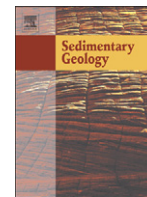




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Wetland sedimentation and associated diatoms in the Pleistocene Olorgesailie Basin, southern Kenya Rift Valley

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ABSTRACT

The Olorgesailie Basin in the southern Kenya Rift Valley contains a variety of lacustrine, wetland and terrestrial facies that were laid down during the last 1.2 million years. This study integrates diatom, ichnofossil, and rhizolith (silica and carbonate) evidence in order to identify and characterize shallow wetland deposition at the top (Member 14; ca. 493 ka) of the Olorgesailie Formation. A key feature of these deposits is the presence of facies with aquatic indicators (diatoms) that are overprinted by ichnofossils and rhizoliths that suggest drier conditions.

Diatom floras include several fresh water *Aulacoseira* spp. and saline indicators such as *Thalassiosira rudolfi*, *T. faurii*, *Cyclotella meneghiniana* and *Anomoeoneis sphaerophora*. The main indicators of shallow fresh to mildly saline waters include *Epithemia argus*, *Rhopalodia gibberula*, *Encyonema muelleri*, and *Synedra* spp. Three main suites of ichnofossils indicate varying water table depths during their formation. These consist of 1) horizontal tunnels that suggest saturated substrates; 2) vertical burrows formed in substrates with relatively lower water tables; and 3) termite, hymenopteran, and beetle ichnofossils that indicate dry substrates.

Member 14 of the Olorgesailie Formation also contains carbonate and siliceous rhizoliths, which occur both together and separately. Four possible models are suggested to explain the silica and carbonate rhizolith formation: 1) a complex of spring-fed marshes and dry areas; 2) ephemeral wetlands and floodplains; 3) wetlands with abundant organic decay, and 4) initial carbonate rhizoliths that were replaced by silica. Preservation of cellular structures and the reworking and incorporation of rhizoliths in overlying younger strata suggest that they formed early during diagenesis.

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1. Introduction

Sedimentation in modern and ancient lake basins has been the focus of numerous multidisciplinary studies during the last few decades. In eastern Africa, research has focused on developing environmental stratigraphies for deeper-water lakes and also on relating these environmental changes to orbital forcing (e.g. Kingston et al., 2007; Trauth et al., 2007). In contrast, the geological and hydrological characteristics of shallow water environments have received comparatively little attention. These diverse settings include both hot and cold springs, swamps, wetlands, and palustrine situations. There have been relatively few geological studies of these shallow water environments because their deposits can be difficult to recognize in the sedimentary record.

During the last decade, there has been an increasing interest in modern spring and wetland sediments, particularly in East Africa, and the criteria that might be used to recognize them (e.g., Ashley et al., 2002; Deocampo, 2002a,b; Owen et al., 2004, 2008a). Some springs form mounds of travertine and tufa (Renaut and Jones, 2000) or silica sinter deposits (Jones and Renaut, 2003), but many springs produce no obvious chemical precipitates. Springs supply water to wetlands, which are often characterized by extensive fine-grained, bioturbated sediments (Laporte and Behrensmeyer, 1980; Ashley and Liutkus, 2002; Scott et al., 2007) and by spatial changes in silica, carbonate, and microfossil content (Ashley et al., 2004). Deocampo and Ashley (1999), for example, suggested that variations in organic decay in wetlands control pH and, in turn, calcite precipitation and silica dissolution.

Research into fossil springs and wetlands is less commonly reported. Dunkley et al. (1993) noted the presence of fossil sinter and travertine in the northern Kenya Rift. Casanova and Renaut (1987) and Roure et al. (2009) have described Pleistocene spring-fed tufas near Lakes Bogoria and Baringo, respectively. Renaut et al. (2002) described hot-spring

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travertine containing silicified plant casts near the Lothidok Hills (NW Kenya). The occurrence of silicified plants in spring-fed wetlands has also been reported by R.A. Owen et al. (2008) at Lake Bogoria (Kenya) and by Liutkus and Ashley (2003) at Olduvai Gorge (Tanzania). More recently, Ashley et al. (2009) have reported on the occurrence of spring-fed wetlands between about 1.79 and 1.74 Ma at Olduvai.

The importance of wetlands as potential watering locations for hominins, especially during times of water stress, has recently been pointed out by Owen et al. (2008b) and Ashley et al. (2009). This increases the need for criteria that can be used to identify wetlands in ancient sedimentary basins where hominins evolved. Consequently, this paper presents a new integrated approach to their recognition, and uses diatom, trace fossil, and rhizolith evidence for the development of wetlands in the western Ologesailie Basin. The deposits occur at the top of the Ologesailie Formation and were possibly affected by post-Ologesailie Formation pedogenesis and/or silica diagenesis during a period when erosion was occurring in other parts of the basin. The aims of this paper are to: 1) describe the shallow water sediments, 2) identify criteria for their recognition as wetland deposits, and 3) develop models to explain how these wetlands formed.

2. Geological setting

The Ologesailie Basin occupies a faulted basin, 150 km² in area, in the southern Kenya Rift and extends for about 15 km in an east–west

direction. A north–south trending, faulted basalt horst block divides the area into the western Legemunge Plain and the eastern Oltepesi Plain (Fig. 1). Over most of the basin the sediments are concealed. However, excellent and laterally continuous exposures occur along the Ol Keju Nyiro River and along several of its tributaries. These deposits were laid down on southerly sloping platform of Magadi Trachytes (~1.4–1.7 Ma), which are cut by north–south trending faults. Mt. Ologesailie, a large extinct Pliocene volcano, forms the southern boundary of the basin.

During the last ~1.2 million years, the basin was filled with at least 120 m of lacustrine, wetland, fluvial, and colluvial sediments with palaeosols occurring at several horizons (Potts et al., 1999; Behrensmeyer et al., 2002; Owen et al., 2008b). These water bodies were of variable size and were characterized by fresh to saline, alkaline conditions (Owen and Renault, 1981; Owen and Renault, 1981) that evolved during four depositional cycles (Behrensmeyer et al., 2002). The first cycle (1.2 Ma–493,000 years ago) is represented by the Ologesailie Formation, which comprises diatomites, diatomaceous silts, clayey silts, and volcanoclastic sands and gravels (Isaac, 1978; Deino and Potts, 1990; Potts et al., 1999). The sequence has been divided into 14 Members (M1–M14) with a maximum composite thickness of about 80 m based on exposures (Shackleton, 1955; Potts, 1996; Potts et al., 1999). Deposition of the Ologesailie Formation was terminated by a major episode of fluvial incision.

During the subsequent ~500,000 years before the Holocene, the basin underwent at least three major cycles of valley cutting and filling

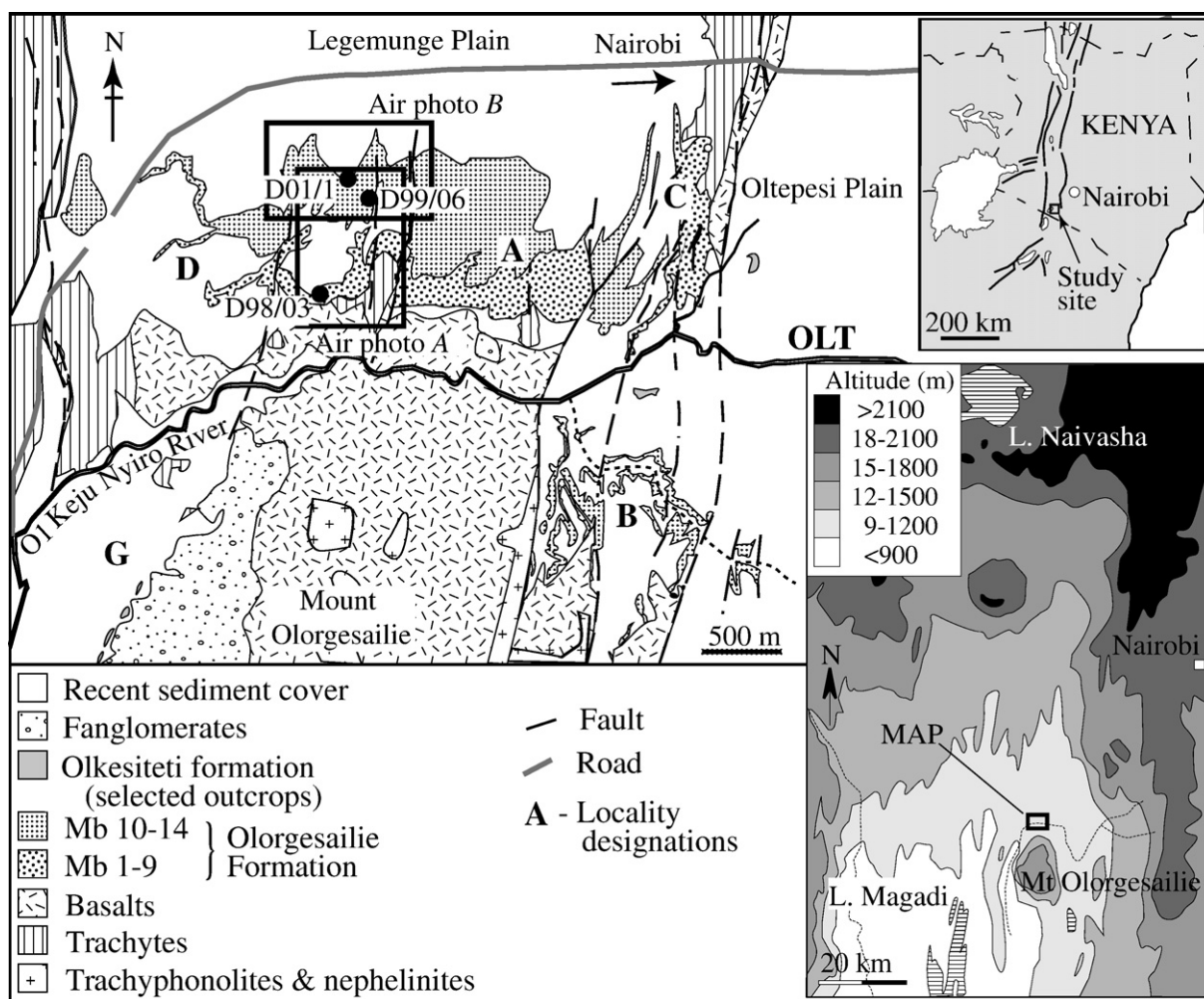


Fig. 1. Location and geological setting of the Ologesailie Basin. Air photographs A and B are shown in Fig. 2. Localities A, B, C, D and G are standard reference areas used by the Ologesailie collaborative project.

that produced post-Olorgesailie Formation sediments referred to informally as the Olkesiteti formation and Oltepesi beds (Behrens-meyer et al., 2002; Brooks et al., 2007).

