Journal of the Royal Society of Western Australia, 78:43-54, 1995

Freshwater biogenic tufa dams in Madang Province, Papua New Guinea

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Manuscript received January 1995; accepted March 1995

Abstract

A large, fresh water calcareous tufa deposit occurs on a minor tributary of the lower Gogol River in Madang Province, Papua New Guinea. The tufa, apparently unique in the area, occurs just downstream of a natural river-tunnel in limestone. The river has a constant flow and is fringed by lowland rainforest. The river runs over a series of terraces formed by tufa dams and is unvegetated by macrophytes. The tufa is complex, consisting of porous, unlaminated calcite, laminated and banded stromatolites, and calcite encrusted insect tubes. Surfaces of the tufa have an epilithic community of insects, green algae, and microbes (rich in cyanobacteria and diatoms) that contributed to tufa formation. The lips of the tufa dams have a greater concentration of insect tubes, stromatolites, and filamentous green algae than elsewhere in the tufa. The associated fauna consists of caddis fly larvae (Trichoptera), midges (Chironomidae) and aquatic lepidopteran larvae (Pyralidae). The deposit is a hybrid of real stromatolites and classical tufa. This unusual equatorial tufa deposit indicates that tube-building insects can play a major role in tufa deposit construction.

Introduction

A series of calcareous tufa dams occur downstream of a river cave in lowland rainforest in equatorial northern Papua New Guinea (Fig 1). The formation is notable because it is apparently unique within a large area and because close inspection in the field shows that it is intimately associated, *inter alia*, with a rich arthropod fauna and stromatolites. This paper describes the context, structure and components of the formation.

Tufa, a spongy, porous, terrestrial, semifriable variety of travertine (Bates & Jackson 1987), is found forming dams and terraces in a freshwater stream in Madang Province, Papua New Guinea. The formation of tufa involves the localized precipitation of calcium carbonate due to processes that range from abiogenic precipitation caused by CO_2 degassing to biotic factors such as photosynthesis that also remove CO_2 (see Pentecost 1981).

Tufa often occurs at the mouths of springs, along streams, and on the shores of lakes (Scoffin 1987, Bates & Jackson 1987). The term 'tufa' apparently has its origin from Pliny (23 to 79 AD) who used the term 'tophus' (*thophus*) for encrustations on plant remains and porous volcanic rocks (Julia 1983, Ford 1989). The term travertine is often reserved for a hard, dense variety of terrestrial calcium carbonate deposit (Bates & Jackson 1987). According to Ford (1989), tufa is more or less synonymous with travertine and he prefers tufa. Julia (1983), on the other hand, uses travertine for all freshwater calcium carbonate encrustations. Chafetz & Folk (1984) use travertine as a general term for all freshwater carbonates around springs while Riding (1991) prefers that travertine be restricted to warm spring carbonate deposits. We follow the usage of Scoffin (1987) and Bates & Jackson (1987).

Most tufas that have been studied are from highly seasonal environments, mainly in the northern temperate and continental regions (Ford 1989). Tufas from low latitude regions, however, are locally abundant (*e.g.* Dunkerley 1981) and may form in seasonally arid settings like those from the Napier Range, Western Australia (Viles & Goudie 1990).

The tufa in Madang Province, Papua New Guinea, is a low latitude deposit that forms dams and terraces along a river draining a karst region (Fig 2). A complex community of aquatic insects, algae, and cyanobacteria is associated with the tufa. Unlike in many other riverine tufa deposits (*e.g.* Pentecost 1987), mosses and macrophytes are not evident. The internal structure of the tufa is variable and ranges from porous, unlaminated carbonate, to complex associations of calcified insect tubes and small stromatolites (with moulds of filamentous microbes). The calcified insect tubes are common in much of the tufa. The association of the complex biota with the tufa, the calcified insect tubes, the stromatolites, the preserved moulds of filamentous microbes, and the organic-rich nature of the tufa suggest that the biota play a major role in the formation of the tufa. The Madang tufa is important because tufas from tropical environments have not been studied in detail; it also indicates that

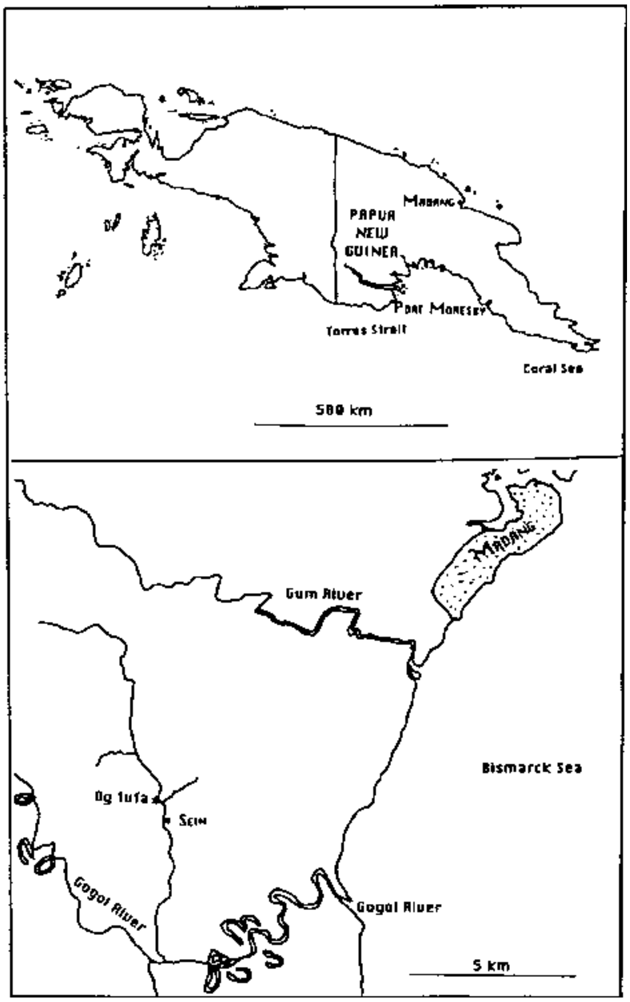


Figure 1. Location map of the Og tufa in Papua New Guinea.

tube-building insects can play a major role in tufa formation and that well-developed stromatolites occur in tufa and contributed to the carbonate buildup.

Description of the area

Location

The tufa deposit occurs in a gorge of a minor lower tributary of the Gogol River (Fig 1), downstream of the exit of a *ca.* 300 m long natural river-cave (the Og Cave) in the Wandokai Limestone; the river runs briefly through this natural tunnel, the remainder of its course being over ground. The locality is *ca.* 0.8 km northwest from Sein village, Madang Province, Papua New Guinea (5°18'S 145°43'E).

Climate

The climate is seasonal. The area comes under the influence of the north-west monsoon from December through March and the south-east trade winds for the rest of the year. The mean annual rainfall of *ca.* 3300 mm masks the high variability (2000-4500 mm over the last 40 years) that results from the strong impact of the El Niño Southern Oscillation (ENSO) on this coast. The high rainfall, together with a mean monthly temperature of between 23 and 33°C support a lowland humid forest on infrequently drying soils overlain by volcanic ash (Bleeker 1983).

