OLIGOCENE TERRESTRIAL STRATA OF NORTHWESTERN ETHIOPIA: A PRELIMINARY REPORT ON PALEOENVIRONMENTS AND PALEONTOLOGY

Bonnie F. Jacobs, Neil Tabor, Mulugeta Feseha, Aaron Pan, John Kappelman, Tab Rasmussen, William Sanders, Michael Wiemann, Jeff Crabaugh, and Juan Leandro Garcia Massini

ABSTRACT

The Paleogene record of Afro-Arabia is represented by few fossil localities, most of which are coastal. Here we report sedimentological and paleontological data from continental Oligocene strata in northwestern Ethiopia. These have produced abundant plant fossils and unique assemblages of vertebrates, thus filling a gap in what is known of Paleogene interior Afro-Arabia. The study area is approximately 60 km west of Gondar, Chilga Woreda; covers about 100 km^2; and represents as few as 1 Myr based on radiometric dates and paleomagnetic chronostratigraphy. The sedimentary strata are 150 m thick, and dominated by kaolinitic and smectitic mudstones and airfall tuff deposits. Five main paleosol types are interpreted as representing Protosols (gleyed or ferric), Histosols, Gleysols, Vertisols, and Argillisols. Varied, poor drainage conditions produced lateral variation in paleosols, and stratigraphic variation probably resulted from lateral changes in drainage conditions through time. Vertebrate fossils occur in sediments associated with ferric Protosols and occur with fruits, seeds, and leaf impressions. Plant fossils also occur as in situ forests on interfluves, leaf and flower compressions associated with in situ carbonized trees in overbank deposits (Gleyed Protosols), and compressions of leaves, twigs and seeds in tuffs. Plant fossil assemblages document diverse forests, from 20-35 m tall, of locally heterogeneous composition, and representing families occurring commonly (legumes) or uncommonly (palms) in forests today. Sedimentological and paleobotanical data are consistent with a nearly flat landscape where a meandering river and ample rainfall supported lush vegetation. Over time, the region was subject to intermittent ashfalls. A unique fauna of archaic mammalian endemics, such as arsinoitheres and primitive hyracoids, lived here with the earliest deinotheres.

Bonnie F. Jacobs. Environmental Science Program, Southern Methodist University, P.O. Box 750395, Dallas, Texas 75275-0395, USA. bjacobs@smu.edu

Neil Tabor. Department of Geological Sciences, Southern Methodist University, P.O. Box 750395, Dallas, Texas 75275-0395, USA. ntabor@smu.edu

Mulugeta Feseha. Institute of Development Research, Department of Geology and Geophysics, Addis Ababa University, P.O. Box 1176, Addis Ababa, Ethiopia. mulugetafy@yahoo.com

Aaron Pan. Department of Geological Sciences, Southern Methodist University, P.O. Box 750395, Dallas, Texas 75275-0395, USA. apan@smu.edu

John Kappelman. Department of Anthropology, University of Texas at Austin, 1 University Station C 3200, Austin, Texas 78712, USA. jkappelman@mail.utexas.edu

Tab Rasmussen. Department of Anthropology, Washington University, Campus Box 1114, St. Louis, Missouri 63130-4899, USA. dtrasmus@artsci.wustl.edu

William Sanders. Museum of Paleontology, University of Michigan, 1109 Geddes Avenue, Ann Arbor, Michigan 48109, USA. wsanders@umich.edu

Michael Wiemann. Center for Wood Anatomy Research, USDA Forest Service, Forest Products Laboratory, One Gifford Pinchot Drive, Madison, Wisconsin 53726-2398, USA. mwiemann@fs.fed.us

Jeff Crabaugh. Oklahoma State University, T. Boone Pickens School of Geology, 105 Noble Research Center, Stillwater, Oklahoma 74078-3031, USA. jeff.crabaugh@okstate.edu

Juan Leandro Garcia Massini. Department of Geological Sciences, Southern Methodist University, P.O. Box 750395, Dallas, Texas 75275-0395, USA. jgarciam@smu.edu

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INTRODUCTION

The Paleogene fossil record is sparse compared with the Neogene record for continental tropical Africa, despite the much longer duration of the Paleogene (43 vs. 23 Ma). The abundance of Neogene fossil localities is related to development of the topographically complex East African Rift, which generated sediment accommodation space and created ample opportunities for fossilization. However, limited exploration for older sites has also contributed to the shortage of Paleogene localities. Continuing investigations of pre-rift sedimentary deposits of eastern tropical Africa aim to fill this gap and have produced significant fossil sites from the Eocene of Tanzania and the Oligocene of Ethiopia (Herendeen and Jacobs 2000; Harrison et al. 2001; Gunnell et al. 2003; Kappelman et al. 2003; Murray 2003; Jacobs and Herendeen 2004; Sanders et al. 2004). These new localities provide unique opportunities to document Paleogene plant and vertebrate evolution, paleoecology, and paleoclimate in interior tropical Afro-Arabia, when the biota was evolving in isolation from those of other continents, and experiencing significant global climate changes.

In this paper we assess the paleoecological implications of late Oligocene fossils and sediments located in Chilga Woreda (henceforth "Chilga"), west of Gondar, on Ethiopia's northwestern plateau (Figure 1). These deposits are remark-ably rich in fossil plants and have produced unique associations of endemic archaic and derived mammals. Abundant paleosols document paleoenvironments independently of the fossils. This wealth of paleontological and palaeoenvironmental data provides information that makes Chilga unique for the African Paleogene.

Geological Background

The study site is located in an area of approximately 100 km^2, 60 km west of Gondar in Chilga Woreda, Amhara Region, northwestern Ethiopia (Figure 1). Geologically, the area is characterized by massive flood basalts as much as 2000 m thick, emplaced approximately 30 million years ago, prior to Miocene rifting (Hofmann et al. 1997). Clastic and volcaniclastic sediments occur interbedded with volcanic deposits in a basin formed by faulting of the basalts in the middle to late Oligocene. Approximately 150 m of fossiliferous sedimentary strata are exposed in outcrops across the basin, but the most complete and best-documented section occurs along the Guang River. In this section, radiometric dates and paleomagnetic reversal stratigraphy constrain the age of about 100 m of sediment to between 27 and 28 Ma, the limits of Chron C9n, or earliest late Oligocene (Feseha 2002; Kappelman et al. 2003; Cande and Kent 1995; Figure 2).

Plant and vertebrate fossils occur throughout the Chilga deposits. Faunal assemblages, domi-
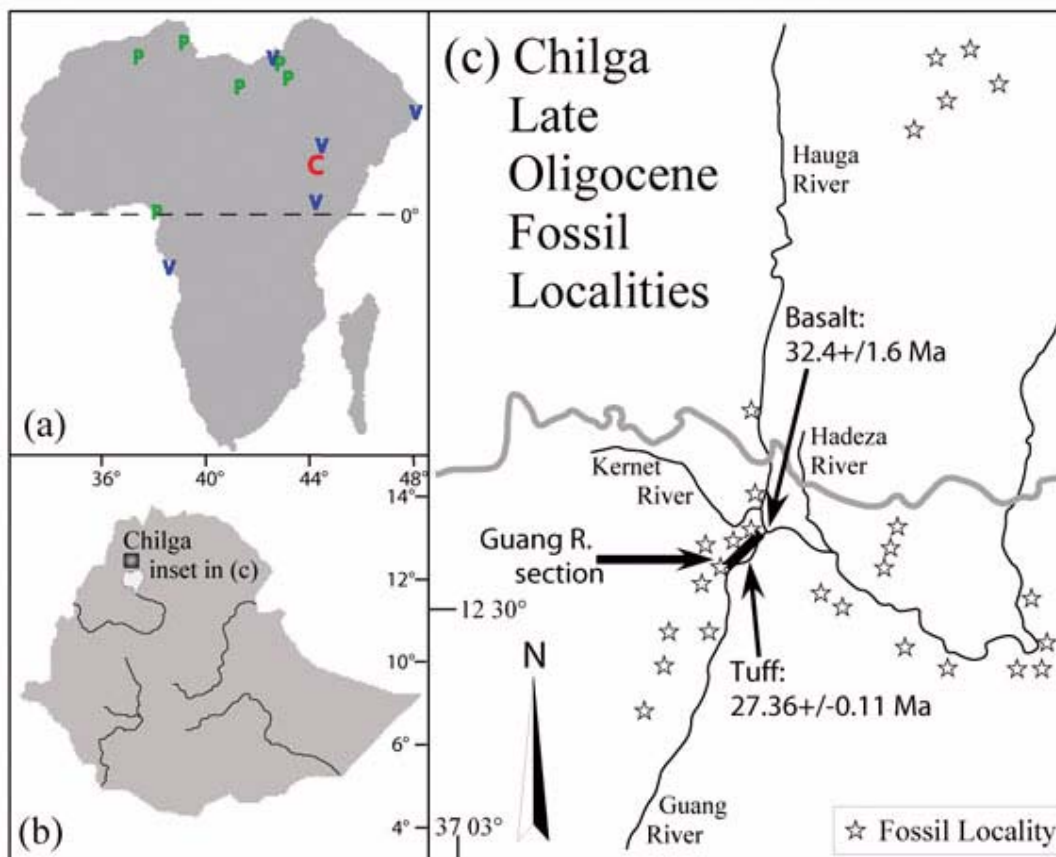
Figure 1. Map of Chilga and surrounding area modified from Kappelman et al. (2003). (a) Map of Afro-Arabia with Chilga (**C;** red), and Paleogene vertebrate and paleobotanical localities marked **P** (blue) and **V** (green) respectively. (b) Location of Chilga in Ethiopia. (c) Detailed map of the Chilga area showing the fossil localities, geological section (see Figure 2) and dated rock samples along the Guang and Hauga rivers.