3. Methods

Section D01/1 was originally logged in 2001 with individual units given letter designations. It was resampled for this study. All other sections are newly described and given numerical designations. Fig. 2

indicates the relationship between the two systems for D01/1. Diatoms were mounted on smear slides using a Naphrax. Taxa were identified using light microscopy and the monographs of Gasse (1986) and Patrick and Reimer (1975). Diatom stratigraphies for each section were drawn using C2, version 1.4 (Juggins, 2005). Only diatoms that form >5% of the flora are shown. Environmental reconstructions are based on training sets and transfer functions provided by the European Diatom Database (EDDI, <http://craticula.ncl.ac.uk/Eddi/jsp/index.jsp>). Diatom species reported in this study match the EDDI

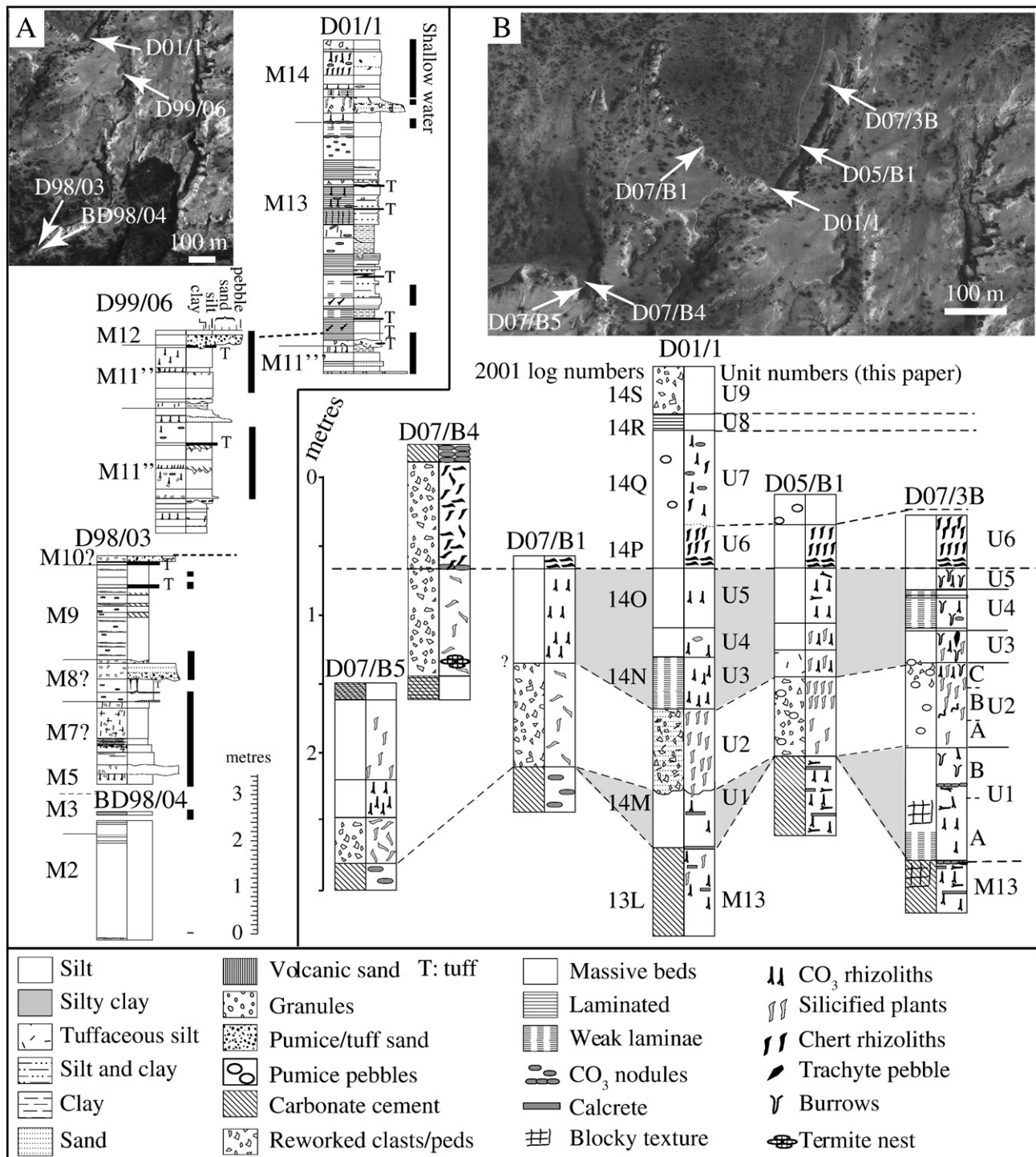


Fig. 2. Lithostratigraphy. A: Composite section for Locality D showing the development of shallow water settings inferred from diatom data (black bars). B: Detailed lithostratigraphy and unit terminology for the upper 3 m of D01/1 and correlative sediments.

classification. Conductivity estimates are based on the EDDI “Combined Salinity Dataset” and “Locally-weighted Weighted Averaging” (LWWA). Trace fossils were examined and photographed in the field, and samples of the smaller ichnofossils were studied in the laboratory. Thin sections of selected examples were examined to determine the cements preserving the traces. Trace types were grouped into recurrent suites observed throughout Members 13 and 14, with a focus on Sections D07/3B, D07/B4, and D07/B5. Further field and laboratory work is required for more detailed ichnotaxonomic treatment.

Major elements were determined by X-ray fluorescence (XRF) at Actlabs (Ancaster, Ontario), as was the loss on ignition (LOI). Organic carbon was determined at Hong Kong Baptist University using a PE2400 Series II CHN elemental analyzer. Rhizoliths were examined in a Leo 1530 Field Emission Scanning Electron Microscope, with elemental data obtained using an Oxford Instruments Energy Dispersive X-ray (EDX) system operated at 8 kV.

4. The wetland sequence

4.1. Stratigraphy and sedimentology

Fig. 2A summarizes the lithostratigraphy for Members 2–14 (M2–M14) in western outcrops of the Ologresailie Formation. Diatom assemblages indicate that shallow water environments developed several times (black bars, Fig. 2A). This study focuses on wetlands that developed during the deposition of M14 (493 ± 1 ka; Deino and Potts, 1990) (Fig. 2A, B).

Fig. 2B shows six sections in laterally extensive (>1 km), horizontally bedded, diatomaceous silt and tuffaceous sand that form a prominent cliff in the north of Locality D (inset photograph, Fig. 2B). Nine informal lithological units are recognized in D01/1—the longest exposed section (U1–9 = 14M–S on 2001 logs for D01/1, Fig. 2). Five units (U1–5) belong to M14. The age of the overlying chert-like rhizoliths and younger sediments (U6–9) is uncertain.

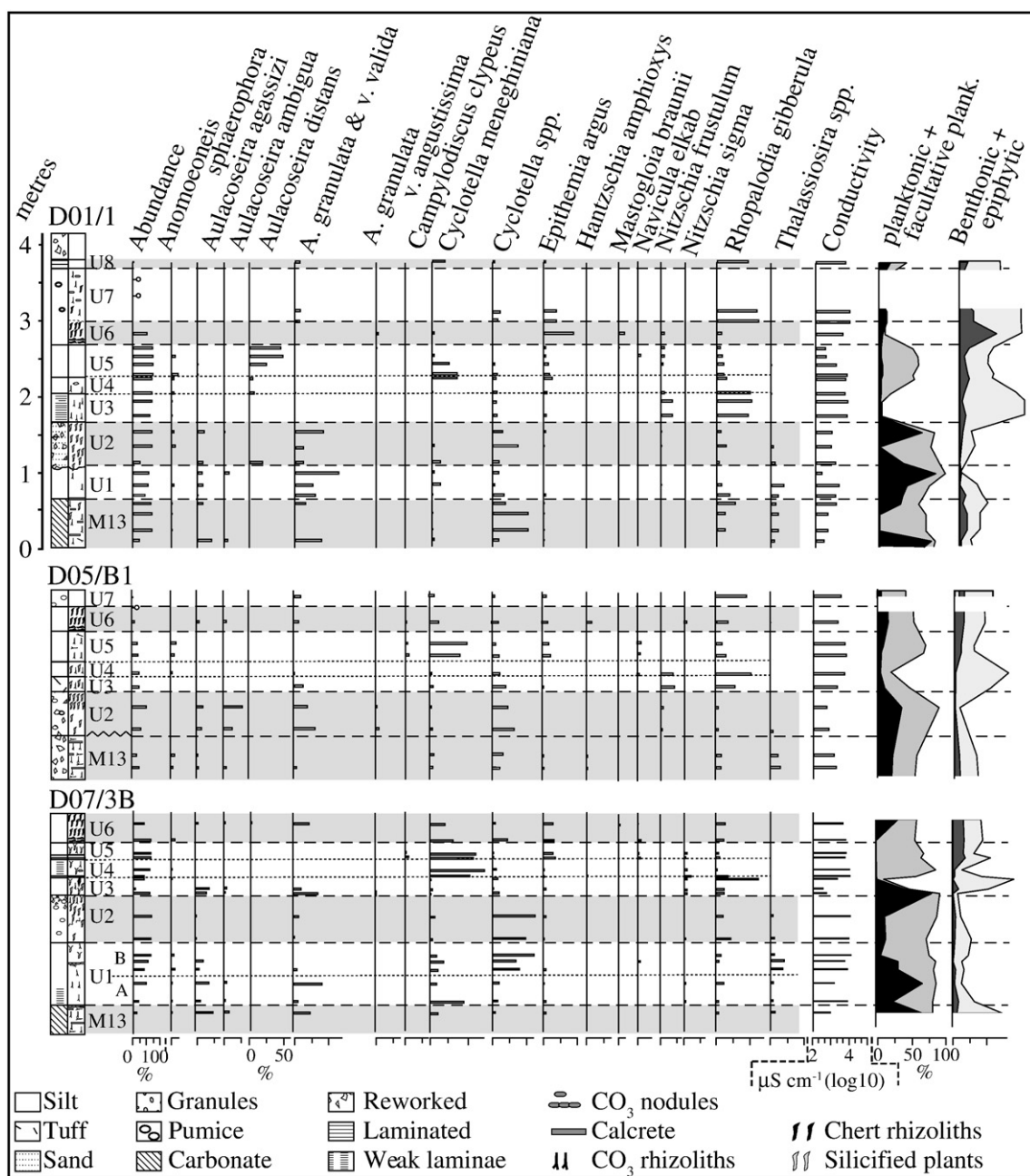


Fig. 3. Diatom stratigraphy for M14 (Ologresailie Fm.). Unit 1 is missing in D05/B1, as is upper Unit 1 in D01/1.

