H. H. Hobbs III

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CONTENTS

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Review of the Microbiology of Underground Environments

by VICTOR CAUMARTIN

ABSTRACT—Studies employing culture methods and optical and electron microscopy have shown that the cave microflora consists of bacteria, actinomycetes, fungi and ultra microscopic forms which are herein described and named *microfusiformentum* of cave clay. Some species require organic material for their nutrition, whereas others derive their energy wholly from the oxidation of inorganic compounds. Certain areas of caves, marked by the absence of fungi, retain the original microflora which existed before contact between the cave and the surface was established. The remaining areas contain a competing surface and underground microflora. The surface forms are characterized by the chemical reduction of iron and the conversion of organic matter into inorganic compounds; whereas the underground organisms are characterized by the oxidation of iron and sulfur, the fixation of nitrogen, and the synthesis of organic compounds. Reports by other authors of so-called fossil microorganisms extracted and cultured from ancient rocks are believed to be invalidated because most rocks have sufficient porosity and permeability to permit continuous contamination by suitably adapted microorganisms. Caves support a complex microbial life and the idea that bacteria are the only significant cavernicole microorganisms must be rejected.

This report is intended mainly to call attention to French studies in cave microbiology and to outline general concepts. The reader should not be surprised to find few references accompanying it, for most of the work in this field is recent, and little has been published.

By definition, the pigmented and photosynthetic organisms living near the entrances of caves are excluded from the cave microflora. Their presence in the entrance passages is explained by their low trophic requirements and perhaps by a special need for intermittent light, but they are also found at the surface. The cave microflora does not necessarily require light, but it may be pigmented, without obvious usefulness. Autotrophic or heterotrophic, it includes bacteria, actinomycetes, and fungi.

Is the cave environment a distinctive one, or does it merely possess the microbiological properties of the soil at the surface except for a few special aspects? The latter situation often prevails, but the conditions in caves are such that the processes, being practically isolated, are much easier to analyze. Study of the surface soil is complicated by the interference of numerous biochemical processes; here one rarely finds an isolated species developing within its own environment. In the case of cave sediment, on the other hand, many places exist where a group of bacteria can be isolated with ease. This is a characteristic which is important to bear in mind.

Only in exceptional cases is a subterranean region protected from contamination by surface deposits. For surface deposits to be lacking, it would be necessary for the cave to be closed and for the surrounding rock to be insulated by an impermeable layer. In most cases, the water which slowly seeps through porous or fissured rock carries a great variety of microorganisms to the surface of the cave sediment as well as organic matter which usually assures their survival.

Often microorganisms are also carried in by air currents.

Numerous studies have been made in this field, beginning as early as the end of the last century; they led to the isolation of the well-known soil bacteria, fungi, cysts of various Protista, pollen grains, and others. A list of all the microorganisms that have been encountered could never be complete and would be of little interest.

A rigorous selection is imposed by the absence of light, by the chemical and mineral composition of the environment, and by the low content of organic matter. Only those organisms survive for which the environment is favorable; the favorable conditions are clearly defined and depend on the characteristics of the surface soil, that is, on the calcareous nature of the bedrock, and on the climate. It is not, then, a matter of adaptation but of rigorous selection. This selection especially affects the heterotrophs which control the consumption of organic matter and often its conversion to inorganic compounds. The products of this conversion remain in the sediment or are washed out, as at the surface, except where they are retained by adsorption on colloidal clay. This is the epigeic character remaining in the microbial processes of caves.

But when the organic deposits and their populations have been eliminated, either temporarily as a result of conversion to inorganic compounds or permanently because the network of joint cracks has been sealed by silt and clay, the presence of sulfur compounds (sulfide and sulfate) and of ferrous compounds, sustains the synthesis of organic material by chemosynthesis. This process is slow but remarkably continuous because the temperature and humidity are nearly constant. This autotrophic life is not typically cavernicole, but conditions there are such that, particularly owing to the long periods of time available, drastic transformations ultimately may be produced. The resulting underground synthesis naturally counteracts the process of breakdown of organic material.

Can surface and underground conditions be superimposed upon one another? They rarely can in their classical form. The surface conversion of organic substances to inorganic compounds is a biochemical process which upsets the chemical balance of the environment. Autotrophism, particularly the iron-bacterial variety, readily adjusts itself to the presence of organic matter but can withstand only certain definite amounts of the products of organic breakdown, so the synthesizing process and the process of organic breakdown are opposed to one another. The speed of surface growth and the slowness of underground growth emphasize the effects produced by this competition. The competition can be found at all levels in the microbial development of surface soil, but we are rarely dealing with organic breakdown alone as the organic material is being constantly renewed and, besides, autotrophs represent only a small part of the population of the surface soil. Only in caves do we observe all the effects of this competition, although it cannot be said that they are confined to subterranean environments.

Another concept relates to the reducing property of clay which results in the protection of the cave system against the propagation of mold. Molds encyst in a chemically reducing medium, chiefly owing to the formation of sulfide ion, and growth is prevented. Their extent, as well as that of the other microorganisms usually accompanying them, reaches no farther than to the limit of the deposits brought in by water and air currents. It is only necessary to investigate mold—which can easily be done with the aid of a Petri dish and a suitable culture medium—in order to locate the zones of contamination in a cave with almost geometric precision and to establish the topographic limit beyond which only autotrophic microbial life of the cave type is encountered. In the remaining underground areas, surface life causing organic breakdown and underground life causing synthesis overlap because of the competition mentioned before.

Defining the uncontaminated areas is useful in several respects, as it permits an investigation of how a cave system became contaminated, for example by water moving through the ceiling, by lateral percolation, and through syphons; by particles carried in by the air; and by other means. It thus becomes possible to pinpoint, with great precision, those areas in caves from which this or that type of sample was taken. Let us hasten to add that caverns affording such protected areas are rare, and the chance of finding one diminishes with each successive visit. Most frequently, a zone of very small size may be found only in an especially favorable location.

Finally, clay supports a population of poorly characterized microorganisms which continue to live so long as the moisture conditions remain the same. These microorganisms can be perceived only with an electron microscope. They are highly sensitive to changes in the chemical composition of their environment, and the problems they post are interesting and quite new. Cave sediment may contain an unusual sort of life. As yet we cannot ascertain its environmental requirements, its influence upon the evolution of caves, or its role in controlling the properties of the water which comes in contact with the clay.

In the following pages some of the concepts outlined in the foregoing will be expanded upon.

Iron Bacteria of Caves

Little cave sediment is devoid of iron bacteria; it may be said that the microbiology of caves depends in large part on the presence of iron. The organisms encountered in these regions live together in a regular fashion; although their exact interrelations are as yet unclear. In many cases, they share—to varying degrees—a mode of primitive life deriving its energy from the simple oxidation of mineral compounds, notably iron compounds. In other words, we may assume the existence of an iron biotype.

Cave sediment lends itself readily to the development of iron bacteria owing to the environmental conditions peculiar to it, for example, its chemical constituents, the presence of needed trace elements, moisture content always at saturation, and, of course, an abundance of iron compounds. In addition, clay-rich soil can retain and neutralize metabolic waste products, which is a factor of considerable importance in biological processes.

The concentration of ions and presence of certain major nutritional elements are vital to the growth of iron bacteria, and the difficulties encountered in their culture have been due mostly to the fact that these properties were not strictly maintained. Studies carried out at the Laboratoire Souterrain at Moulis, Frances, have shown that the ratio of Cl^{-1} and SO_4^{-2} in the culture must not deviate from an average value of 0.1. Above and below this value, the growth curves decline. Analyses of natural soils performed in collaboration with Charles Orliac had previously drawn attention to this equilibrium; under the optimal conditions of growth, the recorded values ranged between 0.2 and 2.0. Exchanges in the silicate lattice, adsorption on colloidal clay, and exchange and combination different from one clay specimen to another, probably lead to a retention of chloride and sulfate in a proportion yielding the ideal ratio. Owing to this fact, good localities for iron bacteria can be found by a chemical analysis for chloride, sulfate, and of course iron. A successful test has been made in St. Catherine Cave, Ariège, France. These studies have also shown that the Ca^{+2}/Mg^{+2} ratio is important; its optimum value is close to 2.5. Calcium and magnesium play the role of trace elements, but an excess of calcium is always desirable, particularly in caves in dolomite rock, to counteract the toxicity produced by magnesium. In addition, the calcium excess determines the solution equilibria—

$$\text{carbonate} \rightleftharpoons \text{bicarbonate} \rightleftharpoons \text{carbon dioxide}$$

thus permitting the mobilization of iron carbonate. Purely chemical mechanisms intervene to permit oxidation for biological purposes, that is, for the growth of microorganisms. We may mention, among these mechanisms, the action of carbonate solution upon ferrous compounds, which gives ferrous carbonate; the role of carbonic acid itself in making the ferrous carbonate soluble; the delay in the decomposition and spontaneous oxidation of ferrous carbonate, this delay being due to the chloride-sulfate equilibrium required for metabolic processes.

A list of mineral substances with oligodynamic activity has been compiled. Oligo-elements, or biocatalysts, are inorganic substances that, in very small quantities, play a part in enzymatic reactions, either as co-enzymes or as activators. These substances produce no effect when very weakly concentrated, but are poisonous when strongly concentrated. There is thus a minimum concentration below which the substance has no effect, a maximum concentration above which the substance acts as poison, and an optimum concentration at which it produces its full effect. The optimum concentrations for certain ions are given below, where the experimentally obtaianed concentration is expressed in gram-ions per liter:

I^-	10^{-9}	Zn^{++}	10^{-6}
Mn^{++}	10^{-8}	Li^+	10^{-6}
TiO_3^{--}	10^{-8}	BO_3^{--}	10^{-6}
Co^{++}	10^{-7}	MoO_4^{--}	10^{-6}
Ni^{++}	10^{-6}	Al^{+++}	10^{-5}
Cu^{++}	10^{-6}	Br^-	10^{-5}

The presence of these substances in clay has been confirmed only for Mn, Al, Ni, and Co, but we have good reason to believe that most of them are present, for an extract of cave clay which was processed in an autoclave under conditions leading to destruction of organic matter (or at least of heat-sensitive organic substances) yielded growth curves typical of oligodynamic action.

At this point it may be appropriate to present certain biochemical data—although they will be discussed further below—as they explain the deleterious effect upon the development of iron bacteria of surface deposits, and of the microorganisms habitually accompanying them. Nitrate and ammonium ions are toxic in low concentrations, often as low as 10^{-5} NO_3^- or NH_4^+ gram-ions per liter, which means that the production of nitrogen compounds in the surface deposits interferes with iron bacteria. Iron bacteria are therefore unlikely to be found in cave areas that are insufficiently protected from external deposits. What is often observed in such cases is the chemical reduction of the iron and its recycling by a different biochemical process involving other bacteria. This problem is now under investigation. Very often, iron sulfide is then formed, which is the most common stable ferrous compound in caverns.

The sulfides, too, are toxic in an S^{--} concentration of 10^{-5}. Iron bacteria avoid cave passages where H_2S solutions drip from the ceiling, where pyrite and other sulfide minerals form on the walls, where water-saturated sediment reduces sulfate in appreciable proportions, and where the iron is reduced to the ferrous state. Their preferred substrates are at the surface of clay veneers affording sufficient oxygenation for aerobic existence.

Iron bacteria in caves include species belonging, for example, to the genus *Sideronema,* to the genus *Siderococcus,* and others. A new species of curious morphology and uncertain taxonomic position, *Parabacterium spelei,* has been identified (A new family would have to be introduced to accommodate iron bacteria from caves). This species is characterized by a pseudomycelium ranging from 0.5-0.6 micron in width and bearing buds near its ends analogous to the yeast-like conidia of the Mucorales (fig. 1). These yeast-like buds have a width of 0.5–0.8 microns and a length of 1.5 micron. On liberation in the culture medium, they develop into ovoid or twin forms 0.5 by 1.5 microns. Twin forms, which are often asymmetric, predominate; these are the forms which appear in cultures and justify the generic name. The sheath is only lightly impregnated with ferric hydroxide, for the bacterium rejects most of its metabolic waste to the external environment in the form of needles 0.1 micron wide and 1.0 long (fig. 2). These needles are usually simple, but they may also exhibit eccentric shapes. After 10 hours in an aqueous suspension, the needles are hydrated and become dilated to spindles 0.4–0.5 micron wide and 1.0–1.3 microns long. This hydration is associated with the nature of the excreta which are said to contain, among other substances, a substance related to the mucilages. If kept in aqueous suspension for more than 10 hours, the spindles become disarranged and the conglutinated organisms can no longer be seen. The transformation of ferric hydroxide into goethite undoubtedly takes place on the clay particles in the course of this hydration.

Common to the iron bacteria is the property of fixing atmospheric nitrogen (which explains the toxicity of ammonium and nitrate salts) and of resisting common sterilization procedures (autoclave at 120°C, 10 percent mineral acid, absolute alcohol). They are stained by a mixture of 1 percent potassium ferrocyanide and 1 percent hydrochloric acid, and they are not killed by standard bacteriological methods of fixation. None of these bacteria, moreover, has flagellate forms. On the contrary, they tend to assume mycelial shapes which cluster in groups difficult to classify.

Figure 1
(Parabacterium spelei), including pseudomycelial and pseudoconidial forms and needle-shaped excreta. X8,000.

SULFUR BACTERIA AND SULFATE REDUCERS

Sulfur bacteria constitute an equally interesting group of cave bacteria, but they are sometimes hard to distinguish from other sulfur oxidizers. It would seem more judicious, therefore, to speak of sulfur oxidizers without specifying the taxonomic groups. Sulfate reducers are also found.

These bacteria play a particularly important part in caves which cut across rocks that are rich in sulfide minerals, such as dolomite rock and shale. But they are found everywhere to some extent, for few caves exist which are not supplied with sulfate. The processes in which they are involved depend entirely on the presence or absence of oxygen. Within clay-bearing sediment, a condition conducive to the reduction of sulfate is created by the lack of oxygen, whereas at the surface of the clay deposit the presence of oxygen leads to the oxidation of sulfide to sulfate.

The bacteria concerned with the movement of sulfur, particularly the autotrophic sulfur bacteria (Thiobacteriales) and the sulfate reducers, constitute an important link in the development of certain minerals in caverns, and they contribute much to an understanding of the development of the varied populations which the subterranean environment affords.

Under the soil with its carpet of vegetation, the bedrock contains sulfate or sulfide minerals which the dissolving water carries downward by gravity and capillarity—slowly owing to their slight solubility but nevertheless to great depth. On contact with the limestone, an equilibrium is established, and the surface solutions move without losing either sulfate or sulfide, until they reach the cave ceiling or sediment. These phenomena operate under geologic conditions with remarkable continuity, but we only observe their results without wholly understanding their mechanism.

An important point to be noted is the possibility that, owing to the permeability of the rock, microorganisms may penetrate simultaneously with the water. The pore size, of course, determines whether or not microorganisms of a given size that are not destroyed by the chemical character or concentration of the solution will be able to pass. This dual capillary and chemical selection has a twofold implication: only resistant (chemoresistant) microorganisms of small size (at least when in the spore state) will reach the cave, and they are for the most part autotrophs and semiautotrophs. The others can exist only in an open system. It follows that, in view of all their distinctive

Figure 2
Needles of ferric hydroxide dilated by hydration. X9,500.

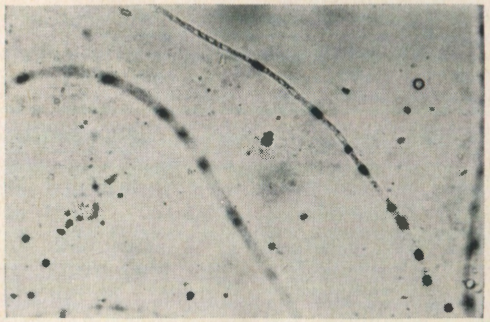

Figure 3
Cultured cysts on young filaments (Penicillium glaucum). X650.

