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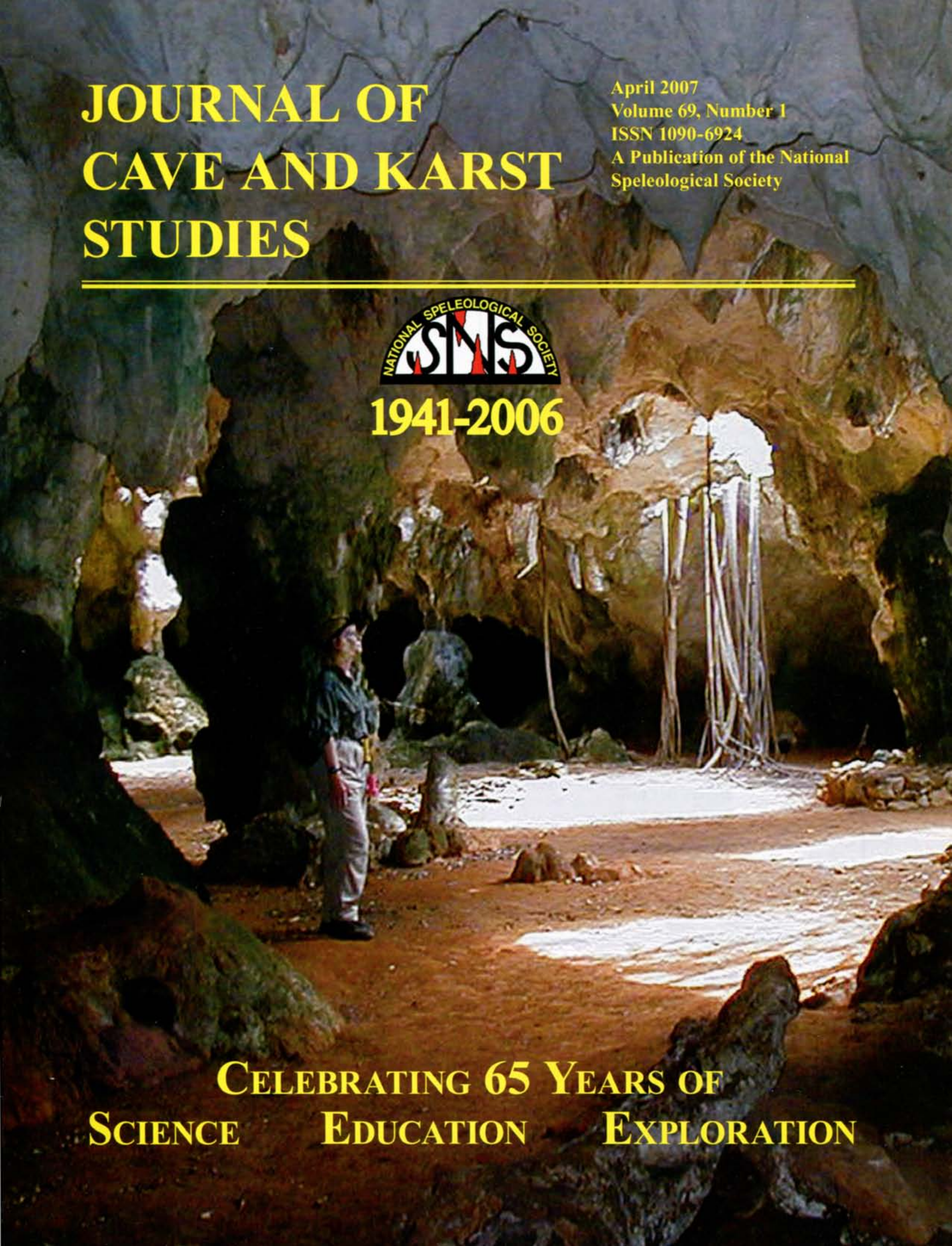

NATIONAL SPELEOLOGICAL SOCIETY

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CELEBRATING 65 YEARS OF
SCIENCE EDUCATION EXPLORATION

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Editor-in-Chief
Malcolm S. Field
National Center of Environmental
Assessment (8623D)
Office of Research and Development
U.S. Environmental Protection Agency
1200 Pennsylvania Avenue NW
Washington, DC 20460-0001
202-564-3279 Voice 202-565-0079 Fax
field.malcolm@epa.gov

Production Editor
Scott A. Engel
CH2M HILL
304 Laurel Street, Suite 2A
Baton Rouge, LA 70801-1815
225-381-8454
scott.engel@ch2m.com

Journal Proofreader
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441 S. Kearney St
Denver, CO 80224
303-355-5283
dgdavis@nyx.net

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Book Reviews
Arthur N. Palmer & Margaret V Palmer
Department of Earth Sciences
State University of New York
Oneonta, NY 13820-4015
607-432-6024 • palmeran@oneonta.edu

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EDITORIAL

Sixty-Five and Still Going Strong

Journal of Cave and Karst Studies

MALCOLM S. FIELD

It is with great pleasure and satisfaction for me that with this Special Issue of the *Journal of Cave and Karst Studies* we mark the 65th Anniversary of the National Speleological Society (NSS) which occurred in 2006. The last such special issue marked the 25th Anniversary of the NSS.

This particular special issue is especially gratifying because it also represents a major change in the way the *Journal* is now put together. Authors, associate editors (AEs), reviewers, and numerous others will find what I believe are major improvements to the *Journal* publishing process.

ARTICLES IN THIS ISSUE

First, I want to point out that for this Anniversary Issue several individuals consented to writing special articles marking the progress in cave and karst studies since the inception of the NSS. Back in 1966, which marked the 25th Anniversary of the NSS, a special issue of the old *Bulletin of the National Speleological Society* (vol. 28, no. 1) included manuscripts on earth sciences and speleology, evolution of cave biology in the United States, cave exploration techniques, and an early history of the NSS. Manuscripts accepted for this special Anniversary issue follow the original concept applied in the 25th Anniversary issue by addressing the major areas of cave and karst studies covered by the *Journal* and some currently less prominent areas, all by some of the most recognized researchers in caves and karst.

For example, earth science and biology papers make up the bulk of papers submitted for publication in the *Journal*. Earth science papers in this issue include manuscripts on the historical aspects of speleogenesis and cave geology (A. Palmer), island cave and karst formation (J. Mylroie and J. Mylroie), cave mineraology and the NSS (C. Hill and P. Forti), hydrology (W. White), cave sediments and paleoclimates (W. White), groundwater tracing (S. Worthington), and pseudokarst (W. Halliday). Life sciences papers include manuscripts on zoogeography and biodiversity in Missouri caves (W. Elliott), and biology and ecology of cave crickets (K. Lavoie, K. Helf, and T. Poulson). Microbiological papers include manuscripts on molecular techniques used in subterranean biogeography (M. Porter), historical perspectives and future research on geomicrobiology in cave environments (H. Barton), biodiversity of sulfidic karst habitats (A. Engel); the latter two crossing the earth science and biological divisions of cave karst studies.

Other significant areas of coverage in the *Journal* in the past, but now more rarely submitted for publication are archaeology, exploration, and social sciences. Cave archaeology and the NSS (G. Crothers, P. Willey, and P. Watson) documents directions the field has taken over the years. The importance of cave exploration and scientific research, a subject area that may be regarded as the legacy of the NSS but that has been sorely lacking over the past several years, is covered in this issue (P. Kambesis). Even more rarely, a social science paper on the creation of a karst database (L. Florea and B. Fratesi) has been included. Lastly, a paper on the human health aspects of exploring and working in caves with elevated levels of radon has been included (M. Field).

PUBLISHING CHANGES WITH THIS ISSUE

As of May 2007 the *Journal* is now accepting all manuscripts via AllenTrack, a web-based system for on-line submission. The AllenTrack web site, http://jcks.allentrack2.net, will be accessible directly from the NSS *Journal of Cave and Karst Studies* web site, http://www.caves.org/pub/journal/. AllenTrack is the same organization that handles publishing of such respected journals as *American Mineralogist*, *Geology*, *Geological Society of America Bulletin*, *Ground Water, Journal of Paleontology*, and *Journal of Sedimentary Research* so it is likely that many authors will already be familiar with the on-line submission process. This change in our publishing process represents a major accomplishment and should greatly enhance the *Journal* while reducing overall publishing costs.

The AllenTrack system is fully integrated so that the editorial staff can fully monitor the review process and more effectively keep the process moving forward. Manuscripts will no longer need to be mailed in triplicate; nor will authors be responsible for determining which AE should receive a particular manuscript. By including selected keywords on the web site when submitting a manuscript, the appropriate AE will automatically be determined, but which may be overridden, as appropriate, by me. All AEs and reviewers will have access to the system whenever and wherever they are as long as they have access to the internet, so reviews and decisions can be made while traveling. Overall, everyone should find the process remarkably easy.

MANUSCRIPT AUTHORS

Manuscript submission is quite easy. After accessing the site for the first time, authors create a login and password and then will enter necessary preliminary manuscript information (authors, addresses, manuscript title, etc.). Then an author will upload their manuscript, figure files, and table files preferably in the original format in which they were created (e.g., DOC, WPD, RTF, TXT, or LaTeX for manuscripts and tables; Excel for tables; and TIFF, EPS, or PDF for figures). Alternatively, manuscripts can be submitted as PDF or HTML files for review purposes only; if accepted the manuscript will need to be resubmitted in one of the listed accepted formats. Tables and figures may be appended to the main document when submitted or tables and figures may be uploaded separately from the main document.

Once uploaded, the system will convert all uploaded files to a single PDF in approximately 10 minutes and a confirmation will be sent to authors via e-mail. Manuscripts already in the system will be uploaded by the editor, but effective June 2007 it is expected that all authors will submit manuscripts using the new internet-based system.

ASSOCIATE EDITORS AND REVIEWERS

Associate editors and reviewers will be able to access submitted manuscripts on-line and will be able to conduct reviews on-line as well. Alternatively, if a hardcopy of the submitted manuscript is desired, then a copy may be downloaded and printed as well. Reviewer's summary opinions, comments, and recommendations for editors, as well as any detailed comments for authors, will all be submitted via the AllenTrack system. Annotated comments on hardcopies can still be returned to AEs if desired, but are no longer necessary.

Associate Editor recommendations and the Editor's decision regarding each manuscript will be sent out to the corresponding author via e-mail. Author-required revisions will also use the AllenTrack web site as will final edits.

Because this is such a significant change in the way manuscripts will be handled in the *Journal,* it will likely require some patience by everyone concerned as we work through the new procedures. However, it is expected that this new *Journal* process will result in monetary savings and speed up the publication process. Overall, it should be a benefit to all concerned.

Arthur N. Palmer – Cave geology and speleogenesis over the past 65 years: role of the National Speleological Society in advancing the science. *Journal of Cave and Karst Studies,* v. 69, no. 1, p. 3–12.

CAVE GEOLOGY AND SPELEOGENESIS OVER THE PAST 65 YEARS: ROLE OF THE NATIONAL SPELEOLOGICAL SOCIETY IN ADVANCING THE SCIENCE

ARTHUR N. PALMER
Department of Earth Sciences, State University of New York, Oneonta, NY 13820-4015, palmeran@oneonta.edu

Abstract: The National Speleological Society was founded in 1941, near the end of a remarkable period in the history of speleogenesis. Many well-known geologists had published on the topic during the previous decade. For various reasons the NSS did not benefit from this wave of interest, and its members were faced with reconstructing the subject from a fresh beginning. The topic was developed mainly by individuals who started as cave explorers and extended that interest into science. Some of the advances over the past 65 years include new field and laboratory techniques, models of cave origin, introduction of sulfuric acid speleogenesis, coastal cave studies, recognition of microbial mediation of cave processes, geochronology and paleoclimatology, digital modeling, and growing attention toward lava caves.

INTRODUCTION

Since its founding in 1941, the National Speleological Society (NSS) has grown from a small regional group into one of the world's largest and most influential organizations in cave science. Over the past 65 years it has helped to foster some of the most notable advances in cave geology and speleogenesis. This paper concerns the history of this field and the role that the NSS has played in its development. There is no need for a rigorous historical record or a detailed description of ideas, as these are provided in recent books edited by Klimchouk et al. (2000), Gunn (2004), and Culver and White (2005). Instead, the aim is to look behind the scenes at the interaction among cave geologists and how their ideas developed.

In summarizing the advances in karst geology for the 25th anniversary of the NSS, Davies (1966) noted that early progress in that field had taken place in spurts, with intervening periods of relative inactivity. He predicted a burst of quantitative advances in speleology in the years to come, and the validity of his prediction is illustrated here.

BEGINNINGS

The NSS was conceived, as Dickens would have said, in both the best of times and the worst of times. During the prior decade there had been a flowering of interest in cave origin, and many of the classic American papers on the subject were produced at that time. The authors include some of history's best-known geologists. William Morris Davis, who wrote a 154-page paper on cave origin (Davis, 1930), is probably the most influential geomorphologist who ever lived. J Harlen Bretz (no period after the J) was one of America's boldest and clear-sighted geologists. Most of his work on caves followed the birth of the NSS (e.g., Bretz, 1942), but he had made his reputation long before. Clyde Malott, who was among Indiana's foremost stratigraphers and geomorphologists, devoted much of his attention for several decades to caves and karst (e.g., Malott, 1937). Allyn Swinnerton was a well-known professor of geology at Stanford, Harvard, and Antioch College (Swinnerton, 1932).

There was considerable disparity of opinion among these early authors. Davis and Bretz championed deep-phreatic cave origin. Swinnerton favored cave origin at or just below the water table. Malott described caves in terms of invasion by surface streams. This brief outline does no justice to any of the authors and omits many others, but it is enough to set the stage. For details see Watson and White (1985) and Lowe (2000).

The founding of the NSS near the end of this period placed it in a position to ride the wave of enthusiasm for speleogenesis, but for several reasons the organization gained little benefit from it. First, none of the contributors to the classic papers were involved in founding the Society. The founders were mainly cave explorers, and although they regarded science as important, they had few credentials in the field.

A second problem was that the ideas developed during this classic period of speleogenesis contradicted one another. They were published before cave maps were widely available, and interpretations lacked the benefit of diverse field experience. With no consensus, it seemed that little solid ground had been gained.

Continental Europeans, with their long tradition in cave science, were astonished by the many contradictory American models for cave origin. The well-known French speleologist Bernard Gèze once said (translated loosely from Trombe, 1952), "It seems that the Americans are trying to reinvent speleology right from square one." But at the same time, western Europeans made almost no reference to the vast amount of contemporary work accomplished in eastern Europe. This insular attitude can be clearly traced to the barriers of language, geography, and politics. The field is much more cosmopolitan today.

The growth of science within the NSS is clear from the first 10–20 years of the *Bulletin of the National Speleological Society* (now the *Journal of Cave and Karst Studies*). *NSS Bulletin* No. 1 was published by the short-lived precursor of the NSS, the Speleological Society of the District of Columbia. Its cover includes a cartoon of a group of cavers scrambling over stalagmites, with one team member burning the seat of the person ahead with his carbide lamp. The issue contains mainly trip reports, and although each shows a well-defined purpose, there is no coordinated scientific focus. Interest in science grew, however, and within a few years scientific articles dominated the *Bulletin*. Several of the early champions of cave geology, including Malott, Swinnerton, and Bretz, were made honorary NSS members, and they responded favorably by contributing articles. American studies of speleogenesis began gradually to rebuild. In 1949 the *Bulletin* included papers on the subject by Ralph Stone and Clyde Malott. In 1950, Allyn Swinnerton contributed a paper on cave mapping, but he did not pursue his ideas on cave origin.

A FORK IN THE ROAD

There may be a reason for Swinnerton's diminished interest in speleogenesis. In 1940, one of the greatest figures in petroleum geology and hydrology, M. King Hubbert, published a seminal paper, *The theory of groundwater motion*, in the *Journal of Geology*, in which he developed the principles of hydraulic potential and the influence of potential fields on ground-water motion. In it, he explicitly criticized Swinnerton's diagrams of cave origin for being incompatible with potential theory and violating the law of conservation of mass. Although Hubbert was not entirely wrong, he failed to take into account the distortion of laminar ground-water patterns by conduit growth (Hubbert, 1940).

Hubbert's paper was hardly noticed by speleologists at that time, but it was a turning point for ground-water hydrologists. For many, ground water became a technical field that relied as much on mathematics and physics as on geology. Today Hubbert is best remembered for his concept of peak oil, but his legacy in hydrology also lives on.

Although no one realized it at the time, this was the third and greatest obstacle faced by cave geologists during the early years of the NSS. Since the turning of hydrology in mathematical directions, speleology has been dismissed as hardly a science at all by most hydrologists, the very people who could benefit the most from cave geology.

A FRESH START

By the 1950s, several NSS members emerged as leaders in cave geology. Ralph Stone (former State Geologist of Pennsylvania) contributed an entire *NSS Bulletin* on Caves of Pennsylvania (Stone, 1953) an update of work that he had prepared earlier for the State Geological Survey, and which includes considerable geologic detail. William Davies, of the U.S. Geological Survey, wrote books on the caves of Maryland (Davies, 1950) and of West Virginia (Davies, 1959). He also advanced the study of speleogenesis with observations of cave levels and their correlation with river terraces (e.g., Davies, 1957). Both he and Stone served as NSS president. Bretz wrote a book on caves of Missouri (Bretz, 1956) and co-authored another on the caves of Illinois (Bretz and Harris, 1961). E.R. Pohl, long-time Kentucky geologist and one of the founders of the Cave Research Foundation, contributed important work on the origin of vertical shafts in limestone caves (e.g., Pohl, 1955).

George Moore, of the U.S. Geological Survey, recognized that it was time for American speleologists to review the status of speleogenesis. In 1959, he convened a symposium on cave origin, sponsored jointly by the NSS and the Geological Society of America. The proceedings were published as *NSS Bulletin* 22, No. 1 (Moore, 1960). This was probably the most important point in NSS history in terms of advancing the field of speleogenesis. Besides Moore, participants included Bretz, Davies, Rane Curl, George Deike, William Halliday, Arthur Lange, John Thrailkill, and William White. Bretz and Davies were already well known in the field, and each of the others also went on to make substantial contributions to speleogenesis. Some are still active in cave geology today.

White (1959) had already published a discussion of speleogenesis in his local grotto newsletter. He reviewed the classic papers of the 1930s and early 1940s and came to the conclusion that no one agreed on anything. But it was made clear during the 1959 symposium that much of the confusion was only a matter of conflicting terminology. In the words of Halliday (1960),

> There seems to be less and less divergence of basic concepts, and more and more argument over classification and terminology, which can be carried to the point that two authorities holding similar views are unable to recognize their agreement.

This warning applies as well today as it did in 1959. But at that time, field experience and cave data were growing rapidly, and the answers to many fundamental questions in speleogenesis seemed within reach. Little did the symposium participants realize how far they had to go.

PHYSICS AND CHEMISTRY ENTER THE PICTURE

An understanding of speleogenesis requires as much knowledge of hydraulics and chemical kinetics as it does of geology. Laboratory experiments by non-speleologists Kaye (1957) and Weyl (1958) showed that the rate of limestone dissolution depends on the velocity of acidic water. This approach promised to solve some of the basic questions about cave origin, but they used hydrochloric acid, which behaves differently from carbonic acid, which is involved in most cave development, and so the results were not as helpful as they once seemed. They did, however, point the way. From his experiments, Weyl estimated that acidic water could not penetrate very far along a typical fracture in limestone before losing most of its solutional capacity.

On the basis of this research, William White and Judith Longyear concluded that none of the previous conceptual models of cave origin were incorrect, but that they were all irrelevant. In each model, caves were tied to their position relative to the water table, whereas, in fact, they form wherever the ground-water flow is greatest (White and Longyear, 1962). White and Longyear also predicted a substantial jump in dissolution rate when the flow changes from laminar to turbulent as the conduit grows.

Alan Howard applied chemistry and hydraulics to cave origin and estimated that the laminar-turbulent transition would increase the solution rate by a few times (Howard, 1964a). This estimate was much smaller than White and Longyear's, but more accurate. Several other projects and academic dissertations by NSS members were devoted to pursuing the kinetics of carbonate dissolution, with the specific goal of clarifying rates of cave origin (e.g., Howard and Howard, 1967; Rauch and White, 1970; Herman and White, 1985).

The idea of a threshold in cave development was expanded further by White (1977). He noted that as a cave grows and its flow becomes turbulent, the water also acquires the ability to transport sediment at nearly the same time. From then on, sinkholes open more rapidly, and abrasion can augment the dissolution rate in caves. White also applied experimental data from Plummer and Wigley (1976) to show that, in a typical cave, the dissolution rate of calcite increases abruptly at about the same time as the onset of turbulence and sediment transport. All three processes enhance the growth rate of caves at more or less the same point in a cave's evolution.

Rane Curl, since the late 1950s, had been concerned with the origin of solutional scallops in the bedrock surfaces of caves. By applying hydraulics and dimensional analysis, he showed how it is possible to determine past flow velocities from scallop lengths. This gave a great boost to the interpretation of cave paleohydraulics. His latest paper on the topic (Curl, 1974) is the most accessible.

Curl also investigated the statistical aspects of cave distribution and morphology. By quantifying these variables, the processes that form caves can be discriminated. He continued to pursue these topics for several decades (e.g., Curl, 1986). This approach is useful to scientists, such as petroleum geologists, who need to predict the distribution of porosity.

Similar advances were taking place simultaneously in Europe. It is worth noting how bursts of activity often take place almost simultaneously around the world under the direction of a few leading researchers, as suggested by Davies (1966). Today, with rapid worldwide communication, this tendency is even more prevalent.

Academic Alliances

William White became a professor at Pennsylvania State University, where he nurtured a long string of graduate students with interests in cave geology and hydrology, as he continues to do today in semi-retirement. Speleogenesis was gradually becoming inseparable from karst hydrology. One by one, he and his students tackled the fundamental problems in these fields.

In the early 1960s, Derek Ford arrived in North America from Britain and soon joined the faculty at McMaster University (Hamilton, Ontario). He threw himself into exploring and interpreting the karst of his vast new homeland and almost singlehandedly put Canada on the map of important karst regions. He joined the NSS and began publishing in the *Bulletin*. A large number of talented graduate students obtained their training under his direction, and the list continues to grow today.

A steady stream of karst scientists from overseas began to pass through both McMaster University and the Pennsylvania State University to observe the research programs at these schools and often to linger as visiting scholars. Inevitably, the two groups began to meet periodically to combine socializing and science. Karst geology and speleogenesis were among the main topics of discussion. These occasional meetings were so successful that other karst scientists began to take part from all over the continent. Soon some of the meetings were held at other locations. In 1974, at a meeting at the University of West Virginia, the still-informal group acquired the name Friends of Karst. There were no rules, no official membership, officers, dues, or newsletter. Since then, many FOK meetings have been held throughout North America, as well as in Puerto Rico, San Salvador, and Romania.

Meanwhile, several Penn State and McMaster students went on to establish their own academic programs in karst or related fields, while similar programs at other universities sprouted from different seeds. A spirit of camaraderie bound them all together, as it still does today, partly owing to the eclectic nature of cave science. It is difficult to retain one's professional dignity while crawling through mud. Some of the unity also stemmed from the impression that few other people seemed to care about caves.

Developments in Cave Geology

Early studies of speleogenesis were hampered by the paucity of field data on cave geology. In the first half of the 20th century there was almost no quantitative information on the relation between caves and their surrounding geology, beyond visual and non-systematic observations. At that time, the situation was more favorable in Europe, where standards of cave mapping were more advanced. By the late 1940s, American geologists began to relate cave patterns to details in the surrounding geology. Such studies were most numerous in the Appalachians (E.L. Krinitzky, 1947; Davies, 1959, 1960; Deike, 1960), and in Mammoth Cave, Kentucky (Deike, 1967). In the Black Hills of South Dakota, Deal (1962) and Howard (1964b) related Jewel Cave and Wind Cave to their complex geologic and hydrologic settings.

In the 1960s, Richard Powell, of the Indiana Geological Survey, developed hand-leveling techniques to map the subtle geologic structure of caves in strata with dips so gentle that they cannot be distinguished by eye. His work at Wyandotte Cave, Indiana, was perhaps the first of its type (Powell, 1968, 1976). His associates, Arthur and Margaret Palmer, extended the technique to caves elsewhere in the country (e.g., Palmer, 1972, 1989). Recently, Roy Jameson has used the leveling method to obtain even greater detail through an analysis of the individual segments in each cave passage (Jameson, 1985, 2006).

This work showed that even in places of almost negligible dip, the trends of many cave passages are controlled by local structures that are too subtle to appear on geologic maps based on surface exposures. Such details provide the necessary criteria for distinguishing whether cave levels (i.e., stories, or tiers) are controlled by geomorphic events, by geologic structure, or by favorable stratigraphy. Earlier studies, such as those of Davies (1957) showed a general relationship between cave elevations and river terraces. Detailed geologic mapping makes it possible to validate the relationship between cave levels and former base levels in some caves (e.g., Powell, 1970) and to reject the relationship in others (e.g., Palmer and Palmer, 1989). As a complication, stress release around entrenched surface valleys helps to localize cave development (Sasowsky and White, 1994). As the dating of cave deposits becomes more sophisticated, caves that are convincingly related to base-level history can be used to interpret the drainage history of entire drainage basins (e.g., Granger et al., 2001; see details below).

Specialized topics in cave geology have emerged. In cave mineralogy, for example, Moore (1952) promoted the word *speleothem* to refer to secondary mineral deposits in caves. The literature on the subject is so vast that readers are referred simply to the massive summary by Hill and Forti (1997). By comparison, detrital cave sediments have received little attention, even though they are integral features of caves and important to cave development. Studies by William Davies and E.C.T. Chao at Mammoth Cave showed how it was possible to interpret source areas for cave sediments (Davies and Chao, 1959). Elizabeth and William White described the dynamics of sediment transport through caves and the relationship between sediments and cave origin (White and White, 1968). Current knowledge on cave deposits, both mechanical and chemical, is summarized in a book edited by Sasowsky and Mylroie (2004).

A common topic at meetings is the regional approach to karst and cave science, in which all aspects of the subject are discussed within a given geomorphic province. An example is the Appalachian Karst Symposium, held at Radford University, Virginia, with proceedings edited by Kastning and Kastning (1991).

In recent decades, cave scientists have begun to apply their knowledge to other fields not generally associated with caves. Examples include the relationship of caves to petroleum geology and mining (Furman, 1993; Hill, 1995), dolomitization (Thrailkill, 1971), the evolution of porosity in carbonate rocks (Queen, 1973, 1994), and the interpretation of tectonic history from the distribution of caves (DuChene and Cunningham, 2006). Other examples of how caves can provide information about the geologic history of the surrounding region are described below.

CONCEPTUAL MODELS OF CAVE ORIGIN

Devising conceptual models of cave origin continues to be a common goal of American speleologists. The tangled web left from earlier decades has finally been sorted out, so that the disparate interpretations finally made sense. None of the early work has been discarded. Instead it is periodically re-examined in the light of new knowledge and incorporated into new models where appropriate. Over the past few decades, several conceptual models have been proposed in an attempt to explain the origin of all caves with a single model.

RELATION TO AQUIFER TYPE

William White described karst aquifers according to their hydrogeologic settings and noted the types of caves that were most typical in each (White, 1969 and later). Diffuse-flow aquifers contain few caves, and they tend to be small and irregular. Free-flow aquifers may or may not be overlain by an insoluble cap-rock. Sinkholes are the main water inputs in the exposed type, and short caves with high sediment load are common. Capped aquifers are fed by vertical shafts around the eroded perimeters of the cap-rock, and long integrated caves extend beneath the cap-rock. Confined aquifers in which impermeable beds force water to flow below the regional base level tend to contain inclined three-dimensional mazes, and the sandwich variety of confined aquifer, which is confined between thin impermeable beds, contains horizontal two-dimensional mazes.

RELATION TO FISSURE FREQUENCY

Derek Ford proposed a model of cave patterns based on the evolution of fissure frequency (spatial density) within an aquifer (Ford, 1971). Fissure frequency is low at first but increases with time as erosion and cave development proceed. The result is a four-state model: (1) At low fissure frequency only a few phreatic loops develop, which extend well below the water table and rise in their downstream ends. (2) With increasing fissure frequency, loops become more abundant but shallower. The water table drops as the permeability increases. (3) Eventually a mixture of phreatic and water-table cave segments develops. (4) Fissure frequency may become so great that phreatic loops cannot form, and cave passages develop almost entirely along the water table. Many caves exhibit more than one state, or they may bypass one or more of them. Two other conditions are possible (Ford, 1988): state 0, in which no fissures at all are present and caves cannot develop; and state 5, in which there are so many small openings that ground water is too diffuse to form significant caves. Artesian conditions are considered a special case in which maze caves form by slow, lengthy dissolution.

LINKAGE OF CAVE PASSAGES

Ralph Ewers demonstrated how individual cave passages link together to form complex caves (Ewers, 1982). Given various inputs at different distances from an outlet, those with the shortest paths are the first to form cave passages. Incipient caves fed by multiple inputs compete with each other, and the first to break through to a spring outlet becomes the main conduit. As the head decreases in the main passage, the flow from more remote inputs is drawn toward it to form tributaries. To develop these concepts, Ewers used models constructed of gypsum, plaster, and salt, into which he injected water under pressure along artificially prepared fissures. In some the water was injected along the flat bottom of the soluble block and viewed from below through a transparent bladder pressed against the block. The linkage mechanism is so robust that there was little or no interference caused by the contrasts in hydraulic gradient and dissolution kinetics between the models and real karst aquifers. As these ideas developed, they were combined with those of Ford in a single paper (Ford and Ewers, 1978).

ORIGIN OF CAVE PATTERNS

Arthur Palmer attributed branchwork caves to recharge through karst surfaces (e.g., through sinkholes and minor sinking streams) (Palmer, 1975). In contrast, he considered that maze caves form either by intense floodwaters (e.g., by recharge from major sinking streams) or by diffuse recharge such as seepage into soluble rock through overlying or underlying insoluble rocks. The model was later expanded (Palmer, 1991) by combining hydraulics and chemical kinetics, with the aid of earlier measurements of limestone dissolution rate (e.g., Plummer et al., 1978): Early cave enlargement depends on the ratio of discharge Q to flow length L (Q/L). The enlargement rate increases with Q, but only up to a certain limit. Further increase in Q raises the enlargement rate only slightly. For a flow path to grow into a cave, its discharge must increase with time. Only a few of the original flow paths reach cave size, as is typical of branchwork caves. The exception is where all openings grow at high rates from the beginning, to form maze caves, in which many alternate routes have large Q/L. Examples include recharge through an adjacent insoluble rock (small L), or periodic floodwaters (large Q). Aggressiveness produced by mixing, oxidation of sulfides, or cooling of thermal water also tends to produce mazes. Fully confined artesian conditions are not sufficient by themselves to form maze caves. The time required to form a cave increases with flow distance and temperature, and decreases with initial fissure width, hydraulic gradient, and CO_2 concentration.

VERTICAL LAYOUT OF CAVES

Stephen Worthington, as an outgrowth of his 1991 Ph.D. dissertation at McMaster University, contributed two important papers on the vertical distribution of cave passages (Worthington, 2004, 2005). He notes that most large springs draining regional karst aquifers have high sulfate concentrations, and that the caves being initiated within them must encounter soluble gypsum or anhydrite beds. Maximum cave depth below the original water table is related to the extent of the cave from headwaters to spring. He re-interpreted cave levels, not in terms of successive stages of valley entrenchment, but instead as being part of the natural evolution of a cave. He based his idea on the fact that warm water at depth has a lower viscosity than cold water and is able to flow faster under a given hydraulic gradient. Utilizing a large personal database on caves from around the world, he devised empirical formulas for cave depth in relation to end-to-end length and other variables. Because of its reliance on field data, it is a rare example of a predictive model.

These constitute the main speleogenetic models developed in America in recent decades. Others have been offered by European speleologists (see Klimchouk et al., 2000). Despite the different approaches, all of these ideas are complementary. Each author is acquainted with the work of the others and has a lengthy familiarity with caves. There is still healthy debate about details, but one hopes that this always remains the case.

Besides the general models for cave origin described above, there have been several more tangible advances in cave geology. Additional styles of bedrock dissolution have been documented, beyond the typical carbonic acid reaction in meteoric water. New methods have been developed for determination of cave ages and paleoclimates. Digital models of cave growth have been devised. Cave information has been widely applied to the interpretation of regional geologic history. These topics are discussed in detail below.

SEACOAST CAVES

Studies in the 1970s by the U.S. Geological Survey (e.g., Plummer, 1975; Back et al., 1984) established that carbonate dissolution could be caused by mixing between fresh water and seawater along limestone coasts. This process was accepted without debate by speleologists, especially by scuba divers, but it was not until the late 1980s that full attention was given to the topic. The leaders in the field have been John Mylroie and James Carew, both of whom were former New Yorkers capable of facing the rigors of research on tropical beaches. Their studies in the Bahamas (e.g., Mylroie and Carew, 1990) clarify the origin, distribution, and ages of caves in carbonate islands, as well as their relation to present and former sea levels. The topic is summarized in the carbonate island cave model (Mylroie and Vacher, 1999). The result of this work has been embraced by a diverse group including sedimentologists, geochronologists, paleoclimatologists, and petroleum geologists. Cave studies are most welcome where they help to address problems in other fields.

SULFURIC ACID CAVES

In the 1970s, when it seemed that the main controversies in speleogenesis were finally being ironed out, an unexpected mode of cave origin was revealed. In a preview of things to come, David Morehouse suggested that sulfuric acid from pyrite oxidation could account for certain caves in eastern Iowa (Morehouse, 1968). Soon afterward, Stephen Egemeier, for his dissertation at Stanford University, chose to study a group of caves in Wyoming's Bighorn valley (such as the Kane Caves), which smelled strongly of hydrogen sulfide. He soon realized that the caves were still in the process of forming by sulfuric acid produced by the oxidation of H_2S, both in the cave stream and on the walls and ceilings above (Egemeier, 1973, 1981). Sulfuric acid attack of the bedrock left a rind of gypsum, which occasionally spalled off, fell to the floor, and was carried away in solution by cave streams. Egemeier briefly visited Carlsbad Cavern (New Mexico) and noted similarities to what he had observed in Wyoming.

This was not the first time sulfuric acid had been linked to cave origin. As early as the 1930s, researchers in Italy, Russia, Hungary independently proposed the process, but their studies were neither detailed nor well publicized.

The idea of sulfuric acid speleogenesis took hold among several western speleologists (e.g., Davis, 1980). Meanwhile, David Jagnow recognized the role of sulfuric acid in the origin of caves in the Guadalupe Mountains, New Mexico, but attributed them to oxidation of pyrite in overlying beds (Jagnow, 1977). Independently, J. Michael Queen noted gypsum replacement in the walls of caves in the Guadalupe Mountains of New Mexico and interpreted the cave inception to mixing between fresh water and underlying sulfate-rich brine (Queen, 1973).

Carol Hill measured sulfur isotopes in the Carlsbad gypsum and found a light isotopic ratio that suggested biological redox reactions, and that the original H_2S must have come from reduction of deep-seated sulfates, followed by oxidation to sulfuric acid where the H_2S rose to the water table in the adjacent limestone mountains (Hill, 1981). By the time she published her full study (Hill, 1987), the concept of sulfuric acid speleogenesis was well accepted by most speleologists. The topic is covered thoroughly in a special issue of the *Journal of Cave and Karst Studies* (DuChene and Hill, 2000).

The Guadalupe cave studies were hampered by the fact that the caves are inactive relics. Evidence to support a sulfuric acid origin is circumstantial. Eventually NSS researchers become aware of an H_2S cave far more active than the ones Egemeier had studied. In the late 1980s, James Pisarowicz and Warren Netherton were apparently the first Americans to enter Cueva de Villa Luz, in Tabasco, Mexico. It contains sickeningly high H_2S concentrations, as well as gypsum crusts, long microbial filaments with highly acidic drips, and many features resembling those of the Guadalupes. A combined team of geologists and biologists examined the cave and gave support to the interpretations of cave origin and modification that had been developed in the Guadalupes (Hose et al., 2000). Although Villa Luz is much more potent than the Kane Caves, re-visits to the Kane Caves showed that they contain many of the same features (e.g., Engel et al., 2004).

The recognition of sulfuric acid speleogenesis opened the door to other types of deep-seated cave origin. This was a field well known in eastern Europe but barely recognized in America until the mid-1980s (e.g., Bakalowicz et al., 1987). In one of the clearest examples, Fred Luiszer combined a study of cave sediments with geochemical analysis of nearby springs to show that Colorado's Cave of the Winds is the product of mixing between deep high-CO_2 water and shallow low-CO_2 water (Luiszer, 1994).

A promising new tool in hydrology is the use of rare elements, including helium isotope ratios, to identify water that has risen from deep igneous sources. Michael Spilde et al. (Spilde et al., 2005) have used this technique to determine that about 6% of the water in Cueva de Villa Luz comes from these deep sources.

THE GEOMICROBIOLOGY OF CAVE ORIGIN

The study of active sulfuric acid speleogenesis led to an explosion of interest in cave geomicrobiology. Before 1990, reports of fossil bacterial filaments in paleokarst were met with skepticism. Were these simply a geologic aberration? Only a few years later, at a meeting of the Karst Waters Institute, at which biologists and geologists from many diverse fields were brought together, the idea suddenly gelled that microbiology is the key to many karst processes (see proceedings edited by Sasowsky and Palmer, 1994). The main importance to speleogenesis is that microbial mediation controls many karst-related redox reactions, including the production rate of H_2S and sulfuric acid (Cunningham et al., 1995; Northup et al., 2000). The quantitative effect of microbial mediation is still uncertain, but no one questions its significance. Cave microbiology has branched off as a major field of cave biology. An intriguing offshoot of these studies is the idea that cave microbiology may provide a window to extraterrestrial life (Boston, 2000).

Geochronology and Paleoclimatology

Speleogenesis can be understood only in terms of geologic time, and quantitative methods of dating cave deposits have helped greatly to advance the field. Many of the techniques in radiometric dating of speleothems were developed at McMaster University by Derek Ford, Henry Schwarcz, and their students (e.g., Harmon et al., 1975). Most speleothem dating involves uranium-series methods, which yield fairly accurate results as far back as 600,000 years (ten times the range of C-14 methods). Recent advances in uranium-lead dating can theoretically reach back as far as Earth's origin, but the technique is fairly complex and does not work with all samples. An example of the technique is given by Lundberg et al. (2000).

The McMaster team was also among the first to apply oxygen and carbon isotopic signatures to the interpretation of paleoclimates and changes in overlying vegetation. This approach makes it possible to determine conditions on a precise local scale, whereas most other methods provide generalized global averages. In the past couple of decades this field has been taken up by many researchers who do not consider themselves to be speleologists.

Throughout geologic time, the magnetic field of the earth reverses itself periodically, and this change is recorded in a tiny residual magnetism locked in rocks and sediments. Victor Schmidt (Schmidt, 1982) measured the paleomagnetism of sediments in Mammoth Cave, Kentucky, and determined that the middle levels of the cave pre-date the last magnetic reversal, i.e., they are older than 780,000 years. This approach has been carried on by Ira Sasowsky and Greg Springer to clarify entrenchment rates in Tennessee and West Virginia (e.g., Sasowsky et al., 1995; Springer et al., 1997). Paleomagnetism can also be measured in many calcite speleothems (Latham et al., 1979), and, where it is also possible to date them radiometrically, the history of magnetic variations can be calibrated.

One problem with dating cave deposits is that the dates are inevitably younger (often much younger) than the caves that contain them. But some minerals are alteration products of sulfuric acid attack on clay and presumably date from the latest phase of sulfuric acid speleogenesis. Some, like alunite ($KAl_3(SO_4)_2(OH)_6$) can be dated radiometrically. Victor Polyak and his co-researchers sampled this mineral in caves at various elevations in the Guadalupe Mountains and showed that their ages range from 12 million to 4 million years, from highest to lowest elevations (Polyak, et al., 1998). Many researchers assume that the decrease in cave age with decreasing altitude indicates a gradual rise of the Guadalupe block with time, while the water table stayed fixed at approximately the same elevation. In contrast, DuChene and Cunningham (2006) suggest that a decline in the water table was caused by loss of the original catchment area by the foundering of fault blocks in the headwater regions. The alunite dating technique is now being applied elsewhere, such as Grand Canyon, in an attempt to determine the history of tectonic uplift and river entrenchment.

Quartz-rich sediment at the earth's surface is continually bombarded by cosmic radiation. Minute amounts of radioactive aluminum and beryllium isotopes (^{26}Al and ^{10}Be) are produced in a certain ratio. When the sediments are buried or carried underground, these isotopes are no longer replenished, and the remaining ones decay. ^{26}Al decays faster than ^{10}Be, so with time the $^{26}Al/^{10}Be$ ratio decreases. By measuring this ratio, the age of the sediment burial can be estimated. Darryl Granger was the first to apply this technique to caves (e.g., Granger et al., 2001; Anthony and Granger, 2004). These studies have helped to sort out the evolution of the Ohio River drainage. After more than a century of explaining caves in terms of surface erosion, speleologists can now reverse the trend by using caves to explain the history of surface erosion.

Digital Modeling

As computer technology has become more powerful and accessible over the past few decades, digital modeling of cave origin has become feasible. The first working models of limestone cave development were developed in the early 1980s by Arthur Palmer to determine the functional relationships among the variables involved in speleogenesis (initial fissure width, hydraulic gradient, flow distance, etc.). The results formed the basis for one of the conceptual models described above (Palmer, 1991). Chris Groves and Alan Howard developed similar models in two-dimensional grids but found that computer technology was not yet advanced enough for them to realize the full potential of the method (Groves and Howard, 1994; Howard and Groves, 1995). Groves reports that one model tied up the mainframe computer at Western Kentucky University for an entire night.

Soon afterward, as technology advanced, karst researchers in Germany and France developed computer models capable of solving complex two-dimensional problems of speleogenesis. Work in this field has progressed at a rapid pace. The results tend to support earlier conceptual models, but they also provide quantitative estimates of the relative importance of such processes as mixing between waters of different chemistry. Dreybrodt and his co-researchers have summarized the advances in the field in a book accompanied by an interactive compact disk. They and other European researchers are now the undisputed leaders in the digital modeling of karst (Dreybrodt et al., 2005).

NON-SOLUTIONAL CAVES

Throughout the history of the NSS, there has been continued but low-level interest in non-solutional caves and pseudokarst, but in the past 15 years the study of lava caves has grown enormously (Halliday, 2004). Kazumura Cave, a 60-km-long lava cave in Hawai'i, is not only the world's longest explored lava cave, but also by far the deepest American cave of any kind (deep, that is, in greatest vertical extent, but not in depth below the surface). The Hawaiian Speleological Survey and Cave Conservancy of Hawai'i now involve many local researchers as well as frequent visitors from the mainland. New discoveries are made every year, especially on the big island of Hawai'i, and they provide a fresh perspective on cave origin.

CURRENT ROLE OF THE NSS IN CAVE GEOLOGY

Today the NSS works closely with many other karst organizations, both in America and in other countries. Over the history of the NSS, many affiliated groups have branched off, but they have all complemented the goals of the Society and have many members in common. The scientific status of the NSS has been strengthened by this mutual cooperation.

The NSS has recently published the book *Speleogenesis: The evolution of karst aquifers*, edited by an international team (Klimchouk et al., 2000), which includes contributions from authors around the world. This book has provided a foundation for the Web site www.speleogenesis.info, which publishes articles in the field, both new and from related journals, and serves as a clearing-house for information about the topic. The *Journal of Cave and Karst Studies* includes reviews of all other major international karst journals, which helps to publicize work in speleology throughout the world. The NSS also offers several research grants, the largest and most prestigious of which is the Ralph Stone Graduate Fellowship in Cave and Karst Studies.

The status of geologic cave research in America has blossomed in recent years. For example, special sessions and symposia in the field are frequently sponsored by NSS members at annual and regional meetings of the Geological Society of America. At some recent national meetings, karst sessions outnumbered those in all but a handful of major fields in geology. In 2004, Derek Ford and William White were jointly honored by GSA for their lifetime contributions to karst (see commemorative volume edited by Harmon and Wicks, 2006).

The reasons for this explosion of interest are clear. Recent advances in dating, paleoclimatology, porosity evolution, and geomicrobiology have applications to many other fields. Several high-profile journal articles in cave geology and speleogenesis have brought widespread attention. Highly regarded books on karst hydrology and geomorphology have been produced by NSS members (e.g., White, 1988; Ford and Williams, 1989; White and White, 1989). New academic centers of karst research have appeared in recent years, as a quick Web search can show.

An organization does not make scientific discoveries: individuals do. But the NSS as a whole has contributed to the field in a unique way. The Society provides a sense of shared purpose in which the scientists share common ground with explorers and mappers, without whose achievements the science would not be where it is today.

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A BRIEF HISTORY OF KARST HYDROGEOLOGY: CONTRIBUTIONS OF THE NSS

William B. White

Materials Research Institute and Department of Geosciences, The Pennsylvania State University, University Park, PA 16802 USA, wbw2@psu.edu

Abstract: The hydrology of karst aquifers has been of interest since early historic times with caves serving as water-carrying pathways. The modern period of karst hydrology can be said to have begun roughly in the 1960s with the work of the International Hydrologic Decade and with the recognition of the relationship of cave exploration to groundwater basins. A theme for the 40 year period between the 25th anniversary of the NSS and the present is the gradual melding of traditional hydrogeology, which does not work well in karst, and the contributions of cave explorers who have provided tremendous detail about the conduit systems in aquifers. Important progress has been made in techniques for water tracing in karst areas and in systematic mapping of karst groundwater basins. Qualitative studies have largely been replaced by quantitative measurements of spring flow and water chemistry. The current research front deals with the construction of flow models for karst aquifers.

Introduction

The most direct interface between cave exploration and the earth sciences is the hydrology of karst aquifers. No wonder. Here goes a survey team of cavers, splashing through a base level water cave up to their belly buttons (or chins) in the karst water table. How much more intimate a connection can there be? Cavers have a deep understanding of the movement of groundwater in carbonate rocks, but it took some time to convince the professional community that they were worth listening to.

The purpose of this article is to trace the gradual evolution of understanding of karst aquifers by the professional community and the role that cavers have played over the past 40 years. Cavers with their detailed maps and their deep understanding of the layout of conduit systems can take credit for a substantial portion of the modern view of karst hydrology. The article does not claim to be a comprehensive review of karst hydrogeology as a whole. For more traditional and extensive reviews see White (1993, 1998, 2002, 2006).

Some Historical Perspective

Although the primary focus of this article is karst hydrology as it has evolved during the past 40 years, it is of interest to look much farther back to see how caves have figured in the precursor history. Summaries of these prescientific roots of hydrology may be found in Adams (1954) and LaMoreaux and Tanner (2001).

Ancient History

Because some of the earliest writings on the natural world come from Greece, a country that is largely karst, it is not surprising that springs and caves were strongly linked. Early Greek writers such as Plato and Aristotle incorporated caves as channel ways carrying water from the sea up into the mountains from which it emerged from springs to form rivers. Springs were of great importance as water sources in the ancient world and many were karst springs, fed by obvious cave passages. The ancient writers were also aware of a version of the hydrologic cycle, perhaps best said in Ecclesiastes (Chapter 1, verse 7). "All the rivers run into the sea; yet the sea is not full; unto the place from whence the rivers come, thither they return again." It was not, however, our contemporary hydrologic cycle in which water evaporates from the sea, drifts over land, and falls as rain. The means by which "thither they return again" were thought to be caves.

After the long hiatus of the Dark Ages, one of the most elaborate models for cavernous flow of groundwater was proposed by Athanasius Kircher in his *Mundus Subterraneus* in 1664. Kircher proposed that water from the sea moved through an elaborate system of conduits to discharge into large cavernous chambers in the hearts of mountains from which it emerged as springs at the heads of rivers. Kircher also postulated subterranean fires and when the feeder conduits passed near the fires, the water emerged as hot springs. Springs and underground rivers acquired a large literature prior to the extensive work that appeared in the late 1800s and early 1900s. See Shaw (1992), especially Chapters 13 and 14.

The Early European Views of Karst Aquifers

Two developments took place in Europe in the latter years of the 19th Century. One was the beginning of systematic cave exploration especially by Schmidl in Austria and Martel in France. The second was the emergence of geomorphology as a science. Geomorphology had two fathers – William Morris Davis in the United States and Albrecht Penck in Vienna, Austria. These two towering intellects laid the foundations of geomorphology and both had at least a passing interest in karst. They even participated in a joint excursion through the Adriatic karst in 1899 (Davis, 1901). Penck's influence on karst research was amplified by his student Jovan Cvijić with his 1893 *Das Karstphänomen*, although a sequence of circumstances greatly delayed final publication of his ideas (Cvijić, 1960). Another Penck disciple, Alfred Grund, was the primary contributor to one of the main European views of karst hydrology. Davis' influence on karst research remained minor until his classic interpretation of cave origins published many years later (Davis, 1930).

European thought on the behavior of water in karst aquifers divided into two distinct schools (Roglić, 1972). The karst groundwater school, championed by Grund (1903), was that sinking streams drained down into a central body of groundwater. The groundwater body had a water table that rose continuously from the sea into the hinterlands and was essentially stagnant. Underground streams were peripheral to the main water body. The opposing view was that water drained through the karst as independent rivers, flowing at different levels, and eventually draining through springs with no common groundwater. In many ways these were an essentially phreatic concept and an essentially vadose concept. The independent underground river concept was supported by those with the greatest experience with cave exploration and the observed behavior of cave rivers (von Knebel, 1906; Katzer, 1909; Martel, 1910). As is frequently the case in geological debates, both sides were partially correct. Later stream tracing results showed that many alpine karst regions with rushing underground rivers also contained a deeper and more slowly moving groundwater body (Zötl, 1961).

EARLY VIEWS OF KARST AQUIFERS IN THE UNITED STATES

Discussion of caves in the United States often begins with the Davis (1930) cave-origin paper. But, in fact, studies of water resources were well underway in the United States early in the 20th Century and many of these studies were of karst areas. There was Greene (1908) on southern Indiana, Matson (1909) on the Kentucky Blue Grass, Weller (1927) on the Mammoth Cave area, and Piper (1932) on the Cumberland Plateau of Tennessee. All of these reports recognized the role of joints and bedding-plane partings as permeability in otherwise impermeable massive limestones. All recognized the interrelationships of sinking streams, cave streams, and springs. In general, these papers presented a reasonable qualitative picture of the movement of groundwater in karst aquifers.

The hydrology of limestone terranes was recognized as a distinct subdivision of the rapidly growing science of groundwater hydrology (or hydrogeology) in Oscar Meinzer's classic book (Meinzer, 1942; Swinnerton, 1942). However, the Davis monograph recast the framework from one of sinking streams, caves, and springs to one in which caves were remnant features formed beneath old peneplains and only fortuitously re-excavated and used by contemporary drainage. Debate shifted to the vadose/phreatic mechanism for cave origin and there were fewer investigations from a hydrological perspective.

THE TRANSITIONAL PERIOD 1942–1966

J Harlan Bretz's (1942) monograph marked the end of the early period for both karst hydrology and cave-origin theory. The succeeding several decades, which, curiously, extend up to the appearance of the 25th anniversary volume of the National Speleological Society Bulletin, were a period of transition. Davies' (1966) own review of the earth sciences and speleology has little to say about karst hydrology. But, in fact, the dry period from 1942 to 1957 had ended and the modern period of karst research in general and karst hydrology in particular was well underway.

One of the transitional markers was Davies' (1960) demonstration that caves are graded to present or past local base levels. Other than it's implications for the theory of cave origin, this paper returned caves to their proper role in the hydrology of contemporary karst-drainage basins. In Europe, karst hydrology was high on the list of priorities for the International Hydrologic Decade, 1964–1974. Research shifted from qualitative descriptions of cave systems and karst aquifers to quantitative measurements on aquifer properties and groundwater movement (IASH, 1965). The change in approach was nicely described in Burdon and Papakis' (1963) *Handbook of Karst Hydrology*. Unfortunately, this exceedingly important document appeared only as a manual for a UN training course and never appeared as a more formal publication. As a contribution to the IHD, Stringfield and LeGrand (1969) prepared a comprehensive review of karst hydrology mainly in the United States.

It was at the beginning of the transitional period that the NSS and systematic cave exploration and survey got underway. By the end of the period, systematic cave data had been published for several states including California (Halliday, 1962), Illinois (Bretz and Harris, 1961), Indiana (Powell, 1961), Maryland (Davies, 1950), Missouri (Bretz, 1956), Pennsylvania (Stone, 1953), Tennessee (Barr, 1961), Texas (P.J. White, 1948), Virginia (Douglas, 1964), and West Virginia (Davies, 1949). Conditions were in place for a melding of the groundwater hydrologist's approach to karst aquifers and the caver's approach to karst aquifers. What has happened in the succeeding 40 years is the topic for the remainder of this review.

CAVE EXPLORATION AND SURVEY: A NEW PERSPECTIVE

Cave exploration in the old days was a straightforward business. Cavers went to areas where there were known caves, talked to farmers, hunters, and the good-old-boys hanging out at the general store, and with some luck were instructed as to where they could find new caves. Having hiked across the fields following "over yonder in that clump of trees," they would sometimes be rewarded with a nice new entrance yawning at the head of a wooded ravine. Exploration was a matter of poking through all of the accessible passages. Some would end in breakdown. Some were choked with sediments and some by flowstone. Regardless, all caves were thought of as ending. Some caves descended to flowing streams and some did not. Some caves were entered at spring mouths or at stream sinks. Others were entered high on the hillsides. Regardless, all caves were tallied separately. Cave catalogs and cave data bases listed as separate caves those that were clearly fragments of a once continuous master cave. Likewise, every passage that could be accessed through the same entrance was considered to be part of the same cave. A large cave might contain high level passages dating far back into the Pleistocene and also base level stream passages that are part of the contemporary drainage system. No matter, it was considered to be a single cave.

Sometime in the 1960s came the gradual recognition that caves in general do not end. Cave passages are fragments of conduits that once carried water from some recharge area, possibly a sinking stream, to an outlet at a spring. These once continuous conduits are broken up by processes of collapse, truncation by surface valleys, and by sediment in-filling. This gradual realization was not a documented discovery although Brucker (1966) formalized it as a way of splicing together the passage fragments that make up what was then the Flint Ridge Cave System. With this understanding, it became possible to consider individual caves as simply puzzle pieces of a larger master drainage system.

With the insight of continuous conduits, cave explorers could search for the missing pieces, either by digging, moving breakdown, sump diving within the cave or by excavating new entrances from the surface. Sometimes a long and persistent effort paid off with a map of an entire drainage basin. Over the past 40 years, a considerable number of examples have been documented. One example is the Mystery Cave – Rimstone River Cave complex in Perry County, Missouri (Fig. 1). Extensive exploration and survey have produced a detailed map of 40 km of mainly two south-north master stream passages along with many more kilometers of disconnected cave fragments (Walsh, 1988, 1989). Those who think such data are easy to obtain are advised to read Walsh's (2002) account of the actual history of the exploration and survey.

CAVE MAPS AND MAPPING

Perhaps the caver's greatest contribution to karst hydrology is their current "map as you go" philosophy. From the earliest days, cavers have prepared cave maps. The reason is simple. On the land surface, a view from a high ridge or an over flight in a small plane gives an excellent perspective of the landscape. However, one cannot see a cave. A caver can see only a small section of passage at any one time. Without mapping, cavers must depend on memory and have no way to accurately display the layout of the cave or to share their discoveries with others.

An accurate traverse line is important but so also is an accurate sketch. For geological or hydrological interpretation of cave maps, it is the accuracy of the sketching that is most useful. One of the early pioneers in precise renditions of cave passages was the late Bernard Smeltzer in Pennsylvania. One of the finest examples, drawn in 1951, is the Fleming Caves in Huntingdon County (Fig. 2). There is accurate floor detail, the walls are sketched with an artist's eye, and the cross sections show the relation of the cave to the structure of the bedrock. Other pioneers were Paul Johnson, Tex Yocum, Lang Brod, and their colleagues in the Missouri Cave Survey, whose outstanding maps began appearing in the early issues of *Missouri Speleology* in the late 1950s and early 1960s.

There have been great strides in the processing and display of cave survey data. Computer programs are available for compiling, plotting, and adjusting closure errors. Maps can be displayed electronically so that they can be expanded, contracted and rotated. Maps stored electronically can have embedded photographs or additional passage detail. Behind the computational magic, however, the primary data source remains the compass and tape measurements and the notebook sketches of the cavers patiently slogging their way through the cave, station by station. From the point of view of the hydrogeological use of cave maps, current concerns with cave conservation have an unfortunate side effect. Most of the early cave data bases, such as those referenced above, were public documents, many even public domain documents. As population has increased over the past 40 years, access to caves has become more limited at the same time that sport caving has become more popular. Cave maps and cave data bases have become proprietary information, often highly restricted. Hydrogeologic investigations that require access to extensive quantities of cave survey data also require investigators to establish confidence and good working relations with the caving community.

CAVE DIVING

The active conduit-drainage systems can often be accessed either from cave entrances at stream sinks or from cave entrances at spring mouths. Unfortunately, these accessed caves often terminate at sumps. As equipment and techniques for SCUBA diving have improved, many of these sumps have been penetrated to the great improvement of our understanding of conduit systems.

Ford and Ewers (1978) laid to rest the vadose/phreatic debate of the 1930s by showing that caves could form in any relation to the water table depending on the local geologic setting. One of the most common geologic settings was a bedding and fracture guided conduit that would, at

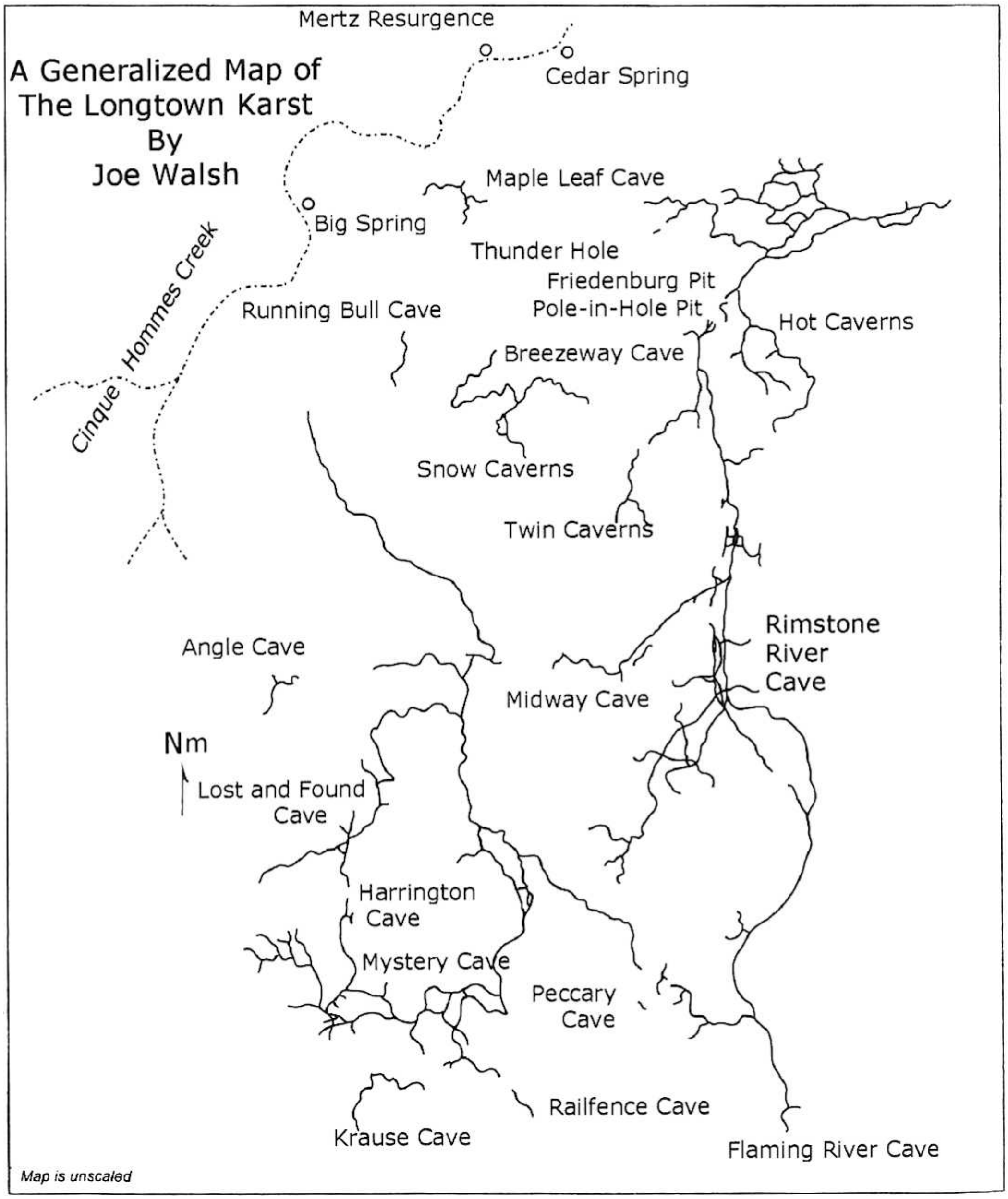

Figure 1. Stick map of Mystery Cave, Rimstone River Cave, and associated smaller caves in Perry County, Missouri. These collections of caves represent two master drainage lines carrying water north to Cinque Hommes Creek. From Walsh (2002).

base flow, consist of a sequence of air-filled, open-channel-flow cave segments interspersed with flooded, pipe-flow segments. Any segment that happened to have an entrance would appear as a stream cave sumped both upstream and downstream. A number of such conduits have been explored by divers and indeed, sumps are often relatively shallow, relatively short, and link segments of air-filled stream cave. Diving also shows the existence of deep conduits well below present day base levels.

An example of the value of diving as part of a hydrogeological investigation is Tytoona Cave, Blair County, Pennsylvania, now an NSS Cave Nature Preserve (Fig. 3). The entrance to Tytoona Cave, in a karst window, gives access to about 300 meters of open streamway. At the end is a sump, followed by a chamber, a second sump, a small chamber, a third sump, and finally, a long streamway ending in a fourth sump. From the resurgence end, at Arch Spring, there is immediately a deep sump, then a streamway ending in a deep sump which is likely the downstream end of the 4th sump in Tytoona Cave. The diver's sketch map here reveals both the undulating pipe/open channel flow system and also the presence of a deep system into which the present day drainage has collapsed.

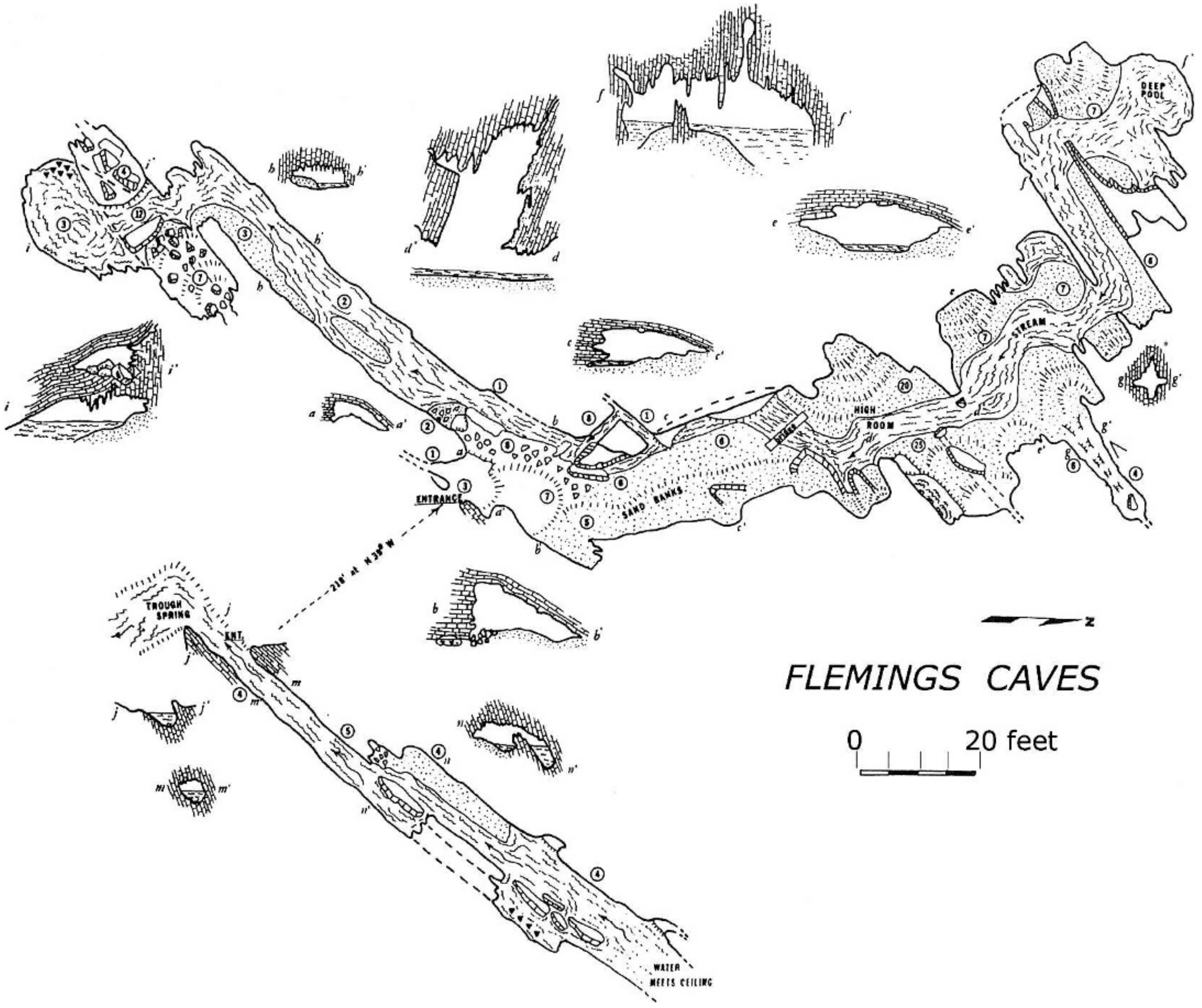

Figure 2. Map of Fleming Caves, Huntingdon County, Pennsylvania. A Bernard Smeltzer map illustrating the early presentation of geologic detail. Map from the files of the Pennsylvania Cave Survey.

Tracer Technology

The routes of underground streams from their surface sources to their emergence in springs have been traced by a variety of methods since the 19th Century. The original method was to add large quantities of dye, often tens or hundreds of kilograms, at the sink point and wait for colored water to appear at the spring. In addition to the necessity of having observers stationed at all possible rise points, springs and streams were often turned green or red to the great consternation of local citizens and the authorities. Although other tracers such as spores and salt brines are occasionally used, fluorescent dyes have remained the tracer of choice, although with many modern improvements.

The first major innovation was the invention of the charcoal dye receptor by J.R. Dunn (1957). Dunn discovered that activated coconut charcoal would effectively sorb dye from water and more importantly, would not release the dye as more water flushed over it. This meant that inexpensive charcoal packets could be placed in all suspected resurgences and collected at the investigator's convenience. The dye could be elutriated with an alcoholic solution of strong alkali and its presence determined by the color or by the fluorescence of the elutriate. Charcoal packets eliminated the need for continuous observation. The charcoal also accumulated dye as the pulse passed by, thus allowing smaller charges of dye to be used so that visual coloring of the resurgence is unnecessary.

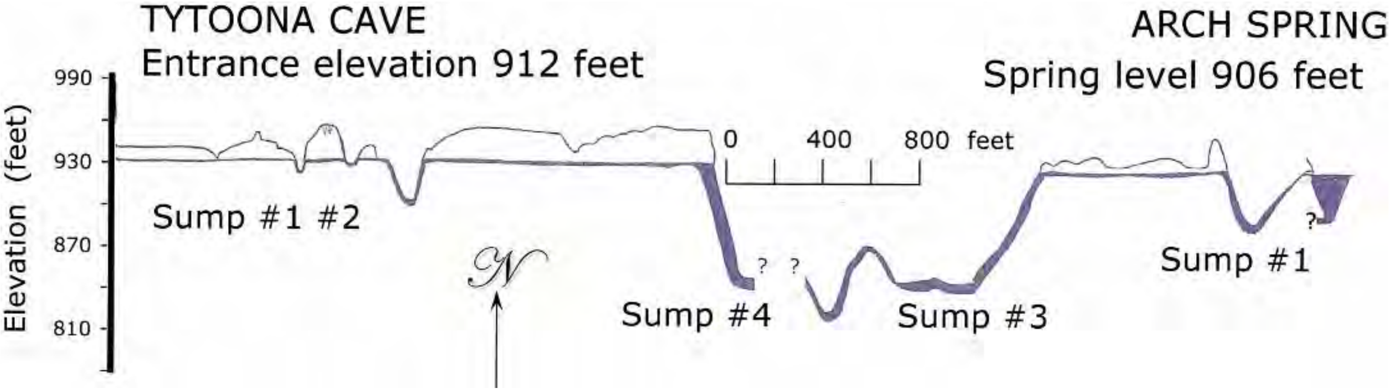

Figure 3. Profile of Tytoona Cave – Arch Spring, Blair County, Pennsylvania. Constructed from sketches by John Schweyen and other divers. Entrance and spring elevations by altimeter measurement.

The second major innovation was the use of quantitative fluorescence spectroscopy to identify dyes and determine dye concentrations. A great variety of dyes have been used for water tracing although only a few are routinely used (Table 1). Each has a characteristic fluorescence peak wavelength. By measuring the fluorescence spectrum instead of simply observing the color, multiple dyes can be distinguished at the same time. Fluorescence bands of organic dyes are broad and overlap, but because the line-shape is Gaussian, computer programs such as Peak-Fit can be used to separate the dye fluorescence bands and thus determine dye concentrations of each. Thus multiple injection points as well as multiple resurgence points can be tested.

A third major innovation was the introduction of quantitative tests using automatic water samplers. Because of the high sensitivity of modern spectrofluorophotometers, small concentrations of dye can be measured directly from water samples rather than from charcoal elutriates. By collecting water samples at regular time intervals and analyzing dye concentrations in each, a dye breakthrough curve can be constructed that displays the dye travel time and sometimes gives information on the geometry of the flow path (Jones, 1984).

Dye tracing is one of the most powerful tools in the karst hydrogeologist's toolkit. Following the introduction of charcoal dye receptors, the drainage patterns for many underground drainage systems were worked out. The Swago Creek basin in West Virginia (Zotter, 1963) was an early example. Contaminant transport over distances of tens of kilometers was demonstrated (Aley, 1972). With the increased sensitivity of modern spectrofluorophotometers, dye detection limits reached the part per trillion level. With high sensitivity came the necessity for careful protocols for dye injection and recovery to avoid cross-contamination and misleading results. Use of dye tracing in legal and regulatory issues forced more careful attention to quality control and chain-of-custody issues. Dye toxicity became an issue fairly early (Smart and Laidlaw. 1977; Smart, 1984) and some otherwise useful dyes were rejected.

Modern dye tracing requires a well-equipped laboratory and a great deal of practical experience. But in spite of the elaborate precautions needed and the equipment required for analysis, the details of the procedures are described mainly in reports and private publications (Alexander and Quinlan, 1992; Field, 1999; Aley, 2002). European practice, however, is laid out in detail by Käss (1998).

The Conceptual Description of Karst Aquifers

At the time of the 25th anniversary Bulletin, karst hydrology was pretty well divided into two camps. There

Table 1. Some commonly used tracer dyes for water tracing.

		Fluorescence Wavelength (nm)[a]	
Common Name	Color Index	Elutriate	Water
Sodium fluoresceine (uranine)	Acid Yellow 73	515.5	508
Eosin	Acid Red 87	542	535
Rhodamine WT	Acid Red 388	568.5	576
Sulpho Rhodamine B	Acid Red 52	576.5	585
Fluorescent Brightener 351	Tinopal CBS-X[b]	398	397

Data courtesy of Crawford Hydrology Laboratory, Western Kentucky University.

[a] Fluorescence wavelengths (intensity) vary significantly with differing instruments and many of the listed values will be found to be in variance with reported fluorescence wavelengths in other publications (e.g., fluorescence wavelength for sodium fluorescein in water is typically reported to be 512 nm (the editor).

[b] Common Name for Tinopal CBS-X provided by the editor.

were the professional hydrogeologists, well educated in the intricate mathematical details of groundwater behavior in porous media and there were the cavers, not yet quite ready to call themselves hydrogeologists. The professionals drilled wells, ran pump tests, and made calculations. Sometimes, as when they drilled into a highly fractured dolomite, they got reasonable results. Sometimes, as when they drilled into a water-bearing conduit, their results were nonsense. There was a considerable effort (White and Schmidt, 1966) to convince the professional community that underground streams had something to do with hydrology. Cavers were accumulating maps and data on stream sinks, springs, and underground-drainage patterns, but generally didn't pay much attention to the mass of rock that surrounded the caves. One of the most important accomplishments of the past 40 years has been merging these divergent points of view.

The Ground-Water Basin Concept

The framework for discussion of groundwater is the aquifer. Aquifers are characterized by the distribution and anisotropy of hydraulic conductivity among the various rock units that make up the aquifer. Aquifers often have well-defined thicknesses, but rarely is one concerned with the area of an aquifer. The framework for discussion of surface water is the drainage basin. Drainage basins have well-defined areas and a certain pattern of stream channels. For geologic settings other than karst, groundwater concepts and surface-water concepts rarely intersect. In karst they are completely entangled.

Just as the notion of reconstructing conduits from observable caves crept into karst thinking without much notice, so also did the concept of the groundwater basin. At some time it began to occur to karst researchers that it was more profitable to think of karst hydrology in terms of drainage basins with both surface and subsurface components rather than thinking of a karst aquifer. For the most part, it was a concept introduced by cavers because it provided guidance about where to search for new caves. Certainly the concept was established when Jones (1973) wrote his report on the karst-drainage basins in Greenbrier County, West Virginia. Jones was one of the first to use extensive dye tracing to map out the entire drainage system and subdivide spring catchments into distinct groundwater basins. An even more elaborate groundwater basin map was prepared by Quinlan and Ray (1981; Quinlan and Ewers, 1989) for the Mammoth Cave area in southcentral Kentucky. Underground drainage in southcentral Kentucky flows either northwest to the Green River or southwest to the Barren River. Quinlan and Ray used cave data, geologic data, more than 500 dye traces, and 1400 well observations to subdivide the Mammoth Cave area into 28 groundwater basins, show the main flow paths, and contour the water table. Many groundwater basins have now been mapped, especially in West Virginia (Jones, 1997) and in the series of drainage-basin maps for Kentucky compiled by J.A. Ray and J.C. Currens.

If the groundwater basin divide can be accurately established, the basin area can be measured. Precipitation within the basin and discharge from the basin can both be measured. Essentially, the existence of a basin boundary puts a mass-balance constraint on water moving through the system. The various statistics developed for surface-water basins can be applied to groundwater basins. If the basin of interest discharges at a spring, the spring can be gauged and a record of discharge established over long periods of time. From these data can be calculated the mean flow either over one water year or over the entire period of record, the mean base flow, and the mean annual peak flow (known as the annual flood for surface basins). The normalized mean base flow is the base flow divided by the basin area. This quantity has been found to be unusually small for karstic basins compared with other surface water basins (E.L. White, 1977) because of the low hydraulic resistance of the conduit system which allows the aquifer to drain during period of low recharge. If a numerical value for the normalized mean base flow can be established for a given region, the basin areas of other springs can be calculated by simply multiplying the measured mean base flow of the spring of interest by the normalized mean base flow for the region. A comparison of various basins by Quinlan and Ray (1995) showed that this simple calculation works well if the local hydrogeology is taken into account. The calculation is a powerful check on spring ground basin areas estimated by other methods.

The boundaries of surface water basins are usually clearly defined by topographic highs and can be easily drawn from topographic maps. The boundaries of groundwater basins are more problematic. The boundaries of contributing sinking-stream basins can be delineated, but boundaries through the karst must be inferred from known stream caves, from tracer tests, from the local geology and from water-table maps constructed from depth-to-water measurements in wells. Unlike surface-basin boundaries, groundwater basin boundaries may shift with increasing or decreasing discharge. Generally, high gradient basins have the most sharply defined boundaries whereas low-gradient basins may have fuzzy boundaries. Tracer tests near the basin boundaries may indicate flow into several adjacent basins. Piracy routes and high-discharge spill-over routes are also common.

Porosity and Permeability

The treatment of a karst system as a groundwater basin leads to certain insights. Treatment of the karst system as an aquifer leads to other insights. These two conceptual frameworks have existed comfortably side-by-side for the 40 year period of this review. The most fundamental properties of an aquifer are its porosity and permeability. It was recognized early on that the permeability (or porosity) of karst aquifers has three components: the matrix permeability of the bedrock itself, the permeability produced by fractures (joints, joint swarms, bedding-plane partings, and some faults), and the permeability due to conduits. This has now been somewhat formalized and researchers speak of the triple permeability model (Worthington, 1999).

The matrix hydraulic conductivities of most compacted limestones are in the range of 10^{-9} – 10^{-11} m s^{-1} and for most practical purposes can be ignored. The exceptions are the young limestones, especially those on carbonate platforms, that have never undergone deep burial or been subject to orogenic forces. For these, the matrix permeabilities are in the range of 10^{-6} to 10^{-7} m s^{-1} and matrix flow is an important component. For information on the hydrogeology of young limestones see Martin et al. (2002). Matrix flow in porous limestones is Darcian and not intrinsically different from flow in other porous media.

Limestones and dolomites are brittle rocks and subject to fracturing by tectonic forces and by stress relief caused by either erosion or glacier unloading. Fracture flow occurs in other brittle rocks such as sandstones and granites. Groundwater in fractures is a major component of the stored water and is the reason that wells drilled into limestone often produce useful quantities of water without the well having penetrated a conduit. Fracture flow is a major emphasis in contemporary hydrological research as attempts are made to model fractures with irregular apertures and also to model fracture networks.

The practical boundary between fracture permeability and conduit permeability occurs at an aperture of about one centimeter. In groundwater basins with typical gradients, a one-centimeter aperture corresponds to the onset of turbulence, to velocities sufficient to begin to transport clastic sediment, and to an increase in the rate of dissolution of the carbonate rock. Caves as conduit fragments, can be mapped by human explorers down to an aperture of about 0.5 m. Between 0.01 m and 0.5 m are solution openings that are too small for direct mapping but large enough to behave hydraulically as conduits. Very little is known about the conduit porosity in this size range. Some insight into the flow behavior can be obtained from the distribution of travel times obtained from tracer tests (Fig. 4). The distribution is log-normal with a considerable tail of the low velocity side. These measurements may indicate tracer dyes moving through small and hence low velocity pathways.

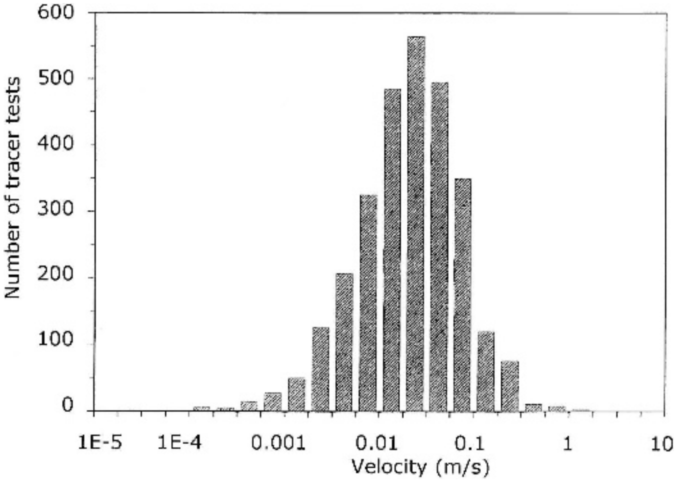

Figure 4. Distribution of travel velocities as determined from 2877 tracer tests between sinking streams and springs. From Worthington et al. (2000).

Importance of the Geologic Framework

The flow of water through karst aquifers is determined by relatively simple principles of fluid mechanics and the interaction of the water with the carbonate bedrock by relatively simple principles of physical chemistry. As in most of the Earth sciences, the devil is in the details. One of those details that was widely overlooked in the early development of karst hydrology was the geologic setting. What karstic rocks are available and how are they arranged with respect to other rocks? Any karst groundwater basin is a work in progress. It evolved from some precursor basin to its present configuration and the present configuration will evolve further into the future. The hydrology of the basin is controlled to a large extent by the underlying stratigraphy and structure.

The geological variables that distinguish one karst drainage basin from another include:

- Thickness of karstic rock units
- Placement of karstic rocks with respect to non-karstic rocks and location within drainage basin
- Bulk lithology: limestone, dolomite or gypsum
- Detailed lithology: micritic limestone, crystalline limestone, shaley limestone
- Stratigraphic homogeneity: bedding thickness, lithologic variations, shale or sandstone confining layers
- Large scale structure: folds, faults
- Small scale structures: density and connectivity of vertical joints, bedding plane partings, few master fractures vs. many smaller fractures

A great variety of karst drainage basins is possible depending on the listed parameters. A variety of placements of karstic rocks with respect to other strata were described early in the review period (White, 1969) and these possibilities have been embellished by others. Most of the karst of eastern United States is developed in at most a few hundred meters of limestone producing fluviokarst landscapes. In locations such as the Cumberland Plateau or the Ozark Plateau, the combination of low dip, limestones located under valley floors and on valley walls, and a protective sandstone and shale caprock on the plateau surface provides ideal conditions for the development of long caves and vertical shafts. Other locations such as the folded Appalachians, with carbonate rocks mainly in the valley floors, produce strike-oriented caves and more limited drainage basins.

The most recent calculations on cave development (Dreybrodt et al., 2005) show that the patterns of conduit-drainage systems are determined during the initiation phase of cave development. At this time, the system is highly sensitive to details of the fracture pattern and to the presence of confining layers. A few centimeters of shale interbedded in the limestone is sufficient to deflect the initial pathway that will later become a cave passage.

A great deal of the literature on karst hydrology consists of studies showing how a particular drainage basin developed in response to its specific geologic setting.

Quantitative Hydrology: Spring Hydrographs

The flow of karst springs is often variable, rising and falling in response to storms. Some springs become muddy during storm flow. Springs can be gauged to produce a continuous recording of discharge as a function of time, a curve known as a hydrograph. The water flowing from a spring represents a composite of all inputs and flow systems upstream in the basin. Use of spring hydrographs to characterize karst aquifers developed early in Europe (Burdon and Papakis, 1963; Milvanović, 1981) and has been developed to a considerable mathematical elegance in France (Mangin, 1984; Labat et al., 2001). Only in the 1980s and later were spring hydrographs extensively used in the United States. In part, this was not due to ignorance but to the fact that most karst hydrology research was being conducted by academics and cavers on shoe-string budgets. Continuous stage recording was desirable but not financially achievable.

Examination of a large number of spring discharge records reveals a range of responses on a scale between two end-members. There are karst groundwater basins with very rapid response times so that the spring hydrograph has peaks corresponding to each individual storm. The other extreme are springs that exhibit essentially no response at all to individual storms and at best rise and fall a little in response to wet and dry seasons. In between are hydrographs with varying degrees of response (Fig. 5).

The aquifer characteristics that control hydrograph pattern are not completely understood. The very flashy response with individual storm peaks requires a small open aquifer with an overall transport time from recharge to spring less that the spacing between storms. Less well-resolved hydrographs can arise from aquifers sufficiently large such that individual storm inputs are damped before they reach the spring. Hydrographs with little storm detail can arise from aquifers in which most of the recharge is through the epikarst which tends to hold water in temporary storage. Springs fed by fracture flow will have less detail in their hydrographs, but a flat hydrograph is not evidence for the absence of conduits. The big Florida springs have almost no detail in their hydrographs but most are known to be fed by very large water-filled conduits.

Sudden intense storms that follow several weeks without rain are the best probes of aquifer behavior. Figure 6 illustrates schematically the parameters that can be measured. The lag time between the storm and the time that storm water appears at the spring is a measure of travel time only if the conduit is an open streamway from sink to spring. If all or a portion of the conduit is flooded, rising head at the upstream end will cause water to discharge from the downstream end responding to a pressure pulse that travels through the system at the speed of sound. The time between the storm and increased flow at the spring can be very short. The ratio of the maximum flow to base flow is a measure of the flashiness of the aquifer, although this ratio also depends on storm intensity. The recession limb of the hydrograph can usually be fitted with an exponential curve (or several). The fitting parameter for the exponential has been called the exhaustion coefficient and has been used (Burdon and Papakis, 1963) to calculate the volume of water held in dynamic storage. The inverse of the exhaustion coefficient has units of time and can be taken as the response time of the aquifer.

Chemical Hydrology

On of the most important accomplishments of the 40 year period was to work out the chemistry of carbonate dissolution in considerable detail. The equilibrium chemistry of both dissolution and precipitation came first and is described in detail in several textbooks (White, 1988; Langmuir, 1997). The equally important kinetics of dissolution and precipitation rates, although more complicated and not so solidly established, has been largely worked out. The dissolution rates of carbonate minerals are important to many areas of science, resulting in a huge literature. Much of it has been reviewed by Morse and Arvidson (2002). Dissolution kinetics combined with flow hydraulics forms the basis for current theories of speleogenesis. A major contributor has been Wolfgang Dreybrodt and his students and collaborators at the University of Bremen in Germany (Dreybrodt et al., 2005). Studies of speleogenetic processes can be considered aquifer modeling along the time axis by calculating the evolution of the conduit permeability through a sequence of initiation, enlargement, stagnation, and decay phases. Although much as been accomplished (Klimchouk et al., 2000), this subject is outside of the scope of the present review.

Although many analyses of karst waters had been obtained, about the best that could be done with them was to plot the concentration of dissolved carbonates on the calculated calcite solubility curve, which then gave some indication of whether the water sample was saturated, supersaturated, or undersaturated (aggressive) with respect to calcite. In the early 1970s there were a number of efforts

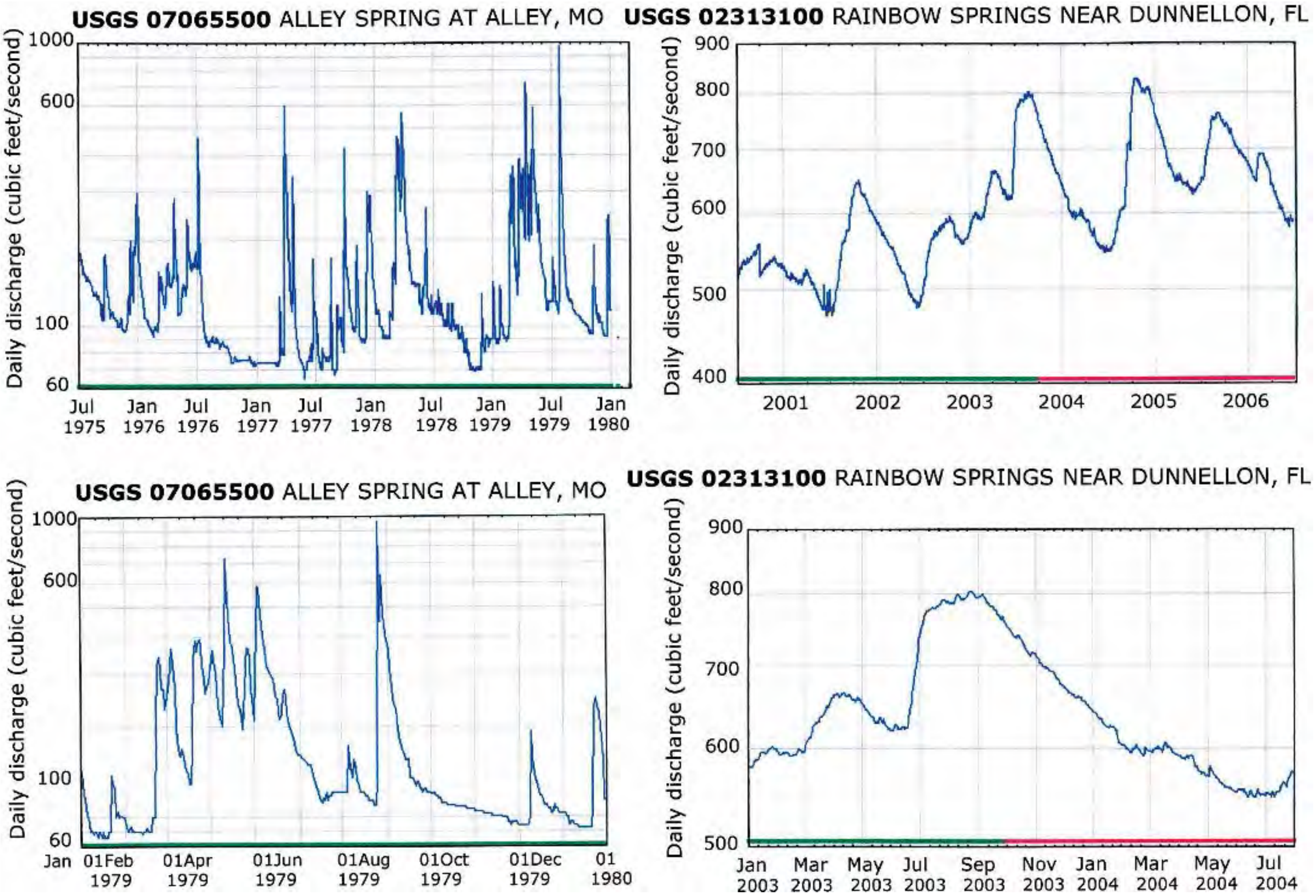

Figure 5. Some representative hydrographs for karst springs. These are selected from U.S. Geological Survey surface water records which are available online (http://waterdata.usgs.gov). Alley Spring is representative of the flashy, fast-response springs where individual storm events appear on the hydrograph. Rainbow Spring displays an annual rainy season/dry season response but does not respond to individual storms.

to more accurately measure the saturation state of cave waters. Most successful of these was the introduction of the saturation index and also the calculated CO_2 partial pressure (Langmuir, 1971). These calculations and other aspects of aqueous chemistry quickly evolved into a collection of computer programs that have continued to evolve down to the present time (Jenne, 1979; Melchior and Bassett, 1990).

In the late 1960s and early 1970s there began studies of spring-water chemistry in which the springs were sampled at regular intervals, typically one or two weeks (Pitty, 1968; Shuster and White, 1971). The dissolved carbonate content of some springs remains essentially constant through the year irrespective of the season or the influence of storm flow. Other springs exhibit a widely fluctuating chemistry and also a fluctuating temperature. There ensued a debate concerning the cause of the chemical fluctuations, with degree of conduit development, percentage of sinking-stream recharge, and flow-through time being offered. Then came the results of Dreiss (1989) who measured a continuous record of the chemistry of Meramec Spring, Missouri. It turned out that the fluctuations observed in previous studies were due to a small number of sampling points extracted from a continuous curve (now known as a chemograph). Chemographs of carbonate species typically are the inverse of hydrographs and represent the dilution of the resident water in the aquifer by injected storm water (Fig. 6). Since their first introduction, chemographs has been constructed for many chemical parameters including groundwater contaminants.

The concentration of dissolved carbonate species in karst aquifers is proportional to the specific conductance of the water. Because specific conductance is easy to measure and easy to record on a data logger, such measurements allow easy determination of carbonate chemographs. Many such have been measured and, in combination with hydrographs, provide additional information on aquifer response. What is observed is that there is a sharp rise in the hydrograph in response to storms. However, there may or may not be an equivalent dip in the chemograph. If the

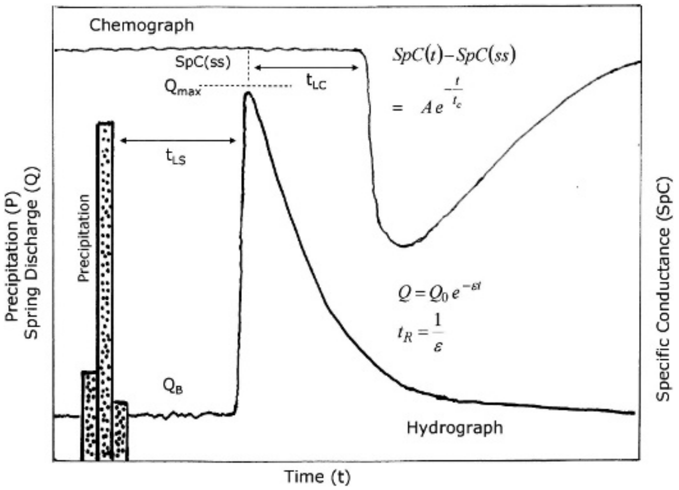

Figure 6. Schematic hydrograph and chemograph for a karst spring showing various measurable parameters. Q_B = base flow. Q_{max} = peak flow for the storm hydrograph. Two time lags are shown: t_{LS} for the lag between the storm and the rising limb of the hydrograph and t_{LC} for the lag between the rising limb of the storm hydrograph and the dip in the chemograph. Both the recession limb of the hydrograph and the recovery limb of the chemograph can be fitted with the functions shown.

rising hydrograph and falling chemograph are coincident, it indicates that the conduit is an open streamway and the rising hydrograph marks the arrival of storm water at the spring. In other cases, there is a delay between the rising limb of the hydrograph and the falling limb of the chemograph. This delay, along with the spring discharge, is a measure of the volume of water pushed out of flooded conduits by the storm pulse (Ryan and Meiman, 1996).

Can Karst Aquifers Be Modeled?

At the end of the review period, much contemporary research on karst hydrogeology consists of attempts to construct a useful, perhaps even valid, general model for karst aquifers. The object of any groundwater model is to reduce the recharge, storage, and flow hydraulics of an aquifer to a computer program. With an accurate model, one should be able to calculate well yields and distribution of hydrostatic heads within the aquifer, as well as the response of the aquifer to varying recharge and to extraction of water for water supply. For a karst aquifer, an accurate model also should be able to reproduce the expected spring hydrographs in response to a specified precipitation event. Much karst hydrological research over the past several decades has been efforts to construct such a model. Results have been decidedly mixed. Summaries of some of the attempted approaches may be found in Jeannin and Sauter (1998) and Palmer et al. (1999).

The guiding parameter for any groundwater model is the hydraulic conductivity. The hydraulic conductivity can be anisotropic and different values can be used for different rock formations, but it should be constant within these constraints. One of the most important difficulties in modeling karst aquifers is that the hydraulic conductivity is scale dependent. It was pointed out by Sauter (1991) and Quinlan et al. (1992) that hydraulic conductivities for highly karstic aquifers can vary over 8 orders of magnitude depending on the scale of measurement (Fig. 7). In an aquifer with this range in values over short distances, any attempt to reduce the aquifer to a single value of hydraulic conductivity can best be described as nonsense.

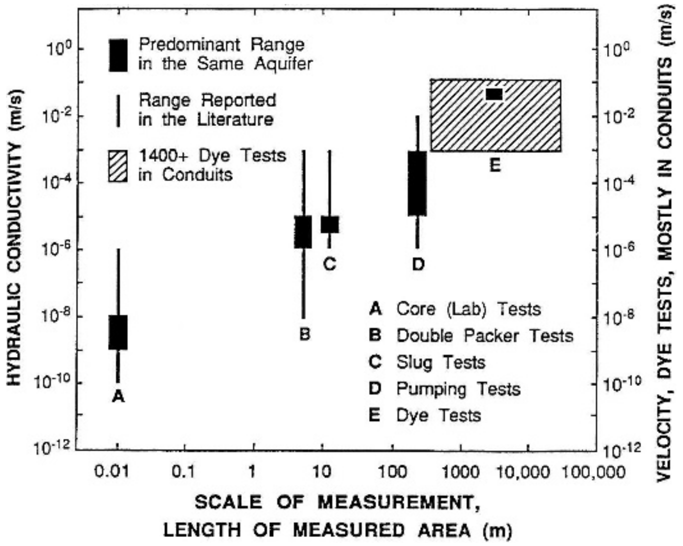

Figure 7. Dependence of hydraulic conductivity on the scale of measurement. From Quinlan et al. (1992).

Without going into very much detail, the main approaches to karst-aquifer modeling are summarized below. Only a few key references are given. This subject is beginning to develop a very large literature.

Equivalent Porous Media Models

Standard porous-media models such as the USGS MODFLOW program assume that at large enough scales, the heterogeneities of the karst aquifer are smoothed out and can be represented by an average hydraulic conductivity. Scanlon et al. (2003) had some success in applying this type of model to the Edwards Aquifer in Texas. Equivalent porous media models work best for aquifers in which the karstic-flow paths are dispersed and consist mainly of solutionally-widened fractures. They work least well for aquifers with well developed conduit systems, particularly those with large inputs of allogenic recharge.

Pipe Flow Models

Equivalent porous-media models ignore the conduit permeability and its localized turbulent flows. Pipe-flow models focus entirely on the conduit system. Pipe-flow models treat the conduit system as a network of pipes subject to the usual laws of fluid mechanics. The drawback of the pipe flow models is that conduits are not exactly pipes. They have varying cross sections, complicated interconnections, and are often further modified by breakdown and sediment infillings. Much detail about conduit pattern is needed. However, calculations of travel times, head losses, and discharges for known conduit systems have been generally successful (Halihan and Wicks, 1998; Jeannin, 2001).

COUPLED CONTINUUM/PIPE-FLOW MODELS

Eventually, karst-aquifer modeling must face the reality of the combined matrix, fracture, and conduit components of the permeability. The conduit system is strongly coupled to surface water through sinking streams and closed depressions and so has a very dynamic response to storms. The fracture and matrix systems receive most of their recharge through the epikarst and have a slower response. A dominant component of the total flow system is the exchange flow between the conduits and the surrounding fractured matrix. During storm flow, heads in the conduit system rise rapidly and water is forced into the surrounding fractures. After the storm flow recedes, the conduit system drains rapidly, heads reverse, and the water stored in the fractures drains into the conduits.

Models have been constructed in which the fracture and matrix system is described as a continuum with Darcy flow. The conduits are put in by hand and described by pipe-flow models. There is an exchange term that describes the influx and outflux of water between the fracture system and the conduits. This model was developed for the Gallus Spring in southern Germany (Sauter, 1992). This model worked well in the sense that it accurately reproduced the storm hydrographs measured at the spring. The drawback is that the conduits must be put in by hand. Tracer studies and cave exploration must supplement the strictly model calculation. Continued development of this approach to modeling has been very promising (Bauer et al., 2003; Liedl et al., 2003).

INPUT – OUTPUT MODELS

All of the modeling approaches described above require considerable knowledge of the aquifer – the geometry of the conduit system, the hydraulic conductivities of the fracture and matrix systems, and any geologic-boundary conditions. In general, the more pre-knowledge available, the more accurate the model. Of course, if all available knowledge is used to construct the model, there may be nothing left for the model to calculate. The diametrically opposite approach is to treat the aquifer as a black box and assume nothing about its internal properties. Instead, models are built from inputs and outputs, both of which can be measured directly. These models make use of linear-systems theory as pioneered by Dreiss (1982, 1989) with more recent applications described by Wicks and Hoke (1999). The idea is to use measured input and output data to construct a kernel function (the black box) which will connect all other relations between input and output.

CONCLUSIONS

In the 40 years since the 25th anniversary Bulletin, knowledge of karst hydrology has made giant forward strides. By borrowing concepts from both groundwater hydrology and surface-water hydrology, an excellent conceptual model for karst aquifers has been developed. There is good understanding of the physical and chemical processes that take place in karst aquifers. The current cutting edge is the development of a reasonable and accurate model to describe the flow behavior within the aquifer. Although there has been some success, a complete model has yet to be obtained. However, the eventual construction of such a model does not seem as remote as it did only a few years ago.

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George Crothers, P. Willey, and Patty Jo Watson – Cave archaeology and the NSS: 1941–2006. *Journal of Cave and Karst Studies,* v. 69, no. 1, p. 27–34.

CAVE ARCHAEOLOGY AND THE NSS: 1941–2006

George Crothers[1], P. Willey[2], and Patty Jo Watson[3]

Abstract: Like most other branches of speleology, cave archaeology in the U.S. grew and developed significantly during the mid to late twentieth century. Originally viewed as marginal to mainstream Americanist archaeology, pursuit of prehistoric and historic archaeology underground is now widely accepted as making valuable contributions to knowledge of human past. The National Speleological Society played a central role in that development and continues to do so. We outline the establishment and growth of cave archaeology in North America, with special emphasis on relations between the NSS and archaeology performed in dark zone, deep cave interiors.

Introduction

The NSS has directly participated in cave archaeology through cooperation, education, and conservation. Members of the Society have made notable contributions to the science by reporting the location of archaeological sites, participating in their investigation, and by equipping scientists with the techniques and technology needed to work safely in the cave environment (Damon, 1991, p. 283).

Cave archaeology was a central NSS concern from the first days of the Society's existence. There was an Archaeology Committee as well as Committees on Membership, Grottos, Records, Publications, Photography, Exploration, Mapping, and Publicity at least as early as 1948 (Damon, 1991, p. 196). At the second Annual Meeting of the NSS in 1945 (the first such meeting was in 1941; the three subsequent meetings were cancelled because of World War II), a featured speaker was Frank Hibben talking about his archaeological work in Sandia Cave, New Mexico, and about putatively pre-Folsom artifacts from that site. A few years later, Hibben was the banquet speaker again at the 1953 NSS convention, presenting a lecture entitled "Ancient Cave Life in the Southwest."

Archaeologists were also included on the NSS award lists during the 1950s. Emil Haury (1951), Henri Breuil (1955), and Carl Miller (1957) all received Honorary Membership in the NSS for their work in cave archaeology: Haury for his Ventana Cave, Arizona, research, Breuil for his research on Paleolithic painted caves in France, and Miller for his excavations in Russell Cave, Alabama.

According to brief summaries in Damon (1991), papers on archaeological topics were often presented in the annual convention sessions. Specific mention of such papers is made in passing for the 1949, 1952, 1953, 1954, and 1956 conventions. In 1958, Carl Miller as the banquet speaker described his archaeological work at Russell Cave showing movies made there by the National Geographic Society. At the 1970 convention, some of Russell Trall Neville's silent movies filmed in various caves (including Salts Cave, Kentucky) were shown. The NSS still owns copies of these Neville films, which were made during the 1920s and 1930s by "the Caveman," as Neville was often called.

Despite interest in cave archaeology within the NSS governance and some portion of the membership during the first few decades after the organization was formed, systematic, long-term archaeological research by professional archaeologists in the dark zones of big caves in the Americas did not get underway until the 1960s. There are probably several reasons for this, but primary among them is the difference between rock shelter archaeology and archaeology conducted in subterranean spaces never illuminated by natural light. Research in rock shelters has been a normal part of field archaeology since the earliest days of the discipline everywhere it was practiced, but the only aspect of cave archaeology widely recognized before the 1980s was documentation of Upper Paleolithic paintings in southwestern Europe. (And, in fact, the authenticity of those dark-zone paintings was established only after a long period of heated debate beginning in the late 1800s and continuing well into the early twentieth century.) Most archaeologists specializing in the early culture history of the Americas did not think that cave dark zones, if they thought about them at all, were places frequented by or even known to ancient human groups. Therefore, cave interiors were outside the research realm of mainstream, mid-twentieth century Americanist archaeology.

Nevertheless, as the NSS and affiliated or associated organizations, such as state and regional surveys (e.g., the Tennessee Cave Survey) and voluntary but formally constituted research groups (e.g., the Association for Mexican Cave Studies and the Cave Research Foundation) grew and proliferated, cavers began making archaeological, biological, geological, and paleontological discoveries that drew increasing numbers of non-caver scientists into the underground world.

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[1] Department of Anthropology, University of Kentucky, Lexington, KY 40506 USA, george.crothers@uky.edu

[2] Department of Anthropology, California State University-Chico, Chico, CA 95929 USA, pwilley@csuchico.edu.

[3] 2870 Solterra Lane, Missoula, MT 59803 USA, pjwatson@artsci.wustl.edu.

A SHORT HISTORY OF DARK-ZONE CAVE ARCHAEOLOGY IN THE UNITED STATES

Because our focus here is on cave archaeology in subterranean spaces with extensive dark zones, we maintain a distinction between archaeology in rock shelters and small caves with no true dark zones, and archaeological research in the dark zones of deep cave interiors. The distinction merits emphasis because rock shelters are so often referred to as caves, and because

> In the most fundamental sense, archaeology in caves is simply archaeology, with all the characteristics of field archaeology done anywhere . . .. But, of course, archaeology underground is different in one significant detail from archaeology done in other terrestrial locales: archaeology done inside a cave interior means archeology done in the dark. Adequate lighting is a problem for every single individual at every moment (Watson, 1998, p. 5; see also Watson, 2001).

Moreover, so far as we know, no ancient people ever actually inhabited cave dark zones, although there is ample evidence that they often explored them, quarried them, and/or used them as storage locales, depositories for the dead or places to contact the spirit world. Hence, archaeologically speaking, cultural deposits in deep cave contexts are usually special purpose sites, secular or sacred or both. Moreover, in dry caves, which make up a large proportion of dark zone sites, preservation of anything and everything left in a specific underground location is virtually complete no matter how delicate or how old or young it may be. This means that the basic techniques used in aboveground sites (including rock shelters and deposits at the mouths of large or small caves) for identifying relative ages and cultural sequences can seldom be applied underground. Radiocarbon or other archaeometric means of dating (all of which are rather expensive) must be secured for individual items to obtain the basic chronological information that all archaeologists require: how old are these remains?

Technical problems of the sort just indicated may help explain the marginal position of cave archaeology in the U.S. before the 1980s, but in fact any and all cave sciences were generally regarded as rather peripheral endeavors until the latter part of the twentieth century (e.g., White, 2003).

THE BEGINNINGS OF SYSTEMATIC CAVE ARCHAEOLOGY: 1890–1960

In the late eighteenth and early nineteenth centuries, when Euroamericans began exploring large, dry caves in the eastern U.S., such as Mammoth and Salts caves in Kentucky and Big Bone and Hubbards caves in Tennessee, they noted that prehistoric people had preceded them in many instances. Much of the Euroamerican exploration was driven by the saltpeter mining business, especially during the War of 1812 and on a smaller scale during the American Revolution. Archaeological remains preserved in these dry caves became antiquarian curiosities, especially the desiccated or mummified bodies of prehistoric Indians found in remote passages or unearthed during nitrate mining (George, 1990).

Stories of these discoveries quickly spread in print and in folklore, with numerous artifacts and a few of the mummies coming to rest in museums. While these discoveries generated further interest in caves and helped build a fledgling cave tourist business following the War of 1812, archaeology as a discipline did not develop as a scientific field until the late nineteenth and early twentieth centuries.

Beginning in 1858, William Pengelley's systematic excavation of archaeological and paleontological deposits at Brixham Cave and Kent's Cavern in England was a revolutionary advance in archaeological recording techniques, and helped prove the co-existence of humans and extinct Pleistocene animals in Europe by demonstrating their co-occurrence in the same geological deposits (see McFarlane and Lundberg, 2005). A young archaeologist, Henry Mercer, used these new techniques in America in an attempt to answer a similar question: the antiquity of humans in the New World (e.g., Mercer, 1896, 1897, 1975). While Mercer never successfully identified human remains or artifacts of human manufacture in the same stratigraphic layer with Pleistocene remains, he systematically sought out cave sites from eastern North America to the Yucatan, including dark-zone deposits, in what was one of the first formally scientific archaeological research programs in the Americas.

A later example of systematic work in dark-zone cave archaeology was that of Alonzo Pond. An archaeologist employed by the National Park Service, Pond was sent to Mammoth Cave by the NPS Chief Historian in 1935 to investigate a desiccated body discovered by two cave guides. The body of this prehistoric Indian was found on a ledge some two miles into the dark zone from the natural entrance. The ancient caver had been crushed to death by a large breakdown block he had apparently undermined while digging through crystal-bearing sediment underlying it. Most of Pond's work in the cave was to oversee raising the multi-ton boulder and removing the body, but he also collected numerous artifacts from other locales in the cave and made observations on the nature of prehistoric mining activity there (Pond, 1937).

CAVE ARCHAEOLOGY COMES OF AGE: 1960–1970

Interest in the archaeology of Mammoth Cave accelerated in the 1960s, as reflected in popular publications by Douglas Schwartz (1960, 1965) and Robert Hall (1967). The Cave Research Foundation (CRF) also began long-term archaeological work in the Mammoth Cave area at this time. The CRF Archeological Project, directed by Patty Jo Watson, began working in Salts Cave (Watson, 1969a), then in Mammoth and other smaller caves in and near Mammoth Cave National Park (Watson, 1974).

The CRF Archeological Project marks the beginning of more systematic integration of the caving community into scientific archaeological work. Although CRF was organized as a private non-profit foundation distinct from the National Speleological Society in order to conduct research in National Park Service managed caves, most of its members are also members of the NSS. The CRF Archeological Project also was the beginning of concerted efforts to bring dark-zone cave archaeology into the mainstream of scientific archaeological research and publication in the U.S. Research undertaken by the Project was funded in part by the National Endowment for the Humanities, the National Geographic Society, and the National Science Foundation. Watson and other CRF archaeologists frequently presented papers at regional and national archaeological conferences, such as the annual meeting of the Society for American Archaeology, and published their results in *American Antiquity*, the leading archaeological journal for work in the Americas (Bennington et al., 1962; Robbins, 1971; Watson and Yarnell, 1966). Results of research by CRF Archeological Project personnel were also published in the *NSS News* (Ehman 1966; Watson, 1966), in the *NSS Bulletin* (Freeman et al., 1973), and in the *Proceedings* for the 4th International Congress of Speleology (Watson, 1969b).

While the CRF Archeological Project was underway in Kentucky, NSS cavers made a spectacular archaeological discovery in the southwestern U.S. (Ellis and Hammack, 1968). Feather Cave, New Mexico, was a well-known site that had been excavated during the 1950s. In 1964, members of the Sandia, Pecos Valley, and El Paso NSS grottos joined forces to explore a small lead that had not been investigated by the archaeologists. After crawling approximately 12 meters through the tight passage, the NSS cavers entered a room of moderate size that seemed to be undisturbed, and contained masses of ceremonial offerings including hundreds of miniature arrows, miniature bows, and pahos (prayer sticks), as well as several pictographs. Realizing the significance of their discovery, the cavers left the remains undisturbed and reported them to the regional chairman of the NSS, Robert Willis, who contacted archaeologist Florence Hawley Ellis. Because news of the discovery had spread, it was decided to collect all materials in the cave after everything had been recorded and documented in place. It was suggested that the cave was a Mogollon shrine dedicated to Earth Mother and Sun Father, visited during biannual solar ceremonies, and was probably about 600 years old. Today, such a find would probably not result in removal of the artifacts. Rather, the first priority would be to keep the discovery quiet, gate and otherwise protect the site, leaving the material in place to respect the beliefs of Pueblo Indians who still visit such caves for ritual purposes.

CAVE ARCHAEOLOGY ENTERS MAINSTREAM AMERICANIST ARCHAEOLOGY: 1970–PRESENT

During the late 1970s and 1980s, NSS cavers began reporting archaeological remains in several dark-zone caves of the eastern U.S. A group of cavers, exploring and mapping a large Tennessee cave that came to be known as Jaguar Cave, discovered a remote passage containing a series of human footprints preserved in the mud floor. Carefully avoiding the track way, the cavers kept their discovery quiet but alerted Watson to the find. Over a number of years the footprint passage was carefully mapped, resulting in the documentation of 274 complete footprints left by nine different individuals. Radiocarbon dating of torch charcoal associated with the prints indicates that the prehistoric cavers entered this passage some 5,400 years ago (based on calibrated radiocarbon ages), the earliest dark-zone cave exploration yet known for the eastern U.S. (Robbins et al., 1981; Watson et al., 2005).