Unit 1 (U1) is discontinuous and may have filled gentle topographic irregularities on M13. At least part of Unit 1 also appears to have been locally eroded prior to the widespread deposition of Unit 2, based on diatom analyses. In the three eastern sections, Units 3–5 consist of white diatomaceous silts that show lateral variability in rhizolith composition (i.e. silica vs. carbonate), bedding, texture, and trace fossils. Unit 6 is dominated by horizontal and vertical chert-like rhizoliths in a diatomaceous silt matrix. These rhizoliths are reworked into the silt of Unit 7. Unit 8 consists of laminated white diatomaceous silt. Unit 9 was only sampled at its base, where it consists of non-diatomaceous mineral silt. The diatom content of weathered surface rubble above the base of Unit 9 is uncertain.

White to light grey, or light yellow, diatomaceous silt is present in all the sections, forming massive or weakly laminated beds up to 90 cm thick in parts of Units 1, 3, and 4 (Fig. 2B). Insect traces and burrows are common. Broken gastropods are present in a 1 cm thick bed at the base of Unit 4 in D07/3B. Carbonate rhizoliths and silicified plant stems are common, particularly in Units 2–5, but both types occur separately in successive layers or are spaced apart laterally over meters to tens of meters within the same unit. Bedding planes are sharp and planar. Poorly-sorted diatomaceous tuffaceous sand and gravel, with reworked diatomite, pumice and small obsidian pebbles, occur in a small fluvial

channel in Unit 2 (D01/1) that cuts into Unit 1. Laterally, pumice and diatomite clasts occur in diatomaceous silt, but with no clear incision of the underlying sediments. Unit 6 is comprised of diatomaceous silt and horizontal and vertical, grey chert-like rhizoliths (Fig. 2).

XRF data indicate that total SiO₂ (52–65% in section D01/1) does not attain the level of a true diatomite as defined by Owen (2002). The proportion of lithogenic silica in feldspar and other minerals can be estimated using the Al₂O₃ content, which is 2.8–9%. Baker (1958) reported average SiO₂/Al₂O₃ ratios of 4.3 for the dominant alkali trachytes in the basin, which suggests a volcanoclastic component of ~12–38% in the M14 sediments. The remaining silica (48–62%) occurs as diatoms, minor phytoliths and sponge spicules, fragments of silicified plants and chert-like rhizocretions, and possibly minor opaline silica cement.

Loss on ignition (LOI) ranged between 10.68–17.72% with organic carbon at <0.59%. High percentages for Ca (1.88–11.57%) correlate with elevated LOI values reflecting the presence of disseminated calcium carbonate. Horizontal plates (<2 cm thick) and vertical crack fills of grey calcite are present in several horizons, especially in basal Unit 1. Carbonate nodules locally coalesce to form more extensive sheet-like structures. Calcite rhizoliths are common in all units, except for Units 2A, 2B, 8 and 9 (Fig. 2), where they are rare or absent.

Table 1
Summary descriptions and interpretations of invertebrate trace fossils from M14.

Trace type	Material	Description	Interpretation	Icon in Fig. 4
Horizontal traces	1 Many examples from M14, Units 1B–2A, D07/3B	Open, dominantly horizontal, mm-scale tunnels, in general, do not branch, but possible in some examples, curving to occasionally meandering, mainly along bedding planes	Suite 1, moist to saturated substrates	
Small vertical burrows	2 Many examples from M14 Units 1B–2C, D07/3B	Unlined, open, vertical to oblique burrows, non-branching, 3–5 mm diameter, up to ~20 cm in length	Suite 2a, lower water tables than Suite 1	
	3 1 example from M14 Unit 2A, D07/3B	Lined, open, vertical burrow, non-branching, 5 mm diameter, lining reddish brown and different from host	Suite 2a, lower water tables than Suite 1	
	4 Several examples from M14 Units 1B–2C, D07/3B	Unlined, pellet-filled, vertical to oblique burrows, non-branching, 3–5 mm diameter, fill may be brownish and different from host or whitish and similar to host	Suite 2a, lower water tables than Suite 1	
Large vertical burrows	5 Several examples from M14 Unit 3, D07/3B	Unlined, open, vertical burrows, non-branching, 8–10 mm diameter, length up to ~40 cm	Suite 2b, lower water tables than Suite 2a	
	6 Several examples from M14 Unit 3, D07/3B	Unlined, pellet-filled, vertical to oblique burrows, may branch (Y-shaped), fill different than host and may be passive fill of open burrows, 8–10 mm diameter, length up to ~40 cm	Suite 2b, lower water tables than Suite 2a	
Backfilled branching burrows	7 Examples from M14 Units 5–6, D07/B4	Branching network of backfilled burrows, orientations horizontal, oblique, and vertical, fill different from host and not meniscate	Suite 3, associated with thin-walled cells	
Lined, oval cells	8 Several examples in M14 Units 5–6, D07/3B	Smooth-lined, ovoid cells arranged in clusters; no central burrow observed; Ichnofamily Pallichnidae of Genise, 2004	Suite 3, lower soil moisture than for Suite 2b	
Thick-walled, spherical balls	9 Three examples from M13 north of D07/3B	Thick-walled spherical brood balls, ~4 cm diameter, attached in groups <4, roughly circular shaped hole/opening in one example, preserved as balls of carbonate cement; Ichnofamily Coprinisphaeridae of Genise, 2004; associated burrows up to 4 cm in diameter and also preserved by carbonate	Suite 3, lower soil moisture than Suite 2b	
Thin-walled spherical to ovoid cells	10 Several examples from M14, Units 5–6, D07/B4 and Units 3–5, D07/01	Thin-walled spherical to oblong cells arranged in clusters and associated with backfilled burrows, fill similar to host; walls same as host; Ichnofamily Celliformidae of Genise, 2004	Suite 3, lower soil moisture than Suite 2b	
Concentrically backfilled traces (termite galleries)	11 Several examples from M13, Unit 1A, and Units 3–5, D07/01 and D07/3B	Variable size (1 cm–8 cm diameter) and orientation (horizontal to oblique to vertical), branching, concentrically backfilled with poorly sorted and sometimes pelletal material, fill generally more reddish brown in color than host	Suite 3, lower water tables than Suite 2b	
Termite nests	12 One example from M14 Units 3–5, D07/B4	~2 m diameter, pear-shaped complex social insect trace with open, diffuse galleries <2 cm diameter, one vertical pipe at top, ca. 10 cm diameter, nest light brown, host white	Suite 3, lower water tables than Suite 2b	

4.2. Diatoms

Fig. 3 shows the diatom stratigraphy for the ~200 m SSW-to-NNE transect, ~200 m long, formed by sections D01/1, D05/B1, and D07/3B. M13 occurs at the base of all sequences and is dominated by planktonic *Aulacoseira granulata*, *A. granulata* var. *valida*, *A. agassizi*, and *A. ambigua*. Unit 1 of M14 is thickest in D07/3B, absent in D05/B1, and relatively thin in D01/1 probably due to varying degrees of erosion at the base of Unit 2. In D07/3B, the base of Unit 1A is dominated by *Cyclotella meneghiniana* (= *Cyclostephanus meneghiniana*), which gives way to *A. granulata* and *A. granulata* var. *valida* with less common *Cyclotella* cf. *meneghiniana*. Unit 1B is characterized by abundant *C. cf. meneghiniana* (resembling small *C. meneghiniana*; Owen et al., 2008b) with less common *C. meneghiniana* and *Thalassiosira* spp. The Unit 1A flora is present in D01/1, but Unit 1B is missing.

Unit 2 is dominated by *C. cf. meneghiniana* (Fig. 3), which is most common in D07/3B, with percentages decreasing southwards. In contrast, *A. granulata* and *A. granulata* var. *valida* are most common in D01/1. *Rhopalodia gibberula* forms a common to minor component of the flora, with *Thalassiosira* spp. occurring infrequently, except at the top of Unit 2 where they are absent.

Thalassiosira spp. are absent in Unit 3 and above. *R. gibberula* and *Nitzschia frustulum* dominate in Unit 3 and the basal part of Unit 4, with the latter diatom being less common in D07/3B. *A. granulata*, *A. agassizi* and *A. ambigua* are common in the lower part of Unit 3 in D07/3B, but rare or absent in the southerly sections. Units 4 and 5 are characterized by a decline in *R. gibberula* and *N. frustulum* and an increase in *C. meneghiniana*. *Epithemia argus* is common for the first time in Unit 5, with *Aulacoseira distans* dominating at the top, but only in Section D01/1.

C. meneghiniana dominates with *E. argus* and *R. gibberula* in silt between chert-like rhizoliths (Unit 6) in D07/3B, but declines southwards. D05/B1 is co-dominated by all three taxa, with the southernmost D01/1 containing mainly *E. argus*. Unit 7 lacks diatoms except near the base where *R. gibberula* is common. This taxon also dominates in Unit 8 (D01/1).

4.3. Trace fossils

Animal traces are common and diverse in the sediments and are unrelated to the modern landscape. Full ichnotaxonomic treatment of the trace fossils in Members 13 and 14 is beyond the scope of this paper, but summary descriptions are given in Table 1. Preliminary analysis has shown that three primarily insect trace fossil suites are recurrent in M13 and M14, and these suites can provide valuable information on paleomoisture conditions during the periods of their formation. Interpretations are based on a variety of features including the trace fossil orientation, fill, details of the wall, shape, architecture, and the general type of trace (e.g., beetle brood balls, termite nests and galleries, hymenopteran cells) and their cross-cutting relationships, together with sedimentological characteristics of the host sediments (e.g., fine lamination). The three suites summarized below are roughly consistent with the widely accepted continental ichnofacies Mermia, Scoyenia, and Coprinisphaera (Genise et al., 2000; Buatois and Mángano, 2007).

