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How to cite

NEUMANN, Katharina et al. The Early Holocene palaeoenvironment of Ounjougou (Mali) : Phytoliths in a multiproxy context. In: Palaeogeography, palaeoclimatology, palaeoecology, 2009, vol. 276, n° 1-4, p. 87–106. doi: 10.1016/j.palaeo.2009.03.001

This publication URL: <https://archive-ouverte.unige.ch/unige:14409>

Publication DOI: [10.1016/j.palaeo.2009.03.001](https://doi.org/10.1016/j.palaeo.2009.03.001)



Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

The Early Holocene palaeoenvironment of Ounjougou (Mali): Phytoliths in a multiproxy context

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ARTICLE INFO

Article history:

Received 17 October 2008

Received in revised form 25 February 2009

Accepted 1 March 2009

Available online xxx

Keywords:

Phytoliths

Pollen

Charcoal

Palynofacies

Micromorphology

Pottery

Early Holocene

Grassland

West African Sahel

ABSTRACT

The site complex Ounjougou on the Dogon Plateau (Mali) comprises sediments up to 100,000 years old with numerous Pleistocene and Holocene sequences. The site Ravin de la Mouche (11.4–10.2 ka) is of special archaeological significance because in its Early Holocene deposits, pottery sherds have been found which are among the oldest in Africa. For a better understanding of the environmental conditions which might have contributed to the innovation of pottery making, a multi-proxy approach was applied to the sediments of Ravin de la Mouche, including phytoliths, pollen, palynofacies, micromorphology and charcoal. The multi-proxy approach also allows reconstructing the complex taphonomy of the site.

In our phytolith study, we applied a combination of the general and the indices approaches. We recorded a maximum of morphotypes and used the summarized data for a calculation of the indices D:P, Ic, and Iph, in comparison with modern surface samples and data from other African phytolith studies. With the general approach, a number of morphotypes could be detected which are useful in describing the Late Pleistocene and the Early Holocene vegetation.

Phytoliths were extracted from the Pleistocene base and the early Holocene layers HA1, HA2 and HA3. The Pleistocene sediment samples, with an age of ca. 30–40 ka BP, have no grass short cell phytoliths (GSCP) and their composition is difficult to interpret. HA1 is a coarse fluvial deposit with mainly redeposited phytoliths of Pleistocene origin. The palaeosol in HA2 contains phytolith assemblages developed *in situ* from a terrestrial plant cover. The vegetation was an open tropical grassland and a gallery forest with palms and Marantaceae. Annuals from the grass subfamilies Chloridoideae and Panicoideae, probably with a low biomass production, dominated the grassland. This might explain the insignificant role of fire, as indicated by the very low number of micro-charcoals. HA3 results from a rhythmic deposition of alluvial sediments, pointing to pronounced seasonality of rainfall and discharge. It contains pollen, charcoal, and phytolith assemblages with a similar composition as in HA2.

The Early Holocene annual grassland on the Dogon Plateau probably harboured a high number of species from the grass subfamily Panicoideae with edible grains. We suggest that the massive expansion of useful Panicoid grasses during the Early Holocene triggered the development of important cultural innovations, mainly pottery production. Cooking wild cereal grains in a ceramic container would have enabled a very effective exploitation of the vast Sahelo–Sudanian grasslands, which remained to be successful until modern times.

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1. Introduction

During the Upper Pleistocene and Early Holocene distinct environmental changes occurred in West Africa which are visible in marine cores off the West African coast (Dupont and Weinelt, 1996; Jahns, 1996; DeMenocal et al., 2000; Lézine et al., 2005) and in terrestrial pollen profiles (Maley, 1981, 1991; Lézine, 1989; Lézine and

Casanova, 1989; Salzmann and Waller, 1998; Salzmann et al., 2002; Waller et al., 2007). After the hyperarid Late Pleistocene, lake levels had already been rising as soon as 14.5 ka, indicating higher precipitation (Gasse, 2000; Shanahann et al., 2006), but a clear response of the vegetation is not documented in the terrestrial records before 11.5 ka, after the end of the Younger Dryas. Poaceae, indicating grassland, dominate the Early Holocene pollen records of the Sahel, where tropical trees only start to expand after 8.7 ka (Salzmann and Waller, 1998; Waller et al., 2007). In the only pollen diagram of the Sudanian zone (Lake Tilla/Nigeria), percentages of tropical trees

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increase directly after the end of the Pleistocene after 11.0 ka, but grasses remain dominant throughout the Holocene (Salzmann et al., 2002). It can be assumed that contemporary with the changes in the woody vegetation, the composition of the grass cover also distinctly changed during the Holocene, but it remained unknown due to the difficulties of identifying grass pollen below family level.

Phytolith analysis is a valuable tool for the study of palaeo-grasslands. Phytoliths, amorphous silicon dioxide particles, are produced in all species of the grass family (Poaceae) and in many other plant families. Their durability in soils and sediments is an advantage where other organic remains like pollen and charcoal have not been preserved. Grass short cell phytoliths (GSCP) allow identification below family level and therefore a much more detailed reconstruction of grasslands. Grassland phytolith analysis has been successfully applied in the Great Plains of North America (e.g. Fredlund and Tieszen, 1994, 1997; Kurmann, 1985), and recent studies have shown the promising potential of phytolith analysis for Africa, a continent which is largely covered by grasslands and savannas (Alexandre et al., 1997; Mworira-Maitima, 1997; Barboni et al., 1999, 2007; Scott, 2002; Bremond et al., 2005a,b, 2008). Although Early Holocene archaeological sites are still sparse in West Africa, it is reasonable to assume that the dramatic environmental change after the end of the hyperarid Pleistocene had a profound impact on humans and their behaviour. Therefore, a better knowledge of the grasslands and savannas inhabited by Early Holocene populations is a key for the understanding of cultural development.

The site complex of Ounjougou (Fig. 1) comprises a series of gullies cut into a succession of Quaternary aeolian, alluvial and colluvial deposits (Rasse et al., 2006; Lespez et al., 2008). Situated on the Dogon Plateau about 10 km east of the city of Bandiagara, the complex includes numerous archaeological sites within a zone of 10 km² on the sloping valley of the Yamé, a tributary of the Niger. The 16 m thick stratigraphic sequence has yielded archaeological material from the lower Palaeolithic to modern times (Huysecom, 2002). For the reconstruction of

West African palaeoenvironments, Ounjougou is unique because of its exceptionally rich and well preserved Holocene plant remains which have been mainly deposited during phases of stillwater accumulation (Rasse et al., 2006; Eichhorn and Neumann, in press). Five principal Holocene occupation phases can be distinguished, based on chronostratigraphic, archaeological and palaeoenvironmental data (Huysecom et al., 2004; Rasse et al., 2004). The site Ravin de la Mouche (14°24'41"N, 3°31'32"W) is a key site for the Early Holocene phase I in the 12th and 11th millennium cal BP. In its lower unit HA1, a techno-typological complex with pottery and small bifacial armatures has been found, reflecting important innovations at the beginning of the Holocene. The ceramic sherds of Ravin de la Mouche are among the oldest of the African continent (Huysecom et al., in press).

For an assessment of the environmental conditions which might have contributed to the innovation of pottery making, we applied a multi-proxy approach to the sediments of Ravin de la Mouche. We present here the results from phytolith, pollen, palynofacies and charcoal analyses, combined with the microstratigraphy of the site. This paper focuses on phytoliths, as they yield the principle information about the Early Holocene vegetation and were preserved in almost all layers of the profile. Phytolith research is still developing in Africa, and the methodology is not yet standardized. It is therefore first necessary to explain the general principles we applied in our study.

2. Indices vs. general approach

There are two basic approaches of palaeoenvironmental phytolith studies in Africa: the indices (or specific) and the general approach, as defined by Strömberg (2002, 2004). The indices approach uses a narrow size fraction (usually < 60 µm) and a limited number of well-defined morphotypes (8–13, depending on the study) for the calculation of four indices to describe the vegetation types of Africa in correlation with climatic parameters, such as temperature and

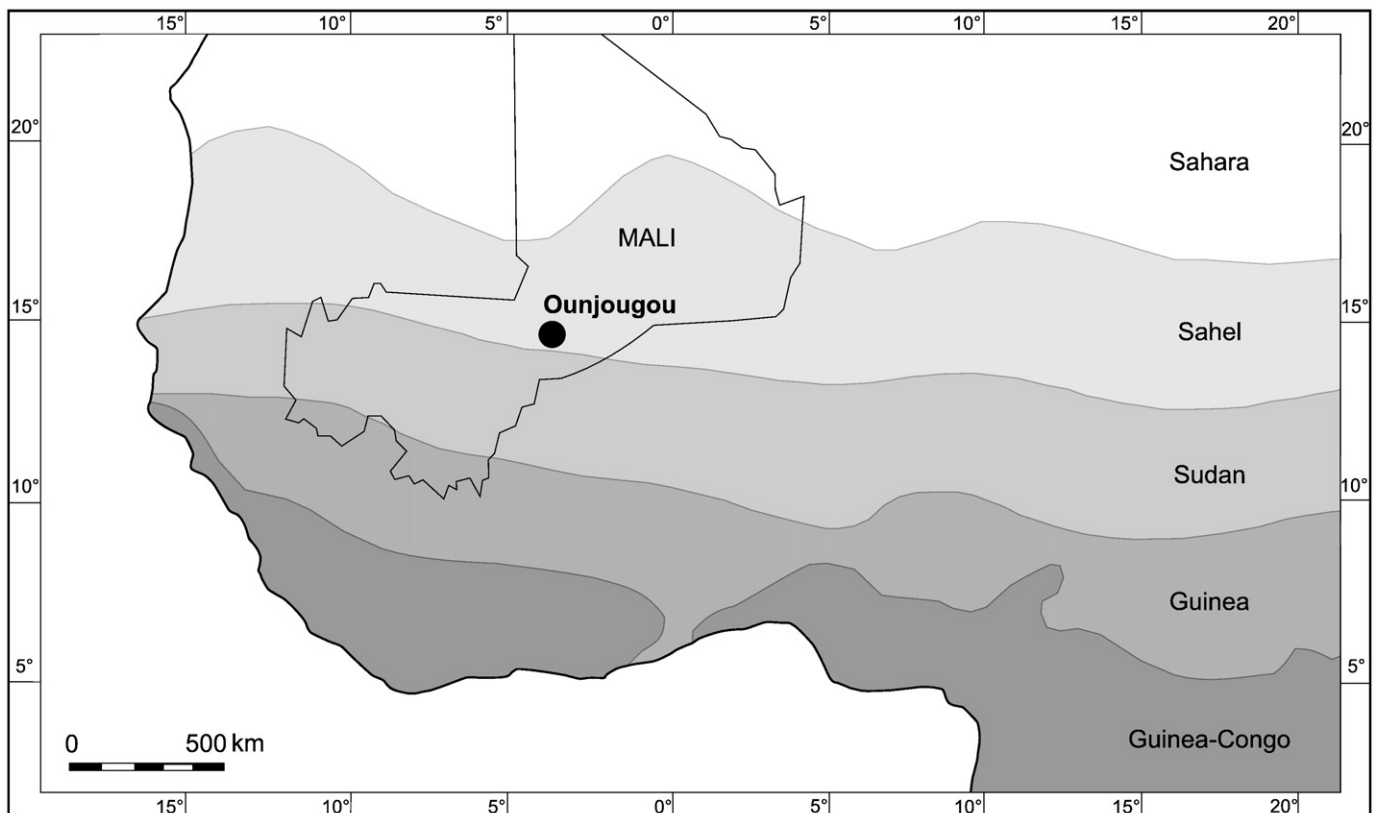


Fig. 1. Map of West Africa with vegetation zones (after White, 1983) and the site complex Ounjougou.

degree of aridity (Alexandre et al., 1997; Barboni et al., 1999, 2007; Bremond et al., 2005a,b, 2008; Alexandre and Bremond, 2009; Strömberg, 2009a,b). The general approach (Strömberg, 2004) considers all morphotypes and size fractions, and is represented in Africa mainly by the work of Runge (1996, 1999, 2000a,b, 2001), Mercader et al. (2000), Vrydaghs and Doutrelepon (2000), Albert et al. (2006, 2009), and Bamford et al. (2006).

Three indices work with different ratios of morphotypes exclusively deriving from Poaceae. They are valuable tools for tracing changes in grasslands and savannas, the dominant formations among African vegetation types. The Ic index (Twiss, 1992) describes the relative proportions of C3 grasses versus C4 grasses mainly in correlation with temperatures. In Africa, the Ic increases with elevation and reflects the increasing dominance of the C3 grass subfamily Pooideae at higher altitudes (Bremond et al., 2008). The Iph index, first proposed by Diester-Haas et al. (1973), is a proxy for the ratio of Chloridoideae versus Panicoideae and indicates the dominance of short-grass or long-grass savannas along an aridity–humidity gradient (Bremond et al., 2005b). The Fs index is defined as the percentage of fan-shaped bulliforms versus the sum of grass phytoliths minus elongates and serves as an indicator for water stress (Bremond et al., 2005b).

The indices developed in Africa work under the premise, originally formulated by Twiss et al. (1969) and Twiss (1992), that certain short cell morphotypes characterize grass subfamilies: trapezoids and rondels are commonly associated with the Pooideae, saddles with the Chloridoideae, and bilobates/crosses with the Panicoideae. Comparative studies on North American (e.g. Brown, 1984; Mulholland, 1989; Fredlund and Tieszen, 1994) and South American grasses (e.g. Gallego and Distel, 2004; Fernandez Honaine et al., 2006; Piperno and Pearsall, 1998), as well as the seminal works of Metcalfe (1960) and Watson and Dallwitz (1994 onwards) have generally confirmed the Twiss classification, but also demonstrated that numerous genera have deviating patterns of short cell phytoliths. However, the indices approach does not refer to single phytoliths diagnostic for species or genera, but to phytolith assemblages (Fredlund and Tieszen, 1994). Several African studies have demonstrated that the relative abundance of saddles, bilobates, crosses and rondels characterizes different grassland types, correlated with the relative phytolith productivity of the grass subfamilies.

