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Biogenic structures in exhumed surfaces around saline lakes: An example from Lake Bogoria, Kenya Rift Valley

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ABSTRACT

Five overprinted suites of animal and plant traces around saline, alkaline Lake Bogoria, Kenya, are described from a set of interfingering Late Pleistocene and Holocene exhumed surfaces that reveal a complex story of changes in lake level and environmental controls on trace assemblages through time. These stratigraphic surfaces are amalgamated and form a co-planar surface. The sediments were first deposited during intermediate lake levels, then reworked and cemented during low lake levels, and were subsequently overlain by transgressive lacustrine sediments during higher lake levels. Ongoing exhumation of the surface near the present shoreline has reactivated the sediments as a substrate for the activities of epifaunal and infaunal animals, as well as plant growth. The modern environmental setting at Lake Bogoria is very similar to that of the preserved exhumed surfaces, which allows comparisons between observed sets of environmental factors affecting animal behaviour and their representation in the fossilized examples. Pronounced lateral environmental heterogeneity around saline and hypersaline lakes may lead to concentrations of life around sites with vital resources, such as freshwater. At Lake Bogoria, groups of fault-controlled hot springs represent these “oases”, and have been a relatively consistent feature in and around the lake during the development of the exhumed surfaces.

Together, the diverse assemblage of animal trace suites from Lake Bogoria represent the *Mermia* and *Scoyenia* ichnofacies, but can be divided into five suites that reveal details of laterally heterogeneous sets of environmental factors, and are useful indicators of lake level, substrate moisture content, substrate cohesion, etc. Suite 1 comprises the traces of chironomid larvae (Diptera: Chironomidae) formed in subaqueous lacustrine settings. Suite 2 includes the traces of flamingos (*Phoeniconaias minor* and *Phoenicopterus ruber*) formed at the shoreline. Suite 3 compares well with the *Mermia* ichnofacies and comprises trails and burrow systems associated with relatively fresh, saturated to extremely shallow subaqueous substrates. Suite 4 is comparable to both the pre- and post-desiccation suites of the *Scoyenia* ichnofacies, is the most diverse suite at Lake Bogoria, and mainly comprises the burrows of beetles, earwigs, and their larvae as well as a diverse set of rhizoliths and vertebrate tracks. Suite 5 contains a moderately diverse set of traces attributed to termites and ants.

1. Introduction

The complexities of continental sedimentary successions and their associated trace fossils have the potential to provide high-resolution information on the paleoenvironmental factors that control the distribution of plants and animals in continental settings. Lateral variations in environmental controls such as sediment texture, moisture, and salinity result in spatial variability of trace assemblages. This is particularly pronounced in hydrologically closed lake basins that commonly experience fluctuations in lake level and salinity of variable duration (“underfilled” basins of Carroll and Bohacs, 1999; Bohacs et al., 2000). Such changes in lake level lead to recurrent deposition and erosion of interfingering lake margin, deltaic, and shallow littoral sedimentary deposits that, in turn, give rise to complex vertical and lateral successions of trace assemblages when animals and plants respond to those environmental changes.

Changes in lake level and depth of water table affect how animals and plants interact with lake margin sediments (e.g., Gierlowski-Kordesch, 1991; Buatois and Mángano, 2004, 2007; Hasiotis, 2007). Around saline lakes, biota and their activity also respond to any inputs of freshwater to the lake, such as rivers, springs and groundwater discharge zones (e.g., Scott et al., 2007a; Owen et al., 2008). In some saline lake basins, vital resources like freshwater may only be available to plants and animals around springs and associated wetlands. The lateral variability of lake- and pore-fluid chemical compositions, and associated suites of authigenic minerals (e.g., Renaut et al., 1986; Owen et al., 2008), is also

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controlled by many of the same environmental factors that influence the composition and distribution of trace assemblages. For example, early cementation of lake margin sediments during periods of lake level fall (e.g., Renaut, 1993) can preserve animal and plant traces in sediments that resist erosion during subsequent lake level rise or fall. Later overprinting of the trace suites in such exhumed surfaces by different tracemakers reflects the complexities of these processes and controls, and the variability in the chemical composition of pore-waters and substrate conditions, both laterally and through time.

This paper presents a study of exhumed sediment surfaces around the margins of saline, alkaline Lake Bogoria in the Kenya Rift Valley that preserve Late Pleistocene and Holocene invertebrate tracks, trails and burrows, a variety of vertebrate traces (Scott et al., 2008), and several types of rhizoliths (Renaut, 1982, 1993; Owen et al., 2008). Previous work on the sedimentology, pedogenesis, paleontology, and ichnology of modern and ancient depositional environments at Lake Bogoria (McCall et al., 1967; Farrand et al., 1976; Tiercelin,1981; Tiercelin et al., 1981; Renaut, 1982, 1993; Tiercelin and Vincens, 1987; Renaut and Owen, 1988, 1991; Renaut and Tiercelin, 1994; Ashley et al., 2002, 2004; Driese et al., 2004; Owen et al., 2004, 2008; Scott, 2005; Scott et al., 2007a, 2008), has made it possible to place the exhumed surfaces and their associated plant and animal traces into a broader basin-scale context.

2. Environmental setting

2.1. Geological setting

Lake Bogoria is a shallow, perennial, saline (60–100 g^{-1} Total Dissolved Salts: TDS), alkaline (pH: ~10–10.5) lake with Na–HCO_3–CO_3 waters located in a young half-graben basin in the Kenya Rift Valley near the equator (Fig. 1). Sodium carbonate evaporites and organic muds are preserved in the basin centre (Renaut and Tiercelin, 1994). The lake is bounded by Neogene volcanic rocks of the ~700 m high Bogoria and Emsos escarpments to the east and south, and by Pleistocene trachyphonolites and basalts on the west. Rocks exposed in the drainage basin (Fig. 1) are primarily basalts, trachytes, and phonolites. The northern margin of the basin is defined by the spill-over point into the drainage for Lake Baringo. The drainage divide is controlled by a deeply buried, NW–SE tectonic lineament (WMTZ in Fig. 2) that obliquely intersects the N–S trending rift (Le Turdu et al., 1995), and by an alluvial fan located where the Sandai River enters the rift floor (Renaut, 1982).

Alluvial silts, siltstones and sandstones, informally termed the Loboi Silts (McCall et al., 1967), lie in the southwestern area of the Baringo basin (Fig. 1) and extend across the drainage divide into the northern part of the Bogoria basin, where they underlie the modern Sandai delta-plain (Figs. 1,2,3). The age of the Loboi Silts is very poorly constrained. They are laterally time transgressive and represent a period of valley-floor alluvial sedimentation that occurred after the faulting that terminated the Pleistocene Kapthurin sedimentation (at ~200 Ka) (Tallon, 1976), through until the latest Pleistocene (Tiercelin and Vincens, 1987). On the central Sandai Plain, the Loboi Silts are locally lithified. The Bogoria Silts were deposited after ~10,500 BP when Lake Bogoria was fresher than today, and form a northward-thinning wedge of weakly lithified silts, sands and muds that disconformably overlies the Loboi Silts paleoland surface (Farrand et al., 1976; Renaut, 1982, 1993). Stromatolitic limestone crusts that reach the height of the spill-over into the Baringo basin at ~999 m O.D. formed at between ~4500 and 3800 BP, and coat boulders, bedrock, travertine, plant roots and stems, and some exhumed Late Pleistocene surfaces around the lake margins (Renaut, 1982; Casanova, 1986; Vincens et al., 1986) (Fig. 4).

2.2. The exhumed “surfaces”

Partially lithified clastic sediments that have been buried by younger sediments then subsequently exhumed by erosion, sometimes on multiple occasions, are exposed on delta margins and around the lake shore in several places. These surfaces are not necessarily contemporary with each other because the processes that led to their cementation may have recurred many times at the same lake level whenever conditions were favourable. These old surfaces are exposed mainly on the Sandai, Loburu, and Emsos delta-plains, and in places along the eastern shoreline (Fig. 3).

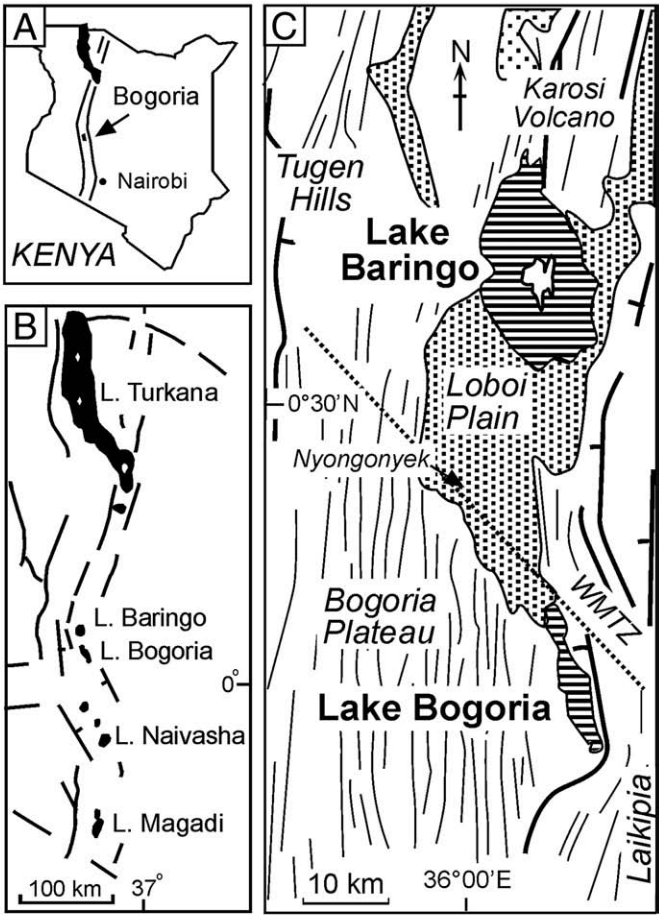

Fig. 1. Maps of the Kenya Rift Valley and the Baringo–Bogoria basin. (A, B) Kenya, showing the rift valley and location of Lake Bogoria. (C) Map of the Baringo–Bogoria basin, showing main localities mentioned in the text.

The uppermost surface of the Loboi Silts on the Sandai delta-plain is locally cemented by analcime, clay minerals and calcite. The zeolites formed mainly through replacement of poorly crystalline smectitic clays and/or minor volcanic glass that reacted with saline, alkaline pore fluids. Calcite likely precipitated by evaporative concentration of meteoric waters infiltrating the sediments from above and by evapotranspiration of shallow groundwater (Renaut, 1993; Scott et al., 2007a), but may also have been bio-mediated by plants and microbes in the substrate (cf. Scott, 2005). The degree of cementation varies laterally and vertically and is greatest on the central parts of the plain. Pockets of the exhumed “surface” have been exposed by erosion of the overlying Bogoria Silts by deflation, fluvial incision and sheet-flooding during lake lowstands, and by wave erosion during minor lake transgressions. The age of the sub-Bogoria Silts disconformity surface is unknown. If the Bogoria Silts are mainly Holocene (cf. Tiercelin and Vincens, 1987), the Loboi Silts, parts of which have been cemented and exhumed, are probably of late Pleistocene age. Renaut (1993) suggested that cementation of the surface probably occurred during an extended dry phase in the late Pleistocene based partly on an association with meter-scale desiccation polygons with cracks also cemented by zeolites, but there is no absolute age for the exhumed Loboi Silts land surface. Based on the Pleistocene to

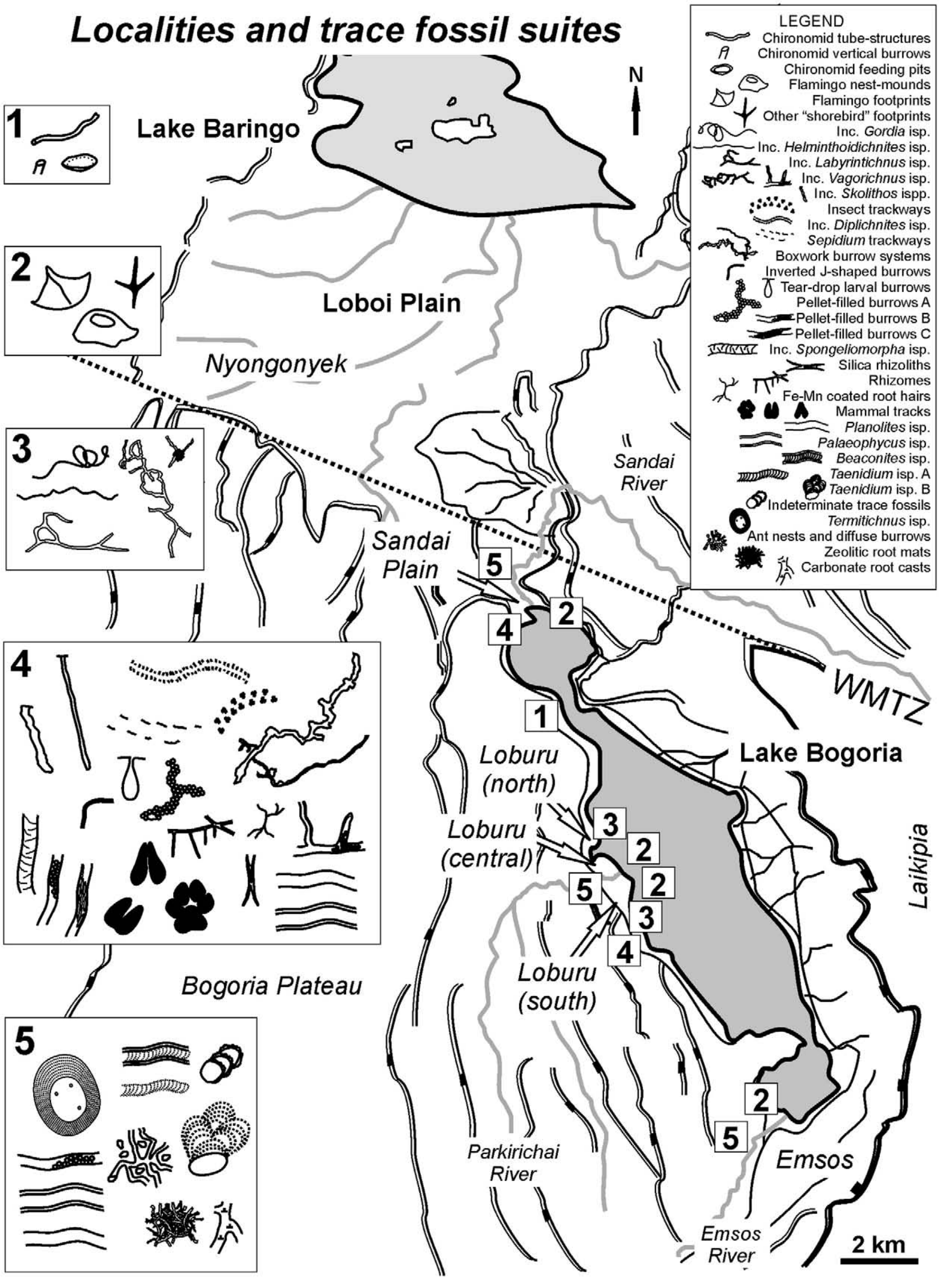

Fig. 2. View from south of the main trace-preserving localities around Lake Bogoria, trace suites identified in this study, and their general distribution. WMTZ: Waseges-Marmanet Transverse Zone (see Le Turdu et al., 1995, for details).

recent history of the Baringo–Bogoria basin, the uppermost Loboi Silts are likely time-transgressive, with the oldest deposits in the south-western Baringo basin near Nyongonyek (Fig. 1).

On the Sandai Plain, the exhumed "surface" that forms uppermost Loboi Silts shows a lateral zonation of sedimentary features that is similar to those of the present lake margins around Lake Bogoria (Fig. 3).