nated by the weathering-resistant teeth of larger mammals, show little change during the time interval represented at Chilga. The plant assemblages, some of which occur in direct association with vertebrate fossils, provide an excellent record of the environment in which the animals lived and, with sedimentological data, provide a fine-scale assessment of spatial and temporal environmental variation. Below, we document and integrate sedimentological and paleontological data in order to better understand the landscape and climate at Chilga.

METHODS

Both sediments and plant fossils were systematically collected for paleoenvironmental analysis. Paleosols were logged and described in the field following previously established methods (Tabor et al. 2002; Tabor and Montañez 2004). Pedogenic horizons within the Chilga strata were recognized using the criteria of Kraus and Aslan (1993). Paleosol tops were identified on the basis

of a marked change in lithology or sedimentary features, whereas profile bases were delineated at the highest occurrence of unaltered parent material. Field descriptions of paleosols (e.g., thickness, color, type, and distribution of mottling; soil structure and mineralogy; size, morphology, and distribution of authigenic minerals) follow the methods of Retallack (1988). Paleosol and lithologic colors were identified in the field with dry samples using Munsell color charts (Munsell Color 1975). In order to avoid recent weathering, outcrop faces were dug back minimally 60 cm to provide a fresh surface for describing and sampling the paleosols. Approximately 500 g of paleosol matrix was collected from each paleosol horizon and stored in either canvas or plastic bags.

The mineralogical composition of sand-size and coarser grains, as well as soil microfabrics, were determined petrographically from doubly-polished thin sections following the methods of Moorhouse (1959) and Brewer (1976). Powdered bulk samples were analyzed by X-ray diffractometry to determine the mineralogical composition of several
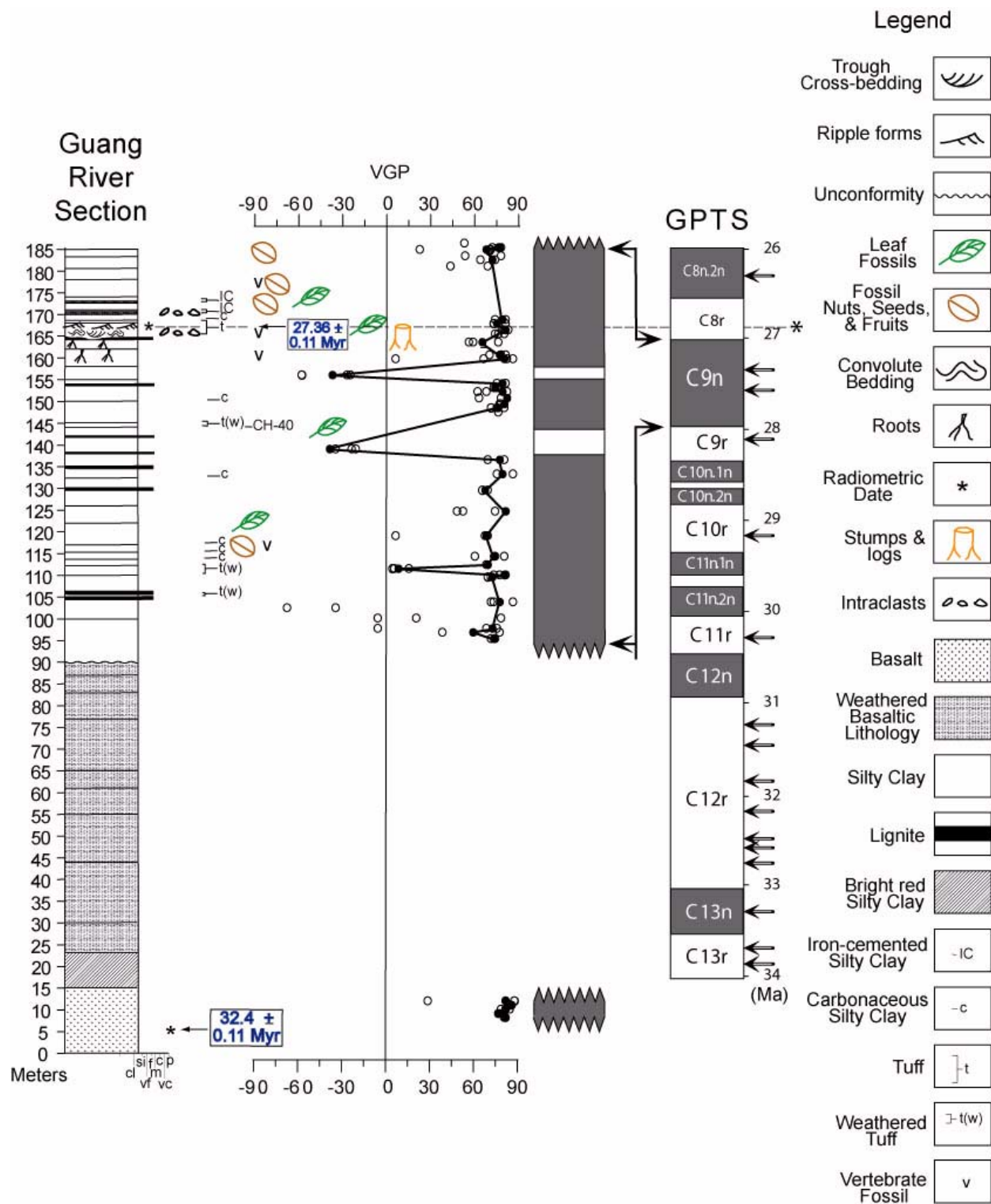
Figure 2. The Chilga section including the upper sedimentary strata and underlying weathered basalt modified from Kappelman et al. (2003). The Ages to the immediate right of the Geomagnetic Polarity Time Scale panel are in Myr. V, vertebrate localities. VGP, virtual geomagnetic pole. White circles, paleomagnetic samples; black circles, site polarity means. Black bars, normal polarity; white bars, reversed polarity. Arrows refer to minor variations in the paleomagnetic record (Cande and Kent, 1995).

different paleosol horizons. X-ray diffraction analyses were performed on a Rigaku Ultima III X-ray diffraction system configured with a vertical Theta:Theta wide angle goniometer, using CuKα at 40Kv and 30mA. Measurements were performed with step-scan increments of 0.01° 2θ, counting times of 2s per increment, 0.5/1.0 mm for the primary slits and 0.2/0.3 mm for the receiving slits. Mineralogical composition of the samples was determined following the methods of Moore and Reynolds (1997).

