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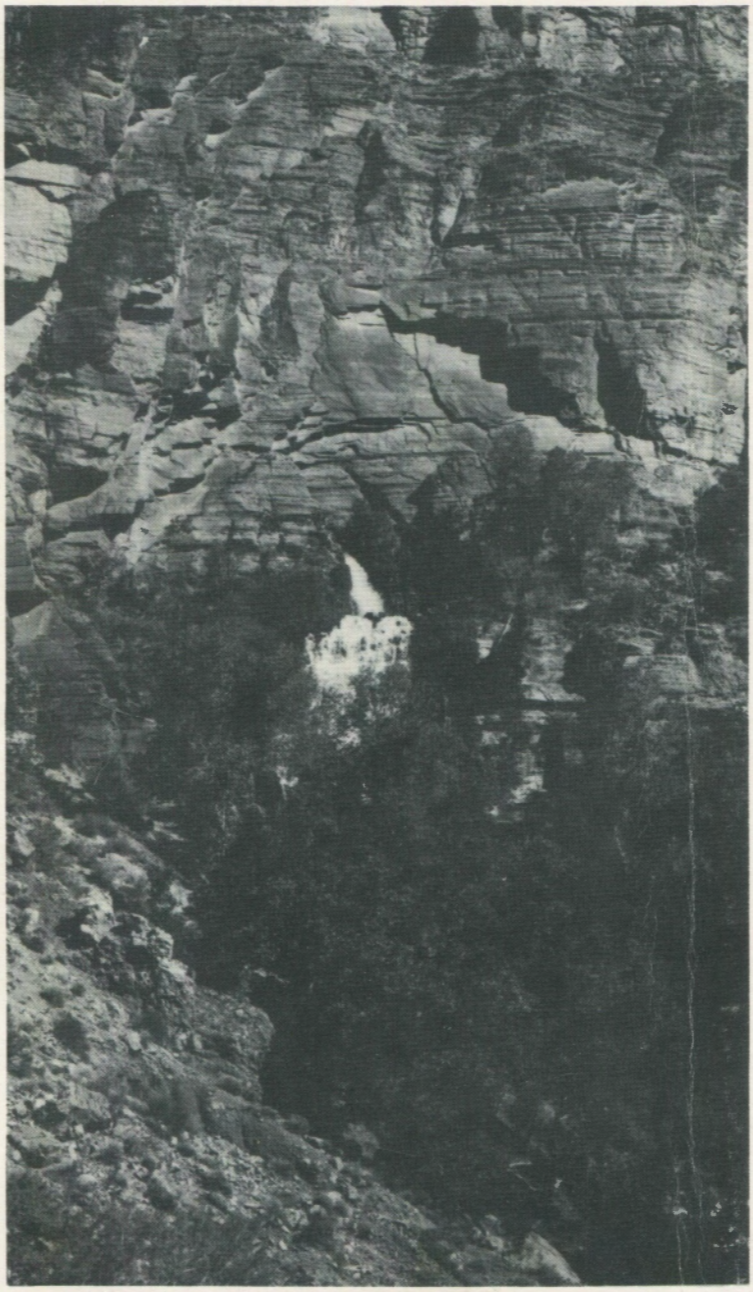

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CONTENTS

COVER PHOTO — Spring at Thunder Cave, Arizona, one of several subterranean tributaries to the Colorado River in the Grand Canyon. Photo by Stewart Peck (see p.57).

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ALPHA RADIATION LEVELS IN TWO CAVES RELATED TO EXTERNAL AIR TEMPERATURE AND ATMOSPHERIC PRESSURE

SUMMARY

Radon and radon daughter concentrations in Carlsbad Cavern are directly related to daily external air temperature minima and, to a much smaller extent, atmospheric pressure. Conversely, more than 50% of the fluctuation in radon-induced alpha radiation at New Cave is associated with changes in atmospheric pressure, while outdoor air temperatures have no significant effect.

The different effects of temperature and pressure on alpha radiation levels in the two caves are related to differences in the size and configuration of each cave.

Gary M. Ahlstrand

National Park Service Cooperative Studies Unit
Department of Range and Wildlife Management
P.O. Box 4169
Texas Tech University
Lubbock, Texas 79409

ALPHA RADIATION levels in cave air attributable to radon and its shortlived daughter isotopes are determined by radon emanation from cave surfaces and the exchange rates of cave air with external air. Emanation is controlled by the concentration of radium in the parent material in the cave, physical structure of the parent material, and atmospheric pressure (Clements and Wilkening 1974; Wilkening, *et al.* 1974). Exchange rates between cave air and outside air are dependent upon cave configuration (Yarborough, *et al.* 1979) and temperature-induced differences between the densities of cave and outside air (Ahlstrand and Fry 1979; Yarborough, *et al.* 1979). Wilkening (1979) proposed a model for predicting radon levels in Carlsbad Cavern from seasonal temperature minima that gave results in close agreement with levels subsequently measured in the cave during a yearlong study (Ahlstrand and Fry 1978).

The objective of this study was to examine the effects of external air temperature and atmospheric pressure on levels of short-lived radon daughter isotopes present in Carlsbad Cavern and New Cave. In addition, the relationship between external air temperature and the radon concentration in Carlsbad Cavern was examined. Both caves are located on the northeastern slope of the Guadalupe Mountains in Carlsbad Caverns National Park, New Mexico. Data were obtained over a two-year period that began in September, 1975.

METHODS

Alpha radiation in regularly visited portions of Carlsbad Cavern and New Cave was sampled periodically to determine the concentration of short-lived radon daughter isotopes present in the air. The sampling frequency at Carlsbad Cavern averaged more than three times per week, and New Cave was sampled at approximately weekly intervals. Consecutive 5 min walking samples were taken along established routes in each cave. Samples were obtained by drawing a known volume of air through a fiberglass filter. Radon daughter levels were determined by measuring the alpha activity of daughter isotopes trapped on the filter with an alpha scintillation counter. Short-lived radon 222 decay products were sampled according to procedures described by Budnitz (1974), and daughters of radon 220 (thoron) were determined by methods given by Rock (1975).

Atmospheric concentrations of radon daughter isotopes are reported in working levels (WL). A WL is any combination of radon daughters in one liter of air that will ultimately release 1.3×10^5 MeV of alpha energy during decay to lead 210. It is also often described as the latent energy inherent in one liter of air containing 100 pCi each of polonium 218, lead 214, bismuth 214 and polonium 214.

Radon concentrations were recorded hourly at a centrally located sampling station in Carlsbad Cavern, using a monitoring system designed by and on loan from personnel at the Denver Mining and Research Center, U.S. Bureau of Mines. The main components of the system consisted of a controlled airflow system, a scintillation detector, and a data acquisition system. Air was drawn continuously at a constant velocity through a filter and the detector. Alpha pulses produced in the detector were amplified, counted, and recorded hourly.

Daily temperature minima were obtained from a maximum-minimum thermometer housed in a weather instrument shelter located approximately 150 m from the natural entrance to Carlsbad Cavern. A continuous record of atmospheric pressure was available from a barograph located with the radon monitoring system.

RESULTS AND DISCUSSION

Radon and radon daughter isotope concentrations for Carlsbad Cavern during warm and cool seasons and for transition periods are summarized in Table 1. Carlsbad is a "right-side-up" cave (Yarborough, *et al.* 1979) because all of its more than 33 km of passages lie below the level of the known entrances. The major portion of the cave lies more than 200 m below surface openings, and some parts extend more than 300 m beneath the entrances. Outdoor daily minimum temperatures from November through March are usually less than cave temperatures; thus, external air mixed readily with the less dense cave air, thereby reducing alpha radiation levels in the cave. Radon and its daughter isotope concentrations were higher from May through September because relatively stable air conditions prevailed in the cave during this period, since outdoor air temperatures seldom fell below temperatures in the cave. Relatively stable air conditions prevailed in the cave during this period. Transition periods in April and October were typified by intermediate radiation level means with standard deviations approximately twice as great as those for the warm and cool seasons (Table 1).

A distinct positive relationship was shown between outdoor minimum daily temperatures and radon concentrations (r=.93; Fig. 1) and between outdoor minimum daily temperatures and radon daughters (r=.93; Fig. 2). The relationship was nearly linear during the cool season, when external temperatures were below those in the cave. Radiation levels increased rapidly during the warm season, as cave air stability increased with rising outdoor temperatures.

Although most of the differences detected in alpha radiation in Carlsbad Cavern were seasonal, temperature - related ones, some of the fluctuations were associated with daily changes in atmospheric pressure (Fig. 3). Emanation of radon from cave surfaces is reduced as atmospheric pressure increases (Wilkening 1979), but this effect was not nearly as pronounced in Carlsbad Cavern as was that related to external temperature changes.

New Cave has 3.2 km of passages; the maximum vertical relief below the main entrance is 76 m. Nearly all of the cave lies below the entrances. All portions of the cave are less than 1 km from an opening to the outside, and the volume of New Cave is proportionally smaller in comparison to that of Carlsbad Cavern. New Cave is an "upside-down-cave", in the terminology of Yarborough, *et al.* (1979). The exchange of air in this cave with external air should occur at a nearly constant rate throughout the year. Relatively stable levels of radon daughter isotopes detected in New Cave during the study support this view. These isotopes averaged 0.23 ± 0.05 WL for the first year of the study and 0.22 ± 0.04 WL during the second year. More than half of the variation in radon daughter levels at New Cave were associated with changes in atmospheric

Table 1. Periodic variation of the mean radon concentrations (pCi/1) and short-lived radon daughter isotope levels (WL) in Carlsbad Cavern.

Period	Radon	Radon Daughters
Warm season: May-September	63.5 ± 5.1	0.32 ± 0.05
Cool season: November-March	20.1 ± 5.2	0.12 ± 0.03
Transition: April	40.6 ± 10.7	0.26 ± 0.09
October	35.3 ± 11.0	0.22 ± 0.08

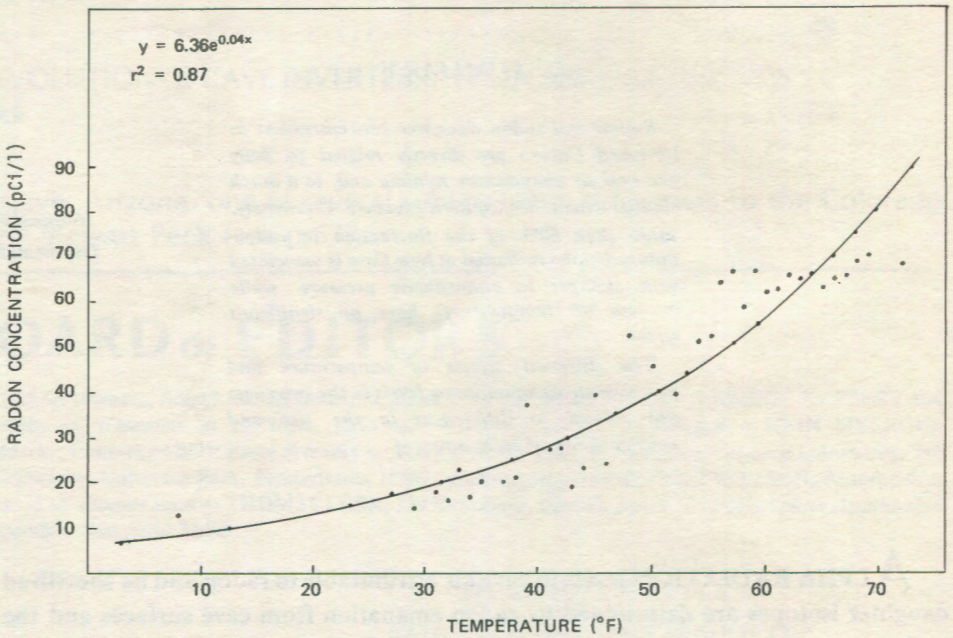
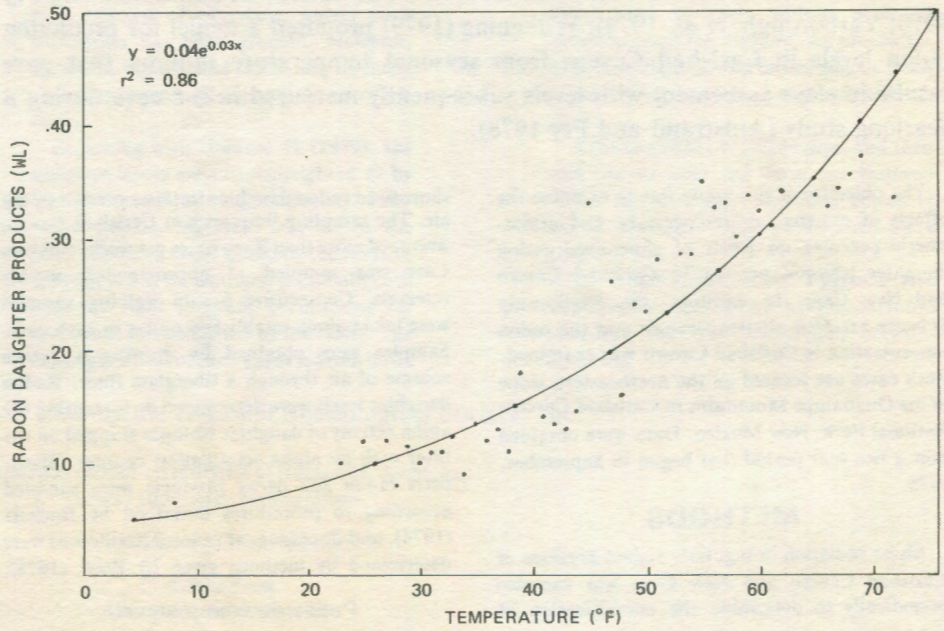


Figure 1. (above) Relationship between outdoor air temperature and mean radon concentration in Carlsbad Cavern.

Figure 2. (below) Relationship between outdoor air temperature and mean radon daughter product concentration in Carlsbad Cavern.



pressure (r=.74; Fig. 4). This inverse relationship is apparently due to the influence of atmospheric pressure on radon emanation from the cave walls rather than to temperature-induced changes in the rate of exchange between cave and outdoor air.

