

PALEOBOTANY AND SEDIMENTOLOGY OF LATE OLIGOCENE TERRESTRIAL STRATA FROM THE NORTHWESTERN ETHIOPIAN PLATEAU

J.L. García Massini, B.F. Jacobs, and N.J. Tabor

ABSTRACT

This paper describes the sedimentology and paleobotany of a Late Oligocene (27.36 ± 0.11 Ma) succession of volcanoclastic strata from the Margargaria River region, northwestern Ethiopian Plateau. Sedimentology indicates fluvial deposition of clay- and silt-rich strata during the early sedimentary phases, whereas organic-rich deposits and massive and fluvially-reworked ash layers are increasingly more common in the middle and upper parts of the succession, respectively. Periods of interrupted deposition are indicated by three paleosol types present in the basal and middle parts of the succession. Paleobotany documents an exclusively angiosperm flora typical of riparian environments in the lower parts of the succession, and a flora dominated by ferns and a few angiosperm taxa typical of disturbed environments in the middle and upper parts. Sedimentology and paleobotany, combined, indicate a riparian environment inhabited by angiosperms for the lower part of the succession, characterized by rather calm deposition by meandering streams. The middle and upper parts of the succession represent transient environments colonized by pioneer vegetation consisting of a diverse fern community and fewer pioneer angiosperms, characterized by deposition of organic- and ash-rich strata in situ in ephemeral ponds and by small-scale crevasse-like channels and by aerial means on the landscape, respectively. Physiographic changes are interpreted to have resulted directly from the influence of volcanism on the surface environment. In summary, this study shows that the volcanic activity associated with the elevation of the northwestern Ethiopian Plateau during the Oligocene repeatedly influenced the development of plant communities and paleoenvironments, favoring the succession of heterogeneous ecosystems on short temporal and spatial scales. Finally, this study is the first that combines paleobotanical and sedimentological data for paleoenvironmental reconstruction and understanding of plant community dynamics in Paleogene deposits from Africa, and it demonstrates the advantages of a multiproxy approach for assessment of paleoecosystem dynamics on an unstable landscape.

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PE Article Number: 13.1.6A

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Submission: 27 July 2008. Acceptance: 19 January 2010

García Massini, J.L., Jacobs, B.F., and Tabor, N.J., 2010. Paleobotany and Sedimentology of Late Oligocene Terrestrial Strata from the Northwestern Ethiopian Plateau. *Palaeontologia Electronica* Vol. 13, Issue 1; 6A: 51p;
http://palaeo-electronica.org/2010_1/184/index.html

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Key words: Ethiopia, Oligocene, microstratigraphy, paleosols, ferns, angiosperms

INTRODUCTION

Volcanogenic deposits are valuable for the creation and preservation of in situ sequential stages of biotic change not commonly represented in the fossil record (e.g., Spicer et al. 1985; Taggart and Cross 1991; Hoffman et al. 1997; Falcon-Lang and Cantrill 2002; Johnson 2007). These might otherwise be represented by fluvial or lacustrine sediments, which are more likely to preserve transported and time-averaged fossil plant assemblages (e.g., see Spicer 1991; Georgieff et al. 2004). Additionally, volcanogenic sediments offer the possibility of age control using radiometric analysis, biochronology, and paleomagnetic reversal stratigraphy (e.g., Kappelman et al. 2003). This paper describes autochthonous and parautochthonous plant assemblages preserved within Oligocene volcanoclastic strata from Chilga Woreda (Chilga), northwestern Ethiopia, that show increasing, although intermittent, activity in terms of ash supply.

The Paleogene of Africa is represented by a limited number of fossil localities, most of which are coastal (e.g., Late Eocene - Early Oligocene Fayum, Egypt [Bown et al. 1982]). Late Oligocene (27 Ma) terrestrial fossiliferous deposits from Chilga discussed in this paper are among the few known Paleogene examples from the inland African tropics (Kappelman et al. 2003; Feseha 2005; Jacobs et al. 2005; Jacobs 2006). In addition, Chilga contains the only known Late Oligocene strata in Africa that preserve both plant macrofossils and vertebrates (Kappelman et al. 2003; Jacobs et al. 2005; Pan et al. 2006). Fossil assemblages from Chilga consist of fruit, seed, and leaf taxa with Guineo-Congolian and East African affinities and an Afro-Arabian endemic fauna (Kappelman et al. 2003; Sanders et al. 2004; Jacobs et al. 2005; García Massini et al. 2006; Pan et al. 2006). Among these plant remains are fern and angiosperm macrofossils. Ferns in particular are poorly represented elements of Cenozoic plant communities and contribute relatively little to environmental

reconstructions in Africa based upon macrofossils (Jacobs 2004, 2006; García Massini and Jacobs 2009). In fact, only a limited number of African fern macrofossils are known (e.g., García Massini et al. 2006). However, based on their Cenozoic palynological record, ferns were diverse, although generally not as diverse as angiosperms (see e.g., Sah 1967; Yemane et al. 1987a, 1987b). The depauperate African fern macrofossil record relative to angiosperms may be a reflection of lower fossilization rates, lesser abundance and diversity, greater challenges to identification, or a combination of these factors. Ferns, in general, do not shed their leaves or other macroscopic plant parts. Instead, they weaken, rot, or fragment while still attached to the parent plant and are most likely to enter the fossil record when buried in situ (Spicer 1991). This suggests that even if ferns were as abundant and diverse as angiosperms during the Cenozoic, they may not have been fossilized without rapid in situ burial, such as in instances of volcanogenic ash deposition.

Deposits from Chilga include a number of tuffaceous strata deposited in a moist tropical climate (Feseha 2005; Jacobs et al. 2005), which accumulated during early development of the East African Rift in association with flood basalt eruption (Hoffman et al. 1997). Sedimentological and paleobotanical data presented herein from a coherent set of tuffs, called Ash-IV, document plant assemblages preserved within an unstable landscape characterized by rapid, and perhaps catastrophic, deposition of volcanic ash-derived sediments. The objective of this paper is to reconstruct the evolution of the paleoenvironment represented by the Ash-IV sequence by high-resolution (cm-dm) analysis of sediments, lithologies, paleosols, and plant macrofossils. A thin set of volcanoclastic strata immediately below Ash-IV is also described and used as a point of reference for paleoenvironmental conditions prior to deposition of the more tuffaceous strata.

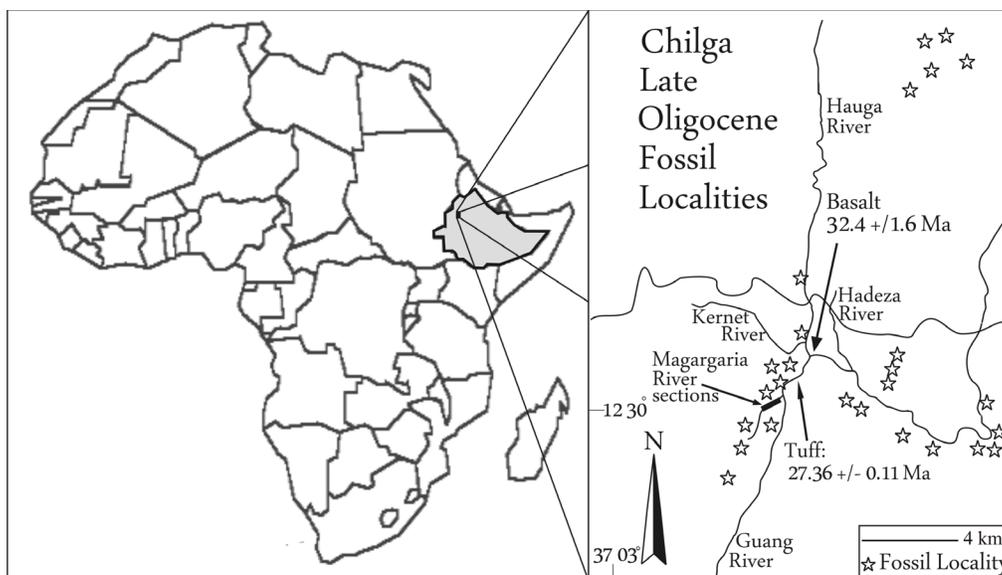


Figure 1. Map of Africa with Ethiopia depicted in gray color. Enlarged area (modified from Kappelman et al. 2003) shows Late Oligocene fossil localities along the Margargaria River in Chilga on the northwestern Ethiopian Plateau. Radioisotopically dated tuff and basalt samples were collected from the areas indicated by arrows.

GEOLOGICAL SETTING

The study area is part of a series of terrestrial deposits that form an informal lithostratigraphic unit named Chilga strata (or Chilga beds). These strata are located 60 km west-southwest of Gondar on the northwestern Ethiopian Plateau (Figure 1). The Chilga beds (~100 km²) consist of a succession (up to 150 m thick) of volcanoclastic sediments and paleosols intercalated with volcanic deposits (Feseha 2005; Jacobs et al. 2005). These strata overlie a plateau of massive flood basalts extruded during Oligocene volcanism (Yemane et al. 1987a; Jacobs et al. 2005; Hoffman et al. 1997). A K-Ar radiometric age of 32.4 ± 1.6 Ma was obtained from basalt that directly underlies the Chilga sedimentary strata (Figure 1) (Kappelman et al. 2003).

The Ash-IV sequence occurs stratigraphically above the dated basalt and is the thickest (up to 20 m) and the least weathered of the tuff sequences in Chilga. This tuff sequence has been used as a guide to correlate sedimentary units laterally across the basin, and contains abundant plant macrofossils (García Massini et al. 2006). An ⁴⁰Ar/³⁹Ar age of 27.36 ± 0.11 Ma was obtained from the Ash-IV sequence itself where it is exposed along the margins of the Guang River (Figure 1) (Kappelman et al. 2003). Sections of Ash-IV and of the thin set of volcanoclastic strata immediately below are exposed along the margins of the Margargaria River (12° 30' 31.3", E 37° 6' 57.3") and are the subject of this paper (Figures 1, 2).

MATERIALS AND METHODS

Three stratigraphically equivalent sections that span the entire (Ash-IV and pre-Ash-IV strata) sequence of volcanoclastic strata exposed along the Margargaria River were excavated, sampled, and described in detail (Figure 3). These range in thickness from 6.31 (southernmost) to 7.01 meters (northernmost), and represent a total lateral distance of approximately 30 meters. A total of 80 sedimentary layers were described among these three sections based on sedimentology, lithology, distribution of plant macrofossils, and paleosols (Figure 3). Based upon observable differences in bedding, grain size distribution, texture, sedimentary structures, biogenic structures, and fossil content, these 80 sedimentary layers were assigned to seven different depositional units (A-G). Complementary data about the mineralogy of the sediments of the different depositional units were obtained from petrographic analysis of thin sections following established methods (Moorhouse 1959). In addition, the mineralogical composition of host matrix sediments for strata representative of the different depositional units was determined by X-ray diffraction analysis of powdered samples using a Rigaku Ultima III X-ray diffraction system equipped with CuK α radiation (Moore and Reynolds 1997). Data were collected over 2-70° 2 θ in continuous scanning mode at 1° 2 θ /min, 30mA and 40 kV.

Paleosols were distinguished based on organic matter content, soil structure and mineral-



Figure 2. Panoramic view of a continuous outcrop from Late Oligocene volcanoclastic strata, exposed along the margins of the Margargaria River (12°30'31.3" N 37°6'57.3" E) in Chilga, northwestern Ethiopian Plateau. Geologic sections excavated and studied in detail are indicated by the red arrows.

ogy, mottling, horizonation, and color (Retallack 1988; Mack et al. 1993; Tabor et al. 2002). The fossils discussed herein were collected from layers distributed among the three geological sections (Figure 3). Geological section CH-79 was collected more intensively, preferentially collecting potentially identifiable specimens rather than every fossil fragment. Plant macrofossils were identified by comparisons with published modern reference materials and use of a variable pressure SEM and standard light microscopy. The total number of specimens from each section (CH-79=247, CH-93=68, CH-89=47) represents a minimum number because most samples (i.e., rocks) contain more than one leaf, megaspore, or other plant part of the same or different taxa.

RESULTS

Sedimentological Data

The sedimentary strata described in this paper have been assigned to seven different depositional units in order to provide a standardized geological framework for analysis of the distribution of sediments throughout the three stratigraphic sections. Each of these stratigraphically equivalent sections is depicted in Figure 3. A systematic description of the different depositional units among the stratigraphic sections is provided below (Table 1, Figure 4.1-4.3).

Depositional unit A (cross-laminated sand). This depositional unit is characterized by cross-laminated fine to very fine sandstones (Figures 3, 4.1-4.2, Table 1). Commonly, these sandstones are bounded by finer-grained horizons, from which they are separated by sharp to hummocky contacts; there is one example where an A sandstone is underlain by a massive sandstone (Figure 3, CH-89, unit 8). Some A units can be traced stratigraphically between sections (Figure 3, CH-79, unit 17 and CH-93, unit 18). The A sandstones are poorly

sorted and contain ferruginized horizons and intraformational clasts. Other less important macrofeatures include small rooting structures, root halos, and rare mud drapes, which include concentrations of fossil organic matter. Petrographic analysis of these sandstones documents abundant concentrically-arranged iron-oxide nodules in a matrix whose main micro-feature is partial to complete coating by reddish iron-rich cement, whereas interstitial spaces are sometimes filled with chalcedony cement (Figure 5.1). Also present are abundant angular volcanic rock fragments and other grains including subrounded to angular feldspars, hornblende, and pyroxene (Figure 5.2-5.4). Sedimentary units also display opaque particles and disseminated bits of organic matter (Figure 5.5). XRD analysis indicates the presence of smectite and kaolinite in addition to the previously mentioned minerals/rocks (Appendix 1).

Interpretation of A depositional units. Based upon the presence of cross laminations and intraformational clasts, A sandy depositional units represent fluvial deposits of low to medium flow speed (Miall 1996). In particular, based on the fact that these sandstones are commonly adjacent (in a vertical sense) to finer-grained horizons, their deposition implies an ephemeral, energetic discharge of sediments, and, in this sense, they may represent levee/crevasse deposits typical of fluvial environments (Miall 1996; Boggs 2006). Such a change in the intensity of sedimentary discharge with respect to vertically adjacent depositional units, and therefore the origin of these types of deposits, can be the result of changes in slope, sediment size, and/or the presence of easily erodible bank materials (Mader 1985). Some A depositional units can be traced stratigraphically between sections, which is consistent with their being sheet-like deposits formed during flooding of the overbank. The abundance of macro- and micro-scopic accumulation of iron indicates well-oxygenated depositional condi-

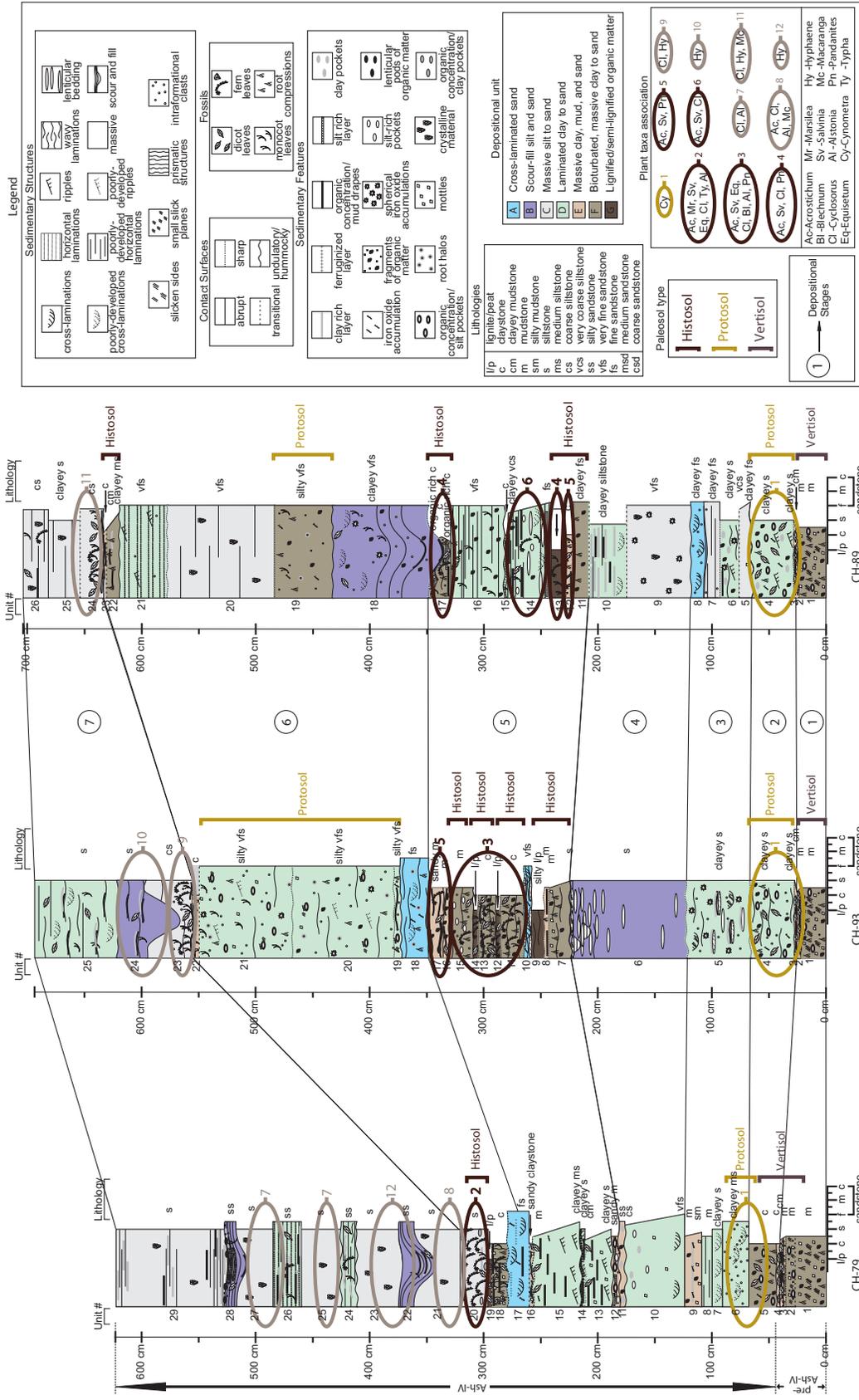


Figure 3. Detailed stratigraphic representation of the three (CH-79, CH-93, CH-89) geologic sections from Late Oligocene volcaniclastic strata exposed along the margins of the Margargaria River in Chilga, northwestern Ethiopian Plateau. Horizontal and oblique lines connecting the sections indicate stratigraphically correlatable sedimentary units and delineate different depositional stages.

Table 1. Classification of Late Oligocene Margargaria River strata into depositional units.

| Facies code | Depositional unit | Sedimentary structures | Interpretation |
|-------------|-------------------------------|--|---|
| A | Fine to very fine sand | Cross-laminated | Ephemeral fluvial deposit of low to medium flow speed (i.e. crevasse splay) |
| B | Silt and very fine sand | Scour and fill and faintly cross-laminated | Ephemeral small scale channel deposit (i.e. chute) |
| C | Silt to fine sand | Massive to faintly laminated | Sediment-gravity flow deposits (i.e. airfall ash) |
| D | Clay to fine sand | Cross- to horizontally-laminated | Reduced traction flood deposits (i.e. overbank deposit) |
| E | Clay, mud and, very fine sand | Massive | Organic- and clay-rich lag deposits from small streams (i.e., mud drape) |
| F | Clay to very fine sand | Massive and bioturbated | Root bed (i.e. paleosol) |
| G | organic matter | Poorly-laminated | <i>In-situ</i> deposits of organic matter (i.e. lignite) |

tions, which is consistent with the sudden discharge of these fluvial deposits (Miall 1996; Boggs 2006). The presence of rooting structures and root halos indicates subaerial exposure and plant colonization of some of these sandstones. A volcanic origin for these sediments is inferred from the abundance of volcanic rock fragments and feldspars, hornblende, and pyroxene. Smectite and kaolinite in the A depositional unit probably originated from rapid weathering of available local or regional volcanic source rocks, and their co-occurrence in these strata is consistent with variable (mild to moderate) weathering and diagenetic intensity and duration regulated by the availability of water in the environment (Bohor and Triplehorn 1993; Moore and Reynolds 1997). In particular, kaolinite indicates better drained, more acidic, more extensively weathered, and more diagenetically altered soils than smectite (Bohor and Triplehorn 1993; Moore and Reynolds 1997). Kaolinite may have also formed *in situ* by acidification of the soil through plant material decomposition (Khademi and Arocena 2008; Bohor and Triplehorn 1993).

Depositional unit B (scour-fill silt and sand).

This depositional unit includes siltstones and very fine sandstones that show scour and fill structures and also may contain well- to poorly-developed trough cross-laminations (Figures 3, 4.1, 4.3, Table 1). Typically, the lower limits of B depositional units scour the upper boundary of the preceding (underlying) unit or have a flat boundary, while laterally some units grade into A depositional units (e.g., Figure 3, CH-89, unit 18 and CH-93, unit 18). Towards the upper contact of some B depositional units, lenses of ashy material and small-scale channel-like structures that grade into the succeeding unit are present. B depositional units are poorly

sorted and contain intraformational clasts, spherical iron oxide accumulations, clay- and organic-rich layers, and other organic remains, including poorly preserved leaves and twigs usually concentrated at the base of the unit. Petrographic data document a massive to finely-laminated silt- and organic-rich matrix that includes abundant volcanic grains, such as elongated glass shards and other angular fragments (Figure 5.6). These units also include bentonite bubbles, angular to subangular feldspar crystals, which are sometimes coated by iron-rich cement, and microscopic intraformational clasts (Figures 5.7-5.8). Other less abundant microfeatures are small pyroxene crystals, opaque particles, and concentrically arranged iron oxide accumulations and halos, which sometimes are rimmed by chalcedony cement (Figure 5.9). XRD analysis of the sediments indicates the presence of smectite, illite-smectite, kaolinite-smectite, and albite (Appendices 2-3).

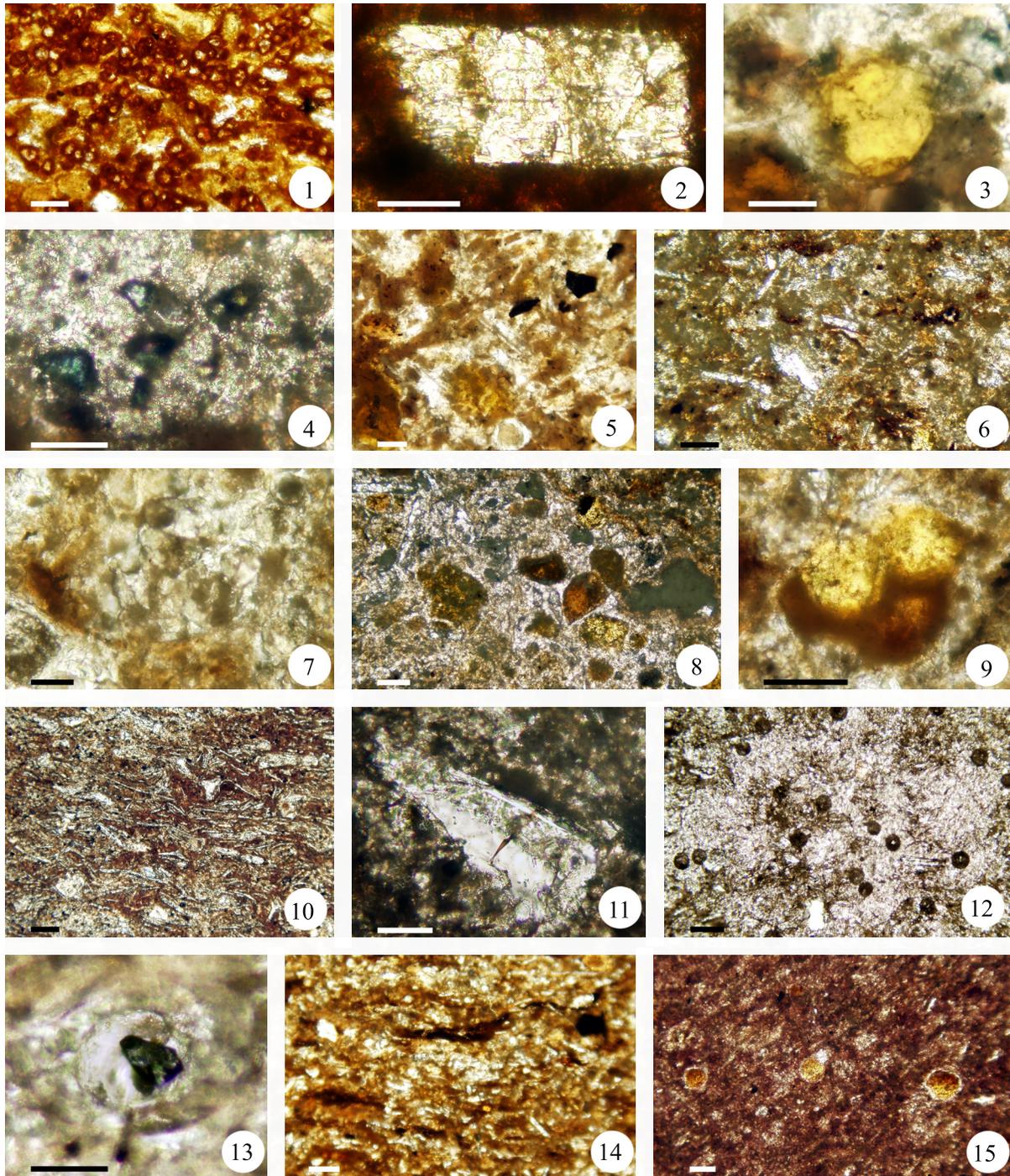
Interpretation of B depositional units. Based on the features observed, B depositional units are interpreted as small channel-like incisions formed during episodes of rapid erosion followed by more or less gentle deposition (Miall 1996). Deposits of this kind are associated with fluvial environments and can be produced by means of high energy ephemeral streams of intermittent sedimentary discharge (Boggs 2006). Occurrence of these types of streams and their associated sedimentary deposits is promoted by an abrupt increase of sediment load, resulting in rapid clogging and avulsion across a floodplain (Boggs 2006). B and A depositional units are gradational deposits differing in discharge intensity of stream sedimentation cutting across the banks of a floodplain, where the former represents a more energetic deposit based on the deeply scoured top of the preceding unit (Miall



Figure 4. Field-scale photographs of Late Oligocene volcanoclastic strata in the Margargaria River localities, north-western Ethiopian Plateau. 4.1 General view of outcrop showing strata arranged into seven different depositional units (A- cross-laminated sand, B- scour-fill silt and sand, C- massive silt to sand, D- laminated clay to sand, E- massive clay, mud, and sand, F- bioturbated, massive clay to sand, G- lignified/semi-lignified organic matter). Man (Mr. Gebre Meskal) for scale = 175 cm. 4.2 Close-up view of A, C, D, E, F, and G depositional units showing their relative thicknesses, sedimentary structures, and contact surfaces. See text for discussion. Scale bar equals 25 cm. 4.3 Close-up view of C and B depositional units showing their relative thicknesses, sedimentary structures, and contact surfaces. See text for discussion. Tape measure equals 62 cm.