The index D:P (Dicotyledons:Poaceae), first proposed by Alexandre et al. (1997), describes tree cover densities and is the ratio of the globular granulate morphotype, produced in tropical woody dicotyledons, versus morphotypes typical for grasses. In Africa, evergreen rainforest and semi-deciduous forest-savanna mosaics can be successfully separated from grassland and savannas with the D:P (Barboni et al., 2007). The applicability of the D:P is still in its testing phase, and its calculation formula has been modified over time. Alexandre et al. (1997) included short cells, trichomes, long cells, and fan-shaped bulliforms in the Poaceae group, while Barboni et al. (1999, 2007) and Bremond et al. (2005a,b) excluded long cells for being non-diagnostic. Trichomes, long cells and bulliform cells have all been excluded from the latest D:P calculations (Bremond et al., 2008), as their abundance may be environmentally controlled, and only the grass short cell phytoliths (GSCP) are considered as valuable indicator for grasses. In her study on the Tertiary grasslands in the Great Plains of North America, Strömberg (2002) added the elongate faceted morphotype to the diagnostic woody dicotyledon group. If the D:P is to be used in a new study and compared with published data, it should be guaranteed that the calculation basis is equivalent.

The overall validity of the D:P for indicating tree cover densities has been questioned by Strömberg (2002, 2004). Strömberg (2004) follows a general approach including analysis of all size fractions, the use of an expanded reference collection, and the definition of indicator morphotypes for woody plants and closed shady vegetation. Comparative evaluation of the palaeo-data from North America has shown that the indices and the general approach, applied on the same

samples, produce markedly different interpretations concerning the openness of habitats. In many cases, the indices approach suggests the presence of grasslands, whereas the general approach indicates relatively closed habitats, typified by the presence of bambusoid grasses, woody and herbaceous dicotyledons, and palms. It seems that in temperate environments, the D:P does not accurately reflect the woody plant cover, because the globular granulate morphotype is only produced by certain plant families mainly distributed in lowland tropical forests. In East African montane forests, the D:P also underestimates the tree cover (Barboni et al., 2007; Bremond et al., 2008).

For a more precise reconstruction of the palaeo-vegetation and its land-use potential, the use of the indices is limited. With the general approach additional morphotypes can be detected which allow for a better understanding of the different vegetation types in a small-scale regional context. The general approach also includes the three-dimensional observation of grass short cell phytoliths which has been successfully applied for several regional grass floras, but not yet in Africa (e.g. Piperno and Pearsall, 1998; for an overview see Piperno, 1988, 2006 and the references therein). Rotation in a liquid medium and three-dimensional observation of short cell phytoliths out of their cellular context reveals a wide variation of forms which can be diagnostically exploited. In combination with the revised taxonomy and phylogeny of the grass family (GPWG, 2001), a finer characterization of the subfamilies in terms of their short cell assemblages seems now possible (Piperno, 2006, pp. 27–34).

For grassland reconstruction in Africa, three aspects are especially important: 1. 3D morphology allows a finer sub-division of bilobates typical for certain sub-families. Characteristic bilobate types for the Bambusoideae, Ehrhartioideae (including *Oryza*, rice), Panicoideae, Chloridoideae and Aristidoideae can be distinguished. 2. The Bambusoid sub-family, in Africa only represented by three species, is now well separated from other basal Poaceae families and produces distinct irregularly shaped short cell phytoliths (Piperno and Pearsall, 1998). 3. The subfamily Arundinoideae, formerly a complex of taxonomically disperse genera and including the genus *Aristida*, has been revised and more strictly defined. The Aristoideae, now recognized as a separate subfamily, have a special type of bilobate with long shafts and rounded end lobes. The characteristic bilobates have been mainly studied in the subfamilies of New World grasses and remain to be confirmed for the African grass floras. As a working hypothesis, we assume that the types described by Piperno (2006) are also distinctive in the African Poaceae.

For the purpose of this study, we decided to apply a twofold approach. We recorded a maximum of phytolith morphotypes, including the 3D GSCP identified after the classification of Piperno (2006). We also studied three modern surface samples and a modern phytolith reference collection of West African species for comparison. From the results of the general approach, we extracted and summarized the data necessary for calculation of the indices D:P, Iph, and Ic. For a comparison with other phytolith data from Africa, we have used the D:P formula of Bremond et al. (2008), i.e. the ratio of the globular granulate morphotype versus GSCP. The published data for comparison were re-calculated accordingly. In the calculation of the D:P from our own data, D is the sum of globular decorated phytoliths (including nodular) minus the echinate type.

3. Classification

Our classification and description of the phytolith morphotypes is presented in Table 1 and Figs. 2 and 3. For the assignment of the morphotypes to the taxonomic groups we used the available literature (Brown, 1984; Ollendorf et al., 1988; Piperno 1988, 2006; Runge, 1996, 1999, 2001; Kondo et al., 1994, Kealhofer and Piperno, 1998; Piperno and Pearsall, 1998; Barboni et al., 1999; Mercader et al., 2000; Blinnikov et al., 2002; Strömberg, 2004; Zucol et al., 2005; Albert et al., 2006) and a reference collection of phytoliths from modern West

Table 1
Morphotype classes used in this study.

Major plant group	Class no.	Name	Fig. no	Morphotype description	Size (µm)	Observed in	n	References
Woody dicotyledons	A1	Elongate faceted	2a	Elongate straight to slightly curved with large facets	35–175	Sclereids, terminal tracheids or silicified intercellular spaces in L of woody dicotyledons	10	Postek, 1981; Runge, 1999 (A4); Mercader et al., 2000; Piperno, 2006 (Fig. 2,6); Strömberg, 2004 (D2)
	A2	Polyhedral faceted	2b	Irregular shapes, surface with large facets	25–90	Sclerenchyma in L of woody dicotyledons	33	Runge, 1999 (C2, C3); Kondo et al., 1994 (Pl. 19a–c); Kealhofer and Piperno, 1998 (figs. 28, 29, 39); Mercader et al., 2000; Strömberg, 2004 (D2)
	A3	Globular decorated	2c–f	Spherical to irregular ellipsoid with various surface decorations: verrucate (wart-like projections), columellate (straight-sides pillar-like projections), tuberculate (smooth rounded projections), granulate (grainy surface), nodular	10–50	L, W of certain woody dicotyledons (L of certain grasses)	54	Piperno, 1988, 2006; Barboni et al., 1999; Runge, 1999 (B2); Bowdery et al., 2001; Strömberg, 2004 (D1); Madella et al., 2005
	A4	Tracheary element	2g	Irregular cylindrical to ellipsoid, densely covered with pilate to dendriform projections	30–70	Pitted tracheids in L of certain dicotyledons, perhaps specific	8	Kondo et al., 1994 (Pl. 20); Piperno, 2006 (Fig. 2,7)
	A5	Thin branched sclereids	2h	Curved and branched fragments of mesophyll intercellular spaces, with distinct concave facets	35–120	L of woody (and herbal?) dicotyledons, observed in L of <i>Syzygium</i>	10	
Ferns, woody or herbaceous dicotyledons	B1	Globular psilate		Globular to subglobular, surface psilate	13–60	L, W of certain dicotyledons, monocotyledons, gymnosperms and ferns	14	Kondo et al., 1994 (Pl. 10); Runge, 1999 (B1/B7); Strömberg, 2004 (E7); Madella et al., 2005
	B2	Globular faceted small	2i	Globular with small facets	13–21	Unknown, resembles some New World Cucurbitaceae, but smaller in size	12	Bowdery et al., 2001; Madella et al., 2005; Piperno, 2006 (Fig. 3,6)
	B3	Blocky polyhedron	2j	Polyhedral or plate-like bodies with large facets, may be related to A2	35–110	L, W of certain conifers and woody dicotyledons	20	Blinnikov et al., 2002 (Fig. 1,16); Strömberg, 2004 (E4)
Family-/genus-specific	C1	Cyperaceae (sedge) type	2k	Tabular, pentagonal or hexagonal, surface psilate or favose, with a central rounded cone	15–35	L of Cyperaceae	7	Ollendorf, 1992; Runge, 1999 (G7/D5); Albert et al., 2006; Piperno, 2006 (Fig. 2,16a); Barboni et al., 2007
	C2	Globular echinate, Arecaceae (palms)	2l	Globular to subglobular with conical spines	8–30	L, W, R of Arecaceae	13	Piperno, 1988, 2006 (Fig. 2,8); Barboni et al., 1999, 2007; Runge, 1999 (B3); Mercader et al., 2000; Strömberg, 2004; Albert et al., 2006
	C3	Marantaceae	2m	Hexagonal to rectangular in side view, lower part with a finely echinate surface, upper part a truncated cone with psilate surface	13–21	F/S of certain Marantaceae	17	Piperno, 1988, 2006 (Fig. 2,16); Runge, 1999 (D3); Mercader et al., 2000
	C4	Annonaceae/Cucurbitaceae type	2n	Globular to subglobular with large facets	25–35	L/F of Annonaceae, Cucurbitaceae, Burseraceae	9	Runge, 1996, 1999 (B4); Piperno, 1988, 2006; Mercader et al., 2000
	C5	<i>Hibiscus</i> type	2p	Tabular with one slightly convex side, upper and lower surface psilate, convex side surface decorated, probably verrucate	14–30	L of <i>Hibiscus</i> , perhaps specific	6	Runge, 1996
	C6	Podostemataceae	2o	Flat, multilobed with columellate to pilate projections	20–30	Highly diagnostic for the family, origin in specific tissue unknown	3	Piperno, 2006 (Fig. 2,15a)
D Grass short cell phytoliths (GSCP)	D1	a) Aristoid	3a	Long shanks (> 10 µm) and rounded/convex, non-sculptured end lobes	24–38	L, I of Aristidoideae	6	Mulholland, 1989; Piperno & Pearsall, 1998; Gallego and Distel, 2004; Piperno, 2006
		b) Panicoid	3b	Mostly with straight end lobes that may have indentations or sculpturing, shafts pronounced, but usually shorter (< 10 µm) than in the Aristoid type	14–23	L, I of Panicoideae	5	Mulholland, 1989; Fredlund and Tieszen, 1994; Piperno, 2006; Fahmy, 2008

	c) Chloroid	3c	With flared, convex edges, resemble saddles in overall outline	10–17	L, I of Chloridoideae	5	Mulholland, 1989; Piperno, 2006
	d) Ehrhartioid	3d	Lobes distinctly scooped, top plateau-like with scooped ends	26	L of Ehrhartioideae	1	Piperno, 2006
	e) Stipa-type	3e	Lower part with rounded lobes and reduced shank, top smaller, plateau-like or bilobate, without ridges or other secondary facets	14–23	L, I of Stipa (Pooideae) and Andropogoneae (Panicoideae)	6	Mulholland, 1989; Fredlund and Tieszen, 1994; Piperno, 2006
	f) undiff.		Bilobates that cannot be classified into any of the above categories, often in side view	10–24	Attributed to Panicoideae in this study	3	
	D2	Trilobate	With three lobes in linear arrangement	23–38	L, I of Panicoideae	4	Piperno and Pearsall, 1998; Madella et al., 2005; Piperno, 2006; Fahmy, 2008
	D3	Cross, a) Panicoid	3f, g Top mirror-image (var.1), or sloping plateau/with raised corners (var. 5/6)	13–20	L, I of Panicoideae	8	Piperno, 1984, 2006
		b) undiff.	Crosses that cannot be clearly classified into a specific variant, often in side view	13–21	Attributed to Panicoideae in this study	8	
	D4	Rondel	3m, n Base rounded, top conical or keeled with pointed ends	6–15	Commonly produced by Pooideae, but also in I of other grass subfamilies	10	Mulholland, 1989; Fredlund and Tieszen, 1994; Piperno and Pearsall, 1998; Piperno, 2006
	D5	Saddle a) squat	3h Saddle-like, long axis parallel to convex sides, or the two axes of equal dimensions	10–15	L, I of Chloridoideae	15	Piperno and Pearsall, 1998; Piperno, 2006
		b) tall	3i Saddle-like, long axis parallel to concave sides	10–22	L, I of Chloridoideae	20	Piperno and Pearsall, 1998; Piperno, 2006
		c) plateaued	3j, k, l Base saddle-like, top smaller, distinctly saddle-like with raised convex edges or flat plateau	12–20	Resemble "saddle-topped short trapezoids" described from Phragmites; maybe a special form from Chloridoideae	10	Ollendorf et al., 1988; Piperno and Pearsall, 1998; Piperno, 2006
		e) undiff.	Saddles that cannot be classified into the above categories, often in side view	8–30	Attributed to Chloridoideae in this study	17	
	D7	Trapeziform sinuate	3o Trapeziform, base with wavy edges, top a rectangular, psilate plateau	40	Typically in L of Pooideae, rarely in Chloridoideae and Panicoideae	1	Mulholland, 1989; Piperno, 2006;
E Poaceae, non-diagnostic	E1	Cuneiform bulliform	Fan-shaped bulliform cells	30–75	L of grasses	22	Barboni et al., 2007; Kondo et al., 1994 (Pl. 9); Barboni et al., 1999, 2007; Mercader et al., 2000; Madella et al., 2005; Strömberg, 2004
F Non-diagnostic	F1	Parallelepipedal bulliform	Parallelepipedal bulliform cells	20–50	L of Poaceae, also attributed to bark of woody dicots (Albert et al., 2006)	23	Kondo et al., 1994 (Pl. 9); Runge, 1999 (G2); Gallego and Distel, 2004; Fernandez Honaine et al., 2006; Albert et al., 2006
	F2	Elongate psilate/ echinate	Elongate rectangular plates with smooth, sinuous or echinate edges	20–170	L of monocots, certain conifers, ferns	37	Piperno, 1988; Kondo et al., 1994; Barboni et al., 1999, 2007; Strömberg, 2004
	F3	Point-shaped/ trichomes	Spindle and triangular bodies	13–160	L, R of grasses, sedges and other taxa	21	Barboni et al., 1999, 2007; Runge, 1999
	F4	Cylindric	Elongate, circular in cross-section	140	L of dicots and monocots	1	Runge, 1999 (A1); Madella et al., 2005
	F5	Elongate parallelepipedal	Parallelepipedal, straight, with edges along the body	40–110	Grasses and non-grasses	11	Runge, 1999 (A3); Mercader et al., 2000; Madella et al., 2005
	F6	Elongate, tapering ends	Elongate, straight, slightly faceted, with tapering ends	40–140	Grasses	23	Runge, 1999 (A5)
	F7	Vessels/tracheids	Cylindric, with spiral thickenings or pitted, often with oblique ends	25–175	Tracheary elements of mainly non-grass plants	21	Runge, 1999 (A2); Strömberg, 2004 (E5)

F = fruits; I = inflorescence; L = leaves; R = roots; S = seeds; W = wood.

