Phytoliths from Archaeological Sites in the Tropical Forest of Ituri, Democratic Republic of Congo

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Phytoliths record late Quaternary vegetation at three archaeological sites in the Ituri rain forest. The oldest deposits, dated to ca. 19,000 to 10,000 ^{14}C yr B.P., contain abundant phytoliths of grasses but also enough arboreal forms to show that the landscape was forested. The late-glacial forests may have had a more open canopy than today's. Younger phytolith assemblages show that the northeast Congo basin was densely forested throughout the Holocene. Archaeological materials among the phytoliths show that people lived in this region during the Pleistocene. Therefore, Pleistocene and Holocene prehistoric foragers probably inhabited tropical forests of the northeast Congo basin many millennia before farming appeared in the region. © 2000 University of Washington.

Key Words: **Ituri; Democratic Republic Congo; central Africa; phytoliths; Later Stone Age foragers; last glacial maximum; vegetation dynamics; "refugia."**

INTRODUCTION

Paleoecological data and climate models indicate that lowland tropical forests underwent large climatic and vegetational changes during the Pleistocene (Kutzbach *et al.,* 1998; Van der Kaars and Dam, 1995). However, such changes appear to have been more complex than the simple cycles of forest contraction and expansion resulting from climatic aridity that are proposed by refugial theory (Haffer, 1969; Hamilton, 1972). For example, some lowland forests contained species associations not seen today (Colinvaux *et al.,* 1996; Maley and Brenac, 1998), such as admixtures of evergreen lowland taxa with montane elements and trees characteristic of seasonal formations. Seasonal forests, for their part, were replaced by mixtures of savanna and thorny scrub vegetation (Van der Hammen and Absy, 1994). These changes were brought about by both sig-

nificantly cooler and drier climates and, perhaps, by markedly reduced CO_2 (Jolly *et al.,* 1998). Plant physiological adaptations to low CO_2 (Cowling, 1999) suggest that late glacial maximum tree taxa would produce smaller leaves and, thus, promote tropical forests with a more open canopy and concomitant increase in grasses.

This paper applies phytolith analysis to the forested core of the African continent using phytoliths from three Later Stone Age archaeological sites ($>18,800 \pm 100$ [14]C yr B.P. to $<715 \pm 45$ [14]C yr B.P.) located in the Ituri rain forest, Democratic Republic of Congo. In Africa, phytolith analysis has been used for paleoenvironmental reconstruction in Senegal, People's Republic of Congo, Kenya, and Ethiopia (Alexandre *et al.,* 1997; Mworia-Maitima, 1997; Barboni *et al.,* 1999). These studies show that phytolith data from lake cores and archaeological sites record both regional and local variations in climate and vegetation in the grassland belt. The aim of this paper is to show the various types of environmental contexts in which ancient *Homo sapiens* colonized the Congo Basin during the late Pleistocene and the Holocene. Some authors have questioned whether humans could have survived in tropical forests without engaging in agriculture (Bailey *et al.,* 1989). Our work suggests that the northeastern Congo Basin was forested when it was settled by humans in the late Pleistocene and that the region remained settled while its forest changed in structure and composition thereafter.

SETTING

The Ituri region is located in the northeast corner of the Guineo-Congolian tropical forest of central Africa (White, 1983), just north of the equator (Fig. 1). In the Ituri region, between the Western Rift and the Congo Basin, are hilly granitic uplands of the north and east, and plains of the center, south, and west. Altitudes range from 1000 m for the highest uplands in the east to 600 m for the plains to the west. The sites studied are 700–800 m above sea level.

Although little rain falls in January and February, an annual rainfall of 1600–1900 mm (Bultot, 1971) allows most of the Ituri district to support evergreen and semievergreen forests. Some of the forests are dominated by one taxon, while others are mixed (Hart, 1985). In the monodominant forests, common in the south and west, *Gilbertiodendron dewevrei* accounts for more than 90% of the canopy. In mixed forests, scattered through the region, no single species forms more than 40% of the canopy. In the Ituri district, monodominant forests have far fewer species per hectare (10) than do mixed forests (53) (Hart and Hart, 1986). Evergreen species make up 94% in monodominant forests and 86% in mixed environments (Hart and Hart, personal communication, 1995). The most common species of trees in the lowland rain forest of Ituri are *Gilbertiodendron dewevrei* (Caesalpiniaceae), *Cynometra alexandrii* (Caesalpiniaceae), *Julbernardia seretii* (Caesalpiniaceae), *Klainedoxa gabonensis* (Irvingiaceae), *Cleistanthus michelsonii*

(Euphorbiaceae), *Erythrophleum suaveolens* (Caesalpiniaceae), *Fagara macrophylla* (Rutaceae), and *Canarium schweinfurthii* (Burseraceae). The most common herbaceous family is the Marantaceae (T. Hart and C. Ewango, personal communication).

The Ituri forest occupies a granitic domain (Lavreau, 1982) shaped in part by neotectonics from the neighboring Rift. Grabens, inselbergs, and tors are common in that section of the forest nearest the Rift, as are boulders and rock shelters of granitoid rocks (Fig. 2) (González, 1997). The shelters, which have attracted repeated human occupation, developed either near inselberg peaks or on hill slopes. Located in outcrops 10 to 15 m, the caves have their mouths randomly oriented, with variable light and temperature conditions and enclosed habitable spaces (average: 51.9 m^2), including dry and wet areas. The geochemistry of the cave deposits in which phytoliths were found is described by Mercader (2000).

ARCHAEOLOGY AND CHRONOLOGY

Archaeological surveys in the lowland forest of Ituri identified over 50 archaeological sites in just 8.5 km^2 (Mercader, 1997). This density of sites suggests that the Ituri forest was settled extensively during prehistoric times. Ten rock shelter sites were excavated, over a period of 12 months, with up to 2 m^2 excavated per shelter. The results indicate that by the last glacial maximum prehistoric Later Stone Age foragers had settled tropical forest environments. Occupation of diverse habitats continued throughout the Holocene, many millennia before the first archaeological indications of the appearance of farming in the region (Mercader *et al.,* 2000).

