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Structural Control Of Cavern Development In Howe Caverns, Schoharie County, New York

William J. Gregg *

ABSTRACT

Development of the main, 4000-ft passage of Howe Caverns, Schoharie County, New York, previously has been attributed to solution along a local fault partially exposed in a nearby quarry. Various features of passage morphology within the Caverns have been correlated with the fault zone by previous authors and these features have been cited as evidence supporting a general concept describing the development of the largest cavern systems in New York State. Current investigations show that the fault in question has not been a significant factor in the development of the main passage of Howe Caverns. This passage is related to cavern development subparallel to the regional strike of bedrock, with modifications of passage morphology through joint control. The hypothetical extension of this fault to the Northwest Passage of McFail's Cave, as attempted by previous workers, has been justified neither by the author's survey nor by those of other workers presently involved in field investigations.

Field studies have shown that the presence of a fault within a cavern does not necessarily imply that faults are more important as zones of groundwater infiltration than are joints and that, in certain instances, faults may act as relatively insoluble zones during passage development.

INTRODUCTION

Howe Caverns is located in east-central New York State, on the northern front of the Helderberg Plateau, at N42° 41′ 45″, W74° 23′ 54″ (Fig. 1). The present entrance to the commercial section of the Caverns is situated on a hillside 4 miles east of the village of Cobleskill, in Schoharie County. Access to the Caverns is primarily by State Route 7, which runs from Albany, N. Y. to Binghamton, N. Y. and the Pennsylvania line. A two-lane paved highway leaves Route 7 in the vicinity of Braymanville, N. Y., heads north across the Cobleskill, and passes the private road leading to the commercial entrance to the Caverns.

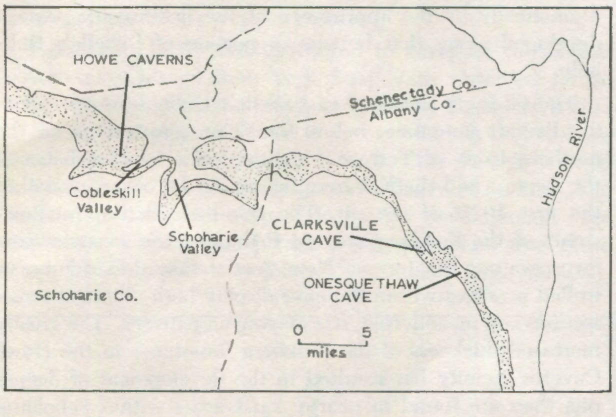

Fig. 1. Map of study area—shaded portion represents outcrop belt of cavernous limestone sequence.

GEOGRAPHIC SETTING

The Helderberg Plateau, within which the Caverns lie, is a dissected upland surface of early Tertiary (Eocene) age dipping gently to the south. Subsequent erosion has resulted in southward retreat of the escarpment and simultaneous development of a second, late Tertiary, surface surrounding the escarpment (Goldring, 1935). Retreat of the northern front of the plateau during the late Tertiary was accompanied by entrenchment of streams within the plateau, leading to the development of down-dip incisions through the limestone sequence into the Ordovician shales below. In the study area, Schoharie Valley is the largest such incision. Next in size are its tributaries, Fox Creek and the Cobleskill. Development of the largest cavern system in northeastern United States, McFail's Cave, as well as that of Howe Caverns itself, is associated with subterranean drainage into the incised valley of the Cobleskill.

Pleistocene glaciation mantled the karst with drift, thus precluding detailed study of the pre-glacial karst surface. Areas of exposed bedrock can be found adjacent to existing cliff-lines, where post-glacial erosion has removed drift deposits, and within areas where solutionally enlarged surface joints and sinkholes have removed the surrounding drift. Fossil cliff-lines, predating glaciation, can be traced under extensive drift deposits throughout the area.

The removal of glacial drift during development of limestone quarries in the area affords one the opportunity to examine freshly exposed bedrock. Exposures show extensive glacial striations and record bevelling of the former karst to a relatively barren surface. The existence of fresh striations and the lack of rudimentary mesoscopic solution features point to negligible solution of the rock surface below the organically deficient glacial covering. Post-glacial surface features are limited to modifications of the rims and walls of pre-existing cutters and sinkholes, where surface runoff from nearby basins is concentrated.

The partial map of the commercial section of the Caverns (Fig. 2) is the work of Homberger and others (Clymer, 1937), with additions by the author. Measurements of structural features and cross-sections of the Caverns were taken by the author during 1972 and 1973. For additional information concerning the continuation of passages beyond the commercial section of Howe Caverns, the reader is referred to previous workers (Addis, 1969).

STRATIGRAPHIC SETTING

Table 1 is a stratigraphic section for the Howe Caverns area (Gregg, 1973). Thicknesses measured by the author are based upon lithological boundaries established by Rick-