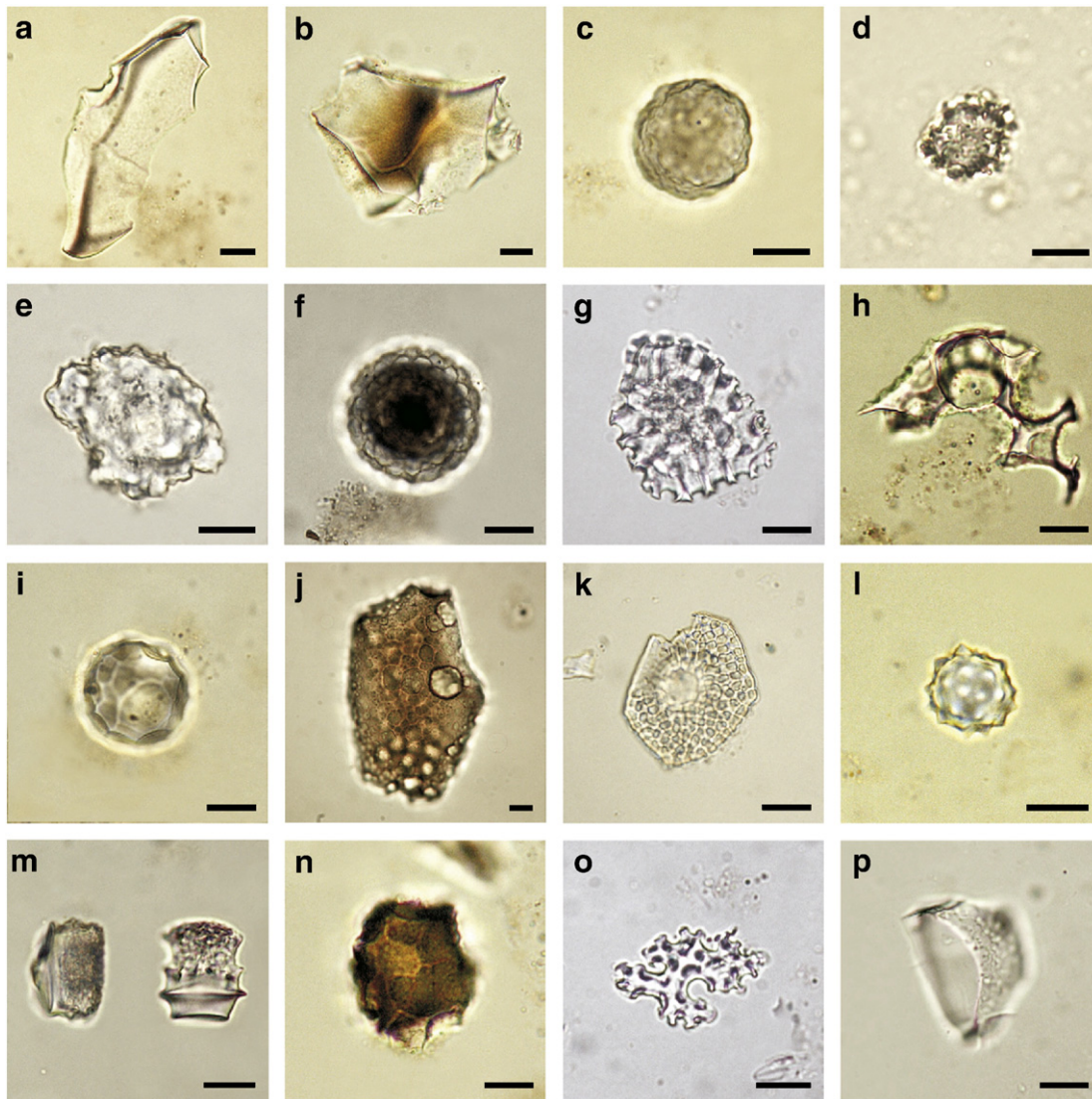


Fig. 2. Photomicrographs of phytoliths in modern samples from the Dogon Plateau (g, k, o) and in fossil samples from the site Ravin de la Mouche (a–f, h–j, l–n, p) (see Table 1 for explanation): (a) elongate faceted (A1); (b) polyhedral faceted (A2); (c–f) globular decorated (A3): (c) verrucate, (d) columellate, (e) nodular, (f) tuberculate; (g) tracheary element (A4); (h) thin branched sclereid (A5); (i) globular faceted small (B2); (j) blocky polyhedron (B3); (k) Cyperaceae (C1); (l) globular echinate, palms (C2); (m) Marantaceae (C3); (n) Annonaceae/Cucurbitaceae type (C4); (o) Podostemataceae (C6); (p) *Hibiscus* type (C5). Scale bar 10 μ m.

African plant species. Whenever possible, we applied the standardized terminology of the International Code for Phytolith Nomenclature, ICPN (Madella et al., 2005). Grass short cell phytoliths (GSCP, class D) were described using the classification of Piperno (2006).

A major problem of phytolith analysis is multiplicity (several morphotypes occur in the same species) and redundancy (the same morphotype occurs in different taxonomic groups) (Rovner, 1971). Both patterns are inherent to phytolith production in plants. The ICPN (Madella et al., 2005) has recognized two different categories which should be considered when assigning taxonomic significance of morphotypes. A phytolith should only be described as “diagnostic” when it is exclusively present in a given taxon or taxonomic group. When a morphotype has been found in a plant, but without sufficient information about its wider taxonomic significance, it should be described as “observed”. Given the preliminary state of phytolith research in Africa and the very limited number of taxonomic phytolith studies, it seems currently impossible to meet the strict requirements of the ICPN that “a phytolith diagnostic at family level must occur in all genera of that particular family, and be absent in other families belonging to the same order or group” (Madella et al., 2005). Therefore, all described morphotypes of this study must be regarded

as “observed”, according to the ICPN definition as “found in a taxon but maybe present in other taxa”. Following the terminology commonly used in palynology (Birks and Birks, 1980), the family- or genus-specific phytoliths (Class C) are all classified as “types”. Current studies on modern grasses (Fahmy, 2008, and work in progress) corroborate the diagnostic value of the bilobate phytoliths established by Piperno (2006) for the subfamilies Panicoideae, Chloridoideae, Ehrhartoideae, Aristoideae and Bambusoideae in the West African flora. However, they also must also be regarded as types, produced abundantly in the respective subfamily, while their rare occurrence in other subfamilies cannot be excluded.

One morphotype among the GSCP merits special attention: the plateaued saddle D6 (Fig. 3j–l). It resembles the “saddle-topped short trapezoid” described by Ollendorf et al. (1988) and Piperno and Pearsall (1998) as characteristic for *Phragmites communis* (Arundinoideae). In the fossil and modern material from Ounjougou an origin from *Phragmites* is not probable, because the only West African *Phragmites* species, *Ph. australis*, is not growing under tropical climatic conditions in the modern Sahel (Hepper, 1972). More modern reference material must be studied to clarify the origin and the palaeoecological significance of this morphotype.

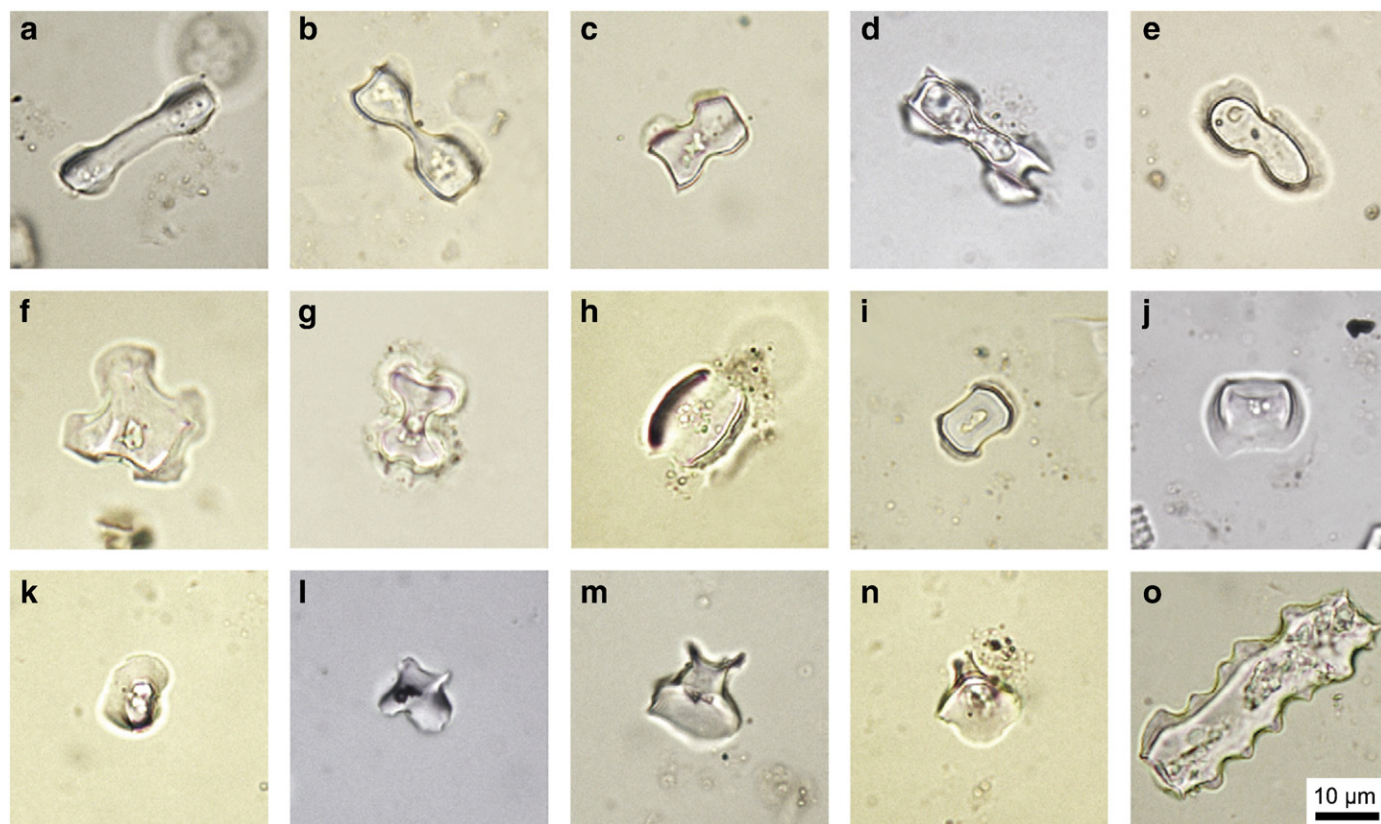


Fig. 3. Grass short cell phytoliths (GSCP) in modern samples from the Dogon Plateau (d) and in fossil samples from the site Ravin de la Mouche (a–c, e–o): (a–e) bilobate, (a) Aristidoid, (b) Panicoid, (c) Chloridoid, (d) Ehrhartioid, (e) Stipa type; (f, g) Panicoid cross; (h) squat saddle; (i) tall saddle; (j–l) plateaued saddle; (m, n) rondel; (o) trapezoid sinuate.

The polyhedral faceted morphotype A2 (Fig. 2b), with irregular shapes, has only rarely been described in the literature. It seems to originate from the leaves of certain woody dicotyledons and has been found in plant material from New Zealand (Kondo et al., 1994, Pl. 19) and Southeast Asia (Kealhofer and Piperno, 1998, Figs. 28, 29, 39). It probably corresponds to type C3 mentioned by Runge (1999) and Mercader et al. (2000). This type is dominant in the Pleistocene samples and could have a diagnostic value for indicating woody vegetation. The thin branched sclereid A5 (Fig. 2h) has not been described so far. It was found in the leaves of modern *Syzygium guineense* and is tentatively attributed to the woody dicotyledons class.

Within the general approach, a finer classification of the globular morphotypes according to their surface decoration (Bowdery et al., 2001; Madella et al., 2005) might have a great potential in the future. In our study, we observed globular phytoliths with columellate, tuberculate, granulate, verrucate, and nodular texture (Fig. 2c–f). However, with a light microscope the surface decorations are not always clearly visible and overlapping occurs. Therefore, we decided to subsume all globular morphotypes with a decorated surface and the nodular type into the class A3 globular decorated.

4. Ravin de la Mouche: stratigraphy and site formation

Ravin de La Mouche is a steep incision, ca. 10 m deep, in the Pleistocene silty formations of the right bank of the river Yamé. Holocene alluvial sediments deposited by the Yamé have filled it up (Rasse et al., 2004, 2006; Lespez et al., 2008). The perennial discharge of the Yamé is characterized by a strong variability reflecting the seasonal rainfall regime of the Soudano–Sahelian belt. The dry season, from October to June, accounts for the parallel duration of a low but constant base flow fed by the sandstone aquifers. In this way the main channel remains active and temporary small floodplain lakes prevail throughout the dry season. The rainy season from June to September,

related to the northwards displacement of the monsoon front, brings notable precipitations (average of 560 mm at Bandiagara). They generally fall in the form of intense rainstorms generating flows with high velocity and channel avulsion at the valley bottom.