Radiometric AMS dating (Table 1) suggests that human occupation in this sector of the Congo Basin had already taken place by $18,800 \pm 100$ [14]C yr B.P., before the last glacial maximum (LGM). Additional ages ($10,530 \pm 50$ [14]C yr B.P.; $10,015 \pm 55$ [14]C yr B.P.) show that approximately 8000 years later, by the start of the Holocene, forager groups continued to settle the Ituri region. Hunter-gatherer groups were still present in the area in the middle Holocene (6025 ± 70 ^{14}C yr B.P.; 2970 ± 70 ^{14}C yr B.P.) and in the late Holocene (1080 ± 41 ^{14}C yr B.P.; 971 ± 33 ^{14}C yr B.P.; 840 ± 70 ^{14}C yr B.P.; 825 ± 30 ^{14}C yr B.P.; 813 ± 35 ^{14}C yr B.P.; 715 ± 45 ^{14}C yr B.P.).

Among ten excavated sites, three were selected for phytolith analysis: Matangai Turu NW (northern Ituri), Makubasi NW (eastern Ituri), and Lengbe (central Ituri) (Figs. 1 and 2). The oldest direct date available in a site for which phytolith analysis was carried out is $10,530 \pm 50$ [14]C yr B.P., obtained on charcoal from a depth of 1.25 m from the site of Matangai Turu NW. Because this layer is underlain by 0.9 m of cultural deposits that contain chipped stone representative of the Later Stone Age, and because major changes in the Matangai Turu NW paleoenvironmental assemblages occur just below this culturally dated stratum, we infer that the basal layers of this site are no younger than the LGM.
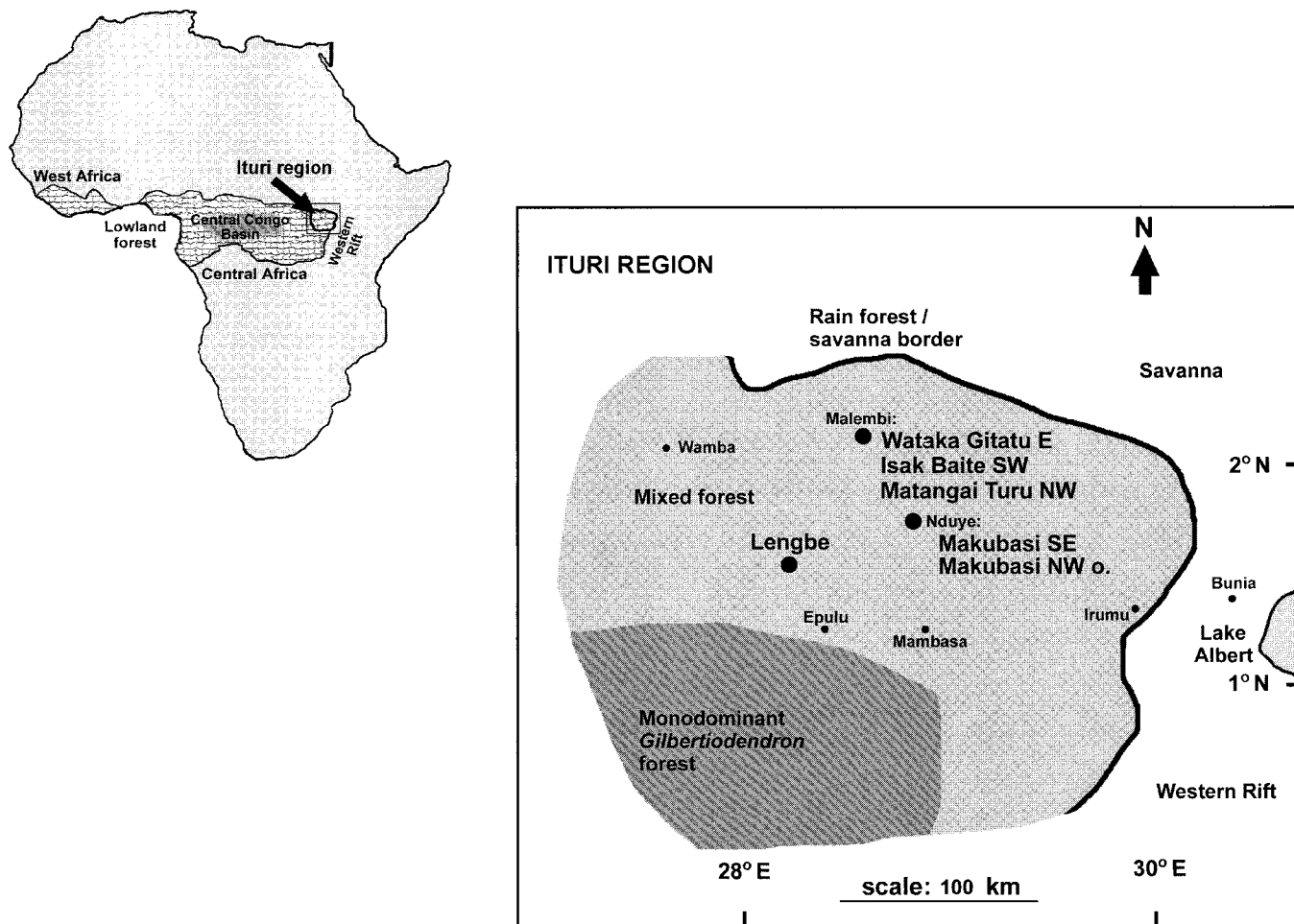
FIG. 1. Map of the study area, showing the extent of central African lowland forest, the Congo Basin, and the Western Rift. The Ituri region shows the forest–savanna border, the geographical distribution of mixed and monodominant forests, and the archaeological sites mentioned in this paper.

FIELD AND LABORATORY PROCEDURES

Archaeological sediment for phytolith analysis was recovered, depending on feasibility, either by scraping sediments out into a plastic bag or by inserting an aluminum frame into excavation unit walls. Spacing between samples was 10–15 cm and soil boundaries were avoided. Sample weight averaged 250 g. The volume of one sampling unit was 10 cm by 10 cm in area and 5 cm deep, a standard volume of sediment in archaeology.

