2 Adaptation

The study of adaptation is often a curious mixture of the obvious and the controversial. On the obvious side are observations that organisms living in a particular environment, say a desert, are better able to survive and reproduce in that environment than in environments where they do not naturally occur, say, a mesic forest. The controversies about adaptation are whether it is an optimization process (Lewontin 1979, Maynard Smith 1978), and whether it is universal. Adaptation and optimization require, first, the presence of genetic variation in fitness for the trait or traits being studied and, second, the absence of conflicting selective pressures or genetic constraints such as linkage that override or confuse the optimization process. For example, to state that the optimal solution to survival in the food-poor environment of caves is reduced metabolic rate (or increased metabolic efficiency) assumes that genetic variation in metabolic rate existed at some point and that there are no conflicting selective pressures, such as selection for rapid growth to escape predation.

Potential selective factors are often easier to identify in caves than in other environments. This chapter begins with a review of the abiotic and biotic conditions in caves that are likely to be important in selection. Then I will examine four predicted adaptations: the evolution of increased tactile and chemical senses to compensate for lack of light in caves, the evolution of metabolic economy, the evolution of adaptations to high moisture and humidity levels, and the evolution of neoteny. The focus throughout is on individual adaptation. The related question of the effect of individual fitness on population growth is discussed in chapter 3.

The Physical Environment

Since most biological work has been done in limestone caves in temperate climates, these are what I emphasize. It is worth noting that caves are not limited to limestone and are not limited to temperate regions. They occur in ice, such as Paradise Ice Cave on Mount Rainier, in tropical limestones, and in lava tubes throughout the world (Halliday 1974).

As a general rule, the physical environment of caves varies less than the surrounding surface environment. Physical conditions do vary, not only over time but also between caves and between areas within a cave. Relative to above-ground conditions, however, there is less variation below ground.

The temperature in caves approximates the mean annual temperature of the region. In parts of large caves remote from any entrance, the temperature scarcely varies at all. In remote parts of the Flint Ridge–Mammoth Cave system, air temperature varies between 13.6°C and 13.9°C (Barr and Kuehne 1971). In most caves, the temperature variation is greater. Figure 2–1 shows the annual temperature limits for Sainte-Catherine Cave in France. Such a temperature profile is typical of many small caves, with fluctuations of several degrees for most of the length and even greater variation near the entrance. Available evidence indicates that terrestrial cave organisms are very sensitive to variation in temperature. Juberthie (1969) found that the cave-limited beetle *Aphaenops cerberus bruneti* was present only at sites with low minute-to-minute fluctuations in temperature 2 mm above the soil (Fig. 2–2).

Relative humidity, even in dry passages, rarely falls below 80 percent. However, most terrestrial cave organisms are found in areas of near saturation. It is rare to find cave-limited species in areas that are not visibly damp or wet, and the terrestrial cave fauna is often restricted to the edges of streams and drip pools. Coping with high humidity and standing water may be a major feature of cave adaptation (see below and Howarth 1980).

Cave waters show a similar pattern of relative stability. Because of

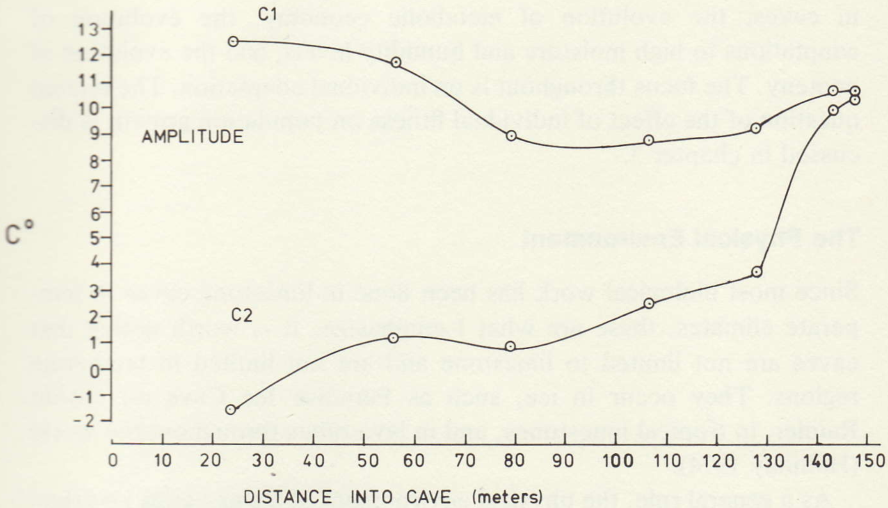


Figure 2-1 Annual temperature fluctuations throughout Sainte-Catherine Cave, Ariege, France. C1 is the maximum temperature profile, and C2 is the minimum temperature profile. (From Juberthie 1969.)

the porosity of karstified limestone, drainage basins in karst have moderate flood peaks compared to other drainage basins. Current velocity and discharge levels vary less in cave streams and in the rivers that are fed by cave waters as well. Pardé (cited in Jennings 1971) found that the mean monthly discharges of the River Nera, which drains a karst area, varied within only 17 percent of the mean annual discharge. By contrast, the Tiber varied up to 95 percent of the mean. On a smaller scale, White and Reich (1970) discovered that peak discharge rates were much lower for small karst streams than for nonkarst streams, but high discharge rates occurred over a longer time (Fig. 2-3). Many cave animals, however, are very sensitive to current flow. Spring floods are a major cause of mortality for cave amphipods (Culver 1971a), and reproduction is often cued to spring floods (Ginet 1960). Furthermore, caves with more variable hydrologic regimes have fewer species. In the Greenbrier Valley in West Virginia, caves with relatively mild hydrologic regimes had more cave-limited amphipod and isopod species ($\bar{x} = 2.3$, S.D. = 1.1, $n = 15$) than caves with severe floods that occasionally filled the cave passages ($\bar{x} = 0.8$, S.D. = 0.7, $n = 13$).

Chemically, cave waters are characterized by high alkaline hardness and relatively high pH (Table 2-1). Spring high water reduces alkaline hardness and pH, but both are still higher than in most surface streams.

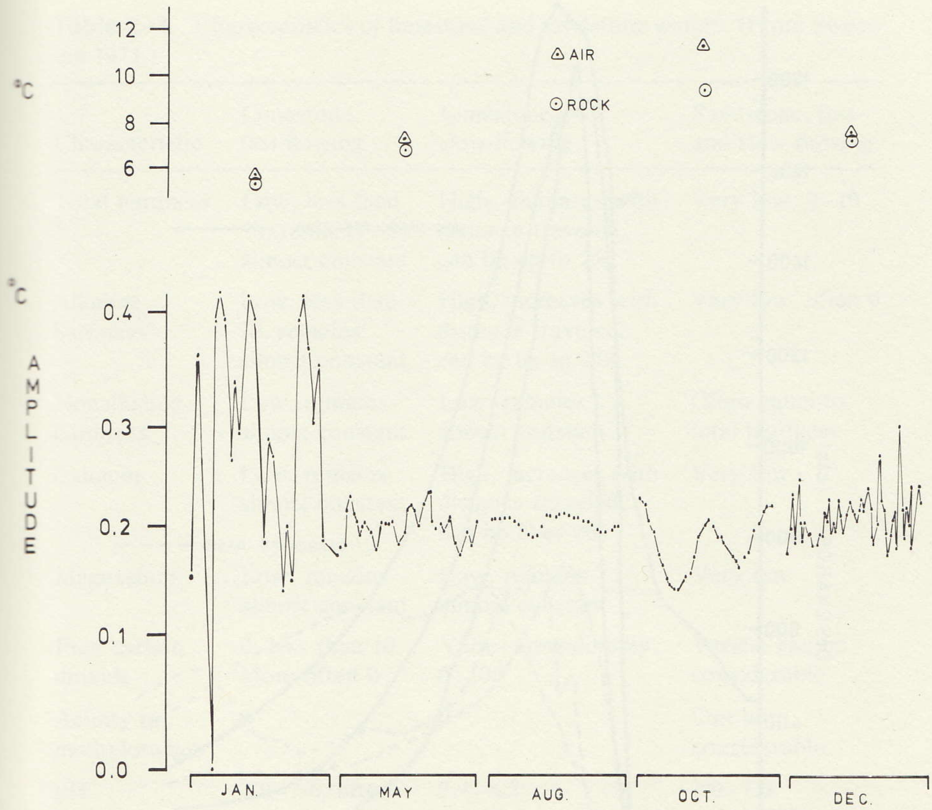


Figure 2–2 The effect of microclimate on the distribution of the beetle *Aphaenops cerberus bruneti* in Sainte-Catherine Cave. *Top panel,* mean temperature of air and rock. *Bottom panel,* deviation from the mean at 10-second intervals 2 mm above the soil. *Aphaenops* was absent in January and December when fluctuations were greatest. (Adapted from Juberthie 1969.)

In cave streams oxygen concentration is usually high, although in rimstone pools fed by slow drips and seeps it can be quite low. An extreme case is the water in Banner's Corner Cave in Virginia, which is polluted by septic tank leakage. Holsinger (1966) found pools there with less than 3 mg/l of oxygen. However, cave isopods (*Caecidotea recurvata*) and planarians (*Phagocata gracilis*) were very common.

