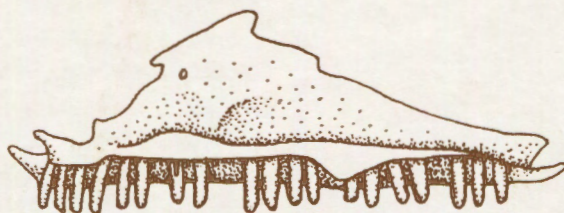


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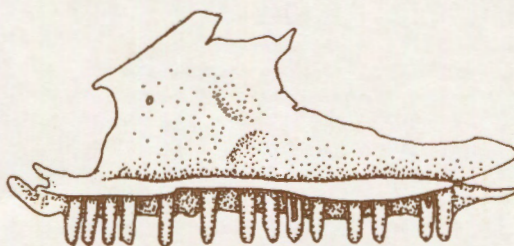
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AN ANALYSIS OF THE COLEOPTERA OF MITCHELL CAVERNS, SAN BERNARDINO COUNTY, CALIFORNIA

ROLF L. AALBU*

A survey was conducted of the Coleoptera of Mitchell Caverns, San Bernardino County, California. Ethylene glycol pitfall traps were used to survey the Coleoptera at selected sites inside and outside the caverns. The study was conducted for a period of one year. Four trapping series, to approximate seasonal variation, were examined. One troglobite, thirteen troglaphiles, six habitual troglloxenes, seven occasional troglloxenes and four accidentals were trapped in the caverns. Four factors were found to influence the cavernicolous fauna trapped: (1) the distance the traps were placed from an outside entrance, (2) the substrate composition in the area of the trap, (3) the humidity of the area, and (4) the subdued climatic seasonal influences bringing into the caverns its associated troglloxene and accidental fauna. Limited, careful use of ethylene glycol pitfall traps was found to be an effective method for surveying cave microfauna.

INTRODUCTION

The following is a condensed version of a report submitted to the State of California Department of Parks and Recreation by the author in 1979 with the same title as above.

Mitchell Caverns Natural Reserve is located on the eastern slopes of the Providence Mountains in San Bernardino County, California, and is part of the Providence Mountains State Recreation Area. The Providence Mountains are one of the highest mountain ranges in the eastern part of the Mojave Desert, an area of relatively sparse vegetation. Mitchell Caverns are located at about 1340 m (4,400 ft) elevation on the eastern slope of the central portion of the mountains, which rise to 2,185 m (7,171 ft) at Edgar Peak. The eastern slope descends to Clipper Valley and rises to the east to Wild Horse Mesa, at approximately the same elevation as the caverns.

Mitchell Caverns are situated in the lower portion of a thick sequence of marine limestone of Permian origin which lines the mountainside for several miles to the north and south of the caverns (Emery & Easton, 1951). The caverns are believed to have originated about 12 million years ago (Miocene) when Wild Horse Mesa extended to the level of the caves (Emery & Easton, 1951). Tropical climate characterized this epoch, the mesa being covered with rain forest. During this period of heavy rainfall, ground water rich in carbon dioxide from decomposing organic matter saturated the limestone layers. As time passed, the area around Wild Horse Mesa eroded to its present level, dropping the level of ground water and exposing the cavities to the air. This caused the formation of calcite crystals which

eventually formed stalagmites, stalagmites and other cave formations present today. At the present time, water activity in the caverns has generally ceased except during periods of heavy rainfall, when a little water does drip through into the caverns.

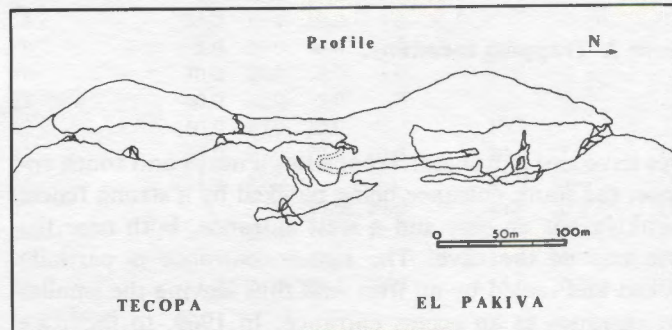


Figure 1. Profile of Mitchell Caverns.

There are over 20 known caves in the Providence Mountains State Recreation Area. Mitchell Caverns actually refers to two separate caves. These caves were exploited as a tourist attraction in the 1930's by a prospector named Jack Mitchell. The north cave, called El Pakiva (Fig. 1), means "pool of water from the eye of the mountain." The south cave, Tecopa, is named after a Shoshonean chief. A Shoshonean tribe, the Chemehuevi, inhabited this area within the last 500 years. A burial site has been found in Tecopa.

Both caves are at about the same level, although El Pakiva contains a secondary, lower chamber at the far south end, which is approximately 60 feet lower (Fig. 1). Both

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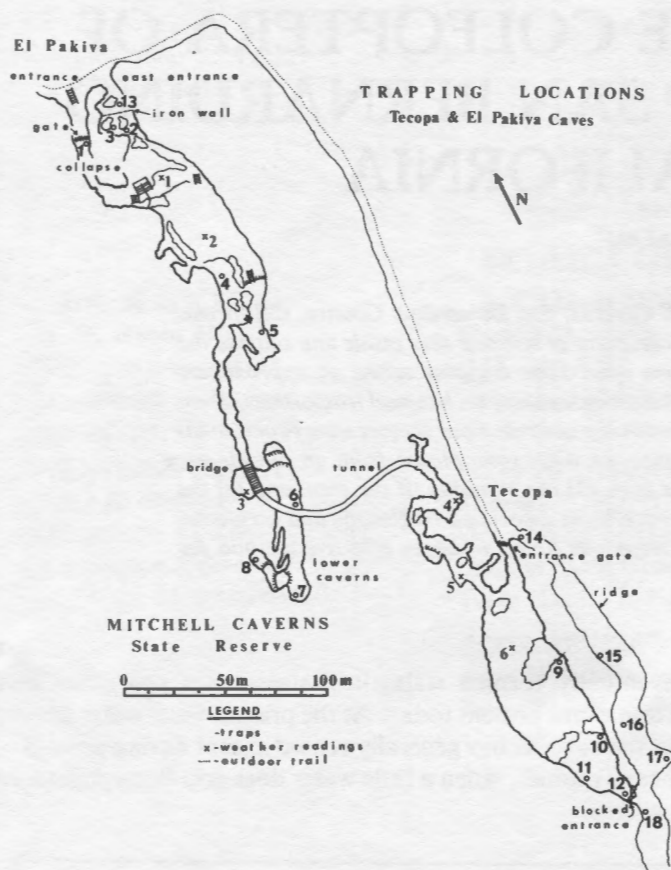


Figure 2. Trapping locations.

caves have two entrances: Tecopa has a north and south entrance, the south entrance being blocked by a strong fence; El Pakiva has an east and a west entrance, both near the north end of the cave. The eastern entrance is partially blocked and sealed by an iron wall thus leaving the smaller west entrance as an access entrance. In 1969, to facilitate visitor tours, excavation was begun on a tunnel designed to connect the two caves. The tunnel was completed in 1970.

MATERIALS AND METHODS

Pitfall traps have been a commonly used method of collecting terrestrial arthropods at ground level. Barber (1931) was one of the first to suggest the use of semi-permanent traps, having bait placed above them, for the collection of cave insects. After experimenting with a number of different solutions for trapping cave beetles under bait, Peck (1973), found best results with a 50/50 mixture of laboratory grade ethylene glycol and water. Aalbu (1977), using three different commercial brands of ethylene glycol (antifreeze) without bait, found that seven of the most abundant families of Coleoptera trapped seemed to indicate a differential attraction to one or more of the different brands. Especially convincing was the trapping of certain species of

Coleoptera where 88% and 94% of all specimens were found in only one antifreeze brand. Of the three brands used (Aalbu, 1977), Dow (Dowguard) seemed to be the most "favorable" for insect sampling, capturing the most numbers of specimens and showing much diversity in species. For this reason, Dowguard antifreeze was chosen exclusively for use in traps during this study.

The ground traps were aluminum one-pound coffee cans of approximately 13.5 cm depth with a 10 cm diameter opening. Plastic inserts 8 cm deep with a 10 cm opening were fitted into the openings of the cans. The lip of the plastic inserts extended 2 cm above the upper edge of the metal can. This facilitated removal of the ethylene glycol and trapped material from the trap without removing or dislodging the metal can from the substrate. The inserts were filled with approximately 250 ml of the ethylene glycol. The traps were then buried in the ground to the rim of the insert. On the outside traps, a large rock of approximately 15 x 15 cms was placed on three or four smaller rocks to protect the can from rain and larger animals but permit arthropods to enter the trap.

Table 1. Trapping Periods

	Locality	Time Span (Summer)	Number of Days in Series
Series 1	cave only	V-27-78 to VIII-26-78	91
		(Fall)	
Series 2	cave & outside	VIII-26-78 to XII-31-78	127
		(Winter)	
Series 3	cave & outside	XII-31-78 to III-17-79	77
		(Spring)	
Series 4	cave & outside	III-17-79 to VI-16-79	92
Total Days Traps Operated			387

If the cave area is small and many traps are used, cave fauna may be drastically reduced altering sometimes delicate ecological balances within the cave. For this reason only few traps were set. This allowed sampling from various areas of the caverns without unduly upsetting the arthropod populations. At the conclusion of this study, all traps were removed from the caverns.

The trapping survey was conducted for slightly more than one year. On May 5, 1978, 12 traps were established in the caverns and activated. These included five traps in the main section of El Pakiva cave, three traps in the lower caverns of El Pakiva and four traps in Tecopa cave (Fig. 2). On August 26, 1978, during the first gathering and replacement of the traps, additional traps were established on the outside of the caverns. These included one at the outside of the blocked east entrance to El Pakiva (#13), and five along the ridge separating the two exits of Tecopa cave (Fig. 2). Trapping periods were segregated into four series, each averaging 97

days or approximately three months. These four trapping series were intended to sample seasonal differences during an entire year (Table 1).

The distances from the nearest outside entrance to the trap locations is indicated by Table 2. Note that with the addition of the man-made tunnel connecting El Pakiva and Tecopa, the distance from the outside to the lower caverns of El Pakiva cave was shortened by approximately 20 m. This connection may have affected the local climate of the lower caverns. Furthermore, the blocking of the larger east entrance of El Pakiva by an iron wall reduced the outside influence into the cave (as well as lengthened the distance from an entrance to the area of traps 2 & 3, see Fig. 2).

The inserts, gathered after each sample period, were cleaned by flushing the ethylene glycol from the material

Table 2. Trap Distance From Cave Entrances

Trap #	Cave	Outside of Cave	Distance to Nearest Entrance	Name of Nearest Entrance
1	EP		-10.5 m	EP
2	EP		-33.0 m	EP
3	EP		-35.1 m	EP
4	EP		-49.5 m	EP
5	EP		-60.0 m	EP
6	EP		-80.4 m	TE
7	EP		-97.8 m	TE
8	EP		-99.9 m	TE
9	T		-24.3 m	TE
10	T		-14.1 m	TF
11	T		-12.0 m	TF
12	T		- 2.4 m	TF
13		EP	+ 0.0 m	EP
14		T	+ 5.7 m	TE
15		T	+20.4 m	TF
16		T	+ 7.2 m	TF
17		T	+ 6.9 m	TF
18		T	+ 5.1 m	TF

EP : El Pakiva

T : Tecopa

TE : Tecopa exit

TF : Tecopa fenced entrance

with water through a 0.075mm mesh brass sieve. The contents were then sorted under a dissecting microscope into Coleoptera and other arthropods. Only Coleoptera were considered and analyzed during this study. Other arthropods were forwarded to appropriate specialists for analysis.

For a better understanding of the faunal composition within the caves, the geological fill and substrates found within the caverns were examined. These can normally be divided into three main components: (1) Collapse Breccia; large limestone blocks which have collapsed from the roof during the history of the cave. These were found abundantly near the cave entrances and especially near the entrance to El Pakiva. (2) Dripstone; this includes stalagmites,

stalagmites, columns and cave veneer. These were found to be most abundant at the south end of the main chamber of El Pakiva and the north end of Tecopa. Emery and Easton (1951) suggested that in fact Tecopa and El Pakiva caves were once continuous, but that the accumulation of dripstone along a transverse fault zone in the area separated them. (3) Cave Dust & Debris; this usually consists of fine grained pebbles, sand, silt, and clay along with larger rocks of calcite or limestone together with a small amount of organic material. The organic material is made up of nuts, seeds, stems, old leaves, and various rodent fecal pellets and bones. Cave dust was found present throughout the caverns. In some areas of the caverns (especially around the inside of the east entrance of El Pakiva and near trap #9 of Tecopa) packrats (*Neotoma lepida* Thomas) have active nest sites. Ground cover in these areas has a very high concentration of

Table 3. Trap Area Substrate Analysis: Percent By Volume

Substrate Composition:	A	B	C	D	E	F	G	Substrate TYPE
Trap #								
1	30.0	55.0	5.0			10.0		I
2	5.0	25.0	30.0	40.0				II
3	5.0	25.0	30.0	40.0				II
4	60.0	30.0		10.0				I
5	25.0	75.0						I
6	40.0	40.0	5.0		15.0			III
7	45.0	15.0	5.0	5.0	30.0			III
8	35.0	15.0	10.0	5.0	35.0			III
9	5.0	15.0	40.0	40.0				II
10	70.0	20.0	5.0	5.0				I
11	60.0	30.0	5.0	5.0				I
12	60.0	20.0	10.0			10.0		I
13	35.0	20.0	20.0	10.0		10.0	5.0	I
14	5.0	55.0				25.0	15.0	IV
15		20.0	20.0	20.0		20.0	20.0	IV
16		35.0		10.0		40.0	15.0	IV
17		60.0				30.0	10.0	IV
18	5.0	20.0	20.0	20.0		15.0	20.0	IV
Cave Traps								
Total	37.7	30.4	11.7	12.9	6.7	1.6	0.0	
Outside Traps								
Total	7.5	35.0	10.0	10.0	0.0	23.5	14.0	

A: Cave Dust.

B: Calcite, Limestone, pebbles & rocks.

C: seeds, bones, insect parts, bark, sticks, twigs, cactus spines.

D: *Neotoma* fecal pellets.

E: organic dust & clay conglomerate.

F: epigeal dirt and soil.

G: epigeal plant and animal materials.

- I. Area with fine cave dust, calcite and limestone pebbles and rocks, and a small amount of organic matter.
- II. Areas with a strong packrat influence having a very high organic content with much organic debris of both plant (seeds, bark, twigs, cactus spines) and animal matter (*Neotoma* fecal pellets, bones, insect parts, etc.).
- III. Lower caverns area with very fine, highly organic dust and conglomerate (dust-clay-rocks).
- IV. Outside (epigeal) substrate.

fecal pellets and plant debris. At certain times in the past, El Pakiva cave has been partially to entirely flooded. The evidence for this is found in the lower caverns where the cave dust, clay and debris forms a conglomerate which is now mostly partially reduced to a fine powder with a highly organic, musky smell. During the construction of the tunnel between the two caves, much of the dirt and rocks blasted from the limestone was deposited on the floor of the main chamber of El Pakiva cave and now forms the present level floor.

An analysis was made of the substrate composition found near each trap. From the data gathered (Table 3), four general types of substrates were found in the trapping area: 1, basic cave substrate consisting of fine cave dust, calcite and limestone pebbles and rocks, and a small amount of organic matter; 2, areas with a strong packrat influence having a very high organic content with much organic debris of both plant (seeds, bark, twigs, cactus spines) and animal (*Neotoma* fecal pellets, bones, insect parts, etc.) matter; 3, the lower caverns area with very fine, highly organic dust and conglomerate (dust-clay-rocks); and 4, outside (epigean) substrate (Table 3).

DISCUSSION AND RESULTS

Upon completion of this study, all traps were removed. No disturbance was found by man, animals, or weather to any of the traps or their contents. No decay was noted in any specimens. A total of 1,873 Coleoptera were trapped during

this study, 1,266 of these inside Mitchell Caverns (Table 4). Of these, 57 species of Coleoptera were identified, 30 from the caverns (Table 5). At least four of these species are new to science.

Compared to epigean (outside) ecosystems, cave ecosystems are very simplified and limited. Three main factors influence the fauna found in caves. These are temperature, humidity, and light. The deeper a burrow extends down from the surface, the less diurnal temperature fluctuation and less variation in relative humidity will be present at the bottom, although a great range in both temperatures and humidities may be encountered when moving from the surface to the bottom of a burrow (Hadley, 1970). Aside from the total absence of light, excepting near entrances, caves are usually characterized by relatively constant humidities and temperatures which correspond to the yearly mean of the area (Barr, 1968).

Table 5. Numbers of Coleoptera Species Trapped

Trap #	S-1	S-2	S-3	S-4	Total S1-S4
1	(8)	(8)	(6)	(11)	(18)
2	4	(5)	(3)	(10)	(13)
3	(3)	(5)	2	4	(7)
4	(3)	2	3	1	(7)
5	(2)	5	1	1	(5)
6	3	2	3	1	4
7	1	1	1	0	2
8	0	1	1	0	2
9	(4)	4	2	3	(7)
10	(9)	4	2	4	(12)
11	7	8	3	3	13
12	9	(4)	3	(6)	(14)
13		8	4	13	16
14		7	9	8	18
15		14	13	15	24
16		15	6	9	21
17		8	4	13	19
18		15	10	14	22
Total	(19)	(27)	(26)	(38)	(53)
El Pakiva main cave	(14)	(13)	(10)	(16)	27 *
El Pakiva lower cave	3	2	3	1	4
Tecopa	(14)	10	7	(8)	23 *
Total in caves	(19)	(19)	(14)	(18)	37 *
Total outside		27	17	31	37

Note: Since the two species of *Ptomophagus* (Leiodidae) and the three species of Aleocharinae (Staphylinidae) were grouped as one species during the survey, traps containing these species or totals reflecting these species are marked in parentheses (). Totals marked with an asterisk * correctly reflect the number of species.

During the period of this study, readings were taken of the temperature and humidity of Mitchell Caverns. Wisehart (1979) measured the temperatures and humidities at six different points within the caverns on a weekly basis during the period from October 3, 1978, to April 18, 1979 (Fig. 3). The relatively level interior of Mitchell Caverns along with

Table 4. Numbers of Coleoptera Specimens Trapped

Trap #	S-1	S-2	S-3	S-4	Total S1-S4
1	23	29	11	55	118
2	7	18	9	27	61
3	9	9	2	8	28
4	7	5	32	20	64
5	40	71	1	1	113
6	20	49	24	39	132
7	3	1	1	0	5
8	0	2	1	0	3
9	37	4	4	14	59
10	437	52	2	38	529
11	65	24	10	12	111
12	11	8	3	21	43
13		32	14	67	113
14		34	23	15	72
15		63	41	58	162
16		48	13	14	75
17		25	7	23	55
18		55	19	56	130
Total	659	529	217	468	1873
El Pakiva main cave	86	132	55	111	384
El Pakiva lower cave	26	52	26	39	143
Tecopa	550	88	19	85	742
Total in caves	659	272	100	235	1266
Total outside		257	117	233	607

the man-made tunnel connecting the two caves allowed a free air passage within the caverns. For this reason the air in Mitchell Caverns were found to be fairly dynamic, the temperatures varying within 10 degrees centigrade and the relative humidity varying 58%. Readings taken at the deepest area (near the tunnel: station #3, Fig. 2) indicated only a 5 degree temperature range and 34% relative humidity variation. Periods of rainfall were found to increase the relative humidity within the caverns.

Without the presence of light energy, cave ecosystems are almost entirely dependent for survival on the transfer of organic food energy from the outside (Barr, 1968). Mitchell Caverns does have a system of electric lights which run the length of the caverns. This system, which is used only during tours, does sporadically attract a few flying forms, such as moths and flies, from the outside to the inside lights.

Most available food energy enters desert caves by way of rodents, bats, and occasionally birds. Since food is a limiting factor in caves, most species found in caves are euryphagous, adaptable to a wide range of food. Other forms are carnivorous, fungus feeders or detritivores. By far the most food energy in Mitchell Caverns comes in with desert packrats or wood rats (*Neotoma lepida*). These bring in organic materials, such as twigs, cacti, grass, leaves, etc., collected outside and brought into their nests. These materials in turn slowly decay, thus providing substrates for fungi and molds to grow during periods of increased humidity. Packrats and other rodents, such as mice, also leave fecal pellets, which are found sometimes in great numbers in the caverns. This dung also provides food for a number of insects. Rodents also bring in associated commensal fauna, pholeophiles, which include a number of species well adapted for living in caves, as they often live in

Table 6. Account of Coleoptera of Mitchell Caverns: Total

Trap #	1	2	3	4	5	6	7	8	9	10	11	12	T
Carabidae													
sp-1	1			1	3								5
sp-2											1	1	2
sp-3	1	2	3		1					1	2		10
sp-4				2		1				3	6	1	12
Cicindelidae													
sp-1		1											1
Cleridae													
sp-1	3								2	2		1	8
Cryptophagidae													
sp-1	1	3									1	1	6
sp-2	16									1			17
Elateridae													
sp-1												1	1
Histeridae													
sp-1	1	1	3						3	3	6	4	19
sp-2	4												4
Lathridiidae													
sp-1		6	2								1	3	12
sp-2	2	1		3					48	463	50	9	575
sp-3		1										1	2
Leiodidae													
sps-1&2	42	31	7	3					3	1	2	8	97
Melyridae													
sp-1	1												1
sp-2	1										10	3	14
Ptinidae													
sp-1	1	1	5	53	105	123	2	2					292
sp-2	3	1							3	2		1	8
Staphylinidae													
sp-1	8	7								1	1		17
sp-2	2												2
sp-3-5	25	2	6	1	3					2	28	8	75
Tenebrionidae													
sp-1			1		1	4	3	2	1	50	2		64
sp-2	6	4				4				2	1		17
sp-3				1						1			2
sp-4	1												1
Trogidae													
sp-1												1	1

underground rodent burrows and nests. Bats, which were at one time common in Mitchell Caverns, are now uncommon. Their associated guano, which supports a number of cave forms in other caves, is relatively unimportant in Mitchell Caverns, as most guano found in the caverns is hard and dry.

The classification of cave animals used in this study was adapted from Barr (1968). These major categories include: I, Cavernicoles (animals living in caves); II, Accidentals (epigean species not morphologically suited for cave environments which stray into caves but usually do not survive for long periods); and III, Epigean (outside species not found in caves). Among cavernicoles the following categories are recognized: A, Obligate Cavernicoles or Trogllobites which are species unable to survive except in caves or similar underground habitats. These are usually known only from caves and exhibit morphological and physiological adaptations such as reductions of eyes, slender body appendages, development of pubescence including hypertrophy of femoral and elytral setae and loss of normal pigmentation for life in caves. B, Facultative Cavernicoles include both Troglaphiles (species which live, reproduce, and complete their entire life cycles within caves although they may be found outside of caves in dark, sheltered microenvironments and do not exhibit the same degree of evolutionary modifications as trogllobites) and Troglloxenes (species which commonly occur in caves but return to the surface for at least part of their life cycle). Troglloxenes usually are more common on the outside and include common epigean species for the most part. Troglloxenes are further divided into Habitual and Occasional or Threshold Troglloxenes. Other characteristics usually associated with cave organisms include delayed reproduction, increased longevity, smaller number of total eggs produced by females, and larger eggs (Culver, 1982).

A survey of cave animals strongly suggests that the presence of Trogllobites in caves is not the result of purely random events. Troglaphiles seem preadapted to living in caves, usually being found in moss, leaf litter, soil, mammal burrows or underground nests, under decaying logs, rocks, or similar dark microhabitats. It is now in general agreement among biospeleologists (Barr, 1968, Mitchell, 1969, and others) that many trogllobites are "relict" populations of previous troglaphiles which became in some way isolated in caves usually during warmer weather cycles as interglacial periods. These surviving populations, in caves after many years of isolation, develop morphological and physiological adaptations which restrict them to a cave existence.

ACCOUNT OF COLEOPTERA TRAPPED, WITH BIOLOGICAL NOTATIONS

(Refer to Tables 5 & 6)

Abbreviations used: S1-S4 (series 1 through 4); #, in-

dicates trap number; (x), indicates classification status; [sp. #] indicates species number used in tables.

CANTHARIDAE

One cantharid was taken from S4-#14. (Epigean). Phytophagous.

CARABIDAE

Carabids are commonly found under logs, stones, leaves, bark, debris or on the ground. Most species are nocturnal and many are predaceous on insect eggs, immatures or, adults. There are more known trogllobites in the Carabidae than in any other family of Coleoptera. Most occur widely in Europe, Eastern United States and Asia. As may be suspected, there are also a number of carabid Troglaphiles and Troglloxenes.

Rhadine sp. [Det. Barr, personal communication] (Troglaphile) [sp. #1]. Most common in moist situations under rotting logs, rocks, in mammal burrows and in caves, this genus contains a number of known trogllobitic and troglaphilic species (Barr, 1960). These seem to be preadapted to a cave existence characterized not only by their habits, but morphologically having elongate appendages and an absence of pigmentation normally found in related carabids. One trogllobitic *Rhadine*, *R. subterranea* Van Dyke, feeds predominantly on eggs of cave crickets in the genus *Ceuthophilus* (Barr, 1968), a genus found commonly in both caves of Mitchell Caverns. Although only a few specimens of *Rhadine* were captured during the survey (8), out of these, 63% were found in the caverns and in El Pakiva only. The outside specimens were trapped during winter S3-#14, (15 & 16) which suggests that perhaps these emerge to the outside during more moist cool conditions.

Anisodactylus sp. (Epigean). Only 1 specimen captured, outside of the caverns: S2-#16. A species of this genus is known to occur in caves in eastern United States as a Troglloxene (Barr, 1964).

Calosoma sp. (Epigean). This large species feeds mostly on Lepidoptera larvae. The single specimen was found in S3-#15.

Cymindis arizonensis Schaeff. [Det. Barr] (Occasional Troglloxene) [sp. #2]. Out of the 54 specimens trapped, only two were found in Tecopa cave S2, all others being from outside traps S2-(31), S3-(20) and S4-(1), which seems to indicate a strong fall/winter occurrence.

Pterostichus (Hypherpes) new species, related to *P. algidus* LeConte [Det. Barr] (Habitual Troglloxene) [sp. #3]. This genus is known to occur in caves as troglloxenes or accidentals. Twenty-seven percent (10) of the specimens trapped were found in the caverns as well as 16% (6) from trap #13 at the entrance to El Pakiva. This species was more abundantly trapped in El Pakiva. Out of the 57% (21) trapped outside the caverns, most were from S2 & S3.

Pterostichus (Hyperpes) congestus Men. [Det. Barr] (Habitual Trogloxene) [sp. #4]. Only 15% of this species were found in the caverns and more abundantly in Tecopa. This was also one of the few species trapped in the lower caverns of El Pakiva. The large size and high mobility of this species perhaps accounts for this.

CHRYSOMELIDAE

Brachycoryna hardyi Van Dyke. (Epigeal). S3-#14.

Crepidodera sp. (Epigeal). S2-#18, S3-#14 & 18, and S4-#17 & 18.

Glyptina sp. (Epigeal). S3-#16.

Longitarsus mancus LeConte (Epigeal). S3-#16.

CICINDELIDAE

Amblycheila schwartzi Horn (Habitual Trogloxene). This uncommon species is known only from a few localities in the Mojave Desert, usually in very rocky, moist situations. Like all cicindelids, it is a predator feeding on a number of insect larvae. A single specimen was trapped in S1-#2 in El Pakiva, although another specimen, not part of this study, was collected under a rock near a spring area near the main visitor center.

CLERIDAE

Members of this family are mainly carnivorous, both as larvae and adults, although there are some scavengers. *Cymatodera latefascia* Schaeffer, (Troglophile) [sp. #1]. One hundred percent of this species were found in both caves of the caverns, in S1 & S2.

Lecontella gnara Wollcott (Epigeal), found in S2-#16.

CRYPTOPHAGIDAE

Members of this genus feed on microfungi and are often found in an assortment of environments where molds develop, as in litter of nests of mammals and birds.

Cryptophagus near *politus* Casey, (Occasional Trogloxene) [sp. #1] Only 6% (6) were from the caverns and mainly near entrances.

Cryptophagus near *fumidulus* Casey, (Occasional Trogloxene) [sp. #2]. Although 32% of this species were trapped in the caverns, all were from traps near the entrances.

CURCULIONIDAE

Eucyllus vagans Horn (Epigeal). One specimen from S2-#18.

Macrophysus sp. (Epigeal). S2-#16, S3-#18.

DACODERIDAE

Dacoderus striaticeps LeConte (Epigeal) S2-#15, S4-#14.

DERMESTIDAE

Trogoderma sp. (Epigeal) Members of the genus

Trogoderma are mostly predators although some are scavengers. None of these were trapped in the caverns. S4-#14, 16, & 17.

ELATERIDAE

Although most elaterids are foliage feeders, some are predaceous.

Estesopus mitis (Horn), (Accidental). Found in trap #12 near an entrance and outside: S2, S3, & S4.

HISTERIDAE

Geomysaprinus (Priscosaprinus) n. sp.? [det. D. Verity] (Troglophile) [sp. #1]. This genus contains many undescribed species (D. Verity, personal communication). Most of these breed in animal burrows and are rarely found elsewhere. Some come to dung and carrion. They are not known from packrat nests. Over 82% (19) were found in the caverns, mostly in Tecopa. Only 3 specimens were trapped outside in S2-#16, S4-#15 & 17.

?*Hister* sp. (Epigeal). These are commonly found in dung. S4-#18.

Saprinus discoidalis LeConte (Occasional Trogloxene) [sp. #2]. This common epigeal species is widespread in deserts of North America. It is usually found on carrion. Twenty-five percent (4) of these were trapped in the caverns (S1, S2-#1), 11 from trap #13, and only 1 from an outside trap.

LATHRIDIIDAE

Lathridiids live on ground litter where they feed on microfungi, slime molds, or decomposing plant material. *Akalyptoischion* n. sp. (det. Andrews), (Habitual Trogloxene) [sp. #1]. The immature stages and food preference of this genus are not known. They are associated with litter and probably feed on microfungi. Thirty-nine percent were found in the caverns, mostly in El Pakiva.

Metopthalmus rudis Andrews (Troglophile) [sp. #2]. Little is known about the life history of these beetles as well, but they probably feed on spores and hyphae of microfungi. This species is mainly found in California. It was the most abundant beetle trapped during the survey: 99% + (575) of these beetles were found commonly in the caverns, with 463 of these found in only 1 trap (#10) in Tecopa and mainly in S1.

Metopthalmus trux Fall (Epigeal). This species also is mainly from California but ranges east to Texas. Only 1 specimen was trapped from S2-#18.

Microgramme n. sp. (det. Andrews) (Occasional Trogloxene) [sp. #3]. Only 2 specimens of this new species were trapped both from the caverns near the entrances in S3 & S4.

LEIODIDAE

Leiodids are mainly scavengers found on decaying organic matter such as humus, carrion, dung, and fungi.

Out of 36 known species of *Ptomophagus* in the subgenus (*Adelops*), 16 are cave specialized troglobites (Peck, 1973). This subgenus contains species specialized to five ecological habitats: forest litter, animal burrows and nests, soil, troglaphiles, and troglobites (Peck, 1973). Forty-seven percent (97) of these were found in the caverns with an additional 27% (56) found in entrance trap #13. Out of the specimens trapped in the caverns, most were found not too far from the entrances in the packrat areas. Two species were identified from the cave but the species composition was not determined. These are probably pholeophilic.

Ptomophagus (Adelops) fesus Horn [Det. S. Peck] (Troglophile) [sp. #1]. Not common in caves but around animal burrows in xeric areas.

Ptomophagus (Adelops) californicus (LeConte) [Det. S. Peck] (Troglophile) [sp. #2]. A more mesic species also found in rodent burrows including *Neotoma* nests and in caves in central California.

MELANDRYIDAE

Members of the family are phytophagous and usually found in dry wood or under bark.

Anapsis sp. (Epigeon). Only 2 specimens were trapped from S2-#13 & 16.

MELYRIDAE

Melyrids consist of both scavengers and carnivores.

Attalusinus submarginatus LeConte (Occasional Trogloxene) [sp. #1]. Although 93% (15) of this species were found in the cave all specimens were from traps near the entrances S3-#11, S4-#1, #11.

Collops sp. (Accidental) [sp. #2]. One specimen was trapped near the entrance to El Pakiva in S1-#1. Species of Dasytinae (Epigeon) S4-#17. Species of Malachiinae (Epigeon). One specimen was trapped from S4-#17.

PTINIDAE

Both the larvae and adults of these beetles feed on dried plant and animal substances.

Niptus n. sp. [det. Aalbu & Andrews] (Troglobite) [sp. #1]. One hundred percent (293) of this new species was found in the caverns, only in El Pakiva. This is also one of the few species to be found in numbers deep in the lower caverns of El Pakiva (only 1 specimen was found near an entrance S4-#13). *Niptus* was slightly more abundantly trapped in the fall but present in large numbers throughout the year. The biology of this species is discussed in Aalbu and Andrews (in review).

Ptinus clavipes Panzer (Habitual Trogloxene) [sp. #2]. This species has a wide geographical range. It is known to feed on dried vegetable matter and animal substances. One hundred percent (8) of these beetles were found in the caverns equally from both caves. Most were found near the entrances.

SALPINGIDAE

Cononotus sericans LeConte, (Epigeon). One specimen was trapped from S4-#16.

SCARABAEIDAE

Onthophagus velutinus Horn (Pholeophile, Habitual Trogloxene). This scarab, which is believed to feed exclusively on packrat dung, was found abundantly in the outside traps, especially near *Neotoma* nests in S2, S3, & S4. These specimens are the first of this species recorded from California. Previous records are from *Neotoma* nests in Texas.

STAPHYLINIDAE

Staphilinids are known to frequent caves. They are usually associated with decaying materials, particularly dung, carrion, or fungi. They are known to occur under stones and in animal nests. Most species are predaceous both as adults and larvae, feeding on arachnids and larvae of Diptera and other Coleoptera. Some feed on minute insects.

Sunius ?mollis (Casey) or new species near [Det. A. F. Newton] (Troglophile) [sp. #1]. This member of the tribe Paederini is usually found under bark, stones or near water. Almost 90% (17) of these were found in the caverns, mainly in El Pakiva. All the others were found in trap #13 at El Pakiva entrance.

Hapalaraea (Dropephylla) cacti (Schwarz) [Det. M. K. Thayer] (Accidental) [sp. #2]. Only two specimens were found in El Pakiva S2 & S4-#1 near an entrance. 3 species of Aleocharinae (Troglophiles). [Det. A. F. Newton] [sp. #3, 4, & 5]. The Aleocharinae contains a large group of staphilinid beetles which are poorly understood. Some are parasitic on fly puparia and some on mammals. Others are adapted for living in soil litter or decaying vegetable matter. Some are found in mammal burrows and nests. Eighty-three percent (75) of these were found in the caverns almost equally in El Pakiva and Tecopa. Only 5% of these were trapped in outside traps. Species composition was not determined.

Pseudopsis minuta Fall [Det. A. F. Newton] (Epigeon). One specimen from S4-#18.

Tachyporus sp. (Epigeon). Two specimens from S4-#17.

TENEBRIONIDAE

Tenebrionids have extremely varied feeding habits feeding on almost any organic matter. Most are found under bark, logs, stone, or walking about on the ground usually at night. A number are known troglobites and many are troglaphiles and troglaxenes.

Anepsius delicatulus LeConte (Epigeon) A total of 8 specimens were trapped; 2 from S2-#16 & 18 and 6 from S4-#16, 17 & 18.

Anchomma costatum LeConte (Epigeon) This rather rare species of Stenosini is known from leaf litter, usually of oak. One specimen was found in S4-#15.

Argoporis bicolor LeConte (Epigeal) Three specimens were trapped in S4-#15, 17 & 18.

Cerenopus concolor LeConte (Epigeal) One specimen of this widespread desert species was found in S2-#15.

