

The Cave Environment

Limestone caves provide unique natural laboratories for studying biological and geological processes.

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During the past 10 years more scientific research has focused on the cave environment. This is because caves are simple natural laboratories. The cave climate is stable and easily defined. The cave communities are simple and can be studied *in toto*. This simplicity allows detailed analysis of processes that are difficult to study in more complex environments.

Here we discuss two classes of problems in detail. First, we consider the interrelation between cave formation and the origins of cave animals. Karst hydrologists study the movement of water through the drainage complex, and biogeographers describe the origin of cave organisms and their dispersal and distribution among the various surface and underground habitats. Second, we treat the cave as a specialized natural laboratory and give specific examples of problems in ecology, evolution, and mineralogy.

Historical Background

Scientific interest in caves began in 17th- and 18th-century Europe with the development of elaborate (but erroneous) theories of the hydrologic cycle in which cave systems were essential elements (1). The beginnings of a correct understanding of the geology of caves date from about 1850 in Europe and 1900 in North America. In Europe, emphasis was on karst hydrology, par-

ticularly on subterranean streams (2). Early biological studies emphasized faunal surveys and descriptions of the degenerate eyes of cavernicolous animals (cavernicoles) (3); only after 1900 were a few experimental studies made (4).

In the early 20th century Racovitza and Jeannel sparked the spectacular rise of modern biospeleology in Europe. This period was, in general, an interlude for cave science in the United States, during which the only additions to knowledge about North American caves and their life were made by Europeans on field trips in North America (5).

Biospeleology advanced slowly in the United States from 1930 to 1950, even though this was the time of a lively debate over the origin of caves. The central point was whether caves form above or below the local water table. Davis (6) proposed cave development deep below the water table, by random circulation of slowly percolating groundwater ("phreatic" origin). This view became textbook doctrine for many years. Other theories placed the zone of cave development at or above the local water table ("vadose" origin). This debate and Davis' reputation as an authority had two stifling effects on cave studies: (i) the implied random pattern of cave development discouraged search for specific hydrological mechanisms causative of cave system patterns, and (ii) the argument over the location of the water table tended to reduce the

research that was done to a sterile classification of some particular cave as having a vadose or phreatic origin.

Factors influencing reactivation of geological cave research and continued progress in biospeleology in the past decade include amassment of a large body of descriptive data collected mainly by nonprofessional explorers and surveyors within the National Speleological Society; growing acquaintance with the large body of European literature that had been largely ignored by American theoreticians of the 1930's; near-completion of a systematic description of many groups of cave organisms and their distribution (7), which permitted biologists to turn to ecological and physiological problems; and, finally, involvement of younger researchers whose interest arose from exploration and field experience. Today, research in the cave-related sciences is being pursued in a number of universities and by three specialized organizations: the Cave Research Foundation, the Institute of Speleology at the University of Kentucky, and the Cave Research Associates.

The Cave Environment

The cave environment is usually thought of as being separated into a twilight zone near the entrance, a middle zone of complete darkness and variable temperature, and a zone of complete darkness and constant temperature in the deep interior. The twilight zone has the largest and most diverse fauna; the middle zone has several very common species which may commute to the surface. We are concerned with the deep interior, where the unique aspects of the cave environment and its obligate (troglobitic) fauna appear (8).

Green plants cannot live in permanent darkness. Thus, deep within caves, the troglobite must find other forms of food, and food is scarce. Leaves, twigs, and soil fall into, or are

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washed into, caves and, in general, constitute the food base of the troglobite. Near cave entrances there are troglomenes such as pack rats and hibernating bats and insects, but these contribute little to the food base of species that dwell in the deep interior. In the main, troglobites live in caves of the temperate regions. In tropical caves and in a few caves in southern temperate regions, perennial colonies of bats or birds (swiftlets or the oilbird) are important sources of food for the abundant facultative species (troglophiles); there are few troglobitic species in these caves.

The overall climate of the cave interior is much less variable than surface environments. The temperature is approximately the mean annual temperature of the region. Thus, caves at high altitude or in high latitudes may contain perennial ice, and tropical caves are noted for their high temperatures. The cave atmosphere is humid, regardless of altitude or latitude. Relative humidities may be as low as 80 percent, but more commonly they vary between 95 and 100 percent. Evaporation rates are usually low, but the cave air is not necessarily still. Air currents and even strong winds occur at great distances from entrances, activated by chimney effects and by changes in barometric pressure. A resonance phenomenon known as "cave breathing" occurs, in which air currents throb back and forth through constricted passages, with periods of a few seconds to a few minutes. A tabulation of macroclimatological variables for caves in temperate regions ("temperate caves") is given in Table 1.

The terrestrial cave environment has been less well studied than the aquatic cave environment. Much of the terrestrial fauna inhabits the cave floor, probably because inwashed food, soil, and chemosynthetic bacteria are there. Mineralogical processes are mainly those of deposition by aqueous transport, but the aqueous phase is limited to thin films of moisture or water droplets. Floor materials include clastic sediments such as sand, silt, and clay (originating both as weathering detritus from the limestone and by transport from distant sources by subterranean streams). Fallen rock slabs from the cave ceiling are also a frequently occurring substrate.

The aquatic environments include running streams, and pools fed by dripping water. The pools are characterized by high pH, high concentration of dissolved carbonates, low content of organic matter suitable for food, and a

sparse fauna. The running streams, with connections to outside food sources, have a lower pH, are often undersaturated with respect to carbonates, and have a richer fauna. Some typical values for the biotic and chemical parameters for temperate caves at low altitudes are also given in Table 1.

Hydrological Regimes in

Karst Regions

Caves are truncated fragments of the larger conduits of the karst drainage net and must be interpreted according to their hydrologic role. Some caves are now active as drainage conduits; others have been abandoned as base levels receded and are useful for the record they retain of past flow conditions and connections.

Karst drainage nets have three principal types of tributary systems connecting to water inputs. Smaller tributaries are typically of high pH and low organic content. They derive their diffuse flow from the bottoms of sinkholes and from cracks and crevices in the limestone surface. They are not directly observable, so details of their pattern are not known. Larger tributaries are characterized by moderately high pH and food content. One kind of large tributary is the vertically flowing tributary seen in many karst regions of the Appalachian plateaus and Interior Lowlands, where flat-bedded rocks are overlain with shales and sandstones which cap the ridges. In these circumstances it is common to find groundwater bodies (aquifers) perched in the overlying rocks. When the bases of these perched aquifers are sealed with shale aquicludes, as they are in much of Kentucky, Tennessee, and West Virginia, the water of low pH drains from them, emerging in small surface springs and in seeps on hillsides or along the edges of plateaus. Much of this water seeps underground again after it has flowed over the aquiclude and moves rapidly through the aquifer, forming large cylindrical vertical shafts (9). Shaft drains, usually of small dimensions, carry the shaft water to nearby trunks as tributaries. The third major tributary type is the sinking stream. Surface streams which rise on non-carbonate rocks bordering the carbonate aquifer often sink when they reach the limestone contact, forming a sharply focused recharge point. Such swallow points form an upstream interface between the surface and underground

drainage nets. Dry stream beds formed on carbonate rocks accumulate debris which can be an important source of food for cave organisms when the dry streams flood during spring rains.

The chemical process by which the aquifer is modified into networks of conduits and caves is the solution of limestone by CO₂-charged groundwater. The resulting pattern may be highly complicated in terms of details of lithology and geologic structure. If the dissolving solutions were percolating through all available joints and bedding planes, one would intuitively expect the flow system to have a "swiss-cheese" pattern. Such patterns are rarely observed. Most karst waters are not in thermodynamic equilibrium with the carbonate wall rock. Dripping waters are often supersaturated; flowing streams are often undersaturated, especially during spring flooding. The time constants for water movement in these large flow nets, relative to the *kinetics* of the chemical reactions, are such that waters can flow the length of the aquifer before becoming saturated. This in itself provides a mechanism for the development of cave passage far from water inputs. Thus, many drainage nets consist of long major horizontal conduits of uniform cross section which pass beneath clastic-rock-capped ridges with no change in morphology.

A second mechanism which allows solution of rock near the water table is the mixing of the vertically and laterally moving waters (10). Vertically moving waters often trend toward equilibration with the high carbon dioxide partial pressures of the surface soil, while laterally moving waters approach the much lower saturation carbon dioxide pressure of the atmosphere. When two such waters mix, because of the nonlinear relation between carbonate concentration and carbon dioxide pressure, the mixed water is again undersaturated and can dissolve more carbonate.

