

BULLETIN

OF THE

NATIONAL SPELEOLOGICAL SOCIETY

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Contents

UNDERGROUND FLOODPLAIN CHARACTERISTICS

DISCUSSION OF "THE CAVE ENVIRONMENT" AND REBUTTAL

CARBIDIMITE FORMATIONS

JULY 1971

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CONTENTS

CHARACTERISTICS OF THE UNDERGROUND FLOODPLAIN.....	William K. Jones	105
BIOGEOGRAPHY OF TROGLOBITES: A DISCUSSION OF "THE CAVE ENVIRONMENT" by Poulson and White.....	Thomas C. Barr and John R. Holsinger	115
A REPLY TO "BIOGEOGRAPHY OF TROGLOBITES"— Thomas L. Poulson and William B. White		119
ADDITIONAL DATA ON THE CARBIDIMITE FORMATION.....	Paul L. Broughton	123

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The BULLETIN is published quarterly in January, April, July, and October. Material to be included in a given number must be submitted at least 90 days prior to the first of the month of publication.

Characteristics of the Underground Floodplain

William K. Jones*

ABSTRACT

Open channel flow through clastic sediment deposits in limestone solution conduits often exhibits characteristics of a surface stream flowing in an alluvium filled valley. An underground floodplain of aggradation is formed by the deposition of clastic sediments in a solution conduit. This creates a perched, "free-surface" stream flowing in an alluvium filled channel. Various reaches of West Virginia caves provide examples of the classic forms of alluvial stream channel development: braided streams, sine-generated meander curves, river bars, and deep v-shaped canyons. Solutional enlargement of the conduit can occur only where the water can reach unprotected limestone. Therefore, horizontal development is most likely on the outside of meander bends, and vertical enlargement may assume an alluvial pattern if the stream downcutting through the alluvial fill reaches bedrock.

INTRODUCTION

Most American publications on cave development have ignored the presence of clastic sediments or have relegated them to secondary importance in the development of the passage. White and White (1968) have shown that sediment transport by fast moving water is an integral part of the development of many of the solutional conduits which comprise the karst drainage net. Curvilinear cave forms have been described by Ongley (1968), Deike and White (1969), and Bretz (1942). Although the basic hydrodynamic process of stream meandering is still unknown, relationships of the channel width, the sediment load, and the mean annual discharge to the "wavelength" of the meander have been described (Leopold, Wolman, and Miller, 1964; Schumm, 1967).

The object of this paper is to examine streams perched on clastic sediments in

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limestone solution conduits and to describe them in terms of surface streams flowing on an alluvial floodplain of aggradation. An attempt is made to show that alluvial channel patterns may be transferred to bedrock and play an important role in shaping the cross sectional appearance of the conduit.

The maps and illustrations for this paper are all of specifically selected reaches (segments) from master trunk conduits in Greenbrier and Monroe counties, West Virginia. These are very short segments of an extensively developed drainage net. The maps represent an attempt to show the pattern of the stream and its present position within the conduit; photographs are used to show the cross section of the passage.

THE ROLE OF CAVE SEDIMENTS

Many limestone aquifers transmit water through an interconnected series of solution conduits which form a drainage net. In a mature karst region, all drainage from the

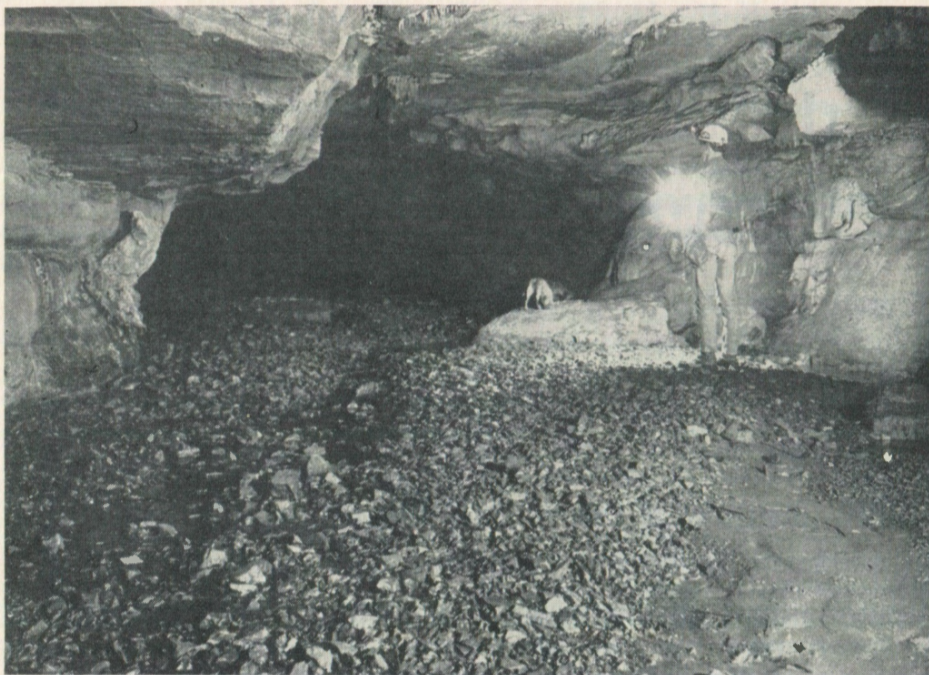


Figure 1. Braided stream. In small interconnected channels, the stream occupies the entire floor of the conduit. Cobble armoring is also evident on the stream bed. Coffman Cave, West Virginia.

area often moves underground through master trunk conduits because the surface stream systems have been pirated underground. Surface weathering and erosion continue, and blind valleys often form, indicating that the subterranean drainage must transmit not only water but also the clastic material eroded from the surface. The clastic sediments are transported by turbulent flow as either suspended load or as bedload, and that portion deposited within the conduit forms the varied sequences of cave fills (White and White, 1968).