Geology

The Wandokai Limestone is of Pleistocene-Holocene age and forms the bedrock of the region. This limestone is a massive and crudely bedded biocalcarenite, calcarenite, calcilutite, and calcareous mudstone with subordinate lithic arenite, conglomerate, and clay (Robinson *et al.* 1976). Although there is noticeable surface drainage, the area is a cavernous karst with predominantly underground drainage.

Methods

The tufa deposit was mapped (Fig 3) to Grade 5-3 using standard speleological methods (Ellis 1976) employing a tape measure, compass, and inclinometer (Suunto). Samples of the deposit and water were collected for laboratory analyses. Some tufa pieces were fixed in neutral formalin in a local laboratory for later microbiological studies.

Samples of the fauna from a number of distinct habitats within the tufa deposit (Fig 4) were taken for identification. Organisms were also extracted from the collected tufa samples. Sweep net samples were taken during the day from the vegetation fringing the pools and collections made at night on the tufa using a black light.

In situ oxygen concentration was measured using a Hanna Instruments HI 8543 portable dissolved oxygen meter. *In situ* hydrogen ion concentration was measured using a Beckman 031 pH meter, calibrated before and after use with Labchem calibration solutions. Water temperature was measured *in situ* using the pH meter calibrated against a certified thermometer. All other measures of water chemistry were made on samples collected (both filtered and unfiltered) in triple acid-washed bottles and kept frozen for later analysis.

Ca^{2+}, Mg^{2+}, K^{+}, and Na^{+} were analyzed by atomic absorption spectrophotometry (Varian/Spectra 30/40) and other analyses followed Strickland & Parsons (1972). X-ray powder diffraction analysis of one tufa sample (SBO305) was performed using a Philips Powder Diffractometer (12045/P3) and Random Technology controller (DFC-331 B).

Microorganisms were examined as wet mounts prepared from tufa preserved in neutral formalin. The outer surface of the tufa was scraped off and the calcite dissolved in dilute HCl. The insoluble materials were then washed with deionized water and a wet mount prepared. Samples were examined using a Zeiss Photoscope II under white light, phase contrast, and Nomarski Interference Contrast. Freshly fractured surfaces were examined under a Nikon SMZ-10 stereomicroscope to determine the extent to which larger microbes may occur below the surface.

Tufa samples were cut with a rock saw and freshly cut surfaces were examined by eye, hand lens, and a Nikon stereomicroscope. Thick (*ca.* 45 µm) petrological

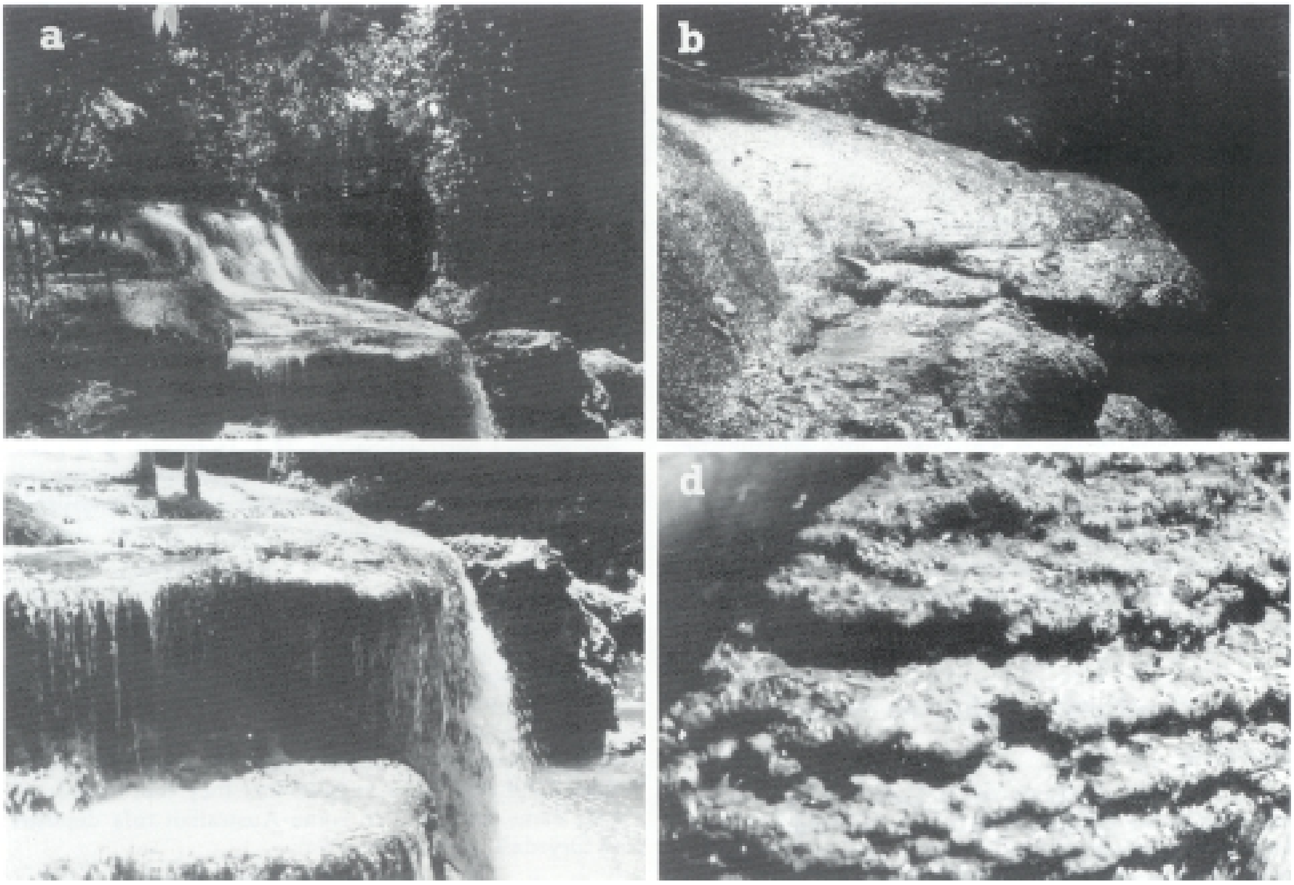


Figure 2. Parts of the Og tufa. **a.** general view of lower left section of Fig 3, **b.** 'riffle' flow over gently sloping tufa denoted by the broad tufa areas in Fig 3, **c.** detail of "a" showing overgrowth of lip, **d.** scalloped area of Fig 5 *in situ* with water partly diverted by arm (upper left).