1996). B depositional units are increasingly more common up section (Figure 3), which is consistent with a gradual development of a braided stream pattern (Boggs 2006). Macro- and micro-features, such as the presence of lenticular bedding and intraformational rip-up grains support a fluvial origin for the sediments and sudden deposition from sediment-saturated streams during flooding events. A volcanic origin for the sediments is

inferred from the abundance of volcanic rock fragments, feldspar crystals, and bentonite bubbles. XRD analysis also supports the volcanic characteristics of the sediments. In particular, formation, fluvial transport, and accumulation of smectite in poorly-drained, topographic low areas is interpreted to result from rapid weathering and burial of available local or regional volcanic source rocks during periods with great availability of water



(Awad and Breir 1993; Yemane et al. 1987a; Moore and Reynolds 1997). In addition, based on the co-occurrence of smectite, illite-smectite, and kaolinite-smectite clay mineralogy, B depositional units probably correspond to rapid burial (Moore and Reynolds 1997). The presence of albite also supports a volcanic origin and is consistent with moderate weathering and rapid burial (Moore and Reynolds 1997).

Depositional unit C (massive silt to sand). This depositional unit consists of massive to faintly-laminated clayey siltstones to fine sandstones (Figures 3, 4.1-4.3, Table 1). Unweathered crystalline volcanic material is a common characteristic of most C depositional units, while fewer units also include spherical iron oxide cement/nodules and clayey intraformational clasts. C units are generally well sorted and rarely fossiliferous, preserving thin (up to 2 cm) layers and lenses that include plant impressions and poorly-preserved compressions. Some C depositional units are part of an upward-fining sequence, while others are typically bound by reworked deposits of coarser or equal grain size. Bases of C units are non-scoured and vertical transitions to units of other depositional units are commonly sharp (~ 1-2 cm at CH-89, units 9-10). Laterally, some C units can be traced stratigraphically between sections, especially in the upper

parts of all sections (e.g., CH-79, unit 20, CH-93, unit 23, CH-89, unit 24). Petrographic analysis shows a massive to faintly laminated silt-rich matrix that is filled with angular elongate volcanic rock fragments, including abundant detrital glass shards and feldspar (mainly sanidine), which results in a “splintery” texture (Figure 5.10-5.11). Also present are very fine sand-size angular to subangular hornblende and pyroxene crystals, and bentonite bubbles that in some cases are rimmed by chalcedony or iron-rich cement and contain crystal inclusions (Figure 5.12-5.13). XRD analysis of C depositional units indicates the presence of feldspathic volcanic material (e.g., anorthite) and smectite (Appendix 4).

Interpretation of C depositional units. Massive sedimentary structure and upward-fining grain-size distribution within C depositional units indicate deposition by gravity (Miall 1996). Based on this, C depositional units are interpreted as airfall ashes. Presence of abundant volcanic rock fragments including feldspar, hornblende, and pyroxene supports the volcanic nature of these horizons (Moore and Reynolds 1997; Boggs 2006), while the common occurrence of bentonite bubbles is consistent with deposition by aerial means (Lentfer and Torrence 2006). The abundance of C depositional units, some of which can be traced stratigraphically

Figure 5 (previous page). Cross-Nichols photomicrographs of thin-sections from Late Oligocene volcanoclastic strata in the Margargaria River localities, northwestern Ethiopian Plateau. 5.1 A depositional unit matrix showing abundant concentrically-arranged iron-oxide nodules, where the main micro-feature is partial to complete coating by reddish iron-rich cement. Whitish material in interstitial spaces is chalcedony cement. CH-79-62TS. Scale bar equals 100 μm . 5.2 Angular plagioclase feldspar crystal sharply-rimmed by iron-rich cement from A depositional unit. CH-79-62TS. Scale bar 50 equals μm . 5.3 Angular hornblende crystal with its borders partially overgrown by reddish iron-rich cement from A depositional unit. CH-93-26TS. Scale bar 50 equals μm . 5.4 Cluster of small size angular pyroxene crystals partly coated by iron-rich cement from A depositional unit. CH-93-22TS. Scale bar 25 equals μm . 5.5 A depositional unit matrix showing opaque particles and disseminated bits of organic matter embedded in reddish iron-rich cement. CH-89-25TS. Scale bar equals 100 μm . 5.6 Massive to finely-laminated silt- and organic-rich B depositional unit matrix. Note abundant large angular volcanic rocks fragments and other angular to subangular rocks partly coated by iron-rich cement. CH-89-25TS. Scale bar equals 100 μm . 5.7 Approximately spherical bentonite bubbles in silt-rich B matrix. CH-89-24TS. Scale bar equals 50 μm . 5.8 Angular to subrounded intraformational clasts in B depositional unit matrix. CH-89-25TS. Scale bar equals 100 μm . 5.9 Concentrically-arranged iron-oxide nodules in B depositional unit matrix. Note rim of chalcedony cement surrounding the nodules. CH-89-24TS. Scale bar equals 100 μm . 5.10 Massive to faintly laminated silt-rich C depositional unit matrix. Note abundant angular elongate detrital glass shards and other volcanic rock fragments that delineate a “splintery” texture. CH-89-7TS. Scale bar equals 200 μm . 5.11 Angular elongate sanidine crystal from C depositional unit. CH-79-65TS. Scale bar equals 50 μm . 5.12 C depositional unit matrix showing numerous bentonite bubbles widespread in the matrix. CH-79-65TS. Scale bar equals 100 μm . 5.13 Single bentonite bubble from C depositional unit. Note rim of chalcedony cement and tiny crystal inclusion on the perimeter and inside bentonite bubble, respectively. CH-89-9TS. Scale bar equals 50 μm . 5.14 Massive to horizontally-microlaminated clay-rich D depositional unit matrix. Note abundant angular to subangular volcanic rock fragments, irregularly developed microscopic layers enriched in clay/organic content, and irregular to angular clasts of organic matter. CH-89-17TS. Scale bar equals 50 μm . 5.15 D depositional unit clay-rich matrix showing possible plant spores rimmed by chalcedony cement. CH-79-49TS. Scale bar equals 100 μm .

between sections (e.g., Figure 3, CH-79, unit 20; CH-93, unit 23, CH-89, unit 24), is consistent with airfall ash deposition on ample parts of the landscape. Evidence of slight fluvial reworking in some C depositional units is indicated by scarce intraformational clasts and poorly developed ripples and cross-laminations on upper bedding plane surfaces. Contorted plant fossils of various sizes occur in several of these airfall deposits, which is consistent with rapid *in situ* burial of vegetation by aerially deposited ash (Spicer et al. 1985; Wing et al. 1993; Johnson 2007). A volcanic origin for C depositional units is supported by smectite and anorthite (plagioclase feldspar) documented by XRD analysis. A neoformational origin for smectite is most likely considering the volcanic origin of the sediments, but, in those units with evidence of fluvial transport, a detrital origin and deposition in topographic lows can also be assumed (Wilson 1999). Anorthite is consistent with moderate to mild weathering conditions (Moore and Reynolds 1997).

Depositional unit D (laminated clay to sand).

This depositional unit consists of ripple cross-laminated siltstones and fine sandstones and horizontally-laminated claystones and mudstones that include variable amounts of sand-, silt-, and clay-size particles (Figures 3, 4.1-4.2, Table 1). Several of the D depositional units show more than one type of lamination or have parts with massive structure, which commonly grade upward from cross, to ripple, to horizontal laminations to massive. Some of these units exhibit upward fining of sediments. Additionally, a few thin units consist of laminated claystones and siltstones hardened by calcitic cement. Some D units are vertically and laterally adjacent to other D units that can be coarser or finer, or bound between finer-grained massive layers of the C depositional unit (e.g., Figure 3, CH-79, unit 26). This depositional unit may also preserve scattered rooting structures, root halos, plant and other unidentifiable organic remains, and is generally poorly sorted. Also, some units contain spherical iron-oxide accumulations, intraformational clasts, mottles, and pockets or poorly-developed layers of organic material, silt, and clay (~mud drapes). Petrographic analysis documents a clay-rich matrix that is structurally massive to horizontally-microlaminated and that contains angular to subangular volcanic rock fragments, irregularly-developed microscopic layers enriched in clay/organic content, and irregular to angular clasts of organic matter rimmed by chalcedony cement (Figure 5.14-5.15). Other, less conspicuous petrographic features are angular to subangular feldspar

crystals coated with brown iron-rich cement, iron oxide concretions/nodules and halos, some of which are rimmed by chalcedony cement, and small crystals of pyroxene and hornblende. Some units also have subangular to subcircular masses of partly weathered volcanic and other rock fragments and intraformational clasts formed by claystone, organic matter, and volcanic fragments rimmed either by iron-rich or chalcedony cement (Figure 6.1). XRD analysis indicates the presence of smectite, kaolinite, and mesolite (Appendices 5-6).

Interpretation of D depositional units. Based upon the features observed, D depositional unit represents settling out of deposits from slow-moving, sediment-saturated streams (Miall 1996). This kind of sedimentary deposit is formed in fluvial environments and commonly represents overbank deposits (Miall 1996). Some D depositional units, individually or taken as small groups, show more or less upward fining concomitant with fading (laterally or vertically) of laminations. These features, to some extent, mimic parts of heterolithic cross stratification sequences that characterize deposits of a meandering river (Thomas et al. 1987). Other units appear as poorly defined, horizontally laminated, layers that are intercalated with finer-grained massive siltstones of the C depositional unit. These may represent parts of levees deposited by sediment-saturated streams, similar to a braided pattern (Boggs 2006). Some of these horizons are bioturbated and include abundant organic material, indicating subaerial exposure and colonization of their surface by plants and other organisms. Macro- and micro-features suggest an abundant supply of sediments from local volcanoes. Clay mineralogy supports the role of volcanic material as primary weathering products of detrital and also possibly neoformational origin (smectite) (Wilson 1999). Also present in some horizons is kaolinite, which implies extensive leaching of the sediments, in environments with abundant water, which is consistent with the interpretation that this depositional unit represents overbank parts of a floodplain associated with a variable water table (Bohor and Triplehorn 1993; Moore and Reynolds 1997). In addition, deposition of mesolite in D depositional units is probably related to erosion and fluvial transport of volcanics in uplands, as this mineral belongs to the zeolite group of tectosilicates, which are found as constituents of volcanic rocks, especially basalts (Artoli et al. 1986).

Depositional unit E (massive clay, mud, and sand). This depositional unit is represented by

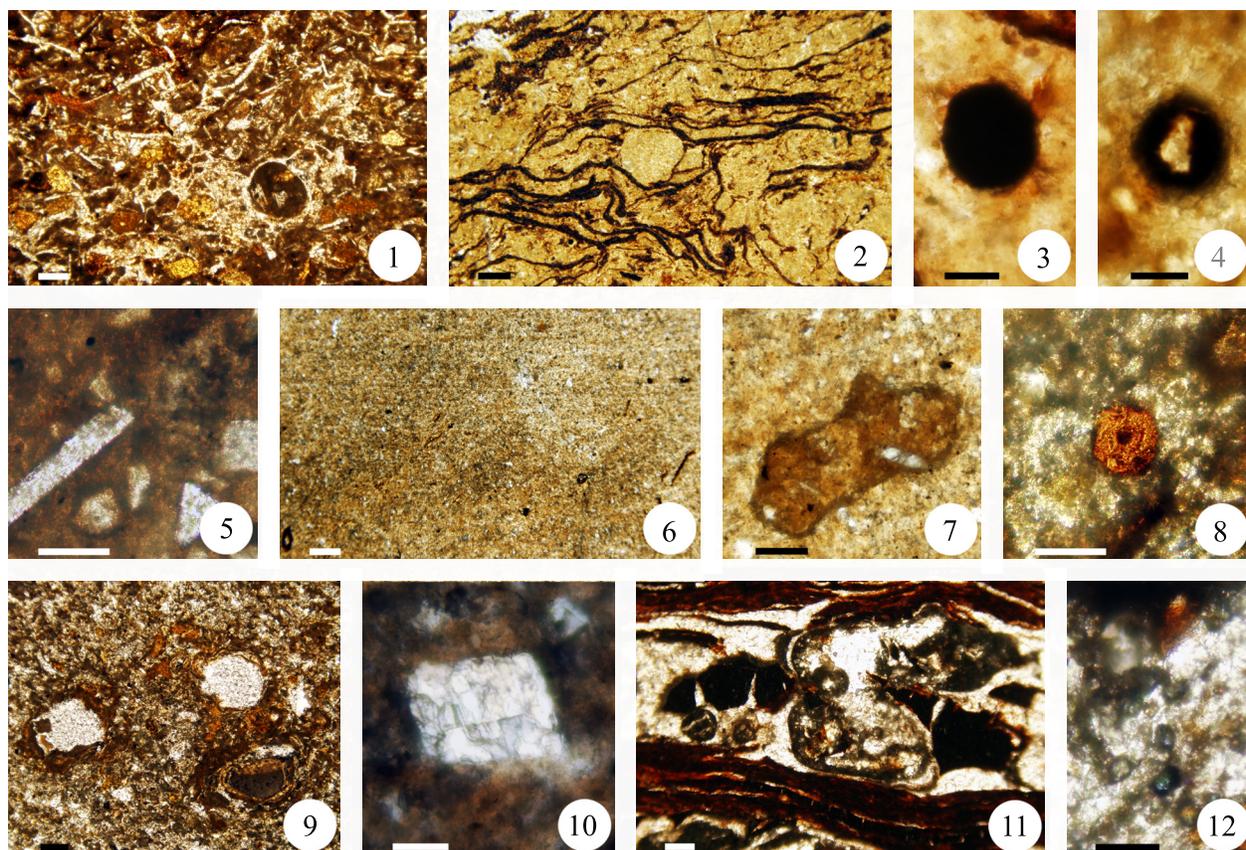


Figure 6. Cross-Nichols photomicrographs of thin-sections from Late Oligocene volcaniclastic strata in the Margargaria River localities, northwestern Ethiopian Plateau. 6.1 D depositional unit matrix showing abundant subangular to subcircular masses of volcanic rock fragments and intraformational clasts. Note larger spherical intraformational clast (right side of image) formed by claystone, organic matter, and volcanic rock fragments and rimmed by chalcedony cement. CH-79-57. Scale bar equals 115 μm . 6.2 Microlaminated to massive, clay-rich, E depositional unit matrix. Note volcanic rock fragments, feldspar crystals (whitish angular particles), and abundant microlenses (\sim micro mud drapes) of organic matter in matrix. CH-79-45. Scale bar equals 140 μm . 6.3 Subrounded organic clast (possible plant spore) in E depositional unit matrix. CH-79-45. Scale bar equals 50 μm . 6.4 Subrounded organic clast (possible root fragment) in E depositional unit. CH-93-12. Scale bar equals 50 μm . 6.5 Subrounded volcanic rock fragments and feldspar crystal (larger fragment on left of image) in clayey E depositional unit matrix. Note reddish iron-rich cement coating rocks and crystal. CH-79-45. Scale bar equals 50 μm . 6.6 Massive to weakly-laminated clay- and organic-rich F depositional unit matrix. CH-79-45. Scale bar equals 200 μm . 6.7 Microscopic lens/pocket of organic-rich material in F depositional unit matrix. CH-79-44. Scale bar equals 100 μm . 6.8 Possible plant spore in F depositional unit matrix. CH-79-63. Scale bar equals 50 μm . 6.9 Roots cross to oblique sections in F depositional unit matrix. Note dark-reddish iron-rich cement bordering roots. CH-89-26. Scale bar equals 50 μm . 6.10 Blocky siderite crystal in F depositional unit matrix. CH-79-44. Scale bar equals 50 μm . 6.11 Coarsely to finely-laminated organic-rich G depositional unit matrix. Note laminated structure represented by undulating and convoluted layers not firmly appressed to each other. CH-89-13. Scale bar equals 100 μm . 6.12 Small rounded volcanic rock fragments in free spaces between organic layers of the G depositional unit matrix. CH-89-13. Scale bar equals 50 μm .

massive, thin, organic-rich claystones, mudstones, and very fine sandstones with variable amounts of silt-size grains (Figures 3, 4.1-4.2, Table 1). Other characteristics include abundance of lenses, pockets, and layers of organic, clayey, and silty material that obscure other features. In addition, these units are well to poorly sorted and exhibit irregular, fine

color mottles. A number of these units are stratigraphically correlatable among all or two sections and consist of thin, generally irregular layers where leaves and leaflets and other plant and organic remains (root fragments and amorphous organic matter) are concentrated. In particular, E units that occur in the basal part of all three sections, where

mainly leaves and leaflets preserved in firmly indurated layers are present, represent the boundary between Ash-IV and pre-Ash-IV strata (Figure 3, CH-79 units 3-4, CH-93, units 2-3, CH-89, units 2-3). E depositional units representing the boundary between Ash-IV and the strata immediately below are underlain and overlain by coarser-grained sediments of variable organic content. Other organic-rich E units are underlain by coarser-grained sediments and overlain by layers that consist almost entirely of organic matter or are intercalated with mainly unfossiliferous layers of variable grain sizes. Petrographic thin sections show a clay-rich matrix filled with poorly developed to irregular microlaminations and microlenses (~micro mud drapes) of organic matter along with less numerous volcanic rock fragments and feldspar crystals (Figure 6.2). Also present are subrounded to irregular organic clasts of various sizes and shapes (Figure 6.3-6.4). Volcanic rock fragments and feldspars are angular to subangular and typically coated by clay, chalcedony-, or iron-rich cement (Figure 6.5). Other micro-features in some E units include hornblende, pyroxene, iron oxide accumulations, and opaque material. A small number of sandy E units are dominated by rounded to subrounded organic clasts, volcanic rock fragments, and very fine sand-size angular to subangular feldspar crystals. XRD analysis indicates the presence of smectite and kaolinite-smectite (Appendix 7).

Interpretation of E depositional units. E depositional units represent organic-rich lag deposits from streams (Miall 1996). In particular, organic-rich sandy and finer-grained E units bound by coarser-grained, organic-poor sediments can be interpreted as sheet-like deposits from shallow braided streams, associated with parts of a floodplain characterized by a high water table (Miall 1996). The presence of irregular to undulate organic-rich macro- and micro-layers that include some identifiable fossil plant parts (spores, root, and/or stem) is consistent with deposition by sediment-saturated streams. Sandier E units that include numerous intraformational clasts, clay and bentonite pockets, and iron-rich accumulations indicate fluvial deposition by sediment-saturated streams on better-drained surfaces and at more proximal parts of the floodplain (McLoughlin and Drinnan 1997). Mineralogical evidence inferred from thin sections, such as the presence of feldspars and pyroxene, is consistent with a volcanic origin for the sediments, which is also supported by data from the XRD analysis. In particular, the presence of smectite indicates the occurrence of poorly-drained areas,

where deposits accumulated by fluvial transport of volcanic weathering products from elsewhere in the basin (Wilson 1999). In addition, the presence of kaolinite-smectite implies increasingly greater weathering under very humid conditions and better drainage (Moore and Reynolds 1997).

Depositional unit F (bioturbated, massive clay to sand). This depositional unit is characterized by massive, intensely bioturbated claystones to very fine sandstones (Figures 3, 4.1-4.2, Table 1). A number of F depositional units also display poorly-developed wavy laminations, which consist of layers rich in organic, clay-, and silt-size particles or a combination of these. The characteristic common to all F depositional units is widespread occurrence of rooting structures and other organic debris including leaf impressions and compressions. Other macroscopic features of some of these units are fine color mottles, root halos, slicken-side surfaces, and pockets or lenses that are either made of organic-, clay-, or silt-rich sediments or a combination of these. F depositional units are generally well sorted, are bound by coarser- or finer-grained sediments or a combination of these, and commonly grade vertically and laterally into organic-rich horizons (E and G depositional units), or, as in the pre-Ash-IV strata (Figure 3, CH-79, units 1-2, CH-93, unit 2, CH-89, unit 1), are stratigraphically continuous between sections. Petrographically, the F depositional units are characterized by a massive to weakly-laminated clay- and organic-rich matrix (Figure 6.6). Some units also display microscopic lenses/pockets of organic-rich material and irregular to subrounded grains of organic matter; especially abundant are root sections bordered by iron-rich cement (Figure 6.7-6.9). Other microfeatures include subangular to subrounded volcanic rock fragments and feldspars. Also present in some units are blocky siderite crystals, concretionary iron-oxides, and opaque particles (Figure 6.10). XRD analysis of the sediments indicates the presence of smectite, kaolinite, and siderite (Appendices 8-9).

Interpretation of F depositional units. F depositional units indicate plant-populated horizons associated with pedogenesis (Miall 1996). Abundance of macro- and micro- rooting structures, organic clasts possibly representing spores or other plant parts, and poorly preserved clay- and organic-rich microlaminations is consistent with fluvial deposition from suspension and at a slow pace alternating with plant growth intervals, in proximal/distal parts of a floodplain. Gradation of F depositional units into organic-rich horizons indicates an

increasingly higher water table, while stratigraphically correlatable units (pre-Ash-IV) indicate more extensive and temporally durable soil formation than individual units. Occurrence of blocky siderite crystals in some of these horizons indicates formation in a reducing environment, low concentrations of aqueous sulfide, circum-neutral pH, and soil $pCO_2 > 100,000$ ppmV (Pearson, 1979; Postman, 1982). However, concretionary iron-oxide nodules in F depositional units are consistent with more oxidizing conditions, slower sedimentation rate, and subaerial exposure. The often mottled appearance of the F units is consistent with temporal variation of the water table resulting in periods characterized by periodically alternating anoxic and oxic conditions. Macro and micro-features and XRD data indicate a volcanic origin for the source sediments. In particular, smectite and kaolinite, which are the most common phyllosilicates preserved in these units as well as in the other depositional units described, are consistent with variable weathering conditions depending upon availability of water in the environment and duration of erosion and deposition processes (Moore and Reynolds 1997). As such, their presence is consistent with rather limited weathering and rapid burial of sediments of volcanic origin (Moore and Reynolds 1997). The co-occurrence of all these minerals can result from rapid evolution of the fluvial landscape. As a result, these minerals represent moderate weathering and demonstrate the temporary nature of this soil-forming environment (Borchardt 1989 and references therein).

Depositional unit G (lignified to semi-lignified organic matter). This depositional unit consists of thin layers of organic matter, including poorly-preserved plant fragments (Figures 3, 4.1-4.2, Table 1). G depositional units are thinner than most other depositional units, not laterally correlatable between sections, and are bound by coarser-grained sediments from which they are separated by sharp erosional or gradational contacts. Petrographic thin sections document a matrix that consists of coarse to fine-laminated organic matter, where most of these laminations appear as undulating and convoluted layers not firmly appressed to each other (Figure 6.11). In the spaces left between these layers usually are found small rounded volcanic rock fragments (Figure 6.12). XRD analysis of G units indicates the presence of smectite and kaolinite (Appendix 10).

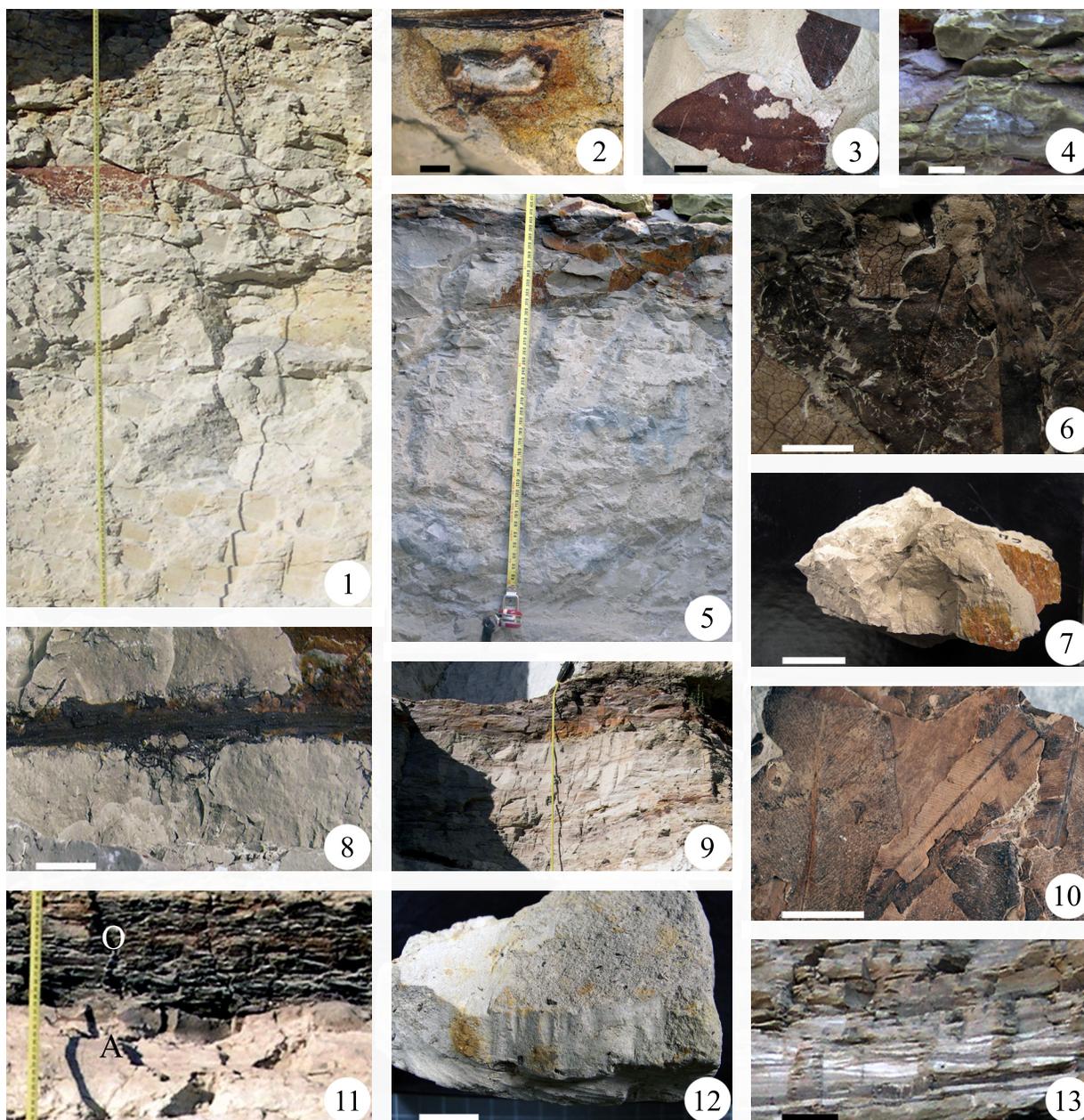
Interpretation of G depositional unit. Based on the features observed, G depositional units represent in situ accumulations of organic matter (~lig-

nites) in shallow, ephemeral pools of water located in parts of a floodplain characterized by a high water table (Miall 1996). The distinction between the E, F, and G depositional units is mainly based on the ratio of organic matter to mineral content within a horizon, while common to them is that their deposition occurred on parts of a floodplain characterized by a high water table (Miall 1996). In the case of the G depositional unit a consistently high water table prevailed, promoting the accumulation of organic matter and inhibiting oxidation. However, the microlayered structure of the G depositional unit, consisting of undulating and convoluted layers of variable thickness, indicates periods of intermittent deposition characterized by periodic subaerial exposure and drying (Boggs 2006). Origin of smectite and kaolinite in the G unit is most probably detrital and consistent with variable weathering of volcanic rocks (Moore and Reynolds 1997; Wilson 1999). In particular, kaolinite commonly accumulates in swampy environments characterized by abundant water leaching through sediments and, therefore, its presence is consistent with an environment with abundant precipitation and well-drained soils (Bohor and Triplehorn 1993). However, peat does not accumulate in well-drained soils. Therefore, kaolinite present in these horizons must have either been transported from well-drained environments or formed by leaching of organic acids and chelates related to the transformation of peat to coal in the burial environment (Bohor and Triplehorn 1993). Smectite forms in poorly drained soils rich in alkaline material and weathers to kaolinite under humid conditions, which is consistent with increasing weathering and rapid burial of the sediments in topographic lows of the floodplain (Moore and Reynolds 1997).

