AQUATIC INSECT LARVAL CONSTRUCTIONS IN TROPICAL FRESHWATER LIMESTONE DEPOSITS (TUFA): PRESERVATION OF DEPOSITIONAL ENVIRONMENTS

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Summary

Tufas are known worldwide as useful archives of palaeoenvironmental information. Recognition of structures within tufas that preserve depositional environments will ensure maximum information is obtained from fossil tufa sequences. Here we document distinctive characteristics that allow recognition of aquatic insect larval constructions within tufa deposits and the depositional environments under which each develops. In tufas from the Gregory River (NW Qld, Australia), fixed-dwelling tubes built by larval midges (Diptera: Chironomidae) represent tufa deposition under flowing or standing water conditions. In thin sections of chironomid tufa, the tubes appear as rings approximately 600 μm in diameter composed of micrite and organic matter. A combination of chironomid tufa and larval caddis-fly (Trichoptera: Hydropsychidae) fixed retreats and nets is a common tufa dam fabric, and indicates deposition in flowing water. The hydropsychid retreats are preserved as 2 mm diameter rings of calcite arranged in a lacework pattern. Tufas formed under spray hydraulic conditions on pool banks near waterfalls contain marquees built between cyanobacteria colonies by larval moths (Lepidoptera: Pyralidae). In thin section, these marquees appear as a calcite encrusted silken sheet up to 5 mm long.

Keywords: tufa, Riversleigh, Gregory River, Chironomidae, Hydropsychidae, Pyralidae

INTRODUCTION

Freshwater limestone deposits (tufas) are important potential sources of palaeoenvironmental information (Drysdale and Head 1994; Andrews *et al*. 2000; Horvatincic *et al*. 2000), and have been used successfully to reconstruct climate histories (e.g. Andrews *et al*. 1994). Such climate information is essential for the development of accurate predictive models of future climatic change, which are validated through studies of both contemporary climate patterns and environmental responses to past climate change (Williams *et al*. 1998). Incorrect interpretation of fossil tufa sequences (e.g. "*Oocardium* tufa" of Bradley (1974), reinterpreted as arrays of calcified caddis-fly (Insecta: Trichoptera) larval cases by Leggitt and Loewen (2002)), may hinder palaeoenvironmental reconstructions. Thus, recognition of structures that reflect a particular tufa depositional environment will aid correct interpretation of fossil tufa sequences.

Depositional models assist in deciphering palaeoenvironments preserved in rock sequences (Tucker 2001). Such models for tufa environments have thus far only been derived from studies of temperate and semi-arid depositional systems (e.g. Pedley 1990). However, recent research at the Gregory River in northwest Queensland, Australia (Figure 1) has revealed significant disparities between tufa sequences in this tropical environment and those of existing extra-tropical models (the authors, unpublished data). One notable difference in tufas forming under tropical climatic conditions is the importance of aquatic insect larval constructions, which persist all year because of the warm and stable water temperatures.

Aquatic insect larvae play an important role in tufa formation in Madang Province, Papua New Guinea (Humphreys *et al*. 1995) and Louie Creek, northwest Queensland (Drysdale 1998; 1999), whereas they are less significant in most temperate locations (Pentecost *et al*. 2000) where larval activities are restricted to spring-summer (Janssen *et al*. 1999). The insect larvae not only enhance the rate at which the rock forms, but also encourage growth of new tufa deposits and re-growth on older tufa surfaces (Drysdale 1999). Larval constructions, particularly dwelling tubes and feeding nets, become incorporated into the tufa (Cranston 1997), and result in distinctive tufa fabrics (Humphreys *et al*. 1995; Janssen *et al*. 1999). Because each insect family occurs within specific hydraulic zones (Drysdale 1998), accurate recognition of larval tufa may be invaluable for interpreting fossil tufas.