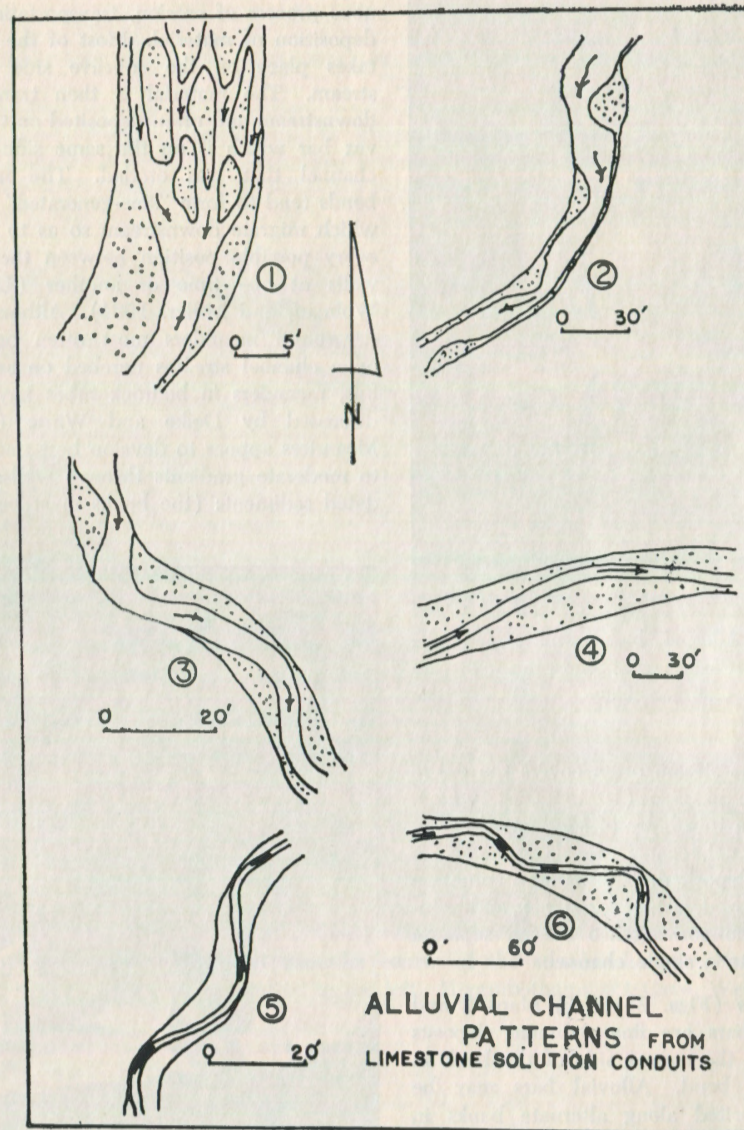
A solution conduit, partially filled with clastic sediments, differs from an alluvial filled valley mainly in that it is entirely enclosed by bedrock walls and a roof. In this case alluvial fill protects the bedrock from the solution and erosional action of the stream, and the stream is actually flowing on a plain raised above the bedrock floor of the conduit. A cave stream flowing en-

tirely within its sediment fill has perched itself (White and White, 1968). This condition is analogous to a "floodplain of aggradation" of a surface stream.

DESCRIPTIONS OF SEDIMENT CONTROLLED STREAM CHANNELS

All of the classic stream channel patterns characteristic of alluvial valleys were found in trunk conduits from caves in Greenbrier and Monroe Counties, West Virginia. These patterns develop under open channel flow conditions and are best observed when low base flow conditions are present.

Braided (Anastomosing) Stream (Fig. 1, Map 1). A braided stream flows in several dividing and reuniting channels and is caused by an over-abundance of easily erodable sediment surrounding the stream channel. An excellent example of a braided stream is found in Coffman Cave, West Virginia. The gradient of the conduit is very



Maps 1-6. 1. Braided Stream. See Figure 1. Coffman Cave, West Virginia. 2 Alluvial-bars. See Figure 2. Coffman Cave, West Virginia. 3. Meander bends with point-bars developing on convex (inside bend) side of bends. See Figure 3. Pecks Cave, West Virginia. 4. Curvilinear stream channel perched on clastic sediments. See Figure 6, Buckeye Creek Cave, West Virginia. 5. Meandering stream downcutting a bedrock canyon. Hern's Mill Cave, West Virginia. 6. Meander channel resulting from secondary stream flow into former discharge opening. See Figure 8. Greenville Saltpeter Cave, West Virginia.

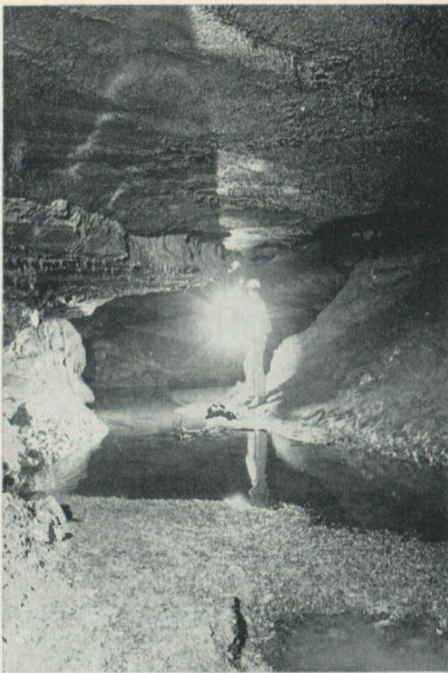


Figure 2. Alluvial bars. Riffles developing against alternating banks in the stream channel. Coffman Cave, West Virginia.

low, and the stream often covers the entire floor of the passage (10 to 20 ft. wide), flowing on a thin layer of sand. Within the stream channel, coarse gravels and cobbles have been deposited. The braided condition is very localized, lasting for 100 ft., and terminates at the convergence of the separate channels into a single channel.

Point-bars (Figs. 2 and 3; Maps 2 and 3). Point-bars are fine sediment deposits growing on the convex side of the bank in a meander bend. Alluvial bars may be found deposited along alternate banks in straight reaches of stream channel. The point bars and alluvial bars coincide with eddies which concentrate the expenditures of energy and localize erosion (Leopold, Wolman and Miller, 1964).

Stream Meanders (Figs. 4, 5, and 6; Maps 4, 5, 6, and 7). Curvilinear stream

meanders are a classic stream channel form. They develop in alluvium through a continuous process of erosion, transportation, and deposition of material. Most of the erosion takes place on the concave side of the stream. The material is then transported downstream and often deposited on the convex bar which is on the same side of the channel that was eroded. The meander bends tend to form "sine-generated" curves, which migrate downstream so as to occupy every possible position between the valley walls at one time or another (Leopold, Wolman, and Miller, 1964). Although underground meanders most often occur as open channel streams perched on sediment fills, meanders in bedrock tubes have been discussed by Deike and White (1969). Meanders appear to develop best under low to moderate gradients through well-consolidated sediments (the banks must be firm).



Figure 3. Point-bar. A point bar developing on the convex side of a meander curve has thrown the stream flow to the right. Pecks Cave, West Virginia.



Figure 4. The past and present meander course of the stream channel. Note benches abandoned as stream course shifted to the left. Higginbothams #1 Cave, West Virginia.