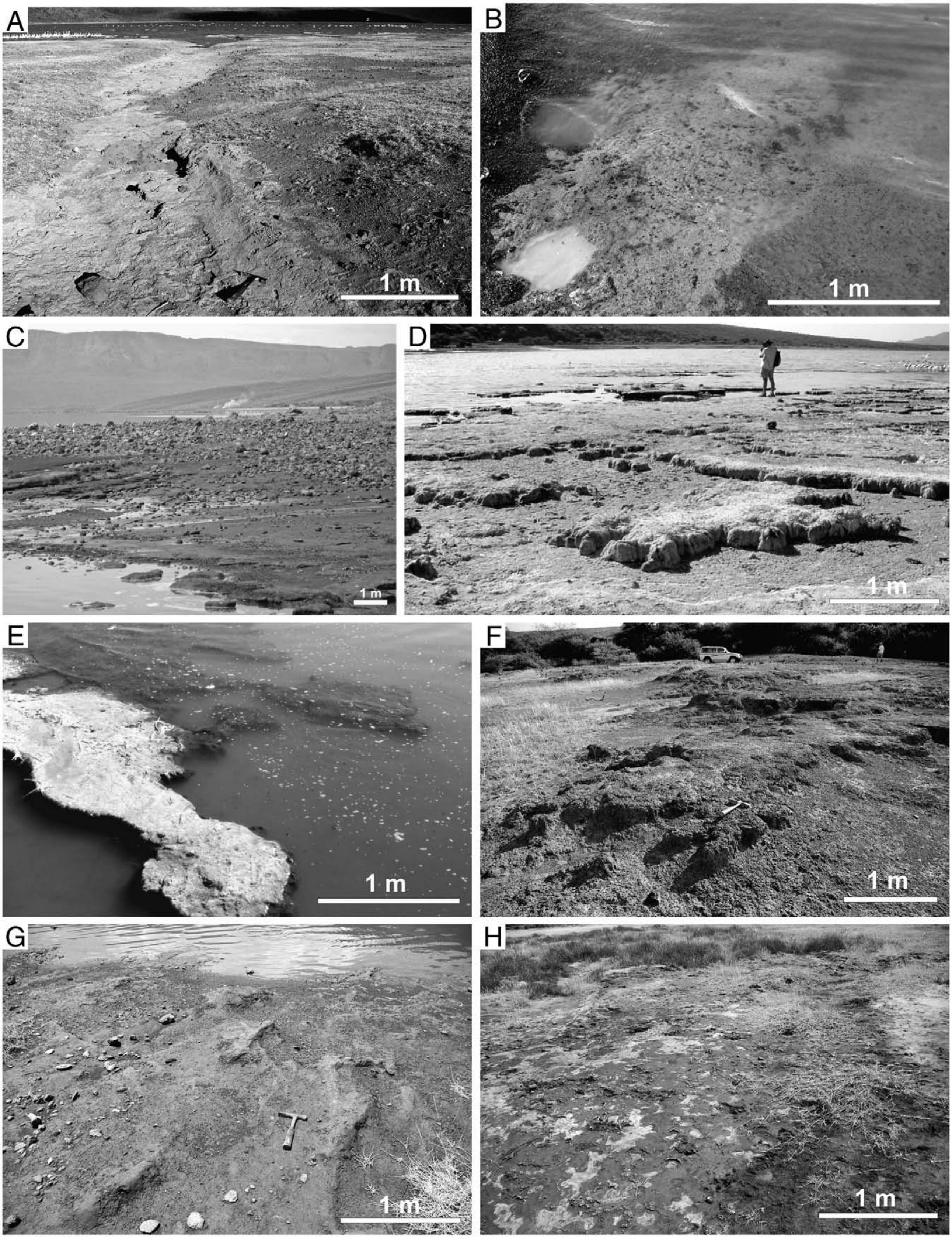

Fig. 3. Photographs showing the exhumed surfaces around Lake Bogoria. Scale bars are 1 m. (A) The uppermost Loboi Silts on Sandai Plain, exposed in an ephemeral channel into Holocene beach deposits. (B) Close up of the uppermost Loboi Silts at the north shoreline of the lake. (C) Portion of the exhumed surface underlying recent colluvium north of the Loburu delta in 2006. (D) The exhumed surface near the main group of hot springs at central Loburu, showing flamingo-modification of the surface and modern salt efflorescence on the surface in 2002. (E) Close up of the flamingo-modified surface at the shoreline of the Loburu delta in 2002. (F) The exhumed surface on the central Loburu delta near the lake basin bounding Hannington trachyphonolites. (G) The exhumed surface at the shoreline at Emsos. (H) Modern surface at the southern lobe of the Loburu delta showing zebra tracks and rhizomous grasses.

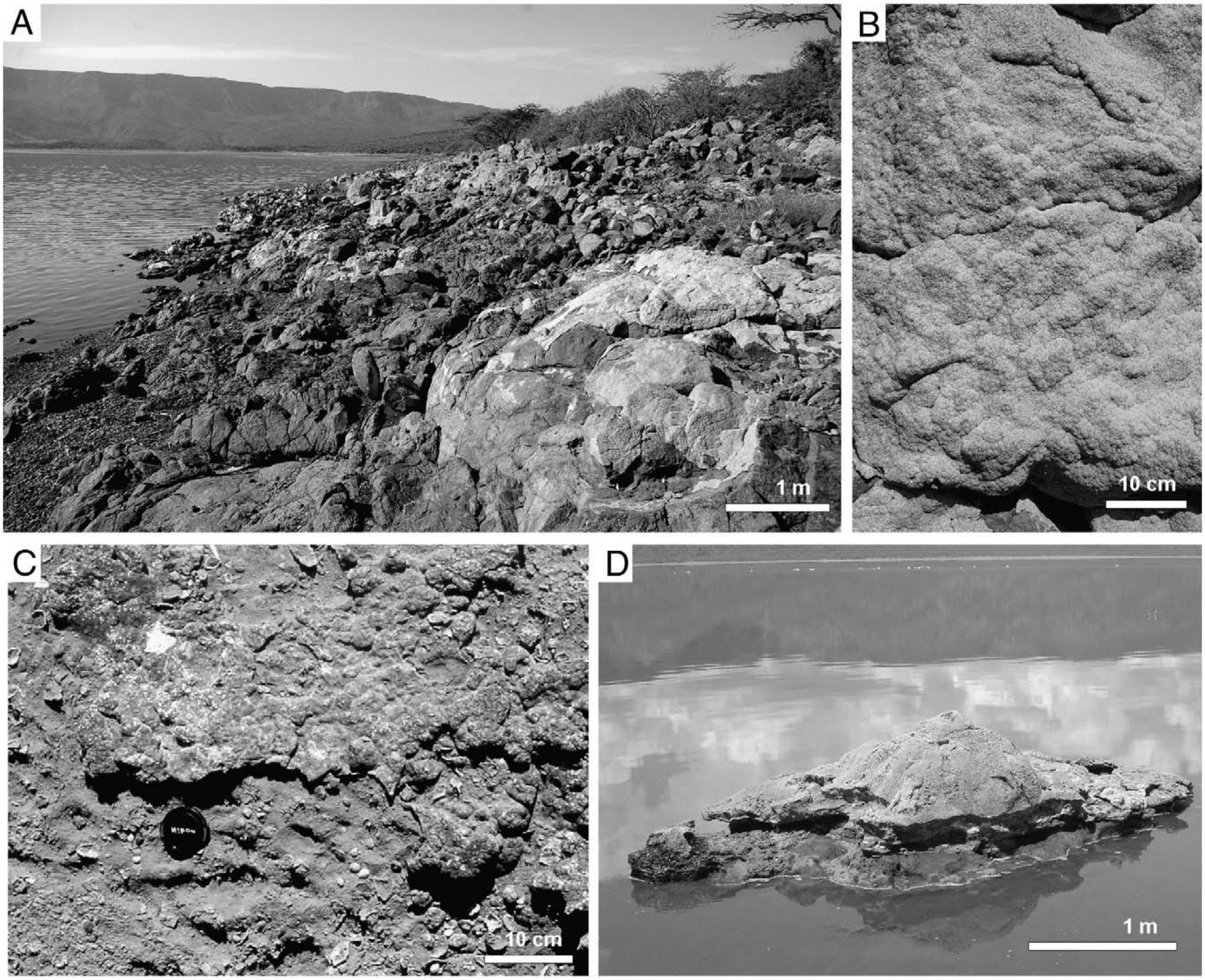

Fig. 4. Photographs of the stromatolitic coating around Lake Bogoria. (A) Stromatolite-coated boulders above the shoreline in 2007. Scale is 1 m. (B) Close up of stromatolitic texture. Scale is 10 cm. (C) Small "patch" of stromatolitic coating on an exhumed surface at the central Loburu delta. Scale is 10 cm. (D) Stromatolitic coating on travertine deposit at the main group of hot springs, Loburu delta. Scale is 1 m.

The surface dips lakewards at ~2–4° and is a buried platform upon which younger sediments have been deposited (e.g., Bogoria Silts, alluvial fans, etc.). The uppermost Loboi Silts of the Sandai Plain appear to have been deposited in a similar depositional setting to the modern delta. Renaut (1993) described a zeolitic–calcitic root-mat approximately 1 km north of the present-day shoreline; Scott et al. (2008) reported fossil vertebrate footprints, including a hominid track, at several sites ~200–800 m landward of the shore.

Erosion between 2002 and 2007 exposed a more laterally continuous exhumed surface than was previously recognized, which preserves a diverse assemblage comprising five suites of invertebrate, vertebrate, and plant trace fossils. Parts of this old surface are exposed in shallow channels near the modern shoreline where they are subject to modern modification by salt efflorescence (cf. Cohen et al., 1991; Scott, 2005; Scott et al., 2007a), and bioturbation by invertebrate burrowers and plant roots where the surface is weakly cemented. The distribution of modern burrowers and plants into the exhumed surface is controlled by similar environmental factors to those that control the lateral distribution of modern traces in all substrates at Lake Bogoria (Scott et al., 2007a).

2.3. Limnological and ecological setting

Lake Bogoria is fed by the Sandai River, several ephemeral streams, almost 200 hot springs, and by ephemeral sheetfloods and direct precipitation on the lake surface (Fig. 2). The lake itself is ~17 km long, up to ~3.5 km wide, and is ~10–12 m deep in the central sub-basin (Tiercelin and Vincens, 1987). The lake is divided into three sub-basins, each with a different sediment package that reflects the type of clastic influx and salinity (Renaut and Tiercelin, 1994). The climate is semi-arid, with 600–900 mm annual precipitation on the rift floor but >2500 mm annual evaporation. Mean annual temperatures range between ~23 and 26 °C. There is little seasonal temperature variation, but two rainy periods occur annually in April–May and August–October (Ashley et al., 2004). Annual lake-level fluctuations are typically several decimeters (<50 cm), but rises of >2 m can occur in El Niño years.

Two deltas, the Sandai delta and the Loburu delta on the mid-western shoreline, provide the most extensive habitat for grasses. Wetlands along parts of the shoreline and near hot springs are vegetated by sedges and other grasses (Onkware, 2000; Owen et al., 2004; Owen et al., 2008). *Acacia* and *Combretum* woodland and scrub is present on the relatively steep slopes around most of the lake margin and along some river channels. The cyanobacterium *Arthrospira fusiformis* is abundant in the lake waters, but only one invertebrate species, *Paratendipes* sp. (Chironomidae) inhabits the lake itself (Harper et al., 2003). Many trace-making beetles and earwigs and their larvae live in the damp to wet substrates around the lake margins (Harper et al., 2003; Scott et al., 2007a). Within the Lake

Bogoria National Reserve, vertebrates include approximately 250 species of birds, several species of bovids, warthogs, zebras, monkeys, baboons, as well as snakes, crocodiles, and monitor lizards (North-Lewis, 1998; Harper et al., 2003).

3. Methods

Observations of modern sedimentological processes, environmental factors that influence trace and substrate taphonomy, and interactions between trace-making animals and plants in lake margin sediments have been recorded as part of a long-term study of the lake (e.g., Tiercelin et al., 1981; Renaut, 1982, 1993; Renaut et al., 1986; Tiercelin and Vincens, 1987; Renaut and Owen, 1988, 1991; Renaut and Tiercelin, 1994; Owen et al., 2004, 2008). Continuing neo- and paleoichnological investigations were undertaken between June and August of 2001, 2002, 2006, and 2007 (Scott, 2005; Scott et al., 2007a, in press). Suggestions for tracemakers are based on personal field observations (J.J.S. and R.W.R.) and the work of Harper et al. (2003).

Sediment samples were collected where appropriate and feasible, and standard laboratory methods included thin section petrography, X-ray Diffraction (using a Rigaku RU200 X-ray diffractometer), electron microprobe (JEOL JXA 8600), and scanning electron microscopy (JEOL 840A SEM) to determine the mineralogy of cements and to infer early diagenetic processes on trace-preserving substrates. Systematic ichnologic descriptions were made of modern and fossil invertebrate traces collected in the field. Where sampling was impossible, photographs are the primary data source.

4. Trace types of plants, invertebrates, and vertebrates at Lake Bogoria

Plant and animal traces in the exhumed surfaces are preserved in five suites, each containing ichnocoenoses that reflect varying hydrological conditions through space and time. A diverse assemblage of plant stem casts and rhizoliths has been described in detail by Renaut (1982) (aqueous stromatolitic stem casts), Renaut (1993) (zeolite- and calcite-cemented root mats) and Owen et al. (2008) (silica-, calcite-, fluorite-, Mn–Fe oxyhydroxide-, and zeolite-cemented rhizoliths) (Fig. 5). These plant trace fossils provide valuable information on the pore-water chemistry and the processes of early mineralization. Root trace morphology and architecture provide information on the depth of the water table and proximity to the shoreline (Cohen, 1982) and (or) wetlands. Modern roots also bioturbate the same exhumed surfaces. Plant traces are briefly described in Table 1 and discussed below.

The focus of this section is the animal traces that are preserved in the sediments of the exhumed surfaces and those produced by recent burrowing into the older, more indurated substrates ("overprinting") (Table 2). The modern traces of beetles (Coleoptera) and earwigs (Dermaptera) into slightly indurated silts and very fine-grained sands of the southern Loburu delta-plain (Fig. 3H), but which are not part of the "exhumed surfaces", are included in the descriptions here because they form a suite of traces that is partly represented in the preserved examples, and contribute to understanding the succession of trace overprinting and the significance of taphonomic controls on the resulting assemblages. Following Bromley (1996, p. 164), "incipient" is used where the traces were observed from modern substrates and where the ichnotaxonomic affinity of the traces were recognizable; in some cases, there are examples of the particular trace types from both modern substrates and the exhumed surface. Scott et al. (2007a) described modern vertebrate and invertebrate traces from the Sandai Plain and Loburu delta, and provided a framework for comparing the modern and fossil trace assemblages. Scott et al. (2008) described the vertebrate track assemblage preserved in the uppermost Loboi Silts and provided a model for the preservation of vertebrate footprints in the surface, their burial, and exhumation.

4.1. Systematic invertebrate ichnology

4.1.1. Chironomid tube structures and associated burrows (Fig. 6)

4.1.1.1. Description (described from modern traces). Millimeter-sized, straight to curved, non-branching, horizontal tube structures are approximately 0.5 cm to 4 cm in length and comprised of loose detritus and organic material that settled on an exhumed surface. They are associated with small (~3 mm diameter) vertical burrows and larger (<1 cm diameter) shallow, circular- and irregular-shaped "pits" into a moderately indurated substrate (Fig. 6).

4.1.1.2. Remarks. Although vertically oriented, U-shaped, and Y-shaped burrows attributed to chironomid larvae (e.g., *Polykladichnus*, Gingras et al., 2007; cf. Uchman and Álvaro, 2000) were not observed in soft, modern sediments, horizontal larval tube structures associated with <3 mm diameter vertical burrows and <1 cm diameter "pits" were found on the exhumed surface during low lake levels of 2006. Horizontal tubes are constructed by chironomid larvae when <10 mm thickness of soft sediment is available, and they build vertically oriented, U-shaped or J-shaped tubes when there is more than 10 mm of soft substrate (McLachlan and Cantrell, 1976). Chironomid larvae prefer microbe-rich substrates (e.g., Edgar and Meadows, 1969), but incorporate available materials including organic and clastic detritus in their tubes, which are held together with a salivary secretion (Brennan and McLachlan, 1979). Materials for tube construction are gathered from around the opening of the tubes, which may leave visibly excavated areas around the tubes if the density of larvae is low enough (Ólafsson and Paterson, 2004). The examples from Lake Bogoria (Fig. 6) show a very small amount of available loose sediment and benthic microbial mats on the subaqueous portion of an exhumed surface that was likely used by chironomids for both tube-building and feeding. The small (<3 mm diameter), circular burrows (up to ~5 cm deep in one example, Fig. 6F) in the associated exhumed surface were likely made by chironomids, although these burrows may have also been made during lower lake levels by tiger beetle larvae. Larger (<1 cm), circular shallow "pits" into the surface may be a result of the sediment excavation for tube-building (Fig. 6E).