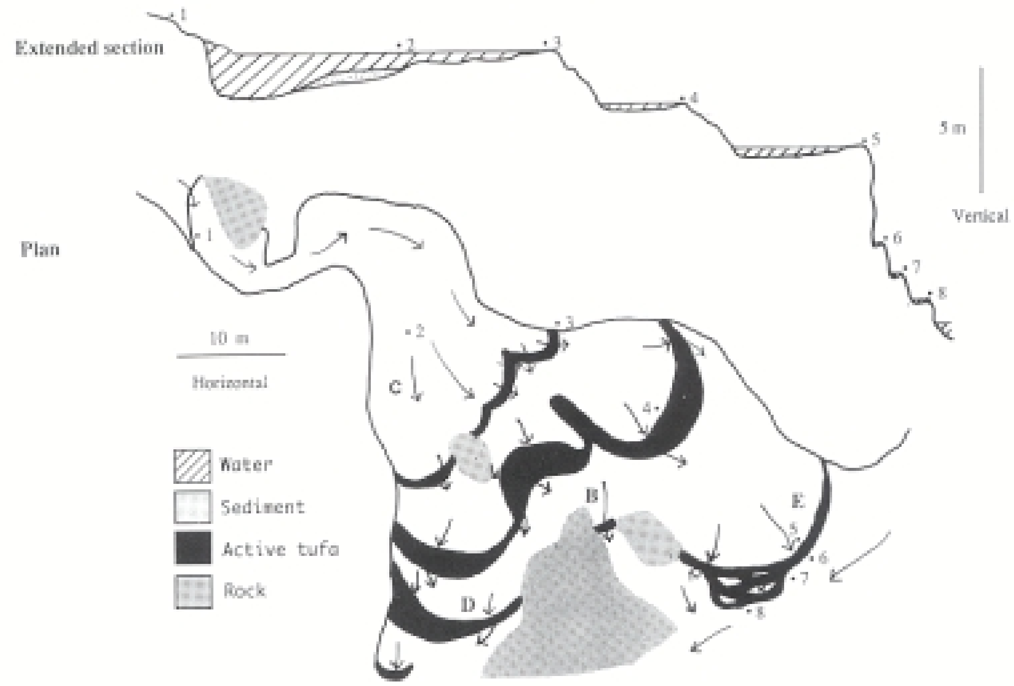


Figure 3. Plan and extended section of the tufa deposit below Og Cave with the apparently active tufa faces shown in black. The stream emerges from Og Cave (1) and spreads through a series of pools formed by tufa dams (3-8), before the confluence with another stream below the final dam (8). Some tufa dams have a narrow sill and a nearly vertical downstream face from which the water falls (3, 5-8; see Fig 2c), while others have a broad sloping sill over which the water has a riffle flow (4, D see Fig 2b). Main dam (5); B marks the site of the sill referred to in the text; dam of the upper pool (3); D denotes sites from which tufa samples were collected; E marks the approximate site of the fracture in the lower tufa dam caused by an earthquake in 1972.

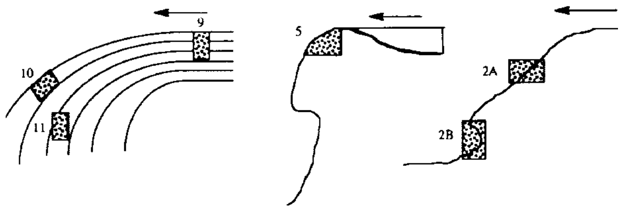


Figure 4. The location of the tufa samples: diagrammatic downstream profiles of three tufa dams indicating the relative positions from which the tufa samples were cut (numbered blocks). Left, gentle slope as in Fig 2b; middle, lip overgrowth as in Fig 2c.

sections, 151 x 176 mm in size, were prepared from six different tufa samples. These were examined under a Zeiss Photomicroscope II and Nikon SMZ stereomicroscope, with white and polarized light.

Morphological parameters of the tufa and its components (*e.g.* lamina thickness, size of microbes, and insect tube diameter) were analyzed using Optimas image analysis software (Bioscan). Statistics were performed using Microsoft Excel and SPSS for Windows.

Description of the tufa deposit

Overview

Owing to its proximity to Og Cave, we have named the deposit the Og tufa. The tufa is apparently unique within the extensive area known to the people of Sein (>10,000 km^2) although superficial deposits of tufa, lacking dams or insect tubes, are found coating rocks associated with seepages entering the Sein River from its west bank, as well as downstream of the Og confluence. The Og tufa occurs in a gorge about 20-30 m deep and 7-40 m wide, that is fringed by lowland tropical vegetation. Hence, the solar radiation incident on the tufa deposit is quite restricted, especially close to the cave. The tufa commences within 20 m of the outflow from Og Cave and extends for approximately 60 m downstream to a confluence with another tributary. There is no visible tufa deposit at the tunnel outflow but it may be obscured by a recent rockfall. The river descends 12.5 m through a series of tufa dams over a horizontal distance of approximately 60 m (Fig 3). The volume of tufa represented in Fig 3 is estimated to be in the order of 2000 m^3, assuming a constant gradient in the underlying rock. We have not measured the rate of flow for the waters in the study area.

Og Cave contains large bat colonies (thousands of bats belonging to at least several species; T Reardon, *pers. comm.* 1994), leeches (V M van der Lande, *pers. comm.* 1994), amblypygids, and millipedes. The downstream water sometimes smells of bat guano.

A fracture associated with an earthquake in 1972 split the tufa dam of the main pool near the left bank (Fig 3, site E). This caused the pool to drain and it is the only time known to the people of Sein, who use the pools daily, that water has not flowed over the face of the tufa dams. While the fissure is still visible to within 15 cm of the next drop-off, it has since been filled naturally with gravel; there has been no regrowth of tufa in the fissure. This lack of overgrowth by tufa suggests a slow rate of tufa formation in this environment. The general morphology of the deposit and the fissure suggest that the system develops by downstream progression with only minimal vertical accretion at the rims.

The river level is reported to be have been constant, even during periods of the ENSO drought. A massive log wedged in the tunnel indicates occasional major flooding. At the time of sampling in May 1990, the mean depth of water flowing over the lip of the main dam was 19±3 mm (n=20) and this depth was reported to be normal by the people of Sein.

The Og tufa is highly variable in morphology, especially at a fine scale, and we present our description of the tufa at four observational levels: megastructure, macrostructure, mesostructure, and microstructure (K Grey, S M Awramik, J Bertrand-Sarfati, H J. Hofmann, B R Pratt, MR Walter & Zhu Shixing, unpublished observations) and we focus on those features that stand out at the observational level under discussion.

Megastructure

The large-scale configuration of the tufa deposit, as seen in the field, consists of a series of dams, a few to several metres wide and up to 17 m long, that stand from less than a metre to four metres high above the next, lower tufa/pool complex (Fig 3). The upper pool contains a series of crescent shaped lips and their constant level and shape suggest that they represent fossil tufa dams, as found in some Australian tufa deposits (R Drysdale, *pers. comm.* 1994).

The lips occur between 8 and 22 m upstream of the retaining dam and are progressively deeper in the pooled water upstream, the successive mean depths (± standard deviation, n) being 22±8(8), 32±3(8), and 50±1(3) cm.