Other discoveries by NSS cavers soon followed the Jaguar Cave work. 3rd Unnamed Cave, Tennessee, first reported to contain a few aboriginal footprints preserved in a remote passage, was found during subsequent archaeological investigation by Watson to be a significant chert quarry, which also contained petroglyphs on the ceiling of the quarry passage. The glyphs and associated quarrying activity, which dates to the Late Archaic and Early Woodland periods, was first published by Charles H. Faulkner (1988), and later was more thoroughly described by Jan Simek (et al., 1998). Twelve of fourteen radiocarbon dates from 3rd Unnamed Cave fall between 2800 and 3800 years B.P. (calibrated ages; Crothers et al., 2002). Analysis of the chert quarrying activity eventually became Jay Franklin's Master's thesis project at the University of Tennessee, Knoxville (Franklin, 1999).

Also during the 1980s, members of the Detroit Urban Grotto, who were mapping the Fisher Ridge cave system east of Mammoth Cave National Park, discovered a few isolated prehistoric footprints and a large crosshatched petroglyph far back in the dark zone of this extensive cave. CRF Archeological Project personnel documented the prints and petroglyph and obtained two radiocarbon dates on associated charcoal (2800–3600 calibrated years B.P.; Kennedy et al., 1984), but the site has not been fully published.

Under the auspices of the CRF Archeological Project, Crothers completed a Senior Honors Thesis at Washington University in 1981 documenting the remains left by would-be rescuers in Sand Cave, Kentucky, during their failed attempts to free Floyd Collins, who was trapped and died there in 1925. One of the first applications of historical archaeology to a cave setting, this thesis was published in the *NSS Bulletin* (Crothers, 1983).

In the early 1980s, a local caver discovered prehistoric drawings on mud-coated walls in an east Tennessee cave, which he reported to Howard Earnest, a U.S. Forest Service archaeologist, and Charles H. Faulkner at the University of Tennessee, who agreed to investigate the site. Faulkner enlisted the help of NSS cavers from the East Tennessee area, especially the Smoky Mountain Grotto, to document and ultimately to gate this important late prehistoric (Mississippian) ceremonial locale (Faulkner et al., 1984; Faulkner, 1986). Faulkner's work at this site, which came to be known as Mud Glyph Cave, initiated a cave archaeology program at Tennessee that continues today. The Mud Glyph Cave project was particularly important because it alerted the caving community to these fragile remains, and many more such subtly decorated caves have now been reported for the Kentucky-Tennessee-Alabama-Georgia karst region (e.g., Faulkner, 1988, 1997; Faulkner and Simek, 1996; Simek et al., 1997).

In May 1986, for example, NSS cavers attending the annual Louisville Grotto's Speleofest found an extensive array of geometric renderings traced in the mud floor of a large, low room well back in the dark zone of a cave now known as Adair Glyph Cave. The cavers notified Philip DiBlasi, a University of Louisville archaeologist, who subsequently obtained a radiocarbon determination for charcoal in the glyph room, indicating that the glyphs date to the Late Archaic period (3500–4200 calibrated years B.P.; DiBlasi, 1996), similar in time to the 3rd Unnamed Cave dates.

Another very important discovery of ancient symbolic renderings in a cave dark zone was made during the early 1990s at a site in Missouri known as Picture Cave (Diaz-Granados and Duncan, 2000, Plates 12–17). In contrast to Adair Glyph Cave and Mud Glyph Cave, the artwork in Picture Cave (which is late prehistoric, hence much closer in age to the renderings in Mud Glyph than to those in Adair Glyph Cave) consists primarily of pictographs created in red, black, and, rarely, white pigments. Many of the items and entities depicted can be fairly readily referred to themes, events, or supernatural beings described in the complex oral traditions of ethnographically and ethnohistorically known midcontinental American Indian groups.

In 1981, NSS cavers from the Clayton County Cavers Grotto rediscovered evidence of prehistoric human activity in Big Bone Cave, Tennessee (Blair and Sneed, 1983; Matthews, 2006, p. 145), the same cave that Henry Mercer visited in 1896. Blair and Sneeds's much more recent discoveries and subsequent reporting to Watson eventually led to Crothers's Master's thesis project at the University of Tennessee (Crothers, 1986, 1987). Big Bone Cave, like Mammoth and Salts caves, has exceptional preservation and contains numerous torch remnants, gourd bowls, woven bags, and footwear left by prehistoric gypsum miners. In fact, one important result of Big Bone Cave archaeology is demonstrating that pre-Columbian gypsum mining was a widespread activity extending well beyond the Mammoth Cave region.

Larry Matthews' summary of Big Bone Cave speleological history has just been published by the NSS (Matthews, 2006). This volume contains numerous illustrations and descriptions of historic and prehistoric remains in the cave, and is a good guide to the abundant literature on this famous Tennessee site.

In 1988, NSS cavers discovered a small cave, high up in the Colorado Rocky Mountains, that they named Hourglass. Subsequently, while mapping passages several hundred meters into the dark zone of Hourglass Cave, they came upon human skeletal remains they thought were prehistoric. They contacted archaeologists and other appropriate personnel whose investigations revealed that the bones are those of a man approximately 45 years old who died in the cave nearly 8000 years ago (Mosch and Watson, 1997). This seems to be the earliest record in the Americas of dark-zone exploration in a high-altitude cave.

Beginning in the 1960s when the Association for Mexican Cave Studies was initiated (for a history, see http://www.amcs-pubs.org/), and becoming especially noticeable since the 1980s, NSS cavers have been actively involved in Mesoamerican cave archaeology. One recent result is the NSS Maya Caves Project (Schaeffer and Cobb, 1991). Archaeologists and cavers have been particularly active in Belize (McNatt, 1996; Moyes, 2002; Peterson, 2006), Guatemala (Brady and Scott, 1997), and Mexico (Hapka and Rouvinez, 1997; Rissolo, 2003). The NSS 2004 Ralph Stone Graduate Fellowship was awarded to a study of karstic and sacred landscapes at a Late Classic site in Guatemala. Even more recently, several NSS members exploring high-altitude caves in South America (Peru) have found numerous archaeological materials, including human remains (Knutson, 2006).

Through the 1980s and into the 1990s new archaeological discoveries in caves clearly had a synergistic effect, driving discoveries of more archaeological material in cave dark zones. As cavers reported sites and these finds became known through presentations and publications, more cavers came forward with other discoveries. Watson also taught a summer field course in cave archaeology during the mid-1980s at Mammoth Cave through Western Kentucky University's Center for Cave and Karst Studies that was popular among NSS cavers. Somewhat later in the 1980s and 1990s, two Earthwatch Institute funded volunteer projects were begun that integrated cavers into structured archaeological research projects. One is the Maya Ceremonial Caves Project (1988–1992), the other is the Cultural Resources Survey of Mammoth Cave (1993–2005). Such specialized courses and active archaeological projects that welcome volunteers can introduce cavers to the nature of archaeological remains found in caves and to the wealth of information that can be obtained when resources are protected and carefully studied.

BIOARCHAEOLOGY IN THE DARK ZONE OF CAVES

Bioarchaeology is the study of human biology revealed in archaeologically-recovered human remains, most often whole or partial skeletons. This information provides insights into the lives and biological characteristics of past peoples, such as population structure, health, illness, and diet. Cave bioarchaeology is bioarchaeology applied to human remains found in caves.

Cave bioarchaeology focuses upon several different data sources: human skeletal and mummified remains, paleofeces, and footprints. Before information of any sort can be gained, however, such materials must be recognized and reported to relevant specialists who can carry out appropriate research while protecting these fragile remains (Hubbard, 1996). The NSS and its members have contributed to bioarchaeological knowledge by reporting human remains found underground.

Human remains in caves are either mummies or skeletons. As noted above, mummies have been described from caves in Peru (Knutson, 2006) as well as from Kentucky and Tennessee caves (Robbins, 1971; Tankersley et al., 1994; Watson and Yarnell, 1986). Contrary to nineteenth century practices (see George, 1990, 1994; Meloy, 1971), mummies are now usually examined *in situ* in caves and left there if security can be guaranteed. Where remains are not threatened by destruction, preservation in place is the preferred alternative to collection and curation of human remains, in deference to wishes of many Native Americans.

More often than mummies, prehistoric skeletons or partial skeletons are found in caves. There are several NSS-related summaries concerning cave skeletons for several southeastern U.S. states (Hubbard and Barber, 1995, 1997; Turner, 1985; Willey, 1985).

Sometimes skeletons in caves have been studied *in situ*, and in other cases they have been removed for laboratory analysis and curation. As just noted for mummies found in caves, it is preferable to leave human skeletal remains *in situ* underground unless they are threatened by looting or other destruction. *In situ* analysis may limit the information that can be gathered, but in some situations, such as pit caves where remains are exposed in the talus cone, basic data can be collected without disturbing the bones. Bull Thistle Cave, Virginia, is an example of an undisturbed pit cave where human bones exposed on the floor of the pit were documented, and then the cave was gated to protect the site (Willey and Crothers, 1986).

Unfortunately, remains in caves are vulnerable to looting, so bioarchaeologists may have to remove skeletal material for curation above ground. There are, however, some instances of remains looted from Tennessee caves that were subsequently recovered, analyzed, and published (Whyte and Kimball, 1997; Willey et al., 1988).

Reports of recently excavated and described cave skeletons include those from Texas pits (Bement and Turpin, 1991; Ralph et al., 1986; Turpin, 1985), from Hourglass Cave in the Rocky Mountains (Mosch and Watson, 1997), from a northwest Georgia cave (Crothers, 1991; Sneed and Sneed, 1991; Willey, 1991), from southwest Virginia caves (Boyd and Boyd, 1997), from central Kentucky caves (Haskins, 1988), and from an East Tennessee cave (Faulkner, 1987). In one case, analysis of skeletons occurred decades after they were excavated (Tucker, 1989).

Most of these skeletal reports are descriptive, usually including basic data for each individual (age at death, and sex), paleopathology (diseases and injuries, such as healed fractures), and alterations to the bones after original deposition. Such reports are quite general, and usually lack problem-oriented approaches. In contrast, there are a few specialized analyses of human bones from caves. These include the use of geographic information systems and estimations of the minimum number of individuals from Honduran caves (Herrmann, 2002), rodent modifications of bones in a Middle Tennessee cave (Klippel and Meadows, 1991), reconstruction of diet based on the dental pathology characteristic of remains found in a Texas cave (Marks et al., 1991), DNA analysis of the Hourglass Cave skeleton (Stone and Stoneking, 1996), and inference of prehistoric diets based on stable isotope data for skeletons from a Virginia cave (Trimble and Macko, 1997).

The most common bioarchaeological remains found in caves, other than human bone, are human paleofecal deposits. Paleofecal analysis was an important part of the CRF Archeological Project because of the direct dietary information they contain (Gremillion and Sobolik, 1996; Marquardt, 1974; Stewart, 1974; Yarnell, 1969, 1974). In addition to dietary constituents of the paleofeces, analysts have studied pollen (Bryant, 1974; Schoenwetter, 1974) and endoparasites (Dusseau and Porter, 1974; Fry, 1974), and have even retrieved hormonal data to determine sex of the defecator. In a study of 12 specimens, all twelve indicated male hormonal ratios (Sobolik et al., 1996). In a study of human paleofeces from Big Bone Cave, Charles T. Faulkner (Faulkner, 1991; Faulkner et al., 1989) examined dietary components and evidence for endoparasitic infection. His analysis was aided by a grant from the NSS to radiocarbon date one of the specimens.

Prehistoric footprints are perhaps the rarest of all bioarchaeological materials, having been found in only a few caves. NSS cavers discovered most of the prehistoric footprints documented in North American caves. So far, only the prehistoric footprints in Jaguar Cave have been adequately described (Robbins et al., 1981; Watson et al., 2005; Willey et al., 2005), thanks in large part to support by NSS members who reported the discovery, mapped the cave, and aided in photographing and casting the foot impressions.

CONCLUSIONS

Archaeology in the dark zones of caves has come into its own as the NSS celebrates its sixty-fifth anniversary. There are a growing number of archaeologists who specialize in the nuances of doing archaeology underground. It is now more common to include chapters on the archaeology of cave resources in synthetic and regional works (e.g., Crothers et al., 2002), and there are now enough practitioners to make up large portions of edited volumes (e.g., Carstens and Watson, 1996) or entire journal issues (e.g., Sherwood and Simek, 2001; Steele, 1997). National and regional archaeological conferences now commonly have entire symposia dedicated to archaeological cave topics (e.g., Symposium: Cave Archeology in the Appalachian Mountains, Journal of Cave and Karst Studies v. 59, p. 132–165). Archaeologists are also beginning to investigate saltpeter mining cave sites in a systematic fashion (Duncan, 1997), an aspect of historic archaeology in caves that has been too long neglected.

In addition to the CRF Archeological Project and several Mesoamerican cave archaeology projects (see the Mesoamerican Cave Archaeology Network http://www.calstatela.edu/academic/anthro/mesocave.html for a current listing), there are active cave archaeology programs at California State University-Los Angeles (directed by James Brady), the University of Kentucky (directed by George Crothers), and the University of Tennessee-Knoxville (directed by Jan Simek). Although there are now many more formally trained specialists carrying out research in cave archaeology than ever before, NSS avocational cavers will continue to be indispensable to the discovery and documentation of archaeological remains in the dark zones of caves.

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Carol A. Hill and Paolo Forti – Cave mineralogy and the NSS: past, present, future. *Journal of Cave and Karst Studies,* v. 69, no. 1, p. 35–45.

CAVE MINERALOGY AND THE NSS: PAST, PRESENT, FUTURE

Carol A. Hill[1] and Paolo Forti[2]

Abstract: The purpose of this paper is to trace the National Speleological Society's past, present, and future involvement with the science of cave mineralogy, in accordance with the celebration of the NSS's 65th Anniversary. In the NSS's first decade (1940s), a number of articles covering mineralogy topics were published in grotto newsletters, the *NSS News* and *NSS Bulletin*, but it wasn't until the 1950s and 1960s that it published professional scientific papers on this subject. The Society's first huge commitment to this field was in their publication of *Cave Minerals* in 1976, the first book in the world on cave minerals and the first book ever published by the NSS. The book series *Cave Minerals of the World*, the second edition of which was published in 1997, has become the standard reference on the subject. Important fields of future research in cave mineralogy that the NSS may become involved with are those of paleo-environments, microbiology, and minerals ontogeny.

Introduction

The National Speleological Society (NSS) has been instrumental in promoting the science of cave mineralogy through its publication of the *NSS Bulletin* (now the *Journal of Cave and Karst Studies*), the *NSS News*, and three editions of *Cave Minerals/Cave Minerals of the World*. We will first describe the early years from 1940 (when the first issue of the *NSS Bulletin* came out) to 1976 when the Society published its first book, *Cave Minerals*. Then we will specifically trace the history of the *Cave Minerals* book series involving both of the authors, and finally we will present what we feel are some promising areas for future cave mineralogy work. For a voluminous, descriptive text on cave minerals and speleothems, the reader is referred to the NSS's book *Cave Minerals of the World* (Hill and Forti, 1997). For shorter reviews on the different classes of cave minerals and speleothem types refer to the articles by Hill and Forti (2004a, b) and Forti and Hill (2004) in the *Encyclopedia of Caves and Karst Science*.

Past

The Early Years (1940–1975)

The National Speleological Society's support of cave mineralogy in the early years was mainly through three avenues of publication:

(1) Grotto publications, where members writing trip reports on caves they had been mapping or exploring also mentioned the minerals and speleothems observed therein. An excellent example of such early grotto publications is the numerous reports by William Halliday in the late 1940s and 1950s in the *California Caver* and *Salt Lake City Grotto Newsletter*.
(2) *NSS News* publication of short mineral descriptions regarding specific caves.
(3) *NSS Bulletin* publication of scientific reports related to cave mineralogy.

These reports constituted the most important aspect of the NSS's early involvement with cave mineralogy because they set the foundation for future scientific publications, including the first *Cave Minerals* book.

While it is not within the scope of this paper to include all of the early articles that contributed to this scientific foundation, some of the more important work will be mentioned, both with regard to the recognition of new minerals or speleothem types, and with regard to early NSS attempts to form committees or symposia on the topic of cave mineralogy.

The first published account of cave minerals/speleothems in the *NSS Bulletin* was by Roy Holden in 1940, in the very first issue of the *Bulletin*, where he described the Luray Caverns helictites and offered modes of origin (Holden, 1940). Holden was also the first to report the fluorescence of calcite speleothems in a United States cave in 1944 (Holden, 1944a), and he chaired the first NSS committee on minerals and formations in 1944 (Holden, 1944b). William Foster in 1949 reported on mineralogic data in speleothem work, and he also chaired the NSS committee on formations and mineralogy in 1951 (Foster, 1949, 1951). Henderson (1949) was the first to describe anthodites as a speleothem type from Skyline Caverns, Virginia, and Warwick (1950) was the first to observe and report in the *NSS Bulletin* the occurrence of calcite bubbles, which also became a new speleothem type. While all of these 1940 articles were important first attempts to describe cave minerals and speleothems, overall

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[1] Earth and Planetary Sciences, University of New Mexico, 200 Yale Blvd., Northrop Hall, Albuquerque, NM, USA 87131, carolannhill@aol.com.
[2] Instituto Italiano di Speleologia, Via Zamboni 67, Bologna, Italy 40127, forti@geomin.unibo.it.

there wasn't much happening in the NSS in cave mineralogy prior to the 1950s.

In 1952, George Moore introduced the term speleothem for any secondary mineral deposit formed in caves (Moore, 1952). Despite some objections to this term over the years, it has stuck and is now the official name in the *Glossary of Geology* for what used to be referred to as a cave formation. Later in the 1950s, Crisman (1956) reported both monocrystalline helictites and stalactites from the Caverns of Sonora, Texas, the first report of monocrystalline speleothems in a United States cave. Davies and Moore (1957) were the first to report a cave occurrence of the minerals endellite and hydromagnesite anywhere in the world, and Good (1957), also working in Carlsbad Cavern at the same time as Davies and Moore, was the first to report a cave occurrence of the mineral montmorillonite anywhere in the world.

In the early 1950s a young undergraduate chemistry student, who took a special interest in cave mineralogy, emerged from the NSS caver ranks to become one of the leaders in this field for the next five decades: William B. White. White published a number of mineral descriptions in grotto publications in the late 1950s and went on to publish a review of cave mineral studies for 1955–1960 in 1961 (White, 1961), and also to chair the first NSS symposium on cave mineralogy (White, 1962). This symposium was held in December, 1960 at the New York meeting of the American Association for the Advancement of Science, and was one of the first attempts to merge cave mineralogy into mainstream science. This symposium was also the most professional of all the publications done by the NSS on cave mineralogy up to this time.

George Moore continued to write seminal papers in the *NSS Bulletin*, one on the origin of helictites in 1954 (Moore, 1954) and another on the growth of stalactites in 1962 (Moore, 1962), plus he was the first to report dolomite as a cave mineral in 1961 (Moore, 1961). Another NSS member who contributed important scientific papers on cave mineralogy in the *NSS Bulletin* in the 1960s–early 1970s was Rane Curl, who published on the aragonite-calcite problem in 1962 and on the minimum diameter of stalactites and stalagmites in 1971 (Curl, 1962, 1971). Thayer (1967) was the first to propose in the *NSS Bulletin* the name conulite for a new speleothem type that he described as simple drip-drilled mud pits lined with calcite.

Among all of the early (1940–1975) workers in U.S. cave mineralogy who published with the NSS, William (Bill) Halliday, George Moore, and William (Will) White stand out as the three persons who probably contributed the most information to this field.

HISTORY OF THE NATIONAL SPELEOLOGICAL SOCIETY'S BOOK *CAVE MINERALS OF THE WORLD*

1970

It all began on January 18, 1970, when Allan P. Haarr, former NSS Executive Vice President and member of Elaine Hackerman's Miscellaneous Publications Committee, asked Carol Hill to write a chapter on cave minerals and speleothems for the NSS's *Caver's Handbook*. Al Haarr knew that Carol was interested in cave mineralogy and that she had been collecting a number of articles on the topic. He also knew that because Carol had moved to New Mexico, she had been working on the mineralogy of Carlsbad Cavern and other caves in the Guadalupe Mountains. Thus, Al Haarr asked Carol to contribute an approximately 50 page-long chapter to the *Caver's Handbook*, remarking: "I see this chapter as a fairly complete article on the various speleothems and their theories of formation." What Al Haarr didn't know is that in Carol's view complete really meant complete, and that Carol rarely writes anything short. Thus began the saga of *Cave Minerals of the World.*

1970–1971

For two years Carol Hill gathered together all of the United States cave mineral/speleothem articles she could find, and from this information and her own personal research wrote a chapter on cave mineralogy for the *Caver's Handbook*. However, this manuscript turned out to be much longer than the 50 pages originally intended by the Miscellaneous Publications Committee. Also by this time, a number of photographs had been obtained for the chapter, especially from cave photographer Pete Lindsley. Thus a dilemma arose within the NSS: What to do with this much-longer-than-anticipated manuscript?

1972

To resolve this dilemma, Dave Irving, then on the NSS board of governors (BOG), suggested that the chapter be made into a book to be sold externally to the public as well as to NSS members. This suggestion generated a major controversy within the NSS, the fear being that the book would promote vandalism once the general public found out what treasures actually exist in caves. Al Haarr remarked in his February 8, 1972 letter to Carol Hill that: "I feel your chapter is needed and useful but not worth an internal fight" (within the NSS), and he thus favored publication only to NSS members and geologists, and then only if the book contained a strong conservation message. Other NSS board members disagreed and thought that the publication of a book on cave minerals was an excellent way to educate the public as to cave conservation. Also, sale of the book could be a way of bringing much needed revenue into the NSS. It was finally decided that Carol's book, *Cave Minerals*, would be published, albeit with a strong conservation message and with no cave locations divulged. A Special Publications Committee then emerged from the former Miscellaneous Publications Committee to handle *Cave Minerals* and other potential book manuscripts. In June of 1972, *SpeleoPress* provided the lowest bid out of five, and was awarded the contract to print *Cave Minerals*.

1973

It was the NSS's plan to have *Cave Minerals* printed and available for sale by the 1973 NSS Convention, but by this time the act of publishing the book had turned into a total fiasco, to quote Al Haarr. The problems were two-fold: (1) Carol Hill had never written a book before, and (2) the NSS had never published a book before. There was no person on the Special Publications Committee that actually had the experience to handle such things as dealer quotes, book orders, price fixing, reprint rights, production schedules, interfacing with printers, advertising/marketing, etc., all of which needed to be spelled out and approved by the BOG. In addition, BOG member Dwight Deal felt compelled (or was compelled by the BOG) to take on the daunting task of making sure the book met professional standards and was properly reviewed. So the publication of *Cave Minerals* dragged on and on.

1976

By March of 1976, the book had been languishing at *SpeleoPress* for many months and had still not been printed. Therefore, then-NSS Executive Vice President James (Moose) Dawson gave *SpeleoPress* an ultimatum: either have the book printed in time for the Morgantown, West Virginia Convention in June, or the NSS would cancel its contract with *SpeleoPress*. Thus it was that *Cave Minerals* became the first book published by the National Speleological Society for a general audience, and the very first book in the world published on the topic of cave mineralogy (Hill, 1976). *Cave Minerals* was 137 pages long and contained 475 references, which included most of the U.S. cave mineralogy literature and some references from Great Britain and Australia, but which barely touched upon the non-English European literature. The book had a colored cover: The Butterfly from Caverns of Sonora by Pete Lindsley (Fig. 1), but the rest of the photographs were in black and white.

1978

By 1978 the sale of *Cave Minerals* had waned because of the failure of the NSS to advertise the book, even to NSS cavers, who approached Carol Hill asking where they could buy the book. This prompted Carol to write to then-NSS president Charlie Larson and the BOG to ask for an NSS commitment to properly sell the book. However, one important person who was able to buy a copy of *Cave Minerals* was Paolo Forti of the Institute of Speleology in Bologna, Italy. Paolo was perhaps only one of a couple of Europeans who read all of the *NSS News* issues, and in this way he had become aware of the existence of Carol's book. Paolo immediately bought probably the first copy of *Cave Minerals* sold in Europe. Paolo was extremely interested in Carol's book because at that time he was putting together a short booklet of his own on European cave minerals. Paolo sent a copy of this booklet, and many other of his publications, to Carol and a mutual correspondence flourished. By now Carol realized that the bulk of what had been written on cave minerals resided in Europe, and that *Cave Minerals* had barely scratched the surface of this knowledge base.

1981

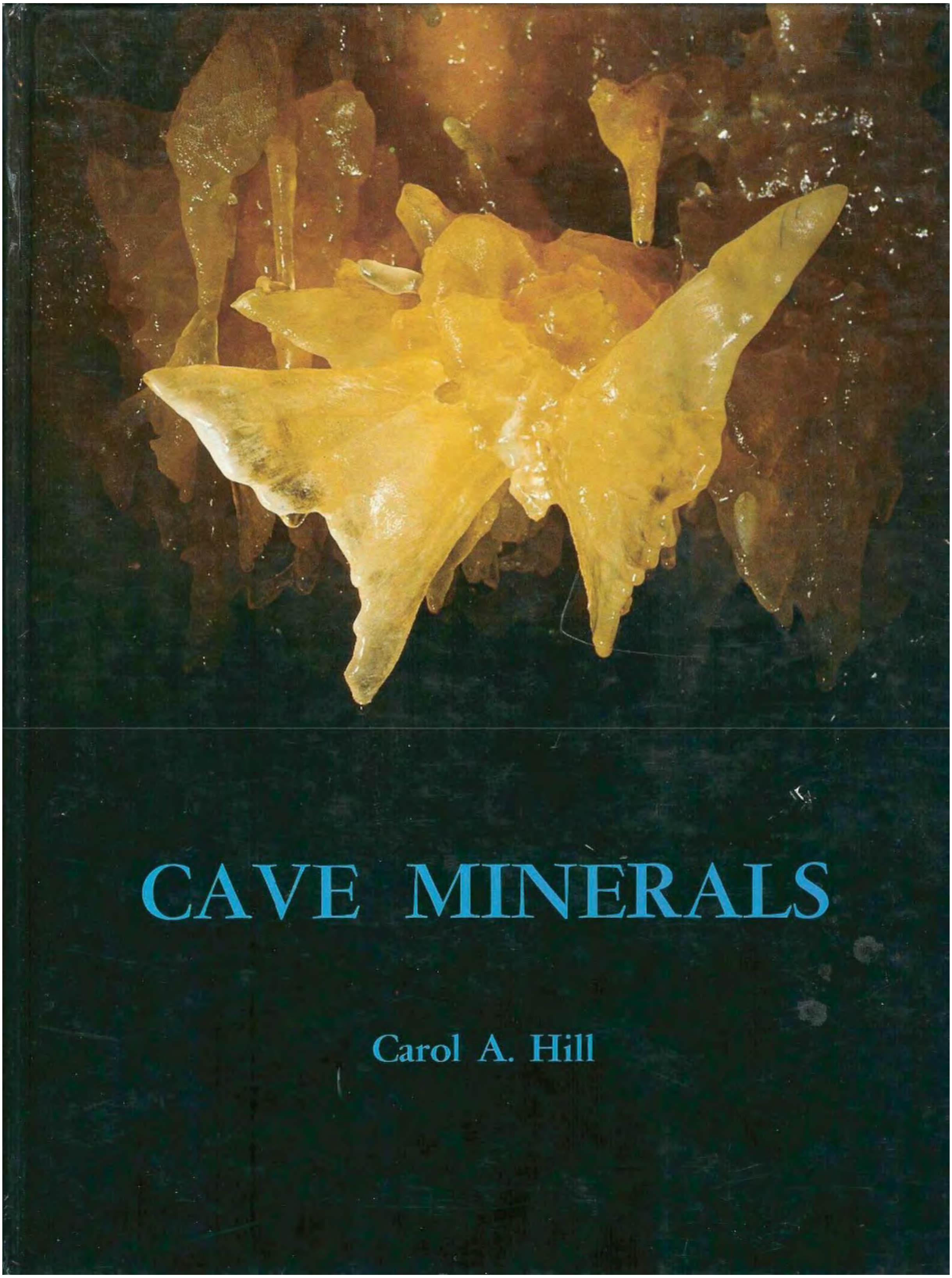
Carol Hill met Paolo Forti for the first time at the 8th International Congress of Speleology in Bowling Green, Kentucky in the summer of 1981. Since the NSS had expressed an interest in publishing another edition of *Cave Minerals*, Carol asked Paolo to be co-author of this new edition, now to be entitled *Cave Minerals of the World*. Paolo was very happy and excited to be a co-author, but did not yet realize the tremendous amount of work that this commitment would entail. The ambitious intent of Carol and Paolo was for *Cave Minerals of the World* to include all of the work done in cave mineralogy around the world up to that time, including all of the papers written on speleothems in the very early years of speleology (Fig. 2). Thus, they invited cave historian Trevor Shaw of Great Britain to write a Historical Introduction to the book.

1982–1985

In 1982 the collaboration of Carol and Paolo on the first edition of *Cave Minerals of the World* (CMW1) began, but with the Atlantic Ocean separating them and with no internet available at that time. For two years the authors labored on the manuscript, with Paolo Forti doing the lion's share of the new work because of the enormous amount of European literature on the subject in a variety of languages. Paolo's wife Giovanna complained that she was not able to see much of him during this time because he was always reading and translating cave mineralogy-related articles. In 1984, when the CMW1 manuscript was almost finished, the NSS decided to print the book in Italy because it was envisioned that most of the European sales would occur during the forthcoming International Congress in Barcelona, Spain. So CMW1 was contracted to an Italian printing house for a prescribed amount of Italian lira, which at that time was very weak with respect to the U.S. dollar. In the summer of 1985, Paolo flew to Albuquerque in order to prepare the final manuscript and choose photos with Carol, and after five full days of immersion (with only one hour of walking in the garden during those five days), CMW1 was ready to go to the printers. As a "gift" to Paolo, Carol and her husband Alan took Paolo on a whirlwind trip through Carlsbad Cavern.

1986

The first edition of *Cave Minerals of the World* (CMW1) was published just in time for the 9th International Congress of Speleology in Barcelona, Spain, but not without problems (Hill and Forti, 1986). It turned out that between 1984 and 1986 the exchange rate of dollars to lira had lowered more than 30%, and as a consequence this caused a major disagreement in pricing between the NSS



CAVE MINERALS

Carol A. Hill

Figure 1. Cover of *Cave Minerals*, published in 1976 by the NSS. This photo by Pete Lindlsey of "The Butterfly" in the Caverns of Sonora was the only color photo in the book.

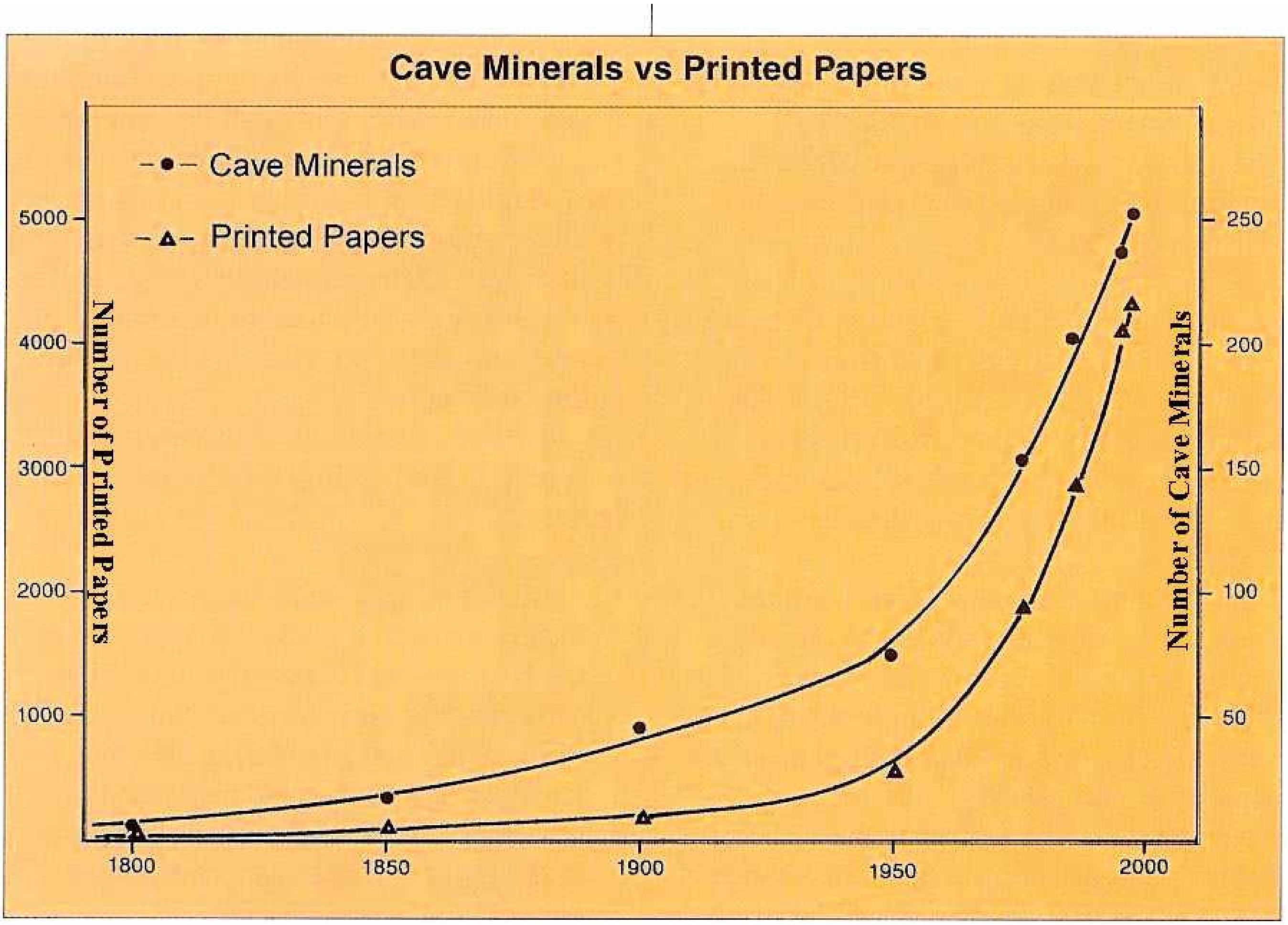


Figure 2. A cumulative graph showing the number of identified cave minerals and printed papers on cave mineralogy from 1800 to the present. Note how this explosion of knowledge has increased almost exponentially with time. From Hill and Forti (1997).

and the Italian printing house. This difficult situation led a very frustrated go-between with Paolo Forti on the European end of things to write to Carol Hill in July of 1986: "I am a University Professor, not a clerk of the NSS." However, CMW1 did make it to Barcelona on time and sold well at the Congress. The prime objectives of this first CMW1 edition were to: (1) set a classification standard for the field of cave mineralogy, and (2) cover cave minerals and speleothems worldwide. The first edition, CMW1, contained over 3,000 references and was 238 pages long. It had a front (Fig. 3) and back colored cover and an insert section of 33 color plates. However, this endeavor so exhausted Carol and Paolo that neither of them planned to write another edition.

1994

In 1994 Paolo Forti, who was by now rested from writing CMW1, became convinced that there needed to be yet another edition of *Cave Minerals of the World* that would: (1) bring CMW1 up-to-date since 1986, (2) provide a new format (reorganization) of the book, which would be more professional and easier to use, and (3) include the finest and most complete set of photographs of cave minerals/speleothems ever assembled. So Paolo, during the Workshop, Breakthroughs in Karst Geomicrobiology and Redox Geochemistry, held in Colorado Springs, Colorado in February of 1994, convinced a reluctant Carol that another edition was needed.

The job of doing *Cave Minerals of the World*, second edition (CMW2) turned out to be much easier than CMW1 due to the fact that the internet and e-mail now allowed us to work together in real time. Because of the time shift between Italy and New Mexico, Paolo's updates could reach Carol by early afternoon, while Carol's material could then reach Paolo by early the next morning, his time. This advancement in computer exchange of information also allowed Carol to more quickly edit Paolo's "Fortian" writing (a hybrid of English-Italian) into standard English. This time around the most difficult task was to obtain full information on cave mineral research in Eastern European

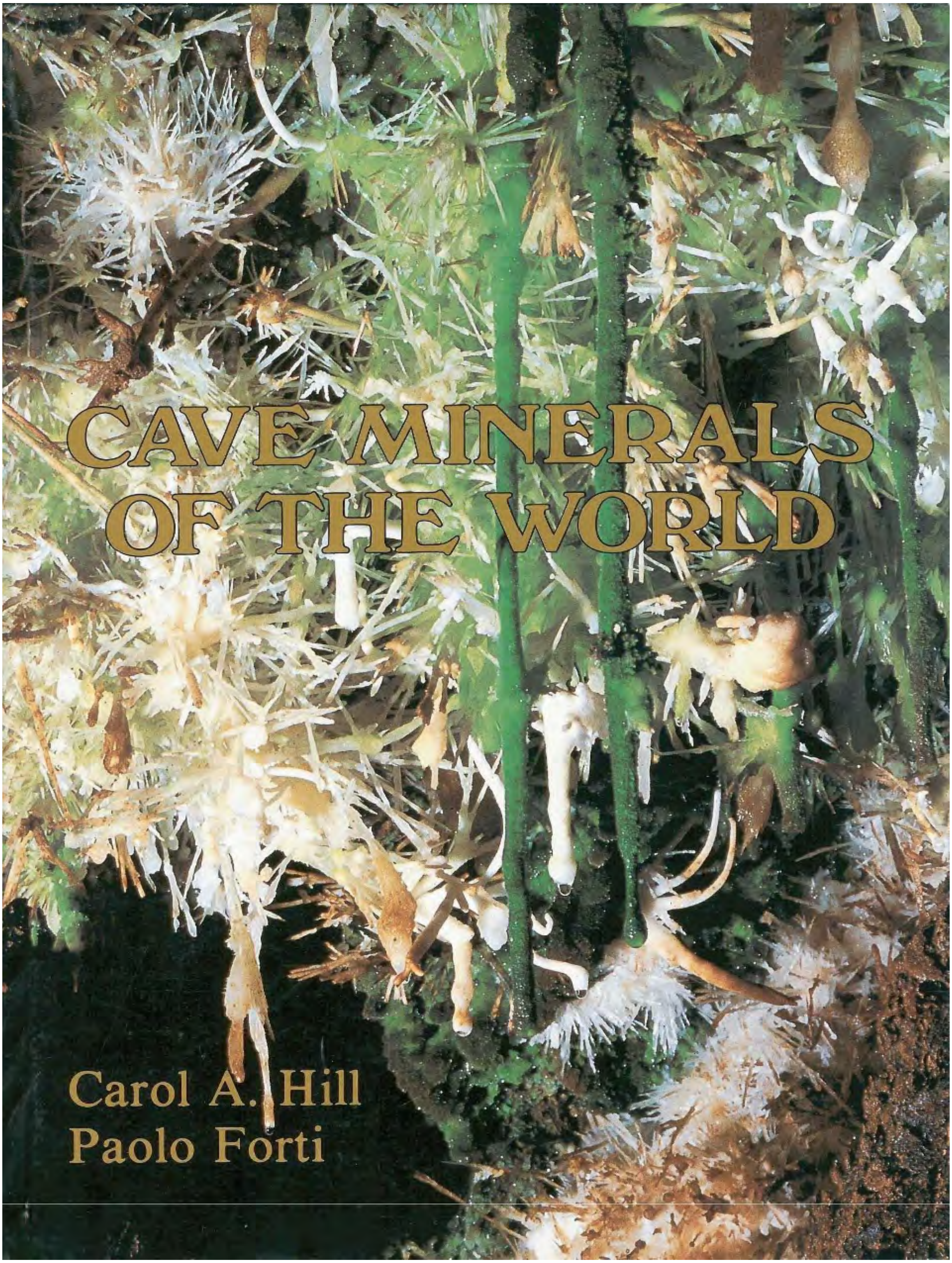


Figure 3. Front cover of *Cave Minerals of the World*, first edition, published by the NSS in 1986. This first edition of CMW1 had color front and back covers and an inset series of 33 color plates.

countries, which had been under-represented in CMW1 because of the adverse political conditions there in the early 1980s. Over a two-year time period, Paolo was obliged to fly to Russia (three times), Bulgaria (two times), Romania, Slovenia, and the Czech Republic besides traveling to Spain, France, Switzerland, and Austria. During these trips over 10,000 slides were selected and over 200 hours of discussion were spent by Paolo with local cavers and scientists. Truly, this book had now become *Cave Minerals of the World*.

In the summer of 1996, another rush trip was made by Paolo to the Hill house in Albuquerque (on this visit, the time was so short that not even a walk in the garden was permitted) in order to select all of the photographs for CMW2 and to finalize the manuscript. From Albuquerque, Paolo and Carol drove by car to the NSS Convention in Salida, Colorado, where all of the material for CMW2 was given to David McClurg, chair of the Special Publications Committee. This time CMW2 would be printed in the United States under David's direct scrutiny.

1997

The second edition of *Cave Minerals of the World* (CMW2) arrived at the 1997 11th International Congress of Speleology in La Chaux de Fonds, Switzerland on time, due mainly to the Herculean effort of David McClurg. At the Swiss Congress CMW2 won the UIS award for Best Cave Book for the previous four years (since the Hungarian Congress). The second edition of *Cave Minerals of the World* is 463 pages long and has 28 co-authors of the Special Topic and Top Ten Caves sections, over and above the contributions of authors Hill and Forti and again-co-author Trevor Shaw (Fig. 4). CMW2 was published by the NSS in *full* color, including the back and front covers (Fig. 5) and 333 color photos and figures. It also includes more than 5,000 references, which essentially did in both Carol and Paolo. The authors now consider their work to finally be *complete* and anticipate writing no further editions. And, as a positive assurance of that, after publication of CMW2, Carol Hill mailed all of her *Cave Minerals of the World* material to Paolo Forti at his Institute of Speleology in Bologna, where it now resides for all to access.

PRESENT

In the decade since CMW2 was published by the NSS, the book has had a great impact among cavers and scientists, as testified by the fact that it is the speleological book which has obtained the highest number of citations in both speleological and non-speleological papers. The names and related properties of the main speleothem types and subtypes have been definitively standardized. The book has also been important in increasing the number of scientists involved in cave mineral research all over the world, whereas before this time such research was limited to a dozen or so persons working in relatively few countries. As a consequence of the NSS publishing this series of three books, new minerogenetic processes are now understood and new minerals for science have been described. And happily, the fear of the NSS in the early 1970s, that the book would promote vandalism, has not been realized. Rather, the publication of the *Cave Mineral* book series has helped to educate the public as to the importance of conserving cave minerals and speleothems. Finally, the book has been essential in making all people aware of the beauty and fragility of the cave environment and its need for protection.

FUTURE

The authors recognize that CMW2 is not the final word in cave mineralogy, but that this science will evolve and be carried on by a new generation of speleologists. As a way of promoting that future, the authors will attempt to identify three areas of future research that they feel are promising for advancing the field of cave mineralogy.

PALEO-ENVIRONMENTS/PALEOCLIMATOLOGY

One of the most important future areas of research in cave mineralogy is the study of paleoclimate and paleo-environment as it relates to the current concern over global warming. An excellent overview paper concerning the dating of calcite speleothems and its application to paleo-environments is by Derek Ford (1997), who has been one of the pioneers and leaders in this field for the last three decades. However, while up to the present calcite and aragonite speleothems have been used almost exclusively for such analyses, in the last few years other cave minerals have begun to be used to determine paleo-environments, minerals such as elemental sulfur as an indicator of high hydrogen sulfide concentration, or opal substituting for calcite as an indicator of rainfall increase over time. An explosion of interest is expected toward the hundreds of different cave minerals whose deposition in caves is controlled by boundary conditions, which in turn are related to the environment or paleo-environment.

The application of speleothems to paleoclimate studies not only involves dating. It also involves determining stable isotope, trace-element, color-banding, and luminescent analyses and profiles of these speleothems (White, 2007). Especially important to the problem of global warming are paleoclimate studies done on Holocene-age speleothems, such as was done by Polyak et al. (2001), who depicted changes in climate over the last 3,200 years from studying mites preserved in stalagmites from Hidden Cave, New Mexico. The presence of these mites, encased in travertine that was dated by the uranium-series method, implies that a wetter and cooler climate existed 3,200 years ago than is present today in the Guadalupe Mountains.

Figure 4. Paolo Forti and Carol Hill autographing copies of their updated second edition of *Cave Minerals of the World*, which made its debut at the International Congress of Speleology in La Chaux de Fonds, Switzerland, in the summer of 1997. Many of the 28 co-authors of CMW2 were at the Congress and formed a long line of book autographers along side of Carol and Paolo.

MICROBIOLOGY

Another field where it is anticipated that research will develop substantially is the inter-relationship between microbiology and cave mineralogy. Microorganisms (mainly bacteria) are responsible for many, if not most, of the low enthalpy processes leading to the deposition of cave minerals (Forti, 2002; Contos, 2001). Such studies, most of which are only a few decades or less old, also have economic importance because they reflect the same mechanisms that cause the mobilization and/or re-deposition of ore bodies in chemoautotrophic environments (Onac et al., 2001). Biominerals, such as form in caves, may also have application to industry and medicine.

One of the most important areas of future research with respect to microbiology-cave mineralogy is that of proving biogenicity, that is, catching microbes in the act of forming minerals. This proves to be a very difficult task, as the products of microbial precipitation often mimic those formed during inorganic processes (Barton et al., 2001; Jones, 2001). And just because fossilized microbes exist in speleothems does not necessarily mean that they played active roles in the precipitation of that speleothem. Even when dealing with living microbes, proving biogenicity is difficult because biogenic mineral production cannot be verified with culturing techniques alone. As discussed by Northup (2006), a process called molecular phylogeny must be used whereby extracting and analyzing DNA provides a genetic tree that can help identify the role that microorganisms play in the creation of mineral deposits. These results can then guide microbial culturing efforts to more closely study the actual mineral production by microorganisms. Such studies are on the forefront of knowledge in understanding the dual organic-inorganic reactions involving the precipitation of cave minerals and speleothems.

MINERALS ONTOGENY

Cave Minerals of the World, like Dana's classic *Manual of Mineralogy*, is mainly a *descriptive* work, one that

Figure 5. Front cover of *Cave Minerals of the World*, second edition, published by the NSS in 1997. This second edition was in full color, containing 333 color photographs and figures as well as color front and back covers.

describes what a speleothem or cave mineral looks like. One of the most important futures of cave mineralogy lies in the subject of minerals ontogeny, which studies the growth of speleothems and cave minerals from a *genetic* perspective rather than from a descriptive perspective. Ontogeny of cave minerals as a scientific study has been developed in Russia, but is poorly understood in the West. As a first step in bringing this subject to the general attention of speleologists and cavers, Charles Self and Carol Hill published an introduction to minerals ontogeny in the August, 2003 issue of the NSS's *Journal of Caves and Karst Studies* (Self and Hill, 2003). This paper introduced the basic principles of minerals ontogeny and explained a hierarchy scheme whereby mineral bodies can be studied as crystal *individuals*, *aggregates* of individuals, associations of aggregates (termed *koras* by the Russians), and as sequences of koras (*ensembles*). However, ontogeny is not simply a new classification system for minerals. It is a method by which past crystallization environments can be deciphered from the mineral bodies themselves. (For example, needles in frostwork-type speleothems never touch each other because of the type of selection encountered within a capillary film environment.) The structure and texture of mineral bodies can be directly related to environmental factors, and speleothems in caves prove to be ideal subjects for this type of study.

In September, 2005, at the Athens-Kalamos, Greece, International Congress of Speleology, the UIS Commission on Cave Mineralogy formed a sub-committee composed of Charles Self (chair) of Great Britain, Bogdan Onac of Romania, Kyung Sik Woo of Korea, and William White and Carol Hill of the United States, to further investigate and promote the subject of minerals ontogeny. As of this writing, Will White is composing a paper for publication entitled: "Speleothem microstructure/speleothem ontogeny: A comparison of crystal growth concepts between Western and Russian conceptual frameworks and between mineralogy, ceramics, metallurgy, and semiconductor technology." Perhaps these endeavors in minerals ontogeny will turn into the subject of another cave mineralogy-related book that the NSS will publish sometime in the future.

CONCLUSION

The National Speleological Society is to be commended on its 65 years of protecting the cave environment, and specifically the speleothems and cave minerals within that environment. The authors especially thank the NSS for disseminating the wonderful and beautiful world of cave minerals to cavers and the public alike through their books *Cave Minerals* and *Cave Minerals of the World*.

ACKNOWLEDGMENTS

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Patricia Kambesis – The importance of cave exploration to scientific research. *Journal of Cave and Karst Studies,* v. 69, no. 1, p. 46–58.

THE IMPORTANCE OF CAVE EXPLORATION TO SCIENTIFIC RESEARCH

Patricia Kambesis

1906 College Heights Blvd, Hoffman Environmental Research Institute, Western Kentucky University, Bowling Green, Kentucky 42101, Pat.Kambesis@wku.edu

Abstract: Of the many objects of scientific interest, caves present a unique challenge because, except for entrance areas, caves are largely hidden from view. As a consequence, caves have not generally attracted the attention of mainstream scientists. With the exception of cave entrances noted on some topographic maps, most caves are not apparent from topographic maps, satellite and LANDSAT imagery, or aerial photographs. Caves and their features exist in an environment with no natural light and contain a myriad of physical and psychological obstacles. It is the cave explorer who ventures past these obstacles, motivated by curiosity and the desire to find and document places previously unknown. Systematic cave exploration is a two-fold process that involves the physical pursuit and discovery of caves and cave systems, and field documentation that provides baseline data in the form of cave survey data and notes, cave entrance and cave/karst feature locations and inventories, written observations, and photo-documentation. These data are synthesized into cave maps, topographic overlays, narrative descriptions, and reports that serve as exploration tools for finding more passages and caves. Systematic documentation and its derivative products also bring the hidden nature of caves and their features to the attention of scientists and provide a basis not only for cave-related research but for a wide range of related scientific endeavors.

Introduction

Caves present a unique challenge to scientific study because, except for entrance areas, caves are largely hidden from view. As a consequence, caves have not generally attracted the attention of mainstream scientists. With the exception of cave entrances noted on some topographic maps, most caves are not apparent from topographic maps, satellite and LANDSAT imagery, or aerial photographs which are the tools that many earth scientists use to visualize the shape, form, and orientation of landforms (Kambesis, 2003). Caves and their features exist in an environment with no natural light and contain a myriad of physical and psychological obstacles. It is the cave explorer who ventures past these obstacles, motivated by curiosity, and the desire to find and document places previously unknown.

In scientific research, there are a variety of questions that provide direction to the pursuit of knowledge. In cave exploration, the initial question is very simple: Does it go? This is the question that hooks the cave explorer and drives her/his curiosity toward an answer. But that answer only brings more questions such as how far, how long, how deep? During the exploration process, as a cave system or cave area reveals its complexity, the questions also change. For example, what is the cave's relationship to the surface, and to surrounding caves? What are the features and obstacles that the cave contains? Those involved in serious cave exploration know that the only way to answer these questions is with systematic documentation in the form of cave and surface surveys, detailed notes and observations, cave/karst feature locations and inventories, and photo-documentation. The data are synthesized into cave maps, narrative descriptions, and reports that can serve as a set of exploration tools for finding more passages and caves. The field documentation and its derivative products also serve as the baseline data for all types of cave-related research.

The most important derivative products of systematic cave exploration are maps, which illustrate the extent and layout of the cave, shapes of passages, and if a profile is included, the three dimensional relationship of the passages. A map not only portrays the geography of a cave, but depending on its level of detail, can show the location of features within the cave. Cave/karst feature inventories are becoming more common in the documentation process, especially because of the increased availability and access to GIS technology which allows more detailed cave/karst feature data to be integrated with the survey and cartographic data. Photography is another important aspect of cave documentation; a description of underwater helictites, u-loops, or chandemites pales in comparison to the photographs that record their existence. Systematic documentation and its derivative products such as cave maps, topographic overlays, reports, inventories, and photographs bring the hidden nature of caves and their features to the attention of scientists and provide a basis not only for cave-related research, but for a wide range of scientific endeavors such as archaeology, evolutionary biology, hydrogeology, geology, geomicrobiology, mineralogy, and paleoclimate studies, to name just a few.

In order for exploration documentation to be of value, it must be accessible. Much of the early information generated by cave exploration in the United States was not published in peer-reviewed journals, publications, or popular magazines. With the formation of the National Speleological Society and its many chapters (grottos) came national and regional publications that served as venues for accounts of cave explorations, maps, cave survey/research project reports, and photographs. State cave surveys, usually organized by active cavers within a state or region, served as archives and catalogs of cave data. Many of the state cave surveys published maps, reports, regional overviews, and results of scientific research in caves of their respective areas. Often these are the resources that scientists use to access information about caves, their characteristics, and features.

Systematic cave exploration and documentation provide an essential foundation for cave research. In turn, the results of cave research also serve the cave explorer in her/his efforts in finding more cave. Two case studies are presented to illustrate how cave exploration affects the course of cave science and vice versa. Systematic explorations in the Mammoth Cave area in Kentucky, and in the Guadalupe Mountains of New Mexico, are submitted as examples of how the tangible results of cave exploration (i.e., survey notes, initial observations, and photographs), and their derivative products (i.e., cave maps, topographic overlays, field notes, and summary reports) provided the basis for the cave research that followed.

CASE STUDY 1: EXPLORATION AND SCIENTIFIC RESEARCH IN THE MAMMOTH CAVE AREA

Efforts to survey Mammoth Cave began after the War of 1812 (Smith, 1960) with the purpose of establishing the relationship between cave passages and surface properties for commercial development of caves for tourism. Other surveys were made in support of construction projects for tourist entrances, walkways, and lighting systems. Due to commercial competition among show caves in the Mammoth Cave area and the marketability of calcite and sulfate deposits, most of the surveys and maps were kept secret. Access to the caves for scientific study was usually denied (Smith and Watson, 1970).

In 1930, world-renowned geographer and geomorphologist William Morris Davis published a scientific paper arguing that caves were not formed above the water table, as was commonly supposed, but were instead the result of underground water circulating deep below the water table (Davis, 1930). Because of Davis' long and impressive reputation as an earth scientist, the paper was embraced by the U.S. scientific community though it contained little supporting field evidence. Davis used some of the existing maps of Mammoth Cave to help develop his theory (Watson and White, 1985). Unbeknownst to him, most of the early maps were not accurate representations, but were at best, fanciful renditions of the cave which portrayed its morphology as a giant labyrinth (Fig. 1), rather than having a modified dendritic pattern (Watson and White, 1985). In 1942, J Harlen Bretz published a paper on cave development that attempted to provide field evidence in support of Davis' theory (Bretz, 1942). What followed was a fifteen year hiatus in which little of consequence appeared in the scientific literature of North America on cave development (White, 1973). It was not until systematic explorations in the Mammoth Cave area began documenting the nature, extent, and layout of the Mammoth Cave system, was it realized that Davis' theory on cave development might be flawed (White et al., 1970).

MODERN EXPLORATION UNDER FLINT AND MAMMOTH CAVE RIDGES

Modern exploration in the Mammoth Cave area began on Flint Ridge in 1947 by Dr. E. R. Pohl, Jim Dyer, and Bill Austin. Their focus included not only extending the physical limits of the caves under Flint Ridge, but also conducting scientific investigations. In 1954 the National Speleological Society sponsored a week-long expedition in Crystal Cave, which in the past had been operated as a show cave. Though no major discoveries were made during that expedition, it proved to be a learning experience in cave project management and in systematic exploration and survey techniques, and ultimately resulted in the establishment of the Cave Research Foundation (CRF) in 1957. The goal of CRF was to explore and map caves for the purposes of furthering scientific research and understanding of caves (Watson, 1981).

CRF adopted a method of systematic exploration that involved mapping cave passages, correlating the surveyed cave passages and their elevations with topographic maps, aerial photographs, and elevation controls such as geographic surface benchmarks (Brucker et al., 1966). Detailed trip reports containing passage and feature descriptions were also important to the systematic documentation process. With these tools, the extent of the Flint Ridge and Mammoth Ridge caves began to be realized along with the establishment of a geographic context for scientific work on cave origin and development.

CRF's work began on Flint Ridge where five major caves and a number of smaller caves were located. The impetus for these efforts was the potential for connections between the major caves of the Mammoth Cave area. This potential was first expressed by E. A. Martel after he visited Mammoth Cave in 1912 (Martel, 1912). He predicted that Flint Ridge and Mammoth Cave systems would some day be physically linked to make a system 241 km in length (Brucker and Watson 1976). Accomplishing such a challenge was a great motivator to the cave explorers and drove them to diligently push and map all varieties of cave passages large and small, dry and wet, magnificent and miserable.

Systematic explorations in Flint and Mammoth ridges not only racked up significant survey footage, but also

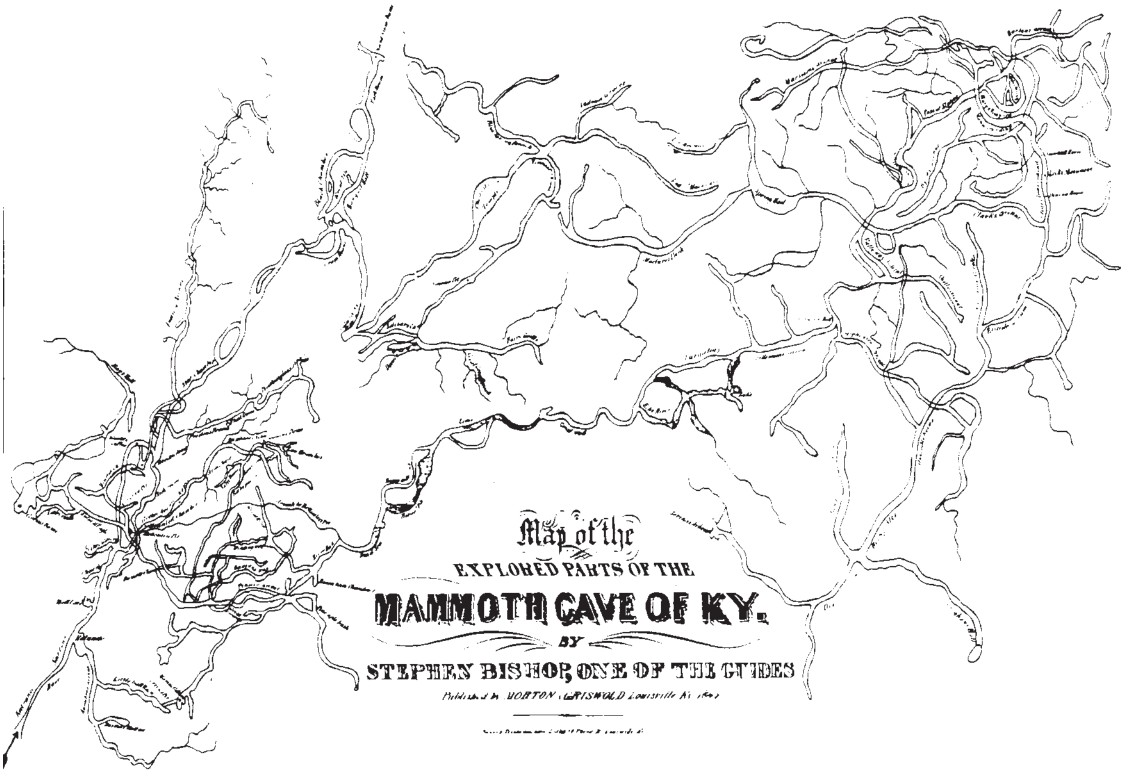


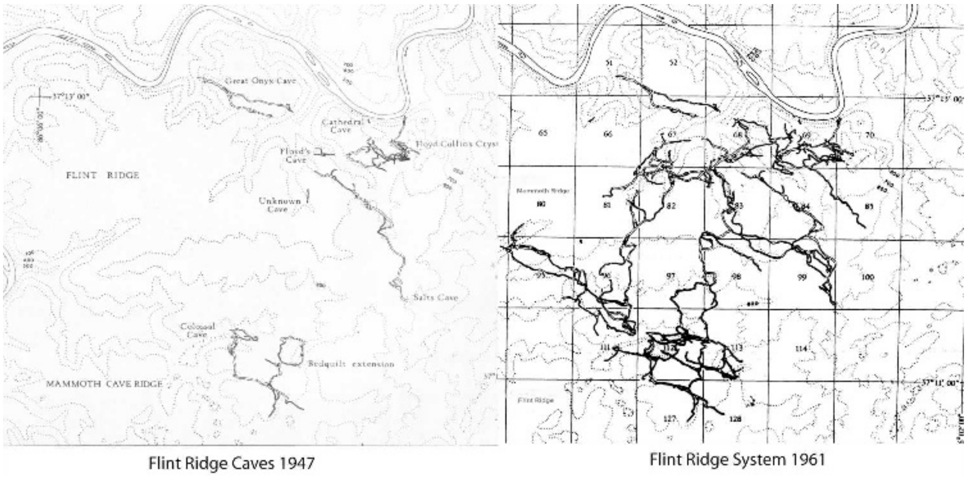
Figure 1. Stephen Bishop's map of Mammoth Cave, 1842 (CRF, 1976)

provided important observations that would impact future explorations and science. Map overlays showed that cave passages could extend out from the major ridges and under the valleys in the Mammoth Cave area (Smith, 1960). Many of the large cave passages were determined to be segmented pieces of longer passages that had been dissected by valley development (Brucker, 1966). Vertical shafts that were very common in the Mammoth Cave area could penetrate through tiers of horizontal passages giving access to previously unexplored cave (Brucker et al., 1972).

By 1961, the major caves of Flint Ridge, including Crystal, Unknown, Colossal, and Salts Cave were connected (Fig. 2). In addition to the speleological accomplishment of connection, systematic exploration also began to confirm and answer geological questions and to cast doubt on Davis' theories on the origins of limestone caves (Smith, 1960). Survey notes, working draft maps, written observations, and detailed reports revealed not only the geographic extent of the caves, but noted the cross-sectional shapes of passages and the features within the passages. These were the types of details necessary to successfully explore a cave system, and also to begin understanding how cave systems formed. Topographic overlays gave geographic context to the morphology and extent of cave passages. In effect, exploring and describing the Flint Ridge System made it possible to begin a rational description of both the cavern-forming process in general, and the history of the Flint Ridge cave complex in particular (Smith, 1964).

One of the first geologic questions that was addressed by the systematic exploration/survey method was the origin of vertical shafts in the caves of Flint Ridge. Though a number of theories were proposed to explain them, a geographic context was missing. Pohl (1955) set forth the hypothesis that the vertical shafts were related to the solutional enlargement of vertical cross joints and that their development was related to the process of headward and areal advance of surface valleys. Cave surveys which located vertical shafts, when added to the topographic overlays, confirmed that the vast majority of these features were indeed located at the edges of the sandstone-capped ridges (Fig. 3). Observations made during survey trips indicated that there was no relationship between the vertical shafts and lateral passages and that shaft drainages use lateral passages only when these passages occur at base level and beneath actively forming shafts (Smith, 1957). Systematic exploration confirmed that vertical shafts were not speleogenetically related to the vast passages and rooms that they intersected (Brucker et al., 1972).

The occurrence and significance of breakdown was another question whose answer was augmented by the observations of cave explorers. According to observations by Davies (1951), limestone and sandstone breakdown can occur where passages are close to the surface, especially where horizontal cave passages are intersected by hillsides. The intersection of large passages could also result in breakdown. However, there were areas in the Flint Ridge caves where none of those conditions existed, but



Flint Ridge Caves 1947

Flint Ridge System 1961

Figure 2. Flint Ridge System 1962 (CRF, 1966).

breakdown still occurred. Cave explorers reported white crystalline coatings and crusts associated with breakdown, and the samples brought back by explorers were identified as gypsum and other sulfates. With that information, it was determined that *in situ* mineral growth of gypsum and other sulfates along bedding planes and joints put pressure on these zones of weakness and caused the rock to peel off the ceiling and walls, thus forming breakdown (Smith, 1957).

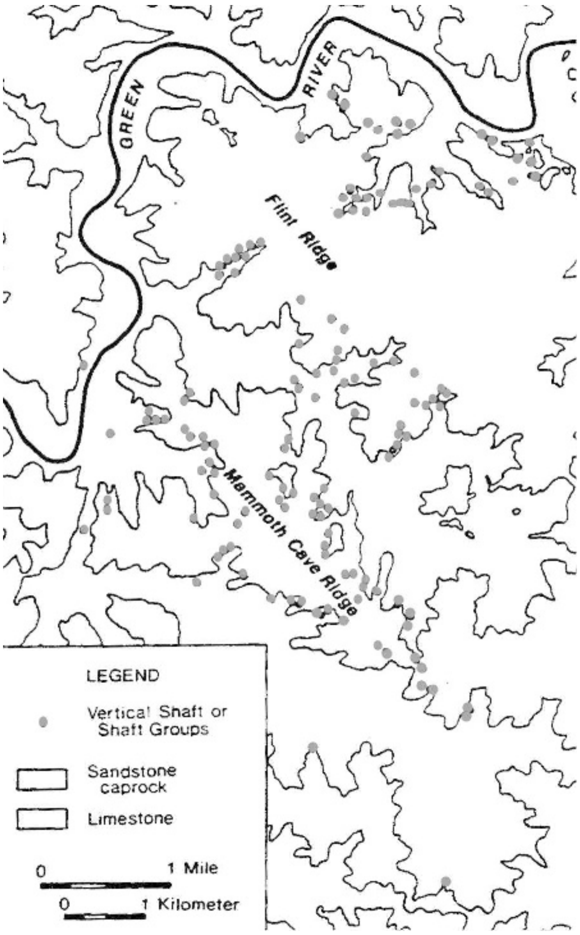


Figure 3. Vertical shafts in the Mammoth Cave area (from White, 1988).

Exploration of new passages in Flint Ridge revealed unusual, previously undescribed speleothems. Photographs were made of the new features and samples were later collected by the exploration team. Laboratory analysis showed that gypsum could combine with other soluble sulfates to produce metastable sulfate minerals like mirabilite. The results of this study were published in an issue of Science (Bennington, 1959) and revealed that thermodynamically unstable mineral phases developing at relatively low temperatures might indicate the occurrence of complex heterogeneous reactions worthy of further kinetic studies (Smith, 1960).

Black coatings observed on the ceilings of passages in Mammoth and Salts Caves were initially thought to be manganese. However, analysis revealed that the coatings were organic; specifically soot (Smith, 1960). Exploration teams reported that soot coatings were always found in association with archaeological material (unpublished Cave Research Foundation reports 1957–1965). As systematic exploration progressed into previously unknown territories, more archaeological artifacts and traces of activities were discovered. In 1962, Watson began a systematic inventory of archaeological features. Not only did she determine that ancient people had used the cave for mining purposes (Watson, 1969), her research ultimately revealed that the prehistoric people in Kentucky and the Eastern Woodlands were among the few indigenous populations in the world to independently develop an agricultural economy, well before domesticated plants were introduced from Mexico (Watson, 1992). Watson was inducted into the National Academy of Sciences in part because of this work.

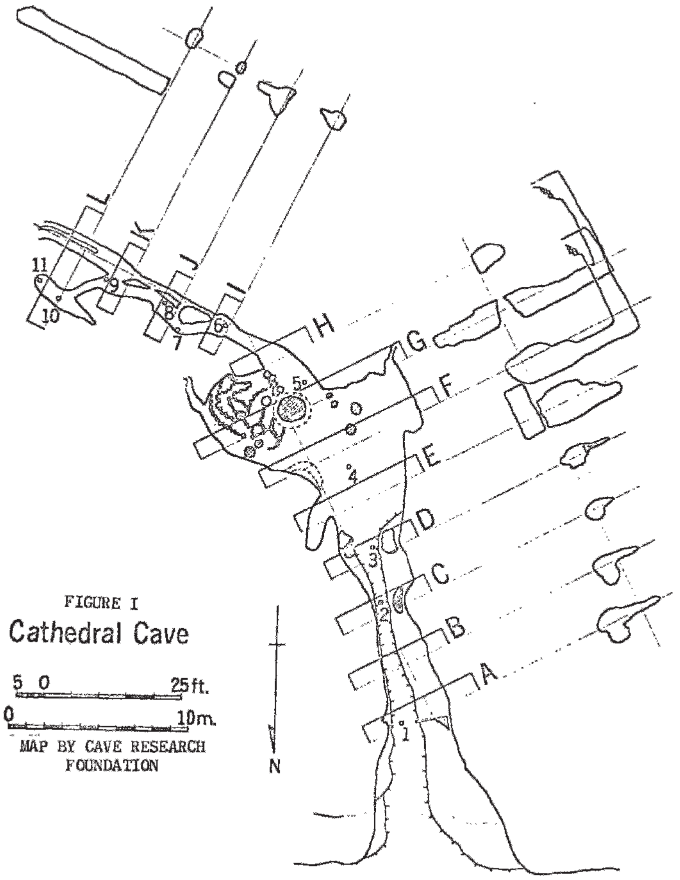


Figure 4. Cathedral Cave, Mammoth Cave National Park (CRF, 1961)

CRF helped support biologic research on cave animals by producing cave maps for baseline ecologic studies. The map of Cathedral Cave (Fig. 4) in Mammoth Cave National Park, with base line transects noted, was provided to researchers who were conducting studies on population dynamics of cave fauna (CRF, 1961). This was the beginning of many biologic studies in the Mammoth Cave area. The observations by survey teams about the composition of sediments and other material on cave passage floors (substrates) provided important information for research on cave ecology. Kane and Poulson (1976) studied the foraging habits of cave beetles in heterogeneous mixes of substrates and homogeneous substrate (uncompacted sand) in Little Beauty Cave and in Great Onyx Cave, respectively. Studies on the long-term effect of weather on cricket populations within White Cave and Little Beauty Cave demonstrated the importance of weather patterns on cricket populations (Poulson, et al., 1995). Poulson (1991) established that aquatic subterranean faunal populations were important indicators of groundwater quality.

The systematic exploration conducted by CRF provided the field evidence necessary for scientists to begin to formulate a regional overview of the geologic processes and cave development of the Mammoth Cave area. As a result of this extensive field work and the interpretation of the data by White et al. (1970), a paper titled "The Central Kentucky Karst" was published in *The Geographical Review*. The paper discussed the geology, mineralogy, and hydrogeology, and their relationship to underground karst features. The work outlined the physiographic evolution of the Mammoth Cave area and classified karst as a dynamic system. This new perspective on cave development replaced the Davisian model of deep phreatic-cave development for the Mammoth Cave region.

After the 1961 connections at Flint Ridge, CRF extended their efforts to Mammoth and Joppa ridges. In 1969 the Flint Ridge System became the longest in the world at 108 km in surveyed length. Concurrent systematic explorations at Mammoth Cave brought its surveyed length to 73 km making it the third longest behind Hoelloch (Switzerland). These impressive accomplishments in speleology were just interim goals for those who were dedicated to systematic exploration. With their eyes on the next prize, CRF explorers aimed at connecting the first and third longest caves in the world. Long and difficult cave trips guided by working maps and the observations and reports of many survey teams pushed the limits of the Flint Ridge System under Houchins Valley and into Mammoth Ridge. In 1972, a small team of CRF cavers, representing the cumulative efforts of all of those before them, connected the Flint Ridge System to the Mammoth Cave System making it the longest cave in the world with a length of 232 km (Brucker and Watson, 1976).

In 1978, cave explorers discovered a subterranean river under Joppa Ridge and it was ultimately connected to the Flint-Mammoth Cave System. Systematic exploration pushed the upstream extent of the Logsdon River east under a valley toward Toohey Ridge, the home of Roppel Cave, whose exploration and survey was a project of the Central Kentucky Karst Coalition (CKKC). In 1983, CRF and CKKC connected Roppel Cave to the Flint-Mammoth Cave System (Borden and Brucker, 2000). The new connection brought the surveyed length of the Flint-Mammoth-Roppel System to 493 km.

While active exploration efforts extended the physical limits of the Flint-Mammoth Cave System into triple digits, scientific research that utilized the baseline data and derivative products generated from cave surveys flourished. In the early seventies, researchers began a leveling and geologic survey in Floyd Collins Crystal Cave with the goals of determining the stratigraphic section in which the Flint-Mammoth Cave system is developed, to clarify the presence of passage levels and their geomorphic significance, and to make a detailed map of the cave (Palmer, 1987). They used copies of the original survey notes that spanned twenty-five years of exploration effort to construct a base map. In 1974, the stratigraphic column from Crystal Cave was extrapolated to most of the major cave passages in the Flint-Mammoth Cave System. Passage levels were

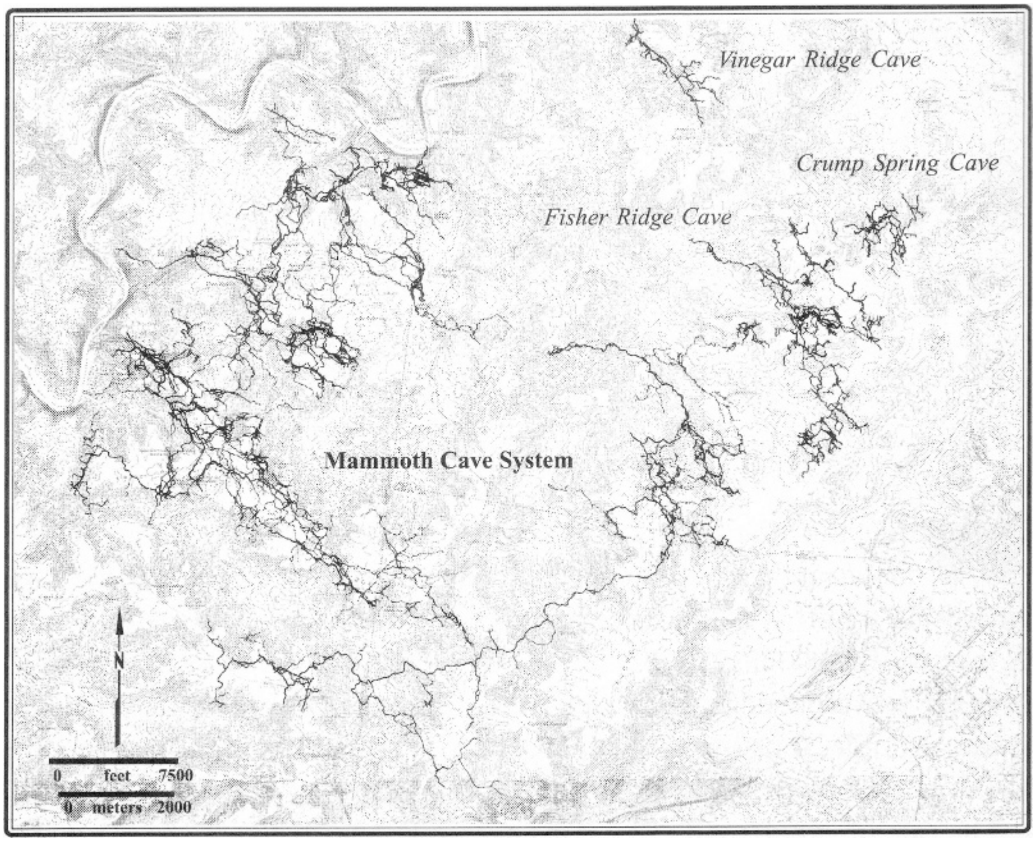


Figure 5. Caves of the Mammoth Cave region (Borden and Brucker, 2000).

described and correlated with the geomorphic history of the surrounding landscape (Miotke and Palmer 1972). The relevance of the passage level data from the geologic and leveling study was augmented with cosmogenic dating of gravels from Mammoth Cave. The results of this collaboration illustrated the far-reaching effects of Pleistocene glaciation on the evolution of the Ohio River valley, on the Green River, and ultimately on the Flint-Mammoth Cave System (Granger et al., 2001).

Hydrogeology is an important research frontier in the Mammoth Cave area. With a current extent of over 608 km, the Flint-Mammoth Cave System consists of a huge collection of active, semi-active, and inactive conduits that are parts of a vast karst aquifer.

Early work on hydrogeology in the Mammoth Cave area was conducted by White et al., (1970), White (1976), Hess and White (1973, 1974), and Miotke (1975). Extensive dye tracing and geochemical analysis by Jim Quinlan, who worked as the geologist for Mammoth Cave National Park, augmented the ongoing hydrogeologic studies. Quinlan maintained that systematic cave exploration/survey was the key to discovering and understanding the hydrology of the flow system of a principle karst aquifer (Quinlan et al., 1983). CRF provided support for Quinlan's hydrogeologic studies in the form of cave maps that he considered critical for his research inside Mammoth Cave National Park (Zopf, 1982). Quinlan also utilized teams of cave explorers who worked outside of the National Park to provide the data and insight necessary to study the vast aquifer of the Mammoth Cave region (Quinlan et al., 1983). His teams discovered and documented an underground distributary system on the Green River, the Hidden River Complex that was hydrogeologically related to Hidden River Cave in Horse Cave, Kentucky (Coons, 1978). They also discovered and conducted systematic exploration in Whigpistle Cave which Quinlan proved via dye traces to be hydrogeologically connected to the Flint-Mammoth Cave System (Coons, 1978). Exploration-related data augmented Quinlan's study of the movement of groundwater in the Mammoth Cave region. His research ultimately revealed that agricultural and industrial contaminants were entering the Flint-Mammoth Cave System from places outside of the national park (Quinlan, 1989).

A specific example of the practical application of Quinlan's findings involved his identification of a sewage treatment plant in Horse Cave, Kentucky as a source of groundwater pollution. The seriousness of the pollution was reflected in Hidden River Cave, located in the middle of town. The stench of sewage rose from the cave entrance and permeated the downtown area. The treatment plant was discharging heavy metals into the groundwater and

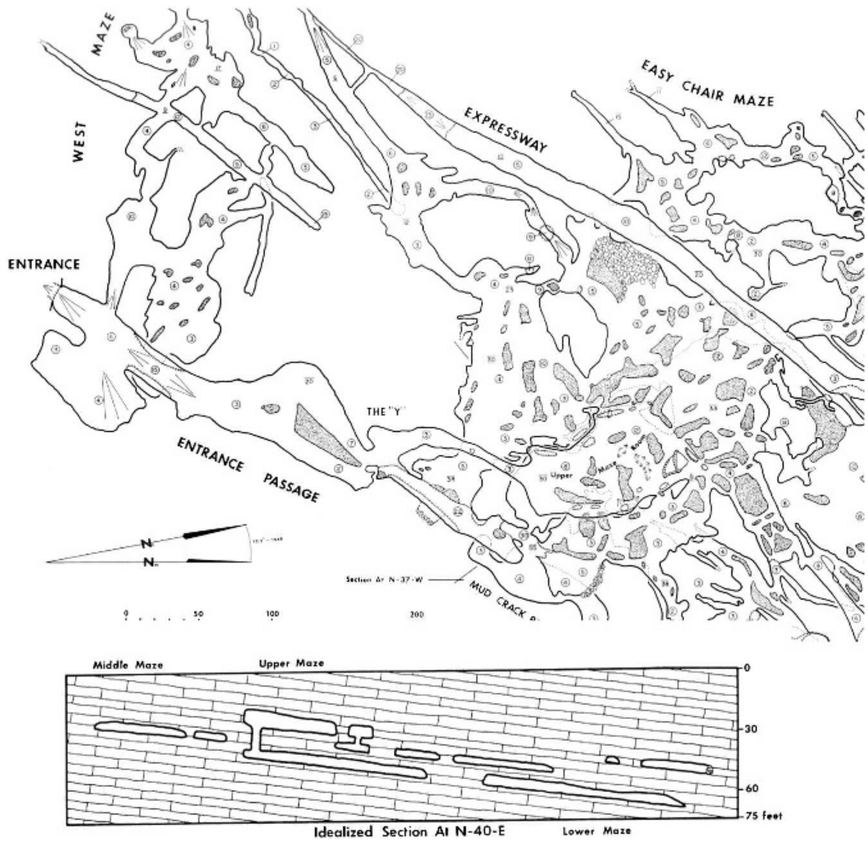


Figure 6. A section of Endless Cave, New Mexico (from Kunath, 1978).

was not effectively treating sewage (Quinlan, 1989). Once the physical functioning of the sewage treatment plant was upgraded, there were significant improvements in the water and air quality of Hidden River Cave.

The 1978 discovery of the Logsdon River made it possible for scientists to study the behavior and characteristics of a karst aquifer from the inside. Based on cave survey and cave radio-locations, Quinlan instigated the drilling of an entrance shaft and a series of wells directly into the Logsdon River to facilitate ongoing hydrogeology-related research. The new entrance shaft allowed the installation of data-logging equipment that monitored changes in stream flow and groundwater chemistry over a variety of timescales. Groves and Meiman (2001) were able to quantify that large storm events play a significant role on karst aquifer development. Groves et al. (2001) also observed that interstitial cave-stream fluids showed evidence of bacterial functions that may influence aquifer evolution.

A regional map of the Mammoth Cave area (Fig. 5) shows the results of fifty years of systematic cave exploration in the region. Over 833 km of passages have been explored and mapped not only within the Flint-Mammoth Cave System, but in other caves located outside of the national park. Quinlan et al., (1983) suggested that the potential for over 1,600 km of human-sized passages exists in the Mammoth Cave area. This potential continues to motivate cave explorers to extend the limits of the world's longest cave system, and for cave scientists to expand the frontiers of knowledge about such topics as karst aquifers, ancient human use of caves, water-rock interactions and their effects on cave development, and the role of microbiology in speleogenesis.

CASE STUDY 2: CAVE EXPLORATION AND SCIENCE IN THE GUADALUPE MOUNTAINS, NEW MEXICO

The caves of the Guadalupe Mountains have long held the fascination of cave explorers and cave scientists alike. In the early days of cave exploration and research, the caves proved to be enigmatic to both groups because of the morphology and layout of the caves, by the seeming lack of relationship between cave and surface features, and by the occurrence of massive gypsum deposits and other unusual mineralogy. The first two factors made caves difficult to find, explore, and map. All three proved puzzling within the scientific context of what was known about cave development.

Earliest explorations of caves in the Guadalupe Mountains began in the latter part of the 19th century (Kunath, 1978). Jim White first entered Carlsbad Cavern in 1898 (Selcer, 2006) and extensively explored it for thirty years (White, 1932). In the early part of the twentieth century, Nymeyer (1978) photographed many of the caves in the Guadalupe Mountains and published photographs along with accounts of his explorations in a book titled *Carlsbad, Caves and a Camera*. However, systematic exploration and mapping of Guadalupe Mountain caves did not begin until the 1960s (Kunath, 1978) with work by the Texas Speleological Survey, the Guadalupe Cave Survey (which later became part of Cave Research Foundation) and, some of the local grottos in Texas and New Mexico. The cave maps produced from those efforts illustrated the complex three-dimensional morphology of the caves (Fig. 6). Some sections of cave maps were intentionally omitted due to the difficulty of graphically rendering multi-level mazes in two dimensions (Lindsley and Lindsley, 1978). Detailed descriptive summaries written by cave explorers provided information about cave features (Kunath, 1978) and reported on unusual mineralogy (Davis, 1973).

The first geologist to study Guadalupe Mountain caves was Willis T. Lee. He participated in two expeditions to Carlsbad Cavern sponsored by the National Geographic Society. Lee's contributions were mostly descriptive in nature and he made a preliminary survey of the cavern which was published in National Geographic Magazine along with photographs by Ray Davis (Lee, 1924, 1925). J Harlen Bretz conducted scientific field work in Guadalupe Mountain caves in 1948 (without the benefit of cave maps), proposing that the caves were phreatic in origin. Bretz (1949) identified the gypsum deposits he observed as a type of gypsum flowstone. Other geologists hypothesized that massive gypsum was the result of a late-stage backup of water from the Castile Formation of the Delaware basin (Jagnow et al., 2000).

As cave scientists began to develop models for speleogenesis in the Guadalupe Mountains, they realized that the models needed to take into account the morphology and layout of the caves had to explain the lack of relationship between cave and surface features, and needed to account for the occurrence of massive gypsum deposits and other unusual mineralogy (Smith, 1978).

Queen (1973) and Palmer et al., (1977) suggested that the gypsum deposits might be related to a process of speleogenesis rather than being the result of vadose secondary mineralization. According to their speculations, the origin of the gypsum deposits could result from replacement of carbonate rocks by gypsum as a result of fresh meteoric water mixing with gypsum-saturated brine already in the rock. Palmer prefaced the hypothesis by expressing caution in accepting it without substantial field evidence (Smith, 1978).

Stephen Egemeier suggested that Carlsbad Cavern may have been dissolved by sulfuric acid (Egemeier, 1971). Other geologists began to see evidence from their field work and observations, of the possibility of a sulfuric acid origin of caves in the Guadalupe Mountains (Davis, 1973; Jagnow, 1978; Hill 1981).

In 1986, an important cave exploration breakthrough in Lechuguilla Cave provided a unique opportunity to test and expand the ideas of a sulfuric acid speleogenesis model and ultimately shifted the focus of research from Carlsbad Cavern to Lechuguilla Cave (Jagnow et al., 2000).

EXPLORATION OF LECHUGUILLA CAVE: A BIGGER PIECE OF THE PUZZLE

For decades, cave explorers had been intrigued by a small guano cave located above Walnut Canyon in Carlsbad Caverns National Park. The cave had a vertical entrance, was not very extensive, and did not contain any speleothems of interest. It was mined for guano for a short time, but then abandoned (Frank, 1988). However, a gale of air issued from a breakdown pile at the base of the entrance shaft. On some days, it sounded like an underground freight train and wisps of dusty sediment were blown up the 27 m long entrance shaft. The source of that wind enticed cave explorers to attempt digging the sediment encrusted breakdown pile at the base of the entrance shaft. Several digging projects were conducted by different caving groups beginning in the 1950's. A group of Colorado cavers re-energized the digging effort in 1984 and in May of 1986 they lucked out when a section of breakdown collapsed into going cave passage (Bridges, 1988). The breakthrough in Lechuguilla Cave would become one of the most significant discoveries of the twentieth century both in terms of cave exploration and cave science (Turin and Plummer, 2000).

The gale-force winds issuing from the breakdown pile in the entrance of Lechuguilla Cave practically guaranteed the existence of a vast cave system. And cave explorers knew that the geology of the area provided the potential for significant depth. The Lechuguilla Cave Project (later replaced by Lechuguilla Exploration and Research Network formed in 1991) was formed in 1987 to provide structure to the systematic exploration effort. Survey standards were established that were similar to those utilized by CRF. However, a much stronger emphasis was placed on vertical control and all surveys were required to include running vertical profiles (Kambesis and Bridges, 1988).

Cave explorers from all over the US and the world participated in the exploration and survey of Lechuguilla Cave. Exploration and mapping moved at breakneck speed with the discovery of 33 km of new passages within the first year (Reames et al., 1999). In order to keep up with the large volume of survey data generated by the exploration effort, computer programs were specifically written to process and plot the survey data (Petrie, 1988). Project members took turns inputting survey data to the ever-expanding database that grew by leaps and bounds after each trip. This mode of exploration and survey assured that the next team who continued the exploration would have a plot of passages that had already been mapped and a view of the relationship between areas of ongoing exploration.

Figure 7. Massive gypsum in Lechuguilla Cave.

This tag-team style of exploration ensured that survey data was continuously being produced for the entire duration of each expedition (Bridges, 1988). Exploration teams consulted the survey notes, line plots, and trip reports, and used the information to plan their next push.

Photography was a regular part of the documentation effort. As exploration progressed, so did photo-documentation of incredible new areas, spectacular speleothems, and highly unusual sediments and mineralogy. Each survey team was required to write a detailed account of their findings, including routes to the survey area, descriptions of unusual cave features, observations about air movement, location of water, and a summary list of unexplored leads. At the end of each expedition, a detailed summary report, with survey statistics, line plots, and trip reports was submitted to the cave specialist at Carlsbad Caverns National Park. Photographs were provided as they became available.

With each expedition, the depth of the cave survey plummeted until it was stopped in the lower part of a water-filled fissure where the cave attained a vertical extent of 489 m (Davis, 1990). Explorers speculated that this was the water table, which was an unprecedented find in any cave of the Guadalupe Mountains (Kambesis, 1991). Exploration reports described the existence of superlative speleothems, some never before documented (Davis, 1990). Fluffy piles of sediment, initially identified as corrosion residues, were observed to occur in hues of tan, red, yellow, black, and brown. Massive gypsum glaciers (Fig. 7) and mounds of sulfur covered the floors of some passages. Though the cave was situated under the Chihuahuan Desert, each expedition revealed the existence of more pools and lakes throughout the vertical extent of the cave. Flowing water was even observed in the Far East section of the cave (Kambesis, 1991). By 1990, the explorers of Lechuguilla Cave had discovered and mapped over 83 km of passages. In 1998 the cave length had reached 166 km with a vertical extent of 489 m.

ON THE HEELS OF EXPLORATION

The availability of line plots and preliminary maps, elevation data, detailed reports, and spectacular photographs from the exploration effort instigated field work for cave research to follow on the heels of exploration.

When the profile map of Lechuguilla Cave was correlated to the stratigraphic section of the Guadalupe Mountains, it revealed that the cave spanned most of the Permian-aged reef complex from the back reef Yates formation, through the massive Capitan Formation and down to the Goats Seep (Jagnow, 1989). The profile illustrated that the cave cut through the heart of the fossil reef (Jagnow, 1989; DuChene, 2000). From the study of cave maps came insights into the characteristic morphologies and patterns of caves formed by sulfuric acid (Palmer, 1991).

Researchers conducted a geologic survey of Lechuguilla Cave and other caves in the Guadalupe Mountains in order to relate geomorphic features of the caves to past hydrologic- and geochemical-dissolution regimes (Palmer and Palmer, 2000). The discovery of alunite, natroalunite, and dickite in Lechuguilla Cave (Palmer and Palmer, 1992), and the subsequent finding of the same minerals plus a suite of uranium-vanadium minerals and hydrobasaluminte in other Guadalupe Mountain caves (Polyak and Mosch, 1995; Polyak and Provencio, 1998) established that these minerals, along with sulfur and gypsum, and the occurrence of gypsum deposits, were characteristic of the sulfuric acid mode of cave dissolution. In addition, the sulfuric acid model of speleogenesis seemed to account for the cave patterns and morphologies, and explained the lack of relationship between surface and cave features in

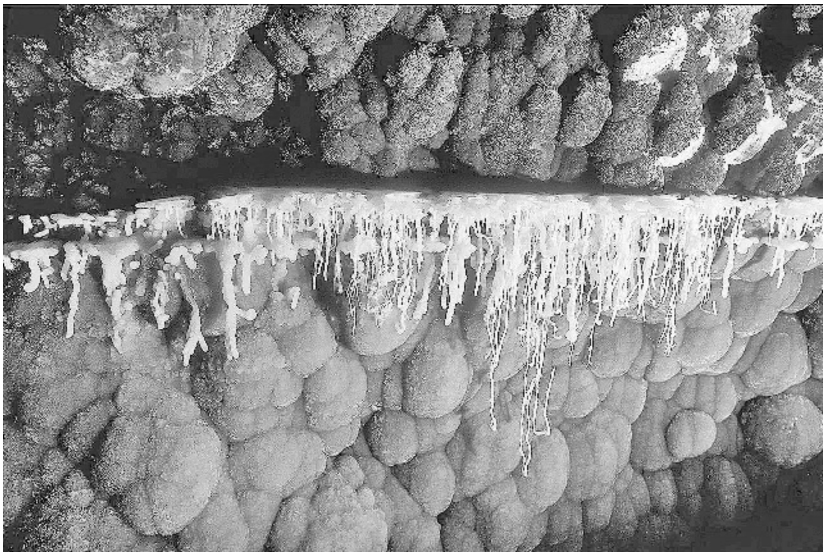


Figure 8. Underwater helictites, Lechuguilla Cave.

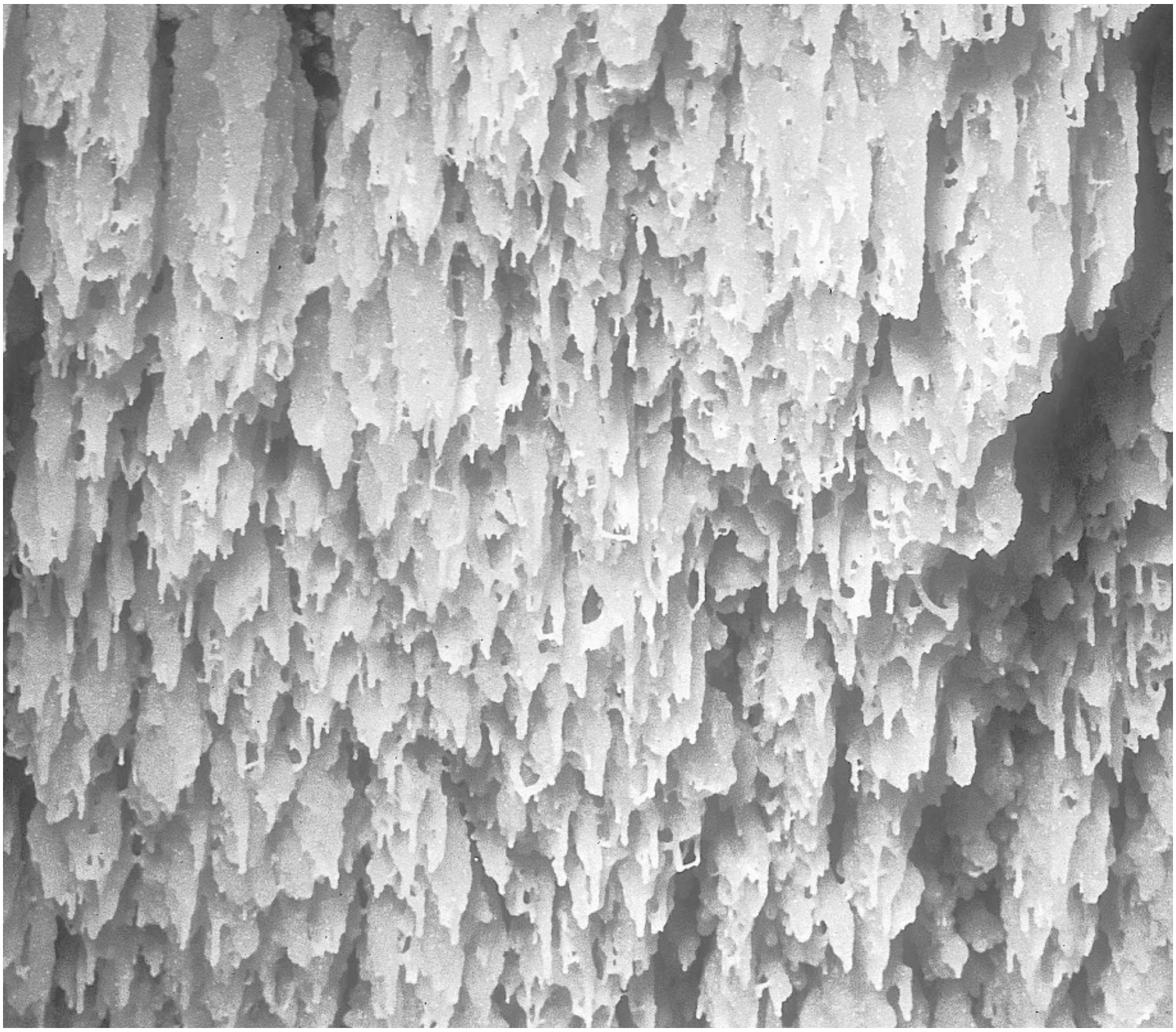


Figure 9. Webulites in Lechuguilla Cave.

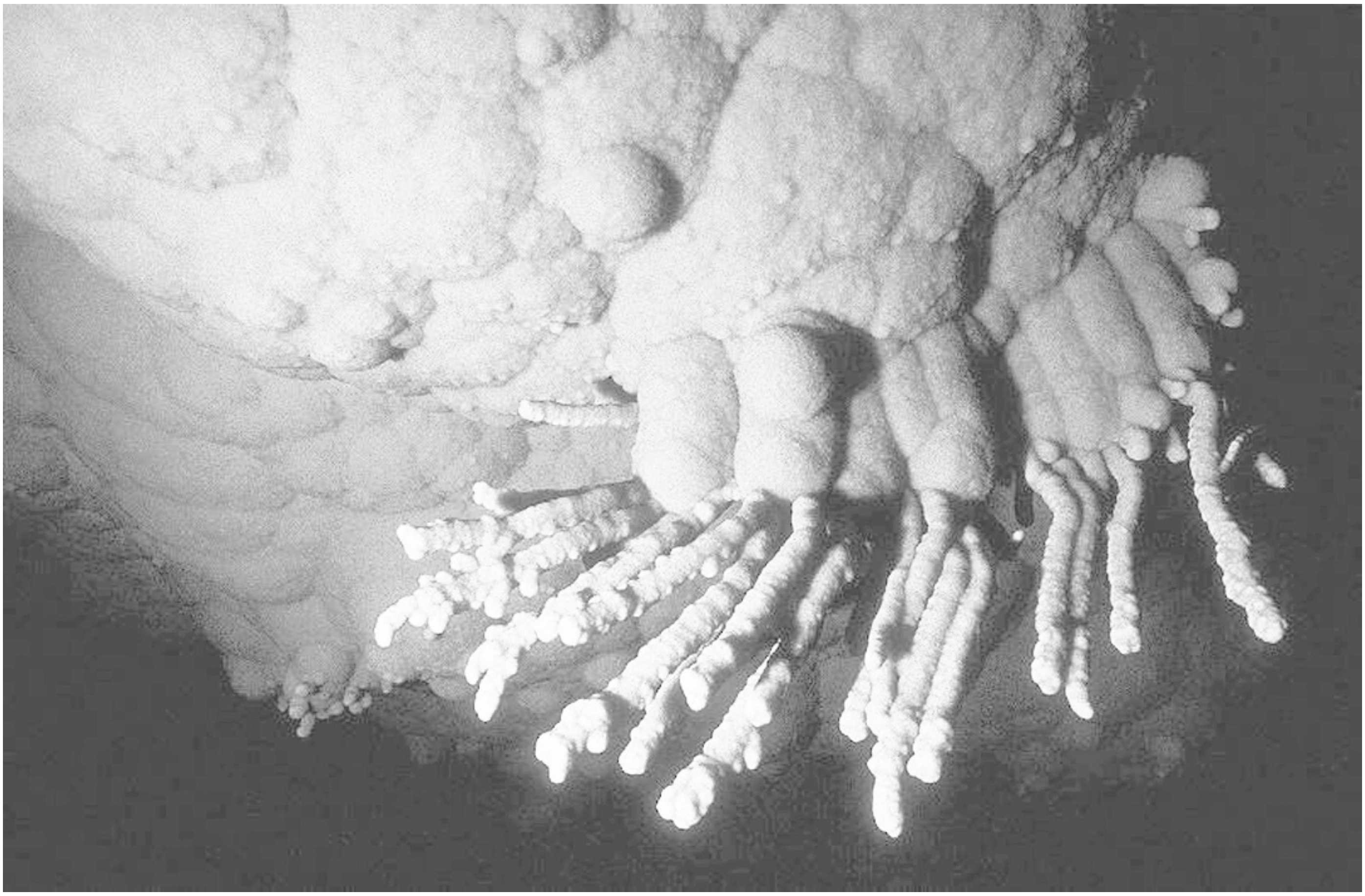


Figure 10. Pool fingers in Lechuguilla Cave.

Guadalupe Mountain caves. The model also established a characteristic set of minerals that were considered definitive indicators of sulfuric acid dissolution. And finally, from $^{40}Ar/^{39}Ar$ dates on alunite, absolute dates were determined for four elevation levels that were correlated across a series of Guadalupe Mountain caves (Polyak and Provencio, 1998).

Water sampling in the numerous pools scattered throughout the vertical extent of Lechuguilla Cave commenced shortly after these features were first reported. Water analyses indicated that the pools represented isolated samples of vadose-zone water infiltrating along separate and independent flow paths (Turin and Plummer, 2000). Pool composition, which is a function of precipitation chemistry, bedrock, and the occurrence of gypsum deposits, could also affect the development of some speleothems such as underwater helictites (Fig. 8). The geochemistry of water from the deep points in the cave confirmed that the water table had indeed been reached (Turin and Plummer, 2000).

Analyses of pieces of some of the more unusual speleothems reported on and collected by cave explorers (with permission of Carlsbad Caverns National Park) revealed a totally unexpected result. Features such as webulites and u-loops (Fig. 9) appeared to be calcified filamentous microorganisms (Cunningham et al., 1995). Pool fingers (Fig. 10) provided evidence of possible bacterial/mineral interaction in their formation (Northup et al., 1997). Iron oxide speleothems (rusticles) showed the presence of organic filaments in their cores (Davis et al., 1990). Corrosion residues, which are common throughout Lechuguilla Cave and also occur in many other caves in the Guadalupe Mountains, are composed of iron oxide and manganese materials containing bacterial and fungal communities (Cunningham, 1991; Cunningham et al., 1995). Northup et al. (1997) proposed that microbes could dissolve cave features via acidic metabolic byproducts.

Recent studies on the ecologic interactions of bacteria that exist in Lechuguilla Cave have shown that the enzymes they produce may be beneficial to the treatment and potential cure for some human diseases (Northup et al., 1997). Researchers from NASA, who have been looking for extreme environments on the earth that may be analogous to life on other planets, have been studying the microorganisms in Lechuguilla Cave (Boston, 2000).

Though exploration and survey have been ongoing in Lechuguilla Cave for the past twenty years, the full extent of the cave system has not yet been realized. Despite great progress in defining the processes that formed the cave, the boundary conditions that resulted in its development are not yet fully understood. As explorers venture into unknown territories in their pursuit of more cave passages, they will uncover more evidence that will result in the continued evolution of theory on Guadalupe Mountain cave development. Cave scientists will continue to pursue the fruits of exploration for analysis and study.

Conclusion

Systematic cave exploration involves not only the physical pursuit and discovery of caves and cave systems, but also includes the systematic documentation of those discoveries. The field documentation that defines systematic cave exploration includes cave and surface surveys, detailed notes and observations, cave and karst feature inventories, and photo-documentation. The data are synthesized into cave maps, narrative descriptions, and reports that can serve as a set of exploration tools for finding more passages and caves and also serve as the baseline for all types of cave-related research. Cave exploration is a fundamental element of cave research and cave-related science.

Acknowledgements

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[1] Editor's Note: Quinlan (1989) has never been published although it was released selectively in draft form.

J.R. Mylroie and J.E. Mylroie – Development of the carbonate island karst model. *Journal of Cave and Karst Studies,* v. 69, no. 1, p. 59–75.

DEVELOPMENT OF THE CARBONATE ISLAND KARST MODEL

JOAN R. MYLROIE AND JOHN E. MYLROIE
Department of Geosciences, Mississippi State University, Mississippi State, MS 39762 USA, mylroie@geosci.msstate.edu

Abstract: The development of a comprehensive conceptual model for carbonate island karst began in the Bahamas in the 1970s. The use, initially, of cave and karst models created for the interior of continents, on rocks hundreds of millions of years old, was not successful. Models developed in the 1980s for the Bahamas, that recognized the youthfulness of the carbonate rock, the importance of fresh-water mixing with sea water, and the complications introduced by glacioeustatic sea-level change produced the first viable model, the flank margin cave model. This model explains the largest caves in carbonate islands as being the result of mixing zone dissolution in the distal margin of the fresh-water lens, under the flank of the enclosing land mass. The flank margin model, taken from the Bahamas to Isla de Mona, Puerto Rico, in the early 1990s, provided the first viable explanation for the very large caves there. Field work in the geologically-complex Mariana Islands in the late 1990s resulted in the development of the Carbonate Island Karst Model, or CIKM, which integrated the various components controlling cave and karst development on carbonate islands. These components are: 1) Mixing of fresh and salt water to create dissolutional aggressivity; 2) Movement of the fresh-water lens, and hence the mixing environments, by 100+ m as a result of Quaternary glacioeustasy; 3) The overprinting of glacioeustatic changes by local tectonic movements, where present; 4) The unique behavior of eogenetic (diagenetically immature) carbonate rocks; and 5) The classification of carbonate islands into simple, carbonate cover, composite, and complex categories. Current research involves the use of flank margin caves as predictors of past and present fresh-water lens configuration, the analysis of flank margin cave morphology as a measure of the processes that create them, and the CIKM as an indicator of paleokarst distribution.

INTRODUCTION

This paper is designed to present to the National Speleological Society reader an understanding of the unique and unusual types of caves and karst that form in tropical carbonate islands. It will also summarize how, for the last 35 years, we have pursued island caves around the world, and attempted to figure out why they are there, and how they formed. Given that it has been 40 years since the JCKS published an anniversary issue such as this one, the time frame is about right to present a review article that takes the reader through the development of ideas about caves and karst on islands, and what we understand today. The research began in the Bahamas, which as will be seen, was fortuitous as they represent some of the simplest carbonate islands that can be found anywhere. (We use the term carbonate island, instead of limestone island, to take note that the rocks we are dealing with contain three carbonate minerals: calcite and aragonite which are different forms (or polymorphs) of calcium carbonate, $CaCO_3$; and dolomite, a calcium-magnesium carbonate, $CaMg(CO_3)_2$.)

We explored and mapped (crudely) our first island cave, Hunt's Cave on New Providence Island, Bahamas, while on a tourist visit in 1971. As northeastern U.S. cavers, we found the heat of the caves and the ever-present biota, especially cockroaches, to be quite a shock (we came back in 1990 and mapped it properly). In 1974 we accompanied Art and Peg Palmer, of Oneonta State University, to Bermuda at the invitation of Mike Queen (then at the Bermuda Biological Station), to map caves and to examine the unusual karst processes in operation. As it turned out, Bermuda caves are somewhat unique, even among island caves, and the team could not agree on how the caves were forming. Beginning in 1976, we began making annual field trips with James Carew, now at the College of Charleston, and our students to the Bahamas, first to North Andros Island in 1976, then to San Salvador Island from 1977 to the present. The hook was set, and we have been captivated and intrigued by island caves ever since. The research began as a two steps forward, one step backward experience as our ignorance of island karst processes was slowly replaced by a growing appreciation for the specialized environment we were observing.

EARLY RESEARCH

For over a decade we applied the models and theories of cave development established by research on continental caves to the caves of the Bahamas, and we had little luck in

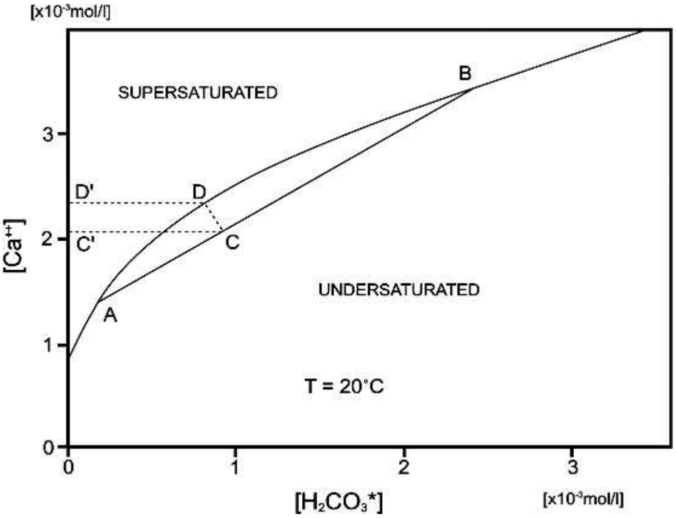

Figure 1. Equilibrium curve for $CaCO_3$, after Dreybrodt (2000). See text for explanation.

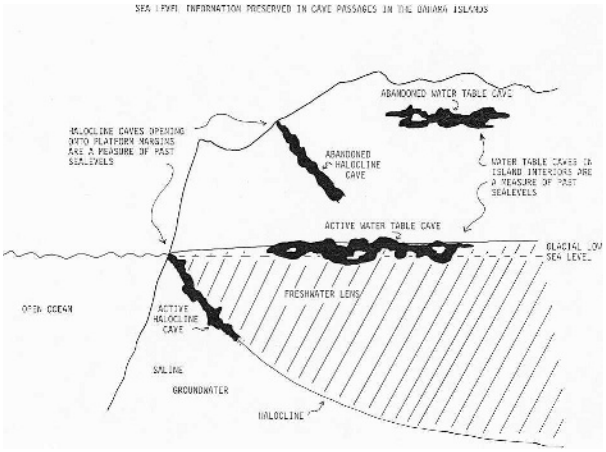

Figure 2. Figure 6 of Mylroie and Carew (1988b). This figure shows water table caves as mixing chambers and not true conduits. The halocline cave's apparent steep dip is a result of vertical exaggeration, and is shown as a conduit discharging directly to the sea. Sea level controls are also evident.

understanding what was going on. In 1991, Palmer (1991) described two major classifications of caves: epigenic caves that are coupled to the surface hydrology, and commonly have sinking streams, caves as turbulent flow conduits, and springs. The second classification was hypogenic, meaning that the cave formed by dissolution in the subsurface as a result of mixing of waters of different chemistry; these caves lack sinking stream inputs or conduits carrying turbulent flow to discrete springs because they are uncoupled from the surface hydrology. Our initial investigations treated the caves of the Bahamas as epigenic in type, although the term hadn't been published yet. We then began to consider what was unique about the island setting, and started to back away from continental theories. We recognized that sea level controlled the position of the fresh-water lens in islands, but we still were conceptually tied to the idea of continental stream caves (Carew et al., 1982; Mylroie, 1983; Mylroie and Carew, 1988a). Some of these ideas, in hindsight, are quite amusing. We also generated some papers, based on amino acid racemization (AAR) dating of rocks in the Bahamas, that attempted to portray cave development as occurring in very short time periods (Mylroie and Carew, 1986a, 1986b, 1987). It turns out that we were correct about the rapid cave development, we just had the wrong time window in the Quaternary because of the bad dates from the AAR work (see Carew and Mylroie, 1997, for a discussion of the AAR problem).

Palmer et al. (1977), drawing on the geochemical work of Bögli (1964, *in* Bögli 1980) and Plummer (1975), had advanced a theory that mixing of marine and fresh waters under carbonate islands could create an environment of enhanced dissolution, and so explain cave development on Bermuda. In the late 1970s and early to mid 1980s, Bill Back and his co-workers published a series of papers (Back et al., 1986 and references therein) that used the mixing of sea water and fresh water under carbonate coasts as a way of explaining porosity and permeability development, dolomitization, and coastline evolution in the Yucatan Peninsula. The essential geochemistry is presented in Figure 1 (Dreybrodt, 2000). Because the saturation curve for $CaCO_3$ is convex upward, waters saturated at two different initial conditions, as at A and B in the figure, when mixed create a water body, C, that is beneath the saturation curve, and so is unsaturated. This water body now has renewed dissolutional potential and will dissolve $CaCO_3$ until it again reaches the saturation curve at D. The amount of Ca^{2+} put in solution is shown by the step from C' to D'. Seawater, and the fresh-water lens in carbonate islands, are usually saturated with respect to $CaCO_3$, but they did so at different initial conditions. Therefore their mixing produces an unsaturated solution, and dissolution will create caves. It was also recognized that descending vadose water, upon reaching the top of the water table at the fresh-water lens, could also mix and create a site of renewed dissolutional aggressivity.

Examination of how these ideas could affect island karst were presented in a paper published in 1988 (Mylroie and Carew, 1988b), that focused on the migration of the fresh-water lens as sea level changed during the Quaternary (Fig. 2). An important misconception arose out of this figure. The fresh-water lens was drawn as commonly found in textbooks and research papers, that is, with vertical exaggeration that shows the halocline descending steeply downwards. However, a 1 km-wide island commonly has a fresh-water lens less than 10 m thick, so the aspect ratio is 10 m/1000 m, or 1 part in 100. The lens margin does not dip steeply. The idea of a steeply descending lens margin was reinforced by the report of cave divers Rob Palmer and Dennis Williams (Palmer and Williams, 1984), who reported that they were able to follow the halocline downwards in cave passages at a relatively steep angle. We now recognize that the existence of the cave passage distorted the flow pattern in the lens, causing the lens to utilize the cave passage as a short-cut to the sea. As sea level has migrated numerous times during the Quaternary, many dissolutional environments have been overprinted, creating a complex of dissolution voids and collapses, forming caves with a significant vertical component. It is these caves that appear to be distorting the modern fresh-water lens, as opposed to the modern lens creating the entire cave complex (the halocline cave of Fig. 2).