To sample the modern "phytolith rain," we collected topsoil from directly underneath tropical forest plots of known species composition (identifications by T. Hart; see Mercader, 2000). Two transect areas, each 500 m by 200 m, were placed in monodominant (Lenda 1) and mixed (Edoro/Afarama 1) forests. Each such area was divided into 250 units of 20 m by 20 m. Out of a total of 500 units available for the survey, 10 units (2% of the total) were chosen for their typical floristical composition. Spacing between units was 40 m. Five individual soil samples were collected at 5-m intervals along the southern

or northern side of each of the 10 units chosen. Samples were retrieved from the uppermost part of the A horizon; after removal of surface litter, a soil area of 10 cm by 10 cm by 5 cm depth was sampled. It is likely that topsoil samples contain phytolith palimpsests from multiple successional phases in the late Holocene, when tropical rain forests persisted in the area in which samples were collected (Hart *et al.,* 1996).

We used four steps to extract the phytoliths: (1) Deflocculation of 10–50 g dry soil material in tetrasodium diphosphate decahydrate ($Na_4P_2O_7H_2O$) in 1 liter of distilled water, placed in an automatic shaker overnight, then washed in distilled water and dried. (2) Separation of sand (63–2000 μm) by wet sieving; removal of clay (<2 μm) and fine and middle silt (2–20 μm), and coarse silt (20–63 μm) by gravity sedimentation; and drying. (3) Removal of organic matter after heating in a sand bath in 30% solution of H_2O_2; washing in distilled water; drying. (4) Phytolith extraction from the sand and silt fractions in a solution of $ZnBr_2$, HCl, and distilled water (specific gravity 2.3) centrifuged at 1000 rpm for 10 min.
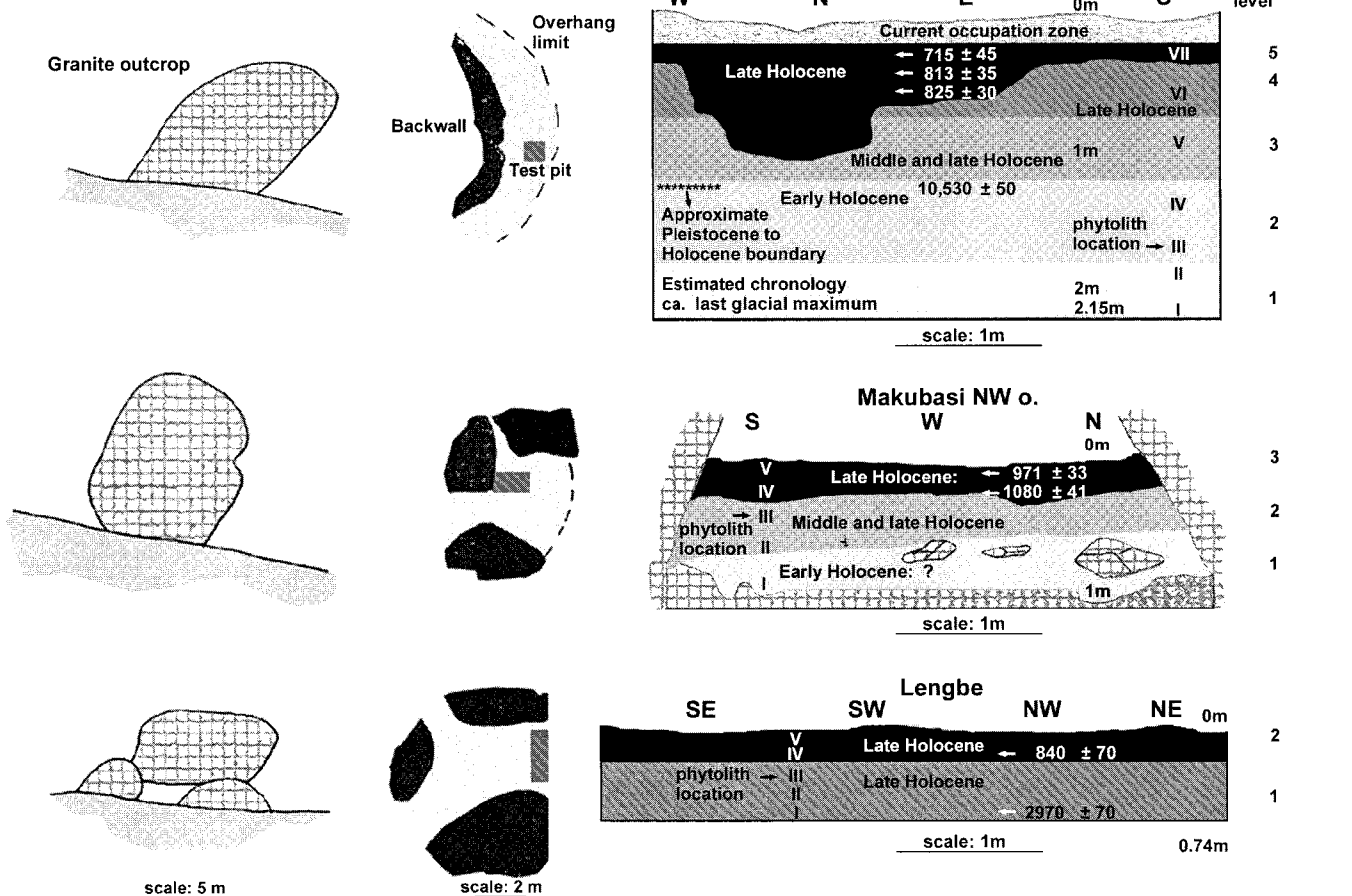
FIG. 2. Drawings of Ituri rock shelters, showing cross sections, views of available space for habitation, test pit locations within the shelters, stratigraphic sections, and radiocarbon ages (in ^{14}C yr B.P.). Shade variations show distinct cultural levels. Archaeological contents of these levels are as follows. Matangai Turu NW levels: 1, 2, 3, lithics; 4, lithics and ceramics; 5, lithics, ceramics, and metal. Makubasi NW o. levels: 1, 2, lithics; 3, lithics and ceramics. Lengbe levels: 1, lithics; 2, lithics and ceramics.