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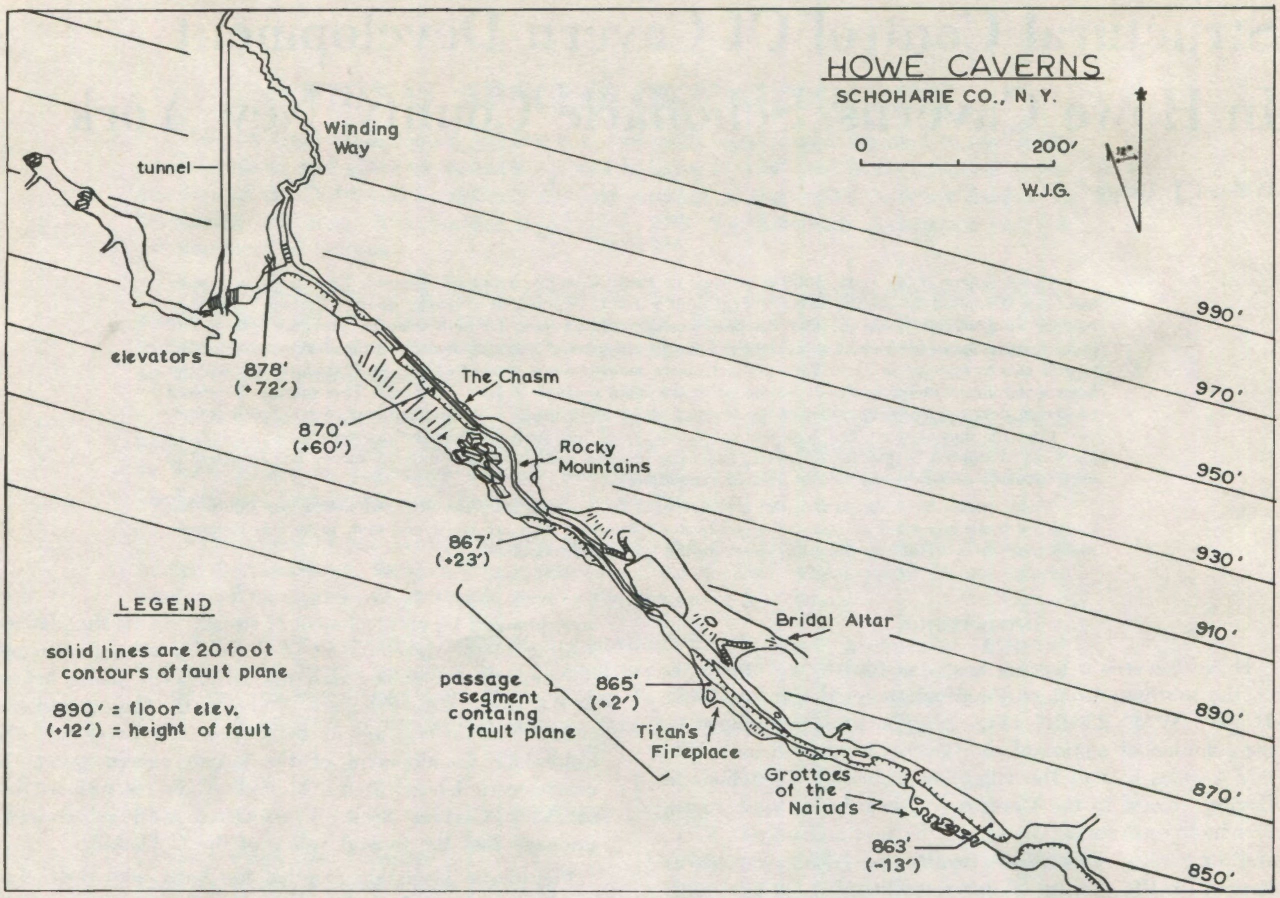

Fig. 2. Map of the commercial portion of Howe Caverns, showing relation of fault plane to cavern passages.

ard (1962). The New Scotland formation, consisting largely of calcareous shales, is conspicuously absent in the Howe Caverns area. The westernmost exposure of this formation is on the east side of Schoharie Valley. Here, it is in its normal stratigraphic position, 43 ft above the basal beds of the Kalkberg. The New Scotland formation at this locality is approximately 46 ft thick and is capped by 14 ft of strata clearly belonging to the Kalkberg formation. On the western side of Schoharie Valley, this 46-ft section has undergone a facies change, becoming identical in lithology to the Kalkberg formation. The transition is marked rather dramatically by the appearance of the first cavern passage developed along that horizon, a portion of LaSelle's Hellhole.

TABLE 1. Stratigraphic thicknesses at (A) Howe Caverns, (B) Schoharie Village, and (C) Gallupville. Order of lettering runs from west to east. Data from Rickard (1962) and Gregg (1973).

FORMATION—Member	Thicknesses (in feet) A	B	C
Becraft—Becraft limestone	20	23	14
Kalkberg—Kalkberg limestone	absent	14	14
New Scotland—New Scotland shaley limestone	absent	46	46
Kalkberg—Kalkberg limestone	104	43	42
Coeymans—Ravena limestone	54	51	49
Manlius—Thacher limestone	36	42	46
Rondout—Chrysler dolomite	37	28	23
Cobleskill—Cobleskill limestone	9	9	8

The 62-ft pit entrance to LaSelle's Hellhole is opened in the Becraft limestone, below the Onondaga terrace on the northern front of Terrace Mountain. The contact between the Becraft and the Kalkberg below can be observed within the first 10 ft of the pit. The thin-bedded, impure limestones of the Kalkberg are 104 ft thick at this location, now incorporating the former New Scotland section. Joint-controlled passages within the cave display both elliptical cross-sections and meandering, stream-canyon patterns. The greatly increased thickness of the Kalkberg limestones in the Howe Caverns vicinity has resulted in the development of deeper pits than are found in nearby karst areas within Schoharie and Albany Counties.

The Coeymans, Manlius and Rondout formations can be successively observed as one travels downstream in Howe Caverns. From the vicinity of the elevators to the dock on the "Lake of Venus", the tour level of the Caverns is predominantly developed in the Manlius formation. Abundant polygonal mudcracks, ripple marks, and cross-bedding can be observed along the ceiling and walls of the passage. The contact between the blue-grey "inch beds" of the Manlius formation and the buff-weathering straticulate beds of the Rondout formation below can be observed at the dock on the "Lake of Venus".

STRUCTURAL CONTROL

Jointing and regional structure

The heterogeneous fabric brought about by systematic vertical jointing in the limestone is the most important structural feature governing passage orientation and cavern development in the Howe Caverns vicinity. The author's study of joint systems in the area has produced slightly different results from those of the Barton Hill Project, 6 miles to the east (Anderson, 1961). The principle orientations of the regional joint pattern are N18E and N85W. Fig. 3 presents an analysis of 83 joints within the Caverns. In addition to the principal orientations already mentioned, a few less frequent joint sets also can be observed. The frequency distributions represented in Fig. 3 range from 24% for the more pronounced joint set to a mere 1% of the total readings for the three weakest joint sets shown. The measurements were taken at many different horizons throughout the Manlius limestone. Units within the formation which are more massive in bedding character often show stronger and more frequent jointing than units which are thinly bedded. Joints frequently are not continuous from one horizon to another, but master joints throughout the cave represent the full spectrum of joint orientations shown in Fig. 3.

The limestone sequence strikes N70W to N80W and dips 1½ to 2 degrees south. Relatively minor variations in the orientation of bedding may have significant effects on passage trends (Palmer, pers. comm.).