Particular patterns of suite overprinting depend on the initial depositional environment, subsequent environmental changes (e.g., lake-level, water table depth), and the relative penetration depths of the various traces. Each trace type has a specific “tier”, or depth relative to the land surface or sediment/water interface at the time of formation. For instance, horizontal tunnels of Suite 1 are relatively shallow compared to vertical burrows of Suite 2, which are relatively shallow compared to the nests and burrows of Suite 3 (cf. Genise et al., 2000; Buatois and Mángano, 2007). Three suites of trace fossils were recognized:

Suite 1 – saturated substrates; horizontal tunnels. Weakly laminated diatomaceous silt in M14/Units 1B–2A (D07/3B, Fig. 4) preserves mm-scale open, horizontal tunnels that lack linings or walls, and which are

present along bedding planes (Fig. 5B). The traces in this low-diversity suite may be attributable to insect larvae and/or nematodes.

Suite 2 – moist, firm substrates; relatively lower water tables and vertical burrows. This suite consists of open, spherical pellet-filled, and lined, small (<5 mm diameter, < ~20 cm length), vertical to oblique, non-branching burrows that locally cross-cut Suite 1 (Fig. 5B–E). Potential tracemakers include beetle larvae and adults and larval earwigs (cf. Scott et al., 2009). Larger (<8–10 mm diameter), longer (<50 cm), open and pellet-filled vertical burrows that sometimes branch upwards (Y-shaped) are preserved in Units 1 and 3 (Section D07/3B) (Fig. 5F). The pellet-fill of these burrows is mixed with silt and clay, and may be passive fill by pellet-rich surficial sediment produced by termites (cf. Crossley, 1986; Jungerius et al., 1999). Potential tracemakers include spiders, beetles, aestivating gastropods, and termites (Ratcliffe and Fagerstrom, 1980; Hasiotis, 2003; Scott et al., 2009). These traces, which indicate relatively dry ground at or above the water table, are associated with carbonate nodules and carbonate root casts. Unlike typical occurrences of the Scoyenia ichnofacies, this suite can be compared with the assemblage of incipient (modern) trace types present in mudflats at Lake Bogoria, which also lacks meniscate burrows (cf. Scott et al., 2007, 2009).

Suite 3 – dry substrates; termites, hymenopterans, and beetles. Concentrically backfilled termite burrows occur in M13 in D07/3B (Figs. 4, 5G,H). North of D07/3B, M13 also preserves the thick-walled brood cells of beetles (e.g., dung beetles, Fig. 5A; cf. Halffter, 1977; Genise and Bown, 1994). Together, this suite indicates relatively low water tables. Termite nests and their associated backfilled, walled, and open, diffuse galleries occur at D07/3B and D07/B4 (Fig. 5H). These are associated with concentrically backfilled and pellet-filled large ‘burrows’ (4–8 cm diameter) attributed to termites (Fig. 5G) and mature termite nests (Fig. 5H). Suite 3 also includes clusters of open, smooth-lined ovoid-shaped pupation chambers of the ichnofamily Pallichnidae Genise, 2004, which are hymenopterans (Fig. 5I; cf. Ritchie, 1987; Hasiotis, 2003; Genise, 2004), clusters of thick-walled spherical cells of the ichnofamily Coprinisphaeridae Genise, 2004 (Fig. 5J), and isolated thin-walled spherical cells associated with backfilled burrows that are attributed to beetles and/or hymenopterans of the ichnofamily Cellichnidae Genise, 2004 (Fig. 5K) (cf. Ritchie, 1987; Hasiotis, 2003; Genise, 2004). The termite nests are attributable to the extant family Macroterminae (cf. Darlington, 1984, 2005; Sands, 1987), and the ichnogenera *Termitichnus* (Bown, 1982) and *Syntermesichnus* (Bown and Laza, 1990).

4.4. Rhizoliths

Calcite rhizoliths, white opaline silica (opal-A) plant casts, and grey chert-like rhizoliths are common in the studied section, and occur separately from each other, except in Units 3 and 4 (Fig. 2B) where both carbonate rhizoliths and silicified plants co-exist at the same stratigraphic levels. Locally, former root channels indicated by Mn-oxyhydroxide stains along their margins. Micrite and pore-filling microsparite occur as both vertical and (sub)horizontal calcite rhizoliths. The carbonate rhizoliths have a sub-circular, 1–2 cm cross section and most are <8 cm long, but with one specimen exceeding >30 cm in length (Fig. 6G). They commonly possess a central void lined with sparry calcite, with minor Mg appearing in EDX spectra (Fig. 6H–I, L).

Silicified plants with square to triangular cross-sections, characteristic of sedges, are common. Small (<2–8 cm long; 2–10 mm wide) stems occur with vertically oriented long axes, although some are also oblique or horizontal, suggesting that these had been reworked. The

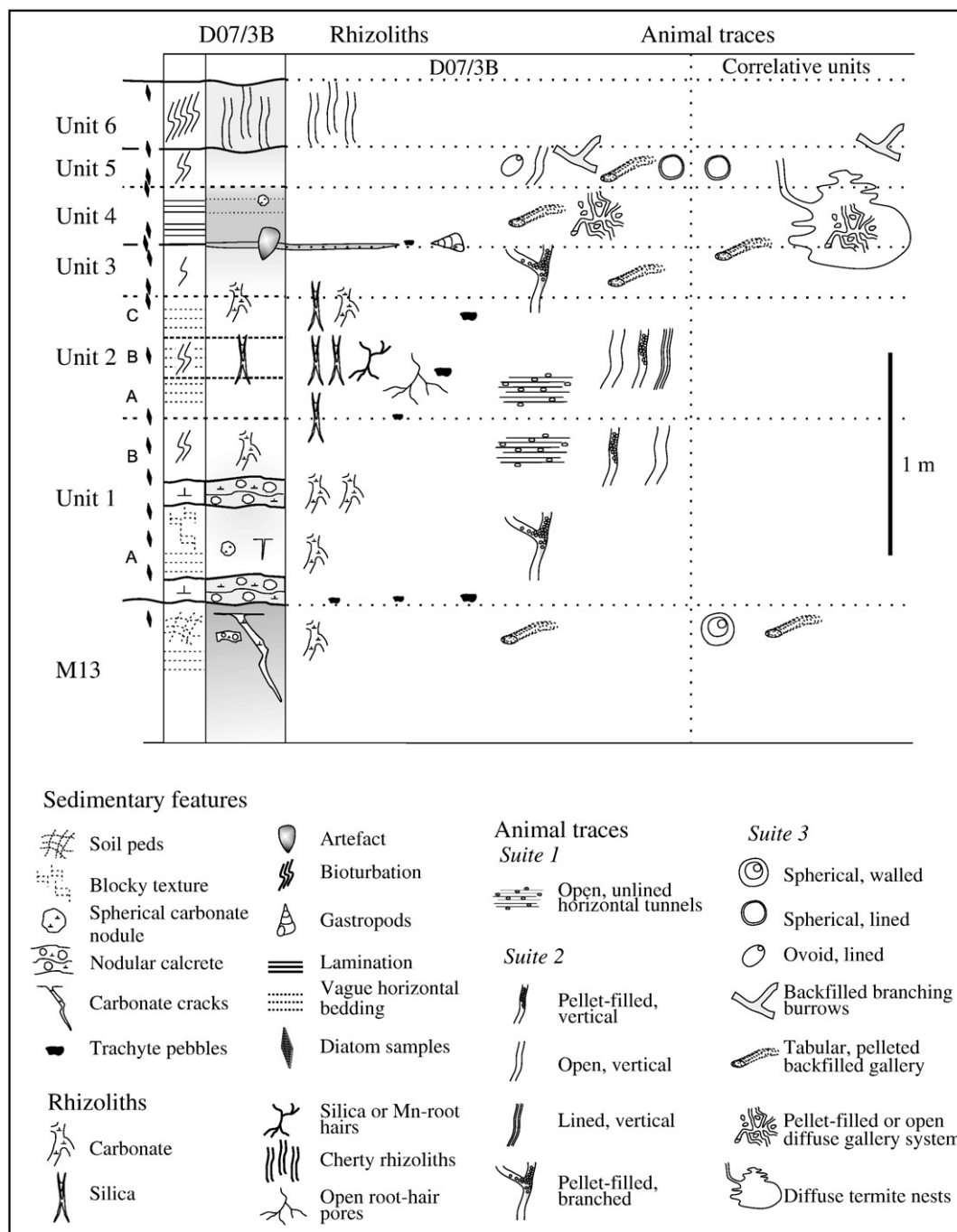


Fig. 4. Ichnofossils and rhizoliths in Section D07/3B. In contrast to the diatom floras, these generally indicate dry substrate conditions.

longer vertical stems occur in dense, closely spaced clusters. They are straight to mildly undulate and without bifurcations. Surfaces are striated parallel to their length axes and cellular structures are well preserved by homogeneous opaline silica permineralization (Fig. 6E–F, L). Spherical nanospheres and microspheres of opal-A up to 5 µm in diameter are present in a few silica rhizoliths.

Pure silica also forms a network of grey chert-like rhizoliths, also composed of opal-A (Fig. 6A–C, J). In the eastern sections, there are basal horizontal rhizoliths (~1 cm thick) overlain by vertical root structures. A central void is often present in these rhizoliths (Fig. 6B) that is surrounded by homogeneous silica, with no crystalline structure visible in SEM images. In western outcrops (D07/B4, Fig. 2), randomly oriented, possibly reworked, chert-like rhizoliths overlie nodular carbonates.