CONCLUSIONS

The exchange rate of cave air with outdoor air, as determined by temperature-induced differences in air densities, was the dominant factor related to alpha radiation levels in Carlsbad Cavern. The levels were low during the cool season, due to the mixing of outdoor air with cave air by gravitational flow. During the warm season, little flow of this type occurred, because the cave air was denser than the warmer external air. This led to greater air stability in the cave and resulted in higher alpha radiation levels. Atmospheric pressure changes accounted for part of the differences detected in alpha radiation levels in Carlsbad Cavern, but these differences were seldom of the magnitude associated with outdoor air temperature minima.

The greatest single factor related to alpha radiation levels in New Cave was atmospheric pressure and its effect on radon emanation in the cave. Due to the configuration of this cave, gravitational flow was of little consequence in determining air exchange rates; thus, little seasonal difference was noted in alpha radiation levels at New Cave.

ACKNOWLEDGMENTS

I am indebted to Dr. Marvin H. Wilkening and Dr. Ernest B. Fish for helpful criticism of the manuscript. Special thanks to Patricia L. Fry for her generous assistance in sampling alpha radiation levels.

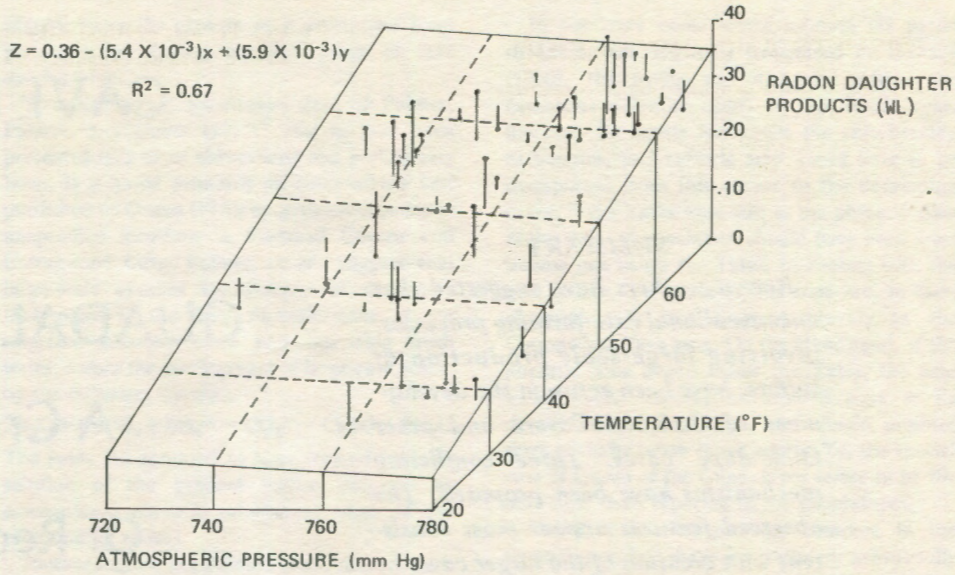
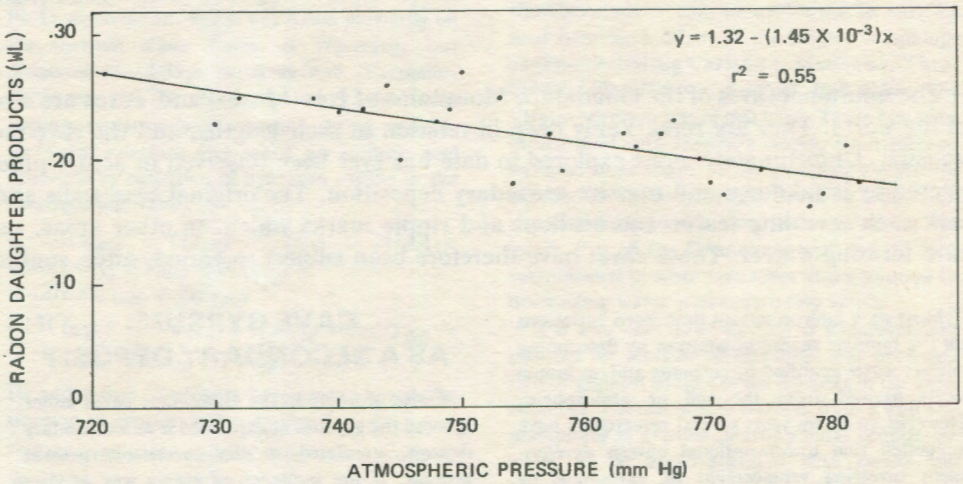


Figure 3. (above) Relationship of atmospheric pressure and outdoor air temperature to radon daughter concentration in Carlsbad Cavern.

Figure 4. (below) Relationship between atmospheric pressure and mean radon daughter product concentration in New Cave.



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CAVE DEVELOPMENT IN THE GUADALUPE MOUNTAINS

A Critical Review Of Recent Hypotheses

SUMMARY

Recent workers have suggested that unconventional cave-forming processes, involving large-scale production of sulfate, have been active in the development of Carlsbad Cavern and other Guadalupe caves. Three conflicting mechanisms have been proposed. The observed features appear most consistent with creation of the larger caves by ascending water charged with sulfuric acid, produced by oxidation of hydrogen sulfide.

Donald G. Davis*

Route 1, Box 93-A, Parachute, Colorado 81635

The solutional caves of the Guadalupe Mountains of New Mexico and Texas are among the most interesting, yet most cryptic in the world. They are remarkably deep in relation to their lengths, and the cave morphology and deposits are in many ways unusual. Unfortunately, none explored to date has ever been observed in actual process of enlargement, and most are heavily altered by breakdown and massive secondary deposition. The original cave walls and sediments, even where visible, generally lack such revealing features as scallops and ripple marks which, in other areas, serve as clues to the nature and source of cave-forming waters. These caves have therefore been subject to varied, often conflicting interpretations.

Most such interpretations have been variations on the familiar theme of solution by descending surface water acidified by carbonic and/or humic acids derived from the soil or atmosphere. However, in recent years several researchers have suggested that unconventional cavern development involving replacement of carbonate by sulfate, or solution of carbonate by a mechanism involving sulfate precipitation, has been important in the origin of Guadalupe caves. Their ideas are based primarily on the presence of remnants of massive gypsum deposits in the larger caves. These deposits, some of which are more than ten feet thick, are evidently indicative of some regionally widespread mechanism, because similar gypsum remnants have been observed in at least Carlsbad Cavern, Spider Cave, New Cave, the McKittrick Hill caves, Pink Panther, Black, Hell Below, Cottonwood, and Virgin caves. These are up to 30 mi distant, in all parts of the Guadalupe Mountains, and range in elevation from about 3650 ft (Big Room, Carlsbad Cavern) to 6800 ft (Cottonwood Cave and Virgin Cave).

CAVE GYPSUM AS A SECONDARY DEPOSIT

Earlier workers in the Guadalupe caves either ignored the gypsum or explained it as a secondary deposit, unrelated to the cavern-enlargement process. If the sequence of events was as they described it, any other interpretation would face serious problems. Bretz (1949, p. 454) stated that the massive gypsum in Carlsbad Cavern is "younger than some carbonate flowstone." Good (1957, p. 21) repeated this, describing "thin friable layers that are thought to represent buried flowstone floors" interbedded in clay and sand deposits underlying massive gypsum. Bretz also considered some of the stalagmites in New Cave to show signs of re-solution. They accordingly believed that the caves had been deeply re-flooded after initial drainage and that the gypsum was deposited during this re-flooding episode. The flooding was attributed to a rise in the regional water table caused by temporary filling of the Pecos Valley with more than 1300 ft of Ogallala gravel in late Pliocene time. Good speculated that saline surface lakes then formed in the area, and that water from these lakes, as it invaded the caves, cooled and caused gypsum to precipitate.

Smith (1978) has criticized this idea on the grounds that "it is unlikely that gypsum was precipitated from cooling waters because the saturation point of gypsum in water increases with falling temperatures." This, however, is true only for temperatures above about 40°C (Hardie, 1967) and would thus be relevant only if the Guadalupe caves were formed by thermal waters, a claim which no one has made.

Nevertheless, other aspects of the Bretz/Good concepts are questionable. I have been unable to recognize evidence for large-scale re-flooding following drainage of any Guadalupe cave. The reported re-solution of speleothems is not useful evidence, since effects of re-solution in Guadalupe caves have not been adequately distinguished from those of dehydration, evaporite-crystal wedging, or other processes, such as bell-canopy formation (Hill, 1978), which may mimic re-

*Statements in this review, where not attributed to other sources, are based on my own observations in Guadalupe caves from 1960 through 1979, including work as a guide in Carlsbad Cavern in 1971-72 and trips with the Guadalupe Cave Survey/Cave Research Foundation.

solution effects. The lower levels of some caves, including Madonna, Three Fingers, Cottonwood and Virgin, do contain mud layers and shelfstone indicating local re-flooding, but these episodes are never associated with gypsum deposits. The massive gypsum, in my experience, is always in direct contact with either bedrock (as is conspicuous near the Lower Cave overlook in Carlsbad Cavern) or deposits of sediment which could be either residual or carried in by phreatic water. The leached "flowstone" of Bretz and Good could also, on the basis of descriptions, be interpreted as a subaqueous calcite encrustation.

Furthermore, the cause invoked by Bretz for the alleged gypsum-depositing re-flooding (Ogallala filling of the Pecos Valley) has been called into question by Bachman (1974, 1976), who states that the Pecos Valley south from Roswell, as a through-flowing regional drainage, is of post-Pliocene origin and that his work "does not support an interpretation of thick Ogallala fill southwest of The Divide. In fact, the Ogallala Formation may not have been deposited in the Pecos depression southward from Carlsbad." (Bachman, 1974, p. 19.) The gravel remnants and sandstone-filled fissures "sand dikes") on the Guadalupe ridge, regarded as Ogallala by Bretz, have been variously interpretated as Cretaceous (Hayes, 1964) or as partly Permian and partly Pliocene (Jagnow, 1978). Moreover, for reasons I will consider later in this review, it is by no means certain that the major Guadalupe caves were created as early as Ogallala time. Thus, there appears to be no sound evidence that these caves have actually experienced two major phreatic episodes separated by a period of drainage.

The character of the Guadalupe cave gypsum also suggests that the gypsum was deposited *before* the caves had begun to grow secondary speleothems. The gypsum is never mingled visibly with calcite, as might be expected in a secondary deposit; where overlain by later calcite (as near the Rock of Ages in the Big Room of Carlsbad Cavern), the gypsum/calcite contact is sharp and non-transitional. The gypsum-deposition chemistry invariably appears incompatible with simultaneous deposition of carbonate. This supports the likelihood that the gypsum arose as an integral aspect of cavern development by one or more of the sulfate-creating mechanisms.

GYPSUM AS A CAVE-DEVELOPMENT RESIDUE

Three different proposals involving sulfate as a direct product of the cave-development process have been put forth. The theory most widely published is that of Jagnow (1977, 1978). Inspired by the work of Howard (1960) and Morehouse (1968) in Iowa, he proposed solution by sulfuric acid derived from oxidation of pyrite in the Yates formation overlying the cave-bearing carbonate rocks. The chemistry is summarized as follows:

$$4FeS_2 + 15O_2 + (8 + n)H_2O + 16CaCO_3 \rightarrow 2Fe_2O_3 \cdot nH_2O + 8Ca^{++} + 8CaSo_4 + 16HCO_3^-$$

Jagnow views the gypsum as a precipitate from ponded water during the final stage of cave development.

A more radical hypothesis, that of Palmer, Palmer, and Queen (1977)*, has to date been presented only in an abbreviated and preliminary form. It is based primarily on observations first published by Queen (1973) on gypsum deposits at unspecified locations in Carlsbad Cavern and Cottonwood Cave. Palmer, *et al.*, suggest that large-scale gypsum replacement of carbonate took place in the deep phreatic zone at the interface between brine and intruding fresh water, *before* the development of large cave voids, by the following reaction:

$$2H_2O + CaCO_3 + SO_4^{--} \rightarrow CO_3^{--} + CaSO_4 \cdot 2H_2O$$

The voids are assumed to have formed by later solution of the gypsum bodies followed by conventional phreatic solution of some of the surrounding rock.

Neither Jagnow nor Palmer, *et al.*, discuss work by Stephen Egemeier, who was the first to suggest that gypsum in Guadalupe caves might be intimately involved in the cave-development process. He brought forth the possibility in 1971 in an unpublished paper sent to Carlsbad Caverns National Park and developed it further in his Ph.D. dissertation, which was based primarily on the thermal Kane Caves of Wyoming, but discussed Guadalupe caves as well (Egemeier, 1973, pp. 69-72). He proposed a three-step gypsum-replacement mechanism acting near the air/water interface and based on sulfuric acid produced by oxidation of hydrogen sulfide in the cave-forming water:

$$(1)\ 2H_2S_{(aq)} + O_{2(aq)} \rightarrow 2S_{(s)} + 2H_2O_{(1)}$$

$$(2)\ 2H_2O_{(1)} + 2S_{(s)} + 3O_{2(aq)} \rightarrow 2HSO_4^-{}_{(aq)} + 2H^+{}_{(aq)}$$

$$(3)\ H^+{}_{(aq)} + HSO_4^-{}_{(aq)} + H_2O_{(1)} + CaCO_{3(s)} \rightarrow CaSO_4 \cdot 2H_2O_{(s)} + CO_{2(g)}$$

He added that "Dolomite is converted by similar reaction to gypsum and epsomite."

Let us consider each of these three proposals in detail.

SULFURIC-ACID SOLUTION VIA PYRITE OXIDATION

Jagnow's suggestion of solution by sulfuric acid descending from oxidizing pyrite in the Yates sandstone caprock at first seems a clear, simple model for a cave-development process having gypsum as a by-product. Jagnow's type specimen cave formed by this mechanism is Queen of the Guadalupes Cave, a 200-ft pit series which underlies a gossan mass of oxidized pyrite and shows vertical vadose flutings. This particular cave does demonstrate features consistent with Jagnow's theory; unfortunately, he generalizes the hypothesis to phreatic Guadalupe caves without explaining how his mechanism could account for their typical distribution and morphology.

*Queen is actually senior author (A.N. Palmer, pers. comm., 1977).