Plant fossils were collected at 50 localities across the basin in the course of surveying, but systematic excavations at three localities have produced the majority of >1100 specimens. One locality, exposed laterally along 60 m of one stratigraphic level at the Guang River section, was subdivided and excavated at four sublocalities. To minimize collecting bias, even fragmentary excavated plant fossils were collected if there was any chance of identification. When necessary, fossils were prepared with a fine-point airscribe. Cuticle was collected from fossil specimens by chipping off an approximately 1 cm^2 sample, which was then prepared using hydrofluoric acid to dislodge inorganic matrix and a weak solution of bleach or hydrogen peroxide to oxidize the organic matter to transparency. Specimens were digitally imaged using one or all of the following: a high resolution single lens digital reflex camera, a digital camera mounted on a reflected or transmitted light microscope, and a LEO 1450 variable pressure scanning electron microscope.

Plant fossil specimens were compared with modern representatives from herbarium and live collections at Missouri Botanical Garden, Royal Botanic Gardens, Kew, or Fairchild Tropical Gardens, and in consultation with botanists who specialize in the relevant plant groups (see Acknowledgments).

Large vertebrate fossils were located by surface prospecting, and all bone and dental fragments were collected. Many localities were suitable for excavation, and some of these sites produced associated postcranial remains. Specimens were subsequently prepared with an airscribe as needed. In an effort to locate small vertebrate fossils, fine-grained sediments were screen-washed at several promising localities. However, the deposits did not yield small bones or teeth.

RESULTS

Lithologies

Chilga sedimentary strata are primarily composed of claystone and mudstone, indicating that clay and silt-size particles were the primary sediments deposited in this basin. Sandstones are relatively rare and, where present, consist primarily of very fine-grained reworked airfall tuffs, feldspars, reworked siderite nodules, and mud and clay aggregates similar in appearance to sandstones composed of pedogenic mud aggregates that have been described from other basins of various ages (Gierlowski-Kordesch and Gibling 2002 and references therein). These observations suggest that allochthonous sand-sized sediment likely entered the basin as airfall deposits. Nevertheless, there is evidence for reworking and transport of Chilga sediments by fluvial processes and pedogenic alteration on the floodplains.

Stream Channel Deposits. Relatively few stream channels have been recognized in the Chilga strata. The general absence of these features may reflect, in part, the generally very fine-grained nature of the Chilga sediments and our inability to discern channel-like structures within rocks with these grain-size characteristics. However, trough-cross bedding and inclined heterolithic cross stratification, similar to point-bar deposits in meandering streams (e.g., Walker and Cant 1984), were observed within the very fine and fine-grained sandstone deposits of reworked airfall tuffs, suggesting that alluvial processes were an important means of sedimentary transport in the Oligocene sedimentary strata.

Overbank Deposits. Overbank deposits in the Chilga region consist primarily of claystones and mudstones. Very fine sands are locally present as thin tabular beds with sharp, non-scoured bases and are typically structureless, but may exhibit planar laminations and asymmetrical ripple cross-laminations. Individual sandstone beds range in thickness from a few centimeters to ~40 cm. These thin sandstone units are interpreted as crevasse splay and levee deposits or airfall tuffs.

Mudstone and claystone beds consist of structureless to finely laminated units ranging from a few centimeters up to 5 m thick. However, some claystones and mudstones exhibit ripple cross-lamination, and many units contain abundant carbonaceous material and plant fossils that grade upward into organic-rich lignite layers (Figure 3C). Most overbank lithologies of the Chilga sedimentary strata were subject to varying degrees of pedogenesis. Because of their abundance, paleosols are an important component of the overbank lithofacies architecture in the Chilga strata.

Figure 3. A. Tabular and branching lignitic root impression from a Type A paleosol (Protosol). Long axis of hand lens is 5 cm across. **B.** Laterally extending lignitic root in a medium to coarse angular blocky silty claystone horizon from a Type C paleosol (Gleysol). Hammer is 40 cm long. **C.** Organic rich O horizon (black layer) overlying a massive to coarse angular blocky silty claystone in a Type B paleosol (Histosol). The thin white layer (8 cm thick) is interpreted to be an altered ashfall layer that briefly halted in situ accumulation of plant material. **D.** Transition zone between a Type C paleosol (Gleysol) with a thin lignite layer at upper surface (left) changing to Type D paleosol (Vertisol, right). The dark line denotes mukkara subsurface structure, which forms from periodic shrink-swell of expansible clay minerals during wet-dry cycles. The lignite layer pinches out toward the right side of the diagram. However, approximately 70 meters to left of this photograph, the lignite layer becomes ~50 cm thick and defines the upper surface of a Type B paleosol (Histosol). Jacob staff in upper center of photograph is 150 cm long. See Text for discussion. **E.** Medium wedge-shape aggregate structure from a Type D paleosol (Vertisol). See text for discussion. **F.** Medium angular blocky silty claystone with thick, continuous argillans (shiny, reflective surfaces) along ped surfaces within an argillic Bt horizon from a Type E paleosol (Argillisol). See text for discussion.

Paleosols

Based on the field inspection of over 141 paleosol profiles distributed across the western region of Chilga strata, we have recognized five morphologically distinct paleosol types that represent the majority of the observed variability (e.g., horizonation, structure, fabric, color, mineralogy; Table 1; Figures 3A-F, 4A-F). Below, we present generalized descriptions of the characteristics of the five paleosol types. We also discuss the morphological variability within a given paleosol type, its stratigraphic and lateral distribution within the study area, and classify each paleosol type according to the Mack et al. (1993) paleosol classification system to indicate the closest estimated soil taxon within the context of the USDA Soil Classification System (Soil Survey Staff 1975, 1998). In order to avoid genetic terms that relate to the character of the paleosol types, we arbitrarily refer to these five paleosol-types as A through E. The paleosol types are vertically and laterally distributed through the Chilga sedimentary strata. Horizon descriptions for each paleosol type are listed in Table 1.

Type A Paleosols. *Description:* The only significant pedogenic features in Type A paleosols are rooting structures, obliteration of original depositional features, and very weak development of soil structures, such as slickensides and wedge-shaped aggregate structure with little or no horizonation (e.g., Figure 3A). These paleosols occur as claystone-or mudstone-rich profiles and very fine sandstone-rich profiles that range from ~20 to >150 cm thick. Claystones are generally gray (5Y 4/1) to olive (5Y 5/2), with few, fine and prominent orange (7.5YR 5/8) mottles and common, medium to coarse, faint gray (5Y 5/2) mottles. Very fine sandstone-rich Type A paleosols are light yellow (5Y 7/3) with massive or single-grain (i.e., sand grains) structure that may grade upward into massive, reddish-orange (7.5YR 5/4), Fe-cemented horizons. Rooting structures are typically composed of lignitic organic material or fine-grained silica (Figure 3A). Type A paleosols that are composed of very fine sandstone are associated with channel and crevasse-splay sandstones, ash-fall tuffs and fine-grained overbank deposits of the floodplain facies. Type A paleosols have highly variable lateral continuity throughout the Chilga strata; these profiles grade laterally into Type B and Type C paleosol profiles.

Interpretation: Paleosols with these characteristics are classified as Protosols, which exhibit weak development of pedogenically altered horizons (Mack et al. 1993). Specifically, profiles composed of grayish-green claystones are Gleyed Protosols (Mack et al. 1993), a category that roughly covers the range of characteristics observed in the USDA Soil Taxonomy soil suborders Aquents and Aquepts. Profiles composed of very fine sandstone with Fe-cemented horizons are Ferric Protosols (Mack et al. 1993), which correspond to the USDA soil great group Petraquept (Soil Survey Staff 1998). The presence of protosols in the Chilga strata indicates that sedimentation within the basin (i.e., upon the floodplains and along stream channels) ceased long enough for colonization by terrestrial flora in poorly drained environments (Buol et al. 1997).

