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The effects of volcanism on Oligocene-age plant communities from the Ethiopian Plateau, and implications for vegetational resilience in a heterogeneous landscape

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ABSTRACT

Substantial volcanism and associated volcaniclastic sedimentation took place in association with East African Rift formation, and in some cases this would have had substantial ecological impacts. Ethiopian Late Oligocene (27.36 ± 0.11 Ma) fossiliferous volcanogenic strata provide opportunities to evaluate the magnitude of disruptive impact of volcanism on forest communities (before development of the Main Ethiopian Rift), and to assess their resilience. Fine-scale sampling and palynological analyses from the Magargaria River region of the northwestern Ethiopian Plateau tests the hypothesis that volcanism had a regional and significant disrupting effect on forest vegetation. These studies are compared with macrofossil and sedimentological data representing more local conditions previously reported from the same sediments. Results indicate that while some forests gave way to open environments dominated by herbaceous taxa, other communities remained or recovered quickly. Volcanic influences on sedimentary processes altered an existing forest ecosystem by creating a spatially heterogeneous landscape that also varied through time. This study supports the inherent significance of palynological data as indicators of ecological change at a regional scale relative to the more local view that macrofossils can provide, and underscores the importance of both kinds of fossils whenever possible for the study of the ecological dynamics of plant communities. The presence of forest taxa after repeated ashfalls indicates a degree of forest community resilience consistent with relatively limited burial by ash during the studied volcanic episodes. This study also suggests that taphonomic and diagenetic processes strongly affected the composition of palynomorph assemblages, skewing them towards thick-walled individuals, especially fungi.

1. Introduction

Flood basalts and associated volcanic eruptions characterized initiation of East African Rift development, which began in Ethiopia in the middle to Late Eocene (George et al., 1998), and ultimately became the major physiographic feature it is today, spanning more than 4000 km in eastern Africa. The East African Rift influences regional climate today, and likely had an influence on plant communities during the course of its development. Late Oligocene plant fossils from Chilga Woreda, northwestern Ethiopia, were present after flood basalt eruption, but before rifting, and provide a unique opportunity to document the extent to which disturbance from volcanism impacted tropical forest communities (e.g., Yemane et al., 1987a,b; Kappelman et al., 2003; Jacobs et al., 2005; García Massini et al., 2006) (Fig. 1). This question has relevance for understanding the ecological resilience of ancient tropical forest communities, and by implication, whether rift volcanism itself could have had a significant impact on long-term community composition and distribution.

A fine-scale study of plant macrofossils and sedimentary facies in seven meters of volcaniclastic strata from Chilga provided a local paleoenvironmental view of associations between plant community structure and landscape variation triggered by volcanism and associated hydrological changes (García Massini et al., 2010). The environment apparently changed from one dominated by riparian woody plant communities to one characterized by more open wetland and pioneer taxa in response to intermittent deposition of organic-rich and volcanic ash sediments, but the climatic context appears to have remained seasonally dry as documented by sedimentology and plant macrofossil compositions (García Massini et al., 2010). The volcaniclastic strata documented previously, and by this study, constitute a significant marker traced to other areas within the approximately 100 km^2 region, suggesting that the inferred impact of volcanism on the biota might have been relatively widespread across the Chilga region.

In this paper we examine the palynological composition of the same volcaniclastic sequence previously documented by García Massini et al. (2010) to test whether paleoenvironmental changes measured here on a regional scale by palynology are consistent with

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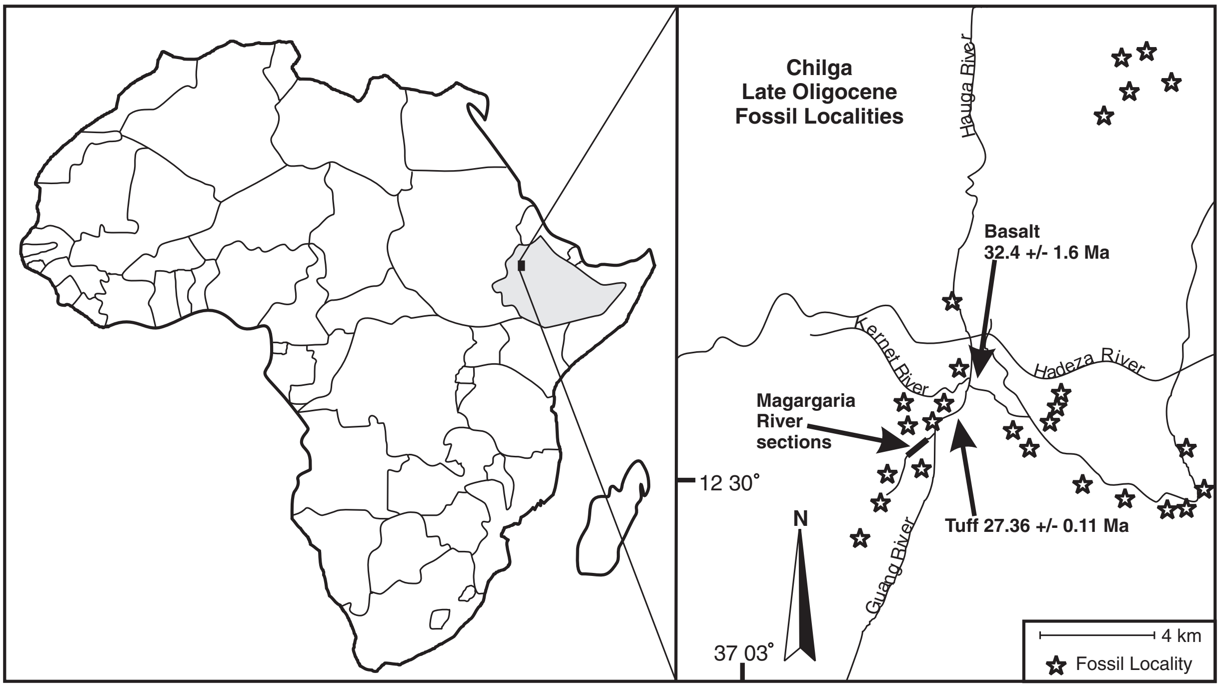


Fig. 1. Map of Africa with Ethiopia depicted in gray color. Enlarged area (modified from Kappelman et al., 2003) shows Late Oligocene fossil localities along the Magargaria River in Chilga, northwestern Ethiopian Plateau. Radioisotopically dated tuff and basalt samples were collected from the areas indicated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

the local signal derived earlier from plant macrofossils and sediments. Our objectives were to (1) compare variation in relative frequencies of three ecologically distinct palynomorph groups (pollen, fern and fungal spores), and (2) to use taxa of known ecological characteristics as more precise indicators of temporal and spatial changes in habitat type. In addition, we examined the influence of taphonomy on palynomorph composition by considering the relative frequency of most abundant taxa and the sedimentological contexts created by volcanism and fluvial processes.

2. Geological setting

The Chilga strata or beds consist of a series of terrestrial deposits located 60 km west-southwest of Gondar at about 1900 m above sea level on the northwestern Ethiopian Plateau (Fig. 1). They consist of volcanic and volcaniclastic sediments, up to 150 m thick, deposited in fluvio-lacustrine environments or as airfall in a ~100 km^2 area overlying a plateau of massive Early Oligocene flood basalts (Yemane et al., 1987a,b; Hoffman et al., 1997; Kappelman et al., 2003; Jacobs et al., 2005). A K–Ar age of 32.4 ± 1.6 Ma was obtained from basalt directly underlying the Chilga strata (Fig. 1) (Kappelman et al., 2003).

The palynological samples reported here come from a sedimentary sequence consisting of a thin set of clay and organic-rich strata overlain by a coherent set of ashes, called Ash-IV, that occur stratigraphically above the dated basalt. Ash-IV is the thickest (up to 20 m in one case) and the least weathered of several tuffs in the Chilga section. In addition, the Ash-IV sequence has been used as a guide to correlate sedimentary units laterally across the Chilga basin, and contains abundant plant macrofossils (Jacobs et al., 2005; García Massini et al., 2006). An ^{40}Ar/^{39}Ar age of 27.36 ± 0.11 Ma was obtained from the Ash-IV sequence itself (Fig. 1) (Kappelman et al., 2003). A seven-meter thick exposure of the Ash-IV sequence and a thin set of fossiliferous strata immediately below it were documented at a fine scale (cm–dm) in three stratigraphic sections exposed in a cliff-face along the Magargaria River (12° 30′ 31.3″, E 37° 6′ 57.3″; García Massini et al., 2010) (Fig. 1).

3. Materials and methods

Samples for palynological analysis were collected from 80 sedimentary horizons documented among three stratigraphically equivalent geologic sections spanning the Ash-IV sequence and the thin set of strata immediately below it (Fig. 2). Palynological samples were prepared using standard techniques (Batten, 1999). At least 300 palynomorphs were counted for each productive sample and individuals were assigned to three ecological groups reflecting different habits and trophic levels: pollen, fungi, and ferns. Relative frequencies of pollen, fungi and ferns and of selected taxa within each of these groups were calculated, and their distributions were analyzed among the three previously described vertical sequences (Figs. 2–6) (Bennett, 2003; García Massini et al., 2010). Selected pollen and spores were identified by comparing specimens to fossil and modern palynomorph collections published in print and online (e.g., African Pollen Database website; Yemane et al., 1987a,b; Barnett and Hunter, 1998; Kalgutkar and Jansonius, 2000).