Eleodes californicus Blaisdell, Mitchell Caverns Population. (Troglophile) [sp. #1]. This species, known from rocky areas of the Mojave Desert and the northern part of the Colorado Desert is usually uncommon. This subgenus (*Metablapyllis*) is very closely related to the subgenus (*Caverneleodes*) which contains cave modified species having slender, elongate antennae and legs (Triplehorn, 1975). This species was found in both caves although more abundantly in Tecopa. Ninety-two percent (64) of this species were found in the caverns, only 6 specimens being trapped on the outside. It was one of the few species trapped in the lower caverns, 13% (9) being trapped there.

Helops attenuatus LeConte (Epigeal). One specimen was trapped in S2-#16.

Schizillus laticeps Horn (Epigeal). This species is known from rocky areas of the Mojave Desert. Of the 5 specimens trapped during this survey (S4-#15 & 18), one specimen was found near one of the cave entrances, none was found inside the caverns. Others were found near the park visitor center.

Schizillus nunenmacheri Blaisdell (Troglophile) [sp. #2]. *S. nunenmacheri* clearly exhibits a high degree of evolutionary modification associated with cave organisms. It differs from the preceding species, *S. laticeps*, by being more slender, by the elytra being less sculptured, and by having a much more slender antennae (the third segment being more than twice as long as in *S. laticeps*), longer legs, long adult and larval life, smaller number of total eggs produced by females, and larger eggs, all evolutionary characteristics associated with cave beetles (Aalbu, in manuscript). *Schizillus nunenmacheri* is quite rare in collections. The type specimen was found near Goldfield, Nevada, but no other ecological data was given. One hundred percent of this locally abundant species was found in Mitchell Caverns or in entrance trap #13. Although trapped in both caves, it was more abundant in El Pakiva. Not only was it one of the few species to be trapped in the deep lower cavern, but many larvae of this species were found living in the deepest pit of the caverns, near trap #8. These may feed on the highly organic cave dust and debris of the area. *Schizillus nunenmacheri* also seems to be associated with packrats (*Neotoma* spp.) and has been trapped just outside of packrat nests in other rocky areas.

Stibia imperialis Blaisdell (Occasional Trogloxene) [sp. #3]. Only 2 specimens of this species were trapped, both in the caverns; one in S2-#10 of Tecopa and one in trap S3-#13 of El Pakiva. This genus is not known to inhabit caves.

Typhlusechus chemehuevii Aalbu & Andrews (Endogean-Pholeophile-Troglophile) [sp. #4]. This recently described species of a rare, small, soil dwelling genus is closely associated with packrats, living in their nests and only com-

Table 7. The Cavernicolous Coleoptera of Mitchell Caverns

	TROGLOBITES
PTINIDAE	<i>Niptus</i> n. sp.
	TROGLOPHILES
CARABIDAE	<i>Rhadine</i> sp.
CLERIDAE	<i>Cymatodera latefascia</i> Schaeffer
HISTERIDAE	<i>Geomysaprinus</i> (<i>Priscosaprinus</i>) sp.
LEIODIDAE	<i>Ptomophagus</i> (<i>Adelops</i>) <i>fisus</i> Horn
	<i>Ptomophagus</i> (<i>Adelops</i>) <i>californicus</i> (LeConte)
LATHRIDIIDAE	<i>Metopthalmus rudis</i> Andrews
STAPHYLINIDAE	<i>Aleocharinae</i> 3 sp.
	<i>Sunius ?mollis</i> (Casey)
TENEBRIONIDAE	<i>Eleodes californicus</i> Blaisdell
	<i>Schizillus nunenmacheri</i> Blaisdell
	<i>Typhlusechus chemehuevii</i> Aalbu & Andrews
	HABITUAL TROGLOXENES
CARABIDAE	<i>Pterostichus</i> n. sp.
	<i>Pterostichus</i> (<i>Hyperpes</i>) <i>congestus</i> Mene.
CICINDELIDAE	<i>Amblycheila schwartzi</i> Horn
LATHRIDIIDAE	<i>Akalypsoischiom</i> n. sp.
PTINIDAE	<i>Ptinus clavipes</i> Panzer
SCARABAEIDAE	<i>Onthophagus velutinus</i> Horn
	OCCASIONAL TROGLOXENES
CARABIDAE	<i>Cymindis arizonensis</i> Schaeffer
MELYRIDAE	<i>Attalusinus submarginatus</i> LeConte
CRYPTOPHAGIDAE	<i>Cryptopphagus</i> near <i>politus</i> Casey
	<i>Cryptopphagus</i> near <i>fumidulus</i> Casey
LATHRIDIIDAE	<i>Microgramme</i> n. sp.
HISTERIDAE	<i>Saprinus discoidalis</i> LeConte
TENEBRIONIDAE	<i>Stibia imperialis</i> Blaisdell
	ACCIDENTALS
ELATERIDAE	<i>Estesopus mitis</i> (Horn)
MELYRIDAE	<i>Collops</i> sp.
STAPHYLINIDAE	<i>Hapalaraea</i> (<i>Dropephylla</i>) <i>cacti</i> (Schwartz)
TROGIDAE	<i>Trox punctatus</i> Germar

ing out at night. Eighty percent of the specimens were collected in two traps: S4-13 located in the cave along a packrat runway along a wall near a nest and S2-15 located outside against a stone cliff with a packrat burrow entrance hole approximately a foot above the trap. Others were found in S2-#1 in El Pakiva and outside in S2-18 and S4-17 near packrat nests. For additional information see Aalbu & Andrews (1985).

TROGIDAE

Trox punctatus Germar (Accidental). This species is associated with dry animal carcasses where it feeds on the hide and dry tissues. Only one specimen was trapped, in S1-#12 near an entrance.

SUMMARY

Twenty-three species of cavernicolous Coleoptera were found to inhabit Mitchell Caverns. These included 1 Troglobite, 13 Troglophiles, 6 Habitual Trogloxenes and 7 Occasional Trogloxenes. Four species of non-cavernicolous Coleoptera were found as accidentals wandering into the caverns (Table 7). El Pakiva maintained the greater amount

of cavernicolous species with 1 Troglobite, 12 Troglophiles, 5 Habitual Troglloxenes and 6 Occasional Troglloxenes. Only 1 Troglobite, 2 Troglophiles and 1 Habitual Troglloxene were found to inhabit the lower caverns of El Pakiva. This is perhaps a function of the relative isolation of the lower caverns, receiving a much lesser regular amount of organic food energy from the outside.

Although the tunnel connecting the two caves was completed in 1970, some species of cavernicolous Coleoptera seem to remain concentrated or even completely restricted to one cave, even after 9 years. *Niptus* n. sp. is a prime example, being found abundantly in both the main section and the lower caverns of El Pakiva but absent in Tecopa.

The seasonal abundance and variation of the cavernicolous Coleoptera seem to be less accentuated than in the epigeal populations. The mean number of species of Coleoptera found in Mitchell Caverns for each trapping season was 17, with a seasonal range of 6. This compares to an outside mean of 25 species with a seasonal range of 14, although there seems to be a general decline in the number of species and specimens trapped in series 3 (winter series) in both the cavernicolous and epigeal populations.

Due to their larger size and visibility (black against the lighter limestone), *Schizillus nunenmacheri* and *Eleodes californica* were the most commonly encountered beetles in the caverns. They were found throughout the caverns walking on the ground, on the slick dripstone walls, or on stalactites. A number of these were actually found hanging upside down from the tips of stalactites in the deeper areas of the caves. This is perhaps a method for getting water droplets during drier periods.

Four factors were found to influence the cavernicolous fauna trapped in Mitchell Caverns: (1), the distance the traps were placed from an outside entrance, which relates to the amount of available organic food energy; (2), the substrate type in the vicinity of the trap; (3), the amount of water activity in the caves, which varies somewhat with seasonal rainstorms; and (4), the subdued influence of the seasons, bringing into the caverns the associated troglloxene and accidental fauna.

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Jones, State Geologist of Alabama and director of the Alabama Museum of Natural History. He pioneered the systematic study of Alabama caves and initiated and sponsored the sampling and study of their invertebrates.

GEOLOGY AND PHYSIOGRAPHY

An introduction to the regional geology and geomorphology can be found in King (1977) and Thornbury (1965). Since the distributions of caves and some cave animals are controlled by regional geology, it is necessary to present a summary of the geology of Alabama. Details can be found in the volume of Alabama geology by Adams et al. (1926) and on physiography by Johnston (1930). The best overview has been presented by Veitch (1967) and a summary from this rare work is presented as follows. The physiographic divisions of northern Alabama are shown in Figure 1.

Physiography

A geological and geographical view of Alabama extends back 500 million years, to the Paleozoic seas of a great trough called the Appalachian Geosyncline. Intermittently, for 300 million years, the deposits to become the Appalachians formed beneath its shallow, shifting seas. Gradually, at the end of the Paleozoic Era, the sea was destroyed by lateral compressions that lifted, folded, and faulted its deposits, raising mountains that persisted until the end of the Mesozoic Era when Cretaceous seas again prevailed over parts of their eroded roots. Then, probably beginning in late Cretaceous times, when the area to become Alabama was a low plain with rivers meandering across flat and folded sedimentary and metamorphic rocks alike, the land was again arched upward. The seas receded slowly southward and erosion began shaping the topography of today.

The Coastal Plains (Fig. 1) are composed of flat-lying sedimentary rocks which lie unconformably on the eroded Paleozoic rocks of the Appalachian Highlands. Their northern boundary is the Fall Line of the Atlantic states which runs through Alabama from Columbus, Georgia, west to Tuscaloosa, and then northward to the northwest corner of the state. The northernmost of these rocks are Upper Cretaceous. Lying unconformably upon them are Cenozoic rocks. Together they cover over half the state, forming a rolling, hilly upland, often with incised stream valleys. They are a succession of sandstones, limestones, shales, and marls, often thin-bedded, sometimes poorly consolidated. Caves are few, scattered, and small.

North of the Coastal Plains in east-central Alabama are the Piedmont Uplands; a triangular area with Columbus, Georgia; and Clanton and Cleburne Counties at its corners. It is a stream-cut upland of caveless Precambrian metamorphic and igneous rocks whose general structure reaches

along the seaward flank of the Appalachians into Pennsylvania.

Above the Piedmont Uplands is the Valley and Ridge Province, a highly folded and faulted area of Paleozoic rocks running through and south of Birmingham, and reaching northward along the western flank of the Appalachians into Pennsylvania. Its disrupted strata form hills and valleys running northeastward: the Weisner Ridges, Coosa Valley, Coosa Ridges, Cahaba Valley, Cahaba Ridges, and the Birmingham-Big Canoe Valley. In the south, around Birmingham, their relief is about 500 ft (150 m); to the north it approaches 1000 ft (300 m). Its rocks are Paleozoic limestones, dolomites, sandstones, and shales, sometimes metamorphosed. Caves are generally few and scattered, but may be large.

The Cumberland Plateau, north of the Valley and Ridge Province, is a part of the Appalachian Plateaus that reach north to the St. Lawrence River, and in which so many eastern American caves are found. In Alabama, the Cumberland Plateau forms a rough inverted triangle with Tuscaloosa at its apex and its base along the Tennessee-Alabama state line. The southeastern side of the Cumberland Plateau is composed of folded Paleozoic rocks forming synclinal plateaus and anticlinal valleys running southwest. The Sequatchie Valley, which contains the Tennessee River northeast of Guntersville, is the first of these; to the southeast, in order, are Sand Mountain, Wills Valley, and Lookout Mountain. In the north the mountains dominate the landscape; to the south they diminish and finally disappear to the northeast of Birmingham. Caves occur in the sides and floors of the valleys.

The remaining parts of the Cumberland Plateau are composed of flat-lying Mississippian and Pennsylvanian rocks that dip gently southward and pass beneath the rocks of the Coastal Plains. They form four physical districts, three of which contain well over half of Alabama's caves: the Jackson County Mountains, the Warrior Basin, and Little Mountain. The remaining district, the Moulton Valley, between Little Mountain and the Warrior Basin, is too low to contain caves. The Jackson County Mountains lie east of Huntsville and north of the Tennessee River. They are the edge of the Cumberland Plateau itself, stream cut, and sandstone capped. Streams running down to the Tennessee River have cut deeply into the original plateau surface, forming a maximum relief of 1000 ft (300 m) in the steep-sided valleys to the north. Along the Tennessee River the valleys are wider and the original surface cut into monadnocks such as Monte Sano. These isolated portions are given mountain names such as Keel Mountain or Green Mountain. Little Mountain (locally better known as Brindley Mountain) is developed by the resistant Hartselle Sandstone where it is exposed south of the Tennessee River westward from Morgan County. Its northern edge forms a scarp over-

looking the Tennessee River and its surface is a rolling upland cut by streams, which slopes southward to pass under the limestone of the Moulton Valley. Along its northern flanks there are many incised sink valleys with many caves, such as the well-known Newsome Sinks. The Warrior Basin is a dissected plateau with a prominent scarp as its northern boundary, its surface developed in the same Pottsville Formation that caps the Jackson County Mountains. It overlooks the Tennessee River between Gunterville and US-231, then falls back from the river, passing between Falkville and Cullman, and reaches westward toward the state of Mississippi.

The Highland Rim portion of the Interior Low Plateaus is best developed in Tennessee, but extends into and across northwestern Alabama. It is a rolling upland with a total relief of about 400 ft (120 m), at an average elevation of about 600 ft (180 m). North of the Tennessee River several south-flowing streams occupy entrenched meanders with cliff-like walls, and limestone cliffs as high as 200 ft (65 m) border the river. Both north and south of the Tennessee River the underlying Tusculumbia (= Warsaw) Limestone contains many springs, sinks, and caves.

Geology of the Cumberland Plateau

The flat-lying rocks of the Cumberland Plateau bear more detailed mention because they contain most Alabama caves. They are a succession of Mississippian and Pennsylvanian limestones, sandstones, and shales, with limestone predominating. The topography is controlled by their southward slope of about 50 feet per mile and by their relative resistance to erosion. The plateau-like tops of the Jackson County Mountains, Sand and Lookout Mountains, and the steep, north-facing scarp of the Warrior Basin are the result of the resistant Pottsville sandstones. Where the cap has been destroyed by erosion, as in the river valley west of Huntsville and from Morgan County westward, the land is lower and there is less relief. A formation of lower resistance, the Hartselle Sandstone, has formed a second, north-facing scarp. These two formations, easily identifiable both by being sandstone and by their unmistakable physical features, serve as markers for a general identification of the cave-bearing limestones beneath them.

The first (lowest) horizontal formation to crop out over a wide area is the Ft. Payne Chert, a generally dark, shaley and sandy limestone that weathers to crinoidal chert. It is exposed over much of the area east of Huntsville and north of the Tennessee River, as well as in the areas of disturbed strata where it forms conspicuous ridges. Above the Ft. Payne chert is a succession of limestones totalling over 1000 ft (300 m) in thickness. In the western part of the state they are interspaced with several local sandstones and often contain shaley or sandy members. The most prominent of these is the Hartselle Sandstone which extends eastward past Huntsville. These grade out eastward, however, and east of

Keel Mountain (Huntsville) these formations are almost entirely limestone. The lower formation of these is the Tusculumbia Limestone—more properly differentiated as the Warsaw and St. Louis Limestones—which lies unconformably upon the Ft. Payne. It is a light, thick-bedded, coarse-grained, and fossiliferous limestone. It forms most of the Tennessee River valley west of Huntsville and the lower slopes and valleys of the Jackson County Mountains.

Unconformably upon the Tusculumbia is the St. Genevieve Limestone, thick-bedded, dark to light grey, and oolitic. Its oolitic nature is a visual differentiation between it and the underlying St. Louis. It crops out on the slopes of Little Mountain and on the lower-middle slopes of the Jackson County Mountains. On Monte Sano it is 75 ft (23 m) thick, its bottom 200 ft (61 m) above the valley floor; it is 75 to 100 ft (23 to 30 m) thick in the Jackson County Mountains, thinner to the west. Above the St. Genevieve is the Gasper Formation, a thick-bedded, light grey, usually oolitic limestone that is visually similar to the St. Genevieve. It crops out on the middle slopes of the Jackson County Mountains and on the upper slopes of Little Mountain where it underlies the Hartselle Sandstone. The St. Genevieve and Gasper are now often combined as the Monteagle Limestone. The Hartselle Sandstone above the Gasper is generally thick-bedded and well cemented. It is about 200 ft (61 m) thick in the western part of the state, thins to about 10 ft (3 m) on Monte Sano, and disappears east of Keel Mountain. In Morgan County it is about 50 to 100 ft (15 to 30 m) thick.

Above the Hartselle, or the Gasper where the Hartselle is absent, is the Bangor Limestone. It is a dark blue, thick-bedded, oolitic, very thick limestone that forms the upper slopes of the Jackson County Mountains, where it is about 400 ft (122 m) thick; the upper slopes of Sand and Lookout Mountains, where it is up to 700 ft (213 m) thick; and the lower and middle slopes of the Warrior Basin scarp, where it is about 500 ft (152 m) thick. The floor of Newsome Sinks is formed in the Bangor and the pits of Jackson County descend through it. Above the Bangor is the Pennington Formation, a shaley limestone 50 to 200 ft (15–61 m) thick, often interbedded, and identified, by red shale members. Upon the Pennington, forming the plateau-like surfaces of the Jackson County Mountains, Sand and Lookout Mountains, and the Warrior Basin, is the resistant Pottsville Formation, a succession of thin-bedded sandstones and shales, often interbedded with coal members.

These same formations also occur in the northern parts of the Valley and Ridge Province, though most of that area is composed of older Paleozoic rocks. Where they are found they are tilted, folded, and faulted and usually of small and interrupted extent. Sand and Lookout Mountains have the same sequence of rocks but on their margins in the Sequatchie, Wills, and Shinbone Valleys there are older rocks in the exposed roots of anticlinal folds.

The effects of geology and geography on the distributions

of cave organisms will be presented in part III of this series.

Caves

Over 2000 caves are now known in Alabama. Most of them are in Madison, Morgan and Jackson Counties, in the northeastern corner of the state. Their location is controlled by geology. Counties in which caves have been studied for invertebrates are shown in Figure 2. Data on cave locations and descriptions can be found in Jones and Varnedoe (1968, 1980), Varnedoe (1973, 1975, 1981) Veitch (1967), and the



Figure 2. Counties in Alabama from which terrestrial cave invertebrates are known. Abbreviations are the first letters for the following counties; Blount, Calhoun, Clarke, Colbert, Conecuh, DeKalb, Franklin, Jackson, Jefferson, Lauderdale, Lawrence, Limestone, Madison, Marshall, Morgan, Shelby, St. Clair, and Talladega.

publications of the Huntsville Grotto. Cave origins in the Cumberland Plateau of Alabama have been discussed by Wilson (1977). Anyone interested in studying these caves should contact the Huntsville Grotto or the National Speleological Society, Cave Avenue, Huntsville, Alabama 35810.

Information on caves in adjacent states can be found in Knight et al. (1974) for Mississippi, and Barr (1961) and Mathews (1971) for Tennessee.

CAVE FAUNAS

One of the most fascinating aspects of cave faunas is their evolutionary adaptation to life in rigorous subterranean environments. General background information on the evolution and ecology of cave animals can be found in Barr (1968), Barr and Holsinger (1985), Culver (1982), Holsinger (1988), and Howarth (1983).

Regional cave faunal surveys have been made for much of the southeastern United States. Examples are: Florida (Peck 1970), Georgia (Holsinger and Peck, 1971), and Tennessee and Virginia (Holsinger and Culver, 1988). The present report is a contribution to an understanding of the cave invertebrates of Alabama, at the junction of the southern Appalachians and the Gulf Coastal Plain.

History of Alabama Cave Biology

The rich fauna of the southern Appalachians has long been recognized by biologists. The habitat offered by the caves of the region is no exception. The recognition of the richness of Alabama cave fauna goes back to what has been called the "early period" of American cave biology by Barr (1966), when Cope and Packard (1881) published descriptions of a new crayfish, amphipod, isopod, and cricket from Nickajack Cave, in Marion County, Tennessee, and Jackson County, Alabama. They pointed out that the fauna seemed to indicate membership in a different faunal region from that of Mammoth Cave, in Kentucky.

No other studies of Alabama cave faunas appeared until the initiation of the work on cave carabid beetles by J. Manson Valentine in the "middle period" of American biospeleology (Barr, 1966). He and Walter B. Jones, then State Geologist of Alabama and Director of the Alabama Museum of Natural History, initiated the first broad collecting program of the cave faunas of Alabama and other states. Their collections provided material for numerous specialists who have contributed to the knowledge of the systematics of Alabama cave faunas.

In 1965 John Cooper organized the project "Biological Survey of Alabama Caves" which attempted to involve local cavers in helping to collect the fauna (Cooper and Cooper, 1966). Some of the records presented here were made by these people.

Dr. Jones discontinued active collecting of cave fauna in

1955 when the number of known Alabama caves stood at 170. Since then William W. Varnedoe and other members of the Huntsville Grotto of the National Speleological Society have coordinated the cataloging of Alabama cave locations and descriptions, as the Alabama Cave Survey.

The literature on the cave fauna of Alabama is scattered. To ease the task of later students who need a complete bibliography of the fauna, I have included all appropriate references. This list will serve as a starting point for future studies on the identification and distribution of the cave fauna.

It should be noted that the Alabama House of Representatives and Senate passed a cave conservation law in 1988. In addition to other protection measures, it makes illegal the collecting, killing, or harming of cave life, except for recognized scientific purposes (Churchill and Moss, 1988).

Field Study

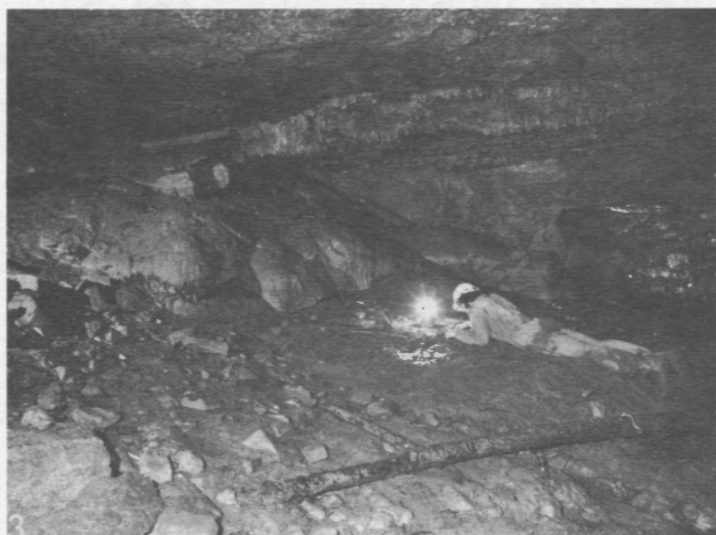
Collecting efforts in Alabama caves have been as extensive and as intensive as possible. In addition to direct visual searching I have used Tullgren funnel extraction of arthropods from organic debris and have extensively used dung and carrion baits.

Since 1963, I have devoted some 50 weeks of full-time field work to Alabama cave faunas. A total of 543 research visits have been made to 213 caves in 14 Alabama counties. Collecting by others brings the total to about 250 caves that have received some biological study. Faunas of the dark zone of the caves received emphasis. Entrance and twilight zone faunas are under-represented in this study as are cave litter and soil faunas and parietal (wall-inhabiting) faunas.

The latter have been emphasized in studies of cave faunas in other areas (Peck, 1988; Peck and Christiansen, 1989).

ANNOTATED FAUNAL LIST

Cave-inhabiting animals usually fall into one of the four ecological-evolutionary categories commonly used in cave biology (Barr, 1968). (1) *Troglobites* are obligatory cave species which are morphologically specialized for, and restricted to, cave habitats, and are unable to live in non-cave habitats. (2) *Troglophiles* are facultative cave species, which frequently inhabit caves and complete their entire life cycles there, but many occupy ecologically similar (cool, moist, and dark) habitats outside of caves. (3) *Trogloxenes* are species which often occur in caves but are incapable of completing their entire life cycle in caves. They must at some time leave the cave, usually for feeding purposes. (4) *Accidentals* are species which accidentally wash, wander, or fall into caves and can exist there only temporarily. Although these may serve as food sources for regular cave inhabitants, the accidentals are of no importance in distribution or evolutionary analysis of cave fauna. I have listed most species judged to be accidentals (but excluded obvious herbivores such as leaf hoppers), even though this category could potentially, through time, come to embrace much of the fauna in the area containing the cave. In many cases, it is still too early to judge the relative degree of cave association of many species. I think it better to include the species than to lose the information. By so doing, patterns of cave association that are not yet apparent may emerge through the compilation of additional data (as was found for cantharid beetle larvae, Peck, 1975b), and the category to which the species is assigned may be changed.



Figures 3 and 4. Invertebrate habitats in caves in Madison County, Alabama. (3) Barclay Cave. Invertebrates are concentrated on organic debris and under rocks on a silt terrace

above the seasonally flooded end of the cave. (4) Cold Spring Cave. Invertebrates occur on rotting wood at the base of the entrance slope of this small cave.

The ecological term *endogean* or *edaphobite* may also be used for cave animals. These are species that normally live in soil, such as earthworms, and their occurrence in caves is usually sporadic.

Many of the species found in the following list are still inadequately known in their distribution outside Alabama and in their ecology; their assignment to one of the above ecological-evolutionary categories should be considered tentative and subject to readjustment when additional information is available. The following abbreviations, placed after the organisms' names, have been employed: TB = troglobite; TP = troglophile; TX = troglaxene; ED = edaphobite; AC = accidental.

Some of the taxa found in this list are still poorly known and, therefore, could not be determined to species. Other forms, such as millipedes, are not being studied and specific names are not available. Still other material represents undescribed species, for which names and descriptions have not been published. Because of these reasons, this list should be regarded as subject to later refinement. However, considering the number of sites sampled, the data given in this list are believed to form a nearly complete picture of the invertebrate fauna of the caves of the region.

Because of space limitations, we do not give supporting data for species records presented here, such as date of collection, collector's name or collection containing the specimens. Records not found in the references listed for each species should generally be assumed to be new records made by me or provided by the specialists acknowledged at the end of the paper. Unpublished records made by other collectors are followed by the initials of the collector. These initialed collectors are listed in the acknowledgements.

Published cave names that do not agree with present usage are placed in parentheses following the currently accepted cave names. Sometimes, there is more than one cave in a county with the same name. When this occurs, the Alabama cave survey number (e.g., AL 60) is used to indicate the identity of the cave.

Where species names and names of higher taxa do not correspond to those given in some of the older literature, it is because we have used names based on more recent revisional studies. Where more recent studies have shown older literature locality records to be based on inaccurate identifications, I have not listed the erroneous localities.

The higher taxa have been listed in generally accepted phylogenetic sequence. Genera within families, and species within genera have been listed in alphabetical order. Localities are listed alphabetically by county within the state, and by cave within the county.

Counties are useful geographical units under which caves can be grouped. They may or may not have natural physiographic boundaries that relate to cave faunas. The Alabama counties mentioned in the following faunal listing are shown in Figure 2. Some new records are given for poorly known

invertebrates in adjacent states, to help document their distributions.

Notes on some cave localities.

Two caves listed below have been destroyed. Town Creek Cave (AL 40) has been flooded, and Toll Gate Natural Well (AL 61) has been filled in.

Nickajack Cave has its sole entrance in Tennessee, but it extends under Jackson County, Alabama, so has been included as an Alabama cave site. The entrance passage is now flooded by a TVA impoundment, but the terminal rooms, in Alabama, should be above the water level.

Early collections by Walter B. Jones were made in the following caves which can no longer be identified or located; Spring AL 31; Terrill AL 32, Kelly Natural Well AL 49, Ingram AL 70, Clemons AL 73, Wolf Den AL 83, Dickey AL 84, Spring AL 85, Pack Rat AL 89 caves.

Phylum Annelida
Class Oligochaeta
Order Opisthopora

Family Lumbricidae

Allolobophora trapezoides (Duges), ED. Dekalb County; Cherokee Cave. This species is European in origin. It has been recorded from caves in Arkansas, Kentucky, Tennessee, and West Virginia (Gates, 1959).

Bimastos tumidus (Eisen), ED. Colbert County; McKinney Pit. Dekalb County; Cherokee Cave. Madison County; Shelta Cave. This is an endemic American species. It has been recorded from caves in Virginia and Tennessee (Gates, 1959).

Dendrobaena rubida (Savigny), ED. Calhoun County; Weaver Cave. Dekalb County; Manitou Cave. Jackson County; Salt River Cave. This species is European in origin. It is known from many caves in Europe and the United States (Gates, 1959).

Octolasion tyrtaeus (Savigny), ED. Dekalb County; Cherokee and Section 26 Caves.

Family Megascolecidae

Diplocardia caroliniana Eisen, ED. Marshall County; Cathedral Caverns. These are very abundant worms in the silt banks along the cave stream (Gates, 1959).

Pheretima diffringens (Baird), ED. Blount County; Bangor Cave. Calhoun County; Weaver Cave. This species is Asiatic in origin (Gates, 1959).

Family Sparganophilidae

Sparganophilus sp., ED. Calhoun County. Weaver Cave. Material unidentifiable to either family or genus. Blount County; Bangor Cave (5 juveniles). Conecuh County; Sanders Cave (2 juveniles). Dekalb County; Sequoyah Caverns. Jackson County; Jess Elliott (10 juveniles) and

Salt River Caves (9 juveniles). Morgan County; Cave Spring Cave.

Phylum Mollusca
Class Gastropoda

Land snails can often be found in the cool and moist twilight zone of caves, where they may feed on dead organic matter, or rasp films of algae and other plants from moist rock surfaces. Hubricht (1985) has given an overview of the distribution of all native eastern species of land snails. In an attempt to determine which species can maintain themselves in the dark of caves, collections reported here are only from the dark zone. Dead shells are often washed into the dark zone.

Order Archeogastropoda

Family Helicinidae

Helicina orbiculata (Say), AC. Jefferson County; Cedar Pole Cave (immature, dead). This species is widespread in the southeastern United States, but is otherwise recorded from caves only in Texas (Reddell, 1965).

Order Stylommatophora

Family Carychiidae

Carychium exile (H.C. Lea), AC. Marshall County; Cathedral Caverns (dead) and Guffey Cave. The species is widespread in the southeastern United States. It is reported from caves in Kentucky and Tennessee (Hubricht, 1964, 1965).

Carychium mexicanum Pilsbry (= *C. floridanum* Clapp), AC. Clarke County; Cave 2 mi SE of Gainstown (L. Hubricht). A widespread southeastern species.

Family Endodontidae

Discus patulus (Deshayes), TP. Blount County; Bangor Cave (L. Hubricht). Jackson County; Indian Rocks Cave. Lauderdale County; Collier Cave (dead). Madison County; Aladdin Cave. This is a wide ranging southeastern species (Archer, 1941c, Hubricht, 1960; 1964).

Helicodiscus barri Hubricht, TB. Colbert County; Georgetown (immature) and McKinney Caves. Lauderdale County; Collier Cave. Madison County; Byrd Spring and Shelta Caves. The species is known only from the dark zone of caves, where it often feeds on guano. It is also reported from caves in Tennessee and Georgia (Hubricht, 1962, 1964, 1985).

Helicodiscus fimbriatus (Wetherby), AC. Jackson County; House of Happiness Cave. Madison County; Burwell Cave (dead).

Helicodiscus hadenoecus Hubricht, TP. Madison County; Aladdin and (Chapman Mountain) Cave Spring (AL 60)

Caves. This species is known from caves in Kentucky and Tennessee, from cricket guano, but is also found in soil and deep in rock slides. (Hubricht, 1962, 1964, 1985).

Helicodiscus inermis H. B. Baker. TP. Clarke County; Cave 2 mi SE Gainstown (L. Hubricht). Conecuh County; Sanders Cave. Dekalb County; Kelly Girls and Lykes Caves. Jackson County; Guess Creek, Indian Rocks, Rainbow, Russell, and Williams Saltpeter Caves. Madison County; Shelta Cave. Morgan County; Royer Cave. This is a wideranging southeastern species, in many habitats, and is also recorded from caves in Tennessee and Virginia (Holsinger and Culver, 1988; Hubricht, 1964, 1985).

Helicodiscus notius notius Hubricht, TP. Blount County; Bangor and Bryant Caves. Dekalb County; Bartlett Cave (dead). This is a wide-ranging southeastern subspecies, also recorded from a cave in Tennessee and Kentucky (Hubricht, 1962, 1964, 1965, 1985).

Family Polygyridae

Mesodon appressus (Say), TP, Figure 5. Marshall County; Merrill (immature) and Painted Bluff Caves. The species ranges from Virginia to Indiana and south to northern Alabama. It is recorded from caves in Tennessee, Virginia and Kentucky (Hubricht, 1964).

Mesodon inflectus (Say), AC? Madison County; Shelta Cave. The species ranges widely in the southeast, and is known from 50 counties in Alabama, but is recorded from caves only by this record and two from Kentucky (Hubricht, 1964).

Mesodon perigraptus (Pilsby), AC. Blount County; Horseshoe Crump Cave. Jackson County; Cornelison Cave.

Mesodon sargentianus (Johnson and Pilsby), TP. Jack-

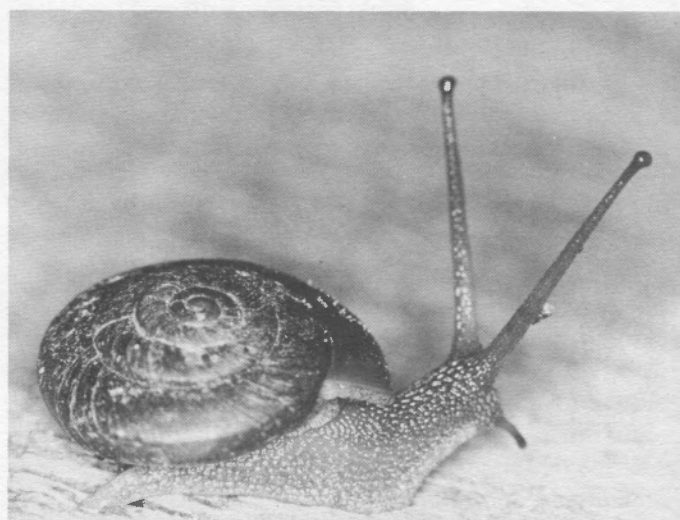


Figure 5. The troglophilic snail *Mesodon appressus*. Its eyes are at the tips of its tentacles. Most snails in Alabama caves live in the twilight zone.