Examination of the solutional sculpturing on cave walls and geometrical considerations of spring discharges as a function of the feeder-trunk cross section place the flow velocities in many passages in the range of 0.03 to 0.3 meter per second. These velocities are high compared with the velocities (in meters per year) usually cited for movement of groundwater in other aquifers. Calculations of Reynolds numbers for channels place most of these flows well into the turbulent regime.

It is not to be inferred from the fore-

Table 1. Typical environmental parameters for caves. The data were compiled from various sources and are intended to be typical rather than representative of any one cave. [Data from Poulson except as indicated in footnotes]

Environment	Chemical parameters*						Physical parameters		Biotic parameters			
	P_{O_2} (torr)	P_{CO_2} (torr)	pH	$M_{Ca^{++}}$ (parts per million)	$M_{Mg^{++}}$ (parts per million)	$M_{HCO_3^-}$ (parts per million)	Temperature (°C)	Relative humidity (%)	Number of species	Diversity	Biomass (gram/hectare)	Substrate organic (% wt. loss on ignition)
<i>Terrestrial</i>												
Entrance	160	0.25					—10–30	10–60	100–300	1.5	1,000,000	5–20
Twilight zone							0–20	10–80	50	0.5	300	2–10
Variable T zone							3–13	30–90	10	.2	100–5,000	1–5
Under cap rock							10–13	80–95	0–3	.4	20	0.1–1.0
Passage with drip		2.5	7.5–8.0†	27†	27†	164†	12–13	90–100	3–7	.9	30	.2–1.0
Stream bank							7–15	95–100	5–11	1.1	20	.5–5
<i>Aquatic</i>												
Sinking stream	180		6.8‡	3.6‡	1.2‡		11.5‡		100	2.0	2,500	5–15
Cave stream, diffuse input	140		7.3	50.3	5		10		0–3	0.5	100	.5–1
Cave stream, concentrated input	180		7.2	60	9		10.5		2–7	1.0	325	1–2
Cave stream, underground course of surface stream	160		7.5	37	3		11.8		8–20	0.4	50	2–6
Vertical flow			7.76§	42.5§	3.8§	110§	12§		0–3	.2	5	0.5–1.5
Drip pools	100		7.86	64.4	16.8	447	15.8		0–2	.2	1	.1–0.5

* M = concentration. † Drip-water data from Murray (40). ‡ Stream data from Brush Valley, Pennsylvania [W. B. White and J. A. Stellmack, *Proc. Intern. Congr. Speleol.*, 4th (1968), vol. 3, p. 261]. § Vertical-shaft data from M. W. Reams [thesis, Washington University (1968)]. || Pool data from Holland *et al.* (38).

going discussion that all limestone aquifers can be treated as integrated-flow net systems. Some are highly interconnected joint and fissure systems without well-defined flow paths, and indeed differ only slightly from noncarbonate aquifers. The dolomite aquifers of northern Ohio and Illinois are of this type. Other such aquifers are in artesian situations where flows, although through open solution cavities, are at great depth and under hydrostatic head. Even among those aquifers to which the model best applies, the degree of interconnectivity between underground drainage basins may be high (11).

Origin and Dispersal of Cave Animals

The number of species in the caves of a region is the result of a balance between colonization and extinction (12). In the early stages of karst development, underground solution is the predominant geological process. Connections to the surface are rare, and so there is little cave colonization. Passages are small and poorly integrated, so there is little movement between caves. The very low food input also makes colonization difficult, but the constant physical conditions are conducive to survival. Trogllobites are most common in the intermediate stages, when diffuse connections to the surface allow colonization and when integration of passage allows move-

ment between caves, but they become less common in the latest stages. As caves are dissected by erosion and filled by deposition, there may be many sinking streams and numerous collapse entrances which increase the chances for colonization but limit movement between caves. A high food input also increases the chances for colonization, but the more variable physical conditions are less conducive to survival (see 13).

In the case of trogllobites we must also consider the chances for genetic isolation, because there must be both cave colonization by a troglophile and extinction of the intervening surface populations before a troglophile becomes trogllobitic. On the worldwide basis the predominant restriction of trogllobites to temperate areas of Europe, North America, Japan, and New Zealand is undoubtedly related to high rates of isolation of troglophiles by climatic changes associated with glaciation. In the stable climates of the lowland tropics there is little chance for isolation, and high rates of erosion may result in ephemeral caves and in high rates of extinction of trogllobites (14).

The ability of trogllobites to move between caves depends mainly on their size. Small species attain wide geographic distribution because they can move through stream gravels and soil outside of caves as well as through interstitial routes represented by minor joint and bedding planes in the lime-

stone. Small terrestrial groups, such as mites and springtails, use such routes, but the most spectacular examples are among the small aquatic species. The efficacy of interstitial distribution for two species of amphipod, *Stygobromus mackini* and *Crangonyx antennatus*, is attested by their large populations in drip pools of upper-level passages that never flood and by the fact that they occur in 75 to 90 percent of suitable caves within their geographic ranges (15).

The large trogllobites do not disperse through interstitial routes outside of caves, so distributions of such species tells us about the extent of underground connections between caves. If there is no morphological differentiation of a series of populations of a species, then the caves the species are found in must be connected. In many cases man can explore, or use stream-tracing dyes to directly demonstrate connections, but in other cases this is not possible. Terrestrial trogllobites move through upper-level passages which are unexplored or inaccessible and not subject to dye tracing. Similarly, there are unexplorable aquatic connections which cannot be inferred by means of dye tracing because they flow only during floods. For example, underground streams have been explored in West Virginia which flow in open passages transverse to, and beneath, major ridges under 330 meters of overburden. However, the flood drainage may follow completely different and inaccessible routes to

surface outlets far removed from the low flow outlets (11) and so allow troglobites to disperse to another basin far beyond the boundaries of both topographic and underground divides. If there is morphological differentiation of a series of cave populations, then the relative magnitude of differentiation gives an index of how long the caves have been separated, and its pattern suggests the positions of former connections. For example, honeycombs of solution channels as far as 60 meters below some river bottoms (16) are problems for engineers building dams and are proven dispersal paths for aquatic troglobites, but rivers are barriers to the dispersal of terrestrial troglobites. As such rivers become larger, older, and more sedimented they become barriers to aquatic species as well. Morphological differentiation of the cave fish *Amblyopsis spelaea* (see cover and Fig. 1), but not of the crayfish *Orconectes inermis*, on either side of the Ohio River suggests that there is a recent barrier, probably dating from the last Pleistocene glacial outwash that filled the river bed and solution channels with sediment.

Biogeography of Troglobites

The composition of an entire troglobitic fauna depends both on interconnectivity of caves and on the balance between colonization and extinction. Here we compare the Appalachian and Interior Low Plateau cave region of southern Indiana to the cave region of northern Alabama to illustrate how these factors influence speciation and rate of adaptation to life in caves. These two regions are similar with respect to (i) the geological time available for colonization and (ii) the groups of troglaphiles available as colonizers.

Limestone outcrops in the Appalachian Valley-Ridge are typically long and narrow, paralleling the characteristic Appalachian folding. The caves typically consist of a single conduit parallel to the ridges; large lateral extents are relatively rare. The limestones do not have a protective cap rock, so the caves are subject to relatively easy attack by the process of truncation and collapse. The limestones of the Interior Plateaus, in contrast, are nearly flat-lying and often occur under sandstone and shale-capped, mesa-like ridges. These caves are related to much larger drainage basins than the caves in the

Appalachians and have a larger lateral extent and a higher interconnectivity. The capping beds protect the caves from decay, so they exist for a long time. In general, it may be said that the integrated drainage basins of the Interior Plateaus are larger, perhaps by a factor of 10, than the drainage basins of the Appalachian valleys.

Barr has analyzed the biogeography of trechine beetles, a group of animals which show extreme contrast in characteristics, depending on geography, those from the Appalachian Valley-Ridge area differing markedly from those from the Interior Low Plateaus of Indiana, Kentucky, and Tennessee. Like certain other groups (17) the Valley-Ridge beetle fauna is characterized by (i) high density of species; (ii) rare co-occurrence of related species (sympatry); (iii) limited distribution, including only some of the potentially habitable caves, frequently only one cave; (iv) extreme rarity in any one cave; (v) small modal size of individuals; (vi) only one or two genera in each group; and (vii) few groups of troglobites in any one cave. In contrast, the troglobitic fauna of the Interior Low Plateaus, such as Mitchell Plain of Indiana and the Pennyroyal and Cumberland plateaus of Kentucky and Tennessee, is characterized by (i) low density of species; (ii) frequent sympatry; (iii) wide distribution, including many of the potentially habitable caves; (iv) moderate-to-large populations in a cave; (v) moderate-to-large modal size of individuals; (vi) commonly three or four genera in each group; and (vii) many groups of troglobites in any one cave.

