

Ichnology Moves Out of the Water:
The Work of Insects and Vertebrates

BIOGENIC ACTIVITY, TRACE FORMATION, AND TRACE TAPHONOMY IN THE MARGINAL SEDIMENTS OF SALINE, ALKALINE LAKE BOGORIA, KENYA RIFT VALLEY

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ABSTRACT: Actualistic studies of the distribution, formation, and taphonomy of vertebrate and invertebrate traces at saline (60–100 g l⁻¹ TDS), alkaline (pH: 10.5) Lake Bogoria in the Kenya Rift Valley have revealed a diverse trace assemblage in the lake-margin sediments. Although hypersaline lakes like Lake Bogoria restrict lacustrine faunal diversity, local marginal subenvironments, including hot springs and ephemeral streams, provide favorable areas for the activities of many species of insects, mammals, birds, and reptiles. Several factors, including sediment texture and moisture content, substrate cohesion, substrate consolidation, and the presence of a food source (i.e., vegetation, microbes, animal waste, flamingo carcasses), control the distribution of traces at Lake Bogoria by influencing the behavior of vertebrates (e.g., “dirt bathing” and nest building) and invertebrates (mainly feeding and locomotion). The distribution of vertebrate traces is also controlled by the proximity to fresh water, but the relationship between invertebrate trace formation and pore-water salinity is less clear.

Many characteristic features of closed-basin lakes, including frequent changes in lake level and shoreline position, the presence of thermal springs, and evolved fluid compositions resulting from evaporation, can have direct impacts on trace taphonomy. Notable taphonomic factors include efflorescent salt crystallization, which may temporarily cement substrates or destroy traces during crystal growth in the capillary fringe; substrate wetting and drying, which can induce soil crusting and the shrinking and swelling of smectitic clays, which in turn can modify trace morphology; and the presence of benthic microbial mats and biofilms, which can temporarily stabilize substrates or contribute to their early cementation by mediating carbonate precipitation. Semiarid environments, such as the Kenya Rift, are favorable settings for the early cementation of substrates by carbonates (e.g., calcite), and, during prolonged, stable dry phases, the preservation of trace fossils and their substrates by zeolites and other minerals (Mn- and Fe- oxyhydroxides).

INTRODUCTION

The marginal environments of continental saline lakes have received little study by ichnologists compared to marginal marine settings. Saline lakes are commonly considered inhospitable locations for the formation of trace fossils because their high salinities inhibit most organisms other than prokaryotes and a limited group of salt-tolerant metazoans (e.g., Hammer, 1986; Buatois and Mángano, 2004). Nonetheless, observations around the saline, alkaline lakes in the Kenya Rift Valley confirm that many organisms inhabit or traverse their margins. The modern marginal sediments show abundant evidence for surficial and infaunal biogenic activity, including locally abundant footprints, trails, burrows, and general bioturbation.

The preservation potential of those biogenic traces is, however, unclear. Saline-lake margins undergo frequent fluctuations in water level, and the sediments can be modified by surface waters and groundwaters of variable compositions. Although burial by sedimentation during rising lake waters can enhance preservation, falling lake waters can lead either to sediment disruption and erosion or to preservation by early near-surface cementation. Little is yet known of the processes and preservation potential of traces in this environment.

This paper describes the results of a study of the impact of biogenic activity on the sediments around the margins of Lake Bogoria, a saline, highly alkaline lake in the Kenya Rift Valley (Fig. 1). The aim of the study was to determine which organisms

are present around the lake margins, to assess their impact on the sediments, and to evaluate the long-term preservation potential of any biogenic traces that they produce. Emphasis is given to understanding the environmental and sedimentological factors that are most likely to enhance the preservation and destruction of the biogenic traces. An understanding of the development, diversity, and taphonomy of traces in modern saline mudflats will help their recognition in the fossil record and help to distinguish them from those associated with freshwater-lake margins.

ENVIRONMENTAL SETTING

Geological and Physiographic Setting

Lake Bogoria lies in a narrow, asymmetric half graben in the central Kenya Rift Valley, 20 km north of the equator (Fig. 1). East of the lake, the Lake Bogoria Escarpment, a major fault scarp, rises up to 700 m above the lake surface and defines the eastern edge of the Bogoria half graben. The scarp face exposes a succession of Miocene to Pleistocene basalts, trachytes, and phonolites (Griffiths, 1977; Hackman, 1988). A flexure in the fault system toward the southwest provides the southern closure of the lake. West of the lake, the northward-dipping Bogoria Plateau is composed of grid-faulted Pleistocene (< 1 Ma) trachyphonolites and basalts. North of the lake, the Sandai Plain is a narrow, sparsely vegetated plain, composed of late Pleistocene and Holocene deltaic, alluvial, and colluvial sediments (Renaut, 1993). A major NW–SE

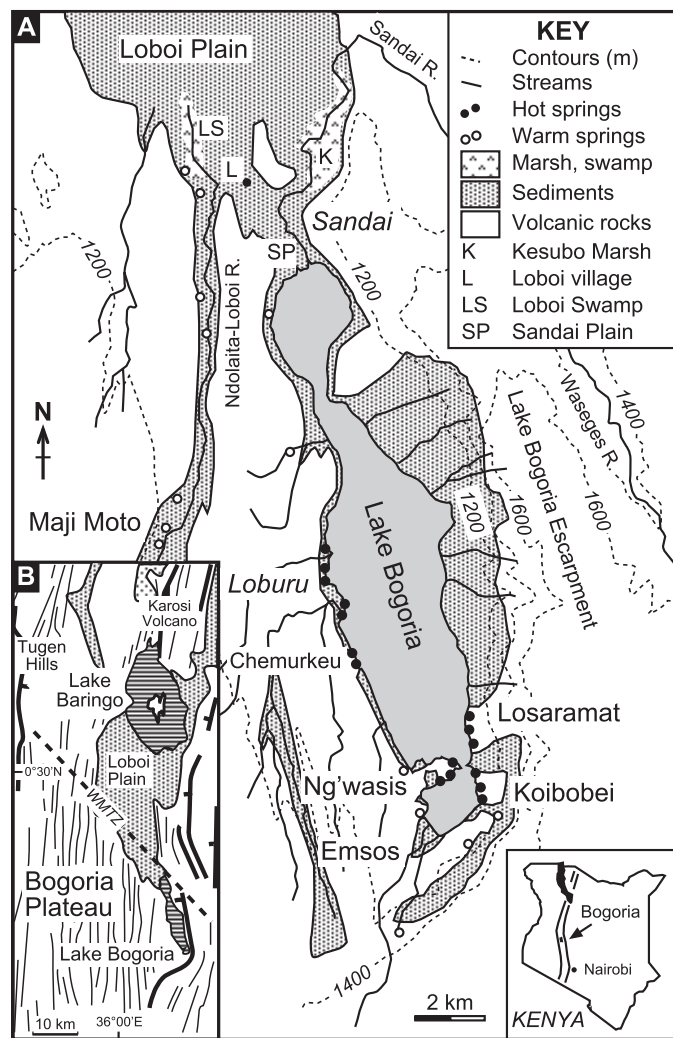


FIG. 1.—Location and setting of Lake Bogoria. **A)** General setting showing location of the Sandai Plain and Loburu, and other localities mentioned in the text. **B)** Simplified geological setting of the Baringo–Bogoria basin (after Le Turdu et al., 1999). WMTZ: Wasages–Marmanet Transverse Zone. General pattern of faulting is shown; thicker lines are major faults.

lineament, the Wasages–Marmanet Transverse Zone (WMTZ), marks the northern margin of the Bogoria basin. North of this lineament, which is a deep structure rooted in metamorphic basement rocks (Le Turdu et al., 1999), lie the alluvial Loboi Plain and Lake Baringo, a freshwater lake (Fig. 1B).

Climate and Limnology

The climate of the Lake Bogoria region is semiarid. Annual precipitation on the valley floor is typically $\sim 700 \text{ mm y}^{-1}$, compared to an annual evaporation rate of $> 2000 \text{ mm y}^{-1}$. Rains are highly seasonal. The “long rains” fall from April to August, commonly as late afternoon convective storms; the “short rains” are mainly in October and November. Mean air temperatures range from ~ 18 to 32°C . Winds are funneled N–S along the axis of the lake by day and commonly reverse during late afternoon, which produces local flooding of littoral mudflats.

Lake Bogoria is a shallow (10 m), meromictic, saline ($60\text{--}100 \text{ g l}^{-1}$ total dissolved salts; TDS), alkaline (pH: 10.5) lake with $\text{Na-CO}_3\text{-Cl}$ waters (Renaut and Tiercelin, 1994). The lake is hydrologically closed and is fed by the Sandai and Emsos rivers, ephemeral streams, direct precipitation, nearly 200 alkaline hot springs, and sublacustrine hydrothermal discharge (Fig. 1A). Lake level ($\sim 990 \text{ m OD}$) fluctuates frequently over time spans ranging from years ($\pm 1.5 \text{ m}$), to decades ($\pm 3 \text{ m}$), to $10^2\text{--}10^3$ years ($\pm 10 \text{ m}$). Most short-term fluctuations are responses to changes in the precipitation/evaporation ratio, but tectonics can also play a role on longer time scales. Although always alkaline, the surface-water (mixolimnion) salinity decreases markedly during periods of higher lake level (Tiercelin, 1981; Tiercelin and Vincens, 1987; Renaut and Tiercelin, 1994).

Flora and Fauna

Lake Bogoria has been a protected National Reserve since November 1970 and was declared a Ramsar Site in 2001. Despite its small size, the reserve contains a large diversity of mammals (discussed below) and one of the largest flamingo populations in the world.

Local vegetation is dominated by wooded grassland and mosaic evergreen bushland, with abundant *Acacia*, *Combretum*, and *Terminalia*. The steep scarps along the lake margins are dominated by *Acacia* bushland. Littoral spring-fed wetlands, including *Cyperus laevigatus* marsh, are present at several sites near the shoreline (Onkware, 2000; Owen et al., 2004). Aspects of the local ecology are discussed by North-Lewis (1998) and Harper et al. (2003).

METHODS

Field Methods—Actualistic Studies

Observations of vertebrates at Lake Bogoria during June–July in 2001 and 2002 form the basis for behavioral interpretations of their traces. Observations of distribution and morphology of invertebrate traces were also made. Associations of these traces with sedimentological and other factors that contribute to their morphology and taphonomy were recorded. A nine-consecutive-day study was made to determine the environmental factors that influence animal behavior and the distribution of various trace morphotypes on the Sandai Plain. Six plots, each $\sim 16 \text{ m}^2$ and located at various distances from the shoreline (Fig. 2A), were monitored daily, following wind-induced flooding, reactivation of the trace surfaces, and retreat of the lake waters from the previous afternoon. Sheet flooding of the delta plain also occurred during the observation period. Different trace morphologies were photographed, and inferences were made regarding weather-related processes (i.e., substrate baking, rain, etc.) and the degree of substrate saturation at the time of print formation. Several important taphonomic factors were identified from these data.

Laboratory Methods

Modern, Holocene, and Pleistocene sediment samples were collected both from beds that contained animal traces and from beds along transects that did not contain traces. Thin sections of trace-bearing sediments were prepared, many of which needed impregnation with epoxy. The bulk mineralogy and clay minerals ($< 2 \text{ m}$) were identified by X-ray diffraction using a Rigaku RU200 X-ray diffractometer. Qualitative energy-dispersive X-ray analyses (EDS) of very fine (clay to fine silt) sediment particles

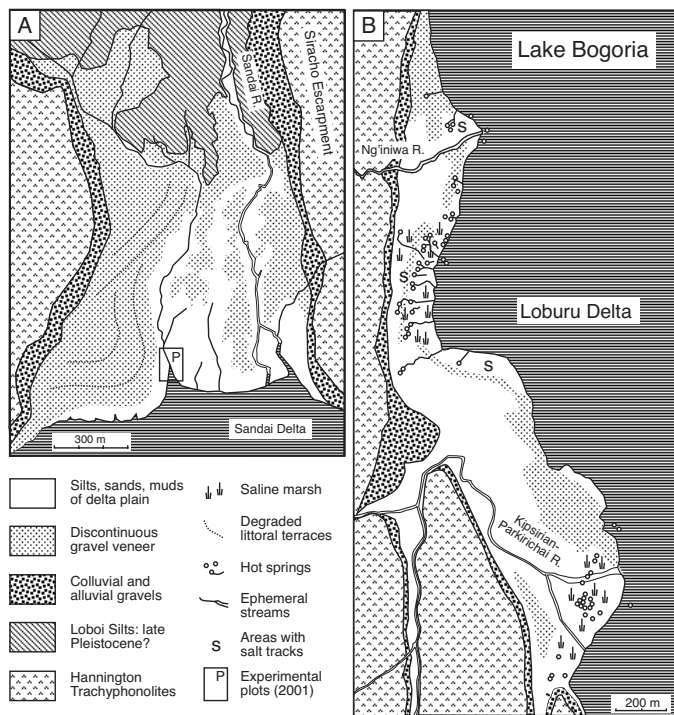


FIG. 2.—Geological setting of A) Sandai Delta and B) Loburu Delta of Lake Bogoria.

were made from polished thin sections using a JEOL JXA 8600 electron microprobe to help confirm mineralogical interpretations.

LAKE-MARGIN ENVIRONMENTS OF LAKE BOGORIA

The margins of Lake Bogoria consist of: delta plains and fan-delta plains; narrow littoral plains, some of which are gravel strewn with patchy grass cover; narrow (15–250 cm) sand and fine gravel beaches; and scattered bedrock outcrops (Renaut et al., 1986, fig. 3; Renaut and Tiercelin, 1994). Biogenic traces are limited mainly to the delta shorelines (Fig. 3A) and, to a lesser extent, the littoral plains and other low-energy zones (e.g., protected embayments), where surficial sediments are composed of fine sand, silt, and mud.