4. Results

Previous work on the Magargaria sections provides a context for the results and interpretations of this palynological study. García Massini et al. (2010) documented airfall tuff, fluvially-reworked, and *in-situ* alluvial deposits comprising seven types of Depositional Units according to differences in bedding, grain size, texture, sedimentary structures, biogenic structures, and fossils (Depositional Units are color-coded in Fig. 2). The following list provides interpretations for these Depositional Units, which are arranged in order of decreasing rate of deposition and increasing organic content: A, ephemeral fluvial deposits of low to medium flow speed (crevasse splay); B, ephemeral small scale channel deposits (chute); C, sediment-gravity flow deposits (airfall ash); D, reduced traction flood deposits (proximal overbank); E, mud drape deposits (distal overbank); F, root bed (incipient paleosol); and G, *in-situ* deposits of organic matter (vegetated floodplain ephemeral pools). Sedimentological characteristics were also used to delineate seven

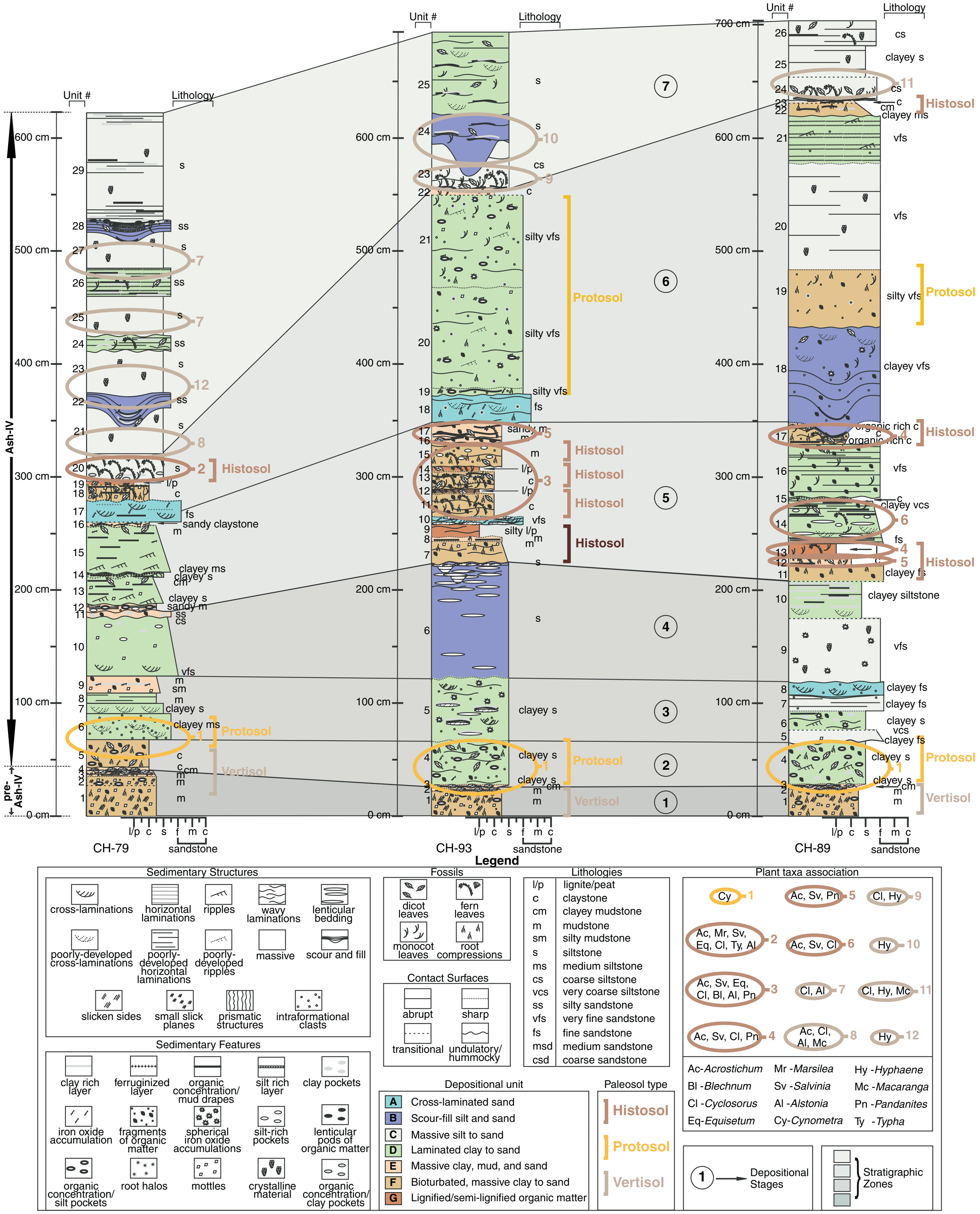
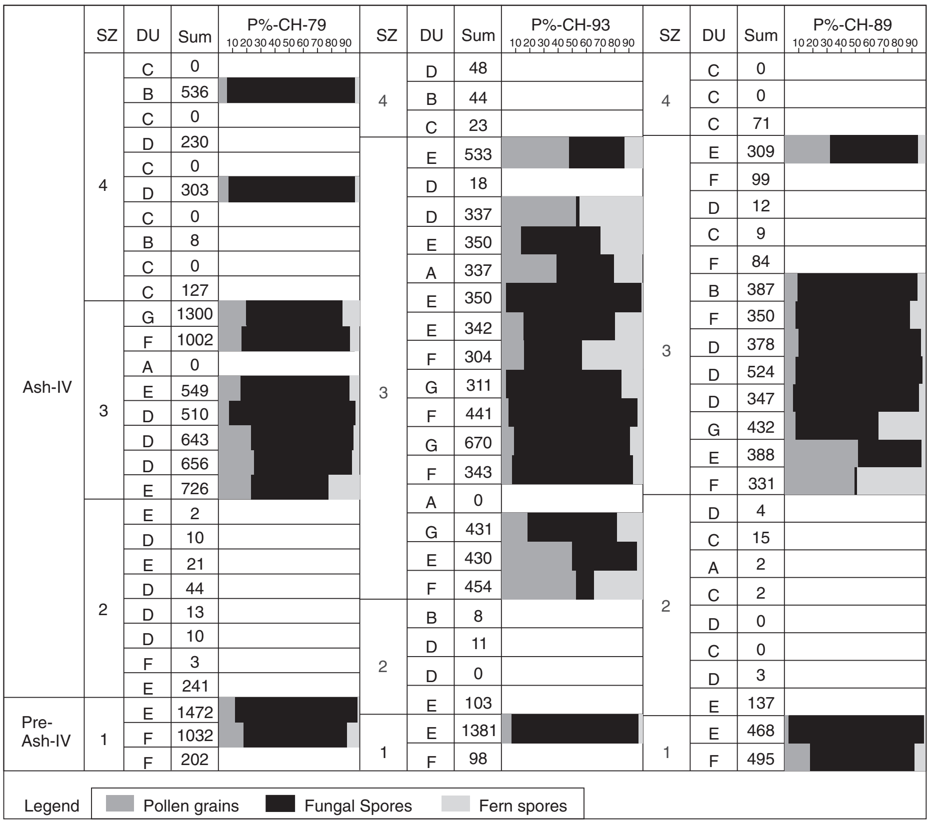


Fig. 2. Detailed stratigraphic representation of the three geologic sections (from W to E: CH-79, CH-93, CH-89) exposed along the margins of the Magargaria River. Sedimentological and macrofossil depositional stages (circled numbers), palynofloral stages (gray shades), Depositional Units (color-coded), Paleosol Types (in brackets), and macrofossil associations (circled) are shown on the sections, which also indicate traditional sedimentary structures and lithologies. Depositional stages are correlated across the three sections.