The most critical factors determining the faunal differences seem to be density, size, and connectivity of caves. To paraphrase Barr (17), the number of trechine species per unit area of limestone terrain is high in the Valley-Ridge area because the limestone is highly discontinuous and there is more speciation when different segments of a once-continuous population are isolated in caves by extinction of the intervening surface populations. The low number of trechine species of the Interior Low Plateaus of Indiana, Kentucky, and Tennessee is attributed to a high potential for subterranean dispersal. We agree with Barr but extend his argument to explain the other biological differences between the two regions.

We suggest that the small size of individuals, the low populations, and

the low number of genera in the Valley-Ridge caves reflect both high chances for extinction and slow rates of evolution. With few caves there can be few colonizations, and each colonizing population will be small, so chances for extinction are high. Also, the rate of adaptation will be slow, since the total variation of the ancestral population on which natural selection can act is minute; in other words, there is a genetic bottleneck (18). This problem is accentuated by the low potential for mixing of different genes between caves of the Valley-Ridge. However, in the Interior Low Plateaus more caves are available, the caves (and thus the colonizing populations) are large, and a high potential for intercave dispersal results in a greater gene pool and faster rates of adaptation. We believe that this explains the greater proportion of "successful" or well-adapted species in the caves of the Interior Low Plateau. Barr has indeed recognized this success by designating the large trechine beetle species, with their wide distributions, large populations, and wide ecological tolerance, members of separate genera.

Caves as Ecological Laboratories

Rules that govern community structure and evolution can be discerned in studying cave communities. Here the community boundaries are discrete, and most of the species can be studied and manipulated in the field and in the laboratory. In this section we consider the control of species diversity and two related phenomena, competition and rarity.

Examination of the basis for local differences in species diversity is of interest because ecologists have speculated about the basis for latitudinal differences—for example, between the arctic and the tropics—without understanding local differences that involve a common group of species. Poulson and Culver, in their studies of species diversity in terrestrial communities of the Mammoth Cave area in Kentucky (19), show that there are definite local differences in the 110 kilometers of the Flint Ridge cave system even though the potential species pool is the same for each local area. They categorize explanations for the control of diversity as primary, secondary, and tertiary. The time available for dispersal between, and adaptation to, habitats is considered a primary factor, as are differences in climatic

rigor, variability, and predictability. The factors of spatial heterogeneity and availability of food are considered secondary, whereas competition, niche overlap, and predation are tertiary. The Flint Ridge system has been in existence since the late Pliocene, so the time factors are constant. Other explanations are based on significant negative correlations of diversity with microclimatic rigor and variability and on positive correlations with spatial heterogeneity and availability of food. The results on microclimatic rigor and spatial heterogeneity are in accord with the results of previous studies of latitudinal diversity, but food supply is usually negatively correlated with diversity. The explanation may be that the persistence of larger cave species tends to be governed by the availability of food.

The design of Poulson and Culver's study does not allow tests of niche relationship, though such tests are quite practical with simple cave communities. So far, conclusions about niche relationships in troglobites have been mainly inferences based on change in morphology or habitat of related species in parts of their geographic ranges where they occur in the same cave. However, Culver (20) is making a direct analysis of niche relationships of stream communities in 20 caves where the potential species pool includes three amphipods, one isopod, one salamander, and one crayfish. Within a single habitat the only pairs of amphipod species found are *Gammarus minus*/*Stygonectes spinatus* or *S. emarginatus*/*S. spinatus*, presumably because each pair involves a large and small species which avoid contact through predominant restriction of habitat to superficial rocks in the case of the larger species and to deeper gravels in the case of the smaller. In simple laboratory experiments in finger bowls, individuals of each species choose rocks over mud, possibly as an adaptation to avoid current and predation by crayfish and salamanders. Similar experiments with pairs of individuals substantiate some conclusions based on field data. With pairs whose members are of different species and use of a large rock, *G. minus* excludes *S. emarginatus*, which in turn excludes *S. spinatus*, but this dominance order is reversed when a small rock is used. In tests with pairs whose members are of the same species, only *S. spinatus* exclude one another. However, this microspacing does not explain the rarity of *S. spinatus*, since, in nature, this species is clumped in samples 0.3 meter square. In nature

there is a constant order of abundance, with *Gammarus minus* very common, *Stygonectes spinatus* rare, and *S. emarginatus* very rare. *Stygonectes* is a weak swimmer, so part of its rarity is due to high mortality at the time of spring floods. The washout rate in an artificial stream is what one would predict from the swimming ability and relative abundance in nature: the washout rate for *G. minus* is less than that for *S. emarginatus* and *S. spinatus*, the latter two rates being about equal.

Rarity in a cave can be accidental or real. A species can be said to be accidental in caves if its presence in different seasons or years fits a Poisson or a negative binomial distribution. Some aquatic interstitial and terrestrial twilight-zone species may fit into this category (13).

There are two explanations for the rarity of a species that is a regular member of a cave community. Rarity of a troglophile or a recently isolated troglomite may result from marginal adap-

tation to caves. This rarity is accentuated by competition when one species is less well adapted than another. The troglophilic crayfish *Cambarus bartoni* is much rarer in the deep cave when the troglotitic *Orconectes inermis* is present. Similarly, the troglophilic fish *Chologaster agassizi* is restricted to entrance areas when *Typhlichthys* occupies areas remote from entrances, where less food is available. Such competition may restrict multiple invasions by a second or third species into caves—for example, in areas of successive glacial advances and retreats—if the first species isolated has been isolated for a very long time. Thus *Typhlichthys* has been able to invade cave areas occupied by *Amblyopsis* only in central Kentucky in the very large Flint Ridge and Mammoth Cave systems, where the habitat is sufficiently diverse to allow segregation by habitat (21).

The rarity of recently isolated troglomites differs from the rarity of relicts. Recent invaders occur in many caves, show extensive variation where there are barriers to dispersal from cave to cave, and are only slightly modified; examples from the Valley-Ridge province of the Appalachians are discussed above. Relicts are often found in only one cave and have no closely related living relatives. They are highly modified and were isolated in caves as long ago as 100 million years, when their surface relatives became extinct. These two kinds of rarity must be considered in the context of adaptation to life in caves.

Caves as Evolutionary Laboratories

We hypothesize that, when an organism invades the stable cave environment, selection no longer acts to maintain its ability to adjust ecologically and physiologically to variable conditions. The loss of adjustment on these levels may be associated with a decrease in genetic variability. There are also changes toward the lowering of population size, reproductive rate, and metabolic rate and toward the lengthening of life and development. These are strategies which do not lead to success in variable or unpredictable environments, where being an opportunist is important for survival. Consistent supporting evidence for our hypothesis is available for many groups of troglomites (22), but only two groups are well enough known to test the hypothesis (23). We will discuss the amblyopsid fish, because one of us has studied them

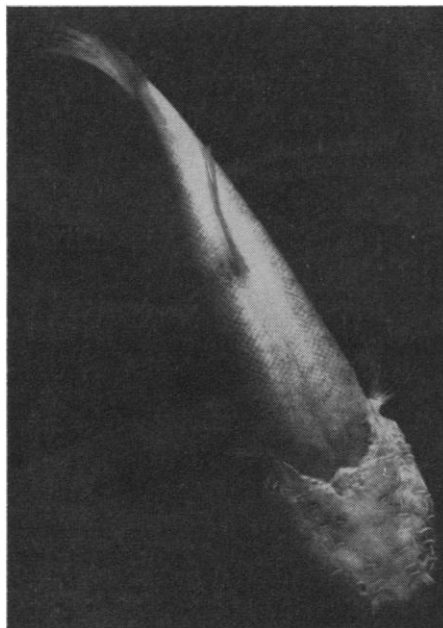


Fig. 1. Dorsal view of *Amblyopsis spelaea*. The paired structures at the front of its head are olfactory organs; the degenerate eyes are embedded in tissue next to the brain with its degenerate visual centers. The lateral-line sense organs, the neuromasts, are free on the fish's surface and are grouped in visible rows, called "stitches," each with 10 to 30 neuromasts. A neuromast has many sensory cells with cilia embedded in a gelatinous rod, the cupula, which is free to move in response to local changes in water movement. The pattern of water movement produced by a moving prey or produced as the fish approaches an obstacle is sensed by the numerous neuromasts and analyzed by the hypertrophied lateral-line centers of the central nervous system.

in detail and because the whole range of cave adaptation is represented in a single small family (24, 25). Amblyopsids are large enough to be suitable subjects for physiological studies, and we know how long each troglobitic species has been isolated. The family includes one surface species, *Chologaster cornuta*, and one troglophile, *C. agassizi*. From the relative degeneration of eyes and pigment cells in different species, it appears that the four troglobitic species have been isolated for different lengths of time (26). Listed in the order of length of isolation, these species are *Typhlichthys subterraneus*, *Amblyopsis spelaea*, *A. rosae*, and a relict species described by Cooper and Kuehne from a cave in northwestern Alabama. In the discussion that follows we compare the troglophile to the older

troglobites and then consider the oldest troglobite, the relict.