Previous suggestions regarding fault control

The effects of fault zones on cavern development have been discussed by several workers and two lines of thought are apparent in the literature. Rutherford (1971) and Werner (1972) demonstrate the effects of low-angle thrust faults to be, primarily, changes in passage morphology. On the other hand, workers such as Krinitzsky (1947) and Ford (1965) are concerned with the importance of fault zones as determinants of cavern orientation.

Egemeier (1969) has attempted to correlate the largest cavern passages in New York State with observed faults. Most notable among the examples given by Egemeier is that of the main passage of Howe Caverns, which is said to have been developed entirely along a fault. This passage is cited as evidence for the relatively greater efficacy of faulting than of joint control with respect to cavern development, "because cracks along fault planes usually are wider than those along bedding planes or joints" (Egemeier, 1969, p. 100).

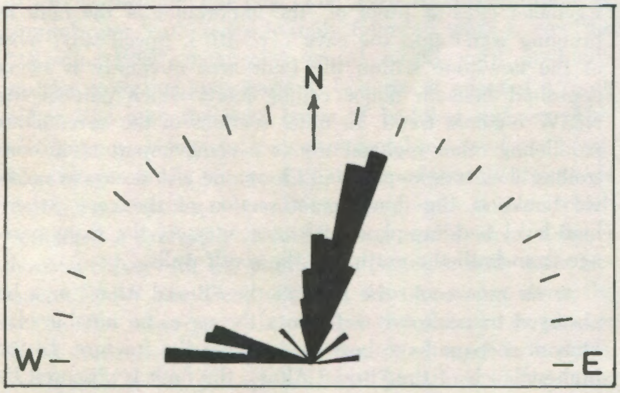

Fig. 3. Equal area circular histogram for vertical joints in Howe Caverns, Schoharie County, N. Y.

Egemeier infers two different strikes for the fault, based upon the diagrams presented (N48W and N62W). The former bearing is used to link the Howe Caverns fault with the fault appearing to the east at Veenfliets Cave, while the latter bearing is used to demonstrate a proposed link between the Howe Caverns fault and another thrust fault dipping precisely the opposite way in the Northwest Passage of McFail's Cave to the west.

The Howe Caverns fault

A low angle thrust fault can be observed in the limestone quarry operated at the village of Howe's Cave, ¾ mile southeast of the commercial entrance to the Caverns. This fault strikes N75W, dips 14° to the south, and has a mean displacement of 1 ft 8 in. along the western side of the quarry. The structure was recognized in the 1960's by Harold Davis (Davis, et. al., 1966), who believed it to strike north towards Grosvenors Corners. The fault cannot be traced outside the quarry, due to extensive drift deposits. The various extensions of the fault postulated by Egemeier are difficult to substantiate. Particular difficulty is encountered in proving the eastern extension, because of the existence of an intervening valley filled with glacial drift.

Within the quarry, the offset is easily seen along the west wall in the lower, massive layer of the Thatcher member of the Manlius formation. Minor amounts of water can be seen trickling from the fault in a few locations during wet seasons, but the significance of the fault plane as an important zone of groundwater infiltration is open to question. Blasting on the quarry face may have drastically increased the flow of water into this zone; the limestone everywhere around the quarry exhibits severe conchoidal fractures from quarrying operations. It has not been possible to trace the fault directly from the quarry into the Caverns, since the fault becomes hidden by extensive talus long before the entrance to the Caverns is reached. Within passages near the quarry, this fault cannot be seen, because it lies well below the elevation of the Caverns in this area.

Evidence against fault control

The strike of the fault, as measured by the author, differs considerably from that cited by previous workers. Because the fault maintains a linear strike in the Cobleskill area, deviations such as have been suggested by others are not easily explained.

Fig. 2 depicts lines of equal elevation along the strike of the fault plane. Data on which this projection is based were obtained by determining the strike of the fault over a distance of 900 ft within the nearby quarry. This was intended to minimize distortions of the fault surface which occur on a mesoscopic scale, enabling precise correlation of the projection with the fault segment actually observed within the Caverns.

The lowest level of the section at "Titan's Fireplace" is shown in Fig. 2 to be 865 ft above sea level. The elevation of the fault surface at this same location is shown by the contour lines. Figures appearing in parenthesis below base level elevations represent the height (or depth) of the fault plane with respect to the floor of a particular passage segment.

In the southern portion of the map, the fault plane is shown to be more than 13 ft below the Caverns level. The fault trace gradually rises until it appears from beneath a clay bank 20 ft south of "Titan's Fireplace". From this point, the fault can be traced north along the passage, through the mouth of the "Old Witch", gradually rising, and eventually disappearing into the ceiling near the "Rocky Mountains".

Within this section, the fault is best seen along the southern wall of the stream channel. It may also be seen on the northern wall opposite "Titan's Fireplace", though it is less easily discernable there. The pillar containing the "Old Witch" is the only other place along the north wall of the Caverns where the fault can be examined.

To the north of the section indicated, the fault continues to rise, eventually reaching an elevation 72 ft above the floor of the cave near the entrance to the "Winding Way". In the far reaches of the passages beyond the "Winding Way", the fault lies in excess of 200 ft above the Caverns.

It is evident from Fig. 2 that the fault could not have excercised much control over the development of the 4000-ft long main passage, because it intersects the passage only for 300 ft; to the west and to the east of this short section, the fault is, respectively, above and below the level of the cave. Further, the influence of the fault on passage morphology within the 300 ft section is negligible compared to the combined influences of jointing and bedding orientation.

It is worthwhile to note the characteristics of the fault zone where it intersects the cave. Slickensides can be observed on the hanging wall in a number of places, even though this surface has been subjected to prolonged periods of solution and mechanical erosion by the stream. Slight modification of the passage due to the presence of the fault may have occurred in "Titan's Fireplace", but the correlation is not definite. Because structural feature such as faults tend to be propagated along pre-existing zones of weakness in the rock, rather than within relatively competent areas, the small solution pockets which can be observed in this area may reflect characteristics of that particular horizon rather than the effects of the fault plane itself. Indeed, as one travels further downstream and out of the area of the fault, small grottos appear intermittently in the horizon mentioned as well as in higher and lower zones within the Manlius limestone, without any apparent faulting. In "Titan's Fireplace", the fault zone can be seen cutting across the center of one "angel wing" of limestone. If the fault was, indeed, a zone of access by groundwater, such a feature would be highly unlikely to develop.