This paper documents distinctive structures associated with larval tufas in the Gregory River, the largest stream draining the Barkly Tableland (Figure 1). Tufas in the Gregory River host an assemblage of macroinvertebrates, conspicuous dwellings and feeding constructions of larval midges (Diptera: Chironomidae), caddis-flies (Trichoptera: Hydropsychidae) and moths (Lepidoptera:

Pyralidae). Compared with studies of tufas in temperate climates, there is a paucity of studies of tropical tufa systems (Ford and Pedley 1996). Thus, we aim to improve current knowledge concerning tropical tufa formation, to describe in detail a common tufa fabric from this environment, and to outline a set of useful geological recognition criteria for accurate identification of larval tufa. This will assist in correctly interpreting depositional environments preserved in fossil tufa sequences, which is vital for accurate reconstruction of tufa palaeoenvironments.

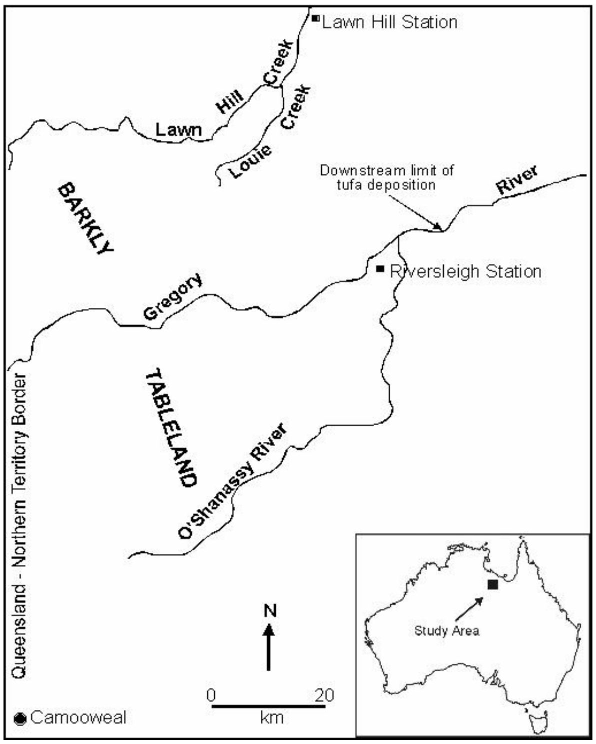

Figure 1. Location of the Gregory River, northwest Queensland, Australia. Tufa is deposited along a reach ~30 km in length. The downstream limit of tufa deposition is located ~11 km downstream of Riversleigh Station (arrow).

MATERIALS AND METHODS

Study site

Located in the seasonally humid tropics, the perennial spring-fed Gregory River is one of four major tufa-depositing streams draining the Barkly Tableland (Figure 1), which has developed in Cambrian limestones and dolomites (Sweet and Hutton 1982). Tertiary Carl Creek Limestone preserved at the study site reveals that tufa deposition has occurred in the area since at least around 20 Ma (Megirian 1992). Freshwater limestones, or tufa, are currently forming as sequences of dams and reefs along a reach extending approximately 30 km from springs in the Barkly Tableland to about 11 km downstream of Riversleigh Station (Figure 1). Precipitation in northern Australia is mainly confined to the summer months and during the wet season is strongly controlled by the strength of the Southern Oscillation Index and variation in the position of the Intertropical Convergence Zone. Average annual precipitation is 535 mm, while mean annual pan evaporation is approximately 3000 mm; consequently the region experiences a significant hydrological deficit. Average annual temperature is approximately 25°C. The dense scrub in the riparian zone is dominated by *Melaleuca* spp. and *Pandanus* spp. whereas vegetation in the surrounding catchment consists of savannah and open woodland.

Sample collection

Sixty samples of fresh tufa were collected from seven sites along the Gregory River in July 2001. All samples were air-dried. Although there is natural variation between individual deposits within the zone of tufa deposition, all are largely indistinguishable with respect to their morphology and the presence and distribution of tufa fabrics. We have also observed comparable tufas in neighbouring Barkly Tableland rivers, and so are confident that the sampling locations chosen are representative of Gregory River tufas.

Microscopy

Air-dried samples were examined by light microscopy. A selection of samples representing individual tufa fabrics, such as larval tufa, moss tufa and microbial tufa, were resin-impregnated then thin-sectioned. The sections were cut to a thickness of 30 μm and were examined in plane-polarised light and under crossed polars.