Phytoliths were identified at magnifications ranging from 400× to 1000× (Zeiss standard light microscope). Opal phytoliths from the sand and silt fractions were counted separately. The number of silt-sized phytoliths per sample studied averaged 120 (range 50–250). The sand fraction commonly contained fewer phytoliths, so that all found on the slide were counted. Phytoliths were identified by comparison with a reference collection of tropical African plants comprising more than 200 species (Runge, 1999). We also consulted catalogs from 2000 species of neotropical plants studied by Piperno and more than 400 species of Southeast Asian plants studied by Kealhofer and Piperno (1998).

Radiometric AMS dates were obtained from charcoal, endocarp, and human bone by four different labs, Utrecht (Holland), Beta (USA), Arizona (USA), and NOSAMS (USA). All charcoal dates relevant to this study were obtained from single samples no more than 2 mm in diameter. No bulk samples were dated.

RESULTS

Present-Day Phytoliths from the Ituri Forest

Phytolith assemblages from soils of the modern Ituri forest (Fig. 3) contain many (40–70%) silt-sized spherical phytoliths (morphotype B), many elongate phytoliths (A4), and few short-cell phytoliths (1–6%) (Alexandre et al., 1997).

Morphotype A comprises elongate phytoliths (Figs. 4a and 4b) mostly produced by trees and shrubs. Morphotype B (Figs. 4c and 4d) is made up of spherical bodies that appear to originate mainly from wood, seeds, and leaves of dicots. Morphotype C (Fig. 4f) is an irregular phytolith of unknown origin

TABLE 1
Radiocarbon Ages

Site	Lab no.	Archaeological level	Material dated	Age (^{14}C yr B.P.)
MSE	Os-21250	basal	1 mm charcoal	$18,800 \pm 100$
MTNW	UtC Nr5075	2	<1 mm charcoal	$10,530 \pm 50$
IBSW	AA33225	basal	endocarp of *Canarium schweinfurthii*	$10,015 \pm 55$
WGE	AA 33226	basal	1 mm charcoal	6025 ± 70
L	Beta 127079	1	endocarp of *Canarium schweinfurthii*	2970 ± 70
MNW o.	UtC Nr 5076	3	2 mm charcoal	1080 ± 41
MNW o.	Os-22251	3	2 mm charcoal	1010 ± 60
MNW o.	UtC Nr 5077	3	2 mm charcoal	971 ± 33
L	Beta 127078	1	endocarp of *Elaeis guineensis*	840 ± 70
MTNW	Os-21235	5	endocarp of *Canarium schweinfurthii*	825 ± 30
MTNW	UtC Nr 5074	5	several 1- to 5-mm fragments of human bone	813 ± 35
MTNW	Os-21251	5	2 mm charcoal	715 ± 45

Note. MSE, Makubasi southeast; MTNW, Matangai Turu northwest; IBSW, Isak Baite southwest; WGE, Wataka Gitatu east; L, Lengbe; MNW o., Makubasi northwest outer cave.

with a distinctive, stippled surface. This stippled phytolith is represented in very high frequencies (62%) in modern monodominant *Gilbertiodendron* forests and has lower representation (5%) in mixed forests. Morphotype D (Figs. 4g and 4h), made up of specific hexagonal and hat bodies, is more common in mixed than in monodominant forests.

Morphotypes E and F (Figs. 4j, 4k, and 4l) are not diagnostic, except for F4. These can be produced by both monocots and dicots. Morphotype G2, subtype 1 (Fig. 4i), comprises the distinctive bulliform cell phytolith produced only in the Poaceae. These and other Poaceae phytoliths are scarce in the modern profiles from the Ituri forest.

Ancient Phytoliths from Archaeological Sites of the Ituri Region

Matangai Turu NW (Malembi). Phytoliths from grasses (e.g., Poaceae, morphotype G2-1) are most common in strata deposited before 10,530 ^{14}C yr B.P. (Fig. 5). In contrast, phytoliths from rain forest trees and herbs (category D1) increase greatly during the Holocene, reaching their maximum values in the last 2000 ^{14}C yr B.P. Some types of phytoliths derived from trees (category B) are most abundant in the Holocene but are present throughout the sequence. Category C, another arboreal indicator, is common during both the late Pleistocene and the Holocene.

Makubasi NW (Nduye). Arboreal phytoliths characterize this sequence, which may be entirely Holocene (Fig. 6). The sequence lacks major variations in the phytolith assemblage. The morphotypes include arboreal (B, C, and D) and herbaceous (e.g., D1) plants typical of rain forest environments.

Lengbe (Epulu). The late Holocene sequence of Lengbe spans the last 3000 ^{14}C yr B.P. As with the sequence from Makubasi NW, its main feature is the dominance of phytoliths

typical of rain forests (Fig. 7). Changes in forest composition during the Holocene may be indicated by phytolith C1, from unknown trees, which is present low in the sequence, disappears in the middle of the sequence, and reappears near the top of the sequence. Phytoliths C3, D, and F peak during the last millennium.

Although all sites suggest diachronic changes in plant use and, perhaps, in local forest composition, only Matangai Turu NW, the sole site with evidence for late Pleistocene through early Holocene human occupation, shows abrupt changes in tree–grass ratios (Table 2). Sample IV, dated to 10,530 ^{14}C yr B.P., contains more arboreal phytoliths and fewer grass phytoliths than do samples from underlying deposits.

DISCUSSION

Phytolith Representation, Source Area, and Identification

Phytoliths generally abound at all the sites examined (Mercader, 2000). They appear to come from a diverse set of plants and plant structures (e.g., tree and herbaceous seeds, tree and herbaceous leaves, bark, woods). Phytoliths consistently present include those from the Annonaceae, Burseraceae, and Marantaceae. Poaceae phytoliths are also well represented at certain time periods. Additional phytoliths, though currently unidentified, probably come from plants of the tropical forest because they abound in "modern" sediments in the region's forests. Such phytoliths include types C1 and C2, which are also common in tropical forests of central and south America (Piperno and Becker, 1996; Piperno, 1998).