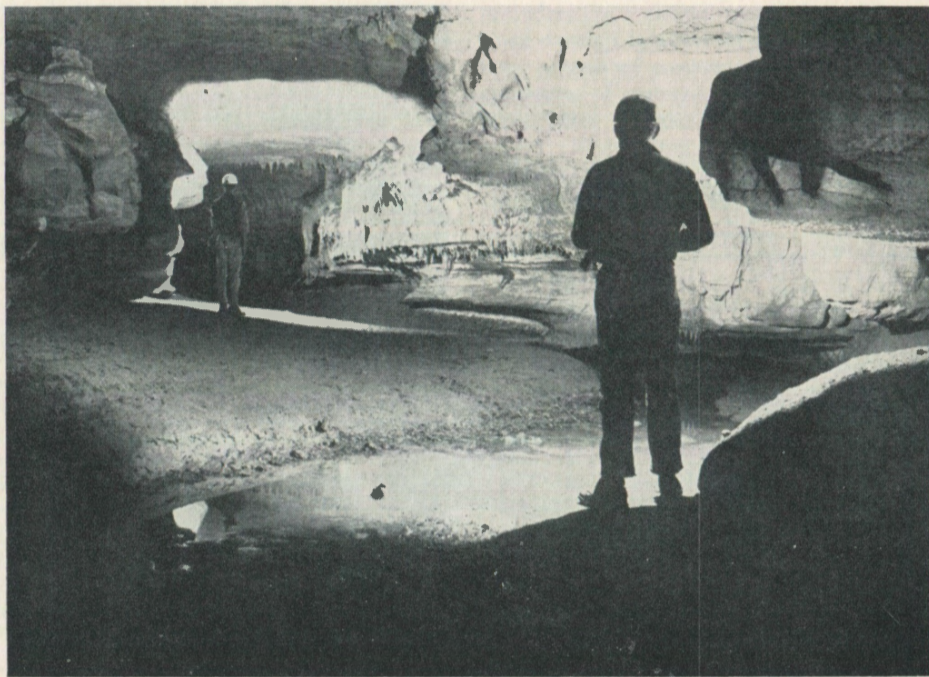


Figure 5. Curvilinear meander. Former horizontal and vertical development of the conduit is shown by former solution positions on the right wall and ceiling of the passage. This is the result of slow downcutting through the sediment fill and increasing amplitude of the meander. Higginbothams #1, Cave, West Virginia.

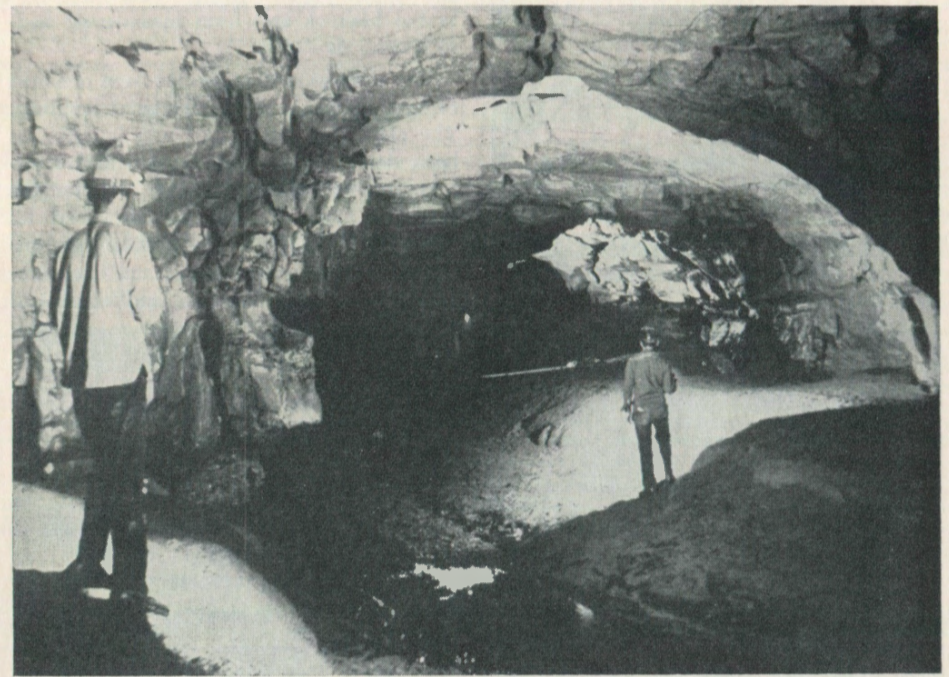
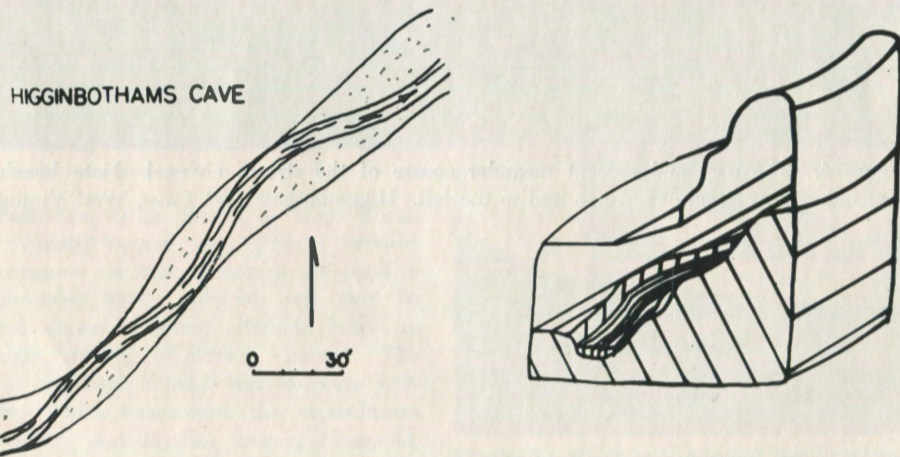


Figure 6. Incised stream meander. The stream, flowing in a long, curvilinear channel has downcut through 5 ft. of alluvial sediments. Buckeye Creek Cave, West Virginia.



Map 7. Sine-generated meander curves. In cross section, the former (ceiling) meander is 180° out of phase with the present stream course. See Figures 4 and 5, Higginbothams #1 Cave, West Virginia.

Deep V-shaped Canyons (Fig. 7). Entrenched v-shaped canyons are developed under conditions of high stream gradients and loosely consolidated sediment deposits. This pattern is typical of large elliptical canyons with thick clastic sediments and low volume, high gradient stream flow. Often the canyons are now entirely dry, the former stream having been pirated to a lower level conduit.

Cobble Armoring (Fig. 1). Cobble armoring refers to the very coarse material (usually pebbles or cobbles) which line the surface of the stream channel, with finer clastic material below this coarser layer. (White and White, in press).

