H. H. Hobbs III

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Contents

JANUARY 1972

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Jaguar *(Panthera onca)* Remains from Big Bone Cave, Tennessee and East Central North America

John E. Guilday* and Helen McGinnis*

ABSTRACT

During a recent survey of Big Bone Cave, Tennessee, jaguar remains were found in an almost virgin passage. The skeletal remains, although fragmentary, were from a single individual that died on the present cave floor. The Big Bone Cave skeleton is compared with other jaguar remains from Tennessee and from eastern North America north of Florida. The results are inconclusive but suggest an age range of 35,000 years BP to 10,000 years BP for the Tennessee jaguars which are believed to belong to an extinct, robust subspecies of the modern jaguar, *Panthera onca*. Sexual, geographical, and chronological variation in the North American remains is discussed.

Introduction

Big Bone Cave, Van Buren County, is one of the best known caves in Tennessee. It was the center of an extensive saltpeter industry during the War of 1812 and the Civil War. Relics of this industry in the form of wooden vats, tramways, and ladders still remain, excellently preserved, in this dry and dusty cave. The cave's name derives from fossil remains of the giant ground sloth, *Megalonyx jeffersonii*, excavated by many individuals during the years 1811 through 1890 (Hay, 1923). The unique feature of this sloth material, now at the Philadelphia Academy of Sciences, is the presence of original horny claw and periosteal fibers still adhering to some of the bones. The cave (lat. 35°46′40″N; long. 85°33′21″ W; alt. 1,020 ft), a solution feature in the Monteagle (Ste. Genevieve-Gasper) Limestone of Mississippian age, is described in Barr, 1961, pp. 451-460.

In June, 1969, the Nashville Grotto of the National Speleological Society began a survey of Big Bone Cave. As of March, 1971, they had surveyed 8.64 miles of cave passage. Ronald Zawislak and John Smyre are preparing a report that will contain a historical account of the cave, accounts of surveying activities and geological studies, and descriptions of over 50 new caves found on Bone Cave Mountain in the vicinity of Big Bone Cave.

Acknowledgments

All data in this paper concerning the description of the cave and the discovery of the jaguar skeleton were furnished by Larry E. Matthews, John Smyre, and Ronald Zawislak of the Nashville Grotto. These men recognized the scientific value of the jaguar remains and preserved them for study. The excellent map (Fig. 1) was drawn by Smyre from the data of the recent survey. We wish to thank Dr. Edward McCrady, University of the South, for supplying us with measurements, Dr. Clayton E. Ray, National Museum of Natural History, and Dr. Alfred Guthe, University of Tennessee, for the loan of specimens. Illustrations are by Alice M.

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* Carnegie Museum, Pittsburgh, Pennsylvania.

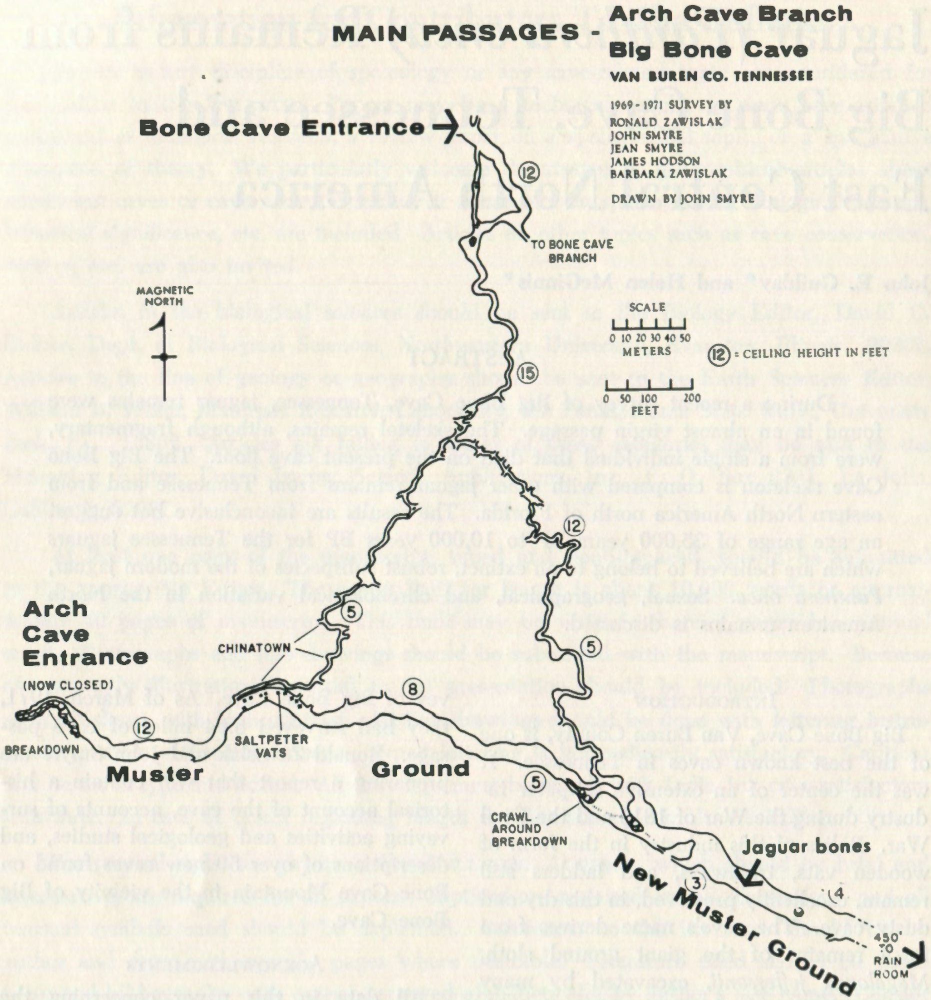

Figure 1. Map of Arch Cave Branch of Big Bone Cave, Van Buren County, Tennessee, showing location of jaguar bones.

Guilday; graphs by Donald Tanner; the photograph (Fig. 5) was taken by Michael B. Collins, University of Texas. Unless otherwise specified, all measurements were taken by the junior author. Research was conducted under National Science Foundation grant no. GB-18706X.

New Discovery in Big Bone Cave

On July 11, 1970, John and Jean Smyre discovered a crawlway leading past two sections of breakdown, possibly of relatively Recent origin, at the east end of the Muster Ground (see Fig. 1) that led to a continuation of the passage which was 50 ft wide and 3 ft high—the "New Muster Ground". During this discovery trip, a small group of bones was observed lying to one side of the survey line 500 ft from the beginning of the passage continuation or 1900 ft from the now closed Arch Cave entrance. The Arch Cave entrance opened into the west end of the Muster Ground from the time of the cave's discovery in 1806 until about 50 years ago, when it reportedly filled with debris.

Crawl marks in the passage suggested that two recent cavers and one or two saltpeter miners may have been down the passage previously. The "New Muster Ground" continues for 1400 ft past the bone site to a point where fill rises to within 6 in. of the ceiling. Several bones were removed by John Smyre on the final surveying trip into the area, November 7, 1970 and turned over to Larry E. Matthews, who submitted them to the Carnegie Museum for determination.

The passageway was floored with a 6-in. layer of desiccated bat guano, gypsum flakes, and rock fragments from the immediate ceiling. This was underlain by dry, cracked mud, which was apparently the original floor when the cave dried out. All exposed surfaces were covered with a thin layer of black dust which is believed to be soot from the torches of the saltpeter miners. Although saltpeter mining was not carried out in the bone-find area, air-borne soot could have drifted into the passage. In addition, torch remains were found in the passageway.

The jaguar bones lay in an area somewhat less than 8 ft in diameter. They were friable, chalky, and broken, with the entire assemblage disarticulated and disoriented. The surrounding area was meticulously examined for bone fragments. Although the skeleton was extremely fragmentary, most of the fragments present were believed to have been collected.

There was no duplication of elements. The skeleton undoubtedly represents a single individual that died on what is essentially the present cave floor. Tracks of saltpeter miners in the soot indicate that they had crawled over the skeleton and apparently moved some bones to the side. Although the skeleton was fragmentary and incomplete, fragments of all portions of the skeleton, with the exception of ribs and vertebrae, were recovered. The bone was soft, friable, and weak. Most of the organic constituents seem to have gone, leaving the bone a chalky white except for those pieces—portions of skull, hipbone, and limb bones—which were evidently exposed on the surface during the time of saltpeter mining, when soot from miners' torches is believed to have covered all exposed areas. In some instances, adjacent major fragments of limb bones were completely different in color, indicating that there had been disturbance of the skeleton prior to soot penetration. The distal end of the left humerus, for instance, had been broken in two. The opposing surfaces of this break were of different colors, one an ivory white surface and the other soot black. Otherwise, the break appeared fresh in the sense that no further damage had taken place along the opposing surfaces. The break may have been caused by early exploration prior to the accumulation of soot or, more likely, disturbance during mining days, exposing some fragments to contamination and burying others in the thin protective layer of the cave floor.

As preserved, the specimen consists mostly of skull fragments, the largest of which are the left maxilla (Fig. 2A) and a left mandible fragment (Fig. 3A). With the exception of one M^1 and one incisor, the crowns of the teeth are broken into small fragments; only the roots remain relatively intact. Limbs are represented by a fragmented but restorable left femur, left and right humerus, fragmentary right femur, right tibia, right ulna, left innominate, and one patella.

At one time the complete skeleton must have occupied a relatively limited area. Recovery methods were designed to collect very small fragments. Several hundred bones or bone fragments were collected, including such small items as 31 phalangeal sesamoids and carpal and phalangeal elements. However, no traces of the vertebral column (with the exception of one chevron bone), ribs, or metapodials other than both left and right first metatarsal were recovered. The sigmoid notch of the ulna had been gnawed by rodents. The skeleton probably was extensively pilfered by the cave rat *Neotoma floridana,* which is notorious for carrying all manner of sticks, bones, etc., to its nest.

