye differentiation should be made on the most highly specialized troglitic species.

There have been numerous attempts to outline mechanisms which would explain satisfactorily present-day eye structure in troglitic salamanders, and in troglitic animals generally. The importance of pre-adaptation usually has been stressed with ample justification (see references listed in Poulson, 1964). Adaptation to some kinds of epigean habitats would lead populations into cave-like habitats and into caves themselves.

Early explanations of eye reduction in troglitic animals were couched in Lamarckian terms of degeneration of unused organs. A similar, but more sophisticated idea, that eyes in troglites are selectively neutral and in the absence of stabilizing selection are lost through accumulation of random mutations, has been popular (Hubbs, 1938; Poulson, 1964; Deamer, 1964). Vandel (1964) has recently supported the curious idea that reduced eyes are a feature of "senile" species which can no longer exist among competitors in epigean habitats, but can survive as re-

licts in caves. According to this idea the "regressive" features of troglites result not from subterranean life, but rather from great phyletic age and resultant species senescence.

Curiously, reduction of eye structure through the ordinary mechanism of evolutionary change, that is, natural selection, has generally been considered unimportant, with the notable exception of Barr's (1968) analysis. The often elaborate alternative explanations have been based on the assumption that well formed eyes are selectively neutral in a cave-dwelling salamander. There actually is no reason to assume such a thing, and there is considerable reason to think that such is not true. Mayr (1963) convincingly doubted that any gene can remain selectively neutral since gene actions may be intimately interrelated and far reaching. It seems highly unlikely that the complex genetic base required for eye differentiation and function would have no pleiotropic influences on phenotypic success. Rosen (1967) argued essentially the same point from the view of optimality theory. It seems likely that selection would operate to reduce eyes in the interest of energy economy.

Eye structure, as well as general body form, of the most specialized troglitic salamanders is largely the result of neotenic trends. Energy conservation resulting from avoidance of metamorphosis may also influence retention in adults of other body features characteristic of early ontogeny. This would be true particularly of structures, such as eyes, which apparently have no important function in cave habitats, but whose presence could be detrimental by requiring energy for differentiation and by providing susceptible sites for mechanical and infectious injury. Natural selection would cause eyes to become less and less differentiated in adults and cranial features to become more embryonic. Hawes, for example (1946), has pointed out adult chondrocranial features in *P. anguinus* which are embryonic in other salamanders.

Wake (1966) noted that the orbitosphe-
noid, which ossifies in larvae of other ple-
thodontid salamanders and is ossified in
adults of other paedogenetic species, never
does ossify in *H. wallacei*, *T. rathbuni* or
T. tridentifera.

Body Pigmentation

Contrary to even recent statements in the
literature that certain troglobitic salaman-
ders lack pigment (*e. g.*, Deamer, 1964;
Vandel, 1964; Wake, 1966), all known
species do have integumentary melano-
phores and retinal melanin. Integumentary
xanthophores can be seen on living *H. wal-
lacei*, and other species probably possess
these as well (see Mohr and Poulson, 1966,
p. 131). In addition, the testes and vasa
deferentia of adult male *G. pallucus*, *T.
rathbuni*, *T. tridentifera* and *E. troglodytes*
are marked with melanophores. Peritoneal
melanophores are present in adult *T. spela-
eus*, *G. pallucus*, *T. rathbuni*, *T. tridenti-
fera*, and *E. troglodytes* which I have seen,
but adult specimens of *H. wallacei* and *E.
latitans* were not available for study.

As a general observation, pigment on the
body surface seems to have been reduced
more than pigment in the peritoneum. Some
adult *T. rathbuni* and *T. spelaus*, for exam-
ple, are more heavily pigmented internally
than externally.

Of the troglobitic salamanders, some
populations of *G. pallucus* are the most
intensely pigmented externally and are
marked with dark spots on a moderately
dark background. Considerable geographic
variation exists in this species, and some
populations are fairly pale. At the other
extreme, the bodies of *H. wallacei*, *T.
rathbuni* and *T. tridentifera* are covered
by relatively few, scattered melanophores
which form no particular pattern; as a re-
sult, the skin has a pale, almost translucent
appearance. Hemoglobin is especially visi-
ble in blood vessels of the gills and limbs
of these species (see Mohr and Poulson,
1966, pp. 99, 131). Ontogenetic regression
of body pigmentation as well as eye struc-
ture occurs in *T. spelaus*. Larvae, especi-

ally those exposed to sunlight, may be
intensely pigmented, whereas larger, cav-
ernicolous larvae and postmetamorphic in-
dividuals are uniformly covered with melano-
phores and the body appears grayish.
The bodies of *E. troglodytes* and *E. latitans*
both bear faint patterns, the latter more
distinctly, but both apparently are less
heavily pigmented than larvae of epigeal
species of *Eurycea*.

There is a positive correlation between
degree of depigmentation and degree of
specialization to cave habitats reflected in
other body features such as neoteny, eye
reduction, tooth numbers, and increasing
head size. Poulson (1964) attempted to ex-
plain depigmentation as a secondary, adap-
tively neutral, result of altered allometric
growth patterns resulting from selection for
slower growth rates. He also commented
that as in the case of eyes pigment may be
reduced by selection through energy econ-
omy. In my opinion the latter is the simpler
and more likely explanation.

Number of Trunk Vertebrae

The most highly specialized North Ameri-
can troglobitic species have among the
fewest trunk vertebrae in the family Ple-
thodontidae (Wake, 1966). It also happens
that among the troglobitic salamanders the
number is directly correlated with degree
of specialization as judged by other criteria
(Table 2). This has led to the conclusion,
probably unwarranted, that a reduction in
number of vertebrae results from troglobitic
specialization (Baker, 1957; Mitchell &
Reddell, 1965). Wake (1966) has pointed
out that in the family Plethodontidae a low
number of trunk vertebrae is probably a
primitive feature, and that the tendency
toward trunk elongation in a genus such as
Eurycea represents specialization. In the
genus *Eurycea* the number of vertebrae
ranges from 14 to 22. The fewest are found
in the eastern species *E. bislineata*, *E.
aquatica*, *E. longicauda* and *E. lucifuga*.
The most are found in the neotenic *E.
tynerensis* which inhabits small, spring-fed
streams in the ozarkian Springfield Plateau,

TABLE 2. Number of trunk vertebrae in North American troglobitic salamanders and some additional species of *Eurycea*.

Species	Number of Vertebrae									
	13	14	15	16	17	18	19	20	21	22
<i>Typhlomolge</i>										
<i>rathbuni</i>	35									
<i>tridentifera</i>	3	11								
<i>Haideotriton</i>										
<i>wallacei</i>	18	2								
<i>Eurycea</i>										
<i>trogloodytes</i>			2	6	4					
<i>latitans</i> *				2	1					
<i>neotenes</i> **					x	x				
<i>pterophila</i> **					x	x				
<i>nana</i> **							x	x		
<i>tynerensis</i> ***								x	x	x
<i>multiplicata</i> ***								x	x	
<i>Typhlotriton</i>										
<i>spelaeus</i>					2	85	60	2		
<i>Gyrinophilus</i>										
<i>palleucus</i>						25	45	2		

* Some data taken from Smith & Potter, 1946.
 ** Data taken from Baker, 1957.
 *** Data taken from Dundee, 1965 a, b.

and in *E. multiplicata* which has a similar but broader range and neotenic tendencies. The non-troglobitic, paedogenetic species of *Eurycea* in the Edwards Plateau of Texas are intermediate in number between the ozarkian species and the Edwards Plateau troglobites.

It may be that the low number of vertebrae in *T. rathbuni*, *T. tridentifera* and *H. wallacei* [the latter is definitely similar to species of *Eurycea* and closely related to them (Wake, 1966)] has nothing to do with adaptation to cave habitats, but rather indicates that they arose from a primitive *Eurycea* stock.

The number of trunk vertebrae in the series from *T. rathbuni* to *T. spelaeus* in Table 2 may indicate the relative time sequence of isolation and differentiation of the various forms from an ancestral stock gradually increasing in vertebral number.

The low number of vertebrae may be relictual rather than specialized.

The two troglobites with the broadest geographic ranges, *T. spelaeus* and *G. palleucus*, show geographic variation in number of trunk vertebrae. The range of number in *G. palleucus* is the same as in its epigeal congener *G. porphyriticus* (Brandon, 1966a). Geographic variation in *T. spelaeus* is clinal (Brandon, 1966b), and seems to be clinal also in *G. palleucus* (Brandon, 1965b and unpublished data) although some populations may be isolated.

Broad, Flattened Heads

Some of the troglobitic salamanders characteristically have proportionally larger heads than most salamanders have, and in addition the snouts are elongate, flattened, broadened and truncate. The most extreme example of this is in *T. rathbuni*, and to a progressively decreasing degree it occurs

in *T. tridentifera*, *G. palleucus*, *H. wallacei*, *T. spelaeus*, *E. latitans* and *E. troglodytes* (see profile sketches in Mitchell & Reddell, 1965, and Brandon, 1966a). Flattening and broadening of the head are not restricted among salamanders to cave-adapted species, but are found also in such bottom dwellers as the mudpuppy (*Necturus* spp.) and the hellbender (*Cryptobranchus alleganiensis*). Among fishes and amphibians living as bottom dwellers in still or slowly moving waters, broadening and flattening of the head are rather common.

The altered head shape, by providing a broader gape, may result in more efficient feeding movements. In addition, Walters and Walters (1965), extrapolating from the relation between head size and lateral line development in amblyopsid cave fishes (Poulson, 1963), have suggested that the broad, blunt snout in cavernicolous populations of the poeciliid fish *Poecilia sphenops* is a structural adaptation to facilitate nonvisual navigation. Broad heads of troglobitic salamanders probably also result in more efficient functioning of neuromasts. The importance of neuromasts in locating aquatic prey under conditions of total darkness may also have been a strong inducement in selection for neoteny.

Poulson (1963) has shown that the mechanism bringing about a proportional increase in head size in troglobitic fishes

involves altered allometric growth patterns. There are differences in relative growth rate of the head in different troglobitic salamanders, as indicated by differences in slopes of regression lines fitted to plots of head width and length versus body length (Table 3). Generally, the head increases in size relatively faster ontogenetically in the more highly specialized species. Thus, the head appears particularly large in large, adult individuals of *T. rathbuni* and *G. p. gulolineatus*. There are rather great differences in relative growth rate of the head in the subspecies of *G. palleucus*.

Attenuation of Limbs

One of the most striking morphological features of *T. rathbuni* is its long, slender legs. Comparative data on leg attenuation and elongation in other troglobitic salamanders, however, are not easily obtained. Usually elongation has been expressed as the ratio between body length and leg length either by direct measurements or by overlapping of appressed legs. Such information, however, could be used just as well to show shortening of the body rather than elongation of the legs. Since troglobitic salamanders differ in number of trunk vertebrae from 13 to 20, and therefore differ in body elongation, some sort of adjustment ought to be made when comparing leg lengths between species. If 13 trunk verte-

TABLE 3. Slopes of regression lines, calculated by the least squares method, for plots of head width and head length against body length in North American troglobitic salamanders.

Species	Head Width b	Head Length b
<i>Typhlomolge tridentifera</i> *	0.244	0.356
<i>Typhlomolge rathbuni</i>	0.203	0.319
<i>Gyrinophilus p. gulolineatus</i>	0.200	0.258
<i>Haideotriton wallacei</i>	0.190	0.229
<i>Gyrinophilus p. necturoides</i>	0.161	0.235
<i>Typhlotriton spelaeus</i>	0.147	0.244
<i>Gyrinophilus p. palleucus</i>	0.134	0.229
<i>Eurycea troglodytes</i>	0.118	0.138

* Measurements taken directly from Mitchell & Reddell, 1965.

brae are considered a standard body length, then leg length can be compared more meaningfully among the species as the ratio of leg length to the "adjusted" body length, because variation in length of vertebrae is considerably less than variation in body length. "Adjusted body length" is the portion of the total snout-vent measurement which results from the head and 13 trunk vertebrae.

Even when comparisons are based on adjusted body lengths, *T. rathbuni*, at all size classes, has the longest legs (Figure 9). Those of *G. p. gulolineatus* are second longest, and are considerably longer than those of *G. porphyriticus* and other subspecies of *G. pallescens*. These data, and others not elaborated here, suggest that *G. p. gulolineatus* may actually be a separate species.

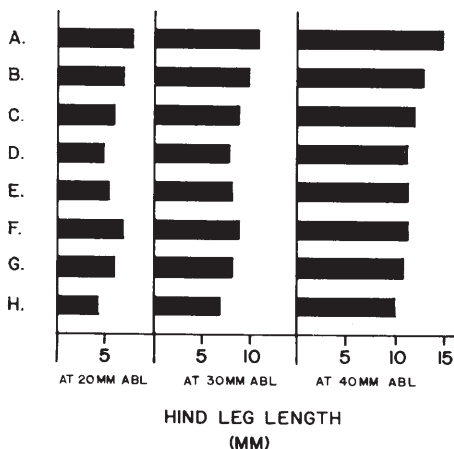


Figure 9. Comparison of hind leg length at three different body lengths in North American troglobitic salamanders. ABL refers to "adjusted body length" as defined in the text. Values of leg length are taken from regression lines fitted to plots of hind leg length versus "adjusted body length". *Typhlomolge rathbuni* (A), *Gyrinophilus pallescens gulolineatus* (B), *Typhlomolge tridentifera* (C), *Haideotriton wallacei* (D), *Typhlotriton spelaeus* (E), *Eurycea troglodytes* (F), *Gyrinophilus pallescens pallescens* and *G. p. necturoides* (G), and *Eurycea latitans* (H).

The legs of *H. wallacei*, *T. tridentifera* and *T. rathbuni* have the appearance of being rather elongated partly because their bodies are short, but also because the legs are attenuated. At small body sizes *E. troglodytes* actually has proportionally longer legs than the more highly specialized *T. tridentifera*; but those of the latter are more slender. The differences between the various troglobitic species in relative leg length are most striking when large specimens are compared, because of allometric growth differences (Table 4). The remarkably elongated legs of *T. rathbuni*, especially of larger specimens, result from a high relative growth rate; they appear even more remarkable because they are attenuate. Legs of *H. wallacei* and *T. tridentifera* are also noticeably attenuate. While there is a big difference between *G. p. gulolineatus* and the other nominal subspecies of *G. pallescens* in relative leg growth, as well as in actual leg length, those of *G. p. gulolineatus* are not attenuated. *E. latitans* is puzzling; its legs are short, but they show surprisingly high positive allometry.

The most likely function of elongated limbs is to raise the body, and particularly the head, above the substrate (Poulson, 1964; Wake, 1966). The excellent photographs in Herald (1952), Mitchell & Reddell (1965) and Mohr & Poulson (1966) show how *T. rathbuni* and *T. tridentifera* stand with their heads lifted high above the substrate. The slow, intermittent locomotion, with body raised, permits greater efficiency in detection of moving prey by the neuromast system. Poulson (1964) also pointed out that longer limbs permit the salamanders to search a larger area per unit of energy expended.

ORIGIN OF *Gyrinophilus pallescens*

The primitive eastern North American genus *Gyrinophilus* contains two polytypic species, the epigean *G. porphyriticus* and the troglobitic *G. pallescens*. *Eurycea* is the only other genus of salamanders known to contain both epigean and troglobitic species.

TABLE 4. Slopes of regression lines, calculated by the least squares method, for plots of hind leg length against "adjusted" body length in North American troglobitic salamanders.

Species	Hind Leg Length b
<i>Typhlomolge rathbuni</i>	0.359
<i>Haideotriton wallacei</i>	0.329
<i>Eurycea latitans</i> *	0.291
<i>Typhlomolge tridentifera</i> **	0.287
<i>Typhlotriton spelaeus</i> (larvae)	0.215
<i>Gyrinophilus p. gulolineatus</i>	0.211
<i>Eurycea troglodytes</i>	0.190
<i>Gyrinophilus p. pallaeus</i> and <i>G. p. necturoides</i>	0.155

* Data from Baker, 1957.

** Some data taken from Mitchell & Reddell, 1965.

G. porphyriticus is a metamorphosing species ranging from eastern Quebec and western Maine through the Appalachian uplift to the Fall Line in Georgia, Alabama, and Mississippi (Figure 10). It shows considerable geographic variation in various traits, most noticeably in body pigmentation, and four subspecies are currently recognized. Its variation and systematics recently have been studied in some detail (Brandon, 1966a). A second neotenic species, *G. lutescens* (Rafinesque), was reported by Mittleman (1942); it is not a distinct species, however, but was based on larvae of one subspecies of *G. porphyriticus* (Newcomer, 1960; Brandon, 1963).

Although the available sample is relatively small, considerable geographic variation is evident in *G. pallaeus*, and three subspecies are currently recognized (Brandon, 1966a; 1967b). They differ in body pigmentation, head width, leg length, eye size, and modal number of trunk vertebrae. About 125 specimens of *G. p. pallaeus* are known to me from five caves in the Crow Creek drainage of Franklin County, Tennessee; 25 of *G. p. necturoides* from one cave in the Elk River drainage of Grundy County, Tennessee; 17 intergrades between the first two subspecies from three caves in the North Sauty Creek drainage of Jackson County, Alabama; 13 of *G. p. gulolineatus*

from two localities in the Ridge and Valley Province of McMinn and Roane counties, Tennessee; and several unidentified populations are known from northwestern Georgia (Cooper, 1968), northern Alabama, and central Tennessee. The full range of this species is not well known, and several workers continue to discover new localities.