In cave sediments of equatorial regions, most phytoliths represent local and *in situ* deposition, as dense vegetation prevents long-distance transport by wind. Anthropogenic materials (e.g., foodstuffs, thatching material, sleeping mattresses, medicinal and ritual plants, leaves brought in with branches
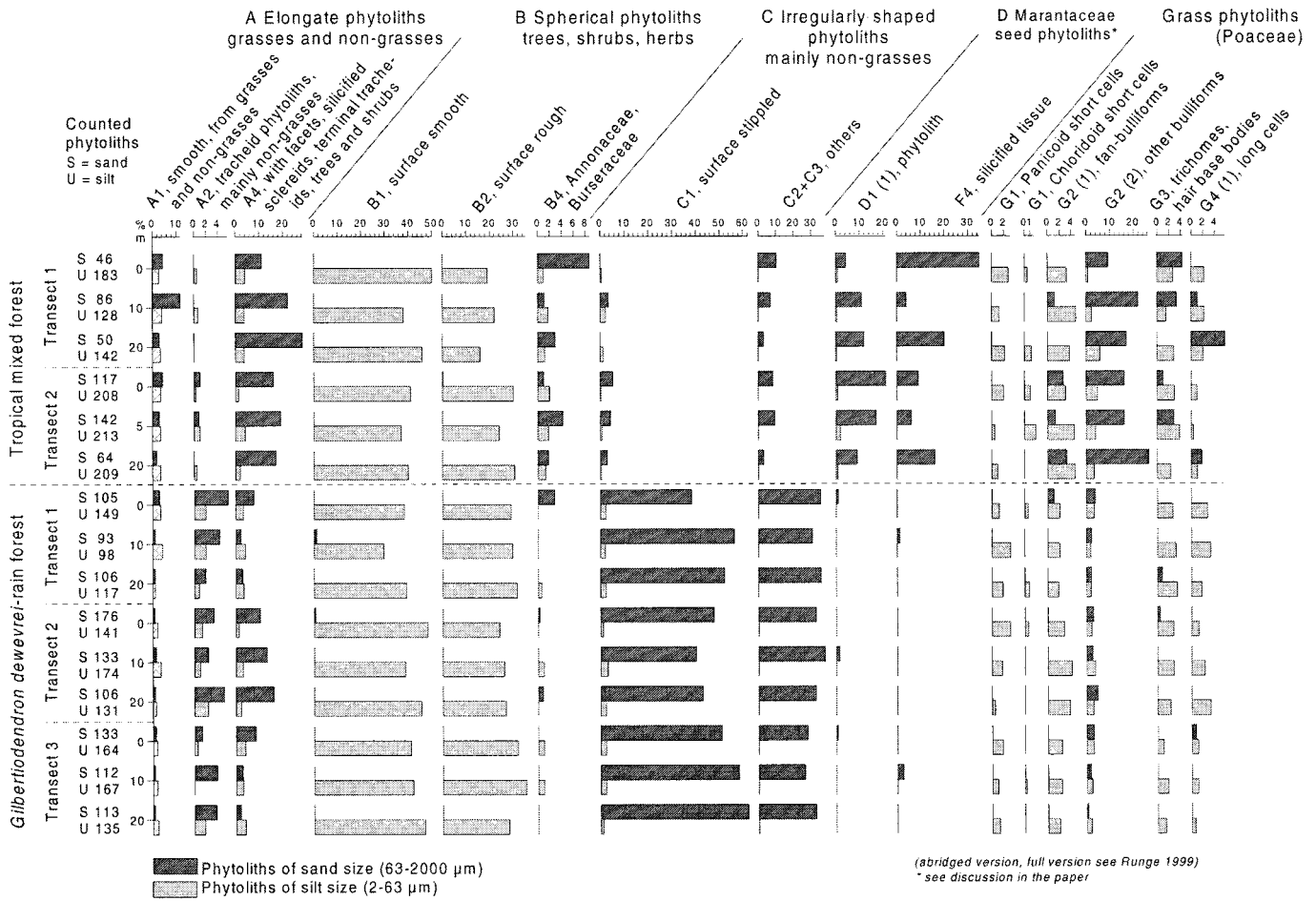
FIG. 3. Phytolith assemblages from modern mixed tropical rain forest (Edoro-Afarama), Epulu, Central Ituri, and modern *Gilbertiodendron* monodominant forest (Lenda), Epulu, Central Ituri.

collected for firewood) and colluvial influx (including plant material growing and decomposing around the rock shelter brought in through the sides of the caves by rain wash) likely account for the great majority of phytoliths present at Matangai Turu NW, Makubasi NW, and Lengbe. Today, in the Ituri forest, plants are collected by women within 0.1–4 km of their camps (Ichikawa, 1992; Bailey, 1991). Ancient tropical forest foragers probably gathered their plant resources from similarly nearby places. It is likely, therefore, that phytoliths represent the plants and the environments that people exploited within several kilometers of rock shelters.

The modern and fossil phytoliths presented here provide direct and indirect evidence for late Pleistocene and Holocene occupation of variably dense tropical forests of the northeast Congo basin by prehistoric Later Stone Age foragers. Phytolith morphotypes A, B, C, and D may emanate largely from forest taxa. Morphotype A comprises elongate phytoliths mostly produced by trees and shrubs. It comes from various vegetal structures, particularly leaves (Piperno, 1988; Postek, 1981). Morphotype B is made up of spherical rugose bodies which