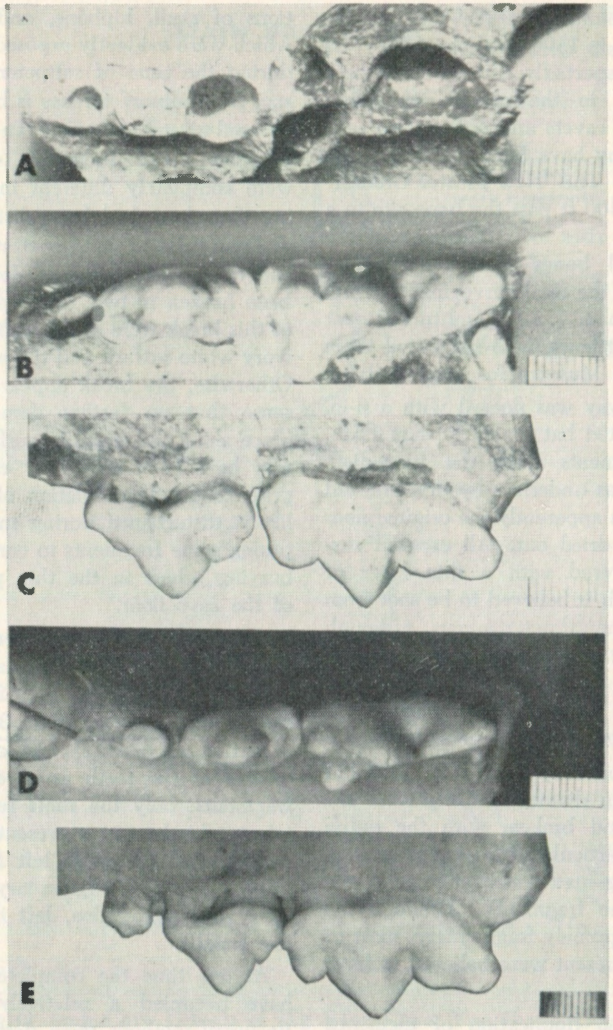

Figure 2. Left maxillae, *Panthera onca*: (A) Late Pleistocene *P. o. augusta*, CM 24369, Big Bone Cave, Van Buren County, Tennessee, crown view, alveoli only, P^2–M^1. (B) Late Pleistocene *P. o. augusta*, UT 110, Little Airplane Cave, Hamilton County, Tennessee, crown view, P^3–M^1, P^2 missing. (C) Same specimen, labial view, P^3–P^4. (D) Recent *P. o. veraecrucis*, CM 3701, Tamaulipas, Mexico, male ?, crown view, P^2–M^1. (E) Same specimen, labial view, P^2–P^4. Scale in millimeters, anterior to left.

This is an instinctive action of no use to cave-inhabiting rats but probably derived from nest-building activities of "normal" surface-dwelling representatives of the genus. Any bone of convenient size for a woodrat to remove and large enough not to escape its notice has apparently disappeared. Any selective removal by man would surely have been at the expense of jaws, teeth, or major limb elements.

The lower jaw is represented by fragments of both sides, but only the left ramus,

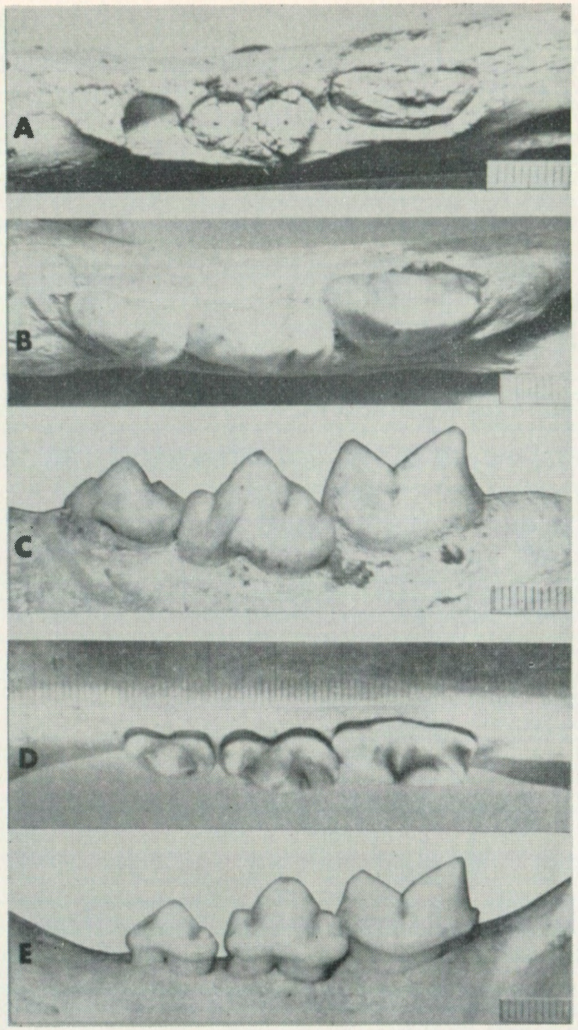

Figure 3. Lower left toothrows, *Panthera onca*: (A) Late Pleistocene *P. o. augusta*, CM 24369, Big Bone Cave, Van Buren County, Tennessee, crown view, P_3–M_1, alveoli and battered root stubs. (B) Late Pleistocene *P. o. augusta*, UT 110, Little Airplane Cave, Hamilton County, Tennessee, crown view, P_3–M_1. (C) Same specimen, labial view, P_3–M_1. (D) Recent *P. o. veraecrucis*, CM 3701, Tamaulipas, Mexico, male ?, crown view, P_3–M_1. (E) Same specimen labial view, P_3–M_1. Scale in millimeters, anterior to left.

with battered tooth roots in place, could be measured (Fig. 3A).

AGE OF SKELETON

The jaguar skeleton from Big Bone Cave is the seventh reported from Tennessee (Fig. 4, localities 1 through 7). All of these finds are variations on the same theme (Fig. 5): a single animal, apparently lost, dying on the present cave floor. Footprints of

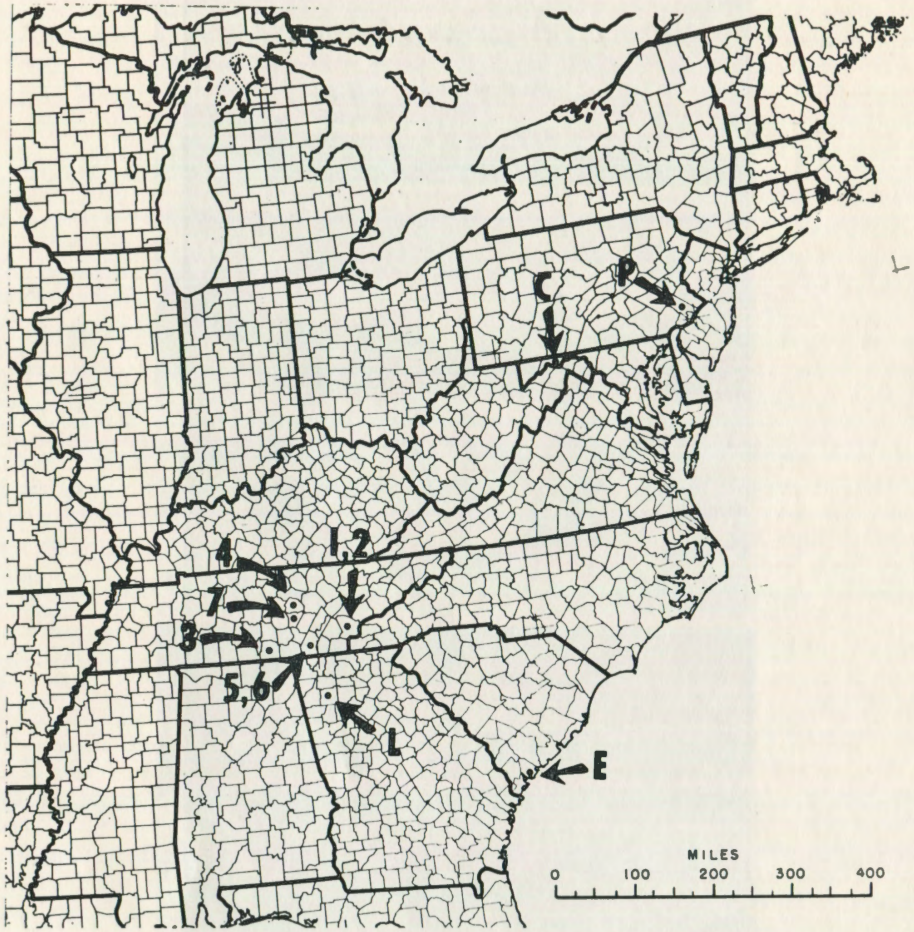

Figure 4. Reported occurrences of Pleistocene *Panthera onca* in eastern North America north of Florida. (1) and (2) Craighead Caverns (The Lost Sea), Monroe County, Tennessee (Simpson, 1941b). (3) Little Salt River Cave, Franklin County, Tennessee (McCrady *et al.*, 1951). (4) Johnson Cave,* Putnam County, Tennessee (McCrady *et al.*, 1951). (5) and (6) Little Airplane Cave, Hamilton County, Tennessee (Parmalee, 1961). (7) Big Bone Cave, Van Buren County, Tennessee (CM 24369). (P) Port Kennedy Cave, Montgomery County, Pennsylvania (Simpson, 1941b). (C) Cumberland Cave, Allegany County, Maryland (Gidley and Gazin, 1938). (L) Ladds Quarry, Bartow County, Georgia (Ray, 1967). (E) Edisto Beach, Charleston County, South Carolina (Ray, 1967).

jaguars were noted and studied from the Craighead Caverns (now commercialized as the Lost Sea) (Simpson, 1941a). The condition of all of the skeletons was much the same, fragile and fragmented. The jaguars found their way to these sites after all speleogenic processes had come to a halt and the caves were stabilized. (The Little

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* See footnote, Table 1.