The rims of the extant dams are up to *ca.* 17 m long, are level (±3 mm), and appear to be self-regulating. A riffle-flow, several metres long, forms as the pool shallows toward the lip of the dam (the water was 19±3(8) mm

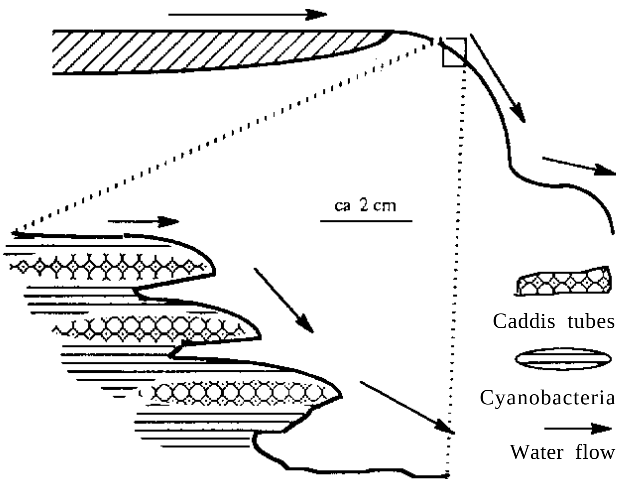
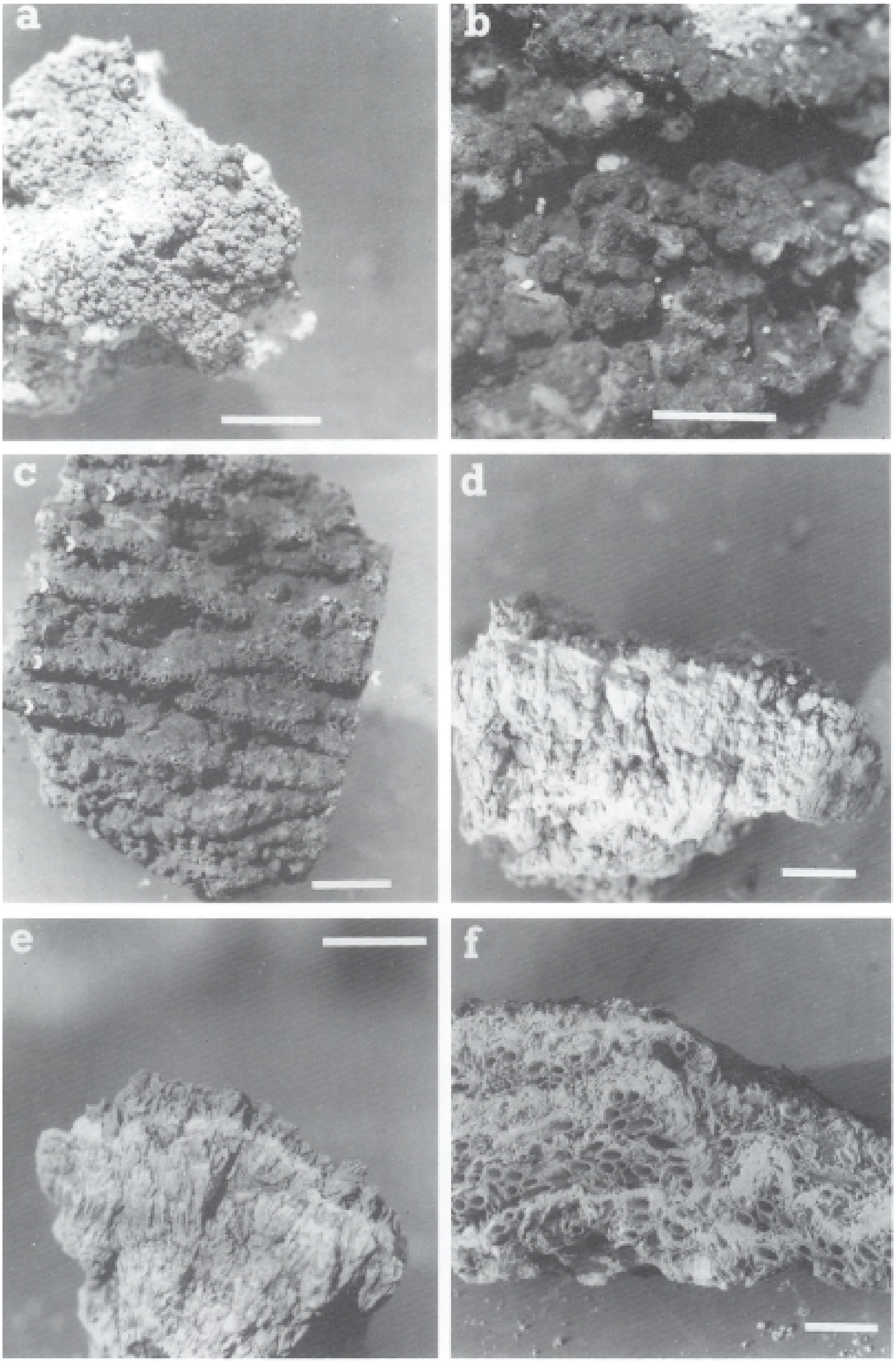


Figure 5. Diagrammatic section through an active face of the tufa formation showing water flow, and detail showing the scalloped edge (*cf* Fig 2d) and the location of caddis fly tubes and cyanobacteria/algal bands.



Figures 6. Photographs of the surface and gross sections of the formation at Sein. **a.** Surface of tufa upstream of the sill showing small protuberances (similar to the chou-fleur type of Freytet & Plet 1990); sample 2a in Fig 4. Scale bar = 10 mm. **b.** Surface growth forms as broad papillae on the sill; sample 2b in Fig 4. Scale bar = 10 mm. **c.** Surface view of the scalloping below the lip of the sill resulting from the alternating layers of cyanobacterial growth and insect tubes (arrows); sample 5 in Fig 4. Scale bar = 20 mm. **d.** Section of Fig 6b above showing the columnar growth form; sample 2a in Fig 4. Scale bar = 20 mm. **e.** Section of Fig 6a above showing the columnar growth form and the banding. Scale bar = 10 mm. **f.** Section of Fig 6c above showing alternating bands of calcareous insect tubes and denser 'algal' layers. Note macroalgae on the surface. Scale bar = 20 mm.

deep on the main dam at the time of sampling). Tufa is deposited on the steep downstream side of the dam and, as well as the expected 'microgours', has in some places a scalloped surface (Figs 2d, 5, 6c).

Macrostructure

The overall structure of the individual components of the tufa is termed the macrostructure. The tufa is primarily massive; nevertheless, there are certain obvious individual components of the tufa such as the banded appearance (Fig 6f) that is present even in the absence of insect tubes, fence-like linear arrays of calcified insect tubes (Fig 6c, 6f), stromatolites (small columns, pseudocolumns, and columnar-layered structures; Fig 6d), and nodules or bumps on the surface (Figs 6a, 6b).