Fig. 4 contains cross-sections of the main passage both east and west of the fault area. Section 'A' is 200 ft west of "Titan's Fireplace", where the fault trace is close to the ceiling. The lower right-hand flowstone bank rests upon a thin layer of clay and sand. Its development can be attributed to water actively dripping from joints in the ceiling, rather than to seepage along an undiscernable fault plane. Section 'B' lies in the center of the fault area and cuts through the "Bridal Altar", located at the upper right of the section. The solid line represents the area where the fault is actually visible, the dashed line represents the hypothetical extension of the fault into the north wall. The apparent southward dip of the cross-section is deceptive, since the north wall is obscured by extensive stream fill. The large joint in the ceiling at the "Bridal Altar" is the only structure introducing water into the cave in that area.

Section 'C' is typical of the majority of the downstream cross-sections of the cave, with the exception of a few rooms developed along major cross joints. There are no faults to be seen here and variations in passage morphology are controlled by jointing, bedding orientation, and differential resistance to weathering between adjacent lithologic units.

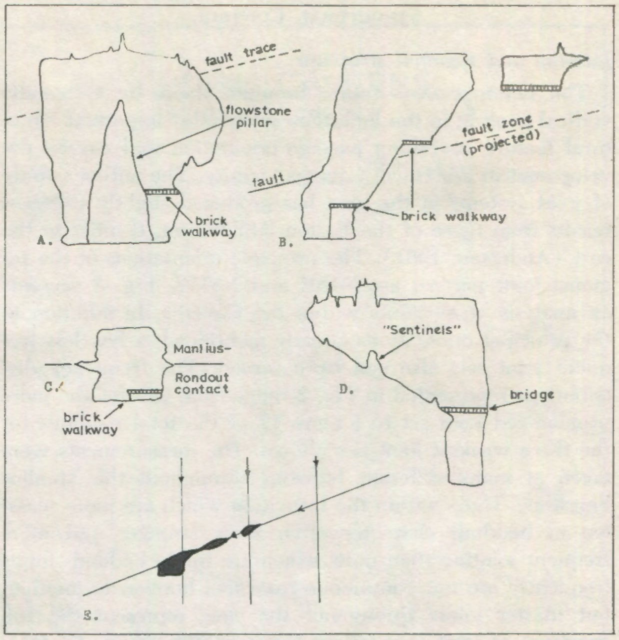

Fig. 4. Selected cross-sections along the main passage of Howe Caverns. (A) west end of Gallery of Titan's Temple, (B) near the Bridal Altar, (C) at the dock on the Lake of Venus, (D) in the Chasm, showing the Sentinels (stalagmites), (E) "typical" section from Egemeier (1969). All sections face west. Vertical and horizontal scale for sections A, B, C, and D is 30 ft per inch.

Section 'D' is taken from the "Chasm", over 400 ft upstream (west) of the fault area. The flowstone terrace on the left can be attributed to water from a series of major joints in the ceiling. The entire terrace rests upon a limestone ledge, although about 6 in. of stream fill intervenes between the bedrock and the flowstone covering. The general slope of the terrace does not reflect fault control, because no faults can be observed along the north wall of the passage at this location. Section 'E' is the cross-section of Howe Caverns which Egemeier presents as "typical". It contrasts markedly with the cross-sections measured by the author.

In addition to the absence of any fault-dominated cross-section, the main passage of Howe Caverns lacks extensive flowstone deposits along the footwall of the fault which Egemeier cites as proof of "the importance of the fault in bringing water into the cave" (p. 107). Specifically, most of the flowstone within the fault area obviously is being deposited beneath major ceiling joints which parallel the N85W regional trend. In other sections of the cave, joints paralleling other regional trends become important in controlling flowstone deposition. Flowstone also occurs as massive banks in the downstream section of the cave, where high-level bedding-plane passages intersect the main passage from both the north and the south walls.

At no time could the fault in the "Bridal Altar" area be observed to transport water into the cave; no notable clay films or seepage have been seen within the fracture. In the highest levels of the "Bridal Altar", the fault is obscured by the clay and mud stream fill which covers the north wall to within two feet of the ceiling. No conclusive observations can be made as to whether or not the fault initially acted as a zone of infiltration here. The fault does not transmit water in the section of the north wall directly opposite "Titan's Fireplace", nor does it modify the passage cross-section.

Other faults within Howe Caverns

The fault thus far discussed is not the only fault to be observed within the Caverns, although it far outweighs the others in terms of extent and displacement. Limestone has been freshly exposed within a new tunnel blasted from the "Winding Way" to the area of the elevator shaft in order to facilitate tourist parties. Minor faults in this section of the cave have various orientations and usually are subparallel to bedding. They cannot be traced out of the tunnel, because their subparallel orientation to primary layering precludes their being identified on a weathered surface. Amounts of displacement are not measurable due to the lack of an adequate marker horizon, but slickensides can be readily observed.

Slickensides usually can be seen only on the calcite "veins" which mark fault zones throughout the section. It is highly unlikely that these calcite veins were deposited by normal cavern processes, because the slickensides show the material to have been in place at the time of faulting. It seems much more likely that the calcite formed by recrystallization of the limestone during faulting, with contemporaneous development of slickensides in the zone of recrystallization. Features related to solution or deposition of carbonate minerals are not visible in any of the fault zones exposed in the tunnel, although newly exposed vertical joints display solutional enlargement and open fissures ranging from 5mm to 20mm in width. It seems likely that, if the faults were important zones of groundwater movement, these joints would show some tendency to have been preferentially enlarged by solution at the plane of intersection of the two features. Instead, one can observe joints passing through the cross-cutting faults with no apparent enlargement at the plane of intersection. One may argue, then, that these faults have been "welded" during the tectonic activity which produced them, and that they are considerably less permeable to groundwater than either joints or, one suspects, even primary layering.

An alternative interpretation

Preliminary observations indicate that the main passage of Howe Caverns was initiated as a low, meandering, strike-oriented, bedding opening. The earliest concentration of groundwater in the cave initially followed what is now the "Winding Way", making its way down-dip until, gradually turning from this joint-controlled course, it adopted a route subparallel with the local strike of bedding surfaces. This change in passage trend may correspond to one of two possible changes in the structure of the limestones. It is possible that the descending stream left a stratigraphic horizon which contained a profusion of N18E joints and entered a lower horizon either with less joint development or with more frequent N85W joint sets, allowing flow to occur along the strike. The other possibility is that the changes in passage trend correspond to barely perceptible changes in bedding orientation at the passage juncture. Situations such as this, in which "vadose" canyons trend down-dip to strike-oriented tubes at the water table, are quite common (A. N. Palmer, pers. comm.) and both of the alternatives cited may be factors influencing changes in passage trends.