Gyrinophilus pallaeus differs from adult *G. porphyriticus* by being paedogenetic, and from its larvae by having smaller eyes, a broader head, a more spatulate snout, a different pattern of body pigmentation and slightly higher tooth counts. In other general body features it is similar to larval *G. porphyriticus*. Specimens which have undergone nearly complete metamorphosis during thyroxin treatment would not be confused with adult *G. porphyriticus*; body pigmentation, head proportions, and certain cranial features remain different. For this reason some workers have considered placing *pallaeus* in a separate genus, but there seems little question that *pallaeus* and *porphyriticus* are closely related. *G. pallaeus* unquestionably is modified for permanent cave dwelling, and is considered taxonomically distinct from *G. porphyriticus*. There is little information bearing on the degree of reproductive isolation between the two species, but such isolation has been assumed to exist. Detailed observations by

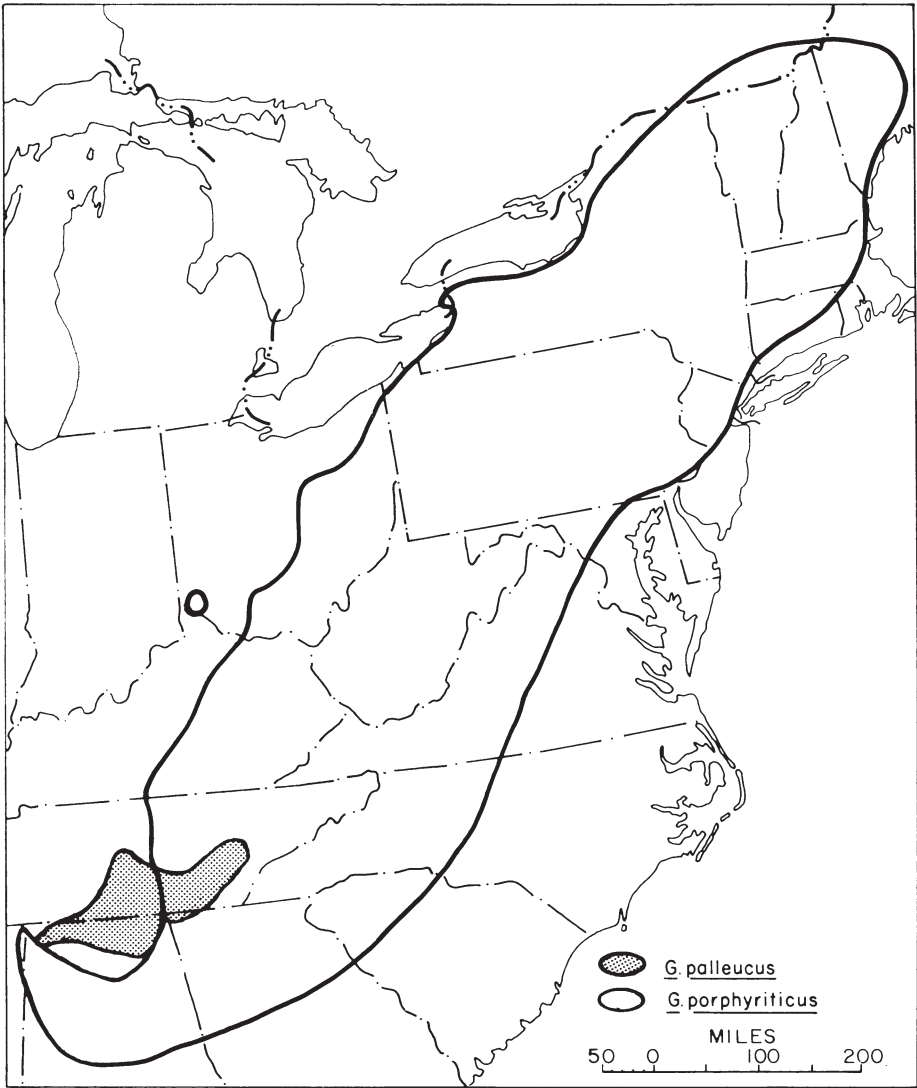


Figure 10. Distribution of *Gyrinophilus porphyriticus* and *Gyrinophilus palleucus*.

Cooper and Cooper (1968) on ranges and habitats of the two species in Alabama show them not to be sympatric there, and leave open the possibility that reproductive isolation results only from geographic or habitat isolation. No tests of hybridization have been attempted yet, and little is

known about the reproductive ecology of either species.

Mechanisms involved in the origin of troglotic species have long been subject to discussion by biologists. *G. palleucus* and its epigeal relative are sufficiently well known to allow consideration of some fac-

tors involved in the origin and modification of a cave dwelling form.

Little is known of the evolution of plethodontid salamanders by direct evidence; fossil remains are few, and there are none of *Gyrinophilus*. Those fossils which are known do not provide sufficient material for phylogenetic considerations (but see Estes, 1965; Wake, 1966). Wake thoroughly discussed the evolution of plethodontid genera, primarily on the basis of osteological evidence.

It seems likely that *G. palleucus* evolved from an epigeal, metamorphosing ancestor, possibly from *G. porphyriticus*. It is impossible to judge the age of *G. palleucus* as a species, but compared with other troglobitic salamanders it seems to be a relatively recent entrant into cave habitats. The present cave systems in Tennessee are estimated to be of Pliocene to Pleistocene age (Barr, 1961).

The known range of *G. palleucus* lies at the periphery of the present-day range of *G. porphyriticus*. Climatic conditions during the Pleistocene may have resulted in the physical isolation of peripheral populations of *G. porphyriticus* and their subsequent adaptation to habitats in and around caves, and finally in restriction to cave habitats as climatic conditions changed.

The present-day ranges of *G. palleucus* and *G. porphyriticus* appear to overlap in eastern Tennessee, but the two species have never been found in the same cave, or even in the same vicinity. In northern Alabama the two species appear to be parapatric (Cooper and Cooper, 1968). Cooper and Cooper (1968) recorded ecological differences between *G. palleucus* caves and *G. porphyriticus* caves and suggested that the first species would have a competitive advantage over the second in cave habitats. The geographic distribution of both species in Tennessee and northwestern Georgia is still rather poorly known, but information is accumulating (Cooper, 1968).

It is certain that preadaptation, especially in regard to neoteny, ecology, and eye

size, played an important part in the invasion of caves by *G. palleucus*.

Neoteny is not known to occur in any population of *G. porphyriticus*, even though this species is a common part of the cave entrance fauna in many parts of its range. Adults, and especially larvae, are found deep within caves, but they differ in no way from individuals collected in epigeal situations in the same areas. The larval period in *G. porphyriticus*, probably three years (Bishop, 1941), is the longest of any plethodontid salamander. It would thus lend itself readily to development of neoteny by selection for slower developmental and growth rates in response to a generally low food supply in caves. Comparisons of developmental growth rates of these two species, however, are not yet available. Indeed, extremely little information of this nature is available for either species. The most obvious biotic difference between epigeal stream and spring habitats where *G. porphyriticus* occurs and *G. palleucus* cave streams is in abundance of potential food. *G. porphyriticus* is aggressively carnivorous, even cannibalistic (Bishop, 1941). Many specimens examined by radiography have salamanders in their stomachs. Larvae and adults seem to feed primarily on a diverse fauna of aquatic invertebrates supplemented by smaller salamanders and some terrestrial invertebrates. Stomachs of *G. palleucus* contain at most a few isopods and few other invertebrates (Brandon, 1967a). The aquatic invertebrate fauna in their caves is neither diverse nor abundant, and stomachs of many specimens are empty.

Cooper and Cooper's (1968) observations of differences between feeding habits of a larval *G. porphyriticus* and a *G. palleucus* under laboratory conditions are probably not as significant as they seem. Feeding behavior in young salamanders is fairly labile, and the reactions of captive specimens to food probably reflect their histories of conditioning to natural sources of food. Striking examples of conditioning to unusual foods or methods of introduction have

been observed in laboratory colonies of other salamanders (Brandon, pers. observ.). Of 12 live *G. palleucus* kept in my laboratory for a year, some fed immediately on beef liver and earthworms, whereas others even now feed on these foods only sparingly and hesitatingly. In general, individuals of *G. palleucus* eat less (and grab it less voraciously) than do larval *G. porphyriticus* and perhaps have a lower metabolic rate (note Cooper and Cooper's comparison of heart-beat rates—1968, p. 23).

There is considerable geographic variation in eye size in both *G. palleucus* and *G. porphyriticus*, but the eyes of the former are consistently smaller (Brandon, 1966a). Within *G. porphyriticus*, Canadian larvae have the largest eyes, while those from the southern Appalachian mountains and Piedmont have the smallest. If *G. porphyriticus* is the parent species, *G. palleucus* would have developed from these southern populations which have the smallest eyes. Subsequent selection for further eye reduction is likely.

Differences among the nominal subspecies of *G. palleucus* in body pigmentation, head

width, leg length, number of trunk vertebrae, eye diameter, and perhaps in adult body size could be the result of more recent local selective pressures, or of genetic drift in partially or completely isolated populations.

This article is based on a paper presented at the meetings of the American Society of Zoologists in Knoxville, Tennessee, December, 1964.

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The Invertebrate Cave Fauna of Georgia

By John R. Holsinger * and Stewart B. Peck **

ABSTRACT

During the early summer of 1967, extensive biological field work was carried out in the caves of northwestern Georgia. Prior to that time the biology of Georgia caves was poorly known. Speleologically, Georgia can be divided into the Appalachian region in the northwest and the Coastal Plain region in the southwest. The majority of caves occur in the Paleozoic limestones of the Appalachians, although a few are found in the early Tertiary limestones of the Coastal Plain.

The data obtained from the collection of invertebrates from 29 caves in Georgia are listed systematically, and a brief discussion of the zoogeographic relationships of the troglobitic forms (obligatory cavernicoles) is given. Based on troglobite distribution, two faunal units are recognized in northwestern Georgia: the Appalachian Plateau and the Appalachian Valley. The former unit is divided into two faunal subunits.

Approximately 130 species of invertebrates are recorded from Georgia caves and between 24 and 27 of them are troglobites. Major animal groups represented by troglobites in Georgia include planarians, snails, isopods, amphipods, crayfish, pseudoscorpions, spiders, millipedes, diplurans, collembolans, and beetles. The invertebrate cave fauna of Georgia also includes a large number of trogliphiles (facultative cavernicoles), with about 25 genera being represented.

INTRODUCTION

The major objective of this study is to give a preliminary annotated listing of all known species of invertebrate cavernicoles of Georgia based principally on field work in June 1967. Moreover, all of the literature pertinent to Georgia cave invertebrates was reviewed and incorporated into the list. Finally, a few new records, obtained by John and Martha Cooper, Tony Iles, and Arthur Dobson subsequent to June 1967, are also included in the list. In addition to being a guide to the invertebrate fauna in Georgia caves, this paper should serve three

other purposes: (a) provide the necessary groundwork for future studies in the ecology and population biology of the cavernicoles of the area, (b) act as a starting point for more detailed studies on the zoogeography and evolutionary biology of the cave fauna of the state as well as for the southern Appalachians, and (c) bring Georgia into line with other major cave-bearing states with regard to the knowledge of its kinds of cave organisms.

Prior to June of 1967, little biological work had been done in the caves of Georgia. In contrast to other southeastern states with major cave and karst regions, the knowledge of Georgia cave fauna was meager. Although a few scattered collections had been made in Georgia caves, no serious attempt had been made to systematically

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investigate or sample the cavernicolous species of this potentially significant area. Previous collecting in Georgia caves had been sporadic, although over the years a few caves were visited biologically by E. Ackerly, T. Barr, K. Dearolf, L. Hubricht, W. Jones, C. Mohr, and J. Valentine. More recent such visits were made by J. and M. Cooper, A. Iles, and A. Dobson. A number of important studies on cavernicoles have given cursory mention to Georgia cave forms, including papers on millipedes by Loomis (1939, 1943) and Chamberlin (1946), amphipods by Hubricht (1943) and Holsinger (1969), planarians by Hyman (1954), beetles by Barr (1965), and general checklists by Dearolf (1953) and Nicholas (1960). Most of these papers, however, covered large areas of the Appalachians, with only one or two caves in Georgia being included.

This report is concerned with the invertebrate cave fauna of Georgia and should serve as a supplement to the biospeleological data already published on other important cave states in the eastern United States. Currently, a number of state cave faunal surveys are in progress or have been published, at least partially. These include Alabama (Peck and Peck, 1967; Cooper, Cooper and Peck, several papers in preparation); Florida (Warren, 1961; Peck, 1970); Texas (Reddell, 1965, 1966, 1967); and Virginia and West Virginia (Holsinger, 1963a, 1963b, and in preparation). More general treatments of state cave faunas are those of Tennessee (Barr, 1961), Virginia (Holsinger, 1964), Pennsylvania (Holsinger, 1971), and Maryland (Franz, in preparation).

Two widely separated and geologically different areas of Georgia contain limestone caves—the Appalachian Plateau and Valley in the northwestern corner, and the Coastal Plain in the southwest. The former area, situated in the “cave rich” Appalachians, is by far the most extensive cavernous region of the two and was, consequently, chosen as the target for the early summer field

work of 1967. Two caves were also investigated in the Coastal Plain at another time by one of us (SBP).

Twenty-nine caves are covered in this study, 27 of which are located in the Appalachians and two of which are located in the Coastal Plain. Figure 1, an outline map of Georgia, shows the location of the two Coastal Plain caves, and Figure 2, a map of the northwestern corner of Georgia, shows the location of 25 of the 27 caves in the Appalachians. During June 1967, 18 of the caves located in Figure 2 were biologically explored by the writers and their assistants; two other caves located in Figure 2 were visited and similarly explored by the writers prior to 1967. The remaining caves located in Figure 2 were investigated by Tony Iles. Three other caves (Saw Mill, Cricket, and Creek Bed caves), all presumably located near Rising Fawn, have been mentioned previously in the literature of Georgia cave faunas (see Dearolf, 1953). These caves could not be identified during



FIGURE 1. Map of Georgia showing the Appalachian Valley and Plateau region (shaded) and two caves located in the Coastal Plain. See Fig. 2 for an enlarged map showing locations of the caves in the Appalachians.

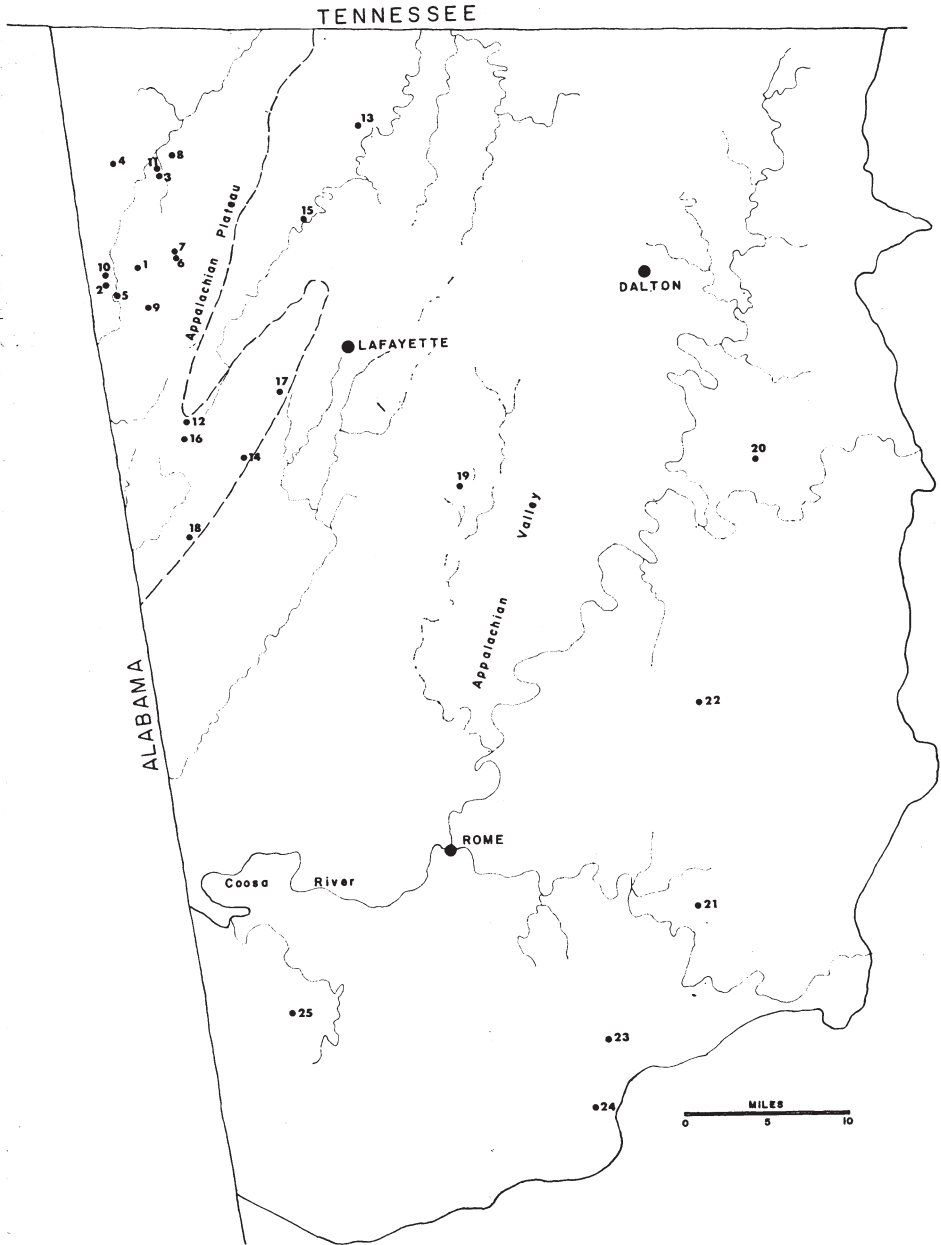


FIGURE 2. Map of the Appalachian Valley and Plateau region of northwestern Georgia showing caves sampled for invertebrate fauna. The names of the caves, keyed to the numbers on the map, are listed in the text.

the field work and are not found in the standardized listing of Georgia caves by the Georgia Speleological Survey. There is good reason to believe, however, that Cricket and Creek Bed caves were names given to the two entrances to what is now called Byers Cave and that Saw Mill Cave could have been another name for Sittons Cave.

Each cave visited in June 1967 was thoroughly searched for invertebrates. The investigation was started just inside of the entrance, and all potential habitats (i. e., damp clay and silt, decaying organic debris, damp rotting wood, pools, streams, etc.) were carefully checked throughout the traversable part of each cave. Bait in the form of liver and carrion was left in some of the caves and checked on a return visit several weeks later.

A list of the caves located on the map in Figure 2 is given below. The numbers assigned to these caves are keyed to the locations shown on the map. Those caves in the list denoted by asterisks were visited by the writers. Some of these caves were either new to the Georgia Speleological Survey or were at best inadequately known. As a service to the Georgia Speleological Survey, Roger Baroody, who assisted with the field work, recorded physical data on all caves visited and subsequently turned over these data to Richard Schreiber for deposition in the files of the Survey. The caves, arranged by county, follow.

Dade County (12 caves): Boxcar (1), * Byers (2), Case (3), * Howards Waterfall (4), Hurricane (5), * Johnson Crook No. 1 (6), * Johnson Crook No. 2 (7), * Morrison and * Morrison Spring (separate caves located $\frac{1}{4}$ mile apart) (8), Running Water (9), Rustys (10), and Sittons (11). *Walker County* (7 caves): * Bible Springs (12), * Cave Spring (13), * Harrisburg (14), * Horseshoe (15), * Mtn. Cove Farm (16), * Pettijohn (17), and Hickman Gulf (located 4 miles NNW of Bible Springs Cave but not shown in figure 2). *Chatooga County* (2 caves): * Blowing Springs (18), and * Parker (19). *Gordon*

County (1 cave): * Roberts (20). *Bartow County* (2 caves): * Kingston Saltpetre (21) and * Yarborough (22). *Polk County* (2 caves): Deatons (23) and * White River (24). *Floyd County* (1 cave): * Cave Springs (25).

AREAL GEOLOGY

The caverniferous limestones of northwestern Georgia occur in two physiographic provinces, the Appalachian Plateau and the Appalachian Valley (Fig. 2). Although there is no clear-cut line dividing these two provinces, the eastern flanks of Lookout Mountain and its associated outlier, Pigeon Mountain, are often regarded as the front of the Appalachian Plateau in this area. A sequence of cavernous limestones (viz., Bangor, Gasper, St. Genevieve, and St. Louis) occurs along the eastern flanks of Lookout and Pigeon Mountains and dips gently to the west. These same limestones, which extend westward, are responsible for the numerous caves developed in extreme northwestern Georgia (Dade County) and northern Alabama (Jackson, Madison, and Marshall counties, etc.). To the east of the plateau front are a series of low ridges and wide valleys, which compose the Appalachian Valley and contain exposures of sedimentary rocks that vary in geologic age from Cambrian to Pennsylvanian. Several of these valleys are floored by Cambrian and Ordovician limestones and dolomites and are intermittently caverniferous. The extensive karst areas found farther north in the Appalachian Valley sections of Tennessee, Virginia, and West Virginia are virtually non-existent in Georgia, and the limestone terrane is usually inconspicuous.