P%-CH-79

	SZ	DU	Sum
Ash-IV	4	C	0
		B	536
		C	0
		D	230
		C	0
		D	303
		C	0
		B	8
		C	0
		C	127
	3	G	1300
		F	1002
		A	0
		E	549
		D	510
		D	643
		D	656
		E	726
	2	E	2
		D	10
		E	21
		D	44
		D	13
		D	10
		F	3
		E	241
Pre-Ash-IV	1	E	1472
		F	1032
		F	202

P%-CH-93

SZ	DU	Sum
4	D	48
	B	44
	C	23
3	E	533
	D	18
	D	337
	E	350
	A	337
	E	350
	E	342
	F	304
	G	311
	F	441
	G	670
	F	343
	A	0
	G	431
	E	430
	F	454
2	B	8
	D	11
	D	0
	E	103
1	E	1381
	F	98

P%-CH-89

SZ	DU	Sum
4	C	0
	C	0
	C	71
3	E	309
	F	99
	D	12
	C	9
	F	84
	B	387
	F	350
	D	378
	D	524
	D	347
	G	432
	E	388
	F	331
2	D	4
	C	15
	A	2
	C	2
	D	0
	C	0
	D	3
	E	137
1	E	468
	F	495

Fig. 3. Composite general palynomorph diagram of a Late Oligocene volcaniclastic sequence from Chilga, northwestern Ethiopian Plateau. The diagram indicates the relative frequencies of pollen, fungi and ferns calculated for three distinct geologic sections (P%-CH), and the four defined areas (PZ) within the volcaniclastic sequence (pre-Ash-IV + Ash-IV) from where palynomorph groups were analyzed. Also indicated are the different Depositional Units (D) to which each stratigraphic unit within the three geologic sections were assigned: A (levee), B (chute-like channel), C (airfall ash), D (proximal overbank), E (distal overbank), F (root bed), G (lignite) (see text and García Massini et al., 2010).

depositional stages that are correlated among the three sections, and are assumed to be time-equivalent laterally (numbered 1–7 in Fig. 2). In addition, plant macrofossil assemblages were grouped according to their composition (colored ellipses in Fig. 2), and three kinds of paleosols were documented. The following results of palynological analyses across the vertical sections are grouped into four stratigraphically cohesive sets of time-equivalent strata representing similar depositional settings and plant macrofossil assemblages. These four stratigraphic zones consist of (1) forest plant fossils concentrated in clay and organic-rich strata below Ash-IV (pre-Ash-IV), (2) fewer forest plant fossils in fluvially-reworked ashes representing the beginning of Ash-IV deposition, (3) wetland and pioneer taxa in lignites and other organic-rich deposits found in the middle part of all sections, and (4) mainly pioneer taxa in airfall ashes and small scale chute-like deposits found in the upper part of all sections (Figs. 2 and 3). Although palynomorph samples are distinctive for each of the four stratigraphic zones, they are not designated “palynozones” because their composition is incompletely known, and two of the zones (2 and 4) are differentiated primarily based upon an absence or very low occurrence of palynomorphs.

Of the 80 samples collected for palynological analyses, 12 were devoid of palynomorphs, 31 had less than 300 palynomorphs per 300 grains of tracer (*Eucalyptus* pollen or *Lycopodium* spores added to each sample before chemical processing), and the remaining 37 yielded at least 300 palynomorphs per 300 grains of tracer. Most palynomorph assemblages were dominated by fungi, followed by pollen and fern spores, although some samples were dominated by pollen or fern spores or both (Fig. 3). Productive palynological samples were concentrated in Zones 1 (pre-Ash-IV strata) and 3 (middle of Ash-IV). Zones 2 (beginning of Ash-IV) and 4 (end of Ash-IV) were barren or poorly productive.

4.1. Zone 1

Palynomorph assemblages from Zone 1 in all sections were from organic-rich clayey floodplain horizons (pre-Ash-IV) deposited prior to emplacement of more tuffaceous strata (Ash-IV) (García Massini et al., 2010). These horizons represent a succession of root-populated and organic-rich clayey to sandy deposits capped by a layer formed by forest litter accumulation (E and F Depositional Units), where palynomorph concentration increases upward. Palynomorph assemblages are dominated by fungi, which occur in greatest number in the uppermost unit of Zone I (Fig. 3). Pollen is slightly more abundant than fern spores in the three sections (Fig. 3).

Most palynomorphs in this zone show some degree of corrosion and are often broken. The best preserved individuals had thicker and melanized walls, and mostly consisted of fungal spores, fruiting bodies, and hyphae. Among the most abundant fungal morphotaxa present in palynomorph Zone 1 assemblages are *Hypoxylonites*, *Brachysporisporites*, *Inapertisporites*, and *Fractisporonites* (Kalgutkar and Jansonius, 2000 and references therein). The first two are assignable to the extant genera *Hypoxylon* and *Brachysporium*, whereas the other two represent variously shaped unicellular spores and multicellular hyphae and conidiophores (spore producing organs) that can be assigned to a number of different extant taxa (Kalgutkar and Jansonius, 2000).

Other less common fungi include *Pluricellaesporites*, *Fusiformisporites*, *Delitschia*, *Spegazzinites*, *Desmidiospora*, *Meliolinites*, and representatives of the Microthyriales. Pollen taxa include *Alchornea* (Euphorbiaceae), *Brachystegia* (Fabaceae), *Albizia* (Fabaceae), and, more sparsely, Sapotaceae-type, *Bombax*-type, grass (Poaceae) and sedge (Cyperaceae) individuals. The ferns are represented by various types of monolete and trilete spores.

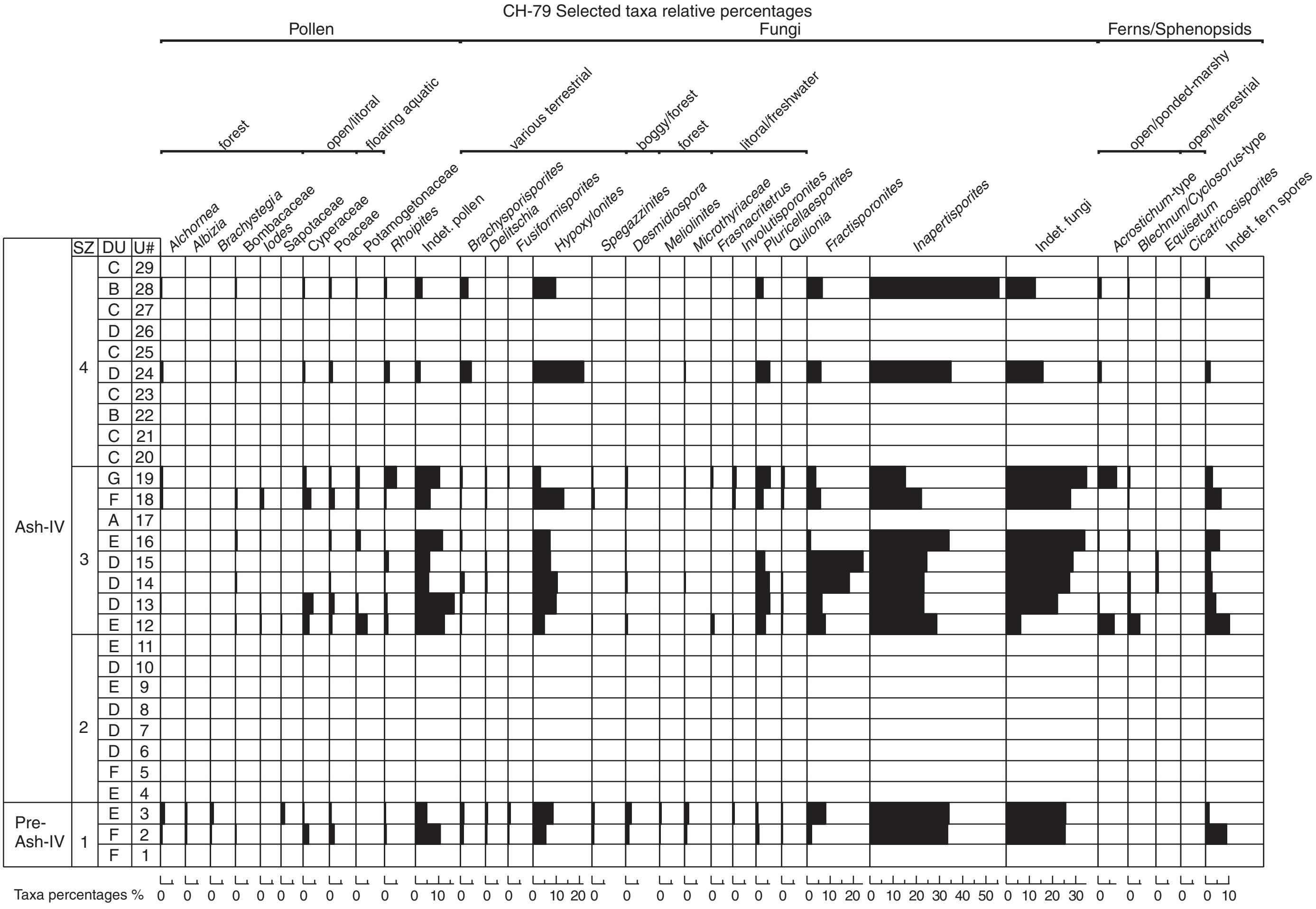


Fig. 4. Palynomorph diagram showing relative percentages of selected taxa from the south (CH-79) geologic section from a Late Oligocene volcaniclastic sequence from Chilga, northwestern Ethiopian Plateau. The diagram also indicates the four defined areas (PZ) within the volcaniclastic sequence (pre-Ash-IV + Ash-IV) from where palynomorphs were analyzed, unit numbers (U#), and the different Depositional Units (D) to which each stratigraphic unit within the three geologic sections were assigned: A (levee), B (chute-like channel), C (airfall ash), D (proximal overbank), E (distal overbank), F (root bed), G (lignite) (see text and García Massini et al., 2010).