From the junction of the "Winding Way" with the main passage, the ancestral cave stream coursed through the high-level channels visible in the ceiling and through the abandoned passage behind the "Bridal Altar". Subsequent lowering of the base level of the cavern stream, probably in response to rapid changes in the Cobleskill Valley, resulted in the successive abandonment of high-level passages when developing bedding-plane passages on lower levels captured their streams.[1] Throughout the developmental stages, modification of passage morphology by minor thrust faults was restricted to mesoscopic solution features. There is no conclusive evidence that faults ever were more important as zones of groundwater infiltration than were master joints in the limestones.

The patterns of the great majority of caverns in New York State (specifically: Skull Cave, Howe Caverns, Schoharie Caverns, Haile's Cave, and Ball's Cave on Barton Hill) are predominantly controlled by factors other than faults. Within nearby McFail's Cave, for example, faulting is apparent only in the Northwest Passage and does not control a majority of the cavern passages. Passages controlled by faults continue to be the exception rather than the rule in the caves of New York State.

The nature of faults in other caverns

Study of faults exposed in other caverns in the Northeast has shown a great diversity in the nature of the relationship between faults and cave passages. The range of influence varies from increased solubility along the fault to situations where the solubility of the fault zone is considerably less than that of the surrounding limestone. The latter relationship is borne out in the Clarksville System, Albany County, N. Y., where well-defined fault planes have an effect on passage morphology similar to that of a resistant layer (Ernst H. Kastning, pers. comm.). Obviously, this type of relationship cannot hold for all faults observed in karst areas, for faults vary in physical properties proportionally to the variation in the tectonic activity that produced them, e.g.: properties of the faulted material, or the temperatures and pressures prevalent within the rock during the time faulting occurs. Further variations in the effects of fault zones on cavern development can be attributed to different orientations of the fault with respect to primary layering and to jointing. The ability of a fault to transmit groundwater may increase as the dip of the fault approaches vertical. In many cases, regional joint patterns are also steeply inclined, so that the observer can easily err in the proper recognition of an observed structure. Such a case can be made with regard to Egemeier's (1969) interpretation of the Clarksville System, where a steeply dipping surface in the northern section of Ward's Cave was mistakenly identified as a fault. The apparent "mismatch" between the walls of the room in question are, in fact, due to recent slumping of the west wall rather than to faulting. Layers of thinly-laminated, stream-laid clay beneath blocks hanging from the west wall

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[1] A situation identical to this has developed at the southeastern end of Howe Caverns, where a totally independent cave system (Baryte's Cave) was discovered during quarrying at the turn of the century. Baryte's Cave runs at a right angle to Howe Caverns, though only 5 feet below it. No water flows through this section of Howe Caverns, because of capture of the flow by Baryte's Cave.

are deformed and the bedding of the west wall, in general, dips inwards toward the center of the room.

Other problems arise in distinguishing individual joints from faults. In Onesquethaw Cave, Albany County, N. Y., a 150-ft passage segment is controlled by what appears to be a fault with a maximum displacement of 0.8 ft (Palmer, 1972). Further investigation disclosed that the trend of this vertical fault is coincident with the predominant trend in the regional joint pattern and that displacement along the fault decreases rapidly as one approaches either end of the passage (Fig. 5). These facts, coupled with the total absence of slickensides and tension gashes within the zone, indicate that the "fault" is, indeed, a joint. The possibility then arises that the development of the cavern passage along this master joint in some way triggered incremental displacements along the joint, in much the same way that mining or quarrying operations may cause instantaneous displacements in the rock through relief of regional stresses.

The preceeding examples illustrate the difficulty one encounters in formulating valid generalizations about the influence of faults on speleogenesis. Fault zones are so variable in physical characteristics that any attempt to ascribe a greater permeability to faults than to joints, or vice-versa, is precluded. A detailed and rigorous examination of the fault zone within each passage in question, strictly adhering to the criteria for verifying the presence of a fault, is the only acceptible method by which the rôle of a particular fault zone in cavern formation can be deduced. Until structural data have been obtained from many different cave systems, a general statement on the relative importance of faulting to speleogenesis will remain beyond reach.

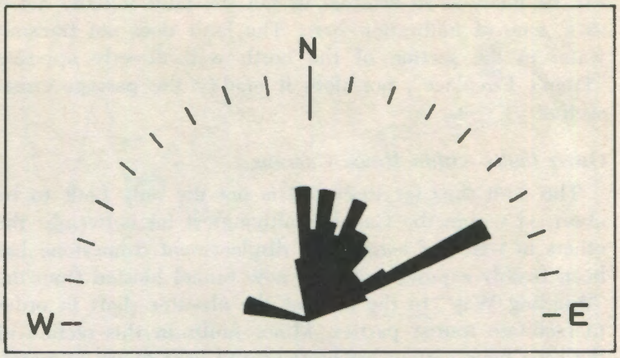

Fig. 5. Equal area circular histogram for vertical joints in Onesquethaw Cave, Albany County, N. Y. Fault discussed in text is excluded from diagram, but parallels largest trend, at N62E.

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The Food of the Salamanders *Eurycea lucifuga* and *Plethodon glutinosus* in Caves

Stewart B. Peck *

ABSTRACT

The contents of the entire digestive tracts were examined in 112 adult *Eurycea lucifuga* and 108 adult *Plethodon glutinosus* salamanders. All specimens were collected in caves. Compared to *P. glutinosus*, *E. lucifuga* was found to have eaten (1) more food items per individual, (2) a greater variety of food types, (3) generally larger types of food items, and (4) more food items from deeper in the cave. The salamanders are opportunistic feeders, but the primary foods of *E. lucifuga* were Mycetophilid and Heleomyzid flies and the primary foods of *P. glutinosus* were ants and mosquitoes. Consequently, it seems that these two salamanders can avoid direct food competition when they occur in the same caves. Laboratory studies showed that it takes about six days for food items to pass through the entire digestive tract of *E. Lucifuga*. Thus, each dissected digestive tract recorded the feeding of the salamander for the six days before capture.