In the Iowa caves where solution via pyrite oxidation was originally recognized by Howard (1960), the pyrite was dispersed within the cavernous dolomite itself. In the Guadalupes, however, the pyrite lies above the cave-bearing carbonates, and sulfuric acid would have to be transported from this source to the developing caves. If the Yates were still in the phreatic zone at the time, then solution should have been most intense just below the Yates, in contact with the acid source. Yet caves in this zone are, in fact, observed only locally, most notably in the Cottonwood Cave area. On the other hand, if the phreatic zone began below the Yates, the acid water would traverse an aerated zone in its descent toward base level, and should produce vertical shafts below input points. Yet the special case of Queen of the Guadalupes seems to be the only such shaft reported in the Guadalupes.

Shafts of another sort are common in the Guadalupes, but these are unfluted, solutionally enlarged fissures or descending tubular conduits, often explorable to depths ranging from two hundred feet to more than five hundred feet. The shafts end in pinchouts, sediment, or rubble, but never in vadose stream outlets, and are generally situated *below*, not above, horizontal chambers which can be attributed to solution near base level. Many of the largest Guadalupe caves—including Carlsbad, Madonna, Three Fingers, Pink Dragon, Sentinel, Hell Below, and Virgin—contain pits of this kind. These pits seem inconsistent with Jagnow's model, since solution initiated from above, in the slow-flow Guadalupe regime, should be limited in depth by sedimentation interfering with deep solution along the joints. Pits of the Guadalupe type are, in fact, very unusual in other cave areas where solution by descending water is demonstrably active.

It is also uncertain whether it is theoretically possible for solution of limestone and precipitation of gypsum to take place together in the same chamber. For calcium to dissolve from a wall and precipitate as gypsum nearby should require the water to be undersaturated with calcite but supersaturated with gypsum at the same time. Yet Egemeier (pers. comm., 1979) has stated to me that, because of the common ion effect, water undersaturated with calcite should be undersaturated with gypsum by about an order of magnitude. The theories of Palmer, *et al.*, and of Egemeier sidestep this problem by asserting that the limestone is directly replaced by gypsum without first going into solution.

SULFATE REPLACEMENT BY BRINE/FRESHWATER MIXING

Palmer, *et al.*, (1977, p. 335) cite the most specific evidence in favor of gypsum replacement, including survival of original-carbonate structures such as fossils, bedding, and pisolites in gypsum in contact with carbonate walls. They have not published exact locations of these features for conservation reasons, but have shown

me unpublished photographs of them which appear to confirm the replacement features (Queen, pers. comm., 1979). Unfortunately, only a small percentage of gypsum in the caves shows such unaltered replacement structures. More typically it appears in one of two forms: white, granular, massive gypsum lacking obvious structure; or gray to buff, dense, fine-grained, massive gypsum which may be faintly banded. (In the west end of the Big Room of Carlsbad Cavern, the granular form is found as a "rind" several inches thick over underlying masses of the dense, massive form, suggesting that the former has recrystallized from the latter.) The massive gypsum has been assumed by most observers to be a precipitate from solution.

Palmer, *et al.*, (1977) challenge this, presenting three observations which they list as "evidence against gypsum deposition in a pre-existing void":

* Gypsum beds never include Pleistocene detrital sediments.
* Gypsum beds never overlie cavern-filling sediments or precipitates.
* Gypsum beds never fill the spongework which often closes peripheral joints and fissures.

These statements, as I understand them, are either questionable or open to other interpretation. The absence of detritus does not necessarily imply that no cave yet existed; it could also mean that gypsum deposition typically took place where free access for detritus was prevented by depth below the surface or a lack of open channels. That gypsum beds never overlie sediments seems contradicted by Good's specific descriptions of clay, sand and calcite layers underlying gypsum in Carlsbad Cavern. The absence of gypsum in spongework might indicate simply that sulfate concentration was insufficient to permit gypsum accumulation during the less active phases of the cave-enlargement process.

Palmer, *et al.*, refer to large-scale gypsum replacement as the "first stage" of Guadalupe cave development. This should be understood as applying only to the particular population of caves which they regard as being of gypsum-replacement origin, not to other early, small, vug-like crystal-lined caves which they believe formed mostly during diagenesis of the limestone (A.N. Palmer, pers. comm., 1979).

In the later caves which do contain gypsum, it is difficult to determine the original gypsum volume because the gypsum survives only in remnants in the drier areas. I see, however, no compelling evidence that gypsum ever filled a large fraction of the present cave volume, as the Palmer/Queen model implies. Had it done so, one might expect wide variations in the ratio of gypsum to open space, with very large masses remaining in protected places. In reality, gypsum depths, at least in larger chambers, seem to fall rather consistently within a range of about 10 to 20 percent of the height of the chamber they occupy (though 50 percent is approximated in the Talcum Passage of Carlsbad Cavern and in a few small passages in Cottonwood Cave). This suggests that the gypsum originated at the same time as the cave spaces, not before or afterward, and that a fairly high ratio of open space to gypsum was maintained during the process.

Another inadequate element in the proposal by Palmer, *et al.*, is the chemistry, which, as published, considers only the chemical species immediately involved in the replacement process, without specifying how the reaction might be driven. They cite Plummer (1975), who proposes phreatic limestone cavern excavation "when low-temperature, saturated, fresh, carbonate ground water at high CO_2 partial pressures is mixed with saline subsurface water," given suitable temperature, pH, and other factors. It is not made clear, however, how gypsum-replacement might fit into Plummer's carbonic-acid mixture-corrosion chemistry, nor do Palmer, *et al.*, explain why the mixture of gypsum-saturated brine with fresh water would not keep the mixture undersaturated, thereby preventing accumulation of gypsum.

Finally, the Palmer/Queen model for brine-mixing gypsum-replacement raises problems because it assumes the process takes place chiefly in the deep phreatic zone. It explains large horizontal rooms such as the Big Room of Carlsbad as the results of mixing at the boundary of dense brine with an overlying lens of fresh water. This could explain the room, but not the pits which often underlie such rooms. Furthermore, gypsum bodies formed at the base of a freshwater lens would undergo phreatic solution as base level dropped and the circulating fresh water body passed downward through the gypsum zone. Such solution, if long continued, could remove all the gypsum before the cave was drained. However, it is not easy to decide whether any such phreatic gypsum solution has actually occurred. Palmer, *et al.*, state that the first solutional event to attack the Guadalupe cave gypsum was phreatic, but the gypsum is so soluble and so porous that it is possible that the rounded surfaces of the blocks were created by vadose drip-spray, condensation water, etc., and that little, if any, gypsum solution was phreatic. The surviving gypsum masses are in places which are protected from dripping and seeping vadose water, not in places where they could have been expected to be out of the way of circulating phreatic water.

SULFURIC-ACID SOLUTION VIA OXIDATION OF HYDROGEN SULFIDE

The Egemeier proposal, having hydrogen sulfide as a sulfuric acid source, appears to fit the observed features of the major Guadalupe caves while avoiding the objections to the Jagnow or Palmer/Queen mechanisms. It provides for gypsum accumulation by means of a powerful sulfate source, mobile in groundwater, and which need not be assumed to have come from above the caves. Hydrogen sulfide, originating with oil and gas deposits, is "commonly found in formation waters throughout most of Eddy County" (Hinds and Cunningham, 1970), a condition which quite likely characterized the Tertiary and early Pleistocene groundwater of the proto-Guadalupe mountains.

Like Palmer, *et al.*, Egemeier considers the gypsum to arise by direct replacement of limestone rather than by precipitation. In Egemeier's model, however, replacement takes place not in the deep phreatic zone, but at the air/water interface. Gypsum replacement at this interface would account for horizontal rooms just as well as replacement at a brine/freshwater boundary, and the air/water interface is the most likely zone for maximum sulfuric acid production with minimal dilution of the resulting sulfate. Moreover, gypsum formed in this zone is more likely to survive, since it is not in danger of removal by phreatic solution as base level drops. Finally, the process has been observed in other caves.

In Egemeier's interpretation of the Wyoming caves that were the primary sources for his hypothesis, sulfide-bearing water rose from deeply buried synclines without causing major cavern enlargement until it had ascended to base level and come in contact with air. The H_2S thereupon reacted with oxygen to create free sulfur which was then further oxidized to sulfuric acid, which attacked the limestone, replacing it by gypsum which in turn fell into the cave stream and dissolved. He called this process "replacement-solution." The active Wyoming replacement-solution caves are simple horizontal streamways, not complex, deep, three-dimensional caverns like those in the Guadalupes. Egemeier did not attempt to account for the differences in cave morphology between the two regions.

These differences, however, are no greater than the differences between caves formed by the carbonic-acid mechanism in areas of dissimilar rock structure and permeability, flow rates and patterns, tectonic history, and other variables. In my opinion, Egemeier's hypothesis can form the basis for a hydrogen-sulfide-based cave development model which is consistent with all known features of gypsum-bearing Guadalupe caves.

COMPREHENSIVE OUTLINE FOR GUADALUPE CAVE DEVELOPMENT

At least two generations of phreatic caves can be recognized in the Guadalupe Mountains. (These should not be confused with the two phreatic episodes postulated by Bretz and Good; Table 1 summarizes the differences between their sequence of events and my own interpretation.)

Scattered through the Guadalupes are many small, simple caves, ranging in size from vugs to caves more than 200 ft long, which are lined with

dogtooth spar crystals. These caves are not spectacular and have received only rare notice in the caving literature (*e.g.*, "Idono Crystal Cave," DuChene, 1967). They are, however, interesting because their relationships to some of the larger caves indicate that the crystal-lined caves are earlier. In a side passage off the main room of Three Fingers Cave, and in a side passage off the Talcum Passage in Carlsbad Cavern, the passages pinch out in crystal-lined terminations where the crystals are progressively dissolved away in the direction of the larger cave. The crystal-lined cavities, in these cases, controlled the later development of large passages, the crystals being preserved at the passage ends because of poor circulation. No gypsum deposits are known in these crystal caves.

There is no evidence that sulfate-replacement played any role in creating these early, small caves. Palmer (pers. comm., 1979) favors an origin by diagenetic alteration of the limestone for at least the smaller ones. I feel that some may have been created by a mixture-corrosion process resembling that suggested by Plummer (1975). The nature of the shift in groundwater conditions which caused deposition of the dogtooth-spar linings is not known. After crystal growth, the caves may have remained in a flooded but basically static condition for an unknown period. Whether caves of this sort formed in more than one epoch is unclear because of lack of observed relationship to datable deposits.

In some large caves, including Virgin and Cottonwood, solution-truncated, brown-cemented breccias are exposed in the walls. Since these are not encrusted with crystals, they may represent a solution event later than the crystal caves but earlier than the main caves. Little is known about them.

Bretz (1949) reported gravel deposits filling a cave remnant on the Guadalupe ridge near Slaughter Canyon; these gravels were interpreted by Bretz as Pliocene Ogallala but by Hayes (1964) as Cretaceous. I do not know to which population this cave belongs, but since the gravel is not later than Ogallala, the cave must be at least of pre-Ogallala age, if not pre-Cretaceous or earlier.

All known larger Guadalupe caves belong to another population which I will designate here as "later generation." These major Guadalupe caves are unlike caves of most other areas in several respects. They are unpredictably located, without reference to surface drainage patterns, and rarely show features such as fluted vertical shafts which would mark points of aggressive water input from above. They are characterized by three-dimensional maze patterns (*e.g.*, Spider Cave; parts of Three Fingers; the McKittrick Hill caves) or by broad but short rooms and passages which are often underlain by deep pits (Carlsbad, Pink Dragon, Virgin, Hell Below). The overlying surface shows no solutional karst features except small rills and tubes. These caves evidently developed after deposition of the ridge-top gravels, since the gravels never infill the caves and some caves cut across the consolidated "sand dikes" associated with the gravels (this is particularly clear at Ogle Cave; see Jagnow, 1978). In this larger-scale cave-forming event, some early caves were rejuvenated and greatly enlarged. During the most active phase in at least some caves, gypsum replaced wall rock and was accumulated in massive deposits on cave floors. The following discussion concerns only these later-generation caves.

AN ASCENDING-WATER/H_2S CONCEPT

I propose that these largest and best-known Guadalupe caves, including Carlsbad Cavern, were developed primarily by *ascending* water on the upwelling limbs of deeply curving flow paths of the pattern defined as "bathyphreatic" by Ford (1977). Evidence for ascending flow from the buried Capitan limestone on the east side of the Delware Basin, in the form of a salt-leached band in the overburden directly above the Capitan, was cited twenty years ago (Moore, 1959) and recently confirmed by Anderson and Kirkland (1980). The western part of the Capitan complex has been exhumed and drained, but the cave patterns described above are consistent with similar ascending flow in former times. In my model, the pits develop on input routes of the ascending cave-forming water. Phreatic solution by water rising under pressure would not be as much inhibited by sedimentation as if the water were descending, since rising water could undermine

Table 1. Guadalupe cave chronology: alternative conceptions.

SEQUENCE ENVISIONED BY BRETZ (1949) and GOOD (1957)		MOST PROBABLE SEQUENCE ENVISIONED IN THIS REVIEW	
Pleistocene	caves drained—major speleothem deposition	Pleistocene	caves drained—major speleothem deposition
			sulfuric-acid cavern development with gypsum accumulation
Late Pliocene	Ogallala valley filling; caves reflooded—secondary gypsum deposition	Pliocene? Cretaceous?	deposition of gravels and 'sand dikes'
Tertiary	caves drained—flowstone and clastic sediment deposition	time unknown	brown-cemented solution breccia
	phreatic cavern solution	time unknown	static phreatic conditions
			phreatic calcite crystal deposition
			small-scale phreatic cave solution
time	*event*	*time*	*event*

sediment-armored surfaces. In this model, the most important aggressive agent in cave development is assumed to be sulfuric acid derived from hydrogen sulfide.

The necessary hydrogen sulfide arises in the petroleum-bearing evaporitic rocks which flank the Guadalupe Mountains, by bacterial reduction of anhydrite using hydrocarbons as energy source at depths where conditions are anaerobic, via a reaction summarized as follows by Kirkland and Evans (1976, p. 2016):

$$CaSO_4 + CH_4 \rightarrow H_2S + H_2O + CaCO_3 + \text{energy}$$

In the process, the anhydrite is replaced by calcite, which is believed to be the mode of origin of numerous "castiles" or limestone buttes which protrude from the gypsum terrain below the Guadalupe limestone escarpment. On becoming aerated, the H_2S will oxidize to sulfur and/or sulfuric acid, which on encountering limestone, may reverse the replacement process involved in the original H_2S production, converting calcite to gypsum. The H_2S must move by diffusion and groundwater circulation from the evaporites into the limestone of the Guadalupe uplift.

