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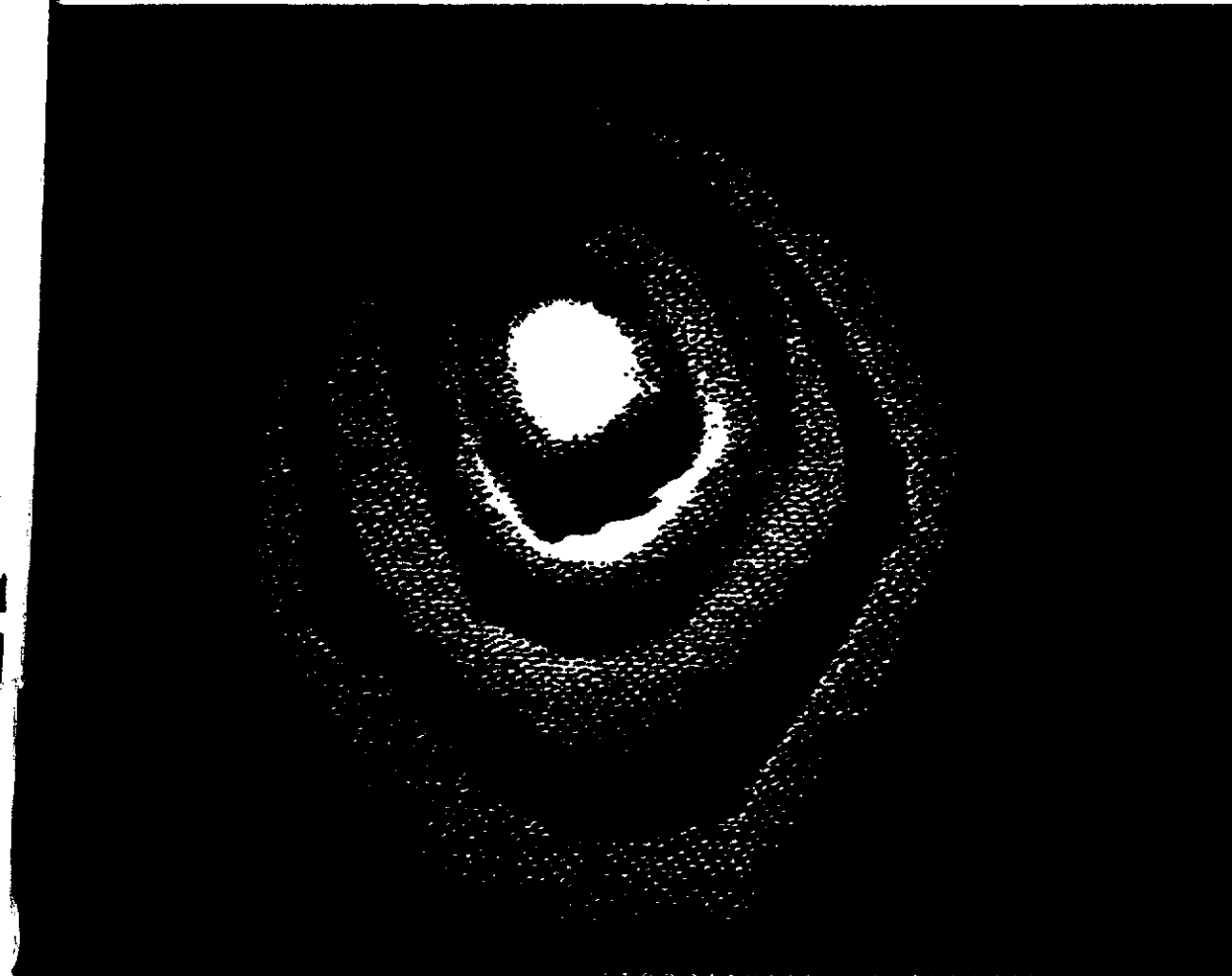
MAMMOTH CAVE NATIONAL PARK

ANNALES DE SPÉLÉOLOGIE

REVUE TRIMESTRIELLE
TOME 26 — FASCICULE 1 — 1971

EXTRAIT

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BIOSPÉOLOGIE

ECOLOGICAL STUDIES IN THE MAMMOTH CAVE SYSTEM OF KENTUCKY. II. THE ECOSYSTEM (*),

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Analyse.

Les niches écologiques possibles de la Mammoth Cave se trouvent près des éboulis terminaux, des puits verticaux actifs, des pierres suintantes actives, et le long des berges des ruisseaux et des mares souterrains. Dans les zones profondes la température reste constante toute l'année, $13,6 \pm 0,2^{\circ}\text{C}$, l'humidité relative est voisine de la saturation, le taux d'évaporation et les déplacements de l'air sont minimaux. Cependant une grande partie de la grotte est sujette à des variations saisonnières du microclimat. Il y a trois sources principales de nourriture dans le système : 1°) le guano, les cadavres et les œufs du Criquet des grottes (*Hadenoeus subterraneus*) ; 2°) les débris végétaux, le méso- et nannoplancton introduits par les eaux ; 3°) les fragments de bois et autres apports dus à l'aménagement touristique de la grotte. Les communautés troglodytes typiques sont associés au bois pourrissant, au guano du Criquet et aux minuscules Oligochètes limivores des bords argileux des rivières souterraines.

Des études du milieu aquatique de la Mammoth Cave ont été faites principalement dans : Echo-roaring River, Styx River, et Crystal Lake. Les paramètres physico-chimiques ainsi que la densité du plancton des rivières sont nettement affectés par les crues hivernales de la Green River. Le Crystal Lake a, au contraire, un taux relativement bas d'oxygène dissous, un pH et un taux d'alcalinité plus élevés ainsi qu'une température plus stable ; la quantité de zooplancton est nettement moins importante dans le Crystal Lake dont la densité de la micro- et macrofaune du fond est aussi beaucoup plus faible.

(*) This investigation was supported by a grant from the National Science Foundation (G-18765). This is the second part of a two-part monograph. Part I, « The Biota », by T. C. Barr, Jr., appeared in Int. Jour. Speleol., 3, 147-203, pl. 37-64.

Les « mares à Crevettes » du Roaring River Passage dans la Mammoth Cave sont un exemple d'une communauté aquatique modérément complexe basée sur la décomposition bactérienne des détritiques entraînés par le courant ; les Protozoaires et autres représentants de la microfaune se nourrissent des Bactéries et sont à leur tour ingérés par les Isopodes, Amphipodes et Crevettes Atyides ; les Ecrevisses et les Poissons Amblyopsides représentent les niveaux trophiques les plus élevés de cette communauté.

Une étude microbiologique préliminaire a montré qu'une grande proportion des Bactéries détectées par nos méthodes ont été vraisemblablement transportées dans la grotte par les eaux, et que la production secondaire dans les argiles du fond des mares et lacs atteint probablement un maximum vers la fin de la saison sèche, en automne. La signification quantitative des microorganismes autotrophes dans l'écosystème reste inconnue.

Areas in Mammoth Cave suitable for existence of cavernicoles occur near terminal breakdowns, active vertical shafts, active dripstone, and along the banks of subterranean rivers and lakes. Deep within the cave the temperature is constant throughout the year at $13.6 \pm 0.2^\circ\text{C}$, relative humidity approaches saturation, and the rate of evaporation and air flow are minimal. Nevertheless many parts of the cave are subject to seasonal microclimatic variations. The system has three main sources of food : 1) guano, dead bodies, and eggs of cave crickets (*Hadenocercus subterraneus*), 2) plant debris and meso- and nannoplankton introduced by percolating and flowing water, and 3) wood fragments and other materials brought into the cave as a result of its development for public visitation. Characteristic troglolitic communities are associated with rotting wood, cricket guano, and small oligochaete worms in the silt banks of underground rivers.

Studies of the aquatic communities were conducted primarily in Echo-Roaring River, Styx River, and Crystal Lake. Winter backflooding of Green River strongly affects physico-chemical factors and plankton density in the cave rivers. Crystal Lake, however, has a rather low level of dissolved oxygen, a higher pH and total alkalinity, and a more stable temperature ; density of both zooplankton and micro- and macrofauna of the silt bottom is also lower.

The « Shrimp Pools » of the Roaring River Passage in Mammoth Cave are an example of a rather complex aquatic cave community based on bacterial decomposition of flood detritus ; protozoans and other microfauna feed on bacteria and are in turn eaten by isopods, amphipods, and atyid shrimps ; crayfishes and amblyopsid fishes are at the highest trophic level in the pools.

A preliminary microbiological study indicates that most of the bacteria demonstrated by our methods have probably been brought into the cave by percolating or flowing water, and that secondary production in the silt banks of lakes and pools reaches a probable maximum in autumn at the end of the dry season. The quantitative importance of autotrophic microorganisms in the Mammoth Cave ecosystem has not been established.

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Introduction.

From the ecologist's viewpoint the Mammoth Cave ecosystem — and almost any other cave ecosystem in the temperate zones of the earth — presents a number of striking contrasts when compared with the more familiar animal and plant communities at the surface. Although many authors in the past have stressed the constancy of the physical environment of a cave, it will be shown that, with the exception of light, which is absent in the depths of the cave, the

constancy of most physical parameters is purely relative. Seasonal fluctuations in temperature, water level, air movements, rate of evaporation, relative humidity, dissolved oxygen, pH, total alkalinity, and so forth, as well as food supply, are of sufficient magnitude in the Mammoth Cave ecosystem to evoke appropriate ecological adjustments in the cave community.

The absence of light prevents primary production of food, except in probably negligible quantities by chemosynthetic autotrophs such as the sulfur and iron bacteria. As a consequence, food must be imported into a cave ecosystem in order to sustain the biotic community. There are two principal agents of food transfer from surface to cave : (1) the troglloxenes, animals which spend much of their time in caves but feed on the outside or in the twilight zone ; and (2) water entering the cave system either as seepage or as flowing streams, transporting bacteria and other microorganisms, zooplankton, larger animals, leaves, sticks, and even logs into the ecosystem. Gravity and air currents may bring food material into the twilight zone, where under suitably moist conditions trogllobites may occur, attracted by the abundance of food. Man himself, with his rotting wooden ladders and bridges, his propensity for littering, and the scraps from his own underground meals has added a further dimension to the food sources available to cavernicoles of the Mammoth Cave system, and has probably introduced more troglphilic species than might otherwise naturally occur.

The extremely low biomass of a temperate zone cave ecosystem is predominantly the result of a limited food supply. Although cavernicoles may be locally abundant in numbers of individuals, their modal size is so small that their contribution to the biomass of the ecosystem is minute. A single example will suffice. One of the most abundant and conspicuous of the terrestrial trogllobites in the Mammoth Cave system is the eyeless carabid beetle, *Neaphaenops tellkampffii* (Erichson). We have conservatively estimated (see below for details) that 750,000 individuals of this species exist in the system. Yet the mean weight of *Neaphaenops* is only 5 mg, so that the entire population of this species in the Mammoth Cave - Flint Ridge system contributes only 3.75 kg of the biomass, or about 15 g per kilometer of cave passage. Only in those sections of the caves where there are numerous bats does the biomass rise above an infinitesimally low level, but in the Mammoth Cave system most of the bats are hibernators and neither add nor subtract significantly from the energy budget of the ecosystem.

The principal limiting factors of a cave ecosystem are food and water. In a typical small cave the atmosphere is saturated or nearly saturated with water vapor in all its parts, but in the Mammoth Cave system there are many kilometers of dry, even dusty galleries extending beneath an impermeable sandstone cap. Most terrestrial cavernicoles are more or less stenohygrobic, and will consequently be

restricted to moist, humid areas where there is a readily available supply of food. The larger aquatic cavernicoles are, of course, limited to reasonably permanent streams and pools. As a consequence of the uneven distribution of food and water, the organisms constituting the Mammoth Cave community are restricted to the lower stream levels and to wet areas of the upper levels, in places where there is not only sufficient moisture but a suitable food source. In any horizontal plane the cave community appears correspondingly discontinuous, except at the lowest (stream) level, and its essential continuity may be appreciated only in a three-dimensional view of the ecosystem.

There is little direct energy exchange between the aquatic and terrestrial components of the Mammoth Cave ecosystem, and these will be separately considered.

Materials and Methods.

Most of the data upon which this investigation is based were collected at bimonthly intervals between November, 1961, and December, 1962, with occasional non-periodic visits to the cave subsequent to 1962. Temperature of cave air and water was measured with calibrated Anschütz precision-grade thermometers readable to 0.2°C. Relative humidity was determined by Taylor sling psychrometers or — in small pockets or stratified layers of air near the ceiling or floor — with an A + « Hygrophil » thermistor psychrometer. Rate of evaporation was determined by periodic reading of the meniscus of a burette attached to a 5-cm porcelain sphere Livingston evaporimeter bulb. Velocity of air currents was measured with a Hastings-Raydist Model G-11 air meter with portable power pack; this instrument is sensitive to air movements as low as 1.5 m/min. Dissolved oxygen in streams and pools was determined by the Winkler method, free CO₂ by phenolphthalein titration, chloride by silver nitrate titration, and total alkalinity by titration with methyl orange. Hydrogen ion concentration was measured by a portable Coleman pH meter, model 20. Measurements of pH were made in the cave at the site of sample collection, and dissolved oxygen determination was carried as far as the acidification stage immediately after sample collection. Plankton was sampled by 15-cm Turtox towing nets constructed of No. 25 mesh silk bolting cloth (about 32 meshes per cm²). Preliminary studies of aquatic microbial growth in the cave were carried out by 2 and 4 week emplacements of Henrici slides in Crystal Lake, Styx River, and Echo River. Plate counts of soil and water samples were made on various media, principally nutrient agar, cornmeal agar, potato dextrose agar, Czapek's agar, and heart-brain-liver agar, incubated at 10°, 20°, and 37°. For determination of coliform density in water samples the MPN/lactose broth method was employed. The marking-release-and-recapture experiments with *Neaphaenops* were analyzed by means of the positive method of Jackson (1939).

Finally, water level, rainfall, and temperature readings during the period of the investigation were obtained through the courtesy of the United States Geological Survey and the National Park Service.

Acknowledgments.

Without the assistance of the taxonomists previously acknowledged in Part I of this paper, this investigation would not have been possible. We acknowledge with thanks the permission to undertake the study accorded us by Superintendents Perry E. Brown and Paul McG. Miller at Mammoth Cave National Park, and the assistance rendered by their staff, notably naturalists Willard E. Dilley, George Olin, and John Krisko. A number of students from the University of Kentucky aided us in one part of the work or another; we single out for special mention Harrison Ambrose, David Brashear, Stewart Peck, and Bernard Pivo. Our colleague, Professor Ralph Wiseman, made helpful suggestions and rendered other assistance in the preliminary microbiological study of the cave. W. Ray Scott, National Park Concessions, Inc., kindly gave permission to use some photographs of Mammoth Cave. Finally, we gratefully acknowledge the assistance of Robert L. Cushman, U. S. Geological Survey; and Frederick Benington, Roger Brucker, and other members of the Cave Research Foundation and the National Speleological Society.

THE TERRESTRIAL COMMUNITY.

The Big Clifty sandstone which overlies the limestone strata in which the Mammoth Cave system has been excavated is virtually impermeable to the downward percolation of groundwater. A perched water table in the sandstone permits the development of small ponds atop the ridges, such as the Union City « Marsh », the Beaver Pond at Sloans Crossing, and the pond (now filled) at the junction of the Park entrance road and the Green River ferry road. In the cave system itself, areas sufficiently damp for the existence of cavernicoles occur beneath the hillside slopes beyond the margin of the sandstone cap or along the subterranean rivers.