INTRODUCTION

Very little is known about the biology of cave-inhabiting salamanders. This is especially true for their food and feeding habits. Brandon (1967), Lee (1969), Peck (1973), and Culver (1973) have contributed data on feeding in cave salamanders, but they examined only aquatic species. The only studies on the feeding of terrestrial salamanders in caves are those of Brandon (1971) investigating adult *Typhlotriton spelaeus* in caves in Missouri, Smith (1948) investigating small samples of *T. spelaeus, Eurycea lucifuga*, and *Plethodon glutinosus* in one cave in Missouri, and Hutchinson (1958) investigating a small sample of *E. lucifuga* and *E. longicauda* in caves in Virginia. These three studies found Heleomyzid flies to be the most common food and that there was little seasonal difference in feeding.

In southeastern United States, two salamanders frequently found in terrestrial cave habitats are the plethodontids *Plethodon glutinosus* (the slimy salamander) and *Eurycea lucifuga* (the cave salamander). These species commonly are found together in the same cave.

P. glutinosus occurs throughout most of eastern United States (Highton, 1971) and through much of its range frequently is found in caves, especially in the middle and southern states. Little is known about its ecology other than that reported by Hairston (1951), Highton (1956), and their included references. Studies of the food of various species of *Plethodon* have been reported by Dumas (1956), Duellman (1954), and Jaeger (1972), but I know of no food studies for *P. glutinosus*. Aspects of competition in *Plethodon*, including *P. glutinosus*, have been discussed by Hairston (1951) and by Highton (1971), but food was not considered.

Eurycea lucifuga (Fig. 1) occurs from central Indiana in the north to northern Georgia and Alabama in the south, from Rockbridge County, Virginia in the east, to Mayes County, Oklahoma in the west. In almost all cases, the species is associated with limestone terranes and it is most commonly found in caves. Other aspects of the ecology and distribution of the species are reviewed by Hutchinson (1956, 1958). There are no previous studies, known to me, of feeding in this species, other than those noted above.

Salamanders in the same habitat previously have been compared to determine if they have notably different feeding habits (Martoff and Scott, 1957; Dumas, 1956). When present, the difference apparently results from a partitioning of food resources in response to interspecific competition (Jaeger, 1972). However, Hairston (1949) generalized that "salamanders will eat almost any animal that falls within the proper size range," and that factors other than food are more important in determining the occurrence and abundance of salamanders.

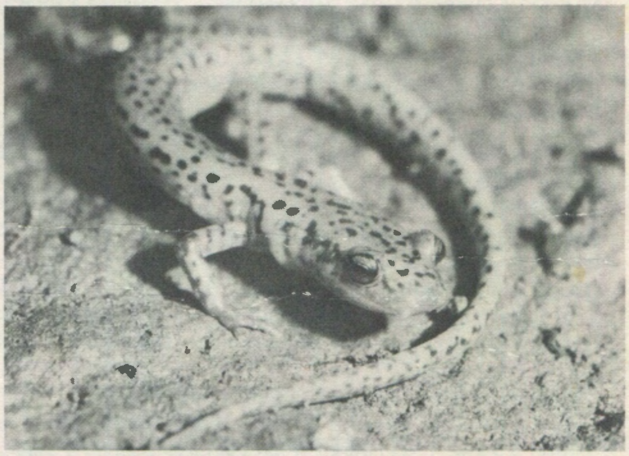

Fig. 1. *Eurycea lucifuga* in Phelps Cave, near Lexington, Kentucky.

This study was designed to provide data on the food of *E. lucifuga* and *P. glutinosus* in caves and to determine if feeding competition exists.

METHODS

Specimens were collected from March to September in 1965 and 1966. Shortly after capture, they were preserved in 70% alcohol to stop their digestive processes. A total of 112 adult *E. lucifuga* and 108 *P. glutinosus* were collected in the same general cave regions. In most cases, caves were found to be inhabited by both species. Thus, it is assumed that the same types of food are roughly available to both species, and that this would not account for feeding differences if any were found to exist. All specimens were dissected in the laboratory, and digestive tract contents were

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identified as completely as possible. In previous studies, such as those of Martoff and Scott (1957), Anderson and Martino (1967), Jaeger (1972), and Hairston (1949), dissections and examinations were made only of the stomach and its contents. In this study, I have examined the contents of the entire digestive tract, from the esophagus through the stomach, small intestine, and large intestine to the rectum. The advantage of examining the entire digestive tract is that it has a greater information content, because it records a greater span of feeding time for each individual. This may be important in cave populations, where stomachs may be empty because of the infrequency of feeding. Few or no problems were encountered in determining the identity of food items in the posterior parts of the digestive tract, even though they had undergone almost complete digestion.

The salamander specimens have been placed in the collections of the Field Museum of Natural History, Chicago, Illinois, and of the Museum of Comparative Zoölogy, Harvard University, Cambridge, Massachusetts.

LOCALITIES

The following data are provided to give an indication of the geographic coverage for each of the species. One hundred and seven *P. glutinosus* were collected from the following sites:

Alabama: (Colbert County) 2 caves, 6 specimens; (DeKalb County) 2 caves, 4 specimens; (Jackson County) 1 cave, 1 specimen; (Lauderdale County) 2 caves, 18 specimens; (Madison County) 5 caves, 63 specimens; (Marshall County) 3 caves, 10 specimens; (Morgan County) 1 cave, 1 specimen.

Florida: (Alachua County) 1 cave, 1 specimen.

Illinois: (Monroe County) 1 cave, 2 specimens.

Tennessee: (Sevier County) 1 cave, 1 specimen.

One hundred twelve *E. lucifuga* were collected from the following sites:

Alabama: (Blount County) 1 cave, 1 specimen; (Colbert County) 1 cave, 1 specimen; (DeKalb County) 3 caves, 5 specimens; (Jackson County) 8 caves, 15 specimens; (Lauderdale County) 2 caves, 4 specimens; (Limestone County) 1 cave, 4 specimens; (Madison County) 8 caves, 18 specimens; (Marshall County) 8 caves, 16 specimens; (Morgan County) 1 cave, 1 specimen.

