

Cave and Karst Science

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Subaerial tufa stalactites: biota and biological processes
Invertebrate fauna of Ogof Ffynnon Ddu, South Wales
Pseudoparonella doveri in the Dark Cave, Malaysia
Algal studies in the Shulgan-Tash Cave, Russia
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Forum

Cave and Karst Science

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Cave and Karst Science

TRANSACTIONS OF THE BRITISH CAVE RESEARCH ASSOCIATION

Volume 31, Number 2

Contents

Papers

Biota and biological processes associated with subaerial tufa stalactites in the tropics. 51
Danko TABOROŠI and Kazuomi HIRAKAWA

The invertebrate fauna of the Ogof Ffynnon Ddu cave system, Powys, South Wales, UK. 63
G T (Jeff) JEFFERSON, Phil CHAPMAN, Julian CARTER and Graham PROUDLOVE

Reports

A uranium-series date from Keld Head Kingsdale, North Yorkshire, UK. 77
Phillip J MURPHY, Joyce LUNDBERG and John N CORDINGLEY

Rediscovery of *Pseudoparonella doveri* (Collembola: Paronellidae) and notes on the 79
Collembola of the Dark Cave (Gua Gelap), Batu Caves, Selangor, Malaysia.
Max MOSELEY

Studies of algae in the Shulgan-Tash (Kapova) Cave, South Ural, Russia. 83
Shamil R ABDULLIN and Marina Yu SHARIPOVA

Abstracts

87

Forum

91

Cover photo:

The open, fault-related chasm of Hull Pot presents a spectacular landmark on the broad but largely drift-covered bench of sub-horizontal Carboniferous limestone between Ribblesdale and the western slopes of Penyghent, one of the "Three Peaks" of the Yorkshire Dales. Normally the surface streambed meeting the open pot on its northern side – the mid-left of the photo – is dry (see plates in the Forum section of this Issue), as the substantial flow of Hull Pot Beck is swallowed by a variety of holes upstream of the main Pot. This image captures the relatively rare occurrence of the beck overtopping its streambed sinks to plunge c.20m to the bouldery floor of the open Pot. The surface stream course and the lip of the waterfall are cut within the Lower Hawes Limestone, with good exposures of the "Girvanella" nodular band upstream of the Pot. Thus, whereas the streambed and upper part of the chasm are cut within the basal limestone bed of the Yoredale Group, the open walls and cave passages below lie within the Malham Formation, the uppermost limestone unit of the Great Scar Limestone Group.

Hull Pot is a classic and mesmerising site in itself, with many questions about its development and past or present hydrological functions remaining to be answered. However, this photograph also has "historical" interest, having been taken during a highly successful BCRA *Geology for Cavers Weekend* fieldtrip in March 1987.

From a photograph by Dave Lowe.

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John Gunn and David Lowe

During the gestation of this issue of *Cave and Karst Science* one of us (JG) has had the good fortune to attend three conferences, whereas the other has spent part of his time in general musings on the future of cave and karst science in Great Britain, with thoughts influenced in no small part by coincidental encounters with related activities in Slovenia. Ideas from both have contributed to the following, which, as always, represents our own opinions and is intended to provoke comment and debate.

The first conference was that of the International Geographical Union (IGU) in Glasgow. This was a huge event attended by around 1500 delegates, of whom only a small number had any direct interest in caves and karst. The IGU has a series of Commissions and Study Groups covering a whole gamut of subject areas, including karst, and the Karst Commission sponsored a pre-Congress field trip to Ireland and three sessions during the actual Congress. Abstracts from the 14 papers presented are included in this Issue. It is interesting to note that nine of these (a clear majority) are concerned with broadly surface karst issues, three involve the use of cave sediments for palaeoclimatic or palaeoenvironmental reconstruction and only two are concerned directly with caves as such. One of these considers the inception, development and destruction of karst caves in central Scandinavia and the other discusses cave conservation in Great Britain.

A lack of research on caves might be expected from a community of geographers, many of whom make no claim to be cavers, although they may visit caves to obtain data and/or samples. However, much more was expected from the work that underpinned the China Caves meeting at the Royal Geographical Society (RGS). In many ways this was a superb event and Andy Eavis deserves a vote of thanks for making it possible – both in terms of his long-term support and involvement in the China Caves Project and specifically for the RGS meeting itself. The amount of exploration that has been undertaken – and the potential that remains – is immense, and the lectures were generally of a high standard, particularly in terms of the visual presentations. However, there was a real paucity of scientific information, and one was left with a feeling that opportunities had been missed.

As we have said many times on these pages, exploration is a vital part of our science, and the preparation of high quality surveys and visual images is essential to our understanding of speleogenesis and related issues. But when we look back to some of the great international explorers of old – Bretz, Casteret, Martel and Schmidl for example – their explorations were accompanied by all manner of observations, including water flow, water quality, cave climate, the nature of the speleothems and the make-up and origin of clastic sediments. More parochially, similar work was done by British explorers, such as Balch, Cullingford, Dunnington, Leakey, Railton, Simpson, Tratman, and many of their contemporaries and more recent explorers – some still active. These British observations were not simply hoarded, but were published, many of them in the predecessors of this journal, the original *Cave Science* (British Speleological Association) and the *Transactions of the Cave Research Group of Great Britain*. Again it is a point we have raised before, but many of these early authors were not university academics but ‘amateur’ cavers who wanted to learn more about the places they enjoyed exploring. It is perhaps worth noting that, based on a very limited number of talks attended at the China Caves meeting, and perusal of journals such as *Karstologia* and *Acta Carsologica*, there seems to be a greater willingness to undertake basic scientific studies amongst cavers in the rest of Europe than there is in Great Britain.

Coincidentally, earlier this year, one of us (DL) was involved in the redrafting of the various forms that are used routinely by Slovenian cavers for recording and describing their explorations for inclusion in the Slovenian Cave Registry. This is the national database and library of all the known caves in Slovenia, and is produced and administered as a joint project between the Speleological Association of Slovenia and the Karst Research Institute of the Scientific Research Centre at the Slovene Academy of Sciences and Arts, which we refer to more commonly as the Karst Research Institute at Postojna. What stood out while working on these forms was first and foremost the virtually total commitment of Slovenian cavers to contribute – and contribute usefully – to this database, which also incidentally collects data from visiting cavers of other nationalities. More striking though was the fact that the forms allow not only for the recording of standard passage descriptions, but also have space for (and invitations to record) a wide range of scientific observations or references to them. Perhaps still more surprising was a more recent request to assist with the editing of a series of cave descriptions for inclusion in *Naše jame* (*The Bulletin of the Speleological Association of Slovenia*), compiled in similar format, relating to explorations carried out in the Philippines by Slovenian and local cavers. Here again the cavers’ descriptions include abundant comments relating to cave development, calcite and clastic deposits, air and water temperature, aspects of geology and observations of cave life. Perhaps such interest and involvement should come as no surprise in a Nation where symposium field trips commonly appear on the National television news and where ongoing aspects of cave exploration and karst research appear to have the same fascination for the general public as they do for active cavers.

And so to Hidden Earth, another excellently organised and well attended event. As at the RGS meeting the paucity of presentations that included a science component was striking. Again there was a talk on cave origins, which was clearly enjoyed by the audience, but this contained material that was at best misleading and at worst factually incorrect! At the same event, the BCRA AGM was very poorly attended – barely quorate – and, although there was some useful debate, the average age of the contributors must have been well over 40. Cavers on the whole eschew ‘politics’, and as editors of *Cave and Karst Science* we try studiously to avoid being drawn into any ‘political battles’. For all that, it is clear to us that there is a real need for increasing scientific awareness among British cavers and hopefully for a greater involvement of cavers in general, both within the day-to-day activities of cave and karst science and in the enhancement and running of both the BCRA and the fledgling BCA.

Biota and biological processes associated with subaerial tufa stalactites in the tropics.

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Abstract: Stalactitic deposits of subaerial tufa are a common feature of humid tropical karst areas. Distinct from classic speleothems by dint of their epigeal locations and tufaceous makeup, and from classic calcareous tufa by dint of their stalactitic form and subaerial depositional settings, these unique and rarely acknowledged sediments are intermediate forms between the two. They contain considerable organic material and provide habitats to a bewildering variety of living organisms, including bacteria, cyanobacteria, fungi, eukaryotic algae, bryophytes, higher plants, and invertebrates.

Tufa stalactites are unique products of inorganic and biogenic carbonate deposition from dripping epikarstic water. The fundamental inorganic mechanisms (CO₂-degassing and evaporative effects) are affected by a plethora of superimposed biological processes. The latter range from the largely inconsequential colonization and minor bioerosion to the significant photosynthetic enhancement of carbonate precipitation and direct biomineralization. These processes operate simultaneously and in complex interrelationships, and may produce distinct biogenic and bioconstructional fabrics and macromorphologies, the most apparent of which are the light-oriented stalactites commonly seen in the entrances of caves.

Keywords: speleothems, outside stalactites, biofilm, biosediments, stromatolites, twilight zone

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INTRODUCTION

Peculiar stalactites, sometimes light-oriented, are commonly seen in cave entrances (Fig. 1a) or plastered to cliffs in humid tropical karst areas (Fig. 1b). Unlike classic speleothems found inside caves, these epigeal deposits are typically friable and porous and are generally composed of microcrystalline calcareous tufa. Unlike conventional tufas, however, they are deposited entirely in a subaerial environment. A centimetre to tens of metres in scale, their overall shape is somewhat irregular, with crooked, bulbous, pendant-like, and deflected forms being common (Figs 1c; d). In addition, analogous drapery-like deposits, rudimentary stalagmites, columns, irregular patches, and bedrock veneers also occur. Their outside surfaces can feel powdery or earthy or be covered by wet and pasty organic coatings (Figs 1e; f; g; h), and they vary in colour from white to grey, purplish, green, brown, or black. They contain considerable organic material and provide habitats to a variety of living organisms.

Surprisingly enough, these features have not been subject to detailed studies, and details of their structure, biology, modes of origin, diversity, and occurrence are virtually unknown. For example, in addition to being regarded as a type of tufa (Viles and Goudie, 1990), they have also been interpreted as erosional features – remnants of former cave speleothems, which have undergone decay and diagenesis after being exposed to outside conditions (e.g., Halliday, 2000). Whereas the latter may be true in some cases, there is now sufficient evidence that these convincingly speleothem-like formations are indeed subaerial deposits of calcareous tufa that form in specific land-surface environments and are not necessarily related to caves (Taboroši *et al.*, 2003; 2004). They are rarely mentioned in literature and are ignored or dismissed in a few sentences even in review articles dedicated to calcareous tufa (Ford, 1989; Ford and Pedley, 1992; 1996; Viles and Goudie, 1990). The deliberations of subaerial tufa, if any, are limited to features associated with the fluctuating air/water interface (Ford and Pedley, 1996). Furthermore, most classification schemes of tufas

(e.g., Casanova, 1981; Chafetz and Folk, 1984; Viles, 1988; Ford, 1989; Pedley, 1990; Ford and Pedley, 1996; with a notable exception of Pentecost, 1993), do not take into account the stalactitic and analogous fully subaerial deposits. Out of 282 references listed in the most detailed global review of tufa to-date (Ford and Pedley, 1996), not a single one describes stalactitic tufa deposits.

Remarkably, this obscurity is not a reflection of rarity, as tufa stalactites are actually a common component of most tropical landscapes. Indeed, they are the subject of cursory references in many expedition reports and general works on tropical karst, where numerous terms have been applied to them. They have been called *aussen Stalactiten* (Lehman, 1954), *Stalactitenvorhang* (Pfeffer, 1978), *outside stalactites* (Sweeting, 1978), *non-vertical stalactites and stalactitic tufa* (Bull and Laverty, 1982), *tufa-like speleothems* (Ford, 1989), *remora* (Pentecost, 1993), etc. Their tufaceous nature and high organic content suggest biological involvement in their formation; and although this has not been formally demonstrated, these deposits are sometimes regarded as biogenic. Thus, Bull and Laverty (1982) classify them as a type of depositional phytokarst, and a few other terms liken them to stromatolites (gigantic stromatolitic stalactites of Forti, 2001; speleothem stromatolites of Wang, 1994; karst cave stromatolites of Wang and Cao, 1993). This threatens to confuse them with the other “cave stromatolites” – the well-documented and possibly related stromatolitic stalagmites (Cox *et al.*, 1989), as well as real stromatolites that grow in certain cave pools (Thurgate, 1996). A further occasional property of these stalactites that points to biogenicity is photo-orientation. This has resulted in yet another series of names applied to these and related deposits, which includes phototropic cave coral (De Saussure, 1961), phototropic phytospeleothems (Lichon, 1992), heliotropic speleothems (Wang and Cao, 1993), etc.

Based on our previous work in Southeast Asia and the Western Pacific (Taboroši, 2002; Taboroši *et al.*, 2003; Taboroši *et al.*, 2004) as well as the research reported here, we believe, however, that the tufa stalactites found in the cave entrances and limestone cliffs in the tropics are not necessarily biogenic, stromatolitic, or light-oriented

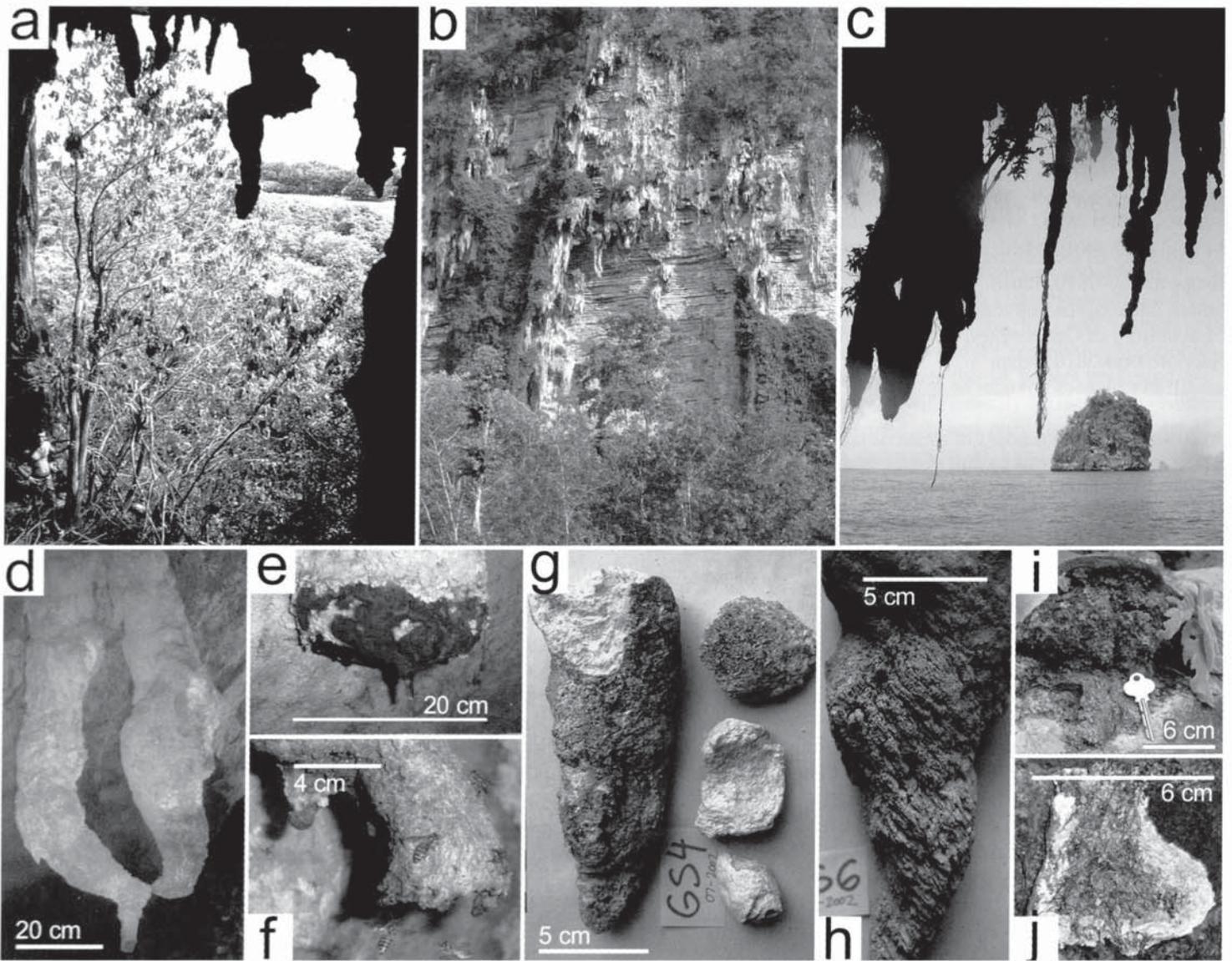


Figure 1. In situ and sampled examples of stalactitic subaerial tufa. a) Tufaceous stalactites in the entrance of a cave in Guam. Note the highly irregular form of the large stalactite. Person for scale. b) Limestone cliff at Ao Nang, near Krabi, Thailand. Note the plentiful stalactites, and the depositional strata visible in the cliff face. If this part of the cliff had once been a back wall of a cave destroyed by cliff retreat (as suggested by Halliday, 2000), then the wall would show dissolutional surfaces or flowstone coatings associated with speleogenesis, rather than the original depositional morphology. c) Massive tufaceous stalactites growing in a coastal overhang at Riley, near Krabi, Thailand. The tips of the longest stalactites are less than 1m from sea level at high tide. Note the plant growth and long roots hanging from the deposits. d) Deflected stalactites in an overhang at the base of the cliff at Riley Lagoon, near Krabi, Thailand. Note the inconsistencies in deflection pattern: stalactite on the left resumes vertical growth, and the curvatures of the two stalactites oppose each other. Also note the lack of moss growth. A pale olive green colouration of the stalactites (not apparent in this greyscale version) is due to microphytes in the surficial biofilm. e) Growing tip of a drapery in a cave entrance in Chong Phli, near Krabi, Thailand. Note the dark grey areas, which are actually a rich, deep dark green coating of algae, limited to the lowest, wettest part of the deposit. Also note that algae are being covered locally by precipitated calcite (white). f) Tip of a highly irregular, deflected tufaceous stalactite in a cave entrance in Chong Phli, near Krabi, Thailand. Note the rich organic coating and the bees swarming around the water source. g) A tufaceous stalactite from Ritidian, Guam. Note the contrast between dark organic coating at the surface and the white colour of the interior. Also note the crumbliness of the deposit. h) Another tufaceous stalactite from Ritidian, Guam. Note the consistently oriented linear features at the surface. They are composed of intertwined calcified filaments of cyanobacteria. The interior of the stalactite is almost entirely composed of such calcified filaments and microcrystalline calcite filling the spaces between them. i) A small mound of bryophyte-deposited subaerial tufa at the base of a cliff in Chong Phli, near Krabi, Thailand. Note the cap of living moss and a colonizer plant. j) Growing tip of a small tufaceous stalactite from Tinian, Mariana Islands. Cut open, the deposit reveals a core entirely filled by plant roots.

(deflections from the vertical axis, if any, can actually be away from the light, or random and inconsistent with other nearby specimens; see Fig.1). Rather, they are an extremely varied array of allied deposits that includes some truly bio-mediated, and even bio-constructural forms on one end of the spectrum, and essentially inorganic layered microcrystalline calcite aggregates (of unsorted and randomly oriented crystallites a few microns in size) on the other. Both “inorganic” and “organic” microfabrics are commonly observed within single specimens, indicating that precipitation is finely controlled by numerous physico-chemical and biological factors, each of which may dominate the others under specific environmental conditions. Thus, just like more conventional types of tufa (fluvial, springline, palludal, etc.) these subaerial tufa deposits are not necessarily biogenic, but do consistently provide complex habitats hosting a wide range of biota, including bacteria, cyanobacteria, eukaryotic algae, fungi, mosses, higher plants, and

invertebrates. Whereas it is, therefore, clearly a generalization and an exaggeration to say that they are all biogenic or stromatolitic in character, the fact remains that these deposits, irrespective of their predominantly biological or inorganic origin, are regularly coupled with a plethora of living organisms.

The intriguing biology of subaerial tufa stalactites, however, has hardly been investigated, despite the fact that biological aspects of conventional (aquatic) tufa are rather well documented (e.g., Pevalok, 1935; Scholl and Taft, 1964; Irion and Muller, 1968; Pentecost, 1978; 1985; 1996; Pentecost and Lord, 1988; Pedley, 1992; Davis *et al.*, 1989; etc.). This observation prompted the research presented in this paper, whose goals are to: (1) provide a primary assessment of the range of biota associated with tufa stalactites, and (2) conjecture a conceptual model of biological processes involved, their interrelationships, and overall contribution, if any, to deposit formation.

MATERIAL AND METHODS

We have examined a total of seventy-eight subaerial tufa stalactites from surface settings in Southeast Asia and the Western Pacific. Of these, ten samples came from Guam and thirty from Tinian in the Mariana Islands, two from Okinawa and two from Okinoerabu-jima in the Ryukyuu Islands, four from the Bukit Peninsula in Bali, and thirty from the Krabi area in southern Thailand. The sampling locations included cliff faces of coastal and inland cliffs, associated notches and overhangs, entrances of inland and coastal caves, walls of widened fractures, and talus caves amid breakdown boulders. For comparison purposes, six real stalactites from caves (two from Guam, two from Tinian, and two from Krabi) were also examined. Samples were removed by hammer and chisel and were not treated with any preservation methods. The collected specimens were allowed to dry and were kept at room temperature in the lab for several weeks prior to analyses. For Tinian samples only, small fragments were also conserved in 70% ethanol as an attempt to better preserve organic structures for microscopic observations (this later proved to be unnecessary as SEM micrographs were quite comparable to those of air dried specimens). Following cutting, and macroscopic and binocular microscope examination (7.5x to 60x magnification), the samples were studied through conventional transmitted-light microscopy of resin-impregnated petrographical thin sections (one transverse and one longitudinal per specimen). Additionally, small fragments (two or three per specimen) were glued to aluminum stubs, sputter-coated with platinum, and observed with a Hitachi S-3000H Scanning Electron Microscope (SEM), under operating conditions at 20kV and 60 μ A. Mineralogy was ascertained by X-ray diffraction (XRD) analyses on a Bruker AXS MX-Labo powder diffractometer with Cu radiation at 40kV and 20mA.

BIOTA

Tufa stalactites seen on cliffs and in cave entrances are associated with numerous living organisms. Inside caves, normal stalactites and other speleothems have been reported to contain some microbes (e.g., Went, 1969; Dickson, 1975; Polyak and Cokendolpher, 1992; Cunningham *et al.* 1995; Northup *et al.*, 2000); but their density and diversity are severely limited by locations in total darkness, low nutrient levels, and the prodigiously inorganic nature of the sparry calcite substrate. However, in the case of tufa stalactites found in epigeal and transitional epigeal–spelean settings, the locations that are reached by daylight (very low levels to full sunlight), the ample nourishment by dripping epikarstic and meteoric water, and the soft and porous nature of host material (Fig. 1g) all translate into intricate microhabitats, which harbour an extremely wide range of biota living in dense populations and complex interrelationships with each other. Even a casual look at in situ specimens reveals thick surficial coatings by algae, fungi, and bryophytes and, in some cases, growth of higher plants. Detailed investigations uncover an even more complex picture of porous sediments teeming with bacteria, cyanobacteria, algae and fungi forming not only elaborate three-dimensional surficial biofilms, but also permeating the interiors of the deposits and, in some cases, even producing the deposits themselves. Protozoa and invertebrates (both terrestrial and marine, in inland and littoral settings respectively) are commonly encountered. All this testifies that stalactitic deposits of subaerial tufa are well-established habitats supporting a wide range of living organisms, including both autotrophs and heterotrophs. Of these, many are undoubtedly simple opportunistic colonizers, but others are probably specialized organisms obligate to these particular settings.

The following is an assessment of this range of biota, which aims to provide an introduction to the unique and previously unstudied subaerial tufa microhabitat and a departure point for future in-depth research. No identification of microbes was attempted beyond determining their basic affinities, since these identifications are usually established by molecular methods and are considered unreliable if based on morphology (Jones, 1995).

Bacteria

Whereas microcrystalline calcite appears pale coloured or transparent when viewed in plane light on a petrographical

microscope, we have often observed it to be opaque and brown (Fig. 2a). Many of the specimens we investigated contain considerable amounts of this dark micritic material, which is in some cases pure and homogeneous, but is more commonly associated with masses or layers of plain microcrystalline calcite (Fig. 2a). In addition, we have observed numerous, distinct spherical to ovate opaque bodies, coloured various shades of brown, randomly distributed within the deposits (Fig. 2b). Jones and Motyka (1987), Chafetz and Meredith (1983), Chafetz and Folk (1984) and Folk *et al.* (1985) have all recognized comparable opaque micrite and bodies in thin sections of various travertine deposits and attributed them to bacterial activity.

Individual bacteria are most apparent on SEM micrographs of outer surfaces of the deposits. They are a ubiquitous component of the complex surficial biofilms, in which they are observed on calcite substrate, organic substrate, or other microbes. They occur in many morphological types, and are seen isolated or grouped in chains or clusters (Fig. 3a).

Cyanobacteria

Cyanobacteria are a key component of organic coatings on tufa stalactites. They occur amidst other microbes in the biofilm, but also form nearly pure colonies. The latter are composed almost exclusively of cyanobacterial filaments that are calcified, for the most part. These colonies are actually recognizable in hand specimens, where they are responsible for many unusual surface textures of tufaceous stalactites (Fig. 1h). They are striking under binocular microscope (Fig. 2c).

In addition to thriving at the exterior surfaces, cyanobacteria are commonly fossilized within the deposits. In fact, some of the arguably most spectacular microfabrics of tufa stalactites are constructed solely by filamentous cyanobacteria. Such deposits are composed almost entirely of calcified filaments surrounded by a microcrystalline matrix (Fig. 2d). The filaments can be grouped in clusters oriented along consistent axes (Fig. 3b), or chaotically intertwined (Fig. 3c). Their length is estimated to be several millimeters. They show no apparent branching and consist of open, isodiametric central tubes, surrounded by one or more layers of calcite. The tubes are circular in cross-section, 2 to 6 μ m in diameter. There are at least four general types of enclosing calcite, and their morphology is highly variable. Usually, the calcite adjacent to a cyanobacterial cell is composed of unsorted crystallites that are less than 1 μ m in size; in some examples, this microcrystalline armour is all that is present (Type 1). In most cases, however, there is an additional outer layer of larger crystals, which may be unsorted or sorted. When unsorted, the outer layer crystals are a few μ m long and exhibit erratic shapes and a disorderly pattern around the filament (Type 2). More common are sorted patterns in which the outer crystals exhibit regular size (about 10 μ m), shape, and arrangement (Type 3; Fig. 3d). Their orientation can be sub-parallel to the filament, but can also extend at near 90° angles to the cyanobacterial cells, forming crystal spikes up to 20 to 30 μ m long (Fig. 2f). Finally, some filaments lack the layered calcite altogether, being composed entirely of dendritic (Jones and Kahle, 1986) crystals (Type 4; Fig. 3e).

In most cases, the pore space between the filaments is partially or completely occluded by microcrystalline or in some cases by sparry calcite (Fig. 2e). In early stages, however, this space is empty, as evidenced by some extremely soft, pasty and porous build-ups on more solid tufa or bedrock substrates (Figs 2g; 3f). In these initial deposits, which are composed solely of entangled filaments, individual sheathed trichoms of cyanobacteria can be observed emerging from the partially calcified tubes (Fig. 3f).