4.2. Zone 2

The boundary between Zone 1 (pre Ash-IV) and Zone 2 (Ash-IV) is a rather sharp transition from low energy deposition of organic rich claystones to higher energy, increasingly ashy and less organic-rich, massive to fluvially-reworked sediments (Depositional Units B, C, D, E, and F). Sedimentary units within palynomorph Zone 2 have only a few or no palynomorphs except for the stratum representing the beginning of the deposition of Ash-IV (Depositional Unit E), where a moderate number of fungi exceed the abundances of pollen and fern spores (total palynomorphs per 300 grains of tracer were less than 300) (Fig. 3). This stratum is dominated by unicellate robust fungal spores of the morphogenus *Inapertisporites*, while thick-walled hyphae fragments and some filiform multicellate spores of the morphogenera *Fractisporonites*, *Pluricellaesporites*, *Scolecosporites*, and *Polycelleasporonites* are second in abundance. Angiosperms and ferns are poorly represented by only a few *Alchornea*, grass, sedge, and Sapotaceae-type pollen grains, and monolete and trilete fern spores.

4.3. Zone 3

Zone 3 is characterized by lignitic and organic-rich horizons (Depositional Units E, F, G) intercalated in parts by a few ashy laminated and massive strata (Depositional Units B, C, D). These represent high water-table environments where ephemeral ponds and adjacent parts of a floodplain received intermittent, but increasing, amounts of airfall ash through time (García Massini et al., 2010). Most assemblages (30 out of 37) had high enough concentrations to count at least 300 palynomorphs, making this the most productive zone of the volcaniclastic succession. Generally, palynomorphs are dominated by fungi in most units (20 of 37), pollen in 3 units, fern spores in 1 unit, or both pollen and fern spores (6 units) (Fig. 3). When fungi are omitted from consideration, pollen is more abundant than fern spores in 21 of 30 productive samples and pollen and fern spores have similar percentages in three units (Fig. 3). Fungi are generally less abundant than pollen and fern spores at the basal part of this zone in the central and north sections (CH-93 and CH-89) (Fig. 3).

As in the pre-Ash-IV strata in Zone 1, assemblages in Zone 3 are characterized by individuals with generally degraded and thick, highly-melanized walls (especially fungi). Some palynomorphs are conspicuous throughout all sections including pollen of *Alchornea*, *Brachystegia*, *Albizia, Iodes*, *Potamogeton*, Sapotaceae-type, *Bombax*-type, grass, sedge, and *Rhoipites*. Spores of the fungal morphogenera *Inapertisporites*, *Hypoxylonites*, *Brachysporisporites*, *Fractisporonites*, and *Pluricellaesporites*, as well as morphologically diverse monolete and trilete fern spores are also common. Some of these are particularly abundant, including *Rhoipites*, grass, sedge, and *Potamogeton* pollen, *Inapertisporites*, *Hypoxylonites*, *Involutisporonites*, *Pluricellaesporites* and *Fractisporonites* fungal unicellular and multicellular filiform spores and hyphae and conidiophore fragments, and Blechnaceae/Thelypteridaceae-type and *Acrostichum*-type fern spores. Other palynomorphs present in some sedimentary units but in smaller numbers, include *Cicatricosisporites* and *Equisetum* spores and the fungal morphogenera

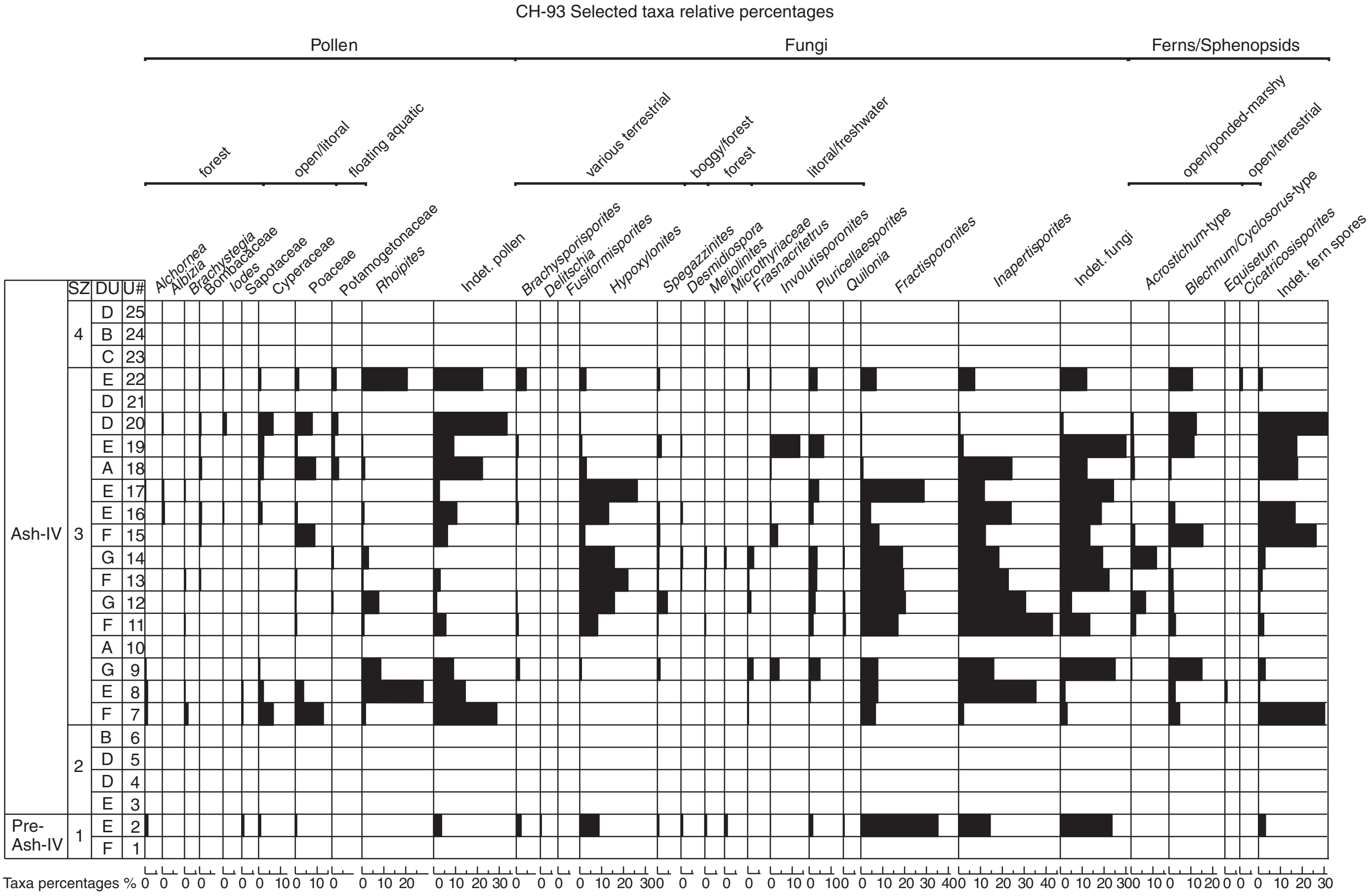


Fig. 5. Palynomorph diagram showing relative percentages of selected taxa from the central (CH-93) geologic section from a Late Oligocene volcaniclastic sequence from Chilga, northwestern Ethiopian Plateau. The diagram also indicates the four defined areas (PZ) within the volcaniclastic sequence (pre-Ash-IV + Ash-IV) from where palynomorph were analyzed, unit numbers (U#), and the different Depositional Units (D) to which each stratigraphic unit within the three geologic sections were assigned: A (levee), B (chute-like channel), C (airfall ash), D (proximal overbank), E (distal overbank), F (root bed), G (lignite) (see text and García Massini et al., 2010).

Spegazzinites, *Quilonia*, *Frasnacritetrus*, *Desmidiospora*, Microthyriaceae-type, *Meliolinites*, *Delitschia* and *Fusiformisporites*.

4.4. Zone 4

Palynomorph assemblages from Zone 4 were recovered from airfall and reworked ash layers (Depositional Units B, C, D) that are interpreted as deposits (overbank, channel, levee) of a braided river (García Massini et al., 2010). Palynological samples from this zone are generally barren (or have a low concentration of palynomorphs), and are productive enough for a count in only two sedimentary units of the south section (CH-79) out of a total of sixteen samples among the three sections (Fig. 3). These two assemblages are dominated by fungi and followed in abundance by pollen and fern spores, respectively (Fig. 3). Of the remaining units containing some palynomorphs, fungi are usually most abundant except for the layer that represents the beginning of the deposition of the ash-rich strata in this palynomorph zone (e.g., CH-79 unit 20), where pollen, fern spores, and fungal spores occur in decreasing order of abundance. However, this stratum does not show a high enough concentration of palynomorphs to be considered fertile, and thus this pattern may only be a result of filtering by taphonomic processes. From a morphostructural point of view, assemblages are dominated by individuals having thick melanized walls and include several fungal morphotypes, including *Inapertisporites*, *Hypoxylonites*, *Brachysporisporites*, *Fractisporonites*, and *Pluricellaesporites*. Among the pollen are sparse grains of *Albizia*, *Bombax*-type, *Potamogeton*, grass, sedge, and *Rhoipites*, whereas ferns consist of trilete and monolete spores. Some types are more abundant in some units than in others, including the fern *Cyclosorus*/*Blechnum*-type (Depositional Unit C) and the fungi *Inapertisporites* and *Hypoxylonites* (Depositional Units B and D).