The Sandai Plain (~ 1.2 km²), fed by the Sandai River and a small ephemeral stream, extends across the width of the northern sub-basin of the lake and is confined laterally by fault scarps (Figs. 2A, 3B, 3C). The delta plain within 200 m of the lake lacks vegetation and is generally flat, but is broken locally by dendritic shallow (< 50 cm; 1–4 m wide), ephemeral channels. The surficial sediments near the lake margin are mainly unconsolidated feldspathic fine sands and silts that become generally more clay-enriched toward the shoreline and on the ephemeral channel floors and embayments that are periodically flooded by lake water. Efflorescent salts (thermonatrite, trona, halite, gaylussite), which form thin surficial crusts and interstitial crystals in the vadose zone, are common in the lake margin. With increasing distance northward from the shoreline, the delta plain gradually becomes higher (slope < 3°), the water table becomes deeper, and the surficial sediments become progressively more lithified and locally covered by patchy grasses and scrub. Shallow sections and pits through the delta show a vertical series of northward-

thinning sedimentary units that record periodic onlaps and offlaps across the delta plain (Renaut, 1982). A widespread discontinuity, visible in some channel sections, shows Holocene delta-plain and delta-front sediments overstepping red zeolitic siltstones and sandstones of probable late Pleistocene age (Renaut, 1993).

The smaller Loburu Delta (0.5 km²), which lies on the midwestern shoreline, abuts against low (20–40 m high) escarpments of Pleistocene trachyphonolites. The delta has two lobes that are separated by a marshy interdistributary embayment (Fig. 2B). The ephemeral Kipsirian and Parkirichai rivers feed the larger southern lobe, and the Ng'iniwa stream feeds the smaller northern lobe. About sixty alkaline hot springs (~ 4.5 g l⁻¹ TDS) discharge along extensions of two fault lines that cut the volcanic rocks west of the delta. Much of the delta plain is vegetated by patchy grasses and shrubs (Onkware, 2000), but the cover decreases shoreward (Fig. 3D). Alkali-tolerant marsh, dominated by *Cyperus laevigatus* and *Sporobolus spicatus*, is present in the interdistributary embayment, but the cover is thin following periods of high lake level. The deltaic sediments are mainly silts and fine sands, with ribbon (channel and beach) and sheetlike (littoral plain) interbeds of gravel. The distal saline mudflats of the southern lobe are sparsely vegetated, and are locally covered by efflorescent trona, thermonatrite, and halite crusts.

Similar littoral delta-plain environments are present at the Emsos (Turkupmakau) Delta at the southern end of the lake (Fig. 1), and along parts of the eastern shoreline. Marginal sediments east of the lake are commonly coarser than at Sandai and Loburu because they originate in large coalescent alluvial fans.

VERTEBRATE TRACES IN THE LAKE-MARGIN ENVIRONMENTS

Mammals

Many large mammals are attracted to the local freshwater subenvironments provided by the ephemeral streams and springs (Fig. 4). Some large grazing mammals, including zebras and warthogs, venture onto the deltaic and littoral plains to feed on grasses because the adjacent topography is steep, rugged, and wooded. Similarly, browsers that are more common in woodlands (e.g., greater kudus) are also present along the shoreline. Vervet monkeys and olive baboons are common in the wooded slopes around the lake. Hyenas and leopards are the only carnivores whose traces were confirmed in marginal environments at Lake Bogoria, although lions, caracals, servals, genets, African wild cats, civets, wild dogs, honey badgers, and mongooses are present in the region (North-Lewis, 1998). The diversity and abundance of large mammal species are higher at Lake Bogoria than at Lake Baringo, partly because Lake Bogoria is a protected National Reserve; minor livestock grazing is permitted in parts of the reserve, but human settlements and agriculture are excluded.

Bovids (Figs. 5A, 5B, 5C).—

The frequency and concentration of the bovid traces are controlled by the species behavior and the ecological variations between each subenvironment (e.g., vegetation type). Bovids in the reserve are mainly Grant's gazelles (*Gazella granti*), impalas (*Aepyceros melampus*), greater kudus (*Tragelaphus strepsiceros*), and African buffaloes (*Syncerus caffer*). During the last 120 years, however, bushbucks (*Tragelaphus scriptus*), waterbucks (*Kobus ellipsiprymnus*), Coke's hartebeests (*Alcelaphus buselaphus cokei*),

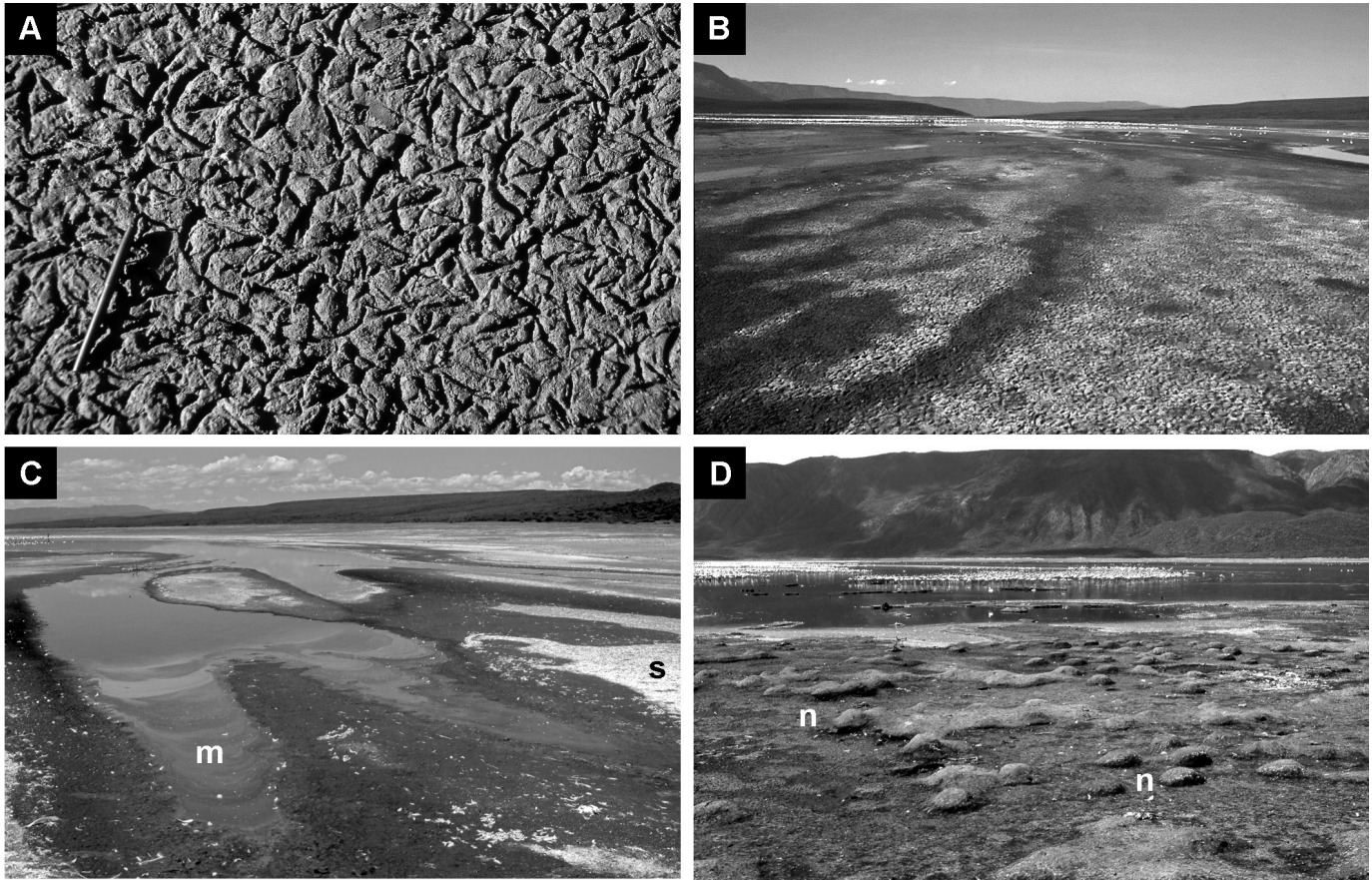


FIG. 3.—Saline mudflats on the margins of Lake Bogoria. **A**) Abundant flamingo prints on saline muddy silts. Such prints commonly seed locations of desiccation cracks. Sandai Plain, ~ 20 m from shoreline. Pen is 17 cm long. **B**) Saline mudflats with puffy efflorescent trona crusts on flamingo-trampled muddy silts. Sandai Plain, looking south toward Lake Bogoria Escarpment (left). **C**) Small inlet at mouth of ephemeral stream along the shore of Sandai Plain. Detrital green *Arthrospira* mats (m) have washed onto the damp mudflats; s, efflorescent salt crusts on slightly higher (5–10 cm) ground. **D**) Eroded flamingo nest mounds (n) on the southern shore of Loburu delta. Flamingos are visible offshore.

and other bovids have been reported (Von Höhnell, 1894; Jobe-Akeley, 1929; North-Lewis, 1998). The species present today are browser / grazers or browsers that rely at least partly on a woodland food source (Estes, 1991). Greater kudu and buffaloes are concentrated at the southern end of the lake, where there is less human disturbance. Grant's gazelles (Fig. 5A) and impalas, however, often venture onto the open Sandai Plain and Loburu Delta. Bovid traces on the Sandai Plain and Loburu Delta are concentrated near freshwater sources but are rare along most of the shoreline. Although prints of greater kudu were seen near hot springs at the southern Loburu Delta (Fig. 5B), buffalo traces were encountered only in wooded areas near the lake and at the Sandai River (Fig. 5C). Bovids tend not to frequent the muddy shorelines and have little effect on lake-margin sediments at Lake Bogoria. Their traces are common in silts and sands on the delta plains, but trampling and sediment reworking are low because their traces are found in discrete trackways, usually impressed to a few centimeters depth.

Suids (Figs. 5D).—

Warthogs (*Phacochoerus africanus*) are common, especially at Loburu Delta, where they graze on grasses, drink from hot-spring effluent, and bathe in littoral sands and gravels saturated

with hot waters. They were not observed on the drier Sandai Plain. Warthogs inhabit burrows in the woodland-scrub areas within a few hundred meters of the shoreline. Their imprint on lake-margin sediments is much higher than that of the bovids, mainly because of their frequent presence in grassed areas. The amount of trampling of the delta-plain substrates by warthogs is generally low, but their bathing holes rework the lake-margin sediments to ≤ 1 m depth, especially near hot springs.

Aardvarks (Fig. 5E).—

Aardvarks (*Orycteropus afer*) are secretive, slow-moving, nocturnal mammals that have an impact on dry sediments surrounding the lake by digging large burrows (~0.5 m in diameter). These burrows, which are common near the mounds of termites (their food source), can be adapted later for use by warthogs (Cumming, 1975). An aardvark trackway was found ~ 500 m from the shoreline on dry and deflated silty sands on the Sandai Plain, presumably heading to and from the Sandai River (Fig. 5E).

Equids (Fig. 5F).—

Zebras (*Equus burchelli*) are common at Loburu Delta, and, like warthogs, feed on salt-tolerant grasses. They also “bathe” on

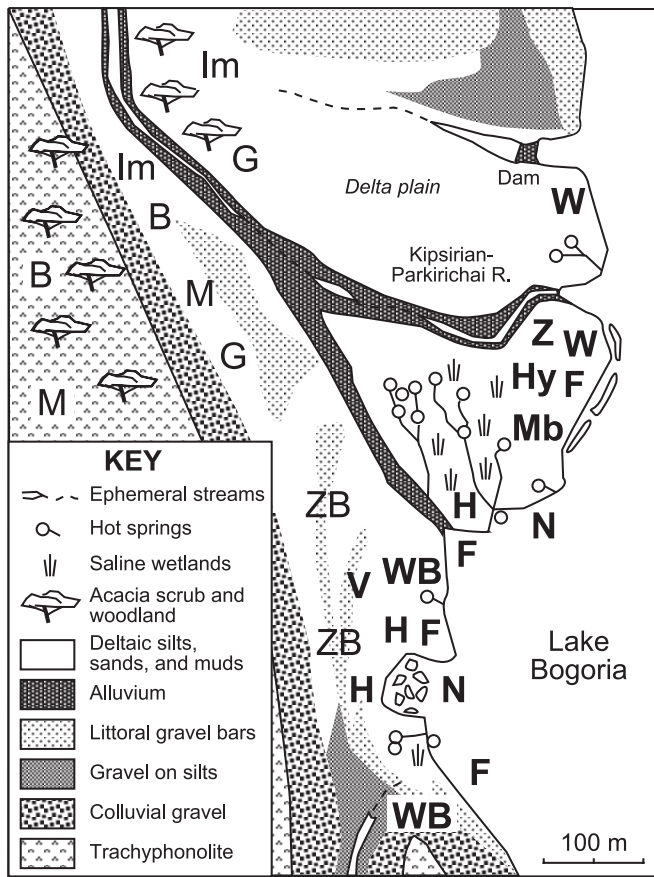


FIG. 4.—Sketch map of southern Loburu Delta showing the main subenvironments and the distribution of animals during June and July of 2001 and 2002. Letters representing animals are located where they were observed most commonly during daylight hours, and where their traces were recorded most commonly. Letters in bold represent those animals whose traces have the highest potential of being fossilized. Most lie in areas of muddy sediments. B, baboon; F, flamingos (prints); G, gazelle (mainly Grant's); H, horizontal tunnels; Hy, hyena; Im, impala; M, monkeys (mainly vervet); Mb, marabou stork; N, flamingo nest mounds; V, vertical burrows; W, warthog (prints); WB, warthog (baths); Z, zebra (prints); ZB, zebra (baths).

dry relict sandy beach berms and littoral terraces composed mainly of silt and fine sand. Unlike warthogs, zebras appear to avoid entering isolated shallow-water pools. Zebras have minimal impact on the lake-margin sediments because their footprints are usually found in firm and moist, but not water-saturated, substrates, and are usually impressed to depths of < 3 cm. On the dry silts and sands of the Loburu Delta, however, they rework the sediment when bathing and destroy the surfaces of any desiccated and potentially trace-preserving beds.

Carnivores (Figs. 5G, 5H).—

Hyena (*Crocuta crocuta*) trackways, oriented normal to the shoreline, were seen near the shorelines of Sandai Plain and Loburu Delta, and indicated a tendency to travel directly to the lake (Fig. 5G). During 2001 and 2002, several hundred flamingos

died daily at Lake Bogoria (cf. Krienitz et al. 2003), attracting scavenging hyenas whose footprints were found associated with traces of flamingos and marabou storks, mainly in water-saturated muds and silty sands.