Type B Paleosols. *Description:* Type B paleosols have two primary components, a lower mineral layer of fine-grained siliciclastic material and an upper layer composed mainly of organic material (Figure 3C). The mineral layers consist of primarily drab (5Y 5/1), structureless to very coarse, angular, blocky kaolinitic claystone or mudstone with mm-scale spherulitic siderite nodules (e.g., Figure 4E). These pedogenically altered horizons grade upward from laminated to thinly bedded sediment. The organic layers are laminated to thinly bedded lignites that range from 10 mm to 700 mm in thickness. The lignite beds are (almost entirely) composed of monocot leaf and stem compressions, and parting lineations within these layers commonly exhibit jarosite and gypsum.

Type B paleosols are distributed throughout the Oligocene strata of the Chilga basin within laminated to thin-bedded claystones and mudstones of overbank depositional environments. The organic-rich horizons define regional "lenticular structures" that can be traced over a few 10's of meters to over 2 km, where they pinch-out and change laterally to Type A and Type C paleosols.

Interpretation: Paleosol Type B is a Histosol based on an inferred surficial accumulation of organic material (Mack et al. 1993; Soil Survey Staff 1998). Modern, laterally discontinuous Histosols form in low-lying, waterlogged regions characterized by anoxic pore waters that promote in situ accumulation of organic horizons (O horizons). Laterally discontinuous, organic accumulations in Type B paleosols are interpreted as O- horizons (Soil Survey Staff 1975, 1998) that formed by in situ accumulation of plant material. The abundance of fossil root traces that exhibit shallow and tabular morphology and base-depleted kaolinitic layers immediately underlying O horizons may correspond to eluvial A-horizons that formed as a result of intense hydrolysis or acidolysis due to seasonally poor drainage (cf. van Breeman and Harmsen 1975). However, the presence of spherulitic siderite nodules in horizons below the inferred surface

Table 1. Characteristics of five major types of paleosols represented in the Chilga strata.

Paleosol Type and Stratigraphic Occurrrence	Horizon[1]	Thickness (m)*	Nodule and rhizolith composition	Mineralogy[2]	Interpreted Drainage Class	Interpreted Surface Runoff
A: Protosol Throughout Chilga Beds	A	0-0.12	Lignitic roots and silicified rhizoliths	M, K, I	Moderately Well to Very Poorly Drained	Very Slow to Slow
	AC, BCss	0.13-0.95	Lignitic roots and silicified rhizoliths	M, K, I		
	C	0.07->1.50	-	M, K, I		
B: Histosol Throughout Chilga Beds	Oa, Oe, Oi	0.10 to 0.70	Lignitic roots	-	Very Poorly Drained	Ponded
	Ag, Aj	0.05-0.21	Lignitic roots	-		
	Bcg	0.09-0.53	Lignitic Roots and mm-scale spherulitc siderite	K, M, S, I		
	Cg	0->1.50	-	-		
C: Gleysol Throughout Chilga Beds	Oa, Oe	0-0.10	Lignitic roots		Very Poorly to poorly drained	Ponded to very slow runoff
	A	0-0.12	Lignitic roots	K, M		
	Bcg1	0.14-0.47	mm-scale spherulitic siderite and hematite	K, S, M		
	Bcg2, Bcnss	0-0.72	mm-scale spherulitic siderite and hematite	-		
	Cg	0- >1.50	-			
D: Vertisol Throughout Chilga Beds	AB	0-0.23			Poorly to somewhat poorly drained	Seasonally ponded to very slow runoff
	Bss	0.21-1.37				
	Bgss1	0.23-0.47		M, K		
	Bgnss	0.35-0.59	mm-scale spherulitic siderite and hematite	M, K, S		
	C	0->1.50				
E: Argillisol Upper 40 m of Chilga Beds	A	0-0.08			Moderately well to somewhat poorly drained	Very Slow runoff
	ABt	0.10-0.14				
	Bt, Btss	0.25-0.37		M, K		
	BC, Bss	0-0.47				
	C	0->1.50				

*The range of thicknesses, in meters, of the various pedogenic horizons represented within paleosols. Note that not all horizons shown may be present in every paleosol (i.e., why some horizons have a range that includes 0 m).

[1]Horizon names and properties follow the USDA Soil Survey Staff (1975; 1998) guidelines. Soil horizon names: O horizon – surface layer dominated by in situ accumulation of organic material, primarily vegetable matter; A horizon – "topsoil" layer, zone of organic matter accumulation and mineral removal (eluvial layer); B horizon – "subsoil" layer(s), zone of soil structural development and mineral accumulation (illuvial layer) that is derived from overlying eluvial layers; AB horizon – a near surface horizon exhibiting intermediate properties between an A and B horizon; C horizon – subsoil layer(s) composed of barely weathered material; C-horizons occur beneath A or B horizons. Subordinate indicators of soil properties: a – highly decomposed organic matter, very few to no recognizable plant parts; used only with O horizons; c – presence of concretions or hard nodules; e – partly decomposed organic matter, <1/2 of mass composed of recognizable plant parts; used only with O horizons; g – evidence for strong gleying, or highly reducing and wet soil conditions. Generally Indicated by chromas < 2.; i – slightly decomposed organic matter, >1/2 of mass composed of recognizable plant parts used only with O horizons; j – accumulation of jarosite; ss – presence of slickensides. Numerical descriptors (e.g., Bgc1, Bgc2 denote two horizons with similar morphologies, but at different depths from the paleosol surface.

[2] Mineralogical composition of bulk fraction as determined from powder X-ray diffraction. M = Montmorillonite; K = Kaolinite, I = Illite, and S = Siderite.
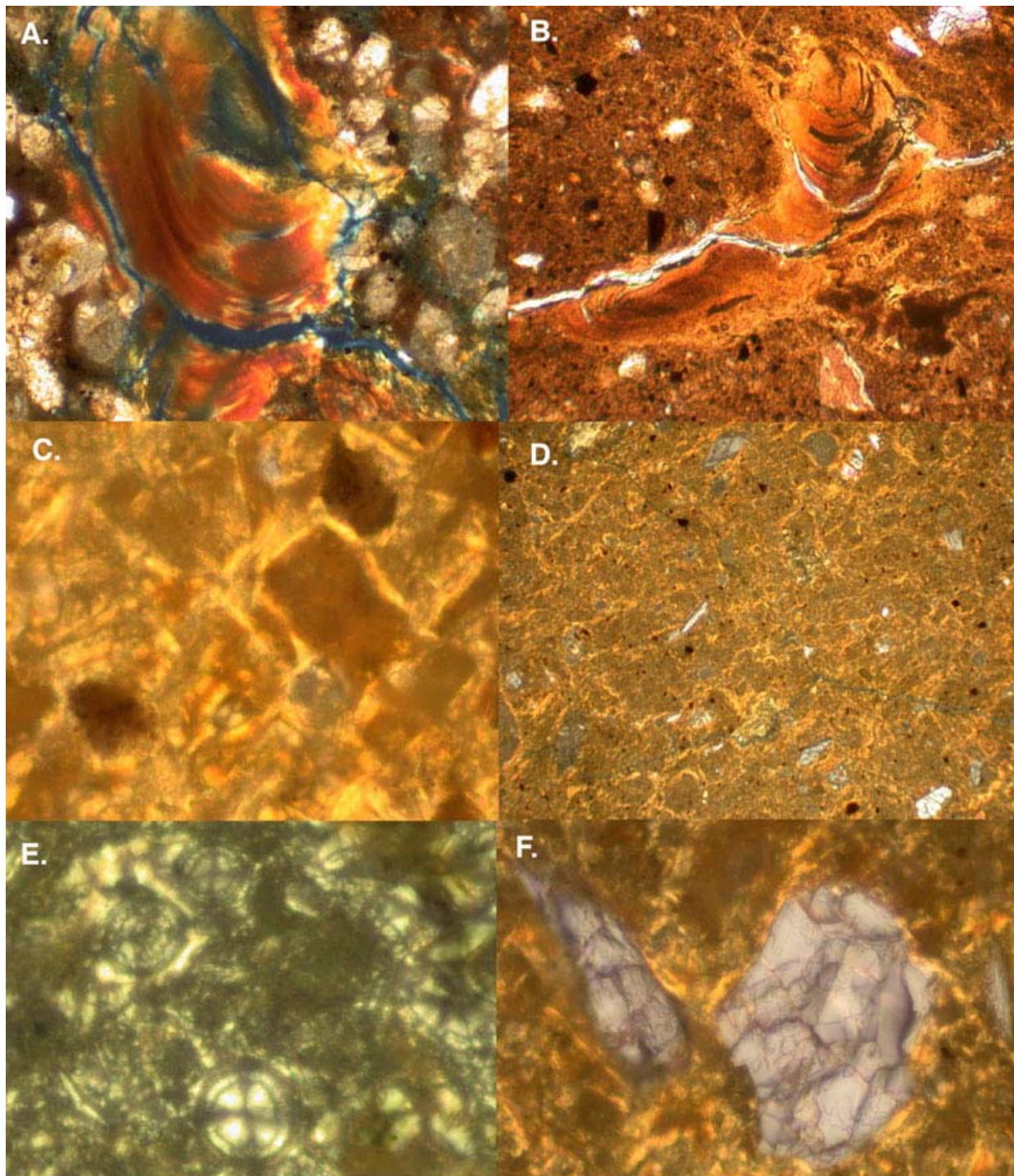
Figure 4. Cross-Nichols photomicrographs. **A.** Void-filling argisepitubule soil microfabric (highly birefringent material in center of micrograph) in a Bt horizon from a Type E paleosol (Argillisol) that formed after an airfall tuff. Field of view is 2 mm across. **B.** Void-filling argilstriotubule soil microfabric in a mudstone matrix from a Bt horizon in a Type E paleosol (Argillisol). Opaque areas in mudstone matrix are hematite-rich grains. Field of view is 5 mm across. **C.** Latticesepic soil microfabric in a Type D paleosol (Vertisol). Field of view is 0.5 mm across. See text for discussion. **D.** Oosepic soil microfabric in a Type C paleosol (Gleysol). Field of view is 2mm across. See text for discussion. **E.** Sphaerosiderite concretions in a silty claystone from a Type C paleosol (Gleysol). Field of view is 15µm across. **F.** Blocky siderite crystals from the mineral horizon of a Type B paleosol (Histosol). Field of view is 0.5 mm across.