After a decade of fieldwork in the Bahamas, we began to see a pattern in the largest dry caves found on the islands (for a review of Bahamian geology, see Carew and Mylroie, 1995a; 1997). The large caves commonly were entered where a hillside had been breached by erosion or had collapsed. The caves were found at elevations of 1 to 7 m, which was in agreement with the position of at least one earlier sea level during the Quaternary, the last interglacial associated with Oxygen Isotope Substage 5e (OIS 5e), which lasted from 131 to 119 ka (Chen et al., 1991). This sea level reached 6 m higher than at present, as glacial ice melted back a bit more than it has today. Given that the Bahamas are tectonically stable, only a glacioeustatic sea-level highstand could have elevated the fresh-water lens above modern sea level, and so placed the fresh-water lens at, and slightly above, that elevation. Cave morphology was predictable and consistent: large chambers near the edge of the hill containing the cave, numerous ramifying passages near the back of the cave, and many cross-links and connections. Cave chambers were wider than they were high, with curvilinear and cuspate margins. Remnant bedrock pillars were common. Passages heading inland commonly ended in blank bedrock walls. As important as what the caves contained was what they did not contain: no turbulent flow markings such as wall scallops, no stream-laid sediments, no sinking stream or spring entrances. To explain these caves, we developed the *flank margin cave* model to interpret the size, shape, position and configuration of the caves (Mylroie and Carew, 1990). The name is derived from the interpretation that the caves develop in the distal *margin* of the fresh-water lens, just under the *flank* of the enclosing landmass (Fig. 3). At this location, the mixing environment of the vadose input to the water table is superimposed on the mixing environment of the fresh-water lens with underlying marine water, increasing dissolution beyond what either environment could do alone. Additionally, the lens cross section decreases at the lens margin, so flow velocities increase, transporting reactants in, and products out, faster than elsewhere in the lens (Raeisi and Mylroie, 1995). Finally, both the top of the lens, and the halocline, are density interfaces that can trap organic material. Oxidation of the organics creates CO_2 that can drive more dissolution; excess organics can create anoxic conditions and drive H_2S-mediated dissolution. The H_2S model appears supported by ^{34}S analysis of intergranular gypsum from some flank margin caves on San Salvador, which showed depletion values associated with biomediation of sulfur in anoxic zones (Bottrell et al., 1993).

Cave development by mixing dissolution in the margin of the lens, under the flank of the land mass, explained the features found in the caves (Fig. 4). The caves were not conduits, but mixing chambers, so the caves showed no evidence of turbulent flow. The greatest amount of mixing took place near the hillside, which, during an elevated sea level, was the shoreline. This action placed the largest chambers near the hillside. The ramifying and cross-linked passages represented migration of the dissolutional front inland. The large width to height ratio mimicked the shape of the distal margin of the lens. The wall morphology displayed dissolution by mixed waters, and mimicked wall and passage morphologies found in other mixed-water environments, such as the hypogenic caves of the Guadalupe Mountains of New Mexico (Palmer, 1991). Only a small amount of hillside erosion was necessary to breach into the caves, which formed initially without human-accessible entrances. It seemed that a significant puzzle regarding island cave development had been explained.

Flank margin caves were the largest, but not the only, type of cave found in the Bahamas. Two other types of dry caves were abundant. Pit caves are found all over the Bahamas, sometimes in very dense clusters, and occasionally at the top of hills. As the name suggests, these are vertical shafts that descend typically 5 to 10 m (Fig. 5). They rarely intersect flank margin caves. Their walls show classic vertical grooves formed by supercritical laminar flow of descending vadose water. During major rain events, they can be observed to efficiently collect water from the epikarst and conduct it downwards as vadose fast-flow routes. Their high density in places was initially thought, based on water budget considerations, to indicate much higher rainfall conditions at a past time. The high pit cave density is now understood to reflect competition and piracy among pit caves, such that some lose their recharge to upstream competitors (Harris et al., 1995). These caves can be complex as a result of this competition, which commonly leads to intersection of pit caves by one another. Pit caves form independently of sea level and fresh-water lens position, and can form in any exposed carbonate rock on an island.

The remaining major dry cave type is the banana hole. Banana holes are circular to oval chambers 5 to 10 m in diameter, and 1 to 3 m high, with phreatic morphologies but lacking the size and passage ramifications found in flank margin caves (Fig. 6). They are located in positions of 0 to 7 m above sea level, but laterally well away from where the lens margin would have been with sea level at

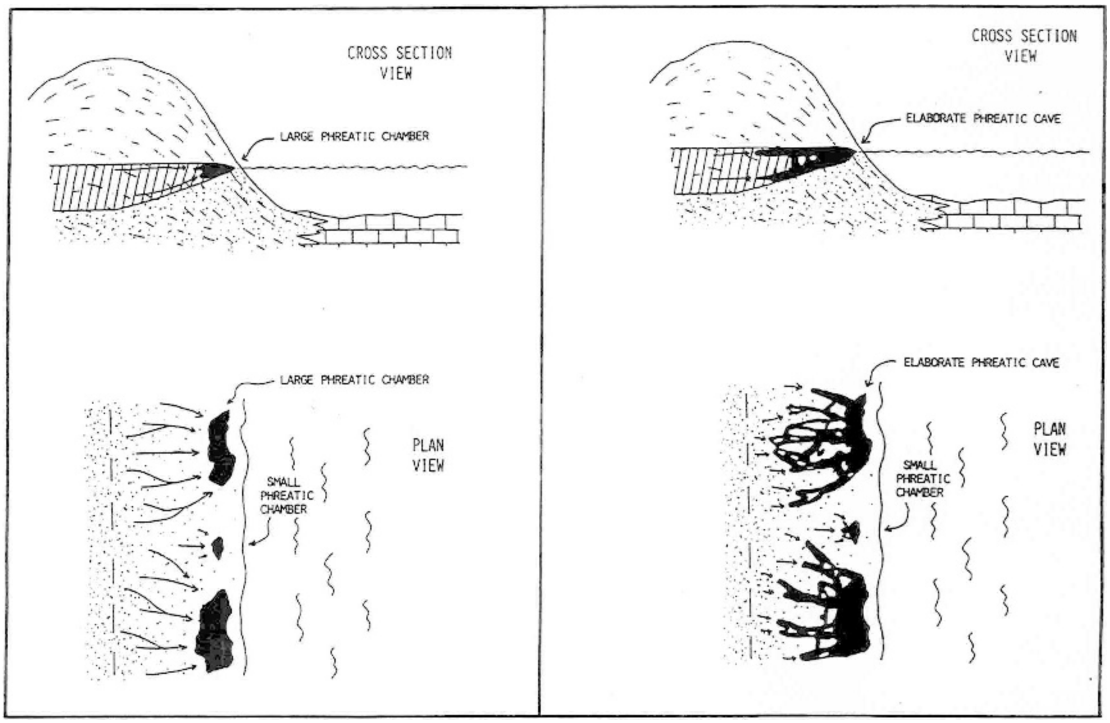

Figure 3. Figure 22 C&D of Mylroie, 1988 (reprinted in Mylroie and Carew, 1990). First display of the flank margin model, showing superposition of the mixing zones at the top and bottom of the fresh-water lens.

that elevation. They are entered where their ceilings have collapsed, or rarely where a pit cave has intersected them. They can be found in dense concentrations, up to 3000 per km^2 (Harris et al., 1995). Occasionally, a collapsed banana hole has a connection with an adjacent, uncollapsed banana hole. Their name is derived from their use to grow specialty crops, such as bananas. The collapses commonly collect soil, vegetative debris, and water, and so provide an excellent location for crop growth. Banana holes were initially thought to be vadose structures, formed by preferential dissolution in low spots on the ground surface (Smart and Whitaker, 1989). These low spots would collect extra water and organic debris, and generate CO$_2$ to drive dissolution at levels above what could be supported by simple meteoric water on adjacent, higher areas. The presence of wall morphologies of a phreatic nature, and the discovery that chambers with intact roofs existed, required that another explanation be considered. Downward-working vadose processes could not be invoked for roofed chambers showing phreatic morphology. Dissolution at the top of the fresh-water lens, by mixing of the lens water with descending vadose water, appears to be the mechanism (Harris et al., 1995). The dominant occurrence of banana holes has been in the Bahamas, which can be explained by considering the relief of those islands. Much of the Bahamas are a lowland plain 6 to 8 m above sea level. San Salvador, for example, is 49% such topography (Wilson et al., 1995). During the last interglacial, the fresh-water lens would have been very close to the land surface, such that the phreatic dissolutional voids formed by vadose water/fresh-water lens mixing would have had very thin roofs, in the order of 0.5 to 2 m thick. These voids would be prone to expression by collapse. Once drained by sea-level fall and open to the surface, they may have enlarged by the vadose organic-mat mechanism envisaged by Smart and Whitaker (1989). The lack of banana hole reports from carbonate islands other than the Bahamas may reflect the greater relief of those islands, such that banana hole voids are roofed by tens of meters of rock, and do not express by collapse. The occasional low and wide phreatic chambers found in deep quarries and high road cuts in the interior of islands such as Guam may represent banana holes.

In addition to the dry caves of the Bahamas, there are many caves that are under water and are accessible only by cave divers. The most spectacular of these are the famous blue holes, which can range from little more than ponds, to sensational deep shafts and kilometers-long cave systems (Fig. 7). Unlike flank margin caves and banana holes, which had to be generated in the relatively short time that sea level has been above modern levels, blue holes reflect the accumulated speleogenesis of many sea-level oscillations. During sea-level lowstands, vadose speleothems such as stalagmites and flowstone grew in what were air-filled shafts and caves. The U/Th dates of these formations range from 15 ka back to the limit of the U/Th technique at 350 ka (Carew and Mylroie, 1995b). The fresh-water lens and its mixing zones have passed up and down the section of rock containing the blue holes many times during the

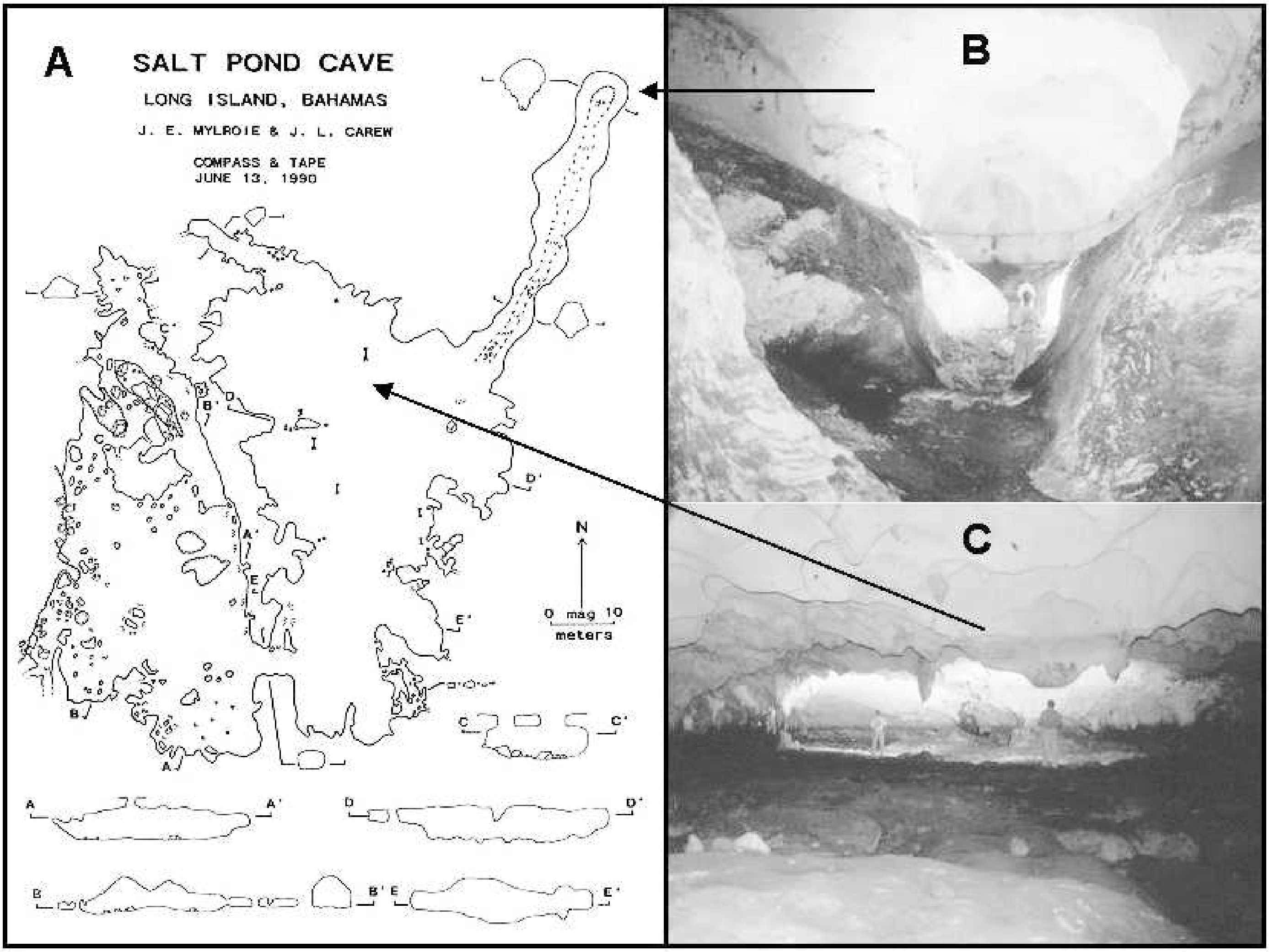

Figure 4. Salt Pond Cave, Long Island, Bahamas. A) Map of the cave, showing passage shape and configuration. B) Interior of Salt Pond Cave, showing a long, tubular passage ending in a blank bedrock wall; the site of the dissolution front when sea level fell at the end of the last interglacial sea-level highstand. C) Interior of Salt Pond Cave, demonstrating the great width relative to height in flank margin caves, indicative of their formation in the thin distal margin of the fresh-water lens.

Quaternary. The amount of over-printing by fresh-, mixed- and salt-water environments, vadose conditions, and collapse is immense. Because of the extensive use of blue holes by recreational divers, in the late 1980s there was confusion about what a blue hole was and how they should be defined. After consulting with Bahamian blue hole explorer Rob Palmer, cave scientist Pete Smart, and Bahamas geographer Neil Sealey, the following definition for blue holes was proposed (Mylroie et al., 1995a, p. 225): "subsurface voids that are developed in carbonate banks and islands; are open to the earth's surface; contain tidally-influenced waters of fresh, marine, or mixed chemistry; extend below sea level for a majority of their depth; and may provide access to submerged cave passages." As blue holes can be found in island interiors, or in lagoons, a further description was added: "ocean holes open directly into the present marine environment and contain marine water, usually with tidal flow; inland blue holes are isolated by present topography from marine conditions, and open directly onto the land surface or into an isolated pond or lake, and contain tidally-influenced water of a variety of chemistries from fresh to marine" (Mylroie et al., 1995a, p. 225). A different approach to defining and describing blue holes can be found in Schwabe and Carew (2006). Blue holes are polygenetic, forming by drowning of pit caves, flank margin caves and banana holes; by progradational collapse; by bank margin failure; and by marine flooding of paleoconduits (Fig. 8). Blue holes are known to react to tides, sometimes with strong currents, especially for ocean holes. Smaller holes, found on inland water bodies in the Bahamas, have been called lake drains (Mylroie et al., 1995b). These are very cryptic features that help regulate

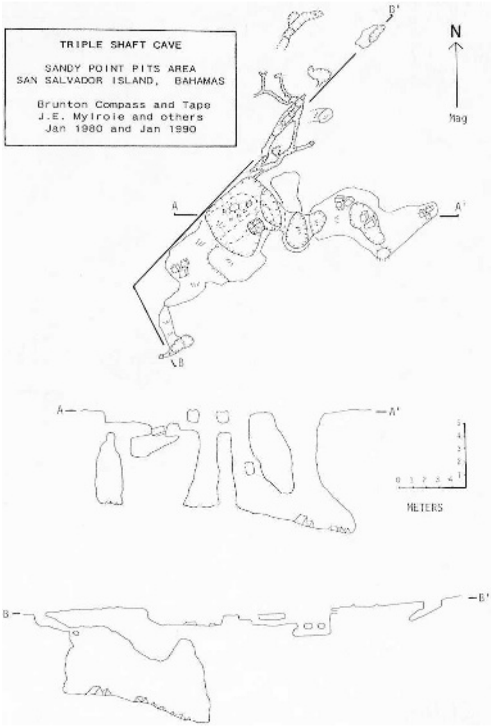

Figure 5. Triple Shaft Cave, a pit cave complex, San Salvador Island, Bahamas. Meteoric water collected in the top few meters of the epikarst passes downward through the vadose zone, forming pit caves, which compete and interact to produce complexes as shown here.

the salinity of inland water bodies by supplying normal salinity sea water, but their nature and configuration is unknown.

THE SECOND RESEARCH PHASE

As noted earlier, the Bahamas, with their youth, relatively simple geology, and lack of tectonics were a good starting point to figure out the complexities of cave and karst development in carbonate islands. The record of cave genesis for the dry caves of the Bahamas was well understood, but questions remained about what had happened during the sea-level oscillations of the Quaternary. The first opportunity to examine this question came in the early 1980s, when the Johnson SeaLink submarine was made available to researchers on San Salvador Island (Carew and Mylroie, 1987). Dives were made on the wall of the carbonate bank on which San Salvador rests, to a depth of 1000 feet (305 m; the depth gauge of the submarine was calibrated in feet, as are U.S. scuba diver depth gauges, so those units are reported first here). The purpose was to locate possible horizons of cave openings that might reflect past sea level, and hence fresh-water lens, positions. In the 1980s, studies from blue holes showed that they did not exceed 300 feet (~90 m) in depth. That depth value was taken in some quarters as an indication that the maximum sea-level lowstand was at −300 feet (~ −90 m), and hence blue holes did not penetrate any deeper. Subsequently (Wilson, 1994), Dean's Blue Hole on Long Island, Bahamas was found to be an astounding 660 feet (201 m) deep, indicating that there was no geologic floor to blue hole depth. Drilling records indicated large voids as deep as 4,082 m (Meyerhoff and Hatten, 1974). The submarine dives were another means of checking the blue hole data. The dives did not examine the wall of the island at depths above 200 feet (~60 m), as modern coral overgrowth obscured the bedrock wall. Caves were found 13 times at a depth of 343 feet (105 m), and twice more at 412 feet (126 m), but nowhere else between 200 feet and 1000 feet depth (Carew and Mylroie, 1987). These data suggest a sea-level lowstand at those depths. The 126 m depth agrees with the oxygen isotope sea-level curve, which indicates the maximum eustatic sea-level lowstand in the Quaternary to be about −125 m. The implication of these observations is that during Quaternary sea-level oscillations, sea level is rapidly changing, either rising or falling in response to ice volume change on the continents, and therefore the fresh-water lens is never in one spot long enough to develop large, observable flank margin caves. Only when sea level has reached a peak (as during the last interglacial, OIS 5e), or reached a trough, and sea level must then reverse its position to make the next oscillation, is the fresh-water lens at one position long enough to make flank margin caves. The trouble with the caves found by the submarine is that we don't know their ages. While the Bahamas are tectonically stable, they are slowly subsiding at a rate of 1 to 2 m per 100 ka (Carew and Mylroie, 1995b). It could be argued that the observed caves could have formed at shallower depths, and have subsided to their observed location. The caves cannot be too old, however, as the steep walls of the Bahama Banks commonly fracture and fail (Daugherty et al., 1987; Mullins and Hine, 1989), and flank margin caves would be preferentially removed. The two horizons, at 105 m depth, and 125 m depth, may indicate the sea-level lowstands associated with OIS 4 (~50 ka) and OIS 2 (~20 ka), respectively.

The Bermuda caves remained a concern, as they did not fit into the cave development model created for the Bahamas, despite having very similar geology (Mylroie et al., 1995b). Similar, however, is not identical. Bermuda has two main differences from the Bahamas. First, it is in a wetter climate, which means its surface rocks erode by meteoric dissolution faster than land surfaces do in the drier Bahamas (especially San Salvador Island, which has a negative water budget). Second, Bermuda sits on a volcanic pedestal that is mantled by the carbonates that make up Bermuda's land surface. In contrast the Bahamas carbonates extend continuously to a depth of 5 km or more (Meyerhoff and Hatten, 1974). Flank margin caves are rare in Bermuda, known only from a few locations. The reason is climatic. In the higher denudation environment of Bermuda, hillsides erode more rapidly than in the

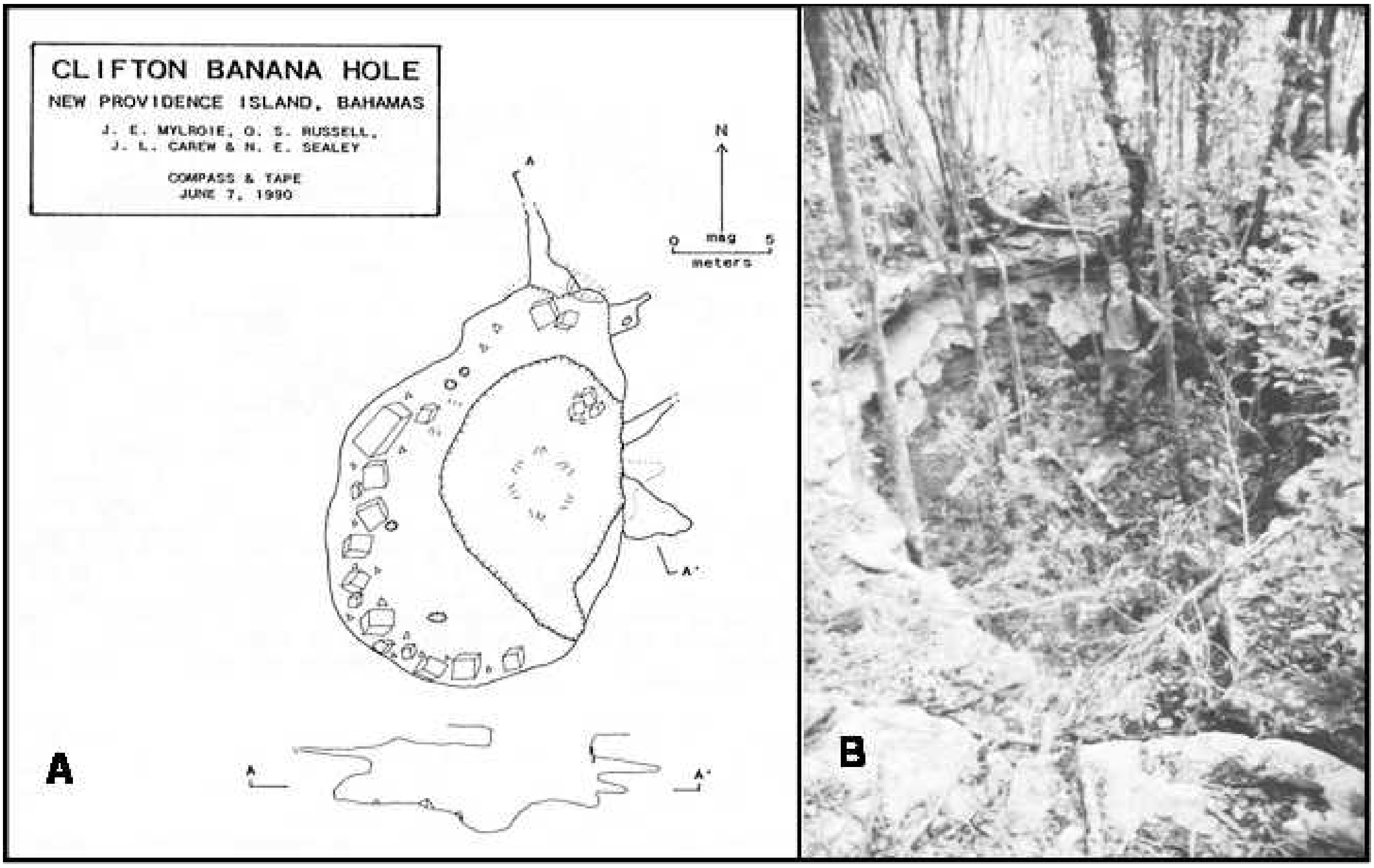

Figure 6. A) Map of Clifton Banana Hole, New Providence Island. Dissolution at the top of the fresh-water lens creates voids. B) Banana hole, unnamed, San Salvador Island; the proximity of the land surface to the top of the lens creates thin ceilings that are prone to failure by collapse.

Bahamas, and the flank margin caves formed during OIS 5e sea-level highstand, 125 ka, are now eroded away (Mylroie et al., 1995b). Their position of formation under the flank of the enclosing landmass made them vulnerable to surficial erosive processes. The famous caves of Bermuda are instead large collapse chambers, with extensive piles of breakdown that can be followed by scuba divers well below sea level. Rock surfaces showing phreatic dissolution are extremely rare in these caves. The mixing dissolution model proposed for Bermuda by Palmer et al. (1977), which proved to be the key to understanding flank margin cave development, does not seem to be the major cave-forming factor on Bermuda. The volcanic pedestal of Bermuda is now almost entirely below sea level, such that a fresh-water lens exists across the length and breadth of the island. However, during glacial ice maxima in the Quaternary, sea level would have been up to 125 m lower, and the volcanic pedestal, though mantled by carbonates, would have been above sea level, partitioning the fresh-water lens. Descending vadose water would have hit the carbonate/volcanic contact, and followed the topography of that interface downward to the fresh-water lens. Such aggregation of water as traditional stream passages would have created large chambers. It is the subsequent collapse of these chambers, and their progradation upward to the elevations seen today, that have created the unique caves of Bermuda (Mylroie, 1984; Mylroie et al., 1995b).

In 1992, at the invitation of Joe Troester of the U.S. Geologic Survey, research began on Isla de Mona, Puerto Rico, located in the Mona Passage halfway between Puerto Rico and the Dominican Republic. Mona is located very near the boundary between the North American plate and the Caribbean plate, and so is in a tectonically active area. The island itself has been uplifted such that it has vertical cliffs on three sides, which are up to 80 m high (Fig. 9). The island is entirely carbonate, as a limestone unit overlying a dolomite. Our initial interest in Mona was that it looked today, because of tectonic uplift, as San Salvador would have looked 20,000 years ago during the glacial ice maximum, when sea level was far below today's position. We knew from published reports that it had many large caves, and we thought the flank margin model might apply, as earlier reports had obviously been uncertain how the caves formed. Jim Quinlan (Quinlan, 1974) had described the caves as phantasmagorical, and reluctantly

Figure 7. Deans Blue Hole, Long Island, Bahamas. This blue hole is the deepest in the Bahamas at 200 m. Its position in a lagoon makes it an ocean hole, subject to direct marine influence. People on far cliff for scale.

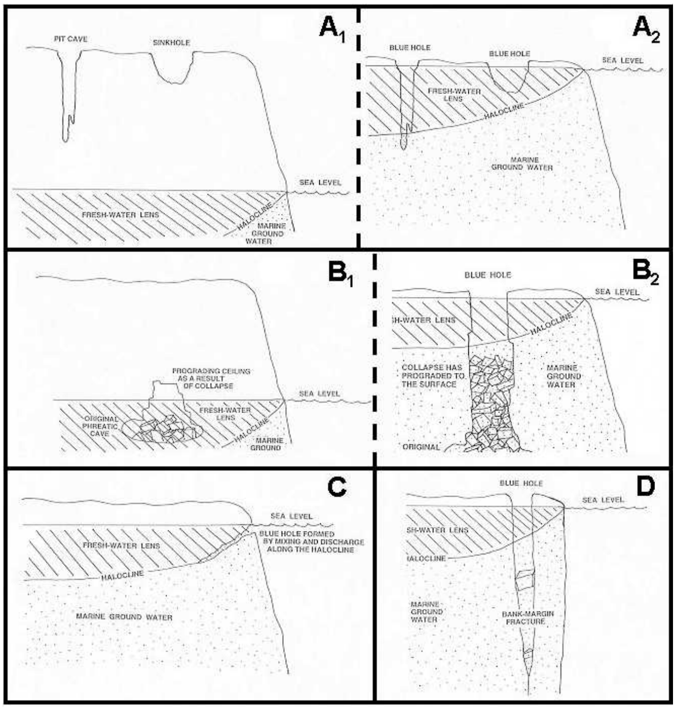

Figure 8. Four ways in which blue holes could form. A) By flooding of sinks and pits. B) By progradational collapse of deep voids. C) By bank margin failure. D) By flooding of conduit caves; note here the vertical lens exaggeration mentioned in Figure 2, still creating the incorrect impression. Adapted from Mylroie et al., 1995a.

placed them in the sea cave category, as he recognized that the caves were not traditional turbulent-flow conduits. Upon field examination, we determined the caves were clearly flank margin caves (Frank et al., 1998), but at an immense scale. The Lirio Cave System eventually mapped out at 20 km, and wrapped around the curving edge of the island (Fig. 10). The question then became why were the caves so large? Caves of over 1 km of linear survey are known in the Bahamas, but 20 km was astounding. The answer lay in the age of the caves. Working with Bruce Panuska, from our Geosciences Department (Panuska et al., 1998), we established, based on paleomagnetic reversal patterns in cave sediments and speleothems, that the caves were at least 1.8 million years old. The caves had developed in the Pliocene, before the onset of the high amplitude, short wavelength sea-level oscillations that characterize the Quaternary. Therefore sea level, and fresh-water lens position, had been stable at a given horizon for a much longer time than had been available in the younger rocks of the Bahamas. This longer time of lens stability had allowed extremely large flank margin caves to develop. Uplift then had placed the caves far above the influence of Quaternary sea-level change, effectively preserving the caves. The Bahamas demonstrated that significant flank margin caves could form in short time windows of approximately 10,000 years. Mona showed that once formed, such caves could survive for more than a million years. Flank margin caves are high-resolution, long-duration repositories of speleological information.

The work in Bermuda and the Bahamas was summarized in Mylroie et al. (1995b) and the Isla de Mona work was summarized in Mylroie & Carew (1995) and in Frank et al. (1998). One of the results of this early work was the recognition that closed contour depressions (commonly labeled in karst areas as sinkholes, uvalas, poljes, etc.) in these young islands were primarily constructional. That is, the depressions were the result of differential deposition of the carbonate rock to create closed contour depressions that drained by karst processes and therefore avoided becoming lakes and ponds. In the Bahamas, the swales between large carbonate eolian dunes had the appearance of very large closed depressions covering thousands of square meters. In other cases, the closed depression was a former lagoon, developed during the 6 m sea-level highstand of the last interglacial (OIS 5e), and now drained because sea level is not as high as it was at 125 ka. Most sinkholes in the 1 to 10 m diameter range found in the Bahamas are cave collapses, the majority a result of banana hole formation that was discussed earlier. The Bahamas differ from continental karst not only in the caves, but also in the depressions. Whereas most depressions, large and small, in continents are the result of dissolutional processes acting from the surface downward, in the Bahamas the large depressions are constructional and the small ones are collapse features from dissolution acting at a variety of depths, in a hypogenic mode.

Figure 9. Uplifted north side of Isla de Mona, Puerto Rico. Cliff is 70 m high, with flank margin caves visible at the top, along the limestone/dolomite contact.

The Current Research Phase

In 1997, John Mylroie was asked to present a keynote address on "Land Use and Carbonate Island Karst" at the *Sixth Multidisciplinary Conference on Sinkholes and the Engineering and Environmental Impacts of Karst* held in Springfield, Missouri in April of that year. The paper published from that conference (Mylroie and Carew, 1997) made the first attempt to view karst development on carbonate islands as a result of a predictable hierarchy (Fig. 11). The differences between some types of island cave and karst development could be attributed to interactions (or the lack thereof) of carbonate rocks with non-carbonate rocks that are commonly found on many islands. The announced presentation on carbonate island karst induced John Jenson, of the Water and Energy Resource Institute of the Western Pacific (now the Water and Environmental Research Institute, or WERI) at the University of Guam, to attend the conference to talk about his karst land use problems in Guam. From that meeting began a fruitful collaboration to investigate the tectonically active, geologically complex carbonate islands of the Mariana Archipelago.

Work in the Mariana Islands began on Guam in July of 1998. As with Isla de Mona, the carbonate rocks in the Marianas, while Cenozoic, were older than those of the Bahamas, and tectonic uplift played an important role. Unlike Isla de Mona, however, non-carbonate rocks outcropped on the surface. These outcrops created allogenic recharge, which upon reaching the contact with carbonate rocks, formed sinking streams, stream caves, and cave springs; typical epigenic caves. Guam provided field proof of the predicted third island category from Fig. 11C. In the vicinity of non-carbonate outcrops, allogenic water created caves similar to what can be found on continents. In the carbonate outcrop at a distance from those non-carbonate rocks, autogenic recharge controlled karst development. And in the carbonate coastal areas, classic flank margin cave development dominated. Isla de Mona, while tectonically uplifted, did not show any evidence of uplift in the last 125 ka (Frank et al., 1998). Guam and the other Mariana islands showed evidence of uplift throughout the Quaternary and up to the present day (Dickenson, 1999). The Mariana Islands presented an island karst environment of much greater complexity than had previously been studied. The field work, done in collaboration with John Jenson and his students, resulted in the first comprehensive interpretation of cave and karst development on Guam (Mylroie et al., 2001). The M.Sc. thesis from the Guam work by Danko Taboroši (Taboroši, 2000) instigated a series of publications addressing karren formation (Taboroši et al., 2004), cave development and distribution (Taboroši et al., 2005), and speleothem formation (Taboroši, 2006) as part of a Ph.D. program at Hokkaido University. The Marianas work continued on to Saipan (Wexel et al., 2001), Aquijan (Stafford et al., 2004), Tinian (Stafford et al., 2005), and Rota (Keel et al., 2006) islands, culminating in a review article of the caves and karst of the Marianas Archipelago (Jenson et al., 2006). The Saipan work (Jenson et al., 2002) resulted in a modification of the island category hierarchy to include a fourth category, the complex island, to represent situations in which complex faulting, and syndeposition of carbonates and volcaniclastics resulted in very complex compartmentalization of the fresh-water lens. One of the unusual outcomes of such compartmentalization is protection of water resources from upconing and saltwater intrusion during aquifer pumping. Another unexpected

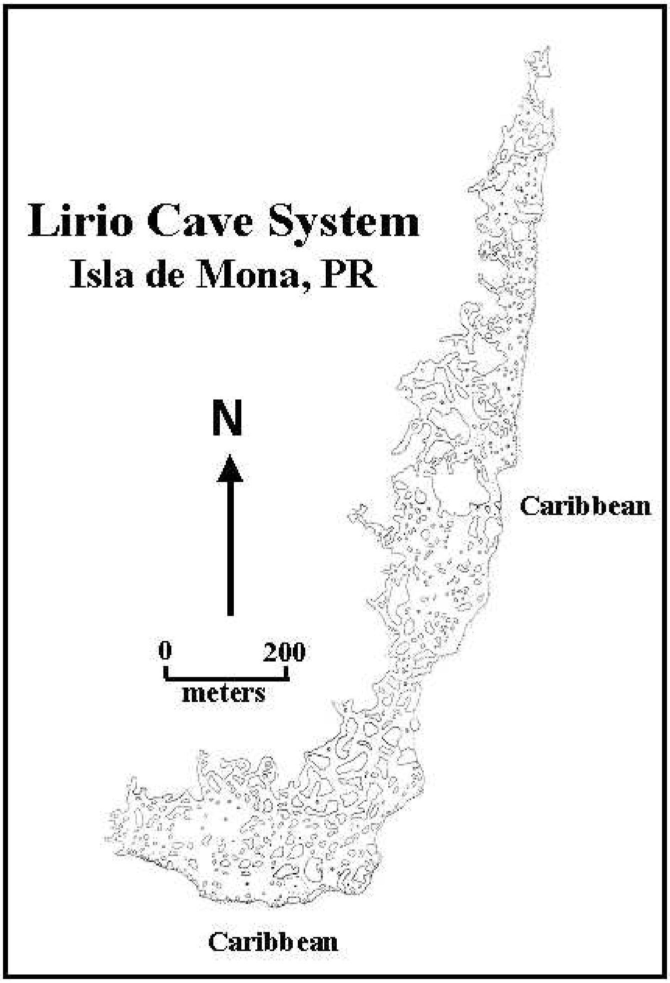

Figure 10. Map of the Lirio Cave Complex, Isla de Mona, Puerto Rico. Note that the cave is maze-like, with larger chambers towards the coast; that the cave does not penetrate very far inland but does wrap around the island coastline.

outcome was the development of confined aquifers, creating phreatic lift tubes to carry water out of the aquifer compartment, as in Kalabera Cave, Saipan (Jenson et al., 2006).

The island categories (Fig. 11) established in Mylroie and Carew (1997), were modified in Mylroie et al. (2001) to reflect advice from H. Len Vacher at the University of South Florida (Mylroie and Vacher, 1999) that not all carbonate islands showing non-carbonate outcrops had the carbonate rocks as a rim, so the third category was modified from carbonate-rimmed island to composite island. That action, and the addition of the complex island category resulted in the creation of a new, four panel figure to express the island type hierarchy (Fig. 12).

Understanding of water flow dynamics in carbonate islands had been pioneered by H. Len Vacher (e.g., Vacher, 1988). The key to that work was the recognition that carbonate aquifers are unique in hydrology in that they are capable of extensive self-modification through dissolutional and depositional processes involving $CaCO_3$. This self-modification is extremely important in the young carbonate rocks that make up carbonate islands today. One of the unexpected outcomes of this work was that the longer a fresh-water lens sat in a given section of young carbonate rock, the more permeable the rock became. As shown in Figure 2, the fresh-water lens exists because a slope, or head, of water is needed to drive the meteoric water collected at the water table to the island perimeter. The less permeable the rock, the steeper the necessary slope (as an analogy, consider a car on a slope; if the axles are rusted, it takes a steep slope to move the car; if the axles are greased, the car moves on a gentler slope). As the fresh-water lens floats in a 1 to 40 ratio based on its density difference with sea water (1.000 versus 1.025 g cm^{-3}), the lens is 40 times as thick below sea level as it is above sea level as a result of buoyancy. Therefore, as the lens becomes more permeable by dissolution, its slope becomes less, its elevation above sea level becomes less, so its thickness becomes less. In the Bahamas, the thickest fresh water lenses are found in the recent Holocene sands (Wallis et al., 1991). While these sands have very high primary porosity, that porosity is not organized into high permeability, and the lens is relatively thick as water flow is not efficient. In the adjacent, older Pleistocene rocks, which may have seen two or more sea-level highstands and associated fresh-water lens events, the permeability is higher and the lens is thinner. Building on these studies, Vacher and Mylroie (2002, p. 183) defined the term eogenetic karst as "the land surface evolving on, and the pore system developing in, rocks undergoing eogenetic, meteoric diagenesis." The term eogenetic was derived from Choquette and Pray's (1970, p. 215) studies of rock age and diagenesis; they defined "the time of early burial as eogenetic, the time of deeper burial as mesogenetic, and the late stage of associated with erosion of long-buried carbonates as telogenetic." Most karst in continental settings is the result of dissolutional processes acting on telogenetic rocks, rocks that are diagenetically mature, recystallized, and lack significant primary porosity. In eogenetic karst, caves are created directly within the eogenetic rocks, bypassing diagenetic maturation, uplift, and telogenetic dissolution (Fig. 13).

The parameters that controlled the development of karst on islands were initially outlined by Mylroie and Vacher (1999) and codified as the Carbonate Island Karst Model, or CIKM, which first appeared by that name after the initial study of Guam (Mylroie and Jenson, 2000; Mylroie et al., 2001). The CIKM has been tweaked and modified over the years. The principles of the CIKM include:

1. Mixing of fresh and salt water at the boundaries of the fresh water lens results in a localized area of preferential porosity and permeability development. Collection of organics at these boundaries may also

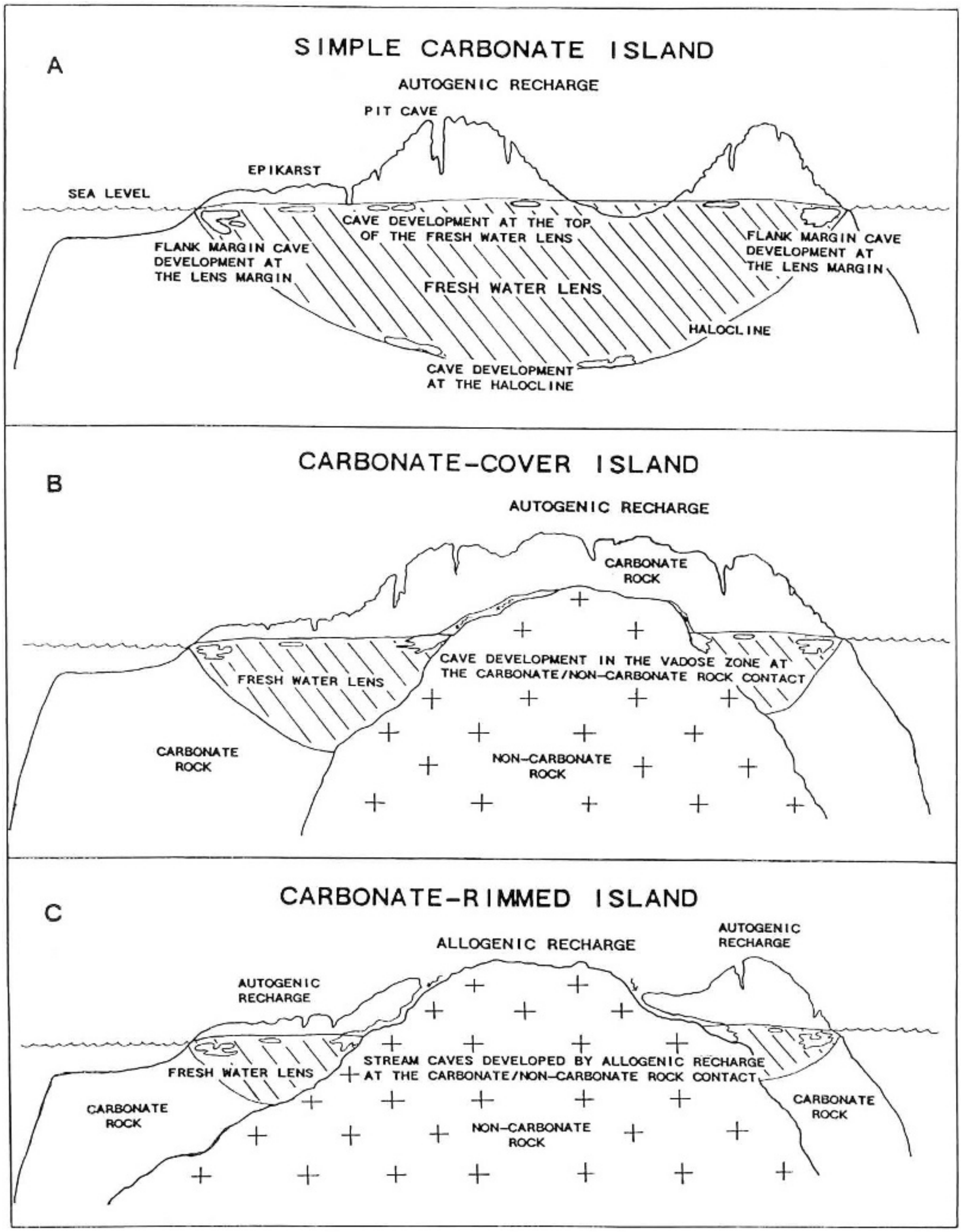

Figure 11. First presentation of a karst classification of carbonate islands, from Mylroie and Carew (1997). The Bahamas fit the (A) Category, Bermuda (at sea-level lowstands) fits the (B) Category, and Guam fits the (C) Category.

enhance dissolution. The maximum dissolution occurs at the lens margin, where the water table and halocline mixing zones are superimposed.

2. Glacioeustacy has moved sea level, and thus the fresh water lens position, up and down more than 100 m throughout the Quaternary.
3. Local tectonic movement can cause overprinting of dissolutional and diagenetic features developed during different glacioeustatic events.
4. The karst is eogenetic in that it has developed on rocks that are young and have never been buried below the zone of meteoric diagenesis.
5. Carbonate islands can be divided into four categories based on basement/sea level relationships (Figs. 11 and 12).

   A. Simple Carbonate Island—Only carbonate rocks are present (Fig. 11A). Meteoric catchment is

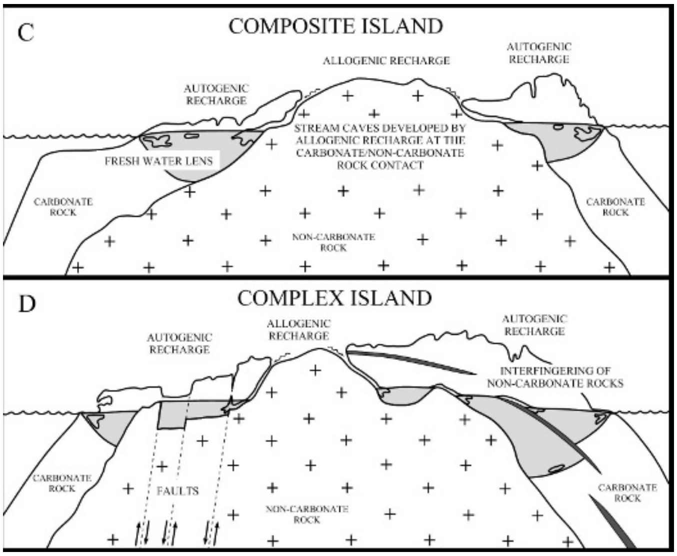

Figure 12. Updated karst classification of carbonate islands, changing Figure 11C from carbonate-rimmed island to composite island, and adding a new category, the complex island, best represented by Saipan.

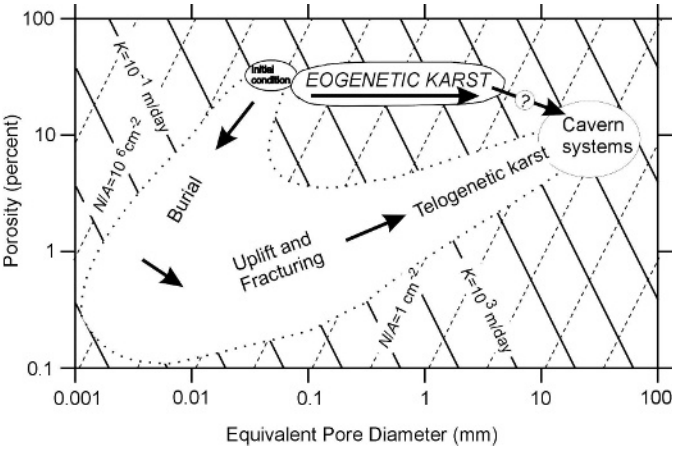

Figure 13. The evolution of eogenetic karst. Slanting solid lines are hydraulic conductivity, K, in m/day. Slanted dashed lines are tube density (number of tubes per unit area, or N/A), a measure of the degree of enlargement of the pore structure (with a consequent decrease in pore number). Eogenetic karst takes a short cut from the original depositional environment to cave development without going through burial, massive diagenesis, and uplift. After Vacher and Mylroie, 2002.

entirely autogenic and flow within the fresh water lens is controlled entirely by properties of the carbonate rock. The Bahamas are examples of simple carbonate islands.

B. Carbonate-Cover Island—Only carbonate rocks are exposed at the surface and the catchment is entirely autogenic (Fig. 11B). Non-carbonate rocks exist under carbonate rocks and may partition and influence flow within the lens, including conduit flow at the contact. Bermuda, at a sea-level lowstand, is an example of a carbonate-cover island.

C. Composite Island—Both carbonate and non-carbonate rocks are exposed at the surface (Fig. 12), allowing for allogenic and autogenic catchment. The lens is partitioned and conduit cave systems can develop at the contact of the carbonate and non-carbonate rocks. Barbados and Guam are examples of composite islands.

D. Complex Island—Carbonate and non-carbonate rocks are complexly interrelated by depositional relationships and/or faulting (Fig. 12). Perching, isolation, and confining of the fresh-water lens is possible. Saipan is an example.

Vacher and Mylroie (2002) also differentiated between island karst, and karst on islands. Island karst develops under the influence of the CIKM. Karst on islands develops in uplifted regions of island interiors, and behaves much the same way as karst on continents at the same latitude. The flank margin caves of Isla de Mona or the Bahamas are examples of island karst. The cockpits of Jamaica, or the mogotes of Puerto Rico, are examples of karst on islands, as they are isolated from glacioeustasy and fresh water/salt water mixing. They are similar to the karst landforms of Belize, a tropical but continental setting.

The karren (dissolutional sculpture at the centimeter to meter scale) of carbonate islands differ from those found in continental interiors of the mid to high latitudes, where most karren research has been done. The jagged, pitted and irregular karren of the coastal environment of tropical carbonate islands is well known, and the classic study is by Folk et al. (1973). That work, and many later works (e.g., Viles, 1988) ascribed the unique nature of this island karren to marine spray, boring endolithic algae, and grazing by gastropods, among other reasons. Folk et al. (1973) called it *phytokarst*, based on the large degree to which the endolithic algae had penetrated and permeated the rock surface. Taboroši et al. (2004) were able to demonstrate that the key factor was the eogenetic nature of the rock. The lack of diagenetic maturity made all weathering processes, organic and inorganic, responsive to the texture, composition, porosity, and cementation of the allochems (particles) that made up the young carbonates. Taboroši et al. (2004) called such karst etching eogenetic karren. Endolithic algae were able to colonize such weak and porous rock in high abundance, which initiated the entire organic aspect of karren development in the coastal carbonates of tropical islands. Endolithic algae do not colonize dense, recrystallized teleogenetic rocks to a similar extent. On southern Guam, in the interior away from CIKM effects, are limestone units ranging in age from

Oligocene to Pliocene. Analysis of these rocks and their karren showed that as diagenetic maturity increased, the karren became less distinctive as eogenetic karren, and resembled more closely the telogenetic karren of continental interiors (Taboroši et al., 2004).

FUTURE RESEARCH

The current state of affairs regarding island karst is very promising. One of the interesting applied research areas is the potential for island karst to be preserved as paleokarst in the rock record, therefore becoming a host for mineralization or hydrocarbons. As eogenetic carbonate rocks are found proximal to their environment of deposition, all that needs to happen to preserve those rocks, and any included karst features, is for subsidence to lower them and continued carbonate deposition to bury them. To preserve an existing telogenetic conduit cave system in a continental interior setting would require major adjustment of plate tectonic motion, to depress the landmass and allow burial to occur. While all this plate adjustment was occurring over millions of years, the existing cave system would need to avoid destruction by erosion. It is clear that eogenetic karst is predisposed to preservation, and that paleokarst in the rock record is most likely former eogenetic karst.

To locate and assess paleokarst in the subsurface, it is important to determine what to search for. Imagine a large carbonate unit in the subsurface, a disk 100 m thick and 10 km in diameter, once exposed at the earth's surface and subjected to karst processes, and now buried. If one assumes telogenetic, conduit cave karst, then one looks for voids extending from the center of the disk to the margin in a few places, as conduit caves that drained the interior of the feature. If one assumes that eogenetic mixing zone karst was active, then one looks for dissolutional voids spaced around the perimeter of the feature. There is a 90° difference in search strategy depending on which model is chosen.

The unique pattern of flank margin caves has called attention to how they develop. Unlike teleogenetic conduit caves, for which a large and extensive data base exists, the eogenetic island cave data base has been built from scratch over the last three decades by a very small group of workers. As a result, until recently the patterns that drive eogenetic caves such as flank margin caves were not easily interpreted. A rank order plot of flank margin caves based on areal footprint (Fig. 14), from the Bahamas, shows that the caves self-select into three size categories (Roth et al., 2006). Areal footprint, or cave area, was selected as the size determiner because it is the best measure of how much dissolution has occurred. Given that flank margin caves form in the distal margin of the fresh-water lens, their vertical variation is minimal as the lens is so thin at that location. Calculating area using the outside perimeter, and removing the area of any inner bedrock pillars, creates a measure of the amount of dissolution. For stream caves in telogenetic settings, cave length is a good measure of the amount of dissolution, as those caves are very long compared to their widths.

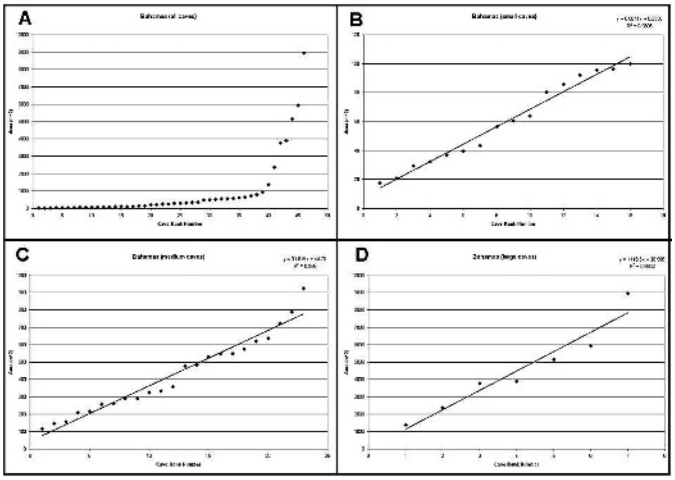

Figure 14. Rank order plots of flank margin cave size (as determined by areal footprint). A) Complete plot, which has 3 straight line segments, each reproduced in (B) small caves, 100 m^2, R^2 = 0.9805, slope = 6.024; (C) medium caves, 100–1000 m^2, R^2 = 0.956, slope = 31.815; and (D) large caves, over 1000 m^2, R^2 = 0.9302, slope = 1,113.3. The line slope changes indicate the point at which major cave chamber intersections occur, creating a jump in cave size. From Roth (2004).

Flank margin caves begin as tiny voids that grow through time. As the dissolutional environment is restricted to the edge of the lens, this dissolution occurs in a band that runs from the coastline of the island inland just a few tens or hundreds of meters. In such a setting, the growth of small voids can continue, but at some stage, adjacent voids, of various sizes, will intersect. When they do, cave size then makes an immediate jump in size. As these cave clusters continue to grow, they then intersect other clusters, and there is again a large jump in cave size. Fig. 14 shows three straight line segments, with slopes that are approximately the square of the previous slope, that represent small (100 m^2 or less), medium (100–1000 m^2) and large caves (over 1000 m^2). The data indicate that as small dissolutional voids grow at random in the thin lens margin, their amalgamation occurs as discrete steps, even though within each size category there is a wide range of sizes depending on the initial size of the individual chambers, and how many became connected. Dissolution continues after chamber amalgamation, and such amalgamations have a greater chance of adding to chambers by connection than the smaller size class does. Computer modeling of this cave generation procedure generates line slopes that are identical to the empirical database (Labourdette et al., 2006), but include a 4th set at 1–2 m^2 in area. This 4th small

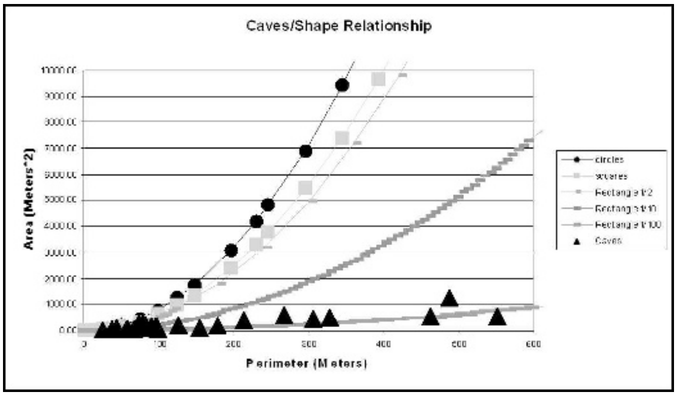

Figure 15. Plot of flank margin cave perimeter versus area, compared to standard geometrical objects. Globular dissolution chambers would expect to plot as a curve, much like circles and squares do. The high degree of perimeter complexity, produced by intersection of dissolutional voids, creates a linear plot instead, approximating a rectangle with a 1 to 100 aspect (width to length) ratio. From Roth (2004).

area group does not appear in the island data base as voids that small are not mapped as caves.

A further test of cave growth by aggregation of smaller caves can be done by plotting cave area versus cave perimeter. For these data, the internal area of bedrock columns and "islands" was removed from the areal footprint, but the perimeter of such internal features was retained, as it was a water-rock contact during cave development. As the perimeter grows linearly (m), but area by the square (m^2), simple geometric shapes produce an exponential curve as they get larger (Fig. 15). Flank margin caves, however, plot as an approximate straight line, which indicates their perimeters must be progressively more complex as the caves increase in size, compensating for the increase in area by the square. The easiest way to create this perimeter complexity is to aggregate smaller cave clusters to create a ramiform pattern, supporting the data created by the rank-order versus area plot (Fig. 14). Flank margin cave growth by cave aggregation is much different than conduit cave growth by surface water capture, further reinforcing how different island karst is from continental karst.

Area issues work not only at the cave level, but also at the island level. As islands get bigger, their perimeter becomes less relative to the island area. Or, in hydrological terms, the recharge area increases exponentially, but the discharge region increases only linearly. As islands get bigger, ever larger amounts of meteoric water must exit through the perimeter. For example, in an island with a radius of 1 km, its area (A) is 3.14 km^2, and its perimeter (P) is 6.28 km, for an A/P ratio of 0.5 km. If the island has a 100 km radius, A is 31,416 km^2, P is 628 km for an A/P ratio of 50 km. Mylroie and Vacher (1999) hypothesized that at some perimeter/area relationship, diffuse flow in the fresh-water lens must become inefficient, and conduit flow will initiate. Evidence of such a relationship can be seen today in the Bahamas and Bermuda. The dry flank margin caves seen today formed in hills that at a past +6 m sea level, were islands with linear dimensions of a few km. However, if sea level dropped 20 m below today's level, the broad, shallow Bahama Banks would become very large islands, with linear dimensions of hundreds of km. The same is true for Bermuda. Did this larger size cross a threshold and generate conduit flow systems? Cave divers have found long, linear conduit caves at depths of 20 to 30 m on Great Bahama Bank (Farr and Palmer, 1984), and at a similar depth on the Bermuda Platform (Vacher and Harmon, 1987). These depths are less than 60 m, and so were not observed during the submarine work on San Salvador Island. The field evidence would suggest that island size controls water flow from islands, favoring conduit flow at large island sizes.

As noted earlier, some of the most classic work on fresh water/salt water mixing and dissolution was done in the Yucatan area (Back et al., 1986). The large, complex cave systems of Quintana Roo State are known as intricate conduit systems discharging water from the interior to the sea (Smart et al., 2006). The Yucatan Peninsula can be considered a very large island, which would be expected to generate conduit flow. One question is: Does that conduit flow negate the development of flank margin caves in the areas along the perimeter where conduits are not present? Field work in the Akumal area of Quintana Roo has demonstrated that the Pleistocene coastal eolianites there contain flank margin caves (Kelley et al., 2006). During the last interglacial (OIS 5e), while the interior of the Yucatan Peninsula was discharging fresh water to the sea at depths of 10 to 20 m, an entirely different sort of cave was developing under hypogenic conditions in the distal margin of the fresh-water lens. Epigenic conduit flow caves and hypogenic flank margin caves can form and function in the same locality and at the same time.

Recent work has taken us to Fais Island, 220 km east of Yap, Federated States of Micronesia, in the far western Pacific. The island is an uplifted carbonate platform 1.2 km by 2.9 km, with elevations up to 28 m. The island obtains its fresh water from rainfall catchment, and following droughts or typhoons, suffers from water-supply problems. Research was undertaken to determine if the CIKM could assist in determining how to exploit the island's ground-water resources. The island beaches are underlain by a tightly-cemented reef flat that extends seaward, and that acts as an aquitard, restricting fresh-water lens discharge to the sea. Flank margin caves were not found in high ground behind the beaches, but only where headlands crossed the reef flat towards the open ocean. These observations indicated that fresh-water discharge in the past was directed through these headlands to bypass the low-permeability reef flats. Analysis of uplifted flank margin caves could be used as a proxy to locate preferred discharges for fresh water today. Using the lowest negative tides of the year, it was found (Mylroie et al., 2005) that ancient flank margin cave positions above modern sea level identified existing fresh-water discharge sites. It was also found that what was believed to be a blue hole or a large cave collapse feature was actually a sand-filled embayment, and a dug well from the Japanese occupation prior to WWII. As with the Holocene sand aquifers of the Bahamas discussed earlier, this sand-filled embayment had the largest amount of fresh water. In this latter case, it was the ability of the CIKM to successfully interpret a pseudokarst feature that helped address the water problem.

SUMMARY

The development of the Carbonate Island Karst Model, or CIKM, required four major accomplishments:

1) Intellectual separation from cave and karst development models that had been produced in continental settings, in telogenetic rocks assuming conduit (or epigenic) flow.
2) Understanding the unique flow systems and geochemistry of isolated carbonate island aquifers, and applying those understandings to cave and karst development.
3) Collection of a sufficiently large data base within each island type to allow patterns to be expressed. In other words, find, explore, and map a lot of caves.
4) Study of a wide variety of carbonate island types to allow compare and contrast studies to be made. In other words, go to a lot of islands, and find, explore, and map a lot of caves.

The progression of the fieldwork from the simplest environment, in the Bahamas, to progressively more complex environments in Bermuda, Isla de Mona and the Marianas allowed the CIKM to be built modularly, expanding in a logical progression to accommodate each successive complication. If we had started our work in the Marianas, we may have well floundered for decades before piecing the puzzle together.

Cave and karst science is like any other science: discovery comes at unexpected times as a result of persistence, preparation, an open mind, and a little bit of luck. For the last 35 years we have traveled widely and sought out islands and their caves. Initially it was enough to find the caves. Then it was enough to map them. But finally, it wasn't enough until we understood why they were there. We didn't set out to become island cave and karst experts, but it sure has been fun.

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CAVE SEDIMENTS AND PALEOCLIMATE

William B. White
Materials Research Institute and Department of Geosciences, The Pennsylvania State University, University Park, PA 16802 USA wbw2@psu.edu

Abstract: This paper is a review of cave sediments: their characteristics and their application as paleoclimate archives. Cave sediments can be separated into two broad categories, clastic sediments and chemical sediments. Of these, stream-transported clastic sediments and calcite speleothems are both the most common and also the most useful as climatic records. Techniques for dating cave sediments include radiocarbon and U/Th dating of speleothems and paleomagnetic reversals and cosmogenic isotope dating of clastic sediments. Cosmogenic isotope dating of clastic sediments in caves with multiple levels or which occur at different elevations provide a geomorphic record of cave ages and river system evolution over the past 5 Ma. Isotope profiles, trace element profiles, color banding and luminescence profiles of speleothems, mainly stalagmites, produce a detailed paleoclimate record with very high time resolution over the past several hundred thousand years. There is potential application of these methods to late Holocene climates with implications for evaluation of current concern over global warming.

Introduction

Caves are open cavities in the earth. As such they are natural sediment traps. No caver needs to be reminded that caves are muddy. Closer inspection, however, shows that cave deposits are remarkably complicated as are the transport mechanisms that carry the sediments into the caves. Cave sediments have been recognized for as long as there has been scientific interest in caves. However, only in the past several decades has it been recognized that cave sediments contain both hydrogeological and paleoclimatological records. In part, this late recognition is due to the recent development of techniques for assigning dates to cave sediments. With an accurate chronology, the cave archives can be correlated with events on the land surface above. The investigation of cave sediments has moved from an obscure corner of karst science to one of today's hottest topics (e.g., Sasowsky and Mylroie, 2004). There is the very real possibility that cave sediments will take their place along side of ocean sediment cores and continental ice cores (Greenland and Antarctica) as the most important records of how Earth's climate has evolved over the past several million years.

The objective of the present paper is to summarize some of the current state of knowledge of cave sediments. As will be seen, the subject has grown much broader than it was in 1966 on the occasion of the 25th anniversary volume. The literature has become very large. What follows are examples to give some feel for what has been accomplished, particularly in the past 10–20 years. It is not a comprehensive review.

Some Historical Background

There has always been a distinction between speleothems and clastic sediments in caves. Speleothems are aesthetically pleasing and their bizarre shapes give caves much of their charm. It takes a special point of view to see the same scientific value in a mud bank as in a cluster of stalagmites.

The first descriptions of speleothems are lost in the mists of antiquity. Shaw's (Shaw, 1992) monumental treatise on cave science prior to 1900 devotes 13 chapters to speleothems including accounts of early and somewhat fanciful attempts to explain them. Many descriptions of the various forms of speleothems have appeared, and one of the best and most detailed descriptions of their crystal structures was written nearly a century ago (Prinz, 1908). The correct chemical reaction for the deposition of calcite in caves was described as early as 1812 by Cuvier and in 1820 by Benjamin Silliman the elder (Shaw, 1992). In a now classic paper, Holland et al. (1964) set forth a detailed chemical model for calcite deposition that remains the accepted explanation to the present time.

Clastic sediments are rarely mentioned prior to 1900 (Shaw, 1992). The two main categories, breakdown and stream deposits, are only briefly mentioned in the two most important early 19th Century textbooks (Kyrle, 1923; Trombe, 1952). Clastic sediments did play a central role in the Bretz (1942) model for cave development. According to Bretz, caves formed deep below the water table and then filled with red unctuous clay which filtered down from overlaying soils. Later dissection of peneplains and draining of the caves allowed the sediments to wash out, leaving behind the open cave passages we see today. Many of Bretz's field observations were in Missouri caves where the sticky muds are particularly common. In response, Reams (1968) devoted an entire Ph.D. dissertation to demonstrating that many of the Missouri cave sediments are, in fact, river sediments carried in through sinkholes and by sinking streams. In contrast, Davies (1960) used the sand and gravel sediments in Appalachian caves to demonstrate that the caves were formed by fast-moving water close to local base levels and not by slow percolation deep below the water table.

Caves sediments came into their own as a significant part of cave science in the 1960s with an important symposium on both chemical and clastic sediments (Dell'Oca, 1961) and the comprehensive research of Renault (1967–1969). The paleoclimatic significance of clastic sediments was recognized in European alpine caves by Schmid (1958). The first two English language textbooks on caves (Jennings, 1971; Sweeting, 1972) had chapters devoted to cave sediments although the coverage was predominantly on chemical sediments. Clastic sediment research in the United States got underway in the mid-1960s with the work of Frank (1965) on the caves of Texas and later work in Australia (Frank, 1969, 1971). Many of these early studies treated clastic sediments in caves as a peculiar sort of sedimentary rock with emphasis on in-cave stratigraphy and provenance of the sediment. One of the most comprehensive studies of sediment source and deposition was an unpublished Ph.D. thesis (Wolfe, 1973) describing cave sediments in the Greenbrier karst of West Virginia.

CLASSIFICATION OF CAVE SEDIMENTS

There is no generally accepted classification scheme for cave sediments. Each of the more recent textbooks on caves and karst (Bögli, 1980; White, 1988; Ford and Williams, 1989, Gillieson, 1996) presents a classification of sediments. These have many points in common but also significant differences. The classification in Figure 1 is a compromise. It lists the main categories of sediment, but does not attempt to provide a pigeon hole for every possible material that might accumulate in a cave.

I. CLASTIC SEDIMENTS
  A. Autochthonous Sediments
    1. Weathering Detritus
    2. Breakdown
    3. Guano
  B. Allochthonous Sediments
    1. Entrance Talus
    2. Infiltrates
      a. Soil Washdown
      b. Gravitational Debris
    3. Stream Transported Sediments
      a. Organic In-Wash
      b. Alluvial Sediments
      c. Glacial In-Wash
      d. Volcanic In-Wash
    4. Debris Flows
    5. Aeolian Deposits

II. CHEMICAL SEDIMENTS
  A. Travertine
    1. Flowstone
    2. Dripstone
  B. Evaporites
    1. Crusts
    2. Bulk Deposits
  C. Phosphates
  D. Resistates
  E. Ice

Figure 1. A classification of cave sediments.

Sediments are divided into two broad categories: clastic sediments and chemical sediments. Clastic sediments are moved mechanically whereas chemical sediments are formed in place, precipitated from solution in seeping, dripping, or flowing water. Clastic sediments can then be subdivided again into materials that are derived locally within the cave and materials that are transported into the cave from the outside. These are known respectively as autochthonous sediments and allochthonous sediments. Chemical sediments are subdivided into categories based on their composition.

Locally derived clastic material consists of weathering detritus, breakdown, and guano. Weathering detritus is the insoluble component of the bedrock, left behind when the bedrock dissolved. Weathering detritus is one source of the sticky clays found in some caves that have no evidence of stream action. Weathering detritus can include sand, silicified fossil fragments, and chert, the latter in some limestones being a major component of the clastic sediment. Breakdown consists of fragments of broken bedrock in a wide range of sizes. The classification of breakdown and the geologic processes responsible for cave passage collapse is more complex than expected (White and White, 1969; Jameson, 1991). Guano is the fecal material deposited in caves by bats and birds. In caves with large bat populations, guano is present in sufficient quantities to be classified as a sediment.

The composition of allochthonous sediment varies depending on the rock types and other materials available in the drainage basin in which the cave is embedded. Cave entrances are usually sites of intensive weathering and the combination of breakdown, downslope movement from other rock units above the cave, soil slumping, and incorporated plant material creates a characteristic pile of roughly stratified debris known as entrance talus. Entrance talus is of importance because it often houses paleontological or archaeological deposits. Infiltrates are sediments that migrate into the cave from the land surface above. They subdivide into soil washdown which is mainly soil from the epikarst that is washed into the cave through solutionally-widened fractures, and gravitational debris which is coarser-grained material that falls down open shafts. Sinking streams carry a great variety of materials into caves including alluvial sediment, glacial tills, volcanic ash and any other unconsolidated material that may be picked up by the stream. Debris flows are essentially avalanches that flow underground. These provide rare but dramatic cave deposits, for example those found in the caves of the New Guinea highlands (Gillieson, 1986). Finally, quantities of sand and loess can be blown into caves directly by wind action to produce aeolian deposits.

Most common of the chemical sediments are the travertines. The word travertine is here used as a blanket label for fresh-water carbonate deposits of all types. Travertine is used as a rock name whereas speleothem refers to the specific external morphology of the deposits. Cave travertines are chemically similar to the calcareous tufas found as spring and fresh water deposits throughout the world and to the geothermal travertines (Ford and Pedley, 1996). Tufas generally are porous and contain a great deal of plant material in comparison to both cave and geothermal travertines, which are usually dense and compact. Tufas also contain paleoclimatic records (Andrews, 2006).

The term evaporite is used for cave sediments in much the same way that it is used for surface sediments; assemblages of minerals formed by evaporating water. Most common in caves is gypsum, $CaSO_4 \cdot 2H_2O$, but there exist a selection of other sulfate minerals as well as occasional halite deposits. The remaining categories of chemical sediments listed in Figure 1 are volumetrically rather minor. Phosphates, mainly hydroxyapatite, are associated with old and decomposed guano deposits. The resistates, iron and manganese oxides, are usually limited to coatings. Perennial ice occurs in alpine caves and so can reasonably be considered a cave sediment.

CLASTIC SEDIMENTS

Figure 1 provides a systematic categorization of clastic sediments in terms of source area. However, the conduit system acts as a mixing chamber so that the sediments observed in caves or emerging from karst springs contain components from all of the sources. Figure 2 gives the overall concept. The key parameters are flow velocities, flow volumes, particle density, and particle size. Although there may be some contribution of relatively light organic material, most clay, silt, sand, cobbles and boulders have densities not greatly different from that of quartz (2.65 g cm^{-3}). Density variations are not a very significant variable. The size of clastic particles varies over six to eight orders of magnitude from sub-micrometer colloidal and clay particles to boulders approaching one meter. The clastic sediments remaining in caves and the flux of clastic sediments through the aquifer are determined mainly by storm flow and by particle size. Clastic particles flushed through the system are part of the hydrology; clastic particles remaining after the caves are drained become the sediment record.

TRANSPORT MECHANISMS

Sediment transport in open channels occurs by two mechanisms: suspended load and bedload. The suspended load consists of particles taken in suspension by the turbulence of stream flow. Such particles tend to settle out, but are held in suspension by the turbulence. The energy required to hold particles in suspension and the rate at which they settle out of suspension depend on particle size. If flow velocities decrease, for example by an expansion of the passage cross-section or by ponding of water behind an obstruction, coarse sediments drop out rapidly but very fine-grained sediments may remain in suspension. Flowing water moves bedload by dragging it along the bed because of the boundary shear between the moving water and the bed material. It is not required that these flows be turbulent although they usually are. The boundary shear necessary to put bed particles in motion increases almost linearly with the particle size and with the square of the flow velocity.

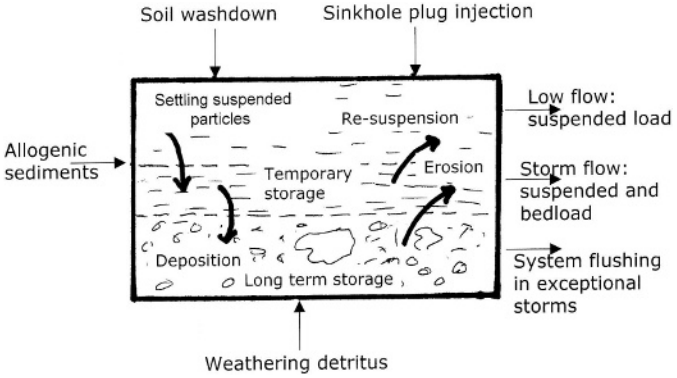

Figure 2. Sketch showing clastic sediment sources and the role of the conduit system as a mixing chamber.

There is a wide range in particle sizes for the material injected into the conduit systems from the sources sketched in Figure 2. Velocities vary along the conduit depending on whether a particular segment is pipe-full or flowing in an open channel, depending on passage cross-sectional area, and depending on obstacles or blockages within the conduit. Velocities also vary depending on whether the system is at base flow or storm flow, and if at storm flow, on the magnitude of the storm. As a result there is a very complex mixing and partitioning of sediment within the conduit system. Small particles in the colloidal or fine clay size range may remain in suspension and provide a continuous flux of sediment at the spring even during base flow conditions. Clay and silt sized particles may settle into temporary storage during base flow but are re-suspended and carried to the spring during storm flow, thus causing the spring to become muddy. Very coarse pebble to cobble size sediments may be swept into the conduit system during large storms and remain in the system in long-term storage until they are swept on through by another exceptional storm. There is a continuous interchange of sediment depending on flow conditions.

Much recent research has been concerned with the hydraulics of sediment transport and with the appearance of suspended sediments at karst springs. Because of the open conduits, many springs discharge very small particles even under base-flow conditions (Atteia et al., 1998). The fine-grained particles are of importance because they provide a transport mechanism for bacteria (Mahler et al., 2000) and heavy metals (Vesper and White, 2003). Turbid or muddy spring water makes the springs unsuitable as water supplies and as a result there have been many studies of suspended sediment transport to springs (Mahler and Lynch, 1999; Drysdale et al., 2001; Amraoui et al., 2003; Massei et al., 2003; Dogwiler and Wicks, 2004). There has been relatively little recent work on the mechanisms of transport of the coarse fraction that makes up much of the sediment seen in caves. Gale (1984) was able to use the observed sediment particle sizes to back calculate the hydraulic characteristics of the conduit in which they were found. One recent study (Hart and Schurger, 2005) estimated the rate of sediment injection through sinkholes to be 111 Mg km^{-2} yr^{-1} for a watershed in central Tennessee.

Lithofacies

Ultimately, of course, the composition, mineralogy, and lithology of cave clastic sediments depend on the material available in the source areas. Within this constraint, however, the sedimentary deposits depend on the internal dynamics of the conduit system. Thus, cave clastic sediments occur in facies that reflect the way in which injected sediment has been rearranged and deposited. There have been a number of facies schemes proposed depending on the criteria used for identifying the facies (e.g., Gillieson, 1986; Springer and Kite, 1997). The scheme sketched in Figure 3 (Bosch and White, 2004) describes facies according to particle size and the degree of sorting. It will be noted that the axes in Figure 3 have no scale. Further, the boundaries between the facies domains are exceedingly fuzzy.

The widest range of particle size and particle sorting occurs in the most common stream deposits in caves, the channel facies. They occur as roughly stratified layers of sands, silts, and cobble deposits most easily observed where more recent streams have cut through earlier sediments thus exposing the layering in the stream bank. Any given exposure of channel facies is likely to show distinct bedding, but this stratigraphy is rarely continuous along the cave passage. The thalweg facies is a derivative of the channel facies. Thalweg facies are the coarse cobble armoring that forms the beds of many active cave streams. The coarse material is a residual deposit formed by stream action winnowing out the fine-grained material from the channel facies. The other three facies sketched in Figure 3 each involve different transport processes.

Slackwater facies are the thin layers of fine grained silt and clay that often form the final top layer of clastic deposits. This facies is often found in blind side passages, pockets, and other niches in caves unlikely to be reached by flowing streams. The slackwater facies appear to be deposited from suspended sediment that has settled out of flooded cave passages. Rising floodwaters fill all available spaces and are then ponded for extended periods of time until the flood recedes. During the time when the passage is water-filled, suspended sediments have time to settle out and form a sediment layer. An investigation of this facies in Agen Allwedd Cave in the UK (Bull, 1981) revealed distinct laminae which were interpreted to be the result of a rhythmic pulsing of sediment-laden water into subterranean lakes in response to surface climate. Careful examination of this microstratigraphy revealed a sequence of climatic events extending back 17,000 years (Bull, 1980).

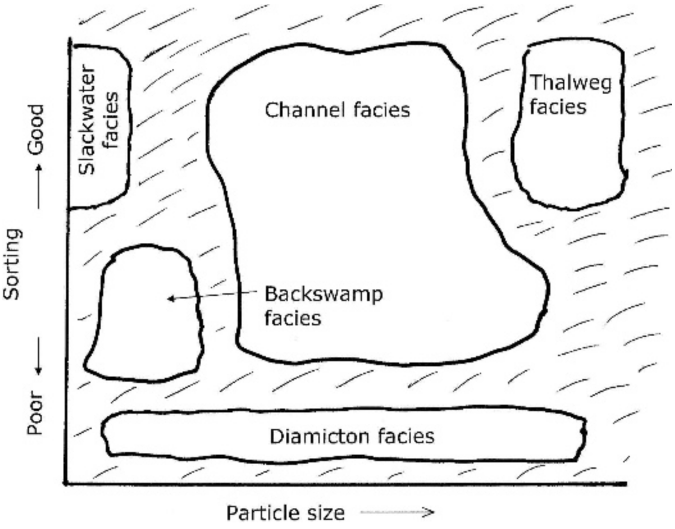

Figure 3. Facies of clastic sediment. Adapted roughly from Bosch and White (2004).

Diamicton facies are the result of debris flows. These are chaotic deposits containing particles ranging from clays to cobbles tossed together with no bedding and no sorting. Special circumstances, mainly extreme storm intensities and high gradient cave passages, allow entire sediment deposits to be taken into suspension and swept down a cave passage to later be deposited in an undifferentiated mass. Diamicton facies were described from the high gradient caves in New Guinea (Gillieson, 1986).

In some caves, particularly network mazes, flow velocities never reach threshold values for sediment transport. The sediments in these caves tend to be locally derived, either the residual insoluble material from dissolution of the limestone or infiltrating soil from the land surface above. The term "backswamp facies" was chosen because, hydraulically, network mazes and other slow-flow caves tend to behave as the underground equivalent of swamps.

Chemical Sediments

Mineralogy

Caves, where temperature, water vapor partial pressure, carbon dioxide partial pressure and other environmental

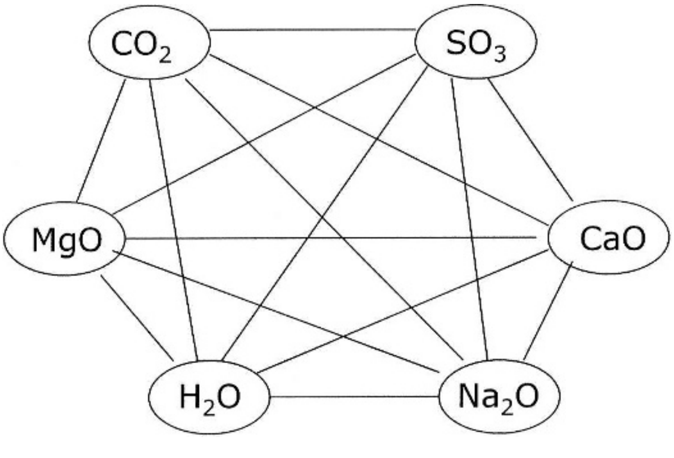

Figure 4. Interconnections of the six oxide components that make up most common cave minerals.

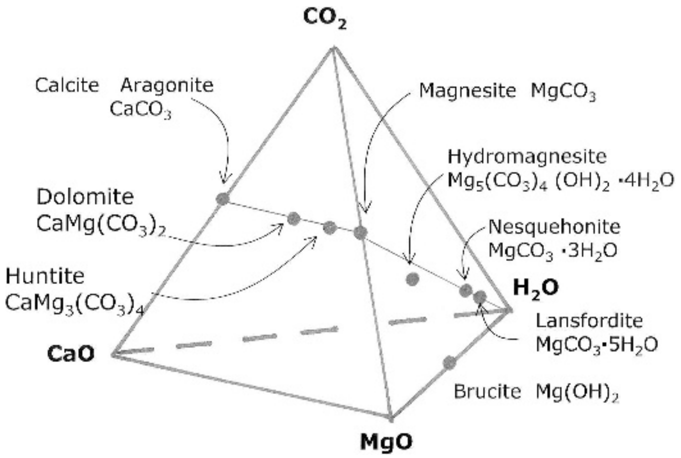

Figure 5. Compositions of the cave carbonate minerals represented on a regular tetrahedron.

parameters either remain constant or cycle through fixed patterns over long periods of time, are effective deposition sites for a surprising range of minerals. Hill (1976) described 74 minerals mainly from caves in the United States. By 1997 when the expanded *Cave Minerals of the World* reached a second edition (Hill and Forti, 1997), the number of identified cave minerals had reached 255. Very few of these occur in sufficient volume to be important as cave sediments.

Ions that occur commonly in carbonate ground waters and would be available for the formation of cave minerals are Ca^{2+}, Mg^{2+}, Na^+, HCO_3^-, and SO_4^{2-}, plus, of course, water. Because caves, with some interesting exceptions, are oxidizing environments, the resulting minerals can be described in terms of their component oxides. The system would be $CaO – MgO – Na_2O – CO_2 – SO_3 – H_2O$. Because any material object contains 100 percent stuff, the total concentrations of all components must add up to 100 percent. Therefore, the number of independent composition variables is always one less than the number of components. The chemical system of six oxides requires a five-dimensional space to plot the compositions which is difficult on a two-dimensional sheet of paper. Figure 4 shows the topological relations. If the components are selected four at a time, the compositions of any minerals in these sub-systems can be represented in three dimensions, namely by plotting any combination of four components on the apices of a regular tetrahedron. The principal Ca-Mg-carbonate minerals can be displayed in this fashion (Fig. 5).

Of the minerals plotted on Figure 5, only calcite and to a lesser extent aragonite are significant constituents of cave sediments. In spite of the common occurrence of caves in dolomite rocks, dolomite rarely precipitates from karst waters. Magnesium appears either as a solid solution in calcite or as the fine-grained hydrated magnesium carbonate minerals known as moonmilk.

The sulfate minerals require the five-component subsystem $CaO – MgO – Na_2O – SO_3 – H_2O$ to cover the common minerals. Gypsum, $CaSO_4{\cdot}2H_2O$ is the second most common cave mineral and, in terms of sediment volume, is by far the most important sulfate mineral. Others include epsomite, $MgSO_4{\cdot}7H_2O$ and mirabilite, $Na_2SO_4{\cdot}10H_2O$. Both are highly water-soluble and are found only in extremely dry caves. The stability of these minerals can be described in terms of the temperature and water vapor partial pressure (White, 1997).

DEPOSITION OF CALCITE AND ARAGONITE

The deposition of both calcite and aragonite in caves is described by the deceptively simple chemical reaction

$$Ca^{2+} + 2HCO_3^- \rightarrow CaCO_3 + CO_2 + H_2O \qquad (1)$$

The same reaction written in reverse describes the dissolution of limestone. The equilibrium concentration of dissolved carbonate depends on the partial pressure of CO_2, the temperature, reactions among the various carbonate species, and also on the ionic strength, other ions in solution, and various complexes that may form. Carbonate chemistry is now understood in considerable detail and appears in a variety of textbooks (e.g., Langmuir, 1997). The equilibrium concentration of dissolved Ca^{2+} in a system open to CO_2 is given by

$$m_{Ca^{2+}} = P_{CO_2}^{1/3} \left[\frac{K_1\ K_C\ K_{CO_2}}{4\ K_2\ \gamma_{Ca^{2+}}\ \gamma^2_{HCO_3^-}} \right]^{1/3} \qquad (2)$$

In this equation, K_1 and K_2 are the first and second dissociation constants for carbonic acid, K_{CO_2} is the Henry's law constant for the solubility of CO_2 and the γ's are the activity coefficients for the Ca^{2+} and HCO_3^- ions. The same equation describes the solubility of aragonite if K_C, the solubility product constant for calcite, is replaced by K_A, the solubility product constant for

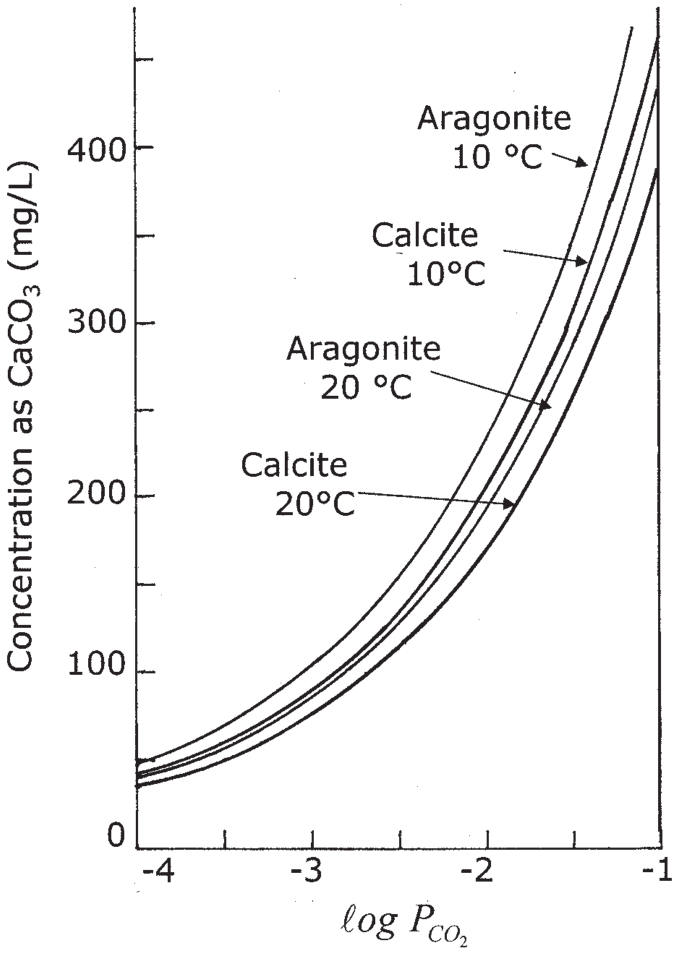

Figure 6. Solubility of calcite and aragonite as a function of CO_2 pressure. Calculated from equation (1) for 10 °C and 20 °C.

aragonite. Numerical values for the constants at various temperatures are given by White (1988). Calculated solubilities for calcite and aragonite are plotted in Figure 6.

The solubility curves in Figure 6 provide a model for the chemistry of carbonate mineral deposition. Rain water contains CO_2 at the concentration of 0.037 volume percent ($log\ P_{CO_2} = -3.43$) but essentially zero dissolved carbonate. When rain water percolates through organic-rich soils, the CO_2 concentration may rise as high as 10% ($log\ P_{CO_2} = -1$). When the CO_2-rich water reaches the bedrock it dissolves the limestone taking Ca^{2+} ions into solution. Ca^{2+}-ion concentrations may reach values in the range of 400 mg L^{-1} as $CaCO_3$ as given by equation (2). These CO_2- and Ca^{2+}-rich percolation waters seep downward along joints until they emerge from the ceilings and walls of cave passages. The CO_2 concentration in cave atmospheres is typically about ten times that of the surface atmosphere ($log\ P_{CO_2} = -2.5$) so in this environment, the dripping waters are highly supersaturated. CO_2 is degassed into the cave atmosphere and $CaCO_3$ is precipitated, until (at equilibrium) the concentration falls back to about 100 mg L^{-1}. Because the cave environment is usually water-saturated, the surfaces of the growing speleothems remain wet. Each successive drop deposits its small load of $CaCO_3$ in register with the ions already present on the growing crystal surface. Thus individual calcite crystals in speleothems in sealed caves tend to be large, often much larger than any that have been grown in the laboratory.

The rate at which calcite dissolves has been the subject of a huge number of investigations (for review see Morse and Arvidson, 2002). Dissolution rate studies are pertinent to the interpretation of cave development (speleogenesis). The reverse rates for calcite or aragonite precipitation and thus of speleothem growth at saturation conditions far from equilibrium tend to follow the same laws as calcite dissolution (with some signs reversed) (Reddy et al., 1981). Near equilibrium, which is the condition in most cave depositional environments, the mechanisms are much more complicated. In order for calcite crystals to grow, the feed solutions must be supersaturated. However, if the supersaturation is too large, new calcite crystals will be nucleated and, instead of one large crystal, the speleothem will consist of many small crystals. $CaCO_3$ growth rates have been studied in the laboratory by controlling supersaturations and measuring growth rates (Gutjahr et al., 1996).

More insight into the details of the process at the atomic scale have been obtained by using the atomic force microscope to actually measure the rate of growth of individual layers within the crystal (Teng et al., 2000). The agreement is generally good between laboratory measurements, calculations of growth rate, and growth rates directly measured in caves (Baker et al., 1998). The trade-off between growth rates of individual crystals and the nucleation and growth of multiple crystals results in a variety of microstructures (also called fabrics or textures) in speleothems which can be examined by polarized light microscopy or by scanning electron microscopy (Frisia et al., 2000). Trace quantities of Mn^{2+} or rare earth elements fluoresce under cathode-ray activation, providing a better visual image of growth patterns than those that can be seen by white light microscopy. Cathodoluminescence microscopy has been used to observe growth patterns in speleothems and produce a paleoclimatic interpretation (Richter et al., 2004).

It has long been established that calcite is the stable polymorph of $CaCO_3$ at all temperatures under ambient pressures (Carlson, 1983). Pressures of 300–500 MPa are required to stabilize the orthorhombic aragonite structure. In what seems to be a direct violation of thermodynamics, aragonite occurs commonly in caves forming anthodites, frostwork, aragonite bushes, and bulk stalactites and stalagmites. The literature on the aragonite problem is very large (see review by Carlson, 1983). Two factors seem to be responsible. One is the sensitivity of calcite nucleation and growth to the presence of impurities. The other is the solubility of aragonite which, as a metastable phase, must be larger than that of calcite. However, as shown by the curves in Figure 6, the solubility of aragonite is only about 10% greater than that of calcite over a wide range of CO_2 pressures at the same temperature. Indeed, the aragonite curve at 20 °C is almost coincident with the calcite curve at 10 °C. Unlike calcite, aragonite nucleates easily and its growth is relatively insensitive to impurities. It is only necessary to inhibit calcite nucleation sufficiently to allow the supersaturation to build past the aragonite solubility curve and aragonite will precipitate. Sr^{2+} enhances aragonite growth by precipitating a Sr-rich nucleus with the aragonite structure. This acts as a template on which aragonite can grow. Mg^{2+} has long been known as a calcite growth inhibitor (Berner, 1975), an effect confirmed by more recent direct measurements with the atomic force microscope (Davis et al., 2000).

Growth of bulk speleothems, of which stalagmites have been of greatest interest, combines consideration of the growth of individual calcite crystals with considerations of precipitation, flow paths from the surface to the cave, and carbon dioxide concentration contrasts between the soil and the cave atmosphere. A further consideration for near-entrance environments is the role of evaporation as a competitive process with CO_2 loss. Because drip-rate (related to precipitation) and CO_2 pressure vary seasonally in most locations, speleothems develop an annual layering with layers that vary in texture and also sometimes in calcite/aragonite content. The rate of growth can be determined by dating the stalagmite layers, either by counting the layers in contemporary stalagmites or by U/Th dating of samples taken along the stalagmite axis. Typical values are in the range of 0.01 to 0.1 mm y^{-1}. The relationship between growth rate and stalagmite shape has been modeled by Kaufmann (2003).

The thickness, texture, and mineralogy depend primarily on precipitation as the most important external parameter, thus measurement of these quantities provides a paleoclimate indicator. Growth layering has provided information from the past several millenia where confirmation from historical records is possible. Such measurement gave a rainfall proxy record for the past five centuries in Madagascar (Brook et al., 1999). Several thousand years of record of the intensity of Indian monsoons was extracted from a stalagmite from Nepal (Denniston et al., 2000a). Spectral analysis of the layering pattern in the Shihua Cave, China appeared to track climatic cycles (Qin et al., 1999). Older records are also possible.

DEPOSITION OF GYPSUM

Gypsum deposition is a matter of the evaporation of sulfate-bearing solutions. No chemistry is involved. The reaction is:

$$Ca^{2+} + SO_4^{2-} + 2H_2O \rightarrow CaSO_4 \cdot 2H_2O \qquad (3)$$

The concentration of dissolved gypsum exactly in equilibrium with crystalline gypsum is given by

$$C_{gyp} = M_{gyp}\left[\frac{K_{gyp}}{\gamma_{Ca^{2+}}\,\gamma_{SO_4^{2-}}}\right]^{1/2} \qquad (4)$$

C_{gyp} is the concentration of dissolved gypsum in g/L, M_{gyp} is the molecular weight of $CaSO_4 \cdot 2H_2O$, K_{gyp} is the solubility constant for gypsum and the gammas are the activity coefficients for calcium and sulfate ions. M_{gyp} = 172.17 atomic mass units. The solubility of gypsum does not depend on pH or CO_2 pressure but does vary with temperature. Other ions in solution affect gypsum solubility through the activity coefficients.

K_{gyp} as a function of temperature is given by

$$\log K_{gyp} = 68.2401 - \frac{3221.51}{T} - 25.0627 \log T \qquad (5)$$

Equation (5) is taken from Langmuir and Melchior (1985). In this equation, T is the absolute temperature in kelvins. At the standard reference temperature of 25 °C, the calculated value is $\log K_{gyp} = -4.581$, a value that has been accepted by several contemporary textbooks (e.g., Langmuir, 1997; Drever, 1997). This number is based on direct solubility experiments and is recommended against other values that have been calculated from thermodynamic data.

The sources of gypsum in caves vary depending on the specific cave. Sources that have been identified include:

- Dissolution, transport, and redeposition of gypsum beds that occur interbedded with the carbonate units.
- Oxidation of H_2S to sulfuric acid followed by reaction of the acid with the limestone to form gypsum. This is the source of gypsum in sulfuric acid caves.
- Oxidation of pyrite, FeS_2, that occurs dispersed in the limestone followed by reaction with the limestone to form gypsum.
- Oxidation of pyrite from overlying strata followed by transport of sulfate-bearing solutions to the cave where reaction to gypsum takes place.

Residual gypsum is a key part of the mechanism for the formation of sulfuric-acid caves (Hill, 1987, 1990). Thus far, gypsum has not been found to contain any significant paleoclimatic record. Another sulfate mineral, alunite, $KAl_3(SO_4)_2(OH)_6$, has been found to retain ^{40}Ar from the decay of ^{40}K so that $^{40}Ar/^{39}Ar$ dating of the alunite from Carlsbad Caverns and other Guadalupe Mountain caves was possible (Polyak et al., 1998). Ages ranged from 3.89 Ma in Carlsbad Cavern to the oldest and highest cave examined, Cottonwood Cave, at 12.26 Ma.

ICE

Seasonal ice forms in many caves where winter temperatures fall below freezing. Often the ice takes the form of spectacular, if transient, speleothems near cave entrances. Caves with perennial ice are less common and

Figure 7. Ice speleothems, Scărişoara Ice Cave, Romania.

Figure 8. Ferrihydrite speleothems, Rohrers Cave, Pennsylvania.

usually occur only at high altitudes. Fossil Mountain Ice Cave in Wyoming is an example in the United States. Best known are the big ice caves of the European Alps such as the Eisriesenwelt and the Rieseneishöhle in Austria. Some of the best paleoclimatic records have been recovered from ice cores drilled in the continental glaciers of Greenland or Antarctica. It would seem that drilling the perennial ice in an ice cave would be valuable. Studies have been undertaken in the Scărişoara ice cave in the Apuseni Mountains of Romania (Racovită and Onac, 2000) (Fig. 7).

Resistates: Iron and Manganese Oxides

Among the more widespread minor cave sediments are the oxides and hydroxides of iron and manganese. These compounds are highly insoluble in neutral pH water and so are known as resistates.

Goethite (FeOOH), ferrihydrite ($Fe(OH)_3$) and other hydrated and hydroxylated iron oxides occur widely in caves. Goethite is usually crystalline at the X-ray diffraction scale but the other iron oxides and hydroxides are usually non-crystalline at the X-ray scale. Speleothems of iron hydrates have been found and are well developed in Rohrer's Cave, Lancaster County, Pennsylvania (White et al., 1985) (Fig. 8).

Black coatings that occur widely on stream sediments are usually described as manganese oxide. Usually the manganese oxides appear only as thin (< 1 mm) coatings although thicker and more massive deposits occur. Although at least nine manganese oxide minerals have been reported from caves (Hill and Forti, 1997), most of the identified deposits are composed of birnessite, the δ polymorph of MnO_2, but with a composition approximately $(Na,Ca,Mn^{2+})Mn_7O_{14}\cdot 2.8H_2O$. The manganese oxides act as scavengers for heavy metals. Concentrations from parts per million to more than one percent of Zn, Cu, Ni, Co, V, and Cr have been found. Likewise, rare earth elements have been found in manganese oxide deposits (Onac et al., 1997). Deposition of the manganese oxide minerals requires oxidation of Mn^{2+} in the cave water to Mn^{4+}, a process that is likely microbially mediated (Tebo et al., 1997; Northup and Lavoie, 2001).

AGE MEASUREMENTS ON CAVE SEDIMENTS

The widespread interest in cave deposits as paleoclimate archives arises because of well-developed and reliable methods for assigning dates to the deposits. Different sediments provide different information and different methods are used to date them. The sections that follow give a short summary of the most important of the dating techniques.

CARBON 14

Spallation of ^{14}N by cosmic rays in the upper atmosphere produces the radioactive isotope of carbon, ^{14}C. The ^{14}C is oxidized to $^{14}CO_2$ which then mixes with other $^{12}CO_2$ in the lower atmosphere thus producing a constant radioactive component. The same constant radioactive background is present in plants which grow by extracting CO_2 from the atmosphere. The basis for C-14 dating is that when plants die, the exchange of CO_2 with the atmosphere ceases, the incorporated ^{14}C begins to decay according to its 5730 year half-life. Measurement of the residual ^{14}C in wood and charcoal then allows the calculation of the time that has elapsed since the wood or charcoal was part of a growing plant. The usual time limit for C-14 dating is about ten half-lives or 50,000 years, but there are many corrections and caveats to the calculation of dates (Taylor et al., 1992).

The calcite in speleothems is derived from limestone dissolved at the soil/bedrock contact above the cave for which the chemical reaction is

$$CaCO_3 + CO_2 + H_2O \rightarrow Ca^{2+} + HCO_3^- \qquad (6)$$

In the cave the calcium and bicarbonate ions are recombined to precipitate calcite in the growing speleothem. Half of the carbon in the precipitated calcite comes from CO_2 and the other half from the $CaCO_3$ in the limestone. The CO_2 is derived partly from the atmosphere and partly from the decomposition of organic material in the soil. The organic material originated as living plants and thus also contains the background concentration of ^{14}C. One might expect, therefore, that the carbon in the bicarbonate ions that form speleothems should consist of about half young carbon from the atmosphere and soil CO_2 and half old, dead, carbon from the limestone. C-14 dating of speleothems should therefore be possible by taking account of the fraction of young, zero age, carbon in the calcite.

The isotopic chemistry of calcite deposition is more complicated. There is carbon-isotope exchange in the soil and in the dissolution and deposition processes. As a result, speleothems typically contain about 85% young carbon, a circumstance that actually makes C-14 dating a little easier. There have been relatively few C-14 dates of speleothems. One critical comparison on speleothems in the Lobatse II Cave (Holmgren et al., 1994) showed that C-14 dates compared well with U/Th dates back to 20,000 years.

U/TH DATING OF SPELEOTHEMS

U/Th-dating has become the gold standard for speleothem dating (Dorale et al., 2004; Richards and Dorale, 2003). The common uranium isotope, ^{238}U, undergoes a long and complicated decay chain before reaching the stable isotope ^{206}Pb (see Figure 1 in Field, 2007). Along that chain of mostly short-lived intermediates are two long-lived isotopes, ^{234}U (half life = 248,000 years) and ^{230}Th (half-life = 75,200 years). Measurement of the ratio of $^{234}U/^{238}U$ and $^{230}Th/^{234}U$, assuming no thorium in the initial sample, allows the calculation of an age. What makes U/Th isotope dating particularly useful for calcite speleothems is a quirk in the geochemistry of these two elements. Both uranium and thorium have 4+ valence states which produce compounds that are highly insoluble. Uranium also has a 6+ valence state which usually appears as the UO_2^{2+} ion. Thorium does not. The uranyl ion further complexes in carbonate waters and becomes highly mobile (Langmuir, 1997). As a result, speleothems often contain tens to hundreds of parts per million uranium but no thorium. The radiogenic thorium that accumulates in the calcite is a direct measure of the time elapsed since the calcite was deposited.

Uranium/thorium dating of speleothems was pioneered by Derek Ford, Henry Schwarcz, and their students at McMaster University. Age dates combined with oxygen isotope ratios and deuterium ratios produced paleoclimatic records for caves in West Virginia (Thompson et al., 1976). These early measurements used alpha particle spectroscopy to measure uranium and thorium isotope concentrations, a technique that required tens of grams of sample (Harmon et al., 1975). Many dates were obtained by multiple laboratories and a picture was framed for northern North America and northern Europe of abundant speleothem growth during the Holocene and during the Eemian (Sangamon) interglacial (isotope stage 5; 100,000–130,000 years B.P.). Relatively little growth occurred during the periods of glacier advancement (Hennig et al., 1983; Gascoyne, 1992). Although some U/Th dating by alpha-counting continues, for example, the demonstration of four episodes of speleothem deposition in level IV of the Demanova Caves in Slovakia (Hercman et al., 1997), better resolution is necessary to probe the paleoclimate records in detail. The breakthrough was the use of heavy ion mass spectroscopy to measure isotope concentrations (Li et al., 1989). More precise isotope concentrations allowed extension of the dating range from 350,000 years for alpha counting techniques to approaching the theoretical limit of about 600,000 years. Heavy ion mass spectroscopy and later accelerator mass spectroscopy also reduced the required sample size so that dates could be obtained from milligrams rather than tens of gram quantities of speleothem. Thus a stalagmite could be

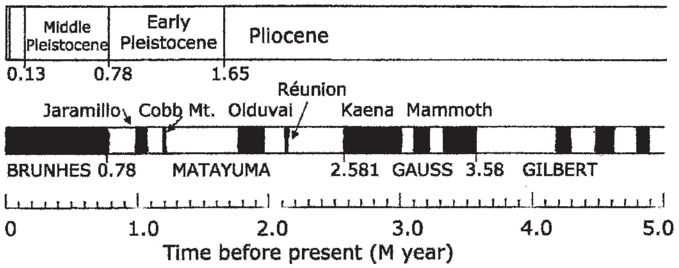

Figure 9. Geomagnetic time scale through the Pliocene. Drawn from data of Cande and Kent (1995), Berggren et al. (1995) and Singer et al. (2004). The precise dates for some of the reversal events are not in complete agreement between literature sources. Labeling at bottom gives the main paleomagnetic periods (or chrons). At top are labeled some secondary events.

sectioned along its long axis, then sampled at close intervals along the axis to obtain a complete chronology of the stalagmite's growth history.

PALEOMAGNETIC CHRONOLOGIES

The Earth's magnetic field reverses at irregular intervals during which the magnetic north pole and the magnetic south pole exchange places. Intervals where the north pole is near its present location are called normal; the other intervals are called reversed. The geophysics of the magnetic field have been extensively investigated (e.g., Channell et al., 2004) and a geomagnetic stratigraphy established well back into geologic time. The paleomagnetic time scale shown in Figure 9 has been drawn only for the past five million years since this is the time interval of most interest in karst processes.

Fine-grained clastic sediments contain small amounts of magnetic minerals. As these sediments settle, the magnetic grains rotate to orient with the Earth's magnetic field as it was at the time of the event. Once the grains have settled, their magnetic orientation is locked in place and can be determined by careful measurement of the magnetic properties of oriented samples. The measurements require very high sensitivity equipment because there are only a small number of magnetic grains and most of these have only weak magnetic moments

If paleomagnetic reversals can be identified in cave sediments, they provide time markers and thus dates for sediments and the passages in which they occur. Because of the long time spans between reversals, the method is best applied to tiered caves where the total sequence of cave passages and their sediments represent equally long times. Within a single cave passage, sediments are expected to be stacked in the usual stratigraphic fashion with the oldest sediments on the bottom. Cave passages, however, are arranged in the opposite order, with the youngest passages near present day base levels and older passages higher on the ridges (Fig. 10). This arrangement must be taken into account in the interpretation of paleomagnetic data. The best samples are obtained from the slackwater facies where the sediment grains settle out in quiet water. Often what is available are the channel facies, and these may very well have been reworked by later flood events so that the paleomagnetic signals are scrambled. If a complete sedimentary sequence is not available, identification of a reversal in a sediment pile in a high-lying cave leaves open the question of which reversal is being observed.

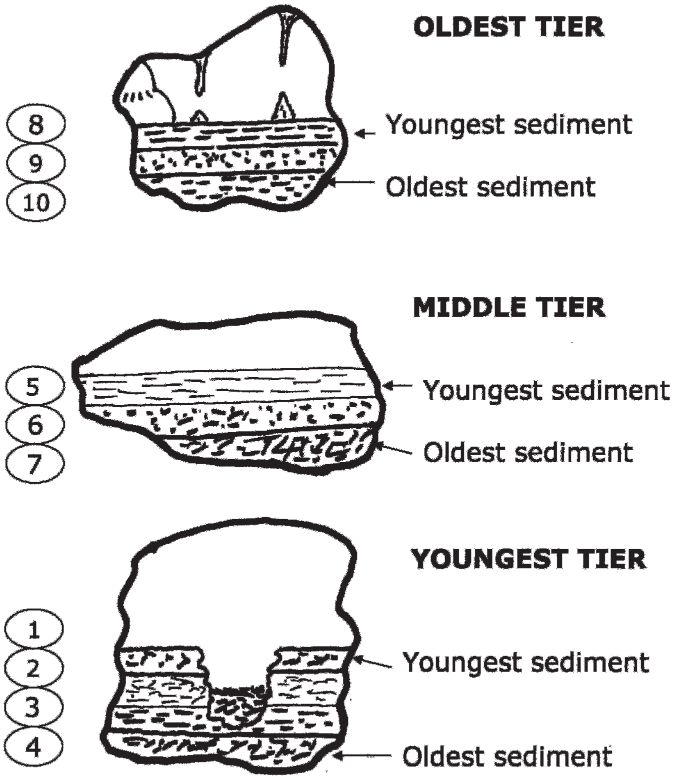

Figure 10. Sketch showing sediment stratigraphic relations in tiered caves. The schematic sediment layers are numbers from youngest to oldest, 1 to 10.

Paleomagnetic stratigraphy has been determined for clastic sediments in Mammoth Cave (Schmidt, 1982), the caves of the Obey River Gorge in the western Cumberland Escarpment of Tennessee (Sasowsky et al., 1995), the caves of the Cheat River Gorge in West Virginia (Springer et al., 1997), and Kooken Cave, Pennsylvania (Sasowsky et al., 2004). Because of limited availability of sensitive magnetic measuring apparatus, and because the reversals provide only widely spaced time markers, this method of sediment dating has seen limited application.

COSMOGENIC ISOTOPE DATING

The Earth is under constant bombardment by cosmic rays, which are extremely energetic particles from space. These particle streams and their spallation products from collisions in the upper atmosphere, rain down on the surface where they can induce nuclear reactions in surface materials. These reaction products are known as cosmogenic isotopes and can be used as an interpretative tool (Gosse and Phillips, 2001). The isotopes of importance for cosmogenic isotope dating of cave sediments are ^{10}Be (half-life = 2.18 Ma) and ^{26}Al (half-life = 1.02 Ma). Both are formed from the secondary cosmic ray neutron and muon bombardment of quartz, ^{10}Be from oxygen and ^{26}Al from silicon.

If quartz, either as pebbles or sand, is left exposed on or near the land surface, a certain very tiny concentration of ^{10}Be and ^{26}Al will build up. If sinking streams then wash the quartz sediment into a cave, the quartz will be shielded from cosmic rays and the accumulated ^{10}Be and ^{26}Al will begin to decay. Although the initial concentrations of the cosmogenic isotopes are not known, the ratio of the concentrations will change so that the time since burial can be extracted (Granger and Muzikar, 2001). Careful sample preparation is needed and, because concentrations are measured in millions of atoms, an accelerator mass spectrometer is needed to determine the isotope ratios.

Cosmogenic isotope dating is one of the most promising recent techniques. It covers a time scale back to 5 Ma which is the time scale for most active karst systems. The quartz that is dated is part of the channel facies sediment load and these materials are usually deposited when the cave passage is part of the active drainage system. To a reasonable approximation, the cosmogenic date of the sediment is also a measure of the age of the cave passage. By using cosmogenic isotope dating of cave sediments, it was possible to establish a rate of downcutting for rivers in the Sierra Nevada (Stock et al., 2004).

The Paleoclimatic Record

Available Archives

The study of cave sediments, as has been demonstrated above, has come a long way. From a beginning of simply trying to understand why speleothems have their observed shapes and mineralogy, investigations of cave sediments are now delving into sediments as archives of critically important paleoclimatic information. Cave sediments have come into their own as the unopened history book of the Pleistocene.

Of the main classes of cave sediments listed in Figure 1, carbonate speleothems have the greatest information content. Clastic sediments appear as facies which reflect the hydraulics of the flow systems that deposited them. Previous episodes of intensive flooding can sometimes be recognized, but clastic sediments do not record much detail and do not provide much time resolution. Speleothems, in contrast, are deposited from solution and thus carry a record of texture, mineralogy, trace element content, and isotope content. Dated speleothems provide a microstratigraphy with a very high time resolution (Perrette, 1999).

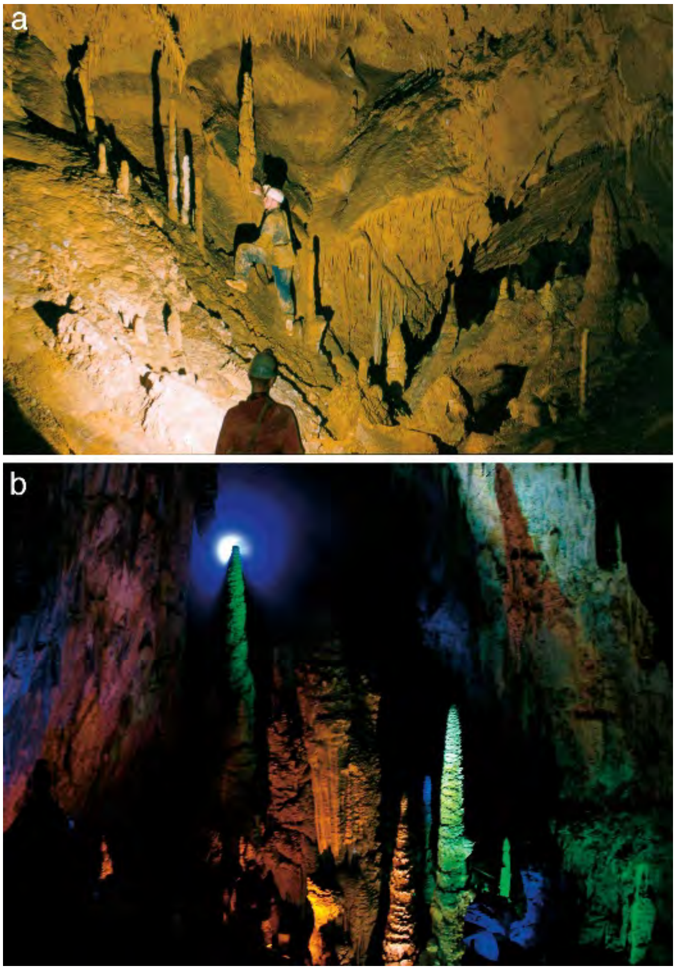

Figure 11. Cylindrical stalagmites. (a) Type of stalagmites typically sampled for paleoclimatic studies. Sites Cave, Pendleton County, W.Va. (b) Large stalagmites in Furong Cave, Chongqing Province, China.