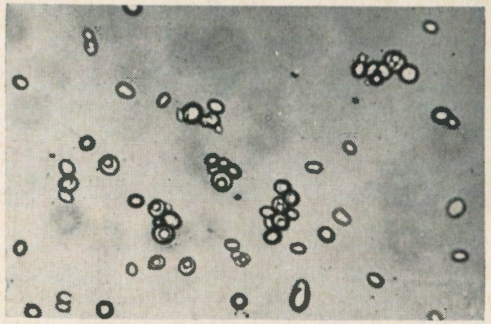

Figure 4
Cultured cysts on yeast (Saccharomyces cerevisiae). X650.

characteristics, caves do not furnish new bacteria but can support chemically resistant ones in greater numbers than anywhere else. This is what makes the cave environment distinctive. Certain species find ideal conditions for their development here without the need for competing with other species; they are accordingly easy to recognize in caves, whereas at the surface they are masked and escape detection.

It is always possible to extract from any rock microorganisms which can be cultured, regardless of the age of the rock, provided it is permeable, as is usually the case. If an appropriate culture medium for chemically resistant cave bacteria is employed, the usual growth is obtained. Under such conditions, experiments for the revival of "fossil" bacteria may be said to be invalidated from the start by a serious error of interpretation and therefore to be worthless.

The environment within a moist rock is reducing, as free oxygen is absent. Sulfate is reduced by sulfate-reducing bacteria to sulfide, which the water slowly carries away. It may be that the sulfur materials which are found, such as pyrite, originate in this way, and the odor of dolomite rock, when it is struck with a hammer, may be due, at least in part, to earlier or present activity of this type.

When a sulfide solution reaches free air, either because it is directed toward a cave by gravity or because it is lifted to the surface of the ground by capillary action, oxidizing bacteria convert it in the presence of oxygen into a sulfate solution. Acidification of the environment is prevented and continuance of the process assured by, among other substances, calcium carbonate, which neutralizes the sulfuric acid being formed. This biochemical mechanism is in large part responsible for the disintegration of calcareous rocks on sunny slopes. The property of dolomite rock to disintegrate into grains under these conditions is attributable to the abundance of sulfide minerals through the intermediary of sulfate ions. The film of water on the cave wall slows oxidation, and the sulfates most commonly wash away; no corrosion occurs, but gypsum deposits form, if evaporation permits.

Thus solutions containing sulfur compounds cannot pass through the bedrock without undergoing changes. Exceptions occur only where rapid infiltration follows wide cracks in the rock or where the path of travel is too short and the rock cover is insufficient or excessively dry. Such phenomena, depending as they do on infiltrating water and on soil processes, are thus wholly dependent on surface conditions; and, in temperate climates, they are closely linked to the rhythm of the seasons. Even in caves, despite the exceptionally even temperature and humidity, the processes are affected by the rhythm of the seasons.

The organisms which contribute to oxidation and reduction have been identified and are known, but we are far from having made an inventory of the organisms existing in all French caves.

Biospeleologists find other fascinating subjects for research in this area, for bacteria utilizing sulfur compounds produce vitamins which in many cases belong to the B-vitamin group. The effects of these vitamins on growth, metabolism, functioning of the nervous system, and so forth, are well known. Among vitamins which have already been isolated from the cells of sulfur bacteria or from their secretions, and the synthesis of which is theoretically possible, may be cited nicotinic acid, pantothenic acid, riboflavin, pyridoxine, and vitamin B_{12}. Those cave microorganisms which live in complete darkness, in isolation from the external world, can thus find organic compounds in the clay covering the walls and filling the fissures—as well as rare mineral substances—which we had long thought were available only to the populations exposed to sunlight. This life in darkness is quite surprising; under the most fortunate circumstances it lacks nothing, provided clay is present.

DETRIMENTAL EFFECT OF SURFACE HETEROTROPHS

Surface heterotrophs are responsible for the destruction of dripstone and of the mineral and organic equilibria prevailing in subterranean sediments.

An organic deposit on dripstone, no matter how small, rapidly becomes a site of decay which leads to local liberation of carbon dioxide and impairs the stability of the crystal structure. In addition, this decay liberates organic acids, in the neutralization of which the carbonate minerals are destroyed.

Thus, the surfaces of stalactites, stalagmites, and flowstone disintegrate. There remains, in relatively dry places, a white, more or less powdery material and, in moist places, a curdled substance which speleologists call *moonmilk*.

These are complex phenomena to which the numerous contaminants of the environment are traceable. The bicarbonate-bearing solution containing calcium, which gives rise to dripstone, emerges from the soil containing, in addition to calcium, silica, manganese, magnesium, soluble phosphate, sulfate, chloride, ferrous iron, and trace elements. In combination, these substances create qualitatively favorable conditions for the development of microorganisms. If ferrous iron occurs, it is oxidized into ferric iron in the presence of iron bacteria even during the growth of dripstone, particularly so where transported organic deposits occur, with the result that a red coloration is produced and a process of latent corrosion is set in motion. This explains the presence of Fe^{+++} near calcite crystals; the iron has been transported in the form of Fe^{++}.

This oxidation of iron is generally accompanied by nitrogen fixation and by the formation of organic acids and often of succinic-acid derivatives. The phenomenon may assume significance if the equilibrium conditions enumerated above are established. It is accelerated in the presence of organic matter and leads to the implantation of an ordinary soil microflora in the cave and to the formation of tartrates, succinates, nitrates, and so forth. The organisms encountered include, in addition to bacteria, actinomycetes and molds which aid in the conversion of the organic matter to inorganic compounds.

After gradually losing their coating of flowstone, the cave walls turn first ocherous and then brownish; they then serve as support for a microsoil as new deposits are added. The water droplets covering this microsoil often give off bronze-colored reflections due to the presence of microorganisms (molds, actinomycetes, and others) which have a certain amount of pigmentation, even when growing in the dark.

The origin of the organic matter poses an interesting problem. Material is brought in by flooding, by capillary flow along the walls and through fissures, but especially by air currents; the last method, for example, carries microscopic algae belonging to the Cyanophyceae and Chlorophyceae. This discovery answers a question regarding moonmilk which has long remained unsettled; besides calcite needles, moonmilk had been found to contain more or less twisted calcite bodies which turned out to be the remains of algae. Certain algae can live heterotrophically in darkness in the presence of organic matter; they produce no chlorophyll under these conditions. In this substratum, rich in dissolved calcium carbonate, the cell walls of these algae become impregnated with a more or less calcitic mineral deposit and become petrified.

The discovery just mentioned is of great importance. Not only does it explain the presence of the twisted bodies and trace their origin, but it also supports the theory of the biochemical origin of some corrosion. If moonmilk can form directly from a solution of calcium bicarbonate, and if other moonmilk deposits can result from local resolution of calcium carbonate, most of the moonmilk appearing in open cave systems is simply an aspect of biochemical corrosion ultimately due to currents of air carrying organic material.

The hetereotrophs responsible for corrosion and decay, on reaching favorable locations in the cave environment, rapidly destroy the rare deposits accumulated there over the years; moreover, they alter the equilibrium which is so vital to the iron bacteria. We find a great many surface forms which convert organic matter here, but note should be taken of the behavior toward proteins that is encountered in the environment. Three possibilities should be considered: (1) the protein is utilized directly and rapidly disappears from the sediment; (2) it is neither transformed nor utilized; and (3) it is converted to inorganic compounds, with ammonification and nitrification. in the usual fashion.

Protein utilized directly.—Protein is utilized by microorganisms such that after 10 days of incubation, reactions for protein, ammonium and nitrate are negative. This is what is found in clay veneers in contact with stalagmitic floors, in decayed dolomite, and rarely, in isolated masses of clay and in the sediment of rimstone pools and syphons. These deposits are poor in actinomycetes—sometimes containing none at all—but they are heavily populated with bacteria and particularly rich in protists. The bacteria include the majority of the heterotrophs that survive in caves. It may be assumed that the bacteria either utilize the protein directly or after only partial digestion with the result that their population is increased and protists are attracted which feed on the bacteria. The rapid disappearance of proteinaceous compounds at such localities causes an equally rapid regeneration of these localities, which therefore recover their autotrophic populations unharmed.

Protein neither transformed not utilized.—These localities are poor in bacteria, poor in Protista—the two usually go hand in hand—and equally poor in actinomycetes. Samples which give these results in the laboratory correspond to samples from sites rich in sulfur derivatives, such as sulfate and sulfide ions, which inhibit the microflora. It is interesting to note that actinomycetes always disappear from places where organic material from external deposits is no longer broken down.

Protein converted to inorganic compounds.—These localities, which are very numerous and for the most part open, contain a relatively high proportion of actinomycetes in addition to the usual cave heterotrophs and ordinary soil bacteria. It is to be noted that nitrification appears more rapidly in some cases than in cultivated soil, and that all traces of organic matter are quickly eliminated in well aerated places. The same phenomena are observed during culture on synthetic media. In the foregoing we have repeatedly called attention to the chemoresistance of cave microorganisms and to the enhancement of the autotrophic function in

Figure 5
Natural cysts separated from clay in a filtering column. The cysts stuck to a particle of mineral matter while being separated. X700.

combination with this resistance. It is conceivable that an excess of organic matter in the soil may bring about a decline in autotrophic power. It must also be noted that the elimination of nitrate, at the rate of its formation, prevents poisoning of the bacteria and thus speeds the phenomenon. It is a general rule in biology that the continuity of a phenomenon is assured only if waste material is carried off or rendered insoluble.

Also appearing in aerobic environment are nitrate-reducing bacteria; they are in fact always present. The reduction products are practically undetectable. In the laboratory, reduction stops at the nitrate stage. At the surface of the sediment, oxidation and removal are no doubt completed very rapidly, the nitrate constituting only a temporary stage. The nitrate reducers arrive at the same time as the organic matter; their chemical resistance is much lower than that of the other bacteria. They are especially sensitive to ferric iron, to the magnesium in dolomite, and to aeration in places where dessication is going on.

The organisms that have the most deleterious effect on them are the nitrifying bacteria which actively mobilizes calcium carbonate. These bacteria play a major role in corrosion without leaving any trace of their passage; the tests for nitrate (diphenylamine, brucine, and so forth) are always very weakly positive.

Special attention must be called to the role played by the actinomycetes. This is a group of organisms still poorly known, except in systematics and antibiotic research. They adapt themselves to the most diverse situations, but most of them live in the soil. There they play a part in the humification of the surface organic substances and in causing them to be completely broken down. Their pseudobacterial forms sometimes create confusion, and the things that they do in caves are often mistakenly attributed to ordinary bacteria. Some of them give off a peculiar odor suggesting both wet earth and moldiness which is the characteristic odor of cave entrances. Others synthesize carotene, even in the dark. Together with the cysts of *Fusarium*, the actinomycetes are, as far as we know today, the source of the carotene of cave clay and of the pigmented organisms of the genus *Thecamoeba* which it encloses. In mineral environments we commonly find an association which is intensely red, imparted by carotene and entirely free from chlorophyll. The association is capped by *Thecamoeba verrucosa* and depends on a fungus —generally *Fusarium,*—or on an actinomycete which synthesizes the pigment, and on bacteria for the organic synthesis. At the surface, in daylight, such associations are to be found particularly on limestone, for example on the chalk overlying the chert of the Craie, on dolomite rock, and on calcareous sandstone. In these cases the carotene is supplied by a fungus. Underground, the fungus is often replaced by an actinomycete. The carotene of certain cave-inhabiting insects may be derived from the same source.

In view of the capacity of the actinomycetes to cause decay in the subterranean environment, attention should be called particularly to the role they may play in the disappearance of prehistoric evidence and in corroison in general.

Behavior of Molds in Underground Environments

In referring to molds in what follows we shall include under this term, for the sake of convenience, fungi that are commonly called green molds and belong to the Aspergillales (Ascomycetes) and those called white molds and belonging to the Mucorales (Phycomycetes). Their behavior in subterranean environments is similar.

Molds exist in caves, but there are no ready-made explanations for the facts which have been observed regarding them.

Organic debris, such as bait left by entomologists, dead insects, bat guano, and so forth, does not necessarily mold. Near cave entrances, such debris is often very rapidly covered over with propagative forms belonging to the genera *Aspergillus* or *Penicillium* or, more rarely, *Mucor,* and so disappears. Nothing like this occurs in certain deep passages where the decomposition is slow. Thus the chance for attack by mold varies from one locality to another.

Numerous investigators have carried out systematic studies of the species existing in subterranean regions, using cultures for this purpose. These studies have shown that caves contain most of the species also found on the surface. It is interesting to note, however, that identification often proves difficult and can be carried no further than the genus. The studies have also shown that, although mycelial filaments can be found at entrances and on partly dry walls, they are never found on clay, except under special conditions, as when the clay is isolated in a receptacle and allowed to dry. In the latter case, a fine mycelium appears at the surface of the medium, probably originating from contact with organic material at some depth below the surface.

Some of the experimental results are worth reporting: (1) Numerous spores can be collected when glycerin or agar plates were placed close to entrances. Of course, no selection was involved; we only found what the air currents had brought, and this included nothing unusual. (2) Cultures of clay samples taken with care to avoid contamination under aseptic conditions, using suitable media such as Raulin, Czapeck, and Rose Bengal streptomycin, always gave positive results, except in certain deep-lying parts. (3) Analysis of clay samples with the aid of a filtering column, permitting the separation of the physical and biological constituents of the clay according to their diameter, seldom yielded spores corresponding to the species mentioned above, except when the sample was taken from a rimstone pool near the cave entrance.

The redox potential of the environment plays an important role in the behavior of molds. In a reducing environment, with H_2S present, spore formation does not occur, and the mycelial filaments disappear. Microscopic analysis has shown that the young thalli divide their protoplasm into a certain number of portions, which usually are 4 to 5 times smaller than the spores and are enclosed by a resistant, more or less chitinous wall. This reaction appears to be linked to the dividing of the nuclei. In Mucorales with multi-energid membrane structure, this phenomenon is often seen in an apocyte; in the others it often appears before the appearance of the cell walls. When transplanted, these portions again produce mycelial filaments; they are called mycelial cysts (fig. 3 and 4).

By contrast, mycelial growth is strongly promoted—and consequently spore formation occurs—in the presence of ferric ions in an oxidizing medium.

This appears to be a general characteristic of the living protoplasm of a certain number of fungi; it affects the young mycelial branches in proportion—as we have said above—to the nucleus-dividing activity. Resting nuclei are no longer in a position to react against the environmental conditions. The same characteristic is found in closely related species, such as the yeasts. These unicellular fungi form 1 to 3 cysts in the presence of sulfide ions, whereas after the action of ferric salts the buds stretch out, in close association, on the cells just formed by budding.

It is the conclusion of these observations concerning the subterranean environment that mycelial cysts form under the action of sulfide ions.

These mycelial cysts (the conditions of formation of which have thus been experimentally established) can be isolated by means of a filtering column (fig. 5). We have found them mainly in water-saturated clay which was amply supplied with sulfide ions and bacteria producing them. It seems that, to the extent that sulfide formation is insufficient or lacking, the fragile mycelial structures that emerge, instead of encysting, rapidly fall prey to bacteria owing to the humidity and the slight impregnation with organic matter. In most cases, however, subterranean clay contains enough sulfide so that mycelial cysts—in varying numbers—form practically wherever the spores are carried.

In an environment lacking sulfide ions that contain a high proportion of organic matter and is aerated, with sulfide oxidizers and iron bacteria present, the mycelial cysts will develop. Aberrant fructifications are sometimes observed, notably on the genus *Penicillium.* These are molds that are generally classified as "fungi imperfecti," which accounts in large part for the difficulties encountered in subterranean mycology.