Hiatuses: Formation of Paleosols

Three different paleosol types have been identified within the bottom and middle parts of the stratigraphic sections exposed along the Margarita River (Figure 3). In particular, based upon evaluation of the relative importance of a series of pedogenic features/processes including relative organic matter content, soil structure and mineralogy, mottling, horizonation, and color, these three paleosols types are classified according to Mack et al. (1993). Morphological characteristics and lateral and vertical distribution of each paleosol are described below.

Yellowish claystones and clayey siltstones containing rooting structures that partly obliterate original sedimentary structures (ripples), a massive



to weakly-developed blocky structure, lack of clear horization, whole to fragmented leaves throughout, and bluish-gray elliptical to variously-shaped mottles characterize the lower part of all sections corresponding to the beginning of Ash-IV deposition (Figure 7.1-7.4). This succession is stratigraphically continuous between the sections (e.g., Figure 3, CH-79, unit 5, CH-93, unit 4, CH-89, unit 4) and is interpreted as a Protosol due to its lack of well-developed soil structure or horization (Mack et al., 1993). A similar paleosol profile, also classified as a Protosol occurs in the middle-upper parts of the north and central sections, but it appears

that this has been eroded in the south section (Figure 3, CH-93, units 19-21, CH-89, unit 19). This upper Protosol differs from the Protosol in the basal part of the sections in that it consists of a succession of silty very fine sand layers that contain poorly-preserved plant remains and rooting casts (up to 2.5 cm thick), filled with cherty cement, and hardened by ferruginous cement (Figure 7.2). The features displayed by these Protosols are consistent with soil formation upon proximal to distal parts of a seasonally inundated floodplain (Mack et al. 1993), whereas, in particular, the less well developed Protosol in the middle-upper parts of the

Figure 7 (previous page). Field photographs of paleosols of Late Oligocene volcanoclastic strata in the Margargaria River localities, northwestern Ethiopian Plateau. 7.1. Succession of massive to rippled claystones and clayey siltstones representing a Protosol. Tape measure equals 120 cm. 7.2 Root cast filled with cherty material within Protosol profile. Note reddish iron-rich rim around root perimeter. Scale bar equals 0.5 cm. 7.3 Whole to fragmented dicot leaves in Protosol profile. Scale bar equals 0.5 cm. 7.4 Bluish-gray elliptical mottle in Protosol profile. Scale bar equals 3 cm. 7.5 Succession of gley-colored mudstones representing a Vertisol. Note variously shaped bluish mottles in Vertisol profile. Tape measure equals 41 cm. 7.6 Dicot leaves mat in the upper, organic-rich, horizon of the Vertisol. Scale bar equals 1 cm. 7.7 Wedge-shaped aggregate structure of Vertisol. Note slicken-side surface (reddish surface on right side of block) of Vertisol. Scale bar equals 1 cm. 7.8 Detail of Vertisol showing compressed organically-preserved root. Scale bar equals 0.5 cm. 7.9 Succession of organic-rich siliciclastic horizons capped by a semi-lignified horizon of plant material (~lignite) of a Histosol profile. Tape measure equals 95 cm. 7.10 Ferns, monocots, roots, and other organic remains in upper semi-lignified horizon in Histosol profile. Scale bar equals 1 cm. 7.11 Detail of lower siliciclastic (A-horizon) and upper (O-horizon) semi-lignified layers in Histosol profile. Note blocky to prismatic structure of lower siliciclastic horizons. Tape measure equals 38 cm. 7.12 Reddish-gray subspherical mottles of Histosol lower siliciclastic layer. Scale bar equals 1 cm. 7.13 Discontinuous and irregular silt-rich lenses and pockets in lower siliciclastic layer of a Histosol profile. Scale bar equals 5 cm.

sections may indicate several shorter cycles of exposure, pedogenesis, and burial. The presence of smectite and kaolinite indicates varied weathering conditions probably reflecting a seasonally changing water table, while kaolinite-smectite, which is also present in these strata, is consistent with rapid burial of the sediments (Appendix 7-8) (Moore and Reynolds 1997).

The basalmost units in all three stratigraphic sections, which correspond to the thin set of strata below Ash-IV (e.g., Figure 3, CH-79, unit 1-3), consist of a succession of poorly-developed, gley-colored, organic-rich, mudstones horizons that grade upward to a layer enriched in organic content (O-horizon) containing abundant leaves (Figure 7.5-7.6). Gley coloration refers to low chroma, greenish-blue-grey soil colors typical of wetland conditions (Mack et al. 1993). The roots (up to 3 cm wide and ~20 cm in long) consist of compacted organic matter oriented vertically and obliquely relative to the orientation of the strata (Figure 7.8). Based on these features and on the presence of homogeneously distributed elliptical to variously shaped bluish mottles and a structure consisting of coarse, wedge-shaped aggregates with slicken side surfaces and fossilized roots (Figures 7.5, 7.7), this succession is interpreted as a Vertisol (Mack et al. 1993).

Vertical rooting structures indicate free-drainage, and therefore at least intermittent well-drained conditions (Retallack 1990). Slicken planes in this profile indicate shrink-swell processes probably related to periodic rise and fall of the local water table, or seasonal flooding from overland flow (Mack et al. 1993). These features may also be observed in poorly developed Gleysols as well as in Vertisols (Mack et al. 1993). Clay minerals present in the strata representing this Vertisol are domi-

nated by smectite, kaolinite, and kaolinite-smectite, all most likely detrital in origin and representing variable weathering conditions (Appendices 7-8). These data are consistent with soil formation upon proximal parts of a floodplain in a seasonal environment (Mack et al. 1993; Tabor and Montañez 2004).

Sets of strata consisting of an organic-rich siliciclastic horizon(s) (A-horizon) that grade into a lignified/semi-lignified organic matter horizon (~lignite, O horizon) that apparently accumulated in situ occur in the middle part of all sections. Numerous compressions and impressions of fronds, leaves, and tabular roots are present in these profiles (Figure 7.10). The mineral layer(s) characteristically is structureless to faintly laminated, or sometimes blocky to prismatic, silty claystone to clayey fine sandstone of rather limited vertical extent (up to ~ 15 cm) (Figure 7.11). Siderite is present in the lower mineral horizon, while kaolinite and smectite are found in both the lower and upper horizons that make up these paleosols (Figure 6.10, Appendices 8-10), which are classified as Histosols (e.g., Figure 3, CH-89, unit 11-13, Figures 7.9, 7.11; Mack et al. 1993). Other individual strata showing increasing organics consisting of variously preserved plant parts appear as partly eroded Histosols (e.g., CH-89, unit 17). Histosol horizons are characterized by their gley coloration, which is more intense as the organics concentrate. Small (up to 1cm across), subspherical reddish mottles occur in the lower layer of siliciclastic material (Figure 7.12). Discontinuous and irregular silt-rich layers or pockets commonly occur within the mineral horizon (Figure 7.13).

Smectite is consistent with slight weathering and rapid burial of sediments of volcanic origin (Moore and Reynolds 1997). Kaolinite is a clay

mineral precipitated in acidic solutions, depleted in bases, and its formation in soils is related to periods of around ten thousand years, precipitation exceeding evaporation, and its presence in the Histosols indicates greater weathering than smectite (Keller 1956; Wilson 1999). The episodic supply of volcanic ash onto the paleolandscape probably provided most of the material that, after leaching, weathered to kaolinite, which accumulated in lowland areas where small ponds developed. Additionally, it is also possible that leaching of organic acids from plant remains during peat formation equally contributed to the presence of kaolinite in the Histosols (Bohor and Triplehorn 1993). The deposition of volcanic ash results in impermeable horizons that promote pond development, which may have favored the formation of kaolinite in the lignites (Crowley et al. 1989, 1994). Co-occurrence of siderite and poorly consolidated plant remains, including tabular roots are consistent with in situ accumulation of organic rich horizons in low lying, waterlogged substrates characterized by a shallow, anoxic or dysoxic water table (Staub and Cohen 1978; Mack et al. 1993; Retallack 1990). The presence of Fe mottles indicates intermittent change between oxic and anoxic soil atmosphere (Vepraskas 1994), while pockets/lenses of ashy material are probably related to erosion by small-scale streams that traversed the landscape; as a result these paleosols appear to have formed by several separate episodes of sediment deposition and plant growth.

Paleobotanical Data

Collection of macrofossils from the volcaniclastic strata studied here yielded a flora that consists of vegetative and reproductive fern and angiosperm specimens, including *Acrostichum* (Pteridaceae), *Marsilea* (Marsileaceae), *Equisetum* (Equisetaceae), *Salvinia* (Salviniaceae), *Cyclosoorus* (Thelypteridaceae), *Blechnum* (Blechnaceae), *Cynometra* (Fabaceae), *Typha* (Typhaceae), *Alstonia* (Apocynaceae), *Pandanites* (Pandanaceae), *Hyphaene* (Arecaceae), and *Macaranga* (Euphorbiaceae) (García Massini et al. 2006; García Massini and Jacobs 2009). In addition to these fossils, there are remains of other less well-preserved plants including ferns (e.g., *Actiniopteris*-like) and angiosperms (e.g., *Rubus*-like), which are mentioned here to more clearly show the stratigraphic distribution of ferns and angiosperms relative to each other. Ferns occur singly or in combination as the dominant vegetation in several units of all depositional units starting at around the middle part of

all sections, except for the A depositional unit, which does not contain macrofossils (except for some root fragments). Angiosperms co-occur with the ferns as subordinate elements in most of these units, except for the lowermost units of all sections of Ash-IV and the thin set of strata below, where angiosperms dominate and ferns are absent.

Ferns

Family PTERIDACEAE Kirchner, 1831
Genus *ACROSTICHUM* Linnaeus, 1753
Acrostichum sp.

Specimens. CH-79-199A (Figure 8.1, 8.3-8.4) and CH-79-21B (Figure 8.2).

Description and type of preservation. This fossil consists of impressions and compressions of fragments of linear-lanceolate sterile and fertile pinnae (Figure 8.1). A few fossils consist of fragments of leaves showing petiolate pinnae. Diagnostic features of this fossil include reticulate venation without included free veinlets and acrostichoid arrangement of stalked sporangia (Figure 8.1-8.4). Additional *Acrostichum* leaf remains were previously described from the Margargaria River and other tuffaceous strata of the Chilga beds, but those did not include fertile specimens, and therefore they were assigned to a fossil species that includes only sterile remains (García Massini et al. 2006).

Stratigraphic distribution and mode of preservation. Remains of the hydrophilic fern *Acrostichum* occur commonly lying flat in organic-rich layers (D, E, F, and G depositional units in CH-89; E, F, and G in CH-93; F and G in CH-79) in all three geologic sections (e.g., Figure 3, CH-79, unit 18-19) and embedded in one airfall tuff in the south section (C depositional unit) (Figure 3, CH-79, unit 20).

Modern distribution and ecology. Extant members of this genus occur inland in wetland settings and in coastal environments associated with mangroves in acidic to neutral pH and high salinity organic- and clay-rich soils (Rao et al. 1973; Tomlinson 1986). Generally, the occurrence of *Acrostichum* today is promoted by increasing soil acidification and by both anthropogenic and natural ecological disturbance (Rao et al. 1973; Tomlinson 1986; Thanikaimoni 1987; Saenger 1998). The ecological distinctiveness that allows *Acrostichum* to inhabit these kinds of environments derives at least partially from its dispersal ability as a pioneer plant adapted to rapid colonization of disturbed

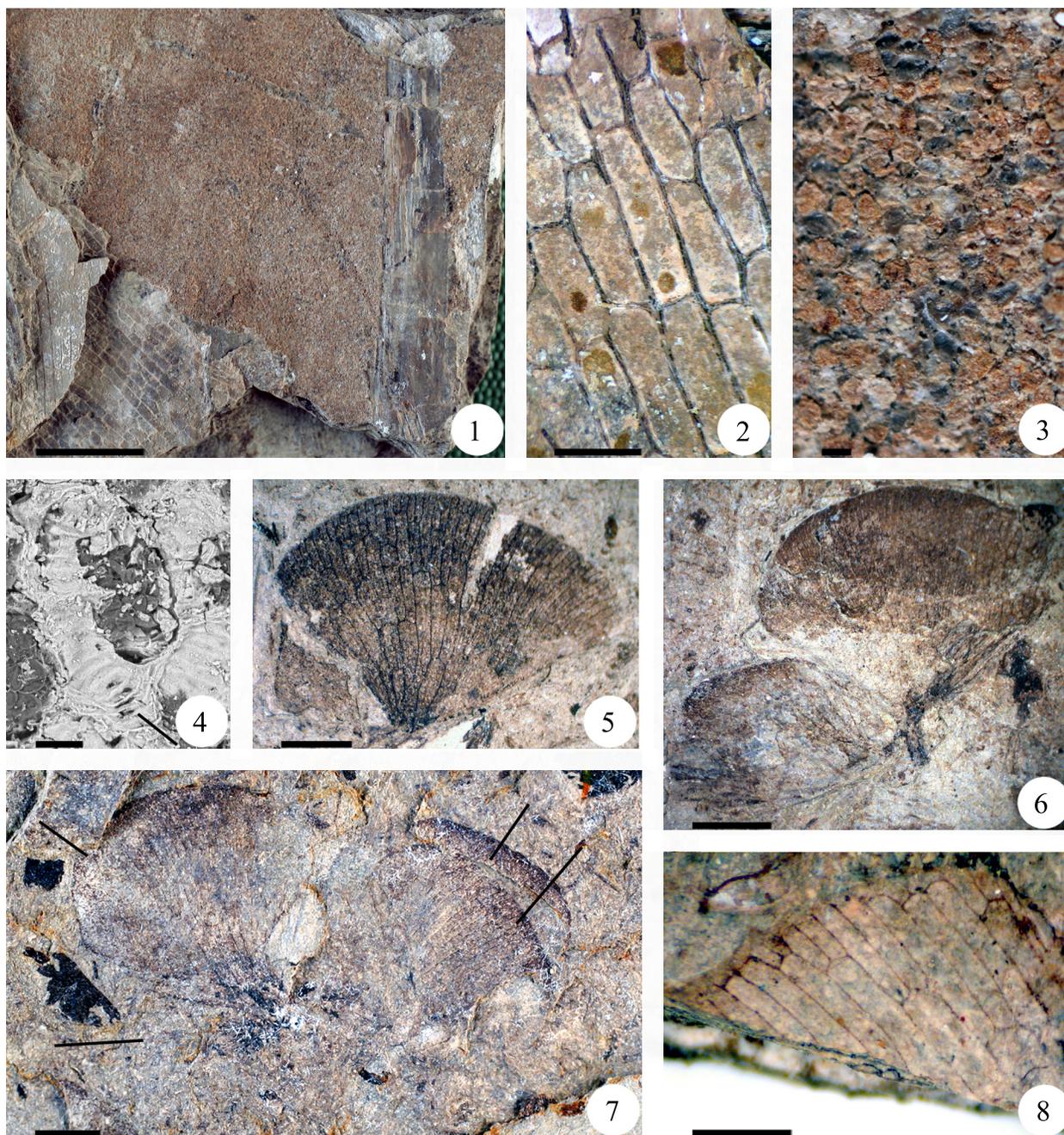


Figure 8. Compressions and impressions of *Acrostichum* pinnae and sporangia and *Marsilea* leaflets from Late Oligocene volcanoclastic strata in the Margargaria River localities, northwestern Ethiopian Plateau. 8.1 General view of fragments of sterile and fertile *Acrostichum* pinnae. CH-79-199A. Scale bar equals 0.5 cm. 8.2 Detail of *Acrostichum* pinnae showing typical reticulate venation consisting of areoles without included free veinlets. CH-79-21B. Scale bar equals 0.5 cm. 8.3 Acrostichoid sporangia arrangement on underside of *Acrostichum* pinnae. CH-79-199A. Scale bar equals 200 μ m. 8.4 SEM of stalked sporangia in situ on underside of *Acrostichum* pinnae. Oblique black bar in picture indicates sporangium stalk. CH-79-199A. Scale bar equals 50 μ m. 8.5 Dispersed individual fan-shaped *Marsilea* leaflet. CH-79-229B. Scale bar equals 0.25 cm. 8.6 *Marsilea* leaflets pair joined by a common petiole. CH-79-227. Scale bar equals 0.25 cm. 8.7 Whole *Marsilea* leaf showing four leaflets attached to a common petiole. Each oblique black bar points to an individual leaflet. CH-79-230A. Scale bar equals 0.25 cm. 8.8 Detail of *Marsilea* leaflet showing typical anastomose venation of secondary veins that results in elongated areoles. Note common marginal vein connecting secondary veins. CH-79-32B. Scale bar equals 0.25 cm.

habitats devoid of local vegetation (Tomlinson 1986; Saenger 1998).

Paleoecological significance. In this regard, the presence of this fossil within the E, F, G, and C depositional units of the Ash-IV tuff sequence at the Margargaria River is consistent with the ecological role of modern *Acrostichum*.

Family MARSILEACEAE Mirbel, 1802
Genus *MARSILEA* Linnaeus, 1753
Marsilea sp.

Specimens. CH-79-229B (Figure 8.5), CH-79-227 (Figure 8.6), CH-79-230A (Figure 8.7), and CH-79-32B (Figure 8.8).

Description and type of preservation. This fossil consists of impressions and compressions of fan-shaped isolated individual leaflets and a few pairs of leaflets with discernible portions of a third and fourth leaflet diverging from a common straight petiole (Figure 8.5-8.7). Venation is dichotomous with veins that anastomose and form fusiform areoles that end in a marginal vein (Figure 8.8). Leaf morphology and venation pattern of the fossil are identical to extant *Marsilea* (Tryon and Tryon 1982). All other fossil *Marsilea* known worldwide were transferred to the morphogenus *Marsileaphyllum* based on a similar, but not identical, leaf morphology and venation (Nagalingum 2007).

Stratigraphic distribution and mode of preservation. *Marsilea* fossils from the Margargaria River localities occur more or less flat along bedding planes in a ~10 cm, massive, overbank silt-rich layer (F depositional unit) in the middle part of the south section (Figure 3, CH-79, unit 18). This layer grades upward into a thin, poorly-consolidated lignite (G depositional unit) in which badly-preserved *Marsilea* leaflets are also found.

Modern distribution and ecology. Extant members of *Marsilea* occur worldwide in temperate to tropical environments rooted in sandy but especially in muddy substrates in ponded settings and in ephemeral aquatic habitats from lowlands up to 1950 meters, such as in some areas of Ethiopia (Johnson 1986; Launert 2003). *Marsilea*'s diversity is greater in Africa than in all other continents, and this has been interpreted to be the result of evolutionary processes related to adaptation to seasonally dry, semi-arid climates (Kornás 1985).

Paleoecological significance. The presence of *Marsilea* in these layers is interpreted to represent ponded settings of ephemeral nature. In addition, *Marsilea*, a cosmopolitan member of the heterosporous water ferns, of high diversity in Africa, is

considered a drought-tolerant taxon usually found in seasonal environments. On this basis, its presence in the Margargaria River localities indicates a seasonally dry climate (Kornás 1985; Launert 2003; Aldasoro et al. 2004; Nagalingum et al. 2007). Moreover, *Marsilea*'s occurrence in Africa is negatively correlated with humidity, which led to the hypothesis that its greater diversity in the Namibia-South Africa region is due to the early development of deserts during the Cenozoic (Aldasoro et al. 2004), and this also supports the interpretation that seasonally dry climatic conditions should have characterized *Marsilea*'s habitat in the Margargaria River.

Family EQUISETACEAE Michaux ex De Candolle, 1804
Genus *EQUISETUM* Linnaeus, 1753
Equisetum sp.

Specimens. CH-79-35A (Figure 9.1) and CH-93-85 (Figure 9.2).

Description and type of preservation. Fossil *Equisetum* has been identified based on the presence of dispersed fragments of impressions and compressions of hollow ribbed stems with nodes formed by a sheath of material representing the remains of whorled leaves (Figure 9.1- 9.2) (Tryon and Tryon 1982; Verdcourt 1999 a; Smith et al. 2006).

Stratigraphic distribution and mode of preservation. *Equisetum* stems occur rooted in situ or lying flat in organic-rich overbank reworked muddy and clayey layers (F and G depositional units) in the central and south sections (e.g., Figure 3, CH-79, unit 18).

Modern distribution and ecology. *Equisetum* inhabits wetland settings and other habitats characterized by a high water table, such as by rivers and streams, in temperate to tropical latitudes including one species native to North, East, Central, and South Africa that occur at elevations as high as 2100 meters (Tryon and Tryon 1982; Verdcourt 1999a). This fern is characterized by being a rapid colonizer of disturbed habitats (Tryon and Tryon 1982; Verdcourt 1999 a). Examples of modern *Equisetum* that dominated early colonization of volcanically disturbed environments by regenerating from buried rhizomes, broken plant fragments, and spores are known from temperate and tropical latitudes of North America (Spicer 1991; Weber et al. 2006). In addition, fossil *Equisetum* has been found elsewhere preserved in situ in swampy to marshy, floodplain, and volcanic paleoenvironments in association with other ferns, which has

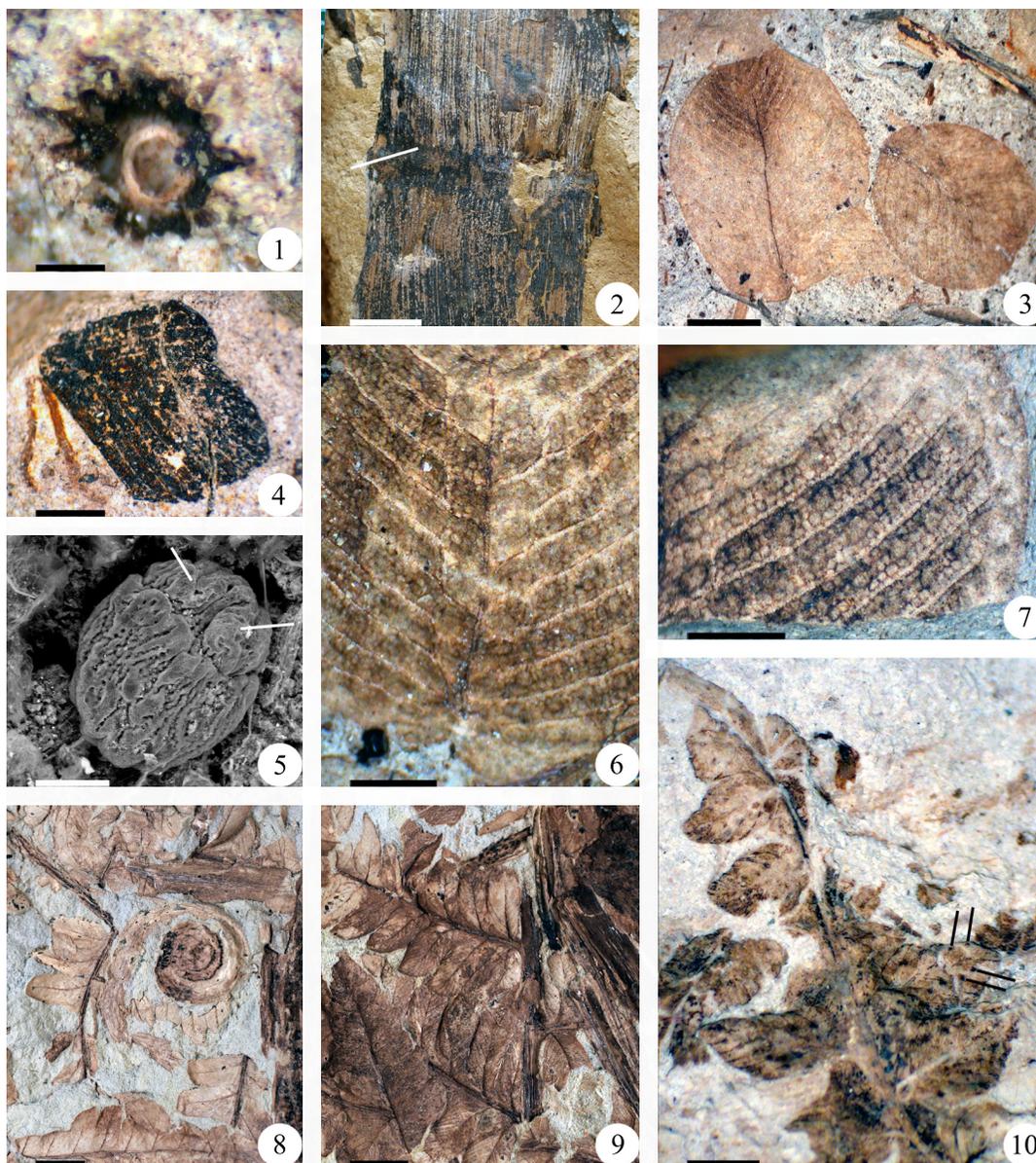


Figure 9. Compressions and impressions of *Equisetum* stems, *Salvinia* leaflets and megaspores, and *Cyclosorus* pinnate leaves from Late Oligocene volcanoclastic strata in the Margargaria River localities, northwestern Ethiopian Plateau. 9.1 Cross section of an in situ *Equisetum* stem with a characteristic hollow central part and ribbed margin pattern. CH-79-35A. Scale bar equals 0.1 cm. 9.2 *Equisetum* stem fragment with enlarged node covered by a sheath of material that represents a whorl of leaves. White oblique bar indicates whorl of leaves. CH-93-85. Scale bar equals 0.5 cm. 9.3 Dispersed ovate-ovovate *Salvinia* leaflets. CH-93-62B. Scale bar equals 0.25 cm. 9.4 Folded *Salvinia* leaflet pair bearing remains of a submerged leaf (reddish-brown filaments) attached to the distal end. CH-93-48A. Scale bar equals 0.25 cm. 9.5 Ellipsoidal *Salvinia* megaspore. Oblique white bars in the picture indicate 2-lobed acrollamella. Note coarsely rugulate surface ornamentation. CH-79-21A. Scale bar equals 100 μ m. 9.6 Fragment of *Salvinia* leaflet showing thick midvein and proximally-curved anastomosed secondary veins forming irregular to polygonal areoles. CH-93-69B. Scale bar equals 0.1 cm. 9.7 Detail of *Salvinia* leaflet venation showing large areoles subdivided into smaller polygonal areoles and marginal vein connecting terminal secondary veins. CH-93-81. Scale bar equals 0.1 cm. 9.8 General view of *Cyclosorus* pinnate leaf fragment showing circinate venation. CH-79-43B. Scale bar equals 0.5 cm. 9.9 *Cyclosorus* pinnate leaf fragment showing alternate secondary pinnae arrangement. Note gradually reduced pinnate leaf fragment on bottom left side of image. CH-79-43B. Scale bar equals 0.5 cm. 9.10 Possible fertile *Cyclosorus* pinnate leaf fragment. Oblique black bars point to possible clusters of sporangia consisting of approximately circular organic remains on pinnules secondary veins. CH-87-1A. Scale bar equals 0.1 cm.

been interpreted to have resulted from rapid sedimentation (e.g., Collinson 1988; Falder et al. 1999; Falcon-Lang and Cantrill 2002; Cantrill and Hunter 2005 and references therein).

Paleoecological significance. The presence of *in-situ* *Equisetum* stems in the same layer preserving *Marsilea* supports the interpretation that this setting was of ephemeral duration. Co-occurring with *Marsilea* and *Equisetum* is *Acrostichum*, and this also suggests that this setting resembled a short-lived inundated terrain, such as a floodplain where the water table was temporarily high or an ephemeral pond.

Family SALVINIACEAE Martynov, 1820

Genus SALVINIA Séguier, 1754

Salvinia sp.