Some oddities of Guadalupe cave morphology can be understood as phenomena related to hydrogen sulfide as a major acid-forming agent. The wide but short passages are consistent with Egemeier's designation of blind passage terminations as characteristic of this mechanism. These terminations reflect the fact that solution via H_2S is not uniformly active along the entire path of flow, but is abruptly increased when sulfuric acid is produced at points where anaerobic sulfide-bearing water becomes oxygenated. This will usually be where the water comes in contact with air, and some of the widest Guadalupe chambers, such as the Big Room of Carlsbad Cavern and the Cavernacle in Virgin Cave, are relatively level and show undercuts in the ceilings which may indicate solution when the rooms were partly flooded. As in Wyoming, much of the actual gypsum replacement may have taken place well above the water surface, on the walls and ceilings of the rooms, whence the gypsum fell into the water where enough was dissolved away to create the existing voids. The ceilings are not now crusted with gypsum, but even slight amounts of seeping or condensing water would suffice to loosen and detach it.

To explain the Guadalupe pits, a variation on Egemeier's mechanism must be introduced. In the Wyoming H_2S caves, large-scale cavern enlargement was observed *only* at the air/water interface. This was probably because the impermeable caprock prevented any oxygenated surface water from mixing with the synclinal waters at depth. In the more permeable Guadalupe rocks, localized flows of oxygenated water probably penetrated deep into the phreatic zone in places, where mixture with ascending sulfide-bearing water produced sufficient acid to enlarge the conduits to explorable pits. Such deep-phreatic pits probably develop primarily by direct solution rather than replacement, because when oxygen must be delivered in slow-flowing water, the sulfuric acid reaction will be strong enough to dissolve caves, but sulfate will be too dilute to permit solid gypsum to accumulate. I have rarely, if ever, seen gypsum on ledges in the pits, and its absence should be expected if the above is correct. Egemeier's "replacement-solution" is thus too narrow a concept to cover the entire Guadalupe cave-forming process, and should be regarded as a special case of a more general mechanism of sulfuric-acid cave development via H_2S. This subject is now under study by R. Mark Maslyn (for preliminary report see Maslyn, 1978).

An acceptable model must also explain why massive gypsum is common in the Guadalupe caves but is absent from H_2S-related caves in other areas such as Glenwood Canyon in Colorado. The answer is probably that in the Guadalupes, where the H_2S arises by sulfate reduction, groundwater charged with H_2S will also be high in sulfate. When more sulfate from the sulfuric acid reaction is added, the system may be pushed to a concentration so near saturation that gypsum is not removed by water circulation as fast as it forms. This agrees with my observation that gypsum is most abundant in chambers which have features consistent with development at the air/water interface, where oxygen for sulfuric acid production is most available, and where oxygenation need not involve the diluting effects of freshwater mixing. Gypsum deposition in this zone might be further enhanced by slow evaporation at the water level.

If the sulfuric acid reaction is needed to force sulfate concentration over the threshold of gypsum deposition, then caves where this reaction was weak may grow without ever forming gypsum deposits, while other caves may accumulate gypsum during the height of sulfuric-acid activity but not during less active phases at the beginning and end of the cave-forming episode. This may be why there are gypsum-free sediments beneath some gypsum in Carlsbad Cavern, and why peripheral spongework (of early or late origin?) lacks gypsum.

Cave solution via H_2S associated with hydrocarbon deposits is based on an agent in limited supply, and must be more time-limited than ordinary carbonic-acid solution based on atmospheric and soil sources. The process must begin when some tectonic event establishes sufficient groundwater circulation to sustain a continuing sulfuric acid reaction, and end (or continue via the carbonic acid reaction) when all available H_2S-rich water has been oxygenated, drained, or displaced by incoming fresh water. Dating of these events in the Guadalupes is speculative. If any of the "sand dikes" cut by the caves, or associated ridge-top gravels deposited before the Guadalupe uplift, are of Ogallala age, then the gypsum-bearing caves must be post-Ogallala.

The succession of levels in Carlsbad Cavern suggests that this cave was at least intermittently enlarging through most of the main uplift of the Guadalupes. The literature, however, is not unanimous as to when this took place. DuChene (1978), for example, places the climax of deformation in the late Tertiary, presumably in post-Ogallala but pre-Pleistocene time. Another source states that the youngest fauna in the Ogallala may be as old as 4.6 ± 1.0 million years (Izett, quoted by Bachman, 1974, p. 48). If, as Bachman states, Ogallala deposition was followed by a period of tectonic stabilization nearly three million years long, ended by rejuvenation of mountain building in early Pleistocene time, then the main Guadalupe uplift, and associated major cave development, would have been early to mid-Pleistocene. This is later than assumed by Bretz (1949) but agrees with the work of Motts (1959).

A stalagmite from Ogle Cave has been dated as growing between 205,000 and 125,000 years before present (Harmon and Curl, 1978), showing that caves as low as 4600 ft elevation had been drained by the later Pleistocene. Some uplift has continued since drainage; survey of a water-level line in Carlsbad Cavern (Jagnow, 1977) indicates a "true dip of nearly 26 ft/mi (0.28) toward N52°E." Another phenomenon in the Big Room of Carlsbad Cavern is also indicative of post-drainage earth movement: I have seen broken stalactites up to six inches in diameter, which show some old, inactive regrowth, near the Temple of the Sun. The damage is too inaccessible to have been done by animals and too early to be man-caused; it can only be the result of earthquake shock.

Flow rates in Guadalupe cave development were apparently slow, and it is probably because of this that the rooms are often broad and high but short, and lack evidence of streamways. However, it does not follow that cave development rates were correspondingly slow. Since sulfuric acid is a strong acid, it is quite possible that maximum cave-growth rate at the peak of activity in a given cave could be much greater, for at least a short time, than could be attained by the comparatively weak agency of carbonic acid. The gypsum floor deposits, which are presumably the residues of the primary cave-forming process, do show evidence of rapid accumulation. The gypsum is virtually free of visible clastic impurities and breakdown, and lacks the variability and discontinuities which are seen in other deposits, such as dripstone, which are known to be deposited slowly over a long period. Jagnow (1978, p. 14) describes the banding in the gypsum in the trail tunnel in the Big Room of Carlsbad Cavern as "1 to 2 mm varves." If these are true varves representing yearly increments, then a gypsum accumulation rate of more than three feet per thousand years would be indicated, with a correspondingly fast removal of limestone. However, it has not been proven that these structures are actually varves. Egemeier (pers. comm., 1979) has reported replaced stromatolites, with varve-like banding, in the same area. Other impossible interpretations, such as banding caused by sequential replacement, should be investigated.

Cave distribution in the Guadalupe Mountains, as well as cave features, is consistent with an

ascending-water concept. The extreme southwestern end of the mountains, now in Guadalupe Mountains National Park, is the highest, wettest part of the range but seems to have the fewest and smallest caves. This was probably the first area to be raised above base level; it could therefore have acted as first input area to drive ascending circulation in lower-lying parts of the Capitan complex, but this highest area may have lacked a source to drive its own ascending circulation that would have been needed to activate the H_2S mechanism there. However, Jagnow (1977) has propounded a plausible alternative explanation for the sparsity of caves at the high end of the range: the more rapid uplift there would have provided less time for cave development at any given level.

Well-drawdown data indicate substantially less hydraulic connectivity in the Capitan after it dips into the subsurface east of the Pecos River (Hiss, 1975); it appears that cave development downdip from the Pecos River has been inhibited by limited circulation.

The hypothesis of ascending-water speleogenesis by sulfuric acid via H_2S seems to have considerable explanatory value for specific Guadalupe caves. In the case of Carlsbad Cavern, it would apply as follows: Water from an underlying source rose by way of the Bottomless Pit and smaller deep pits such as one below the Mystery Room, and followed a sinuously ascending route through a proto-Big Room and up the Main Corridor to a base-level outlet above the present entrance level. With successive drops in base level, new horizontal levels were developed, probably at the air/water interface, in adjustment to progressively lower outlets, at Bat Cave, Guadalupe Room, Big Room, Left Hand Tunnel and finally Lower Cave levels. The Main Corridor and Bottomless Pit, which are anomalous in a descending-water model, are integral feeder conduits in the ascending-water model. The sequence of horizontal base-level passages is the same in either model. Lake of the Clouds passage, which resembles Bottomless Pit but does not issue in a large base-level chamber, is puzzling, but perhaps can be attributed to a higher sulfuric acid concentration with a lower flow rate. Thick calcite-raft deposits in this passage indicate that the sulfuric acid reaction was exhausted before drainage of this lowest part of the Cavern.

The caves of McKittrick Hill, in an otherwise largely caveless area, are situated in an anticline, which would have been a logical focal point for ascending water movement.

Cottonwood Cave has some unusual features which may indicate that it was developed in a locus of particularly high sulfuric acid concentration. It is a cave of large volume in dolomitic rock. Since dolomite dissolves more slowly than limestone, this suggests either stronger acid action or longer time for enlargment than most Guadalupe caves. The latter is unlikely, since the cave is in the more rapidly uplifted part of the range. Since Cottonwood Cave is just below the pyrite-bearing Yates, it may be that sulfuric acid from H_2S oxidation was augmented there by pyrite oxidation in accord with Jagnow's theory. The presence of free sulfur in the cave's gypsum deposits (Davis, 1973) is also consistent with a high ratio of sulfide to oxygen. Such a situation would enhance sulfur production and preservation. Egemeier emphasized free sulfur as a normal step in the oxidation of H_2S to sulfuric acid, at least when the reaction is subaerial; but where H_2S in dilute solution encounters oxygen in excess, all the sulfide should be rapidly converted to sulfuric acid, the reaction becoming, in effect, simply $H_2S + 2O_2 \rightarrow H_2SO_4$. This may be why free sulfur has not been observed in other Guadalupe caves, except for the special cases noted below.*

It is likely that H_2S-related cave development is still taking place, on a scale commensurate with the present cirulation of groundwater, toward the northeast end of the Guadalupes where the Capitan complex dips beneath the Pecos Valley. Bjorklund and Motts (1959, App. B, Fig. 48), from water-well data, have profiled a zone of freshwater/brine mixing in this area. A "potable mixed-water zone in the reef aquifer" underlies a band about four miles wide, between Hackberry Draw and an eastern limit about a mile east of the Pecos River. They infer from the well data deeply-curving flow paths which focus on ascending discharge to springs along the river; this flow pattern is precisely like that which I have inferred for the drained section of the Guadalupes on the basis of cave morphology.

Oil-well data also confirm the existence of flooded, sulfur-bearing caves in this region. Hinds and Cunningham (1970, pp. 9-10) reproduce an oil-well log from the SW¼ NE¼ Sec. 3, T.22S., R.26E., at 3325 ft ASL, just west of the town of Carlsbad. The sequence recorded includes "open cavern" at 65 ft depth; "first water" at 146 ft; "open flowing river of water" at 345 to 355 ft; "cave, strong sulphur water" at 535 ft; "open cave, black sulphur coating tools" at 807 ft.

One H_2S cave has also been reported actively developing in the zone of aeration, in a limestone butte in the gypsum plain a few miles south of the Guadalupe Mounains, in the NW¼ of BK61, TWP2 in Texas. It is described as "a roughly cylindrical, vertical cavern about 10 to 15 ft in diameter and about 100 ft deep," issuing H_2S and partly lined with sulfur (Kirkland and Evans, 1976, p. 2014). This confirms that cave development does occur in this area in a manner close to that proposed by Egemeier, but it differs in two ways from typical caves of the Guadalupe Mountains proper: it is inside the H_2S source area so that phreatic water flow need not be involved in its origin; and the cave is forming at a depth shallow enough to intersect the surface.

No natural entrances have been found to typical Guadalupe H_2S-related caves which are still being enlarged. This is to be expected; since the acid source is below, the process does not require solution channels between the overlying surface and the zone of reaction near base level; and the active zone is likely to be deep enough to minimize the likelihood of collapse entrances. In the early history of such caves, the only entrances are likely to be active or abandoned base-level outlets.

I would expect that dry areas with climate and geology like those of the Guadalupe Mountains, but where gypsum basin deposits and petroleum deposits or other sulfide sources are sparse, would be less cavernous. A case in point may be the Big Bend region of Texas, where there are several ranges having up to 1200 ft of massive Cretaceous limestone, but in which solution caves are few and small. It is also possible, however, that differences in the tectonic or climatic histories of the two regions have been important in causing the differences in cave distribution.

In closing, I should emphasize that neither I nor the authors reviewed here intend to present sulfate-replacement solution and carbonic-acid solution as mutually exclusive processes. Carbonic acid is, in fact, a secondary product of sulfuric-acid solution, and has undoubtedly been active to some degree in the same caves in which the sulfate reaction is viewed as the main reaction. Nor do I presume that the hypotheses favored here will prove to be correct in all respects. Guadalupe cave development has probably been more complex than my outline indicates, and it is quite possible that some elements of almost every idea ever proposed are applicable to some caves.

The conflicting possibilities inferred by different workers from the sulfate deposits should be tested by more sophisticated methods. The Guadalupe cave gypsum needs detailed petrographic study for better evidence as to the degree to which replacement or precipitation has produced it. Chemical analysis for trace materials, such as chloride, would be helpful in determining whether the caveforming water was briny; and since bacterial sulfur is isotopically "light" (Kirkland and Evans, 1976), isotopic analysis should be useful in deciding whether biogenic H_2S was really involved in developing the Guadalupe caves.

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*Cottonwood Cave is no longer the only typical Guadalupe cave known to contain elemental sulfur. In October 1980, Carol Hill discovered a small deposit of finely-granular yellow sulfur irregularly disseminated in a gypsum "rind" on massive gypsum at the second trail tunnel in the Big Room of Carlsbad Cavern [Note added in press].

