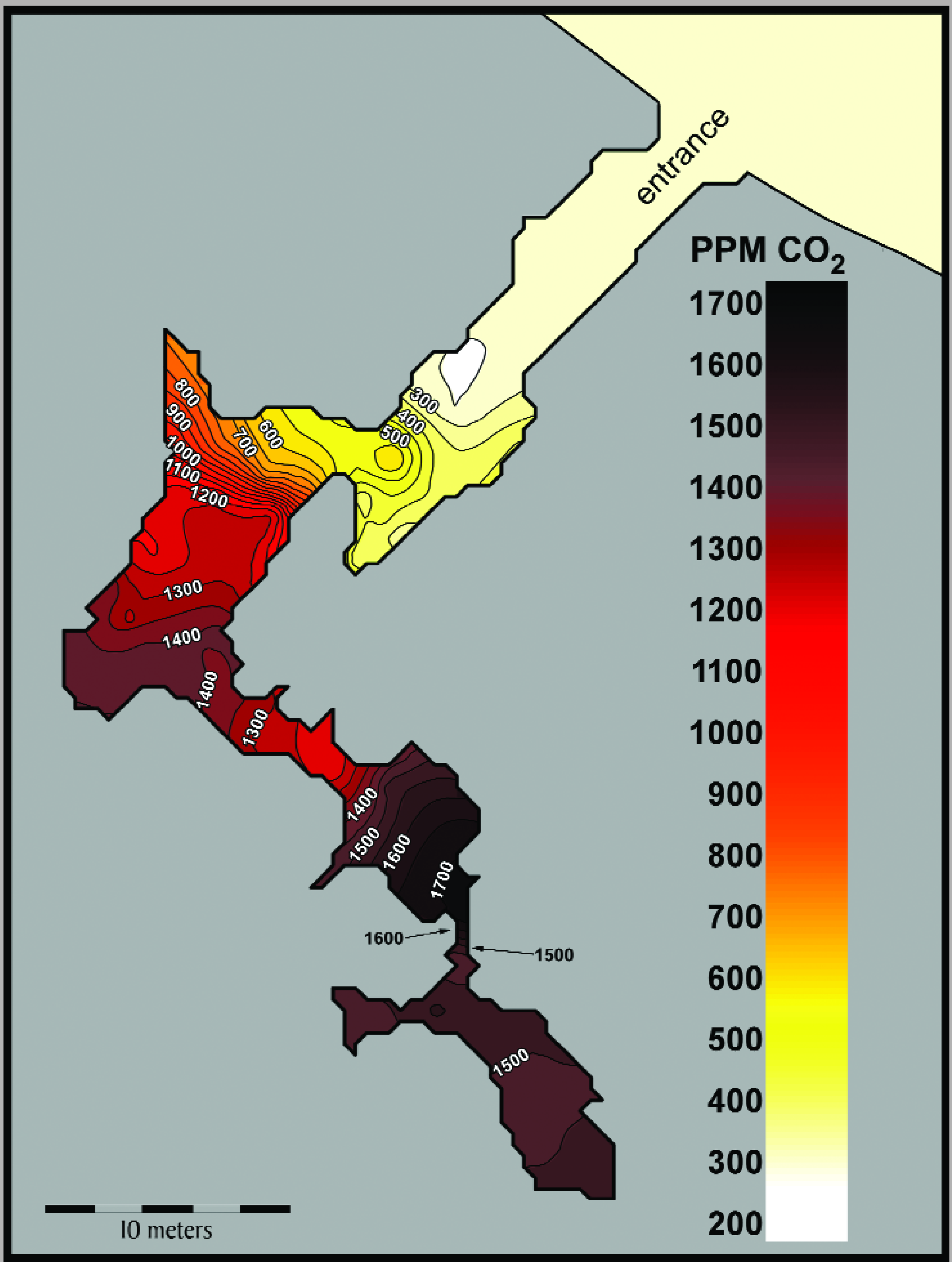
JOURNAL OF CAVE AND KARST STUDIES

April 2006
Volume 68 Number 1
ISSN 1090-6924
A Publication of the National Speleological Society



Journal of Cave and Karst Studies of the National Speleological Society
Volume 68 Number 1 April 2006

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The *Journal of Cave and Karst Studies* (ISSN 1090-6924, CPM Number #40065056) is a multi-disciplinary, refereed journal published three times a year by the National Speleological Society, 2813 Cave Avenue, Huntsville, Alabama 35810-4431 USA; (256) 852-1300; FAX (256) 851-9241, e-mail: nss@caves.org; World Wide Web: http://www.caves.org/pub/journal/. The annual subscription fee is $23 US, $44 US for 2 years, and $65 US for 3 years. Check the *Journal* website for international rates. Back issues and cumulative indices are available from the NSS office. POSTMASTER: send address changes to the *Journal of Cave and Karst Studies*, 2813 Cave Avenue, Huntsville, Alabama 35810-4431 USA.

The *Journal of Cave and Karst Studies* is covered by the following ISI Thomson Services: Science Citation Index Expanded, ISI Alerting Services, and Current Contents/Physical, Chemical, and Earth Sciences.

Front cover: Contour map of CO_2 concentrations throughout Ballynamintra Cave. See James U.L. Baldini, Lisa M. Baldini, Frank McDermott and Nicholas Clipson, p. 4–11.

SUBMITTING MANUSCRIPTS TO THE *JOURNAL OF CAVE AND KARST STUDIES*

MALCOLM S. FIELD

OVERVIEW OF THE PROCESS

Over the past two years that I have been Editor of the *Journal of Cave and Karst Studies* it has become apparent to me that many individuals do not know to whom they should submit their manuscript or in what form to submit it. Generally speaking, the simplest and the most effective manner in which to submit a manuscript and to whom are not the same.

Most often, authors of manuscripts will want to submit their manuscripts directly to the Associate Editor whose listed area of expertise on the *Journal* masthead appears to most closely match the manuscript subject matter. If an author is unsure to whom a manuscript should be submitted, a request can be e-mailed directly to me for my opinion, or the manuscript can be sent directly to me. Either way will entail a minor delay in the review process as I make the necessary inquiries and/or send the manuscript on to the appropriate Associate Editor.

PREFERRED SUBMISSION APPROACH

The best approach for an author to use when submitting a manuscript to the *Journal of Cave and Karst Studies* is to contact the appropriate Associate Editor directly by e-mail to inquire as to how the Associate Editor prefers to have the manuscript submitted (*e.g.*, e-mail, hardcopies, and/or CDROM). Such an approach will facilitate a smooth transmission procedure. Based on the description of the paper (*e.g.*, size of files, special symbols contained, *etc.*) the Associate Editor can provide the prospective author with the necessary guidance to facilitate transmission of the manuscript in question to the Associate Editor who will in turn send it out for reviews. It is here recommended that all future authors of manuscripts communicate directly with the appropriate Associate Editor prior to actually submitting their manuscript to the *Journal of Cave and Karst Studies*. After communicating with an Associate Editor, it is expected that one of two methods for manuscript submission will be suggested.

SUBMISSION METHOD NO. 1

The first, and perhaps simplest, method to submit a manuscript to the *Journal of Cave and Karst Studies* is as an attachment to an e-mail message. The *Journal of Cave and Karst Studies* requires that all prospective manuscripts be submitted as single column, double-spaced MS Word files with tables and figures included in separate files. In most instances these can be downloaded and saved to the hard drive of an Associate Editor's computer from a received e-mail message, but not always. Often the files are too large, especially figure files, for sending and receiving by e-mail. In addition, there are times when computer operating systems are incompatible, which causes additional problems. However, for foreign authors e-mail may be the best method available.

Unfortunately, problems with e-mail submission may, at times, arise. For example, very large files may not be easily transferred by e-mail. Also, unusual characters, fonts, or symbols that are readily available on the author's computer may not be available on the Associate Editor's or reviewer's computer, which leads to confusion and delays.

SUBMISSION METHOD NO. 2

A second and reasonably effective method for submitting a manuscript to the *Journal of Cave and Karst Studies* is to use the U.S. Postal Service to deliver the manuscript in question. Specifically, three hardcopies of the actual manuscript, figures, and tables along with a CDROM of the manuscript, figures, and tables in separate files would be necessary.

Problems may still arise with the files on the CDROM. Specific fonts, special characters, etc., may still not be readable on the Associate Editor's computer. However, the submission of a hard copy should alleviate the problem of incompatible computer files.

SUMMARY

The easiest and most effective way to ensure a smooth manuscript submission process for the *Journal of Cave and Karst Studies* is to communicate directly with the appropriate Associate Editor. Through discussions between the manuscript author and the Associate Editor, the best method for efficient manuscript submission will likely emerge.

James U. L. Baldini, Lisa M. Baldini, Frank McDermott and Nicholas Clipson – Carbon dioxide sources, sinks, and spatial variability in shallow temperate zone caves: Evidence from Ballynamintra Cave, Ireland. *Journal of Cave and Karst Studies*, v. 68, no. 1, p. 4–11.

CARBON DIOXIDE SOURCES, SINKS, AND SPATIAL VARIABILITY IN SHALLOW TEMPERATE ZONE CAVES: EVIDENCE FROM BALLYNAMINTRA CAVE, IRELAND

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Carbon dioxide concentrations in Ballynamintra Cave, S. Ireland, generally increase with distance from the entrance, but this trend is non-linear because physical constrictions and slope changes compartmentalize the cave into zones with distinct P_{CO_2} signatures. In this cave, CO_2 originates from the soil and enters the cave by degassing from dripwater and by seeping through fractures, and is then transported throughout the cave by advection. Elevated concentrations in roof fissures, joints, and adjacent to walls suggest that these locations shelter CO_2 gas from advection and permit local accumulation. CO_2 enrichment was noted over a sediment accumulation, suggesting that microbial oxidation of organic compounds in the sediment provided an additional CO_2 source distinct from the soil zone above the cave. Advection driven by external barometric pressure variations caused ventilation, which is the principal CO_2 sink. The data presented here underscore the need for high resolution data to adequately characterize cave air P_{CO_2} variability.

Introduction

Carbon dioxide partial pressure (P_{CO_2}) in the unsaturated zone is an important rate-determining factor in a variety of geochemical processes occurring in the subsurface. Dissolution of atmospheric and soil CO_2 into percolation waters forms carbonic acid (H_2CO_3), the principal agent responsible for limestone dissolution and cave development. Generally, soil P_{CO_2} is substantially higher (typically 1,000–10,000 ppm) than atmospheric values (~380 ppm) (Troester and White, 1984; White, 1988), and is largely responsible for the total dissolved CO_2 in vadose water. In a closed system, limestone dissolution occurs until the dissolved carbon dioxide is completely consumed. Conversely, an open system maintains constant contact between the percolating water and soil CO_2, increasing the amount of total carbonate dissolution. In reality, most systems are open until a certain depth, past which contact with the soil zone stops and closed system behavior ensues. The geochemical system then remains at equilibrium until the water reaches void spaces with lower P_{CO_2} than the dissolved P_{CO_2} of the water, at which point degassing of the dissolved CO_2 occurs, followed by calcite precipitation. Thus, P_{CO_2} variability throughout a cave can influence the spatial distribution of calcite deposition. Previous research suggests that stalagmite growth rate is a proxy for paleotemperature (Genty *et al*., 2001), vegetation (Baldini *et al*., 2005), and rainfall (Genty and Quinif, 1996; Railsback *et al*., 1994). Thus, understanding CO_2 distribution and dynamics in caves is important for palaeoclimate research using stalagmites because their growth rates partially depend on cave atmosphere P_{CO_2} (Kaufmann, 2003; Kaufmann and Dreybrodt, 2004; Spötl *et al*., 2005).

While CO_2 degassing may cause calcite precipitation, water condensing from high-humidity cave air onto calcite surfaces in a cave may absorb CO_2 from the air, producing carbonic acid and subsequent calcite dissolution. This phenomenon is termed condensation corrosion, and the rates are dependent on cave atmosphere P_{CO_2}. Previous research has demonstrated that although condensation corrosion is most prevalent in hydrothermal caves (Bakalowicz *et al*., 1987; Cigna and Forti, 1986), it can occur in non-thermal caves (De Freitas and Schmekal, 2003; Dublyanski and Dublyanski, 1998; Jameson, 1991; Sarbu and Lascu, 1997; Tarhule-Lips and Ford, 1998). Opinions on the speleogenetic importance of condensation corrosion vary, but the potential risks to speleothems and cave pictographs are well-documented (Carrasco *et al*., 2002; Pulido-Bosch *et al*., 1997). Understanding the behavior of CO_2 in caves is therefore critical for the preservation of cultural heritage sites and heavily visited commercial caves, and may also affect the vadose modification rate of existing cave passage.

Many researchers have measured P_{CO_2} in caves, but very few high-spatial resolution datasets of P_{CO_2} exist. Gewelt and Ek (1983) published a comparison of the spatial P_{CO_2} variability in two Belgian caves where respired CO_2 was absorbed by a breathing apparatus filled with sodium carbonate. A linear relationship existed between the distance from the cave entrances and cave air P_{CO_2}. Based on the CO_2 distribution in the caves, the soil zone and an underground stream flowing through one of the caves were inferred as CO_2 sources.

Another study presented data from Belgium and numerous other countries, and demonstrated that P_{CO_2} is positively correlated with above-ground temperature (Ek and Gewelt, 1985) and that P_{CO_2} concentrations are higher near the ceiling of passages. A study of the Aven d'Orgnac in France suggested that air enriched with biogenic CO_2 moved through bedrock fissures into the cave (Bourges *et al*., 2001).

The P_{CO_2} data presented here are used to develop a high spatial resolution survey of carbon dioxide concentrations for Ballynamintra Cave, Ireland. Whereas previous research on spatial variability of cave atmosphere CO_2 [*e.g.*, (Ek and Gewelt, 1985; Gewelt and Ek, 1983)] was conducted using chemical pump detectors that were relatively imprecise and cumbersome, the current research was conducted using an infrared CO_2 probe, greatly increasing the precision and decreasing the time necessary per measurement. Consequently, the entire cave was surveyed with a spatial resolution better than one point per five meters, both horizontally and vertically. This high resolution also facilitates the development of air circulation models that identify sources and sinks. To our knowledge, this is the first cave air P_{CO_2} survey created using high-precision CO_2 loggers coupled with breathing apparatuses to minimize the effects of operator-respired CO_2.

SITE DESCRIPTION

Ballynamintra Cave is located approximately 11 km NW of Dungarvan, County Waterford, Ireland, and is developed in lower Carboniferous (Mississipian) limestone strata (Fig. 1). It is a very short cave, with only 95 m of surveyed passage and a depth of 14 m (Ryder, 1989), but is divided by slopes and constrictions into three distinct sections. The large (~3 m diameter) entrance leads immediately to the first section, a relict phreatic tube approximately 3 m in diameter that also has a smaller entrance near the far end via a collapse skylight. A narrow, excavated passage leads 3 m downwards from here into the cave's main section, which consists of a large chamber 12 m long, 3 m high, and 3 m wide. This chamber continues south until a large (6 m long, 2 m wide, and 4 m high) accumulation of soil. A vertical passage (called The Hole) at the accumulation's base leads through very narrow passages to the lowest point in the cave, which terminates at a sump. This is the only small area that was not included in the CO_2 survey, because the extremely tight nature of these tunnels prevented passage of the operators and breathing apparatuses. The top of the soil accumulation is approximately 2 m below the ground surface, and plant roots are observable extending into the cave at this point. A very tight (0.25 m high, 1 m wide), excavated passage leads downwards to the cave's third distinct section, a very well decorated chamber 10 m long, 3 m wide, and 2 m high at approximately the same level as the main chamber.

The cave is developed in the side of an escarpment overlain by a small, well-developed mixed beech and oak wood with substantial undergrowth, though pasture surrounds the escarpment in all directions. The soil is well-developed with distinct O and A horizons. The epikarstic zone is reached after approximately 50 cm, but depth varies considerably at different locations on the escarpment.

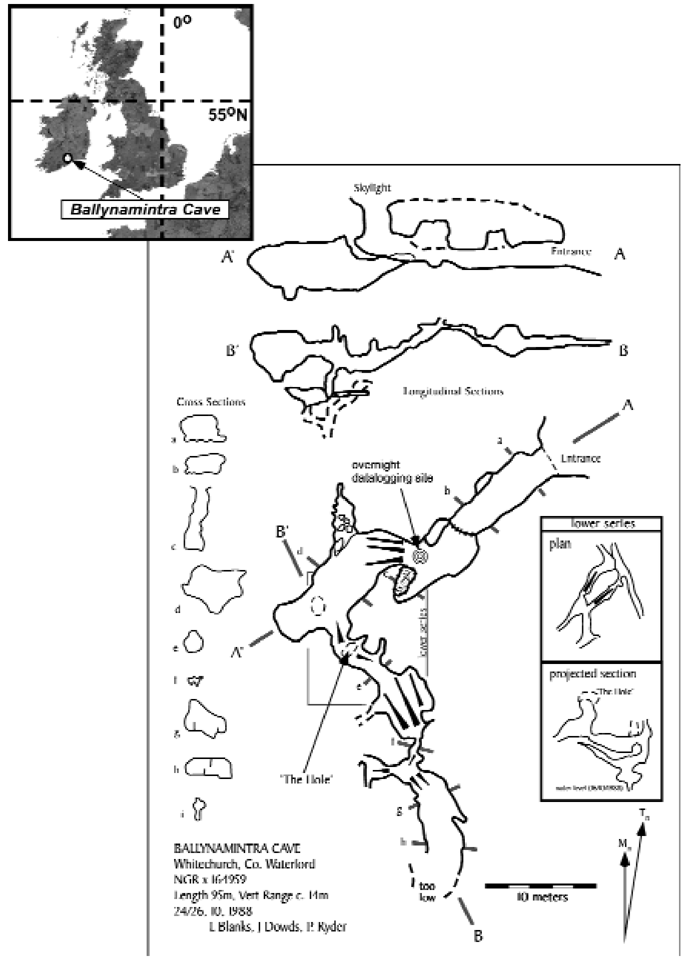

Figure 1. Map and location of Ballynamintra Cave, County Waterford, Ireland. The concentric circles indicate the overnight logging site. Adapted from the original survey by L. Blanks, J. Dowds, and P. Ryder (Ryder, 1989).

Mean annual surface temperature at Cork Airport (50 km to the SW) is 10.1 ºC and mean annual rainfall is 1,191.7 mm.

METHODS

Temperature and CO_2 concentrations were determined using a calibrated Vaisala GM70 CO_2 meter, which calculates P_{CO_2} by measuring the absorption of an infrared beam by CO_2 molecules. The precision for the P_{CO_2} measurements is better than ±30 ppm (2σ), and the temperature measurement precision is ±0.02 ºC (2σ). All P_{CO_2} values are presented as ppm (volume) and were corrected for barometric pressure. Measurements for the survey were made on September 9, 2005.