A number of traits of the Amblyopsidae have degenerated as a result of (i) reduced selection for maintenance in permanent darkness, (ii) lack of predators, or (iii) constant temperature and oxygen pressure in caves. We have already considered eye and pigment cell morphology. The older troglobites no longer show escape responses when they are disturbed, and they seem to have lost some resistance to pathogens. There is reduced regulation of metabolic rate when the oxygen pressure is sharply lowered. An older troglobite, *Amblyopsis rosae*, shows a fourfold increase in metabolic rate when the temperature rises from 10° to 15°C, in contrast to the more usual one- to twofold increase, with full acclimation, in the youngest

troglobite, *Typhlichthys*. The older troglobites retain circadian oxygen consumption but have lost circadian activity, and their rhythms cannot be set by (entrained to) light-dark cycles. We view this as evidence that a circadian clock mechanism is basic to biological organization but that the coupling of the clock to the environment through entrainment of activity cycles, as seen in the spring-dwelling *Chologaster agassizi*, is not maintained by selection in a cave environment which lacks daily cycles (27). These kinds of degeneration and decreased genetic variability are associated with adaptation to an unvarying environment. A decrease in genetic variability is suggested by decreased phenotypic variance in eye size and in morphological traits, such as the lateral-line sensory systems, that are selected in caves (see 24, 25, and Fig. 2).

Among the traits that are selected in caves, we have recently studied endogenous annual (that is, circannian) rhythms of reproduction. Caves are without seasonal cues, so a circannian clock is adaptive in allowing females to be prepared to lay eggs when the chances for reproductive success are at a maximum. There is some evidence for circannian reproductive rhythms in amblyopsids, but crayfish are more suited to experimental analysis since the reproductive state of individuals can be followed by external observation in the field or laboratory. Field data collected over a 3-year period suggested a circannian cycle. We have now confirmed the occurrence of such a cycle by following 36 crayfish for as long as 3 years under constant laboratory conditions. Individuals became slightly out of phase with each other, due to differences in the period of their free-running rhythms, but in nature their rhythms are reset and synchronized each year. The cue that resets the rhythm is probably the same one that triggers egg-laying—possibly the subtle drop in temperature that is associated with spring rains, when food input to the cave is at a maximum (28).

Efficiency in utilizing and finding scarce food is the basis of many adaptations of troglobites. Less food is required when growth and metabolic rates are lowered (29), and there is evidence suggesting that utilization efficiency is also increased in troglobitic amblyopsids. For example, despite a metabolic rate only half that of *Chologaster*, *Amblyopsis* is no less ac-

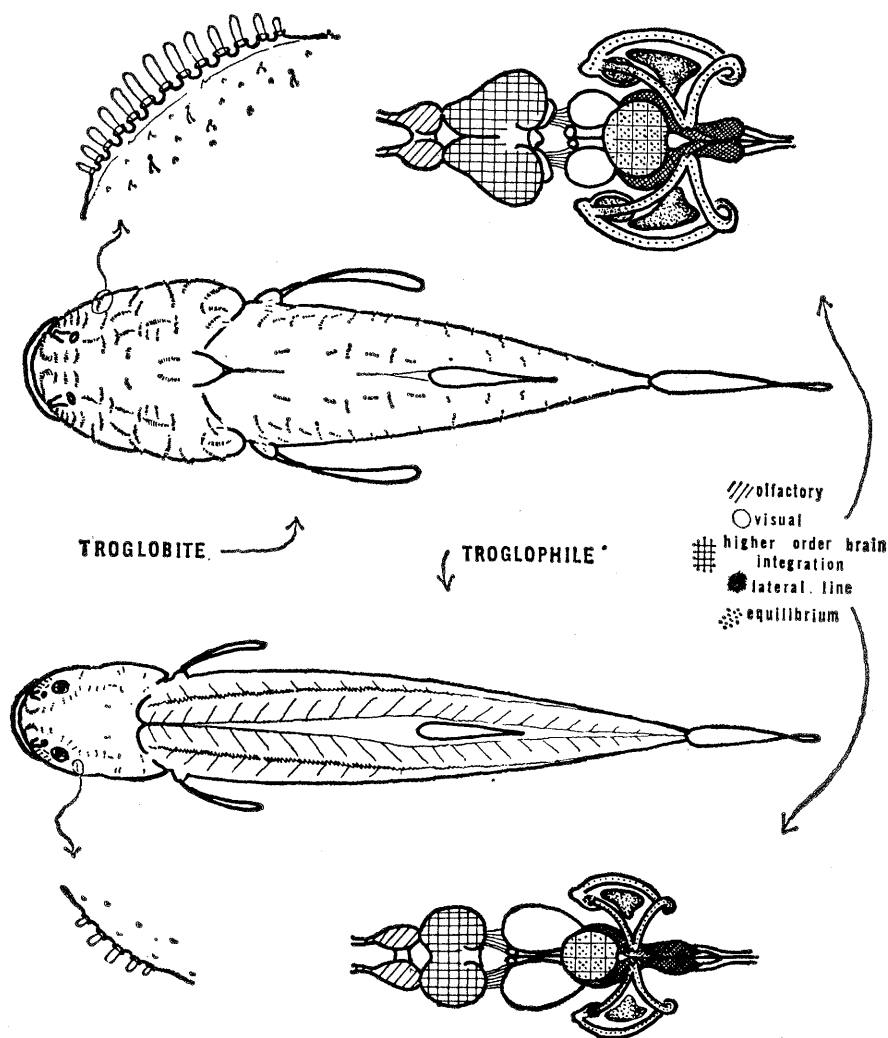


Fig. 2. Diagrams contrasting *Amblyopsis spelaea* with its troglophilic relative *Chologaster agassizi*. Each of *Chologaster*'s "stitches" has fewer neuromasts, and only the cupula projects into the water. Note also that the tactile receptors are fewer in kind and density in *Chologaster* than in *Amblyopsis*. The troglobite's large head displaces more water and so makes detection of obstacles more efficient. This large head is no disadvantage for the slow-swimming *Amblyopsis*; in fact, *Amblyopsis*'s longer fins allow it to move twice the distance that *Chologaster* moves for each coordinated pectoral-caudal fin stroke. (See also the legend to Fig. 1.)

tive than *Chologaster*. Differences in food-finding efficiency are also important. As discussed above, this explains why there is an exclusion of troglaphiles to areas near cave entrances and of troglobites to deep cave zones. We are analyzing this in the laboratory. To simulate the density of prey near cave entrances, we introduced ten water fleas into a fish's 5-liter aquarium. *Chologaster agassizi* found the first prey sooner than *Amblyopsis* did and had eaten all ten before *Amblyopsis* had eaten the fourth one. However, in 100-liter aquaria with only one water flea for each species, *Amblyopsis* found the prey hours before *Chologaster* did. This situation is analogous to the deep cave, where finding food, which is scarce and widely dispersed, requires efficient searching. *Amblyopsis* swims very slowly but, in contrast to *Chologaster*, is active 24 hours a day. Furthermore, it swims a greater distance before turning and so samples a wider area in its search. Finally, its more developed lateral line allows it to locate prey farther from its body and to achieve greater success in capturing the prey after locating it. In summary, *Amblyopsis* covers ten times as much territory and searches 30 times as much water as its troglaphilic relative does.

Evolution of metabolic economy in troglobites is associated with lowered rates of population growth. Increased metabolic efficiency in amblyopsid troglobites has led to more frequent reproduction by a higher proportion of females, but population size and potential rate of increase are still markedly lower for these troglobites than for their surface or troglaphilic relatives. For example, *Amblyopsis* lays larger and fewer eggs than *Chologaster*. This results in a longer period of development, but the fry are larger when they leave the mother's gill cavity and so can better avoid cannibalism and can feed on larger prey. Thus, more of the young survive. Despite the large eggs, the caloric cost of reproduction is less for *Amblyopsis* than for *Chologaster* because *Amblyopsis* lays fewer eggs and is metabolically more efficient in producing them (see 24 and Fig. 3). A number of other life-history phenomena are associated with the small populations characteristic of most troglobites. Long life and low rates of development, growth, and maturation also result in an age structure dominated by the older age classes and thus also contribute to a low rate of popu-

lation growth. The relict species of amblyopsid shows still lower rates of growth, longer life, probably lower metabolic rate, and definitely better development of its lateral-line system. This suggests that the rarity of other specialized relict troglobites also results from long periods of adaptation in a stable environment with low food supply (30).