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FLUCTUATIONS IN A POPULATION OF THE CAVE SALAMANDER

Eurycea lucifuga

Albert A. Williams

Department of Zoölogy
University of Wisconsin — Milwaukee
Milwaukee, Wisconsin 53201

SUMMARY

A field study of a small population of the common cave salamander Eurycea lucifuga, *in Union Point Cave, Union Co., Illinois, indicated seasonal variation both in density and in the spatial distribution of the visible population in the cave. The changes in population density are possibly associated with seasonal migrations into the cave for courtship and breeding purposes, while the spatial distribution is shown to be a function of seasonal changes in availability of suitable wet substrate within the cave. The intrusion of the investigator into the stable cave habitat is seen to have a marked effect on the salamander population, complicating interpretation of this and other hypogean ecological studies. Behavior of the salamanders in response to sudden disturbances is described.*

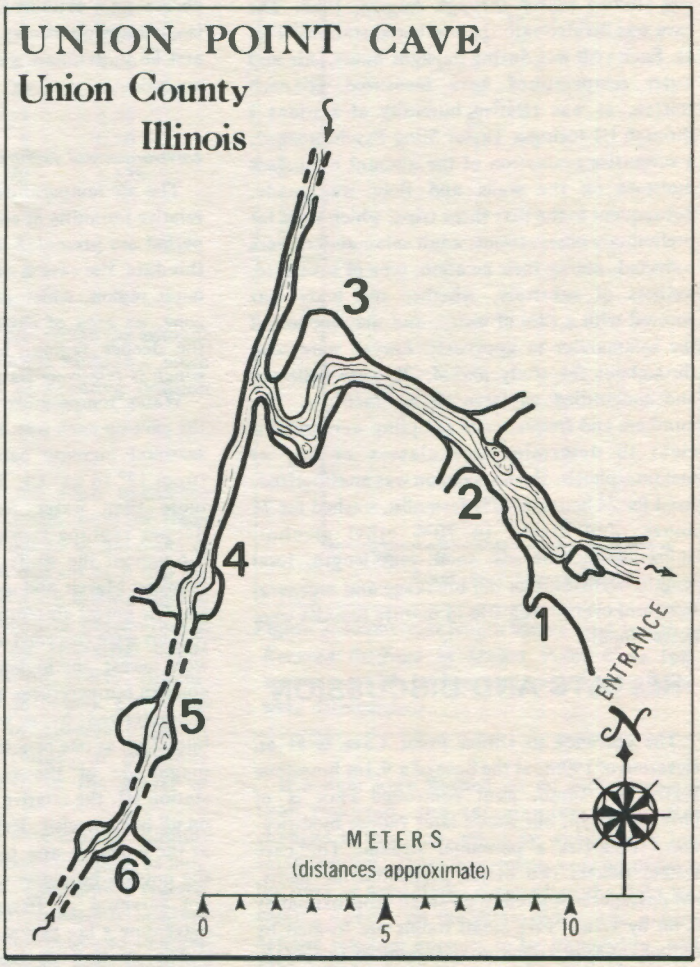

Figure 1. (left) Sketch of Union Point Cave, Union County, Illinois. Distances are approximate. Numbers indicate stations discussed in the text.

INTRODUCTION

THE CAVE SALAMANDER, *Eurycea lucifuga* Rafinesque, is a common species distributed through an extensive portion of east-central United States. It is found associated with caves throughout its range, both deep within them as well as in adjacent terrestrial epigean habitats. The twilight zone is considered to be its most common habitat. Although some ecological and developmental aspects of its life history have been investigated, it remains a very common but little studied animal familiar to anyone caving in the eastern US. In this paper, I report on the activity patterns, spatial distribution, relative abundance, and associated environmental fluctuations of a population within a small cave in southern Illinois.

METHODS

Union Point Cave, 16 miles south of Carbondale, Illinois (SW¼, NE¼, sec. 1, T. 11 S., R. 2 W Alto Pass quadrangle, Union County, Illinois) was studied March through August, 1968. The cave was divided into six numbered stations (Fig. 1). Each visit was during daylight hours. Air and water temperatures were measured at each station, as was relative humidity at stations I through III (using a Taylor Sling Psychrometer); a subjective evaluation of the amount of surface moisture on the walls and floor was made. Subsequent to the first three trips, which were for preliminary observations, adult salamanders were collected, noting their location, type of substrate, wetness of substrate, whether the body was covered with a film of water, and the reaction of the salamander to approach. Larvae were seen throughout the study period: 26 were collected and indentified as larva of *E. lucifuga*. The numbers and frequency of sampling were insufficient to determine age classes or age at metamorphosis. Each specimen was anesthetized, fixed for 24 hours in 10% formalin, washed for 24 hours, and stored in 70% ethyl alcohol. Subsequently, the sex, snout-vent length, total length, occurrence of tail breakage and regeneration, and ovarian egg size in mature females were determined.

RESULTS AND DISCUSSION

The entrance to Union Point Cave is at an elevation of 190m, at the base of a 9.1m limestone bluff. The small, joint controlled cave is of phreatic origin, but shows later vadose modification. It carries a perennial stream. The cave system follows two major perpendicular joints, the passages being relatively small (approximately 0.9m by 1.2m). Five small rooms are formed by ceiling collapse at the intersections of secondary joints. The cave extends well beyond my study area and has never been fully explored.

The owner indicated that the stream issuing from the cave has never dried up and during heavy rains has flooded to a depth of four feet. This degree of flooding is not common and would still leave ample wall space suitable for salamanders within the cave above the high water mark.

During the study period, a breeze blew out of the cave at a velocity of 40 to 45m per minute. The velocity was slower within the cave, due to the larger cross section of the passages. This cool, moisture laden air from the deeper portions of the cave maintained the temperature and humidity of the twilight zone at a relatively constant level. Hutchison (1958) reported a similar situation in one of the four caves he studied.

The mouth of the cave is never subjected to direct sunlight, and the size of the twilight zone did not exhibit any seasonal variation in size between March and August. The last traces of light are discernible (to human eyes after 5 minutes' accommodation) in the second room of the cave, approximately 31m from the entrance (station III).

The cave was visited during daylight hours once during March, approximately every five days during April and May, twice a month during June and July, and once during August. A total of 108 observations of adult *Eurycea lucifuga* were made (some individuals may have been seen repeatedly) and 68 individuals were removed for laboratory analysis.

Environmental factors

The air temperature, water temperature, and relative humidity at each station during the study period are presented in Table 1. On the basis of this data, the cave is divided into two regions: the outer region, which corresponds to the twilight zone, an area of environmental variability, and the deeper region, beyond the twilight zone, which is relatively stable.

Water temperature was uniform throughout the cave on each trip, although there was a slight seasonal increase between March and August (from 12° to 14° C). Air temperature fluctuated more than water temperature, although the deeper regions remained relatively constant throughout the study, warming up only 2.5° C between March and August (from 11.5° to 14° C). The lowest air temperatures for the inner cave regions were recorded when epigean temperatures were lowest, the highest cave temperatures when epigean temperatures were highest. Station I was characterized by a widely fluctuating relative humidity: as one penetrated the twilight zone, the magnitude of the fluctuations decreased. At station III, the relative humidity was 95 to 100% on all but one visit. Relative humidity was lowest at the entrance and highest on those days when the outside humidity was highest. The cave was not surveyed at frequent enough intervals to determine a lag period.

The amount of moisture on rock and clay surfaces within the cave fluctuated greatly, from flowing films of water to none. During March and April, all surfaces within the cave were wet. From May through August, there was progressive drying. The drying commenced at the entrance and progressed back through the twilight zone during the early summer months. The drying was periodially interrupted by drainage of water from the surface for a few days following local rains. Changes in the quantity of surface moisture did not appear to influence the relative humidity.

Every salamander seen during the study was either on a wet surface with a film of water covering both the substrate and its body, or in the stream. If a salamander escaped while being captured, it did not hesitate to run over a dry area, but one was never found naturally on such a surface.

Population density

There appeared to be both seasonally and environmentally induced variations in the position and density of the visible population of *E. lucifuga*. Peck and Richardson (1976) observed *Eurycea* throughout the entrance, twilight, and dark regions of caves, but indicated that the population density was greatest in the entrance and twilight regions during the spring and summer. Most previous investigations had indicated a preference for the twilight zone. Green, *et al.* (1967) postulated a random distribution throughout the cave system. I found that the salamander population was concentrated in particular regions, and that locations of these concentrations within the cave varied between the wetter spring months and the relatively dry summer months: during the summer, the population moved deeper into the cave. This is best indicated by the percentage of the monthly sample observed in each region of the cave (Table 2), and is correlated with the disappearance of surface moisture in the front portions of the cave. Hutchison (1958) also concluded that the distribution of the salamanders is influenced by the amount of moisture on the walls and floors of the caves.

Changes in the size of visible populations of this species within caves have been noted by Ives (1951) and Hutchison (1958). Hutchison noted that population size reached a peak during April through June, declined during July and August, and remained low during the fall and winter months. I observed similar fluctuations at Union Point Cave. The average number of individuals observed per trip increased from April through June (April, 2.5; May, 8.4; June, 11.5), and then the number declined during the later summer months (July, 5.0; August, 6.0).

Hutchison (1958) noted that as the saturation deficit of the deeper cave regions increased, the population size dwindled. At Union Point Cave, both relative humidity and temperature fluctuated randomly during the period when the population size increased and decreased. This agrees with the data obtained by Hutchison for the months of March through September. Only when the relatively high saturation deficits of the winter months are included in Hutchison's graph does his relationship emerge. Fluctuations in the visible population must be related to some factor

Table 1. Environmental fluctuations in Union Point Cave.

Date	Water Temperature (°C) Station I	II	III	IV	V	VI	Air Temperature (°C) Station I	II	III	IV	V	VI	Relative Humidity (%) Station I	II	III
March 6	12.0	12.0	12.0	12.0	12.0	12.0	12.5	12.0	11.5	11.5	11.5	11.5	83	89	95
April 7	12.5	12.5	12.5	12.5	12.5	12.5	14.0	13.0	12.0	12.5	12.0	12.0	74	88	100
April 20	13.0	13.0	13.0	13.0	13.0	13.0	26.5	16.5	14.0	14.0	14.0	14.0	82	94	100
April 25	12.0	12.0	12.0	12.0	12.0	12.0	13.5	11.0	11.0	11.5	11.0	11.0	57	78	87
April 30	12.5	12.5	12.5	12.5	12.5	12.5	13.0	11.0	11.5	11.0	11.0	11.0	88	100	100
May 4	12.0	12.0	12.0	12.0	12.0	12.0	12.5	12.5	12.0	12.0	12.0	12.0	83	89	97
May 9	12.5	12.5	12.5	12.5	12.5	12.5	12.0	12.0	12.0	12.0	12.0	12.0	100	100	100
May 15	13.0	13.0	13.0	13.0	13.0	13.0	16.0	14.5	12.5	12.5	12.5	12.5	89	94	95
June 22	14.0	14.0	14.0	14.0	14.0	14.0	22.0	19.0	13.0	13.0	13.0	13.0	75	83	100
June 30	13.5	13.5	13.5	13.5	13.5	13.5	23.0	15.0	13.5	13.5	13.5	14.0	74	84	100
July 21	13.5	13.5	13.5	13.5	13.5	13.5	18.5	14.0	13.0	13.5	13.0	13.0	82	98	98
Aug 11	14.0	14.0	14.0	14.0	14.0	14.0	23.5	17.5	13.5	14.0	14.0	14.0	78	83	96

Table 2. Percentage of the monthly sample observed in each region and sex ratios at Union Point Cave.

Month	**	II	**	III	**	IV	**	V	VI	N	Ratio Males/Females
March	----	80.0	----	20.0	----	----	----	----	----	5	0.25
April	----	16.7	----	33.3	16.7	16.7	----	16.7	----	6	1.00
May	16.0	64.0	16.0	----	----	----	----	4.0	----	25	1.08
June	----	39.1	----	8.7	----	17.4	----	17.4	17.4	23	1.88
July	----	----	----	20.0	----	60.0	----	20.0	----	5	1.50
August	16.7	----	----	----	----	66.7	16.7	----	----	6	0.50
										70	1.125

**Passages between the major stations.
No specimens were collected from Station I or from between stations V and VI.

other than the saturation deficit or relative humidity during the spring and summer months.

An analysis of population size and movements is complicated by the effect that the investigator has on the community being studied. Both Hutchison and I noticed that there is a marked reduction in the size of the visible population of *Eurycea lucifuga* after the first visit to a cave. Hutchison (1958) reported a drop in the visible population (from 20 to 3, 15 to 4, 13 to 4, and 3 to 0) in four caves, three days after the first trip. On the first visit to Union Point Cave, 26 *Eurycea lucifuga* were observed. Twelve days later, only 6 were observed (none of the original 26 had been captured). The natural variation in the population may be impossible to determine accurately due to this effect that the investigator has on the population.

What actually controls fluctuations in size of the visible populations is as yet not understood. One hypothesis would relate the increase in population size to an influx of individuals from outside the cave at the onset of the breeding season. The little information that is available concerning the breeding season indicates that courtship occurs in midsummer (Organ, 1968; Williams, 1976) and oviposition in the fall and winter. Thus, the population increase might be associated with courtship. Other, less likely, possibilities would be that the size of the population is controlled by changes in the amount of surface moisture or relative humidity, since these factors are involved in dictating position within the cave.

Habits

Approximately 16% of the adult specimens were collected from the stream, most of these from beneath rocks. Since not all of the rocks in the stream bed were turned over on each trip the relatively high percentage of adult salamanders in water might be even greater. This observation is in marked contrast with the terrestrial habits described by Banta and McAtee (1906), Hutchison (1956), and Green, *et al.* (1967). Either the terrestrial/aquatic habits of *Eurycea* differ in various portions of its range, or previous investigators did not search in the gravel of stream beds.

When cave salamanders were initially illuminated in the cave, they remained motionless as long as the light stayed on them. They always reacted quickly after being touched, commonly heading for pools or the stream. If they managed to enter the water before being captured, they generally eluded capture. Many animals, first observed on rock walls beside the stream, escaped by jumping from the wall and dropping into the stream. Water is an effective escape route, when available.

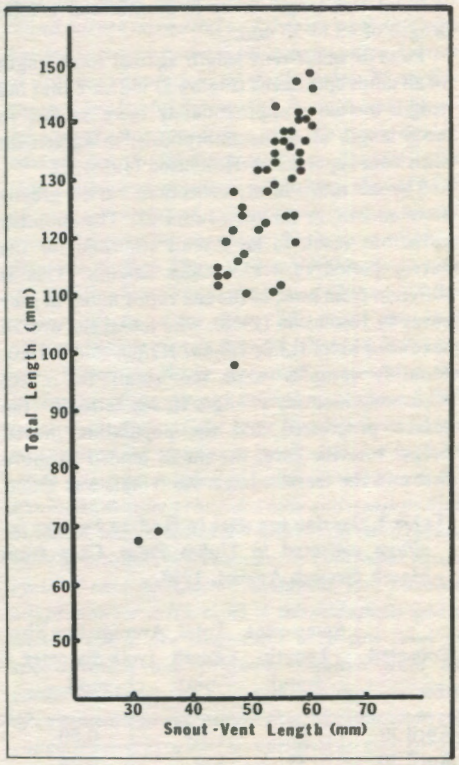

Figure 2. Snout-vent length versus total length of *Eurycea lucifuga* at Union Point Cave (all specimens with broken and regenerating tails were disregarded).