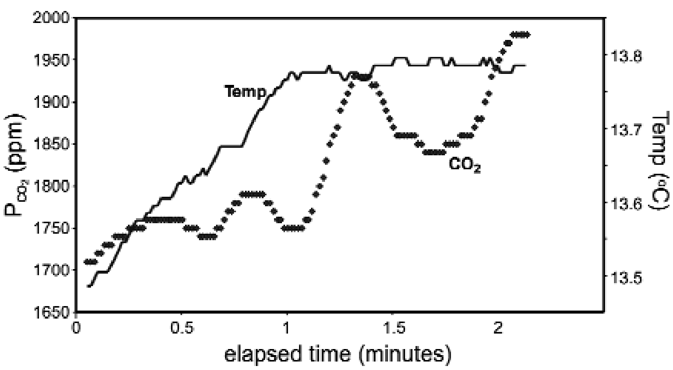

Figure 2. Time-series dataset of P_{CO_2} and temperature obtained after removal of breathing apparatus. Solid line represents temperature data and filled diamonds represent P_{CO_2} measurements.

Error due to respired CO_2 contributions into the cave atmosphere was minimized by using a breathing apparatus that allowed normal breathing but expelled respired air through a 20 m long flexible tube and into the atmosphere in previously surveyed portions of the cave. Because of the measurement rapidity (less than 2 minutes in most cases), the respired air did not have sufficient time to diffuse into the sections of the cave where measurements were actively being taken. Electric lights were used exclusively.

P_{CO_2} and temperature measurements (n = 137) were taken along short transects in the cave, and the location of each measurement relative to datum measured with a compass, clinometer, and calibrated tape. P_{CO_2} measurements were often taken in vertical profiles; the mean of these points was determined to create a single point in an x–y grid. These points were then used to create horizontal two-dimensional contour maps. All contour maps were created using Surfer 8®. Data were also logged overnight every 15 minutes in the phreatic tube section of cave near the entrance to the more poorly ventilated section of cave (see Fig. 1 for location) to observe whether any shifts associated with colder nighttime temperatures occurred.

Results and Discussion

Impacts of Respiration

Removal of the breathing apparatus near the furthest point away from the cave entrance after completion of the survey (in a small tunnel approximately 2 m high and 2 m wide) demonstrated that respiration immediately caused CO_2 levels to rise from 1,700 ppm to 1,980 ppm, an increase of 16% in just over 2 minutes (Fig. 2). This is broadly consistent with previous studies that suggest increases of 32% after 5 minutes respiration from 3,800 to 5,000 ppm (Ek and Gewelt, 1985; Gewelt and Ek, 1983). The increase was punctuated with minima and maxima, suggesting that direct, high-P_{CO_2} respiration reached the CO_2 meter only occasionally, depending on the breathing direction of the operators. A human breath contains approximately 40,000 ppm CO_2 (Miotke, 1974), considerably higher than atmospheric values (380 ppm) and cave air values (mean value in Ballynamintra Cave 1,050 ppm), and therefore can significantly alter cave air concentrations. When long measurement times are necessary, as with CO_2 meters dependent on chemical pump detectors, significant error is introduced. Studies not using techniques to mitigate the effects of respired CO_2 will likely report erroneously high P_{CO_2} values.

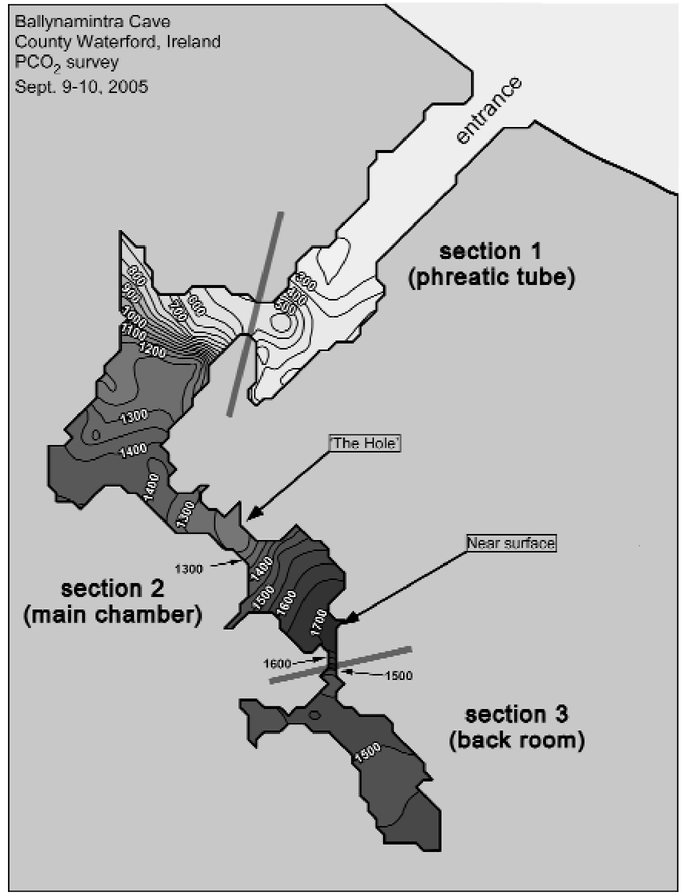

Figure 3. Contour map of CO_2 concentrations throughout Ballynamintra Cave. Contour interval is 50 ppm. Points used to construct contour map are shown as black circles.

The temperature measurements taken simultaneously with the P_{CO_2} measurements suggest that the presence of two people raised the temperature of the small chamber by at least 0.3 °C in two minutes, though because the operators were present in the room before logging began, the effect likely exceeds this estimate. Because of this potential error, temperature measurements are not precise enough to create a detailed temperatures contour map; however, general spatial trends in temperature are apparent and will be discussed below.

Cave Air CO_2 Distribution

Ventilation caused by the large entrance combined with the smaller skylight entrance results in considerably lower P_{CO_2} in the phreatic tube section of cave than in the other sections (Fig.

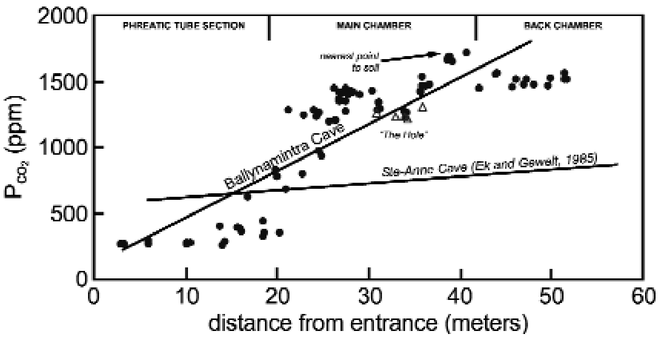

Figure 4. CO_2 concentrations plotted against distance from the entrance of Ballynamintra Cave. Unfilled triangles represent data points obtained in the lower level of the cave ('The Hole') that were not included in the survey shown in figure 3. Regression lines describing the data from this study and from a previous study (Ek and Gewelt, 1985) in Ste-Anne Cave, Belgium, are shown. The slope for the regression line describing the data obtained in the current study (*m* = 34.29) is greater than that for the older study (*m* = 5.3) because the small passages and constrictions present in Ballynamintra Cave inhibit air circulation more effectively than the larger passages in Ste-Anne Cave.

3). P_{CO_2} values reach a local maximum (550 ppm) directly adjacent to the narrow, inclined constriction leading to the deeper main section of cave. A plume of CO_2 rich air exists protruding from this constriction into the phreatic tube section, where advection likely prevents accumulation to more elevated P_{CO_2} values. Values increase very steeply from the well-ventilated phreatic tube entrance passage into the cave's second, main section, reaching local peak concentrations of 1,450 ppm before decreasing gradually to values of 1,250 ppm towards the extremely tight passage known as The Hole that leads downwards towards a sump. Values obtained within this tight vertical passage are the lowest of the entire cave (1,230 ppm), with the exception of the phreatic tube section closest to the entrance. Carbon dioxide partial pressure values increase again as the cave ceiling approaches the ground surface, eventually reaching the most elevated values in the entire cave (1,720 ppm). The passage here is developed at the top of a large accumulation of sediment, and roots growing in roof fissures indicate the close proximity of the soil. This was confirmed by comparing the survey to a GPS measurement of surface altitude, suggesting that this section of cave is less than two meters below the surface. P_{CO_2} values gradually decrease downward through a tight constriction into the third section of the cave (Fig. 3). Values in this isolated chamber are approximately 1,500 ppm and do not vary considerably, suggesting that the single small entrance to the chamber prevents significant air exchange.

CONTROLS ON CAVE AIR P_{CO_2}

The trend towards more elevated P_{CO_2} values with distance from the entrance (Fig. 4) suggests that air circulation is the most important control governing CO_2 distributions, and that physical constrictions in the cave impede air movement. Diffusion of CO_2 out of the highest P_{CO_2} area was calculated using an equation derived from Fick's First Law:

$$J = -D\frac{dC}{dx} \tag{1}$$

where:
- J = flux [(kg m^{-2} s^{-1})]
- D = diffusion coefficient of CO_2 in air (m^2 s^{-1})
- dC = concentration change (g m^{-3})
- dx = distance (m)

Using values of $D = 3.0 \times 10^{-6}$ (m^2 s^{-1}), $\Delta C = 1{,}500$ (g m^{-3}) (concentration change between high concentration area to phreatic tube area), and $\Delta x = 50$ m (approximate distance from high concentration area to phreatic tube area), the flux (J) out of the high P_{CO_2} area is calculated as -1.989×10^{-10} (kg m^{-2} s^{-1}). The amount of CO_2 contained within the high P_{CO_2} region of cave at the back of the main chamber is 0.11 kg, assuming the volume of the high P_{CO_2} area of cave is 33.3 m^3 and the P_{CO_2} is 2,000 ppm. Using a cross-sectional area value for the passage of 6.0 m^2, diffusion will homogenize CO_2 concentrations throughout the cave in approximately 3 years. This time period is long compared to the probable time required to ventilate the cave via differential pressures caused by changes in surface atmospheric barometric pressure, and is thus probably not an important mechanism for CO_2 transport in Ballynamintra Cave.

The steepest gradients in P_{CO_2} occur immediately after tight passages separating different sections of Ballynamintra Cave (Fig. 4). The regression line between P_{CO_2} and the distance from the entrance in Ballynamintra Cave has a steeper slope (m = 34.29) than the regression line calculated by Ek and Gewelt (1985) for Ste-Anne Cave, Belgium, (m = 5.3) and probably results from the difference in cave morphologies. Ballynamintra Cave is small with several tight constrictions, while Ste-Anne Cave is larger with wider passages, allowing more ventilation and air exchange. Although the maximum P_{CO_2} reached in the main passage of Ste-Anne Cave is much greater than that reached in Ballynamintra Cave (3,200 ppm versus 1,720 ppm), the value reached after 50 m (the maximum distance from the entrance, Ballynamintra Cave) is much lower (800 ppm compared with 1,720 ppm), supporting the hypothesis that the differences in the slopes of the regression lines results from more air circulation in Ste-Anne Cave. This interpretation is also supported by evidence from other caves with very large dimensions that have very low P_{CO_2} values (Ek *et al*., 1989).

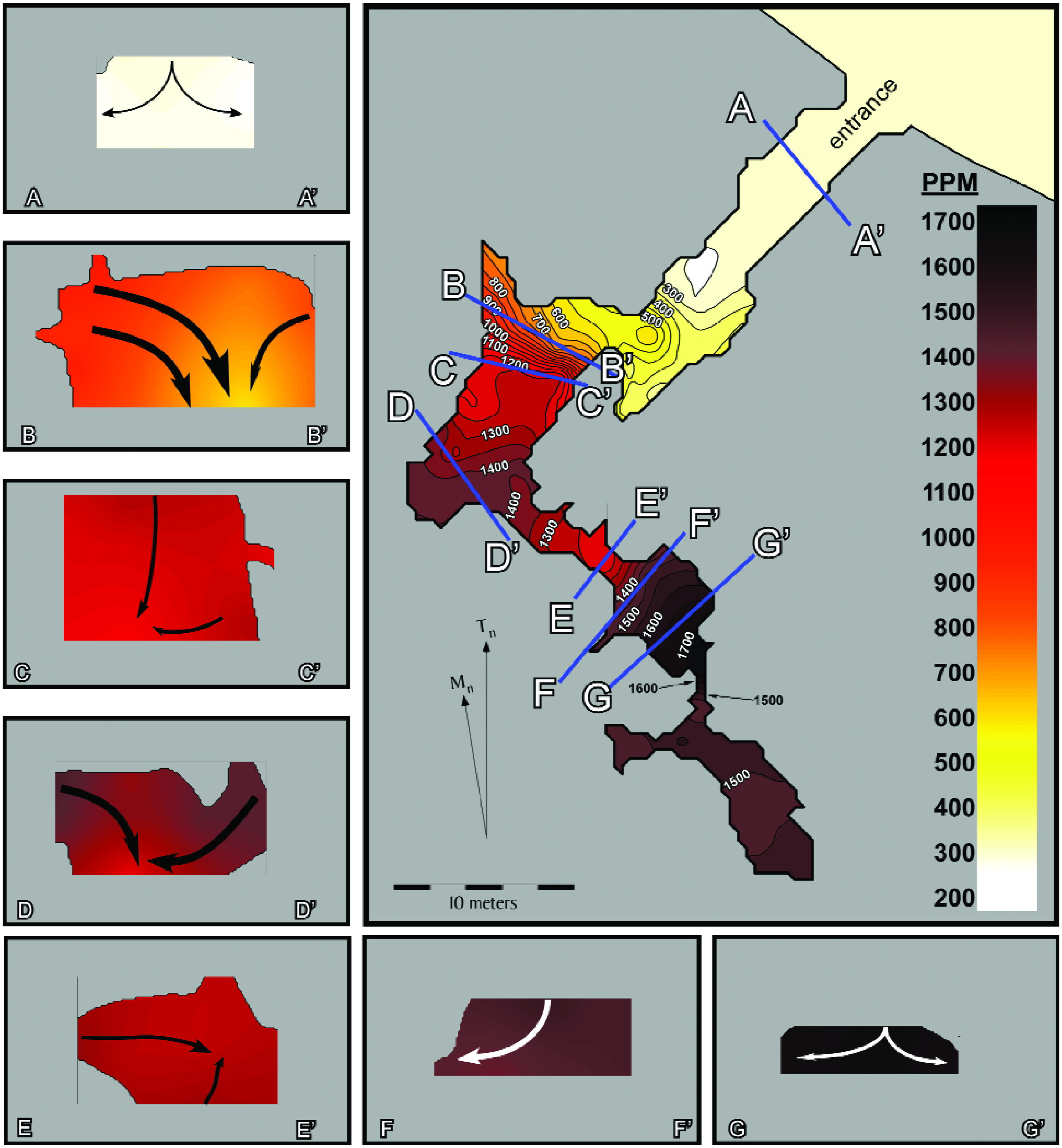

Figure 5. Contour maps of P_{CO_2} values (ppm) at various cross-sections of passages in Ballynamintra Cave. All values use the same contour interval (10 ppm). Arrows indicate inferred direction of CO_2 flux, from high P_{CO_2} to low P_{CO_2}. The gradient strength is reflected schematically by the size of the arrows; larger arrows indicate a stronger P_{CO_2} gradient. Solid grey indicates rock.

A widespread misconception is that because CO_2 is approximately 1.5 times heavier than typical air, it sinks to deeper sections of cave. This mechanism will only affect caves with temperatures near absolute zero, when gas molecules lose nearly all their vibrational energy, and so is not an important factor anywhere (Smith, 1999). Several other mechanisms may increase cave atmosphere P_{CO_2} (James, 1977): 1) degassing of dissolved CO_2 from cave waters that generally obtain elevated CO_2 contents from the soil, 2) production of CO_2 from the respiration of micro-organisms in the cave, usually associated with decaying organic matter, 3) CO_2 flow through fractures connected to the soil, and 4) deep-seated CO_2 seepage from porous reservoirs, usually igneous in origin. Only the first three mechanisms are relevant in Ballynamintra Cave.

The first mechanism (CO_2 degassing) is identifiable by a vertical gradient in P_{CO_2} concentrations in a passage with no organic matter accumulation. The high P_{CO_2} locus depends on the drip rate of the degassing water. If drips are very rapid, water does not have sufficient time to degas on the cave ceiling but instead degasses near the floor, creating locally high concentrations near the base of a passage. Conversely, slow drips will degas on the ceiling and will result in locally high P_{CO_2} values at the top of passages. In both cases, degassing rates must exceed gas diffusion and advection rates; otherwise the CO_2 will spread evenly throughout the chamber. The second mechanism (CO_2 flux from fissures) also results in elevated P_{CO_2} values near the ceiling, but is distinguished from the degassing mechanism by the lack of active drips and the presence of vertical cracks or fissures. The third mechanism (microbially-produced CO_2) is generally associated with the presence of organic material.

In Ballynamintra Cave, most passage cross-sections demonstrate higher CO_2 concentrations near the ceiling or fractures (Fig. 5), suggesting that the dominant mechanisms involve CO_2 degassing from drip waters or CO_2 fluxes from fissures. A major exception occurs in the cross-section of the passage at the top of the sediment accumulation (Fig. 5f). Carbon dioxide concentrations are greatest near the passage base, suggesting that this localized CO_2 maximum reflects microbially-induced organic matter decay in the sediment. Sheltered areas typically have elevated P_{CO_2} values (Fig. 5), suggesting reduced advective CO_2 dispersion. This suggests that air movement through the cave is analogous to water movement in streams, with a central zone of greatest flow (the thalweg in surface streams) and lateral zones of reduced velocity due to either friction or physical sheltering.

The distribution of CO_2 in Ballynamintra Cave and the association of locally elevated concentrations with ceiling fissures strongly suggest that the gas originates predominantly from the soil. A soil P_{CO_2} logger permanently installed directly above the cave indicates that P_{CO_2} values greater than 5,000 ppm are typical during the summer. This soil gas is dissolved in percolation water, transported into the subsurface, and degassed in the cave. Additionally, soil gas may also diffuse downward through fissures into the cave. Downward soil gas diffusion is probably the dominant source of CO_2 to Ballynamintra Cave because of its proximity to the soil zone and lack of high discharge drips. Calculations based on the P_{CO_2} of cave waters and estimated number of drips suggest that if drips were the only source of CO_2 into the cave, it would take at least 50 years to produce the accumulation of CO_2 observed in the high P_{CO_2} sections, assuming the complete absence of any CO_2 sinks. This calculation and the association of high P_{CO_2} areas with fissures therefore suggest that downward soil gas diffusion, rather than degassing from drips, is the dominant source of CO_2 to Ballynamintra Cave. However, because fracture frequency and width in karst areas decreases with depth (Baker *et al*., 1997), downward diffusion of gaseous CO_2 is probably a more important source at Ballynamintra Cave than at deeper caves.