Sources of Food

Except for a few chemosynthetic autotrophic bacteria that use iron and sulfur as an electron donor (Caumartin 1963), primary producers are absent. Thus, in a general sense, cave communities are decomposer

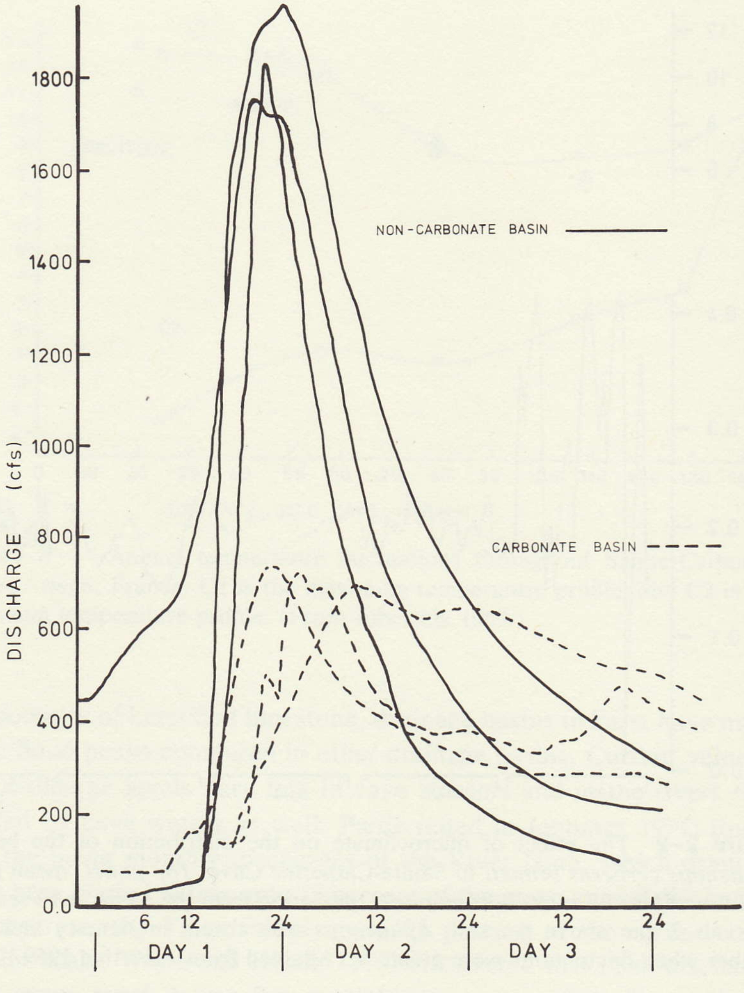


Figure 2–3 Peak discharges in cubic feet per second (cfs) for a carbonate and a noncarbonate basin in Pennsylvania for three days. The carbonate basin drains 145 km^2 and the noncarbonate basin drains 95 km^2. (From White and Reich 1970.)

communities. Food is brought in by both biological and physical agents continuously or in pulses and in different spatial configurations. Food enters a cave in three main ways. Organic matter is carried directly by streams and vertical shafts, and this source can be important for the terrestrial as well as the aquatic community because a layer of plant detritus is often left by receding flood waters. Another important source of food is the dissolved organic matter, bacteria, and protozoa in water

Table 2–1 Characteristics of limestone and sandstone waters. (From Sweeting 1973.)

Characteristic	Limestone, fast-flowing	Limestone, slow-flowing	Sandstone, fast- and slow-flowing
Total hardness	Low, less than 70, remains almost constant	High, increases with distance traveled, can be up to 250	Very low, 0–10
Alkaline hardness[a]	Low, less than 70, remains almost constant	High, increases with distance traveled, can be up to 250	Very low, often 0
Nonalkaline hardness	Low, remains almost constant	Low, remains almost constant	Often equal to total hardness
Calcium	Low, remains almost constant	High, increases with distance traveled, can be over 200	Very low
Magnesium	Low, remains almost constant	Low, remains almost constant	Very low
Free carbon dioxide	0–less than 10. More often 0	Varies considerably, 0–100	Varies, can be considerable
Acidity to methylorange	0	0	Can be considerable
pH	7.0–7.6, often constant	7.4–8.5	3.0–7.0
Color	Usually slightly colored	Colorless	Often highly colored

a. mg $CaCO_3$, per 1,000 ml.

percolating into the cave through the limestone rock. Finally, there are the feces of animals that regularly enter and leave the cave and eggs deposited by cave "crickets" (see below). In some caves, food may enter in more exotic ways. One most interesting special case is the Hawaiian lava tube caves, where exudates from tree roots are the major food source (Howarth 1972).

In the terrestrial cave environment there are at least five major sources of food: cave cricket eggs and guano, microorganisms, plant detritus left by flooding, bat guano, and feces of other mammals.

In many North American caves, cave crickets in the family Rhaphidophoridae, for example, *Euhadenoecus* and *Hadenoecus* in the east (Fig. 2–4) provide a major source of food. *Hadenoecus* leaves the cave

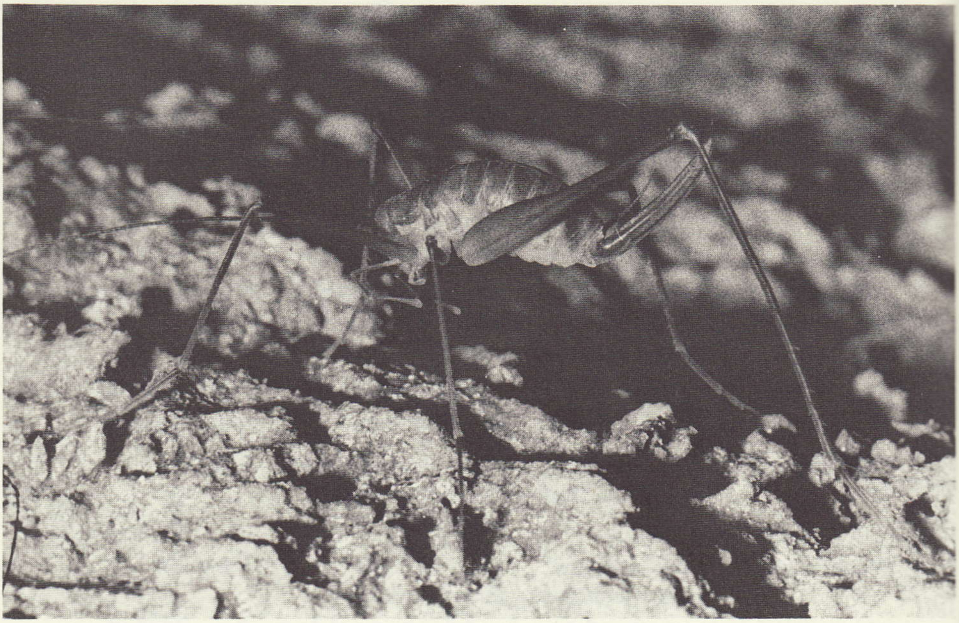


Figure 2–4 *Euhadenoecus fragilis* in Sweet Potato Cave, Lee County, Virginia. (Photo by author.)

at night and feeds "opportunistically and omnivorously as a scavenger" (Hubbell and Norton 1978), and cricket guano is an important food source for many species. Some of the most diverse terrestrial cave communities occur in areas where cricket guano is splattered on walls and floors. The female crickets oviposit inside the cave, usually in sandy substrates; in parts of the Edwards Plateau of Texas and the Interior Low Plateau in Kentucky, cave cricket eggs are the major dietary item for some beetle species (Mitchell 1968, Norton, Kane, and Poulson 1975). In some caves, this interaction comes close to being a naturally isolated predator–prey pair. In the absence of sandy substrates, the crickets oviposit in substrates that are difficult for beetles to excavate, and this interaction is absent.

Microorganisms occur on a variety of substrates, including wood, dung, and plant detritus, and are at least part of the diet of many terrestrial cave invertebrates. Microfungi appear to be more important than bacteria or actinomycetes. In a study of several Virginia caves, Dickson and Kirk (1976) found that the abundance of the cave-limited invertebrates was correlated with abundance of microfungi and with high fungal–bacterial ratios, but not with abundance of bacteria or ac-

Table 2–2 Average plate counts of microorganisms in and around Old Mill Cave, Virginia. (Modified from Dickson and Kirk 1976.)

Sample description	No. samples	Microfungi × 10^{-3} per gm of substrate	Ratio of bacteria: actinomycetes: fungi
A-horizon, forest soil	3	500	23:7:1
Entrance room	3	11	91:8:1
Dung, entrance room	1	7,160	6:0:1
Dark passages, floor	5	12	87:12:1
Floor with decayed chitin	1	490	25:0:1
Passages with stream	9	10	35:13:1
''Dry'' passages	6	1	865:69:1

tinomycetes (Table 2–2). As expected, resource levels were lower in the cave than in forest soil, but there were exceptions. Dung in the entrance area and mud floors with chitin remains had high plate counts. The apparent correlation of high humidity and abundance of microfungi makes it difficult to know which factor is more important.