Cylindrical (broomhandle) stalagmites are the speleothem of choice (Fig. 11a). Stalagmites grow, layer by layer, as water drips onto their tops. A stalagmite of uniform diameter is evidence of uniform growth rate over long periods of time. Uniform growth also implies uniform drip rates and uniform chemistry. Stalagmite growth rates mostly fall in the range of 0.01 to 0.1 mm y^{-1}. If there are no breaks in the growth, such stalagmites provide time spans of 100,000 years to 10,000 years per meter of stalagmite. Most stalagmites examined thus far have been less than two meters in length. Much larger stalagmites exist (Fig. 11b). Measurements on these stalagmites pose the technical problem of removing and longitudinally sawing the specimen. Speleothem work also raises a very serious ethical question: Is the scientific information obtained from the stalagmite worth the damage done to the cave in order to collect it?

Because annual growth layers in a typical stalagmite are fractions of a millimeter thick, high time resolution depends on micro-samples and micro-analysis. With sufficient micro-sampling it is possible to construct parameter profiles along the stalagmite axis, which, of course, is also a time axis. Quantities that have been measured include:

- Oxygen isotope ratios
- Carbon isotope ratios
- Deuterium/hydrogen ratios
- Trace elements – typically Mg, Sr and Ba, and many others
- Layer-to-layer color variations (color banding)
- Layer-to-layer variations in luminescence intensity (luminescence banding)

Most widely measured are the isotope ratios for $^{18}O/^{16}O$ and $^{13}C/^{12}C$. The oxygen isotope ratio is related to temperature and is widely interpreted as a paleoclimate thermometer. However, a temperature calibration depends on speleothem deposition under conditions of isotopic equilibrium which may not be achieved (Hendy, 1971; Mickler et al., 2006). The carbon isotope ratio is related to the type of vegetation on the land surface above and has been used to distinguish forest from grassland.

Calcite speleothems appear in a variety of colors mostly ranging from white to shades of tan, orange, and brown. The most common sources of color are humic substances derived from the overlying soil (White, 1981). Likewise, speleothem calcite is usually strongly phosphorescent under long wave UV excitation due mostly to the fulvic acid fraction of the humic substances (van Beynen et al., 2001). An important discovery made in the 1980s by Yavor Shopov (Shopov et al., 1994) is that the luminescence is banded on a micrometer scale and that the individual bands represent an annual cycle. There has been a tremendous amount of interest in luminescence and color banding. These appear to be a measure of precipitation, but calibration in terms of specific climatic variables has been difficult.

There are a range of pertinent time scales and associated questions. These are dealt with individually in the following sections. For a much more complete discussion of the other paleoclimatic data into which the speleothem results are merged, see Bradley (1999).

The Pliocene/Early to Middle Pleistocene: 5 Ma to 300 ka

Much of today's landscape, including most of the caves and surface karst, has been sculptured during the past 5 Ma, that is the Pliocene, the Pleistocene and the Holocene. Near the beginning of this period the mild climate of the Eocene and Miocene gave way to a climatic cycling from warm to cold and back to warm periods. In high northern and southern latitudes and at high altitudes these cycles were accompanied by advances and retreats of glaciers. Sea level rose and fell as significant volumes of water were sequestered in continental ice sheets and later released as the ice melted. The climatic oscillations occur in regular cycles: 41,000 years at the beginning of the period of oscillations and switching to a 100,000 year cycle about 800,000 years ago. The cycles are known in considerable detail because of data extracted from the long ice cores drilled in Greenland and Antarctica (Fig. 12).

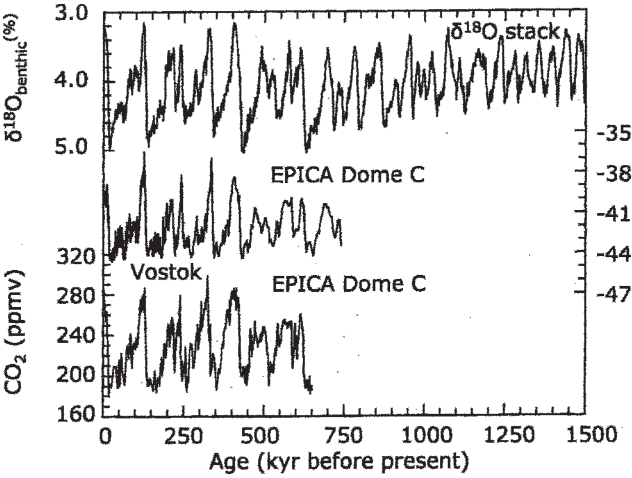

Figure 12. Climatic cycles over the past 1.5 Ma based on ice core records. From Brook et al. (2006). Oxygen isotope data are the benthic record. Vostok and Epica Dome C are ice cores from Antarctica.

Events prior to about 500,000 years are beyond the range of U/Th dating. Information from the Pliocene and Early to Middle Pleistocene must be extracted from clastic sediments which can be dated by cosmogenic isotope methods and by paleomagnetic reversals. At about the time that the 25th anniversary issue of this journal was being published, Davies' (1960) view that master trunk caves were formed close to regional base levels was becoming accepted (White and Schmidt, 1966). Fossil caves could, in principle, be dated by their relation to nearby river terraces. However, the evolution of surface valleys is destructive, with earlier valley floors and channels being dissected and lost as surface streams continue to downcut. As a result, the dating of terraces was always highly uncertain. In recent years, the situation is reversed. Cosmogenic isotope dating of clastic sediment in master trunk caves gives very accurate dates which can then be applied to the terrace level toward which the cave passage is graded.

Cosmogenic isotope dating has been used to establish a chronology for the main trunk passages in Mammoth Cave (Granger et al., 2001) and for major caves in the western Cumberland Plateau of Kentucky and Tennessee (Anthony and Granger, 2004). The caves chosen for dating span the entire time period of cave and karst development in the south-central Kentucky karst and the Appalachian plateaus. The main conclusions from these investigations are summarized in Figure 13. These studies have locked in a time scale for most cave development in the eastern

MAMMOTH CAVE	CUMBERLAND PLATEAU
	Caves graded to Highland Rim (Harrisburg Surface?) 5.7 – 3.5 Myr
Level A: Highest level passages 3.6 Myr Sediment infilling	Caves related to Parker Strath 3.5 – 2.0 Myr
Level B: Main cave in Mammoth 2.15 Myr Sediment infilling	Caves graded to stillstands in Cumberland River. 2 – 1.5 Myr
Level C: Mid-level tubes with little sediment infilling 1.55 Myr	
Level D: Smaller passages 1.45 Myr	Caves formed after 1.5 Myr
Massive regional sedimentation event at ~0.8 Myr	

Figure 13. Chronologies for caves and erosion surfaces in the Mammoth Cave area and the Cumberland Plateau. Information compiled from Granger et al. (2001) and Anthony and Granger (2004).

United States. By relating the oldest Cumberland Plateau caves to the dissection of the Highland Rim surface at 5.7 to 3.5 Ma, by implication, the same time scale should apply to caves related to the Harrisburg Surface in the Valley and Ridge Province of the Appalachians (White and White, 1991).

One of the events common to both Mammoth Cave and the Cumberland Plateau was a massive sediment in-filling at about 800,000 years B.P. Such a sedimentation event implies high precipitation and flooding on the land surface above. This time interval also corresponds to the transition from 41,000 year to 100,000 year climatic cycles. Whether this is merely a coincidence or whether the cave sedimentation is recording the global shift in climatic cycles should be further investigated.

THE LATE PLEISTOCENE AND THE EEMIAN INTERGLACIAL

The younger end of the Pleistocene lies in the time range for U/Th dating so that full use can be made of the speleothem records. For reference, Figure 14 gives the usual time divisions. It was a period of extensive climatic variation with both glacial and interglacial periods.

In areas of coastal karst, lowering sea levels during the glacial maxima allowed the development of air-filled caves that were then flooded when the glacial ice melted. These caves often contain speleothems which can be U/Th dated and there may be overgrowths on the speleothems that deposited after the caves re-flooded. One of the first accomplishments of U/Th dating of speleothems was to identify sea-level lowering during the Illinoian glaciation (Gascoyne et al., 1979). Sea level minima can be tracked by dating speleothems from submerged caves (Lundberg and Ford, 1994; Richards et al., 1994). Likewise sea level stands higher than present sea level can be measured by dating the overgrowths that form under phreatic conditions (Vesica et al., 2000).

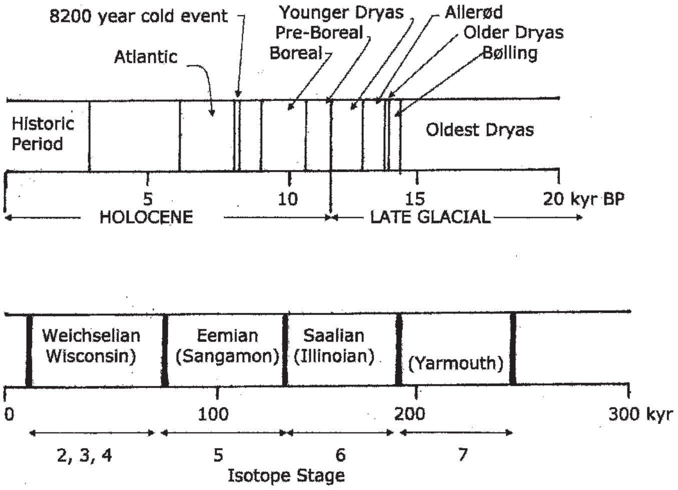

Figure 14. Sketch showing climate periods of the late Pleistocene and the Pleistocene-Holocene transitional period, the period most easily accessible to U/Th dating.

Oxygen isotope profiles along Tasmanian stalagmites produced an oxygen isotope profile from the Eemian interglacial well into the Wisconsin glacial period (Goede et al., 1986; Goede et al., 1990). The profiles were interpreted in terms of temperature changes during the period of record. Deuterium/hydrogen profiles obtained by extracting fluid inclusions in dated spelethems traced temperature over the past 140 ka in the eastern Mediterranean (McGarry et al., 2004). It has long been argued that the arid regions of the Near-East were much wetter during interglacial periods. A speleothem record from Oman shows rapid calcite growth and an oxygen isotope record consistent with high rainfall at 6.5–10.5, 78–82, 120–135, 180–200, and 300–325 ka (Burns et al., 2001). An oxygen and carbon-isotope record in three stalagmites from Missouri clearly shows transitions from forest to savanna to prairie to forest through the Wisconsin glacial period, 75 to 25 ka (Dorale et al., 1998).

THE END OF THE LAST ICE AGE: EXTREME CLIMATIC OSCILLATIONS

The end of the Wisconsin ice age was a tumultuous time with some extreme climatic excursions before the climate settled into the more stable period of the Holocene. Figure 14 names these periods and gives their approximate time intervals. It should be noted that not all sources give the same time boundaries for these periods. The cold glacial climate of the Oldest Dryas gave way to a period of warming, but oscillating climate in the Bølling/Older Dryas/Allerød. At about 12,900 years B.P., according to ice core data (Alley et al., 1993), the northern climate plunged into a 1300 year cold period, the Younger Dryas, from which it emerged with an abrupt warming marking the beginning of the Holocene at 11,640 years B.P. The transition from glacial cold to pre-boreal climate apparently required no more than a decade. The last gasp of the ice age was an event at 8200 years B.P., an abrupt cold snap that lasted for about 200 years. It was identified in ice cores among other records (Alley et al., 1997).

Much of the data on climatic events at the close of the last glaciation come from studies at northern latitudes. There is always the question of how these climatic excursions appeared in temperate or tropical climates or in the southern hemisphere. The intense cooling period of the Younger Dryas appeared in a speleothem record from Australia (Goede et al., 1996). Climatic fluctuations appeared in speleothem records from New Zealand (Williams et al., 2004). Speleothem texture combined with trace element concentrations and heavy metal isotopes were used to sort out wet/dry and warm/cool periods in the Soreq Cave, Israel (Ayalon et al., 1999).

In the American Southwest, there was the onset of a wet climate at 12,500 years B.P. near the beginning of the Younger Dryas. Based on stalagmite growth as dated by U/Th methods, the wet period persisted about 2000 years taking it into beginning of the Holocene and ending at 10,500 years B.P. when the climate shifted to the present arid regime (Polyak et al., 2004). The 8200 year B.P. event appeared as a weakened monsoon in tropical Costa Rica according to speleothem data (Lachniet et al., 2004). It was also found as an anomaly in trace element profiles in a stalagmite from Crag Cave, southwestern Ireland (Baldini et al., 2002)

The Holocene: 11,650 Years to Present

There were climatic fluctuations during the Holocene, but these were generally less pronounced than those at the end of the glacial period. The Holocene is usually considered to extend from a beginning at 11,500 to 11,700 years B.P. (variably stated in different sources) to the present. The beginning date given above is from Alley et al. (1993). Shifts in climate as reflected in the oxygen isotope profiles of dated speleothems have been measured for Europe (McDermott et al., 1999), Israel (Frumkin et al., 1999), southern Africa (Lee-Thorpe et al., 2001), and China (Wang et al., 2005; Zhang et al., 2004).

A series of studies of carbon isotopes from a variety of caves in the American Midwest has allowed the tracking of vegetation over the course of the Holocene (R.G. Baker et al., 1998; Denniston et al., 1999a; Denniston et al., 1999b; Denniston et al., 2000b). Nearly all trees, shrubs, and cool-season grasses preferentially are enriched in the ^{12}C isotope (C_3 vegetation) whereas grasslands (C_4 vegetation) contain more of the ^{13}C isotope. A pattern of shifts from forest to grassland and back to forest has been documented, but the timing of the shifts varies with location. Generally, there is good agreement with pollen records.

Measurement of ^{87}Sr/^{86}Sr ratios in a speleothem from Harrison's Cave, Barbados, showed a systemic change through the Holocene (Banner et al., 1996). This record correlates with rainfall.

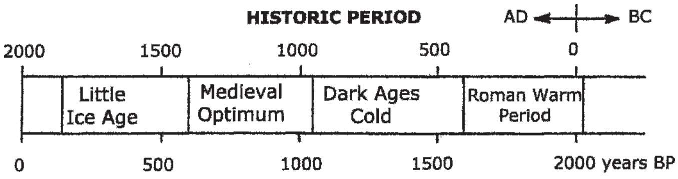

Figure 15. Sketch showing climate periods for the historical period as recorded in Europe. The boundaries are not sharp and vary somewhat between regions.

The Historic Period: The Past Several Thousand Years of The Holocene

An issue of national and international importance at the time of this writing is that of global warming. It seems that on the average, winters have become warmer, summers hotter, glaciers are retreating, hurricanes have increased intensity, and sea levels are rising. On one side are those who assign these changes to a greenhouse effect brought on by the anthropogenic increase in carbon dioxide and other greenhouse gases in the atmosphere. On the other side are some who assert that the whole idea of human-induced global warming is a myth and that these fluctuations are part of a natural cycle. The implications are enormous. Prolonged warming sufficient to melt the Greenland and Antarctic ice caps (as well as other glacial ice) would raise sea levels, shift ocean currents, drown coastal cities, and change atmospheric circulation patterns so that productive farm lands might become dust bowls. Are human beings creating a disaster or are we simply riding yet another climatic cycle, this one on a centuries time scale?

Climate has indeed oscillated over the past several millennia with a period of oscillation of several centuries (Fig. 15). The warm climates during the flowering of the Roman Empire gave way to cold climates in Europe during what is known as the Dark Ages. Climate warmed again during the Medieval period and then shifted into what historically has been called the Little Ice Age. Since the late 19th Century, climate in North America and Europe has been warming. The "grandfather winters" are fading from memory.

There is some accumulating evidence that these more subtle recent climatic events can be teased from the speleothem record. Spikes in the ^{13}C record in a stalagmite from Belize over a 30 year period from 1970 to 2000 correlated with the southern oscillation index – a measure of El Niño events (Frappier et al., 2002). Oxygen isotope profiles taken from three stalagmites from a cave in southern Oman provided a 780 year record of monsoon activity. The record revealed the transition from the Medieval Warm Period to the Little Ice Age at AD 1320 (Fleitmann et al., 2004). Speleothem records from South Africa indicate that the Little Ice Age, which extended from roughly AD 1300 to 1800, was about 1 °C cooler than present while the Medieval Warm Period may have been 3 °C warmer (Tyson et al., 2000). The boldest proposal has been to calculate a 3000 year temperature record from stalagmite color banding from South Africa (Holmgren et al., 2001). What is needed, and what more accurately calibrated speleothem records may provide, is an assessment of whether the present day warming is comparable to other warm periods of the past several millennia, or whether we are entering a new, and possibly quite dangerous, climatic regime.

CONCLUSIONS

Cave sediments have the potential for providing detailed paleoclimate archives with value comparable to ice cores and deep sea sediment cores. Techniques for establishing accurate dates on high resolution records in speleothems are in place for the time scale from the late Pleistocene to the present. Cosmogenic isotope dating of clastic sediments extends the measurable time scale back to the early Pliocene but with much less time resolution. The problem remains of establishing reliable relationships between measurable parameters, trace element profiles, isotope profiles, color and luminescence profiles, and the actual climatic variables for which the measurements are a proxy (McDermott, 2004).

Climate, as recorded in cave sediments, is very much a matter of the local climate in the immediate vicinity of the cave. In order to obtain a broader regional or even global picture of climate at some time interval, many more data are needed. Cave sediment – paleoclimate studies are in their infancy.

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GROUNDWATER RESIDENCE TIMES IN UNCONFINED CARBONATE AQUIFERS

Stephen R.H. Worthington
Worthington Groundwater, 55 Mayfair Avenue, Dundas, Ontario, Canada, L9H 3K9, sw@worthingtongroundwater.com

Abstract: Tracers have been widely used in unconfined carbonate aquifers to measure groundwater velocities and travel times. Injected tracers have largely been used to measure travel times from sinking streams to springs. Environmental tracers have largely been used to estimate overall residence times in an aquifer, and give times that are typically one hundred times longer than estimates from injected tracers. Use of both environmental and injected tracers has enabled residence times and storage volumes to be calculated for both diffuse and conduit components in a number of aquifers. With the addition of permeability data it is possible to calculate storage and flow components for the matrix, fracture and channel components. Results show that the matrix of the rock provides almost all storage, but has very long residence times, especially in older carbonates. Channels provide little storage, account for most of the flow, and have very short residence times. Fractures play an intermediate role between the matrix and channels and have low storage and moderate residence times. These same contrasts are found in many different aquifers and are likely to be found in all unconfined carbonate aquifers. Thus these aquifers are marked not so much by ranging from conduit flow to diffuse flow types, but rather in having triple porosity with contrasting flow and storage properties in the matrix, fractures and channels. The combination of environmental and injected tracers provides a powerful tool for elucidating these contrasting properties.

Introduction

There are widely divergent views on groundwater residence times in unconfined carbonate aquifers. One view is derived from the long history of measuring groundwater velocities; it has been estimated that more than 90% of all groundwater traces have taken place in carbonates (Quinlan, 1986). Such testing as well as cave exploration has led to the view that most carbonate aquifers are dominated by flow through conduits. A contrasting view usually comes from well tests, where transmissivity and hydraulic conductivity values are broadly similar to those from sand aquifers. Consequently, many hydrogeologists assume that carbonate aquifers function in a similar way to sand aquifers and behave as equivalent to porous media with the water, in general, moving slowly through the rock.

White and Schmidt (1966) recognized that carbonate aquifers have both localized flow in conduits and diffuse flow through fractures and the matrix of the rock, and Atkinson (1977) calculated the proportions of conduit and diffuse flow for the Cheddar groundwater basin in England. It appeared to be logical that there might be a range between carbonate aquifers where diffuse flow dominates and the water seeps slowly through the aquifer, and others where conduit flow dominates, and a number of such conceptual models have been proposed (White, 1969; Atkinson and Smart, 1981; Smart and Hobbs, 1986; Quinlan et al., 1992).

An alternative possibility is that both diffuse flow and conduit flow are present in most, if not all, carbonate aquifers, and that the perceived differences are largely a function of the types of measurements made. Thus tracer tests from sinking streams to springs are an excellent way to demonstrate conduit flow with rapid velocities, whereas a borehole is unlikely to intersect a major conduit so pumping test results generally reflect diffuse flow properties. Worthington et al. (2000) analyzed data from four contrasting limestone and dolostone aquifers in terms of flow and storage in channels, fractures and the matrix. They concluded that at least 96% of storage is in the matrix and that at least 94% of flow is through channels in the aquifers studied, thus showing that widely different carbonate aquifers function in similar ways.

Tracers have been very useful in helping determine the proportions of matrix, fracture and channel flow in carbonates, and this paper reviews a number of studies with contrasting results.

Injected and Environmental Tracers Used to Measure Travel Times

The most common tracing in carbonate aquifers is between sinking streams and springs, and well over ten thousand such tests have been carried out. Worthington (1999) compiled the data from 2,877 such tests, which have an approximately log-normal distribution with a geometric mean of 1,770 m d^{-1}. In the data set there is a wide range in distance traced, with the median distance being 4,000 m and 576 traces being over distances of at least 10 km

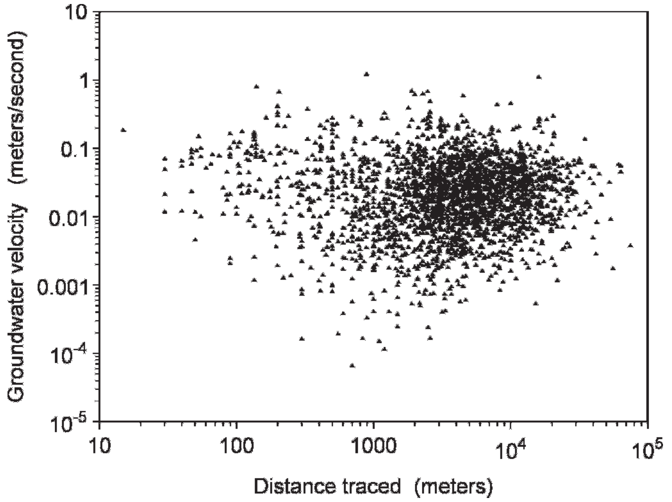

Figure 1. Ground-water velocities and traced distances for 2,877 sink to spring tracer tests.

(Fig. 1). The large number of traces over long distances with rapid flow clearly indicate that extensive networks of interconnected conduits on a scale of many kilometers are common.

There have been a number of studies from dolines or from the surface to drip points in caves 10–100 m below the surface (Friederich and Smart, 1981; Bottrell and Atkinson, 1992; Kogovšek, 1997). Tracer arrival times are typically minutes to hours, but there is commonly high dispersion so that mean residence times are much greater. There have also been a number of tracer tests between wells and these typically give travel arrival velocities of tens to hundreds of meters per day. The existence of velocities $>100 \text{ m d}^{-1}$ from sink to spring, surface to conduit and from well to well tracer tests clearly show that there are many pathways in carbonate aquifers where there is rapid flow.

A wide range of environmental tracers have been used to determine residence times, including water temperature, chemical variables such as total hardness and both stable and radioactive isotopes. Sampling in shallow conduits has shown that average residence times in the vadose zone are typically months or longer (Pitty, 1968; Yonge et al., 1985). These times are much longer than the tracer arrival times from injected tracers and demonstrate the large variance in residence time. Similarly, there have been many tritium measurements at springs that have demonstrated mean residence times of years while in the same aquifers tracers have shown flow-through times of days, and a number of these studies will be described below.

The broad conclusion to be made from all the tracer studies is that environmental tracers tend to give much greater aquifer residence times than injected tracers. This apparent anomaly can be resolved by accounting for the multiple porosity elements in a carbonate aquifer.

CALCULATION OF RESIDENCE TIMES IN CARBONATE AQUIFERS

A simple and useful way to consider carbonate aquifers is in terms of flow and storage in one-, two- and three-dimensional elements of the aquifer (Worthington, 1999). The one dimensional elements have generically been called channels (Worthington and Ford, 1995). Channels with diameters less than a few centimeters commonly provide most of the inflow to boreholes during pumping tests, and in caves are best seen as the vadose flows and drips that form stalactites and stalagmites. Larger channels are called conduits when flow becomes turbulent, which is commonly at a threshold diameter of about 1 cm (White, 1988, p. 290–293). Caves are large conduits that a person can enter. The two dimensional elements in carbonate aquifers are joints and faults. The three dimensional elements are the matrix blocks that lie between the fractures.

The calculation of residence times in porous-medium aquifers is straightforward. In such aquifers flow lines are parallel and particle tracking numerical models such as the U.S. Geological Survey program FLOWPATH can give estimates of travel between two points in an aquifer and therefore of residence time. The calculation of residence times in carbonate aquifers is only straightforward in two simple situations. One is where all the flow is along a conduit from a sinking stream to a spring. In these situations there is no mixing between water particles of different ages and thus a simple piston-flow model of advective flow from sink to spring provides an accurate model. The second simple situation may occur where recharge is through a thick porous medium overburden such as sand. Soil is unlikely to behave as a porous medium because of preferential flow via channels caused by root casts, animal burrows or dessication shrinkage of clays. In a downgradient direction in carbonate aquifers there is increasing mixing between waters that have followed different flowpaths and thus have a range of ages. Consequently, the variance of the age will generally increase in a downgradient direction.

RESIDENCE TIMES FROM ENVIRONMENTAL AND INJECTED TRACERS

There have been a number of studies where both environmental and injected tracers have been used (Table 1). Each of these studies involved analysis of a number of tritium samples as well as multiple traces from sinking streams to springs.

The east-flowing Danube River loses flow at sinkpoints in its bed in southern Germany. Tracer testing in 1877 using salt and the fluorescent dye uranine showed that the flow crosses the European continental divide and resurges 12 km to the south at Aach Spring, which is on a tributary of the west-flowing Rhine River. This spring is the largest in Germany with an average discharge of $8.5 \text{ m}^3 \text{ s}^{-1}$, and

Table 1. Groundwater velocities from injected and environmental tracers.

Location	No. of ^{3}H samples	Mean flow path length (km)	Residence time ^{3}H (years)	Velocity from ^{3}H (m d^{-1})	Traced distance (km)	Velocity from injected tracer (m d^{-1})	Reference
Aach, Germany	10	9	10	2.5	12 – 18	1000 – 4800	Batsche et al., 1970
Areuse, Switzerland	23	6	0.75 – 2	8 – 22	6 – 14	350 – 4800	Müller and Zötl, 1980
Kiveri, Greece	40	15	2	20	3 – 42	160 – 4300	Morfis and Zojer, 1986
Vaucluse, France	57	30	10	8	23 – 46	200 – 2300	Puig, 1990; Mudry and Puig, 1991; Couturaud and Puig, 1992
Hölloch, Switzerland	24	5	0.5 – 1.7[a]	8	0.4 – 11	600 – 5300	Bögli and Harum, 1981; Jeannin et al., 1995

[a] From both ^{2}H and ^{3}H

losses from the Danube account for a major fraction of the flow (Batsche et al., 1970; Käss, 1998). Tracing from these sinks to Aach Spring gave travel times of 2.5 to 13 d, with the travel time being inversely related to discharge at the spring. However, tritium analyses gave a mean residence time of 6 to 14 yr. The age of water at two major sinks on the Danube is 2 to 6 yr and 6 to 14 yr, respectively (Batsche et al., 1970), so the actual residence time in the aquifer of the old component of flow is uncertain.

The Areuse Spring in the Swiss Jura Mountains has a mean flow of 4.7 m^3 s^{-1}. Tracer tests from five sinking streams to this spring helped delineate the catchment area and give conduit velocities. Tritium and discharge measurements showed that the rapid component of flow was 20% of total discharge, with the remaining 80% of discharge having a mean residence time of 9 months to 2 yr (Müller and Zötl, 1980).

In the Peloponnese peninsula in Greece there are a series of enclosed basins with large sinking streams, surrounded by mountains that rise up several hundred meters. The mean residence time of more than 80 springs in this area was determined from tritium samples, with most springs having residence times in the range of 2 to 10 yr (Morfis and Zojer, 1986). Some of the larger springs were selected for intensive tritium sampling. For instance, monthly samples were collected at Kiveri Spring for a period of three years and a further 14 samples were collected during a three month period while tracer tests were being carried out. Kiveri Spring is a coastal spring and is one of the largest springs in Greece. Six injected tracers were recovered at this spring, with flow paths of 3–42 km and much faster groundwater velocities than the tritium indicated (Table 1). There was similar intensive sampling at springs at Stymfalia, Ladon, and Kefalari which yielded groundwater ages of 5 yr, 4.5 yr, and 4 yr, respectively. Injected tracers recovered at these three springs days to weeks after injection gave similar results to Kiveri, with most tracers giving velocities >1000 m d^{-1} (Morfis and Zojer, 1986).

The Vaucluse Spring is the largest spring in France and has a groundwater catchment of about 1,100 km^2. The spring has been explored to a depth of −308 m by a remote-operated submersible vehicle (Mudry and Puig, 1991). Tritium measurements at the spring have shown that there is a mixture of water of different ages; at high flows recent precipitation predominates, while at low flow there is a large component of water with a residence time of more than 30 yr. Similarly long residence times have also been measured in boreholes in the catchment area (Puig, 1990). The short residence time component has been demonstrated by seven tracer tests over distances of 23–46 km, where tracer residence times have varied from 2 weeks to several months (Couturaud and Puig, 1992).

Hölloch is the longest cave in Western Europe, with a mapped length of 190 km. There have been extensive studies of the cave and its hydrology (Bögli and Harum, 1981; Jeannin et al., 1995; Jeannin, 2001). Measurements with deuterium and tritium gave estimated mean residence times of 1.6 yr and 1.7 yr, respectively, for the long residence-time component which accounted for a minimum of 30% of total discharge. Deuterium gave a mean residence time of 6 months for the total spring flow, and tracer tests gave residence times of 10 h to a week.

The residence times and velocities of the above five studies are summarized in Table 1. The tritium analyses gave an age for the groundwater that yielded an average velocity of 2–22 m d^{-1} whereas the injected tracers gave velocities that were about one hundred times faster.

Recent studies at Wakulla Spring (Florida) have given an even larger contrast between the results of the two techniques. Environmental tracers gave a groundwater residence time age of 39 years from ^{3}H/^{3}He analysis, and Katz (2001) suggested that such ^{3}H/^{3}He dating "provides a realistic assessment of the susceptibility of the UFA [Upper Floridan Aquifer] to contamination by approximating the travel time for contaminants to reach a particular zone in the aquifer." This interpretation is based on the assumption that the aquifer behaves as a porous medium. However, recent tracer testing with fluorescent dyes from the sinking streams of Munson Slough, Fisher Creek and Black Creek has given groundwater ages of just days to weeks (Loper et al., 2005). This confirms that the aquifer behaves as a double or triple porosity aquifer rather than a single porosity porous medium aquifer. Additionally there has been extensive cave exploration upstream from Wakulla Springs, which have a mean discharge of 11 m^3 s^{-1} (Wisenbaker, 2006). The combination of the massive discharge from a single location and the cave exploration gives further information on the conduit fraction of flow.

The very large differences between groundwater ages from injected tracers and environmental tracers in all the above studies are complementary rather than contradictory because they measure different aspects of the porosity. The tracers injected into sinking streams and recovered at springs give velocities and residence times of conduit flow, the fastest component of flow through the aquifer. The environmental tracers give an average age of the groundwater, including not only the rapid flow component through conduits, but also the slow flow component through the matrix and fractures in the bedrock as well as the soil and epikarst.

The combination of environmental and injected tracers in the above studies clearly shows that there are multiple residence times in carbonate aquifers and that residence time is a function of the parameter being measured. There have been a number of studies that have considered the volumes and residence times of the different porosity components in carbonate aquifers, and one single-porosity, three double-porosity, and two double-porosity models are discussed below.

RESIDENCE TIMES AND STORAGE VOLUMES IN SINGLE- AND DOUBLE-POROSITY MODELS

Jordtulla Cave is an almost straight 580 m long submerged conduit in Paleozoic marble that drains Glomdal Lake in Norway and provides an example of a simple sink to spring conduit. The cave survey showed the conduit volumes is 1.35 $\times 10^4$ m^3 and continuous discharge measurements over a period of 20 months gave a mean discharge of 2.5^{3}m s^{-1} (Lauritzen et al., 1985; Lauritzen, 1986). The mean residence time of the flow through the conduit is thus 13,500/2.5 s or 90 min. This calculation ignores the gain along the conduit from autogenic recharge from matrix, fracture or conduit flow. The autogenic catchment is 2.6% of the total catchment and the proportions of flow through the rock matrix, fractures, or channels have not been measured or calculated. The matrix flow is likely to be extremely low in this low-porosity marble, so it is likely that almost all autogenic recharge flows rapidly through fractures and channels and consequently may also have a short residence time. Residence time in the conduit is inversely proportional to discharge, which varies substantially in this mountainous subarctic environment. The residence time has been measured by more than forty traces at flows between 1 m^3 s^{-1} and 10 m^3 s^{-1} (Lauritzen, 1986; Smart and Lauritzen, 1992). At extreme flows of 0.1 m^3 s^{-1} and 50 m^3 s^{-1} the calculated residence time is 38 h and 4.5 min, respectively.

The Cheddar Springs have a mean discharge of 0.73 m^{3}s^{-1} and drain an estimated 39 km^2 of the Mendip Hills in England, and both conduit and non-conduit fractions of flow and storage were calculated by Atkinson (1977). The lag between the arrival of a flood pulse and the arrival of low-conductivity sinking stream water was used to estimate a conduit volume of 1.1 $\times$ 10^5 m^3. Integration of the discharge recession curve gave a baseflow storage of 3.3 $\times$ 10^6 m^3, showing that conduits only account for 3% of total storage. A non-conduit transmissivity of 0.031 m^3 s^{-1} was calculated from the baseflow recession and from the storage coefficient, which enabled the fraction of non-conduit flow of 30% to be estimated, with the remaining 70% of flow being through conduits (Atkinson, 1977). The residence time for non-conduit flow can be calculated by dividing the non-conduit volume by the discharge of 0.22 m^3 s^{-1}, giving an average residence time of 170 d. Similarly, the average residence times for conduit flow can be calculated by dividing the conduit volume by the conduit discharge of 0.51 m^3 s^{-1}, giving a residence time of 2.5 d. The groundwater catchment is 10 km in length so this time would represent an average velocity of 2 km d^{-1} over an average flow path length of 5 km. Smart (1981) carried out repeat tracing along the Longwood Swallet to Cheddar Springs flow path and found that conduit velocity was directly proportional to discharge and ranged from 110 m d^{-1} to 6400 m d^{-1}, with 13 of the traces exceeding

2 km d^{-1} and 11 traces being less than 2 km d^{-1}. Thus the repeat tracing lends credence to the estimate of conduit volume by Atkinson (1977).

The Höllengebirge in the Northern Limestone Alps of Austria are a high mountain range with autogenic recharge. Seasonal discharge, ^{18}O variations and low-flow tritium concentrations were used to calculate storage volumes and residence times for conduit and non-conduit flow and storage (Benischke et al., 1988). Results showed that concentrated recharge and rapid flow through conduits accounted for 72% of flow, but this only accounted for 4% of aquifer storage.

The Central Styrian Karst in Austria has a major sinking stream, the Lurbach, as well as a limestone plateau with autogenic recharge. The sinking stream accounts for 64% of the spring discharge of 0.29 m^3 s^{-1}. Conduit volume was calculated from the spring discharge between tracer injection and recovery times during 17 repeat tracer tests, and non-conduit storage was calculated from 29 tritium measurements from samples collected over a period of two years (Behrens et al., 1992).

The results from the four areas described above are summarized in Figure 2. The three double-porosity models give broadly similar results, with 4% or less of storage being in conduits, but most of the flow being in them. There are also some substantial differences. The small conduit volume in the Styrian karst is because the calculation is only of the main conduit from the Lurbach sinking stream and does not include conduits in the autogenic fraction of the catchment. The large differences in matrix/fracture residence times are probably at least partly due to the differences in the method of calculation, with the two Austrian examples using tritium and Cheddar using baseflow recession. However, all three double-porosity models show that conduit residence times are orders of magnitude less than non-conduit residence times.

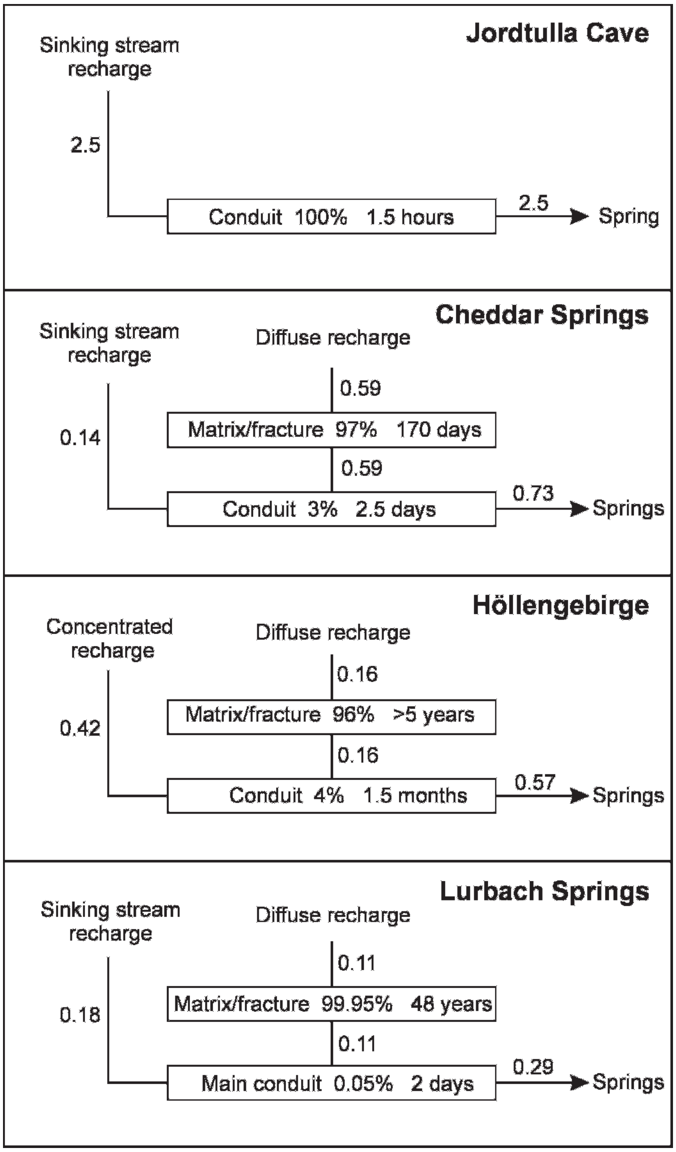

Figure 2. One and two-box models for carbonate aquifers, with fraction of storage (in percentage) and residence time in each box and flow in (m^3 s^{-1}) between boxes. See text for details.

Residence Times and Storage Volumes in Triple-Porosity Models

Triple-porosity models can potentially give a more accurate picture than double-porosity models of groundwater residence times in carbonate aquifers, and two examples are shown in Figure 3, the Manavgat River basin in Turkey and the Turnhole Spring basin in Kentucky.

The Manavgat River basin drains a topographic basin of 928 km^2 and in addition several closed basins, giving an estimated total drainage area of 9,100 km^2 (Yurtsever and Payne, 1986). This area has both the longest groundwater traces and one of the largest springs in the world (Bakalowicz, 1973; Chabert, 1977; Karanjac and Gunay, 1980). A total of 41 tritium samples were collected between 1963 and 1980 at the Oymapınar gauging station, where long-term discharge records are available. Tritium concentrations were found to vary by more than an order of magnitude, with the maximum of 684 tritium units being measured in a sample collected in April 1963. Part of the variation over time was due to decreasing atmospheric concentrations following the cessation of atmospheric nuclear weapons testing, but there was also a factor of four variation in concentration between high-flow and low-flow periods. From recession curve analysis, Yurtsever and Payne (1986) inferred that there were two storage elements in the aquifer with average residence times of about 3 months and 9 months, respectively, plus a baseflow component with a longer residence time and a discharge of 29 m^3 s^{-1}. Best-fit analysis to match modeled and measured tritium values gave mean residence times of 2 months, 9 months and 12 yr for the three components of

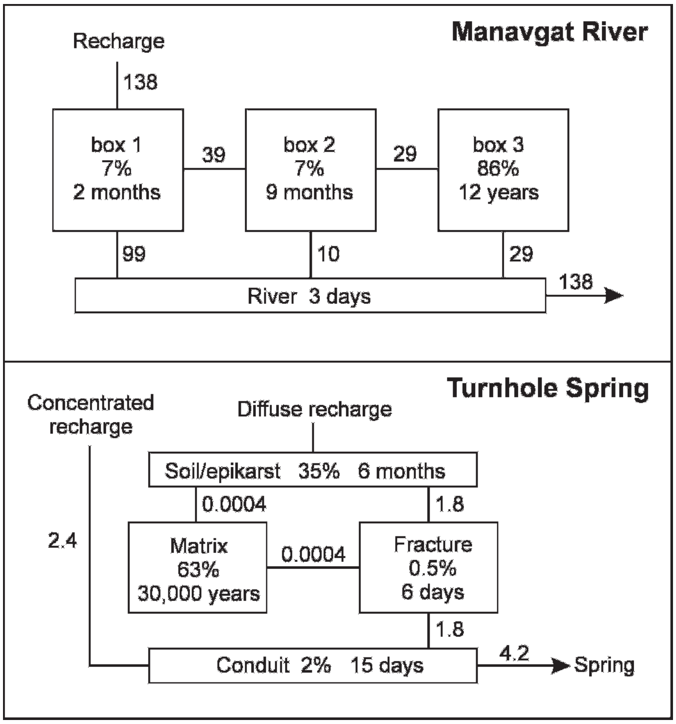

Figure 3. Multiple-box models for carbonate aquifers, with fraction of storage (in percentage) and residence time in each box and flow in (m^3 s^{-1}) between boxes. See text for details.

flow, with 86% of storage being in the long residence time component (Figure 3).

The Turnhole Spring basin drains an area of 217 km^2, including part of Mammoth Cave (Quinlan and Ewers, 1989). Worthington et al. (2000) calculated matrix, fracture and channel fractions of flow and storage. Matrix porosity and hydraulic conductivity were measure from core and hand samples. Fracture hydraulic conductivity was determined by pump and slug tests in boreholes, and fracture porosity was calculated from estimated fracture apertures. Channel porosity was determined from the lag between the arrival of a flood pulse and the arrival of low-conductivity sinking-stream water and from tracer-test velocities. Channel flow was determined from runoff calculations. Finally, the effective aquifer thickness was estimated from the looping of cave passages in Mammoth Cave, which are up to 23 m below the contemporaneous water table. Results gave 96–97% of storage in the matrix of the rock (Worthington et al., 2000). However, the study only considered bedrock storage and flow, and soil and epikarst properties were not included. Gunn (1986a, b) showed that such storage can be a considerable fraction of total storage where there is thick soil or overburden above a carbonate aquifer. The depth of soil and moisture content in the Turnhole Springs catchment have not been measured, but an estimated 300 mm of storage would have a mean residence time of 6 months and would then account for 35% of total storage in the groundwater basin (Fig. 3).

Residence Time Distributions of Flow and Storage

From the above studies it is possible to estimate residence time distributions for the respective aquifers. However, there are two very different definitions of residence time distribution (Worthington et al., 2000). These are

$$T_r = T_m R_m + T_f R_f + T_c R_c \qquad (1)$$

$$T_s = T_m S_m + T_f S_f + T_c S_c \qquad (2)$$

where T is residence time, R is recharge to the aquifer, S is the storage in the aquifer, the subscripts m, f, and c refer to matrix, fracture and channel, respectively; T_r is the residence time of water recharging the aquifer, and T_s is the residence time of the water within the aquifer. The three components of R and S are dimensionless fractions, the sum of which are both unity.

Jordtulla Cave and the Turnhole Spring basin are the simplest and most complicated models, respectively, of the examples that are shown in Figures 2 and 3. Residence time distributions for them were calculated using Equations 1 and 2 and assuming that the residence time of each flow component in the bedrock has a log-normal distribution. Examples of log-normal distributions include the tracer velocity distribution in Figure 1, which has a standard deviation of 0.54 log units. Similarly, hydraulic conductivity data also have a log-normal distribution, with the standard deviation usually being between 0.5 and 1.5 log units (Freeze and Cherry, 1979, p. 31). For instance, the slug test data from nine boreholes in the Turnhole Spring basin have a geometric mean of 6×10^{-6} m s^{-1}, with a standard deviation of 0.94 log units.

In calculating the residence time distributions, the residence times for Jordtulla Cave are based on the flow duration data (Lauritzen et al., 1986). For conduit flow at Turnhole Spring, residence times are based on a mean groundwater pathway of 11 km and on the histogram of tracer-velocity distribution in Worthington et al. (2000); these data are shown in Figure 1. For matrix flow and fracture flow it is assumed that the residence time distributions are log-normal with a standard deviation of 2.0 log units. This large standard deviation reflects not only the variation in hydraulic conductivity, but also the large variation in distance flowed. For the soil/matrix a standard deviation of 1.0 is used because flow through soil is likely to be approximated by piston flow and the substantial differences in residence time may be largely due to differences in soil thickness.

Results are shown in Figure 4. Jordtulla Cave is modeled as a single-porosity aquifer, so the residence time distributions from Equations 1 and 2 are identical (Fig. 4a). However, the two distributions for Turnhole Spring are very different. In terms of recharge to the

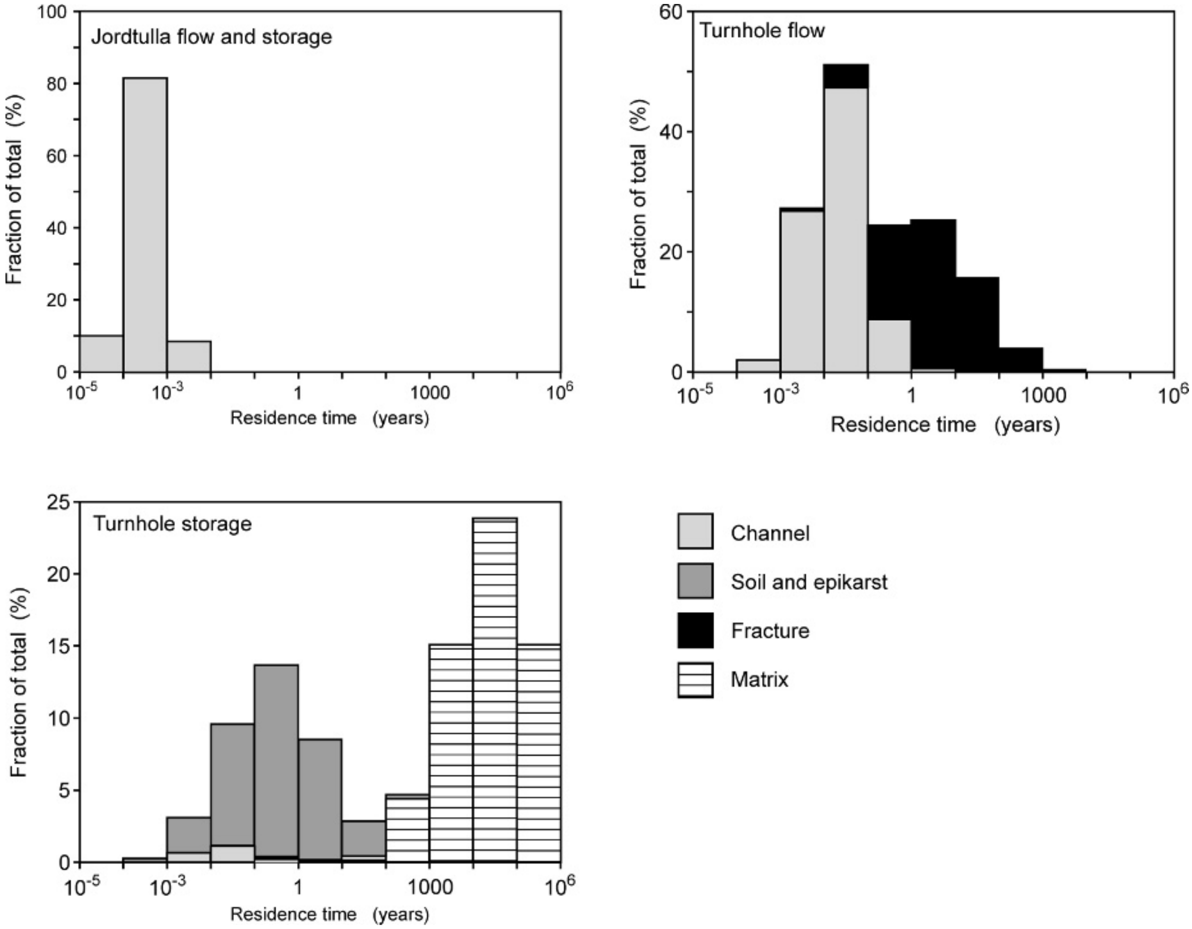

Figure 4. Residence times for both flow and storage in Jordtulla Cave (top left), flow in the Turnhole Spring basin (top right), and storage in the Turnhole Spring basin (bottom left).

aquifer (or discharge from the aquifer), most of the water passes quickly through it and the mode is 0.01–0.1 yr, or 4–37 d (Fig. 4b). This reflects the large proportion of concentrated recharge at sinking streams or dolines which has been shown by tracing to quickly travel to Turnhole Spring. The residence time of storage is bimodal and is dominated by soils and epikarst storage, with a residence time of months, and by matrix storage, which has a very long residence time (Fig. 4c). From Equation 1, the mean residence time of recharge to the aquifer is 4 years. The mean residence time of storage in the aquifer is given by

$$T_s = T_m S_m + T_f S_f + T_c S_c + T_e S_e \qquad (3)$$

where terms for residence time (T_e) and storage fraction (S_e) in the soil and epikarst are added to the variables in Equation 2. Equation 3 gives a mean storage residence time of 19,000 years; this is dominated by the large fraction of total storage that is in the matrix and by its long storage time. The estimated residence times are only first approximations as they are based on very limited data.

DISCUSSION AND CONCLUSIONS

The models in Figures 2 and 3 are all simplifications of the carbonate aquifers discussed. The range in residence times may be more of a continuum rather than the discrete ages that these figures imply because there is a continuum of aperture sizes. These range from pore throats less than 1 μm in width to fractures, many of which have apertures in the 10–100 μm range, to channels. The smallest channels, such as those feeding slow-dripping stalactites, have calculated apertures in the 0.05–1 mm range (Worthington, 1999). The largest channels, such as those close to high-discharge springs, have apertures greater than 10 m.

There are a number of factors influencing the estimated residence times of the different aquifers discussed, including the use of different tracers and different methodologies to calculate residence times as well as differences in the aquifers themselves.

The aquifers discussed in this paper are all unconfined. In some confined carbonate aquifers, such as deep synclinal basins, extremely high total dissolved solids (TDS) concentrations show that flow is sluggish, and in these situations there may have been little karstification unless it occurs at an early pre-burial stage. However, in other confined aquifers such as the Edwards Aquifer in Texas, there are large springs with low TDS and the aquifer is well-karstified (Lindgren et al., 2004).

Detailed consideration of advective flow and of diffusion have shown that fractured rocks are unlikely to behave as porous media (Pankow et al., 1986). Furthermore, the self-organization due to the positive feedback loop between flow and dissolution means that carbonate aquifers are less likely than other fractured rocks to behave as porous media. The use of both injected and environmental tracers is an excellent way of demonstrating the multiple porosities and large range in residence times in carbonate aquifers. There have been a number of conceptual models that have suggested that carbonate aquifers range from conduit-flow to diffuse-flow types. However, the present study better supports the conclusions of Worthington et al. (2000) that unconfined carbonate aquifers all have great similarities, with all having triple porosity with contrasting flow and storage properties in the matrix, fractures and channels.

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PSEUDOKARST IN THE 21ST CENTURY

WILLIAM R. HALLIDAY
Hawaii Speleological Survey, 6530 Cornwall Court, Nashville, TN 37205, wrhbna@bellsouth.net

ABSTRACT: Karst is a specific type of terrain (or landscapes) with characteristic suites of well-known surface and subsurface dissolutional features. The latter result from integrated subsurface drainage. A variety of nondissolutional processes forms terrains analogous to certain types of karst; these are termed pseudokarst. Before 1906, these generally were believed to be karst somehow formed in poorly soluble rocks. They share a considerable range of features, resources and values with karst, commonly (but not invariably) including caves, and the two are linked across a wide spectrum of processes and features (e.g., between dissolutional and piping caves). Unlike karst, integrated subsurface drainage may not be present. Isolated caves define neither karst nor pseudokarst. Multiprocess terrains and landscapes are not uncommon. Based largely on conclusions of a working session of the 1997 International Congress of Speleology, eight types of pseudokarst are identified, with notably different implications for extraterrestrial habitats: rheogenic pseudokarst, glacier pseudokarst, badlands and piping pseudokarst, permafrost pseudokarst, talus pseudokarst, crevice pseudokarst, compaction pseudokarst and consequent pseudokarst. Some appear to exist on Mars. Speleologists expert in their differentiation should serve as consultants to planetary geologists.

INTRODUCTION

The 65th anniversary of the National Speleological Society also is the 65th Anniversary of the use of the term pseudokast in the title of a scientific article (Floridia, 1941). Now, studies of pseudokarst and pseudokarstic caves constitutes a rapidly expanding subdivision of speleology. Numerous articles in publications of the National Speleological Society concern pseudokarst and its caves in lava, in and under glaciers, in seacoasts, in badlands and landslide topography, crevice caves and terrains in a variety of rocks, and even multiprocess caves. In part, this trend has resulted from emphasis on pseudokarst in planetary geology, but many are fascinating in their own right. The International Union of Speleology now has a full-fledged Commission for Pseudokarst as well as another Commission on Volcanic Caves, and a third which maintains that seemingly pseudokarstic glacier features actually are karstic, not pseudokarstic.

HISTORY

Landforms now generally recognized as pseudokarstic were written about in China perhaps 2,300 years ago (Liu et al., cited by Pewe et al., 1995) and at Italy's Mount Etna only a little later (Carus, T., cited in Banti, 1993). A map of Iceland's Surtshellir system was published in 1759 (Halliday, 2004). During the early 20th Century the term originated independently in several European languages, for several types of features and widely varying terrains. The German geologist von Knebel (1906) appears to have been the first to use it in print, identifying crevice terrain in Iceland which engulfs a river as pseudokarstic. Many of these early writers were far from centers of learning and were not academics. Commonly their accounts were in obscure publications. Many were in languages which were not widely read. Locally invented terminologies tended to baffle readers, especially those which attempted to apply karstic concepts to phenomena which only looked karstic.

Beginning around 1927, Russian scientists pioneered the study of karst-like features in permafrost and in poorly soluble rocks. In 1931 and 1935 F. P, Savarenskij wrote about karst-like phenomena in loess and clayey sediments, terming them loess karst and clay karst (Savarenskij, 1931, 1935 [cited by Alexander Klimchouk, written comm.]). In 1947, N. A. Gvozdetskiy recommended qualified use of the term pseudokarst, correctly pointing out that its processes are real, not pseudo. A breakout occurred in mid-century when central European speleologists began publishing English-language summaries, then entire papers in English (e.g., Kukla, 1950; Kunsky, 1957). Vulcanospeleology developed separately, with initially discrete Italian and American roots which merged as a result of international symposia beginning in the 1970s. Initial momentum in glaciospeleology also had a separate beginning, entirely European. In July 1886 Forel mapped a newly discovered 250-meter cave in the Arolla Glacier at 1:5000, and described and discussed it a year later (Forel, 1887). In 1892, a glacial outburst from the Tete-Rousse Glacier killed some 150 Swiss villagers. The Director of the Mont Blanc Observatory investigated and found a glacier cave 175 m long leading to a drained glacial lake (Anon., 1892; Vallot et al., 1892). In 1895 Sieger followed with a lengthy article entitled *Karstformer der Gletscher*. It summarizes several earlier reports of glacier caves in various parts of the world (Sieger, 1895). Three years later, proceedings of

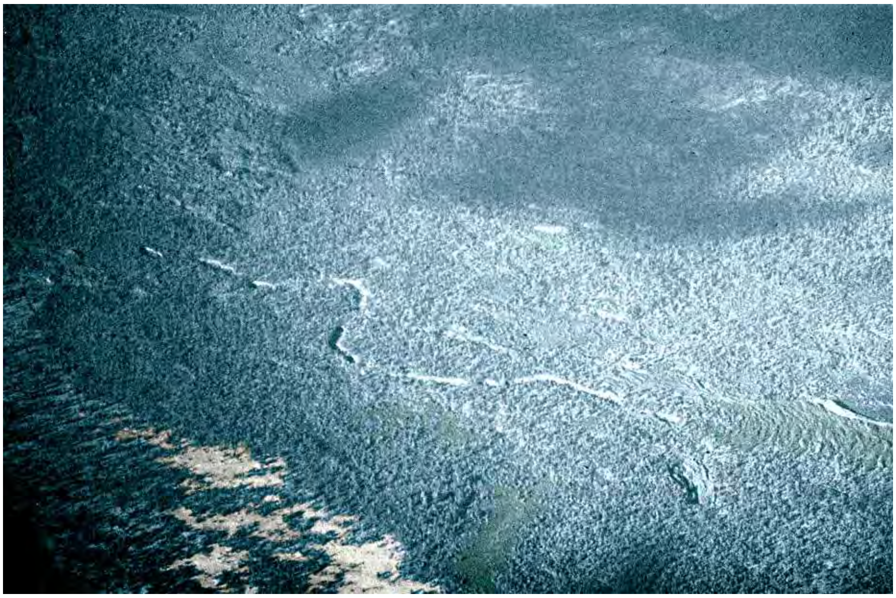

Figure 1. Rheogenic pseudokarst. Oblique aerial photo of partially collapsed lava tube cave, El Malpais National Monument, New Mexico. Compare with Figure 7 showing rectilinear crevice pseudokarst.

a symposium on glacial hydrology were published in Spelunca No. 16.

DEFINITION

A working session of the 1997 International Congress of Speleology concluded that "pseudokarsts are landscapes with morphologies resembling karst, and/or may have a predominance of subsurface drainage through conduit-type voids, but lack the element of long-term evolution by solution and physical erosion" (Kempe and Halliday, 1997). Not clearly covered by this definition, however, are some landscapes arising in talus with an active streamflow (e.g., Colorado's Lost Creek Cave System, discussed below). An older, simpler definition now seems more desirable: karst-like morphology primarily produced by a process other than dissolution.

TYPES OF PSEUDOKARST

On a global basis, the 1997 working session specifically identified:

1) rheogenic pseudokarst (pseudokarst on lava flows)
2) glacier pseudokarst
3) badland and piping pseudokarst (including loess)
4) permafrost pseudokarst
5) talus pseudokarst (including boulder fields and roofed streamcourses)

Time limitations precluded consideration of two other important types, and a third is identified here for the first time:

6) crevice pseudokarst (including littoral pseudokarst)
7) compaction pseudokarst
8) consequent pseudokarst

Other pseudokarstic types exist (e.g., tower pseudokarst, as discussed by Wray [1997]).

RHEOGENIC PSEUDOKARST

Rheogenic pseudokarst includes those portions of lava flows which are shaped by the presence of open lava tubes (Fig. 1). Its caves and pits include lava tube caves, hollow tumuli, hollow lava rises, hollow flow lobes and tongues, open vertical volcanic conduits, tree and animal mold caves, hollow hornitos, and a very few hollow dikes. Spaciousness and near-level floors of numerous terrestrial lava tube caves suggest that they may be a major extraterrestrial resource (Halliday, 1966). The Commission on Volcanic Caves of the International Union of Speleology has taken a proactive approach to identification and documentation of rheogenic caves and pits throughout the world, and a global file of maps of lava tube caves is funded by NASA and maintained at Arizona State University.

In the last half-century, studies of lava tube caves have revealed that they are resources scarcely second to dissolution caves, with many features in common. Some contain a greater range of minerals than do karstic caves and some contain biota as specialized as those of karstic caves and mesocaverns. While significant differences exist in their hydrogeologic mechanisms, lava tube caves pose virtually the same disease hazards as dissolution caves. A few contain cave art, habitations, fossil localities and other cultural features. Others are notable recreational sites including show caves.

Figure 2. Glacier pseudokarst. Multiple entrances to the Paradise Ice Cave system ca. 1970.

The longest known lava tube cave is Hawaii's Kazumura Cave which has a slope length of 65.6 km. Never more than 20 m below the surface, it has a vertical extent of 1,100 m. Its floor plan basically is sinuous, with local braiding. It is especially notable for drained plunge pools up to ~20 m wide. The deepest known open vertical volcanic conduit is Iceland's Thrinukagigur, 204 m deep. Hawaii's Na One pit crater contains a smaller open vertical volcanic conduit which begins on a ledge near the bottom of the pit crater. Their combined depth is 268 m. Divers have descended 122 m in the water-filled vertical conduit of Hawaii's Kauhako Center, with the bottom beyond reach of their lights.

Other volcanic islands with especially notable rheogenic pseudokarst and caves include Iceland, Honshu (Japan), Jeju Island (Korea), Azores Archipelago, Canary Islands, Comoro Archipelago, Galapagos Archipelago, Samoa and Rapa Nui (Easter Island). Major continental sites include Italy (Mt. Etna), Kenya and Australia. Other locations include Syria, Jordan, Saudi Arabia, Rwanda, Chile, Argentina and Tanzania where a unique carbonatite rheogenic pseudokarst exists in the crater of Ol Doinyo Lenggai volcano. In the conterminous United States, notable rheogenic pseudokarst is present in most of the states west of the Great Plains (Montana and Wyoming are exceptions; a single open vertical volcanic conduit recently was identifield in Nevada, and to date, examples of this type of pseudokarst in Colorado are minor).

Glacier Pseudokarst

Glaciospeleology is the study of caves and streams within and beneath glaciers and firn (Fig. 2). Fountain and Wilder (1998) have provided an excellent overview albeit with minimal reference to caves. Current studies are especially active in Iceland, Greenland (especially of moulins), Svalbard (Spitzbergen), Siberia and southern South America. Such studies have lagged in Antarctica where the world's largest glacier cave either underlies the Ross Ice Shelf or is the intraglacial cave containing Lake Vostok. Geothermal caves on Mount Erebus are receiving increasing study. U.S. Geologic Survey geologist, Israel Russell, was the father of American glaciospeleology. He produced several notable reports on the 4,000 km^2 (1,500 mi^2) Malaspina Glacier in Alaska (e.g., Russell, 1893) with special reference to their caves and hydrogeology. A long hiatus followed Russell's work, but additional glacier pseudokarst was found in Alaska and elsewhere in the northwestern United States and in the part of British

Columbia bordering the Alaskan panhandle. Aside from the small, anomalous low-elevation Big Four Ice Caves (Washington State), the most accessible was on 4,392 meter Mount Rainier. Its well-known Paradise Ice Caves originally were in a terminal lobe of its Paradise Glacier. By 1908 attractive pictures of these caves adorned local guidebooks. Also, geothermal caves were identified in craters of several northwestern volcanoes. The largest were atop Mount Rainier. On Oregon's Mount Hood, gas emissions in such a cave are lethal at least intermittently (Anonymous, undated, reprinted, 1994a). Geothermal caves of Mount Baker were found and studied much later.

In the 1940s, the Paradise Ice Caves at the snout of the Paradise Glacier disappeared as their lobe shriveled and vanished. A few years later, similar caves were found in the nearby Stevens Glacier. Through the 1950s and 1960s they gradually enlarged and the name Paradise Ice Caves was transferred to them. Also on Mount Rainier, an outburst flood from a previously unknown cave in the Kautz Glacier caused considerable damage, but decades passed before the flood and the new-found cave were correlated. Much the same happened on Oregon's Mount Hood in 1921 (Anonymous, undated, reprinted 1994b).

The year 1968 marked the beginning of a short golden era of American glaciospeleology centered in the Alaska-British Columbia ice fields (e.g., MacKenzie and Peterson, 1968) and on the new Paradise Ice Caves (e.g., Anderson et al., 1994). In the latter, Anderson and co-workers found and mapped a total of almost 25 km of ephemeral passages. These passages appeared, enlarged into spacious rooms, collapsed and disappeared as this glacier lobe also shriveled, expanded, shrivelled again and finally disappeared. Maximum length at any given time was 13.25 km (Anderson et al., 1994). Ice speleothems and glare ice and firn inclusions in the glacier were especially notable features. Part of the system reappeared briefly in firn in the mid-1990s.

In 1970, climbers, cavers and geologists became interested in geothermal ablation caves in the summit craters of Mount Rainier. Eugene Kiver and co-workers mapped 1.8 km of passages in the east crater and 305 m in the smaller west crater. It contained a small lake at an altitude of 4,329 m. Evaluating mudflow hazards, Lokey (1973) spent 42 consecutive days in these craters and their caves.

Studies of similar, comparatively accessible caves in the crater of Mount Baker were underway when Mount St. Helens erupted in 1980. The impact of the eruption refocused all northwestern speleological activity, and no further work has been done in the Mount Baker geothermal caves.

BADLANDS AND PIPING PSEUDOKARST

Piping is the horizontal, graded or vertical grain-by-grain removal of particles by channelized ground-water flow in a granular material and in some poorly soluble rocks (Fig. 3). Parker and Higgins (1990) and Dunne (1990, p. 1–28) present different mind-sets and different vocabularies in the same volume. It long was recognized primarily as a cause of serious engineering problems. In recent years, extensive piping caves have become recognized as important individual features. Piping was first recognized in loess and loess-like silt in China, but natural caves are not characteristic of loess topography.

Figure 3. Gigglers Caves, Kenya, a piping cave in hard granular tuff.

The pure form of piping is the pseudokarst extreme of a speleogenetic spectrum with 100% karstic dissolution at the other. Between these extremes is an intermediate interface in impure carbonates and evaporite rocks and limy sandstones and other poorly soluble rocks. Piping also participates in development of large multiprocess caves in some tropical quartzites and in development of compaction pseudokarst (see below).

Some badlands topography is riddled with pipes, piping caves, funnel-shaped sinks, dry valleys and other features of centripetal subsurface drainage commonly observed on karstic terrains. Locally these form specific landscapes. Many of their individual features are short-lived; some last only from one storm to the next. The overall landscape, however, tends to persist through long periods of scarp

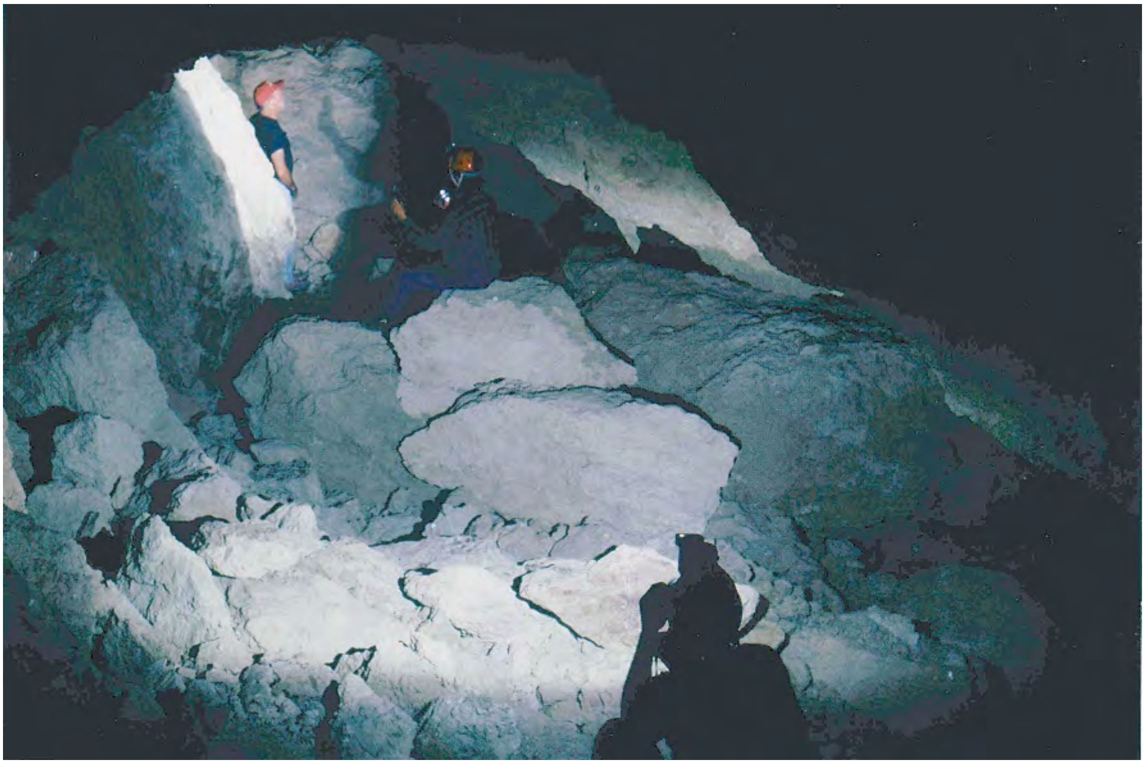

Figure 4. Small room in Officer's Cave, Oregon, a piping cave in a pyroclastic landslide. In more consolidated rock with less frequent rockfall, piping caves may provide extraterrestrial shelter.

retreat. Badlands National Park (South Dakota) is the American type locality, and Petrified Forest National Park also contains notable examples. In Oregon's John Day Country, 345-meter Officers Cave (Fig. 4) was described as an isolated geological curiosity in 1964 (Parker, 1964). A few years later, Texas and California speleologists began describing increasingly large, complex piping caves in a variety of poorly consolidated dry lands. Beginning with Anvil Points Claystone Cave in 2001, Davis unleashed a seeming flood of reports on examples in drylands in western Colorado (e.g., Davis, 2001). Pipes also are common in boglands, with slutch caves up to 50 m long reported in England. The longest recorded American piping cave is 804 m Christmas Canyon Cave, formed in a thin layer of unconsolidated volcanic ash between a surficial basalt layer and a mudflow deposit. It serves as a seasonal resurgence for much of the Cave Basalt lava flow on the south side of Mount St. Helens, Washington (Halliday, 2004).

In more consolidated rocks, piping forms complex caves in sandstones in Minnesota and Arkansas, and participates in formation of others in hard granular tuff and in partially soluble lakebed deposits in Kenya. The latter include Kitum Cave, formerly believed to have been excavated by elephants seeking salt. Perhaps the longest piping cave on record is 8 km Bohemia Cave in New Zealand, said to have been formed largely by ground-water erosion in phyllites underlying marble.

PERMAFROST PSEUDOKARST

Roughly 10% of the earth's surface is underlain by permafrost. In areas where it is covered by tundra or taiga, a combination of thawing and piping produces curvilinear thaw ponds, steep-walled depressions, funnel-shaped pits, ponors, dry valleys, small caves and other karst-like features. These are largely of interest as engineering problems, but Russian and some other geologists have discussed them specifically as important pseudokarst features. Somewhat similar features are present where residual soil of melting glaciers takes the place of tundra or taiga. In Europe, the term thermokarst has been applied to permafrost pseudokarst, but there is nothing dissolutional in the processes which form any of it. Marjorie Sweeting is among those who have decried this unfortunate term, pointing out its confusing similarity to thermal karst.

TALUS PSEUDOKARST

Talus caves are receiving increasing attention in the world speleologic literature, but talus pseudokarst is rarely mentioned. Nevertheless, talus accumulations occasionally form important landscapes and American speleologists tend to underestimate the occurrence and significance of talus caves per se (Fig. 5). In some parts of Europe, they are the largest and commonest type of cave. Sjoberg (1989a) found that 15% of Swedish talus caves have high scientific and/or recreational values; Sweden's Bodagrottorna has more than 2,500 m of passage. In temperate climates such caves may serve as important glacieres or provide other microclimates favorable to specialized life forms. In arid regions, some minimize evaporation of running or ponded water. Especially in granite and anorthosite, some provide delightful recreational caving. A few have been developed as show caves. In Southern California and probably elsewhere, some talus caves served as human habitations well into the 20th Century.

In the United States, talus caves exist almost exclusively in one of two settings: hillside or cliff-bottom rockpile fields which form talus pseudokarst, and steep-walled stream gullies. Sjoberg (1989b) also described neotectonic boulder caves in Sweden. Some of these are end products of roches moutonnees, smoothed and rounded by glacial erosion, then fractured by tectonic activity after deglaciation. This combination of processes has preserved the overall contour of the roche moutonnee, and produced a localized talus pseudokarst.

Rockpile and rockslide talus caves characteristically are slope failure features found especially in boulder fields at the bases of cliffs, on slopes or in narrow stream gorges, or, rarely, in narrow grabens. A variety of processes is involved: block glide, grusification of granite, and others. Some represent a stage of disintegration of crevice caves affected by differing rates of downslope movement. In California and in parts of the northeastern United States, those partially filling narrow, steep-walled granite gorges are locally termed, purgatory caves. Some of these are active multiprocess caves, with active vadose solution, grusification, piping and scouring of talus and bedrock alike. The alpine Lost Creek system of Colorado has formed a distinctive narrow dendritic pseudokarst 5 km long, with large pseudokarstic windows, flat-stacked boulders and ridges of partially grusified granite up to 60 m high. Here, Lost Creek repeatedly disappears into swallet caves, reappearing to flow across flat-bottomed sinkholes (Hose, 1996). Enormous quantities of granitic sand debris have been cleared from caves and sinkholes in this unusual system. Smaller examples have been described in Europe.

Malin and Edgett (2000) have reported several Martian features resembling certain terrestrial talus pseudokarst. Some are immediately downslope from presumed outbursts of water. These are potential Martian glaciers. Others may serve as small habitation sites.

Crevice Pseudokarst

The first identification of a terrain as pseudokarst described a crevice pseudokarst in Iceland (von Knebel, 1906). Where karst and karstic caves are readily accessible, however, all but the most spectacular crevice caves and crevice pseudokarst (e.g., Fingal's Cave, Island of Staffa, Scotland) are commonly ignored. Consequently they are much more common than is generally recognized. They occur in both littoral and inland terrains; the former includes littoral zones of now-dry inland Pleistocene lakes. Littoral examples are formed by hydraulic wedging by waves and other forms of marine erosion. These may form fractures extending hundreds of meters inland, readily traceable on the surface (Fig. 6). Especially where sinkholes develop along such fractures, small but interesting pseudokarstic landscapes may be identified. Examples include the island of Staffa, Scotland, the Ballybunion coastal area of Ireland, sections of the Oregon coast including the Devil's Punchbowl and the area of Sunset Cliffs, San Diego County, California. Because of their origin and geometry, few such caves are inhabitable.

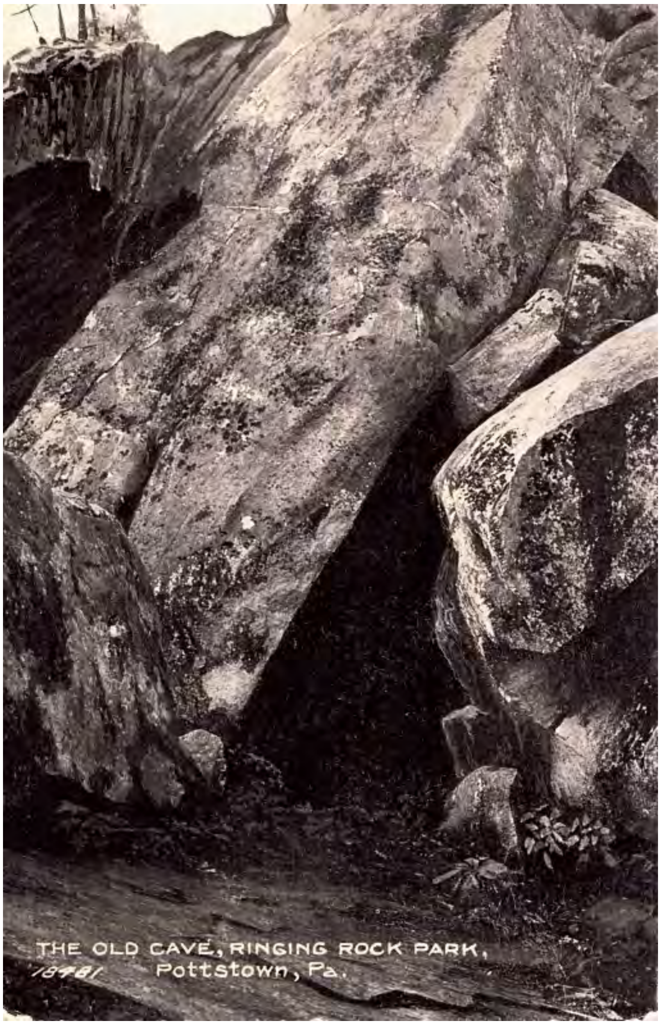

Figure 5. Talus pseudokarst at Pottstown, Pennsylvania. Because the general public is more interested in talus caves than are speleologists, old postcards are a useful resource in identifying them.

Inland crevice caves vary greatly in size. A few have extraordinary parameters, such as Devil's Hole in the small Nevada section of Death Valley National Park. The small near-surface section of this feature is complex and karstic, but most of it consists of a single spacious crevice in

Figure 6. Littoral crevice pseudokarst, island of Staffa, Scotland. The right hand opening is the entrance to Fingal's Cave.

limestone occupied by warm ground water apparently much more than 100 m deep (the National Park Service prohibits cave diving here). It apparently formed as a result of structural tension in the Great Basin and its water is part of a major regional aquifer (Riggs et al., 2000).

Smaller inland crevice caves vary from isolated cracks in cliffs to narrow rectilinear networks on slopes. Many of the latter are an intermediate stage of breakup of competent rock masses due to mass movement or gravity-sliding enhanced by local subsurface drainage. Where the movement is not uniform across the length of such a crevice, bedrock blocks slide and rotate at different speeds and in different directions, converting part or all of crevice caves into one or more talus caves. Basalt and granite commonly develop curvilinear crevice caves rather than rectilinear forms. Some deep caves in tropical quartzite are crevice caves, but others are multiprocess caves extensively modified by piping. Crevice terrains in Arizona appear to be of one of two types. Some in northern Arizona are believed to be the product of subsidence caused by deeply buried karst. Others in areas of especially deep alluvium appear to be the result of excessive drawdown of ground water (Harris and Allison, 2006). Tectonic and solutional caves occur along the former.

Most of the island of Hawaii lacks surface drainage as a result of crevice pseudokarst formed as a result of fractures in brittle basalts secondary to various volcanic and seismic events. Most of these crevices are concealed by vegetation or by volcanic ash, or by subsequent lava flows. But the Great Crack in the southwest rift zone of Kilauea volcano is a kilometer-wide zone of en echelon crevices of various widths and depths, locally open to the surface (Figs. 7 and 8). An implausible concept of its origin is that the weight of Kilauea volcano is tilting that part of the island of Hawaii away from Mauna Loa volcano, and that Kilauea volcano ultimately will slide or topple into the Pacific Ocean. More plausible is the possibility that this is a self-propagating crevice, enlarged and elongated by injection of pressurized magma into initially small fractures in the wall of Halemaumau crater. Within it, mapping teams have reached a depth of 183 m. At several levels, one or more lateral coatings or lava reveal lateral flow of lava at depth. The Great Rift of south central Idaho is another very large inland crevice in a basalt flow field (Fig. 9). At least one eruptive fracture on Mount Etna (Italy) extends downslope in the form of a lava tube cave (Giudice and Scalia, 1994).

Unless block glide has been active, crevice caves characteristically taper downward. Localized floors generally are formed by wedged breakdown blocks. Thus extraterrestrial crevice caves are unlikely to be suitable habitation sites.

COMPACTION PSEUDOKARST

Compaction is common in landslide and avalanche deposits. This facilitates piping (see above). Pseudokarst may be formed by such compaction, and is discussed here for the first time. Initially, drainage of such deposits tends to be internal and their surfaces may be pitted with large and small punched out or conical crater-like depressions (Fig. 10). A notable example formed in unconsolidated material at the northern base of Mount St. Helens (Washington State) on May 18, 1980. Here, virtually the entire northern side of the volcano avalanched moments

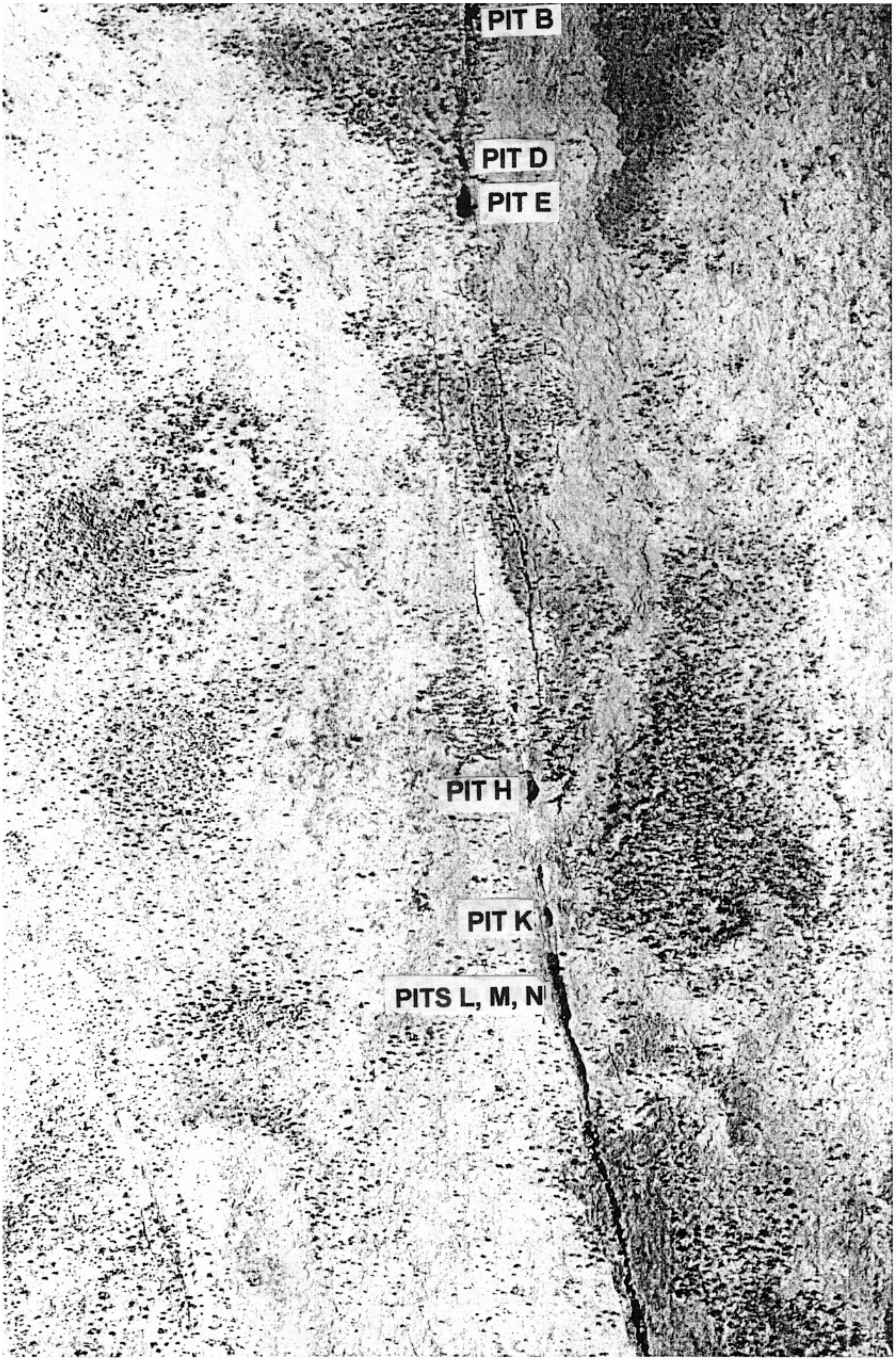

Figure 7. Crevice pseudokarst in a 2 km segment of the Southwest Rift Zone of Kilauea Volcano, Hawaii. Individual pits along the Great Rift are lettered from north to south; Pit H is near the center of the photo. It has been mapped to a depth of 186 m. Note that smaller en echelon crevices are mostly hidden by vegetation.

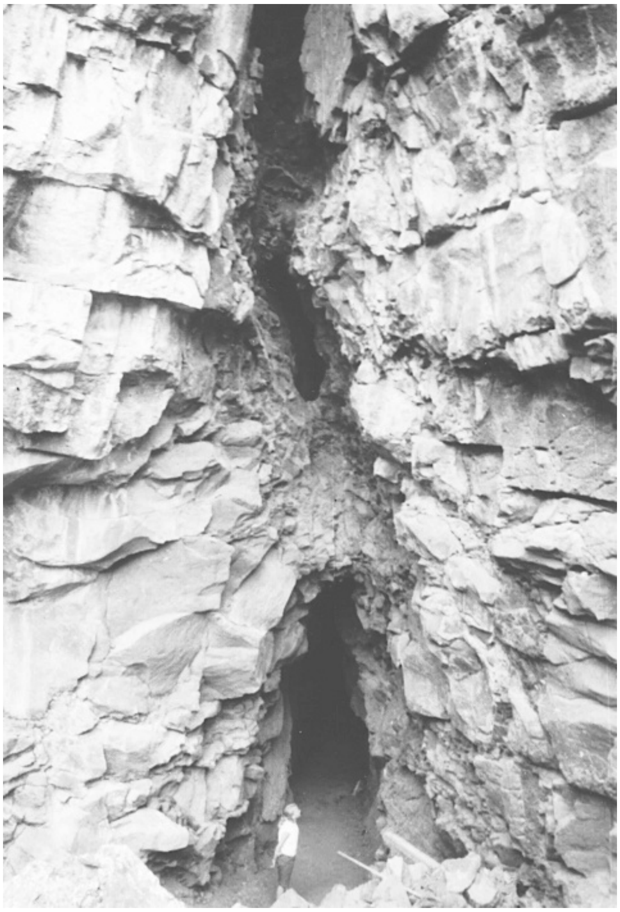

Figure 8. A short segment of the Great Rift, Idaho, seen from a large skylight. The flat is an artificial pathway constructed to permit visitor access.

before a lateral ash-cloud eruption covered its slump with several meters of slightly cohesive volcanic sand. The avalanche layer contained large and small fragments of fractured glaciere as well as shattered blocks of bedrock. Some were transported laterally for several kilometers in their original upright position. All was heated, but the degree of hydrothermal injection varied. Almost at once, melting and compaction began to generate crateriform and punched-out depressions varying widely in size.

The overlying ash cloud deposit underwent rapid erosion, with formation, enlargement and headward erosion of new gullies followed by coalescence of closed depressions and pond formation. During the first few months, vertical piping was prominent locally. As gullies enlarged, deepened and pirated their neighbors, parallel crevices formed in the pyroclastic ash cloud sand, elongating up-slope. Some were partially roofed by block slumping, and piping developed along their bases. More extensive roofing formed a few short-lived pyroclastic caves.

A 1 m layer of quicksand atop one temporary pond supported the weight of investigators, but did not withstand the impact of large rocks which sometimes broke loose and rolled down the steep slope of the closed depression. The resulting orifice revealed muddy water in a low cavern roofed by the quicksand layer.

Overall, this pseudokarst evolved rapidly. With each seasonal rain, the surface of the ponds rose disproportionately as the ash cloud deposit washed into them. Surface drainage developed, and all but the largest depressions disappeared within 15 years. After 25 years the area still could be recognized as pseudokarstic.

In southern Nevada and adjacent Utah, several small caves and pits have been identified in alluvium including Alluvium Cave. Some, but not all, are the result of piping.

Consequent Pseudokarst

Consequent pseudokarst is karst-like terrains resulting from action of natural processes on shallow mines, underground quarries and other subsurface works of man. Although the U.S. Geological Survey has studied many such occurrences, the term and the unifying concept were developed late in the 20th Century by Istvan Eszterhas of Hungary. Some of the affected areas contain extensive caverns formed by natural stoping, bounded on all sides by talus or by fracture surfaces. Their surface features tend to be rectilinear, and they commonly cause serious engineering problems. Underground drainage is minimal or absent.

The Future of Pseudokarst

Despite 20th Century progress in this rapidly emerging field, documentation and study of pseudokarst inevitably has lagged behind those of karst. Application of hard-learned calcareospeleological exploration techniques to some volcanic pseudokarst, however, has shown that many long-established techniques are easily modified to meet new conditions as needed (e.g., hyperthermal, hypothermal, hypoxic, and hypercarbic caves).

If this is to be man's century of breakout into space, speleologists everywhere need to stay alert to the great volume of relevant data now pouring back from Mars and beyond, and to volunteer our assistance in the interpretation of data already seen to demonstrate confusingly varied terrains. This is an area of progressively narrow specialization and we cannot expect planetary geologists, or even terrestrial geologists lacking in experience with various types of terrestrial pseudokarst, to recognize and properly utilize their extraterrestrial analogues. Already on Mars, what appears to be a typical crevice cave has been identified as a potentially habitable lava tube. Plans relying heavily on such misidentifications open the way to disaster.

Perhaps the first step should be breaking down the language barrier which still hinders definitive communication between central European pseudokarst specialists and those of the rest of the world. If necessary, travel to a series of international meetings on pseudokarst should be subsidized. The National Speleological Society and the

Figure 9. Landing created by wedging of rockfall, the Great Crack, Hawaii. Terrestrial caves of this type are unsuitable for human habitation.

Figure 10. Subsidence pseudokarst. This conical depression in the Spirit Lake pseudokarst (Mount St. Helens, Washington State) was photographed in an early stage of its evolution. A thin ash-cloud tephra deposit is still present on the flats formed on top of the landslide deposit containing the sinkhole.

International Union of Speleology should take the lead in such endeavors. The survival of man in space may depend on it.

ACKNOWLEDGEMENTS

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Kathleen H Lavoie, Kurt L Helf, and Thomas L Poulson – The biology and ecology of North American cave crickets. *Journal of Cave and Karst Studies,* v. 69, no. 1, p. 114–134.

THE BIOLOGY AND ECOLOGY OF NORTH AMERICAN CAVE CRICKETS

Kathleen H. Lavoie[1], Kurt L. Helf[2], and Thomas L. Poulson[3]

Abstract Cave and camel crickets are widely distributed in caves throughout the world, and in North America they make up the bulk of the biomass in many caves. Most caves do not have large populations of bats, so the guano, eggs, and carcasses of these cavernicolous crickets are dependable sources of fixed energy for troglobites (Mohr and Poulson, 1966; Barr, 1967; Barr and Kuehne, 1971; Richards, 1971; Harris, 1973). The crickets often are a true keystone species, maintaining cricket guano communities and specialized egg predators, as well as providing more dispersed energy inputs that increase overall ecosystem diversity. They are all commonly referred to as crickets, and are all in the same Order (Orthopterans) with grasshoppers, crickets, and katydids. Most cave crickets actually are grasshoppers. Cave crickets in Hawaii are true crickets (Gryllids). Because cave crickets are relatively large and abundant, they have received more study as a group than most other cavernicolous invertebrates, but there are still a lot of things we don't know about cave crickets and some continuing mysteries.

Classification And Genetics

Early researchers were fascinated by the bizarre life forms frequently encountered in caves, and spent a lot of effort looking for confirmation of their evolutionary ideas. In his 1888 *The Cave Fauna of North America*, Packard was surprised to find that cave crickets collected from deep inside a cave showed the same eye morphology as those collected near an entrance. He invoked a complicated explanation of acceleration and retardation to explain differences in ovipositor length instead of attributing differences to a range of sizes and ages in crickets.

Cavernicolous members of the tribe *Ceuthophilini* are widely distributed throughout the United States and into Mexico, while cavernicolous members of the tribe *Hadenoecini* are restricted to the American southeast. The taxonomic relations and geographical distributions of the tribe *Ceuthophilini* have been reported by Hubbell (1936) and tribe *Hadenoecini* by Hubbell and Norton (1978). In May of 2006, Northern Arizona University announced the discovery of a new genus of cave cricket and two new species of cavernicolous *Ceuthophilus*. These new crickets were found as part of a survey of 24 caves in the Grand Canyon-Parashant National Monument in Arizona (www.onlinepressroom.net/nau/).

Rhaphidiphorids are wingless, with long antennae. They have robust hind legs for jumping, and are sometimes called camel crickets because the back is humped up with the head bent down. Both males and females have two cerci at the end of the abdomen that are rich in sensory receptors. Adult female crickets have an ovipositor between the two sensory cerci. Cavernicolous crickets show a range of adaptations (troglomorphy) to the cave environment. Some species, such as *Ceuthophilus stygius* camel crickets in Kentucky, use the cave only as a refuge during the day. They forage and lay eggs outside in the forest. The young crickets hatch, and many over-winter just inside cave entrances. They are clearly trogloxenes. *Hadenoecus subterraneus* cave crickets in Mammoth Cave and *Ceuthophilus conicaudus* in Carlsbad Cavern leave the cave only to feed, and all other aspects of their life cycle occur in caves, so they are habitual trogloxenes or troglophiles. Some species, such as *Caconemobius varius* found in the lava tube Kaumana Cave in Hawaii, feed and reproduce in caves without ever leaving, and are true troglobites.

In Carlsbad Cavern there are three different species of *Ceuthophilus* crickets that represent a range of troglomorphic adaptations (Fig. 1). The least cave-adapted species is the robust *C. carlsbadensis* that is common in areas with bat guano. The most cave adapted species, *C. longipes*, lives in remote areas of Carlsbad where food is very limited. The intermediate species, *C. conicaudus*, is widely distributed in smaller caves throughout the Park.

A very interesting and diverse group of true gryllid crickets live in lava-tube caves of the Hawaiian archipelago (Fig. 2). Howarth (personal communication) states that there are more different kinds of cave crickets in Hawaii than in all of continental North America. There are at least two *Caeconemobius* species that live in Kaumana Cave on the big island of Hawaii and another species in small interstitial spaces on the lava flow. Both the cave crickets and the lava flow cricket are presumably evolved from a large, dark, eyed species that lives in the wave-splash zone of rocky beaches. The lava flow cricket retains its eyes and shows a slight reduction in pigmentation and a great

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[1] State University of New York College at Plattsburgh, 101 Broad St., Plattsburgh, NY 12901 lavoiekh@plattsburgh.edu

[2] Division of Science and Resource Management, Mammoth Cave National Park, Mammoth Cave, KY 422259 kurt_helf@nps.gov

[3] 318 Marlberry Circle, Jupiter, FL 33458-2850 tomandliz@bellsouth.net

Figure 1. Comparison of the three Carlsbad *Ceuthophilus* crickets, left to right, *C. carlsbadensis, C. conicaudus*, and *C. longipes*. Adult males.

reduction in size. The highly-cave adapted species is very small, blind, and has lost nearly all of its pigment. What is particularly noteworthy is that this divergence from a common ancestor must have happened between 700,000 and 1,000,000 years ago, which is the maximum age of the big island of Hawaii (Howarth, 1983, 1987; Otte, 1994).

The genetics of nine species of cave crickets from sites in Pennsylvania through Alabama were analyzed by Caccone and Sbordoni (1987) and Caccone and Powell (1987). The results show that populations of cave crickets in areas where the limestone is continuous, but highly fractured, are genetically more variable than populations from regions where the limestone distribution is more disjointed. This pattern suggests that cricket movement between populations through subsurface conduits is important in maintaining genetic variability. A lack of genetic differentiation among populations of the trogloxenic camel cricket, *Ceuthophilus gracilipes*, was reported by Cockley et al. (1977) over a 1,000 km^2 (386 mi^2) area in the eastern United States. This species is found in caves and in the forest under logs and loose bark. Their findings suggest that the forest populations may serve as a genetic bridge among cave populations.

Genome size is an important taxonomic factor because it influences cell size and how long it takes a cell to divide. Genome size in orthopterans averages 8.2 pg ± 0.5 for haploid DNA. The smallest known orthopteran genome size is 1.55 pg in *H. subterraneus* (Gregory, 2001).

LIFE HISTORY

The life history of *Hadenoecus subterraneus* begins when a female cricket inserts her ovipositor into sandy soil, and inserts an egg below the surface. The egg, about the size and shape of a grain of long rice, stays buried for about

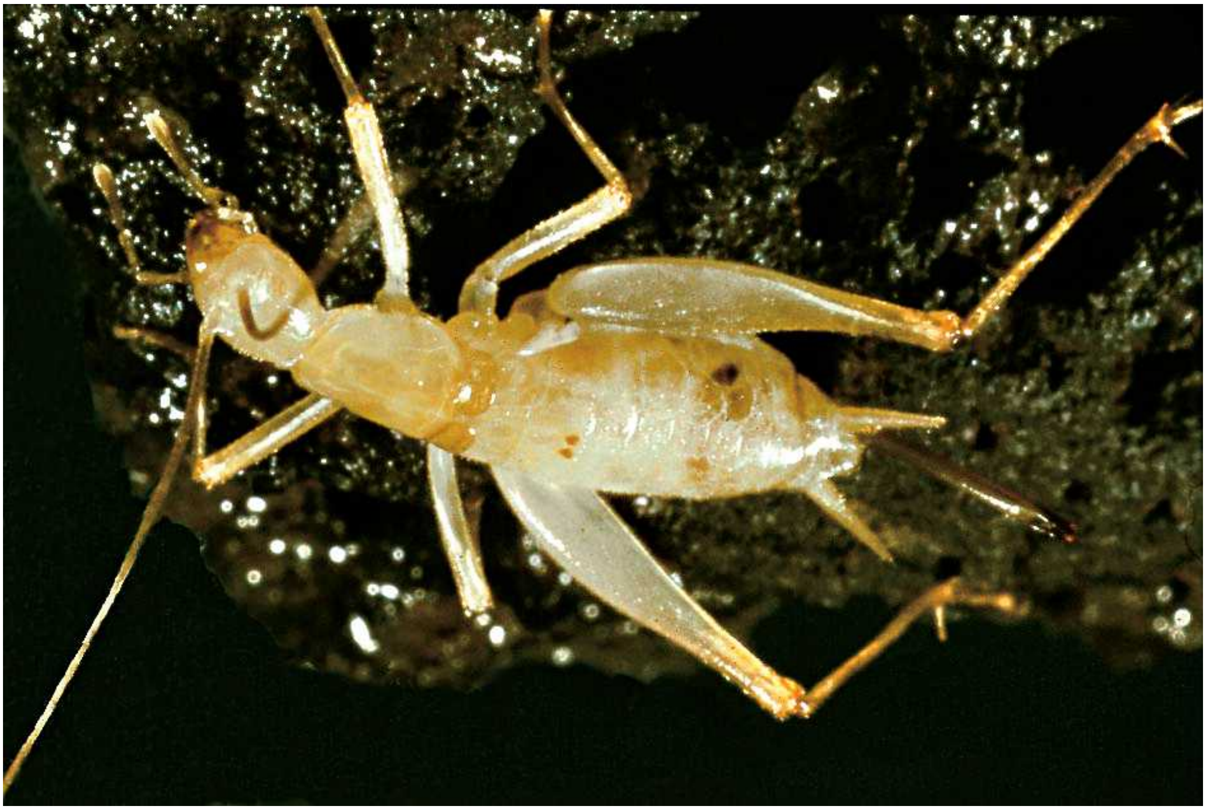


Figure 2. Undescribed underground tree cricket (*Thaumatogryllus sp*) from caves on Maui. Adult female.

12 weeks before the nymph hatches. The nymph is not completely developed; it has yolk where its digestive tract will be, but the longer the egg stays in the sand, the more likely it will be eaten by a specialized egg predator, the sand beetle *Neaphaenops tellkampfii*. Once it hatches, the nymph works its way out of the soil and moves to the walls and ceiling of the passage where it has less chance of being eaten. Crickets at this stage completely lack pigment, and are called whities.

Many measures of cricket size have been used by field biologists, including head width and leg lengths. For *Hadenoecus subterraneus*, we have reliably measured the length of the drumstick (i.e., the femur of the hindmost pair of legs, or Hind Femur Length [HFL]). Whities have HFL of slightly less than 5 mm. As crickets molt they go through many stages or instars. They first begin to develop secondary sexual characteristics at around 10 mm HFL and reach a gangly teen-age stage at around 15 mm HFL and are grayish-brown in color. They make their final molt to adults at HFL usually greater than 20 mm HFL. We rarely (0.5–3.8%) find a sexually mature adult cave cricket with a HFL less than 20 mm. Most adults have a HFL of around 23 mm; we have never measured a *Hadenoecus* cave cricket larger than 26 mm HFL. Sexually mature adult crickets are darker brown than sub-adults due to hardening and tanning (sclerotization) of legs and ovipositors. We hypothesize that the crickets take up to three to four years to reach adult size that is probably influenced by their success in finding food. Crickets may live another three to four years (or longer) as a sexually mature adult. One of the best lines of evidence we have for this extreme longevity is the frequency of observed molting crickets. *C. stygius*, which lives for a year, routinely has 2–6% of the population molting, compared to *H. subterraneus*, where the rates are 0.1–0.01% (based on one molting cricket of 512 observed, one of 969, and one of 1,024 on different census dates, and many thousands of crickets observed with no molts).

Reproductive studies on cave crickets have concentrated on the presence and size of mature gonads, egg-laying rates, and reproductive behaviors. Seasonal dissections of crickets for spermatophores in males and ova in females suggest that *H. subterraneus* are capable of reproduction in all months with the possible exception of July. (Cyr et al., 1991). These data support the observed seasonality in reproduction reported by Hubbell and Norton (1978) and Griffith and Poulson (1993).

Measurable ova were found in *Ceuthophilus stygius* only in August, September, and October samples, indicating marked seasonality in reproduction in this annual species (Cyr et al., 1991). Parasitism by hairworms markedly affects number and size of ova formed in *C. stygius* (Studier et al., 1991). Six non-parasitised *C. stygius* contained 25.5 ± 4.2 ova/female while nine parasitized females collected at the same time contained an average of 2.2 ova. Seven parasitized females had no ova at all.

Northup and Crawford (1992) studied two of the *Ceuthophilus* species in three passages in Carlsbad Cavern. Some seasonality in reproduction and frequency of adults of *C. carlsbadensis* was noted, but the pattern is not as strong for the more cave-adapted *C. longipes*. *C. carlsbadensis* females (n=745) contained 0–60 eggs, with a mean of 6.34 (+/−1.09) eggs per female. *C. longipes* (n= 43) had a range of 0–4 eggs per female, with an average of 0.67 eggs (+/−0.17). Seventy-two percent of adult female *C. carlsbadensis* had eggs compared to only 37% of adult *C. longipes*. *C. longipes* produces significantly fewer and larger eggs, as expected of a more cave-adapted animal. Patterns of distribution of immature and adolescent crickets were highly variable in both time and location. The authors suggest that both species of camel crickets are able to reproduce throughout the year.

Total annual egg production by *H. subterraneus* was estimated by Cyr et al. (1991). During winter, 20–30 eggs were laid by individually caged female crickets in a 2–3 day period of rapid egg laying, while in early summer, the rate was 1–3 eggs laid every eight days. If average eggs laid per year is based on maximum egg-laying rates for each period of observation, then the annual egg production is 96 to 371 eggs laid per year per female. It is unlikely that crickets maintain measured maximum egg-laying over extended time periods. Three pairs of caged cave crickets, collected *in copulo*, however, laid an average of 0.46 eggs/day over a 154 day interval from March to August, which corresponds to an annual egg-laying rate of 167 eggs/year. The time span studied was not the peak time for egg production, and the 154 day interval is also longer than the estimated 12 weeks needed for eggs to hatch, so this rate estimate is probably low. Compared to other Orthopterans, the estimated range is somewhat low. In a year, the common house cricket lays 728 eggs, German cockroaches lay 218–267 eggs, and American cockroaches lay 200–1000 eggs (Altman and Dittmer 1972).

Individually-caged adult female *H. subterraneus* showed seasonal differences in the amount of egg-laying in Mammoth Cave (Cyr et al., 1991). At a deep cave site in Sophy's Avenue, many more eggs were laid in two day intervals from October to February (4.3 ova/day) than in April and July (0.6 ova/day). Egg-laying at the Frozen Niagara Entrance site averaged 0.1–0.8 ova/day in spring through fall. The influence of seasonal environmental conditions is shown in the winter data, where the greatest number of eggs were laid in Sophy's Avenue, and no eggs were laid in Frozen Niagara. At that study time the entrance door to Frozen Niagara was damaged, which allowed cold, dry air to enter and extend approximately 75 m into the cave where the females were caged. Half of the caged females died, and none of the survivors laid any eggs or even made any ovipositor holes.

POPULATION SIZE

The size of individual *H. subterraneus,* and the side passages and alcoves we can't access, make complete direct population counts extremely difficult and of limited reliability. And except in small caves, exactly where is the end of the cave for purposes of a census? Only a few attempts at population studies have been made and only for large cave crickets. In general, results are more consistent in very small caves, such as Little Beauty Cave and White Cave in Mammoth Cave National Park.

One technique used to estimate total population size is known as mark-recapture. All individuals (marked and unmarked) are counted and marked with a different color on days 1 and 2 and counted again on day 3. Crickets can be marked successfully with dots of different colored office correction fluid or paint on their backs, by gluing on numbered bee tags, or using UV bright paint. Total numbers of marked and unmarked crickets on each day are used to calculate a statistical estimate of total population size. Attempts to do mark-recapture studies of cave cricket populations are often complicated by the large turnover of animals from accessible staging areas where we can see and mark them, to roost areas that are inaccessible to humans. Problems with mark-recapture studies are a continuing mystery.

A mark-recapture study by Hellman (1989) from fall to winter for the Frozen Niagara Entrance of Mammoth Cave estimated that there were 976.8 (± 209.4) adult crickets in October 1987, but only 70.6 (±35.9) crickets in February 1988. The differences are not due to a huge population crash, but reflect the reduced movement of crickets in the winter months. Hobbs and Lawyer (2002) marked 769 adult *Hadenoecus cumberlandicus* cave crickets from a parthenogenic population (all females) in Coon-in-the Crack Cave in Kentucky. Based on the mark-recapture rate, they estimate the total adult population size in this cave as 5,508 individuals.

During a long-term biomonitoring project at Mammoth Cave National Park, Poulson et al. (1998) found some interesting differences among *H. subterraneus* populations at nine monitored entrances. They collected census data by dividing crickets into four size classes, 1–4, with size one being the smallest juveniles, and size four being sexually mature adults as estimated by size and degree of tanning of ovipositors and legs. Instead of existing as one meta-population with roughly equal interactions among sub-populations, there are source and sink populations. In a source population there is a greater number of smaller size classes relative to larger size classes, which suggests a population that is increasing, although small crickets never outnumber large adults. A sink population is greatly skewed to the larger adult and sub-adult size classes, with low levels of local reproduction. The sink populations are maintained by immigration of crickets from source populations. There were source populations at three of nine entrances, and sinks at the remaining six. There is no relationship between total population size and whether an entrance is a source or a sink. In general, source populations are located in entrances that have ceiling pockets that provide a refuge above the influx of surface air and are close to suitable reproductive areas. Most of the source entrances are located in sinkholes or in mature forests that offer good foraging opportunities and a protected microclimate. Both types of populations should be protected since emigration of adults from a sink can repopulate a source population should it be wiped out.

INTRACAVE DISTRIBUTION

In many caves, crickets are difficult to find, but in other caves you can easily see hundreds of individuals in a relatively small area. These numbers may change drastically with time of day and season. Cave crickets gather around entrances as roosts and in staging areas where they can evaluate surface conditions before leaving the cave to forage. They are also found in stable deep cave areas away from human-sized entrances, but close to cricket-sized entrances.

Cathedral Cave, a small cave in a limestone bluff overlooking the Green River in Mammoth Cave National Park, was the site for a three year study of the migration patterns of *H. subterraneus* by Brother Nicholas and his students (Nicholas, 1962). Crickets were the only important source of food input into the cave. The small cave was divided into 12 3.1 m (10 ft) long transects. A different color paint was assigned to each transect, and all large crickets in each transect were marked, a total of 3,750 individuals. Ninety-seven percent of marked individuals were found in their original 3.1 m (10 ft) quadrant each day (Nicholas, 1962). Daily observation showed that about 1/3 of the crickets emerged each night to forage under optimal environmental conditions. This regular exiting of 1/3 of the population is not consistent with more recent metabolic studies, as discussed below. We also observe great reductions in the numbers of marked crickets over longer periods of time.

Neilsen (1989) took advantage of the very flat ceiling in Floyd Collins Crystal Cave, Mammoth Cave National Park, for a study of *H. subterraneus* distribution over six days. He mounted a light on a tripod with a grid over the end to project a pattern of one meter squares on the ceiling in the first 28 meters of the cave. Every six hours, every other day for three census days, he and a team mapped the location of every individual cricket. They found that the distribution of total crickets was very uneven (Fig. 3), with some areas having large numbers of individuals of all sizes, and other areas consistently having none. The distribution is probably related to local microclimate differences with less wind flow or higher moisture for the crickets.

Total counts of roosting *H. subterraneus* show a cyclical pattern with respect to day and time of collection. Highest

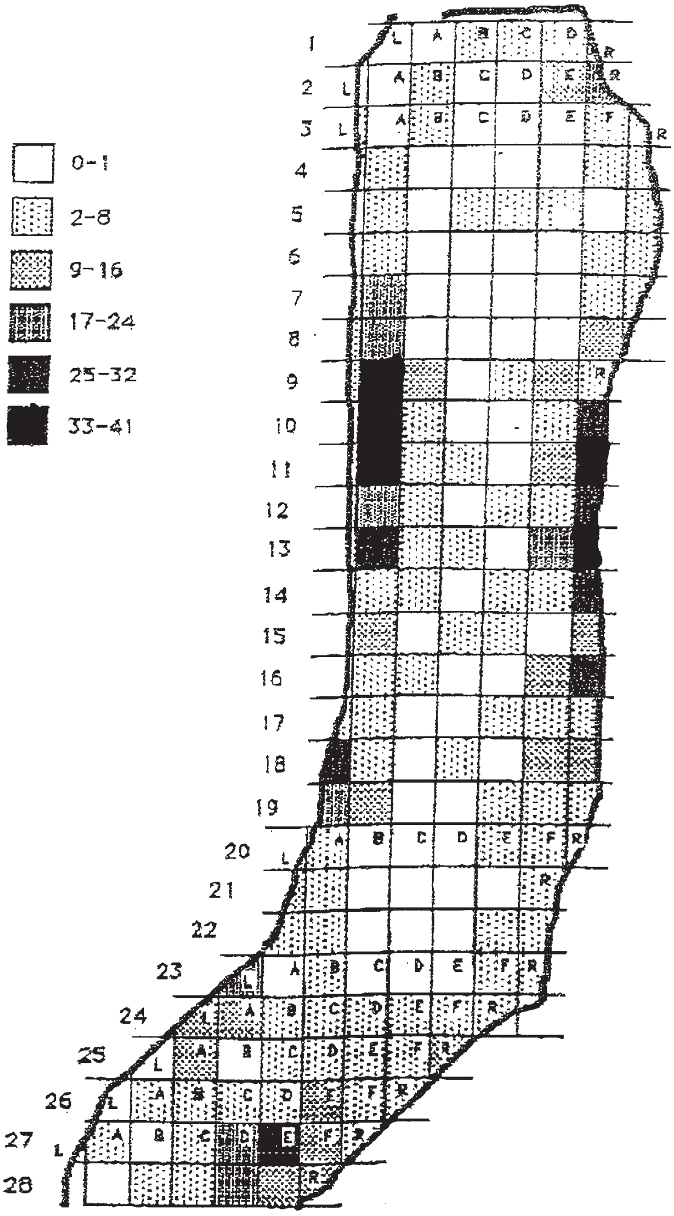


Figure 3. Cave cricket distribution summed over all census counts in Floyd Collins Crystal Cave (Neilson 1989).

population counts in the entire census area are in the evening at 1800 hours (367 individuals) while the lowest count is in the early morning at 0600 hours (255 individuals). Emergence of more crickets into the study area during the 1800 hour count is consistent with crickets sampling entrance conditions in the evening to see if epigean climate is appropriate for foraging (Studier et al., 1986). Numbers also fluctuate with time as crickets retreat to and emerge from sites that are inaccessible to humans. Crickets were observed at distances into the cave greater than the 28 meters sampled in this study. Where the crickets go when they leave the accessible sites is one of the mysteries of the cave.