of these paleosol profiles indicates a relatively low partial pressure of O_2, but high concentration of CO_3^{2-} at depth in these soils (e.g., Mozley 1993). The shallow, tabular distribution of root traces further reflects the poorly drained conditions under which Type B paleosols formed (cf. Retallack 1988, 1990).

Type C Paleosols. *Description:* Type C paleosols consist of massive to medium to coarse, angular blocky, gray (5Y 5/3) to yellow-green (5Y 5/2) claystones and mudstones with fine to medium reddish-orange (7.5YR 6/4) mottles. These pedogenically altered layers grade upward from finely laminated to massive sediment or occur superimposed upon older paleosols. These paleosols range from ~450 mm to >2 m thick and contain abundant mm-scale spherulitic siderite nodules and finely disseminated micritic siderite cements that indurate entire horizons (Figures 3B, 4E, and F). In addition, the upper 10 to 100 mm of Type C paleosol profiles may consist of organic-rich lignitic horizons. Type C paleosols change laterally into Type A, B, and D paleosol profiles.

Interpretation: Paleosols with these characteristics are interpreted as Gleysols, which exhibit morphological characteristics indicative of formation in poorly drained areas near the interface with the local or regional groundwater table (Mack et al. 1993). Gleysols roughly correspond to the USDA soil great group Aquepts (Soil Survey Staff 1998). The drab greenish-gray paleosol matrix colors, reddish mottling, subsurface accumulation of spherulitic siderite nodules, and in situ accumulation of surficial organic matter collectively indicate that Type C paleosol profiles developed in areas characterized by high water tables and poor soil drainage across the Oligocene floodplains.

Type D Paleosols. *Description:* Type D paleosols are composed of smectite-rich claystones and silty claystones that grade upward from laminated fine-grained sediments or partially overprint underlying paleosols, such as Type C paleosols. Type D paleosols generally exhibit weakly developed slickenplanes and wedge-shaped aggregate structures that range from 50 to 200 mm across, with secondary coarse angular blocky structure and abundant clay pressure faces at depth (Buol et al. 1997). The lower horizons also typically contain mm-scale spherulitic siderite nodules. The upper boundaries of these horizons are distinct and wavy (Figure 3D), grading upward to greenish-gray (5Y 3/5) horizons with well-defined, wedge-shaped aggregate structure (Fig. 4E), slickenplanes and fine to medium, prominent, reddish-orange (7.5YR 5/4) mottles. Internally, the microfabric of the paleosol matrix in these horizons exhibits striated highly oriented, birefringent clays oriented in a "boxwork" (lattisepic) to continuous, highly oriented, birefringent clays oriented in concentric "spheroids" (Oosepic; Brewer and Sleeman 1976). (Figure 4C, D), micromophology that is typical of modern, clay-rich soils characterized by seasonal wetting and drying (Brewer and Sleeman 1988). The uppermost horizons generally exhibit coarse prismatic structure with secondary medium angular blocky structure. Smectite clays dominate the mineralogy (Table 1), indicating that these soils were not deeply weathered. These paleosols are broadly distributed throughout the stratigraphic succession and may be traced laterally in excess of 1 km across the Chilga strata. Type D paleosol profiles are observed to change laterally to Type C, Type B, and Type E paleosols.

Interpretation: Type D paleosols are Vertisols, based on their high clay content (>35%), presence of slickensides, and v-shaped desiccation cracks, which together indicate seasonal soil wetting and drying (Mack et al. 1993; Soil Survey Staff 1998). Hematitic redox concentrations and low-chroma matrix colors throughout much of the profile support a more specific paleosol classification as gleyed Vertisols (Mack et al. 1993) or the soil sub-order Aquerts (Soil Survey Staff 1998). Modern Vertisols typically form on flat terrain with strongly contrasted, wet and dry seasonal or monsoonal climates (Buol et al. 1997). Seasonal wetting and drying of expandable 2:1 phyllosilicate minerals (e.g., smectite) leads to shearing of plastic soil materials, slickenside formation and development of Vertisol morphology. Vertisols require a period of soil-moisture deficit and sparse vegetation to maintain a high concentration of basic cations, thereby preserving expansible clay minerals in the soil matrix (Retallack 1990; Duchaufour 1982). We interpret Type D paleosols to have formed under wet conditions, given the presence of gley colors and redoximorphic features, with relatively short periods of soil-moisture deficit. Furthermore, Type D paleosols developed in clay-rich overbank deposits of the Chilga floodplains likely characterized by a short period of soil drying.

Type E Paleosols. Description: Type E paleosols are comprised of several well- developed mudstone and claystone horizons. The uppermost horizon is dusky-red (7.5YR 3/2) mudstone, underlain by several yellowish-gray (5Y 5/2) claystone horizons that grade upward from thinly laminated to ripple-cross laminated claystones and mudstones. The lowest of the claystone horizons contains slickensides with wedge-shaped aggregate structure and secondary, medium to coarse, angular

blocky structure with thin, discontinuous clay skins (argillans; Figure 4A, B; Brewer 1976). Overlying horizons contain medium to fine, angular blocky structure with thick, continuous clayskins and ferrans (2.5YR 5/5) upon ped surfaces and in soil pores (Figure 3E). Mixtures of kaolinite and smectite dominate the <2μm fraction in the claystone layers. In addition, abundant root halos (sensu Retallack 1990) are present in the upper horizons of Type E paleosols. Type E paleosols are found only in the upper ~40 meters of the Chilga sequence, and they change laterally to Type C and Type D paleosols.

Interpretation: The clay-enriched horizons with abundant clayskins upon ped surfaces likely correspond to an argillic horizon (Retallack 1990; Soil Survey Staff 1998). In this regard, Type E paleosols are Argillisols (Mack et al. 1993), which roughly corresponds to the soil orders Alfisols and Ultisols (Soil Survey Staff 1998). The dominant pedogenic process in soils with these characteristics is translocation of clay via leaching of Ca^{2+} from clay-exchange sites in the soil profile (Franzmeier et al. 1985). Significantly, argillic horizons form only in seasonal climates, upon well-drained, stable portions of the landscape, indicating that these Argillisols must have formed upon drier parts of the paleolandscape. Mixtures of kaolinite and smectite clays suggest that these soils underwent more significant weathering, possibly attributed to better drainage and/or duration of pedogenesis, than all other paleosol types discussed here. However, the presence of gley colors in Type E paleosols likely corresponds to sufficiently long periods of soil saturation and anoxic conditions to facilitate leaching of ferric Fe from the profiles. Vertic features in these paleosols indicate seasonal wet-dry cycles, suggesting seasonal precipitation in this region of tropical Africa.