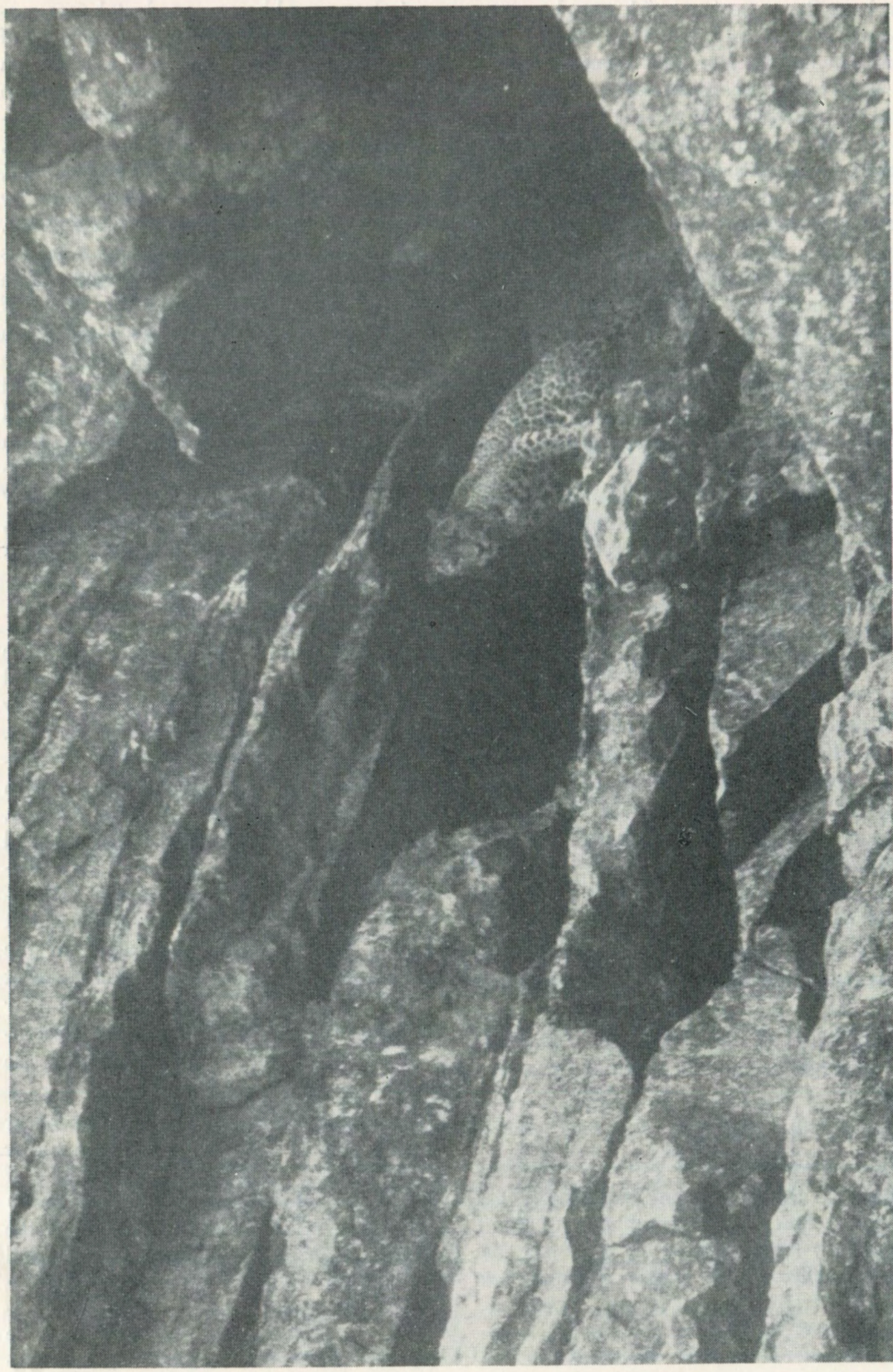

Figure 5. Jaguar at entrance to a cave at Tampico, Mexico, January 1969. Photograph by Michael B. Collins.

Airplane Cave specimen #1 was, however, covered in part by flowstone.) This places them late in the late Pleistocene, probably in early post-Wisconsinan times. The poor state of preservation in what is an essentially stable environment, the obvious size differences between this extinct population sample and the modern adjacent race of *Panthera onca,* and the fact that jaguars no longer occur north of southern Texas and apparently did not do so at least in late Indian times, all argue for some degree of antiquity. There is evidence (Martin and Wright, 1967) for a major wave of large mammal extinctions about 10,000 years ago, and these Tennessee jaguars were probably able to survive until whatever prey species they depended upon, perhaps peccary, became extinct. There has been no attempt to date any of the jaguar finds by isotopic methods. The Big Bone Cave specimen is too powdery and too small a sample while the older finds are contaminated with preservatives. One possible age parallel which may shed some light is the skeleton of the spectacled bear, *Tremarctos floridanus,* from Grassy Cove Saltpeter Cave, Tennessee (Guilday and Irving, 1967). Like the jaguars, it was a single individual found in an obscure passage on the present cave floor. Even the state of preservation of the bone was similar—chalky, fragmentary, and extremely light. The carbon-14 date was 33,660 ± 3,980 years BP. If this date can be accepted at its face value, there would seem to be no reason why the jaguar skeletons could not be equally as old. An age range of 35,000 years BP to 10,000 years BP is tentatively suggested for the Tennessee jaguars.

TENNESSEE JAGUARS

Despite the fact that remains of seven jaguars are available from Tennessee caves, the fragmentary condition of most of them makes any observations as a population sample difficult. No single measurement could be duplicated on all seven specimens. The greatest number of comparable measurements were those of dentitions, and in no instance could any one dental measurement be duplicated in more than four of the seven individuals. This is not enough to assess sexual and individual variation and certainly not enough to permit adequate comparison with other local samples. Those measurements that are available, either taken from the literature or made by the junior author, are presented in Table 1. The figures for each measurement of this Tennessee sample are also averaged. As a group, they fall well within the range of those modern South American races given by Simpson, although they are larger than modern Mexican material (see Figs. 6 and 7). Although McCrady *et al.* (1951) treated *Panthera augusta* as a full species, both Simpson (1941b) and Kurtén (1965) believe it to have been an extinct, especially robust, subspecies of the modern jaguar, *Panthera onca.* We agree with the latter interpretation.

VARIATION

The fragmentary nature of most of the Tennessee material prevents direct dental comparisons with other eastern finds. Only one upper and three lower carnassials (Fig. 6, no. 5; Fig. 7, nos. 5, 6 and 12) are suitably preserved. They agree in size with those of other examples of *P. o. augusta.* They are not exceptionally large and fall short of large examples of Recent *P. o. palustris* from southern South America. Simpson (1941b) states that the southernmost race, *P. o. palustris,* is the largest of the living South American jaguars. Somewhat larger fossil specimens occurring even farther south parallel the North American size increase to the north. Both phenomena are ascribed to Bergmann's response.

Male jaguars exceed females in linear dimensions (Simpson, 1941b). Grouping by sex in Figure 7 seems apparent; a cluster of smaller measurements (nos. 2 through 9) presumably representing females about the size of the one Recent male plotted, and larger specimens (nos. 11 through 14) presumably representing males. A sexual grouping is not apparent in Figure 6, but the length of scatter of the plotted points sug-

TABLE 1. Skeletal measurements (in mm.) of late Pleistocene *Panthera onca augusta* from Tennessee, U. S. A. Specific locations shown in Fig. 4.

CH-1. Craighead Caverns, AMNH 32633. Data from Simpson, 1941b. (locality 1)
CH-2. Craighead Caverns, AMNH 32635. Data from Simpson, 1941b. (locality 2)
LSR. Little Salt River Cave, NMNH 18262. McCrady *et al.,* 1951. (locality 3)
SPC. Saltpeter Cave,* University of the South collection. McCrady, *et al.,* 1951. (locality 4)
LA-1. Little Airplane Cave, specimen #1, UT 110, University of Tennessee collection. (locality 5)
LA-2. Little Airplane Cave, specimen #2, UT 110, University of Tennessee collection. (locality 6)
BBC. Big Bone Cave, CM 24369. (locality 7)
N, X = Number of measurements and average value of all Tennessee specimens (left and right sides of individual specimens averaged).
All hyphenated measurements are left and right side of same individual.

Measurement	CH-1	CH-2	LSR	SPC	LA-1	LA-2	BBC	X	N
			Upper Dentition						
C^1 (ant. margin)–P^4	...	...	...	...	...	83.6	...	83.6	1
C^1 (post. margin)–P^4	...	...	...	...	...	59.9-59.1	61.7	60.2	2
P^4, length	...	...	31.2	...	...	30.8-31.3	...	31.1	2
P^4, ant. width	...	...	...	...	...	15.7-15.7	...	15.7	1
P^4, post. width	...	...	...	...	...	11.3-11.3	...	11.3	1
P^4, length paracone	...	...	...	...	...	10.6-10.5	...	10.5	1
P^4, length metastyle	...	...	...	...	...	13.1-12.7	...	12.9	1
P^3, length	...	19.6	...	...	...	20.1-19.8	...	19.8	2
P^3, width	...	...	...	...	...	9.0-8.9	...	8.95	1
C^1, ant.-post. diameter	...	19.5	...	...	19.9	20.7-21.1	...	20.3	3
C^1, transverse diameter	...	16.3	...	...	16.5	16.8-16.9	...	16.6	3

TABLE 1. Skeletal measurements (in mm.) of late Pleistocene *Panthera onca augusta* from Tennessee, U. S. A. Specific locations shown in Fig. 4 (Continued).