A profile 11 m long and with an average height of 4 m was opened during the excavation (Fig. 4). The Early Holocene deposits are divided into four sedimentary sequences: HA0 to HA3 from bottom to top. HA0 is the earliest sequence of the Pleistocene–Holocene transition, composed of reworked Pleistocene silts. It is directly cut into a channel developed within the yellow silts of the Pleistocene formation U4 (OSL dated between 45 and 40 ka, Lespez et al., 2008). HA1, the main Early Holocene stratigraphic unit, is characterized by clastic alluvial formations consisting of cross-bedded medium to coarse sands and gravels with Pleistocene silty blocks. HA2 is composed of silty sandy alluvial sediments with gray Pleistocene silty blocks. HA3 consists of thin beds of greyish sandy silt containing abundant organic remains, alternating with coarse sand lenses. In general, the Holocene sedimentary sequence indicates sedimentation under conditions of concentrated high-energy flow, strongly contrasting with the underlying Pleistocene silts and more recent Holocene silty formations (Rasse et al., 2004, 2006; Lespez et al., 2008). The dating control is provided by eight ^{14}C dates (Table 2) which place HA2 between 11,390 and 10,740 calBP, and HA3 between 11,170 and 10,210 calBP. The dates of HA2 and HA3 give a secure *terminus ante quem* for HA1 where no reliable material for dating was found. Only a few rounded micro-charcoals with a Pleistocene age were present in HA1, showing the importance of redeposited sediments.

5. Modern vegetation

The Dogon Plateau is situated in the north of the Sudanian zone *sensu* White (1983). The modern natural vegetation on the plateau is a typical Sahelo–Sudanian savanna with shea butter trees (*Vitellaria*

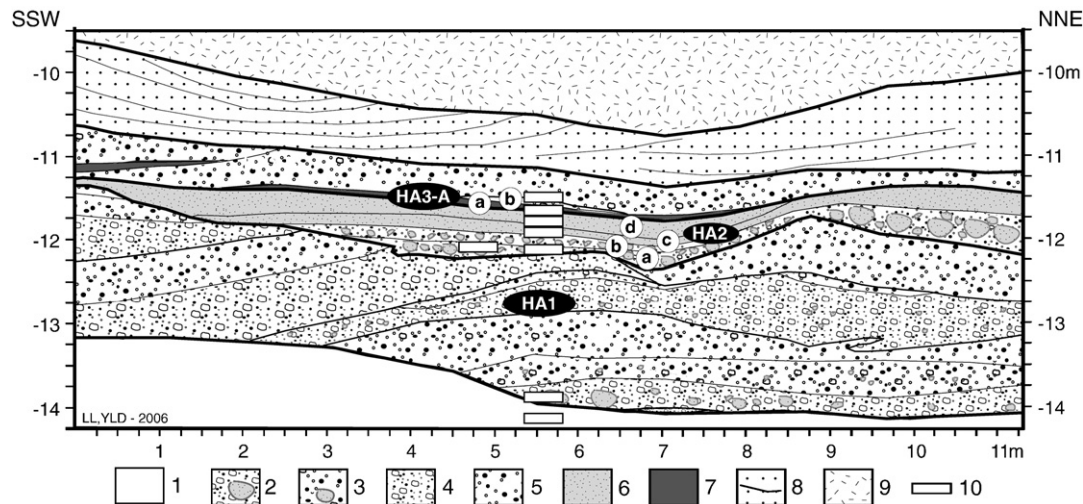


Fig. 4. Profile of the site Ravin de La Mouche: (1) Pleistocene sandy silts; (2) coarse sands, gravels and cobbles with numerous Pleistocene silty blocks; (3) medium and coarse sands with numerous Pleistocene silty small rounded blocks; (4) cross bedded layers with coarse sands, gravels and cobbles; (5) fine to medium compact sands with Pleistocene silty blocks and pedogenetic features; (6) alternating cross-stratified coarse sands and gray silty sandy layers with organic remains; (7) medium to fine sands; (8) recent slope deposits; (9) position of phytolith samples.

paradoxa), *Lannea* spp., *Sclerocarya birrea*, *Daniellia oliveri*, *Parkia biglobosa*, *Terminalia macroptera*, *Khaya senegalensis*, *Vitex* spp., *Prosopis africana* and shrubs such as *Combretum micranthum*, *Heeria insignis* and *Guiera senegalensis*. It has been strongly modified by human activities over several millennia. Intensive agriculture and gardening have created a cultural landscape dominated by anthropogenic plant communities, which today are only rarely affected by bushfires because of the scarcity of grasses. The modern riverine vegetation along the Yamé at Ounjougou has been largely cut, leaving only a few larger individuals of *Syzygium guineense* and *Andira inermis*, an introduced species, whereas the river terraces are almost completely covered with gardens.

In remote, steep and inaccessible valleys on the Bandiagara Plateau, relict forests persist, with a remarkable floristic richness. These Sudano-Saharan gallery forests are protected from clearing and fire and harbour species such as *Cola cordifolia*, *Khaya senegalensis*, *Saba senegalensis*, *Ceiba pentandra* and *Diospyros mespiliformis*. On non-cultivated shallow soils of the plateau, dense grass savannas (after the Yangambi classification, C.S.A., 1956) with low, mainly annual grasses and a very sparse tree cover are found.

6. Materials and methods

6.1. Phytolith, pollen and charcoal sampling

Charcoal samples were handpicked from the profile during the archaeological excavations. Stratified sediment samples for pollen and phytoliths were taken from all lithofacies of the excavated profile in the field campaigns between 2004 and 2007 (see Tables 3 and 4). After micromorphological analysis had indicated soil formation within

re-deposited Pleistocene material of HA2, separate samples from the still visible integer Pleistocene boulders of HA2 were taken in 2007. With this separate sampling, we wanted to answer the question if the phytolith assemblages in HA2 were an inheritance of the Pleistocene, or if they represent the Early Holocene vegetation cover.

Three modern surface samples were taken from the following habitats: Sample 134: grassland vegetation with dominating *Schoenefeldia gracilis* on shallow soil on top of the Dogon Plateau (14°09'34" N, 03°34'39"W). Sample 135: degraded gallery forest with admixtures of savanna species (14°10'04"N, 3°35'30"W). Sample 138: species-rich gallery forest near Ségué (13°51'19"N, 03°45'09"W). For each of the modern surface samples, 10 teaspoon subsamples from the uppermost soil horizon (litter removed) in a 10 m × 10 m plot were taken and mixed together.

6.2. Grain-size and micromorphology

Three sections were selected for sampling. For grain-size analysis, 21 samples were collected in each sedimentary lithofacies. For micromorphological analyses, we sampled sediment blocks from each horizon and across the main horizon boundaries. The intact blocks were impregnated with polyester resin under vacuum following the methodology described by Guilloché (1980). Seven large format thin sections (13 × 6 cm) were prepared and described at 4–400× magnification under petrological microscope according to Bullock et al. (1985). Micromorphological analysis was carried out for the detection of micro-bedded sediment structures, description of lithofacies and pedological features (humification, biological activity, micro-aggregation, hydromorphic features, oxidation and desiccation features).

Table 2

Radiocarbon dates of Ravin de la Mouche. Calibration with OxCal 4.0 (Bronk Ramsay, 2001, 2007), atmospheric data from Reimer et al. (2004).

Sample Nr	Layer	Depth	Date bp	calBP (2σ)	Laboratory number
OUN.M0304-40	Contact HA2d/HA3A	11.59–11.85	9785 ± 70	11390–10870	ETH-28746
OUN.M05-5	HA2 d		9510 ± 70	11180–10740	ETH-31279
OUN.M05-4	HA3 Aa		9610 ± 70	11170–10720	ETH-31278
OUN.0001-M15	HA3 Aa	12.18	9590 ± 70	11100–10590	ETH-23540
OUN.M0304-31	HA3 Aa	11.53	9515 ± 70	11100–10590	ETH-28745
OUN.M03-10	HA3 BC	11.51	9500 ± 75	11100–10580	ETH-27142
OUN.M03-17	HA3 BC	11.70–11.82	9365 ± 70	10760–10300	ETH-27143
OUN.M03-28	HA3 BC	11.60	9150 ± 70	10500–10210	ETH-27144

Table 3
Absolute counts of phytoliths in fossil and modern samples from Ounjougou.

			Fossil samples Ravin de la Mouche							Modern surface samples			
Layer			Pleistocene	HA 1	HA 2 a/b	Pleistocene boulder	HA 2 c/d	HA 2 c/d	HA 3 Aa	HA 3 Ab			
Depth (m)			14.29	14.05	12.25	11.90	11.81	11.76	11.64	11.57			
Sample no.			129	132, 133	130, 131	120, 121	109	116, 117	118, 119	122, 123	134	135	138
Group of plants	Class	Morphotype											
Woody dicotyledons	A1	Elongate faceted		18	34	17	2	54	32	31	2	3	5
	A2	Polyhedral faceted	83	116	278	333	49	270	170	228	13	8	34
	A3	Globular decorated	6	3	2	5	18	19	6	21	30	48	60
	A4	Tracheary element											123
	A5	Thin branched sclereids	2	51	9	48	13	65	95	9		6	4
Ferns, woody/herbaceous dicotyledons	B1	Globular psilate			2	1	7	8	8	3	7	10	18
	B2	Globular faceted small	17	4	3	13	4	29	16	10		1	2
	B3	Blocky polyhedron	4		1	15	13	3	4	23	5		
Family/genus-specific	C1	Cyperaceae type					4	3			13	26	30
	C2	Globular echinate, Arecaceae			2		9	8	2	17	3	5	2
	C3	Marantaceae					25	10		11	1	2	7
	C4	Annonaceae/Cucurbitaceae type			5			6	11	2		2	1
	C5	<i>Hibiscus</i> type					7						
	C6	Podostemataceae											38
Poaceae, grass short cell phytoliths (GSCP)	D1/2	Bilobate/Trilobate			1		70	73		59	81	60	39
	D3	Cross					11	10	1	7	13	26	3
	D4	Rondel					13	16	1	14	23	33	12
	D5	Saddle					89	73		67	151	76	39
	D6	Plateaued Saddle					37	25		36	42	5	8
	D7	Trapezoid sinuate					1						
		Other short cells					3			2			
Non-diagnostic, Poaceae	E1	Cuneiform bulliform	20	8	36	40	143	27	72	35	61	33	64
Non-diagnostic, others	F1	Parallelepipedal bulliform	41	30	75	118	329	113	177	138	113	53	217
	F2	Elongate psilate/echinate	19	7	29	71	185	70	115	176	168	65	106
	F4	Point-shaped/trichomes	50	30	35	60	210	97	73	51	69	104	103
	F5	Cylindric			1	3		15	14	10		2	
	F6	Parallelepipedal elongate	8	3	4	16	4	2	15	12		5	5
	F7	Elongate, tapering ends	14	10	16	19	67	15	17	14	3		
	F8	Vessels/tracheids			2	4	6	5	8	8	2	1	1
		Total	264	280	533	761	1317	1017	834	984	800	574	921
Others		Unclassified	2		6		33	27	8	11	8	10	27
		Sponge spicules	1	2	26	68	15	47	52	31	34	60	198
		Charred grass epidermis								48	3	4	2
		Charred wood fragments						2		429			
		Charred indiff.						11		216	12	16	24

6.3. Phytolith preparation and counting

15–20 g of dried sediment was processed after the standard method described in Piperno (2006), including the following steps: 1. deflocculation with EDTA; 2. removal of coarse sand with a 250 µm mesh sieve; 3. clay removal by gravity sedimentation; 4. removal of carbonates with 10% HCl; 5. removal of organic material with concentrated nitric acid and potassium chlorate; 6. extraction of phytoliths with a heavy liquid (zinc bromide at a specific gravity of 2.30–2.35); storage of phytolith residue in ethanol 95%. 7. mounting on microscope slides. We tested several mounting media for their physical and optical properties. To enable rotation and three-dimensional investigation of short cell phytoliths, observation and counting was done in benzyl benzoate which proved to be most appropriate among the liquid mounting media.

Absolute counts range from 260–1300 morphotypes, depending on the phytolith concentration of the samples. In samples with high concentration, at least 200 diagnostic grass short cell phytoliths (GSCP) were counted to enable a statistical robust interpretation (Albert and Weiner, 2001; Strömberg, 2009a). Diatoms, sponge spicules, and charred grass epidermis and wood fragments were counted, but excluded from the sum, as well as the non-diagnostic morphotypes. The phytolith diagram was prepared with the TILIA package (Grimm, 1987).

We tested the phytolith content of modern wood, leaf and bark (and one fruit) from the gallery forest species present in the charcoal and pollen samples, to determine their input for the fossil phytolith

assemblages. The reference samples were processed by dry and wet ashing after Piperno (2006) from material of the Goethe University Frankfurt collections, and from herbarium specimens in the Herbarium Senckenbergianum Frankfurt.

6.4. Pollen and palynofacies

Standard chemical preparation included removal of the mineral fraction with HCl and HF and humified organic matter with KOH. This technique preserves pollen and other organic matter (OM) analysed as palynofacies with the methods of the organic matter petrography (Combaz, 1964; Caratini, 1994; Tyson, 1995; Batten, 1999; Sebag et al., 2006). Several categories of particulate OM can be distinguished according to their optical properties: amorphous OM with indistinct outlines, discrete elements (recognizable organs or organisms), and phytoclasts (constituents produced by plants or derived from their degradation). Palynofacies is an indicator of depositional palaeoenvironment and transport processes. It may also be used to study the effects of postsedimentary processes and diagenesis in the deposits.

6.5. Charcoal identification

The charcoal fragments were fractured into the three diagnostic planes transverse, tangential and radial, and identified with an incident light microscope. For comparison, the West African wood collection of the Goethe University Frankfurt and a computer aided identification key based on DELTA was used (Neumann et al., 2001).

Table 4
Absolute counts of pollen samples from Ravin de la Mouche.