5. Discussion

5.1. Paleoenvironmental setting

The sharp boundary between M13 and M14 and pedogenic modification of the top of the uppermost part of M13 both indicate a break in sedimentation, perhaps of significant duration, before the lake returned to form Unit 1 of M14. Concentrically backfilled galleries of termites and thick-walled insect brood balls in M13 suggest that relatively dry substrates (cf. Sands, 1987, Genise et al., 2000) existed before deposition of M14. The floras of Units 1–2 (M14) indicate contrasting fully aquatic conditions. The common diatoms, *A. agassizi* and *A. ambigua* document shallow, swampy dilute water (Gasse, 1986). The former taxon is favoured by low salinity (conductivities of <200 µS cm⁻¹), whereas *A. granulata* is

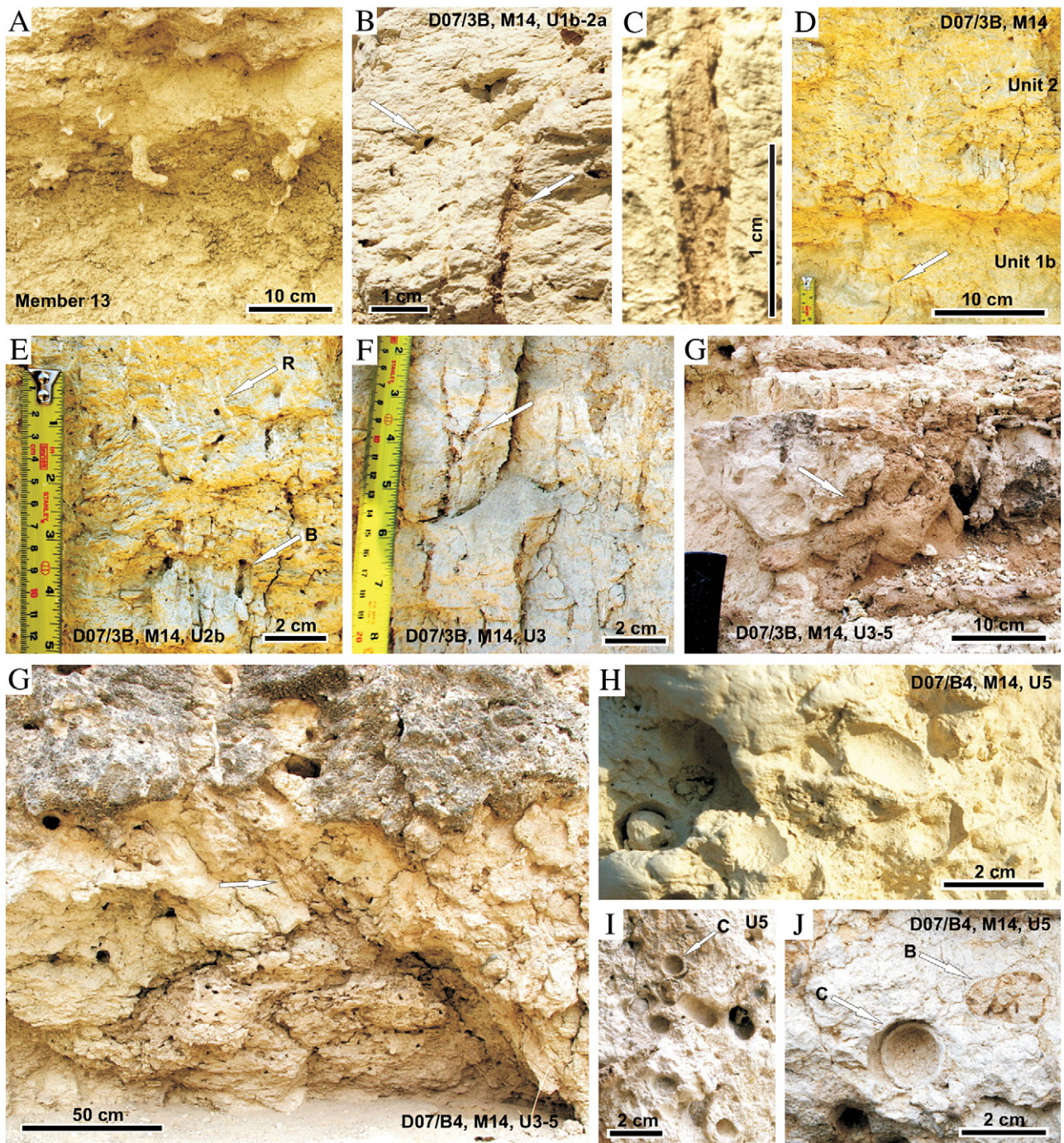


Fig. 5. Animal traces. A: Carbonate thick-walled beetle “brood balls” (Suite 3); B: open, horizontal tunnels (Suite 1, left arrow) and vertical, pellet-filled burrow (Suite 2, right arrow); C: vertical, lined burrow (Suite 2); D: open vertical and oblique burrows (Suite 2). Note higher density of burrows in Unit 2 and extension of Suite 2 burrows into Unit 1b (arrow); E: open vertical and oblique burrows. (B) Burrow. (R) Silica rhizolith. F: Vertical, pellet-filled burrows. Note Y-shape branching at left (arrow); G: large, pelleted, concentrically backfilled termite galleries (arrow); H: large, mature termite nest with open, diffuse galleries. Large exit hole tower above (arrow); I: lined, ovoid cells of beetles or hymenopterans; J: clustered nest cells (C) of hymenopterans; K: thin-walled cell (C) and backfilled burrow (B) attributed to beetles.

associated with deeper water. Perhaps of greater significance is the occurrence of *C. meneghiniana*, small *Cyclotella* spp. (mainly *C. cf. meneghiniana*) and *Thalassiosira* spp. (*T. rudolfi*, *T. faurii*), which are favoured by higher salinities (e.g., Barker et al., 1990). Gasse (1987), for example, reported *T. rudolfi* and *T. faurii* in a groundwater-fed saline pond with conductivities of 10,000–13,000 $\mu\text{S cm}^{-1}$ at Guidimouni (Niger).

Mixing of fresh and saline diatoms is common in many water bodies as a result of stratification, temporal shifts in salinity, or influxes of fresh water (Owen, 2002). A shallow ephemeral wetland with fresh water can be inferred from the dominant taxa. However, the small (<3–5 cm depth) shrinkage cracks, soil peds, insect burrows and insect cells indicate that

the waters dried out for periods of unknown duration. The increased salinity during desiccation would account for the saline diatoms.

Traces characteristic of water-saturated-substrates (Suite 1), preserved in Units 1B and 2A, may have been formed very near the sediment surface, similar to modern larval tunnels along the shoreline and near hot-spring-fed pools at Lake Bogoria (Scott et al., 2007, 2009). Small (<5 mm diameter) vertical burrows (Suite 2) cross-cut these earlier traces and indicate a slight lowering of lake- and groundwater-levels. Calcite rhizoliths probably formed in drier areas at this time (see below). Carbonate-cemented concentrically back-filled galleries of termites were also found near the base of Unit 1 at

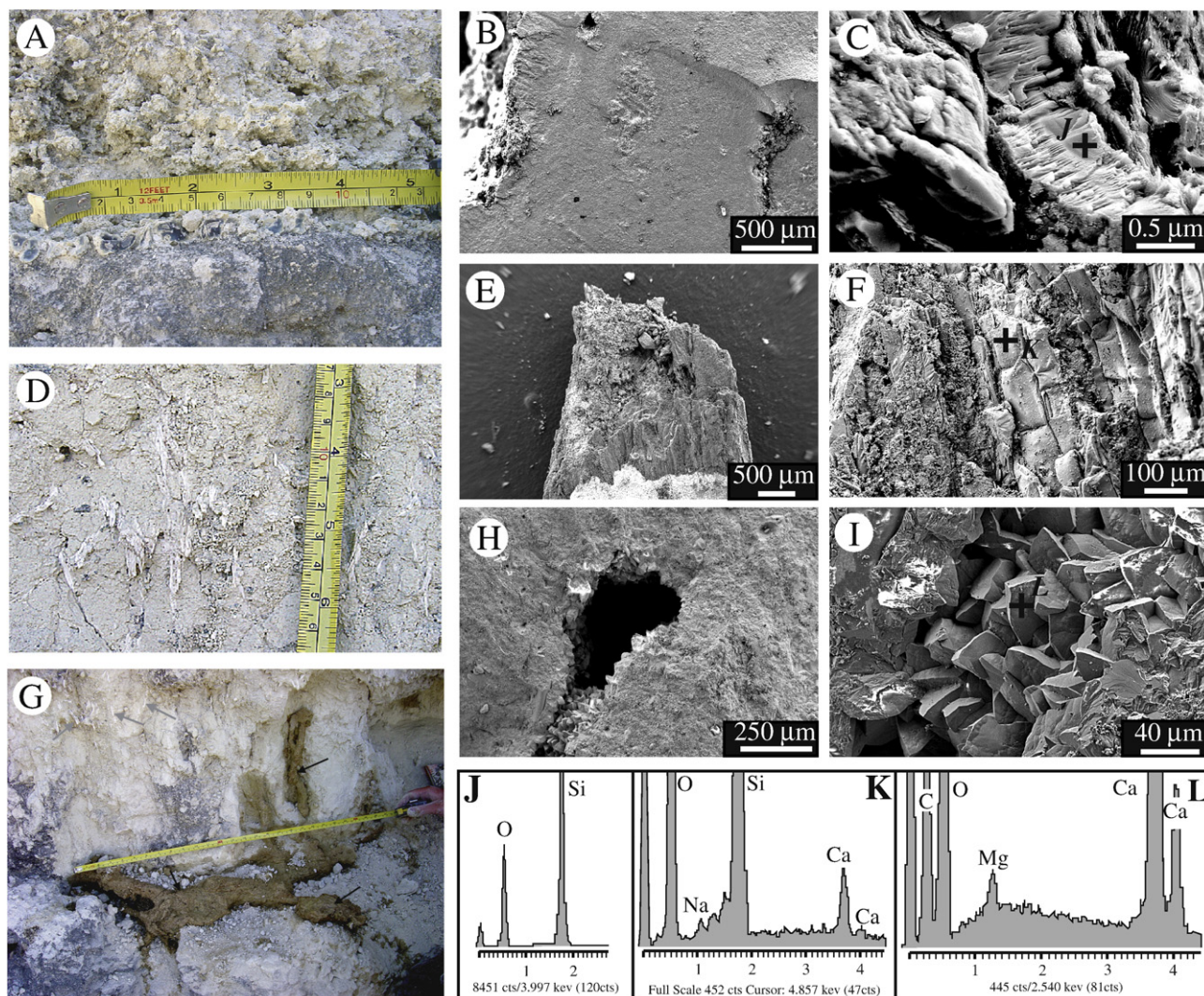


Fig. 6. Rhizoliths. A: “Cherty” rhizoliths on diatomaceous silt; B: SEM of cherty rhizoliths with central pore space to right; C: detail of pore space in “B” with EDX spot location (J); D: silicified, vertical, plant stem casts; E: silicified plant; F: detail of “E” with well-preserved cellular structure. EDX spot analytical point is marked “K”; G: large carbonate rhizolith. Grey arrows are silica stems; H: central pore space of a smaller (1 cm diameter) carbonate rhizolith; I: detail of “G” showing sparry calcite. EDX spot (L); J–L: EDX spot analytical data for the rhizoliths.