Leopard (*Panthera pardus*) traces, although rare, were also found at Sandai Plain and Loburu Delta in dry silty fine sands along game trails in transitional areas between the plains and woodland scrub (Fig. 5H). In one incident, an adult ostrich chased off a leopard that had approached an ostrich family resting on the Sandai Plain during the night. This event was recorded by traces on a freshly wind-deflated surface in dry silty sand with a low density of other footprints. The two carnivore trace types observed in the lake-margin sediments at Lake Bogoria were zoned, apparently due to the distribution of food sources, their hunting/scavenging behavior, and their ecology. Neither species had much influence on the sediments—their footprints are generally very shallow (< 5 mm depth) and form discrete trackways.

Primates (Fig. 5I).—

Other than humans, vervet monkeys (*Cercopithecus aethiops*) and olive baboons (*Papio cynocephalus anubis*) (Fig. 5I) are the only primates in the region today. The footprints of vervets and baboons are common in dry silty sediments along the fringes of wooded areas. Thus, they were observed on the delta plain at Loburu but not on the Sandai Plain.

Birds

Lake Bogoria and local spring-fed wetlands provide habitat for more than 350 resident and migrant bird species (Hartley, 1986; Harper et al., 2003). Several bird species use the habitat along the shoreline and the associated ephemeral streams and hot-spring outflow channels. The traces of these species—mainly flamingos, plovers, geese, teals, storks, herons, and ostriches—are dominant in the deltaic and littoral-plain sediments. Flamingos are the only birds that rely directly on Lake Bogoria for their food source and (practice) breeding sites; the others are generally active at or near sites of freshwater inflow. During rainy periods, when runoff is temporarily ponded, a higher diversity of species approaches the shore.

Flamingos (Fig. 6).—

Lake Bogoria is the deepest of the highly saline, alkaline lakes of the Kenya Rift and the most reliable habitat for flamingos during drought. Up to two million birds have been reported on the lake at one time (Brown, 1973). Two flamingo species inhabit the Kenya Rift: lesser flamingos (*Phoeniconaias minor*), which are endemic to Africa, and greater flamingos (*Phoenicopterus ruber*), which are migrants from Europe. Lesser flamingos feed on cyanobacteria (*Arthrospira fusiformis*) and other plankton in the water column that are filtered using their specialized tongues (Vareschi, 1978; Harper et al., 2003). Several flamingo behavioral patterns are associated with sites of dilute inflow to the lake. Because flamingos depend on both fresh and saline water, their traces dominate the shoreline at Lake Bogoria (Figs. 3A, 3B, 6). Their great impact on lake-margin sediments results from large numbers of individuals, their social behavior, and nest-building activities. Most footprints are made in soft, saturated littoral muds (Fig. 6).

The degree and distribution of substrate trampling depend on shoreline position and climatic influences such as wind direction and intensity, which can cause ephemeral flooding of lake-mar-

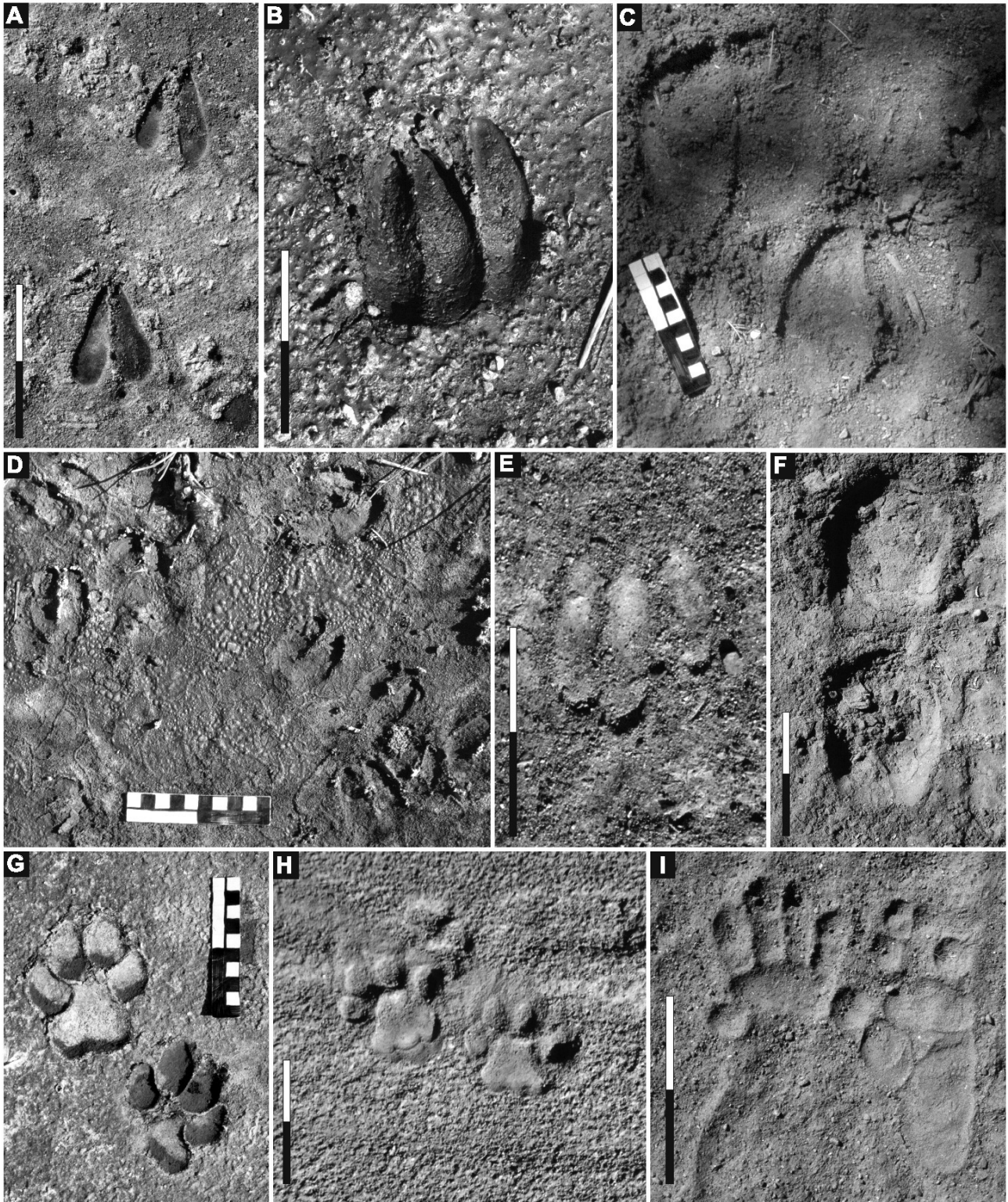


FIG. 5.—Examples of mammal traces in the lake-margin delta plains at Lake Bogoria. Scale bars are all 10 cm. **A)** Adult Grant's gazelle front and hind prints, Sandai Plain. **B)** Greater kudu front and hind prints, southern Loburu Delta. **C)** African buffalo front and hind prints, wooded area near the southern Loburu Delta. **D)** Several warthog prints in lightly trampled area of the southern Loburu Delta, together with *Vagorichmus*-like horizontal tunnels and microbial mat. **E)** Aardvark print, Sandai Plain. **F)** Zebra front and hind prints, southern Loburu Delta. **G)** Hyena front and hind prints, Sandai Plain. **H)** Leopard front and hind prints, Sandai Plain. **I)** Common (olive) baboon front and hind prints, in wooded area near the southern Loburu Delta.

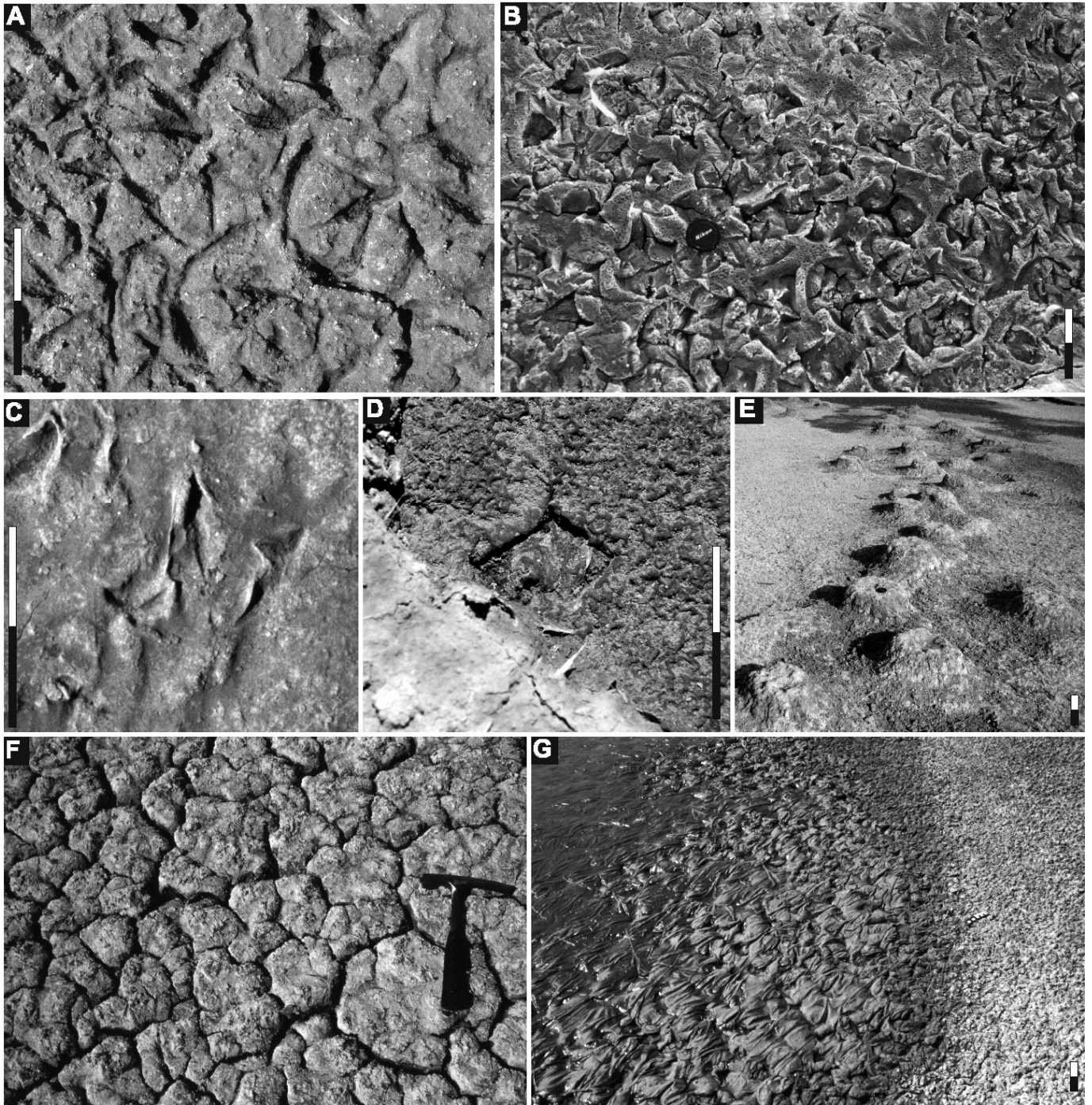


FIG. 6.—Examples of variable flamingo trace morphology and flamingo-modified sediments. All scale bars are 10 cm. **A)** Flamingo-trampled salt- and clay-encrusted surface near shoreline of Sandai Plain, showing effects of swelling clays on morphology. **B)** Flamingo-trampled mud with benthic microbial mat at Loburu Delta, now desiccated with salt efflorescence. **C)** Flamingo footprint formed in wet mud drape near shoreline at Sandai Plain, now partly desiccated just above water table. **D)** Flamingo footprint impressed into partly desiccated benthic microbial mat at Loburu Delta; note wrinkle texture within footprint and adjacent salt crusts. **E)** Recently built flamingo nests near the mouth of the Sandai River on Sandai Plain. **F)** Desiccation-cracked mud near shoreline at Sandai Plain; crack and polygon morphology is dictated by flamingo trampling of the muds; hammer for scale. **G)** Flamingo-created surface texture in soupy mud at shoreline of Sandai Plain; these structures form when many individuals walk through the mud together, splashing mud in the direction of travel.

gin sediments, and heavy rains that induce sheetfloods and form temporary pools of fresh water. Changes in lake level and the volume of dilute fluvial inflow, which are related to the precipitation/evaporation ratio, can cause lateral shifts in the distribution of trampled surfaces. Flamingo footprints and flamingo-trampled surfaces can also dictate the morphology and distribution of desiccation cracks and polygons (Fig. 6F).

At various times of the year, flamingos engage in breeding and display behaviors, and gather in suitable areas to build “practice” nests (Brown, 1973). At Lake Bogoria, nests are built from mud at sites where there is reliable inflow of relatively dilute water near the mouth of the Sandai River (Fig. 6E) and on the Loburu Delta (Fig. 3D). The delta gradients in these two regions are very low, and as lake waters recede during the dry seasons, increasing amounts of soft muddy sediment suitable for nest building are exposed. The impact of nest-building activities on

lake-margin sediments is extensive. The birds completely rework muds in some areas and create biosedimentological features along shorelines, including excavated depressions between nest mounds and “mini-escarpments” (Scott et al., 2003). The effects of flamingo behaviors on shoreline sediments will be reported elsewhere.

Marabou Storks (Figs. 7A, 7B).—

Marabou (*Leptoptilus crumeniferus*) footprints are second to flamingo footprints in abundance and impact on lake-margin sediments, especially by influencing the morphology and nucleation sites of desiccation cracks (Fig. 7A). Their traces are usually associated with flamingo traces near the Sandai River and at Loburu Delta because, like hyenas, scavenging marabous take advantage of flamingo mass mortality.