DISCUSSION AND CONCLUSION

The primary effect of sediment deposits on the floor of a solution conduit is the insulation of the bedrock from solution and mechanical abrasion. Thus, enlargement of

the conduit, particularly by downcutting, is retarded or halted. Solution enlargement of the conduit can occur only where the stream can contact unprotected bedrock. A certain amount of sub-alluvial corrosion of the bedrock (corrosion at the contact of the water saturated alluvial deposits and the bedrock floor) is assumed to occur, but its effect on the development of the conduit is usually negligible because of the relatively higher rate of corrosion from open channel flow. If the regional base level drops while the stream is perched on sediments, a hydrostatic head is created that provides the energy for the stream to downcut through the alluvium or to be converted to another route by piracy (White and White, 1968).

Streams which fill the entire conduit as braided or meandering channels may cause localized horizontal enlargement of the conduit where they contact the bedrock walls. Solution is greatest on the outside (concave

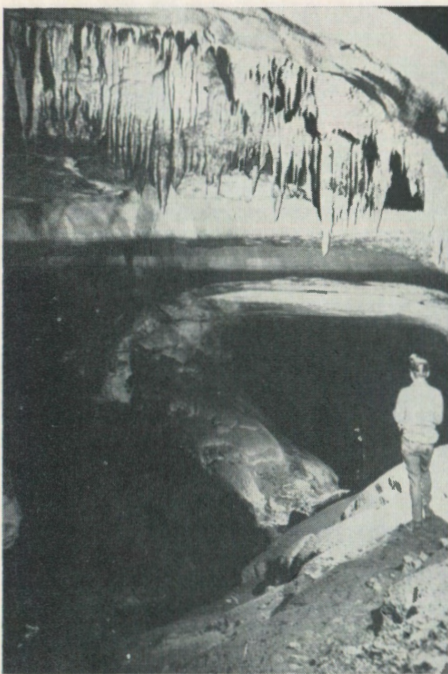


Figure 7. Straight v-shaped canyon. A high gradient stream has cut a 30-ft. deep canyon through loosely consolidated sediments. General Davis Cave, West Virginia.

side) of the channel. In some reaches, the amplitude of the meander is controlled by the width of the conduit, although in other cases the width of the conduit may be a function of the amplitude.

Streams which downcut through their alluvial channel and reach the bedrock floor may recommence solutional enlargement of the primary conduit in a vertical (downward) direction. If the stream path is straight or slightly curving, keyhole shaped canyons may develop. If the streams meander, the meanders may be transferred

to the bedrock and form meandering bedrock canyons (Map 5).

The discussion thus far has been confined to cave segments of primary trunk conduits. The clastic material of cave sediments has been derived by stream erosion and transportation within the recharge area for the conduit. Many caverns contain deep fill deposits and small free-surface streams which have only an "accidental" relationship to the flow direction and conditions which formed the original cavity. A complete flow reversal from a surface stream entering an old discharge opening has been described by Wolfe (1970). Another example of a secondary stream depositing sediments and cutting channels through its alluvium may be seen in Greenville Saltpeter Cave, West Virginia (Fig. 8).

Alluvial channel patterns occurring within solution conduits are a result of the weathering and erosion of a karst landscape. Examination of a short segment of the conduit will show the sculpturing effect of the alluvial patterns; examination of the conduit in relation to the entire drainage basin will reveal the structural (geological) and hydrological controls. The overall form of the drainage net is controlled by the geological and hydrological makeup of the drainage basin; the localized form of the conduit is an expression of localized flow patterns following a hydrological expedient.

ACKNOWLEDGMENTS

The field work for this study was supported in part by the West Virginia Geological and Economic Survey. I would like to thank Henry Rauch and Larry D. Woodfork for reading the manuscript and discussing some of the observations made and conclusions drawn in the paper.

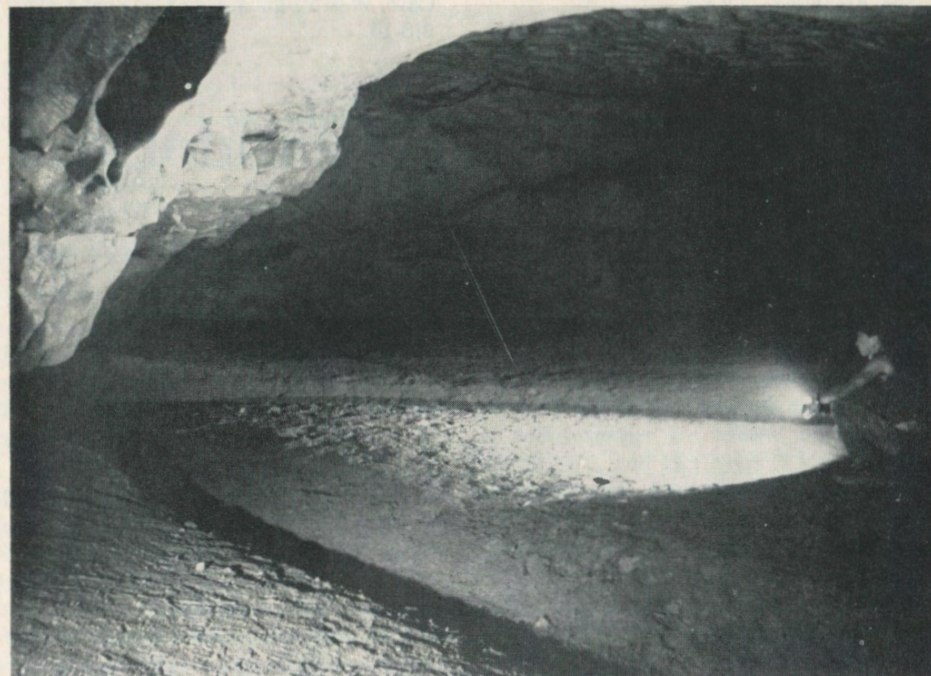


Figure 8. Incised meandering by a secondary stream. An intermediate surface stream, entering a former discharge opening, has cut a 2-ft. deep channel in the alluvial sediments. Greenville Saltpeter Cave, West Virginia.

LITERATURE CITED

- Bretz, J. H. 1942. Vadose and phreatic features in limestone caves. *J. Geology*, 50:675-811.
- Deike, George H., and William B. White. 1969. Sinuosity in limestone solution conduits. *Amer. J. of Science*, 267:230-241.
- Leopold, Luna B., M. G. Wolman, and J. P. Miller. 1964. *Fluvial processes in geomorphology*. W. H. Freeman and Co., San Francisco, 522 pp.
- Ongley, E. D. 1968. An analysis of the meandering tendency of Serpentine Cave, N. S. W. *J. Hydrology*, 6:15-32.
- Schumm, S. A. 1967. Meander wavelength of alluvial rivers. *Science*, 157:1549-1550.
- White, William B., and Elizabeth L. White. 1968. Dynamics of sediment transport in limestone caves. *Bull. Natl. Speleol. Soc.*, 30(4):115-129.
- . (in press). Channel hydraulics of free-surface streams in caves.
- Wolfe, Tom. 1970. Sediments of Bob Gee Cave, West Virginia. *The Canadian Caver*, 2:3-14.