Eukaryotic algae

Walls and speleothems in cave entrances are commonly covered by algal coatings, which are particularly prolific in tropical areas. Algae are a common element of the transitional environment between well-illuminated epigeal settings and dark cave interiors (Cubbon, 1976), and the thickness, colour, and species composition of algal coatings are known to vary in different parts of the caves' twilight zones (Dalby, 1966b). Though present on many cave walls at our study

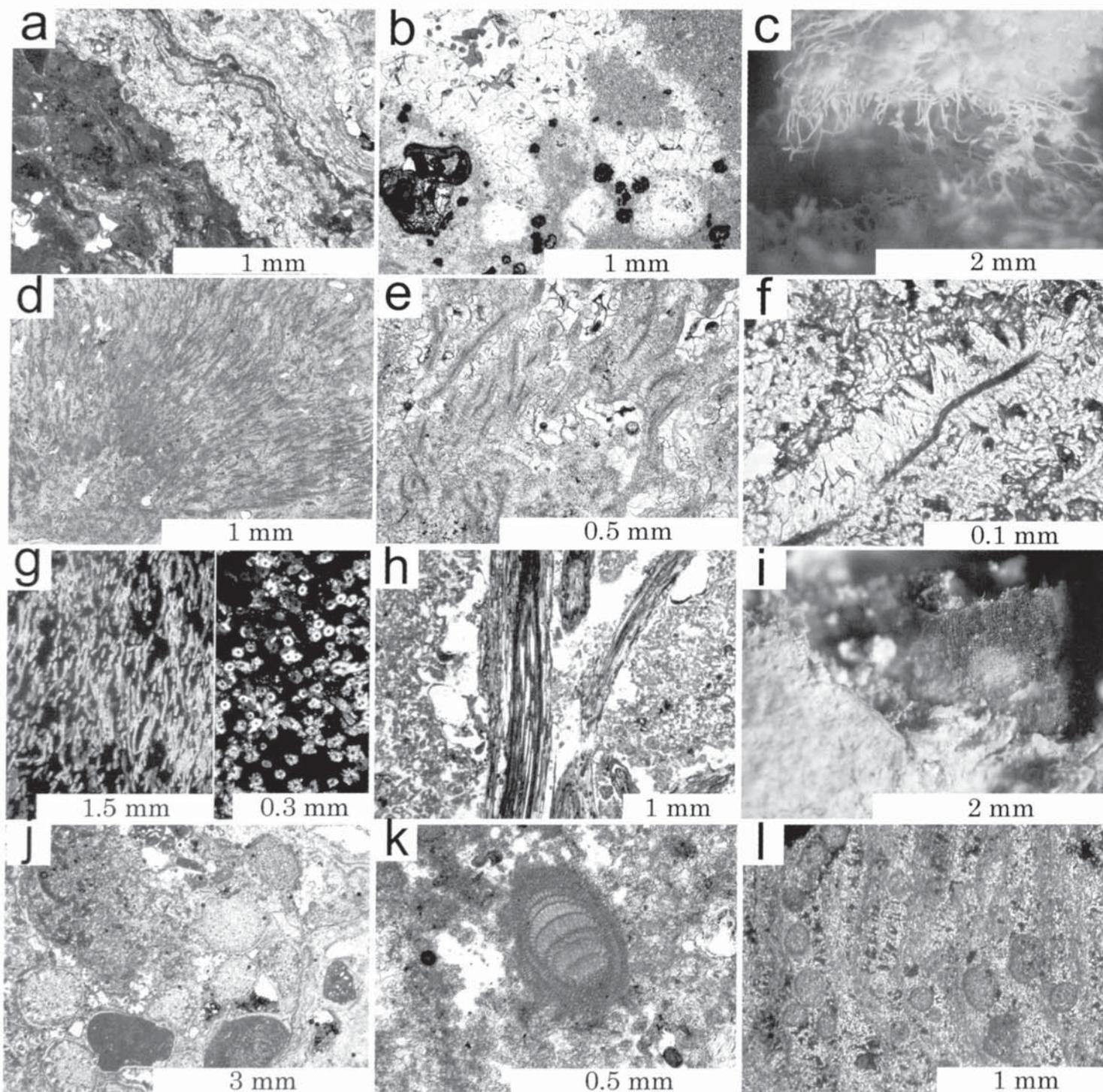


Figure 2. Photo micrographs of tufaceous stalactites: plane light thin sections (a, b, d – f, h, j, k), cross-polarized light thin sections (g, l), and binocular microscope samples (c, i). a) Opaque organic-rich material (dark) intercalated with transparent microcrystalline calcite (pale). Note that each is dominant in different parts of the deposit. Also note the irregular, convoluted aspect of the laminae. b) Numerous dark biogenic bodies, of likely bacterial origin. Note that they are present in pore spaces, as well as in sparry and microcrystalline calcite areas. c) Calcified cyanobacterial filaments at the outer surface of a tufaceous stalactite. Note that the filaments entwine around each other and are freely suspended in open space. Deeper into the deposit, the empty space between the filaments is reduced and filled with calcite. d) A tufaceous stalactite microfabric supported entirely by calcified filaments. Note the radial appearance of the cyanobacterial filament network, infilling by microcrystalline calcite, and little remaining pore space. e) A close-up of a similar microfabric. Note the cyanobacterial trichoms and their calcified sheaths and the near complete occlusion of pore space by calcite. f) A close-up of a calcified filament. Note the cyanobacterial trichom in the central tube, the long spiky crystals attached to it and oriented at approximately 90° angles, and calcite filling the surrounding space. g) A transverse (left) and cross section (right) of a soft, pasty, subaerial tufa build-up consisting of nothing but calcified cyanobacterial filaments. Note the extreme porosity and lack of any infilling of pore space between the filaments. h) Extremely porous tufa with plant root remains. Note the preservation of the roots and the fact that they are neither replaced nor coated by calcite, but simply embedded in it. This indicates that the roots were alive within the deposit. i) Insect chitinous fragment interred in tufa. j) Skeletal grains of marine origin (benthic foraminifera tests and fragments of calcareous algae) embedded in microcrystalline and organic-rich matrix. k) Calcareous red alga embedded in microcrystalline material. l) Spherical, pisolith-like bodies interred among the porous, irregular laminae of a coastal zone tufaceous drapery deposit.

sites, the growth of eukaryotic algae is most luxuriant on stalactitic tufa deposits (Fig.1e), where it is nurtured by localized water seepage. The algal coatings tend to be absent or minimal in locations illuminated by direct sunlight (e.g., cliff faces).

Algae are the principal constituents of the complex biofilms covering the surfaces of tufaceous stalactites, where they live in

close proximity with numerous other microorganisms. We have identified some biofilm microbes as eukaryotic algae, but this is still tentative, since many other filamentous microbes – including cyanobacteria, fungi, and actinomycetes – can exhibit similar morphology, only somewhat separable based on filament diameter and mode and angle of branching (Klappa, 1979). Algal colonies in

biofilms (Figs 3g; 3h) commonly consist of irregularly branching filaments that form web-like, tangled mats (Fig.3g). These filaments are inconsistent in diameter, 5 to 15µm, and are not calcified, except for the accidental calcite grains affixed to them. They appear to have a central longitudinal groove, which may or may not be artifact of desiccation and is similar to that of algae from cave walls in the Cayman Islands, reported by Jones and Kahle (1986). These algal mats provide substrate for numerous other microbes, and are commonly intertwined with them.

Fungi

Veneers of fungi and lichens are macroscopically apparent on many tufaceous stalactites, but are also present on surrounding bedrock. In such situations, they typically grow in single species patches as simple colonizers of available substrates.

Of much more significance are the copious growths of fungi (Figs 3i; 3j), hyphae (Fig.3k), spores (Fig.3l) and mucilage (Fig.4a) that form the major components of biofilms and organic coatings on subaerial tufa stalactites. Fungi commonly grow mats that cover calcite surfaces, and, in turn, provide substrate to a bewildering array of other microbes with which they live in close proximity and complex interrelationships (Fig.4b). Many organic structures in these biofilms are partially covered by what appear to be random calcite crystallites (Fig.4c); others are clearly preferentially calcified; and many remain uncalcified (Figs 4d; e). Calcite crystallites are commonly entwined by fungal hyphae, and are in some places fastened, and even suspended by the hyphae. Fungal spores and fruiting bodies of various microbes are also common in the biofilms. Numerous types can be recognized, including a range of ovate to spherical structures of various sizes, but mostly 10 to 20µm in diameter (Fig.3l). Sporangia, containing closely packed clusters of spores, include some highly distinctive forms (Fig.4b).

Bryophytes

The association of bryophytes (mosses) with conventional tufa deposits has long been recognized by bryologists (e.g., Pia, 1934), and is also common in the case of tufaceous stalactites. About one fifth of our samples (excluding those from littoral settings) exhibited some bryophyte growth, and a few were quite thoroughly covered by them. In general, moss growth on subaerial tufa stalactites is patchy and limited to the sunlight-facing portions of the deposits, and is secondary to deposit formation, being simply a result of mosses colonizing suitable habitats.

However, in some cases, bryophyte growth was seen to influence and guide the deposition of subaerial tufa. Portions of stalactites coated by bryophytes are in some cases underlain by highly distinctive, extremely porous rock, comparable to conventional tufa fabrics deposited by mosses (e.g., Weijermars *et al.*, 1996). This is particularly striking in cross-sections of hand specimens, in which the moss-covered, sunlight-facing portion is made of sponge-like rock, while the other parts are usual microcrystalline calcite layers. We have also encountered a few minor deposits where bryophytes appeared to be the principal builders. These grow on bedrock in well-lit areas below rock overhangs, directly underneath dripping tufaceous stalactites, and appear as mini-phytoherm mounds (<20cm tall) of spongy tufa capped by bryophyte mats (Fig.1i).

Higher plants

Higher plants are a ubiquitous feature of tufa stalactites and are commonly growing in them. In case of some massive formations in the Krabi area in Thailand, entire trees were rooted in these deposits. Plant roots emerging from and extending many metres down from the central holes of tufa stalactites are frequently seen (Fig.1c).

Roots of higher plants were recognized in approximately 10% of all thin sections prepared, with amounts varying from trace to considerable (Fig.2h). In some specimens, roots were a minor component, merely a result of plants colonizing and penetrating suitable substrate. In others, they formed the core, extended throughout, and appeared to precede and provide critical support for the growth of tufa. An illustration of this phenomenon is provided by tufaceous stalactites formed entirely around hanging roots and rootlets (Fig.1j) and tufa coatings that preferentially cover plant

roots exposed on bedrock surfaces. In some tufa stalactites that had plant roots hanging from their central holes, we observed the exposed roots being partly encased in separate masses of tufa, which were suspended in mid-air and discontinuous with the main stalactite body.

Terrestrial invertebrates

Insects and other arthropods are commonly observed on tufa stalactites, which hold particular appeal to them during the dry seasons when freshwater sources are more limited. Diptera, Lepidoptera, Hymenoptera (Fig.1f), and Diplopoda (millipedes) are especially common, and in coastal areas we have also seen many hermit crabs (Decapoda: Anomura) climb up and cling onto tufa stalactites that drip freshwater.

Although insects associated with tufaceous stalactites can be numerous, we have seen no evidence that they directly contribute to subaerial tufa deposition, as can be the case with some aquatic tufas (Stirn, 1964; Bramwell and Shotton, 1982; Poluzzi and Minguzzi, 1998). Chitinous fragments of insects and other arthropods are commonly interred in the organic coatings surrounding tufaceous stalactites (Fig.2i). These are generally too disintegrated to be identified, but appear to belong primarily to the first three orders mentioned above. This organic debris provides nutrients to heterotrophic microbes in the biofilm. Jones (1995) reported that certain microbes on cave walls congregate on insect remains.

In addition, spider webs, insect eggs, oothecae (e.g., Blattaria: Blattidae), and especially mud-cell nests of wasps (Hymenoptera: Sphecidae) are commonly attached to some tufa stalactites. Shells of terrestrial snails, in some cases less than 1mm across, are also found in the biofilm as well as buried in tufa.

Marine organisms

A discrete category of tufa stalactites occurs within spray and splash zones of tropical coasts (Taboroši *et al.*, 2003). In such areas, the interplay of distinct climatic, hydrological and biological factors impresses a unique character on the deposits, resulting in a separate, marine littoral variety of subaerial tufa. In addition to some morphological and mineralogical idiosyncrasies (size less than 30cm, dominance of patchy and globular shapes and coralliform textures, rarity of deflected forms, and presence of aragonite in addition to calcite), it is the biology of these deposits that clearly separates them from tufa stalactites from inland sites, and indeed, from all other types of tufa.

These coastal deposits lack bryophyte and plant growth; and their strikingly dark to black colour attests to the presence of unique marine littoral biofilms (Fig.4f). Although composed of the same general groups (bacteria, cyanobacteria, eukaryotic algae and fungi) and just as prolific as corresponding biofilms from inland locations, they are more diverse and quite distinct in their species composition (Fig.4g). In that aspect, they are reminiscent of biofilms on intertidal rocks. Marine epilithic diatoms (Figs 4h; 4i) and foraminifera (Fig.4j), for example, are a common occurrence here, but were not encountered on inland tufa stalactites. Bioerosional borings (Fig.4k) and other evidence of marine organisms (Fig.4l) are also plentiful.

In addition to the unique microbial assemblages at their exposed surfaces, these littoral deposits also contain marine organisms fossilized within the tufa. Most of these are incidental calcareous grains incorporated following the death of the organism, and include whole and broken tests of benthic foraminifera and skeletal fragments of corals, calcareous algae, and molluscs (Figs 2j; 2k). These vary widely in incidence, and can appear as isolated single grains floating in the precipitated matrix or large groups of grains cemented together. Some of the latter are cemented by an isopachous layer of acicular aragonite as in beachrock, but are more commonly simply embedded in microcrystalline calcite (Fig.2k). In addition to marine skeletal grains, these deposits commonly contain extremely convoluted layers and pisolith-like bodies (not found in any inland specimens) of probable biological origin (Fig.2l).

Vertebrates

Larger animals play marginal roles. Whereas vertebrate fossils have been reported embedded in tufa (Bramwell and Shotton, 1982) as

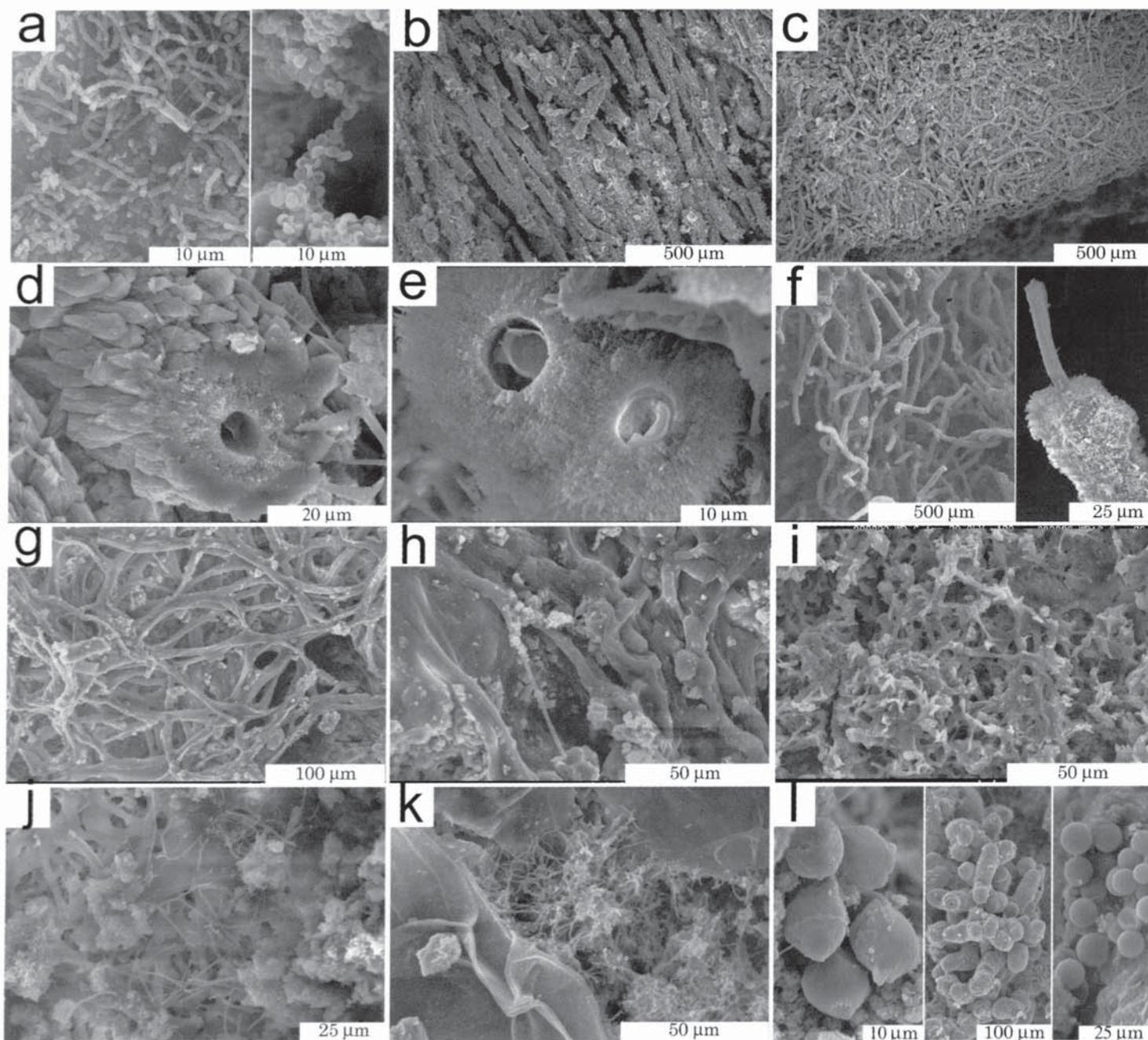


Figure 3. SEM micrographs of organisms associated with tufaceous stalactites. a) Microbes, arranged in chains (left) and clustered (right). Note that many of the chains have broken apart, and the constituent, autonomous units lay scattered. b) Tufaceous stalactite fabric composed entirely of straight, consistently aligned calcified cyanobacterial filaments. c) Tufaceous stalactite fabric composed entirely of chaotically intertwined calcified cyanobacterial filaments. d) Cross-section of a calcified filament. Note the small size of the crystals adjacent to the central canal and the large size and regular arrangement of crystals forming the periphery. Also note that a small part of the organism is visible in the central hole. e) Cross-sections of two calcified filaments. Note that they are composed of dendritic crystals, in stark contrast with the previous micrograph. Also note that portions of organic filaments are clearly visible in the tubes. f) Calcified cyanobacterial filaments at the outer surface of a tufaceous stalactite (left) and a close-up of one (right). Note that the filaments extend in open space and form a chaotic network. The organic filament sheath clearly emerges from the calcified tube. g) Biofilm dominated by irregularly branching filaments forming a web-like, tangled mat. Note the lack of calcification. h) Biofilm composed of apparent algal or fungal filaments fused into a continuous mass. i) and j) Biofilms dominated by irregular mats and filaments, associated with calcite crystals and clumps of bacteria. k) Possible fungal hyphae and sporangia. l) Probable microbial spores found attached to the biofilm.

well as in flowstone deposits in caves (Hill and Forti, 1997), no such remnants have yet been associated with tufa stalactites. The only relatively common occurrences are gecko (Squamata: Sauria: Gekkonidae) eggs laid into minor hollows. In an isolated case, a shed snakeskin was observed wrapped tightly around a tufaceous stalactite in Krabi, Thailand. Its fragments could conceivably become incorporated into the deposit and used as a nutrient source by the heterotrophic microbes. In the same area, we have often observed tree shrews (Scandentia: Tupaiidae) and macaques (Primates: Cercopithecidae) climb animatedly up massive stalactitic deposits in cave entrances and on cliff faces.

BIOLOGICAL PROCESSES

Traditional theory has emphasized the role of abiotic precipitation in the formation of tufa: percolating meteoric waters first mobilize

CaCO_3 in the presence of elevated CO_2 levels in the soil and, subsequently, precipitate it when they emerge from springs and CO_2 degasses to attain equilibrium with the atmosphere (Atkinson and Smith, 1976; Dreybrodt, 1988). In addition, increased evaporation effects at the land surface are an important contributing factor. They cause rapid precipitation of calcite from water, resulting in poorly arranged and randomly oriented microcrystalline aggregates. These mechanisms imply a very close genetic relationship between tufa and speleothems, which is perhaps nowhere as obvious as in the case of tufa stalactites – the ignored “missing link” between classical tufa and cave deposits. However, while carbonate speleothems are considered generally abiotic (Forti, 2001), a variety of biological processes contributes to the formation of tufa (Pedley, 1992). These processes are numerous, complex, and commonly poorly understood, and involve hundreds, probably thousands, of species in

an impressive range of prokaryotes and algae (Freytet and Verrecchia, 1998), heterotrophic microbes (Krumbein, 1979), bryophytes (Zhaohui and Pentecost, 1999), higher plants (Pedley, 1990), and even fauna (Drysdale, 1999).

Correspondingly, in the case of subaerial tufa stalactites, physico-chemical precipitation and evaporative processes maintain significant influence on the deposition, but are profoundly affected by superimposed biological processes, which interact in complex ways to produce the observed fabrics and features (Fig.5a). Whereas the exact relationships between abiotic and biotic processes and, indeed, the nature of biological involvement in tufaceous stalactite formation remain largely unknown, there are several biological processes that are important. Although the complexity and integration of these processes may not warrant it, the key mechanisms are discussed here separately, primarily because each of them, when dominant, produces recognizable fabrics and even distinct morphologies of tufaceous stalactites. We have grouped them into macrophyte-mediated and biofilm-mediated processes.

Macrophytes

Macrophytes are known to contribute to the deposition of certain types of tufa, and are especially involved in lacustrine and paludal tufas (Pedley, 1990). They generally include semi-aquatic and aquatic plants, such as bryophytes (Pentecost, 1987), liverworts, and partly submerged higher plants, which provide substrates for calcite precipitation and microbial colonization on the fringes of their stems and leaves. As a consequence, they commonly develop carbonate coatings and provide primary frameworks for tufa precipitation (Pedley, 1992).

In contrast, macrophytes that mediate the formation of tufaceous stalactites are bryophytes and terrestrial plants, and it is primarily their roots that enhance the deposition of tufa. They (1) provide substrate and physical support for the formation of subaerial tufa stalactites, and (2) enhance calcite precipitation by increasing CaCO_3 saturation levels through photosynthetic CO_2 uptake.

Substrate and physical support

The relative importance of simple physical support provided by macrophytes to incipient deposits is difficult to estimate, as associated photosynthetic and microbial metabolic processes also influence preferential accumulation of calcite on plants. The physical support that is afforded to subaerial calcite deposits by plants is perhaps best seen in the darkness of caves, where the roots, which enter cave passages in search of water, are frequently covered by and fossilized in calcium carbonate (Hill and Forti, 1997). However, this process may be augmented by biological activity of the roots (Johnson, 1967). Correspondingly, in epigeal environments, the association of plants and their roots with tufaceous stalactites is commonly a result of calcite deposition on plant roots; but it can also be a matter of simple colonization of tufa by plants. In either case, when present, roots clearly support and strengthen the tufaceous stalactites, as we saw when tips of certain root-supported tufaceous stalactites could not be sampled by the usual hammer and chisel, nor be plucked by hand, but had to be cut off by gardening scissors. What came first, root or tufa, is irrelevant, and both situations certainly occur.

What appears to be unique about the relationship between tufaceous stalactites and macrophytes is that the deposition of tufa around plant roots and the growth of roots inside the tufa can be viewed as positive-feedback processes. Unlike roots hanging inside cave passages and encased in calcite (and indeed, most roots associated with carbonate concretions; see Klappa, 1980), which offer no benefit to the living plant, tufa can actually sustain the plants associated with them. Plants receive growth space and nourishment from the uniquely soil-like, porous, and aerated tufa comprising the stalactites, whose locations at the termini of preferential pathways of groundwater in the epikarst offer ample water. The non-compacted nature of tufa enhances root penetration and growth (Gliński and Lipiec, 1990), which, in turn, enhances the deposition of tufa by providing physical support and nucleation sites for crystals, substrate for the development of calcifying microbial biofilms, and possibly directly modifying local geochemistry.

Although the general view is that roots increase acidity in neighboring soil, roots can actually lower the pH of the soil adjacent to them (Gray and Williams, 1971).

Photosynthetic enhancement

The fact that autotrophs can contribute to carbonate deposition by removing photosynthetic CO_2 from water is well-documented (Golubic, 1974; Pentecost, 1978; Merz, 1992). In many cases, the bulk of this photosynthesis-mediated precipitation is due to autotrophic microbes in epilithic biofilms (Pedley, 1992; 1994), but macrophytes also play a role (Pentecost, 1984; 1987; Zhaohui and Pentecost, 1999). Bryophyte photosynthesis, for example, affects water chemistry and, in certain tufa deposits, accounts for 6 to 12% of the total carbonate deposition, the rest being precipitated inorganically (Pentecost, 1996). The same also occurs in subaerial tufa deposits, and is particularly obvious in cave entrances where mosses produce distinct tufaceous build-ups (Fig.1i) and speleothem-like deposits (Dalby 1966a; Pearce, 1975; Lichon, 1992), many of which show a clear and striking deflection toward the source of light. Moss-directed growth and moss-deposited fabrics are evident in some specimens we investigated, although deflections from the vertical axis are more commonly due to biofilm processes.

Biofilm

Subaerial tufa stalactites are covered by up to several mm thick microbial coatings. These biofilms are complex tri-dimensional structures composed of diverse microbial assemblages and copious amounts of communal mucus (extracellular polymeric substances). The importance of biofilms to the formation of freshwater carbonates has been highlighted by Pedley (1992) who showed that the "complex associations of microbes and mucus mediate much of the constructional activity." Working on biofilms on cave walls, Jones (1995) argued the same for cave twilight zones, stating that the biofilm "provides a medium in which a broad spectrum of destructive and constructive processes operate" and that the destructive processes are more common than constructive ones. Located in comparable environmental settings, biofilms coating tufa stalactites are similar to those described by Jones (1995), but the net result is clearly constructive.

Whereas classical tufa deposits are subaqueous and extensive, bestowing broad, relatively stable, and somewhat buffered environments for biofilm development, tufa stalactites are subaerial and situated in specific "spot" locations, providing for a wider range and greater spatial variability of microclimatic and other environmental parameters. This makes them an excellent field laboratory for studies of environmental influences on biofilm composition and dynamics. Even our preliminary observations by SEM, without any quantitative or enumerative approach, have shown that a bewildering array of different biofilms is associated with tufa stalactites, exhibiting profound differences between specimens and even within single specimens. We have identified at least five important parameters that determine the composition of species able to thrive, and thus control the nature of biofilm and the type and intensity of operative biological processes (Fig.5b). These are gradient-based variations in (1) illumination – ranging from full sunlight on cliff faces to shaded settings under overhangs and canopy and low light levels of cave entrances; (2) microclimate – humidity and temperature showing the greatest range in the least protected sites, and little variation deeper in cave entrance zones; and (3) proximity to the sea – ensuing different amounts of sea spray, if any. There are also largely random variations in (4) water availability and geochemistry, as individual stalactites are fed by separate epikarstic pathways and are characterized by different drip rates and chemical properties. These four factors exert control over yet another important aspect, that is (5) lithology and mineralogy of the precipitated substrate. Texture, hardness, porosity, and crystal size are partly environmentally determined and can affect the species composition and nature of colonizing biofilms. However, they are also interdependent with the same biofilms, considering that microbial biological processes, in turn, do affect lithological and mineralogical properties of the deposit whose precipitation they mediate. Adding to the complexity is the fact that environmental aspects can show pronounced seasonal changes, introducing

temporal variation to the nature of biofilm.

The processes operating in epilithic biofilms on carbonates are extremely complex and are only beginning to be understood (Chafetz and Buczynski, 1992; Pedley, 1992; 1994). Based on this first look at the biofilms on tufa stalactites, we have tentatively identified several key processes for which there is direct petrological evidence. Constructional processes are (1) photosynthetic enhancement of precipitation; (2) encrustation of cyanobacteria; (3) precipitation by heterotrophic microbes; and (4) trapping and binding of detrital material. In addition, erosional processes, notably (5) micritization; and (6) boring are also apparent but their impact is clearly overwhelmed by precipitation.

Photosynthetic enhancement

Photosynthetic activity by autotrophs in the biofilm is highly conducive to calcite precipitation (Pedley, 1992; 1994). It increases the local pH and thus augments the physico-chemical precipitation of microcrystalline calcite from the water. Calcite is spontaneously precipitated both on the individual micro-organisms (calcifying many in the process), as well as in the communal mucus.