Where all the necessary conditions for development are not present, the cysts may be preserved in the clay in a latent state. Being unable to go back far enough, we could not determine the life span of such cysts, but we did obtain normal cultures from preparations that were 3 years old. It should be noted that the tendency to encystment and preservation of cysts differs greatly from one group to another; the most favored genera are *Penicillium* and *Fusarium,* while the Mucorales often form cysts which are large but highly fragile.

We now understand why molds develop only in partly dry parts of the cave system, where aeration of the substrate resists the formation of sulfide ions. Because of the scant supply of organic matter, the development is always of short duration. Organic waste products mold only in places where cysts are present, unless they contain the necessary spores within them.

The formation of cysts counteracts the formation of spores, hence reproduction. Accordingly, clay sediment receiving no external deposits are free of mold. This is surprising at first sight, but the mechanism is so strictly adhered to that zones subject to external deposits can be topographically reconstructed in a cave with the aid of a well-chosen culture medium, such as Czapeck medium, which is inoculated with sediment samples taken under conditions to avoid contamination. This is the test which made it possible for us to determine the areas where uncontaminated cave populations may be found.

Note also that the mycelial cysts secondarily impregnate their walls with mineral salts and retain their shape after death. We have been able to obtain them in cores several meters deep taken from clay banks. It may be assumed that they pass into a fossil state, for similar shapes are present in thin carbonaceous shale layers. The only fossil fungi known before were sclerotia. We may take it that the mycelial cysts constitute peculiar fossils of molds which appear under well-defined conditions and the study of which may lead to interesting conclusions.

A systematic study of mycelial cysts in cave clay remains to be undertaken, and we cannot very well dwell on this subject. Still, it may be worth while to cite some statistical

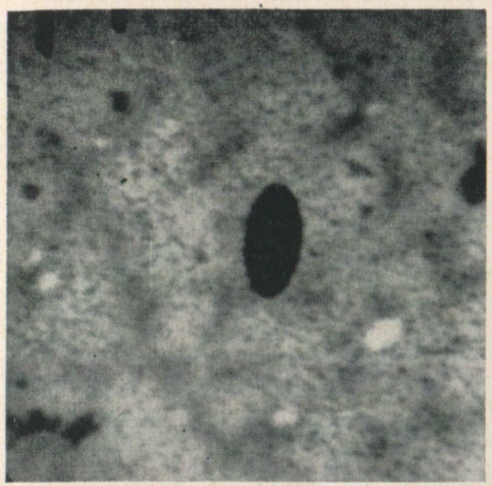

Figure 6
Dilated spindle extracted from blocks of clay from En Gorner Cave, eastern Pyrenees. X10,000.

Figure 7
Elongated spindles from limonitic clay from St. Catherine Cave, Ariège, France. X5,000.

Figure 8
Budding spindles from limonitic clay from St. Catherine Cave. X5,000.

Figure 9
Cultured spindles. Note increase in size and motile organ at one end. X1,000.

data, since they support the experimental results we have discussed. The following results have been obtained by the culture of clay samples: 15 percent of the cultures examined belonged to the genus *Aspergillus* and could be determined to species; 4 percent belonged to the genus *Penicillium* and could be determined to species; 63 percent could not be accurately identified, representing either a depauperate *Penicillium* or filaments which did not fructify; 11 percent of the cultures were considered to belong to the genus *Fusarium.* All the samples taken together thus made up 74 percent of "fungi imperfecti," which is a much higher proportion than is found in ordinary environments.

Only 7 percent Mucorales were found in our analyses.

MICROFLORA OF CAVE SEDIMENT VISIBLE ONLY WITH AN ELECTRON MICROSCOPE

The study of the microflora of clay with the electron microscope involves magnifications ranging between 2,500 and 5,000 times and sometimes exceeding 10,000 times. It reveals morphologic types which are spindlelike, dilated across the short axis, tapered, truncated at the ends, or threadlike. as well as very small cocci and hexagonal shapes (fig. 6, 7, 8, and 9). Such assemblages are often found at solution levels and in rimstone-pool sediment in association with cocci and bacilli (these require a magnification of no more than 1,500-3,000 times).

The common "coccus" and "bacillus" forms are thus associated with organic deposits. The forms peculiar to clay are spindle-like; because of their frequent occurrence we may consider them as typical for this type of environment. The physical nature of the substrate probably orients their morphology.

The results we are citing were obtained by a statistical analysis of more than 150 samples from caves in the Pyrenees, the Causses, the Alps, the Jura Mountains, and the part of France bordering on the Mediterranean, thus covering a sufficiently large area to substantiate a study of this kind.

Experiments to enrich media with various chemicals, such as sulfate, chloride, phosphate, silicate, and nitrate compounds, asparagine, glucose, and others, disclosed that the morphologic changes are controlled by the chemical composition and the presence of organic material. These experiments were run in a passage which was particularly safe from common contaminants; the test clay had been scrupulously examined beforehand.

There can be no question here of spores belonging to microorganisms that populate other environments, for budding forms (budding is often found on organisms inhabiting unfavorable environments) appear frequently; the buds adhere to the mother cell for a long time. Culturing, when possible, does not prevent budding but merely alters its form and size. It should be noted, however, that a motile organ sometimes appears in a liquid medium.

The classification of similar microorganisms is not an easy task owing to the existence of very marked morphologic variations which are not easy to follow because of the nature of the natural environment. We shall provisionally categorize the whole group of spindle-shaped organisms in the clay of caverns, and associated organisms, as the "microfusiformetum" of cave clay.

CONCLUSIONS

In the foregoing, a few of the known microbiological aspects of subterranean regions have been examined. Their distinctiveness from biological and biochemical viewpoints has been considered at some length along with some applications of the information that immediately occur to the speleologist and particularly to the biospeleologist. The value of such a study, however, lies not so much in the possible discovery of new organisms (were it not for the excessive complexity of the heterotrophic surface area, we would undoubtedly have long ago solved most of these problems), it arises from the fact that certain phenomena, having been clearly isolated here, can now be more easily studied. Biology has also been shown to play a previously unsuspected role in the formation of certain minerals, and it also has a part in the life of cave-dwelling animals that, though indeed suspected, had never been proved. The future of cave microbiology, therefore, rests not so much on systematic studies as on the study of biochemical and ecological relations within the very heart of the cave sediment.

Caves are able to sustain a complex microbial life in the absence of light. Even though the species involved are not restricted to caves, it is essential to recognize that this varied life exists, and the opinion that bacteria are the only significant microorganisms in the cave environment should be rejected.

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The Survey and Improvement of Natural Caverns for Use as Fallout Shelters in North Alabama*

by THOMAS E. BAILEY, Illustrations by J. R. McCLAIN

ABSTRACT—During the National Fallout Shelter Survey recently completed, a significant amount of shielded space was found to exist in natural caverns. In the nine county area of North Alabama potential shelter space for 25 percent of the population was found to exist in caves. Conditions such as remote locations, difficult access to shelter rooms, ventilation, filtration of air, stream flow into entrances, infiltration of surface water, dampness, rough floors, etc., indicate that improvements will be required before the average cave could be put to use as a shelter. In nearly all cases there appears to be a feasible and logical solution to each of these improvement problems. A test shelter program in which improvements would be designed, constructed and operated in a selected cave would be the next logical step in studying this important problem.

INTRODUCTION

During the spring and summer months of 1962 engineering firms throughout the United States were engaged in a National Fallout Shelter Survey and Marking Program under the direction of the U. S. Army Corps of Engineers. The primary purpose of the project was to locate spaces within existing buildings which could be used by the public in the event of nuclear attack. In addition to a survey of building facilities, special facilities such as mines, tunnels, and caves were also designated for investigation.

Brown Engineering Company of Huntsville, Alabama performed the survey in the area of North Alabama shown in figure 1. During the course of the survey the possibility of using some of the many natural caverns in this limestone area were considered. With the assistance of the Huntsville Grotto of the National Speleological Society, survey teams conducted extensive field investigations which revealed that a surprising number of shelter spaces could be made available

PROBLEM CONSIDERATIONS

The primary consideration in fallout shelter planning is to place as much mass as possible between the shelter occupants and the by using the caves provided that proper improvements were made. field of radioactive contamination. A secondary and less satisfactory solution is to place as much distance as possible between the occupants and the field. Emphasis must also be placed upon the fact that radioactive particles must be prevented from entering the shelter area.

It is important to note at this point that there are two basic types of fallout. First and most important is "early fallout." This is the result of the return to earth of highly radioactive particles formed during a nuclear explosion. These particles come down within 24 hours of the burst and range in size from 50 to 500 microns, and would resemble average beach sand in size, with all the particles visible to the naked eye. Immediately following their formation these particles begin a process of decay, during which time their radioactivity decreases rather rapidly at first, and more slowly as time passes.

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*Views expressed in this paper are those of the author and do not reflect official policy of the Office of Civil Defense, Department of Defense or of the National Speleological Society.

The second type of fallout, "long term" fallout, consists of very fine particles produced in a nuclear explosion. These particles remain aloft for long periods of time and are distributed over large areas by high altitude winds. Although it is possible that long term fallout may cause some delayed genetic problems, it is not a serious immediate hazard. Shelters under consideration in this discussion are concerned only with immediate survival by protection from early fallout.

In considering natural caverns as potential fallout shelters it is obvious that the shielding capabilities of most caves would be unsurpassed due to the shielding masses involved. Some caverns, however, would not be suitable. Open pits would allow the fallout particles to enter directly during their normal descent through the atmosphere. This would result in contamination of the floor of the proposed shelter.

Some caverns are structurally unsound and for that reason could not be considered for habitation. In north Alabama several caves located at the point where the Hartselle Sandstone overlies the Gasper Limestone were found to be unstable, with evidence of extensive recent breakdown. Caverns which remain flooded much of the time would also be unusable.

Prior to the beginning of the shelter survey certain criteria were established by the Corps of Engineers relative to acceptable shelter size. This criteria stated that each shelter area must accommodate at least 50 people (allowing 10 square feet per person); and must have a minimum head room of 6½ feet for at least half of the shelter area, and at least 4 feet for the remainder. These size requirements resulted in the rejection of many of the smaller caverns in the area.

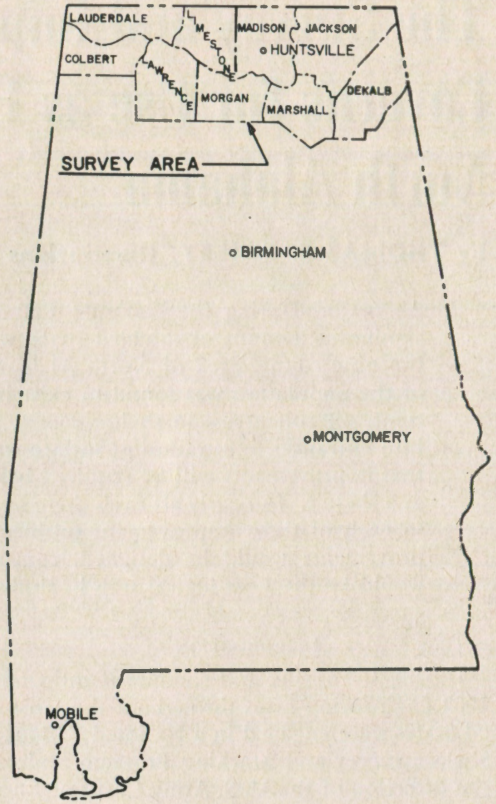


Figure 1
Nine county fallout shelter survey area in northern Alabama.

Access—In many cases, caves which met the general requirements were located in a remote area far from any population center. Inaccessibility presents a problem, but this is not insurmountable. At least one half hour and perhaps as much as six hours will be available for the population to seek shelter following a nuclear attack. This would be enough time for many people to reach even a remote shelter. In order to make this possible it would be necessary to construct roads to within practical walking distance of the remote shelters. Primitive type graded roadways or improved walkways or trails from the nearest highway would be of great help in speeding the flow of persons to these shelters.

Many caves have small entrances which would need enlarging in order to allow people to enter rapidly. Stairways or steps will often be required both outside and inside the entrances.

Large rooms suitable for use as shelters are often found well back in a cave and may only be reached by employing the techniques of rope climbing or perhaps by crawling through endless muddy wet passages. In this instance two solutions are available. First, the improvement of the existing passage to the shelter room could be undertaken by enlargement of crawlways and placement of required bridges and walkways. A less obvious but often more practical solution would be the driving of a horizontal or sloping adit directly to the shelter room from the surface. This entrance problem and its solution are illustrated in figure 3. Since experience indicates that many caves follow the general contour of the ground above (and are therefore often quite close to the surface) this second approach could well be the most practical and economical solution to a difficult access problem.

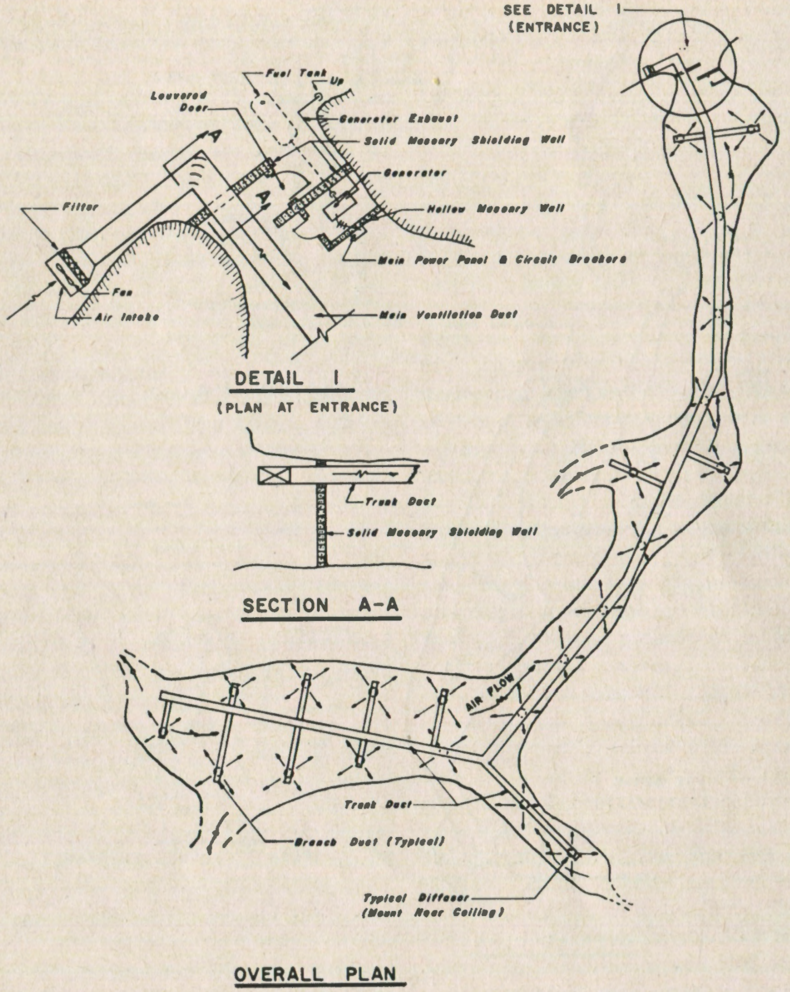
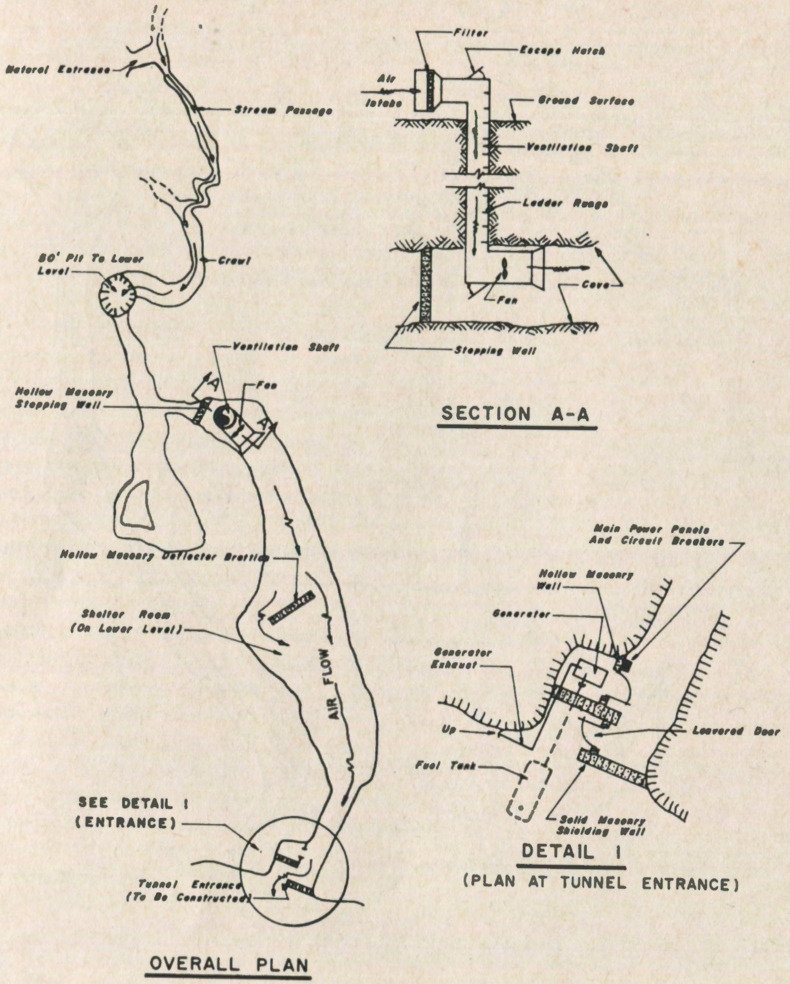


Figure 2
Ventilation system for a cave shelter.