D07/3B associated with carbonate rhizoliths. Additional evidence for receding waters comes from a small fluvial channel at the base of Unit 2 and localized erosion of parts of Unit 1.

The Unit 2 sediments were partly laid down as the fill of a fluvial channel that eroded into underlying U1 and adjacent strata, and contain abundant *C. cf. meneghiniana*, which dominate in Unit 1B of D07/3B. Their presence could be due to reworking of this relatively robust taxon or the resumption of wetland conditions similar to those of Unit 1B. Plants that grew in the channel and in laterally correlative deposits became silicified (see discussion below). Suite 1 traces are cross-cut by Suite 2 vertical burrows that extend downwards into Unit 1 (Fig. 5D). The vertical burrows appear to originate from several “horizons” within Unit 2 and are most concentrated in Unit 2B (Fig. 5E), where there is a higher abundance of silica rhizoliths. These features collectively suggest fluctuating water levels in this area and frequent periods of alternating deposition and subaerial exposure.

The diatomaceous sediments of Unit 3 and lower Unit 4 are dominated by either *R. gibberula* and *N. frustulum*, or *A. granulata* var. *valida* and *A. agassizi*. The former taxa record shallow saline swamps, whereas the latter document deeper water, fresher conditions. Together, they indicate a wetland that varied spatially and temporally. *C. meneghiniana* locally dominates in Units 4 and 5. These diatoms are common today in alkaline lakes or hot springs with conductivities $>6000 \mu\text{S cm}^{-1}$

(Gasse, 1986). *C. meneghiniana*, for example, is abundant in shallow (<2.5 m), saline (16–23‰ TDS) Lake Manzala in the coastal Nile Delta (Zalat and Servant-Vildary, 2005). Elevated salinities are also indicated by the presence of *Anomoeoneis sphaerophora* and *Campylodiscus clypeus*. In contrast, the presence of *A. distans* var. *africana* in the upper part of Unit 5 (D01/1) suggests fresh swampy conditions with $\text{pH} < 7$ (Gasse, 1986).

Both calcite and silica rhizoliths occur in growth positions in Units 3–5 but vary in abundance between different sections. The traces of termites become common in M14, Unit 3, with well-developed termite nests and concentrically backfilled galleries overprinting Units 3–5 in D07/3B (Fig. 5G) and D07/B4 (Fig. 5H). Larger, open and pellet-filled vertical burrows also possibly attributable to termites (cf. Hasiotis, 2003) appear to originate from a horizon below Unit 4 in Section D07/3B. Unit 4 lacks traces from Suites 1 or 2 in section D07/3B, but was reworked by Suite 3 traces. Unit 5 is massive and bioturbated by Suite 3 traces. Burrows and nests of bees and beetles (Fig. 5J–K) are restricted to Units 4 and 5, and they likely formed from paleosurfaces lying above Unit 5 at about the same time as the termite nests were formed in areas that would have had low water tables. However, there is no clear indication of the time needed to form these traces, except that the development of large termitaries would take at least several years to decades (cf. Grassé, 1958; Sands, 1987). It is also possible that the termitaries were replaced well after local water tables had been lowered during the initial downcutting of the older

Olorgesailie Formation sediments. In general, the paleoenvironments of Units 3–5 were complex spatially and temporally with both dry and moist emergent areas, fresh shallow wetlands, saline swamps and perhaps local spring-fed habitats.

Stratigraphic relationships of the rhizoliths in the uppermost sediments can be interpreted in several ways, with three possible explanations currently under consideration: 1) U6–9 and the contained rhizoliths are also part of M14; 2) these upper sediments are part of M14, but the rhizoliths formed during post-Olorgesailie Formation time (i.e. after ~493 ka); and 3) both the upper sediments and the contained rhizoliths post-date the Olorgesailie Formation. These three possible scenarios also have implications for when the termite nests and associated burrows were formed. Carbonate-cemented termite galleries are present in Unit 1, Section D07/3B, and are common throughout Units 3–5 in Sections D07/3B and D07/B4, along with un-cemented examples that also have reworked sediments of Units 3–5. The timing of bioturbation by termites is difficult to reconstruct, partly because it is probable that there were several periods of low water tables before, during, and after the deposition of Units 6–9.

The dense network of chert-like rhizoliths in Unit 6 suggests that abundant in situ macrophytes were established during the time of their formation. Intervening silts contain diatoms that vary laterally, but include saline species (*C. meneghiniana*) and taxa associated with swampy, moderately saline wetlands (*E. argus*, *R. gibberula*). The rhizoliths rest upon a laterally extensive planar surface that indicates a flat paleotopography and/or possibly a stable water table. The fossilized plants might have either been silicified during or soon after growth in an area locally supplied by silica-rich fluids, or have been silicified later by replacement of carbonate rhizoliths (see discussion below). Unit 7 lacks diatoms, except for a shallow swamp flora (mainly *R. gibberula*) at the base, and probably accumulated under terrestrial conditions. Scattered, randomly oriented chert-like rhizoliths in Unit 7 imply local reworking of older Unit 6 sediments.

The diatom floras and fine laminations in Unit 8 indicate a return to swampy conditions.

5.2. Depositional models

A distinctive characteristic of the sediments is a lack of coarse-grained facies (sand and gravel), apart from the fill of one minor channel in Unit 2 (D01/1, Fig. 2). This is true for much of the exposed Olorgesailie Formation, except for pumiceous sand and gravel in M4 and M10. This is surprising given the basin was bounded by steep faulted margins and an extinct, eroding volcano during sedimentation. There are several possible explanations. Firstly, sediment may have been trapped by marginal or wetland vegetation (e.g. Johnston et al., 1984; Dieter, 1990), as may have been the case near Pleistocene paleosprings at Olduvai Gorge in Tanzania (Ashley, 2007). Secondly, at times, much of the lake water may have been derived from dilute springs and/or groundwater seepage around the lake margins. Discharge from these sources would contain little detrital sediment apart, perhaps, for very minor aeolian components, but would have sufficient discharge to be capable of minor incision. The lack of a large sediment load would, in turn, reduce turbidity, decrease dilution of diatoms by siliciclastic sediments, and help to explain for the high diatom abundance in the Olorgesailie Basin. Thirdly, although less likely, the paucity of coarse-grained deposits may reflect the weathering products of the trachyte bedrock. Renaut and Owen (1991), for example, attributed an apparent lack of coarse sand at Lake Bogoria to the breakdown of the volcanic bedrock (mainly trachyphonolites and phonolitic trachtes) into the component silt-sized alkali feldspars that form most of the groundmass, and alteration of other silicates and glass into clays.

Any depositional model for the wetland sequence described needs to account for several lines of evidence. The diatoms indicate recurrent shallow, fresh to moderately saline, wetlands. Trace fossils document drier periods. In particular, the ichnofossil suites reflect three

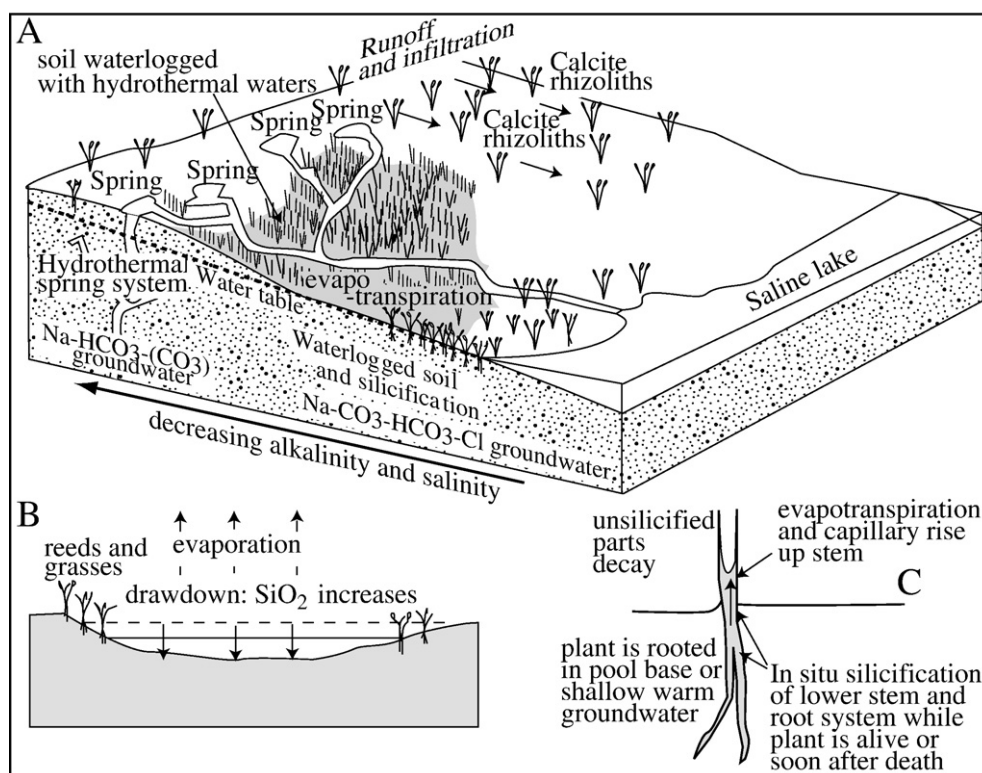


Fig. 7. Wetland model A. Spring-fed wetland supplied by silica-enriched water. Further concentration by evaporation (B) leads to increased silica, which reaches the point of precipitation following evapotranspiration (C). Silicified lower stems/roots remain after upper part decays. Carbonate rhizoliths form in areas fed by meteoric waters with higher Ca²⁺ concentrations.

geomorphological–hydrological situations: 1) sediments that were constantly wet; 2) low-lying areas with sediments above the water table; and 3) dry locations well above the water table. Traces that represent prolonged periods of substrate stability and low water tables (e.g., well-developed termite nests, Suite 3) cross-cut earlier traces that signify constantly wet and periodically moist substrates (Suites 1 and 2, Fig. 5A–F), indicating a likely fall in groundwater. With deeper water table, vertical burrows (Suite 2) increase in length, and termite galleries and associated burrows (Suite 3) reach deeper into the substrate to rework and overprint older sediments and traces. Paleoenvironmental models also need to account for the periodic development of soil peds, minor planar erosion surfaces, and local minor channeling. Finally, there is a need to explain the spatial separation of carbonate rhizoliths and silicified plants and to clarify why silicified plants are common in these sediments (and post-Olorgesailie Formation deposits), yet are absent or scarce in the older members (pre-M14) of the Olorgesailie Formation. Four models for the wetland environments are suggested.