5. Interpretation of palynological data

5.1. Zone 1

The palynological assemblages of Zone 1, which were deposited prior to Ash IV volcanic activity, are dominated by fungi, followed in abundance by pollen and ferns, respectively (Fig. 3). Fungi are commonly two or more times as abundant as the other two palynomorphs together in this zone, and dominate nearly everywhere. The fungi-rich palynomorph assemblages generally have a high proportion of thick-walled, highly-melanized individuals, especially fungi, and others with variously corroded and broken walls. This suggests that depositional paleoenvironments favored the preservation of resistant fungal propagules. A number of studies have shown that taphonomic processes can significantly influence palynomorph assemblages leading to the differential preservation of thick-walled or degraded and corroded individuals (e.g., Andersen, 1984; Crowley et al., 1994). In particular, Andersen (1984) showed that the abundance of thick-walled, highly-melanized hyphae in soils increased their concentration through time aided by their greater resistance to breakdown by microorganisms than thinner-walled and less pigmented palynomorphs. These processes are probably exacerbated when fluctuating water levels allow substrates to dry periodically, such as at or near the soil surface, rather than when substrates are permanently submerged.

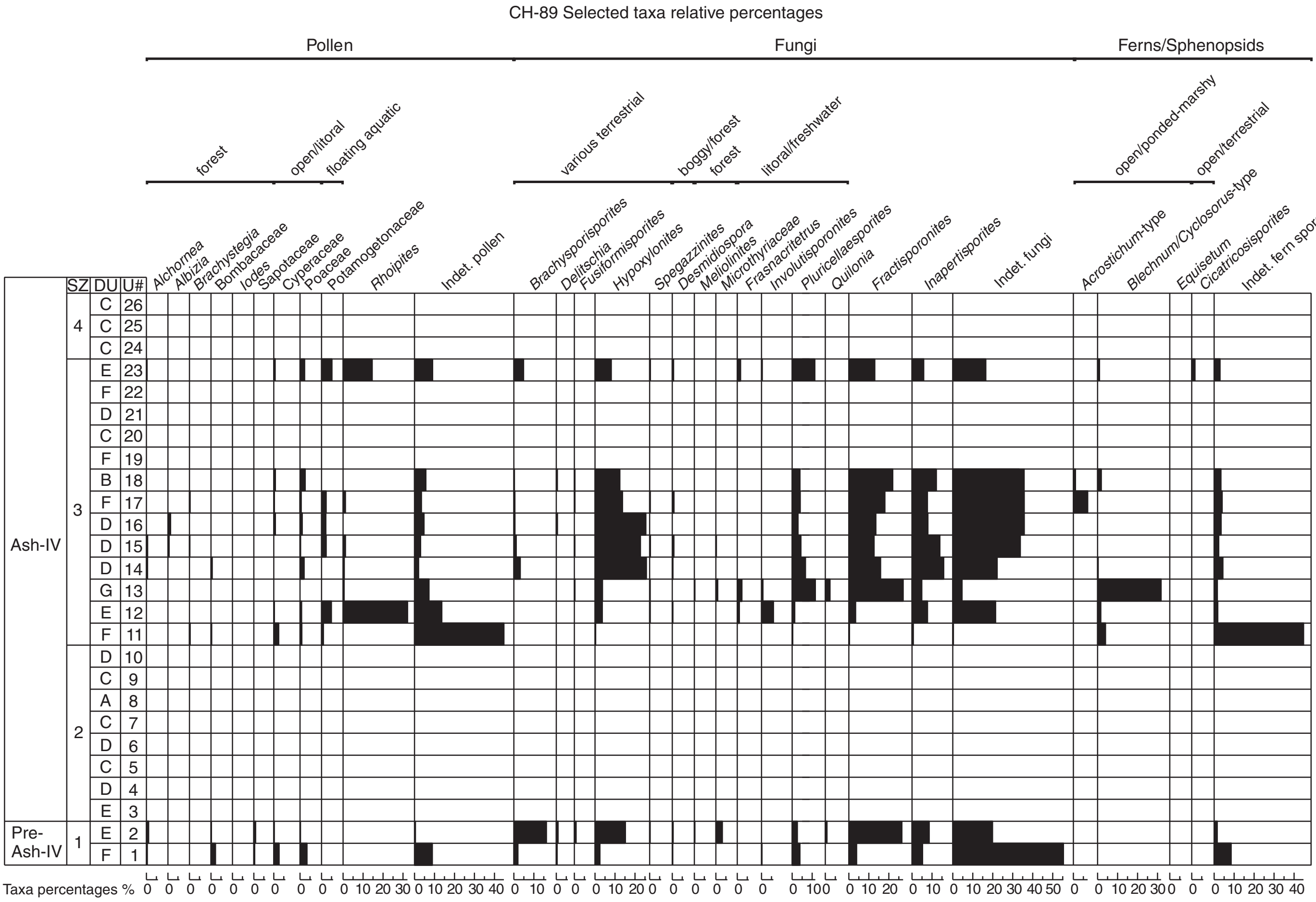


Fig. 6. Palynomorph diagram showing relative percentages of selected taxa from the north (CH-89) geologic section from a Late Oligocene volcaniclastic sequence from Chilga, northwestern Ethiopian Plateau. The diagram also indicates the four defined areas (PZ) within the volcaniclastic sequence (pre-Ash-IV + Ash-IV) from where palynomorph were analyzed, unit numbers (U#), and the different Depositional Units (D) to which each stratigraphic unit within the three geologic sections were assigned: A (levee), B (chute-like channel), C (airfall ash), D (proximal overbank), E (distal overbank), F (root bed), G (lignite) (see text and García Massini et al., 2010).

Moreover, these cycles in the water table positively influence fungal abundance by encouraging sporulation (Cohen, 1973; Cohen and Spackman, 1977; Webster and Descals, 1981; Chapela and Boddy, 1988a,b; Chmura et al., 1999), and have a greater corrosive effect on thinner-walled palynomorphs (e.g., pollen) (Elsik, 1971, 1996; Fernández Pinto da Luz et al., 2005; Traverse, 2007). Independent evidence for alternating wet and dry conditions is provided by the overprint of a vertic paleosol on Zone 1 sediments (Fig. 2).

Despite probable filtering by taphonomic processes, the palynomorphs of Zone 1 are informative for paleoecology. The abundance of fungi in the forest litter horizon (CH-79, unit 3, CH-93, unit 2, CH-89, unit 2; Figs. 2–6) is consistent with observations of modern forest floors with an accumulation of leaf and other organic debris (Bandoni, 1981; Webster and Descals, 1981; Andersen, 1984). Two of the most abundant fungal morphotaxa in palynomorph Zone 1 (*Hypoxylonites* and *Brachysporisporites*) are morphologically identical to extant common saprotrophs found on bark, wood, and decaying vegetation and animals. Other fungi in this zone are also morphologically most similar to extant saprotrophs such as *Cookeina* (=*Fusiformisporites*), *Delitschia*, and *Spegazzinia* (= *Spegazzinites*), which are common on soil, dung, and other organic substrates (Carmichael et al., 1980; Barnett and Hunter, 1998). These same taxa also include some weak parasites of vascular plants (Bandoni, 1981; Webster and Descals, 1981; Sherwood-Pike, 1988; Webster and Weber, 2007).

A number of fungal morphotaxa in Zone 1 assemblages can be assigned to extant epiphyllous types, including *Meliola* spores, *Desmidiospora* propagules, and Microthyriaceae-type fruiting bodies (Carmichael et al., 1980; Barnett and Hunter, 1998; Kalgutkar and Jansonius, 2000; Cannon and Kirk, 2007; Webster and Weber, 2007). The Microthyriaceae is a group of leaf and stem saprotrophs and pathogens on moist tropical to temperate forest species worldwide (Kalgutkar and Jansonius, 2000; Kirk et al., 2001; Cannon and Kirk, 2007; Webster and Weber, 2007). *Meliola* is a widespread genus of plant pathogens typical of moist tropical forests (Webster and Weber, 2007). *Desmidiospora* has been interpreted as either germlings of Microthyriaceae or appressoria identical to those produced by extant pathogenic taxa, such as *Meliola*, to penetrate the underlying host plant tissue during the infection process; however, other authors considered this morphotaxon to be dispersed conidia or sporangia, such as those of *Desmidiospora myrmecophila* and *Entophlyctis lobata*, which are common in bogs (Dilcher, 1965; Bradley, 1967; van Geel, 1978; van Geel et al., 1981; Jarzen and Elsik, 1986; Elsik, 1992).