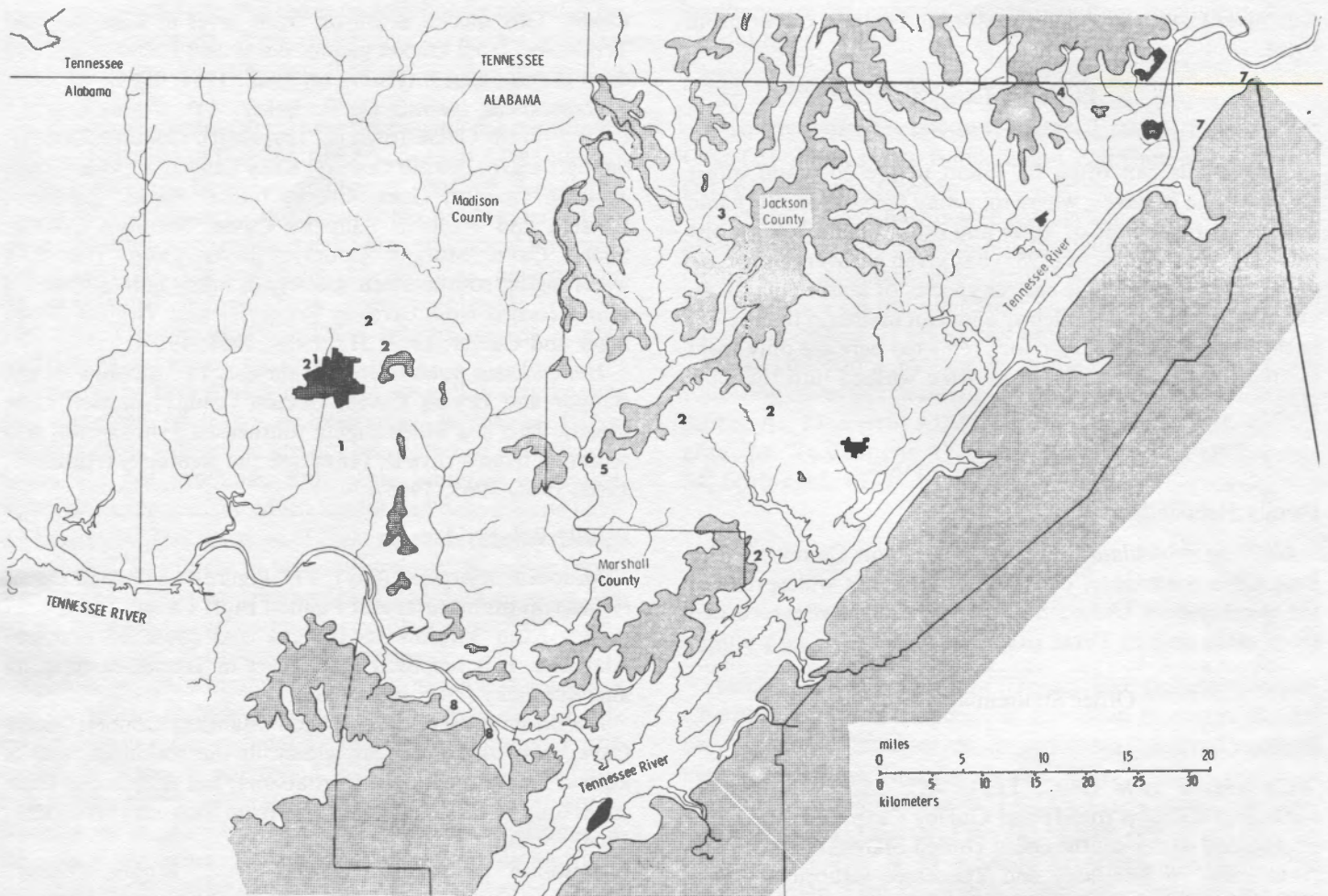


Figure 6. Distribution of some troglobitic invertebrates in northeastern Alabama. Stippling represents the Pottsville sandstone remnants of the cap rock of the Cumberland Plateau, locally called the Jackson County Mountains. Caves do not exist under this cap rock. Consequently, these plateau remnants, as well as the large rivers and streams and their alluviated valleys, represent barriers to subterranean

terrestrial dispersal. One and two are the land snails (1). *Helicodiscus barri* and (2). *Glyphyalina specus*. (3). is a terrestrial isopod, *Miktoniscus* sp. 4-8 are pseudoscorpions (4). *Apochthonius russelli*, (5). *Lissocreagris eurydice*, (6). *Lissocreagris mortis*, (7). *Lissocreagris nickajackensis*, (8). *Alabamocreagris pecki*.

son County; Crossing, House of Happiness, Nat, Mink (Out) entrance of Gross-Skeleton, Sheldons (immature) and Pig Pen Caves. Madison County; Aladdin (immature), Hurricane, Jacks and Scott Caves. The species occurs only in Jackson and Madison counties, Alabama (Hubricht, 1985).

Polygyra fatigitata (Say), AC. Lauderdale County; Collier Cave (dead). This is the only Alabama record for the species, otherwise known only from Indiana, Kentucky and Tennessee (Hubricht, 1985).

Stenotrema spinosum (Lea), AC. Lauderdale County; Key Cave (J.E. Cooper).

Stenotrema turbinella (Clench and Archer), AC. Dekalb County; Manitou Cave. The species occurs only in northern Alabama and adjacent parts of Tennessee and Georgia (Hubricht, 1985).

Family Zonitidae

Gastrodonta interna (Say), AC. Madison County; Aladdin Cave. Shelby County; Anderson Cave. This is a wide-ranging southern species, known to occur in over 30 Alabama counties (Hubricht, 1985).

Glyphyalina cryptomphila (Clapp), TP? Blount County; Bangor Cave. This is a widespread species, sometimes found in caves (Hubricht, 1985).

Glyphyalina indentata (Say), TP. Calhoun County; Dauge Cave No. 1. Colbert County; McKinney Pit (dead). Conecuh County; Sanders Cave. Dekalb County; Cherokee and Talley Caves. Jackson County; Cornelison Cave. Lauderdale County; Collier Cave (dead). Madison County; Barclay, Burwell (dead) and Hurricane Caves. The

species is widely distributed in the southeastern states, and occurs in almost every county in Alabama.

Glyphylinia pecki Hubricht, TB. Jefferson County; Cedar Pole and Crystal (McClunney) Caves. The species is known only from these caves (Hubricht, 1966, 1985).

Glyphyalinia latebricola Hubricht, TP. Jackson County; Doug Green and Swaim Caves. This species is otherwise known only from under rocks on Burwell Mountain, near Jeff, Madison County (Hubricht, 1968, 1985).

Glyphyalinia sculptilis (Bland), AC. Shelby County; Anderson Cave.

Glyphyalinia specus Hubricht, TB? Jackson County; Hall, Mink (Out) entrance of Gross-Skeleton Cave, and Schiffman Caves. Madison County; (Chapman Mountain) Cave Spring (AL 60), Cold Spring, and Shelta Caves. The species is known only from the dark zones of caves, but over a wide range in Tennessee, Kentucky and West Virginia (Hubricht, 1985).

Ventridens gularis (Say), AC. Madison County; Burwell Cave (dead). The species ranges widely in the southeast, and is known from over 30 Alabama counties (Hubricht, 1965, 1985).

Zonitoides arboreus (Say), TP. Blount County; Bangor Cave. Conecuh County; Sanders Cave (dead). Jackson County; Cross, Indian Rocks, and Hall Caves. Madison County; Aladdin and Shelta Caves. Marshall County; Cave Mountain Cave. Morgan County; Royer Cave (dead). St. Clair County; McGlendon Cave. The species is widespread throughout the United States. It is known from caves in Kentucky, Tennessee, Texas, and Virginia and I report it here from Bat Cave, Alachua County, Florida (Archer, 1941c, Hubricht, 1964, 1965, 1985; Reddell, 1965).

Phylum Arthropoda
Class Crustacea
Order Isopoda

Cave-inhabiting terrestrial isopods of North America are reviewed by Schultz (1981). Most are litter or soil inhabiting species that are scavengers in moist caves; only a few are troglobites. Troglobitic *Amerigoniscus* are known from Georgia and Tennessee, and so might be expected in Alabama (Vandel, 1977).

Family Porcellionidae

Porcelio laevis Latreille, TP. Jackson County; Nickajack Cave. The species is introduced from Europe, and is widespread in North America. It usually occurs in drier areas in cave habitats (Vandel, 1950).

Family Cylisticidae

Cylisticus convexus (DeGeer), TP. Limestone County; Rockhouse Cave. Marshall County; Painted Bluff Cave. The species is introduced from Europe, and is widespread. It

is known from caves in Georgia, Indiana, Kentucky, Tennessee, Texas, and Virginia (Schultz, 1970).

Family Ligidae

Ligidium elrodii (Packard), TP. Marshall County; Green Bar Cave. This widespread forest litter species seems to have differentiated into local subspecies populations in caves in Virginia, Tennessee, and Georgia (Schultz, 1970). It is probably more frequently found in caves rather than forests at lower elevations and in more southern parts of its range.

Family Trichoniscidae

Miktoniscus medcofi Van Name (= *M. alabamensis* Muchmore), TP. Jackson County; Hall, Moody, Schiffman Cove, and Two Way Caves. Madison County; Shelta Cave. Marshall County; Guffey and Steves Caves. This eyed and pigmented species is widespread in the eastern United States, from Florida to Ohio. It occurs in caves over much of its range (Muchmore, 1964; Schultz, 1976; Vandel, 1965) and more frequently in caves than in forests at lower elevations and the more southern parts of its range.

Miktoniscus morganesis Schultz, TP. Morgan County; Cave Spring Cave (type locality). The species is reported only from this cave (Schultz, 1976).

Miktoniscus sp, TB? Marshall County; Buds Cave. This seemingly undescribed species is eyeless and without pigment. Additional specimens are needed.

Class Arachnida
Order Scorpiones

Family Vejovidae

Vejovis carolinianus (Beauvois), AC. Jackson County; Sheldons Cave (in a dry crawlway).

Order Pseudoscorpiones

Cave-inhabiting pseudoscorpions of North America are reviewed by Muchmore (1981). About 150 species (30% of the North American fauna) have been found in cave habitats. Many more species of these secretive and hard-to-find predators remain to be discovered.

Family Chernetidae

Hesperochnes cf. *mirabilis* (Banks), TP. Blount County; Catfish and Horse Caves. Colbert County; McCluskey and McKinney Caves. Dekalb County; Cherokee and Dunham Caves. Jackson County; Bucks Pocket, Doug Green, Pig Pen, Swaim Caves, and Two Way. Jefferson County; Cedar Pole and Crystal Caverns Cave. Lauderdale County; Basket, Colliers, Slough, Bone, and Key Caves. Madison County; Burwell (Burnett), Hurricane, and Spook Caves. Marshall County; Cave Mountain, Dunham, Merrill, Painted Bluff, Steves, and Warrenton Caves. Members

of this genus are most often found in Alabama caves in association with bat guano and raccoon dung, and in decaying debris in pack rat nests (Muchmore, 1974).

Family Chthoniidae

Aphrastochthonius tenax Chamberlin, TB. Blount County; Bangor (type locality) and Catfish Caves. The genus is not closely related to any other in the family, and may be a distributional relict. Other than for Alabama species, the genus is known to contain 10 species living in caves or hypogean situations in New Mexico, California, Cuba, Mexico and Guatemala (Chamberlin and Malcolm, 1960; Chamberlin, 1962; Muchmore, 1972, 1984, 1986).

Aphrastochthonius pecki Muchmore. TB. Jefferson County; Crystal Caverns (type locality). Known only from this cave (Muchmore, 1968).

Apochthonius russelli Muchmore, TB. Jackson County; Russell Cave (Pig entrance) (type locality). The genus contains many undescribed species and is widespread throughout much of the United States. It occurs commonly in forest litter. Troglobitic species occur in California, Oregon, West Virginia, Virginia, Indiana, Missouri, Ohio (unpubl.) and Arkansas (Benedict, 1979; Benedict and Malcolm, 1973; Muchmore, 1976, 1980).

Apochthonius spp., TP. Colbert County; McKinney Cave. Jackson County; Paint Rock and Reece Caves. Madison County; Burwell, Ellis, Hutton (WBJ), and Spook Caves. Morgan County; Vandever Cave. St. Claire County; McGlendon Cave. This is undetermined material (Muchmore, 1976).

Chthonius tetrachelatus (Preysler), TP? Lawrence County; Saltpeter Cave (WBJ). Limestone County; Rockhouse Spring Cave. Marshall County; Painted Bluff Cave. The species is widely distributed in the eastern United States but has not been previously reported from Alabama (Hoff, 1958).

Kleptochthonius multispinosus Hoff, AC. Marshall County; Griffiths Cave. The species is widespread in the southeastern states and has previously been found in Alabama forests (Hoff, 1958; Malcolm and Chamberlin, 1961).

Kleptochthonius sp., TP? Jackson County; McFarland Cave. Madison County; Spook Cave. St. Claire County; McGlendon Cave. Many cave restricted species of this genus occur in Tennessee, Kentucky, Virginia, and West Virginia (Muchmore, 1965).

Tyrannochthonius spp., TB, TP. Blount County; Bangor and Ingram Caves. Jackson County; Cave Stand entrance of Gary Self Pit, Crossings, Driftwood, Fern, House of Happiness, Jess Elliott, Indian Rocks, Mink (Out) entrance of Gross-Skeleton, Paint Rock, Reese, Salt River, and Two Way Caves. Madison County; Aladdin, Barclay, Burwell, Byrd, Spring, Cave Spring (AL 60), Big (Huntsville) Spring,

Matthews, Shelta, Sinks, Twin, and Varnedoe (RG) Caves. Marshall County; Cave Mountain, Eudy, Gamble, Guffey, Honeycomb, Line Point, and Keller Caves. Some 11 species and subspecies remain to be described from Alabama Caves (Chamberlin and Malcolm, 1960). The only named species of this genus in the United States is *T. floridensis* from forests in Florida and Alabama (Muchmore, 1985).

Family Neobisiidae

Trisetobisium fallax (Chamberlin), TP. Colbert County; Gist Cave (type locality). Lawrence County; Thomas Cave. The species is also known from a forest in North Carolina (Chamberlin, 1962; Curcic, 1982).

Lissocreagris eurydice (Muchmore), TB. Jackson County; Kenamer Cave (type locality). Known only from this cave. Troglobites are those listed here and species in Nevada, California, Oregon, Washington, and Texas (Muchmore, 1969). The species listed here in this family were formerly in the genus *Microcreagris* and have been placed in this or other newly formed genera (Curcic, 1984).

Lissocreagris mortis (Muchmore), TB. Jackson County; Fern Cave (the Morgue entrance) (type locality). Known only from this cave (Muchmore, 1969).

Lissocreagris nickajackensis (Muchmore), TB. Jackson County; Nickajack and Horseshull Caves (type locality). Known only from these caves, the first now flooded by a TVA impoundment (Muchmore, 1966, 1969).

Lissocreagris persephone (Chamberlin), TP? Marshall County; Davidson (type locality), Driftwood, Gamble, and Keller Caves (Chamberlin, 1962; Curcic, 1984; Muchmore, 1969).

Lissocreagris pluto (Chamberlin), TP? Marshall County; Terrell Cave (type locality). Known only from this cave (Chamberlin, 1962; Curcic, 1984).

Lissocreagris pumila (Muchmore), TP? Blount County; Bryant Cave (type locality). The species is also known from litter in Blount County and a cave in Chatooga County, Georgia (Muchmore, 1969).

Lissocreagris subatlantica (Chamberlin), TP? Colbert County; Dickey and Spring (type locality) Caves. Morgan County; Anvil Cave. The species is also known from litter in Shelby and Blount Counties, and from a cave in Georgia (Chamberlin, 1962; Curcic, 1984; Muchmore, 1969).

Lissocreagris sp., TP? Blount County; Catfish Cave. Marshall County; Hampton (Hampden), Kellers, and Old Blowing Caves. Undetermined material.

Alabamocreagris pecki (Muchmore), TB. Marshall County; Beech Spring and Old Blowing Caves (type locality). Known only from these caves (Curcic, 1984; Muchmore, 1969).

Novobisium ingratum (Chamberlin), TP? Jackson County; McFarland Cave (type locality). The species is also known from an epigean locality in Putnam County, Tennessee (Chamberlin, 1962; Curcic, 1984; Muchmore, 1967).

Order Araneae

Family Agelenidae

Calymmaria cavicola (Banks), TP. Blount County; Bangor and Randolph Caves. Colbert County; Gist, Little Bear, McCluskey, and Wolf Den Caves. Jackson County; Engle Double Pit (McFarlen Blowing entrance), Roadside, Gary Self Pit (Rousseau entrance), and Tony Caves. Lauderdale County; Bat Cave. Madison County; Aladdin, Cave Spring (AL 60), Herrin, Kelly Natural Well, Moon, Natural Well, Scott, and Toll Gate Natural Well Caves. Marshall County; Honeycomb, Honeycomb School, and Town Creek Caves. Morgan County; San Souci Cave. The species is widely distributed in the Appalachian region, both in and out of caves.

Cicurina brevifaria Bishop and Crosby, TP? Jackson County; Copper as (= Pack Rat) Cave (WBJ). The species is recorded from Tennessee caves (Barr, 1961).

Cicurina minima Chamberlin and Ivie, TP. Calhoun County; Weaver Cave (Lady) (WBJ). Jefferson County; Pinson (Hickman) Cave (WBJ). Lawrence County; Thomas Cave (WBJ).

Cicurina sp., TP. Jefferson County; Cedar Pole Cave, and Crystal (McClunney) Cave. This species is eyeless and is undescribed.

Coras lamellosus Keyserling, TP? Marshall County; Town Creek Cave (WBJ).

Tegenaria domestica Clerck, TP. Blount County; Horseshoe-Crump Cave. Calhoun County; Meadows, and Weaver Caves. Jackson County; Sauta Cave (Barr and Reddell, 1967). Madison County; Candlestand (Goat) Cave. Though it has a predilection for dark sheltered places it is rarely found in caves.

Family Araneidae

Allepeira conferta (Hentz), AC. Colbert County; Georgetown Cave. This species is abundant in shaded gullies in central Alabama (Archer, 1941a).

Aranea cavatica (Keyserling), AC. Jackson County; (Honey [Clear] Creek) Saltpeter Cave (A 74). This species is also recorded as occurring in unspecified cave entrances on Monte Sano, Madison County (Archer, 1940a, 1940b).

Azilia vagepicta Simon, TP. Blount County; Cedar Grove River Cave. Colbert County; Wolf Den Cave. Jackson County; Small Cave. Marshall County; Merritt and Town Creek Caves. The species is also known in caves in Jackson County, Florida (Archer, 1940a, 1940b, 1941a; Peck, 1970).

Eustala anastera (Walckenaer), AC? Reported as occurring in caves and their entrances, but no locations are given for it (Archer, 1940b).

Leucauge venusta (Walckenaer), TP? Morgan County; Baz, Cave Spring and Trinity Caves. This is a widespread species recorded from caves and their entrances (Archer, 1940b).

Mangora placida Hentz, AC. New records. Morgan County; Cave Spring Cave (WBJ & AFA).

Meta menardi (Latreille), TP. Dekalb County; Sequoyah Cave. Jackson County; Gary Self Pit (Cave Stand entrance), Gross-Skeleton, Hambrick (WBJ), (Honey Creek) Saltpeter, Horseshoe, Pack Rat (WBJ), Rainbow, and Small Caves. Lawrence County; Thrasher (WBJ) and Thomas (WBJ) Caves. Limestone County; Rockhouse Cave. Madison County; Henson (WBJ), and Jett Sinkhole (WBJ) Caves. Marshall County; Bishop MacHardin and Merritt Caves. Morgan County; Houston (WBJ) and Power Line (WBJ) Caves. This species is widespread in the eastern United States, and often occurs in caves. It reaches its southern limit in northern Alabama (Archer, 1940a, 1940b; and Barr, 1961).

Neoscona benjamina (Walckenaer), AC. The species is mentioned as frequenting caves and their entrances, but no locations are cited (Archer, 1940b).

Tetragnatha versicolor Walckenaer, AC. Calhoun County; Weaver Cave. This species forms webs over streams at cave entrances (Archer, 1940b).

Theridiosoma radiosum (McCook), TP? Calhoun County; Weaver Cave. Colbert County; Gist Cave. Madison County; Hering Cave. Morgan County; Cave Spring Cave. The species is recorded as living in caves with permanent streams, and is recorded from Tennessee caves (Archer, 1940a, 1940b; Barr, 1961).

Wixia ectypa (Walckenaer), AC. This species is adventitious in cave entrances on Monte Sano, Madison County (Archer, 1940a, 1940b).

Family Clubionidae

Anahita punctulata (Hentz), TP? Colbert County; Gist Cave (WBJ & AFA), and Spring Cave (WBJ & AFA). Jackson County; Engle Double Pit (McFarlen Blowing entrance Cave (WBJ & AFA). Madison County; Kelly Natural Well (WBJ). Marshall County; Bishop Cave (WBJ & AFA). Morgan County; Bat (WBJ), and Trinity Caves (WBJ & AFA).

Anyphaena celer (Hentz), AC. Morgan County; Cave Spring Cave (WBJ & AFA).

Anyphaenella albens (Hentz), AC. Morgan County; Cave Spring Cave (WBJ & AFA).

Aysha gracilis (Hentz), AC. Morgan County; Cave Spring Cave (WBJ & AFA).

Chiracanthium inclusum (Hentz), DC. Marshall County; Honeycomb Cave (AFA).

Liocranoides unicolor Keyserling, TB? Blount County; Bangor (WBJ), Bryant, Cedar Grove River, Horseshoe-Crump, and Randolph Caves. Calhoun County; Weaver (Lady) Cave (WBJ & AFA). Colbert County; Dickey (WBJ & AFA), Georgetown, Gist (WBJ & AFA), McKinney (WBJ & AFA) Caves. Dekalb County; Cemetery, Manitou, Se-

quoyah, Stanley Carden, and Talley Caves. Jackson County; Clemons (WBJ & AFA), Cornelison No. 1, Crossings, Driftwood, Gamble, Geiger, Gross, House of Happiness, Indian Rocks, Jess Elliott, Keel (WBJ & AFA), Kyles, McFarland, Engle Double Pit (McFarland Blowing entrance), Nat, Out, Paint Rock, Pig Pen, Rousseau Salt River, Schiffman, Sauta, Sheldons, Talley Ditch, Tupelo, and Wynne Caves. Jefferson County; Crystal (McClunney) Cave. Madison County; Aladdin, Byrd Spring, Cave Spring AL60, Hurricane, Moring, Taploe, Toll Gate Natural Well (WBJ & AFA), Glover (Water) Caves. Limestone County; Rockhouse Cave. Marshall County; Cave Mountain, Davidson, Dunham, Gamble, Hambrick, Honeycomb School (AFA), Keelers, Line Point (WBJ), Painted Bluff, Steves, Walnut, and Warrenton (WBJ) Caves. Morgan County; Cave Spring, Horseback, and Talucah Caves. This large, pale hunting spider is also recorded from caves in Tennessee (Barr, 1961). It was described from Mammoth Cave, Kentucky.

Family Ctenidae

Ctenus hibernalis Hentz, AC. Marshall County; Painted Bluff Cave. Shelby County; Lous Crawl Cave.

Family Hypochilidae

Hypochilus thorelli Marx, AC. Jackson County; (Clear Creek) Saltpeter (AFA), McFarland (WBJ & AFA) Caves. Madison County; Clark Bluff, Hurricane, Moring Caves. Marshall County; Painted Bluff Cave. This very primitive spider is widely distributed in the southeast along the Cumberland Plateau from southern Kentucky and adjacent Virginia to northern Alabama. It makes its webs in shady and protected places and is also known from caves in Tennessee (Archer, 1940a; Barr, 1961; Forster et al., 1987).

Family Dictynidae

Dictyna florens Ivie and Barrows, AC. Morgan County; Cave Spring Cave (WBJ & AFA).

Family Leptonetidae

In this family of minute spiders, 44 species occur in North America, with 15 in the southeastern states, and 9 of these in caves (Gertsch, 1974). Many of the Alabama species are called troglophiles, but if cave-restricted and showing various stages of eye loss, they may be nascent troglobites. Searching in litter and talus slopes may reveal some of these species outside caves. The rich Alabama fauna suggests that more species remain to be discovered.

Leptoneta alabama Gertsch, TP. Calhoun County; Kilgore (near Weaver Station, unknown to Alabama Survey), Lady and Weaver Caves. Dekalb County; Cemetery Cave. Marshall County; Painted Bluff Cave (type locality). Known only from these caves (Gertsch, 1974).

Leptoneta jonesi Gertsch, TP. Jefferson County; Crystal (McClunney) Caverns (type locality). Known only from this cave (Gertsch, 1974).

Leptoneta serena Gertsch, TB. Lauderdale County; Collier Cave (type locality). Known only from this cave (Gertsch, 1974).

Leptoneta credula Gertsch, TP. Lauderdale County; Bat Cave (type locality). Known only from this cave (Gertsch, 1974).

Leptoneta blanda Gertsch, TP. Blount County; Ingram Cave (type locality). Known only from this cave (Gertsch, 1974).

Leptoneta barrowsi Gertsch, TP. Blount County; Bangor Cave (type locality). Known only from this cave (Gertsch, 1974).

Family Linyphiidae

Centromerus denticulatus (Emerton), TP. Jackson County; Crossings Cave. Marshall County; Bishop Cave. This is a wide-ranging species (Van Helsdingen, 1973) also known from caves in Georgia (Horseshoe Cave, Walker County) and Tennessee (Round Mountain Cave, Franklin County, and Quarry Cave, Bradley County).

Centromerus latidens (Emerton), TP. Blount County; Cedar Grove River Cave. Calhoun County; Weaver (Lady) Cave (WBJ & AFA). Jackson County; Paint Rock Cave. Limestone County; Indian Cave. Madison County; Barclay, Burwell, Hutton (WBJ), Jacks (WBJ), Matthews, Natural Well (WBJ), Sinks (TCB) Toll Gate Natural Well (WBJ) caves. Marshall County; Davidson, Griffith (WBJ), and Hampton caves. Morgan County; Horseback and Royer (WBJ) caves. Shelby County; Anderson Cave. Talladega County; DeSoto (Kymulga) Cave (WBJ & AFA). The species is also known from caves in Florida and Kentucky. It is widely distributed in eastern North America and is often found in forest litter (Van Helsdingen, 1973).

Centromerus cornupalpis (O.P.-Cambridge), AC. Blount County; Bangor Cave. This is a widespread species, rarely found in caves (Van Helsdingen, 1973), but records are known for caves in Tennessee.

Eperigone eschatologica Crosby, AC. Marshall County; Quarry Cave.

Eperigone maculata (Banks), AC. Jackson County; Tony Sinks (Cox) Cave (WBJ). Madison County; Barclay Cave.

Eperigone tridentata (Emerton), AC. Calhoun County; Weaver Cave (WBJ & AFA).

Islandiana muma Ivie, TP (or TB?). Colbert County; Wolf Den Cave. Lawrence County; Ivy Hollow Cave. This species is otherwise recorded only from one cave in Virginia (Ivie, 1965).

Lepthyphantes sabulosa (Keyserling), TP. Madison County; Jacks Cave (WBJ), Kelly Natural Well, Toll Gate Natural Well (WBJ & AFA) (Archer, 1940a).

Meioneta spp., AC. Conecuh County; Sanders Cave. Dekalb County; Stanley-Garden Cave. Two undescribed species are represented in this collection.

Phanetta subterranea (Emerton), TB. Colbert County; Georgetown, Keeton, McKinney and McKinney Pit Caves. Dekalb County; Lykes, Section 26, and Sequoyah Caves. Jackson County; Tony Sinks (Cox) (WBJ & AFA), (Honey [Clear] Creek) Saltpeter (WBJ & AFA), Horseshoe, Jess Elliott, Keel (WBJ & AFA), McFarland Engle Double Pit, (McFarlen Blowing entrance) (WBJ & AFA), Moody, Paint Rock, Sheldons, Swaim and Tate Caves. Jefferson County; Crystal (McClunney) Caverns. Lawrence County; Ivy Hollow Cave. Lauderdale County; Bat (WBJ), Collier, and Key Caves. Limestone County; Indian and Rockhouse Caves. Madison County; Hurricane, Scott and Shelta (WBJ) Caves. Marshall County; Beech Spring, Cathedral Caverns, Honeycomb (AFA), Line Point (WBJ) and Merrill Caves. Morgan County; Bat (WBJ), Cave Spring (WBJ), Horseback, Hughes and Talucah Caves. St. Clair County; McIendon Cave (WBJ). This species is widespread throughout the eastern United States. It is known only from cave habitats (Archer 1940a; Barr, 1961).

Porrhomma cavernicolum (Keyserling), TB. Limestone County; Spence Cave. The species is at the southern margin of its distribution in northern Alabama.

Taranucnus durdenae Ivie, AC. Jackson County; Rainbow Cave. Madison County; Green Grotto.

Tapinocyba sp., AC. Blount County; Catfish Cave.

Family Lycosidae

Arctosa sublata Montgomery, AC. Dekalb County; Talley Cave.

Pirata sp., AC. Blount County; Bangor Cave. Madison County; Barclay Cave.

Family Micryphantidae

Ceraticelus fissiceps (O.P. Cambridge), AC. Colbert County; Wolf Den Cave (WBJ & AFA). Morgan County; Cave Spring Cave (WBJ & AFA).

Origanates rostratus (Emerton), AC. Jackson County; McFarland Cave (WBJ & AFA).

Family Mimetidae

Mimetes notius Chamberlin, AC. This species is predatory on other species and wanders into cave entrances. Archer (1940a).

Mimetes puritanus Chamberlin, AC. This species is recorded from an overhanging ledge at the entrance of Cave Spring Cave, Morgan County (Archer, 1941b).

Family Nesticidae

Gaucelmus augustinus Keyserling, TP. Blount County; Dixon and Catfish Caves. Clarke County; Broadenax and

McVay Caves. Colbert County; Wolf Den Cave. Jefferson County; Crystal Caverns. Lawrence County; Ivey Hollow Cave. Marshall County; Line Point and Lower 4 Lane Caves. Morgan County; Lipscomb, and Lost Mule Caves. The species is distributed from Florida and the Gulf States, through Texas, to Mexico and Panama, and the West Indies. In the United States it is most often found in caves (Gertsch, 1984). Other members of the genus occur in Mexico, Central America, and the West Indies.

Eidmanella pallida (Emerton), TP. Blount County; Bangor and Bryant Caves. Calhoun County; Lady, Millers, and Weaver Caves. Conecuh County; Sanders Cave. Limestone County; Carruth Cave. Jackson County; Limrock Blowing Cave. Madison County; Byrd Spring, Matthews, and Shelta Caves. Marshall County: Line Point. Morgan County; Talucah Cave. The species is widespread in North America from Eastern Canada southward to Costa Rica. It has spread with commerce to Hawaii and Europe. It is frequently found in caves and has been listed under the generic name *Nesticus*.

Nesticus barri Gertsch, TB. Jackson County; Boxes, Cornellison, Driftwood, Fern, Gross-Skelton, Guess Creek, Hall, Upper Rainbow (Happy Hollow), Horseshull, Indian Rock, Isbell Spring, Jess Elliott, Kennamer, Kyle, Larkin, Limrock Blowing, Montague, Moody, Nickajack, Mink (Out) entrance of Gross-Skeleton, Pigpen, Rainbow, Ridley, Russell (Pig entrance), Salt River, Sheldons, Schiffman, Steele Saltpeter, Tally Ditch, Tate, Tumbling Rock, and Wynne Caves. Marshall County; Bishop, Cathedral (= Bat), Devils Dungeon, Guffey, Honeycomb, Kellers, Kristys, MacHardin, Porches Spring, Royal Shaft, and Quarry Caves. The species also occurs in caves in adjacent Franklin and Marion Counties, Tennessee (Gertsch, 1984). The Nickajack and Horseshull records are on the other side of the Tennessee River from all other records and should be reconfirmed. The record (Gertsch, 1984) from Tuckaleechee Caverns, Blount County, Tennessee, must be an error because troglobitic *Nesticus* do not have such a distribution. Currently, 14 species of cavernicolous *Nesticus* are known in the southern Appalachians, and another 10 are epigeal species. Others are likely to be found (Gertsch, 1984).

Nesticus jonesi Gertsch, TB. Morgan County; Cave Spring Cave (type locality). Known only from this cave (Gertsch, 1984).

Family Oxyopidae

Oxyopes salticus Hentz, AV. Morgan County; Bat (WBJ), Cave Spring (WBJ), and Trinity (WBJ) Caves.

Family Pholcidae

Pholcus sp., TP. Jackson County; Sheldons Cave. Marshall County; Dunham, Painted Bluff and Porches Spring Caves. This species is undescribed. Archer (1940a) reports

P. phalangioides from caves and their entrances "all over the state," and Barr (1961) records it from Tennessee caves.

Family Pisauridae

Dolomedes vittatus Walckenaer, AC. Marshall County; Line Point Cave (WBJ). Madison County; Cave Spring AL 60 (WBJ & AFA) and Scott Caves. Morgan County; Cave Spring Cave (WBJ & AFA). This fishing spider occasionally wanders along streams into caves.

Pisaurina micra Walckenaer, AC. Madison County; Kelly Natural Well (WBJ). Morgan County; Cave Spring Cave (WBJ & AFA).

Family Salticidae

Stoidis aurata (Hentz), AC. Talladega County; DeSoto (Kymulga) Caverns. (WBJ & AFA).

Family Symphytognathidae

Maymena ambita (Barrows), TP. Madison County; Aladdin, Cave Spring AL 60, and Jacks Caves. Marshall County; Line Point, Rockhouse, and Warrenton Caves. This species is recorded by Gertsch (1960) from a cave in Tennessee and caves in Kentucky, and in epigean sites in Tennessee and Alabama. This is disjunct, for the genus otherwise occurs in Mexico and the Caribbean.

Family Theridiidae

Achaearanea globosa (Hentz), AC. Madison County; Buford Cave. This species is a common and widespread species that occurs at cave entrances. Archer (1946) recorded it as *Hentziectypus globosus*.

Achaearanea porteri (Banks) TP. Blount County; Bangor Cave (WBJ). Calhoun County; Lady Cave. Colbert County; Dickey and Spring Caves. Jackson County; McFarland Cave. Lauderdale County; Key Cave. Madison County; Buford Cave. Jackson County; Sauta Cave (JMV; TCB). Lauderdale County; Collier Cave (WBJ). Limestone County; Rockhouse Cave. Marshall County; Hambrick Cave. Morgan County; Trinity Cave (AFA). This species is also known from other north Alabama localities that are not caves, but only sheltered areas. This species was listed by Archer (1946) as *Theridion redemptum* Gertsch and Muliak.

Achaearanea rupicola (Emerton), TP. Madison County; Buford Cave, Moore Cave. Marshall County; Honeycomb School Cave. Jackson County; Saltpeter Cave AL74 (AFA). This species occurs in numerous habitats in north Alabama, as well as caves and their entrances. Archer (1946) listed the species as *Theridion rupicola*.

Achaearanea tepidariorum (C. Koch), TP. Calhoun County; Weaver Cave (WBJ & AFA). Colbert County; Bridge Cave (WBJ). Lauderdale County; Gravelly Springs Cave (WBJ). Madison County; Candlestand (Goat), Keel and Scott Caves. Marshall County; Hambrick Cave. Morgan County; Cave Spring, Bat, Sans Souci, and Trinity

Caves. The species is statewide in distribution and is often associated with buildings as well as caves and their entrances. Archer (1940a, 1946) lists the species in the genus *Theridion*.

Argyrodes partita (Walckenaer), AC. Morgan County; Bat (WBJ), Cave Spring (WBJ), and Trinity Caves (WBJ). This species was listed by Archer (1940a) as *A. cancellatus*. It is recorded as living symbiotically in the webs of other spiders in cave entrances.

Argyrodes rufa (Walckenaer), AC. Morgan County; Cave Spring Cave. The species is statewide and occurs in many habitats, in addition to caves and their entrances. It lives in the webs of other spiders, and is listed as *A. trigonum* by Archer (1946).

Conopistha nephilae (Taczanowski), AC. Madison County; Caves on Monte Sano. This species is recorded from webs of *Aranea cavatica* at cave entrances. It is nearly statewide in distribution (Archer, 1946).

Paidisca marxi (Crosby), AC. Colbert County; Spring Cave. Jackson County; McFarland Blowing Cave. This is a widespread, but secretive species (Archer, 1946). It also occurs in Griers Cave, Randolph County, Georgia.

Theridion flavonotatum Becker, AC. Morgan County; Cave Spring Cave. A statewide species, it commonly occurs in forests (Archer, 1946).

Theridion glaucescens Becker, AC. Morgan County; Cave Spring Cave. This species is widespread in forests and within buildings (Archer, 1946).

Theridion kentuckyense Keyserling, AC. Colbert County; Wolf Den Cave (WBJ & AFA).

Theridion lyricum Walckenaer, AC. Colbert County; Wolf Den Cave. A statewide species, often associated with buildings (Archer, 1946).

Theridula opulenta (Walckenaer), AC. Morgan County; Cave Spring Cave. This species is widespread in the southern two-thirds of Alabama. It is listed by Archer (1946) as *T. ventillans* Keyserling.

Tidarren sisypoides (Walckenaer), AC. Madison County; Shelta Cave. This species is widespread in the state, and is frequently associated with cave entrances (Archer, 1946). Archer (1940a) reported it from cave entrances as *T. for-dum*.