Specimens. CH-93-62B (Figure 9.3), CH-93-48A (Figure 9.4), CH-79-21A (Figure 9.5), CH-93-69B (Figure 9.6), and CH-93-81 (Figure 9.7).

Description and type of preservation. *Salvinia* consists of dispersed individual ovate-obovate leaflet impressions and compressions (Figure 9.3-9.4). Also present are coarsely rugulate, ellipsoidal megaspores with a prominent 2-lobed acrollamella that obscures the trilete mark (Figure 9.5). A few specimens of *Salvinia* consist of two leaflets folded on top of each other from which emerge two filaments that resemble a submerged root-like leaf (Figure 9.4). Secondary venation consists of proximally-curved lateral veins that arise from a prominent midvein and anastomose, forming irregular to polygonal areoles that collect together into a marginal common vein (Figure 9.6-9.7). The areoles further anastomose into smaller components that appear clustered, resembling the bases for insertion of trichomes observed in extant taxa (Figure 9.7). This fossil has been assigned to extant *Salvinia* based on venation and morphology of leaflets, while megaspores also are morphologically identical to extant members of this genus (Tryon and Tryon 1982).

Stratigraphic distribution and mode of preservation. *Salvinia* leaflets are mainly found lying flat or slightly curved along breaking planes in poorly laminated to massive mudstones, claystones, and lignites (F and G depositional units) in the central and north sections (e.g., Figure 3, CH-93, unit 11-13, CH-89, unit 17). These fossils are also poorly-preserved lying flat on some coarser-grained overbank layers in the central (E depositional unit; e.g., CH-93, unit 17) and north sections (D and E depositional units; e.g., Figure 3, CH-89, units 12-14). *Salvinia* megaspores are found in all sections in

organic-rich claystones and lignites (F and G depositional units) (e.g., CH-79, unit 18).

Modern distribution and ecology. Extant *Salvinia* is a rapidly growing taxon that inhabits rivers or other aquatic settings mainly in tropical latitudes including Africa with one species mainly native to the eastern part of the continent (Schelpe 1961; Tryon and Tryon 1982; Verdcourt 2000). Colonies of *Salvinia* that grow over generations form mats centimeters thick that create an anoxic environment below (Schelpe 1961). In addition, *Salvinia* co-occurs with *Marsilea* in dry regions of Africa, which is consistent with the fact that both ferns, independently, are negatively correlated with humidity (Aldasoro et al. 2004).

Paleoecological significance. The presence of this fossil in overbank layers separated and capped by lignites supports previous data indicating frequent inundation and formation of ponded settings in the environment. In particular, *Salvinia* occurrence could have contributed to organic matter preservation in the lignite units, especially in the central section (CH-93, units 11-14) where this fern is most abundant. *Salvinia* leaflets and megaspores co-occur with the remaining ferns in these overbank layers and in similar layers in the north section (e.g., CH-89, unit 17), except for *Marsilea*, which only occurs with *Salvinia* megaspores in the south section (CH-79, units 18-19). This probably reflects landscape heterogeneity, suggesting that these two aquatic ferns were contemporaneous in the environment, but restricted to different ecological niches. *Salvinia* is not adapted to terrestrial conditions, in contrast with *Marsilea* (Schelpe 1961; Kornás 1985; Tryon and Tryon 1982; Schneider and Pryer 2002), and therefore it must have lived in a wetter part of the environment.

Family THELYPTERIDACEAE Pichi Sermoli, 1970

Genus CYCLOSORUS Link, 1833

Cyclosorus sp.

Specimens. CH-79-43B (Figure 9.8-9.9), CH-87-1A (Figure 9.10), and CH-79-234B (Figure 10.1).

Description and type of preservation. This fern consists of alternately arranged, sterile and, apparently, fertile, bi-pinnate frond fragment impressions and poorly-preserved compressions that are gradually reduced and that are circinate in the bud (Figure 9.8-9.10). Possible fertile specimens from a locality collected elsewhere in the Chilga basin display a series of black rounded spots, reminiscent of sori, borne in two parallel rows on the secondary veins of each pinnule (Figure 9.10). Pinnules are pinnately veined and have a typical venation over-

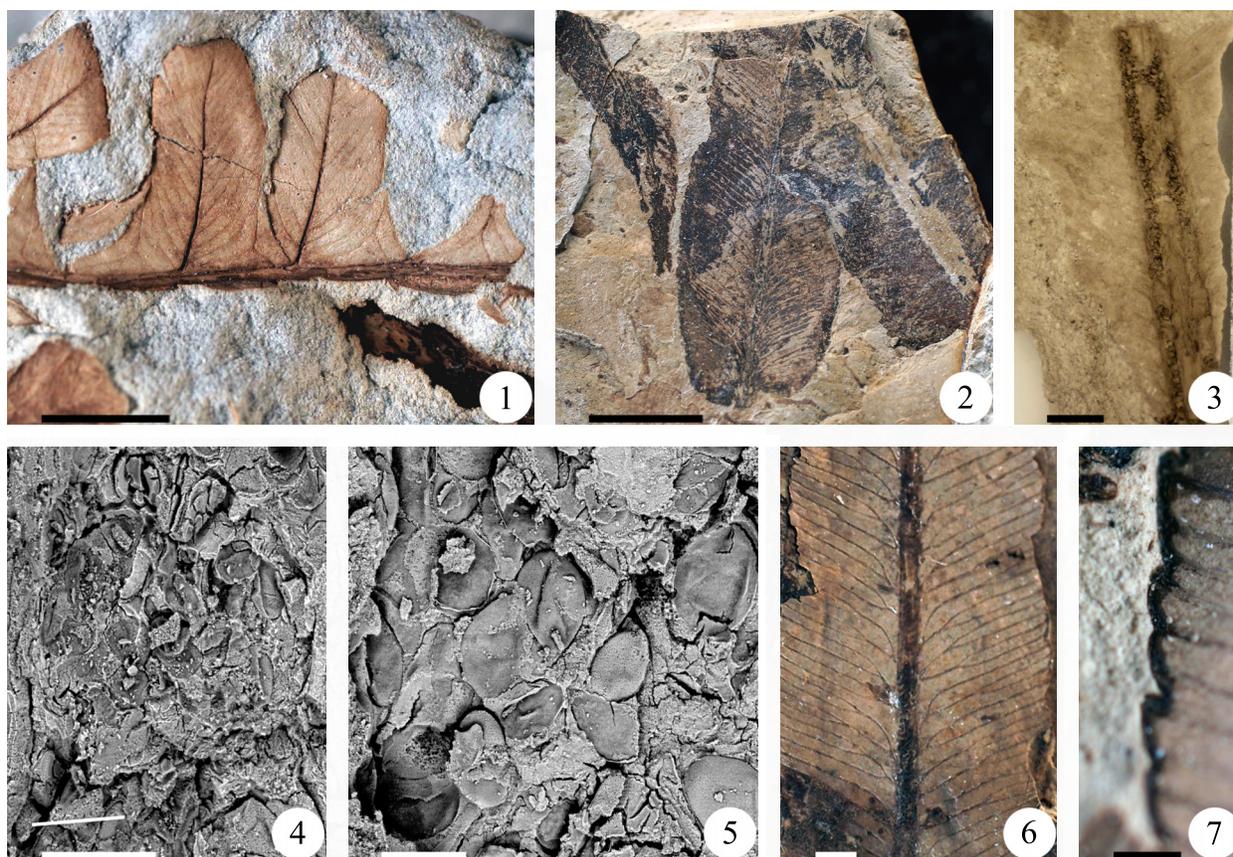


Figure 10. Compression of *Cyclosorus* pinnate leaf and compressions and impressions of *Blechnum* pinnae, sporangia and spores from Late Oligocene volcanoclastic strata in the Margargaria River localities, northwestern Ethiopian Plateau. 10.1 Detail of *Cyclosorus* pinnate leaf fragment showing a characteristic pinnate venation pattern. Note the first pair of secondary veins of adjacent pinnules fused into a single common vein that is arranged perpendicular to the costa and that is joined at its upper limit by the following pair of secondary veins of each pinnule. CH-79-234B. Scale bar equals 0.5 cm. 10.2 Dispersed linear lanceolate *Blechnum* pinnae fragments. CH-93-90. Scale bar equals 0.5 cm. 10.3 Fertile *Blechnum* pinnae fragment showing two rows of sporangia, arranged on a commissure along each side of the costa. CH-87-8. Scale bar equals 0.1 cm. 10.4 SEM of stalked sporangia *in-situ* on *Blechnum* pinnae. Oblique white bar in picture indicates sporangium stalk. CH-87-8. Scale bar equals 50 μ m. 10.5 SEM of *Blechnum* stalked sporangia with *in-situ* monolete spores. CH-87-8. Scale bar equals 25 μ m. 10.6 Detail of *Blechnum* pinnae fragment showing typical dichotomous venation. Note that secondary veins bifurcate once or twice. CH-93-70. Scale bar equals 0.1 cm. 10.7 Detail of *Blechnum* pinnae fragment showing dentate margin. CH-93-70. Scale bar equals 250 μ m.

all, in which the distal and proximal veins of adjoining pinnules meet at the sinus and fuse into a single vein that extends vertically and perpendicularly away from the costa (Figure 10.1). The following veins of each pinnule meet at the sinus, synchronically or nearly so, but do not fuse and end at its upper limit (Figure 10.1). Fossil fronds have been assigned to *Cyclosorus* (Thelypteridaceae) based on pinnule venation and pinnae arrangement and morphology (Tryon and Tryon 1982; Kramer and Green 1990).

Stratigraphic distribution and mode of preservation. In situ *Cyclosorus* frond mats, where indi-

viduals embedded within an airfall tuff (C depositional unit) can be traced vertically and laterally for a short distance within this unit, occur as the dominant vegetation in the south section (Figure 3, CH-79, unit 20). Smaller *Cyclosorus* frond fragments embedded or lying-flat in airfall tuffs, lignites, and overbank layers (C, F, and G depositional units) are also found, singly or co-occurring with some or all of the other ferns in all three sections (e.g., Figure 3, CH-79, units 19; CH-93, unit 23; CH-89, unit 17) and in some reworked tuffs (D depositional unit) in the south and north sections (e.g., CH-79, unit 26; CH-89, unit 14).

Modern distribution and ecology. Today's distribution of *Cyclosorus* includes swampy habitats in the tropics and subtropics of South America and Africa, especially the southeastern and western parts of this continent (Tryon and Tryon 1982; Kramer and Green 1990). This fern is characterized by its ability to colonize disturbed sites such as landslides and roadside banks (Tryon and Tryon 1982; Judd et al. 2007).

Paleoecological significance. The presence of *Cyclosorus* in the Margargaria River is consistent with the pioneer ecological role of extant taxa in this genus (Barthel 1976; Riegel et al. 1999; Collinson 2002), and indicates the common occurrence of short-lived settings during the deposition of the Ash-IV sequence.

Family BLECHNACEAE Newman, 1844

Genus *BLECHNUM* Linnaeus, 1753

Blechnum sp.

Specimens. CH-93-90 (Figure 10.2), CH-87-8 (Figure 10.3-10.5), and CH-93-70 (Figure 10.6-10.7).

Description and type of preservation. This fossil consists of impressions and compressions of linear lanceolate fertile and sterile dispersed individual pinnae (Figure 10.2-10.3). Fertile specimens, which were recovered at a different locality than the Margargaria river localities, show two rows of exindusiate sporangia arranged in a linear pattern in a commissure that runs parallel to the midvein (costa) (Figure 10.3). Stalked sporangia are preserved as compressions and contain discrete numbers of ellipsoidal monolet spores (Figure 10.4-10.5). Venation is free dichotomous, where secondary veins bifurcate twice (Figure 10.6). Secondary veins end at the margin forming a toothed-crenulate pattern (Figure 10.7). The presence of fossil *Blechnum* (Blechnaceae) from Ash-IV is inferred based on morphology of sterile and fertile fronds (Tryon and Tryon 1982).

Stratigraphic distribution and mode of preservation. Numerous *Blechnum* pinnae occur flat or curved along bedding planes in lignites and overbank layers in the central section (F and G depositional units) (e.g., Figure 3, CH-93, unit 11-13) and in overbank layers in the north section (F depositional unit) (Figure 3, CH-89, unit 17); it co-occurs with all the other ferns, except *Marsilea*.

Modern distribution and ecology. *Blechnum* is a cosmopolitan genus best represented in cooler temperate zones or higher altitudes in Africa (1500-2300 meters high) (Kramer and Green 1990;

Aldasoro et al. 2004; Parris 2006). In addition, extant members of this family inhabit montane wet evergreen forests, wet grasslands, and swamps, and form thickets in disturbed sites in tropical latitudes (especially in the Southern Hemisphere) (Tryon and Tryon 1982; Kramer and Green 1990; Parris 2006; Judd et al. 2007).

Paleoecological significance. The presence of *Blechnum* in the Ash-IV deposits at the Margargaria River localities, ~1800 m above sea level today, may indicate similar environmental conditions and substantial uplift of the Ethiopian Plateau by the Late Oligocene (Hoffman et al. 1997 and references therein). The ability of *Blechnum* as a pioneer taxon is consistent with the biology of the other ferns present in these deposits and, independently, also indicates a landscape characterized by a rapidly changing physiography.

Angiosperms

Family FABACEAE Lindley, 1836

Genus *CYNOMETRA* Linnaeus, 1753

Cynometra sp.

Specimens. CH-79-110 (Figure 11.1, 11.3), CH-79-92A (Figure 11.2), CH-79-85 (Figure 11.4), CH-79-124 (Figure 11.5).

Description and type of preservation. This fossil consists of impressions and compressions of small-sized, slightly oblong-elliptic, dispersed leaflets with an oblique-acute base (Figure 11.1). Leaflets are asymmetrical, have a short, pulvinate, petiolule, a slightly eccentric primary vein, faint secondary brochidodromous venation, an entire margin, paracytic stomata, and an acute emarginate apex with a mucron (Figure 11.2-11.5). All these features combined associate this fossil with extant *Cynometra* (Mackinder 2005; Hawthorne and Jongkind 2006).

Stratigraphic distribution and mode of preservation. *Cynometra* leaflets occur contorted along bedding planes or lying flat in weakly laminated clayey siltstones, mudstones, and silty claystones (D, E, and F depositional units) in the basalmost units of Ash-IV in all sections and in the thin stratum immediately below (pre-Ash-IV), respectively (e.g., Figure 3, CH-79, unit 3-5). *Cynometra* is qualitatively the most abundant fossil plant from these basal units.

Modern distribution and ecology. Living *Cynometra* are trees or shrubs common to western and central Africa in lowland rain and swamp forest, often along rivers (Hawthorne and Jongkind 2006; Judd et al. 2007). Members of this genus are also

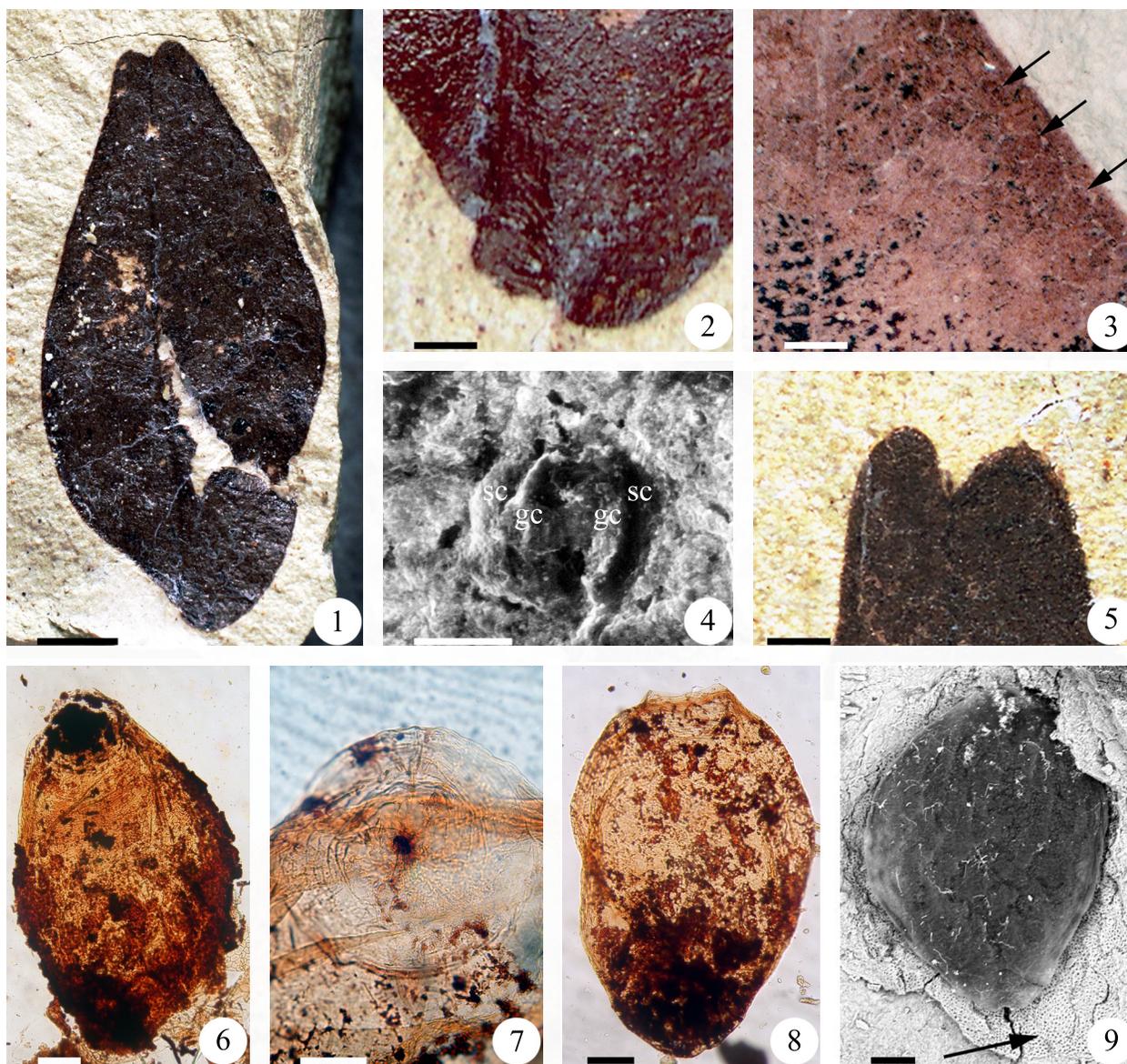


Figure 11. Compressions and impressions of *Cynometra* leaflets and *Typha* seeds from Late Oligocene volcanoclastic strata in the Margargaria River localities, northwestern Ethiopian Plateau. 11.1 General view of a slightly oblong *Cynometra* leaflet. Note oblique asymmetric base and emarginate apex. CH-79-110. Scale bar equals 0.25 cm. 11.2 Detail of *Cynometra* leaflet base showing pulvinate short petiolule. CH-79-92A. Scale bar equals 0.1 cm. 11.3 Detail of *Cynometra* leaflet brochiodromus venation. Arrows point to secondary veins arching and anastomosing with each other before reaching leaflet margin. CH-79-110. Scale bar equals 0.1 cm. 11.4 SEM of *Cynometra* leaflet surface showing paracytic stomata, where each guard cell (gc) is accompanied by a subsidiary cell (sc) with which is parallelly aligned. CH-79-85. Scale bar equals 10 μ m. 11.5 Detail of *Cynometra* leaflet emarginate apex bearing a small mucron. CH-79-124. Scale bar equals 0.1 cm. 11.6 General view of a barrel-shaped *Typha* seed with operculate (circular darkened area) proximal end. CH-79-4. Scale bar equals 125 μ m. 11.7 Detail *Typha* seed proximal end showing circular operculum. CH-79-26. Scale bar equals 50 μ m. 11.8 General view of a *Typha* seed without an operculum. Note ragged collar of cells resulting from operculum detachment. CH-79-26. Scale bar equals 125 μ m. 11.9 *Typha* seed showing possible remains of bristles (part of the perianth) surrounding its perimeter (impressions of a micro-pitted area indicated by arrow). CH-79-4. Scale bar equals 125 μ m.

present in seasonally dry forest, woodland, and bushland or thicket, where some species grow gregariously and form dominant stands (Mackinder 2005).

Paleoecological significance. Because of the wide range of environments in which species of *Cynometra* can be found today, the paleoecological setting cannot be determined more narrowly than bushland to rainforest based upon this genus. However, additional *Cynometra* leaves have been found previously in the Guang River locality of the Chilga beds, approximately 20 meters stratigraphically below the *Margargaria* species described here, forming part of a parautochthonous plant assemblage that was interpreted to represent a riparian forest community (Pan 2007). *Cynometra* from the *Margargaria* River localities is morphologically indistinguishable from the Guang River fossil, and therefore, it may be assumed that they both represent the same taxon and inhabited comparable riparian environments separated in time and space.

Family TYPHACEAE Jussieu, 1789

Genus *TYPHA* Linnaeus, 1753

Typha sp.

Specimens. CH-79-4 (Figure 11.6, 11.9) and CH-79-26 (Figure 11.7-11.8).

Description and type of preservation. This fossil consists of compressions of barrel-shaped seeds (Figure 11.6-11.9). Characteristic of these seeds is an operculum that occludes the proximal end, where a ragged area representing a collar of cells is seen in those individuals that lack an operculum (Figure 11.6-11.8). A darker zone of cells is commonly present towards the base of these seeds (Figures 11.6, 11.8) and may represent the chala-zal region present in modern taxa. A micro-pitted area surrounding the perimeter of some of the specimens (Figure 11.9) is reminiscent of the part of attachment for bristles (part of the perianth) present in modern taxa. The features displayed by the fossil are consistent with extant *Typha* (Herendeen and Crane 1995; Judd et al. 2007).

Stratigraphic distribution and mode of preservation. Numerous small (~0.1 cm long) *Typha* seeds laying along bedding planes in clayey organic rich and lignitic layers in the south section (F and G depositional units) (Figure 3, CH-79, unit 18-19) co-occur with *Marsilea*, *Cyclosorus*, *Salvinia* (megaspores), *Acrostichum*, and *Alstonia*.

Modern distribution and ecology. Members of the family Typhaceae or “cat tails” are cosmopoli-

tan taxa that inhabit river or sedge meadows, swamps, and fresh water marshes (Judd et al. 2007). They can be found in sandy, shallow-water settings with fluctuating water tables; in soils that may be saturated seasonally and undergo periodic drying, in habitats that may show moderate peat development and, especially, in disturbed habitats (Smith and Kaul 1986; Zomlefer 1994). In particular, an increase in the abundance of *Typha* has been related to the spread of swampland following forest disturbance in successional volcanic environments in New Zealand and in Mount Saint Helens in North America (Spicer 1991; Wilmshurst and McGlone 1996). One reason *Typha* may rapidly colonize open landscapes could be the large number of very small seeds produced by a single plant facilitating transportation by wind currents in open landscapes (Smith and Kaul 1986; Zomlefer 1994). Each wind-dispersed unit comprises an achene-like fruit plus bristles (persistent perianth or “pappus”) that, after dispersal, ultimately split lengthwise to release the single seed (Smith and Kaul 1986).

Paleoecological significance. Abundance of *Typha* seeds in the studied units indicates an open landscape with a shallow freshwater pond or a slow flowing stream with abundant aquatic vegetation, something that may have been promoted by volcanic disturbance of the environment. Co-occurrence of *Typha* with *Salvinia* megaspores, *Marsilea*, and *Acrostichum*, each of which are known to occur in swampy settings but within more or less discrete zones among these (i.e., emergent, shoreline-rooted vegetation), is consistent with high sedimentation rates that rapidly buried the vegetation allowing its preservation as a whole. Further, the occurrence of dicot leaves (*Alstonia*) towards the top of this layer is consistent with the idea that as the swamp or pond dried, the zone of rooted vegetation gradually increased.

Family APOCYNACEAE Jussieu, 1789

Genus *ALSTONIA* Brown, 1810 a

Alstonia sp.

Specimens. CH-79-5A (Figure 12.1), CH-79-32A (Figure 12.2), and CH-79-8 (Figure 12.3-12.4).

Description and type of preservation. This fossil consists of lanceolate to oblanceolate petiolate leaf impressions and poorly-preserved compressions with an entire margin, a decurrent base, and an acute-acuminate apex (Figure 12.1-12.3). Venation is pinnate with many pairs of secondary veins coming off the main vein at a right to acute angle and parallel to each other (Figure 12.4). In addition, all

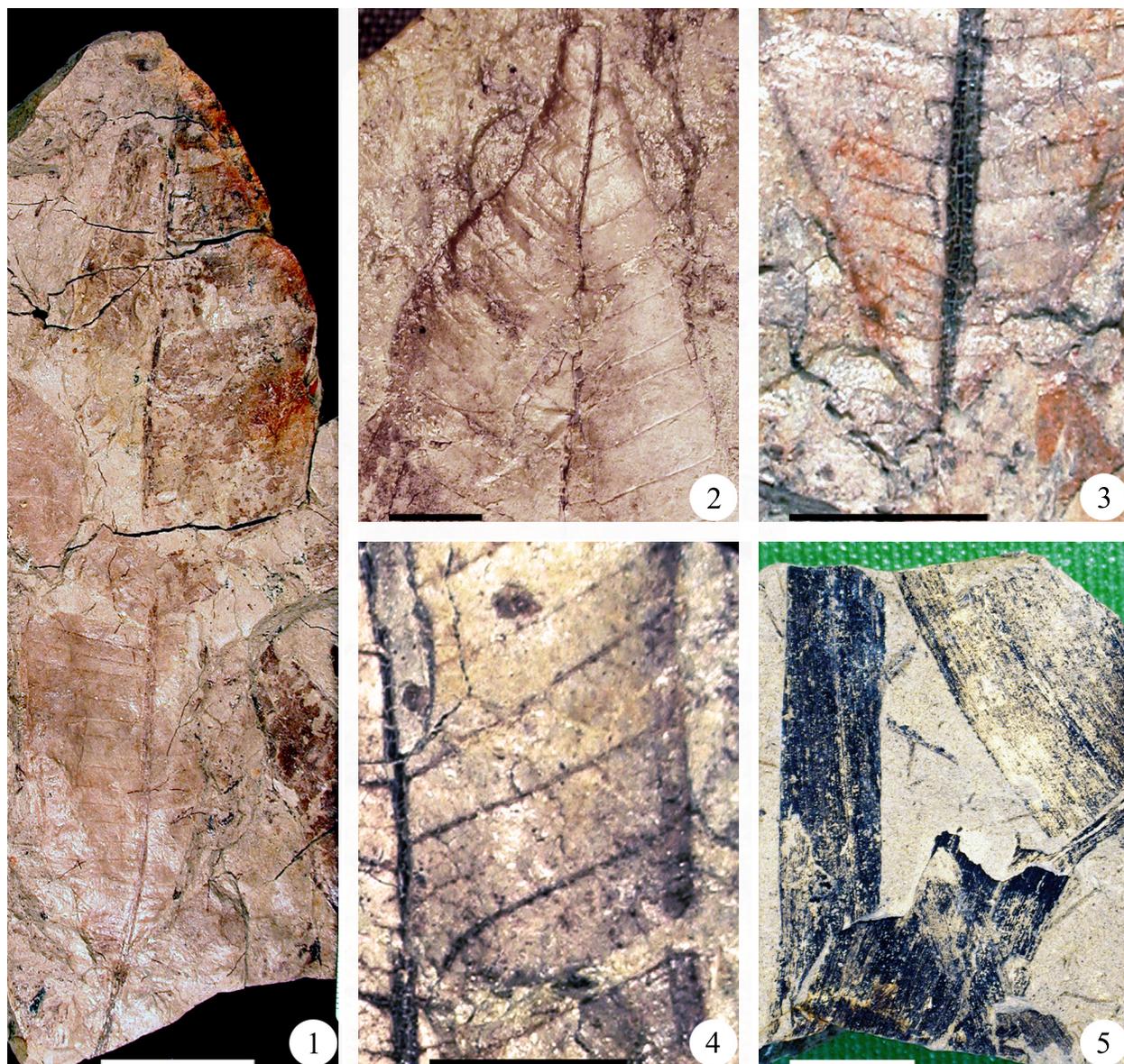


Figure 12. Compressions and impressions of *Alstonia* and *Pandanites* leaves from Late Oligocene volcanoclastic strata in the Margargaria River localities, northwestern Ethiopian Plateau. 12.1 General view of lanceolate *Alstonia* leaf. CH-79-5A. Scale bar equals 2 cm. 12.2 Detail of *Alstonia* leaf showing acute-acuminate apex. CH-79-32A. Scale bar equals 0.5 cm. 12.3 Detail of *Alstonia* leaf showing decurrent base. CH-79-8. Scale bar equals 0.5 cm. 12.4 Detail of *Alstonia* leaf showing pinnate venation, where parallel secondary veins come off the main vein at a right to acute angle and connect with each other via a thick marginal vein. CH-79-8. Scale bar equals 0.5 cm. 12.5 General view of fragments of strap-like *Pandanites* leaves. Note specimen in bottom part of image appearing M-shaped in oblique transverse-section. CH-79-89. Scale bar equals 1 cm.

secondaries run to the margin where they collect in a thick common marginal vein (Figure 12.4). These characters, especially the presence of a large and thick marginal vein where parallel secondary veins collect, are found in the extant genus *Alstonia* (Hawthorne and Jongkind 2006).