If a light were flashed on an individual and then removed, the salamander quite often changed its position, often by withdrawing into small crevices. These movements only occurred in the dark or semi-dark, never when the light was shining directly on the salamander. The natural defense reaction appears to be immobility, with subsequent movement only when the salamander is cloaked in darkness or disturbed.

Of the salamanders captured, 28.3% had broken and regenerating tails. Hutchison (1956) reported only 4% natural tail breakage. This may be an indication that there was more predation on

the salamanders in Union Point Cave than in the caves Hutchison studied. Hutchison reported that 11.4% of the tails of his specimens were broken during capture, no tails were broken during capture in this study. Since Hutchison was marking his specimens and then releasing them he was forced to handle them more than I was, possibly accounting for the greater tail breakage in his study.

Females average slightly smaller in the mean snout-vent length, 50.1 ± 1.32 ($\bar{x}$ ± SEM, n=32) than males, 54.9 ± 0.77 (n=36). The smallest metamorphosed individual was a 31 mm female, and the largest larva was 33 mm. The total lengths of these specimens were 68 and 70 mm respectively. The larva is 12 mm larger than the maximum size (58 mm) reported by Hutchison (1966). Metamorphosis generally occurs between a snout-vent length of 25 to 35 mm and a total length of 45 to 55 mm.

Plots of snout-vent length against total length of all adult specimens (Figure 2) indicate that tail length increases approximately twice as fast as body length after metamorphosis, in agreement with data reported by Hutchison (1956).

The sex ratios in my collections varied greatly from month to month (Table 2). The monthly variations result in an overall sex ratio for the survey period of 1.125 males/females. This is different from most of the sex ratios noted in four caves by Hutchison (1958), who found the overall sex ratios to be 1:3.0, 1:0.65, 1:1.60, and 1:1.10. Monthly samples were too small to reflect accurately monthly changes in sex ratio. As the season progressed and the population moved deeper into the cave, the males tended to move first and the females later. No female was found deeper in the cave than a male, but males were often found deeper in the cave than females.

Ovarian eggs gradually increased in size during the study period (Table 3). Females smaller than 50 mm were considered to be juveniles since all, no matter when they were collected, had small unyolked eggs (generally less than 0.5 mm diameter). The study was terminated before the maximum egg size had been reached. According to Bardon and Kezer (1944), Myers (1958), Green, *et al.* 1967), and Organ (1968), the eggs at ovulation are approximately 3 mm in diameter. By August, the average ovarian egg size was slightly larger than 2.0 mm; however, the rate of increase in egg size had slowed down during the summer months and, thus, it was impossible to extrapolate from the available data exactly when the maximum size would be reached.

Table 3. Ovarian egg sizes (yolked) in *Eurycea lucifuga* collected in Union Point Cave from March through August, 1968.

Collected	Snout-vent Length (mm)	Total Length (mm)	Average Egg Size (yolk diameter mm)
April 30	52	126*	0.50
April 30	53	122	0.75
May 4	59	146	1.5
May 4	55	134	1.0
May 4	57	124*	1.0
May 9	56	128*	1.0
May 9	50	116*	0.75
May 9	55	120*	
May 9	53	131	1.0
May 9	55	111	0.75
May 15	56	137	0.75
June 22	58	117	1.75
June 22	59	136	2.25
June 22	61	148	2.0
June 22	54	93*	1.75
August 11	53	104*	2.0
August 11	53	128	2.0
August 11	50	111	1.5

*Specimens with broken and regenerating tails.

CONCLUSIONS

Population dynamics of cave dwelling vertebrates, including the cave salamander, warrants further investigation. Particular problems exist concerning the effect of investigator intrusion on the stable cave habitat, diel cycling and its regulatory cues, density dependent and independent regulation of population size, individual spacing within the population, and dispersion of the population within the available habitat.

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erratum

NSS Bulletin v. 42, p.34, in the abstract entitled "^{230}Th-^{234}U Ages of Speleothems from Mystery Cave, Minnesota," the age for line MC #3 (base) should be >350**.

Peck, S.B. (1980)—Climatic Change and the Evolution of Cave Invertebrates in the Grand Canyon, Arizona: *NSS Bulletin:* 42:53-60.

CLIMATIC CHANGE AND THE EVOLUTION OF CAVE INVERTEBRATES IN THE GRAND CANYON, ARIZONA

Stewart B. Peck

Department of Biology, Carleton University, Ottawa, Ontario, Canada K1S 5B6

SUMMARY

The invertebrate cave faunas of three stream caves, located in the lower part of the Upper Sonoran Desert life zones of the Grand Canyon, Arizona, were investigated. Of the 15 species found, all are terrestrial and five are probably now limited to stream caves in the canyon as troglobites or disjunct populations of troglophiles. These five species probably descended from forest litter-inhabiting ancestors living near the caves during past glacial-pluvial climates. These climates, with their cooler and/or wetter conditions, should have allowed a lowering of at least some components of nearby spruce-fir montane forest communities from the Kaibab Plateau some 1000 m down into the middle elevations of the Grand Canyon, in the vicinity of the caves. This "life zone" lowering occurred most recently from 24,000 to 14,000 years ago. When the forest retreated upwards at the beginning of the present interglacial (about 8,000 years ago), some of the litter invertebrates which had entered the caves were locally isolated in them when adjacent epigean populations went extinct. Examples may be a rhagidid mite and a campodeid dipluran, and these could represent the most recent wave of invaders in a climatically controlled taxon cycle of cave occupation, isolation, and possible adaptation (or extinction). A telemid spider and a leiodid beetle are troglobites at a low level of specialization and probably resulted from an earlier (probably the Sangamon) interglacial wave of cave isolation and adaptation. An entomobryid collembolan is assumed to represent an even earlier period of subterranean isolation.

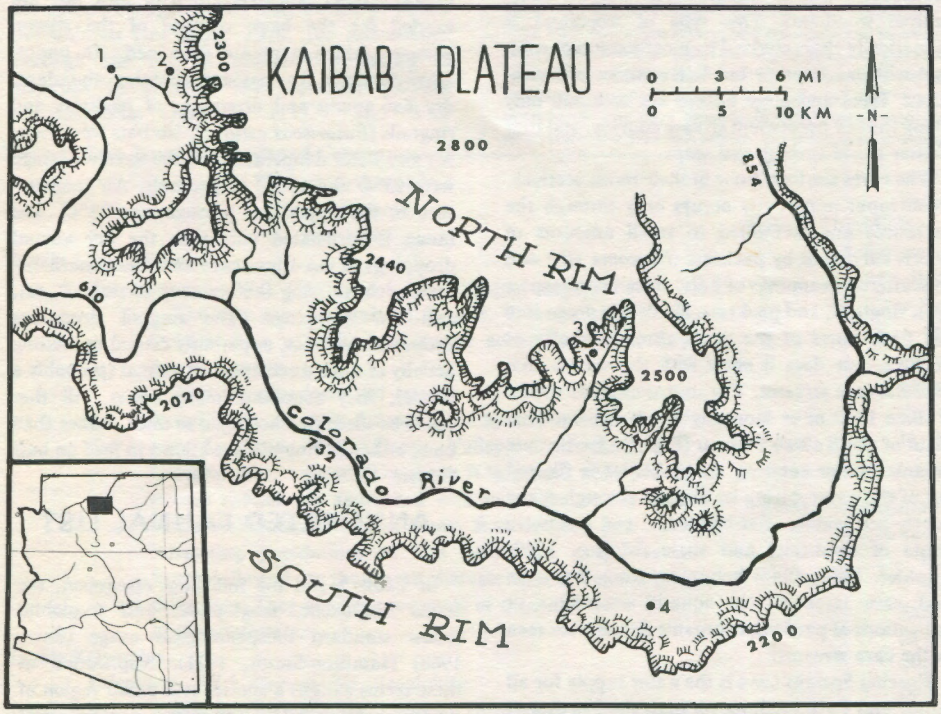

Figure 1. Schematic map of part of the Grand Canyon of the Colorado river in northern Arizona, showing locations of sites mentioned in the text. 1. Thunder Cave. 2. Tapeats Cave. 3. Roaring Springs Cave. 4. Caves on Horseshoe Mesa. Elevations are given in meters.

INTRODUCTION

Little is known of the invertebrate inhabitants of caves of southwestern United States, outside of those of Texas and of the vicinity of Carlsbad Cavern, New Mexico (see Mitchell, 1969, and the review of Welbourn, 1978). In a discussion of the relative lack of highly evolved cave-invertebrate faunas in the southwest, I (Peck, 1978) suggested that terrestrial litter invertebrates that have an evolutionary potential for cave specialization (that are "preadapted" for cave colonization) are known to be present in cool-moist montane forests in the southwest. These invertebrates should have had access to caves during the cooler and more moist climates of the glacials (pluvials), when such forests existed over a greater area and at a lower elevation. The lack of a cave-evolved invertebrate fauna is then due not to a lack of suitable ancestral colonists but is more likely a result of past and present periods of regional aridity. These would have eliminated most of the fauna that previously had access to and inhabited these caves.

The mode of action of aridity in the extinction of aquatic cave invertebrates is obvious: The groundwater fauna is eliminated as groundwater habitats vanish. The mode of elimination of an already existing terrestrial troglobitic fauna probably occurs in a two-fold manner: Terrestrial troglobites generally have very thin integuments and poor physiological control of water loss. They are generally intolerant of even small amounts of environmental desiccation within a cave. Secondly, increased regional aridity diminishes the net primary productivity of the epigean plant community that ultimately feeds the cave community and diminishes the transport of this food into the cave by runoff waters (Peck, 1976) or the percolation of water containing dissolved and particulate organic materials. Interestingly, some arid zone caves may experience increased food input from bat guano, but this, too, tends to eliminate troglobites (see Mitchell, 1969).

Parallels exist between southwestern United States and Australia, a continent with many limestone and karst areas and many cave systems but which has had an interglacial and Recent history of intensive and extensive aridity (Galloway, 1965). Australia has a poorly developed fauna of cave-evolved invertebrates (Hamilton-Smith, 1967) with only some 30 species of troglobites (most of which have been discovered since 1967) (B.P. Moore, A.M. Richards, personal communications), as compared to over 350 such species in the United States (Barr, 1968). The effects of aridity in causing this faunal impoverishment have been suggested (Moore, 1964; Richards, 1970). Additionally, Australia is a comparatively flat continent, and this has limited the development of extensive temperate montane forests with their deep, cool, and moist accumulations of litter and moss. As a consequence, few arthropods became adapted to such litter habitats and were thus preadapted (sensu Barr, 1968) to the occupation of Australian caves. My field work in both areas has convinced me that conditions in Australian *Nothofagus* (southern beech) forests most closely approximate those of the upper elevation forests of the southeastern and southwestern United States, and that these are the prime sites of the events of litter adaptation (and cave preadaptation). The argument is reinforced by the fact that the Australian troglobitic fauna is richest in Tasmania, and it is here that *Nothofagus* forests are the most extensive and the opportunities for litter adaptation are best developed.

A field test of these hypotheses on the impact of aridity on cave fauna biogeography and evolution in southwestern United States could be made in "desert" caves that have not experienced internal drying and that are near a montane source of litter-inhabiting invertebrates. Such caves should contain a cave-evolved terrestrial fauna, which should have a relationship with the past and present litter community in the montane forests. In an effort to verify these expectations, three major stream caves below the North Rim of the Grand Canyon, Arizona, were examined for invertebrate inhabitants in September, 1977.

This paper is a contribution toward the development of a more general, historical, and dynamic model of the evolution, distribution, and composition of terrestrial cave invertebrate communities.

THE CAVES

All three caves lie in the Cambrian Muav Limestone, above its contact with the impermeable Cambrian Bright Angel Shale. Permanent streams flow from their mouths. The caves are at elevations from 1160 m to 1580 m. This elevation range now possesses a sparse shrub vegetation, depending on slope and exposure. It includes the transition of the Lower to the Upper Sonoran Desert life zones of the southwest, where blackbrush desert merges into pinyon pine-juniper woodland. This type of woodland is climatically characterized by mostly summer rain, and with mild winter but hot summer temperatures. Trees and large bushes are common only along the few permanent stream courses, and they cluster about springs and seeps.

The caves are food-poor in their moist sections. Food input apparently occurs only through the entrances and is limited to small amounts of debris carried in by packrats (*Neotoma* sp.) and to scattered droppings of bats, mice (*Peromyscus* sp.), ringtails, and packrats. No debris drops into the back parts of the caves through shafts or crevices, nor does it enter with the waters that feed the cave streams. The source of these waters is some 1000 m or more higher on the sinkhole plain of the Kaibab Plateau (Fig. 1). Particulate organic matter entering the sinkholes is filtered out of the water during its descent through many poorly-permeable, flat-bedded, and massive strata of sandstone and shale (McKee, 1969; Strahler, 1944, 1948) before entering the caves and cave streams. No aquatic organisms or indications of particulate organic debris were seen in the cave streams.

Roaring Springs Cave is the water supply for all visitor and Park facilities on both the North and South rims of the canyon. Human entry is restricted. The cave is about 3.5 km long and is a system of high and generally narrow vadose passages. It is at an approximate elevation of 1580 m, or about 1000 m below and 7 km from the head of the Kaibab Trail. Invertebrate fauna was found only in the twilight zone or about 150 m into the dark zone from the western entrances (unpub. 1964-1965 map by the Central Arizona Grotto, in Park files; Seagle, 1935). Bats are scarce or absent. Packrat nest debris is present, but only in very dry areas. Air and water temperatures were 12°C.