Family Uloboridae

Uloborus globosus Walckenaer, AC. The species is reported as occurring in cave entrances in Jackson, Lawrence, Madison, Marshall, and Morgan Counties (Archer, 1940a).

Class Arachnida Order Opiliones

Cave-Inhabiting harvestmen of North America are reviewed by Goodnight and Goodnight (1960, 1981).

Family Sabaconidae

Sabacon jonesi Goodnight and Goodnight, TP. Madison County; Natural Well. The species is reported only from this locality (Goodnight and Goodnight, 1942). Shear (1975) indicates that this may be a synonym for the widely distributed species *S. cavicolens* (Packard), which is occasionally found in caves, especially in the southern part of its range, as far west as Arkansas (Peck and Peck, 1982).

Family Ceratolasmetidae

Hesperonemastoma pallidimaculosa (Goodnight and Goodnight), TB. Marshall County; Rockhouse Cave (type locality). Morgan County; Lamons Cave (TK). The species is eyeless, and known only from these localities (Goodnight and Goodnight, 1945; Gruber, 1970). Its sister species may be *H. inops* (Packard) of Kentucky. See Shear (1986) for notes on family names of this and the preceding family.

Family Gagrellidae

Leiobunum sp., TX. Cooper and Cooper (1966) reported amazingly large concentrations of harvestmen on the walls and ceilings of Alabama caves. Although no specific cave names were given, the animals were reported to be known from many caves. The animals in question were not identified but they are surely members of the genus *Leiobunum*, which are well known for their populous aggregations (Cockerill, 1988) and their very long, thin legs. Cooper and Cooper are probably incorrect in listing these animals as troglophiles, they are more likely troglloxenes, which leave the caves at night to feed as predators in nearby forests or fields.

Family Cladonychidae (= Erebomastriidae)

Thermomaster brunnea (Banks) (? = *Phalangodes archeri* Goodnight and Goodnight), AC. Jackson County; McFarland and Engle Double Pit (McFarlen Blowing entrance) Caves. Madison County; Aladdin Cave. The species is a forest litter inhabitant, and also occurs in forests at higher elevations in Georgia, Tennessee, and North Carolina (Briggs, 1969; Goodnight and Goodnight, 1942, 1960).

Family Phalangodidae

Bishopella jonesi Goodnight and Goodnight, AC. Jackson County; McFarland Cave (type locality). This seems to be an otherwise unknown forest litter species (Goodnight and Goodnight, 1942).

Bishopella laciniosa (Crosby and Bishop), TP. Blount County; Horseshoe-Crump, and Ingram Caves. Calhoun County; Lady and Weaver Caves. Colbert County; Dickey, Galleymore (= Gilleymore), Georgetown, Gist, McCluskey, McKinney, McKinney Pit, and Wolf Den Caves. Dekalb County; Cherokee, Kelly Girls, Manitou, Sequoyah, Section

26, and Talley Caves. Cherokee County; Wright Cave. Jackson County; Gary Self Pit (Cave Stand entrance), Clear Creek Saltpeter, Cornellison No. 1, Devils Stairstep, Forty Eight Ten, Gross-Skeleton, House of Happiness, Jess Elliott, Indian Rock, Isbell Spring, Kyle, McFarland, Engle Double Pit (McFarlen Blowing entrance), Nickajack, Mink (Out) entrance of Gross-Skeleton, Putman, Rainbow, Sauta, Tumbling Rock, and Williams Saltpeter Caves. Jefferson County; Cedar Pole and Crystal (McClunney) Caves. Lauderdale County; Basket, Butler, and Collier Caves. Lawrence County; Ivy Hollow Cave. Limestone County; Pope Cave. Madison County; Shelta Cave. Marshall County; Dunham, Gamble, Griffith, Hampton, Honeycomb, Line Point, MacHardin, Steves, and Terrill Caves. Morgan County; Cave Spring, Inge, Roper, Royer, and Talucah (Bat) Caves. St. Clair County; McIendon and Terrell No. 1 Caves. This species is also known from higher elevation forest litter collections from Alabama, Georgia, North and South Carolina, and Tennessee, and cave collections from Georgia, Tennessee and Jackson County, Florida (Barr, 1961; Crosby and Bishop, 1924; Goodnight and Goodnight, 1942, 1960; Holsinger and Peck, 1971; Peck, 1970). The proper genus for this species may be *Phalangodes*.

Crosbyella spinturnix (Crosby and Bishop), TP. Calhoun County; Daugette Cave No. 1. Shelby County; Anderson Cave. Talladega County; DeSoto (Kymulga) Caverns. The species is reported from forest litter localities in Alabama, Arkansas, Louisiana, Mississippi, and Florida, and caves in Arkansas, Georgia and Florida (Crosby and Bishop, 1924;

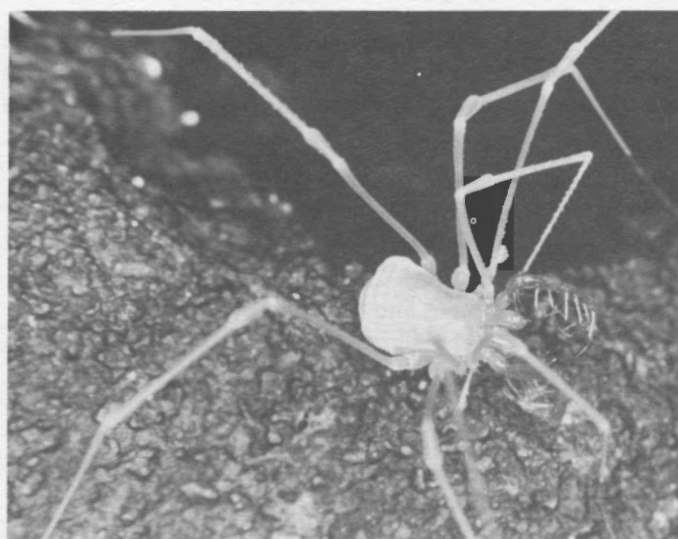


Figure 7. The troglobitic harvestman *Phalangodes apalachius*. This elegant species is known from only one Alabama cave, but from many others in Tennessee. In forest-dwelling species, eyes are present on a tubercle at the front of the head.

Goodnight and Goodnight, 1942; Holsinger and Peck, 1971; Peck, 1970; Peck and Peck, 1982). The proper genus name for this species may be *Phalangodes*.

Phalangodes (= *Tolus*) *appalachius* (Goodnight and Goodnight), TB, Figure 7. Jackson County; Jess Elliott Cave (T. C. Barr). The species occurs in Tennessee along the western Cumberland escarpment northeast to Overton County. Known Tennessee records (TCB) are Coffee County; Lusk Cave. Franklin County; Walker Spring and Wet Caves. Grundy County; Big Mouth; Crystal, and Wonder Caves. Marion County; Monteagle Saltpeter Cave. Overton County; Mill Cave. Putnam County; Bridge Creek Cave. Van Buren County; Big Bone and McElory Caves. Warren County; Cumberland Caverns. This species is probably the sister species to *P. armata* Tellkamp, a troglobite of south-central Kentucky and adjacent north-central Tennessee. Goodnight and Goodnight (1981) hint that these two taxa should be synonymized, resulting in a disjunction of distribution difficult to explain for a troglobite.

Order Acarina

Mites ectoparasitic on bats in Alabama are reviewed by Brennon and White (1960).

Unidentified material. Blount County; Bryant Cave (debris), Jackson County; Coon Creek Cave (guano), Doug Green Cave (debris), Limrock Blowing Cave (*Neotoma* nest), Sauta Cave (guano). Jefferson County; Crystal (McClunney) Caverns. Madison County; Barclay Cave. Marshall County; Dunham Cave (*Neotoma* nest), Painted Bluff Cave (guano), Porches Spring Cave.

Comments. Many species of mites have been encountered in Alabama caves. The above is a partial listing of collections and observations.

Family Rhagidiidae

Robustocheles (*Lewia*) *hilli* (Strandtmann), TP. These mites have been seen in several Alabama caves, but specimens are not available to confirm the above identification. This is the most frequent cave rhagidiid, and is known from caves in Arizona, Georgia, Kentucky, Tennessee, Virginia, West Virginia, and Washington State; and epigean sites elsewhere. Other genera and species also occur in caves (Zacharda, 1985; Zacharda and Elliott, 1981).

Class Diplopoda

A review of the cavernicolous millipedes of the United States is given by Shear (1969).

Order Cambalida

Family Cambalidae

Cambala annulata (Say), AC. Talladega County; DeSoto (Kymulga) Caverns. The species is distributed in eleven eastern states, but is rarely found in caves (Chamberlin and

Hoffman, 1958; Hoffman, 1958; Loomis (*Cristula*), 1943; Shelley, 1979).

Cambala minor (Bollman), TP. Blount County; Catfish and Randolph caves. Colbert County; McCluskey, McKinney, McKinney Pit, and Murrells Caves. Dekalb County; Cemetery, Lois Killian, and Steward Spring (JAC) Caves. Cherokee County; Wright Cave. Jackson County; Limrock Blowing and Talley Ditch caves. Lauderdale County; Butler No. 1, Collier, and Key Caves. Lawrence County; Ivy Hollow Cave. Limestone County; Forked Stream Cave (not in Alabama Survey). Madison County; Matthews, Barclay, and Byrd Spring Caves. Marshall County; Old Blowing Cave. Morgan County; Royer Cave. Talladega County; Dulaney Cave (WBJ). The species is widespread in epigean localities in the eastern states and is known from many caves in Arkansas, Illinois, Indiana, Missouri, Oklahoma, Tennessee, Virginia and West Virginia (Causey, 1959; Shelley, 1979).

Cambala ochra Chamberlin (= *Cambala* or *Troglocambala loomisi* Hoffman), TP. Conecuh County; Sanders (= Turks or Brooklyn) Cave (type locality for *T. loomisi* Hoffman). The species ranges from southern Indiana, through central Kentucky, and the Cumberland Plateau of Tennessee to the Gulf Coastal Plain and east Texas (Shelley, 1979). There seem to be no other cave populations, although this one was very abundant, feeding on bat guano (Causey, 1964; Hoffman, 1956).

Order Chordeumatida

Family Cleidogonidae

Cleidogona sp., AC. Colbert County; McKinney Pit. Jackson County; Nat Cave. Probably an epigean species washed into the caves.

The *eburnea* species group

Pseudotremia eburnea Loomis, TB. Jackson County; Nickajack Cave. Marshall County; Davidson Cave. The species is otherwise known from Cricket Cave (type locality) Walker County and Case Caverns, Dade County, Georgia. *P. aeacus* Shear is also known from caves in Dade County, Georgia (Loomis, 1939; Shear, 1972). This and the following species belong in this group with many epigean and cave species in Alabama, Tennessee, Georgia, and North Carolina.

Pseudotremia nyx Shear, TB. Marshall County; Cathedral Caverns (type locality). Known only from this cave (Shear, 1972).

The *cottus* species group

Pseudotremia minos Shear, TB. Jackson County; Russell Cave (type locality). Known only from this cave (Shear, 1972). This is the only troglobite in this group, which occurs otherwise in eastern Tennessee.

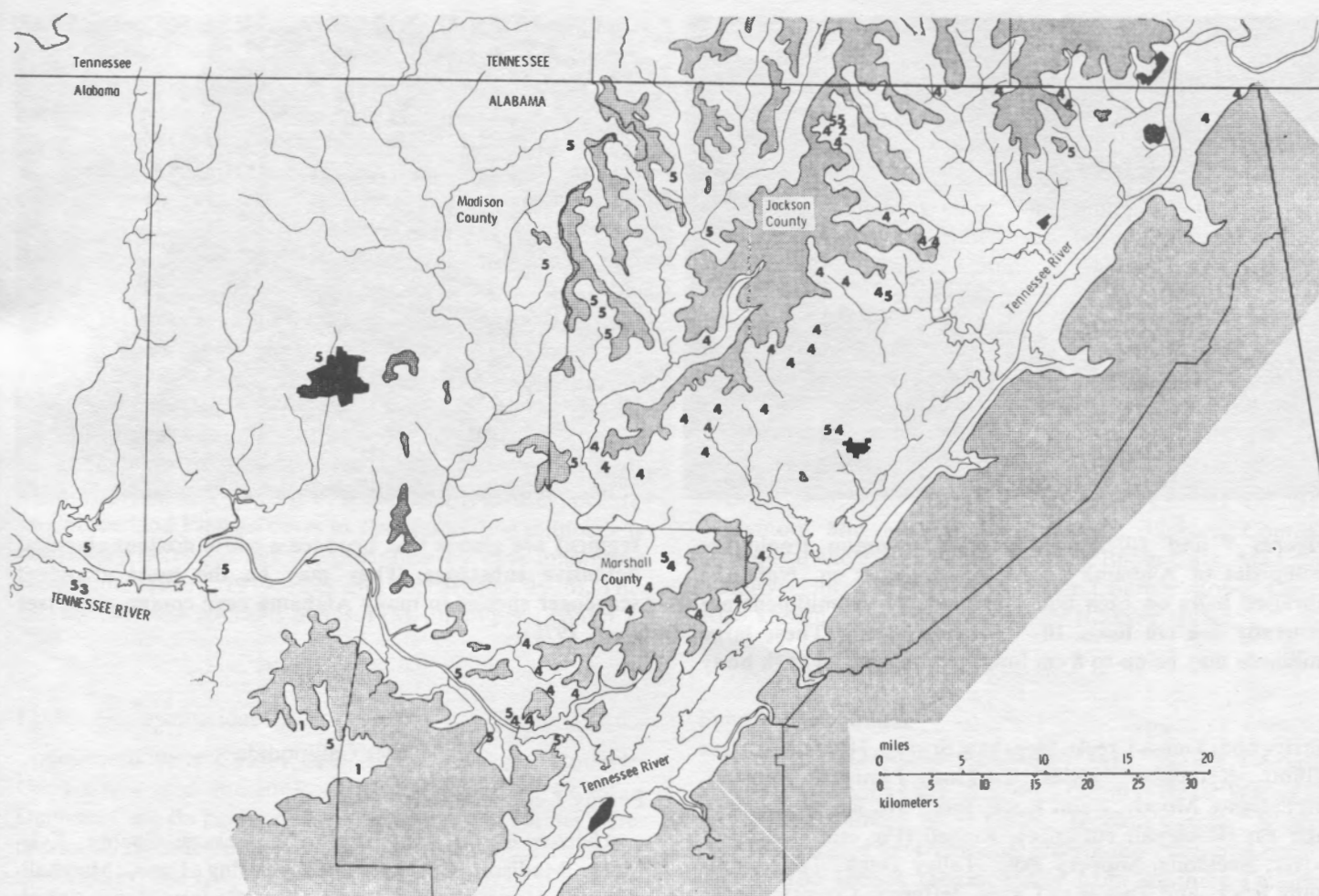


Figure 8. Distributions of some troglobitic invertebrates in northeastern Alabama. One and two are harvestmen, (1). *Hesperonemastoma pallidimaculosa*, (2). *Phalangodes apalachius*. All the others are spiders. 3. *Nesticus jonesi*. 4.

Nesticus barri; limited to the eastern flanks of the Jackson County Mountains. 5. *Phanetta subterranea*; this species has a wider distribution to the west, south and east in Alabama and in other states.

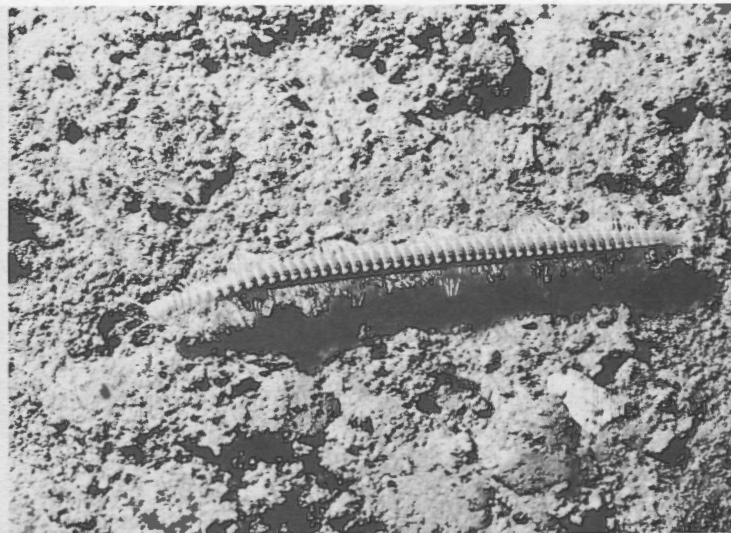
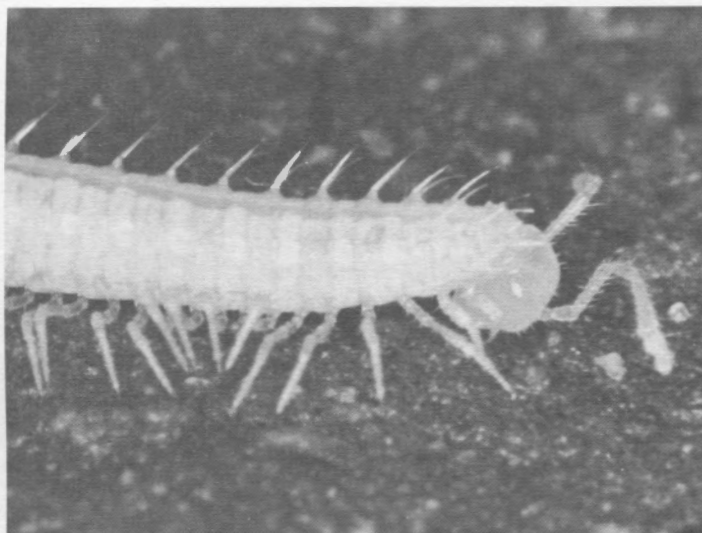
Pseudotremia spp., TP and TB. Colbert County; Georgetown, Keeton, and McKinney Pit Caves. Dekalb County; Cherokee, Kelly Girls, Section 26, Sequoyah, and Stanley-Garden (JEC) Caves. Jackson County; Cagle, Horseshoe, Horseskull, Long Island Saltpeter (WT), McFarland, Rainbow, Ranie Willis, Ridley, Roadside, Russell (Pig Entrance), Salt River, Sheldons, Steele Saltpeter, Talley Ditch, The Morgue (WT), The Sinks, Vandever, Williams Saltpeter, and Wynne Caves. Lauderdale County; Basket and Collier Caves. Limestone County; Rockhouse Cave. Madison County; Barclay, Chapman (WT), Cold Spring, and Sinks Caves. Marshall County; Beech Spring, Bishop, Dunham, Eudy (WT) Hampton, King School (JEC) Ledbetter, (RG), Merrill, Merritt, Old Blowing and Terrill (WT) Caves. Morgan County; Cave Spring, Horseback, Intreken, Laughlin Spring (JEC), and Vandiver Caves. This interesting material remains to be

studied. It may help to understand the trends in cave evolution in this genus (Causey, 1959, 1960; Loomis, 1943; Shear, 1972).

Family Trichopetalidae

Scoterpes austrinus austrinus Loomis, TB. Dekalb County; Manitou Cave (Type locality). Also reported from White River Cave, Floyd County, Georgia (Loomis, 1943; Shear, 1972). The subspecies *A. austrinus nudus* Chamberlin is recorded only from Kingston Saltpeter Cave, Bartow County, Georgia.

Scoterpes spp., TB, Figure 9. Blount County; Bangor, Bryant, Catfish, and Randolph Caves. Calhoun County; Green Valley Cave (LG); Colbert County; McKinney Cave. Dekalb County; Bartlett, Cherokee, Kelly Girls, Killian, Lykes, Sequoyah, and Stanley-Garden Caves. Jackson County; Bell Spring, Bucks Pocket, Buds, Cagle, Crossing,



Figures 9 and 10. The two most common troglotic millipedes in Alabama caves. 9. *Scoterpes* sp. Note the upraised hairs on each body segment. These millipedes are generally 1–2 cm long. 10. *Tetracion jonesi*. These large millipedes may be up to 8 cm long. At the sides of each body

segment are glands that produce a white noxious chemical defensive substance. They may be the most abundant scavenger species in many Alabama cave communities (see Peck 1976).

Driftwood, Guess Creek, Henshaw Spring, Horseshoe, Jess Elliott, Kennamer, Kyles, Larkins, Limrock Blowing, McFarland, Moody, Paint Rock, Rainbow, Roadside, Gary Self Pit (Rousseau entrance), Russell (Pig entrance), Salt River, Sheldons, Slippery Pole, Talley Ditch, Tate, Tumbling Rock, and Two Way Caves. Jefferson County; Cedar Pole and Crystal (McClunney) Caves. Limestone County; Indian and Rockhouse Caves. Madison County; Aladdin, Barclay, Burwell, Byrd Spring, Cave Spring (AL60), Ellis, Hering (Herrin), Oakwood, Shelta, Glover (Water) and Vann (New Hope Cave Spring) Caves. Marshall County; Cathedral Caverns, Gamble, and Steves Caves. Morgan County; Royer and Talucah Caves. Shelby County; Anderson Cave. St. Clair County; McLendon Cave. This rich material awaits study, to unravel the course of evolution in this cave restricted genus. Records of *S. copei* from caves in Dade County Georgia, and Franklin and Hamilton Counties, Tennessee, are errors, because that species is limited to caves in south-central Kentucky. This group offers a substantial challenge to a student of cave-faunal evolution in the southeast (Causey, 1959, 1960; Chamberlin, 1946; Loomis, 1939, 1943; Shear, 1969, 1972).

Trichopetalum syntheticum Shear, TB. Jackson County; Crossings Cave (type locality). Marshall County; Buds Cave. Known only from these caves (Shear, 1972). The genus contains more species in caves and forests in the central Appalachians. The distribution on both sides of the Tennessee River is puzzling.

Order Callipodida

Family Lysiopetalidae

Abacion magnum Loomis, AC. Jackson County; Kyle Cave. Madison County; Sneed Spring Cave. Marshall County; Honeycomb Cave. Shelby County; Lous Crawl Cave. This genus of large millipedes, with chemical defenses which ooze from their lateral crests, shares a common ancestor with the troglotic genus *Tetracion* (Chamberlin, 1946; Loomis, 1943). The record of *A. lactarium* (Say) (Loomis, 1943) from Kingston Saltpeter Cave, Bartow County, Georgia, is probably this species.

Tetracion jonesi Hoffman, TB, Figure 10. DeKalb County; Kelly Girls Cave. Jackson County; Beanfield, Bell Spring, Blue River (WT); Doodlebug Hole (Blowing entrance) (JEC). Borderline (WT), Bouldin, Boxes Cove, Bucks Pocket, Buds, Cagle, Cornellison No. 1, Crossings, Doug Green, Driftwood, Dripping Spring, Engle Double Pit (McFarland Blowing entrance), Fourth of July, Forty Eight Ten, Gary Self (RG), Geiger, Guess Creek, Hall, Upper Rainbow (Happy Hollow), Henshaw Spring, Horseshoe, House of Happiness, Indian Rocks, Isbell Spring, Jess Elliott, Kennamer, Larkin, Kyle, Limrock Blowing, Little Sink, McFarland, Merritt, Moody, Moon Spring, Nat, Mink (Out) entrance of Gross-Skeleton, Paint Rock, Pigpen, Putman, Rainbow, Ranie Willis, Roadside, Salt River, Sauta, Sheldon, Small, Steele Saltpeter, Swaim, Tate, Talley Ditch, Tumbling Rock, Two Way, Tupelo and

Williams Saltpeter Caves. Madison County; Aladdin, Burwell, Cave Spring AL 60, Vann (New Hope Cave Spring), Candlestand (Goat), Hurricane, Jacks, Scott, and Glover (Water) Caves. Marshall County; Beech Spring, Bishop, Cave Mountain, Clark Bluff, Dunham, Keller, Kirkland, Line Point, MacHardin, Merrill, Old Blowing, Painted Bluff, Steves, Walnut, and Warrenton Caves. Morgan County; Hughes Cave. There is interesting variation between and within populations of these large-sized and very common millipedes. Populations east and south of the Tennessee River may differ. An analysis of this variation might give interesting conclusions on the evolution of this species. Two subspecies have been named (*T. j. jonesi* from Cathedral Caverns, Marshall County; and *T. jonesi antaeum* from Barclay Cave, Madison County, Hoffman, 1956). The species extends into caves in Franklin County, Tennessee. Another species, *T. tennesseensis* Causey, occurs in Cumberland Plateau caves in Tennessee. The millipede is chemically defended against predation by cave-inhabiting salamanders (Peck, 1974; Peck and Richardson, 1976). The defense chemical contains p-cresol (M. Blum pers. comm.).

Order Julida

Family Nemasomatidae

Ameractis satis Causey, TB or EB? Jackson County; Coon Creek and Indian Rock Caves. Marshall County; Dunham Cave (in packrat nest). The genus and species were previously recorded only from caves in five Tennessee counties (Causey, 1959, 1960).

Order Polydesmida

All members of this order are eyeless scavengers in litter and soil. In this case eyelessness is not an indication of cave adaptation.

Family Platyrrhacidae

Euryurus leachii Author, AC. Conecuh County; Sanders Cave. Jackson County; Gross-Skeleton Cave. Jefferson County; Crystal Caverns. Madison County; Shelta Cave. Marshall County; Honeycomb Cave. This usually epigeal species may be abundant in caves on rotting wood (Loomis, 1943). The name *E. erythropygus* (Brandt), was erroneously applied in the past.

Family Eurydesmidae

Brachoria sp., AC. Jackson County; Pigpen Cave.

Pachydesmus crassicutis Wood, AC. Jackson County; Mink (Out) entrance of Gross-Skeleton Cave. Madison County; Cave Spring Cave.

Family Polydesmidae

Pseudopolydesmus sp., ED or AC. Blount County;

Bangor Cave. Colbert County; McCluskey Cave. Dekalb County; Little Creek (JEC) and Goat House (RG) Caves. Jackson County; Driftwood, Ranie Willis, Gary Self Pit (Rousseau entrance) Caves. Madison County; Barclay Cave. Marshall County; Beech Spring, Davidson, and Dunham Caves. Talladega County; Dulaney Cave (WBJ).

Pseudopolydesmus pinetorum (Bollman), AC. Jackson County; Larkin and Hall caves. Madison County; Cold Spring Cave, Marshall County; Gamble Cave. Creek Bed Cave, Rising Fawn, Walker County, Georgia is listed by Loomis as a site for *Polydesmus americanus* Carl (Loomis, 1939).

Scytonotus probably *granulatus* (Say), AC. Jackson County; Swaim Cave.

Family Macrosteronodesmidae

Chaetaspis, near *mollis* Author, TP. Colbert County; Gallymore and McKinney Pit Caves. Jackson County; Driftwood Cave. Lauderdale County; Butler Cave. Madison County; Hurricane Cave. Morgan County; Royer Cave. Also known from Tennessee caves (Causey, 1960).

Order Spirobolida

Family Spirobolidae

Narceus americanus (Beauvois), AC. Blount County; Horseshoe-Crump Cave. Marshall County; Grant Waterfall (JEC), and Painted Bluff Caves. Jackson County; Nickajack Cave (listed as *Arctobolus marginatus* (Say) by Loomis (1939). The species ranges widely from southern Ontario and Illinois to Florida and east Texas, but is only accidental in caves (Keeton, 1960).

Class Chilopoda

Centipedes occur in caves infrequently. They are active predators on small arthropods in soil and litter habitats. A few may be troglaphiles, and a very few in North America may be troglobites.

Order Lithobiomorpha

Family Lithobiidae

Lithobius atkinsoni Bollman, TP. Blount County; Bangor and Bryant Caves. Calhoun County; Daugette No. 1 and Weaver Caves. Dekalb County; Section 26 Cave. Madison County; Clark Bluff Cave. Marshall County; Gamble, Honeycomb, Keller, Painted Bluff and Steves Caves. This is a widespread eastern species (Chamberlin, 1925). Other cave records are Gerards and Milton Caves, Jackson County, Florida, and Fisher and John Hollins Caves, Cannon County, Tennessee.

Garibus, probably *alabamiae* Chamberlin, AC. Madison County; Barclay Cave.

Garibius ?, sp., AC. Marshall County; Hampton Cave (two males, seemingly a new species or genus, lacking sclerotized caudal glands associated with the setigerous tibial lobe of the last legs). The same species appears to be in Jackson Cave, Cannon County, Tennessee.

Nampabius, probably *mycophor* Chamberlin, AC. Jackson County; Rainbow Cave.

Paitobius arienus (Chamberlin), AC. Jackson County; Sheldons Cave. The species also occurs in North and South Carolina (Chamberlin, 1922).

Paitobius, probably *juventus* (Bollman), AC. Marshall County; Gamble Cave.

Paitobius carolinae (Chamberlin), AC. Blount County; Horseshoe-Crump Cave.

Typhlobius coecus (Bollman), ED or TB? Blount County; Bryant Cave. Jackson County; Kennamer Cave. Morgan County; Vandiver Cave. This species is eyeless, with weak pigmentation, a large organ of Tomosvary, long antennae,

and general setose body and appendages. It is otherwise recorded from North Carolina and Tennessee (Chamberlin, 1922), and here from Fox and Overall Caves, Dekalb County, Tennessee.

Watobius anderisus Chamberlin, AC. Calhoun County; Weaver Cave.

Order Scolopendromorpha

Family Scolopendridae

Scolopocryptops sexspinosus (Say), TP. Blount County; Bangor Cave. Colbert County; McCluskey and Murrells Caves. Conecuh County; Sanders Cave. Dekalb County; Manitou, Sequoyah and Talley Caves. Jackson County; Crossings, Paint Rock, and Williams Saltpeter Caves. Lauderdale County; Collier Cave. Limestone County; Rockhouse Cave (WBJ). Madison County; Barclay, Hurricane, and Shelta Caves. Marshall County; Terrill Cave.

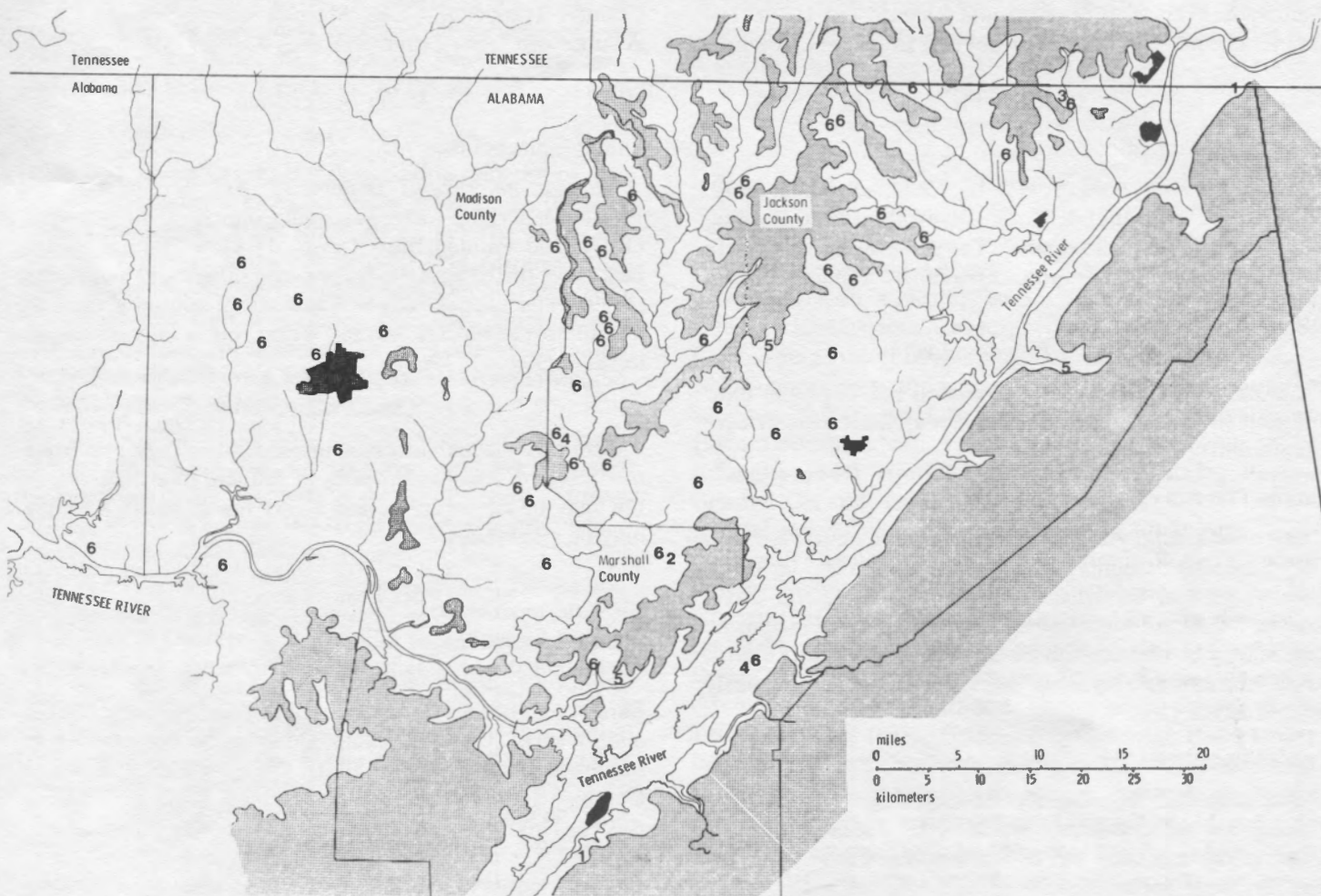


Figure 11. Distributions of troglobitic millipeds in north-eastern Alabama. 1. *Pseudotremia eburnea*. 2. *Pseudotremia nyx*. 3. *Pseudotremia minos*. 4.

Trichopetalum syntheticum. 5. *Ameractis satis*. 6. *Scoterpes* spp.; this genus is more common in caves in the Highland Rim than are any other group of troglobites.

This is a widespread eastern species. I also have a record for Trussel Cave, Grundy County, Tennessee.

Class Symphyla

Family Scutigerellidae

Scutigerella sp., ED. Madison County; Byrd Spring Cave. Jackson County; Gary Self Pit (Rousseau entrance) Cave. Records are also from Johnson Crook Cave, Dade County and Hickman Gulf and Harrisburg Caves, Walker County, Georgia; and Round Mountain Cave, Franklin County; Tennessee. Little is known of these strange soil dwellers in the United States (Michelbacher, 1942; Edwards, 1959).

Family Scolopendrellidae

Symphylella sp., ED. Jackson County; Talley Ditch Cave.

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THE FOSSIL HERPETOFAUNA (PLEISTOCENE: IRVINGTONIAN) OF HAMILTON CAVE, PENDLETON COUNTY, WEST VIRGINIA

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INTRODUCTION

Each of three Irvingtonian herpetofaunas from caves in south-central Texas (Holman and Winkler, 1987), West

Virginia (Holman, 1982), and Maryland (Holman, 1977) are much more similar to the modern herpetofaunas of the areas than the fossil mammalian faunas are to the modern mammalian faunas, a situation that has posed some compelling questions. Thus, the availability of a fourth Irvingtonian herpetofauna, more taxonomically diverse than any of the other three, is of considerable interest. This herpetofauna is from Hamilton Cave, Pendleton County, West Virginia, located about 5.6 km south of Franklin (Fig. 1). The cave is especially important in that it has produced a virtually complete skeleton of the "American Cheetah" *Acinonyx* (*Miracinonyx*) sp.

The Hamilton Cave Irvingtonian Bone Bed.—Hamilton Cave lies at 38°36'20" N. Lat., 79°22'15" W. Long. at an elevation of 617.2 m. The cave entrance is on a ridge about 55 m above the south fork of the Potomac River. The cave formed in Devonian limestone and is thought to have first become accessible to large mammals in the early Pleistocene. The interior of the cave is a maze of numerous small passageways at right angles to one another (Fig. 2). The total length of all of these passageways is over 7.4 km. The fossils of the present paper came from two sites designated "Cheetah" and "Smilodon 2." Both of these sites were in an area of the cave near its eastern end about 152 m from the entrance (Fig. 2). The fossil skeletons of the large carnivores using the cave (cheetah, jaguars and bears) are well preserved, showing little effect of water transport. But much of the herpetological material is quite fragmentary, possibly coprolitic. The amphibian and reptile bones came from cave earth surrounding the larger bones. This matrix was collected in bags and hauled out of the caves to be sieved through standard-mesh mosquito net bags.