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NOTE: In this article Barr and Holsinger discuss a paper on the cave environment written by Poulson and White which appeared in *Science* in 1969. A rebuttal by Poulson and White follows.

Biogeography of Troglobites

Thomas C. Barr¹ and John R. Holsinger²

Although we are in broad agreement with Poulson and White (1969) on the unusual potential of caves as biological and geological study areas, some of their interpretations have alternative explanations.

(1) "The ability of troglobites to move between caves depends mainly on their size." This generalization is too broad. We believe mobility and niche breadth are also significant. Many large troglobites, such as the cavefish *Typhlichthys subterraneus* and the blind crayfish *Orconectes australis*, have extensive geographic ranges, and many small ones, such as the isopod *Asellus stygius*, the spider *Phanetta subterranea*, and the amphipod *Stygonectes allegheniensis*, also have extensive ranges. Among blind trechine beetles, the larger species usually, but not invariably, have larger ranges than the smaller ones, but this generalization does not hold for all troglobites; furthermore, we suspect that range extent in various species of cave trechines reflects varying mobility

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and niche breadth. Some of the smallest troglobites of Alabama and Tennessee caves are the minute bythinine pselaphid beetles of the genus *Speleochus* Park; approximately a dozen species are known, each from a single cave, and two caves 5 km apart are inhabited by distinctly different species (Barr and Steeves, in prep.). Subterranean amphipods of the genus *Apocrangonyx* are among the smallest (2-5 mm) species in the entire family Gammaridae, yet without exception the cavernicolous species of *Apocrangonyx* have very local distributions with individual species known only from one or two caves (Holsinger, 1969a). In marked contrast are several comparatively large (8-20 mm) species of amphipods belonging to *Stygonectes* and *Stygodromus* which have extensive ranges (Holsinger, 1967, 1969b).

(2) The composition of troglobitic faunas depends, according to Poulson and White, "both on interconnectivity of caves and on the balance between colonization and extinction." The Interior Low Plateaus (IL) and the Appalachian Valley and Ridge province (AV) are said to be "similar with respect to . . . the groups of troglolithes

available as colonizers." We believe that historical factors are also very important and that part of the differences between IL and AV cave faunas may be explained by regional differences in the ancestral surface faunas. At the generic level, there are about 25 genera which contain troglotic species in both the IL and AV cave regions, about 30 genera whose troglitic representatives are restricted to the IL region, and less than 10 genera whose troglitic species occur only in the AV region. Although we cannot say how many trogliphile genera were present during Pleistocene colonization of the caves in these regions, the considerable differences in the extant cave faunas and in many groups of non-cave invertebrates now occupying the IL and AV regions are evidence that the Pleistocene ancestral faunas may also have been rather different. That there probably are more Pleistocene cave relicts in the IL region than in the AV region we attribute to enhanced opportunities for successful speciation and subsequent survival in the physically larger and biotically more diverse ecosystems of IL caves.

(3) "We agree with Barr but extend his argument to explain the other biological differences between the two regions. We suggest that the small size of individuals, the low populations, and the low number of genera in the Valley-Ridge caves reflect both high chances for extinction and slow rates of evolution." Poulson and White are not in fact extending Barr's argument but are offering explanations other than those which Barr (1967) himself suggested. He explained lower species diversity in AV cave communities as a direct result of the fragmentation of caverniferous limestone into many isolated pockets. The transformation of a trogliphile into a troglote is a special case of multiplication of species (Barr, 1968). We assume (a) that successful speciation in caves as elsewhere is an event of comparatively low probability and (b) that most trogliphiles cannot use interstitial means of dispersal from one cave to another, while most troglotes can do so.

Since there is a much higher degree of interconnectivity in IL caves, successful troglote speciation in an IL cave may open a hundred or more caves to eventual occupation by the troglote. A newly speciated troglote in an AV cave may find its hypogean horizons limited to the caves of a single valley. Cave communities in the Interior Low Plateaus were thus evolved by commingling and coadaptation of a number of troglotes which speciated at different times and places. This was possible only to a limited extent in AV caves.

The populations of troglotes in AV caves are not invariably low, but there is considerable evidence that the size of the populations may fluctuate considerably from year to year. Barr (1967) attributed such fluctuations to the instability of AV cave communities, which include few species.* Increased stability of IL cave communities is related to greater community complexity. More complex communities offer more niches, since there are more elements from which niches can be formed. If modal size is a measure of niche size, as suggested by Hutchinson and MacArthur (1959), then a larger modal size should be permitted in IL caves than in AV caves.

(4) We attribute a greater role to the founder principle developed by Mayr (1963) and applied by Barr (1968) to troglote speciation. Poulson and White make no clear distinction between extinction of founder populations, which we think was a common occurrence, and extinction of troglote species, which we think has been less frequent. In applying the MacArthur-Wilson (1963) theory that an island community is the result of an equilibrium between colonizations and extinctions, Poulson and White have in our view neglected some

* The Mississippian limestone plateaus of the Interior Lowlands and the Valley and Ridge province are regarded as type areas which illustrate in an especially clear fashion the ecological phenomena discussed. The Greenbrier River Valley of eastern West Virginia, despite its geographic proximity and geological affinities to the Valley and Ridge province, is a region in which the numerous cave communities have ecological characteristics of the IL type.

basic differences between caves and islands. Since most of the troglotes show taxonomic affinity with cold-adapted epigeal animals, the probability is high that opportunities for colonization were limited to brief periods at the onset of the interglacials (Holdhaus, 1933; Barr, 1968). In both IL and AV caves the colonizing periods were similarly short, with the result that the cave faunas were probably initially unsaturated. In IL caves, however, the high dispersal potential for troglotes in extensive networks permitted mixing of many local faunas as the more mobile species expanded their geographic ranges in various directions. Low dispersal potential for troglotes in AV cave systems is reflected by the low species diversity.