Ventilation—Most single entrance caves examined during the course of the survey exhibited no noticeable natural current of air. Under this condition it was decided that a mechanical ventilation system would be necessary to meet the Corps of Engineers criteria which states that 3 cubic feet per minute of air must be provided for each person.

Some caves having more than one entrance



OVERALL PLAN

SECTION A-A

DETAIL I

(PLAN AT TUNNEL ENTRANCE)

Figure 3
"Flow-through" type ventilation system for a cave shelter.

and with entrances at differing elevations exhibited strong natural air currents. These currents could not be considered as dependable sources of air for the shelter occupants since there would be unpredictable variations in quantity and direction of flow depending upon the season. There has also been some speculation as to the fact that these natural currents might carry particles of radioactive dust into the shelter area. This is unlikely since the particles are of reasonably large size and would tend to settle out near the entrance if the velocity of the air stream were not too high. Some of the lighter particles could conceivably reach the shelter, however, and in order to insure protection the air flow would probably need control of some sort.

Sealing of all the cracks where the air enters the cave might well be an impossible task. In many cases it would not be possible to locate all of these cracks. Fortunately the problem may be solved much more easily than this by installing a ventilation system as shown in figure 2. This system provides a filtered intake and fan located a short distance from the entrance. This location is critical since the intake must be separated as much as possible from the generator exhaust which is piped out at the entrance. In addition the filter will become highly radioactive as it collects the fallout particles from the air. For this reason the shelter area must be shielded from the filter. The best way to accomplish this shielding is to place the filter at some distance from the entrance in such a way that the shelter would not be directly exposed to it. The air would be forced by the intake fan into a trunk duct mounted at the ceiling, and would be supplied to the shelter through branch ducts and ceiling diffusers. This system would place the shelter area under a positive pressure, making all air leakage from the inside to the outside. The used air would leave the shelter through a louvered door at the entrance. Some of this used shelter air could be used to cool the generator by routing it through the generator room and using dampers and louvers for control. The positive control afforded by a ventilation system such as described would make the shelter air supply safe from radioactive penetration.

An alternate arrangement is illustrated in figure 3. In this case a cave room separated from the natural entrance by water filled crawlways and a hazardous pit, would be made accessible by driving a short horizontal tunnel from the surface. Ventilation would be provided through a vertical shaft connecting with the surface at the rear of the room. The intake with its filter is located at the surface in a position not directly exposed to the shelter below. The air is pulled down the shaft by a fan mounted in the shelter area. A stopping wall would be erected behind the air shaft to prevent backflow into unused areas of the cave. The system shown in which the air drifts through the shelter is a "flow through" type (without ductwork) in which the air drifts through the shelter room via the path of least resistance (from the fan to the louvered door at the tunnel entrance).

One advantage offered by this system is that the vertical airshaft could also serve as an emergency exit if ladder rungs were provided in the shaft and necessary escape doors provided in the duct work and enclosures. The shelter area would be under positive pressure in this illustration and would be safe from radioactive penetration. It should be noted, however, that the control would not be as good as with a system of ductwork. In the "flow through" system it might be necessary to construct some deflector brattices which would direct the air into all areas of the shelter.

Water Flow—It appears at this time that water entering the cave shelter will be one of the most difficult of the problem considerations. A surface stream flowing into a cave entrance would definitely carry radioactive material into the shelter area. The degree of contamination would depend upon many variables and would be difficult to predict. The only positive solution to this problem would be stream diversion. In many caves this would be so expensive that it would be impossible. Most of the caves with streams flowing into their entrances would therefore be unusable. Fortunately only a few of the caves considered as shelters had surface streams entering.

A more common water problem is the case where surface water seeps into the cave via the joint system in the limestone. In many cases this water would receive adequate filtration during the time of seepage. Since the process of infiltration is slow, in many cases there would be time for the radioactive particles being carried by the water to decay to a safe level before reaching the shelter. The only positive answer to the problef of infiltration would be an extended period of observation in each individual shelter area to determine the extent and time of infiltration under varying meteorological conditions. The practical answer might be to divert some of the surface water above the cave shelter in the hope of drying out certain areas where ceiling drips indicate large amounts of seepage. If this approach were successful the shelter areas would become much more comfortable in addition to becoming much safer from radioactivity.

Habitability—The fact that most caves are damp and muddy and appear to be very uncomfortable dwelling places causes them to be somewhat undesirable as shelters in their existing condition. Improvements such such as drainage tile for removing excess water, gravel floors, and sleeping spaces on a deck above the floor would do much to relieve some of the unpleasantness. Diversion of surface water above the cave and the installation and operation of a ventilation system would both be instrumental in helping to dry out the shelter area.

Most cave floors are rough and uneven, and in places covered with breakdown. It would be necessary to rearrange this material, preferably in the form of steps or shelves, in order to make more efficient use of the space in the shelter area. This method would also provide some degree of separation for the shelter occupants. Fallout shelters are presently being stocked with supplies to provide for a two week stay time. It is very likely, however, that the shelter occupants could leave the shelter, at least for short periods of time, after two or three days. This of course would depend upon the nature of the attack, which is difficult to predict. Although the living conditions in the average cave might not be very healthful it is safe to say that the chances of recovery from a case of pneumonia would be better than chances of recovery from radiation sickness.

SURVEY RESULTS

The first step in the survey of caves consisted of an examination of the Alabama cave listing which had been prepared by the Huntsville Grotto of the National Speleological Society. Several sessions were held with survey project personnel and Grotto members in attendance, during which time a listing of 252 potential caves was prepared.

Following this, survey crews went into the field to visit each cave in order to verify its usability on the basis of size, headroom, structural stability, etc. At the same time an estimate of the approximate size was made and the owner's name and address obtained. During this field investigation several caves which had not appeared on the state listing were added to the inventory of potential cave shelters. Of the 252 caves visited only 102 were found suitable for use under Corps of Engineers criteria. Twenty-three new caves were added, however, bringing the total to 125. Maps of the 23 "discovered" caves have been turned over to the Huntsville Grotto for inclusion in the National Speleological Society files.

TABLE I

County	No. of Potential Cave Shelters	Improved Capacity of Potential Cave Shelters	Population
Lawrence	7	2,524	24,501
Limestone	3	1,189	36,513
Colbert	5	4,210	46,506
Lauderdale	4	2,779	61,622
Morgan	14	19,250	60,454
Marshall	17	27,388	48,018
Dekalb	9	8,259	41,417
Jackson	27	42,432	36,681
Madison	8	9,711	117,348
TOTALS	94	117,242	473,060

The next step in the survey operation was to either obtain or make an accurate map of each cave so that the area and volume of the shelter area could be determined. In many cases the maps furnished by the Huntsville Grotto served as excellent guides for this work. The information shown in plan was generally accurate and adequate, however most of the maps were very vague as to the location of the cave and the room heights within the cave. In all cases the caves were revisited during this phase to verify the existing map, add information to it, or make a new map.

After the maps had been prepared the capacity of the shelter area was computed. Preliminary designs for improvements to access, habitability, entrance shielding, ventilation, and electric power and lighting were made. Finally the cost of these various improvements was estimated and all of the data developed was set down on a Standard Data Collection Form. While making detailed investigations during this phase it was found that some of the caves previously thought to be usable were in fact either too small or structurally unsound or uninhabitable for some other reason. The final tabulation indicated that a total of 94 caves could be considered usable. Of these, 60 would be usable to some extent without improvement and 34 would need improvement prior to use.

Table I shows the results of the survey by county, and compares the number of improved shelter spaces which could be made available, with the population. Worthy of note is the fact that 25% of the total population of the nine county area could be sheltered in caves provided proper improvements were made. It is also interesting to note that cave shelters could provide 117,742 spaces while building shelters in the same nine county area could only be improved to provide 99,220 spaces. In addition to the cave and building shelters already mentioned two large underground limestone quarries which were similar to caves in many respects, were discovered to have an improved capacity of 30,311. These facilities were officially designated as mines and are not included in Table I, although they would be treated very much like caves in the design of improvements.

The results of the survey serve to point up the importance of considering underground shelters in general, and caves in particular, very carefully in view of their apparent potential shelter capabilities.

CONCLUSIONS

At first glance it may appear that the difficulties involved in improving caves for use as shelters would be such that all caves should be dismissed from consideration for this purpose. The results of the survey, however, indicate that a great deal of shielded space exists in caves. This significant amount of space demands that very careful consideration be given to cave shelters prior to turning our backs to their possibilities and going on to other shelter development programs.

Most cave owners have been most cooperative in giving their permission to both survey and use caves located on their property. This has not been universally true of building owners, however, due to the fact that space in buildings is already in use and the owner exercises caution in releasing the space for another use. It is not felt that any difficulty would be encountered in obtaining permission to improve a cave as a shelter.

The fact that cave shelters are already being favorably considered is evidenced by the fact that the Corps of Engineers is presently engaged in placing marking signs at each of the 60 caves in the North Alabama survey area which are usable as they exist. These signs are steel, mounted on pipe columns set in concrete at the cave entrance. Inside the cave steel signs are being permanently mounted on the wall near the center of the shelter area. In the near future these marked caves will be stocked with food, water, and equipment by Civil Defense Authorities. The materials for stocking these shelters are on hand in many areas and will be placed as soon as arrangements are made to provide safe storage places inside the caves.

Since very little construction has been tried in caves and certainly no shelter improvements made, it is difficult to predict just how some of the proposed systems will work under actual conditions. Prior to embarking on an extensive program of shelter improvement construction it would be desirable that some of the proposed systems be tested, and a uniform approach be developed. For this reason serious consideration should perhaps be given to a program involving construction of some "test shelters" in caves. Such a program of "test shelter" construction would insure that any further work in cave shelters would be properly accomplished. The costs of both design and construction could be observed and would give an accurate indication of what to expect costwise in the future.

Once a test shelter were placed in operation certain items that might be worthy of monitoring are:

1. Sound levels resulting from operation of standby power generation equipment.
2. Operation of electrical switching arrangements in a damp atmosphere.
3. Foot candle levels produced by lighting in caves.
4. Adequacy of air supply and circulation.
5. Percent of floor space found usable.

In addition to the above, many engineering techniques for cave surveying would no doubt develop during the design stage. It is even possible that the design might dictate the need for changes in the present shelter criteria as established by the Corps of Engineers.

Once the test shelter has served its purpose from a construction standpoint, it might be used with the cooperation of Civil Defense Authorities as a trial shelter for tests under actual use conditions. Further engineering data could be gathered during these tests. For example, a National Guard or similar military unit might be placed in a cave for a period of time, simulating actual nuclear attack conditions. During this period observations could be made as follows:

1. Temperature rise due to personnel in the shelter area.
2. Extent of drying of the cave floor due to operation of the ventilation system.
3. Methods of disposing of waste materials.
4. Sleeping arrangements in cave shelters.
5. Reaction of shelter occupants to cold, dampness, and confinement.

Following these use tests the test shelter could be stocked with the necessary provisions and materials for future use by the public in the event of nuclear attack. Follow-up checks could then be made for:

1. Low temperature and high humidity effects on supplies and equipment.
2. Maintenance required to keep permanent shelter improvements such as electrical and ventilation systems in working order.

In view of all the many possible uses to which a test cave shelter might be put, and due to the apparent relative importance of this type shelter in some regions of the country, it is very desirable that further study be given to cave shelters prior to dismissing them from consideration. It is felt that a test shelter project would represent the next logical step in such a study program. There are indications that such a project might possibly be included in the Civil Defense Shelter Research Program which will be underway in early 1963.

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HUNTSVILLE, ALABAMA

Annotated Checklist of the Macroscopic Troglobites of Virginia With Notes on Their Geographic Distribution[1]

by JOHN R. HOLSINGER

ABSTRACT—Extensive field work in recent years has facilitated the publication of a checklist of Virginia's troglobitic species. A large number of pertinent range extensions remain to be worked out, however, and in addition, several new species probably remain to be discovered. Forty-one troglobitic species are presently recognized from Virginia, including planarians (2), amphipods (4), isopods (3), millipeds (9), collembolans (4), beetles (10), pseudoscorpions (4), and spiders (5). At least fifteen more species are known but have yet to be described in the literature.

The isolation of certain species in caves and genetic changes within cave-dwelling animal populations are believed to be causative factors in troglobitic speciation. Many present-day cave species have probably evolved from surface forms already partially adapted for a subterranean existence. Certain cavernicolous groups like the anophthalmid beetles, pseudotremid millipeds, and cave pseudoscorpions are restricted to very small geographic areas and in some cases, only one cave system. Other cavernicolous groups like linyphiid spiders and various species of collembola are not restricted to isolated areas, but their range extends over a wide geographic region. With the exception of spiders and collembolans, aquatic troglobites seem to be more widely dispersed than terrestrial troglobites. The limestone region of Virginia which was remote from Pleistocene glaciation contains more than three times as many troglobitic species as the limestone area in Pennsylvania which was close to Pleistocene glaciation.

The first attempt to present a systematic checklist of all the known macroscopic troglobites of the United States was by Nicholas (1960a). Previous to this, Nicholas had published preliminary lists of troglobites for the states of Missouri (1960b) and Pennsylvania (1960c). One year later, Warren (1961) published a checklist of the obligative cavernicoles of Florida. Recently, the need was felt for a similar treatment of this subject in Virginia, and the author began to compile data for such a presentation. The extensive collecting carried on by T. C. Barr, Jr. in 1958 and more recently by members of the Biological Survey of Virginia Caves has provided considerable information on range extension relative to many of the little-known troglobitic species of this state. Unfortunately, most of the undescribed material obtained during this period remains to be worked out and could not be included in the formal list. In addition to the concentrated collecting efforts mentioned above, earlier workers had already added appreciably to the knowledge of Virginia cave fauna prior to 1950.

Both Nicholas (1960a) and Warren (1961) used the term obligative cavernicole in reference to those animals which are more or less completely adapted to the hypogean environment, thus permanent cave dwellers. Warren considered the two terms obligative cavernicole and troglobite to be synonymous.

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[1] Contribution Number Eight from the Biological Survey of Virginia Caves, a research project of the National Speleological Society.