Stratigraphic distribution and mode of preservation. *Alstonia* leaves occur lying flat or slightly contorted along bedding planes within organic-rich claystones and mudstones and semi-consolidated lignitic layers (G and F depositional unit) in the south and central sections (e.g., Figure 3, CH-93, unit 15, CH-79, unit 18-19). Leaves of *Alstonia* are also found embedded and completely curled up in

some reworked and airfall tuffs (B, C, and D depositional units) in the south section (Figure 3, CH-79, units 20, 22, 24, 26).

Modern distribution and ecology. Extant *Alstonia* are trees and shrubs that occur as pioneer taxa in primary and especially in secondary swamp successional forests (Hawthorne and Jongkind 2006). They have a buttressed base when they live in swampy settings, which are sometimes characterized by a seasonal climate, at low and medium altitudes in sub tropical to tropical latitudes, including west, central, and northeastern Africa and southern Asia (Hawthorne and Jongkind 2006; Judd et al. 2007; African Flowering Plants Database).

Paleoecological significance. The presence of *Alstonia* is consistent with the occurrence of an early successional open swampy environment of reduced extent, which supports the paleoenvironmental interpretation based on other angiosperm and fern taxa (*Marsilea*, *Salvinia*, *Acrostichum*, *Typha*) in the same strata.

Family PANDANACEAE Brown, 1810 b
Genus *PANDANITES* Tuzson, 1913
Pandanites sp.

Specimens. CH-79-89 (Figure 12.5) and CH-89-69 (Figure 13.1).

Description and type of preservation. This fossil is characterized by narrow, strap-like, leaf impressions and compressions that appear M-shaped in transverse section and that have their margins ornamented with numerous regularly-spaced, hook-like, upwardly-oriented, small teeth (spines) (Figures 12.5, 13.1). Other features include numerous parallel veins of one order, pairs of which appear to be connected by perpendicularly to slightly obliquely (weakly-developed) secondary veins (Figure 13.1). Some specimens display a keel, or a slightly inflexed or thickened part of the leaf (Figure 13.1), where additional spines are present in modern *Pandanus*, but it appears that these have been lost in the fossil. Despite the absence of this last character, the morphological features present in this fossil are consistent with its affinity to *Pandanites*, which is the fossil representative of the extant genus *Pandanus* (Hawthorne and Jongkind 2006; Kvaček and Herman 2004; Burger 1967).

Stratigraphic distribution and mode of preservation. *Pandanites* occurs lying flat or slightly curved along bedding planes within organic rich claystones and mudstones (G, E, and F deposi-

tional units) in the central and north sections (Figure 3, CH-93, unit 11-13, CH-89, unit 17).

Modern distribution and ecology. Modern Pandanaceae are trees, climbers, or shrubs with prop roots that inhabit lowland swamps including coastal environments in oceanic islands, riverine forests, and the shores of rivers in evergreen forests up to 1400 meters in the Old and New World tropics and subtropics (Burger 1967; Beentje 1993; Hawthorne and Jongkind 2006). It also occurs in secondary forest as gregarious patches along streams and around swamps (Beentje 1993; Hawthorne and Jongkind 2006).

Paleoecological significance. The presence of *Pandanites* is consistent with a moist and warm environment in a landscape traversed by rivers and dominated by swamps. *Pandanites* would have concentrated where the water table was high.

Family ARECACEAE Schultz-Schultzenstein, 1832
Genus *HYPHAENE* Gaertner, 1788
Hyphaene sp.

Specimen. CH-93-99A (Figure 13.2).

Description and type of preservation. This fossil consists of compressed petiole fragments that are armed with robust spines of similar size (Figure 13.2). The spines in some specimens are paired and regularly spaced while, in others, it is not possible to determine due to poor preservation (Figure 13.2). Spines are either curved or perpendicular to the petiole, and have relatively broad, flat, arcuate bases that connect with adjacent ones (Figure 13.2). The presence of armed petioles bearing spines with these characteristics indicates affinities with the palm genus *Hyphaene* (subfamily Coryphoideae) (Hawthorne and Jongkind 2006; Pan et al. 2006; Uhl and Dransfield 1987).

Stratigraphic distribution and mode of preservation. *Hyphaene* petiole fragments occur embedded at variable orientations in airfall and reworked tuffs in the central (B and C depositional units; CH-93, unit 23-24) and north sections (C depositional unit; Figure 3, CH-89, unit 24, 26).

Modern distribution and ecology. *Hyphaene* occurs in Africa in arid to semi-arid climates, particularly associated with seasonal streams (Burger 1967; Uhl and Dransfield 1987; Hawthorne and Jongkind 2006). *Hyphaene* species are found in gallery and coastal forests, floodplains, palm savannahs, and along creeks behind mangroves (Burger 1967; Hawthorne and Jongkind 2006).

Paleoecological significance. The presence of *Hyphaene* in Ash-IV is consistent with a riparian

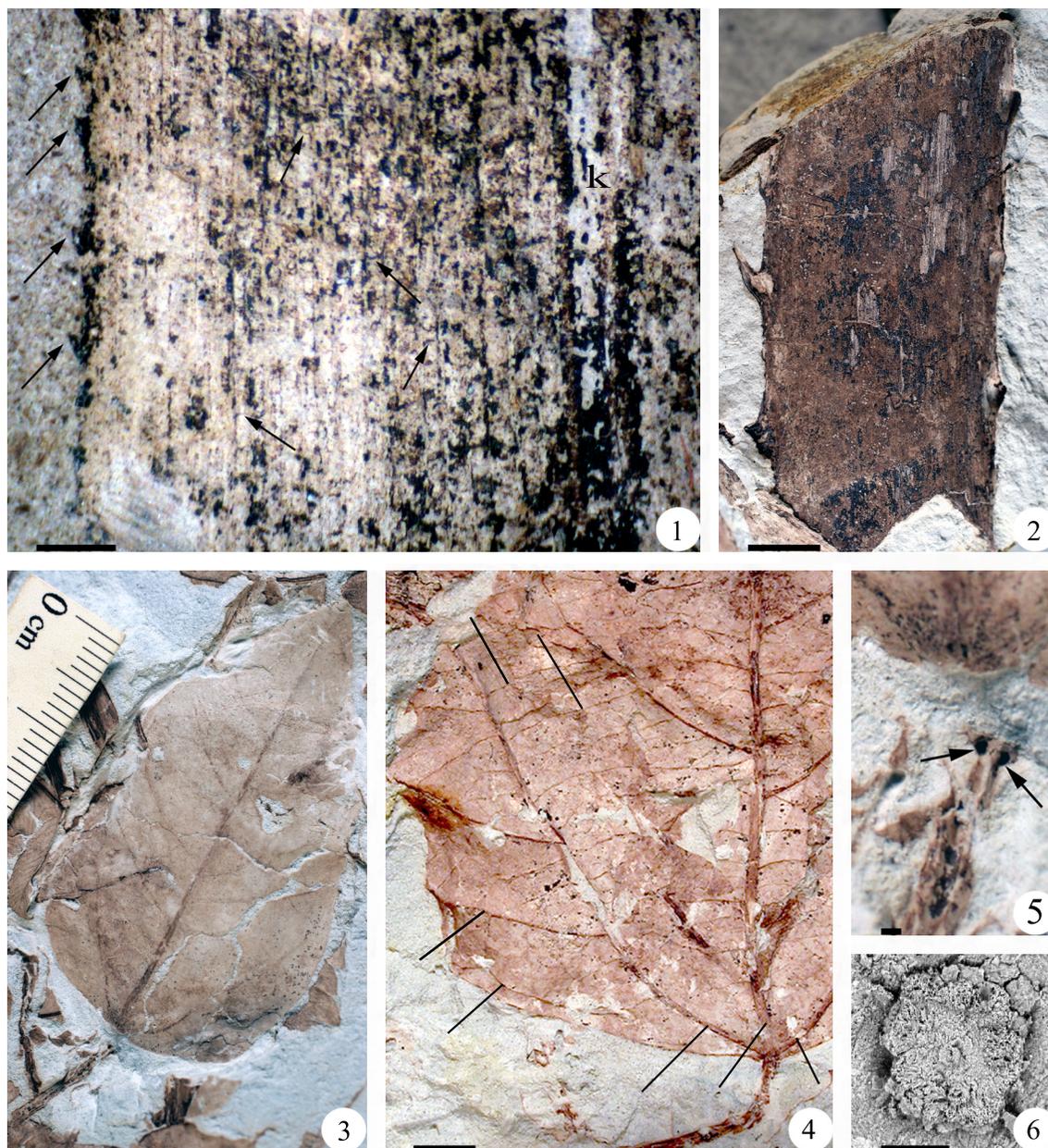


Figure 13. Compression of *Hyphaene* petiole and *Pandanites* leaf and compressions and impressions of *Macaranga* leaves from Late Oligocene volcanoclastic strata in the Margargaria River localities, northwestern Ethiopian Plateau. 13.1 Detail of *Pandanites* leaf showing marginal, regularly-spaced, upwardly-oriented, hook-like small teeth (aligned oblique arrows on left side of image) and numerous parallel veins of one order connected by perpendicularly to slightly obliquely weakly-developed secondary veins (central oblique arrows). Note slightly inflexed area possibly representing a keel (K). CH-89-69. Scale bar equals 0.1 cm. 13.2 General view of a fragment of a *Hyphaene* armed petiole. Note approximately regularly-spaced, curved, spines connected to each other through relatively broad flat arcuate bases. CH-93-99A. Scale bar equals 1 cm. 13.3 General view of a broadly lanceolate *Macaranga* leaf with cuneate to obtuse base, acute apex, and entire margin. CH-79-236. Bar subdivisions equals 0.1 cm. 13.4 Detail of *Macaranga* leaf tri-nerved (actinodromous) venation showing prominent primary veins (oblique bars on right side of image). Note intersecondary veins that split off from the lateral main veins, arch, and reach the margin of the leaf (oblique bars on bottom left side of image). Oblique bars on upper left side of image indicate tertiary veins arranged in a more or less scalariform pattern (alternate percurrent). CH-79-20B. Scale bar equals 0.5 cm. 13.5 Detail of *Macaranga* petiole-leaf intersection. Note hollow petiole and extrafloral nectaries (two small dots indicated by the arrows). CH-79-236. Scale bar equals 0.25 cm. 13.6 SEM of *Macaranga* leaf surface showing a disc-shaped gland. CH-79-232. Scale bar equals 0.1 cm.

environment, but as palms have been previously found occurring in early colonization stages of volcanically disturbed environments during the Cenozoic (e.g., see Collinson 2001 for references), its presence probably also reflects adaptation to disturbance. A *Hyphaene* species different from the taxon described here has been found in older strata in Chilga in both airfall tuff and organic-rich mudstones (Pan et al. 2006), consistent with *Hyphaene* from Chilga characterizing seasonal, ecologically unstable, environments.

Family EUPHORBIACEAE Jussieu, 1789

Genus *MACARANGA* Thouars, 1806

Macaranga sp.

Specimens. CH-79-236 (Figure 13.3, 13.5) CH-79-20B (Figure 13.4), and CH-79-232 (Figure 13.6).

Description and type of preservation. This fossil consists of leaf impressions and poorly-preserved compressions that are broadly lanceolate, have a cuneate to obtuse base, an acute apex, and an entire margin (Figure 13.3). Venation is tri-nerved (actinodromous), where the primary veins are prominent and robust (Figure 13.4). Intersecondary veins split off from the lateral main veins, arch, and reach the margin independently (Figure 13.4). Tertiary venation is difficult to observe but it looks more or less scalariform (alternate percurrent) (Figure 13.4). The petiole is relatively long and appears hollow (Figure 13.5). Two small dots at the end of the petiole in a few specimens represent extrafloral nectaries (Figure 13.5). Also, disc-shaped glandular hairs are present in some specimens (Figure 13.6). The range of features displayed (i.e., extrafloral nectaries and disc-shaped glandular hairs) associates this fossil to both *Macaranga* and *Mallostus* of the Euphorbiaceae; however, the absence of stellate or stellately bundled hairs, the leaf shape, and a long petiole indicates a closer relationship with *Macaranga* (Kulju et al. 2007).

Stratigraphic distribution and mode of preservation. *Macaranga* occurs flat or contorted, sometimes completely curled up, in some airfall tuffs (C depositional unit) in the south and north sections (e.g., Figure 3, CH-79, unit 20, CH-89, unit 24).

Modern distribution and ecology. Extant *Macaranga* is a fast growing pioneer species of tropical to subtropical montane evergreen forest, and may locally be common to dominant in wetter vegetation types, such as swamp forests, gallery forests, and open seasonally swampy settings (Hawthorne and Jongkind 2006; Judd et al. 2007). It regenerates vigorously in clear-felled areas, secondary for-

est, forest edges, riverine forests, and especially in ecologically disturbed places (Slik and van Welzen 2001).

Paleoecological significance. The presence of fossil *Macaranga* is consistent with the presence of an open landscape with at least seasonally abundant water in a periodically disturbed area.

In addition to the fossils already described, there are other plant remains that cannot be assigned confidently to any known group, although they display enough features to allow suggestion of affinities to extant taxa. These fossils are briefly commented on here since they provide additional information about the distribution of ferns and angiosperms within the studied geologic sections. In addition, taphonomy of these additional plants generally corresponds with depositional setting. For example, lignitic strata preserve mostly horizontal and flat-lying fossil assemblages, whereas airfall deposits preserve ferns and angiosperms embedded in ash, sometimes curled, and rarely horizontal. In most cases plant fossils appear to have come from local communities determined by disturbance and/or edaphic setting.

After ferns, the most abundant fossil plants present in these sections are impressions and compressions of angiosperm leaves, leaflets, and, to a lesser extent, fruits. Many of the leaves and leaflets are characterized by their pulvinate petioles or petiolules and the fruits consist of pods of various sizes and shapes, as in the Fabaceae or bean family (Judd et al. 2007). These fossils are found in all depositional units (except A, which, other than for the presence of rooting structures, is non-fossiliferous), but are most abundant in over-bank layers (D, E, and F depositional units). Leaves and leaflets are most common in the basal-most part of all sections of Ash-IV and the thin set of strata below (CH-79, unit 3-5, CH-93, unit 2-4, CH-89, unit 2-4), where ferns are absent and where they co-occur with the leaves of *Cynometra*, discussed above. These assemblages form a continuous mat of leaves that are concentrated in two indurated clayey mudstone to siltstone layers that represent the boundary between Ash-IV and pre-Ash-IV. These units are stratigraphically continuous between sections and probably represent forest litter accumulation (E depositional unit; CH-79, unit 3-4, CH-93, unit 2-3, CH-89, unit 2-3). The widespread occurrence of Fabaceae remains in all sections may be related to their efficiency as N₂-fixing plants for obtaining soil nutrients, which allows them to thrive in environmentally unstable habitats (Schulze et al. 2005).

Whole to fragmented Fabaceae fruit compressions and impressions occur in several horizons throughout the sections, but appear more abundant in some overbank layers (F depositional unit) (i.e., CH-79, unit 18). Despite the common presence of legume fruits in some horizons, fern and parallel-veined monocot-like leaf impressions and compressions dominate in the overbank and lignitic horizons (D, E, F, G depositional units) occurring in the middle part of all sections. In these, ferns and monocots co-occur with impressions and compressions of *Pandanites*, a possible grass flower, poorly-preserved dicot leaves and leaflets (some of which are covered with extensive fungal hyphae networks), armed palm petioles, and fragments of plicate palm fronds (e.g., CH-79, unit 18-19, CH-93, unit 11-14, CH-89, unit 12-14). In most cases, ferns in these horizons are so abundant that it is not uncommon to find numerous dispersed sporangia, spores, megaspores, frond fragments, and other parts completely carpeting the fossil deposit. Some of these remains could have been produced by ferns other than those already described, including a fern that is preserved as contorted to flat-lying compressions in an overbank layer in the south section (F depositional unit, CH-79, unit 18). This fern consists of poorly-preserved creeping rhizomes bearing slightly grooved stems terminated in flabellate tufted fronds that divide dichotomously into linear segments. This fossil is most similar morphologically to *Actiniopteris* (Pteridaceae), a terrestrial taxon commonly found in rather arid settings in East Africa (e.g., lava hillsides, bushland and woodland, dry forests) (Johns 1991; Verdcourt 1999 b; Smith et al. 2006). If this fossil is in fact an ancient representative of extant *Actiniopteris*, then its presence would indicate a seasonally arid environment, which would agree with the inferred environmental conditions based on the presence of other taxa (e.g., *Marsilea*) present in the same fossil horizon.

Palm impressions and compressions, including *Hyphaene*, other spiny petioles of the Coryphoid and Calamoid type (Uhl and Dransfield 1987), and fragments of plicate fronds occur in airfall and the reworked tuff horizons (C and D depositional unit) towards the top of the central and north sections (CH-93, unit 23-25, CH-89, unit 24); plicate palm fronds are also found in stratigraphically equivalent airfall tuff layers in the south section (e.g., CH-79, units 24, 26). In addition, other palm frond fragments are found in some lignitic and airfall tuff horizons in all sections (e.g., CH-79, unit 18, CH-93, unit 14, CH-89, unit 26). Co-occurring

with these palms and some of the described ferns (e.g., *Cyclosorus*) present in a number of tuff layers, are impressions of three morphotypes of poorly preserved dicot petiolate leaves, one of which consists of stipulate compound leaves with a serrate margin that are reminiscent of the extant genus *Rubus* (Rosaceae) (Hawthorne and Jongkind 2006). This is a cosmopolitan genus, with representatives in Africa occurring commonly in wet mountain regions (up to 3000 meters); some of these taxa are known as early colonizers of open patches of primary and secondary forest successions following volcanic or other types of disturbance (Spicer 1991; Hawthorne and Jongkind 2006; Wilmshurst and McGlone 1996; African Flowering Plants Database).

Another monocot that is part of this plant assemblage consists of organically-preserved large hollow septate stems (culms), filled with ashy material, with enlarged internodes, much like bamboos (Poaceae) (Judd et al. 2007). This is present in two reworked tuffs (D depositional unit) (CH-79, units 24, 26) in the south section. Extant bamboos are known as successful colonizers (Judd et al. 2007), based on which an early colonizer role is suggested for the fossils present within Ash-IV. A previous record of bambusoid grasses preserved in airfall tuff layers from the Miocene of Kenya is consistent with the interpretation that bamboos were associated with disturbed environments in the past (Jacobs and Kabuye 1987).

The distribution of plants within the three geologic sections discussed here indicates that riparian vegetation preserved as a forest litter accumulation horizon, which includes the genus *Cynometra* within the legumes family, typical of seasonal environments, and other dicot angiosperms of unknown affinity, characterized the early depositional stages of Ash-IV and pre-Ash-IV. The occurrence of plant assemblages consisting of in situ and transported aquatic and terrestrial ferns and a few angiosperms typical of ponded or wetland settings distributed in the lignitic horizons around the stratigraphic middle part of all sections is interpreted to represent a series of fluvial environments characterized by high water table inundated floodplains. The airfall and slightly fluvially-reworked horizons in the upper part of all sections is characterized by ecological pioneer taxa and other individuals of less clear affinity, among which are in situ preserved ferns and angiosperms, which is interpreted as indicating open ash-covered floodplains where airfall ash deposition preserved early ecological stages of plant community succession.

In summary, the Ash-IV unit and the thin set of strata below it (pre-Ash-IV) contain a succession of plant communities that reflect the temporal physiographic variations of the environment resulting from increasingly frequent volcanic activity.

DISCUSSION

Despite the frequent and widespread occurrence of Cenozoic volcanoclastic deposits, fine-scale paleoenvironmental reconstruction through a continuous geological section has been attempted only in a few instances (e.g., Yuretich 1984; Crowley et al. 1989, 1994; Falcon-Lang and Cantrill 2002; Jago and Boyd 2005). Most studies have focused on single sedimentary events that represent a snapshot of the plant community at a given moment. In these cases, the dynamics of plant community changes as influenced by concomitant changes in the environment, particularly by volcanic activity, remain unsampled. Moreover, inferences of environmental conditions based on data from a single sedimentary event is assumed to be a good representative of landscape heterogeneity at the time of deposition, but may be misleading in rapidly changing regions, such as those influenced by catastrophic events. The study presented here is among the few that have used a combined approach, including sedimentology, stratigraphy, and paleobotany, to infer the evolution of the environment at fine temporal and spatial scales, and its focus on the poorly known Paleogene of tropical Africa makes it unique.

Interpretation of Sedimentology

The main characteristic of the strata represented in the sections studied here is that they are thin, incompletely/poorly-developed, and often randomly truncated or mantled by massive ash layers. These attributes most likely resulted from stochastic variation in sediment discharge influx and therefore irregular rates of deposition. In particular, sedimentary structures present in these strata can be related to fluvial processes associated with channel and overbank depositional environments (e.g., Currie et al. 2009). The distinction between these depositional environments is not sharp, but gradual since the sedimentary structures concerned represent adjacent areas of the same fluvial environment. Characteristics that help to distinguish between these depositional environments are the association of particular sedimentary structures and the grain size of the sediments (e.g., Currie et al. 2009). In this study, most depositional units are formed of fine-grained particles, which

indicate that they represent overbank and nearby areas of a fluvial environment.

The lower portion of the stratigraphy, named stage 1 in Figure 3, consists of fine-grained sediment and organic-rich layers (E, F depositional units; all beneath Ash-IV), classified here as a Vertisol paleosol, suggesting a relatively long depositional hiatus in the overbank depositional environment. Emplacement of the stage 1 strata are laterally continuous among the geological sections, and the abundant organic remains (e.g., leaves) concentrated in a thin horizon capping the sequence probably represent forest litter accumulation. The overlying stage 2 strata (Figure 3; beginning of Ash-IV deposition) consist of weakly-laminated claystones, mudstones, and siltstones (D, E, F depositional units), and include fossil leaves and root traces that are most abundant in a thin horizon at the base of the sequence. Stage 2 sediments are interpreted as a Protosol paleosol created by suspension-settling after flooding in a vegetated overbank environment relatively distant from the effects of fluvial-channel depositional processes. Both stage 1 and 2 strata (Figure 3) are consistent with fluvial deposition characterized by meandering streams (Thomas et al. 1987), whereas the latter probably represents a shorter time interval and closer proximity to the channel environment based on generally coarser-grained and relatively lower organic content of the sediments. The thin organic-rich horizon at the base of the stage 2 strata also probably represents forest litter accumulation, but for a shorter period of time relative to stage 1.

Stage 3 (Figure 3) includes organic-rich, poorly developed cross- and horizontally-laminated fining upward strata that represent partially preserved heterolithic cross stratification (A, C, D, and E depositional units). Stage 3 is interpreted to represent parts of point-bar deposits associated with lateral accretion processes in a fluvial environment (Thomas et al. 1987). However, bedding contact surfaces within this succession can be hummocky to erosional, suggesting that these strata may alternatively represent a succession of thin levee deposits in overbank environments characterized by deposition from a meandering stream.

Stage 4 (Figure 3) consists of relatively thicker, massive to poorly-laminated and ripple-cross-laminated, siltstones and very fine sandstones (C, B depositional units) formed by gravity-flow deposition. This deposition mode commonly occurs in channels when overbank slumping results in the sudden formation of a sedimentary

deposit (Miall 1996; Boggs 2006). However, the strata considered here consist mainly of volcanic ash that was not already part of the system, but rather was supplied by local to regional volcanic eruptions. This indicates that part of the extra sediment supply released into the environment was directly deposited on parts of the floodplain, while some of it choked streams and promoted sluggish sedimentation. As a result, sedimentary features characterizing these tuffaceous strata are associated with the channel/overbank transitional part of the depositional environment, much like the preceding units.

Stage 5 consists of poorly-developed (i.e., partially unconsolidated organic matter) lignites and other poorly-laminated organic-rich layers (e.g., Figure 3, CH-93, unit 11-13). The majority of these strata are classified within the fine-grained and organic-rich depositional units (D, E, F, and G) and therefore they represent sedimentary structures typical of the overbank depositional environment (Miall 1996). Their presence is consistent with autochthonous and parautochthonous deposition of organic matter in ephemeral ponds or other parts of the floodplain characterized by a high water table (Miall 1996; Boggs 2006). The origin of these ephemeral pools of standing water can be the result of the obliteration of topographic differences and sealing of soils and other surfaces on the floodplain by the episodic deposition of volcanic ash (Crowley et al. 1989, 1994).

Stage 6 includes cross-laminated, thin, fine sandstones which scour underlying sediments of succession 5 and are, in turn, overlain by massive to poorly-laminated finer-grained layers. This upper part of the succession also shows increasing bed thickness and decreasing organic content toward the north section (CH-89). A thin and continuous organic-rich clayey layer caps the succession. The more coarsely laminated layers are interpreted as fluvial deposits associated with flash flood events, while the massive to poorly reworked strata probably represent rapidly deposited airfall to stream-deposited tuffs buried in a more or less proximal position on a floodplain. The laminated strata represent sedimentary structures formed in the overbank environment; in particular, based upon their gradual thickening and development of scour sedimentary structures in a south (CH-79) to north direction (CH-89), these sedimentary structures represent transition from lower levee deposits to crevasse channel deposits in a position proximal to stream channel environments (Miall 1996).

Additional massive to poorly-laminated siltstones, some of which also show a concave shape, akin to scour and fill structures, characterize stage 7. These have been assigned to the C, B, and D depositional units and are interpreted as sedimentary structures formed or deposited in the overbank environment (Miall 1996). In particular, the horizontal to wavy laminated layers and the layers showing scour and fill structures represent various transitional parts ranging from the overbank to the channel depositional environments, respectively (Miall 1996). The massive siltstones are interpreted to have been aerially deposited on different parts of the fluvial landscape, where they created deposits on the floodplain and choked streams resulting in the formation of multiple small channels according to a braided pattern.