We interpret Type E paleosols to have developed upon the more stable and well-drained areas of the Chilga region. This interpretation is based on the fine-grained nature of the strata associated with the profiles and pedologic features, such as argillic horizons, that formed upon older, more stable portions of the landscape (Soil Survey Staff 1975; Buol et al. 1997).

Paleobotany

A field survey of the Chilga basin in 2001 documented abundant and widespread plant fossil localities, which have now produced over 1000 leaf, fruit, seed, flower, and wood specimens. These specimens allow us to fill a large temporal gap in the tropical African plant fossil record, and to address Paleogene plant evolution, biogeography, and paleoclimate. The plant fossils occur in a variety of depositional settings, the majority of which fall into the following five categories: (1) overbank or pond deposits, which preserve autochthonous organic litter consisting of leaf, flower, insect, and twig compressions associated with pollen and in situ carbonized trees (associated with paleosol Type A, Protosols; Figure 5A, C); (2) airfall tuffs, which preserve leaf and seed compressions and impressions, in many cases associated with *in situ* silicified tree stumps (Figure 5D); (3) tuffaceous ironstones, which preserve fruit and seed casts associated with leaf impressions and vertebrate fossils (associated with paleosol Type A, Protosols; Figure 5E); (4) lignites, which grade from compressed peat containing leaves and stems to low-grade undifferentiated coal (associated with paleosol Type B, Histosols); and (5) silicified in situ forests in a variety of interfluvial depositional settings (Figure 5B).

In the following sections, we summarize what is known from the plant fossils found among these five preservational settings, and then integrate our results with those from geological and vertebrate paleontological research on the same deposits.

Overbank or Pond Deposits. These organic-rich deposits are to date the most productive in terms of density of plant fossils and quality of preservation. One of us (A. Pan) is focusing on the study of a single depositional unit (~ 30 cm thick) from which four sublocalities have been collected along a lateral exposure of approximately 60 m. Macrofossil compressions of at least 30 taxa among 533 specimens have been documented along this exposure, and include palm leaflets, petioles, and flowers representing the subfamilies Calamoideae, Coryphoideae, and Arecoideae; leaflets of *cf. Sorindeia* (Anacardiaceae), *Dioscorea* (Dioscoreaceae, section *Lasiophyton*), and Fabaceae (legumes); a flower of *cf.* Rubiaceae, leaves provisionally referred to the families Sapotaceae and Malvaceae *s.l.*; and one insect wing. Leaf cuticle and morphological features, such as hairs and glands, have been instrumental in providing key characters necessary for identification. The concentration of palm fossils and presence of at least three of the five extant subfamilies together at this site are unusual compared with the limited diversity of palms usually found in living African forests (Moore 1973). On the other hand, the presence of *Dioscorea* and Fabaceae species is more typical of living African forest communities.

Table 2 allows a comparison of preliminary taxonomic lists among the four sublocalities, which range from 11 to 37 m apart from one another. Between 18% and 75% of the taxa recorded (to

Figure 5. A. leaf compression from Sublocality CH-40 (leaf litter assemblage), **B.** Silicified tree trunk from in situ fossil forest, **C.** pollen grain from leaf litter assemblage matrix, **D.** palm leaf impression in ash IV, **E.** seed cast from tuffaceous ironstone, 62mm diameter.

date) at each sublocality are unique to that sublocality. Furthermore, neighboring sublocalities share very few, if any, taxa with each other. The limited local distribution of taxa in the small sampling area documents heterogeneity of composition within the original plant community (cf. Burnham 1993). As our study has progressed, both diversity and heterogeneity have increased, and while the numbers shown in Table 2 may change somewhat with further work, we consider this variability of local plant

composition comparable to that of modern forests of tropical West Africa (Richards 1996).

Plant community physiognomic information is provided by the presence of two charcoalified and partially compressed tree trunks lying prone at the base of the leaf bed (Sublocality 2). Leaf fossils were found draped over the trunks, but not below them. Thus, a forest gap was created by tree falls, perhaps associated with a fire, at a time prior to leaf-bed deposition, but not long enough before to allow for decay of the fallen trees. Upright, in situ,

Table 2. Distribution of plant taxa at four sublocalities, arranged here from south to north, along a 60 m lateral exposure of an organic-rich overbank deposit. The number of specimens from each of the sublocalities is shown in the second row (total = 533). Key to text coloration is at base of table.

SOUTH	Sublocality 4 CH-54	Sublocality 3 CH-41	Sublocality 1 CH-40	Sublocality 2 CH-52	NORTH Total Count
No. of Specimens	103	103	195	132	533
Taxa	Arecaceae	cf. Alismataceae	Sapotaceae (cf. *Mimusops*)	Eremospatha	
	Hyphaene	Anacardiaceae (cf. *Sorindeia*)	?*Celtis/Strychnos*	3 Legume taxa	
	Unknown 9	Unknown 12	*Dioscorea* sect. *Lasiophyton*	?Celtis/Strychnos	
	Unknown 18	Unknown 13	Fabaceae (cf. *Bauhinia*)	Sapotaceae (cf. Mimusops)	
		Unknown 14	Unknown 17	Unknown 10	
		Unknown 15	Unknown 1	Flower (cf. Rubiaceae)	
		Unknown 16	Unknown 2	Calamoideae (cf. Lepidocaryeae group)	
		Arecoideae	Unknown 11	Arecoideae	
		Unknown 3	4-5 Legume taxa	Palm flowers	
		Unknown 4	Unknown 7	Unknown 8	
		Unknown 5	Palm inflorescence		
		Unknown 6	Palm flower (cf. calamoid)		
Minimum # Taxa - Estimate	4	12	14	11	
Proportion of Unique Taxa	0.75	0.58	0.21	0.18	

Taxon found at 2 or more sublocalities
Taxon unique to one sublocality
Taxon may or may not be limited to one sublocality

charcoalified tree stumps also occur along this outcrop (Sublocalities 1, 2, and 4), but appear to be rooted in the paleosol below the leaf bed. Thus, leaves and other forest debris fell around the bases of the in situ trees following a fire (presumably the same fire responsible for the tree falls).

Airfall Tuffs. Five ash horizons can be traced laterally within the basin (for - 5 km), and the least weathered of these (ash IV) was fossiliferous at all locations visited. While these deposits show some sedimentary structures associated with transport by water, there is evidence of at least periodic direct airfall consistent with the preservation of delicate fern fronds, which indicate rapid burial without transport more than a short distance. One fern taxon, *Acrostichum*, is found in ash IV at several locations. This genus grows today in edaphic settings associated with high salt content or poorly drained, swampy conditions (Mabberly 1993). Other plants from ash IV include a small pinnatifid fern, legume fruits and leaflets, fan palm leaves, broad-leaved dicot impressions, and in situ silicified tree trunks including palms. An Ar[40]/Ar[39] age of 27.36+/-0.11 Ma on ash IV glass shards provides precise time control for the plant fossils (Figure 2; Kappelman et al. 2003).

Tuffaceous Ironstone. Fruit and seed casts are abundant in these deposits, which have also produced the majority of vertebrate fossils from Chilga. These sediments can be recognized everywhere in the basin by their red and black color derived from iron and manganese oxides. Organic plant material (i.e., cuticle) has not been found, but some leaf impressions show detailed venation and the fruit and seed casts preserve diagnostic surface features. Preliminary identifications include Arecaceae (palm) fruits, Fabaceae (legume) fruits and leaflets, and the seeds of at least three morphologically distinct species of *Anonaspermum* (Annonaceae).

Lignite. Macrofossils preserved in the lignites consist of robust stems and shoots. These have not yet been studied, but fieldwork in December 2004 documented the rare occurrence of cuticle in some lignite deposits. Thus, there is potential for further work on plant cuticle from the macrofossils and for the assessment of these deposits palynologically.