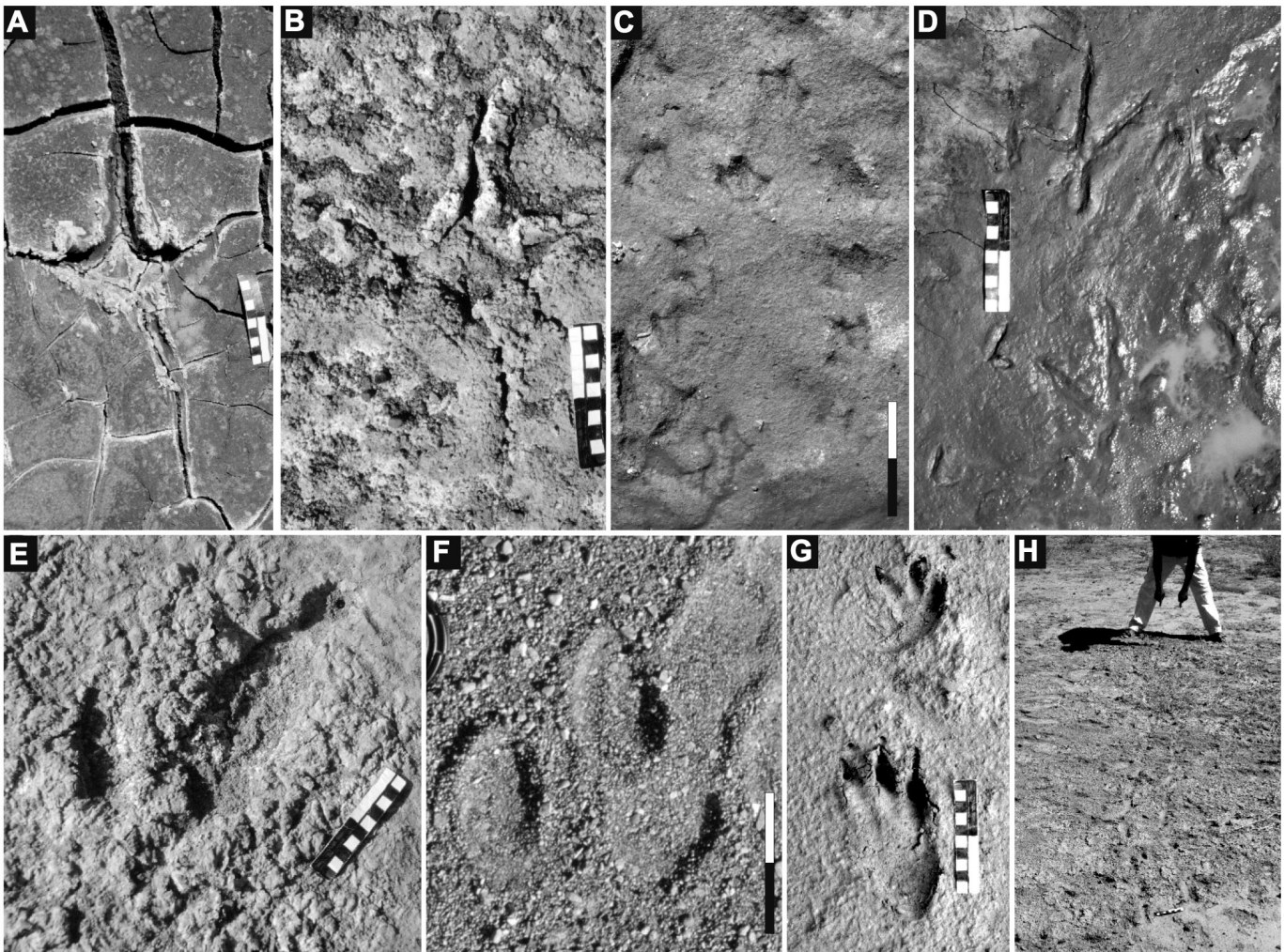


FIG. 7.—Examples of bird and reptile traces at Lake Bogoria. Scale bars are 10 cm. **A)** Marabou stork print and associated desiccation cracks in smectitic mud in drying channel of the Sandai River. **B)** Salt-deformed marabou stork print on Sandai Plain. **C)** Several teal prints in mud-draped drying ephemeral channel on the Sandai Plain. **D)** Grey heron prints along margin of drying channel of the Sandai River; plover prints at bottom left. **E)** Adult ostrich print in flamingo-trampled and salt-encrusted silts and fine sands near shoreline at Sandai Plain; note only two digits. **F)** Juvenile ostrich print in coarse sands and gravels on Sandai **G)** Crocodile left front and hind prints in wet sands of the Sandai River. **H)** Tortoise trackway in dry sands of the Loburu delta plain; man for scale.

Geese, Plovers, Cranes, Yellow-Billed Storks, Herons, and Teals (Figs. 7C, 7D).—

The traces of other wading birds (e.g., yellow-billed storks: *Mycteria ibis*) at Lake Bogoria are generally associated with fresh-water sites near the shoreline. Egyptian geese (*Aloochen aegyptiacus*) and plovers (*Vanellus* spp., *Charadrius* spp.) nest on the flat areas surrounding the lake, and crowned cranes (*Balearica* spp.) nest near wetlands near Lobo village (Fig. 1A). Herons (*Ardea* spp.) (Fig. 6D) nest at Lake Baringo but visit Lake Bogoria, probably to feed on insects (Kimeli, personal communication, 2002). The footprints of the migrant green-winged teal (*Anas capensis crecca*) were observed along an ephemeral stream after storm-related sheet flooding on the Sandai Plain (Fig. 7C).

Ostriches (Figs. 7E, 7F).—

Adult and juvenile ostrich (*Struthio camelus massaicus*) trackways, “dirt-bathing” traces, and “sleeping” traces were observed on the Lobo Plain and Sandai Plain, but not at Loburu Delta. Their traces are common in open, flat areas, which also tend to be dry, although their footprints were observed occasionally near the Sandai shoreline.

Reptiles

The traces of crocodiles (*Crocodylus niloticus*), monitor lizards (*Varanus* spp.), snakes (many species), and tortoises (*Kinixys* spp., *Geochelone* spp.) are locally common in the marginal environments around Lake Bogoria. However, only traces of crocodiles and monitor lizards are found in wet sediments near the shoreline. Several Nile crocodiles inhabit the Sandai River; their traces are found on the riverbanks and in ephemeral channels (Fig. 7G). Monitor lizards are common in the more secluded, forested area at the south end of the lake, where the Emsos River and outflow from a cool spring enter the lake (Fig. 1A). Rare traces of snakes have been observed on dry fine sandy sediments on the Sandai Plain and in the transitional zone between the Loburu Delta and woodland scrub. Trackways of tortoises are common in dry sediments around the lake but were not observed in the wetter areas near the shoreline (Fig. 7H).

INVERTEBRATE TRACES IN THE LAKE-MARGIN ENVIRONMENTS

Introduction

Only one benthic invertebrate species (a chironomid) has been recorded in Lake Bogoria (Harper et al., 2003). Nevertheless, several invertebrates that are known to be potential tracemakers inhabit the saline lake margins (Table 1). The lake-margin springs locally provide fresh and brackish water that favor rich microbial communities (Renaut et al., 1998; Hindák, 2001; Krientiz et al., 2003), which provide food for some of the invertebrate tracemakers. Microbial mats and biofilms at Loburu, for example, provide food for beetles. Ants and termites are very common on the dry well-drained plains north of the lake, where termitaria are abundant, and on dry slopes distant from the lake margins, but are uncommon near the shoreline. Funnel spiders are also common. An unusual feature first reported on the saline mudflats at Lake Bogoria is the formation of “salt tracks and trails”, which are ephemeral traces “preserved” as salt crystals (Renaut et al., 1986, fig. 6). In this section, the nature, origin, and significance of the salt tracks are discussed, and a brief description of the main types of invertebrate traces and their distribution is presented.

TABLE 1.—Potential trace-making insects at Lake Bogoria (sources: Harper et al., 2003, except * = J.S. personal observations).

Family	Genus	Species
Chironimids (midges)	<i>Paratendipes</i>	sp.
Coleoptera: Tenebrionid	<i>Gonocephalum</i>	sp.
	<i>Sepidium</i>	spp.
	<i>Vietomorpha</i>	spp.
	<i>Rhytinota</i>	<i>praelonga</i>
	<i>Zophosis</i>	spp.
Cicindelids (tiger beetles)	<i>Lophyra</i>	<i>boreodilatata</i>
	<i>Prothyma</i>	<i>methneri methneri</i>
	<i>Cylindera</i>	<i>rectangularis</i>
	<i>Myriochile</i>	<i>vicina pseudovicina</i>
	<i>Tithoes</i>	<i>confinis</i>
Cerambycids (longhorn beetles) inc. the Prionids	<i>Macrotoma</i>	<i>palmata</i>
Scarabaeidae (rutelids and metholonids)	None given	
Elaterids (click beetles)	<i>Tetralobus</i>	spp.
?Staphylinidae *		
?Heteroceridae *		
Dermoptera (earwigs) *		

Invertebrate Ecology at Lake Bogoria

The limited ecological research at the Lake Bogoria National Reserve has emphasized the high microbial productivity in the lake and the flamingo population. Harper et al. (2003) briefly described the terrestrial invertebrate fauna and discussed the ecology of the only benthic detritivore, *Paratendipes* sp. (Diptera: Chironomidae). These chironomids (midges) are locally plentiful in the shallow (2–4 m) oxygenated lake waters. The extremely low benthic diversity, a single dominant phytoplankton species (*Arthrospira fusiformis*), and the absence of macrozooplankton reflect the high salinity of the lake waters (Harper et al., 2003).

The most diverse invertebrate fauna today comprises insects found within the “draw-down” zone around the shoreline, where accumulated flamingo feathers and carcasses, bird excrement, and vegetal debris have attracted many beetles (Table 1; Harper et al., 2003). Although not reported by Harper et al. (2003), other trace-making beetles (e.g., staphylinids, heterocerids; Tony Drane, personal communication, 2005) and earwigs (Order Dermoptera; J.S., personal observations) were also identified, and appear to be represented in the lake-margin trace assemblage.

Salt Tracks and Trails

An unusual feature on saline mudflat surfaces at Loburu is the development of “salt tracks” (Figs. 8, 9). These consist of small (0.3–1 cm diameter by 0.1–0.5 cm high) mounds of very finely crystalline soluble salts that exhibit a wide range of trackway and trail patterns (Fig. 8C). The patterns resemble invertebrate locomotion and grazing traces, and show great variation in length (< 3–200 cm), width (1–12 mm), and sinuosity. Many, but not all, of the traces are paired, parallel lines of mounds. The mounds can be conical, star-shaped, tumuliform, or display barbed, featherlike patterns. Mounds of salts “preserve” traces in positive relief on the surface (convex epichnia), while they apparently represent shallowly buried (< 1 cm) traces in negative relief (concave epichnia) on the upper surfaces of older, palimpsest bedding

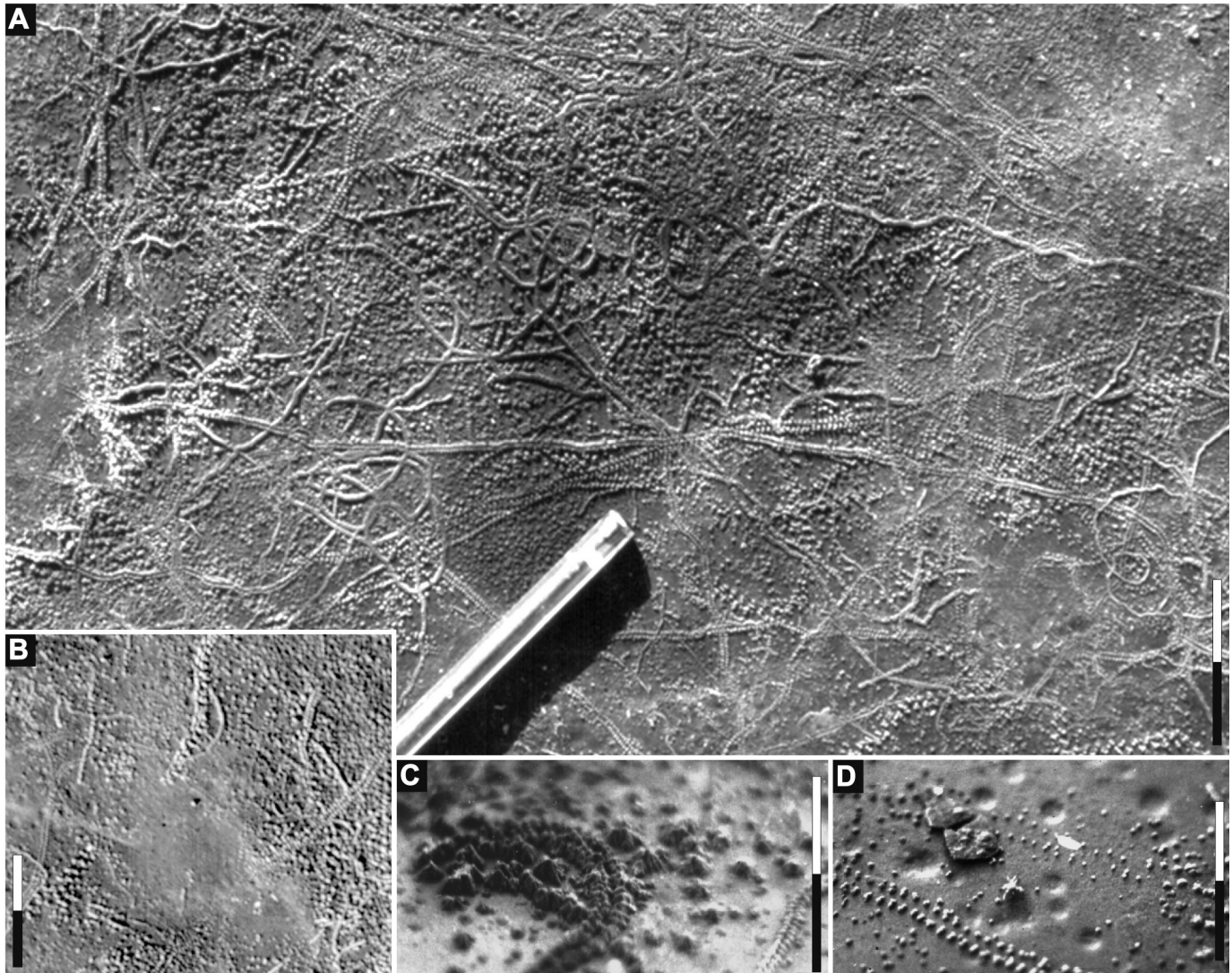


FIG. 8.—Salt tracks and their formation. Scale bars are 2 cm. **A)** “Salt-tracked” surface at Loburu Delta, an hour after heavy rains. **B)** “Missing” portions of salt trackways demonstrate that the subsurface invertebrate traces were formed before salts crystallized on surface. **C)** Oblique closeup of salt “mounds” on wet surface. **D)** Raindrop impressions in wet silts shortly after rains stopped are salt-free, but salt tracks are beginning to form.

planes. In a sense, the salt tracks are “elite” traces (cf. Bromley, 1996); that is, it is through diagenetic processes that they become visible on the surface following rains. The mounds are best developed on damp cohesive clayey silts and silty clays, and poorly developed in loose sediments. X-ray diffraction analyses show that they are variably composed of nahcolite (NaHCO_3), trona ($\text{NaHCO}_3 \cdot \text{Na}_2\text{CO}_3 \cdot 2\text{H}_2\text{O}$), or natron ($\text{Na}_2\text{CO}_3 \cdot 10\text{H}_2\text{O}$).