The cave region of northwestern Georgia is drained by two major river systems. Streams located north and northwest of La Fayette flow into the Tennessee River, and streams located east, south and southeast of La Fayette flow into the Coosa River which is part of the Mobile Basin drainage and ultimately joins the Alabama River.

The greatest concentration of caves in the Appalachian region of Georgia is along the

eastern flank of Pigeon Mountain and in the outcrops of Mississippian limestones west of Lookout Mountain in Dade County. Most of the caves in the Appalachian Valley are developed in various limestone and dolomite members of the Knox group. In the computer print-out list issued by the Georgia Speleological Survey in 1967 approximately 124 caves were recorded. Undoubtedly many more caves exist, and significant discoveries, such as the one mentioned below, will be made there in the future. In late 1968, an exhaustive exploration of Ellisons Cave, located on the eastern side of Pigeon Mountain in Walker County, revealed it to be one of the deepest and most significant caves in the eastern United States (Schreiber and McGuffin, 1969a, 1969b). This cave contains more than 9.5 miles of surveyed passage and a vertical extent of 981 feet (Schreiber and McGuffin, 1969b). Its most interesting geologic feature is Fantastic Pit, a huge dome pit 570 feet deep. The breakthrough in Ellisons Cave alone is good evidence of the speleological potential of northwestern Georgia. Other large caves, such as Byers, Pettijohn, and Cemetery Pit, also occur in this part of the state, but unfortunately little published information on these caves is available.

Only a few scattered caves occur in the Coastal Plain of southwestern Georgia and most of these are not of great extent. However, these caves are developed in a physiographic region significantly different from the Appalachians and in limestones of much more recent origin. The carbonate rocks of this area are of early Tertiary age and are members of the stratigraphic series which contains several important caves in adjacent northern Florida (Jackson and Washington counties).

ANNOTATED LIST

The Schiner system of the ecological classification of cavernicoles, as revised by Racovitza and recently redefined and clarified by Barr (1963b, 1968), is used in the following list. Cavernicoles usually fall into one of four ecological categories: (1) *trog-*

lobites—obligatory cave species which are morphologically specialized for, and restricted to, cave habitats and are unable to survive on the surface; (2) *troglophiles*—facultative cave species which frequently inhabit caves and complete their life cycles there but may occupy ecologically suitable habitats on the surface; (3) *trogloxenes*—species which often occur in caves but frequently return to the surface or near the surface (*i. e.*, cave entrance zone) for food; (4) *accidentals*—species which accidentally wander, fall, or are washed into caves and can exist there only temporarily. The ecological term *edaphobite* also is sometimes applied to cavernicoles. Edaphobites are obligatory deep-soil animals that may occasionally occur in caves, but if so, their occurrence is usually sporadic (Barr, 1968, p. 43). The term *endogean*, as defined by Vandel (1964), is also used to designate this category of occasional cavernicoles.

Many of the forms found in the following list are still inadequately known as to distribution and ecology and their assignment to one of the ecological categories is tentative pending further study. The following abbreviations, placed in parentheses after names, have been employed: TB = troglobite, TP = troglophile, TX = troglaxene, ED = edaphobite.

Some of the taxa found in this list are still poorly known taxonomically and therefore could not be determined to species. Other forms, such as the planarians, terrestrial isopods, and diplurans, currently are being studied and specific names are not yet available. Still other material represents undescribed species, and to date descriptions and names have not been published. Because of these reasons and the fact that a number of major caves in Georgia remain to be biologically investigated, this list should be regarded as preliminary. However, considering the number of caves sampled and their random distribution in the limestone areas, the data given in this list are believed to be generally representative of the invertebrate cave fauna of the state.

PHYLUM PLATYHELMINTHES

Class Turbellaria

ORDER TRICLADIDA

Family Planariidae

Sphalloplana georgiana Hyman (TB)

Georgia Records.—Dade Co.: Howards Waterfall Cave (Type Locality).

Comments.—This species was described by Hyman (1954) on the basis of material collected by Mr. Charles E. Mohr.

Sphalloplana sp. (TB)

Georgia Records.—Dade Co.: Byers and Johnson Crook caves.

Comments.—This material is presently being studied by Dr. Roman Kenk of the Smithsonian Institution; it may well represent new records for *S. georgiana*, since these two caves are not far from the type locality of this species (see above).

PHYLUM ASCHELMINTHES

Class Nematomorpha

ORDER GORDIOIDEA

Family Gordiidae

Gordius sp. (Accidental)

Georgia Records.—Polk Co.: White River Cave.

Comments.—A single, undetermined, adult specimen of this genus was collected from a shallow, mud-bottom pool in this cave. Gordian worms occasionally occur in caves (Vandel, 1964; Reddell, 1965) but are probably accidentally introduced as parasitic larvae by crustacean or insect hosts.

PHYLUM ANNELIDA

Class Oligochaeta

ORDER OPISTHOPORA

Family Lumbricidae

Allolobophora trapezoides Duges (ED)

Georgia Records.—Dade Co.: Morrison Cave.

Comments.—This species is of European origin and was probably accidentally introduced into this country through commerce. It has also been recorded from caves in Arkansas, Kentucky, Tennessee, and West Virginia (Gates, 1959).

Octolasion tyrtaeus Savigny (ED)

Georgia Records.—Dade Co.: Johnson Crook Cave No. 2.

PHYLUM MOLLUSCA

Class Gastropoda

ORDER STYLOMNATOPHORA

Family Endodontidae

Helicodiscus barri Hubricht (TP)

Georgia Records.—Chatooga Co.: Parker Cave.

Comments.—This small, terrestrial snail is known only from caves to date and is recorded from Dickson and Davidson counties, Tennessee (Hubricht, 1962, 1964a) and

Colbert, Lauderdale, and Madison counties, Alabama (Peck, in prep.; Cooper, in press).

Helicodiscus inermis Baker (TP)

Georgia Records.—Polk Co.: White River Cave.

Walker Co.: Blowing Springs Cave.

Comments.—This species ranges from New Jersey westward to Missouri and Texas, and south to the Gulf of Mexico. It has been recorded from caves in Van Buren and Grundy counties, Tennessee (Hubricht, 1964a), from caves in six counties in Alabama (Peck, in prep.), and from one cave in Bath Co., Virginia (Holsinger, unpublished data).

Family Polygyridae

Mesodon perigraptus (Pilsbry) (TX)

Georgia Records.—Chatooga Co.: Parker Cave.

Mesodon (Patera) sp. (TX)

Georgia Records.—Walker Co.: Harrisburg Cave.

Comments.—This species was previously recorded from three counties in Georgia (Hubricht, 1964b).

Family Zonitidae

Gastrodonta interna (Say) (TX)

Georgia Records.—Walker Co.: Blowing Springs Cave.

Comments.—This species ranges from West Virginia westward to Indiana and southward to central Alabama (Hubricht, *in litt.*). It has been recorded from one cave in Alabama (Hubricht, 1964a) and from 22 counties in Georgia (Hubricht, 1964b).

Glyphyalinia paucilirata (Morelet) (TP or TX)

Georgia Records.—Walker Co.: Harrisburg Cave.

Comments.—This species has been reported from caves in Kentucky and Tennessee (Hubricht, 1964a).

Glyphyalinia sculptilis (Bland) (TX)

Georgia Records.—Walker Co.: Bible Springs Cave.

Comments.—This species is also recorded from a cave in Kentucky (Hubricht, 1964a) and from eight counties in Georgia (Hubricht, 1964b).

Glyphyalinia specus Hubricht (TB)

Georgia Records.—Chatooga Co.: Parker Cave.

Dade Co.: Morrison Cave. Walker Co.: Cave Spring and Pettijohn caves.

Comments.—This species was previously known only from caves in Kentucky, Tennessee, and Alabama. It is white and apparently blind (Hubricht, 1965).

Zonitoides arboreus (Say) (TP)

Georgia Records.—Walker Co.: Blowing Springs and Pettijohn caves.

Comments.—This species is widely distributed in the United States and is known from 45 counties in Georgia (Hubricht, 1964b). It has also been recorded from caves in Ala-

bama, Kentucky, Tennessee, and Texas (Hubricht, 1964a; Reddell, 1965; Peck, in prep.; Cooper, in press).

PHYLUM ARTHROPODA

Class Crustacea

ORDER EUCOPEPODA

Family Canthocamptidae

Attheyella pilosa Chappuis (TX)

Georgia Records.—Chatooga Co.: Blowing Springs Cave.

Comments.—See Bowman, et al. (1968) for a discussion of the systematics and ecology of this species. *A. pilosa* was found in association with *Cambarus* in the above cave.

Family Cyclopidae

Cyclops (Acanthocyclops) vernalis Fisher (TP)

Georgia Records.—Bartow Co.: Kingston Salt-petre Cave.

Comments.—Four specimens of this species were collected from a shallow, mud-bottom pool. According to H. C. Yeatman (*in litt.*), this is an extremely variable and widespread epigean species that is frequently found in caves.

ORDER ISOPODA

Family Asellidae

Asellus richardsonae (Hay) (TB)

Georgia Records.—Chatooga Co.: Blowing Springs Cave. Dade Co.: Byers and Johnson Crook caves. Floyd Co.: Cave Springs Cave. Walker Co.: Horseshoe and Mtn. Cove Farm caves.

Comments.—Steeves (1963) published a re-description of this species and added several new localities. *A. richardsonae* is widespread and is distributed from southwestern Virginia south-southwestward to northwestern Georgia and northern Alabama. Although the type locality (Nickajack Cave, Marion Co., Tennessee) of this species is situated only a few feet from the northwestern corner of Georgia, *A. richardsonae* was previously un-recorded from Georgia.

Asellus sp. (TB)

Georgia Records.—Walker Co.: Pettijohn Cave.

Comments.—This undescribed species is known from material (ca. 15 specimens) collected from a drip pool and the cave stream.

Lirceus sp. (TP or TX)

Georgia Records.—Chatooga Co.: Blowing Springs Cave.

Comments.—Nine lightly pigmented specimens were collected from pieces of wood submerged in a small stream. *Lirceus* occasionally occurs in cave streams (*viz.*, Tennessee and Virginia) but most populations do not represent troglitic species.

Family Armadillidiidae

Armadillidium vulgare (Latreille) (TX)

Georgia Records.—Walker Co.: Horseshoe Cave.

Comments.—Eight specimens of this common and widespread species were collected from this cave.

Family Ligiidae

Ligidium elrodii chatoogaensis Schultz (TX)

Georgia Records.—Chatooga Co.: Blowing Springs Cave.

Comments.—This species was fairly abundant in the stream passage in and around damp to wet organic debris. This subspecies was recently described by Schultz (1970) on the basis of material collected in this cave. Other subspecies of *L. elrodii* are described from caves in southwestern Virginia and eastern Tennessee by Schultz (1970).

Family Oniscidae

Cylisticus convexus (De Greer) (TX)

Georgia Records.—Dade Co.: Morrison Cave. Floyd Co.: Cave Springs Cave. Walker Co.: Bible Springs and Cave Springs caves.

Comments.—This species is common throughout the United States and has been reported from caves in Indiana, Kentucky, Tennessee, Texas, and Virginia (Schultz, 1970).

Family Trichoniscidae

Caucasonethes sp. (TB)

Georgia Records.—Chatooga Co.: Blowing Springs Cave. Dade Co.: Byers Cave. Walker Co.: Bible Springs, Horseshoe, Mtn. Cove Farm, and Pettijohn caves.

Comments.—This material is currently being studied by Professor Albert Vandel of Toulouse, France. Several species are apparently represented in this collection, one or more of which may be undescribed.

Miktoniscus sp. (TP)

Georgia Records.—Chatooga Co.: Blowing Springs and Parker caves. Decatur Co.: Climax Cave. Randolph Co.: Griers Cave.

Comments.—Several species of this genus occur in caves of the eastern United States and at least one of them is probably a troglobite (*i.e.*, *M. racovitzaei* Vandel) (Vandel, 1965). The most common cavernicolous species, however, is *M. alabamensis*, a troglophile which ranges from Virginia southwestward to Alabama and Florida and may well be the species represented by the above material.

ORDER AMPHIPODA

Family Gammaridae

Crangonyx antennatus Packard (TB)

Georgia Records.—Chatooga Co.: Blowing Springs Cave. Dade Co.: Byers, Howards Waterfall, and Sittons caves. Floyd Co.: Cave Springs Cave. Walker Co.: Harrisburg, Horseshoe, Mtn. Cove Farm, and Pettijohn caves.

Comments.—This species is common in caves of the southern Appalachian region, and its range extends from the upper Tennessee River basin in southwestern Virginia, south-southwestward to Floyd Co., Georgia, and west along the Tennessee River valley to northwestern Alabama and south-central Tennessee (Holsinger, 1969).

Stygobromus sp. (TB)

Georgia Records.—Chatooga Co.: Blowing Springs Cave. Dade Co.: Byers, Howards Waterfall, and Rustys caves. Walker Co.: Pettijohn Cave.

Comments.—This undescribed species is closely related to *S. mackini* (a common species in southern Appalachian Valley caves) and possibly ranges westward into Jackson Co., Alabama (Holsinger, 1969).

Stygobromus sp. (TB)

Georgia Records.—Chatooga Co.: Parker Cave. Comments.—Only five specimens of this large, rather unusual species (undescribed) have been taken from temporary, mud-bottom pools in the lower level of this cave. This species may be distantly related to *S. mackini*.

Stygobromus sp. (TB)

Georgia Records.—Floyd Co.: Cave Springs Cave. Polk Co.: White River Cave.

Comments.—This undescribed species is known largely on the basis of several collections made from White River Cave by Ernest Ackerly during the late 1940's. This species has also been recorded from a cave in Calhoun Co., Alabama. Its morphological affinities are with *S. mackini* (Holsinger, 1969).

ORDER DECAPODA

Family Astacidae

Cambarus cryptodytes Hobbs (TB)

Georgia Records.—Decatur Co.: Climax Cave. Comments.—Although this is the only known Georgia record for this species, it has been recorded from a well and five caves in Florida (Warren, 1961).

Cambarus latimanus LeConte (TP or TX)

Georgia Records.—Chatooga Co.: Blowing Springs Cave. Dade Co.: Byers and Hurricane caves. Walker Co.: Mtn. Cove Farm Cave.

Comments.—According to Hobbs (1959), the range of this species extends from North Carolina to Florida. Apparently this species has also been taken in northern Alabama (Martha Cooper, pers. comm.), but its occurrence in Georgia caves was previously un-recorded. At least five, rather pale specimens of *C. latimanus* were taken from a single stream pool in Blowing Springs Cave.

Cambarus sp. (TP or TX)

Georgia Records.—Chatooga Co.: Blowing Springs Cave. Walker Co.: Bible Springs Cave.

Comments.—Both of these records are based on single females, which, according to H. H. Hobbs, Jr. (*in litt.*) possibly represent an undescribed species, closely related to *C. striatus*. In Blowing Springs Cave, this species occurs with *C. latimanus*.

Class Arachnida

ORDER PSEUDOSCORPIONIDA

Family Chernetidae

Pseudozoaona sp. (TP)

Georgia Records.—Chatooga Co.: Parker Cave. Dade Co.: Johnson Crook No. 1, Morrison, and Morrison Spring caves. Walker Co.: Cave Spring, Hickman Gulf, and Mtn. Cove Farm caves.

Comments.—This genus is often found in caves of the eastern United States in association with various kinds of mammal dung.

Family Chthoniidae

Apochthonius sp. (TB or TP)

Georgia Records.—Chatooga Co.: Parker Cave. Dade Co.: Morrison Cave.

Kleptochthonius magnus Muchmore (TP ?)

Georgia Records.—Dade Co.: Johnson Crook Cave. Walker Co.: Mtn. Cove Farm Cave.

Comments.—This species was originally described from a cave in Franklin Co., Tennessee and is only slightly, if at all, modified for cave life (Muchmore, 1966a). It has never been collected from an epigeal habitat, however.

Family Neobisiidae

Microcreagris subatlantica Chamberlin (TX)

Georgia Records.—Chatooga Co.: Parker Cave. Comments.—This species was originally described from caves in Colbert Co., Alabama, but it is also found on the surface and is not modified for cave life (Chamberlin, 1962). The new record (above) was recently published by Muchmore (1969).

Microcreagris pumila Muchmore (TP or TX)

Georgia Records.—Chatooga Co.: Parker Cave. Comments.—This species was recently described by Muchmore (1969) on the basis of material collected from the above cave and a cave and an epigeal locality in Blount Co., Alabama. The genus *Microcreagris* is Holarctic in distribution and contains a number of epigeal and cavernicolous species. Troglotic species of the genus have been described from Alabama, Tennessee, and Virginia (Chamberlin, 1962: Muchmore, 1966b, 1969) but none have been found in Georgia to date.

Microcreagris sp. (TP or TX)

Georgia Records.—Dade Co.: Johnson Crook Cave. Walker Co.: Pettijohn Cave.

Comments.—A single female of this undetermined species was collected.

ORDER ACARINA

Family Rhagidiidae

Rhagidia sp. (TB or TP)

Georgia Records.—Bartow Co.: Kingston Salt-petre Cave. Dade Co.: Byers and Morrison caves. Walker Co.: Bible Springs and Pettijohn caves.

Comments.—Rhagidiid mites are frequently found in caves of the eastern United States, where they usually occur in damp areas associated with particles of organic debris. This genus is also represented in damp leaf litter habitats on the surface (especially in mountainous areas). To date only two cavernicolous species have been described from North America (Holsinger, 1965), but additional (undescribed) species, including the material recorded above, await further study.

ORDER OPILIONES

Family Phalangodidae

Phalangodes (*Bishopella*) *lacinosus* Crosby and Bishop (TP)

Georgia Records.—Chatooga Co.: Blowing Springs Cave. Dade Co.: Byers and Sittons caves. Polk Co.: White River Cave. Walker Co.: Bible Springs, Cave Spring, Harrisburg, Horseshoe, and Pettijohn caves.

Comments.—This species is abundant in caves in northern Alabama and central Tennessee (Barr, 1961; Goodnight and Goodnight, 1942, 1960; Peck, in prep.). It has been collected occasionally from epigeal situations in Alabama, Georgia, North and South Carolina, and Tennessee; and from both inside and outside of caves in Jackson Co., Florida (Crosby and Bishop, 1924; Goodnight and Goodnight, 1942, 1953, 1960; Peck, in prep.).

Phalangodes (*Crosbyella*) *spinturnix* Crosby and Bishop (TP)

Georgia Records.—Decatur Co.: Climax Cave. Comments.—This species is known from caves in Alabama, Arkansas, and Florida and from epigeal localities in Alabama, Arkansas, Florida, and Mississippi (Goodnight and Goodnight, 1942; Peck, in prep.).

ORDER ARANEAE

Family Agelenidae

Calymmaria cavicola (Banks) (TP or TX)

Georgia Records.—Chatooga Co.: Parker Cave. Dade Co.: Byers Cave. Walker Co.: Bible Springs and Mtn. Cove Farm caves.

Comments.—This species also inhabits caves in nearby Tennessee (Barr, 1961) and is known from 22 caves in Alabama (Peck, in prep.).

Cicurina arcuata Keyserling (TP or Accidental?)
Georgia Records.—Walker Co.: Cave Spring Cave.

Cicurina pallida Keyserling (TP or TX)

Georgia Records.—Randolph Co.: Griers Cave.