A CO_2 sink is inferred to exist in The Hole because of anomalously low concentrations present in and around the vertical passage. The presence of water at the passage base suggests that the water P_{CO_2} is lower than the cave atmosphere P_{CO_2}, and is actively absorbing CO_2 from the atmosphere. Unfortunately, the very tight passages prevented the researchers from reaching the water to obtain any measurements.

Temperature Distribution

The temperature above-ground on the day of the survey was measured as 17 ºC and was only slightly lower in the phreatic tube section, with a mean measurement of 15.5 ºC. Once past the constriction leading into the main chamber, the recorded temperature decreased to approximately 12.5 ºC and remained stable until The Hole when temperatures dropped noticeably to 11.5 ºC. This is the deepest section of cave and probably has the least exchange with the external atmosphere. The presence of water may also have contributed to the lower temperature. Temperatures increased dramatically near the top of the sediment accumulation to almost 14 ºC, but this may partially result from the presence of two cavers in a small space for a prolonged period of time (as mentioned above). However, it may also reflect the proximity of warmer 17.0 ºC above-ground air two meters away through the overburden. The temperature in the deeper back chamber was approximately 12.5 ºC and stable throughout.

Temporal CO_2 Variability

Carbon dioxide and temperature measurements were logged every 15 minutes between 8:39 p.m. and 11:39 a.m., September 8–9, at the top of the steep passage connecting the phreatic tube section to the main chamber (Fig. 6). The measurements vary from very low (200 ppm, value below atmospheric probably because of forest photosynthetic effects) late in the logging interval to a maximum of 1,390 ppm occurring at 1:39 a.m., suggesting that CO_2 rich air was expelled from the

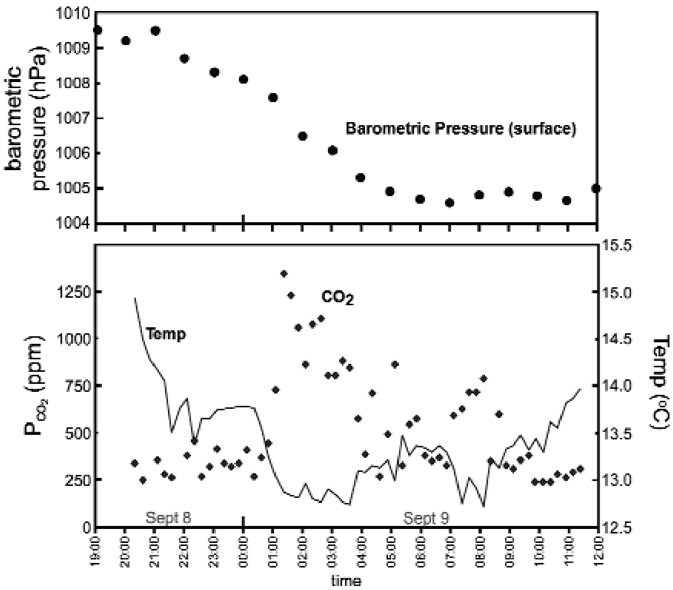

Figure 6. Temperature (solid line) and P_{CO_2} variations (filled diamonds) measured every fifteen minutes between 8:39 p.m. and 11:39 a.m., September 8–9, at the top of the steep passage connecting the phreatic tube section to the main chamber. Maximum P_{CO_2} values were recorded at 1:39 a.m. (1390 ppm). The top panel displays the hourly barometric pressure at Cork Airport (closest meteorological station to cave, 40 km to the west) during the measurement period.

cave during the night. The maximum concentration recorded is comparable to the concentrations characteristic of the rest of the cave; therefore a barometric pressure reduction that occurred on the surface overnight may have caused the cave to exhale, resulting in an extension of the high-P_{CO_2} plume (Fig. 3). The interpretation is supported by the temperature data, which reach their lowest values (12.8 ºC) coincident with the highest P_{CO_2} values. The similarity between this temperature value and typical cave air temperature (12.5 ºC) suggests that both the high P_{CO_2} and the low temperature values reflect advection of air from deeper in the cave. Longer term CO_2 concentration datalogging in the main chamber of Ballynamintra Cave demonstrates the presence of quasi-periodic, large P_{CO_2} spikes reaching maximum values of over 3,000 ppm. These may correspond to periods of decreased barometric pressure on the surface, which cause the extraction of CO_2 rich air from fissures (Baldini *et al.*, in prep.). Conversely, high external barometric pressure pushes in atmospheric air, reducing cave air P_{CO_2}.

IMPLICATIONS

The distribution of CO_2 in Ballynamintra Cave implies that the elevated P_{CO_2} values found deeper in caves will result in reduced degassing from dripwater, consequently reducing calcite deposition rates. This study therefore suggests that stalagmite calcite precipitation rates must vary spatially throughout a cave, even if all other parameters affecting precipitation remain unchanged. Furthermore, a large overnight P_{CO_2} shift suggests that calcite precipitation may vary temporally as well as spatially in response to the P_{CO_2} variations induced by external barometric changes. The hypothetical creation of an entrance (either naturally through erosion or artificially) to a cave previously with no entrance will ventilate the cave and produce a rapid P_{CO_2} drop. This phenomenon would result in a rapid stalagmite growth rate increase that may resemble the effects of a climatic amelioration (Baldini *et al.*, 2002; Genty *et al.*, 2003). Paleoclimate studies using stalagmite growth rate or isotopic proxies must consider the possibility of rapid ventilation in relevant situations. A comparison of stalagmite $\delta^{13}C$ and growth rates could distinguish between the two effects (ventilation and climatic amelioration). Both effects would result in increased calcite deposition rates, but ventilation would raise $\delta^{13}C$ values while a climatic amelioration would reduce stalagmite $\delta^{13}C$ (because of increased surface bioproductivity).

Because the research presented here indicates that concentrations of CO_2 are not homogenous throughout caves, heterogeneities must also exist in the rates of speleogenetic processes that are affected by P_{CO_2}. Condensation corrosion will affect areas of elevated P_{CO_2} preferentially over other areas of lower P_{CO_2}, particularly when associated with high humidity (Dublyanski and Dublyanski, 1998). The heterogeneous spatial and temporal distribution of CO_2 concentrations also affects gypsum deposition in caves via the Palmer Model, where low P_{CO_2} drip water containing sulphate ions absorbs CO_2 from the cave atmosphere, dissolves the surrounding limestone, and redeposits gypsum (Palmer, 1986). Because gypsum has a higher molar volume than calcite, this replacement can lead to the formation of breakdown and cavern enlargement (White and White, 2003). This chemical model is highly sensitive to the cave air P_{CO_2}, and relatively small variations may either initiate or inhibit gypsum deposition.

CONCLUSIONS

The CO_2 distribution in Ballynamintra Cave demonstrates that CO_2 concentrations generally increased with distance from the entrance, but that local sources and sinks countered this trend. Constrictions in the cave compartmentalized areas with distinct P_{CO_2} signatures. In this cave, most CO_2 apparently enters the cave through the ceiling; either dissolved in dripwater or more likely by seeping in the gas phase from the soil to the cave through fractures, though a combination of both mechanisms is probable. Transport throughout the cave occurs by advection induced by barometric pressure differences between the surface and cave. Concentrations in fissures, cracks, and adjacent to walls were higher than those in the centers of passages, suggesting that these locations partially shelter CO_2 gas from advection. Cave air P_{CO_2} may also increase locally due to microbially produced CO_2 originating from a soil accumulation near the end of the cave. A sump located at the cave's lowest point may act as a CO_2 sink.

These data indicate that one P_{CO_2} measurement will not accurately characterize cave air P_{CO_2}. Because of the importance of CO_2 on calcite deposition, condensation corrosion, speleogenetic processes, and the preservation of cave pictographs, the distribution of CO_2 in caves should be researched further. The simple, efficient technology involved permits the construction of high-resolution surveys of larger caves, testing whether the relationships observed in Ballynamintra Cave are applicable on larger scales. Future studies in deeper caves, caves containing active rivers, and commercial caves would provide interesting supplements to the results reported here. Additionally, future research should apply natural or artificial tracers to more positively identify sources and sinks of CO_2. Isotopic studies would help identify potential CO_2 sources, and would also evaluate the response of stalagmite calcite carbon isotopic ratios to P_{CO_2} variations.

Acknowledgments

We thank Dr. David Drew and Professor Christoph Spötl for helpful reviews that improved the manuscript. Professor Camille Ek is thanked for providing relevant reprints. We also thank the landowners for permitting access to the site. This research was supported by Enterprise Ireland Basic Research Grant 3750/92201/R8965.

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THE JABAL AL QARAH CAVES OF THE HOFUF AREA, NORTHEASTERN SAUDI ARABIA: A GEOLOGICAL INVESTIGATION

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The Jabal Al Qarah Caves, located approximately 13 km east of Al Hofuf, Eastern Province of Saudi Arabia, are an intricate cave system developed in the calcareous sandstone, marl and clay of the Upper Miocene to Lower Pliocene Hofuf Formation. Physiographically, the hill of Jabal Al Qarah is an outlier mesa that is located at the eastern edge of the Shedgum Plateau, the southern extension of the As Summan Plateau, and the larger Syrian Plateau to the north. Based on cave morphology and interpreted evolutionary history, the Jabal Al Qarah caves appear to be significantly different from other limestone caves reported in the As Summan Plateau. Jabal Al Qarah is known for its tall, linear cave passages and narrow canyons. The boxwork of linear passages is better developed here than any other known cave locations in the Eastern Province. Field observations, including orientations of the escarpment face of the Shedgum Plateau, joints, and fractures, coupled with a review of the tectonic history of the region, suggest that these caves resulted from erosional enlargement of a series of very deep and narrow joint-controlled fissures in the Hofuf Formation. Petrographic data, especially an abundance of well-preserved palygorskite type clay minerals, suggests that the Hofuf Formation was deposited in a mudflat-dominated coastal plain environment.

INTRODUCTION

The Al Hofuf area of the Eastern Province of Saudi Arabia (Fig. 1) is a part of the Shedgum Plateau (Fig. 2), the eastern edge of the greater As Summan Plateau. The Shedgum Plateau is covered by a succession of Tertiary carbonates and evaporites of the Um er Radhuma, Rus, Dammam, Hadrukh, Dam and Hofuf formations (Fig. 3). The Shedgum Plateau, including the Hofuf area, is dotted with numerous karstic features including sinkholes, solution cavities and caves (Pint, 2000, 2003). Edgell (1990a, 1990b) reported over 58 caves in an area of 500 km^2 in the As Sulb area of the Summan Plateau.

Jabal Al Qarah, which hosts the Jabal Al Qarah Caves (N 25º 24.69'; E 49º 41.62' at the main cave entrance), is approximately 130 km southwest of Dammam, and 10 km northeast of Al-Hofuf, in the Eastern Province of Saudi Arabia (Fig. 1). The jabal, named after a large, well-known village in proximity of the mountain, is technically an outlier mesa located close to the eastern escarpment of the As Summan Plateau (Hotzl *et al*., 1978). Locally known as Ghar Al Nashab (t*he Cave of the Archer*) and also as Ash-Shab'an (*the Satiated*), the Jabal Qarah caves have developed in the Upper Miocene to Lower Pliocene Hofuf Formation (Fig. 3). The cave is an interesting and popular geologic and geomorphic feature. Its cool protected passages have been a gathering place for visitation and commerce for generations. Hotzl *et al*. (1978) provided a brief description of the geomorphology of the cave area, and a map of the cave was prepared by Hotzl and Maurin.

GEOMORPHOLOGY

The area immediately east of the Shedgum escarpment contains several isolated erosional remnants, as outliers, buttes and mesas, including Jabal Al Qarah, Barqa Ar Rukban, Jabal Burayqa and Jabal Sha'bah. The main entrance of the cave system is located at the eastern edge of Jabal Qarah overlooking the date plantations of the Al-Hasa Oasis. At the main cave (Ghar An Nashab I, Hotzl *et al*., 1978) entrance, the top of the hill is approximately 75 m above the local street level. Jabal Al Qarah is characterized by an alternation of small plateaus and near-vertical cliffs. Like most of the hills around the area, Jabal Al Qarah is a flat-topped hill with a maximum elevation of about 225 m above mean sea level (Fig. 2). The eastern edge of the Jabal, close to the cave entrance, is interpreted to be bounded by several north-south trending high-angle normal faults with throws of up to 10 m. The mushroom-like pillars of the Hofuf Formation observed close to the cave entrance appear to be on one of these down fault blocks. The cave system has approximately 28 linear passageways totaling about 1.5 km in length, in a rectangular area roughly 132 m x 216 m (Fig. 4).

A meter-thick limestone bed that caps the Hofuf Formation elsewhere in the region is not present at Jabal Al Qarah. This zone is characterized by a cap of caliche (Fig. 5a). When caliche covers the top of the isolated pillar-like erosional remnants of the Hofuf Formation, they have an appearance resembling giant mushrooms (Fig. 5b). Well-developed caliche caps commonly overlie the Hofuf and Dam formations elsewhere in the Shedgum Plateau, including the escarpment face to the east of the cement factory close to Al Ayun, north of Al Hofuf.

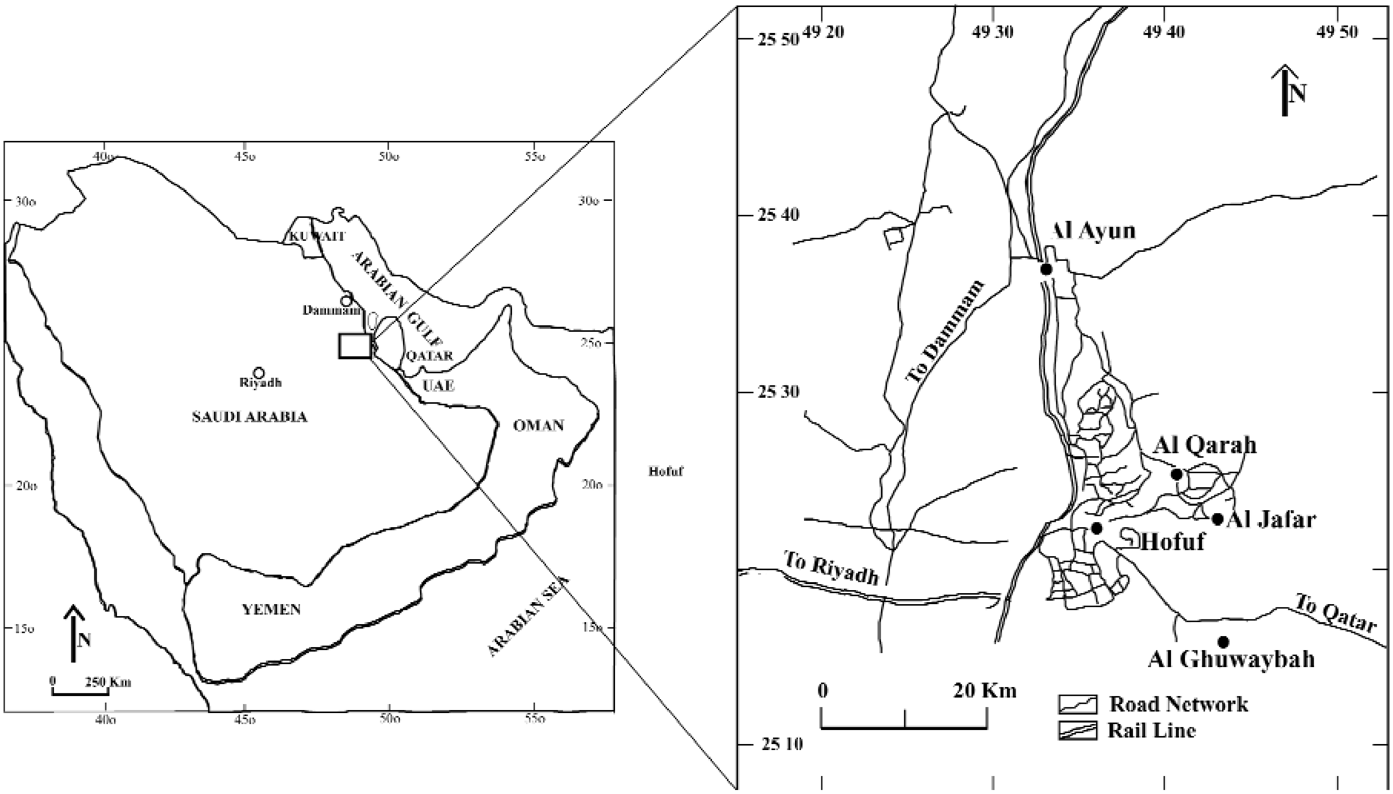


Figure 1. Location map. The Jabal Al Qarah caves are located approximately 10 km east of Hofuf, Eastern Province, Saudi Arabia.

Stratigraphy and Sedimentology of the Host Formations

The rocks exposed at Jabal Al Qarah consist of limestone, marls and clays of the middle Miocene Dam and Hofuf formations (Fig. 6). The basal section of the Hofuf Formation at Jabal Al Qarah is a thin layer of marl overlain by a conglomerate bed, up to 17 m thick, followed by an 18 m thick sequence of lacustrine sandy limestone. At the cave section, however, the Dam and the basal part of the Hofuf Formation are not exposed. The sandy limestone is overlain by an approximately 75 m thick sequence of light grey calcareous sandstone with reddish marl/silty marl intervals (Fig. 7a,b). A thin limestone bed, up to 2 m thick, caps the sequence.

The Hofuf Formation, that hosts the main Jabal Al Qarah cave section, is a white to light grey, massive, calcareous sandstone inter-bedded with soft, reddish to yellowish brown marl and clay. The cave section (including the interior of the caves) of Jabal Al Qarah is characterized by two distinct reddish marl/silty clay intervals of which the thicker one, approximately 5 m thick, is at ground level close to the main entrance of the cave. The other reddish interval is thinner, up to 2 m thick, and is at the mid-level of the jabal. The reddish marl/clay intervals appear continuous to the west and north of the jabal. When freshly exposed, these horizons often show an intricate network described by Hotzl *et al*. (1978) as a *"network of cemented small pipes of roots"* (Fig. 8). Goldring (pers. comm., 2000) believes that these features are *rhizocretions* of possible mangrove plant origin. Concretionary bodies, of possible algal origin, range in diameter from 10 to 30 cm and are common in the grey horizons.

Unlike many of the limestone caves in the As Summan Plateau, where the cave floor, walls and ceiling are characterized by the presence of various features including stalactites, stalagmites, cave pearls, guano, different mineral deposits, and wind-blown fine dusts (Pint, 2000; Pint, 2003), the interior of the Jabal Al Qarah caves is either clean or covered only by a thin veneer of wind-blown dust and guano.