Plant detritus may also be an important food source. A layer of mud and finely divided leaves, often rich in oligochaetes, is deposited in many caves by slowly receding flood waters. Such areas often have a rich fauna. In caves subject to severe, rapid flooding, clumps of twigs and leaves are left behind, and the fauna on these resource patches is relatively distinct, usually of species not limited to caves, such as the isopod *Ligidium elrodii* (Schultz 1970, Holsinger, Baroody, and Culver 1975).

In stone-bottomed cave streams most of the food is plant detritus. Microorganisms are present, but in very low numbers. In slow-moving streams usually with mud bottoms, and in drip and seep pools isolated from the main stream, microfungi are more common and are correlated with the abundance of macroscopic invertebrates (Dickson and Kirk 1976). Plankton are scarce (Fig. 2–5), and are mostly washed into caves, but plankton populations apparently reproduce in the cave during the summer and autumn (Barr and Kuehne 1971).

A few caves harbor large bat colonies with large guano concentrations beneath, and in these caves food is comparatively abundant and continuously present. Thus selective pressures are different, and it is not surprising that the fauna feeding on guano is quite different from the rest of the cave fauna. Many guano-feeding species are not found in caves without guano, and these species display little of the eye and pig-

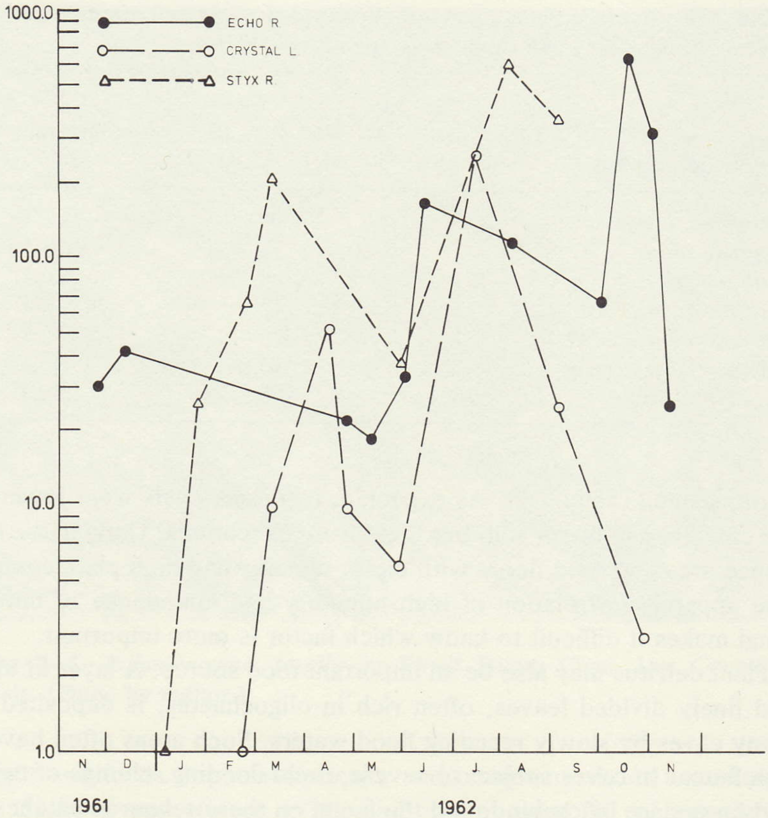


Figure 2–5 Plankton densities per 100 m of tow in three aquatic habitats in Mammoth Cave over a 12-month period. Peaks apparently correspond to heavy rainfall and spring snow melt. (From Barr and Kuehne 1971.)

ment reduction often found in cave organisms (Mitchell 1970, Peck 1971).

Besides serving as a substrate for microfungi, dung and dead animals are important food sources. Peck (1973a) has used dung as a very effective bait for catopid beetles. Poulson (1978) has found that there are differences in caloric content and in predictability of feces availability of mammals and invertebrates that enter caves, and that each fecal type has a more or less distinct community associated with it.

There remains the question of how much food is actually available to cave animals. The best comparative study is that of Peck and Richardson (1976), who compared the stomach contents of cave salamanders (*Eurycea lucifuga*) from the entrances and from the dark zones of caves in Tennessee and Alabama. Salamanders collected at the entrance, where one would expect food to be more abundant, had 18.6 prey items, with a volume of 0.14 ml, per stomach. By contrast, those from the dark zones had only 3.4 prey items, with a volume of 0.05 ml, per stomach.

Sensory Compensation

Perhaps the most cherished tenet of biospeleology, dating back at least to the neo-Lamarckians at the turn of the century, is that the fragile, delicate morphology of cave animals results from selection for increased sensory organs on appendages, which in turn results in lengthened appendages. This conjecture depends on two main points. The first is that the number (or size) of sense organs is increased by increasing the length of appendages bearing sense organs, or by increasing the density of sense organs per surface area, or by increasing surface area by appendage elongation. The second assumption is that increased number or size of sensory organs increases fitness. Since fitness is difficult to measure, it is not surprising that there is little evidence on this point. What is surprising is the paucity of evidence on the first point.

There are certainly cave organisms with very long appendages and a generally fragile appearance, of which *Euhadenoecus fragilis,* shown in Figure 2–4, is but one example. But how general is the phenomenon, and what is its adaptive significance? Morphometric studies are not that common in the biospeleological literature, and many suffer from inappropriate comparisons. For example, a comparison of European subterranean amphipods in the genus *Niphargus* with fresh- and brackish-water amphipods in the genus *Gammarus* (for example, Ginet 1960) is suspect, because *Niphargus* probably did not arise from *Gammarus,* and in fact the two genera are placed in separate families (Bousfield 1977). Inappropriate comparisons can work both ways. Albert Vandel, the noted French cave biologist, held to the outmoded orthogenetic theory that cave organisms are both phylogenetically and individually senescent (Vandel 1964) and therefore did not believe that adaptation to the cave environment occurs. Many of his often inappropriate comparisons of cave and surface populations show no lengthening of appendages of cave populations (p. 572).

To investigate whether appendages of cave organisms are indeed longer, two comparisons must be made. First, the appendage lengths of cave populations should be compared with those of their closest noncave relatives. But since the ancestors of cave organisms often occur in habitats sharing some characteristics of caves, especially reduced light levels, they are likely to be "preadapted" to cave life. The second comparison should be between the appendage lengths of the ancestors or relatives of cave species and those of other noncave populations. Such a morphometric study of preadaptation has not been attempted and indeed would be very difficult because of the very large number of measurements required. Morphometric studies of cave and related noncave populations have been made, but most of these studies have involved only adults, and little information on ontogeny is available, making it difficult to interpret the allometry equation $y = bx^a$ (Gould 1971).

The amphipod *Gammarus minus* is common in springs and caves in much of the Appalachians. Populations in the large caves of Greenbrier County, West Virginia, and Tazewell County, Virginia, are noticeably paler and longer, with reduced eyes and elongated appendages. A reanalysis of data for these populations given by Holsinger and Culver (1970) shows that the increase in length of the first antennae in cave populations is not due to positive allometric effects, where an increase in body size causes a proportionally greater increase in antennal length. Fits of both the large cave and the spring populations to the allometry equation $y = bx^a$, where x is length and y is antennal length, yielded values of a slightly less than, but not significantly different from, 1. The linear slopes are significantly different (0.52 for springs, 0.71 for large caves), resulting in quite different morphologies (Fig. 2–6). The large cave forms also show considerable eye degeneration, and in fact Bousfield (1958) suggested that the large cave form might be a separate species. These morphometric changes would seem to support the claim that increased appendage length is a result of adaptation to the cave environment. However, the genetic basis of these changes is unclear. In an analysis of electrophoretic variants of soluble enzymes, Gooch and Hetrick (1979) found considerable geographic variation, but almost no differences between spring and cave populations. This suggests that adaptation to cave life does not require a large reorganization of the genome. Finally, there is no direct evidence that the morphometric changes observed are the result of selection or that they even have a genetic basis.