		HA3 B	HA3 Ab	HA3 Aa			
		—11.53	—11.57	—11.59	—11.61	—11.65	
Trees	Alchornea	7	17	22	21	11	
	Syzygium	6	7	5	6	2	
	Uapaca	3	2	13	15	3	
	Celtis	2	1	9	7	2	
	Combretaceae	2	4	5	4	3	
	Pterocarpus		1	2		1	
	Detarium	2	1	2	1	1	
	Sapotaceae		1				
	Bombax		1	1			
	Lannea/Sclerocarya	1		3	2		
	Ziziphus			1			
	Hymenocardia				1		
	Securinega			1			
	Diospyros	1		2	1		
	Mitragyna	1	2	2	1		
	cf. Nauclea	1					
	cf. Acacia				1		
	cf. Dichrostachys		1				
	cf. Elaeis			1			
	Herbs	Poaceae	69	79	188	109	77
Tubuliflorae		2	4	4	6	2	
Liguliflorae		2	2	2	5	1	
Chenop./Amaranth.		5	3	1	4	1	
Acanthaceae		2	2	1	2	1	
Mitracarpus		1		1			
Borreria			1		1		
Rubiaceae		1					
Euphorbiaceae		1	1	1	1		
Phyllanthus			1				
Polycarpea			1	1			
Indigofera					1		
Nyctagynaceae				1		1	
Caryophyllaceae		1		1	1		
Cucurbitaceae				1			
Boraginaceae			1				
Fabaceae		1			1		
Aquatics		Cyperaceae	2	3	5	7	1
		Nymphaea	2	1	4	2	1
		Typha	1	2	1	1	
	Ipomoea			1			
	Polygonum t. senegal.	1		1	1		
	Spore trilete			2	1		
	Monocot. indet.			1	1		
	Indeterminate		2	4	1		
	Indeterminable	3	10	9	5	2	
	Pollen sum	120	151	299	210	111	
	Concentricystes		2	3		1	

7. Results

7.1. From lithofacies to depositional environments (Figs. 4–6)

HA1 is 2 m thick and consists of five sequences, each composed of two units. The basal contact of each lower unit is erosional. Their lithofacies are red to ochre gravel and coarse sand with gray Pleistocene silt blocks. The mean grain size is >2.5 mm, showing moderate to poor sorting ($So > 1.6$). Finer units characterized by cross-bedded coarse sand with thin gravel layers (2–4 cm) overlay them. Grain-size is 1–2.5 mm, the sediment is better sorted ($So < 1.4$) and characterized by fining up. The alluvial architecture and the grain-size parameters suggest bed and bars deposits in a braided or wandering river system. It signifies phases of pulsed high-energy floods and channel mobility (Figs. 4–6).

The contact between HA1 and HA2 is erosional. HA2 is divided in two main units, each composed of different material. The average thickness of the yellowish base unit (HA2 a/b) is 30 cm. It is constituted by rounded sandy silt blocks (3–20 cm), mainly reworked from the Pleistocene sandy silty deposits, in a medium sand matrix. The upper unit HA2 c/d is also around 30 cm thick but, in contrast

with the lower one, it is composed of brownish sandy silt smaller blocks (0.5–5 cm) and seems more homogeneous because the boundaries of the blocks are more diffuse and faint. HA2 c/d micromorphology shows fragments of limpid clay coatings and amorphous organic material in the groundmass and microlaminated limpid clay coatings along channels and planes (Fig. 5).

At first, the sediments of HA2 result from erosion into the Pleistocene deposits probably by stream incision and riverbank erosion. Afterwards, they had experienced a pedogenesis during the Early Holocene indicating that HA2 is part of a buried palaeosol. The clay coatings in the channels and planes suggest the beginning of clay migration under well-drained conditions. It attests to contemporaneous stream incision in the previous floodplain and the development of a low alluvial terrace, which was rarely flooded. Furthermore, the pure infillings along the channels and planes point to a pedogenesis under a protective vegetation cover preventing significant soil erosion.

HA3 is 20–50 cm thick; its basal contact is erosional and explains the truncation of the palaeosol HA2. HA3 has three sequences (A, B, C), each composed of two successional units. The lower unit is composed of cross-stratified coarse sand poorly sorted with an average thickness of 20 cm. The upper unit corresponds to a gray sandy silt layer, 1–4 cm thick. Under the microscope, micro-laminations and numerous

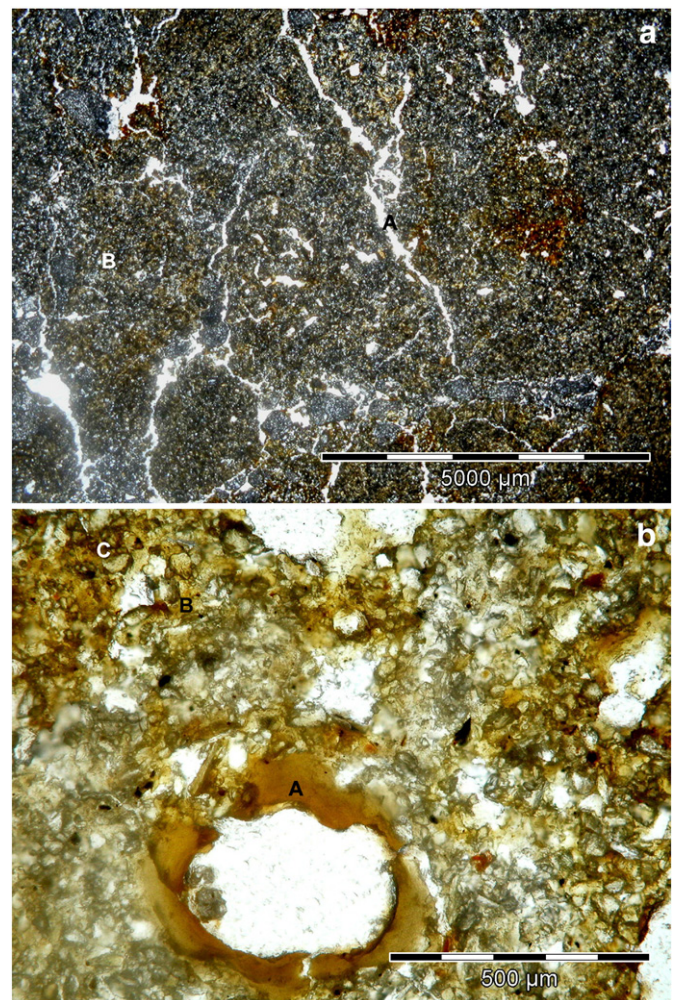


Fig. 5. Photomicrographs of thin sections of HA2 deposits. (a) H2c/d deposits (non polarized light), channels (A) and subangular blocky peds (B) which testify a developed pedogenesis; (b) H2c/d deposits, detail (non polarized light), microlaminated clay coating around a channel (A), fragmented and dispersed clay coating (B) and amorphous organic matter in the groundmass (C).

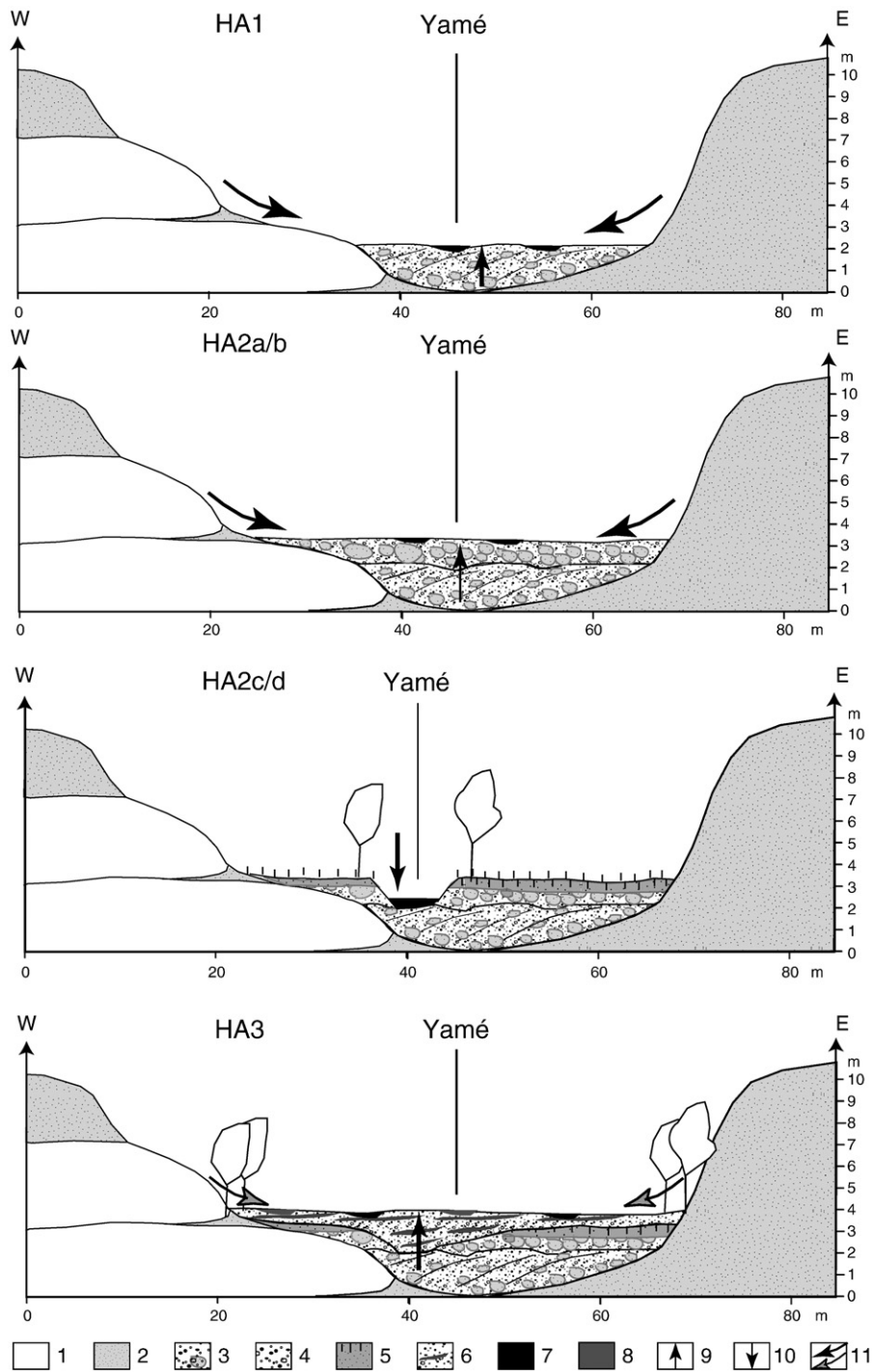


Fig. 6. Schematic sketch of the fluvial system changes during the early Holocene. (1) sandstone; (2) Pleistocene sandy silts; (3) coarse sands, gravels and cobbles with numerous Pleistocene silty blocks; (4) cross bedded medium and coarse sands with gravels and cobbles; (5) fine to medium compact sands with Pleistocene silty blocks and pedogenetic features; (6) alternating cross-stratified coarse sands and gray silty sandy layers with organic remains; (7) channel; (8) permanent small lakes; (9) alluvial filling; (10) stream incision; (11) river bank erosion (strong/weak).

organic remains (leaves, micro-charcoal) characterize the layers. These sequences result from alternating succession of channel deposits, overlaid by suspension to decantation sediments deposited in a quiet environment. In relation with the current sedimentary pattern of the Yamé River, HA3 represents the earliest Holocene rhythmic sediments resulting from alternating wet and dry season alluvial sedimentation. They indicate a wandering or meandering river, with a coarse load during the rainy season, flowing in a floodplain with permanent small lakes. The layer HA3 Aa sampled for

phytoliths and pollen corresponds to the dry season sedimentation, HA3 Ab to the wet season sedimentation, including a larger catchment area.

7.2. Phytoliths (Table 3, Fig. 7)

The Pleistocene Sample 129 has a very low phytolith concentration and the absolute sum of counted morphotypes is low. Although the grass morphotype cuneiform bulliform is common, the absence of

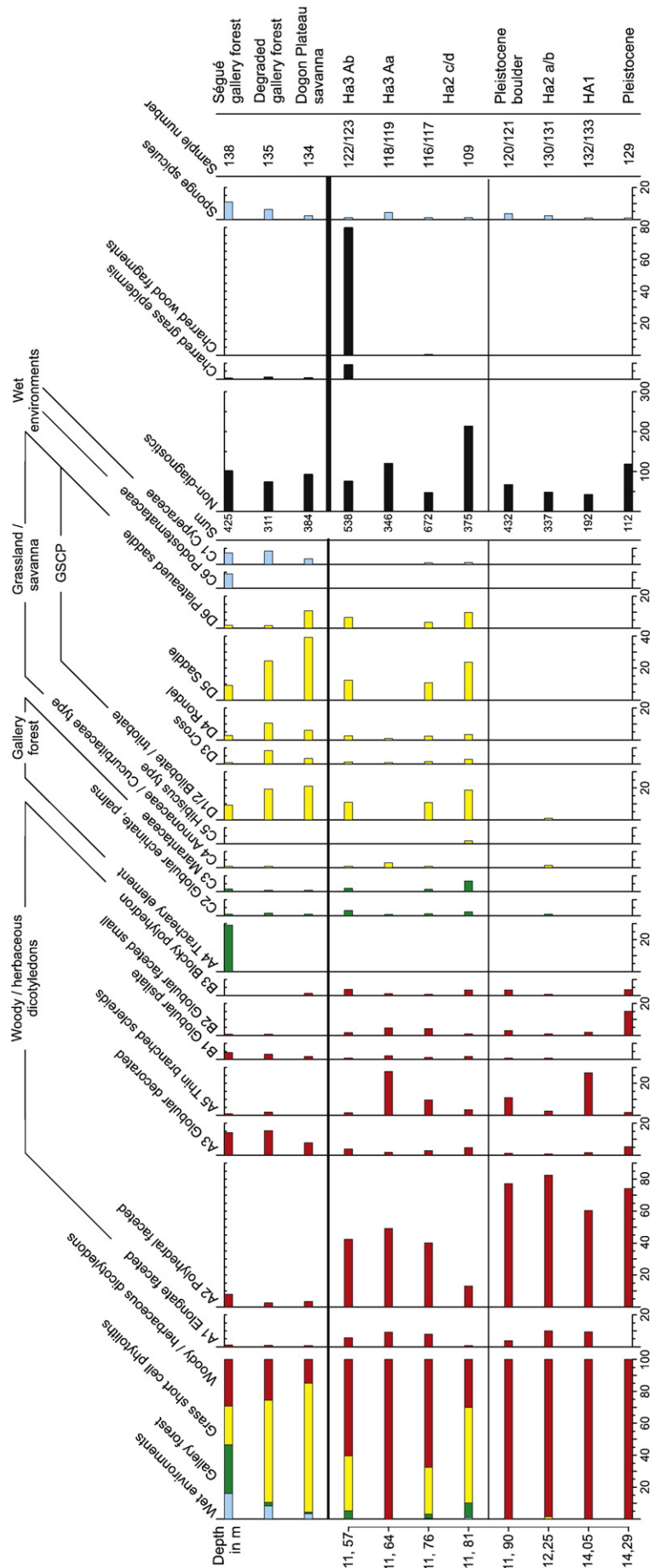


Fig. 7. Percentage phytolith diagram of Ravin de la Mouche in comparison with three modern samples from the Dogon Plateau; analysis: K. Neumann and A. Fahmy.