Thin-section petrography confirmed that the light grey unit is a calcareous sandstone comprising fine- to medium-grained quartz sand embedded in a calcareous or clay matrix or cement (Fig. 9). Sand and silt-sized calcite grains are also common in this horizon. The sand is poorly sorted and shows a bimodal grain-size distribution.

Clays recognized (x-ray diffraction and scanning electron microscopy) in the grey intervals of the Hofuf Formation often occur both as pore-filling and pore-lining cement. Palygorskite $(Mg,Al)_2Si_4O_{10}(OH)•4(H_2O)$ and smectite are the two dominant clay types recognized (Fig. 10a,b). SEM study shows bundles of fiber-like palygorskite radiating out from a smectite core (Fig. 10b). Palygorskite is a common mineral in the soils from the Arabian Peninsula (McKenzie *et al.,* 1984). Jenkins (1976) reported abundant palygorskite from the soils from the

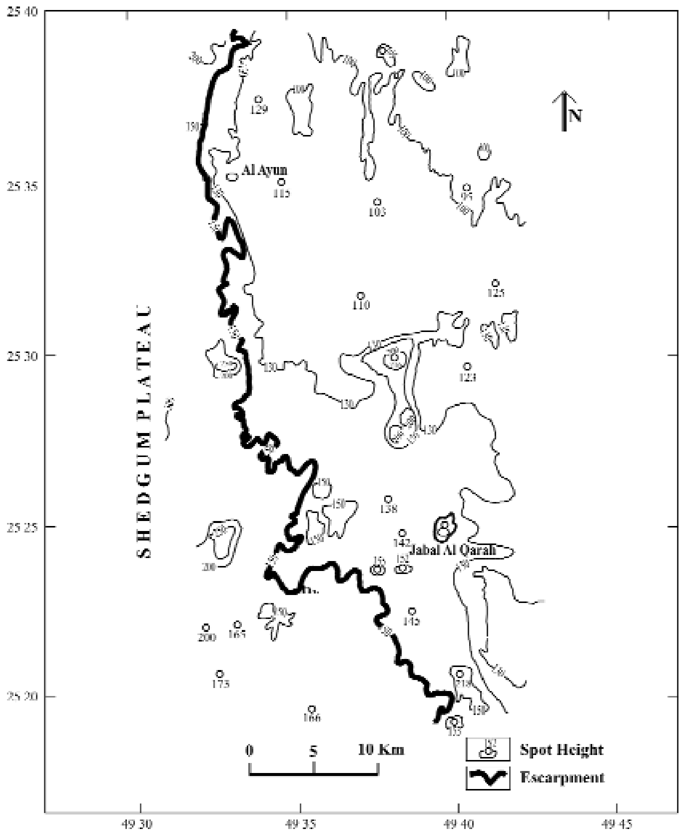


Figure 2. Topographic map of part of the Shedgum Plateau showing Jabal Al Qarah and the surroundings. (modified after Hotzl *et al*., 1978).

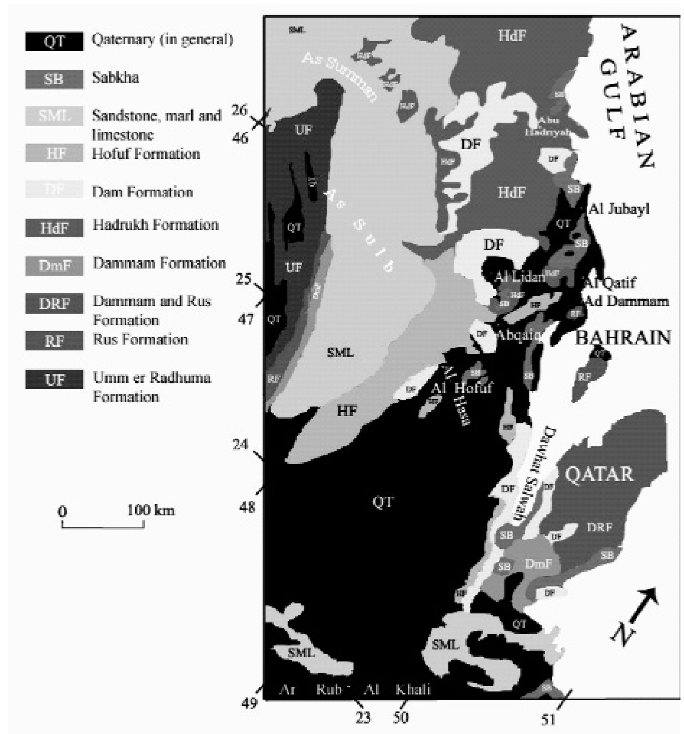


Figure 3. Geologic map of part of the Shedgum Plateau. Al Hofuf and adjoining areas including Jabal Al Qarah are covered by the Mio-Pliocene age Hofuf Formation. (modified after Hotzl *et al*., 1978).

Hofuf area. According to Ingles *et al*. (1998), Mg-rich smectite is common in modern and ancient saline lakes. Palygorskite, however, often forms in ephemeral saline lakes and saline flood plains either by the transformation of precursor clay minerals or by dissolution-precipitation mechanism (Velde, 1985; Jones and Galan, 1988). Ziegler (2001) discussed the tectonics, paleogeography and deposition of the post-Paleozoic sequences in the Arabian Peninsula, and noted that during the Miocene-Pliocene, a halo of mainly continental (Hadrukh Formation) to transitional-marine sediments (Dam Formation) were deposited around this region. The Hofuf Formation is the age-equivalent lacustrine sediments deposited in the interior of the Arabian Plate.

Compared to the grey horizons, the grain size of the reddish to yellowish brown horizons is fine and composed of both marl and clay (Fig. 11). SEM study shows that in addition to calcite and clay, both gypsum and halite are common in the reddish intervals (Fig. 12a,b). Owing to the loose and friable nature of the marl and clay, the reddish horizons appear to weather more readily than the grey calcareous sandstone horizons.

FORMATION OF THE JABAL AL QARAH CAVE

Limestone caves usually form by dissolution and erosional enlargements of the hosts along zones of relatively soluble rocks, or zones of textural and structural weakness. Such caves often consist of irregular underground chambers constituting a series of passages. The cave chambers and passages are often characterized by the presence of various dripstone features such as stalactites and stalagmites. Most of the limestone caves reported in Saudi Arabia are of this category (Pint, 2000; Forti *et al*., 2003; Pint, 2003). Caves of various shapes and sizes are common in the Shedgum Plateau and these isolated hills including Jabal Al Qarah. The dominant caves of Jabal Al Qarah are joint-controlled, steep-walled, and located above most of the nearby terrain (Fig. 13a,b). The caves are at varying stages of development with heights ranging from a few meters to tens of meters, and are up to 3 m wide. Devil's Thumb Cave (N 25º 52.62, E 48º 45.83) is another cave in the area that exhibits tall linear passages similar to Jabal Al Qarah. Other common cave types in the Hofuf area of the Shedgum Plateau include dissolution-controlled caves and caves formed by collapse of the overlying strata resulting from weathering, erosion, and removal of the underlying strata. One such cave (Fig. 13b) is located at the west side of the Jabal Al Qarah close to the base of the wireless (radio) station (N 25º 24.32, E 49º 40.89).

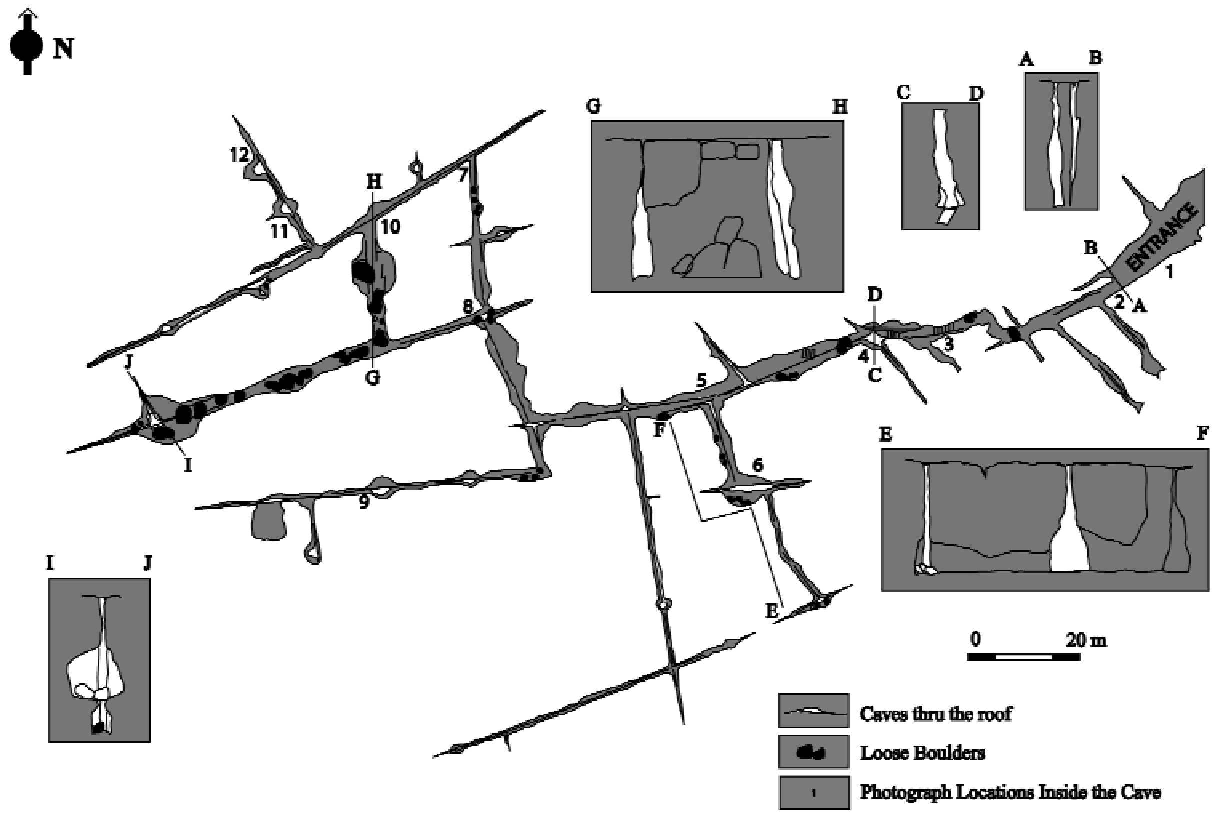


Figure 4. Distribution of major cave chambers in the Jabal Al Qarah caves. The dominant NNW and NE orientations of the caves coincide with the orientations of the regional joint/fracture systems (Figure 16). (modified after Hotzl *et al*., 1978).

Earlier workers investigating the Jabal Al Qarah caves including Hotzl *et al*. (1978) believe that marine erosion in a sea-cliff setting was responsible for the development of the caves in the Jabal. The model proposed by Hotzl *et al*. (1978) suggests that breakers and tides associated with a high sea level during the Quaternary, as well as infiltrating precipitation in the past, played a role in the development of the cave system in Jabal Al Qarah. In support of the role of marine erosion, they cited the presence of numerous wave-cut gorges along the joint openings, and several levels of wave-cut platforms (terrace). One such gorge is up to 10 m wide, reaching almost 300 m in extent into the Jabal. The elevation of cave-bearing sec-

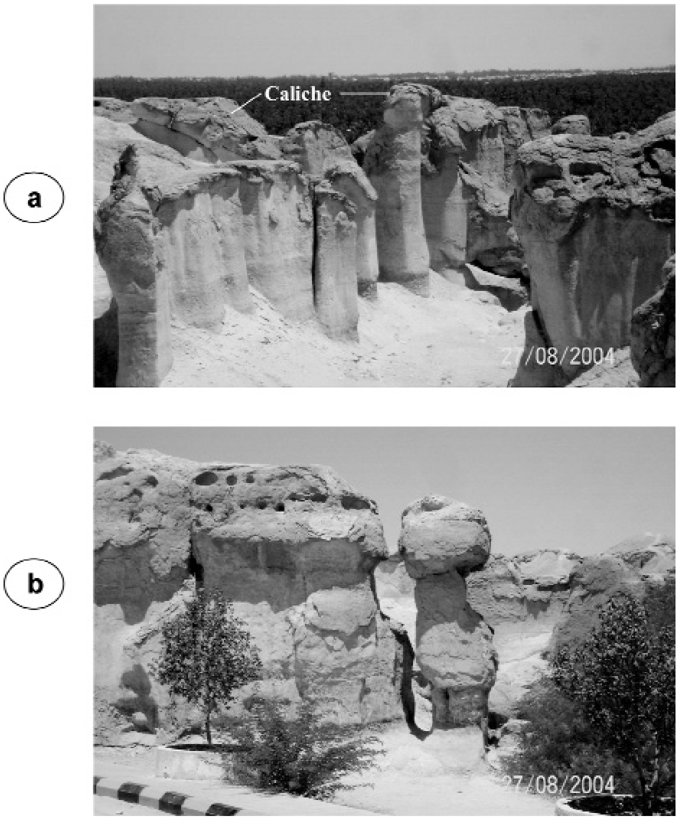
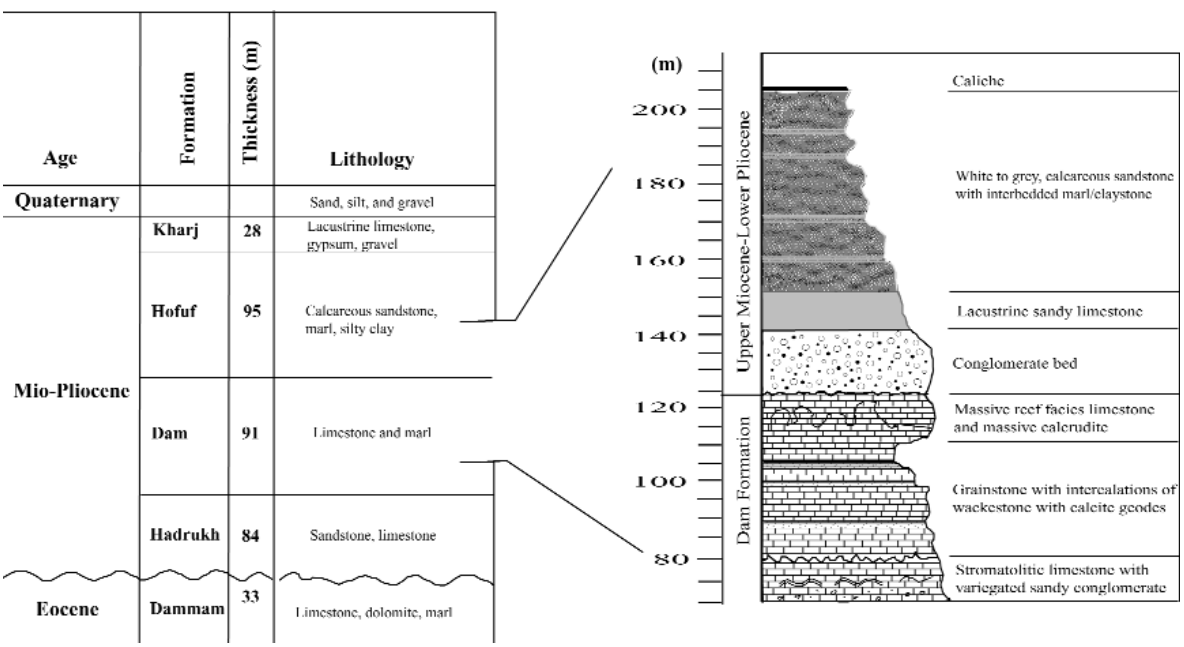


Figure 5. These photographs show the nature and extent of weathering in the Hofuf Formation (a & b). Mushroom-shaped pillars are weathered Hofuf Formation close to the main entrance of the caves. Note well-developed caliche horizons (dark) capping the pillars.

Figure 7. Lithology of the exposed Hofuf Formation at Jabal Al Qarah. As seen in these photographs (a & b), the Hofuf Formation at the jabal comprises an alternation of grey, massive calcareous sandstone and reddish brown marl/silty clay. These photographs were taken on the eastern edge of the jabal close to the main entrance.

Figure 6. Generalized stratigraphy of the Hofuf area. The Jabal Al Qarah caves are hosted in the Mio-Pliocene Hofuf Formation.



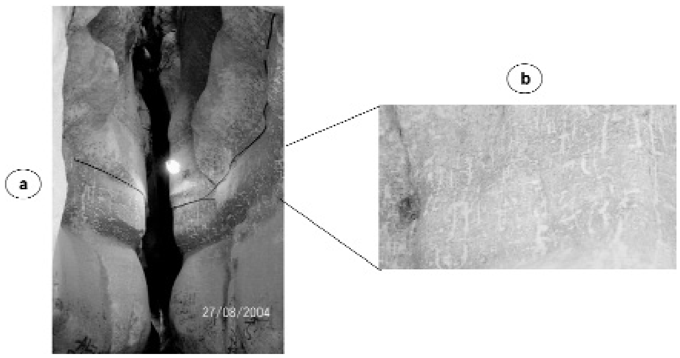


Figure 8. Closer views of the red interval of the Hofuf Formation at Jabal Al Qarah. (a) Outside wall of the main entrance. (b) Cave interior. Intricate textures observed in this interval are interpreted as *rhizocretions* of possible mangrove plant roots.

tions of the Jabal Qarah is over 205 m above present sea level, however, and as the highest Quaternary sea level in the area is less than 100 m (Fairbridge, 1961; Darwish and Conley, 1990; Evans and Carter, 2002; Fig. 14), the role of marine erosion in forming the caves is unlikely.