Measurement	CH-1	CH-2	LSR	SPC	LA-1	LA-2	BBC	X	N
			Lower Dentition						
C_1-M_1	106.0	...	...	...	...	95.0-94.3	...	98.4	2
C_1, ant.-post. diameter	26.0	...	...	...	18.9	20.4-20.2	20.8±	21.2	4
C_1, transverse diameter	22.0	...	...	...	17.1	16.2-15.4	15.0±	17.1	4
P_3-M_1	66.0	...	...	...	...	56.7-57.1	57.1	59.2	3
P_3, length	18.2	...	...	...	...	16.4-16.1	16.2±	16.7	3
P_3, width	9.0	...	...	...	...	8.4-8.3	...	8.6	2
P_4, length	24.7	...	...	...	...	21.9-21.9	19.3±	21.9	3
P_4, width	12.4	...	...	...	...	10.6-10.1	10.1±	10.8	3
M_1, length	24.6	...	...	...	22.0-22.0	19.9-22.1	19.8±	21.4	4
M_1, width	12.7	...	...	...	11.8-11.8	11.9-11.7	...	12.0	3
			Mandible						
depth ant. to P_4	42.0	...	...	...	...	33.6-36.0	37.1	37.2	3
depth post. to M_1	43.0	...	...	...	...	38.0	37.4	39.4	3
thickness at M_1	17.5	...	...	...	...	19.3	17.8	18.2	3
depth at diastema	44.5	...	...	...	...	39.1	40.1	41.2	3
			Humerus						
humerus, length	...	...	263.0	...	...	256.0	262.0-259.0	260.0	3
width, distal end	...	...	69.5	...	...	...	67.1-68.2	68.3	2
shaft, transverse width	...	...	24.7	...	...	23.2+-23.0	24.3	23.8	3
			Radius						
length	...	...	222.0	...	...	229+	...	225.5	2
width, distal end	...	...	46.7 - 48.6	...	...	...	...	47.6	1
			Ulna						
length	...	...	269.0+-279.0	...	...	...	...	274.0	1

TABLE 1. Skeletal measurements (in mm.) of late Pleistocene *Panthera onca augusta* from Tennessee, U. S. A. Specific locations shown in Fig. 4 (Continued).

Measurement	CH-1	CH-2	LSR	SPC	LA-1	LA-2	BBC	X	N
			Femur						
length	...	...	291.0	286.0	...	...	297.0	291.3	3
head, ant.-post. diameter	...	...	32.9	...	...	...	31.4	32.1	2
shaft, transverse diameter, mid-length	...	...	27.9	...	...	...	28.4-28.4	28.2	2
shaft, ant.-post. diameter, mid-length	...	...	24.7	...	...	...	25.5-25.1	25.1	2
width, distal end	...	...	59.9-62.1	62.0	...	...	57.5	60.4	3
			Tibia						
length	...	...	254.0-255.0	248.0	...	...	248.0	251.2	3
transverse diameter, proximal end	...	...	63.2-62.8	63.0	...	...	56.4	61.3	3
transverse diameter, distal end	...	...	45.4-45.5	45.0	...	45.1	40.9	44.4	4
ant.-post. diameter, distal end	...	...	31.0-31.8	...	...	29.4	27.7	30.0	3
			Astragalus						
length	...	...	44.8-45.3	...	...	43.5	...	44.5	2
width	...	...	43.4-44.6	...	...	39.1	...	42.4	2
neck, width	...	...	21.9-21.0	...	...	18.7	...	20.5	2
head, width	...	...	25.6-25.7	...	...	25.3	...	25.5	2
			Calcaneum						
length	...	...	85.3-86.5	...	...	84.8	...	85.5	2
width	...	...	34.0-34.0	...	...	34.7	...	34.2	2
width at cuboid facet	...	...	25.0-25.0	...	...	23.1	...	24.4	2
			Navicular						
length	...	...	31.2-32.4	...	...	35.0	...	32.9	2
width	...	...	22.7-22.4	...	...	24.2	...	23.1	2
			Trapezoid						
width	...	...	19.7	...	...	18.0	19.6-19.3	19.1	3

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* Larry E. Matthews (letter, Nov. 10, 1971) states that this is actually Johnson Cave, Putnam County, Tennessee, and that McCrady concurs.

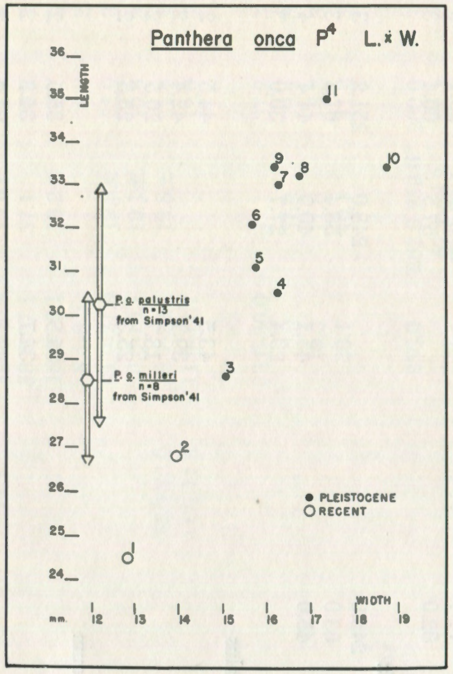

Figure 6. Upper carnassial (P^4), *Panthera onca*, Pleistocene and Recent. Ordinate = crown length (mm.); abscissa = crown width (mm.). Data from Simpson, 1941b = observed range and mean of modern subspecies. Lefts and rights of same animal averaged where possible.

No.	Catalog no.	Locality	Measurement	Reference
		Recent		
1.	ISM 1068 (female)	Nayarit, Mexico	24.5 x 12.8	Kurtén, 1965
2.	CM 3701 (male ?)	Tamaulipas, Mexico	26.8 x 13.9	*
		Wisconsinan		
4.	FDT 487	Santa Fe, Florida	30.5 x 16.2	Kurtén, 1965
5.	UT 110 #2	Little Airplane Cave, Tennessee	31.1 x 15.7	*
7.	UTBEG 40673	Laubach Cave, Texas	33.0 x 16.2	Slaughter, 1966
10.	USNM 11411	Vero, Florida	33.4 x 18.7	Kurtén, 1965
		Pre-Wisconsinan, Illinoian?		
3.	UF 3004	Haile II B, Florida	28.6 x 15.0	Martin, in press
6.	CM 24328	Cumberland Cave, Maryland	32.1 x 15.6	*
11.	GSF V-5695	Reddick, Florida	35.0 x 17.3	Kurtén, 1965
		Late Pleistocene, unassigned		
8.	USNM 125	Niobrara River, Nebraska	33.2 x 16.7	Kurtén, 1965
9.	USNM 23486	Ladds Quarry, Georgia	33.4 x 16.1	Ray, 1967

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* Measurements made by junior author for this paper.

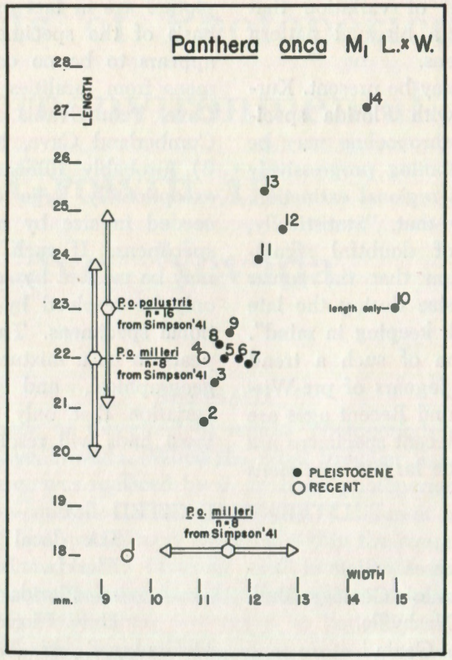

Figure 7. Lower carnassial (M_1), *Panthera onca*, Pleistocene and Recent. Ordinate = crown length (mm.); abscissa = crown width (mm.). Data from Simpson, 1941b = observed range and mean of modern subspecies. Lefts and rights of same animal averaged where possible.

No.	Catalog no.	Locality	Measurement	Reference
		Recent		
1.	ISM 1068 (female)	Nayarit, Mexico	18.0 x 19.5	Kurtén, 1965
4.	CM 3701 (male ?)	Tamaulipas, Mexico	22.0 x 11.1	*
		Wisconsinan		
2.	USNM 11470	Melbourne, Florida	20.7 x 11.1	Kurtén, 1965
5.	UT 110 #1	Little Airplane Cave, Tennessee	22.0 x 11.5	*
6.	UT 110 #2	Little Airplane Cave, Tennessee	22.0 x 11.8	*
12.	AMNH 32633	Craighead Caverns, Tennessee	24.6 x 12.7	Simpson, 1941b
13.	UTBEG 40673	Laubach Cave, Texas	25.4 x 12.3	Slaughter, 1966
		Pre-Wisconsinan, Illinoian?		
3.	UF 14765	Waccasassa River, locality 6, Fla.	21.5 x 11.3	Martin, in press
7.	—	Coleman IIA, Florida (smallest individual measured)	21.9 x 12.0	Martin, in press
8.	UF 8879	Reddick, Florida	22.3 x 11.4	Kurtén, 1965
9.	UF 3003	Reddick, Florida	22.5 x 11.6	Kurtén, 1965
10.	—	Port Kennedy Cave, Pennsylvania	23.0 x ?	Simpson,'41b,p.8
14.	—	Coleman IIA, Florida (largest individual measured)	27.2 x 14.4	Martin, in press
		Late Pleistocene, unassigned		
11.	USNM 23486	Ladds Quarry, Georgia	24.0 x 12.2	Ray, 1967

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* Measurements made by junior author for this paper.

gests an undue amount of variation that may resolve itself into a bisexual pattern with additional specimens.