There are at least three types of wet microhabitats, but the classification is not a hard and fast one and the types often merge. (1) Since development of much of the cave antedates the present surface topography, erosion of surface valleys often bisects cavern galleries. Such galleries are abruptly truncated by talus of limestone slabs and sandstone rubble, through which trickle small streams of water from the surface. Among the more spectacular breakdowns of this nature are Rafinesque Hall and Violet City in Mammoth Cave and the east terminus of Floyds Lost Passage in the Flint Ridge system. Brucker (1966) has discussed this phenomenon in detail. (2) The occurrence of vertical shafts, or « domepits », is closely correlated with the position of the edge of the sandstone cap. (Pohl,

1955), where acid drainage from the Big Clifty itself, or springs in the overlying, calcareous Haney member of the Golconda formation sink into the Girkin limestone. Many of these shafts (Fig. 1) are still

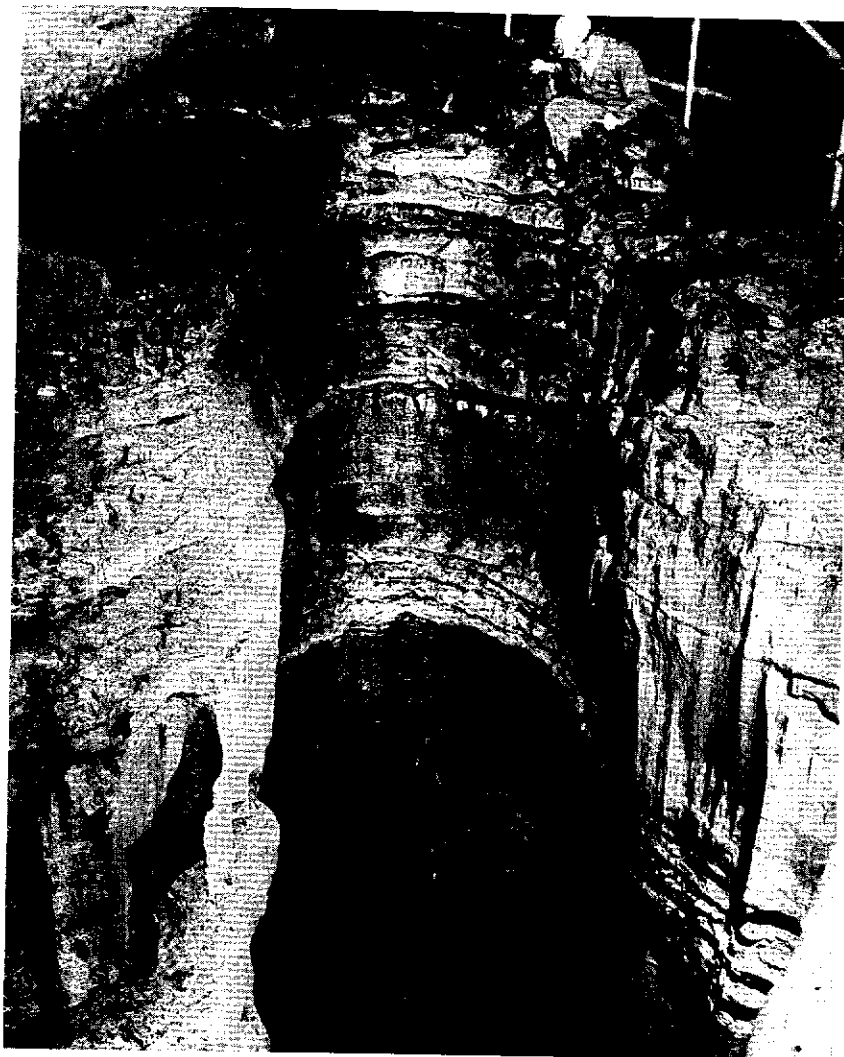


FIG. 1. — Side-Saddle Pit in Mammoth Cave, a typical vertical shaft, or « domepit ».

active, and wet spray and pools are found during most of the year in Washington's Pit, Bottomless Pit, Mammoth Dome, Lee's Cistern (Gratz Avenue), and Cathedral Domes in Mammoth Cave, and in

Colossal Dome in Flint Ridge. (3) Slow percolation of ground water into the cave has led to local deposition of dripstone, though to a lesser extent than in many other caves. Such areas are usually wet and humid, and may contain seasonal pools in rimstone pockets (gours). Some major dripstone areas in the system are Frozen Niagara, Gothic Avenue, Violet City, New Discovery Entrance, Nelson's Discovery (Briggs Avenue), and Mammoth Dome in Mammoth Cave; White Cave; the entrance region of Great Onyx Cave; the Attic Room of Crystal Cave; and the end of the old tourist route in Colossal Cave.

Air Temperature, Relative Humidity, and Air Currents. — Air temperature in the Mammoth Cave system fluctuates between 7.2°C and 15.2°C. In the deeper parts of the cave, uninfluenced appreciably by air currents and surface water, air temperature fluctuates between 13.2° - 14.0°, mean about 13.6°C (Table 1). Winter air currents

TABLE I.

Mammoth Cave mean temperatures, 1961-1963.

(Anschutz precision-grade thermometer or calibrated 225-mm mercury thermometer. Approximately 12 readings per month; terminal breakdowns and readings immediately after floods excluded, but such areas are normally 0.8° - 2.2°C lower in winter and 0.2° - 0.8°C higher in summer).

	°C
January.....	13.8
February.....	13.3
March.....	13.6
April.....	13.8
May.....	13.9
June.....	13.9
July.....	13.7
August.....	13.9
September.....	13.9
October.....	13.9
November.....	13.6
December.....	13.6

sweeping into entrances and ground water seeping through breakdowns and into domepits cools certain areas in winter and early spring — e.g. the Rotunda and the first 1000 m of Broadway, Audubon and Little Bat avenues, Rafinesque Hall, the Moonlight Dome area, Mammoth Dome, River Hall, Shakespeare's Galleries, and other passages along the rivers in Mammoth Cave; also Floyds Lost Passage and Pike Chapman Entrance in the Flint Ridge Cave System, and the first 200 m of Great Onyx Cave. Typical winter temperatures from these areas range between 11.4° - 12.8°C.

The relative humidity, even in dusty, dry areas, rarely falls below 80 %, and in parts of the cave inhabited by cavernicoles, ranges between 94 % and saturation. The humidity of the air layers near wet ceilings, walls, and in sheltered pockets is often higher than the average value obtained by sling psychrometer readings in the middle of a passage ; a thermistor psychrometer fitted with a long, slender, aspirator tube is necessary to determine this. Even in remote parts of the cave system a light air current is present, the flow through a typical gallery being analogous to the flow of water through a pipe. In the middle of the gallery a typical rate of air movement is 6 to 12 meters per minute, with the rate decreasing toward the walls, ceilings, and floors, less than 1.5 meters per minute at a markedly irregular surface such as an undulating floor or a floor strewn with small rocks. The Bernoulli effect is observed at narrow constrictions (such as Elbow Crevice between Gothic and Gratz avenues). A periodic reversal of flow is often associated with horizontal galleries in communication with vertical shafts open to the exterior (as in Marion Avenue near the 81.5-meter elevator shaft to the surface).

Seasonal Changes in Terrestrial Cave Microclimates. — Seasonal climatic changes at the surface affect the terrestrial environment in as drastic a manner as winter and spring floods affect the aquatic environment. The familiar « breathing phenomenon » observed in caves, in which cave air flows out of entrances in summer, is usually attributed to density gradients between surface and cave air. The rate of air flow between surface and cave is directly proportional to the temperature difference between the two air masses. Barometric winds in the cave, responding to low pressure of surface air, complicate the situation in a manner not yet carefully investigated for the Mammoth Cave system (see Conn, 1966, for a comprehensive discussion of barometric winds in Jewel Cave, South Dakota). The effect of summer exhalation is to extend the habitable, humid microclimate of the deep cave much closer to the entrance. In winter, however, the effects of inhalation of surface air are ecologically severe. Not only is the surface air much drier than cave air, but it absorbs moisture from the cave as it warms up to cave temperature. In spring and autumn, when days are warm and nights are cool, reversal of the air flow may occur twice during a 24-hour period. The theoretical annual distribution of inhalations, exhalations, and reversals, assuming a constant cave temperature of 13.4°C, is plotted in Figure 2.

Typical temperature and humidity profiles in Great Salts Cave (Flint Ridge) and Mammoth Cave for late fall and winter are shown in Tables 2, 3, and 4. The main avenue of Great Salts Cave, 1.5 kilometers long with an average height of 8 meters and width of 18 meters, is a rather dry, first and second level gallery of the Flint Ridge cave system. For most of its length it lies beneath the sandstone cap and has a meager fauna. The Mammoth Cave data illustrate the cooling and drying effect of cold surface air (Stations B, C, D, E). Ther-

mal stratification of lower (outside) and upper (cave) air layers is demonstrated by measurements at Station B. Table 5 is a profile of temperature, relative humidity, and rate of air flow along a 2.5 km course through Pohl and Turner avenues in the Flint Ridge System in early November.

Rate of evaporation in Mammoth Cave is always lower than on the surface, but the winter air stream flowing into an entrance markedly increases evaporation. Livingston atmometers (5-cm porcelain spheres) placed in Audubon Avenue and the Radio Room, respectively, during the winter and spring of 1956-57 showed an average evaporative rate 15.5 times higher in Audubon Avenue, where the instrument was located in the air stream flowing from the Historic En-

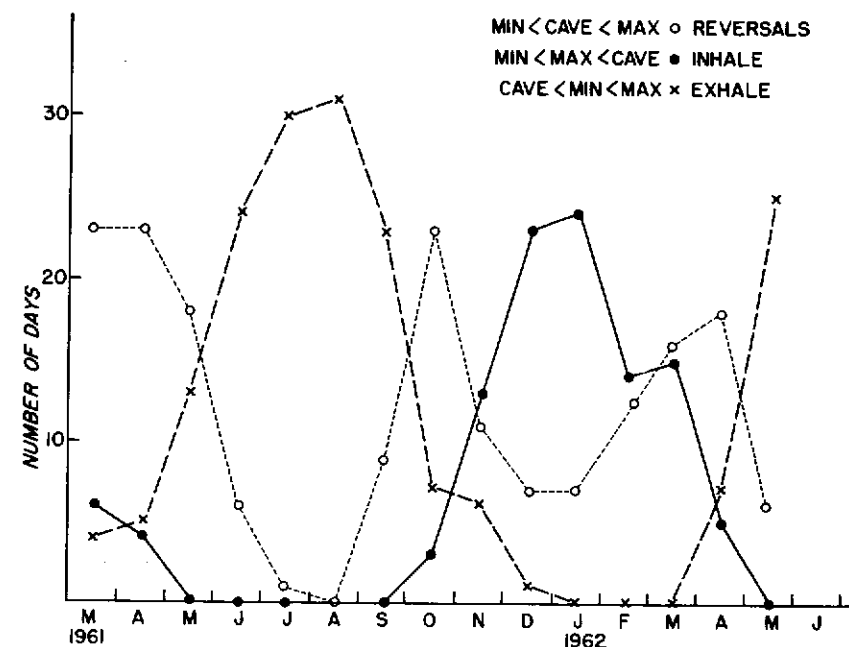


FIG. 2. — Hypothetical monthly distribution of air flow in and out of entrances of Mammoth Cave ; based on records of maximum and minimum daily surface temperatures, assuming a « deep » cave temperature of 13.4°C and neglecting possible effect of barometric winds.

trance about 550 meters distant (data from Barr, 1958). For the 171-day period from 9 December 1956 to 19 May 1957 the Audubon Avenue atmometer lost water at an average rate of 0.0248 ml/hr. During this period relative humidity determinations fluctuated between 92 % and 94 % and the air temperature was 11.7° - 12.8°C. For the 202 day period from 9 December 1956 to 19 June 1957 the Radio Room atmometer, at a site protected from direct effects of winter

TABLE II.
*Temperature and Relative Humidity in Great Salts Cave,
 Kentucky, XII.8.1956.*
 Data from Barr, 1958).

Station	Location	Temperature °C	Relative Humidity %
A	Second Room	13.2	94
B	Second Breakdown	13.8	92
C	Entrance to Lower Level	13.8	92
D	50 m beyond C in Upper Level; wall and rocks damp; <i>Hadenoeus</i> present	13.8	94
E	80 m beyond C in Upper level; fungus on dry wood	13.8	94
F	Near Mummy Valley	13.8	88
G	Far side Mummy Valley; desiccated <i>Lasiurus borea-</i> <i>lis</i> on wall	13.8	88
H	100 m before Pike Chapman (closed) entrance; desic- cated <i>Neotoma</i> with <i>Psyl-</i> <i>lipsozus</i>	12.8	92
I	Pike Chapman entrance; collapsed artificial shaft; seepage; <i>Neaphaenops</i> , <i>Stygobromus</i>	12.2	94

TABLE III.
*Temperature and Relative Humidity in Mammoth Cave,
 Kentucky, XII.9.1956.*
 Data from Barr, 1958).

Station	Location	Temperature °C	Relative Humidity %
A	Surface, hotel parking lot	1.0	81
B	Houchins' Narrows, 1 m above floor	7.2	85
	Houchins' Narrows, 2 m above floor	10.0	96
C	Rotunda	11.7	90
D	Audubon Avenue	12.2	92
E	Methodist Church	12.2	86
F	Base of Mammoth Dome	12.8	100
G	Richardson's Spring	12.8	99
H	Dead Sea, 5 m above water level	13.3	100
I	Radio Room	13.3	100

air flow, lost water at an average rate of only 0.0016 ml/hr. Relative humidity was 99 % - 100 % and temperature was constant at 13.4°C during this period. Most of the common terrestrial troglobites inhabiting the cave have been taken at one time or another in the Radio Room. At the Audubon Avenue station only an occasional *Hadenoeus* was observed near the atmometer, although *Neaphaenops* and *Phalangodes* occurred among wet rocks in the bottom of Rafinesque Hall 100 meters away.

TABLE IV.
*Temperature and Relative Humidity in Mammoth Cave,
 Kentucky, II.13.1965.*

Station	Location	Temperature °C	Relative Humidity %
A'	Historic Entrance	3.8	66
B	Houchins' Narrows, 1 m above floor	5.0	79
	Houchins' Narrows, 2 m above floor	8.0	97
B'	50 m beyond Sta B'		
	1 m above floor	8.3	81
	2 m above floor	9.4	88
C	Rotunda	11.9	89
D	Audubon Avenue	12.2	83
D'	Rafinesque Hall	11.7	94
D''	Little Bat Avenue	13.1	97
F	Base of Mammoth Dome	13.0	97
F'	Crevice Pit (top of Mammoth Dome)	13.3	97
J	Sparks and Sylvan avenues, junction	13.3	92
J'	100 m beyond Sta. J, toward River Hall	13.3	92
J''	Vanderbilt University Hall	12.6	92
H'	Styx River (bottom of steps)	13.1	97

The contrasting effect of cave and surface air on evaporative rate in a small grotto 50 meters from the Frozen Niagara (artificial) Entrance, near the top of Moonlight Dome, is graphically depicted in Figure 3, which shows an inverse relationship between epigeal temperature and rate of evaporation in the cave. The ambient winter evaporative rate is seen to exceed the summer minimum by a factor of up to 200 times. The air stream flowing into the Frozen Niagara Entrance may — in the coldest weather — attain a velocity of about 60 meters per minute with the door closed, but air currents impinging on the atmometer bulb have never been measured at more than 2 m/min.