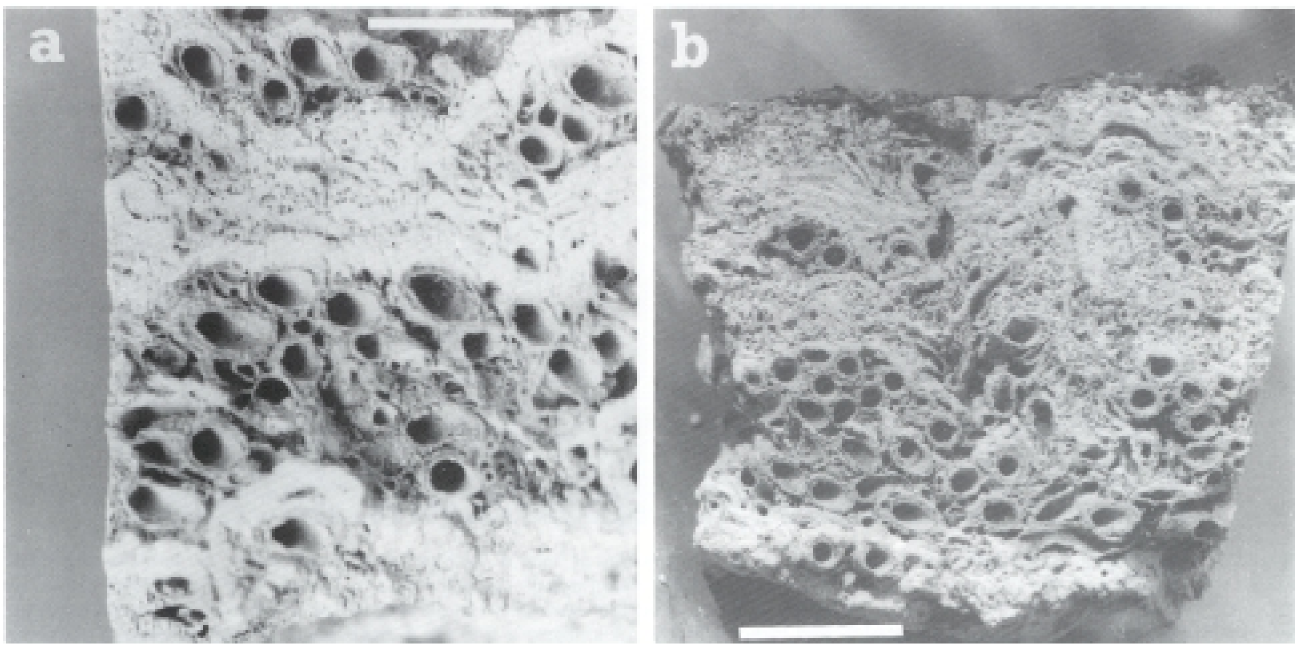
The surface of the tufa is dominated by bumps or nodules. These often appear as small protuberances, commonly a few millimetres in size but up to 2 cm across and up to 0.8 cm high (Figs 6a, 6b). Many of the nodules, when studied in cut specimens and in thin sections, appear to be the product of the complex growth of columnar-layered and pseudocolumnar stromatolites, some with a pillared microstructure (Figs 6a, 6e). Upstream of the sill (site B in Fig 3) the surface of the tufa is not regularly sculptured, but below the lip it is often deeply scalloped (Figs 2d, 5, 6c) with indentations on the order of 2.5 cm deep. The scalloping appears to be produced by the alignment of aquatic insect tubes (Figs 5, 6c, 6f, 7a). The general scalloping associated with the leading edge of the sill seems to be influenced by algae/cyanobacteria, an hypothesis that is supported by the highest density of stromatolites in these samples (Figs 6f, 8d).

Mesostructure

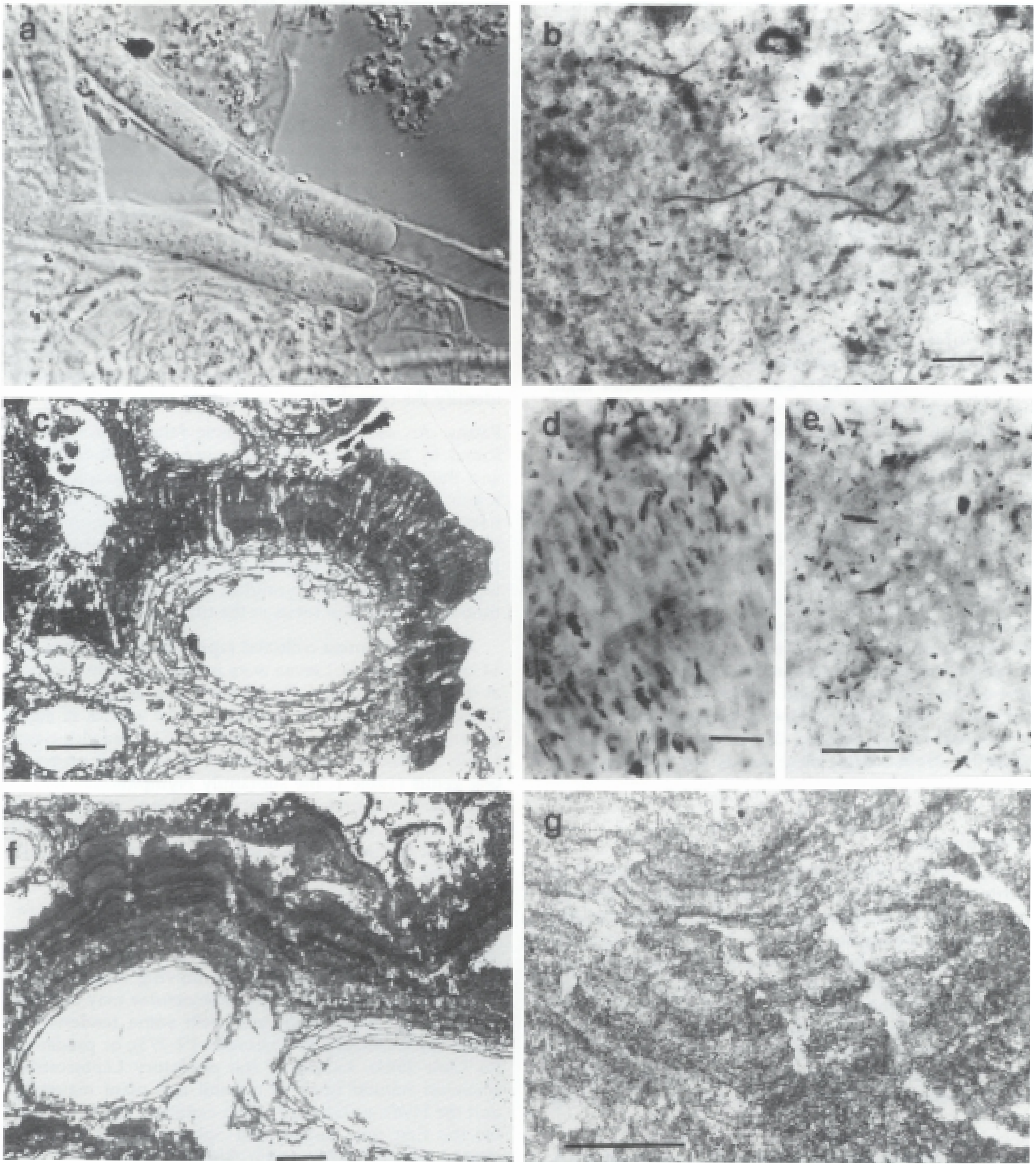
The mesostructure features (at a scale between macrostructure and microstructure; see below) include insect tubes, stromatolites and their lamination (and banding), and other small-scale features observable with the eye or hand lens.

The tufa is variable from site to site and our limited sampling constrains our ability to discern any but the most superficial patterns. Edges of dams (sills) and other areas of greater water turbulence appear to have the densest occurrence of insect tubes. Sites with denser (less porous) tufa have few large insect tubes but many smaller tubes, and a fabric that is characterized by pillared to arborescent micritic bushes often originating on insect tubes with stromatolites oriented normal to the upper surface (Fig 8c). The best-developed stromatolites (Fig 8d) occur in tufa with dense accumulations of insect tubes (Figs 6f, 8a, 8b); however, thin, somewhat columnar, columnar-layered, and pseudocolumnar stromatolites are common in all samples (terminology from K Grey, S M Awramik, J Bertrand-Sarfati, H J. Hofmann, B R Pratt, MR Walter & Zhu Shixing, unpublished observations). In samples with few insect tubes, nodules appear to be formed by pseudocolumnar tufa and stromatolite formation (Fig 6d).