Yet another variable may be present. Kurtén (1965), working with Florida specimens, suggests that a chronocline may be present, the animal becoming progressively smaller as it approaches regional extinction. He concludes (p. 232) that, "Statistically, these differences are of doubtful significance, but the indication that the jaguar tended to decrease in size during the late Pleistocene is well worth keeping in mind". There is little indication of such a trend from Figures 6 and 7. Jaguars of pre-Wisconsinan, Wisconsinan, and Recent ages are plotted, and while the Recent specimens are obviously smaller and the largest specimens plotted are in fact pre-Wisconsinan, on the basis of the specimens plotted here there appears to be no consistent trend. Specimens from localities such as Port Kennedy Cave, Pennsylvania (Fig. 7, no. 10) and Cumberland Cave, Maryland (Fig. 6, no. 6), probably Illinoian in age, are neither exceptionally large or small and are exceeded in size by many late Wisconsinan specimens. If such a trend is present, it may be masked by sexual variation and can only be resolved by future study of additional specimens. The present situation appears to be a mixture of individual, sexual, geographical, and perhaps chronological variation that only the addition of more fossil finds will resolve.

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The Effects of Photoperiod and Some Microenvironmental Factors on Plant Growth in Lehman Cave, Nevada

Lillian Sheps [*]

ABSTRACT

A study was made of the effect of regular photoperiods on the growth of plants in Lehman Cave, Nevada. When the usual irregular lighting, governed by numbers of daily tours, was replaced by 6- or 12-hr photoperiods, growth greatly exceeded that in non-controlled areas. A number of different microenvironments containing different plant species were observed within the overall relatively stable cave environment. Some factors involved in these microenvironments are light, temperature, soil moisture, relative humidity, and pH. The plant potential of the cave was found to exceed existing vegetation in both lighted as well as dark areas, as shown by the rapid appearance of algae when lights were introduced into a previously dark area, the successful transplanting of cave lower plant species to lighted areas devoid of vegetation, and the introduction, through seeds, of higher plants. Animal interaction was observed, especially with higher plants. Cultures of cave plant species did poorer under apparently more optimal controlled laboratory conditions than in the cave.

INTRODUCTION

One of the outstanding characteristics of caves is their relatively stable environment. Temperature remains more or less constant throughout the year. The normal cues of day and night are absent, and in general one senses an eerie timelessness. The lack of normal daily and seasonal changes presents an extraordinary habitat for living organisms, whose vitality generally depends on synchronization of their endogenous rhythms with environmental ones (Bünning, 1964). The occurrence of endogenous rhythms, even in organisms living in apparently cue-less environments, was demonstrated by the discovery of a circadian rhythm in the ancient cave crayfish *Orconectes pellucidus* which has lived for millions of years in Mammoth Cave, Kentucky (Jegla and Poulson, 1968).

The requirement of light by most plants means that those growing in the interior of caves are subject to some sort of light rhythm. Usually, however, introduced lighting is irregular. This is especially true of Lehman Cave, which was the locale of this study.

Lehman Cave (Fig. 1) is developed in marble, originally limestone altered by intense heat and pressure, and contains large numbers of speleothems (Moore, 1960). It is located in eastern Nevada (80.5 km east of Ely) at about 2200 m elevation, in pinyon-juniper country on the eastern flank of Wheeler Peak. The cave forms a part of Lehman Caves National Monument.

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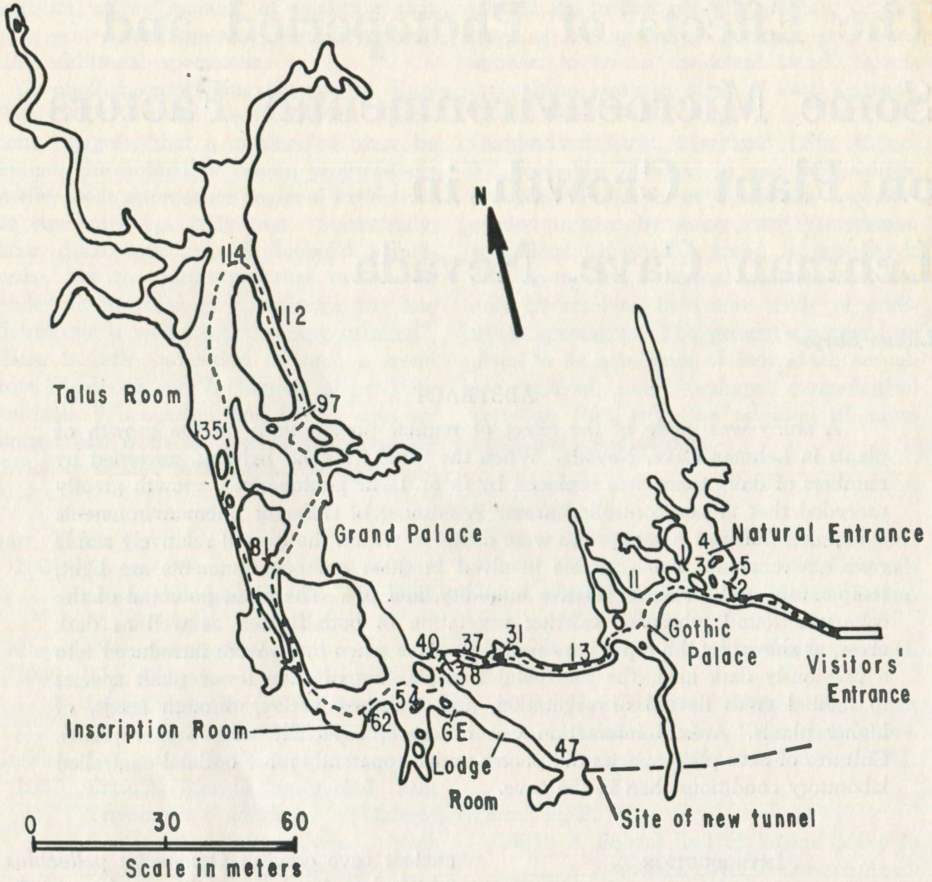

Figure 1. Map of Lehman Cave, Nevada. Numbers indicate locations of lights at experimental sites. GE refers to an unnumbered light at the "Giant's Ear."

Plant spores and seeds have access to the cave through visitors (human and animal) or through air and water entering by the visitors' tunnel, by a small opening in the plastic cover over the original entrance, or by other unknown vents. Existing vegetation is essentially cryptogamic and centers around the artificial lights, which were introduced in most of the cave chambers in 1939-40 and in the Talus Room in 1960. During daily tours (between 08:00 and 17:00), individual sections of the cave are lighted just long enough (about 20 min.) to accommodate each group. With considerable daily and seasonal variation in numbers of visitors, photoperiods are consequently highly irregular.

Apart from the superimposed erratic light rhythms and some obvious moisture differences, the overall cave environment gives the impression of being quite stable. A number of different microenvironments, not always obviously related to moisture, are, however, distinguishable to the plants that vary in kind, abundance, and size throughout the cave.

The object of the present work was to study the effects of different photoperiods and some microenvironmental factors on existing and potential plant life. Cave studies were supplemented with controlled laboratory ones.

This research formed part of an ecological survey commissioned by the National Parks Service, partly in order to determine the possible consequences of opening a new visitors' tunnel (see Fig. 1). Other publications to date on this project include studies of air movements (Went, 1970), fungi associated with stalactite growth (Went, 1969), and microecosystems (Stark, 1969).

METHODS

To facilitate present and future work, 175 of the more accessible cave lights were mapped and inconspicuously numbered. Figure 1 shows the locations of the various experimental sites chosen for study as being representative of different types of microenvironments throughout the cave. Each station covered an area of approximately 625 cm^2.

The microenvironmental factors studied were:

1. Soil temperature, °C, taken with a Yellow Springs Instrument Co. telethermometer.
2. Light readings in foot candles.
3. Light wattage.
4. Percent soil moisture, determined by percent weight lost in screened samples during heating to constant weight at 55°C.
5. pH, determined by a portable Specific Ion Meter No. 404 (Ionalyzer) of Orion Research Co.

Tests of growth potential

A. Cave soil germination tests

Some areas that seemingly might support plant life were barren, possibly due to lack of seeds or spores. Also, seedlings of higher plants had been observed in the cave in the past, possibly introduced by humans, animals, or water. To judge the extent to which such potential growth of both lower and higher plants already existed in the cave, as well as possibly to learn something of the habits of animal carriers, 14 soil samples were collected from various cave areas and 4 from outside the cave near the original entrance. Equal portions of all samples were placed in 10 × 10-cm pots in greenhouses at 20°C day and 10°C night and at 30°C day and 20°C night, watered daily, and observed regularly for germination.

B. Germination of higher plants in the cave

The potential for germination and growth of higher plants was tested by sowing seeds of four low-temperature-germinating plants —peas (*Pisum sativum*), barley (*Hordeum vulgare*), beets (*Beta vulgaris*), and chickweed (*Stellaria media*)—in plots of approximately 240 cm^2 in 11 lighted areas and 2 dim ones (3 m from lights) located throughout the cave.

Control germination experiments were carried out in the laboratory at 20°C day, 10°C night and at 30°C day, 20°C night, in both natural photoperiods and total darkness.

C. Transplanting of lower plants

To further test the growth potential and possible microenvironmental specificity of the cave, two species of moss, *Campylium chrysophyllum* (Bird) J. Lange and *Physcomitrium* sp., and an unidentified species of alga were transplanted from Light 40, where growth was good, to different cave locations largely devoid of vegetation. Approximately 3 cm^2 portions of the plants were carefully removed with part of their substrate, placed in shallow furrows in the new area, and watered with 1 liter of water.

Effects of light

A. Effect of introducing light into previously dark area of cave

As a further test of the growth potential in the cave, a 120-Watt light operating on a 12-hr photoperiod time clock was set up in a previously dark but moist area approximately 2 m beneath the "Giant's Ear" (GED).