On February 14, 1965, with a surface air temperature of 4°C and relative humidity of 48 %, air was moving into the cave through the cracks around the closed door of the Frozen Niagara Entrance at a

TABLE V.
Temperature, Relative Humidity, and air flow in Flint Ridge Cave system, XI.5.1961.

Station	Temperature °C	Relative Humidity %	Air Flow, meters/minute
OA. Outside, Austin Entrance	9.4	93.0	—
1. 8 meters inside tunnel	12.0	94.6	4
2. Entrance to Columbian Avenue	12.8	97.6	5 (3 m above floor, Pohl Ave.) 4.7 (inside mouth Columbian Ave.)
3. Meander loop (after trench) on right	13.8 (floor)	94.6	5
	13.6 (+ 2 m)	93.4	25-27
	13.7 (ceiling)	96.4	13-19
4. First pit (<i>Neaphaenops</i> abundant)	12.4 (floor)	98.8	1.3-1.6
	13.0 (+ 2 m)	97.0	7-8
	13.6 (ceiling)	97.0	7-8
5. "Black Onyx"	12.0 (floor)	98.2	2.2
	12.5 (+ 0.3 m)	94.0	3
	12.9 (+ 2.5 m)	92.5	13-22
6. "Mexican Spring" (<i>Neaphaenops</i> , <i>Platymachus</i> , <i>Phalangodes</i> , <i>Hadenocetus</i> , <i>Stygobromus</i>)	11.9 (floor)	100.0	—
	12.5 (+ 1.5 m)	100.0	—
	11.7 (+ 2.5 m)	100.0	26
	10.6 (water)	—	—
7. Turner Avenue (large column)	14.0 (air)	93.0	—
	11.8 (water)	—	—
	11.8 (silt)	—	—
8. "Symmetrical Sand-pile"	15.2 (air)	82.0	—
	14.2 (silt)	—	—
9. Mirabilite stalactites (no fauna)	15.2	86.0	—
10. Barrel Formation (no fauna)	14.5	90.6	—
OB. Outside entrance	9.8	92.4	1-10

rate of approximately 50 m/min, flowing along the left wall of the passage at a reduced rate in the wider portion before reaching St. Peter's Dome, then accelerating and passing the atmometer grotto and plunging into Moonlight Dome (with the door open influx of air

proceeded at a rate of 150 m/min). In the 50 m segment of passage the surface air had warmed to 12° and relative humidity was 91 %. Calculation of the volume of air entering the cave showed that water from the cave walls and ceiling in this segment was being absorbed at the rate of 1.92 kg/hr. In Fig. 3, the first peak in evaporative rate came in December, at the end of the dry season, but declined with winter rainfall and an increase in ground water seeping into the cave. The second evaporation peak occurred during a prolonged cold spell and is directly related to absorption of water by cold air entering the cave.

An aggregation of approximately 150 *Hadenocetus subterraneus* roosts near the atmometer station at Moonlight Dome. During periods of low evaporative rate the cricket guano beneath the colony

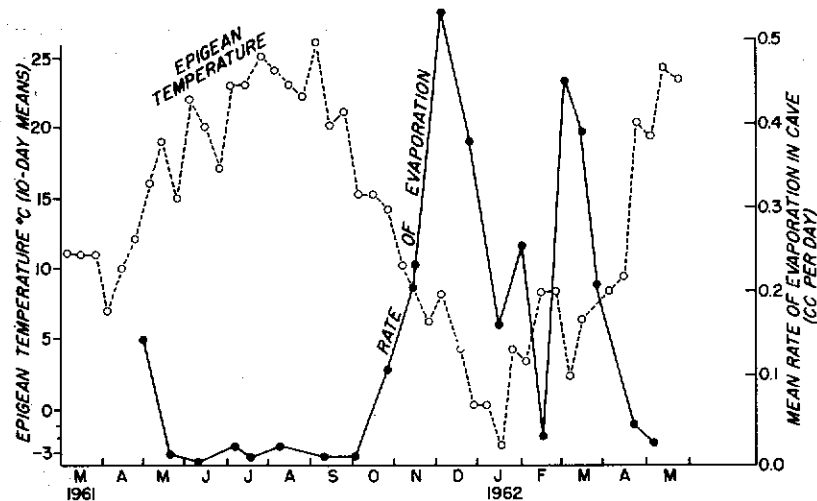


FIG. 3. — Evaporative rate at Moonlight Dome, Mammoth Cave, Livingston 5-cm porcelain sphere evaporimeter bulb ; with parallel plot of epigeal temperatures, 10-day means constructed from records at Mammoth Cave National Park.

teems with dipteran larvae, *Tomocerus*, and *Platymachus hirtus* ; *Pseudanophthalmus menetriesii*, *P. pubescens*, and *Cybaeus* are frequent predators. During very cold weather only the crickets are evident, usually tightly aggregated in dense clusters, with most of the other species secreted in more less inaccessible crevices.

In Floyd's Lost Passage in the Flint Ridge cave system, Cournoyer (in Brucker and Lawrence, 1955) noted a drop in air temperature from 12.5° to 7.2°C and a drop in relative humidity from 97 % to 78 % in an hour's time, 16 February 1954. These changes were attributed to colder air moving into the cave through a breakdown at the east end of the passage, which abuts against the wall of the Green River canyon, and took place during a heavy winter rainstorm at the

surface. Temperature recovery to 12.5° was attained after 2 1/2 hours, but relative humidity did not again reach 97 % (mean relative humidity at the same station February 15, 16 and 17) until 17 1/2 hours had elapsed. Thus even those cavernicoles which inhabit supposedly remote parts of the cave system are not necessarily immune to the deleterious effects of low relative humidity and drastically increased winter rate of evaporation. The prevalence of *Neaphaenops tellkampfi* in Floyd's Lost Passage and similar galleries, while *Pseudanophthalmus* spp. have not been observed there, is probably related to its burrowing capability and its larger size. The silt in which it burrows has a high field moisture equivalent (see below) and its interstices are probably saturated with water vapor. Furthermore, a greater size results in a lower surface/volume ratio and less evaporative loss per unit weight.

Substratum. — Slabs and angular fragments of limestone resulting from ceiling collapse litter much of the floor of the Mammoth Cave system. A description of such breakdown and a theoretical discussion of its mechanics are given by Davies (1951). Terminal passage breakdowns are common in the system, and passages truncated by erosion of surface valleys are usually plugged by talus creep of limestone slabs and sandstone cobbles derived from the overburden (Brucker, 1966).

Cave silt is the predominant substratum for most terrestrial cavernicoles, although they also occasionally crawl over wet flowstone, cave cricket guano, and rotten wood. The high moisture retention of the silt, as opposed to sand and gravel, probably accounts for micro-distributional preferences of beetles, collembolans, campodeids, opilionids, spiders, mites, and possibly other groups. *Neaphaenops* pupates in moist, crumbly silt beneath flat stones, in cells approximately 10 mm in diameter. The imagoes also burrow extensively and, as noted above, may survive temporary surges of cool, drying air by taking refuge in the silt. Damp silt yields a much higher plate count than sands and gravels when sampled for bacteria, molds, and yeasts (see below).

Clastic fills in the Mammoth Cave system include (a) gravel-sand, (b) fine sand, (c) silty sand, (d) sandy silt, (e) silt, and (f) silty clay (Davies and Chao, 1959). True clays (grain size < 0.01 mm) are rare. The most abundant type of fill is silt (grain size 0.01-0.13 mm); the redbrown silts have a higher clay content than the brown or gray varieties. The field moisture equivalent of Mammoth Cave silts is given by Davies and Chao (op. cit.) as 37.3-39.4 %, substantially higher than for the other types of fill. Throughout the system the sequence of fills is much the same - sand near the bottom, giving way suddenly to coarse sands and gravels in the middle and upper portions, overlain by fine silt and a thin layer of silty clay.

Of possible biological interest are clues to the development and Pleistocene history of the cave system that might be revealed by stu-

dy of the composition and sequence of the fills. Davies and Chao (op. cit.) report apparently authigenic barite, celestite, and gypsum occurring in the fills of the upper levels; these are absent in fills now being deposited along Echo and Styx rivers, strongly suggesting that deposition at present taking place in the cave is rather different from depositional processes in the past. Davies and Chao postulated a semiarid stage in the early development of the cave system to account for sufficient sulfates in surface streams to precipitate the barite and celestite. Davies (personal communication) has also pointed out the presence of exceptionally smooth, possibly wind-polished pebbles in the fill in Vanderbilt University Hall (Mammoth Cave) as a possible indicator of a semi-arid climate. However, unless most of the Mammoth Cave species have colonized caves only during the latter stages of the Pleistocene, the hypothesis of an extended semi-arid period is incompatible with the general theory of troglobite colonization, speciation, and subsequent adaptive evolution which was developed in Part I of this paper. Epigeal aridity would result in comparative aridity and reduced food input in the cave system, and the influx of sulfate-laden waters would present pH and osmotic problems for aquatic and possibly terrestrial cavernicoles. The biological theory requires colder, wetter periods alternating with warmer, drier periods. Certainly a climate of the sort now found in southern New Mexico and Arizona would make the prolonged survival of most troglobites highly improbable. The fauna of the caves of the Carlsbad Caverns region includes a large number of troglaphiles and guanobites, but very few troglobites (Barr and Reddell, 1967), a phenomenon attributable to the semi-arid climate, which reduces both food and water input into the ecosystem.

Energetics of terrestrial communities. — There are at present three principal sources of food in the caves of Mammoth Cave National Park. The contributions from bat guano, although probably very significant in pre-Wisconsin Mammoth Cave and perhaps moderately so prior to commercial development of the cave (see part I, pp. 176-177), are today negligible, with the possible exception of the Colossal Cave part of the Flint Ridge system. The existing food sources are 1) rotten wood, most of which has been artificially introduced, and other sporadically introduced materials, 2) the guano, eggs, and dead bodies of cave crickets, *Hadenocercus subterraneus*, and 3) organic detritus, bacteria, protozoans, and other organisms washed into the system by sinking streams and percolating ground water. The role of the microflora is predominantly one of decomposition and transformation, hence of secondary production (see below).

Rotten wood is the most obvious of the many artificially introduced potential foods in Mammoth Cave, most of it coming from removal of old bridges and ladders, the remains of which were thrown out of sight into convenient, dark, side passages. Metal and concrete

are now used extensively along commercial trails, and the rotten wood and its typical troglobitic assemblage will eventually disappear unless reintroduced for experimental purposes in limited areas. Although not naturally occurring in the upper levels of Mammoth Cave, the ecological fate of the wood does not appear to differ significantly from that of wood falling or washing into nearby caves with a similar faunal assemblage. To the long-term use of wooden bridges, railings, and ladders, especially in the Historic Section of Mammoth Cave, must be attributed the early discovery and description of Mammoth Cave's rich terrestrial fauna. This seems to have been especially important in the Labyrinth (Packard, 1888 ; Call, 1897), a part of the cave no longer shown commercially, where the old wooden structures have long rotted away and have been reduced to humus-like piles by earthworms.

The typical « xylophagous » assemblage of primary consumers (saprophiles) in Mammoth Cave includes collembolans (*Folsomia*), diplurans (*Plusiocampa*), millipedes (*Scoterpes*), oligochaetes (lumbricids and lumbriculids), and sometimes snails (*Carychium stygium*, *Zonitoides arboreus*). Typical predators include the trechine beetles (*Neaphaenops* and *Pseudanophthalmus menetriesii*), opilionids (*Phalangodes*), mites (*Rhagidia*), spiders (*Anthrobia*), and less commonly, pseudoscorpions (*Kleptochthonius*). The food web of a pile of rotting wood actually includes at least 3 trophic levels, since the wood must first be altered by the decomposers and transformers before it can be utilized by the primary consumers. One to two years seems to be necessary for this process of wood decomposition before it is able to support a local animal community. The rhizomorphs of polypores commonly extend outward for several meters from a relatively « fresh » pile of wood. The polypores involved are apparently constantly of the group known as the « brown wood rots », although species identification has not been achieved because fruiting does not normally occur in the cave.

Heavy cardboard and paper left in wet places undergoes much more rapid decomposition in the caves. The faunal assemblage, especially in corrugated cardboard or layers of cardboard which create many interstices, usually includes a much higher proportion of the smaller saprophiles and predators (*Folsomia*, *Rhagidia*, *Anthrobia*) listed above, and often a few saprophilic catopid beetles (*Ptomaphagus*) and predaceous pselaphid beetles (*Batrissodes henroti*). The unusually large population of pselaphids in two piles of rotting cardboard in Diamond Caverns, just outside Mammoth Cave National Park, is attributed to the large numbers of *Folsomia*, upon which the beetles are presumed predominantly to feed.

Of other sporadically (artificially or naturally) introduced food materials, the temporal development of micro-communities based on decomposing animal products — meat, fish, cheese, feces, a dead bat or dead cave rat — deserves special consideration. Decomposition and transformation proceeds very rapidly here, in the cave as the

surface, and primary consumers appear within a few days, attracting predators. The most abundant primary consumers are larvae of catopid beetles (*Ptomaphagus hirtus*) and helemyzid flies (*Amoebaleria defessa* and related species). Adult *Ptomaphagus* burrow beneath rocks and silt under and around the food source, and become most abundant about 4 to 6 weeks after introduction of the food. The most common predators are mites (*Macrocheles* sp.) and — especially near entrances to the cave — larvae and adults of staphylinid beetles (Aleocharinae, *Homaetarsus* sp.). The mites are phoretic on *Amoebaleria*. Other common troglobitic predators — *Neaphaenops*, *Pseudanophthalmus*, *Anthrobia*, *Rhagidia*, *Kleptochthonius* — are not infrequently encountered around the food source.

Cricket guano, as well as cricket eggs and dead crickets form a major food source based on the abundant troglophile, *Hadenoeus subterraneus* (Park and Barr, 1961). This species is highly important not only for the Mammoth Cave community but also for most of the cave communities of the Pennyroyal plateau in Kentucky, as well as for those of the margin of the Cumberland plateau in eastern Kentucky ; *H. subterraneus* appears to be absent from the Bluegrass and the western slope of the Cumberland saddle between the Pennyroyal and the Cumberland plateau, with the peculiar exception of its isolated type locality at Hickmans Landing (Camp Nelson), Jessamine County, Kentucky (Part I). Similar large, highly cavernicolous *Hadenoeus* spp. are of major significance in the food webs of many caves in central Tennessee, notably in the Cumberland plateau. In addition to the guano itself, *Hadenoeus* contributes its eggs, which are a major component of the food of *Neaphaenops tellkampfi* in the caves of the Pennyroyal and Mammoth Cave plateau. Similar feeding habits have been observed in another large, cursorial trechine beetle, *Darlingtonia kentuckensis* Valentine, in the Cumberland plateau caves.