Morphological studies of other cave organisms have yielded a variety of results. An analysis of Shear's (1972) data for type specimens of species in the milliped genus *Pseudotremia* indicates that the cave-limited species do not have proportionately longer third antennal segments than other species (Table 2–3). Using the allometry equation

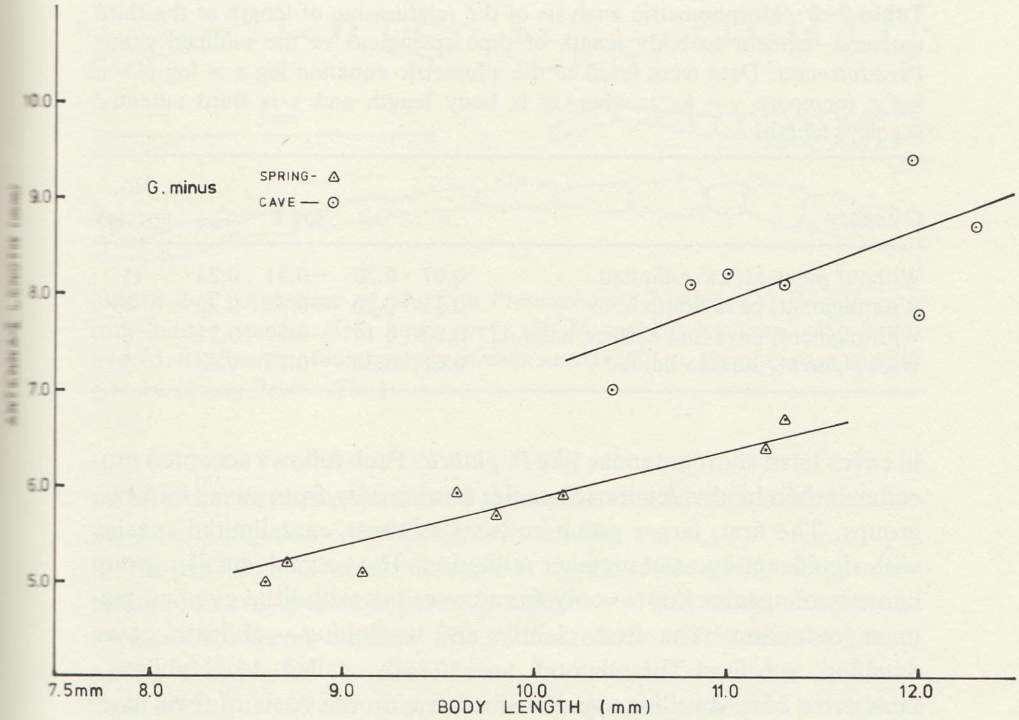


Figure 2–6 Average body length plotted against length of first antennae in mature male *Gammarus minus* from eight spring and seven cave populations in Virginia and West Virginia. (Modified from Holsinger and Culver 1970.)

$y = bx^a$, neither b nor a was consistently higher for cave-limited species. The only group that showed consistent differences were cave-limited species that retained pigment. They had a lower slope, but a higher intercept than either surface species or cave-limited species lacking pigment.

Peck's (1973a) study of *Ptomaphagus* beetles, on the other hand, indicates that cave species do have elongated antennae. Although he only gives ratios or drawings of antennae, making allometric analysis impossible, it is clear from his drawings that the cave species have longer antennae. Peck suggests that long antennae are advantageous to cave species because they allow greater searching ability and disadvantageous to surface species because space is a constraint in their soil-litter habitats. Antennae of Mexican *Ptomaphagus* are shown in Figure 2–7. Most of the cave-limited *Ptomaphagus* have antennae like *P. troglomexicanus,* but a small group of species that are regularly found

Table 2–3 Morphometric analysis of the relationship of length of the third antennal segment to body length of type specimens of the milliped genus *Pseudotremia*. Data were fitted to the allometric equation $\log y = \log b + a \log x$ (compare $y = bx^a$), where x is body length and y is third antennal segment length.

Category	a	s_a	$\log b$	$s_{\log b}$	No. species
Without pigment, cave-limited	0.67	0.20	−0.81	0.24	15
With pigment, cave-limited	0.35	0.20	−0.38	0.26	8
With pigment, cave and surface habitats	0.80	0.14	−0.99	0.21	8
With pigment, surface-limited	0.61	0.30	−0.77	0.43	5

in caves have short antennae like *P. elabra*. Peck follows accepted procedure when he divides those species known only from caves into two groups. The first, larger group consists of those cave-limited species with significant eye and pigment reduction. The second, smaller group consists of species known only from caves but with little eye and pigment reduction. The first clearly are troglobites—obligate cave-dwelling species. The second are usually called troglophiles—facultative cave-dwelling species—because on the basis of their morphology, it is assumed that they will be found in noncave habitats.

It is also widely held that gene exchange with surface populations prevents troglophiles from fully adapting to the cave environment. There is an obvious circularity in this argument, because species that do not show appendage elongation or regressive evolution are assumed to be swamped by gene flow or to have not been in caves long enough to adapt (see Hamilton-Smith 1971). However, many of these troglophiles are very successful in caves, at least numerically. The best examples are the little-studied cave Diptera, which are common in many caves. Gene flow and insufficient time may have constrained the amount of appendage elongation, but it is also possible that not all cave species are subject to selection pressures for sensory compensation and appendage elongation. Some credence is given to this view by Franz and Lee's (in press) suggestion that cave-limited crayfish are adapted to different resource levels, and by Poulson's (1978) data showing that some less modified cave species specialize on locally abundant but patchily distributed resources. The most parsimonious explanation of the morphometric data is that some cave populations undergo considerable appendage elongation, probably the result of selection for increased nonvisual sense organs in the food-poor environ-

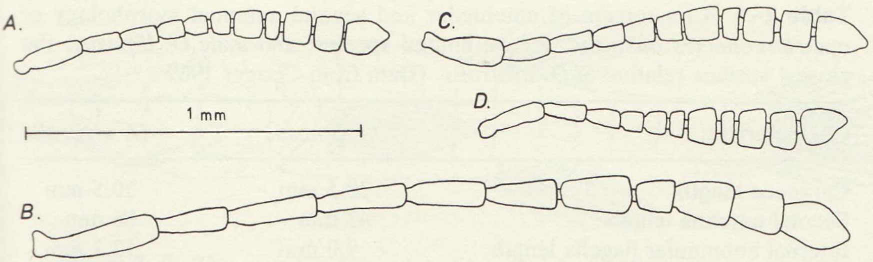


Figure 2–7 Antennae of Mexican *Ptomaphagus* beetles: (*A*) *P. elabra,* a cave-limited species with large eyes; (*B*) *P. troglomexicanus,* also cave-limited; (*C*) *P. altus,* found only in forests; and (*D*) *P. leo,* found in caves and in forests. (From Peck 1973a.)

ment. Other cave populations do not, and it is at least possible that appendage elongation is not being selected for.

One especially clear-cut example of the evolution of increased sense organs in cave species is given in Cooper's (1969) study of cave and surface *Orconectes* crayfish. She minimized allometric effects by comparing crayfish of the same size. As indicated in Table 2–4, the cave-limited *Orconectes australis* has longer antennae and antennular flagellae, more antennular asthetascs, and longer asthetascs than the surface-dwelling *O. limosus,* the closest surface relative to *O. australis*. Apparently both chemoreceptors (asthetascs on the external flagellum) and mechanoreceptors (various organs on the internal flagellum and second antenna) are used to locate food. In a series of laboratory experiments Cooper showed that *O. inermis,* a cave-limited species very similar to *O. australis,* located injured *Enchytraeus* worms twice as fast as *O. limosus* whose eyes had been painted with enamel.

Vandel (1960) has provided counterexamples of evolution of decreased sense organs in cave species. Eyeless, unpigmented cave-dwelling isopods in the genus *Androniscus* have fewer antennular asthetascs than the species Vandel believed closest in morphology to the ancestral stock, *A. dentiger,* even though the cave-limited species have the same body length. Vandel's interpretation is that these data support the orthogenetic hypothesis of phyletic senescence of cave species and their lack of adaptation. A more modern interpretation is that as with *Pseudotremia,* discussed above (see Table 2–3), there has not been selection for appendage elongation and increased sense organs in cave-dwelling species. That antennular asthetascs are actually reduced

Table 2–4 Comparison of antennular and second antennal morphology of male *Orconectes australis,* a cave-limited species, and male *O. limosus,* the closest surface relative of *O. australis.* (Data from Cooper 1969.)

Characteristic	*O. limosus*	*O. australis*
Carapace length	30.5 mm	30.5 mm
Second antenna length	42 mm	86 mm
Internal antennular flagella length	9.0 mm	12.2 mm
External antennular flagella		
Length	10.5 mm	11.4 mm
No. segments	31	36
No. bearing asthetascs	18	22
No. asthetascs/segment	7	7
Asthetasc length	0.12 mm	0.18 mm

in cave-limited *Androniscus* is open to question. All species in the subgenus *Dentigeroniscus* have three antennular asthetascs except for *A. dentiger.* All species, including *A. dentiger,* are found in caves, but some, for example, *A. brentanus* and *A. dentiger,* are found outside caves as well. Furthermore, other sense organs may display different patterns.

The classic case of sensory compensation and cave adaptation in general is Eigenmann's (1909) and Poulson's (1963) studies of amblyopsid fish. Since these studies have become a paradigm, they are worth examining in some detail. At the outset I should point out that cave amblyopsids are the top predators in the aquatic cave food chain, and to a degree that is extreme even for cave populations their food is both diffuse and scarce. It presents a most likely case to look for sensory compensation.