appear to derive mainly from wood, seeds, and leaves of dicots. It is the most common type of phytolith found in tropical forests, including those of Central and South America and Southeast Asis (Piperno, 1993, 1998; Kealhofer and Piperno, 1998; Runge, 1999). Significantly, spherical rugose phytoliths from dicots are scarce in phytolith assemblages from modern tropical savanna and steppe environments (Barboni *et al.,* 1999; Alexandre *et al.,* 1997). Morphotype C is a phytolith of unknown origin with a distinctive, stippled surface. C1 is produced by several tree taxa and is found in large quantities in modern soils of Amazonian forests (Piperno and Becker, 1996) but never in phytolith assemblages from modern tropical savannas of Africa (cf. Alexandre *et al.,* 1997; Mworia-Maitima, 1997; Barboni *et al.,* 1999) or America (Piperno, 1988, 1998). In the Ituri forest, however, C1 may indicate a monodominant *Gilbertiodendron* stand. Morphotype D abounds in mixed forests and belongs to the Marantaceae, perhaps to the Burseraceae. Therefore this phytolith type is a potential indicator of a closed canopy. In contrast, Poaceae phytoliths are scarce in the modern profiles from the Ituri forest, reflecting their low occurrence in the shady understory of this habitat today.
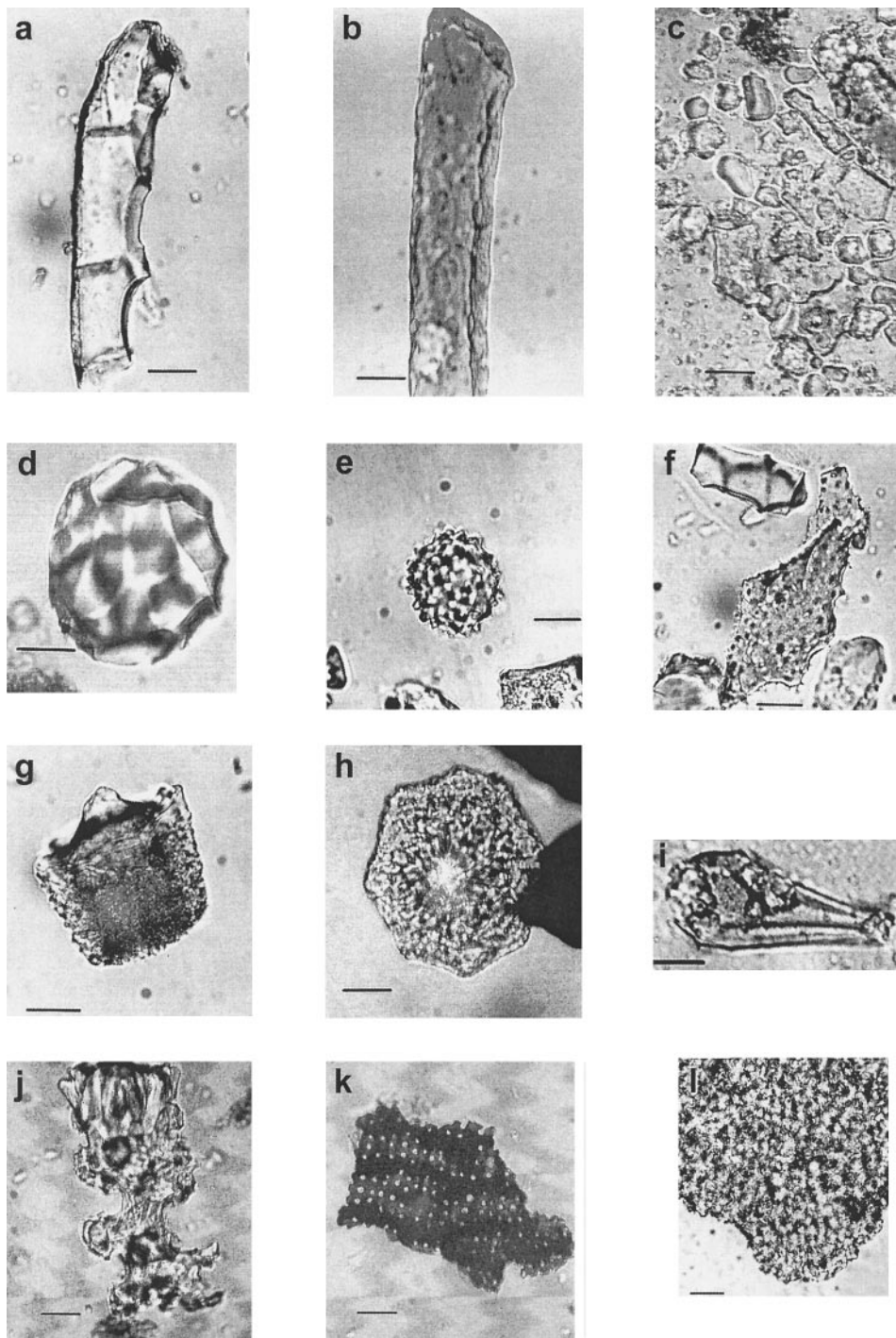
FIG. 4. (a) Modern sample from mixed forest, Central Ituri. Type A4; elongate body with facets; silicified terminal tracheid. Length 154 μm (scale bar: 20 μm). (b) Archaeological sample from Lengbe I. Type A3; elongate phytolith with a nearly smooth surface and edges along the body. Length 166 μm (scale bar: 20 μm). (c) Modern sample from *Gilbertiodendron* monodominant forest, Central Ituri. Types B1 and B2. Examples of dicot and monocot sphericals with smooth and rough surfaces. Diameter: 8–20 μm (scale bar: 20 μm). (d) Archaeological sample from Matangai Turu NW VII. Type B4; nearly spherical phytolith with facets. Size 70 × 57 μm (scale bar: 20 μm). (e) Palm phytolith. Diameter: 46 μm (scale bar: 20 μm). Reprinted with permission of Elsevier. (f) Modern sample from *Gilbertiodendron* monodominant forest, Central Ituri. Type C1; irregularly shaped phytolith with a stippled surface. Length 100 μm (scale bar: 20 μm). (g) Modern sample from *Gilbertiodendron* monodominant forest, Central Ituri. Type D1, subtype 1; shape variation with a round apex; length 60 μm, breadth 52 μm (scale bar: 20 μm). (h) Archaeological sample from Matangai Turu NW VII. Type D1, subtype 1. Diameter ca. 80 μm (scale bar: 20 μm). Perhaps a fruit-seed phytolith from the Marantaceae. (i) Archaeological sample from Matangai Turu I. Type G2, subtype 1; fan-shaped bulliform phytoliths from Poaceae (Paniceae?): 23, length 56 μm; 24, length 55 μm; 25, length 66 μm (scale bar: 20 μm). (j) Modern sample from mixed forest, Central Ituri. Type D2; specific phytolith, "head" and "body" with outgrowths. Possible origin: *Marantaceae* seeds. Length 126 μm (scale bar: 20 μm). (k) Modern sample from mixed forest, Central Ituri. Type E1; platelet with alternating amber-colored and opaque stripes, regular perforations occur in the amber-colored stripes only. Possible origin: achene epidermis of *Compositae* (scale bar: 20 μm). (l) Modern sample from mixed forest, Central Ituri. Type F4; strong silicified tissue; thick and irregularly rough; composed of puzzle-piece-shaped cells (scale bar: 20 μm).
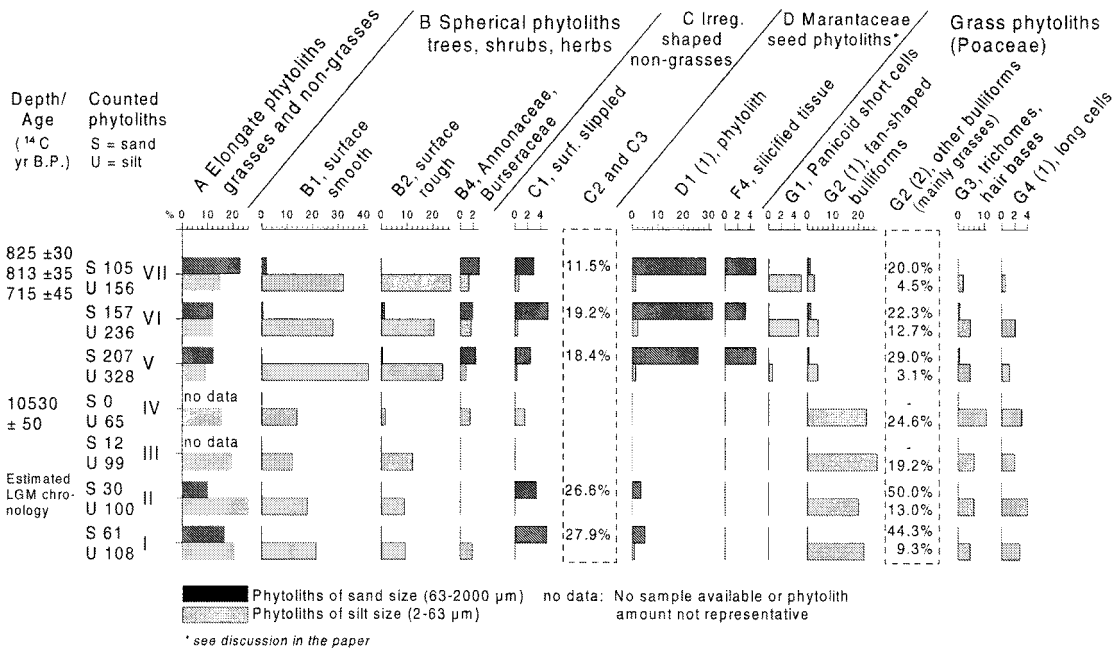
FIG. 5. Opal phytolith assemblage from archaeological site Matangai Turu NW, Northern Ituri. "No data" means small numbers of sand-sized phytoliths.