The guano itself accumulates in a thin layer (up to 5-10 mm deep) beneath roosts of colonies of *Hadenoeus* (Fig. 4) and may also occur in small increments beneath more isolated, but favored, roosting spots. The crickets feed almost entirely on forest floor arthropods outside the caves at night, returning to their roosting spots during the day. Guano production is thus largely limited to the warmer months of the year, although the crickets do make occasional epigeal forays on warm, wet nights during the winter. Reichle, Palmer, and Park (1965) have demonstrated a persistent rhythmic locomotor activity in crickets collected in White Cave, linking their feeding times with the surface regimen of day and night. The crickets begin moving toward entrances in late afternoon and emerge at twilight ; at night they are often seen several hundred meters from cave entrances. Winter aggregations in the cricket roosts — appearing near the end of October — are more compact than summer roosting colonies. From the few observations of copulation in *H. subterraneus*, impregnation of females takes place throughout the late fall,

winter, and early spring, but is most frequent about the time of formation of the winter roosts.



FIG. 4. — Guano deposits of the cave cricket *Hadenoeus subterraneus* (black material on flowstone) ; near entrance of Great Onyx Cave, Mammoth Cave National Park.

Animal communities based on the crickets, their excreta, and their eggs are best developed in White Cave (part I, p. 149, fig. 7), Proctor Cave (on Joppa Ridge), Great Onyx Cave (Flint Ridge), and since

1960, inside the original entrance to Crystal Cave, which is no longer shown to tourists. The most diverse of these communities is undoubtedly the one found in White Cave, the entire animal life of which is dependent on the crickets and, to a lesser extent, on a few pieces of rotten wood near the end of the cave. A generalized food web for this community is shown in Fig. 5. The saprophiles subsisting on the partially decomposed cricket guano include snails (*Carychium stygium*, *Glyphyalinia specum* [rare]), isopods (*Miktoniscus mammothensis*), millipedes (*Scoterpes copei*, *Antriadesmus fragilis*), collembolans (*Folsomia cavicola*, *Tomocerus bidentatus*), diplurans (*Plu-*

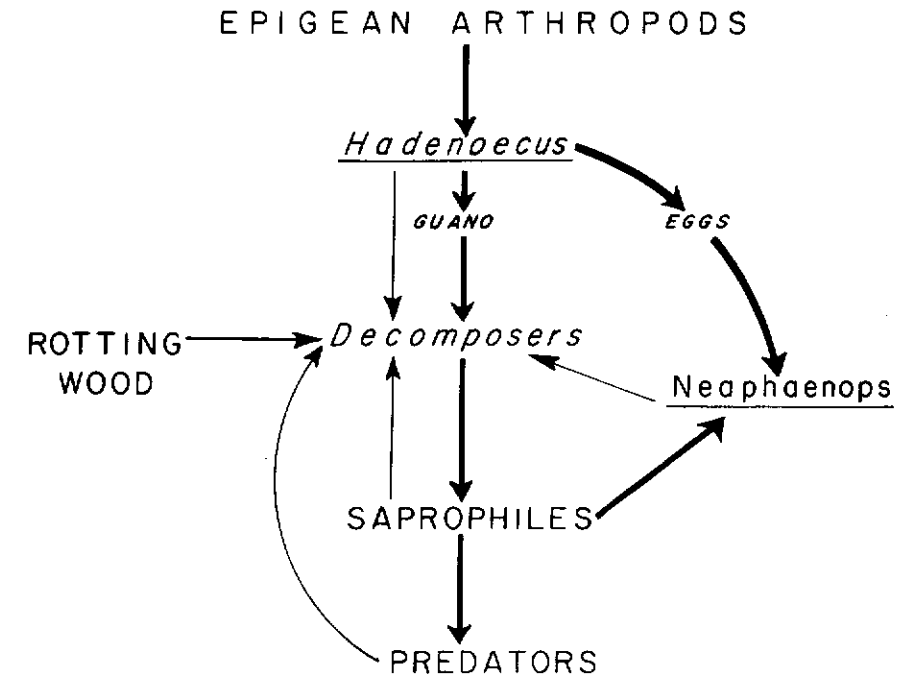


FIG. 5. — Schematic food web in White Cave, Mammoth Cave National Park ; major food energy input consists of guano, eggs, and dead bodies of cave crickets (*Hadenoeus subterraneus*), with a smaller input of old wood. See text for list species classified as « saprophiles » and « predators ».

siocampa cookei), and catopid beetles (*Ptomaphagus hirtus*). The predators include spiders (*Anthrobia monmouthia*), opilionids (*Phalangodes armata*), pseudoscorpions (*Pseudozaona mirabilis*, *Kleptochthonius cerberus*), and trechine beetles (*Pseudanophthalmus menetriesii*, *P. pubescens* [rare], *P. audax* [rare], *P. inexpectatus* [rare]). The precise details of the prey-predator relationships are poorly understood ; it is unlikely that any of the predators are highly specialized, but at the same time it is probable that certain

predators feed much more heavily on some of the primary consumer species than others. *Neaphaenops tellkampfi*, which is quite capable of eating any consumer species which it can catch (as revealed by offering various saprophile species as food in the laboratory), occupies a special position by virtue of its feeding on the eggs of *Hadenoeus*, which it extracts from the silt into which they are pressed by the long ovipositors of the female crickets. Adult *Hadenoeus*, in turn, does not discriminate in its feeding between epigean and hypogean arthropods, but eats *Neaphaenops* and probably other cave arthropods as well. Further complications in the web (not illustrated) involve the presence of a number of troglonemes and facultative troglonemes, especially dipterans and orb-weaving spiders (*Meta menardi*), which are moderately abundant within the first 75 meters of White Cave.

Stream detritus. — Large fragments of wood, twigs, leaves, and so forth are rarely carried into the Mammoth Cave system, but are locally significant in a few places in the Flint Ridge system and in the Cedar Sink-Turnhole system. Their subaerial decomposition and subsequent utilization follows the same pattern as already described for rotten wood. Many finely triturated fragments, together with microorganisms and mesoplankton are regularly transported into the cave via Echo and Styx rivers, which deposit them along with heavy silt on their subterranean banks. Bacterial plate counts from samples of mud along the rivers are among the highest recorded in the cave. Secondary production by mud bacteria supports dense populations of minute, slender oligochaetes (tubificids and enchytraeids) in the riparian silts. The relative productivity of such areas may be roughly assessed at a glance by noting the density and extent of castings of the worms. Many species of trechine beetles in the Interior Low Plateaus regularly feed on riparian oligochaetes, and thus constitute the highest of three trophic levels. Among these species is *Pseudanophthalmus striatus*, which is moderately abundant along the rivers in the Mammoth Cave system, but extremely rare elsewhere in the cave. Both *Neaphaenops tellkampfi* and an occasional *P. menetriesii* also feed on the oligochaete banks. *P. pubescens* — rare in Mammoth Cave itself — is common along the streams of the Cedar Sink-Turnhole system and in many caves of the Pennyroyal, where it coexists with *P. striatus* and sometimes with other species.

Population Density. — An estimate of the numbers of individuals in local populations of *Neaphaenops tellkampfi* was attempted in three areas of Mammoth Cave — 1) Marion Avenue, 2) Sophies Avenue (which joins Marion Avenue about 150 meters before study area # 1), and 3) the Radio Room, near Frozen Niagara. Areas selected for investigation were marked off somewhat arbitrarily into gallery segments, the boundaries of which correspond to points at which *Neaphaenops* are no longer commonly seen walking about on

the floor. Specimens were collected by hand and placed in large glass jars and held for marking in the cave. Marking was accomplished by placing a small amount of a cellulose acetate-amyl acetate paint on the elytra of each specimen. The specimen was then placed in a second jar long enough for the paint to dry, and all marked specimens were released near the center of the study area. Since the possible deleterious effects of the marking paint were not known, 11 specimens were heavily marked and placed with 13 unmarked specimens in a square glass aquarium (area approximately 0.37 m²), on the bottom of which was a layer of cave silt 5 cm deep. The container, with the control specimens, was left on the floor in area # 1 for 7 days, at the end of which all 24 specimens were active and apparently in normal condition. Although the paint showed a tendency to flake off the painted beetles, all of them retained sufficient paint to be readily recognizable as marked. There is a very low probability that some of the beetles in the later samples had previously been marked and could not be recognized because all of the paint had flaked off; if this occurred, then our estimates of population density may be slightly higher than the true population density.

The results of our marking-release-recapture observations are shown in Table 6, together with computation of modified Lincoln-Petersen indices, using the positive method of Jackson (1939), in which only the initial sample was marked. In area 1 (300 m²) our estimate shows a total population of 880 beetles. This was perhaps the most « open » of the three study areas; a rocky floor immediately before the area boundary was never observed to harbor *Neaphaenops*, but an occasional specimen was encountered wandering along Marion Avenue beyond the area. Of the 97 specimens marked on 24 March 1963 in this area, none was found outside the area on 29 March nor 6 April. On 13 April one specimen was found approximately 24 meters beyond the boundary and another approximately 67 meters beyond. In area 2, which is slightly damper, beetles appear to be much more abundant from visual inspection, and our results confirm this, with an estimate of 2761 individuals for a passage segment 10 m wide × 40 m long (400 m²), slightly less than 7 beetles per square meter of floor space. Pupae were found in this area, under stones in silt chambers, during the study period (April 1963) and have since been discovered here in May and June of later years. In area 3, the Radio Room (about 300 m²), an estimate of 816 individuals in the population was obtained.

If only two such *Neaphaenops* areas per kilometer of cave passage occur in Mammoth Cave and the other caves of Mammoth Cave National Park, the total population of this species within the Park is probably close to 750,000 individuals (average of 1486 specimens per area X 2 X estimated 250 kilometers of known passages). Despite this large population size, the total biomass contribution of *Neaphaenops* imagines to the ecosystem, with an average weight of

about 5 mg per individual, is only about 3.75 kg. Furthermore, if the estimates are fair approximations to the true population size in the sample areas, these data shown that anywhere from 6 to 25 per cent of the population is removed if all specimens which can be found in an area by diligent collectors are captured. The actual proportion of specimens actively crawling about on the cave floor is substantially less, since 1/4 to 1/2 of the specimens in each sample were obtained under stones. The active proportion of the Marion Avenue and Radio Room populations is therefore probably on the

TABLE VI.
Neaphaenops marking-release-recapture experiment
employing positive method of Jackson.

Area and Location	Date	Total Captures	Marked Recaptures	Corrected Recaptures
1. Marion Avenue, Mammoth Cave	III-24-63	97	—	—
	III-29-63	118	10	$y_1 = 8.75$
	IV-06-63	127	7	$y_2 = 5.70$
	IV-13-63	133	6	$y_3 = 4.64$
$r_+ = \frac{y_2 + y_3}{y_1 + y_2} = 0.715 \quad a_o = \frac{y_1 + y_2}{r_+} - y_1 = 11.46$				
$P = \frac{100}{1} \times \frac{100}{a_o} = 880$				
2. Sophies Avenue, Mammoth Cave	III-24-63	100	—	—
	III-29-63	128	5	$y_1 = 3.90$
	IV-06-63	168	2	$y_2 = 1.19$
	IV-13-63	177	4	$y_3 = 2.26$
$r_+ = 0.678 \quad a_o = 3.61 \quad P = 2761$				
3. Radio Room, Mammoth Cave	III-30-63	200	—	—
	IV-06-63	133	16	$y_1 = 6.02$
	IV-13-63	108	8	$y_2 = 3.70$
	IV-20-63	102	3	$y_3 = 1.47$
$r_+ = 0.532 \quad a_o = 12.25 \quad P = 816$				

order of 10 per cent and that of the Sophies Avenue population may be near 5 per cent. It is conceivable that there is a much higher rate of immigration and emigration in Sophies Avenue, especially up and down the walls of the adjacent pit, so that the apparently resident population is actually drawn from a wider area, and actually more than 5 per cent of the population is active at any given time. Since the apparent density of *Neaphaenops* in Sophies Avenue is more than 2 1/2 times that of the other two areas, this may be the case,

although it is also possible that Sophies Avenue is simply a more productive habitat.

Obviously there are at least two rather different types of populations in these 3 samples, and it is not really feasible to make broad generalizations to all the populations in the Mammoth Cave system. We have casually observed many other populations and suspect that most of them will prove to be similar to the Marion Avenue — Radio Room type, with the Sophies Avenue type relatively infrequent. Still other types certainly must exist, especially along the banks of perennially flooded subterranean streams, where the silt is less suitable for extensive burrowing and where interstices normally available for inactivity periods may be silt-filled. It may be much easier to obtain density estimates for such populations, since the majority of individuals should be readily accessible. It should also be noted that heavy collecting in these areas can decimate or almost completely remove the entire population.

TABLE VII.
Relative abundance of cave trechines in Kentucky.

		Calculated from $\sum_{i=1}^r \frac{1}{n-i-1}$	Observed
Walnut Hill Cave, Barren County 9 Aug. 1966	<i>P. menetriesii</i>	38.02	35
	<i>P. pubescens</i>	19.78	20
	<i>N. talkampfii</i>	10.72	14
	<i>P. striatus</i>	4.56	4
Diamond Caverns, Barren County 23 Aug. 1965	<i>P. menetriesii</i>	29.33	29
	<i>P. pubescens</i>	13.33	14
	<i>P. striatus</i>	5.33	5
Cave City Cave, Barren County 24 Aug. 1965	<i>P. pubescens</i>	24.44	26
	<i>P. menetriesii</i>	11.11	12
	<i>P. striatus</i>	4.44	2

Relative Abundance of Trechines. — Collections of trechines in the Mammoth Cave system usually show a preponderance of *Pseudonophthalmus menetriesii* in the upper levels and of *P. striatus* along the rivers, with numerous *Neaphaenops talkampfii* in both places. Other species occur sporadically, usually in very small numbers. However, in small, more homogeneous caves of northern Barren County (about 15 - 20 km south of Mammoth Cave), the relative abundance of *P. menetriesii*, *P. pubescens*, and *P. striatus* appear closely to approximate the broken stick model proposed by MacArthur (1957), at least in late summer samples (Table 7).

Tests of MacArthur's model for diverse groups of animals and plants have shown good fits to groups of rather closely related species in homogeneous environments (MacArthur, 1957, 1958; King, 1964), but not to highly diverse assemblages of species in heterogeneous biotopes (plankton in a river, trees in a forest, all animals in a cave, and so forth). As shown in the data for Walnut Hill Cave, *Neapphaenops* may also be included in collections from small, homogeneous caves, without undue departure from the model. However, if larger caves with both wet and dry, sandy areas are completely sampled, then the large number of *Neapphaenops* from the sandy areas will cause the sample to depart radically from the distribution predicted by the model. In Diamond Caverns, the entire sample was collected from a wet, artificially enlarged terminal passage containing a few rotting boards.

MacArthur (1957, 1958) originally interpreted a close fit to the model to mean that the resources of the environment are randomly assorted among the species involved, although both MacArthur (1966) and Hairston (1969) have seriously questioned whether the model has any ecological meaning. It should be noted that the rank of the component species is not predicted by the model, nor is rank the same in Cave City Cave as it is in Walnut Hill Cave and Diamond Caverns, since in Cave City Cave *P. pubescens* displaces *P. menetriesii* as the most abundant species.

THE AQUATIC COMMUNITY.