Operative in many carbonate deposits, this photosynthetic enhancement of "background" inorganic precipitation is particularly obvious in subaerial tufa stalactites. This is because the vertical aspect and partly shaded locations of these deposits entail unequal illumination, causing the photosynthetic processes to be localized. The simple and often cited outcome is that the growth of photosynthetic prokaryotes and microphytes is usually more intensive on the daylight-facing sides of the stalactites. This results in the preferential deposition of calcite in those areas, and the "leaning" of the stalactites toward the light source (e.g., Bull and Laverty, 1982). It must be noted, however, that the same mechanism can cause the leaning of tufaceous stalactites away from the light. Considering that the photosynthetic organisms resident on tufaceous stalactites are commonly specialized for low light conditions of cave twilight zones (Cox and Marchant, 1977), their growth in certain locations may be inhibited by direct sunlight, causing the preferential growth to occur on the shaded sides of the deposits. Other biotic and abiotic factors that contribute to the non-vertical growth of tufa stalactites (both positively and negatively light-oriented, as well as erratic) certainly include the growth of macrophytes (both shoots and roots); patchy precipitation of calcite by heterotrophic microbes; localized decay of organic matter; influence of air currents and sea spray direction; and particularly the spatial and temporal variations in the microclimate (notably evaporation rates), which are atypical inside caves but broad in epigeal environments.

Encrustation of cyanobacteria

Unlike passive calcification by autotrophs, which is generated by photosynthetic modification of the medium and leads to spontaneous precipitation, the calcification of many cyanobacteria appears to be a more active process, in which they initiate and control the precipitation (Pentecost and Riding, 1986; Merz, 1992; Schneider and Le Campion Alsumard, 1999).

The type of cyanobacterial calcification most relevant to tufa stalactites is encrustation (Kobluk and Risk, 1977b; Jones and Motyka, 1987), which is the precipitation of calcite on the surfaces of cyanobacterial filaments. We have seen no evidence of organic filament replacement by calcite or calcite precipitation within the filaments (which would give rise to rod-like rather than the tubiform calcified filaments that we observed; see Klappa, 1979). Regarding the timing of calcification, it appears to occur during the life of the organisms. Whereas in some cases filament calcification is thought to occur only on dead cells (e.g., in the shallow marine environment; Kobluk and Risk, 1977a), this appears not to be the case in tufa stalactites. The preservation of filament structure, constant diameter and form, and lack of collapsed filaments (as reasoned by Jones and Kahle, 1986), all indicate that the calcification occurred prior to any decay. Furthermore, in our micrographs of outer surfaces of tufa stalactites and similar deposits, portions of resident cyanobacteria are clearly visible inside the tubes' central holes (Figs 3d; e). This makes the calcified filaments reported here quite unique, as no remnants of organic structures inside the calcite tubes have been

seen in vadose settings elsewhere. Therefore, these filaments are not merely fossils, as reported from other carbonate settings (James, 1972; Kahle, 1977; Knox, 1977; Klappa, 1979; Jones and Kahle, 1986; Jones and Motyka, 1997; Phillips *et al.*, 1987), but are structures contemporaneous with (and still occupied by) the living organisms responsible for them. In the outermost surfaces of some deposits, exposed organic filaments can be seen extending at least 30 μm out of their calcified tubes (Fig. 3f).

Another valuable insight comes from the extremely porous, several cm-thick, soft tufa patches that locally coat limestone bedrock and older tufa. These pasty deposits are pure cyanobacterial colonies, appearing as tangled webs of calcified filaments without any matrix filling the voids between them. It has previously been suggested that the source of CaCO_3 in calcified cyanobacteria are limestone clasts, which are serving as substrate (Schroeder, 1972); but this is clearly not possible where calcified filaments are in contact only with other identical filaments and not with the bedrock. Instead, the source of CaCO_3 are most likely epikarstic and meteoric freshwater, which, as they seep out from the rocks or trickle across exposed limestone surfaces mobilize enough ions that are subsequently used by cyanobacteria to precipitate calcite.

The calcification mechanisms are not clear, but uniform shapes and sizes and orderly arrangement of crystals surrounding the filaments indicate that their formation is controlled by the cyanobacteria. Whereas it has been suggested that such regular patterns are not necessarily controlled by the cells, but rather by fluid geochemistry and crystallization rates (Pobeguín, 1954), this is not likely to be the case (1) where unique crystals surround only cyanobacterial filaments and are not found in adjacent areas with other potential nucleation sites (organic and inorganic substrates) and (2) distinct patterns of regular and organized crystals form successive layers surrounding cyanobacterial filaments. All this indicates that calcification is initiated and managed by the cyanobacteria, possibly by internal ordering of organic constituents of their mucilaginous sheets (Riding, 1977). Additional evidence of direct participation of cyanobacteria in calcite precipitation rests in the fact that numerous calcified filaments we observed are composed of dendritic crystals of calcite, a rare crystal form we have not seen on any other nearby substrates (including other types of intimately associated microbes). Dendritic crystals of calcite described by other authors (e.g., Barron, 1975; Jones and Kahle, 1986; Merz, 1992) were also reported as site-specific to certain cyanobacteria, which prompted Jones and Kahle (1986) to state that "*the algae itself or something associated with the algae must, somehow, be responsible for encrustation of the filaments...*".

The consequence of cyanobacterial encrustation are unique microfabrics and even entire stalactitic deposits that are essentially colonies of calcite-armoured cyanobacteria. In such deposits, only cells at the outer surfaces are alive, whereas those in the interior are fossilized in calcite (precipitated at the nucleation sites provided by the calcified filaments). Calcite gradually fills all pore spaces between the filaments (and also the voids within the filaments, transforming them from original tubular structures to solid rods). The final result are solid, case-hardened deposits, which are a truly bioconstructional variety of tufa stalactites.

Precipitation by heterotrophic microbes

The important role heterotrophic microbes play in the formation of some tufa has been demonstrated by Chafetz and Meredith (1983), Chafetz and Folk (1984), Folk *et al.* (1985), Chafetz (1986), etc. Both bacterially induced mineralization (Braissant *et al.*, 2003) and constructional activity by fungi (Jones and Pemberton, 1987) in terrestrial carbonates have been experimentally validated, although many of the numerous and complex metabolic pathways and direct precipitation processes remain poorly known (Castanier *et al.*, 1999).

Extensive masses of opaque micritic material found within some tufa stalactites are thought to be a result of heterotrophic microbial activity. In stark contrast with the transparent microcrystalline and sparry calcite attributed to inorganic precipitation from epikarstic water, they are comparable to bacterially constructed tufa of Chafetz and Folk (1984). These organic-rich fabrics are locally homogeneous masses lacking obvious structure, but elsewhere appear as dark

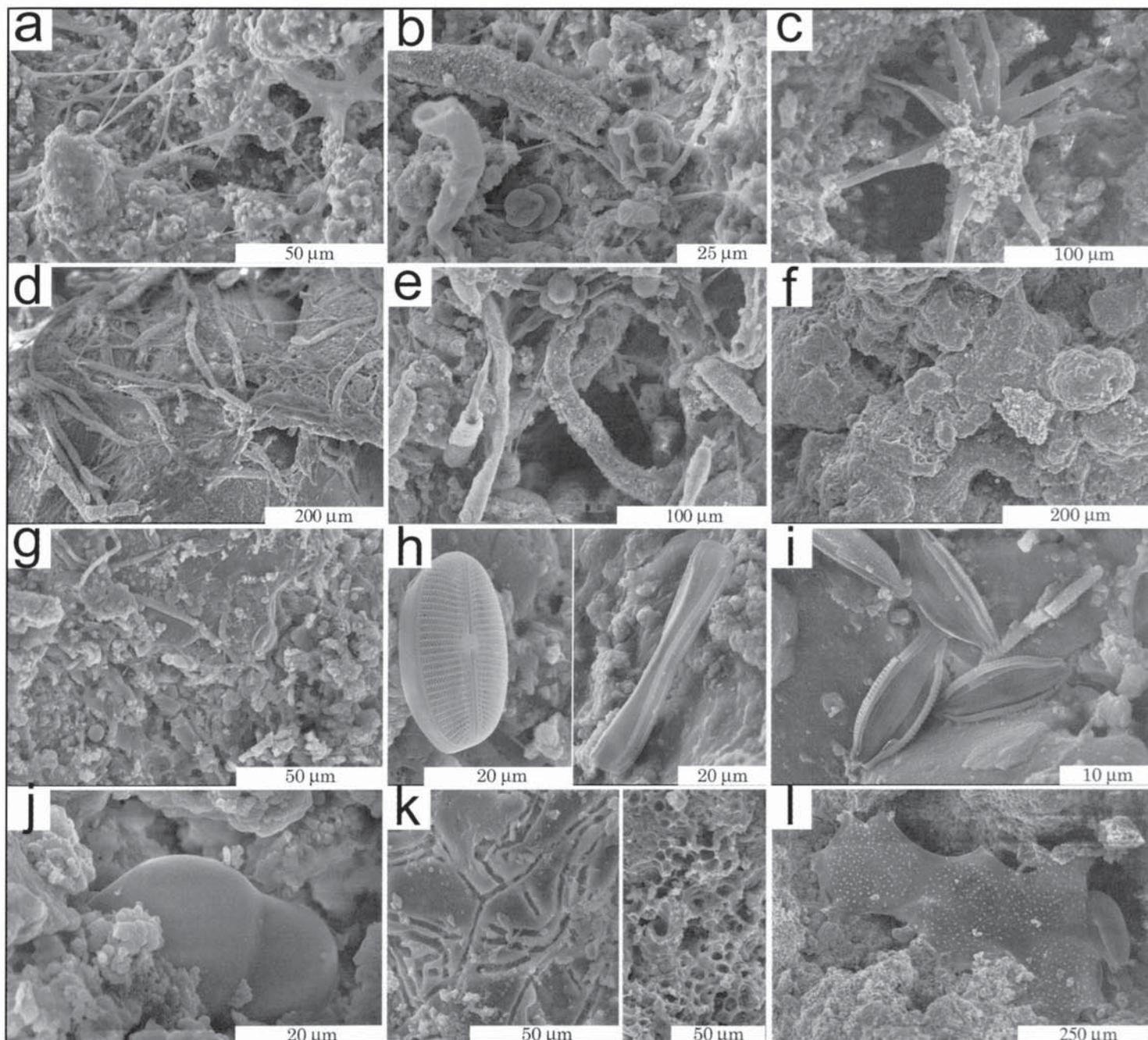


Figure 4. SEM micrographs of organisms associated with tuffaceous stalactites. a) Strands of mucus in the biofilm stretched on organic substrate. b) Bewildering array of microbes, spores, and calcified filaments on fungal or algal substrate. The unusual structure to the right of the centre may be a sporangium. c) An unusual biological structure partly covered by calcite crystallites. d) and e) Complex biofilms dominated by filamentous microbes. Note that only some of the filaments are calcified. f) Surface of a coastal zone tuffaceous stalactite deposit. Note that it is entirely composed of organic material. g) Biofilm at the surface of a coastal tuffaceous deposit. Note the fungal or algal mat substrate, and calcite grains and great variety of micro-organisms superimposed on it. h) and i) epilithic diatoms. j) Foraminiferal test interred in marine supratidal zone tufa. k) Traces of microbial boring at the surface of a tuffaceous stalactite in supratidal zone. l) Suspected eggs of an unidentified organism covered by a protective secretion, at the surface of a coastal zone tufa deposit.

layers curiously intercalated with plain microcrystalline calcite (Fig.2a). Such layering is never fine, dense, and regular as in speleothems, but rather irregular, convoluted, and discontinuous, which further evokes biological activity. The morphology of the dark organic-rich laminae (also recognized in certain speleothems and considered biogenic by Thraikill, 1976 and Jones and Motyka, 1987) suggests that bacteria-rich biofilms can dominate the outward-growing surfaces of stalactitic tufa deposits and, at times, be engulfed by succeeding layers of inorganically precipitated calcite from dripping vadose water. The alternations of light (plain microcrystalline calcite) and dark (organic rich) laminae could possibly be a result of seasonal variations in water availability, which are quite pronounced in tropical areas and affect the dynamics of surficial biofilms, likely causing shifts between inorganic and biogenic precipitation mechanisms.

In addition, the pisolith-like accretions found in tufa stalactites in marine coastal zones are also one likely result of bacterial activity. Consisting of fine, concentric laminae and reaching 15mm in diameter, they are a minor but evident constituent of subaerial tufa

forming within reach of surf and spray, and not found in deposits from inland areas. They are produced by coralliform growth (see Figs 5c and 6b in Taboroši *et al.*, 2003) at the outer surfaces of these coastal tufa deposits, and are comparable to numerous other bacterially-formed coated grains (e.g., Chafetz, 1986).

Trapping and binding

Much of the surface of tufa stalactites is lined by dense, tangled mats of filamentous microbes. These, combined with the ever-present fungal hyphae and plentiful mucus, are capable of trapping, binding, and incorporating detrital grains and organic material. This is the operative process responsible for the presence of various incidental inclusions, such as insect fragments, in the precipitated material. This role of the epilithic biofilm was also recognized by Jones (1995), who identified insect parts buried in the biofilms that coat cave walls in the Cayman Islands. Whereas this process implies certain genetic links with stromatolites (Riding, 1991), it is unlikely that it contributes significantly to deposit growth, because the amounts of alloigenous material available in the subaerial setting are

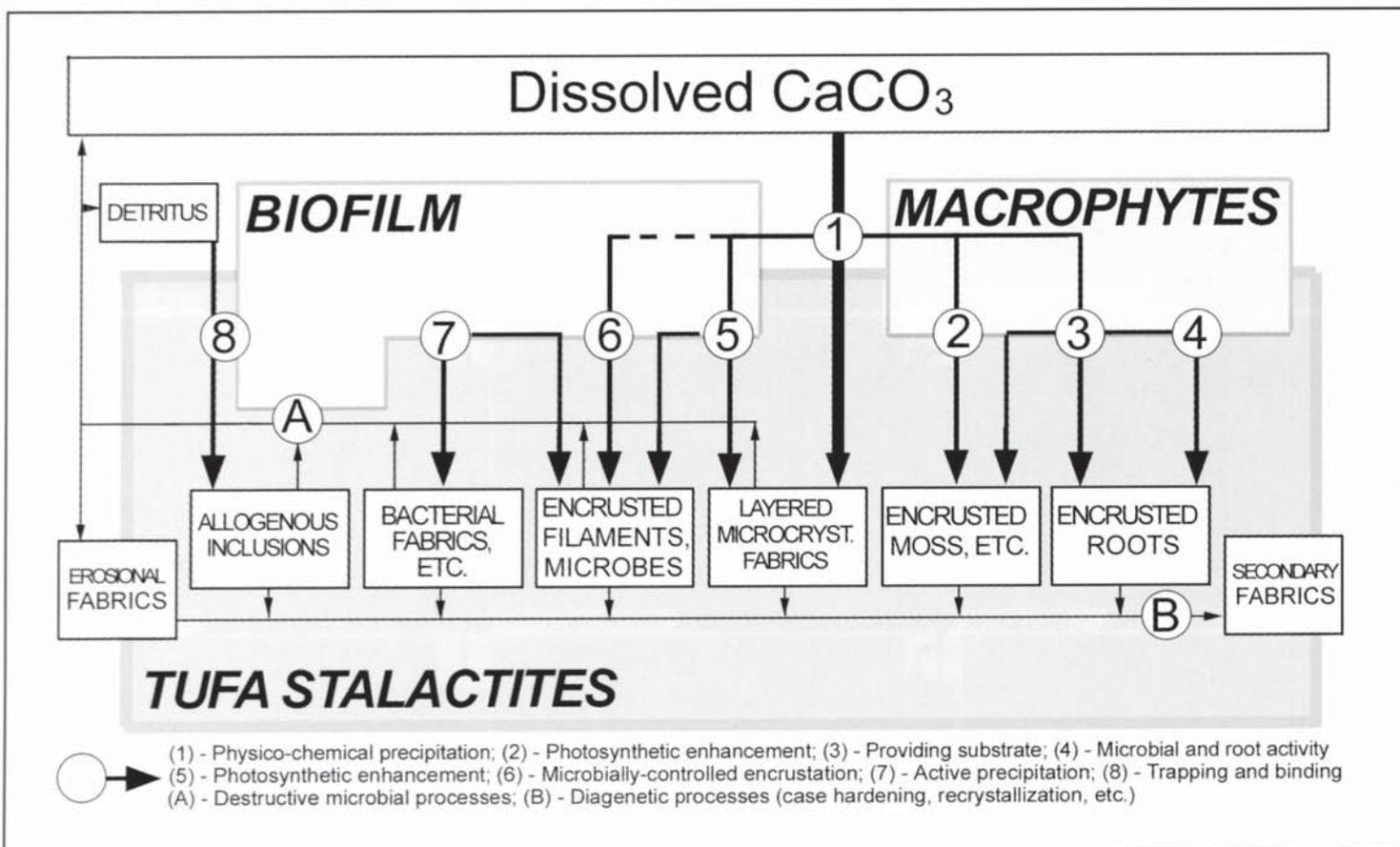


Figure 5. a) Conceptual model of the formation of subaerial tufa stalactites, outlining the main biological processes superimposed on physico-chemical precipitation and the resultant microfibrils.

minimal. In tufa stalactites, the trapped and bound material is usually limited to organic detritus, loose calcite grains, and aeolian particles, just like in the case of subaerial stromatolitic stalagmites described from cave entrances in Australia (Cox *et al.*, 1989; James *et al.*, 1994). A special case occurs on cliffs and overhangs in the marine supratidal zone, where tufaceous stalactites incorporate skeletal grains of marine origin. These grains can form substantial parts of some deposits (as a result of temporary contact with calcareous beach sand, for example) and are, to the best of our knowledge, the only example of allogenous marine carbonates interred in calcareous tufa.

The already discussed bioconstructional deposits of calcified cyanobacterial filaments and calcite matrix are also reminiscent of stromatolites, but a fundamental difference is secondary material that is precipitated in situ rather than transported, trapped, and stabilized as in typical, aquatic cyanobacterial stromatolites (Pentecost and Riding, 1986).

Erosional processes (micritization and boring)

Not all microbial activity in tufa stalactite biofilms is constructional. At least two erosional processes – micritization and boring – take place, but their overall impact is limited due to strong constructional activity.

Jones and Motyka (1987) have argued that microcrystalline calcite in some speleothems is a result of biological erosional activity, and Jones (1995) has shown clearly that biofilms in twilight zones of caves can have erosional effects on the substrate and produce a range of destructive microfibrils, including microcrystalline calcite produced by the biologically mediated breakdown of sparry calcite substrate (sparmicritization). This is highly significant to the study of subaerial tufa stalactites. It has been suggested that soft and porous stalactites exposed in surface settings in the tropics are not depositional tufa at all, but remnants of cave speleothems that have decayed following exposure to the out-of-doors (e.g., Halliday, 2000). Any residual calcite so modified by sparmicritization would be morphologically similar to precipitated microcrystalline calcite and difficult to distinguish from it.

Nevertheless, it is the precipitated and not the sparmicritized

microcrystalline calcite that forms the bulk of subaerial tufa deposits. Microcrystalline calcite of tufaceous stalactites forms metre-scale deposits, and it is highly implausible that they could form by decay of sparry calcite. Sparmicritization has been demonstrated to occur only up to 6µm from the rock surface (Jones 1987) and we have observed crumbly micritic material to a depth of just a few mm at the surfaces of indisputable cave speleothems that were exposed to sunlight and outside conditions by cave collapse. We have never encountered a tufa stalactite sample that would show a hypothesized sparmicritization front advancing from the surface toward what should remain a hard crystalline core. In addition, most tufaceous stalactites exhibit clear and undisturbed internal laminations, which presumably would be obliterated by sparmicritization. Although the possibility that sparry calcite of normal cave speleothems can decay into tufa-like masses remains to be considered in future research, we are convinced that the bulk of the microcrystalline material of the epigeal, tufaceous stalactites discussed in this paper was precipitated as such. Some biologically mediated micritization almost certainly occurs on the outside surfaces, but it is overwhelmed by the depositional facets of the biofilm.

A more obvious mark of microbial erosional activity is provided by various borings, which are common in the outer surfaces of tufa stalactites, particularly in the coastal zone, but do not penetrate beyond 1mm depth.

CONCLUSION

Stalactitic deposits of subaerial tufa (tufa stalactites) are a common feature of tropical karst areas, where they occur in a variety of epigeal (e.g., scarps, overhangs, and the undersides of collapse boulders) and transitional epigeal–spelean settings (e.g., cave entrances and widened fractures). Genetically and morphologically related to both speleothems and classical tufa deposits, these features can be viewed as intermediate forms between the two. Like cave speleothems, tufa stalactites are produced by vadose water, which emerges from the bedrock, degasses CO₂ to attain equilibrium with the atmosphere, and precipitates CaCO₃. However, because tufa stalactites form in epigeal settings, the increased evaporation effects

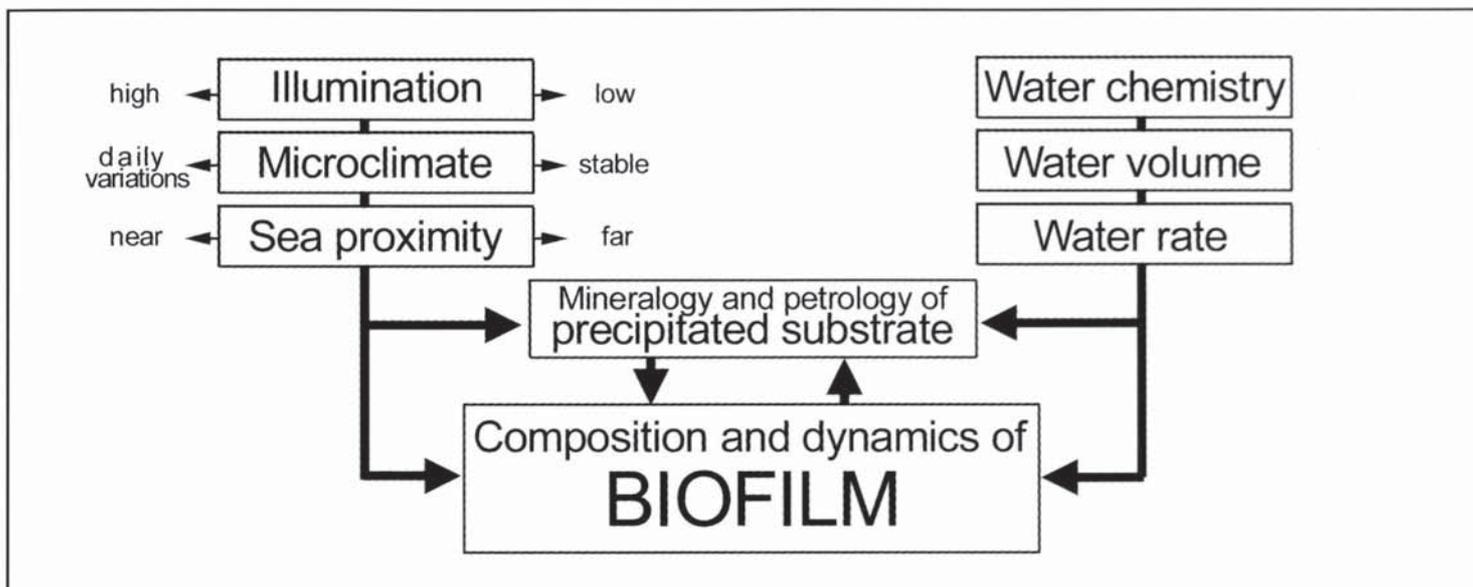


Figure 5. b) Inorganic factors determining the species composition and dynamics of epilithic biofilms on subaerial tufa stalactites.

induce rapid deposition of calcite, which results in crystals of more random orientation and smaller size compared to those of normal carbonate speleothems.

The soft and porous nature of the resultant tufaceous deposits, combined with locations reached by daylight and ample nourishment by water translate to intricate microhabitats harbouring a wide range of biota. We have identified bacteria, cyanobacteria, fungi, eukaryotic algae, bryophytes, higher plants, and invertebrates, all living in association with the tufa stalactites and in complex inter-relationships with each other. This implies a variety of biological processes, ranging from the largely inconsequential colonization and minor bioerosion to the significant photosynthetic enhancement of carbonate precipitation and direct biomineralization. These complicated and poorly understood biological influences are superimposed on the essentially inorganic underlying mechanism; and based on the relative contribution of biological versus inorganic factors, they produce a bewildering array of allied fabrics and deposits, including some biogenic and bio-constructural forms.

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The invertebrate fauna of the Ogof Ffynnon Ddu cave system, Powys, South Wales, UK.

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Abstract: The Ogof Ffynnon Ddu cave system is one of the largest in Great Britain and supports a rich and diverse fauna. At least 62 taxa have been recorded, including 3 troglobites, 4 stygobites, 26 troglaphiles, 8 stygophiles, 2 threshold troglaphiles, 5 threshold troglaxenes, and 14 accidental taxa. Taxonomically the fauna is composed of 1 platyhelminth, 3 annelids, 1 mollusc, 10 Crustacea (including 4 stygobites), 3 diplopods, 13 Collembola (including at least 2 troglobites), 2 Trichoptera, 2 Lepidoptera, 1 hymenopteran, 9 Diptera (with 1 troglobite), 11 Coleoptera, 3 Araneae and 3 Acari. It is very likely that some components of the current fauna, most probably the stygobitic Crustacea, survived some or all of the Pleistocene glaciations within the system.

Dedication: *To the memory of Jeff Jefferson, the most articulate cave biologist of his generation. He took the data collected by many, collated by Mary Hazelton into the Biological Records, and produced several seminal reviews, which not only informed but also provide deep insight into many important problems in biospeleology.*

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PREFACE

This paper is based principally upon a study carried out by the first two authors in 1979. Jeff Jefferson obtained a grant from the Nature Conservancy Council (NCC) to study the invertebrate fauna of Ogof Ffynnon Ddu II. Jeff and Phil Chapman carried out this study between January and March 1979. Their findings were compiled into a report for NCC (Jefferson and Chapman, 1979) but never

published. Since this work is of great significance, the successor to NCC in Wales, the Countryside Council for Wales (CCW), and Phil Chapman, were approached for permission to put the work into the public domain. They agreed to this and the fourth author prepared the present paper, incorporating data from the original report, new distribution data provided by the third author, and additional data from other sources.



Figure 1. Androniscus dentiger a common troglaphilic isopod. Photograph by Phil Chapman.

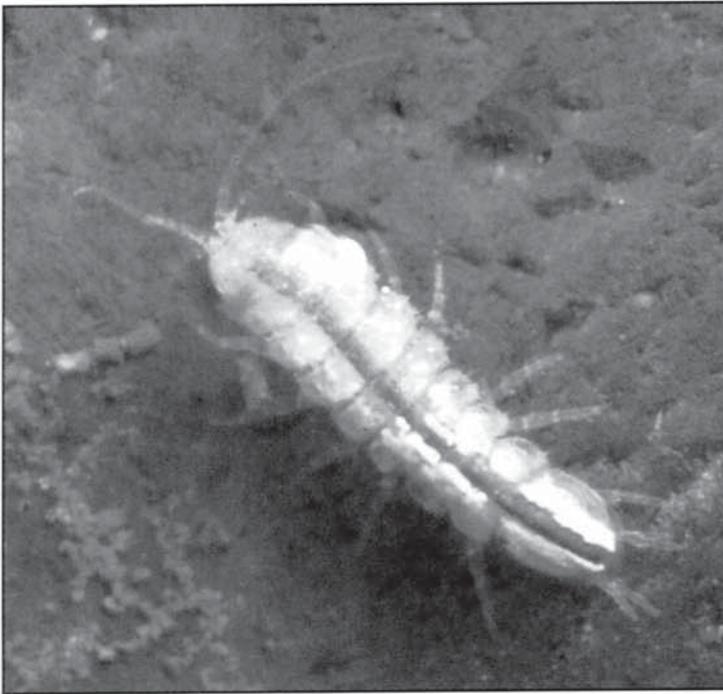


Figure 2. *Proasellus cavaticus* is a stygobitic isopod. Photograph by Phil Chapman.

INTRODUCTION

Ogof Ffynnon Ddu (OFD) is an extensive cave system situated in the Tawe valley, Powys, South Wales (NGR SN 848 152). It was first entered in 1946 (OFD I), with major extensions in 1966 (OFD II) and 1967 (OFD III). With well over 50km of surveyed passage it is the third longest cave in the British Isles, and, at 300m, the deepest. It is among the 50 longest caves in the world. The system displays enormous complexity, with great diversity in passage age and morphology and in the nature and magnitude of sedimentary deposits and speleothems. Passage types range from active streamways with fast-flowing streams, which are susceptible to powerful scouring floods, to high-level, relict, tunnels with clastic sediments and speleothem growth.