In summary, from the sedimentological data analyzed, it is inferred that most subenvironments of a fluvial environment, except for the most distal parts of the floodplain, are preserved within the succession of strata associated with the Ash-IV unit and the thin set of strata below. An overview of the sedimentary structures of the deposits analyzed is consistent with initial (pre-AshIV strata) deposition by meandering streams on a seasonally inundated floodplain. With the beginning of Ash-IV deposition, calm sedimentation was interrupted by rapid accumulation of ash on different parts of the landscape. Numerous thin lignitic horizons intercalated with these sediments in the stratigraphic middle part of the sections indicate in situ deposition of organic matter in ephemeral pools of stagnant water distributed on the floodplain during volcanic quiescence. Increased frequency of airfall and fluvially reworked ashes, in the upper part of all stratigraphic sections, indicate environments characterized by ash-covered floodplains and fluvial deposition according to a braided pattern. The distribution of depositional units and paleosols indicating the rapid evolution of a system characterized by rather calm deposition on seasonally inundated floodplains to more energetic deposition by braided streams is consistent with stochastic variation of sedimentary discharge rates, which probably reflects the increasing influence of episodic volcanic activity on the landscape through time.

Interpretation of Plant Assemblages

Among the fossil plants preserved, angiosperms occur throughout the basalmost layers of Ash-IV and the thin set of strata below (pre-Ash-IV) with leaf remains concentrated in two thin horizons

probably representing forest litter accumulation. Numerous compressions and impressions of, apparently, several different angiosperm morphotypes occur in these basal horizons, but most of these are impossible to differentiate, since they overlap and are tightly appressed, thus precluding the possibility of identification. The most abundant fossil in these two horizons and the only taxon present in the overlying layer of Ash-IV in all sections is *Cynometra*, which is also present in stratigraphically older strata of the Chilga beds (Pan 2007). There, *Cynometra* is part of a paraautochthonous plant assemblage that was interpreted as representative of a riparian forest environment (Pan 2007) and it is reasonable to assume the same is true in this case.

Plant communities adjacent to or within depositional areas above the basal horizons characterized by forest litter accumulation appear less rich taxonomically up section, where angiosperms are generally underrepresented and ferns dominate. Fossil ferns have been shown to be the principal component of low diversity plant communities in other studies of environments subject to disturbance by volcanic activity (Jago and Boyd 2005; Lentfer and Torrence 2006). In these communities, dominance by ferns has been attributed to their role as ecological pioneers (Went 1959; Richards 1996). Accordingly, the decline in richness of the vegetation through time (up section) is probably a result of the influence of the recurring disrupting effect of episodic volcanism on the environment, which positively influenced the occurrence of ferns and other ecological pioneer plants. Moreover, this work shows that, although the Ash-IV unit is useful for stratigraphic correlation throughout the basin, it does not represent a geologically instantaneous event. Rather, these data indicate that deposition of the pre-Ash-IV and Ash-IV units was a progression towards an ash-dominated depositional system (Figures 3, 14). Nevertheless, fossil floras undergo an almost instantaneous (years to decades) transition from angiosperm-dominated to fern-dominated throughout emplacement of the Ash-IV strata. This pattern of fossil preservation is best characterized as an ecological threshold change (Gordon et al. 2008).

A number of studies have shown that volcanic ash deposition in fluvial environments can cause sealing of soils and choking of rivers, promoting flooding and consequent erosion and runoff (Wilcox 1959; Burnham and Spicer 1986). Other authors have indicated that leaching and deposition of volcanic ashes also results in impermeable

horizons, which promotes pond development (Crowley et al. 1989, 1994). Pond development is associated with a change of vegetation, where ferns can dominate in the early stages (Cohen and Raymond 1984). The abundance of ferns may also be attributed to their capacity to live in poorly oxygenated, waterlogged settings, as well as their ability to be early ecological colonizers (Wing et al. 1993; Page 2002). Accordingly, the abundance of ferns in all the lignites and similar organic rich layers is interpreted as an occurrence of ephemeral ponds across the sampled area in response to volcanic influence on the landscape and the ability of this plant group to live in this kind of setting.

The possibility that the occurrence of more fern remains in the lignitic/peaty layers relative to angiosperms was the result of taphonomic processes should also be considered. Spicer (1989) suggested that reed vegetation growing around the margins of swamps could form a natural barrier preventing entrance and sedimentation of water-transported plant fragments from elsewhere. The few angiosperm remains preserved in the Ash-IV lignites could have been windblown. However, there is a consistency in the composition of the ferns and angiosperms, which are always disturbance taxa (e.g., *Macaranga* and *Cyclosorus*) (Slik and van Welzen 2001). These occur immediately above the lignitic/peaty horizons in some of the massive to slightly reworked tuffs, which are interpreted as open ash-covered landscapes created by volcanic activity. As a result, it seems more plausible that ferns and angiosperms characterizing both lignites and ash layers are a reflection of local low diversity plant communities rather than a consequence of taphonomic processes restricting the preservation or input of angiosperms. This interpretation is consistent with previous research showing that plant communities subjected to recurrent volcanism are characterized by poor taxonomic diversity (Jago and Boyd 2005; Lentfer and Torrence 2006).

Interestingly, up-section, the ferns from Chilga often co-occur with several palms (including Calamoid and Coryphoid taxa), a plant association documented before in paleoenvironments directly influenced by volcanic activity (Wing et al. 1993). Some palms are known as early colonizers in successions from herbaceous to forest swamps, and where they are adapted to saline conditions (Coetzee and Rogers 1982; see Collinson 2001 for other examples where an early successional role has been attributed to palms). Although sediments from the Margargaria River localities do not indi-

cate saline conditions, the association of palms with some or all of the fern taxa (*Acrostichum*, *Blechnum*, *Cyclosorus*, *Equisetum*, *Marsilea*, *Salvinia*) interpreted here as early ecological colonizers is consistent with a similar role for palms. Previous research on palms from Chilga documents their occurrence in a variety of sediment types representing similar and different edaphic settings compared to those described here, which is consistent with ecological versatility and the ability of palms to live in rapidly changing environments (Pan et al. 2006).

Plant assemblages described in this study appear compositionally and ecologically unique when compared to other Paleogene communities from Africa (see e.g., Jacobs 2006; García Massini and Jacobs 2009; Jacobs et al. 2009). This appears evident considering the scale of interpretation of the Margargaria localities analyzed here, the scarcity and uneven distribution of Paleogene macrofloras in Africa, and the poor age control of most known plant assemblages for this period (see e.g., Jacobs 2006; García Massini and Jacobs 2009; Jacobs et al. 2009). Nevertheless, some of the plant taxa present in the Margargaria River localities are also found in similar environments from the Paleogene in Africa. For example, *Acrostichum*, *Salvinia*, and *Typha* macrofossils are known from possible Eocene coastal swampy/marshy environments from Nigeria (Seward 1924). These same three taxa are known from the Late Eocene of Egypt (Fayum depression) in what are interpreted as mangrove and brackish (*Acrostichum*) and marshy habitats (*Salvinia* and *Typha*), while other taxa in the same deposits, characterized by angiosperms that are not found in the plant assemblages from the Margargaria River, indicate gallery forests inland (Tiffney 1991). *Acrostichum* macrofossils are also known from Uganda (Middle Tertiary) and Ethiopia (Oligocene; to the south of Chilga) in woodlands or savannahs and in lacustrine deposits, respectively, both set in volcanic environments (Chaney 1933; Beauchamp et al. 1973). Co-occurring with *Acrostichum* in the two latter places are a number of dicot angiosperm taxa, none of which, except for the presence of the family Fabaceae, are present in the Margargaria River localities (Chaney 1933; Beauchamp et al. 1973). In fact, the Fabaceae appears to be the most abundant family preserved as macrofossils (leaves and wood) and palynomorphs in African Cenozoic assemblages, although the genus *Cynometra*, which characterizes some of the strata from the Margargaria River, is only known from

younger strata of Chilga and from Middle Eocene deposits from Tanzania (Jacobs 2006; Pan 2007). In this latter deposit, *Cynometra* occurs as part of a legume-dominated plant assemblage characterized as a seasonal woodland environment (Herendeen and Jacobs 2000). This is to some extent consistent (i.e., both represent seasonal forest environments) with the depositional environment interpreted for the occurrence of *Cynometra* from the Margargaria localities. Other than these four taxa, the Margargaria River flora shares a record of *Pandanus* (seeds) from the Fayum depression (Kräusel and Stromer 1924), but this evidence has been questioned by Chandler (1954).

Palynologically, *Macaranga*-type pollen and *Acrostichum*, *Salvinia*, and *Marsilea* spores have been recorded from a series of settings ranging from coastal mangrove and swampy settings to inland semi-deciduous forest with humid woodland West and East Africa (e.g., Caratini et al. 1991; Vincennes et al. 2006); however, identification of palynomorphs relative to macrofossils, especially for dispersed spores, is less precise due to fewer diagnostic characters (e.g., see Collinson 2001, 2002). Moreover, edaphic settings for those assemblages are not comparable to the Margargaria River, where volcanism was the driver for the occurrence and rapid deposition of plant assemblages.

As a result, the scarce representation of the macrofossils from the Margargaria River at other Paleogene localities in Africa and the particular setting that volcanism associated with the development of the East African Rift represents make the Ethiopian plant assemblages considered in this study unique. Notwithstanding, some of the taxa present in the Margargaria River localities, such as *Acrostichum*, *Salvinia*, and *Typha*, are also found to be common in similar settings (swamp/marshy habitats, sometimes influenced by volcanism) in other African Paleogene deposits, which may be indicating ecological consistency for these taxa during this period in this continent. These same taxa, as well as *Blechnum*, *Cyclosorus*, and various palms are also common, single or in combination, throughout North America-Europe during the Paleogene. This supports the common association of these taxa in similar habitats characterized as wetland that were in some instances directly influenced by volcanism during the Paleogene (Collinson 2001, 2002 and references therein).

In summary, the Ash-IV deposits and the thin set of strata below (pre-Ash-IV) contain a succession of compositionally and ecologically unique

plant communities that are a reflection of the physiographic characteristics of the environment. In particular, the angiosperm taxa characterizing the early depositional stages of Ash-IV, as well as the thin set of strata below (pre-Ash-IV), correspond to riparian forest vegetation typical of seasonal environments. Taxa in the middle and upper part of the geological sections can be characterized as ecological pioneers, where their presence reflects the influence of rapid and episodic modifications of the landscape triggered by volcanic activity. Volcanism provided an inorganic, fresh surface of ash for colonization by pioneer plants and a sealant that preserved the pre-existing vegetation at the time of each eruption. This indicates that, as the physical settings within the environment were episodically disturbed, so were plant communities reset to earlier stages of development and, in this sense, these deposits preserve several stages of plant recovery, particularly those stages associated with early colonization. This is consistent with low diversity plant assemblages and the mode of preservation and size disparity of plant parts preserved, especially in the airfall tuffs, all of which indicate poor sorting and rapid deposition. Therefore, plant taxa in the middle and upper parts of the studied sections can be interpreted as the fittest available vegetation source following each particular volcanic eruption rather than the temporally-directed (undisturbed by major catastrophic events) evolution of a single plant community through ecological succession.

Summary of Paleoenvironmental Stages Based on Paleobotany and Sedimentology

Stratigraphic correlations among the three sections described from Ash-IV and the thin set of strata below delineate a general evolutionary pattern of ecosystem change through time (Figure 3, Figure 14.1-14.7).

Rather calm sedimentary conditions, dominated by a meandering river, correspond to the initial depositional stages (pre-Ash-IV) (Figure 3, Figure 14.1). During the second to third stages (beginning of Ash-IV deposition) (Figure 3, Figure 14.2-14.4) increased deposition rates result from intermittent ashfall. Some of this ash was aerially deposited, as is indicated by the presence of massive strata, and some was reworked and deposited fluvially. The upwards increasing presence of fill and scour structures internally cross-laminated to lenticular-bedded implies continuous ingressions of ash that rapidly filled and choked streams with sediment. These structures indicate that small-scale

braided streams, instead of large meandering streams gradually developed on the landscape.

Apparent sedimentary calm is inferred from the presence of vertically and laterally alternating lignites and organic-rich strata dominated by ferns (Figure 3, Figure 14.5). This indicates widespread low-lying areas where deposition of organic material occurred in situ. The presence of ashy material within these deposits indicates that ashes covered a vast part of the landscape, and that intermittent fluvial deposition reworked some of this ash into environments characterized by peat accumulation. With time, volcanism gradually resumed and fluvial sedimentation occurred by means of numerous small penecontemporaneous channels in a braided stream system. This relatively unstable environment resulted in fewer plants able to occupy the environment and in situ organic accumulation became less common across this region of the landscape (Figure 3, Figure 14.6). Increased abundance of massive tuffs up section indicates active volcanic activity, while the vertical repetition of scour and fill structures, intercalated with the ashy horizons, is evidence of the sporadic deposition by means of high energy braided streams (Figure 3, Figure 14.7). The abundance of ferns and a few other pioneer colonizers in some of these strata is consistent with an unstable environment, where only those plants adapted to the rapidly changing physiography were able to endure.

In summary, the data presented here show that episodic volcanic activity directly influenced the evolution of the environment and plant community, where a forested landscape characterized by rather calm fluvial deposition was replaced by one dominated by ferns and characterized by aerial and dynamic fluvial deposition.

CONCLUSIONS

1. This research shows that the combined study of paleobotanical and sedimentological data from these deposits allows for a dynamic picture of landscape evolution in a relatively rarely studied tropical upland setting. In particular, this paper provides a first view of the dynamics of ecological succession in Paleogene forests of Africa subjected to repeated disturbance by major volcanic activity, such as those associated with rift development.
2. Analysis of macrofossils and sediments show that physiographic changes brought about by volcanism characterizing the Late Oligocene of northwestern Ethiopia influenced paleoenvironmental conditions and plant communi-

Hypothetical Reconstruction of Landscape Evolution Based on Sedimentological and Paleobotanical Data

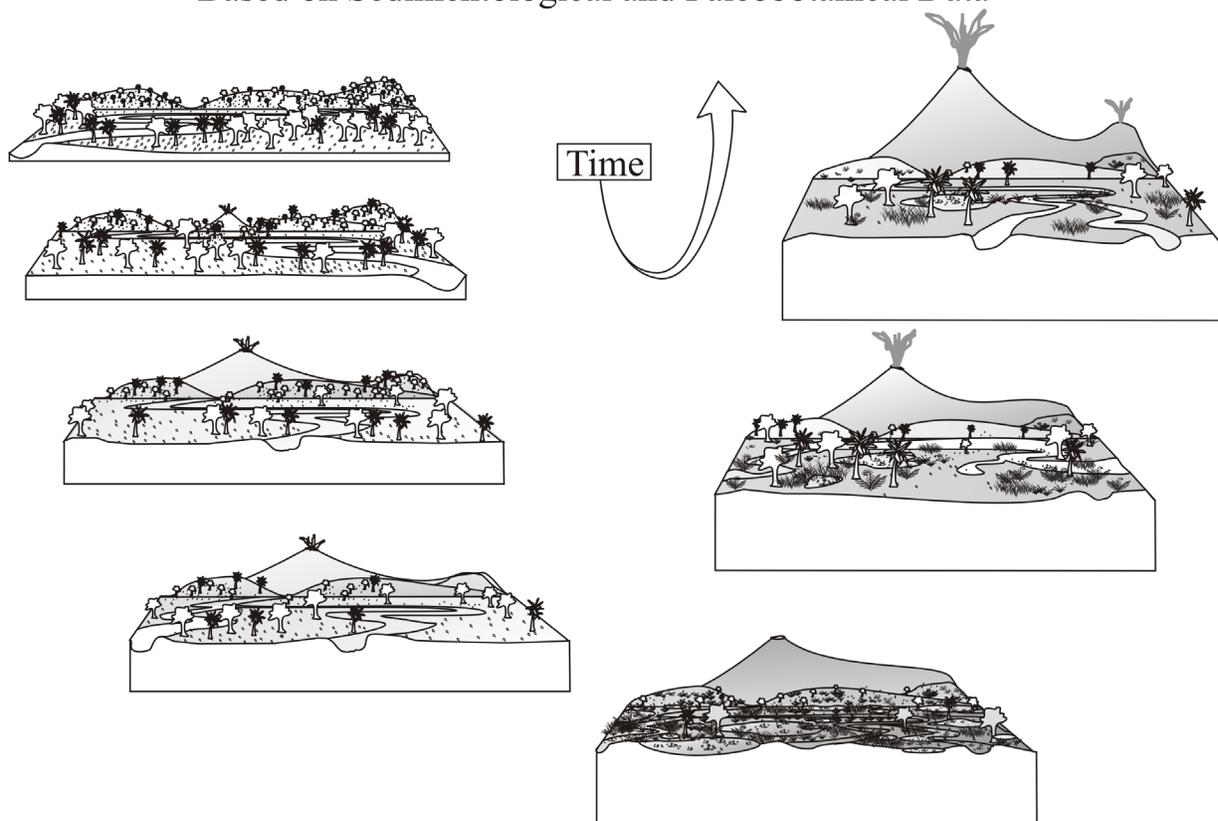


Figure 14. Inferred paleoenvironmental stages for the deposition of the Late Oligocene volcanoclastic strata from the Margargaria River localities, northwestern Ethiopian Plateau. 14.1 and 14.2 Initial stages of paleoenvironment evolution depicting a forested landscape characterized by fluvial deposition associated with meandering streams. 14.3 and 14.4 Intermediate stages of paleoenvironment evolution showing moderate volcanic activity, altered forest vegetation, and sedimentary deposition gradually following a braided pattern. 14.5 Intermediate stage of paleoenvironment evolution showing landscape dominated by reed and fern vegetation inhabiting ponds and other water-saturated settings of ephemeral duration, where episodic volcanic activity, at times, interrupted in situ deposition of organic matter. 14.6 Intermediate stage of paleoenvironment evolution characterized by increased volcanic activity, sparse vegetation, and fluvial deposition according to a braided pattern. 14.7 Final stage of paleoenvironmental evolution showing a landscape dominated by the presence of ferns and other ecological pioneer plants, where deposition resulted mainly from airfall ash and ephemeral discharge of sediments by braided streams.

ties, transforming a forested landscape inhabited by riparian taxa to transient settings dominated by ferns and a few ecologically pioneer angiosperms typical of disturbed environments.

3. In summary, the common occurrence of ferns associated with only a few angiosperm taxa also known as ecological pioneers at several localities across the Chilga basin (100

km²) suggests that volcanism had a profound effect on plant communities over a large area. Therefore, it can be suggested that the extinction from the Ethiopian highlands of some angiosperms with affinities to modern West and Central African forests, present in older sediments at Chilga, could have been due, at least in part, to repeated volcanism associated with development of the northwestern Ethiopian Plateau.

ACKNOWLEDGMENTS

We thank the Authority for Research and Conservation of Cultural Heritage, the Ministry of Culture and Sport Affairs, Ethiopia, particularly A. Jara, for permission to conduct our ongoing research in the Blue Nile Basin, the Director and staff of the National Museum, Addis Ababa, for their assistance with collections, and the Gondar ARCCH for logistical support. In addition, the authors are grateful to the help provided with the fieldwork by G. Ayele, Y. Desta, Y. Sitotaw, A. Abedom, T. Desta, M. Mekonnen, H. Habtemichael, and E. Addissu. The project was funded by grants from the National Science Foundation EAR-0240251 and EAR-0617306, the National Geographic Society, and the Downey Family Award for Faculty Excellence to BFJ and NT. Funds for this project also came from the National Science Foundation EAR-000 1259 to BFJ and NT the Jacob and Frances Sanger Mossiker Chair in the Humanities, the University Research Institute of the University of Texas at Austin, and the Institute for the Study of Earth and Man (to JLGM). One of the authors (JLGM) wishes to dedicate this paper to Lena Marie Echelle.

REFERENCES

- African Flowering Plants Database. Conservatoire et Jardin botaniques de la Ville de Genève and South African National Biodiversity Institute, Pretoria, "Retrieved [June 2008]", from /www.ville-ge.ch/cjb/bd/africa/index.php.
- Aldasoro, J.J., Cabezas, F., and Aedo, C. 2004. Diversity and distribution of ferns in sub-Saharan Africa, Madagascar and some islands of the South Atlantic. *Journal of Biogeography*, 31:1579-1604.
- Artoli, G., Smith, J.V., and Pluth, J.J. 1986. X-ray structure refinement of mesolite. *Acta Crystallographica*, C42:937-942.
- Awad, M.Z. and Breir, F.E.R. 1993. Oligo-Miocene to Quaternary paleoenvironment in Gezira area, central Sudan, p. 465-470. In Thorweihe and Schandelmeier (eds.), *Geoscientific Research in Northeast Africa*. Balkema, Rotterdam.
- Barthel, M. 1976. Eozäne floren des Geisetales. Farne und Cycadeen. *Abhandlungen des Zentralen Geologischen Instituts, Berlin*, 26:439-498.
- Beauchamp, M.M., Lemoigne, Y., and Petrescu, J. 1973. Les paléoflores tertiaires de Debré-Libanos (Ethiopie). *Société Géologique du Nord Annales*, 43:17-32.
- Beentje, H.J. 1993. Pandanaceae, p. 1-9. In Polhill, R.M. (ed.), *Flora of Tropical East Africa*. Balkema, Rotterdam.
- Boggs, S. 2006. *Principles of Sedimentology and Stratigraphy* (fourth edition). Pearson, Prentice Hall, Upper Saddle River, New Jersey.
- Bohor, B.F. and Triplehorn, D.M. 1993. *Tonsteins: altered volcanic-ash layers in coal-bearing sequences. Geological Society of America Special Paper 285*, Boulder, Colorado.
- Borchardt, G. 1989. Smectites, p. 675-272. In Dixon, J.B. and Weed, S.B. (eds.), *Minerals in soil environments. Soil Science Society of America* (second edition), Madison, Wisconsin.
- Bown, T.M., Kraus, M.J., Wing, S.C., Fleagle, J.G., Tiffney, B.H., Simons, E.L., and Vondra, C.F. 1982. The Fayum Primate Forest Revisited. *Journal of Human Evolution*, 11:603-632.
- Brown, R. 1810 a. On the Asclepiadeae: 64. A Natural Order of Plants Separated from the Apocineae of Jussieu. *Memoirs of the Wernerian Natural History Society*, 1 (1811) 75.
- Brown, R. 1810 b. *Prodromus Flora Novae Hollandiae et Insulae van-Diemen*: 340.
- Burger, W.C. 1967. *Families of Flowering Plants in Ethiopia*. Oklahoma State University-Press, Stillwater, Oklahoma.
- Burnham, R.J. and Spicer, R.A. 1986. Forest litter preserved by volcanic activity at El Chichón, Mexico: A potentially accurate record of the pre-eruption vegetation. *Palaios*, 1:158-161.
- Cantrill, D.J. and Hunter, M.A. 2005. Macrofossil floras of the Latady Basin, Antarctic Peninsula. *New Zealand Journal of Geology and Geophysics*, 48:537-553.
- Caratini, C., Tissot, C., Kar, R.K., Venkatachala, B.S., and Sarr, R. 1991. Palaeocene palynoflora from Walalane borehole, Senegal, p. 123-133. In Heine, K. (ed.), *Palaeoecology of Africa and the Surrounding Islands. Proceedings of the 1st Symposium on African Palynology*.
- Chandler, M.E.J. 1954. Some Upper Cretaceous and Eocene fruits from Egypt. *Bulletin of the British Museum (Natural History) Geology*, 2:147-187.
- Chaney, R.W. 1933. A Tertiary flora from Uganda. *Journal of Geology*, 41:702-709.
- Coetzee, J.A. and Rogers, J. 1982. Palynological and lithological evidence for the Miocene paleoenvironments in the Saldanha region (South Africa). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 39:71-85.
- Cohen, A.D. and Raymond, R. 1984. Peat deposits of Costa Rica. *Geological Society of America, Abstracts with Programs*, 16:474.
- Collinson, M.E. 1988. Freshwater macrophytes in palaeolimnology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 62:317-342.
- Collinson, M.E. 2001. The ecology of Cainozoic ferns. *Review of Palaeobotany and Palynology*, 119:51-68.
- Collinson, M.E. 2002. Cainozoic ferns and their distribution. *Brittonia*, 53:173-235.