At first, it was assumed that these mounds were the result of salts crystallizing preferentially in very small depressions (trackways or trails) left by a range of invertebrates traversing the damp sediment surface. However, observations of their formation near the hot springs at central Loburu (Fig. 2B) show that this is not always the case. Silt and mud surfaces that were flat and salt-free developed dense patterns of salt tracks following rainstorms. The tracks appeared almost simultaneously in their final form, about 10–15 minutes after precipitation ended. No organisms were seen to cross the surface during or following the

storms, and no visible tracks or trails were present on the dry surface before the rains. Within an hour, much of the surface was covered in salt tracks (Fig. 8A). These biogenic patterns evidently existed in final form before salt crystallization (Fig. 8B). Excavations below sites of salt-track formation showed the presence of very shallow, continuous horizontal burrows, only 0.2–0.5 cm below the surface, and other zones of high porosity, including a shallow vesicular layer similar to those that form under clay crusts in semiarid soils (e.g., Sullivan and Koppi, 1991; Anderson et al., 2002).

By a process that is not fully understood, the subsurface trace patterns are “transferred” to the surface as it dries out, appearing as patterns of microcrystalline efflorescent salts. The process may be one of very rapid capillary evaporation (Fig. 9) above zones of enhanced shallow permeability such as subsurface trails, very shallow buried tracks, or soil vesicles and irregular cracks. Raindrop-impact prints do not become primary sites for salt crystal-

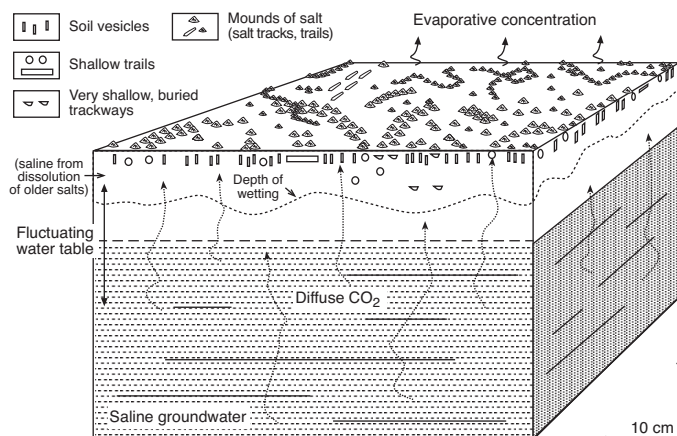


FIG. 9.—Model for formation of salt tracks and trails near hot springs at Loburu. Carbon dioxide gas diffuses upward through saline groundwater (typically 15–30 g l⁻¹ TDS). The CO₂ normally diffuses quietly into the atmosphere, but it is delayed during rainstorms, when the surface layer is water saturated. Rain and runoff dissolve salts near the surface. Within a few minutes of the rain stopping, trapped gases (air and CO₂) escape to form soil vesicles or pass through shallow (< 5 mm) buried traces. At points of escape, salts crystallize rapidly (< 15 minutes) from the saline waters, forming small mounds of nahcolite, trona, or natron, above the shallow zones of high porosity. In so doing, they commonly mimic the shape of the very shallow underlying traces. Competent, cohesive sediments are needed (muddy silts or silty muds) to prevent the shallow trails from collapsing after the organism has passed through the substrate. Very shallow fenestral pores left after decay of buried microbial mats might also act as loci for salt crystallization at the surface.

lization (Fig. 8D), which shows that salt is not crystallizing in a surface trackway.

The mineralogy of the sodium carbonate salts is strongly influenced by temperature and PCO₂. Nahcolite requires high PCO₂ to form (Eugster, 1966) so is normally absent at the land surface. At Loburu, however, CO₂ is probably being degassed through the delta sediments from the shallow geothermal reservoir that feeds the neighboring hot springs. The upward flow of CO₂ can contribute to the rapid crystallization of evaporating Na–HCO₃ runoff and shallow groundwaters and to their nahcolite composition (Fig. 9). Trona forms at sites distant from hot springs where PCO₂ is probably less, and natron crystallizes during cooler nights. Within a few days, the track patterns degrade by deflation. Following the next rainfall, the salt tracks commonly reappear in the same location with the same pattern.

Salt traces, however, are not restricted to mudflats influenced by geothermal activity. Similar patterns have been observed at the Emsos Delta (Fig. 1A), at Lake Magadi (Kenya), and on mudflats around saline lakes in British Columbia, Chile, Bolivia, and Spain. They also form on damp mudflats following rain where concentrated brines lie within a few centimeters of the surface, but they become disguised or destroyed when efflorescent salts gradually encrust the mudflat during desiccation or dissolved during rains. Although the salts do not survive, their presence confirms that benthic invertebrate communities capable of producing a range of traces commonly inhabit saline mudflats (cf. Garcia and Niell, 1991).

Trace Types Represented by Salt Tracks and Trails

Several types of invertebrate traces are represented by the sodium carbonate salts (Fig. 10). They are briefly described and discussed in Table 2. Only a preliminary description and tentative identifications of tracemakers are appropriate because detailed three-dimensional studies have not yet been undertaken. Some patterns likely represent shallow subsurface trackways, whereas others are produced as shallow trails at or just below the buried mudflat surface. The traces are likely to be modern because the unconsolidated sediments are easily disrupted by salt crystallization, desiccation, and more intense bioturbation. Most tracks appear to represent traces along a single, buried bedding plane.

Other Trace Types and Facies Associations

An abundant and moderately diverse assemblage of insect traces was observed in the marginal sediments of Lake Bogoria in June–July, 2001 and 2002, primarily at the Sandai Plain and Loburu. Brief descriptions of the traces and a discussion of their distribution are presented here.

Sepidium Trackways (Fig. 11A).—

Description.—Straight to gently curving, the maximum width of the trackways is ~ 10 mm. Imprints comprise parallel, elongate scratches (< 8 mm length) and perpendicular structures that appear to taper externally (< 3 mm length). Imprint sets have generally alternate symmetry. Stride length is ~ 15 mm.

Discussion.—The tracemaker (*Sepidium* sp.) was directly observed walking on dry, poorly sorted silty sands at Loburu Delta. The differences observed between these trackways and the comparable forms represented by salt tracks (Fig. 10A) likely reflect substrate differences and/or the speed of the tracemakers.

Incipient Skolithos Vertical to Oblique Burrows (Figs. 11B, 11C, 11D).—

Description.—At least three size classes of open, vertical burrows were present on the Loburu Delta: 1–3 mm, 4–6 mm, and 10 mm in diameter. Tumuli were observed at the openings of the smaller burrows, but most had been reworked by rain and/or wind. The largest burrows were commonly associated with pelleted tumuli at their openings; if muddy, they persisted as muddy domes around the burrow opening after rains (Fig. 11D).

Discussion.—The vertical burrows at Lake Bogoria are attributed to the activity of beetles. Both sub-adult and adult tiger beetles (Coleoptera: Cicindelidae) construct dwelling and “temporary shelter” burrows (Stanley and Fagerstrom, 1974) in moist silt to fine sand near the shoreline, accounting for two of the size classes observed: a) adults: 4–6 mm diameter, and b) sub-adults: 1–3 mm diameter.

The larger vertical and oblique burrows (10 mm diameter) were less common than the almost ubiquitous tiger-beetle burrows. The tentative assignment to a staphylinid tracemaker (*Bledius*) is supported by the positive identification of this genus at Lake Bogoria (Tony Drane, personal communication, 2005). The acquisition of three-dimensional data will likely increase the ichnotaxonomic diversity of vertical burrows to include, for example, the ichnotaxon *Polykladichmus*, which has been associated with bifurcated *Bledius* burrows by Uchman and Álvaro (2000). *Bledius* burrows are common in the wet peripheral zones

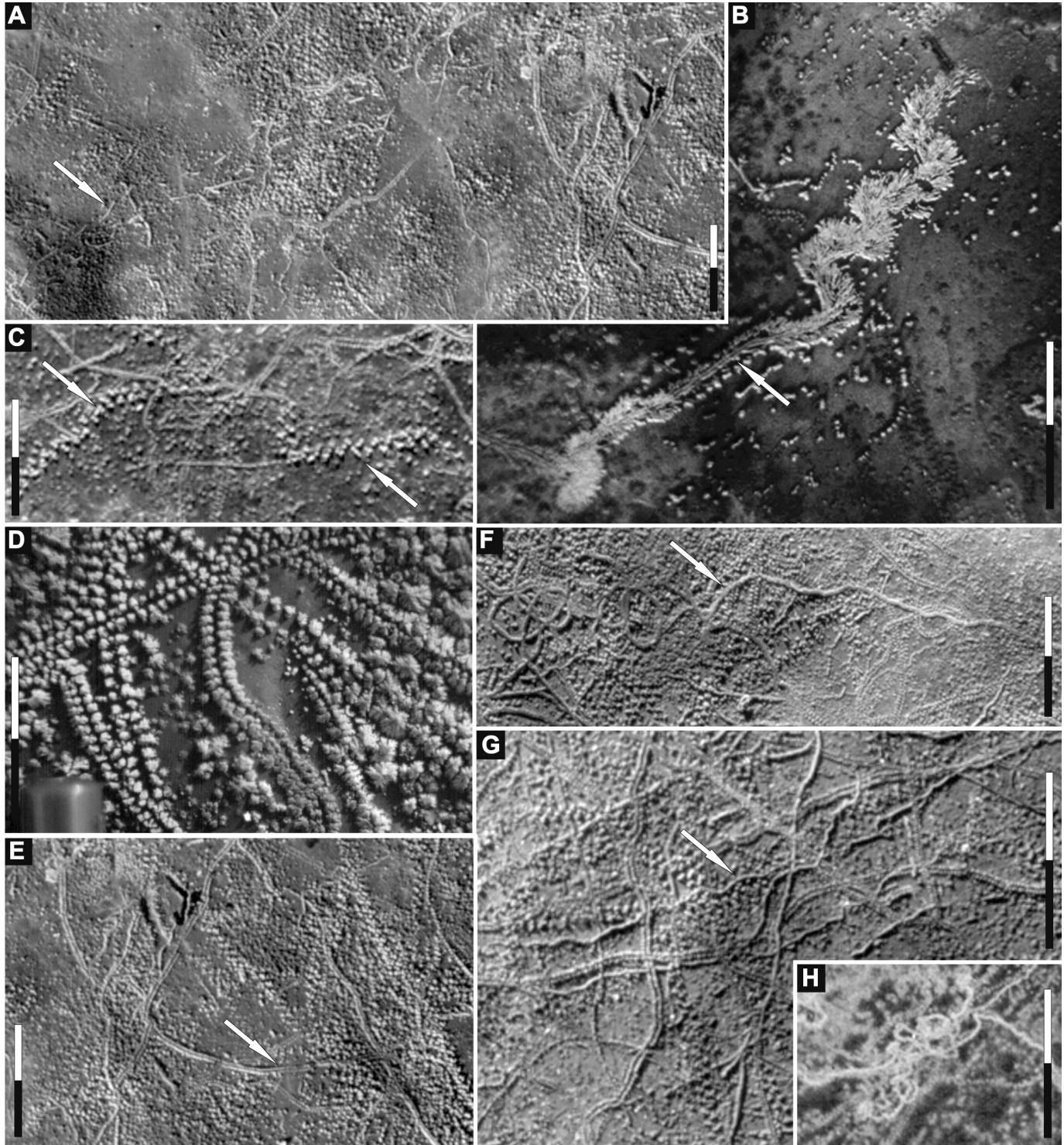


FIG. 10.—Trace types represented by salt tracks and trails. All scale bars are 2 cm. **A)** *Sepidium*-like beetle trackway; arrow highlights trackway. **B)** Incipient *Siskemia* trackway; arrow highlights two continuous grooves along trackway midline. **C)** *Indet.* trackway **A**; arrows highlight groups of three imprints. **D)** Incipient *Diplichnites* trackways with salt mounds beginning to form between traces. **E)** Incipient *Diplopodichnus* trackways; individual imprint impressions are not visible in photograph; arrow shows position of trackway. **F)** Highly looping incipient *Diplopodichnus* trackway; individual imprint impressions are not visible in photograph; arrow highlights position of trackway. **G)** Incipient *Helminthoidichnites* trails; arrow highlights meandering portion of trail. **H)** Incipient *Gordia* trail showing intense looping and unspecialized feeding behavior.

TABLE 2.—Salt tracks and trails. Description and brief discussion of different types and their taphonomy.