Cicurina sp. (TB ?)

Georgia Records.—Dade Co.: Byers Cave.

Comments.—According to W. J. Gertsch (*in litt.*) this is an undescribed species that is more closely related to a species group from Texas than to a common species in nearby Alabama caves. Apparently the genus *Cicurina* is represented by troglobites only in the more southern parts of the cave areas of North America (viz., Georgia, Alabama, and Texas). In the central Appalachian cave region (e.g., Virginia and West Virginia) this genus occasionally occurs in the form of a troglaxene or troglophile such as *C. pallida* (Holsinger, unpubl. data). Barr (1961) reported *C. breviararia* (TP or TX) from Tennessee.

Tegenaria domestica Clerk (TP or TX)

Georgia Records. Walker Co.: Hickman Gulf Cave.

Comments.—This species has also been taken in northern Alabama and southern Tennessee caves.

Wadotes calcaratus (Keyserling) (Accidental?)

Georgia Records.—Dade Co.: Johnson Crook No. 1 Cave.

Family Argiopidae

Meta menardi (Latreille) (TP)

Georgia Records.—Dade Co.: Morrison Cave. Walker Co.: Harrisburg and Mtn. Cove Farm caves.

Comments.—This species is common in caves throughout the eastern United States and is usually found near entrances.

Family Clubionidae

Liocranoides unicolor Keyserling (TP)

Georgia Records.—Chatooga Co.: Parker Cave. Dade Co.: Byers and Morrison caves. Walker Co.: Bible Springs, Hickman Gulf, Horseshoe, and Mtn. Cove Farm caves.

Comments.—This species is also common in caves of south-central Tennessee and northern Alabama (Barr, 1961; Gertsch, *in litt.*).

Family Leptonetidae

Leptoneta sp. (TB or TP)

Georgia Records.—Dade Co.: Byers Cave. Walker Co.: Harrisburg and Pettijohn caves.

Comments.—According to W. J. Gertsch (*in litt.*) these collections represent a new species. The genus *Leptoneta* is also represented by a number of troglobitic species in the Edwards Plateau region of central Texas (Gertsch, pers. comm.; Reddell, 1965.) This group also occurs in caves around the Mediterranean (Vandel, 1964).

Family Linyphiidae

Centromerus denticulatus (Emerton) (TP)

Georgia Records.—Walker Co.: Horseshoe Cave.

Comments.—This species is also found occasionally in caves of southeastern Tennessee and northern Alabama.

Phanetta subterranea (Emerton) (TB ?)

Georgia Records.—Dade Co.: Byers, Howards Waterfall, Johnson Crook No. 1, Morrison, and Sittons caves. Floyd Co.: Cave Springs Cave. Walker Co.: Cave Spring and Harrisburg caves.

Comments.—This species is common in caves all over the eastern United States (*i.e.*, Appalachian region and Interior Low Plateaus).

Porromma cavernicolum (Keyserling) (TB ?)

Georgia Records.—Bartow Co.: Kingston Salt-petre Cave.

Comments.—This species is also widespread in the Appalachian and Interior Low Plateau cave regions but is apparently not as common as *P. subterranea*.

Family Lycosidae

Pirata sp. (Accidental)

Georgia Records.—Walker Co.: Horseshoe Cave.

Family Nesticidae

Nesticus pallidus Emerton (TP or TX)

Georgia Records.—Floyd Co.: Cave Springs Cave. Randolph Co.: Griers Cave.

Comments.—This species is a common troglone in caves of the United States and even Mexico.

Family Pholcidae

Pholcus sp. (TP or TX)

Georgia Records.—Floyd Co.: Cave Springs Cave.

Comments.—The family Pholcidae is also represented in Texas and Mexico by cavernicolous species (Nicholas, 1962; Reddell, 1965). In addition, Barr (1961) reported the group from Tennessee caves.

Family Salticidae

Maevia vittata Koch (Accidental)

Georgia Records.—Walker Co.: Hickman Gulf Cave.

Family Symphytognathidae

Maymena ambita (Barrows) (TP)

Georgia Records.—Walker Co.: Horseshoe Cave.

Comments.—This species is known primarily from caves in Alabama, Kentucky, and Tennessee (Gertsch, 1960).

Family Theridiidae

Achaearanea tepidariorum (Koch) (TP)

Georgia Records.—Gordon Co.: Roberts Cave. Polk Co.: White River Cave. Walker Co.: Bible Springs Cave.

Comments.—This species is also recorded from a few caves in nearby Alabama and Tennessee, and as far north as Monroe Co.,

West Virginia (Gertsch, *in litt.*). Another species of this genus (*A. porteri*) is a common troglophile in Texas caves (Reddell, 1965) and is also reported from Tennessee caves (Barr, 1961).

Class Symphyla

Family *Scutigere* sp. (ED)

Georgia Records.—Dade Co.: Johnson Crook Cave No. 2. Walker Co.: Harrisburg Cave.

Comments.—Although symphylans are depigmented and anophthalmic, they are members of the soil fauna (endogean or edaphic) and are not true cave inhabitants (Vandell, 1964).

Class Chilopoda

ORDER GEOPHILOMORPHA

Family Geophilidae

Arenophilus bipuncticeps (Wood) (TX or Accidental)

Georgia Records.—Chatooga Co.: Blowing Springs Cave.

ORDER LITHOBIOMORPHA

Family Lithobiidae

Lithobius atkinsoni Bollman (TP)

Georgia Records.—Randolph Co.: Griers Cave.

Comments.—This species is found in caves on the southern Coastal Plain and in epigeal habitats farther north (Peck, 1970).

Neolithobius voracior (Chamberlin) (TP)

Georgia Records.—Decatur Co.: Climax Cave.

Comments.—This species is also reported from three localities in Mississippi (Chamberlin, 1925).

Paitobius sp. (TX or Accidental)

Georgia Records.—Dade Co.: Morrison Spring Cave.

Comments.—This species is probably *P. adelus* Chamberlin, which is also known from one cave in Alabama (Peck, *in prep.*).

Pampibius sp. (TX or Accidental)

Georgia Records.—Walker Co.: Cave Spring Cave.

Comments.—This material apparently represents a new species in a previously monotypic genus.

ORDER SCOLOPENDROMORPHA

Family Cryptopidae

Scolopocryptops sexspinosus (Say) (TX or Accidental)

Georgia Records.—Dade Co.: Johnson Crook and Morrison caves. Walker Co.: Pettijohn Cave.

Comments.—This species is common in the eastern United States and is known from one cave in Alabama.

Class Diplopoda

ORDER CHORDEUMIDA

Family Cleidognoidae

Pseudotremia eburnea Loomis (TB)

Georgia Records.—Dade Co.: Byers and Johnson Crook No. 1 caves. Walker Co.: Hickman Gulf, Mtn. Cove Farm, and Pettijohn caves.

Comments.—Loomis (1939), in his description of this species, designated Cricket Cave, Dade County as the type locality. As pointed out earlier, however, this cave could not be identified during the field work. Loomis (1939), and also Dearolf (1953), listed *Pseudotremia* sp. (immatures) from Creek Bed Cave, Dade Co., but the latter cave could not be identified either.

Pseudotremia sp. (TB or TP)

Georgia Records.—Dade Co.: Case, Howards Waterfall, Morrison, Morrison Spring, Running Water, and Sittons caves. Walker Co.: Bible Springs and Harrisburg caves.

Comments.—Most of the above material is known from immatures and females and could not be specifically determined.

Family Lysiopetalidae

Abacion magnum (Loomis) (TX)

Georgia Records.—Dade Co.: Byers Cave. Chatoga Co.: Blowing Springs Cave. Polk Co.: White River Cave.

Comments.—This species was originally described from Madison Co., Alabama (epigean habitat) by Loomis (1943). Chamberlin (1946) reported *A. lactarium* from Kingston Saltpetre Cave, Bartow Co., Georgia, but this was probably an error for *A. magnum* (Causey, *in litt.*). The former is known from the Coastal Plain and Piedmont of the eastern United States (Chamberlin and Hoffman, 1958) but not from the Appalachian Valley or Plateau. Reddell (1965) reported another species of this genus (*A. texense*) from several caves in central Texas.

Family Striariidae

Striaria sp. (TX)

Georgia Records.—Chatoga Co.: Parker Cave.

Comments.—This genus is represented by two troglobitic species in the United States (Shear, 1969).

Family Trichopetalidae

Scoterpes austrinus Loomis (TB)

Georgia Records.—Bartow Co.: Kingston Saltpetre Cave. Chatoga Co.: Blowing Springs Cave. Dade Co.: Johnson Crook No. 1 and Morrison caves. Polk Co.: Deatons and White River caves. Walker Co.: Bible Springs, Horseshoe, Mtn. Cove Farm, and Pettijohn caves.

Comments.—At least two subspecies (species ?) of *S. austrinus* occur in Georgia caves—

S. a. austrinus and *S. a. nudus* Chamberlin (1946). The latter is known only from its type locality (Kingston Saltpetre Cave) but should now be re-examined in light of the new material as it may well represent a distinct species. *S. a. austrinus* was originally described from Manitou Cave, DeKalb Co., Alabama by Loomis (1943), but recent collecting shows it (or a very closely related form) to be rather common in northwestern Georgia. *Scoterpes copei* (Packard) has also been reported from Georgia (*i.e.*, Sawmill Cave, Dade Co.) and Tennessee (Loomis, 1939, 1943; Dearolf, 1953; Chamberlin and Hoffman, 1958), but the range of this species should be restricted to south-central Kentucky (Causey, *in litt.*). It should be noted that Sawmill Cave, like Creek Bed and Cricket caves, could not be identified during the field work and is probably known to the Georgia Cave Survey by another name.

Scoterpes sp. (TB)

Georgia Records.—Chatoga Co.: Parker Cave. Dade Co.: Sittons Cave. Walker Co.: Harrisburg Cave.

Comments.—The specimens from Sittons and Harrisburg caves were immature or females and could not be determined. The material from Parker Cave represents an undescribed species (Causey, *in litt.*).

ORDER JULIDA

Family Nemasomatidae

Ameractis satis Causey (TB or TP)

Georgia Records.—Dade Co.: Morrison Cave.

Comments.—This species was first described from a cave in White Co., Tennessee by Causey (1959). More recently, Barr (1961) reported the range as extending from Overton County to Hamilton County, Tennessee, and Peck (*in prep.*) collected it from two caves in Alabama. The Georgia and Alabama records extend the range of this species to the southeast.

Blaniulus guttulus (Bosc) (ED)

Georgia Records.—Dade Co.: Morrison Cave.

Comments.—This eyeless soil inhabitant is the only known species of the genus in North America and is apparently an introduced form from Europe.

ORDER PLATYDESMIDA

Family Andrognathidae

Andrognathus corticarius Cope (TX)

Georgia Records.—Floyd Co.: Cave Springs Cave.

Comments.—This epigean species has been reported from several states in the southeastern United States (Chamberlin and Hoffman, 1958).

ORDER POLYDESMIDA

Family Paradoxosomatidae

Oxidus gracilis (Koch) (TP)

Georgia Records.—Decatur Co.: Climax Cave.
Floyd Co.: Cave Springs Cave.

Comments.—The range of this species is tropicopolitan. It has apparently been introduced into the United States, where it has become well established in the south and west (Chamberlin and Hoffman, 1958). Although *O. gracilis* is commonly found in greenhouses, it is reported from several caves in Texas (Reddell, 1965) and one cave in Pennsylvania (Loomis, 1939). This species has also been collected from caves in Mexico and one cave in Alabama (Peck, in prep. and unpubl. data).

Family Polydesmidae

Polydesmus sp. (or *Pseudopolydesmus* ? sp.) (TX)

Georgia Records.—Dade Co.: Creek Bed Cave (of Loomis and Dearolf).

Comments.—A single male from this cave was said by Loomis (1939) to be close to, if not identical with, *Polydesmus pinetorum*. (= *Pseudopolydesmus pinetorum*—Chamberlin and Hoffman, 1958).

ORDER SPIROSTREPTIDA

Family Cambalidae

Cambala annulata Say (TP)

Georgia Records.—Randolph Co.: Griens Cave.
Comments.—This species is also known from caves in Jackson Co., Florida and central Alabama and from many epigeal localities in the Appalachians (Hoffman, 1958; Shear, 1969).

Cambala minor Bollman (TP)

Georgia Records.—Chatooga Co.: Parker Cave.
Dade Co.: Morrison Cave. Walker Co.: Horseshoe and Pettijohn caves.

Comments.—This species (or species complex—see Shear, 1969) is a common inhabitant of forested areas in the eastern United States. It frequently occurs in caves, however, and has been reported from such habitats in Alabama (Peck, in prep.), Kentucky (Shear, 1969), Tennessee (Barr, 1961), and Virginia—West Virginia (Holsinger, unpubl. data).

Cambala sp. (TP)

Georgia Records.—Chatooga Co.: Blowing Springs and Parker caves. Polk Co.: Deatons and White River caves. Walker Co.: Cave Spring Cave.

Comments.—Although these records are based on immature specimens, they probably represent *Cambala minor* or a closely related form.

Class Insecta

ORDER COLLEMBOLA

Family Entomobryidae

Pseudosinella hirsuta (Delamare-Deboutteville) (TB)

Georgia Records.—Bartow Co.: Kingston Saltpetre Cave. Chatooga Co.: Blowing Springs Cave. Dade Co.: Johnson Crook, Howards Waterfall, Morrison, Running Water, and Rustys (?) caves. Polk Co.: Deatons Cave. Walker Co.: Bible Springs, Harrisburg, Horseshoe, Mtn. Cove Farm, and Pettijohn caves.

Comments.—This common troglobite is also known from caves in Alabama, Kentucky, Tennessee, and the extreme tip of southwestern Virginia (Christiansen and Culver, 1968).

Family Sminthuridae

Arrhopalites sp. (TP)

Georgia Records.—Bartow Co.: Kingston Saltpetre Cave. Walker Co.: Mtn. Cove Farm Cave.

Comments.—This genus is a widespread, Holarctic group with a number of well known trogliphilic species (Christiansen, 1966).

Family Tomoceridae

Tomocerus bidentatus Folsom (TP)

Georgia Records.—Chatooga Co.: Parker Cave. Dade Co.: Byers and Morrison caves. Walker Co.: Bible Springs Cave.

Comments.—This widespread species is known from numerous epigeal and subterranean localities in the eastern United States. It is especially common in caves in the Appalachian region (Christiansen, 1964).

Tomocerus dubius Christiansen (TP)

Georgia Records.—Bartow Co.: Kingston Saltpetre Cave.

Comments.—This species has been recorded from a number of caves and surface sites in the southeastern United States; it has also been reported from several epigeal localities in California (Christiansen, 1964).

Tomocerus flavescens (Tullberg) (TP)

Georgia Records.—Dade Co.: Johnson Crook Cave. Walker Co.: Cave Spring and Horseshoe caves.

Comments.—This species occurs across the entire North American Continent and has been reported from many caves (Christiansen, 1964).

ORDER THYSANURA

Family Nicoletidae

Nicoletia sp. (TB or TP)

Georgia Records.—Walker Co.: Horseshoe Cave.

Comments.—This undescribed species may be the same as that collected from two caves

in northeastern Alabama (Peck, in prep., Cooper, in press). Furthermore, this form may be an inhabitant of the deep soil (edaphic) rather than a true cave dweller. Reddell (1966) reported a rather common troglotic species of *Nicoletia* from caves in central Texas.

ORDER DIPLURA

Family Japygidae

Unidentified genus and species (ED)

Georgia Records.—Chatooga Co.: Blowing Springs Cave. Walker Co.: Mtn. Cove Farm Cave.

Comments.—Single specimens of this unidentified form were collected from damp spots under rocks (with *Plusiocampa*, see below) in the above caves. Virtually nothing is presently known about the distribution of this rare group in eastern North American caves.

Family Campodeidae

Plusiocampa sp. (TB?)

Georgia Records.—Chatooga Co.: Blowing Springs Cave. Dade Co.: Johnson Crook No. 2 and Morrison caves. Walker Co.: Bible Springs, Cave Spring, Mtn. Cove Farm, and Pettijohn caves.

Comments.—Only five cavernicolous species of this genus have been described from North America (Condé, 1949), although a wealth of un-studied material from southern Appalachian caves indicates a number of undescribed forms. Two of the five described cave species occur in nearby Alabama (i.e., Madison County), but it is presently impossible to say whether the Georgia records represent new species or only mark range extensions of the Alabama forms.

ORDER ORTHOPTERA

Family Gryllacrididae

Ceuthophilus ensifer ensifer Packard (TX)

Georgia Records.—Dade Co.: Byers, Howards Waterfall, Johnson Crook, Morrison, and Morrison Spring caves.

Comments.—This subspecies is also known from localities in eastern Jackson Co., Alabama, and southern Hamilton and Marion counties, Tennessee (Hubbell, 1936 and *in litt.*). In addition to caves, this species inhabits forested talus slopes and cliffs.

Ceuthophilus gracilipes (Haldeman) (TX)

Georgia Records.—Bartow Co.: Yarborough Cave. Dade Co.: Byers, Morrison, and Morrison Spring caves. Gordon Co.: Roberts Cave. Walker Co.: Bible Springs Cave.

Comments.—The distribution of this common species runs in a wide band from Massachusetts and New York southward along the Appalachians to Alabama and northwestern Florida, and then northward to southern Missouri (Hubbell, 1936 and *in litt.*). This

species also occurs in a variety of forested habitats.

Hadenocerus puteanus Scudder (TX)

Georgia Records.—Dade Co.: Byers, Howards Waterfall, Johnson Crook, and Morrison Spring caves (plus Creek Bed, Cricket, and Saw Mill caves of Dearolf, 1953). Gordon Co.: Roberts Cave. Polk Co.: White River Cave. Walker Co.: Bible Springs and Mtn. Cove Farm caves.

Comments.—The range of this species extends from northeastern Ohio and southern New York southward along the Cumberland Plateau, Appalachian Valley, and Piedmont to northeastern Alabama and northern Georgia. It has been recorded from Charlton County in southeastern Georgia and perhaps in error from Lawrence Co., Mississippi. This species lives in cave entrances, along cliffs and talus slopes, and in mesic forests (Hubbell, *in litt.*).

ORDER PSOCOPTERA

Family Psocidae

Psillipsocus ramburii Selys-Longchamps (TP)

Georgia Records.—Bartow Co.: Yarborough Cave. Walker Co.: Cave Spring and Harrisburg caves.

Comments.—This species is known from Europe and North America, and in the latter its range extends from Michigan to Mexico. *P. ramburii* also occurs in caves in Alabama, Tennessee, and Texas and is usually found on organic matter in the drier parts of these caves (Gurney, 1943; Mockford, 1950; Barr, 1961; Reddell, 1966; Peck, in prep., Cooper, in press).

ORDER LEPIDOPTERA

Family Tineidae (?)

Unidentified genus and species (TX)

Georgia Records.—Dade Co.: Byers Cave. Walker Co.: Harrisburg, Mtn. Cove Farm, and Pettijohn caves.

Comments.—Several moths were collected from the droppings of the cave rat (*Neotoma*) in the above caves.

ORDER HYMENOPTERA

Family Braconidae

Aspilota sp. (TX)

Georgia Records.—Bartow Co.: Yarborough Cave. Dade Co.: Johnson Crook Cave. Walker Co.: Horseshoe and Mtn. Cove Farm caves.