Angiosperms are not very diverse or abundant in palynomorph Zone 1 and include only a few recognizable types. These include Sapotaceae, *Alchornea*, *Brachystegia* and *Albizia*, which based on their modern distributions today in Central, West, and East Africa, together indicate forest, sometimes swampy, settings (e.g., Robertson and Luke, 1993; Hawthorne and Jongkind, 2006). The presence of graminoid pollen in low numbers indicates periaquatic/aquatic settings such as can occur in open patches of forest or similar settings around the fringes of swamps (e.g., Burger, 1967; Yemane et al., 1987a,b). *Bombax*- type pollen, which is morphologically more similar to living *Bombax* and *Ceiba* than to *Adansonia* (a more xerophytic genus), is also present in Zone 1. *Bombax* and *Ceiba* commonly occur in association with swampy settings; low relative percentages compared to the other pollen taxa, especially at the forest litter horizon capping Zone 1, might reflect one or more of the following: (1) occurrence in more open areas of the environment in closer association with grasses and sedges (which are wind-pollinated and likely to be produced in larger numbers), (2) low detectability within these palynomorph assemblages (due to low productivity of parent plants), and (3) diagenetic processes that disproportionately affect their preservation (Figs. 4–6). Ferns in this palynomorph zone consist of monolete and trilete spores of unknown affinity (Figs. 3–6).

In summary, the presence of fungi that commonly occupy forest-floor litter and the phylloplane implies a well-established forest plant community with a network of biological interactions. Similarly, the pollen results indicate the presence of forest formed by a combination of trees and herbs and a few ferns (Figs. 4–6). The independent sedimentary record, which documents significant organic debris accumulation via fairly low-energy deposition on a seasonally inundated floodplain, is consistent with copious fungal remains and the distribution of macrofossils in this zone (Fig. 2) (García Massini et al., 2010).

5.2. Zone 2

Zone 2 is a succession of fluvially-reworked and airfall ashes (Depositional Units B, C, and D) and corresponds to the initial deposition of the more tuffaceous part of the volcaniclastic sequence (Fig. 2) (García Massini et al., 2010). Sedimentary units in this zone are mostly barren or have low palynomorph counts, except for moderate numbers (less than 300 individuals/palynomorphs assemblage) in the basal horizon (Depositional Unit E; Fig. 3). This horizon, which consists of a silty ash layer containing organic debris that in part may have been reworked from the underlying forest litter horizon, produces more than 50% fungi in all three sections, followed by up to 32% pollen and up to 3.5% ferns. Taxonomic composition of Zone 2 is similar to that of Zone 1, although somewhat less diverse. In addition, the basal horizon is dominated by thick-walled fungal spores; particularly common are the *Inapertisporites* and *Fractisporonites* morphogenera of unknown affinity, and broken and degraded fungi, pollen, and fern specimens. The abundance of *Inapertisporites* and *Fractisporonites* probably reflects taphonomic bias toward preservation of more resistant propagules as a result of fluvial reworking and chemical changes of the substrate due to the addition of ash, but it could also represent unidentifiable saprotrophs or other types of fungi that thrive on river shores (e.g., see Barnett and Hunter, 1998; Webster and Weber, 2007). Other fungal remains observed in these basal samples include fragments of typical freshwater filiform spores in the *Pluricellaesporites* and *Quilonia* morphogenera (e.g., see Ingold, 1975; Marvanová, 1997). These represent a greater percentage of the fungi in this layer than in that of the underlying forest litter horizon, indicating either biased preservation, or a switch towards more aquatic conditions, or both. Also present are Sapotaceae-type and *Alchornea* pollen grains, which indicate forest environments. A few grains of sedge and grass also form part of this assemblage, and these might have occupied aquatic or periaquatic parts of the landscape either in forest openings, or along herb-dominated river edges. The presence of the fungus *Desmidiospora* is consistent with forest or boggy conditions (Dilcher, 1965; Bradley, 1967). The presence of a few spores of the fungal morphogenus *Polycelleasporonites*, which are most similar to those of the extant cosmopolitan genus *Alternaria*, is consistent with an open landscape and humid conditions (Elsik, 1992, 1996; Barnett and Hunter, 1998). Overall, the sediments of palynomorph Zone 2 were unfavorable for palynomorph preservation and accumulation. Only the basalmost horizon preserved moderately abundant assemblages. If they are not reworked, taxa present in these assemblages indicate freshwater and open environments, but some tree taxa indicate forests remained at least as patches of vegetation outside of the immediate area of deposition. This result is consistent with paleoenvironmental interpretations based on plant macrofossils and sediments, which indicate rapid depositional rates on point bars and adjacent parts of a floodplain inhabited by a few riparian taxa (Fig. 2) (García Massini et al., 2010).

5.3. Zone 3

Zone 3 is characterized by a series of organic and ash-rich claystones, siltstones, and lignites (Depositional Units E, F, and G) representing the most productive strata of the entire volcaniclastic succession (30 out of the 37 productive horizons; Fig. 3). There are no temporal trends in relative abundances of pollen, ferns, and fungi, but lateral variation in relative percentages of selected taxa are consistent with environmental differences previously inferred from macrofossils and sediments (García Massini et al., 2010). In general, the samples show that environmental conditions in most cases favored proliferation and preservation of fungi over pollen and fern spores, probably as a result of periodic ashfall on seasonally moist settings (e.g. see Bilderback and Slone, 1987; Crowley et al., 1994; Suberkropp, 2001) (Fig. 3). In contrast, the absence or poor representation of fungi from the pollen and/or fern dominated assemblages probably reflects reducing conditions and a more stable water table level, conducive to the preservation and accumulation of pollen and spores, but biased against fungi. Pollen productivity and rapid sedimentation may also have played a role, as there is evidence for an increase in thin-walled, psilate, and hyaline palynomorphs produced by highly productive wind-pollinated herbaceous plants relative to animal-pollinated forest taxa in the environment (Traverse, 2007; Kalgutkar and Jansonius, 2000).

Among the most abundant morphotaxa present within the fungi-dominated assemblages of Zone 3 are thick-walled *Inapertisporites* spores of unknown affinity followed in abundance by *Hypoxylonites* (a morphogenus identical to extant *Hypoxylon* spores) and hyphae and conidiophore fragments (*Fractisporonites*). Less abundant are broken and intact filiform and coiled propagules morphologically most similar to taxa (*Pluricellaesporites*, *Quilonia*, and *Involutisporonites*) common in freshwater and transitional environments between aquatic and terrestrial areas (e.g., Ingold, 1975; Marvanová, 1997; Barnett and Hunter, 1998; Kalgutkar and Jansonius, 2000). The abundance of these and other fungi increases at the top of short sequences of increasingly organic-rich strata near the beginning of palynomorph Zone 3 deposition in the central and north sections (CH-93 and CH-89), varies little in overbank units in the middle part of this zone, and decreases in lignites and other organic-rich strata towards the end of this zone (Figs. 3–6). The relative percentages of morphotaxa characterized by filiform and coiled spores (e.g., *Pluricellaesporites*, *Quilonia*, and *Involutisporonites*) increase relative to those of almost all of the remaining fungi in some of the lignites (e.g., CH-79, units 18-19) (Figs. 3–6). The modern counterparts of such fungi can live on submerged dicotyledon leaves, twigs, wood, grasses, sedges and other organic debris. They sporulate when exposed to the air as a result of surface drying, thus, the abundance of such fungi is consistent with habitats characterized by organic-rich substrates in seasonally wet environments (Bandoni, 1981; Webster and Descals, 1981; Barnett and Hunter, 1998).

Other less abundant fungal morphotaxa are present in palynomorph Zone 3 assemblages, including *Brachysporisporites*, *Spegazzinites* and *Fusiformisporites*, which are morphologically most similar to the extant saprotrophs *Brachysporium*, *Spegazzinia*, and *Cookeina*, respectively. These are consistent with a diverse fungal saprotrophic flora (Sherwood-Pike, 1988; Barnett and Hunter, 1998; Kalgutkar and Jansonius, 2000). In addition, the increase of the relative percentage of tetraradiate spores assignable to the morphogenus *Frasnacritetrus* in the lignitic horizons (G Depositional Unit), which are morphologically identical to *Tetraploa*, an extant taxon that occurs on grasses and carices in both terrestrial and aquatic environments including ponds and slow flowing streams, is consistent with an open landscape having a variable water table (Figs. 3–6) (Wolf, 1966; Elsik, 1986, 1992; Barnett and Hunter, 1998; Kalgutkar and Jansonius, 2000). Moreover, the near absence of epiphyllous fungal morphotaxa, in most horizons, indicates rather open environments with local plant communities generally depleted in arboreal taxa and probably enriched in herbs and other small plants not contributing their leaves to the deposits (Figs. 3–6). An exception is the occurrence of a few Microthyriaceae and *Desmidiospora* in some lignitic horizons, which probably indicates the likely presence of more mature environments having herbs as well as tree plant taxa in close proximity to the standing, organic-rich water that produced the lignitic units (Figs. 4–6).