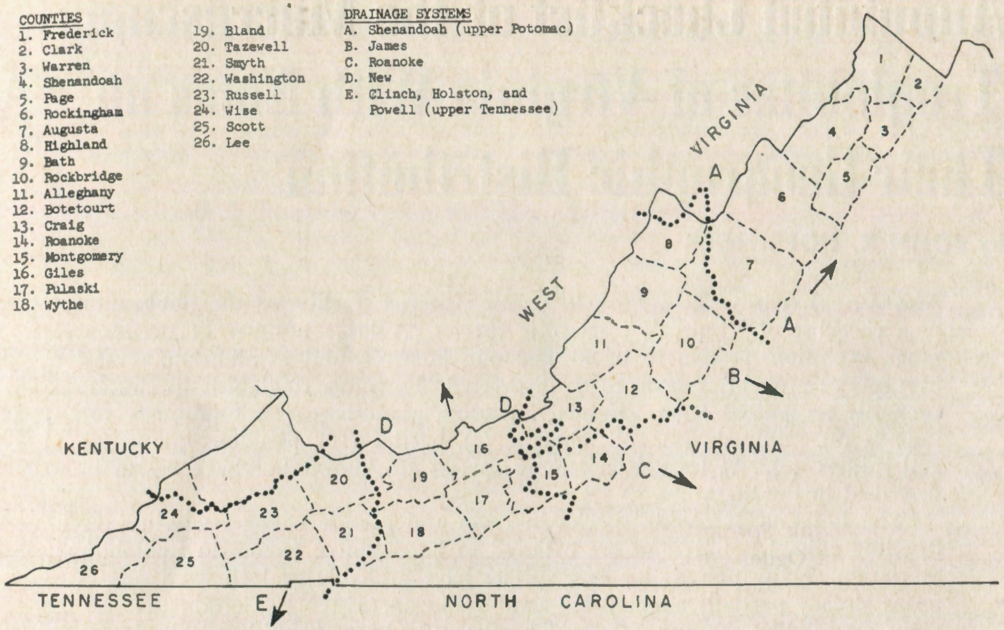

Figure 1
Map of the caverniferous limestone areas in the Appalachian region of Virginia. Dots indicate boundaries of major drainage basins; arrows indicate general direction of flow in drainage basins.

The author has adopted the term troglobite, and finds the following definition convenient: *members of a species which exist only in the cavern environment and complete their life cycles in absolute darkness* (troglobites are never found on the surface unless they are washed out of a cave by flooding). Through modification and regressive evolution these organisms usually possess characteristic features such as loss of sight (their eyes being rudimentary or lost), slender bodies, loss of toleration to such stimuli as light and heat, longer appendages, and some or complete loss of integumentary pigmentation.

As would be expected, strict limitation of species to this definition has lead to the exclusion from the checklist of several cavernicoles which, because of their almost complete modification to subterranean life, might otherwise have been included.[2] Three examples immediately come to mind: *Nesticus pallidus* Emerton, *Tomocerus bidentatus* Folsom, and *Phalangodes flavescens* (Cope). All three forms, when found in caves, undoubtedly complete their life cycles there. The occurrence, however, of these same species in epigean surroundings provided the necessary criterion for their exclusion.

The greatest shortcoming to presenting a checklist at this time was the impossibility of including many of the recently acquired but as yet undescribed troglobites that are known to exist. In many instances, whole complexes remain to be studied and worked out. In other cases further collecting is needed before definite ranges can be accurately plotted, The author has personally collected at least five and possibly six new forms which remain to be described. In addition, ten or more other new forms, collected by other workers in earlier times, are also in need of description. Several groups need a modern review before meaningful names and data can be published. The present situation, while regretable, is not surprising considering the tedious task and enormous amount of time required to complete some of these necessary jobs. In view of this, the author feels justified at this time to mention some of the undescribed forms and give the reader an idea of their present status.

Blind, unpigmented snails (fam. Bithyniidae) have been obtained from five cave streams and three springs in Virginia. Seven of these forms have been tentatively assigned to the genus *Fontigens*. The other one is an undescribed species of the genus *Lartetia*, a relict form collected only from travertine pools in Skyline Caverns, near Front Royal, Warren County. *Fontigens* is known from the following localities: Witheros Cave, Bath County; Paint Bank Spring, Craig County; Ogdens Cave and Ogdens Spring, Frederick County; Tawneys Cave, Giles County; George Hinkin Spring, Shenandoah County; and Skyline Caverns, Warren County. All specimens have been deposited with J. P. E. Morrison, United States National Museum.

As a result of work by Causey (1960) many of the problems regarding the taxonomy and geographic distribution of the zygonopid millipeds have been clarified. Another problem, similar to the one which once plagued the zygonopids, remains to be resolved for the genus *Pseudotremia*. Major problems concern the variation and speciation of this group, especially in the southwestern portion of the state. In addition, a totally new species of pseudotremid was recently obtained in Porters Cave, Bath County, and will be described by N. B. Causey in the near future.

Two new species of isopods of completely different families have been discovered since 1958. One, a cirolonid, was collected from Madison Cave, Augusta County by T. C. Barr, Jr. and possibly belongs to the otherwise European genus, *Sphaeromides*. In 1960 the author collected a new species of asellid isopod from three caves in southwestern Virginia. With subsequent collecting, *Asellus sp.* is now known from five localities, all within the upper Tennessee River drainage system. Specific locations for this species are Crouses and Unthanks Caves, Lee County; Rock House and Seven Springs Caves, Russell County; and Parsons Cave, Wise County. H. R. Steeves, III, (pers. comm.) now has a description of this isopod in press. Several undetermined and possibly new species of terrestrial isopods (fam. Trichoniscidae) have been collected from Lowmoor Quarry Cave, Alleghany County and Bucks Hill Cave, Rockbridge County.

Many additional specimens of troglobitic amphipods, some of which may be new forms, have been discovered since the informative work of Hubricht (1943). When further work has been accomplished, new range extensions can undoubtedly be mapped. All amphipod material is at present in the care of the author.

A great deal of important work on the troglobitic trechines (essentially of the genus *Pseudanophthalmus*) has been accomplished in recent years by T. C. Barr, Jr. Many new species have been obtained in west central and southwestern Virginia, and a monographic treatment on this interesting group of cavernicoles is expected in the near future.

Little has been reported regarding the range or habits of the troglobitic pesudoscorpions. Malcolm and Chamberlain (1961) have recently described two new species from caves in southwestern Virginia, but owing to the secretive nature and comparative rarity of these organisms, few specimens have ever been obtained. To date, however, every cave (with one possible exception) in which pseudoscorpions were collected have yielded what will probably turn out to be discrete new species. These include *Apochthonius sp.* and *Pseudozaona sp.* from Cave Run Pit Cave, Bath County; *Mundochthonius sp.* from Helsleys Cave, Shenandoah County; a form similar to the European genus *Pseudoblothrus* from Maddens Cave, Shenandoah County; and *Kleptochthonius* (*Chamberlinochthonius*) *sp.* from Porters Cave, Bath County.

Continued field work will doubtlessly add considerable knowledge to the ranges of many of the known troglobites of the state. It also stands to reason that a few more new species will be uncovered from time to time. This is especially true of the organisms with-

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[2] Because of its reported existence in a grave, *Pseudosinella argentea* Folsom might be an exception to this rule. The author, however, feels that a grave (while possibly endogeic) could in most instances be regarded as possessing all of the factors that ordinarily constitute a hypogean habitat. It might also be added that all other records for this species are strictly from caves.

in the groups that consist of pseudoscorpions, pseudotremid millipeds, and carabid and pselaphid beetles. In order to keep pace with the inevitable addition of pertinent data, the author plans to publish supplementary checklist as warranted.

Geographic Distribution

It is beyond the scope of this paper to make more than a few brief comments relative to the many problems regarding the distribution of troglobitic species in the Appalachians of Virginia. Intense speciation, which is so characteristic of cavernicolous groups like the trechine beetles, pseudotremid millipeds, and cave pseudoscorpions, is undoubtedly a dramatic result of geographic isolation in caves. Of the eight presently recognized species of the carabid genus *Pseudanophthalmus* from Virginia, one is known from a single cave while the remaining seven are restricted to but a few caves closely related to each other by their geographic proximity. Four of these anophthalmid species are represented by subspecies (see checklist), and with the exception of *P. hubbardi limicola, P. p. potomaca,* and *P. p. pusio,* each subspecies is known from only one cave. In Clover Hollow and Tawneys Caves, Giles County, *P. gracilis* and *P. punctatus* are sympatric, but each species occupies its own niche within the cave habitat.

Three of the six described troglobitic species of the milliped genus *Pseudotremia* are, to date, known only from their type locality. The other three species, while not restricted to one cave, are however, found only in caves that exist in continuous or contiguous beds of limestone within a relatively small area. Three species of the completely troglobitic genus *Zygonopus* have been described from Virginia, but all three fail to demonstrate the high degree of endemism that is so characteristic of the cave species belonging to the genus *Pseudotremia*. In Virginia species ranges seem roughly to follow drainage basin outlines. Close scrutiny, however, reveals that this is not a general rule, especially in the neighboring state of West Virginia. The tendency to overlap into an adjacent drainage basin is noted in Augusta County, Virginia, where the range of *Zygonopus weyeriensis* extends into the upper Potomac drainage and comes to within approximately ten miles of the range of *Zygonopus whitei*. A similar situation is found in Pendleton County, West Virginia, where the range of *Z. weyeriensis* also extends into the upper Potomac drainage basin and comes to within approximately five miles of the range of *Z. whitei*. Comparable situations are also noted in Roanoke County, Virginia, and Greenbrier County, West Virginia.

Information regarding cave pseudoscorpions is rare, but of the four recognized species each has so far been collected from only a single cave. In contrast, other cavernicolous groups like spiders (linyphiids and several nesticids) and collembolans (three species of the family Entomobryidae) contain extremely vagile species which, in several cases, are distributed in caves throughout the limestone areas of the entire southeastern United States. If isolation is a definitive factor here, then it has not yet shown itself in any appreciable amount of speciation. This seemingly unusual situation might be explained if consideration is given to the distribution pattern of ancestors, to the length of time that these species have actually been isolated within a cave, and to their susceptibility to genetic drift. If it is assumed that isolation has occurred in fairly recent times, then it might also be assumed that divergence has not had enough time to advance to the point where phenotypic differences can be properly recognized.

In some respects, aquatic troglobites present different zoogeographic distribution problems than do terrestrial troglobites, and must be studied from a slightly different viewpoint. As Barr (1960a) has pointed out, the dispersal of aquatic troglobites by underground routes is probably more easily facilitated than terrestrial troglobites since subterranean watercourses are probably less readily closed by silting, erosion, and flowstone deposition than drier courses. This hypothesis may well account for the wide range of the cave isopod, *Asellus pricei*, which occurs in caves in the Susquehanna River drainage system in Pennsylvania southwestward to the James River drainage system in Virginia and possibly as far south as the New River drainage basin. None of the divides separating these drainage systems are more than a few miles wide and all consist of limestone strata. If, as Piper (1932) has observed, surface and subterranean erosion can proceed at different rates then it might be predicted that there are one or more underground waterway connections between these aforementioned basins. If these hypothetical connections exist, they could greatly favor gene exchange between populations living in caves situated along basin headwaters. It should be pointed out, however, that a totally different species of *Asellus* exists in caves located along the upper Tennessee River drainage in southwestern Virginia, and, according to H. R. Steeves, III (pers. comm.), this undescribed species is more closely related morphologically to certain Tennessee and Kentucky forms that it is to the *pricei* group in northern and west central Virginia.

Cavernicolous amphipods, with the exception of the widely distributed troglophile, *Gammarus minus* Say, seem to be restricted to specific drainage systems. *Stygobromus spinosus* appears to be the most isolated of these species and is know so far from only two locations in the upper Potomac drainage basin in the Shenandoah Valley.

In comparison, aquatic cave planarians present so many range anomalies that an explanation for their dispersal by the usual means, i.e., intra-drainage or inter-drainage, is impossible at the present time. *Sphalloplana virginiana* is restricted to only one cave in Rockbridge County, while *Phagocata subterranea* is widely but sparsely distributed over an area covering the states of Indiana, Pennsylvania, and Virginia.

It is interesting to compare the number of troglobitic species of the Paleozoic limestone terrane in Virginia to those in the glaciated or glacial-affected areas of Pennsylvania. Twelve true cave forms have been discovered in Pennsylvania in contrast to forty-one which have been described from Virginia. It is perhaps significant, that of these twelve species, all are aquatic organisms except for one milliped and two spiders. Five of the species found in Pennsylvania caves are also found in Virginia caves and three of these are aquatic. Doubtless the inundation of caves by glacial floodwaters and the correspondingly lower temperatures must have had a devastating effect on many of the cave forms which were living in Pennsylvania caves during the Pleistocene. It is conceivable, however, that many of the aquatic troglobites of that period were able to escape extinction by virtue of the fact that they would not have been vulnerable to drowning or drastically affected by the supposed temperature drop of underground water. Hazelton and Glennie (1953) indicated that the European cave amphipod, *Niphargus*, might have escaped annihilation during the Pleistocene glaciation of the British Isles if the ground water below the ice remained at a temperature above 4°C. (39°F.). An alternate theory might assume that all troglobites in Pennsylvania were exterminated by one or more of the lethal effects of glaciation, and that most of the aquatic forms present in Pennsylvania today have migrated there through subterranean watercourses from unglaciated areas since the late Pleistocene. Still a third hypothesis might argue that all troglobitic forms present in Pennsylvania have evolved since glacial recession. The third postulate, however, fails to account for the comparatively large number of aquatic species in contrast to the relatively small number of terrestrial ones. If the latter hypothesis is accepted, then it must be assumed that any of the same species living in Virginia (e.g., *Asellus pricei* or *Phagocata subterranea*) have also evolved in the interval of 10,000 to 15,000 years since the last glacial period. That troglobitic evolution could have taken place in this comparatively short period of time is not necessarily ruled out, if one takes into consideration the fact that many ancestors of currently existing troglobites were probably already preadapted for cavern dwelling and that small isolated populations might be very prone to the accidental fixing of mutations.

One of the most tantalizing zoogeographic problems yet encountered involves two relict troglobitic species only recently discovered in the Shenandoah Valley. As already pointed out, a troglobitic snail, *Lartetiia sp.*, known in this country only from Skyline Caverns, has its closest affinities with a European cave form found in several caves in the Rhine River Valley. Similarly, a cirolanid isopod from Madison Cave seems to be much closer related to a European species, *Spaeromides raymondi* Dollfus (known only from a single cave in France), than to a previously known North American species, *Cirolanides texensis* Benedict, known from several caves in Texas. Such phenomena are probably the result of several complex, interrelated factors and are almost certain to have zoological as well as geological implications. It is not uncommon to find like genera on both sides of the Atlantic, but, to find two such closely related forms as those indicated above, in remotely isolated caves, separated by an insurmountable geological barrier, is unique.

CHECKLIST

In the following checklist, specific cave localities have been listed as part of the range of a species in Virginia. Where the troglobite has no record outside of the state, specific localities are cited under the General Range category. Cave location data have been made consistent with information in the files of the Virginia Cave Survey. Caves listed as specific localities but not consistent with records of the Virginia Cave Survey are noted with an asterisk. Where caves have been known by more than one name the currently accepted one is listed first with the former name in parentheses.

The author is grateful to the following for their aid in identifying specimens and their helpful comments regarding the taxa included: Dr. Thomas C. Barr, Jr., Carabidae; Dr. Nell B. Causey, Chordeumida; Dr. Kenneth A. Christiansen and Dr. David L. Wray, Collembola; Dr. Willis J. Gertsch, Araneae; Dr. Libbie H. Hyman, Turbellaria; Dr. David R. Malcolm and Dr. William B. Muchmore, Chelonethida; Mr. Harrison R. Stevens, III, Asellidae. The author is also indebted to Dr. Horton H. Hobbs, Jr., Brother G. Nicholas, F. S. C., and Mr. John E. Cooper for their helpful suggestions in the preparation of the manuscript. The latter is an investigator in the Biological Survey of Virginia Caves, and has contributed to the field work upon which this report is based. Mr. Lyle G. Conrad has also assisted in field work.