Comments.—These small wasps are commonly found on bait left in caves in northern Alabama as well as the caves mentioned above. They are probably parasitic upon the fly larvae that are initially attracted to the bait.

ORDER DIPTERA

Family Heleomyzidae

Aecothea specus (Aldrich) (TP or TX)

Georgia Records.—Dade Co.: Johnson Crook Cave. Polk Co.: White River Cave. Walker Co.: Bible Springs, Cave Spring, Horseshoe, and Mtn. Cove Farm caves.

Comments.—This species is distributed from Alaska to California and eastward to Ontario (Canada), Ohio, and Georgia, and is common in caves (Gill, 1962). Dearolf (1953) reported *Aecothea fenestralis* Fallan from Saw Mill Cave but this may be a misidentification for *A. specus*.

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

Georgia Records.—Dade Co.: Morrison, Running Water, and Rustys caves (plus Saw Mill Cave of Dearolf, 1953). Walker Co.: Harrisburg, Mtn. Cove Farm, and Pettijohn caves.

Comments.—This species was previously known to range from Michigan eastward to Pennsylvania and south-southwestward to Missouri and Alabama. The new Georgia records mark a range extension. *A. defessa* is common in caves of the eastern United States and has been collected as deep in caves as 150 yards from the entrance (Gill, 1962, 1965). A population with a morphology similar to the one formerly assigned to *Amoebaleria sackeni* Garrett was found in Mtn. Cove Farm Cave, but this species was recently synonymized with *A. defessa* (Steynskal, 1968).

Heleomyza brachypterna (Leow) (TP or TX)

Georgia Records.—Walker Co.: Harrisburg and Mtn. Cove Farm caves.

Comments.—The above records are based on females and should be confirmed with males if and when available. This species has been collected from caves but was previously unrecorded from Georgia. (Gill, 1962).

Family Muscidae

Chaetogenia sp. (Accidental)

Georgia Records.—Bartow Co.: Yarborough Cave.

Comments.—This collection was made from human feces.

Family Mycetophilidae

Unidentified genus and species (TP or TX)

Georgia Records.—Walker Co.: Bible Springs and Mtn. Cove Farm caves.

Comments.—These collections were made from carrion traps.

Family Psychodidae

Psychoda sp. (TP or TX)

Georgia Records.—Bartow Co.: Kingston Saltpetre Cave. Walker Co.: Pettijohn Cave.

Comments.—These flies are frequently found in moist, shady places with decaying organic debris (Curran, 1965; Stone et al., 1965).

In the above caves these flies were taken from carrion traps and human feces.

Family Sciaridae

Sciara sp. (TP or TX)

Georgia Records.—Bartow Co.: Kingston Saltpetre Cave. Dade Co.: Byers, and Johnson Crook caves. Polk Co.: White River Cave. Walker Co.: Mtn. Cove Farm Cave.

Comments.—These small, dark, delicate flies are found in moist places where their larvae feed on fungus (Curran, 1965; Stone et al., 1965). Several species may be represented by the above collections, most of which were collected within a few hundred feet of the cave entrances in traps baited with carrion.

Family Spaeroceridae

Leptocera sp. (TP or TX)

Georgia Record.—Chatooga Co.: Blowing Springs Cave. Dade Co.: Johnson Crook Cave. Walker Co.: Bible Springs, Mtn. Cove Farm, and Pettijohn caves.

Comments.—These small, dark flies are common in caves, where they are frequent scavengers on decaying organic matter (Curran, 1965; Stone et al., 1965).

Family Tipulidae

Unidentified genus and species (TX ?)

Georgia Records.—Dade Co.: Johnson Crook Cave. Walker Co.: Bible Springs Cave.

Comments.—The above collections were made in the twilight zone. Tipulids are often found in small swarms in cave entrances, perhaps using the moist entrances as day-time retreats.

Family Phoridae

Megaselia sp. (TP or TX)

Georgia Records.—Bartow Co.: Yarborough Cave. Chatooga Co.: Blowing Springs and Parker caves. Dade Co.: Byers, Johnson Crook, and Morrison caves. Polk Co.: White River Cave. Walker Co.: Cave Spring, Harrisburg, Horseshoe, Mtn. Cove Farm, and Pettijohn caves.

Comments.—These small, dark flies are common around decomposing organic matter in caves. Several species are represented in the above collections which were made mostly from *Neotoma* dung and carrion bait.

ORDER COLEOPTERA

Family Cantharidae

Unidentified genus and species (TX)

Georgia Records.—Chatooga Co.: Parker Cave. Walker Co.: Harrisburg, Mtn. Cove Farm, and Pettijohn caves.

Comments.—The above collections were all larval forms and were taken from damp areas just inside the dark zone. These beetle larvae have also been encountered in caves in Alabama and Tennessee.

Family Carabidae

Agonum (Rhadine) caudatum (LeConte) (TP)

Georgia Records.—Dade Co.: Rustys Cave.

Comments.—This species is a common troglophile in the caves of Alabama, Tennessee, and Virginia (Barr, 1964). It was previously unrecorded from Georgia caves.

Anillinus sp. (TX ?)

Georgia Records.—Dade Co.: Morrison Cave.

Comments.—This undescribed, forest-soil inhabiting species has also been found in Alabama caves (Barr, 1969; Peck, in prep.).

Atranus pubescens (Dejean) (TP)

Georgia Records.—Walker Co.: Bible Springs Cave.

Comments.—This species occurs in caves of the eastern United States, the Ozarks, and Texas (Barr, 1964).

Harpalus (Pseudophonus) sp. (Accidental)

Georgia Records.—Dade Co.: Morrison Cave. Walker Co.: Bible Springs Cave.

Pseudanophthalmus digitus Valentine (TB)

Georgia Records.—Dade Co.: Byers and Johnson Crook caves.

Comments.—This species was previously known only from two females taken in Tennessee Caverns, Hamilton Co., Tennessee (Barr, 1965).

Pseudanophthalmus fulleri Valentine (TB)

Georgia Records.—Dade Co.: Byers, Howards Waterfall, Johnson Crook, Morrison, and Sittons caves. Walker Co.: Horseshoe Cave.

Comments.—This species was previously known only from its type locality (Tennessee Caverns, Hamilton Co., Tenn.) and Howards Waterfall Cave (see above) (Barr, 1965). The new records above not only extend the range of this species but also indicate that it is not as rare as previously thought (see Barr, 1965, p. 66).

Pseudanophthalmus sp. (TB)

Georgia Records.—Chatooga Co.: Blowing Springs Cave. Walker Co.: Mtn. Cove Farm and Pettijohn Caves.

Comments.—These collections represent an undescribed species.

Tachys (Tachyura) ferrugineus (Dejean) (TP)

Georgia Records.—Decatur Co.: Climax Cave.

Comments.—This species occurs rarely in caves in the eastern United States but is known from four caves in Alabama (Peck, in prep.). According to Barr (1964), this species is common in caves in Texas.

Family Leiodidae (subfamily Catopinae)

Catops gratiosus Blanchard (TP or TX)

Georgia Records.—Chatooga Co.: Parker Cave. Dade Co.: Morrison Cave. Walker Co.: Mtn. Cove Farm Cave.

Comments.—All of the above collections were made from rotting liver bait in the dark zone. This species was previously recorded from Washington (state), Ontario (Canada), and New England southward to Kentucky

and Virginia (Hatch, 1933). Most of the southern records are from caves.

Nemadus sp. (TP or TX)

Georgia Records.—Dade Co.: Morrison Cave. Walker Co.: Cave Spring, Horseshoe, and Mtn. Cove Farm caves.

Comments.—All of the above collections were made from liver bait in the dark zone. Members of this genus are only occasionally encountered in caves, where they may exist in large populations on bat guano.

Prionochoeta opaca Say (TP or TX)

Georgia Records.—Chatooga Co.: Blowing Springs Cave. Walker Co.: Bible Springs, Cave Spring, Horseshoe, and Mtn. Cove Farm caves.

Comments.—All of the above collections were made from liver bait in the dark zone. This species was previously recorded from Quebec (Canada) and New Hampshire south to North Carolina and west to Arkansas (Hatch, 1933).

Ptomaphagus whiteselli Barr (TB)

Georgia Records.—Dade Co.: Byers, Case, Morrison, and Sittons caves.

Comments.—This species was originally described from Sittons Cave by Barr (1963a) and was also reported from Sequoyah Caverns, DeKalb Co., Alabama by Peck (1966).

Ptomaphagus sp. (TB)

Georgia Records.—Walker Co.: Bible Springs, Mtn. Cove Farm, and Pettijohn caves.

Comments.—This undescribed species appears to be more closely related to a species from Jackson Co., Alabama than to *P. whiteselli* from nearby caves in Dade County.

Ptomaphagus sp. (TP)

Georgia Records.—Dade Co.: Johnson Crook No. 2 and Morrison caves. Walker Co.: Bible Springs Cave.

Comments.—This undescribed species has also been collected from forest litter in Georgia and Alabama and from caves in Alabama (Peck, in prep.).

Sciodrepoides fumatus terminans LeConte (TX?)

Georgia Records.—Walker Co.: Cave Spring Cave.

Comments.—Hatch (1933) called this species *Catops (Sciodrepoides) terminans* and gave its range as extending from British Columbia and New Brunswick south to Illinois and North Carolina. This species was collected from liver bait in the above cave where it was probably accidental rather than trogloneic.

Family Pselaphidae

Batrissodes globosus (LeConte) (TP)

Georgia Records.—Decatur Co.: Climax Cave.

Comments.—This is the best known and most widely distributed species in the genus and occurs throughout eastern North America (Park, 1947). This species has also been

taken from Sanders Cave, Conecuh County, in southern Alabama (Peck, in prep.).

Batriasymmodes spelaeus Park (TP)

Georgia Records.—Chatooga Co.: Blowing Springs Cave. Walker Co.: Bible Springs Cave.

Comments.—This species was previously reported from caves in nine Alabama counties and four Tennessee counties; more recently it was collected from a sandstone rockshelter in Alabama (Park, 1951, 1958, 1960, 1965; Peck, in prep.; Steeves, in litt.).

Subterrochus sp. (TB)

Georgia Records.—Walker Co.: Mtn. Cove Farm Cave.

Comments.—This undescribed species is apparently a troglobite (Park, 1960; Steeves, in litt.).

Family Staphylinidae

Atheta sp. (TP)

Georgia Records.—Bartow Co.: Yarborough Cave. Chatooga Co.: Blowing Springs and Parker caves. Dade Co.: Byers, Johnson Crook, and Morrison caves. Walker Co.: Bible Springs, Cave Spring, Horseshoe, Mtn. Cove Farm, and Pettijohn caves.

Comments.—The above collections, mostly from carrion traps and liver bait, probably represent at least three species of this genus.

Geodromicus brunneus Say (TX ?)

Georgia Records.—Walker Co.: Bible Springs and Mtn. Cove Farm caves.

Comments.—This species might be an accidental rather than a troglone.

Lesteva pallipes LeConte (TP)

Georgia Records.—Chatooga Co.: Blowing Springs Cave. Walker Co.: Bible Springs and Mtn. Cove Farm caves.

Comments.—All of the above collections were made from carrion traps or liver bait.

Oxyopoda sp. (TX ?)

Georgia Records.—Bartow Co.: Yarborough Cave.

Philonthus cyanipennis Fabricius (Accidental)

Georgia Records.—Walker Co.: Pettijohn Cave

Comments.—This species was collected from liver bait.

Philonthus sp. (TP or TX)

Georgia Records.—Walker Co.: Bible Springs Cave.

Comments.—This species is presently undescribed.

Quedius fulgidus Fabricius (TP)

Georgia Records.—Polk Co.: White River Cave.

Comments.—This species is distributed across the United States and is known from caves in Illinois and Kentucky (Peck, unpubl. data).

Quedius erythrogaster Mannerheim (TP)

Georgia Records.—Dade Co.: Morrison Cave. Walker Co.: Harrisburg, Hickman Gulf, and Pettijohn caves.

Comments.—This species ranges across the northern United States and into Canada and is common in caves of the eastern part of the country.

Tachinus fimbriatus Gravenhorst (Accidental)

Georgia Records.—Walker Co.: Pettijohn Cave.

Comments.—This single record is from a male specimen collected from a carrion trap just inside the cave entrance.

ZOOGEOGRAPHIC RELATIONSHIPS

Of the approximately 130 invertebrate species presently recorded from Georgia caves, between 24 and 27 are troglobites. The troglobites represent approximately 20 percent of the total invertebrate fauna and about 45 percent of them are apparently endemic to northwestern Georgia. Owing to the fact that taxonomic studies are still in progress and that further field work will undoubtedly yield additional species, these figures must be regarded as provisional. The troglobitic species are taxonomically distributed as follows, with the number of Georgia endemics given in parentheses. Planarians, 1 (1); gastropods, 1; asellid isopods, 2 (1); trichoniscid isopods, 1 (1?); gammarid amphipods, 4 (1); crayfish, 1; chthoniid pseudoscorpions, 1 or 2 (1); spiders, 3 or 4 (2); chordeumid millipedes, 2 or 3 (2 or 3); diplurans, 1? (1?); collembolans, 1; carabid beetles, 3 (1); leiodid beetles, 2 (1); and pselaphid beetles, 1 (1).

More than one-half of the troglobitic species of northwestern Georgia are also found in caves of nearby states, notably in neighboring Alabama and Tennessee. *Cambarus cryptodytes*, a troglobitic crayfish recorded from Climax Cave in southern Georgia, is also known from northern Florida.

Although taxonomic and distributional data are still incomplete, it is nevertheless possible to analyze the distribution of the troglobitic species of the Georgia Appalachians. In northwestern Georgia two zoogeographic faunal units, the Appalachian Plateau unit and the Appalachian Valley unit, can be designated. These units correspond to the physiographic units of the same name

and are geologically defined on the basis of theoretical dispersal barriers.

The Plateau unit lies on the eastern margin of the Appalachian (Cumberland) Plateau which, in turn, continues northward into south-central Tennessee and westward into northern Alabama. With some exceptions it may correspond zoogeographically to the Cumberland Plateau faunal unit designated by Barr (1967). However, the Plateau of Georgia is exceptional because: (a) its geological and physiographic relationship to the Cumberland Plateau is marginal, (b) its limestones lie in close proximity to those of the Appalachian Valley, and (c) its limestones are extrinsically isolated from those which form the broad, caverniferous western edge of the Cumberland Plateau in Alabama and Tennessee, the area more precisely designated as the Cumberland Plateau faunal unit by Barr (1967).

The Plateau faunal unit can be subdivided into (1) the Lookout Valley subunit, situated entirely within Dade County and defined as the cavernous area lying between Sand Mountain on the west and Lookout Mountain on the east; and (2) the eastern Lookout Mountain subunit (including Pigeon Mountain) which lies mostly within Walker County.

Five distinct patterns of troglobite distribution are distinguishable. (1) There are a few species which are not only common in caves in both faunal units of northwestern Georgia but are also found in much of the southern Appalachian cave region. These species show comparatively little range restriction and include the snail, *Glyphyalinia specus*, the isopod *Asellus richardsonae*, the amphipod *Crangonyx antennatus*, the spiders *Phanetta subterranea* and *Porrhomma caverniculum*, millipedes of the *Scoterpes austrinus* complex, and the collembolan *Pseudosinella hirsuta*. (2) There are a number of forms which occur in both subunits of the Plateau but not in the Valley and include an undetermined (undescribed?) species of the terrestrial isopod *Caucasonethes*, an undescribed species of the amphipod *Stygobromus*, the pseudoscorpion *Kleptochthonius magus*, an undescribed species of the spider *Leptoneta*,

the milliped *Pseudotremia eburnea*, and an undetermined (undescribed?) species of the dipluran *Plusiocampa*.

(3) There are a few species which occur in caves in one or the other Plateau subunits but not in both: the Lookout Valley fauna includes the planarian *Sphalloplana georgiana*, an undescribed species of the spider *Cicurina*, the millipede *Ameractis satis*, the carabid beetle *Pseudanophthalmus digitus*, and the leiodid beetle *Ptomaphagus whiteselli*; the eastern Lookout Mountain fauna includes an undescribed species (one each) of *Asellus*, *Pseudanophthalmus*, *Ptomaphagus*, and *Macherites*. (4) Two species occur in the Plateau (Lookout Valley) and also in the Appalachian Valley and include an undetermined (or undescribed?) species of the pseudoscorpion *Apochthonius*, and the carabid beetle *Pseudanophthalmus fulleri*. (5) Only two species (both undescribed) of the amphipod *Stygobromus* are known exclusively from the Appalachian Valley caves—one from Parker Cave and one from caves in Floyd and Polk counties.

Although not formally covered in this paper, the troglobitic vertebrates of Georgia might also be mentioned in passing, since their presence in the state further emphasizes the zoogeographic significance of this area. Three species of vertebrate troglobites have been reported from Georgia caves—two salamanders and one fish. *Haideotriton wallacei* (Carr), a rare troglobitic salamander, was first described from a deep well at Albany, Dougherty Co., Georgia, and has since been found in a number of caves in Jackson Co., Florida and in Climax Cave, Decatur, Co., Georgia (Pylka and Warren, 1958; Warren, 1961). A more widely distributed troglobitic salamander, *Gyrinophilus pallescens* McCrady, previously recorded from caves in southern and eastern Tennessee and Jackson Co., Alabama (Brandon, 1966), was recently reported from Harrisburg Cave in Walker County, Georgia by Cooper (1968). This is the first and only known record to date for this species in Georgia. The southern cavefish, *Typhlichthys subterraneus* Girard, a rather widely distributed troglobite whose range extends

from Missouri to southern Indiana and south through Kentucky and Tennessee to northern Alabama, was recently discovered in Twin Snakes Cave in Dade Co., Georgia, by A. Iles and A. Dobson (Cooper and Iles, this issue). This is the first Georgia record for this species.

By and large, the troglomorphic species of Georgia have much wider ranges than the troglobitic species and most are not restricted to any one given faunal unit or subunit. Since, by definition, these species are not necessarily restricted to cave habitats, their powers of dispersal are usually greater than those of troglobites and, consequently, their ranges are less narrowly defined. Approximately 20 genera which are represented by troglomorphic species throughout most of the southeastern cave region (Appalachians and Interior Low Plateau) are also found in Georgia. Four other genera which contain troglomorphs in Georgia are known otherwise only from caves in the Interior Low Plateau region, primarily from northern Alabama, central Tennessee and Kentucky.

Of some interest are four species of Georgia troglomorphs which show a habitat shift going from north to south along their ranges. These four species—the millipede *Cambala annulata*, the opilionid *Phalangodes spinturnix*, the carabid beetle *Tachys ferrugineus*, and the leiodid beetle *Prionochoaeta opaca*—are more common in caves on the southern ends of their ranges, especially in the Coastal Plain, than on the northern ends. In the northern parts of their ranges, especially in the Appalachians, these species are more common in the cool, moist habitats of forest floors. The preference for caves in the Coastal Plain is probably influenced to a large extent by the absence of ecologically suitable habitats on the surface.