(5) [Relicts] "are highly modified and were isolated in caves as long ago as 100 million years, when their surface relatives became extinct." We believe there is no basis for supposing that any relict species which can be called strict troglotes are much older than late Pliocene, i. e., they may have been isolated in caves as long ago as 1.5-2.0 million years. A number of primitive and ancient crustacean groups—bathynellids, thermosbaenaceans, phreatocoids, spelaeogriphaceans, and ingolfiellids—occur in phreatic waters and occasionally in caves. Most of these taxa are represented by interstitial, phreatobitic species, however, and their presence in caves is usually sporadic and probably fortuitous. The great age of these crustaceans does not imply that the caves they inhabit are similarly ancient. These groups have apparently been distributed in groundwater far longer than the time since the excavation of existing caves. The minute syncarid crustaceans of the order Bathynellacea occur in cave pools, wells, and other ground water, but are not restricted to limestone regions. Since fossil syncarids are known from fresh-water

Carboniferous deposits (Vandel, 1964), bathynellids are probably very ancient relicts. But the Carboniferous syncarids are not bathynellids, and even if they became subterranean long before the Pleistocene, the existing bathynellid species cannot be said to have been "isolated in caves as long ago as 100 million years."

(6) "Caves are without seasonal cues, so a circannual clock is adaptive in allowing females to be prepared to lay eggs when chances for reproductive success are at a maximum." In the same paragraph the authors proceed to cite temperature change as a seasonal cue. Although it is conceivable that certain remote, deep-lying, very dry (hence uninhabitable) areas of some large caves are wholly without seasonal cues, the climatological constance of the cave environment is purely relative. Potential cues are numerous in both aquatic and terrestrial environments, ranging from late winter and spring floods to seasonal reversal of air movements in and out of the cave entrances and to increased percolation of vadose ground water into cave passages (Hawes, 1939; Ginet, 1969; Juberthie, 1969; Barr and Kuehne, in press).

(7) "Competition will be reduced, because of low population densities and low rates of population growth, and competitive exclusion is rare, or difficult to reconcile with the high species diversities found within single habitats." This is a priori reasoning, since the authors make a point (p. 975) that most conclusions on niche relationships are based on indirect analysis. The only direct analysis currently available is the study of D. Culver (1970), which does demonstrate spatial exclusion. Furthermore, the indirect data, including Poulson's own work on amblyopsid fishes (Poulson, 1963), strongly support the concept of relatively rigid exclusion.

LITERATURE CITED

- Barr, Thomas C., Jr. 1967. Observations on the ecology of caves. *Amer. Nat.*, 101:475-492.
- . 1968. Cave ecology and the evolution of troglobites. *Evolutionary Biology*, 2:35-102.
- Barr, T. C., Jr. and R. A. Kuehne (in press) *Annales de Spéléologie*.
- Barr, T. C., Jr. and Steeves. In preparation.
- Culver, D. C. 1970. Analysis of simple cave communities: niche separation and species packing. *Ecology* 51:949-958.
- Ginet, R. 1969. Rythme saisonnier des reproductions de *Niphargus* (Crust. Amphip. hypogé). *Annales de Spéléologie*, 24(2): 387-397.
- Hawes, R. S. 1939. The flood factor in the ecology of caves. *J. Animal Ecology*, 8:1-5.
- Holdhaus, K. 1933. Die europäische Höhlenfauna in ihren Beziehungen zur Eiszeit. *Zoogeographica*, 1:1-53.
- Holsinger, John R. 1967. Systematics, speciation, and distribution of the subterranean amphipod genus *Stygonectes* (Gammaridae). *Bull. U. S. Natl. Museum*, 259:1-176.
- . 1969a. The systematics of the North American subterranean amphipod genus *Apocrangonyx* (Gammaridae), with remarks on ecology and zoogeography. *Amer. Midl. Nat.*, 81:1-28.
- . 1969b. Biogeography of the freshwater amphipod crustaceans (Gammaridae) of the central and southern Appalachians, pp. 19-50. In P. C. Holt (ed.), *The distributional history of the biota of the Southern Appalachians. Part I: Invertebrates*. V.P.I. Press, Blacksburg, Virginia.
- Hutchinson, G. E. and R. H. MacArthur. 1959. A theoretical ecological model of size distribution among species of animals. *Amer. Nat.*, 93:117-125.
- Juberthie, C. 1969. Relations entre le climat, le microclimat et les *Aphaenops cerberus* dans la grotte de Sainte-Catherine (Ariège). *Annales de Spéléologie*, 24(1):75-103.
- MacArthur, R. H. and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. *Evolution*, 7:373-387.
- Mayr, Ernst. 1963. *Animal species and evolution*. Harvard University Press, 797 pp. (see especially Chapter 17).
- Poulson, Thomas L. 1963. Cave adaptation in amblyopsid fishes. *Amer. Midl. Nat.*, 70:257-290.
- Poulson, T. L. and W. B. White. 1969. The cave environment. *Science*, 165:971-981.
- Vandel, A. 1964. *Biospéologie: la biologie des animaux cavernicoles*. Gauthier-Villars, Paris, 619 pp.

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A Reply to "Biogeography of Troglobites"

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To answer Barr and Holsinger's critique of our article on "The Cave Environment" (Poulson and White, 1969), we will discuss the points that they raise in the same order as presented above.

(1) *Movement of troglobites between caves.* In discussing the importance of size in movement between caves, we were concerned with broad generalities when we discussed ability (meaning potential for movement), whereas Barr and Holsinger are discussing mobility, meaning actual movement by a particular species. We may both be right. If modal size divided by niche breadth is a constant (This is by no means certain. See point 3.), then a species that is physically small *could* move through tiny interstitial channels between caves more easily than a larger species but it has such a narrow niche that its realized mobility *would be* limited.

(2) *Biogeography of ancestral troglaphiles.* We do not agree that the higher number of troglobite genera in IL caves today necessarily reflects a higher number of ancestral troglaphile genera in IL than in AV cave regions. It is equally possible to argue that the opposite held in pre-Pleistocene times and that the greater chances for successful colonization of IL caves left a disproportionate number of surviving generic relicts as troglobites in the IL cave regions. Lacking

fossil evidence to prove either point, we preferred to argue that the ancestral faunas available for cave colonization were similar and thus to stress the effects of regional geology on the composition of the cave faunas in the two regions.