The insect tubes, produced primarily by caddis fly larvae (Trichoptera), occur in all samples studied and range in size from 0.18 to 3.06 mm in diameter (mean=0.93 mm; median= 0.64 mm; n=384). They have arbitrarily been grouped into small (≤0.64 mm) and large (>0.64 mm) tubes. Tubes are not uniformly distributed with respect to size and density. For example, the sample illustrated in Fig 6f has dense arrays of large tubes with a mean diameter of 1.7 mm (median=1.83 mm; n=109). In another sample (SBO304) which has abundant tubes (ranging in size from 0.19 to 2.41 mm dia; mean=0.56 mm; median=0.44 mm; n=107), large tubes (>0.64 mm in diameter) are rare. Walls of the calcified tubes, which are up to 1 mm thick, are composed of



Figures 7. Gross sections of the formation at Sein. **a.** Section of Fig 6c showing alternating bands of calcareous insect tubes and denser layers which are stromatolites or microbial carbonates. Scale bar = 10 mm. **b.** End view of Fig 6f. Scale bar = 20 mm.



Figures 8. Photomicrographs of microbes in formalin preserved samples and thin sections of dried tufa. **a.** Oscillatoriacian cyanobacteria on surface of tufa (from formalin preserved sample). Scale bar *ca.* 10 µm. **b.** Filamentous cyanobacteria in laminae of the stromatolites. Scale bar *ca* 25 µm. **c.** Portion of stromatolite on calcified insect tube with pillared microstructure or tufts; pillars are separated by voids filled with sparite. Scale bar = 1 mm. **d.** Microbial carbonate with radiating filamentous microbial fossils (clear tubes) in a micritic matrix, forming small, dense bushes. Scale bar *ca.* 25 µm. **e.** Cross section of filamentous microbial fossils (arrows) similar to Fig 8d. Scale bar *ca.* 25 µm. **f.** Stromatolite encrusting and bridging calcified insect tubes. Scale bar = 1 mm. **g.** Coarsely laminated stromatolites. Scale bar = 1 mm.

laterally discontinuous micritic layers often organized in a lacework to cellular pattern (Figs 8c, 8f). The inner surface of tubes often has a yellowish-brown stain. Tufa specimens with moderate to abundant calcified insect tubes also appear to have the most stromatolites. In thin section, the laminae of the stromatolites are seen between and encrusting insect tubes (Fig 8f).

Frequently, a variety of small (<1 cm dia) calcareous tubes is found in tufa (*e.g*. Wallner 1935; Heimann & Sass 1989). Some of these are carbonate precipitated around plants (Pedley 1992) while others are calcified insect tubes (Scholl & Taft 1964). In contemporary deposits, direct observation can be made of the organisms making the tube but in ancient tufa deposits it may be difficult to differentiate between plant and insect tubes. However, in fossilized examples a limited variability in tube diameter would suggest that small plants (*e.g.* bryophytes) and insects were involved, whereas tubes many centimetres in length would indicate plant stems or roots (root hairs may be preserved). We suggest that the nature of the calcified wall, like the lacework found in the Og tufa insect tubes, may be a feature characteristic of tube-building insects that could be used to identify them in ancient tufas.

The tufa contains numerous small (<1 cm dia) pseudocolumnar and columnar-layered stromatolites (columnar forms are rare), less than a centimetre high, that frequently encrust masses of calcified tubes (Fig 8f). The stromatolites appear to be most abundant in tufa with the densest population of tubes and these occur at the sill; however, they are not abundant in tufa with the fence-like arrays of tubes (Fig 6c).

The thickness of the stromatolitic laminae varies considerably. However, there is a clear pattern of predominantly light laminae (average 114.8 µm thick) and dark laminae (average 56.4 µm thick). Some areas have a coarsely laminated, banded appearance (Fig 8g) which is a variety of stromatolitic laminae (Fig 8f). The bands are alternating layers of thinner dark micrite and thicker light-colored microspar and differ from stromatolite laminae in their more diffuse boundaries and overall coarseness of the calcite. Unlike banding in many lacustrine stromatolites, these bands are not composed of finer laminations.

Microstructure

Much of the tufa is structureless and composed of micrite with numerous voids. Thin sections of this tufa appear very dull, blue-green in color under cathode luminescence indicating primary, fresh calcite that has not be influenced by meteoric/diagenetic processes. There are two obvious microstructures, pillared and stromatolitic. Stromatolitic microstructure consists of alternating laminae of thinner dark micrite and thicker light microsparite (see above). The preservation of the material is sufficient to preserve filamentous microbial fossils (presumably cyanobacteria) in the laminae (Fig 8b).

An interesting microstructure is a pillared form which is dominant in sample SBO 305. The pillars consist of small, possibly cylindrical structures (25 to 82 µm dia), some occasionally bifurcate, arranged in a radial manner on large calcified insect tubes, and composed of micrite (Fig 8c). Individual pillars have a fibrous internal structure and are composed of remnants of microbial filaments arranged parallel to the long axis of the pillar. This structure resembles the stromatolitic tufts described by Freytet & Plaziat (1982, Plate 9a on page 113). Most filaments are not well preserved and it is uncertain if the filaments branch. The diameter of filament moulds of clear calcite is approximately 3 µm. Filaments of this size are apparently common in tufa (*e.g.* Pedley 1987).

Biogenic elements in the tufa

Cyanobacteria and algae. In formalin preserved specimens, the surface of the tufa contains a complex microbial community dominated by filamentous cyanobacteria (Fig 8a) and diatoms. Green algae live on the surface of the tufa, but we have not found compelling evidence of green algae preserved in the tufa. The pillared microstructure shown in Fig 8c contains in longitudinal section what might appear to be the remains of large filaments. However, we have not found circular cross sections of the same diameter that would support this interpretation (see Figs 8d, 8e). While the cyanobacteria appear to dominate numerically, the larger green algae would dominate the photosynthetic biomass. Because of limited sampling of fixed material and the degradation that occurred between the time samples were collected and fixed in the laboratory, we have not attempted to identify the cyanobacteria or algae in more detail.

Fauna. An abundant and diverse fauna is sometimes found in and on tufa deposits (*e.g.* Dürrenfeldt 1978) and the Og tufa is no exception. Faunal samples were taken for identification from a number of distinct habitats within the system. The dominant biomass of these samples is for several species of sedentary caddis fly (Trichoptera), Diptera ('midges') and aquatic lepidopteran larvae (Pyralidae; two species). Some of these species inhabit tubes in the tufa, and spin nets.

Adult Trichoptera collected represent eight genera (*ca.* 14 species; Table 1). Larvae were present in various instars at the one time observed. Adults of the dipteran family Chironomidae represent probably eight species of eight genera (P Cranston, *pers. comm.*). The lepidopteran family Pyralidae was represented by larvae of probably one genus (Table 1; the subfamily Nymphulinae within Australasia requires revision; J Hawking, *pers. comm.*). In addition, an errant fauna including flatworms (Turbellaria) and water mites (Hydracharina) was observed.