B. Effect of regular photoperiod on plant growth in the cave

The usual irregular cave lighting was replaced by regular photoperiods operating on time clocks in two cave areas with established plant communities. With 120-Watt bulbs, photoperiods of 12 hrs (from 08:00

to 20:00) and 6 hrs (from 08:00 to 14:00) were set up in the "Giant's Ear" (GE) and at Light 54 respectively. The former community consisted of abundant growth (approximately 90% cover) of the moss, *Campylium chrysophyllum*, plus unidentified algae and fungi. The latter community, though drier, still supported a reasonably good growth (approximately 30% cover) of *Campylium chrysophyllum* and some algae. The same moss growing well at Light 40 with normal cave photoperiods was used as control. Measurements of the moss were made at marked reference points chosen for comparable initial size (20 mm) and light intensities (70 f.c.) at the "Giant's Ear" (GE) and Light 40. At Light 54, positioning of the light was such that light intensity at the plot was 20 f.c. and initial size was 15 mm.

Specimens of *Campylium chrysophyllum* as well as other cave species collected in sterile vials were also cultured in the laboratory at 20°C day, 10°C night and at 10°C day, 6°C night, both with 12-hr photoperiods.

RESULTS AND INTERPRETATION

Relationship of microenvironmental factors to cave plant growth

Table 1 summarizes some microenvironmental factors for 26 microenvironments in Lehman Cave, sampled on different occasions, together with qualitative descriptions of the more obvious components of their plant communities. This sampling shows that, despite an apparently stable environment, there are a number of different microenvironments that individually are subject to fluctuation of such factors as temperature, moisture, and light, and that support various plant communities.

The cave consists of relatively dry areas up to the Lodge Room, fairly moist areas from there to the Talus Room, and very dry areas in the Talus Room. Cold dry air entering the cave in winter affects moisture as well as temperature (see Table 1). The local moisture fluctuations correspond partly with the air flow data of Went (1970) and probably are also affected by seepage of exterior precipitation.

Although, in general, the amount of vegetation correlates with degree of moisture (Spearman Rank correlation coefficient +0.68, significant at 99% level for 16 lighted stations), a number of exceptions indicate that other factors may be involved. Thus some areas with apparently adequate moisture and light were barren (e. g., Lights 13 and 112) whereas others with lower moisture supported vegetation (e. g., Light 54).

Because of various installations and reflectors, comparable wattage and distance from lights resulted in very different light readings (see Table 1). Light intensities at most growth sites were low but adequate for support of lower plants. Algae were found below 20 f.c. and mosses at somewhat higher intensities, although transplant experiments showed that mosses can also survive at lower intensities.

Soil temperatures on given dates were found to vary by several degrees throughout the cave, largely as a result of distance from and intensity of lights. Spearman Rank Correlation coefficients for 3 stations (GE, GED, and Light 54) were all −1. This temperature gradient has a profound effect in some cases, such as at the "Giant's Ear," where an increased temperature within 3 cm of the light (GEB) resulted in sufficient decrease in moisture level to prevent vegetation (see Table 1).

A pH range from 8.0 to 9.6 was found within the cave proper and from 6.2 to 8.6 in the original entrance area. The tendency to acidity in the latter reflects the high concentration of carbon dioxide and lack of calcite deposits.

A degree of specificity of plants to substrate is indicated by the relationship of moss and algae to pH. *Campylium* and *Physcomitrium* occurred only at pH 9.2 or higher, while *Bruchia* was found at pH 8.4. No algae or moss were found at a pH below 8.4, although moisture might have been a limiting factor at some sites.

Other indications of specificity of microenvironment are shown by mosses. Thus, *Bruchia* occurs at high moisture and rela-

TABLE 1. Plant Communities and Microenvironmental Factors in Lehman Cave, 1968.

		Date (and time) of Observations												
		% Soil Moisture			% Relative Humidity*			Soil Temperature, °C					Light,	Distance of
Station Near Light No.	Type of Vegetation (and % Cover)	26 IX	24 X	4 XII	IX	X	XII	26 IX (10:00)	24 X (20:00)	7 XII (09:00)	pH 4 XII	Watts	Ft. c. at site	site from light, cm
11	No apparent vegetation	5.4	4.7	3.4	91	84	60	12.8	12.0	12.5	8.0	150	225	25
13	No apparent vegetation	8.1	3.2	2.2				12.6	12.6	11.8	8.1	100	90	30
31	No apparent vegetation	3.7	4.1	4.1				12.0	11.2	11.8	8.0	150	4	250
37	Algae; Moss, *Physcomitrium* sp. (85%)	16.3	18.7	16.7				12.6	12.6	12.3	9.4	100	40	30
38	(Dark area below light) Algae on wall (80%)	..	10.2	9.6				11.0	11.0	11.4	8.9	100	0	190
40	Luxuriant algae; moss, *Physcomitrium* sp. (95%)	11.1	12.4	11.1				11.4	12.6	10.2	9.3	150	70	35
47	Algae; moss, *Bruchia* sp. (90%)	70.5	66.3	62.1	97.6	99.6	90.6	11.9	11.9	12.2	8.4	150	20	90
47a	(Dark area 3 m into new tunnel) No apparent vegetation	..	31.4	34.7				10.5	10.9	11.0	8.7	150	0	330
GE†	Luxuriant algae, fungi; moss, *Campylium chrysophyllum* (Bird) J. Lange (90%)	8.2	7.2	3.7				12.0	12.4	13.4	9.2	120	70	30
GEB	(Near base of light) No apparent vegetation	0.9	0.8	0.8				15.5	18.4	...	9.3	120	400	3
GED	(Previously dark area beneath GE, newly lighted) No apparent vegetation	24.4	22.4	23.9				14.0	14.4	13.3	9.2	120	150	60
54	Algae; moss, *Campylium chrysophyllum* (30%)	0.5	1.0	0.7				15.0	16.0	13.9	9.6	150	20	15
62	No apparent vegetation	11.2	9.0	9.3				...	14.4	13.6	8.4	150	10	25
81	Algae (80%)	34.3	33.9	34.9	95.8	99.1	98	...	14.5	12.7	9.6	100	13	45
97	Algae (60%)	8.2	9.2	9.4				...	14.2	13.8	9.4	100	15	40
97	(Dark area below light) No apparent vegetation	..	30.4	16.5				...	12.2	11.9	9.0	100	0	200
112	No apparent vegetation	..	9.3	9.1				...	12.7	12.4	8.2	75	25	25
114	No apparent vegetation	4.8	4.5	9.0				...	11.0	13.0	8.4	500	6	87
114	(Dark area) No apparent vegetation	2.2	..	3.3				...	12.9	12.8	..	500	0	400
114	(Dark area) No apparent vegetation	1.6	..	2.4				...	12.8	12.4	..	500	0	500
135	Algae (75%)	..	11.7	21.7				...	12.6	12.4	9.5	100	12	40
Original Entrance Area (No artificial lights)														
1	(Dark area) No apparent vegetation	..	..	..				...	...	19.3	7.6		0	
2	(Under natural light) Algae	..	..	..				...	...	13.7	8.5		5	
3	(Under natural light) No apparent vegetation	..	..	..				...	...	16.2	7.1		1	
4	(Dark area) Fungi	..	..	..				...	...	18.7	6.2		0	
5	(Dark area) Fungi	..	..	..				...	...	10.9	8.6		0	

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* Monthly averages from records of Lehman Caves staff.
GE† = "Giant's Ear".

tively low temperature, *Physcomitrium* at intermediate moisture and temperature, and *Campylium* at relatively low moisture and higher temperature (Table 1).

The importance of time in the establishment of cave communities is shown by the sparse vegetation in the Talus Room, which has been lighted for only 9 years, compared with the considerably greater abundance and variety in the remainder of the cave which has been lighted for 30 years. Thus, of 15 lights surveyed in the former, only 13.3% had algae and none had mosses; whereas in the latter, of 146 lights, 45.2% had vegetation, 43.2% with algae and 15.8% with moss. In addition to the species mentioned above, *Amblystegium serpens* (Hedw.) BSG, *Pohlia wahlembergii* (Web and Mohr) Andr., and other unidentified species were noted in the longer lighted areas.

Tests of growth potential

A. *Cave soil germination tests*

No natural germination occurred in the soil samples from the interior of the cave during a 3-month observation period. However, intruders of some nearby greenhouse plants currently in seed showed that cave soil can support growth of higher plants. Other evidence reported later indicates that animals utilize seed and other plant material as food, which could account for the lack of germination.

A number of grasses and dicotyledons characteristic of the area exterior to the cave germinated in the four samples taken from outside the cave. The moss, *Physcomitrium* sp., appeared in a sample from the original entrance area, presumably from spores that had entered the opening in the entrance cover.

B. *Germination of higher plants in the cave*

Except for chickweed, which failed to germinate under any laboratory conditions, all other controls showed more than 80% viability at the lower temperatures.

In the cave neither temperature nor pH were critical. A local moisture level of approximately 8%, however, was found to be a limiting factor for germination. No germination was observed in the dry entrance area up to Light 37 nor in the Talus Room, but seedlings of beets and peas were found at Lights 40, 47, "Giant's Ear" (GE), the newly lighted area below GE (GED), and Light 81. The greatest germination percentage found was 90% for beets at GED, with 24% moisture. Interestingly enough, chickweed germinated at two cave locations (Light 37 and GED) but not in the laboratory.

Effect of photoperiod

The positive influence of regular photoperiod on growth of cave seedlings was shown by the fact that after 1 month beet seedlings in the "Giant's Ear" with a 12-hr photoperiod had a mean height of 25±3 mm, whereas those at Light 47 with irregular lighting were only 12±1 mm. This corroborates other growth results reported later.

Animal interactions

Many of the plots throughout the cave were disturbed by animals, revealing that they utilize the cave as trogloxenes. Frequent deposits of pine nut shells at lights, as well as the greater disturbance of plots closest to lights, indicate that the animals might be attracted by the warmth of the lights.

Animals apparently displayed a preference for higher protein content in their selection of seed. Many barley and pea seed hulls were found at the plots, and no barley seedlings at all were observed. The smaller beet and chickweed seeds were less disturbed, although several beet seedlings were pulled out or chewed on.