(3) *Small modal size and fluctuating populations of AV troglobites.* We think that Barr and Holsinger's arguments about modal size and population fluctuation in relation to AV vs. IL faunas are circular. In regard to modal size, they argue that . . . More complex communities (in IL caves) offer more niches since (due to high cave interconnectivity) there are more elements (=species?) from which niches can be formed. (Thus?) if modal size is a measure of niche size, as suggested by Hutchinson and MacArthur, then a larger modal size should be permitted in IL than in AV caves. The crux of Hutchinson and MacArthur's argument is that smaller animals "see" smaller patches in the environment and so can use smaller habitat niches than larger animals. Smaller animals might also have a lower mean free path and be able to eat a smaller range of food sizes than larger animals. However, we find that the mean free paths of large (*Neaphaenops tellkampfi*), medium (*Pseudanophthalmus striatus* and *P. menetriesei*), and small (*P. inexpectatus*) trechine beetles of the Mammoth Cave systems (IL cave region) are similar and extensive relative to substrate patchiness and thus prey patchiness. Also, they show no significant differences in substrate choice (mud,

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sand, or rocky gravel) in the laboratory. Furthermore our preliminary data show that the size of these predatory beetles, which is in the ratio of 1.00:0.50:0.21 by volume, does not affect the size of prey that they can handle. Thus size is not the basis for slight differences in habitats of these beetles in Mammoth Cave (Barr, 1966 and 1967) and the actual basis for niche separation remains obscure. Some clue as to the meaning of the relation of small modal size to population fluctuations, seasonality, and rarity in AV caves may be gained through our studies on an IL species with similar characteristics, namely the small (1.5 mg) *P. inexpectatus*. Whatever the basis for these characteristics, we do not agree with Barr and Holsinger that low or fluctuating population size of small AV trechines is due to instability of AV caves which they imply to be a result of fewer species (=fewer alternate food types) in AV than in IL caves. We think this is a circular argument and there is more inwashed food in AV than in IL caves. We think that any instability of AV caves is due to their unpredictable and rigorous "climatic" regime, especially as regards flooding. Compared to IL cave areas, the AV drainage basins that feed into caves have less exposed limestone relative to the bordering clastic rocks, and these clastics, with their free-surface streams, have greater relief. The result is larger flood pulses which carry in more and rockier sediment into AV caves, even with unpredictable moderate or small storms in summer and fall.

(4) *Equilibrium between colonization and extinction.* Despite Barr and Holsinger's unhappiness with the analogy of caves to islands, we find equilibrium models instructive. They are correct in pointing out that we did not make the important distinction between: (a) chances for colonization, *i.e.* genetic isolation of troglaphiles, and extinction of the colonizing founder populations in the limited time span at the beginning of interglacials and (b) the continuing chances for extinction of both founder populations and established troglobites. In this

context we were concerned with founder populations and their extinction being more likely in AV than IL cave regions. In the AV region Culver (1970a) has used a non-interactive equilibrium model to explain differences in species number in caves with aquatic species, like some amphipods and isopods, that can use interstitial routes of dispersal. His use of the model deals with contemporary differences in number of species from caves in one karst valley whereas our example was for regional faunas and thus was using the island equilibrium analogy to explain differences in number of species between different karst valleys or karst regions. Put another way each cave or series of potentially interconnected caves can be regarded as an island with a species equilibrium in ecological time even though caves as a class are not saturated with species in evolutionary time.

(5) *Age of relicts.* We disagree with Barr and Holsinger's view that all ancient relicts are sporadic and probably of fortuitous occurrence in caves, and so we hold open the remote possibility that some troglobites or their ancestors might have been isolated in caves as long as 100 million years ago. Geologically it seems clear that no caves or even cave regions have been continuously available for occupancy for this long, but this does not mean that some of these ancient groups were not intermittently occupying caves and groundwater during this long time. Barr (1968) has emphasized that an organism can be both phreatobitic (in groundwater) and troglobitic. Barr and Holsinger argue that the ancient relicts are primarily phreatobitic whereas we ask only that they hold open the possibility that some relicts have been primarily troglobitic at times in the geological past and even today, as is demonstrably the case for some amphipods of the genus *Stygonectes* and isopods of the genus *Asellus* that are found both in groundwater and in caves. Culver (1971) has shown that some species in these genera occur continuously in and reproduce in cave streams. Their greater rarity and unpredictable occurrence, on a

presence/absence basis, in drip pools fed by groundwater above stream flood level can be construed as evidence that the groundwater is the accidental or less optimum habitat, not the cave stream.

(6) *Annual clocks in troglobites and seasons in caves.* We were ambiguous in our statement that ". . . caves are without seasonal cues, so a circannian clock is adaptive in allowing females to be prepared to lay eggs when chances for reproductive success are at a maximum." In fact there are proximate cues to season, in late winter and spring, associated with floods or increased percolation of ground water, but no cues which allow prediction of these events. Outside of caves photoperiod is a reliable cue which allows advance preparation for spring, but in caves a circannian (=endogenous yearly) clock is required if the animals are to be prepared to take advantage of an unpredictable influx of food which may occur anytime from late winter to early summer (Jegla and Poulson, 1970).

(7) *Competition and species diversity.* Here we mean species number; there may also be differences in relative abundance of troglobitic species in AV and IL caves but we do not know of any data on relative abundance for AV caves. We agree that we were using a priori reasoning in relating high species diversity to reduced competition. We were trying to point out that competitive exclusion has been overemphasized in explaining the high species diversity in old, stable, non-rigorous environments like the lowland wet tropics and deep sea abyssal plain. Chances for exclusion might be reduced in a local patch of environment if the outcome of competition were indeterminate. Interminancy could result from periodic subtle biotic or abiotic perturbations especially in species, such as many troglobites, which have low population densities, long lives, and low intrinsic rates of natural increase. The trechine beetles discussed in

point 3 seem to fit this description. In aquatic habitats of caves competitive exclusion seems to be more important than in the terrestrial habitats occupied by the beetles, but even in the aquatic habitats we insist that Barr and Holsinger have not made the important distinction between invariant habitat selection and character displacement, *e.g.* habitat selection, that results only when congeners co-occur. Invariant habitat selection may be a result of either intra- or interspecific competitive interaction in the past whereas character displacement in areas of co-occurrence reflects ongoing competitive exclusion that results from some kind of interference. Thus, in the triad of amphipod species studied by Culver (1970b) the smallest, *Stygonectes spinatus*, is separated on a microspatial level by invariant habitat selection. The larger two, *S. emarginatus* and *Gammarus minus*, are in separate habitats only when they co-occur and this ongoing spatial exclusion is based on interference competition. A similar contrast can be made for amblyopsid cave fish. In the Mammoth Cave region three species show invariant habitat selection whether alone, in pairs, or in a triad. We suggest that this is the evolutionary result of competitive interaction in a cave region with enough habitat heterogeneity to allow habitat segregation by several species. In other cave regions there is not as much habitat heterogeneity, and the solution to competition has been to have only one species per cave, *i.e.*, ongoing competitive exclusion. Thus, when the surface populations of the troglaphilic ancestors of present day *Typhlichthys* became extinct, survival in caves was possible only for those founder populations in caves not already occupied by established troglobites, either *Amblyopsis spelaea* or *A. rosae*. Also, present distributions of *Typhlichthys-Amblyopsis* pairs suggests that competitive exclusion still prevents their co-occurrence in single caves outside of the Mammoth Cave region (Poulson, 1963).