PLATYHELMINTHES

TURBELLARIA

TRICLADIDA

Kenkiidae

Sphalloplana virginiana Hyman

Sphalloplana virginiana Hyman, 1945. Am. Midl. Nat., 34:477.
Type locality—Showalters Cave, 1 mile south of Lexington, Rockbridge, Co., Virginia.
General range—Known only from type locality.
Comments—Small population observed in small, muddy-bottomed pool several hundred feet from entrance. Cave is subject to flooding and type pool dries up during summer months. Habitat also with a wealth of organic matter and contains other organisms, including isopods, collembolans, and salamander larvae.

Planariidae

Phagocata subterranea Hyman

Phagocata subterranea Hyman, 1937. Trans. Am. Microscop. Soc., 56:474.
Type locality—Donaldsons Cave, 4 miles east of Mitchell, Lawrence Co., Indiana.
General range—Caves of Lawrence and Monroe Cos., Indiana; Goss Cave, Mifflin Co., Pennsylvania (L. H. Hyman, pers. comm.); and Russell Co., Virginia.
Virginia localities—Known only from Rock House (Banners Corner) Cave, Russell County.
Comments—In Rock House Cave a large population lives in several rimstone pools which are highly contaminated with septic tank leakage from above. The population exists in close association with annelid worms, isopods, and salamanders.

ARTHROPODA

CRUSTACEA

AMPHIPODA

Gammaridae

Crangonyx antennatus Packard

Crangonyx antennatus Packard, 1881. Am. Nat., 15:880.
Type locality—Nickajack Cave, Shellmound, Marion Co., Tennessee.
General range—Caves in Alabama, Tennessee, and Virginia.
Virginia localities—Known only from Cudjos Cave, Lee Co.
Comments—Collected from a stream in Cudjos Cave (Hubricht, 1943).

Stygobromus mackini Hubricht

Stygobromus mackini Hubricht, 1943. Am. Midl. Nat., 29:695.
Type locality—Sikes Cave,* 4.5 miles north of Lebanon, Russell Co., Virginia.
General range—Indian Cave, Grainger Co., Tennessee; and caves in Russell and Tazewell Cos., Virginia.
Virginia localities—Type locality and Chimney Rock (Chimney) Cave, Tazewell Co.

Stygobromus spinosus (Hubricht and Mackin)

Cragonyx spinosus Hubricht and Mackin, 1940. Am. Midl. Nat., 23:203
Stygobromus spinosus (Hubricht and Mackin) Hubricht, 1943. Am. Midl. Nat., 29:697.
Type locality—A spring near Hawksbill Mountain, Skyline Drive, Madison Co., Virginia.
General range—Type locality and Luray Caverns, Page Co.
Comments—Hubricht (1943) reported 100 female specimens from drip pools in Luray Caverns.

Synpleonia pizzinii Shoemaker

Synpleonia pizzinii Shoemaker, 1938. Proc. Biol. Soc. Wash., 51:137.
Type locality—Wetzel's Spring, Grover Archbold Park, just west of Georgetown, Washington, D. C.
General range—Springs in Washington, D. C. and southern Pennsylvania, and caves and springs in northern Virginia.
Virginia localities—Spring, Fairfax Co.; Massanutten Caverns, Rockingham Co.; Skyline Caverns, Warren Co.
Comments—Collected from cave streams and pools and from springs.

ISOPODA

Asellidae

Asellus pricei (Levi)

Caecidotea pricei Levi, 1949. Notulae Nat., no. 220:2.
Asellus pricei (Levi) Mackin, 1959. In Ward and Whipple's Fresh Water Biology: 876.
Type locality—Refton Cave, Lancaster Co., Pennsylvania.
General range—Caves in Pennsylvania and northern and west central Virginia.
Virginia localities—Barterbrook Springs Cave, Augusta Co.; Ogdens Cave, Frederick Co.; Will Mauck Cave, Page Co.; Billy Williams, Showalters, Tolleys Caves and Graham Spring, Rockbridge Co.; Endless and Massanutten (spring in front of cave) Caverns, Rockingham Co. This species has also been reported from Better Forgotten and Butler Caves, Bath Co.; Eagle Rock Cave No. 2, Botetourt Co.; and Tawneys Cave, Giles Co., but these records are unconfirmed at the present time.
Comments—Usually found in small numbers in quiet pools but sometimes under rocks in streams. This species has been observed to feed on dead frogs and toads. Asellids (but not *A. pricei*) have been found to eat cave planarians in Rock House Cave, Russell Co. It should be noted that on several occasions in the past this species was erroneously determined as *Caecidotea stygia* Packard in Virginia as well as in Pennsylvania.

Trichoniscidae

Caucasonethis henroti (Vandel)

Amerigoniscus henroti Vandel, 1950. Arch. Zool. exp. Gen., 87:191.
Caucasonethis henroti (Vandel) Vandel, 1953. Pacific Sc., 7:175.
Type locality—Gilleys Cave, Pennington Gap, Lee Co., Virginia.
General range—Known only from type locality.
Comments—According to T. C. Barr, Jr. (pers. comm.), this species lives on wet, rotting wood near the entrance to Gilleys Cave.

Miktoniscus racovitzai Vandel

Miktoniscus racovitzai Vandel, 1950. Arch. Zool. exp. Gen., 87:197.
Type locality—Luray Caverns, Luray, Page Co., Virginia.
General range—Known only from type locality.

DIPLOPODA

CHORDEUMIDA

Conotylidae

Zygonopus packardi Causey

Zygonopus packardi Causey, 1960. J. New York Entomol. Soc., 68:77.
Type locality—Pattons Cave, Monroe Co., West Virginia.
General range—Caves in Bland, Botetourt, Giles, and Roanoke Cos., Virginia; and Greenbrier, Mercer, and Monroe Cos., West Virginia.
Virginia localities—Hamilton and Newberry-Bane Caves, Bland Co.; Perry Saltpeter Cave, Botetourt Co.; Clover Hollow, Starnes, Straleys, and Tawneys Caves and Giant Caverns, Giles Co., Dixie Caverns, Roanoke Co.
Comments—Usually found in small numbers around decaying wood and leaf litter, or on moist clay banks. Collected from wet stalactites in Dixie Caverns.

Zygonopus weyeriensis Causey

Zygonopus whitei Ryder, 1881 (in part). Proc. U. S. Nat. Mus., 3:527.
Zygonopus weyeriensis Causey, 1960. J. New York Entomol. Soc., 68:75.
Type locality—Grand Caverns (Weyers Cave), near Grottoes, Augusta Co., Virginia.
General range—Caves in Augusta, Bath, and Rockbridge Co., Virginia; and Greenbrier, Pendleton, and Pocahontas Cos., West Virginia.
Virginia localities—Type locality and Madison Cave, Augusta Co.; Boundless, Butler, Porters, and Starr Chapel Caves, Bath Co.; Billy Williams Cave, Rockbridge Co.
Comments—Habits are similar to *Zygonopus packardi* (discussed above).

Zygonopus whitei, Ryder

Zygonopus whitei Ryder, 1881. Proc. U. S. Nat. Mus., 3:527.
Type locality—Luray Caverns, Luray, Page Co., Virginia.
General range—Caves in Augusta, Page, Rockingham, and Shenandoah Cos., Virginia; and Pendleton Co., West Virginia.
Virginia localities—Glade Cave, Augusta Co.; type locality and Ruffners Cave, Page Co.; Endless Caverns and Stephens Cave, Rockingham Co.; Maddens Cave and Shenandoah Caverns, Shenandoah Co.
Comments—Habits are similar to other zygonopids. Specimens of this species were collected under raccoon feces in Glade Cave and on rocks barely submerged in a stream in Endless Caverns.

Cleidogonidae

Pseudotremia cavernarum Cope

Pseudotremia cavernarum Cope, 1869. Proc. Am. Philos. Soc., 11:179.
Type locality—Erharts Cave, 5 miles east of Christiansburg, Montgomery Co., Virginia.
General range—Known only from type locality.
Comments—In most instances, troglobitic pseudotremids are found crawling on damp clay or mud banks. In Erharts Cave, *P. cavernarum* is very abundant on rotting wood at the bottom of the entrance slope (T. C. Barr, Jr., pers. comm.).
In Porters Cave, Bath Co., two specimens (*Pseudotremia sp.*) were collected from the decaying carcass of a turtle.

Pseudotremia hobbsi Hoffman

Pseudotremia hobbsi Hoffman, 1950. J. Wash. Acad. Sci., 40:90.
Type locality—Chestnut Ridge Cave,* 2.5 miles northwest of Clifton Forge, Alleghany Co., Virginia.
General range—Caves in the upper James River drainage system in Alleghany and Bath Cos., Virginia, and McClungs Cave, Greenbrier Co., West Virginia.
Virginia localities—Hoffman (1950) reports this species from 11 caves in Alleghany and Bath Cos., but unfortunately, these records are not presently available. One additional record is known—Second Dam Cave, Alleghany Co.

Pseudotremia nodosa Loomis

Pseudotremia nodosa Loomis, 1939. Bull. Mus. Comp. Zool., 86:175.
Type locality—English Cave, near Harrowgate, Claiborne Co., Tennessee.
General range—Caves in Claiborne and Anderson Cos., Tennessee, and Lee Co., Virginia.
Virginia localities—Crouses Cave and possibly Gilleys and Jones (Ewing) Saltpeter Caves, Lee Co. Note: A larger series of material is needed before accurate determinations can be made on the pseudotremids of Lee Co.

Pseudotremia sublevis Loomis

Pseudotremia sublevis Loomis, 1944. Psyche, 51:67.
Type locality—Tawneys Cave, near Newport, Giles Co., Virginia.
General range—Type locality, Big Stony,* Clover Hollow, and Spruce Run Caves, Giles Co., Virginia.
Virginia localities—There is a good possibility that this species has been collected in caves other than those listed under general range, but data on these locations are not presently available.
Comments—Cope (1869) reported *Pseudotremia cavernarum* from Big Stony and Spruce Run Caves, Giles Co., in addition to Erharts Cave, Montgomery Co. Hoffman (1958) explored these Giles County caves for millipeds and reached the conclusion that they were inhabited by *Pseudotremia sublevis* and not *P. cavernarum* as originally reported by Cope. As a result, the type locality and range of *P. cavernarum* was restricted to Erhart's Cave (see checklist, above).

Pseudotremia tuberculata Loomis

Pseudotremia tuberculata Loomis, 1938. Bull. Mus. Comp. Zool., 86:171.
Type locality—Cassel (Cassel Farm) Cave, Burkes Garden, Tazewell Co., Virginia.
General range—Known only from type locality.
Comments—Abundant on raccoon feces in type locality.

Pseudotremia valga Loomis

Pseudotremia valga Loomis, 1943. Bull. Mus. Comp. Zool., 92:377.
Type locality—Cudjos (King Solomons) Cave, Cumberland Gap, Lee Co., Virginia.
General range—Known only from type locality.
Virginia localities—See note on *P. nodosa.*

INSECTA

COLLEMBOLA

Entomobryidae

Pseudosinella argentea Folsom

Pseudosinella argentea Folsom
Pseudosinella argentea Folsom, 1902. Psyche. 9:366.
Type locality—A grave in Washington, D. C.

General range—Caves in Arkansas, Georgia, Kentucky, Missouri, Tennessee, Virginia, and a grave in Washington, D. C.
Virginia localities—Known only from Madison Cave, Augusta Co.

Pseudosinella orba Christiansen

Pseudosinella orba Christiansen, 1960. Psyche. 67:20.
Type locality—Morrill Cave, Sullivan Co., Tennessee.
General range—Single localities in Tennessee and Virginia.
Virginia localities—Known only from Hamilton Cave, Bland Co.

Sinella hoffmani Wray

Sinella hoffmani Wray, 1952. Bull. Broklyn Entomol. Soc., 47:95.
Type locality—Lowmoor Quarry Cave, near Clifton Forge, Alleghany Co., Virginia.
General range—Caves in Bath, Botetourt, Rockbridge, and Tazewell Cos., Virginia; and Monroe, Pendleton, and Pocahontas Cos., West Virginia.
Virginia localities—Type locality, Alleghany Co.; Boundless, Breathing, Butler, Crossroads, Porters, Starr Chapel, and Witheros Caves, Bath Co.; Perry Saltpeter Cave, Botetourt Co.; Buck Hill and Doll House Caves, Rockbridge Co.; Stonleys (Divides) Cave, Tazewell Co.
Comments—This species is sometimes very plentiful on decaying organic debris and occasionally on moist clay banks. Several specimens were collected from the surface of a small pool in Lowmoor Quarry and Stonleys Caves.

Sminthuridae

Arrhopalites ferrugineus (Packard)
Smynthurus ferrugineus (Packard), 1888. Mem. Nat. Acad. Sci., 4:67.
Arrhopalites ferrugineus (Packard) Christiansen, 1960. Am. Midl. Nat., 64:40.
Type locality—Endless Caverns (New Market Cave), 4 miles south of New Market, Rockingham Co., Virginia.
General range—Type locality and Grand Caverns, Augusta Co., Virginia.

COLEOPTERA

Carabidae

Aphanotrechus virginicus Barr

Aphanotrechus virginicus Barr, 1960. Coleopterists' Bull., 14:65.
Type locality—Hugh Young Cave, 0.5 mile southeast of Maiden Spring, Tazewell Co., Virginia.
General range—Known only from type locality.
Comments—This form is known from a single female collected on a rock above the cave stream (Barr, 1960b).

Pseudanophthalmus gracilis Valentine

Pseudanophthalmus gracilis Valentine, 1932. J. Elisha Mitchell Sci. Soc., 47:253.
Type locality—Tawneys Cave, near Newport, Giles Co., Virginia.
General range—Type locality and Clover Hollow Cave, Giles Co., Virginia.
Comments—The anophthalmids are usually found near cave streams or pools and frequently under rocks or organic material.

Pseudanophthalmus hirsutus hirsutus Valentine

Pseudanophthalmus hirsutus hirsutus Valentine, 1932. J. Elisha Mitchell Sci. Soc., 47:252.
Type locality—Cudjos (King Solomons) Cave, Cumberland Gap, Lee Co., Virginia.
General range—Known only from type locality.

Pseudanophthalmus hirsutus delicatus Valentine

Pseudanophthalmus hirsutus delicatus Valentine, 1932. J. Elisha Mitchell Sci. Soc., 47:270.
Type locality—Gilleys Cave, Pennington Gap, Lee Co., Virginia.
General range—Known only from type locality.

Pseudanophthalmus hubbardi hubbardi (Barber)

Anophthalmus hubbardi Barber, 1928. J. Wash. Acad. Sci., 18:196.
Pseudanophthalmus hubbardi (Barber) Jeannel, 1928. L'Abeille, 35:130.
Pseudanophthalmus hubbardi hubbardi (Barber) Jeannel, 1931. Arch. Zool. ex. Gen., 71:450.
Type locality—Luray Caverns, Luray, Page Co., Virginia.
General range—Known only from type locality.

Pseudanophthalmus hubbardi avernus Valentine

Pseudanophthalmus hubbardi avernus Valentine, 1945. Trans. Conn. Acad. Arts and Sci., 36:648.
Type locality—Endless Caverns, 4 miles south of New Market, Rockingham Co., Virginia.
General range—Known only from type locality.

Pseudanophthalmus hubbardi limicola Jeannel

Pseudanophthalmus hubbardi limicola Jeannel, 1931. Arch. Zool. exp. Gen., 71:450.
Type locality—Maddens Cave, 1.5 miles northwest of New Market Station, Shenandoah Co., Virginia.
General range—Type locality, Shenandoah Caverns and Shenandoah Wild Cave, Shenandoah Co., Virginia.