RESULTS

Evidence of larvae from three insect families is preserved within Gregory River tufas (Table 1). The dominant chironomid genus is *Rheotanytarsus*, while hydropsychids are mainly represented by the genus *Cheumatopsyche*. Chironomids, hydropsychids and larval pyralids are also conspicuous throughout other tufa-depositing streams in the Barkly Tableland (Drysdale 1998). Distinctive larval structures (Figure 2) and associated fluvial environments preserved in tufas associated with each insect family are reported below.

Chironomidae

Based on tube morphology and geographic distribution, we have identified Gregory River chironomid tube-builders as larvae of the species *Rheotanytarsus flabellatus* (Glover). Ridges along each chironomid tube, extended to become arms at

Table 1. Distinctive characteristics of larval constructions commonly preserved in Gregory River tufas, and hydraulic environments each represents. These hydraulic environments are described in Table 2.

LARVAE	LARVAL CONSTRUCTIONS	GEOLOGICAL RECOGNITION CRITERIA	HYDRAULIC ENVIRONMENTS
Diptera: Chironomidae	Fixed dwelling tubes	Ring of micrite and organic particles 5 circular objects within ring Diameter of ring: 600 μm Thickness of ring: 150 μm	Flow, lap, standing
Trichoptera: Hydropsychidae	Fixed retreats	Lacework calcite ring Diameter: 2 mm Thickness: 1 mm	Flow, lap, impact
	Silk capture nets	Arcuate microridges Height: up to 10-20 mm	
Lepidoptera: Pyralidae	Silk marquee	Thin sheet perpendicular to tufa growth direction Length: 5 mm	Flow, lap, spray
	Burrows	Cylindrical hollows within tufa Diameter: 5 mm	

the tube's anterior, are visible in Figure 2(a). This type of tube is only constructed by *R. flabellatus*; other species build the arms on the rim of the tube (Cranston 1997).

In the Gregory River, masses of chironomid tubes (Figure 2a) or, less commonly, individuals, cover portions of tufa dams, woody debris dams, gravel riffles and the channel base in flow zones (Table 2). They are less common in lower energy zones, but may be present on the channel banks in lap zones and on leaf litter in standing water hydraulic zones (Table 2). The chironomid tubes are always constructed parallel to the direction of water flow with the arms facing into the stream current (Figure 2a). The tubes are gradually incorporated into tufa deposits as calcification occurs, enhancing the apparent tufa accumulation rate by increasing its porosity.

Thin sections cut transverse to the long axis of Gregory River chironomid dwelling tubes show that the porosity of chironomid tufa is approximately 60%. Each chironomid tube is preserved as a ring of micrite (microcrystalline calcite, grain size less than 4 μm (Tucker 2001)) and organic matter (Figure 2b). Evidence for tube calcite encrustation is preserved in isopachous calcite fringes surrounding each ring (Figure 2b). Figure 2(b) shows that the rings may be up to 600 μm in diameter and about 150 μm thick. Ridges formed from tube arm structures are preserved within the ring. These ridges appear as five, evenly spaced, 100-150 μm diameter circular features composed of organic material (Figure 2b).

The number of these features is comparable with the number of arms on each tube. Voids surrounding the organic matter indicate that the ridge material has begun to decay. Tube arm structures preserved within thin sections through chironomid tubes are just one characteristic that allows the chironomid tubes to be distinguished from hydropsychid retreats, which are described below.

Hydropsychidae

In the Gregory River, *Cheumatopsyche* larvae prefer high-energy hydraulic conditions and arcuate arrays of the retreats and nets aligned transverse to flow direction (Figure 2c) cover all surfaces in lotic (flowing water) situations (Table 1). Thin sections cut perpendicular to vertical retreat orientation show that hydropsychid retreats are readily distinguished from chironomid tubes (Figure 2). Not only are the hydropsychid retreats larger, but also they are quite different structurally. Hydropsychid retreats are preserved as a sub-circular ring approximately 2 mm in diameter (Figure 2d). Walls of the retreat are up to 1 mm thick and consist of sparite (calcite crystals larger than 4 μm (Tucker 2001)) arranged in a lacework pattern (Figure 2e).