The cave's length and complexity developed over a very long period. Few absolute dates are available, but one flowstone sample from a high-level passage near the highest entrance (Top Entrance) has been dated to 267 thousand years before Present, and was deposited during the Hoxnian Interglacial (Smart and Christopher, 1989). A major vadose passage, The Traverses, is 50m high and lies 28m above the current active stream. Data from the Yorkshire Dales suggest that vadose downcutting occurs at 5 to 20cm 1000^{-1} years (Gascoyne, *et al.*, 1983). On the basis of the evidence above, using an average downcutting rate of 10cm 1000^{-1} years, The Traverses



Figure 3. *Niphargus fontanus* is a stygobitic amphipod which probably preys on *Proasellus cavaticus*. Photograph by Phil Chapman.

and the current streamway have taken 780,000 years to form. It is likely that the OFD system has been developing for at least 1 million years. The cave has been described by O'Reilly *et al.* (1969) and Stratford (1995), with geological and other details in Smart and Christopher (1989).

The first fauna collected from OFD was the millipede *Blaniulus guttulatus*, collected by Aubrey Glennie on January 2nd 1949 (Hazelton, 1959, p.14) (30 years to the day before the start of the Jefferson and Chapman study). The first stygobite, the amphipod *Niphargus fontanus*, was collected by Mary Hazelton on 31st July 1949 (Hazelton, 1959, p.15). Since then many more animals have been collected and there are now at least 62 taxa known throughout the system (Appendix 1). Most of these were collected, or observed, *ad hoc*, and the only systematic and extensive study is that of Jefferson and Chapman (1979). The following pages record their findings together with complementary information from other sources. Taken together, the 1979 survey, and other studies reported below, these data form a statement of the current biological knowledge of this extensive cave system.

The Jefferson and Chapman 1979 survey of OFD II

The NCC contract ran from January 2nd to March 16th 1979. OFD II was covered as fully as possible, with visual searches for animals being the main activity, although a certain amount of baiting was also undertaken. Animals were only collected if they could not be identified in the cave. Observations of abundance, behaviour and habitat were made and some samples taken for determination of organic matter content. Temperature and humidity values were recorded in some places (Appendix 2). Cave sites where animals were found were recorded onto a survey plan. These distribution maps are included in the report to NCC (Jefferson and Chapman, 1979) but it is not possible in some cases to determine with certainty exactly where the animals were found. For this reason the maps are not included here.

FAUNA RECORDED DURING THE 1979 SURVEY OF OGOFF FFINNON DDU II, WITH ECOLOGICAL NOTES

Annelida ("worms")

Oligochaeta

Aeolosomatidae

Aeolosoma hemprichi. Stygophile.

Abundant in a small, drip-fed, pool in OFD II (Jefferson, 1989, p.59). Living in a layer of silt and feeding on bacteria or detritus.

Lumbricidae

Undetermined. Stygophile.

Found in sediments where it is probably a detritivore.

Enchytraeidae

Undetermined. Stygophile.

Widespread and probably common, though inconspicuous. In organic detritus, dipteran carcasses and "peaty" sediment. Amphibious and probably a detritivore.

Annelida of various families are probably much more important in aquatic sediments, and elsewhere, than currently recognised.

Mollusca

Stylommatophora

Zonitidae (snails)

Oxychilus cellarius. Troglophile

Living animal not recorded. Remains (shells) locally common below known or suspected entrances.

Crustacea

Ostracoda

Only one species of ostracod (*Cavernocypris subterranea*) has been

recorded (Jefferson, 1989) but it is of great interest. It was first recorded in OFD by Eddington and Jefferson on 3rd August 1965, in Column Passage (Hazelton, 1967, p.230). Apart from this cavernicolous population in OFD, it is known from only three springs in southern England (in Surrey, Sussex and Buckinghamshire), and a spring near Malham Tarn (Yorkshire) (Proudlove *et al.*, 2003). Within OFD, Chapman (1993, p.156) notes that "...[*Cavernocypris*] *subterranea* is quite numerous in the mesocavernous seepage water running over flowstone slopes". It is very likely that the population of *C. subterranea* in OFD is effectively stygobitic, as there is no possibility of genetic exchange with other populations. In Europe it is known from cave and hyporheic habitats (Meisch, 2000, p.386). Meisch (2000, p.386) records that it is widely distributed throughout Europe, excluding Ireland. Further studies of this population are required.

Copepoda

Cyclopidae

Stygophiles

Three species of copepod (*Paracyclops fimbriatus*, *Acanthocyclops vernalis*, *Megacyclops viridis*) have been recorded. Nauplii locally common (adults less so) on peaty sediments of shallow, sluggish streams. It is probably benthic, feeding as a detritivore and/or scavenger. Copepods are probably widespread and common in aquatic habitats in OFD. They were not searched for specifically, as their small size demands special equipment.

In common with the Annelida it is very likely that copepods are of great importance in the subterranean ecosystem of OFD. Two of the species recorded here (*Acanthocyclops vernalis* and *Megacyclops viridis*) are very common in groundwater and are also known from the Dan yr Ogof system on the other side of the Tawe valley (Eddington, 1977).

Isopoda

Trichoniscidae (wood lice)

Androniscus dentiger. Troglophile. (Fig.1)

Attracted to liver bait close to Top Entrance. This is the commonest troglophilic isopod in British caves and is also common in caves across Europe. Genetic studies by Gentile and Sbordoni (1998) have demonstrated that individual populations of this species, in separate caves, are very distinct and do not exchange genes with other cave populations or with surface populations.

Asellidae (water lice)

Proasellus cavaticus. Stygobite. (Fig.2)

Widespread and common in water films on flowstone, in shallow gour pools, under rocks in larger trickles. Frequent where flowstone is covered with slimy brown film, possibly bacterial in origin. Diet probably consists largely of filamentous bacteria/fungi.

P. cavaticus appears to be common in thin films of water on brown-stained flowstone (8 out of 13 records in OFD II). From the dark gut contents of specimens in such habitats it appears that the fine dark brown sediment present on such flowstones is frequently ingested. Bacteriological examination of both the silt and of surface scrapings from the flowstone itself should be included in a future study. Another potential energy source in such habitats is a thin brown bacterial bloom (visible due to the interference colours produced in low-angle incident light) that occurs on the more "static" water films of such slopes. However in order to feed upon this the animals would need to break the surface film of the water in which they live and such behaviour has not been observed. Several known *P. cavaticus* habitats of the above type were observed contemporaneously with a heavy flooding of the main water conduits (11th March 1979). There appeared to be very little increase in water flow at most of the sites. We have never seen *Niphargus fontanus* (probably the main predator of *P. cavaticus* in the cave) on steep stalagmitic walls, although they may be present in nearby pools. We therefore conclude that *P. cavaticus* frequents such walls for at least three reasons: 1. There is an adequate food supply, 2. It is a stable habitat with little washout risk, 3. It is free from at least one major predator.

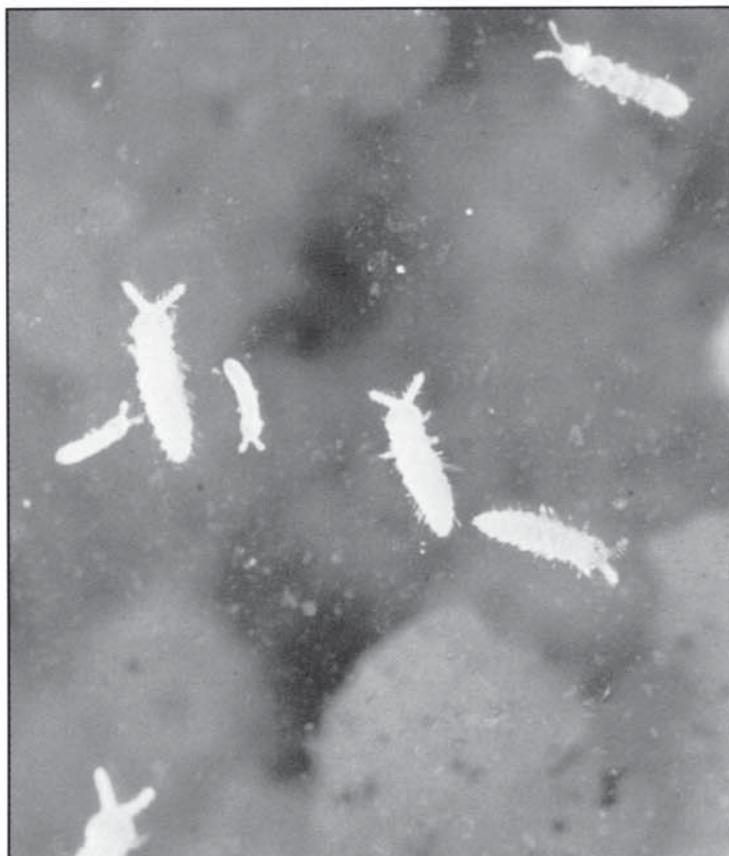


Figure 4. *Collembola* in the *Schaeffereria emucronata* group on a pool surface. Photograph by Phil Chapman.

P. cavaticus has been seen intermittently in other habitats such as the edges of a small stream entering Arete Chamber and a nearby stream close to Gnome Passage. Also in a small, calcite depositing, trickle in Chasm passage, in Columns Hall, and in a single isolated pool close to the Big Chamber Near the Entrance. Examination of the first two failed to reveal any specimens during the severe flood of 23rd March 1979. This was not surprising as there are few refugia, and water flow had increased to the point where it was able to move small pebbles, let alone small isopods. This extreme habitat instability suggests that such streams represent only marginal habitats for this species.

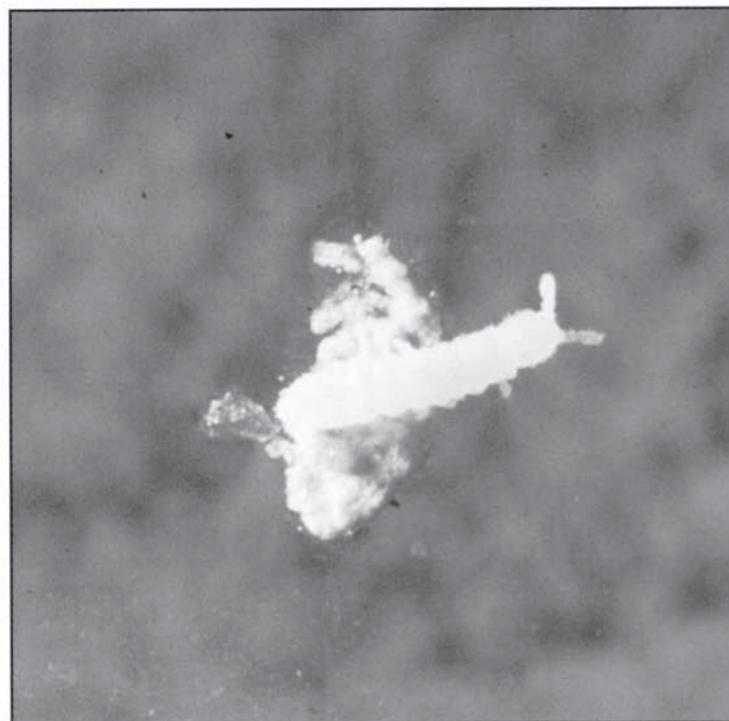


Figure 5. *Archaphorura schoetti*, a troglotic collembolan, on a raft of *exuviae* with a single large egg. Photograph by Phil Chapman.



Figure 6. The caddis fly *Stenophylax permistus* aestivates in caves during the summer. Photograph by Phil Chapman.

P. cavaticus is exceptionally sedentary. In one case the same individual was seen in the same part of the same small static pool at least weekly from 8th January to 11th March 1979. Such behaviour (or lack of it) may be adaptive in conserving the scarce energy resources available in certain habitats.

Subsequent observations by JC during the 1990s to the present day confirm many of Jefferson's and Chapman's original observations of *P. cavaticus* in OFD. *P. cavaticus* continues to be found throughout the cave, but usually limited to one or two individuals in small pools and water seeps. However large numbers of *P. cavaticus* have been observed on a number of occasions. During 1995 a visit to a high-level series, the Great Oxbow Series, revealed large numbers of *P. cavaticus* in a gently ascending passage ending in a static sump. The flowstone floor had numbers of *P. cavaticus* exceeding 20m⁻² for a considerable length of the passage. This also included numerous individuals of *Niphargus fontanus*. This passage is in a part of the cave that is not regularly visited, but has yet to receive a repeat visit by the third author.

P. cavaticus has also been observed in large numbers in the OFD I main streamway, in areas such as the 'Step'. In areas of calmer water, and in the lee of large rocks, large adult specimens of *P. cavaticus* can be found. The lower the main streamway water level the easier it is to observe this population. It is unclear whether these animals have been washed out of the upstream sump complex or actively able to maintain their position in the main streamway.

Amphipoda (freshwater "shrimps")

Niphargidae

Niphargus fontanus. Stygobite. (Fig.3)

Widespread in trickle-fed pools and small streams, often in crevices, under stones or in mud cracks. Predator/detritivore, may supplement diet with bacteria-rich silt. Silt is a known, and important, part of the diet of stygobitic amphipods including various *Niphargus* species (Ginet, 1960) and *Crangonyx antennatus* (Dickson, 1979).

Although widespread *N. fontanus* is not common. Records are usually of single individuals, so perhaps no more than a dozen specimens in all were seen during the course of this study. Typical habitats are quiet pools in small streams. The animal's shape and semi-cryptic habits allow it to escape the ravages of floods and it is consequently found in some fairly flood-labile streams. Tracks, probably made by this species, are common in the mud floors of pools in some passages from which the animal itself is not recorded. Such tracks were seen in a series of isolated pools in one passage, suggesting that short out-of-water migrations took place from pool to pool.

Recent observations by JC confirm that *Niphargus fontanus* is widespread in OFD. Continued observations show *N. fontanus* to be still present at many of the sites examined by Jefferson and Chapman in OFD II. *N. fontanus* was also observed among a large aggregation of *Proasellus cavaticus* in the Upper Oxbow Series of



Figure 7. The Herald moth, *Scoliopteryx libatrix*, hibernates in caves during the winter. Photograph by Phil Chapman.

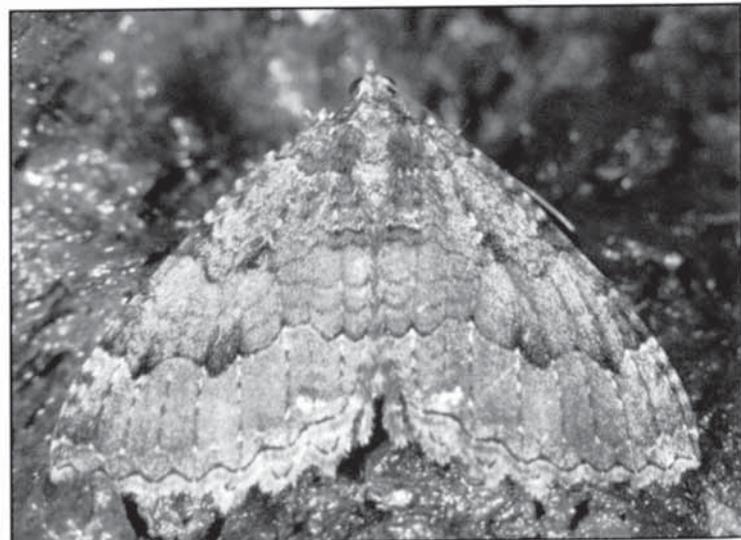


Figure 8. The Tissue moth, *Triphosa dubitata*, hibernates in caves during the winter. Photograph by Phil Chapman.

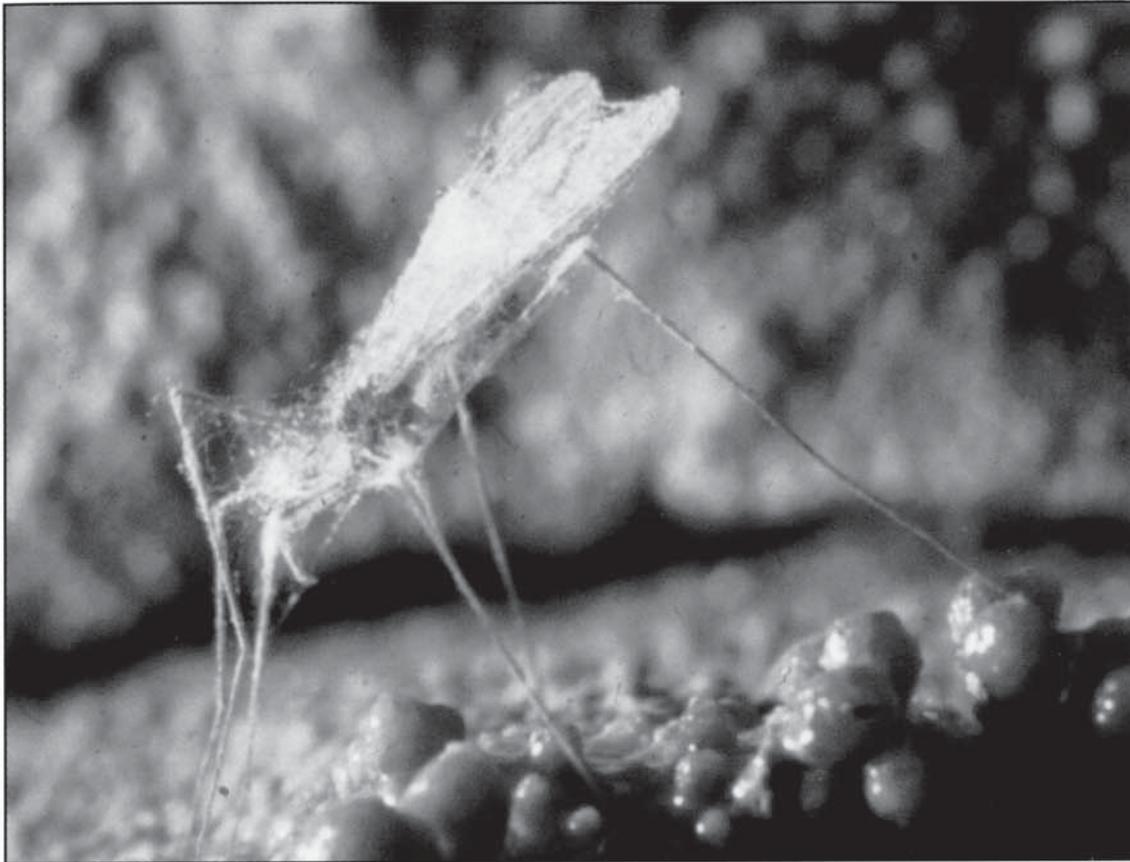


Figure 9. *Trichocera maculipennis* adult. Photograph by Phil Chapman.

OFD II during 1995. It also appears that *N. fontanus* can be highly mobile. Many of the pools and small streams that hold *N. fontanus* populations dry out periodically during prolonged dry periods. Yet, when water returns, then so do the *N. fontanus* populations. Another interesting observation has been the absence or presence of *N. fontanus* in pools along the main "trade routes" [the routes followed most commonly by cave explorers] in the cave. Regular observation of a series of pools along the trade route in OFD I showed many potentially good *N. fontanus* sites to lack the amphipods. However a few such pools do contain good populations of *N. fontanus*, despite being shallow and well trodden by passing cavers. A good example of this is a broad, but shallow trickle-fed pool at the 'Junction' in OFD I. This pool usually contains 5 to 10 individuals of *N. fontanus*.

OFD contains three stygobitic Crustacea, the ostracod *Cavernocypris subterranea*, the amphipod *Niphargus fontanus* and the isopod *Proasellus cavaticus*. All of these species have very poor dispersal abilities and it seems improbable that they have migrated into this area since the last glacial maximum c.18,000 ybp. It is certainly possible to hypothesise that they have been resident within OFD throughout the Pleistocene. A phylogeographical study using DNA divergence rates is currently being planned to address this question (Proudlove *et al.*, 2003, Proudlove and Wood, 2003).

Insecta

Collembola (springtails)

A note on the taxonomy of Collembola

The taxonomy of Collembola that are recorded from Britain and Ireland is in a state of flux. After a long period when this group received little serious study it is now the subject of major revisions. Dr Steve Hopkin of the University of Reading is reviewing the whole collembolan fauna and it is very likely that his work will result in numerous alterations to taxonomy and nomenclature. In the following discussion currently accepted names are used and notes are appended where necessary. Hopkin's ongoing work can be accessed at the following site, where URLs for the relevant maps and descriptions for each species are provided:

(www.ams.rdg.ac.uk/zoology/collembola/maps/)

Hypogastruridae

Schaefferia emucronata group. Troglophile. (Fig.4)

Locally abundant on pool surfaces near entrances. Favours small pools in flowstone containing floating organic detritus (e.g. collembolan exuviae and dipteran carcasses), probably feeding as an omnivore. Also recorded near The Confluence. Recorded by Jefferson and Chapman (1979) as *Schaefferia lindbergi*. The component species of the *emucronata* group (which includes *lindbergi*) cannot be separated reliably.

(www.ams.rdg.ac.uk/zoology/collembola/maps/030SCemu/)

Onychiuridae

Archaphorura schoetti. Troglobite. (Fig.5)

Widespread and common, particularly on pool surfaces. Seems equally at home in eutrophic and highly oligotrophic regions of the cave. Sluggish in movement. Probably feeding as an omnivore. This is the most common troglitic collembolan having been recorded from many caves in Great Britain as widely separated as Sutherland (Scotland) and Devon. It is also found in mines, but how it colonises these is not known. Also recorded from caves in Ireland (Proudlove and Hopkin unpublished). Recorded by Jefferson and Chapman (1979) as *Onychiurus schoetti*.

(www.ams.rdg.ac.uk/zoology/collembola/maps/091ARsch/)

Protaphorura armata group. Troglophile.

Single immature specimen on a pool surface in the Nave (a deep cave habitat). Recorded by Jefferson and Chapman (1979) as *Onychiurus armatus* group.

(www.ams.rdg.ac.uk/zoology/collembola/maps/119PRarm/)

Onychiurus fimetarius group. Troglophile.

Surface of a single pool covered by a "greasy" film containing bodies of Diptera. Omnivore. *Onychiurus 'fimetarius'* is a species complex whose relationships are not yet resolved. Specimens from OFD should probably be given the name *O. cebennarius*.

(www.ams.rdg.ac.uk/zoology/collembola/maps/103ONfim/)

Isotomidae

Isotoma notabilis. Troglophile.

Widespread and common on larger, muddier pool surfaces away from entrances. Often in considerable numbers on pools with no 'greasy' surface film. Probably an omnivore.

(<http://www.ams.rdg.ac.uk/zoology/collembola/maps/296ISnot/>)



Figure 13. *Speolepta leptogaster* (larva) on its web of silk threads. Photograph by Phil Chapman.

seen moving along these threads and while thus suspended, the head is slowly passed to and fro over the cave wall in a series of sweeping movements. We interpret this as feeding behaviour, and suggest that the larvae are grazing on micro-flora present on the cave wall. In addition to providing a rapid pathway across the feeding area, the threads appear to serve a second important function. Prior to pupating, the larvae assume a head-down vertical position in the web, suspended by the tip of the abdomen. The pupa retains this position and it may well be that the web, by suspending it clear of the cave wall, serves to protect the pupa from fungal attack. It may be that a selective advantage accrues from pupating on the drier parts of cave walls and this may in part explain the presence of larvae in such apparently trophically-poor habitats. An obvious strategy would seem to be for larvae to spend their period of active growth on the damper, trophically-rich, parts of the cave wall and then to migrate to the drier regions in order to pupate. We have not observed such behaviour, but one larva on damp flowstone was observed to have moved about 40cm over a two-week period, spinning new scaffolding web as it moved. Obviously much more could be learned about the behaviour of this most interesting animal by further regular observations in OFD II.

The principal study of this species is that of Matile (1962). In England Laurence (1982, 1989) studied a population in a London cellar. This population differed from the OFD one in that larvae were never seen, and were assumed to be hidden in cracks in the wall.

***Exechia parva*. Accidental.**

Single specimen beneath rock just inside Top Entrance.

Sciaridae

***Sciara* or *Bradysia* sp. adults. Troglophile.**

Remains widespread and common. Living animals widespread in damper passages. Unlike *Speolepta*, adults much more common than larvae. Remains of adult sciarids are relatively common throughout the cave, though living animals are less frequently seen. However their exact place in the cave ecosystem is quite baffling. It is not even clear how many species are represented (possibly at least three).

***Sciara* or *Bradysia* sp. larvae.**

Only one sciarid larva has been taken, and this was on a small patch of well-decomposed vegetable detritus some way from the entrance.



Figure 14. *Heleomyza serrata*. Photograph by Phil Chapman.

Heleomyzidae

Heleomyza serrata. Accidental (?). (Fig.14)

Adults locally abundant near known, or suspected, entrances. Numerous observations of copulation during February and March 1979, although no larvae were seen. Adult presence in cave is enigmatic. Entry may be accidental due to orientation to air currents, positive thermotaxis in late autumn, or it may be deliberate. May enter as larvae showing positive geotaxis just prior to pupation. Adults may hibernate in caves, but this is unlikely as significant numbers are present all year round.

This is perhaps even more baffling in its occurrence in caves than is *Sciara*. Adults are abundant close to Top Entrance and above the pitch that leads into Column Hall. In OFD they are present in considerable numbers throughout the year and so they are obviously not hibernating in the cave. Larvae have not been recorded from the cave, which would suggest that the species is not troglomorphic. We can only conclude that they are probably accidentals. One possibility is that the larvae feed on sheep droppings on the surface above the cave, and on burrowing into the soil to pupate, accidentally enter crevices connected to cave passages. The newly-emerged adults may move towards the comparatively warmer air of the cave and be unable to find their way out. This explanation rests on a number of suppositions that it might be possible to test in the laboratory.

Many flies succumb to fungal attack while in the cave, and bodies in various stages of decomposition are extremely common in several passages (Fig.15). These, together with their fungal attackers, might seem to present a major source of food for cavernicolous invertebrates. However there are no records of any cave invertebrate being taken on either dead fly or fungus, apart from one instance where Collembola and enchytraeid worms were taken on a single, well-decomposed *Heleomyza* carcass on a pool surface near the Mini Columns. In this one case it appears likely that the fungal spores filling the carcass were the attractant food source, and it may be that such spores released by mature fungi on the walls provide an important dietary requirement of Collembola on pool surfaces nearby. Nevertheless, in view of the numbers of animals that are able to survive in the very trophically-deprived deep cave environment, it is quite extraordinary that such an obviously rich energy source as the carcasses and their fungal attackers should be almost totally neglected by the cavernicolous fauna.

This interpretation of the biology of *H. serrata* is at odds with that of Harvey (1977). He studied this species in a mine in Scotland and found that it used the mine for hibernation between August and March. This behaviour was also noted in Springs Wood Level, Yorkshire, by Richardson (information in Harvey, 1977). In common with the flies in OFD many of the mine tunnel flies became fungally infected.



Figure 15. *Heleomyza serrata* attacked by fungus. Photograph by Phil Chapman.

Arachnida

Acari (mites)

Veigaiidae

Veigaiia sp. Troglophile.

One specimen attracted to liver bait near Top Entrance. Predator on Collembola and other small insects.

Rhagidiidae

Rhagidia spp. Troglophiles (possibly troglobites).

Widespread, but infrequent. On pool surfaces, under rocks or detritus. Predators on Collembola. At the time the original report was prepared the acari had not been identified beyond genus and there may be more than one species of *Rhagidia*, one or more of which may be troglitic.

Mammalia

Chiroptera (bats)

Remains widespread but infrequent away from entrance regions. No live records.

Chiroptera droppings

Observed in various places.