Pseudanophthalmus hubbardi parvicollis Jeannel

Pseudanophthalmus hubbardi parvicollis Jeannel, 1931. Arch. Zool. exp. Gen., 71:450.
Type locality—Battlefield Crystal Cave, 2 miles northeast of Strasburg, Shenandoah Co., Virginia.
General range—Known only from type locality.

Pseudanophthalmus hubrichti Valentine

Pseudanophthalmus hubrichti Valentine, 1948. Geol. Surv. Alabama, Mus. Pap. no. 27:13.
Type locality—Doughertys Cave, 3 miles northwest of Lebanon, Russell Co., Virginia.
General range—Type locality and Rock House (Banners Corner) Cave, Russell Co., Virginia.

Pseudanophtalmus petrunkevitchi Valentine, 1945.

Pseudanophthalmus petrunkevitchi Valentine, 1945. Trans. Conn. Acad. Arts and Sci., 36:652.
Type locality—Skyline Caverns, 2 miles southwest of Front Royal, Warren Co., Virginia.
General range—Type locality and Woods Cave, Page Co., Virginia.

Pseudanophthalmus potomaca potomaca (Valentine)

Pseudanophthalmus potomaca Valentine, 1932. J. Elisha Mitchell Sci. Soc., 47:262.
Pseudanophthalmus hubbardi potomaca Valentine, 1945. Trans. Conn. Acad. Arts and Sci., 36:651.
Pseudanophthalmus potomaca potomaca (Valentine) Jeannel, 1949. Notes Biospeol, fasc. 4, Publ. Mus. Nat. Hist. Paris, no. 12:63.
Type locality—Kenny Simmons Cave, Pendleton Co., West Virginia.
General range—Single localities in Virginia and West Virginia.
Virginia localities—Known only from Van Devanters Cave, Highland Co.

Pseudanophthalmus punctatus Valentine

Pseudanophthalmus pusio var. punctatus Valentine, 1931. J. Elisha Mitchell Sci. Soc., 46:250.
Pseudanophthalmus punctatus Valentine, 1932. J. Elisha Mitchell Sci. Soc., 47:266.
Type locality—Tawneys Cave, near Newport, Giles Co., Virginia.
General range—Type locality, Clover Hollow and Spruce Run Caves, Giles Co., Virginia.

Pseudanophthalmus pusio pusio (Horn)

Pseudanophthalmus pusio Horn, 1868. Trans. Am. Entomol. Soc., 2:124.
Pseudanophthalmus pusio pusio (Horn) Valentine, 1932. J. Elisha Mitchell Sci. Soc., 47:268.
Type locality—Erharts Cave, 5 miles east of Christiansburg, Montgomery Co., Virginia.
General range—Type locality, Agnew and Thorn Hill Caves, Montgomery Co., Virginia.

Pseudanophthalmus pusio bathycola Valentine

Pseudanophthalmus pusio bathycola Valentine, 1932. J. Elish Mitchell Sci. Soc., 47:268.
Type locality—Aunt Nellies Cave, 3 miles southeast of Blacksburg, Montgomery Co., Virginia.
General range—Known only from type locality.

Pselaphidae

Arianops (Arispeleops) jeanneli Park
Arianops (Arispeleops) jeanneli Park, 1956. J. Tenn. Acad. Sci., 31:85.
Type locality—Gilleys Cave, Pennington Gap, Lee Co., Virginia.
General range—Known only from type locality.
Comments—Cavernicolous pselaphids are usually found in damp areas near organic material, close to cave entrances. Only one specimen of this species is known.

ARACHNIDA

CHELONETHIDA

Chthoniidae

Apochthonius coecus (Packard)

Chthonius coecus Packard, 1884. Am. Nat., 18:203.
Apochthonius coecus (Packard) Chamberlin and Malcolm, 1960. Am. Midl. Nat., 64:111.
Type locality—Grand Caverns (Weyers Cave), near Grottoes, Augusta Co., Virginia.
General range—Known only from type locality.

Kleptochthonius (Chamberlinochthonius) gertschi Malcolm and Chamberlin

Kleptochthonius (Chamberlinochthonius) gertschi Malcomb and Chamberlin, 1961. Am. Mus. Novitates, no. 2063:17.
Type locality—Gilleys Cave, Pennington Gap, Lee Co., Virginia.
General range—Known only from type locality.

Kleptochthonius (Chamberlinochthonius) lutzi Malcolm and Chamberlin
Kleptochthonius (Chamberlinochthonius) lutzi Malcolm and Chamberlin, 1961. Am. Mus. Novitates, no. 2063:19.
Type locality—Cudjos Cave, Cumberland Gap, Lee Co., Virginia.
General range—Known only from type locality.

Syarinidae 1X OR TP, NOT TB

Chitrella cavicola (Packard)
Obisium cavicola Packard, 1884. Am. Nat., 18:201.
Chitrella cavicola (Packard) Chamberlin and Malcolm, 1960. Am. Midl. Nat., 64:113.
Type locality—Endless Caverns (New Market Cave), 4 miles south of New Market, Rockingham Co., Virginia.
General range—Known only from type locality.

ARANEAE

Linyphiidae

Bathyphantes weyeri (Emerton)

Linyphia weyeri Emerton, 1875. Am. Nat., 9:279.
Bathyphantes weyeri (Emerton) Barr, 1960. Am. Midl. Nat., 64:5.
Type locality—Grand caverns (Weyers Cave), near Grottoes, Augusta Co., Virginia.
General range—Virginia and Pennsylvania west to Kentucky and Wisconsin.
Virginia localities—Known only from type locality.

Phanetta subterranea (Emerton)

Linyphia subterranea Emerton, 1875. Am. Nat., 9:279.
Phanetta subterranea (Emerton) Keyserling, 1886. Spinnen Amerikas, Theridiidae, 2:125.
Type locality—Wyandotte Caverns, Crawford Co., Indiana.
General range—Virginia and Pennsylvania west to Indiana and southeast to Alabama.
Virginia localities—Lowmoor Quarry Cave, Alleghany Co.; Fountain and Madison Caves, Augusta, Ca.; Boundless, Breathing, Cave Run Pit, Clarks, and Starr Chapel Caves, Bath Co.; Hamilton Cave, Bland Co.; Perry Saltpeter Cave, Botetourt Co.; Ogdens Cave, Frederick Co. Clover Hollow, Starnes, Straleys, and Tawney's Caves, Giles Co. Olingers Cave, Lee Co.; Luray Caverns, Page Co.; Massanutten Caverns and Stephens Cave, Rockingham Co.; Jessie Cave, Russell Co. Grigsby Cave, Scott Co.
Comments—Usually found in or under rotting vegetable matter, decaying animal feces and sometimes on damp clay banks. This species is quite often found to live in close association with collembolans on which it may be predacious.

Porrhomma cavernicolum (Keyserling) new combination[3]

Willibaldia cavernicola Keyserling, 1886. Spinnen Amerikas, Theridiidae, 2:123.
Linyphia incerta Emerton, 1875. Am. Nat., 9:280.
Porrhomma emertoni (Emerton) Roewer, 1942. Katalog der Araneae, 1:603.
Troglohypantes cavernicola (Keyserling) Bonnet, 1959. Bibligraphia Araneorum, 2(5):4721.
Type locality—Reynolds Cave, Barren Co., Kentucky.
General range—Virginia west to Missouri and southwest to Arkansas.
Virginia localities—Glade and Madison Caves, Augusta Co.; Clarks, Crossroads, Porters, and Witheros Caves, Bath Co.; Clover Hollow Cave, Giles Co.; Unthanks Cave, Lee Co.; Luray Caverns and Ruffners Cave, Page Co.; Buck Hill Cave, Rockbridge Co.
Comments—The habits for this species seems to be approximately the same as for *Phanetta subterranea.*

Nesticidae TP

Nesticus carteri Emerton

Nesticus carteri Emerton, 1875. Am. Nat., 9:279.
Type locality—Mammoth Cave, Edmonson Co., Kentucky.
General range—Caves in Kentucky, Tennessee, and Virginia.
Virginia localities—Cudjos Cave, Lee Co.; Buck Hill and Doll House Caves, Rockbridge Co.

Nesticus tennesseensis (*Petrunkevitch*)

Ivesia tennesseensis Petrunkevitch, 1925. Ann. Entomol. Soc. Am., 18:321.
Nesticus tennesseensis (Petrunkevitch) Jackson, 1944. Bull. Nat. Speleol. Soc., 6:57.
Type locality—Indian Cave, 5 miles northwest of New Market, Jefferson Co., Tennessee.
General range—Caves of Kentucky, Tennessee, Virginia, and West Virginia.
Virginia localities—Rumbolds Cave, Alleghany Co.; Fish Hatchery and Walkthrough Caves, Craig Co. Giant Caverns, Glenlyn,* and Starnes Caves, Giles Co.; Burton (Burtons Indian) Cave, Russell Co.

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Hazelton, Mary and E. A. Glennie, 1953, Cave

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[3] New combination recommended by W. J. Gertsch, Curator of Arachnida, American Museum of Natural History.

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BIOLOGICAL SURVEY OF VIRGINIA CAVES
NATIONAL SPELEOLOGICAL SOCIETY
FALLS CHURCH, VIRGINIA

Fossilization of Bat Skeletons in the Carlsbad Caverns

by JAMES K. BAKER

ABSTRACT—Cave deposits are important sites for the large accumulation and preservation of animal remains. Most of what we know about fossil bats is derived from cavern sediments.

Bats estimated to number in the trillions have lived within the Carlsbad Caverns over a period of at least 17,000 years. Vast deposits of their guano and skeletal remains are found throughout the Caverns. In those rooms which are now, or have been inhabited, both guano and bone material is found. In other rooms, skeletal remains only are found.

These latter rooms are not inhabited intentionally, but, having small entrances through which bats might enter accidentally on a random flight, they act as natural traps. Becoming lost and trapped, the bats die within these rooms and their bones accumulate in the pits and depressions in the floors.

Fossilization of some of the bones occurs beneath silt and calcite which covers them. Some bats are preserved *in toto* within the tops of active formations (speleothems) by the rapid deposition of calcite. Most skeletons, however, are disarticulated. A few bones become the nuclei for the forming of cave pearls.

The large deposits of bat skeletons in the Carlsbad Caverns are probably the most extensive of any found in the large bat caves of the Southwest.

Caves are important sites for the accumulation and preservation of large deposits of animal remains and these have contributed greatly to our knowledge of life in the past. Generally, caves are of such a nature they become the habitats for numerous kinds of vertebrate animals. Some of these are carnivorous species and they bring into the caves other animals as food items and an assortment of bones may be accumulated which represent the fauna of a wide area around the cave entrance. Therefore, a distinct advantage to cave deposits, over others, is that large samples frequently are available which give a good idea of former local faunas.

The conditions which favor the preservation of fossils are relatively rare and the fossilization of bone material is a matter of such rare occurrence that of the millions of individuals that must have existed in the past, it was perhaps an exception that an animal was in such a position that its skeleton was preserved in a hardened matrix. The conditions by which fossilization occurs can not always be known precisely but in the Carlsbad Caverns there are at present large quantities of bat skeletons being fossilized by the deposition of silt and calcite and the exact methods which lead up to the accumulation and preservation of large quantities of these mammal skeletons can be observed in detail.

Bats seem almost synonymous with animals that are cave inhabitants and they have been hanging head downward in caves for over 50 million years. Much of what we know of fossil bats is derived from cavern sediments and of such a nature are the remarkably preserved fossil bats of the Eocene from the "Braunkohle" of Messel in Darmstadt. Germany (Revilliod, 1917). Numerous North American Pleistocene local faunas, especially those of the Wisconsin epoch, include bats and all except one of these occurrences are from cave deposits (Merriam and Stock, 1925; Schultz, 1938; Skinner, 1942; Handley, 1955; and Jones, 1958). In 1960, Lawrence described another Pleistocene bat, from the ancient guano deposits of New Cave, New Mexico, a large cave near the Carlsbad Caverns.

The Carlsbad Caverns in New Mexico have long been famous for their large colo-

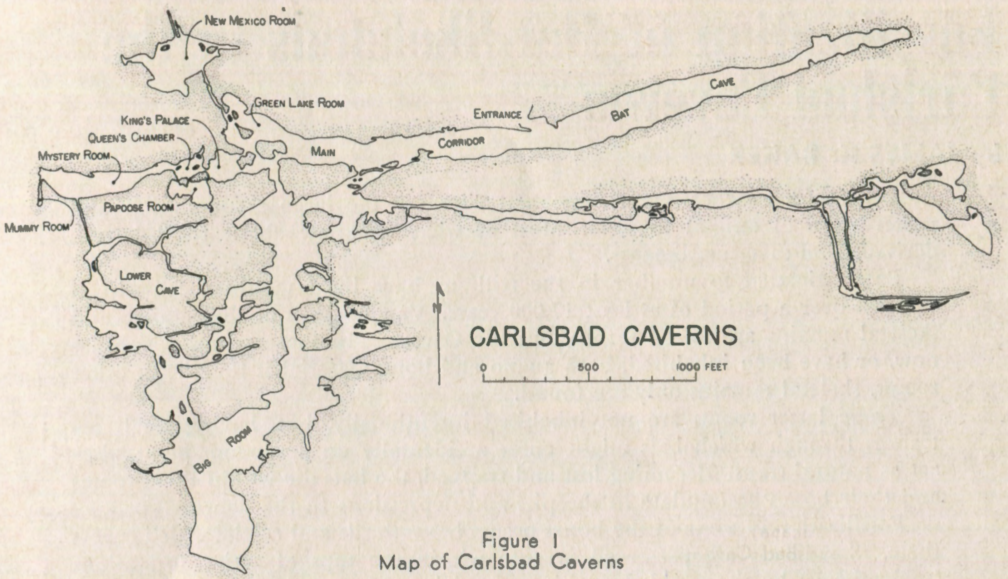

Figure 1
Map of Carlsbad Caverns

nies of freetail bats, *Tadarida brasiliensis mexicana*. More than one million of them may live at once within the Caverns and exit flights may last for as long as three hours. When these flights are at their densest, up to 5,000 bats a minute will pass a given point. The moving mass resembles black smoke from a distance, rising from the hillside, and it is believed that sight of these flights led to the discovery of the Caverns in the early 1880's.

In addition to the Mexican Freetail, eight other bat species are recorded from the Caverns. Carbon-14 datings of the ancient guano deposits from nearby New Cave (Libby, 1954) indicate that bats have used New Cave for at least 17,800 years. Since the extinct Pleistocene freetail is found also in the Carlsbad Caverns, bats no doubt have been living in these caverns for just as long. It would, of course, be impossible to make even an approximate estitmate of the total numbers of bats which have dwelled inside the Carlsbad Caverns, but quantities in the trillions are feasible and certainly not unlikely. If we can assume, as an average, just 1/2 million bats per year, the total would be over 8 trillion in 17,000 years. The vast guano deposits which were mined from the caverns from about 1903 to 1940, an estimated 100,000 tons covering thousands of square feet of cave floors and in places to 50 feet in depth, help make this total figure a little more realistic and comprehensible.

With such multitudes of bats, great numbers must have died inside the Caverns and many hundreds still die each year. Their bones become deposited in abundance and in places are several inches deep covering many square feet of the Cavern floor. In rooms where bones are most abundant, it is difficult to walk without stepping upon them.

Various rooms of the Caverns have been occupied by bats at one time or another, and these contain both guano and skeletal remains. Other rooms which have not been occupied intentionally contain no guano but may have quantities of skeletons. These are rooms which are too inaccessible for daily habitation but are entered occasionally by bats in random flight. Becoming lost and trapped they soon die and it is in these rooms that the best preserved skeletal remains are found. Bats can be found in all stages of decomposition from freshly dead to ancient bones.