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The Southern Cavefish, *Typhlichthys subterraneus*, at the Southeastern Periphery of its Range

By John E. Cooper * and Anthony Iles **

ABSTRACT

Two populations of the troglolithic amblyopsid fish, *Typhlichthys subterraneus* Girard, have been discovered in Deer Head Cove headwaters of tributaries of the Tennessee River, including the first reported in Georgia. These are the nearest known localities to Walden Gorge, which divides the Tennessee into an eastern and a western portion. Another locality for this fish in the Coosa River drainage of Alabama is now known. Additional specimens from Sell's Cave, Alabama, the only previously known Coosa locality, have been collected. The Mobile Basin populations do not differ significantly in morphology from several Tennessee River drainage populations.

INTRODUCTION

The troglolithic amblyopsid fish, *Typhlichthys subterraneus* Girard, has the most extensive range of any North American cave fish. This range is discontinuous, with a western component including northeastern Oklahoma, central and southern Missouri, and northern Arkansas, and an eastern component which begins in the south-central tip of Indiana, extends south in a narrow band through central Kentucky, widens in central Tennessee, and covers most of northern Alabama along both sides of the Tennessee River (although few populations from south of the river are known). It has recently been discovered in southeastern Kentucky as well (Cooper and Beiter, in

MS). The range apparently does not include those parts of eastern Missouri, southern Illinois, southwestern Indiana, and western Kentucky which lie between the southernmost limits of Wisconsin glaciation and the northern limits of the Cretaceous shoreline of the Mississippi Embayment.

The southeastern periphery of the range of this fish was for some time thought to lie along the main Tennessee River drainage in northern Alabama and adjacent Tennessee. However, Boschung (1961) reported specimens from Sell's Cave (Al 876), near Collinsville, DeKalb County, Alabama, which clearly indicated that at least one population of *T. subterraneus* existed in the Coosa River system across the drainage divide. A member of this population is figured in Smith-Vaniz (1968). The following new information concerning *Typhlichthys* on the southeastern edge of its range, including the initial record for the state of Georgia and

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the closest records to Walden Gorge, which divides the Tennessee River into an eastern and western portion near Chattanooga, is a result of the work of the Biological Survey of Alabama Caves, a research project of the National Speleological Society. This paper is Contribution Number 5 from the Survey. Numbers in parentheses following some cave names refer to the Alabama Cave Survey system of identifying and locating caves (Tarkington, *et al.*, 1965), which avoids the confusion sometimes resulting from the fact that many Alabama caves have the same or similar names.

COLLECTIONS AND DISCUSSION

Georgia

Dade County, Twin Snakes Cave—The first Georgia specimen of *Typhlichthys subterraneus* was captured here in April, 1969. Numerous visits had been made to the cave during the preceding year, but water there had either been impossibly high for collecting or non-existent. In February, 1969, A. Dobson and A. Iles saw a large specimen in an inaccessible sump at the far end of the cave. Several subsequent trips were made to the cave, but they were all fruitless until the April trip. In addition to the lone specimen collected at this time, another, in excess of 50 mm long, was observed but not captured.

Twin Snakes Cave lies in a small bluff bordering Allison Creek, about 1.7 km north of Deer Head Cove Cave, discussed below. The entrance is a few meters above stream level, and the cave itself is short, having probably only about 60 m of accessible passage. It is normally dry, but after prolonged rain the water table rises slowly and floods the cave with clear water, sometimes completely.

Other members of the aquatic community here include the crayfish *Cambarus bartoni cavatus*, and a small, unidentified, gilled salamander which eluded capture because of mud stirred up in crawling through the water. As in many other caves, when the water is rising in Twin Snakes the fish

and crayfish move up with it, probably seeking food.

Fred Byers, a local resident and cave explorer, says that he has seen white fish in Hurricane Cave, Dade County, a cave of debouché at or near the valley floor draining the east side of Fox Mountain. A search in late 1967 did not yield any indication of fish here. This is far from conclusive evidence that they don't exist in this area, though, since it took many trips to Deer Head Cove before a specimen was ever seen.

Alabama

DeKalb County, Deer Head Cove Cave (Survey number not available)—The second specimen of *T. subterraneus* from Deer Head Cove was collected in this cave in the spring of 1969 by Dobson and Iles. Deer Head Cove Cave is the main resurgence site for the drainage of Deer Head Cove, which lies between Fox Mountain to the east and Pudding Ridge to the west, and most of which lies in Alabama. The water here goes to ground through a number of sinks scattered throughout the cove, then coalesces and re-emerges as Allison Creek. This eventually joins Lookout Creek, a northeast-flowing tributary of the Tennessee River. The main cave here has an impressive cross-section but is only penetrable for some 30 m before it ends in a sump. Attempts by The Descenders, a diving and cave-exploring club from Atlanta, Georgia, to penetrate to the large cave hypothesized to lie beyond the sump, have met with no success. On the surface, about 135 m behind the expansive entrance, lies a small hole which opens onto a steep slope descending into a room floored with boulders. Along the far edge of the room at the water table is a small lake where *Typhlichthys* was found. This lake probably connects with the resurgence stream, since it rises and falls rapidly in response to epigeal conditions, is sometimes highly turbid, and appears to flow as a mass.

At the time the fish was captured the main cave stream was in flood. Lakes in the

cave were several feet higher than normal and very turbid. Some time had been spent in vainly trying to locate a specimen in the opaque waters. The capture of a single fish was finally accomplished by a blind sweep of a net through deep, swirling water. A very small specimen had been previously observed in the cave on a routine collecting trip in December, 1968, but capture was not possible. On each of two subsequent visits a single fish was observed which also proved too elusive for capture.

Other aquatic fauna found in this cave were a single specimen of the petromyzontid, *Lampetra sp.*, and an observed specimen of a large, gilled salamander which may have been *Gyrinophilus pallescens*, recently reported from Georgia caves by Cooper (1968).

DeKalb County, Sell's Cave—(AI 876)—Boschung (1961) first reported *Typhlichthys* from the Mobile Basin on the basis of 10 specimens collected at this locality by him, R. E. Smith, and J. White on June 29, 1958 (UAIC 656). Two additional specimens (AU 2067) were collected here by W. Smith-Vaniz and G. N. Greene on August 20, 1964. On June 22, 1968, Cooper, with the help of R. Graham, A. Dobson, and L. Guy, collected four specimens and observed a number of others here by diving in the cave. Individual fish on this occasion were found within 10 cm of the surface and as deep as nearly 2 m, but each was within 30 cm or less of a limestone wall, submerged ceiling, or ledge. None was seen on or near the bottom in deep water. All of the captured specimens had heavy concentrations of melanophores along the lateral line and myoseptal divisions, and two had concentrations in the dorsal midline. In addition, one specimen had a reticulate pattern on the posterior half of the body. This concentrated condition of melanophores in cave fish is usually (but not always) associated with openness of the habitat to light, and that is the situation at Sell's.

The only other macroscopic aquatic fauna seen in the cave were two larvae of the salamander, *Eurycea longicauda longicauda* X *guttolineata*, which were observed on silt in shallow water at the entrance. A recently metamorphosed specimen of this salamander was found under a rock on moist soil 0.5 m from the water's edge.

Sell's Cave is in a deep, wooded sink at an elevation of 213 m, some 120 to 150 m northwest of Big Wills Creek, a tributary of the Coosa River. It is primarily a large, subterranean lake, some 15 m long and 3 to 5 m wide, which opens to the surface through a medium-sized, horizontal entrance. The edge of the lake is directly exposed to light, although it is shaded from bright sun by forest canopy for most of the year. Because of the steepness of the sink there is no outflow from the lake at the entrance. The water is very clear and cold; Boschung (1961) recorded the temperature on June 29, 1958, as 14° C. Dr. J. Ramsey has provided the following physico-chemical data collected on August 20, 1964 by Smith-Vaniz and Greene: water temperature, 13.3°C.; air temperature, 20.6°C. in cave; dissolved O₂, 7.4 ppm; CO₂ 8 ppm; HCO₃⁻, 171 ppm; CaCO₃, 82 ppm. The floor of the lake slopes sharply down from the entrance, and water depth quickly increases from just a few cm to around 3 m. At its furthest accessible point the lake is 5 to 6 m deep. There is considerable air space above the water in the lake room and there is rumored to be a short section of dry passage beyond and above this. No accessible underwater leads were found by Cooper in 1968.

DeKalb County, Browder Cave (AI 445)—This cave is the second Coosa drainage locality where *T. subterraneus* has been found. On March 15, 1969, R. Graham, E. Steenburn, and A. Dobson observed three specimens here and collected two of them. Browder Cave is in the drainage of Big Wills Creek, about 5 km north of Fort Payne and 29 air km from Sell's Cave. The accessible cave consists of a single, medium-

sized room with a short side passage. The floor of the room slopes very sharply from the entrance, and it was at the bottom of this slope that the water containing the fish was found. The water was covered with muddy scum, an invariable sign of rising water in such caves. According to the owner of the cave, it floods completely and water flows from the entrance when groundwater rises in response to heavy spring rains. Cooper visited the cave in July, 1968, and found it completely dry. No other aquatic organisms have been seen in Browder Cave.

In first reporting *Typhlichthys* from the Coosa River drainage, Boschung (1961) "tentatively assigned" the specimens to the species *T. subterraneus*. Smith-Vaniz (1968) apparently had no difficulty assigning his specimens from Sell's Cave to this species. It was reasonable to suspect that this peripheral population, in a drainage system from which the species was previously unknown, might be significantly divergent when compared with others, but this is not now indicated by the morphological evidence. These specimens exhibit no consistent phenotypic differences when compared with other populations from the Tennessee River drainage in northern Alabama. This observation will be elaborated in a future paper dealing with variation in southern *Typhlichthys* populations. Woods and Inger (1957) indicate that *T. subterraneus* shows considerable variation with respect to some characters throughout its range, but the inter-populational differences show no consistent geographic pattern and are of no taxonomic significance. A very thorough study of variation in cave-dependent and cave-independent characters in *Typhlichthys* populations is in order. A partial analysis for nine populations has been made by Poulson (1961).

It has been suggested that genetic continuity in some aquatic troglobites may be facilitated by exchange through groundwater systems which are more-or-less auto-

nous from surface drainage patterns. See, for example, Woods and Inger (1957) and Holsinger (1969). Ehrlich and Raven (1969), however, present strong evidence that phenetic similarity in possibly allopatric populations, including those of the troglobitic collembolan *Pseudosinella hirsuta*, carefully analyzed by Christiansen and Culver (1968), may be more a matter of similar selective regimes than any significant gene flow.

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Biology of Cave and Deep Sea Organisms: a Comparison

By Thomas L. Poulson *

ABSTRACT

A panel discussion held at the 1969 AAAS meeting is summarized. The cave and deep sea environments have many similarities for the organisms which have adapted to life in them. The similarities and differences in these adaptations are examined for insight into evolutionary ecology and community structure in the two environments. The characteristics of life history and age distribution, sensory adaptation, and metabolic efficiency are discussed. The effects of geographic isolation and Pleistocene invasions are contrasted. Species diversity and the factors influencing it are discussed.

The intent of this paper is to summarize a panel discussion held at the 1969 Boston Meeting of The American Association for the Advancement of Science. I arranged the program which was sponsored by the Biology Section of The National Speleological Society. My summary, of course, represents my own distillation of the proceedings and so may not adequately reflect the views of my colleagues. I hope that anything lost in that regard is balanced by cohesion.

PROGRAM OUTLINE

- I. General introduction (Poulson)—Characterization of the two environments and reasons for interest in caves and the deep sea.
- II. Life history, sensory and metabolic adaptations—Evidence for the importance of metabolic economy?
 - A. Life history and age distributions
 1. Amblyopsid cave fish; a paradigm for decreased reproductive potential (Poulson)
 2. Deep sea brittlestars; an exception to the rule? (Schoener)

3. Evolutionary trends in cave beetles (Peck)
 4. Age distributions of deep sea mollusks: inferences from growth of inshore and deep sea species (Turner and Rhoades)
 - B. Sensory adaptations: inference from allometry and body proportions and behavioral evidence (Poulson)
 - C. Metabolic efficiency: is it general?
 1. Amblyopsid cave fish: increased metabolic efficiency with increased time of isolation in caves (Poulson)
 2. Cave amphipods: an exception? (Culver)
 3. Deep sea animals: no difference from inshore species? (Teale)
 - D. Is food limiting in the deep sea?
 1. Problems of defining food and its availability (Darnell)
 2. Is depth zonation of animals related to food supply? (Rowe)
 - E. Open discussion
- III. The fauna
 - A. History of the biota—Effects of the Pleistocene, persistence of relicts,

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and multiple invasion vs in situ speciation

1. Terrestrial cave organisms (Peck)
 2. Aquatic cave organisms (Holsinger)
 3. The deep sea epifauna and infauna (Sanders)
- B. Explanations of species diversity
1. Indices of diversity, general hypotheses, and examples from caves (Culver)
 2. The stability/time hypothesis: in-shore vs deep sea (Sanders)
- C. Open discussion

PARTICIPANTS

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INTRODUCTION

The major basis for this discussion is the similarity in the environmental problems faced by organisms that live permanently in caves and those that live permanently on the ocean bottoms at depths below 2000 meters (the bathybenthic). It seems likely that the animals in these environments share morphological, physiological, and life history specializations due to lack of light and food limitation. These adaptations may relate to similarities in community structure which are of interest to the evolutionary ecologist. Finally, there was the hope that communication between students of the two environments might yield insights into the basis for community structure in other environments.

Both caves and the bathyenthos are of a class of environments that can be char-

acterized as old, climatically stable, and non-rigorous (Poulson and White, 1969). They are therefore predictable in time. There are, however, major differences between these two natural laboratories. Improved sampling has revealed (Sanders and Hessler, 1969) that the bathybenthic oozes contain large numbers of species (infauna) including many species in the same genus feeding by ingesting the sediment and extracting bacteria, protozoa, or dissolved organic matter. This raises fascinating questions about the role of competitive exclusion, particularly since it appears that a given species pattern may be repeated over wide areas even on both sides of an ocean basin. In caves the habitat is more dissected in space and in character, both inter- and intracave. There is the question whether cave communities are stabilized in evolutionary time; certainly cave faunas are more recent than deep sea faunas. Finally, the low average densities of small animals in caves, .0001-1.0/m², make one wonder whether competitive exclusion is even possible. These densities approach those seen for comparable sized animals in a photographic survey of the deep sea epifauna, .01-10/m² (Rowe and Menzies, 1970), but are nowhere near the high densities, 25-200/m², for the deep sea infauna (Sanders and Hessler, 1969).

Cave animals, unlike bathybenthic animals, can be maintained in the laboratory and studied behaviorally or physiologically under natural and experimentally modified conditions. There are few enough cave species so that it is possible to study the biology of each species of the community and its interactions with other species. Thus it will be possible to determine which species characteristics or interactions are associated with communities of high or low diversity. This level of analysis is not yet possible in the deep sea, mainly because of logistic and sampling problems. Defined sampling of the infauna at one location will be necessary to define interspecific and interindividual interactions. Photography is used to sample the larger and less diverse epifauna, but with this method the more mobile groups, like fish and shrimp, are

disturbed and rarely recorded on film. For the infauna the problems at the initial taxonomic level are staggering in themselves. Often groups apparently have as many as 10-25 species in a sample. To be sure that they are really separate species it is necessary, as Hessler has done for one genus of isopods, to compare all life history stages of each species to assess whether the fine morphological differences between supposed species are constant and therefore real. The next level of analysis, of habitat or food selection and of metabolic needs, is underway in caves but is not yet possible in the deep sea. For whatever reason, and it does not seem to be temperature or pressure, live specimens have not long survived the trip to the surface and so have scarcely been studied alive. Hopefully perfection of deep submersibles will soon allow biologists to circumvent these problems by in situ observation.

LIFE HISTORY AND AGE DISTRIBUTIONS

I started this discussion by using amblyopsid cave fish (Poulson, 1963 and 1969) as a paradigm for the decreased compound interest rate of population growth selected by food limitation over a long period of evolutionary time. The evolutionary series of swamp, spring-cave, and cave fish shows decreased fecundity associated with increased egg size and parental care, increased generation time associated with increased age at first reproduction and longevity, and a tendency toward skewing of age distributions toward older age classes. This evolutionary series culminates in a life history or reproductive strategy which is the antithesis of the "opportunism" shown in seasonal and rigorous environments, and I proposed that long life and the chance for repeated reproduction allows eventual reproductive success in an environment that may not be conducive to reproduction every year because of food or mate scarcity and predation.

Peck reviewed his work on scavenger beetles (1968 and in progress) which, as with most cave organisms (Poulson, 1964), supports the paradigm given for cave fish.

Peck described a series of elegant studies in which he raised surface, troglomorphic, and troglobitic species of the genus *Ptomaphagus* through their life cycles in the laboratory. The more specialized troglobites show longer life cycles, but the development of a non-feeding larva, small clutch size, and large eggs seen in European species is inexplicably absent in the North American species. Perhaps the problem of a sedentary larva finding a rare and superdispersed food supply is circumvented by adult feeding of young in the specialized species. This seems a reasonable possibility to me since the larvae of N. American species do not have the degenerate sense organs or mouthparts seen in European forms that never feed.

The data on bathybenthic species are scattered and fragmentary, especially on size or age distributions, but it is clear that some epibenthic groups do not conform to the paradigm set up for cave fish. Schoener showed that the brittlestars have an inverse relation between fecundity and egg size but, except for a few brooding species, all lay hundreds to thousands of small eggs. Each of these species has a depth range of 1 to 5 thousand meters, and their fecundities do not have the same rank order as specialization inferred from narrowness of depth distribution. Apparently the epibenthic crabs show a similar mix of brooding species with few large eggs and non-brooding species with many small eggs and free-living planktonic larvae (Marshall, 1954). From fragmentary data it appears that a higher proportion of the infauna show large eggs and direct development (Sanders and Hessler, 1969).

The few data available that suggest low growth rates have not yet been translated into age or even size distributions. Rhoades has started to analyze scanning electron micrographs of growth rings in the shells of bivalve mollusks (nuculoids) from the intertidal to the deep sea. His preliminary data show about twice as many rings in deep sea as for similar sized inshore species, but it is not yet clear whether these rings are equivalent because the daily and tidal

reabsorption of shell inshore is absent in the deep sea. Data available on the size distributions of deep-sea forms are suspect because of the possible size sorting and loss of small individuals during retrieval of the sampling gear from the ocean depths. Here the core sampling being done by Sander's group will provide important information on a comparative basis even if there are no data on growth rates to translate size into age distributions. Despite lots of unambiguous data on size distributions of troglobites, growth rates have been determined only for fish.

SENSORY ADAPTATION

Cave and bathybenthic organisms face similar selective pressures, so we would expect parallels in sensory adaptations. However, unlike caves, the presence of luminescent organs in some species of bathybenthic animals (but not in as high a proportion as in the bathy- or mesopelagic) results in maintained selection for eyes and pigmentation. On the other hand, deep sea and cave animals both have to hunt in the dark because the deep sea is still basically aphotic. Unfortunately it is not yet possible in the case of deep sea forms, as it has been for cavefish (Poulson, 1963; Poulson and White, 1969) and some invertebrates (Poulson, 1964; Cooper, 1969), to relate relative food limitation to efficiency of food finding.