Patchy distributions of female *Hadenoecus cumberlandicus* cave crickets in sheltered locations were reported by Hobbs and Lawyer (2002). Yoder et al. (2002) report that aggregation behaviors in these cave crickets serve to protect them from dehydration. Increasing cricket group size (1, 5, 10, and 20) caused lower water loss rates in caged crickets. The protective group effect was eliminated when they used dry flowing air. They proposed that the protection from clustering is from increased local relative humidity.

Few studies examine the intracave movement and dispersal of cave crickets. Hobbs and Lawyer (2002) marked 2,378 adult female and juvenile *Hadenoecus cumberlandicus* cave crickets from Coon-in-the-Crack Cave in Kentucky. Based on tagged individuals, the majority of crickets moved an average of 10–15 m d^{-1}, with a mean of 41 m. Downing and Hellman (1989) also examined in-cave movement of *H. subterraneus* from White Cave, Mammoth Cave National Park. They used different colors of typewriter correction fluid to mark adult cave crickets near the entrance (10–15 m from the entrance) and those found deeper in the cave (35–40 m from the entrance). The distribution of the marked adult crickets was monitored daily for a week by 5 m transects from the entrance to 50 m into the cave. Within 24 hours there was a general movement of crickets from the front of the cave towards the rear, including one individual that moved 25 m. Crickets marked from deeper in the cave tended to move around less. On the morning of day 4, after the one warm night during the study period, there was movement of crickets from the back to the front of the cave. A similar rhythmic movement pattern was observed by Campbell (1976) with *C. conicaudus* in Spider Cave in New Mexico.

SEASONAL DISTRIBUTION AND ABUNDANCE

In some cave entrances in central Kentucky, *H. subterraneus* co-exist in very large numbers with much smaller numbers of *C. stygius*. Large numbers of crickets were collected in their roosting caves during all four seasons from White Cave, Walnut Hill Cave, the Frozen Niagara Entrance to Mammoth Cave, and Floyd Collins Crystal Cave (Studier, et al., 1988). Crickets were collected by hand, sexed when large enough, and hind femur lengths (HFL) measured to the nearest 0.1 mm. Considerable care was taken in searching for and collecting all sizes of crickets since smaller crickets are easily overlooked because they roost in small crevices and stay away from open spaces.

The distribution of crickets by HFL for all caves studied for each season is presented in Fig. 4. *H. subterraneus* of all sizes are present in all seasons, and adults (HFL > 19.9 mm) make up the greatest fraction of each population in all seasons. There is no apparent seasonal difference in distribution by size, and no traceable peaks for the smaller

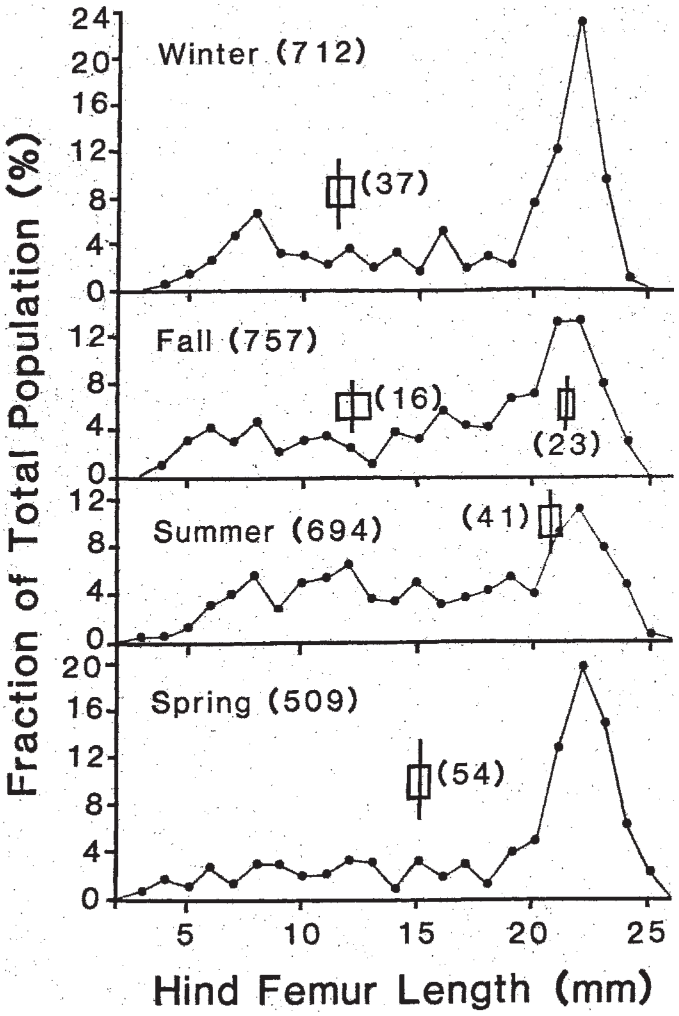


Figure 4. Seasonal distribution by hind femur length (HFL) of *H. subterraneus* (data points) and *C. stygius* (box of mean, width is 95% confidence interval) from four entrances in Kentucky (Studier, et al. 1988).

sized crickets that would indicate a seasonal period of intense reproduction within the populations, despite reported marked seasonal differences in reproductive effort in this species (Barr, 1967; Kane and Poulson, 1976; Hubbell and Norton, 1978). Differences could be because all sites sampled for this study are entrance sites in contrast to deep cave sites as discussed later in this paper.

The population structure for *H. subterraneus* shown in Figure 4 where adults predominate, is typical of a long-lived population. We know from recovery of marked, numbered, individuals that adult cave crickets can live as adults at least 17 to 24 months, considerably longer than the 7 to 11 months reported by Hubbell and Norton (1978). The preponderance of large, sexually-mature adults at all times of the year shows that cave crickets are relatively long-lived, perhaps living for four years or more.

Data for *C. stygius* are also presented in Figure 4 as discrete boxes, where the vertical line is the mean HFL of crickets measured, and the width shows 95% confidence intervals (Studier et al., 1988). Camel crickets are typically found in discrete size categories in each season due to their yearly life cycle. *C. stygius* shows a big jump in size from spring to summer with a period of rapid growth and attainment of sexual maturity. A new cohort of young appears in the fall to join the cohort of current adults. By winter, mostly small camel crickets over-winter to become the next season's cohort of adults as they emerge in the spring to feed.

The same data from Figure 4 shows that total crickets by gender among sub-adults (15.0–19.9 mm; 263 females and 231 males) have a sex ratio close to 1:1. Adult crickets by gender (713 females: 509 males) have a sex ratio that is significantly different in which females predominate. Lack of a gender bias among sub-adults and the preponderance of females among adult crickets suggests a differential mortality with greater death rates for adult male crickets. Male crickets must leave the safety of the cave to feed more frequently and they stay out longer than females, which probably results in a higher mortality rate for males (Studier, et al., 1986). Alternatively, females may simply live longer than males. Norton (personal communication) found unpredictable variations in male: female ratios of *H. subterraneus*, so this is another mystery of the cave.

Entrance vs. Deep Cave Sites

Hubbell and Norton (1978) suggest that there may be differences between entrance populations of cave crickets and deep cave populations. An entrance site is a location that can be used by humans to enter the cave. A deep cave site is located away from an entrance accessible to humans and does not experience the seasonal changes in temperature and humidity at an entrance site. Because of a dome-pit arrangement at the Sophy's Avenue site and at Bubbly Pit in Great Onyx Cave, dense cold winter air flows directly past the roost site with little effect on roost temperature or relative humidity. In all cases, successful reproduction requires an area with a suitable sand-clay substrate. *H. subterraneus* cave crickets are very negatively affected by air that is not water-saturated and by temperature fluctuations (Studier et al., 1987b; Studier and Lavoie, 1990).

Our long term biomonitoring study shows that the populations from these two areas can grade into one another. Our best example comes from the New Discovery entrance, where a large population of crickets of all sizes, with adults predominating, is found in the first 20 meters from the entrance ready to exit the cave and forage. Continuing into the cave for 100 meters shows a switch to a deep cave site where the main function of the population is reproduction and there are only adults and small young crickets present.

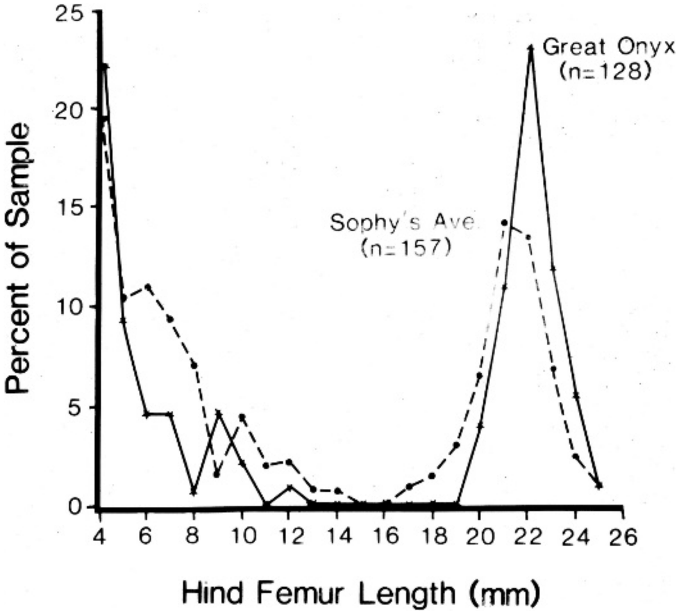


Figure 5. Distribution of *H. subterraneus* by hind femur length (HFL) at two deep cave sites in Mammoth Cave National Park. (Studier and Lavoie unpublished data.)

Seasonal averages of ova (eggs) per female *H. subterraneus* are quite consistent, but do show site-related differences. Crickets in entrance areas show consistently low levels of reproduction as evidenced by the number of eggs per female cricket (average 6.7 ova/female), while females from a deep cave site show strong seasonal differences in reproduction and egg-laying (average 18.1 ova per female) (Cyr et al., 1991). Hubbell and Norton (1978) report average numbers of large ova for females in July and January at the entrance at Great Onyx at 2.1 and 5.3, from deep in Great Onyx at 5.6 and 7.0, and from January in Parkers Cave at 3.6 in the entrance and 7.6 deeper in the cave.

Another striking difference is the size-class distribution between *H. subterraneus* in entrance sites and deep cave sites. Entrance sites (Fig. 4) show a majority of adults and a fairly even representation of crickets in other size classes. Data collected from two deep cave sites are shown in Figure 5 (Studier and Lavoie, unpublished data). There are many large adults and many small juveniles, but the intermediate size classes are nearly absent. Adults are skewed to a male sex bias, and males and females have much less food in their crops than in entrance areas. The deep cave sites serve as reproductive and nursery areas where crickets go to mate and lay eggs (Hubbell and Norton, 1978; Kane and Poulson, 1976). The eggs hatch and the young crickets go through several molts in the cave before leaving to roost around entrances where they can leave the cave to feed. Young crickets in the deep cave areas may feed mostly on other individuals of their species (Levy, 1976). The actual number of molts to reach adult size is estimated by Hubbell and Norton (1978) as eight. They reported that caged hatchlings stayed in the non-feeding white stage for five weeks, molted to feeding second instars for ten weeks, and they were unable to raise the crickets beyond that.

METABOLIC RATES AND WATER BALANCES

Low metabolic rates are assumed to be a troglomorphic characteristic. Studies of the metabolism and water balance of *H. subterraneus* and *C. stygius* were made by caging adult individuals in the cave and measuring weight loss as a function of time (Studier et al., 1986, 1987a, 1987b; Viele and Studier, 1990). These were wild-caught animals, and we selected for crickets that appeared to have more crop contents. Dissected crops, carcasses, gonads, and combined wastes were analyzed in the lab for moisture content and caloric value. The metabolic rates for *H. subterraneus* are one-half that of surface insects of similar mass (Studier et al., 1986). The relationship between body mass and HFL differs by sex for *C. stygius* and is the same for both sexes for cave crickets. This relationship has a high predictive value ($R^2 = 0.902$) and allows us to measure the hind femur length and weight of a cricket, and by extrapolation determine its crop contents without having to sacrifice the cricket, using the equation:

$$\text{CEL W (mg)} = 2.698\ \text{HFL2} - 50.07\ \text{HFL} + 274.1 \qquad (1)$$

In this study, wild-caught females started at 101% of their crop-empty live weight. These adult female *H. subterraneus* lost weight at a rate that would make them crop-empty in 11.5 days. Adult males lost weight at a slower rate, but they had consumed only 72% of their body weight, so these males should leave the cave to feed at least every 9.9 days. *H. subterraneus* exiting White Cave had nearly empty crops and 65.2% of exiting crickets were males (Studier et al., 1986). Helf (2003) reports that some crickets can consume in excess of 200% of their body weight in food in a single feeding. Most full wild-caught crickets had 110–130% of their crop-empty live weight (CELW) in their crops. Higher starting crop contents would extend these projections of time between feedings by up to 2– 2.5 times which would be the maximum time they could stay in the cave before leaving to feed to avoid using up body energy reserves.

Adult *C. stygius* lost weight at two rates over the five days of the study, which we interpret as a rapid phase due to crop-emptying, followed by a slower rate of weight loss when fat reserves are being utilized (Studier et al., 1986). If they are to avoid using fat reserves, female camel crickets must forage at least every 3.0 days and males every 2.3 days. *C. stygius* are able to consume only 34% to 39% (males *vs.* females) of their body weight in food. Because camel crickets have very little flexibility in how often they

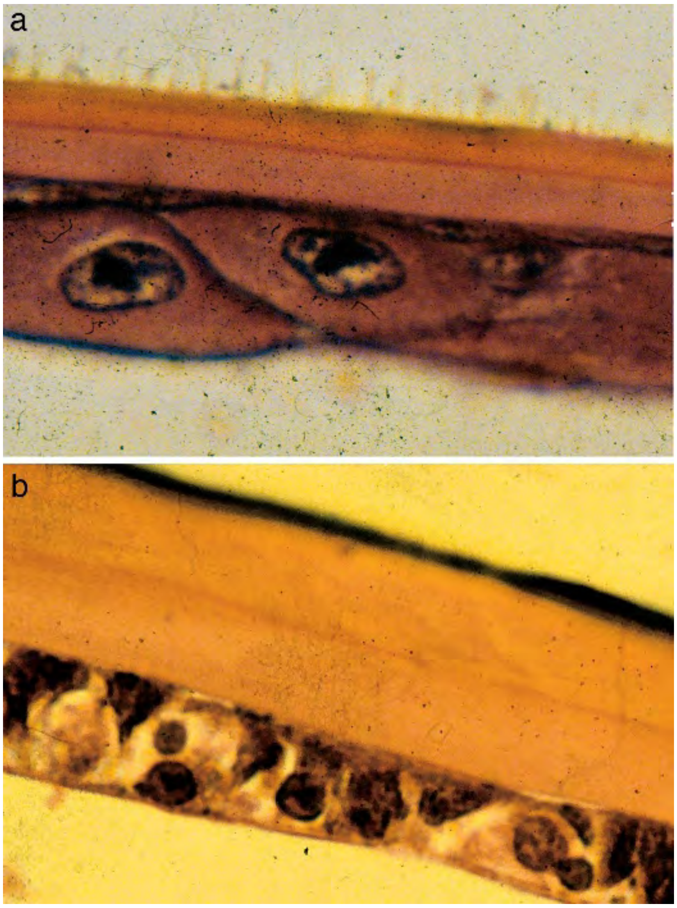


Figure 6. Cross section of the cuticle of a) *H. subterraneus* and b) *C. stygius* taken at 400×.

must feed to maintain their fat reserves, they must be able to leave the cave more frequently and endure a wider range of environmental conditions than cave crickets.

Cave crickets are also very sensitive to moisture loss by evaporation because their outer cuticle is thin compared to camel crickets (Fig. 6). The cuticle of *H. subterraneus* is approximately half as thick and appears to lack epicuticular wax compared to *C. stygius*. Yoder et al. (2002) reported that extractable cuticular lipids were significantly lower from *H. cumberlandicus* compared to *C. stygius*.

The metabolism of the three species of *Ceuthophilus* crickets from Carlsbad Cavern show the expected differences with degree of troglomorphy (Northup et al., 1993). Based on an in-cave weight loss study, calculated metabolic rates (cal h^{-1}) were 1.04 for *C. carlsbadensis* and 0.52 for *C. longipes*. These metabolic rates are half those predicted for epigean species of similar size. The long-term weight loss patterns are linear for all three species over the five days of the weight loss study. Foraging intervals are inferred for females and males, respectively, of 5.1 and 4.4 days for *C. carlsbadensis*, 4.6 and 5.7 days for *C. longipes*, and 5.0 and 4.2 days for *C. conicaudus*. Again, these wild-caught crickets had fed at some unknown earlier time, and the actual feeding intervals are certainly longer.

Responses to Temperature and Relative Humidity

In central Kentucky, cave crickets must forage for food outside the cave, but foraging is very restricted by surface temperature and relative humidity (Leja and Poulson, 1990; Studier and Lavoie, 1990; Helf, 2003). Outside temperatures must be close to cave temperatures of 13°C (55°F) and relative humidity must be close to saturated. Tracings from an electric eye cricket counter are shown in Figure 7 for two times of the year at Mammoth Cave (Helf, 2003). In summer, a pattern of two peaks (exit and entry) is seen every night. In winter, crickets do not leave the cave when the temperature drops below about 5°C. Large numbers of crickets leave only on the warmest nights. Weather records for Mammoth Cave National Park indicate that on most nights throughout the year for at least a short time, surface conditions allow foraging. There are only a few weeks during the hottest months of summer and the depth of winter that are completely off-limits to foraging. Five degrees celsius was the lower temperature limit for surface foraging. At these low temperatures, *H. subterraneus* experience high evaporative water loss that may be made up by consumption of moister foods.

H. subterraneus rapidly lose water and die above even the mild temperature of 20°C (62°F). At 13°C, *H. subterraneus* lost water (0.35–0.53 mg% h^{-1}) at a much higher rate than *C. stygius* (0.08 mg% h^{-1}). At 23°C water loss was about 5 to 9 times higher for both species of crickets, but *H. subterraneus* (1.49–1.52 mg% h^{-1}) again greatly exceed water loss for *C. stygius* (0.27 mg% h^{-1}). In terms of Q10, a rough measure of the effect of temperature on physiology, the Q10 at 9.5°C–15°C was about 1.2, indicating no effect, temperatures from 15°C–20°C and 20°C–25°C were 2.5–3.0, which is a typical physiologic activity range. At 25°C–30°C, the Q10 was lethal.

Ectotherms such as invertebrates, fish, and reptiles, cannot metabolically regulate their body temperatures, so body temperature changes in response to changes in environmental temperature. The metabolic rate in these animals is expected to increase with increasing temperature. The absolute increase in metabolic rate is much greater in *H. subterraneus* than in *C. stygius* (Studier and Lavoie, 1990). The fact that *H. subterraneus* die very quickly and could not even be tested at temperatures exceeding 25°C indicates that they have much greater thermal sensitivity than *C. stygius*. These marked thermal sensitivities indicate adaptation to nearly constant ambient cave temperature and result in greatly increased metabolic demands at higher temperatures. As a result, we expect voluntary epigean foraging at ambient temperatures much above cave conditions to be reduced.

Because *H. subterraneus* forages on the surface throughout the year, it is exposed to highly variable climatic conditions relative to those in the subsurface environment. Helf (2003) examined the impact of climatic conditions on *H. subterraneus* exit patterns in Mammoth

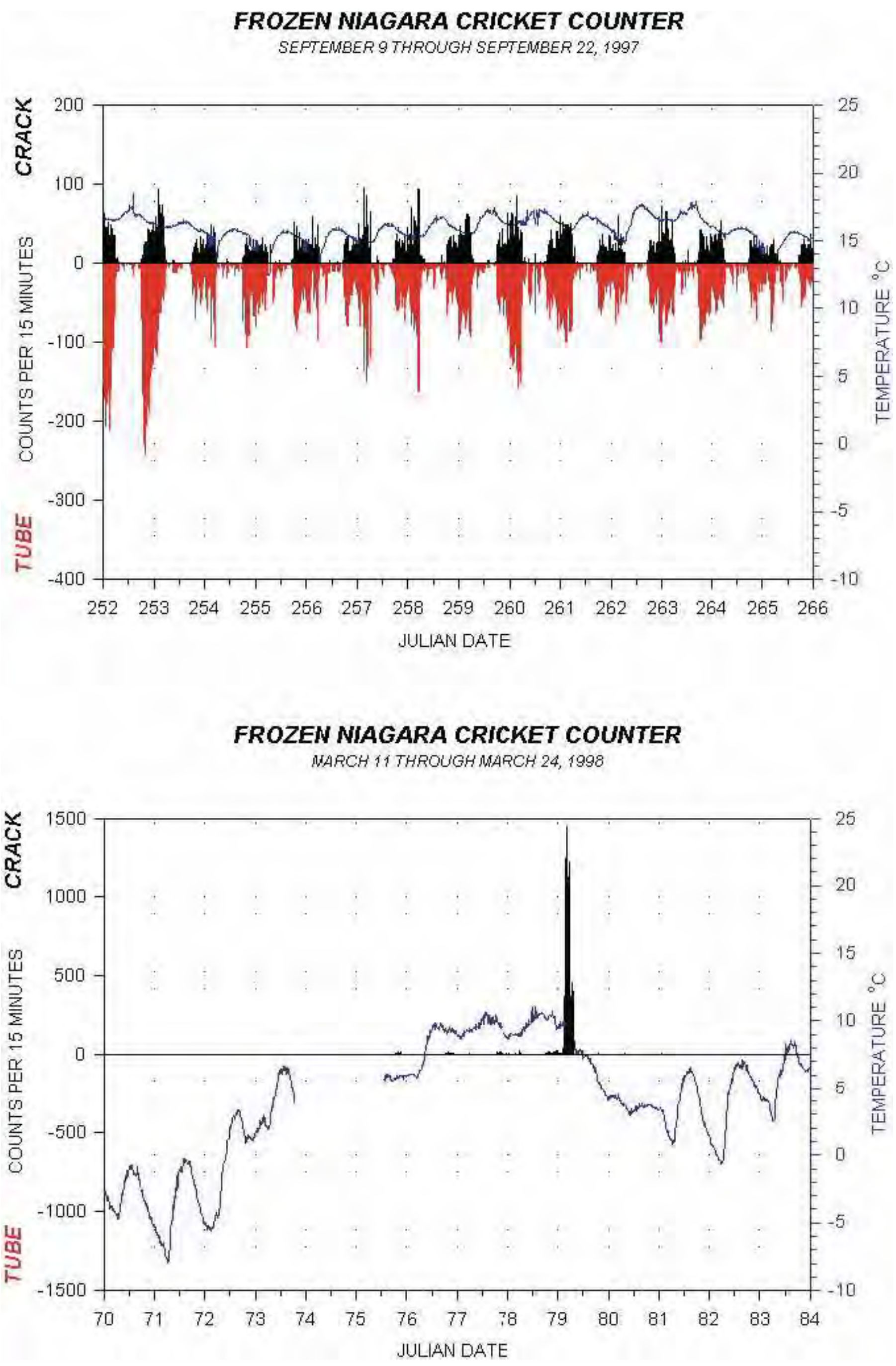


Figure 7. Counts of exiting crickets at Frozen Niagara Entrance, Mammoth Cave during optimal foraging temperatures in 1997 and suboptimal foraging temperatures in 1998. Solid Lines reflect crickets exiting through a crack 3 m above ground level. Dotted lines indicate temperature (Helf 2003).

Cave National Park. He analyzed data from 1996 to 1998 on surface temperature, precipitation, and *H. subterraneus* exit patterns using an electronic eye placed at a narrow crack just outside a cave entrance known to be heavily used by crickets. Overall, significantly greater numbers of cave crickets exited the cave nightly in summer (approximately 460 ± 50/night) versus winter (approximately 190 ± 25/night). In spring/summer, there was a significant positive correlation between numbers of cave crickets exiting caves and rainfall. Cave cricket biology supports this conclusion in that evenings with significant rainfall would reduce their evaporative water loss and increase the volatility of odoriferous food patches, thus increasing cricket success in finding food.

Even more important is the effect of cold winters and summer droughts on cricket survival. From 1994–1997 we censused *H. subterraneus* populations 2–6 times per year in nine cave entrances in Mammoth Cave National Park (Poulson et al., 1998). The overall numbers of size classes 1 (smallest), 2, 3 and 4 (large adults) generally increased in all caves over the four years with mean numbers per cave of 1,026, 1,998, 1,645, and 2,670. In the two caves with the largest populations there was a steady increase of 1,250, 2,180, 2,895, and 4,148 both for a weak source cave (Great Onyx) and 1,980, 2,133, 2,597, and 2,695 for a sink cave (White). The initial low numbers were probably the lingering effect of a severe late 1980s drought and severe early 1990s winters. From 1994 to 1997 the Taylor Drought Index generally decreased as did the number of long winter cold snaps that absolutely preclude foraging by crickets. We also know from indirect evidence of cricket guano communities that drought has had a negative effect on cricket populations in the interval from the early 1970s to late 1980s (Poulson et al., 1995). The presumed mechanism is that crickets preferred moist and/or rotting fruit, feces, micro-carrion, and mushrooms are largely unavailable during droughts. In this context it is not surprising that our best source caves have moist, protected, mature forests around their entrances.

The three closely related gryllid cricket *Caconemobius* species from Hawaii are an appropriate comparison among a cave-adapted species and its two closely related surface species. Ahearn and Howarth (1983) studied water balance physiology and metabolic rates of these species and, as expected, found that their ability to conserve water is strongly correlated with their environment. *C. sandwichensis*, the marine rock zone ancestor, is rarely, if ever, subjected to extremes in temperature or to relative humidity less than 98%. *C. fori*, the lava flow species, is exposed to extremes in temperature and relative humidity from daily cycles, and may also have to contend with geothermal heat. The cave species, *C. varius*, lives in a constant temperature environment and is extremely sensitive to relative humidity below saturation. After 12 hours in a dry environment near their normal ambient temperature (19 °C), the cave species lost significantly more water (14.7 ± 0.7% of body mass) than did either surface species, *C. fori* (8.8 ± 0.7%) and *C. sandwichensis* (11.5 ± 0.6%).

DIET AND DIGESTION

What do crickets eat in the wild is a simple question, yet is one of our enduring mysteries of cave cricket biology. They act as scavengers, eating whatever is smelly enough to get their attention and soft enough to chew. *H. subterraneus* have been observed eating mushrooms, dead insects, animal droppings, berries, and flowers. Taylor et al. (2005) observed one foraging *C. secretus* cave cricket with a live hemipteran in its mandibles. Crickets come readily to a wide range of baits, including rotten liver, limburger cheese, cat food, grape jelly, and peanut butter. Examination of gut contents shows mostly unidentifiable mush, with an occasional recognizable insect part or piece of moss (Levy, 1976). Crickets seem to eat a much more varied diet in summer than in winter. They are also cannibalistic and will eat any cricket that is injured, but they will not eat the crop of the injured cricket. Crops may be a source of injury or death, and crickets may avoid eating them to prevent the cricket equivalent of food poisoning (Janzen 1977).

A study of caged *H. subterraneus* fed different types of foods one at a time (Lavoie et al., 1998, Helf 2003) shows that crickets do not eat partially decomposed leaf litter, moss, lichen, or live earthworms. Crickets gained 5–35% of their crop-empty live weight (CELW) on overripe fruit, deer fecal pellets, or fresh mushrooms. Crickets gained 70–120% of CELW from eating rotting mushrooms. Offering crickets artificial baits of cat food or wet cereal caused them to really tank-up, eating 100–250% of their CELW. We have done extensive searches for cricket foods in the wild, and we have a lot less success at it than the crickets do with their well-developed sense of smell. The natural crop contents are low in sodium relative to potassium, and low in total calories, which suggests that the crickets do not commonly find such high-quality foods as carrion or dead insects in the wild (Studier, 1996).

Organisms that consume plant detritus, decaying fruit, rotting wood, and herbivore dung ingest a variety of bacteria, protozoa and fungi along with their food (Martin and Kukor, 1986). If ingested microbes survive and proliferate in the digestive tract or excrete enzymes that remain active in the gut, then ingested microbes can augment or extend the digestive and metabolic capabilities of the organism that consumes and harbors them (Martin and Kukor, 1986, Kaufman and Klug, 1991). The crop of *H. subterraneus* is a very thin-walled structure that lies between the esophagus and hindgut (Fig. 8). These crickets frequently eat to the point of physical distortion by consuming very large amounts of food in a single foraging bout. The crop may act as a storage and fermentation chamber where an assemblage of microbes pre-digests the food. Some Orthopterans, including crickets, grasshoppers and cockroaches, depend on both resident and ingested microbes to aid in digestion, fermentation, and production of secondary metabolites, including potential toxins.

H. subterraneus may be partially restricted to a narrow temperature range to keep their crop microbes, including bacteria and yeast, under control. As reported by Studier and Lavoie (1990), cave crickets die in a few hours if held at temperatures above room temperature (23°C). Some of these crickets, as well as an occasional field-collected specimen, had crops visibly distended with gas, occasionally to the point of rupture. We think that crickets were killed by unregulated growth of crop microbes that produce excessive gaseous or toxic metabolites at elevated temperatures.

Most microbes isolated at 20°C from cave cricket crops or hindguts grew best above ambient cave temperatures of

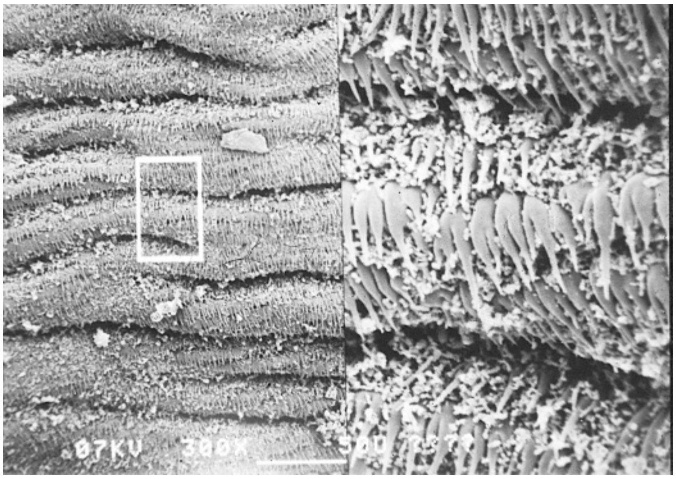


Figure 8. *Hadenoecus* cave cricket crop walls have chitinous structures for grinding and mixing food, and large numbers of resident bacteria.

13.5°C with only one isolate showing optimum growth at cave ambient temperature (Phillpotts, 1989). The pattern of growth at different temperatures is largely due to the activity of enzymes at different temperatures. Enzyme activity generally increases up to the temperature optimum, and crop enzyme activity was optimum at 23°C. One limitation on cave cricket foraging is the need to slow down the metabolic activities of crop microbes that are largely responsible for food digestion. When cave crickets were fed diets rich in either carbohydrates or protein and compared to the natural diet, the activities of specific enzymes responded rapidly to the different diets, as would be expected if microbes were producing the digestive enzymes (White, 1989; Coller, unpublished data).

Whatever the reason or reasons for the extreme thermal sensitivity observed in *H. subterraneus*, even a modest increase in cave ambient conditions could have profound negative effects on cave crickets. Since caves maintain the average annual temperature of the area where they are located, global warming would result in increased cave temperatures. Even a modest increase of 2–6°C over the next 50 years (Schneider, 1989) would greatly increase metabolic demands and evaporative water loss, which would force more frequent foraging bouts and exposure to surface conditions and predators. These changes would probably result in extinction of cave crickets and the concomitant loss of the major source of fixed carbon energy inputs into caves in central Kentucky and many other areas around the world (Poulson, 1991).

FORAGING

Most cave crickets must leave the cave to forage for food. They have to consider many factors in deciding when to leave the cave. They will leave only when it is dark and conditions on the surface are close to cave conditions of 15 °C and 100% humidity, which are obviously influenced by season. How full the cricket is and its risk of being eaten are other factors they have to consider. Adult crickets have the advantage of having greater fat reserves than juveniles, so they can afford to wait longer for better foraging conditions than smaller crickets.

Campbell (1976) used a directional electric eye counter to show that decreasing light intensity was the trigger for *C. conicaudus* to emerge from Spider Cave. Total numbers emerging were influenced by temperature, relative humidity, and moonlight intensity. Numbers could change drastically in a short time. From July 3–4, 110 crickets emerged compared to July 7–8 when 1,195 crickets emerged. In lab studies, hungry crickets were more active. The highest emergence occurred on nights with low temperatures, high relative humidity, and low light intensity.

Levy (1976) observed that *H. subterraneus* use odor to differentiate among food choices. Small crickets are less fussy about what they eat than medium or large crickets. Small crickets fed on the first food item they encountered, compared to larger crickets with longer legs and antennae that can sense food from a greater distance away, and get to pick and choose among the different feeding opportunities. She described *H. subterraneus* as scavengers on stilts. Odor is highly correlated with caloric value; smelly foods tend to have more calories, but Levy could not determine whether crickets showed a real preference for higher calories or just smell.

DeLong (1989) did a deceptively simple caloric density preference study in the cave by offering *H. subterraneus* a buffet of three food choices. He used two extremes; pure peanut butter, which has a strong smell and is high in fat and calories (5.9 Kcal g^{-1}), and pure corn starch, which has no odor and is a pure carbohydrate with much lower caloric value (4.1 Kcal g^{-1}). A third bait choice was a 50:50 mixture that reduced available calories (down to 5.0 Kcal g^{-1}), but kept the strong odor associated with peanut butter. The bait buffet was offered for one hour under separate live traps (a plastic ring capped with screening and propped up with a stick), traps were set by remotely yanking a string attached to the stick, and captured crickets were counted, sexed, and had their HFL measured (Table 1).

Consistent with Levy's scavenger on stilts model (Levy, 1976), non-sexable small crickets (HFL $<$ 10 mm) were evenly distributed among the baits, while large adult (HFL $>$ 20 mm) and medium (HFL 10–19 mm) crickets were preferentially found in the higher calorie baits. These size-related differences suggest that small crickets do not forage for the optimum caloric pay-off, but stop to feed at the first available foodstuff. These results also show that medium and large crickets do select for higher calorie foodstuffs based on odor, but are not able to select the highest calorie food. Data by gender for medium and large crickets show nearly equal numbers of males and females attracted to the 100% and 50% PB baits.

Table 1. *H. subterraneus* captured by size at three different energy level baits.

Bait	Large[a]	Medium[b]	Small[c]	Total
100% Peanut butter with 0% cornstarch	18	17	22	57
50:50 Peanut butter and cornstarch	13	22	23	58
0% Peanut butter with 100% cornstarch	2	1	22	25

HFL=Hind Femur Length (DeLong 1989).

[a] Large crickets = HFL>20 mm

[b] Medium crickets = HFL 10–19 mm

[c] Small crickets = HFL< 10 mm

Understanding the extent of the distance away from an entrance that cave crickets forage is an important consideration in cave management. If the crickets are the base of the food input into the cave, efforts have to be made to ensure that they have suitable habitat for foraging. Taylor et al. (2005) used UV bright paint to mark about 2000 *C. secretus* out of about 15,000 as they exited at night from Big Red Cave in Texas in late spring and summer 2003. The researchers used UV lights to locate marked crickets on the surface over a total of 17 sampling nights. The location of all 291 crickets on the surface (marked and unmarked) was recorded with GPS and a flag, and later measured and mapped. About half the crickets (51.1%) were located within 40 m of the entrance. Densities were uniform out to about 80 m, and some (8.1%) were located up to 105 m from the entrance, which is much greater than expected. On average, adults were found further from the entrance than sub-adults, and no male:female differences in distribution were noted. Crickets were typically found close to the ground, and almost evenly distributed in grasses, leaf litter, or herbaceous vegetation, although the authors noted that the vegetation type, such as cacti, may have influenced search efforts. In addition to managing suitable foraging environments around entrances, the authors noted the need to control fire ants in these areas.

Foraging And Predation Risk

During a foraging bout on the surface, cave crickets likely use their prodigious jumping ability as their primary means of escape from predators. However, cave crickets' highly distensible crop enables them to increase their weight by more than >200% which could compromise their jumping ability and thus their means of escaping from predators. Helf (2003) showed that increasing crop fullness compromised large cave crickets' jumping ability (Fig. 9). Thus, cave cricket foraging decisions may be based on the tradeoff between food intake and biotic factors with the strongest impact (e.g., perceived predation risk or competition).

Helf (2003) hypothesized that the advantage a full crop conveys to an adult cricket would be outweighed by the negative effects it has on their jumping ability and predicted there would be a negative correlation between how much food large cave crickets eat at bait patches and its distance from a cave entrance. Helf (2003) used color-coded bait patches placed at different distances from cave entrances to examine what effect *H. subterraneus* perceived risk of being eaten has on their foraging behavior. The data from these experiments, numbers, sizes, and fullness of crickets that fed at the bait patches on a given night, were obtained by censusing and weighing colored crickets in the cave the day following a foraging bout. There was no significant difference in food intake among bait patch distances. The data suggest that cricket foraging behavior was not affected by predation risk. Average food intake at all patch distances (ca. 100% of body weight) were well below cricket crop capacity of ≥200%.

Helf (2005) found aggregative responses to food patches in *Ceuthophilus secretus*, a widespread species in central Texas, can also lead to intense intraspecific competition (Fig. 10). Helf (2005) used bait patches centered on cave entrances at the four cardinal directions set just outside cave entrances, at 5 m, and at 10 m away to examine the foraging behavior of *C. secretus* at six caves in Government Canyon State Natural Area (GCSNA) in San Antonio, Texas. During summer and fall months the amount of food consumed by *C. secretus* declined significantly as a function of patch distance from cave entrances. Videotaped foraging bouts showed fierce intraspecific competition among *C. secretus* at bait patches. There was a significant positive

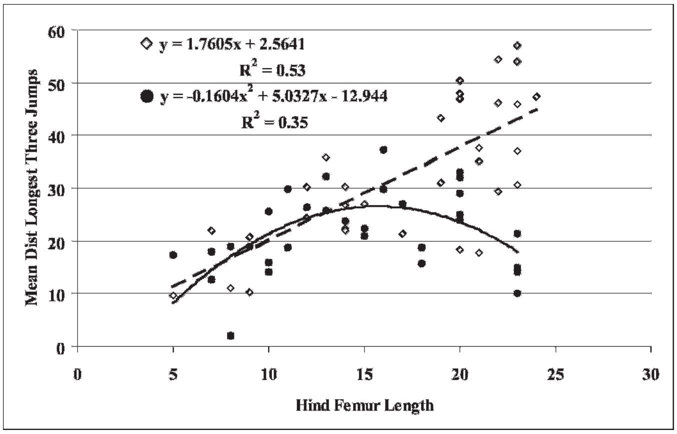


Figure 9. Effect of crop fullness on jumping ability of various sizes of *Hadenoecus* cave crickets. Error bars are ±1 standard deviation (Helf 2003).

Figure 10. Intense intraspecific competition among *Ceuthophilus secretus* at bait patches.

correlation between their time spent feeding in bait patches and patch distance.

Red Imported Fire Ants (*Solenopsis invicta*) were usually found in large numbers at food patches, but 2003, a drought year, saw the largest numbers of *S. invicta* using the bait patches. Similarly, *C. secretus* food intake at bait patches was highest during 2003. GCSNA staff treated *S. invicta* mounds at half the study caves with boiling water that effectively reduces their number. Surprisingly, *C. secretus* consumed significantly less food from bait patches at treated caves relative to untreated caves. These data suggest that at caves with reduced *S. invicta* numbers, *C. secretus* was released from interspecific competition and so was able to exploit all available bait patches. At untreated caves, *C. secretus* increased food intake was likely due to their avoidance of distant bait patches being used by great numbers of *S. invicta*. Overall there were fewer available bait patches being exploited by many crickets. On one occasion there was a significant negative correlation between *C. secretus* time spent feeding in bait patches and patch distance (Helf, 2005).

A study of numbers of three species of *Ceuthophilus* in three central Texas caves was made by Elliott and Sprouse from 1993 to 1999 (Elliott, 1994). Lakeline Cave was heavily impacted by construction of a mall, which left an undisturbed area around the cave entrance of only 0.9 ha (2.3 ac) in comparison to two other caves in large undisturbed areas. Cave cricket numbers in Lakeline Cave showed a steady decline with time while populations in the other two caves remained stable. These crickets generally forage 50–60 m from a cave entrance, showing the need for a larger undisturbed area around the entrance.

Movement and Elongated Appendages

Elongated appendages and gracile appearance are widely regarded as troglomorphic characteristics of cave animals. Elongated appendages, particularly antennae,

Table 2. Averages of ranges [in brackets] of hind femur length (HFL), crop-empty live weight (CELW), and attenuation index ($CELW/HFL^3$) for cricket species, both Rhaphidophoridae and Gryllidae.

Species	Cave status	Number Location	CELW, mg (S.E.)	HFL,mm (S.E.)	Attenuation Index $CELW/HFL^3$
Rhaphidophoridae					
Hadenoecus subterraneus	TP	425 KY	[11.3–556.8]	[7–25]	0.0334 [0.0296–0.0380]
Ceuthophilus longipes	TP	21 NM	120.2 (0.1)	12.6 (0.1)	0.0602
Ceuthophilus stygius	EP/TX	247 KY	[108.5–1338]	[10–25]	0.0996 [0.0508–0.1214]
Ceuthophilus conicaudus	EP/TX	20 NM	166 (9.3)	10.2 (0.2)	0.1546
Ceuthophilus carlsbadensis	EP/TX	29 NM	283.6 (0.1)	11.5 (0.1)	0.1879
Gryllidae					
Caconemobius varius	TB	19 HI	34.0 (2.4)	6.1 (0.1)	0.1474
Caconemobius fori	EP/TX	19 HI	59.4 (0.1)	7.2 (0.2)	0.1571
Caconemobius sandwichensis	EP	14 HI	80.9 (4.0)	7.4 (0.2)	0.1998
Gryllus pennsylvanicus	EP	20 MI	291.7 (0.1)	10.1 (0.1)	0.2831
Acheta domestica	EP	20 ???	142.2 (4.0)	7.4 (0.2)	0.3543

Values in parentheses are standard errors. Crickets are ranked specifically by attenuation index and in decreasing order by status of cave adaptation where TB=troglobite, TP=troglophile, TX=trogloxene, and EP=epigean. (Studier *et al.*, 2002).

could increase sensory perception, while elongated legs may be an adaptation for walking on irregular surfaces in total darkness (i.e., in a three-dimensional dark maze where stepping across gaps may be safer than jumping or walking around). Elongated appendages also could be an adaptation for metabolic economy; with longer legs, the animal could move farther with each step. Continuing Levy's (1976) scavenger on stilts concept, long legs and antennae allow crickets to reach above surface boundary layers to detect food or mates better. Vandel (1965) generalizes very broadly that cavernicolous crickets show extreme appendage elongation, even within a group that tends to have long appendages.

Studier et al. (2002) did a study of leg attenuation in a range of cave and surface crickets. When possible, they measured a range of sizes of individuals of each species and found that a relationship exists between body mass and a linear measurement of hind femur length. In both *H. subterraneus* and *C. stygius*, the relationships differ between sexes, with adult females routinely being heavier than adult males of similar HFL. With *H. subterraneus*, the relationships also differ by season. Individuals of similar HFL are lightest in the spring and heaviest in the fall. We have a limited amount of information from other species, but adults of the three *Ceuthophilus* species from Carlsbad and the three *Caconemobius* species from Hawaii generally fit the proposed model. An attenuation index of the ratio of crop empty live weight to hind femur length, cubed ($CELW/HFL^3$) inversely ranks the studied cricket species to their level of adaptation to a cavernicolous existence, and is proposed as a potentially useful non-lethal quantitative indicator of the extent of cave adaptation in crickets (Table 2).

Jumping behavior in *H. subterraneus* was studied by Sevick (unpublished data). He used a photographic system with a strobe light to evaluate the cricket jumping response to a threat. The pictures reveal something quite unexpected; the crickets somersault during their escape jump. He thought that the somersault allows the cricket to make contact with the underside of a ledge or the ceiling of the cave, which are safer places to avoid predators than just landing on the floor several centimeters away from where it started.

The evasive behavior of *H. subterraneus* has also been studied. Individual cave crickets were captured and tested in the cave by forcing them to hop to exhaustion (Fig. 11), defined as being unresponsive to touch (Mason, 1989). Crickets with longer hind femurs hopped greater distances both per hop and cumulatively, while the amount of food in the crop reduced the hop length, but not the total distance hopped. In winter 1988, 32 adult crickets with HFL≥ 20 mm, hopped an average of 11.5 ± 0.6 times (range 7–20 hops). The average hop length was 36.7 ± 1.2 cm (range 23.8–46.9 cm) for a total average distance hopped of 419 ± 1.2 cm (range 212–898 cm). Time to exhaustion was 15.3 ± 0.2 seconds (range 8–24 seconds). The compass direction of the initial and subsequent hops were random. Comparing winter to summer, crickets showed an increased ability to hop for a longer time and total distance, although the average hop length remained the same.

Helf (2003) measured the impact of surface temperature on large *H. subterraneus* locomotory ability by measuring the distance they walked and jumped over sixty seconds at a temperature conducive to foraging (9°C) and a temperature that precluded foraging (3°C). There was a significant decrease in the distance walked by large crickets from 9°C to 3°C. No statistical comparison was even possible for jumping ability between 9°C and 3°C because crickets could not jump during the 3°C trials. As an ectotherm, *H.*

Figure 11. Exhausted *Hadenoecus* cave cricket does not respond to touch and is unable to use its hind legs for jumping (muscles are in tetany).

subterraneus cannot respond to the negative effect of low surface temperatures, so it waits inside the cave for better conditions.

In the Mammoth Cave entrance biomonitoring study, Poulson, Helf and Lavoie expressed concern about plans to develop gates for some entrances to the Mammoth Cave system. The use of airlock doors would eliminate the evening movement of *H. subterraneus* out of the cave to forage and their morning return to roosts in the caves. We wanted to know what size openings would need to be left around gates to permit free movement of cave crickets. Four large adult crickets were placed in a fiberglass window screen bag attached to PVC tubing of different lengths and shapes. The bags were placed horizontally on the ground and the number of crickets remaining after one hour and 12 hours was noted. A diameter of 1 ¼ in was the minimum that allowed for free movement of adult crickets. The shape of the tubing had no appreciable effect on cricket movement, so baffling the tubes should be possible to reduce air flow without a negative effect on crickets. We recommended that several openings be included in the design of airlock gates, with a single 3–4 in opening low down for movement of cave rats (*Neotoma* spp.) and multiple openings of 1 ½ in closer to the ceiling for crickets. Salamanders could make use of any of these openings. The Park Service agreed. Caves with gated bat entrances would already allow free movement of crickets and rats, and were not part of these recommended modifications.

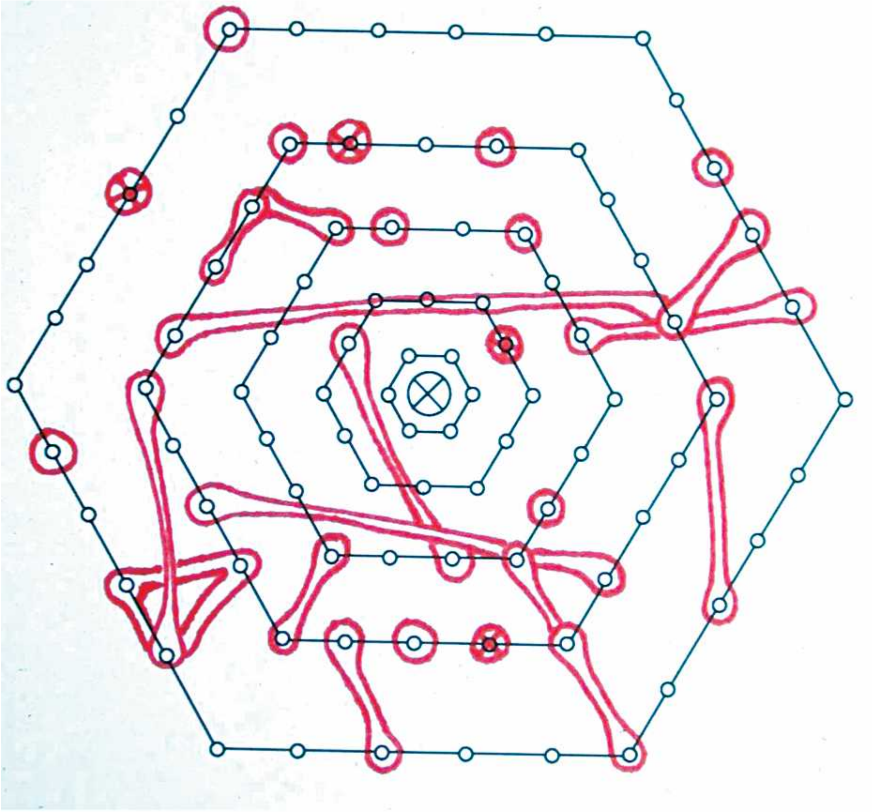
CRICKETS AS PREY

If you have ever watched a nature show, you have probably noticed that many things like to eat crickets and grasshoppers. Cave crickets are no exception. Inside the cave, they are preyed upon by spiders and salamanders. In some caves, specialized beetles prey on cricket eggs and injured young crickets. Outside the cave, crickets are eaten by many animals, in particular, mice. In Texas caves *Ceuthophilus* are eaten by many species including a scorpion and a spider. In addition dead crickets are scavenged by a rove beetle, a harvestman, and springtails, if other crickets do not find them first.

A cave sand beetle, *Neaphaenops tellkampfi*, is a specialized predator on cricket eggs in Kentucky. Some aspects of the relationship between crickets and beetles have been well studied (Poulson, 1975; Norton et al., 1975; Kane and Poulson, 1976; Griffith, 1991). Beetles dig in areas of sandy soil that have been disturbed by oviposition. It has been suggested that female crickets from caves with populations of beetles have co-evolved to have longer ovipositors than females from un-predated populations (Hubbell and Norton 1978). The difference is only one millimeter, but inserting eggs that much deeper decreases the risk of the egg being found by a sand beetle. In laboratory studies, Griffith (1991) carefully measured the depth of buried cricket eggs and the depth of holes dug by beetles. The overlap of graphs showed that beetles are likely to find only 25% of eggs laid. A reduced harvest rate due to lower, seasonal cricket egg availability was shown by Griffith and Poulson (1993) to decrease beetle fecundity. Cave cricket eggs that escape predation hatch into nymphs that move to the ceiling where they are less vulnerable to predators (Norton et al., 1975). A similar situation of coevolution or parallel evolution between predator and prey is seen in the Cumberland Plateau area, involving *H. cumberlandicus* and a different species of cave beetle, *Darlingtonea kentuckensis* (Hubbell and Norton, 1978; Marsh, 1969), *Ceuthophilus* in Texas by *Rhadine subterranea* (Mitchell, 1968).

Ceuthophilus maculatus, a cave cricket, may be an intermediate host for an intestinal parasite of mice. Fish (1974) studied the food of two species of meadow mice (*Microtus* sp.), and determined that the mice would eat these crickets when they encountered them in a confined space. The mice discarded the hard parts of the crickets, eating only internal organs. The lack of identifiable cricket parts in the stomachs of the mice may have led researchers to underestimate the use of insects in the diet.

The use of cave entrances by mice *(Peromyscus leucopus*) as a reliable source of food in the form of cave crickets was studied by Viele and Studier (1990). At some entrances, numbers of exiting crickets can be in the hundreds or even thousands per night. Viele and Studier set up a grid of traps around the entrance to a small, biologically rich cave in Mammoth Cave National Park called White Cave. Sherman live traps were set at 10 m intervals and baited with peanut butter. Traps were set at night and checked in the morning for several days. Trapped mice were marked to identify specific individuals and then released. The data were plotted to determine the home range of each trapped mouse. Only four white-footed deer



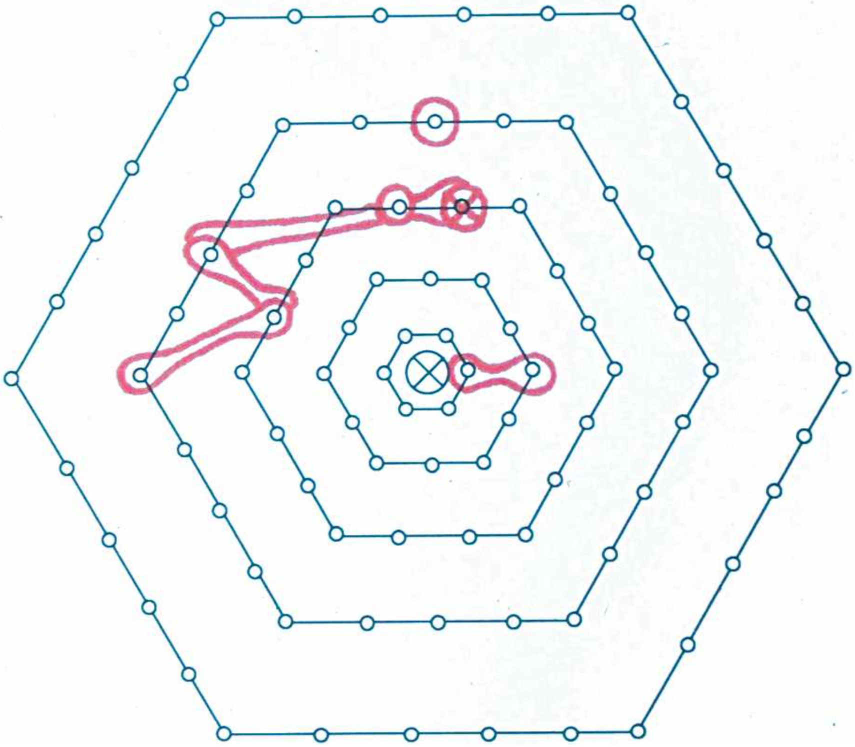


Figure 12. Sherman live trap grid of 90 live traps at Great Onyx cave 6–8 June, 1996. The upper grid was centered on the cave entrance used by crickets and the lower grid was set in similar terrain without a cave entrance several hundred meters away from the cave grid. All traps in the grid were 10m from the next nearest trap. Marks indicate captures of white-footed mice (*Peromyscus leucopus*). Connected points and circles with an 'X' indicate multiple captures of one individual (Helf 2003).

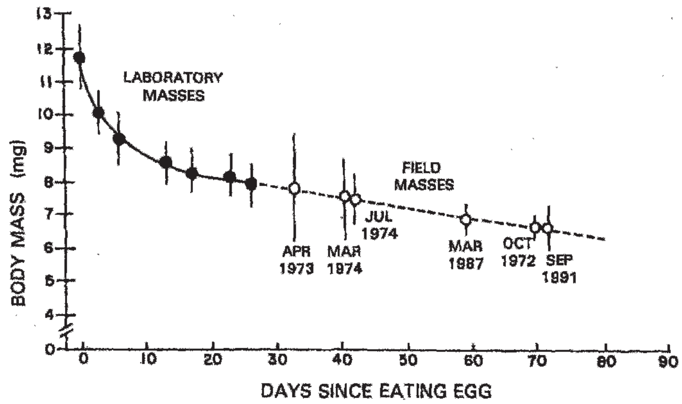


Figure 13. Mass loss in *Neaphaenops* sand beetles (mean +/− SD). Solid circles represent mass loss in the laboratory after consuming a single cricket egg (distended). Open circles are field masses, placed on an extended line (—) at a slope of 0.031 mg/d that equals the average rate of mass loss of non-distended beetles (Griffith and Poulson 1993).

mice were captured, but the home ranges of three of the mice were not randomly or evenly distributed. Three of the mice had home ranges that overlapped at the cave entrance, indicating the importance of the cave entrance to the mice.

Helf (2003) examined the effect of a cave entrance actively used by foraging *H. subterraneus* on the density of *P. leucopus* at Great Onyx Cave in Mammoth Cave National Park. Helf set a 90-trap grid centered on the cave entrance with another 90-trap grid set several hundred meters away in similar terrain without a cave entrance. Helf (2003) found 26 *P. leucopus* individuals within 50 m of the cave entrance whereas only six *P. leucopus* individuals were found in the control area (Fig. 12). Helf concluded that such high *P. leucopus* densities, since they are insectivorous, could affect the local community around cave entrances.

Studier (1996) measured the size, mass, nitrogen and mineral concentrations of crop-free carcasses of *H. subterraneus*, their eggs, and the egg predator sand beetle, *Neaphaenops tellkampfi*. Body magnesium, iron, and nitrogen concentrations decrease with size in the cave crickets, and accumulation of these minerals occurs very slowly in hatchling cave crickets. Nutrients needed for egg growth greatly exceed needs of the cricket for growth. Compared to cricket eggs, the beetles contain similar concentrations of iron and calcium, lower concentrations of magnesium and potassium, and higher concentrations of nitrogen and sodium. Growth rates of body mass in crickets is about one-tenth the growth expected for epigean insects, so nitrogen and mineral accumulations are likewise expected to be very slow.

A single cricket egg represents about 75% of the mass of a *N. tellkampfi*, making it a huge meal. Based on a weight-loss study in the laboratory (Griffith and Poulson, 1993), a single cricket egg will sustain a beetle for 2–3 weeks before it has to begin using body fat reserves (Fig. 13). As an example of you are what you eat, the nitrogen and mineral composition of the *N. tellkampfi* carcass is quite different from levels found in other beetles, and much more similar to that of cave cricket eggs (Studier, 1996).

Female *H. subterraneus* exhibit two strategies to avoid egg predation. One strategy is predator satiation, in which timing of egg production results in an overabundance of eggs for a short duration. Predators become satiated during this short period, and the surviving young quickly grow beyond a size easily handled by the predator (Smith, 1986). One cricket egg completely satiates a sand beetle for approximately a week or two (Norton et al., 1975; Griffith and Poulson, 1993). A reduction in predation rates is associated at the population level with high egg densities (Kane and Poulson, 1976). The second predator avoidance strategy involves making large numbers of ovipositor holes to increase search time for *Neaphaenops* beetles, which preferentially dig in areas of disturbed substrate. Caged crickets consistently made more ovipositor holes than eggs laid. Both of these strategies may increase egg survival rate. Oviposited eggs have a minimal hatching success rate of 82.6%, with an approximate time to hatching of 12 weeks, which agrees with estimates by Hubbell and Norton (1978). Females may also be testing the soil for suitable conditions of egg development. None of these explanations is mutually exclusive.

Ten-meter transects (32.8 ft transects) of nine entrances in Mammoth Cave National Park were censused regularly from 1995–1997 by the authors. All entrances had *Nesticus* spiders or a similar-sized spider, while only five had populations of the large orb-weaver *Meta americana* (Fig. 14). At the five entrances with *Meta*, there was a positive correlation between spider number and reproduction, and cave cricket abundance both in transects in a cave and between caves. This finding suggests that cricket prey numbers have a strong influence on success of the spider predator.

Fungi may have the potential to reduce cave cricket populations. In a study of the internal and external species of fungi associated with a trogloxenic cave cricket, *Hadenoecus cumberlandicus*, Benoit et al. (2004) isolated a range of soil saprophytes that you would expect to find in a cave. Two internal isolates were species of plant pathogenic fungi, which they attributed to feeding. One external isolate was a genus of fungus that is an insect pathogen. Presence alone does not indicate activity, but we occasionally observe dead crickets covered in a white mycelium of *Isaria densa* (Cali, 1897). We refer to them as cricket marshmallows, for obvious reasons (Fig. 15). We are not sure if the fungus kills the cricket or grows on it after the cricket dies, but it is certainly present at the time of death. The fungus is in a race with crickets and other scavengers for the carcass.

Figure 14. *Meta americana* spider with web. These large spiders are able to catch and consume adult cave crickets.

CAVE CRICKETS AS KEYSTONE SPECIES

The cave cricket is often considered a dominant species in cave ecosystems because of the large numbers of individuals and their contribution to the food base in many caves. Cave crickets enhance biodiversity in food-limited caves by a combination of their feces, eggs, and dead bodies. This might have been predicted just by their high importance value as by far the largest, the most numerous, and the highest metabolic rate species in caves where they occur. Their actual contribution to biodiversity has only been well studied in Texas caves by Mitchell (Mohr and Poulson, 1966) and in Kentucky (Poulson, 1992).

In the Mammoth Cave area their guano under entrance roosts only occasionally has the right moisture to support a very diverse community, but their scattered feces away from entrances support a community that includes some of the most troglomorphic springtails, beetles, millipedes, and spiders. In addition, their eggs are eaten by a carabid beetle, *Neaphaenops tellkampfii*, which occurs in high densities where crickets lay most of their eggs in sandy or silty substrates away from entrances. The beetle's feces in turn support a moderately diverse community that includes springtails, mites, a pseudoscorpion, a dipluran, and a spider.

In Texas caves *Ceuthophilus* guano can also be an important community food base, supporting populations of troglobites and troglophiles (S. Taylor, personal communication). And, though not studied, the feces of a carabid beetle (Rhadine) that eats cricket eggs are certainly the basis of another community.

Long-term studies of cave cricket guano communities in two small caves in Mammoth Cave National Park show large fluctuations in the numbers of animals censused over 24 years between 1971 and 1994 (Fig. 16). Poulson et al. (1995) pose four hypotheses to explain the observed variation. The first hypothesis is that anthropogenic disturbances by cave tours cause the crickets to move their roosts to other areas, thus preventing renewal of the guano. After considering the frequency, group size, and path

Figure 15. Cricket marshmallow: A dead *H. subterraneus* cricket surrounded by a dense white fungal mycelium.

followed by tour groups, we rejected this hypothesis. A second hypothesis is that weather directly affects the guano, making it too dry or two moist to support the guano community. This hypothesis is rejected because the data are not consistent with the model. The third hypothesis is that weather changed the cave microclimate, causing the crickets to roost elsewhere, which reduces guano input to the community. However, we have observed that crickets do keep the same roosts for long periods of time, and new guano communities are not established elsewhere.

The final hypothesis, and the one supported by observations, is that weather effects are indirectly seen on the guano communities because weather forces change in cricket foraging, guano deposition, and cricket survival. Data comparing species diversity and abundance of the guano community with an increase in cricket numbers coincided with a period of favorable weather. Poor surface weather conditions negatively affect cricket foraging and the trophic cascade based on guano resupply.

PERSPECTIVES

Cave crickets are often important keystone species that support cave ecosystems by production of eggs, carcasses, and guano that serve as the food base in many caves. Tom Poulson is fond of using the phrase, Mysteries of the Cave, when discussing something we just don't understand about caves and cave life. The challenge of field research is to find answers to these mysteries (Poulson, 1996). Any research project in the field can be a humbling experience. You review what you know, develop alternate hypotheses to test, think, plan, and plan again, get your materials together, build devices, travel to the field site, and then nothing works as you planned. Generally, most experiments require two or more modifications, and plenty of duct tape, before they work. Cave cricket research is no exception. Although we know a lot about a few species, there are still tremendous opportunities for further study of cave crickets in order to solve more mysteries of the cave.

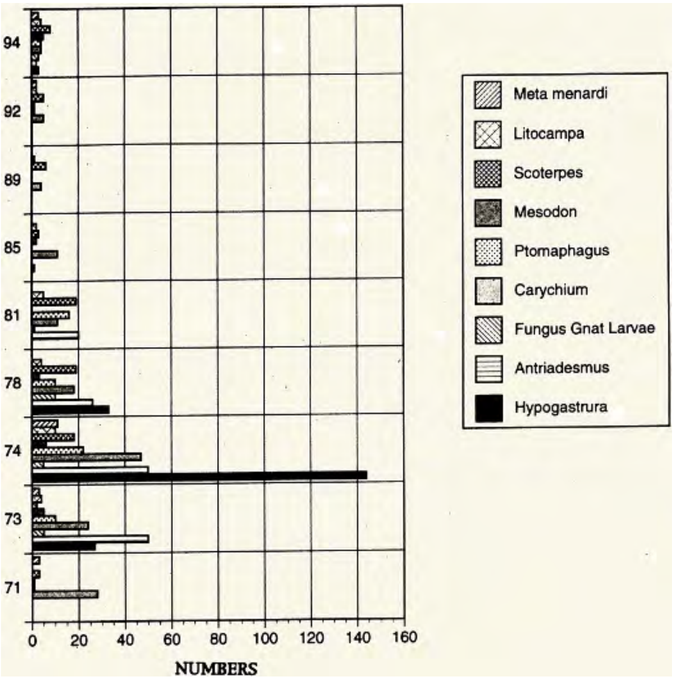


Figure 16. Changes in abundance of cave cricket guano community organisms in White Cave over 24 years from 1971–1994 (Poulson *et al.,* 1995).

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W.R. Elliott – Zoogeography and biodiversity of Missouri caves and karst. *Journal of Cave and Karst Studies,* v. 69, no. 1, p. 135–162.

ZOOGEOGRAPHY AND BIODIVERSITY OF MISSOURI CAVES AND KARST

William R. Elliott
Missouri Department of Conservation, Resource Science Division, 2901 West Truman Boulevard, Jefferson City, MO 65102-0180, Bill.Elliot@mdc.mo.gov

Abstract: The Missouri Cave Life Database contains 927 species and about 12,500 observation and collection records. About 1,038 (17%) of Missouri's 6,200 caves and cave springs are biocaves with at least one species record, but only 491 sites (8%) have five or more species recorded. Missouri has 82 troglobites (67 described, 15 undescribed), including 49 aquatic and 33 terrestrial species. The aquatics include 30 described and six undescribed stygobites, plus 13 described phreatobites. The terrestrials include 24 described and nine undescribed species. Six of the troglobites (four described) may actually be troglophiles, edaphobites or neotroglobites. There are about 215 troglophiles (17 aquatic), 203 trogloxenes (20 aquatic) and 407 accidentals or of uncertain ecological classification (27 aquatic).

Karst zoogeographic regions include the broad Springfield and Salem plateaus; the Boone, Hannibal, St. Louis, Jefferson-Ste. Genevieve, and Perryville karsts; and an isolated area, Caney Mountain. Troglobites are currently known from 728 Missouri sites, including 597 caves (10% of known caves). Twenty-five troglobites, eight of which are new species, occur at single sites only. Missouri shares 48 troglobites with other states, exhibiting relatively low diversity in terrestrial troglobites compared to areas east of the Mississippi River, but high aquatic biodiversity.

Values for species richness (SR), troglobites, site endemism (SE) and biodiversity (B) were derived to rank and compare caves for conservation planning. Many species and biologically important biocaves were added to the Missouri Natural Heritage Database and the Comprehensive Wildlife Conservation Strategy, a long-range, statewide conservation plan. Further work should focus on poorly known regions.

Introduction

The purpose of this paper is to summarize and analyze data derived from the Cave Life Database (CLD), which the author developed at the Missouri Department of Conservation (MDC) to track Missouri's cave fauna. Peck and Lewis (1978) compared the eastern Missouri cave fauna to Illinois and other regions, and they extensively discussed the origins and relations of the faunas. An updated overview of the State's cave zoogeography is provided, but the focus of this paper is more on cave biodiversity and how to prioritize caves for conservation planning.

The purpose of the CLD is to bring together all pertinent checklists and data sources into a relational database. The CLD draws on published and unpublished records from the scientific literature, agency reports, speleological literature, databases (such as the Missouri Natural Heritage Database), and unpublished records from experienced observers and biologists. The database is used to track collections and observations, to produce checklists for any cave, county, or taxon, and to study zoogeography, biodiversity and conservation issues. The analyses help in recognizing knowledge gaps, planning studies and wildlife conservation work, drawing species range maps, updating the Natural Heritage Database and developing educational materials and publications.

The CLD is too large to publish here, so summary statistics, analyses, tables, maps, photographs and species checklists are provided for the top three caves for biodiversity. Readers may contact the author for checklists and specialized reports.

Literature Review

Missouri caves (Figs. 1 and 2) are mentioned in some of the earliest American biospeleological literature. Girard (1852, 1859) reported on cave crayfishes and described *Typhlichthys subterraneus* (the Southern cavefish) from Kentucky; the species was later found in Missouri. Ruth Hoppin (Hoppin, 1889) sent her collection of Ozark cavefish from Sarcoxie Cave, Jasper County, in 1888 to Harvard professors Samuel Garman (Garman, 1889) and Walter Faxon. Faxon (1889) described *Cambarus setosus*, the Bristly Cave Crayfish (Fig. 3). Schwarz (1891) described the beetle, *Ptomaphagus cavernicola*, from Marvel (Marble) Cave, Stone County, and it also was collected in 1897 by C. H. Merriam in Hamilton Cave, Washington County. Stejneger (1892) described the Grotto salamander, *Typhlotriton spelaeus* (now *Eurycea spelaea* according to

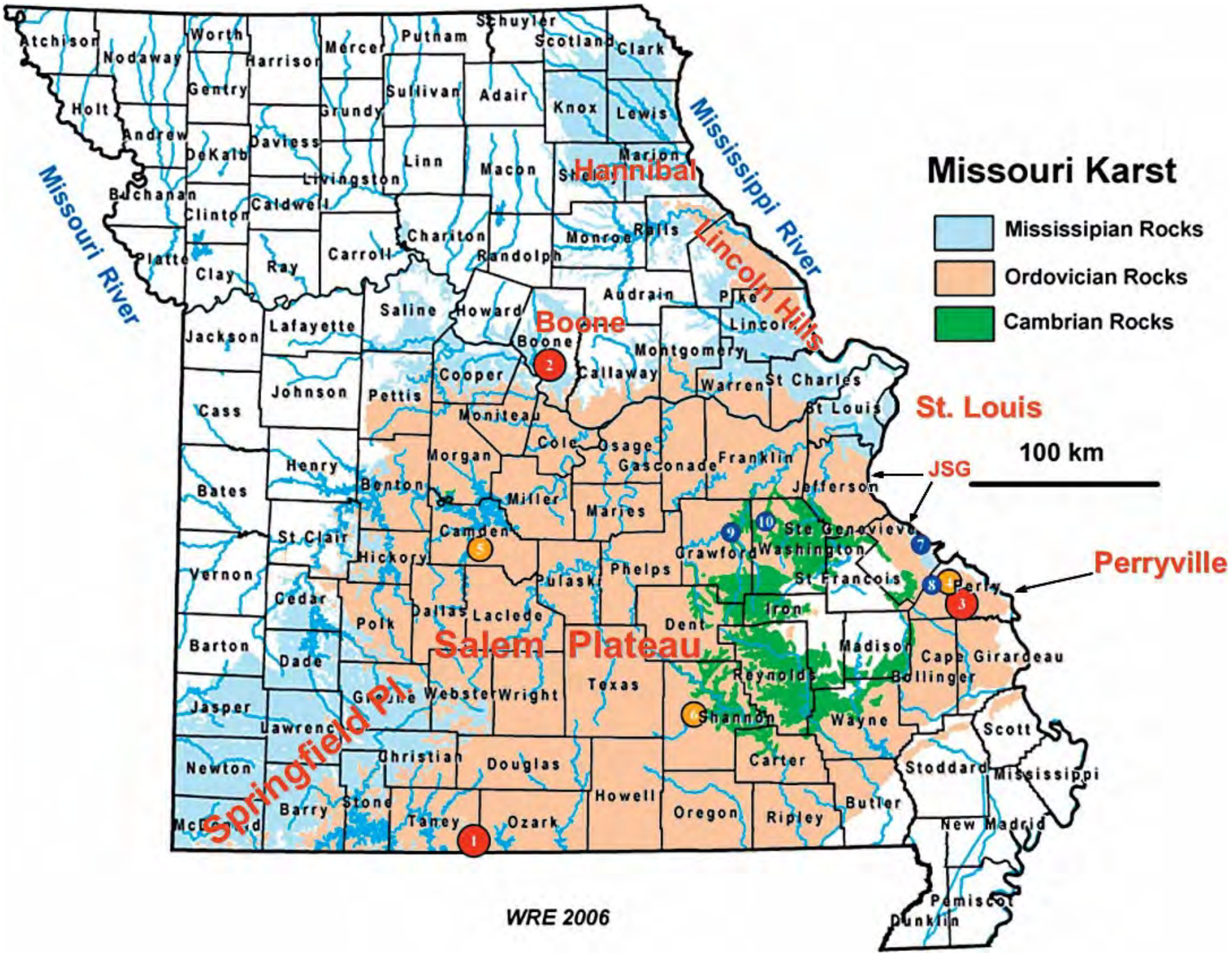

Figure 1. Missouri karst map showing the three principal ages of dolomites and limestones, karst zoogeographic regions and the top ten biocaves. 1) Tumbling Creek Cave, Taney County; 2) Devil's Icebox Cave, Boone County; 3) Mystery Cave, Perry County; 4) Berome Moore Cave, Perry County; 5) River Cave, Camden County; 6) Branson Cave, Shannon County; 7) Kohms Cave, Ste. Genevieve County; 8) Tom Moore Cave, Perry County; 9) Jagged Canyon Cave, Crawford County; 10) Great Scott Cave, Washington County.

Bonett and Chippindale, 2004). Eigenmann (1898, 1899, 1901, 1909) described the Ozark cavefish, *Amblyopsis rosae* (Fig. 4), and published many other papers on Missouri cavefish and salamanders.

The first third of the 20th century saw few reports on Missouri cave life. A troglophilic spider was reported by Crosby (1905) from Rocheport (Boone) Cave, Boone County; later it was described as *Cicurina cavealis* by Bishop and Crosby (1926). J. W. Mackelden collected the Grotto salamander from Marble Cave, Oregon County, in 1906. A. D. Newman collected amphipods from a well at Harrisonville, Cass County, from 1915–1917. Unknown collectors worked in Talking Rocks Cavern (Fairy Cave), Stone County, in 1919. Grotto salamanders were taken in Sarcoxie Cave in 1927, apparently by B. C. Marshall, and by E. P. Creaser and E. B. Williamson from several caves in 1929–1930. These early records came from several museum catalogs.

In the second third of the 20th century, Hubbell (1934, 1936) published many descriptions of *Ceuthophilus* crickets (Fig. 5), including five species in Missouri caves. The legendary Leslie Hubricht studied many caves and springs from 1931 to 1969. He found and described numerous new species of amphipods, isopods, and aquatic snails (Hubricht, 1940, 1941, 1942, 1943, 1950, 1959, 1971, 1972; Hubricht and Mackin, 1940, 1949). Kenneth Dearolf and Hubricht collected four species of millipedes in 1938, which were described by Loomis (1939), including *Causeyella*

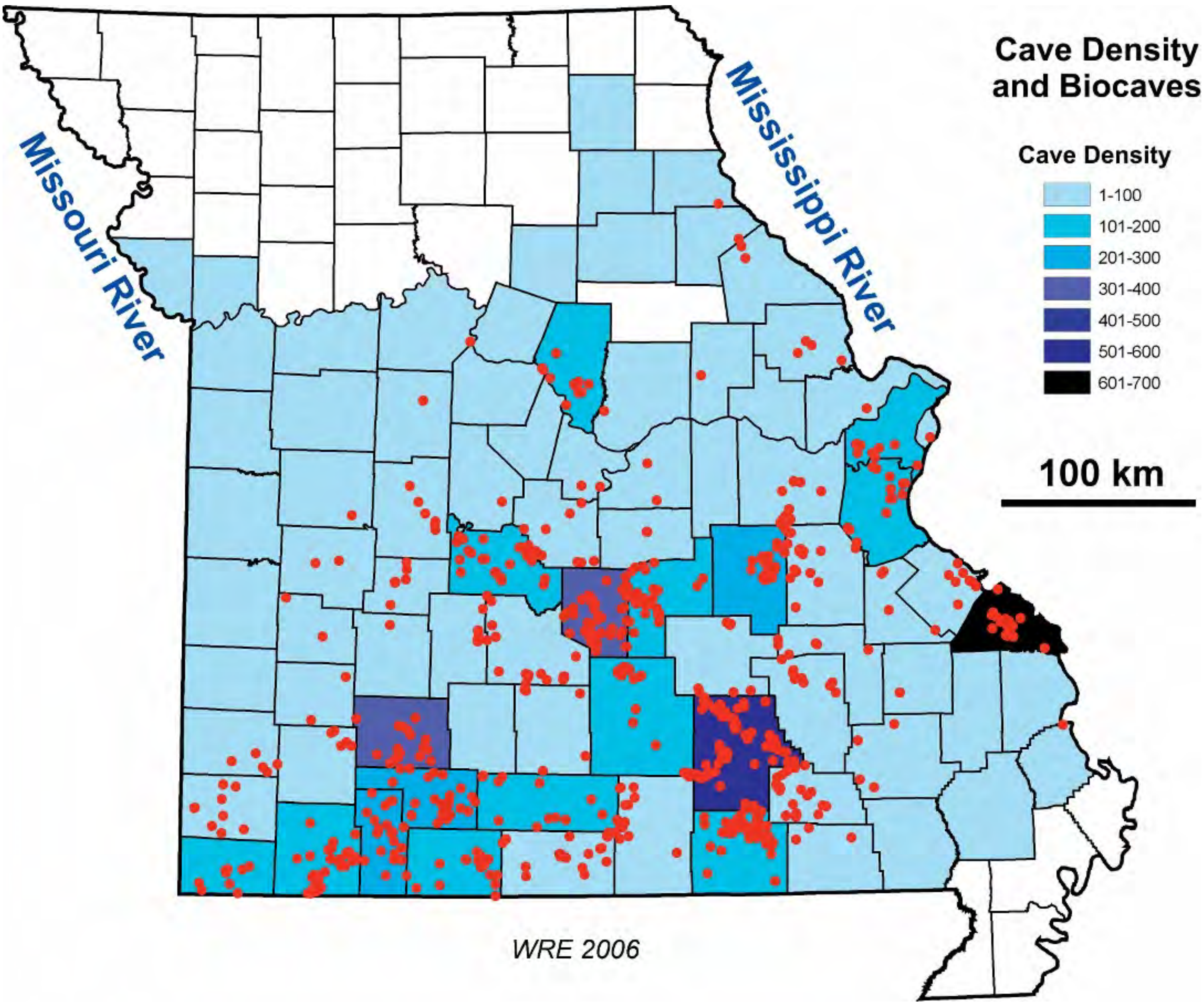

Figure 2. Cave density by county (about 6,000 caves) and biocaves (about 900).

dendropus (Fig. 6), a widespread troglobite. Hubricht published the first general paper on Ozark cave invertebrates in 1950. Hyman (1945, 1956) described the flatworms *Sphalloplana hubrichti* from Illinois and Missouri, and *Macrocotyla glandulosa* from Devil's Icebox Cave, Boone County. *Macrocotyla* was placed under the older genus name, *Kenkia* (Sluys and Kawakatsu, 2006). Kenneth Christiansen collected springtails in 42 Missouri caves between 1950 and 1986, and he provided many other identifications (Christiansen, 1964, 1966) (Table 1). Thomas C. Barr, Jr. studied seven caves in 1958 and 1965, and he described and identified numerous beetles. Causey (1960) provided a key to six species of millipedes, two of them troglobites.

In the last third of the 20th century cave research increased as more speleologists became active. John R. Holsinger made four collecting trips to Missouri between 1964 and 1988, visiting 30 caves and springs in search of amphipods and hydrobiid snails, at times with Rusty Norton and Robert Hershler (Holsinger, 1967, 1971, 1989). In 1999 the author worked in the field with Holsinger's Ph.D. student, Stefan Koenemann, and Ulrike Englisch in search of *Bactrurus* amphipods (Koenemann and Holsinger, 2001). These trips and papers provided a monograph on the systematics of *Stygobromus* (then *Stygonectes*); descriptions of *S. barri, S. ozarkensis, Allocrangonyx hubrichti* and *Bactrurus pseudomucronatus*; the new family Allocrangonyctidae; and new locality records for

Figure 3. ***Cambarus setosus,*** **Bristly cave crayfish, Turnback Cave, Lawrence County, Missouri.**

S. alabamensis, S. clantoni and *B. brachycaudus*. New species of Missouri *Stygobromus* will be described in the near future.

In 1966 Thomas J. Aley purchased Tumbling Creek Cave (Bear Cave), Taney County, and began the Ozark Underground Laboratory, which sponsored many scientific studies over the next 40 years (Aley and Thomson, 1971; Thomson and Aley, 1971; Hershler et al., 1990; Elliott et al., 2005; Elliott and Aley 2006). John L. Craig studied cave invertebrates, focusing on caves threatened by the proposed Meramec Park Lake in eastern Missouri (Craig, 1975, 1977). LaVal et al. (1977) completed an evaluation of bat caves in the proposed Meramec Park Lake and Union Lake project areas. Many important caves would have been inundated by the Meramec Lake. These studies, along with reports from caver Don Rimbach and others, influenced public opinion, and the projects died for several reasons, including imminent loss of scenic and recreational values.

Figure 4. ***Ambyopsis rosae*****, Ozark cavefish, Ben Lassiter Cave, McDonald County.**

Figure 5. ***Ceuthophilus gracilipes*****, a female camel cricket.**

Lewis (1974) extensively studied Mystery Cave, Perry County, one of the top three Missouri caves for biodiversity. Kenk (1975, 1977) described the flatworms *Macrocotyla* (now *Kenkia*) *lewisi* and *Sphalloplana evaginata* from Perry County; the latter was later found in Camden County by Slay et al. (2006). Peck and Lewis (1978) compared the richness of eastern Missouri caves to Illinois and other areas. Christiansen (1983) analyzed cave Collembola patterns across the eastern USA.

Since 1978 MDC's Richard Clawson contributed voluminous census data on bats from 103 caves and three mines in 38 counties, primarily of endangered Gray and Indiana bats (Table 1).

From 1978 to 1984, MDC's James E. (Gene) Gardner collected numerous invertebrate specimens from 436 caves and 10 springs, providing important baseline information on subterranean biodiversity and the core data in the CLD

Figure 6. ***Causeyella dendropus*** **(formerly** ***Scoterpes*****), Smallin Cave, Christian County.**

Table 1. Principal contributors to the Cave Life Database, starting with Gardner's 1986 study. Christiansen collected an unknown number of Collembola representing 28 species.

Collector	Observed	Collected	Sites	Counties
D. Ashley and students	5,200	1,200	57	17
K. Christiansen (Collembola)			42	24
R. Clawson (Chiroptera)	9,680,000		106	35
W. R. Elliott and assistants	1,525,000	1,800	130	36
J. E. Gardner	390,000	4,500	446	41
M. Sutton	483,000	>1,000	174	21
Exclusive totals	16,207,494	>12,500	960	63
Caves	647	615		
Counties	54	61		

(Gardner, 1985, 1986) (Table 1). Gardner worked with many agencies and landowners to study their cave life and provide management recommendations. He listed 414 invertebrate species, of which 52 species (13%) were considered troglobites (39 described, 13 undescribed). The numbers of other ecological types were uncertain because of limited ecological data, but were in the range of 90–130 troglophiles (25–31%), 135–167 trogloxenes (32–40%) and 142 accidentals (34%). No comprehensive list of Missouri's cave vertebrates has been published, but a computer printout with a large number of observations was contributed by Gardner to the CLD.

MDC's Natural History Division provided many observations to the Natural Heritage Database from 1985–2006, and these were imported into the CLD. Koppelman and Figg (1993) published a preliminary study on the genetics of cave crayfish. William Pflieger published important summaries of Missouri crayfishes (Pflieger, 1996) and fishes (Pflieger, 1997), including cave forms. Many other MDC staff participated in cave studies (see Acknowledgments).

Oesch and Oesch (1986) studied caves at Fort Leonard Wood, Pulaski County. Elliott and Clawson (2001) studied the temperatures of Indiana and Gray bat caves, including Fort Leonard Wood. Taylor and Slay (pers. comm.) conducted detailed cave invertebrate surveys at Fort Leonard Wood.

Michael J. Sutton studied at least 174 caves in 21 counties for the Cave Research Foundation, mostly in the Mark Twain National Forest and the Ozark National Scenic Riverways (Sutton, 1993, 1998, 1999). He also conducted a census study (2004) of the Pink Planarian, *Kenkia glandulosa,* in Devil's Icebox Cave, Boone County, a stygobite unique to that cave. The species is threatened by water pollution, and it appears to have variable population size. Sutton contributed many invertebrate identifications and observations (Table 1). In 2005 and 2006, Sutton and Sue Hagan (*pers. comm.*) discovered an undescribed species of trechine beetle, *Pseudanophthalmus,* about 5 mm long, in Branson Cave and Round Spring Cavern, Shannon County. Thomas C. Barr, Jr. is studying this species, which would be the third species of troglobitic beetle in Missouri.

David C. Ashley studied at least 57 caves in 17 counties with his students from Missouri Western State University and others since 1993 (Ashley, 1993, 1996, 2003). The studies included bioinventory, community ecology, and many cavesnail censuses of the endangered *Antrobia culveri* in Tumbling Creek Cave, Taney County (Table 1). Ashley and Elliott (2000) provided an overview of Missouri cave life.

Lewis (2002, 2004) described *Chaetaspis aleyorum*, a polydesmoid millipede, and *Brackenridgia ashleyi,* a trichoniscid isopod, from Tumbling Creek Cave. Shear (2003) redescribed *Scoterpes dendropus*, placing it in the new genus *Causeyella*, which contains two other species in Arkansas.

Population estimates of the endangered *Antrobia culveri,* Tumbling Creek Cavesnail (Fig. 7), by Ashley and Paul McKenzie, United States Fish and Wildlife Service (USFWS), have documented their decline since 1996 (Ashley 2003, U.S. Department of the Interior 2001, 2003). The Tumbling Creek Cavesnail Working Group was founded by Paul McKenzie to bring together experts from the region.

Elliott (2000a, 2000b, 2001, 2003a, 2003b, 2004, 2005, 2006b) joined MDC in 1998, and he worked with eight research partners and others to study Missouri's cave life (see Acknowledgments). He collected about 1,800 invertebrate specimens in 130 caves, springs, wells and mines in 36 Missouri counties, and he observed an aggregate of 860,000 animals (1,525,000 with assistants). In 1999 his team discovered a new species of cave crayfish, *Orconectes stygocaneyi* (Fig. 8), from Caney Mountain Conservation Area, a significant addition to our understanding of cave crayfish systematics and zoogeography (Hobbs, 2001). Elliott and Ireland (2002) led a year-long study of 40 caves, involving members of the Missouri Caves and Karst Conservancy. Elliott and Ashley (2005) characterized Missouri cave and karst communities. MDC

Figure 7. ***Antrobia culveri*, Tumbling Creek cavesnail, Taney County.**

Figure 8. ***Orconectes stygocaneyi*, Caney Mountain cave crayfish, Ozark County.**

cave biology interns, Michael E. Slay, Stephen T. Samoray, Sara Gardner, and resident cave ecologist, James E. Kaufmann, contributed 860 invertebrate specimens and counted a total of 1,050,000 bats, mostly using near-infrared video (Elliott et al., 2006); they also counted about 260 other vertebrates. Slay et al. (2006) and Graening et al. (2006) provided new data on planarians and *Cambarus setosus* in the Ozarks.

MATERIALS AND METHODS

DATABASE DESIGN

In 1998 the author began work on the CLD for MDC using a species database that he had previously designed in Texas. Significant amounts of data were added with the help of research partners and assistants since 1999 (Table 1). Additional research partners recently joined the project. The design is frequently upgraded, and the author is interested in collaborating with other states that may want to expand the database to their areas.

A large database of cave life images also was developed, some of which is posted on the *Biospeleology* web site (Elliott, 2007). The image database consists of hundreds of scanned and digital photographs, mostly in jpeg format, maintained in the ACDSee® program by ACD Systems, Inc. A description field holds pertinent data about each image, including the cave, county, state, subject, photographer, date and keywords. Images may be found by searching folders, file names, or words in the description field. This program has a self-maintaining database function. Many of these photos are available for scientific and educational use.

The CLD was developed using Microsoft Access®, a Windows® application. The CLD is a relational database with three central relations: the tables Species and Localities, and a query object, Unique Cave Names, which is based on the Localities table. This query could be replaced in the future by a table of official cave names derived from the Missouri Speleological Survey; however, the query functions well in tracking known county/cave name combinations, new cave names that are not yet registered with the Missouri Speleological Survey (MSS), and 279 noncaves, such as wells, mines, smaller springs, and some epigean (surface) sites.

A relational database is a software system that ties together related data through certain key fields held in common, such as county and cave name, species number, cave accession number and so on. This type of database is used for everything from parts inventories to biological data. Space does not allow a complete description of all the many fields and objects in the CLD, but such is available from the author on request.

The Species table, with 31 fields, contains extensive taxonomic and ecological information about each species, including published remarks of various authors. Notations can be added. The conservation status of the species in the *Missouri Species and Communities of Conservation Concern* (Missouri Department of Conservation, 2005) checklist is noted in the Status field, including whether it is a threatened or endangered species on the Missouri or Federal lists. The Status field matches information in NatureServe's national Natural Heritage Database, and proposed data can be recorded there for species that are not yet in the Heritage system. If a species is revised taxonomically, those changes are made one time in the appropriate fields. Each species is assigned a unique Spnum (species number), which is used to relate it to the Localities table in a one-to-many relationship. Thus, basic taxonomic information does not

Table 2. Ecological types of cave-dwelling species, described and undescribed. Included as troglobites are 36 stygobites, 13 phreatobites and 6 possible troglophiles, edaphobites or neotroglobites. Included in the troglophile category are 35 possible trogloxenes and 3 possible stygoxenes.

Ecological Type	Terrestrial	Aquatic	Total
troglobites	33	49	82
troglophiles	198	17	215
trogloxenes	203	20	223
accidentals	380	27	407
Totals	814	113	927

have to be repeated for each new locality record. Another field, ITIS, contains the Integrated Taxonomic Information System's Taxonomic Serial Number (TSN), if such has been assigned (U.S. Department of Agriculture 2006). Currently 979 species are in the Species table, 51 of which are placeholders for generic identifications, such as unsorted collection or *Stygobromus sp.* About 927 species are known from Missouri caves, 82 of which are troglobites (Table 2), and 57 Spnums were added for cooperative work with Arkansas. The author, as data manager, maintains the CLD with data from colleagues and the literature. A new version is issued on compact disc to the partners once a year.

The Localities table, with 59 fields, contains data on observations and collections. Each partner enters new data through data entry forms, viewing either one species or one cave at a time. One can find a species and its Spnum in several ways, then enter its Spnum for a new record within a cave, in which case the county and cave name are automatically inserted in the record. If one uses a species form, one can fill in the county and cave name, then the Spnum for that species is automatically inserted, thereby insuring that the proper relation is maintained. New data records are automatically tagged so that the data manager can separate them from old data when the users send in their data. The user can input the date, number observed, number collected, temperatures, names of observers, field notes and other fields, which allow one to record if an identification is tentative, specimen and vial numbers, taxonomist, date collections were sent to a taxonomist, museum catalog number, identification date, and other data. This provides a complete tracking system for field collections until they are indentified and curated. A special query allows the printing of small specimen labels. Literature records may be entered and the references included.

Another table, Cave Trips, is related to Unique Cave Names, and is used for trip reports and preliminary data. These can be used for inputting a preliminary report, from which a user can then copy data into the main tables via forms on the same screen.

Many queries were created for special purposes, and they can be copied to spreadsheets or a geographic information system (GIS) for analysis and reformatting. The queries can select fewer fields or composite multiple species records into presence/absence form. Trends in bat colony size can be graphed from such queries. Report forms can be printed for a particular cave, area or taxon, or sent to a word processor for editing. The design allows expansion of the database to other states or countries.

The CLD does not include precise cave location data, but only the county, cave name and cave accession number. Ongoing collaboration with the MSS and the Missouri Caves & Karst Conservancy (MCKC) enables the CLD to be temporarily related to a state cave database, for zoogeographic analysis and cave management. Such data tables are used only in a secure GIS. Potential uses would be creating species range maps and mapping biodiversity and conservation problems. Such products are important for environmental review of construction projects that may threaten cave resources and ground water. In Missouri these tools were used for mapping Cave Focus Areas for long-term wildlife conservation planning (Elliott, 2006). The end products were maps at scales that do not reveal precise cave locations. Many caves are degraded by individuals who have discovered cave locations on their own, but it is not necessary to worsen the problem by publicizing precise cave locations.

BIODIVERSITY COMPUTATIONS

For biodiversity computations in this paper, I include stygobites (aquatic troglobites) and phreatobites under the general term troglobite or troglobiont, which some authors now reserve for terrestrial troglobites. In Elliott (2003a) and this paper, I consider a phreatobite an inhabitant of ground water, exhibiting troglomorphy, but not necessarily limited to karst systems. Many authors may prefer the term stygobite or stygobiont for all subterranean, aquatic, troglomorphic species, and avoid the term phreatobite.

Limited funding for cave conservation work requires that we prioritize caves. One goal was to identify caves rich in species and high in endemism for long-range, statewide, wildlife conservation planning (Elliott, 2003b, 2006). Generally, Missouri caves with rare, endemic species also have many other species, but that is not always the case. Troglobites generally are the most endemic cave dwellers, whereas troglophiles often have large ranges, therefore the focus was on troglobites and species richness.

For MDC's Missouri Comprehensive Wildlife Conservation Strategy project in 2004, important bat caves and large karst springs also were taken into account because they represent important components in the karst ecosystem (Elliott, 2006).

There are various methods for measuring biodiversity. The author developed a cave biodiversity index for individual caves based on three elements that could be computed with queries in the CLD: *SR* (species rich-

Table 3. Troglobites and phreatobites in Missouri (82 total, 15 undescribed in bold). A = aquatic, T = terrestrial. Endemism is the inverse of the number of sites.

Sciname	Author	Year	Common Name	Eco Type	Habitat	Sites	Endemism
Allocrangonyx hubrichti	Holsinger	1971	Hubricht's long-tailed amphipod	PB	A	8	0.13
Amblyopsis rosae	(Eigenmann)	1897	Ozark cavefish	TB	A	44	0.02
Amnicola stygia	Hubricht	1971	Stygian cavesnail	TB	A	2	0.50
Antrobia culveri	Hubricht	1971	Tumbling Creek cavesnail	TB	A	1	1.00
Apochthonius colecampi	Muchmore	1967	Colecamp pseudoscorpion	TP or TB	T	3	0.33
Apochthonius mysterius	Muchmore	1976	Mystery Cave pseudoscorpion	TB	T	1	1.00
Apochthonius typhlus	Muchmore	1967	Stone County cave pseudoscorpion	TB	T	2	0.50
Arrhopalites clarus	Christiansen	1966	Clarus cave springtail	TB	T	8	0.13
Bactrurus brachycaudus	Hubricht and Mackin	1940	Short-tailed ground-water amphipod	PB	A	88	0.01
Bactrurus hubrichti	Shoemaker	1945	Sword-tailed amphipod	TB	A	1	1.00
Bactrurus pseudomucronatus	Koenemann and Holsinger	2001	False sword-tailed cave amphipod	PB	A	23	0.04
Brackenridgia ashleyi	Lewis		trichoniscid isopod	TB	T	7	0.14
Caecidotea ancyla	(Fleming)	1972	Ancyla cave isopod	TB	A	11	0.09
Caecidotea antricola	Creaser	1931	Antricola cave isopod	TB	A	106	0.01
Caecidotea beattyi	Lewis and Bowman	1981	Beatty's cave isopod	TB	A	2	0.50
Caecidotea dimorpha	Mackin and Hubricht	1940	Dimorphic ground water isopod	PB	A	2	0.50
Caecidotea extensolinguala	Fleming	1972	St. Francois ground water isopod	PB	A	1	1.00
Caecidotea fustis	Lewis	1981	Fustis cave isopod	TB	A	16	0.06
Caecidotea kendeighi	Steeves and Seidenberg	1971	Kendeigh's ground water isopod	PB	A	1	1.00
Caecidotea n. sp.			Devil's Icebox Cave isopod	TB	A	1	1.00
Caecidotea packardi	Mackin and Hubricht	1940	Packard's cave isopod	TB	A	1	1.00
Caecidotea salemensis	Lewis	1981	Salem cave isopod	TB	A	31	0.03
Caecidotea serrata	(Fleming)	1972	Serrated cave isopod	TB	A	2	0.50
Caecidotea steevesi	(Fleming)	1972	Steeves' cave isopod	TB	A	1	1.00
Caecidotea stiladactyla	(Mackin and Hubricht)	1940	Slender-fingered cave isopod	TB	A	4	0.25
Caecidotea stygia	Packard	1871	Stygian cave isopod	TB	A	7	0.14
Cambarus aculabrum	Hobbs & Brown	1987	cave crayfish	TB	A	1	1.00
Cambarus hubrichti	Hobbs	1952	Salem cave crayfish	TB	A	23	0.04
Cambarus setosus	Faxon	1889	Bristly cave crayfish	TB	A	44	0.02
Causeyella dendropus	(Loomis)	1939	Causeyella cave millipede	TB	T	14	0.07
Chaetaspis aleyorum	Lewis	2002	Aleys' cave millipede	TB	T	3	0.33
Cottus sp. 8			Grotto sculpin	TB	A	8	0.13
Crangonyx packardi	Smith	1888	Packard's ground water amphipod	PB	A	5	0.20

Table 3. Continued.

Sciname	Author	Year	Common Name	Eco Type	Habitat	Sites	Endemism
Diacyclops clandestinus	Yeatman		Copepod	PB	A	1	1.00
Eumesocampa n. sp.			cave dipluran	TB	T	6	0.17
Eurycea spelaea	(Stejneger)	1892	Grotto salamander	TB	A	200	0.01
Fontigens antroecetes	(Hubricht)	1940	Enigmatic cavesnail	TB	A	8	0.13
Fontigens proserpina	(Hubricht)	1940	Proserpine cavesnail	TB	A	5	0.20
Haplocampa or Litocampa n. sp. 1			cave dipluran	TB	T	5	0.20
Haplocampa or Litocampa n. sp. 2			cave dipluran	TB	T	1	1.00
Haplocampa or Litocampa n. sp. 3			cave dipluran	TB	T	1	1.00
Islandiana speophila	Ivie		cave spider	TB	T	2	0.50
Kenkia glandulosa	(Hyman)	1956	Pink planarian	TB	A	1	1.00
Kenkia lewisi	Kenk	1975	Lewis' cave planarian	TB	A	3	0.33
Mundochthonius cavernicolus	Muchmore	1968	cave pseudoscorpion	TB	T	1	1.00
Mundochthonius n.sp. near cavernicolus			cave pseudoscorpion	TB	T	1	1.00
Oncopodura hoffi	Christiansen & Bellinger	1980	Hoff's cave springtail	TB	T	2	0.50
Oncopodura iowae	Christiansen	1961	Springtail	TP or TB	T	4	0.25
Onychiurus n. sp. nr. paro			cave springtail	TB or TP?	T	1	1.00
Onychiurus n.sp., nr. pseudofimetarius			cave springtail	TB or TP?	T	5	0.20
Onychiurus obesus	Mills	1934	Obese springtail	TP or TB	T	1	1.00
Orconectes stygocaneyi	Hobbs	2001	Caney Mountain cave crayfish	TB	A	1	1.00
Phanetta subterranea	(Emerton)	1875	cave spider	TB	T	3	0.33
Porrhomma cavernicola	(Keyserling)	1886	cave spider	TB	T	10	0.10
Pseudanophthalmus n. sp.	Barr (in ms)		blind trechine beetle	TB	T	2	0.50
Pseudosinella espana	Christiansen	1961	Espana cave springtail	TB	T	5	0.20
Pseudosinella sp. 1, argentea group			cave springtail	TB	T	8	0.13
Sinella avita	Christiansen	1960	Avita cave springtail	TB	T	3	0.33
Sinella barri	Christiansen	1960	Barr's cave springtail	TB	T	3	0.33
Sinella cavernarum	(Packard)		Cavern springtail	TP or TB	T	5	0.20
Spelobia tenebrarum	(Aldrich)	1897	Cave dung fly	TB	T	90	0.01
Sphalloplana evaginata	Kenk	1977	Perryville cave planarian	TB	A	4	0.25
Sphalloplana hubrichti	(Hyman)	1945	Hubricht's cave planarian	TB	A	3	0.33
Stygobromus n. sp. a	Holsinger (in ms)		cave amphipod	TB	A	1	1.00

Table 3. Continued.

Sciname	Author	Year	Common Name	Eco Type	Habitat	Sites	Endemism
Stygobromus alabamensis alabamensis	(Stout)	1911	Alabama cave amphipod	PB	A	23	0.04
Stygobromus barri	(Holsinger)	1967	Barr's ground-water amphipod	PB	A	3	0.33
Stygobromus clantoni	(Creaser)	1934	Clanton's ground-water amphipod	PB	A	2	0.50
Stygobromus n. sp. g	Holsinger (in ms)		Gardner's cave amphipod	TB	A	27	0.04
Stygobromus heteropodus	(Hubricht)	1943	Pickle Springs amphipod	PB	A	1	1.00
Stygobromus n. sp. 2, onon. gp.			cave amphipod, to be revised	TB	A	1	1.00
Stygobromus n. sp. 3, onon. gp.			cave amphipod, to be revised	TB	A	1	1.00
Stygobromus onondagaensis	(Hubricht and Mackin)	1940	Onondaga Cave amphipod	TB	A	38	0.03
Stygobromus ozarkensis	(Holsinger)	1967	Ozark cave amphipod	TB	A	10	0.10
Stygobromus subtilis	(Hubricht)	1943	Subtle ground-water amphipod	PB	A	1	1.00
Tingupa pallida	Loomis	1939	Tingupa cave millipede	TB	T	72	0.01
Tomocerus missus	Mills	1949	Missus cave springtail	TB	T	6	0.17
Typhlichthys subterraneus	Girard	1859	Southern cavefish	TB	A	29	0.03
Uncinocythere pholetera	(Hart and Hobbs)	1961	cave ostracod	TB	A	1	1.00
Uncinocythere xania	(Hart and Hobbs)	1961	cave ostracod	TB	A	1	1.00
Xenotrechus condei	Barr and Krekeler	1967	Northern Xenotrechus cave beetle	TB	T	2	0.50
Xenotrechus denticollis	Barr and Krekeler	1967	Southern Xenotrechus cave beetle	TB	T	2	0.50
Zosteractis interminata	Loomis	1943	Zosteractis cave millipede	TB	T	5	0.20

Table 4. Species checklist for Tumbling Creek Cave, Taney County, Missouri.

Rank	Species	Common Name	Type	Status
1	*Agkistrodon contortrix*	Copperhead	AC	
2	*Antrobia culveri*	Tumbling Creek cavesnail	TB	S1 G1G2
3	*Arctoseius cetratus*	Long-leg small shiny longsnout mite	AC	
4	*Arrhopalites clarus*	Clarus cave springtail	TB	S3 G4
5	*Arrhopalites pygmaeus*	springtail	TP	
6	*Arrhopalites whitesidei*	springtail	TP	
7	*Atheta troglophila*	rove beetle	TP	
8	*Bakerdania sp.*	hairy mite	AC	
9	*Banksinoma sp.*	slender knobby-legged oribatid mite 2	AC	
10	*Bembidion sp.*	small black ground beetle	TP	
11	*Brackenridgia ashleyi*	Ashley's isopod	TB	S2 G2
12	*Bradysia sp.*	dark-winged fungus gnat	TP	
13	*Caecidotea ancyla*	Ancyla cave isopod	TB	S1 G1G3?
14	*Caecidotea antricola*	Antricola cave isopod	TB	S4 G5
15	*Calvolia sp.*	mite	AC	
16	*Carpelimus sp.*	rove beetle		
17	*Castor canadensis*	Beaver	TX	
18	*Causeyella dendropus*	Causeyella cave millipede	TB	SU GNR
19	*Ceratozetes sp.*	winged oribatid mite	AC	
20	*Ceuthophilus seclusus*	Secluded camel cricket	TX	
21	*Ceuthophilus silvestris*	Forest camel cricket	TX	
22	*Ceuthophilus uhleri*	Uhler's camel cricket	TX	
23	*Chaetaspis aleyorum*	Aleys' cave millipede	TB	S1 GNR
24	*Cicurina cavealis*	Cicurina spider	TP	
25	*Crosbyella sp.*	harvestman	TP or TB?	
26	*Cottus bairdi*	Mottled sculpin	TX	
27	*Dendrolaelaps near latior*	short-leg small shiny longsnout mite	AC	
28	*Eptesicus fuscus*	Big brown bat	TX	
29	*Ereynetes sp.*	small velvet mite	AC	
30	*Eurycea longicauda*	Dark-sided salamander	TP	
31	*Eurycea lucifuga*	Cave salamander	TP	
32	*Eurycea spelaea*	Grotto salamander	TB	S2S3 G4
33	*Ferrissia fragilis*	limpet	TX	
34	*Folsomia candida*	springtail	TP	
35	*Hesperochernes occidentalis*	guano pseudoscorpion	TP	S3 G4G5
36	*Histiosoma sp.*	small lumpy mite	AC	
37	*Hoploscirus sp.*	longsnout velvet mite	AC	
38	*Hydra sp.*	freshwater hydra		
39	*Hypena humili*	quadrifid moth		
40	*Hypoaspis sp.*	large shiny longsnout mite	AC	
41	*Iphidozercon reticaelatus*	small squat mite	AC	
42	*Islandiana sp.*	cave spider	TP or TB?	
43	*Ixodes sp.*	tick		
44	*Lasiurus borealis*	Eastern red bat	TX	
45	*Lasiurus cinereus*	Hoary bat	TX	
46	*Leptocera sp.*	small dung fly		
47	*Leptocera tenebrarum*	dung fly	TP?	
48	*Limonius flavomarginatus*	click beetle	TP	
49	*Lirceus sp.*	Lirceus isopod	TP or TX?	
50	*Macrocera nobilis*	webworm, fungus gnat	TP	
51	*Macrocheles penicilliger*	brown shiny mite	AC	
52	*Macronyssus jonesi*	black squat or hairy shiny bat mite	AC	

Table 4. Continued.

Rank	Species	Common Name	Type	Status
53	*Monunguis near streblida*	large velvet mite	AC	
54	*Multioppiea sp.*	slender knobby-legged oribatid mite 1	AC	
55	*Myotis grisescens*	Gray bat	TX	S3 G3 SE FE
56	*Myotis lucifugus*	Little brown bat	TX	
57	*Myotis septentrionalis*	Northern long-eared bat	TX	S3 G4
58	*Myotis sodalis*	Indiana bat	TX	S1 G2 SE FE
59	*Neobisnius sp.*	rove beetle	AC	
60	*Onychiurus sp.*	springtail	TP	
61	*Orconectes neglectus neglectus*	Ringed crayfish	TX	
62	*Palaeacarus sp.*	black-hair oribatid mite	AC	
63	*Physa gyrina*	physid snail	TP?	
64	*Pipistrellus subflavus*	Eastern pipistrelle	TX	
65	*Platynus tenuicollis*	large black ground beetle	TP	
66	*Plesiodamalus sp.*	hairy knobby-legged oribatid mite	AC	
67	*Plusiocampa sp.*	cave dipluran		
68	*Poecilochirus necrophori*	Split-back shiny mite		
69	*Poecilophysis weyerensis*	rhagidiid mite	TP	
70	*Polyaspis sp.*	large squat mite	AC	
71	*Proctolaelaps hypudaei*	pale shiny mite	AC	
72	*Pseudopolydesmus pinetorum*	polydesmid millipede	TP	
73	*Pseudosinella argentea*	springtail	TP	
74	*Pseudozaona sp.*	pseudoscorpion		
75	*Psyllipsocus ramburii*	book louse	TP	
76	*Ptomaphagus cavernicola*	cave leiodid beetle	TP	
77	*Rana palustris*	Pickerel frog	TX	
78	*Rhizoglyphus sp.*	large oval mite	AC	
79	*Sancassania? sp.*	tiny oval mite	AC	
80	*Semotilus atromaculatus*	Creek chub	AC	
81	*Spelobia tenebrarum*	Cave dung fly	TB	
82	*Stigmaeus sp.*	hairy medium oval mite	AC	
83	*Stygobromus onondagaensis*	Onondaga Cave amphipod	TB	S3? G5
84	*Stygobromus ozarkensis*	Ozark cave amphipod	TB	S3? G4
85	*Trichocera sp.*	winter crane fly	TX	
86	*Trombidium sp.*	thin-legged chigger mite	AC	
87	*Tyrophagus sp.*	side-dot mite	AC	
88	*Undetermined sp.*	generic amphipod, crangonyctid		
89	*Undetermined sp.*	generic ant, black	AC	
90	*Undetermined sp.*	generic ant, red	AC	
91	*Undetermined sp.*	generic beetle, antlike flower	AC	
92	*Undetermined sp.*	generic beetle, click	AC	
93	*Undetermined sp.*	generic beetle, darkling	AC	
94	*Undetermined sp.*	generic beetle, dermestid larva	AC	
95	*Undetermined sp.*	generic beetle, ground	TP, TX or	
96	*Undetermined sp.*	generic beetle, rove	TP?	
97	*Undetermined sp.*	generic beetle, wrinkled bark	AC	
98	*Undetermined sp.*	generic bug, bed	PR	
99	*Undetermined sp.*	generic bug, jumping ground		
100	*Undetermined sp.*	generic bug, true		
101	*Undetermined sp.*	generic centipede	TX	
102	*Undetermined sp.*	generic crayfish		
103	*Undetermined sp.*	generic dipluran	ED	
104	*Undetermined sp.*	generic fluke, Mongenea	PR	
105	*Undetermined sp.*	generic fly, moth	TX	

Table 4. Continued.

Rank	Species	Common Name	Type	Status
106	*Undetermined sp.*	generic gnat, fungus	TX or TP?	
107	*Undetermined sp.*	generic leafhopper	AC	
108	*Undetermined sp.*	generic midge 446	TX	
109	*Undetermined sp.*	generic millipede		
110	*Undetermined sp.*	generic mite, large velvet	AC	
111	*Undetermined sp.*	generic mite, spinturnicid star	PR	
112	*Undetermined sp.*	generic pseudoscorpion, small, white		
113	*Undetermined sp.*	generic spider, pale		
114	*Undetermined sp.*	generic springtail, huge pigmented	AC?	
115	*Wespus sp.*	harvestman	AC	

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ness or number of all species in the cave), *T* (number of troglobites, stygobites and phreatobites), and *SE* (site endemism, which is the aggregate of troglobite endemism at the site). Lacking troglobite population estimates in most cases, a simple metric was found for comparing how endemic a species is within Missouri, as follows.

$$SE = \sum e \tag{1}$$

where *e* (endemism) represents the reciprocal of the number of known Missouri sites. For example, the Grotto salamander, *Eurycea spelaea*, has 200 known sites in Missouri, so

$$e = \frac{1}{200} = 0.005 \tag{2}$$

The total number of sites for *E. spelaea*, which ranges through four states in the Ozark region, is not currently published, however, for such a species the endemism value becomes so small as to be relatively unimportant in calculating a cave's *SE*. One could also use the *S* or *G* values from the Natural Heritage Database, but these values are not as up-to-date and do not take into account the many undescribed species that are known to cave biologists.