Bats are good flyers in total darkness, yet this does not keep them from becoming lost within the twisting passageways of a large cavern system such as the Carlsbad Caverns. Once lost in rooms having small entrances, they become trapped as it is difficult for them to find the opening and escape. The rooms may have other adjoining passageways and be filled with domes, pits, and large solution pockets which lead nowhere. Several rooms of this type which can trap bats are found in the Carlsbad Caverns.

Figure 2
Mummified body of a Mexican Freetail bat, (Tadarida brasiliensis mexicana), in the Mummy Room, Carlsbad Caverns.

Upon entering the Caverns from the outside, bats fly in an easterly direction towards the Bat Cave (fig. 1), a large room approximately 1/2 mile in length with ceiling heights to 100 feet. It is this section of the Caverns that is most used by bats. They prefer to roost in places where the ceiling is domed and guano deposits beneath these domed areas are several feet in depth. Dead and dying bats may be found in abundance scattered over the surface of the guano, but are covered quickly by the continual deposition of this material. Some sections of the Bat Cave contain deposits of fossilized guano, capped by several inches of flowstone, and scattered through it are the bones of the extinct Pleistocene freetail.

In the direction opposite the Bat Cave, the Main Corridor leads into the more extensive portions of the Carlsbad Caverns. Bats infrequently roost in the Main Corridor, using certain crevices in the ceiling area adjacent to the Cavern entrance. Large deposits of fossilized guano found deeper in the Main Corridor indicate that this area was once more heavily used. To enter the Main Corridor, bats may fly straight from the Bat Cave or may turn 180 degrees as they come in from the entrance. Observers have noted that they do both. When an occasional bat or group of bats flies the entire length of the Main Corridor, they are funneled downward into one of several rooms collectively called the "scenic rooms." These are the New Mexico Room, Green Lake Room, King's Palace, Queen's Chamber, Papoose Room, Mystery Room, and the Mummy Room.

Why bats should fly as far as these rooms is not understood. To reach them, bats must descend over 800 feet beneath the surface and in a direction opposite that of the Bat Cave and cave entrance. Generally, bats enter a cavern only as far as is necessary to find the first dark room suitable for habitation. To go any further is needless and only increases the chances of their becoming lost. It is likely, however, that in flying from the Bat Cave toward the outside, some bats may occasionally miss the entrance and in searching for it will continue down the length of the Main Corridor. These two sections of the Caverns are hollowed along the same fracture lines and are nothing more than extensions of one with the other. They are arbitrarily divided at the location of the entrance area and it is a straight flight from one room into the other. Also, since it is usual for the bats to continually mill around in small numbers in the area of the entrance for several minutes prior to leaving the Caverns, it may be that during this time a few wander off into the Main Corridor and, becoming confused, penetrate into the deeper parts. Small flights of bats are seen occasionally in the scenic rooms.

The geography of the scenic rooms is significant to the bat remains found in them. A few bat skeletons are found in the Green Lake Room and the King's Palace but because of the proximity of these two rooms to the Main Corridor, bats that may be trapped temporarily can escape easily back into the Main Corridor. Often, they will

Figure 3
A bat which died on a sloping surface. The main portion of the skeleton is being imbedded in calcite but the arm and finger bones of the left wing are being carried slowly down slope by water action.

penetrate deeper and once past the Green Lake Room and the King's Palace they can be considered lost. From the Green Lake Room some enter the New Mexico Room by way of a long narrow corridor, and many bat bones are found in this isolated room.

Some of the more extensive deposits of bone material occur in the Papoose Room. Until the 1930's this room could be entered only through a small opening from the Queen's Chamber, yet many hundreds of bats found their way into it. The present connection between the Papoose Room and King's Palace is a man-made tunnel, the construction of which has upset the ecology of the Papoose Room. The tunnel is large enough and in such a position that it may be found easily and bats are no longer trapped. In addition, the opening into the Queen's Chamber has been enlarged, furthering the chances for escape.

From the Queen's Chamber, bats enter a large opening leading into the Mystery Room and they are seen frequently flying back and forth between these two rooms. In the ceiling of the Mystery Room a small opening leads directly into the Lower Cave. That bats enter the Lower Cave from the Mystery Room is evidenced by numerous skeletal remains found in the Lower Cave near this opening. Probably, however, most of the bats that enter the Lower Cave come in from the direction of the Big Room which shows much evidence of former usage. The Big Room has some extensive, ancient guano deposits indicating bats used this room for a long period of time in the past. It is believed the bats entered the Big Room

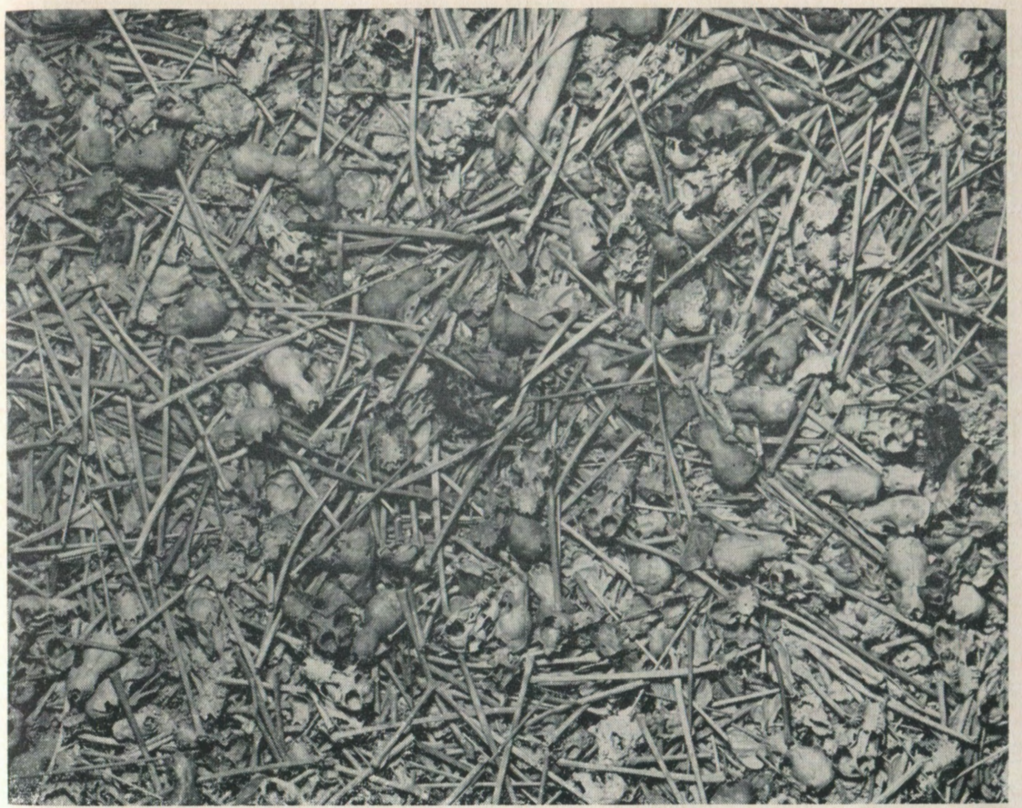

Figure 4
A natural accumulation of disarticulated skeletons of Mexican Freetail bats, (Tadarida brasiliensis mexicana), in the Papoose Room, Carlsbad Caverns.

through a former opening over the south end of the room which has since been sealed by slumping.

The Mummy Room extends as a small grotto off the end of the Mystery Room and is quite difficult to enter, yet a few bats have managed to find their way into it. Because of the dryness of this area, the dead bats mummified. Many of the mummies are hanging on the walls, ceilings, and formations (fig. 2) and most are in excellent stages of preservation. Mexican Freetails are the most numerous, but there are mummies of the genera *Myotis, Lasiurus,* and *Eptesicus.* It is somewhat surprising that *Lasiurus,* a tree bat rather than a cave bat, would be found in the Caverns, yet numerous mummified bodies and skeletal remains of *Lasiurus borealis* and *Lasiurus cinereus* prove that these species frequented the Carlsbad Caverns at least in the past. Recent specimens have been reported, however, from other caves (Beer, 1954). Perhaps their abundance in the past is indicative of a more boreal climate than the arid conditions that prevail today in the area of the Carlsbad Caverns.

In rooms where the larger bat skeletal deposits are found, bones are scattered unevenly across the floors. Wherever one steps some bones are found but for the most part they are deposited only in certain areas. The cave floors are highly irregular with many pits, shallow depressions, sloping surfaces, and formations. The bats may die in any location but their bones tend to accumulate at the base of the slopes or in the bottoms of the pits and depressions. Dripping water is responsible for most of the movement of

Figure 5
Depression in the floor of the Mystery Room, Carlsbad Caverns, showing a deposit of silt and bat bones. Note where dripping water bored a hole through the silt revealing more skeletal material. In upper left corner limb bones occur which have been cemented to the floor by calcite.

the bones but no doubt dying bats crawling around over the floor break up many of the skeletons and cause them to slide or roll down sloping surfaces (fig. 2). Most skeletons become disarticulated in the processes of accumulation and the bones become scattered at random throughout a deposit (fig. 3). The sorting appears in several cases to be the results of intermittent pooling actions of dripping water.

In the Mystery Room silt and sand accumulates in some of the floor depressions along with the bat skeletons and the bones are buried. In one such deposit the recent dripping of water has bored a hole down through the silt for several inches exposing the bones buried in it (fig. 4). More often, however, calcite fills a depression to cover the bones and the whole area becomes cemented as a "coquina" of bat bones. As newer bones are deposited on top of the calcite, they too are cemented. Where bats die directly in a depression or are carried into one before decomposition occurs, the skeleton may remain intact and be preserved *in toto* (fig. 5). Many thousands of bat bones are encased in the flowstone of the scenic rooms and in one section of the Papoose Room the whole floor is nothing but calcite and bone material.

Frequently bats die clinging to the tops or sides of active formations (speleothems) and as the formations grow the bats are embedded in the deposit of calcite (fig. 6). On many formations the barest outlines only are discernible of the bats which have died upon them. In one formation a bat was found preserved in its center, completely hidden from view.

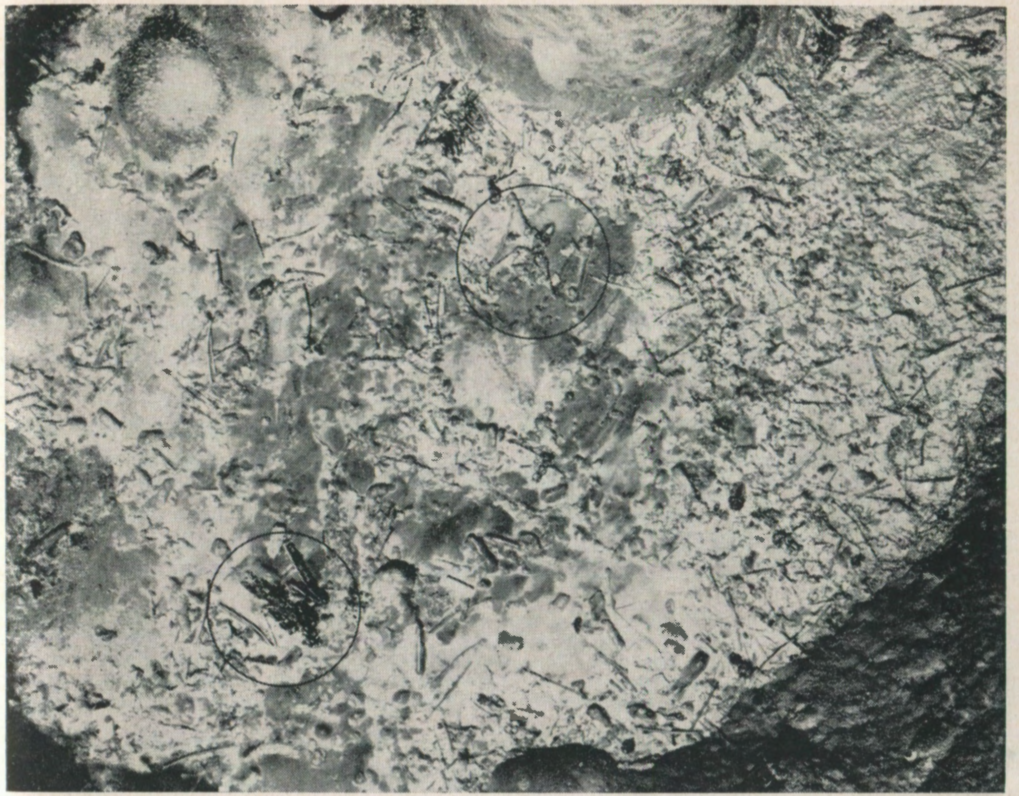

Figure 6
Bat bones and broken bits of formations (speleothems) accumulated in a floor depression and now being imbedded in calcite. Most skeletons are disarticulated from sliding down adjacent sloping surfaces but some skeletons are intact. A recently dead bat is in a depression (lower circle). A bat partially buried (in toto) is in the upper circle.

On rarer occasions a single bone, usually a limb bone, becomes the nucleus for the forming of a cave pearl. Dripping water deposits calcite around the bone and the force of the dripping water continually turns it keeping it from being cemented to the floor. Eventually a cave pearl is formed which may be several millimeters in diameter and rounded longitudinally with the limb bone in its center.

Although great numbers of bat bones are being fossilized at present and have been in the past, there are perhaps more that deteriorated completely and never achieved fossilization. Bats often die in places unsuitable for their preservation. These are areas where silt and calcite are not being deposited and the high humidity of the cave air causes the bones to soften and crumble.

It is fortunate though that the Carlsbad Caverns have rooms such as the scenic rooms in which large quantities of bone material collects and is displayed. There is no guano deposition to bury them and, other than those places where they are embedded in silt or calcite, the bones lie exposed, loose, and easy of access. They can be scooped by the handfuls. Because of this abundance, the Carlsbad Caverns may be outstanding for the bat remains found in them.

Ironically, the Carlsbad Caverns are the largest known, yet they have one of the smallest bat populations of the several large

Figure 7
Body of a bat which died hanging from the top of an active formation (speleothem) and is being covered by a deposit of calcite. Papoose Room, Carlsbad Caverns.

bat caves in the Southwest, especially those on the Edwards Plateau of central Texas. The other bat caves, however, are not extensive enough to contain the distant rooms and twisting passageways which can trap bats and the few large rooms they may have are all habitually used. They are blackened with the stains from bat excreta and guano covers the floors from wall to wall, burying the majority of the bat bones found in the rooms. The bones in the guano are disarticulated by the host of scavenger organisms, especially the dermestid beetle larvae, which feed on the dead bats and continually churn through the guano. Guano, however, is a poor medium for the preservation of large numbers of bat bones, relative to the methods described by silt and calcite. In addition most of the other bat caves are easily accessible to vertebrate scavengers or predators which enter periodically to feed upon the dead and dying bats, thus decreasing the potential for large bone deposits. Also, the guano in these caves is mined intermittently and in places where good bone material may have existed, the areas have been trampled and scraped over and it is likely that even bone carrying silt deposits have been sacked and mixed with the guano.

In the Carlsbad Caverns, the Bat Cave section is little different. Guano covers large areas of the floor and has been mined extensively. Scavenger animals feed upon the bats and generally there are no good bone deposits in the guano or elsewhere in the Bat Cave. Yet, the Caverns are extensive enough that all rooms have not been used for bat occupancy and as this paper describes, there are those rooms which are uninhabited but which act as bat traps; hence their skeletons can accumulate in great numbers and under such conditions that they are becoming fossilized. In addition, the rooms are far enough from the entrance and so erratic are the times and numbers of bats which become trapped in them, that scavenger animals have not reached them or have been able to survive in them.

In conclusion it is well to point out that the large deposits of bat remains found in the Carlsbad Caverns offer an excellent opportunity for studies of the skeletal features of Pleistocene and Recent bats.

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