The presence of water in Mammoth Cave is rather closely controlled by surface topography and proximity to the water table. The sandstone caprock channels drainage laterally and produces an effective shield for the passages directly beneath, which despite high relative humidities are virtually devoid of flowing or standing bodies of water. Surface drainage enters the cave at the margins of the sandstone cap, often carrying visible amounts of organic material. The terminal breakdown in Rafinesque Hall (Mammoth Cave) is sufficiently wet to support populations of *Asellus* and *Stygobromus*, and *Stygobromus* occurs in capillary films at Pike Chapman Entrance (artificial, Salts Cave), but most breakdowns are more noteworthy for their terrestrial fauna. Large amounts of water plunge 40 to 50 m via domepits almost to the water table, but some water moves laterally for short distances as streams, seeps, and « springs », reaching the water table in a series of steps. Late winter and spring are periods of maximal flow in the cave, and many of the small subterranean streams disappear by late summer or autumn. *Asellus* and *Stygobromus* occur in a few of these streams and pools. *Speophila buchanani* has been observed on several occasions in such a surface-fed stream in Great Onyx Cave. *Chaetogaster* occurs sporadically in temporal drip pools near Frozen Niagara and in a dripstone area in Proctor Cave.

Rimstone pools (gours) form a characteristic feature of White Cave, where they can be more conveniently observed than in less accessible portions of the system. The basins are dry in summer and autumn but fill to maximum depths of a half meter within a few weeks after saturated soils can no longer retain winter precipitation. Water drips into the pools from stalactites or trickles down over columns and flowstone to enter the pools. Organic enrichment is furnished by cricket guano. In late November, 1961, the recently filled pools appeared sterile, but only two weeks later several of them contained *Sphalloplana percaeca*, 3-6 mm in length. The same phenomenon has been observed in subsequent years. The pools were full and inhabited by flatworms in mid-September, 1967, following an unusually wet summer. Ginnet and Puglisi (1964) observed the same pattern of appearance of *Fonticola notadens* in a cave in France, and found that the planarians survived in hygroscopic silts on the bottoms of dried pools, undergoing asexual reproduction by fragmentation during this time. A similar explanation may account for the sudden appearance of relatively large planarians in White Cave. *Asellus stygius* has been found on the wet flowstone of White Cave and was taken from one of the pools on a single occasion.

The largest known body of water situated above flood levels in Mammoth Cave is Crystal Lake in the Frozen Niagara section. It fills the bases of two narrowly connected domepits and is ponded to a maximum depth of about 3.5 m by a flowstone dam at one end, artificially grouted and cemented. Surface area is about 120 m². Water is supplied only by ceiling drip and wall flow after heavy surface precipitation. Levels are highest in late winter and slowly fall about 0.3 to 0.5 m by the following autumn. The lake contains no macroscopic organic material; bottom sediments are free of odor when brought to the surface. Enrichment is assumed to be meager, coming mainly from cricket guano and soil microorganisms carried into the cave by ground water. Grab samples made near baited areas revealed the presence of *Asellus stygius*, *Stygobromus vitreus*, tests of *Diffugia* sp., the exuvium of a tardigrade, and one or two unidentified nematodes. Two *Orconectes pellucidus* were observed on most visits. The results of plankton sampling are discussed below.

The abundance and permanence of aquatic habitats increases markedly as one descends from the upper levels of the caves into the lower levels. Active and partially abandoned drains of domepits often lead surface drainage back beneath the sandstone cap so that xeric upper passages are underlain by extensive wet areas. Relative humidity always exceeds 98 per cent and permanent water can be maintained by slight and infrequent input. *Orconectes pellucidus* joins the cave isopods and amphipods as a characteristic species of such waters. Streams in the intermediate levels of the system are generally of short extent; they usually flow sluggishly over flat limestone with silt, sand, and fine gravel lying in shallow pockets,

eventually disappearing into floor crevices. Depths in the flat stretches seldom exceed a few centimeters.

Echo (Fig. 6), Roaring (upper Echo), and Styx rivers represent the surface of the water table in Mammoth Cave. Similar large streams have not yet been discovered in the cavern complex beneath Flint Ridge, although substantial populations of amblyopsid fishes and *Orconectes pellucidus* are maintained in Eyeless Fish Trail. These larger aquatic cavernicoles are also reported for Colossal River (T. L. Poulson, personal communication). The two Flint Ridge

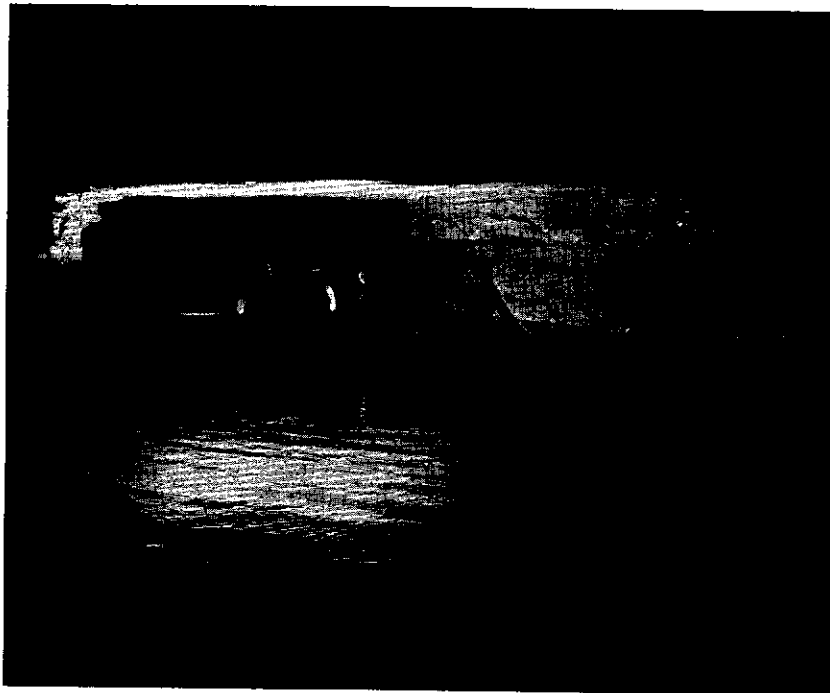


FIG. 6. — Echo River, Mammoth Cave. Photo by W. Ray Scott, courtesy National Park Concessions, Inc.

streams also occur at or very close to the water table surface. *Amblyopsis*, *Typhlichthys*, and *Orconectes* are abundant in the large subterranean river which courses through the Cedar Sink-Turnhole system in Joppa Ridge. In Mammoth Cave isolated flood pools, notably in the Roaring River passage, are associated with the major rivers, and will be separately discussed.

The cave rivers occupy the floor of galleries which are quite similar to the dry upper passages in dimensions and contours. Except under extreme flood conditions the rivers appear much like surface

streams with long pools and short riffles. In the Echo system the largest pools may exceed 100 m in length, but widths seldom surpass 10 m. Styx River is first seen through a floor window (the « Dead Sea »), and can be followed for about 100 m before its channel becomes heavily silted, when most of the flow apparently takes place in inaccessible lateral conduits. Residual pools in the silted area (« Lake Lethe ») exhibit little or no flow in late autumn, and are normally less than 1 m deep, although two of them are approximately 3 m deep even at low water. In the Echo system, pool depths of 3 to 4 m are common. Occasionally siphons carry the rivers beneath rubble or dipping ceiling beds, and it is as impenetrable siphons that they debouche into the narrow valley of Green River. Echo-Roaring River is less depositional in character than Styx River, and finer sediments are usually restricted to deeps pools, backwater, and gradually sloping banks. In summer the streams are extremely clear and without appreciable flow, but they become badly roiled by even small rises, and have high turbidity virtually all winter. In an unobstructed river passage deposition produces a V-shaped cross-section along the stream, the thickest deposits occurring at the sides, where rate of flow is minimal.

The hydrology of the cave rivers is complex and worthy of description here as a basis for interpretation of our results and as a ready summary for future workers. The Mammoth Cave plateau has only a few wet-weather streams and these vanish into sinkholes after short courses. In effect the cave receives all local precipitation which is not transpired or evaporated directly back to the atmosphere. Styx River may derive its flow from this catchment plus some Green River water, but Echo River is much larger and probably gathers water from still farther south and west. Well level records from the Sinkhole Plain south of the plateau reveal that the water table slopes toward Green River (Robert Cushman, personal communication). Still farther south several creeks, varying in length from 1 to 15 km, sink beneath the surface and contribute to the water table of the Sinkhole Plain (Kuehne, 1966). It seems probable that Echo River rises from several of these surface tributaries at least 20 km from its mouth, although it gathers much of its volume from the Sinkhole Plain and Mammoth Cave plateau. The present level of Green River has been raised approximately 2 m by a low navigation dam at Brownsville, downstream. This artificial disturbance in the ecology of the cave river systems may account for the depositional character of Styx River in its lower reaches and for the fact that some Green River water normally flows into its mouth. The mixture of surface and cave water thus feeds into lower Echo River and emerges at Echo River spring. This situation has been well documented by Hendrickson (1961), who made effective use of a high chloride difference between Green River and the cave streams to trace water masses and dilutions. Major floods on Green River reverse the flow of both cave streams, which rise in response to each

flood crest and sometimes completely fill the river passages. As the floods subside the cave streams disgorge a mixture of their own storm waters and those of Green River.

Unfortunately, most limnological work in the Mammoth Cave system, including that of this paper, has necessarily been restricted to the accessible areas which are influenced by Green River. The upper sections of the Echo-Roaring river system are infrequently accessible because of slight flooding; a low ceiling 250 m inside the Roaring River passage makes the river impassable except at lowest water stage (about 1 m). Removal of the navigation dam at Brownsville would open the stream to biological exploration throughout much of the year.

Water levels. — Figure 7 illustrates the relationship between precipitation and water levels in the cave streams between October 4,

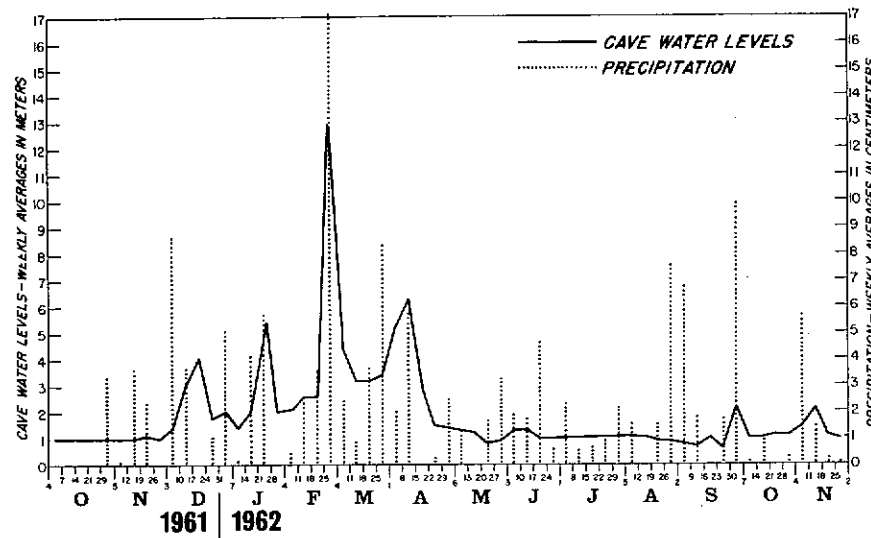


FIG. 7. — Cave water levels in Mammoth Cave, October 1961 — November 1962, showing relationship to local precipitation. Cave data averaged from U.S. Geol. Surv. nitrogen bubbler manometer gauge at Dead Sea, or from corrected daily gauge readings at Echo River outlet; precipitation data from National Park Service weather station at Mammoth Cave.

1961, and December 2, 1962. Precipitation data were recorded by the National Park Service weather station on Mammoth Cave Ridge. Most water levels are based on a continuous record from the Dead Sea (Styx River) made by the U.S. Geological Survey's nitrogen bubble manometer housed directly above at the surface. Weekly values are based on a number of daily averages. The manometer was occasionally inoperative, especially during the spring and summer of 1962. At such times cave water levels were estimated by correcting

readings from the standard stream gauge at Echo River outlet. The 1 m level on the graph represents normal low level of Styx River and any values below this are accompanied by the disappearance of most of the shallow pools in Lake Lethe, but not in Echo River.

Low and stable water levels prevailed through late autumn of 1961, but were finally disturbed by heavy rains on 10 December and a subsequent increase in gauge height. A still larger flood occurred in late January as a result of precipitation hardly greater than that causing the previous rise, but rainwater falling on previously saturated soils apparently drained more quickly and more completely into both the cave streams and into Green River. Heavy precipitation falling on the entire Green River basin for two days preceding 2 March 1962 produced a record flood in Mammoth Cave. In River Hall the waters rose to 16.5 m above normal low water level (1 m), and even normally dry portions of the cave were inundated. After a fourth major rise in April the cave waters quickly fell to near normalcy. Each of the floods had left behind a coating of silt and sand which occasionally held recognizable bits of finely triturated plant material. A few larger pieces of wood were sparsely distributed through the stream galleries.

Most of the summer of 1962 was dry and gauge height remained near normal until August, when a slow decline became apparent. Shallow pools along Lake Lethe disappeared and actual flow was reduced to a mere trickle. A series of thunderstorms in late August and early September had no measurable effect on cave water level, but subsequent rains in early October produced a 1 m crest. A similar rise resulted from the first cold rains of November, 1962.

Figure 7 illustrates the general annual pattern of water levels in Mammoth Cave, although the low, stable period in the fall of 1961 was somewhat longer than usual, and the flood of March 1962, was greater than usual. One or more major floods occur during the colder months of every year, while low and stable water levels normally prevail during the warmer months. Summer flooding up to 3 or 4 m follows prolonged and heavy precipitation in the Green River basin, but summer floods are sporadic and occur only in wet years (e.g. 1963 and 1967). The normal pattern is closely associated with the growing season. Interception and transpiration of rainwater by the deciduous forest canopy reduce surface runoff and dry the soils to considerable depth. Leaf fall is maximal in October and subsequent precipitation restores soil moisture. Small streams resume flow and respond quickly to precipitation. The stage is then set for major flooding of Green River and the cave streams. Physical and chemical conditions of the cave waters are closely associated with the precipitation and water level picture, as are plankton counts in Echo River and the importation of organic materials into the cave by backflooding of Green River. The sources of the waters investigated thus differ markedly from that of the pools and droplets studied in Luray Caverns by Holland et al. (1964). In restricted areas of the

Mammoth Cave system, particularly where dripstone is abundant, the discussion of these authors is probably much more pertinent.

Physical and chemical conditions. — The results of physical and chemical factors measured for the cave rivers and for Crystal Lake are shown in Figures 8, 9 and 10, and in Table 7. When points on the curves are separated by more than a month's time, they are connected by a dashed line. Crystal Lake, near the Frozen Niagara entrance, is easily accessible in all seasons, allowing us to accumulate a better record here than in either of the rivers. The rivers were occasionally approached via Silliman Avenue, at which times Echo River was sampled at Fourth Landing and Styx River samples were omitted. Normal access was via River Hall and Shakespeare's Galleries, and water levels determined our sampling sites. Third Landing was chosen for Echo River sampling, but floods and silt deposition isolated this site during winter when variations in physicochemical parameters were greatest. Styx River was sampled along Lake Lethe, the foot of the steps beyond Rapier's Pit, or even in River Hall, depending on flood stage.