4.1.2. Incipient Gordia (Fig. 7A)

4.1.2.1. Description (described from modern traces). Epichnial, horizontal, unbranched, small (1–2 mm), unilobed trails that are self-crossing and looping and were observed to be up to 10 cm in length (Fig. 7A).

4.1.2.2. Remarks. These simple horizontal traces were observed in modern saturated substrates near slightly brackish water (4–5 g/l TDS) hot springs at the southern and north-central Loburu delta; they appear to be laterally restricted to these areas. Scott et al. (2007a, Fig. 10A, Table 2) reported incipient *Gordia*, *Helminthoidichnites*, and *Diplopodichnus* as "salt trails", a type of elite trace (*sensu* Bromley, 1996), which indicated shallow subsurface trails on the modern delta surface at Loburu. Small (1–2 mm diameter), open horizontal burrows were observed in cross-section in "modern" slightly indurated substrates, and appear to be along bedding planes in laminated, slightly indurated silts at southern Loburu.

4.1.3. Incipient Helminthoidichnites (Fig. 7B)

4.1.3.1. Description (described from modern traces). Epichnial, horizontal, unbranched, small (1–2 mm), unilobed trails up to several centimeters in length that are straight to slightly curved.

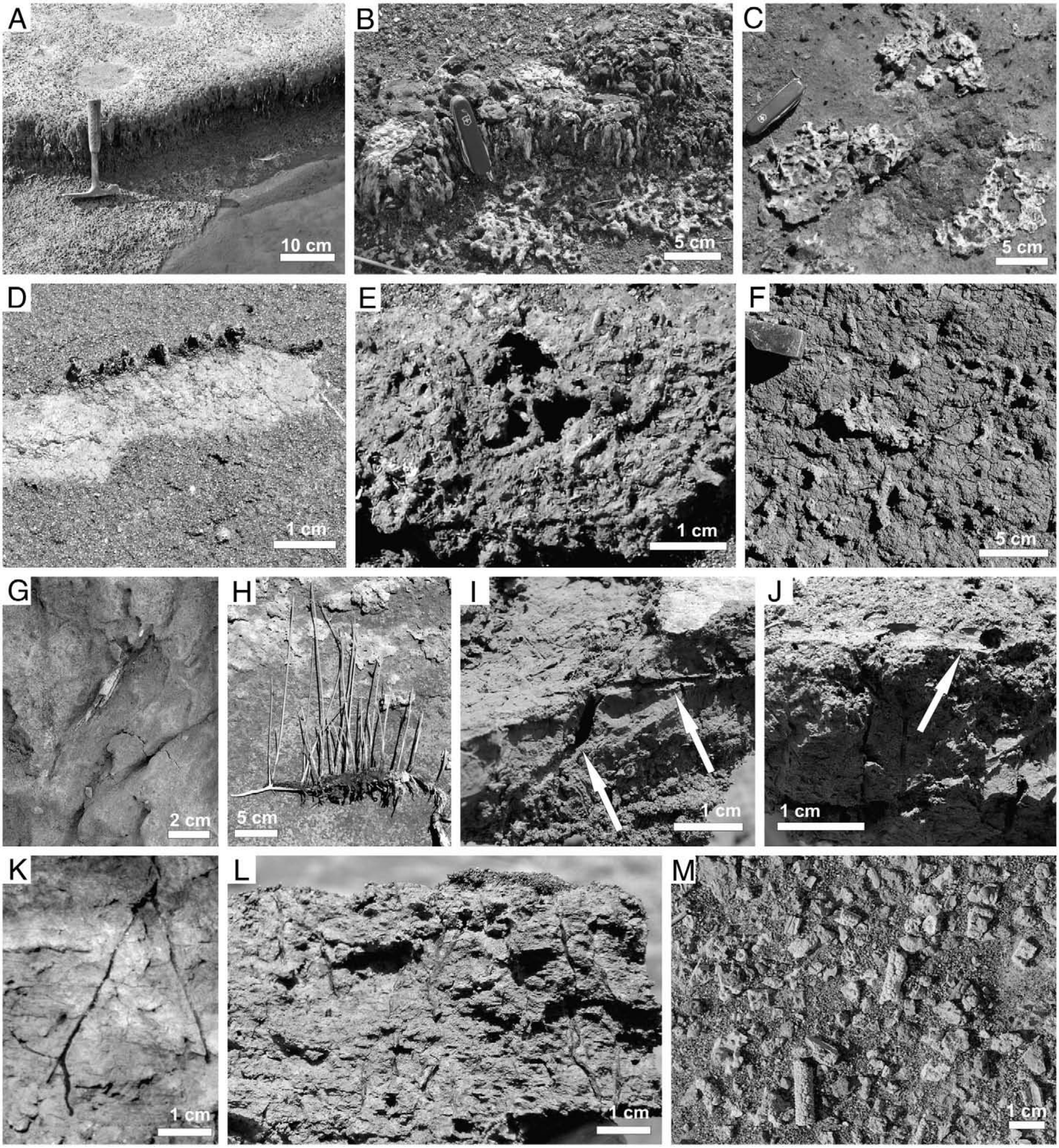

Fig. 5. Photographs of modern and fossil plant traces at Lake Bogoria. (A) Silica rhizoliths, Loburu delta. Scale bar is 10 cm. (B) Clustered silica rhizoliths, Loburu delta. Scale bar is 5 cm. (C) Horizontal mat with rhizoliths, Loburu delta. Scale bar is 5 cm. (D) Bulbous fluorite rhizoliths, Loburu delta. Scale bar is 1 cm. (E) Close up of zeolitic root mat, Sandai Plain. Scale bar is 1 cm. (F) Carbonate root casts, Loboi Silts, Nyongonyek. Scale bar is 5 cm. (G) Carbonate root cast around modern root, Loboi Silts, Nyongonyek. Scale bar is 2 cm. (H) Modern rhizomous roots, southern Loburu delta. Scale bar is 5 cm. (I) Horizontal to oblique, open, “lined” branching root traces of modern rhizomous sedge. Note that the branches of the trace have different diameters (arrows), southern Loburu delta. Scale bar is 1 cm. (J) Close up of horizontal root trace with “lining” (arrow), southern Loburu delta. Scale bar is 1 cm. (K) Close up of Fe- and/or Mn-oxyhydroxide “lined” branching root-hair trace, Emsos. Scale bar is 1 cm. (L) Example of buried, vertically oriented, branching, open root traces, some still containing roots, Loburu delta. Scale bar is 1 cm. (M) Stromatolitic stem casts associated with tufa mound, Sandai Plain. Scale bar is 1 cm.

4.1.3.2. Remarks. These traces are associated with incipient *Gordia* as “salt trails” (Scott et al., 2007a), but are more commonly observed in perennially saturated substrates around hot springs, and may also be represented as 1–2 mm wide open horizontal burrows in the deltaic silts of southern Loburu.

4.1.4. Incipient Labyrintichnus isp. (Fig. 7C–H)

4.1.4.1. Description (described from modern traces). Mainly horizontal, smooth-walled, convex epichnial branched networks comprised of intersecting and crossing, open, straight to curved, and sometimes

Table 1
Descriptions of modern and fossil plant traces at Lake Bogoria

Type of plant trace	Preserved by	Reference	Localities	Description	Corresponding trace suite and figure #
Siliceous vertical rhizoliths	Opaline silica	Owen et al. (2008), Fig. 4A	Loburu delta: lake-marginal plain	White to pale brown, straight, vertically oriented, and generally unbranched, circular and tapering rhizoliths, usually 2–4 mm diameter and up to 20 cm long	4; Fig. 5A
Clustered siliceous rhizoliths	Opaline silica, flourite, calcite	Owen et al. (2008), Fig. 4B, E	Loburu delta: lake-marginal plain; near hot springs	White to bluish, dense clusters of siliceous rhizoliths forming irregular, knobby surfaces; individual rhizoliths are ~1–4 mm in diameter and ~5 cm long	4; Fig. 5B
Root and stem moulds in horizontal mats	Open moulds or siliciclastic casts associated with opaline silica mats	Owen et al. (2008), Fig. 4G, H, J	Loburu delta: lake-marginal plain, near hot springs; Sandai Plain: fossil tufa mound	Circular and ovoid moulds (5–10 mm diameter) penetrate white to brown siliceous mats, and may be filled with siliciclastics. Also associated with mats are horizontal, reticulate, siliceous rhizoliths that appear to have been rhizomes (3–10 mm diameter)	3, 4; Fig. 5C
Silica–calcite rhizoliths	Calcite and opaline silica	Owen et al. (2008), Fig. 4F	Loburu delta: lake-marginal plain	Calcite-cemented siltstone nodules that form around siliceous vertical rhizoliths ~2–4 mm in diameter and 2–5 cm long.	4; –
Bulbous fluorite rhizoliths	Fluorite, calcite and opaline silica	Owen et al. (2008), Fig. 4D	Loburu delta: lake-marginal plain	Irregular spheroidal to ovoid flourite-rich knobs ~1 cm in diameter and 2 cm long that are associated with silica–calcite rhizoliths	4; Fig. 5D
Zeolitic root mats	Analcime, calcite, authigenic clays, Fe-oxyhydroxides	Renaut (1993); Owen et al. (2008), Fig. 10A	Loboi Silts, Sandai Plain	Dense networks of hollow tubes ~3 mm in diameter and several centimeters long	5; Fig. 5E
Calcite root casts	Calcite (micrite and micro-sparite)	(Renaut (1993); Owen et al. (2008))	Loboi Silts, Sandai Plain and Nyongonyek	Sandai: horizontal and vertical root casts ~1–5 cm long and 0.3–1.5 cm in diameter with irregular surface textures; Nyongonyek: horizontal and vertical, often branching root casts ~1–3 cm in diameter and up to 2 m in length	5, 6; Fig. 5F,G
Branching rhizome open networks	Open holes in siliciclastics	This paper	Loburu delta; Emsos delta	Shallow, open branching networks of sedges and grasses in littoral wetlands; rhizome holes may taper and have smooth hole "linings" with no ornamentation; vertical branches (~4 mm) are commonly at ~90° to horizontal rhizomes (~4–6 mm in diameter)	4; Fig. 5H–J
Lined, branching root-hair pores	Open holes in siliciclastics with Mn- and/or Fe-rich linings	This paper	Loburu delta; Emsos delta	1–3 mm in diameter, these branching networks may branch obliquely upwards or downwards; larger examples tend not to branch and are vertically oriented; all are lined with red to black Mn- and/or Fe-rich linings	4, 5; Fig. 5K
Open root-hair pores	Open holes in siliciclastics with no lining	This paper	Loburu, Emsos, Sandai, and Nyongonyek	1–2 mm in diameter open, branching root-hair networks with predominantly vertical and oblique orientation of individual root-hair pores	4, 5, 6; Fig. 5L
Stromatolitic stem casts	Calcite	Renaut (1982)	Sandai Plain: fossil tufa mound; Emsos, Mwanasis	Greyish brown, mammillary, stromatolitic encrustations on plant stems, twigs, and tree stumps; associated with stromatolitic coating around the shoreline and tufa mound on Sandai Plain	– ; Fig. 5M

looping horizontal tunnels in two size modals (1–2 mm wide and 3–4 mm wide). The burrow system is three-dimensional and has oblique to vertical tunnels that connect the horizontal networks which can be up to ~2 m in length. Vertical dimensions of the networks were not measured.

4.1.4.2. Remarks. The lined tunnel networks of incipient *Labyrintichnus* (Uchman and Álvaro, 2000) at Lake Bogoria have been observed in subaerial, but saturated, and extremely shallow (few mm) subaqueous substrates associated with thin surficial microbial films, especially near hot spring outflow on the Loburu delta (Fig. 7D). Horizontal networks may be associated with pelleted tumuli (i.e. piles of excavated material at burrow opening) which suggest that the burrow systems remain open while they are excavated.

4.1.5. Incipient Vagorichnus isp. (Fig. 7I, J)

4.1.5.1. Description (described from modern traces). Lined, three-dimensional, hypichnial and endichnial branched network of straight to slightly curving walled tunnels (4–5 mm width) that are actively filled (cf. Buatois et al., 1995), commonly with <1 mm spherical pellets. In the examples at Bogoria, the pellets appear to be made up of sediment identical to the host substrate. The size of the networks can be up to several meters in horizontal dimensions, and depths of up to 10 cm were observed.

4.1.5.2. Remarks. The incipient *Vagorichnus* tunnel systems at Lake Bogoria are common in subaerial, but wet, microbe-rich substrates in areas associated with high water tables and (or) near hot springs (e.g., southern Loburu). The Lake Bogoria examples may be either pellet-filled or open. Incipient *Vagorichnus* networks described by Scott et al. (2007a) are probably better assigned to *Labyrintichnus* based on the nature of the fill, but the two types may be transitional with one another at southern Loburu. Incipient *Vagorichnus* isp. in the modern setting at Lake Bogoria may also be transitional with the pellet-filled A burrow networks (Section 4.1.6), although these examples are only lined at the sediment–air interface.

4.1.6. Pellet-filled burrows A (Fig. 8A–D)

4.1.6.1. Description (described from modern traces). Unwalled, pellet-filled (pellets are <1 mm), branching endichnial burrow systems composed of horizontal burrows (<4–5 mm diameter) along buried bedding planes and regular, perpendicular vertical branches less than ~10 cm below the sediment–air interface. Pellets are composed of material similar to the host sediment in grain size and colour. These systems are connected with convex epichnial, branching, pellet-walled burrow systems at the surface (Fig. 8B).

4.1.6.2. Remarks. These burrow systems are found in damp to wet, microbe-rich silty substrates on the southern Loburu delta, and are found on bedding planes, including the sediment–air interface.

Table 2
Distribution of modern and fossil animal trace types around Lake Bogoria

	Sandai Plain	Emsos delta	Loburu delta (north hot springs)	Loburu delta (central)	Loburu delta (southern plain; springs)
Suite 1	←	?	Chironomid tube-cases CHIRONOMID BURROWS CHIRONOMID FEEDING PITS	?	→
Suite 2	FLAMINGO NEST MOUNDS	**Flamingo nest-mounds**	FLAMINGO NEST MOUNDS	FLAMINGO NEST MOUNDS	Flamingo nest-mounds
	FLAMINGO MODIFIED SURFACES	**Flamingo modified surfaces**	FLAMINGO MODIFIED SURFACES	FLAMINGO MODIFIED SURFACES	Flamingo modified surfaces
	Flamingo and other bird footprints		Flamingo and other bird footprints	Flamingo and other bird footprints	Flamingo and other bird footprints
Suite 3			Inc. *Gordia* isp.		Inc. *Gordia* isp.
		Inc. *Helminthoidichnites* isp.	Inc. *Helminthoidichnites* isp.		Inc. *Helminthoidichnites* isp.
		Inc. *Labyrintichnus* isp.	Inc. *Labyrintichnus* isp.		Inc. *Labyrintichnus* isp.
			Inc. *Vagorichnus* isp.		Inc. *Vagorichnus* isp.
Suite 4	VERTEBRATE FOOTPRINTS	Vertebrate footprints	Vertebrate footprints	?VERTEBRATE FOOTPRINTS	Vertebrate footprints
	INC. *SKOLITHOS* ISP.	Inc. *Skolithos* isp.	INC. *SKOLITHOS* ISP.	*SKOLITHOS* ISP.	Inc. *Skolithos* isp.
	***Planolites* isp.**	***Planolites* isp.**	***Planolites* isp.**	***Planolites* isp.**	*Planolites* isp.
	Horizontal tunnels of boxwork burrows	PELLET-FILLED BURROWS A	Boxwork burrows	PELLET-FILLED BURROWSB	Pellet-filled burrows A
	Pellet-filled burrows B	PELLET-FILLED BURROWS B	Insect trackways	***Palaeophycus* isp.**	Pellet-filled burrows B
		INC. *SPONGELIOMORPHA* ISP.	RHIZOMES	Insect trackways	Pellet-filled burrows C
		Earwig burrows	FE-MN-LINED ROOT HAIRS	**Indeterminate root traces**	Tear-drop larval burrows
		RHIZOMES	**Silica rhizoliths**	FE-MN-LINED ROOT HAIRS	Inverted J-shape burrows
		FE-MN-LINED ROOT HAIRS		**Silica rhizoliths**	Inc. *Vagorichnus* isp.
					Inc. *Spongeliomorpha* isp.
					Insect trackways
					Rhizomes
					Fe-Mn-lined root-hairs
Suite 5	***Planolites* isp.**	***Planolites* isp.**		***Planolites* isp.**	
	***Palaeophycus* isp.**	***Palaeophycus* isp.**		***Palaeophycus* isp.**	
	***?Beaconites* isp.**	***Termitchnus* isp.**		***?Beaconites* isp.**	
	***Taenidium* isp. A**	ANT NESTS		***Termitchnus* isp.**	
	***Taenidium* isp. B**			**Ant nests**	
	Interdeterminate isp.			**Carbonate root casts**	
	***Termitchnus* isp.**				
	Carbonate root casts				
	Zeolitic root mats				
	ANT NESTS				

Legend – Traces associated with the exhumed surfaces
Trace type ………………… Modern examples only
Trace type …………… Fossil examples only
TRACE TYPE ……………… Modern and exhumed surfaces

4.1.7. Pellet-filled burrows B (Fig. 8E)

4.1.7.1. Description (described from modern traces). Unlined/unwalled, vertical and horizontal, unbranched, endichnial burrows ~4 mm in diameter that are partly to completely filled with spherical pellets (~0.5 mm diameter) of material similar to the host sediment.