Pollen- and/or fern-dominated assemblages in palynomorph Zone 3 are in general characterized by low diversity. This could indicate that taphonomic characteristics favored preservation of tougher, more resistant individuals and/or types less susceptible to degradation by soil microorganisms (Elsik, 1971, 1996). However, the general underrepresentation of fungi and degraded individuals and the morphological characteristics of the palynomorphs preserved, especially the most abundant types (psilate, light-colored, and thin-walled) instead suggests limited microbial activity, and a relatively accurate representation of low diversity plant communities. Rapid deposition associated with massive ashy strata (Depositional Units E, F), probably explains the reduced microbial activity, dominance of pollen and spores in the assemblages, and the preservation of a few most abundant types.

The relatively high abundance and diversity of ferns in Chilga was previously noted by Yemane et al. (1987a,b), who pointed out that this is rare in palynomorph assemblages and comparable to the even more diverse palynoflora from the Miocene of Burundi (Sah, 1967). This abundance was interpreted as reflecting high rainfall and runoff in humid, closed, forest environments (Yemane et al., 1987a,b). We suggest that high fern abundance and diversity is not necessarily a reflection of a closed wet-forest environment at Chilga. In another study of palynomorph assemblages in organic-rich deposits, fern-dominated horizons were recorded right after ash deposition on peat mires (Crowley et al., 1994). This was explained to be a result of sealing off of soils by volcanic ashfall, promoting ponding and abundance of taxa adapted to inundated settings, including ferns. We suggest that similar factors apply to Chilga in depositional units where ash fall affected the local hydrology in ways favoring fern diversity. Fern abundance in these units probably reflects their ability to live in poorly oxygenated, waterlogged settings and their capacity to function as pioneer plants, as noted in modern studies of colonization of ash after deposition (Spicer et al., 1985; Burnham, 1994; García Massini et al., 2010).

Among the fern-dominated assemblages within palynomorph Zone 3, two types dominate over other palynomorphs, as documented in the lignites and other organic-rich sedimentary units of this zone (D, E, F, and G Depositional Units) (Figs. 4–6). One type is a kidney-shaped, psilate, monolete fern spore. Spores of this kind are among those produced by a number of genera, such as *Cyclosorus* and *Blechnum*, in the Thelypteridaceae and Blechnaceae, respectively (Tryon and Tryon, 1982; Kramer and Green, 1990; Tryon and Lugardon, 1991). The other common type is a triangular, proximally scabrate, trilete spore morphologically most similar to those produced by a number of extant genera including *Cyathea* and *Acrostichum* in the Cyatheaceae and Pteridaceae, respectively (Tryon and Tryon, 1982; Kramer and Green, 1990; Tryon and Lugardon, 1991). *Blechnum*, *Cyclosorus*, and *Acrostichum* macrofossils have been identified from the central part of the three sections in the same and different stratigraphic horizons (García Massini et al., 2006, 2010; García Massini and Jacobs, 2009). In particular, *in-situ Acrostichum* and *Blechnum* spores morphologically identical to the dispersed individuals have been found attached to some of the macrofossils suggesting a connection between all the dispersed spores of these types and these taxa (García Massini et al., 2010). Dispersed and *in-situ Blechnum*/*Cyclosorus*-type (under various fossil names, e.g., *Laevigatosporites* and *Stiropteris*) and *Acrostichum*-type spores and macrofossils are known from deposits associated with early colonization events of disturbed environments, particularly by ashfalls (Kramer and Green, 1990; Collinson, 1996, 2001, 2002 and references therein). In addition, the widespread occurrence of these and other fern (*Salvinia*, *Marsilea)* and sphenopsid macrofossils (*Equisetum*) in the same and different horizons has been cited before as evidence of poorly-vegetated wetland environments dominated by pioneer taxa (García Massini et al., 2010), so even if fern spores are dominant among these assemblages only in a few cases, their abundance in these horizons, especially the *Blechnum*/*Cyclosorus*-type and the *Acrostichum*-type, support similar ecological and environmental characteristics at least locally. The increase in the relative percentage of spores of *Equisetum*, in a number of horizons stratigraphically below where stems of this sphenopsid have been found previously (CH-79, units 14–15, CH-93, unit 8), and *Cicatricosisporites*, a taxon associated with extant arid-adapted ferns (*Mohria* sp.) (Salard-Cheboldaeff, 1981; Tryon and Lugardon, 1991), at a horizon stratigraphically continuous with *Marsilea* leaflets (CH-93, unit 22, CH-89, unit 23), is also consistent with the interpretation from macrofossils indicating local ponded settings of ephemeral nature in rather seasonally dry environments (Figs. 4–6) (García Massini et al., 2010).

Angiosperm pollen in Zone 3 includes a diversity of taxa (most of them also present in pre-Ash-IV strata). The most abundant of these is *Potamogeton*, a common inhabitant of freshwater settings, sedges, which usually occur in moist soils along rivers and ponds in open and poorly-drained environments, grasses, which are usually common in aquatic or open areas, and the morphogenus *Rhoipites*, a morphotaxon of unknown affinity that is not well understood ecologically (Burger, 1967; Kolstad, 1986; Larson and Barker, 1986; Sutherland, 1986; de Villiers and Cadman, 1997). *Rhoipites* is the single most abundant taxon in some units (e.g., CH-93, unit 8) and accounts for the largest number of pollen present in the entire volcaniclastic sequence. The relative percentage of *Rhoipites* increases towards the tops of short successions of increasingly organic-rich strata (F to E and F to G Depositional Units) along with *Potamogeton*, sometimes one or so units stratigraphically above grasses, and sedges, which both decrease (Fig. 4–6). These sedimentary sequences were interpreted as evidence of cycles of ponding and drying (García Massini et al., 2010). Inverse patterns of abundance between herbs on the one hand, and *Rhoipites* and *Potamogeton* on the other, are particularly evident around the base and top of palynomorph Zone 3, whereas intervening strata show a variety of relative percentages of pollen and spore types (Figs. 4–6).

The relative percentage peaks of herbaceous taxa (grasses and sedges) coincide with peaks of fern spores (*Acrostichum* and *Blechnum*/*Cyclosorus*) in some horizons (Depositional Unit F, CH-79, unit 12), suggesting open areas characterized by a high water table (Figs. 4–6). However, the inverse is observed in other units (Depositional Unit G), where the relative abundance of *Acrostichum* and *Blechnum*/*Cyclosorus* spores increases along with *Potamogeton* and *Rhoipites*, whereas grasses and sedges decline (Figs. 4–6). Moreover, the abundance of these ferns also peaks in other lignites showing an overall decrease in pollen (CH-89, unit 13, CH-93, units 7–9) (Figs. 4–6).

These observations suggest that, regardless of the particular association, ferns show a preference for ponded or waterlogged soils. The poor representation of arboreal angiosperms in most strata of palynomorph Zone 3 suggests that they primarily occurred in relatively small patches or were located away from the immediate depositional area on better drained substrates (Figs. 4–6). In addition, forest taxa may have been predominantly entomophilous or otherwise animal-pollinated, thus characterized by relatively low pollen productivities (Traverse, 2007). Herbaceous macrofossils are present throughout the volcaniclastic sequence, but are most abundant in association with fern macrofossils, implying short-lived, poorly-drained, settings in rather open environments depleted in arboreal taxa, likely created by ashfall on the landscape (Fig. 2) (García Massini et al., 2010).

Of the other pollen taxa present in some of these Zone 3 assemblages, *Alchornea*, Sapotaceae-type, *Bombax*-type, *Iodes*, *Albizia*, and *Brachystegia* show similar low relative abundances. These plant taxa may be interpreted as having been present, occasionally, in swampy or ponded areas locally in parts of the landscape with a high water table or in forest patches remaining regionally. *Iodes*, which is a climbing vine that prefers moist settings, probably lived in close contact with *Alchornea* and Sapotaceae in secondary forests. *Brachystegia* and *Albizia* are only represented by a few pollen grains whose relative percentages more or less mirrors that of *Rhoipites,* and probably also indicate patches of forest characterized by distally better drained substrates. (Figs. 4–6) (Burger, 1967; Yemane et al., 1987a,b; Hawthorne and Jongkind, 2006). Pollen assemblages indicating swamp/waterlogged conditions are associated with relatively low numbers of tree pollen taxa and are most common in the organic-rich parts of the sequence. This is consistent with paleoenvironmental characteristics inferred from macrofossils, where, for example, *Pandanus*, *Alstonia*, and *Typha* from the upper part of Zone 3 were also interpreted as indicators of swampy settings with a few larger trees (García Massini et al., 2010).