The Amblyopsidae comprise six species in four genera. *Chologaster cornuta* is nocturnal and lives in swamps in the Atlantic coastal plain; *C. agassizi* is found in springs and caves, more commonly in springs; and the remaining four species are limited to caves. Assuming no differences in the rates of regressive evolution among the species, it is possible to rank these four according to the length of time they have been in caves by comparing relative eye and pigment cell degeneration (Poulson and White 1969, Cooper and Kuehne 1974). *Typhlichthys subterraneus* shows the least regressive evolution, followed by *Amblyopsis spelaea, A. rosae,* and *Speoplatyrhinus poulsoni.* There appear to be two main phyletic lines (Woods and Inger 1957): the *Chologaster–Typhlichthys* line and the *Amblyopsis* line. The anatomi-

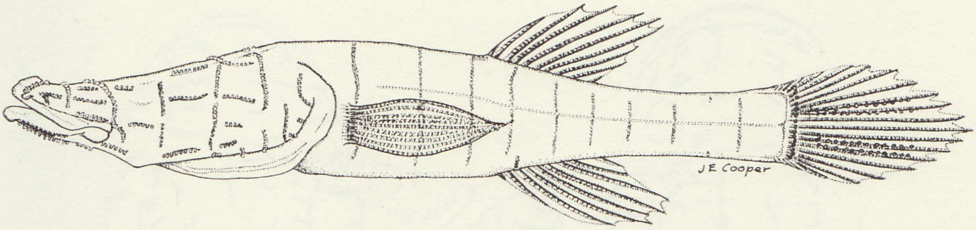


Figure 2–8 The cave fish *Speoplatyrhinus poulsoni*. (Drawing by Dr. John E. Cooper, courtesy North Carolina State Museum of Natural History.)

cal affinities of *Speoplatyrhinus* are obscure, suggesting a third line; this remarkable fish is shown in Figure 2–8.

The most striking sensory hypertrophy is in the lateral line system, shown in Figure 2–9. This hypertrophy appears to increase food-finding ability at low, but not at high, prey densities. When one *Daphnia* was introduced into a 100-liter aquarium, *A. spelaea* found it hours before *C. agassizi* did (Poulson and White 1969). In contrast *C. agassizi* ate all ten *Daphnia* introduced in a 5-liter aquarium before *A. spelaea* had eaten half. The results at high prey densities probably result from a low maximum food intake of *Amblyopsis*. Table 2–5 shows reaction distances of the amblyopsids to various prey. Because of differences in neuromast morphology, *Typhlichthys* is more sensitive to general water movement, and *Amblyopsis* is more sensitive to direction (Poulson 1963).

Brain anatomy also undergoes adaptive changes with increasing time of isolation in caves (Fig. 2–10). The optic lobe decreases in size, but more interesting are the increases in size of the telencephalon, cerebellum, semicircular canals (dynamic equilibrium receptors), otoliths (static equilibrium receptors), eminentia granularis (input path for lateral line and semicircular canal–otolith input), and cristae cerebellum lobe (input path for tactile receptors) (Poulson 1963). The only exception to this trend is the smaller cerebellum size in *Speoplatyrhinus* (Cooper and Kuehne 1974). Obstacle avoidance and spatial memory are increased in the cave-limited species, especially *Amblyopsis*, as a result of these changes.

Since there has been selection for food-finding ability because of a food-scarce environment, one would also expect selection for increased metabolic efficiency in these species, and in fact this is the case. All three cave-limited species have metabolic rates considerably

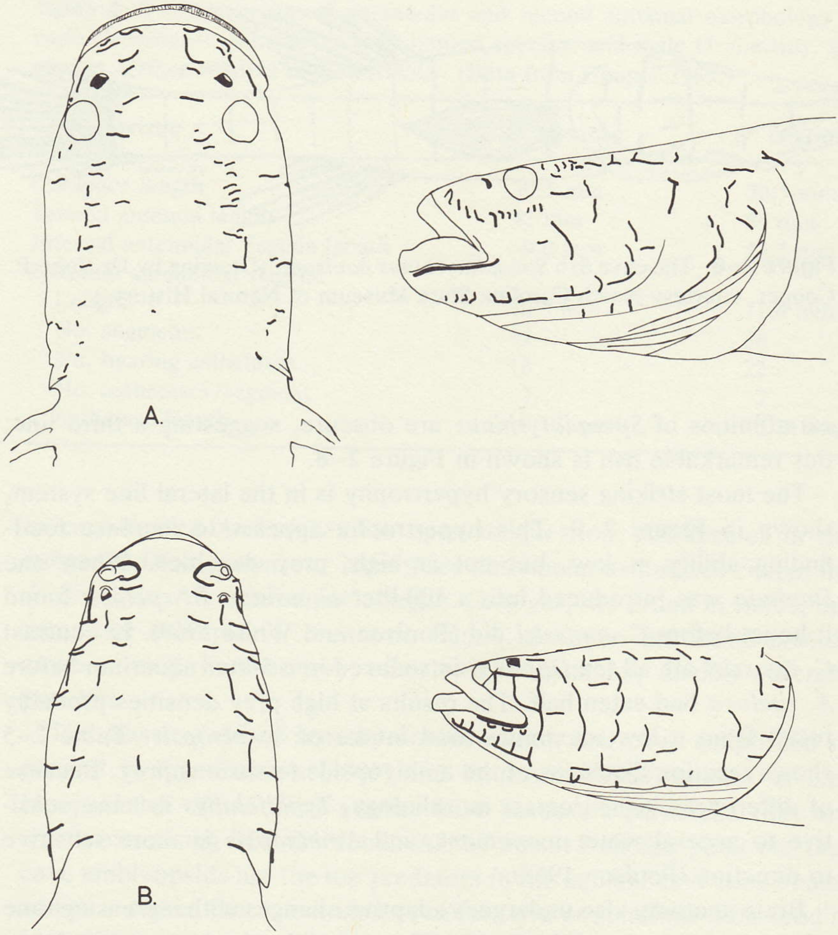
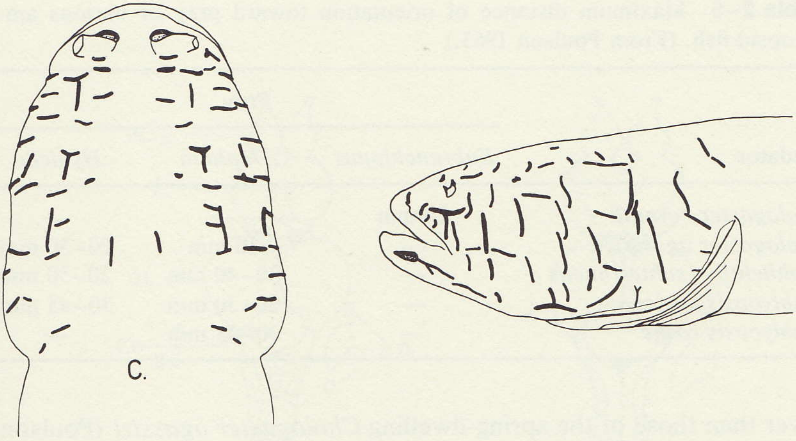


Figure 2–9 Dorsal and lateral views of the head lateral line system of (*A*) *Chologaster agassizi,* (*B*) *Typhlichthys subterraneus,* (*C*) *Amblyopsis spelaea,* (*D*) *A. rosae,* and (*E*) *Speoplatyrhinus poulsoni.* (Modified from Eigenmann 1909, Poulson 1963, and Cooper and Kuehne 1974.)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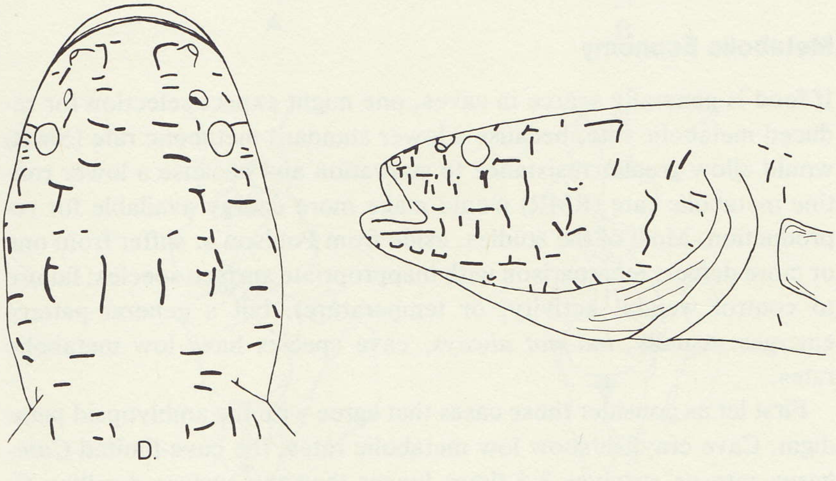
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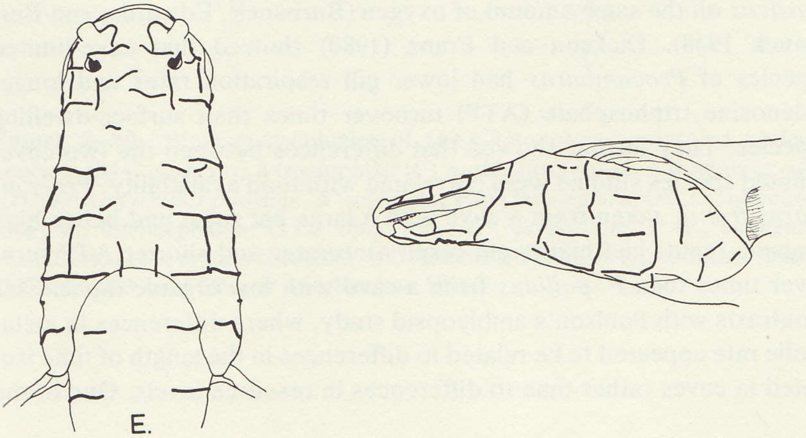
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Table 2–5 Maximum distance of orientation toward prey of various amblyopsid fish. (From Poulson 1963.)