Analogous ichnotaxon	Fig.	Description	Remarks
<i>Indet.</i> Trackways A: <i>Sepidium</i> Trackways	10A	Straight to gently curving, the maximum width of this trackway is < 10 mm. Imprints are narrow scratches (1 mm width) that are parallel and sometimes oblique to the midline and are ~ 3–8 mm long, with a stride of ~ 12–15 mm. Track rows are simple. Symmetry is generally opposite, but alternate when turning.	This type is similar to those produced by the tenebrionid beetle <i>Sepidium</i> in dry saline silts of the Loburu Delta in 2002 (Fig. 11A).
Incipient <i>Siskemia</i> Trackway	10B	Trackways (< 5 mm wide) with two grooves along the midline (0.5 mm) and elongate, scratch-like imprints oriented obliquely to the midline. Track rows are simple. The trackway is straight to meandering, and shows angular changes of direction.	Earwigs are the probable trace maker of the <i>Siskemia</i> -like trackways. They have two posterior “pinchers” that could be capable of producing the double groove along the midline of the trackway. Similar trackways have been described from the Devonian Old Red Sandstone of Scotland (Walker, 1985).
<i>Indet.</i> Trackways B	10C	Trackways show alternate symmetry of imprint groups with three circular-shaped imprints per group, although it was difficult to determine the number of imprints per set due to the nature of the salt crystallization. No continuous traces are present. External widths are 4–6 mm; spacing between imprint groups is generally < 2 mm. Individual imprints are < 1 mm in diameter. Trackways commonly crosscut one another and are generally straight, but show angular changes of path direction.	These trackways are very common but are not distinct, mainly because groups of imprint impressions are scattered throughout the surface and are not necessarily part of continuous trackways. Some of these isolated “imprints” may be small (< 1 mm) gas bubbles of associated microbial mats.
Incipient <i>Diplichnites</i> Trackways	10D	Transitional with small <i>Diplopodichnus</i> -like trackways, these trackways are straight to gently curving. Imprints are not grouped, are opposite across the midline, are perpendicular to the midline, and are ellipsoidal to circular in shape, although the shape may be obscured by salt crystallization. There are three size classes: 1) 1–2 mm, 2) 2–3 mm, and 3) 3–4 mm maximum external widths.	The propensity for <i>Diplichnites</i> -like trackways to grade into <i>Diplopodichnus</i> -like trackways is highest for the smallest size class, and not observed for the largest size class. Because of the nature of taphonomic processes involved, this phenomenon may simply be related to salt crystal size, which obscures the distinction between individual imprints in the smallest trails. The three size classes of trackways may correspond with sub-adult stages, perhaps in a (as yet unidentified) beetle.
Incipient <i>Diplopodichnus</i> Trackways	10E, 10F	Straight to gently curving, locally looping or meandering, these bilobed trails are ~ 1–4 mm wide. Width of the median longitudinal furrow is < 0.5 mm. Very closely spaced perpendicular, ellipsoidal imprints are distinguishable and are oriented opposite to one another. The trackways commonly crosscut one another and also other trails and trackways, especially when looping (Fig. 10F).	These trails are transitional with <i>Diplichnites</i> -like trackways, and possibly demonstrate differences in substrate consistency. In some cases, the trackways are unlobed (with a corresponding reduction of external width in half to 1–2 mm), showing imprints from just one side of the midline, again likely demonstrating variations in substrate consistency. Particularly if the maximum external width is < 2 mm, the median furrow is locally not apparent, possibly because the nahcolite crystals are larger than the furrow; thus, the furrow is obscured and the trackway appears unlobed in sections. Similarly, due to apparent taphonomic causes, some examples of the <i>Diplopodichnus</i> -like traces may appear like <i>Cruziana problematica</i> , but with closer inspection, subtle imprints are locally visible. The highly looping and smaller forms likely represent unspecialized feeding behaviors together with locomotion.
Incipient <i>Helminthoidichnites</i> Trails	10G	Unbranched, straight to curving and slightly meandering in places, small (1 mm width), simple, smooth unlobed horizontal trails.	The trails may parallel other traces, such as a ? <i>Sepidium</i> trackway that the <i>Helminthoidichnites</i> -like trail appears to follow along a section of its length. Potential tracemakers may be beetle larvae.
Incipient <i>Gordia</i> Trails	10H	Unbranched, small (1–2 mm maximum width) unlobed trails that are highly looping and self-crossing.	Potential tracemakers of these simple horizontal tunnels are likely the larvae of beetles (e.g., Elateridae: click beetle larvae).

of saline lakes (Gerdes et al., 1985; Hammer, 1986) and are made only in cohesive (moist or microbe-rich) sediments finer than very coarse sand (Smith and Hein, 1971; Garcia and Niell, 1991). The impact of the burrowing activities of these beetles is potentially high: tumuli reintroduce sediment to the surface, where it can be deflated (Smith and Hein, 1971), and vertical shafts can obscure laminations and disrupt buried tunnels and/or vertebrate traces.

Boxwork Burrows (Fig. 11E, 11F).—

Description.—Sediments bioturbated by boxwork burrow systems were observed along the margins of exhumed surfaces that formed “mini-escarpments” at the lake shoreline, and along the margins of pools fed by hot-water seepage (Fig. 11E). Burrows/tunnels are not backfilled, and their diameters are in two size classes: 10–20 mm and 5–6 mm; they may represent adult and sub-adult forms of the same species.

Discussion.—These burrow systems resemble those described for mole crickets (Orthoptera: Gryllotalpinae) by Chamberlain (1975) and Ratcliffe and Fagerstrom (1980); these insects, however, have not yet been positively identified from Lake Bogoria (Harper et al., 2003.). Earwigs observed on the Loburu Delta during this study could be the tracemaker of these boxwork burrows. Similar types of burrows have been reported from Plio-Pleistocene saline, alkaline lake deposits from Tanzania (Schlüter and Kohring, 1992) and Tertiary evaporite-rich (gypsum) lake deposits from Spain (Rodríguez-Aranda and Calvo, 1998).

Incipient Vagorichnus Tunnels (Figs. 11G, 11H, 11I).—

Description.—These smooth, branched and bifurcating, straight to gently curving to looping, open horizontal tunnels may crosscut one another but are generally connected and apparently reused. Pellet-comprised tumuli may be associated with points from which several tunnels radiate, suggesting a possible third dimension to these systems. There are two size classes: 1–2 mm and 3–4 mm width. These traces were observed only where sediments contained thin, moist microbial biofilms.

Discussion.—The horizontal feeding tunnels in saturated sediments at Loburu Delta are very similar to those made by Coleoptera: Heteroceridae: *Heterocerus* (Chamberlain, 1975; Clark and Ratcliffe, 1989) or by Carabidae: *Bembidion*, species tentatively identified from Lake Bogoria (Tony Drane, personal communication, 2005.). Carabid beetles produce burrow systems of horizontal tunnels and vertical shafts (Ratcliffe and Fagerstrom, 1980) that may explain the tumuli associated with some horizontal systems at Loburu.

Heterocerus-like horizontal tunnels associated with tibial spine-scratch ornament were observed in a drying pool near the Sandai River (Fig. 11J) and are also similar to the horizontal tunnels associated with boxwork burrows (Fig. 11F). Two principal factors that control the distribution of *Heterocerus* burrows appear to be sediment cohesion and grain size: enough clay must be present to hold the sediment forming the tunnel “roof” together as it dries (Clark and Ratcliffe, 1989). If the tunnel is at an insufficient depth below the surface, and the tunnel roof is desiccated, the roof may split or collapse (Fig. 11H).

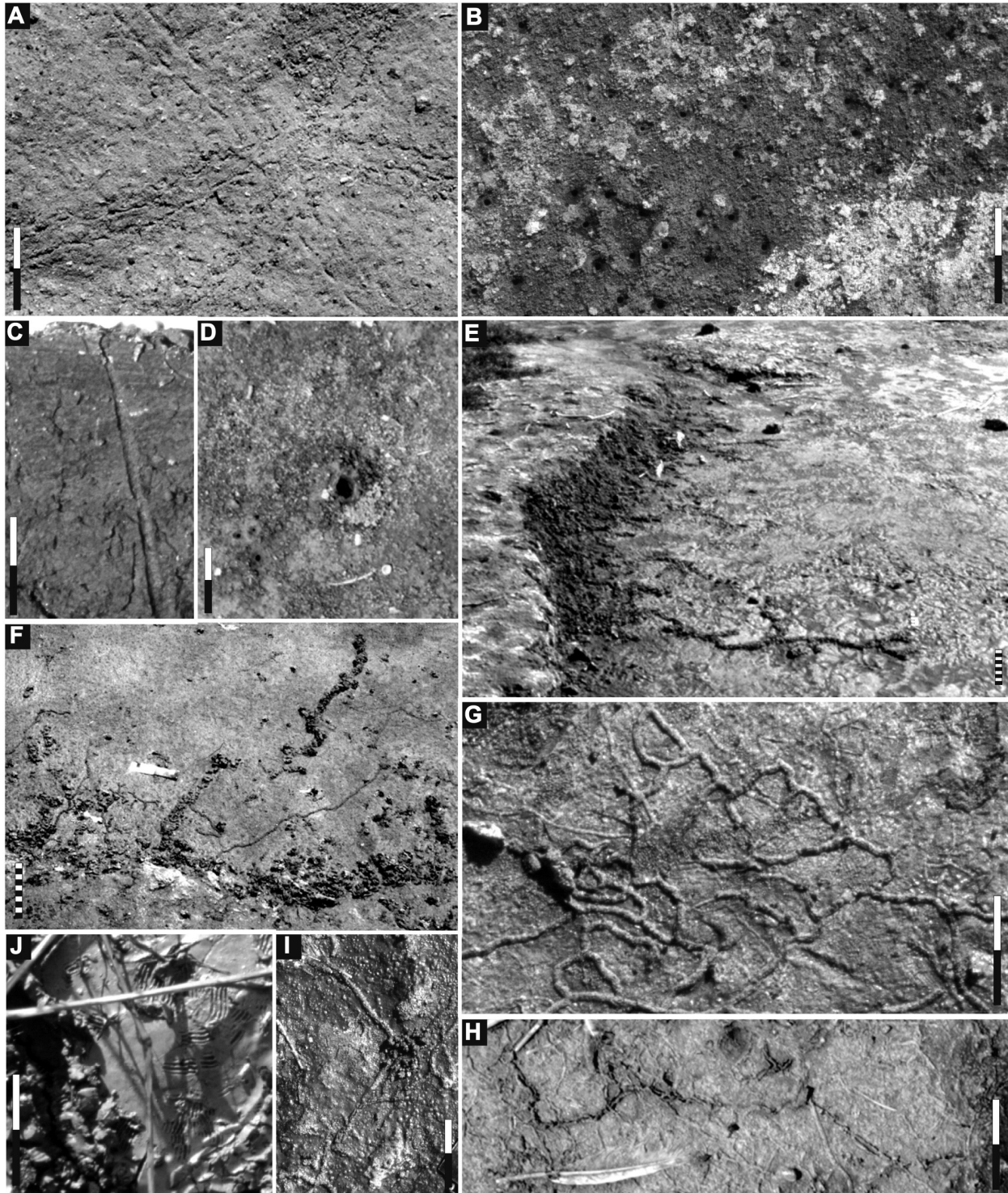


FIG. 11.—Insect traces at Lake Bogoria, 2001 and 2002. All scale bars are 2 cm. **A)** Tenebrionid (?*Sepidium*) beetle trackways on dry salty silts and sands, Loburu Delta. **B)** Plan view of incipient *Skolithos* vertical burrows of tiger beetles in damp, moist silts and sands of the southern Loburu Delta. **C)** Section through slightly oblique tiger-beetle burrow from same locality as burrows in Part B. **D)** Muddy tumulus at opening of larger incipient *Skolithos* burrows at Loburu Delta. **E)** Boxwork burrows in exhumed (semi-lithified) surface at Loburu Delta; tunnels are in recent muds; surface texture is created by flamingo trampling. **F)** Plan view of horizontal ?beetle tunnels associated with boxwork burrows in recent muds at Loburu Delta. **G)** Incipient *Vagorichnus* tunnels in wet, microbe-rich mud at the southern Loburu Delta. **H)** Dried and broken roofs of incipient *Vagorichnus* tunnels. **I)** Tumuli at intersection of incipient *Vagorichnus* tunnels. **J)** Scratch traces of ?*Heterocerus* tibial spines in mud of drying pool near Sandai River.

Vagorichnus, defined by Buatois et al. (1995) from Jurassic lacustrine turbidites, was interpreted as a feeding trace. Commonly, the Jurassic traces were actively backfilled, while those at Lake Bogoria remained open. If preserved, an alternative analogous ichnotaxon for the traces at Lake Bogoria could be *Labyrinthichnus*, described from Tertiary lacustrine deposits in Spain (Uchman and Álvaro, 2000). This ichnogenus is passively filled and includes traces that are composed of irregular nets, locally with vertical or oblique shafts (Uchman and Álvaro, 2000). Uchman and Álvaro (2000) noted the similarity between *Labyrinthichnus* and traces made by carabid or heterocerid beetles.

Invertebrate Trace Assemblages

Despite the lack of backfilled meniscate burrows at Lake Bogoria, most of the traces fall within the *Scoyenia* ichnofacies. This saline-lake-margin assemblage resembles the one described from Permian playa-lake deposits in western Argentina (Zhang et al., 1998), which also lacks backfilled meniscate burrows. It is also similar to the assemblage described for desiccated overbank deposits in arid to semiarid settings in general (Buatois and Mángano, 2004). In summary, Lake Bogoria is a hypersaline lake with an extremely small benthic lacustrine invertebrate fauna (Chironomidae), but with a moderately diverse lake-margin fauna that produces an impoverished *Scoyenia*-like assemblage of traces.

Factors Affecting Distribution of Invertebrate Traces

The most important factors that appear to affect the distribution of invertebrate traces at Lake Bogoria [i.e., (1) substrate cohesion, (2) sediment moisture (cf. Gierlowski-Kordesch, 1991), and (3) the presence of a food source] are strongly related to lake level and proximity to hot springs. Substrate cohesion, for example, is influenced both by the presence of microbes in the sediment, which are abundant near hot springs, and by the clay content, which varies with lake level and proximity to shoreline. Most invertebrate traces at Loburu are in deltaic, moist to saturated silts and fine sands (Fig. 4). Some types of traces are pervasive (e.g., vertical burrows of adult tiger beetles), while others are distributed locally around hot springs and are associated with microbial mats (e.g., incipient *Vagorichnus* tunnels). At Lake Bogoria, incipient *Skolithos* traces do not represent high-energy lacustrine environments, but indicate the sediment moisture levels desired by tiger beetles (cf. Smith and Hein, 1971). Like the deep lacustrine, simple grazing traces within the typical *Mermia* ichnofacies (Buatois and Mángano, 1998), the distribution of incipient *Vagorichnus* horizontal tunnels at Lake Bogoria is related to the abundance of food, which in this case is the microbial films that are associated with saturated substrates and hot-spring outflow.