Many of the caddis-fly larvae (Trichoptera: Hydropsychidae: Philopotamidae) represented in the samples mostly strain food (algae, fine organic particles and small invertebrates) from the flowing water by constructing capture nets of silk. Leptoceridae may be large or small particle detritivores with some tendency to herbivory (especially in *Triaenodes* PT-773), or predatory (St Clair 1994). Larvae of the predatory Leptoceridae construct tubular cases of mineral and plant materials, and the Hydroptilidae, or micro-caddises, are free-living for the first four instars and only construct a purse-shaped case in the fifth instar (Neboiss 1991).

The Nymphulinae (Lepidoptera) have aquatic larvae which may be case-making, web-spinning or free-living, and feed on algae or aquatic plants, and may live in flat cases formed from pieces of the food plant.

The chironomid taxa represented are all rheophilic, with the possible exception of ?*Bryophaenocladius,* which belongs to a terrestrial/semi-terrestrial clade. Most are relatively cosmopolitan genera, although *Riethia* has South American/Australian affinities, and *Skusella* has Afrotropical/Australian affinities. *Microtendipes* is apparently monotypic and quite uncommon in Australia, and the only adult species that has been named is

Table 1

Insect larvae (L) identified from the tufa, and adults (A) collected at a black light situated above the Og tufa.

Species	Family
TRICHOPTERA	
Cheumatopsyche sp PT-1862	Hydropsychidae (A)
Cheumatopsyche sp PT-1863	Hydropsychidae (A)
Cheumatopsyche sp PT-1868	Hydropsychidae (A)
Cheumatopsyche sp	Hydropsychidae (L)
Chimarra sp PT-1864	Philopotamidae (A)
Chimarra sp nr *C. goroka* Sykora PT-1866	Philopotamidae (A)
Chimarra sp nr *C. papuana* Kimm. PT-1865	Philopotamidae (A)
Chimarra sp	Philopotamidae (L)
Ecnomus sp	Ecnomidae (A)
Hellyethira sp nov A Wells (in press)	Hydroptilidae (A)
Oecetis sp; ?*O. buitenzorgensis* Ulmer	Leptoceridae (A)
Orthotrichia sp nov[1]	Hydroptilidae (A)
Tinodes sp; ?*T. aberrans* Kimm	Psychomyiidae (A)
Triaenodes sp PT-1867	Leptoceridae (A)
Triaenodes sp B	Leptoceridae (A)
?genus	Leptoceridae (L)
Triaenodes sp C (different from PT-1867)	Leptoceridae (A)
?genus sp 2	Hydrophilidae (L)
DIPTERA: CHIRONOMIDAE	
genus nr *Thienemannimyia*	Tanypodinae: Pentaneurini
Cricotopus cf *albitibia* Kieffer	Orthocladiinae (A)
Riethia ?*stictoptera*	Chironominae (A)
Rheotanytarsus	Chironominae (A)
Rheocricotopus	Orthocladiinae (A)
nr *Bryophaenocladius*	Orthocladiinae (A)
genus nr *Skusella*	Chironominae (A)
Microtendipes sp	Chironominae (A)
LEPIDOPTERA: PYRALIDAE	
Potamomusa sp	Nymphulinae (L)
EPHEMEROPTERA	
? genus	Caenidae (L)
Baetis sp	Baetinae (L)

[1] to be described by A Neboiss

conspecific with the Afrotropical species, although rearing would be required to confirm this (P Cranston, *pers. comm.)*.

Water chemistry

The general water chemistry from samples collected above and below the Og tufa are presented in Table 2. The pH of the water increased significantly while flowing over the formation rising from pH 7.6 to *ca.* pH 8.0 ($F_{1,4}$ = 36.7; p= 0.004) but the temperature (26.7±0.33°C; n=10) and oxygen content (mean 7.8 ±0.13 ppm O_2, n= 14) showed no trend, with the latter being *ca.* 95-99% saturated throughout its passage across the formation. The water is nutrient rich (as reflected by the nitrate levels; Table 2) having received the waste products of a large bat colony inhabiting the tunnel immediately upstream.

Table 2

The mean constituents of water flowing over the Og tufa on 24 May 1990 (n=2).

	mg L^{-1}
Calcium	27.65
Magnesium	2.15
Potassium	0.35
Sodium	2.3
Total iron	0.34
Nitrite-N	0.006
Nitrate-N	0.47
Ammonium-N	0.39
Phosphate-P	0.025
Total-P	0.031

The water chemistry is unremarkable except that the calcium concentration of <30 mg L^{-1} is very low for a tufa-depositing stream and perhaps provides support for the biotic involvement in the tufa formation. By comparison, fresh groundwater in a tropical karst in Cape Range, Western Australia, has a mean of 82 mg L^{-1} Ca^{2+} (sd= 4.9, n= 7). Detailed examination of the water and tufa chemistries is required to determine the relative contribution of physical and biological processes to tufa deposition and nature of the carbonates involved.

Microenvironment

The water velocity increases as it approaches the lip of the sill (dam) and passes down the face. The distribution of the taxa with respect to the sills in the tufa is shown in Fig 9. The front face is saw-toothed with the lee positions of the formation being occupied by tubes of net-making caddis flies; the growth appears to be by forward progression of the cyanobacteria-rich laminae (Fig 5). The internal structure of the formation varies in a manner apparently related to the nature of the water flow in the area. Sections of the rock show clearly that tufa growth has progressed outwards and that it has changed position (elevation; see fossil sills in Fig 3) so that the deposited band of tufa/calcite is sinuous, similar to turbulent water flow (Figs 6f, 7a, 7b).

The rows of net-trapping Trichoptera were mostly collected under the overhangs on the face of the dams, while the bigger, long-jawed caddis flies were more frequent in the riffles, with tube-living chironomids throughout. These are different microhabitats even within the front face of the falls. The microturbulence of the water may be of considerable importance in determining suitable microhabitats for the cyanobacteria, algae, and the arthropods.

Although many of the insects inhabiting the formation are net-builders, they would trap little non-calcareous material from the stream; the acid insoluble fraction of the tufa comprised only 0.8% by weight (range 0.30 to 1.0; n=3); this compares with from 4-9.1% acid insoluble fraction in tufas from Europe and Australia (Viles & Goudie 1990) and a mean of 3.44% (range1.0-10.55%) in ten accreting deposits from active sites in Great Britain (Pentecost 1993).