Paleoenvironmental Changes

At present, few paleoenvironmental data are available from the lowland evergreen forests of the Congo's watershed. Reconstructions of Quaternary environments are based on data from lakes located in mosaic areas (Elenga *et al.,* 1994), the far northwestern corner of the central African forest at its transi-

tion to the West African domain (Maley and Brenac, 1998), and West Africa (Talbot and Johannessen, 1992). Other contexts include pollen data from the neighboring Western Rift (Sowunmi, 1991; Bergonzini *et al.,* 1997; Marchant *et al.,* 1997), cave pollen from savanna–forest mosaic environments in their transition to both Western Rift savannas and the afro-
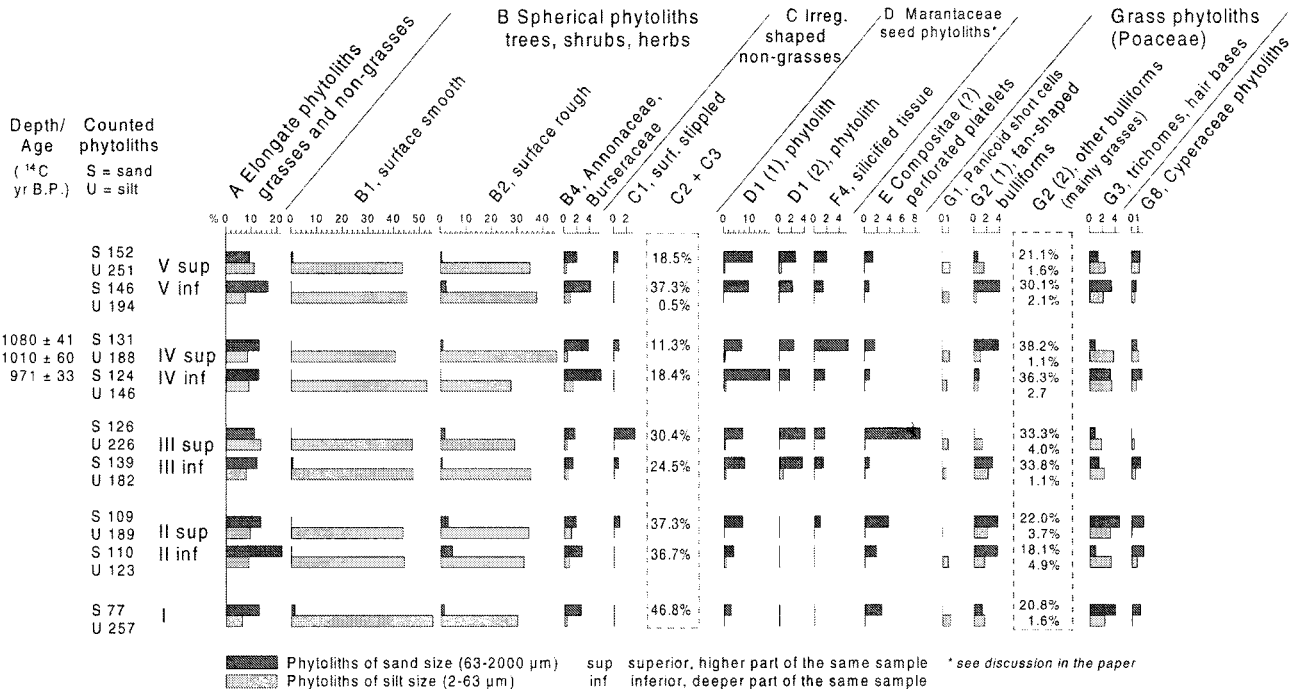