In contrast, the Tumbling Creek cavesnail, *Antrobia culveri*, is an endangered species known from one cave, so

$$e = \frac{1}{1} = 1 \tag{3}$$

Tumbling Creek Cave has an *SE* value of 2.92, representing the aggregate endemism of 12 species of troglobites, at least two of which are unique to that cave. So, the more endemic a cave's fauna is, the higher the *SE* value.

To represent all three factors in one score for each cave, they were multiplied to obtain a Biodiversity Index *B*

$$B = SR \times T \times SE \tag{4}$$

which is used for ranking caves for biodiversity. *B* is dimensionless, and minor differences between caves probably are not significant. *B* simply is a way of digesting complex information into one index for broad comparisons. *SE* scores also were computed for certain counties and karst zoogeographic regions, which one could call area endemism, to examine the suite of troglobites within broader areas.

One also could add *SR, T* and *SE* to create a biodiversity index, however, they do not scale the same and *SR* usually would be overemphasized. One can transform *SE* by multiplying it by 10 or 100 to obtain a value in the same order of magnitude as *SR* and *T*. However, the ranks for the top three caves would be the same as multiplying the three factors, although some low scoring caves would rank differently. Multiplication of the factors provides a fairly balanced emphasis of *SR, T*, and *SE*.

The relations of *SR, T*, and *SE* were examined with linear regressions and one-way ANOVA. All regressions were highly significant ($p < 0.001$), indicating that *SE* is highly dependent on high *SR* and *T*. However some interesting outliers resulted, which did not conform well to general trends. Some caves with high *SR* and *T* have much higher *SE* than the general trend would predict; examples are Devil's Icebox Cave, Boone County; Mystery Cave and Berome Moore Cave, Perry County; River Cave, Camden; Kohm's Cave, Ste. Genevieve County; and Branson Cave, Shannon County. Three of these caves are in eastern Missouri, where there is high cave

Table 5. Species checklist for Devil's Icebox Cave, Boone County, Missouri.

Rank	Species	Common Name	Type	Status
1	*Agabus sp.*	predaceous diving beetle	TP	
2	*Agkistrodon contortrix*	Copperhead	AC	
3	*Ambystoma maculatum*	Spotted salamander	AC	
4	*Ambystoma texanum*	Smallmouth salamander	TX	
5	*Arrhopalites pygmaeus*	springtail	TP	
6	*Arrhopalites whitesidei*	springtail	TP	
7	*Bactrurus brachycaudus*	Short-tailed groundwater amphipod	PB	S4 G4
8	*Bembidion sp.*	small black ground beetle	TP	
9	*Brachinus americanus*	ground beetle	AC	
10	*Bufo americanus*	Eastern American toad	TX	
11	*Caecidotea brevicauda*	Short-tailed groundwater isopod	TP	
12	*Caecidotea sp.*	Caecidotea isopod, troglobite	TB	
13	*Cantharis? sp.*	soldier beetle	TX	
14	*Ceuthophilus seclusus*	Secluded camel cricket	TX	
15	*Ceuthophilus silvestris*	Forest camel cricket	TX	
16	*Chrysemys picta bellii*	Western painted turtle	AC	
17	*Crangonyx forbesi*	amphipod	TP	
18	*Crangonyx packardi*	Packard's groundwater amphipod	PB?	
19	*Crangonyx sp., forbesi group*	amphipod	TP	
20	*Dina microstoma*	leech	TP?	
21	*Dineutus sp.*	whirligig beetle	AC	
22	*Dugesia dorotocephala*	planarian	AC	
23	*Eptesicus fuscus*	Big brown bat	TX	
24	*Etheostoma spectabile*	Orange-throat darter	AC	
25	*Eurycea longicauda*	Dark-sided salamander	TP	
26	*Eurycea lucifuga*	Cave salamander	TP	
27	*Eurycea sp.*	Eurycea salamander	TP	
28	*Gammarus pseudolimnaeus*	amphipod	TX	
29	*Hyla versicolor*	Eastern gray treefrog	TX	
30	*Kenkia glandulosa*	Pink planarian	TB	S12G3
31	*Lampropeltis calligaster calligaster*	Prairie kingsnake	AC	
32	*Lepomis megalotis*	Longear sunfish	AC	
33	*Macrocera nobilis*	webworm, fungus gnat	TP	
34	*Mustela vison*	mink	TX	
35	*Myotis grisescens*	Gray bat	TX	S3 G3 SE FE
36	*Myotis lucifugus*	Little brown bat	TX	
37	*Myotis septentrionalis*	Northern long-eared bat	TX	S3 G4
38	*Myotis sodalis*	Indiana bat	TX	S1 G2 SE FE
39	*Oncopodura iowae*	springtail	TP or TB	
40	*Ondatra zibethicus*	Muskrat	AC	
41	*Onychiurus reluctus*	springtail	TP	
42	*Orconectes virilis*	Northern crayfish	TX	
43	*Physa sp.*	physid snail	TP	
44	*Pipistrellus subflavus*	Eastern pipistrelle	TX	
45	*Placobdella sp.*	leech	TX	
46	*Plethodon glutinosus*	Slimy salamander	TX	
47	*Porrhomma cavernicola*	cave spider	TB	S2 G5
48	*Procyon lotor*	Raccoon	TX	
49	*Pseudacris crucifer crucifer*	Northern spring peeper	TX	
50	*Pseudacris triseriata triseriata*	Western chorus frog	AC	
51	*Pseudopolydesmus sp.*	polydesmid millipede	TP	
52	*Pseudosinella argentea*	springtail	TP	
53	*Ptomaphagus cavernicola*	cave leiodid beetle	TP	

Table 5. Continued.

Rank	Species	Common Name	Type	Status
54	*Rana catesbiana*	Bullfrog	AC	
55	*Rana clamitans*	Green frog	TX	
56	*Rana palustris*	Pickerel frog	TX	
57	*Scalopus aquaticus*	Eastern mole	AC	
58	*Semotilus atromaculatus*	Creek chub	AC	
59	*Spelobia tenebrarum*	Cave dung fly	TB	
60	*Thamnophis sirtalis sirtalis*	Common garter snake	AC	
61	*Tingupa pallida*	Tingupa cave millipede	TB	S4 G4
62	*Tomocerus missus*	Missus cave springtail	TB	SU G4
63	*Undetermined sp.*	generic amphipod		
64	*Undetermined sp.*	generic beetle		
65	*Undetermined sp.*	generic beetle, darkling	AC	
66	*Undetermined sp.*	generic beetle, ground	TP, TX or	
67	*Undetermined sp.*	generic beetle, hister		
68	*Undetermined sp.*	generic beetle, predaceous diving	AC	
69	*Undetermined sp.*	generic beetle, rove	TP?	
70	*Undetermined sp.*	generic crane fly	TX	
71	*Undetermined sp.*	generic earthworm, lumbricid	ED	
72	*Undetermined sp.*	generic fly		
73	*Undetermined sp.*	generic fly, sciarid		
74	*Undetermined sp.*	generic mite		
75	*Undetermined sp.*	generic mite, oribatid	AC?	
76	*Undetermined sp.*	generic mite, rhagidiid		
77	*Undetermined sp.*	generic spider		
78	*Undetermined sp.*	generic spider, pale		
79	*Undetermined sp.*	generic springtail, entomobryid		
80	*Vonones sayi*	harvestman	AC	

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endemism, however, they have received extensive study by cave biologists, so they probably have higher values as a result. On the other hand, some prominent caves are deficient in *SE* despite having a high *SR*, such as Great Scott Cave, Washington County; Jagged Canyon Cave, Bear Cave and Onondaga Cave, Crawford County; and Great Spirit Cave, Pulaski County. Four of the five latter caves are in the Meramec River basin, but that may not be significant, and they probably have not received as much study as deserved.

RESULTS

HIGH BIODIVERSITY CAVES

Currently there are about 12,500 observation and collection records. About 1,038 (17%) of Missouri's approximately 6,200 caves and cave springs are biocaves (at least one species), but only 491 sites (8%) have five or more species recorded. The CLD has data on 279 other localities, such as springs, wells, mines and some surface sites.

Missouri has 82 troglobites (67 described, 15 undescribed), including 49 aquatic and 33 terrestrial species (Tables 2 and 3). The aquatics include 30 described and six undescribed stygobites, plus 13 described phreatobites. The terrestrials include 24 described and nine undescribed species. Six of the troglobites (four described) may be troglophiles, edaphobites or neotroglobites. There are about 215 troglophiles (17 aquatic), 203 trogloxenes (20 aquatic) and 407 species of uncertain ecological type (27 aquatic).

Species checklists are provided for three important biocaves: Tumbling Creek Cave, Taney County (Table 4); Devil's Icebox Cave, Boone County (Table 5); and Mystery Cave, Perry County (Table 6). Tumbling Creek Cave ranks first in Missouri for species richness (115 species), number of troglobites (12), and site endemism (2.9154), giving it an overall Biodiversity Value of 4,023.25

Table 6. Species Checklist for Mystery Cave, Perry County, Missouri.

Rank	Species	Common Name	Type	Status
1	*Agonum extensicolle*	ground beetle	AC	
2	*Ambystoma tigrinum tigrinum*	tiger salamander		
3	*Amoebaleria defessa*	heleomyzid fly	TX	
4	*Anisodactylus opaculus*	ground beetle	AC	
5	*Apochthonius mysterius*	Mystery Cave pseudoscorpion	TB	S1 G1G2
6	*Armadillidium vulgare*	pillbug isopod	TX	
7	*Arrhopalites clarus*	Clarus cave springtail	TB	S3 G4
8	*Arrhopalites pygmaeus*	springtail	TP	
9	*Atheta sp. 3*	rove beetle	TP	
10	*Atheta sp.*	rove beetle	TP	
11	*Atranus pubescens*	ground beetle	TP	
12	*Austrotyla specus*	conotylid millipede	TP	
13	*Bactrurus brachycaudus*	Short-tailed groundwater amphipod	PB	S4 G4
14	*Bembidion texanum*	ground beetle	TP	
15	*Bimastos tumidus*	earthworm	ED	
16	*Brachinus fumans*	ground beetle	AC	
17	*Caecidotea antricola*	Antricola cave isopod	TB	S4 G5
18	*Caecidotea brevicauda*	Short-tailed groundwater isopod	TP	
19	*Caecidotea n. sp.*	Caecidotea isopod	TB	
20	*Caloglyphus sp.*	acarid mite	TP?	
21	*Ceuthophilus elegans*	Elegant camel cricket	TX	
22	*Cottus sp. 8*	Grotto sculpin	TB	S2 G1Q
23	*Crangonyx forbesi*	amphipod	TP	
24	*Cunaxa sp.*	cunaxid mite	TP?	
25	*Dactylolabis montana*	crane fly	TP	
26	*Dina microstoma*	leech	TP?	
27	*Diplocardia sp.*	earthworm	ED	
28	*Eumesocampa n. sp.*	cave dipluran	TB	
29	*Fallicambarus fodiens*	digger crayfish	TX	
30	*Folsomia candida*	springtail	TP	
31	*Fontigens antroecetes*	Enigmatic cavesnail	TB	S2 G2G3
32	*Fontigens sp.*	cavesnail	TP	
33	*Galerita bicolor*	ground beetle	AC	
34	*Gammurus troglophilus*	amphipod	TP	
35	*Harpalus fulgens*	ground beetle	AC	
36	*Hawaiia miniscula*	zonitid snail	TX	
37	*Hypogastrura denticulata*	springtail	TP	
38	*Hypogastrura matura*	springtail	AC or TX?	
39	*Hypogastrura sp., denticulata complex*	springtail	TP	
40	*Isotoma notabilis*	springtail	TP	
41	*Isotoma sp.*	springtail	TP	
42	*Isotoma viridis*	springtail	TX	
43	*Kenkia lewisi*	Lewis' cave planarian	TB	S1 G1
44	*Lycoriella sp.*	sciarid fly	TX	
45	*Meta ovalis*	Cave orb weaver	TP	
46	*Neobisnius sp.*	rove beetle	AC	
47	*Oncopodura hoffi*	Hoff's cave springtail	TB	S1S3 G1G2
48	*Paratachys sp., corruscus*	ground beetle	AC	
49	*Pardosa sp.*	lycosid spider	TX	
50	*Patrobus longicornis*	ground beetle	TX?	
51	*Phagocata gracilis*	planarian	TP	
52	*Physa halei*	Hale's Physa snail	TP	
53	*Pseudosinella argentea*	springtail	TP	

Table 6. Continued.

Rank	Species	Common Name	Type	Status
54	*Pseudosinella sp. 1, argentea group*	cave springtail	TB	
55	*Rugilus dentatus*	rove beetle	AC	
56	*Stratiolaelaps sp.*	laelapid mite	TP?	
57	*Undetermined sp.*	generic beetle, ground	TP, TX or	
58	*Undetermined sp.*	generic mite, laelapid	TP?	
59	*Zonitoides arboreus*	snail	TP or TX?	

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(Table 7), but its ranking could change with further studies. Depending on biodiversity measures, Tumbling Creek Cave may have the highest biodiversity for a single cave west of the Mississippi River, rivaled by Tooth Cave and Stovepipe Cave, Travis County, Texas, and perhaps others (Elliott, 1997; Elliott and Aley, 2006). However, the entire Edwards Aquifer in Texas ranks higher in biodiversity (Longley, 1981).

KARST ZOOGEOGRAPHY

Although karst regions and cave faunal units were named by earlier authors, such areas were conceived differently by each. Peck and Lewis (1978), Dom (2002) and Nigh and Schroeder (2002) discussed karst regions, but karst zoogeographic regions in this paper are based on a combination of troglobite zoogeography, physiography, geology and karst type. These regions lack sharp boundaries because of wide-ranging troglobites.

Troglobites are currently known from 728 Missouri sites, including 597 caves (9% of known caves). Twenty-five troglobites, eight of which are new species, occur at single sites only. An interesting example is *Orconectes stygocaneyi* (Fig. 8), the Caney Mountain cave crayfish, known only from a small cave with a perched aquifer on a high hill, geologically and hydrologically isolated from the main Springfield and Salem plateaus. As the only stygobitic *Orconectes* west of the Mississippi, its nearest relative is *O. pellucidus* from Kentucky (Ashley and Elliott, 2000; Hobbs, 2001).

Some aquatic species are wide-ranging. The most ubiquitous troglobite is *Eurycea spelaea*, the Grotto salamander (Fig. 9), with 200 known sites in Missouri, many others in Arkansas and Oklahoma, and one in Kansas. The author considers the Grotto salamander as the trademark cave species of the Ozark Region. It is a neotroglobite that may have evolved from an ancestor ecologically similar to *Eurycea lucifuga* (Fig. 10), but within the *E. multiplicata* complex (Bonett and Chippindale, 2004). Other wide-ranging forms are the millipede *Tingupa pallida* and the amphipod *Stygobromus ozarkensis* (Fig. 11); the latter ranges across most of the Ozarks (mostly caves) into Kansas (wells), more as a phreatobite than a strict stygobite. The isopod *Caecidotea antricola* (Fig. 12) has an even larger range. The amphipod *Allocrangonyx hubrichti* was considered a rare stygobite, but Robison and Holsinger (2000) found it in an Arkansas well and Sarver and Lister (2004) found it in 16 epigean streams in 14 Missouri counties. Individuals from caves typically were larger than those from epigean sites, which usually were gravel substrates in pools.

Missouri shares 48 troglobites with other states (Table 8), has relatively low diversity in terrestrial troglobites compared to areas east of the Mississippi River, but has high aquatic biodiversity. There is nearly equal similarity to faunas east and west of the Mississippi River. Missouri ranks about seventh among the United States in troglobite richness (Table 9).

SPRINGFIELD PLATEAU

This broad karst and physiographic region (Fig. 1) comprises limestones of Mississipian age, but it has smaller springs than the Salem Plateau. The plateau stretches into northern Arkansas, northeastern Oklahoma and the southeastern corner of Kansas. Representative species are *Amblyopsis rosae*, the Ozark cavefish (44 sites, Fig. 4), and *Cambarus setosus*, the Bristly cave crayfish (44 sites, Fig. 3), which co-occur in 16 sites (22%). Subpopulations of these species are found in semi-isolated parts of the aquifer. The geologic influence on cavefish distributions was discussed by Noltie and Wicks (2001). There are 21 troglobites in this large area, with the second highest area endemism in Missouri. However, none of the top 10 biocaves are in this region. Turnback Cave, Lawrence County, is the most biodiverse, with 40 species, seven troglobites (including Ozark cavefish and Bristly cave crayfish), but relatively low *SE* (Table 7).

BOONE KARST

This karst is formed in Mississippian limestones, and it might be considered an extension of the Springfield Plateau, along the Missouri River in Boone and adjacent counties. This karst was not glaciated during the latest (Wisconsin) glacial, but it may have been glaciated during the Illinoian and earlier. The Boone Karst lacks cavefish

Table 7. The top 50 biocaves in Missouri ranked by overall Biodiversity Index (B).

Rank	Cave	County	*SR*	*T*	*SE*	*B*
1	Tumbling Creek Cave	Taney	115	12	2.9154	4,023.25
2	Devil's Icebox Cave	Boone	80	9	2.7530	1,982.18
3	Mystery Cave	Perry	59	11	2.6875	1,744.16
4	Berome Moore Cave	Perry	28	10	2.0205	565.75
5	River Cave	Camden	41	8	1.6800	551.05
6	Branson Cave	Shannon	54	7	1.1997	453.48
7	Kohms Cave	Ste. Genevieve	38	7	1.5208	404.53
8	Tom Moore Cave	Perry	33	7	1.1811	272.82
9	Jagged Canyon Cave	Crawford	64	7	0.4478	200.63
10	Great Scott Cave	Washington	55	6	0.4222	139.34
11	Bear Cave	Crawford	62	5	0.4125	127.88
12	Brawley Cave	Shannon	27	7	0.6110	115.47
13	Kelly Hollow Cave	Oregon	21	7	0.7829	115.09
14	Chimney Rock Cave	Barry	40	7	0.4079	114.22
15	Bounds Branch Cave	Shannon	23	4	1.0623	97.73
16	Turnback Cave	Lawrence	40	7	0.3318	92.90
17	Possum Trot Hollow Cave	Shannon	18	4	1.0513	75.69
18	Bat Cave	Crawford	42	4	0.4354	73.14
19	Round Spring Cavern	Shannon	25	5	0.5394	67.43
20	Panther Cave	Ripley	10	5	1.2585	62.93
21	Zorumski Cave	Phelps	30	2	1.0323	61.94
22	Creech Cave	Lincoln	27	2	1.0114	54.61
23	Hamilton Spring Cave	Washington	15	6	0.6016	54.14
24	Turner Spring Cave	Oregon	38	5	0.2628	49.93
25	Fisher Cave	Franklin	20	4	0.5817	46.54
26	Old Spanish Cave	Stone	11	5	0.7859	43.22
27	Upper Camp Yarn Cave	Carter	22	5	0.3728	41.00
28	Mushroom Cave	Franklin	25	4	0.4058	40.58
29	Smallin Cave	Christian	9	4	1.1086	39.91
30	Mushroom Rock Cave	Barry	16	4	0.6161	39.43
31	Lewis Cave	Ripley	8	4	1.0918	34.94
32	Camp Branch Cave	Washington	11	3	1.0357	34.18
33	Davis Cave	Shannon	27	5	0.2519	34.00
34	Powder Mill Creek Cave	Shannon	35	5	0.1842	32.24
35	Cooks Cave	Reynolds	27	2	0.5769	31.15
36	Running Bull Cave	Perry	8	5	0.7756	31.03
37	Great Spirit Cave	Pulaski	46	4	0.1657	30.50
38	Onondaga Cave	Crawford	52	5	0.1171	30.46
39	Mossy Spring Cave	Washington	28	5	0.1965	27.51
40	Pipe Spring Cave	Oregon	23	6	0.1907	26.32
41	Lone Hill Onyx Cave	Franklin	37	3	0.2250	24.98
42	Bat Cave	Shannon	19	5	0.2606	24.76
43	Woods Cave	St. Louis	23	4	0.2568	23.62
44	Martin Cave	Shannon	17	4	0.3394	23.08
45	Wood Cave	Christian	29	5	0.1554	22.53
46	Green Cave	Washington	27	3	0.2627	21.28
47	Mud Cave	Ozark	10	2	1.0435	20.87
48	Crevice Cave	Perry	12	4	0.3958	19.00
49	New Liberty Cave	Oregon	23	6	0.1199	16.55
50	Rice Cave	Jefferson	8	5	0.4024	16.09

SR = total number of species or species richness, T = number of troglobites and phreatobites, SE = site endemism value, $B = SR \times T \times SE$.

Figure 9. *Eurycea spelaea*, Grotto salamander, Tumbling Creek Cave, Taney County.

Figure 11. *Stygobromus ozarkensis*, Tumbling Creek Cave, Taney County, is a stygobite found in the Springfield Plateau of southwestern Missouri and adjacent parts of Arkansas and Oklahoma.

and cave crayfish and its cave fauna is different. Devil's Icebox Cave is a large cave with an extensive sinkhole plain feeding its stream, with two endemics, *Kenkia glandulosa*, the Pink Planarian, and a new, undescribed species of *Caecidotea* (Table 5). The system is nutrient-enriched from sinkhole ponds, suburban development and livestock, and it has a large Gray bat colony and abundant cave life. Other large caves, such as Hunter's Cave and Rocheport (Boone) Cave, have few troglobites and are largely fed by epigean waters (Lerch et al., 2000). The area has 10 troglobites and moderate endemism.

HANNIBAL KARST

This karst is formed in Mississippian rocks and some Devonian and Silurian rocks near Hannibal, Marion County. Somewhat isolated from the other karsts, it has two common troglobites, *Bactrurus brachycaudus* (Fig. 13) and *Tingupa pallida*, but it has received little study.

LINCOLN HILLS KARST

Formed in Mississippian rocks along the Lincoln Fold in Pike and Lincoln counties, this region has three troglobites and a moderate amount of endemism: *Bactrurus brachycaudus, Caecidotea packardi* and *Mundochthonius cavernicolus.*

SALEM PLATEAU

This broad area is mostly a dolomitic karst of Ordovician age, with Cambrian rocks ringing the central Ozark Dome, a structural, igneous feature known as the St.

Figure 10. *Eurycea lucifuga*, the troglophilic Cave salamander, Keyhole Cave, Shannon County.

Figure 12. *Caecidotea antricola*, a widespread phreatobite/stygobite, Cooks Cave, Reynolds County.

Table 8. Troglobites and phreatobites shared between Missouri and other states. Numbers shared with regions east and west of the Mississippi are for those regions as a whole.

State	Species
Arkansas	22
Iowa	4
Kansas	7
Oklahoma	14
West of Mississippi	31
West of Mississippi only	23
Illinois	22
Indiana	10
Kentucky	10
Tennessee	9
West Virginia	1
East of Mississippi	26
Widespread both sides	6
Missouri only	34
Total shared with Missouri	48

Francois Mountains. This plateau could be divided into many karst zoogeographic regions, particularly river basins such as the Meramec, Gasconade, Osage, Niangua, Current/Jacks Fork, Eleven Point and others. However, interbasin transfer of ground water is common, and there are very large recharge areas, therefore stygobites can cross from one basin to another. For example, the record-holding, long-distance dye trace in the USA ran for 64 km to Big Spring, Carter County (Aley, 2000).

High biodiversity is found in some caves such as Tumbling Creek Cave, Taney County, and Branson Cave, Shannon County. A cavefish/crayfish pair co-occurs in nine (21%) of 52 caves: *Typhlichthys subterraneus*, Southern cavefish (29 sites), and *Cambarus hubrichti*, Salem cave crayfish (23 sites). These two stygobites are absent from some stream caves, even though they may occur in springs nearby (e.g., Powder Mill Creek Cave, Shannon County). A new species of troglobitic carabid beetle, Tribe Trechini, was recently found in two caves near the Current River, the first *Pseudanophthalmus* west of the Mississippi River and a link to eastern faunas (Michael J. Sutton and Tom Barr, Jr., pers. comm.). The three karst regions below can be considered eastern subdivisions of the main Salem Plateau, separated from it by the St. Francois Mountains.

Figure 13. *Bactrurus brachycaudus*, a phreatobite, Devil's Icebox Cave.

ST. LOUIS KARST

Nigh and Schroeder (2002) recognized the Florissant Karst and the St. Louis Karst, based on surface vegetation, soils and geology, but they are lumped together here, as there is no distinction in cave zoogeography. Woods Cave contains a widespread species that is rare in Missouri, *Caecidotea stygia.* Many of the caves have been obliterated by urbanization. Nevertheless, there are 11 troglobites and

Table 9. The top ten states in troglobite biodiversity (described species). Data from Hobbs, Culver and Elliott (2006) and the CLD. Missouri has a total of 82 troglobites (67 described, 15 undescribed), including 49 aquatic and 33 terrestrial species. The aquatics include 31 described and 6 undescribed stygobites, plus 13 described phreatobites. The terrestrials include 24 described and 9 undescribed species.

Rank	State	Stygobites	Phreatobites	Terrestrial Troglobites	Total
1	Texas	58	2	119	179
2	Tennessee	40	1	120	161
3	Alabama	23	2	120	145
4	Virginia	38	12	89	139
5	Kentucky	29	0	90	119
6	West Virginia	32	1	42	75
7	Missouri	31	13	24	68
8	Indiana	22	3	32	57
9	California	8	7	42	57
10	Georgia	16	0	24	40

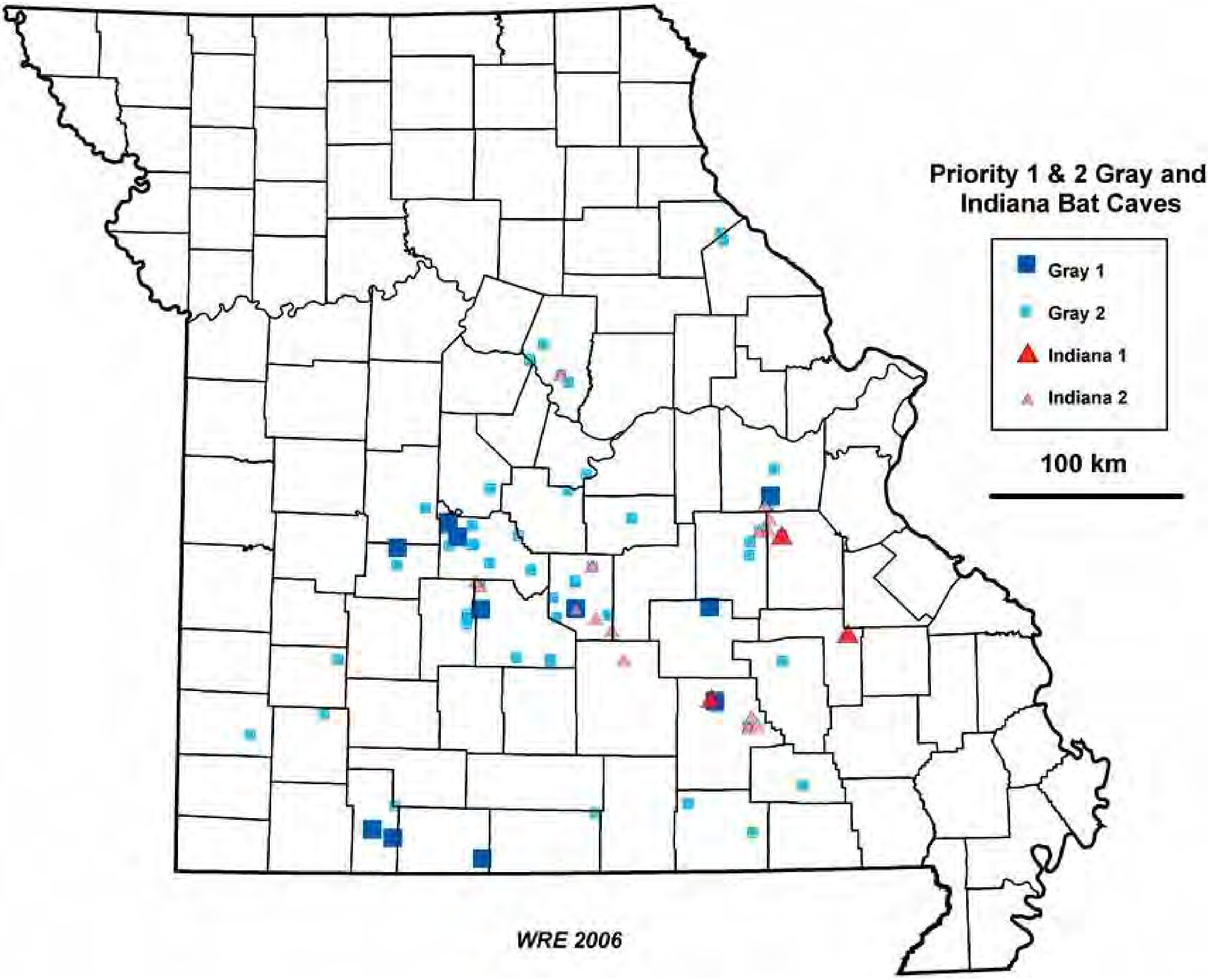

Figure 14. Priority 1 and 2 Gray and Indiana bat caves.

slightly more area endemism than the Lincoln Hills to the north. Peck and Lewis (1978) recognized a St. Louis-Ste. Genevieve County Fauna, which are separated here into the St. Louis and Jefferson-Ste. Genevieve karsts.

JEFFERSON STE. GENEVIEVE KARST

This karst is formed in Mississippian and Ordovician rocks in Jefferson and Ste. Genevieve counties, south of St. Louis. There are faunistic similarities to the St. Louis and Perryville karsts. Mississippian rocks crop out in northern and southern blocks containing most of the caves, but a few important biocaves, such as Friedman's and Pleasant Valley, lie in Ordovician rocks in northern Jefferson County. Two endemic cave beetles occur: *Xenotrechus condei*, Northern Xenotrechus cave beetle, and *X. denticollis*, Southern Xenotrechus cave beetle, with only two known caves each. A stygobite, *Sphalloplana hubrichti*, Hubricht's cave planarian, occurs in Illinois and in this area, in two Ordovician springs and in Kohm's Cave, a large stream system with abundant cave life. Kohm's also has *X. denticollis*, a trechine beetle about 3.6 mm long, which may feed on tubificid oligochaete worms on stream banks. *Xenotrechus* is most closely similar to *Chaetoduvalius* and *Geotrechus* from southern Europe (Barr and Krekeler 1967). Extensive bat stains on the edges of domes indicate that a large colony of Gray bats may have roosted in Kohm's Cave, but no longer. No Gray bats are currently known from caves in eastern Missouri. With 19 troglobites, this karst has the highest area endemism in Missouri. Peck and Lewis (1978) thought the Ste. Genevieve Fault separated this area from the Perryville County Fauna to the south.

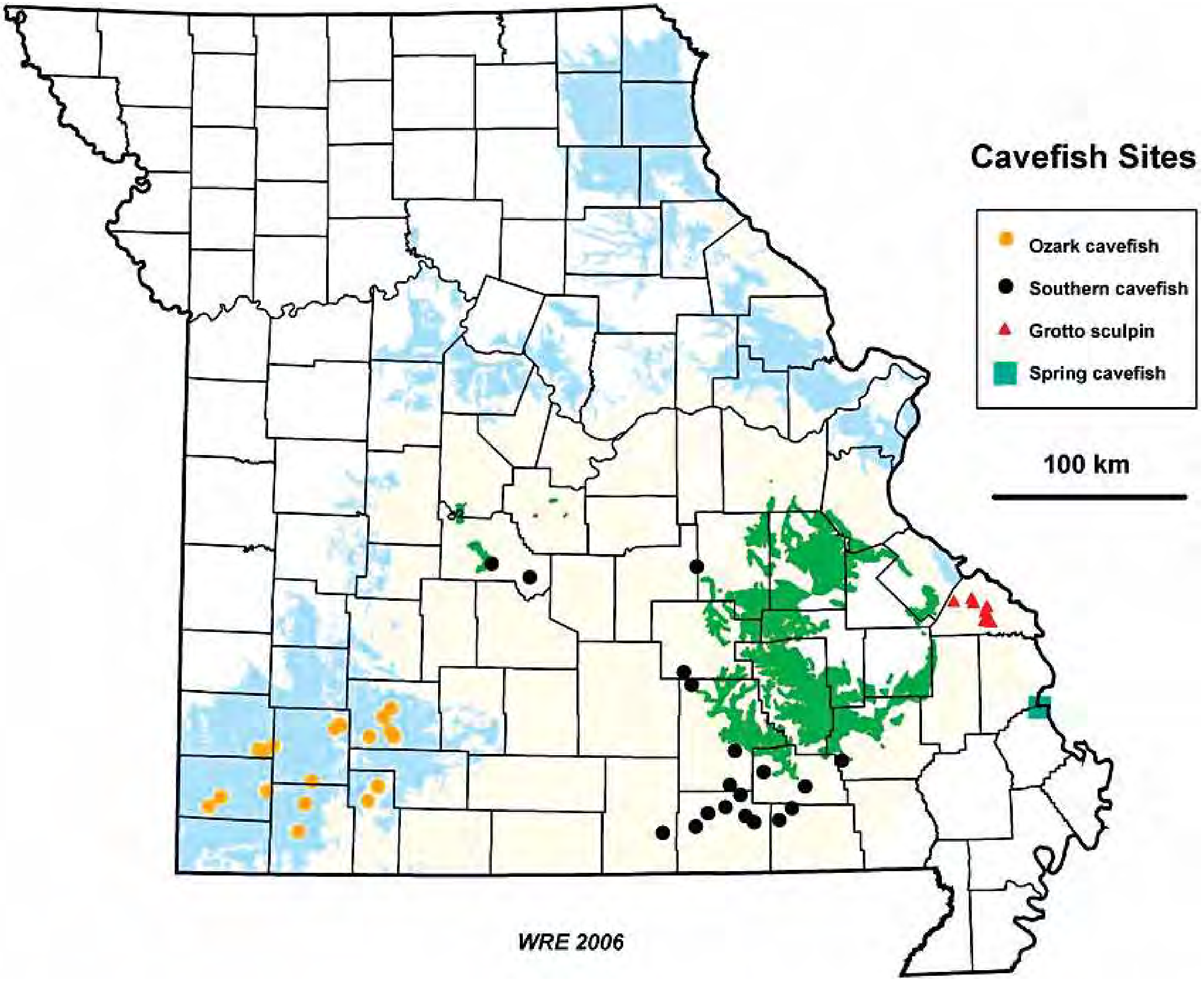

Figure 15. Cavefish sites.

PERRYVILLE KARST

Some of the densest known karst development in the USA occurs in Perry County, in limestones of middle Ordovician age or older. About 700 cave entrances are recorded in the large sinkhole plain, with many large river caves, such as Crevice Cave, the longest in Missouri at 45 km. Large stream caves are especially developed in the Cinque Hommes Creek area. The uplands are covered with up to 10 m of loess derived from the Mississippi River flood plain (Vandike, 1985), and there is heavy row crop agriculture. Biologically similar to the Jefferson-Ste. Genevieve Karst, the Perryville Karst has its own endemics and lacks trechine beetles. Endemic species include *Sphalloplana evaginata,* Perryville cave planarian, *Kenkia lewisi,* Lewis' cave planarian, and *Cottus* sp. 8, the undescribed but distinct Grotto sculpin (Burr et al., 2001), now on Missouri's Species of Concern List. Mystery Cave ranks as third in cave biodiversity in Missouri (Table 7). With 18 troglobites, this karst has high area endemism.

CONSERVATION

Many species and biologically important caves were added to the Missouri Natural Heritage Database and the Comprehensive Wildlife Conservation Strategy, a long-range, statewide conservation plan (Elliott, 2006b).

The term biocave is a cave for which at least one species was recorded in the CLD. Five was considered the minimum number of species indicating that there had been an actual bioinventory instead of a cursory check or a single-species survey. Beginning with a set of about 1200 caves with biological records, a subset of 862 biocaves was

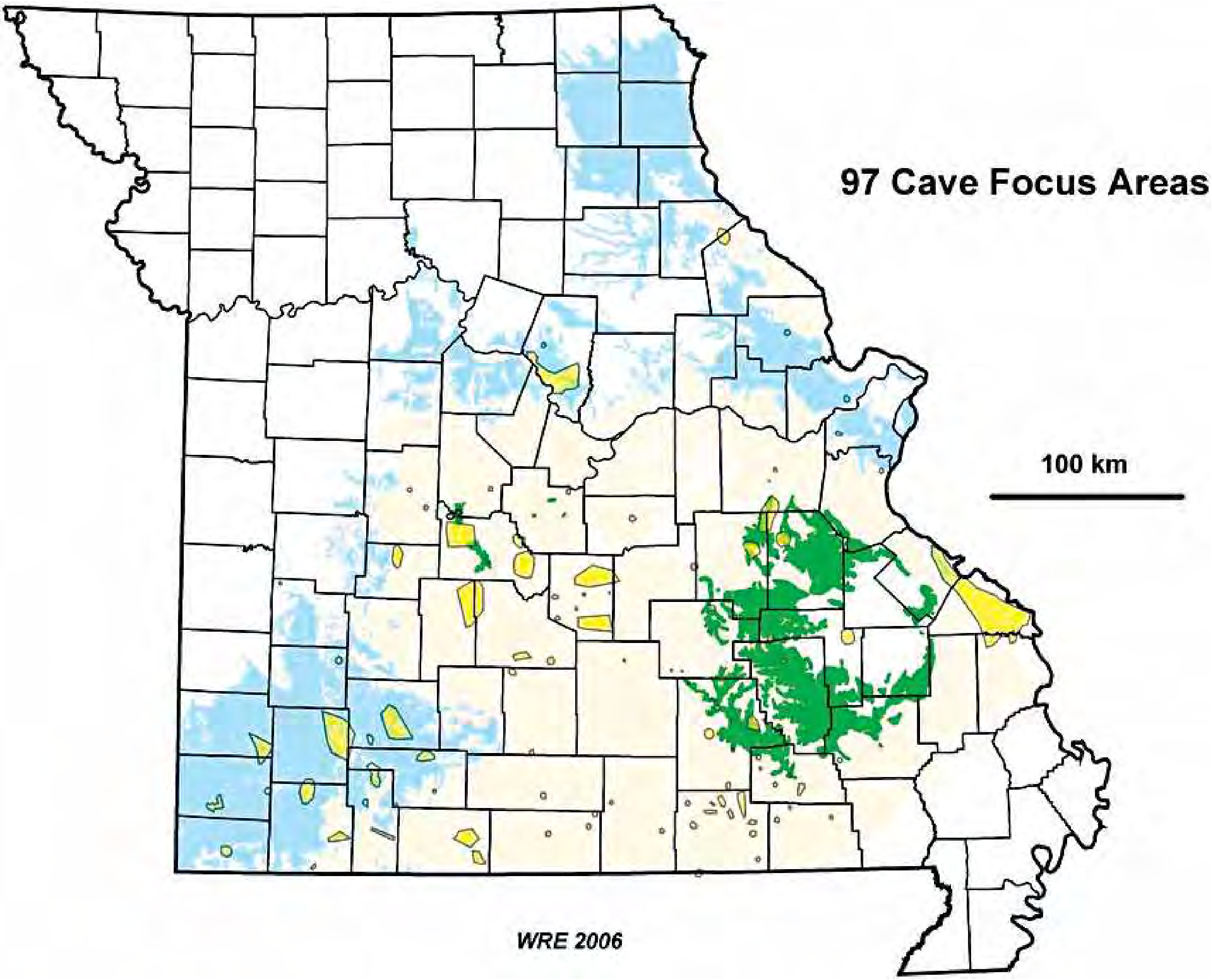

Figure 16. Ninety-seven Cave Focus Areas comprising high biodiversity caves, important bat and cavefish caves, and first magnitude springs.

derived (Fig. 2), then a relation between a table of biocaves and a table of cave locations was temporarily created using decimal-degree coordinates, developed with the help of the Missouri Natural Heritage Database and Hal Baker, Missouri Caves & Karst Conservancy.

The Cave Focus Areas that were derived do not pinpoint caves, but are polygons typically four to eight kilometers in diameter, including one or more important caves or springs. Once the polygon shapefiles were created in ESRI's ArcMap®, the Cave Focus Areas could be included in an overall GIS project for wildlife planning without revealing specific cave locations. Researchers and conservationists may obtain individual cave locations from the Heritage Database or the Missouri Speleological Survey on a need-to-know basis, with written justification.

Caves were ranked for *B* (biodiversity index), as an attribute in ArcMap to examine the geographic distribution of important biocaves (Fig. 1). Figure 14 shows 11 Priority 1 (>25,000–30,000 bats) and 55 Priority 2 (<25,000–30,000) Gray bat caves, and three Priority 1 and 16 Priority 2 Indiana bat caves. These priorities are used by MDC to rate the caves for larger, more important colonies of Gray bats (maternity and hibernacula) and Indiana bats (hibernacula only). See Clawson et al. (2006). Figure 15 depicts cavefish sites.

The final step in delineating Cave Focus Areas (Fig. 16) was to create data layers in ArcMap of the above elements. Polygon shapefiles were drawn around clusters of important caves and first magnitude karst springs, which flow $>2.83\ \mathrm{m^3\ s^{-1}}$ ($100\ \mathrm{ft^3\ s^{-1}}$). The latter springs often contain

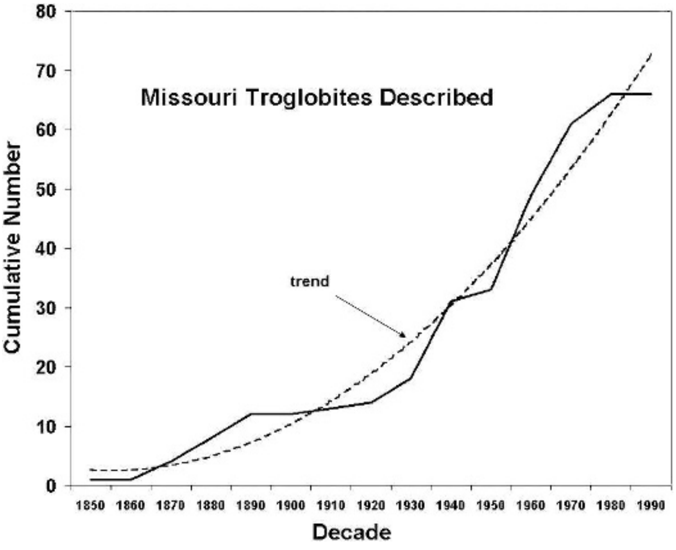

Figure 17. The rate of description of new troglobitic species from Missouri, with fitted polynomial curve.

important ground water species and represent hydrological connections over long distances. The largest, Big Spring, Carter County, flows about 12 m^3 s^{-1} (424 ft^3 s^{-1}), with a peak flow of 37 m^3 s^{-1} (1,307 ft^3 s^{-1}).

DISCUSSION AND CONCLUSIONS

High troglobite endemism occurs in some areas, such as the Jefferson-Ste. Genevieve Karst, Springfield Plateau, Perryville Karst, and the Salem Plateau. Area endemism is generally low north of the Missouri River, Boone County being an exception. Endemism generally increases to the south and the east, but high biodiversity caves occur over a broad area. The top three caves are widely separated by 260–320 km, but more top biocaves are found in eastern Missouri than elsewhere (Fig. 1).

The Ozark Region lacks the rich troglobitic beetle fauna that is common in the eastern United States. Until recently the only trechines in Missouri were the two *Xenotrechus* found in the Jefferson-Ste. Genevieve Karst. The discovery of a new species of relatively small *Pseudanophthalmus* in Shannon County re-opens the question of the low number of troglobitic beetles in the Ozarks, discussed by Barr and Krekeler (1967) and Peck and Lewis (1978). Perhaps we only need to look for smaller beetles to have success. However, Missouri caves lack large colonies of rhaphidoporid crickets, with just four instances in the CLD where an observer counted more than 100 crickets, the maximum being 500 *C. gracilipes.* In contrast, cricket populations often number in the thousands in Texas (several *Ceuthophilus*) and Kentucky (*Hadenoecus* and *Ceuthophilus*), where there are many troglobitic and troglophilic carabid beetles, such as *Rhadine*, *Pseudanophthalmus*, and *Neaphaenops* preying on cricket eggs (Lavoie et al., 2007). Missouri rhaphidophorids are less cave-loving, which may have prevented the co-evolution of cricket-egg-predators, along with a possible lack of ancestral carabids invading the Ozarks from the Appalachians (Peck and Lewis, 1978).

Christiansen (1983) analyzed the distributions and troglomorphy of cave Collembola east of the Great Plains. The greatest biodiversity of troglobites was in the heartland of the nonglaciated Appalachians and Interior Low Plateaus, particularly among the Entomobryinae. The Ozarks have intermediate biodiversity, and caves in glaciated areas have the lowest level of cave adaptation.

Hobbs et al. (2003) provided a list troglobitic species for the United States. Culver et al. (1999, 2003) analyzed regional patterns of troglobites, stygobites and phreatobites across the entire USA. The analysis of Culver et al. looked at the Ozark Region and not Missouri *per se*. For both stygobites and troglobites, only number of caves was a significant predictor, and that seems to be borne out in this study, at least in eastern Missouri. Distance to Pleistocene glacial edges was not important, but there was some influence from proximity to late Cretaceous sea margins, an ancient source of aquatic colonizers. There was no effect from surface productivity (vegetation type).

In this study somewhat different conclusions were drawn than by Culver et al., (2003), but without statistical testing. In this study, high biodiversity as measured in some Missouri caves seems to be related to several factors:

1) Areas with larger and numerous caves with numerous aquatic and terrestrial microhabitats,
2) Location generally south of the Missouri River (away from Pleistocene glaciation),
3) Moderate to high, natural nutrient loads from recharge (essential) and Gray bat guano (not always essential, as in Mystery Cave), as opposed to vegetation type, and
4) High scientific and conservationist interest by the owner or manager, and access by qualified biologists.

The top three biocaves provide excellent examples of the factors given above. Tumbling Creek Cave, the leading Missouri biocave at this time, has received 40 years of study but is still yielding new species (Elliott and Aley, 2006). Martin (1980) studied the extreme arthropod diversity of Tumbling Creek Cave, tabulating 28 mite species, most of which were associated with Gray bat guano. Insofar as half (58) of the 115 species in Tumbling Creek Cave are morphospecies not yet identified to species, including 27 that are not yet identified to genus, there is still some potential for additional, new, endemic species there. Tom Aley (*pers. comm.*) observed troglobitic crayfishes on five occasions in the cave, but no specimens have been obtained yet for identification.

Another example of the above four factors is Devil's Icebox Cave, managed by Rock Bridge Memorial State Park as a wildlife refuge and wild caving venue, where

Table 10. Cave biodiversity in 46 Missouri counties, based on the approximate number of caves known in 2005–2006. Sorted by Success 5, which is the countywide number of troglobites divided by Effort 5 (the number of biocaves with at least five species divided by the number of caves).

County	Caves	Biocaves 1	Biocaves 5	Troglobites	Effort 1	Success 1	Effort 5	Success 5
Perry	656	23	9	19	0.0351	542	0.0137	1385
Jefferson	160	51	3	15	0.3188	47	0.0188	800
Newton	57	20	1	7	0.3509	20	0.0175	399
Lawrence	43	12	1	9	0.2791	32	0.0233	387
Greene	360	29	4	4	0.0806	50	0.0111	360
St. Louis	130	56	5	12	0.4308	28	0.0385	312
Stone	283	31	10	11	0.1095	100	0.0353	311
Douglas	108	17	2	5	0.1574	32	0.0185	270
Ste. Genevieve	72	17	4	12	0.2361	51	0.0556	216
Shannon	535	158	65	24	0.2953	81	0.1215	198
Pulaski	350	70	25	14	0.2000	70	0.0714	196
Dade	55	2	1	3	0.0364	83	0.0182	165
Dent	96	12	3	5	0.1250	40	0.0313	160
McDonald	103	20	4	6	0.1942	31	0.0388	155
Taney	137	27	14	15	0.1971	51	0.1022	147
Christian	220	45	18	11	0.2045	54	0.0818	134
Crawford	205	45	24	13	0.2195	59	0.1171	111
Camden	146	44	20	15	0.3014	50	0.1370	110
Jasper	26	7	1	4	0.2692	15	0.0385	104
St. Francois	19	9	1	5	0.4737	11	0.0526	95
Benton	42	5	2	4	0.1190	34	0.0476	84
Phelps	146	41	23	13	0.2808	46	0.1575	83
Boone	105	32	14	11	0.3048	36	0.1333	83
Washington	81	28	16	15	0.3457	43	0.1975	76
Franklin	97	54	23	17	0.5567	31	0.2371	72
Wright	57	10	7	8	0.1754	46	0.1228	65
Barry	134	60	28	13	0.4478	29	0.2090	62
Laclede	78	28	9	7	0.3590	20	0.1154	61
Reynolds	66	16	6	5	0.2424	21	0.0909	55
Lincoln	36	4	2	3	0.1111	27	0.0556	54
Oregon	140	81	47	18	0.5786	31	0.3357	54
Ozark	80	25	14	9	0.3125	29	0.1750	51
Miller	64	18	5	4	0.2813	14	0.0781	51
Texas	178	46	21	6	0.2584	23	0.1180	51
Madison	20	8	2	5	0.4000	13	0.1000	50
Carter	75	45	26	14	0.6000	23	0.3467	40
Pike	38	4	1	1	0.1053	10	0.0263	38
Maries	36	3	2	2	0.0833	24	0.0556	36
Howell	39	19	9	8	0.4872	16	0.2308	35
Morgan	30	3	1	1	0.1000	10	0.0333	30
Dallas	27	12	2	2	0.4444	5	0.0741	27
Ripley	9	3	3	6	0.3333	18	0.3333	18
Cole	18	3	1	1	0.1667	6	0.0556	18
Iron	25	14	8	5	0.5600	9	0.3200	16
Hickory	21	12	2	1	0.5714	2	0.0952	11
Pettis	5	5	2	2	1.0000	2	0.4000	5

visiting scientists and park staff often conduct faunal surveys and contribute data to the CLD. Mystery Cave received intensive study by Lewis (1974). Few high-biodiversity caves received only cursory study.

The trend of discovering and describing new troglobitic species in Missouri has varied since the 19th Century, but it is gradually increasing (Fig. 17). With a backlog of 15 undescribed troglobites, the pace of description still will increase if there is funding for the few skilled invertebrate taxonomists. The ongoing taxonomic crisis does not encourage the training of new invertebrate taxonomists (Wheeler et al., 2004, Elliott, 2006). If the Missouri trend of discovery continues, we could see many more troglobites eventually, or else an ever-increasing backlog of undescribed species and unrecognized biodiversity.

Additonal work is needed in many areas. Many Missouri caves are good candidates for having high biodiversity, but they have not yet received adequate study. Three examples are Carroll Cave, Camden County; Crevice Cave, Perry County; and Bruce Cave, Pulaski County. All are large, with extensive streams and terrestrial habitats, large recharge areas and reportedly abundant cave life. Table 10 shows cave biodiversity in 46 Missouri counties, based on the number of caves known in 1998. Of the 1,274 sites with biological records, 1,038 are caves or cave springs and 491 are caves with five or more recorded species. Effort1 is the number of Biocaves1 (with at least one recorded species) divided by the number of caves in that county. A similar calculation was done for Effort5 (caves with at least five species). Success1 is the number of troglobites divided by Effort1 for a county (similarly for Success5). The list is ranked in descending order of Success5, a measure of success in finding troglobites in caves that have been studied somewhat adequately. Perry and Jefferson counties rank high because many troglobites were found with relatively little effort, indicating the high endemism found in those karst areas. Table 10 is a guide to where future work should be concentrated. Besides the three prominent caves mentioned above, counties with many caves, but modest success to date, probably are good candidates for intensive study. An exception may be the urban areas of Greene and St. Louis counties, but the more rural areas may yet contain high biodiversity. Some counties have received little cave exploration, but still may have high speleological potential (e.g., Stone and Douglas counties).

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Hazel A. Barton and Diana E. Northup – Geomicrobiology in cave environments: past, current and future perspectives. *Journal of Cave and Karst Studies,* v. 69, no. 1, p. 163–178.

GEOMICROBIOLOGY IN CAVE ENVIRONMENTS: PAST, CURRENT AND FUTURE PERSPECTIVES

Hazel A. Barton[1,*] and Diana E. Northup[2]

Abstract: The Karst Waters Institute *Breakthroughs in Karst Geomicrobiology and Redox Geochemistry* conference in 1994 was a watershed event in the history of cave geomicrobiology studies within the US. Since that time, studies of cave geomicrobiology have accelerated in number, complexity of techniques used, and depth of the results obtained. The field has moved from being sparse and largely descriptive in nature, to rich in experimental studies yielding fresh insights into the nature of microbe-mineral interactions in caves. To provide insight into the changing nature of cave geomicrobiology we have divided our review into research occurring before and after the Breakthroughs conference, and concentrated on secondary cave deposits: sulfur (sulfidic systems), iron and manganese (ferromanganese, a.k.a. corrosion residue deposits), nitrate (a.k.a. saltpeter), and carbonate compounds (speleothems and moonmilk deposits). The debate concerning the origin of saltpeter remains unresolved; progress has been made on identifying the roles of bacteria in sulfur cave ecosystems, including cavern enlargement through biogenic sulfuric acid; new evidence provides a model for the action of bacteria in forming some moonmilk deposits; combined geochemical and molecular phylogenetic studies suggest that some ferromanganese deposits are biogenic, the result of redox reactions; and evidence is accumulating that points to an active role for microorganisms in carbonate precipitation in speleothems.

INTRODUCTION

Life on Earth has been microscopic for much of its 3.7 billion year history (Schopf and Walter, 1983). Nonetheless, the metabolic activity of these organisms has left its mark on every conceivable planetary structure, from isotopic fractionation of ore deposits in the deep subsurface to the oxygenation of the atmosphere (Newman and Banfield, 2002; Schopf and Walter, 1983). Such metabolic activities continue to be critically important in the maintenance of the biosphere, where microorganisms sustain higher forms of life through primary production, nitrogen fixation and organic carbon mineralization. Despite the planetary evolution of our bio- and geospheres, historically researchers tended to ignore microbial activity in geological environments due to an ability to explain many geochemical reactions through purely inorganic chemistries and the inability to culture microorganisms from these sites (Amann et al., 1995). Eventually these limitations were removed with the development of molecular-scale geochemistry, while molecular biology allowed investigators to examine such environments without the need for cultivation (Banfield and Nealson, 1997; Hugenholtz et al., 1998; Newman and Banfield, 2002; Pace, 1997).

Such techniques, and their resultant findings, also facilitated the interactions of microbiologists and geologists to understand the natural history of life processes and biogenic changes identified under geologic conditions (Banfield and Nealson, 1997). This scientific revolution at the boundary of geology and biology, which became known as geomicrobiology, extended into all arenas of geology and revealed processes occurring under previously unrecognized physical and chemical conditions (Newman and Banfield, 2002). Historically, as investigators began to examine cave environments in closer detail, they identified unusual structures that hinted at the important role that microbial species might play in these systems (Cunningham et al., 1995; Hess, 1900; Høeg, 1946).

In creating a comprehensive review of the advances in cave geomicrobiology, we have built upon the earlier reviews (Northup and Lavoie, 2001; Northup et al., 1997) and have chosen to use the Karst Waters Institute *Breakthroughs in Karst Geomicrobiology and Redox Geochemistry* conference in 1994 (hereafter referred to as the Breakthroughs conference; Sasowsky and Palmer, 1994) as a watershed event in the history of such studies within the US. This conference brought together an international group of scientists to present their microbiological research, allowing ideas to be discussed and debated between karst and non-karst researchers. These cross-disciplinary interactions sparked a greater recognition and quickening of cave geomicrobiology within the US. Indeed, a search of the literature indexed in *Scisearch* (1977–present), *BIOSIS* (1969–present), and *Zoological Record* (1978–present), using search keywords representative of the secondary

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* Corresponding Author Address: Department of Biological Sciences, Northern Kentucky University, SC 204D Nunn Drive, Highland Heights, KY 41099; bartonh@nku.edu; Ph: 859-572-5303; Fax: 859-572-5639; www.cavescience.com

[1] Department of Biological Sciences, Northern Kentucky University, Highland Heights, KY 41099

[2] Department of Biology, University of New Mexico, Albuquerque, NM 87131

minerals, microorganisms, and caves, returned 165 articles of which 134 were published after 1994. To highlight the rapid evolution of cave and karst geomicrobiology, we will review studies on the secondary deposits identified in caves carried out in the years preceding the Breakthroughs conference and then examine the representative studies that followed. The latter clearly demonstrates the impact that mainstream geomicrobiological techniques have had on cave geomicrobiology and how subterranean processes in caves have led new investigators to enter the field.

CAVE GEOMICROBIOLOGY BEFORE 1994

Initial work on cave microbiology prior to the 1990s tended to concentrate on descriptive studies, with many investigators noting the presence of microorganisms in cave secondary mineral environments. Generally, such observations were dismissed as the result of transport into the system through air movement or vectors (animal or human) (Cunningham et al., 1995; Northup et al., 1994; Palmer, 1991). Researchers suggested that due to geologic isolation from allochthonous surface energy input, microbial species would be limited to the relatively few able to eek out an existence in this extremely starved environment (Palmer, 1991). Nonetheless, certain geochemical processes were difficult to explain by purely inorganic processes.

NITRATES

Cave nitrate (a.k.a. nitrocalcite or calcium nitrate) is the saltpeter commonly found in dry cave sediments and historically was an important component of gunpowder manufacture (Faust, 1949). As early as 1900, Hess questioned the origin of such deposits and proposed a seeping ground-water hypothesis in which bacterial decomposition of organic matter above the cave released nitrate ions that were transported via ground water. Subsequently, evaporation of water in dry passages would result in a buildup of nitrate in the saltpeter earth (Hess, 1900). Hill (1981), Hill et al. (1983), and Pace (1971) proposed modifications on this seeping ground-water mechanism, suggesting that organic-rich ammonia or ammonium ions were carried in from surface soils. Other suggested sources of nitrates in caves included bat guano (Hill, 1987); ammonium–urea from amberat (cave rat feces and urine) (Moore and Sullivan, 1978); bacterial nitrogen fixation (Faust, 1949, 1968; Lewis, 1992); fertilizers and sewage; volcanic rocks; and forest litter (Hess, 1900; Hill, 1981; Moore, 1994). Studies in Mammoth Cave demonstrated the presence of nitrifying bacteria, specifically *Nitrobacter* spp., in densities 100 times higher than surface soils, although no consensus was reached on a biogenic source for these nitrates (Fliermans and Schmidt, 1977).

SULFUR

Early studies of sulfur in caves concentrated on descriptive studies of microorganisms in caves with sulfide inputs. Principi (1931) first proposed sulfuric acid-driven speleogenesis, and suggested that a small Italian cave was created by the interaction of sulfidic waters with limestone (noted in Vlasceanu et al., 2000, who also reviews early non-cave and karst sulfuric acid corrosion). Morehouse (1968) first described cave dissolution by sulfuric acid in the English-language literature based on his studies in Level Crevice Cave, Iowa. Of particular interest in establishing a microbial role in sulfuric acid-driven speleogenesis was the first documentation of isotopically light sulfur and gypsum deposits. These lighter isotopes are preferentially used by cellular enzymes; and thus, such fractionation usually indicates biological activity. Hill (1987) provided the first $\delta^{34}S$ values for a range of geological environments, including sulfur isotope analyses on sulfur and gypsum deposits from several Guadalupe caves. The comparison of observed data with theoretical values led her to conclude that biological fractionation had occurred in the pathways leading up to the cave deposits. In a later publication Hill (1994) concludes that biogenic fractionation comes from the initial reduction of sulfate to hydrogen sulfide; that the cave elemental sulfur deposits are not biogenic, while the gypsum deposits are. Since these early papers, other studies have implicated sulfuric acid in the formation of numerous caves (Davis, 1980; Egemeier, 1981; Galdenzi, 1990; Hill 1987, 1990; Jagnow, 1979; Korshunov and Semikolennyh, 1994); however, in these inactive cave systems, the cause and effect of microbial metabolisms on speleogenesis remained elusive.

CARBONATES

An early morphological study of limestone types by Shoji and Folk (1964) first indicated the possible role that microorganisms might play in carbonate deposition, revealing inclusions within rock that were later shown to be microbial in origin (Folk and Chafetz, 1980). At the same time, geologists were recognizing a microbial component to carbonate precipitation in stromatolites from the fossil record (Logan et al., 1964), which provide evidence of some of the earliest life on Earth (Schopf and Walter, 1983). While studies on stromatolites suggested that microbial activity was limited to the trapping of calcite crystals within an algal film, subsequent work demonstrated that changes in the microenvironment through photosynthetic activity induced this precipitation of calcite (Walter, 1976). While much early work concentrated on saltwater environments with photosynthetically-driven calcite precipitation, Chafetz and Folk (1984) began to examine calcite precipitation in freshwater, travertine deposits. These investigators were among the first to recognize that the high temperatures and sulfide chemistry of these environments limited algal growth and photosynthesis. As a result, they were able to demonstrate that as much as 90% of the deposited travertine in these springs was bacterially precipitated (Chafetz and Folk, 1984). These investigators went on to demonstrate that local changes in geochemistry altered the

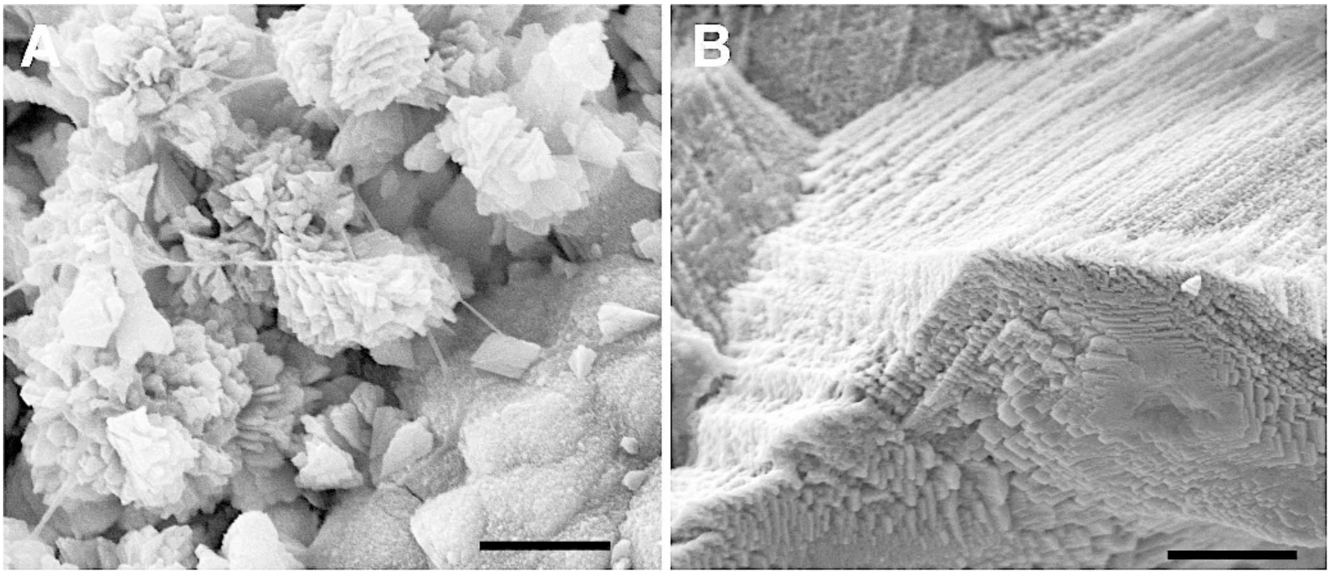

Figure 1. Scanning electron micrographs of calcite crystals formed on Boquet B-4 media (Boquet et al., 1973) by bacteria isolated from a cave environment. A, Calcite crystals forming on a bacterial colony; filaments of individual bacterial cells are visible (scale bar 5 μm). B, Individual calcite crystal formed on a bacterial colony, confirmed by energy dispersive spectroscopy (EDX; scale bar 10 μm).

crystal structure of such deposits, allowing the nature of such biogenic deposits to be identified within the geologic record (Chafetz, 1986; Chafetz and Folk, 1984; Love and Chafetz, 1988).

At the time of the discoveries by Chafetz and Folk (1984), the possibility that microorganisms were involved in calcium carbonate ($CaCO_3$) precipitation was not new. Indeed, the earliest indication of such deposition was made by Wollny in 1897 (as referenced in Hall and Miller, 1905). Later investigators went on to conclude that such precipitation was caused by biological surfaces that could coordinate ions and facilitate biologically controlled mineralization (Chafetz and Buczynski, 1992). Nonetheless, it was not until the experiments of Boquet et al. (1973) who grew soil bacteria on agar plates that contained calcium, but lacked any source of carbonate, that the importance of bacterially controlled mineralization (BCM) was realized (Fig. 1). Interestingly, the work of Boquet et al. suggested that the ability to precipitate calcite was a common occurrence among soil bacteria and is conserved across multiple evolutionary domains. Buczynski and Chafetz (1991) were able to confirm the importance of BCM by showing that only metabolically active bacteria could precipitate $CaCO_3$, and that the subsequent mineral structures (calcite versus aragonite) were dependent on the viscosity of the medium on which they were grown. Such results emphasized the importance of the terrestrial environment on calcite precipitation (Buczynski and Chafetz, 1991; Chafetz and Buczynski, 1992).

With the stimulus of such work being carried out in carbonate precipitation, it is not surprising that the myriad of speleothems found in caves prompted early studies to examine the potential role of microorganisms in the formation of these deposits. In the 1960s, Thrailkill (1964) was the first to suggest a link between the origin of cave popcorn and microorganisms, while Went (1969) suggested that fungi played an important role in stalactite growth (Fig. 2), although no biogenic component was identified by Folk and Assereto (1976). In 1983, Danielli and Edington demonstrated that bacterial species isolated from secondary cave deposits displayed a greater capacity to precipitate $CaCO_3$ than surface species (Danielli and Edington, 1983). Such activity led the authors to suggest a metabolic link between using an organic calcium salt for energy and excreting calcium ions as a waste product, which would result in precipitation when the calcium exceeded the solubility threshold (Danielli and Edington, 1983). Additional support for the role of microorganisms in speleothem formation was primarily circumstantial and consisted of a number of investigators finding micro-fossils within carbonate speleothems (e.g., Cox et al., 1989; Jones and Motyka, 1987; Polyak and Cokendolpher, 1992), until the identification of pool fingers by Davis et al. (1990). These subaqueous pool fingers demonstrated a truly biogenic structure, with parabolic u-loops connecting pendant fingers, the formation of which was difficult to describe using solely abiotic processes (Fig. 3). The associated webulites seen with these pool fingers (Davis, 2000) also appeared biogenic in origin, more closely resembling microbial biofilm structures than mineral precipitates.

Another carbonate deposit that has long attracted microbiologists is moonmilk, also known as mondmilch and a variety of other names (Bernasconi, 1981; Reinbacher, 1994). Moonmilk, which has differing structural

Figure 2. Circumstantial evidence, such as this fungal mycelium emerging from the end of a calcite soda straw and its associated calcite crystals, prompted early investigators to postulate on a role for microbial species in the deposition of speleothems.

forms, from a soft, granular paste to a loosely aggregated powder, can be composed of calcite, aragonite or hydromagnesite crystals, depending upon the structure of the cave in which it is deposited (Hill and Forti, 1997). Høeg (1946), in one of the earliest papers on microbial-mineral interactions, suggested that the metabolic activity of microorganisms was the cause of moonmilk deposition, an idea later supported by Davies and Moore (1957). In support of this hypothesis was the work of Went (1969), who demonstrated the ability of fungal hyphae to act as attachment and nucleation sites for $CaCO_3$ precipitation. Nonetheless, with the formation of soft deposited forms of moonmilk on much harder bedrock, other investigators suggested that corrosion rather than deposition mechanisms were responsible. Early studies by Caumartin and Renault (1958) and Caumartin (1963) suggested that

Figure 3. Small, double u-loops connecting the pendant-like pool-fingers in Hidden Cave, New Mexico. These small structures were difficult to explain using abiotic processes. It is now known that such structures are biogenic in origin.

moonmilk could be the result of microbial metabolic products that corroded underlying bedrock. Despite numerous hypotheses, at the time of the Breakthroughs conference, no clear picture emerged of whether these intriguing deposits are biogenic or abiotic in origin.

OTHER MINERALS

Of the other secondary mineral species observed in caves, an abundance of circumstantial evidence for iron biomineralization exists: Caldwell and Caldwell (1980), Caumartin (1963), Crabtree (1962), Dyson and James (1981), Jones (1991), Jones and Motyka (1987), Klimchouk (1994), Luiszer (1992), Maltsev (1997). One of the only experimental studies was that of Peck (1986), who recovered the iron-oxidizing species *Gallionella ferruginea* and *Leptothrix* sp. from cave pools, sumps and moist Fe/Mn structures in Level Crevice Cave near Dubuque, Iowa. This study established that sterile controls showed no iron precipitation, while live inoculations of subterranean bacterial species precipitated iron hydroxides (*Gallionella ferruginea* cultures) and iron-impregnated sheaths (*Leptothrix* sp). Such iron-encrusted filaments were also identified in the rusticles of Lechuguilla Cave, wherein Davis et al. (1990) used scanning electron microscopy (SEM) to show the filamentous bacterial shapes associated with these interesting formations.

Several early studies also proposed microbial participation in the formation of cave manganese deposits: Broughton (1971), Cílek and Fábry (1989), Crabtree (1962), Hill (1982), Jones (1992), Laverty and Crabtree (1978), Moore and Sullivan (1978), Peck (1986) and White (1976). A range of manganese forms are found, such as coatings on walls or speleothems (Gascoine 1982; Hill, 1982; Kashima, 1983; Moore and Sullivan 1978; Rogers and Williams, 1982), soft deposits in clastic deposits (Cílek and Fábry, 1989), and consolidated crusts (Hill, 1982; Jones, 1992; Moore, 1981; Peck, 1986). Moore (1981) found manganese-oxidizing bacteria such as *Leptothrix* in a stream in Matts Black Cave, West Virginia, and attributed the formation of birnessite in this cave to the precipitation of manganese around sheaths of bacteria. The presence of rods, sheets, strands, and smooth spheroid morphologies in the fossil remains of manganese precipitates in stalactites, karst breccia and root calcrete crusts in Grand Cayman caves led Jones (1992) to conclude that some of these manganese precipitates were biogenic; however, as with much of the pre-1994 cave geomicrobiology literature, many of these studies provide only descriptive, circumstantial evidence. The degree to which the phylogenetically diverse group of microorganisms known to oxidize reduced manganese can promote such oxidation, passively or enzymatically, is debated. Microorganisms can increase the rate of manganese oxidation by up to five orders of magnitude (Tebo et al., 1997) and the large accumulations of manganese oxides that occasionally occur in caves represent potentially microbial mediated production.

Literature on other biogenically mediated mineral structures from caves is limited; studies of silicate speleothems and clay mineral forms have been conducted mainly in Japan and Venezuela. Early studies of microorganisms associated with opal speleothems demonstrated the presence of microbial morphologies in the speleothems (Kunicka-Goldfinger, 1982; Urbani, 1976, 1977). *Meolosira*, a silicaceous algal diatom, were found in twilight zone coralloids in Togawa Sakaidanipdo Cave, Japan (Kashima, 1986; Kashima, et al., 1989). Little early work exists on clay-containing speleothems such as vermiculations, although Anelli and Graniti (1967) hypothesized that the halo surrounding vermiculations is caused by acids and other organic substances secreted by fungi.

CAVE GEOMICROBIOLOGY AFTER 1994

At the beginning of the 1990s, new molecular techniques increased the number of environments that could be successfully studied by microbiologists (Pace, 1997). Such techniques allowed researchers to examine the complex chemical interactions of microbial physiology with redox active minerals, in what had previously been considered abiotic, geological environments (Banfield and Nealson, 1997; Newman and Banfield, 2002). The bringing together of cave geologists and biologists at the Breakthroughs conference mirrored the evolution of the science of geomicrobiology; biologists brought alternative principles (respiration across redox gradients) and unique techniques (DNA purification and molecular phylogenetics) to their geologic peers (Newman and Banfield, 2002). Geologists likewise exposed biologists to the principles of mineralogy and novel techniques (x-ray powder diffractrometry and energy dispersive spectroscopy) (Banfield and Nealson, 1997). The introduction of new tools and techniques provided opportunities to pose novel questions in cave environments. While this initial euphoria was not without its drawbacks [the *de facto* hypothesis for many biologists is that everything is biogenic, with the converse being true for geologists (Barton et al., 2001)], the initial discoveries brought cave geomicrobiology to a new found audience. This work also showcased the significance of cave microbiology to speleologists and allowed them to recognize potentially important geomicrobial structures during exploration (Davis, 2000; Davis et al., 1990). The melding of such activities has taken the value of such research beyond the interest of speleologists and into the broader scientific realm (Newman and Banfield, 2002).

NITRATES

George Moore's 1994 title, "When will we have an accepted explanation for cave nitrate deposits?" captures the essence of a debate that has spanned more than a century. Despite the significance of cave nitrates in the early history of cave microbiology, there has been little work that has advanced our understanding beyond the hypotheses reviewed in the earlier section of this paper. The stable isotope work of Jameson et al. (1994) did demonstrate that saltpeter is enriched in the lighter isotope of nitrogen, supporting the hypothesis that microbial activity is involved in the formation of cave nitrates. Microbiologists have continued to debate the degree to which bacteria, such as *Nitrosomonas* and *Nitrobacter*, facilitate the creation of the cave saltpeter deposits and the origin of the nitrogen. Nonetheless, to date, no consensus exists to explain the formation of these minerals in caves, likely a reflection of the loss of any commercial value for such deposits with the advent of industrial chemistry. Even so, nitrogen is a limiting nutrient for microbial growth in all environments and a clear understanding of how such deposits form would lead to a greater understanding of how microbial growth can be supported in subterranean environments (Newman and Banfield, 2002).

SULFUR

The intense exploration of Lechuguilla Cave and the discoveries of massive sulfur related deposits provided substantial support for the theory of sulfuric acid driven speleogenesis (Spirakis and Cunningham, 1992; Cunningham et al., 1993, 1994) [an expanded history of this idea in the Guadalupe Mountains is traced in Jagnow et al., 2000]. Nonetheless, the metabolic role of microorganisms in producing such sulfuric acid was based almost entirely on the study of inactive cave systems in which cavern enlargement through active microbial processes was no longer occurring. The rare exception were initial studies in Parker Cave (Kentucky), which suggested that sulfur and gypsum deposited on artificial substrates in Sulphur River resulted from extensive bacterial sulfide-oxidizing activity (Angert et al., 1998; Olson and Thompson, 1988; Thompson and Olson, 1988). Other investigators also began examining microbial sulfur cycling in active cave systems, leading to a greater understanding of the role of bacteria in cave dissolution. Our discussion of this work will be brief as readers are referred to the current review of sulfuric acid speleogenesis by Engel (this issue).

In the underground aquifer of the Bahamas and Yucatan Peninsula, the hydrology results in the formation of anchialine caves. These caves contain an upper freshwater lens, a brackish mixing zone (halocline), and underlying seawater that intrudes from the coast (Bottrell et al., 1991; Moore et al., 1992) and creates a stratified water column within the cave system, based on chemical, temperature and density gradients (Moore et al., 1992; Pohlman et al., 1997; Stoessell et al., 1993). Within the halocline itself, stratified zones of SO_4^{2-}, NO_3^-, NO_2^-, and pH have been observed, suggesting the presence of an active microbial ecosystem (Pohlman et al., 1997; Socki et al., 2001; Stoessell et al., 1993). Work by Socki et al. (2001) has shown that $\delta^{34}S$ values for the sulfide in these systems are isotopically light, as much as $-63.2^{o}/_{oo}$, suggesting that the H_2S comes from bacterial cycling, and not from degradation of plant material entering through the cenote, supporting microbially driven sulfuric-acid production (Marcella et al., 1994; Martin and Brigmon, 1994). The importance of such subterranean sulfur-cycling is emphasized by the discovery by Sarbu et al. (1994) of a sulfur-based cave ecosystem in Movile Cave, Romania, where a macroscopic-ecosystem is supported by chemoautotrophic bacterial communities (Sarbu et al., 1996). The basis of this ecosystem was a staggering level of dissolved H_2S in the water, approaching 1300 µM, although the majority of microbial mats in this system developed on the surface of pools in isolated air pockets, rather than in a stratified water column (Sarbu et al., 1994, 1996). The discovery of such a diverse subterranean ecosystem driven by chemoautotrophic microorganisms was a significant advance in our understanding of biological diversity. Other cave systems have similarly contributed to our understanding of biologically mediated sulfuric acid speleogenesis, including Cueva de Villa Luz, Mexico (Hose et al., 2000), Frasassi Cave, Italy (Galdenzi and Menichetti 1995; Vlasceanu et al., 2000), Cupp Coutunn Cave System, Turkmenia (Maltsev 1997), Lower Kane Cave, Wyoming (Engel et al., 2004), and Cesspool Cave, Virginia (Engel et al., 2001). These systems demonstrate many of the subaerial microbial activities thought to have occurred within Lechuguilla Cave, confirming a broader biogenic component in the speleogenesis of sulfuric acid caves (Davis, 2000).

In order to better understand the microbial metabolic processes that lead to cavern enlargement, Engel et al. (2004) demonstrated localized dissolution of carbonates by *Epsilonproteobacteria* in Lower Kane Cave, Wyoming. The bacteria locally produced sulfuric acid that dissolved the host rock, leaving behind obvious solution pockets where the microorganisms attached to the surface of the mineral

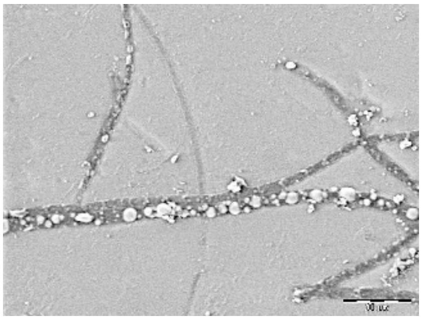

Figure 4. Unpreserved calcite chip and filamentous microbial cells (some with intracellular sulfur globules) examined with environmental scanning electron microscopy; calcite chip was exposed to the microbial mat for three months, resulting in an etching of the surface by the microbial activity. Scale bar 10 µm.

(Fig. 4). Surprisingly, these investigators demonstrated that dissolved H_2S in the cave spring was quickly consumed by sulfide-oxidizing bacteria before it could generate inorganic sulfuric acid, in direct contradiction to the classic sulfuric acid speleogenesis model of Palmer (1991; Engel et al., 2004). In contrast, other caves such as Cueva de Villa Luz have aggressive subaerial microbial activity resulting in the presence of microbial biofilm communities (snottites; Fig. 5) with observable sulfuric acid production (Hose et al., 2000). Such communities are actively producing gypsum precipitates that slough off the walls to enlarge the cave and rillenkarren that were taken as evidence of past microbial activity within Lechuguilla Cave (Davis, 2000). In order to identify the microbial activity responsible for the formation of caves on the scale of Carlsbad Caverns and Lechuguilla Cave, Barton and Luiszer (2005) recently proposed a metabolic model wherein sulfite and sulfuric acid could be produced in such systems in the absence of significant oxygenated water input. This theory also suggested that subaerial dissolution in the presence of oxygen would result in localized pockets of aggressive dissolution, as has been seen in both Lechuguilla and Villa Luz cave systems (Hose et al., 2000; Davis, 2000). Whatever the microbial mechanisms in place, there remain important questions regarding observable differences in speleogenesis and cavern enlargement on the molecular and geological scales (Engel et al., 2004; Klimchouk et al., 2000) that promise to be an exciting and innovative area in cave geomicrobiology as we work toward a comprehensive model of sulfuric acid speleogenesis.

Figure 5. Microbial biofilms, such as these snottites from Cueva de Villa Luz, produce water droplets with a pH of 0 to 2. Such biofilms play important roles in secondary dissolution processes within sulfidic cave systems.

CARBONATES

In the past decade, there has been a rapid expansion in our understanding of carbonate biogeochemistry and the deposition of $CaCO_3$ in reactions that range from the molecular to environmental scale (Banfield and Nealson, 1997; Banfield et al., 2005; Mozely and Davis, 2005; Neuweiler et al., 2000; Newman, 2001; Woods et al., 1999). Together, these investigations are piecing together a more complete understanding of the role that biological processes, whether direct or indirect, play in the formation of $CaCO_3$ deposits within the geologic record (Banfield and Nealson, 1997; Bosak and Newman, 2003; Neuweiler et al., 2000; Woods et al., 1999). Likewise, the importance of speleothems as terrestrial travertine deposits has led to greater research in these environments, increasing our understanding of the potential role that microorganisms play in the structure and formation of such cave deposits (Cacchio et al., 2004; Frisia et al., 2002; Galy et al., 2002; Melim et al., 2001; Saiz-Jimenez, 1999; Sanchez-Moral et al., 2003; Tooth and Fairchild, 2003). Together this work indicates that, as has been observed in hot spring travertines, the local geochemistry, temperature, rate of CO_2 off-gassing and precipitation, and microbial activity all play critical roles in carbonate deposition and structure (Fouke, et al., 2000; Frisia et al., 2002; Sanchez-Moral et al., 2003).

There has been a greater recognition of the different roles that biologically induced and biologically controlled precipitation play in $CaCO_3$ biomineralization (Bosak and Newman, 2005; Braissant et al., 2005); biologically induced precipitation (BIM) refers to the effect that organismal

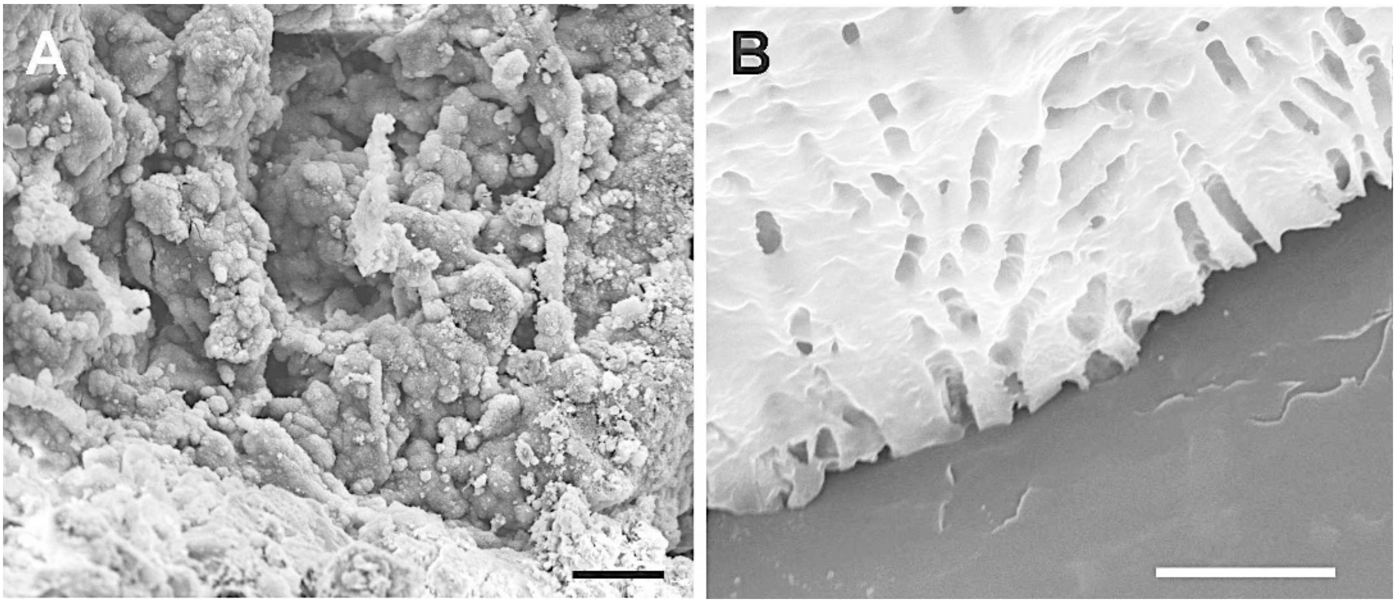

Figure 6. Microorganisms growing on the wall of a cave in Kentucky have become encased in a calcite matrix (A), as confirmed by EDX analysis (scale bar 20 µm). Viable bacterial cells were isolated from this area and shown to also become encased in calcite during growth on B-4 media, leaving behind cell-shaped cavities when washed from the precipitated calcite (B; scale bar 5 µm).

metabolic activities and by-products have on the local physiochemical environment, favoring conditions that promote precipitation (Frankel and Bazylinski, 2003). Biologically controlled precipitation (BCM), also called organic matrix-mediated mineralization or boundary-organized mineralization, refers to the role that cellular substrates play in promoting coordination and growth of biominerals (Bazylinski and Frankel, 2003; Simkiss and Wilbur, 1989).

Microorganisms can promote $CaCO_3$ precipitation through processes of BCM by altering the saturation index (SI) of the solution, or by removing kinetic inhibitors of crystallization, such as magnesium, sulfate or phosphate ions (Bosak and Newman, 2005, and references therein). While such BCM activities have been shown to play an important role in calcite crystal morphology (Bosak and Newman, 2005; Braissant et al., 2005; D'Souza et al., 1999; Orme et al., 2001; Schultze-Lam et al., 1992), it has been more difficult to assess a role for BIM in $CaCO_3$ deposition and the role of microorganisms in speleothem development. Castanier et al. (1999) have suggested that bacterial autotrophic processes cause CO_2 depletion surrounding the cell, favoring the precipitation of calcium ions as $CaCO_3$. Other investigators have proposed that heterotrophic processes of nitrogen fixation and release play a critical role in raising the pH of the local environment, again favoring the precipitation of carbonates (Cacchio et al., 2004; Hammes and Verstraete, 2002). In cyanobacterial species, fixation of CO_2 increases the concentration of bicarbonate ions, which may be excreted into the extracellular medium, causing $CaCO_3$ precipitation if calcium ions are present (Badger and Price 2003; Hammes and Verstraete 2002). While such photosynthetic reactions are not possible in cave environments, the carbonic anhydrases responsible for CO_2 uptake are common among bacterial species (Merlin et al., 2003). McConnaughey and Welan (1997) also suggested that bacterial calcification may generate energy for nutrient uptake in starved environments and may explain the ubiquitous nature of calcite precipitation originally observed by Boquet et al. (1973).

Intellectually a problem arises in that as microorganisms carry out calcite precipitation, such activity invariably leads to entombment within the growing crystal and death (Barton et al., 2001) (Fig. 6). This makes understanding an evolutionary advantage for such activity difficult to assess. It is known that bicarbonate ions can serve as a buffer, which allows microorganisms to carry out cellular processes that would otherwise lead to acidic conditions; if bicarbonate ions were serving this function under such conditions, Ca^{2+} would quickly accumulate to toxic levels. Nonetheless, evidence is starting to emerge that bacteria, like their eukaryotic counterparts, have Ca^{2+} antiporter protein pumps that selectively detoxify calcium from the cell by pumping it into the extracellular medium (Cai and Lytton, 2004). Indeed, a study by Anderson et al. (1992) demonstrated that under toxic calcium concentrations, *Pseudomonas fluorescens* actively precipitated calcite.

This work is further supported by Cacchio et al. (2004), who demonstrated a selective enrichment for microbial species capable of carrying out $CaCO_3$ deposition from speleothems within Cervo Cave, Italy. These investigators demonstrated that bacterial species isolated from different speleothems displayed an unusually high rate of carbonate precipitation, when compared with organisms from non-karst environments; however, these investigators relied on cultivation techniques that favored microorganisms capable of surviving the transition from the starved, oligotrophic conditions of cave environments to the eutrophic conditions of a nutrient plate. Such cultivation strategies selectively identify microbial species that are known to display the metabolic phenotypes consistent with carbonate precipitation, including *Pseudomonas* and *Bacillus* species (Boquet et al., 1973; Cacchio et al., 2003, 2004; Koch, 1997). Nonetheless, these investigators did demonstrate using oxygen and carbon isotopic fractionation that three distinct processes appeared to be involved in bacterial calcite precipitation (Cacchio et al., 2004). Whatever the metabolic process responsible for calcite deposition (and the work of Cacchio et al., (2004) suggests they may be numerous) it is important to remember that a balance must exist between biological and inorganic processes in such precipitation (Fouke et al., 2000; Palmer, 1996).

Regardless of the metabolic activity directly responsible for $CaCO_3$ deposition within caves, investigators have continued to examine such deposits for the presence of microfossils, petrographic fabrics that are indicative of microbially mediated precipitation and isotopic fractionation of the carbonate (Melim et al., 2001; Boston et al., 2001). Using SEM, Melim et al. (2001) examined the layered calcite pool fingers, first identified by Davis (2000) as potentially biogenic in origin. These investigators found an abundance of fossil filaments within micritic layers, but not in the inter-layered clear calcite spar. They also found a small shift in the carbon isotope composition of the micritic versus clear calcite layers. Together, this association suggested that microorganisms were involved in the deposition of this formation (Melim et al., 2001). Such work was recently supported by Baskar et al. (2006), who demonstrated microcrystalline deposition of calcite within stalactites that appeared to be mediated by microbial processes. A study by Contos et al. (2001) also demonstrated the presence of subaqueous calcite precipitates associated with microbial biofilms in Weebubbie Cave, Australia. These deposits formed in waters well below the saturation index of calcite and demonstrated a unique structure, which could only be replicated *in vitro* with the addition of organic acids (Orme et al., 2001). Such results led the investigators to conclude that the surface of the *Gammaproteobacteria* species found within the bacterial filaments of the cave (Holmes, et al., 2001) played a crucial role in calcite deposition (Contos et al., 2001).

The most convincing evidence of microbial involvement in speleothem formation comes from the formation of moonmilk (Cañaveras et al., 2006). While moonmilk was one of the earliest calcite cave deposits to be associated with microbial activity (Høeg, 1946), its needle-fiber structure is delicate and easily altered by the constructive or destructive processes of diagenesis (Jones, 2001). Thus it has remained difficult to determine the role that microorganisms play in the structural formation of moonmilk. By using a combination of cultivation, molecular phylogenetics and petrographic analyses, Cañaveras et al. (1999, 2006) demonstrated that moonmilk does not contain fungal filaments, but rather numerous filamentous *Proteobacteria* species that demonstrate a calcite precipitation phenotype. Morphological evidence suggested that moonmilk forms through the microbial colonization of rock surfaces, followed by calcite deposition along bacterial surfaces, microstructural breakdown, and accumulation of collapsed fibers (Cañaveras et al., 2006). As this process repeats through seasonal oscillations, moonmilk deposits become thicker, forming the significant deposits observed in numerous caves (Cañaveras et al., 2006). These investigators also identified the presence of *Crenarchaeota*, members of the Archaea, in these moonmilk deposits; their role in moonmilk formation remains unclear (Gonzalez et al., 2006). Together, such work represents one of the most complete pictures of the physiological and geochemical relationships of biogenic deposit formation within cave environments.

While a significant amount of work has been geared toward understanding microbial involvement in carbonate constructive processes, there is an increasing interest in the destructive, erosional processes of microbial activity (Jones, 2001). Even while microbial surfaces may bind Ca^{2+} ions, increasing the likelihood of calcite crystallization (Bosak and Newman, 2005), certain biological molecules have a sufficiently high affinity for these ions that they actually promote dissolution (Perry et al., 2004; Friis et al., 2003). Such structures include exopolysaccharide (a major component of biofilms), siderophores and other secreted chelators, and even the bacterial cell wall (Perry et al., 2004; Friis et al., 2003). Through their metabolic processes, bacteria also secrete a number of organic acids, which actively dissolve carbonates. Conversely, a number of microbial structures, including lipids and phospholipids, actually inhibit dissolution, while soil derived humic acids, which form a significant portion of the organic carbon found within cave drip waters (Saiz-Jimenez and Hermosin, 1999), also inhibit calcite dissolution. It is likely that the governing factors controlling microbial involvement in calcite constructive or destructive development will involve a balance between the local conditions, the geochemistry and physiochemistry of the local environment, and the microbial metabolic processes that predominate under such conditions (Pohl and Schneider, 2002; Vlasceanu et al., 2000).

OTHER MINERALS

Two decades ago, Peck (1986) described the presence of microbial species in manganese and iron oxides within caves and proposed the possibility of chemolithotrophic primary producers in these systems. Unfortunately most

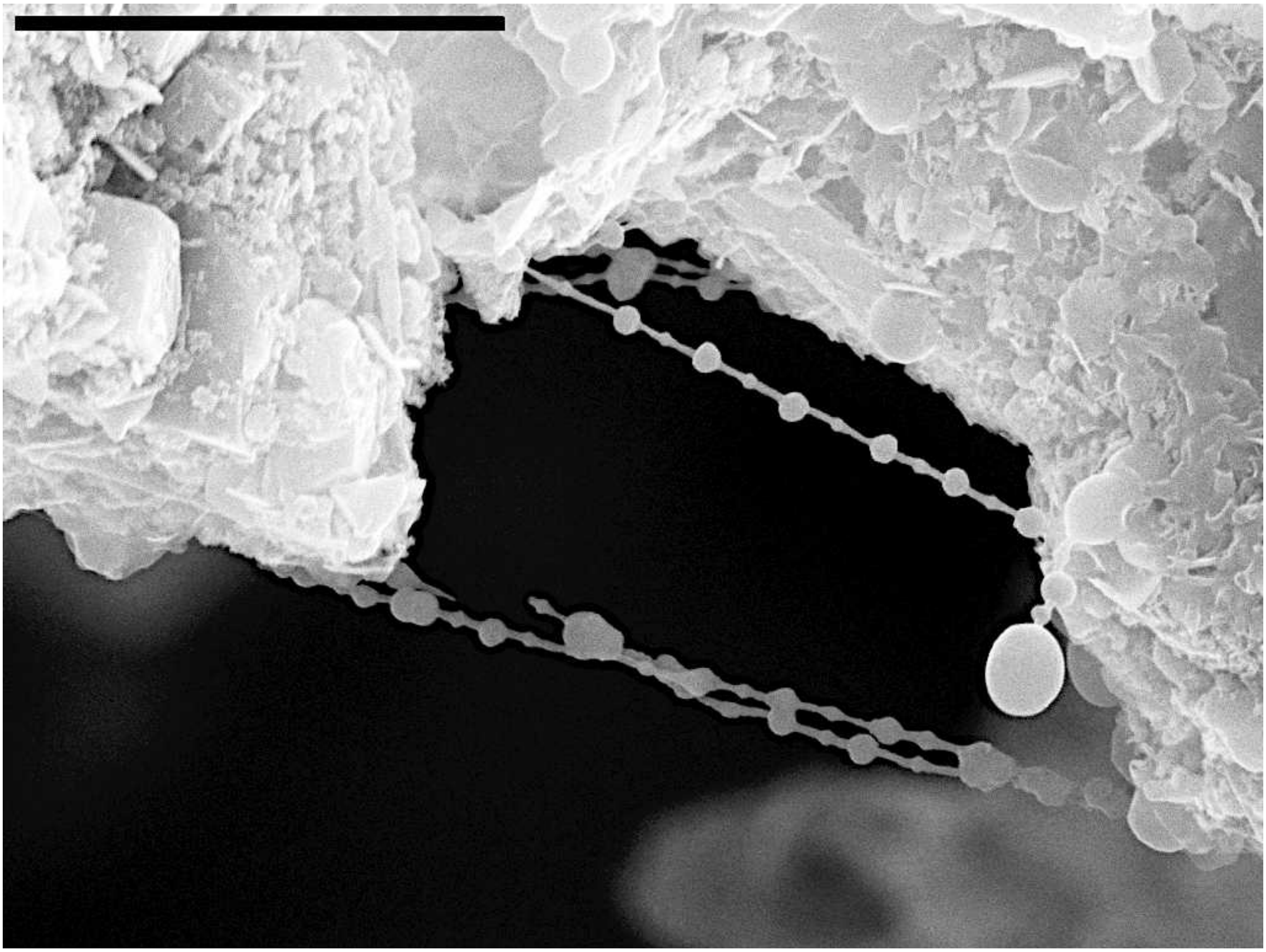

Figure 7. Unusual beads-on-a-string morphologies of manganese-oxidizing bacterial species are seen throughout several of the ferromanganese deposits from Snowing Passage in Lechuguilla Cave. EDX analyses show that the mineral matrix is manganese oxide. (Scale bar 5 μm).

biologists did not recognize the significance of this observation. Such indifference mirrors the general lack of interest by microbiologists (primarily due to the funding climate at the time), who tended to concentrate on medically important pathogens. Events in the exploration of Lechuguilla Cave, first explored in the same year as Peck's study, would provide the impetus to explore microbe-mineral interactions on manganese and iron environments in caves; one of the deposits that generated the greatest interest were the colorful deposits on walls and ceilings (Cunningham, 1991). These iron and manganese oxide-rich layers were initially believed to be the insoluble residue from the attack of corrosive air on the carbonate bedrock and were called corrosion residues (Queen, 1994; Cunningham, 1991). These corrosion residues, now referred to as ferromanganese deposits, occur in a range of colors and are diverse in composition with variable amounts of clay and Al-oxide minerals; all are rich in Mn- and Fe-oxides (Spilde et al., 2005). The work of Cunningham was the first to recognize an association between microbial species and ferromanganese deposits within Lechuguilla Cave (Cunningham et al., 1995). Inspired by Cunningham, the team of Boston, Northup, Spilde and others established the presence of a diverse community of microorganisms, some of whom were related to known manganese- and iron-oxidizing bacteria and others who appear to be previously unknown (Northup et al., 2003) (Fig. 7), and documented the presence of metabolically active bacteria in the punk rock underlying the ferromanganese deposits (Spilde et al., 2005). Their geochemical studies documented a four-fold enrichment of reduced manganese between the bedrock and ferromanganese deposits. Spilde et al. (2005) also demonstrated that some of the mineral species identified in these deposits can be reproduced *in vitro* by microbial species inoculated from these environments and fed a chemical diet of the reduced metal ions present within the rock of the cave, while killed controls did not produce the crystalline forms. While this does not conclusively demonstrate a cause-and-effect, it takes a significant step toward understanding the microbial activities responsible for the formation of such deposits.

Somewhat similar deposits to the ferromanganese deposits of Lechuguilla Cave are those found in Ochtiná Aragonite Cave in Slovakia. These deposits, termed ochres, contain goethite, birnessite, and asbolane (Bosák et al., 2002). Besides the co-occurrence of goethite and birnessite in these deposits and those in Lechuguilla Cave, Ochtiná ochres also contain occasional occurrences of La-Nd-bearing phosphate. Lechuguilla ferromanganese deposits also contain instances of rare earth elements associated with phosphate minerals. Bosák et al. (2002) suggested that the manganese oxides were the result of microbial precipitation in pool bottoms in a manner similar to that described by Andrejchuk and Klimchouk (2001). Chelius and Moore (2004) performed a phylogenetic analysis of the Wind Cave (South Dakota) paleofill samples that contained some manganese and iron. Interesting similarities exist between the archaeal phylogenetic trees of this study and those of Northup et al. (2003). Closest relatives for both included clone sequences from the South African gold mine study (Takai et al., 2001), which were obtained from pore water that passes over wad (manganese oxide) fill (T.C. Onstott, *pers. comm.*). What role archaeal species may play, if any, in production of manganese oxides is currently unknown.

Additional forms of poorly crystalline manganese oxides and hydroxides (pyrolusite, romanechite, todorokite, and rhodochrosite) have been described from caves (Onac, et al., 1997; Gradzínski et al., 1995; Northup et al., 2000). Irregularly shaped crusts of manganese flowstone (2–20 mm thick) are found in Jaskinia Czarna Cave (Tatra Mountains, Poland). Filaments and globular bodies are interpreted as bacterial or fungal cells that participated in the formation of the flowstones, as evidenced by their three-dimensional morphology and the amorphous character that is more common in biogenic manganese oxides. The high Mn/Fe ratio of 72.1:1 in the crusts was attributed by Gradzínski et al. (1995) to biologically mediated precipitation. A little studied type of ferromanganese oxide deposit is the black coatings of littoral Mediterranean submarine caves. Allouc and Harmelin (2001) concluded that black coatings in these caves were biosedimentary deposits that form from the interaction of slime, associated with microorganisms, and dissolved manganese from the seawater. The study includes some fascinating SEM micrographs of biofilm and microbial structures and makes the observation that the Mn/Fe ratio is negatively correlated with level of nutrients.

Kasama and Murakami (2001) attempted to ascertain the microbial contribution to iron precipitation on stalactites composed of ferrihydrite. Microscopy studies showed a variety of microbial morphologies associated with the stalactites. Their experiments demonstrated that in comparison to inorganic processes, microorganisms enhanced precipitation rates by up to four orders of magnitude. The authors argued that exopolysaccharides and microbial surface characteristics were more important than metabolic processes in the precipitation of iron in this cave.

FUTURE PERSPECTIVES ON GEOMICROBIAL ACTIVITIES IN CAVE SYSTEMS

Since the emergence of geomicrobiology as a science, our understanding of microbial interactions with minerals has evolved beyond a preliminary appreciation of their role in carbon, sulfur and nitrogen cycling. It is now recognized that many important mineral transformations, originally considered to be inorganic in nature, can be mediated by microorganisms; from the microbial precipitation of dolomite in groundwater (Roberts et al., 2004; Warthmann et al., 2000); transformation of smectite to illite clay (Kim et al., 2004); to the production of iron, uranium and even gold deposits (Newman and Banfield, 2002). Likewise, through a more thorough understanding of geochemistry, we have expanded our knowledge of the range of habitable environments on Earth; from endolithic environments of extreme temperatures (Friedmann and Ocampo, 1976; Bell, 1993) to the deep subsurface, where hydrogen produced from volcanism, serpentinization and even radiolysis provides sufficient energy to support microbial growth (Chapelle et al., 2002; Coveney et al., 1987; Lin et al., 2005). While such work allows us a more comprehensive understanding of life on Earth, it also opens a window into the possibility of life under other geochemical conditions, such as on Mars or Europa. Due to the absence of liquid water on the surface of these planetary bodies, extant life will be restricted to the subsurface (Boston et al., 1992), making it critical to understand the processes that support microbial life in all subsurface environments.

While, as the title suggests, this review primarily addresses the interactions between microbes and minerals in cave environments, microbiology in cave environments also provides information on subterranean chemolithotrophic ecosystems (Barton et al., 2004; Chelius and Moore, 2004; Groth et al., 1999, 2001; Laiz et al., 1999, 2003; Schabereiter-Gurtner et al., 2002). Together these investigations suggest that without sunlight energy and through geologic isolation, caves are extremely starved environments where the levels of available organic carbon to support heterotrophic microbial growth are often a thousand-fold lower than starved terrestrial environments (Barton, unpublished, 2006). Examining microbial ecosystems surviving under such starved conditions suggests that they produce a myriad of energy conserving reactions; from obtaining energy from the minuscule organic material percolating into the system and fixing available nutrients from the atmosphere, to reducing the trace minerals within the rock of the cave itself (Barton et al., 2004; Chelius and Moore, 2004; Northup et al., 2003; and Spilde et al., 2005). Recent studies have also suggested that the Archaea may play important roles in cave microbial ecosystems (Chelius and Moore, 2004; Gonzalez et al., 2006; Northup et al., 2003), although an identifiable metabolic role for these microorganisms has yet to be determined.

By understanding how microorganisms survive the extreme starvation of caves, we can understand and limit human impacts on such hypogean environments (Cigna, 1993). In doing so, such work can preserve cultural treasures, such as Paleolithic paintings in the caves of northern Spain, where tourist activity altered the cave environment and brought in heterotrophic microorganisms that threaten to damage these images (Cañaveras et al., 2001; Groth et al., 1999; Laiz et al., 2003). An understanding of such processes also facilitated the development of microbially precipitated calcite coatings, which can help to preserve historical monuments and sculptures (Hoppert et al., 2004; Rodriguez-Navarro et al., 2003). Presently it is hard to predict the similar outcomes from the increasing number of microorganisms being cultured from cave environments, although they range from such beneficial activities as bioremediation to drug discovery.

Even as we write this review, new techniques are being developed in materials science, chemistry, physics, geology and biology that will allow investigators to ask more complex questions of the interactions between microorganisms and mineral surfaces. For example, in materials science, attenuated total reflectance Fourier transformed infra-red (ATR-FTIR) spectroscopy allows real-time analysis of chemical changes on surfaces through microbial activity (Omoike et al., 2001), while atomic force microscopy allows us to examine the intra-molecular forces that allow microorganisms to acquire energy from mineral surfaces (Lower et al., 2001). Within microbiology, new techniques that allow us to probe inter-species and ecosystem interactions (Caldwell et al., 2000), and advances in genomics, metagenomics and proteomics, will allow us to ask questions of community interactions within caves that could previously only be addressed under *in vitro* conditions. All the while, caves continue to be discovered, presenting new environments to be examined. As a result, our understanding of microbial activity in such subterranean systems can only continue to grow, as present questions are addressed and new questions are posed. As we look back over the advances in cave geomicrobiology since the Breakthroughs conference, we can predict that the science of cave geomicrobiology will continue to grow in both prominence and regard within the greater scientific community.

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SUBTERRANEAN BIOGEOGRAPHY: WHAT HAVE WE LEARNED FROM MOLECULAR TECHNIQUES?

Megan L. Porter
Department of Biological Sciences, University of Maryland Baltimore County, Baltimore, MD 21250 USA

Abstract: Subterranean faunas have unique distributional attributes, including relatively small ranges and high levels of endemism. Two general models have been proposed to account for these distributional patterns–vicariance, the isolation of populations due to geographic barriers, and dispersal, an organism's ability to move to and colonize new habitats. The debate over the relative importance of each of these models in subterranean systems is ongoing. More recently, biogeographical studies of subterranean fauna using molecular methods have provided new perspectives into the distributional patterns of hypogean fauna, reinvigorating the vicariance versus dispersal debate. This review focuses on the application of molecular techniques to the study of subterranean biogeography, and particularly the contribution of molecular methods in estimating dispersal ability and divergence times. So far, molecular studies of subterranean biogeography have found evidence for the common occurrence of multiple independent colonizations of the subterranean habitat in cave-adapted species, have emphasized the importance of the genetic structure of the ancestral surface populations in determining the genetic structure of subsequent hypogean forms, and have stressed the importance of vicariance or a mixed model including both vicariant and dispersal events.

Introduction

Cave-adapted fauna have intrigued scientists for centuries. Part of this fascination has been focused on understanding the unique geographic distribution patterns over space and time (i.e., biogeography) of subterranean organisms. However, the unique suite of regressive (eye and pigment loss) and progressive (appendage elongation, enhanced non-visual sensory modes) traits termed troglomorphy (Christiansen, 1962) characterizing cavernicoles often hinder distributional studies because the highly convergent form can obscure taxonomic relationships among cave-adapted species and among closely related cave and surface species. Compared to surface species, cave-adapted faunas generally have small geographic ranges and high levels of endemism at all scales of measurement, making their biogeography distinct (Culver and Holsinger, 1992; Gibert and Deharveng, 2002; Christman et al., 2005). There are numerous records of single cave endemics in both terrestrial (troglobionts) and aquatic (stygobionts) cave-adapted species (Paquin and Hedin, 2004; Christman et al., 2005). These distinctive geographic patterns have lead to investigations of how, why, and when species colonize, adapt, and persist in subterranean environments. In general, understanding the biogeography of cave-adapted fauna offers insights not only into the evolution of the troglomorphic form, but also into the formation and persistence of subterranean faunas, providing important information relative to cave conservation and management issues.

There has been a long running debate regarding the mechanisms responsible for the distribution of cave-adapted fauna, beginning as early as the late 1800s (Packard, 1888). The crux of the debate has been over the relative roles of different biogeographic models, particularly dispersal (an organism's ability to move to and to colonize new habitats) and vicariance (isolation of populations due to geographic barriers). Over the years, various studies have supported one model or the other (see Culver et al., 2007 for a brief historical review). However, it has recently been recognized that subterranean faunal distributions are more clearly explained by a combination of both vicariance and dispersal events, with many reflecting processes occurring in ancestral surface populations before the invasion of the subsurface (Christiansen and Culver, 1987; Verovnik et al., 2004; Buhay and Crandall, 2005; Leféburе et al., 2006). With respect to the classic debate, subterranean distribution patterns are likely the result of complex processes both internal (e.g., dispersal capabilities) and external (e.g., vicariant events, habitat connectivity) to the species of interest. Therefore, rather than investigating biogeographical patterns in terms of one mechanism versus another, it has become more important to understand the combination of factors involved in creating current distribution patterns, including dispersal ability, potential vicariant events, and rates of evolution and extinction (Holsinger, 2005; Culver et al., 2007).

Given that there are ecological disparities controlling the distributional differences between troglobiotic and stygobiotic species (e.g., modes of colonization, rates of migration and extinction, types of geographic barriers), considerations in subterranean biogeography first include understanding the role of habitat on these factors (Holsinger, 2005). Subterranean aquatic environments are generally connected over wider areas (due to hydrology) compared to the connectivity of karstic terrestrial habitats. Hydrologic connectivity provides stygofauna greater dispersal potential and, therefore, generally larger distributional ranges (Culver et al., 2007). Furthermore, the relative contribution of dispersal versus vicariance is dependent on factors such as the scale of investigation, ranging from faunal distributions under individual rocks, within cave stream riffles, in cave stream segments from a single system, within cave and karst basins of a single river drainage, from cave systems in different drainages, to regional and continental patterns (Culver and Fong, 1994). Investigating these diverse geographical and geological scales produces distributional patterns corresponding to differences in time and dominant processes, with large scale patterns (cave systems, regions, continents) occurring over geological / evolutionary timescales being strongly affected by vicariant and dispersal events, and distributions within cave systems occurring in ecological timescales with influences from processes such as competition, predation, mutualism, and migration.

As subterranean biogeographers begin to assess the relative roles of dispersal and vicariance in subterranean faunal distributions, molecular techniques, involving the characterization of genetic material like DNA, RNA, and proteins, have become an increasingly powerful tool, complementing the significant amounts of taxonomic and biogeographic research devoted to searching cave and karst systems for animals. The main goal of this overview is to explore the contributions of molecular data to our understanding of subterranean biogeography. I will discuss how recent molecular methods have provided the analytical tools to estimate phylogenetic relationships, population parameters (e.g., migration rates, population structure), and divergence times essential for gaining deeper insights into the colonization, persistence, and adaptation of fauna in subterranean settings. Molecular perspectives are also presented on several different scales, including populations versus species and karst basins versus continental distributions.

THE MOLECULAR PERSPECTIVE

Although classical genetics, where individuals from different populations are crossed to examine the heritability of particular traits, have a long history in biospeleology (Breder, 1943; Sadoglu, 1956), molecular techniques aimed at investigating the genetic variability of cave populations only began in the 1970s with the development of the first major molecular markers, allozymes (protein variants) (Avise and Selander, 1972; Carmody et al., 1972; Hetrick and Gooch, 1973; Laing et al., 1976; Cockley et al., 1977; Turanchick and Kane, 1979; Sbordoni et al., 1979). As the available number of molecular markers increased and the associated analyses became more sensitive and refined, investigations of subterranean biogeography from a genetic perspective became feasible (see Sbordoni et al., 2000 for review).

Currently, molecular studies using mitochondrial gene sequences to investigate population and species level questions are common, including the genes for 12S and 16S rRNA, cytochrome oxidase I, cytochrome B, and NADH dehydrogenase. Nuclear genes (e.g., 28S rRNA) have been less commonly used, and are generally more suitable for higher-level (among species, genera, families) phylogenetic studies. At the level of populations, genetic analyses utilizing molecular data, such as microsatellites (a sequence of DNA containing tandemly repeated units, where the number of repeats varies within and among populations) and DNA sequences, now allow for a vast range of parameters to be estimated and assessed for a particular species. These parameters include estimates of the number of genetic populations, migration rates (i.e., levels of gene flow), and effective population sizes (N_e is a measure of genetic diversity, calculated as the size of a hypothetical population where all of the adults contribute gametes to the next generation; N_e is usually smaller than the actual number of individuals in a population) (see Pearse and Crandall, 2004 for a review of recent advances in population genetics). At higher taxonomic levels (species and genera), molecular markers offer large numbers of characters to be used in phylogenetic (evolutionary) methods, increasing the sensitivity and resolution of the analyses. The following sections describe specific areas of investigation where, in coordination with the strong foundations of traditional biogeographic studies, molecular techniques have the potential to substantially increase our understanding of subterranean biogeography.