The mammalian fauna as a whole resembles the late Irvingtonian faunas of Cumberland Cave, Maryland, and the neighboring Trout Cave of West Virginia (Gidley and Gazin, 1938; Grady, 1987). This would mean that the age of the bone beds is approximately 600,000 to 700,000 years

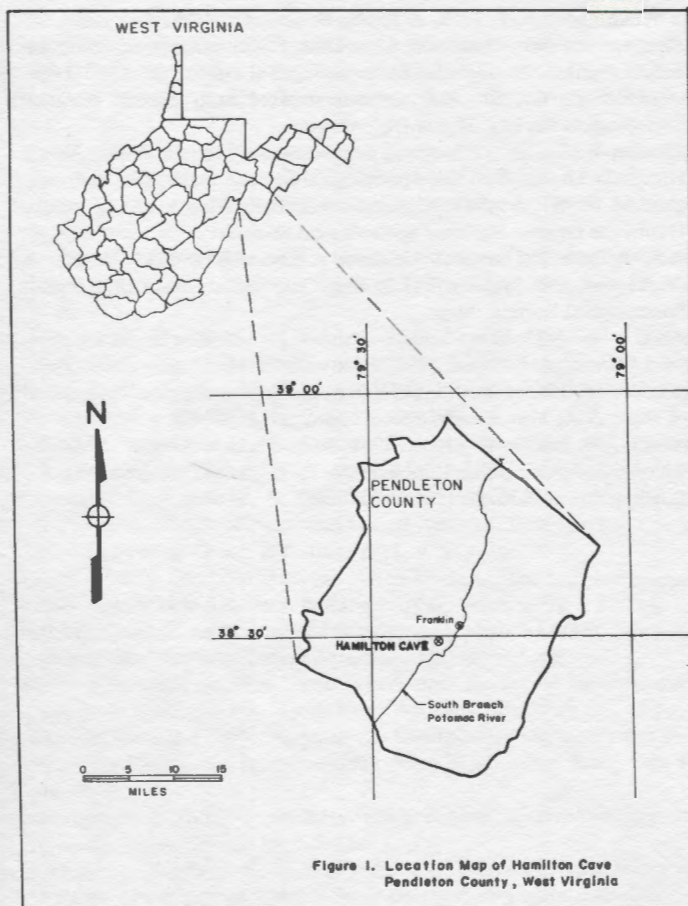


Figure 1. Location Map of Hamilton Cave, Pendleton County, West Virginia.

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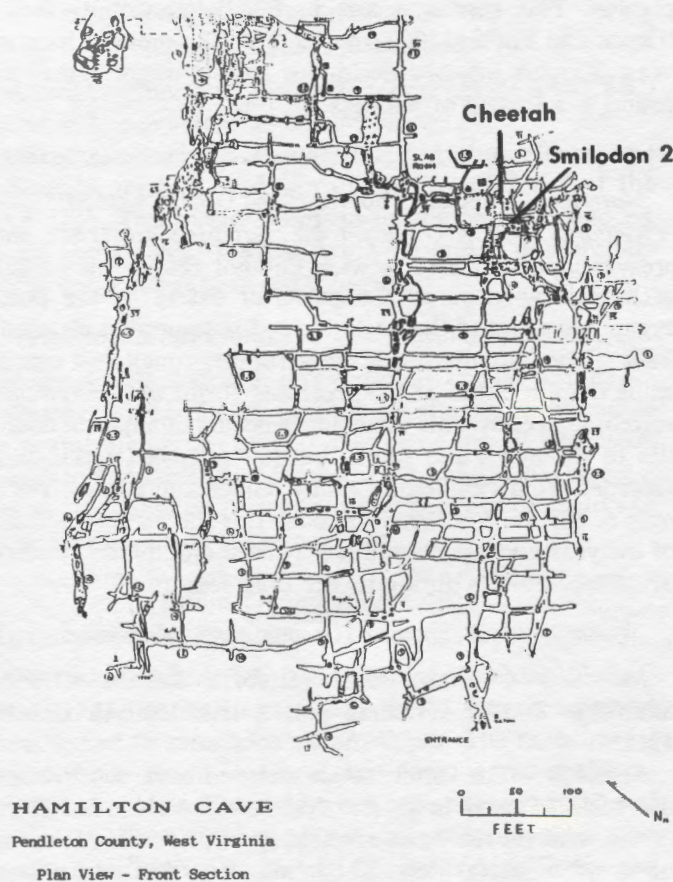


Figure 2. Hamilton Cave, Pendleton County, West Virginia. Plan View, Front Section.

before the present. Thus far about 60 mammalian species have been identified from the Hamilton Cave bone beds. Seventeen of these are extinct. Moreover, nine forms no longer occur in the area of the cave today, but occur elsewhere in the modern fauna of North America. There is no evidence of temporal mixing in the mammalian fauna, with the exception of a few easily recognizable bones of current cave bats, late rodents, and one peccary specimen. A checklist of amphibians and reptiles identified from the Hamilton Cave bone bed follows.

CHECKLIST OF HAMILTON CAVE IRVINGTONIAN HERPETOFAUNA

Salamanders

- Cryptobranchus* sp. indet. hellbender
- Notophthalmus viridescens* eastern newt
- Ambystoma jeffersonianum* complex Jefferson salamander complex species indet.
- Ambystoma maculatum* spotted salamander
- Ambystoma opacum* marbled salamander
- Ambystoma tigrinum* tiger salamander

- Desmognathus fuscus* dusky salamander
- Desmognathus ochrophaeus* mountain dusky salamander
- Desmognathus monticola* seal salamander
- Gyrinophilus porphyriticus* spring salamander
- Gyrinophilus* sp. ? neotenic form or neotenic species of spring salamander

Anurans

- Bufo americanus* American toad.
- Bufo woodhousii fowleri* Fowler's toad
- Hyla chrysoscelis* or *H. versicolor* cryptic gray treefrog or gray treefrog.
- Hyla crucifer* spring peeper
- Rana catesbeiana* bullfrog
- Rana clamitans* green frog
- Rana pipiens* complex *Rana pipiens* complex species indet.
- Rana sylvatica* wood frog

Turtles

- Emydidae indet. indeterminate emydid turtle

Lizards

- Sceloporus undulatus* eastern spiny lizard
- Eumeces laticeps* broadhead skink
- Eumeces fasciatus* five lined skink

Snakes

- Carphophis amoenus* eastern worm snake
- Coluber constrictor* racer snake
- Elaphe* sp. indet. rat snake
- Lampropeltis triangulum* milk snake
- Nerodia sipedon* northern watersnake
- Storeria* sp. indet. brown or redbelly snake
- Thamnophis* sp. indet.
- Crotalus horridus* timber rattlesnake

SYSTEMATIC PALEONTOLOGY

Numbers are of the National Museum of Natural History (USNM). Habitats of modern West Virginia amphibians and reptiles are from Green and Pauley (1987).

Class Amphibia

Family Cryptobranchidae

- Genus *Cryptobranchus* Leukart, hellbenders
- Cryptobranchus* sp. indet., hellbender

Material.—Cheetah: forty-one vertebrae, two epihyals USNM 421548. Smilodon 2: ten vertebrae, right scapula, two left dentaries USNM 421549.

Remarks.—Holman (1977) described a new species, *Cryptobranchus guildayi*, from the Irvingtonian of Cumberland Cave, Maryland, on the basis of a single dentary, and later reported *C. guildayi* from the Irvingtonian of Trout Cave,

West Virginia, on the basis of dentaries and additional skeletal elements (Holman, 1982). Naylor (1981) has questioned the validity of *C. guildayi* and believes it may be *C. alleganiensis*, the modern form.

The Hamilton Cave scapula and dentaries are similar to *C. guildayi*, but the epihyals are similar to *C. alleganiensis*. Since only two skeletons of adult modern *C. alleganiensis* are available to us at present, it seems best to refer the Hamilton Cave fossils to *Cryptobranchus* sp. indet. until more modern comparative material is available. The genus does not occur in Pendleton County today (Green and Pauley, 1987, map p. 47), but occurs in all of the adjoining counties to the west. Modern hellbenders in West Virginia prefer clear, cool mountain streams.

Family Salamandridae

Genus *Notophthalmus* Rafinesque, eastern newts
Notophthalmus viridescens (Rafinesque), eastern newt

Material.—Cheetah: ten vertebrae USNM 421550.

Remarks.—Holman and Grady (1987) pointed out characteristics of individual vertebrae of *Notophthalmus*. We are unable to find any consistent differences between the Hamilton Cave vertebrae and those of *Notophthalmus viridescens*, the only species of the genus that occurs north of Florida and southern Georgia today. The eastern newt occurs in Pendleton County today (Green and Pauley, 1987, map p. 59). Modern adult eastern newts live in many aquatic habitats, especially lentic ones.

Family Ambystomatidae

Genus *Ambystoma* Tschudi, mole salamanders
Ambystoma jeffersonianum complex, Jefferson salamander complex

Material.—Cheetah: four vertebrae USNM 421551. Smilodon 2: one vertebra USNM 421552.

Remarks.—Vertebrae of the *A. jeffersonianum* complex (*A. jeffersonianum*, *A. laterale*, *A. platineum*, and *A. tremblyi*) are elongated and have a narrow postzygapophyseal area, the neural arch ends anterior to the posterior extent of the postzygapophyses, and the posterior end is depressed. *Ambystoma jeffersonianum* is the only species of this complex that occurs in Pendleton County today (Green and Pauley, 1987, map p. 51). Modern *A. jeffersonianum* in West Virginia are said to spend most of their lives underground or in stacks of wet leaves.

Ambystoma maculatum (Shaw), spotted salamander

Material.—Cheetah: five vertebrae USNM 421553. Smilodon 2: five vertebrae USNM 421554.

Remarks.—Vertebrae of *A. maculatum* are shorter than in the *A. jeffersonianum* complex and have a wider, more flared postzygapophyseal area. The neural arch usually extends posterior to the posterior extent of the postzygapophyses, and the posterior end of the vertebra is de-

pressed. This species occurs in Pendleton County today (Green and Pauley, 1987, map p. 52). The modern form in West Virginia inhabits deciduous forests where it may be found in a variety of habitats.

Ambystoma opacum (Gravenhorst), marbled salamander

Material.—Cheetah: two vertebrae USNM 421555.

Remarks.—In *A. opacum* the vertebrae are short, the prezygapophyseal area is wide but not flared, the neural arch ends anterior to the posterior extent of the postzygapophyses, and the posterior end is somewhat elevated. This species usually has a more robust, roughened neural spine than in either of the preceding forms of *Ambystoma* vertebrae. Today, this salamander occurs in adjacent counties to the north and south, but has not been specifically recorded from Pendleton County (Green and Pauley, 1987, map p. 54). In West Virginia today this species spends most of the year underground, but may be found under a variety of surface objects during its breeding season.

Ambystoma tigrinum (Green), tiger salamander

Material.—Cheetah: four vertebrae USNM 421556. Smilodon 2: two vertebrae and a left humerus USNM 421557.

Remarks.—The vertebrae are assigned to *A. tigrinum* on the basis of their large size, proportions given in Tihen (1958), and on the basis of their upswept neural arches as observed in lateral view. The humerus is from a very large individual, and differs from that of *A. maculatum* in having a much wider ulnar-condylar base.

Ambystoma tigrinum probably does not occur in West Virginia today (see discussion in Green and Pauley, 1987, p. 189). The nearest it gets to the fossil area is in central Maryland and eastern Virginia about 150 kilometers to the east (Conant, 1975, map 205). A similar occurrence of *A. tigrinum* out of its modern range was reported by Holman (1977) for the Irvingtonian Cumberland Cave site, Allegany County, Maryland. Today, this species is absent from most of the Appalachian area.

Family Plethodontidae

Genus *Desmognathus* Baird, dusky salamanders
Desmognathus fuscus (Green), dusky salamander

Material.—Cheetah: four vertebrae USNM 421558. Smilodon 2: two vertebrae USNM 421559.

Remarks.—The posterior end of the neural arch in *D. fuscus* is much less notched than in *D. ochrophaeus*, and differs from *D. monticola* which usually has the posterior end of the neural arch slightly convex or flattened. *Desmognathus fuscus* occurs in Pendleton County today (Green and Pauley, 1987, map p. 61) where it lives near the edges of woodland streams and brooks.

Desmognathus ochrophaeus Cope,
mountain dusky salamander

Material.—Cheetah: three vertebrae USNM 421560. Smilodon 2: one vertebrae USNM 421561.

Remarks.—These *Desmognathus* vertebrae have the moderately notched condition of the posterior end of the neural arch. This species occurs in Pendleton County today (Green and Pauley, 1987, map p. 62) and it is more terrestrial in its habits than is *D. fuscus*.

Desmognathus monticola Dunn, seal salamander

Material.—Smilodon 2: one vertebrae USNM 421562.

Remarks.—This *Desmognathus* has the posterior end of the neural arch convex. This species occurs in Pendleton County today (Green and Pauley, 1987, map p. 63) where it lives in cool mountain streams, tunneling into the banks or living under rocks in the stream bed.

Genus *Gyrinophilus* Cope

Gyrinophilus porphyriticus (Green), spring salamander

Material.—Smilodon 2: five vertebrae USNM 421563.

Remarks.—Holman and Grady (1987) discuss vertebral characters of *Gyrinophilus porphyriticus*. The notochordal canals of the above vertebrae are closed as in metamorphosed individuals. The only other unquestioned species of this genus, *G. pallescens*, is neotenic. *Gyrinophilus porphyriticus* occurs in Pendleton County today (Green and Pauley, 1987, map p. 79). This species is found in boggy areas near springs and in caves in West Virginia today.

Gyrinophilus sp. ? neotonic form

Material.—Cheetah: two vertebrae USNM 421564.

Remarks.—These two vertebrae both have widely open notochordal canals and are much larger than the above five *Gyrinophilus* vertebrae. The two vertebrae may represent an extinct neotenic form, or less likely they could represent *G. pallescens*, a neotenic salamander that occurs only in south-central Tennessee, northern Alabama and extreme northern Georgia (Conant, 1975, map 223). Besharse and Holsinger (1977) described a troglodytic species of *Gyrinophilus*, *G. subterraneus*, from General David Cave in Greenbrier County, West Virginia, but Blaney and Blaney (1978) considered it to be a variant of *G. porphyriticus*. Since *G. "subterraneus"* and some troglodytic *G. porphyriticus* show some neotenic characters (Green and Pauley, 1987), it would be of interest to ascertain the extent of the closure of the notochordal canals in these forms.

Family Bufonidae

Genus *Bufo* Laurenti, toads

Bufo americanus Holbrook, American toad

Material.—Cheetah: five left and three right ilia USNM 421565.

Remarks.—Ilia of *B. americanus* and *B. woodhousii fowleri* may be difficult to separate, but in most cases *B. americanus* tends to have wider, lower ilial prominences. Ilia with quite low ilial prominences were assigned to *B. americanus*, while those with quite high, narrow prominences were assigned to *B. w. fowleri*. Intermediate ilia were not assigned to species. The American toad occurs in Pendleton County today (Green and Pauley, 1987, map p. 94). This species migrates into uplands after the breeding season in West Virginia today where it occupies a variety of situations including both open and woodland areas.

Bufo woodhousii fowleri Hinkley, Fowler's toad

Material.—Cheetah: three left and two right ilia USNM 421566.

Remarks.—The subspecies *B. woodhousii fowleri* may be readily distinguished from its western counterpart *B. w. woodhousii* in that it has a distinctly lower ilial prominence. Fowler's toad occurs in Pendleton County today (Green and Pauley, 1987, map p. 95) where it frequents sandy flood plains and river bottoms as well as brushy thickets and woodland borders.

Family Hylidae

Genus *Hyla* Laurenti, treefrogs

Hyla chrysoscelis or *versicolor*, gray treefrogs

Material.—Cheetah: two right ilia USNM 421567. Smilodon 2: right ilium USNM 421568.

Remarks.—The cryptic species *H. chrysoscelis* and *H. versicolor* have a composite range in eastern United States today (Conant, 1975, map 278). The ilia of these two species appear to be identical to each other, but they may be separated from those of *H. crucifer* in having the dorsal prominence roughened or ovaloid (more rounded in *H. crucifer*), located more posteriorly on the bone, and in being much larger. Only *H. versicolor* has been recorded from Pendleton County today (Green and Pauley, 1987, map p. 101). Both species are found in open woodlands where they live in thickets and on tree branches in West Virginia today.

Hyla crucifer Wied, spring peeper

Material.—Smilodon 2: right ilium USNM 421569.

Remarks.—This small treefrog occurs in Pendleton County today (Green and Pauley, 1987, map p. 100) where it inhabits woods and thickets.

Family Ranidae

Genus *Rana* Linnaeus, true frogs

Rana catesbeiana Shaw, bullfrog

Material.—Cheetah: left ilium of a juvenile specimen USNM 421570. Smilodon 2: two left and one right ilia USNM 421571.

Remarks.—Ilia of juvenile *R. catesbeiana* are quite porous in the area around the acetabular fossa, and because

of this characteristic, it may be distinguished from ilia of *R. clamitans* of the same size. Both *R. catesbeiana* and *R. clamitans* ilia may be separated from those of the *R. pipiens* complex on the basis of the much steeper slope of the dorsal acetabular expansion into the ilial blade in the former two. *Rana catesbeiana* is found in Pendleton County today (Green and Pauley, 1987, map p. 107) where it inhabits a variety of permanent, still bodies of water.

Rana clamitans Latreille, green frog

Material.—Cheetah: four left and five right ilia USNM 421572. Smilodon 2: two right ilia USNM 421573.

Remarks.—This species is found in Pendleton County today (Green and Pauley, 1987, map p. 108) where it occurs in a variety of aquatic habitats.

Rana pipiens complex, leopard frogs

Material.—Cheetah: 23 left and 26 right ilia USNM 421574. Smilodon 2: 31 left and 16 right ilia USNM 421575.

Remarks.—The only *R. pipiens* complex frog that has been reported from Pendleton County today is *R. palustris* (Green and Pauley, 1987, map p. 114), but *R. pipiens* has been reported from adjoining counties to the north and the south (Green and Pauley, 1987, map p. 112). Both species may wander rather far from water into grassy areas in West Virginia today.

Rana sylvatica Le Conte, wood frog

Material.—Cheetah: four left and four right ilia USNM 421576. Smilodon 2: three left ilia USNM 421577.

Remarks.—Holman (1984) has given characteristics for separating ilia of *R. sylvatica* from those of other species of *Rana*. Mainly, the ilial blade tends to have a rounded, robust protuberance on the posterodorsal portion of its lateral surface that separates it readily from other *Rana* species. This species occurs in Pendleton County today (Green and Pauley, 1987, map p. 110) where it is found in moist woodlands with well-developed leaf litter.

Class Reptilia
Order Testudines
Family Emydidae
Emydidae indet.

Material.—Cheetah: two fragmentary carapacial bones USNM 421578.

Remarks.—These two very small bones are too fragmentary for generic identification.

Order Squamata
Family Iguanidae

Genus *Sceloporus* Wiegmann, spiny lizards

Sceloporus undulatus (Latreille), eastern spiny lizard

Material.—Cheetah: left partial maxilla USNM 421579.

Remarks.—*Sceloporus undulatus* is easily separated from other lizards in the Appalachian region in having narrow, weakly tricuspid teeth. This species occurs in Pendleton County today (Green and Pauley, 1987, map p. 141) in open wooded areas.

Family Scincidae

Genus *Eumeces* Wiegmann

Eumeces laticeps (Schneider), broadhead skink

Material.—Cheetah: partial left and partial right dentary USNM 421580.

Remarks.—The dentary of *E. laticeps* differs from those of *E. anthracinus* and *E. fasciatus* in having the teeth in labial view (1) lower crowned, (2) blunter, and (3) thicker. Moreover, the dentary is much larger and more robust in *E. laticeps* than in either of the other two species. The Hamilton Cave dentary represents a specimen having a snout-vent length well in excess of 110 mm based on modern skeletal material. This exceeds the maximum snout-vent length of modern *E. fasciatus* (8.6 cm, Conant, 1975) and *E. anthracinus* (7.0 cm, Conant, 1975). *Eumeces laticeps* has not been recorded in Pendleton County today (Green and Pauley, 1987, map p. 145) but has been recorded from Jefferson County to the northeast and Calhoun County to the west. This species is chiefly arboreal in West Virginia today and is much rarer than *E. fasciatus*.

Eumeces fasciatus (Linnaeus), five lined skink

Material.—Cheetah: seven left and two right dentaries, one left and two right maxillae USNM 421581. Smilodon 2: one left dentary USNM 421582.

Remarks.—The dentary of *E. fasciatus* may be separated from that of *E. anthracinus* in that the anterodorsal border of the Meckelian groove (viewed lingually) is much thicker, especially in the terminal part of the bone. The maxilla of *E. fasciatus* may be distinguished from that of *E. anthracinus* (and *E. laticeps*) in that its nasal border slopes much less abruptly into the anterior maxillary process (Fig. 3). *Eumeces fasciatus* occurs in Pendleton County today (Green and Pauley, 1987, map p. 144) where it lives in a wide variety of terrestrial habitats.

Family Colubridae

Genus *Carphophis* Gervais, worm snake

Carphophis amoenus (Say), eastern worm snake

Material.—Cheetah: 21 vertebrae USNM 421583. Smilodon 2: nine vertebrae USNM 421584.

Remarks.—The vertebrae of *Carphophis* and *Diadophis* are quite similar, as both have very low neural spines, depressed neural arches, and wide, flat hemal keels. Nevertheless, most *Carphophis* vertebrae have lower, thinner, less posteriorly projecting neural spines than in *Diadophis*. This snake occurs in Pendleton County today (Green and Pauley,

1987, map p. 163) where it is a forest animal of moist, rocky soil.

Genus *Coluber* Linnaeus, racers
Coluber constrictor Linnaeus, racer

Material.—Cheetah: five vertebrae USNM 421585. Smilodon 2: one vertebra USNM 421586.

Remarks.—The vertebrae of *C. constrictor* differ from those of other large colubrid snakes in North America of the Appalachian region in being elongated, having a very thin neural spine and hemal keel, a vaulted neural arch, and prominent epizygapophyseal spines. The racer occurs in Pendleton County today (Green and Pauley, 1987, map p. 165) where it may be found in a wide variety of terrestrial habitats.

Genus *Elaphe* Fitzinger, ratsnakes
Elaphe sp. indet., ratsnake

Material.—Cheetah: four fragmentary vertebrae USNM 421587. Smilodon 2: two fragmentary vertebrae USNM 421588.

Remarks.—These vertebrae are too fragmentary to identify to the specific level. The only ratsnake that occurs in Pendleton County today is the black rat snake, *Elaphe obsoleta*, (Green and Pauley, 1987, map p. 171). The fox snake, *Elaphe vulpina*, a species that occurs much to the northwest area today (Conant, 1975, map 148) has been reported from the Irvingtonian of nearby Trout Cave, West Virginia, and the nearby Cumberland Cave, Maryland (Holman, 1977, 1982). One of the vertebrae from Hamilton Cave is quite "vulpina-like," but it has an area of the neural spine missing that is critical for specific determination.

Genus *Heterodon* Latreille, hognose snakes
Heterodon platyrhinos Latreille, eastern hognose snake

Material.—Smilodon 2: three vertebrae USNM 421589.

Remarks.—The vertebrae of *H. platyrhinos* have a moderately high neural spine, but a depressed neural arch and a wide, flat hemal keel. The hognose snake occurs in Pendleton County today (Green and Pauley, 1987, map p. 160) where it frequents dry, open sites.

Genus *Lampropeltis* Fitzinger, kingsnakes and milksnakes
Lampropeltis triangulum (Lacepede), milksnakes

Material.—Cheetah: five vertebrae USNM 421590. Smilodon 2: four vertebrae USNM 421591.

Remarks.—This species is readily identified based on its depressed vertebral shape, low neural spine, and a moderately wide and flat hemal keel. This species occurs in Pendleton County today (Green and Pauley, 1987, map p. 177) where it occupies a wide variety of habitats.

Genus *Nerodia*, watersnakes
Nerodia sipedon (Linnaeus), northern water snake

Material.—Cheetah: three vertebrae USNM 421592.

Remarks.—Brattstrom (1967) gives characters for the identification of the genus *Nerodia* and Holman (1967) has given characters that distinguish the individual vertebrae of *N. sipedon*. This species occurs in Pendleton County today (Green and Pauley, 1987, map p. 151). This snake is said to occur in almost every aquatic situation in West Virginia today.

Genus *Storeria* Baird and Girard, brown and redbelly snakes

Storeria sp. indet. brown or redbelly snake

Material.—Cheetah: ten vertebrae USNM 421593. Smilodon 2: three vertebrae USNM 421594.

Remarks.—The vertebrae of *Storeria* are tiny, have very low neural spines, and hypapophyses that are quite pointed and directed posteriorly. We are unable to separate the vertebrae of *S. dekayi* and *S. occipitomaculata*. The former species has not been recorded from Pendleton County today, but occurs in the adjoining counties to the north and west (Green and Pauley, 1987, map p. 152). The latter species occurs in Pendleton County today (Green and Pauley, 1987, map p. 153).

Genus *Thamnophis* Fitzinger, garter and ribbon snakes
Thamnophis sp. indet., garter or ribbon snake

Material.—Cheetah: 27 vertebrae USNM 421595. Smilodon 2: eleven vertebrae USNM 421596.

Remarks.—Brattstrom (1967) has discussed the identification of individual *Thamnophis* vertebrae. The Hamilton Cave *Thamnophis* vertebrae are too fragmentary for specific identification. Two species of *Thamnophis*, *T. sauritus* and *T. sirtalis*, occur in West Virginia today. The former species has not been recorded from Pendleton County, but occurs in adjacent counties to the north and west (Green and Pauley, 1987, map p. 154). The latter species occurs in Pendleton County today (Green and Pauley, 1987, map p. 156).

Family Viperidae

Genus *Crotalus* Linnaeus, rattlesnakes
Crotalus horridus Linnaeus, timber rattlesnake

Material.—Cheetah: 13 vertebrae USNM 421597.

Remarks.—This species has very tiny paracotylar foramina and a low neural spine compared to other *Crotalus* species. The timber rattlesnake occurs in Pendleton County today (Green and Pauley, 1987, map p. 181) where it is found in mountainous areas where there are brushy ridges and rocky hillside ledges.

DISCUSSION

The Hamilton Cave herpetofauna is the most taxonomically diverse Irvingtonian herpetofauna known. At least eleven salamanders, eight anurans, one turtle, three lizards and nine snakes are represented by the fossils. None of these are extinct, with the possible exception of the

Gyrinophilus fossils that may represent neotenic forms and *Cryptobranchus*, although 17 of about 60 mammalian species from Hamilton Cave are extinct. Moreover, the Hamilton Cave herpetofauna is similar to the herpetofauna that lives in the area today.

Five forms, *Cryptobranchus* sp. indet., *Ambystoma opacum*, *A. tigrinum*, the presumed neotenic *Gyrinophilus*, and *Eumeces laticeps*, have not been recorded from the modern herpetofauna of Pendleton County. But other than the *Gyrinophilus*, all may be found living relatively nearby (see systematic discussion section this paper and Conant, 1975), and their absence may reflect local changes in recent years or lack of local collecting.

The presumed neotenic *Gyrinophilus* was possibly a cave inhabitant and might reflect a higher water table at the time of the deposition of the sediments and bones.

When all of the Irvingtonian cave herpetofaunas of the United States are compared (Table 1), a striking feature of all of them is their similarity to herpetofaunas that would occur in each of the areas today. Such modern analogs are not found in Irvingtonian mammalian faunas of the United States (Kurten and Anderson, 1980).

This apparent paradox might be explained as follows (Holman and Grady, 1987). Unlike mammalian species, no strictly tundra or boreal herpetological species exist today. Thus, if northern herpetological species were displaced southward by advancing glaciers, they could not be detected in fossil faunas. But strictly boreal and tundra species of mammals do exist and have been easily detected in North American Pleistocene faunas.

On the other hand, herpetological species confined to more westerly regions do exist today and have been detected in Irvingtonian cave faunas (Table 1 and Holman, 1977 and 1982). *Elaphe vulpina* and *Sistrurus catenatus* have been detected in Appalachian cave faunas (Table 1) and their presence has been attributed to a Pleistocene "Prairie Peninsula."

A second explanation of the herpetological and mammalian paradox may be that cave herpetofaunas may represent animals from the immediate vicinity of the cave, but that the mammals may have been transported from afar by predators, thus representing a more regional aspect of the paleoenvironment.

A final comment is that it is becoming increasingly evident that herpetological genera and species have been very much more stable in the face of whatever forces caused the massive extinction of mammalian genera and species at the end of the Pleistocene.

ACKNOWLEDGMENTS

The National Geographic Society provided a research grant that aided in the collection of specimens from Hamilton Cave by F. Grady. The National Speleological Society, owner of Hamilton Cave, gave permission to make collections of fossil vertebrates from the cave. Many

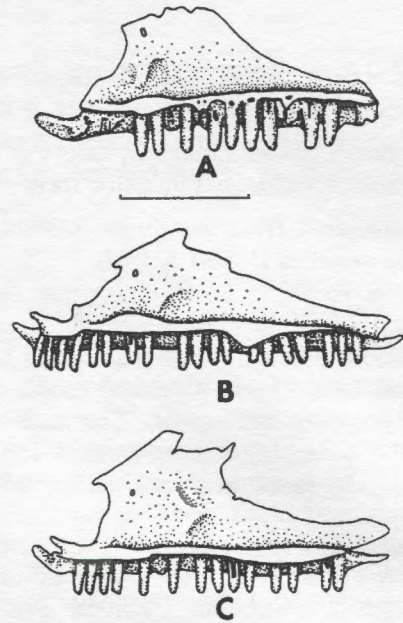


Figure 3. Left maxillae of *Eumeces*. A, *E. fasciatus* from the Pleistocene (Irvingtonian) of Hamilton Cave, West Virginia USNM 421581. B, modern *E. fasciatus* from Kansas MSU 1500. C, modern *E. anthracinus* from Maryland MSU 217. The line equals two mm and applies to all drawings.

volunteers helped haul bags of bone-bearing matrix out of the cave, in particular Tom Kaye, Dave West, Bob Hoke, Miles Drake, Donald Keller and Cindy Keller. Lisa Hallock made the drawing (Figure 3), E. Ray Garton made Figure 1 and Dave West made Figure 2.

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Table 1. Irvingtonian Amphibians and Reptiles from United States Caves. (E) = extinct species. (*) = extralimital form.

Taxon	Hamilton Cave West Virginia	Trout Cave West Virginia	Cumberland Cave Maryland	Fyllan Cave Texas
<i>Cryptobranchus guildayi</i> (E)		X(*)	X(*)	
<i>Cryptobranchus</i> sp. indet.	X(*)			
<i>Ambystoma jeffersonianum</i> complex	X			
<i>Ambystoma maculatum</i>	X		X	
<i>Ambystoma opacum</i>	X	X	X	
<i>Ambystoma tigrinum</i>	X(*)	X(*)	X(*)	X
<i>Desmognathus fuscus</i>	X			
<i>Desmognathus ochrophaeus</i>	X			
<i>Desmognathus monticola</i>	X			
<i>Notophthalmus viridescens</i>	X		X	
<i>Notophthalmus</i> sp. indet.				X(*)
<i>Plethodon glutinosus</i>		X		
<i>Gyrinophilus porphyriticus</i>	X		X	
<i>Gyrinophilus</i> (neotenic form) (?E)	X			
<i>Pseudotriton ruber</i>			X	
<i>Bufo americanus</i>	X	X	X	
<i>Bufo woodhousii fowleri</i>	X		X	
<i>Bufo</i> sp. indet.				X
<i>Hyla chrysoscelis</i> or <i>versicolor</i>	X			
<i>Hyla crucifer</i>	X		X	
<i>Pseudacris triseriata</i>			X	
<i>Rana catesbeiana</i>	X			
<i>Rana clamitans</i>	X		X	
<i>Rana sylvatica</i>	X	X	X	
<i>Rana pipiens</i> complex	X	X	X	
<i>Kinosternon flavescens</i>				X
<i>Geochelone</i> sp. indet. (E)				X(*)
<i>Clemmys muhlenbergi</i>			X	
<i>Terrapene carolina</i>			X	X
<i>Chrysemys picta</i>			X	
<i>Crotaphytus</i> cf. <i>C. reticulatus</i>				X(*)
<i>Sceloporus</i> near <i>S. olivaceus</i>				X
<i>Sceloporus undulatus</i>	X	X	X	
<i>Sceloporus</i> near <i>S. undulatus</i>				X
<i>Eumeces fasciatus</i>	X	X	X	X
<i>Eumeces laticeps</i>	X			
<i>Eumeces obsoletus</i>				X
<i>Ophisaurus</i> sp. indet.				X
<i>Coluber</i> or <i>Masticophis</i>				X
<i>Coluber constrictor</i>	X	X	X	
<i>Elaphe guttata</i>				X
<i>Elaphe vulpina</i>		X(*)	X(*)	
<i>Elaphe</i> sp. indet.	X			
<i>Lampropeltis getulus</i>				X
<i>Lampropeltis triangulum</i>	X	X	X	X
<i>Opheodrys vernalis</i>			X	
<i>Heterodon platyrhinos</i>	X	X	X	
<i>Diadophis punctatus</i>			X	
<i>Carphophis amoenus</i>	X		X	
<i>Tantilla</i> sp. indet.				X
<i>Nerodia fasciata</i>				X
<i>Nerodia sipedon</i>	X		X	
<i>Storeria</i> sp. indet.	X			X
<i>Thamnophis</i> sp. indet.	X	X	X	X
<i>Tropidoclonion lineatum</i>				X
<i>Micrurus fulvius</i>				X
<i>Agkistrodon contortrix</i>		X		
<i>Crotalus atrox</i>				X
<i>Crotalus horridus</i>	X	X	X	X
<i>Sistrurus catenatus</i>		X(*)		

BAT POPULATION STUDY FORT STANTON CAVE

MATTHEW SAFFORD*

SECTION I INTRODUCTION AND BACKGROUND

The purpose of this study is to determine the size, stability and trends of the winter bat population using Fort Stanton Cave. This information will be used to develop a plan of action for managing use of the cave and bat protection. Research needs will be identified.

Reports of bats using Fort Stanton Cave date back to the 1950s (Ballinger and Smith, 1959). An absence of significant bat guano deposits indicates that the cave has been used only as a winter roost/hibernaculum throughout its history. In

1966/67 an intensive study was conducted by D. J. Howell to determine what ambient conditions are preferred by hibernating bats in Fort Stanton Cave.

During the hibernating season of 1976/77, vandals entered the cave illegally and killed 355 bats, an estimated $\frac{1}{3}$ of the population at that time. This incident led to an ongoing project of monitoring the winter bat colony. Three years later, because of drastically declining population numbers, visitation to the cave was restricted to BLM-escorted groups only during the winter months (BLM, 1980). This restriction is still in effect and annual bat counts have continued. The resulting ten years of information is presented in Section IV.