In concluding this section we suggest that evolution in caves is similar in many of its aspects to evolution in other stable environments, such as the lowland tropics and the deep sea. The most striking parallels are the probable reduction of genetic variability and a reduction in the rate of population growth that must accompany parental care, longer maturation, longer life, and smaller population size (31). These two features limit the potential for fast evolutionary change, but this is not of major significance for species survival in an environment that changes only subtly and slowly over geologic time. Competition will be reduced, because of low population densities and low rates of population growth, and competitive exclusion is rare, or difficult to reconcile with the high species diversities found within single habitats (32). We suggest that the relatively low species diversity in caves and the extremely high species diversity in lowland tropics and the deep sea are due primarily to the span of geologic time over which each environment has been stable and, secondarily, to the species pool of possible colonizers. Thus, caves show the least species diversity because caves have the most variable "climate," the shortest geologic history, and the smallest species pool.

Microflora of Caves

Cave bacteria are of interest to bio-speleologists because they are important to the survival of troglobitic animals and not because they are in any way unique. Caumartin has shown that the cave bacterial flora is a selected representation of noncave species. He believes that the deep-cave bacteria produce antibiotics which exclude many molds and higher fungi (33). This would explain the zonation of microflora from entrance zones to deep-cave zones, and it may be related to the use of bacterial clays by troglobites. Such clays have food value (34), but this is not enough to explain the impaired ability to survive observed in

many troglobites not given access to them.

In the case of amphipods, Gounot has shown experimentally that something produced by the bacteria is responsible for the salutary effect of cave clays on the survival and growth of the amphipods (35). The important item may be a vitamin or an antibiotic. It is tempting to suggest that adaptation to a local microflora and its antibiotics explains why some terrestrial troglobites reared on soil other than that from their native cave habitat show impaired ability to survive and impaired reproductive efficiency (36).

Caves as Mineralogical Laboratories

One group of cave minerals is interesting because of its peculiar mineralogy and the possible involvement of bacteria in their formation. These are soft cottage-cheese-like masses found fairly frequently in caves and known by the collective name of "moonmilk." Moonmilk consists of a variety of carbonate minerals, some of which are associated with particular species of bacteria. Most of the moonmilks analyzed from temperate caves of the eastern United States have been hydromagnesite ($3 \text{ MgCO}_3 \cdot \text{Mg}(\text{OH})_2 \cdot 3\text{H}_2\text{O}$), although nesquehonite ($\text{MgCO}_3 \cdot 3\text{H}_2\text{O}$), huntite ($\text{CaCO}_3 \cdot 3\text{MgCO}_3$), aragonite, magnesite, and dolomite have also been reported. Moonmilks from high altitudes may not be related to bacterial activities. These are mainly calcite and are thought to originate from the dehydration of the compound $\text{CaCO}_3 \cdot \text{H}_2\text{O}$ (37).

Many cave processes are freshwater analogs of processes occurring on the ocean floor. Carbonate deposition, in particular, can be studied *in situ*, and the geochemical parameters of the process measured. The mineralogy of caves can be fairly complex if one takes into account the interaction of carbonate minerals with organic materials or with vein minerals in the wall rock. Most interesting are the "normal" cave minerals, which are calcite, aragonite, gypsum, a variety of rare sulfates, and a variety of hydrous carbonates (the moonmilks).

The deposition of calcite in the cave environment turns out to be a remarkably complicated process. Holland and his colleagues (38) have shown three stages in the evolution of the calcite-depositing waters: (i) the equilibration of the groundwater in the soil zone;

(ii) the transport of the solution without loss of carbon dioxide through joints to the cave passage; and (iii) the reequilibration of the solution to the carbon dioxide pressure of the cave atmosphere, which is probably not much higher than that of the surface atmosphere. The final step of calcite deposition takes place mainly through

loss of carbon dioxide rather than through evaporation. This idea is confirmed by field observation that the most prolific and perfect calcite growth takes place in cave passages which are completely sealed from the outside, often by water traps in the channel. The humidities of these chambers remain at 100 percent, and evaporation

should be negligible. The formation of an entrance and subsequent lowering of humidities often degrades the calcite deposits.

Aragonite is a common mineral in caves, and its occurrence in this environment is as much of an enigma as is its occurrence in sea-bottom sediments. Cave aragonite is deposited

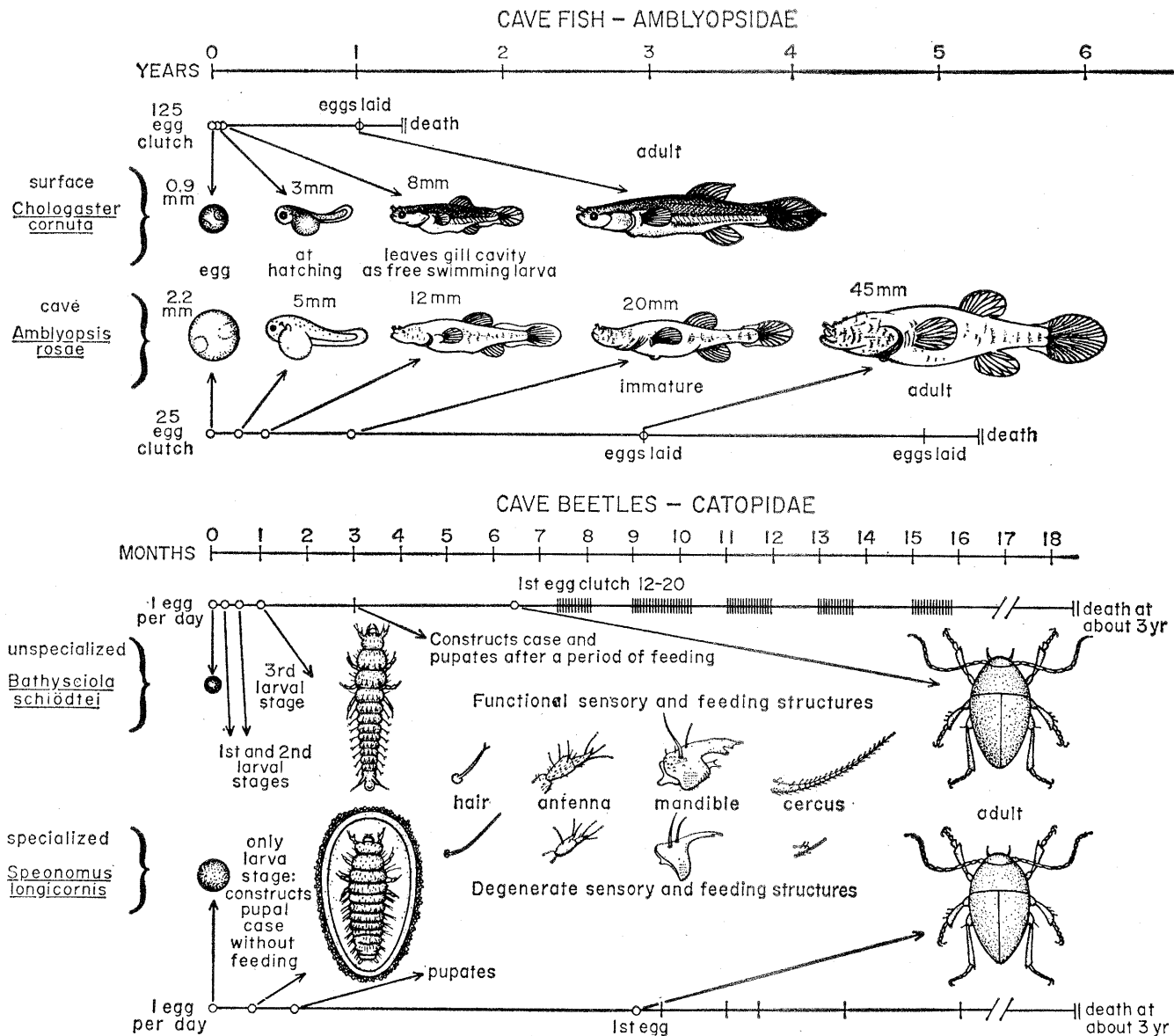


Fig. 3. Diagrams illustrating the life history of troglobites. Selection for life-history adaptations in cave fish and cave beetles is based on a low food supply in caves (22). The time scale is in years for both species of fish and in months for the beetles. For each species a horizontal "time line" is given, on which ages at different developmental stages are indicated by open circles. An arrow connects each circle to the drawing or designation of the stage in question. *Chologaster cornuta* (the surface species of fish) leaves the gill cavity of the female at the age of 1 month, grows quickly, becomes mature and lays eggs at the age of 1 year, and dies. Because the eggs are larger, *Amblyopsis rosae*, the troglobitic species, takes about 4 months to become free-swimming but is then larger, more mobile, and able to eat larger plankton than its surface relative is. It does not mature until it is 3 years old. Its caloric cost for reproduction is less, overall, and less in proportion to its caloric cost for routine maintenance, than that for the surface species, and its rate of survival is higher. The catopid beetle's adaptation to the condition of low food supply differs from that of the cave fish. The unspecialized troglomorphic species that live near cave entrances where there is a lot of detrital food have a typical beetle life history. The female lays eggs—one or two small ones per day for several weeks—periodically throughout her life. Each egg hatches into a small larva that feeds, grows, and molts three times before constructing a pupal case in which it metamorphoses to the adult stage. The specialized troglomorphic catopid beetles live far from entrances, in a part of the cave where food is so rare and highly dispersed that a normal larva, having limited mobility, would starve. In the course of evolution these species have essentially dispensed with the larval stage. The mobile adult searches widely for food and, at irregular intervals, lays single large eggs each of which hatches into a mature larva, all intermediate larval stages having been by-passed. Immediately after hatching, the mature larva constructs its pupal case without feeding; it is plump and has degenerate sensory and feeding structures.