Tapeats Cave lies behind Tapeats Spring, a tributary to Tapeats Creek. It is reached by trail from Monument Point or Little Saddle (near Indian Hollow Camp) via Thunder Spring, or by bushwacking from Crazy Jug Point. It is 18 km and a 1200 m descent from Little Saddle to Thunder Springs alone. The cave is at an elevation of 1180 m. An entrance section of small-diameter walking passage leads into a large-diameter trunk passage about 2 km long containing the river. Collections were made in only the first 200 m of the cave, because a raft and exposure suit are necessary to proceed beyond this region (Beck, 1958, 1959; unpub. 1974 map in Park files). Invertebrate fauna was found only on the few scattered items of debris (packrat droppings and food and nest materials).

Thunder Cave lies behind Thunder Spring, at about 1160 m. It is 1 km long and is reached by trail from Monument Point. This is a difficult and unpleasant cave to enter and traverse. The ledge traverse and rock climb to the entrance should be attempted only with a belay. The stream section is a narrow and scoured "sewer" passage above a deep, swift stream (Beck, 1959; unpub. 1959 map in Park files). An exposure suit and raft are needed for the back sections of the stream passage, which were not examined. An upper, large-diameter dry passage contains abundant, dry bat guano and droppings of packrats and ringtails (*Basariscus astutus*). No bats were seen. Air and water temperatures in the stream passage were 13°C and 11°C, respectively. Air temperature in the upper dry passage was 23°C. The fauna is associated only with the dry animal droppings of the upper cave and was remarkably scarce, considering the quantity of ringtail, rat, and bat droppings. The ringtail droppings showed some holes, apparently caused by feeding activity of some undetermined animal (probably a beetle); they contained many bones. All that could be identified belonged to mice, rather than bats, although ringtails are known to feed on bats (Murie, 1975:45).

ANNOTATED FAUNAL LIST

In Table 1 and the following discussion, the terms trogloxene, troglophile, and troglobite follow standard biospeliological usage (Barr, 1968) Hamilton-Smith, 1971). Application of these terms assigns a species to a broad region of the full spectrum of ecological and morphological specializations that invertebrates may develop for cave life. For the evolutionary and biogeographic purposes of this paper, it is useful to separate troglophiles into two sub-categories. Non-disjunct populations of troglophilic species are those known or expected to occur in suitable epigean environments in the immediate vicinity of the caves in which they occur. There is thus actual or potential genetic contact between the cave and epigean populations (see Christiansen and Culver, 1969, for exceptions in Collembola). In contrast, disjunct populations of troglophilic species are those not known or not expected in epigean environments in the immediate vicinity of the caves in which they occur. These are altitudinal or latitudinal disjuncts, and epigean populations would be expected or are known at higher elevations or latitudes in cool-moist forest litter or similar favorable habitats. Caves are then refuges for the survival of the disjunct low altitude

and/or latitude populations of the species. There is no present genetic contact between disjunct cave and epigean populations, and the cave populations are potential troglobites. These two sub-divisions are similar to but not exact equivalents of Hamilton-Smith's (1967, 1971) categories of first level and second level troglophiles, respectively.

EVOLUTIONARY AND DISTRIBUTIONAL INTERPRETATIONS

Much of the evolution of cave-limited invertebrates is thought to have been precipitated by Pleistocene climatic change and the subsequent isolation of populations in caves (see Barr, 1968; and Peck and Lewis, 1978, for references). It is well documented that climatic changes occurred in the American Southwest, and that these caused widespread changes in the distribution of plants and animals (see Peck, 1978, for references). Through the use of radiocarbon dating of materials in ancient, low elevation packrat middens, Van Devender (1977) and Van Devender, *et al.* (1977) have shown that woodland vegetational and faunal communities throughout the southwest changed in comparative synchrony to desert or grassland about 8,000 years ago, during a climatic shift to the present interpluvial (characterized by a reduced winter rainfall). Phillips (1977) and Cole (1979) using packrat middens from the Grand Canyon, found that vegetational zones (or at least major components of them) were displaced as much as 1,000 m below their present lower elevational limits on the canyon rims*. During the last glacial-pluvial, the coolest (but probably not wetter) summer conditions and wettest (but not significantly colder) winter conditions occurred from 24,000 to 14,000 years ago. We should expect that at this time at least part of the Canadian and Hudsonian spruce-fir forest life-zone floras (Rasmussen, 1941) and components of their litter faunas could spill from the Kaibab Plateau, down into the canyon to the vicinity of the caves. This must also have happened during earlier glacial-pluvials.

We can now ask whether any of the invertebrates found in the Grand Canyon caves reflect these changes in climates and distributional ranges? The trogloxenes and non-disjunct

*Pleistocene paleobotanical and palynological research is increasingly showing that modern plant associations have not had a fixed composition through time but that they should be considered as short-term assemblages. Each species has a unique distribution based on requirements or tolerances which differ from those of other species. Thus, past range shifts as a response to changing climates have been individualistic, and not as well-ordered and uniform movements of complete floral and faunal "community" units. Plant associations are then seen as temporal and somewhat random associations of species that arrived in an area and have been able to survive (See Matthews, 1979, for references). Among the animals in such communities, it is likely that some "litter" invertebrates have more dynamic dispersal abilities than the plants that characterize their habitats, and that they could occupy favorable and newly available sites sooner than woody plants. Movement ahead of the plants that normally form the litter, and that buffer it against climatic extremes, could occur through slopes and fields of talus which could have similar buffering properties. This dynamic potential for "litter" species movements has implications for the historical composition of communities of terrestrial cave invertebrates. They are generally patterned in that they contain members in the same higher taxa, but their initial specific composition in a specific cave must have a significant component of variability because of the historical accidents involved in dispersal. They will also not be stable through time, because of the random processes that promote extinction, and because each interglacial will introduce a new pulse of different species into the interacting mix in a cave.

Table 1. Cave fauna of the Grand Canyon.

Phylum Arthropoda

Class Arachnida

Order Aranea

Family Loxoscelidae

Loxosceles sp., W.J. Gertsch det., non-disjunct troglophile.

Thunder cave, 1 male, 1 female, 4 immatures, from webs at base of walls near guano accumulations in dry upper passage.

This is an undescribed species and is the fourth to be found in the genus in Arizona. The species is most closely related to one from Death Valley, California (W.J. Gertsch, pers. comm.). The genus is large and widespread; several species are associated with caves (especially near entrances) in the Caribbean Basin. Both epigean and cave-inhabiting populations of this genus are only weakly hygrophilic and are thus more characteristic of warmer and drier sites. They are not occupants of montane forest litter in the southwest.

Family Telemidae

Telema sp., W.J. Gertsch det., troglobite.

Roaring Springs Cave, 1 female, from small web in damp area with large rocks.

This small spider is an undescribed species with long legs, and small, widely separated eyes. It is the only known spider from an Arizona cave that seems to be cave-adapted (as a low level or relatively unspecialized troglobite) as well as being the first record of the family from Arizona. Other species (W.J. Gertsch, pers. comm.) occur in moist forest litter habitats in northern Utah, California, and the Pacific Northwest. For instance, *T. gracilis* occurs all over northern California in ground debris and occurs in caves in Calaveras and adjacent counties. Separate Californian species in Subway and Samwell caves, both in Shasta County, seem to have been derived from it. *T. pacifica,* known from British Columbia, Washington, Oregon, Montana, and into Northern Utah, is a probable ancestor for the Roaring Springs Cave species. The genus is a generalized one, probably once widely distributed over the world, but now surviving only as relicts in restricted areas. Epigean species occur in Africa, and other cave populations include *T. mayana* from a cave in Guatamala, another species from a cave in Ecuador, and *T. tenella* from caves in western France (W.J. Gertsch, pers. comm.).

Family Theridiidae

Achaeranea canionis (Chamberlin and Gertsch), W.J. Gertsch det., non-disjunct troglophile or trogloxene.

Tapeats Cave, 1 female; Roaring Springs Cave, 2 males.

These small spiders were in small webs where damp walls and floors meet. The species occurs in cave and mesic epigean situations over a wide area from New Mexico, through Utah and Arizona, to California. Other species in in the genus are frequently found near cave entrances.

Order Opiliones

Family Phalangiidae

Leiobunum, cf. *townsendi* Weed, W.A. Shear, det., trogloxene.

Roaring Springs Cave.

Many of these harvestmen occur just inside the cave's dark zone. They probably leave the cave at night to forage as predators. This species is widespread through the southwest and various species in the genus frequently occur in cave entrances throughout the United States.

Order Acari

Family Rhagidiidae

Rhagidia sp., cf. *hilli* Strandtman, Evert Linquist det., troglobite or disjunct troglophile.

Roaring Springs Cave, one at mouse (bat?) dropping on moist sand.

Rhagidia are known from cave locations in eastern and western United States and Mexico, as well as cool-to-cold and wet forest litter. *R. hilli* itself is reported only from Alaska and the Northwest Territories (Strandtmann, 1971), where it occurs under logs and rocks and in moss and lichens. Careful study could detect no differences between the Roaring Springs Cave specimen and the illustrations of *R. hilli.* However, neither the genus or the species are well enough known to say that they are or are not now distributed in suitable habitats in western and southwestern mountain forests. The specimen is clearly not the closely related species *R. grahami,* Elliott (1976), geographically the closest known described species, occurring in a cave in northern Utah.

(Table 1, continued)

Class Collembola

Order Entomobryomorpha

Family Entomobryidae

Tomocerus sp., K. Christiansen det., troglobite.

Roaring Springs Cave, several on scattered mouse (bat?) droppings on moist sand in dark zone.

This undescribed species has only four known close relatives, all from caves (three in the U.S. and one in Japan). One of these is *T. grahami* from Terrero Cave, Santa Fe County, New Mexico. Another is *T. missus* from caves in Missouri, Illinois, and Kentucky (discussed by Peck and Lewis, 1978). All of these are probably relicts of an extinct Asiamerican species group of troglophiles, which was similar in distribution to that of the present day troglophile *T. bidentatus*. This extinct form has been replaced on the surface by *T. flavescens*, but its derivatives persist in scattered cave systems. If this is so, additional related species should be found in other western caves (K. Christiansen, pers. comm.).

Class Insecta

Order Diplura

Family Campodeidae

Haplocampa sp., troglobite or disjunct troglophile.

Tapeats Cave, three specimens found on droppings on silt along wall in main trunk passage.

Various genera of campodeids are commonly found in caves and forest litter in eastern and montane western United States. *Hoplocampa* has a distribution of relict populations in the Rockies and Cascades, in lava tubes in the west, and limestone caves in Illinois and Missouri (Ferguson, 1975, Peck and Lewis, 1978).

Order Orthoptera

Family Rhaphidophoridae

Ceuthophilus sp., trogloxene.

Roaring Springs Cave, two teneral female camel crickets were found in the entrance zone.

The genus is often associated with caves throughout most of the United States.

Order Psocoptera

Family Psocidae

Psyllipsocus ramburii Selys-Longchamps, E.L. Mockford det., non-disjunct troglophile.

Tapeats Cave, one specimen on decayed leaf on moist rock floor in dark zone.

The species is known from Europe; in North America, it ranges from Michigan to Mexico. It is frequently found associated with dry debris in caves. The species is parthenogenetic, and most collections contain only females.

Order Coleoptera

Family Leiodidae

Ptomaphagus cocytus Peck, troglobite.

Roaring Springs Cave, 18 adults and many larvae were found feeding on a few scattered mouse (or bat?) droppings on moist sand. Tapeats Cave, 6 adults and 6 larvae on droppings and decaying cottonwood leaves on moist floor in dark zone.

The species was described and previously known from only four specimens from Roaring Springs Cave (Peck, 1973). The new material generally supports the previous description of the species. The wings, which extend slightly beyond the elytral tips in the Tapeats populations, are slightly longer than in the Roaring Springs populations, but they are still useless for flight. Although the species has reduced eyes, they are functional and are not as reduced as in other cave-specialized *Ptomaphagus*. The combination of reduced eyes, wings, and pigmentation, and the elongated appendages, suggest that the species is limited to caves and can be considered a low level or relatively unspecialized troglobite. All other western *Ptomaphagus* are widespread in epigean (or animal burrow) habitats except for two species specialized for deep litter (or talus) in high-elevation New Mexican forests (Peck, 1978).

Family Tenebrionidae

Eschatomoxys sp., C.A. Triplehorn det., non-disjunct troglophile.

Thunder Cave, one specimen on wall above guano in dry upper passage.

The genus is a peculiar triorophine tenebrionid with a narrow head and pronotum and unusually elongate antennae. These characteristics seem to be adaptations not for caves, but for scavenging in animal nests and burrows. Two species have been described from deserts in California, Baja California, and Utah; these or other species are known from Arizona, including Rampart Cave, Grand Canyon (Blaisdel, 1935, 1936; Sorenson and Stones, 1959; Triplehorn, pers. comm.). A prolonged fire in the Pleistocene ground-sloth dung deposit in Rampart Cave in 1976 has undoubtedly eliminated this beetle population as well as much of the inestimably valuable paleoclimatic record preserved in the dung. Other genera and species of tenebrionid beetles have recently been described and reported from caves on Horseshoe Mesa, on the south rim of Grand Canyon (Triplehorn, 1975).

Order Lepidoptera

Family Noctuidae

Pronoctua typica Sm., Eugene Munroe det., trogloxene.

Roaring Springs Cave.

Several of these moths were on the ceiling and walls of the cave, just inside the dark zone. The moth is widespread in the West, from British Columbia to California and Arizona. Other members of the subfamily Noctuinae (=Agrotinae) are also known to occur in caves, where they hibernate or aestivate.

Order Diptera

Family Tipulidae

Tipula (*Bellardina*) *rupicola* Doane, Herbert Teskey det., trogloxene.

Roaring Springs Cave.

Several of these large crane flies were in dark ceiling pockets in the twilight zone. They were probably using the cave as a daytime retreat.

Family Mycetophilidae

Mycetophila sp., cf. *fungorum* (DeG.), R. Vockeroth det., trogloxene.

Roaring Springs Cave; one female collected and several seen inside the dark zone.

This fungus gnat is widespread from Quebec to Alaska and southwards to Mexico, and is known from other western caves.

Family Sciaridae

Sciara sp., non-disjunct troglophile?

Tapeats Cave, one adult found with rotting leaves in dark zone near cave entrance.