The interpretation of results of oxygen and temperature measurements in Mammoth Cave are greatly simplified by the absence of diurnal patterns which are superimposed on seasonal changes in surface waters. In late autumn (Fig. 8) oxygen values are at or near their annual low point and water temperatures are about in equilibrium with cave air. Winter floods oxygenate the water while depressing temperature.

Crystal Lake affords the clearest picture because it is isolated from Green River, has a small input of water, and was frequently sampled. Temperature fell to a brief annual low during December, 1961, and January, 1962. Direct heat exchange and evaporative cooling are thought to have been effective in producing a marked change here. The lake lies quite close to the Frozen Niagara entrance, an artificial opening loosely closed by a wooden door around which winter air finds easy ingress. Cold, dry air flows along the floor and spills over into the dome pit in which part of the lake is located. Water entered the lake as a thin film which flowed down the walls of the shaft with little or no splash effect and consequently minimal oxygenating action. The minimum temperature measured was 11°C in January and the maximum was 13.8°C in August. Dissolved oxygen rose from an annual low of 7.2 ppm in November, 1961, to a high of 10.4 ppm the following January, and again in March. The spring fluctuations probably resulted from rapid percolation of water from the surface. During the dry summer and autumn months the dissolved oxygen decreased gradually, then increased sharply to 10.8 ppm after the heavy October rainfall restored a flow of water down the walls of the pit.

The winter and spring changes in dissolved oxygen and temperature in the cave rivers were partially monitored in Styx River but

were virtually missed in Echo River. An inverse relationship in winter is indicated more clearly than for Crystal Lake. Styx temperatures dropped from 13.4°C in November, 1961, to 8.6° the following January, while oxygen rose from 9.6 ppm to 12.6 ppm during the same period, producing a slightly supersaturated condition.

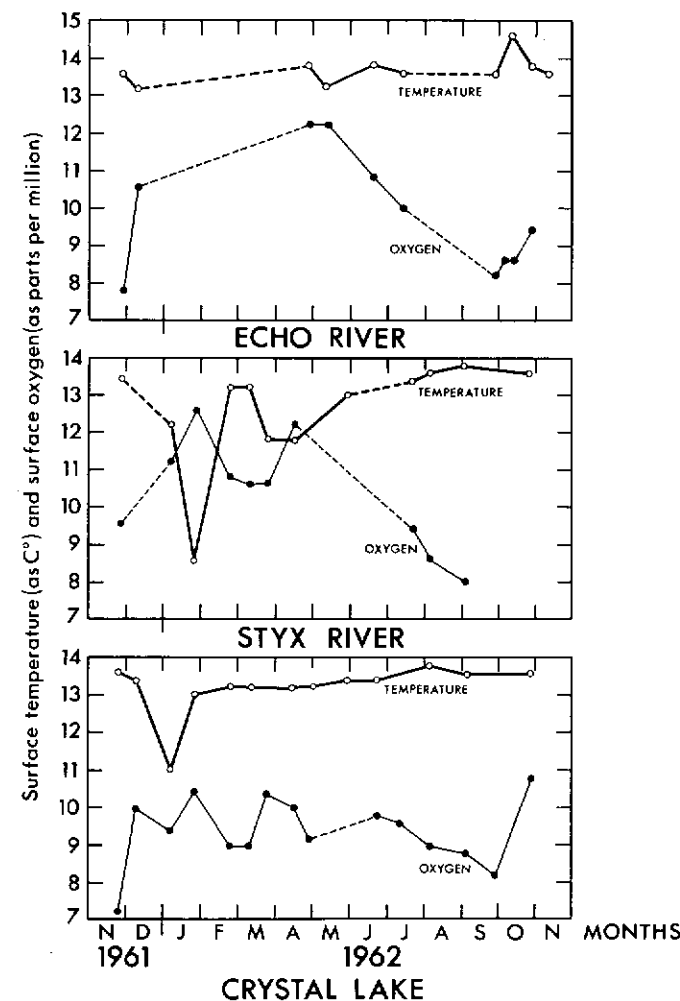


FIG. 8. — Surface temperature and surface oxygen in Mammoth Cave waters ; temperature readings from Anschütz precision-grade thermometer, oxygen determinations from standard Winkler method.

Following a return to higher temperatures and lower oxygen tensions the pattern was again recorded during the last flood of March and April. Other fluctuations of temperature and oxygen probably occurred between our sampling periods. Stable temperature

and declining oxygen values characterized the summer and early autumn months. Several readings were obtained on Echo River at the time of the small October rise caused by heavy thunderstorms. Water temperature rose a degree to 14.6°C and oxygen content rose 0.8 ppm to 9.4 ppm, but remained well below saturation level.

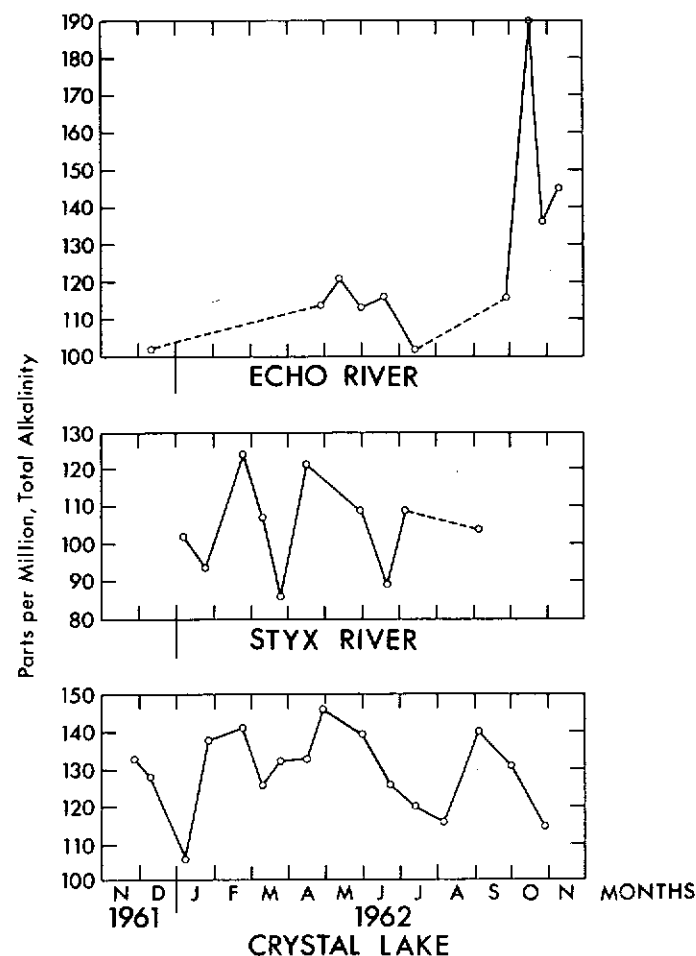


FIG. 9. — Total alkalinity (methyl orange titration) in Mammoth Cave waters.

Oxygen tensions are the result of interaction of several biological and physical factors. Oxygen replacement can come about only through a restricted number of physical means. In contrast to surface waters, oxygenation through convection currents or wind action is virtually absent in the cave streams. Considerable mixing does result from turbulence of cave streams, particularly in flood stage,

but this effect dwindles almost to nothing by the end of summer. A large volume of quite cold surface waters enters the cave from time to time during winter and much of it is violently agitated before reaching the rivers. The tendency of the cave rivers to be slightly supersaturated with oxygen in winter and early spring probably results from heat transfer from the surrounding rocks.

Though the density of aquatic cave organisms is low, their activity constitutes a steady demand for oxygen. The physical factors operative in winter and spring overshadow biological demand, but in summer our results indicate that a gradual oxygen depletion to 80 % or less of saturation occurs in quiet, undisturbed pools. The rate of loss is distinctly greater in Styx and Echo rivers than in

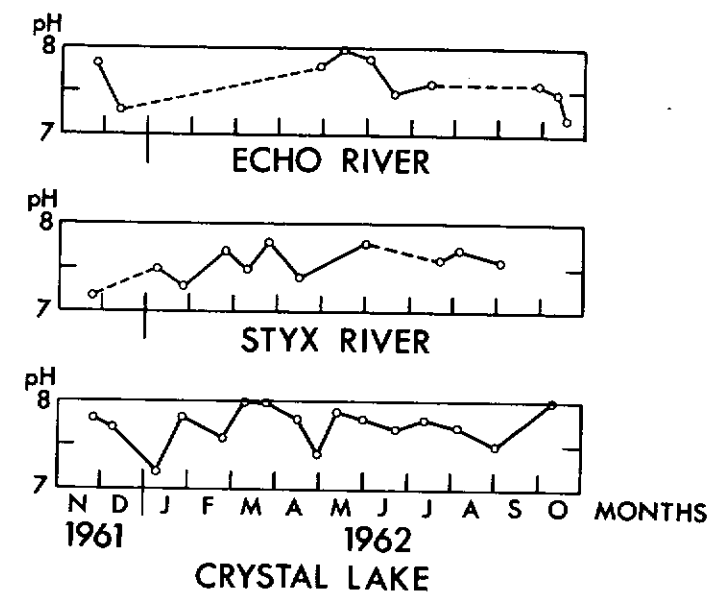


FIG. 10. — pH in Mammoth Cave waters ; Coleman Model 20 portable pH meter.

Crystal Lake, where biomass is much lower. It should prove feasible for future investigators to estimate summer and fall community metabolism in cave pools by monitoring oxygen depletion, correcting for the rate of diffusion at the air-water interface and the slight air and water circulation which may occur.

Total (methyl orange) alkalinity and pH were also monitored during the study (Figures 9 and 10), but the results are not subject to easy analysis. Differences in the source of water may be involved in independent behavior of the three study areas. Crystal Lake receives water from the limestones directly above, but part of this may have originated on the sandstone caprock of Mammoth Cave Ridge. Echo River collects water from above and from a large limes-

tone area to the south of the cave. The origin of Styx River is probably similar to that of Echo but considerable mixing with less alkaline Green River water is known to occur.

Values of pH varied from 7.2 to 8.0 in Echo River, 7.2 to 8.1 in Crystal Lake, and 7.2 to 7.8 in Styx River. Our data show that the first major floods of winter cause a depression in pH and that higher, but variable, values occur during the remainder of the year.

Lower pH values in Styx River paralleled lower total alkalinity values, which varied during the year between 86 ppm and 124 ppm. The annual range in Crystal Lake was 106 ppm to 146 ppm, while that of Echo River was 102 ppm to 190 ppm. Minimal alkalinity always occurred during winter floods, when the great amount of surface runoff and infiltration dilutes dissolved solids. The great peak in Echo River came at the time of the resumption of flow following a long, dry summer. Similar peaks in surface streams have been recorded by previous authors and are explained as the uptake of solids that have accumulated in or at the surface of soils.

Neel (1951) made a detailed analysis of physical and chemical conditions in a surface limestone stream lying approximately 160 km northeast of Mammoth Cave under regional temperature and rainfall conditions similar to those of the cave region. Comparison of his data with our findings reveals some interesting similarities and differences. The discharge patterns of the surface and cave streams are quite similar. Major floods in the surface stream were confined to winter. Discharge decreased through spring and summer and streams ceased to flow by late summer. Steady flow resumed overnight from heavy November rains and the stream was subject to winter floods thereafter. Neel found a much greater range of variability in temperature and dissolved oxygen, and the maxima fell at different times from those in the cave system. Oxygen was maximal in spring when algal photosynthesis was greatest, although temperatures had already risen above their lowest marks. As in the cave streams, minimal oxygen values occurred in autumn. However, Neel noted a precipitous and short-lived drop in oxygen tension which started with October leaf fall and ended with resumption of flow. Temperatures followed a seasonal curve with a slight lag, being maximal in July and minimal in January.

Neel's values for pH were consistently low (7.1-7.4) during autumnal decomposition and consistently high (8.7-9.1) throughout spring. Summer values remained above 8.0 and reached 9.0 over algal mats in tributaries to the main stream. Major winter floods reduced pH levels to 7.0, but they returned to 8.0 or higher between floods. Our minimal pH values are very close to Neel's and also came during winter, but the cave rivers never displayed high pH compared to surface limestone streams. Total alkalinity in the surface streams varied with source of flow, whether derived from springs, soil seepage, or surface runoff, and was generally modified by photosynthetic activity, especially over riffles. Heavy winter rains reduced

methyl orange alkalinity values to as low as 122 ppm, while the highest values of 217 ppm occurred in early October. Although environmental conditions in the cave are seemingly less complicated, we still found alkalinity to be inexplicably variable.

Although the annual range of variability is smaller for physical and chemical parameters in Mammoth Cave waters than for surface waters, the rate of change is great at the beginning of winter. These sharp variations may prove to be important cues for aquatic cave troglobites, which are not subject to diurnal and seasonal changes that condition the activities of surface animals. Poulson (1963) and Woods and Inger (1957) have shown that reproduction in troglotic amblyopsid fishes occurs during or just after the winter floods. We have seen the atyid shrimp *Palaemonias ganteri* carrying eggs between April and November, the largest number of eggs occurring in April. It is logical to suppose that other troglobites will be shown to display reproductive peaks at times that assure young of the best opportunities for feeding.

Supplementary Physical and Chemical Data. — A few additional samples (Table 8) have been taken in years following the main study period. The more recent readings at the regular Mammoth Cave stations fall close to anticipated values for the appropriate season.

On 21 February 1964 surface and bottom samples were made in Crystal Lake for temperature, dissolved oxygen, alkalinity, and chlorides. Oxygen values were the same (8.4 ppm) at the surface and on the bottom at depth of 3 m. Chlorides were also the same (1 ppm) at both levels, and only a slight difference of 3 ppm in alkalinity was recorded. Surface temperature was 0.2°C lower than bottom temperature, suggesting that movement of cold air into the shaft above the lake was sufficiently great to produce slight chilling and probably convective mixing.

Oil brine pollution of Green River upstream from Mammoth Cave has greatly abated since Hendrickson's (1961) study, but a chloride gradient from Green River (23 ppm) through Styx River (11 ppm) to lower Echo River (2 ppm) was still evident on 11 October 1963. With the exception of Annette's Dome, which lies beneath a recently abandoned septic field, chloride content of local surface drainage into the cave system was only 1 ppm or 2 ppm. Areas of the cave affected by backwater flooding from Green River may have slightly more chloride, as shown by the values obtained for Echo River (3 ppm) and the Roaring River Shrimp Pools (4 ppm) on 6 July 1963. Chlorides are higher in Styx than in Echo, which reflects the persistent addition of Green River water to Styx River.

The relatively low alkalinity of sandstone-derived waters above the cave may persist in percolating water which has recently entered the cave system, as at Roosevelt Dome and the ceiling spout near Frozen Niagara. Intermediate alkalinity has been recorded at

Richardson's Spring, which lies at moderate depth in the cave. Particularly cold water (8.2°C) was recorded during winter from the cascade at the base of Annette's Dome. On warming, such waters would become supersaturated with oxygen before reaching ambient cave temperature.

TABLE VIII.
Supplementary physical and chemical data.