A NOTE ON PREDATORS IN THE OGOFFYNNON DDU SYSTEM

One of the striking features of the OFD system is the great scarcity of terrestrial predators. The only well-represented genus is *Rhagidia* and there may be several species present. They occur infrequently, but widely, throughout the system on pool surfaces and damp silt, amongst detritus and under rocks. Remains of two other troglomorphic predators, *Trechoblemus micros* (Coleoptera: Carabidae) and *Lesteva pubescens* (Coleoptera: Staphylinidae), are scarce and living beetles are rare (only one recorded in three months despite the use of attractant baits). Another potential predatory group, the spiders, have not been recorded from the dark zone of the cave. This absence is a reflection of the generally very poor trophic resources of the cave (excluding streamways and the inexplicably under-utilised resource represented by *Heleomyza serrata*). It may also reflect the timing of the survey (January – March) and may change later in the year.

Aquatic predators are represented by *Niphargus fontanus* and by partially depigmented trout (*Salmo trutta*) in the main streamway. The main streamway (Nant Newydd) is fed by a sinking stream that carries considerable numbers of aquatic insect larvae into the cave. These presumably provide the bulk of the diet for the trout. Away from the streamway food is scarce (though less so in aquatic than terrestrial habitats).

Phoridae

Phora sp. Accidental.

Single dead specimen above and near Column Hall.

Kjaerandsen (1993) studies the Diptera of caves and mines in southern Norway. He found *T. maculipennis* uncommon but *C. pipiens* and *H. serrata* common. All of the *C. pipiens* individuals were female. He did not record *S. leptogaster*.

Coleoptera (beetles)

Carabidae

Trechoblemus micros. Troglophile. (Fig.16)

Remains widespread but infrequent. Feeding as a predator. This beetle is one of the commonest in British caves and its apparent rarity in this large cave is anomalous.

Staphylinidae

Lesteva pubescens. Troglophile. (Fig.17)

Infrequent. One specimen near Top Entrance in small, low-level passage. Probably feeding as a predator.

ASSOCIATIONS BETWEEN PAIRS OF SPECIES OF COLLEMBOLA

OCCURRING ON POOL SURFACES IN OFD II

Presence/absence of 10 species of Collembola was recorded from 48 pool surfaces throughout OFD II. Three species occurred on only one or two pools and are not considered further. A fourth species, *Maegalothorax minimus*, is too small to identify positively in the field and is also difficult to catch, and it too is not considered. Results for the remaining six species were tested by using a contingency table. This yields a measure of significant association between species pairs in the form of values of the corrected chi-squared (X^2) greater than 3.84 (Southwood and Henderson, 2000). Significant values of chi-squared may be converted to a coefficient of mean square contingency (CMSC) giving values from +1 (complete positive association) to -1 (complete negative association). The results are given in Table 1.

Species pair	Corrected X^2	CMSC *
<i>A. schoetti</i> / <i>S. emucronata</i> group	-1.40	
<i>A. schoetti</i> / <i>A. pygmaeus</i>	-63.5	-0.40
<i>A. schoetti</i> / <i>I. notabilis</i>	-4.26	-0.34
<i>A. schoetti</i> / <i>Folsomia</i> sp.	-1.14	
<i>A. schoetti</i> / <i>P. "dobati"</i>	-0.43	
<i>S. emucronata</i> group / <i>A. pygmaeus</i>	+0.44	
<i>S. emucronata</i> group / <i>I. notabilis</i>	0	
<i>S. emucronata</i> group / <i>Folsomia</i> sp.	+13.26	+0.61
<i>S. emucronata</i> group / <i>P. "dobati"</i>	+0.04	
<i>A. pygmaeus</i> / <i>I. notabilis</i>	+10.78	+0.56
<i>A. pygmaeus</i> / <i>Folsomia</i> sp.	-0.05	
<i>A. pygmaeus</i> / <i>P. "dobati"</i>	+0.04	
<i>I. notabilis</i> / <i>Folsomia</i> sp.	-0.12	
<i>I. notabilis</i> / <i>P. "dobati"</i>	+0.28	
<i>Folsomia</i> sp. / <i>P. "dobati"</i>	+0.46	
* Coefficient of mean square contingency (Southwood and Henderson, 2000)		

Table 1. Presence / absence of ten species of Collembola on 48 pools in OFD II. Results were tested using a contingency table that yields a measure of significant association between species pairs in the form of values of the corrected chi-squared (X^2) greater than 3.84. Significant values of chi-squared can be converted to a coefficient of mean square contingency (CMSC) giving values from +1 (complete positive association) to -1 (complete negative association).

Scaefferia emucronata group and *Folsomia* sp.

These species were well represented next to known entrances, or at least where there is relatively little overburden. *Folsomia* lacks pigment and eyes (though a single corneal remnant is present close to each postantennal organ). However these are probably the result of an endogean, rather than hypogean, existence. *S. emucronata* group has pigmented eyes and may have some scattered grey pigment when mature. It is widespread and common in British caves, though favouring comparatively eutrophic shallow passages. Both species are commonly found on pools with an obvious greasy surface film and/or flotsam of dead insects or collembolan exuviae (Fig.5). *S. emucronata* group is also found in pools above the main streamway (close to the Confluence) that contain bodies of accidentally introduced Trichoptera and Diptera. In view of their very similar and limited ranges, a positive association is to be expected on pool surfaces. However an association as strong as that indicated by this study suggests that there is little competition between the species.

Isotoma notabilis and *Arrhopalites pygmaeus*

These species are usually found some distance from the entrance in the deeper passages. They are often present in considerable numbers on pools that do not have a visible surface film. They are presumably able either to utilize rather different energy sources from those available to *Scaefferia emucronata* group and *Folsomia* sp., or else are far more efficient in their use of the energy available to them. Once again, the strong positive association suggests that these two species do not compete significantly.

Archaphorura schoetti

This species is widely distributed and is found with all four of the above species. It is found very commonly in pools where no other species occur (13 of 48 pools examined). Although close to the upper limit of its range, it occurs freely with *S. emucronata* group and *Folsomia* sp., showing no marked tendency of positive or negative association. On the other hand it shows a strong negative association with *I. notabilis* and *A. pygmaeus*, which occur in the central part of its range. This suggests competitive exclusion. *A. schoetti* no doubt has lower energy requirements than *I. notabilis* or *A. pygmaeus*, but in situations where the food supply is close to the limits of the requirements of the latter two species it appears unable to compete with them. However, its smaller energy requirements allow it to occupy pools trophically beyond their limits.

CONCLUSION

The main achievement of this work has been the establishment of a comprehensive, although clearly incomplete, fauna list for the OFD system (Appendix 1) with detailed information about distribution within the cave, type of habitat, behaviour and so on. At least 62 taxa have been recorded from the system as a whole (Table 2, Table 3). This is a typical post-glacial fauna, dominated by trogloniles but with the remnants of a stygobitic fauna that possibly survived glaciations within the cave.

The work has been particularly fruitful in the case of Collembola.

Troglobites	3
Stygobites	4
Troglophiles	26
Stygophiles	8
Threshold trogloniles	2
Threshold troglonenes	5
Accidental	14
Total	62

Table 2. A breakdown of the ecological status of the invertebrate fauna recorded from the OFD System.

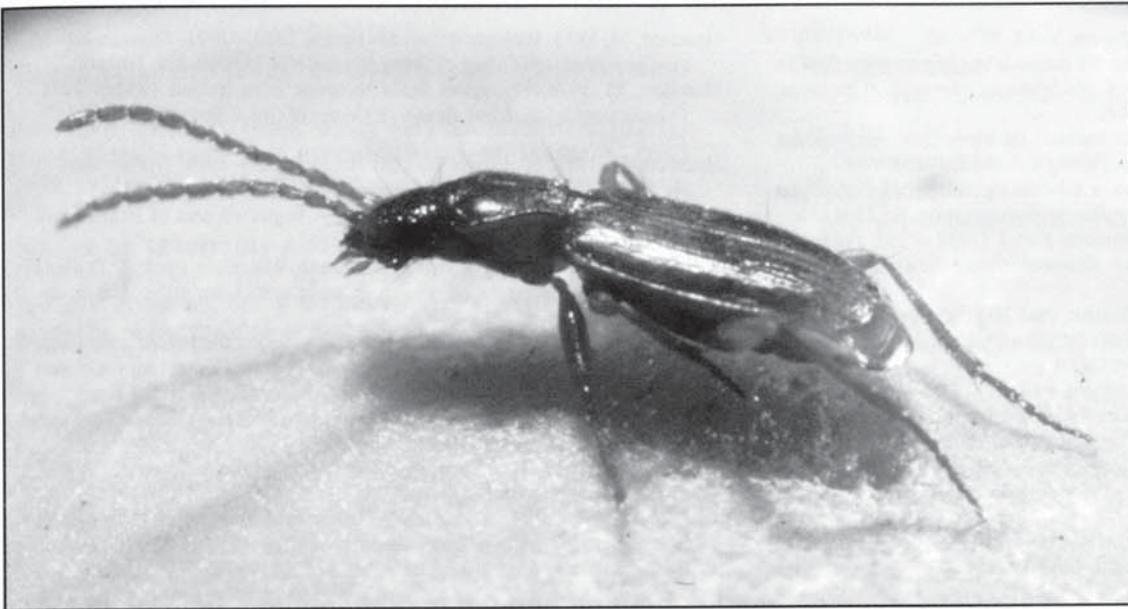


Figure 16. *Trechoblemus micros*. Photograph by Phil Chapman.

Platyhelminthes	1	
Annelida	3	
Mollusca	1	
Crustacea	10	
Ostracoda		1
Copepoda		3
Isopoda		3
Amphipoda		3
Diplopoda	3	
Insecta	38	
Collembola		13
Trichoptera		2
Lepidoptera		2
Hymenoptera		1
Diptera		9
Coleoptera		11
Arachnida	6	
Araneae		3
Acari		3
Total	62	

Table 3. A breakdown of the taxa recorded from the OFD System

There is the distinct possibility that at least one of the species found in the deep cave environment may be a troglobite new to Britain. Various degrees of association between different species of Collembola have come to light and it will be interesting to see whether further data confirm these results.

Distribution mapping has confirmed that some cavernicoles show a measure of zonation, and this seems to be correlated to proximity to entrances and/or depth of overburden. In some cases this may represent recruitment from outside, but in others it seems to be

linked with the availability of exogenous organic matter. The nature of this organic matter and its means of ingress are far from clear, as also is the source of energy utilised by the deep cave inhabitants.

The Diptera of OFD II pose some interesting problems. Observations already made on the larvae and pupae of *Speolepta leptogaster* throw some light on the biology of this interesting fly and it should not be difficult to make further progress. Similarly with *Heleomyza serrata*: further observations and experimental work should enable the ecological status and role of this species to be clarified. The enigma of *Trichocera maculipennis* may be more difficult.

A great deal remains to be done, but it is clear that cave ecology is a profitable area for research. Ogof Ffynnon Ddu, being a National Nature Reserve and a very large system, is particularly suitable for such studies.

ACKNOWLEDGEMENTS

Adrian Fowles and Richard Preece of the Countryside Council for Wales (the successor to the Nature Conservancy Council in Wales) were both very positive and helpful in granting permission for the "In Confidence" NCC report to be published. They are thanked for allowing this important study to see the light of day. Phil Chapman, one of the authors of the original report, was also enthusiastic, and is thanked for allowing the fourth author to convert the report into a publication. I hope it meets his very high standards but I doubt that it does. The Committee of the South Wales Caving Club were most encouraging. Rhian Hicks and Paul Wood reviewed the manuscript and provided valuable comments.

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Figure 17. *Lesteva pubescens* larva. Photograph by Phil Chapman.

APPENDIX 1

Fauna recorded from the Ogof Ffynnon Ddu System

Data from Jefferson (1989), which were compiled from Hazelton (1955, 1956a,b, 1958, 1959, 1960a,b, 1961, 1963, 1965, 1967, 1968, 1970, 1971, 1972, 1974, 1978).

A note on taxonomy and nomenclature

Since the original report was written a number of names have changed. In the list below the older name is given first, then the current name and the source of the alteration.

Insecta: Collembola

Onychiurus schoetti = *Archaphorura schoetti* (S. Hopkin pers. comm.)

Schaefferia lindbergi is now considered as a member of the *Schaefferia emucronata* group and individual species within this group cannot be easily separated (S. Hopkin pers. comm.)

Myriapoda: Diplopoda

Polymicrodon polydesmoides = *Nanogona polydesmoides* (Blower, 1985)

Crustacea: Ostracoda

Cypridopsis subterranea = *Cavernocypris subterranea* (Meisch, 2000)

Crustacea: Copepoda

Acanthocyclops viridis = *Megacyclops viridis* (F. Stoch pers. comm.)

Platyhelminthes

Turbellaria

Tricladida

Planariidae

Phagocata vitta (Duges, 1830) (stygophile)

Annelida

Oligochaeta

Aeolosomatidae

Aeolosoma hemprichi Ehrenberg, 1828 (stygophile ?)

Lumbricidae

Undetermined species (stygophile)

Enchytraeidae

Undetermined species (stygophile)

Mollusca

Gastropoda

Zonitidae

Oxychilus cellarius (Muller, 1774) (troglophile)

Arthropoda

Crustacea

Ostracoda

Cyprididae

Cavernocypris subterranea (Wolf, 1920) (local stygobite)

Copepoda

Cyclopidae

Paracyclops fimbriatus (Fischer, 1853) (stygophile)

Acanthocyclops vernalis (Fischer, 1853) (stygophile)

Megacyclops viridis (Jurine, 1820) (stygophile)

Isopoda

Asellidae

Proasellus cavaticus (Leydig, 1871) (stygobite)

Trichoniscidae

Trichoniscus pusillus Brandt, 1833 (accidental ?)

Androniscus dentiger Verhoeff, 1908 (troglophile)

Amphipoda

Crangonyctidae

Crangonyx subterraneus Bate, 1859 (stygobite)

Gammaridae

Gammarus pulex (Linnaeus, 1758) (stygophile)

Niphargidae

Niphargus fontanus Bate, 1859 (stygobite)

Diplopoda

Craspedosomidae

Nanogona polydesmoides (Leach, 1815) (troglophile)

Polydesmidae

Brachydesmus superus Latzel, 1884 (troglophile)

Blaniulidae

Blaniulus guttulatus (Fabricius, 1798) (troglophile)

Insecta

Collembola

Hypogastruridae

Schaefferia emucronata group Absolon, 1900 (troglophile)

Onychiuridae

Protaphorura armata (Tullberg, 1869) group (troglomite ?)

Onychiurus fimetarius group (Linnaeus, 1767) (troglophile)

Archaphorura schoetti (Lie Petterson, 1897) (troglomite)

Isotomidae

Folsomia "diplophthalma" (Axelson, 1902) (troglophile)

Folsomia fimetaria (Linnaeus, 1758) (troglophile)

Folsomia "agrelli" Gisin, 1944 (troglophile)

Istoma notabilis Schaffer, 1896 (troglophile)

Entomobryidae

Pseudosinella "dobati" Gisin, 1966 (troglomite)

Pseudosinella immaculata (Lie Petterson, 1896) (troglophile)

Neelidae

Megalothorax minimus Willem, 1900 (troglophile)

Sminthuridae

Arrhopalites caecus (Tullberg, 1871) (troglophile)

Arrhopalites pygmaeus (Wankel, 1861) (troglophile)

Trichoptera

Polycentropidae

Plectrocnemia geniculata McLachlan, 1871 (accidental)

Limnephilidae

Stenophylax permistus McLachlan, 1895 (threshold troglaxene)

Lepidoptera

Geometridae

Triphosa dubitata (Linnaeus, 1758) (threshold troglaxene)

Noctuidae

Scoliopteryx libatrix (Linnaeus, 1758) (threshold troglaxene)

Hymenoptera

Proctotrupidae

Codrus longicornis Nees, 1834 (accidental)

Diptera

Trichoceridae

Trichocera maculipennis Meigen, 1818 (troglophile ?)

Tipulidae

Limonia nubeculosa Meigen, 1804 (threshold troglaxene)

Culicidae

Culex pipiens Linnaeus, 1758 (threshold troglaxene)

Chironomidae

Spaniotoma sp. (accidental)

APPENDIX 2

Mycetophildae

Speolepta leptogaster (Winnertz, 1863) (troglobite)

Mycetophila ocellus Walker, 1848 (accidental)

Sciaridae

Bradysia forficulata (Bezzi, 1914) (troglophile)

Phoridae

Megaselia rufipes (Meigen, 1804) (accidental)

Heleomyzidae

Heleomyza serrata (Linnaeus, 1758) (accidental ?)

Coleoptera

Carabidae

Leistus spinibarbis (Fabricius, 1775) (accidental)

Nebria brevilcollis (Fabricius, 1792) (accidental)

Trechoblemus micros (Herbst, 1784) (troglophile)

Pterostichus aethiops (Panzer, 1796) (accidental)

Calathus fuscipes (Goeze, 1777) (accidental)

Leiodidae

Choleva agilis (Illiger, 1798) (accidental)

Catops nigricans (Spence, 1815) (troglophile)

Staphilinidae

Lesteva pubescens Mannerheim, 1830 (troglophile)

Ochtheophilus aureus (Fauvel, 1871) (troglophile)

Quedius mesomelinus (Marshall, 1802) (troglophile)

Chiloporata longitarsis (Erichson, 1837) (accidental)

Arachnida

Araneae

Tetragnathidae

Meta menardi (Latreille, 1804) (threshold troglophile)

Metellina merianae (Scopoli, 1763) (threshold troglophile)

Linyphiidae

Lepthyphantes zimmermanni Bertkau, 1890 (accidental)

Acari

Veigaiidae

Veigai nemorensis (Koch, 1839) (troglophile)

Rhagidiidae

Rhagidia punkva Zacharda (troglophile)

Rhagidia spelaea (Wankel) (troglophile)

Temperature and humidity measurements in OFD II

The Relative Humidity (RH) measurements are approximate, especially at higher values, as they were measured with a whirling hygrometer. Where no difference could be observed between wet and dry bulb temperatures, the RH is given as 98%+. Air temperature values are from the dry bulb of the hygrometer.

Locality	Date	Grid Ref.	Temp. (°C)	RH (%)	Comments
Low passage	30/01/1979	86381589	4.75	c. 95	Near entrance
Entrance passage	08/02/1979	86381590	7	c. 97	Gate closed
Entrance passage	23/02/1979	86381590	5	c. 76	Gate open
Entrance passage	26/02/1979	86381590	3.8	c. 78	Gate open
Entrance passage	05/03/1979	86381590	5	98+	Gate closed
Small chamber	08/01/1979	86371591	7.25	98+	Near entrance
Small chamber	30/01/1979	86371591	7	c. 97	—
Small chamber	01/02/1979	86371591	8	98+	—
Small chamber	26/02/1979	86371591	7.2	c. 78	—
Small chamber	05/03/1979	86371591	7.5	98+	—
Pool in small chamber	08/01/1979	86371591	8	—	Water temperature
Pool in small chamber	30/01/1979	86371591	7	—	Water temperature
Pool in small chamber	01/02/1979	86371591	8	—	Water temperature
Pool in small chamber	26/02/1979	86371591	7.2	—	Water temperature
Pool in small chamber	05/03/1979	86371591	7.5	—	Water temperature
Big Chamber	13/01/1979	86431596	8.5	c. 97	—
Big Chamber	26/02/1979	86431596	8+	98+	—
White Candle Chamber	01/02/1979	86371589	8.8	98+	High-level chamber
Proscenium Arch	01/02/1979	86421584	8.7	98+	—
Salubrious Passage	08/02/1979	86451575	9	98+	—
Mud Junction	08/02/1979	86471566	9.2	98+	—
Upper North Canyon	23/02/1979	86381583	9.2	98+	—
Bhowani Junction	26/02/1979	86681601	8.7	98+	—
Columns Pitch (top)	05/03/1979	86401608	8.8	98+	—

A uranium-series date from Keld Head Kingsdale, North Yorkshire, UK.



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Keld Head is a large spring located in the glaciated valley of Kingsdale (Fig. 1 and Plate 1). The bulk of the emergent water comes from both the east and west sides of Kingsdale, with additional input from the Marble Steps area farther to the west. To date approximately seven kilometres of flooded passage have been explored, making it the longest submerged cave system yet explored in the UK. Keld Head was the site of pioneering cave dives by Graham Balcombe in 1945 (Farr, 1991) and has remained a major focus of cave diving activity ever since. A description of each section of the system, intended for the use of visiting divers, is given by Monico (1995). The Keld Head system and particularly one of its influent cave systems (Swinsto Hole), has been proposed as the type

example of cave development in the Yorkshire Dales (Waltham *et al.*, 1981).

Speleothems that are now underwater have been recorded on a number of occasions by those exploring the system. The presence of these speleothems indicates that a lower water level was maintained at some time in the past. The recorded speleothems fall into two groups, one group in the entrance area, where there are stalagmites reaching 20 to 30cm below the present day minimum discharge level (e.g. Hrudnji, 1978; Cordingley, 2000), and a second group of flowstone-type deposits several metres beneath the water level more than 500m from the entrance, in the Marble Steps Branch (e.g. Monico, 1995, p.130; Skorupka, 2000). The possible significance of



Plate 1: Keld Head, Kingsdale. Water rises at the near left corner of the pool and flows rightwards (towards the east) to join the north-south surface course of Kingsdale Beck.

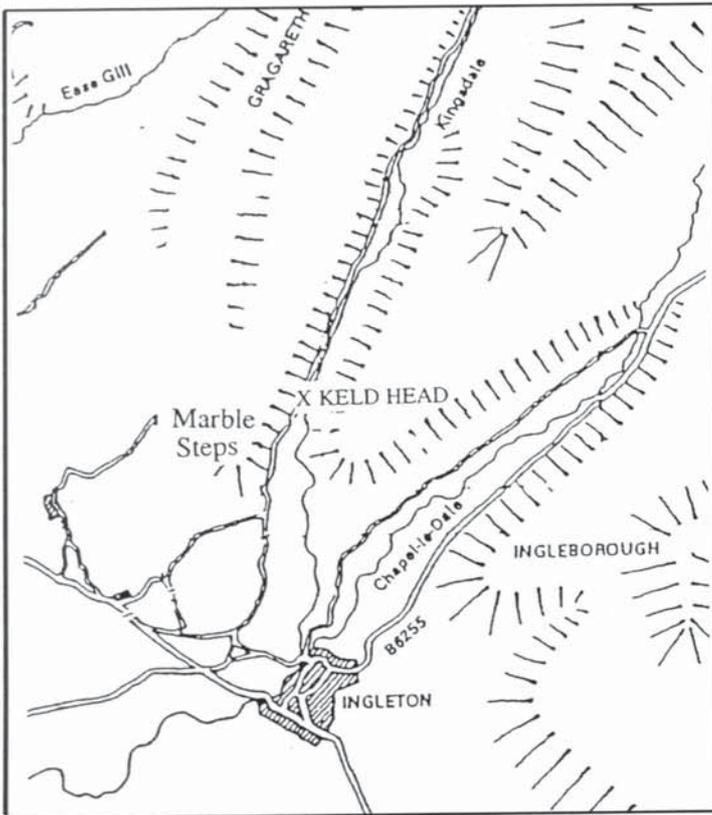


Figure 1: Location of Keld Head. Reproduced, with permission, from Brook et al., 1994.

these deposits in constraining the chronology of cave development has been mentioned by Brook (1969), Brook (1974) and King (1976), though no attempt to date the deposits was made prior to that leading to this publication.

Cordingley (2000) reported the occurrence of "... jagged stal. curtains hanging below water level like large fangs" beneath an air bell situated 30m from the entrance (see Fig.2). During a period of very low discharge in July 2002 a sample of stalagmite was removed from a depth of 18cm below water level at the point labelled "stal. airbell" on Fig.2. Uranium-series disequilibrium dating by thermal ionisation mass spectrometry was conducted at Carleton University. This yielded a date of 2489 ± 31 years BP (see Table 1)

During the decay of the last (Devensian) icesheet a retreat moraine was deposited at Raven Ray, down valley of Keld Head. This feature impounded a lake, the infilling of which resulted in the development of the flat floor of Kingsdale. The present water level in Keld Head is maintained by the presence of sediment on the floor of Kingsdale, but until now the timing of the last depositional episode, which resulted in the drowning of speleothems in Keld Head, has been a matter of conjecture. Brook (1969) suggested that the final episode of deposition was as a result of Kingsdale Beck redistributing solifluction debris as it meandered across the site of the post-glacial lake, but King (1976) suggested that the raising of the water level was a direct result of the infilling of the lake. The Uranium-series date published in this Report shows that the sediment maintaining the present water level was deposited within the last 2500 years. As this postdates the beginning of settled

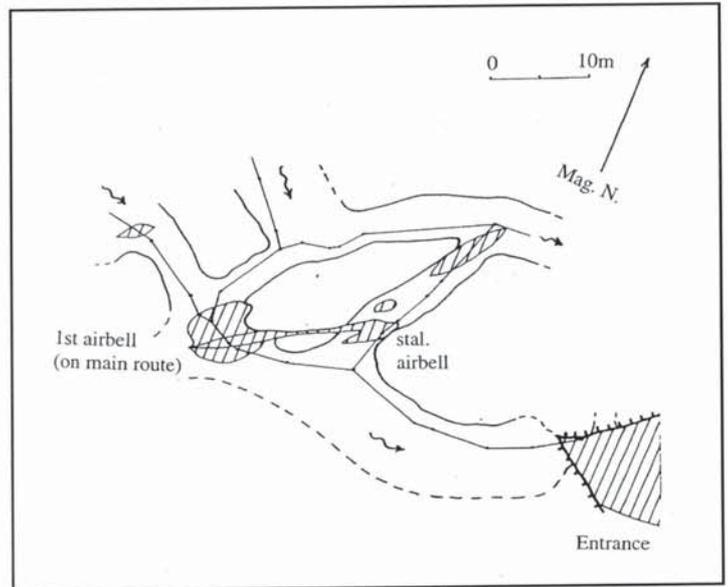


Figure 2: Plan of the passages in the entrance area of Keld Head. Reproduced from Cordingley, 2000.

farming in the area, a possible anthropogenic cause for the raising of the water level cannot be ignored, and this may even have been as recently as the 1820s, when the course of Kingsdale Beck was straightened artificially. Further dating evidence and a detailed study of the sediment fill of Kingsdale will be needed before the origin of the drowned speleothems in Keld Head is fully understood.

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Sample Code	Age (years BP)	U conc. (ppm)	Th conc. (ppm)	$^{230}\text{Th}/^{234}\text{U}$	$^{234}\text{U}/^{238}\text{U}$	$^{230}\text{Th}/^{232}\text{Th}$	Initial $^{234}\text{U}/^{238}\text{U}$	$^{234}\text{U}/^{232}\text{Th}$
KH1	2489 ± 31	0.097	0.084	0.02254 ± 0.00028	1.10044 ± 0.00174	4.158 ± 0.054	1.1012 ± 0.0017	184

Table 1: U-series data. All errors quoted are 2σ. All ratios are activity ratios.



Rediscovery of *Pseudoparonella doveri* (Collembola: Paronellidae) and notes on the Collembola of the Dark Cave (Gua Gelap), Batu Caves, Selangor, Malaysia.

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Abstract: *Pseudoparonella doveri* is an unusual troglomorphic springtail that appears to have no close epigeal relatives. Previously it was known only from specimens collected in the Dark Cave, Batu Caves, Malaysia, almost 80 years ago. The species was recently rediscovered on gour pool-dripstone habitat in the same cave. A brief qualitative survey of this and other habitats in the Dark Cave was also carried out to improve our knowledge of the little-known collembolan fauna of this important speleobiological site.

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INTRODUCTION

The Dark Cave (Gua Gelap), is the longest cave in a group, collectively known as Batu Caves, formed in an isolated limestone hill 13km north of Kuala Lumpur, Selangor, Malaysia.

The invertebrate fauna of the Dark Cave was one of the first in the tropics to be investigated (Ridley, 1899). Frederick Dover made a collection representing many invertebrate groups in the 1920s, and subsequently Elliot McClure and a team from the Malayan Nature Society (McClure, 1965; McClure *et al.*, 1967) carried out extensive resurvey of the cave. In addition there have been several minor studies (see bibliography in Price, 1998). In total the specimens collected there constitute the largest and most comprehensive collection of cave organisms ever made in a Southeast Asian cave (Deharveng and Bedos, 2000), and this, together with the fact that records go back more than a century, presents an invaluable and probably uniquely comprehensive database.