	Prey		
Predator	*Eubranchippus*	*Daphnia*	*Hyalella*
Chologaster cornuta	20 mm	—	—
Chologaster agassizi	—	10 mm	20–30 mm
Typhlichthys subterraneus	—	30–40 mm	20–50 mm
Amblyopsis spelaea	—	20–30 mm	30–45 mm
Amblyopsis rosae	—	30–45 mm	—

lower than those of the spring-dwelling *Chologaster agassizi* (Poulson 1963); see Fig. 2–11.

Metabolic Economy

If food is generally scarce in caves, one might expect selection for reduced metabolic rate, because a lower standard metabolic rate (SMR) would allow greater resistance to starvation and because a lower routine metabolic rate (RMR) would make more energy available for reproduction. Most of the studies, aside from Poulson's, suffer from one or more defects (comparison with inappropriate surface species; failure to control weight, activity, or temperature), but a general pattern emerges: usually, *but not always,* cave species have low metabolic rates.

First let us consider those cases that agree with the amblyopsid paradigm. Cave crayfish show low metabolic rates; the cave-limited *Cambarus setosus* survives 3.5 times longer than the surface-dwelling *C. rusticus* on the same amount of oxygen (Burbanck, Edwards, and Burbanck 1948). Dickson and Franz (1980) showed that cave-limited species of *Procambarus* had lower gill respiration rates and longer adenosine triphosphate (ATP) turnover times than surface-dwelling species. They further showed that differences between the two cave-limited species studied were correlated with food availability. *Procambarus franzi,* taken from a cave with a large bat roost and hence high organic input, had higher gill respiration rates and shorter ATP turnover times than *P. pallidus* from a cave with low organic input. This contrasts with Poulson's amblyopsid study, where differences in metabolic rate appeared to be related to differences in the length of time isolated in caves rather than to differences in resource levels. One of the

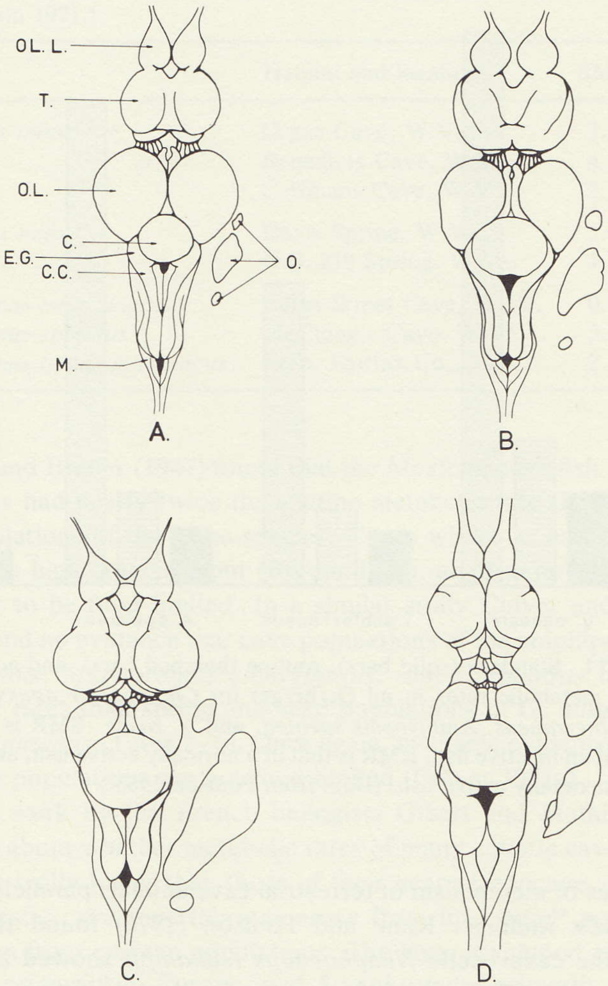

Figure 2–10 Brain morphologies of (*A*) *Chologaster cornuta,* a surface species; (*B*) *C. agassizi,* a troglophile; (*C*) *Amblyopsis rosae,* a troglobite; and (*D*) *Speoplatyrhinus poulsoni,* a troglobite. Parts labeled are: OL.L., olfactory lobe; T., telencephalon; O.L., optic lobe; C., cerebellum; E.G., eminentia granularis; C.C., cristae cerebelli; M., medulla oblongata; O., otoliths. (From Poulson 1963, and Cooper and Kuehne 1974.)

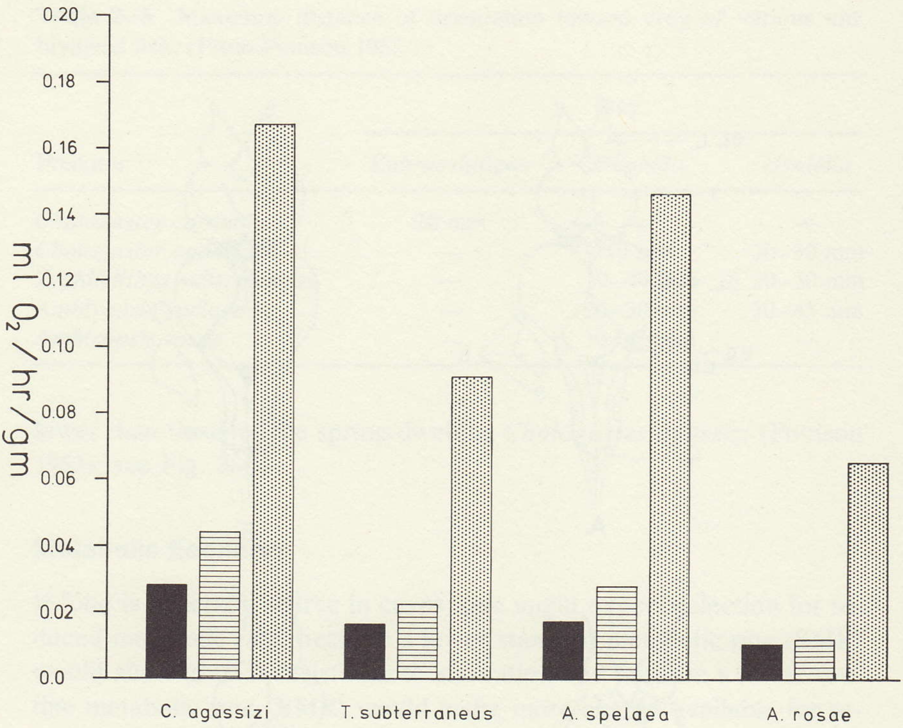

Figure 2–11 Standard (solid bars), routine (hatched bars), and active (stippled bars) metabolic rates in ml O_2/hr/gm for *Chologaster agassizi, Typhlichthys subterraneus, Amblyopsis spelaea,* and *A. rosae.* SMR is the metabolic rate of an inactive fish, RMR is that of a normally active fish, and AMR is that of a maximally active fish. (Data from Poulson 1963.)

few studies of metabolism of terrestrial cave animals parallels Dickson and Franz's findings. Kane and Poulson (1976) found that when starved, the cave beetle *Neaphaenops tellkampfi* showed about half the percentage of daily weight loss on sand and mud substrates than the cave beetle *Pseudanophthalmus menetriesii.* On litter substrates *N. tellkampfi* showed a nonsignificant reduction in weight loss compared to *P. menetriesii.* The most reasonable interpretation of these differences is that *P. menetriesii* is less food limited, its Collembola prey being locally abundant but patchily distributed. Other cave species that show reduced metabolic rates include the isopod *Caecosphaeroma serrata* and the amphipod *Niphargus longicaudatus* (Derouet 1959). Poulson (1964) reviews evidence for some other cases.

Reduction in metabolic rate is not universal in cave organisms.

Table 2–6 Standard Metabolic Rates (SMR, no activity) and Routine Metabolic Rates (RMR, normal activity) for cave and spring amphipods from Virginia and West Virginia. Rates are given in μl O_2/0.01 g/hr. (Data from Culver and Poulson 1971.)