DISTRIBUTIONS OF CAVE ADAPTED SPECIES

One of the foundations of biogeographic studies is a solid understanding of the distribution of the species of interest, which can be difficult for cave-adapted species for several reasons. First, cave-adapted faunas are characterized by a suite of unique morphological (loss of eyes and pigmentation, elongation of appendages, hypertrophy of non-optic sensory organs) and physiological (increased life spans and development times, reduced metabolic rates and numbers of eggs) traits. These troglomorphic traits, exhibited on a global scale across diverse taxonomic groups, are one of the most powerful examples of habitat-driven convergence of form (Porter and Crandall, 2003) and one of the few demonstrated cases where convergent morphology can strongly mislead phylogenetic analyses (Wiens et al., 2003). The combination of regressive (lost) and progressive (enhanced) features found in cave-adapted faunas can lead to the existence of cryptic species, where two genetically different species are given one name based on morphological similarities. Even when species are diagnosed properly, convergent morphologies often lead to hypotheses of close evolutionary relationships among highly cave-adapted species, when in fact they represent more distant lineages (Wiens et al., 2003). In some cases, troglomorphic morphologies have led to incorrect taxonomic designations above the species-level; molecular studies of the stygobiotic catfish *Prietella phreatophila* and *Prietella lundbergi* indicate that each is more closely related to species from different genera than they are to each other (*P. phreatophila* to *Ictalurus* species and *P. lundbergi* to *Ameiurus* species; Wilcox et al., 2004). In the absence of obvious morphological differences due to extreme convergence, molecular phylogenetic studies of troglobiotic and stygobiotic species have been successful at diagnosing the presence of taxonomic incongruencies based on cryptic morphologies, thereby changing our understanding of the distribution of subterranean fauna, and their relationships with each other and with epigean species (Chippindale et al., 2000; Parra-Olea, 2003; Buhay and Crandall, 2005).

Due to low population densities, the rarity of encountering some species, and the difficulties associated with collecting in some cave environments, our understanding of the distribution of cave fauna is also hampered by the difficulty in obtaining adult specimens, which are required for accurate species identification and taxonomic scrutiny. These constraints can be overcome by using molecular data to compare immature specimens to adult types of known species. For example, this approach has been used successfully with the *Cicurina* species from Texas, extending the range of the federally endangered *C. madla* to more than twice the number of previously reported caves; however, it is noted that this approach must remain a part of a balanced taxonomic approach by maintaining a taxonomic framework based upon multiple types of biological information (e.g., morphology, molecules, and ecology [Paquin and Hedin, 2004]).

DISPERSAL ABILITY

The phrase "limited dispersal ability" is common throughout the biospeleological literature (Holsinger, 1991; Coineau, 1994; Caccone and Sbordoni, 2001; Baratti et al., 2004). This assumption leads to hypotheses related to the isolation and speciation of cave faunas; limited dispersal abilities result in little to no genetic exchange between populations, allowing isolated populations to become genetically distinct, ultimately to the point of becoming different species. However, this dispersal assumption can be difficult to test empirically, particularly for species that may spend a significant amount of time traversing realms of the karst landscape and associated ground-water habitats that are inaccessible to the human researcher. For example, Buhay and Crandall (2005) used molecular studies of the mitochondrial 16S rRNA gene to investigate the stygobiotic *Orconectes* species in the Appalachians; larger than expected effective population sizes were used to infer the occurrence of a ground-water network unknown to humans but accessible to the crayfish. Furthermore, limited dispersal ability is a qualitative statement, providing no information useful for determining dispersal capabilities relative to habitat or other species. Yet, this tenet of limited dispersal is a central assumption to postulates of the importance of vicariance in subterranean distributions.

Using molecular methods, biospeleologists have begun to quantify the dispersal ability of subterranean fauna, in both relative and absolute terms. Comparing estimated gene flow among populations of cave and forest-dwelling cricket species, Caccone and Sbordoni (1987) demonstrate that cave species have lower rates of gene exchange than epigean species, with the degree of genetic differentiation in hypogean species correlated with the continuity of the limestone habitat. Similarly, in aquatic systems, population differentiation is related to habitat connectivity (Sbordoni et al., 2000). Given that ecological studies have shown that wide-ranging movements are possible for some stygobiotic species, particularly those capable of moving through interstitial habitats, such as ostracods (Danielopol et al., 1994), and that aquatic habitats have generally higher connectivity, stygobionts should have greater dispersal potential and capabilities than troglobionts (Lamoreaux, 2004).

At the heart of this issue are basic questions such as: What constitutes a cave population? What is the vagility of a particular species? How connected are these populations? Is habitat connectivity limiting dispersal? Was the habitat more or less connected in the past? These questions are affected both by intrinsic and extrinsic factors, making a complete answer dependent on understanding both the ecology (dispersal capability) and habitat (dispersal potential) of an organism. Molecular methods can address all of these questions, as the evolutionary history (including past and present dispersal events) is reflected in the genetic differences among populations, species, and genera of subterranean fauna. By delineating populations using genotypic clustering methods, the connectivity of a system can be investigated. For example, different caves in the same hydrologic system representing a single, randomly mating population can readily be identified. Conversely, patterns of genetic differentiation can be used to identify either unseen barriers to gene flow or gene flow across hypothesized geographic barriers; by estimating the phylogenetic structure and divergence times of the stygobiotic amphipod, *Niphargus virei*, Lefébure et al. (2006) found evidence for recent dispersal through apparent geographic barriers.

One of the few cases where molecular studies show strong support for an active migration (dispersal) model is in the anchialine gastropod, *Neritilia cavernicola* (Kano and Kase, 2004). *N. cavernicola* is a stygobiont found in anchialine caves on two islands in the Philippines situated 200 km apart. Genetic studies found no evidence of isolation between the islands, indicating the presence of a marine planktotrophic phase capable of migrating between the islands via ocean currents (Kano and Kase, 2004). Kano and Kase hypothesize that this active migration model, dependent on a larval stage tolerant of marine waters, may be common in anchialine stygobiotic fauna exhibiting disjunct insular distributions.

Migration rates and population structures may be the most interesting genetic parameters to estimate among troglobionts and stygobionts as a method to test the hypothesis that cave-adapted species are indeed poor dispersers relative to epigean organisms, and to quantify the differences in dispersal abilities among troglobionts and stygobionts, and among stygobionts from different subterranean habitats (epikarstic vs. phreatic).

VICARIANCE

In the classic model of vicariance, a once widely distributed ancestral species is fragmented within its range by an external (geological or climatic) event. This fragmentation leads to isolation of different segments (populations) of the species, allowing for genetic differentiation, and often speciation. Important to this model is timing; dating the event leading to fragmentation also provides the time since divergence of the derived set of species. Because this model is tied to external events, examples of vicariance-driven biogeography patterns are most obvious at large scales, including continental movements via tectonic events (Holsinger, 2005; Culver et al., 2007). One of the most widely used (and convincing) methods in biogeography to demonstrate these large scale vicariance patterns is to look for congruence in area cladograms constructed for different sets of species that have similar distributions. Basically, evolutionary relationships are reconstructed among diverse sets of species from a given area, and correlated with geography. If similar patterns of geographic patterning partitioned by evolutionary relationships emerge in many different taxa, there is strong evidence for large-scale vicariant events. Krejca (2005) proposed an even more rigorous test, where an *a priori* hypothesis of divergence patterns is created based on geologic history of a region, which is then tested by comparison to phylogenies constructed for the subterranean fauna of that region. Molecular phylogenetic methods assist these endeavors by making it possible to quickly generate cladograms for large numbers of populations and species. However, these types of broad studies using molecular data have not yet been widely employed to investigate subterranean biogeography (see Krejca, 2005 for an example).

The clearest examples of vicariant events in karst systems are 1) marine regressions (Culver et al., 2007) and 2) extirpation of surface populations from a species with both epigean and hypogean populations. However, in karst systems, patterns resulting from these types of vicariant events are virtually indistinguishable from a distribution resulting from dispersal (Culver et al., 2007). Therefore, perhaps the most promising way to investigate the relative influence of dispersal versus vicariance in karst settings is to study species where both hypogean and epigean populations still co-exist or where closely related surface species have not yet been extirpated. However, even if a surface ancestor still exists, it can be difficult to identify due to the radical morphological changes present in the subterranean morphotype. Higher-level molecular phylogenetic studies offer increased resolution for comparisons across large geographic scales by providing more characters for phylogenetic analyses in organisms where convergence can make morphological characters difficult, and can help elucidate relationships among extant hypogean and epigean relationships (Cooper et al., 2002; Wiens et al., 2003).

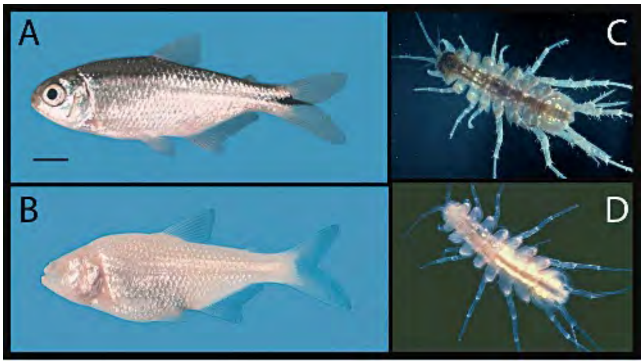

Figure 1. Epigean (A) and hypogean (B) forms of *Astyanax mexicanus*. Scale bar in A = 1 cm. Epigean (C) and hypogean (D) forms of *Asellus aquaticus* (photos provided by B. Sket). Specimen length in each panel = ca. 10 mm.

Some of the best-studied examples of species with both epigean and hypogean populations include the isopod, *Asellus aquaticus*, and the fish, *Astyanax mexicanus* (Fig. 1). In these species, cave-adapted populations occur in the same drainages as epigean populations, offering the ability to investigate processes involved in the colonization and isolation of subsurface populations at the incipient stages of speciation.

Molecular studies of *A. aquaticus* incorporating estimates of population structure indicate that surface populations colonized caves to form stygobiotic populations three times within the Dinaric karst of Slovenia (Verovnik et al., 2004). Furthermore, estimates of divergence time indicate that the subsurface was invaded after the ancestral populations were isolated by vicariant fragmentation, demonstrating the genetic footprint ancestral surface population structures leave in hypogean populations and species. Similarly, molecular investigations of *A. mexicanus* indicate multiple origins of cave populations, representing at least two independent invasions from surface populations, with no measurable gene flow occurring between surface and cave populations (Dowling et al., 2002; Strecker et al., 2003). Again, the phylogenetic analyses indicate that the evolutionary history of the surface ancestors controls the genetic differentiation of the hypogean populations, with three of the four cave populations investigated originating from an ancestral source different from the contemporary surface populations (Strecker et al., 2003, 2004).

Using molecular techniques, this pattern of multiple invasions into subterranean aquatic habitats has been documented for many stygobiotic species (Kano and Kase, 2004; Lefébure et al., 2006), including the stygobiotic dytiscid diving beetle fauna found in calcrete aquifers from western Australia (Cooper et al., 2002; Leys et al., 2003). The dytiscid fauna from this region has invaded the subsurface independently at least 26 times (18 times within the tribe Bidessini and eight times within the tribe Hydroporini; Leys et al., 2003) and based on divergence time estimation shows an evolutionary pattern consistent with a climatic vicariant event, where increasing aridity in the region extirpated a widespread epigean ancestor, driving the evolution of the subterranean diving beetles (climatic relict hypothesis; Cooper et al., 2002; Leys et al., 2003).

From these studies, the importance of the distribution and genetic structure of the ancestral surface species is emphasized in controlling subterranean biogeographic patterns and current genetic relationships. The difficulty lies in elucidating the influence of extinct epigean population structure on subterranean biogeography from processes occurring after the colonization of caves.

DIVERGENCE TIMES

Perhaps one of the most important parameters that can be estimated using molecular data is lineage ages. Placing dates on the origins of a particular cave-adapted lineage is an interesting and thought-provoking exercise, which leaves open the temptation to correlate divergence times with timing of cave colonization. However, it is necessary to remember that the age of a particular lineage does not necessarily correlate with the time of cave invasion (Verovnik et al., 2005). Particularly in highly fragmented surface habitats, epigean populations can be highly isolated, and therefore genetically divergent prior to cave invasion (see previous section [Verovnik et al., 2004]); this situation results in estimated lineage ages much older than time of cave occupancy, leading to misinterpretation of biogeographic determinants. Conversely, if dispersal and subsequent isolation are an important determinant of subterranean biogeography, it is possible for lineages to be younger than time of karst inhabitation. However, by knowing these stipulations and acting conservatively, estimating lineage ages is still a worthwhile endeavor. When combined with information on regional geologic histories, large-scale biogeographic patterns can be linked to either vicariant or dispersal events. Interestingly, most of the studies estimating divergence times using molecular clock methods have investigated stygobionts, and have postulated vicariance models or a mixed model of repeated range expansions and vicariant isolation (Table 1) (Ketmaier et al., 2003; Buhay and Crandall, 2005; Lefébure et al., 2006). In those studies where mixed models were invoked, however, vicariant events were related to larger scale phenomena while dispersal was linked to smaller scale phenomena within karst basins.

Many molecular studies of cave fauna have used gene sequence data to estimate divergence times based on molecular clocks, the assumption that DNA sequences change at a constant rate over time (Table 1) (Zuckerkandl and Pauling, 1965). With an estimate of sequence divergence between two species and a mutation rate in number of base pair substitutions per unit time, preferably calibrated to the taxon of interest, the age since the split can be inferred. There are a number of caveats associated with this type of analysis, however. When rates of evolution are compared within closely related species for the same DNA region, it is generally assumed they display clock-like behavior; however, most datasets appear to violate the clock model (Graur and Martin, 2004). Yet this assumption is rarely tested in studies of cave animals (see Caccone and Sbordoni, 2001 and Leys et al., 2003 for examples testing the assumption of a molecular clock) and the prevalence of many ancient cave adapted lineages may significantly violate any assumption of clock-like evolution. Second, usually mutation rates have not been estimated for the species of interest, so mutation rates from other, sometimes not so closely related, organisms are used. As this rate is used to convert sequence divergence to time, this is a critical assumption. Third, because mutation rates vary among genes, usually estimates are based on a single genetic marker. However, even considering all of these issues, in the absence of good fossil data or geologic events of a known age, molecular clock estimates provide a reasonable first approximation of time (Cooper et al., 2002). In a study of troglobiotic Bathysciine beetles from Sardinia using mitochondrial sequence data from the cytochrome oxidae I gene (COI), Caccone and Sbordoni (2001) illustrate how these caveats can be resolved. First, the assumption of a molecular clock was tested by investigating the linearity of evolution in the COI gene. Next, rates of COI evolution were empirically derived by calibrating sequence divergence to dates from well-defined geological events related to the splitting of the beetle lineages (Caccone and Sbordoni, 2001). These types of studies are extremely useful for calibrating rates of evolution in cave fauna, for investigating the evolution of the troglomorphic form, and for providing rate estimates for divergence time estimations in cave species where well-defined geological events correlating to lineage splitting are lacking.

More recent phylogenetic methods in estimating divergence times relax the assumption of clock-like sequence evolution and allow for multiple molecular markers to be incorporated into the estimate (Thorne et al., 1998; Sanderson, 2002; Thorne and Kishino, 2002; Yang, 2004), but these methods also require calibration points (i.e., fossils or geographic events associated with lineage splitting of known ages) to calculate divergence times

Table 1. Representative studies using molecular data to investigate the biogeography of troglobiotic and stygobiotic species.

Taxa	Genes[a]	Biogeographic model[b]	Region	Estimated Ages of Biogeographic Events	Reference
Troglobiotic					
Arachnida					
Araneae					
Nesticus	ND1	V, D, C	Appalachians, U.S.A.	…	Hedin, 1997
Hexapoda					
Coleoptera					
Ovobathyscioloa	COI	V	Sardinia, Italy	Sea level oscillations 16–5.5 Ma	Caccone and Sbordoni, 2001
Patriziella	COI	V	Sardinia, Italy	Pliocene climate change	Caccone and Sbordoni, 2001
Orthoptera					
Dolichopoda	16S, COI	V	Mediterranean	Pleistocene	Allegrucci et al., 2005
Crustacea					
Isopoda					
Littorophiloscia	COI	V, D	Hawaii, U.S.A.	…	Rivera et al., 2002
Hawaiioscia	COI	V, D	Hawaii, U.S.A.	…	Rivera et al., 2002
Stygobiotic					
Hexapoda					
Coleoptera					
Dytiscidae	COI, 16S, $tRNA_{leu}$, ND1	V	Western Australia	Late Miocene / Early Pliocene	Cooper et al., 2002; Leys et al., 2003
Crustacea					
Amphipoda					
Niphargus virei	COI, 28S	V, D	France	13 Ma	Lefébure et al., 2006
Isopoda					
Asellus aquaticus	COI, 28S	V, D	Dinaric Karst, Europe	8.9–2.9 Ma	Verovnik et al., 2004, 2005
Typhlocirolana	12S, 16S	V	Mediterranean basin	Tethyan events	Baratti et al., 2004
Stenasellus	COI	V, D	Corsica, Sardinia, Tuscany, Pyrenees, Italy	Miocene events and Quaternary glaciations	Kentmaier et al., 2003
Decapoda					
Orconectes	16S	V, D	Appalachians, U.S.A.	Cretaceous	Buhay and Crandall, 2005
Gastropoda					
Neritilia cavernicola	COI	D	Philippines	…	Kano and Kase, 2004
Vertebrata					
Teleostei					
Astyanax mexicanus	cytB, ND2	V, D	North and Central America	4.5–1.8 Ma	Dowling et al., 2002; Strecker et al., 2003; Strecker et al., 2004

[a] Gene region abbreviations: COI = cytochrome oxidase I, cytB = cytochrome B, ND1 = NADH dehydrogenase subunit 1, ND2 = NADH dehydrogenase subunit 2, 16S = 16S ribosomal RNA, 12S = 12S ribosomal RNA, $tRNA_{leu}$=leucine transfer RNA, 28S = 28S ribosomal RNA. All genes included in this table are mitochondrial, except for 28S which is a nuclear gene.

[b] V = vicariance, D = dispersal, C = competition.

across a phylogeny. These schemes are only recently being applied to subterranean biogeographic questions (Leys et al., 2003; Lefébure et al., 2006), and offer interesting research avenues that can correlate the age of a cave with phylogenetic estimates of hypogean divergence times. Using a method that relaxes the molecular clock assumption, Leys et al. (2003) investigated the timing of the transition from surface to subterranean life in the remarkable diversity of stygobiotic dytiscidae found in calcrete aquifers in Western Australia. By estimating divergence times between epigean and hypogean species, and between closely related species pairs that diverged after invasion of the subterranean calcrete habitat, a window was estimated for when the hypogean transition took place. The estimated ages for the eight pairs of species occurring in the same calcrete aquifers ranged from 3.6–8.7 Ma, representing the minimum age of the subterranean lineages. Estimates from hypogean species pairs occurring in different calcrete aquifers (representing independent subterranean invasions) provide a maximum age from 4.8–8.9 Ma, making the window of transition from surface to subterranean habitats from 8.9–3.6 Ma. Interestingly, there was a latitudinal pattern in divergence times coinciding with the onset of aridity, with species pairs from northern localities diverging earlier than southern localities (Leys et al., 2003).

THE FUTURE OF SUBTERRANEAN BIOGEOGRAPHY

There is still much to learn about the processes driving current distributional patterns of organisms from caves and karst systems, and the combination of molecular techniques with the extensive work of subterranean biogeographers offers the potential to refine the questions being asked. Molecular phylogenetics and population genetics offer subterranean biogeography the ability to identify cryptic species, to link unidentifiable juvenile specimens to rare adult morphotypes to expand distributional ranges, to determine dispersal abilities via estimates of gene flow, population structure, and migration rates, and to estimate divergence times. Current molecular studies of hypogean populations overwhelmingly invoke either vicariant hypotheses, of either the ancestral surface or cave populations, or propose a mixed model, linking vicariance with range expansions (i.e., dispersal), to explain subterranean distributional patterns (Strecker et al., 2004; Verovnik et al., 2004; Buhay and Crandall, 2005; Lefébure et al., 2006); few studies have found evidence for a dispersal-only model of biogeography (Kano and Kase, 2004). However, at smaller scales (karst basins), molecular investigations of dispersal abilities offer insights into the connectivity of the subterranean realm. As molecular estimates of parameters such as population structure, migration rates, and divergence times, become more common, it will be possible to investigate how the disparities between troglobiotic and stygobiotic species affect genetic divergence and speciation, and to begin to quantify the dispersal abilities of cave organisms in general. The molecular biogeographical studies of subterranean fauna thus far have provided new perspectives into the distribution patterns of hypogean fauna, reinvigorating the vicariance versus dispersal debate. Finally, many of the molecular analyses used in biogeographic studies (population structure, gene flow, distributions) are also of supreme importance when considering conservation and management issues for subterranean fauna (Buhay and Crandall, 2005). Continued molecular investigations will provide information necessary for identifying the most imperiled cave species needing conservation.

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Annette Summers Engel – Observations on the biodiversity of sulfidic karst habitats. *Journal of Cave and Karst Studies,* v. 69, no. 1, p. 187–206.

OBSERVATIONS ON THE BIODIVERSITY OF SULFIDIC KARST HABITATS

Annette Summers Engel
Department of Geology and Geophysics, Louisiana State University, Baton Rouge, LA 70803 USA, aengel@geol.lsu.edu

Abstract: Recognition of the metabolic process of chemosynthesis has recently overthrown the ecological dogma that all life on earth is dependent on sunlight. In complete darkness, complex ecosystems can be sustained by the energy and nutrients provided by chemosynthetic microorganisms. Many of these chemosynthetically-based ecosystems result from microbial manipulation of energy-rich sulfur compounds that can be found in high concentrations in groundwater. Subsurface environments in general can be highly stressful habitats (i.e., darkness, limited food, etc.), but in the case of sulfidic groundwater habitats, organisms must also tolerate and adapt to different stresses (e.g., toxic levels of gases or lethally low oxygen concentrations). Nevertheless, these habitats, and specifically cave and karst aquifers, have a richly diverse fauna. This review focuses on the biodiversity (as the number and types of species) of sulfur-based cave and karst aquifer systems. The relationships among ecosystem productivity, biodiversity, and habitat and ecosystem stresses are explored. The relatively high numbers of species and complex trophic levels could be attributed to the rich and plentiful, chemosynthetically-produced food source that has permitted organisms to survive in and to adapt to harsh habitat conditions. The geologic age and the hydrological and geochemical stability of the cave and karst aquifer systems may have also influenced the types of ecosystems observed. However, similar to non-sulfidic karst systems, more descriptions of the functional roles of karst aquifer microbes and macroscopic organisms are needed. As subterranean ecosystems are becoming increasingly more impacted by environmental and anthropogenic pressures, this review and the questions raised within it will lead to an improved understanding of the vulnerability, management, and sustainability challenges facing these unique ecosystems.

Introduction

Caves represent discontinuous continental subsurface habitats that are characterized by complete darkness, nearly constant air and water temperatures, relative humidity near saturation, and generally a poor supply of nutrients. Excluding climatic fluctuations that could bring thermally- or chemically-contrasting air or water into a cave's interior, the physical arrangements and constraints of most subterranean habitats have remained relatively unchanged for thousands, if not millions, of years (e.g., Gale, 1992). For most people who have sat in the sunless silence of a cave, the concept that life could flourish in such conditions for even a short period of time is profound. Indeed, colonizing the subsurface requires specific adaptations to the stresses of living in darkness and to the extreme environmental conditions encountered, such as nutrient and energy limitations, the possibility of experiencing oxygen deprivation, high-water pressures due to living at deep aquifer depths, or geochemically variable solutions. Recently, studies have focused on the metabolic and evolutionary mechanisms that address the survival of subsurface- or cave-adapted faunas (e.g., Jones et al., 1992; Howarth, 1993; Hervant et al., 1999a; Porter and Crandall, 2003; Hervant and Malard, 2005; Hüppop, 2005; Lefébure et al., 2006). Due to such specialized adaptations, many species of obligate subsurface troglobites (living in terrestrial habitats) or stygobites (living in aquatic habitats) have high degrees of endemism (Barr, 1967; Culver et al., 2003).

The paucity of a continuous nutrient supply is one of the critical extreme conditions affecting subsurface-adapted fauna, as most are quite dependent on the flux of nutrients and energy from the surface, specifically from photosynthetically-produced organic matter. Often, this material comes in the form of wind-blown, meteoric-, and stream-derived detritus (e.g., particulate matter like leaves or woody debris, or as dissolved organic carbon), or from bat and other animal guano (Barr, 1967; Culver, 1976; Brown et al., 1994; Poulson and Lavoie, 2000; Gibert and Deharveng, 2002; Simon et al., 2003; Hüppop, 2005). Consequently, organisms reliant on the transport of easily-degraded organic matter may experience prolonged periods of starvation. Numerous studies have shown that increased feeding efficiency, lower metabolic rates, slower growth rates, and reduced fecundity are linked to nutritional stress (e.g., Hervant et al., 1999b; Hüppop, 1985, 2005). However, a growing body of evidence reveals that some subsurface and cave ecosystems do not rely exclusively on surface-derived organic matter (e.g., Stevens, 1997; Krumholz, 2000; Amend and Teske, 2005).

In the absence of light, reactive rock surfaces and mineral-rich groundwater provide a wide assortment of potential energy sources that microbial *chemolithoautotrophs* (translated loosely as rock-eating self-feeder) can use to gain cellular energy while making organic carbon molecules from inorganic carbon (i.e. CO_2, HCO_3^-). Chemolithoautotrophs are distinguished from photosynthetic organisms based on whether the energy source is from inorganic chemicals (*litho-*) or from light (*photo-*). Conversely, *heterotrophs* use organic carbon for cellular energy and as a carbon source, and *chemoorganotrophs* use organic compounds for a carbon source and obtain cellular energy from chemical transformations. Chemolithoautotrophs are important to global biogeochemical cycles and ecosystem-level processes because they can cycle various elements simultaneously while generating considerable amounts of organic carbon and serving as the base of ecosystem food webs. Some researchers have hypothesized that subsurface chemolithoautotrophic primary productivity may surpass the activity of photosynthetic organisms on the Earth's surface (e.g., Stevens, 1997).

Prior to the 25th anniversary issue of the Bulletin of the National Speleological Society in 1966, and in the years that followed, the concept that chemosynthesis could sustain subsurface ecosystems was not commonly accepted (nor understood), as chemolithoautotrophic activity was considered insufficient to support ecosystem-level processes (e.g., Schreiber, 1929; Wolters and Schwartz, 1956; Barr, 1966, 1967; Caumartin, 1963; Poulson and White, 1969; Ginet and Decou, 1977). The discovery of chemolithoautotrophically-based ecosystems at the deep-sea hydrothermal vents in the late 1970s (e.g., Jannasch, 1985; Deming and Baross, 1993) toppled the dogma that all life on earth was dependent on sunlight. In 1986, another important breakthrough further changed perceptions of life in the continental subsurface, and of cave ecosystems in general; that discovery was the uniquely diverse chemolithoautotrophically-based ecosystem from the hydrogen sulfide-rich (*sulfidic*) groundwater associated with the Movile Cave, Romania (Sarbu, 1990; Sarbu et al., 1996).

Sulfur, as the 14th most abundant element in the Earth's crust, is biogeochemically important because proteins and other cellular components of all life are comprised of at least 0.5–1% sulfur by dry weight (Zehnder and Zinder, 1980). Nearly all organisms get their required sulfur either from consuming organic sulfur compounds or from assimilatory sulfate reduction. Sulfur exists in a variety of valence states, from the most reduced form as hydrogen sulfide (H_2S) to the most oxidized form as sulfate (SO_4^{2-}). Changes in valency are attributed to the geochemically reactive nature of the various sulfur compounds (e.g., Millero et al., 1987; Megonigal et al., 2005), and prokaryotes (from the domains *Bacteria* and *Archaea*) can gain energy by transforming one valence state to another. Many of the transformations within the sulfur cycle are catalyzed almost exclusively by microorganisms, and biological sulfur cycling must be tightly coupled with oxidation-reduction (redox) reactions to out-compete the abiotic reactions (for a review, see Megonigal et al., 2005). The relationship between the metabolic requirements for sulfur and oxygen (O_2) causes many sulfur-dependent microbes to occupy interface, or gradient, habitats with a range of O_2 concentrations from highly-oxygenated (*aerobic*) to O_2-deprived (*anaerobic*).

Chemolithoautotrophic ecosystems have been identified from marine sediments (e.g., D'Hondt et al., 2002; Amend and Teske, 2005), continental aquifers (e.g., Stevens and McKinley, 1995; Stevens, 1997; Amend and Teske, 2005), and other caves and karst settings (e.g., Pohlman et al., 1997; Vlasceanu et al., 2000; Engel et al., 2004a). In some deep, isolated continental aquifers, chemolithoautotrophic methanogenic microbial communities are supported by the geochemical production of molecular hydrogen (H_2) (Stevens and McKinley, 1995; Amend and Teske, 2005). No higher trophic levels, including microscopic eukaryotes, have been reported to date from these microbial ecosystems; this starkly contrasts with the trophic diversity found at the deep-sea vents and from sulfidic karst systems where sulfur compounds are exploited by chemolithoautotrophs (e.g., Jannasch, 1985; Sarbu et al., 1996; Engel, 2005).

Here I explore the biodiversity of sulfidic cave and karst ecosystems. The motivation for this review was to evaluate the relationships among ecosystem productivity, biodiversity (as the number and types of species), and habitat and ecosystem stresses with respect to ecosystem stability. Of the known locations for sulfidic karst (Fig. 1), there is generally a clumped distribution of systems in North America and Europe. This could relate to the abundance of (bio)speleologists on these continents, but also to the geologic and hydrostratigraphic history of the karst. It is likely that more sulfidic karst systems are distributed worldwide; as such, considerable adventures await. This review concludes with a perspective on the directions of future work.

ORIGIN OF SULFIDIC CAVE AND KARST SYSTEMS

The classic speleogenesis model invokes carbonic acid dissolution of carbonate rocks, usually at shallow depths and rarely far below the water table (e.g., Palmer, 1991). The alternative karstification process of sulfuric acid speleogenesis was initially proposed by S.J. Egemeier from work in Lower Kane Cave, Wyoming (Egemeier, 1981), where groundwater bearing dissolved sulfide discharges as springs into the cave passage. Hydrogen sulfide gas

Figure 1. Approximate locations for sulfidic caves and karst aquifers reported in the literature. Some of the sites are discussed in detail herein.

volatilizes from the groundwater to the cave atmosphere[1] and is oxidized to sulfuric acid on moist subaerial surfaces:

$$H_2S + 2O_2 \leftrightarrow H_2SO_4 \qquad (1)$$

The acid reacts with and replaces carbonate with gypsum ($CaSO_4 \cdot 2H_2O$),

$$CaCO_3 + H_2SO_4 + H_2O \leftrightarrow CaSO_4 \cdot 2H_2O + CO_2 \qquad (2)$$

This speleogenetic process has been suggested to explain the formational history of active cave systems globally (Hubbard et al., 1990; Sarbu et al., 1996; Galdenzi and Sarbu, 2000; Hose et al., 2000; Sarbu et al., 2000), ancient caves like Carlsbad Cavern, New Mexico (Hill, 1996; Polyak and Provincio, 2001), and some continental karst aquifers at or just below the water table (Hill, 1990, 1995; Schindel et al., 2000). Lowe and Gunn (1995) suggest that sulfuric acid may be important for all nascent subsurface carbonate porosity generation, and Palmer (1991, 1995) further speculates that sulfuric acid speleogenesis is more important for the evolution of carbonate-hosted petroleum reservoirs than it is for the origin of caves, as the process has been linked to the karstification of reservoirs, e.g., the Lisburne field in Prudhoe Bay, Alaska (Jameson, 1994; Hill, 1995).

Various biological, geologic, and hydrostratigraphic parameters generate H_2S. As all life generates small amounts of H_2S from the breakdown of sulfur-containing organic compounds (e.g., proteins), H_2S is produced during the decay and decomposition of organic matter, such as in swamps. Microbial reduction of sulfate-bearing minerals, such as gypsum, or dissolved sulfate in marine or fresh water generates H_2S (see discussion below). Microbial

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[1] **A Safety Note:** Cave explorers and researchers working in active sulfidic caves are exposed to harsh conditions, including toxic gases and the possibility of reduced oxygen levels. Hydrogen sulfide is a colorless flammable gas that can cause headaches, dizziness, nausea, and irritability with prolonged, low-level exposure. The rotten eggs odor (detectable to 0.5 ppbv in air) is not a good indicator of the atmospheric concentration; exposure dulls the sense of smell. At higher exposure levels, this desensitization can lead to coma and death. Above 20 ppmv, H_2S causes eye and mucous membrane irritation, and pulmonary edema in few cases. In some caves, concentrations exceeding 100 ppmv have been reported (e.g., Hose et al., 2000). It is recommended that cave air be monitored for H_2S and oxygen, as well as other gases (CH_4, CO) using a multigas monitor (e.g., PhD Ultra Atmospheric Monitor, Biosystems, Middleton, CT) at all times while working in active sulfidic caves. Although the concentration of H_2S may be less than both the OSHA and NIOSH short term exposure limit (STEL) of 10 ppmv for 10 min, acute irritation is possible. Level-C respiratory protection, such as a half-face air-purifying gas mask with organic/acid vapor cartridges (H_2S escape), should also be worn. Such masks are effective for SO_2, organosulfur gases, and radon, but have only short term protection against high H_2S. At high levels, a full-face mask should be used to protect the eyes and facial mucous membranes. Cartridges should be changed regularly when working in sulfidic conditions. H_2S gas negatively affects the sensitivity of oxygen sensors, and any air monitoring device should be checked periodically. Ambient air contains approx. 20.8% oxygen; under no circumstances should anyone enter a cave or passage when oxygen concentrations are $<19.5\%$ unless they have supplied oxygen available to them. According to OSHA, physical work at oxygen levels $<19.5\%$, even with no toxic gases, is impaired due to reduced coordination, dizziness, irritability, and possibly poor circulation. At oxygen levels $<10\%$, vomiting, mental failure, and unconsciousness occur. Concentrations $<6\%$ for 8 min can cause respiratory failure and death.

sulfate reduction is commonly associated with petroleum reservoirs, and basinal brine solutions naturally associated with petroleum often have high concentrations of H_2S; the gas will migrate updip from reservoirs and dissolve into groundwater. Stable sulfur isotope ratio analysis has established that the source of sulfide for many cave and aquifer systems can be attributed to microbial sulfate reduction (e.g., Rye et al., 1981; Stoessell et al., 1993; Hill, 1996). When karst is proximal to volcanic terranes, volcanism gives off H_2S and other gases. Groundwater discharging as geysers, hot springs, or underwater vents will often have high dissolved sulfide content. For example, the source of H_2S and other gases was evaluated by analyzing the N_2/He and He/Ar content and He isotopes of the springs discharging into Cueva de Villa Luz (also known as Cueva de las Sardinas), Mexico (Spilde et al., 2004). The dissolved gases were found to have an upper mantle origin that could be related to El Chichón volcano ~50 km to the west of the cave system (Spilde et al., 2004).

MICROBIAL DIVERSITY WITHIN THE SULFUR CYCLE

Some of the earliest microbiological research regarding chemolithoautotrophic metabolism was done in the late 1880s with sulfur bacteria from sulfidic springs (e.g., Winogradsky, 1887). Much later, the microbiology of sulfidic caves was observational and predominately involved microscopy and culturing (e.g., Caumartin, 1963; Symk and Drzal, 1964; Hubbard et al., 1986, 1990; Thompson and Olson, 1988; Grubbs, 1991; Stoessell et al., 1993; Brigmon et al., 1994; Sasowsky and Palmer, 1994; Mattison et al., 1998; Ulrich et al., 1998; Humphreys, 1999; Latella et al., 1999b). Because cell morphology does not accurately determine species identity, and because most microbes in nature have not been grown in laboratory cultures, especially autotrophs (it has been estimated that <1% of known microbes are culturable; Amann et al., 1995), researchers have turned to genetic studies (culture-independent methods; Amann et al., 1990; Amann et al., 1995) involving the characterization and comparison of (predominately) 16S rRNA gene sequences and their evolutionary relationships. Recently, Barton (2006) summarized some culture-independent genetic methods that have been used to describe microbes from caves. Moreover, to understand the microbial metabolic pathways and the consequences of microbial metabolism on ecosystem function, stable and radiolabelled isotope ratio analyses of the habitat (water, rocks, air, etc.) and the microbial biomass have been done (e.g., Langecker et al., 1996; Sarbu et al., 1996; Airoldi et al., 1997; Pohlman et al., 1997; Humphreys, 1999; Porter, 1999; Vlasceanu et al., 2000; Engel et al. 2004a; Hutchens et al. 2004).

The use of genetic methods has significantly expanded our knowledge of the microbial diversity in active sulfidic cave and karst systems (Vlasceanu et al., 1997; Angert et al., 1998; Vlasceanu et al., 2000; Engel et al., 2001; Holmes et al., 2001; Brigmon et al., 2003; Engel et al., 2003a; Engel et al., 2004a; Hutchens et al., 2004; Barton and Luiszer, 2005; Herbert et al., 2005; Meisinger et al., 2005; Macalady et al., 2006). Evaluation of 16S rRNA gene sequences retrieved from microbial mats from active sulfidic karst systems reveal a diverse range of microorganisms. Available 16S rRNA gene sequences were compiled from various sources and public databases (e.g., GenBank <http://www.ncbi.nih.gov/>); this file consists of 345 partial and full-length sequences (as of May 2006) and is provided as supplemental data for future analytical work <http://geol.lsu.edu/Faculty/Engel/geomicrobiology_publications.htm>. A simple comparison of the available sequences indicates that members of the *Bacteriodetes/Chlorobi* and *Proteobacteria* phyla, and especially bacteria associated with the gamma and epsilonproteobacterial classes, have been identified from all of the studied, active sulfidic caves (Table 1). It is noted, however, that none of the caves have been exhaustively sampled to verify that a microbial group is truly absent from an ecosystem. Moreover, the simple retrieval of gene sequences from a particular habitat does not necessarily mean that those microbes are active in a community. Similarly, metabolic function of uncultured microorganisms is only cautiously assumed from close genetic affiliation to cultured organisms.

To place the microorganisms that have been identified from sulfidic caves and karst systems into the context of the sulfur cycle, an overview of the metabolic diversity of organisms follows. It is not my intention to exhaustively cover each sulfur cycle transformation pathway here and the reader is guided to excellent recent reviews for more information (e.g., Amend et al., 2004; Brimblecombe, 2005; Canfield et al., 2005; Megonigal et al., 2005). Figure 2 illustrates the sulfur cycle in the context of other elemental cycles, including the carbon, nitrogen, and oxygen cycles.

SULFUR OXIDATION

Despite the fact that high concentrations of reduced sulfur compounds, like H_2S gas or elemental sulfur (S^0), are toxic to most organisms (e.g., Somero et al. 1989; Megonigal et al., 2005), these compounds serve as electron donors for microbial metabolism, such as in H_2S oxidation. O_2 is the electron acceptor in this reaction:

$$H_2S + 2O_2 \leftrightarrow SO_4^{2-} + 2H^+ \tag{3}$$

For the purposes of this review, any microbe capable of oxidizing any reduced sulfur compound will be generally referred to as a sulfur-oxidizer. For a vast majority of the sulfur-oxidizing microbes, sulfate is the end product (e.g., Canfield et al. 2005). For others, intermediate products may form, like sulfite ($SO_3{}^{2-}$), thiosulfate ($S_2O_3{}^{2-}$) (Equation 4), tetrathionate ($S_4O_6{}^{2-}$), and S^0 as intra- or

Table 1. Major affiliations for microbial communities found in sulfidic cave or karst systems.

Major Taxonomic Affiliation	Movile Cave (Romania)[a]	Frasassi Caves (Italy)[b]	Lower Kane Cave (Wyoming)[c]	Parker's Cave (Kentucky)[d]	Big Sulphur Cave (Kentucky)[e]	Cesspool Cave (Virginia)[f]	Glenwood Springs (Colorado)[g]
Bacteria							
Acidobacteria	•	•	•				
Actinobacteria			•				•
Bacteroidetes/Chlorobi	•	•	•	•	•	•	•
Chloroflexi		•	•				•
Deferribacteres		•					
Fibrobacter			•				
Firmicutes/ low G+C	•	•	•				•
Flexistipes							•
Nitrospirae	•		•				•
Proteobacteria			•				
Alphaproteobacteria	•		•				
Betaproteobacteria	•	•	•		•	•	
Deltaproteobacteria	•	•	•			•	•
Gammaproteobacteria	•	•	•	•	•	•	•
Epsilonproteobacteria	•	•	•	•	•	•	•
Planctomycetes	•		•		•		
Spirochaetes			•				
Termite Gut 1		•					
Verrucomicrobium	•	•	•				
Candidate Divisions	•	•	•	•			•
Archaea							
Euryarchaeota							
Thermoplasmata							•
Methanomicrobia	•	•	•				
Fungi	•			•			

[a] 16S rRNA gene sequences from Vlasceanu et al. (1997), Vlasceanu (1999), Hutchens et al. (2004), and Engel and Porter (unpublished data).
[b] 16S rRNA gene sequences from Vlasecanu et al. (2000) and Macalady et al. (2006).
[c] 16S rRNA gene sequences from Engel et al. (2003a), Engel et al. (2004a), and Meisinger et al. (2005).
[d] 16S rRNA gene sequences from Angert et al. (1998).
[e] 16S rRNA gene sequences from Engel and Porter (unpublished data).
[f] 16S rRNA gene sequences from Engel et al. (2001) and Engel and Porter (unpublished data).
[g] 16S rRNA gene sequences from Barton and Luizer (2005), and Engel and Porter (unpublished data).

extra-cellular sulfur globules (Equation 5); these intermediates can be further oxidized to sulfate (Equations 4 and 6) (Fig. 2):

$$S_2O_3^{2-} + H_2O + 2O_2 \leftrightarrow 2SO_4^{2-} + 2H^+ \qquad (4)$$

$$HS^- + {}^1\!/_2O_2 + H^+ \leftrightarrow S^0 + H_2O \qquad (5)$$

$$4S^0 + 6O_2 + 4H_2O \leftrightarrow 4SO_4^{2-} + 8H^+ \qquad (6)$$

Because of the large cell size and filamentous nature of some species (Fig. 3A), sulfur-oxidizing bacteria can be readily observed in conspicuous and sometimes extensive microbial mats that either attach to substrata or float in the water column in sulfidic cave streams (Fig. 3B), in karst aquifers (Fig. 3C), or in anchialine cave and stratified cenote systems (water-filled sinkholes) (Fig. 3D, in this case showing non-white mats) (e.g., Hubbard et al., 1986, 1990; Olson and Thompson, 1988; Thompson and Olson, 1988; Grubbs, 1991; Brigmon et al., 1994; Sarbu et al., 1996; Airoldi et al., 1997; Vlasceanu et al., 1997; Angert et al., 1998; Mattison et al., 1998; Humphreys, 1999; Hose et al., 2000; Sarbu et al., 2000; Gary et al., 2002; Engel et al. 2003a; Garman and Garey, 2005; Barton and Luiszer, 2005; Macalady et al., 2006; Randall, 2006). Many of the species from the alpha- ($\alpha-$), beta- ($\beta-$), gamma- ($\gamma-$), and epsilonproteobacterial ($\varepsilon-$) classes found in microbial mats from caves are associated with sulfur oxidation. Although some *Archaea* have been identified (e.g., *Thermoplasma acidophilum* from the Glenwood Hot Pool Spring, Colorado; Barton and Luiszer, 2005), *Archaea* capable of oxidizing reduced sulfur compounds (e.g., Canfield et al., 2005) have not been found from sulfidic caves to date.

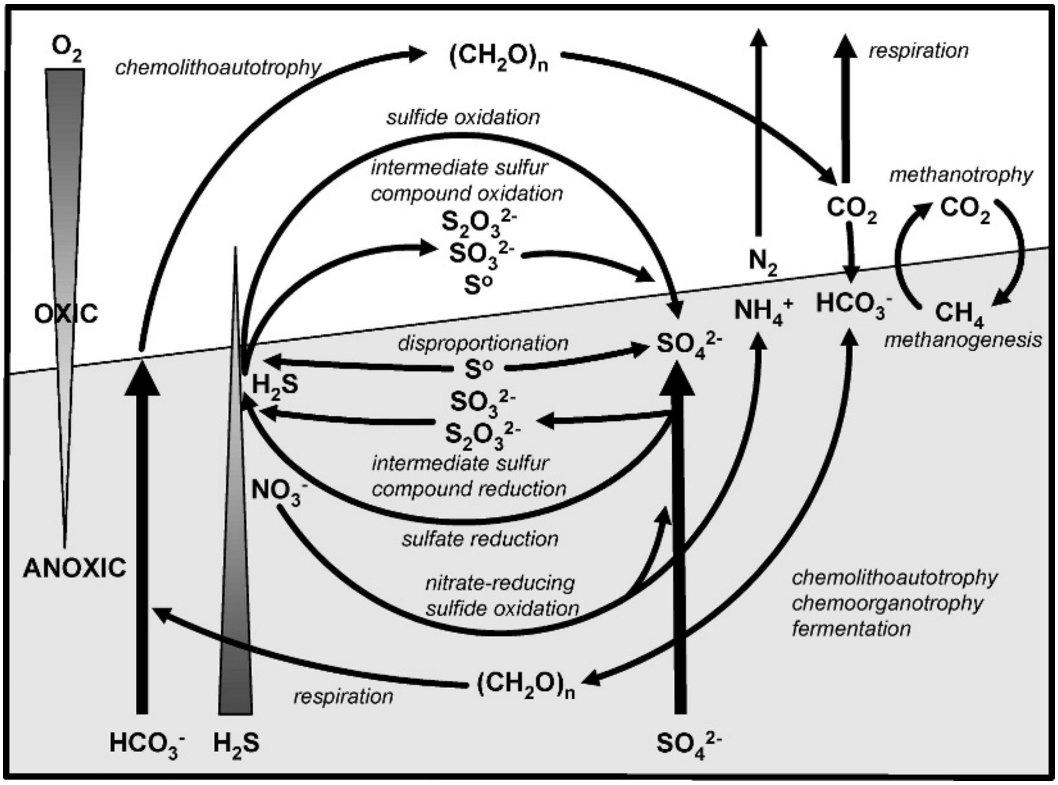

Figure 2. Schematic of integrated biogeochemical cycling in microbial ecosystems related to the sulfur, oxygen, carbon, and nitrogen elemental cycles.

Recent research demonstrates that sulfur-oxidizing bacterial communities in cave microbial mats depend on relatively stable O_2 concentrations and availability (Engel et al., 2004a), although some species can tolerate, and may even prefer, extremely low concentrations of O_2 (<1 mg L^{-1} dissolved O_2) for prolonged periods of time (e.g., Takai et al., 2003). If the concentration of O_2 is too low for growth, nitrate can be used as an electron acceptor (e.g., Sayama et al., 2005); depending on the metabolic pathway, either N_2 (Equation 7) or ammonium (NH_4^+) can form (Equation 8):

$$5H_2S + 8NO_3 \leftrightarrow 5SO_4^{2-} + 4N_2 + 4H_2O + 2H^+ \quad (7)$$

$$H_2S + NO_3^- + H_2O \leftrightarrow SO_4^{2-} + NH_4^+ \quad (8)$$

Some microbes, such as *Beggiatoa* spp., form S^0 from the oxidation of H_2S with nitrate (Equation 9), which can be further oxidized with nitrate (Equation 10) (e.g., Sayama et al., 2005):

$$4H_2S + NO_3^{2-} + 2H^+ \leftrightarrow 4S^0 + NH_4^+ + 3H_2O \quad (9)$$

$$3NO_3^- + 4S^0 + 7H_2O \leftrightarrow 3NH_4^+ + SO_4^{2-} + 2H^+ \quad (10)$$

Because many fresh water systems are nitrogen-limited, the nitrate-reducing sulfur-oxidizing bacteria (NRSOB) generate nitrogen compounds that other organisms in the ecosystem can use (e.g., $NH^+{}_4$), thereby linking the sulfur cycle to the nitrogen cycle (Fig. 2). NRSOB have been identified from several cave and karst aquifers (e.g., Lawrence and Foster, 1986; Mattison et al., 1998), and these organisms may extend the depths to which sulfur, and consequently carbon and nitrogen, are cycled in oxygen-depleted waters of sulfidic karst aquifers (Engel et al., 2004b).

The presence of ε-*proteobacteria* in all of the sulfidic caves studied thus far is exciting. A recent study of ε-*proteobacteria* by Campbell et al. (2006), using a large dataset of geographic, genetic, and ecological information, reveals that members of this class are not only in sulfidic caves, but also numerous other sulfur-rich habitats, including marine waters and sediments, deep-sea hydrothermal-vent sites and vent-associated animals, groundwater associated with oilfields, and from terrestrial and marine sulfidic springs. The best studied terrestrial system where ε-*proteobacteria* have been described is Lower Kane Cave (Campbell et al., 2006). Quantification of different microbial groups using genetic approaches reveals that up to 100% of some samples is comprised of ε-*proteobacteria*, making Lower Kane Cave the first non-marine natural system known to be driven by the activity of filamentous ε-*proteobacteria* (Engel et al., 2003a). The majority of the 16S rRNA sequences could be assigned to two lineages distinct at the genus level, LKC group I and LKC group II (Engel et al., 2003a; Engel et al., 2004a), and LKC group II was found to be predominately responsible for sulfuric acid

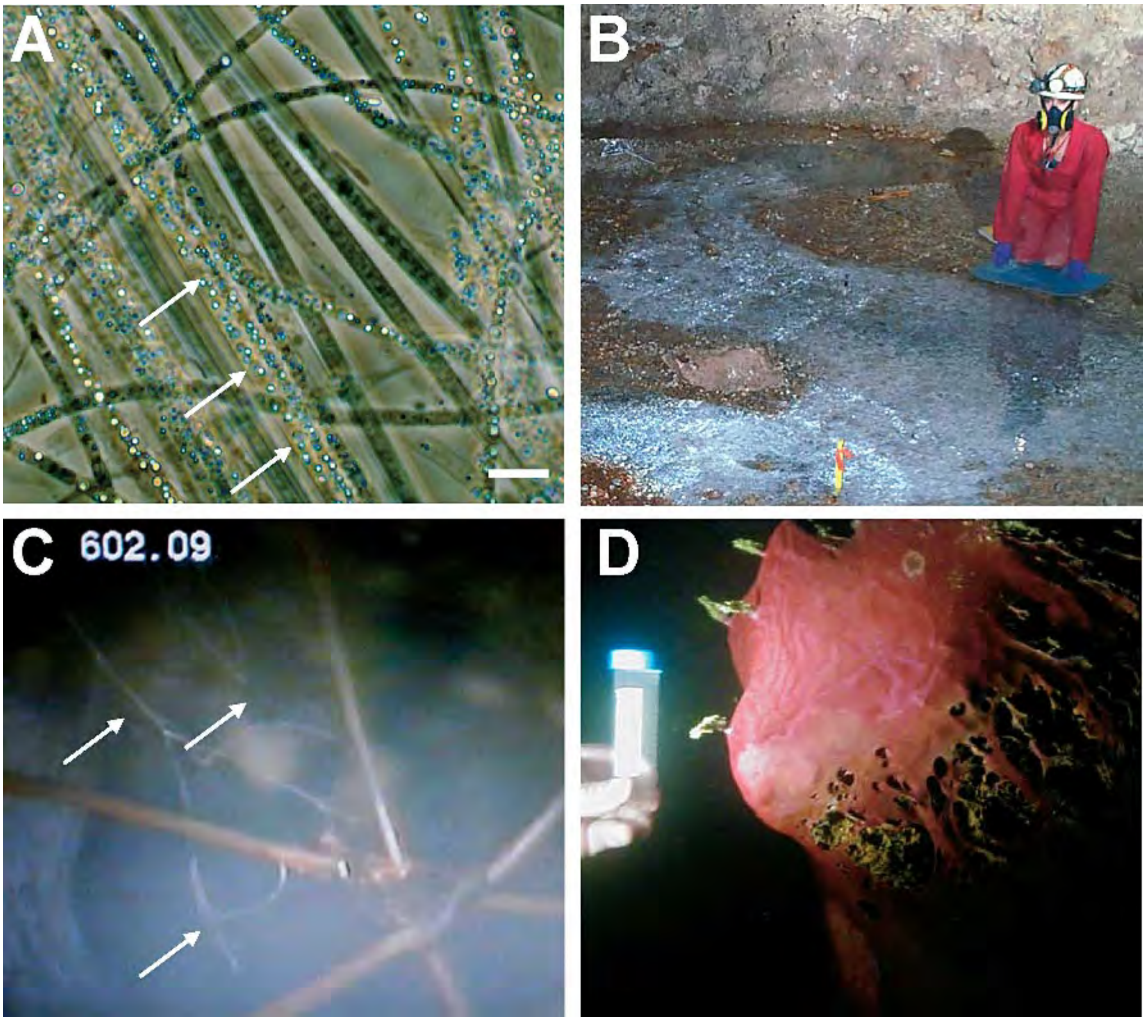

Figure 3. (A) Filamentous and rod-shaped microbial cells of sulfur-oxidizing bacteria. Arrow, sulfur globules. Scale is 10 microns. (B) White microbial mat in sulfidic stream, Lower Kane Cave, Wyoming. (C) Arrows pointing to white filaments suspended in sulfidic water of an open-hole well in the Edwards Aquifer. Field of view is ~6 inches. Number at upper left refers to well depth in feet (183.5 m) from the surface (image digitally captured from video provided by the Edwards Aquifer Authority, San Antonio, Texas). (D) Biofilm of purple sulfur bacteria covering carbonate rock in La Pilita cenote, of the Sistema Zacatón, Mexico.

dissolution of the cave host limestone (Engel et al., 2004b). Certain ε-proteobacterial groups correlated to high dissolved sulfide and low dissolved O_2 content in the cave streams, suggesting that some species prefer different geochemical conditions (Engel et al., 2004a).

Another diverse group of microbes that use H_2S (or H_2) as an electron donor during anoxygenic photosynthesis includes the purple sulfur bacteria (e.g., *Chromatium*, *Thiocapsa*, *Ectothiorhodospira*), the purple nonsulfur bacteria (e.g., *Rhodobacter*), the green sulfur bacteria (e.g., *Chlorobium*, *Pelodictyon*), the green nonsulfur bacteria (*Chloroflexus*, *Oscillochloris*), and the *Heliobacteria* (e.g., Brimblecombe, 2005; Canfield et al. 2005). Some of the species oxidize reduced sulfur completely to sulfate (Equation 11), while others form intermediate sulfur compounds (Equation 12), where CH_2O represents organic carbon compounds made during photosynthetic CO_2 fixation:

$$3CO_2 + H_2S + 2H_2O \leftrightarrow 2CH_2O + SO_4^{2-} + 2H^+ \quad (11)$$

$$CO_2 + 2H_2S \leftrightarrow CH_2O + H_2O + 2S^0 \quad (12)$$

These organisms have been found in sulfidic springs (e.g., Elshahed et al., 2003; Barton and Luiszer, 2005) and cenotes (e.g., Stoessell et al., 1993; Humphreys, 1999; Gary et al., 2002; Herbert et al., 2005) (Fig. 3D), and are likely to be significant contributors to ecosystem sulfur and carbon cycling in those habitats. Because of the need to photosynthesize, these groups should not be found in complete darkness; however, *Chloroflexus* spp. have been described from Lower Kane Cave (Meisinger et al., 2005) and the Frasassi Caves (Grotta Grande del Vento-Grotta de Fiume-Grotta Sulfurea), Italy (Macalady et al., 2006) (Table 1), and may be present in Cueva de Villa Luz (Cueva de las Sardinas), Mexico (Hose et al., 2000). It is suspected that these species may be able to grow in the dark using alternative pathways for energy and carbon fixation (e.g., Canfield et al., 2005).

Generally, abiotic conditions influence the types of organisms that a habitat can support. Most sulfur-oxidizers require neutral pH conditions to buffer metabolic acidity (Ulrich et al., 1998; Brimblecombe, 2005), and the buffering capacity of dissolving carbonates may be one reason why sulfur-oxidizers are prevalent in karst. Yet, some sulfur-oxidizers (e.g., *Acidothiobacillus*) thrive in low pH environments as acidophiles (acid-lovers). In active sulfidic caves, such as in Cueva de Villa Luz, extremely low pH habitats have been described, especially on subaerial cave-wall surfaces. Biofilms on subaerial, cave-wall surfaces (also described as snottites, mucotites, microbial draperies, or cave-wall biofilms by different investigators over the years) have been described from active sulfidic caves and mines (Johnson, 1998; Vlasceanu et al., 2000; Engel et al., 2001; Engel et al., 2003b). In Cueva de Villa Luz, for example, measured cave-wall pH associated with 'snottites' was 0 (Hose et al., 2000). Culture-dependent and culture-independent studies revealed diverse populations of *Thiobacillus, Sulfobacillus*, *Acidimicrobium*, and other groups, such as the *Firmicutes* (Hose et al., 2000; Vlasceanu et al., 2000; Engel et al., 2001; Engel et al., 2003b).

SULFATE REDUCTION AND SULFUR DISPROPORTIONATION

Reduced sulfur compounds originate from several sources, including abiotic processes (e.g., volcanism), the degradation of organics (e.g., proteins), or dissimilatory sulfate reduction whereby oxidized compounds (e.g., $SO_4{}^{2-}$) serve as electron acceptors under anaerobic conditions; elemental sulfur can also be reduced to H_2S (Fig. 2). Sulfate (or S^0) can be reduced using H_2 as the electron donor (Equation 13) or using organic compounds, such as acetate (Equation 14) or lactate (although numerous organic compounds can be used):

$$4H_2 + SO_4^{2-} + H^+ \leftrightarrow 4H_2O + HS \qquad (13)$$

$$CH_3COO + SO_4^{2-} \leftrightarrow 2HCO_3^- + H_2S \qquad (14)$$

The utilization of organic compounds by sulfate-reducers, either as complete oxidation (e.g., acetate) to CO_2 or the incomplete oxidation of other compounds, again links the sulfur and carbon cycles.

Molecular investigations of some sulfidic aquifers, including those associated with oilfields, have documented sulfate-reducers (Voordouw et al., 1996; Ulrich et al., 1998); thus far, studies identifying these organisms in active sulfidic caves have been limited to Lower Kane Cave and the Frasassi Caves (Engel et al., 2004a; Meisinger et al., 2005; Macalady et al., 2006). A genetically varied group of microbes are known to carry out dissimilatory sulfate reduction, but the sulfate-reducers that have been found in sulfidic karst systems predominately fall within the *δ-proteobacteria* class (Table 1). The other groups of sulfate-reducers grow at 70 to 105 °C (Brimblecombe, 2005; Canfield et al., 2005), well above the temperatures of currently explored, active sulfidic cave and deep aquifer systems.

Another recently recognized, environmentally significant sulfur transformation pathway is disproportionation (e.g., Brimblecombe, 2005; Canfield et al., 2005). During disproportionation, intermediate sulfur compounds that were produced during incomplete oxidation, such as S^0 or $S_2O_3{}^{2-}$ (Equation 15), form both reduced and oxidized forms of sulfur (Fig. 2):

$$S_2O_3^{2-} + H_2O \leftrightarrow H_2S + 3SO_4^{2-} \qquad (15)$$

Several groups of microbes disproportionate sulfur compounds, including anoxygenic phototrophs, some sulfate-reducers (e.g., *Desulfovibrio* and *Desulfobulbus* spp.), and sulfate-reducing bacteria that perform sulfur disproportionation as their sole metabolism (e.g., *Desulfocapsa* spp.). In general, characterization of sulfate- and S^0-reducing or sulfur-disproportionating microbes from sulfidic caves and aquifers has not been thoroughly done, although *Desulfocapsa thiozymoxenes* has been found in Lower Kane Cave and the Frasassi Caves (Engel et al., 2004a; Meisinger et al., 2005; Macalady et al., 2006). Where O_2 can abiotically oxidize reduced sulfur compounds, the reductive and disproportionation pathways generate supplemental sulfide that sulfur-oxidizing bacteria within the microbial mats can use (Engel et al., 2004a).

FAUNAL INVENTORIES

The fauna of cave and karst aquifer ecosystems have not been exhaustively sampled nor characterized (i.e. large, conspicuous animals are easy to see and describe), and obligate cave fauna have been inadequately identified (e.g., Culver et al., 2004). Similarly, microscopic eukaryotes (e.g., fungi, molds, protozoa) and micro-invertebrates (e.g., copepods) are almost virtually unknown for most subterranean systems, despite the extensive work done on microbes involved in sulfur cycling and descriptions of the chemolithoautotrophic microbial communities (see previous section of text) (e.g., Angert et al., 1998; Engel et al., 2004a; Hutchens et al., 2004; Barton and Luiszer, 2005; Macalady et al., 2006) (Table 1). Nevertheless, Culver and Sket (2000) illustrate that some of the most biologically diverse karst ecosystems (based on the numbers of species, exclusively) are associated with sulfidic waters, especially when considering systems with a high number of endemic populations. Such systems include the Movile Cave, the Edwards Aquifer in Texas, and the anchialine Washingham Caves in Bermuda. Most notable on their list is the chemolithoautotrophically-based ecosystem of the Movile Cave, with 30 terrestrial species (24 are cave-adapted and endemic) and 18 aquatic species (9 cave-adapted and endemic) (Sarbu et al., 1996; Culver and Sket, 2000). However, not all sulfidic caves or aquifers are known for high species numbers, as is the case for Lower Kane Cave with only four identified species (Porter, unpublished data) (Table 2). Part of this difference in the number of higher trophic level species in sulfidic cave and karst systems may be attributed to the invasion history of animals in the region (e.g., Christman and Culver, 2001) and the age of the system, as Lower Kane Cave is likely to be quite young geologically (e.g., Stock et al., 2006) compared to the other caves (e.g., Longley, 1986; Oetting et al., 1996; Engel, 1997; Groscehen and Buszka, 1997; Sarbu et al., 2000).

For the purpose of this review, the known faunal inventories for some sulfidic caves and karst aquifers are provided (Table 2); the compiled lists of species numbers (available at <http://geol.lsu.edu/Faculty/Engel/geomicrobiology_publications.htm>) result from combing through the literature, the World Wide Web (<http://www.karstwaters.org/kwidata.htm>), and by personally contacting individual research groups. To my knowledge, no summary like this has been previously assembled for sulfidic cave and karst aquifer systems. A note of caution: these lists are not inclusive and they likely contain errors because they were compiled from many different, including previously unpublished, sources. Although the biodiversity of some submarine caves has been studied (e.g., Grotta Azzura; Mattison et al., 1998), the focus of the next section is limited to continental systems.

In short, sampling caves is tricky work, but sampling sulfidic caves is definitely more complicated (see footnote 1). Similarly, sampling groundwater can also be difficult (e.g., Ghiorse and Wilson, 1988; Krumholz, 2000). Therefore, sampling biases may have caused the incomplete and inaccurate picture of species richness and distribution for sulfidic systems (e.g., Culver et al., 2004; Schneider and Culver, 2004; van Beynen and Townsend, 2005). Certainly, the novelty of the Movile Cave ecosystem may have prompted the years of investigations (e.g., Plesa, 1989; Sarbu, 1990; Georgescu and Sarbu, 1992; Decu and Georgescu, 1994; Decu et al., 1994; Georgescu, 1994; Poinar and Sarbu, 1994; Weiss and Sarbu, 1994; Sarbu et al., 1996; Vlasceanu et al., 1997; Manoleli et al., 1998; Porter, 1999; Vlasceanu, 1999; Hutchens et al., 2004). Moreover, in some faunal descriptions, organisms were only characterized to the family or order levels, and some genus- and species-level identifications have changed over the years due to more detailed systematics and molecular phylogenetics. Future work should concentrate on completing and verifying the list because these issues obviously inhibit a thorough statistical comparison of sulfidic karst-system biodiversity and presently hinder any evaluation of the possible economic value of these systems (e.g., Fromm, 2000; Gibert and Deharveng, 2002; van Beynen and Townsend, 2005).

MICROSCOPIC EUKARYOTES

The diversity of the microbial eukaryotes (e.g., fungi, protists, etc.) in sulfidic cave and karst aquifers has been poorly measured, despite the importance of these organisms to ecosystem function. Several fungal groups have sulfur-based metabolism, like sulfur gases consumption and production, and fungi also play a role in concrete corrosion associated with methanethiol (CH_3SH) consumption. These studies suggest that fungi may be an overlooked part of the sulfur cycle in these systems, and may be important to limestone dissolution (e.g., Burford et al., 2003). Fungi, ciliated protozoa, and rotifers have been described from the sulfidic waters in Grotta di Fiume Coperto, Italy (Latella et al., 1999a; Maggi et al., 2002) (Tables 1 and 2). Not shown in Table 2, however, are the results from a survey from the Sulphur River passage of Parker's Cave, Kentucky, which identified 13 genera of protozoa (from eight orders), including species common to sulfidic habitats and associated with grazing (Thompson and Olson, 1988). Fungi and rotifers (also unclassified) have been reported from Movile Cave (Sarbu, 1990).

INVERTEBRATES

Phylum Platyhelminthes

Although the diversity of the flatworms is high in non-sulfidic subterranean settings, only *Dendrocoelum* sp. has been reported from Movile Cave (Sarbu, 1990). Flatworms have also been observed in Lower Kane Cave and Cueva de Villa Luz, but no identification was done.

Phylum Nematoda

Several new species of stygobitic nematodes have been described from sulfidic karst aquifers (e.g., Moravec and Huffman, 1988; Poinar and Sarbu, 1994). Although *Chronogaster troglodytes* sp. n. from Movile Cave is bacterivorous, *Rhabdochona longleyi* sp. n. from the Edwards Aquifer was found infecting the intestines of the two blind catfishes, *Trogloglanis pattersoni* Hubbs & Bailey 1947 and *Satan eurystomus* Eigenmann 1919 (Moravec and Huffman, 1988).

Phylum Annelida

This group is represented by aquatic worms and leeches, both of which have been described from just two sulfidic cave systems (Table 2). Most notable is *Haemopis caeca* Manoleli, Klemm & Sarbu 1994, the cave leech endemic to Movile Cave and the surrounding sulfidic karst aquifer (Manoleli et al., 1998). Annelids have been reported from the Sulphur River passage of Parker's Cave, but no details are given (Thompson and Olson, 1988). Tubificid worms

Table 2. Estimated number of species reported for sulfidic caves and karst aquifers, including accidentals (i.e. surface invaders); bats and salamanders are not included in the aquatic counts. * refers to a possible occurrence, but no formal description (the symbol is also used if an origin could not be verified). Note that some organisms are not limited to the sulfidic portions of the systems, but have been described from the freshwater component of a cave or aquifer (e.g., in the case of the Frasassi Caves). For the Edwards Aquifer, however, taxa recorded from only the sulfidic part of the system are enumerated. Full species lists can be found at <http://geol.lsu.edu/Faculty/Engel/geomicrobiology_publications.htm>.

	Movile Cave (Romania)		Frasssi Cave (Italy)		Grotta di Fiume Coperto (Italy)		Cueva de Villa Luz (Mexico)		Edwards Aquifer (Texas) aquatic	Lower Kane Cave (Wyoming)	
	terrestrial	aquatic	terrestrial	aquatic	terrestrial	aquatic	terrestrial	aquatic		terrestrial	aquatic
Oligohymenophorea (ciliate protozoa)						1					
Rotifera		2				1					
Platyhelminthes (flat worms)		1						*			*
Nematoda (round worms)		3							1		
Annelida											
Oligochaeta (aquatic worms)		3		1							
Hirudinea (leeches)		1				1					
Mollusca											
Gastropoda (snails)		1		1	2	1	*	1			1
Archnida											
Acari (mites, ticks)	1		1				~80				
Aranaea (spiders)	5		5		3		13			1	
Pseudoscorpiones (false scorpions)	3		1		2		6				
Schizomida (whip scorpions)							1				
Scorpiones (scorpions)					1		*				
Crustacea											
Copepoda (copepods)		3				3		*			
Ostracoda (ostracods)		1									
Amphipoda (amphipods)		2		1		1			*		
Isopoda (isopods)	4	1	1		3	1		*			
Decapoda (shrimp, crayfish, crabs)								1			
Myriapoda											
Chilopoda (centipedes)	3				3						
Diplopoda (millipedes)	1				1						
Symphyla (garden centipedes)	1						*				
Hexapoda											
Ellipura (collembola)	3		2				23			1	
Insecta											
Coleoptera (beetles)	4		2		3		6				
Diptera (flies)	2				2		*	1			
Hymenoptera (wasps, ants, bees)							10				
Orthoptera (crickets, cockroaches)					2		*				
Lepidoptera (moths, butterflies)					1		*				
Hemiptera (bugs, aphids)							1				
Heteroptera (true bugs)		1				1		2			
Psocoptera (barklice, booklice)							1				
Thysanura (silverfish)							2				
Vertebrata											
Osteichthyes (fish)								1	2		
Anguilliformes (eel)				*				*			
Totals	27	19	12	3	23	10	~143	~6	3	2	2

have also been described from sediments in sulfidic cave streams where surface water can back-flood into the cave passages (e.g., Lower Kane Cave), although no formal descriptions have been made.

Class Mollusca

Even though non-sulfidic caves can be colonized by both terrestrial and aquatic snails, few descriptions of gastropods from sulfidic caves and aquifers are known (Table 2). In the case of land snails, this is most likely due to the lack of communication with the surface whereby snails can be washed into a cave. Described aquatic snails include the endemic prosobranch snail, *Heleobia dobrogica* Bernasconi 1991, from Movile Cave (Bernasconi, 1997), populations of *Islamia* spp. in the sulfidic stream portions of the Grotta di Fiume Coperto and the Frasassi Caves (Latella et al., 1999a; Sarbu et al., 2000; Maggi et al., 2002), and the endemic snail *Physella* (formerly *Physa*) *spelunca* Turner & Clench 1974 from the sulfidic streams in Lower Kane Cave (Porter et al., 2002; Wethington and Guralnick, 2004). A sister species, *Physella johnsoni* Clench 1926, has also been reported from sulfidic springs (one in a cave) on Sulphur Mountain in Banff National Park, Canada (Lepitzki, 2002; Wethington and Guralnick, 2004). The *P. spelunca* population in Lower Kane Cave is tremendous, with an estimated 6,800 individuals per square meter (Porter et al., 2002). *P. spelunca* was originally described as being troglomorphic (i.e. pigmentless, no eyes), but observations indicated there were at least two other color morphs (red and black) although genetic variation from the cave populations has not been identified to date (Porter et al., 2002). Two species of snails, with high population densities, have been observed, but not yet described, from Cueva de Villa Luz (K. Lavoie, personal communication).

Class Arachnida

Because many of the sulfidic caves are in poor communication with the surface, the colonization of these caves by arachnids (e.g., mites, spiders, scorpions) has been limited, except in the case of systems with many entrances or with large bat populations. These have high arachnid diversity (Table 2). Most notable are the numbers of different arachnid species reported from Cueva de Villa Luz, and the ~80 species of acarians, representing five orders. The microarthropods have been the subject of extensive research by one group and of several Masters theses (Palacios-Vargas et al., 1998; Palacios-Vargas et al., 2001;Estrada, 2005; Pastrana, 2006); the account of the arachnids in this one cave is likely due to that concentrated effort. Moreover, seven species of bats representing three different families have been described from Cueva de Villa Luz, and most of the microarthropods were found associated with bat guano or surface-derived material proximal to cave entrances (Palacios-Vargas and Estrada, personal communication). Several acarians (*Sejus* sp., *Gamasellodes* sp., *Protolaelaps* sp.) are found near the sulfidic cave stream and the microbial mats (Palacios-Vargas and Estrada, personal communication). Two possibly new species of mites, *Dactyloscirus* sp. and *Neoscirula* sp. (Cunaxidae family), have been found near the microbial mats in the sulfidic water of Cueva de Villa Luz (Estrada and Mejía-Recamier, 2005). Undescribed acarians have also been reported from the Sulphur River passage of Parker's Cave (Thompson and Olson, 1988). Troglobitic spiders have been described from both Movile Cave (five species, each representing their own order) and the Frasassi Caves (two species from one order) (e.g., Georgescu and Sarbu, 1992; Georgescu, 1994; Weiss and Sarbu, 1994; Sarbu et al., 2000). *Nesticus* spp. have been reported from acidic cave walls in both of these caves, and spider webs commonly have low pH droplets hanging from them. Drops also form on webs from the linyphiid spider, *Phanetta subterranea* Emerton 1875, in the Sulphur River passage in Parker's Cave (Thompson and Olson, 1988).

Subphylum Crustacea

Much like the microbial eukaryotes, micro-invertebrates have been poorly studied from sulfidic caves and karst aquifers. Several species of copepods and ostracods have been described from only two caves (Table 2). Movile Cave hosts an endemic copepod and ostracod (Plesa, 1989). Additionally, within the Order Amphipoda there are few described species from sulfidic caves or aquifers (Table 2); however, given the prevalence and diversity of amphipods in non-sulfidic caves globally (e.g., Culver and Sket, 2000; Gibert and Deharveng, 2002), and their metabolic flexibility and high tolerance of hypoxia (e.g., Macneil et al., 1997; Hervant et al., 1999a; Hervant et al., 1999b; Kelly et al., 2002; Lefébure et al., 2006), it is surprising that more amphipods have not been identified. A few stygobitic isopods have been characterized from sulfidic systems, although comparatively more troglobitic isopods have been described (Table 2).

One habitat that has high potential for crustaceans is sulfidic groundwater (despite the fact that even fresh groundwater has not been adequately sampled). Longley (1981) asserted that the Edwards Aquifer in Central Texas had the potential to be the most diverse subterranean biological community on earth, although little work has been done to verify the proclamation. The sulfidic (badwater) portion (Rye et al., 1981; Oetting et al. 1996; Ewing, 2000) of the aquifer has been virtually unexplored biologically and has the potential to host a unique fauna (see description below of the Osteichthyes), including microbes (e.g., Grubbs, 1991). The non-fungal microbiology has recently been described for a portion of the sulfidic aquifer in the San Antonio area (Randall, 2006; Engel, unpublished data). Overall, ~91 species or subspecies of animals have been described from the entire Edwards Aquifer, including 44 endemic stygobites (Ourso and Horning, 2000). One sampled artesian well in San Marcos, Texas, reportedly has ~10 species of amphipods, from numerous families (Holsinger, 1980). Several descriptions of stygobitic amphipods indicate that some species, such as *Artesia subterranea* Holsinger 1980, were retrieved from warm mineral water from artesian wells (Holsinger, 1966, 1980), which may be taken to mean that the species was retrieved from a sulfidic well. This phenomenal crustacean diversity deserves attention, and verification is needed if any of these species are living in the sulfidic portion of the aquifer.

Superclass Hexapoda

The types of hexapods described from sulfidic cave and karst systems include collembolans and insects, and the group is dominated by terrestrial species (Table 2). Among the species described, endemic troglobites have been reported from Movile Cave (e.g., Decu and Georgescu, 1994) and the Frasassi Caves (Sarbu et al., 2000). Numerous hexapods, particularly among collembolans and hymenopterans, have been inventoried from Cueva de Villa Luz as part of thesis research (Estrada, 2005; Pastrana, 2006). Although considered a terrestrial taxon, the larva stage of chironomid midge is found in high abundance in the sulfidic waters in Cueva de Villa Luz (Lavoie and Evans, 2002). Many hexapods are considered to be grazers in the cave food webs, predominantly consuming microbial biofilms; some may also be omnivorous. One notable heteropteran is the endemic, stygobitic water scorpion, *Nepa anophthalma* Decu et al. 1994, from Movile Cave (Decu et al., 1994); *Nepa cinerea* Linnaeus 1758 has been identified from Grotta di Fiume Coperto (Latella et al., 1999a).

Vertebrates

Among the organisms found in caves, perhaps the vertebrates have elicited the most attention, even though many are accidental in caves (from birds to skunks). Bats are frequent visitors to sulfidic caves with entrances to the surface, such as Cueva de Villa Luz and the Frasassi Caves (Hose et al., 2000; Sarbu et al., 2000) (a species list is provided in the supplement at <http://geol.lsu.edu/Faculty/Engel/geomicrobiology_publications.htm>, but not in Table 2). For this review, only aquatic vertebrates are described in detail.

Class Osteichthyes

Two different families of fishes have been described from sulfidic karst settings. *Poecilia mexicana* Steindachner 1863 (the cave molly, family Poecilidae) is prevalent in the sulfidic waters of Cuvea de Villa Luz and nearby sulfidic springs (Langecker et al., 1996; Hose et al., 2000; Tobler et al., 2006). This small fish, having reduced eye size and pale coloration compared to surface-dwelling populations, is the center of attention for the ritual celebration of native villagers (Langecker et al., 1996; Hose et al., 2000). For probably a thousand years, kilograms of fish are sacrificed annually during the ceremony, but the population appears to be robust (Tobler et al., 2006). The sources of food for the fish are considered to be microbial mats and chironomid larvae (Langecker et al., 1996; Lavoie and Evans, 2002).

The deep sulfidic waters of the Edwards Aquifer host the two endemic blind catfishes, *T. pattersoni* and *S. eurystomus* (both from family Ictaluridae), whose origin has been traced back to the Pliocene or Miocene (Langecker and Longley, 1993). Both fish show remarkable adaptations to the deep aquifer, having been retrieved from over 400 m water depth, including the lack of pigment, loss of eyes and pineal organs, and the lack of the swim-bladder (which is typical for deep-sea fishes). Each of the aquifer species also has unique morphological features that are attributed to their respective ecological niches. *T. pattersoni* has a sucker-like mouth distinct from any other species in the family that is suggestive of grazing (Langecker and Longley, 1993), and Longley and Karnei (1978) report partially degraded fungus in the gut. The catfish was probably full of sulfur-oxidizing bacteria instead of fungus, as the bacteria form extensive biofilms on the aquifer walls (Grubbs, 1991; Randall, 2006) (Fig. 3C). In contrast, *S. eurystomus* had gut contents resembling stygobites (e.g., amphipods), suggesting that it was probably a predator (Langecker and Longley, 1993).

Class Anguilliformes

Hundreds of well-preserved, 30–70 cm long, adult eel fossils (*Anguilla anguilla*) have been found in the Frasassi caves, ~5 m above the present day water table (Mariani et al., 2004). Isotopic comparisons between the eels and river and cave animals indicated that the eels were not endemic to the sulfidic cave waters, but instead to the surface river. Reconstructed ^{14}C ages were consistent to the cave paleolevels, dating back as far as 9,000 years ago. An eel has been reported from Cueva de Villa Luz (Hose et al., 2000), although it is unclear whether it is endemic or accidental.

The Role of Chemolithoautotrophy in Shaping the Biodiversity of Sulfidic Karst Ecosystems

As previously discussed, the major energy and food sources in most cave and karst aquifers are from photosynthetically-produced organic matter that is brought into the system from the surface by air, water, or animals. Prolonged periods of limited to no food can cause widespread starvation (e.g., Hüppop, 2005), which undoubtedly results in stress (see discussion below) (Howarth, 1993). Accordingly, individuals who are stressed may expend greater energy for survival and would require more food in order to cope with habitat-induced pressures (e.g., Howarth, 1993; Hüppop, 2005; Parsons, 2005). For sulfidic systems, one of the consequences of chemolithoautotrophic primary productivity is an increase in the quality and quantity of organic carbon (Poulson and Lavoie, 2000;

Engel et al., 2004a). This rich and abundant food source may have a significant impact on biodiversity and an organism's ability to endure habitat stresses.

The carbon to nitrogen ratio (C:N) of microbial biomass can be related to food quality. The lower the ratio (~3–5), the better the quality because of limited influx and processing of surface-derived material that would increase the nitrogen content of the organic matter (Engel et al., 2004a). Microbial biomass from Movile Cave and Lower Kane Cave have C:N values of ~5 and are comparable to periphyton in surface streams and bacteria from deep-sea vents (Kinkle and Kane, 2000; Engel et al., 2004a). In contrast, high C:N ratios indicate that there is an abundant carbon supply, likely due to storage of biomass, but a reduction in nitrogen availability.

Stable isotope ratio analyses (SIRA) and radiolabeled-carbon assimilation studies confirmed that chemolithoautotrophic primary productivity was prevalent in the microbial mats from various caves (Sarbu et al., 1996; Airoldi et al., 1997; Pohlman et al., 1997; Mattison et al., 1998; Humphreys, 1999; Porter, 1999; Kinkle and Kane, 2000; Sarbu et al., 2000; Vlasceanu et al., 2000; Engel et al., 2004a; Hutchens et al., 2004). For carbon isotope systematics, the two carbon isotopes of importance are ^{12}C and ^{13}C, whereby the incorporation of carbon into living tissues invokes significant kinetic isotope fractionation. Specifically, biological (e.g., enzymatic) processes discriminate for the lighter isotope (^{12}C), leaving the heavier isotope (^{13}C) behind. Differences in the isotopic composition are expressed in terms of the delta (δ)-notation of a ratio of the heavy versus the light isotopic values for a sample relative to a standard, measured in per mil (‰). In general, biogenic carbon is isotopically lighter (more negative) than the inorganic reservoir (e.g., CO_2 or dissolved HCO_3^-); chemolithoautotrophic carbon fixation pathways have some of the largest fractionation effects, with resulting δ^{13}C values of chemolithoautotroph-dominated microbial biomass ranging between −30 and −45‰ compared to surface organic matter at ~−20‰ (Fig. 4). Variations in the δ^{13}C composition of microbial biomass are due to the taxonomic groups present and different compositions of dissolved inorganic carbon. Excretion, respiration, and heterotrophic carbon cycling are (for the most part) considered negligible carbon isotope fractionation processes, and the isotopic composition of heterotrophic organic matter will be the same as, or slightly higher than, the source organic carbon (essentially, in SIRA, the you-are-what-you-eat motto prevails).

The literature describing elaborate food webs is extensive for surface ecosystems (e.g., forests, soils, lakes), but studies of chemolithoautotrophically-based ecosystems and the structure and dynamics of their food webs are fairly limited (Sarbu et al., 1996; Pohlman et al., 1997; Vlasceanu et al., 2000; Sarbu et al., 2000). Trophic structure of most cave ecosystems is characterized by a lack of predators and extensive omnivory (Gibert and Deharveng, 2002). There has been relatively little done with regard to evaluating the biogeochemical and ecological roles of the dominant groups in the sulfidic ecosystems. The limited SIRA studies do support that predators are lacking in sulfidic systems, although it is possible that the predators are not known or that the identified species have not previously been considered predators (e.g., amphipods; Kelly et al., 2002). True predators (e.g., spiders) are present in the Movile Cave ecosystem and the δ^{13}C values for those organisms (−37 to −44‰) demonstrate that they eat grazers, who in turn have δ^{13}C values consistent with consumption of the microbial mats (Fig. 4). The δ^{13}C compositions of the microbial mats suggest chemolithoautotrophic productivity, and are distinct from surface organic matter (Fig. 4). Langecker et al. (1996) explored the food web of Cueva de Villa Luz using sulfur SIRA and found that the analyses could only partially define energy flow within the food web.

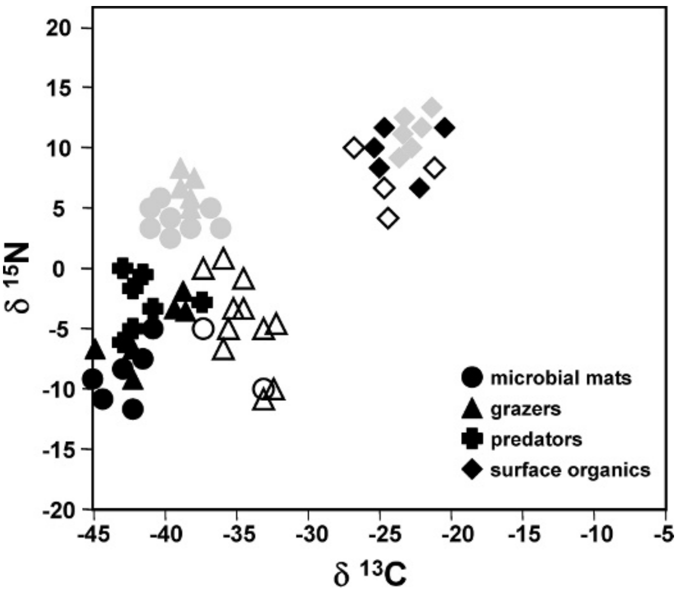

Figure 4. Stable carbon and nitrogen isotope ratio analyses for Movile Cave (solid symbols) the Frasassi Caves (open symbols), and Lower Kane Cave (shaded symbols) from Sarbu et al. (1996), Vlasceanu et al. (2000), and Engel et al. (2004a), respectively. Circles are microbial mat samples from each cave; triangles are for grazers; crosses are for predators (only Movile Cave has predators); diamonds are surface organics. Variations in the δ^{13}C composition of microbial biomass for the caves are due to the taxonomic groups present, which may have distinct carbon fixation pathways, and different starting compositions of dissolved inorganic carbon.

Assimilation studies have been done with microbial biomass from several sulfidic cave systems using ^{14}C-bicarbonate to estimate chemolithoautotrophic productivity and ^{14}C-leucine to estimate heterotrophic productivity (Porter, 1999; Engel et al., 2001) (Fig. 5). Autotrophic rates

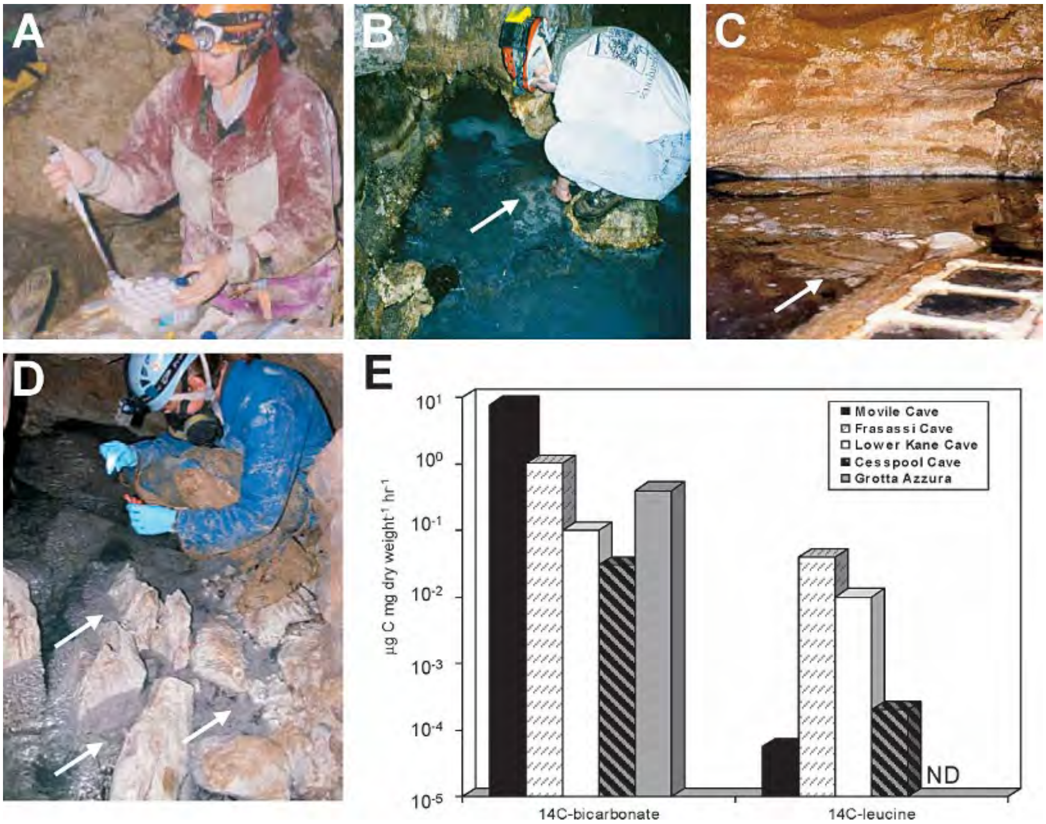

Figure 5. (A) Set-up for radiolabelled-isotope experiment in the Frasassi Caves, Italy. (B) Sampling in Cesspool Cave, Virginia; arrow pointing to mats. (C) Floating microbial mats (arrow) in Movile Cave, Romania. Grid is ~10 cm on a side. (D) Sampling stream mats in the Frasassi Caves, Italy; arrows pointing to mats. (E) Comparison between cave microbial mats for ^{14}C-bicarbonate and ^{14}C-leucine incubations to estimate chemolithoautotrophic primary productivity and heterotrophic productivity, respectively (Porter, 1999). Autotrophic productivity only was estimated for Grotta Azzura, Italy (ND = no data for leucine test) (Mattison et al., 1998).

were highest for the Movile Cave and lowest for Cesspool Cave, but in all of the caves examined, autotrophic productivity was significantly greater (from one to five times) than heterotrophic activities (Porter, 1999; Engel et al., 2001). Similar rates of autotrophic productivity were estimated for microbial mats from the submarine cave, Grotta Azzura, at Cape Palinuro, Italy (Mattison et al., 1998). Microbial heterotrophic processing of autotrophic biomass was low, with heterotrophs processing a minor fraction of the available autotrophic productivity (Porter, 1999; Engel et al., 2001). For Lower Kane Cave, the estimate is ~30% of the autotrophic productivity is processed through heterotrophy in Lower Kane Cave, which compares well with estimates of ~20–40% of autotrophic productivity processing by heterotrophy for the open oceans (Porter, 1999).

The consequences of a rich and abundant food source relate to biodiversity (as the number of species), ecosystem function, and food web dynamics. First, nutritional stress may simply be negligible because members of the ecosystem do not need to rely on outside food or energy (e.g., Howarth, 1993). Organisms consuming the chemolithoautotrophically-produced food may also have a greater ability to endure habitat stresses, such as low O_2 and high H_2S (see discussion below). Moreover, the low C:N ratios and low heterotrophic productivity indicate that there is a limited microbial detrital loop and that nutritional quality of the biomass is high. These factors should correlate to a high number of grazers and other trophic levels that could be supported by microbial mat consumption (Engel et al., 2001). However, one argument asserts that a rich and plentiful food source may increase functional redundancy at various trophic levels (thereby increasing the total number of species in an ecosystem; e.g., Wohl et al., 2004; Hooper et al., 2005), if the food can not be accessed by high trophic levels. Another argument suggests that the stability of the overall habitat and the rich food source may support lower diversity (Gibert and Deharveng, 2002; Wohl et al., 2004), especially if there is a limited influx of surface organisms to replenish the gene pool or to increase competition (e.g., Barr and Holsinger, 1985; Hooper et al., 2005). As is apparent in the preceding faunal inventories, more thorough descriptions of the functional roles of the organisms in sulfidic karst systems are needed to address these arguments fully.

THE ROLE OF HABITAT STRESS IN SULFIDIC KARST ECOSYSTEMS

Subsurface environments can be highly stressful habitats for life, with stress defined as a potentially damaging condition in the biological system (e.g., Howarth, 1993). The ability of subterranean organisms to tolerate, adapt, and evolve under stressful habitat conditions has been the subject of recent research (e.g., Howarth, 1993; Hüppop, 2005). For most organisms, stress avoidance is probably the first line of defense (e.g., Badyaev, 2005; Parsons, 2005). However, obligate troglobites and stygobites have conspicuous adaptations to subsurface conditions (i.e. darkness, limited food, etc.), including the reduction in and loss of structures (eyes, pigments, wings, etc.), loss of time-keeping abilities (and circadian rhythm), slower metabolic rates, and reduced fecundity, but also the elongation of appendages, enhanced sensory structures, etc. Organisms living in the sulfidic conditions not only manifest similar morphological, behavioral, and physiological adaptations compared to non-sulfidic subsurface animals, but they also must deal with different environmental stresses, such as toxic levels of gases like H_2S, CO_2, and CH_4, and variable pH.

Excluding nutritional stress, one of the most significant stresses for organisms living in sulfidic habitats is hypoxia (dissolved O_2 concentrations <2.0 mg L^{-1}) (Hervant et al., 1997; Malard and Hervant, 1999; Hervant and Malard, 2005). Note: the solubility of oxygen is complicated by temperature, pressure, elevation, and salinity, but in general the solubility decreases with increasing temperature and salinity; so in mesothermal (>10 °C) waters that are common for continental sulfidic systems, dissolved O_2 levels can be <0.01 mg L^{-1}, or considered anoxic. Because darkness precludes photosynthesis, O_2 is not produced *in situ*, and abiotic and biotic consumption, particularly if organic carbon is plentiful, can rapidly diminish the concentration of O_2. Moreover, slow to negligible air exchange with groundwater, or limited air circulation in cave passages, not only results in atmospheric stagnation, but also causes the accumulation of noxious gases, such as CO_2, CH_4, and H_2S. Utilization of O_2 as an electron acceptor for metabolic processes (e.g., through sulfur oxidation or heterotrophy) would also keep the concentration of dissolved O_2 exceedingly low. Therefore, microbial communities play a fundamental role in maintaining habitat physicochemistry, such as possibly causing and maintaining hypoxia in sulfidic aquifers.

Although it seems that microbes can easily and readily adapt to extreme habitat conditions, and that chemolithoautotrophy provides a rich and plentiful energy source for animals, one question remains: how do higher organisms live in such a harsh habitat? Much like the dogma that all life on earth is dependent on sunlight, there has been an ecological tenet that all life on earth requires O_2, and a lot of it, to live. Clearly, the biological diversity of groundwater systems in general, and sulfidic cave and karst habitats specifically (Table 2), points toward the fact that life certainly has adaptive strategies to living in these extreme environments (e.g., Howarth, 1993; Badyaev, 2005; Parsons, 2005).

Numerous studies have shown that groundwater crustaceans can live and grow under hypoxic conditions for several months and can survive anoxia for >48 hr. This is in stark comparison with surface-dwelling crustaceans who could survive for only a few hours to one day (Malard and Hervant, 1999; Hervant and Malard, 2005). Moreover, Bishop et al. (2004) found that the respiration rates of seven orders of stygobitic crustaceans living at dissolved O_2 levels of <0.6 mg L^{-1} in anchialine caves were lower than surface-dwelling organisms or similar to organisms living at slightly higher O_2 levels. Metabolic strategies and adaptations have been examined for stygobites and troglobites (e.g., Hervant and Malard, 2005), whereby the activity of various enzymes, and specifically high levels of malate dehydrogenase, indicate that some stygobites are poised for anaerobic metabolism (Bishop et al., 2004). The research also demonstrates that organisms rapidly recover from prolonged hypoxia by efficient removal of lactate and other anaerobic waste products (Hervant et al., 1999a; Hervant and Malard, 2005). Similar results have been reported for deep-sea vent organisms, in that those animals use anaerobic metabolism to support activity at low O_2 levels, while regulating O_2 consumption, and maintaining efficient circulatory systems and high-affinity hemoglobin.

Despite these adaptations, however, living at hypoxia still brings noxious gases, such as H_2S, into an organism's body. Tolerance of, and survival in, high H_2S concentrations for cave animals in sulfidic settings (such as anchialine caves) have not been studied in detail. For some organisms, like those at the deep-sea vents, symbiosis with microbes may be an evolutionary mechanism to deal with high H_2S levels (e.g., Somero et al., 1989). However, some studies of polychaete tube worms demonstrate the animals can survive up to four days when they switch to anaerobic metabolism under anoxic conditions with high sulfide (up to millimolar levels), which may be aided by special epidermal tissue structures independent of bacterial symbiosis (Hourdez et al., 2002; Menon et al., 2003).

CLOSING REMARKS

Cave-adapted organisms have the potential to be some of the rarest and most threatened species on Earth (e.g., van Beynen and Townsend, 2005). Subterranean biodiversity is quite high globally (Gibert and Deharveng, 2002), and is considered to be strongly linked to the (hydro)geologic age and permanence of the karst setting (e.g., Culver, 1976; Barr and Holsinger, 1985; Jones et al., 1992). With continual isolation from the surface, organisms disperse and migrate, and populations can become separated from each other and speciation can occur. For non-sulfidic karst systems, it has been estimated that >50% of obligate cave-adapted species can be found in <1% of the land, at least for the United States (Culver et al., 2000). For sulfidic habitats, local geological and hydrostraigraphic controls (e.g., Christman and Culver, 2001) will impact the distribution of organisms endemic to sulfidic systems, as conditions that lead to sulfide production are needed. Consequently, the distribution of species in sulfidic karst aquifers may be even more restricted. How does one actually measure the spatial distribution of an animal whose potential habitat is a 100 km^2 aquifer? Is this a small distribution, or a large distribution?

Although it is evident that the intimate dependence of subsurface ecosystems on surface-derived nutrients and energy has catalyzed the mandatory protection of many karst systems from above-ground, usually anthropogenic, disturbances (van Beynen and Townsend, 2005), sulfidic ecosystems may not rely on surface-derived organics and may be potentially buffered from such disturbances. To attempt to understand more fully the vulnerability, management, and sustainability challenges facing these systems, as well as the potential that these systems may have a monetary value, the amount of future work is considerable. I suggest that exciting avenues for future research will not only be in the exploration of new systems, but in the rediscovery of old systems. We have known about some of the sulfidic caves and karst aquifers for nearly 100 years, but we still must shed light on many outstanding questions, including: what is the true nature of species diversity and distribution, how are the ecosystems structured, what are the ecological functions of organisms within the system, how do species adapt to habitat stresses, how does habitat stress affect ecosystem diversity and structure, and what are the roles of geochemistry and geology on habitat development and modification of these subterranean sulfidic ecosystems? Uncovering the answers to these questions will certainly provide years of fruitful study.

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Malcolm S. Field – Risks to cavers and cave workers from exposures to low-level ionizing α radiation from ^{222}Rn decay in caves. *Journal of Cave and Karst Studies,* v. 69, no. 1, p. 207–228.

RISKS TO CAVERS AND CAVE WORKERS FROM EXPOSURES TO LOW-LEVEL IONIZING α RADIATION FROM ^{222}RN DECAY IN CAVES

MALCOLM S. FIELD
Office of Research and Development, U.S. Environmental Protection Agency, Washington, D.C. 20460, field.malcolm@epa.gov

Abstract: Human health risks posed by exposure to elevated levels of ^{222}Rn in caves are not well documented. Various studies throughout the world have detailed the often very high ^{222}Rn gas concentrations in caves and exposures to cavers and commercial tour guides and other employees, but without a consequent assessment of the overall impact on human health. Although ^{222}Rn concentrations in caves are considered high relative to most above ground dwellings, the levels identified are also considered to be low for ionizing α radiation. Low-level ionizing radiation impacts on human health are deduced by application of the linear no-threshold theory (LNT) of radiation carcinogenesis. Comprehensive reviews of the published literature and an understanding of exposure time suggests that commercial cave workers (e.g., tour guides) and commercial ^{238}U-mine workers are both exposed for the same number of hours per month ($\sim$170 h), but cave workers are exposed to much lower ^{222}Rn concentrations than are mine workers. Cavers will generally be exposed for a smaller number of hours per month. Risk estimates suggest that cavers will likely be subject to insignificant risks, but that cave workers may be subject to low-level risks of developing lung cancers from elevated levels of ^{222}Rn gas concentrations in caves.

INTRODUCTION

This paper was developed to provide the National Speleological Society reader with an intensive investigation of the potential health effects posed by exposure to elevated levels of radon in caves. To the author's knowledge, no other publication on radon in caves has delved into the risks to cavers from exposure to radon in caves to the extent that this paper does.

Radon-222 is generally regarded as a naturally occurring inert radioactive gas with a half life of 3.824 days and is produced within the ^{238}U decay series (Fig. 1), the process of which is described in detail in Field (1994, p. 52–60) and where the phenomenon of radioactivity is described in detail in Ivanovich (1992, p. 1–33). In fact, ^{222}Rn is only partly inert. Radon-222 may also be regarded as a metalloid[1], an element that lies on the diagonal of the Periodic Table between the true metals and nonmetals (Fig. 2). Because ^{222}Rn is a metalloid, it exhibits some characteristics of both metals and nonmetals, such as forming a series of clathrate compounds[2] (inclusion compounds), and reacts readily with fluorine and fluorides (Stein, 1987; Cigna, 2005).

Radon-222 poses a substantial threat to human health when build-up occurs in confined spaces such as homes, mines, and caves (ICRP, 1994a, p. 1) and when exposure time is sufficiently long. The average annual per person radiation dose from exposure to ^{222}Rn from caves is estimated to be 1 nSv (0.1 μrem)[3], although cavers and cave workers are expected to receive much higher doses (ATSDR, 1997, p. 217). Show caves are a recognized hazard in terms of ^{222}Rn exposure to cave workers (tour guides, maintenance personnel, employees working in shops built over cave entrances, etc.) (IAEA, 2003, p. 5–6 and 46), but because of the sensitive nature of cave environments, high ^{222}Rn gas concentrations cannot easily be remediated (IAEA, 2003, p. 60). Forced air ventilation in caves is regarded as unthinkable because of the likely deleterious effects on the microclimates and biota (Yarborough and Meyers, 1978, p. 28 and 73). The U.S. Environmental Protection Agency (EPA) believes that the risks posed to human health by low levels of ^{222}Rn gas in single-family residences to be more significant than the risks to uranium miners exposed to very high levels of ^{222}Rn gas because the miners are only exposed for 170 h per month in the mine (1 Working Level Month) while homeowners spend more time in their dwellings and receive a greater overall exposure (Abelson, 1991). The principal threat is by the formation of lifespan shortening lung cancer, pulmonary emphysema, and pulmonary fibrosis through damage to the respiratory epithelium (Samet, 1997; Cross, 1987, p. 215–216).

The existence of elevated concentrations of ^{222}Rn in caves is well established in the literature (Table 1). Table 1 is a sampling of the literature that contains extensive ^{222}Rn concentration values, but does not list all of the basic literature on caves and ^{222}Rn (see for example, Cigna, 2005; Gunn, 2003, p. 617–618). However, the risks to

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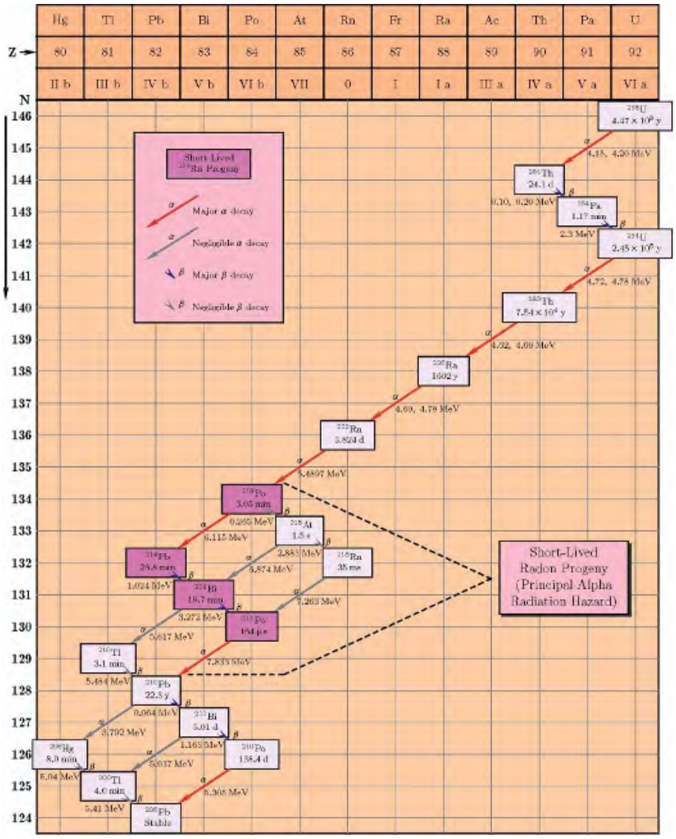

Figure 1. Uranium-238 decay series. The horizontal scale, Z, is the number of protons in the nucleus, and the vertical scale, N, is the number of neutrons in the nucleus. Also shown are the half-lives, type of decay (either by α- or β-particles), and the major radiation energies (in MeV) of ^{238}U and its progeny. Modified from Cothern (1987, p. 7) and NRC (1988, p. 26). Negligible percentage decays included even though they are not a human health concern. See Table 12 in the Appendix for the historic names of the ^{222}Rn progeny.

cavers and cave workers from exposure to the relatively high ^{222}Rn concentrations in caves are poorly understood and rarely reported in the literature (Kobal et al., 1986, 1987; Vaupotič et al., 1998, 2001).

The purpose of this paper is to explore the risks posed to the health of cavers and tour guides as a result of exposure to low-level ionizing radiation from ^{222}Rn gas and its progeny. Radon-219 and ^{220}Rn (commonly known as thoron) do not represent as serious a concern as does ^{222}Rn because (1) ^{219}Rn is relatively rare and has a very short half life ($T_{1/2}$ = 4 s) and (2) ^{220}Rn has a very short half life ($T_{1/2}$ = 56 s) (ATSDR, 1990, p. 11). Radon-219 has only rarely been found at elevated levels in caves (Yarborough and Meyers, 1978, p. 42).

Particular attention will be directed at the linear no-threshold theory (LNT) of radiation carcinogenesis because this is the accepted model for estimating risks posed by exposure to ^{222}Rn gas and its progeny (Dicus, 2001; Kellerer and Nekolla, 2000; NCRP, 2001; NAS, 2005; NRC, 1999, p. 69) even though there is some dispute as to its appropriateness (e.g., Bond et al., 1996; Cohen, 2000). There is, however, good reason to continue relying on the LNT even with all its attendant problems because it is a reasonable risk model (Oughton, 2006).

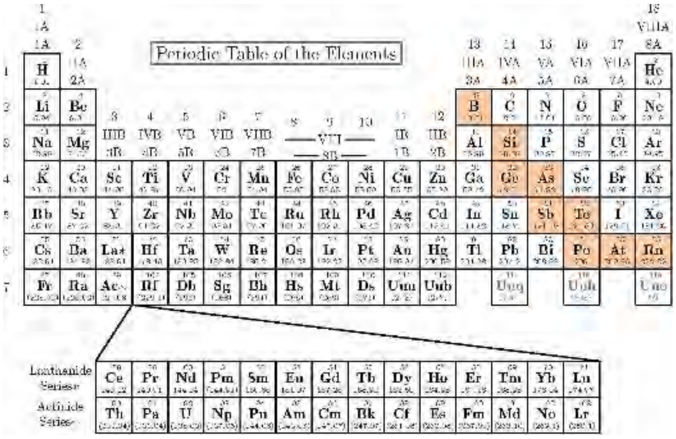

Figure 2. Arrangement of the metalloid elements (dark shading) in the Periodic Table (modified from Stein (1987).

THREATS POSED BY ^{222}RN AND ITS PROGENY

Radon-222 is the heaviest of the noble gases and because it is a relatively nonreactive gas that exists everywhere in the environment, it tends to migrate to and concentrate in enclosed spaces (e.g., basements, caves, tunnels, etc.). However, ^{222}Rn is not a major health risk by itself.

High concentrations of ^{222}Rn progeny (^{218}Po, ^{214}Pb, ^{214}Bi, and ^{214}Po) are widely recognized as a source of lung cancer and possibly other cancers (Henshaw et al., 1990; Bridges et al., 1991) through the emission of α- and β-particles with dense ionization along their tracks although it is the α-particles that are most responsible for the resulting high-linear energy transfer (LET)[4] because of its large +2 charge and relatively large mass (~8,000 times that of an electron). Emission of β-particles (high-energy electrons) results in low-LET because of its ±1 charge and much smaller mass than α-particles. In either case, both low and high LET interactions can cause significant DNA damage (ATSDR, 1997, p. 30–31), but it is the densely ionizing radiation produced by α-particle decay that causes many double strand DNA breaks that are most difficult for cell repair and are most likely to give rise to cancer formation (Craven and Smit, 2006). According to Craven and Smit, sparsely ionizing radiation typically results in single strand DNA breaks which are much easier for cells to repair.

Cothern (1989) states that "between 4,000 and 30,000 fatal lung cancers occur each year due to exposure to radon in indoor air," but does not offer any supporting data or references for such a contention. The EPA had projected

Table 1. Summary of ^{222}Rn literature (modified from Hyland and Gunn (1994). Note that many of the references include ^{222}Rn measurements from several sources[a].

Country	Mean ^{222}Rn Concentration (Bq m^{-3})	Number of ^{222}Rn Measurements	Max. ^{222}Rn Concentration (Bq m^{-3})	Min. ^{222}Rn Concentration (Bq m^{-3})	Reference
Australia	610	274	4,045	9	Solomon et al. (1996)
China[b]	141	32	278	38	Wiegand et al. (1995)
Czech Republic	1,235	60	21,000	200	Burian and Stelcl (1990)
Great Britain	2,907	820	46,080	10	Hyland and Gunn (1994)
Great Britain	…	2,000	155,000	100	Hyland and Gunn (1994)
Great Britain	35,890	34	155,000	7,400	Gunn et al. (1991)
Great Britain	9,306	13	12,552	68	Gillmore et al. (2000)
Great Britain	365	42	3,187	26	Gillmore et al. (2002)
Great Britain	315	28	3,047	34	Gillmore et al. (2002)
Greece	25,179	6	88,060	185	Papastefanou et al. (1986)
Hungary	3,300	25	14,000	500	Somogyi et al. (1989)
Hungary	2,468	8	13,200	200	Lenart et al. (1990)
Ireland	4,127	26	7,940	200	Duffy et al. (1996)
Japan	11	5	20	< 1	Miki and Iauthora (1980)
Malaysia	596	39	1,978	100	Gillmore et al. (2005)
Poland	1,166	279	4,180	60	Przylibski (1999)
Russia	2,390	14	8,550	373	Gunn (1991)
Slovenia	1,412	101	7,220	15	Kobal et al. (1986)
Slovenia	965	66	5,920	60	Kobal et al. (1987)
Spain	108	301	488	5	Dueñas et al. (1998)
Spain	3,564	8,587	7,120	186	Lario et al. (2005)
South Africa	267	63	2,319	3	Gamble (1981)
Switzerland	25,000	6	40,000	2,000	Surbeck (1990)
United States	1,927	60	9,350	37	Yarborough (1976)
United States	2,589	11	9,460	370	Eheman et al. (1991)
United States	1,475	…	2,350	740	Ahlstrand (1980)
United States	…	860	1,850	333	Ahlstrand and Fry (1976)
United States	11,678	37	82,177	11	Bashor (undated)

[a] Data quality control likely varies for each study conducted for each country which should be regarded as problematic.

[b] Measurements taken in Chinese cave dwellings built in the Chinese Loess Plateau which is mainly composed of Mesozoic sandstones overlain by Tertiary red clays that are covered by Quaternary loess tens to over one hundred meters thick (Wiegand et al., 1995) where the number of inhabitants exceed three million (Yanada, 2003)

14,000 lung-cancer deaths per year from residential ^{222}Rn exposure with an uncertainty range of 7,000 to 30,000 (Page, 1993), but now estimates 21,000 lung-cancer deaths per year from residential ^{222}Rn exposure with an uncertainty range of 8,000 to 45,000 (U.S. EPA, 2006). In fact, the expected lung cancers and other adverse health effects may be more a result of smoking than of inhalation of ^{222}Rn gas (Pisa et al., 2001). In addition, the expected lung cancers in cavers and cave workers appear to be conspicuously missing from the published literature, perhaps because no one has yet linked lung cancers in cavers and cave workers to long-term exposure to high ^{222}Rn concentrations (Halliday, 2003).