Even so, the list of the fauna inhabiting the Dark Cave remains far from complete, as indicated by the species inventories of McClure (1965) and McClure *et al.* (1967). Some of the more-conspicuous invertebrates, such as the Coleoptera, as well as relatively obscure and taxonomically difficult groups such as the Acari remain largely uninvestigated.

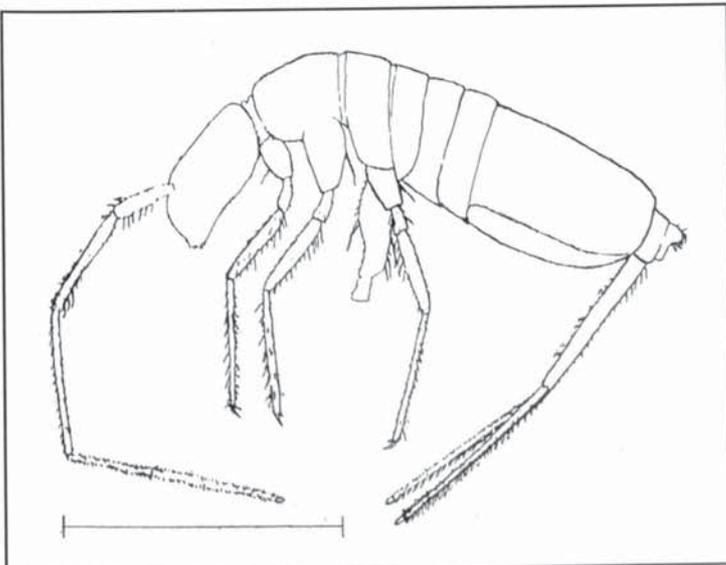


Figure 1. Early sketch of *Pseudoparonella doveri*, reproduced from Carpenter, 1993. The scale line represents approximately 1mm.

Still less is known about the ecology of the invertebrate fauna. The site is commonly thought of as a "guano cave" but this is only partly true and thus somewhat misleading: the Dark Cave is actually an extensive series of caverns (>2000m surveyed length according to Price, 2002) with many different terrestrial and aquatic habitats that range from high-energy bat guano accumulations to oligotrophic gour pool-dripstone sites. The guano habitats themselves are not uniform, because different species of bat tend to roost in different areas of the cave, and there are also large variations in humidity and other environmental parameters from place to place. There is very little published information on the distribution of invertebrates in these diverse habitats, and the food webs proposed by McClure (1965) are obviously simplified and, although reasonable, largely speculative.

Both taxonomically and ecologically the Collembola are among the least known of the invertebrate groups inhabiting the cave. Carpenter (1933), working with the specimens collected by F Dover, listed only two: *Sinella caeca* ("caeca" is now considered to be a species group) and a new cavernicolous species that he named *Pseudoparonella doveri*. Yosii (1959) reported neither of these, but added six further taxa: *Xenylla similata* Denis, *Brachystomella contorta* Denis, *Sinella höfti* Schaeffer, and three new species: *Willemia nadchatrami*, *Callyntrura bukit-timahensis* and *Callyntrura zonata*. However the validity of some of these records is in doubt because they were based on inadequate material (in some cases single specimens). McClure (1965) added nothing new, basing his list on the earlier publications. Habitat data are almost non-existent for any of these Collembola: Carpenter (1933) gives almost no useful information, whereas Yosii (1959) did not provide habitat notes.

P. doveri Carpenter was previously known and described only from a series of specimens collected almost eighty years ago by F Dover in July and September 1926 (Carpenter, 1933), at which time it seems to have been quite common. Yosii (1959) did not report finding this fairly large collembolan and, whereas they did include it in their faunal list, McClure and his co-workers also do not appear to have themselves reconfirmed the presence of the species in the cave. In recent years, despite many visits, members of the Malaysian Nature Society were unable to find it (Price, *pers. comm.* 2003), and it has not been reported elsewhere in the region (Deharveng, *pers. comm.* 2003).

In the decades since *P. doveri* was discovered the Dark Cave has suffered a considerable degree of ecological change, as a result of guano mining, the building of concrete walkways inside the cave and increasingly frequent human visitation. It was therefore thought

Site number	Zone	Description	Associated fauna recorded	Collembola collected
I	Threshold	Main (tourist) entrance chamber. The collecting site was an area of damp soil and broken rock with plant litter, near the wall on the northwest side.	Diverse, soil/litter threshold assemblage with earthworms (Megascolecidae), millipedes (Cambalopsidae), isopods (Armadillidae, Trichoniscidae), ants (Formicidae), microdriles (Enchytraeidae), beetles, spiders and flies.	<i>Lepidocyrtus (Acrocyrtus)</i> sp.
II	Deep Threshold	Main (tourist) entrance chamber. Southeast facing wall: coated with a film of wet bat guano.	Abundant small (?cave-adapted) grazing snails (Gastropoda); bat leeches.	<i>Xenylla yucatanana</i>
III	Deep Threshold	Cavern A. Floor. Dry friable bat guano with rocks, small stones and some fragments of wood. All the Collembola collected here were on or immediately under these pieces of wood.	Cave Cockroach (<i>Pyconoscelus striatus</i>) and <i>Periplaneta</i> spp. (invasive) extremely abundant. Sporadic beetles (Tenebrionidae), various mites (including Uropodidae, Oribatidae).	<i>Cyphoderus</i> sp. <i>Sinella (Coecobrya)</i> sp. <i>Isotomiella</i> sp.
IV	Dark Zone	Cavern B. Damp soil with rocks.	Sporadic eyeless isopods (Trichoniscidae), ants (Formicidae), Diplura.	<i>Sinella (Coecobrya)</i> sp.
V	Dark Zone (Transition Zone)	Cavern D: "Geometric Pools" Localized area of active gour pools and dripstone. An oligotrophic area with little terrestrial fauna: with the exception of the springtail the species found here were attracted to baits and apparently came from adjacent areas of the cave.	Various beetles (Coleoptera), isopods (Trichoniscidae) and adult flies (Diptera). A few doratodesmid millipedes (<i>Ascetophacus macclurei</i>).	<i>Pseudoparonella doveri</i>
VI	Dark Zone (Deep Cave)	Cavern C (north end). Deep actively accumulating damp to waterlogged accumulations of bat guano cover the floor. There is some broken rock, and a small stream crosses the collecting area.	The most biodiverse study site. Abundant troglobitic snails (Gastropods) and cambalopsid millipedes (<i>Plusioglyphiulus grandicollis</i>) almost everywhere on the floor. Many different flies (Diptera) are attracted to light. <i>Gryllotalpa fulvipes</i> (Orthoptera), Hemiptera, Acari and other fauna in the guano with, usually under stones, sporadic centipedes (<i>Ostostigmus</i> and an unidentified geophilid), <i>Amyntas indicus</i> (Megascolecidae), <i>Pyconoscelus</i> and other fauna.	<i>Xenylla yucatanana</i> <i>Cyphoderus</i> sp. <i>Lepidocyrtus (Ascocyrtus)</i> sp. <i>Pararrhopalites</i> sp.

Table 1: Location and details of study sites in the Dark Cave, Batu Caves, Selangor, Malaysia. (The nomenclature of locations and topographic features within the caves follows McClure et al. 1967).

possible that this relatively conspicuous and formerly common springtail had become extinct.

According to Carpenter's description (1933), *P. doveri* (Fig.1) is a troglomorphic, eyeless springtail, up to 2mm in length and pale yellow in colour. Deharveng (1987) suggested that it might belong to the Genus *Troglopedetes* (Paronellidae). It has no known epigeic relatives (Deharveng, 1987) and no other closely related cave-adapted species are reported from the Malay Peninsula. The species is thus of considerable taxonomic interest and perhaps evolutionary significance, and it is important to know whether it still exists.

Accordingly, following a reconnaissance in 2000, I visited the Dark Cave several times in 2003 with the aim of ascertaining whether *P. doveri* is still present and, if so, to collect a series of specimens requested by Dr Louis Deharveng for a taxonomic review of the species. At the same time I took the opportunity to make a more general survey with the aim of confirming, if possible, the earlier records, expanding the list and also gathering preliminary distributional and ecological information.

METHODS

Collembola were sampled qualitatively (March 2000, June–August 2003) from six different habitats within the Dark Cave (Table 1), using hand searching, pitfall traps, cheese bait and by flotation from guano and cave soil samples. Habitat and locality field records were made for all collections. Specimens were preserved and forwarded to Dr Deharveng for expert taxonomic identification. Reference material was retained in the collection of Dr Deharveng (duplicates of most taxa were deposited in the author's collection).

The nomenclature of locations and topographic features within the cave follows that of McClure et al. (1967).

RESULTS

P. doveri was found in small numbers only at Site V, where it was hand-collected from gour pools and adjacent damp flowstone surfaces. Additional specimens required for taxonomic study were secured from the same site using cheese bait.

Family	Taxon	Field Records	Ref.	Notes
Brachystomellidae	<i>Brachystomella contorta</i> Denis	Many, September 1958. Habitat not reported.	Yosii, 1959	Troglophile or troglaxene. Found in both the Old World and the New World tropics.
Hypogastruridae	<i>Willemia nadchatrami</i> Yosii	10 examples, September 1958. Habitat not reported.	Yosii, 1959.	This species was described from Batu material, and has subsequently been found elsewhere (epigeal) in South Thailand and Indonesia.
	<i>Xenylla yucatanana</i> Mills	Abundant, Site II, March 2000; common, Site VI, July 2003.	This report.	Guanophile: cosmopolitan, in guano caves.
	<i>X. similata</i> Denis ?	One example, January 1958. Habitat not reported.	Yosii, 1959.	Record needs confirmation: based on a single specimen, so possibly misidentified, or a stray.
Cyphoderidae	<i>Cyphoderus</i> sp(p).	Common, Sites II and VI, June–July 2003.	This report.	<i>Cyphoderus</i> spp. are common in caves, ants' nests and epigeal habitats worldwide. The Southeast Asian species are in need of revision.
Entomobryidae	<i>Sinella (Coecobrya)</i> sp(p).	One, on stream, November 1926; one, 800 ft. from entrance, August 1926 (both as <i>S. caeca</i>); one (as <i>S. höfti</i>), September 1958; many, on damp wood, Site III, June 2003; several, in soil, Site IV, June 2003.	Carpenter, 1933 Yosii, 1959 This report.	One or more eyeless <i>Coecobrya</i> spp. are generally distributed in the cave in soil, damp wood, etc., but seem never to be associated with guano. Many of the spp. found in the caves of Southeast Asia are very similar and cannot be identified reliably from single specimens, thus the records of " <i>caeca</i> " and " <i>höfti</i> " from the Dark Cave are unreliable.
	<i>Lepidocyrtus (Acrocyrtus)</i> sp.	Many, Site I, June 2003.	This report.	In caves probably merely a threshold dweller.
	<i>Lepidocyrtus (Ascocyrtus)</i> sp.	In wet guano, Site VI, June 2003.	This report.	Guanophile?
Paronellidae	<i>Pseudoparonella doveri</i> Carpenter	Several, in side passage, July 1926; large numbers, on stream, September 1926; several, on gour pools, wet dripstone and cheese bait, Site V, June–July 2003.	Carpenter, 1933 This report.	Troglobite. (See text for discussion).
	<i>Callyntrura bukit-timahensis</i> Yosii	4 examples, April 1958. Habitat not reported.	Yosii, 1959	Troglophile? The species was described from material collected at Batu and epigeal sites in Singapore.
	<i>C. zonata</i> Yosii ?	One female, April 1958. Habitat not reported.	Yosii, 1959	Record needs confirmation: based on a single specimen so possibly misidentified, or a stray.
Isotomidae	<i>Isotomiella</i> sp.	Many on, and in guano under, damp wood, Site III, June 2003.	This report.	Regular troglaxene?
Sminthuridae	<i>Pararrhopalites</i> sp.	In wet guano, Site VI, July 2003.	This report.	May be undescribed.

Table 2: Summary of records of collembolan taxa from the Dark Cave (see Table 1 for location and details of study sites).

Eight collembolan taxa, representing six Families (Hypogastruridae [1], Cyphoderidae [1], Entomobryidae [3], Paronellidae [1], Isotomidae [1] and Sminthuridae [1]), were identified in the collections (see Table 2 for list and details).

Six taxa were found in dark zone sites (Sites IV, V, and VI), four in the deep threshold (Sites II and III), and one in the threshold (Site I). Six taxa were associated with guano (Sites II, III and VI), whereas only one was collected from the oligotrophic study site (V). (Table 1).

With the possible exception of *S. höfti*, confirmation of which must await further taxonomic work on the new *Sinella* (*Coecobrya*) material from the cave, none of the taxa reported by Yosii (1959) were found.

DISCUSSION

Although Carpenter (1933) believed that *P. doveri* was common in the cave, the new collections now suggest that it is restricted to the relatively small areas of oligotrophic gour pool-flowstone habitat (represented by study site V). It is not surprising to find a troglomorphic form in this habitat. However, Carpenter (1933) appears to have been mistaken in describing the species as eyeless: all examples collected in 2003 have pigmented (black) ocelli (Deharveng, *pers. comm.*). Considering that the material had been stored in alcohol for a number of years prior to description it is possible that ocelli were present but were overlooked because the pigment had faded.

It is not at all obvious why none of the Collembola reported by Yosii (1959) were recorded. Admittedly, some of his records are doubtful for reasons presented above, but this is not the case for all of his reported taxa. One explanation could be that he collected from a distinct habitat that was not included in the current survey, presumably in the threshold, because most of his species are epigeal, not cave springtails. Anyway, assuming this is the case there are now records for eleven taxa representing seven Families (Brachystomellidae [1], Hypogastruridae [2], Cyphoderidae [1], Entomobryidae [3], Paronellidae [2], Isotomidae [1] and Sminthuridae [1]). In addition, two doubtful records (Hypogastruridae [1] and Paronellidae [1]) await confirmation (Table 2).

Some of these Collembola belong to groups that are in need of taxonomic revision, and hence cannot at present be identified reliably beyond the generic level. Because of this, and the limited data, few useful generalizations can be made. As a whole the fauna is dominated by entomobryoids (7 taxa), whereas poduroids are relatively poorly represented (3 taxa). Only one symphleponid is known from the cave. the guano-associated fauna is apparently the most taxonomically diverse, whereas only one species was found in the oligotrophic site. the ecological status of most of the species is not yet certain. *P. doveri* is almost certainly a troglomite and, although it is possible that there are other obligate cavernicoles represented, and some of the species are probably trogophiles or guanophiles, several taxa, including the *Acrocyrtus* and *Isotomiella*, may be primarily epigeal animals normally, in caves, confined to the threshold zone. A complete understanding of the nature of the collembolan fauna of the Dark Cave must await taxonomic revision of some genera, as well as further competent systematic collecting.

The findings of the current project provide further evidence that, despite the extensive literature on the subject, there is still much work to do before we can reach more than a preliminary understanding of the invertebrate fauna of the Dark Cave. A systematic resurvey, group-by-group, is highly desirable, as is a

better understanding of the distribution of species within the varied habitats in the cave.

CONSERVATION IMPLICATIONS

The Malaysian Nature Society controls the Dark Cave under lease, but currently no agreed conservation management plan is in effect, and the cave is subject to continuing disturbance including frequent tourist trips and occasional illegal guano mining.

At present the collembolan *P. doveri* is known only from a single collecting site in this isolated cave (where it is probably endemic), and it has been recorded there only in small numbers during the recent survey. It is believed to be a taxonomically significant cave-dwelling collembolan, so urgent consideration should be given to its protection and conservation. Certainly, now that its survival has been confirmed and a satisfactory study series secured, there must be no further collecting of the species without convincing scientific justification.

As one of the best and most comprehensively documented exemplars of a tropical Southeast Asian cave, the Dark Cave is of considerable speleobiological importance. In particular the extensive guano deposits may well serve as regional type-examples of such habitats. There is thus a very strong case for the introduction of effective measures to protect and preserve the ecology of the cave. Much additional research on the invertebrate fauna is necessary in order to develop and implement effective conservation management measures.

ACKNOWLEDGEMENTS

I am much indebted to Dr H Steiner, who searched the extensive and widely scattered literature on the Batu invertebrates, and sent me copies, and to Dr L Deharveng, who kindly and promptly identified the springtails. Thanks are also due to the Malaysian Nature Society for granting access to the site, and to L Price of that Society for help in the field. Finally, thank you to the anonymous BCRA reviewer who read and critiqued an early draft version of the report.

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Studies of algae in the Shulgan-Tash (Kapova) Cave, South Ural, Russia.

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Summary: Algal flora in the Shulgan-Tash (Kapova) Cave (South Ural, Russia) was investigated. 61 algae species, varieties and forms were found in this cavern during investigations in 2000 and 2001. Algae with filamentous thalli, belonging to the **Cyanophyta (Cyanobacteria)** Division, were found to dominate during both years. Among the several algal divisions recognised **Bacillariophyta** was found to exhibit the highest resemblance between the 2000 and 2001 studies, whereas wall growths displayed the highest resemblance among the various recorded biotopes. Divisions and genera of underground algae that dominate in the caverns all over the world were found also to prevail in the Shulgan-Tash Cave. Several species that are common worldwide were revealed during this and foregoing investigations. It was also found that entry of algae to this cave is related to the "inflation" of surface waters via open fissures and karst cavities.

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INTRODUCTION

Cave algae investigations have been carried out since the beginning of the 20th century (Maheu, 1903, 11–15). Claus (1955, 1–26) in Hungary and Friedmann (1955, 439–445) in Israel initiated systematic exploration of these organisms.

By 1994 specimens from each known algae Division except Raphidophyta, Charophyta, Phaeophyta and Cryptophyta, had been found in caves all over the world. 332 species and varieties from 117 genera, had been described. 23 were identified to generic level as cave algae (Coute and Chauveau, 1994, 371–380).

In Russia, cave algae have been investigated at the Botany Department of Bashkir State University since 1996, when the entrance zone of the Shulgan-Tash (Kapova) cave was studied (Sharipova and Dubovik, 1999, 7–9). To date the research group has examined the algal flora of nine different caves in the South Ural region. 95 algal species and varieties have been checked in these caves. The different biotopes including cave floor deposits, stream and lake beds, cave waters and cave walls (respectively 'g', 'b', 'w' and 'wl' in Fig.1). Both the quantitative and qualitative compositions of the biotopes were analysed (Abdullin and Sharipova, 2002, 56–57).

There are no published data on the ways that algae enter caverns, although some studies (Jones, 1965, 491–516; Kol, 1964, 19–24) touch upon this question. The aim of this investigation, besides the gathering of data about the algal flora of the Shulgan-Tash (Kapova) cave, was to supply experimental results about some ways that algae enter caves.

MATERIALS AND METHODS

Shulgan-Tash Cave, which was formed by the Shulgan River, lies on the right bank of the Belaya River in the Burzyan region of the Bashkortostan Republic (Russia). More than 3km of galleries and halls on three levels have been surveyed in the system. The greater part of the lowermost and youngest level is flooded by the Shulgan River. This river, which goes underground several kilometres from the cavern, appears in the Hall of the Abyss, a remote part of the cave, and forms the Blue Lake near the entrance, rising from a depth of 82m. The cavern entrance, which is known as the Portal, is a huge hollow in the rock. From the Portal the middle level stretches for 360m to the Hall of Chaos. Accessible from a hole under the roof of Stalagmite Hall in the middle level, the upper level, ends at the Big Distant well, leading to the Hall of the Abyss. All the cave passages are excavated in Devonian and Carboniferous limestones, but calcite sinter covers the cavern walls and the cave floor comprises clay, detrital minerals, sand and calcite.

Both the Near and Remote lakes are situated within the upper cave level, and the Remote Lake carries running water. Water

flowing from the roof of the Hall of Chaos forms the Lukyanka stream, which flows into the Lake of the Dome hall, which also transmits running water. These waters flow under the stones to enter the Shulgan river by diverse routes. Study of the cave's development history indicate that it can be classified within the river type of the karst caves (Lobanov, 1979).

In 1959 drawings dating from the Late Palaeolithic period were discovered in the cave by A V Ryumin (Kudryashov, 1969; Lyakhnitsky, 2002).

On 27 to 28 July 2000 twenty-three samples were collected from all sections of the cavern other than the most distant parts. A further thirty-five samples were collected on 25 to 27 August 2001, again from all parts of the cave and in the Shulgan river sinkhole. Samples were taken from cave floor deposits, stream- and lake-beds, cave waters and cave walls during both years. Material was gathered carefully using sterilized instruments and placed into sterile collecting packets, and water was collected into sterile vials.

During the collecting period, air and water temperature, humidity, and level of illumination in the entrance zone were measured. In 2000 the air temperature was 6.8 to 14.5°C and water temperature was 5 to 8°C. In 2001 the air temperature was 6.8 to 11.0°C and the water temperature was 5 to 8°C. Relative humidity was 81 to 100% both years. On the basis of the measured light intensity two zones were picked out in the cave: the lighted zone (extending approximately 60m from the entrance) and the dark zone (comprising all other parts of the cavern).

In the laboratory the cave wall samples were immediately examined microscopically. The rest of the material was transferred under sterile conditions into autoclaved Erlenmeyer flasks filled with sterile mineral Gromov's solution. The flasks were placed in a culture chamber where they received illumination for 12 hours per day. Portions of the stream/lake bed and cave floor deposit samples were placed on cultivation plates under "growth slides". According to published sources (Hollerbach and Shtina, 1969), this method permits recognition of the presence of actively vegetating algae. Material on the plate is covered with 4 to 5 microscope slides and then covered with distilled water; after a while algae grow out on the slides. The water samples were filtered through isoporous membranes (average pore diameter 0.5 µm) and then also placed in Erlenmeyer flasks with sterile mineral Gromov's solution. All material was examined periodically during seven months of cultivation, and all algae were identified by means of light microscopy.

Occurrence frequency of species was determined using the formula: $F = a/A \cdot 100\%$; where "a" is the amount of samples in which the species was recorded and "A" is the total number of samples. Serensen Resemblance Coefficient (SRC) was applied for the floristic analysis.

TAXONOMY

Year 2000 investigations

Cyanophyta (Cyanobacteria)

Chroococcaceae

Family Coccobactraceae

1. *Synechocystis minuscula* Woronich
2. *Synechocystis sallensis* Skuja

Hormogoneae

Family Nostocaceae

3. *Nostoc paludosum* (Kütz.) Elenk.
4. *Nostoc punctiforme* f. *populorum* (Geitl.) Hollerb.

Family Anabaenaceae

5. *Anabaena bergii* f. *minor* (Kissel.) Kossinsk.
6. *Cylindrospermum minutissimum* Collins.
7. *Cylindrospermum muscicola* Kütz.

Family Rivulariaceae

8. *Calothrix elenkinii* Kossinsk.

Family Oscillatoriaceae

9. *Oscillatoria amphibia* Ag.
10. *Oscillatoria brevis* Kütz.
11. *Oscillatoria neglecta* Lemm.
12. *Oscillatoria tenuis* Ag.
13. *Oscillatoria terebriformis* f. *grunowiana* (Gom.) Elenk.
14. *Phormidium ambiguum* f. *majus* (Lemm.) Elenk.
15. *Phormidium autumnale* (Ag.) Gom.

Family Schizothrichaceae

16. *Microcoleus vaginatus* (Vauch.) Gom.

Family Plectonemataceae

17. *Plectonema boryanum* Gom.

Bacillariophyta

Centricae

Family Aulacoseiraceae

18. *Aulacoseira* sp.

Pennatae

Family Naviculaceae

19. *Navicula contenta* Grun.
20. *Navicula mutica* Kütz.
21. *Navicula mutica* var. *binodis* Hust.
22. *Navicula mutica* var. *nivalis* (Ehr.) Hust.
23. *Navicula pelliculosa* (Bréb.) Hilse

Family Nitzschiaceae

24. *Hantzschia amphioxys* (Ehr.) Grun.
25. *Nitzschia palea* (Kütz.) W.Sm.

Xanthophyta

Family Pleurochloridaceae

26. *Pleurochloris imitans* Pasch.

Chlorophyta

Chlorophyceae

Family Chlorococcaceae

27. *Chlorococcum infusionum* (Schrank.) Menegh.
28. *Chlorococcum* sp.

Family Chlorellaceae

29. *Mychonastes homosphaera* (Skuja) Kalina et Punč.

Family Coelastraceae

30. *Coelastrum microporum* Näg.

Family Chlorosarcinaceae

31. *Chlorosarcinopsis minor* (Gern.) Herndon

Family Ulothrichaceae

32. *Ulothrix variabilis* Kütz.

Year 2001 investigations

Cyanophyta (Cyanobacteria)

Chroococcaceae

Family Coccobactraceae

1. *Synechocystis aquatilis* Sauv.
2. *Synechocystis crassa* Woronich.

Family Merismopediaceae

3. *Merismopedia tenuissima* Lemm.

Hormogoneae

Family Nostocaceae

4. *Nostoc paludosum* (Kütz.) Elenk.

Family Anabaenaceae

5. *Anabaena* sp.1
6. *Anabaena* sp.2

Family Oscillatoriaceae

7. *Oscillatoria amphibia* f. *tenuis* (Anissim.) Elenk.
8. *Oscillatoria rupicola* Hansg.
9. *Phormidium ambiguum* Gom.
10. *Phormidium lividum* Näg.
11. *Phormidium molle* f. *tenuius* W. et G.S. West
12. *Phormidium mucicola* Hub.-Pestalozzi et Naum.

Family Schizothrichaceae

13. *Microcoleus delicatulus* W. et G.S. West
14. *Schizothrix lardaceae* (Ces.) Gom.

Family Plectonemataceae

15. *Plectonema boryanum* Gom.
16. *Plectonema boryanum* f. *hollerbachianum* Elenk.

Bacillariophyta

Centricae

Family Aulacoseiraceae

17. *Aulacoseira* sp.

Pennatae

Family Naviculaceae

18. *Navicula contenta* Grun.
19. *Navicula minima* Grun.
20. *Navicula pelliculosa* (Bréb.) Hilse
21. *Navicula subminuscula* Manguin.
22. *Navicula* sp.1
23. *Pinnularia* sp.1
24. *Pinnularia* sp.2
25. *Stauroneis anceps* Ehr.

Family Cymbellaceae

26. *Amphora veneta* Kütz.

Family Nitzschiaceae

27. *Hantzschia amphioxys* (Ehr.) Grun.
28. *Nitzschia palea* (Kütz.) W.Sm.
29. *Nitzschia sublinearis* Hust.

Chlorophyta

Chlorophyceae

Family Chlamydomonadaceae

30. *Chlamydomonas globosa* Snow.

Family Chlorococcaceae

31. *Chlorococcum* sp.
32. *Neospongiococcum* sp.

Family Chlorellaceae

33. *Chlorella* sp.1
34. *Chlorella* sp.2
35. *Chlorella* sp.3
36. *Mychonastes homosphaera* (Skuja) Kalina et Punč.

Family Selenastraceae

37. *Ankistrodesmus falcatus* (Corda) Ralfs.
38. *Chlorolobion lunulatum* Hind.

RESULTS AND DISCUSSION

The material collected during the two years has been determined to consist of 61 species, varieties and forms of algae distributed as follows: **Cyanophyta (Cyanobacteria)** – 31 species (51%); **Bacillariophyta** – 16 species (26%); **Xanthophyta** – 1 species (2%); **Chlorophyta** – 13 species (21%). Two families among 20 were most species-rich: *Oscillatoriaceae* – 21.3% (13 species); *Naviculaceae* – 18.0% (11 species). Among 29 genera found in the cave *Navicula* (13.1%), *Oscillatoria* (11.5%) and *Phormidium* (9.8%) were most rich in species. *Nostoc paludosum* (Kütz.) Elenk. (F = 31%), *Plectonema boryanum* Gom. (F = 55%), *Nitzschia palea* (Kütz.) W.Sm. (F = 40%) and *Mychonastes homosphaera* (Skuja) Kalina et Punč. (F = 24%) were the species most commonly revealed in the cavern.

Cyanophyta (Cyanobacteria) with filamentous thalli dominated the collections in both years. Most of the **Bacillariophyta** and **Chlorophyta** were unicellular algae. One species of **Xanthophyta** was also a unicellular alga.