Substrate consolidation also plays a role in trace distribution (Buatois and Mángano, 2004). At Lake Bogoria, vertical burrows were ubiquitous in exhumed delta-plain surfaces that were somewhat consolidated, but moist, while boxwork burrow systems were found along the erosional escarpments of these surfaces (Fig. 11E). No other trace types were observed on or in the more lithified sediments. Other types of traces (e.g., incipient *Vagorichnus* horizontal tunnels) are distributed according to substrate consolidation, moisture content, and lithology. Bown and Kraus (1983) found that each trace-fossil type in the Eocene Willwood Formation was associated with a particular grain-size range and fluvial subenvironment. The association of certain trace types with sediment texture at Lake Bogoria may simply reflect the proximity to the lake shoreline, which also

contributes to the other factors noted (i.e., cohesion, moisture content).

It is unclear whether the formation of efflorescent Na-CO₃-Cl salts is a factor in the activity of the invertebrate tracemakers at Lake Bogoria (cf. Verschuren et al., 2000), although it certainly could affect the distribution of trace fossils. In the slightly saline lake deposits of the Jurassic East Berlin Formation, New England, evaporitic gypsum might have played a role in the patchy distribution of trace-fossil suites, but their distribution could also have been related to the distribution of ephemeral pools (Gierlowski-Kordesch, 1991). In Carboniferous nonmarine rocks from New Brunswick, Pickerill (1992) reported an absence of ichnofaunas in alluvial-plain ichnofacies, despite the preservation of rhizoliths. A similar situation is present on the modern and late Pleistocene Sandai Plain at Lake Bogoria. Although rare observations of invertebrate traces were made on Sandai Plain, all were near the shoreline or in isolated brackish pools, and not on the dry, salt-encrusted surfaces of the delta plain.

PRESERVATION OF BIOGENIC STRUCTURES IN LAKE-MARGIN SETTINGS

Many factors are known to influence or control the taphonomy of vertebrate and invertebrate traces (e.g., Laporte and Behrensmeyer, 1980; Scrivner and Bottjer, 1986; Cohen et al., 1991; Bromley, 1996; Zhang et al., 1998; Buatois and Mángano, 2004). In continental environments, these factors include sediment texture and mineralogy, sediment moisture levels, frequency of wetting and drying, and many factors specific to the organism that is producing the trace, such as its shape, body mass, behavioral characteristics, and habitat. Some factors are common to all continental environments. Sediment desiccation, for example, produces mudcracks that disrupt traces in many different sub-aerial settings, including supratidal and intertidal mudflats, floodplains, and playas. Similarly, early erosion of traces by water or wind is not limited to a specific environment. In contrast, erosion of traces by ice advance or mineral crystallization, which are restricted by climate, are examples where trace taphonomy is dominated by specific environmental factors.

Saline lake margins provide some unusual controlling factors on trace taphonomy that are absent or less effective in other settings. In this section, we highlight some specific processes that play an important role in preservation and (or) early destruction of traces around the saline-lake margins. Some of these processes (e.g., salt crystallization) also occur in other settings, including marine sabkhas and salinas (marginal lagoons); other processes (e.g., substrate calcification) occur on floodplains and in other nonmarine settings.

Interactions among these factors are especially important: the most obvious changes in trace morphology and impacts on preservation potential are commonly a product of not just several factors acting on the substrate simultaneously, but of the particular interactions among those factors. Some of the factors identified (i.e., clay mineralogy, salinity of pore waters, and the rate of substrate drying) were tested experimentally to determine how they interact to alter impression morphology and lead to the stabilization or destruction of the traces (Scott and Renaut, 2004; Scott, 2005). Other factors were assessed by interpreting processes of preservation at three Pleistocene trace-fossil localities in the Baringo-Bogoria basin.

Impact of Efflorescent Salt Crystallization

The saline, alkaline pore and lake waters at Lake Bogoria play an important role in the taphonomy of vertebrate and inverte-

brate traces, and of primary sedimentary structures in lake-margin environments (e.g., Fig. 7B). The high net evaporation at Lake Bogoria leads to capillary evaporation of saline, alkaline, lake-margin pore waters that contribute to the formation of efflorescent Na-CO₃-Cl salts, both as surface crusts and as interstitial crystals in the shallow vadose zone. Evapotranspiration also locally concentrates salts in littoral marsh settings. The form, quantity, and effects of salts on the sediments are determined mainly by the daily and seasonal weather patterns, sediment texture, the depth and salinity of the associated fluids, and the frequency of inundation by runoff and lake water (e.g., Smoot and Lowenstein, 1991; Renaut, 1993; Smoot and Castens-Seidell, 1994).

The preservation potential of animal traces and primary sedimentary structures is affected dramatically by this salt crystallization, and, depending on environmental conditions, salts may either help to stabilize the substrate temporarily or break it up. The formation of thin crusts on footprint surfaces, commonly produced by evaporated runoff or lake water, can stabilize the substrate and temporarily inhibit deflation (field observations, 2001; e.g., Fig. 6A). Conversely, if salt crystals continue to grow, mainly by capillary evaporation, they will contribute to the disaggregation of the substrate. Sediment grains are physically raised and separated by crystal growth, later collapsing when salts are dissolved by rain or runoff or are removed by deflation (Fig. 7B). By these processes, the morphology (including dimensions) of traces may be modified before burial. These effects were confirmed by experimental studies to determine their impact on impression morphology and to test their interactions (Scott and Renaut, 2004; Scott, 2005). The destructive influence of efflorescent salts on modern vertebrate prints at Lake Manyara, Tanzania, was also mentioned by Cohen et al. (1991).

Zhang et al. (1998) discussed the preservation of invertebrate traces of the Scoyenia ichnofacies in Permian playa-lake deposits of Argentina. They found rare trace fossils in regressive playa and mudflat facies associated with gypsum salts, but also many well-preserved arthropod traces and desiccation cracks at the base of transgressive sheetflood sands. This phenomenon may be related to varying degrees of aridity (Zhang et al., 1998) and the formation of trace-destroying efflorescent salts during arid periods. The invertebrate trace assemblages reported from Tanzanian Plio-Pleistocene (Schlüter and Kohring, 1992) and Spanish Tertiary (Rodríguez-Aranda and Calvo, 1998) saline lakes and their margins are composed only of endichnia. Rodríguez-Aranda and Calvo (1998) also found rhizolites and only rare vertebrate traces that were preserved on muddy bedding planes, perhaps demonstrating the preservational biases against surface trackways in these environments. In fully subaqueous Tertiary lacustrine deposits from the Calatayud-Teruel basin of Spain, only *Beaconites filiformis* was preserved; the lack of other elements of the Mermia ichnofacies and the association with evaporites were attributed to hypersaline conditions (Uchman and Alvaro, 2000).

At Lake Bogoria, the water table is much shallower at the distal parts of Loburu Delta than on the distal Sandai Plain, and the delta gradient at Loburu is lower. Thick salt crusts do not form at Loburu, nor does interstitial salt formation appear to disrupt lamination. Nevertheless, horizontal burrows just below the sediment surface are quickly destroyed by efflorescent salts when the sediment is no longer saturated by hot-spring discharge or littoral groundwater seepage. The higher diversity of the trace assemblage at Loburu may be due to the fresher water input from hot springs (< 5 g l⁻¹ TDS) and the adjacent uplands, and the relatively high water table, which limit the effects of capillary evaporation and salt crystallization by maintaining moisture at the surface.

Sediment Texture and Composition

Sediment texture and consistency not only influence the morphology of animal traces by contributing to the behavioral response of the animal to the substrate and the initial morphology of the traces, but can also influence taphonomic processes that later modify the substrate. Sediment texture directly influences the formation of efflorescent salt crusts by capillary evaporation, by being more effective in fine-grained than in coarse-grained sediments. Similarly, texture can control the rate of percolation of meteoric water through the surface sediments and, where drainage is impeded, may influence the development of sheetfloods (e.g., Lado et al., 2004).

Smectite, illite, and interstratified illite-smectite are common clay minerals in several depositional environments in the East African Rift, particularly in semiarid areas with more evolved saline, alkaline fluids and volcanic or volcanoclastic catchment rocks (e.g., Yuretich and Ervin, 2002; Deocampo, 2004). At Lake Bogoria, X-ray diffraction analyses of the < 2 μm fraction have shown that many recent lake-margin clays are randomly interstratified illites-smectites or smectites. Shrinking and swelling of these clays can have a dramatic effect on trace preservation both by potentially altering trace morphology (e.g., Fig. 7A) and by contributing to trace destruction. Statistical analyses of experimental data have shown that changes in impression morphology due to the swelling and shrinking of smectitic clays were quantifiable, and that the behavior and influence of these clays are partly dependent on pore-water salinity (Scott and Renaut, 2004; Scott, 2005).

Clay mineralogy also has an important effect on "seal" formation in soils from the Lobo Plain (Fig. 1) in the Baringo-Bogoria basin. Lado et al. (2004) showed that kaolinitic and illitic soils, such as the Molo soils on the Lobo Plain, are less prone to seal formation than soils that contain smectites. Rain-resistant seals and crusts form periodically at the surface of the smectitic sediments on the Sandai Plain (e.g., Fig. 6A). The interaction of Na-CO₃-Cl-rich fluids with these sediments can increase dispersion of clays between pores, decrease soil permeability, and lead to formation of seals and soil crusts (cf. Goudie, 1983). Such seal formation can help to maintain the original trace morphology and stabilize surfaces. However, because rainfall infiltration rates are much lower on surfaces with these surface seals, the erosive energy from runoff can increase, thereby enhancing erosion of the underlying sediments (Lado et al., 2004) once the surface crust is broken.

Microbial Mats and Biofilms

Organic matter in sediments generally increases the retention time for pore water, encourages grain cohesion, and thus promotes temporary stabilization of the substrate (e.g., Forster and Nicolson, 1981). Microbial mats and biofilms, which may be detrital or benthic, can facilitate substrate stabilization, especially if composed of benthic filamentous cyanobacteria (e.g., de Winder et al., 1989; Noffke et al., 2003). At Lake Bogoria, the detrital films of planktonic cyanobacteria that settle onto lake-margin muds from retreating lake waters may retard destruction of surface structures by delaying desiccation (Fig. 3C). Benthic mats (< 1 cm thick) and thin biofilms commonly line the base of vertebrate prints impressed in wet littoral sediments (e.g., Figs. 5D, 6B, 6D). With burial by fine mud, the mat-lined prints could resemble skin impressions after lithification, or if buried rapidly under anoxic conditions, the mat may be preserved as a thin carbonaceous film that lines the print surface.

Isolated cyanobacterial communities may also temporarily stabilize *dry* sediments with filaments and extracellular muci-

lage, which may then form a surface crust that is resistant to deflation (e.g., Campbell, 1979; de Winder et al., 1989). These crusts become hydrophobic when desiccated, and inhibit water infiltration, causing runoff and sheet flooding (de Winder et al., 1989). Aggregates formed by microbial trapping of grains have also been shown to reduce wind erosion and to increase the moisture content of the substrate (Forster and Nicolson, 1981). These processes are likely to be active on the Sandai Plain and the Loburu Delta, where hard surface crusts associated with cyanobacteria were observed.

The modern lake, hot-spring, and lake-margin groundwaters at Lake Bogoria contain little Ca^{2+} (Tiercelin and Vincens, 1987; Cioni et al., 1992). If, however, those waters were dilute and Ca-bearing, then benthic cyanobacterial mats on footprinted substrates could become calcified during microbial photosynthesis (e.g., Casanova, 1994; Castanier et al., 2000), enhancing preservation of the substrate. Pleistocene ichnofossils in the Baringo–

Bogoria basin (Fig. 12) are associated with microbial-mat surface textures and stromatolitic coatings into which bird footprints are impressed (Figs. 12C, 12D). Contemporary pore waters at those localities were probably much fresher than those at Lake Bogoria today, based on the extensive calcite cementation (Scott, 2003, 2005). By analogy, calcified stromatolites are forming today on rocky littoral substrates around the northern shores of Lake Baringo, which has a salinity of $< 1.5 \text{ g l}^{-1}$ TDS (Renaut et al., 2000; Tarits et al., 2006).

Microbial mats are clearly an important factor for preservation of some traces, especially where the microbes mediate early calcification of the substrate. Their role, however, is strongly controlled by local environmental conditions, particularly the hydrology and hydrochemistry. Many surficial microbial films on the Sandai Plain are detrital scums (Fig. 3C). With retreat of the lake, the green organic (*Arthrospira*) films desiccate and oxidize, or are incorporated into the shallow sediments when trampled by