Jabal Al Qarah is marked by well-developed joint systems with dominant trends to the N 5–30º W and N 55–60º E (Fig. 4). Many of the major caves in the Shedgum Plateau, including those of the Jabal Al Qarah, are oriented along these two general directions (Saner *et al*., 2005, Fig. 15a–g). These joint-controlled caves have vertical or near-vertical walls that often extend from the floor all the way to the roof. When extended through to the roof, these joints often appear as straight-line openings along these general directions (Fig. 16a,b). As indicated by the fresh rock exposures along the cave walls, the

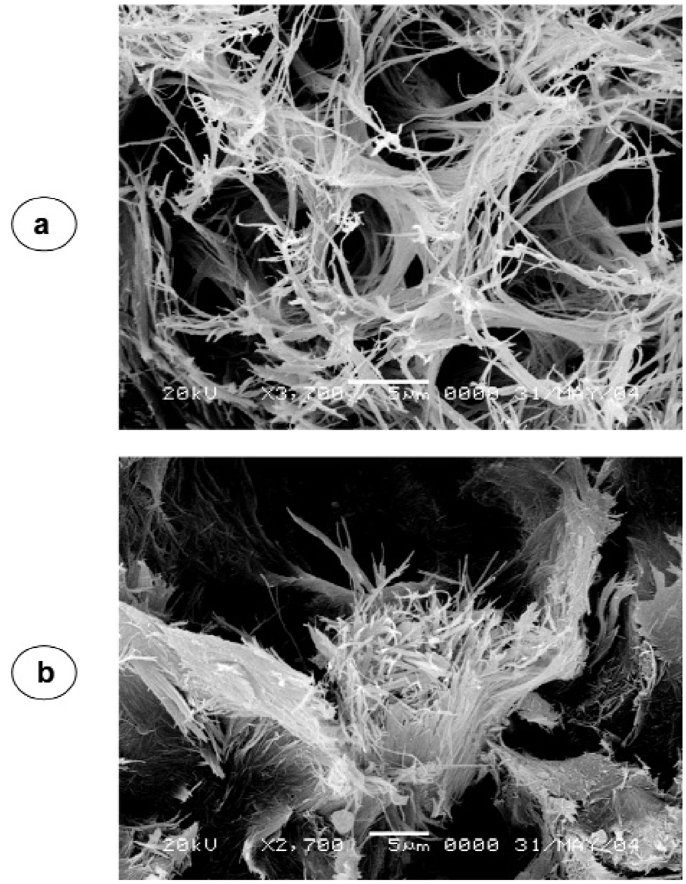
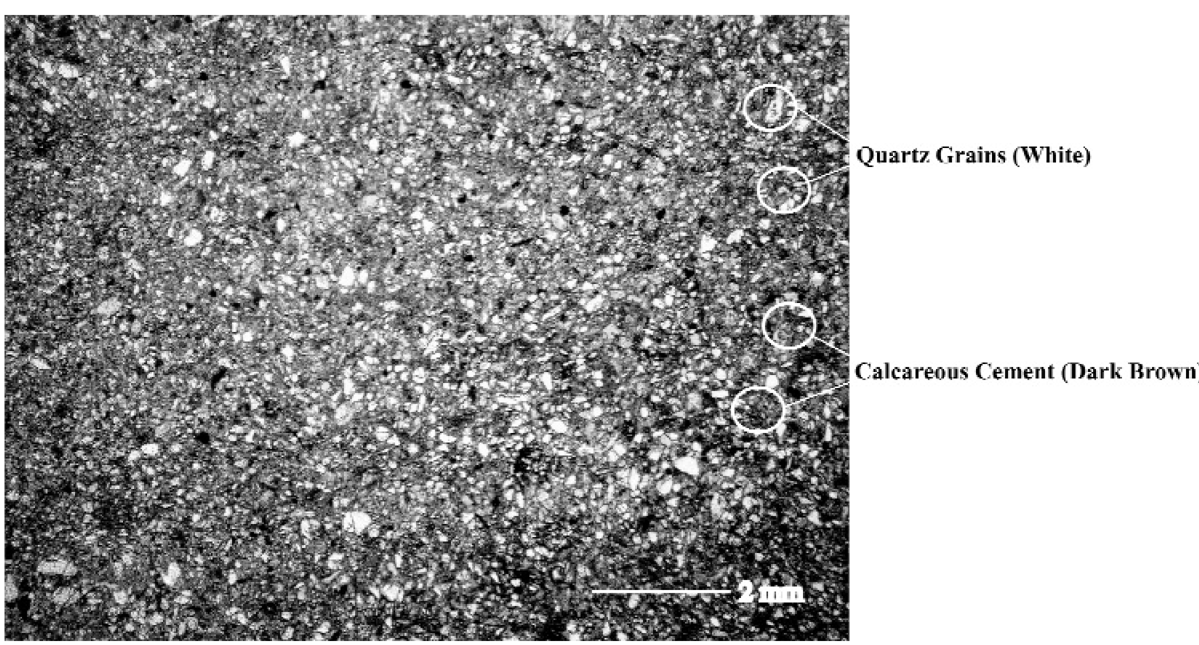


Figure 10. SEM images showing clay type in the grayish intervals. (a) Palygorskite showing typical bundle-shaped morphology, (b) Palygorskite radiating out from a smectite core. Palygorskite and Mg-smectite are common clay minerals in saline lake and coastal plain type depositional settings.

Figure 9. Photomicrograph of a representative sample from the grey horizon. The grey horizon comprises fine to medium-grained quartz embedded in a calcareous or clay matrix/cement.



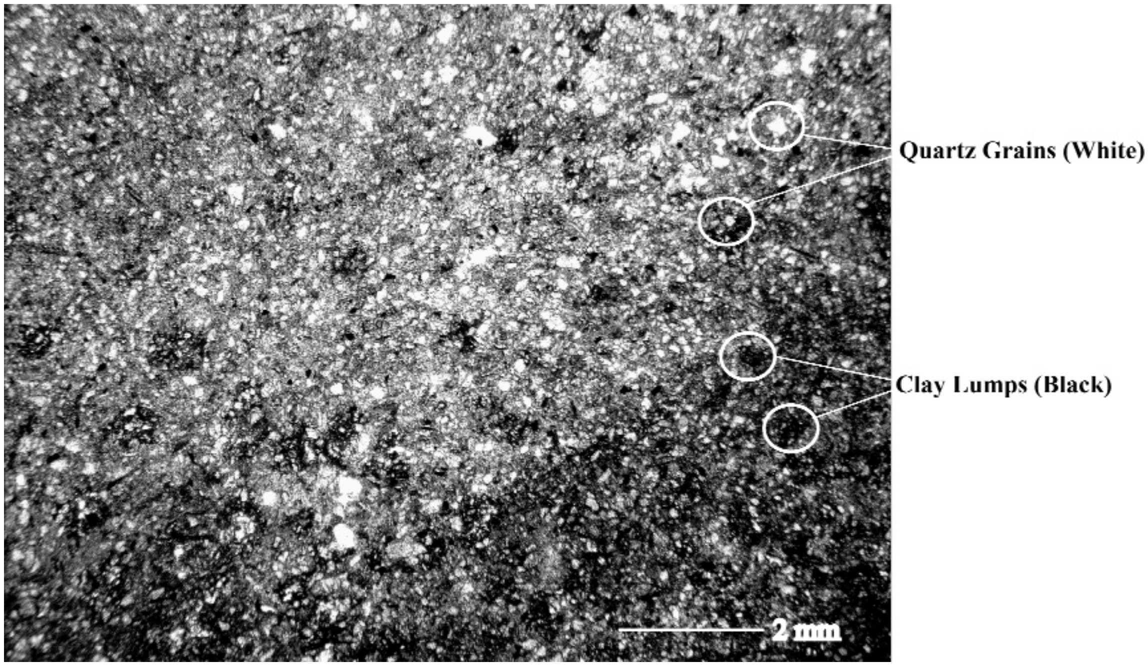


Figure 11. Photomicrograph of a representative sample from the reddish horizon. Compared to the composition of the grey horizons, the reddish horizons are made of finer grained sediments and consist dominantly of marl and clay.

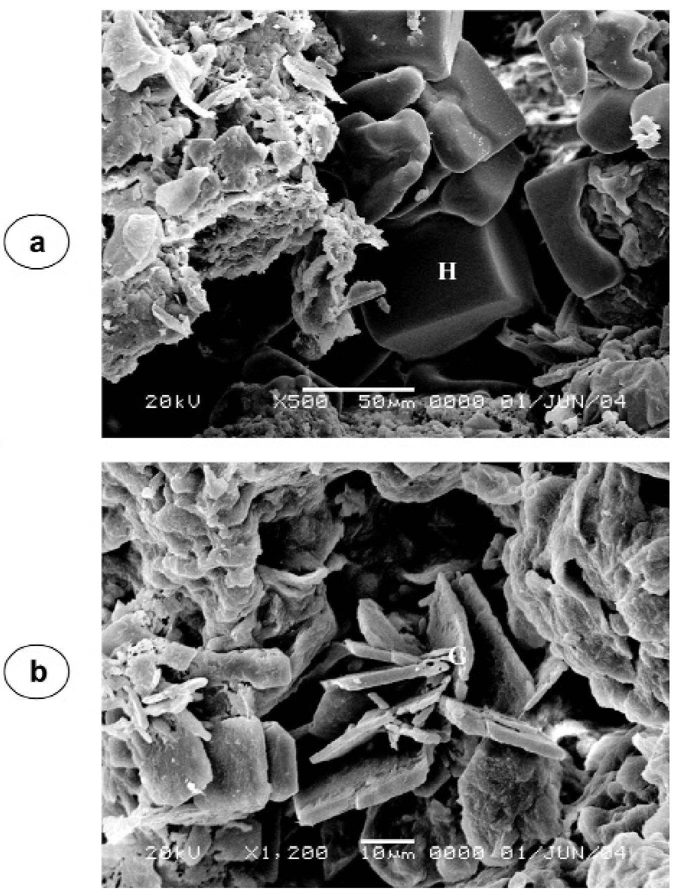


Figure 12. SEM images showing details of a sample from the reddish horizon (a & b). Note that in addition to calcite and clay, both halite (H) and gypsum (G) are also common in this horizon.

Figure 13. Different types of caves recognized in the Shedgum Plateau. (a) Joint-controlled, steep-walled caves at the escarpment face near to the cement factory north of Al Ayun (N 25º 41.62'; E 49º 29.05') approximately 10 km north of Al Hofuf. (b) A dissolution-dominated circular, flat-bottomed cave at the western face of the Jabal al Qarah, close to the wireless/microwave tower (N 25º 24.32'; E 49º 40.89').

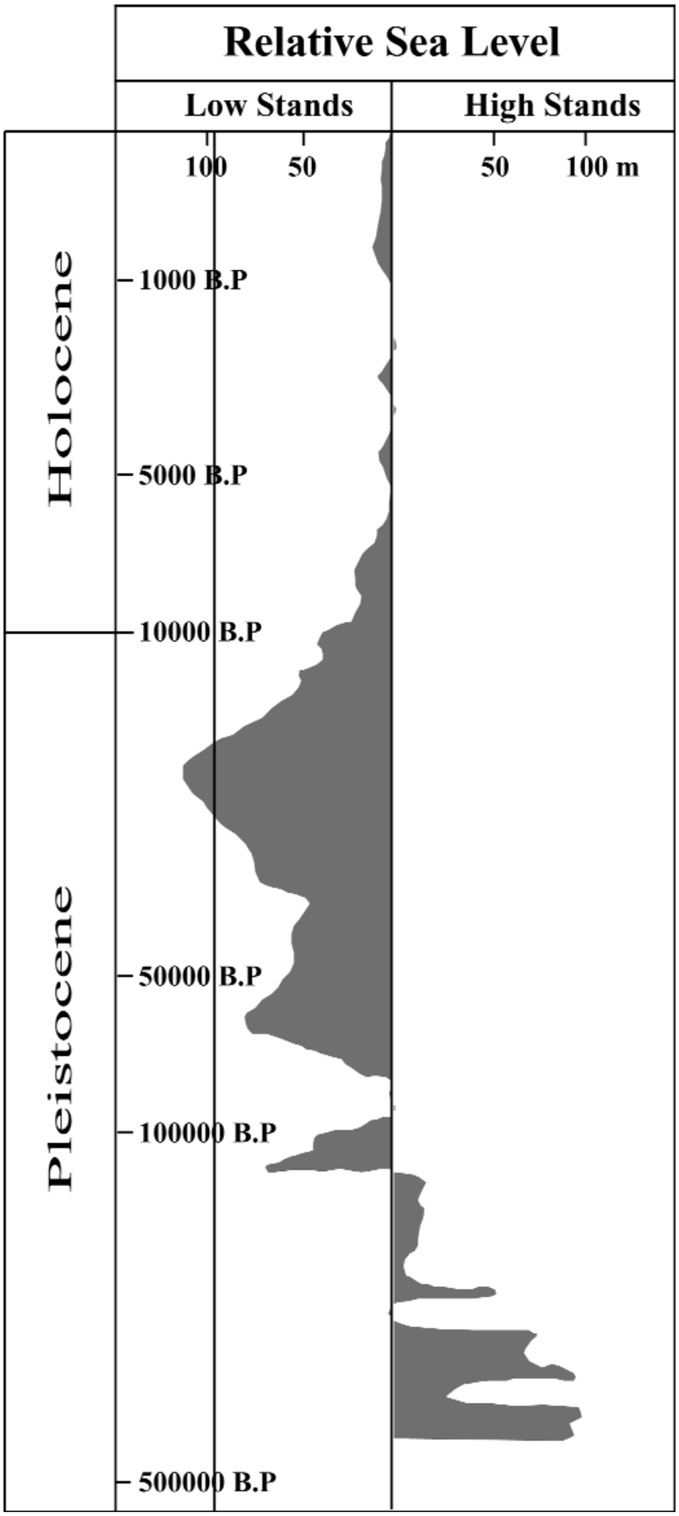


Figure 14. Quaternary sea level changes in the Arabian Gulf area. (Data source: Fairbridge, 1961; Darwish and Conley, 1990).

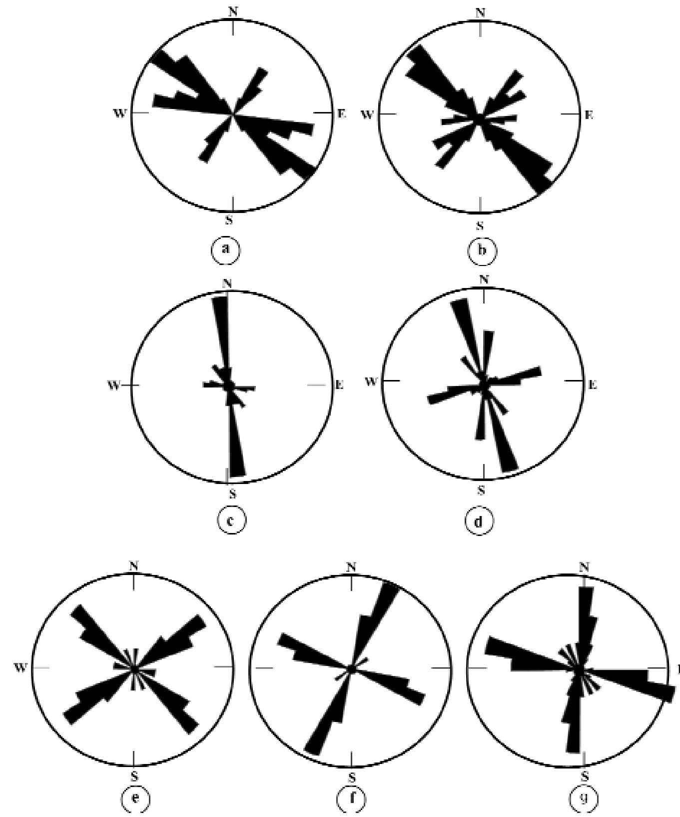


Figure 15. Orientations of the joint/fracture systems in the exposed upper Tertiary formations in the Shedgum Plateau. (a) Orientation of the major cave chambers and branches, Jabal Al Qarah, (b) Hofuf Formation, entrance of Jabal Al Qarah caves. (N 25º 24.690', E 49º 41.616'; n = 43), (c) Dam Formation. (N 25º 39.143', E 49º 29.356'; n = 39), (d) Dam Formation. (N 25º 32.871', E 49º 31.879'; n = 74), (e) Hofuf Formation. N 25º 42.621', E 49º 30.437'; n = 20), (f) Hofuf Formation. (~ 300 m east of e; n = 16), (g) Hofuf Formation. (N 25º 40.137', E 49º 28.828'). (Data source: Saner *et al.*, 2005; present study).

cave-forming processes are still in progress, suggesting normal subaerial weathering and enlargement of the joints as a dominant cave-forming process.

A DISTINCT TYPE OF SAUDI ARABIAN CAVE

Caves are common geomorphic features in any karstic terrane, and Saudi Arabia is not an exception. These caves form largely due to dissolution of limestone by slightly acidic ground water at the shallow subsurface. As noted earlier, such limestone dissolution caves are common features in limestone terranes of Saudi Arabia including the Shedgum Plateau. However, the Jabal Al Qarah caves lack many features that often characterize limestone-dissolution caves. For example, limestone-dissolution caves are often irregular in shape and contain many dripstone features like stalactites, stalagmites,

Figure 16. Surface openings in the Jabal Al Qarah cave chamber through the roof. (a) A N–S oriented straight-line opening. (b) An E–W oriented opening. Such openings usually form when erosional enlargement of the caves extends all the way to the top of the jabal.

etc. In contrast, the distribution of the majority of the Jabal Al Qarah caves is strongly controlled by the distribution of the joint/fracture systems of the host Hofuf Formation. Table 1 compares the the Jabal Al Qarah caves with other known caves in Saudi Arabia.

Conclusions

Jabal Al Qarah represents a mesa comprising the Upper Miocene to Lower Pliocene Hofuf Formation in front of the escarpment that marks the eastern edge of the As Summan or Shedgum Plateau.

The Hofuf Formation hosting the Jabal Al Qarah caves consists of an alternation of red and grey intervals of dominantly calcareous sandstone. Based on overall lithology (calcareous sandstone), and more specifically, the presence of palygorskite showing delicate morphological features, the sediments of the Hofuf Formation hosting the Jabal Al Qarah caves were deposited in a mud flat to lacustrine depositional setting.

Unlike most of the caves reported from the As Summan Plateau, formed by dissolution of limestone by ground water, the Jabal Al Qarah caves represent an above ground (street level) cave system that appears to have developed due to subaerial weathering and enlargement of the well-defined joint and fracture systems in the Hofuf Formation. Due to subaerial development, the caves in Jabal Al Qarah do not show many cave features typical of other caves in eastern Saudi Arabia.

Table 1. Comparison of the features of the Jabal Al Qarah caves with other limestone caves in northeastern Saudi Arabia.

Feature/Parameter	Jabal Al Qarah	Limestone Caves in Saudi Arabia (Benischke *et al*., 1997; Pint, 2000, 2003)
Ground position	Above the street level	Below the street level
Lithology	Calcareous sandstone and marl	Dominantly limestone and dolomite
Cave deposits	Mostly wind-blown dust and weathered debris from the cave walls	Stalactite, stalagmite, wind-blown dust and sand
Structural (joints, faults) controls	Prominent	Not commonly recognized
Role of ground water in cave development	Uncertain. Well above the regional ground water level	Dominant. Many caves still contain water
Distribution	Confined to the areas with jointed and fractured rocks	Anywhere in the karstic terrain with soluble rocks
Internal cave structure	Vertical or semi-vertical	Irregular
Surface opening	Straight continuous linear opening or isolated linear opening along a straight line	Usually circular; semi-circular and irregular

Acknowledgements

The author would like to acknowledge several individuals of the Earth Sciences Department at King Fahd University of Petroleum & Minerals (KFUPM), Dhahran, including Dr. Mustafa Hariri and Mr. Mushabbab Al Asiri for their active support in different phases of this project. Constructive review and comments by Dr. Geriant Wyn Hughes of Saudi Aramco and Mr. John Pint of the Saudi Geological Survey at Jeddah helped in clarifying few concepts and further improvements of the manuscript. We thank three anonymous reviewers for their constructive criticisms and suggestions for further improvements of the manuscript.