4.1.7.2. Remarks. These burrows may have both vertical and horizontal components and are most common in damp to wet substrates with variable degrees of induration, including the exhumed surfaces at the present shoreline at Emsos.

4.1.8. Pellet-filled burrows C (Fig. 8F,G)

4.1.8.1. Description (described from modern traces). Unlined/unwalled, vertical burrows ~4 mm in diameter that are partly filled with elongate fecal pellets (<0.5 wide, 4–5 mm long) similar in colour and grain size to the host sediment. Observed examples were less than 5 cm in length.

4.1.8.2. Remarks. These burrows have only been observed as vertical burrows in damp to wet, slightly indurated substrates at southern Loburu, but not in the exhumed surfaces.

4.1.9. Inverted J-shaped burrows (Fig. 8G)

4.1.9.1. Description (described from modern traces). Small (1–2 mm wide), straight, open, unlined/unwalled tunnels that curve from vertical tunnels onto buried bedding planes, making an inverted J-shape.

4.1.9.2. Remarks. These traces are common in wet, slightly indurated substrates like those at southern Loburu. The depth of the "J" was observed to be within ~3 cm of the sediment–air interface, but more examples are required to establish an average depth of the "J" and whether or not the change in direction may be related to particular bedding plane characteristics or just the depth below the surface.

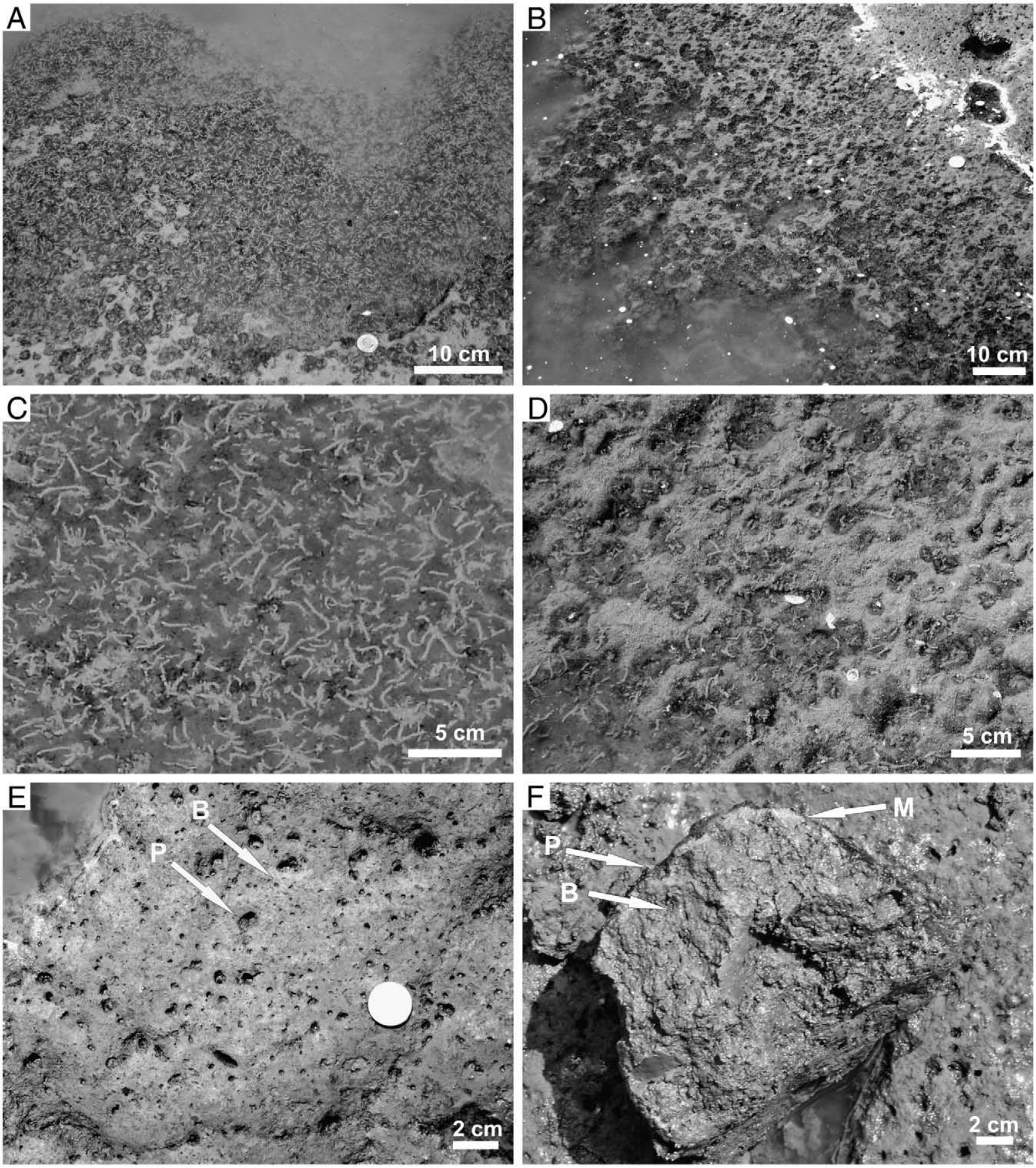

Fig. 6. Modern traces of chironomid larvae (Suite 1). (A) View of horizontal tube structures of chironomid larvae and thin layer of detritus and sediments on a subaqueous exhumed surface. Scale bar is 10 cm. (B) View of chironomid cases, benthic microbial mat, and exhumed surface at the shoreline. Note the circular "feeding territories" of the larvae into the mat. Scale bar is 10 cm. (C) Close up of horizontal tube structures of chironomid larvae made from detritus and fine sediments on an exhumed surface. Scale bar is 5 cm. (D) Close up of chironomid tube structures and benthic microbial mat. Scale bar is 5 cm. (E) Close up of exhumed surface at shoreline with possible chironomid traces. B: tiny larval burrows; P: circular "pits" into surface. Scale bar is 2 cm. (F) Close up of broken piece of the anoxic exhumed surface showing an oxidized "rind" <1 cm thick underlying a thin microbial mat (M). B: tiny larval burrows; P: circular "pits" into surface. Scale bar is 2 cm.

4.1.10. Tear-drop larval burrows (Fig. 8H)

4.1.10.1. Description (described from modern traces). Vertically oriented, tear drop-shaped, open endichnial burrows up to 5 mm in diameter, with short 1–2 mm wide vertical open burrows that exit to the air–sediment interface. The tear drop may contain ~0.5 mm diameter spherical pellets of similar composition to the host substrate, but the exit hole to the surface remains open.

4.1.10.2. Remarks. When in use, these tear-drop domiciles of beetle larvae (pers. obs. J.J.S.; Fig. 8H) lie within ~2 cm of the surface. They were most commonly found in wet to saturated zones of southern

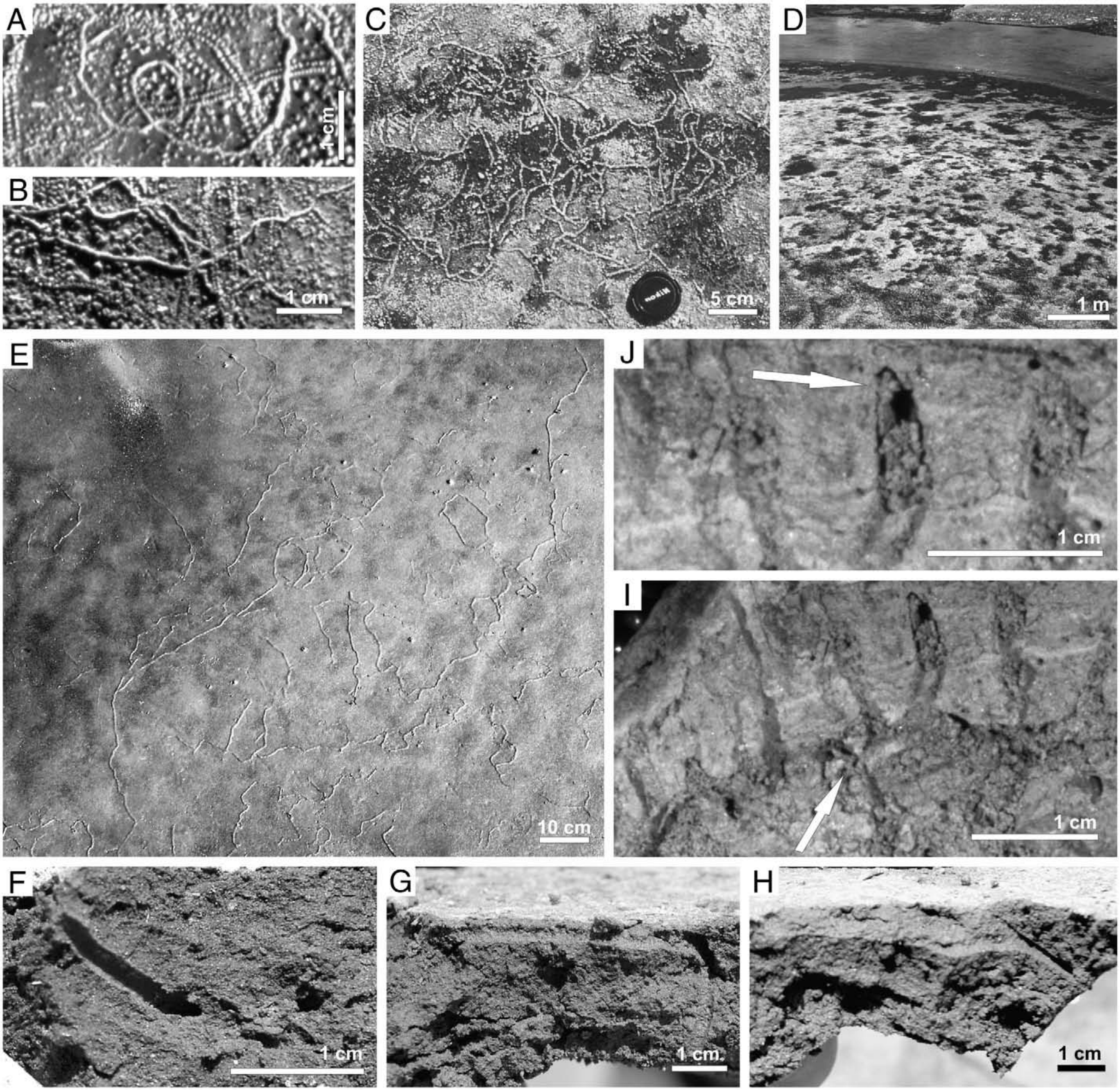

Fig. 7. Photographs of animal traces in Suite 3 and 4. (A) “Salt trace” of incipient *Gordia* isp. Scale bar is 1 cm. (B) “Salt trace” of incipient *Helminthoidichnites* isp. Scale bar is 1 cm. (C) Incipient *Labyrintichnus* isp. on drying surface with salt efflorescence. Scale bar is 5 cm. (D) View of area covered in incipient *Labyrintichnus* isp. adjacent to hot-spring outflow channel. Scale bar is 1 m. (E) Incipient *Labyrintichnus* isp. under shallow film of relatively freshwater. Scale bar is 10 cm. (F) Close up of oblique, endichnial incipient *Labyrintichnus* isp. showing slightly lighter coloured burrow lining/wall. Scale bar is 1 cm. (G) Close up of incipient *?Labyrintichnus* isp. showing vertical burrowing and horizontal tunneling just below sediment–air interface. Scale bar is 1 cm. (H) Close up of incipient *?Labyrintichnus* isp. showing obliquely oriented branching. Scale bar is 1 cm. (I) Close up of walled, branching, endichnial incipient *Vagorichnus* isp. Note main horizontal tunnel with roughly perpendicular vertical branches (arrow). Scale bar is 1 cm. (J) Close up of walled, pelletal backfilled portion of incipient *Vagorichnus* isp. (arrow). Scale bar is 1 cm.

Loburu, where water tables are high and hot-spring fluids (including steam) escape from hundreds of small (cm scale) vents across the delta plain.

4.1.11. Arthropod trackways (Fig. 9A)

4.1.11.1. Description (described from modern traces). Several types of arthropod trackways including incipient *Diplichnites* (3–4 mm wide), incipient *Siskemia* (<5 mm wide), trackways of tenebrionid beetles (*Sepidium* spp.; pers. obs. J.J.S.) (<10 mm wide), and indeterminate trackways A (4–6 mm wide) and B (20 mm wide) were observed as “salt tracks” and in modern lake margin dry silts up to several cm in length (Fig. 9A).

4.1.11.2. Remarks. Epichnial insect trackways are relatively common on the dry silt- to very fine sand-sized sediments near the lake margin, and have been observed as “salt tracks” on top of wet, slightly indurated substrates. The timing when the salt trackways were made initially is unknown, but they were likely made in stabilized substrates (e.g., stabilized by clays or microbial biofilms and/or mats; Scott, 2005; Scott et al., 2007a) and buried to shallow depths by silts.

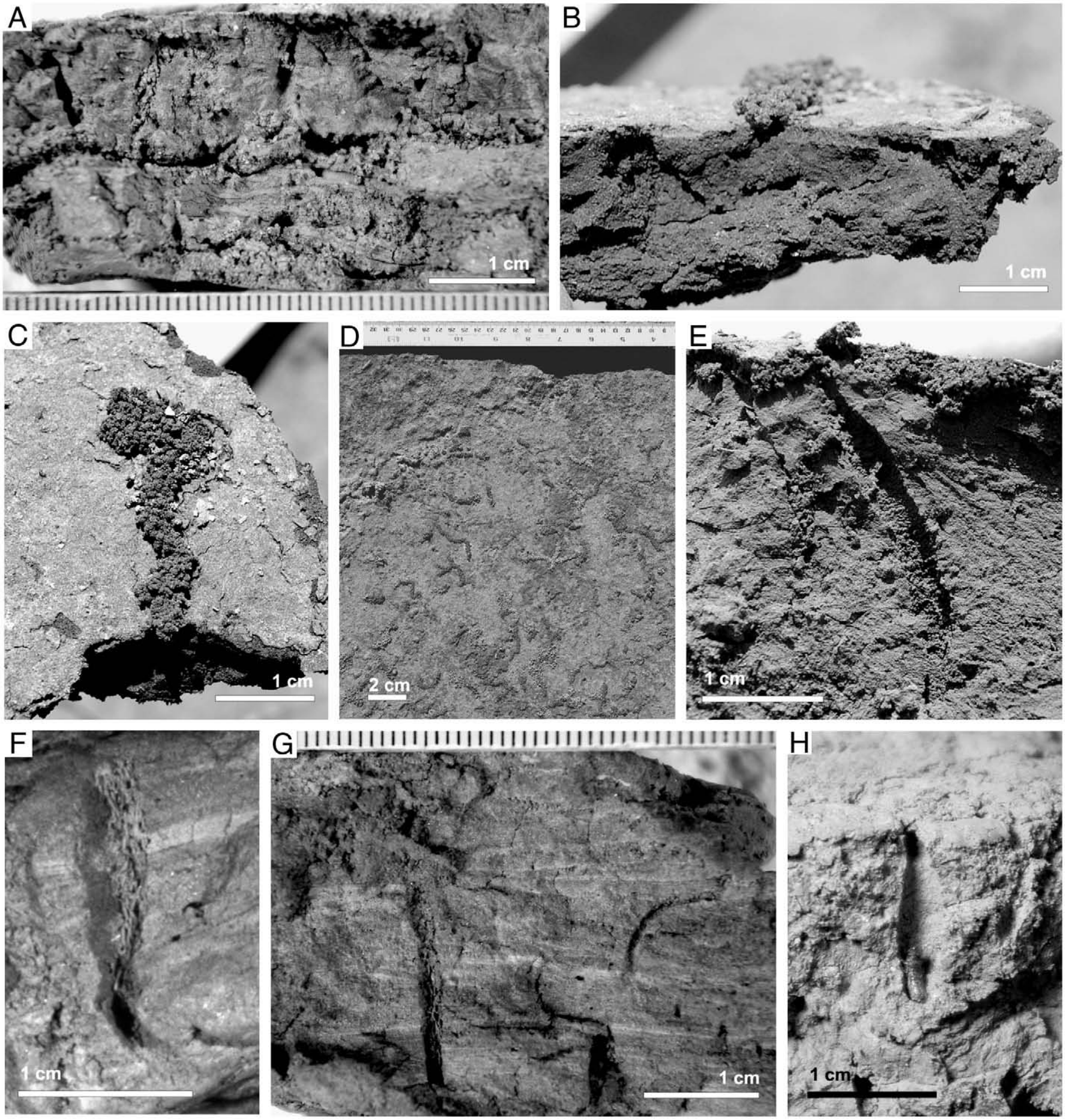

Fig. 8. Photographs of animal traces in Suite 4. (A) Pellet-filled burrow system A. Note lack of walls and main horizontal tunnel with perpendicular vertical burrows. Scale bar is 1 cm. (B) Close up of pellet-filled burrows A at sediment–air interface. Note vertical and horizontal unwalled tunnel leading to the pelleted tunnel roof on the surface. Scale bar is 1 cm. (C) View of pelleted tunnel roof from above. Scale bar is 1 cm. (D) View of many pelleted burrows A from above. Scale bar is 2 cm. (E) Pellet-filled vertical burrow B showing oblique orientation and spherical pellet fill. Scale bar is 1 cm. (F) Close up of pellet-filled vertical burrow C. Note elongate fecal pellets. Scale bar is 1 cm. (G) Pellet-filled burrow C and inverted J-shaped burrow in laminated silt. Scale bar is 1 cm. (H) Tear-drop larval burrow opening to surface. Note larvae still within burrow. Scale bar is 1 cm.