- Crowley, S.S., Dufek, D.A., Stanton, R.W., and Ryer, T.A. 1994. The effects of volcanic ash disturbance on a peat-forming environment: environmental disruption and taphonomic consequences. *Palaios*, 9:158-174.
- Crowley, S.S., Stanton, R.W., and Ryer, T.A. 1989. The effects of volcanic ash on the maceral and chemical composition of the C coal bed, Emery coal field, Utah. *Organic Geochemistry*, 14:315-331.
- Currie, B.S., Colombi, C.E., Tabor, N.J., Shipman, T.C., and Montañez, I.P. 2009. Stratigraphy and architecture of the Upper Triassic Ischigualasto Formation, Ischigualasto Provincial Park, San Juan, Argentina. *Journal of South American Earth Sciences*, 27:74-87.
- De Candolle, A.P. 1804. *Essai sur les propriétés médicales des plantes, comparées avec leurs formes extérieures et leur classification naturelle*: 49.
- Falcon-Lang, H.J. and Cantrill, D.J. 2002. Terrestrial paleoecology of the Cretaceous (Early Aptian) Cerro Negro Formation, South Shetland Islands, Antarctica: a record of polar vegetation in a volcanic arc environment. *Palaios*, 17:491-506.
- Falder, A.B., Stockey, R.A., and Rothwell, G.W. 1999. In situ fossil seedlings of a *Metasequoia*-like taxodiaceous conifer from Paleocene river floodplain deposits of central Alberta, Canada. *American Journal of Botany*, 86:900-902.
- Feseha, M.Y. 2005. Sequence stratigraphic interpretation of the Chilga Basin sediments, northwest Ethiopia. *Ethiopian Journal of Science*, 28:75-92.
- Gaertner, J. 1788. *De Fructibus et Seminibus Plantarum*, 1:28.
- García Massini, J.L. and Jacobs, B.F. 2009. Cretaceous-Cenozoic record of ferns in Africa, p. 201–220. In van der Burgt, X., van der Maesen, J. and J.-M. Onana (eds.), *Systematics and conservation of African plants*. Royal Botanic Gardens, Kew.
- García Massini, J.L., Jacobs, B.F., Pan, A., Tabor, N., and Kappelman, J. 2006. The occurrence of the fern *Acrostichum* in successional volcanic and fluvio-lacustrine strata in the Oligocene of the northwestern Ethiopian Plateau. *International Journal of Plant Sciences*, 167:909-918.
- Georgieff, S.M., Herbst, R., Esteban, G.I., and Nasif, N. 2004. Análisis paleoambiental y registro paleontológico de la Formación Desencuentro (Mioceno Superior), Alto de San Nicolás, La Rioja, Argentina. *Ameghiniana*, 41:45-56.
- Gordon, L.J., Peterson, G.D., and Bennett, E.M. 2008. Agricultural modifications of hydrological flows create ecological surprises. *Trends in Ecology & Evolution*, 23:211-219.
- Hawthorne, W. and Jongkind, C. 2006. *Woody Plants of Western African Forests: A Guide to the Forest Trees, Shrubs and Lianas from Senegal to Ghana* (first edition). Kew Publishing, Royal Botanical Gardens, Kew.
- Herendeen, P.S. and Jacobs, B.F. 2000. Fossil legumes from the Middle Eocene (46.0 Ma) Mahenge flora, Singida, Tanzania. *American Journal of Botany*, 87:1358-1366.
- Herendeen, P.S. and Crane, P.R. 1995. The fossil history of the monocotyledons, p. 1-21. In Rudall, P.J., Cribb, D.F., and Humphries, C.J. (eds.), *Monocotyledons: Systematics and Evolution*. Royal Botanical Gardens, Kew.
- Hoffman C., Courtillot, V., Feraud, G., Rochette, P., Yirgus, G., Ketefo, E., and Pik, R. 1997. Timing of the Ethiopian flood basalt event and implications for plume birth and global change. *Nature*, 389:838-841.
- Jacobs, B.F. 2004. Palaeobotanical studies from tropical Africa; relevance to the evolution of forest, woodland and savannah biomes. *Philosophical Transactions of the Royal Society of London B*, 359:1573-1583.
- Jacobs, B.F. 2006. The plant fossil record and implications for phytogeography in tropical Africa, p. 191-203. In Ghazanfar S.A. and Banerjee H.J. (eds.), *Biodiversity, Ecology, Phytogeography and Taxonomy*. Royal Botanic Gardens, Kew.
- Jacobs, B.F. and Kabuye, C.H.S. 1987. A middle Miocene (12.2 my old) forest in the East African Rift Valley, Kenya. *Journal of Human Evolution*, 16:147-155.
- Jacobs, B.F., Tabor, N., Feseha, M.Y., Pan, A., Kappelman, J., Rasmussen, T., Sanders, W., Wiemann, M., Crabaugh, J., and García Massini, J.L. 2005. Oligocene terrestrial strata of northwestern Ethiopia: a preliminary report on paleoenvironments and paleontology. *Palaeontologia Electronica*, Vol. 8, Issue 1; 25A:19p, 825KB; http://paleo-electronica.org/paleo/2005_1/jacobs25/issue1_05.htm
- Jacobs, B.F., Pan, A.D., and Scotese, C. 2009. A review of the Cenozoic vegetation history of Africa. In Werdelin, L. and Sanders, W. (eds.), *Cenozoic Mammals of Africa*. University of California Press.
- Jago, L.C.F. and Boyd, W.E. 2005. How a wet tropical rainforest copes with repeated volcanic destruction. *Quaternary Research*, 64:399-406.
- Johns, R.J. 1991. *Pteridophytes of Tropical East Africa: A Preliminary Checklist of the Species* (first edition). Royal Botanical Gardens, Kew.
- Johnson, D.M. 1986. Systematics of the new world species of Marsilea (Marsileaceae). *Systematic Botany Monographs*, 11:1-87.
- Johnson, K.R. 2007. Forests frozen in time. *Nature*, 447:786-787.
- Judd, W.S., Campbell, C.S., Kellogg, E.A., Stevens, P.F., and Donoghue, M.J. 2007. *Plant Systematics: a phylogenetic approach* (third edition). Sinauer Associates, Inc., Sunderland, Massachusetts.
- Jussieu, A.L. 1789. *Genera Plantarum*, 25.
- Kappelman, J., Rasmussen, T., Sanders, W.J., Feseha, M.Y., Bown, T.M., Copeland, P., Crabaugh, J., Fleagle, J.G., Glantz, M., Gordon, A., Jacobs, B.F., Maga, M., Muldoon, K., Pan, A., Pyne, L., Richmond, B., Ryan, T.J., Seiffert, E.R., Sen, S., Todd, L., Wie-

- mann, M.C., and Winkler, A. 2003. New Oligocene mammals from Ethiopia and the pattern and timing of faunal exchange between Afro-Arabia and Eurasia. *Nature*, 426:549-552.
- Keller, W.D. 1956. Clay minerals as influenced by environments of their formation. *American Association of Petroleum Geologists Bulletin*, 40:2689-2710.
- Khademi, H. and Arocena, J.M. 2008. Kaolinite formation from palygorskite and sepiolite in rhizosphere soils. *Clays and Clay Minerals*, 56:429-436.
- Kirchner, E.D.M. 1831. *Schul-Botanik, oder, Kurze Naturgeschichte der Pflanzen Überhaupt*, Berlin, 109.
- Kornás, J. 1985. Adaptive strategies of *Marsilea* (Marsileaceae:Pteridophyta) in the Lake Chad Basin of N.E. Nigeria. *Fern Gazette*, 13:231-243.
- Kramer, K.U. and Green, P.S. 1990. The families and genera of vascular plants, p. 68-74. In Kramer, K.U. and Green, P.S. (eds.), Volume 1, *Pteridophytes and Gymnosperms*, Springer-Verlag, Berlin.
- Kräusel, R. and Stromer, E. 1924. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens, IV. *Abhandlungen der Bayerischen Akademie der Wissenschaften Neue Folge*, 30:1-48.
- Kulju, K.K.M., Sierra, S.E.C., Draisma, S.G.A., Samuel, R., and van Welzen, P.C. 2007. Molecular phylogeny of *Macaranga*, *Mallotus*, and related genera (Euphorbiaceae S.S.): insights from plastid and nuclear DNA sequence data. *American Journal of Botany*, 94:1726-1743.
- Kvaček, J. and Herman, A.B. 2004. Monocotyledons from the Early Campanian (Cretaceous) of Grünbach, Lower Austria. *Review of Palaeobotany and Palynology*, 128:323-353.
- Launert, E. 2003. Marsileaceae, p. 1-16. In Bentjee, H.J. and Ghazanfar, S.A. (eds.), *Flora of Tropical East Africa*. Lisse, Balkema Publishers.
- Lentfer, C. and Torrence, R. 2006. Holocene volcanic activity, vegetation succession, and ancient human land use: unraveling the interactions on Garua Island, Papua New Guinea. *Review of Palaeobotany and Palynology*, 143:83-105.
- Lindley, J. 1836. *Edward's Botanical Register*, Volume 22.
- Link, J.H.F. 1833. *Hortus Regius Botanicus Berlinensis*, 2:128.
- Linnaeus, C. 1753. *Species Plantarum*. Tomus I[II], Impensis Laurentii Salvii, Holmiae, Stockholm.
- Mack, G.H., James, W.C., and Monger, H.C. 1993. Classification of paleosols. *Geological Society of America Bulletin*, 105:129-136.
- Mackinder, B. 2005. Tribe Detarieae, p. 69-110. In Lewis, G. Schrire, B., Mackinder, B., and Lock, M. (eds.), *Legumes of the World*. The Royal Botanical Gardens, Kew.
- Mader, D. (ed.) 1985. *Aspects of fluvial sedimentation in the Lower Triassic Buntsandstein of Europe. Lecture notes in Earth Sciences, Volume 4, Braidplain, floodplain and playa lake, alluvial-fan, aeolian and palaeosol facies composing a diversified lithogenetical sequence in the permian and triassic of South Devon (England)*. Springer Verlag, Berlin, 15-64.
- Martynov, I.I., 1820. *Tekhno-Botanico Slovar*, 559.
- McLoughlin, S. and Drinnan, A.N. 1997. Fluvial sedimentology and revised stratigraphy of the Triassic Flagstone Bench Formation, northern Prince Charles Mountains, East Antarctica. *Geological Magazine*, 134:781-806.
- Miall, A.D. 1996. *The geology of Fluvial Deposits: Sedimentary Facies, Basin Analysis, and Petroleum Geology* (first edition). Springer-Verlag, Berlin.
- Mirbel, C.F.B. 1802. *Marsileaceae*. In *Historie Naturelle des Végétaux*, 5:126 (Lamarck & Mirbel, 21 Nov. 1802).
- Moore, D.M. and Reynolds, R.C. 1997. *X-ray Diffraction and the Identification and Analysis of Clay Minerals*. Oxford University Press, New York.
- Moorhouse, W.W. 1959. *The Study of Rocks in Thin Section*. Harper and Brothers, New York.
- Nagalingum, N.S. 2007. *Marsileaphyllum*, a new genus for Marsileaceous macrofossils: leaf remains from the Early Cretaceous (Albian) of southern Gondwana. *Plant Systematics and Evolution*, 264:41-55.
- Nagalingum, N.S., Schneider, H., and Pryer, K. 2007. Molecular phylogenetic relationships and morphological evolution in the heterosporous fern genus *Marsilea*. *Systematic Botany*, 32:16-25.
- Newman, E. 1844. *History of British Ferns*, Edition, 2:8.
- Page, C.N. 2002. Ecological strategies in fern evolution: a neopteridological overview. *Review of Palaeobotany and Palynology*, 119:1-33.
- Pan, A.D. 2007. The Late Oligocene (28 – 27 MA) Guang River Flora from the northwestern plateau of Ethiopia. *Southern Methodist University, Department of Geological Sciences*, Dallas, Texas.
- Pan, A.D., Jacobs, B.F., Dransfield, J., and Baker, W.J. 2006. The fossil history of palms (Arecaceae) in Africa and new records from the Late Oligocene (28-27 Ma) of northwestern Ethiopia. *Botanical Journal of the Linnean Society*, 7:101-111.
- Parris, B.S. 2006. Blechnaceae, p. 1-11. In Beentje, H.J. and Ghazanfar, S.A. (eds.), *Flora of Tropical East Africa*. Royal Botanic Gardens, Kew.
- Pearson, M.J. 1979. Geochemistry of the Hepworth Carboniferous sediment sequence and origin of the diagenetic iron minerals and concretions. *Geochimica et Cosmochimica Acta*, 43:927-941.
- Pichi Sermoli, R.E.G. 1970. *Webbia*, 24:709.
- Postman, D. 1982. Pyrite and siderite formation in brackish and freshwater swamp sediments. *American Journal of Science*, 282:1151-1183.
- Rao, T.A., Mukharjee, A.K., and Banerjee, L.K. 1973. Is *Acrostichum aureum* L. truly a mangrove fern? *Current Science*, 42:546-547.

- Retallack, G.J. 1988. Field recognition of paleosols, p. 1-20. In Reinhardt, J. and Sigleo, W.R. (eds.), *Paleosols and Weathering Through Geologic Time: Principles and Applications. Geological Society of America Special Paper 216*, Boulder, Colorado.
- Retallack, G.J. 1990. *Soils of the Past: An Introduction to Paleopedology*. Unwin Hyman, Boston, Massachusetts.
- Richards, P.W. 1996. *The Tropical Rain Forest: An Ecological Study* (second edition). Cambridge University Press, Cambridge.
- Riegel, W., Bode, T., Hammer-Schiemann, G., Lenz, O., and Wilde, V. 1999. The paleoecology of the Lower and Middle Eocene at Helmstedt, northern Germany – A study in contrasts. *Acta Palaeobotanica, Supplement*, 2:349-358.
- Saenger, P. 1998. Mangrove vegetation: an evolutionary perspective. *Marine and Freshwater Research*, 49:277-286.
- Sah, S.C.D. 1967. Palynology of an Upper Neogene profile from Rusizi Valley, Burundi., *Annales du Musée Royal de L'Afrique Central, Série 8, Sciences Géologiques, Mémoires*, 57:1-173.
- Sanders, W.J., Kappelman, J., and Rasmussen, T. 2004. New large-bodied mammals from the Late Oligocene site of Chilga, Ethiopia. *Acta Paleontologica Polonica*, 49:365-392.
- Schelppe, E.A.C.L.E. 1961. The ecology of *Salvinia auriculata* and associated vegetation on Kariba Lake. *Journal of South African botany*, 27:181-187.
- Schneider, H. and Pryer, K.M. 2002. Structure and function of spores in the aquatic heterosporous fern family Marsileaceae. *International Journal of Plant Sciences*, 163:485-505.
- Schultz-Schultzenstein, K.H. 1832. *Natürliches System des Pflanzenreichs nach seiner inneren Organisation : nebst einer vergleichenden Darstellung der wichtigsten aller früheren künstlichen und natürlichen Pflanzensysteme*, 317. Berlin, Germany.
- Schulze, E.D., Beck, E., and Müller-Hohenstein, K. 2005. *Plant Ecology*. Springer, Berlin.
- Séguier, J.F. 1754. *Plantae Veronenses, seu Stirpium quae in Agro Veronensi Reperiuntur Methodica Synopsis*, Veronae, 3:52.
- Seward, A.C. 1924. A collection of fossil plants from south-east Nigeria. *Bulletin of the Geological Survey of Nigeria*, 6:66-81.
- Slik, J.W.F. and van Welzen, P.C. 2001. A phylogeny of *Mallotus* (Euphorbiaceae) based on morphology: indications for a pioneer origin of *Macaranga*. *Systematic Botany*, 26:786-796.
- Smith, S.G. and Kaul, R.B. 1986. Typhaceae Juss., the cat-tail family, p.1237-1239. In McGregor, R.L., Barkley, T.M., Brooks, R.E., and Schofield, E.K. (eds.), *Flora of the Great Plains*. University of Kansas Press, Lawrence, Kansas.
- Smith, A.R., Pryer, K.M., Schuettpelz, E., Korall, P., Schneider, H., and Wolf, P.G. 2006. A classification for extant ferns. *Taxon*, 55:705-731.
- Spicer, R.A. 1989. The formation and interpretation of plant fossil assemblages. *Advances in Botanical Research*, 16:95-191.
- Spicer, R.A. 1991. Plant Taphonomic Processes, p.71-113. In Allison, P.A. and Briggs, D.E.G. (eds.), *Taphonomy: Releasing the Data Locked in the Fossil Record, Volume 9 of topics in Geobiology*. Plenum Press, New York.
- Spicer, R.A., Burnham, R.J., Grant, P., and Glick, H. 1985. *Pityrogramma calomelanos*, the primary, post eruption colonizer of Volcán Chichonal, Chiapas, Mexico. *American Fern Journal*, 75:1-5.
- Staub, J.R. and Cohen, A.D. 1978. Kaolinite-enrichment beneath coals; a modern analog, Snuggedy Swamp, South Carolina. *Journal of Sedimentary Petrography*, 48:203-210.
- Tabor, N.J. and Montañez, I.P. 2004. Morphology and distribution of fossil soils in the Permo-Pennsylvanian Wichita and Bowie Groups, north-central Texas, USA: implications for western equatorial Pangean paleoclimate during icehouse-greenhouse transition. *Sedimentology*, 51:851-884.
- Tabor, N.J., Montañez, I.P., and Southard, R.J. 2002. Mineral and stable isotopic analysis of pedogenic proxies in Permo-Pennsylvanian paleosols: implications for paleoclimate and paleoatmospheric circulation. *Geochimica et Cosmochimica*
- Taggart, R.E. and Cross, A.T. 1991. Plant successions and interruptions in Miocene volcanic deposits, Pacific Northwest, p. 57-68. In Lockley, M.G. and Rice, A. (eds.), *Volcanism and Fossil Biotas. Geological Society of America Special Paper 244*, Boulder, Colorado.
- Thanikaimoni, G. 1987. Mangrove palynology. *Published by UNDP/UNSECO Regional project on training and research on mangrove ecosystems, RAS/79/002, and the French Institute, Pondicherry. Institute Français de Pondichéry, Travaux de la Section Scientifique et Technique, Tome 24*.
- Thomas, R. G., Smith, D. G., Wood, J. M., Visser, J., Calverley-Range, E. A., and Koster, E. H. 1987. Inclined heterolithic stratification – terminology, description, interpretation and significance. *Sedimentary Geology*, v. 53, p. 123-179.
- Thours, L.M.AP. 1806. *Genera Nova Madagascariensia*, 26.
- Tiffney, B.H. 1991. Paleoenvironment of the Oligocene Jebel Qatrani Formation, Fayum depression, northern Egypt, based on floral remains. *Abstracts 23rd GSA meeting*, 456.
- Tomlinson, P.B. 1986. *The Botany of Mangroves*. Cambridge University Press, Cambridge.
- Tryon, R.M. and Tryon, A.F. 1982. *Ferns and Allied Plants*. Springer Verlag, New York.
- Tuzson, J. 1913. Adatok Magyarország fosszilis flórájához Magyarország fosszilis flórájához (Additamenta ad floram fossilem Hungariae III). *A magyar királyi földtani intézet évkönyve*, 21:209-233.

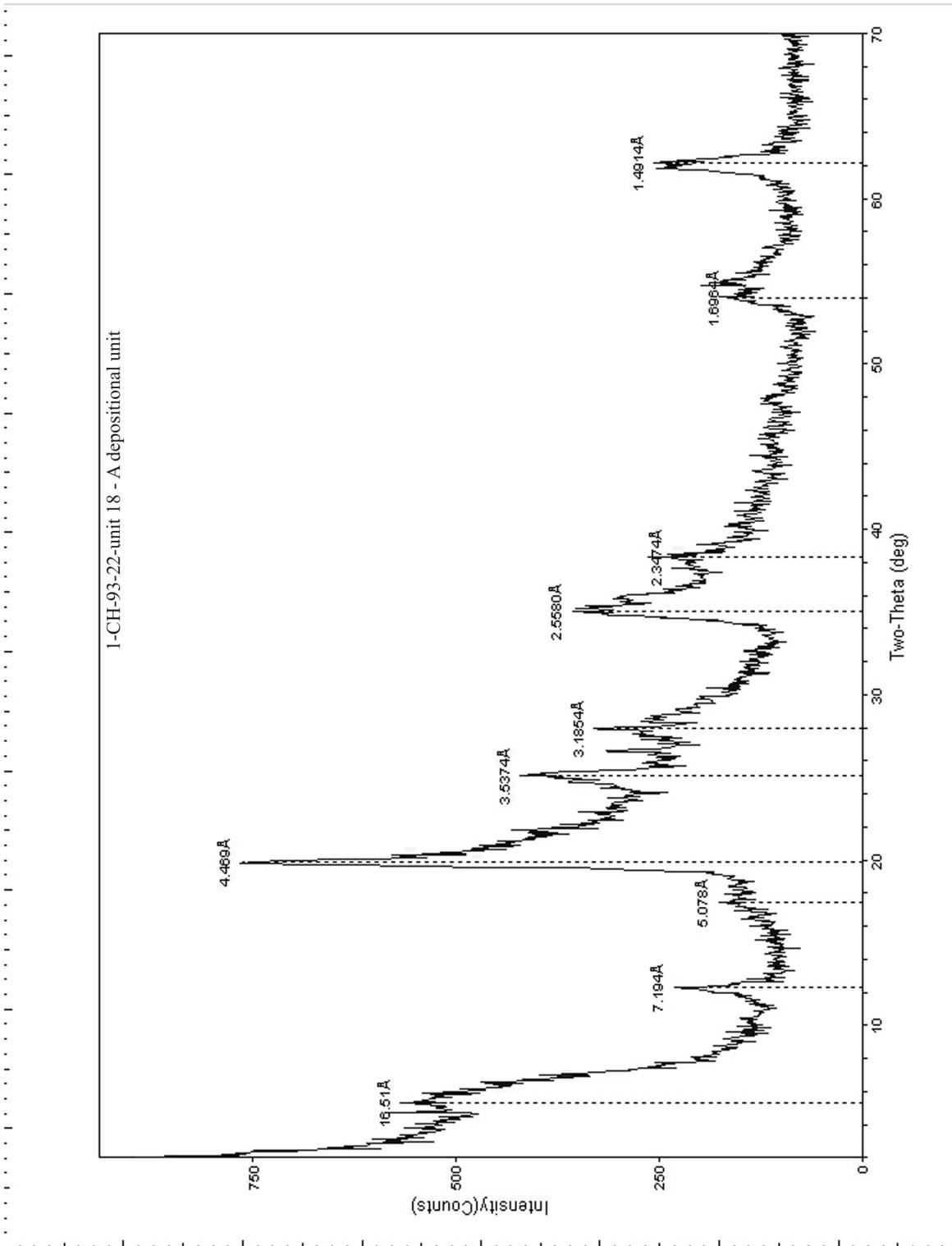
- Uhl, N.W. and Dransfield, J. 1987. *Genera Palmarum. A Classification of Palms Based on the Work of Harold E. Moore Jr.* Allen Press, Lawrence, Kansas.
- Vepraskas, M.J. 1994. Redoximorphic features for identifying aquic conditions. *North Carolina Agricultural Research Service Technical Bulletin*, Raleigh.
- Verdcourt, B. 1999a. *Flora of tropical east Africa. Equisetaceae*. Royal Botanical Gardens, Kew.
- Verdcourt, B. 1999b. *Flora of tropical east Africa. Actinopteridaceae*. Royal Botanical Gardens, Kew.
- Verdcourt, B. 2000. *Flora of tropical east Africa. Salviniaceae*. Royal Botanical Gardens, Kew.
- Vincennes, A., Tiercelin, J., and Buchet, G. 2006. New Oligocene-early Miocene microflora from the southwestern Turkana Basin paleoenvironmental implications in the northern Kenya Rift. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 239:470-486.
- Weber, M.H., Hadley, K.S., Frenzen, P.M., and Franklin, J.F. 2006. Forest development following mudflow deposition, Mount S. Helens, Washington. *Canadian Journal of Forest Research*, 36:437-449.
- Went, F.W. 1959. The plants of Krakatoa. *Scientific American*, 181:52-54.
- Wilcox, R.E. 1959. Some effects of recent volcanic ash falls with especial reference to Alaska. *USGS Bulletin*, 1028:409-474.
- Wilmshurst, J.M. and McGlone, M.S. 1996. Forest disturbance in the central North Island, New Zealand, following the 1850 BP Taupo eruption. *The Holocene*, 6:399-411.
- Wilson, M.J. 1999. The origin and formation of clay minerals in soils: past, present and future perspectives. *Clay Minerals*, 34:7-25.
- Wing, S.L., Hickey, L.J., Swisher, C.C. 1993. Implications of an exceptional fossil flora for Late Cretaceous vegetation. *Nature*, 363:342-344.
- Yemane, K., Robert, C., and Bonefille, R. 1987 a. Pollen and clay mineral assemblages of a Late Miocene lacustrine sequence from the northwestern Ethiopian highlands. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 60:123-141.
- Yemane, K., Bonefille, R., and Faure, H. 1987 b. Palaeoclimatic and tectonic implications of Neogene microflora from the Northwestern Ethiopian Highlands. *Nature*, 318: 653-656.
- Yuretich, R.F. 1984. Yellowstone fossil forests: new evidence for burial in place. *Geology*, 12:159-162.
- Zomlefer, W.B. 1994. *Guide to Flowering Plant Families* (first edition). The University of North Carolina Press, Chapel Hill, North Carolina.

APPENDICES

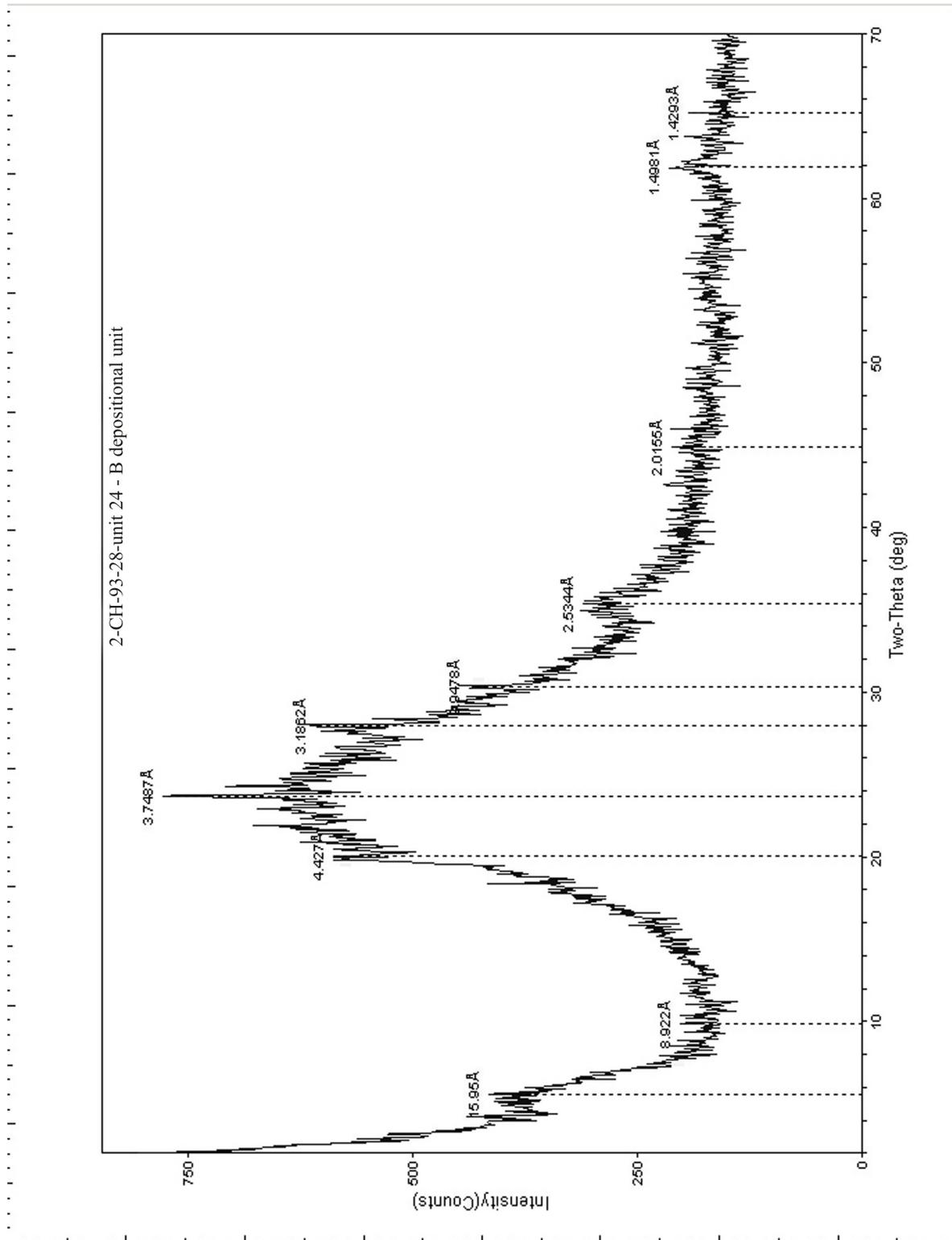
Appendices 1-10. X-Ray Diffractograms of powdered samples from 1) A depositional unit; 2, 3) B depositional unit; 4) C depositional unit; 5, 6) D depositional unit; 7) E depositional unit; 8, 9) F depositional unit; 10) G depositional unit. Peak positions that were used for mineralogical identification are marked by dashed lines. Spacing (for Cu-K α given in angstroms) is given above the dashed lines. 1-CH-93-22-unit 18) peaks near 18.4 Å and peak near 7.1 probably indicate the d (001) of 2:1 phyllosilicate smectite and 1:1 phyllosilicate kaolinite, respectively. Other peaks in the diffractogram correspond to other d (hkl) indices for smectite and kaolinite not discussed here; 2-CH-93-28-unit 24) peak near 15.9 Å probably indicate the d (001) of 2:1 phyllosilicate smectite. Peaks near 3.1, 3.2 and 3.7 probably indicate d (001, 002) of plagioclase feldspar albite. Other peaks in the diffractogram correspond to other d (hkl) indices for smectite and albite not discussed here; 3-CH-89-24-unit 18) peaks near 3.3 and 9.3 and 7.2 and 3.5 Å probably indicate the d (001, 002) of the 2:1 interstratified clay mineral Illite-smectite and Kaolinite-smectite, respectively. Other peaks in the diffractogram correspond to other d (hkl) indices for illite-smectite and kaolinite-smectite not discussed here; 4-CH-79-65-unit 20) peak near 15.7 Å probably indicate d (001) of 2:1 phyllosilicate smectite. Peaks near 3.1 and 3.2 Å probably indicate d (001, 002) of plagioclase feldspar anorthite. Other peaks in the diffractogram correspond to other d (hkl) indices for smectite and anorthite not discussed here;

5-CH-93-4-unit 4). Peaks near 14.4 and 7.1 Å probably indicate d (001) of 2:1 phyllosilicate smectite and 1:1 phyllosilicate kaolinite, respectively. Other peaks in the diffractogram correspond to other d (hkl) indices for smectite and kaolinite not discussed here; 6-CH-79-67-unit 24) peaks near 15.3 and 2.86 and 6.45 probably indicate the d (001) and d (001, 002) 2:1 phyllosilicate smectite and tectosilicate mesolite, respectively. Other peaks in the diffractogram correspond to other d (hkl) indices for smectite and mesolite not discussed here; 7-CH-93-26-unit 22). Peaks near 16.8 and 7.2 and 3.5 Å probably indicate d (001) of 2:1 phyllosilicate smectite and d (001, 002) of the 2:1 interstratified clay mineral Kaolinite-smectite, respectively. Other peaks in the diffractogram correspond to other d (hkl) indices for smectite and kaolinite-smectite not discussed here; 8-CH-89-1-unit 1) peaks near 7.1 Å probably indicate d (001) of 1:1 phyllosilicate kaolinite. Other peaks in the diffractogram correspond to other d (hkl) indices for kaolinite not discussed here; 9-CH-89-23-unit 17) peaks near 16 and 2.7 Å probably indicate d (001) of 2:1 phyllosilicate smectite and iron carbonate siderite, respectively. Other peaks in the diffractogram correspond to other d (hkl) indices for smectite and siderite not discussed here; 10-CH-89-13-unit 12) peak near 15.7 a d 7.1 Å probably indicate d (001) of 2:1 phyllosilicate smectite and 1:1 phyllosilicate kaolinite, respectively. Other peaks in the diffractogram correspond to other d (hkl) indices for smectite and kaolinite not discussed here.