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John C. Landolt, Steven L. Stephenson, and Michael E. Slay – Dictyostelid cellular slime molds from caves. *Journal of Cave and Karst Studies*, v. 68, no. 1, p. 22–26.

DICTYOSTELID CELLULAR SLIME MOLDS FROM CAVES

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*Dictyostelid cellular slime molds associated with caves in Alabama, Arkansas, Indiana, Missouri, New York, Oklahoma, South Carolina, Tennessee, West Virginia, Puerto Rico, and San Salvador in the Bahamas were investigated during the period of 1990–2005. Samples of soil material collected from more than 100 caves were examined using standard methods for isolating dictyostelids. At least 17 species were recovered, along with a number of isolates that could not be identified completely. Four cosmopolitan species (*Dictyostelium sphaerocephalum*,* D. mucoroides*,* D. giganteum *and* Polysphondylium violaceum*) and one species (*D. rosarium*) with a more restricted distribution were each recorded from more than 25 different caves, but three other species were present in more than 20 caves. The data generated in the present study were supplemented with all known published and unpublished records of dictyostelids from caves in an effort to summarize what is known about their occurrence in this habitat.*

Introduction

Dictyostelid cellular slime molds (dictyostelids) are single-celled, eukaryotic, phagotrophic bacterivores usually present and often abundant in terrestrial ecosystems (Raper, 1984). These organisms represent a normal component of the microflora in soils and apparently play a role in maintaining the natural balance that exists between bacteria and other microorganisms in the soil environment. For most of their life cycle, dictyostelids exist as independent, amoeboid cells (myxamoebae) that feed upon bacteria, grow, and multiply by binary fission. When the available food supply within a given microsite becomes depleted, numerous myxamoebae aggregate to form a structure called a pseudoplasmodium, within which each cell maintains its individual integrity. The pseudoplasmodium then produces one or more fruiting bodies (sorocarps) bearing spores. Dictyostelid fruiting bodies are microscopic and rarely observed except in laboratory culture. Under favorable conditions, the spores germinate to release myxamoebae, and the life cycle begins anew. Dictyostelids are most abundant in the surface humus layer of forest soils, where populations of bacteria are the highest and microenvironmental conditions appear to be the most suitable for dictyostelid growth and development (Raper, 1984).

While the primary habitat for dictyostelid cellular slime molds (or dictyostelids) is the leaf litter decomposition zone of forest soils, these organisms are known to occur in other types of soils. Among these are soils of cultivated regions (Agnihothrudu, 1956), grasslands (Smith and Keeling, 1968), deserts (Benson and Mahoney, 1977), and both alpine (Cavender, 1973) and arctic (Cavender, 1978; Stephenson *et al*., 1991) tundra. In addition, dictyostelids have been reported from the layer of soil-like material (canopy soil) associated with the epiphytes that occur on the branches and trunks of tropical trees (Stephenson and Landolt, 1998). Dictyostelids also occur on dung and were once thought to be primarily coprophilous (Raper, 1984). However, perhaps the most unusual microhabitat for dictyostelids is the soil material found in caves. Few studies have considered the dictyostelids associated with caves. In what apparently represents the first published report of dictyostelids in caves, Orpurt (1964) reported two species (*Dictyostelium mucoroides* and *Polysphondylium pallidum*) from a cave located on Eleuthera Island in the Bahamas. Later, Waddell (1982) reported eight species from Blanchard Springs Cavern in Arkansas. One of these (*Dictyostelium caveatum*) was new to science. In the most extensive study to date, Landolt *et al*. (1992) investigated 23 caves in West Virginia. Nine species of dictyostelids were recovered, and three of these were present in at least 10 different caves. One of these three species (*Dictyostelium rosarium*) was of particular interest, since it had not been recorded from soil samples collected from above-ground sites in an earlier study of the distribution and ecology of dictyostelids in West Virginia (Landolt and Stephenson, 1990). In general, based on available data, the distribution of dictyostelids in caves appears to be rather patchy, but in the microsites where they do occur, these organisms can exhibit surprisingly high levels of abundance and diversity.

The objective of the present study was to extend the earlier investigation of dictyostelids in West Virginia caves (Landolt *et al*., 1992) to caves at a number of other localities, with particular emphasis placed on caves in the Ozark region of Arkansas, Missouri and Oklahoma (Landolt *et al*., 2005). In addition, these data were supplemented with all known published (Waddell, 1982; Landolt and Stihler, 1998; Reeves *et al*., 2000; Reeves, 2001; Nieves-Rivera, 2003) and unpublished records of dictyostelids from caves in an effort to summarize what is known about their occurrence in this habitat.

Material and methods

The caves considered in the present study are located in Alabama, Arkansas, Indiana, Missouri, New York, Oklahoma, South Carolina, Tennessee, West Virginia, Puerto Rico, and San Salvador in the Bahamas. All of these were sampled during the period of 1990 to 2005. Samples of cave substrate material, from the floor and from ledges, were collected from arbitrarily selected locations within each cave. Most samples were collected in conjunction with other cave survey work. In general, sample sites within a cave were chosen to represent the variety of different substrates available in that cave. If present, samples containing guano, plant debris or detritus were included along with mineral substrate samples. Depending upon the particular cave, samples ranged in texture from powdery dry dust or gravel to very wet clay mud. Samples were stored in sterile plastic bags, returned to the laboratory and processed as soon as possible following collection, using procedures similar to those described by Cavender and Raper (1965). In this procedure, 5–10 g of sample are suspended in sterile, distilled water to make a soil dilution ratio of either 1:10 or 1:25. An aliquot of the suspension (containing 0.02 g soil) is added to each of 2–3 plastic culture dishes containing a phosphate buffered (pH 6.0), filtered hay infusion agar. This medium is prepared by autoclaving 10–20 g of dry hay/L distilled water, filtering and adding 1.5 g KH_2PO_4, 0.62 g $Na_2HPO_4 \cdot 7H_2O$, 15 g agar/L filtrate. Each dish received approximately 0.3 mL of *Escherichia coli*, and culture plates were incubated under diffuse light at 10–25 °C. Each plate was carefully examined at least once a day for several days following appearance of initial aggregations and the location of each aggregate colony marked. When necessary, particular isolates were subcultured to facilitate identification. Nomenclature used herein follows that of Raper (1984).

Results

The data obtained from the caves examined in the present study along with other published and unpublished records of

Table 1. Summary data (obtained in the present study or reported in the literature) on caves sampled for dictyostelids. The figure given for the Ozarks represents the combined total for Arkansas, Missouri and Oklahoma.

Region	No. of caves investigated	No. of caves with dictyostelids	Percentage (%)	No. of species recovered
West Virginia [a, c]	61	58	95	12
Arkansas [b, c]	17	6	35	5
Missouri [c]	15	11	73	7
Oklahoma [c]	3	3	100	4
Ozarks (Subtotal)	35	20	57	8
Georgia [d]	2	2	100	6
South Carolina [e]	1	1	100	4
New York [c]	2	1	50	1
Indiana [c]	2	2	100	4
Tennessee [c]	3	3	100	6
Alabama [c]	4	4	100	8
Puerto Rico [c, g]	8	6	75	9
Bahamas [c, h]	5	5	100	5
Total	123	102	83	18

[a] Landolt *et al*., 1992
[b] Waddell, 1982
[c] Present study
[d] Reeves *et al*., 2000
[e] Reeves, 2001
[f] Davidson, unpublished data
[g] Nieves-Rivera, 2003, and unpublished data
[h] Landolt and Stihler, 1998

Table 2. Occurrence of dictyostelids in caves considered in the present study. The figure given for the Ozarks represents the combined total for Arkansas, Missouri and Oklahoma.

Region	Dsp[a]	Dmu	Dro	Dgi	Dmi	Dau	Ddi	Dpu	Dca	Dma	Dte	Dci	Dpo	Dvi	Pvi	Ppa	Pca	Pte	Total Species
West Virginia	41	26	16	16	17	20	6	5							6	3	1	1	12
Arkansas	2	2	3	2			1	2	1						4	2			9
Missouri	1	3	7	2				2							5	4			7
Oklahoma	1					1									1	1			4
Ozarks (Subtotal)	4	5	10	4		1	1	4	1						10	7			10
Georgia	1	1		1		2		1							2				6
South Carolina	1	1													1	1			4
New York	1																		1
Indiana	2	1					1								1				4
Tennessee		2		2	3	1		2								1			6
Alabama		4	2	3	1	1		2							4	3			8
Puerto Rico		1		2		2		3		2	1	1			1	5			9
Bahamas								5					2	2	3			1	5
Total Records	50	41	28	28	21	27	8	22	1	2	1	1	2	2	28	20	1	2	

Note: Total records refers to the number of caves from which the species in question has been recorded.

[a] Dsp = *Dictyostelium sphaerocephalum*, Dmu = *D. mucroroides*, Dro = *D. rosarium*, Dgi = *D. giganteum*, Dmi = *D. minutum*, Dau = *D. aureo-stipes*, Ddi = *D. discoideum*, Dpu = *D. purpureum*, Dca = *D. caveatum*, Dma = *D. macrocephalum*, Dte = *D. tenue*, Dci = *D. citrinum*, Dpo = *D. polycephalum*, Dvi = *D. vinaceo-fuscum*, Pvi = *Polysphondylium violaceum*, Ppa = *P. pallidium*, Pca = *P. candidum* and Pte = *P. tenuissimum*.

dictyostelids in caves are summarized in Table 1. Based on these data, dictyostelids would seem to be consistently present in the assemblages of microorganisms found in caves, with 102 of the 123 (83%) caves known to have been examined for the presence of dictyostelids yielding at least one species. In West Virginia, the region for which the most data exist, dictyostelids were recovered from 95% of the 61 caves investigated. Most records of dictyostelids in caves are from temperate North America, but these organisms also were recovered from 11 of 13 (85%) caves surveyed in Puerto Rico and the Bahamas.

At least 17 species of dictyostelids were isolated from samples of cave soil collected during the course of the present study (Table 2), along with a number of isolates that could not be identified completely. *Dictyostelium giganteum*, *D. mucoroides*, *D. rosarium, D. sphaerocephalum* and *Polysphondylium violaceum* were the most common species, and each was recorded from more than 25 different caves. Three other species (*D. aureo-stipes*, *D. purpureum* and *P. pallidum*) were recovered from more than 20 caves. Most of the other species recovered from caves were much less common, and several *(e.g.*, *D. citrinum*, *D. macrocephalum* and *D. polycephalum*) were recorded from only a single cave. Just one species (*D. caveatum*) reported in the literature from caves was not encountered in the present study. This species, recovered by Waddell (1982) from a cave in Arkansas, has not been reported since, either from caves or from aboveground sites.

Discussion

The considerable body of data compiled for dictyostelids in caves in eastern North America indicates that these organisms should be considered part of the common microflora found in cave habitats. As a general observation, the species of dictyostelids that occur in caves are much the same as those most likely to be recovered from samples of above-ground soil (especially forest soil) in the general region of the cave in question. For example, with a single exception, all of species now known from more than 25 caves are generally considered to be among the most common inhabitants of forest soils (Raper, 1984; Swanson *et al*., 1999). Interestingly, samples from caves in subtropical regions (Puerto Rico and the Bahamas in the present study) yielded species of dictyostelids (*e.g.*, *Dictyostelium citrinum* and *D. macrocephalum*) thought to have distributions centered in tropical/subtropical regions of the world (Swanson *et al*., 1999). As such, the absence of these species in caves located in temperate regions, which was the case for the vast majority of caves sampled in the present study, is not surprising.

Dictyostelium rosarium appears to be the one major exception to this general pattern. This species appears to have an unusual and rather restricted distribution in nature (Raper, 1984). It has been found in North America only occasionally in dry/saline soils above ground (Benson and Mahoney, 1977) but was reported to occur with a surprising degree of regularity in caves in West Virginia by Landolt *et al*. (1992). In the present study, *D. rosarium* was commonly recorded from caves, including additional caves in West Virginia as well as others sampled in Alabama, Arkansas, and Missouri. The relative abundance of *D. rosarium* in caves in at least temperate North America is particularly noteworthy because the species appears to be rare outside of North America. For example, only a single isolate is known from the entire Southern Hemisphere (Cavender *et al*., 2002).

Three genera are currently recognized for the dictyostelids. While two of these (*Dictyostelium* with 14 species and *Polysphondylium* with four species) appear to be well represented in cave habitats, there are apparently no records of any member of the third genus (*Acytostelium*) from cave habitats. Species of *Acytostelium* are generally smaller and more delicate than members of the other genera, and it is possible that such forms simply do not survive well in caves, for reasons that are not yet known. Evidence for such a conclusion is suggested by the apparent absence of *D. lacteum* from caves. This species is common in forest soils throughout eastern North America but also is smaller and apparently more delicate than the majority of dictyostelids known from caves.

Unlike many microorganisms, dictyostelids produce spores that appear to have a rather limited potential for dispersal. In the dictyostelid life cycle, the unicellular amoeboid cells that represent the vegetative stage aggregate and form a structure called a pseudoplasmodium, which then gives rise to one or more fruiting structures (sorocarps), each bearing one to several masses of spores (sori). Since the spores are embedded in a mucilaginous matrix that dries and hardens, they stand little chance of being dispersed by wind (Cavender, 1973; Olive, 1976). It has been demonstrated (Suthers, 1985; Stephenson and Landolt, 1992) that various animals, ranging from invertebrates to amphibians, small mammals, and birds are capable of dispersing the spores of dictyostelids by means of ingestion-defecation. For example, Stephenson and Landolt (1992) isolated dictyostelids from the fecal material of bats and suggested that the latter may introduce dictyostelids to caves. In the present study, virtually all of the caves sampled for dictyostelids were known to support populations of bats. Indeed, actual collecting of sample material was carried out in the context of studies related to monitoring the bats present in a particular cave. It is very likely that organisms other than bats can serve as vectors for dictyostelid spores. Cave crickets (*Ceuthophilus gracilipes* [Halderman]) collected from one cave in Arkansas have been demonstrated to carry dictyostelid spores on the surface of their body (Stephenson and Slay, unpub. data). Since these crickets forage in the litter layer of forests outside of the cave, it is possible that they could introduce dictyostelid spores into the cave in addition to transporting spores from one place to another within a given cave. This aspect of the dictyostelid ecology warrants additional study. A few of the caves included in the survey are visited frequently by humans, but the great majority of the caves are sparsely visited by people because of such factors as small size, difficult access or restricted access for the protection of bat colonies.

Since dictyostelids depend upon a variety of aerobic bacteria for food, almost certainly the guano produced by bats represents a factor of considerable importance, although dictyostelids were rarely recovered directly from guano piles. Limited data obtained for a series of five samples obtained from the center of a guano pile outward suggest that dictyostelids are most abundant in the zone just outside the actual pile (Stephenson *et al*., unpub. data). As such, the question of whether bats introduce dictyostelids to caves still remains problematic, but it seems likely that bats are largely responsible for providing sufficient organic material to permit dictyostelids to survive in caves. Except for deposits of guano, organic material subject to bacterial decomposition is usually sparse in caves (Dickson and Kirk, 1976). Some caves may receive additional organic input as a result of surface water flow into the cave, and in one or two caves included in this study, cave rodent activity was specifically noted by sample collectors.

In summary, although caves might seem to represent an unusual habitat for dictyostelids, they do provide environmental conditions (*i.e.*, high humidity along with stable temperatures) that are reasonably suitable for these organisms, as indicated by the data presented in this paper.

Acknowledgements

Appreciation is extended to Dr. J. C. Cavender for examining some of the dictyostelids isolated in the present study and to Dr. Paul G. Davison for providing some of the data reported herein. We thank Chuck Bitting, Rick Clawson, Steve Hensley, Steve Samoray, and Blake Sasse for assistance with collection in Arkansas, Missouri, and Oklahoma caves. The research reported herein was supported in part by a grant (DEB-0316284) from the National Science Foundation and by a grant from the Shepherd University Alumni Association.

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CHARACTERISTIC ODORS OF *TADARIDA BRASILIENSIS MEXICANA* CHIROPTERA: MOLOSSIDAE

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*The odors in a central Texas cave with a large roosting population of Mexican free-tailed bats (*Tadarida brasiliensis mexicana*) were identified and related to captive individual bats. Solid phase microextraction (SPME) was used to sample and concentrate the volatile organics from the cave and individual bats. Odors were detected organoleptically and simultaneously quantified and identified. The characteristic odor for* T. b. mexicana *is due principally to 2'-aminoacetophenone.*

Introduction

Olfactory cues play many roles in the lives of bats, from feeding to social communication, kin recognition and group identification (Suthers, 1970; Gustin and McCracken, 1987; Loughry and McCracken, 1991; De Fanis and Jones, 1995; Bloss, 1999; Bouchard, 2001). Some bats prefer odors of roost mates, and both sex discrimination and roostmate recognition have been associated with the use of olfactory cues (De Fanis and Jones, 1995; Bouchard, 2001; Bloss *et al*., 2002). Male quality is associated with olfactory cues in *Saccopteryx bilineata* (Voight and von Helversen, 1999; Voight, 2002).

As with many other mammals, body odors derive from a variety of sources on bat's bodies. Urine, feces, glandular products and fermentation products all have been associated with typical odors (Voight and von Helversen, 1999; Scully *et al*., 2000; Voight, 2002).

Female bats use chemical cues to identify their young among millions of pups, and males can discriminate their own odors from those of other males (Gustin and McCracken, 1987). The roosts of bats often assume the odors of the residents, and Mexican free-tailed bats (*Tadarida brasiliensis mexicana*) are a good example because many bat biologists readily use the characteristic odor to recognize roosts. Human observers can sense the characteristic roost odor at considerable distances from roosts. The distinctive "corn tortilla" or "taco shell" aroma is a sure indicator of a *T. brasiliensis* roost. Closer to the roost, the overall odor is stronger and at the same time more complex. Here the single taco shell descriptor is no longer adequate to describe the roost (Wright *et al*., 2005).

The goals of our study were first to use GC-MS to identify the compound in the colony odor responsible for an aroma similar to taco shells, and second, by sampling known roosts and bats' bodies, to determine where the odor originates. We collected data from a known cave roost and from captive bats and their roosts.