Model A (Fig. 7) is based on one presented by R.A. Owen et al. (2008) for Holocene sediments on the margins of saline, alkaline Lake Bogoria in the central Kenya Rift, where shallow lake-marginal marsh (*Cyperus laevigatus*, *Sporobolus spicatus*) is fed by perennial hot-spring effluent. By analogy, diatoms inhabited relatively cool distal spring sites and areas subject to periodic lake flooding (cf. R.B. Owen et al., 2004, 2008a). Trace fossils were formed in drier areas, which shifted laterally as spring effluent moved or spring vents changed their

activity. In situ silicification of plants occurred where springs supplied elevated aqueous silica, with amorphous silica saturation being achieved mainly by evapotranspiration. This caused permineralization by opal-A that began while the plants were alive (Renaut et al., 2002; R.A. Owen et al., 2008; Fig. 7B). Subsequently, silica build-up killed the plants, but abiotic capillary evaporation from the partially silicified tissues allowed silica precipitation to continue for a period after death. According to this model, calcite rhizoliths formed in areas where water tables were shallow but without the direct influence of hot springs, since the deep thermal fluids were depleted in Ca^{2+} and thus unlikely calcium sources. Surface runoff and shallow meteoric (non-thermal) alkaline groundwater supplied Ca^{2+} to drier areas. In contrast, calcite formation would be less likely in the wetlands, since organic decay might have lowered the pH, sufficiently to allow silicification (Knoll, 1985; Deocampo and Ashley, 1999).

A problem with this model is the laterally extensive distribution of the silica rhizoliths at Olorgesailie. At Lake Bogoria, they are only associated with hot springs. No evidence has yet been found for silica-rich high-temperature springs in the Olorgesailie Basin. Nonetheless, hot ($>80^\circ\text{C}$) alkaline springs, with $>90\text{ mg l}^{-1}\text{ SiO}_2$ discharge into lake Nasikie Engida, a saline lake 25 km southwest of Olorgesailie, but they leave no sediment record (i.e. no sinter or travertine) because they are undersaturated with respect to amorphous silica and contain $<1\text{ mg l}^{-1}\text{ Ca}$ (Renaut and R.B. Owen, unpublished data). Furthermore, R.A. Owen et al. (2008) reported that fluorite is common in the

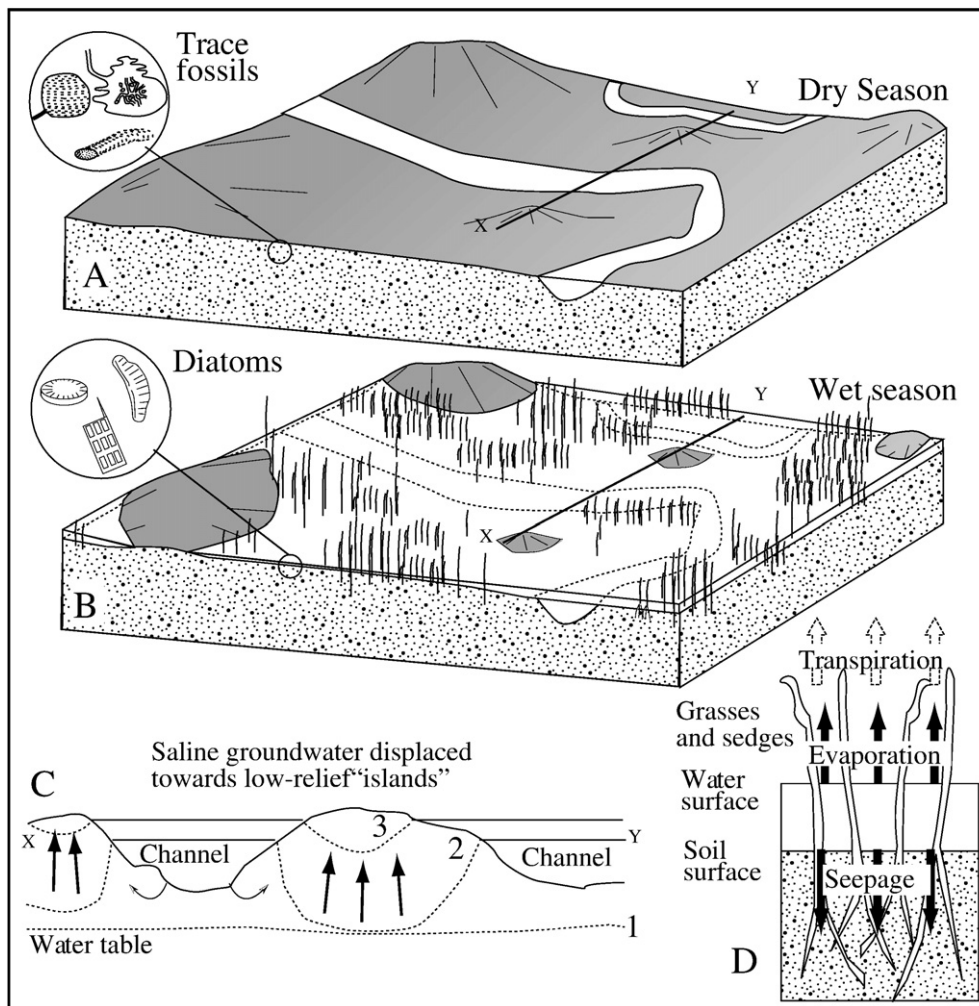


Fig. 8. Wetland model B. During dry periods insects burrow into subaerial substrates (A). Flooding periodically inundates the area (B). Water floods in along channels and permeates down and laterally (C), displacing the water table from position 1 to 2 and then 3. This has the effect of raising the older saline groundwater below low-rising islands (note vertical scale is exaggerated). Water is lost from groundwater by transpiration while surface water is lost by evaporation (D). In the Okavango swamp transpiration exceeds evaporation.

Holocene sediments at Lake Bogoria, including rhizoliths, which was attributed to the high F content of the thermal waters. Although F is common in many Kenya Rift springs (e.g., Nair et al., 1984), no fluorite has been found in the strata examined for this study at Olorgesailie.

Fig. 8 shows Model B, which is based on observations by McCarthy and Ellery (1995) and McCarthy et al. (1998) of the flood cycle in the Okavango Delta in Botswana, a broadly flat region with fluvial channels and areas of slightly higher ground similar to that suggested for the paleowetlands, but differing in the presence of sand. They noted that silica precipitation was induced from groundwater by evapotranspiration from rooted plants, whereas carbonates precipitated in wetland island soils below minor topographic highs. During floods diatoms would be deposited in the submerged sediments, whereas during dry seasons infaunal insects could burrow into the exposed deposits. Carbonate and silica precipitation would have been driven by seasonally abundant water and high evapotranspiration rates. In this setting, evapotranspiration loss from rooted grasses and sedges would exceed evaporative loss from surface waters alone (Fig. 8D). Consequently, there would have been a greater increase in the groundwater salinity (and Si and Ca concentrations). At the start of each new flood cycle, runoff would initially infiltrate the subsurface sediments below and adjacent to shallow channels, displacing pre-existing saline groundwater, which would then migrate to areas below slightly higher ground (Fig. 8C).

The data from Okavango indicated minimal dilution or mixing between floodwater and older groundwater despite the obvious differences in fluid density. Instead, saline groundwater became localized

beneath the low-lying islands over multiple flood cycles. The net effect was that silica saturation was reached along the margins of stream channels and in areas of relatively low topography, eventually leading to formation of silica rhizoliths. In contrast, both silica and carbonate saturation was attained in shallow fluids below gently sloping topographic highs, resulting in the formation of calcite and/or silica rhizoliths. A similar model, based on local subtle variations in salinity linked to topography, could potentially account for the spatially separated areas of silica and carbonate–silica precipitation at Olorgesailie.

The chert-like rhizoliths are not easily explained by either of these models. The silica rhizoliths referred to in Models A and B were permineralized during growth or soon after the plants died, but before decay. This was not necessarily the case with the chert-like rhizoliths. These appear to surround a central void similar to those found in carbonate rhizoliths, which probably formed as rhizocretions around roots (cf. Klappa, 1980).