In a second planting later in the fall, more seeds were apparently removed, resulting in less germination. The growing scarcity of food with onset of colder weather probably stimulates the animals to become more acute and less selective hunters.

C. *Transplanting of lower plants*

Figure 2 illustrates the results of transplanting the moss *Campylium chrysophyllum* and an associated alga taken from Light 40, where it was well established, to various locations throughout the cave. Except for algae at Light 81 none had any obvious vegetation initially.

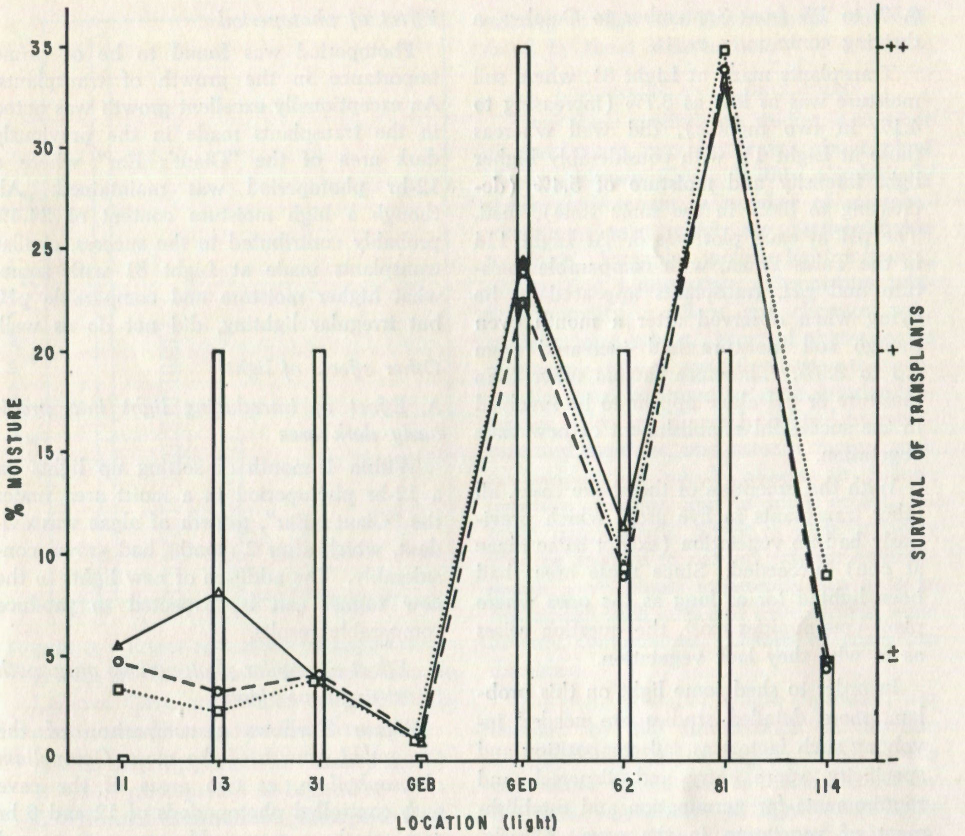

Figure 2. Relationship of soil moisture to survival of algae and moss (*Campylium chrysophyllum*) transplanted to various locations in Lehman Cave. Soil moistures: △———26 IX 68; O-------24 X 68; □. . . . 4 XII 68. Height of bar = survival of transplants: ++ = excellent, showing some growth; + = established but no measurable growth; ± = barely surviving; − = died. GEB = within 3 cm of light at GE; GED = previously dark area beneath GE.

At very low levels, soil moisture appears to be critical in establishing the transplant. Thus, at the immediate base of the light in the "Giant's Ear" (GEB), where a drying effect resulted in a soil moisture of 0.8%, the transplants died. At a distance of 30 cm from the same light, where the moisture was 8.2%, there was a luxuriant growth of the transplanted species. The increased temperature of about 3°C at the base of the light is not critical, because laboratory cultures survived at considerably higher temperatures. Nor is pH critical, since other areas with the same pH supported the transplants.

Although moisture appears to be critical in establishing a transplant, this apparently is not so in existing communities. Observations throughout the cave revealed that *Campylium chrysophyllum* can thrive at relatively low moisture levels and high temperatures (see Table 1). For example, at Light 54, where soil moisture varied from

0.5% to 1% from September to October, a thriving community exists.

Transplants made at Light 31, where soil moisture was as low as 3.7% (increasing to 4.1% in two months), did well whereas those at Light 11, with considerably higher light intensity and moisture of 5.4% (decreasing to 3.4% in the same time), died. The pH at each plot was 8. At Light 114 in the Talus Room, with comparable moisture and pH, transplants appeared to be dying when observed after a month even though soil moisture had increased from 4.8 to 9.0%. Therefore factors other than moisture or pH alone appear to be involved in the successful establishment of new cave vegetation.

With the exception of the above cases, all other transplants in five areas which previously had no vegetation (except some algae at one) succeeded. Since these areas had been lighted for as long as the ones where plant communities exist, the question arises as to why they lack vegetation.

In order to shed some light on this problem, more detailed studies are needed involving such factors as soil composition and specificity, spore entry and dispersal, and requirements for germination and establishment of vegetation in the cave. Clearly, given the opportunity, much more vegetation could exist, but since measurable growth is generally slow under natural cave conditions, long term studies are needed.

Of interest will be the observation of the effects of the new tunnel and proposed enlargement of the original cave entrance opening, which should bring in new spores, seeds, and animals. Not only can this be expected to alter the appearance of the cave in terms of new vegetation, but gradually the changes in CO_2 concentration effected by photosynthesis and respiration could also have some bearing on the speleothems. The recent curious discovery by Went (1969)—that fungi are involved in stalactite growth—means that an increased fungi population could have particularly interesting potential effects on cave formations.

Effect of photoperiod

Photoperiod was found to be of prime importance in the growth of transplants. An exceptionally excellent growth was noted in the transplants made in the previously dark area of the "Giant's Ear" where a 12-hr photoperiod was maintained. Although a high moisture content of 24.4% probably contributed to the success, similar transplants made at Light 81 with somewhat higher moisture and comparable pH, but irregular lighting, did not do as well.

Other effects of light

A. *Effect of introducing light into previously dark area*

Within 1 month of setting up lights on a 12-hr photoperiod in a moist area under the "Giant's Ear", growth of algae was evident, which after 2 months had grown considerably. The addition of new lights in the new tunnel can be expected to produce comparable results.

B. *Effect of regular photoperiods on growth of existing cave plants*

Figure 3 shows a comparison of the amount of growth of the moss, *Campylium chrysophyllum*, at two areas of the cave with controlled photoperiods of 12 and 6 hr respectively, a comparable area with normal intermittent cave lighting, and two controlled laboratory cultures. In a little over two months, plants of originally comparable size showed very different growth increments. Those given a 12-hr photoperiod showed 3.5 times as much growth as those with intermittent lighting, and just over twice as much as those with a 6-hr photoperiod. The plots at the 12-hr photoperiod and intermittent lighting had comparable ranges of soil moisture and light intensity. At the 6-hr photoperiod, despite considerably lower soil moistures and light intensity, growth was still 1.7 times as great as at the intermittent lighting.

These results, as well as previous ones with seedlings of higher plants and transplants of lower plants, show that increased lighting given as regular photoperiods in the cave greatly enhances growth.

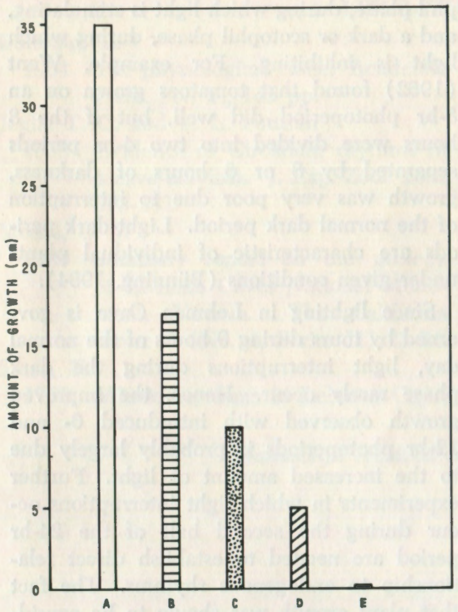

Figure 3. Effect of various photoperiods on growth of *Campylium chrysophyllum* in Lehman Cave and under controlled laboratory conditions after 2-1/3 months.

A = 12-hr photoperiod in "Giant's Ear."
B = 6-hr photoperiod at Light 54.
C = Normal intermittent photoperiod at Light 54.
D = Controlled laboratory, 12-hr photoperiod at 10°C, 12-hr dark at 6°C.
E = Controlled greenhouse, 12-hr photoperiod at 20°C day, 10°C night.

Growth of cave plants in controlled laboratory conditions

Campylium chrysophyllum, cultured in cool (10°C day, 6°C night) and warm (20°C day, 10°C night) conditions with 12-hr photoperiods, showed considerably less growth than in any of the cave conditions (Fig. 3). At the lower, more cave-like temperatures after 3 months, a small amount of growth occurred, but none was observed at the higher temperatures. Other cave species of mosses and algae followed a similar pattern. The important influence of temperature and possibly other unknown factors existing in the cave environment are indicated by these observations.

DISCUSSION AND CONCLUSIONS

From these preliminary studies, a number of conclusions may be drawn about plant life in Lehman Cave. Within a relatively stable environment, a number of microenvironments exist which are distinguishable to plants. Variables include light intensity, photoperiod, temperature, soil moisture, relative humidity, air flow, and chemical substrate among others. Most of these are in a dynamic state of some fluctuation throughout the year, governed by such interior factors as lights which partly control temperature and moisture, and exterior factors such as temperature which affects air inflow, moisture changes, and to some extent, interior temperature. Slight as such variables may be relative to natural exterior environments, cave plants apparently are able to distinguish such cues and have formed some definite communities. Details of some are discussed.