Methods and Materials

We sampled organic compounds in the Bracken Cave environment via an artificial ventilating shaft that had a continuous draft of air from the interior. Five SPME fibers (Carboxen/PDMS, 85 µm, 2 cm length, 23 gauge, on Stableflex™ Supelco, Supelco Park, Bellefonte, PA, 16823-0048) each were suspended in the airflow from the cave for 120 minutes on June 30, 2001. We made four additional collections on August 31, 2001. After sampling, the fibers were wrapped in conditioned aluminum foil and analyzed within 1–2 days after collection.

In 2001, we sampled fabric roosting pouches of five captive *T. brasiliensis* originating from central Texas on September 7 (2 roosts), September 24 (1 roost) and October 12 (2 roosts). Samples were collected by inserting an SPME fiber into each cloth roosting pouch for various lengths of time. The cloth pouches were used by only one individual but were open to ambient air. Unused pouches also were sampled and analyzed as blanks.

We collected urine samples from captive *T. brasiliensis* bats originating from central Texas on September 16, 2001 (3 specimens) and on September 30, 2001 (5 specimens). For comparison, we also collected urine samples from a female *Lasiurus cinereus* on October 30, a female *Lasiurus intermedius* on October 31, a male *Nycticeius humeralis* on October 30, and a male *Myotis velifer* on October 30. The bats' urine was collected in glass pipettes and the samples were placed in 40 ml Eagle-Picher EPA vials. We sampled the gular glands of two captive male *T. brasiliensis* and the anus of one captive male *T. brasiliensis* on September 16, 2001. These samples also were placed in EPA vials. We inserted SPME fibers into the vials through the vial septa and exposed them to the urine and glandular volatiles for various lengths of time.

Table 1. Selected volatile organic compounds and principal odors of Bracken Cave.

Retention Time (min)	Identification (odor)	Retention Time (min)	Identification (odor)
1.74	acetaldehyde (fermented)	17.13	acetylpyrazine (roasted)
1.76	methyl mercaptan (skunky)	17.21	decanal
2.02	Not identified (foul)	17.42	isovaleric acid (foul, rancid)
2.16	carbon disulfide	17.83	acetophenone
3.89	2 & 3-methylbutanal (foul, aldehydic)	18.27	methionol
4.13	benzene	18.28	3-methylfuranone
6.71	dimethydisulfide	18.39	1-chloro-4-methoxybenzene
6.73	1-aza-1,3-butadiene	18.43	geraniol
7.01	isoxazole	18.69	2,6,6-trimethylcyclohex-2-en-1,4-dione
7.34	isobutanenitrile	18.86	acetamide
7.41	hexanal	19.58	2-methylpropanamide
8.77	pyrazine	19.80	4-ethyl-3-methyl-2H-pyran-2-one
9.07	2,3-dihydro-4-methylfuran (sweet, phenolic)	20.51	2-chlorophenol
9.35	an amine	20.52	ethyl decanoate
9.98	an amine	20.61	hexanoic acid
10.24	methylpyrazine	20.85	guaiacol
10.71	2-propanone oxime	21.05	butamide
10.75	N-nitrosodimethylamine	21.52	thyjopsene (musty)
11.06	beta-myrcene	21.61	phenylethyl alcohol
12.08	dimethylpyrazine isomers (roasted, nutty)	21.63	methylcumate
12.15	limonene	22.17	benzoacetonitrile
12.19	1-octen-3-one (earthy)	22.66	not identified (moldy)
12.38	octanal (sweet, aldehydic)	23.12	phenol
12.61	cumene	23.72	p-anisaldehyde
13.22	acetic acid (sour)	23.73	1,2,3,4-tetrahydro-1,6-dimethyl-4-(1-methylethyl) naphthalene (grainy, floral)
13.26	Dimethyltrisulfide (skunky, foul)		
13.75	trimethylpyrazine	23.92	5-methyl-2-pyrazinylmethanol
14.58	1H-pyrrole (musty, burnt)	24.03	4-(2,6,6-trimethyl-1-cyclohexenyl)-3-buten-2-one (floral, herbaceous)
14.59	2-nonanone		
14.95	nonanal	24.02	m-cresol
15.00	2-methyl-6-vinyl-pyrazine	24.61	p-cresol (musty)
15.06	propionic acid	25.03	2,4-dimethylquinazoline
15.25	benzaldehyde	25.62	2,4-dichlorophenol
15.83	isobutyric acid	25.65	2,6-dimethylphenol
16.29	2-pentylthiophene	26.22	2’-aminoacetophenone (taco shell)
16.64	benzonitrile	27.95	cedrol
16.66	dihydro-5-methyl-2(3H)-furanone	27.45	6-methyl-2H-1-benzopyran-2-one
16.79	camphor	28.85	indole
16.81	butyrolactone	28.91	benzoic acid
16.98	trans-2-nonenal	31.42	1-(2-aminophenyl)-1-butanone

Table 2. Roosting Odors *(Tadarida brasiliensis)*

No.	Retention Time (min)	Male A	Male B	Male C	Female A	Female B	Identification
1	8.60	Not described				Foul	
2	12.18			Roasted	Meaty	Nutty, roasted	
3	12.46		Sweet, aldehydic		Sweet		
4	12.59			Roasted		Roasted, savory	
5	13.16		Not described		Foul, sour	Acidic	
6	14.89				Sweet	roasted	
7	16.29		Foul, musty		Not described		
8	16.53		Soapy, aldehydic	Sweet, floral	Sweet, aldehydic	Sweet, floral	
9	16.74				Foul, soapy	Foul	
10	17.30		Foul acidic	Stale	Acidic	Acidic	
11	17.84		Foul			Musty	
12	18.64				Sweet	Foul	
13	19.26		Foul			Floral	
14	20.32		Meaty		Animal	Resiny	
15	22.26		Not described	Herbaceous		Herbaceous	
16	23.89		Musty	Sweet			
17	24.01		Aldehydic		Sweet, aldehydic		
18	26.22	Taco shell	Taco shell	Taco shell	Taco shell	Taco shell	2'-aminoacetophenone
19	31.40				Sweet		1-(2-aminophenyl)-1-butanone

We performed odor analysis on a standard configuration AromaTrax™ instrument (Microanalytics, Round Rock, TX). The inlet for the thermal desorption of the SPME fibers was equipped with a Merlin Microseal™ septum. Odor volatiles were separated on the AromaTrax™ system using the standard arrangement of tandem BP1 and BP20 columns and detected simultaneously with photoionization (PID), mass spectral (MS) and olfactory detectors. We recorded the sniff port olfactory response using AromaTrax™ odor tracking software.

To identify the hundreds of volatiles in the Bracken cave samples, we used the multidimensional gas chromatography (MDGC) capability of the AromaTrax™ system to enhance separation and identification of individual odor compounds. Identification of odor compounds was made by use of Benchtop/PBM Software Library Search program (Palisade Corp., N. Y.). Simultaneous detection of the resolved odors was done using PID, MS and olfactory detection.

Results

During the time when we obtained our samples, Bracken Cave was occupied by an estimated 20 million Mexican free-tailed bats. Samples from both dates gave essentially the same odor compositional results. We detected hundreds of volatile compounds and present data for the principal odors detected (Table 1). In the samples, 2'-aminoacetophenone was the most concentrated compound in the air exhausting from the roost. This also was the most intense odor sensed at the sniff port during GC-O analysis and the odor most characteristic of the cave roost. The next most intense odors are the earthy odor of 1-octen-3-one, the phenolic odor of 2-chlorophenol and the floral or herbaceous aroma of the tentatively identified 4-(2,6,6-trimethyl-1-cyclohexen-1-yl)-3-buten-2-one.

Roost pouches of five captive *T. brasiliensis* corrected for odors common to unused pouches indicated the dominant presence of 2'-aminoacetophenone (taco shell) for all five individuals (Table 2). One male had two detectable odors while others had seven to 12 odors. Five of 19 odors from individual profiles were among the major odors from Bracken Cave including octanal, acetic acid, isovaleric acid, 4-(2,66-trimethyl-1-cyclohexenyl)-3-buten-2-one and 2'-aminoacetophonone (Table 1).

All seven *T. brasiliensis* had the characteristic taco shell odor of 2'-aminoacetophonone in their urine (Table 3). Except for acetic acid and butyric acid detected in most samples, there was considerable variation in other odor compounds among the seven bats' urine. Ten of the odors found in urine samples also were found in roosting pouches.

We did not find the odor of 2'-aminoacetophenone in the urine of *Lasiurus cinereus*, *Lasiurus intermedius*, *Nycticeius humeralis* or *Myotis velifer* (Table 4). *Lasiurus cinereus* had a strong characteristic amine odor identified as trimethylamine, but no single strong characteristic odor was detected from *Lasiurus intermedius*, *Nycticeius humeralis* or *Myotis velifer*.

We found only acetic acid and another somewhat sour odor in the sample from the gular gland of a male *T. brasiliensis* while gular gland extract from a second male *T. brasiliensis* had sour acetic acid propionic acids, a nutty pyrazine odor and 2'-aminoacetophenone. The other odors we detected also were present in the unused roosting pouch material.

Table 3. Urine Odors (*Tadarida brasiliensis*).

Retention Time (min)	Female A	Female C	Female D	Male A	Male A (anus)	Male B	Male D	*Identification*
6.62	Foul							Trimethylamine
7.01						Foul		
7.40						Not described		
8.51	Not described							
8.96		Savory Pyrazine						
10.02			Sweet			Not described		
10.61			Sweet					
11.80				Savory				2, 5-dimethylpyrazine
12.17	Sour							
12.28		Savory	Earthy	not described	Earthy	Earthy, foul	Musty, foul	
12.36		Foul				Foul		
12.60		Sweet						
13.28	Sour	Sweet	Acidic	Acidic	Acidic	Sour		Acetic acid
14.58							Sweet	Dichlorobenzene
15.10	Not described	Not described		Not described				
15.35		Foul			Foul	Musty, foul		
15.47						Sweet		
16.12	Foul							
16.56	Sour, acidic			Acidic	Acidic	Foul, acidic	Sweet	Butyric acid
17.05		Aldehydic						
17.30						Sour, acidic		
17.55		Not described						
19.15	Foul							
19.87	Sour							
21.32		Aldehydic						
21.65					Floral	Sweet		Phenylethyl alcohol
23.70		Not described				Animal	Not described	
23.90		Not described			Not described			
26.01		Not described						
26.26	Taco shell	Taco shell	Taco shell	Taco shell	Taco shell	Taco shell	Taco shell	2'-aminoacetophenone
31.53	No odor	No odor	No odor	No odor	Not described	No odor	Slight odor	1-(2-aminophenyl)-1-butanone

DISCUSSION

Our data indicate that 2'-aminoacetophenone is the principal odorant responsible for the characterisitic taco shell odor of *Tadarida brasiliensis mexicana* roosts. This odor carries in the air for a considerable distance from the roost and is readily recognized by humans because of its unique character. It also may be used by the bats to identify their roosts. The fact that 2'-aminoacetophenone is a polar molecule that is strongly absorbed on solid surfaces and dust particles (Wright *et al*., 2005) means that it accumulates in the roost and, over time, also is concentrated on surfaces around the roost. The odor can be quite intense when the ambient temperature is high and when local surfaces are wet with rain or other moisture, leading to displacement of the compound into the air (Wright *et al*., 2005).

There are many other odorants present that contribute to the roost odor. One of these is the polar odorant p-cresol. P-cresol acts in a similar way to 2'-aminoacetophenone in terms of its absorption and desorption properties. Most of the odors, however, have less polarity than 2'-aminoacetophenone or p-cresol and do not accumulate on surfaces to the same degree. They generally dissipate after traveling a short distance from the roost. Near the roost, the combination of all the odors is very intense and not well tolerated by humans. Further from the roost, only a few polar odorants dominant.

A significant source of 2'-aminoacetophenone is *T. brasiliensis* urine. In our study, four other species of bats (*Lasiurus cinereus*, *L. intermedius*, *Nycticeius humeralis*, and *Myotis velifer*) did not have detectable levels of 2'-aminoacetophenone and therefore had no taco shell odor.

One of several metabolites of skatole (3-methylindole), 2'-aminoacetophenone, is a metabolite of tryptophan and is produced in the gut of many animals by microbial action (Diaz, *et al*., 1999). Skatole is known to be a pneumotoxin in domestic animals (Diaz, *et al*., 1999), and this property may be important for understanding the chemical makeup of the roost environment. If skatole is toxic to *Tadarida brasiliensis mexicana*, then the accumulation of this compound from 20 million bats in a restricted area could cause health problems for that population. The fact that skatole is not detected under the conditions of analysis in the Bracken Cave roost may mean it is effectively metabolized by microbial action somewhere in the environment or within the bats themselves, thus reducing this potential health hazard for the bats.

Table 4. Urine Odors (select species).

Retention Time (min)	*Lasiurus cinereus* (female)	*Lasiurus intermedius* (female)	*Nycteceius humeralis* (male)	*Myotis velifer* (male)	*Identification*
1.67	Amine				Trimethylamine
2.17	Amine				
3.39		Not described			
4.83	Must				
5.08	Musty				
6.40		Not described		Not described	
6.68				Not described	
7.54	Foul				
8.81			Foul		
12.10			Not described	Musty	
12.24	Musty				
13.28	Acidic	Foul	Acidic	Acidic	
15.27	Not described	Not described	Not described	Not described	Acetic acid
16.55	Acidic	Acidic, rancid			
20.81		Aldehydic		Floral	
21.47	Not described			Floral	
22.35				Sweet	
26.26	Not detected	Not described	Not detected	Not detected	2'-aminoacetophenone

Considering the high concentration of 2'-aminoacetophenone in the Bracken Cave roost and the apparent good health of the 20 million bats in the colony, 2'-aminoacetophenone does not appear to pose a health risk to *T. brasiliensis*. Subsequent work may lead to answers to the larger question of what factors contribute to creating and maintaining the chemical composition of ambient air in long established confined animal areas such as this cave, which could have commercial application in domestic animal production. In addition, the odor collection technique used in this study has implications for the identification of otherwise inaccessible bat roosts.

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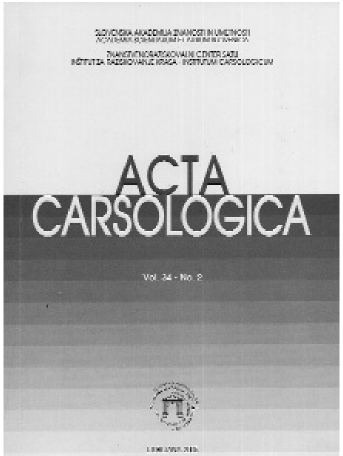

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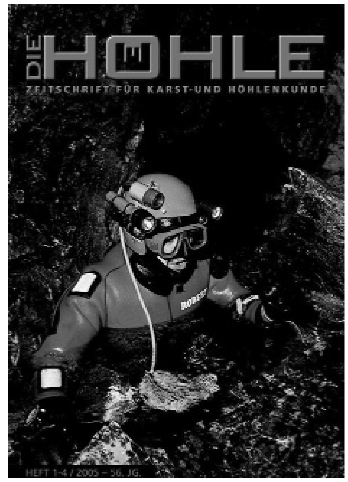

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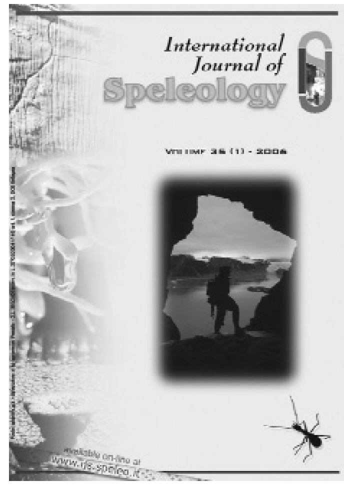

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Relationships between deflector faults, collapse dolines and collector channel formation: some examples from Slovenia. Šušteršič, France, 1–11 (Re-published from: *Speleogenesis and Evolution of Karst Aquifers* 1 (3), www.speleogenesis.info).
Salt ingestion caves. Lundquist, Charles F. and Varnedoe, William W., Jr., 13–18, (Paper presented during the 14th International Congress of Speleology, Kalamos, Greece, August 21–28, 2005).
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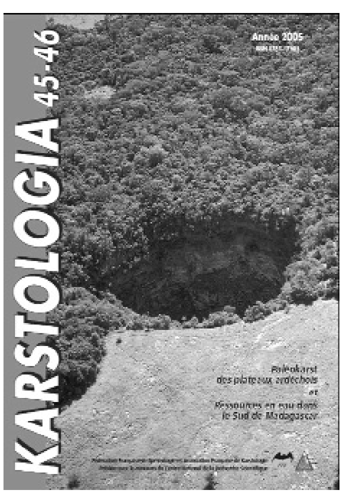

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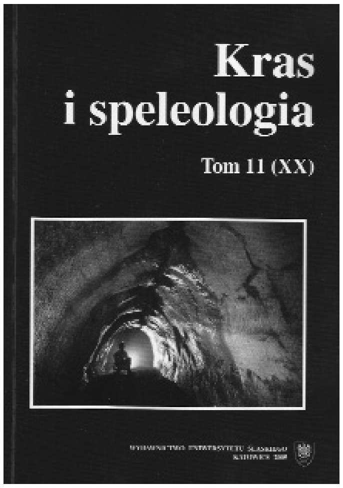

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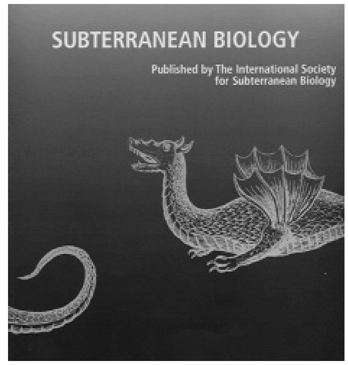

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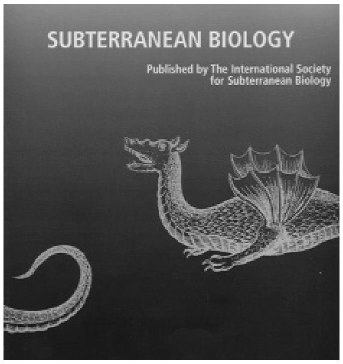

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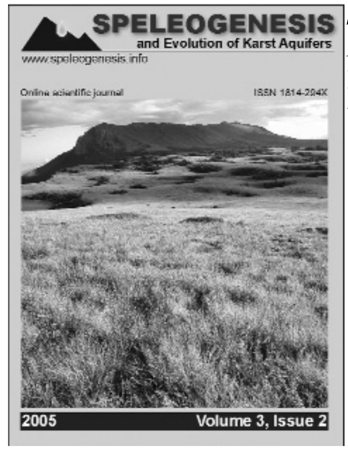

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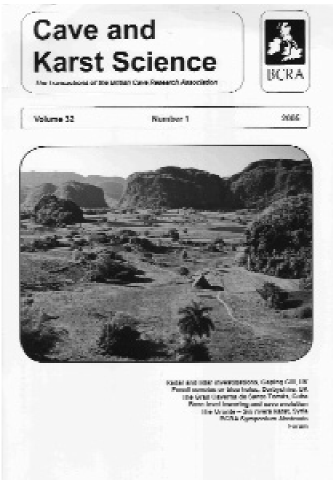

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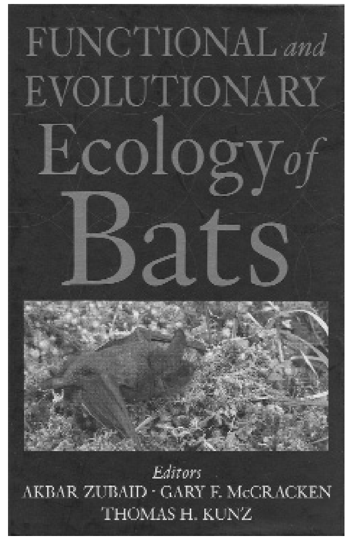
BOOK REVIEWS



Functional and Evolutionary Ecology of Bats

Akbar Zubaid, Gary F. McCracken, and Thomas H. Kunz (eds.), 2006, Oxford University Press, New York, 342 p. ISBN 9-780195-154726, hardcover, 6¼ 9½ inches, $74.50.