Species	Habitat and locality	SMR	RMR
Gammarus minus	Organ Cave, W.Va.	3.3	3.4
	Benedicts Cave, W.Va.	4.1	4.3
	Coffmans Cave, W.Va.	2.5	2.6
Gammarus minus	Davis Spring, W.Va.	5.0	5.2
	U.S. 219 Spring, W.Va.	1.5	2.1
Stygobromus emarginatus	Court Street Cave, W.Va.	0.8	—
Stygobromus spinatus	McClung's Cave, W.Va.	2.9	—
Stygobromus tenuis potamacus	Seep, Fairfax Co., Va.	2.1	—

Schlagel and Breder (1947) found that the Mexican cave fish *Astyanax mexicanus* had nearly twice the routine metabolic rate (RMR) of surface populations of the same species. Caves where *A. mexicanus* are found have high organic input (Breder 1942), and the populations are not likely to be food limited. In a similar study Culver and Poulson (1971) found no evidence that cave populations of the amphipods *Gammarus minus, Stygobromus emarginatus,* and *S. spinatus* had lower metabolic rates than spring and seep populations of *G. minus* and *S. tenuis potamacus* (Table 2–6). Once again, available evidence suggests that these populations are not food limited (Culver 1971a).

Recent work by the French biologists Gibert and Mathieu raises questions about whether metabolic rates of many aquatic cave invertebrates are really lower than those of their nearest noncave ancestors. Some aquatic cave invertebrates arose from interstitial[1] populations rather than from epigean populations. The large amphipod genera *Niphargus,* primarily in Europe, and *Stygobromus,* primarily in North America, occur mostly in noncave habitats, with cave species apparently derived from these (Holsinger 1978). A similar situation may obtain with isopods (Magniez 1976) and flatworms. Gibert and Mathieu (1980) found that starved cave *Niphargus virei* depleted lipid and carbohydrate reserves more rapidly than interstitial populations of *N. rhenorhodanensis,* which suggests that *N. virei* has a higher metabolic

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[1] The term "interstitial" and its many partial synonyms are used in several ways. Here the term means any nonkarstic, noncave subsurface habitat, for example, riverine gravels. See chapter 7 for more details.

rate. Mathieu (1980) also found that cave populations of *N. rhenorhodanensis* were more active than interstitial populations, which also suggests a higher routine metabolic rate for cave populations. The most reasonable explanation for these data are that many interstitial habitats are even more food poor than cave habitats. Since the metabolic rate of *N. virei,* a cave species, is lower than that of any other amphipod reported in Wolvekamp and Waterman's (1960) review, it is likely that for *Niphargus,* both cave and interstitial environments are usually food poor.

Adaptation to High Moisture

Terrestrial cave species must adapt to a water-saturated atmosphere. Howarth (1980) reviews the evidence that there is an upper limit to humidity tolerance for surface-dwelling terrestrial arthropods and suggests that cave-limited species have evolved effective water excretory mechanisms that conserve salts and that this involves cuticular reduction, resulting in increased cuticular permeability. If cuticular permeability is increased as a result of adaptation to saturation or near-saturation—and there is no direct evidence on this point,—then in less humid conditions these species will lose water rapidly. This may explain the extreme moisture sensitivity of terrestrial troglobites (see Howarth 1980). Alternatively, cuticle reduction may be the result of selection for metabolic economy, since cuticle formation and maintenance incur a significant metabolic cost (T. L. Poulson, personal communication). Or cuticle reduction may be the result of relaxed selection. In any case, one would expect the evolution of mechanisms to insure that terrestrial cave organisms remain in areas of high humidity and low saturation deficit.

One clear case of evolution of humidity-detecting sensory structures is the highly developed internal antennal vesicles found in cave beetles in the family Catopidae (Peck 1977, Accordi and Sbordoni 1978). Peck found that compared to those of epigean species, the sensory hairs on the surface of antennal segments were longer in cave species of *Ptomaphagus* and that there was an increase in structural complexity of the internal antennal vesicle in the seventh antennal segment (Fig. 2–12). European cave catopids also show a structural elaboration of the internal antennal vesicles, although they are structurally quite different from those of North American species. From the experiments of Lucarelli and Sbordoni (1978), it is clear that a major function of these organs is humidity detection.

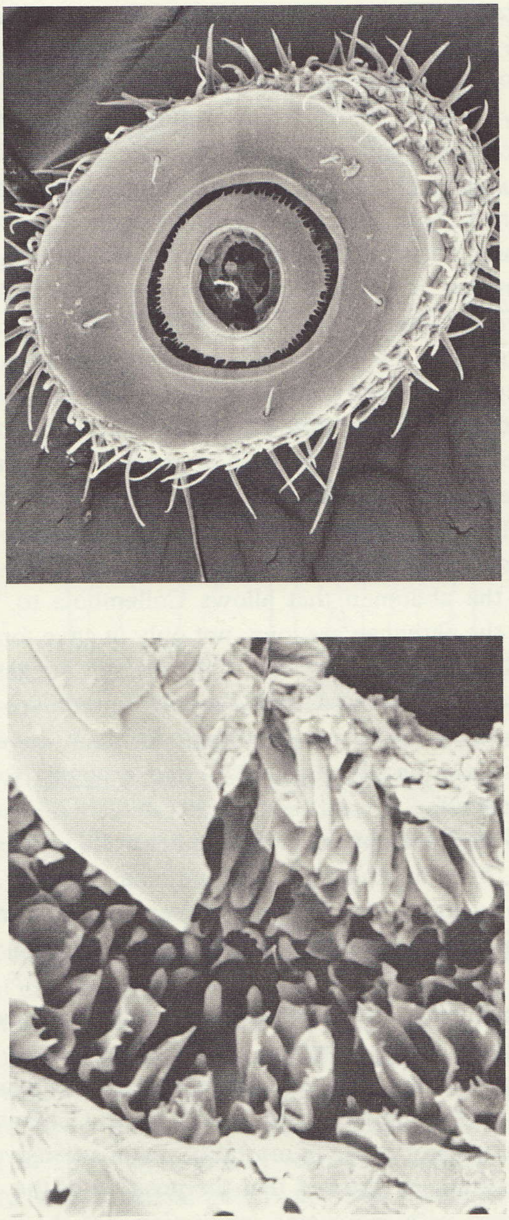

Figure 2–12 Scanning electron micrographs of internal antennal vesicle of *Ptomaphagus hirtus*. *Top,* antennal joint socket is in the middle, surrounded by ringlike slit opening (periarticular gutter) into sensory vesicles. *Bottom,* sensory pegs line the sensory vesicle. (Photos courtesy of Dr. Stewart B. Peck, Department of Biology, Carleton University, Ottawa.)

The importance of adaptation to high moisture, especially standing water, can be seen in cave Collembola in the genera *Sinella* and *Pseudosinella,* whose morphologies are probably the most thoroughly studied of any cave organisms. Christiansen (1961) compared Japanese and Nearctic *Sinella* and European and Nearctic *Pseudosinella,* and divided morphological characters into two groups—those that were cave independent and those that were cave dependent. Cave-independent characters, such as head chaetotaxy and labial papillae, showed no consistent changes between troglophilic (facultative) and troglobitic (obligate) cave species, but were useful in determining taxonomic and phyletic position. On the other hand, cave-dependent characters, such as antennal length, showed consistent differences between troglophilic and troglobitic species. The cave-dependent characters of highly modified troglobites are similar regardless of genus or geographic location. Cave-dependent characters that are both well studied and widespread are shown in Fig. 2–13; a larger list is given in Christiansen and Culver (1968). The mucro is at the end of the furcula, a tail-like structure folded under the abdomen that allows Collembola to "jump." This structure and the antennae are long, not only in cave forms but also in species that live on free surfaces. Christiansen suggests that these changes increase the animal's ability to detect predators and to escape quickly. Collembola are major prey items for many cave beetles (McKinney 1975, Kane and Poulson 1976) and probably for spiders and harvestmen as well.

Both highly modified cave species and deep soil species, such as the Onychiuridae, have an enlarged third antennal segment organ. Christiansen (1961) suggests that this organ is sensitive to humidity or temperature and notes that highly modified cave forms are very sensitive to both.

The tenet hair, empodial appendage, and unguis are part of the claw complex. Changes in this complex are clearly related to the ability of Collembola to walk on wet, smooth surfaces, wet clay, and water (Christiansen 1965). In many caves, pools act as Collembola traps and are likely to be a major cause of mortality. In an extensive series of observations Christiansen showed that the position of the claw on these surfaces changes with increasing adaptation. Of the animals with a stage 3 (highly cave-adapted) claw complex (see Fig. 2–13), 90 percent were able to move over a water surface, compared with only 4 percent of those in stage 1 (unmodified). Figure 2–14 shows the claw positions of non-cave-modified and cave-modified forms on wet clay. Similar differences between species in claw position on wet smooth surfaces and on water indicate the adaptive nature of the morphological changes.