Pyralidae

In the Gregory River, larval pyralids construct rectangular marquee-like shelter structures (Figure 2f) across tufa surfaces and also build retreats in the

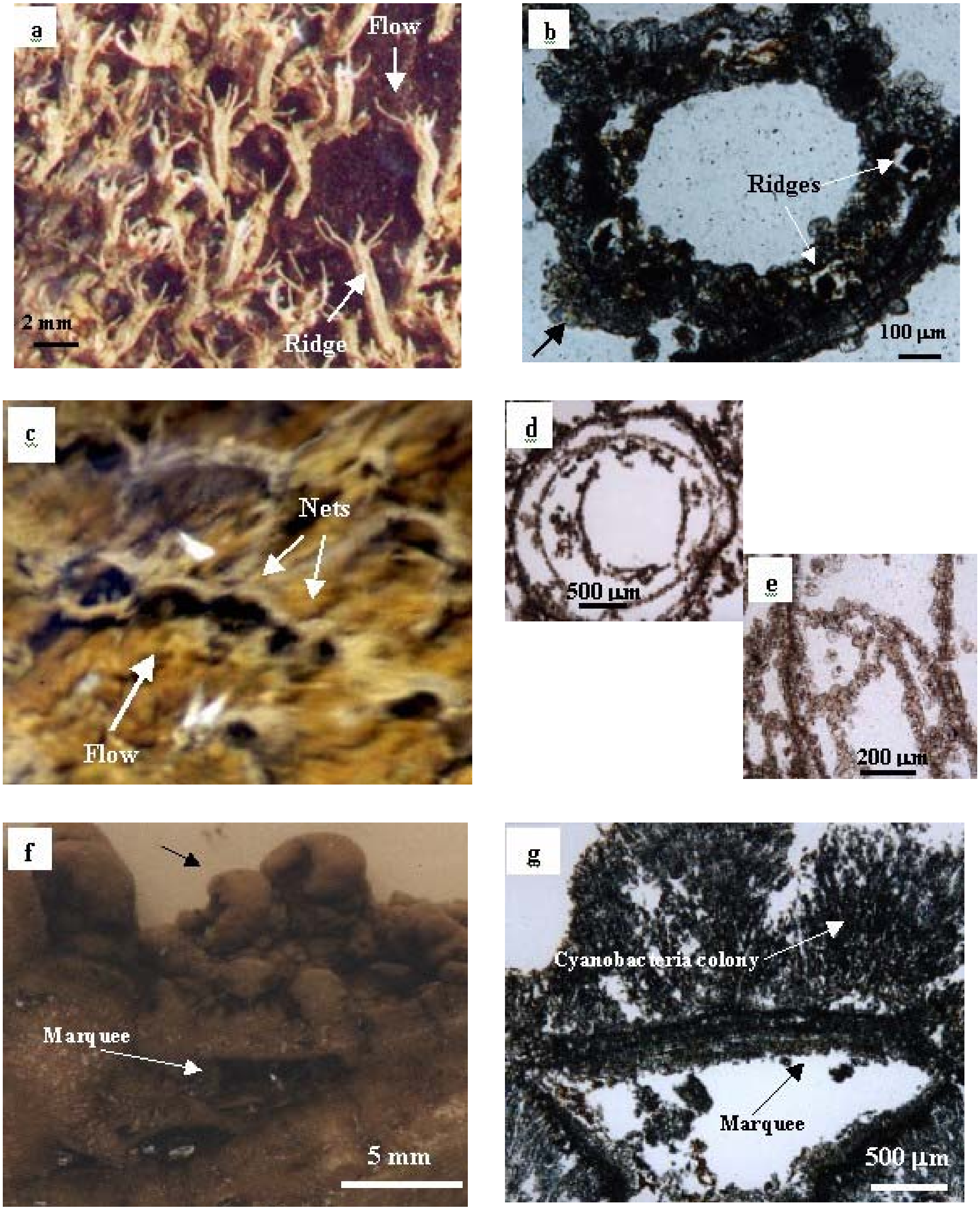

Figure 2. Gregory River larval tufas. (a) Larval chironomid dwelling tubes with distinctive ridges extended to form arms. (b) These ridges are preserved in thin sections through the chironomid tubes, which appear as a ring of micrite and organic material. The tubes are encrusted with calcite (black arrow). (c) Arcuate arrays of larval hydropsychid nets aligned perpendicular to the direction of water flow. (d) In thin section, each larval hydropsychid retreat appears as a ring of calcite arranged in a lacework pattern. (e) Detailed view of a hydropsychid retreat wall in thin section, showing unique arrangement of sparite. (f) Larval pyralid marquees within a tufa deposit. Although the larvae build the silken marquees across the surface of the rock, these marquees have been incorporated into the tufa and provided a new substrate for microbial tufa growth. The contemporary tufa surface is indicated by a black arrow. (g) Pyralid marquee in thin section. Cyanobacteria colonies have formed microstromatolites above the abandoned marquee.