4.1.12. Boxwork burrow systems (Fig. 9B,C)

4.1.12.1. Description (described from modern traces). These burrow systems are primarily made up of horizontal, branching, open, roofed tunnels formed just below the air–sediment interface. Internally, the burrow margins are circular, but the exterior margin is irregular because of the manner of excavating the tunnel by pushing mud to the sides and above. There are two size classes (5–6 mm wide and 10–20 mm wide) of burrows in the horizontal branching system. A vertical component of this burrow system was also observed in indurated substrates near the present-day shoreline to have depths of up to ~30 cm from the uppermost surface to the base of the burrow system at the water table (pers. obs. J.J.S., 2002).

4.1.12.2. Remarks. Scott et al. (2007a) described modern boxwork burrow systems at the Loburu delta, and during subsequent fieldwork

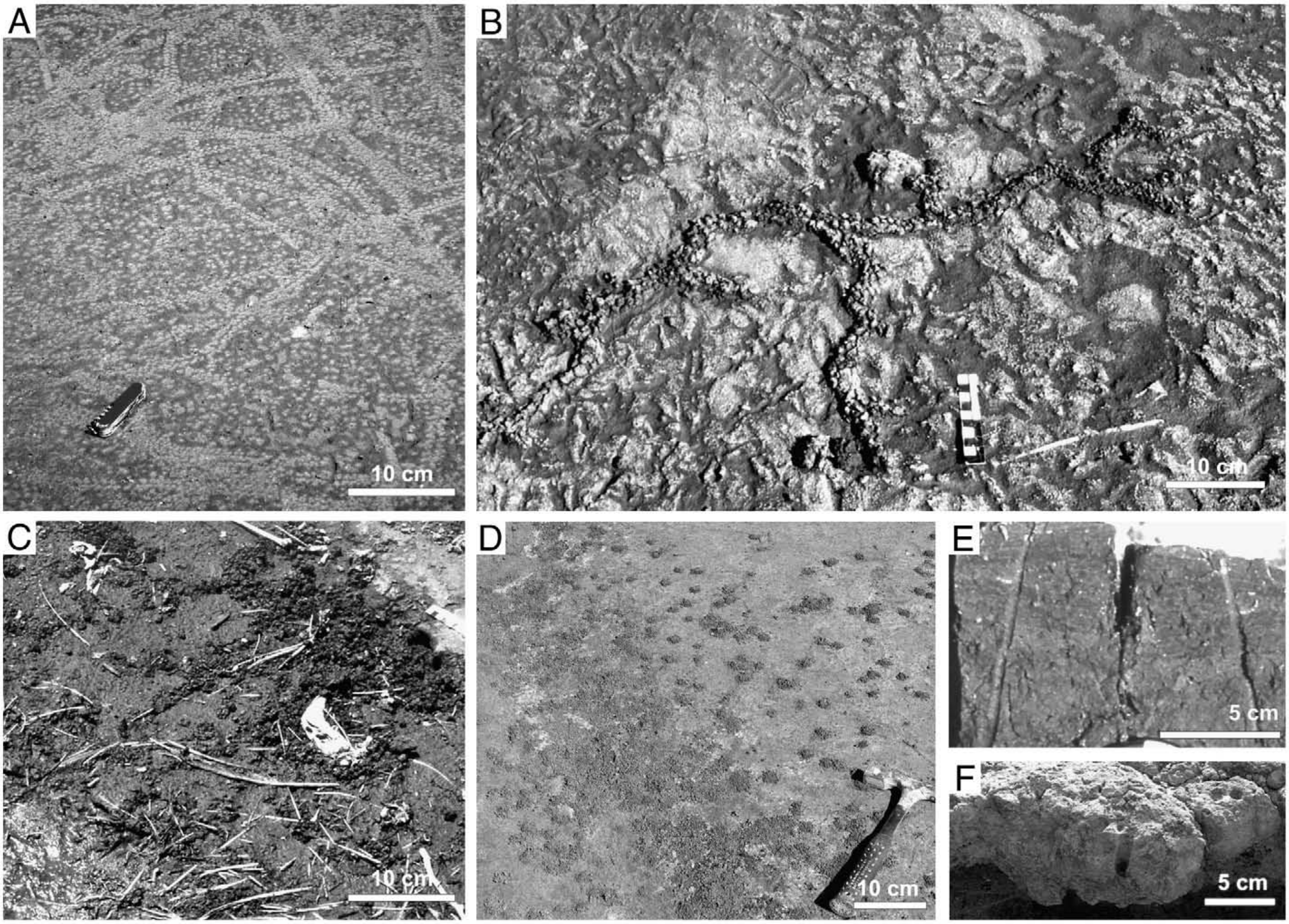

Fig. 9. Photographs of animal traces in Suite 4. (A) Surface with insect trackways (indeterminate ichnotaxa), Loburu delta. Scale bar is 10 cm. (B) Horizontal portion of branching boxwork burrows. Note irregular tunnel roof cross-cutting flamingo-trampled surface texture. Scale bar is 10 cm. (C) Boxwork burrow bioturbation and horizontal tunnels at shoreline, Loburu delta. Scale bar is 10 cm. (D) View of tumuli (piles of excavated material) on surface associated with tiger beetle vertical burrows. Scale bar is 10 cm. (E) Oblique vertical burrow of tiger beetles. Scale bar is 5 cm. (F) Fossil example of 12 mm diameter *Skolithos* isp. in exhumed surface at central Loburu delta. Scale bar is 5 cm.

similar traces were also found preserved in the sediments of the exhumed surface. The fossilized examples show the branching patterns and irregular margins to the burrows, but do not retain the tunnel roofs.

4.1.13. Incipient Skolithos ispp. (Fig. 9E,F)

4.1.13.1. Description (described from modern and fossil traces). Vertical to oblique, unlined/unwalled, unbranched burrows in three size classes: 1–3 mm, 4–6 mm, and 10–12 mm. The depths of the burrows are ~5–20 cm. The burrow margins may be ornamented with “wrinkles” if made in slightly indurated substrates. Modern examples may or may not be associated with pelleted tumuli at the sediment surface (Fig. 9D).

4.1.13.2. Remarks. Beetle larvae and adults and spiders are the likely tracemakers of incipient *Skolithos* ispp. at Lake Bogoria. Tiger beetle (Coleoptera: Cicindelidae) larvae are attributed to the 1–3 mm size class, tiger beetle adults to the 4–6 mm size class (Fig. 9E), and unknown beetles, possibly Staphilinid adults, or spiders to the 10–12 mm size class (Fig. 9F). Tracemaker suggestions are based on personal field observations (tiger beetles and spiders), Smith and Hein (1971), and Harper et al. (2003).

4.1.14. Earwig larval burrow systems (Fig. 10A–C)

4.1.14.1. Description (described from modern traces). Open or pellet-filled, branching three-dimensional burrow systems. Burrows range from 4 to 8 mm in diameter, and may have ornamented burrow margins depending on substrate consistency. Portions of the burrows may be backfilled with spherical pellets that tend to be darker than the host sediment (Fig. 10A).

4.1.14.2. Remarks. Earwig adults and larvae have been observed (pers. obs. J.J.S.) burrowing into indurated substrates at the present margin of Lake Bogoria, including exhumed surfaces. Depending on the water content and consolidation of the substrate, the traces may be considered as *Spongeliomorpha* isp. because they can have transverse to oblique “wrinkles” (Fig. 10A,C).

4.1.15. Incipient Spongeliomorpha isp. (Fig. 10A,C)

4.1.15.1. Description (described from modern traces). Unwalled, vertical to oblique, locally branching burrows and burrow systems with ornamented burrow margins that show wrinkle-like transverse patterns. Burrows may be open, but are commonly filled with dark pelletal material (<1 mm) distinctly different from the exhumed surface substrate. The burrows range from 4 mm to 8 mm in diameter.

4.1.15.2. Remarks. Incipient *Spongeliomorpha* were found in the exhumed surface in wet to saturated areas at the present-day shoreline at Emsos, and in one example, incipient *Spongeliomorpha* isp. was directly associated with open, unornamented burrows presumably made at approximately the same time (Fig. 10A).

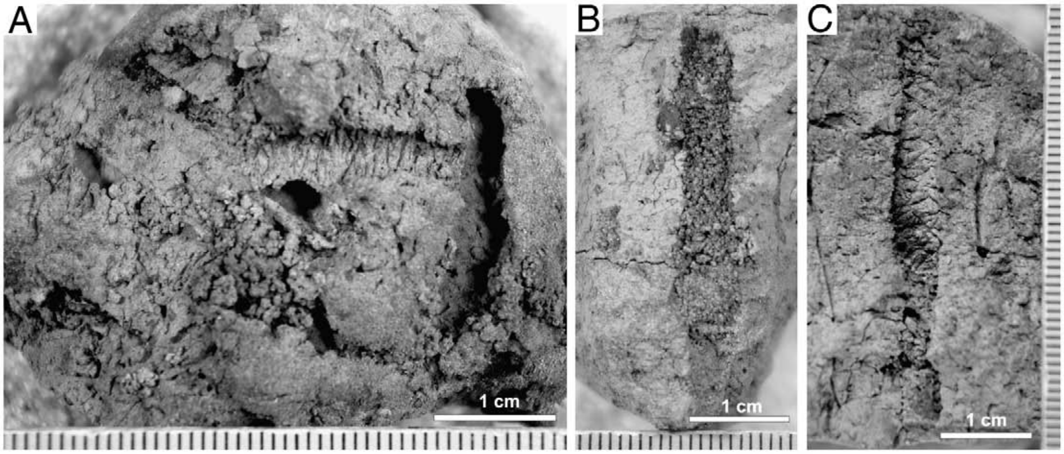

Fig. 10. Photographs of earwig burrows (Suite 4) into the moist exhumed surface at the present-day shoreline at Emsos. (A) Branching burrow system showing contemporary incipient *Spongeliomorpha* isp. branching with open burrow and associated with pellet-filled burrows. Scale bar is 1 cm. (B) Vertical pellet-filled burrow of earwigs. Note different sizes of pellets, but generally spherical shape, and the darker colour of the pelleted infill. Scale bar is 1 cm. (C) Incipient *Spongeliomorpha* isp., partly pellet-filled. Scale bar is 1 cm.

4.1.16. *Planolites* isp. (Fig. 11A–C)

4.1.16.1. Description (described from fossil material). Unlined, horizontal to oblique, straight to curving, endichnial burrows (6–8 mm wide) filled with non-pelletal and pelletal material different in colour from the host sediment but of the same grain size (Fig. 11A–C).

4.1.16.2. Remarks. It is unclear whether or not the *Planolites* examples from Lake Bogoria were passively or actively filled, although it is likely that they were actively backfilled because the burrows are horizontal and preserved as endichnia. Examples are found primarily in fine sandstones of the exhumed surface on Sandai Plain.

4.1.17. *Palaeophycus* isp. (Fig. 11D, E)

4.1.17.1. Description (described from fossil material). Smooth-walled, horizontal to oblique, straight to curving, endichnial burrows (<~12 mm wide) that are either open or filled with material similar to the host sediment.

4.1.17.2. Remarks. These burrows are associated with other traces in the exhumed surface at Sandai Plain such as *?Beaconites* isp., which also have smooth walls, but are backfilled (e.g., Keighley and Pickerill, 1994; Smith et al., 2008).

4.1.18. *?Beaconites* isp. (Fig. 11C)

4.1.18.1. Description (described from fossil material). Thick-walled, meniscate backfilled, straight, unbranched, horizontal burrows preserved as endichnia, and are ~8 mm in diameter including the wall. Infill is partly pelleted, and partly composed of the poorly sorted host sediment.

4.1.18.2. Remarks. *?Beaconites* isp. burrows were found in porous sandstones of the exhumed surface on Sandai Plain, and based on the nature of the "pelleted" and poorly sorted host sediment infill. In one example, *?Beaconites* isp. grades directly into *Taenidium* isp. A (Fig. 11F).

4.1.19. *Taenidium* isp. A (Fig. 11F, G)

4.1.19.1. Description (described from fossil material). Unwalled, meniscate backfilled, straight to curving horizontal to oblique, unbranched endichnial burrows, from 5–6 mm in diameter to more than 2 cm. Infill may be partly pelleted, and partly composed of the poorly sorted host sediment.

4.1.19.2. Remarks. *Taenidium* is more common than *?Beaconites* in the exhumed surface at Lake Bogoria, and in one example the two ichnotaxa are continuous and transitional with one another (Fig. 11F). Meniscate backfilled traces at Lake Bogoria were observed only in the exhumed surface on Sandai Plain.

4.1.20. *?Taenidium* isp. B (Fig. 11H)

4.1.20.1. Description (described from fossil material). Concentrically backfilled endichnial burrows composed of adjacent oval-shaped "packets" (i.e. asymmetrical groups of thin, indistinct meniscate fill, *sensu* Smith et al., 2008) approximately 2–3 cm in diameter without constructed walls, directly associated with open, unwalled burrows. The meniscate fill is composed of pelletal (~1 mm) and non-pelletal material that is homogeneous with the host sediment.

4.1.20.2. Remarks. The morphology of these traces is similar to *Taenidium* isp. in that they are unwalled, and the fill is "meniscate" or "concentric" and composed partly of pelleted material. The burrows appear to be formed by excavation, with the concentrically arranged burrow fill representing the changing position of the burrow margin as excavation continued and caused the previously occupied space to be filled. This behaviour and morphology are shown in the "Adhesive Meniscate Burrows" of Smith et al. (2008), but the traces at Bogoria differ in that they do not show "chamber walls" and may also be filled with pelletal material. In one example from Bogoria, the concentrically laminated "packets" and an open, ~1.5-cm wide obliquely oriented burrow appear to be part of the same burrow system (Fig. 11H).

4.1.21. Indeterminate trace fossils. (Fig. 11I)

4.1.21.1. Description (described from fossil material). Open, pellet-walled endichnial burrow ~7 mm in diameter that shows lateral movement of the open burrow and wall, leading to an almost spreiten-containing structure.

4.1.21.2. Remarks. These open burrows are associated with *Taenidium* isp. B, and the spreiten may have resulted from the lateral movement of a walled burrow or gallery.