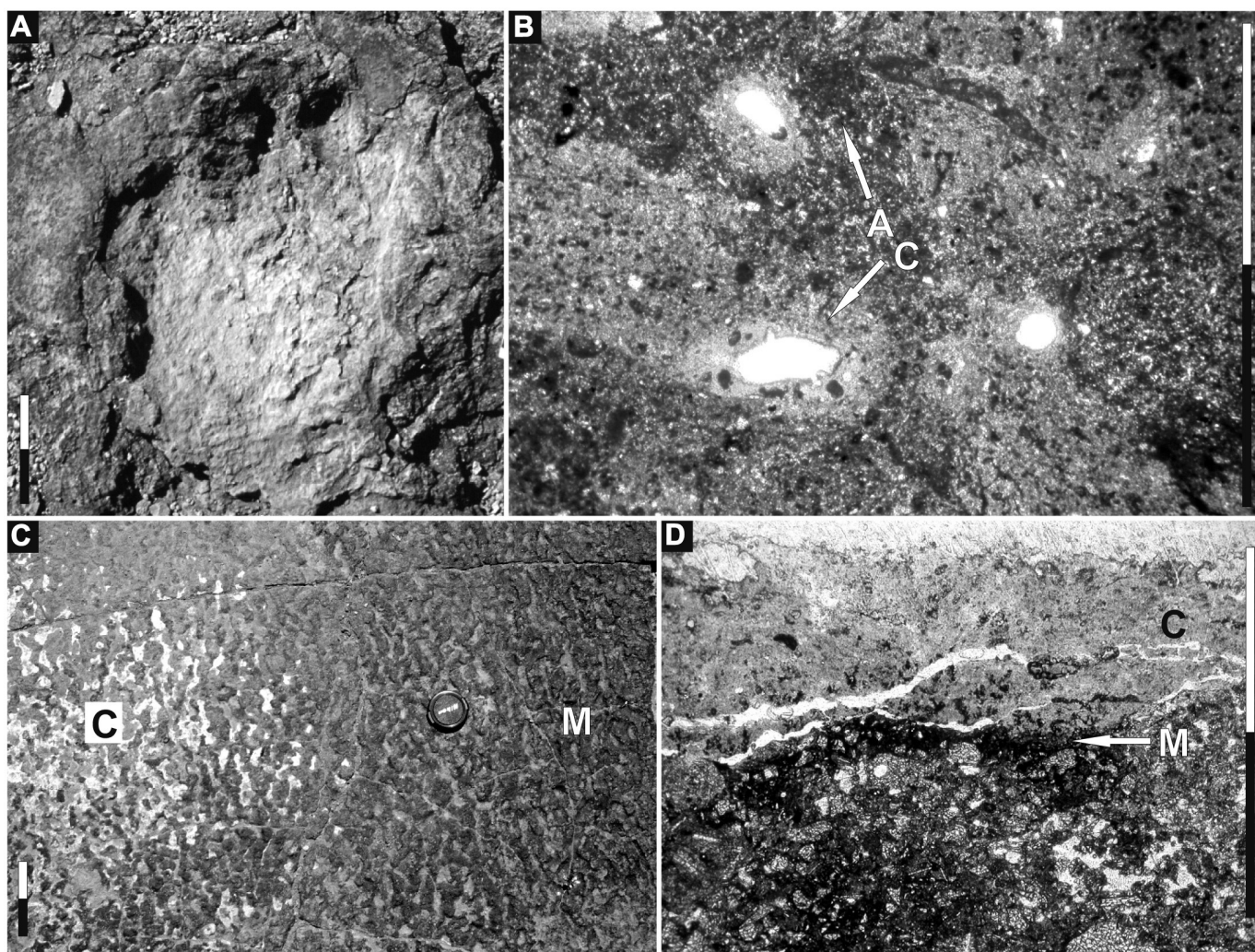


FIG. 12.—Pleistocene trace fossils and preserved surfaces from the Baringo–Bogoria basin. **A**) Pleistocene hippopotamus print preserved in silty sandstone by calcite, zeolites (analcime), and iron oxides; Ilosuwani Formation; scale bar is 10 cm. **B**) Photomicrograph (plane-polarized light) of hippopotamus-print-preserving substrate showing calcite (C) and analcime (A) cements around root hair pores; analcime is also found in the darker sanidine-rich silty groundmass; scale bar is 2 mm. **C**) Pleistocene microbial-mat surface texture associated with preserved bird footprints; whitish surface cements are calcite (C); black surface cements are Mn-oxides (M); scale bar is 10 cm. **D**) Photomicrograph (plane-polarized light) of microsparitic calcite (C) and Mn-oxide-cemented (M) microbial mat surface shown in Part C; scale bar is 2 mm.

flamingos. Any role that these films play in trace preservation is probably temporary or incidental. Only in shallow inlets or abandoned fluvial channels do mats survive for days, weeks, or rarely longer, unless moisture is maintained locally by surface runoff or groundwater seepage. In contrast, the mats at Loburu are mainly benthic, thicker, and more effective in enhancing trace preservation (Fig. 6D). They form where there is nutrient-rich hydrothermal outflow or dilute seepage onto the low-lying littoral sediments of the delta. Not only does this outflow maintain moisture for longer periods than on the Sandai Plain, but the fresher waters attract many animals that produce a higher diversity of prints and invertebrate traces (Fig. 4).

Stabilization by Early Cementation

Preservation of traces is highly favored where the host sediments are cemented during early diagenesis. Processes of cementation are generally slow in siliciclastic sediments compared to carbonate rocks (e.g., Scholle and Ulmer-Scholle, 2003), so unless rapidly buried, most traces are removed by erosion or obliterated by intense bioturbation or compaction before they can be preserved in the rock record. In semiarid environments, however, possibilities for early cementation are much higher than in temperate and humid environments because evaporative concentration can lead to saturation of surface and near-surface waters with respect to several mineral phases at or close to the land surface (Goudie, 1983; Smoot and Lowenstein, 1991; Jones and Deocampo, 2003; Parcerisa et al., 2005).

In saline mudflats, salts may briefly preserve traces by armoring the substrate, as described, but many soluble salts dissolve in runoff at the surface or soon after burial by undersaturated groundwaters (cf. Hay and Leakey, 1982; Smoot and Lowenstein, 1991). Except under extreme aridity, salts are unlikely to cement and preserve traces.

Other minerals, however, can play a role in early preservation. Alkaline-earth carbonates (calcite, aragonite, and Mg-carbonates) are commonly precipitated on saline mudflats as surface crusts and interstitial (vadose) mineral cements where surface and shallow groundwaters undergo evaporative concentration and exsolution of CO₂ (e.g., Eugster and Hardie, 1978; Renaut, 1990; Smoot and Lowenstein, 1991). These processes can be geologically rapid, with partial lithification occurring over time spans of years to tens of years, as shown by anthropogenic artefacts (e.g., bottle caps) cemented in the sediments (e.g., Last, 1992). Biomediation by photosynthetic bacteria and algae can enhance the process (Castanier et al., 2000).

Although the modern mudflats are uncemented, vadose and phreatic calcite cements are present in footprinted surfaces in Holocene and Pleistocene sediments of the Sandai Plain, Loburu, Lobo Plain, and elsewhere in the Baringo-Bogoria basin (Fig. 12). To form these cements implies a periodic supply of relatively dilute (Ca-bearing) surface water or shallow groundwaters, and a sufficient amount of time for cements to form at a given level. A period of environmental stability is needed to cement footprints and invertebrate traces at or just below the land surface. Although the time needed for this cementation remains uncertain, thin sections of footprinted horizons confirm the efficacy of this process (Figs. 12B, D). Once partly cemented, such horizons can then survive multiple episodes of burial and exhumation. Several exhumed calcite-cemented surfaces are present on the Loburu delta plain and the Sandai Plain that preserve vertebrate footprints and flamingo nest mounds (Scott et al., 2003; Scott et al., in press).

Other minerals can also play a role in early cementation of substrates that have been foot printed or host other trace fossils.

Mn- and Fe-oxyhydroxides armor some footprinted surfaces in Pleistocene sediments of the Baringo basin (Scott, 2005), but their origin has not been studied. Some may be similar to desert varnish (e.g., Quade, 2001), implying prolonged stability at the land surface, or a redox process during shallow burial may be involved. Others may form in association with microbial mats (Fig. 12C, D).

Several surfaces with footprints and other trace fossils on the central Sandai Plain, the northeastern margin of the southern lobe of Loburu Delta, and in Pleistocene sediments at Logumukum (Fig. 1), are cemented by calcite and zeolites (mainly analcime: NaAlSi₂O₆·H₂O; Fig. 12A, B). The zeolites formed at the land surface and in shallow soils where clay minerals and volcanic glass reacted with saline, alkaline pore fluids (Hay, 1966, 1970; Renaut 1993; Langella et al., 2001) under semiarid conditions. These reactions can take several thousand years (Hay, 1966), so prolonged stability is again implied for the traces to be preserved after their initial early stabilization.

DISCUSSION

The results of this study confirm that a wide range of vertebrate and invertebrate traces has the potential to be preserved in the sediment sequences of saline lakes. Lake Bogoria, with a salinity of 60–100 g l⁻¹ TDS, has modern traces associated with a diverse mammal, reptile, bird, and invertebrate fauna, most of which need fresh water. Many organisms that produce traces do so at or near sites of freshwater inflow from ephemeral streams, hot springs, and groundwater seepage, including the large flamingo population, which sometimes exceeds a million birds (Fig. 4). In the geological record, however, the strata that contain these traces are intercalated with lacustrine beds containing bedded evaporites and laminated organic-rich mudstones and shales that formed under anoxic conditions (Renaut and Tiercelin, 1994) with few, if any, preserved traces. Significantly, many modern traces are forming in lake-margin environments while hypersaline anoxic sediments are accumulating in the deeper parts of the lake. The two subenvironments are contemporary, but the lateral distance between them is < 2 km in places.

Lake level partly dictates the distribution and the taphonomy of different types of vertebrate and invertebrate traces, as well as the processes that act on substrates in specific regions of lake-margin environments (cf. Cohen et al., 1991; Buatois and Mángano, 2004). At Lake Bogoria, these processes include, for example, efflorescent salt formation and substrate stabilization by microbes in the sediment. The shoreline position is particularly influential on animal behavior and thus the distribution of traces (e.g., Cohen et al., 1993). With vertebrates, shoreline position helps to determine the behaviors in which they may engage at a particular place (e.g., warthogs and mud baths; nest-building activities of flamingos; Fig. 4). Invertebrate behavior is also closely linked to shoreline position, especially because of the influence of lake level on sediment moisture content and microbial food sources along the lake margins (Fig. 4).

The close association of invertebrate and vertebrate trace assemblages with deltaic subenvironments (e.g., areas with freshwater input) at Lake Bogoria implies that changes in lake level will not cause simple linear lateral shifts in trace assemblages with changes in shoreline position. Rising lake level is commonly accompanied by decreasing salinity and vice versa, so trace assemblages respond to the changing ecology as well as shoreline location. Changes in hydrochemistry can modify both animal behavior and early taphonomic processes, especially those involving the formation of efflorescent salts and early cementation. Similarly, subaerial hot-spring outflow on the margins of Lake

Bogoria is important for vertebrate behavior and the growth of benthic microbial mats that encourage the trace-making behaviors of invertebrates. Because the location of most of the springs is stable and related to faults, rising lake level may submerge the springs, if not the entire delta plains, and cause a major change in trace distribution relative to the shoreline.

Changes in lake level reflect climatic and weather patterns, and tectonic influences. Lake-level changes in closed basins often affect large areas, especially at deltas or mudflats where the gradient is low (Smoot, 1985). Trace assemblages may reflect the type of basin (overfilled, balance-filled, or underfilled of Bohacs et al., 2000) because they respond to this temporal variability in lake level and periodic desiccation of the substrate (Buatois and Mángano, 2004).

Although several hundred thousand flamingo prints were present near the shoreline of the Sandai Plain during 2001 and 2002 (Fig. 3A), few are likely to be preserved. Footprinted horizons and invertebrate ichnofossils are present in many saline mudflat sequences (e.g., Scrivner and Bottjer, 1986; Renaut et al., 1999), but some sequences are barren except for a few horizons with rich ichnofaunas. In some cases, this may reflect the total absence of macrofauna (e.g., environmental extremes such as hypersalinity or absence of freshwater), but in other cases (e.g., in massive mudstones) the absence may be due to nearly total disruption or poor preservation.

Desiccation is a commonly cited mechanism (e.g., Tucker and Burchette, 1977; Smith, 1993) for preserving footprints on mudflats, and can be effective in temporarily stabilizing footprints and invertebrate traces along lake margins when water levels are relatively stable or during small-scale lake regression (e.g., ~1–2 m at Lake Bogoria). Such desiccated surfaces may survive nearly intact following low-energy lacustrine transgression, particularly if seals have formed at the surface because of soil crusting or early calcite cementation. Although soil crusts can induce erosion (Lado et al., 2004), the low gradients in the littoral zone prevent incision during periods of stable lake levels, allowing unchanneled waters to flow across the low-angled surfaces. With frequently changing lake levels, however, opportunities for incision (falling) and littoral erosion (rising) increase, reducing opportunities for preservation. On saline mudflats, disruption resulting from salt crystallization tends to increase with falling lake level and the increasing salinity of shallow lake-margin groundwaters. Concurrently, however, runoff is likely to decrease, reducing fluvial erosion on the peripheral mudflats. Rates of lake-level change are also important. A rapid fall in lake level, for example, may remove mudflats from the influence of saline groundwater, whereas a rapid rise across a low-angle deltaic setting may allow burial of the stabilized mudflat surface, particularly if accompanied by increased sediment yield in the catchment.

The conditions that allow preservation of trace fossils in saline mudflats require the complex interplay of many factors, some of which destroy traces, whereas others favor preservation. Semi-arid climates are especially suitable for trace preservation because desiccation events are prolonged and the precipitation of authigenic minerals is enhanced. Periods of lake-level stability (e.g., only ± 2 m range at Lake Bogoria), when the lake is at an intermediate level, are probably the most favorable for ichnofossil preservation in mudflats of closed basins.

Vertebrate and invertebrate trace distribution, morphology, and taphonomy around Lake Bogoria reflect aspects of the geological setting and the various lake-margin subenvironments. Basin morphometry, hydrochemistry, catchment-rock mineralogy, and cool-spring and hot-spring distribution, together with climate and the physiology and behavioral ecology of animal

species, all determine the characteristics of trace assemblages observed at Lake Bogoria.

CONCLUSIONS

Preliminary study of the modern biogenic activity and recent traces in the marginal environments of Lake Bogoria has led to the following conclusions:

1. Although saline lacustrine environments are not conducive to high faunal diversity, local subenvironments around the lake margins (e.g., springs, ephemeral streams), provide areas with moderate vertebrate and invertebrate diversity.
2. Factors that control trace distribution in the lake-margin environments include sediment texture and moisture content, substrate cohesion, substrate consolidation, and the presence or absence of microbes in benthic mats or detrital films.
3. Efflorescent salts derived from capillary evaporation of shallow groundwater and evaporated runoff can modify the morphology of traces or destroy them.
4. Microbial mats and biofilms in which vertebrate and invertebrate traces have been formed or that locally cover tracked or burrowed surfaces may temporarily protect traces, especially where fluid chemistry allows early calcification.
5. Soil crusting and seal formation can help to stabilize mudflat surfaces and protect traces from erosion.
6. Clay mineralogy is important in trace preservation and taphonomic alteration of trace morphology. Smectites and expansive clays, while promoting seal development, can also modify the traces with repeated wetting and drying.
7. Evaporation of dilute surface waters (runoff) and shallow groundwaters can lead to early carbonate cementation, which helps to stabilize the substrate. With prolonged stability, zeolites and other minerals (Mn- and Fe-oxyhydroxides) may cement mudflat surfaces containing traces.
8. Lake level is a fundamental control on the distribution and taphonomy of invertebrate and vertebrate traces. Changes in lake level do not simply cause linear lateral shifts of trace assemblages, but may cause major changes in trace distribution relative to shoreline because of the interaction of several sedimentological processes with evolving surface-water and pore-water chemistry and animal behavior.

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