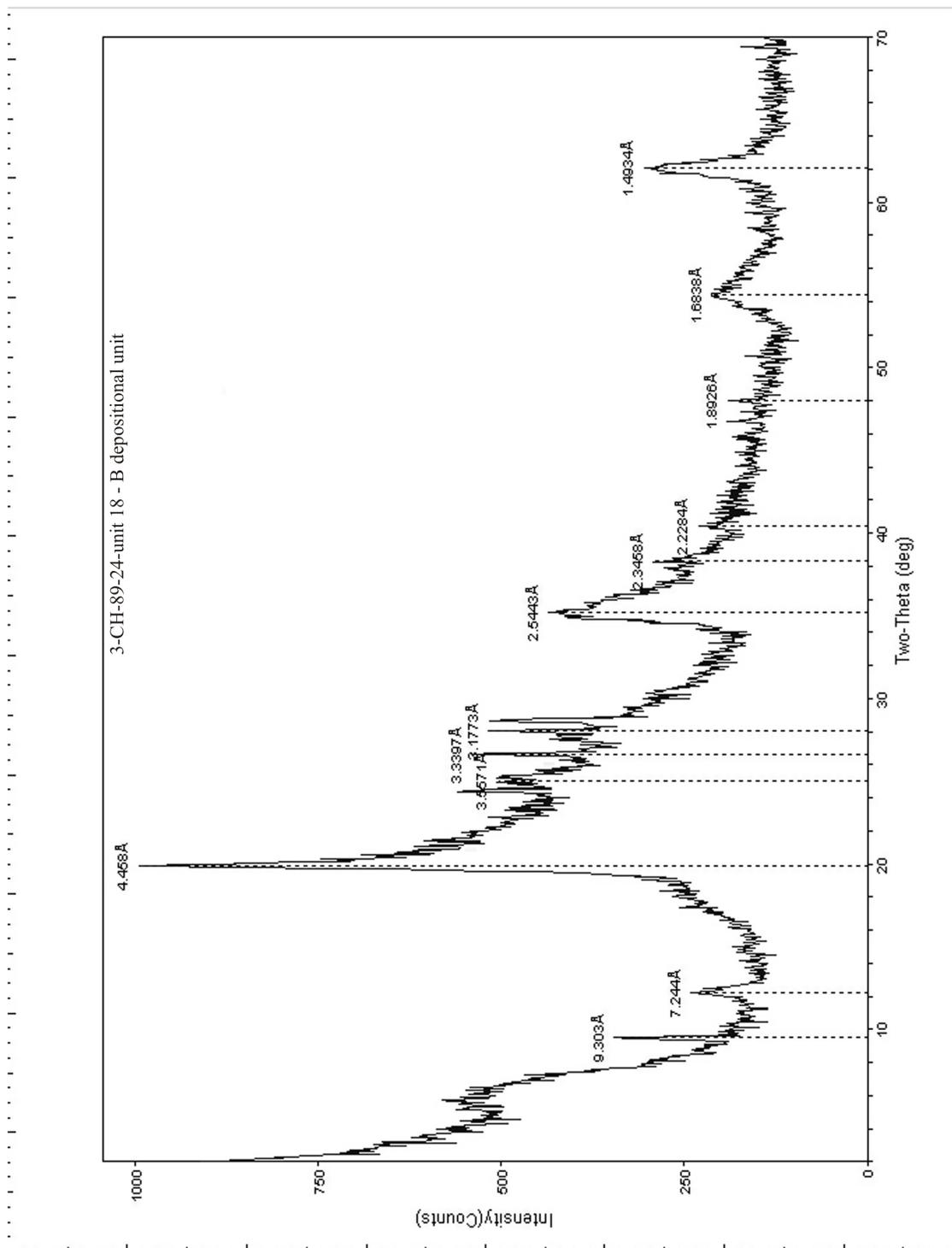
APPENDIX 1.



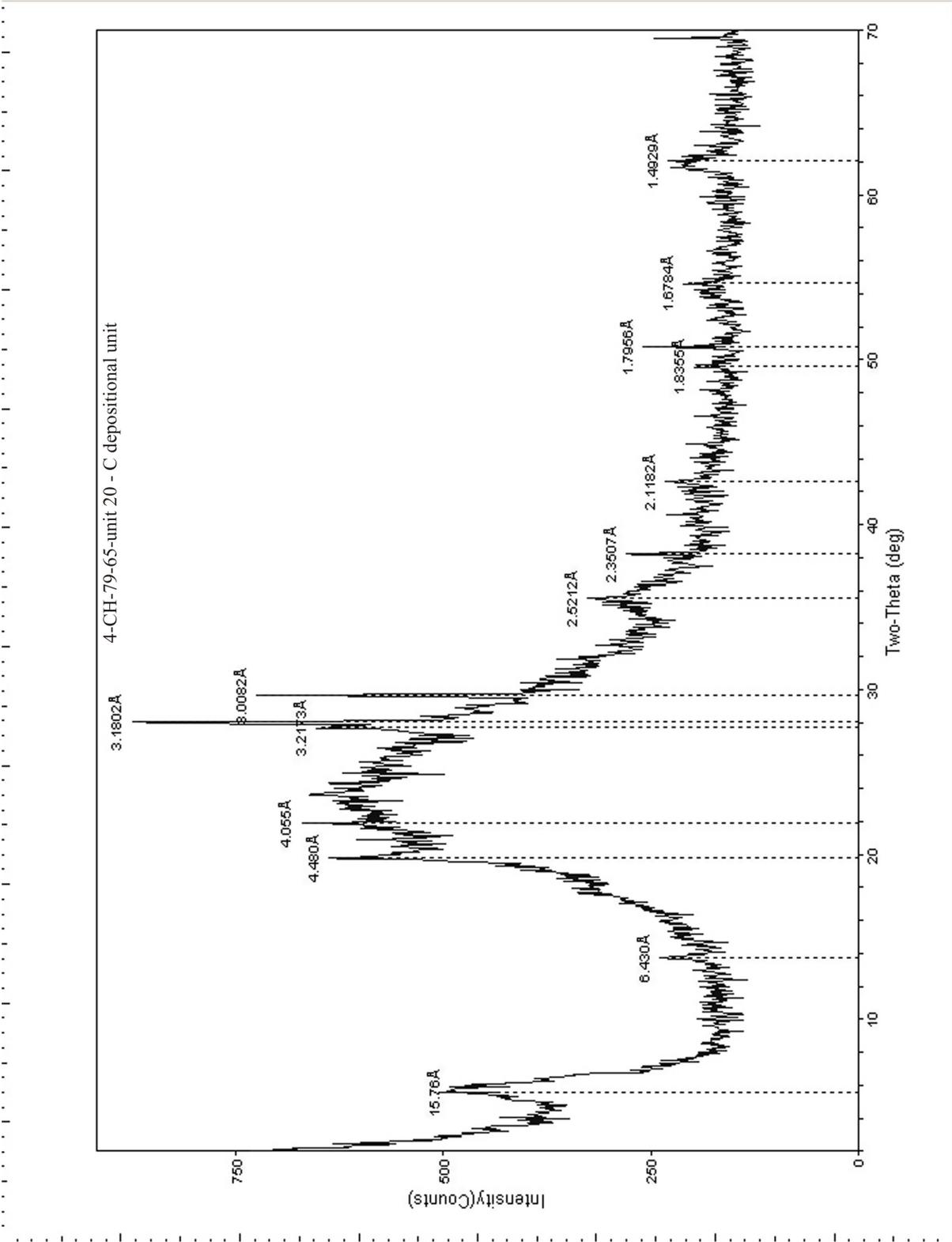
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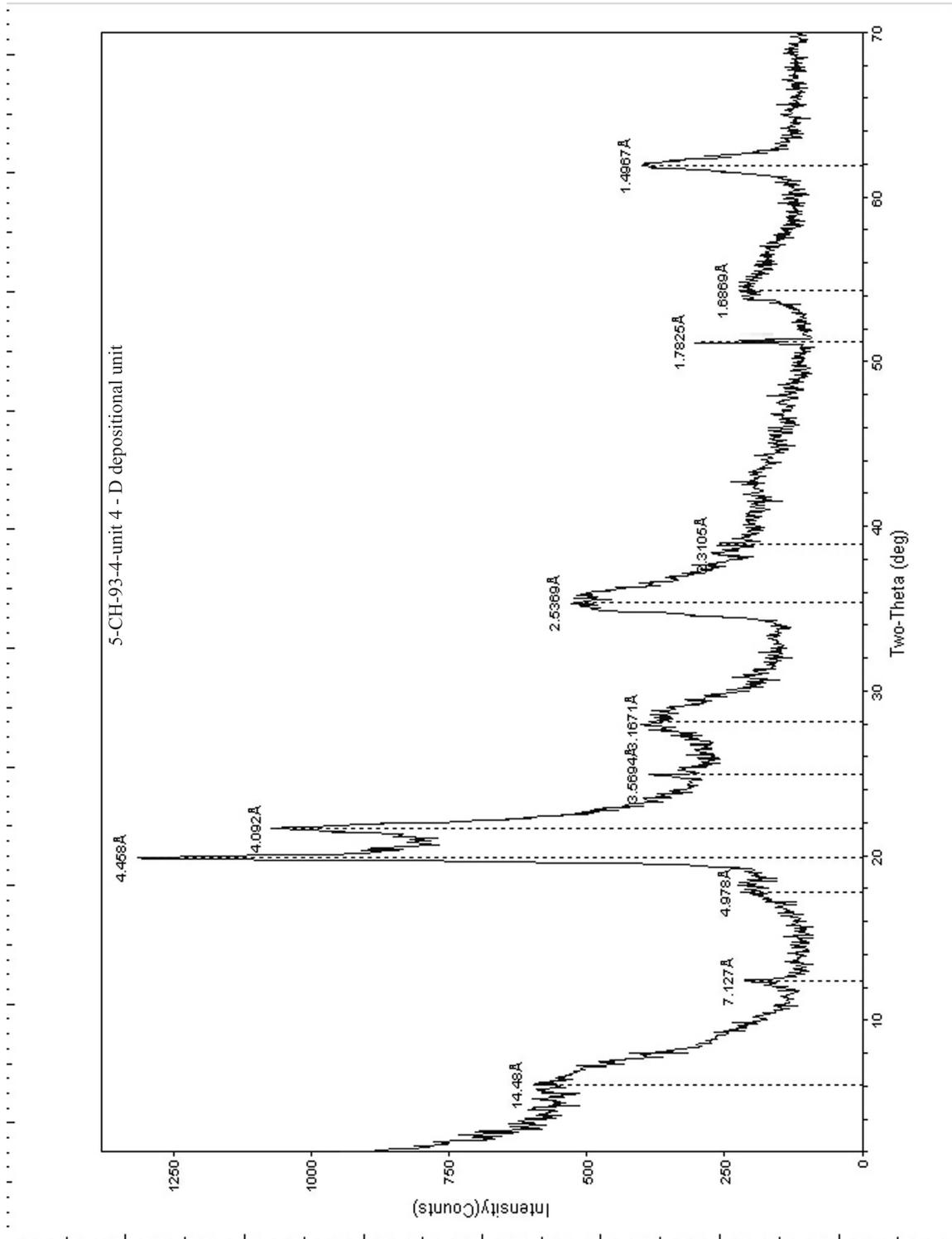
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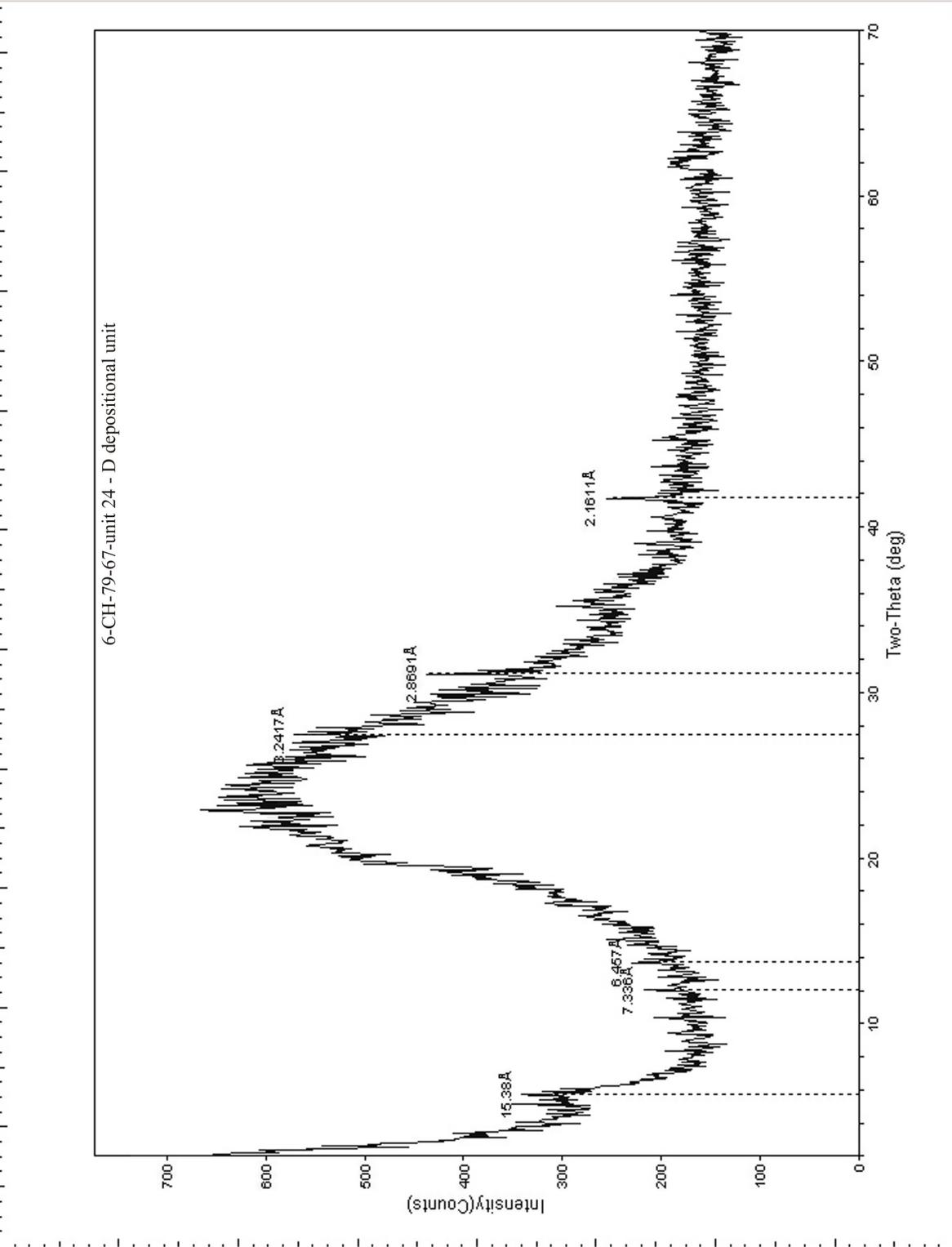
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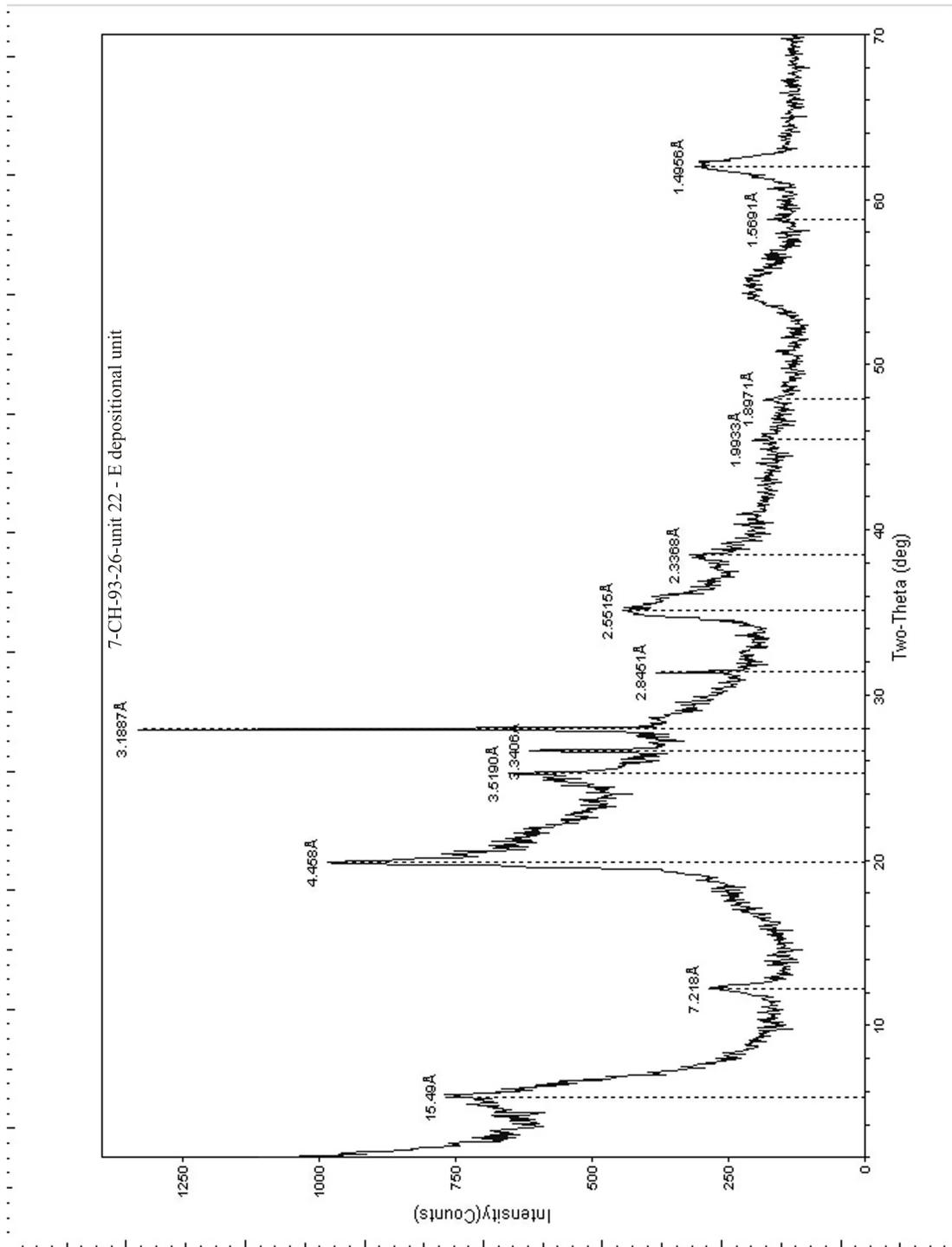
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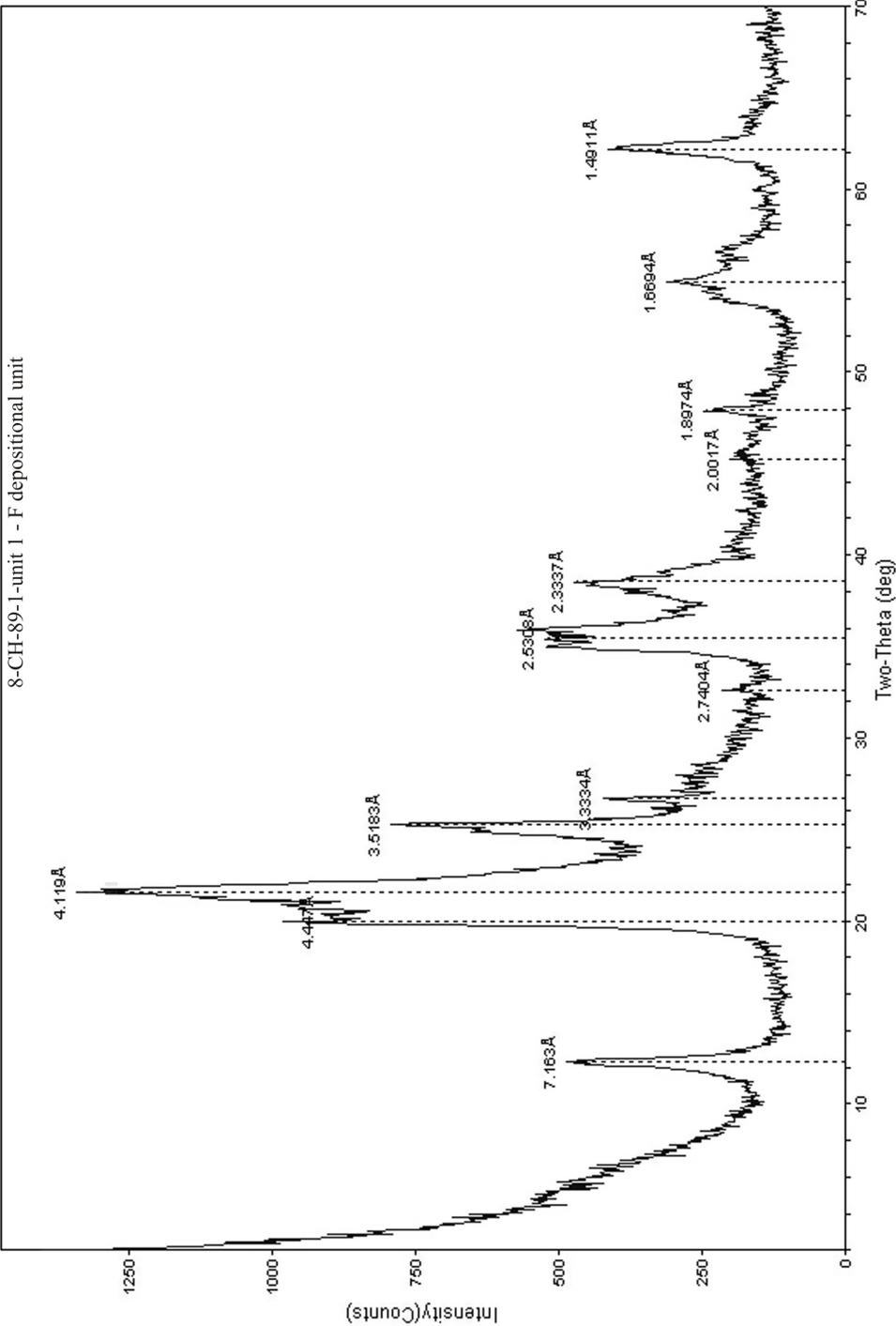
APPENDIX 6.



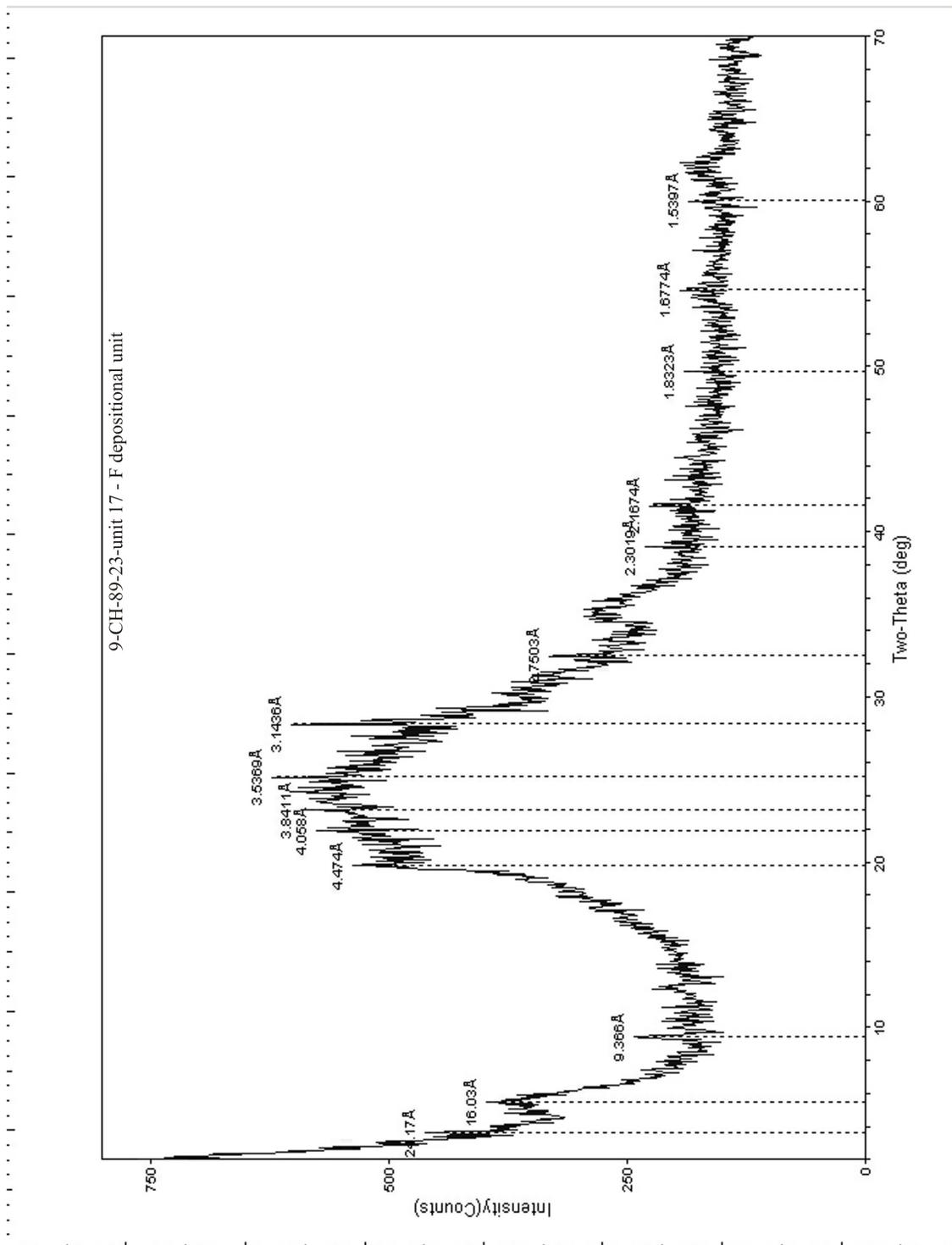
APPENDIX 7.



APPENDIX 8.



APPENDIX 9.



APPENDIX 10.