Location	Date	Temp. °C	Total Alk. (PPM)	pH	Cl- (PPM)	O ₂ (PPM)
Crystal Lake	II-15-63	12.6	140	7.9	—	8.4
» »	VII-05-63	13.6	134	7.8	—	7.8
(surface)	II-21-64	13.0	152	—	1	8.4
(bottom, 3 m)	II-21-64	13.2	155	—	1	8.4
Echo River,						
Third Landing	VII-06-63	13.6	120	7.8	3	9.0
» »	VII-31-63	13.6	118	8.0	2	9.1
» »	X-11-63	13.4	131	—	2	—
Styx River, along board						
walks	X-11-63	13.2	120	—	11	—
» »	IV-05-64	11.2	83	—	4	—
» »	II-13-65	12.4	110	—	3	—
Roaring River, Shrimp						
Pools	VII-06-63	13.4	131	7.4	4	6.0
Roaring River, lower						
end	VII-06-63	—	122	7.8	2	—
Green River at Mam-						
moth Cave Ferry	II-14-65	—	68	—	5	—
Green River at Styx						
Outlet	X-11-63	—	—	—	23	—
Annettes Dome	II-21-64	8.2	125	—	5	13.0
Lake Purity	II-21-64	13.0	140	—	2	10.2
Ceiling spout at Frozen						
Niagara	II-14-65	13.2	25	6.7	1	—
Richardson Spring	IV-05-64	11.6	80	—	2	—
Pool at Jumbo	II-14-65	13.4	104	8.2	1	—
Roosevelt Dome in						
New Entrance, pool	IV-04-64	10.6	49	—	1	10.8
Surface stream flowing						
into New Entrance	IV-04-64	9.8	34	—	1	11.0
sink	II-14-65	4.5	35	6.9	1	—
» »						
Beaver Pond at Sloans						
Crossing (surface	IV-04-64	10.4	35	—	2	—
pond)						
Great Onyx Cave, do-						
mepit near entrance	II-21-64	12.0	—	—	2	9.2
White Cave, rimstone						
pools	IV-04-64	12.2	144	—	2	10.4

Plankton Collections. — Plankton tows were made on most of the occasions when water samples were taken from the river systems. Boats could sometimes be used to make deep midchannel tows in Echo River, but most collections were made from shore or from catwalks, and various depths were sampled. Collections were preserved in formalin and counted later in the laboratory under magnifications of 100 X and 440 X.

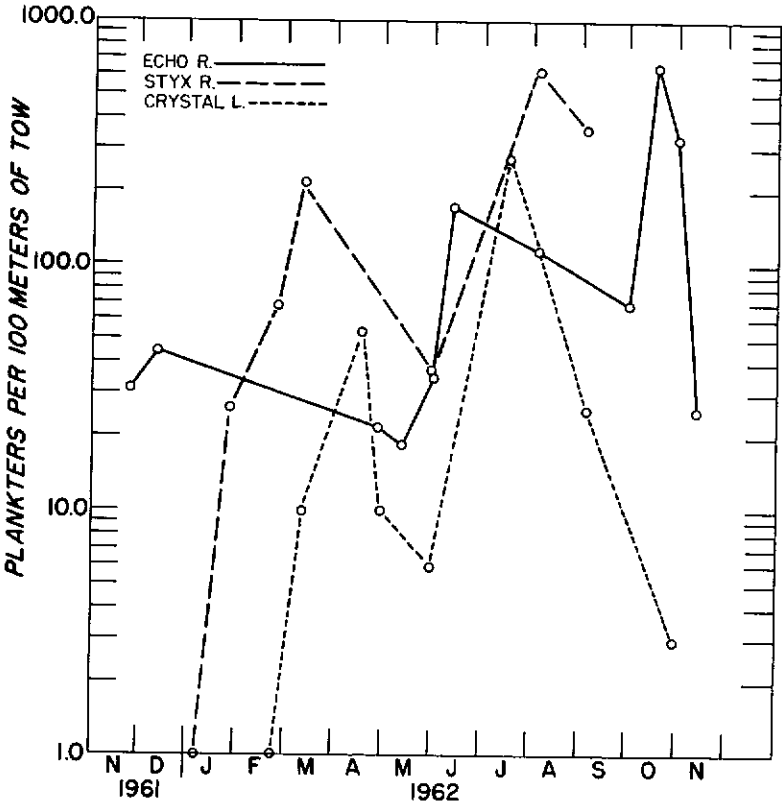


FIG. 11. — Plankton density in Mammoth Cave waters ; semilogarithmic plot.

A few diatoms, filamentous green and filamentous blue-green algae were encountered regularly in spring and summer collections from Echo and Styx rivers. We considered these to be surface algae swept into the cave during backflooding, as Kofoid (1899) had done, and restricted our counts to zooplankton, which may feed and grow in the cave even though ultimately of surface origin. The studies relating to taxonomy of algae from walls, mud, and pools in Mammoth and Crystal caves were reviewed in Part I of this paper.

The most striking feature revealed by analysis of plankton tows is the low density of organisms (Fig. 11). Numbers are presented on

a semilog scale to prevent obscuring the lowest values. « Plankters per 100 m of tow » was used as a convenience; with our nets a 100 m tow strained approximately 1766 liters.

Adult copepods or nauplii were the only group of animals which appeared in every collection made in the rivers and in Crystal Lake. A checklist of species encountered was given in Part I of this paper. *Tropocyclops prasinus* is the most widely distributed and abundant copepod in the samples. All of the species occur commonly in surface waters with the exception of *Cyclops donaldsoni*, which is known only from caves or from streams issuing from caves. This species appeared in a single Roaring River Collection, which was made at a distance from Green River far greater than that of the regular Echo and Styx samples.

Other forms occurring in various plankton samples include testate and ciliate protozoans, nematodes, rotifers, a tardigrade, an ostracod, and the cladoceran *Bosmina longirostris*, which made up one-third of the October peak sample from Echo River, but was otherwise absent from most river collections and from all Crystal Lake samples. The bulk of material collected in tow nets consists of normally benthic microinvertebrates which are adventitious, rather than true plankters. In retrospect, it appears that a more accurate measure of available food microorganisms in the rivers would emerge from samples taken at or near the bottom muds.

Crystal Lake and Styx River show minor peaks in plankton during the period of high water in winter and early spring and still higher peaks in July and August. Echo River could not be sampled in flood stage, but a slight increase in June and a definite peak in October and November were recorded. Copepods with egg sacs and *Bosmina* with young in the brood pouch were common in the latter collections. In Styx River a few copepods with egg sacs were seen in both March and August.

Winter increases in zooplankton are contemporary with the great influx of water and detritus from percolating ground water, sinking creeks, and backflow from Green River. To a major extent this plankton is presumed to be allochthonous. In Crystal Lake it may be trapped and contribute significantly to secondary production, but at least some of the winter plankton of Echo and Styx rivers is again lost to Green River through the mouth of Echo River. It will be a major task to determine the quantitative significance of winter plankton to secondary production in the cave rivers.

By contrast, the summer and autumn increases in plankton counts occur when cave waters are typically more isolated from surface influences. These peaks can possibly be attributed to secondary production based on the detritus left by receding flood waters. The quiet, clear condition of the cave streams is more amenable to biological activity than are the strong currents and high turbidity during winter floods. We conclude that the greatest amount of secondary

production contributing to the aquatic food chain of the cave occurs during summer and autumn.

The paucity of meso- and nannoplankton in open water indicates that most biological activity is localized on or in bottom sediments. Future studies might well concentrate on bottom sampling in spite of the attendant problems of carrying collecting gear into the cave and separating the micro- and meso-fauna from the accompanying silt.

Community Composition of Shrimp Pools. — The Shrimp Pools in Roaring River passage offer the only readily accessible contained area in Mammoth Cave for investigation of the biological aspects of large pool and stream ecology. These pools include about a dozen shallow basins scattered along a 100 m segment of gallery, the floors of which feature scalloped pinnacles, fluted rock surfaces, and massive deposits of silts and sands. The pools lie approximately 3 m above low water level in Echo River (and Roaring River, its upstream extension), and are filled by annual floods, receding very slowly during the dry season, and attaining minimum depth prior to the first heavy rains of late fall or early winter (late October to mid-January, during the period in which we have observed them). The community is thus apparently dependent on winter floods for food input and must survive the dry season in isolation from the Echo River system.

The fishes, *Chologaster agassizi* and *Typhlichthys subterraneus* occur in the larger pools, and *Amblyopsis spelaea* has been observed twice during a 13-year period. *Asellus*, *Stygobromus*, *Orconectes*, *Cambarus tenebrosus*, and *Palaemonias ganteri* are the macroinvertebrates of widespread occurrence in the community. Microscopic examination of fresh samples of bottom sediment — silts and sands — has revealed several species of protozoans (notably ciliates) and occasional nematodes. *Palaemonias ganteri* was observed to strain and filter the bottom sediments through its mouthparts more or less in the same manner described for the Brazilian atyid *Atyoida potimirim* by Müller (1881). The food of these troglobitic shrimps probably consists of microorganisms in the silt. Since their feeding habits thus seem to require relatively large, seasonally replenished basins with a high secondary productivity, the extremely localized occurrence of *Palaemonias ganteri* (known only from the Roaring River passage in Mammoth Cave and the Golden Triangle area in the Flint Ridge system) may be the result of these specialized requirements. When disturbed, a shrimp rises quickly to the surface, quickly swims laterally for several centimeters, then settles again to the bottom. Capture is easily achieved by prodding an individual and then netting it during its brief flight below the surface. Population density was not determined, but generally from one to two square meters of the bottom of the pools were scanned to find each shrimp.

Measurements of two small series of *Palaemonias* are presented in Table 9. Length was measured from the base of the rostrum to

the tip of the extended telson. The material was preserved in 70 % alcohol and weights were made after excess fluid was removed by placing specimens on filter paper. Eggs were removed from gravid females and separately weighed.

TABLE IX.
Measurements of palaemonias ganteri taken from Roaring river passage, Mammoth Cave.
Length from base of rostrum to tip of telson ; weights of specimens do not include egg weights. Material preserved in 70 % ethanol, excess fluid removed on filter paper before weighing.

Date	Length (mm)	Weight (mg)	Sex	No. Eggs	Total Egg Weight (mg)
X-13-1961	23	141	♀	15	21
	22	150	♀		
	22	118	♀		
	20	76	♀		
	18	56	♀		
	14	19	♀		
	13	17	♀		
	12	29	♀		
	12	15	♀		
	10	13	♀		
V-13-1962	23	121	♀	15	4
	22	143	♀		10
	22	114	♀		4
	21	134	♀		10
	21	126	♀		9
	20	129	♀		5
	20	119	♀		4
	20	83	♀		
	17	60	♀		
	15	54	♀		
	14	51	♀		
	14	28	♀		

The spring collection contained 7 gravid females bearing from 14 to 33 small eggs. A single egg-carrying female in the autumn collection carried few (15) but much larger eggs. This suggests that peak egg production occurs in late winter or early spring and eggs are carried into or through summer. Since we neither collected nor saw shrimps less than a centimeter long, we do not know when the eggs hatch and young shrimps join the population, but presumably this occurs between late summer and winter.

A hypothetical food web for energy transfer in the Shrimp Pools is shown in Figure 12. The more speculative portions of the diagram concern the relationships between the larger species — shrimps, crayfishes, and amblyopsid fishes. It is quite probable that small *Palaemonias* and small *Orconectes* are regularly eaten by the larger

amblyopsids, but the crayfishes in turn are not likely to be very efficient predators of shrimps or fishes. The low density of amblyopsids in the pools is at least consonant with the view that they are top carnivores in the food pyramid. It is of interest to note that the system exhibits at least 3 to 5 trophic levels, depending on the pathway of the chain between decomposers (= secondary producers) and top carnivores.

Small oligochaete worms (Tubificidae and Enchytraeidae, gen. et sp. undetermined) form a link between the food web of the pool community and the terrestrial community of the wet silt banks around

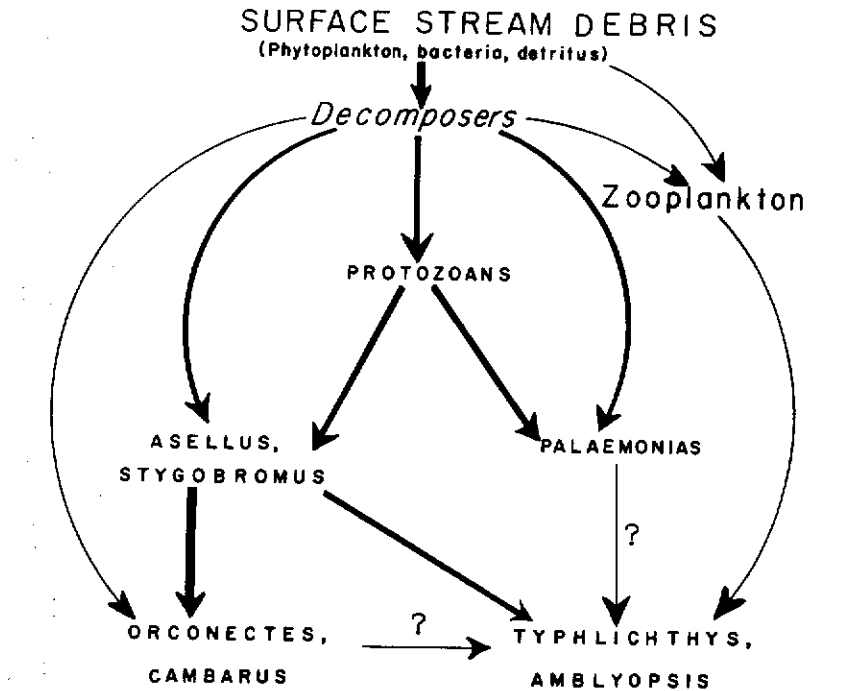


FIG. 12. — Schematic food web for « Shrimp Pools » in Roaring River Passage, Mammoth Cave.

the pools. These minute annelids burrow extensively in wet mud along the pool margins, feeding on microorganisms in the silt. They are in turn preyed upon by trechine beetles, principally *Neaphaenops tellkampfi* and *Pseudanophthalmus striatus*.

THE CAVE MICROFLORA.

The microflora of the Mammoth Cave community includes bacteria, eumycophytes, and algae. The role of the algae in cave ecosystems is not well understood, and in Mammoth Cave studies have

been limited to the systematics of these organisms (see Part I. pp. 179-182 for a summary of these studies) ; they are all presumably heterotrophic. The eumycophytes share with the bacteria the important role of decomposers and transformers, hence of secondary producers, in the breakdown and alteration of wood, leaves, guano, and other materials imported into the ecosystem from the surface.

The prevalence of bacteria and other microflora in cave silts of France, and their activity relating to secondary production in cave communities has recently been investigated in considerable detail by A. M. Gounot (1967). Dudich (1932) and Caumartin (1963) have reported the presence of chemosynthetic bacteria in European caves. In the Mammoth Cave area, Pohl and White (1965) obtained growth of organisms tentatively identified as *Thiobacillus thiooxidans* and *T. ferrooxidans* in a modified Leathen medium (Leathen et al., 1951) adjusted to pH 3.0 and inoculated with samples of pyrite and seepage from pyrite horizons at the contact between the Big Clifty sandstone and overlying Haney limestone. These bacteria could be locally carried into the cave-forming limestones below the Big Clifty by percolating groundwater. While the potential significance of sulfur- and especially iron-bacteria as primary producers in cave ecosystems is recognized, our Mammoth Cave studies suggest that their quantitative contribution is relatively small, except perhaps quite locally in occasional small, isolated pools. Detailed, quantitative investigations on the autotrophic microflora of temperate zone cave systems are badly needed. No organism with either the morphology or the reported chemical capabilities of *Perabacterium spelei* (Caumartin, 1957) was encountered in any of the samples investigated.