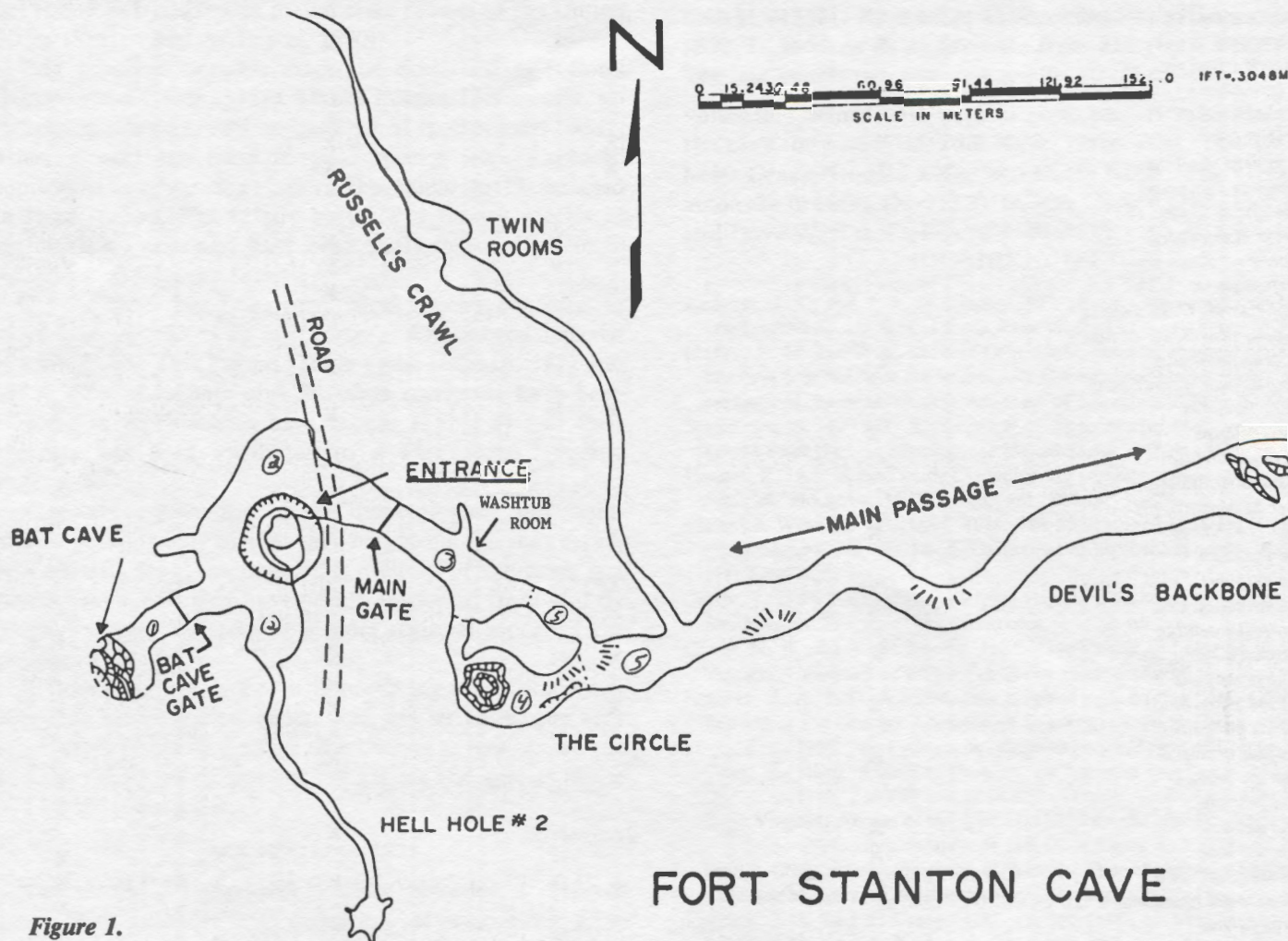


Figure 1.

*Outdoor Recreation Planner, Bureau of Land Management, P.O. Drawer 1857, Roswell, NM 88202-1857.

SECTION II DESCRIPTION OF ENVIRONMENT AND BATS

Fort Stanton Cave

Fort Stanton Cave is located in south-central Lincoln County, New Mexico, at an elevation of 6100 ft (1830m). It is an extensive, joint-controlled limestone cave with over 40,000 ft (14,667 m) of passages. The cave's interior temperature is nearly constant at 54°F (12°C) year around. Temperatures in passages near the single entrance vary with changing weather conditions outside, but are generally several degrees cooler than the remainder of the cave. This may be due to a partial cold-trap effect in the funnel-shaped entrance that inhibits circulation.

The passages used as hibernating roosts are generally wider than they are tall and vary in heights from 20 ft (6 m) to 3 ft (1 m). Temperatures in these areas range from 34° to 48°F (1.1 to 8.9°C). No summer roosts have been found in the cave.

Bat Cave is a separate portion of the cave which is closed to use except for research and is also used as a hibernaculum (Fig. 1).

Bats of Fort Stanton Cave

By far the most populous bat in the study was *Plecotus townsendii pallescens*, the Western Big-Eared bat. This bat is easily identified by its long ears, 1 in. (2.5 cm) or longer, which may be held erect or coiled back along the head depending on the ambient temperature. The bat has a wingspread of 12 to 13 in. (297 to 320 mm) (Barbour and Davis, 1969). It is a cave dweller, seeking out warmer caves for summer roosts and colder caves for hibernating. Individuals may roost singly or in small to medium-sized clusters on open areas of walls or ceiling. The location of the summer roost used by these bats is currently unknown.

The only other species with any significant population is *Myotis subulatus*, the Small-Footed Myotis. This species is recognized by its small size, small feet and black face-mask. It has a wingspread of 8 to 10 in. (212 to 248 mm). It is generally a solitary animal and is most often found jammed into a narrow crack or crevice with only its nose showing. The number of bats of this species observed is probably only a small percentage of the actual number because of their penchant for hiding.

Other species that have been observed are *Eptesicus fuscus*, the Big Brown bat, and *Pipistrellus hesperus*, the Pipistrelle. These were recorded only occasionally as solitary individuals and so are probably transients and not regular inhabitants.

During hibernation, the internal temperature of a bat will drop to within a few degrees of the surrounding temperature. Heartbeat, respiration and metabolic activities will slow tremendously. Disturbing a bat during this period enough to cause arousal will force it to use up important fat

reserves. There are no flying insects out for it to feed on so it may not survive the remainder of the winter.

SECTION III CENSUS METHODS

Population numbers were obtained by direct count of the animals during hibernation. Care was taken not to create undue disturbance and the animals were not handled. If more than one counter was available, multiple counts were tallied and averaged to reach a final number. The cave was divided into sections to facilitate counting and to determine if the bats were changing locations during the winter (Fig. 1). For the first few years of the census, several counts were made during the hibernating season. Recent evidence (Currie, pers. comm.) indicates that *P. townsendii* is highly sensitive to disturbance in hibernation, so counts were limited to one or two during a season in later years.

Temperature readings were taken with a pocket-style alcohol thermometer placed on a wall or ceiling at a level even with the bats. This information was recorded during the last four counts.

SECTION IV

RESULTS

Number of Bats

Annual bat counts were begun in the 1977/78 hibernating season and continued to present (87/88). No data was found for the 83/84 or 84/85 seasons. The data indicates a great deal of variation in the number of bats using the cave as a hibernaculum (Fig. 2). Average numbers were calculated by adding up all bats counted and dividing by number of counts in one season. However, the number of counts varied as did the times that the counts took place. High peak counts occurred in 77/78, 82/83 and 87/88, while low counts were recorded in 79/80 and 85/86.

Figure 3 indicates an average season's population shift. The number of animals increases slowly as winter progresses, then reaches a peak in late January or early February before tapering off in late March.

The numbers presented on the previous graphs indicate the total number of bats in the cave, regardless of species. Figure 4 illustrates the percentages of *P. townsendii* and *M. subulatus* for four sample counts. Occasionally, a third species would be observed, but these were assumed to be accidentals or transients as they were not consistently present.

Temperatures

Temperatures measured varied more in areas near the entrance than those further into the cave as would be expected. Following is a list of temperature ranges for each area (°F): Bat Cave 39–48, Entrance Area 34–45, Washtub Room 34–42, Circle Room 48–56, Main Passage 44–56.

SECTION V
ANALYSIS*Temperatures*

Howell (1967) and Barbour & Davis (1969) suggest that ambient temperature is an important factor in winter roost selection. Howell found that, in Fort Stanton Cave, *Plecotus* will seek roost sites in the temperature range of 43 to 55°F in late fall and early spring but prefer colder areas in the middle of winter (34–45°F). The most populous area of the cave is now the Washtub Room where the temperature has averaged around 40°F (4.4°C). The Entrance Area is well used when temperatures are near 41°F (5°C). Least used area is the Main Passage with an average of 51°F (10.6°C).

Population Numbers

The graph shown in Figure 2 suggests a cyclic pattern of bat colony size. Assuming that the estimation of 1,100 bats in the cave before the bat kill of 1977 is correct (BLM, 1980), there seems to be a 5-year cycle of highs and lows in population numbers. High peak counts occurred in the 77/78 hibernating season (before the bat kill), five years later in 82/83 and again in the latest season, 87/88. Low counts were recorded in 79/80 and 85/86 (the low may have been in 84/85 but the data is missing).

This peak/trough pattern may be the result of any one of the following factors or a combination:

1. Severity of Winter—Colder outside temperatures force more bats into the cave to hibernate.

ANNUAL BAT CENSUS

Ft. Stanton Cave

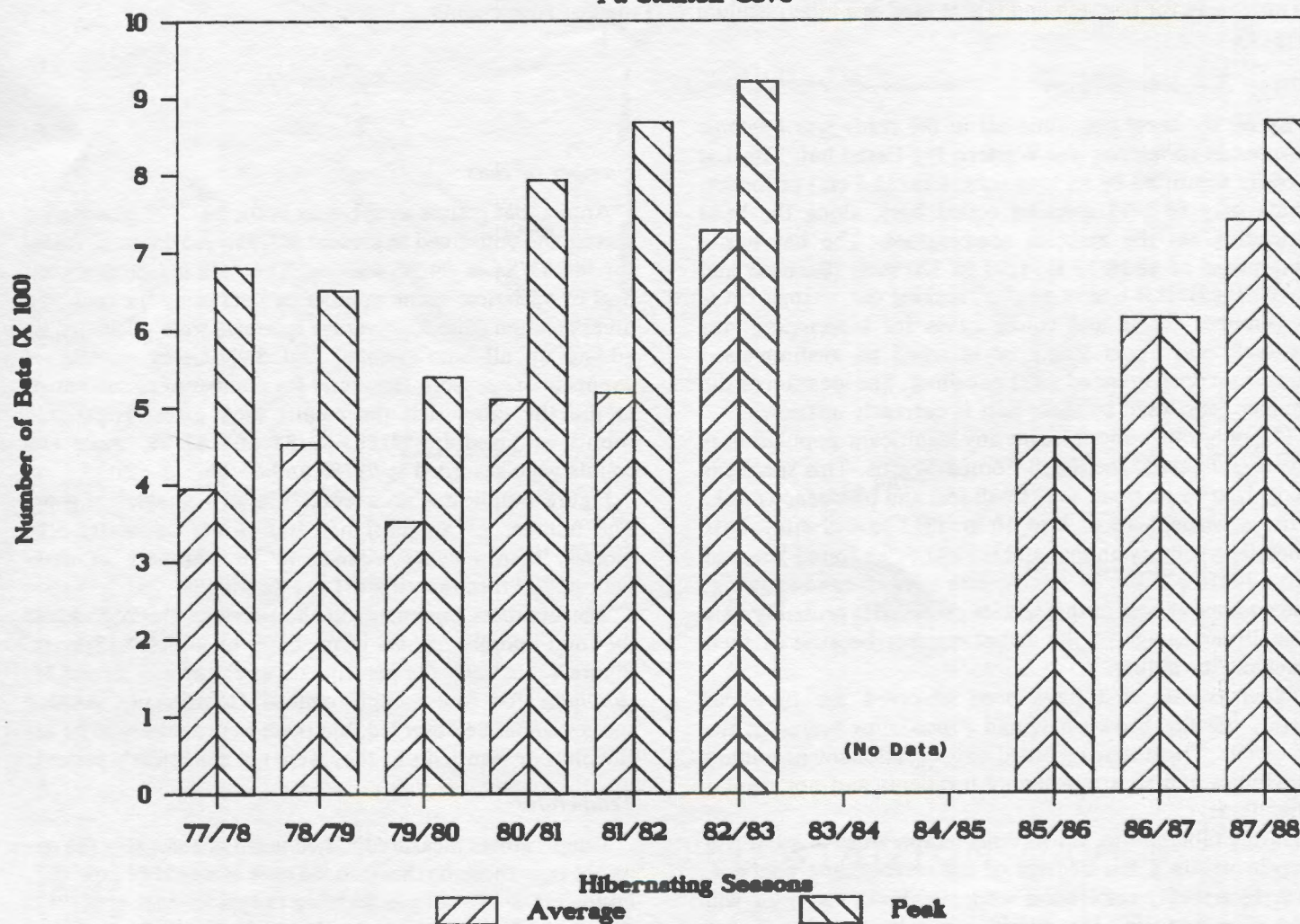


Figure 2.

POPULATION SHIFT

Ft. Stanton Cave

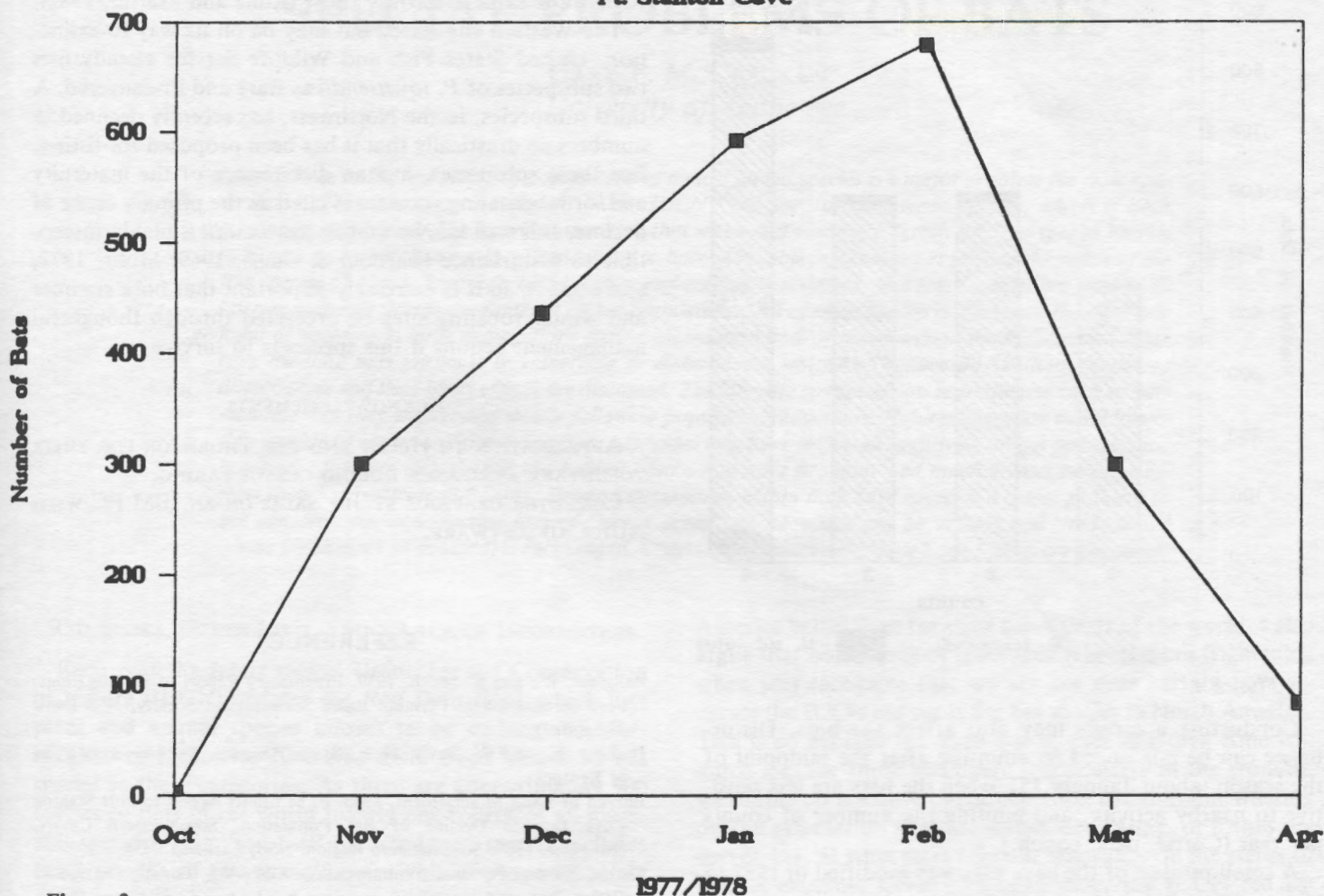


Figure 3.

2. Summer Precipitation—A below-normal amount of summer precipitation in the area will cause a decrease in the number of insect prey available. Therefore, less bats in the summer to stay in winter.
3. Natural Population Dynamics—A population will exhibit normal fluctuations in size due to a variety of factors.
4. Human Disturbance—Increased human activity will cause some bats to abandon the hibernaculum.

SECTION VI

DISCUSSION AND RECOMMENDATIONS

Many diverse factors can influence the management of finite resources such as caves. Outside pressures from oil and gas development, mining, grazing and recreation often come into conflict with protection of the resource. BLM is an agency that must manage the multiple use of land and resources.

The primary objective for cave resource management is to manage public lands in a manner which will protect cave resources . . . (BLM Manual 8380—Cave Resources Management). This provides us the authority to take management actions that are necessary to protect a cave and its contents. With this in mind, a look at what can be done to protect habitat for bats and other spelean life forms is warranted.

Of all the factors listed in Section V, only one can be manipulated: human presence. BLM realized that something must be done when the number of bats in Fort Stanton Cave declined in the late '70s (BLM, 1980). Access to the cave was limited during the hibernating season (November through March) by stipulating that each party be accompanied by a BLM representative to ensure that the bats are not disturbed. This policy should continue and, in addition, recreation trips limited to one per month for the season. Bat Cave should remain closed except for research and administrative trips.

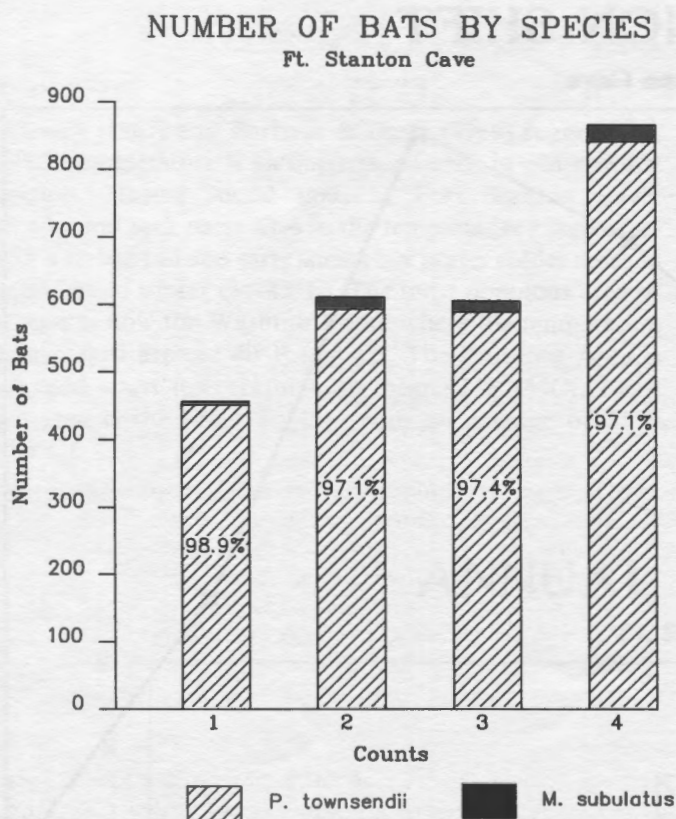


Figure 4.

Conducting a census may also affect the bats. Disturbance can be minimized by counting after the midpoint of the season (about January 15), when the bats are less sensitive to nearby activity, and limiting the number of counts per year (Currie, pers. comm.).

A small portion of the cave gate was modified in 1987 to allow easier bat movement. Additional modification is needed by replacing more of the existing gate with a proven bat-grid design.

Further research is needed to suggest the best methods of reducing human impact. In addition, discovering where the *Plecotus* are spending the warmer months is very important

in managing the colony as a whole because the species exhibits a high degree of site attachment, returning year after year to the same maternity roost (Kunz and Martin, 1982).

The Western Big-Eared bat may be on its way to extinction. United States Fish and Wildlife Service already lists two subspecies of *P. townsendii* as Rare and Endangered. A third subspecies, in the Northwest, has recently declined in numbers so drastically that it has been proposed for listing. For these subspecies, human disturbance of the maternity and/or hibernating roosts was cited as the primary cause of decline. It is well known that *P. townsendii* is highly susceptible to disturbance (Barbour & Davis, 1969; Mohr, 1972; and others), so it is extremely important that both summer and winter roosting sites be protected through thoughtful management actions if this species is to survive.

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COMPUTER GRAPHICS BY JIM SALAS ON AN IBM PC WITH AUTOCAD SOFTWARE.

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CAVE CONSERVATION: SPECIAL PROBLEMS OF BATS

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Ignorance as to the real status of populations of almost all bat species is a major problem for their conservation. This ignorance is reflected in the IUCN "red list" of threatened species, which is both minimalist and biased. The recent proposition that we should construct "green lists" of species known to be secure, rather than red lists, is extended to bats. Available information regarding the status of the five species of North American bats listed as endangered is reviewed, and these species are used to illustrate major problems encountered by bat populations. All of these species rely on cave roosts. Their habit of roosting in large aggregations during hibernation and/or reproduction make these and other cave dwelling bats particularly vulnerable to disturbances which can reduce populations. Types of disturbances and their likely effects are discussed. The long-life spans and low reproductive rates of bats mandate that they will recover slowly following population reductions. Habitat alteration and destruction outside of roosts and poisoning from pesticides also have impacted negatively on bat populations; however, roost site disturbance and habitat destruction have probably had much greater negative effects than has pesticide poisoning. Because disturbance within their cave roosts is a major problem in bat conservation, constructing lists of "green caves" (those which can be visited) and "red caves" (those which must be avoided) is encouraged. Criteria for constructing these lists of caves are discussed.

RED BOOKS, GREEN LISTS, AND A LACK OF INFORMATION

Each year the International Union for the Conservation of Nature (IUCN) updates the *Red Data Book* which lists plant and animal species known to be endangered, vulnerable, or rare. The 1988 *Red Data Book* places 33 bat species in these categories. As there are approximately 900 species of bats in the world (nearly one-fourth of all mammal species), this "red list" of threatened species includes less than 4% of the world's bats. This disproportionately small number should lead anyone with even remote awareness of the worldwide extinction crisis to question whether this list reflects reality with regard to bat species that are threatened. In reality, the red list does not come close to giving an accurate picture of the problem.

First, consider that the red list has a substantial geographical bias toward North American species. The standard reference on North America bats (Barbour and Davis, 1969) lists 39 species of bats in North America, north of Mexico. These 39 species comprise about 5% of the worldwide bat species diversity. However, of the 33 threatened bat species on the IUCN list, 5 are native to North America. So, a fauna comprising 5% of total bat species diversity, accounts for 15% of the species considered as threatened. I argue that this bias does not reflect reality with regard to species endangerment. Rather, this bias reflects our ignorance regarding the status of most bat populations. We simply know the status of bats in North

America better than for most other parts of the world. I also argue that our degree of ignorance is even more frightening when you recognize that we are not even certain how accurate the IUCN red list is for bat species in North America. This is so because for most bat species in North America, much less for those elsewhere (particularly in the tropics), we simply do not have the information to determine whether overall population sizes are stable, decreasing, or if they are decreasing, at what rates? So our ignorance on the status of bats is extreme. Given this ignorance, the IUCN red list gives a highly inaccurate and minimal assessment of our current extinction crisis.

Recognizing this, prominent conservation biologists recently have suggested that the construction of red lists has been a major tactical error by those who wish to preserve the world's biota (Imboden, 1987; Diamond, 1988). Red lists are thought to be a tactical error because the existence of such a list may lead to the assumption that *if a species is not on the list* that species is not in jeopardy. This, of course, is not how the list should be interpreted. Many species that are not on the list should be, but are not, simply because we don't know enough about them. To correct this tactical error, it has been suggested that rather than constructing red lists we should construct "green lists." Green lists would include species that we know are secure. To be on the green list a species should meet the criterion of "known not to be declining in numbers now, and unlikely to decline in the next decade" (Diamond, 1988). With a green list, it is argued, the burden of proof is shifted to those who wish to maintain that all is well with a species.

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Those proposing green lists have been concerned with birds, not with bats. Certainly, much more is known about the status of birds than of bats. However, it is estimated that fewer than $\frac{1}{3}$ of the world's bird species would qualify for inclusion on a green list. This being the case with birds, I also suspect that fewer than $\frac{1}{3}$ of the world's bats likewise would qualify for such a list.

SOME THINGS THAT WE DO KNOW

With our ignorance as a perspective, I wish to consider some of what we do know about the status of bats, particularly cave bats. This requires going back to the red list. Of the 39 bat species in North America, north of Mexico, 18 rely substantially on caves for roosting sites. Some of the remaining 21 species also are occasionally found in caves, but caves evidently are not absolutely essential to them. Of the 18 species for which caves are essential, 13 species utilize caves year-round; both for reproduction and as winter roosts. The remaining 5 species rely on caves as hibernating sites, but roost elsewhere during reproduction. Four of the 5 North American species on the red list require caves year round (Table 1), and one species (the Indiana bat) requires caves for hibernation, but roosts elsewhere during the summer. So all North American bats listed as threatened are cave-dwelling; there appears to be a correlation with cave-dwelling and species jeopardy. However, to hearken briefly back to our ignorance, it is easier (not easy, just easier) to assess the status of cave-dwelling bats than the status of bats that are more dispersed in their roosting habits, and thus more difficult to find and monitor. The bias toward cave-dwelling bats being on the threatened list may in part be a result of relative ease of censusing.

LIFE HISTORY TRAITS PREDISPOSING BATS TO EXTINCTION

Unlike most small mammals, bats have extremely long life spans. Even the smallest bat typically has a life expectancy on the order of 10 years, and individuals are known to live much longer than this. Wild little brown bats, for example, are known to survive as long as 30 years (Keen and Hitchcock, 1980). In addition to long life expectancies, bats have very low rates of reproduction. Many female bats do not reproduce until their second year and, after reaching maturity, females usually produce only a single pup each year. Consequently, bats have far lower potential rates of population growth than are typical of most small mammals. Although bats are often perceived of as similar to rats or mice, the reproductive rates of bats are, in contrast, more similar to those of antelopes or primates. If a bat population is decreased in size, it can recover only slowly.

Bats have other characteristics which contribute to their vulnerability. Among the most significant is their habit of roosting together in large aggregations. The fact that large numbers of individuals often are concentrated into only a

few specific roost sites results in high potential for disturbance. Because of their aggregative roosting habits, species that are very common actually can be vulnerable because they are in only a limited number of roosts. Mexican free-tailed bats (*Tadarida brasiliensis mexicana*) are an excellent example. Single cave roosts of these bats can contain 10's of millions of individuals and the loss of even one such roost would mean the loss of a significant portion of the entire species population.

DISTURBANCE OF ROOSTS BY HUMANS

Aggregations of bats are vulnerable to a variety of human-caused disturbances. At least 3 North American endangered species (Indiana, gray, and Sanborn's long-nosed bats) are known to have abandoned traditional roost sites because of commercial cave development (Humphrey, 1978; Tuttle, 1979; Wilson, 1985a). An important hibernaculum for endangered big-eared bats has been threatened by quarrying (Hall and Harvey, 1976), and I personally have observed numerous examples of vandalism such as burning old tires, or shooting guns inside bat cave roosts. Although intentional disturbance of roosts is well documented, unintentional disturbance often poses an even greater threat. In the temperate zone, aggregations of bats which cavers typically encounter are either hibernating groups that occur in late fall, winter, and early spring, or maternity colonies that occur in late spring or summer. There is no question that disturbances as seemingly trivial as merely entering a roost area, or shining a light on hibernating bats or on a maternity group of females and their pups, can result in decreased survival, perhaps outright death, and possible abandonment of the roost site. Although there is some controversy about the significance of this apparently "innocent" disturbance, my own experience and reading of the literature lead me to the opinion that it can be extremely significant. However, there is no question that the impact of such disturbances are somewhat species-specific, and that the timing of the disturbance is very important.

The results of "innocent" disturbance of a maternity colony can include the following. (1) It can cause individuals to abandon roost sites, particularly early in the reproductive season when females are pregnant. This may result in females moving to other, perhaps less ideal, roosts where their success at reproducing is reduced. (2) Disturbance raises the general level of activity within roosts. This may result in greater expenditure of energy and less efficient transfer of energy to nursing young. This, in turn, may cause slower growth of young and increase the foraging demands on females, thus increasing the time females are outside of the roost and vulnerable to predation. (3) Disturbance can cause outright death of young that lose their roost-hold and fall to the cave floor. (4) Maternity aggregations often result in thermoregulatory benefits. Clustering

bats gain thermal benefits from being surrounded by other warm bodies. However, individuals also may receive thermal benefit because the accumulated body heat of all individuals present serves to raise temperatures within the roost area. Therefore, if the size of a colony decreases, the accumulated thermal advantages to the individuals in that colony may likewise decrease, and it may become energetically less advantageous, or perhaps even energetically impossible for females to raise pups in that roost. Thus, there may be a "threshold," where after a population reaches a certain lower size, roost temperatures cannot be raised sufficiently for rearing young and that roost must be abandoned as a maternity site.

Problems caused by disturbing hibernating bats also relate to their energy requirements. During winter, temperate zone bats go long periods without eating, and allow their body temperatures to drop, often to near freezing. The energy reserves that bats accumulate prior to hibernation are often close to what is needed to survive the winter. Disturbance during hibernation may cause bats to arouse prematurely, elevating their body temperatures and utilizing stored energy reserves which should not be spared. The bats may go back into torpor after the disturbance, but then they may not have sufficient energy to survive the rest of winter. This may not be apparent to the person causing the disturbance.

Roost site disturbance also can seriously impact bats which do not form large aggregations. This is undoubtedly so for many tropical bats which roost in mature, hollow trees, which are being cut as more tropical forest goes into cultivation. To my knowledge, we don't know the trajectories of populations of any of these tree-roosting bats. As an example closer to home, it seems probable that the decline of the Indiana bat may be attributed in part to the loss of roost sites other than caves. Indiana bats hibernate in caves and there is no question that disturbance of hibernacula has contributed to their decline. However, in the midwestern United States, several large hibernacula of Indiana bats are protected from disturbance, yet these cave populations continue to decline (Clawson, 1987). We can only speculate on the reasons for this continued decline, and this again points to our ignorance. However, while Indiana bats hibernate in caves, in summer they roost and give birth in tree hollows and under the loose bark of trees. The loss of tree roosts may very well be a serious factor in the continuing decline of the Indiana bat in the Midwest. That the decline of the Indiana bat may be due in part to factors outside of their hibernacula in no way implies that disturbances at hibernacula are unimportant. Rather, it emphasizes the importance of protecting hibernacula so as not to add additional stresses to these populations.

HABITAT DEGRADATION OUTSIDE OF ROOSTS

Man also has impacted negatively on bat populations by

causing habitat alteration and degradation outside of their roost sites. For example, two species of North American bats on the red list are endangered, in large part, because man's activities have decreased their food resources. Both species of long-nosed bats inhabit desert regions of the southwestern U.S. and Mexico, and both feed on the nectar and pollen of desert flowers (Wilson, 1985a,b; Anonymous, 1988). Wild agave is a major food source of both species. Wild agaves have been severely reduced because they interfere with cattle grazing and because they are harvested by moonshiners for making tequila. Although long-nosed bat populations also have been affected by interference with their cave roosts (Wilson, 1985a, Anonymous, 1988), the reduction in agaves is clearly important in their decline. Long-nosed bats also are major pollinators of both organ pipe and giant saguaro cacti. The well-known decline of these cacti also is evidently directly attributable to the decline of long-nosed bats (Wilson, 1985a,b; Anonymous, 1988).

THE ROLE OF PESTICIDES

Pesticides used to control insect populations have negatively impacted populations of many bats (Clark, 1981). Two effects seem likely; (1) direct poisoning of bats, and (2) reduction in the resource base of bats which eat insects. At present, we know little regarding the effects caused by pesticides reducing the insect prey of bats. However, direct poisoning by DDT (now banned for use in the U.S.) and other organochlorine pesticides has been widely implicated in the decline of many bats (reviewed in Clark, 1981). While pesticide poisoning clearly has caused the decline of local populations of many bats, there has been a tendency to over-emphasize the importance of pesticide poisoning as one of the major factors in the decline of bats (Clark, 1981; McCracken, 1986). In fact, I question whether the general decline of any bat species can be attributed solely or even largely to the toxic effects of pesticides. This is not to exonerate pesticides, but rather to point more strongly at what are the major causes of bat population declines: i.e. roost site interference and the reduction of resources. I suspect that overemphasis of the importance of pesticide poisoning serves to draw attention away from these other causes.

How do I justify these statements? First, the belief that bats are unusually sensitive to pesticides dates from an early paper which purported to document their extreme susceptibility to DDT poisoning (Luckens and Davis, 1964). It is now established that the susceptibility of bats to DDT is in general no greater than that of other similar sized animals (Clark, 1981). Second, there have been many observed, dramatic declines of bat populations that have been attributed to DDT poisoning, without strong data to support these attributions. The most spectacular of these occurred in Eagle Creek Cave, Arizona, where the population of Mex-

ican free-tailed bats declined from an estimated 30 million to an estimated 30 thousand individuals. While other toxins, such as methyl parathion (Clark, 1986), may have contributed to this decline, and human disturbance also seems a likely culprit, there is no evidence that DDT poisoning was a major cause of the loss of this population (Clark, 1981; McCracken, 1986). Again, this is not to say that DDT or other toxins have not directly killed bats. It is well documented, for example, that young Mexican free-tailed bats from Carlsbad Caverns have had potentially lethal pesticide concentrations. However, this is evidently a local problem that has not been reported in other colonies of this species (Geluso et al., 1981). Finally, a natural "experiment" on DDT poisoning has been done for us. In the early 1960's, Cave Springs Cave in Alabama housed a major maternity colony of gray bats. This cave was heavily disturbed by humans and by the early 1970's all its gray bats were gone. However, Cave Springs Cave was then protected by fencing and its gray bat population began recovering to the point that it now houses an estimated 50,000 individuals. Cave Springs Cave is near a former DDT processing plant which also was a major toxic waste dumping site. At present, the bats and bat guano within this cave are substantially polluted with a variety of toxic chemicals including DDE (derived from DDT) and PCB's. Although, this bat colony experiences occasional dieoffs resulting from these toxins, the colony has nonetheless continued to recover in the face of these pollutants; this recovery dating from when the cave was protected (Tuttle, 1986).

RED CAVES/GREEN CAVES

From what we know about human-caused impacts on bat populations, there is little question that roost-site disturbance, vandalism, and habitat destruction have had severe effects. This is particularly so for cave-dwelling bats. My opinion that these impacts are likely to have had greater negative effects than pesticide poisoning is shared by other researchers (Clark, 1981; Tuttle, 1985). People who visit caves, both professionally or for sport, must be acutely aware of the potential damage they can do to resident bats. To minimize such damage, we should recognize that there are caves ("Red Caves") which should not be visited by humans at any time, or only visited during certain times of the year, and other caves ("Green Caves") which are not important to bats or other threatened species and can be open to visitation. Bats select caves as hibernacula or as maternity sites because they fulfill very specific requirements. Fulfilling these requirements depends on cave structure, air circulation patterns, temperature profiles, and the cave's location relative to foraging sites (Tuttle and Stevenson, 1978; Tuttle, 1979). Because the requirements of bats are highly specific, those caves which do fulfill them will be relatively rare and may be absolutely essential to the bats. There may simply be no acceptable, alternative roost

Table 1. Officially endangered North American bats* and their use of cave roosts.

Species	Cave Roost Requirements
Indiana Bat	
<i>Myotis sodalis</i>	Winter Hibernacula
Gray Bat	
<i>Myotis grisecens</i>	Year-Round
Big-Eared Bat**	
<i>Plecotus townsendii</i>	Year-Round
Sanborn's Long-Nosed Bat	
<i>Leptonycteris sanborni</i>	Year-Round
Mexican Long-Nosed Bat	
<i>Leptonycteris nivalis</i>	Year-Round

*These species are listed on both the IUCN Red List and the U.S. Fish and Wildlife Service Endangered Species List.