The plant potential, whose expression was enabled by the introduction of lighting approximately 30 years ago, greatly exceeds the actual vegetation, as demonstrated by the rapid appearance of algae when lights were introduced to a previously dark area, by the successful transplanting of cave plant species and the establishment of seedlings of higher plants in previously barren areas of the cave, and by the occurrence of an exterior moss in an original entrance area soil sample tested in the laboratory. Thus spores may be assumed to be present throughout the cave, but unknown factors prevent their germination in seemingly favorable microenvironments.

Animals were also found to be a source of plant interaction, as both dispersal agents and consumers. With the proposed reopening of the original entrance and with the introduction of new lights, new plant communities can be expected which potentially could have some effects on cave environment and speleothem formation. A long term study of such progress would prove fruitful.

A major controlling microenvironmental factor in the establishment of new plant growth, for both higher and lower plants, was found to be soil moisture. For higher plants, a critical level of approximately 8% is necessary. For lower plants, a level as low as 0.5% can sustain established growth, but a higher level of approximately 4% was found to be necessary for transplants of mature plants. This information conceivably could be used, if desirable, to control cave vegetation, such as preventing establishment of plants by artificial drying.

Microenvironmental factors other than moisture were found to be vital, as shown by the failure of several apparently favorable areas to support transplanted cave species while others with lower moisture content succeeded. Possibly specific soil factors are involved. Further indications of this were found in some specific relations of cave mosses to pH. The fact that cave plants did poorer under apparently more optimal controlled laboratory conditions than in the cave further points to unknown cave factors to be explored.

The most pronounced rhythmic component of the cave environment is the erratic photoperiod governed by numbers of daily visitors. Although existing plants, which are essentially cryptogamic, have adapted to such intermittent lighting, the present work shows that a regular photoperiod of either 6 or 12 hours greatly enhances growth of existing lower plants as well as of introduced seedlings of higher plants.

Apparently, cave plants are able to grow with highly irregular lighting since the light they receive comes within their natural light phase. Circadian rhythms of plants have been shown to consist of a light or photophil phase, during which light is stimulating, and a dark or scotophil phase, during which light is inhibiting. For example, Went (1962) found that tomatoes grown on an 8-hr photoperiod did well, but if the 8 hours were divided into two 4-hr periods separated by 8 or 6 hours of darkness, growth was very poor due to interruption of the normal dark period. Light-dark periods are characteristic of individual plants under given conditions (Bünning, 1964).

Since lighting in Lehman Cave is governed by tours during 9 hours of the normal day, light interruptions during the dark phase rarely occur. Hence, the improved growth observed with introduced 6- and 12-hr photoperiods is probably largely due to the increased amount of light. Further experiments in which light interruptions occur during the second half of the 24-hr period are needed to establish direct relationship to endogenous rhythms. The fact that plant growth was shown to be considerably affected by photoperiod, however, should be a consideration in the installation of new lighting systems, as resulting vegetation becomes an integral part of the cave's ecology.

ACKNOWLEDGEMENTS

I wish to express sincere thanks to Mr. E. L. Robinson, Superintendent, to Mr. R. Graybell, Naturalist, and to all the other members of the Lehman Caves staff for their generous assistance during this work. I am grateful to Dr. F. W. Went for his critical review of the manuscript, to Dr. S. Bamberg for his help in setting up the lighting system and in collection of the data, to Dr. Y. O. Koh for the statistics, and to Dr. Jeanette Wheeler for her help with the figures. Thanks are expressed to the National Park Service for supporting this research.

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A Reply to "The Classification of Australian Cavernicoles with Particular Reference to the Rhaphidophoridae (Orthoptera)"

Elery Hamilton-Smith *

Although I do not wish to unduly prolong any controversy, I feel a brief reply must be made to several points raised by Richards (Natl. Speleo. Soc. Bull. 33:135-139):

1. My paper (Natl. Speleol. Soc. Bull., 33:63-66) is not "based upon" the 1967 paper (J. Aust. Ent. Soc., 6:103-118) as stated by Richards, although this earlier work is cited as an illustration, but upon much more extensive data, covering a much greater number of species, a great deal of which is still unpublished.
2. I was at some pains to point out that my paper was a limited contribution to discussion, based upon Australian experience, and was not presented as an overall scheme for all purposes. Richards says "generalizations from Southern Hemisphere fauna have been made to erroneously include the cave fauna of the world." I did not and do not claim such omniscience.
3. I have not at any time listed *Speotarus lucifugus* among the fauna of the Nullarbor caves and have always referred to specimens from that region as *Speotarus* sp. I detailed the distribution of the total genus as that which Richards assigns to the single species *S. lucifugus*. Present evidence suggests she is correct, but the taxonomy of this genus is still unclear and, at the time of my earlier paper, it was even more unclear.
4. I agree that much more evidence is required to establish the validity of any classification scheme of this kind. However, I fail to see that Richards has produced sufficient evidence to invalidate my division of the troglophiles into two levels. Without venturing into detail at this point, I note that new evidence (generally not cited by Richards) has suggested my classifications of some species in my 1967 paper were incorrect. I am glad that such new evidence has come to light, but I also note that it has not seriously affected the general usefulness of the classification scheme as such.
5. With respect to the Rhaphidophoridae, I admit my error in using the term "diurnal" when "bimodal" might have been preferable. I regret not having described in detail my own observations of 237 *Micropathus tasmaniensis* leaving a single cave entrance in little over an hour, many of which were later observed feeding on vegetation, but would admit that a single night's observation is inadequate evidence for satisfactory ecological classification, even though indicative. I continue to admit my difficulty and confusion in finding a satisfactory treatment for the ecological classification of the Austra-

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lian Rhaphidophoridae. I can only say I am as certain about my uncertainty in this matter as Richards appears certain in insisting that, with some exceptions, they must be treated as troglophiles and never as trogloxenes.

Addendum to "The Classification of Australian Cavernicoles with Particular Reference to the Rhaphidophoridae (Orthoptera)"

Aola M. Richards*

In a recent paper Barr (1971) refers to the cave cricket *Hadenoecus subterraneus* as "the abundant troglophile". As mentioned previously, Hamilton-Smith had used Barr's earlier reference to this species as a trogloxene to support his own classification of cave crickets. Apparently Barr is now in agreement with my classification of these insects.

REFERENCE

Barr, Thomas C., Jr. and Robert A. Kuehne 1971 Ecological Studies in the Mammoth Cave System of Kentucky. II. The Ecosystem. Ann. Speleologie 26(1): 47-96.

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RECENT CAVE BIOLOGY PAPERS APPEARING IN OTHER JOURNALS

Prepared by the Biology Section of the National Speleological Society

Armstrong, J. G., and J. D. Williams. 1971. Cave and spring fishes of the southern bend of the Tennessee River. Journal of the Tennessee Academy of Science 46: 107-115.

Reports on many types of fishes, mostly epigean, associated with cave streams and springs from Walden Gorge through northern Alabama. Very little on the troglobite, *Typhlichthys subterraneus,* but an interesting new record for *Chologaster agassizi* from Franklin County, Tennessee.

Carpenter, J. H. 1970. *Geocentrophora cavernicola* n. sp. (Turbellaria, Alloeocoela): first cave alloeocoel. Transactions of the American Microscopal Society 89: 124-133.

Describes an alloeocoel from John Rogers Cave in Jackson Co., Kentucky and Blowhole Cave, Pendleton Co., West Virginia. No other cavernicolous alloeocoels are known anywhere in the world.

Christiansen, K. 1970. Survival of Collembola on clay substrates with and without food added. Annales de Speleologie 25: 849-852.

The author suggests that chemo-synthetic bacterial activity can furnish a major food source for cave Collembola, especially *Tomocerus* and *Onychiurus.* Cave forms usually survived longer on cave clay than related surface forms.

Christiansen, K. 1971. Factors affecting predation on Collembola by various arthropods. Annales de Speleologie 26:97-106.

Species of Collembola differ strikingly in their susceptibility to predation, the differences being largely associated with size and mobility. Cave adaptation seems to have little relationship to predator escape. Opilionids were more efficient predators than chilopods.

Cooper, J. E. 1971. Interesting new locality records for the southern cavefish, *Typhlichthys subterraneus* Girard (Pisces, Amblyopsidae). Bulletin of the Association of Southeastern Biologists 18:30 (Abstract).

Reports an apparently isolated population from southeastern Kentucky, the first record for Georgia, some localities from south of the Tennessee River, and another locality in the Coosa River system (Mobile Basin drainage).

Cooper, J. E., and M. R. Cooper. 1971. Studies of the aquatic ecology of Shelta Cave, Huntsville, Alabama. Bulletin of the Association of Southeastern Biologists 18:30 (Abstract).

Briefly discusses the faunal aspects of Shelta Cave and the work being done there.

Culver, D. C., and T. L. Poulson. 1970. Community boundaries: faunal diversity around a cave entrance. Annales de Speleologie 25:853-860.

In Cathedral Cave, Kentucky, the authors find some evidence that the number of species and their evenness of abundance is higher in the entrance than in the cave or on the surface. This may be a phenomenon characteristic of ecotones in general.

Kenk, R. 1970. Freshwater triclads (Turbellaria) of North America. III *Sphalloplana weingartneri* new species from a cave in Indiana. Proceedings of the Biological Society of Washington 83:313-320.

The first troglobitic planarian from Indiana is described. It is found in Bronson's Cave in Lawrence County.

Kenk, R. 1970. Freshwater triclads (Turbellaria) of North America. IV. The polypharyngeal species of *Phagocata.* Smithsonian Contributions to Zoology 80: 1-17.

Phagocata subterranea, a blind, white planarian previously believed to be a troglobite, was found not to be a separate species from *P. gracilis,* a form common in surface waters. It is common in caves in much of the southeastern United States.