Georgia: (Walker County) 1 cave, 1 specimen.

Illinois: (Hardin County) 1 cave, 4 specimens; (Monroe County) 1 cave, 1 specimen; (Pike County) 1 cave, 1 specimen; (Pope County) 1 cave, 1 specimen; (Union County) 1 cave, 1 specimen.

Indiana: (Lawrence County) 1 cave, 1 specimen.

Kentucky: (Edmonson County) 2 caves, 21 specimens.

Missouri: (Franklin County) 1 cave, 1 specimen; (Stone County) 1 cave, 1 specimen.

Tennessee: (Bedford County) 1 cave, 8 specimens; (DeKalb County) 1 cave, 1 specimen.

Virginia: (Lee County) 1 cave, 1 specimen.

West Virginia: (Monroe County) 1 cave, 1 specimen.

The comparatively few specimens randomly taken from each site should not have upset or endangered the structure of any particular population, especially in view of the fact that Hutchinson (1958) found each population of *E. lucifuga* that he investigated to have around 60 individuals, even though only a few were visible on each visit to the caves.

SPECIMEN SIZE

Some authors cited above have found salamander size to be related to size of food items taken. This relationship was not investigated closely in this study, but the specimens of *E. lucifuga* were larger than those of *P. glutinosus*. The snout to vent lengths of *P. glutinosus* ranged from 22 mm to 72 mm, with a mean salamander snout-vent length of 41 mm. The snout to vent lengths of *E. lucifuga* ranged from 29 mm to 89 mm, with a mean salamander snout-vent length of 59 mm.

DIGESTION TIMES

It is of interest to know the time involved in the passage of a food item through the digestive tract. Six *E. lucifuga* (snout-vent lengths of 50, 52, 54, 60, 63 and 65 mm) were confined in clear plastic boxes containing moist paper towelling and kept in a dark incubator at 15°C (60°F), a common cave temperature in the southeast. Individual food items, such as beetles and small roaches, were placed in the boxes with the salamanders. Daily records were kept of when the food items were eaten and when they reappeared in feces. Times of passage through the digestive tract were observed and recorded for 35 food items. The small salamanders were found to have a food passage time of four to seven days, while the larger ones had a digestive time of five to nine days. The average time for the six salamanders was six days. Thus, we can conclude that the items in the digestive tracts of *E. lucifuga* represent an average feeding record of the six days prior to capture and preservation. For the 112 *E. lucifuga* dissected, this is a total feeding record of about 670 days. Digestion time for *P. glutinosus* was not measured, but it may be less than six days for this somewhat smaller species.

RESULTS AND DISCUSSION

Table 1 lists the food items found in the dissected salamanders. A full classification is not given for the food items for sake of brevity. A more complete listing of higher and intermediate taxonomic categories for invertebrate cave faunas appropriate for the region under study can be found in Holsinger and Peck (1971).

E. lucifuga ate a broader range of food items than did *P. glutinosus*. A minimum of 73 different food species were found in *E. lucifuga* guts, while a minimum of 27 different food species were found in the guts of *P. glutinosus* (Table 1). *E. lucifuga* also seems more able to locate food, because a higher proportion of specimens contained food items and these had a greater average number of food items per salamander. Only 11 *E. lucifuga* were found with no food items in the digestive tract, while 65 *P. glutinosus* were found to have no food items in the digestive tract. Thus, 101 *E. lucifuga* contained 538 items, an average of 5.3 items per fed salamander. The 43 *P. glutinosus* with food contained 286 food items, an average of 6.7 items per fed salamander. However, if the unusual cases of two *P. glutinosus* specimens which contained 111 mosquitoes are discounted, the average is four food items per fed salamander.

E. lucifuga also can be considered a more successful predator in that its food items generally are larger. These include *Pseudotremia* millipeds and *Hadenoecus* and *Ceuthophilus* crickets. *P. glutinosus*, on the other hand, seems to be able to more successfully locate and eat smaller items, such as small Podurid collembola, mites, and the minute

TABLE 1.

TABLE 1. A comparative table of food items found in digestive tracts of 112 *E. lucifuga* and 107 *P. glutinosus* from caves in the Southeastern quarter of the United States. The frequency occurrence is the number of digestive tracts containing a food category. Percent occurrence is the percent a food category represents in the total of food items consumed by the salamander sample. The food categories marked with an asterisk are normal members of cave communities.