These flies are frequently found in caves on moist, decomposing plant material.

troglophiles suggest little, because they use the caves only as daily or seasonal retreats, or are very wide-ranging species with considerable ecological amplitude. Most of these probably also now reside outside of the caves in the small, mesic groves of hardwood trees and shrubs that border the upper reaches of the streams issuing from the caves (Fig. 2). Even so, the moisture-requiring invertebrates (the flightless ones with poor dispersal mechanisms, at least) in these isolated groves at springs (as well as much of the vegetation) are disjunct remnants of more widespread mesic communities in earlier and more moist climates. In the last pluvial, there undoubtedly were more nearly continuous galleries of mesic vegetation along the better developed systems of permanent streams (but not along the Colorado River itself, which experienced periodic shoreline scouring by spring floods). With the more extensive streamside vegetation, many invertebrates had greater dispersal opportunities through moist litter. However, I know of no studies attempting to investigate the distributional history of the communities of forest litter invertebrates now isolated in the mesic forest remnants preserved in moist canyons and at springs in the southwestern deserts.

In contrast to the above, however, five species of disjunctly distributed troglophiles or troglobites are well enough known and distinct enough in morphology, habitat requirements, and/or geographic range to indicate that they must have reached the caves that they now occupy at some time in the past, during a more favorable cool-moist climate. They do not (and should not be expected to) occur in other habitats outside of, but at the same elevation as, the caves in the canyon.

The *Rhagidia* mite is closest to, if not the same as, a species known otherwise only from Alaska and the Northwest Territories. Since all *Rhagidia* taken outside of caves occur in very wet and cool-to-cold habitats, we can probably expect it today in litter in the spruce-fir forest zone on the high mountains of the southwest, including the Kaibab Plateau. Englemann spruce and Douglas fir still occur in scattered, cool, and protected (mostly northfacing) ravines and slopes on the Kaibab Plateau, above 2,400 m elevation (Rasmussen, 1941). If inhabitants of this forest zone descended some 1,000 m during the pluvial maximum 24,000 to 14,000 years ago, as did components of the lower woodland community, they could have come down to about 1,400 m, or below the elevation of Roaring Springs Cave. The mite could then have had easy access to the cave through colder and wetter litter.

Campodeid diplurans are not well enough known in the southwest to firmly comment on their distribution in general or on that of the species in Tapeats Cave. However, these insects are usually found only in cool and moist forest litter habitats and would not be expected to occur now in the canyon outside of caves. They would be expected, however, in such sites on the Kaibab Plateau. As envisioned for the mite, they probably reached the cave during a pluvial while the forest zone was lower; I assume (since morphological change requires time) the most recent pluvial if the species in the cave and that expected on the Plateau are the same, an earlier one if they are different.

The leiodid beetle *Ptomaphagus cocytus* has evolved from *P. fisus,* a widespread and fully-winged species associated with subterranean rodent nests and burrows throughout much of the southwest (Peck, 1973). I now suggest that it probably separated from *P. fisus* (by cave isolation and the loss of flying ability?) early in the Sangamonian interglacial (not during the Wisconsinan glacial as earlier indicated, Peck, 1973, p. 146). This is a judgement made in the light of what little is known on the rates of genetic differentiation in this genus (Laing, Carmody, and Peck, 1976). The species' adaptations seem too great to have developed in caves in only the present interglacial, but not too extreme to have prevented it from dispersing overland to various caves in the Wisconsinan. If Wisconsinan (or earlier) populations of *P. cocytus* were flightless, they must have used overland dispersal routes through moist litter, talus, and/or animal burrow habitats to reach the two caves that the species is now known to inhabit. Geological structure (faults) and hydrology (see geology review of McKee, 1969) make the existence of subterranean dispersal routes between the two caves, 41 km apart, highly unlikely if not impossible. Dispersal to the region of the caves (unless these were the actual site of its interglacial speciation) was probably in the last glacial-pluvial. At this time, spruce-fir forests probably covered the Kaibab and spilled over the rim and down stream courses to or near the caves (but probably not actually as low as the 1,190 m elevation of Tapeats Cave).

Figure 2. Spring at Thunder Cave, at the base of a 300 m high cliff of sandstones, shales, and limestones. The local vegetation at the elevation of the caves in the canyon is shrub desert (left foreground); except near springs or seeps, where moisture and often - cooler conditions allow mesophytic trees and shrubs to exist. These pockets of vegetation (and at least some of their associated invertebrates) are disjunct remnants of formerly more widespread cool-moist forests that occurred in the canyon during pluvials.

The *Telema* spider also has a comparatively low level of cave-adapted morphology. This suggests that its history may be similar to that of the *Ptomaphagus* beetle and that it may have experienced similar or the same events (in the same places?) of isolation and speciation in the Sangamon, the possibility of some limited dispersal in the Wisconsinan, and recent restriction to Roaring Springs Cave (and others?).

The eyeless *Tomocerus* collembolan is in a genus that generally tends to conserve eyes (K. Christiansen, pers. comm.). The eye loss is then one of several extreme morphological specializations in the species. This and the very relict distribution of the species' relatives indicate a very long period of subterranean evolution, perhaps starting during the Yarmouthian or an even earlier interglacial stage. It is interesting to note that only this remnant of a very old collembolan invasion was found. There are no traces of the most recent wave that colonized so many caves in Texas and New Mexico (Christiansen and Culver, 1969). This suggests some degree of faunal isolation between the Grand Canyon region, and Texas-New Mexico (K. Christiansen, pers. comm.). The barrier may be the lowlands of the Colorado River.

DISCUSSION

The "taxon cycle" concept is of potential use in understanding the evolution of cave-adapted arthropods. Taxon cycles are defined as recurring changes in range expansion and contraction of species on island groups (or habitat islands) as inferred from patterns of geographic distribution and taxonomic differentiation (see Rickleffs and Cox, 1978, for review). As have others before me (see Peck and Lewis, 1978, for references) I see the temperate terrestrial troglobitic fauna of North America to be a generally repetitive and patterned assemblage descending from litter-dwelling ancestors of cool-mesic forests. The ranges of these ancestors fluctuated in response to Pleistocene climatic changes, and some of their descendants are found in caves, which represent restricted islands of suitable environments. A cautious evaluation of the circumstantial clues of distribution and taxonomy may give relative indications of when various components of a terrestrial cave community were introduced into the cycle in caves.

The relative amounts of time spent by a taxon in the cycle are suggested by its geographical and morphological separation from relatives. Several

of the species in a community may represent the same pulsed wave of occupants and should be at a relatively similar stage in the cycle of adaptation. The increasing levels of specialization may represent increasingly longer times of cave occupation. The relative times of entry into a cycle could then be correlated with known times of past climatic suitability for entry into the cycle. Reliability of interpretation may be enhanced by using known events as markers (such as the time a cave became suitable for occupation; for instance, following a period of periglacial unsuitability as in Illinois) or when several components of the fauna show similarities in their patterns. The picture will probably be more clearly seen where climatic change has been more extreme, such as in southwestern U.S., or in the southern end of the Appalachians. The question of how a species or set of species proceeds through the entire cycle in caves is an interesting one that is yet to be fully determined.

When my interpretations of the above data are summarized, they suggest the evolutionary history of the community as reconstructed in Table 2. It is to be expected that future work on the taxonomy and distribution of cave and epigean litter invertebrates in southwestern United States, as well as on regional Pleistocene paleobotany, geochronology, and paleoclimatology, will change some of the details of the scheme. Its major tenents can be tested by additional discoveries of cave and epigean invertebrates in the Grand Canyon region, either as new taxa, or as new localities for known taxa. Both may provide details against which to judge the proposed patterns of dispersal and isolation and their consequent results in morphological and geographical separation. Although the scheme is open to criticism, I offer it as a synthetic framework within which to consider the data that have been gained. I am less concerned that my interpretations be found invalid than that their assumptions might not be tested further in the light of new data.

There are, of course, possible shortcomings to this taxon cycle of thought. They include differences in levels of preadaptation, rates of evolution in different taxa, degrees of selective pressures, genotypic variability, evolutionary-ecological strategies, and so on. These objections should apply, however, less to caves than to other communities which are more complex in their components, biotic interactions, and selective pressures. Even so, the limited studies that are available show that some of these uncertainties are more imagined than real (Rickleffs and Cox, 1978). these potential obstacles should not prevent us from attempting to look for the generalities that may exist. There is now a large body of ecological, evolutionary, distributional, and paleoclimatic fact and theory with which we should attempt to correlate and interpret the results of speleobiological surveys. Cave faunas contain a much more exciting story of biotic migration and change than is presented in a faunal list alone.

Radioisotope studies of cave deposits reveal some of the effects of changing paleoclimates in southwestern caves (Harmon and Curl, 1978), but when specific Grand Canyon caves became open for faunal occupation is not known. Inferences from erosion rates in the canyon (Hunt, 1969) suggest that the caves studied for this paper were available in the Sangamon, but possibly not earlier. The number of interglacial starting points for taxon cycles of speleobiological evolution are also not known, but are probably more than the four recognized in the "classic" sequences of deposits in the central United States (see Harmon, *et al.* 1977, 1978). A stabilized system of terms for time intervals and events in the Pleistocene is also yet to be achieved (Boellstorff, 1978). Wright (1976) and Beaty (1978) see the Pleistocene as a sequence of long-lasting glacials of 80 to 100,000 years punctuated by significantly shorter interglacials of 10 to 15,000 years. This suggests short interglacial periods for population

Table 2. A suggested reconstruction of the evolutionary history of the times of subterranean isolation and evolution (interglacials) and dispersal (glacials) in the invertebrate fauna of Grand Canyon caves.*

Time	*Tomocerus* sp.	*P. cocytus.* *Telema* sp.	Campodeid (?) *Rhagidia* sp.	Non-disjunct Troglophiles and Trogloxenes
"Yarmouthian" (or earlier) Interglacial: caves isolated by desert.	Ancestors cave isolated, form low-level troglobite species in Grand Canyon (?) and elsewhere			
Illinoian Glacial (180,000 to 130,000 years B.P.): forest at or near caves.	Overland dispersal of low-level troglobites into Grand Canyon (?)	Dispersal into northern Arizona (?)		
Sangamonian Interglacial (125,000 to 80,000 years B.P.): caves isolated by desert.	Cave isolation in Grand Canyon, additional evolution of troglobites, epigean ancestor extinction (?)	Cave isolation as disjunct troglophiles, each speciates in single cave to low-level troglobite.	Isolation in Kaibab Plateau forest litter.	
Wisconsinan Glacial (80,000 to 15,000 years B.P.): forest at or near caves at least 24,000 to 14,000 years B.P.	Overland dispersal (?), same species in other caves will suggest this.	Overland dispersal, *P. cocytus* to two caves, *Telema* sp. expected in other caves.	Overland dispersal from Kaibab down into Canyon	Living at lowest elevation sites in Canyon
Recent (interglacial): caves isolated by desert from about 8000 years B.P.	Isolation in one or more caves as highly evolved species, epigean ancestors extinct, very relict distribution of relatives.	Isolation in one or more caves as low-level troglobites, epigean ancestor survives.	Cave isolation in Canyon as disjunct troglophiles, also in Kaibab litter (?)	Move to higher elevations of Canyon and occupy caves and other sites.

*Late Pleistocene pluvial climates in southwestern United States were generally contemporaneous with glacial climates in the northern part of the continent (Van Devender, 1977). The climatic fluctuations that accompanied glacial stadia and interstadia were probably not of sufficient duration to provide adequate time for genetic isolation and population evolution. Such evolutionary time is probably available when these are combined into full glacials and interglacials, as shown in Table 2. The abundant fossil record of terrestrial and semi-aquatic arthropods shows little or no evidence of speciation in the later half of the Pleistocene. This is because these animals met climatic change merely by adjusting their geographic distributions. However, speciation in the later part of the Pleistocene is to be expected where extreme selective pressures operate on small, distributionally immobilized, and genetically isolated populations such as those occurring in caves today as disjunct troglophiles. Modern troglobitic species resulted from the survival of only a small number of such populations. The fate of most troglophiles, when isolated from their epigean populations is extinction. Otherwise, there would be many more species of troglobites.

isolation and genetic reorganization and long glacials for increased opportunities for overland dispersal and biotic "testing" of the new genotypes. All these factors hamper the biogeographer and evolutionist in making generalizations on the historical development of communities of temperate terrestrial cave arthropods.

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Natural Trap

Staging Area: Cody, Wyoming

Discipline: Archaeology

For 20,000 years, a large vertical cavern 15 miles west of the Big Horn Mountains near the Montana border trapped unsuspecting animals at the bottom of its 65-foot shaft. Invisible to animals on the run, the cave is unique for its stratified record of prehistoric fauna, now long extinct. At the bottom lie mammoth, bear, dire wolf, camel, antelope, three kinds of Equus (the ancestor of the modern horse) and possibly a fourth. Few Pleistocene sites have yielded muskox, but Natural Trap has revealed three peculiarly long-snouted specimens that are quite different from modern muskox and noticeably longer-nosed than known ice age forms.

Dr. B. Miles Gilbert and EARTHWATCH will continue to recover materials of extinct Pleistocene animals who so long ago were trapped in a cavern west of the Big Horn Mountains of Wyoming. The Pleistocene is the geological time period (from about 2 million years ago until 10,000 B. C.) during which most mammals, including man, evolved.

In cooperation with the University of Kansas, Dr. B. Miles Gilbert, a physical anthropologist at the University of Missouri, has been excavating Natural Trap with support from EARTHWATCH for the last six years. His evidence appears to indicate that rapid climatic and environmental changes (in a 500-year period during the last 20,000 years) may have influenced the survival and extinction of certain species alleged by some to have been overhunted by early man.

This season, Gilbert will investigate skeletal remains of the earliest and largest animals, many of which are best known from Natural Trap excavations. He needs volunteers to help him continue his research.

EARTHWATCH teams will be instructed in all aspects of excavating, and will assist in the identification, removal, screening and cleaning of specimens. Team members will make the 65-foot descent into the cave daily, either by free-fall rappel or climbing down via scaffolding.

Field conditions: Accommodations are a campsite of tents with no hot water or electricity. Despite these challenges, the atmosphere is friendly and easygoing, with evening discussions around campfires and plenty of opportunity to hike and explore the magnificent Big Horn country. Laundry, swimming pool, and provisions are in a nearby town.

Interests in climbing, photography, geology, spelunking, and zoology welcomed.

EARTHWATCH *news*

Box 127 10 Juniper Road
Belmont, MA 02178

National Speleological Society
Cave Avenue
Huntsville, Alabama 35810

Address Correction Requested

12386 R 0781 NSS 1
HORTON H. HOBBS, III
601 WHITE OAK DR.
SPRINGFIELD, OH 45504