**Two subspecies of big-eared bats are listed. These are the Ozark big-eared bat (*P. t. ingens*) and the Virginia big-eared bat (*P. t. virginianus*).

sites available. These caves must be placed on our red list. Conversely, most caves will not satisfy these requirements and will not be important as bat roosts. These can be placed on a green list. It seems likely that the vast majority of caves would go on the green list. For example, less than 5% of caves surveyed in the southeastern U.S. were found to be physically suitable as gray bat maternity or hibernating roost sites (Tuttle, 1979).

A major problem, of course, will be deciding whether a cave belongs on the green versus the red list. One obvious criterion is that major hibernacula and maternity roosts of threatened or declining bats should be red-listed, at least during the seasons when bats are present. Conversely, caves which are not occupied by bats and for which there is no evidence of prior occupancy should be green-listed. But, obviously, judgments will have to be made, often with only limited information. For example, it can be argued that historically important roosting sites that are now abandoned should be red-listed, at least temporarily, in the hope that they will be reoccupied. It also can be argued that caves with only small colonies should be red-listed, possibly for gene pool conservation, or that caves important to transients during seasonal movements should be red-listed during the relevant seasons. On the other hand, there may be no harm in green-listing some cave roosts of abundant, widely dispersed species (e.g., those of eastern pipistrelles), particularly if those caves have inherent interest to cavers.

Although listing caves for no or restricted access because of their use by roosting bats is likely to be controversial, these listings are necessary to preserve bat populations. Individuals who explore caves for sport or scientific study have a high probability of encountering roosting bats. The NSS, as the largest single organization of cavers, has the opportunity to provide education regarding potential impacts on bat populations to large numbers of people who are likely to encounter bats. In addition, cavers often have knowledge of bat roosting sites, and this knowledge is essen-

tial to informed and responsible listing of caves on red or green lists. Opportunities are abundant for cavers to cooperate with state, national, and private conservation agencies in identifying and preserving sensitive cave habitat. Several NSS grottos have taken the initiative themselves to construct, or are in the process of constructing, red and green lists of caves. These people should be supported in their efforts. Efforts to construct these lists should be expanded.

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HISTOPLASMOSIS: A HAZARD TO NEW TROPICAL CAVERS

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Each new generation of cave explorers wishing to cave in Mexico or the tropics has to face the possibility of sickness from histoplasmosis. Even modest exposure in a tropical cave may result in incapacitating illness. In order to gain immunity it is desirable for the first exposure to be as light as possible. If the amount of initial exposure is misjudged, results may be serious. The fungus is found in tropical and semi-tropical caves around the world and to a lesser degree in temperate zone caves. Many caves known to be infected are reported here along with a review of some of the epidemics associated with them.

While over 90% of all epidemics originate from contact with birds or bird excreta, a significant number originate in caves. If the caver comes from the northern part of the United States or from Canada, England, or other countries of northern Europe, he is likely to lack immunity. Cave scientists, archeologists, northern mining engineers, and newly-employed guano miners are especially at risk. Some suggestions have been made as to ways to minimize initial exposure. Finally, thought is given to the possible development of a protective vaccine.

Histoplasmosis is a fungal infection of interest to cave explorers, particularly to those who are introducing novices to caving or to those planning to explore foreign caves. Many of those who inhale spores of the fungus at any given time will have no adverse reaction because they already have developed immunity. In those who are not immune the reaction is likely to be more severe. Histoplasmosis is not only an infectious disease brought on by inhaling the spores of the fungus but also an allergic disease in which individual susceptibility is determined for the most part by the extent of previous exposure.

The word 'epidemic' is used in this paper in a limited sense only. It designates a group of people who become ill after exposure at one time or place. Cave epidemics are minor compared to those not associated with caves such as that in Indianapolis, Indiana, in which 120,000 people were infected (Wheat, 1981), Montreal, Canada (many thousands) (Anon, 1966), Cincinnati, Ohio (thousands); Mason City, Iowa, in two epidemics (eleven thousand), Delaware, Ohio (354) (Anon, 1971), Mexico, Missouri (several hundred), and Hot Springs, Arkansas (189). In some epidemics the source of the infection has remained unknown in spite of diligent investigation. Each year about 500,000 people in the United States become infected but only a few hundred are infected from caves.

The fungus is dimorphic growing as a mold and as a yeast. In moist enriched soil at moderate temperatures it grows as a filamentous mold. It forms large mycelial mats in piles of guano-enriched soil. Minute spores, 2-3 microns in diameter are formed within the network or on small stalks and released into the air in tremendous numbers. If the wind carries the spores to a warm, moist soil the cycle starts again.

However, if the spores are inhaled by a warm blooded creature like a bat or a human being a different form develops. The spore bores through the alveolar wall of the lung setting up a local inflammatory reaction. The spore is carried to the spleen and invades cells of the reticulo-endothelial system. In these cells it multiplies like a yeast until released into the blood stream to circulate again. The cells may pass into the intestinal tract and be deposited in the soil to start a new cycle.

THE CONTIGUOUS STATES

Oklahoma

The modern study of the underground epidemiology of this disease began in March 1944, when a group of soldiers at Camp Gruber, Oklahoma, became sick with a respiratory illness after taking refuge from a storm in an abandoned storm cellar shared by bats and other animals (Cain, 1947). Their respiratory disease appearing 11 days later did not correspond to any illness known at that time. Many laboratory tests were run by the health authorities. The histoplasmin test of the victims, though turning positive, was thought at that time to be non-specific. Although the diagnosis of histoplasmosis was not made immediately, the index of suspicion for this disease was raised. The fungus eventually was cultured from the sites of exposure at Camp Gruber in 1951 establishing the diagnosis (Larsh, 1955). The fungus was isolated soon after from bats captured in another Oklahoma cave (Byrles, 1969). Similar observations were made of the outbreak at Camp Crowder, Missouri.

Arkansas

Early in the fall of 1945 a rumor of buried treasure was spread about the town of Foreman, Arkansas. Hernando De

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Soto, the Spanish adventurer, it was said, or possibly Jesse James, the notorious outlaw, had buried his treasure in a local cave. Many local residents knew of a chalk mine in a nearby limestone bluff called Rocky Comfort Cave. An Oklahoma couple with a bulldozer had uncovered a flight of stone steps there the previous week and started the treasure hunt. Actually this was an abandoned tunnel of the Kelley plant of the White Cliff's Portland Cement and Chalk Company. The plant had been a source of cement for sidewalks of Little Rock, Arkansas 50 years before this time (Anon., 1947).

Curved steps cut in limestone led into an entrance room and thence to several small rooms joined by crawlways. The rooms were half filled with crumbled rock and debris. The out-of-town discoverers returned to their home in Oklahoma City only to be hospitalized for treatment of acute chest disease. Twenty-five local adults and teenagers went into the cave on or shortly after September 12, 1945. Armed with garden tools and flashlights, they dug for buried treasure. During the search, they dug into the debris with vigor, moving mountains of dirt and raising a great deal of dust. Some of the diggers recalled that they choked on the dust and could scarcely get their breath. Eventually the searchers left the cave after they despaired of finding the hidden treasure.

Four days later several treasure hunters came down with cough and fever. During the next 9 days, 21 out of 25 of those who had spent time in the cave developed a respiratory ailment with chills, high temperature and chest pain (Washburn, 1948; Lehan and Furcolow, 1957; Halliday, 1958). One of the huskiest diggers, a local planter, lapsed into semicoma and remained unconscious for two days. As the fever subsided, it left the victims weak and short of breath. However, after several weeks had passed, each of the adventurers was on the road to recovery.

Meanwhile a local health officer enlisted the aid of the State Health Department and the U.S. Public Health Service. A health team equipped with a Mobile Field Laboratory was dispatched to the scene and many diagnostic tests were run. The residents placed the blame on poor circulation and stale cave air. A bulldozer was used to carve away the face of the bluff obliterating the original entrance and exposing the rooms. The continuing Public Health investigation showed that the victims developed a positive skin reaction to histoplasmin. The picture was made complete sometime later when the pathogenic fungus was grown in the laboratory from soil samples gathered in the cave. This was the first association of an epidemic of cave sickness with a fungus from the site of infection (Washburn, 1948).

Arkansas, along with Missouri, Kentucky and Tennessee are the heart of the Central United States histoplasmosis belt. The zone includes the southern portion of Illinois, Indiana, and Ohio, and extends to the far Southwest. Eighty

percent of young males in the four central states are skin test positive by the time they reach the draft age. The area of general infection extends into all bordering states but the number of positive reactors falls off with distance. It may be more than coincidence that large blackbird roosts are known throughout this area. Arkansas alone has 17 roosts each of which harbors over a million birds.

Missouri

Late in 1958 or 1959, three members of Middle Mississippi Valley Grotto in St. Louis, Missouri, explored Bat Cave in Shannon County, Missouri (MacLeod, Pers. Comm.). This cave is approached from the Current River by boaters who float down the picturesque stream. The cavers, including a teen-age girl, explored crawlways to the back of the cave. This involved some crawling over guano-covered breakdown. Several weeks later two of them came down with a respiratory illness with cough, chest pain and weakness. The young woman showed her spirit by composing a song which was sung to guitar accompaniment around Mid-Mississippi Valley Grotto campfires.

Histoplasmosis

By Barbara MacLeod

A sad story I have to tell
About a caver I once knew well.
He frequented the places where the rain never falls,
Where the sun never shines, where on water-fluted walls
Bats do dwell.

He took his topo map and went to scout
For a cave he had always heard about.
He had talked to all the farmers and he listened with a grin
To the story that they told him where four people had gone
in
And not come out.

He was warned by everyone to stay away,
That he shouldn't go beyond the light of day.
There the enemy was lurking in the dry and dusty air.
But to him it made no difference; he decided to go there
Anyway.

In a short time the entrance he had found.
Feeling just a little scared, he looked around,
But he saw nothing suspicious, so he trolly-dotted on
Knowing nothing had ever happened in the many times
he'd gone
Underground.

He took off down the passage with a bound.
He trolly-dotted through a guano mound,
He could've walked around it and it wouldn't have delayed
him,
But he didn't know that there *Histoplasma capsulatum*
Did abound.

The enemy gathered forces silently
 Waiting for the perfect opportunity,
 When this bold, intrepid caver with the limestone in his
 blood
 Stubbed his toe and fell face forward in the guano-covered
 mud.
 Oh, tragedy!

With disgust he raked the guano from his hair
 At the time he was completely unaware
 Of the sneaky little critters whose primary occupation
 Was to upset respiration and effect contamination.
 (spoken) T.B. or not T.B.?
 No, it's *histoplasmosis*!

Well, they've had him in the fungus ward since then
 And he's gonna be there 'til I don't know when.
 He's had to give up caving and I know he must regret it,
 But as soon as they have cured him he'll go out and he'll get
 it
 Again.

The composer of the above verse has continued to show a
 talent for folksongs and was able later to explore tropical
 caves with impunity because of her acquired immunity.

A year or so later, three young men from the same grotto
 explored Bat Cave in Pulaski County, Missouri
 (*Underground*, 1960). They also pushed narrow crawlways.
 While resting on his way out of the cave, one man
 remembered that his rose bushes were not thriving. He filled
 a plastic baggie with bat guano to fertilize his plants.
 Another caver did likewise. Two weeks later, two of the
 cavers were violently ill. One was sick for months with com-
 plications and eventually lost a lung and one kidney
 (Rothwall, 1960).

Florida

A thirty-two-year-old man got sick in 1955 about three
 weeks after exploring No Name Cave, Citrus County, near
 Floral City, Florida (DiSalvo, 1970). Samples of cave dirt
 were positive for histoplasmosis. Of bats caught there, 64%
 were infected with the fungus (Tesh and Schneidau, 1967).

In October 1966, a college biology student developed
 histoplasmosis ten days after a field trip on which they were
 exploring caves near Gainesville, Florida (Anon., 1968). The
 student reported that one cave contained not only bats but
 also large amounts of guano. Savior Cave and Grant's
 another sinkhole cave nearby, were investigated as possible
 sources of infection. One bat infected with histoplasmosis
 was caught in the first and soil samples were positive in the
 second (DiSalvo, 1970).

Near Newberry, Alachua County, three sinkhole caves
 were studied by a team of Public Health investigators. In-
 fected bats were trapped in Jones Cave. Indian Cave,
 Jackson County, had infected bats and soil, and Small Pic-

nic Area Cave had infected bats. Turnley Cave, Marion
 County, had positive soil samples (DiSalvo, 1970).

In January, 1973, teen-aged members of a church camp
 group explored a limestone cave in Suwannee County,
 Florida (Anon., 1973). This group of twenty-nine, including
 eight girls, had gone into the cave once or twice for about 30
 minutes without ill effect. While attempting to get the bats
 to fly, this group had thrown dirt at them which created a
 great deal of dust. On February 10, 1973, an 18-year-old girl
 from this group was admitted to the University of Florida
 Medical Center in severe respiratory distress (Halliday,
 1973). On her third hospital day it was learned that three of
 her companions also had been hospitalized. Their chief
 symptoms were cough, fever, night sweats, shortness of
 breath on exertion, and chest congestion. In all, twenty-
 three persons were infected in this group. Symptoms ap-
 peared as early as six days and as long as forty-four days
 after exposure. All of them recovered.

Many Florida cavers have a positive skin test showing that
 they have been exposed to the fungus and have some degree
 of immunity. Of a group of fourteen Florida spelunkers, ten
 had positive skin tests. This gives an overall positive rate for
 this group of 71%. The general population of Florida has a
 rate of 4.7% (Haskell, 1973). Most of the residents of
 Florida have not been exposed to this fungus.

Tennessee

During the 1930s Watson Monroe, a geologist, took part
 in an early study for the State of Tennessee of pulmonary
 disease in two counties with differing climate and soil. The
 investigators were sure that the chest disease appearing on
 mass chest x-rays of the general population was more
 prevalent in limestone areas. Only later was it apparent that
 the health team was confusing the x-ray picture of tuber-
 culosis with that of histoplasmosis. In one Tennessee cave
 73% of the gray bats (*Myotis grisescens*) were infected (Tesh
 and Schneidau, 1967). Human cases have originated in Big
 Bone Cave (Sullivan, pers. comm.). The cave area was
 reported to have a higher fox population than other regions
 of the state.

Texas

The fungus was first isolated in the State of Texas from
 infected bats in Frio Cave, Uvalde County (Emmons, 1966).
 A soil sample was positive from Kickapoo Cave, Kinney
 County (Al-Doory and Rhodes, 1968). In Brewster County a
 small undecorated cave was named Histoplasmosis from the
 fungus cultured from it by a San Antonio physician
 (Cochran, pers. comm.).

Mexican free-tailed bats (*Tadarida brasiliensis mexicana*)
 have been found to carry the infection especially the eastern-
 most of the four migratory groups (Group D Cockrum)
 from Mexico. The great bat caves of Texas: Frio, Blowout,

Bracken, Bat Cave Cavern and Devil's Sinkhole, must be considered to be infected until shown otherwise (Emmons, 1966; Al-Doory and Rhoades, 1968). Three biologists became ill after visiting Bracken Cave. They were believed to be the first reported cases from this well known cave (McMurrey and Russell, 1982).

New Mexico

A Public Health Epidemiologist got histoplasmosis after an off-trail visit to Carlsbad Cavern (Furcolow, 1965). He believed that he was immune because he had a positive skin test before going on this trip. His illness was not severe but was accompanied by a rise in serum antibodies. In recent medical literature are recorded a number of cases of reinfection. Apparently no one can be certain that he will not get the disease more than once. Some cases of far-advanced disease are thought to be due to repeated reinfections. A New Mexico state archeologist also got the disease while exploring passages of Carlsbad (Meador, pers. comm.). The organism was found in fresh guano from Carlsbad and in guano from adjacent caves (Kajihiro, 1965).

A caver caught the disease in 1973 while visiting four wild New Mexico caves. Crockett's Cave was considered the most likely source because it entailed much crawling through dust and bat guano (Rhodes, pers. comm.). Months later the caver was still weak and short of breath. A lecturer at Grand Canyon Lodge stated that Tramway Cave, named from its suspended cable, was infected, but had no details.

Members of two families were infected in an abandoned gold mine near Hobbs, New Mexico. The states of Oklahoma, Texas, New Mexico and Arizona form the southwestern extension of the mid-American histoplasmosis zone.

Other United States Sites

Infected soils have been reported from scattered sites in northern and southern Arizona and many species of bats have been found to be infected (DiSalvo, 1969). An infected Little Brown Bat (*Myotis lucifugus*) was found in Montana (Bell cited by Ajello, 1969). Infected cave soil was found in Spirit Mountain Cave, Cody, Wyoming (Enright, 1979) and Maquoketa Caves, Iowa (Cazin, 1967). Maryland, Georgia and Alabama have yielded infected bats (Tesh and Schneidau, 1967). A West Virginia cave is reported as infected (Hixson, pers. comm.). A biologist got histoplasmosis in Virginia after sleeping in the back of a truck in which cave coveralls had been shaken out (Peck, pers. comm.). Attempts to close an infected Virginia cave were dropped after it was pointed out that, because of the starlings, a person was more likely to get the disease by sitting under a tree in the downtown parks of Washington, D.C., than by visiting the cave.

Puerto Rico

In 1963 the Spanish Club from a nearby high school

visited the Aguas Buenas Caves in Puerto Rico. Two weeks later several of the students developed cough, fever, and pneumonia (Sifontes, 1964). One showed erythema nodosum, a blotchy swelling of the skin associated with histoplasmosis. Others had only mild symptoms. Of fourteen in the group, thirteen were found to have positive skin tests. Chest x-rays of many of them showed abnormal shadows. When an equal number of their classmates were tested all were negative. The caves were the only place outside of school where the original group had been together.

Two Public Health officials went to the caves to collect soil samples. They wore paper masks during their trip. Both developed positive skin tests following their visit (Torres-Blasini, pers. comm.). They were alarmed to find that the caves had been designated a Radiation Shelter by the Civil Defense Authority. Civilians had been instructed to report there with their entire families in case of a bomb attack. This order was rescinded because the cave was unsuitable for this purpose. Most of the populace of Puerto Rico have a negative skin test. Five soil samples taken from different parts of the cave were positive for the fungus.

In 1968 an NSS field trip to the Aguas Buenas Caves included six members who had negative skin tests. Fifteen days after entering the caves, three members became ill (Lewis, 1968). They developed high fever, cough, loss of appetite, fatigue, chest pain and headache. Not only was time lost from work but there was also prolonged debility. Three others developed positive skin tests. The caves were posted by health authorities against entry before the group left Puerto Rico. Since then on several occasions it has been proposed that they be reopened for commercialization (Beck, 1973).

In February 1963, a soil sample from the Cueva de las Panes near Utuado was found infected with histoplasmosis (Torres-Blasini, 1966). This cave lies in the west-central part of the island. A 1x2m entrance leads into a series of high-vaulted rooms extending upward about 50m. There are three consecutive chambers with a smaller side chamber opening off the large middle room. The ceiling is decorated with stalactites. Fruit-eating bats, *Artibeus jamaicensis* among others, inhabit the cave. In places, long sprouts of germinating seeds can be seen growing from the guano. The atmosphere is very humid with water dripping from formations to form pools on the floor. Many people visit this cave each year.

Recently, a group of six made an exploratory trip on the Tanama River. This deeply entrenched river near the Aricebo Radio Telescope site goes underground nine times in the course of a few miles. The group slept in caves several times on the trip. A short time later, one of the team, a long-time government naturalist, became ill with an acute disease (Gurnee, pers. comm.). He was flown to a government hospital near Washington, D.C., in critical condition. Eventually his illness was confirmed as histoplasmosis. He had

been hospitalized for three months and was still far from well at the last report.

Mexico

In years past an illness was widely known to the people of North-Central Mexico as the "Fever from Abandoned Mines" (Gonzales-Ochoa, 1957). The cave disease was common knowledge in folklore and in local medical circles. A letter written in 1895 is preserved in the state archives of Nueva Leon. It is from a healing woman of the north to the Fathers of the Sick in Nueva Leon. In it she stated that she was going about curing those individuals stricken with the Fever from old Mines and Caves. She preferred her own simple remedies to those used at that time by the doctors.

Many years ago the disease was associated with the presence of guano. A bat cave close to the village of Torreon, Nueva Leon had a bad reputation. Many cases of chest disease and several fatalities occurred among those men who carried out guano (Gonzales-Ochoa, 1957, 1963). In 1930 the Mayor of the town ordered the cave closed to prevent further cases of this disease. Because of histoplasmosis, caves were given names like La Cueva del Diablo (The Cave of the Devil), La Envenenada (The Poisoned Cave), or Cueva la Eviudadora (The Widow-Maker) (Gonzalez-Ochoa, 1960).

In August of 1948 a party of four explored an abandoned mine, El Refugio, in Lampazos, Nueva Leon. These individuals, a Mexican engineer and his assistant, an American and a Canadian geologist, became ill in six to nine days with fever, cough, and signs of pneumonia (del Valle, 1957). The chest x-rays showed their lungs to be filled with numerous nodules resembling those of tuberculosis. The Canadian geologist succumbed to the disease two weeks later. The others were seriously ill but recovered. Since that time many Canadian mining engineers working in the tropics have suffered the ill effects of histoplasmosis (Anon., 1974).

Another epidemic occurred in 'La Cueva del Diablo' located between Monterrey, Nueva Leon and Laredo, Texas. Fifty men were hired to remove bat guano from this cave to be used as fertilizer. Twenty of the fifty were stricken with a respiratory disease and within a short time eight of them had died (Gonzales-Ochoa, 1957). Visiting cavers in 1966 were warned by a local resident that the cave was "muerta" (dead) (Al-Doury, 1968). In December of 1956, sixteen workmen were hospitalized in the Civil Hospital of Gomez Palacio, Durango, with a respiratory disease (Gonzalez-Ochoa, 1957). One week before they had entered 'Indian Cave' also known as 'Cueva del Guano' near Picardias, Durango, to bring out bat guano. They developed a cough and expectorated bloody sputum. Fourteen had abnormalities on the chest x-ray. Four of these became critically ill and died within the first week. One of the survivors had a negative skin test 20 days later, but was

positive when rechecked in eight months. Two who had minimal involvement by chest x-ray showed complete clearing in six months. Of the four with more serious chest involvement, three were improved six months later on x-ray and one appeared to be worse.

In July of 1954 a man visited the cave of Ixtacumbilix-unan, Yucatan. After twelve days he became ill with a lung disease. His x-rays and skin tests were positive. A follow-up study three years later showed the lung lesions to have healed and to have become calcified throughout.

In October of 1954 five men were investigating an old guano mine near Mapimi, Durango. This mine had not been worked for forty years and large amounts of bat guano had accumulated. Four of the explorers were in the cave for several hours and collected specimens of bat guano for analysis. Each of these became ill seven to fourteen days later (Gonzalez-Ochoa, 1957). One man who remained near the entrance did not get sick. One of the stricken men got rapidly worse and died after a week. Another became skin-test positive after a month but got better. His lungs showed clearing in about eight months' time.

Three students from the University of California explored a cave in the State of Nyarit in the winter of 1955. They later became ill. The cause of their illness was discovered to be histoplasmosis particularly through the efforts of Dr. Smith of Berkeley, California, and by the laboratory of the University of Chicago. The disease was considered to be rare and unusual at that time.

An engineer and his driver in October of 1956 entered an abandoned mine in Queretaro, Queretaro which contained abundant bat guano. Both became gravely ill a few days later (Gonzalez-Ochoa). After twenty days the skin test of one was negative but his serum was very strongly positive with an anti-histoplasmosis titre of 1:128. No higher titre had previously been recorded from a Mexican cave. Both men got worse in spite of intensive medical treatment and died within a month.

In January of 1957 five students from the Institute of Technology in Monterrey, Nueva Leon explored a cave near the highway leading to Ciudad Victoria, Tamaulipas. They found an abundance of guano within the cave. Two of them became ill with symptoms of histoplasmosis. In one of them the diagnosis was confirmed by isolation of the organism from his bronchial secretions by means of injection into a hamster. Both students recovered.

In September of 1956 there was an epidemic in Caca-huamilpa, Guerrero. The cave is situated near the old highway from Cuernavaca to Taxco. This attractively decorated cave boasts a half-mile of huge, electrically lighted passage. Thousands of people have visited this cave including the ill-fated Empress Carlotta who wrote a note on the wall showing how far she had gone. A special party of nineteen tourists including several doctors requested a wild tour beyond the commercial section of the cave. The passage

explored was so poorly ventilated that it was difficult for the party to breathe. The visitors sank in bat guano up to the waist. Thirteen of the party got severe chest congestion. Four patients were treated at the Institute of Health and Tropical Diseases where the diagnosis was confirmed. All recovered.

This cave was also the site of two subsequent outbreaks in 1961. In each instance, local residents, some of whom were working as cave guides, explored back passages in an attempt to discover extensions to the cave. The explorations were discouraged after members of each party became ill from inhalation of infected dust (Bustamente, 1964).

Other Mexican Sites

In September of 1959 four workers got histoplasmosis in a mine, 'La Matona,' near Gomez Palacio, Durango. They were treated in the Civil Hospital of Gomez Palacio and recovered. In 1960 a case occurred in a visitor to a grotto in the state of Morelos and another in San Francisco, Nyarit. In 1962 an epidemic occurred in Cajales, Guerrero. In 1963 there was an epidemic in the grottos of Michapan, Morelos.

Two Texas cavers explored 'La Cueva del Guano,' Durango, also called 'La Cueva de Espana.' They learned later that the cave was closed to guano mining in 1961 when one miner died and others went to the hospital.

'La Cueva Chica,' San Luis Potosi, contains a series of pools through which the explorer must pass, some of which are covered with a deep layer of floating guano. The cave has been the site of extensive biological collecting and is noted for its wide variety of cave life. It is the type location for the first blind characid fish ever found. The New York Zoological Society and the New York Academy of Science were co-sponsors of one scientific expedition to this cave. They not only found the blind fish for which they were searching, but also found a large number of fish in various intermediate phases between surface and fully-adapted subterranean types. These findings were enthusiastically reported to the scientific world. All but two of the members of the expedition developed histoplasmosis. One of the sponsors succumbed a short time later to a respiratory illness possibly aggravated by histoplasmosis (Smith, 1968).

In 1961 eleven men went to work in 'La Joya' of Lerdo, Durango. They were removing mineral salts from the cave floor. This cave lies in a desert region which is very dry. The relative humidity in the cave is 20%. The cave floor is made up of clay and mineral salts with only traces of organic matter. The dry dust was apparently heavily inoculated with spores of histoplasmosis since all eleven of these men became ill and three died.

In 1959 there were cases reported from the Grutas de Cuetzala, Guerrero. Very little has been written about this very large cave. In 1960 a case was reported from Sotano Oreza. This lies in an area of sinks and resurgences in southern Veracruz.

In July of 1966 four Texas cavers explored the 'Cueva del Diablo,' Sabinas Hidalgo, Nueva Leon. The owner of the cave property warned them that the cave air was dangerous. They improvised masks from cotton handkerchiefs. Portions of the cave were moist while others were dry and dusty. A few bats were seen and the smell of ammonia was noted throughout. All four developed positive skin tests following their exposure but only two became ill. They learned later that eleven guano workers had taken sick from work in this cave and that five had died. They urged that no one go in this cave without good reason.

A British-Belgian-U.S.A. expedition to Mexico to explore the Nacimiento de Rio Saludo near San Lucas was aborted when most of them became ill. Several were treated in Mexico City and others were flown to England for treatment. Some of the party felt that they would never survive the severe fever and pain that they suffered. They advised the use of masks or avoidance of dry caves containing bat or bird guano (Gill, 1983). A British specialist thought that their misfortune should not deter others from exploring tropical caves (Frankland, 1983).

Histoplasmosis is endemic in many caves of Mexico. Over a 15-year period 423 cases were reported in 35 epidemics and a few isolated cases (Gonzales-Ochoa, 1963). Cases were reported from Mexican Caves in eleven states. Most of these infections occurred in newly-employed guano workers or first-time explorers of Mexican caves. An unusually large number of local residents seemed to succumb to the disease. This may be due to genetic factors or to heavy initial exposure to the infected dust. The most severe cases developed an overwhelming pneumonia with septicemia and toxemia. Respiration was severely compromised in the inflamed lungs.

Guatemala

In 1969, two Wisconsin scuba divers were part of a Milwaukee Museum Expedition to study the sacred wells of Guatemala. One day when they were not diving, they helped their teammates with archeological work. One task was to fill pails with cave dirt so that it could be sifted for artifacts. A few days later both of them became seriously ill and were taken to a hospital at Oaxaca, Mexico (Spaulding, 1969). A Milwaukee doctor reported that they ran a fever of 105°F. and could not walk twenty steps without getting completely out of breath. They were flown to Mexico City where the diagnosis of histoplasmosis was confirmed. Three months later they had improved to the point that they could leave Columbia Hospital, Milwaukee, for weekends at home. Two other members of the expedition suffered only minor illness from their exposure.

While making cave movies on the Alta Veragay area of Guatemala in 1968, two professional crew members from New York were stricken (Gurnee, pers. comm.). Peter Van Dyke, soundman for ABC, and a companion were flown to

New York seriously ill. Both men were reported to be disabled for nearly a year by pulmonary histoplasmosis. Three people out of seven who entered Cueva de Juan Flores early in 1973 came down with the disease (Breisch, 1973).

Belize

In British Honduras a twelve-year-old boy, the son of North American ranchers, became ill with a respiratory disease. He had been in a cave one week before he got sick. At first his illness was thought to be tuberculosis. He was flown to the United States where further diagnostic tests showed that he had histoplasmosis (MacLeod, pers. comm.).

El Salvador

Infected bats have been trapped near La Libertad, El Salvador.

Panama

On June 20, 1965, a group of seven United States soldiers explored a cave on the shore of Madden Lake. When the lake level is high, parts of the cave are flooded. The soldiers used one of several entrances, a tunnel-like crawlway, to reach the inner part of the cave. They noted many bats flying wildly about. They did no digging and left after twenty or thirty minutes. Three weeks later five of the cavers got sick with an acute respiratory infection with chills, fever, sweating at night, and weakness (Shacklette, 1966). Chest x-rays taken at the army hospital showed the typical infiltration of the lungs and their blood tests were positive for histoplasmosis.

Public Health officials with several cavers returned later to try to determine the infectivity of the cave. One official knew that his skin test was negative, so he went only to the cave entrance. In spite of this he got sick thirty days later with histoplasmosis. Another had had a positive skin test for fourteen years so he went in the cave without hesitation. He also came down with histoplasmosis. Another positive member did not get sick but showed a rise in serum antibodies after the trip. This group isolated the fungus from the air of the entrance as well as in the cave itself. Tests of soil were positive. Laboratory animals exposed to the air in the cave became infected. Of 169 bats they trapped in the cave, eighty were found to be infected (Hasenclever, 1967).

This group also caught infected bats in the Chilibre Caves in the Republic of Panama, in an abandoned gold mine on the Isthmus, and in a shelter on an air field. The Greater Mustached Bat, *Chilonycteris rubiginosa* and Little Big-Eared Bat, *Micronycteris megalotis*, often had the fungus in their feces. When these creatures were dissected, ulcerated sores caused by histoplasmosis could readily be seen in the lining of the intestine. These sores or ulcers discharged infected material into the intestinal tract. In this way the feces became directly infected and spread the infection to the soil

of the cave. Of 623 bats collected in Panama and the Canal Zone in another series, one in ten was infected. By this study, it was demonstrated that the soil could become contaminated at almost any spot where bats rested.

In some Central American countries like Panama with a long warm season and high humidity, almost the entire population is exposed to the disease during childhood. The disease is almost unknown among adult residents.

Off Florida, site unspecified

Two Florida treasure seekers became ill after being escorted to a cave at a secret location in Central America. A third case developed in a man who was believed to have followed the others surreptitiously to the hidden location (*Medical Times, News and Notes*).

Jamaica

The wife of an American biologist is reported to have contracted histoplasmosis while caving in Jamaica (Peck, pers. comm.).

Trinidad, B. W. I.

Several large caves are found on the island of Trinidad which provide shelter for oilbirds and bats. The caves differ in elevation, forest cover, and stream activity. Oropouche Cave in limestone is in low hilly country, partly forested and partly cultivated. The three Aripo Caves lie at a much higher elevation in a humid montane forest. The two Tamana Caves are found in central Trinidad.

In the Aripo Caves, many ledges are occupied by oilbirds. The cave temperature shows little variation from 69°F. Water drips from the roof and two of the caves have streams running through them. The floor is covered with oilbird excrement along with seeds of palms and fruits that have been regurgitated. Histoplasmosis was found in the soil of the first and third Aripo Caves, the Oropouche Cave, and the larger Tamana Cave (Ajello, 1962a, 1962b). All the caves contain bats and the vampire bat is found in the largest Aripo Cave. The Aripo and Tamana bat caves are popular tourist attractions and are visited by many people each year.

Venezuela

The unique oilbird, *Steatoris caripensis*, was discovered by Alexander von Humboldt, the German explorer-naturalist, in 1799. They were in a cave near Caripe, State of Monegas, Venezuela, now called Cave of the Guacheros. This bird is a large nocturnal fruit-eating relative of the whippoorwills and goatsuckers. For several thousand feet from the entrance the ledges of a large hall are occupied by oilbirds. They have a click type of radar and fly in the dark by echolocation. This rather rare chicken-size bird is found in only a few other caves, widely scattered, in Trinidad, Peru, Colombia, Ecuador, and British Guiana (Ajello, 1962a). Histoplasmosis has been found in the Cave of the

Gaucheros and in the soil of two other oilbird caves. Because the birds are few in number, their role in the dissemination of the disease is felt to be minor.

A local industry operated for many years in this area to produce a high grade cooking oil. This oil kept very well in a tropical climate. When the young oilbirds were nearly grown but unable to fly, they were collected from nests on the ledges. Each had developed a very large fat pad from the rich fruit and palm seed diet brought by the parents. The fat was extracted by rendering in large iron vessels and was preserved in earthen pots. Now the birds are protected. The Cave of the Guacheros has been declared a National Monument and is under governmental supervision. Visitors are led through the cave by way of a passage parallel to the hall of the oil birds by trained guides. There is a large bat population found in other sections of the cave.

One of the early victims of histoplasmosis was Dr. de Bellard Pietri, grandmaster of Venezuelan caving, Director of the Section of Speleology of the Venezuelan Society of Natural Science and Conservator of Speleology of the Museum of Natural Science. On March 22, 1951, he explored la Cueva de Na Placida situated in Charallave, State of Miranda. He became acutely ill eight days later and was feverish for seventeen days.

On January 19, 1955, he explored the Cuevas de El Pinon in Ocumare del Tuy, State of Miranda with a young companion. Twenty-one days later the novice caver became violently ill in a similar way with high fever and disseminated bronchopneumonia. The young man was susceptible to the disease while Dr. Pietri was immune because of his prior exposure.

Other Venezuelan caves known to be infected are Cueva del Encanto and Cueva del Agua, State of Anzoategui, La Gruta or Cueva de Carrizalito, State of Falcon, and especially, Cueva del Penon No. 1, State of Miranda.

On February 6, 1954, a group of eleven students and two instructors from LaSalle in Barquisimeto visited the Cueva de la Vieja Miranda. They were inside several hours collecting spiders, pieces of stalactites, and samples of guano. Some descended by use of a rope to a pool lying in the deepest part of the cave. The humidity was high and there were innumerable bats. During the second week following their visit, five developed fever and weakness. One instructor was immune. All the rest got sick. Seven had a benign course of their illness. Two were moderately ill, and two were seriously ill. Skin tests done at a later date showed that each person was positive after visiting the cave.

Several months later a party of five collected soil samples from the cave. All but one were positive before the trip. The negative person wore a mask during the entire trip except for a moment while a photograph was taken. During that moment he held his breath. Nevertheless, in sixteen days he developed acute histoplasmosis. The spores are so small that only a very fine mesh filter is effective and it must fit the

face well. Four out of five soil samples were positive on laboratory study (Campins, 1956).