In Situ Silicified Forests. Trunk diameter measurements from 72 trees at two localities (34 and 38 trees, respectively) provide tree height estimates (Appendix 1) using the regression formulae of Rich et al. (1986) and Niklas (1994). The two sets of estimates are remarkably similar; however, estimates based on the formula of Rich et al. (1986) may be more accurate because the predictive formula was derived from dicotyledonous trees of modern tropical wet forest (Costa Rica), while the formula of Niklas (1994) was derived from a

combination of woody gymnosperms and angiosperm dicots (not exclusively tropical). Both sets of estimates indicate that the trees in these forests stood between about 20 and 35 m tall (Appendix 1). The distribution of trees mapped at one of these localities, using GPS measurements with cm-scale accuracy, documents a density of one tree every 3 m, a minimum considering that not every tree would have been preserved. Identification of the specimens is in progress, but analysis of thin sections to date indicates forest assemblages with richness of - 20 tree species over 6400 m^2.

Vertebrate Fossils

One of the most interesting and long-standing observations of Afro-Arabian vertebrate evolution concerns the dramatic turnover between the endemic archaic faunas of the Paleogene and the more modern largely immigrant faunas of the Neogene (Maglio 1978). Prior to the discovery of the Chilga vertebrates, the general absence of fossil localities dating from between 32-24 Ma offered little evidence as to the tempo and mode of this continental-scale turnover event. Discoveries in the Chilga region have helped to better establish the circumstances of this turnover and point out new research directions.

Vertebrate localities occur through the entire section at Chilga (Figure 2) but are also more concentrated in tuffaceous ironstones associated with Paleosol Type A (Protosols). The remains are usually fragmentary, most commonly represented by teeth and jaws, although limb elements are not rare, and generally represent medium- to large-sized herbivores. The same depositional and preservational characteristics of the sediments that together act to produce such a superb paleobotanical record (see above) apparently work to bias the vertebrate record; mammals smaller than about 20 kg are not represented in our collections and their absence, along with the absence of birds, fish, or other small vertebrates, may be due to diagenetic leaching of bone prior to fossilization (Kappelman et al. 2003).

The Chilga vertebrate fauna (Table 3) is composed of large paenungulate herbivores that are well represented in older Paleogene Afro-Arabian localities (Sanders et al. 2004). The most distinctive form is a new species of *Arsinoitherium* (Order Embrithopoda), *A. giganteum*, larger in size than earlier forms, and representing the youngest known occurrence for this group. The hyracoids are a second group showing moderate diversity at Chilga, with two new species of the common but conservative genera *Pachyhyrax* and *Megalo-*

hyrax, being well represented. A third species is larger in size and is probably related to *Pachyhyrax*, while a fourth is closely related to *Bunohyrax*. Proboscidea are the most diverse order of mammals and are represented by three families and five new species. Three of these new proboscideans belong to the family Palaeomastodontidae (*Phiomia major*, aff. *Palaeomastodon* sp. nov. A, and aff. *Palaeomastodon* sp. nov. B), with the Chilga occurrences representing the youngest known for this group. Deinotheres are also represented by a new genus and species, *Chilgatherium harrisi,* and extend back into time the earliest occurrence of this family by 7 Myr. The third family of Proboscidea is the Gomphotheriidae, with the Chilga occurrence of a new species (cf. *Gomphotherium* sp. nov.) again representing the oldest known for this group (Sanders et al. 2004).

DISCUSSION

Coexisting fossil plants, vertebrates, and paleosols have seldom been reported from Paleogene sites in tropical Africa. At Chilga, the abundance of fossil assemblages, and their association with a range of paleosols, allow us to apply multiple proxies to reconstruct floral and faunal communities all within the context of their paleolandscape.

The most striking characteristics of paleosols in the Chilga sedimentary strata are gley coloration, or the dominance of low chroma colors (e.g., gray or green), and accumulation of organic material (Mack et al. 1993). These features are found within all of the Chilga paleosols, but they are most prominent in paleosol Types A-C. Such soils occur most commonly today in areas with a high water table, where soil horizons are waterlogged and undergo anoxic, or aquic conditions for most of the year (Mack et al. 1993; Buol et al. 1997; Soil Survey Staff 1998). Specifically, the combination of (1) gley colors, (2) diffuse accumulation of organic material, (3) tabular rooting systems, (4) accumulation of minerals associated with low redox potential, such as siderite, and (5) lenticular bodies of organic-matter accumulation at the surface of Type B and C paleosols, is interpreted to represent the poorest soil drainage conditions across the Chilga floodplains, probably corresponding to local ponding of water or very slow surface runoff. In contrast, the presence of redoximorphic features, such as drab soil matrix colors with red and orange color mottling and accumulation of fine hematitic nodules in some of the Type C and D paleosols, suggests seasonal groundwater-table fluctuation and alternating periods of reducing and oxidizing conditions. Furthermore, the wedge-shaped aggregate struc-

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Table 3. Vertebrate fossils known from Chilga sediments (Kappelman et al. 2003; Sanders et al. 2004).

Order	Family	Subfamily	Genus and species
Proboscidea			
	Palaeomastodontidae		Phiomia major
			Palaeomastodon sp. nov. A
			Palaeomastodon sp. nov. B
	Deinotheriidae		
		Chilgatheriinae	*Chilgatherium harrisi*
	Gomphotheriidae		*Gomphotherium* sp. nov.
Embrithpoda			
	Arsinoitheriidae		*Arsinoitherium giganteum*
Hyracoidea			
	Saghatheriidae		*Pachyhyrax* sp. nov.
			Gen. et sp. nov., aff. *Pachyhyrax*
			Megalohyrax sp. nov.
			Bunohyrax sp.

tures and slickenside formation in some of the Type C and all of the Type D paleosols likely indicate periodic wetting and drying of the soil profile, suggesting that these profiles formed upon portions of the landscape that experienced periodic fluctuation of the local groundwater table. Finally, argillic horizons in Type E paleosols require fairly stable, better-drained conditions well above the groundwater table. Thus, we consider most of the lateral and stratigraphic variation in the distribution of paleosol profiles to record differences in the landscape position of soil-forming processes, with respect to the paleo-groundwater table (Figure 6A, B).

Feseha (2002) summarized the tectonic and structural details of the basin that captured the Chilga sedimentary sequence. That summary envisioned four stages of regional faulting and sedimentation spanning 32-12 Ma. For the Oligocene epoch, the inferred paleosol drainage conditions across the exposed areas of the basin provide a meaningful physiographic context for paleoecological reconstruction.

The composition and physiognomy of plant fossils from Chilga reflect local depositional conditions within the context of regional climate. The plants found in overbank or pond deposits close to a stream (in sediments associated with paleosol Type A) consist of taxa often found in those settings in tropical Africa today. These include palms, particularly calamoid or climbing palms, *Sorindeia*, and cf. Alismataceae. However, the entirety of this assemblage, including provisional identifications of Sterculiaceae, Fabaceae, and Dioscoreaceae, is indicative of a climate wet enough to support forest vegetation. Thus, a riparian association does not eliminate the necessity for ample rainfall, which must have been at least 1100 mm/year on average

(the minimum needed to support forest vegetation today; e.g., Jacobs 1999).

Initial results from collection and study of plant specimens from the airfall tuffs (e.g., tuff IV) indicate that these plants grew in substrates that were very wet, perhaps swampy. The fern genus *Acrostichum*, found in ash IV in at least two locations across the basin, is represented today by three living species. These are pantropical and occur in either freshwater swamps or in association with mangrove vegetation (Mabberly 1993). Another pinnatifid fern occurs in this context at Chilga, associated with the leaves of dicots and legume fruits. Elsewhere, the same tuff preserves upright tree stumps, including palms, large palmate palm fronds, and legume leaves associated with pedogenic modification (Type A paleosols), a clear indication of a stratigraphic hiatus within the tuffaceous unit. In addition, tuff IV exhibits trough cross-bedding and sedimentary structures similar to those found in point bar deposits today, consistent with deposition of the airfall tuff in meandering stream channels. Thus, the airfall tuff bed, which is at least 7 m thick in most places, represents episodic ash deposition across a landscape characterized by a range of edaphic settings from swampy to subaerial.