Risks to cavers and cave workers by exposures to high levels of ^{222}Rn may not be as serious as is often presented. The potential overestimation of the risks posed by elevated levels of ^{222}Rn and the belief by many individuals that overestimation may actually be the case, have caused some consternation among some researchers (Cothern, 1989, 1990; Little, 1997). The possibility that ^{222}Rn and its progeny may be responsible for some cancers other than lung cancer also is not strongly supported in the literature (Tomasek et al., 1993). For example, Law et al. (2000) were unable to establish an association between household exposure to ^{222}Rn and the development of leukemia in adults in Great Britain. Lauier et al. (2001) obtained similar results.

A significant reason why ^{222}Rn and its progeny may not be as serious a threat to cavers and cave workers may be because although ^{222}Rn concentrations in caves are considered to be elevated, these levels are also considered to be relatively low in terms of ionizing radiation. For example, employees exposed to radiation in the work place in Great Britain (e.g., cave tour guides) are not allowed to receive annual effective radiation doses[5] above 50 mSv yr^{-1} (10 WLM yr^{-1}) with an action level of 15 mSv

Table 2. Inhalation exposure studies of ^{222}Rn (modified from ATSDR, 1990, pp. 13–15). Superscript numbers next to each entry correspond to data point numbers in Figure 3.

Species	Exposure Frequency/ Duration	Effect	NOAEL (Bq m^{-3})	LOAEL (Effect)		Reference
				Less Serious (Bq m^{-3})	Serious (Bq m^{-3})	
Acute Exposure						
Mouse^{1}	1 d	Death			8.14×10^9 (30 d LD_{50})	Morken (1955)
Mouse^{2}	1 d 5–40 h	Hemato			8.14×10^9 (anemia)	Morken (1955)
Intermediate Exposure						
Rat^{3}	4–6 mo 2 d wk^{-1} 1 h d^{-1}	Death	1.11×10^5			Chameaud et al. (1984)
Rat^{4}	Lifespan 2 d wk^{-1} 90 h wk^{-1}	Death			1.78×10^8 (dec lifespan)	Palmer et al. (1973)
Mouse^{5}	Lifespan 150 h wk^{-1}	Death			1.55×10^7 (dec lifespan)	Morken and Scott (1966)
Hamster^{6}	Lifespan	Death			1.78×10^8 (dec lifespan)	Palmer et al. (1973)
Rat^{7}	Lifespan	Resp			1.78×10^8 (metaplasia)	Palmer et al. (1973)
	2 d wk^{-1} 90 h wk^{-1}	Other		1.78×10^8 (dec bw)		
Mouse^{8}	Lifespan	Resp			1.55×10^7 (metaplasia)	Morken and Scott (1966)
	150 h wk^{-1}	Hemato		1.55×10^7 (dec lymph)		
		Other		1.55×10^7 (dec bw)		
Mouse^{9}	Lifespan	Resp			1.78×10^8 (fibrosis)	Palmer et al. (1973)
	2 d wk^{-1} 90 h wk^{-1}	Other		1.78×10^8 (dec bw)		
Hamster^{10}	Lifespan	Resp			1.78×10^8 (metaplasia)	Palmer et al. (1973)
	2 d wk^{-1} 90 h wk^{-1}	Other		1.78×10^8 (dec bw)		
Dog^{11}	1–50 d 5 d wk^{-1} 20 h wk^{-1}	Resp			2.04×10^7 (fibrosis)	Morken (1973)
Rat^{12}	2.5–8 wk 4 d wk^{-1} 3–6 h d^{-1}	Cancer			1.11×10^7 (CEL-lung)	Chameaud et al. (1982)
Rat^{13}	25–115 d 4–5 h d^{-1}	Cancer			2.78×10^7 (CEL-lung)	Chameaud et al. (1974)
Rat^{14}	6–6 mo 2 d wk^{-1} 1 h d^{-1}	Cancer			1.11×10^7 (CEL-lung)	Chameaud et al. (1984)

Table 2. Continued.

Species	Exposure Frequency/ Duration	Effect	NOAEL (Bq m^{-3})	LOAEL (Effect) Less Serious (Bq m^{-3})	LOAEL (Effect) Serious (Bq m^{-3})	Reference
Chronic Exposure						
Hamster[15]	Lifespan 5 d wk^{-1} 6 h d^{-1}	Death	1.15×10^7			Cross et al. (1978)
Hamster[16]	>1 mo−18 yr (occup)	Resp			$>3.70 \times 10^3$ (tuberculosis)	Waxweiler et al. (1981)
Hamster[17]	Lifespan	Resp			9.62×10^6 (hyperplasia)	Cross et al. (1978)
	5 d wk^{-1}	Hemato	1.15×10^7			
	6 h d^{-1}	Other		9.62×10^6 (dec bw)		
Human[18]	0.5–23 yr (occup)	Cancer			1.26×10^4 (CEL-lung)	Gottlieb and Husen (1982)
Human[19]	(occup)	Cancer			7.40×10^3 (CEL-lung)	Morrison et al. (1981)
Human[20]	0–14 yr (occup)	Cancer			3.70×10^3 (CEL-lung)	Solli et al. (1985)
Human[21]	>29 yr (occup)	Cancer			2.22×10^3 (CEL-lung)	Edling and Axelson (1983)
Human[22]	>1–>20 yr (occup)	Cancer			1.85×10^3 (CEL-lung)	Damber and Larsson (1985)
Human[23]	48 wk yr^{-1} 48 h wk^{-1} (occup)	Cancer			1.85×10^3 (CEL-lung)	Howe et al. (1987)
Human[24]	>10 yr (occup)	Cancer			1.11×10^3 (CEL-lung)	Snihs (1973)
Human[25]	>2–30 yr (res)	Cancer			5.55×10^1 (CEL-lung)	Svensson et al. (1989)
Human[26]	(occup)	Cancer			8.88×10^3 (CEL-lung)	Fox et al. (1981)
Human[27]	>1 mon–18 yr (occup)	Cancer			3.70×10^3 (CEL-lung)	Waxweiler et al. (1981)
Human[28]	>1 mon–30 yr (occup)	Cancer			1.48×10^4 (CEL-lung)	Roscoe et al. (1989)

CEL = Cancer Effect Level
hemato = hematological
resp = respiratory
occup = occupational
dec = decreased
bw = body weight
res = residential

(1.5 rem) (Hyland and Gunn, 1994). This total annual effective dose of 50 mSv yr^{-1} is also applicable in some instances in the United States (U.S. Navy, 2001, p. 4-1 and NRC, 2005, p. 5), although 20 mSv yr^{-1} (4 WLM yr^{-1}) is generally the accepted level (OSHA, 1988, 41 CFR §57.5038) while the NCRP (1993, pp. 34–35) has suggested more flexibility to control worker exposure. However, low-radiation doses are considered to range from near 0 to 100 mGy[6] (0 to 10 rad), medium doses from 100 mGy to 1 Gy (10 to 100 rad), and high doses from 1 Gy to 20–60 Gy (100 to 2,000–6,000 rad) (NRC, 2005, p. 374).

By this definition it would appear that an action level based on an effective dose of 15 mSv may be overly protective. The human equivalent dose H_T is estimated using Equation (1)

$$H_T = \sum_R W_R \, D_{T,R} \qquad (1)$$

and the effective dose E_D is estimated from

$$E_D = \sum_T W_{T_i} \sum_R W_R \, D_{T,R} \qquad (2)$$

Using $W_R = 20$ for α-particles (ICRP, 1980, p. 94) results in an absorbed dose $D_{T,R}$ of 0.75 mGy, which is at the lower spectrum of a low-radiation dose. Using $W_{T_L} = 0.12$ for the lung (0.24 for lungs) (ICRP, 1991, p. 68) results in 6.25 mGy which is still at the lower spectrum of a low-radiation dose.

^{222}RN PROGENY

Although it is true that ^{222}Rn represents a risk to cavers in terms of lung cancer, its relatively long half life (3.824 d) will more often result in the exhalation of ^{222}Rn prior to emanation of an α-particle that could penetrate the epithelium of the lung to cause a cancerous growth. So even though the energy associated with the emission of an α-particle from ^{222}Rn is relatively high (5.49 MeV) and it is possible that α-particle emission from inhaled ^{222}Rn gas may have an adverse affect on human health, it is not likely that α emission will actually occur during the time that the ^{222}Rn gas resides in the lung. This situation is considerably different for ^{222}Rn progeny.

The four ^{222}Rn progeny (^{218}Po, ^{214}Pb, ^{214}Bi, and ^{214}Po) are either metals (^{214}Pb and ^{214}Bi) or metalloids (^{218}Po and ^{214}Po) that are relatively short-lived and emit α-particles with relatively high energy and β-particles with relatively low energy (Fig. 1). It is these features, principally the α-particles, that represent the main risk posed by ^{222}Rn. Each of the four principal ^{222}Rn progeny are quite reactive, which causes them to plate-out[7] in the lung as well as enhancing their tendency to adsorb to smoke and dust particles. The risk of lung cancer occurrence is exacerbated by smoke and dust particles because these metals and metalloids readily react with and adsorb to the particles which are easily inhaled.

Threats from ^{218}Po

Polonium-218 has a half life of 3.05 min and is the immediate progeny resulting from the decay of ^{222}Rn. When ^{218}Po decays, it emits an α-particle with a relatively high energy of 6.12 MeV. With a half life of 3.05 min it is possible that ^{218}Po will emit an α-particle during the time that it resides in the lung. However, its relatively short half life tends to prevent its being easily distributed throughout the body from the lungs.

Threats from ^{214}Pb and ^{214}Bi

Lead-214 and ^{214}Bi are metals with half lives of 26.8 min and 19.7 min, respectively. These two radioisotopes decay by low energy β emission, but are still a threat to human health, although less so than the other short-lived ^{222}Rn progeny that decay by α emission (Fig. 1). Their relatively longer half lives and low energy relegate ^{214}Pb and ^{214}Bi to a slightly lesser threat status. In addition, their half lives are still too short to allow for substantial distribution throughout the body.

Threats from ^{214}Po

Polonium-214 has a very short half life (164 µs). It emits an α-particle with a high energy of 7.69 MeV. With a half life of just 164 µs it is highly likely that ^{214}Po will emit an α-particle during the time that it resides in the lung. Its very short half life and high energy makes ^{214}Po a significant threat to human health. Although the very short half life of ^{214}Po prevents its distribution throughout the body, the relatively long half life of its immediate progeny ^{210}Pb (22.3 yr) can result in serious harm in parts of the body other than the lungs from the decay of ^{210}Pb.

Polonium radionuclides have many of the characteristics of rare-earth elements, are amphoteric, and tend to form hydroxides and radiocolloids *in vitro*[8] and *in vivo*[9]. The latter tends to cause polonium to become phagocytized[10] by cells of the reticuloendothelial system[11] for eventual deposition in the spleen, lymph nodes, bone marrow, liver, and kidneys after parenteral administration[12] (NRC, 1988, p. 161). Fortunately, the half lives of the polonium radionuclides in the immediate ^{222}Rn-decay series are of such a short duration ($T_{1/2}$ for ^{218}Po = 3.05 min and $T_{1/2}$ for ^{214}Po = 164 µs) these problems are generally not a major concern. However, ^{210}Pb with its much longer half life ($T_{1/2}$ = 22.3 yr) is of concern.

HEALTH EFFECT ESTIMATES FROM EXPOSURES TO ^{222}RN AND ITS PROGENY

Inhalation exposure to significant levels of ^{222}Rn and its progeny (assumed to be in equilibrium) have been shown to cause acute and chronic effects on laboratory animals and humans (Table 2 and Fig. 3) (ATSDR, 1990, p. 12–27). However, the processes linking inhalation of ^{222}Rn and its progeny to increased lung cancer risk are complex (ICRP, 1994a, p. 2) primarily because of the numerous confound-

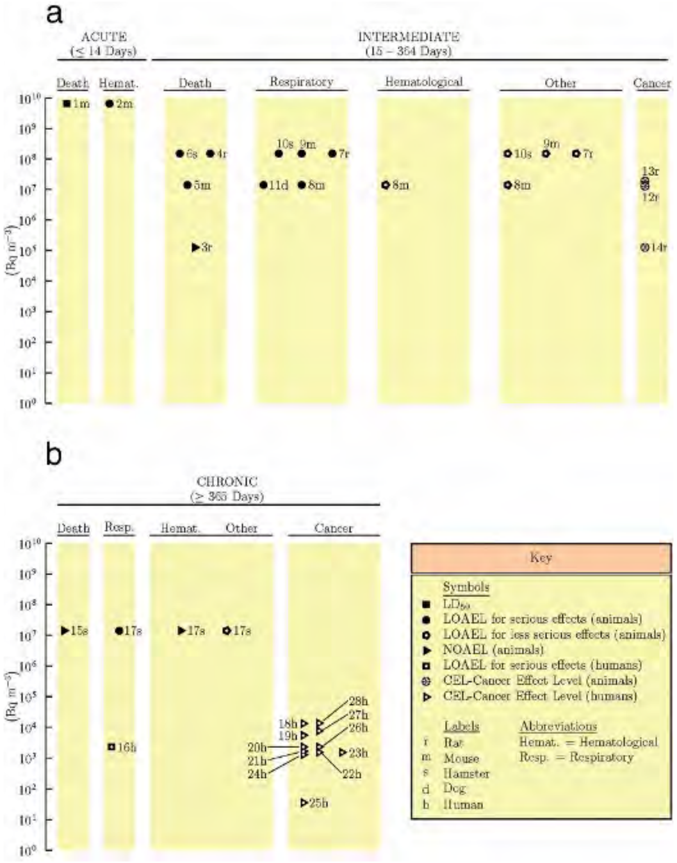

Figure 3. Levels of significant inhalation exposure to ^{222}Rn (modified from ATSDR, 1990, pp. 16–17). Numbers next to each data point correspond to superscripts for each entry in Table 2. Acute and Intermediate effects = a and chronic effects = b.

ing factors[13] (ICRP, 1994a, p. 7) (e.g., smoking). For this reason, many of the epidemiological studies on miners and animals are inadequate so that health research continues.

Review of Selected Animal and Human Studies

The ^{222}Rn concentrations used in the studies cited by ATSDR (1990, p. 12–27) ranged from a low of 56 Bq m^{-3} (human studies) to a high of 8.14 × 10^{9} Bq m^{-3} (animal studies). In the human studies, a cancer effect level in lungs was identified (actual exposure frequency/duration was from >2–30 yr). In the animal studies, mouse mortality and development of hematological (anemia) symptoms occurred after a 30 d Median Lethal Dose (LD$_{50}$) study (actual exposure frequency/duration was from 5–40 h).

Animal Studies

The mouse studies obviously involved much higher doses of ^{222}Rn than would typically be experienced by a caver (see Table 1), but the exposure time would be comparable. The human study and other similar studies cited by ATSDR (1990) include ^{222}Rn concentrations that a typical caver may be exposed to, but the examined exposure times are generally longer than would be typical for a caver (an exception can be made for tour guides, maintenance workers, etc.).

The animal studies listed in Table 2 resulted in few lung cancers (21% in dogs, zero in mice, and 1.3% in Syrian hamsters) even though the ^{222}Rn doses to which the animals were exposed were extremely high (NRC, 1999, p. 43). Syrian hamsters did not develop any tumors at exposures below 3.89 × 10^{5} J s m^{-3} (3.0 × 10^{4} WLM) whereas rats showed a high incidence of respiratory-tract tumors after exposure to ^{222}Rn. However, according to NRC (1999, p. 43–44) the mechanistic bases of these interspecies differences are such that species-to-species extrapolations of absolute risk cannot be used. As a result, direct extrapolation of animal data to humans cannot be used to predict absolute risk.

Human Studies

Epidemiological studies on the effects of ^{222}Rn gas and its progeny on human health consist primarily of studies on ^{238}U and phosphate miners (^{238}U is associated with phosphate deposits). The human studies, except for the Svensson et al. (1989) study (number 25 in Table 2 and Figure 3), mostly tend to cluster in the cancer region for ^{222}Rn concentrations around 1,000 to 10,000 Bq m^{-3} (Figure 3). These epidemiological studies of cohorts of miners confirm that long-term exposure to high levels of ^{222}Rn gas and its progeny represent a very serious threat to human health.

One human study (Svensson et al., 1989) while suggesting a clear link between ^{222}Rn and small cell carcinoma in the lung, also notes that cancers were less prevalent in the rural cohort over the urbanized cohort where ambient air pollution was a positive confounder. This discrepancy is regarded by the authors as a serious flaw in the study. Additionally, according to Snihs (1973) no conclusions regarding dose and effect below 50 mSv (5 rem) may be drawn because of the large uncertainties and statistical errors. This suggests that the risks to cavers and cave workers from exposure to ^{222}Rn in caves may not be overly significant.

Exposure of Cavers and Cave Workers to ^{222}Rn and its Progeny

The formation of ^{222}Rn and its progeny is shown by the decay sequence in Figure 1. Radon-222 readily migrates to areas with a negative air space, such as caves and tunnels. It is also soluble in water and will reside in cave waters and atmospheres in equilibrium (Fig. 4). In addition, the ^{222}Rn parent, ^{226}Ra, will react with and precipitate on cave walls as RaCO$_{3}$ and thus provides a continuous source of ^{222}Rn. The net result is that ^{222}Rn concentrations in caves are considerably higher than typically occur in above ground residences, but are significantly less than those found in ^{238}U mines.

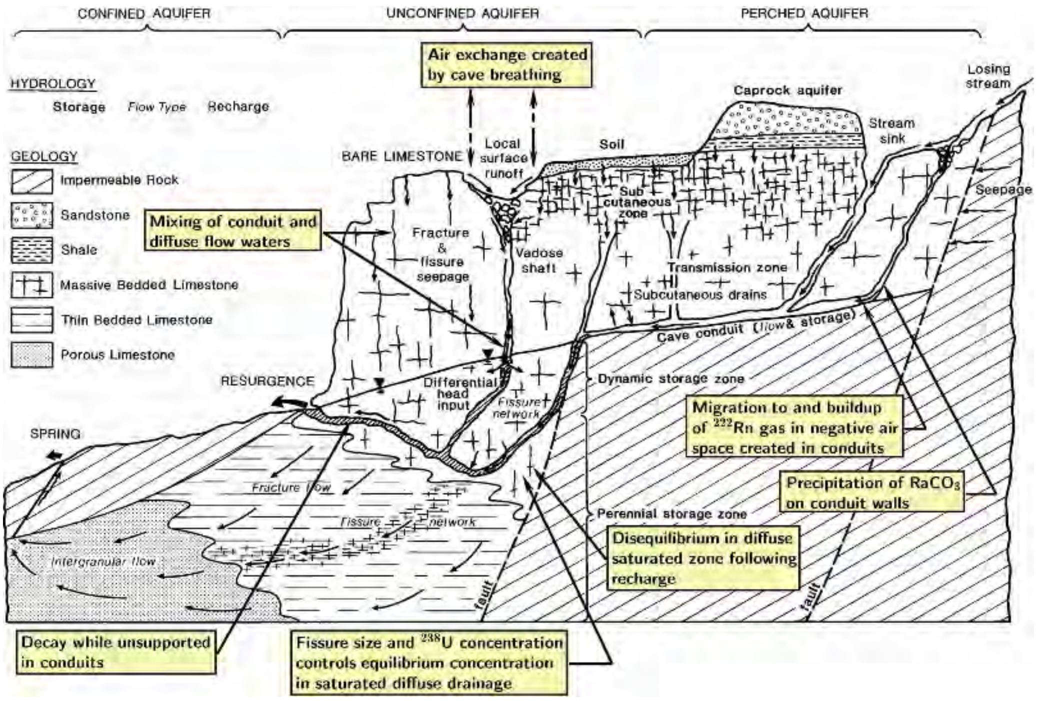

Figure 4. Factors controlling the ingrowth and decay of ^{222}Rn equilibrium activities in a cave system (modified from Smart and Friederich, 1986; Smart, 1991). Radon-222 ingrowth and decay processes in karst aquifer waters provided by Peter Smart (*pers. comm.*). Other important factors include dilution and volatilization. Cave breathing effects on ^{222}Rn concentrations are described in Cunningham and LaRock (1991); Yarborough and Meyers (1978, pp. 22–42. Precipitation of $RaCO_3$ on conduit walls is described in Field (1994, pp. 59–61). Radon-222 secular equilibrium is established after 26 days.

CUMULATIVE EXPOSURE

The decay of ^{222}Rn to its progeny results in secular equilibrium, provided none of its progeny plate out (i.e., adsorb to cave walls). Cumulative exposure C_E has historically been calculated in terms of working levels (WL) with 170 h for a working level month (WLM) and is calculated (in SI units of J h m^{-3}) using (NRC, 1999, p. 178)

$$C_E = \sum_{i=1}^{n} \left(\overline{C}_{Rn}\right)_i \frac{t_i}{170} \tag{3}$$

where $(\overline{C}R_n)_i$ is the average concentration of ^{222}Rn decay products during an exposure interval expressed in J m^{-3} and t_i is the number of hours of the exposure.

The significance to cavers of Equation (3) is the hours of exposure. According to NRC (1999, p. 178), the cumulative exposure for individuals who continuously occupy a residence (commonly known as shut-ins) at a given decay product concentration is greater than four times that for an occupational exposure (8,766 h compared to 2,000 h worked on an annual basis). This means that for cave tour guides who work no more than 170 hours per month will be exposed to one quarter that of individuals who do not leave their dwelling. For recreational caving, exposure will generally be considerably less.

The net result is that individuals living in above ground dwellings, but are not necessarily shut-ins, are annually exposed to 4.8 mSv of ^{222}Rn, as compared to coal and metal miners who are annually exposed to just 0.7 and 2.7 mSv of ^{222}Rn, respectively (Wrixon et al., 2004, p. 40). For cavers and cave workers, radiation doses are likely to be much less because, although ^{222}Rn concentrations in caves are likely to be similar to that of coal mines, they will be lower than in ^{238}U mines while exposure times will typically be much less than that of an occupant of a dwelling.

Comparative Dosimetry

The activity of the ^{222}Rn decay products is described by the Potential Alpha-Energy Concentration (PAEC) which is a non-equilibrium mixture. The PAEC is obtained from the potential alpha energy per unit of activity (Bq) of the considered radionuclide according to $\varepsilon_p/\lambda_r = (\varepsilon_p T_{1/2}/\ln 2)$ (ICRP, 1994a, p. 3). The total airborne PAEC may be obtained from (ICRP, 1994a, p. 4)

$$C_p = \sum_i C_i \left(\frac{\varepsilon_{p,i}}{\lambda_{r,i}}\right) \tag{4}$$

where values for ε_p and λ_r are listed in Table 3. The half life of ^{214}Po is so short ($T_{1/2} = 164$ µs; see Fig. 1) that for all practical purposes it is always in equilibrium with its parent

Table 3. Potential α-energy per atom and per unit activity (modified from ICRP, 1994a, p. 3).

Radionuclide	Half-Life (min)	Potential α-Energy per Atom (MeV)	per Atom (10^{-12} J)	per Unit of Activity, ε_p (MeV Bq^{-1})	per Unit of Activity, ε_p (10^{-10} J Bq^{-1})
^{222}Rn Progeny					
^{218}Po	3.05	13.69	2.19	3,615	5.79
^{214}Pb	26.8	7.69	1.23	17,840	28.6
^{214}Bi	19.9	7.69	1.23	13,250	21.2
^{214}Po	2.73×10^{-6}	7.69	1.23	2.0×10^{-3}	3.0×10^{-6}
Total (at equilibrium), per Bq or ^{222}Rn				34,710	55.6

^{214}Bi and is not needed in the decay chain calculations (NRC, 1999, p. 137). The Potential Alpha-Energy Exposure (PAEE) may then be calculated from (ICRP, 1994a, p. 4)

$$P_p(t) = \int_0^t C_p(t) \tag{5}$$

where time t is expressed as the amount of time an individual is exposed (e.g., one week, one month, etc.).

The equilibrium factor F is defined as the ratio of ^{222}Rn decay product concentration to that of ^{222}Rn and is given by (Hopke et al., 1995)

$$F = \frac{1.18 \times 10^8 \; C_p}{C_{Rn}} \tag{6}$$

where the value of F ranges from 0.2 to 0.8, but typically ranges from 0.35 to 0.40. A default indoor value of 0.4 is recommended by ICRP (1994a, p. 20). However, because of the difficulty of estimating ^{222}Rn decay product concentrations in caves which range from 0.04 to 0.95, a mean value of 0.5 is usually assigned to F for cave studies (see for example, Hyland and Gunn, 1994) although a strong basis for this contention has not been reported. Aley et al. (2006) suggested that, for some notable exceptions, F for most show caves probably ranges between 0.5 and 1.0, although a strong basis for this contention was not supported in this instance either.

Using Equation (6) it is possible to calculate the actual Equilibrium Equivalent Exposure (EEQ) from (ICRP, 1994, P. 4)

$$P_{eq}(t) = \int_0^t C_{eq}(t) \tag{7}$$

where

$$C_{eq} = F \; C_{Rn} \tag{8}$$

The EEQ is a measure of the exposure to ^{222}Rn and its progeny that an individual receives for a given ^{222}Rn concentration. It is the EEQ that determines how seriously an individual has been exposed to a given concentration of ^{222}Rn and its progeny for a given period of time.

RECOMMENDED ^{222}RN EXPOSURES

Allowable exposures to cave workers to PAEC have varied over the years as cancer risks have become better understood. Initial U.S. Government regulations were first set in 1976, but were later revised.

1976 Recommendations

In 1976, the National Institute of Occupational Safety and Health (NIOSH) recognized that ^{222}Rn progeny at several caves managed by the National park Service (NPS) were near the occupational limits as set forth in Occupational Safety and Health Administration (OSHA) standards for ^{238}U miners. NPS caves in which the PAEC exceeded 6.24 μJ m^{-3} (0.30 WL) include Carlsbad Caverns National Park, N.M., Lehman Caves National Monument, Nev., Mammoth Cave National Park, Ky., Oregon Caves National Park, Ore., and Round Spring Cave in Ozark National Scenic Riverways, Mo. Additionally, the PAEC inside the caves and above ground buildings cooled by cave air at Mammoth Cave were 12.48 μJ m^{-3} (0.60 WL) (Baier, 1976). Specific recommendations by NIOSH are shown in Table 4.

Current Recommendations

Current recommended regulations regarding exposures of workers to ^{222}Rn are listed in Tables 5 and 6. The recommendations listed in Table 5 are intended to be conservatively protective. These levels are applicable to cave workers (e.g., tour guides), but are overly restrictive for infrequent cave explorers. According to Strom et al., (1996, p. 5) (citing NCRP, 1993, p. 49) effective dose in the workplace should not exceed 5 cSv (5 rem) in any one year with $A_{ge} \times 1$ cSv as a lifetime limit. If the ICRP (1994a) recommendations are applied, then the the NCRP recommendations convert to 5 cSv (5 rem) in any one year with $A_{ge} \times 7.08$ mJ h m^{-3} or $A_{ge} \times 1$ cSv as a lifetime limit.

Regulations specific to cave workers (and miners) are shown in Table 6. The cave worker regulations were developed and published by OSHA (OSHA, 1988) and Mine Safety and Health Administration (MSHA) (MSHA, 1989). OSHA sets an individual exposure limit equal to 14.0 mJ h m^{-3} = 20.0 mSv yr^{-1} (4.0 WLM yr^{-1}) (OSHA,

Table 4. Recommended regulations by NIOSH for exposure of cavers to ^{222}Rn decay progeny in 1976 (modified from Baier, 1976).

PAEC Level		
(μJ m^{-3})	(WL)	Recommended Regulation
>2.08	>0.1	All-underground smoking stopped
2.08–4.16	0.1–0.2	Monitor workspace at least quarterly
4.16−6.24	0.2–0.3	Monitor workspace quarterly
>6.24	>0.3	Monitor workspace weekly and maintain exposure records on all exposed employees
20.80−41.60	1.0–2.0	Immediate corrective action to lower PAEC below 20.80 μJ m^{-3} (1.0 WL)
>41.60	>2.0	Withdraw all workers not necessary to lower PAEC below 20.80 μJ m^{-3} (1.0 WL)

Cumulative individual exposure shall not exceed 14.0 mJ h m^{-3} yr^{-1} (4.0 WLM yr^{-1}).

1988, 41 CFR §57.5038). MSHA also sets a maximum cumulative dose equal to 14.0 mJ h m^{-3} = 20.0 mSv yr^{-1} (4.0 WLM yr^{-1}) (MSHA, 1989, 30 CFR Part 57). However, ICRP65 was a little more specific in that it set a recommended effective dose at 14.0 mJ h m^{-3} = 20.0 mSv yr^{-1} (4.0 WLM yr^{-1}) averaged over five years and 35.0 mJ h m^{-3} = 50.0 mSv yr^{-1} (10.0 WLM yr^{-1}) in any single year (ICRP, 1994a, p. 21).

Aley et al. (2006) lays out a strategy for reducing total α radiation exposures of show-cave employees to As Low As Reasonably Achievable (ALARA[14]) levels. Although not yet approved in 2006, it is likely that some form of the strategy will be approved by the National Caves Association in which each member will be required to develop a Cave Radiation Management Plan following guidelines developed by OSHA.

DETERMINING ^{222}RN RISKS TO CAVERS

The risks posed by exposure to elevated levels of ^{222}Rn gas have not adequately addressed exposures to recreational cavers and cave workers. Regulations not specific to caves have been promulgated (e.g., MSHA, 2005, §57.5037–§57.5046) while regulations specific to caves have been developed (NPS, 1980) and are being updated (NPS, 2005). These regulations generally specify acceptable Working Levels for individuals, but not exposure rates, absorbed doses, or effective doses which are necessary for determining risks. However, because human health effects caused by elevated ^{222}Rn concentrations are based on epidemiological studies of miners subjected to much higher ^{222}Rn exposures (concentrations and times) as well as confounding factors (smoking, dust, etc.), risk estimates for cavers and cave workers need to be established using the linear no-threshold theory (LNT) even though the associated uncertainty in the cancer risk per unit dose at low dose and dose rate is difficult to quantify (Eckerman et al., 1999, p. 11–12).

APPLICATION OF THE LNT TO ^{222}RN AND ITS PROGENY

The LNT for radiation carcinogenesis is based on the concept that all radiation doses, no matter how small, can cause cancer (i.e., there is no acceptable radiation threshold at which cancers will not be initiated). According to this

Table 5. Recommended regulations by DOE for exposure to ^{222}Rn-decay progeny in 1996 (modified from Strom et al., 1996, p. 6).

	PAEC		PAEE		
Country[a]	(μ J m^{-3})	(WL)	(mJ m^{-3} yr^{-1})	(mSv yr^{-1})	(WLM yr^{-1})
United States	6.93	⅓	14.0	20.0	4.0
Canada, France, Great Britain	8.32	0.4	16.8	24.0	4.8
	…	…	17.5	25.0	5.0[b]
	…	…	35.1	50.0	10.0[c]
	…	…	35.1	50.0	10.0[d]

[a] The United States values are based on U.S. Environmental Protection Agency (EPA), U.S. Department of Energy (DOE), and U.S. Nuclear Regulatory Commission (NRC) regulations.

[b] Values are for any single year — $A_{ge} \times 3.54$ mJ h m^{-3} ($A_{ge} \times 1$ WLM).

[c] Values are for any single year — $A_{ge} \times 7.08$ mJ h m^{-3} ($A_{ge} \times 2$ WLM).

[d] Values are for any single year —14.0 mJ h m^{-3} yr^{-1} (4.0 WLM yr^{-1}) averaged over 5 yr.

Table 6. Published regulations by OSHA and MSHA for exposure of cavers to ^{222}Rn-decay progeny in 1976 (modified from ATSDR, 1990, p. 93–94).

PAEC Level		PAEE Level			
(μJ m^{-3})	(WL)	(mSv yr^{-1})	(WLM yr^{-1})	Published Regulations	Reference
…	…	20.0	4.0	Individual exposure limit	OSHA[a]
2.08	0.1	…	…	Monitor workspace at least once yearly	OSHA[b]
2.08–6.24	0.1–0.3	…	…	Monitor workspace quarterly	OSHA[c]
>6.24	>0.3	…	…	Monitor workspace weekly and maintain exposure records on all exposed employees	OSHA[d]
20.80	1.0	…	…	Immediate corrective action to lower PAEC	OSHA[e]
20.80	1.0	…	…	Instantaneous maximum	MSHA[f]
…	…	20.0	4.0	Maximal cumulative dose	MSHA[f]

[a] (OSHA, 1988, 41 CFR §57.5038).
[b] (OSHA, 1988, 41 CFR §57.5087).
[c] (OSHA, 1988, 41 CFR §57.5037).
[d] (OSHA, 1988, 41 CFR §57.5037).
[e] (OSHA, 1988, 41 CFR §57.5041).
[f] (MSHA, 1988, 30 CFR Part 57).

theory then, if exposure to 1 Gy (100 rad) causes a cancer risk R, the risk from exposure to 10^{-2} Gy (1 rad) is $R/100$, the risk from exposure to 10^{-5} Gy (1 mrad) is $R/10^5$, and so on, which means that only a zero radiation dose will result in a zero risk of cancer (Cohen, 2002).

CANCER RISK MODELING FOR EXPOSURE TO ^{222}RN AND ITS PROGENY

Models intended to address cancer risks from exposure to ^{222}Rn and its progeny have evolved over the years, although all have followed the LNT (Yu et al., 2006). The most current model was developed and published in ICRP66 (ICRP, 1994b).

Human Respiratory Tract Model for Effective Dose Estimation

Using the program LUNGDOSE.F90 (Nikezic and Yu, 2001) which was developed according to the Human Respiratory Tract Model (HRTM), an estimated equilibrium factor F equal to 0.366 was obtained, which closely matches the ICRP65 recommended value ($F = 0.4$) (ICRP, 1994a, p. 5) and the BEIR VI arithmetic average value of 0.408 (James et al., 2003). An average inhalation rate $I_h = 2.16 \times 10^4$ m^3 s^{-1} in a residence resulted in an estimated thoracic dose D_T of 79.20 nSv (Bq h $m^{-3})^{-1}$ (126.112 mSv WLM^{-1}). Most interestingly, LUNGDOSE.F90 resulted in an estimate for a Dose Conversion Factor (DCF) equal to 9.50 nSv (Bq h $m^{-3})^{-1}$ (15.13 mSv WLM^{-1}) which is considerably larger than the epidemiological estimate for a DCF equal to 3.18 nSv (Bq h $m^{-3})^{-1}$ (5.06 mSv WLM^{-1}) for workers and 2.44 nSv (Bq h $m^{-3})^{-1}$ (3.88 mSv WLM^{-1}) for the public (ICRP, 1994a, p. 13). This discrepancy emphasizes the complexities and uncertainties when calculating risks posed by exposure to PAEC (Gourmelon et al., 2005, p. 19).

The difference between the LUNGDOSE.F90 estimate for a DCF equal to 9.50 nSv (Bq h $m^{-3})^{-1}$ (15.13 mSv WLM^{-1}) and the ICRP65 estimate for a DCF equal to 3.18 nSv (Bq h m^{-3}) (5.06 mSv WLM^{-1}) is not regarded as significantly large because of the complex physical and biological issues involved and reasonably matches a previously epidemiologically-estimated value of 9.0 nSv (Bq h $m^{-3})^{-1}$ (14.33 mSv WLM^{-1}) (UNSCEAR, 2000, p. 107). An evaluation of the discrepancy has resulted in the suggestion that the epidemiologically-based estimate for DCF will need to be increased and that for now, the larger DCF value estimated dosimetrically using the HRTM is recommended for use in risk calculations (UNSCEAR, 2000, p. 107). However, others feel that the epidemiologically-based estimates are more scientifically sound (Neal Nelson, *pers. comm.*).

Using the values estimated from Lungdose.F90 developed by Nikezic and Yu (2001) with $I_h = 3.33 \times 10^4$ m^3 s^{-1} to account for a combination of resting, light and heavy exercise (James et al., 2003) typical of caving, the ^{222}Rn concentrations listed in Table 1 and Equation (9) (Wiegand et al., 1995)

$$E_{DA} = C_{Rn}\, F\, T_i\, D_{CF} \tag{9}$$

produced the annual effective doses E_{DA} for ^{222}Rn exposures to recreational cavers (50 h yr^{-1}), professional cavers (600 h yr^{-1}), part-time cave workers (1,760 h yr^{-1}), and full-time cave workers (2,000 h yr^{-1}) (Table 7). Realistically, there is no reliable way to estimate the average number of hours experienced by recreational cavers, professional cavers, and part-time cave workers. The number of caving hours per year for cavers (50 h yr^{-1} and 600 h yr^{-1}) are considered reasonable estimates. Part-time cave worker hours equal to 1,760 h yr^{-1} was used as an estimate because this value is recommended for

Table 7. Estimated annual effective doses using the LUNGDOSE.F90 program[a] for exposures to cavers and cave workers for mean ^{222}Rn concentrations listed in Table 1. Superscript numbers next to each entry correspond to the x-axis on Figures 5–8. Entries without a superscript were not plotted.

	Recreational Caver[b]		Professional Caver[c]		Part-Time Cave Worker[d]		Full-Time Cave Worker[e]	
Country	(mSv yr^{-1})	(WLM yr^{-1})	(mSv yr^{-1})	(WLM yr^{-1})	(mSv yr^{-1})	(WLM yr^{-1})	(mSv yr^{-1})	(WLM yr^{-1})
^{1}Australia	0.14	0.03	1.73	0.35	5.07	1.01	5.77	1.15
^{2}China[f]	0.03	0.01	0.40	0.08	1.17	0.23	1.33	0.27
^{3}Czech Republic	0.29	0.06	3.50	0.70	10.27	2.05	11.67	2.33
^{4}Great Britain	0.69	0.14	8.24	1.65	24.18	4.84	27.48	5.50
Great Britain	…	…	…	…	…	…	…	…
^{5}Great Britain	8.48	1.70	101.77	20.35	298.53	59.71	339.24	67.85
^{6}Great Britain	2.20	0.44	26.39	5.28	77.41	15.48	87.96	17.59
^{7}Great Britain	0.09	0.02	1.04	0.21	3.04	0.61	3.45	0.69
^{8}Great Britain	0.07	0.01	0.89	0.18	2.62	0.52	2.98	0.60
^{9}Greece	5.95	1.19	71.40	14.28	209.44	41.89	238.00	47.60
^{10}Hungary	0.78	0.16	9.36	1.87	27.45	5.49	31.19	6.24
^{11}Hungary	0.58	0.12	7.00	1.40	20.53	4.11	23.33	4.67
^{12}Ireland	0.98	0.20	11.70	2.34	34.33	6.87	39.01	7.80
^{13}Japan	< 0.01	< 0.01	0.03	0.01	0.09	0.02	0.10	0.02
^{14}Malaysia	0.14	0.03	1.69	0.34	4.96	0.99	5.63	1.13
^{15}Poland	0.28	0.06	3.31	0.66	9.70	1.94	11.02	2.20
^{16}Russia	0.56	0.11	6.78	1.36	19.88	3.98	22.59	4.52
^{17}Slovenia	0.33	0.07	4.00	0.80	11.75	2.35	13.35	2.67
^{18}Slovenia	0.23	0.05	2.74	0.55	8.03	1.61	9.12	1.82
^{19}Spain	0.03	0.01	0.31	0.06	0.90	0.18	1.02	0.20
^{20}Spain	0.84	0.17	10.11	2.02	29.65	5.93	33.69	6.74
^{21}South Africa	0.06	0.01	076	0.15	2.22	0.44	2.52	0.50
^{22}Switzerland	5.91	1.18	70.89	14.18	207.95	41.59	236.31	47.26
^{23}United States	0.46	0.09	5.46	1.09	16.03	3.21	18.21	3.64
^{24}United States	0.61	0.12	7.34	1.47	21.54	4.31	24.47	4.89
^{25}United States	0.35	0.07	4.18	0.84	12.27	2.45	13.94	2.79
United States	…	…	…	…	…	…	…	…
^{26}United States	2.76	0.55	33.12	6.62	97.14	19.43	110.38	22.08

[a] Lungdose.F90 program (Nikezik and Yu, 2001) estimate for DCF = 12.92 nSv (Bq h m^{-3})$^{-1}$ (20.75 mSv WLM^{-1}) and D_T = 107.63 nSv (Bq h m^{-3})$^{-1}$ (171.38 mSv WLM^{-1}) for $I_h = 3.33 \times 10^{-4}$ m^3 s^{-1}.

[b] Recreational cavers = 50 h yr^{-1} of caving.

[c] Professional cavers = 600 h yr^{-1} of caving.

[d] Part-time cave worker = 1,760 h yr^{-1} of cave work.

[e] Full-time cave worker = 2,000 h yr^{-1} of cave work.

[f] The measured ^{222}Rn concentrations for the China data listed in Table 1 are better represented by 7,000 h yr^{-1} exposure with an $I_h = 2.16 \times 10^{-4}$ m^3 s^{-1} because these data are from cave dwellings resulting in an E_{DA} = 3.43 mSv yr^{-1} (0.69 WLM yr^{-1}).

outside exposure by UNSCEAR (2000, p. 107), even though UNSCEAR recommended a larger equilibrium factor of (0.6) for external exposures, but which was not used in the calculations because it is not appropriate for caves.

An $I_h = 3.33 \times 10^4$ m^3 s^{-1} resulted in a greater D_T and a greater overall E_{DA} for cavers and cave workers than when an $I_h = 2.16 \times 10^4$ m^3 s^{-1} was used because of the much greater breathing activity. Mean annual effective doses E_{DA} listed in Table 7 typically ranged from much less (0.03 mSv yr^{-1}) to much greater (339.27 mSv yr^{-1}) than the recommended maximums of 20 to 50 mSv yr^{-1}. Unfortunately, the great range of data and variability evidenced make it very difficult to realistically estimate the risks posed to cavers and cave workers from the estimated E_{DA}. However, it appears from Table 7 that recreational cavers and, for the most part, professional cavers are likely to be only minimally exposed to excess ^{222}Rn concentrations whereas cave workers should be more concerned about exposure to excess ^{222}Rn concentrations for the five countries with high mean ^{222}Rn concentrations (Great Britain, Greece, Japan, Switzerland, and the United States) (Table 7).

Figures 5–8 illustrate the threat to cavers and cave workers from exposure to elevated levels of ^{222}Rn gas in caves relative to acceptable limits. From Figures 5–8 it is

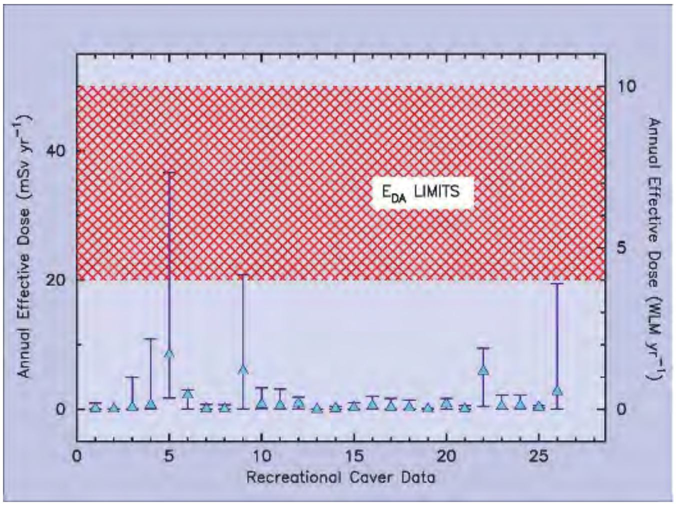

Figure 5. Plot of mean, minimum, and maximum annual effective dose values for recreational cavers from Table 7 relative to published acceptable limits of 20−50 mSv yr^{-1} (4−10 WLM yr^{-1}). The x-axis numerical values correspond to the superscript labels in Table 7. (Note that data sets listed in Table 7 missing mean values [Great Britain and United States] are not plotted).

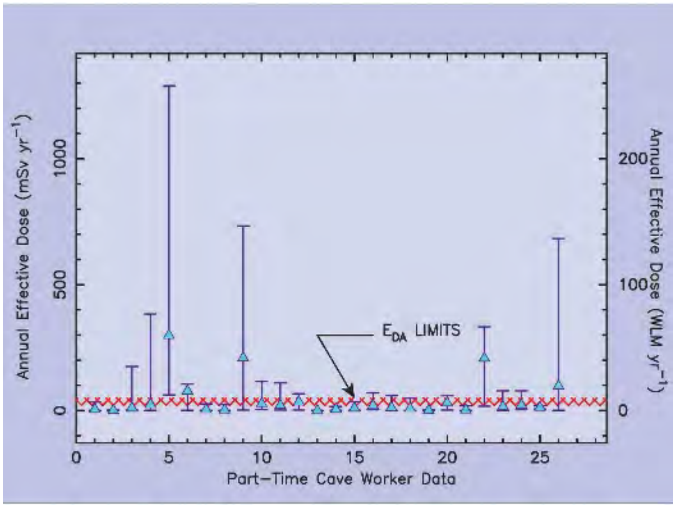

Figure 7. Plot of mean, minimum, and maximum annual effective dose values for part-time cave workers from Table 7 relative to published acceptable limits of 20–50 mSv yr^{-1} (4–10 WLM yr^{-1}). The x-axis numerical values correspond to the superscript labels in Table 7. (Note that data sets listed in Table 7 missing mean values [Great Britain and United States] are not plotted).

apparent that cavers are generally not at risk while cave workers appear to be minimally at risk.

A series of notched boxplots (see Chambers et al., 1983, for a description of notched boxplots) using the data listed in Table 7 and shown in Figure 9 further demonstrate that only cave workers will be minimally impacted at the lower E_{DA} limit of 20 mSv yr^{-1} (4 WLM yr^{-1}). However, the median line of each notched boxplot for the part-time and full-time cave workers are also below the minimum acceptable limit for exposure, suggesting that neither the part-time nor the full-time cave workers are impacted at the lower E_{DA} limit, and only the the more extreme values

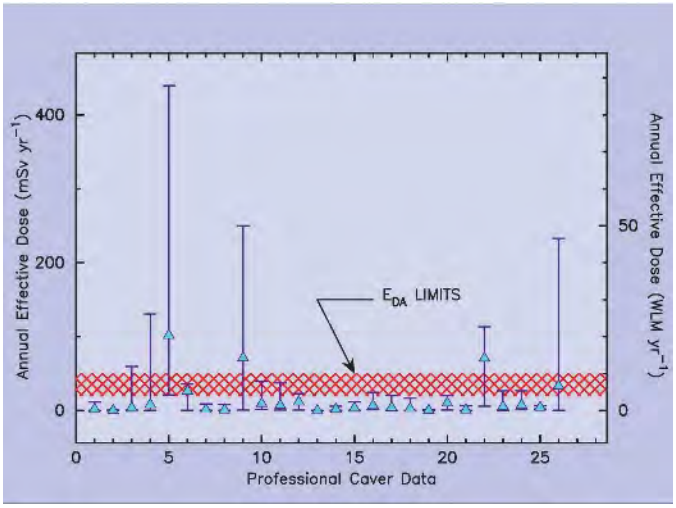

Figure 6. Plot of mean, minimum, and maximum annual effective dose values for professional cavers from Table 7 relative to published acceptable limits of 20–50 mSv yr−1 (4–10 WLM yr^{-1}). The x-axis numerical values correspond to the superscript labels in Table 7. (Note that data sets listed in Table 7 missing mean values [Great Britain and United States] are not plotted).

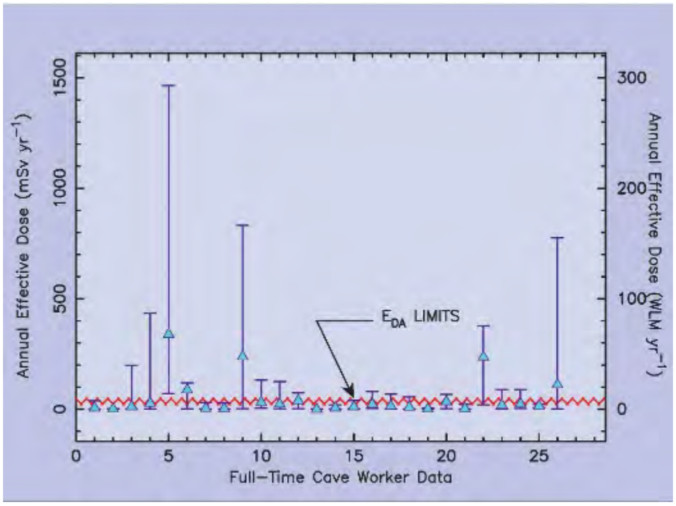

Figure 8. Plot of mean, minimum, and maximum annual effective dose values for full-time cave workers from Table 7 relative to published acceptable limits of 20–50 mSv yr^{-1} (4–10 WLM yr^{-1}). The x-axis numerical values correspond to the superscript labels in Table 7. (Note that data sets listed in Table 7 missing mean values [Great Britain and United States] are not plotted).

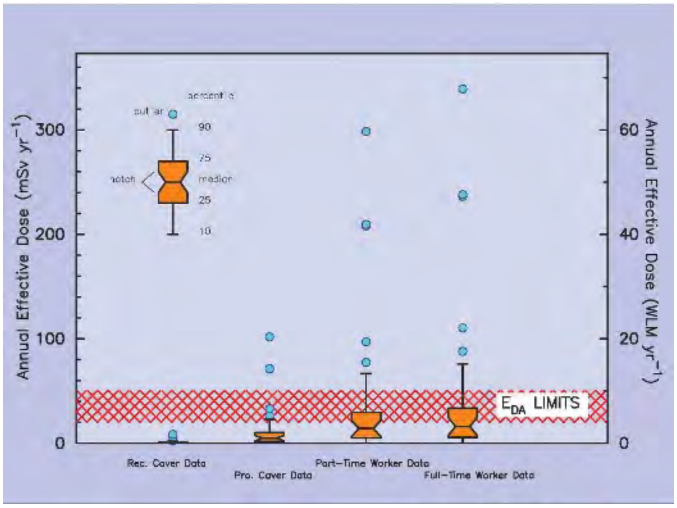

Figure 9. Notched boxplots of estimated annual effective doses relative to acceptable limits. (Note that data sets listed in Table 7 missing mean values [Great Britain and United States] are not plotted).

(i.e., >90th percentile) exceed the 50 mSv yr^{-1} (10 WLM yr^{-1}) limit.

Exposure of Cavers to ^{222}Rn and its Progeny. Exposure of cave workers and cavers to ^{222}Rn and its progeny is obtained from (Eckerman et al., 1999, p. F4)

$$P_{eq}(t) = C_i \int_0^t e^{(-\ln 2t)/T_{1/2}} \tag{10}$$

which considers the decay series of ^{222}Rn through its progeny, of which only the principal progeny identified in Figure 1 are used in the calculations. Each progeny concentration is estimated from the concentration of its respective parent. According to the nuclear decay data listed in Eckerman et al. (1999, p. G19–G20), each radionuclide for the ^{222}Rn decay series decays to between 99.98% and 100% to its principal progeny (e.g., 99.98% of ^{218}Po decay results in ^{214}Pb) (Table 8), which renders insignificant the other progeny shown in Figure 1 (e.g., ^{218}AT and ^{218}Rn).

Applying Equation (10) allows for exposures to cavers from ^{222}Rn and its progeny to be estimated from the ^{222}Rn concentrations listed in Table 1. Estimated exposures are listed in Table 9, where it may be noted that the smallest estimated exposure is produced by ^{214}Po. This appears contrary to the notion that the very short half life of ^{214}Po ($T_{1/2}$ = 164 µs) will result in the greatest lung doses because ^{214}Po will likely emit an α-particle before it can be exhaled. Polonium-214 decays only once, but is in secular equilibrium with its parent radionuclide ^{214}Bi. However, ^{214}Po has the greatest number of decays per unit intake of ^{222}Rn in equilibrium with its progeny. Its half life, therefore, is not a factor (N. Nelson, pers. comm.).

Risks to Cavers from Exposure to ^{222}Rn and its Progeny. Risks to cave workers and cavers need to be estimated from the exposures listed in Table 9 and risk coefficients determined from epidemiological studies when available. Risks include both mortality and morbidity.

The risks of mortality (cancer death) and morbidity (cancer with or without death) from exposure to ^{222}Rn and its progeny are estimated from (Eckerman et al., 1999, p. F-8)

$$R_{M_i} = P_{eq_i}\, S_C\, I_h\, M_{R_i} \tag{11}$$

where a scaling coefficient S_C of 1.11 for inhalation was considered appropriate (Eckerman et al., 1999, p. E-5) and the values for the mortality[15] and morbidity[16] risk coefficients M_{R_i} are listed in Table 10.

The EPA estimates mortality risks from exposure to ^{222}Rn gas as a function of WLM; specifically, EPA expects 5.4×10^{-4} lung cancer deaths per WLM. This methodology was not used here because the WLM does not account for such factors as breathing rates, tidal volumes, or the fraction of progeny unattached to aerosols, which modify the relationship between exposure and risk (Cothern, 1987, p. 26).

Morbidity risks to cavers and cave workers can not be directly calculated because the relevant morbidity risk coefficients exist only for ^{214}Pb and ^{214}Bi (Table 10). The difference between the mortality and morbidity coefficients for ^{214}Pb and ^{214}Bi are relatively insignificant, but the same cannot be said for the other radionuclides listed in Table 10. In general, it is reasonable to expect that the risk of morbidity to cavers and cave workers will be somewhat greater than is the estimated risk for mortality.

In order to develop a rough estimate for the risk of morbidity for cavers and cave workers, the values for the

Table 8. Nuclear decay products and fractions for ^{222}Rn and its progeny (modified from Eckerman et al., 1999, p. G19–G20).

Radionuclide	$T_{1/2}$	Decay Mode	Radioactive Decay Products and Fractional Yield			
			Radionuclide	Fraction	Radionuclide	Fraction
^{222}Rn	3.8325 d	α	^{218}Po	1.0000	…	…
^{218}Po	3.05 min	α β−	^{214}Pb	0.9998	^{218}At	0.0002
^{214}Pb	26.8 min	β−	^{214}Bi	1.0000	…	…
^{214}Bi	19.9 min	α β−	^{214}Po	0.9998	^{210}Tl	0.0002
^{214}Po	164.3 µs	α	^{210}Pb	1.0000	…	…

Table 9. Estimated time-integrated concentration exposures to ^{222}Rn and its progeny for cavers for the mean ^{222}Rn concentrations listed in Table 1[a].

	Inhalation Exposure				
Country	^{222}Rn ($Bq\ s^{-1}\ m^{-3}$)	^{218}Po ($Bq\ s^{-1}\ m^{-3}$)	^{214}Pb ($Bq\ s^{-1}\ m^{-3}$)	Z^{14}Bi ($Bq\ s^{-1}\ m^{-3}$)	^{214}Po ($Bq\ s^{-1}\ m^{-3}$)
Australia	4.82×10^{7}	3.35×10^{4}	3.35×10^{4}	3.35×10^{4}	5.58×10^{-4}
China	1.11×10^{7}	7.74×10^{3}	7.74×10^{3}	7.74×10^{3}	1.29×10^{-4}
Czech Republic	9.76×10^{7}	6.78×10^{4}	6.78×10^{4}	6.78×10^{4}	1.13×10^{-3}
Great Britain	2.30×10^{8}	1.60×10^{5}	1.59×10^{5}	1.59×10^{5}	2.66×10^{-3}
Great Britain	…	…	…	…	…
Great Britain	2.84×10^{9}	1.97×10^{6}	1.97×10^{6}	1.97×10^{6}	3.28×10^{-2}
Great Britain	7.35×10^{8}	5.11×10^{5}	5.11×10^{5}	5.11×10^{5}	8.51×10^{-3}
Great Britain	2.88×10^{7}	2.00×10^{4}	2.00×10^{4}	2.00×10^{4}	3.34×10^{-4}
Great Britain	2.49×10^{7}	1.73×10^{4}	1.73×10^{4}	1.73×10^{4}	2.88×10^{-4}
Greece	1.99×10^{9}	1.38×10^{6}	1.38×10^{6}	1.38×10^{6}	2.30×10^{-2}
Hungary	2.61×10^{8}	1.81×10^{5}	1.81×10^{5}	1.81×10^{5}	3.02×10^{-3}
Hungary	1.95×10^{8}	1.35×10^{5}	1.35×10^{5}	1.35×10^{5}	2.26×10^{-3}
Ireland	3.26×10^{8}	2.26×10^{5}	2.26×10^{5}	2.26×10^{5}	3.77×10^{-3}
Japan	8.69×10^{5}	6.04×10^{2}	6.04×10^{2}	6.04×10^{2}	1.01×10^{-5}
Malaysia	4.71×10^{7}	3.27×10^{4}	3.27×10^{4}	3.27×10^{4}	5.45×10^{-4}
Poland	9.21×10^{7}	6.40×10^{4}	6.40×10^{4}	6.40×10^{4}	1.07×10^{-3}
Russia	1.89×10^{8}	1.31×10^{5}	1.31×10^{5}	1.31×10^{5}	2.19×10^{-3}
Slovenia	1.12×10^{8}	7.75×10^{4}	7.75×10^{4}	7.75×10^{4}	1.29×10^{-3}
Slovenia	7.63×10^{7}	5.30×10^{4}	5.29×10^{4}	5.29×10^{4}	8.82×10^{-4}
Spain	8.53×10^{6}	5.93×10^{3}	5.93×10^{3}	5.93×10^{3}	9.87×10^{-5}
Spain	2.82×10^{8}	1.96×10^{5}	1.96×10^{5}	1.96×10^{5}	3.26×10^{-3}
South Africa	2.11×10^{7}	1.47×10^{4}	1.46×10^{4}	1.46×10^{4}	2.44×10^{-4}
Switzerland	1.98×10^{9}	1.37×10^{6}	1.37×10^{6}	1.37×10^{6}	2.29×10^{-2}
United States	1.52×10^{8}	1.06×10^{5}	1.06×10^{5}	1.06×10^{5}	1.76×10^{-3}
United States	2.05×10^{8}	1.42×10^{5}	1.42×10^{5}	1.42×10^{5}	2.37×10^{-3}
United States	1.17×10^{8}	8.09×10^{4}	8.09×10^{4}	8.09×10^{4}	1.35×10^{-3}
United States	…	…	…	…	…
United States	9.23×10^{8}	6.41×10^{5}	6.41×10^{5}	6.41×10^{5}	1.07×10^{-2}

[a] Only the mean time-integrated concentration exposures are shown here. Maximum and minimum exposure values were calculated from the maximum and minimum ^{222}Rn concentrations listed in Table 1 but are not shown here due to space limitations.

morbidity risk coefficient M_{R_B} for ^{214}Pb and ^{214}Bi were taken from Table 10. For the other radionuclides, the mortality risk coefficients M_{R_T} listed in Table 10 were increased by a factor of 1.5 on the assumption that such an increase will reasonably represent a morbidity risk coefficient M_{R_B} for those radionuclides for which morbidity risk coefficients are not yet available.

Table 10. Mortality and morbidity risk coefficients for ^{222}Rn and its progeny.

	Risk Coefficients	
Radionuclide	Motality (Bq^{-1})	Morbidity (Bq^{-1})
^{222}Rn[a]	3.21×10^{-11}	…
^{218}Po[a]	9.44×10^{-11}	…
^{214}Pb[b]	9.31×10^{-10}	9.81×10^{-10}
^{214}Bi[c]	7.45×10^{-10}	7.84×10^{-10}
^{214}Po[a]	7.12×10^{-17}	…

[a] Risk coefficients source: Puskin and Nelson (1994, p. 53).

[b] Risk coefficients source: Eckerman et al. (1999, p. 71).

[c] Risk coefficients source: Eckerman et al. (1999, p. 72).

Mortality and morbidity risks (Table 11) were averaged over all ages and both genders for a population with specified mortality and morbidity for the mean exposures listed in Table 9. The mean risks of mortality and morbidity ranged from 10^{-5} (1 in 100,000) to 10^{-7} (1 in 10,000,000) where 10^{-6} (1 in 1,000,000) is usually considered an acceptable risk.

The significance of the mortality and morbidity inhalation risks posed to cavers and cave workers is shown in Figures 10 and 11. It will be noted from Figures 10 and 11 that the majority of the mean values are very close to the 10^{-6} acceptable risk level, but the maximum measured risks appear considerably greater than the 10^{-6} acceptable risk level. Only data sets represented by numbers 5 (Great Britain), 6 (Great Britain), 9 (Greece), 22 (Switzerland), and 26 (United States) exhibited mean values substantially greater than the 10^{-6} acceptable risk level.

Table 11. Inhalation risks from ^{222}Rn and its progeny for exposures to cavers and cave workers for the ^{222}Rn concentrations listed in Table 1. Superscript numbers next to each entry corresponds to the x-axis on Figures 10 and 11. Entries without a superscript were not plotted.

Country	Inhalation Motality Risk			Inhalation Morbidity Risk		
	Mean	Maximum	Minimum	Mean	Maximum	Minimum
^{1}Australia	5.9×10^{-7}	3.9×10^{-6}	8.8×10^{-9}	8.8×10^{-7}	5.9×10^{-6}	1.3×10^{-8}
^{2}China	1.4×10^{-7}	2.7×10^{-7}	3.7×10^{-8}	2.0×10^{-7}	4.0×10^{-7}	5.5×10^{-8}
^{3}Czech Republic	1.2×10^{-6}	2.0×10^{-5}	1.9×10^{-7}	1.8×10^{-6}	3.0×10^{-5}	2.9×10^{-7}
^{4}Great Britain	2.8×10^{-6}	4.5×10^{-5}	9.7×10^{-9}	4.2×10^{-6}	6.7×10^{-5}	1.4×10^{-8}
Great Britain	…	1.5×10^{-4}	9.7×10^{-8}	…	2.2×10^{-4}	1.4×10^{-7}
^{5}Great Britain	3.5×10^{-5}	1.5×10^{-4}	7.2×10^{-6}	5.2×10^{-5}	2.2×10^{-4}	1.1×10^{-5}
^{6}Great Britain	9.1×10^{-6}	1.2×10^{-5}	6.6×10^{-8}	1.3×10^{-5}	1.8×10^{-5}	9.8×10^{-8}
^{7}Great Britain	3.6×10^{-7}	3.1×10^{-6}	2.5×10^{-8}	5.3×10^{-7}	4.6×10^{-6}	3.8×10^{-8}
^{8}Great Britain	3.1×10^{-7}	3.0×10^{-6}	3.3×10^{-8}	4.6×10^{-7}	4.4×10^{-6}	4.9×10^{-8}
^{9}Greece	2.5×10^{-5}	8.6×10^{-5}	1.8×10^{-7}	3.6×10^{-5}	1.3×10^{-4}	2.7×10^{-7}
^{10}Hungary	3.2×10^{-6}	1.4×10^{-5}	4.9×10^{-7}	4.8×10^{-6}	2.0×10^{-5}	7.2×10^{-7}
^{11}Hungary	2.4×10^{-6}	1.3×10^{-5}	1.9×10^{-7}	3.6×10^{-6}	1.9×10^{-5}	2.9×10^{-7}
^{12}Ireland	4.0×10^{-6}	7.7×10^{-6}	1.9×10^{-7}	6.0×10^{-6}	1.1×10^{-5}	2.9×10^{-7}
^{13}Japan	1.1×10^{-5}	1.9×10^{-8}	7.2×10^{-10}	1.6×10^{-8}	2.9×10^{-8}	1.1×10^{-9}
^{14}Malaysia	5.8×10^{-7}	1.9×10^{-6}	9.7×10^{-8}	8.6×10^{-7}	2.9×10^{-6}	1.4×10^{-7}
^{15}Poland	1.1×10^{-6}	4.1×10^{-6}	5.8×10^{-8}	1.7×10^{-6}	6.0×10^{-6}	8.7×10^{-8}
^{16}Russia	2.3×10^{-6}	8.3×10^{-6}	3.6×10^{-7}	3.5×10^{-6}	1.2×10^{-5}	5.4×10^{-7}
^{17}Slovenia	1.4×10^{-6}	7.0×10^{-6}	1.5×10^{-8}	2.0×10^{-6}	1.0×10^{-5}	2.2×10^{-8}
^{18}Slovenia	9.4×10^{-7}	5.8×10^{-6}	5.8×10^{-8}	1.4×10^{-6}	8.6×10^{-6}	8.7×10^{-8}
^{19}Spain	1.1×10^{-7}	4.8×10^{-7}	4.9×10^{-9}	1.6×10^{-7}	7.1×10^{-7}	7.2×10^{-9}
^{20}Spain	3.5×10^{-6}	6.9×10^{-6}	1.8×10^{-7}	5.2×10^{-6}	1.0×10^{-5}	2.7×10^{-7}
^{21}South Africa	2.6×10^{-7}	2.3×10^{-6}	2.9×10^{-9}	3.9×10^{-7}	3.4×10^{-6}	4.3×10^{-9}
^{22}Switzerland	2.4×10^{-5}	3.9×10^{-5}	1.9×10^{-6}	3.6×10^{-5}	5.8×10^{-5}	2.9×10^{-6}
^{23}United States	1.9×10^{-6}	9.1×10^{-6}	3.6×10^{-8}	2.8×10^{-6}	1.4×10^{-5}	5.4×10^{-8}
^{24}United States	2.5×10^{-6}	9.2×10^{-6}	3.6×10^{-7}	3.7×10^{-6}	1.4×10^{-5}	5.4×10^{-7}
^{25}United States	1.4×10^{-6}	2.3×10^{-6}	7.3×10^{-7}	2.1×10^{-6}	3.4×10^{-6}	1.1×10^{-6}
United States	…	1.8×10^{-6}	3.2×10^{-7}	…	2.7×10^{-6}	4.8×10^{-7}
^{26}United States	1.1×10^{-5}	8.0×10^{-5}	1.1×10^{-8}	1.7×10^{-5}	1.2×10^{-4}	1.6×10^{-8}

Risks were estimated for the mean, maximum, and minimum ^{222}Rn concentrations listed in Table 1 even though exposures for the maximum and minimum ^{222}Rn concentrations are not shown in Table 9.

Label numbers refer to data position in Figures 10 and 11.

Figure 12 shows a set of notched boxplots for the mortality and morbidity inhalation risks. From Figure 12 it can be seen that the median measure of the mean risk values is only slightly greater than the 10^{-6} acceptable risk level, but the notches extend to the 10^{-6} acceptable risk level, suggesting that the overall risks may be acceptable. However, in individual caves and locations within certain caves, risks may be significant, as evidenced by the fact that the 75th percentile, the 90th percentile, and various outliers extend well beyond the 10^{-6} acceptable risk level.

Discussion and Conclusions

Attempts have been made to regulate exposures to cavers and cave workers to excess levels of ^{222}Rn gas in caves ever since high levels of ^{222}Rn gas were discovered in some caves administered by the NPS (Yarborough and Meyers, 1978, p. 19). Protection levels for cave workers were implemented at the earliest possible time (Baier, 1976) and have continued to evolve as more is learned. Unfortunately, little is still known about the effects of low-level ionizing α radiation from ^{222}Rn and its progeny. Still, it is widely recognized that the development of lung cancers may be expected based on numerous animal studies and epidemiological studies of miners.

Measuring ^{222}Rn is of little value unless these concentrations are converted to risk estimates. Calculating annual effective doses (mSv yr^{-1} or WLM yr^{-1}) is the generally accepted method for determining human-health threats. Using appropriate limits (20 mSv yr^{-1} to 50 mSv yr^{-1}) helps to put the calculated values in a health-risk context.

In general, it would seem that recreational and professional cavers are minimally at risk of developing lung cancers from exposure to ^{222}Rn, part-time cave workers are

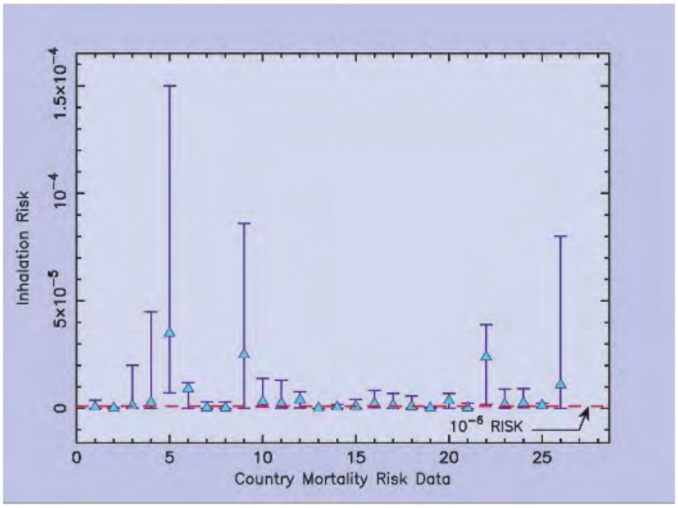

Figure 10. Plot of mean, minimum, and maximum mortality risk values from Table 11 relative to a 10^{-6} acceptable risk. The x-axis numerical values correspond to the superscript labels in Table 11. (Note that data sets listed in Table 11 missing mean values [Great Britain and United States] are not plotted).

somewhat more at risk in some caves, and full-time cave workers more so (Table 7). This conclusion was similarly obtained by Craven and Smit (2006) for non-smokers. Unfortunately, the large degree of uncertainty associated with the calculations and potential discrepancies in the ^{222}Rn measurements, necessitate that the calculations listed in Table 7 be viewed with some degree of skepticism (it is not possible to determine if the calculated annual effective doses in Table 7 are too high or too low or by how much). However, the annual effective doses listed in Table 7 should still be viewed as representative of the potential risks cavers and cave workers might be subject to when spending any significant amount of time underground.

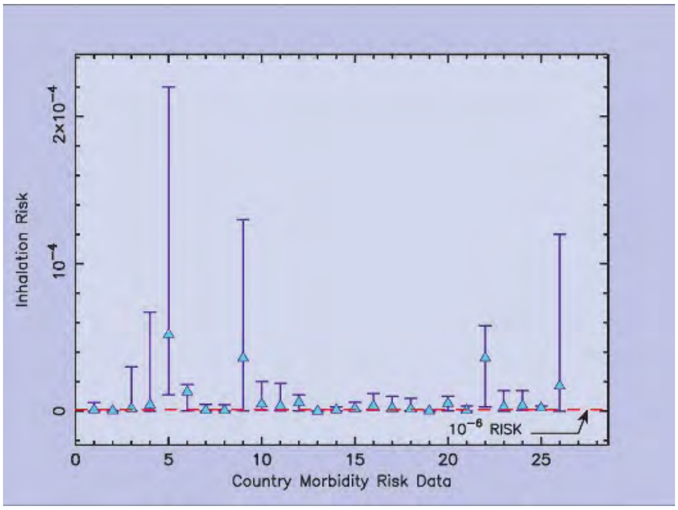

Figure 11. Plot of mean, minimum, and maximum morbidity risk values from Table 11 relative to a 10^{-6} acceptable risk. The x-axis numerical values correspond to the superscript labels in Table 11. (Note that data sets listed in Table 11 missing mean values [Great Britain and United States] are not plotted).

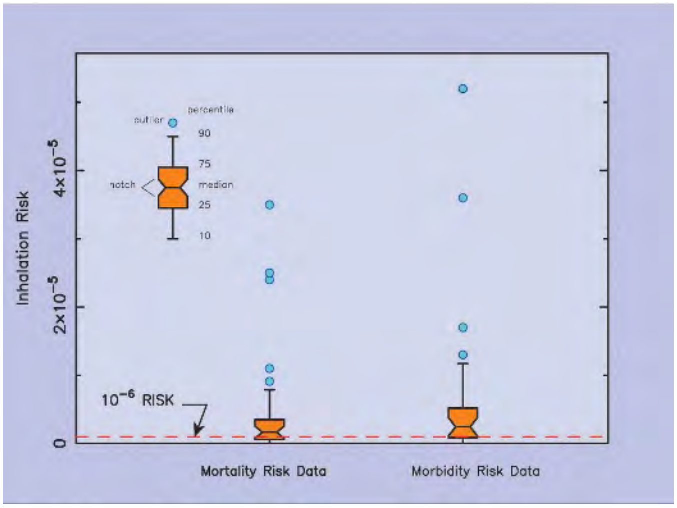

Figure 12. Notched boxplots of estimated mortality and morbidity risks relative to a 10^{-6} acceptable risk. (Note that data sets listed in Table 11 missing mean values [Great Britain and United States] are not plotted).

A less common method of calculating risks posed by low-level ionizing α radiation from ^{222}Rn and its progeny, but which is a more typical method of calculating risks in general, is to use cancer slope factors (mortality and morbidity risk coefficients M_{R_i}) to produce dimensionless risk estimates. The mortality and morbidity risk estimates listed in Table 11 for the ^{222}Rn concentrations listed in Table 1 are of negligible concern.

For short-term exposures, typical of recreational cavers, the risk levels listed in Table 11 for the mean ^{222}Rn concentrations are probably of little concern. The same is probably true for professional cavers. However, for long-term exposures, typical of cave workers, these risk levels warrant some degree of minor concern especially in areas of poor ventilation (Kobal et al., 1988). If the maximum ^{222}Rn concentrations listed in Table 1 are considered, the risks will increase slightly, which may warrant a greater concern.

Overall, it appears that risks to cavers and cave workers are generally low, but in selected caves risks to cave workers may be significant. However, proper cave worker precautions for caves with elevated ^{222}Rn concentrations will minimize the risks. In addition, given the uncertainties associated with use of the LNT, concerns over risks to cave workers may need to depend on the eventual improvements or abandonment of the LNT. Changes to the LNT may result in a reduction or increase in the estimated risks to cavers and cave workers from exposure to elevated levels of ^{222}Rn. Other uncertainties, such as extreme seasonal

Table 12. ^{222}Rn progeny current and historic names.

Current		Historic	
Symbol	Name	Symbol	Name
^{218}Po	Polonium-218	RaA	Radium A
^{214}Pb	Lead-214	RaB	Radium B
^{214}Bi	Bismouth-214	RaC	Radium C
^{214}Po	Polonium-214	RaC′	Radium C′
^{210}Tl	Thallium-210	RaC″	Radium C″
^{210}Pb	Lead-210	RaD	Radium D
^{210}Bi	Bismuth-210	RaE	Radium E
^{210}Po	Polonium-210	RaF	Radium F

variations in measured ^{222}Rn concentrations (Yarborough and Meyers, 1978, p. 22) [e.g. 740 versus 22,165 Bq m^{-3} in Magic Garden, Postojna Cave (Kobal et al., 1988)], further complicate risk calculations.

APPENDIX

RADON-222 PROGENY AND HISTORIC NAMES

When first discovered, the current ^{222}Rn progeny were known as decay products of ^{226}Ra and were formerly designated as Radium A – Radium F. The ^{222}Rn progeny are now known to be the isotopes listed in Table 12.

RADIATION SI UNITS AND CONVERSION TO TRADITIONAL UNITS

Radiation units have evolved over the years. As a result, radiation units can be quite confusing. To alleviate some of the confusion, selected radiation parameters are identified in Table 13 along with the SI special name, symbol, SI derived units, and traditional units.

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Table 13. International System (SI) units and equivalents for traditional units (modified from Taylor, 2001, 1995; Nero, 1988, p. 39).

	SI Derived Unit				
Parameter	Special Name	Special Symbol	Expressed in Terms of Other SI Units	Expressed in Terms of SI Base Units	Conversion for traditional Unit
Activity	becquerel	Bq		s^{-1}	1 Ci = 3.7×10^{10} Bq (1 pCi = 0.037 Bq)
Concentration		Bq m^{-3}			1 pCi L^{-1} = 37 Bq m^{-3}
PAEC[a]		J m^{-3}			1 WL = 1.3×10^{8} MeV m^{-3} = 2.08×10^{-5} J m^{-3}
EEDC[b]		Bq m^{-3}			1 WL PAEC = 3740 Bq m^{-3}
Exposure		J s m^{-3}			1 WLM = 12.97 J s m^{-3} = 3.60×10^{-3} J h m^{-3}
Exposure		Bq s m^{-3}			1 WLM = 73.9 Bq yr m^{-3}
Exposure Rate		J m^{-3}			1 WLM yr^{-1} = 4.11×10^{-7} J m^{-3}
Exposure Rate		Bq m^{-3}			1 WLM yr^{-1} = 73.9 Bq m^{-3}
Absorbed Dose	gray	Gy	J kg^{-1}	m^{2} s^{-2}	1 rad = 1 cGy = 10^{-2} Gy
Absorbed Dose Rate		Gy s^{-1}		m^{2} s^{-2}	1 rad s^{-1} = 10^{-2} Gy s^{-1}
Dose Equivalent[c]	sievert	Sv	J kg^{-1}	m^{2} s^{-2}	1 rem = 1 cSv = 10^{-2} Sv = 10^{-2} J kg^{-1}
Effective Dose		J s m^{-3}			1 WLM yr^{-1} = 5 mSv yr^{-1}

[a] Potential Alpha-Energy Concentration (PAEC).

[b] Equilibrium-Equivalent Decay-Product Concentration (EEDC).

[c] Also known as Biologically Effective Dose.

ing relevant portions to English. This program has been essential to the understanding of ^{222}Rn risks to cavers. The author would also like to thank Ms. Lindsey Bender and Dr. Neal Nelson of the U.S. Environmental Protection Agency's Office of Radiation and Indoor Air for their support and guidance and for providing specific radiation risk guidance materials. Lastly, the author thanks Dr. Neal Nelson and Dr. Ivan Kobal of the Jožef Stefan Institute (Ljubljana, Slovenia) for their critical reading of the manuscript.

NOTATION

A_{ge}	age of an exposed individual (dimen.)
C_{eq}	EEDC — ^{222}Rn concentration that would result if $F = 1$
C_E	cumulative exposure (J h m^{-3})
C_i	activity concentrations for ^{222}Rn and its progeny (Bq m^{-3})
C_p	PAEC — total α-particle energy potentially emitted by any mixture of ^{222}Rn per unit volume of air (J m^{-3})
$(\overline{C}R_n)_i$	average concentration of ^{222}Rn decay products during exposure interval (J m^{-3})
C_{Rn}	^{222}Rn concentration (Bq m^{-3})
D_{CF}	Dose Conversion Factor
$D_{T,R}$	mean absorbed radiation dose to tissue T from radiation R (Gy)
E_{DA}	annual effective radiation dose to organs and tissues (Sv yr^{-1})
E_D	effective radiation dose to organs and tissues (Sv)
F	equilibrium factor (dimen.)
H_T	human equivalent radiation dose to tissue T (Sv)
I_h	inhalation rate (m^3 s^{-1})
M_{R_B}	morbidity-risk coefficient for ^{222}Rn and its progeny (Bq^{-1})
M_{R_T}	mortality-risk coefficient for ^{222}Rn and its progeny (Bq^{-1})
P_{eq}	EEQ — time-integrated exposure to EEDC (Bq s^{-1} m^{-3})
P_p	PAEE — time-integrated exposure to PAEC (J s m^{-3})
R	risk
R_{M_B}	risk of morbidity (dimen.)
R_{M_T}	risk of mortality (dimen.)
S_C	scaling coefficient for a current (mobile) population to a stationary population (dimen.)
t	time (T)
T_i	exposure time — subscript i refers to exposure for part-time cavers (50 h yr^{-1}), full-time cavers (600 h yr^{-1}), part-time cave workers (1,760 h yr^{-1}), and full-time cave workers (2,000 h yr^{-1}) (h yr^{-1})
$T_{½}$	radioactive half-life of considered radionuclide (T)
W_R	radiation weighting factor for various types of radiation (dimen.)
W_{T_i}	tissue weighting factor for differing sensitivities of various human tissues to radiations (dimen.)
ε_p	potential alpha energy per unit of activity (Bq)
λ_r	decay constant for considered radionuclide (dimen.)

ACRONYMS

DCF	Dose Conversion Factor
DNA	Deoxyribonucleic Acid
DOE	U.S. Department of Energy
EEDC	Equilibrium-Equivalent Decay-Product Concentration
EEQ	Equilibrium Equivalent Exposure
EPA	U.S. Environmental Protection Agency
HRTM	Human Respiratory Tract Model
LD50	Median Lethal Dose
LET	linear energy transfer
LNT	linear no-threshold theory
LOAEL	Lowest Observed Adverse Effect Level
MSHA	Mine Safety and Health Administration
NIOSH	National Institute of Occupational Safety and Health
NOAEL	No Observed Adverse Effect Level
NPS	National Park Service
NRC	U.S. Nuclear Regulatory Commission
OSHA	Occupational Safety and Health Administration
PAEC	Potential Alpha-Energy Concentration
PAEE	Potential Alpha-Energy Exposure

NOTES

[1] A metalloid is an element with properties intermediate between those of metals and nonmetals.

[2] Clathrate compounds are formed by trapping the ^{222}Rn in the lattice of surrounding atoms rather than forming chemical bonds.

[3] See Table 13 in the Appendix for a brief overview of radiation SI units and conversion to traditional units.

[4] The linear energy transfer (LET) of radiation is a measure of the spatial energy distribution stated in terms of the amount of energy deposited per unit length of particle track, *dE*/*dx*, with typical units of keV μm^{-1} (NRC, 1990, p. 11). It is the energy lost by charged particles in electronic collisions per unit track length where a low-LET is taken as $<$10 keV μm^{-1} and a high-LET is taken as $>$10 keV μm^{-1} (NRC, 2005, p. 375).

[5] In radiation biology, dose specifically pertains to the amount of energy ionizing radiation deposits in an organ tissue (ATSDR, 1997, p. 35).

[6] Effective dose (Sv) converts to absorbed dose (Gy) according to $1\ \text{Sv} = 1\ \text{Gy} \times W^R$.

[7] The term "plate-out" refers to the attraction of the negatively charged ion to surfaces such as a cave wall or the epithelium of the lung.

[8] *In vitro* refers to the technique of performing experiments in a test tube or in a living organism.

[9] *In vivo* refers to experiments conducted on living tissue of a whole living organism as opposed to a partial or dead organism.

[10] Phagocytized refers to the ingestion of particles or organisms by phagocytosis.

[11] The reticuloendothelial system consists of a group of cells capable of phagocytosis.

[12] Parenteral administration refers to the route of particle administration (transport) through the body.

[13] Confounding factors are associated with the finding of an association for the wrong reason. It is associated with both the risk and the disease being studied, but need not be a risk factor for the disease under study. The confounding variable can either inflate or deflate the true relative risk (Wartenberg et al., 2000).

[14] ALARA means making every reasonable effort to maintain exposures to radiation as far below the dose limits in this part as is practical consistent with the purpose for which the licensed activity is undertaken, taking into account the state of technology, the economics of improvements in relation to state of technology, the economics of improvements in relation to benefits to the public health and safety, and other societal and socioeconomic considerations, and in relation to utilization of nuclear energy and licensed materials in the public interest (U.S.NRC, 2006, 10 CER, 2006,10 CFR § 20.1003).

[15] "A mortality risk coefficient is an estimate of the risk to an average member of the U.S. population, *per unit activity inhaled or ingested for internal exposures or per unit time-integrated activity concentration in air or soil for external exposures*, of dying from cancer as a result of intake of the radionuclide or external exposure to its emitted radiations" (Eckerman et al., 1999, p. 1).

[16] "A morbidity risk coefficient is a comparable estimate [mortality estimate] of the average total risk of experiencing a radiogenic cancer, whether or not the cancer is fatal" (Eckerman et al., 1999, p. 1).

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Lee J. Florea, Beth Fratesi, and Todd Chavez – The reflection of karst in the online mirror: a survey within scientific databases, 1960–2005. *Journal of Cave and Karst Studies,* v. 69, no. 1, p. 229–236.

THE REFLECTION OF KARST IN THE ONLINE MIRROR: A SURVEY WITHIN SCIENTIFIC DATABASES, 1960–2005

LEE J. FLOREA[1], BETH FRATESI, AND TODD CHAVEZ[2]

Abstract The field of cave and karst science is served by a literature that is dispersed across far-flung topical journals, government publications, and club newsletters. As part of an inter-institutional project to globalize karst information (KIP, the Karst Information Portal), the USF Library undertook a structured battery of literature searches to map the domain of karst literature. The study used 4,300 individual searches and four literature databases: GeoRef, BIOSIS, Anthropology Plus, and GPO Access. The searches were based on a list of 632 terms including 321 karst-related keywords culled from three leading encyclopedias and glossaries of cave and karst science. An examination of yearly changes in publication rate indicates that for the last 45 years, the number of cave and karst publications has increased steadily, as has the number of journals in which they appear. In particular, the past ten years cover a period of rapid growth where karst-specific journals achieved peer-review status, and individual journals accepted more cave and karst papers for publication.

INTRODUCTION

Part of what attracts students of geology is the field experience, the idea that the first challenge in studying an outcrop is getting to it. Biology and archaeology share this element of expedition. This challenge is ever-present in karst, even more so than in most other fields. Cave science is not only logistically demanding and physically challenging, but also conceptually intricate and difficult to categorize:

> The idea that there is a science of speleology that includes everything that one might like to know has proved infeasible. Instead of an inwardly focused study on caves, the current generation of cave scientists are finding out that they need to look outward rather than inward. To understand caves, one must also understand the landscape, drainage basins, and rock units in which they occur. One must draw on geochemistry, fluid mechanics, crystallography, and many other disciplines that provide essential understanding of the processes that occur in caves.
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> - White and White, 1998, p. 40

Karst researchers encounter additional challenges in managing an information environment wherein a large amount of the information pertaining to karst originates outside of the academic world. The National Speleological Society is perhaps the largest source and repository for cave data (in the form of maps, trip reports, etc.) in the United States, even though, according to a 2005 survey, only around 15% of NSS members consider themselves professional scientists. Thus, as karst scientists, we enjoy and depend upon the cooperation and companionship of industry professionals, explorers, and amateur scientists whose standards for data-gathering may meet or exceed those of the scientific institution.

Traditionally, little of the data collected by non-scientist cavers makes it into literature with widespread distribution; the information ends up in consulting reports, expedition summaries, and caving-club newsletters. These publications are termed gray literature by virtue of being unavailable through conventional channels of library acquisition (Bichteler, 1991). Library professionals find guidebooks to be particularly frustrating, branding them "sneaky, fly-by-night, changecoat publications [that are] hard to identify, hard to acquire, hard to catalog and retrieve, and hard to preserve" (Walcott, 1990). These gray literature venues rarely find their way into standard bibliographic indices, and are not only difficult for researchers to track down, but may only exist in personal libraries that can suffer from damage or loss. Academic scientists, however, are more concerned with the fact that much gray literature manages to make its way into print while avoiding the peer-review process (Bichteler, 1991, p. 40).

Despite these concerns, recent data indicates that scientists across several disciplines are citing more gray literature (e.g., Mili, 2000, in economics; Osif, 2000, in the transportation sciences). In one particular study of papers from a fisheries management conference, Lacanilao (1997) found that 92 percent of the total number of citations were to gray literature.

Gray literature publications serve an important role in supporting the sciences (Cordes, 2004; Luzi, 2000). Research appearing as an unreviewed abstract or proceedings paper may yet be innovative and is oftentimes the only work on a particular subject. In the karst community, gray literature publications may document the first observations within a cave, the first identifications of new species, or the locations of important archeological sites.

For 65 years the *Journal of Cave and Karst Studies* has provided one avenue by which karst scientists can place

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[1] Department of Geology, University of South Florida 4202 E. Fowler Ave, SCA 528, Tampa, FL 33620, lflorea@chuma1.cas.usf.edu, sfratesi@mail.usf.edu

[2] University Libraries, University of South Florida 4202 E. Fowler Ave, Tampa, FL 33620, tchavez@lib.usf.edu

their research on permanent record and communicate with non-science cavers in the United States and abroad. *GeoRef*, a leading earth science citation database, classified this journal's predecessor, the *NSS Bulletin*, as a non-peer-reviewed journal. This changed in 1995 with the change in name. Moreover, the *Journal* has been indexed with the Institute for Scientific Information (ISI) since 2003.

One example of a pioneering effort to document gray elements of the karst literature is the bibliography of Northup et al. (1998). Published in 1998, *A Guide to Speleological Literature of the English Language, 1794–1996* documents 3,558 works in print concerning caves as of 1996. As this paper demonstrates, the growth in publication of karst related research has increased substantively during the succeeding decade, a fact that has led in part to the Karst Information Portal (KIP) initiative. As a partnership with karst researchers from many perspectives, the KIP promises to be a dynamic descendent to the type of bibliography represented by Northup et al. (1998), providing access to white and gray information sources in multiple formats, a repository facility, and expert evaluation of key resources.

THE KARST INFORMATION PORTAL

Scientists and information specialists from the National Cave and Karst Institute (NCKRI), the University of New Mexico (UNM), and the University of South Florida (USF), concerned about the fragmented distribution of data and literature about karst resources, have initiated the KIP. The intent of the KIP is to gather content and metadata from disparate masses of karst research into one online searchable portal and to facilitate communication among karst scientists.

With an international focus, designers intend the KIP to serve as a one-stop source for sharing information about karst literature. The KIP will include material that is often hard to locate, such as technical reports, conference proceedings, theses and dissertations, newsletters, maps, databases, and photos of karst resources.

Ascertaining the domain of karst literature is one vital step toward establishing the KIP. For instance, identifying journals that publish karst literature will assist information specialists in acquisitions. Tracking publication trends in karst will help plan for the future needs of the KIP. Understanding where karst research occurs and how the karst literature clusters around fields of study and subject keywords, will provide a metric by which administrators can assess the content of the KIP against the real distribution of karst literature.

EXPLORING KARST THROUGH ONLINE DATABASES

To lay groundwork for the KIP, we undertook a survey of the existing karst literature. This survey, primarily conducted between October, 2005 and January, 2006, consisted of more than 4,300 literature searches across four major scientific databases: *GeoRef*, a leading earth-science database administered by the American Geological Institute (AGI); *BIOSIS Previews*, the medical and life-science database of the *ISI Web of Knowledge* owned by the Thompson Corporation; *Anthropology Plus*, managed by Eureka and combining the Anthropological Literature from Harvard University and the Anthropological Index from the Royal Anthropological Institute in the UK; and *GPO Access*, the primary search engine for publications published by the US Government Printing Office.

Part of the goal of this study is to find out what sort of ontology best captures the relevant literature. Our classification of search terms is therefore somewhat rudimentary. We culled a list of 321 cave- and karst-related terms from the glossaries of the *Encyclopedia of Caves* (Culver and White, 2005), *A Lexicon of Cave and Karst Terminology with Special Reference to Environmental Karst Hydrology* (Field, 1999), and the online *Glossary of Speleological and Caving Terms* (ASF, 2004).

We combined lists of terms from all three glossaries and deleted the duplicates. To supplement the list of 1,875 words that remained, we included a list of 30 names of important caves around the world, 26 fields of study related to caves and karst, 24 geographic settings where caves and karst features are found, all seven continents with 37 sub-regions within these continents, and 187 independent nations, former countries, and alternate spellings of these countries. In all, this refined list included 2,186 terms.

From our refined list, we extracted a short list of 15 primary words likely to capture a large number of the English-language citations relevant to caves and karst studies. These words included the word stems karst, cave, and several linguistic variations thereof (e.g. *cueva*). Major related words were included in this list – spring(s), conduit(s), and bats, for instance.

Next we outlined two groups of modifiers for the words in the original list. The higher-level group consists of locations, scientific disciplines, and settings within which karst might be found. For example, the terms paleontology, marine, and Romania are all higher-level modifiers. The lower-level group includes 321 keywords that would fall within the karst field itself (either physically or bibliographically). These are generally more specific, such as sediment and model. The remaining 1,539 terms were either too specific or too general to capture relevant citations and were eliminated.

One set of searches utilizes the primary terms applied to all four databases in this study. The second set of searches consists of each term from the two lists of modifiers, combined with the term cave or karst and the appropriate wildcard symbols, such as an asterisk (*), to capture all of the derivatives. It is important to note that the results of these searches are not filtered for relevance; they are presented in this paper as returned by the search engine.

Table 1. Search results for the primary search terms.

	GeoRef[a]							
Search Terms	All	Peer-Review	Journal	Conference	Books	BIOSIS Previews[b]	Anthropology Plus[c]	GPO Access[d]
bats	251	107	215	41	16	16,062	96	25,253
carbonate aquifer(s)[e]	347	91	278	178	63	31	1	497
carso[f]	3,663	1,402	3,237	802	346	316	0	39,655
cave	24,180	5,199	21,265	6,690	2,595	23,961	8,450	64,988
conduit(s)[g]	2,840	1,131	2,466	1,220	323	6,731	11	26,738
cueva(s)	998	210	768	380	212	178	853	451
grotte	910	89	860	163	45	63	1,813	60
grotto(s)	673	37	632	64	40	75	49	754
karst[h]	27,379	6,570	23,698	10,031	3,407	5,234	269	7,800
limestone aquifer(s)	1,640	390	1,375	684	235	50	0	495
sink	7,893	2,501	6,803	2,870	937	13,625	158	58,659
spring(s)[i]	71,986	29,018	65,504	31,361	4,873	87,528	1,211	349,274
spel(a)eo[j]	10,452	1,748	9,563	3,410	828	696	370	621
stygo	29	10	27	10	1	488	0	158
troglo	84	27	70	21	5	4,853	430	1,291

[a] Search included entire reference.
[b] Topic search.
[c] Keyword search.
[d] General search.
[e] The search string, carbonate aquifer(s), includes the phrase, carbonate aquifer, and the plural form, carbonate aquifers. This construction applies to all search strings with a similar format.
[f] The search string, carso, includes the word, carso and all derivatives that use carso as a prefix. This construction applies to all search strings with a similar format.
[g] The search string, conduit(s) results in many citations that are unrelated to karst studies.
[h] The search string, karst, includes the word, karst, and all derivatives that use karst as a root word and have prefixes or suffixes. This construction applies to all search strings with a similar format.
[i] The search string, springs, results in many citations that are unrelated to karst studies.
[j] The search string, spel(a)eo, includes all terms that contain the root, speleo, or the alternate spelling, spelaeo.

We performed an additional set of searches to net the entire body of citations related to caves or karst within *GeoRef* for each year between 1960 and 2005. We separated these by publication type and extracted a subset of peer-reviewed journal articles. We performed similar general karst searches within the abstract archives of the Geological Society of America.

The Domain of Karst Literature

Primary Terms

The primary search term results are dominated by the term spring, which does not specifically refer to karst springs (Table 1). The search results for spring in *GPO Access* reflects the loose nature of this search engine: a search here returns hits on any document within all U.S. government websites. The results are not restricted to scientific documents; thus the term spring returns almost 350,000 citations, most of which probably refer to the season of rebirth, rather than a point of resurgence (Table 1). Because the results from this search engine appear to have little relevance to the desired body of literature and little advantage over a conventional web-search engine, we eliminated *GPO Access* from all subsequent searches.

Second and third in order of prevalence in the primary search terms are the words karst and cave, the most general of the remaining English-based terms (Table 1). Citations within *Anthropology Plus* refer almost exclusively to caves, with comparatively few references to karst. *BIOSIS Previews* had four times more references to caves than to karst, whereas in *GeoRef* they occur about the same number of times (Table 1).

The relatedness of terms to specific disciplines influences their distribution among the databases. For example, the biology-related terms bats, stygo-, and troglo- returned by far the most results from *BIOSIS Previews*, while geological terms such as carbonate aquifer and limestone aquifer are more prevalent in *GeoRef* (Table 1).

Higher-Order Modifiers

Results for the searches of higher-order modifiers are included in Tables 2 and 3, separated into setting, location, field of study, and subject keywords.

The modifier sea appears as the most frequent geographic setting mentioned in karst-related GeoRef citations (Table 2). This is not surprising; even in studies of mid-continental karst, it is difficult to discuss karst development without invoking sea-level or referring to a base level of some sort. It should be noted that there is likely considerable overlap between sea and the second and third ranking geographic modifiers, marine, and island (Table 2).

With a glance at Table 2, karst appears as a decidedly Eurocentric discipline: Europe is by far the most-cited continent in cave and karst references, with more than three times the number-two continent, Asia. However, although North America comes in at a distant third place as a continent, the United States is the country mentioned the most times overall, with about as many citations as the continent of Europe itself (Table 2). These numbers surely reflect the history of karst (with its European origins), the distribution and impact of journals in different countries, the amount of karst accessible to each region, and other scientific and socio-economic influences, as well as vagaries of the search process. For example:

1) There are about as many references in *BIOSIS Previews* to karst in Norway as there are references to caves in the United States (Table 2). We find that this is because of references to the Norwegian spruce (*Picea abies* (L.) Karst). Only 21 references remain when the species name is excluded from the search.
2) On the other hand, both France and Spain have anomalously large numbers of references to cave in *Anthropology Plus* (Table 2). No doubt these citations reflect a long and distinguished record of cave archeology, particularly as it relates to famous Paleolithic cave art at sites such as Lascaux and Altamira.

The predictable partiality of each database to its own sub-discipline is clearly demonstrated in our search results for the fields of study (Table 2): the geology and geomorphology papers are in primarily in *GeoRef*, the biology and ecology papers are dominant in *BIOSIS Previews*, and archaeology papers comprise the majority of the *Anthropology Plus* results.

Results for the 30 most commonly occurring keywords are presented in Table 3. General rather than specific keywords compose most of this list. Yet, a few more specific terms that refer to specific scientific methods, such as isotope, make the list. The phrase cave system seems to permeate biological literature, whereas phrases such as karst water and karst hydrology occur commonly in geological literature.

Annual Publication Rates in the GeoRef Database

Searches for karst-related GSA abstracts show continued, rapid growth of the field during the past ten years (Fig. 1). Karst-related abstracts now constitute about 2.5% of all GSA abstracts produced each year, more than twice the percentage in 1995. The pattern of peer-reviewed articles not associated with conference proceedings shows a slightly different profile (Fig. 2). Growth of the field during the 1990s yields to a slight downturn after 2003. This may simply be the manifestation of a lag time of data entry in *GeoRef*.

The increase in journal diversity mirrors the increase in number of articles on caves and karst (Fig. 2). Between 1960–2005, karst articles appeared in 437 different peer-reviewed journals. However, as is true of most scientific disciplines, the majority of the karst literature is concentrated in a few core journals (Bradford, 1934). The top 25 journals account for 46% of the karst-related citations. Figure 2 shows this list of 25 journals, ranked by the total number of karst and cave articles from 1960 to 2005.

While karst-specialty journals account for only 8% of the peer-reviewed publications for this time period, it has only been in the last ten years that the *Journal of Cave and Karst Studies*, *Cave and Karst Science*, and *Acta Carsologica* have been included in *GeoRef* as peer-reviewed journals, all three with short but intense histories of publishing karst papers (Fig. 2). *Environmental Geology*, while not exclusively a karst journal, has a similar publication profile. The *Journal of Hydrology* has included several articles concerning karst each year for most years since its inception, making it the top source for karst-related articles from 1960 to 2005.

General science journals such as *Nature* and *Science* have a long history of intermittently including karst articles that are cited by *GeoRef* (Fig. 2). These accumulate large numbers of karst citations through their long life spans. In the major geological sub-discipline journals such as *Chemical Geology* and *GroundWater*, we see a substantial increase in the number of articles over the past ten years (Fig. 2).

CONCLUDING REMARKS

This study represents one in a series of steps to designing an information portal for the karst sciences; a portal that will facilitate worldwide communication on research on karst phenomena. The series of 4,300 literature searches that compose this study identify the scope of cave- and karst-related literature and the changes through time that karst literature experienced. Karst as a science is growing, and the past ten years encompass much of that growth. Our searches reveal several factors that partially explain the increasing volume of peer-reviewed karst literature:

1. The karst-heavy journals achieved peer-review status;
2. The number of journals that publish karst-related articles increased; and
3. The number of cave and karst articles in each journal increased.

With respect to the first point, obtaining peer-review status was a critical step for establishing the credibility of

Table 2. Ranked summary of search results for the top five geographic settings, all continents, and the top 25 countries.

		Search Engine						
		GeoRef[a]		BIOSIS Previews[b]		Anthropology Plus[c]		
Search Area	Rank	Cave[d]	Karst[e]	Cave	Karst	Cave	Karst	Totals
Geographic Setting								
Sea	1	741	1,249	466	191	21	1	2,669
Marine	2	558	874	677	198	10	0	2,317
Island	3	728	624	506	79	66	0	2,003
Plateau	4	566	814	97	95	25	1	1,598
Mountain	5	709	529	157	141	39	3	1,578
Continents								
Europe	1	8,749	10,387	1,203	1,342	435	40	22,156
Asia	2	2,415	3,671	526	183	254	2	7,051
North America	3	2,455	722	887	242	188	2	4,496
Africa	4	1,096	652	537	55	359	0	2,699
Australia	5	951	395	417	64	150	3	1,980
South America	6	530	320	294	62	28	0	1,234
Pacific[f]	7	334	199	189	25	67	1	815
Antarctica	8	0	0	0	0	0	0	0
Countries								
United States[g]	1	12,795	9,336	1,604	265	67	4	24,071
France	2	3,618	1,780	398	205	1,264	17	7,282
Germany[h]	3	2,280	1,251	138	253	138	9	4,069
United Kingdom[i]	4	2,903	497	148	45	0	0	3,593
China	5	1,105	1,961	179	95	126	2	3,468
Spain	6	878	974	358	135	721	5	3,071
Italy	7	1,145	988	423	246	3	8	2,813
Mexico	8	1,016	656	422	70	217	4	2,385
Australia	9	951	395	419	64	245	3	2,077
Norway	10	295	98	48	1,629	3	2	2,075
Canada	11	1,006	600	120	92	14	0	1,832
U.S.S.R.[j]	12	547	1,063	115	72	15	0	1,812
Austria	13	978	508	69	62	55	11	1,683
South Africa	14	726	120	286	11	371	0	1,514
Switzerland	15	672	381	74	51	36	2	1,216
Czechoslovakia[k]	16	506	489	34	106	39	19	1,193
Yugoslavia[l]	17	216	639	168	112	31	15	1,181
Hungary	18	342	460	51	42	50	8	953
Poland	19	346	364	92	112	17	9	940
Slovenia	20	304	359	76	74	13	10	836
Japan	21	435	88	240	26	33	0	822
Israel	22	273	148	98	19	240	1	779
Romania	23	265	278	168	42	7	0	760
Greece	24	168	320	125	21	110	2	746
Brazil	25	193	177	247	42	55	1	715

[a] Search included entire reference.

[b] Topic search.

[c] Keyword search.

[d] The search string, cave, includes the word cave and all derivatives that use cave as a prefix.

[e] The search string, karst, includes the word karst and all derivatives that use karst as the root word and have prefixes or suffixes.

[f] Though not a continent, we included Pacific in this section because it includes a variety of island nations not included within the other continents.

[g] The country search, United States, also includes the search USA, U.S.A., and America.

[h] The country search, Germany, includes the previous states of the Federal Republic of Germany and the German Democratic Republic.

[i] The country search, United Kingdom, also includes the search phrases UK, U.K., Britain, and England.

[j] The country search, U.S.S.R., does not include Soviet Union or Russia which are separate searches.

[k] The country search, Czechoslovakia, does not include Czech Republic or Slovakia which are separate searches.

[l] The country search, Yugoslavia, does not include searches for any of the present countries that comprise the former Yugoslavia.

Table 3. Ranked summary of search results for the top 10 fields of study and the top 30 subject keywords.

Field of Study and Subject Keyword	Rank	Search Engine						Totals
		GeoRef[a]		BIOSIS Previews[b]		Anthropology Plus[c]		
		Cave[d]	Karst[e]	Cave	Karst	Cave	Karst	
Field of Study								
Geomorphology	1	11,554	8,736	22	32	19	3	20,366
Geology	2	12,477	5,408	729	501	91	8	19,214
Ecology	3	487	519	6,373	3,146	44	1	10,570
Biology	4	234	70	6,332	3,855	18	0	10,509
Arch(a)eology[f]	5	1,618	409	476	27	6,592	80	9,202
Hydrology	6	1,965	6,378	18	67	0	0	8,428
Hydrogeology	7	2,134	3,876	5	42	1	0	6,058
Pal(a)eontology	8	3,933	334	74	13	65	1	4,420
Exploration	9	2,065	1,911	123	17	86	0	4,202
Engineering	10	2,146	1,899	79	25	2	0	4,151
Subject Keyword								
System(s)[g]	1	1,859	3,026	20,123	2,111	38	4	27,161
Vertebrat[h]	2	4,067	738	17,656	603	0	1	23,065
Mammal	3	3,238	575	16,436	420	87	0	20,756
Environment(s)	4	3,088	5,685	6,538	3,385	161	11	18,868
Water	5	4,089	10,212	1,865	1,659	6	1	17,832
Sediment	6	6,330	9,610	491	282	148	7	16,868
Region	7	3,087	5,049	6,058	2,124	189	20	16,554
Hydro	8	4,147	10,090	886	484	3	0	15,590
Human(s)	9	925	825	11,727	236	734	10	14,457
Morphology	10	1,322	938	7,906	2,017	54	2	12,239
Cainozoic or Cenozoic	11	7,141	4,429	307	79	0	0	11,956
Ground(-)water[i]	12	2,803	8,333	126	271	3	3	11,539
Quaternary	13	6,766	3,128	451	98	102	4	10,549
Limeston	14	3,157	5,097	343	311	12	1	8,921
Carbon	15	5,528	1,088	503	522	59	3	7,703
Development	16	1,400	2,315	2,579	1,240	15	3	7,552
Strat	17	3,342	2,778	812	245	297	10	7,484
Species	18	581	209	4,808	1,838	8	0	7,444
Pleistocene	19	3,877	1,548	1,238	180	294	9	7,146
Deposit(s)	20	2,137	3,214	896	412	193	2	6,854
Isotop	21	1,785	1,574	2,733	154	41	2	6,289
Mine(s) or mining	22	1,248	2,935	1,162	868	55	5	6,273
Evolution	23	1,838	2,676	1,210	243	242	4	6,213
Mineral(s)	24	1,749	2,251	1,046	839	28	4	5,917
Radio	25	1,316	839	3,394	108	184	5	5,846
Invertebrate(s)	26	289	19	4,619	907	0	0	5,834
Aqui	27	1,138	4,393	72	227	2	1	5,833
Fossil	28	2,636	674	1,654	388	412	4	5,768
Reproduce	29	57	36	5,138	424	1	0	5,656
Model	30	1,277	2,374	448	448	28	0	5,644

[a] Search included entire reference.

[b] Topic search.

[c] Keyword search.

[d] The search string, cave, includes the word cave and all derivatives that use cave as a prefix.

[e] The search string, karst, includes the word karst and all derivatives that use karst as the root word and have prefixes or suffixes.

[f] The search string, arch(a)eology, includes archeology and the alternate spelling archaeology. This construction applies to all search strings with similar format.

[g] The search string, system(s) includes the word system and the plural form systems. This construction applies to all search strings with similar format.

[h] The search string, vertebrat, includes all terms that begin with the root vertebrat. This construction applies to all search strings with similar format.

[i] The search string, ground(-)water includes the forms groundwater, ground-water, and ground water.

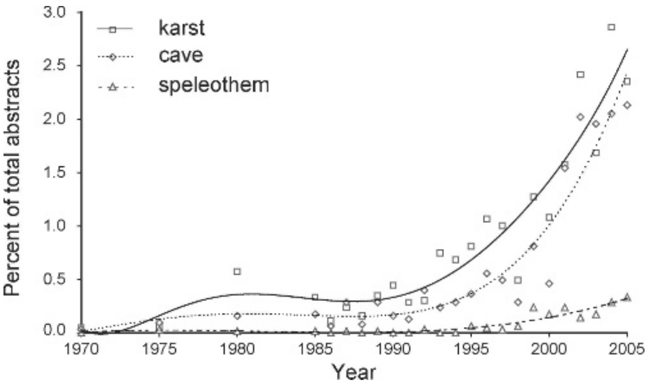

Figure 1. Percent of abstracts related to caves and karst at Geological Society of America meetings. Prior to 1985 percentages are averaged over five years.

karst as a science. Papers in the *Journal of Cave and Karst Studies* and other karst-oriented journals now reach a much broader community of scientists and resource professionals, facilitated by current trends in on-line publishing. Furthermore, all three points reflect upon a conscious effort over several decades by dedicated cavers and karst professionals to advance the science to a point of acceptance by the greater scientific community, particularly within the earth science disciplines. Overall, the numbers from this study elaborate on a statement that karst scientists are gratified to hear:

> Cave geology has come of age. The geological study of caves is now an integrated part of the geological sciences rather than a portion of an exotic borderland science called speleology.
> - White and White (1998, p. 41)

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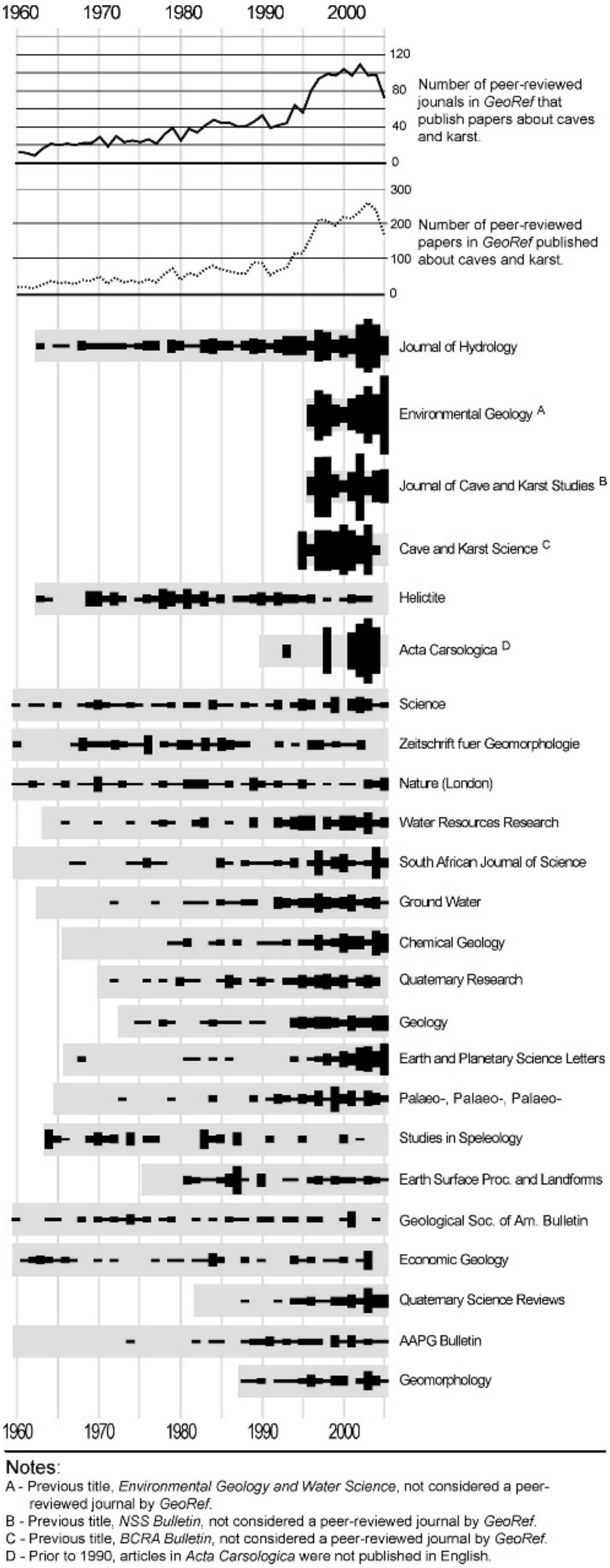

Notes:
A - Previous title, *Environmental Geology and Water Science*, not considered a peer-reviewed journal by *GeoRef*.
B - Previous title, *NSS Bulletin*, not considered a peer-reviewed journal by *GeoRef*.
C - Previous title, *BCRA Bulletin*, not considered a peer-reviewed journal by *GeoRef*.
D - Prior to 1990, articles in *Acta Carsologica* were not published in English.

Figure 2. Ranked summary of the number of cave- and karst-related publications each year by journal. The top graph is the number of peer reviewed journals in *GeoRef* that publish papers about caves and karst, and the lower graph is the number of peer-reviewed papers in *GeoRef* about caves and karst. Each bar graph provides information on the cave and karst publication history for an individual journal. The total height of a single black bar represents the number of relevant papers for that year. For scale reference, the total height of each horizontal, gray bar corresponds to ten articles. The length of each gray bar spans the lifespan of the journal.

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