Peru

In a towering cliff in the Peruvian rain forest lies the vine shrouded mouth of the Cueva de las Lechuzas, a well known archeological site. This enormous "Cave of the Owls" is named for the colony of Guachero birds that make it their home. They have large night-adapted eyes that reflect light like those of an owl. For years some visitors have had an illness called Tingo Maria Fever, after a trip to the cave. This illness was described by Antonio Raimondi in 1874.

In 1955 two students who had visited the cave were reported to have yielded cultures positive for histoplasmosis (Ajello). *H. capsulatum* turned out to be the cause of Tingo Maria Fever. Tests of soil from the cave were positive for this fungus. Also, soil tests from surrounding fields were often positive. Distant fields were usually negative. This suggested that the disease was spread in a radial manner from the cave mouth by defecation of birds or bats in flight (Constantine, 1970) or by infected animals. The use of infected guano as fertilizer also may have spread the fungus to field and garden. Nearby residents were found to have an unusually high percentage of positive reactions to skin tests.

The wife of the director of a California museum went up to the cave entrance but did not go into the cave. Thirty days later she came down with pulmonary histoplasmosis. A notice has been posted at the entrance to the cave warning visitors of the danger.

Columbia

The Macaregua Cave near San Gil, Santander, in central Columbia has been known to science since historical times. It is a stream cave with many large rooms and one known entrance almost closed by sliding rocks. It houses thousands of bats. The cave is said to have been the burial ground of Indians and is reputed to contain fabulous riches buried with the Indians. Strange animals are said to live there. Because it is sacred ground to the Indians, it is rumored to contain a curse and whoever enters becomes ill (Grose, 1970).

Many years ago a group of fifteen people went in hoping to find gold or strange animals. They found darkness, foul air, and confusing passages but nothing of value. Two weeks later all of them became ill. For some time after this the cave remained undisturbed. However, in November 1966 two biologists from the University of the Andes in Bogota explored the cave. Both were known to be Histoplasmin positive. Of the bats they captured twelve were found to have histoplasmosis. In order to test the infectivity of the cave air, seven volunteers who were skin test negative spent two to four hours in the cave collecting bats. Fourteen to sixteen days later, all complained of fatigue, moderate fever, pain on inspiration, and cough. One of the

five was extremely weak for six weeks with generalized disseminated histoplasmosis while the others had the benign form.

Brazil

Brazil has had several epidemics. In one a teacher, twelve scholars, and a dog were affected after visiting a cave (Paula, 1959). Another involved eight people who were infected from bat droppings in a building (Fava Netto, 1967).

Europe

England and most portions of the European continent north of the Alps appear to be free of histoplasmosis. One exception is Rumania from which infected soils have been reported from the cave of Topolnita, Oltenia district (Alteras, 1965). Cases have been reported from Italy (Sotgiu, 1965) and Israel (Ajello, 1977).

Cyprus

A centuries-old labyrinth in the ancient Roman settlement of Curium in southern Cyprus in the Mediterranean was visited by a party of tourists. One man in the party caught a bat and showed it to a friend. Several weeks later these two members of the group became ill (Stoker, 1964). Chest x-rays and skin tests confirmed the diagnosis. They eventually recovered. By way of contrast, a biologist trapped and banded 30,000 bats in northeastern U.S.A and eastern Canada without becoming positive (Fenton, pers. comm.).

Africa

Transvaal

On March 12, 1953, four students explored Johnson's Pothole, a limestone cave in Potgietersrust District, Transvaal. One of the students went only part way into the cave before returning to the surface. The other three continued on and after some hundreds of yards they reached a dead end. The floor was covered by a deep layer of bat guano and they were exposed to the dusty atmosphere for several hours. Fourteen days later each of the three developed an acute pneumonia (Murray, 1957) from which he recovered after a period of three weeks. The fourth student developed no clinical signs but became histoplasmin positive.

On April 26, 1953, four adult Europeans explored a large limestone cave in the Thabazimbi area. They spent three hours in the cave digging through guano at different points to determine its depth. Seven days later all four developed typical attacks of pneumonia from which they recovered after a period of several weeks (Dean, 1957). After the illness all were histoplasmin positive.

On July 16, 1953, seven students explored a limestone cave leading off a 70-foot pothole. Few bats were observed and there was little guano. The cave was very dusty in the

dry portions. The students spent the greater part of the day in the cave. Nine to fourteen days later all developed attacks of pneumonia (Dean, 1957) from which they recovered in three to fourteen days.

An extensive study was made of the immunity of members of the Transvaal Speleological Association. Of twenty-nine regular members of the club who had been caving for some time, twenty-six were found to have positive histoplasmin skin tests. Twenty-two of these had a clear-cut history of respiratory illness after caving. A few members were skin test negative, but had an obvious immunity. Ten new members who had just started caving were recovering from respiratory infections. Within a few weeks or months these ten became positive on skin testing for histoplasmosis (Dean, 1957).

Another test group consisted of fourteen new members of the Society who had never been in caves. Their skin tests were negative. On joining the club they had chest x-rays, blood counts, and the blood serum of each was examined for antibodies against rickettsiae, fungi, and various viruses. In each person there was observed an attack of pneumonia following his first exposure in a cave known to be infected (Dean, 1957).

Subsequent skin tests showed that they had changed from histoplasmin negative to histoplasmin positive, and in most cases changes were found in the chest x-rays. The severity of the illness seemed to be related to the length of the exposure as well as to the particular cave. One cave, Johnson's Pothole, Hennops River, always led to infection of cavers who had not previously suffered from the disease. Laboratory animals exposed in this cave developed histoplasmosis.

Three adults explored a cave in the Skurweberg Range near Pretoria, South Africa. One became ill with a bout of what was thought to be influenza. This was later correctly diagnosed as histoplasmosis. His two companions had x-rays characteristic of the disease. Another adult was found to have calcifications in both lung fields. In 1963, three men were in a party that visited caves in the Congo Caves area of the Cape Province in March (Wolpowitz, 1963). Two of them explored Marcus Cave, Melville's Pot Cave, and Spiesgat Cave. One visited Marcus Cave but only stood in the entrance to Spiesgat and Melville Caves. Each developed acute pulmonary histoplasmosis.

A Rhodesian Geologist explored bat caves in the Urungwe Native Reserve (Dean, 1955). Twelve days later he became ill. Three weeks later he was a desperately sick man. His guides were unaffected. Two persons became ill in 1958 following exploration of the Magwento Bat Cave in the Urungwe Mountains, Mashonaland. Three miners explored an old mine shaft in the Kersworp District in 1950. Four to seven days later they developed a severe febrile illness which because of the x-ray findings was diagnosed as miliary tuberculosis. They recovered completely in three weeks.

Skin tests were done on twenty members of the Cape Speleological Society. All were negative to Histoplasmin until such time as they explored in the Transvaal. The local caves that were regularly visited by this group were apparently free of histoplasmosis.

Rhodesia

In 1953 a visiting overseas archeologist developed a febrile illness after exploring caves in Northern Rhodesia (Zambia). A year later his skin test was positive for histoplasmosis. In 1960, three adult members of an exploring party became ill after visiting Ulster Caves near Sinonia, Southern Rhodesia (Zimbabwe) (Gelfand, 1962). Each developed a positive skin test.

In Rhodesia many local people are fearful of entering the caves. This is not only because the witch doctors carry out secret ceremonials there, but because the caves are thought to be M'tagati or "bewitched." A native constable died three weeks after entering one of the forbidden caves. Six months later a trooper of the South African Police examined a packet of bones and other equipment of witch doctors in a cave. Afterward he got pneumonia and died.

These unfortunate accidents seemed to have spawned a large number of tales of "haunted caves" and "mysterious curses" that cause intruders to become ill. A member of the Rhodesian Geologic Service spent one day in a large cave and ate his lunch there, according to a report. Twelve days later he became acutely ill. He was found to have a positive chest x-ray and skin tests. Histoplasmosis apparently can be acquired by swallowing the organism as well as by inhaling the fungus. The Grotto of Kariba Reserve, Urungwe should be considered a source of this disease. Four miners got sick in Matabeleland while reopening old bat infested portions of a mine (Doy, 1974).

Tanganyika (Tanzania)

In October of 1957, a 29-year-old biologist and his wife became ill after visiting the Amboni Caves near Tanga in Tanganyika (Ajello, 1960b). These caves are a part of a series of caves along a deep gorge cut in compact gray limestone of Jurassic Age. The entrances are pillared by travertine and the walls are covered with it. In the cave there are large vaulted chambers connected by galleries and tunnels that provide a home for several species of bats. For many years the guano has been mined for use as fertilizer. At least one of the explorers examined bat guano closely for insects and ticks. Both persons became ill. Seven of thirteen soil specimens that were tested from this cave were found to be positive.

Members of a caving group of Jadotville, Kantanga, demonstrated the presence of the fungus in the grotto Etienne in the grottoes of Mulungwiski (Richebe, 1960). There are other reports of the disease from Zaire, the Sudan, and a possible case from the caves of Morocco

(Young). In all histoplasmosis has been reported from more than seventeen central African countries, but the limit of distribution of the fungus is unknown.

Malaya

The fungus was found in soil samples from a bat cave in a limestone cliff a few miles north of Kuala Lumpur, Malaya (Ponnampalam, 1963). The cave is 65 to 130 meters high and nearly two kilometers long. Several streams run through it and water drips from the roof. The interior harbors many bats of several species. This was the first isolation of this fungus from soil in Malaysia.

Australia

In September 1972 a group of cavers from the suburbs of Sidney visited Church Cave, Wee Jasper, near Yass, N.S.W., Australia. Because they lived some distance apart it was several weeks later that each learned that the others had been sick. Each had developed bronchitis with fever, blocked nose, cough and headache (Welling, 1972). Public Health authorities responded. Soil studies were made, cave temperatures recorded, and nearby caves investigated. One cave serves as a maternity roost for bats from Church Cave so both are under suspicion. The disease has been reported from New Zealand but no details were given (Anciaux de Faveaux, 1960).

The Philippines

Other reports have come from the Philippines. One cave on the Island of Cebu is known to be infected (Sullivan, pers. comm.). This cave lies in one of a series of limestone ridges that traverse the central part of the island. It is occupied by swallows that nest on the cliffs and vertical walls. The nests are composed of a gelatinous fishy paste with bird saliva and are collected to make bird-nest-soup, an oriental gourmet's delight. Nest collecting has been restricted here because of the hazard of histoplasmosis.

This list does not exhaust the caves or caving areas that are infected. Numerous other examples of illness are rumored following cave exploration. Fortunately most of them are of a benign type and the victim has made a complete recovery. Every caver should familiarize himself with the disease and with infected areas. He should try to protect himself from needless exposure to this fungus and try to help others to avoid heavy exposure until immunity has developed.

SUGGESTIONS

1. Stay upright. Keep your face as far above the guano as possible. Laboratory animals exposed near the floor get more infection.
2. Avoid stirring up dust.
3. Stay out of caves containing large numbers of bats. They not only have own pathogens but they harbor a variety

of biting arthropods that are ready to transfer those pathogens to you. This is also true of other cave animals.

4. Make sure your first exposure is a light one. Do your early caving in an area of lightly infected caves or visit bird roosts.

5. Avoid infected caves unless you have a positive histoplasmin skin test or have had adequate previous exposure.

6. Do not have any contact with the fungus if you have suppressed immunity or have AIDS.

7. Be wary of any dirt brought out of a cave. Do not shake out cave clothing or equipment in such a way that dust will be inhaled. Wash boots in running water if possible. Use care in cleaning survey instruments or brushing the dirt off archeological cave artifacts.

8. In the laboratory handle cultures under a hood. Do not sniff the cultures. Handle cave specimens including soil samples, as if they were highly infectious. Follow standard laboratory safety guides to avoid laboratory infections.

9. Handle bats and other cave creatures with care.

10. Respect both wet and dry caves. Cave dirt can be infective no matter how much moisture it contains. It may be a dry powdery dust, damp dirt, or wet mud. Spores develop in a moist environment. Even a flooded cave may have air filled with spores. If a cave is blowing air outward or bats are flying, an area around the cave mouth may be infected. If there is a crust on the guano, step in such a way as to avoid breaking it.

11. Keep in good physical condition to keep your immunity high. Avoid excessive fatigue and protein depletion. Even if you know you are immune, do not get a heavier exposure than necessary. Do not be misled by well-intentioned persons who have an acquired immunity although their skin test is negative. This only means that the skin test at times lacks adequate sensitivity. Do not invite reinfection.

Exposure to histoplasmosis poses a problem for each new generation of cavers. Usually this is solved in hit or miss fashion by cavers in the U.S. by exploring local caves first and obtaining light exposure. This method is usually effective. One might be tempted to inhale spores from a culture since laboratory infections are a well known way to get the disease (Murray, 1963). Neither of these methods can be recommended since they are uncontrollable. Before doing anything to try to gain immunity, consult your doctor.

The severity of the initial reaction appears to be related in a direct manner to the degree of infectivity of the site, that is the concentration of spores in the inhaled air, and with the length of time of exposure. In group epidemics the lightest case is usually the person with the shortest time in the cave (Lehan, 1957). Development of immunity should be confirmed by a positive histoplasmin skin test. A month should be allowed for immunity to develop. It would seem foolhardy to explore a heavily infected cave if one had no immunity.

The development of a vaccine is not such a remote possibility as it might seem. Dr. Herbert Hasenclever at the National Institute of Allergy and Infectious Diseases asked who would use such a vaccine (Carper, 1969). Possibly we can answer his question. An experimental vaccine already has been produced. Histoplasmosis spores were killed by exposure to steam for ten minutes. When tested on New Zealand White rabbits, killed spores protected them from injection of lethal doses of live spores (Wong and Kwan, 1973). Such a vaccine might be proposed as an "orphan drug" if it met the requirements of the National Institute of Health for government subsidy of development and production. Promotion of a histoplasmosis vaccine might be a suitable project to be taken up by the organized caving community.

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For more information about the diagnosis and treatment of histoplasmosis, please consult any standard textbook of medicine.

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A PARTIAL LIST OF EPIDEMICS AND INFECTED SITES

United States of America

- Arkansas: Rocky Comfort Cave.
- Florida: No Name Cave, Savior Cave, Grant's Cave, Jones Cave, Indian Cave. Small Picnic Area Cave, Turnley Cave, Suwannee County Cave.
- Missouri: Bat Cave, Shannon County; Bat Cave, Pulaski County.
- Oklahoma: Cave near Reed.
- New Mexico: Carlsbad Cavern, Crockett's Cave, Tramway Cave.
- Tennessee: Big Bone Cave.
- Texas: Frio Cave, Kickapoo Cave, Histoplasmosis Cave, Bracken Cave.
- Puerto Rico: Aguas Buenas, Cueva de las Panes. Tanama River.

Mexico:

- Coahuila: Cave near Torreon.
- Durango: La Cueva del Guano (La Cueva de Espana or Indian Cave), Cueva Joya de Lerdo, La Matona.
- Guerrero: Grutas de Cacahuamilpa, Cueva de Cajales, Grutas de Cuetzala.
- Morelos: Grutas de Michépán. Cueva de la Poza de Moctezuma, Cueva del Salitre (Tetecalita).
- Nuevo León: Cueva de la Boca, Cueva del Diablo, Cueva Envenenada, Cueva de la Virgen, Cueva de San Bartolo, El Refugio.
- Nyarit: Unidentified cave.
- Puebla: San Juan Raboso.
- Queretaro: Queretaro Cave.
- San Luis Potosi: San Luis Potosi Cave, La Cueva Chica.
- Tamaulipas: Cueva del Abra, Cueva del Guano de Tamaulipas, Cueva de los Troncones.
- Yucatan: Cueva de Ixtacumbilxunan, Gruta de Pichjabin.

- Guatemala: The Sacred Wells, Alta Veragay Cave, Cueva de Juan Flores.
- Belize: Unidentified cave.
- El Salvador: La Libertad Cave.
- Panama: Madden Lake Cave, Chilibre Caves.
- Jamaica: St. Clair Cave.
- Trinidad, B.W. I.: Oropouche Cave, Aripo Caves, Tamana Caves.

Brazil: Unspecified cave.

- Venezuela: Cave of the Guacheros, La Cueva de Na Placida, Cuevas de El Pinon, Cueva del Encanto, Cueva del Agua, La Gruta (Cueva de Carrizalito), Cueva El Penon No. 1, Cueva de la Vieja Miranda, Cueva Las Guacas.
- Peru: Cueva de las Lechuzas.
- Colombia: Macaregua Cave.

Europe

- Rumania: Cave of Topolnita.
- Italy: Unidentified cave.
- Cyprus: Labyrinth of Curium.

Middle East

- Israel: Mitzpe Yodfat (Bat Cave), Galilee.

Africa

Transvaal: Johnson's Pot Hole, Thabazimbi Cave.

Cape Provinces: Pretoria Cave, Marcus Cave, Melville's Pot Cave, Spiesgat Cave, Magwento Bat Cave, Ulster Caves, Grotto of Kariba Reserve, De Hoop Cave.

Tanganyika: Amboni Caves.

Kantanga: Etienne Grotto.

Congo: Unspecified cave.

Sudan: Unidentified cave.

Morocco: Caves of Morocco.

Zambia: Archeological cave.

Far East

Malaya: Cave near Kuala Lumpur.

Philippines: Cebu, Unnamed cave.

Australia: Church Cave

New Zealand: Unspecified Cave.

SOME HISTORICAL SPECULATIONS ON THE ORIGIN OF SALTPETER

WARREN C. LEWIS, M.D.*

The early history of saltpeter is reviewed with observations made on its natural occurrence and recovery. A number of ancient writers and chemists noted that saltpeter formed as a salty crust on stone and was found in loose earth in sites protected from excessive rain. It could be obtained by soaking these materials in cold water. It was found around manure piles and compost heaps. Later they observed that it would form, although slowly, when these conditions were duplicated by artificial means. The earth once leached of its mineral content under some circumstances retained the ability to form saltpeter. This was a source of continued speculation.

Saltpeter was known in Mesopotamia at the dawn of recorded history. A Sumarian clay tablet written about 2200 or 2100 B.C. refers not only to saltpeter but also black saltpeter. Some historians interpret this and other evidence to mean that refining and processing was already well developed at this time. It is mentioned along with ten other mineral-like substances in the Ebers Papyrus. This scroll which was found in Thebes has been called the oldest book in the world. It was written about 1550 B.C. in Hieratic script, a cursive form of the chiseled hieroglyphics of ancient Egypt. A reference which may apply to saltpeter decay is found in the Bible in the Book of Leviticus (c 570 B.C.). In the 14th chapter, 37th verse, a priest has been called by the owner to examine a house.

If the priest, on examining it, finds that the infection on the walls of the house consists of greenish or reddish depressions which seem to go deeper than the surface of the wall, he shall close the door of the house behind him and quarantine the house for seven days. On the seventh day the priest shall return to examine the house again. If he finds that the infection has spread on the walls, he shall order the infected stones to be pulled out and cast in an unclean place outside the city. The whole inside of the house shall then be scraped and the mortar that has been scraped off shall be dumped in an unclean place outside the city.

It would appear that the chemical properties of saltpeter were unknown to the Israelites, since no value was placed on the material that was removed, but the destructive character of saltpeter corrosion was known.¹

The alchemists in Europe became acquainted with saltpeter in the first century B.C., probably by trade from the East through the Middle-East. In China it was combined with sulfur in definite proportions in the third century and by the seventh century it led to the production of fireworks and firecrackers. In the tenth century during the Sung Dynasty, the Chinese recorded the military use of explosive

mixtures of saltpeter, sulfur, carbon and asphalt called *huo-yo*. Ibn al-Baitar of Málaga, Spain (d.1248), transmitter of Arabic lore, mentions saltpeter as 'Chinese Snow.' Saltpeter was imported to Europe from India during the later Middle Ages. In India it was produced during the dry season from rich organic soils subject to seasonal flooding and dirt obtained near the dwellings. The product was often contaminated with common salt. One Mid-Eastern source was a valley between Mount Sinai and Suez. Saltpeter was also made in Europe at this time, according to early reports, from earth from old dry sheep-stalls and stables.²

Roger Bacon (1214-1292) is credited with the invention of gunpowder in Europe. He wrote about its composition from saltpeter, sulfur and charcoal in 1242. His description remained obscure since it was partially concealed in a cypher. He wrote about it again in 1270.

Marcus Graecus (c.1300), the name given to the compiler of information from various texts in Greek, reported that:

Saltpeter is a mineral found as an efflorescence on stones. This earth is dissolved in boiling water; then the liquor is poured off, filtered, and heated for a day and a night, when little plates of the solid clear salt are found at the bottom.

A monk, 'Black' Berthold Schwartz of Freiburg, probably Constatin (Anklitzen), introduced propulsion to Europe by showing how to fire a missile. Gunpowder was first used in European warfare in the battle of Crécy in 1346. The *Codex Germanicus* (c.1350), gave some details on preparing the constituents of gunpowder. Saltpeter was purified by crystallization from a filtered solution, followed by fusion to expel the last traces of water.³

Vannuccio Biringuccio (1480-1539), Italian chemist and metallurgist, acquired his knowledge of mining and metal working by extensive travels through Italy and Germany. Saltpeter was used at that time in fluxes in the smelting of metals and assay of metallic ores. His work, *De la Pirotechnia*, published in Venice in 1540 said:

Saltpeter is a mixture composed of many substances extracted with fire and water from arid and manurial soils,

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from that growth that exudes from new walls or from that loosened soil that is found in tombs or uninhabited caves where the rain cannot enter. It is my belief that it is engendered in these soils from an airy moisture that is drunk in and absorbed by the earthy dryness.

Then having tested the earth either by taste, or in some other way, to assure yourself that it contains saltpeter, make a great heap of it in the middle of the room where you are to work.

He then outlined his process with quicklime, cerris or oak ashes and water. Leaching was followed by concentration through evaporation, cooling, decanting and crystallization. Alum and lye were used in the refining process.

If you wish to have it purer than usual and completely without gross earthiness, without fatness (excess lye), and without salt, which it must be for making very fine gunpowder and aqua fortis (nitric acid) for parting (separating gold from silver), do it in one of two ways that I shall now teach you. The first, and the one most pleasing to me is with water and the second is by fire.

He went on to describe two processes of refining saltpeter, one by redissolving in water and the other by melting.

Biringuccio wrote in a local vernacular with crude literary style. His work was translated into several languages but due to a poor format and crude illustrations, his work was largely ignored. It gave the earliest complete account of the gathering and preparation of saltpeter. His process of refining of saltpeter by repeated crystallization was unchanged for centuries and his observation that saltpeter was formed under aerobic conditions would be repeated by many subsequent writers. Sixteen years later, in 1556, Agricola published what was essentially Biringuccio's process in elegant Latin in *De re metallica*, and the work became widely known.⁴

Georg Agricola also known as Georg Bauer (1494–1555), German physician, apothecary and metallurgist, after study and travel, settled in Joachimstaal, Czechoslovakia, then one of the most important mining centers of Europe. He was interested in occupational illnesses of miners and metal workers and in all aspects of mining and metallurgy. Day and night he visited the mines and smelters gathering information which he later put in book form. He was also active in politics, and wrote on economics and religion. His books on mining and metallurgy, with material gathered from a number of sources as well as his own observations, were detailed and profusely illustrated with woodcuts. He illustrated the processing of saltpeter and the making of gunpowder. His books were of such high quality that they became the standard texts in that field for the next century.

Saltpeter is made from a dry, slightly fatty earth, which, if it be retained for a while in the mouth, has an acrid and salty taste. Pure saltpeter which has rested many years in the earth, and that which exudes from the stone walls of wine

cellars and dark places, is mixed with the first solution (obtained by his process) and evaporated by boiling.

The earths from which the solution was made, together with branches of oak or similar trees, are exposed under the open sky and sprinkled with water containing saltpeter. After remaining thus for 5 or 6 years, they are again ready to be made into a solution.

His English translators, President Herbert H. Hoover, American mining engineer and his wife, thought that this passage was a description of an artificial niter bed, perhaps the first such description. If so, it is quite incomplete and may even be misunderstood by those trying to follow his procedures. It does indicate that Agricola was familiar with the phenomenon of regeneration of spent saltpeter earth.⁵

Niccolò Machiavelli (1469–1527), Italian statesman and political philosopher, an admirer of the Medici, left provocative and cynical essays on government. In *The Art of War* he discusses gunpowder and its chief ingredient saltpeter. He seems to have followed Agricola when he said:

(Saltpeter) is a mixture of many substances gotten out by fire and water of dry and dusty ground, or of the flower that grows out of new walls in cellars, or of that ground that is found in tombs or desolate caves where rain can not come in.⁶

Hans Breu of Bayreuth explored the Sopheinhöhle in Franconia in search of saltpeter in 1490. In the 16th century saltpeter was needed by many burgeoning industries and crafts. It was used in dying fabrics, making glass, explosives and acids as well as in pharmacy and metallurgy. The collection and purification of saltpeter began to be practiced in systematic fashion in every country of Europe.⁷

Basil Valentine (c1604), probable pseudonym of Johann Thölde of Hesse, in *Fr. Basilii Valentine chymische Schriften* wrote:

Saltpeter: a wonder-salt with an infernal spirit concealed in an ice-like form.

The term 'spirit' at that time referred to one of four substances: saltpeter, sal-ammoniac, quicksilver or sulfur that disappeared entirely upon application of heat.⁸

In 1624 a proclamation was issued in Cambridge, England:

For preservation of Grounds for making of Salt-Peeter. It (shall be) illegal to pave dovecots or cellars, except the part used for wine or beer, with stone, brick, or floor-boards or to lay the same with lime, sand, gravel, or anything that will stop the growth of the Mine of Saltpeter.

It was later copied and made into law by several New England states when they needed saltpeter for munitions.⁹

Johann Rudolph Glauber (1604–1670), German chemist, pharmacist and physician, is credited by some historians with being the first to form artificial niter beds. He started out as an alchemist travelling in quest of spagyric wisdom

and was very successful in furthering pharmaceutical chemistry. He moved, later in life, into an alchemists house in Amsterdam with four large laboratories in the rear. Five or six men were employed at the retorts, distillatory furnaces, ovens, and other equipment of his own design for the production of salts and other pharmaceuticals.

Glauber at the age of twenty-one discovered the medicinal value of sodium sulfate known today as Glauber's Salt. He treated saltpeter with hydrochloric acid in a secret process which enabled him to obtain very pure nitric acid. His most highly-valued synthetic salt was ammonium nitrate, which he fancied Adam brought out of Eden. It was made secretly from saltpeter and ammonia. He also learned how to synthesize saltpeter from other chemicals. Saltpeter was obtained from earth by throwing putrefiable matter of both vegetable and animal origin into pits and adding wood ashes. He extracted from this, in due time, a solution which on evaporation yielded crystals of saltpeter. Glauber believed that the function of the putrid material in the compost heap was to draw the niter from the air.¹⁰

An early woodcut shows a brush of bound fibers and a hand-held pan being used to remove saltpeter from walls. Another illustration shows a factory with saltpeter being chipped off the walls of mounded niter beds and put in a wheelbarrow to be taken inside for leaching and boiling. In some European countries saltpeter was reported to have been collected by washing the walls where dampness and the nature of the materials favored the development of nitrifying bacteria. Sheepfolds, cellars, damp rooms, old broken bricks and plaster, and caves (?), were washed with a solution made with cinders of vegetable matter.¹¹

Edmé Mariotte (1620-1684), French experimental scientist, played a central role in the newly-formed Paris Academy of Science. While known primarily as a physicist, his brilliant work extended over many fields of science. He was known for his cleverness in the design of experiments and he carried them out with a typical frugality. He exposed some saltpeter earth to the air in an upper room of his house. When he later leached it with water, he was unable to obtain "even one gram of saltpeter from it." When he placed the same earth in his cellar it soon became covered with saltpeter.¹²

John Mayow (1640-1679), English physiologist and chemist, was known for work relating to respiration, chemistry of combustion, and muscular action. In order to account for the formation of saltpeter he postulated the existence of a hypothetical "saltpeter" in the atmosphere.¹³

Louis Lémery (1645-1715), French chemist and pharmacist, stated in 1717 that saltpeter was usually obtained from the earth and refuse piles near old lime-plastered walls and in stables and churchyards. He thought that all salts were derived from mineral earth with the exception of saltpeter which derived its acidity directly from acid particles in the atmosphere. He filled three earthen vessels

respectively with lime, potassium carbonate, and leached saltpeter earth. These were exposed on pedestals in the moist air of a dark cellar whose walls and floor were covered with saltpeter. After two years, he found not a trace of saltpeter in any of the three vessels. By simply moistening the contents at frequent intervals with animal substances (urine?), he soon prepared a quantity of saltpeter.¹⁴

Hermann Boerhaave (1668-1738), Dutch physician, botanist, and chemist, not only taught chemistry and medicine but also spoke out strongly against war. His school attracted scholars from all parts of Europe. He published medical books of encyclopedic breadth and said:

Modern niter, or saltpeter, forms octagonal crystals: it is a semi-fossil (semi-mineral) extracted from a bitter nitrous earth; it melts in a moderate fire; it gives off very little water; it is rather fixed; when it is melted, it bursts into flame with all inflammable matter; it dissolves in 6½ (parts) of water.¹⁵

Etienne-François Geoffroy, the Elder, so-called to avoid confusing him with his younger brother (1672-1731), French physician and chemist, to distinguish saltpeter from sodium carbonate, the 'niter,' or natrum, of the ancients, called it the Niter of the Moderns.

Since no Salt-petre is obtainable, except from Earths impregnated with the urinous Salts of Animals or Vegetables, it is doubted by some whether this Salt be of a Mineral or Animal Original. This we leave to be determined by others, but we chuse to follow the Example of the Generality of Chemists, in ranking it among Minerals, because it is extracted immediately from the Earth, and cannot be obtained from the Urine and Faeces of Animals without Earth.¹⁶

The Salpêtrière, an historic Paris hospital for women, was founded in 1656 by a grant of land and some buildings from the king. It took its name from an arsenal at the site on which the hospital was built in which saltpeter had been made. A small saltpeter refinery was in operation in Dijon, France, as early as 1725. Itinerant saltpeter-makers, authorized by the government to collect earth from the stables and cellars of the inhabitants, also demanded free lodging from the villagers and wood for heating their evaporating kettles. For this they were roundly detested. In 1778 Guyton de Morveau with Jean-Baptiste Courtois and others again founded a plant at Dijon, for the artificial production of saltpeter but went bankrupt when they were unable to compete with the cheap product from India.¹⁷

The same Jean-Baptiste and his son, Bernard Courtois, had a change of fortune during the French Revolution when they did a lucrative business. Young Bernard and his father, to convert the alkaline earth nitrates into saltpeter, added wood ashes in the traditional way. Much of the potash from the ashes was lost because it reacted with salts other than nitrates. They conceived the idea of using, instead of wood ashes, the cheaper ash of sea-weeds, especially *Fucus* and *Laminaria*, harvested on the coasts of Normandy and Brit-

tany. The resulting salt, sodium nitrate, could then be converted to potassium nitrate in an economical manner by treatment with wood ashes. The entire industry benefited from their discovery. The ash of these algae, although rich in other salts, was valued at that time only for the alkali content. Bernard achieved fame when he discovered in the leachate of seaweed ashes an unknown element, iodine.¹⁸

Joseph Priestley (1733–1804), English physicist, educator and Unitarian theologian, was best known for his discovery of gases such as oxygen and carbon dioxide. He also studied electricity. After his home and laboratory in England were destroyed by an angry mob he came to America. He suggested, in a paper published in 1809, that weak nitrous acid produced in the atmosphere caused the deposition of saltpeter.¹⁹

Antoine Laurent Lavoisier (1743–1794), French chemist and physiologist, Director of the state gunpowder works, was called the founder of modern chemistry. In the last part of the eighteenth century he greatly improved the French saltpeter industry through modernization and standardization. For many years the state arsenals had furnished saltpeter of various standard grades to the dyers, distillers of nitric acid, glass makers and metal casters. These products formed the heart of the French chemical industry.

Denis Diderot (1713–1784), French encyclopedist and philosopher, was an active force in assembling technical knowledge and liberal ideas in the period of the Enlightenment. In Diderot's *Encyclopedia*, 1776–77, 34 volumes in all, in the section on saltpeter thought to have been written by Lavoisier, it was stated that reanimated earth was an infinitely renewable source of saltpeter.²⁰

Pierre Joseph Macquer (1718–1784), a contemporary of Lavoisier, observed that 'Nitric acid' was never found but in earths and stones that had been impregnated by matters subject to putrefaction. "Salt-peter signifies the 'Salt of Stone'; and in fact Nitre is extracted from the stones and 'plaster' in which it forms."²¹

Two natural sources of nitrates are in a class by themselves. The Nitrières were ancient limestone quarries in the valley of the Seine near Evreux, France, which produced saltpeter for commerce. Nitrates developed on quarry walls facing south, especially in the spring and the fall of the year, but only on the surface. Thin flakes of chalky stone were chipped off the walls by the workmen. After leaching, the chips were piled in rows to renew their nitrate content. The walls could be worked again in about six months and about 15,000 pounds of saltpeter were produced annually. The niter caves of Ceylon, twenty or thirty in number, differed by appearing to be hand-carved, not only out of limestone, but also out of talc and feldspar. For six months of the year, workmen chipped rock off the cave wall to extract nitrate salts. The superficial deposit, although usually not apparent, sometimes formed a visible excrescence. This seemed, according to one mid-nineteenth century author, to

point to the texture of the rock as the cause of nitrification rather than to any supply of organic matter.²²

In 1750, the German Academy of Science offered a prize for the best paper on nitrification. A noteworthy paper was received on the generation of niter. In 1775 the French Academy of Sciences offered a similar prize. Several of the papers submitted to the Academy were reviewed in *Comptes Rendues*, which continues to this day to be an Academy publication of chemical abstracts. It was at this time that concepts of 'aereal acid,' (CO_2 , H_2CO_3) and 'aereal niter,' (N_2 , NO , and NO_2 and their acids), were being actively debated.

Longchamp, Chemist, after studying these papers, reported to the French Academy in 1823 that the earth in caves nitrified itself sufficiently for extraction in eight or ten years. He stated that nitrates were generated from nitrogen of the air and not from that of organic substances.²³

With this, the science and art of forming saltpeter moved, but moved very slowly, into the modern era. It was not until the twentieth century that the two symbiotic bacteria that are the main independent source of nitrates in soil were identified.

ACKNOWLEDGEMENTS

I gratefully acknowledge the help of Marion O. Smith, Angelo I. George, Carol A. Hill, and Bill Torode, librarian, and others who helped in preparing this paper. Opinions expressed here are my responsibility.

¹The writer of the Sumerian tablet is thought to have been a physician. The Ebers Papyrus contains over 800 prescriptions some of which seem to have been compiled from older sources dating back as much as twenty centuries. Leviticus contains the sacrificial and other ritual laws prescribed for the priests of the tribe of Levi. A modern version of the Bible has been selected.

²The transition from simple explosives such as firecrackers to propellants of missiles is not well documented but some inferences can be drawn from Chinese literature. See the *Wu-ching Chung-yao* of Tseng Chung-liang, 1044.

³Chemical knowledge and technology go hand in hand. The use of saltpeter in fireworks may have been well known. It was not until suitable metals could be cast into guns that the explosive potential of nitrates could be utilized.

⁴Much credit once given to Agricola apparently should go to Vannucio Biringuccio, 1540, *The Pirotechnica of Vannucio Biringuccio*, published in translation, 1942, by The American Institute of Mining and Metallurgical Engineers, New York.

⁵Georg Agricola was the leading authority on mining and metallurgy as Europe came out of the Dark Ages. For several terms he served honorably as Catholic mayor of Chemnitz, Czechoslovakia. Unfortunately, he was embroiled in religious controversies and was faced with intolerant attitudes characteristic of his time. When he died, the local Protestant clergy refused to allow him to be buried in the parish church, an honor usually accorded to mayors. A friendly bishop, after four days, arranged for his interment in the next province in the Catholic Cathedral at Zeitz, at which place his memory is honored today.

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