5.4. Zone 4

Sedimentary deposition in palynomorph Zone 4 shows instantaneous burial of lignitic and other organic-rich strata by a succession of airfall and fluvially-reworked ash layers (Depositional Units B, C, D) that are palynologically productive (at least 300 individuals/palynomorph assemblage) in only two of sixteen units (Fig. 3). These two assemblages, which were deposited in overbank and chute-like channel environments (Depositional Units B and D) (García Massini et al., 2010), are largely dominated by fungal remains that would be most resistant to decay. Most of the fungi (~90% of all individuals) are *Inapertisporites* and *Hypoxylonites* spores, and fewer *Brachysporisporites* spores, *Fractisporonites* conidiophore and hyphae fragments, and *Pluricellaesporites* filiform spores (Figs. 4–6). *Hypoxylonites* (=*Hypoxylon*), *Brachysporisporites* (=*Brachysporium*), and *Pluricellaesporites* (=*Xylomyces*) morphotaxa are most similar to extant genera that include mainly saprotrophs and less commonly plant pathogens ubiquitous on decaying soil organic debris and in freshwater settings (Bandoni, 1981; Webster and Descals, 1981; Marvanová, 1997; Barnett and Hunter, 1998; Webster and Weber, 2007). *Inapertisporites* and *Fractisporonites* are less easily associated with any specific extant taxon and may represent a variety of taxa from diverse environments. Pollen and fern spores are poorly represented and only important in the lowermost ash layers of this Zone (Fig. 3) (C Depositional Unit), where a moderately low concentration allowed a count of <300 palynomorphs. Included among the angiosperms present in this and the two more productive assemblages are a few *Alchornea*, sedge, grass, *Bombax*-type, *Rhoipites*, and *Potamogeton* pollen grains in similar relative percentages, whereas ferns do not include any recognizable taxa except for some Blechnaceae/Thelypteridaceae-type spores in lower relative percentages than pollen (Figs. 4–6). The poor representation of palynomorphs within these ash layers and the combination of individuals present in the productive assemblages suggests the strong influence of taphonomic factors favoring accumulation of more resistant types.

Despite the general absence of palynomorphs in this zone, the types present suggest that taxa adapted to freshwater and waterlogged settings were able to proliferate during longer depositional periods (overbank deposits) and/or in more distal parts of the landscape (channel deposits). In particular, the presence of *Alchornea* and *Bombax*-type pollen implies that some forested areas remained in the region, but were probably not very extensive, as suggested by the absence of epiphyllous fungal taxa (Microthyriaceae-type and *Meliola*) (Figs. 4–6). The presence of *Rhoipites* in the stratigraphically middle part of the sections was interpreted before as indicating secondary vegetation growth on increasingly organic-rich substrates. Its presence in palynomorph Zone 4 is consistent with recurrent ashfall on the landscape interrupting normal development of plant communities. The presence of open and probably also water-logged environments is supported by the presence of Poaceae, Cyperaceae and Potamogetonaceae pollen and a few *Blechnum*/*Acrostichum* fern spores (Figs. 4–6). This agrees with macrofossil and sedimentological data, which indicate low-diversity plant communities inhabiting rather open, ash-covered landscapes (García Massini et al., 2010). However, the almost complete absence of palynomorphs from the ashier stratigraphic units representing either airfall or slightly fluvially reworked ashes is not necessarily an indication of regional mass killing of standing vegetation. More likely, it is a consequence of rapid ash deposition. The recovery of a greater concentration of fungal propagules and the presence of a number of tree forest taxa in some of the more time-averaged strata (e.g., chute-like stream and overbank facies) suggests that the effects of volcanism were localized and, even if extensive, not so uniform as to completely destroy plant communities regionally (Figs. 2–6).

6. Discussion and conclusions

This paper tested the hypothesis, developed from previous work on plant macrofossils and sedimentology, that repeated Late Oligocene volcanism over a broad region in the Chilga area had a fundamental effect on plant communities, including regional elimination of forest community structure. Palynological studies of the same volcaniclastic sediments, which sample more regionally than macrofossils (Taggart and Cross, 1990; Spicer, 1991; Traverse, 2007), are inconsistent with this hypothesis because pollen from forest taxa are present both before and after major ash sequence deposition. In addition, the palynomorph assemblages appear to reflect taphonomic processes associated with deposition and preservation that vary nearly independently of temporal and spatial changes in local plant community structure. Our results show that previous knowledge of plant macrofossils and sedimentary context provides critical information allowing one to separate the contributions of organisms from those of depositional and preservational factors to the final composition of palynomorph assemblages.

Local structural and compositional changes in plant communities resulted from hydrological and substrate change associated with ash input, which created heterogeneous ecosystems on short temporal and spatial scales (Fig. 7). The volcaniclastic sequence documents a combination of forest trees, herb taxa (including ferns), and fungi representing a progression from pre-ash tree-dominated to open herb-dominated environments locally with patches of forest remaining regionally. Volcanism did not alter plant communities so drastically as to eliminate forests from the regional landscape, as previously suggested by macrofossils, thus documenting a degree of resilience in the forest ecosystem and likelihood that individual ashfalls were relatively shallow in some areas (del Moral and Grishin, 1999). Precise compositional and diversity changes in regional forest communities in response to repeated ashfalls and successional recovery cannot be documented by this study, but modern analogue studies demonstrate a process dependent upon differential survival of species, plant ecological relationships, species composition of source areas, and stochasticity (del Moral and Grishin, 1999).

In summary, this study shows that a variety of communities coexisted in heterogeneous environments created as a result of

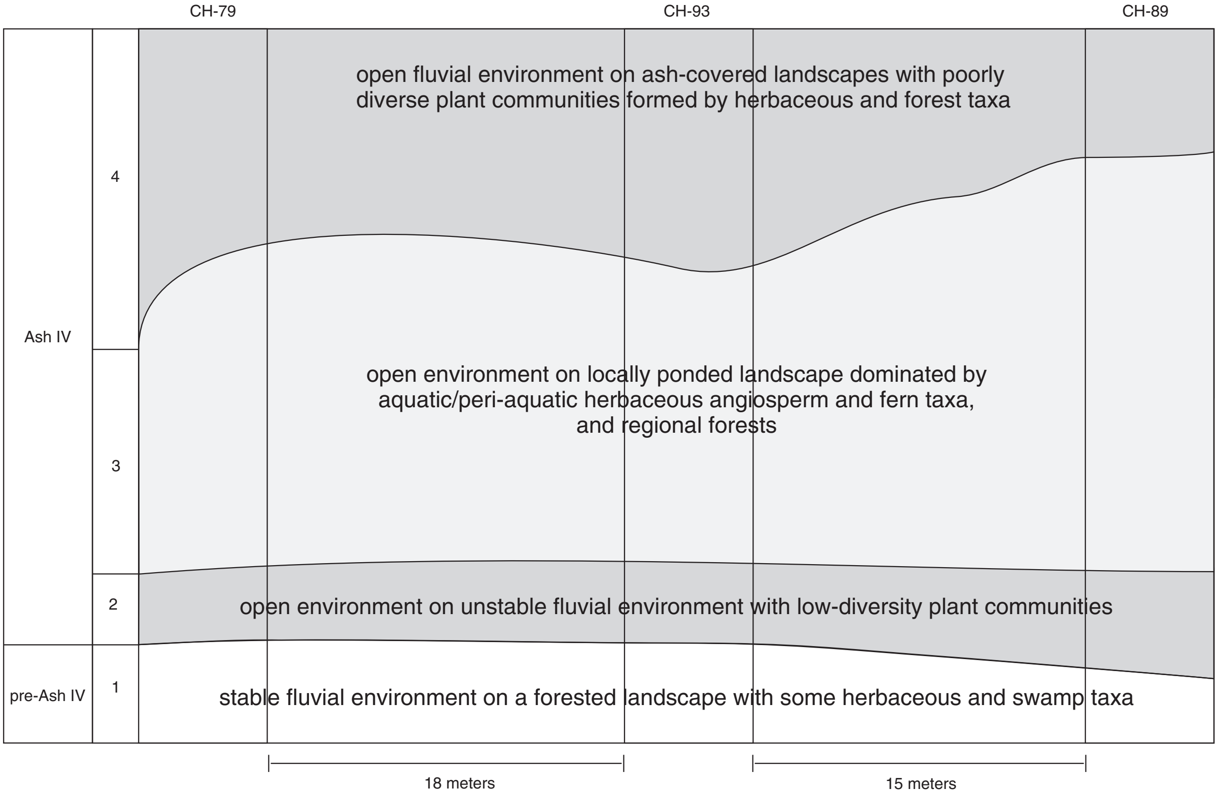


Fig. 7. Chart showing an interpretation of paleoenvironmental changes through time (palynomorph zones 1 to 4) based on palynology, macrofossils and sedimentology combined.

volcanism associated with formation of the northwestern Ethiopian Plateau and associated rifting during the Paleogene. Analysis of the whole flora from the Ethiopian tuffs provides a unique record of ecological dynamics at both local and regional scales that has relevance to the evolution of the East African Rift itself, and the associated impacts on ecosystems by repeated ash deposition and consequent hydrological (water table and stream course) changes.

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