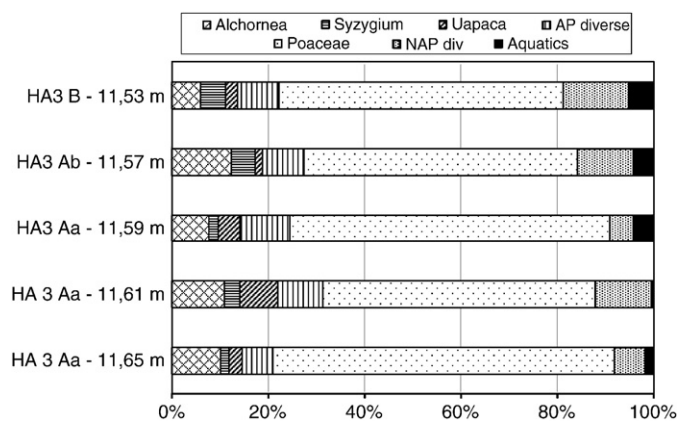


Fig. 8. Percentage diagram of major pollen groups in Ravin de la Mouche, layer HA3; analysis: A. Ballouche.

GSCP is remarkable. The most conspicuous feature of this sample is the high percentage (75%) of the polyhedral multifaceted type, with an admixture of phytoliths from woody and herbaceous dicotyledons (e.g. thin branched sclereids 2%, globular faceted 15%). With 2%, globular decorated phytoliths are weakly represented. Due to the absence of diagnostic GSCP, calculation of the D:P, Iph and Ic indices could not be performed, and the assemblage cannot be attributed to any type of savanna. The Early Holocene HA1 Sample 132/133 is similar to the one from the underlying Pleistocene sediments, indicating reworking and re-deposition of older material (Fig. 7).

The samples from HA2 contain two clearly different types of assemblages. Sample 130/131 from the lower layers HA2 a/b and Sample 120/121 from the Pleistocene boulder have similar assemblages as Sample 129 from the Pleistocene base, pointing to the Pleistocene origin of the re-deposited Early Holocene sediment. GSCP is absent, the polyhedral faceted morphotype dominates, and phytoliths from woody and herbaceous dicotyledons are well represented.

In HA2 c/d, by contrast, the phytolith samples are much richer. The same types as in HA1, HA2 a/b and the Pleistocene layer are still present, but with much lower percentages. Most distinctive is the good representation of GSCP (30–60%), with high numbers of bilobates and saddles, pointing to a tropical grassland. Annonaceae/Cucurbitaceae type and *Hibiscus* type could represent the herb and woody plant component of these savannas. Marantaceae type and the globular echinate morphotype from palms point to an input of phytoliths from a dense, woody vegetation growing under humid conditions. Moist habitats are also indicated by the presence of Cyperaceae type and sponge spicules.

The samples from the seasonal sediments in HA3 Aa and HA3 Ab distinctly differ from each other. In HA3 Aa (sample 118/119, fine-grained sediments with *Syzygium* leaves) the assemblage is similar to the samples from the Pleistocene material in HA0 and HA1, indicating erosion and re-deposition of Pleistocene material in a calm environment. By contrast, sample 122/123 from the coarser sediments of HA3 Ab presents a rich variety of morphotypes and is similar to the samples from HA2 c/d. In addition, it contains a high number of microscopic charcoal fragments and some charred grass epidermis fragments. The ratio of microscopic charcoal fragments vs. charred grass fragments is 10:1, indicating that the majority of the charred material originated from woody plants and not from grasses. The coarse-grained nature of the sediment and the rich phytolith assemblage suggest an origin from a wider catchment area, including erosion of Early Holocene soils in periods of intensive rainfall.

7.3. Pollen and palynofacies (Table 4, Figs. 8, 9)

Pollen is absent in the Pleistocene layer, in HA1 and HA2. Five samples from HA3 provided sporo-pollinic material suitable for a

vegetation reconstruction. Pollen sums in HA3 A lie between 111 and 299, and one sample of HA3 B provided 120 identifiable pollen grains. Despite the poor preservation and the low pollen sums, the taxonomic diversity is significant: 43 taxa in 5 samples. There is no significant difference between the composition of the samples in HA3 Aa and HA3 Ab, except for the better conservation in HA3 Aa (Figs. 8, 9).

Herbal taxa dominate with 70–80% (51–68% grasses). Among the arboreal pollen, *Alchornea* is dominant (7–11% in HA3 Aa and 5% in HA3 Ab), indicating pioneer formations of humid places. *Uapaca*, *Syzygium* and *Celtis* were growing along the borders of permanent streams, while the wetland herbaceous formations are represented by Cyperaceae, *Typha*, *Nymphaea* and *Polygonum*. The regional vegetation on well-drained soils was a dense grass savanna or grassland, including heliophilous and xerophilous taxa such as Asteraceae (Liguliflorae/Tubuliflorae) and Chenopodiaceae/Amaranthaceae. The woody plant cover (Combretaceae, *Pterocarpus*, *Detarium*) was certainly very scattered, with a low diversity.

Organic matter is generally poorly preserved. The palynofacies (after Combaz, 1964; Tyson, 1995) contains mainly agglomerates of structureless amorphous organic matter (AOM), with very few discrete elements or recognizable organs and organisms (phytoclasts, palynomorphs). This indicates intensive pedological degradation and/or biological activity in a sub-aquatic environment (Sebag et al., 2006). Among the structured elements, opaque particles (OP) are dominant, corresponding partially with charcoal particles and organic remains, which have undergone thermal maturation after burial. Pyrofusinites, typical for aerial carbonization of vegetative tissues, are rare. From this we can conclude that the incidence of fires was low.

The quantitative composition can be used to define the conditions of transport and deposition of the organic matter. In the coarse sediments of HA3 Ab the palynofacies equidimensional and rounded opaque particles with small sizes (<20 µm) are dominant, indicating reworking and transport (rainy season). The fine deposits of HA3 Aa have higher proportions of elongated opaque particles and preserved translucent phytoclasts with sizes ranging from 30 to 50 µm, typical for deposition in a calm environment (dry season). The palynofacies thus confirms the existence of seasonal deposits defined by the micro-morphological analysis.

7.4. Charred wood (Figs. 10, 11c–f)

Charcoal is absent in the Pleistocene layer, in HA1 and HA2. From HA 3, 649 charcoal fragments were studied. The dominant taxon in the samples is *Syzygium*, with 85%. The wood most probably belongs to *Syzygium guineense*, a widespread tree in tropical Africa, growing along streams, riverine and swampy forests. Minor taxa with percentages from 1% to 5% are *Prosopis africana*, *Anogeissus leiocarpus*,

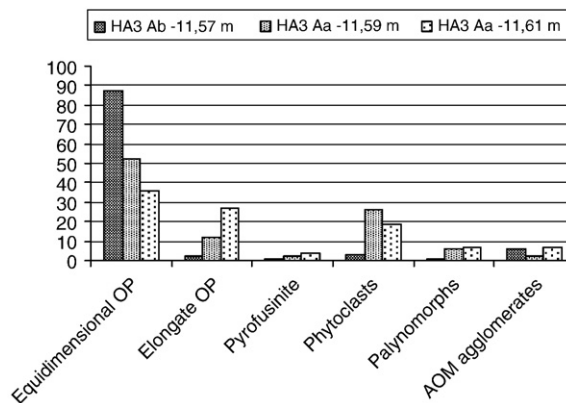


Fig. 9. Percentage palynofacies diagram of Ravin de la Mouche, layer HA3; analysis: A. Ballouche. OP = opaque particles, AOM = amorphous organic matter.

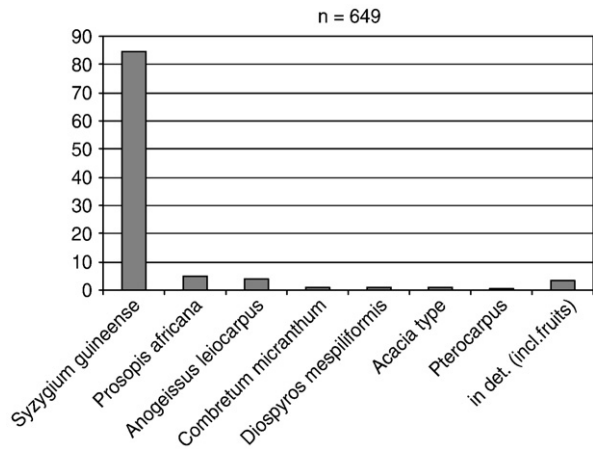


Fig. 10. Percentage charcoal diagram from Ravin de la Mouche, layer HA3; analysis: K. Neumann.

Combretum micranthum, *Diospyros mespiliformis*, *Acacia*, and *Pterocarpus*. Unidentified fragments make up 3% of the total sum. The preservation is moderate to good, and the charcoal fragments are not rounded, indicating either deposition in situ or short-distance transport (Figs. 10, 11c–f).

7.5. Modern phytolith surface samples (Tables 3 and 6, Fig. 7)

The three modern samples have remarkably variable percentages of GSCP: 20% in the undisturbed gallery forest (Sample 138), 65% in

the degraded gallery forest (Sample 135), and 85% in the open Dogon Plateau savanna (Sample 134). Among the GSCP, saddles and bilobates dominate. In the gallery forest samples 135 and 138, rondels make up ca. 15% of the GSCP, and single Ehrhartoid bilobates point to (probably wild) *Oryza* species. Among the morphotypes from woody plants, the globular decorated type is well represented with 7–15%. Cyperaceae, diatoms and sponge spicules in all samples indicate soils with at least seasonal high humidity. Especially interesting is the presence of Podostemataceae and the “tracheary element” morphotype (28%) in sample 138. Podostemataceae indicate the presence of freshwater conditions (Piperno, 2006), and the tracheary elements might be significant for some woody plants of the gallery forest. In all samples, the Marantaceae type and the globular echinate morphotype from *Arecaceae* is present in small quantities, although no palms have been noted in the modern vegetation.

7.6. Reference samples from modern plants (Fig. 11a, b)

The species *Combretum micranthum*, *Anogeissus leiocarpus* (Combretaceae), *Prosopis africana* (Mimosaceae) and *Diospyros mespiliformis* (Ebenaceae) do not seem to produce any phytoliths. The leaves of *Acacia sieberiana* (Mimosaceae) and *Celtis integrifolia* have distinct epidermal hair cells, and the leaves of *Alchornea cordifolia* (Euphorbiaceae) produce globular verrucate phytoliths (ca. 5 µm) which are much smaller than the globular decorated forms in the fossil samples. The endocarp of *Celtis integrifolia* (Ulmaceae) is heavily silicified, consisting of globular to subglobular cells with faceted, finely echinate and nodular structures. In the leaves of *Syzygium guineense* (Myrtaceae) irregular faceted phytoliths and thin branched sclereids were found, comparable to the morphotypes A2 and A5 in the fossil samples (Fig. 11b). The leaves of *Uapaca togoensis* have silicified isodiametric

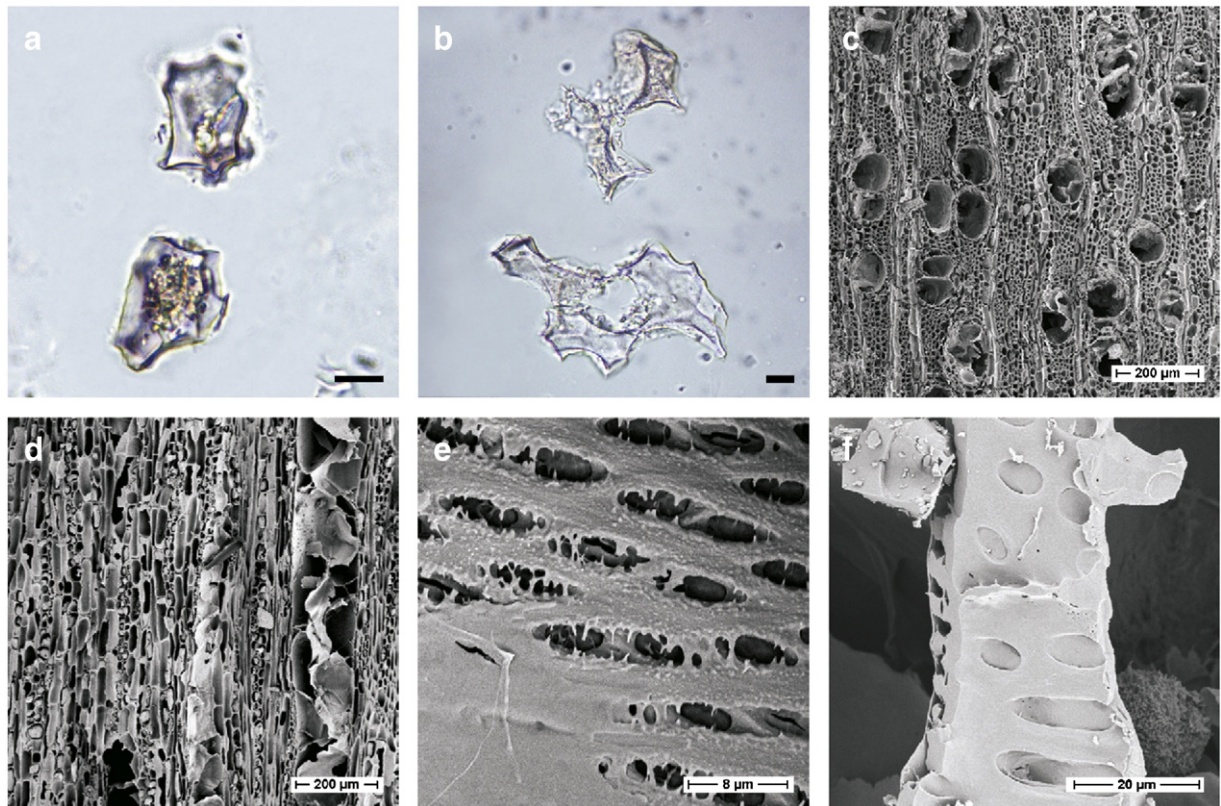


Fig. 11. Microphotograph of leaf phytoliths observed in modern plants: (a) polyhedral multifaceted (*Uapaca togoensis*); (b) thin branched sclereids (*Syzygium guineense*), scale bar 10 µm; SEM photographs of *Syzygium* charcoal from Ravin de la Mouche: (c) transverse view, (d) tangential view, (e) radial view: vested intervessel pits, (f) radial view: vessel-ray-pits with reduced borders.

epidermal tissues and some irregular faceted phytoliths (Fig. 11a). *Uapaca togoensis* was the only species with wood silica, consisting of globular, subglobular to nodular morphotypes with psilate to decorated surfaces. However, with 4–10 μm these are much smaller than those observed in the fossil samples (10–50 μm). Only the leaf phytoliths of *Uapaca* and *Syzygium* show similarities with fossil material and might have contributed to the assemblages. All the other modern morphotypes, especially fragile vessels from leaves, but also the heavily silicified endocarp cells of *Celtis*, are absent in the fossil samples.