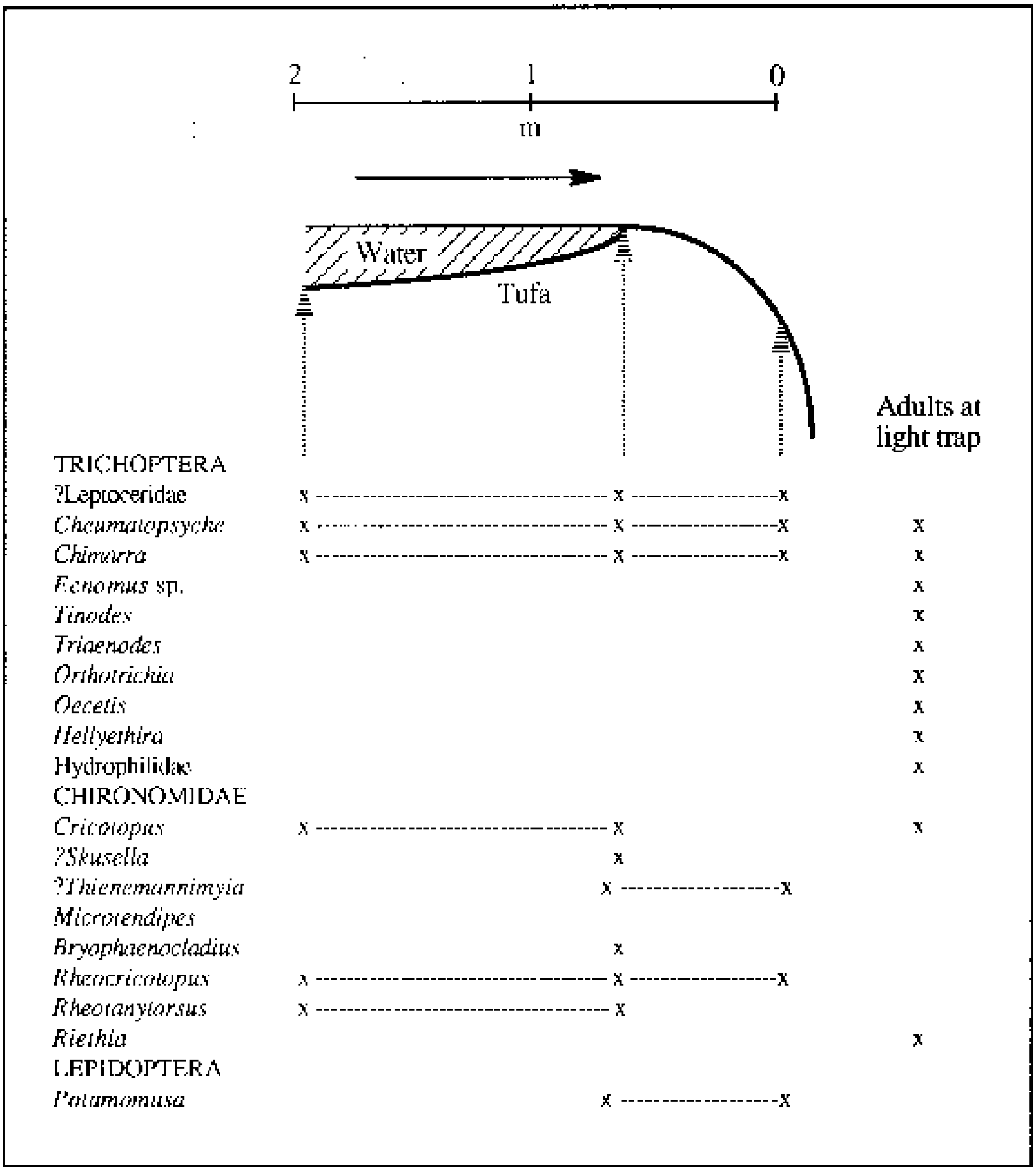


Figure 9. The distribution of the taxa with respect to the sills in the tufa formation. The water is pooled upstream of the sill and then forms riffles over the lip and down the face. The light trap data indicate adults present at the site.

Discussion

The series of drowned tufa dams in the upper pool (Fig 3; another example is also discussed by Ford 1989) provides evidence consistent with the face of the tufa dams both growing in height and progressing downstream. The sweeping convex downstream faces and the remarkable evenness of the lips of the tufa dams suggest they are self-regulating and that they progress most rapidly where the current is strongest in the centre of the stream.

The water is rich in nitrates (Table 2) possibly resulting from bat guano. Marine stromatolites are often prevented from forming by an increase in the nutrient levels in the water which promotes growth of algae over the cyanobacteria (Pentecost 1978, 1992) and the same could occur in non-marine environments. However, with the Og Tufa, algae (other than diatoms) and mosses are not sufficiently abundant, despite the high nutrient levels, to dominate tufa surfaces and prevent cyanobacterial and diatom participation in the construction of the tufa. It is uncertain what factor(s) prevents luxurious growth of higher photosynthesizers.

Tufa dams and terraces are normally discussed in the context of examples from highly seasonal climates in which both diurnal and annual growth layers can be observed in the formations (Ford 1989). Ford's recent review mentions no large tufa deposits from equatorial regions lacking seasonality – the constancy of water flow over the Og tufa was noted above – yet widespread and varied tufa deposits were reported by Hossfeld (1951) to occur in northern Papua New Guinea, including the Madang area.

Five methods of tufa deposition have been identified (Ford 1989): 1) chemical reactions in saline or alkaline lakes; 2) the cooling of thermal waters 3) inorganic degassing of CO_2 (often promoted by microturbulence); 4) indirect biochemical precipitation caused by photosynthetic uptake of CO_2; and 5) direct metabolic precipitation of calcium carbonate by organisms such as cyanobacteria, algae, and mosses. The first two factors are unlikely candidates for the genesis of the Og tufa because the conditions are not appropriate. The third factor is unlikely to be the prime agent in the formation of the Og tufa as there is only minor evidence for tufa formation where it might be expected elsewhere in the system, in the absence of biotic associates. The fourth factor is unlikely as living stems and leaves immersed in the water were not covered by tufa either above or below the Og tufa. The presence of cyanobacteria and algae within the tufa and the development of stromatolites within suggest a role of the fifth factor in the formation of the Og tufa, although the effect might be indirect (Pentecost 1978, 1981, 1984, 1985).

Our study of the Og tufa suggests that a sixth factor needs to be added to the list of tufa depositing agents, namely the presence of tube-building insects living amongst the stromatolitic layers (Figs 6f, 7a, 7b, 8a, 8b). The tubes provide a stable substrate for benthic microbes (like the cyanobacteria and diatoms) that are adapted to an environment characterized by turbulence and the precipitation of calcium carbonate.

The Og tufa is an example of a tufa deposit formed by a combination of factors (3, 5, and 6) where local water turbulence, a rich benthic photosynthetic microbial community, and calcite tube-building invertebrates combine to form tufa.

There is a commonly held notion that microbial mats and stromatolites form in environments that are extreme (*e.g.* Jørgensen & Revsbech 1982). Microbial mats of cyanobacteria and diatoms are very common in a variety of environments and form in areas actively grazed and burrowed by macro and micro invertebrates. The accretion of cyanobacteria into stromatolites in an environment seemingly benign - constant water, equatorial climate, buffered, moderate water chemistry - and biotically rich may be puzzling. However, the key ingredient here is the rapid precipitation of calcite that mineralizes the structure; if mineralization is contemporaneous with microbial growth, stromatolites can form.

Acknowledgements: We are grateful to the landowners of Sein village for permission to work in the area, for their assistance with the work and their hospitality. For determining the fauna we thank Dr A Neboiss, Museum of Victoria (Trichoptera); Mr J Hawking, Murray Darling Fresh Water Research Centre, Albury (Pyralidae) and Dr P Cranston, Australian National Insect Collection (Chironomidae). Laboratory water analyses were conducted by P L Osborne, Department of Biology, University of Papua New Guinea. Caroline Lawrence assisted in the preparation of the map and Douglas Elford printed photographs of the tufa samples. David Pierce performed the XRD analysis and printed photomicrographs. SMA acknowledges the financial assistance of NASA Grant NAGW-1940 on lacustrine stromatolites. The field work was conducted while WFH was in receipt of a Christensen Research Institute Fellowship and with the approval of the Madang Provincial Council. This is contribution 143 from the Christensen Research Institute, Madang, Papua New Guinea. We thank Russell Drysdale for his pertinent comments on a draft of this paper.

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