from fresh groundwater of low ionic strength. The relatively few available measurements of ion activity products (39, 40) indicate that the dripping waters are supersaturated with respect to aragonite. Which minerals are deposited depends on the unpredictable kinetics of the process. Deposition is not random; although quantitative data are lacking, aragonite occurs in profusion in some caves, while in other caves it occurs very sparsely if at all. Analyses of cave aragonites show higher concentrations of strontium in the aragonite than in coexisting calcite. In caves with gypsum deposits the dripstone seems to contain more aragonite than it does in caves that lack such deposits. It is commonly supposed that Sr^{++} and SO_4^{--} ions enhance the precipitation of aragonite, although a cause-and-effect relationship has not been conclusively demonstrated (41).

The sulfate minerals—mainly gypsum, with occasional occurrences of mirabilite ($\text{Na}_2\text{SO}_4 \cdot 10\text{H}_2\text{O}$), epsomite ($\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$), and a number of rarer minerals—pose a different sort of problem. The chemistry of deposition seems to be a straightforward matter of evaporation of imperceptibly small seeping solutions. The sources of the sulfates are more difficult to assess. In many caves in the Southwest the gypsum and other sulfate deposits probably arise mainly from solution, transport, and redeposition of overlying evaporites. In the central Kentucky karst, the source of sulfates has been reasonably well established as pyrite in the Big Clifty Sandstone formation which overlies the cavernous limestones (42). Oxidation of the pyrite is enhanced by the action of the bacteria *Thiobacillus thiooxidans* and *Ferrobacillus ferrooxidans*. The sulfate solutions percolate down through the limestone but do not react with it until the solutions reach the cave passages. The reaction of sulfate ion with calcite under pH conditions near neutrality is very delicately dependent on the carbon dioxide partial pressure. The cave passage, with its good atmospheric circulation, acts as a sink for the carbon dioxide and allows the reaction to proceed forward. The gypsum precipitates in the wall rock of the cave passage, with much replacement of limestone by gypsum and with collapse of passage ceilings from crystal wedging forces. The gypsum flowers and other forms which give the caves much of their beauty appear to result from local recrystallization and transport of

the primary deposits in the wall rock. Not all cave gypsum forms in this manner; in some of the caves of the Highland Rim country of Tennessee, in particular, there are gypsum deposits whose ultimate origin is still completely unknown.

Dolomite is rare in cave deposits, although depositing solutions are supersaturated with respect to dolomite. A few cave occurrences of dolomite have been reported, but it has not been conclusively demonstrated that any of these are primary in the sense that the dolomite was formed directly from solution instead of recrystallized from some precursor mineral phase (43).

The Future

Perhaps the most important use of caves is their use as limited and simple natural laboratories in which we can study the principles governing evolution in more complex stable environments, such as the tropics. Simple field and laboratory experiments should help us to understand the general features of niche structure, and comparisons between the distributions and biologies of cavernicoles from different cave regions should help us to understand the control of species diversity. For this work more detailed knowledge of both surface and cave distribution and of systematics is needed for a variety of groups which contain troglobites. Future studies should include consideration of relative abundances, number of caves inhabited, and variation within a single cave and between caves.

In a practical sense we need to know more about karst hydrology. Hydrologists and geological engineers in the United States have yet to come fully to grips with the problems of karst aquifer systems that have plagued portions of Europe for decades. As the urban development of the "northeast corridor" sprawls westward into the limestone valleys of Pennsylvania and Virginia, much more understanding of the hydrology of these valleys will be needed. Foundation subsidence from de-watering of karst aquifers has already been an expensive problem in Florida, and similar problems have occurred in Pennsylvania and probably elsewhere. Such problems will increase. Pollution will also become a serious problem as pollutants are carried longer distances, in unpredictable ways, in carbonate aquifers. It may be possible to trace the transfer of pollutants, even at low con-

centrations, by observing the structure of bacterial and protozoan communities, but prediction of the destination of pollutants will be possible only when we understand the geometry of the underground drainage.

In the course of urbanizing rural limestone terrains, many interesting cave systems and their unique faunas will be destroyed. Natural cave laboratories are going to be very hard to find. The delicate processes which are in need of study require an uncontaminated system. It is clear that certain of these cave systems should be preserved for scientific study. Some individual caves are being purchased to preserve unique and endangered fauna, but the undisturbed areas around them are too small to insure maintenance of a normal ecology. Mammoth Cave National Park is one obvious place where further measures for the preservation of caves should be taken, because it contains the longest and third-longest cave systems in the world, already partially protected. The longest—the almost pristine Flint Ridge cave system—should be set aside as wilderness; the third-longest—the already heavily used and modified Mammoth Cave—is large enough to accommodate expanded public tours and, in addition, a cave laboratory for studying and comparing the disturbed and undisturbed cave systems (44).

References and Notes

1. D. Pfeiffer, *Z. Deut. Geol. Ges.* **113**, 42 (1961); see also F. D. Adams [*Birth and Development of the Geological Sciences* (Dover, New York, 1954), chap. 12] for an account of Kircher's early attempt to produce a hydrologic cycle by using cave conduits as pipes for returning ocean waters to springs.
2. A. Grund, *Pencks Geograph. Abhandl.* **7**, 103 (1903); J. Cvijic, *Rec. Trav. Inst. Geograph. Alpine* **6**, No. 4 (1918); O. Lehmann, *Die Hydrographie des Karstes* (Deuticke, Leipzig, 1932). Lehmann's paper is quite modern in outlook and conceptual basis; it is too frequently overlooked by North American authors.
3. See T. C. Barr, Jr., *Bull. Nat. Speleol. Soc.* **28**, 15 (1966). A. S. Packard [*Nat. Acad. Sci. Mem. No. 4* (1888), p. 1] treats the subject of degenerate eyes, but the best work is Eigenmann's classic of biospeleology, *Carnegie Inst. Wash. Publ.* **104** (1909).
4. T. L. Poulson, in *Handbook of Physiology*, D. B. Dill, Ed. (Williams and Wilkins, Baltimore, 1964), sect. 4, reviews the experimental work up to 1962.
5. A. Vandel, *Biospéologie* (Gauthier-Villars, Paris, 1964).
6. W. M. Davis's "Origin of Limestone Caverns" [*Bull. Geol. Soc. Amer.* **41**, 475 (1930)] is perhaps the classic American work on cave origin. It develops an elaborate argument to demonstrate that the sites of cave origin are in the deep phreatic zone, below the regional water table. Its principal supporter was J. H. Bretz [*J. Geol.* **50**, 675 (1942)]. Cave formation above the water table in the vadose zone was proposed by J. H. Gardner [*Bull. Geol. Soc. Amer.* **46**, 1255 (1935)] and C. A. Mallott [*Proceedings Geological Society of America* (1937), p. 323]. A. C. Swinnerton argued that cave development takes place in the zone of seasonal water-table fluctuation (the flood-water zone) [*Bull. Geol. Soc. Amer.* **43**, 663