4.1.22. *Termitichnus* isp. (Fig. 12A–E, ?G)

4.1.22.1. Description (described from fossil material). Roughly spherical to oval balls (chambers) with concentric fill composed of material

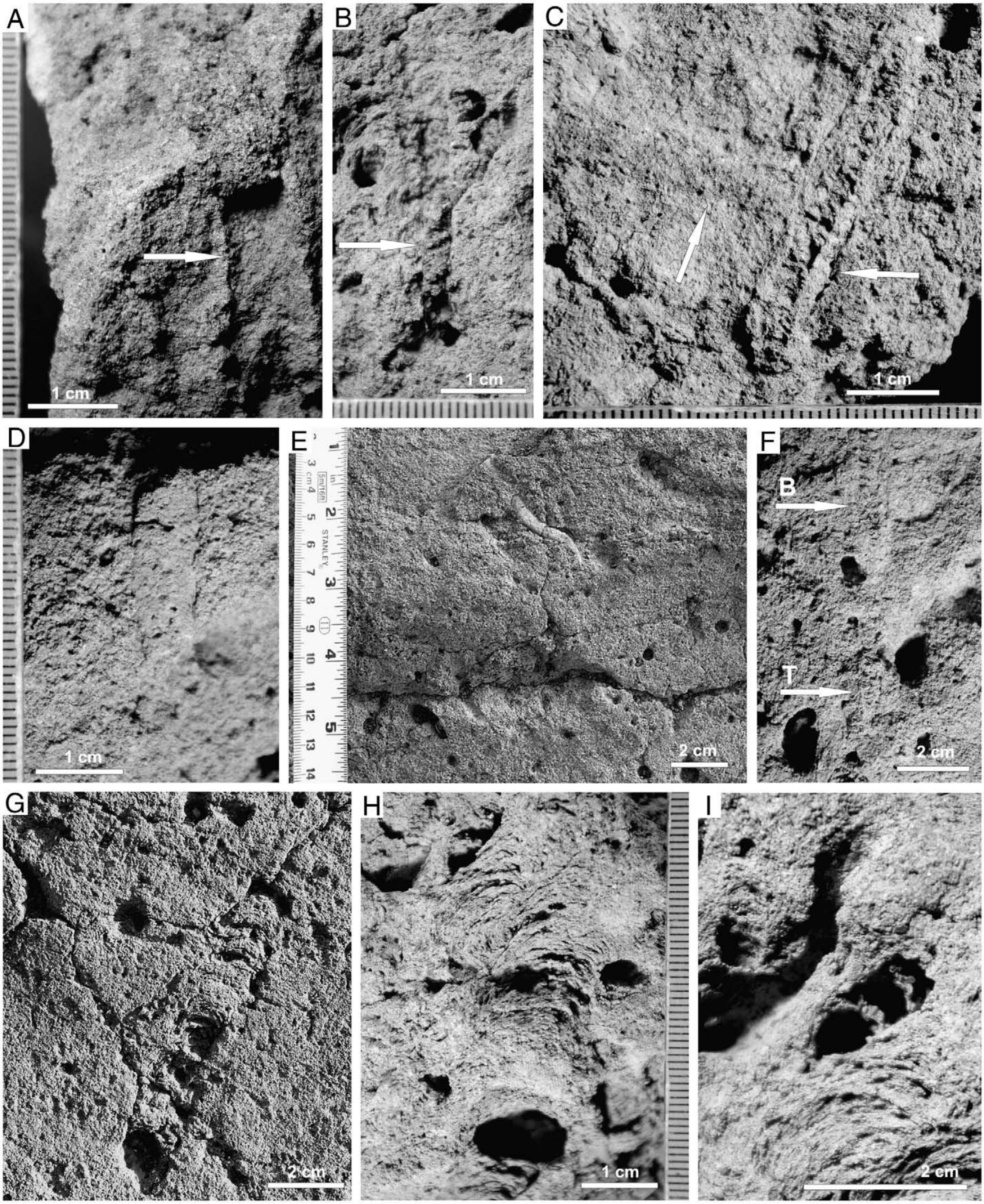

Fig. 11. Photographs of animal traces in Suites 4 and 5, Sandai Plain. (A) *Planolites* isp. (arrow). Scale bar is 1 cm. (B) Pellet-filled burrow, *Planolites* isp. (arrow). Scale bar is 1 cm. (C) *Planolites* isp. (arrow) crosscut by *?Beaconites* isp. (arrow) Scale bar is 1 cm. (D) *Paleophycus* isp. Scale bar is 1 cm. (E) Field photo of *Paleophycus* isp. in uppermost Loboi Silts, Sandai Plain. Scale bar is 2 cm. (F) Transition area between *?Beaconites* isp. (B) and *Taenidium* isp. A (T). Scale bar is 2 cm. (G) Close up of large *Taenidium* isp. A. Scale bar is 2 cm. (H) Close up of *?Taenidium* isp. B showing concentrically backfilled "packets" and associated open burrow. Scale bar is 1 cm. (I) Close up of indeterminate isp. showing pelleted walls (?spreiten) of open burrow. Scale bar is 2 cm.

similar to the host sediment. Chambers range from ~5–25 cm in diameter. Some examples show an internal sphere with a smooth lining (Fig. 12A). The chambers are associated with straight, walled connecting galleries approximately 2–3 cm in diameter, although these galleries were not directly observed exiting the chambers (Fig. 12B, C). Small (5–6 mm diameter), open diffuse galleries are directly associated with the chambers (Fig. 12C–E).

4.1.22.2. Remarks. These traces are similar to *Termitichnus simplicidens* described from Egypt (Genise and Bown, 1994), which were interpreted as of termite chambers connected by straight, simple galleries and having a rind of sediment arranged concentrically. The density of chambers that are connected by these galleries is not sufficiently high for the traces to be assigned to *Vondrichnus* isp. (cf. Genise and Bown, 1994).

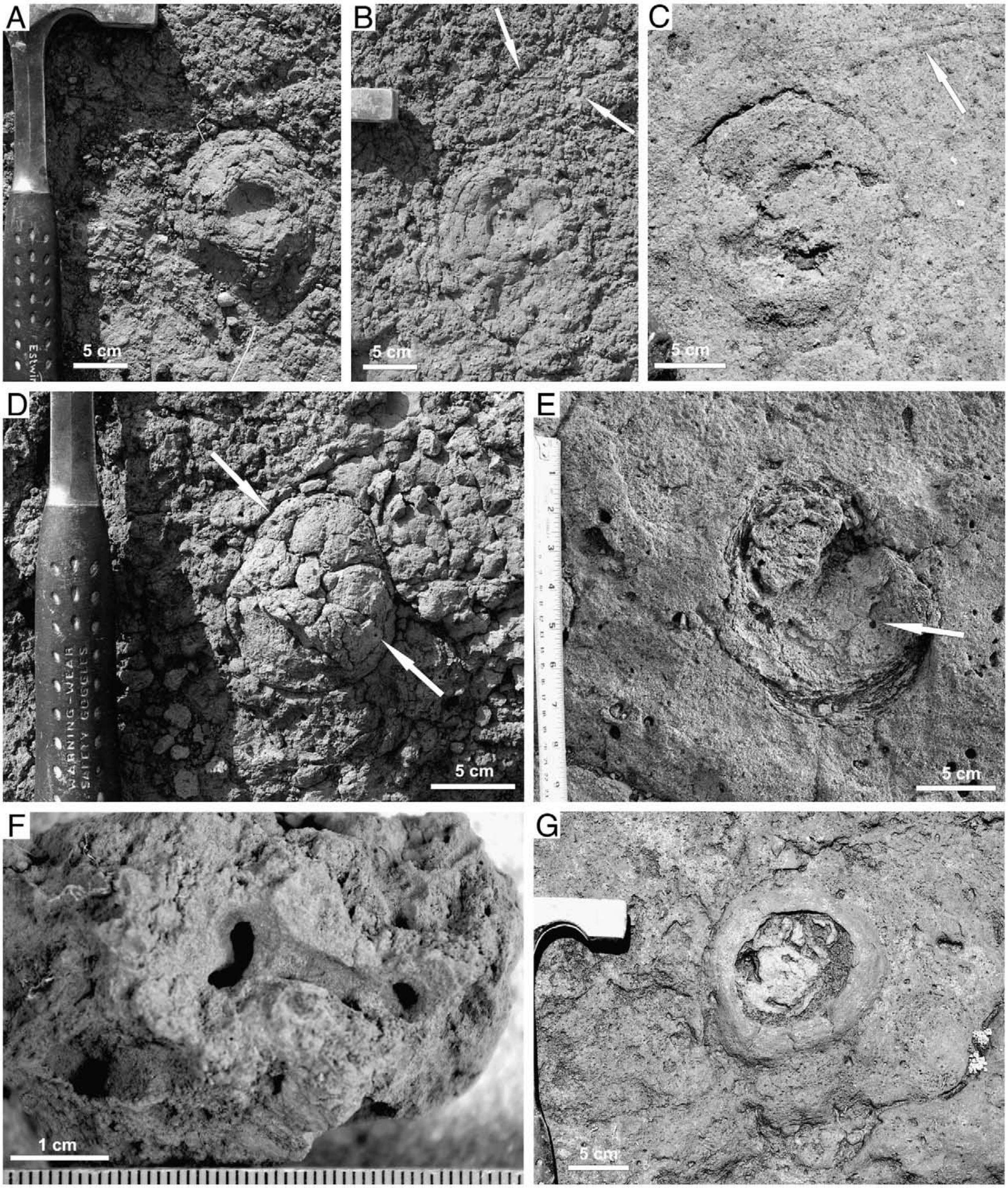

Fig. 12. Photographs of animal traces in Suite 5. (A) *Termitichnus* isp., showing concentric fill and spherical, smooth-walled core, central Loburu delta. Scale bar is 5 cm. (B) *Termitichnus* isp., associated with open, walled galleries (*Palaeophycus* isp.) (arrow), central Loburu delta. Scale bar is 5 cm. (C) *Termitichnus* isp., associated with walled, backfilled gallery (*?Beaconites* isp.) (arrow), Sandai Plain. Scale bar is 5 cm. (D) *Termitichnus* isp., showing spherical shape and open diffuse galleries (arrows). Scale bar is 5 cm. (E) *Termitichnus* isp. showing concentric fill and open diffuse galleries (arrow), Sandai Plain. Scale bar is 5 cm. (F) Modern ant nest burrow system into exhumed surface, Emsos. Scale bar is 1 cm. (G) Spherical nest at Emsos: *?Attaichnus* isp. or *Termitichnus* isp. Scale bar is 5 cm.

4.1.23. Ant nests (Fig. 12F,G)

4.1.23.1. Description (described from modern and fossil material). Open, three-dimensional burrow networks composed of small, somewhat tabular chambers (<3 cm diameter) and intersecting branched tunnels of various sizes (~3–10 mm diameter) that have smooth burrow margins.

4.1.23.2. Remarks. Ant nests were observed both as fossil examples in the exhumed surface on Sandai Plain and also as modern nests excavated into the exhumed surface as a shallow, horizontal maze within 10 m of the present-day shoreline at Emsos. More work is needed to associate these Bogoria traces with other ichnotaxa attributed to ant or termite tracemakers. The modern example is similar to *Socialites* isp. Roberts and Tapanila, 2006 because it is also a burrow network of anastomosing galleries that form an irregular boxwork (Fig. 12F). The examples at Bogoria also strongly resemble the fragments of termite “hives” reported from the Laetoli Formation by Sands (1987) (Fig. 12F). Individual chambers connected by galleries have not been clearly identified from the exhumed surface, except one example at Emsos that is similar to *Attaichnus* isp. Laza, 1982 (Fig. 12G).

4.2. Vertebrate traces preserved in the exhumed surface

4.2.1. Flamingo nest mounds and associated surfaces (Fig. 13A–D)

Lesser and greater flamingos (*Phoeniconaias minor* and *Phoenicopterus ruber*) are normally abundant at Lake Bogoria, and heavily modify the littoral and lake margin sediments by their nest-building activities and trampling of the substrate (Scott et al., 2007a). Flamingo activities and their traces are concentrated along the shoreline, and nests are usually built from wet mud in very shallow lake waters as the lake is receding following higher lake levels in the rainy seasons (e.g., 2001, Fig. 13D). Flamingo nest mounds are trampled and compacted during nest-building and, together with the muddy surfaces on which the nests are built, become relatively resistant to erosion by further trampling, sheetfloods, deflation, and even flooding by the lake. Modern flamingo nest mounds are found near fresh to brackish water sources at Lake Bogoria on the Sandai and Loburu deltas (Fig. 13A, B). Fossil flamingo nest mounds and their associated surfaces are found in the Bogoria Silts, and also in some exhumed surfaces (Fig. 3D; cf. Scott et al., 2008). Low lake levels during 2006 revealed flamingo-modified exhumed surfaces around a much greater portion of the shoreline than just the main deltas (Fig. 13C).

4.2.2. Vertebrate footprints

Vertebrate footprints, including mammals, birds and reptiles, are found around the modern shoreline at Lake Bogoria, but are most common on Sandai Plain and Loburu, particularly near sources of freshwater. Details of the modern assemblage composition, distribution, and taphonomy were given by Scott et al. (2007a). Fossil vertebrate footprints were from an exhumed surface on Sandai Plain (Scott et al., 2008). Further erosion between 2002 and 2007 revealed many more poorly preserved mammal footprints in the same surface (Fig. 3A). The latter footprints were probably deeply impressed into a

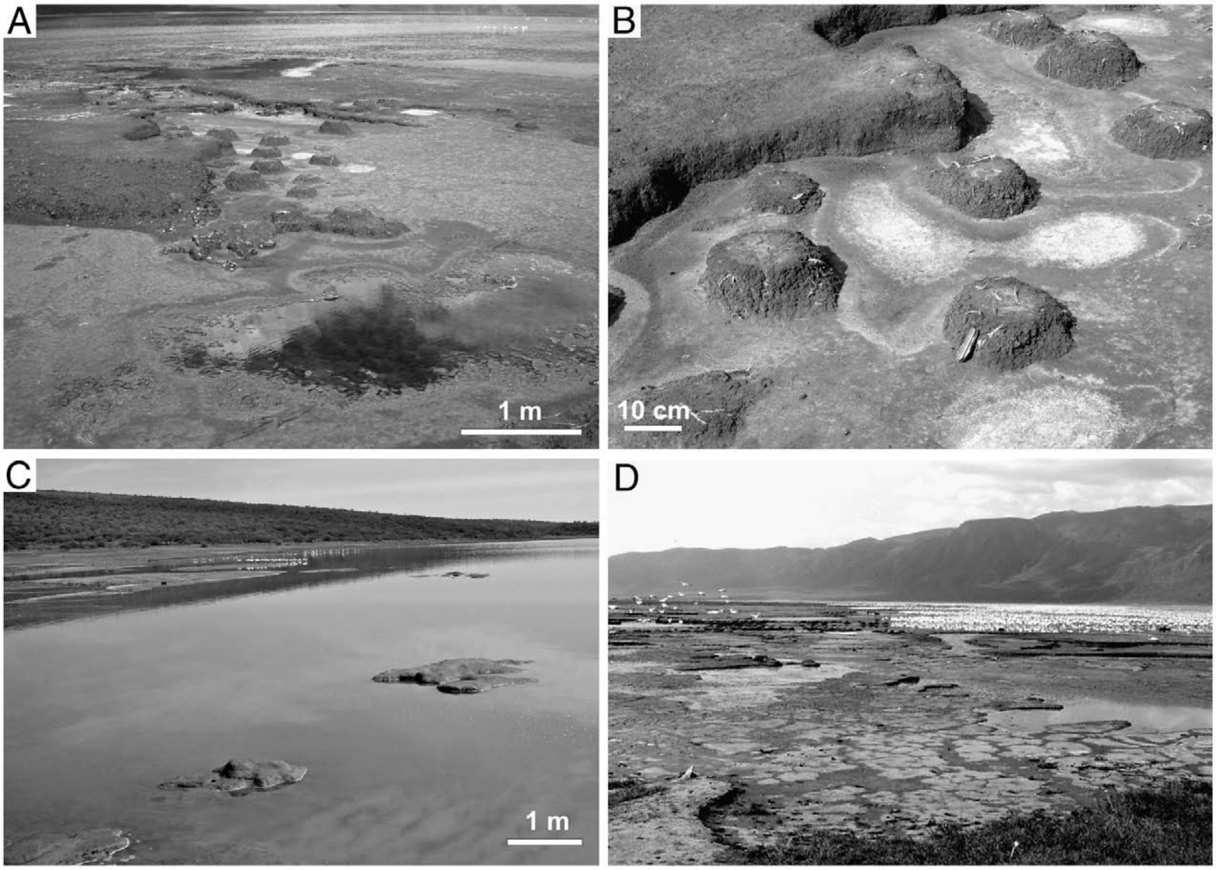

Fig. 13. Flamingo nest-mounds and modified surfaces of Suite 2. (A) Modern nests built where wet mud is available, adjacent to older, compacted surfaces at southern Loburu shoreline in 2006. Note the pool of lake water in foreground, which shows flamingo footprints in trampled mud. Scale is 1 m. (B) Close up of modern flamingo nest-mounds in drying muds as the lake recedes, southern Loburu delta. Scale bar is 10 cm. (C) Flamingo-modified exhumed surface exposed north of the Loburu delta in 2006. Scale bar is 1 m. (D) Active flamingo nest-mound building by lesser flamingos at the southern Loburu delta, 2001. Flamingos in background for scale.

more saturated substrate closer to the present shoreline than those previously described.