Based primarily on papers presented at the 12th International Bat Research Conference (August 2001, Universiti Kebangsasn Malaysia, Kuala Lumpur), Functional and Evolutionary Ecology of Bats highlights many of the innovative methodologies in current use for the study of these elusive and secretive mammals. With 39 invited contributors, this text presents a wealth of detailed information about the interaction of bats and their environment. Chapters are well written and nicely illustrated with clear and relevant graphs, tables, or figures. Each chapter is well referenced.

The book is divided into three sections. Section I focuses on aspects of physiological ecology, emphasizing energetics and metabolism, thermoregulation, and hibernation. Section II presents various aspects of functional anatomy, notably tooth structure, wing form and function, aspects of quadrupedal locomotion, and evolution of skull morphology in relation to feeding behavior in fruit bats. Section III is a consideration of roosting ecology and population biology, including discussions of population genetics, life-history traits, social behavior, mating systems, and roosting ecology.

Throughout the book, species-specific aspects of anatomy, physiology, energetics, and behavior are considered in relation to the animal's environment and lifestyle. Adaptations are discussed with respect to potential benefits and costs. The usefulness of various models in the study of energy metabolism and temperature regulation is presented and put into perspective to habitat selection. The importance of micro- and macrohabitats—both cave and non-cave—is stressed.

In considering various aspects of cave environments in relation to roost suitability and energy metabolism of bats, this volume should have broad appeal to anyone interested in the intricacies of cave biology. It will be of particular interest to environmental physiologists, ecologists, behaviorists, mammalogists, evolutionary biologists, and lay readers with a back-ground in biology and an interest in structural and functional design (i.e., biological form and function). This is an invaluable reference work for bat biologists that calls attention to some of the modern technological breakthroughs being made in the study of bats.

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International Journal of Speleology: 40 Years of Speleological Science

CD ROM reprint compiled by Jo De Waele, 2005. €8 in Europe, €12 elsewhere. Information at www.ijs.speleo.it.

The International Journal of Speleology is the official journal of the International Union of Speleology. It is published by the Società Speleologica Italiana. The full contents of the first forty years of the journal, 1964–2004, were published on a CD for the Fourteenth International Congress of Speleology in Greece in August 2005. The CD comprises 33 volumes. While there have always nominally been four numbers per volume, only volume 6 was actually published in four issues, and there are 59 issues in all. The CD also contains a *Manual of Karst Water Analysis*, by Wieslawa Ewa Krawczyk, undated but apparently from the early nineties. During its early years, the journal was predominant devoted to biospeleology, but more recently all aspects of speleology have been equally represented. Notable single-topic issues include "Symposium on Speciation and Adaptation in Cave Life," published in two parts in volume16 number 1/2 and 17 1/4 (1987–88), "Gypsum Karst of the World," 25 3/4 (1996), and "Proceedings of the Eighth International Symposium on Vulcanospeleology," 27 1/4 (1998).

The CD is readable on both Windows and Macintosh computers and requires a web browser and Adobe Acrobat Reader. The Flash player is also required, but it isn't clear how important it is for anything other than the unnecessary multi-media auto-run file that executes when the CD is mounted. This could be bypassed by directly opening the file *index.htm*, which contains fields allowing searches by issue, author, or word in the titles, abstracts, or keyword lists of all the papers. The searches, however, require special database engines included on the CD, and whether these will work on whatever computer you have five years from now is questionable. Fortunately, the database of information, including pointers to the articles in the 486 MB of PDF files in directory *pdf/*, is present as an ordinary text file *db/articles.xml* or *data/articles_mac.xml*, so you could do simple searches with the Find command on any word processor. Where necessary, all of the titles and abstracts have been translated into English for the database, which facilitates the search but makes it impossible to tell what language the article will turn out to be in. The PDF files of the articles will probably remain readable as long as you have a computer that can read data CDs at all, maybe another twenty years.

Except for the final two volumes, for which the original computer files were available, the PDF files for all articles consist of grayscale facsimile scans. Few pages of the journal have actually included grayscale illustrations, and space limitations and the use throughout of grayscale images have required that the scans be only 100 dots per inch, which is marginal for the text, especially in the small text used for footnotes and captions, and is inadequate for some of the illustrations. I hope that the original scans of thousands of pages were made and archived at a higher resolution, so that it won't eventually have to be done all over again. I was able to produce smaller files by scanning some old papers myself at 200 dpi black-and-white bitmap for the text and 400 dpi, either bitmap or grayscale as needed, only for the illustrations.

All of the content of the CD and the search capability are also free at *www.ijs.speleo.it*, and papers from new issues are being added as they are published. However, the CD is inexpensive and can be ordered on-line with a credit card at the same web site, so I recommend buying a copy. Any one of the single-topic issues would be worth the price.

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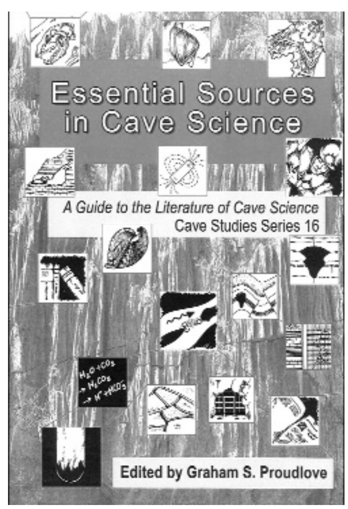

Essential Sources in Cave Science: A Guide to the Literature of Cave Science

Graham S. Proudlove (ed.), 2005. British Cave Research Association, Cave Studies Series 16, 56 p. ISBN 0-900-265-31-0, softbound, 8.1 11.5 inches, £4.50, plus postage. Orders and inquiries: Ernie Shield, Village Farm, Great Thirkleby, Thirsk, Great Britain, Y07 2AT. See publications-sales@bcra.org.uk.

The British Cave Research Association (BCRA) is the scientific arm of the British Caving Association. Essential Sources in Cave Science is an addition to their Cave Studies Series, which consists of introductory publications aimed at two targets: the sport caver who has become interested in scientific speleology, and karst specialists who need to know the major references to work outside their own field. This booklet provides a welcome service to both groups.

An introductory overview describes the scope of cave science and explains the referencing system. In this book the subject is divided into the following sections, each is contributed by a well-known specialist in the field: Geology (Dave Lowe), Geomorphology (Tony Waltham), Hydrology and hydrogeology (Chris Groves), Chemistry (Simon Bottrell), Geophysics (Phil Murphy and Tony Waltham), Radon physics (Clark Friend), Communication in caves (David Gibson), Radiolocation (David Gibson), Other aspects of physical speleology (Graham Proudlove), Speleogenesis (Dave Lowe), Minerals and speleothems (Charlie Self), Paleo-environments (Andy Baker), Biology (Graham Proudlove), Bats (John Altringham), Archaeology and paleontology (Andrew Chamberlain), Conservation and management (Graham Price), and Speleology (Ric Halliwell).

Each category has an introduction explaining the nature of the topic and why it is important, as well as an indication of progress in the field and where the field is headed. The main body of each section is a list of published references organized by author. A very useful feature is a brief description of each publication that indicates its strong points. The book also includes a list of periodicals published by speleological societies, as well as references to their Web sites. A concluding section by Dave Checkley describes the BCRA Cave Research Initiative, which invites members to participate in a variety of cave-science projects.

The reference lists are international in scope and appear to include the most significant publications, although, in keeping with the likely readership, with a strong tilt toward the British literature. Readers with no access to a large university library may have difficulty finding some of the publications. However, each section also includes a highly relevant list of Web-based resources. Who would want to miss browsing the Web site of the Explosives User Group?

The most direct competition is the karst bibliography edited by Northup *et al*. (1998). Although it is much more complete than the BCRA booklet, it obviously does not include publications from the last decade. Other sources of information on karst literature include the recent encyclopedias edited by Gunn (2004) and by Culver and White (2005). All three books are massive and scholarly. In contrast, the slender BCRA publication is less expensive, highlights more clearly the most significant publications, and is probably more inviting to the average caver.

Although this book is aimed at general cavers and karst scientists, it would also be a useful guide for professionals who are unfamiliar with karst but who need to know important sources in karst science to apply to their own fields. In addition it serves as a status report on the progress that has been made in cave science.

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Northup, D.E., Mobley, E.D., Ingham, K.L., and Mixon, W.W., eds., 1998, A guide to the speleological literature of the English language, 1794-1996: St. Louis, Cave Books, 539 p.

LONG CAVES OF THE UNITED STATES

Compiled by Bob Gulden

No.	Cave Name	State	Length Miles	Length Meters	Depth Feet	Depth Meters
1	Mammoth Cave System	Kentucky	367.000	590629	379	115.5
2	Jewel Cave	South Dakota	135.570	218179	632	192.6
3	Wind Cave	South Dakota	120.490	193820	664	202.4
4	Lechuguilla Cave	New Mexico	116.380	187295	1604	488.9
5	Fisher Ridge Cave System	Kentucky	109.284	175876	356	108.5
6	Friars Hole Cave System	West Virginia	45.539	73288	628	191.4
7	Kazumura Cave [Lava Tube]	Hawaii	40.700	65500	3614	1101.5
8	Organ (Greenbrier) Cave System	West Virginia	39.500	63569	486	148.1
9	Blue Spring Cave [Saltpeter]	Tennessee	33.390	53736	233	71.0
10	Martin Ridge System (Wig.,Jackpot,Martin)	Kentucky	32.239	51884	314	95.7
11	Crevice Cave	Missouri	28.201	45385	—	—
12	Cumberland Caverns [Saltpeter]	Tennessee	27.616	44444	200	61.0
13	Scott Hollow Cave	West Virginia	27.000	43452	571	174.0
14	Carlsbad Cavern	New Mexico	25.560	41135	1035	315.5
15	Sloans Valley Cave System	Kentucky	24.640	39654	240	73.2
16	Xanadu Cave System	Tennessee	23.799	38301	230	70.1
17	Hellhole	West Virginia	23.123	37213	519	158.2
18	The Hole (Boggs Cave)	West Virginia	23.003	37020	225	68.6
19	Omega System	Virginia	22.840	36757	1263	385.0
20	Coral Cave System	Kentucky	22.560	36307	340	103.6
21	Sugar Run Cave System	Virginia	22.500	36210	718	218.8
22	Binkley's Cave System	Indiana	22.097	35562	140	42.7
23	Hidden River System (Hicks Cave)	Kentucky	21.100	33957	160	48.8
24	Culverson Creek Cave System	West Virginia	20.820	33507	300	91.4
25	Lilburn Cave	California	20.810	33490	508	154.8
26	Blue Spring Cave	Indiana	20.810	33490	140	42.7
27	Lost River Cave System	Indiana	20.050	32267	87	26.5
28	Chestnut Ridge Cave System	Virginia	20.030	32235	804	245.1
29	Honey Creek Cave	Texas	19.947	32101	124	37.8
30	Leon Sinks Cave System [Under Water]	Florida	18.939	30479	240	73.2
31	Moore Cave System (Berome & Tom)	Missouri	18.000	28968	—	—
32	Windymouth (Wind) Cave	West Virginia	18.000	28968	—	—
33	Fitton (Beauty) Cave	Arkansas	17.500	28164	—	—
34	Thornhill Cave System	Kentucky	17.232	27732	—	—
35	Coldwater Cave	Iowa	17.005	27367	80	24.4
36	Kipuka Kanohina (Kula Kai Caverns) [Lava Tube]	Hawaii	16.500	26554	762	232.3
37	McClung Cave System	West Virginia	16.400	26393	200	61.0
38	Butler-Sinking Creek System	Virginia	16.010	25766	624	190.2
39	Mystery Cave System	Missouri	15.842	25495	—	—
40	Rumbling Falls Cave.	Tennessee	15.695	25259	474	144.5
41	Fern Cave (597)	Alabama	15.630	25154	536	163.4
42	Mountain Eye Cave System [Saltpeter]	Tennessee	15.587	25085	300	91.4
43	Nunley Mtn.Cave System (Maria Angela Grotto)	Tennessee	15.152	24385	350	106.7
44	Cave Creek Cave System	Kentucky	15.010	24156	170	51.8
45	Foglepole Cave	Illinois	15.000	24140	—	—
46	Benedicts (Persinger) Cave	West Virginia	14.746	23731	254	77.4
47	Big Horn - Horsethief Cave System	Wyoming/Montana	14.615	23521	171	52.1
48	Rimstone River Cave	Missouri	14.200	22853	—	—
49	Powell's Cave System	Texas	14.199	22851	75	22.9
50	Bone - Norman Cave System	West Virginia	14.118	22721	186	56.7
51	Emesine Cave (1881 System) [Lava Tube]	Hawaii	12.890	20744	1433	436.8
52	Mystery Cave System	Minnesota	12.790	20584	101	30.8
53	Big Bat Cave	Kentucky	12.680	20406	—	—

DEEP CAVES OF THE UNITED STATES

Compiled by Bob Gulden

No.	Cave Name	State	Length Miles	Length Meters	Depth Feet	Depth Meters
1	Kazumura Cave [Lava Tube]	Hawaii	40.700	65500	3614	1101.5
2	Umi'i Manu System [Lava Tube]	Hawaii	2.415	3887	1869	569.7
3	Hue Hue Cave [Lava Tube]	Hawaii	6.711	10800	1623	494.7
4	Lechuguilla Cave	New Mexico	116.380	187295	1604	488.9
5	Columbine Crawl	Wyoming	2.301	3703	1551	472.7
6	Emesine Cave (1881 System) [Lava Tube]	Hawaii	12.890	20744	1433	436.8
7	Great EX(pectations) Cave	Wyoming	7.854	12640	1408	429.2
8	Omega System	Virginia	22.840	36757	1263	385.0
9	Main Drain Cave	Utah	1.450	2334	1227	374.0
10	Bigfoot Cave	California	12.400	19956	1205	367.3
11	Neffs Canyon Cave	Utah	0.760	1223	1163	354.5
12	Pahoa Cave(s) (segmentation??) [Lava Tube]	Hawaii	9.942	16000	1150	350.5
13	Ellisons Cave	Georgia	12.127	19517	1063	324.0
14	Silvertip Cave System	Montana	3.166	5096	1052	320.6
15	Carlsbad Cavern	New Mexico	25.560	41135	1035	315.5
16	Ambigua Cave [Lava Tube]	Hawaii	1.096	1764	960	292.6
17	Bull Cave	Tennessee	2.272	3653	924	281.6
18	Nielsons Well (Cave)	Utah	1.260	2028	880	268.2
19	Kauhako Crater (Vauhako) [Lava Pit]	Hawaii	—	—	865	263.7
20	Na One Pit (Pit 6083, Pelee's Abyss) [Lava Pit]	Hawaii	—	—	862	262.7
21	Big Brush Creek Cave	Utah	4.920	7918	858	261.5
22	Rich Mountain Blowhole	Tennessee	2.077	3342	840	256.0
23	Papoose Cave	Idaho	3.250	5230	831	253.3
24	MeanderBelt Cave	Montana	0.723	1164	807	246.0
25	Chestnut Ridge Cave System	Virginia	20.030	32235	804	245.1
26	Sunray Cave	Montana	0.832	1338	801	244.1
27	Viva Silva Cave	Alaska	—	—	797	242.9
28	Kipuka Kanohina (Kula Kai Caverns) [Lava Tube]	Hawaii	16.500	26554	762	232.3
29	Big Red Cave [Lava Tube]	Hawaii	2.241	3607	760	231.6
30	Spanish Cave	Colorado	1.090	1754	741	225.9
31	Ka'eleku Caverns [Lava Tube]	Hawaii	1.772	2852	738	224.9
32	Virgin Cave	New Mexico	1.894	3048	723	220.4
33	Sugar Run Cave System	Virginia	22.500	36210	718	218.8
34	Simmons Mingo - My Cave System	West Virginia	6.700	10783	683	208.2
35	Wind Cave	South Dakota	120.080	193250	664	202.4
36	Dorton Knob Smoke Hole	Tennessee	1.023	1646	660	201.2
37	Little Brush Creek Cave	Utah	5.933	9548	658	200.6
38	Lost Creek Siphon	Montana	0.189	304	650	198.1
39	SnowHole	Alaska	0.371	597	649	197.8
40	Fossil Mnt.Ice Cave - Wind Cave System	Wyoming	2.900	4667	644	196.3
41	Flathead Alps Cave	Montana	—	—	642	195.7
42	Jewett II Cave	Tennessee	3.349	5390	636	193.9
43	Jewel Cave	South Dakota	135.570	218179	632	192.6
44	Rawhide Horror Hole	Tennessee	1.136	1829	630	192.0
45	Friars Hole Cave System	West Virginia	45.539	73288	628	191.4
46	Doe Mountain Cave	Virginia	2.712	4365	628	191.4
47	El Capitan Pit	Alaska	0.211	340	625	190.5
48	Butler-Sinking Creek System	Virginia	16.010	25766	624	190.2
49	Sand Hill Multi Drop (3500)	Alabama	1.193	1920	620	189.0
50	Upper Kaupulehu System [Lava Tube]	Hawaii	3.447	5547	617	188.1
51	Jewett I Cave	Tennessee	1.788	2877	615	187.5
52	Keala Cave [Lava Tube]	Hawaii	5.410	8707	610	185.9
53	MOS Cave / Obscure Magnificence (2697)	Alabama	1.001	1611	603	183.8