Table 2. Hydraulic environments inhabited by aquatic insect larvae in the Gregory River.

HYDRAULIC ENVIRONMENT	RELATIVE ENERGY	DESCRIPTION OF HYDRAULIC ENVIRONMENT (adapted from Drysdale and Gillieson 1997)
Standing water	Low	Water body of any depth Flow velocity does not exceed 0.01 ms^{-1}
Spray	Intermediate	Deflected water near waterfalls Spray may range from a fine mist to an intense splash
Lap	Intermediate	Pulses of lapping water along channel or pool banks
Flow	High	Stream flow which is moving at a velocity exceeding 0.01 ms^{-1} Flow may occur at an inclination >0° and can include the passage of water down the steep face of a tufa dam Includes seepage flow
Impact	High	A column of water which becomes detached from a tufa dam crest and strikes the substrate at the base of the dam

form of burrows or cylindrical tubes within the tufa (see Drysdale 1998). The marquees are readily identified in thin sections cut parallel to the direction of tufa growth. They are composed of a silken sheet around 3-5 mm in length, which may be covered in calcite (Figure 2g). Larval pyralid marquees and burrows are present in Gregory River tufas in a range of hydraulic zones (Table 1). Marquees are common within microbial tufa in spray zones (Table 2) where they are constructed between cyanobacteria colonies that appear as dendritic columns (microstromatolites) in thin section (Figure 2g). Larval pyralid burrows are present in Gregory River tufa samples from the channel, tufa dams, and waterfall overhangs in flow and lap zones (Table 1).

DISCUSSION

Geological recognition criteria for larval tufas

Gregory River chironomid tufa has a high porosity and consists of calcite-encrusted larval chironomid dwelling tubes, each with five arm structures on the tube's anterior. Larval *Rheotanytarsus* use detrital and algal material bound with salivary silk secretions to construct cylindrical dwelling tubes (Brennan and McLachlan 1979; Cranston 1997). Tubes are attached to the substrate by silken threads, which protect the larvae from predation and may minimize dislodgement (Berg 1995). *Rheotanytarsus* larvae are filter feeders and use silken strands spun into a net and suspended from arms on the tube's anterior to trap fine particles of food (Benke *et al*. 1984; Cranston 1997). To feed, the larvae remove and ingest sections of the net and then repair the missing section, or they may roll the portion of net into a ball and add it to the tube wall (Oliver 1971). Tube arms are composed of the same type of material as the tube and the type of material used is primarily determined by particle availability (Brennan and McLachlan 1979).

The high porosity of Gregory River chironomid tufa and the size of the encrusted tubes are comparable with chironomid tufa from Louie Creek (Drysdale 1998) and Lawn Hill Creek (Cranston 1997). This agreement suggests that these characteristics may be used to identify chironomid tufa in other tropical streams and in fossil tufa sequences. In addition, the distinctive rings of micrite and organic material preserved in thin sections of chironomid tufa may also be used as geological recognition criteria for this tufa fabric. Gregory River chironomid larvae and subsequent chironomid tufa predominantly occur on tufa dams and the channel base within flow zones, although they may also be present less commonly in standing water zones. These hydraulic preferences are consistent with those reported by Drysdale (1998), Cranston (1997), and Humphreys *et al*. (1995) in other tropical streams. Thus, the presence of chironomid tufa in fossil tufa sequences indicates tufa deposition under predominantly flowing water conditions. Furthermore, palaeoflow direction is preserved by the orientation of the tubes, whose arms point in an upstream direction. Prevailing hydraulic conditions of chironomid tufa may be clarified by the presence or absence of hydropsychid tufa.