The fossil forests at Chilga are a good indication of wet conditions upon interfluvial settings. This inference is consistent with interpretations based on the plant assemblages known from overbank deposits, the presence of waterlogged bog or swamp deposits preserved as lignites, and the paleosol data, all of which point to poorly drained conditions in a generally wet climate.

With respect to mammalian assemblages, it is interesting to note that despite the somewhat more derived aspect of the individual taxa of the Chilga
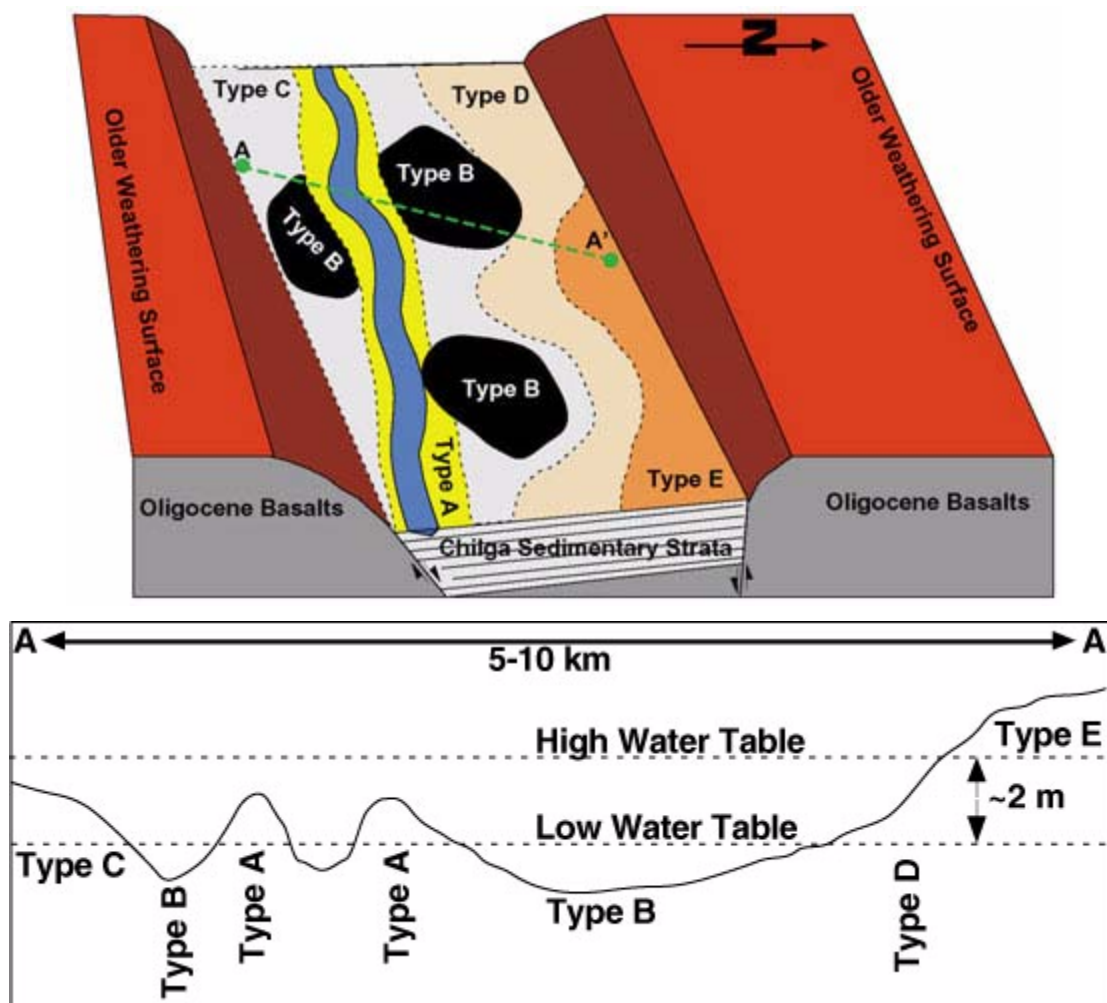
Figure 6. Schematic reconstruction of the Chilga sedimentary basin during Oligocene time. Based on the stratigraphic and lateral relationships of paleosols and sediments, a proposed facies relationship of the different soils is superimposed upon the paleolandscape. The line A-A' marks the lower cross section of the soil landscape. Type A paleosols (Protosols) are associated with sediments indicative of environments characterized by frequent sedimentation, such as stream levees and crevasse splay deposits. Type B paleosols (Histosols) form in local to regional depressions characterized by ponded water or very slow runoff in ever-wet environments, such as swales adjacent to stream levees. Type C paleosols (Gleysols) form in fine-grained sediments characterized by poorly drained and waterlogged environments across the floodplains and interfluves that underwent long periods of anoxia and aquic soil moisture conditions. However, development of soil structure and redoximorphic coloration in the upper horizons of Type C paleosols indicates some periods of better drainage, possibly during periodic fall of the regional groundwater table. Type D paleosols (Vertisols) form in clay-rich sediments characterized by periodic cycles of wetting and drying, possibly related to seasonal fluctuations of the regional water table. Type E paleosols (Argillisols) formed upon the most stable portions of the landscape, likely in paleogeographic positions most distal from depositional centers (i.e., streams) and topographically well above the position of the groundwater table. See text.

fauna, its general composition of arsinoitheres, hyracoids, and paleomastodonts largely matches that of the faunas from older Paleogene localities found around the continental margins of Afro-Arabia (Kappelman et al. 2003). The occurrence of this fauna in the highlands of Ethiopia suggests that these herbivores enjoyed a very widespread distribution across Afro-Arabia and probably occupied generalist niches with broad ecological tolerances. This observation is especially interesting in light of their overall low species diversities across a long temporal interval. In contrast, the dramatic diversification of the Proboscidea in the absence of any overall changes in faunal composition demonstrates that other, probably environmental, conditions were acting to drive their continued evolution. The question as to whether or not the arrival of Eurasian immigrants was responsible for driving the later extinction of the archaic endemics can only be tested by the recovery of new fossil locali-

ties dating closer to the Paleogene-Neogene boundary (23 Ma).

In summary, we envision an Oligocene landscape consisting of a generally flat and broad floodplain in a humid, tropical climate. Despite limited relief, landscape position played a primary role in the distribution of plants and in soil development due to variable but poor drainage conditions across the basin (Figure 6A, B).

We hypothesize that stratigraphic changes in paleosol morphology and plant composition are primarily a reflection of intrabasinal physiography rather than extrabasinal controls, such as regional or global climate change. In addition, episodic ash-falls were literally superimposed upon these evolutionary geomorphic processes and provided a significant (perhaps primary) source of sedimentary material. The ash, depending on where it fell, was reworked to varying degrees, became part of a stable land surface upon which vegetation became established, or was incorporated into standing or flowing water.

Additional, quantitative paleoclimate proxies will provide a basis for evaluating the influence of climate on Chilga fossils and sedimentary characteristics and will allow us to test the hypothesis that climate change was not a primary driver of the physical and biotic changes identified in the sedimentary strata. Fossils and sediments have the potential to provide independent estimates of paleotemperature from the stable isotope composition of pedogenic minerals and fossil wood anatomical characters. Paleotemperature estimates from leaves at tropical sites have been shown to be unreliable (Jacobs 2002), but paleoprecipitation estimates can be derived from fossil leaf assemblages and from elemental composition of paleosols. To test for the occurrence of climate change, the accuracy of paleoclimate estimates derived from plant fossils will be evaluated by intrabasinal comparison of estimates from contemporaneous (stratigraphically equivalent) and facies-equivalent localities (Burnham 1994). If the plant fossils prove to be reliable climate proxies, then comparisons between facies-equivalent assemblages from different stratigraphic levels can assess the occurrence of climate changes through the sequence. Further analysis of plant fossil taxonomy will provide greater resolution of temporal and spatial variability of community composition, yield valuable biogeographic information, and provide historical documentation to complement and test systematic hypotheses generated by molecular phylogenetics.

ACKNOWLEDGMENTS

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