4.3. Trace suites

Five suites of animal traces are recognized in the modern lake margin substrates and the exhumed surfaces in the Bogoria basin, each reflecting variations in substrate moisture levels, proximity to shoreline and depth of the water table, as well as other substrate characteristics such as grain size, salinity, cohesion, presence of microbes, and food source. Together, the suites are representative of the *Mermia* and *Scoyenia* ichnofacies, although not all suites can be easily correlated with any of the ichnofacies (e.g., "chironomid" suite).

4.3.1. Suite 1: "chironomid" suite

The first suite comprises the traces of chironomid larvae, which are represented by modern, fragile, organic-rich horizontal tube structures as well as small (<3 mm diameter) vertical burrows into the exhumed surfaces, and larger (<1 cm diameter) shallow "pits". These may represent their "feeding territories" on microbial mats, accumulated detritus, and the uppermost sediment of the exhumed surface (Fig. 6; Chaloner and Wotton, 1996). Although not seen in modern sediments or in the exhumed surface, it is possible that the vertical, U-shaped, and Y- or J-shaped burrows of chironomid larvae into soft sediment (e.g., *Polykladichnus*) could be found in shallow lacustrine cores taken offshore from water >1 m deep, or beyond the depth to which flamingos wade in shoreline sediments. *Paratendipes* sp. is the only metazoan species in Lake Bogoria today (Harper et al., 2003). If preserved, their traces would form a very low diversity assemblage that represents subaqueous lacustrine substrates above the chemocline (the maximum depth to which chironomids were found by Harper et al., 2003), but below the depth at which flamingos trample the soft shoreline substrate (<~1 m) or feed from the chironomid-rich muds (in the case of *Phoenicopterus ruber*, Jenkin, 1957).

4.3.2. Suite 2: "flamingo nest mound" suite

The second suite is associated with saturated and shallow subaqueous substrates at the shoreline during receding lake levels. It is not necessarily associated with springs, but may be loosely associated with freshwater sources in general including lake margin hot springs and rivers (e.g., the Sandai, Emsos, and Parkirichai rivers). This suite comprises flamingo nest-mounds, and includes flamingo footprints, other bird footprints, and flamingo-trampled surfaces associated with the nests. This suite is comparable to the "shore-bird ichnofacies" (Lockley et al., 1994) and the *Grallator* ichnofacies of Hunt and Lucas (2007), and the consistent association of this suite with the "*Scoyenia* suite" supports the suggestion that it may be best considered as an ichnosubfacies of *Scoyenia* (*sensu* Melchor et al., 2006). The Lake Bogoria example is dominated by flamingo traces, shows very low ichnodiversity (cf. Hunt and Lucas, 2007), and includes nest structures as well as footprints.

4.3.3. Suite 3: "Mermia-like" suite

The third suite of animal traces is roughly consistent with an impoverished *Mermia* ichnofacies (cf. Buatois and Mángano, 1995). The suite comprises trails and tunnels present in water-saturated substrates and in extremely shallow subaqueous areas (<~3 cm depth) associated with fresh to slightly brackish, point-sourced springs and benthic microbial mats and films. Incipient *Gordia* isp., incipient *Helminthoidichnites* isp., incipient *Labyrintichnus* isp., incipient *Vagorichnus* isp., and shallow subaqueous flamingo and mammal footprints that are stabilized by benthic microbial mats are representative traces of the suite. Plant roots that are preserved as holes in microbial mats (Fig. 5C; Owen et al., 2008, type 3, Fig. 4G) are associated with this suite.

4.3.4. Suite 4: "Scoyenia-like" suite

The fourth suite is the most diverse and is broadly consistent with the *Scoyenia* ichnofacies. It is represented mainly by the horizontal and vertical burrows, trackways, and tunnels of beetle and earwig larvae and adults (pers. obs. J.J.S.), and also by a diverse assemblage of vertebrate footprints including mainly birds and mammals (Scott et al., 2007a, in press). *Skolithos* ispp., incipient *Vagorichnus* isp., incipient *Diplichnites*, incipient *Diplodichnus*, incipient *Siskemia*, *Sepidium* trackways, inverted J-shaped burrows, tear-drop burrows, pellet-filled burrows A, B, and C, boxwork burrow systems, *Planolites* isp., and *Spongeliomorpha* isp. are included in this suite. This assemblage is associated with moist to wet substrates in areas with high water tables and cohesive substrates, and was also found near fresh and brackish water sources including hot springs and rivers. *Spongeliomorpha* isp., *Skolithos* ispp., and boxwork burrow systems with ornamented burrow margins are also representative of drying, firmer, and slightly indurated substrates.

Rhizoliths associated with the fourth suite include branching, dark, organic-lined root-hair pores and open holes from rhizomous wetland sedges and grasses (cf. Owen et al., 2008; Fig. 5H–L). This suite of animal traces is also associated with root stems and rhizoliths preserved by opaline silica, fluorite and calcite, the precipitation of which was partly influenced by hot-spring fluids (Owen et al., 2008; Fig. 5A–D). Animal and plant traces from this suite may be found around the entire lake, but environmental factors that restrict biodiversity, such as increased salinity, strongly affect the precise make-up of the suite in the modern setting. For instance, the Loburu delta contains all the trace types listed above, whereas the Sandai Plain, which does not have hot springs, contains a much less diverse assemblage of vertebrate footprints, and rare invertebrate burrows (Scott et al., 2007a). Incipient *Skolithos* isp. formed by tiger beetle adults and larvae (pers. obs. J.J.S.; cf. Stanley and Fagerstrom, 1974) are widespread around the lake, but often comprise a monospecific example of this trace suite.

4.3.5. Suite 5: "Termitichnus" suite

The fifth suite, recognized in the exhumed surfaces around Lake Bogoria, is composed of *Planolites* isp., *Palaeophycus* isp., *?Beaconites* isp., *Taenidium* isp. A, *Taenidium* isp. B, indeterminate isp., *Termitichnus* isp., and ant nests. Plant traces associated with this suite include calcite root casts and zeolitic root mats of grasses (cf. Renaut, 1993; Fig. 5E). This suite is comparable to the assemblage from semi-arid Late Pleistocene South Africa that led to the proposal of the *Termitichnus* sub-ichnofacies by Smith et al. (1993). Although subsequent work by Genise et al. (2000) suggested that the *Termitichnus* ichnofacies should be abandoned (cf. Buatois and Mángano, 1995), it appears that the lack of hymenopteran and beetle nests is valuable information that could be lost if the assemblage reported here was included in the alternative *Coprinisphaera* ichnofacies.

5. Preservation and representation of trace suites in the exhumed surfaces

The exposed portion of the exhumed surface landward of the modern shoreline does not preserve traces from the *Mermia*-like suite (Suite 3), which is associated with freshwater, saturated to subaqueous substrates, and benthic microbial mats and biofilms. It is possible that Suite 3 traces are present but submerged or covered by younger deposits. Any small, delicate *Mermia*-like traces from Suite 3 would probably have been destroyed through surface-trampling by flamingos and mammals or by the formation and deflation of efflorescent salts during periods of low lake level. Tube structures of chironomid larvae (Suite 1) are expected to suffer the same fate as the fragile *Mermia* traces. Extensive flamingo trampling of the shallow, soft sediment, subaqueous zone where chironomids live in Lake Bogoria (Harper et al., 2003) is also expected to have completely destroyed any chironomid larval burrows (e.g., *Polykladichnus*, Gingras et al., 2007), although their head parts could be preserved in the sediment. Chironomid burrows and pits into previously desiccated and indurated substrates, however, are expected to survive, although their distinction from similar-sized tiger beetle vertical burrows (~3 mm diameter) would be difficult.

Flamingo nest mounds from Suite 2 are preserved in the exhumed surface at the northern part of the Loburu delta, Emsos delta, and also in the extensive mudflat deposits exposed in northern Loburu during low lake levels in 2006 (Fig. 3C). Irregular surfaces that appear to have been modified by flamingos are also preserved in the exhumed surface on Sandai Plain (Scott et al., 2008) and in the exhumed surfaces of the central Loburu delta. No clear flamingo footprints are preserved in the exhumed surfaces, probably because the high numbers of trampling flamingos and extreme bioturbation commonly cause destruction of their prints in shoreline sediments. This same trampling, however, can promote the stabilization of the nest mounds and associated surfaces by compaction.

Several trace types from the *Scoyenia*-like Suite 4 are preserved in the exhumed surfaces at the Emsos delta, the central and northern parts of the Loburu delta, and at Sandai Plain. These include pellet-filled horizontal burrows, horizontal and branched expressions of the boxwork burrow systems, *Skolithos* isp., *Planolites* isp., and several types of vertebrate footprints (Scott et al., 2008). Plant trace fossils from Suite 4 are well represented in the exhumed surfaces and include silica rhizoliths, calcite root casts, and open root-hair systems. Meniscate backfilled burrows, possible termite and ant traces, as well as zeolitic and calcitic root-mats, calcite root casts, and well developed pedogenic features are characteristic of Suite 5 in the exhumed surfaces at Sandai Plain, the central part of the Loburu delta, and at Emsos.

Finally, the exhumed surfaces also include some modern traces from Suites 1, 2 and 4. Where the surface near the shoreline is sufficiently wet to encourage the activities of beetle larvae and earwigs, new traces are being formed in older, weakly lithified exhumed sediments. Rhizomes of salt-tolerant littoral wetland sedges (*Cyperus laevigatus*) and grasses (*Sporobolus spicatus*) as well as the branching root-hair systems of grasses penetrate the older sediments. Other modern traces that are overprinting the moist to wet, indurated exhumed surfaces near the present-day shoreline include the tiny burrows and "pits" of chironomids (Suite 1) and recent flamingo nest-mounds added to the resistant surfaces using wet mud and/or just

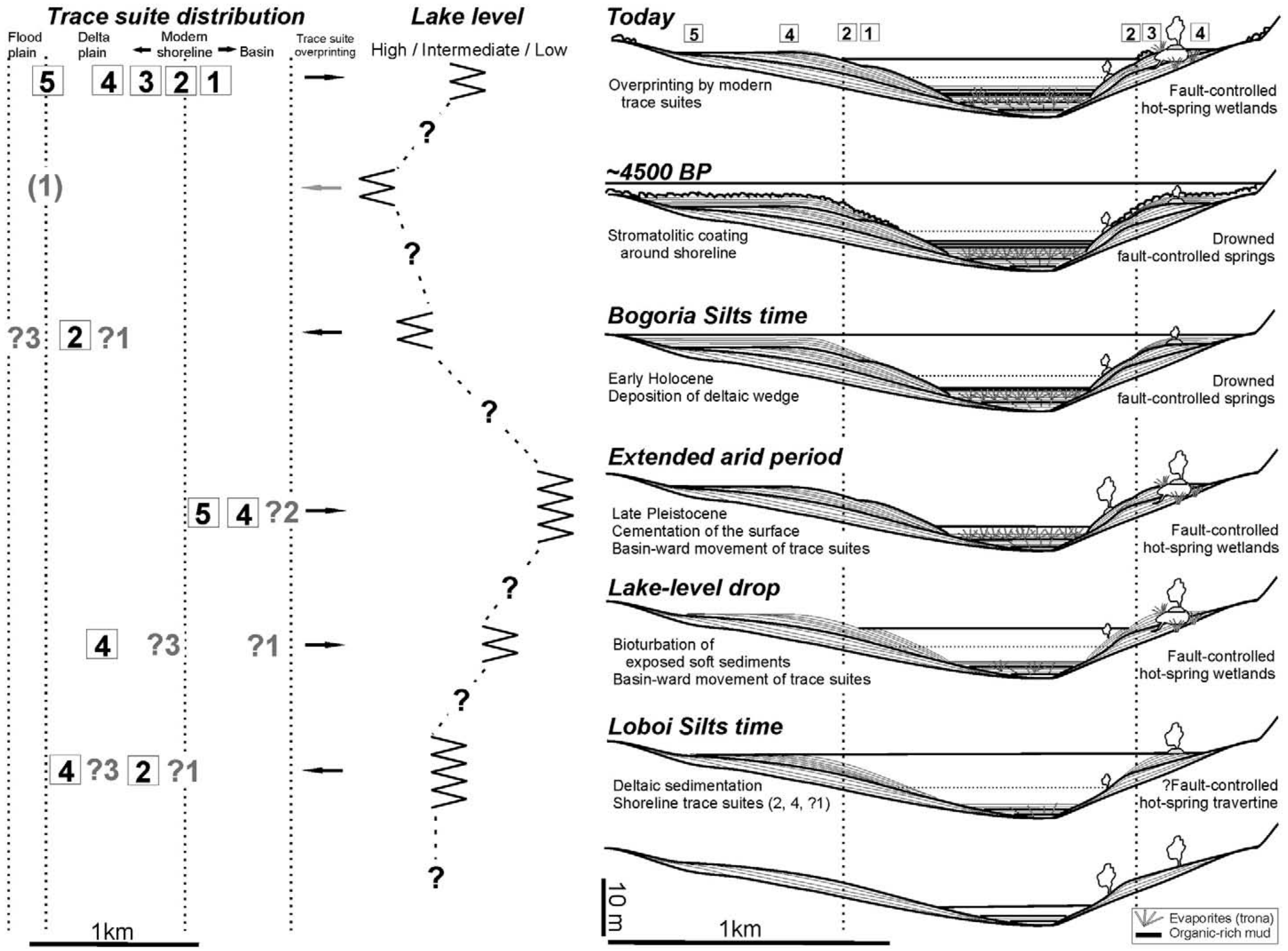

Fig. 14. Schematic reconstruction of lake level changes in the Bogoria basin based on trace fossil suites and previous work on the sedimentology of the lake basin (e.g., Tiercelin et al., 1981; Renaut, 1982; Tiercelin and Vincens, 1987; Renaut, 1993; Renaut and Tiercelin, 1994). The chronology of lake level change is poorly constrained due to difficulties in ^{14}C dating. At left, the lateral movement of trace suites relative to the modern shoreline and direction of overprinting onto the exhumed surfaces is shown with inferred lake levels. Numbered trace suites (in black) are described in the text. Trace suites in grey are either preserved in sediments other than the exhumed surfaces (e.g., in stromatolitic crust), or are expected to have been present originally but are not preserved in the exhumed surface.

feathers where the substrate is too hard (e.g., Fig. 3D) (Suite 2). Incipient *Spongeliomorpha* isp., earwig burrows, pellet-filled burrows A, *Skolithos* isp., boxwork burrow systems, ant nests, and plant roots of Suites 4 and 5 are also reworking the surfaces where lithification is weak. Dry areas of the exhumed surfaces on Sandai Plain and at the central Loburu delta are presently being overprinted by grass roots, but apparently by few burrowing insects.

Taphonomic processes that affect the exposed exhumed surfaces today are primarily destructive and cause the disintegration of the surface by efflorescent salt crystallization near the shoreline where there is capillary evaporation of saline pore-waters (e.g., Fig. 3D), and by the continued trampling by flamingos and other vertebrates such as bovids. Pedogenic processes, such as destruction by roots, and wetting and drying of the surface, lead to the formation of peds and the break-up of the surface. Wave erosion along the shoreline during repeated, small-scale lake level rise has greatly contributed to exposing the surface, but has also led to the destruction of the uppermost and possibly most delicate portions of it (e.g., Fig. 3B, E, G). Taphonomic processes that contribute to the further preservation of the surface include local cementation by calcite precipitated in subaerial portions of the surface by evaporation of meteoric waters, and also possibly by bio-mediation of plants and microbes (Renaut, 1993; Scott, 2005). Cementation of the surface by zeolites (analcime) may be ongoing, but very slow (Renaut, 1993).