LITERATURE CITED

- Barr, T. C. 1966, 1967. Cave Carabidae (Coleoptera) of Mammoth Cave. *Psyche*, 73:284-287; 74:24-26.
- Barr, T. C. 1968. Cave ecology and the evolution of troglobites. *Evolutionary Biology*, 2:35-102.
- Culver, D. C. 1970a. Analysis of simple cave communities. I. Caves as Islands. *Evolution*, 24:463-474.
- . 1970b. Analysis of simple cave communities: niche separation and species packing. *Ecology*, 51:949-958.
- . 1971. Analysis of simple cave communities. III. Control of abundance. *Amer. Midl. Nat.*, 85:173-187.
- Jegla, T. C., and T. L. Poulson. 1970. Circannian rhythms. I. Reproduction in the cave crayfish *Orconectes pellucidus inermis*. *Comp. Biochem. Physiol.*, 33:347-355.
- Poulston, T. L. 1963. Cave adaptation in amblyopsid fishes. *Amer. Midl. Nat.*, 70:257-290.
- Poulson, T. L., and W. B. White. 1969. The cave environment. *Science*, 165:971-981.

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Additional Data on the Carbidimite Formation

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A recent article (Broughton, 1970) described an apparently new type of speleothem that grew entirely from man-dumped carbide waste in Porter's Cave, Bath County,

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Virginia. The name "ice cream" formation was proposed. Previously described formations of this type have been reported to the writer from Fitton Cave, Arkansas (Tichenor, 1970). Recently, additional observations of the speleothem have been reported from

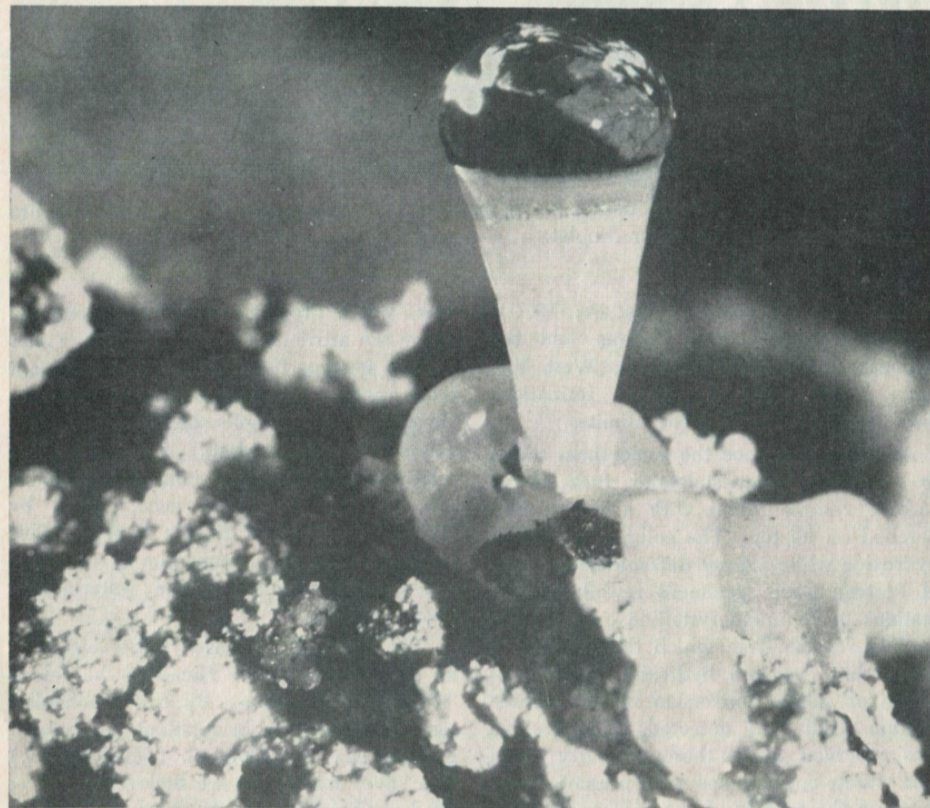


Figure 1. Carbide formations growing from a carbide dump in Porter's Cave, Virginia.



Figure 2. A carbidimite formation in its final stage of development. A calcite film has completely enclosed the water droplet.

Haines Cave, Wisconsin (Hedges, 1970); Leonard Springs Cave, Indiana and the Arbogast-Cave Hollow System, West Virginia (Eddy, 1970). These formations have also been termed carbidimites.

At first appearance the speleothem seems to be a soda straw stalactite stuck in the carbide residue, often with a water drop perched on its top. The color is a calcium hydroxide white. X-ray diffractometer study of Porter's Cave specimens reveal the formations to be microcrystalline calcite. The carbide residue from which they formed is portlandite (calcium hydroxide). No indication of calcite conversion in the carbide residue itself was detected. The residue was observed to be thoroughly dry when carbidimite speleothems were present. However, on the surface of the calcium hydroxide residue, as well as on adjacent wall

rock, water droplets were fairly common. These are attributed to condensation, rather than to seepage from above. The dominant form appears to be a roughly globular or "blister-shaped" fragile shell of calcite enveloping a water drop. Apparently, the relatively insoluble calcium hydroxide is saturated in the water, accompanied by absorption of carbon dioxide from the cave atmosphere. A paper-thin film of calcite is subsequently formed at the water-atmosphere interface.

Through capillary action the water droplet can slowly migrate ahead of the calcite "shell" crystallization. By this mechanism seemingly random orientations of tubular growths can be generated. (See figure 1.) The "live" formations are hollow and water filled. The tubular structure, similar to the photo, is usually filled with a milky-

colored colloidal suspension. The liquid gradually becomes completely clear near the exposed water drop at the "live" end. A sufficient sample of the milky fluid to determine its nature could not be collected. The calcite growth direction is at the exposed water drop end of the speleothem. The terminal stage of the growth is the complete envelopment of the water drop by a calcite film. (See figure 2.) This prevents the water from moving by capillary action, as well as access to atmospheric carbon dioxide to generate calcite. Eventually the water disappears, leaving a hollow calcite speleothem in a carbide dump.

Formations up to 4 cm. high have been observed, but typical carbidimites are 1 to 2 cm. high. They are usually vertical with the live end at the top but have been observed at essentially all angles to the horizontal. Often the columnar shape exhibits an erect bead-chain form, as well as vase-shaped forms flaring towards the top and helictite-like spirals. Diameters vary considerably but are typically about 1 cm. They may be so thin as to be barely visible.

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REFERENCES

- Broughton, Paul, 1970. The ice cream formation—a new speleothem. *NSS NEWS*, 28(7):91.
- Eddy, David, 1970. Written communication to the *NSS NEWS* staff.
- Hedges, James, 1970. Written communication to Paul Broughton.
- Tichenor, John, 1970. Written communication to Paul Broughton.

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