	E. lucifuga			*P. Glutinosus*		
	No. Food Items	Freq. occurrence	% occurrence	No. Food Items	Freq. occurrence	% occurrence
Annelida, Lumbricidae	3	2	.6			
Snails, *Carychium* *	2	2	.4			
Glyphyalinia *	1	1	.2			
unknown	10	7	1.9	8	7	2.8
Crustacea, Decapoda, *Orconectes* *	2	2	.4			
Amphipoda *	2	2	.4			
Isopoda, *Asellus* *	1	1	.2			
Cylisticus	2	2	.4	1	1	.3
unknown terrestrial	3	3	.6			
Diplopoda, *Pseudotremia* *	9	2	1.7			
Julidae	2	1	.4			
Polydesmidae *	13	9	2.4	4	4	1.4
Chilopoda, Scutigeridae	4	4	.7	1	1	.3
Pseudoscorpionida	5	4	.9	3	3	1.0
Acarina	3	3	.6	8	8	2.8
Araneae, *Leiocranoides* *	2	2	.4			
Nesticus *	1	1	.2			
unknown	17	13	3.2	4	3	1.4
Phalangida, *Leiobunum*	1	1	.2			
Collembola, Entomobryidae, epigean	13	7	2.4	1	1	.3
Pseudosinella hirsuta *	6	2	1.1			
Sminthiridae	2	2	.4	3	3	1.0
Poduridae	2	1	.4	15	2	5.2
Thysanura, Machilidae	3	2	.6			
Diplura, Japygidae	1	1	.2			
Orthoptera, Acrididae				1	1	.3
Ceuthophilus *	14	11	2.6			
Hadenoecus *	19	12	3.5			
Plecoptera	2	1	.4			
Trichoptera	2	1	.4			
Psocoptera	1	1	.2			
Hemiptera, Miridae	4	4	.7			
Reduviidae	2	2	.4			
unknown	1	1	.2			
Homoptera, Cicadellidae	4	2	.7			
Cixiidae	2	2	.4			
Neuroptera				1	1	.3
Coleoptera, Carabidae, *Dyschirius*	2	2	.4			
Carabidae, *Pseudanophthalmus* *	2	1	.4			
Carabidae unknown	2	2	.4	1	1	.3
Carabidae, larvae	2	1	.4			
Dytiscidae	3	2	.6			
Leiodidae, *Ptomaphagus* *	13	5	2.4	1	1	.3
Ptomaphagus larvae *	1	1	.2			
Catopocerus *	1	1	.2			
Staphylinidae, *Philonthus* *	1	1	.2			
Staphylinidae, Aleocharinae*				11	8	3.8
Staphylinidae, larvae	4	4	.7	5	2	1.7
Histeridae				1	1	.3
Scarabaeidae, *Aphodius*	1	1	.2			
Anthicidae	1	1	.2			
Oedmeridae	1	1	.2			
Cryptophagidae	4	3	.7			
Elateridae	4	4	.7			
Nitidulidae				1	1	.3
Chrysomelidae	4	4	.7			
Cerambycidae	1	1	.2			
Curculionidae	1	1	.2			
unknown	9	6	1.7			
Lepidoptera larvae, Noctuoidea	10	6	1.9	1	1	.3
Diptera, Tipulidae *	4	2	.7			
Mycetophilidae *	98	15	18.2	2	2	.7
Sciaridae *	23	11	4.2			
Culicidae *	4	2	.7	112	3	38.8
Cecidomyidae	3	2	.6			
Spheroceridae *	33	11	6.1	4	2	1.4
Phoridae *	27	6	5.0	11	1	3.8
Psychodidae *	1	1	.2			
Heleomyzidae *	87	18	16.2	7	4	2.4
Scatophagidae	1	1	.2			
Caliphoridae	1	1	.2			
Muscidae	1	1	.2	1	1	.3
unknown adults	1	1	.2			
maggots	16	7	3.0	13	1	4.5
Hymenoptera, Braconidae	2	2	.4			
Formicidae	5	5	.9	63	10	22.0
Eulophidae				1	1	.3
Ichneumonidae	1	1	.2	1	1	.3
undetermined	2	2	.4			
Total food items	538			286		

Eulophid wasp, which are less than 1 mm long. This difference in food size is more than would be expected for large salamanders with mean sizes differing by only 18 mm.

If we consider as primary food items those which were eaten more than 10% of the time, we find that only Mycetophilidae and Heleomyzidae are primary foods for *E. lucifuga*, and only Culicidae and Formicidae for *P. glutinosus*. However, because these salamanders seem to be opportunistic, they will take advantage of any food "bonanza" that they happen to find. If we were to attempt to adjust the figures in Table 1 by excluding the individuals which had located bonanzas, we would exclude three *E. lucifuga* which had eaten 53 Mycetophilids and two which had eaten (respectively) 21 and 16 Heleomyzids. We would exclude one *P. glutinosus* which ate 11 Podurids, two which ate 111 mosquitoes, one which ate 13 maggots, and two which ate (respectively) 33 and 12 ants. However, this procedure does not result in any other category becoming an exceedingly important primary food. Rather, all other food categories are fairly uniformly raised a few percentage points.

E. lucifuga was found to have eaten more invertebrates from deeper zones of the caves, including quite a few blind (troglobitic) species. Included in these were five aquatic crustaceans. Other than these and, possibly, one Dytiscid beetle, in a total of five *E. lucifuga*, there was no evidence of feeding in aquatic habitats for either salamander species.

Also found in the digestive tracts were non-food materials not associated with food items. Boluses of sand and small stones were found 66 times in 52 *E. lucifuga* and 59 times in 37 *P. glutinosus*. Undeterminable non-arthropod debris, mostly plant material, was found 29 times in 19 *E. lucifuga* and 15 times in 10 *P. glutinosus*. These may or may not represent unsuccessful feeding attempts. If they are interpreted as unsuccessful attempts, then *P. glutinosus* missed more often than *E. lucifuga* in relation to numbers of successful feeding attempts. It is difficult to interpret feeding efficiencies of the salamanders in this sample. If we take the 538 food items in *E. lucifuga* as 538 successful feeding attempts and the total of 95 sand and debris boluses as unsuccessful attempts, we calculate feeding attempts to be 85% successful. Similarly, for *P. glutinosus*, if 286 successful feeding attempts are recorded by the 286 food items and the total of 74 sand and debris boluses are 74 unsuccessful attempts, we calculate a feeding success of 76%. However, these feeding efficiencies should not be given too much weight because of the uncertainties involved in the initial assumptions, as previously discussed (Peck, 1973). The efficiencies likewise are comparable to other observed efficiencies of cave salamander feeding only with caution. The 67% efficiency found in *Haideotriton spelaeus* (Peck, 1973) and the similar efficiency for *Gyrinophilus porphyriticus* (Culver, 1973) were achieved in aquatic situations completely lacking in visual clues for food location and capture. In the present study, it is not known how many salamanders may have used visual clues in locating and capturing their food.

In conclusion, the feeding differences seem to indicate that the two salamanders overlap in their food spectra, but that they can avoid direct competition for invertebrate food in caves in which both salamanders occur. *E. lucifuga* is the more efficient, effective, and successful predator on the cavernicolous arthropod community.

FURTHER STUDY

When this study was completed, several weaknesses were recognized. Data should have been kept on incidence of digestive tract parasites. Detailed notes on the location where each salamander was captured should have been kept to indicate if *P. glutinosus* occurs closer to the cave entrance and if *E. lucifuga* is deeper in the caves, as their feeding seems to suggest. This data also would help to evaluate the question of whether or not salamanders which are in the dark zone of the cave in the daytime might move toward the entrance at night to feed. Lastly, the size of food items should have been measured since it is really more important than numbers of food items. For instance, one cricket can have the food value of many smaller insects.

Data on these questions consequently were collected for 218 *E. lucifuga* from 1967 to 1972 and will be presented in a later paper.

I would like to encourage others to investigate the feeding behavior of these and other cave-inhabiting species of terrestrial salamanders in the way that Culver (1973) has studied the feeding behavior of cave populations of *Gyrinophilus porphyriticus*.

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