This opens the possibility of secondary replacement of carbonate (calcite) by silica at a later stage (Model C; Fig. 9). However, no relic carbonate has been found in the cherty rhizoliths, either in thin section or during SEM examination. Other carbonate rhizoliths would also have been exposed to later silica-enriched fluids, but many are unaltered. Furthermore, the chert-like rhizoliths are locally reworked into the overlying sediments, which strongly suggests early silicification rather than later replacement. Alternatively, the rhizoliths might have initially formed as opaline silica (Model D; Fig. 9) at the time plants were growing. The bulbous nature of the chert-like rhizoliths

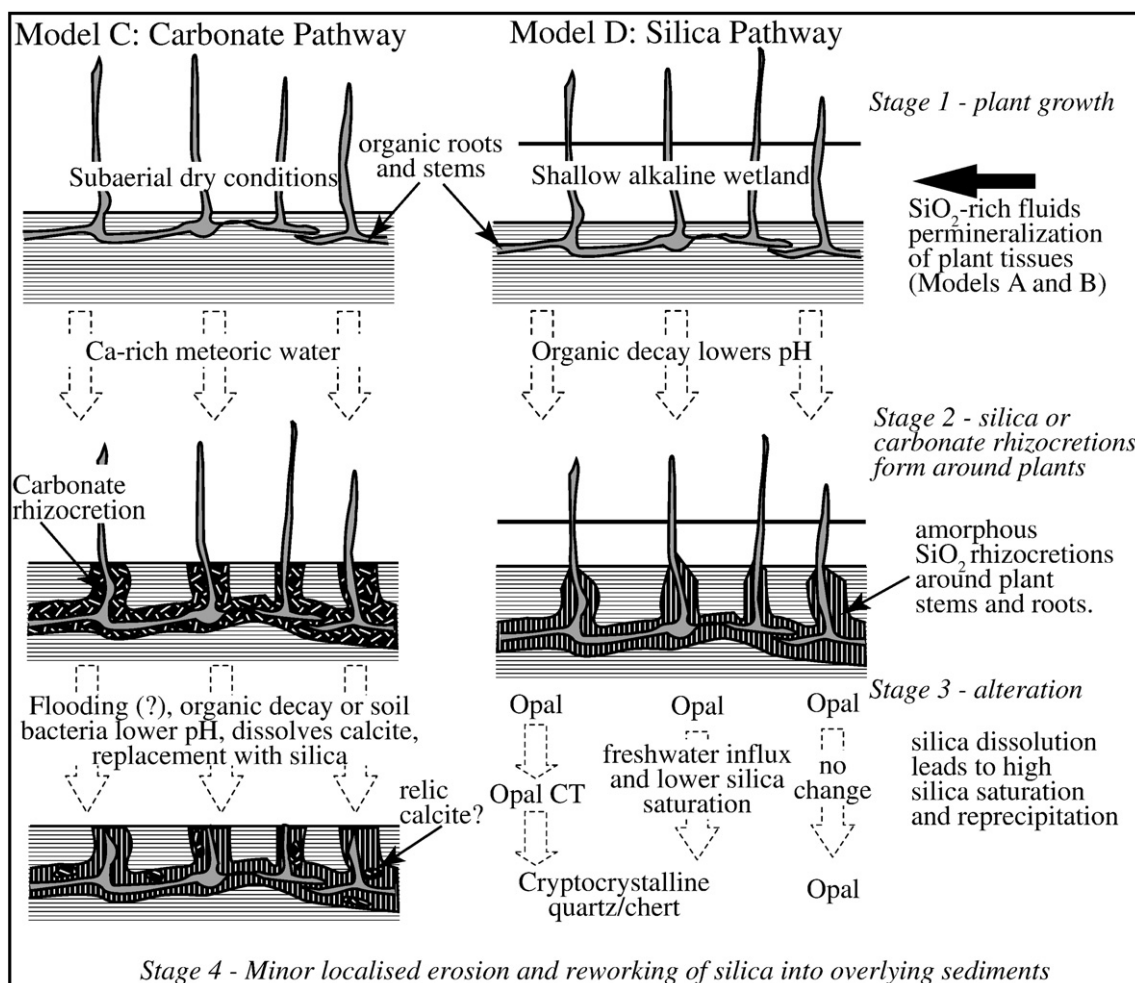


Fig. 9. Wetland models C and D. This shows formation of chert-like rhizocretions. Model C shows a potential carbonate pathway involving rhizocretion formation in an arid setting with its subsequent replacement. Model D shows a silica pathway with initial opaline silica rhizocretions forming in response to pH reduction. A variety of pathways could then lead to chert-like materials, including diagenetic alteration of the opal-A. Subsequent erosion and reworking locally affects the rhizoliths.

contrast with the slender forms of the permineralized silica plants and points to a contrast in processes compared with Models A and B, with silica forming as concretionary masses around plant stems rather than within cells. Model “D” implies that organic decay might have released CO₂, resulting in a lowering of pH if the soil waters were unbuffered. This would, in turn, favour silica precipitation around plant stems and roots, especially if the fluids affected were alkaline as suggested by the diatoms. XRD analysis of a selected few rhizoliths and their appearance in SEM images suggest that they are composed mainly of non-crystalline silica (opal-A). If some are crystalline, then the original opaline silica could later have altered to opal-CT and then cryptocrystalline quartz or chert, or might have crystallized directly to chert. However any later phase of opaline silica dissolution and reprecipitation should also have affected the diatoms in the adjacent porous sediments, yet most diatoms are unaltered or show only moderate dissolution. Similarly, the silica-permineralized plants of other horizons show little evidence of further alteration, suggesting that most silicification occurred during or soon after sedimentation.

An additional consideration in assessing the paleoenvironments is that silicified plants are rare in the rest of the Olorgesailie Formation, a formation with abundant silica-rich diatomaceous and volcanoclastic sediments, but they are common in M14 and post-Olorgesailie Formation strata. This contrast could be the result of a change in the paleohydrological conditions at about the time that M14 was deposited. Behrensmeyer et al. (2002) noted that a period of incision of the Olorgesailie Formation in other parts of the basin was linked to a phase of regional faulting. The early stages of that tectonic activity would probably have altered the regional groundwater regime, perhaps providing permeable pathways for deeper waters, including thermal fluids to reach the surface. Such a change in hydrogeology could have increased spring and groundwater discharge, enhanced the supply of silica to surface waters and shallow groundwaters, and perhaps led to the formation of spring-fed tufas, which overlie some post-Olorgesailie sediments.

6. Conclusions

The deposits at the top of the Olorgesailie Formation contain diatoms indicating shallow water environments that ranged from fresh to moderately saline. However, these aquatic floras provide few clues, other than partial fragmentation of frustules, to indicate phases of subaerial emergence. This study shows that integrating evidence from diatom floras and ichnofossils with normal sedimentological data can yield deeper insights into the complex nature of past wetland settings and their temporal variability.

Much of the sequence preserved in M13–M14 was deposited subaqueously, but these sediments have been overprinted with features that formed during drier periods of subaerial emergence. These features include rhizoliths that record plant growth, in both wet and dry soils, and which provide clues about the soil hydrochemistry and early diagenetic processes. Preserved soil structures (peds, desiccation cracks) also indicate emergent episodes, as do fluvial erosion surfaces. Trace fossils give clues to the former water table depths during their formation and, where they cross-cut each other, can provide physical evidence of the sequence of changing lake levels and water tables through time.

A key to recognizing these shallow lake-marginal and wetland settings is the mix of features that formed in dry, moist and wet conditions, and which are preserved in the same package of sediments. Several palaeoenvironmental models have been proposed to explain their origins. The sediments might have been laid down in point-sourced spring-fed wetlands, more diffuse zones of groundwater seepage near lake margins, or in seasonal wetlands in areas with low topographic relief in the distal parts of an ephemeral drainage system.

Faulting during the later phases of Olorgesailie Formation sedimentation could have played a critical role in the development

of the wetland environments by changing the basin hydrogeology and increasing the amount of groundwater discharge in the basin.

Acknowledgments

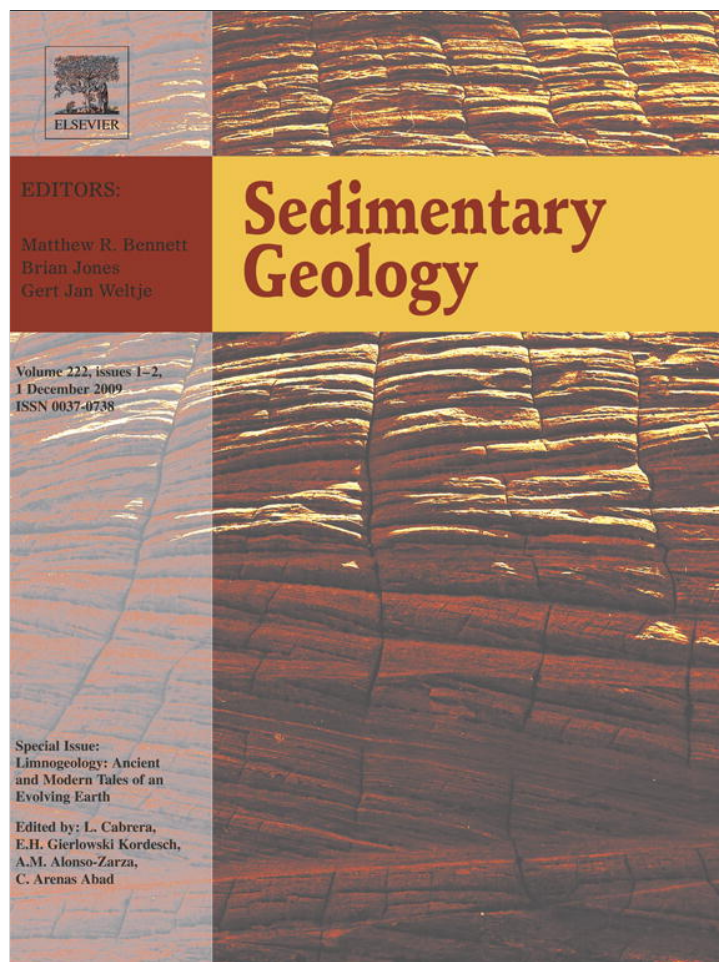
Olorgesailie fieldwork is a collaborative project of the National Museums of Kenya and the Smithsonian Institution. The authors would like to thank the National Museums of Kenya (NMK) and the NMK Palaeontology Section, Department of Earth Sciences, for their support. This research was undertaken under permits issued by the Ministry of Science and Technology, Republic of Kenya, which we gratefully acknowledge. We also thank the Kenya Office of the President for permission to carry out this research. Funding was provided by the Research Grant Council of Hong Kong (HKBU 2013/06P) and by the Hong Kong Baptist University (FRG/05-06/II-50). Further funding was given by the Natural Sciences and Engineering Research Council of Canada (RG 629-03; PGS D Scholarship to J.J.S.), the International Association of Sedimentologists (Postgraduate grant to J.J.S.), the National Science Foundation (HOMINID grant 0218511), and the Smithsonian Human Origins Program. We are grateful for the expertise of Luis Buatois (University of Saskatchewan), who provided valuable advice on the trace fossil identification and interpretations.

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