The preferred hydraulic zone of hydropsychid larvae in the Gregory River is one of flowing water conditions, which corroborates observations made by Drysdale (1998; 1999) and Humphreys *et al*. (1995). Hydropsychid larvae do not inhabit standing water zones (Drysdale 1998). Therefore, it may be concluded that tufa containing both chironomid tubes and hydropsychid constructions must have formed within flowing water. In addition to constructing fixed dwelling retreats, larval *Cheumatopsyche* also build silken capture nets to strain the water for food particles (Drysdale 1999), which may include detritus, algae and small animals (Benke *et al*. 1984; Humphreys *et al*. 1995). Both structures, particularly the nets, may play an important role in tufa formation (Drysdale 1999). The nets and retreats provide materials onto which calcite precipitation occurs and they increase local water turbulence (Drysdale 1999), which significantly increases the rate of calcite precipitation (Liu *et al*. 1995). Hydropsychid tufa in the Gregory River consists of distinctive arrays of retreats and nets that are preserved as arcuate microridges aligned perpendicular to flow direction. In thin section, the retreats consist of calcite arranged in a lacework ring shaped pattern approximately 2 mm in diameter. Similar lacework rings in larval tufa from Papua New Guinea were previously described by Humphreys *et al*. (1995). The unique lacework microstructure allows hydropsychid retreats to be readily distinguished from both chironomid tubes and pyralid marquees.

In the Gregory River, marquee-shaped pyralid shelters are constructed from a rectangular silken sheet up to 5 mm in length. These are the same as pyralid marquees preserved in tufas from other streams in northwestern Queensland (Drysdale 1998). Pyralid constructions may be built in the Gregory River under a range of hydraulic conditions including flowing water and spray. The pyralid preferences described here are comparable to pyralid hydraulic preferences reported by Drysdale (1998) for Louie Creek, Queensland. Pyralid marquees may also be present in association with colonies of cyanobacteria that are common within microbial tufa formed in spray zones. Therefore, the combination of preserved larval constructions and other associated tufa fabrics may provide useful information concerning tufa depositional environments.

Tufa – insect larvae relationships

Although aquatic insect larvae play an important role in tufa formation by increasing rock porosity and enhancing the apparent accumulation rate (Humphreys *et al*. 1995; Drysdale 1998; 1999), tufas may also have a positive impact on populations of insect larvae. Availability of construction material and space in which to construct a dwelling structure or feeding net are important controls on larval numbers (Brennan and McLachlan 1979; Benke *et al*. 1984). Therefore, formation of tufa dams in a channel may result in a positive feedback mechanism that allows considerably larger larval populations by increasing the surface area over which dwelling structures may be built. The increased surface area over which water flows via dams and dam spillways may enhance the proportion of food particles passing through the larval nets compared with the total volume of food being carried through the system. Indeed, Cranston (1997) noted that *Rheotanytarsus* tubes are particularly common below the outfall of dams, where there is plentiful fine particulate organic matter and lotic conditions. Furthermore, calcite encrustation of chironomid tubes enhances tube strength (Irion and Müller 1968), which is important in minimizing predation (Berg 1995). Thus, we suggest that there are positive feedback relationships between tropical tufa systems and populations of insect larvae.

This paper has shown that aquatic insect larvae not only enhance tufa formation rates, but that their populations may benefit from inhabiting tufa-depositing streams. The larvae construct structures that are preserved within the rock and may be used to identify specific tufa depositional environments. Chironomid tufas discussed in this paper represent tufa deposition under flowing or standing water conditions. This tufa fabric predominantly forms on dams, gravel riffles or amongst leaf litter in shallow pools. When found in association with hydropsychid tufa it can be concluded that the tufa formed in a high energy, flowing water depositional environment. A combination of chironomid and hydropsychid tufa fabrics mainly represents deposition on a tufa dam. Pyralid tufa observed with microbial tufa represents deposition under spray conditions on channel or pool banks near a waterfall. Pyralid tufa also forms within the channel and on dams and so may be present with tufa fabrics that represent flowing water depositional conditions. This information will aid correct interpretation of depositional environments preserved in fossil tufa sequences, which is essential for accurate reconstruction of environmental responses to past climate changes.

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