Thirty-two different algae taxa were found during 2000, and thirty-eight taxa in 2001 (Table 1). Algae of the **Cyanophyta (Cyanobacteria)** Division dominated during both years. The *Oscillatoriaceae* and *Naviculaceae* families showed the greatest abundance of species in both years (Table 2). In 2000 the genera *Oscillatoria* (15.6%) and *Navicula* (15.6%) dominated, whereas in 2001 the genera *Phormidium* (10.5%) and *Navicula* (13.2%) were most common. The composition of the most commonly encountered species was different in 2000 and 2001, with only *Nostoc paludosum* (Kütz.) Elenk. and *Plectonema boryanum* Gom. occurring among the dominant species in both years (Table 3). In 2000 two samples were found to be completely sterile, whereas in 2001 all samples contained algae.

Low SRC (26%) was exhibited between the algal floras of different years. The **Bacillariophyta** Division had the highest resemblance (SRC = 48%), whereas the **Cyanophyta (Cyanobacteria)** Division had the lowest resemblance (SRC=12%) in 2000 and 2001.

The lighted zone displayed higher resemblance (SRC = 29%) than the dark zone in the different years. Among the biotopes wall growths ('wl' in Fig.1) showed highest resemblance (SRC = 44%), and the waters ('w' in Fig.1) had the lowest resemblance (SRC = 13%). The greatest part of the lighted zone walls are covered by mosses. We suppose that the mosses form a habitat with a specific microclimate, which is responsible for the algae composition of wall growths being relatively permanent. The lowest resemblance of algae composition, found in the waters, may apparently be explained by the fact that most of the cave water systems comprise running-water.

№	Taxon [Division]	2000	2001
1	Cyanophyta (Cyanobacteria)	17 species (53%)	16 species (42%)
2	Bacillariophyta	8 species (25%)	13 species (34%)
3	Chlorophyta	6 species (19%)	9 species (24%)
4	Xanthophyta	1 species (3%)	–
	All	32 species	38 species

Table 1. Systematic algae composition of Shulgan-Tash Cave in different years.

№	Taxon [Family]	2000	2001
1	Oscillatoriaceae	7 species (22 %)	6 species (16 %)
2	Naviculaceae	5 species (16 %)	8 species (21 %)
3	Chlorellaceae	–	4 species (11 %)

Table 2. Dominant families of algae in Shulgan-Tash cave in different years.

№	Taxon [species]	2000	2001
1.	<i>Nostoc paludosum</i> (Kütz.) Elenk.	26	30
2.	<i>Nostoc punctiforme</i> f. <i>populorum</i> (Geitl.) Hollerb.	39	–
3.	<i>Plectonema boryanum</i> Gom.	65	46
4.	<i>Navicula minima</i> Grun.	–	67
5.	<i>Navicula</i> sp.1	–	42
6.	<i>Nitzschia palea</i> (Kütz.) W. Sm.	–	55
7.	<i>Mychonastes homosphaera</i> (Skuja) Kalina et Punč.	–	30

Table 3. Frequency of occurrence (F.%) of prevailing algae species in Shulgan-Tash Cave in different years.

Cyanophyta (Cyanobacteria) were dominant in Shulgan-Tash Cave, just as they are in other caves investigated all over the world. Species belonging to the genera *Oscillatoria*, *Phormidium* and *Navicula* also outnumber all others in caves throughout the world (Coute, Chauveau, 1994). It can be concluded that the divisions and genera that dominate in the Shulgan-Tash Cave resemble those that dominate in other caves investigated all over the world.

Previous investigations in the cave (Sharipova and Dubovik, 1999; Sharipova, 2001) revealed 45 algae species, varieties and forms, although during the earlier studies samples were taken only from the part section of the system between the entrance and Stalagmite Hall. Probably, the great variety of species recognized is the result of abundant algae colonizing this entrance zone. Comparing these previous data with materials obtained from the same zone during this study revealed that resemblance was low (SRC=19%). Wall growths displayed the highest resemblance, as they did between 2000 and 2001 (SRC=14%). Waters showed no resemblance between the studies. Common species from this and the previous investigations are listed in Table 4.

Although resemblance between this and the previous studies was low, there were some common species in different years (Table 4). Some species (*Nostoc paludosum* (Kütz.) Elenk.; *Hantzschia amphioxys* (Ehr.) Grun.; *Aulacoseira* sp., *Navicula pelliculosa* (Bréb.) Hilse) were found during all the studies. Others (*Plectonema boryanum* Gom.; *Navicula contenta* Grun.; *Nitzschia palea* (Kütz.) W.Sm., *Chlorococcum* sp.; *Mychonastes homosphaera* (Skuja) Kalina et Punč.) were revealed in 2000 and 2001. As mentioned above, the previous study touched only upon the entrance zone of the cave. Many of the species listed in Table 4 were found at the same points in 2000 as in 2001 and thus it is supposed that these algae formed one or several populations in the cavern. Most of these algae were encountered in the lighted zone, but a few (*Nostoc paludosum* (Kütz.) Elenk.; *Plectonema boryanum* Gom.; *Nitzschia palea* (Kütz.) W.Sm.; *Mychonastes homosphaera* (Skuja) Kalina et Punč.) occurred all over the cave in areas without running water during both years. Additionally, in contrast to other species, these species were also found on the "growth slides". Perhaps these algae adapt to live in the darkness.

Algae species amount distribution in the Shulgan-Tash Cave was analysed as a means of revealing the ways that these organisms entered the system. Fig.1 illustrates the quantitative localization of different algae species among various biotopes found in the cavern in 2000 and 2001. The predominant amount of these organisms was found within the entrance zone and also at locations with permanent running-water systems. The light levels, specific microclimates formed by mosses, ease of access to humans and animals, floods and the presence of soil can explain the great number of algae at the entrance zone. But abundant quantities of algal species, especially diatoms, were found in the Hall of the Abyss in 2001. This is unusual for remote cavern areas. The stream/lake bed, cave floor deposit and water samples collected in the Hall of the Abyss and in the Shulgan River sinkhole were studied. 16 species of algae were revealed: **Cyanophyta (Cyanobacteria)** – 7 species (44%); **Bacillariophyta** – 4 species (25%); **Chlorophyta** – 5 species (31%). 10 species of algae were identified in the Shulgan River swallow hole and 13 species were found in the Hall of the Abyss. The Serensen Resemblance Coefficient was high (61%) between these two parts of the cave. Algal flora resemblance between the Hall of

№	Taxon [species]	1996 – 1997	2000	2001
1.	<i>Microcoleus vaginatus</i> (Vauch.) Gom.	+	+	–
2.	<i>Nostoc paludosum</i> (Kütz.) Elenk.	+	+	+
3.	<i>Phormidium ambiguum</i> Gom.	+	–	+
4.	<i>Plectonema boryanum</i> Gom.	–	+	+
5.	<i>Synechocystis sallensis</i> Skuja	+	+	–
6.	<i>Aulacoseira</i> sp.	+	+	+
7.	<i>Hantzschia amphioxys</i> (Ehr.) Grun.	+	+	+
8.	<i>Navicula contenta</i> Grun.	–	+	+
9.	<i>Navicula mutica</i> var. <i>binodis</i> Hust.	+	+	–
10.	<i>Navicula pelliculosa</i> (Bréb.) Hilse	+	+	+
11.	<i>Nitzschia palea</i> (Kütz.) W. Sm.	–	+	+
11.	<i>Chlorococcum</i> sp.	–	+	+
12.	<i>Chlorosarcinopsis minor</i> (Gern.) Herndon	+	+	–
13.	<i>Mychonastes homosphaera</i> (Skuja) Kalina et Punč.	–	+	+

Table 4. Common algae species in Shulgan-Tash Cave in different years.

the Abyss and Blue Lake was lower (SRC = 52%). Algal flora resemblance between the Shulgan River swallow hole and the Blue Lake was lowest (SRC = 50%). Thus, this floristic coefficient is reduced between the following areas: Shulgan River swallow hole → Shulgan River, the Hall of the Abyss → Shulgan River, Blue Lake. Probably, this phenomenon relates to the death of some algae in the underground Shulgan River. It may be supposed that the algal flora of the Hall of the Abyss is formed mainly by the Shulgan River, and that this river also influenced the algal flora of the Blue Lake.

The various rivers and streams flowing into the cave and characterized by high current rates (10 to 1000 m/h and higher) are "influxional" waters (Lobanov, 1979), i.e. surface waters flowing through open fissures and karstic cavities into the karst rock mass. Thus the process whereby algae enter the Shulgan-Tash Cave via the Shulgan River may be termed the influxional waterway subtype of algal entry. Also, it may be supposed that this means of entry is also active in other running-water systems within the cave (the Remote Lake, flowing waters in the Hall of the Chaos, the Lukyanka Stream), and thus the predominant numbers of algae were found at these places.

Near Lake is not running-water, but is filled by infiltration waters and condensation water (Lyakhnitsky and Chuyko, 1999). However, the number of algae species in Near Lake was the same as that in the running-water systems of the cave. Perhaps, this phenomenon relates to human visits, as in the nearest Hall of the Drawings. It is supposed that the low floristic resemblance between the algal floras of different years was connected with the presence of running-water systems in the Shulgan-Tash Cave.

Numbers of algae in cave floor deposit ('g' in Fig 1) and stream/lake bed samples ('b' in Fig.1) were higher in all the running-water systems and in Near Lake, than in other water samples ('w' in Fig.1). Possibly, these biotopes collect and concentrate the algae.

Thus, the results of this investigation revealed permanently resident algae species in the Shulgan-Tash Cave and indicated one of the ways that algae enter caves. The study of the Shulgan-Tash Cave algal flora is continuing.

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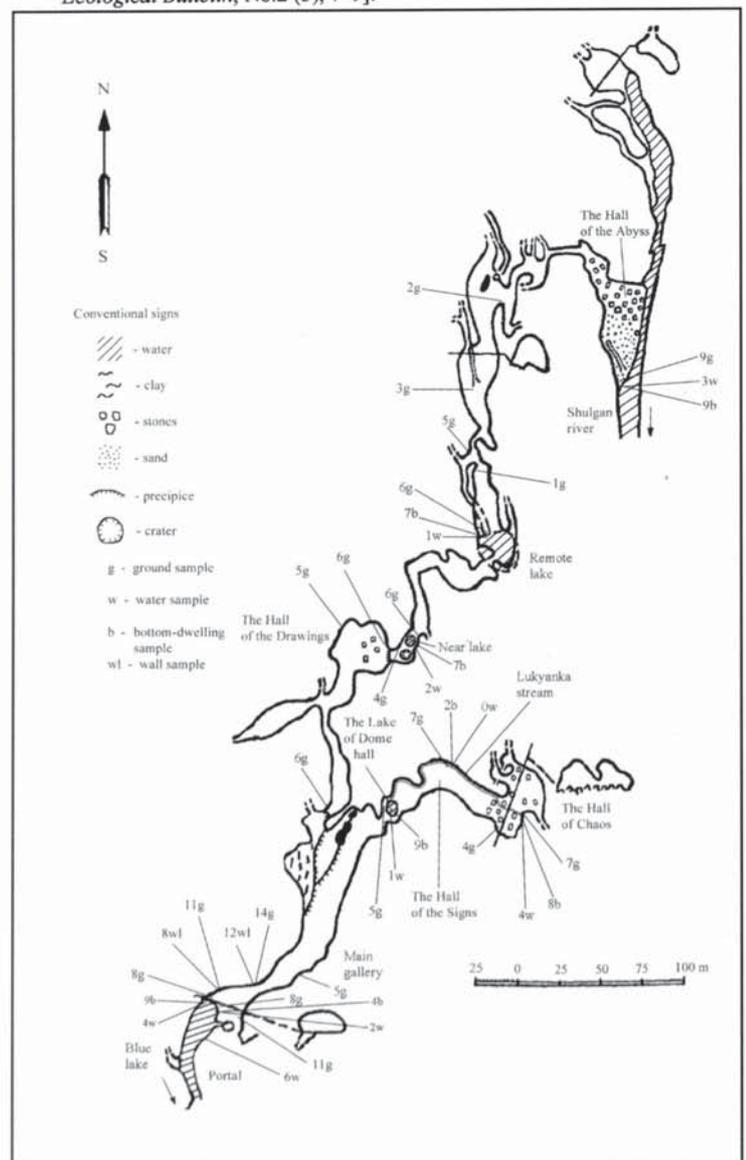


Figure 1: Number of algae species of various biotopes (see text) found in different parts of Shulgan-Tash Cave in 2000–2001.

Abstracts of papers presented at the International Geographical Congress, Glasgow, August 2004

The 14 abstracts that follow are from papers presented orally or as posters at three congress sessions that were sponsored by the IGU Karst Commission. Although an abstracts booklet was provided to participants this is not widely available. Hence it was decided to include them in this issue of *Cave and Karst Science*. The papers were grouped into two themes: "Advances in Karst Geomorphology and Hydrology" and "Karst Resources Management"

One area in which karst geomorphologists have made an important contribution to knowledge is in the reconstruction of past environmental conditions on the basis of evidence from underground and subaerial deposits. The first three papers explore different aspects of paleoenvironmental reconstruction, whereas the fourth considers the hydrology of percolation waters that supply the inputs to speleothems. The next four papers provide new understanding on karst landform evolution in a variety of environments, from the cold regions of Scandinavia, through the now temperate but once glaciated regions of northwest England to the Mediterranean and finally the arid extreme of the Egyptian desert. Two more papers consider palaeokarst and the final destruction of caves when the lowering ground surface intersects their roofs. Three papers address different aspects of resource management in karst terrains: the management of tropical karst terrains, the problems of heavy metal contamination of karst soils in the more industrialised areas of Europe, and the tricky question of how statutory agencies can manage wild caves without actually entering them. The final paper takes a more historical approach, considering the research undertaken by an early karst scientist and what can be learned from his work.

WHERE DO LAMINATED STALAGMITES GROW?

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Over the last ten years, there has been a growing body of research that has identified laminated stalagmites. Rather like the use of tree rings, stalagmite growth rings can be used to both obtain a precise time scale by counting them, as well as evidence of environmental change through the measurement of ring width. However, laminated stalagmites are not ubiquitous, and have a geographical pattern that depends on a variety of factors such as the seasonality of surface climate, overlying soil and vegetation type, and depth below surface. Understanding of the processes of lamina formation should help us to predict both the likely locations of laminated stalagmites as well as their width. Such a process-based study is presented here, which predicts the likely geographical locations of annually and sub-annually laminated stalagmites, as well as their likely lamina width. These predictions are then compared to actual observations of laminated stalagmites from around the world.

UNDERGROUND SEDIMENTARY DEPOSITS AS A NATURAL RECORD: HIGH RESOLUTION STUDY IN VIEW OF PALAEOENVIRONMENTAL RECONSTRUCTIONS (CHORANCHE CAVES, VERCORS, FRANCE).

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The aim of this study is to try to produce palaeoenvironmental reconstructions from an original natural archive: the lacustrine detrital endokarstic deposits. The study of these sedimentary signals implies a very important preliminary work: the understanding of the stressed sedimentary processes peculiar to the underground environment. This work is based on cores and uses essentially

Passage pattern. The poster focuses on the signal processing and statistical methods (high resolution study with granulometry, spectrophotometry, magnetic susceptibility and grey levels). For instance, results obtained by power spectral density and wavelet analysis are discussed. Moreover, in the endokarstic environment, studies of detrital deposits are in high complementarity with all researches conducted around carbonated deposits, (speleothems and especially stalagmites) which is a recurrent topic actually. So, crossing of these two records is a good way to check sediment resolution quality. This work is a contribution to researches about local climatic evolutions.

AN ENVIRONMENTAL MODEL OF FLUVIAL TUFAS OF THE SEASONALLY WET TROPICS, NORTHERN AUSTRALIA.

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Tufa streams in the tropical wet-dry climate zone of northern Australia are influenced strongly by perennially warm water temperatures, high evaporation rates, and monsoonal large-magnitude floods. The history of the Australian monsoon is not fully understood, partly because few sources of palaeoenvironmental information exist in the area. However, fossil tufa deposits, which record terrestrial climate information, have been preserved throughout northern Australia and hold great potential for reconstructing the region's climate history. We present a conceptual tufa model that will aid interpretation of these fossil tufas. In the Barkly karst, northern Australia, tufas form in dam, cascade and pool/waterhole geomorphic environments. Each environment is represented in the rock record by a specific combination of tufa geomorphic units and facies associations. Preservation of particular facies is thought to reflect changes in the strength of monsoonal floods. A strong monsoon is represented by an abundance of flood indicators such as phytoclastic, lithoclastic and intraclastic tufa facies. Conversely, evidence of weak monsoons or a prolonged absence of floods may include oncoids, calcite rafts and thick accumulations of fine carbonate sediments. Fossil tufa sequences at two sites have been interpreted using this new model. The model can be applied to other Barkly karst fossil tufas as well as those in similar environments elsewhere in the world (eg Papua New Guinea).

TRANSMISSION AND PRESERVATION OF CLIMATIC SIGNALS VIA KARSTIC HYDROLOGICAL SYSTEMS.

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There has been a recent upsurge of interest in the capture of past climatic conditions in cave precipitates (speleothems) via the mediation of karst aquifer water with distinctive hydrological and hydrogeochemical properties. The karst system behaviour depends on the properties of the soil zone, the attributes of the main karst aquifer, and the ventilation of the cave cavity. Water residence time is a function of storage capacity and the distribution of matrix and preferential flow routes in the soil and of matrix, fracture and conduit routes within the aquifer. Temporal variations occur in soil and aquifer zone flow pathways in response to rainfall inputs of differing duration and intensity. Resultant karst water chemistries are also constrained by the relative abundance and degree of reactivity of soil and aquifer zone materials. A combination of drip rate and hydrogeochemical properties in karstic waters may display distinctive variations in response to patterns of variation of infiltration in response to atmospheric precipitation, or to seasonal changes in cave ventilation, or both. However there are varying thresholds and sensitivities of different dripwaters to change, and some drips display invariant properties. Where hydrological change occurs there is often a distinctive hydrogeochemical response in terms of higher ratios of trace elements such as Mg and Sr to Ca under drier conditions in response to varying weathering times of bedrock and greater opportunities for degassing and prior CaCO₃ precipitation along the flowpath. Greater rates of ventilation in the winter exacerbate the prior precipitation effect. The hydrogeochemical changes are further modified during the transformation of the signal into a speleothem since varying growth rates of crystals also give rise to changes in trace element composition which exaggerate the seasonal signal in particular. Recent qualitative studies of the aquifer properties that allow these varying hydrogeochemical signals to develop have now been extended, in a study in disused limestone mines of simple geological structure near Bath, UK, into a quantitative predictive model. Quantitative modelling will be much more difficult to achieve in more complex aquifers, but the approach is attractive also in offering opportunities for modelling of dispersed pollutant transport in karstic aquifers.

THE DEGLACIATION OF CENTRAL SCANDINAVIA AND ITS IMPLICATIONS FOR KARST CAVE DEVELOPMENT.

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Models for the inception, development and destruction of karst caves in central Scandinavia have been constructed as part of a wider research project into the speleogenesis of caves in Caledonide metacarbonate rocks. A consequence of the epigeic association of these caves with the landscape is that their speleogenesis can only be understood in the context of the geomorphological evolution of the host region. The key process responsible for present landforms in the study area is the repeated cycle of glaciation and deglaciation that characterised the late Pliocene and the Pleistocene. The Weichselian and earlier deglaciations of central Scandinavia were driven by two summer heat fluxes: warming by sea water that caused the icesheet to retreat eastwards as the melting sea encroached up coastal valleys, and direct solar warming that caused the icesheet to melt and ablate from its upper surface. When nunatak mountains and ridges emerged above the icesheet, ice-dammed lakes were formed alongside them. These grew in size, became integrated with englacial drainage as deglaciation proceeded, and inundated most karst areas for periods up to c. 1000 years. From the latest theories of the physics and

chemistry of the dissolution of limestone, it can be shown that the many relict phreatic passages in the area enlarged to present dimensions within the timescales of these deglacial inundations. The vadose passages were entrenched during interglacials, especially the Holocene.

NEW INTERPRETATIONS OF SURFACE KARST LANDFORMS IN NW ENGLAND.

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Field observations in NW England identified surface limestone landforms with characteristics difficult to explain by karstification only in the 15ka since the Late Devensian. They include large grikes and weathering flares; deeply rannelled bevelled edges; rounded boulders and scars; large holes; tors; and pinnacles. Re-examination of pedestal evidence suggests that the high solution rates necessary for the formation of these 'mature' landforms in this period did not occur and that c.15cm was a probable maximum general solution lowering rate in 15ka in these areas. If the date of erratic deposition on the limestone were much earlier than Late Devensian then rates would be lower. It is proposed that these features survived the Devensian Glaciation at least partly. A modified limestone pavement development model demonstrates major influential factors. Glacial survival relates to factors such as thick, massive rock, and locations sheltered from major Devensian ice-scour, for example, at high altitudes between valleys, in embayments and side valleys, or locations where ice lost power. Identification of similar landform features within apparently glacially scoured pavement areas could indicate their greater age. Possibly some forms are completely unglaciated and exposed by erosion of overlying beds along strong limestones, i.e. palaeokarst, or interstratal features. Thus smaller surface karst features of NW England may be considerably older than previously thought, possibly some are unglaciated and others have evolved since pre-Devensian glaciations.

SUBMERGED KARST IN CROATIA – DEAD OR ALIVE?

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The eastern Adriatic (Croatian) coast is one of the most indented coastlines anywhere in the world and is the *locus typicus* of the Dalmatian type of coast. It is a typical submergent (ingressional) coast, which formed during the last, Late Pleistocene – Holocene transgression, of the order of 125 ± 5m. The rising sea flooded pre-existing karstified areas and their numerous exo- and endokarstic landforms, which were formed in tectonically fractured Mesozoic to Early Palaeogene carbonate sediments (limestones and dolomites). Processes of karstification took place downward to the former erosional base level, which is, in the case of coastal objects, most commonly sea level. Prevalence of easily soluble carbonate rocks in the drainage area of most of the rivers on the Eastern Adriatic coast resulted in a very slow sedimentation rate. Specifically, only approximately 20% of river-borne material is suspended and the rest is dissolved, so most of the erosional and depositional karstic forms, (speleological objects with speleothems, dolines, poljes, karrens, etc.), can still be recognized on the sea floor, in spite of the millennia spent in the sedimentary environment. Most of them seem to be simply submerged, others have changed their function and in some of them the process of karstification continues, despite their position below the present sea level.

KARST FORMS AND KARSTIFICATION IN EGYPT.

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Vast areas of Egypt are covered by karstified rocks. Although present-day dry climatic conditions are barely conducive to karst development, karst forms spread all over Egypt. This means that karst forms in Egypt are relict forms, developed during past wet periods. Geomorphological and geological evidence indicates that Egypt as a whole experienced wet climates with moderate to heavy rainfall during most of the Oligocene, Miocene, Pliocene and Pleistocene. During these wet periods, karstification was active and intense, and wide areas of Egypt were modelled by karst processes. Although some relict forms, such as Djara Cave have been known for a long time, little attention has been given to karst forms and the role of karstification in modelling the surface of Egypt. Recent studies have revealed a wealth of karst heritage in Egypt, including caves, cone and tower karst, solution depressions, tufa deposits, and terra Rosa. Caves are recorded at 16 localities in the Nile Valley sides, the Western and Eastern Deserts. Cone and tower karst can be seen in the region of Bahariya and Farafra Depressions, whereas tufa deposits are mainly recorded along the escarpments of Kharga. These studies also revealed several cycles of karstification, the oldest of which dates back to the Eocene-Oligocene period. Some of the speleothems in the Djara Cave are older than 500 ky.

THE ROLE OF INHERITED SPELEOGENETIC FEATURES IN THE EVOLUTION OF KARST RELIEF.

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The last decade of karst morphology studies, especially in Slovenia, focused on presence of endokarstic phenomena within present-day karst relief. Denuded underground cavities or unroofed caves filled with various sediments became recognized as the common speleogenetic features of karst landscape. These phenomena are usually maintained to represent the oldest speleogenetic phases in the whole geomorphic region. There is a much better database for karst evolution than cave morphology and sediments as well as karst depressions of superficial origin. Unroofed caves with preserved sediments, speleothems and in some cases with preserved cave rock relief raise the possibility of reconstructing past environments. Inherited speleogenetic features influence farther karst relief evolution. Exhumation of inherited karst drainage systems, including surface or subsurface speleogenetic features, is the most effective factor in development of karst-related subsidence. This exhumation takes place by means of both natural and human-induced processes of internal cave sediment evacuation. Steady denudational activity within the carbonate massif could bring endokarstic phenomena to the surface. An important task for future studies is to explain how caves are able to survive speleo-destruction processes and be present within the karst morphology. The presence and dissolutional activity of the epikarst control the possibility of speleogenetic feature inheritance. Epikarsts on different denuded karst plateaux are examined in this paper, and a model of karst relief evolution, including the presence of inherited speleogenetic features in the morphology, is proposed.

KARST DIVERSITY SYSTEMS AND FEATURES IN ALGARVE (SOUTHERN PORTUGAL).

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Portuguese karst areas are developed in the western and in the

southern Mesozoic basins. Though the later area is smaller, we can distinguish two main karst systems with quite different features: one inland karst and a littoral one related not only to karstification but also to mechanical bioerosion. The Algarve inland karst system is developed in limestone and dolomite rocks dipping southwards and closely related to fractures and joint patterns. Closed karst depressions aren't the most common features, although they include several types of dolines (sinkholes) and two polje-like depressions: Nave Barão (closed, 4km long) and Nave Cordeiros (open, 9km long). However this karst system shows a big diversity in what concerns lapiaz (karren) solution forms. Ranging in size from a few millimetres to several metres, from honeycomb weathering, klufkarren (clints associated with grikes), hohlkarren and rundkarren to quite spectacular bogaz, pinnacle and tower-like landforms. These three last features are relict forms resulting from the exhumation of an old karst. Terra rossa-like deposits still wholly or partly cover several of those forms. The littoral karst can be similar to the inland type with deep lapiaz developed in limestones and marls exposed by marine and gully erosion. Another type, developed in carbonated aeolianites, shows an altitudinal zonation (lapiaz, vasques, mares de défoncement de vasques and mares).

HEAVY METAL CONTAMINATION OF THE KARSTIC SOILS IN HUNGARY.

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Although the karst regions in Hungary are much less contaminated by heavy metals than those in other European countries, their investigation is a great importance for the purposes of prevention. If the metals are going through the soil into the karst water, then it becomes unhealthy for the population. Generally the acid soils do not accumulate heavy metal. If the soil has adequate pH value and the organic matter- and clay mineral contents are high enough, it can adsorb a large quantity of heavy metal ions, thereby decreasing the mobility of the ions. In the presentation, the heavy metal contents of the soils and vegetation are surveyed and the present-day pressure levels are evaluated for test areas in the Aggtelek Mountains. The Zn, Pb, and Co contaminations of the soils are not considerable; the Cd and Cr limits are occasionally exceeded. From the analyses of heavy metal concentrations in plants, it is claimed that in the case of oaks and hornbeams the higher Ni content involves higher concentrations of Cu and Zn. The Cr amounts in soils become available for plants, if soil pH is around 5. Pollution of tested karst areas is not too strong, but the growing tendency for metal contamination will be problematic in the near future.

AN ASSESSMENT OF KARST PROTECTION IN THE PHILIPPINES.

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Ms S Restificar, Geography, University of Wisconsin-Milwaukee, USA.

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Of the approximately 35,000km² of karst landscape in the Philippines, about 10,000km², or 29% is designated as protected areas. There is no current legislation that is directed specifically towards the conservation of karst landscapes, but the adoption of a National Caves and Cave Resources Management and Protection

Act in 2001 is a significant step that augurs well for future broader government recognition of the significance of the national karst patrimony. Among existing protected areas, significant karst occurs within the U.N. World Heritage Puerto Princessa National Park on Palawan, within the Central Cebu National Park, and in the Samar Island Natural Park. Also in Samar is the Sohoton Natural Bridge National Park and the Caligba Cave Protected Landscape, which with an area of about 900km² is the largest protected karst area in the country. In Bohol, karst is protected in the Rajah Sikatuna Protected Landscape, and much of the Chocolate Hills is conserved as a National Monument. Significant marine karst is protected within the El Nido Marine Reserve and in the Tubbataha Reefs National Marine Park, which is a Natural World Heritage Site.