Average plate counts from various aseptically collected cave samples are given in Table 10. Although cornmeal agar, potato dextrose agar, Czapek's agar, brain-heart-liver agar, and tryptone glucose extract agar were included among the media initially employed, the highest counts were obtained on nutrient agar, which was plated in serial dilution and routinely incubated at 20°C for 7 days. Both surface and subsurface colonies were counted.

Among the soil samples plated, a series taken from clean, silty sand beneath small stalactites at « Jumbo » a huge flowstone in an isolated, seldom-visited chamber near Frozen Niagara, showed major seasonal fluctuations clearly related to surface rainfall. The site is in a collapse dome with heavily fractured ceiling and shallow overburden. An early October rainfall resulted in a sharp increase of bacteria, followed by decline in numbers. The heavy rainfall of 9 December brought the plate count to over 1 million per gram. The drop to 410,000 per gram by the last week in March presumably reflects a reduction in humus microflora and heavy leaching of the forest floor soil above the cave. The high count in floor silt (8.75 million per gram), from the Radio Room, near « Jumbo », is probably explained by prior introduction of fish and cheese baits into the general area, subsequent proliferation of decomposers, and contamination of the

TABLE X.

Bacterial plate counts from cave samples in Mammoth Cave National Park.

All counts on nutrient agar and samples from Mammoth Cave except where otherwise specified.

Location of Sample	Date	Average Count (2 or 3 plates)
A. Soil Samples		
Wrights Rotunda (Broadway)	X-15-61	$61 \times 10^4/\text{gram}$
Side passage off Wrights Rotunda	III-24-62	$0.6 \times 10^4/\text{gram}$
Marion Avenue, floor silt	X-15-61	$102.5 \times 10^4/\text{gram}$
Radio Room, floor silt	X-15-61	$875 \times 10^4/\text{gram}$
“Jumbo” formation, off Radio Room	IX-30-61	$168 \times 10^4/\text{gram}$
same	X-15-61	$650 \times 10^4/\text{gram}$
same	XI-07-61	$215 \times 10^4/\text{gram}$
same	XII-10-61	$1015 \times 10^4/\text{gram}$
same	III-25-62	$41 \times 10^4/\text{gram}$
Hillside soil above “Jumbo”	XI-26-61	$3650 \times 10^4/\text{gram}$
Dead Sea, mud from bank	III-24-62	$135 \times 10^4/\text{gram}$
Roaring River passage, mud core from bank	XII-09-61	$420 \times 10^4/\text{gram}$
B. Ceiling Paste Sample		
Turner Avenue, Crystal Cave	XI-24-61	$10.7 \times 10^4/\text{gram}$
C. Water Samples		
“Cataract” metal barrel under ceiling spout, Broadway (tryptone glucose extract agar)	X-15-61	37.5/cc
Crystal Lake	X-15-61	$109.00 \times 10^3/\text{cc}$
same	XII-10-61	$21.90 \times 10^3/\text{cc}$
same	III-25-62	$7.50 \times 10^3/\text{cc}$
Lake Lethe	XI-25-61	$0.38 \times 10^3/\text{cc}$
River Styx (flooded)	III-24-62	$14.00 \times 10^3/\text{cc}$
Lake Lethe	V-31-62	$0.14 \times 10^3/\text{cc}$
Echo River	XI-06-61	$0.74 \times 10^3/\text{cc}$
same (flooding)	XII-09-61	$35.00 \times 10^3/\text{cc}$
same	V-31-62	$0.07 \times 10^3/\text{cc}$
Roaring River Shrimp Pool, surface scum	V-31-62	$1.95 \times 10^3/\text{cc}$
D. Mud Samples from Bottom		
Roaring River Shrimp Pool	XII-09-61	$4.5 \times 10^6/\text{gram}$
same	V-31-62	$8.7 \times 10^3/\text{gram}$
Crystal Lake	XII-10-61	$4.8 \times 10^5/\text{gram}$
E. MPN Coliforms (Water)		
Crystal Lake	XII-10-61	17/100 cc
same	III-25-62	33/100 cc
River Styx (flooded)	III-24-62	1600/100 cc
Lake Lethe	V-31-62	45/100 cc
Echo River	XII-09-61	49/100 cc
same	V-31-62	40/100 cc

sample area (about 15 meters away) by trechine beetles (*Neaphae-nops*) which visited the bait and tracked the microorganisms across the floor. The Radio Room sample site is not subjected to ceiling drips, as is the « Jumbo » site. The normal density of microflora of a *Neaphae-nops* feeding-and-breeding ground is probably closer to the average of about 1 million per gram obtained from the Marion Avenue silt sample.

The lowest count (6000 per gram) obtained for a silt sample was taken in a dry, dusty side passage near Wright's Rotunda off Broadway. In the main gallery of the cave (Broadway) nearby, superficially similar dry silt contained 100 times more bacteria. The Broadway site is exposed to slow but persistent air currents flowing between the Historic and Violet City entrances. The mud core sample from the wall of the Roaring River passage, near the Shrimp Pools, was taken 10 December, just as the first flood of the season began, but before the flood waters had reached the sample site; an average count of 4.2 million per gram was obtained. A similar mud sample, taken from the shore of the Dead Sea in late March, 22 days after the crest of a 16.5-meter flood, showed a substantially lower count (1.35 million per gram.).

In a very few places in the caves, areas of walls and ceilings exhibit evident decomposition of the rock, the surface coated with a wet, blue-gray paste 10 - 15 mm thick. A sample of this paste from the ceiling of Turner Avenue, a recently discovered, seldom-visited gallery in the Flint Ridge cave system, yielded an average count of 107,000 per gram. Culture smears revealed small to medium gram-positive cocci in tetrads and (less abundant, growing only on potato dextrose agar smears) gram-positive rods in chains and containing spores. The ceiling limestone decomposition is probably furthered, if not actually initiated (for example, by such organisms as *Thiobacillus thiooxidans* and *T. ferrooxidans*), by bacterial growth.

Open water samples from Lake Lethe - River Styx, Echo River, and the Roaring River Shrimp Pools revealed maximum counts (14,000 — 35,000 per milliliter) during flood stage, with very low counts before and after flooding. Crystal Lake, fed by percolating groundwater from the same hillside which supplies « Jumbo », apparently shows a feeble secondary production peak in late fall, decreasing with rising water levels resulting from winter and spring rains. The « Cataract » sample was taken from a metal drum beneath a small stream of water issuing from the ceiling in a remote part of Broadway. The average count of only 37.5 per milliliter is the lowest recorded.

The very high counts obtained from fine bottom silts in the Roaring River Shrimp Pools and in Crystal Lake suggest, as do the low mesoplankton counts, that (a) most biomass in the aquatic community is concentrated on the substratum, and (b) maximum productivity of the aquatic community occurs near the end of the dry season. Productivity of bottom silts in Crystal Lake is about 1/10 that of

the Shrimp Pools. This observation accords with qualitative examinations of the microfauna in the silts and general abundance of macrofauna in both bodies of water.

Walls, rocks, and pieces of wood submerged in the waters of Echo and Styx rivers or Crystal Lake rather rapidly acquire a slimy coating of bacteria and eumycophytes. Henrici slides suspended vertically near the surface in Echo River, Styx River, and Crystal Lake in September 1961 showed macroscopically visible growth within two weeks. Staining and macroscopic observation revealed the predominance of small to medium bacilli and coccobacilli, some in chains, with a scattering of spirilla, large single rods, and a very few sheathed, possibly branched forms. Slides examined after 4 week's immersion showed heavier bacterial growth, plus — in Crystal Lake and Echo River — overgrowths of phycomycetes, and even a few ciliate protozoans. A limited amount of growth and secondary production by aquatic macroorganisms in Mammoth Cave waters is thus a normal phenomenon independent of the silt substratum. Further investigation is required to establish the order of succession in such microbiological communities and to determine whether these potential food sources require allochthonous nutrients (i.e., organic substances in colloidal form washed into the cave from the surface) or may possibly be initiated and sustained by chemoautotrophs.

Incidental to total plate counts, most probable numbers of coliforms were obtained for several water samples, using the lactose broth method. Cave river water showed MPN's of 40 - 49 per 100 ml when not in flood stage, but an MPN of 1600 per 100 ml 22 days after the flood of 2 March 1962. In Crystal Lake somewhat lower MPN's (17 to 13) were found, with indication of an increase paralleling influx of surface waters down the sides of the domepits. The river water was clearly not potable at any time, and even the water of Crystal Lake is of questionable potability. Knowledge of numbers and seasonal distribution of coliform bacteria in subterranean waters and the extent to which they can be dispersed in limestone aquifers could be readily obtained in the Mammoth Cave system and other caves of the region. Such data are of potential public health significance, especially in karst areas where sinkholes are commonly used for disposal of garbage, dead farm animals, and sewage, as is locally the case in parts of Kentucky. Microorganisms transported by cave streams are not subject to the germicidal action of ultraviolet radiation as in surface streams. Where flow is through tubular solution channels, filtration by and absorption onto the surfaces of sand and silt particles is minimal. Consequently pathogenic microorganisms may be transported much farther by underground streams than by surface streams of similar flow.

The microorganisms in 6 samples from biologically productive areas (Echo River water, Crystal Lake water and bottom silt, Roaring River mud from banks and pools, and soil from beneath « Jumbo ») readily reduced nitrate to ammonia, but no evidence of

nitrogen fixation was obtained in 4 samples (Roaring River mud from banks and pools, Crystal Lake mud, soil from beneath «Jumbo»). Inocula from the latter samples failed to produce growth in either of Stephenson's media (Stephenson, 1949) for *Nitrosomonas* and *Nitrobacter*.

The bulk of our studies have been largely quantitative and rather preliminary, and were designed primarily to provide an index of microbiological activity in various parts of the cave. As a general rule, the microflora of the Mammoth Cave community is much more sparsely distributed than that of epigeal soils and streams and appears to be continually replenished by air currents, percolating ground waters, and backflooding from Green River. The probable significance of the cave microflora in biosynthesis of vitamins, and the apparently close association between many troglobites and cave silt has already been mentioned by Gounot (1960, 1967) and Vandel (1964). During the dry season, decomposition and transformation processes carried on by the microflora constitute an apparently critical link between the imported food sources and the primary consumers. However, in our judgment, the important question of whether or not autotrophic microorganisms contribute substantially to the food energy of cave ecosystems remains unresolved.

ADDENDUM TO PART I.

The following species records were inadvertently omitted from the text of Part I, «The Biota».

OLIGOCHAETA: *Aeolosoma hemprichi* Ehr. - troglophile. This common freshwater annelid was found in bottom silt and cricket guano from the bottom of rimstone pools near the entrance of Great Onyx Cave. More recently, Dr. S. M. Gittleson has cultured this species from a water sample taken from Richardson Spring in Mammoth Cave.

ACARINA: *Ixodes cookei* Packard — troglophile or troglaxene. A specimen of this tick, presumably a bat parasite, was obtained IV-13-1963 from Hundred Domes (= Coach) Cave, Barren Co., Kentucky, by William Russell and determined by Dr. Glen Kohls.

OPILIONES: *Sabacon crassipalpe* (Koch) — threshold troglaxene. This harvestman was collected near the mouth of Brushy Knob Cave, Barren County, and determined by Professor C. L. Goodnight.

Since the appearance of Part I, Gittleson (1969) has published a detailed study of cave protozoans with special reference to Mammoth Cave. He reports finding 33 species, including 7 phytomastigophorans, 8 zoomastigophorans, 5 rhizopods, 7 heliozoans, 2 holotrichs, 1 peritrich, and 3 spirotrichs. Poulson and Culver (1969) discussed species density in cave communities, using terrestrial community samples from Eyeless Fish Trail in the Flint Ridge cave system. White, Watson, Pohl, and Brucker (1970) have written an excellent review of the karst and cave features of the Mammoth Cave region.

Summary and conclusions.

Since much of Mammoth Cave underlies a non-porous sandstone stratum, many of the upper-level galleries are dry and unsuited for habitation by cavernicoles. The habitable microenvironments are: 1) near terminal breakdowns, 2) near active vertical shafts (dome-pits), 3) near active dripstone, and 4) along the banks of subterranean streams and pools. In remote, undisturbed areas of these types the temperature is $13.6 \pm 0.2^\circ\text{C}$ throughout the year, relative humidity is near saturation, and rate of air movement and rate of evaporation are minimal. However, much of the cave, including the habitable areas, is subject to seasonal fluctuation of microclimate because of (a) heat loss to winter seepage or cold streams sinking from the surface, or (b) movement of cold, dry air into the cave during winter, resulting in a decrease in air and soil temperature, a decrease in relative humidity, increased rate of air movement along the galleries, and a drastically increased rate of evaporation. The last factor is especially limiting for troglobites, which are predominantly stenohygrobic, and for many troglaphiles as well.

Food energy enters the terrestrial cave environment of the Mammoth Cave system from 3 primary sources: 1) guano, dead bodies, and eggs of troglaxene cave crickets (*Hadenocetus subterraneus*) which feed on forest-floor arthropods outside the cave; 2) plant debris, mesoplankton, and nanoplankton carried into the system by water; and 3) pieces of wood and other artifacts of commercialization of the cave. Typical troglobite assemblages are associated with rotting wood, cricket guano, and the minute, limivorous tubificid and enchytraeid oligochaetes of the silt banks of subterranean rivers.

Special studies of *Neaphaenops tellkampfi* and *Pseudanophthalmus* spp. (Col., Carab., Trechinae) reveal that, under certain conditions, their relative abundance in small caves near Mammoth Cave closely approximate the broken stick model proposed by R. H. MacArthur. Three local populations of *N. tellkampfi* in Mammoth Cave were sampled, marked, released, and recaptured; their population sizes were estimated by the positive method of C. H. N. Jackson to be 816, 880, and 2761 individuals, respectively.

Aquatic studies were concentrated on Echo-Roaring River, Styx River, and Crystal Lake in Mammoth Cave. The physico-chemical features and plankton density of the rivers are markedly affected by winter backflooding from Green River, which produces abrupt decreases in temperature and pH, generally increases in dissolved oxygen, and has a variable effect on total (methyl orange) alkalinity. In contrast, Crystal Lake has a relatively lower oxygen content, higher pH and total alkalinity, and a more stable temperature. Zooplankton counts fluctuate considerably in all three habitats, but are substantially lower in Crystal Lake, which also exhibits a much lower density of bottom micro- and macrofaunas.

The « Shrimp Pools » of the Roaring River Passage in Mammoth Cave are an example of a moderately complex aquatic community based on bacterial decomposition of stream detritus ; protozoans and other microfauna feed on the bacteria and are in turn eaten by isopods, amphipods, and atyid shrimps ; crayfishes and amblyopsid fishes represent the higher trophic levels in this community.

A preliminary microbiological study showed that (a) bacteria are much less abundant in the cave than in surface soils and streams ; (b) decomposition nevertheless proceeds rather rapidly, at least in moist microenvironments, and the decomposers serve as secondary producers in the ecosystem ; (c) a large proportion of the bacteria detected by our methods was probably transported into the cave by water ; and (d) secondary production in bottom silts of pools and lakes probably reaches a maximum near the close of the dry season, in autumn. The quantitative significance of autotrophic microorganisms in the ecosystem remains unknown.

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