8. Discussion

8.1. Taphonomy and reconstruction of the vegetation using the general approach

The sediments of Ravin de la Mouche originated from a complex series of erosion, re-deposition and soil formation under variable drainage conditions. The taphonomy of phytolith deposition, as inferred from the geomorphological and micromorphological data, has to be considered in the interpretation and reconstruction of the vegetation represented in the Pleistocene and Early Holocene layers. Generally speaking, the profile contains two types of plant remains in the Early Holocene layers: 1. The Pleistocene phytolith heritage is visible in HA2 a/b, in the undigested Pleistocene boulders and the reworked fluvial sediments of HA3 Aa. 2. Remnants of the Early Holocene vegetation in the 12th and 11th millennium BP are the phytoliths in HA2 c/d and HA3 Ab, pollen and charcoal in HA3. The Early Holocene plant remains are interpreted as a whole, as the differences between HA2 c/d and HA3 are due to taphonomic processes and not to changes in the vegetation.

The base of the profile belongs to phase U4 of the Pleistocene chrono-stratigraphy with an age between 45/47 ka and 40 ka (Rasse et al., 2004; Lespez et al., 2008), attributed to Oxygen Isotope Stage 3 with a cooler climate and widespread dry vegetation types in northern tropical Africa (Dupont et al., 2000). The fine ocre-yellow silty sediments indicate pedogenesis, and the phytolith assemblages can be expected to be in situ depositions. The most conspicuous feature of the Pleistocene sample is the complete absence of GSCP. The combination of Poaceae cuneiform bulliforms, polyhedral multifaceted and other morphotypes from woody and herbaceous dicotyledons resembles phytolith samples from the LGM (Late Glacial Maximum) in DR Congo which have been interpreted as representing a light forest with shrubs and herbs in the undergrowth (Mercader et al., 2000). This vegetation has no modern analogue in Africa and might have established under glacial conditions with lower atmospheric CO_2 (Cowling, 1999). An alternative explanation is that changes in production and taphonomy of fossil grass phytoliths might have happened through time, thus aggravating further interpretation (Alexandre et al., 1999).

In HA1, the low phytolith content can be explained with the sandy-gravelly structure of the fluvial sediment. The phytolith assemblage is similar to the Pleistocene sample. It does not represent the Early Holocene vegetation during deposition of the sediment, but the old Pleistocene land surfaces which were eroded and re-deposited.

The sediments of HA2 consist of re-deposited silts originating either from U5, dated between 40 and 30 ka BP, or U4 (Rasse et al., 2004; Lespez et al., 2008). An Early Holocene pedogenesis in the upper part (HA2 c/d) of the Pleistocene silts included the deposition of phytoliths from an in situ vegetation. Soil formation did not reach the lower horizons HA2 a/b which only contain the Pleistocene assemblage. The same is true for the remaining, only partly digested Pleistocene boulders. The phytolith assemblage in the pedogenetically altered areas of HA2 c/d originates from three different sources: 1. the Pleistocene parent material with a high amount of polyhedral multifaceted phytoliths; 2. the early Holocene grassland developed in situ on the land surface and represented by GSCP, Annonaceae/

Cucurbitaceae type and *Hibiscus* type; 3. an early Holocene forest vegetation mainly represented by the globular echinate morphotype and Marantaceae type. Although taphonomically complex, the origin of most morphotypes can be clearly attributed to one of the three sources.

The stratified sediments of HA3 are of fluvial origin and have two quite different phytolith assemblages, according to their seasonal deposition, which is reflected in the granulometry. The fine deposits of HA3 Aa have the same phytolith composition as the Pleistocene material from HA0 and HA2, indicating erosion and re-deposition of Pleistocene layers. By contrast, the coarser material of HA3 Ab, deposited during the early rainy season, shows the same phytolith assemblage as in HA2 c/d and must therefore originate from eroded early Holocene soil material. The pollen samples from HA3, short-lived under oxidizing conditions, reflect the regional vegetation and indicate with their high percentage values of grass pollen the existence of an open grassland.

Marantaceae in HA2 c/d and HA3 Ab are indicators of a closed forest (Strömberg, 2004). In view of the low D:P (see Section 8.2), they cannot be taken as evidence of a larger forested area, but rather of a gallery forest with limited extension. The tree species of the gallery forest, as inferred from pollen and charred wood in HA3, were *Syzygium guineense*, *Prosopis africana*, *Diospyros mespiliformis*, *Pterocarpus*, *Acacia*, *Alchornea*, *Uapaca* and *Celtis*, with the shrub *Combretum micranthum* and Marantaceae in the undergrowth. Palms were also a constituent of the denser woody vegetation along the watercourses. The globular echinate morphotype, originating from palms, is often used as a forest indicator (Piperno and Becker, 1996; Boyd et al., 1998; Shulmeister et al., 1999, 2001). In this case, it points to the existence of a permanent water source, which is essential for palm growth (Strömberg, 2004), and for *Uapaca*. For the phytoliths from the gallery forest, water or wind transport can be assumed. Occasional flooding of the alluvial terraces might have transported and deposited the phytoliths from the nearby dense riverine vegetation. The presence of well-preserved Cyperaceae phytoliths and complete sponge spicules in HA 2 c/d points to short distance transport. Sponge spicules are usually fragmented and corroded in fluvial deposits transported over a long distance (Zucol et al., 2005), while Cyperaceae hat-shaped phytoliths generally do not preserve well in soils (Albert et al., 2006).

The combined analysis of charred wood, pollen and phytoliths from the same Early Holocene deposits clearly shows the taphonomic biases due to different degrees of representation, deposition, preservation and levels of identification. Charred wood is a good indicator of woody vegetation and allows identification to genus or even species level. However, the analysis of the charcoal gives only information about the local gallery forest and does not allow statements about the regional vegetation. The low number of pollen grains restricted to the narrow sediment bands of HA 3 illustrates well the delicate pollen preservation in fluvial sediments. The pollen samples, which in this case are a “snapshot” of one year’s deposition, represent both the regional grassland and the local gallery forest, adding a number of taxa to the reconstruction of the forest. The major advantages of the phytoliths at Ravin de la Mouche is their durability, especially in the early Holocene palaeosoils, their potential for grassland reconstruction, and their significance to represent the regional vegetation in an open landscape. However, they are much less specific for woody vegetation.

8.2. Application of the indices D:P, Ic and Iph (Table 5)

The phytolith assemblage of HA2 c/d and HA 3Ab have D:P values around 0.1 clearly indicating an open grassland or savanna and not a forest. The D:P of the fossil samples is similar to the modern surface samples from the Dogon plateau grassland, whereas gallery forests of the Dogon plateau have D:P values between 0.3 and 0.6. The comparatively low D:P in Sample 138 from the dense gallery forest

underestimates the tree cover, if only the globular decorated morphotype is taken as an indicator for the woody vegetation. The low D:P is in this case not due to the strong input of GSCP, but to the exclusion of other morphotypes from woody plants, in this case the tracheary element A4, from the calculation.

The D:P of the fossil samples are comparable with those of modern African savannas and grasslands which are mostly lower than 1 and in many cases even lower than 0.1 (Barboni et al., 2007; Bremond et al., 2005b). The D:P, however, does not allow us to separate between different savanna types and to trace tree cover densities in West African short grass and long grass savannas. Sparsely wooded Sahelian grasslands and Sudano–Guinean woodlands with a much higher tree cover have very low and markedly similar D:P values (Barboni et al., 2007; Bremond et al., 2005b). This is due to the large biomass production of the tall Sudanian and Guinean grasses and hence the increased input of grass phytoliths to the soil assemblages where they mask the increased production of globular decorated types from woody plants.

The composition of the Early Holocene grassland at Ounjougou can be further specified by the Ic and Iph indices. Ic values around 7 indicate the dominant input of C4 grasses from the subfamilies Chloridoideae and Panicoideae and hence tropical conditions with high temperatures, whereas C3 Pooideae and Danthoioideae do not seem to have contributed to the phytolith assemblages. Assemblages from higher elevations in the East African mountains where these subfamilies dominate, have values between 35 and 95 (Bremond et al., 2008). However, the Ic from the La Mouche samples seems quite high

Table 5

D:P, Ic and Iph indices of fossil and modern phytolith samples from Ounjougou, compared with surface samples from other African sites.

Origin	Sample number	D:P	Ic (%)	Iph (%)
<i>Ravin de la Mouche</i>				
HA 2 c/d	PH 109	0.08	6.33	60.87
HA 2 c/d	PH 116/117	0.09	7.73	51.31
HA 3 Ab	PH 122/123	0.11	7.65	60.95
<i>Dogon-Plateau, Mali</i>				
Dogon Plateau savanna	PH 134	0.10	7.42	67.25
Degraded gallery forest	PH 135	0.30	17.57	52.70
Ségué gallery forest	PH 138	0.59	11.88	54.00
<i>Ethiopia, Middle Awash Valley (Barboni et al., 1999)</i>				
Shrub steppe	MA 94-103	0.17	45.82	49.14
Stream mud	MA 94-106	0.35	31.54	17.73
Riparian forest	MA 94-101	1.26	35.71	36.11
<i>East African tropical mountain area (Bremond et al., 2008)</i>				
Mt Kenya, Afroalpine zone	LAS 3-2	0.00	80.38	23.53
Mt Kenya, Mountain forest	UM 3-1	0.02	51.97	30.00
Afroalpine zone	RGW 24	0.01	40.57	26.98
Mountain forest	RGW 2	0.16	31.58	7.69
Semi-deciduous forest	MAS 7	1.27	1.35	10.96
	MAS 59	2.05	8.11	8.82
<i>West Africa, Sahara to Sudan Zone (Bremond et al., 2005b)</i>				
Sahara	RIM 3	0.17	../.	25.00
	MAU 05	0.03	../.	14.71
Sahel	RIM 11	0.02	../.	47.67
	83-35	0.11	../.	72.97
	83-30	0.04	../.	20.18
	83-48	0.03	../.	32.87
Sudan Zone	83-4	0.31	../.	15.24
	82-78	0.08	../.	9.73
	83-120	0.07	../.	5.58
	83-100	0.07	../.	6.63
<i>Cameroon, rain forest-savanna mosaic (Bremond et al., 2005a)</i>				
Mature Rinorea forest	4	12.58	../.	6.25
	6	10.83	8.70	7.14
Tall grass savanna	22	1.61	16.67	1.94

in comparison to other West African assemblages (Bremond et al., 2005b). For samples from West African savanna soils, the Ic is usually not calculated due to the lack of rondels and trapeziform short cells (Barboni et al., 2007). Trapeziform cells, typical for Pooideae (Piperno, 2006), are practically absent in the La Mouche samples, and the Ic values around 7 are due to the comparatively high numbers of rondels. Rondels are diagnostically less significant as they are produced in many Poaceae subfamilies (Mulholland, 1989). The apparent contradiction between the statement of Barboni et al. (2007, p. 462) that rondels are absent in the West African phytolith assemblages, and their good representation in the Early Holocene samples, but also in the modern samples from the Dogon Plateau, needs further clarification.

With 51 to 61%, the Iph of the fossil samples is very high and even at the upper limit of Iph values from modern Sahelian grasslands, which rarely exceed 40%. Bremond et al. (2005b) have proposed an Iph boundary of 20% to discriminate Sahelian short grass savannas from Sudanian tall grass savannas with significantly lower Iph values. The modern phytolith assemblages from the Dogon Plateau also have very high Iph values between 52 and 67%, pointing to a dominance of Chloridoideae grasses in the vegetation.