THE CONSERVATION OF BRITAIN'S CAVE RESOURCE: AN OVERVIEW.

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The highest level of statutory protection for earth science sites in Great Britain is afforded by designation as a 'Site of Special Scientific Interest' (SSSI) and over 30% of British caves and over 75% of cave passage lie within SSSI. Each SSSI has a citation and a Site Management Brief (SMB) but these are broad and do not provide detailed locations for any interest feature. In 2002 English Nature (EN, the body with statutory responsibility for SSSI in England) commissioned inventories of "Special Interest Features" in each SSSI. These took the form of reports and annotated surveys of individual caves or cave systems. Particular attention was paid to the location of the most vulnerable attributes of each cave (Clastic sediment sequences and Speleothems) with cave passage morphology receiving less detailed attention as it was judged to be less fragile and minimally impacted. Given that there are over 320km of passage in English cave SSSI it would have proved impossible for EN staff to visit them all to check on their condition but, in any event, they were prevented from going underground by the organisation's Health and Safety policy. Instead, individual cavers have taken on this task and achieved considerable success. The paper will review how this has been achieved with respect to the Peak District region.

THE WORK OF BALTHAZAR HACQUET (1739–1815) ON POLJE.

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Cerkniško jezero (Lake of Cerknica), a periodic lake in Cerkniško karst polje (Polje of Cerknica, Dinaric karst, Slovenia), has been known as a curiosity since the days of Antiquity, being shown in the first encyclopaedia, "L'Encyclopédie de Diderot et d'Alembert". The earliest printed descriptions of the lake date from the 16th century. Many authors (e.g. Kircher 1665; Brown 1673; Valvasor 1687; Steinberg 1758) tried to explain its functioning. Valvasor was the first to describe it in detail. To explain it he had to invent 3 underground lakes, connected to the surface lake by numerous and complicated siphons. B Hacquet, who lived in Carniola for 20 years (1766 – 1787) also studied and described Cerkniško polje. His opinion of the karst was surprisingly modern. He knew that water dissolves limestone; he knew that the water penetrates immediately underground through the rocky limestone surface; he noticed caves made completely watertight by clay and flowstone. He knew many underground water connections and he stressed the importance of the difference in level between ponors and springs. In 1778 Hacquet published the first volume of "*Oryctographia carniolica...*" (Physical description of Carniola...) where he described Cerkniško polje in detail (pp. 129–141). He stated explicitly that the main reason for Cerkniško jezero's periodicity was precipitation: when too much rain falls, ponors cannot swallow all of the water (maximised discharge), and thus the polje floor is flooded ("Kesselthal" as Hacquet called it) and a lake appears. And the opposite: when rainfall input is less than the discharge of the ponors, the lake dries up. The director of the "Cabinet of Rarities" at the Vienna Court, J A Nagel, was of the same opinion as Hacquet, but his written report (1748) was never published. Hacquet also undertook three months of "economical travel" to find out how to prevent floods in the poljes of Inner Carniola.

Forum

Readers are invited to offer thesis abstracts, review articles, scientific notes, comments on previously published papers and discussions of general interest for publication in the Forum of *Cave and Karst Science*.

All views expressed are those of the individual authors and do not necessarily represent the views of the Association unless this is expressly stated. Contributions to the *Cave and Karst Science* Forum are not subject to the normal refereeing process, but the Editors reserve the right to revise or shorten text. Such changes will only be shown to the authors if they affect scientific content. Opinions expressed by authors are their responsibility and will not be edited, although remarks that are considered derogatory or libellous will be removed, at the Editors' discretion.

Late 19th or early 20th century photographs of Hull Pot, North Yorkshire, UK.

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Hull Pot, situated on the flanks of Penyghent above Horton in Ribblesdale in North Yorkshire, is a 90m-long, 20m-wide and 20m-deep quarry-like pothole aligned along a minor, slightly mineralized fault plane. The floor of the pot consists of a layer of loose boulders and cobbles of unknown thickness, but a wet shaft in solid rock under the eastern end of the pothole descends to a boulder choke at 60m depth, which may be in the fill beneath the main pothole (Papard, 1977).

At present the surface hole may be descended at the eastern end by a climb down a crack, or at the western end by "...a very exposed step on to a massive collapse block..." (Brook *et al.* 1991). This fallen block is clearly visible on Plate 1, which shows the western end of the open pot. Gemmel (1952) comments on the presence of this block (describing it as a detached pinnacle) and notes that it has obviously slid down from the side, and that this must have occurred relatively recently, as he had seen an old photograph showing a projecting buttress rather than a detached block. Though Gemmel's account was not published until 1952, the visits took place in 1940 (Brook *et al.*, 1991). Mitchell (1937) describes an easy descent route at the western end of the pothole, commenting: "...care must be exercised in passing over the boulders.", presumably referring to a descent route using the fallen block, which is clearly visible in the

photograph between Mitchell's pages 7 and 8. The photograph in Plate 2 also shows the western end of the pothole, and what is now the collapse block described by Brook *et al.* (1991) is still attached to the southern wall of the pothole, though clearly it is severely undercut. Whereas the exact date of this photograph is unknown, it was taken by the prolific Leeds-based photographer Godfrey Bingley (1842–1927), who was active between 1887 and 1913 (Jones, 1987). Thus, the detachment of this large limestone block from the wall of the pothole must have occurred some time between 1887 and 1937.

The photograph in Plate 3 was also taken by Godfrey Bingley, and clearly shows an intact drystone wall surrounding the surface opening. This surrounding wall is also visible in Plate 2. Today only a trace of this wall can be seen around the pothole (see Plate 4). This indicates that the wall has nearly disappeared between 1887 and the present day, and yet another drystone wall, which can be seen farther up the hillside in Plate 3, is clearly seen as still intact in Plate 4. One possible explanation for this is that generations of visitors to the site have thrown rocks from the wall down the hole, so some of the loose material flooring the pothole may have been sourced from the surrounding drystone wall. Some supporting evidence for this supposition is provided by the fact that the part of the surrounding wall that survives intact is on the side of the hole that is least accessible to casual visitors.

REFERENCES

- Brook, A, Brook, D, Griffiths, J and Long, H, 1991. *Northern Caves*, Volume 2, The Three Peaks. [Skipton: Dalesman.]
Gemmel, A, 1952. Damming and diving at Hull Pot. In: Gemmel, A and Myers, J O, 1952. *Underground Adventure*. [Clapham: Dalesman.]



Plate 1: Hull Pot in 2004, looking towards the west, showing the detached pinnacle described in the text.



Plate 2: Late nineteenth or early twentieth century view of Hull Pot, looking towards the west. The detached rock pinnacle visible in Plate 1 remains attached to the southwestern wall. Note also the intact drystone wall that once encircled the Pot [Photo taken by Godfrey Bingley].

DISSERTATION ABSTRACT

Facies changes across the Asbian-Brigantian boundary on the southern part of the Askrigg Block

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M Phil, 2004
University of Sheffield

Abstract

The position of the Asbian-Brigantian boundary on the southern part of the Askrigg Block was located in the shallow-water Dinantian carbonate successions in the Settle district of North Yorkshire, UK. The succession consisted of sedimentary packages less than ten metres thick, above and below the boundary. The distribution of lithofacies and biofacies within individual packages represented deposition during a shallowing-up phase.

Emergent and diagenetic features, including clay wayboards, were described from the carbonate successions studied, and the mineralogy and rare earth element geochemistry of the clay wayboards was determined. Palaeoenvironments were reconstructed on the southern part of the Askrigg Block. These were used to interpret geological events on the southern part of the Block in a sequence stratigraphic context. The styles of sedimentation were influenced by glacioeustatically-controlled cyclic changes in relative sea-level, consisting of 5th order parasequences, dominated by highstand carbonate sediments. Local tectonic movements on the Askrigg Block periodically caused reductions or increases in sediment accommodation potential. Some filling of the accommodation probably occurred by diachronous shoaling across the platform, which could account for lithofacies differences close to the Asbian-Brigantian Boundary at different localities, but autocyclicity did not primarily control the style of sedimentation. Glacioeustatic falls in base level were the primary mechanism that caused emergence, with differences in platform geometry controlling the styles and durations of emergence across the platform.

The mineralogy and geochemistry of the kaolinite-rich clay wayboards indicates that they were of volcanoclastic origin. The wayboards are classed as tonsteins, but their original composition would have been close to a trachyandesite/basalt of within-plate origin, which is part of the alkaline suite of igneous rocks. The volcanic ash was likely to have been fairly locally-sourced, say, within 100 kilometres of the study area, possibly from the area of the present Isle of Man or Derbyshire.

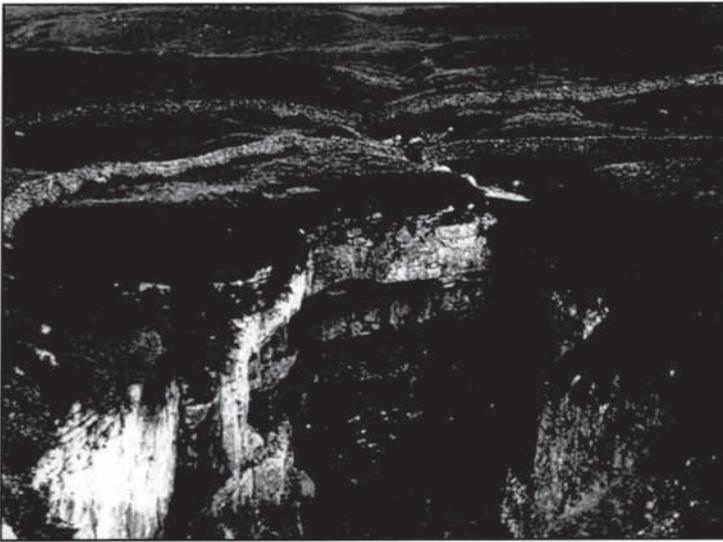


Plate 3: Late nineteenth or early twentieth century view of Hull Pot, looking towards the east. The encircling drystone wall, still intact, is clearly visible [Photo taken by Godfrey Bingley].

Jones, J E, 1987. A Noble Gift: the University of Leeds collection of photographs by Godfrey Bingley. *The University of Leeds Review*, 30, 117-135.

Mitchell, A, 1937. *Yorkshire Caves and Potholes*, 1, North Ribblesdale. [Skipton: Privately published.]

Papard, P, 1977. Hull Pot. *British Cave Research Association Bulletin*, No.15, 7-8.

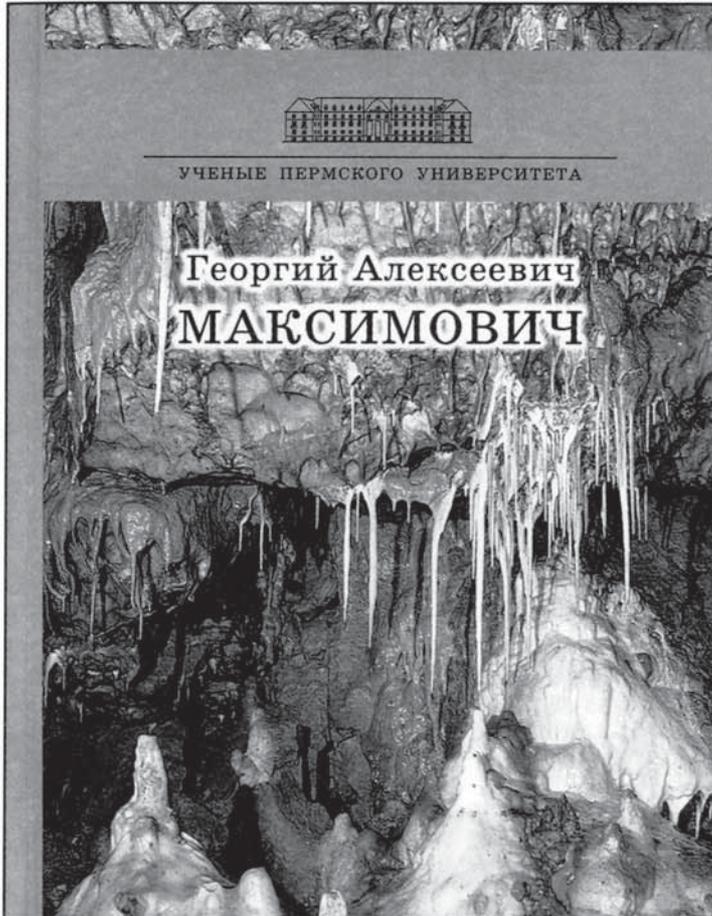


Plate 4: Hull Pot in 2004, looking towards the east. Note that the drystone wall visible in plates 2 and 3 has virtually disappeared, as is also apparent in Plate 1.

PUBLICATIONS

The following information about the subject matter of two recent historical publications was kindly supplied by Elena Larionova, of the Institute of Natural Sciences at Perm State University. The reports are presented virtually verbatim as provided, with only minor grammatical editing.

Maximovich, E G, Maximovich, N G and Kataev, V N, 2004. *George Alekseevich Maximovich*. [Perm: "Cursive" Press.] (in Russian with English summary), 512 pages; photos 32 pages.



This book is devoted to the outstanding Russian geologist and karst researcher, Professor, Doctor of geological-mineralogical sciences, and honorary member of the Geographical Society of the USSR, George Alekseevich Maximovich (1904–1979). It contains his biography, sketches of scientific, pedagogical, international and public activities, as well as a list of his publications. The book also includes memoirs of his colleagues and his correspondence with outstanding Russian geologists and geographers of the Twentieth century, academicians V A Obruchev, V I Vernadsky, A E Fersman and others. It contains many photos reflecting his life and career. On the cover of the book are views of the Maximovich Hall from the Geologists-2 Cave in the Perm Region (Russia).

G A Maximovich's creative heritage is surprisingly varied. These are works on oil geology and hydrogeology, hydrogeochemistry and geomorphology, karst and speleology, seismology and the history of science.

During 53 years of scientific activity he published 544 scientific, popular science and other works, including several monographs. His works are published in Romania, France, Austria, Yugoslavia, Bulgaria, Germany, Czechoslovakia, England and Hungary. His popular science books were published in huge circulations.

The majority of his works were devoted to questions of karstology and scientific speleology. He was the founder of the Soviet scientific school of geological karstology. In his two-volume



Dr George A Maximovich with students in 1936. During preparations for the XVII Session of the International Geological Congress he was the leader of a complex geological expedition from Perm State University.

monograph, *Basics of Karstology*, which became the encyclopaedia for karst researchers, an enormous number of generalizations and new concepts are concentrated. The book was awarded a gold medal at the VI International Speleological Congress. Many classifications, concepts and terms developed by G A Maximovich in the field of karstology have become classical and are found in encyclopedias and dictionaries.

The second scientific direction developed by him was hydrogeochemistry and the chemical geography of waters. His concept of hydrochemical facies is used by experts worldwide. His monograph *Chemical Geography of Land Waters* was awarded a gold medal by the Geographical Society of the USSR.



Dr George A Maximovich in 1960.

The third direction, oil geology and hydrogeology, he developed in 1926–1934 during his work in Chechnya. Later, in the 1960s and 1970s, he devoted himself to this direction again, and developed theoretical bases of oil-and-gas karstology.

George A. Maximovich was born in 1904 in Warsaw, graduated in 1926 from Dnepropetrovsk Mining College, and worked as a geologist in Chechnya in 1926–1934. In 1934 he founded the Chair of Dynamic Geology and Hydrogeology at Perm State University and for 45 years was its Head. He defended his doctor's thesis in 1944, receiving the highest praise from academicians V I Vernadsky and F P Savarensky.

In 1947 he founded the first USSR periodical on karst and speleology, *Speleological Bulletin*, which became *The Caves* in 1961. For 30 years it was the only regular periodical on karst topics in the USSR. G A Maximovich was its editor-in-chief for 17 years, and for 15 years he was also the editor-in-chief of another periodical founded by him, *Hydrogeology and Karstology*.

In 1964 he founded in Perm the first USSR association of karst researchers and speleologists, the Institute of Karstology and Speleology, which coordinated research on karst in the USSR and united experts from 12 Soviet republics.

During 49 years of pedagogical activity G A Maximovich took part in the education and training of thousands of experts in the field of oil geology, hydrogeology, engineering geology, geophysics and other disciplines.

Several caves, as well as notable features within caves, in Russia, in the Ukraine, in Kazakhstan and in the USA are named after him.

Professor G A Maximovich – a scientist with a global name, whose theoretical research has received international recognition.

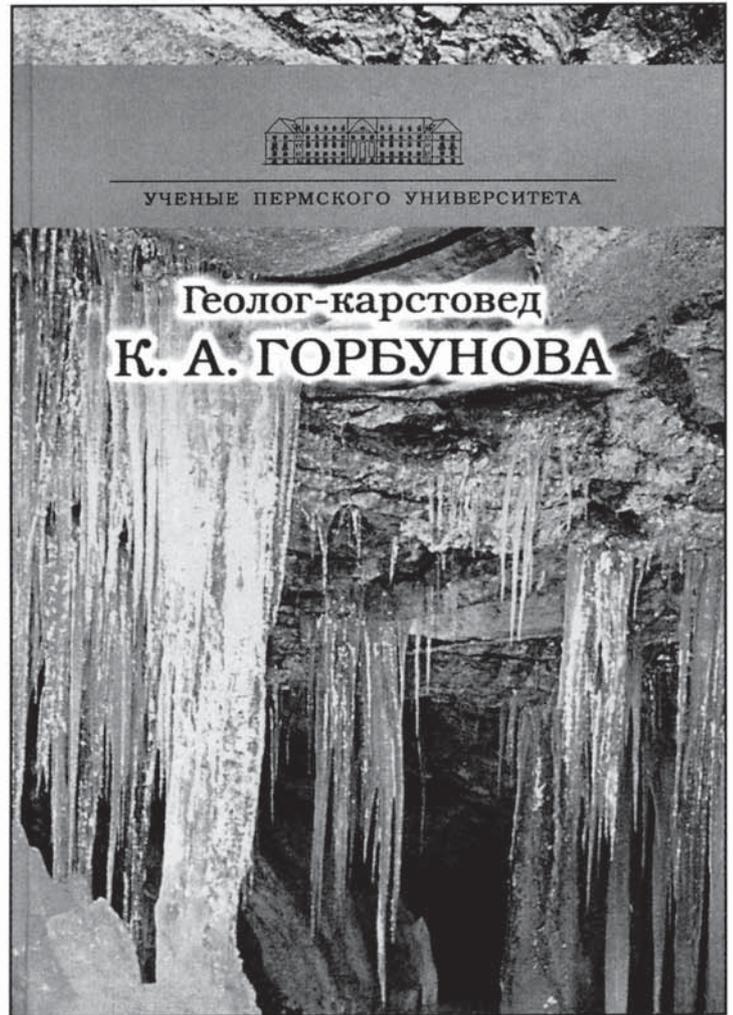
Maximovich, E G and Maximovich N G, 2002. *Geologist – Karst Researcher K. A. Gorbunova*. [Perm: Kursiv.](in Russian with English summary), 240 pages, 36 photos.

This book is devoted to distinguished Russian karst researcher Klara A Gorbunova (1925–1996). It contains a brief biography, sketches of scientific, pedagogical, international and public activities, as well as a list of her publications. The book includes recollections by her colleagues, as well as K A Gorbunova's memoirs regarding her studies at the Perm University and a history of the origin and development of karst science in Russia during the period 1947–1996.

K A Gorbunova made essential contributions to the research of karst regionalization, typology, morphology, hydrogeology, hydrology, geochemistry as well as the history of karstology. Her contribution to the research of gypsum karst is especially noteworthy. Many works are devoted to other areas of geology, some of which include speleology, geomorphology, geocology, as well as engineering geology. She is the author of 334 scientific works, including 8 monographs and a number of popular scientific works. Her last publications are devoted to the history of speleology in Russia and Kungur Ice Cave (Perm Region). Between 1993 and 1996 she was the scientific supervisor of complex studies of Kungur Ice Cave.

Career, scientific and pedagogical activities of K A Gorbunova are connected with the Perm University (1943–1996). She studied in the geological-geographical department between 1943–1948, continued her postgraduate studies at the University between 1948–1951, and successfully defended her PhD. thesis in 1956. K A Gorbunova worked at the Chair of Dynamic Geology and Hydrogeology between 1951–1993, and at the research division between 1993–1996. During 45 years of pedagogical activity, K A Gorbunova took part in the education and training of many experts in the field of hydrogeology, engineering geology, geophysics and several other specialties.

The Institute of Karstology and Speleology – the first association of karst researchers and speleologists in the former USSR – was founded in the city of Perm in 1964 by Professor G A Maximovich.



K A Gorbunova was the Deputy Director of the Institute between 1979–1992, and the Director of the Institute between 1992–1996. She was the editor of 66 editions on karst and other geological topics in 1958–1995, including the famous Russian periodical, "The Caves," which has been published in the city of Perm since 1961.



Dr Klara A Gorbunova.



The participants of the All-union conference on "Karst of Middle Asia and mountains countries", Tashkent City, 1979. From left to right: V. I. Martin, K. A. Gorbunova, V. N. Kozevnikova, N. A. Gvozdeckij.

K. A. Gorbunova was a participant in the IV, VI and X International Speleological Congresses and several additional international forums on karst, speleology and other geological concerns. She was a member of a number of commissions of the International Union of Speleology, and was a participant of the international projects on karst topics. She was in contact with many outstanding foreign karst researchers, and hosted several scientists in the city of Perm between 1990–1995.

K. A. Gorbunova's scientific works are widely used and cited, not only in Russia but also worldwide. Her publications are included in international bibliographic editions; certain monographs became classical works during her lifetime.

The book was exhibited at the International Cave Expo in Samcheok, Korea in 2002.

You can make a request for this book to meg@permonline.ru or the Chair of Dynamic Geology and Hydrogeology of Perm University.

CORRIGENDUM

We apologise to readers and to the authors involved, for the following publishing error within the Paper "*Gypsum karst south of İmranlı, Sivas, Turkey*", which appeared in *Cave and Karst Science* Volume 31, Number 1.

On page 11 of the published Paper, Figure 6 is presented correctly, as described by its caption. However, the same image was also printed, in error, as Figure 7 on the same page. In consequence, the correct Figure 7 image was omitted.

We appreciate that this last-minute compilation error will inevitably have caused annoyance and potential embarrassment to the authors, to whom we repeat our sincere apologies. Equally, we hope that the error did not spoil other readers' enjoyment of this interesting Paper too much.

For those who would wish to see the Paper as it was meant to be we have reproduced the correct Figure 7 image below, at the same size as the original, duplicated, illustration. With no printing on the reverse side of the page, this replacement image can, if required be cut out and pasted into the original Issue.



Figure 7. The Yeşilgöl Collapse Doline, southeast of İmranlı.

RESEARCH FUNDS AND GRANTS

The BCRA Research Fund

The British Cave Research Association has established the BCRA Research Fund to promote research into all aspects of speleology in Britain and abroad. A total of £2000 per year is currently available. The aims of the scheme are primarily:

- a) To assist in the purchase of consumable items such as water-tracing dyes, sample holders or chemical reagents without which it would be impossible to carry out or complete a research project;
- b) To provide funds for travel in association with fieldwork or to visit laboratories that could provide essential facilities;
- c) To provide financial support for the preparation of scientific reports. This could cover, for example, the costs of photographic processing, cartographic materials or computing time;
- d) To stimulate new research that the BCRA Research Committee considers could contribute significantly to emerging areas of speleology.

The award scheme will not support the salaries of the research worker(s) or assistants, attendance at conferences in Britain or abroad, nor the purchase of personal caving clothing, equipment or vehicles. The applicant must be the principal investigator, and must be a member of the BCRA in order to qualify. Grants may be made to individuals or groups (including BCRA Special Interest Groups), who need not be employed in universities or research establishments. Information about the Fund and application forms for Research Awards are available from the Research Fund Administrator (address at foot of page or e-mail research-fund@bcra.org.uk).

Ghar Parau Foundation Expedition Awards

An award, or awards, with a minimum of around £1000 available annually, to overseas caving expeditions originating from within the United Kingdom. Grants are normally given to those expeditions with an emphasis on a scientific approach and/or pure exploration in remote or little known areas. Application forms are available from the GPF Secretary, David Judson, Hurst Barn, Castlemorton, Malvern, Worcestershire, WR13 6LS, e-mail: d.judson@bcra.org.uk. Closing dates for applications are: 31 August and 31 January.

The E K Tratman Award

An annual award is made for the most stimulating contribution towards speleological literature published within the United Kingdom during the past 12 months. Suggestions are always welcome to members of the GPF Awards Committee, or its Secretary, David Judson (see above for contact details), not later than 31 January each year.

BRITISH CAVE RESEARCH ASSOCIATION PUBLICATIONS

Cave and Karst Science – published three times annually, a scientific journal comprising original research papers, reports, reviews and discussion forum, on all aspects of speleological investigation, geology and geomorphology related to karst and caves, archaeology, biospeleology, exploration and expedition reports.

Editors: Dr D J Lowe, c/o British Geological Survey, Keyworth, Nottingham, NG12 5GG, UK, (e-mail d.lowe@bcra.org.uk) and Professor J Gunn, Limestone Research Group, University of Huddersfield, Queensgate, Huddersfield, HD1 3DH, UK (e-mail j.gunn@bcra.org.uk).

Speleology - published three times annually and replacing BCRA's bulletin '*Caves & Caving*'. A magazine promoting the scientific study of caves, caving technology, and the activity of cave exploration. The magazine also acts as a forum for BCRA's special interest groups and includes book reviews and reports of caving events.

Editor: David Gibson, 12 Well house Drive, Leeds, LS8 4BX, (e-mail: speleology@bcra.org.uk).

Cave Studies Series - occasional series of booklets on various speleological or karst subjects.

No. 1 *Caves and Karst of the Yorkshire Dales*; by Tony Waltham and Martin Davies, 1987. Reprinted 1991.

No. 3 *Caves and Karst of the Peak District*; by Trevor Ford and John Gunn, 1990. Reprinted with corrections 1992.

No. 4 *An Introduction to Cave Photography*; by Sheena Stoddard, 1994.

No. 5 *An Introduction to British Limestone Karst Environments*; edited by John Gunn, 1994.

No. 7 *Caves and Karst of the Brecon Beacons National Park*; by Mike Simms, 1998.

No. 8 *Walks around the Caves and Karst of the Mendip Hills*; by Andy Farrant, 1999.

No. 9 *Sediments in Caves*; by Trevor Ford, 2001

No. 10 *Dictionary of Karst and Caves*; by D J Lowe and A C Waltham, 2002.

No. 11 *Cave Surveying*; by A J Day, 2002.

Speleohistory Series – an occasional series.

No.1 *The Ease Gill System – Forty Years of Exploration*; by Jim Eyre, 1989.

BCRA SPECIAL INTEREST GROUPS

Special Interest Groups are organised groups within the BCRA that issue their own publications and hold symposia, field meetings, etc.

Cave Radio and Electronics Group promotes the theoretical and practical study of cave radio and the uses of electronics in cave-related projects. The Group publishes a quarterly technical journal (c.32pp A4) and organises twice-yearly field meetings. Occasional publications include the Bibliography of Underground Communications (2nd edition, 36pp A4).

Explosives Users' Group provides information to cavers using explosives for cave exploration and rescue, and liaises with relevant authorities. The Group produces a regular newsletter and organizes field meetings. Occasional publications include a Bibliography and Guide to Regulations, etc.

Hydrology Group organizes meetings around the country for the demonstration and discussion of water-tracing techniques, and organizes programmes of tracer insertion, sampling, monitoring and so on. The Group publishes an occasional newsletter.

Speleohistory Group publishes an occasional newsletter on matters related to historical records of caves; documentary, photographic, biographical and so on.

Cave Surveying Group is a forum for discussion of matters relating to cave surveying, including methods of data recording, data processing, survey standards, instruments, archiving policy, etc. The Group publishes a quarterly newsletter, *Compass Points* (c.16pp A4), and organizes seminars and field meetings.

Copies of BCRA Publications are obtainable from: Ernie Shield, Publication Sales, Village Farm, Great Thirkleby, Thirsk, North Yorkshire, YO7 2AT, UK.

BCRA Research Fund application forms and information about BCRA Special Interest Groups can be obtained from the BCRA Honorary Secretary: John Wilcock, 22 Kingsley Close, Stafford, ST17 9BT, UK.