- (1932)]. Most recent geomorphologists agree with Swinnerton [M. A. Sweeting, *Geograph. J.* **115**, 63 (1951)]; W. E. Davies, *Bull. Nat. Speleol. Soc.* **22**, 5 (1960); W. B. White, *ibid.*, p. 43; R. A. Watson, *ibid.* **28**, 159 (1966)].
7. A symposium organized by T. C. Barr, Jr. [*Amer. Midland Naturalist* **64**, 1 (1960)] covers the early monographs.
 8. Biota of the deep cave interior are categorized as troglonemes (regular or accidental visitors), troglonemes (facultative species), and troglonemes (obligate species). T. C. Barr, Jr. [*Cave Notes* **5**, 9 (1963)] has given the most recent discussion of this terminology. A review of groups that become troglonitic is given by Vandel (5).
 9. E. R. Pohl, *Nat. Speleol. Soc. Occasional Paper* **2**, 1 (1955); see R. A. Watson [*Intern. J. Speleol.* **2**, 369 (1966)] for a related discussion of underground solution canyons.
 10. The solution of limestone at depth by an undersaturated groundwater formed by mixing two saturated waters with different equilibrium carbon dioxide pressures is discussed in detail by Bögli [*Erdkunde* **18**, 83 (1964)], who called it *Mischungskorrosion*. The effect, implicit in the chemistry of carbonate solution, has been confirmed by others.
 11. For a description of interconnected karst drainage systems, see W. B. White and V. A. Schmidt, *Water Resources Res.* **2**, 549 (1966).
 12. This equilibrium theory was first suggested for islands by R. H. MacArthur and E. O. Wilson [*Evolution* **17**, 373 (1963)].
 13. P. J. Starr [thesis, Yale University (1968)] worked in three caves of the Greenbrier Valley in West Virginia. Greenbrier Caverns and Benedict's Cave are fed by diffuse input and have two troglonitic and one accidental species of harpacticoid copepod. In addition, troglonitic amphipods and isopods are found. Fuller's Cave is fed by sinking streams. It floods during each rain, and severely in the spring. It has seven species of harpacticoid—all accidental species, to judge from their seasonal occurrence and lack of reproduction. No troglonitic amphipods or isopods occur; there are large numbers of aquatic insects from surface habitats.
 14. The lowland tropics have very few troglonites, but there is a great variety of troglonites, with large populations supported by guano from large bat colonies and organic debris washed in during torrential rains of the rainy season [see, for example, M. J. Heuts and N. Leleup, *Ann. Mus. Roy. Congo Belge Ser. 8 Sci. Zool.* **35**, 1 (1954)]. The most complete published faunal list for a tropical cave [H. E. McClure, B. Lim, S. E. Winn, *Pacific Insects* **9**, 399 (1967)] includes only five possible troglonites out of 151 species of invertebrates in 99 families and 23 vertebrate species. As is typical for tropical caves (R. Mitchell, *Southwest Naturalist*, in press), most of the possible troglonites are aquatic and the only certain troglonite is a marine relict. The importance of climatic change and isolation is proved by comparison of the montane areas of Africa and Mexico. In African montane areas there is a rich soil-and-moss fauna of eyeless and wingless trechine beetles. There are no terrestrial troglonites, because the climate has been stable; there is no limestone; and there has been no glaciation to keep the forests to the lower slopes of the mountains and thus give preadapted soil fauna access to the lowland limestone cave areas [N. Leleup, *Ann. Mus. Roy. Congo Belge, Ser. 8 Sci. Zool.* **46**, 1 (1956)]. In Mexico there are limestone caves at altitudes affected by montane glaciation, and it is in these high-altitude caves that the only terrestrial troglonites are known [R. Mitchell, *Southwest Naturalist* **14**, in press; T. C. Barr, Jr., *Newsletter Ass. Mexican Cave Study, Austin, Texas* **2**, 182 (1966); S. B. Peck, *Psyche* **75**, 91 (1968)].
 15. J. R. Holsinger, in "Proceedings of the Conference on the Distributional History of Invertebrate Biota of the Southern Appalachians," P. Holt, Ed. (Virginia Polytechnic Institute, Blacksburg, in press). Holsinger makes the point that such distributions also depend on ability to move through vadose channels in soils and gravels above the water table.
 16. B. C. Moneymaker [*J. Geol.* **49**, 74 (1941)] has discussed such channels, and *Typhlichthys*, a cave fish, has been collected from them in the upper Cumberland River. Terrestrial troglonites can move only across much smaller streams [see 7; T. C. Barr, Jr., and S. B. Peck, *Amer. Midland Naturalist* **64**, 12 (1960)].
 17. T. C. Barr, Jr. [*Amer. Naturalist* **101**, 475 (1967)] uses only trechine beetles of the genus *Pseudanophthalmus* as examples of faunal differences, but less complete data for catopid beetles (S. B. Peck, private communication), millipedes, asellid isopods, collembola, planaria, and perhaps other groups [reviewed by J. R. Holsinger, *Bull. Nat. Speleol. Soc.* **25**, 23 (1963) and thesis, Madison College, Virginia (1963)] suggest that the differences in Valley-Ridge and Interior Low Plateau beetle fauna discussed by Barr are also found in a number of other species.
 18. T. C. Barr, Jr., refers to isolated limestone massifs in this context but does not apply the argument to the Valley-Ridge [17; *Evolutionary Biology*, T. Dobzhansky et al., Eds. (Appleton-Century-Crofts, New York, 1968), vol. 2]. Our explanation of slow adaptation in the Valley-Ridge is based on a report of the evolution of cave-dependent morphology in a collembolan [K. C. Christiansen, *Evolution* **15**, 288 (1961); *ibid.* **19**, 529 (1965)] that has invaded caves in four different areas of the Interior Low Plateaus [— and D. Culver, *ibid.* **22**, 237 (1968)].
 19. T. L. Poulson and W. Culver, *Ecology* **50**, 153 (1969); unpublished data.
 20. D. Culver, *Amer. Zoologist* **7**, 807 (1967); private communication.
 21. T. L. Poulson, unpublished data. We feel that some of Barr's data on trechine beetles at the edge of areas glaciated during the Pleistocene may also be interpreted in this way [*Amer. Midland Naturalist* **63**, 307 (1960)].
 22. For general reviews, see (4) and (5). The beetle data presented in Fig. 2 are part of more thorough studies by S. Deleurance-Glaçon [*Ann. Speleol.* **18**, 227 (1963); *Ann. Sci. Nat. (Zool.) Ser. 12* **5**, 1 (1963)]. The studies of R. Ginot on an amphipod are also of special note [*Ann. Speleol.* **15**, 127 (1960)].
 23. K. C. Christiansen's studies on entomobryid collembola ("springtails") provide the most complete data for a terrestrial troglonite. Studies on food aggregation and competition (personal communication) show parallels to the more detailed studies on amblyopsid fish (24). These studies promise to be exciting because collembola have generation times short enough to make genetic analysis feasible. The statistical analysis of morphological adaptation at the population level (see 18) has already proceeded farther than will ever be possible for cave fish.
 24. C. H. Eigenmann did the best early work on amblyopsid fishes (see 3), and two recent papers have dealt with their systematics and phylogeny [L. P. Woods and R. Inger, *Amer. Midland Naturalist* **58**, 232 (1957); D. Rosen, *Amer. Museum Novitates No. 2109* (1962)].
 25. T. L. Poulson has done almost all the recent natural-history and experimental work [thesis, University of Michigan (1961); *Amer. Midland Naturalist* **70**, 257 (1963); work (unpublished) resulting from collaboration with M. A. Barnett (studies on feeding efficiency), D. Fell (obstacle avoidance), and S. Drezek (regulation of metabolic rate)]. Barnett and Drezek were National Science Foundation undergraduate research participants in the initial phases of these studies.
 26. According to our interpretation, eye size and dioptric apparatus are reduced quickly by selection during the initial stages of isolation in caves because considerable energy and material are required in producing these last stages of growth following completion of morphogenesis. Also, there is a stage in eye degeneration, or in rudimentation of any organ, beyond which there is no further change because the organ shares developmental mechanisms with systems that are maintained by selection. In between these stages the total number of dioptric, retinal, and structural support elements lost or simplified at the embryological stage of maximum eye development gives a relative time scale for isolation in caves. The assumption of random accumulation of loss mutations is supported by absence of pattern in loss between related species, and the assumption of similar mutation rates among related species is probably valid.
 27. T. L. Poulson and T. C. Jegla, in *Proc. Intern. Congr. Speleol.*, 4th (in press), vol. 4. See also E. Gunzler's studies on amphipods [*Biol. Z.* **83**, 677 (1964)] and T. C. Jegla and T. L. Poulson [*J. Exp. Zool.* **168**, 273 (1968)].
 28. T. C. Jegla [*Biol. Bull.* **130**, 345 (1966)] made the initial field study, and T. L. Poulson and T. C. Jegla did the experimental work. The suggestion that temperature is the most reliable cue is based on year-round studies of chemical properties and temperature of cave waters in central Pennsylvania [W. B. White and J. A. Stellmack, *Proc. Intern. Congr. Speleol.*, 4th (1968), vol. 3, p. 261; E. T. Shuster, thesis, Pennsylvania State University (1969)].
 29. The cause of lowered metabolic rate in amblyopsids is a lowered gill-surface area and lowered rate and volume of ventilation. Lowered ventilation rate and heart rate may be associated with lowered brain metabolism [T. L. Poulson and S. Drezek, *Proc. Intern. Congr. Speleol.*, 4th (in press), vol. 4], but lowered growth rates are not associated with decreased thyroid activity.
 30. Similar patterns, where the phylogenetically oldest relicts are rare, found in only a few caves, and highly modified morphologically, are known for such diverse groups as pselaphid beetles [O. Park, *Amer. Midland Naturalist* **64**, 66 (1960)], tomocerine collembola (K. C. Christiansen, private communication), and amphipods in the flagellatus group of the genus *Stygonectes* [J. R. Holsinger, *Amer. Midland Naturalist* **76**, 100 (1966)]. In the United States most relicts are found in peripheral or disjunct limestone areas such as central Alabama and eastern Texas, where the species diversity of troglonites in the cave may be especially high. We suggest that such high diversity in a food-poor environment is allowed in part by the high proportion of well-adapted relicts.
 31. Inference based on morphology and size distributions suggests that, in parallel with troglonites, bathyentonic invertebrates with narrow depth distributions have longer lives and larger eggs than widely distributed species [A. Schoener, *Ecology* **49**, 81 (1968); A. Bruun, *Geol. Soc. Amer.* **67**, 641 (1957); G. Thorson, *ibid.*, p. 461 (1957)], and bathypelagic fish show extreme energy economies [N. B. Marshall, *Discovery Rep.* **31**, 1 (1960)].
 32. H. L. Saunders suggests that stability is the major factor contributing to the high species diversity of deep-sea invertebrates [*Amer. Naturalist* **102**, 243 (1968)]. He finds as many as 96 species in a sample (occupying an area 1 meter square) of only 460 individuals. This raises problems for the competitive exclusion principle, because a high proportion of these species are deposit feeders and there may be 8 to 20 closely related species in an area 1 meter square. T. Dobzhansky has provided the most lucid account of similar situations in the lowland tropics [*Amer. Sci.* **38**, 209 (1950)].
 33. V. Caumartin reviews microbiology of cave soils in an ecological context [*Bull. Nat. Speleol. Soc.* **25**, 1 (1963)].
 34. A. M. Gounot has provided the best quantitative data on natural cave microflora [*Ann. Speleol.* **22**, 23 (1967)].
 35. A. M. Gounot, *ibid.* **15**, 501 (1960).
 36. This phenomenon is known for catopid beetles (see 22) and tomocerine collembola (see 30), but the most thorough data are reported by S. B. Peck for an American catopid [private communication; *Bull. Nat. Speleol. Soc.* **30** (1968)].
 37. G. Baron, S. Caillere, R. LaGrange, T. Pobegu, *Bull. Soc. Franc. Mineral Crist.* **82**, 150 (1959); R. Bernasconi, *Stalactite* **7**, 148 (1967); R. Gradzinski and A. Radomski, *Rocznik Polsk. Towarz. Geol.* **26**, 63 (1956).
 38. H. D. Holland, T. V. Kirsipu, J. S. Huebner, U. M. Oxburgh, *J. Geol.* **72**, 36 (1964).
 39. Chemical analyses of dripping cave waters are rare. Holland's (38) measurements in Luray Caverns are the most complete.
 40. J. W. Murray, *J. Geol.* **62**, 481 (1954) and J. V. Thraikill, thesis, Princeton University (1965).
 41. R. L. Curl, *Bull. Nat. Speleol. Soc.* **24**, 57 (1962); F. R. Siegal, *Sedimentology* **4**, 285 (1965).
 42. E. R. Pohl and W. B. White, *Amer. Mineralogist* **50**, 1461 (1965).
 43. The deposition of secondary dolomite crusts surrounding calcite spar in Jewel Cave, South Dakota, is described by D. E. Deal