The morphological adaptations of the epibenthic deep sea fish and crustaceans may function either to avoid stirring up the soft bottom oozes where food occurs—as in the stilt-fins of the bathypteroid fish, the long thin legs of crabs and shrimp, and the high oil content of the liver that confers neutral buoyancy to a six-gilled shark—and/or as adaptations for finding food and detecting predators. It is also possible that the stilt-fins function as I have suggested for the long spindly legs of specialized cave salamanders (Poulson, 1964 and Brandon, this issue) where the lateral line water movement detection system is given a wider "field of view" by being raised off the substrate. In a more straight forward vein

the open pits in the bathybenthic cetomimid fish (*Gyrinomimus*, Richardson and Garrick, 1964) may serve to expose the lateral line organs and increase their exposure in a different way than in amblyopsid cave fish where the evolutionary solution has been to place the organs in rows on the surface of the head. A large head may reflect increased sensory endowment of the less obvious chemosensory systems in the macrourid and brotulid fish which are also convergent in their 'vacuum cleaner' mouths (Bruun, 1966; Marshall, 1954). Of course some species, like the double-tailed fish *Halophyrus*, have obvious contact chemical sensors on whiskerlike barbels that trail along the bottom as the fish swims above, much as catfish do. Just as increased relative head size gives more area for lateral line or taste organs in fish, so the shape of crustaceans does for tactile and chemoreceptors. Comparing two species of the same body weight, the one with a more "slight" body build and long attenuated limbs has a higher total surface area and so more sense organs per unit body weight. However, this modification in body build does not seem to be common in bathybenthic crabs and shrimp, although it is the general rule in cave crustaceans. These calculations, of course, prove nothing without experimental data like Banta's (in Poulson, 1964). More recently, Cooper (1969) has given behavioral data, in terms of time taken to react and distance moved before capture, for increased food finding efficiency in a cave crayfish vs a related surface form.

METABOLIC EFFICIENCY

There is considerable fragmentary evidence that aquatic troglobites have lower metabolic rates than troglomorphic or surface species of the same group, but in most cases the controls have not been adequate. I argued that amblyopsid fish, which are at the top of the food web, are most likely to be food limited. Indeed it is clear that there is a reduction of growth and metabolic rate in the evolutionary series of surface, troglomorphic, and troglobitic species (Poulson, 1963). This metabolic efficiency is not at the

expense of activity since routine metabolic rate goes down while total foraging activity and percentage of time that a fish is active go up. In contrast, Culver presented data on amphipods that showed no predictable relation between cave adaptation and activity or metabolic rate either between troglomorphic and troglobitic species of the genus *Stygonectes* or within a polytypic troglomorphic species, *Gammarus minus* (Culver and Poulson, 1971a). The fish and amphipod data are rationalized when it is realized that: 1. Amphipods are lower down in the food web than fish; and 2. The caves of the Valley-Ridge (where the amphipods were studied) have discrete organic debris in-washed at all seasons but the caves of the Interior Low Plateaus (where the fish occur) get only diffuse input of unidentifiable organic matter and only in the spring (see Jegla and Poulson, 1970). This is just another example of how caves are a less uniform habitat than the deep sea; the variations in food supply between caves may be equivalent to the variation in food with depth in the deep sea.

The matter of energy economy in deep sea animals rests largely on inference from morphology or distribution of animal biomass and potential food with depth, since food metabolic studies are lacking. Metabolic studies are ambiguous. The epibenthic species came up in poor condition and there are rarely inshore relatives to serve as a baseline for the infauna which came up in good condition protected in the mud. The necessary controls for such studies—related species, comparable size and activity, adjustment to the metabolic chamber—have been recently reviewed by Culver and Poulson (1971a). The data at hand do not meet all these conditions but are worth reviewing. Teale reported neither lower metabolic rates nor any effect of pressure for a few deep sea brittlestars, a sipunculid worm, an isopod, and a clam as compared to inshore species but emphasized the preliminary nature of his results. His techniques are such that routine or acute, and therefore near maximum, metabolic rates are measured. However, Turner

showed lower growth rates for the same species of boring clams in wood panels submerged at 2000 meters than in those submerged at 200 meters, thus suggesting a pressure effect on metabolism.

The morphology of bathypelagic animals is correlated with energy economy (Marshall, 1960), so it is worthwhile to consider such indirect evidence for energy economy among bathybenthic species. Childress (1969 and personal communication) shows that the metabolic rate of bathypelagic shrimp decreases in parallel with depth and that there is a parallel decrease in size, musculature, and gill area. This parallels the morphological deep sea "syndrome" so well described by Marshall for fish where the metabolically expensive swim bladder is vestigial and even the kidney may be reduced to a single renal tubule! Unfortunately neither the bathybenthic shrimp nor fish have been examined in this regard. But I infer, as does Marshall, from specimens and in situ photographs that this syndrome is not present in any bathybenthic fish. They have swim bladders and well developed scales and musculature, and their gills are normally developed. However they do tend to be small, and so the possibility of subtle differences in gill area and growth rate, such as that documented in similar sized cave fish, can not be discounted until metabolic studies can be done.

Rowe argued for the importance of food limitation since, with the exception of deep ocean trenches which act as nutrient traps and would be a good control for the effects of food vs pressure, there is a decrease in abundance and biomass with depth (Menzies and Rowe, 1969; Sanders and Hessler, 1969) which is paralleled by a decrease in potential food. The decrease in biomass below 2000 meters, on the order of 25-50 fold per 500 meters, parallels a decrease in downslope transport of discrete organic matter, such as turtle grass and sargasso weed, but dissolved and fine particulate organic matter that may "rain" down from above shows little variation and shows no clear relation to animal biomass. This brings up the real problem, for cave

as well as the deep sea, as to what is or is not food, for these detrital based food webs.

Cave-bathybenthic comparisons of food limitation must be made with caution because there are no good data on organic matter in or on the substrate and, even when available, it is not clear whether that measured by the usual combustion or oxidation methods reflects energy extractable by organisms. Is the low density and biomass of cavernicoles related to the observation that particulate matter washed into caves may remain for several years and that its nutritive value is therefore low? If so, how do we explain the apparent paradox that deep sea biomass is higher than for caves even though the particulate matter contains less organic matter? The answer may be in the availability to the animals. There is suggestive evidence, even for inshore areas of the sea, for bacterial specialists on cellulose, chitin, and other traditionally refractile organic compounds, for complex recycling of animal secretions, regurgitations, and egestions, and for direct uptake of dissolved organic molecules including amino acids, sugars, and vitamins (see references in Darnell, 1967). The morphology of inshore vs deep sea deposit-feeding bivalves suggests the extremes for recycling of fecal pellets. Inshore the tellinid bivalves have a short gut and the recycling may involve egestion of feces low in protein and high in carbohydrates, growth of bacteria, and repetitions of the cycle until the carbohydrate is gone. In the midwater species the efficiency of digestion presumably increases due to a longer and more coiled gut with fewer recyclings, and in the deep-sea it appears that bacteria have been added to the gut so that there is a symbiosis (Allen and Sanders, 1960).

HISTORY OF THE BIOTA

Many of the relevant ideas about cave biogeography have been either recently reviewed (Poulson and White, 1969) or are discussed elsewhere in this issue (Culver; Peck and Holsinger), so my review will focus on differences between caves and the

deep sea. The major theme of the discussion was the difference in possibility for geographic isolation and subsequent speciation—clearly high in caves, which are discontinuous in time and space, and seemingly low in the deep sea, which is uniform in bottom type and lacks obvious geographic barriers.

Peck and Holsinger showed that the origin of some aquatic troglobites via invasion of seacoast caves or sand and gravel is quantitatively less important than invasion from interior karst areas during glacial advances and retreats. Highland terrestrial species adapted to cool, moist forests or aquatic species adapted to cool streams spread into the lowland during glacial advance and either moved back into the uplands or became restricted to isolated pockets of cool microclimate, such as springs and cave entrances, as the glaciers started to retreat again. As the glaciers continued to retreat, the terrestrial habitats in the lowlands became dry-warm and the streams became warm. As a result, the only cool-adapted populations to persist in the lowlands were those that had access to caves where it remained cool all year. Those species that persisted in caves and evolved into specialized troglobites are said to have been preadapted to caves by their physiological tolerance to cold and their ability to sense food and mates in dark areas like forest litter or under rocks and ledges in streams; thus they were already facultative cave forms, *i. e.* "troglophiles". Generally few of these troglophilic ancestors persisted even in the highlands, and so the troglobitic cave derivatives are said to be relicts.

Like most cave species some of the deep-sea crustaceans are Pleistocene relicts, but others, like the protobranch mollusks that date from the Cambrian, are much more ancient relicts. However, unlike the cave species, it is not clear how the deep sea species became isolated. Perhaps southward spread of a boreal inshore fauna during glacial advance was followed by a down slope instead of northward movement along temperature isoclines as the glaciers retreated. A variant of this is suggested by

the disjunction in faunas at the continental slope thermocline which is amplified at the borders of marine basins such as Mediterranean-Atlantic. During the Pleistocene there may have been little difference between the two basins but, as they diverged postglacially toward the 37.5-39.0 ‰ vs 36.0-36.5 ‰ salinity and 13-14° vs 2.0-2.5°C temperature difference of today, some of the cold adapted Mediterranean deep-sea species could have invaded the Atlantic and so added to its diversity. And, as a third variant, species diversity of a basin could increase if multiple invasions of the same inshore ancestor gave rise to different species as Barr believes happened with some cave beetles and springtails (Christiansen and Culver, 1968 and 1969). In the deep sea, local diversity would be increased when those separate invading populations became adapted and spread enough to overlap in geographic range. This overlap subsequent to multiple invasion is easy to envision for caves but the more striking faunal overlap, on both sides of the Atlantic Ocean, along a depth contour rather than between depths at one spot (Sanders and Hessler, 1969) makes it difficult to explain the deep sea faunal overlap. Whether planktonic larvae of the epibenthic species disperse widely and survive or settle at only one depth is unknown. Whatever the case, the explanation of the narrow depth distribution requires a much narrower physiological tolerance to pressure than has been suggested by my work on ability of cave fish to metabolically compensate for temperature change or even by Teales' work on the effects of pressure on deep sea forms (see above).

Whatever the chances of multiple invasion, it is clear there has been plenty of time for diversity to slowly increase in the deep sea since, unlike caves, the temperatures and salinities have changed little over geologic time, even during the Pleistocene, and so new invasions probably far outnumber extinctions. Put another way, it may not be necessary to invoke *in situ* speciation in the deep sea to explain its high species richness. Sanders, however,

prefers to think that *in situ* microgeographic speciation has been important in the deep sea since there have been such massive adaptive radiations within single genera (Sanders, 1968). Also in his favor is a good correlation between species richness, narrowness of geographic distribution, and life history traits that promote the chances for microgeographic speciation. For example a given area has 5 species of brittlestars, 25 bivalve mollusks, and 85 crustaceans. The crustacean species have the narrowest depth range, suggesting the narrowest physiological tolerance, and the narrowest geographic range, suggesting the most limited larval dispersal. Both traits go along with the presence of few large eggs, brooding of eggs, and absence of planktonic larvae that would disperse over a wide range of depths and geographic areas. Thus the possibilities for microgeographic speciation, particularly in such sedentary infaunal crustaceans, cannot be discounted. The possibilities for such speciation seem large in view of the demonstrated species differences in highly mobile species like fish, between ocean basins and trenches in the bathybenthic rat-tails (*Macrouridae*) and between water masses that differ subtly in salinity, temperature, and nutrients in the mesopelagic lantern fish (*Melamphiidae*).

The influence of the Pleistocene on the deep sea is debated, but it is clear that it has had a major influence on speciation in caves. Despite possibilities for speciation resulting from multiple invasions of one ancestor during one glacial epoch (see Christiansen and Culver, 1969) most workers agree that the diversity in caves is mainly the result of multiple invasions by different troglophiles during three or four Pleistocene advances and withdrawals of the ice sheet. The several grades of morphological specialization in cave millipedes and amphipods and of physiological specialization in cave fish are most easily explained by waves of invasion and isolation that coincide with different glacial epochs. If this is correct, then the drastic runoff, flooding, scouring, and temperature changes suggested by some for periglacial karst areas

either was not so drastic or was not so widespread that species already present could not survive. Even the terrestrial and larger aquatic species, that could not gain access to the well-buffered non-cave groundwater available to the small isopods and amphipods, have survived at least one glacial epoch in caves.

SPECIES DIVERSITY

Culver started this last part of the program with an elementary review of diversity indices. He differentiated between indices which merely reflect species number, i. e. indices of species "richness", and those, like the information theoretic index, that reflect both species number and relative abundance. For example, species richness would not differ between a sample of 3 species with 10 individuals each and 3 with 15, 10, and 5, respectively. However, an information theory index would give the latter a lower diversity because the relative abundance of the three species is less even than in the former sample (see references in Poulson and Culver, 1969 or Culver and Poulson, 1971b for more detail). This distinction is critical with comparisons of within- and between-cave diversity because there are so few species, but in the deep sea each sample contains so many species and individuals that these refinements are not critical. Thus Sanders uses a species richness index and standardizes his measurements to 1000 individuals using a so-called rarefaction method. A typical abyssal plain sample rarified to 1000 individuals contains 5 species of brittlestars, 19-30 bivalve mollusks, 50-70 polychaete worms, and 70-125 crustaceans including 12 taniad shrimp, 23 cumacean shrimp, 30 amphipods, and 35 isopods.

Sanders explained that his stability/time hypothesis for diversity of marine benthic communities has been derived to fit field observations (Sanders 1968; Slobodkin and Sanders, 1969). In his view the low species richness of inshore communities is due to physical control by extreme fluctuations, for example in an estuary where salinity and current change on a daily basis and tem-

perature changes on a seasonal basis. He feels that competition and predation are more severe inshore than in the highly diverse and biologically controlled deep-sea communities where the environment is constant in time with extremely predictable and therefore presumably less intense interactions. I pointed out that the importance of competitive exclusion to an explanation of the high diversity in his samples can only be answered with more detailed sampling. Despite Sanders arguments to the contrary, a repeated species pattern from dredge samples at about the same depth and place but from different directions does not obviate the problem that his samples are too big and uncontrolled to detect small differences in substrate or species composition that may be important to the tiny, sedentary infauna. Sanders' group is now doing the necessary repeated core sampling at one location to answer this criticism. Such sampling will allow him to assess the role of species co-occurrence, and thus presumably interaction, and microhabitat patchiness by correlating shapes of species abundance curves in a series of cores with character of substrate, amount of "food", number of related species or potential predators, etc. If the cores show no differences in microhabitat patchiness, then it will become important to look for coevolutionary interactions, like those plant/pollinator and plant/herbivore interactions that have augmented diversity of plant/insect communities, and feeding specificities, like those shown by fish which specialize on scales, blood, fin rays, and rotting flesh of other fish in the tropics.

The diversity of cave communities is intermediate between the benthic communities of estuaries and the deep sea, but Culver and I (1969 and unpublished) do not believe that this allows us to simply say that control of diversity in caves is intermediate between that in estuaries and the deep sea, i. e. a mix of biotic and physical control. We pointed out that objective categorization of "physical" and "biotic" are necessary to formulate a hypothesis for the control of diversity and to

devise meaningful field and laboratory experiments to test the hypothesis. Culver then summarized a scheme that includes all factors that potentially affect diversity, starting when a new habitat is "opened" for colonization. Initially there is a stochastic non-interactive equilibrium that depends on intrinsic probabilities for colonization and extinction of each potential colonizer. After the numbers of individuals increases, there are three parallel kinds of control. Until we have data to the contrary, we consider that these operate simultaneously: 1. Biotic interaction such as competition, predation, and mutualism; 2. Energy flow as determined by rates of turnover, productivity, and life history and stabilization of energy flow as determined by connectedness of food webs; and 3. Physical control including the subparameters of "climate"—rigor (extremes), variability (variance), and predictability (autocorrelation)—and structural heterogeneity of the habitat. After this introduction, examples were given for terrestrial and aquatic cave communities.

Culver discussed his data (1970; 1971a, b) from 28 West Virginia stream caves where different species combinations are present. He illustrated the random nature of colonization and extinction of an isopod and three species of amphipod in a small cave and suggested that differences in species composition in larger caves where populations are more persistent could also be partially explained by a balance of colonization and extinction. Most of the remaining between-cave variance in community composition is associated with length of the cave stream and its susceptibility to spring flooding. He showed that field data on seasonal changes in amphipod density and laboratory studies on washout and injury in an artificial stream also confirm the importance of flooding to control of community composition. The length of cave is negatively associated with flooding but more important is its positive correlation with number of tributary streams and so with possible avoidance of competition through microhabitat selection. He related field data on microhabitat/amphipod distribution to habitat selection in the labo-

ratory. The small cave amphipod selects small gravels whether or not its larger relative is present thus indicating no present day effect of competition. But the large cave amphipod and the isopod only showed microhabitat selection when the large spring-cave amphipod is present thus indicating ongoing competition. This kind of competition which leads to competitive exclusion is due to active interference of one species with another's behavior. It is hard to envision in a uniform habitat like the deep sea especially with so many species present. In discussion I suggested the possibility that since there has been more evolutionary time available in the deep sea, many deep sea species show invariant microhabitat selection like the small cave amphipod studied by Culver. This suggestion is based on the observation that competitive exclusion cannot even be demonstrated in terrestrial cave communities of Mammoth Cave that are much more complex than the West Virginia stream communities but show nowhere the complexity of the deep sea communities.

As with Culver's study, our work on terrestrial communities in the 110 kilometer Flint Ridge Cave System (Poulson and Culver, 1969 and continuing) has shown a significant negative effect of climatic rigor (flooding and evaporation rate) and a positive effect of structural heterogeneity of the habitat (substrate diversity) on between-habitat species diversity.

Overall the terrestrial system is a better analogue of the deep sea than the aquatic cave system because the terrestrial animals were sampled in 50 sites within a single large cave where all 14 regular species can get to every sampling site, where the characteristics of a sampling site can be replicated to assess any random or seasonal effects, and where there is a triad of related beetle species which allows assessment of the role of competition in control of diversity.

Correlation of species diversity with substrate diversity in our original study and suggestions of fighting during laboratory interactions first led us to look for explana-

tions of species diversity in terms of differential substrate selection by the three beetle species. However, there was no competitive exclusion along the niche dimension defined by substrate since competition coefficients calculated using each species tested alone did not differ from the coefficients found with species tested in pairs or triads. In addition no species showed consistent preference for fine gravel, sand or mud. So what, if any, niche dimension is important in separating these beetles? It appears that differences in species biology are part of the answer. We now have data for three stream passages that do not differ much in substrate diversity or "food" (average weight loss after ignition) but do differ greatly in rigor, variability, and predictability of flooding, food input, and potential drying. The

results thus far are that species diversity, evenness, and repeatability are highest in the least rigorous, least variable, and most predictable passages. The differences in the other cave species found in these three passages lend weight to my current hypothesis that the combination of high mobility, high reproductive potential, and broad physiological tolerance—what I have called ecological opportunism—is characteristic of animals in communities with low species diversity. Thus much of my current emphasis is on beetle biology, particularly physiological tolerance. The other emphasis will be on perturbation studies in nature to test my hypothesis by modifying such things as food to see if, as predicted, the local species diversity drops due to colonization by opportunists, especially crickets.

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The Classification of Cavernicoles

By Elery Hamilton-Smith *

ABSTRACT

A seven-category system for the classification of cavernicoles is proposed, primarily on the basis of Australian experience.

Parasites are separated from the Schiner-Racovitza categories to form a separate category; it is suggested in line with some other workers that the term troglaxene should not be used for accidental species; threshold species not found within the dark zone are also separated, but the complexity of the threshold fauna is emphasized.