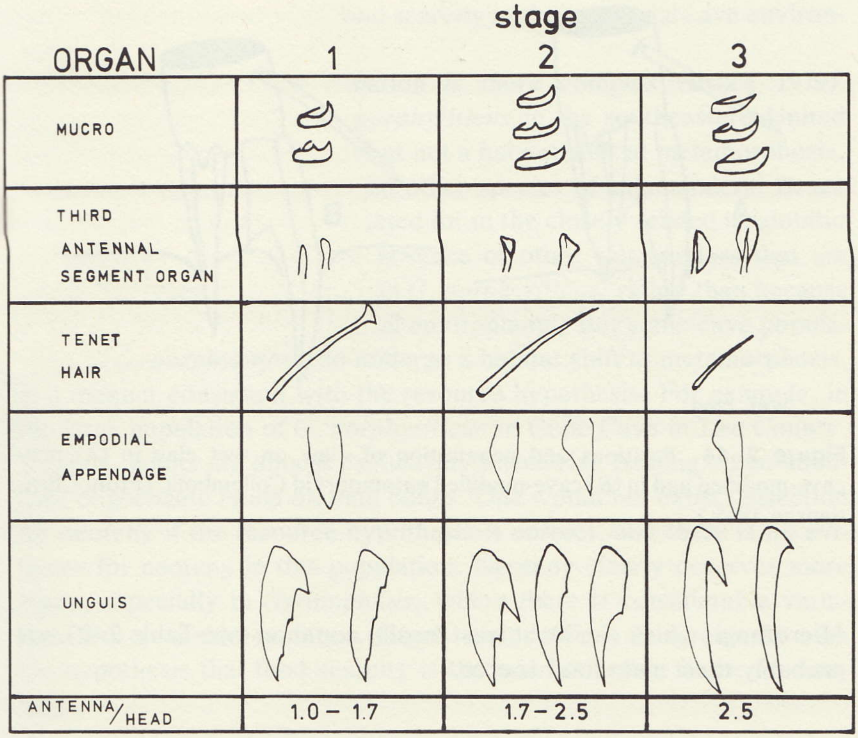

Figure 2–13 Modifications of Collembola morphology with increasing cave adaptation. Stage 1 represents species unmodified to cave life, stage 2 is intermediate, and stage 3 represents highly modified cave forms. (From Christiansen 1961.)

Finally, Christiansen (1961) provides some indirect evidence that the morphological changes increase fitness. Stage 1 species (with unmodified claw complexes) were found in less than ten caves, most within a range of less than 1,600 km^2, although their range in epigean habitats was much greater. Stage 2 species (intermediate modification) were found in more caves and over a greater area. However, they were either limited to caves or found in restricted epigean habitats, both cases reducing their dispersal potential. Stage 3 species (highly modified claw complexes) showed a broad variation in geographic range but were found in as many caves as stage 2 species. Speciation, local adaptation, and restricted movement account for differences in distribution of stage 2 and stage 3 species. But both are more successful in caves, at least as judged by geographic distribution, than stage 1 species.

Although cave Collembola may be modified to cope with food-poor environments, Christiansen (1965) found no evidence to support this.

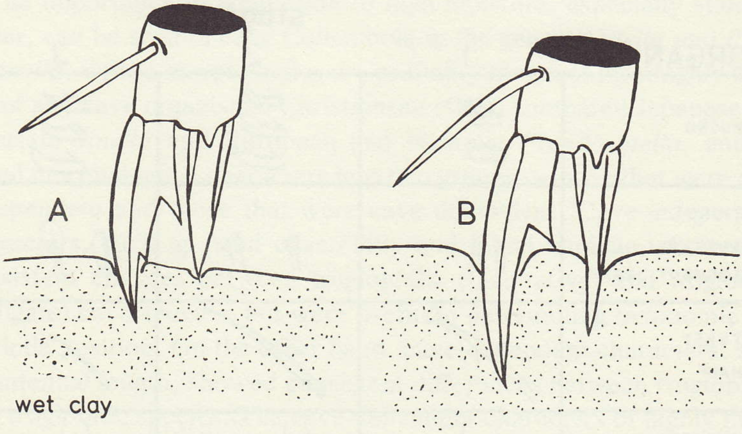

Figure 2–14 Positions and penetration of claw on wet clay in (*A*) non-cave-modified and in (*B*) cave-modified entomobryid Collembola. (From Christiansen 1965.)

Microfungi, which can be at least locally common (see Table 2–2), are probably their main food source.

Neoteny

Paedomorphosis, the retention of juvenile characters in the adult, has been reported for a variety of cave organisms. For example, *Speoplatyrhinus poulsoni,* the most cave-modified amblyopsid fish, shares some characters, such as body size and head size, with immature *Typhlichthys subterraneus*. The best-studied cases are the cave-dwelling plethodontid salamanders. Although there is no direct evidence, it is generally agreed that cave plethodontids are neotenic (retarded somatic development) rather than paedogenic (accelerated sexual development) (Gould 1977, Bruce 1979). Of the nine species of cave-limited salamanders, all but *Typhlotriton spelaeus* and *Gyrinophilus subterraneus* are neotenic and retain larval gills throughout their life (Brandon 1971, Besharse and Holsinger 1977). Of the other seven, only *G. palleucus* can be readily transformed by thyroxin treatments (Brandon 1971). The question that needs to be considered here is whether neoteny is an adaptation to low food supply. Wilbur and Collins (1973) suggest that it evolves in response to an unstable or harsh terrestrial environment compared to the aquatic environment. It is more likely that neoteny in cave salamanders, except for *Gyrino-*

philus, happens because of food scarcity in the terrestrial cave environment.

For *Gyrinophilus* the situation is more complex (Bruce 1979). Epigean stream-dwelling *G. porphyriticus* in the southeastern United States undergo a dietary shift but not a habitat shift at metamorphosis, becoming a specialist feeder on other species of salamanders. Bruce suggests that neoteny was selected for in the closely related troglobitic *G. palleucus* because of the absence of other salamanders that are major diet items of adult epigean *G. porphyriticus,* rather than because of food scarcity in the terrestrial environment. But some cave populations of *G. porphyriticus* do undergo a habitat shift at metamorphosis, in a manner consistent with the resource hypothesis. For example, in the large population of *G. porphyriticus* in Cope Cave in Lee County, Virginia, adults are almost exclusively terrestrial, feeding on an abundant oligochaete fauna on mud banks. One would not expect selection for neoteny if the resource hypothesis is correct, and there is no evidence for neoteny in this population. Neoteny clearly deserves more study, especially in *Gyrinophilus,* where there is considerable variation. But available evidence, largely anecdotal, is in agreement with the hypothesis that food scarcity is the main selective factor for neoteny.

Conclusions

Although the evidence is incomplete, several conclusions can be reached. First, many cave populations are adapted to scarce food supplies. Poulson's work on the Amblyopsidae is the most thorough and unassailable. Other groups, for example, crayfish (Cooper 1969), show adaptations to scarce resources in morphology and food-finding behavior. The high feeding efficiency of cave beetles that eat cricket eggs (Mitchell 1968, Kane and Poulson 1976) is most easily explained by strong selection for food-finding ability. The frequent finding that cave organisms are resistant to starvation also suggests that food scarcity is a dominant selective force.

But the second conclusion is that food scarcity is not a universally dominant selective force. Christiansen's elegant studies of entomobryid Collembola, which are at least numerically dominant in many terrestrial caves, strongly indicate that moisture and humidity, rather than food, have been the dominant selective factors. Other groups, such as *Stygobromus* amphipods, show little evidence of adaptation to low food supplies. Kane and Poulson's (1976) and Dickson and Franz's

(1980) demonstrations that metabolic rate and its correlates are related to levels of food supply indicate that there are at least differences in the intensity of selection for reduced metabolic rate among obligate cave species.

It is also likely that many troglophiles are not "troglobites in training." Many troglophiles have no known surface populations and are classified as troglophiles only because they show little sign of regressive evolution. Other troglophiles have no surface populations near cave populations. For example, *Gyrinophilus porphyriticus* is common in caves in the upper Powell Valley in Virginia and Tennessee, but no surface populations are known from this area. It is very rare to find a population of any cave organism that extends from the surface directly into a cave. In most cases it is unlikely that gene flow is retarding adaptation. It is likely that what are called troglophiles have been in caves for a shorter period of time than what we call troglobites, if only because troglophiles show less regressive evolution (but see chapter 4). Nonetheless, by any measure available, many troglophiles are very successful in caves. Many such as helomyzid and sciarid flies, are found in a large percentage of caves in a given area, and with large populations. More work is needed on these seemingly "uninteresting" species.

Finally, there is considerable evidence that many cave populations are not at an evolutionary equilibrium. If equilibria were widespread, then there would be no reason to expect differences in metabolic rate among amblyopsids based on their length of time of isolation in caves. There would be no reason to expect a fraction of a population of the crayfish *Orconectes pellucidus* to retain circadian rhythms (Jegla and Poulson 1968) or to expect that larvae of *Gyrinophilus porphyriticus* in caves would still occasionally show lunging behavior during feeding, even though it greatly reduces feeding efficiency (Culver 1975). The lack of equilibrium in turn implies either that selection has been weak or that selectable variation in these traits is scarce. It is impossible to know which is more important, but we do know that in many cases selection has had a long time to act; most terrestrial species in north temperate zones probably invaded caves during interglacials in the Pleistocene (Barr 1968), and aquatic species may be much older (Holsinger 1978).