[thesis, University of Wyoming (1962)]. Dolomite occurs in secondary cave deposits in Carlsbad Caverns, New Mexico, where it is believed to be altered from aragonite by reaction with magnesium-rich solutions [J. Thrallkill, *J. Sedimentary Petrol.* 38, 141 (1968)].

44. Shelta Cave, Huntsville, Alabama, is being purchased by the National Speleological Society because of the very large diversity of troglobites and the presence of a unique

shrimp and crayfish. Ezell's Cave in Texas is being purchased by Nature Conservancy because it contains a rare and unique troglitic salamander, *Eurycea rathbuni*, as well as relict species of flatworm, amphipod, and shrimp. The possibility of declaring the Flint Ridge Cave System in Mammoth Cave National Park, Kentucky, an underground wilderness under the Wilderness Act of 1964 is currently a hotly debated topic.

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Vegetational Change Along Altitudinal Gradients

Studies in Ethiopia show that discreteness of zonation varies with steepness of slope.

Edward W. Beals

The controversy among plant ecologists as to whether vegetational variation is predominantly continuous or discontinuous still goes on and occasionally reaches the pages of *Science* (1, 2). The continuum school of thought, originating out of Gleason's individualistic concept of plant associations (3) was originally developed in this country during the 1950's by Curtis and his associates (4) and by Whittaker (5). A parallel development occurred among Polish ecologists (6). The other view, illustrated by Clements' organismic concept of the community (7) and by the elaborate taxonomy of communities put forward by Braun-Blanquet and his colleagues (8), has been staunchly defended by Daubenmire (1), who claims that the continuums described by most authors are artifacts of data manipulation.

It may be significant that continuum concepts originated largely among ecologists living in areas of gentle topography—in Poland and in the Midwest. Braun-Blanquet's ideas were formulated largely in mountainous Switzerland, and Daubenmire's experience has been mostly in the western mountains

of the United States. Whittaker's gradient analysis in the Great Smoky Mountains (5) showed continuity but also some discontinuity in the vegetational changes.

It is apparent to many ecologists that under some conditions vegetation forms a continuum, under other conditions it forms discrete communities, and that most vegetation is somewhere between. The question is, What factors determine the relative continuity of the vegetation? Are there factors operating besides the obvious ones, such as predominance of certain combinations of conditions in an area, or inherent environmental discontinuities, or random fluctuations?

Comparison of the Two Study Areas

Two areas in Ethiopia allow a unique comparison of the effects of steep and gentle altitudinal gradients on vegetational change. One area is located on the Rift Escarpment (11°5'N, 40° to 39°50'E), beginning below the village of Bati and extending westward up to the town of Combolchia. This steep gradient extended from 800 to 2050 meters (a vertical change of 1250 meters) in about 20 kilometers horizontal, and the topography was rugged.

The other area is in the Rift Valley (9°N, 40°10'E to 7°15'N, 38°35'E), from Awash Station southwest to Shashamane. This gentle gradient extends from 1000 to 1900 meters (a vertical change of 900 meters) in about 300 kilometers horizontal, and the landscape, except for a few isolated volcanic peaks, is gently rolling to flat. Though this gradient has less altitudinal range than the other one, its greater geographic range is compensatory, and the vegetational types in the two areas are somewhat similar. The two areas are within 235 kilometers of each other.

One environmental difference, resulting from contrasting topography and causing considerable difference in the vegetation, is the depth and stability of the soil—in the former case shallow, rocky, and poorly developed; in the latter case relatively deep and well developed. The soils throughout both areas of sampling are derived from basic volcanic rock.

Moisture is probably the overriding factor influencing altitudinal zonation. Neither area receives frost. *Acacia* scrub communities occur at lower elevations.

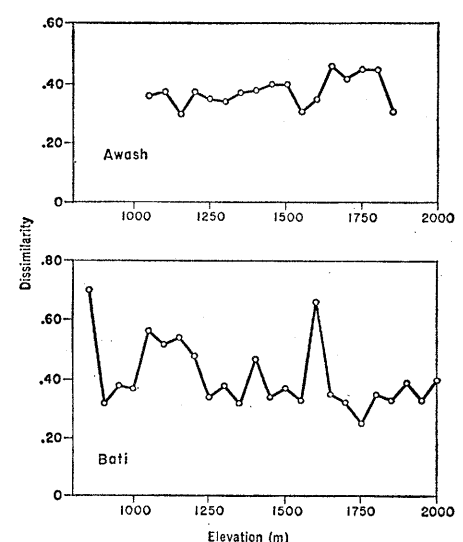


Fig. 1. Dissimilarity (1 — coefficient of similarity) of adjacent segments of the altitudinal gradient along the gentle (Awash) and the steep (Bati) slopes. High values indicate rapid changes in vegetation, low values indicate slow changes.

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