The dark zone fauna is thus separated into four categories: troglaxenes and troglobites as in the Schiner-Racovitza system, with troglaphiles divided into two levels, being those species also occurring in the epigeal environment (first level) and those confined to caves (second level).

The ecological classification of cavernicoles has been widely discussed, and this discussion has led to the coining of elaborate or even picturesque terminology, much of which proved to have been still-born. I hesitate to add to this discussion (and certainly refuse to coin new words) but feel it may be useful to outline my own attempts to gain some greater clarity in this matter. It may well be that my thinking reflects the particular characteristics of the Australian cave fauna or even my own idiosyncrasies, and I stress that this paper is intended as a contribution to discussion, rather than as a presentation of "the new system for classification of cavernicoles."

The generally accepted, but variously interpreted, system which is in use today is based upon the work of Schiner (1854) who divided the fauna of the Adelsberg Caves into troglobites, troglaphiles, and occasional cavernicoles. Racovitza (1907) proposed the term troglaxene to replace Schiner's "occasional cavernicoles", and

these three terms are the basis of present usage.

Alternative patterns of classification or of terminology have been proposed by a number of authors, including Hesse (1924), Thinemann (1926), Dudich (1932), Pavan and Tomaselli (1944-58), and Christiansen (1962). Of these, only Dudich's division of the troglaxenes into the two categories of regular and accidental has gained any acceptance, although even this proposal is open to considerable doubt (see Barr 1963) and will be discussed below. The most useful further contribution to this question was that of Jeannel (1926) who adopted the basic Schiner-Racovitza system, but also drew particular attention to the fauna of the twilight or threshold zone. Jeannel also developed a useful series of categories for the description of specific biotopes within the cave environment and hence for the detailed categorization of fauna within a particular cave. However, this latter classification complements the Schiner-Racovitza system and in no way replaces it.

An examination of the literature shows a variety of definitions being used for each

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of the Schiner-Racovitza categories and an even wider range of interpretations of these definitions. Accepting the idea of Vandel (1965) that each of these categories must inevitably be heterogeneous and the obvious fact that any system of categories must inevitably be limited according to the available data, it seems clear that further clarification and agreement is much to be desired. In striving towards some clarity for my own purposes, I have tried not only to apply general classificatory principles, but to arrive at a series of classes which express something of the relationship between the species and the cave ecosystem.

The term and concept of troglobite is perhaps the most clearly defined and understood, even though formal definitions in common use are often unclear. Thus, Hazleton & Glennie (1962) suggest "species living permanently in the dark zone, and not in the endogean or epigeal domain." However, their usage of the term corresponds with the generally accepted definition, such as that of Barr (1968), "obligatory species which are unable to survive except in caves or similar hypogean habitats."

Greater confusion surrounds the troglaphiles. This is, understandably, a much more heterogeneous category. Although generally clearly enough defined, e.g. Barr (1968), as "facultative species which commonly inhabit caves and complete their life cycles there, but also occur in sheltered, cool, moist epigeal microenvironments", it is well known that many troglaphiles are only recorded from the dark zone of caves. However, in the absence of regressive or adaptive modification, these are by convention treated as troglaphiles rather than troglobites. Barr (1963) cites the example of *Agonum (Rhadine) longicolle* (Benedict), recorded only from Carlsbad Caverns and nearby caves, but possessing large faceted eyes and darker pigmentation than troglabitic members of the genus. He points out that such species might reasonably be considered as potential troglobites, but suggests that they must be currently considered as troglaphiles.

The Australian cave fauna is particularly rich in species of this kind, and the significance of this fact would be disguised if all troglaphiles were treated as a single category. I have therefore adopted the practice of sub-dividing the troglaphiles into two sub-categories:

First-level Troglaphiles — those forms living out their total life-cycle within caves but also known from epigeal habitats.

Second-level Troglaphiles—those forms living out their total life-cycle within caves, known only from caves, but not exhibiting any modification to the cave environment.

The usefulness of this division, even noting the extent to which its application may be biased by lack of information, may be seen from a recent review of the Australian cave fauna (Hamilton-Smith, 1967) which lists 33 species as first-level and 30 species as second-level.

The second source of confusion arises from differing interpretations of the definition. Most authors appear to assume that the definition intends to convey that many individuals of the species will spend their total life within a cave, while other individuals will spend their total life outside of a cave. However, by contrast with this usage, Richards (1968) applies the term troglaphile to the New Zealand species *Pallidoplectron turneri* and *Gymnoplectron waitomensis* (Fam. Rhabdiphoridae), but at the same time describes both species as frequently leaving the cave for periods of two or three hours, feeding, and then returning to the cave. This behaviour pattern is very similar to, if not identical with, that of many troglaxenes and it would seem more appropriate if these species were considered troglaxenic or primarily so. Their relationship to the cave ecosystem is certainly that of a troglaxene, as their behaviour would result in a considerable energy input to the system. Thus, Barr (1968) refers to cave crickets as among the "most important troglaxenes" in terms of energy input to the ecosystem. The treatment of the Rhabphi-

dophoridae as troglaphiles by Richards (*op. cit.*) rests upon her distinctive and atypical interpretation of the category definition which appears to embrace forms usually considered as "habitual troglonexes." It therefore seems confusing and inappropriate.

Dudich (1932) divided the troglonexes into the two categories of "habitual" (Pseudotroglobionte) and "accidental" (Tycho-troglobionte). This pattern has been followed by a number of authors, notably Hazleton and Glennie (1962). Barr (1963) suggested that the term "troglonexe" should not be applied to accidental species. I concur strongly with his suggestion, and reserve the term for those species which frequent caves at specific times within their life cycle, but at other times enter the epigeal domain. Such species are a relatively major and consistent source of energy input to the ecosystem. On the other hand, accidental species are of much less significance in this respect and are certainly not consistent in their energy input.

Obligate parasites constitute a further minor problem. Hazleton & Glennie (1962), while recognizing that these relate to the cave ecosystem only through their host (at least in the case of bat parasites), treat them as troglonexes. I find it less confusing to treat these as a separate category, rather than trying to force them into the Schiner-Racovitza system.

The dwellers within the threshold zone present particular problems in many faunal lists, and, for instance, that of Hazleton and Glennie does not clearly distinguish threshold species from dark zone species. Studies of this fauna are relatively few, although some attention has been paid to individual species, e.g. Graham (1966-68). Vandel (1965) lists a number of European studies

and summarizes this field, but it is clear from his summary that although this is a complex ecological domain there is as yet no satisfactory overall conceptual framework for its study. In terms of considering overall cave fauna it again seems preferable not to force threshold dwellers into the Schiner-Racovitza categories, but to clearly separate them.

The above line of thought leads me to use seven categories which can even be arranged into the customary binary key as shown below.

1. Obligate parasites PARASITES
not obligate parasites 2
2. Does not regularly inhabit
caves ACCIDENTAL
Regularly inhabits caves..... 3
3. Does not live in
dark zone THRESHOLD
Lives in dark zone..... 4
4. Does not spend total life
in cave TROGLOXENE
Spends total life in cave..... 5
5. Also known from FIRST-LEVEL
epigeal habitats TROGLOPHILE
Only known from cave or
similar habitat 6
6. Not modified to SECOND-LEVEL
cave environment..... TROGLOPHILE
Modified to
cave environment..... TROGLOBITE

In summary, the significant points suggested are the division of troglaphiles into two sub-categories, support of Barr (and others) in separating accidental species from troglonexes, and removal of threshold species and parasites from inclusion in the Schiner-Racovitza categories. None are completely novel or original but it is hoped that their integration may prove useful. Comment and discussion will be welcomed.

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Résumé of the 1970 Short Course in Cave Biology

A Short Course in Cave Biology, probably the first of its kind held in the United States, was conducted in conjunction with the annual convention of the National Speleological Society at Pennsylvania State University on August 21, 1970. The Short Course, a day-long event composed of 10 lectures on cave organisms and their ecology, was sponsored by the Biology Section of the N.S.S. The course was attended by 50 persons, many of whom displayed a great deal of interest in the proceedings and expressed the desire for similar courses in the future. Because of the enthusiasm of the participants and the rapidly expanding interest in cave ecology, a sequel to the Penn. State session will follow at the 1971 annual convention at Virginia Polytechnic Institute. The 1971 session will consist of biological excursions into nearby Greenbrier Caverns, West Virginia. The purpose of these excursions will be to point out some of the various kinds of cave organisms in their natural environment.

A very brief summary of the talks given at the 1970 Short Course follow in their order of presentation:

1. *Introductory Remarks* by John R. Holsinger, Old Dominion University. A brief history of the development of biospeleology in the United States was given, followed by a definition of some of the technical terms currently used in the field. The importance of cave laboratories was also pointed out.

2. *Protozoans* by Stephen Gittleson, University of Kentucky. Some of the different types of protozoans recently discovered in North American cave waters were discussed and illustrated. Although troglobitic (i.e., obligatory cavernicolous) protozoans are unknown, a number of species that inhabit subterranean waters exhibit rather unusual trends, such as frequent encystment and extremely small size.

3. *Planarians* by Jerry Carpenter, University of Kentucky. Flatworms or planarians are widespread in cave waters of the eastern and central U. S. and are represented by a number of troglobitic species. Several species were discussed and illustrated, and techniques for collection, preservation, and study were stressed.

4. *Amphipods and Isopods* by John R. Holsinger, Old Dominion University. Amphipods and isopods, two major orders of higher crustaceans, are common in subterranean waters of much of the United States. The similarities and differences of these two groups of cavernicoles were emphasized and various aspects of their ecology were discussed.

5. *Crayfish* by Martha R. Cooper, University of Kentucky. Crayfish, another major group of crustaceans, are represented in cave waters of the eastern and central United States. The troglobitic forms are predominantly restricted to northern Florida, the Interior Low Plateau region, and the Ozark uplift. Most of the important cave species were illustrated and discussed.

6. *Caves as Islands and Archipelagoes* by David Culver, University of Chicago. The community structure of caves was compared quantitatively with those of islands and archipelagoes. Caves, at least when considered from the standpoint of aquatic communities, tend to be more like archipelagoes than islands.

7. *Ecology of Cave Entrances* by Richard Graham, Upsala College. Although cave entrances are quickly by-passed by most cave biologists in their haste to get into the dark recesses, this zone is both significant and interesting. Composition and interaction of species of the transitional zone between the epigeal and hypogeal environment were discussed.

8. *Bats* by Charles E. Mohr, Delaware Nature Education Center. Although bats

are only troglonexes, ecologically speaking, these animals make up a significant fauna of many caves, and studies on their unique behavior are being pursued by a number of researchers. A number of the species associated with North American caves were illustrated and attention was called to two important books recently published on bats.

9. *Composition of Terrestrial Ecosystems* by Thomas L. Poulson, University of Notre Dame. The composition and interaction of species in the terrestrial ecosystems of various caves were discussed and illustrated. Many of the examples used in this presentation were drawn from recent studies conducted in the Flint Ridge and Mammoth Cave systems of central Kentucky.

10. *Amphibians and Fishes* by John E. Cooper, University of Kentucky. Among the cold-blooded vertebrate animals, two groups—salamanders and fishes—are represented by troglobites. Although a number of salamanders are found in caves, only a few are exclusively troglobitic and all but one species are known from the United States. Both cave-associated amphibians and fishes were discussed and illustrated.

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Caves as Model Systems

REVIEW: "Observations on the ecology of caves" by Thomas C. Barr, Jr., *American Naturalist*, 101:475-492. 1967.

In this short paper Dr. Barr has attempted to link what we know about cave communities to the rapidly developing body of ecological theory. The importance of the paper can hardly be overestimated. It has been widely read by ecologists, and together with Poulson's work on amblyopsid fishes (Poulson, 1963; Poulson and White, 1969) it signals the emergence of biospeleology from a long period of taxonomy. The paper has four sections: a general introduction to the cave environment, biogeography of caves, various points of interest about the ecology of cave animals, and a model for speciation in caves.

The general introduction to the cave environment focuses on the contrast between caves of the Appalachian Valley and the Mississippian Plateaus. In this section Barr presents a unified, easily readable picture of the cave environment. However, it is diffi-

cult to know how much credence to give many of his generalizations, since references to the literature are few and far between. For example, he states that "decomposition of the debris (in caves) takes place slowly over the course of several months or years." This may or may not be true (no references are given), but at least cave populations of *Gammarus minus* (Amphipoda) can feed on leaves and/or their microflora after the leaves have been in the water only ten days (Culver, 1970b). However, many of the rather general statements in this section are probably backed up by observations recorded in Barr's legendary field notebooks. It is unfortunate that more data were not presented here to back up his contentions.

In the section on biogeography, Barr confirms two predictions of the geographic theory of speciation. Since cave beetles are limited to subterranean dispersal: (1) there are more species in the Appalachian Valley where the limestone outcrops are discontinuous, and (2) the geographic ranges of the

species are smaller in the Appalachian Valley. Barr misinterprets evidence presented in the investigation of *Pseudosinella hirsuta* (Collembola: Entomobryidae) by Christiansen and Culver (1968). While it is true that *P. hirsuta* represents several invasions by a surface ancestor, each invasion and subsequent dispersal occurred within a single area of continuous limestone. Therefore, *P. hirsuta* confirms Barr's contention that dispersal occurs via subterranean routes, but not the theory of geographic speciation. While subterranean dispersal within limestone outcrops seems to be the rule for terrestrial cave animals, this is not the case for many aquatic species. Holsinger (1969) found that some amphipod species are able to disperse via superficial subsurface water as well as through subsurface water in limestone outcrops.

I found the most interesting part of the paper to be that relating the biology of cave beetles to various ecological theories, particularly those that deal with aspects of diversity. Unfortunately, it is also the most confusing part. It is clear, however, that Barr's main thesis is that geologic features, e.g. continuity of limestone outcrops, are the dominant factors affecting diversity. The confusion arises when he tries to relate diversity of cave beetles to general theories of diversity. There are two bodies of ecological theory that might be applicable: theories about high diversity in the tropics, and stochastic theories of island biogeography. It is unclear which of these Barr considers more useful, and in fact he does not explicitly distinguish the two. Although he presents an analogy between tropical and temperate environments and Mississippian Plateau caves and Appalachian Valley caves, it seems to me that a better analogy than tropical and temperate environments is one with islands or groups of islands. Caves in one karst valley are highly connected, and therefore immigration rates are very high. For example, in the Greenbrier Valley of West Virginia, I have found (Culver, 1970a) that there was no area effect, i.e. an increase in species number with increased area, which is one of the most general characteristics

of islands. Thus we need to compare valleys of different sizes to make a fair test of the area effect. Second, there are two general kinds of equilibria of extinction and immigration (Janzen, 1968): an equilibrium concerning the number of individuals, and an equilibrium concerning the number of species. The relationship of these two equilibria to caves remains unelucidated.

Another source of confusion is Barr's implied contention that the causes of high diversity in the tropics will be the same as the causes of high diversity in Mississippian Plateau caves. There is no reason to believe that this is true.

Since the publication of Barr's paper, more sophisticated theories concerning interactions in complex communities have become available (Levins, 1968), and these make his discussion of the dynamics of higher species diversity out of date. This is just as well, since he seems to argue that more species *per se* make more niches available.

One of Barr's more interesting findings is that beetle abundance in some caves fits what ecologists call a broken-stick distribution (MacArthur, 1957). Such a distribution, however, does not indicate broad niche overlap, as Barr suggests, but rather that the niches of the species are contiguous and non-overlapping.

In the concluding section, Barr discusses the speciation process in troglobites. This theory is greatly expanded in his paper on evolution of troglobites (1968), but my major objection to the section as presented here is that it is too vague and general. The status of troglophile populations with respect to epigeal or surface populations is complex and poorly understood. (Christiansen and Culver, 1969; Holsinger and Culver, in press), yet Barr's discussion here and in his paper on troglobite evolution does not aid in the analysis of such transitional populations. What is needed is a quantitative, rigorous theory of the process of cave adaptation. Since Barr knows the literature of population genetics well, he is the obvious person to develop such a theory.

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REVIEW: "Cave Ecology and the Evolution of Troglobites" by Thomas C. Barr, Jr. *Evolutionary Biology*, Vol. 2:39-102, 1968.

This excellent work is required reading for every student of cave biology. It serves equally well as an introduction to cave animals for the student of evolution and a source for biospeleologists. The analysis of the nature and origin of the cave biomes is the best short summary available. The main body of the work is well-organized, and the topic headings lend themselves to easy reference. The section on the cave ecosystem is largely oriented around nearctic systems but presents a clear view of most of the information about such systems in 1968. One can quarrel with a few minor points (such as the statement that the energy contribution of chemosynthetic autotrophs is probably negligible); however, the

major picture developed is both clear and accurate.

The most important section of the article deals with the evolution of troglobites. An introduction and history of biospeleology is followed by a summary of the where and what of cave animals. After an outline of the nature of physical conditions in caves, there is a more extended treatment of food and food webs. This is followed by a brief discussion of the present evidence for circadian rhythms in cave animals and the effect of geology on troglobite distribution in the East Central U. S. An extended discussion of the question of "regressive" evolution is followed by an analysis of the problems of speciation and adaptation in caves in general. The interesting section on circadian rhythms points up the inconclusive nature of presently available data and sharply poses a number of critical ex-

periments.* The initial historical summary of the question of "regressive evolution" in cave animals clearly exposes much of the barren ground this idea has traversed. Reading the later discussion of speciation and adaptation points out the erroneous nature of the term "regressive" as applied to troglitic change. A far more apt term would be reconstructive evolution. The basic idea clearly presented by Barr that cavernicoles go through a period of isolation followed by a period of reconstruction of

* *Editor's note:* There have been two experimental studies on circadian rhythms published since Barr's paper was written. A study on cave crayfish [T. C. Jegla and T. L. Poulson, Evidence of Circadian Rhythms in a Cave Crayfish. *J. Exp. Zool.* 168:273-282 (1968)] shows that 3 of 7 individuals had statistically significant circadian rhythms of metabolic rate and/or activity and 5 of 7 showed some rhythmicity and other criteria expected of circadian clocks, e.g. resetting after change in a light-dark cycle. A parallel study on amblyopsid cave fish, of which some preliminary results have been published [T. L. Poulson and T. C. Jegla, Circadian Rhythms in Cave Animals. *Proc. IV Internatl. Congr. Speleol. in Yugoslavia*, 4-5:193-195 (1969)], shows that a trogliphilic and three troglitic species all show clear evidence of circadian metabolic rates but that activity rhythms are clear cut only in the trogliphile; they are lost in the troglitic isolated in caves for the longest evolutionary time and show an intermediate state, like that in the cave crayfish, in the troglitic most recently isolated in caves.

the genotype associated with the new direction of evolution furnished by the cave habitat is supported by a considerable body of evidence. The idea that this reconstructive phase can only occur after the extinction of epigeal ancestral forms is a more doubtful hypothesis. A number of recent works have shown that a high degree of population isolation can exist without any apparent physical barrier to interbreeding. It should then be possible for the reconstruction phase to occur locally even in the presence of the epigeal ancestor. The fact remains that the ancestral forms are no longer extant in areas where most troglitics occur. Whether this extinction is a necessary prerequisite of troglitization, or a by product of the stability of the cave environment, is a secondary matter.

While some students of cave biology may disagree with the emphasis on Mayr'sian speciation, or other points in this article, it is on the whole clear, concise, and useful.

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