6. Context and significance of the overprinting trace suites with changing lake levels

The exhumed surfaces around Lake Bogoria preserve many, but not all, of the plant and animal traces present in the modern setting. Except for the *Mermia*-like suite, all other suites found along the modern lake margin setting were at least partly represented in the surfaces. The cross-cutting relationships of the four preserved suites are evidence for frequent lake level fluctuations (cf. Tiercelin et al., 1981; Renaut, 1982; Renaut et al., 1986; Tiercelin and Vincens, 1987; Renaut and Tiercelin, 1994), and demonstrate that trace suites can be used as a tool to help to reconstruct the sequence of events (Fig. 14). The exhumed surfaces represent a set of laterally adjacent and interfingering palimpsest surfaces that, if buried, would reflect an overall hiatus in sedimentation. Through their interaction with such surfaces, preserved animal and plant trace suites provide insights to the paleoenvironmental changes through time that are not necessarily represented by preserved sediments. This can be demonstrated by comparing typical patterns of delta sedimentation with the succession of overprinting of trace suites preserved in those sediments.

6.1. Complexities of deltaic sedimentation at Lake Bogoria

The narrow Bogoria lake basin is laterally confined between the faulted volcanic rocks that form the basin margins. During periods of intermediate lake levels, including today, extensive mudflats surrounding the lake are absent, except along parts of the Sandai and Loburu deltas. Small-scale, short-term lake level changes (<3 m fluctuations) today are thus marked mainly by vertical movements in shoreline position. During prolonged periods of low lake level (~8–10 m lower than present), such as existed during the Late Pleistocene (Renaut, 1993; Renaut and Tiercelin, 1994), more extensive mudflats might have increased the area of lake margin habitats for trace-making plants and animals, especially if springs that were previously submerged became subaerially exposed to provide isolated freshwater point-sources for plants and animals.

The deltas at Lake Bogoria have complex stratigraphic architectures characterized by generally thin (cm to dm scale) beds and shallow channeling that reflect the frequent changes in lake level, lake water salinity and density, and probably tectonic subsidence. Renaut and Tiercelin (1994) discussed the main controls and typical facies. The delta plains and littoral zones are composed predominantly of sands (K-feldspar, lithic grains, glass), feldspathic silts and muds. During periods of relatively high lake level, lake water salinity and density decrease, whereas the siliciclastic sediment supply tends to increase. At the Sandai delta, much of the sediment reaches the lake floor by low-density turbidity currents. Although some progradation takes place, migration of the delta-front upstream during transgression leads mainly to aggradation upon the older platform of the delta plain. At Loburu, in contrast, upstream migration of the delta front is restricted by topography, so sediment progradation during highstands may produce low-angled foreset beds of sand and fine gravel.

At the present intermediate lake levels, only slow progradation is occurring: much of the sediment is deposited as hypopycnal plumes of silt and clay that settled beyond the delta front. At very low lake levels, inflow is strictly ephemeral (except for hydrothermal discharge) and most sediment is likely delivered by very shallow ephemeral washes and sheetfloods across the exposed low-angled mudflats.

The changing styles of deltaic sedimentation that respond mainly to climatically controlled lake level changes (cf. Tiercelin et al., 1981; Tiercelin and Vincens, 1987) are responsible for the complex stratification patterns seen in the delta sediments. Much of the sediment deposited on the delta-plain platforms during lake highstands is reworked subaerially during later lowstands, leading to laterally discontinuous units, common intercalation of delta plain, shoreline and delta front beds, and local channel incision. In contrast, brief transgressive phases, such as those associated with El Niño events, can rework relatively coarse material offshore and deposit it nearshore as sand bars and fine gravel spreads upon the distal delta plains.

The exhumed surfaces that contain ichnofossils are recognized mainly by their somewhat higher degrees of lithification than the overlying sediments. The exhumed surfaces commonly show desiccation cracks, implying that they were subaerial surfaces during periods when lake level was relatively low. The crack networks range in spacing from a few cm to almost a meter (south-central Loburu shoreline). The largest crack networks are filled by younger sediments and likely formed during periods of very low lake level. Most of the cementation that preserves the exhumed surfaces probably occurred during regressive phases.

6.2. Lake level related events and associated trace overprinting

The exhumed "surface" that represents the uppermost (Late Pleistocene) Loboi Silts in the Bogoria basin (Sandai Plain) is interpreted to have been originally deposited in a setting similar to that of today: a slowly aggrading low-angle alluvial delta-plain that interfingers with deltaic and littoral silt and mud, as well as beach berms of sandy gravel and distal colluvial fans. The only other potential deltaic sites preserved around Lake Bogoria that may have been deposited at approximately the same time as the uppermost Loboi Silts, and are similarly well indurated, are those seen today on the central lobe of the Loburu delta (Figs. 2, 3F; Renaut, 1993). The trace assemblage and degree of induration at Emsos is comparable to both Sandai Plain and the central Loburu delta, but the relative timing of initial deposition at Emsos cannot be deduced with the available evidence.

While the uppermost Loboi Silts were being deposited, the lake shoreline was higher than it is today, with the preserved trace assemblage forming as the lake receded. This is, in part, shown by the location of the preserved trace fossils on Sandai Plain (Scott et al., 2008) that show overprinted examples of Suite 2 (flamingo surfaces) and Suite 4 (*Scoyenia*-like suite) <~800 m landward of the present shoreline. Vertebrate track morphology and taphonomy (Suite 4) are particularly useful for interpreting the history of changes in substrate consistency, and with large desiccation cracks, support the interpretation that the bioturbation occurred during lake regression (Scott et al., 2008). Cross-cutting relationships of Suite 5 (*Termitichnus* suite) (e.g., Fig. 11C), which comprises traces that infer lower water tables, in the vertebrate track-preserving surface, suggest that not only did lake regression continue, but that the surface was likely buried to shallow depth before formation of the Suite 5 traces. This assemblage was preserved by the zeolite (analcime) and calcite cementation that occurred during an extended period of aridity and low lake levels (Renaut, 1993; Scott et al., 2008), and which was the most important event in the preservation of the exhumed surface.

The trace assemblage from the central lobe of Loburu delta supports a similar interpretation by showing the preservation of a moderately diverse Suite 5 overprinting Suite 4 and possibly a poorly-preserved Suite 2. Pedogenesis of the cemented sediments has had a greater effect on the break-up of the "surface" at central Loburu than at Sandai. Suite 5 was also preserved at Emsos, again possibly overprinting a very poorly preserved Suite 2. Suite 5 (particularly *Termitichnus* isp.) was not preserved in the "surface" at either the southern Loburu delta, nor was it found north of the central lobe at Loburu where the hot springs have likely been active since the late Pleistocene. Instead, an apparently flamingo-modified surface (Suite 2) with meter-scale desiccation cracks and a diverse assemblage of rhizoliths of Suite 4 (R.A. Owen et al., 2008) is preserved around the hot springs. These findings suggest that either the fossil rhizolith assemblage is younger than the flamingo-modified surface and destroyed any evidence of Suite 5 by overprinting, or Suites 4 and 5 were laterally adjacent during low lake levels, but responded to a different set of paleoenvironmental controls in different lake margin subenvironments (i.e., drying lake margin vs. spring-fed wetland).

The Loboi Silts are unconformably overlain by the early Holocene wedge of Bogoria Silts on Sandai Plain that was deposited during higher lake levels. Flamingo nest-mounds and modified surfaces (Suite 2) are preserved in the Bogoria Silts on Sandai Plain, but more work is necessary to determine the trace assemblages of this unit. The silty and sandy sediments of the section measured in the present-day channel of the Parkirichai River into the southern lobe of the Loburu delta may have also been initially deposited during high lake levels, and perhaps at the same time as the Bogoria Silts on Sandai Plain. The preserved trace assemblage in these sediments is very similar in composition to the Suite 4 that is presently forming on the southern Loburu delta (J.J.S., unpublished results).

A stratigraphically useful, widespread stromatolitic coating dated to ~4500 BP (Vincens et al., 1986) covers portions of the exhumed sediments at the central Loburu delta (Fig. 4C), rhizolith-preserving substrates at the central and northern lobes of Loburu, boulders that form steeper margins around the lake (Fig. 4A,B), and hot-spring travertine deposits around the lake (Renaut, 1982). The stromatolitic coating represents the highest and freshest example of Lake Bogoria known; it reached the basin-sill spill-over height of 999 O.D. Chironomid larval traces of Suite 1 are the only trace fossils expected to be preserved with the stromatolitic coating, and have been found in thick limestone coatings at Ng'wasis at the south end of Lake Bogoria.

Today, lake levels are again in the "intermediate" stage, and erosion of the Bogoria Silts and the stromatolitic coating is ongoing, with progressively more of the Late Pleistocene surfaces being exhumed. As these older sediments again become the active substrate for plant, animal, and sediment interactions, they become more and more reworked by root growth, burrowing, and various other taphonomic processes. Overprinting of the subaerial, shoreline, and subaqueous portions of the surfaces by animal and plant traces that represent Suites 1, 2, 3, 4, and 5 occurs today in response to the various sets of environmental factors that control the lateral distribution of trace ichnocoenoses.

7. Discussion

7.1. Environmental controls on the lateral distribution of animal traces

Scott et al. (2007a,b) discussed the environmental factors that appear to control the distribution of modern animal traces in lake margin sediments at Lake Bogoria. Substrate-related factors include substrate moisture content, substrate cohesion, and substrate consolidation, all of which are partly related to lake level, water table, depth and proximity to hot springs. Other factors include the grain size, degree of induration and cementation, and the presence or absence of microbes in or on the substrate. These factors may be most important for invertebrate traces, but they also play a role in the distribution of vertebrate footprints and their various substrate-related morphologies and taphonomic signatures. The salinity of the sediment pore-waters and lake water is an important control on the assemblage compositions of both vertebrate and invertebrate traces, and can influence their taphonomic stabilization, alteration, and/or destruction (Scott, 2005; Scott et al., 2007a).

The environmental controls observed and inferred at Lake Bogoria are representative of "intermediate" lake levels (cf. Renaut and Tiercelin, 1994), but are expected to be relatively consistent during drier periods when lake levels are somewhat lower. Springs that discharge on the lake margin deltas may play an especially important role in the lateral distribution of preserved animal traces in underfilled, saline lake basins by providing laterally restricted pockets of relatively less-stressed conditions. These point-sourced fresh to brackish water "oases" may contribute to increased lateral environmental heterogeneity, especially around hypersaline lakes that have more extensive mudflats (Scott et al., 2007b). Lake Bogoria, for example, was lower, more saline and bordered by broad mudflats at several stages during the Late Pleistocene and Holocene (Tiercelin and Vincens, 1987). Under extreme aridity and hypersalinity, surface water may be limited to sites near spring inflow, as at modern Lake Magadi (Eugster, 1980). During such times of increased environmental stress with more saline lake waters and greater lateral variability of food and water resources, trace assemblages associated with subaerial springs may represent a concentrated view of the animal life in the basin.

Fault-controlled, lake margin springs like those in the Kenya Rift can also play an important role when they are drowned, even by lake level changes of <1 m where shoreline gradients are low. During relatively wet (and less saline) periods, lake levels rise due to increased precipitation and can submerge lake margin springs, which further decreases the salinity in a littoral zone. The increased lateral distribution of the point-sourced freshwater input dramatically influences the shoreline ecology and sedimentology. At Lake Bogoria in 2007, for example, littoral wetland vegetation covered the shoreline of the Loburu delta, and birds, such as sacred ibis and cattle and little egrets, used the shoreline at Lake Bogoria to breed for the first time in many years (Michael Kimeli, pers. comm., 2007).

Such short-term changes can exert an important ecological control on animal behaviour and plant growth and can take place with only small changes in lake level (e.g., 2–3 m). They can potentially obscure the lateral environmental heterogeneity recorded by traces. For example, the present biological and ichnological assemblages at Sandai Plain and the Loburu delta are dramatically different from one another in composition and degree of diversity. The preserved trace assemblages in the older exhumed surfaces at central Loburu and on the Sandai Plain, however, are much more similar in composition and diversity than the present-day examples (Table 2). This can potentially be explained by two scenarios: 1) during deposition of the uppermost Loboi Silts, Lake Bogoria was fresher, with relatively more laterally homogeneous shoreline ecology than today; and/or 2) continual changes in lake level resulted in sufficient overprinting of trace fossil suites to cause the homogenization of the preserved trace assemblages, despite the notion that at any time, the sets of environmental factors may have varied dramatically between laterally adjacent subenvironments. A major difference between the rhizolith assemblages on the Sandai Plain and the Loburu delta, however, does suggest that hot spring outflow was an important control that was relatively constant throughout much of the history of Lake Bogoria, and which has long been present at the Loburu delta, but not on Sandai Plain (Renaut and Tiercelin, 1994; Owen et al., 2008).

7.2. Stratigraphic significance of the exhumed surfaces

Recent studies have emphasized the importance of ichnology in sequence stratigraphic analysis of lacustrine successions (Buatois and Mángano, 2004, 2007, 2009-this volume). These studies underscored the complexities of stratal surfaces in underfilled lakes (after Bohacs et al., 2000). The analyzed surfaces at Lake Bogoria clearly illustrate the palimpsestic nature of most of these surfaces, providing additional evidence of the hiatus involved in their formation. The five trace suites recorded in the studied exhumed surface reveal the complex interplay of paleoecologic and taphonomic controls. Each of these suites reflects specific conditions of water availability and substrate consistency. In turn, subtle lake level fluctuations in a gently dipping lake margin plain strongly impact on these factors, and are conducive to suite overprinting. Therefore, studies of present exhumed surfaces add support to the notion that taphonomic pathways are essential to understanding the dynamic nature of continental ichnofacies (Buatois and Mángano, 2002, 2004, 2007). In fact, ichnofacies developed along the margins of underfilled lake basins are analogous to those associated with marine omission surfaces, particularly those in carbonates (Bromley, 1975). Most of these carbonate surfaces display complex cross-cutting relationships between softground, firmground, and hardground suites, and form composite ichnofabrics.

The ichnology of similar palimpsest surfaces has been documented in ancient underfilled lakes. Zhang et al. (1998) analyzed Permian playa-lake deposits from western Argentina, which contain a number of omission surfaces associated with lake desiccation and subsequent transgression. These surfaces are dominated by arthropod trackways, commonly showing extremely high density. Cross-cutting relationships are observed on bedding planes, revealing very shallow tier emplacement, a situation typical of Paleozoic continental ichnofaunas given the limited colonization of infaunal ecospace (Buatois and Mángano, 1993; Buatois et al., 1998). Uchman and Álvaro (2000) documented the ichnology of Miocene lacustrine deposits from Spain, which accumulated in an evaporitic underfilled lake. In these deposits, a single sandy marlstone bed contains a number of overprinted suites, spanning a subaqueously emplaced depauperate *Mermia* ichnofacies, the *Scoyenia* ichnofacies (both pre- and post-desiccation) and the terrestrial *Coprinisphaera* ichnofacies (see also Buatois and Mángano, 2009-this volume). Dominance of infaunal elements, typical of post-Paleozoic continental ichnofaunas, was conducive to complex cross-cutting relationships revealed by full-relief endichnial trace fossils.

Intensely bioturbated surfaces with complex cross-cutting relationships, such as those in Lake Bogoria, represent co-planar surfaces. These surfaces, also known as FS/SB (flooding surfaces/sequence boundaries), occur when the subaerial unconformity is modified during subsequent transgression and no lowstand deposits are preserved above the surface. Therefore, co-planar surfaces represent sequence boundaries that are overlain not by the lowstand systems tract, but by the transgressive systems tract. High-frequency lake level changes in underfilled lakes promote widespread development of co-planar surfaces, which in most instances involved more than one transgressive–regressive cycle, resulting in even more complex patterns of trace suite overprinting.

8. Conclusions

Extended periods of low lake levels in underfilled lake basins may permit the cementation of trace-preserving strata by a variety of minerals including calcite and zeolites, such as the siliciclastic, exhumed surfaces around Lake Bogoria, Kenya. Lakes with frequent lake level fluctuations, and which experience extended periods of low lake levels, may not show a net accumulation of sediments in lake margin environments, but instead the exhumation of stratigraphically important, cemented surfaces that continue to be active substrates for animal, plant, and sediment interactions. Complex patterns of trace suite overprinting can potentially be used, in conjunction with sedimentological evidence, to deduce the succession of changes in environmental factors that controlled the distribution and composition of the trace assemblages. Such surfaces may be the key for recognizing saline-lake trace fossil assemblages across basins, and understanding the lateral variability in environmental factors that control the assemblage compositions.

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