8.3. Local or regional signal?

Long-distance transport has long been recognized as a major factor for the formation of phytolith assemblages in soils (e.g. Piperno, 1988, 2006; Fredlund and Tieszen, 1994; Alexandre et al., 1997). Especially under arid or semi-arid climatic conditions and open vegetation, phytoliths may be blown in aerosols over several hundred kilometres. For the phytoliths deposited during the Early Holocene in HA2 c/d, a local (within 20 m), extralocal (between 20 and several hundred meters) and regional component (using the distance scales of Jacobson and Bradshaw, 1981) can be expected. The openness of the grassland as reconstructed from the D:P and Iph indices must have favoured wind-transport. Experiments from North America suggest that 30–70% of the phytoliths deposited in open grasslands soils originate from an extra-local or regional source (Fredlund and Tieszen, 1994). As soil formation is a long-term process, the phytolith assemblages of HA 2 c/d have accumulated over a considerable period. This phenomenon is called inheritance (Fredlund and Tieszen, 1994). Not only on the spatial, but also on the temporal scale, the GSCP assemblages represent an average of the phytolith deposition and are therefore representative for the regional vegetation in the 12th and 11th millennium BP.

8.4. Composition and ecology of the Early Holocene grasslands on the Dogon-Plateau (Table 6)

The contribution of different Poaceae subfamilies to the Early Holocene grasslands at Ounjougou can be further specified from the GSCP assemblages. The differentiation of bilobates according to their sub-family specific types shows that the contribution of Aristidoideae and Chloridoideae bilobates to the assemblages is negligible. As Bambusoideae GSCP have not been found in the samples, the bilobates, trilobates and crosses can be attributed to the Panicoideae, the saddles to the Chloridoideae. The rondels in the fossil samples might originate from the inflorescences of Panicoid grasses where they commonly occur (Piperno and Pearsall, 1998). The plateau saddle phytolith, well represented with 13–20% in the fossil and modern samples, cannot be interpreted so far (Table 6).

It is conceivable that the largest part of the Chloridoideae phytolith input comes from the annual species *Schoenefeldia gracilis*. Under modern conditions on shallow, silty and loamy soils of the Sahel, *S. gracilis* is the dominant grass, often forming almost monotypic stands (Le Houerou, 1989, pp. 71; Müller, 2003). This species is also dominant in the modern grassland on shallow soils of the Dogon Plateau whose phytolith assemblage has an Iph of 67% (Sample 134). The Early

Table 6
Grass short cell phytoliths (GSCP) in fossil and modern sediment samples from Ounjougou: a) Absolute counts, a) Percentages of subfamily specific phytoliths.

	Fossil samples			Modern surface samples		
	Ravin de la Mouche – 11.81 HA2c/d	– 11.76 HA2c/d	– 11.57 HA3Ab	Dogon Plateau savanna	Degraded gallery forest	Ségué gallery forest
<i>a) Absolute counts</i>						
Sample number	109	116/117	122/123	134	135	138
<i>Aristidoid</i>						
Bilobate Aristidoid		1	5	2		1
<i>Panicoid</i>						
Bilobate Panicoid	35	24	21	40	17	10
Bilobate indiff.	33	38	30	14	34	19
Bilobate Stipa type		3	1	16	2	3
Cross Panicoid			3	6	6	
Cross indiff.	11	10	4	7	5	3
Trilobate	1	7	2	3	3	2
<i>Chloridoid</i>						
Saddle squat	30	26	27	86	18	13
Saddle tall	11	21	22	44	15	13
Saddle indiff.	48	26	18	20	43	13
Bilobate Chloridoid	1			5	3	2
<i>Other</i>						
Bilobate Ehrhartioid					1	2
Plateaued Saddle	37	25	36	42	5	8
Rondel	13	16	14	23	26	12
Trapezoid sinuate	1					
Other	3		2			
Sum GSCP	224	197	185	308	178	101
<i>b) Percentages of subfamily specific phytoliths</i>						
Aristidoid		0.5	2.7	0.7		1.0
Panicoid	37.6	45.2	35.5	32.5	39.9	36.7
Rondel (probably Panicoid)	5.0	4.6	5.5	2.9	12.3	11.9
Plateaued saddle	16.7	12.6	19.7	13.6	2.8	7.9
Chloridoid	40.7	37.1	36.6	50.3	44.4	40.5
Ehrhartioid					0.6	2.0
SUM in %	100	100	100	100	100	100

Holocene grasslands on the Dogon Plateau were mainly composed of annuals, due to the edaphic aridity of the weakly developed soils on the sandstone surfaces and in the Pleistocene silts. Therefore the majority of Panicoid grasses, represented by bilobates, crosses and trilobates, were most probably also annuals. Aristidoids with their only Sahelian genus *Aristida* are weakly represented in the phytolith samples, and do not seem to have made a major contribution to the vegetation on the plateau. This can be explained with the edaphic conditions on the silty and loamy soils of Pleistocene origin, which were not suitable for *Aristida*. *Aristida* prefers deep sandy soils, and it is conceivable that *Aristida* species were growing on the sand dunes in the plains off the plateau.

The Early Holocene annual grasslands of the Dogon Plateau were not heavily affected by fire. The large number of micro-charcoals in the phytolith samples of HA3 Ab originated from the gallery forest, not from the grassland, because charred wood is much better represented than charred grass epidermis fragments. The rarity of bush fires is also indicated by the low number of pyrofusinites, typical for aerial carbonization of vegetative tissues, in the palynofacies. Probably the annual grass cover did not provide enough biomass for large-scale bush fires.

The composition of the GSCP in the two surface samples from modern gallery forests is similar to the grassland sample, thus demonstrating the influence of lateral phytolith transport into the closed woody vegetation. In both samples, bilobates of the Ehrhartioid type have been found. Although rare, they might indicate the presence of rice, probably a wild *Oryza* species, in the surrounding area. Together with sponge spicules, diatoms, Cyperaceae and (in one case) Podostemataceae (Fig. 7) they serve as indicators of permanent or semi-permanent waterbodies. Wild rice was an important food plant in the later Holocene (Klee et al., 2000; Murray, 2004). Although

Ehrhartioideae bilobates are absent in Ravin de la Mouche, their diagnostic potential, as an indicator for this important cereal, should be kept in mind for future studies.

8.5. Landuse potential of the Early Holocene vegetation

The presence of ceramics and small bifacial stone tools in HA1 attests to the presence of human populations at Ounjougou during the Early Holocene (Huyssecom et al., 2004, in press). Our palaeoecological data from La Mouche allow for an assessment of the land resources and their potential use. The landscape of Ounjougou included two major landscape and vegetation units as reconstructed from geomorphological evidence and the botanical macro- and micro-remains: 1. the Sahelian grassland composed mainly of annuals, with a sparse tree cover, 2. the meandering river with a gallery forest and a floodplain comprising permanent small lakes. Although the pottery has been found in layer HA1 which is slightly older than HA2 and HA3 and not directly dated, there is good reason to suppose that the Early Holocene grasslands and gallery forest had already been developed from the very beginning of the Holocene.

The river provided a permanent water source with fish, other aquatic animals and waterplants, such as *Nymphaea* with edible tubers. The rivers and lakes attracted herbivores from the surrounding grassland pastures and offered favourable conditions for hunting. Among the gallery forest trees, *Diospyros mespiliformis* and palms provided edible fruits that could be dried and stored. However, tree fruit exploitation, which should become a major economic activity in later periods of the Holocene (Neumann et al., 1998; Kahlheber and Neumann, 2007), probably did not contribute very much to the diet. In comparison with the Middle Holocene woody plant communities of Ounjougou (Eichhorn and Neumann, in press), the Early Holocene

vegetation was poor in woody species and had only a limited potential for their exploitation.

The most important carbohydrate source was provided by the annual Panicoid species in the vast grasslands. Many annual Panicoid grasses have edible grains, such as species from the genera *Brachiaria*, *Panicum*, *Digitaria*, *Cenchrus* and *Echinochloa*. Archaeobotanical and ethnographic studies prove the extensive use of Panicoid grasses in the Sahara and the Sahel from the Early Holocene until modern times (Harlan, 1989; Wasylikowa, 2001; Barakat and Fahmy, 1999; Klee et al., 2000, 2004). Some ethnic groups collect the grains as a staple on a regular basis (Tubiana and Tubiana, 1977; Smith, 1978), while others use them as supplementary famine food (Burkill, 1994; Selleger, 2007). Like in the Near East (Hillman, 1996), the massive expansion of wild cereals under the warm and moist Early Holocene climate seems to have triggered the development of a new resource exploitation behaviour, linked with technological innovations for collection, storage and processing. Before consumption, the starch-rich grains of the wild cereals had to be subject to heat treatment in order to increase their digestibility by amylase in the human body (Stahl, 1989). While bread baking became the predominant form of processing in the Near East, the small grains of the tropical African Panicoideae are typically boiled in a container, as practiced today in the Sahel. Thus the innovation of pottery making, as indicated by the ceramic sherds in Ravin de la Mouche, might have been directly related to the abundant availability of Panicoid grasses in the Early Holocene landscape.

8.6. Ravin de la Mouche in a West African palaeoclimatic context

Ravin de la Mouche is one of the few West African sites illustrating the vegetation development after the end of the Younger Dryas and the beginning of the Holocene. This drastic arid-humid transition, matching a major Greenland warming event, is placed between 11.7 and 11.0 ka BP in tropical Africa (Gasse, 2000) and was correlated with an abrupt resumption of the African Monsoon, the onset of a strongly seasonal rainfall regime (Garcin et al., 2007) and exceptional high stands of the water level in Lake Bosumtwi/Ghana (Shanahann et al., 2006). The reconstructed Early Holocene vegetation of the Dogon Plateau shows remarkable similarities with pollen evidence from sites in the Sahelian Manga Grasslands of Nigeria (Salzmann and Waller, 1998; Waller et al., 2007). In the Manga Grasslands dune depressions, freshwater vegetation with *Typha* established after 11.5 ka BP, followed by a swamp forest with *Alchornea*, *Uapaca* and *Syzygium* after 10.5 ka BP. The grasslands of the surrounding dune fields remained very open and Sudanian savanna trees are only recorded after 8.7 ka BP. In both areas, there is an obvious time lag between the onset of climatic and hydrological humid conditions at ca 11.5 ka BP and the establishment of Sudanian savannas at least 2000–3000 years later (Waller et al., 2007; Eichhorn and Neumann, in press).

9. Conclusion and perspectives

At Early Holocene Ounjougou, the rarity of trees in the zonal vegetation, the presence of Chloridoid/Panicoid annual grasses and the absence of fire in the grassland point to the existence of stable “climatically determined savannas” (Sankaran et al., 2005), which were additionally favoured by edaphic poor soils on the sandstone-derived silts. These grasslands were distinctly different from the Middle Holocene tropical savannas in West Africa, with their much higher tree cover and regularly affected by fire (Salzmann, 2000; Salzmann et al., 2002; Eichhorn and Neumann, in press). Trees were mainly restricted to gallery forests along rivers or lakes. The major resources were the grains of Panicoid grasses, wildlife and a few edible fruits from gallery forest trees. Their seasonal availability probably exerted a strong influence on mobility patterns of the prehistoric population.

The analysis of the plant remains from Ravin de la Mouche shows the potential of phytolith research on buried soils and alluvial sediments in Africa. With micro-morphology and phytolith analysis, ancient land-surfaces and paleosoils can be detected. The former upper horizons of the paleosoils contain the phytoliths deposited by a local in situ vegetation plus a regional component, whereas alluvial deposits represent allochthonous plant remains from a wider catchment area.

A combination of the general and indices approaches is an appropriate tool for phytolith based vegetation reconstructions in Sub-Saharan Africa. The indices D:P, Ic and lph are useful for a broad-scale overview on palaeovegetation and climate. Application of the general approach on the samples from Ravin de la Mouche shows new perspectives for future phytolith research in Africa:

1. A finer subdivision of GSCP allows us to assess the contribution of different grass-subfamilies to the assemblages. More studies on GSCP of modern grasses could increase the chances to find morphotypes specific for tribes, genera or even species, e.g. *Oryza*. This approach can also be applied, complementary to palynology, for a differentiation of the hitherto unknown grassland composition in Holocene and Pleistocene lake sediment cores.
2. Besides the globular decorated type, other phytoliths seem to be valuable indicators for woody vegetation, mainly the elongate faceted and the irregular shaped faceted morphotypes. Their indicator value has to be tested with modern reference material from plants and surface samples. So far, no indicator has been found for the woody plant cover of the West African savannas. It remains open if the woody plants in a savanna are “silent” in their phytolith signal, i.e. masked by the overrepresentation of grass phytoliths. The Holocene gallery forest can be successfully described with the Marantaceae type, the globular echinate morphotype from palms and the globular decorated morphotype. The latter subsumes spherical phytoliths with various surface decorations, which might be exploited in the future.
3. It is highly probable that there are many family- or genus-specific phytolith morphotypes in the African flora which add information about the past vegetation. Examples in this study include the Annonaceae/Cucurbitaceae, the *Hibiscus* type and the Podostemataceae type. They can be detected with the general approach, and with more studies of reference material from modern plants.

Acknowledgements

We thank our Malian colleagues and the members of the Ounjougou team for their help in the field and for inspiring discussions, especially Michel Rasse, Barbara Eichhorn, Yann le Drezen and Sylvain Ozainne. Dolores Piperno (Smithsonian Institution, Washington D.C.), generously hosted two of us (A.F. and K.N.) and patiently discussed with us the phytolith data. Thanks to Monika Heckner for drawing and editing the figures, Jennifer Markwirth for processing the samples, Manfred Ruppel for taking the SEM photos, Astrid Stobbe for her help with TILIA, and Richard Byer for language editing. We thank Georg Zizka and Stefan Dressler (Senckenberg Research Institute, Frankfurt) for hosting us in the laboratories and giving access to the herbarium collections. Our work is part of the project APPD (Archéologie du Paysage en Pays Dogon) funded by the DFG (Deutsche Forschungsgemeinschaft) and the ANR (Agence Nationale de Recherche). From 2005–2007 the French team was given financial support by the program ECLIPSE II (INSU-CNRS). The excavations were funded by the Swiss National Foundation for Scientific Research (FNRS), the Swiss-Liechtenstein Foundation for Foreign Archaeological Research (SLSA) and the Faculty of Science of the University of Geneva. A.F. conducted his laboratory work in Frankfurt with grants provided by the Humboldt Foundation and the

DAAD. The comments of one anonymous reviewer greatly helped to improve the paper. For any shortcomings, however, the authors are fully responsible.

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