FIG. 6. Opal phytolith assemblage from archaeological site Makubasi NWo., Eastern Ituri.
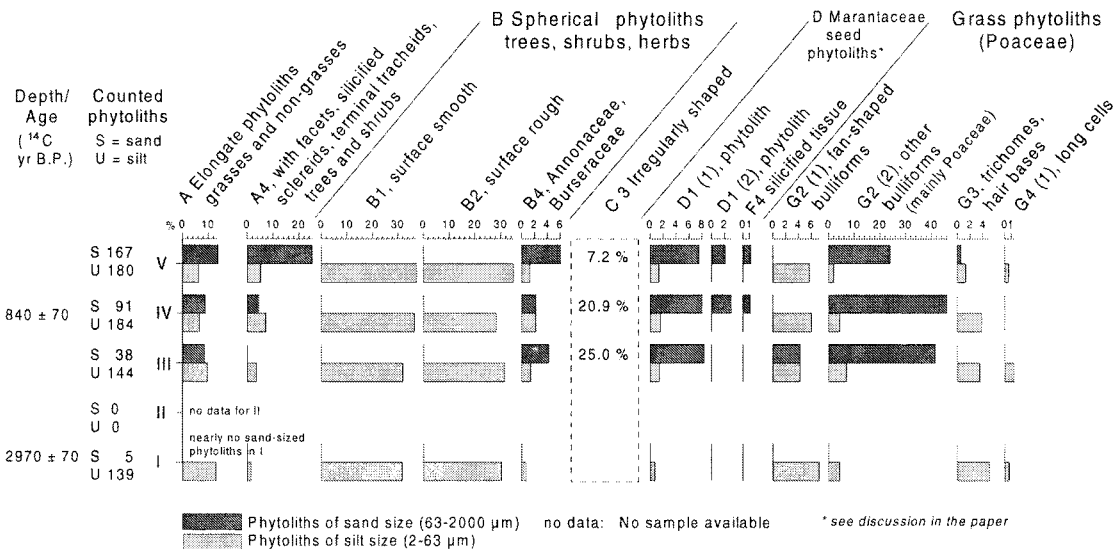
FIG. 7. Opal phytolith assemblage from archaeological site Lengbe, Central Ituri. "No data" means small numbers of sand-sized phytoliths.

montane belt (Brook *et al.,* 1990), and paleoenvironmental interpretations of pedogenesis in "stone-lines" (Runge, 1995). The climate and vegetation records studied by these authors support the idea that major dry and cool periods occurred during the last glaciation, between 22,000 and 10,500 ^{14}C yr B.P. (Talbot and Johannessen, 1992). During dry and cool intervals of the late Pleistocene, tropical forest formations probably retreated and intermixed with savannas (Elenga *et al.,* 1994), gave way to open environments (Brook *et al.,* 1990; Sowunmi, 1991; Runge, 1995), or interfingered with montane

elements (Maley and Brenac, 1998; Marchant *et al.,* 1997). But in other cases humid and cool environments may have supported forested landscapes, as shown by Jahns *et al.* (1998) and this study, with open canopies, abundant shrubs, and more forest herbs and grasses.

As for Pleistocene phytolith assemblages from Ituri, the forest cover appears to have been reduced during the last glacial cycle, but not enough to convert tropical forest to grassland. Dumbbell, cross, polylobate, and saddle phytolith morphologies from Panicoid and Chloridoid C_4 grasses sug-

TABLE 2
Abundance of Phytoliths (Percentages)

Sample no.	Arboreal morphotypes					Herbaceous morphotypes					In silt
	B1	B2	B4	C1	Total	Short-cell	G2-1	G3	G4	Total	
MTNW VII	32	27	1	1	61	10	1	2	1	14	7
MTNW VI	28	20	1	1	50	6	4	5	2	17	5
MTNW V	42	20	1	1	64	2	4	5	1	12	4
MTNW IV	14	2	1	2	19	3	24	11	3	41	1
MTNW III	12	12	0	0	24	0	28	6	2	36	1
MTNW II	18	8	0	0	26	2	22	6	4	34	1
MTNW I	22	8	2	0	32	6	22	4	3	35	1
MNW o. V	43	35	1	0	79	2	2	3	0	7	34
MNW o. IV	40	46	1	0	86	1	1	4	0	6	27
MNW o. III	46	28	1	0	74	2	1	2	0	5	21
MNW o. II	44	34	1	0	78	1	2	4	1	8	17
MNW o. I	56	30	1	0	86	1	2	2	1	6	6
L V	38	36	1	1	76	1	6	1	1	9	6
L IV	36	28	2	0	66	1	6	4	0	11	4
L III	32	32	2	0	66	3	4	4	1	12	3
L II		no data									
L I	32	30	1	1	64	4	8	5	1	18	3

Note. MTNW, Matangai Turu northwest; MNW o., Makubasi northwest, outer cave; L, Lengbe.

gestive of savannas are rare in the Pleistocene phytolith assemblages from the Ituri region. Indeed, the presence of this type of aridity marker in the Ituri assemblages is very low (5–10%, Figs. 5–7, Table 2), while they largely abound (22–40%; Alexandre *et al.,* 1997) in the phytolith assemblages from the savannas and forest–savanna mosaics of the Guineo-Congolian region (Alexandre *et al.,* 1997). These changes suggest that the Pleistocene to Holocene transition in the area was marked by a shift to a denser forest cover. Nevertheless, because arboreal taxa are represented throughout the sequence, the Ituri lowlands probably remained forested during the final millennia of the late Pleistocene. Perhaps the forests contained a dense understory of many shrubs and herbaceous plants. Such conditions are predicted by models of vegetational changes that consider the effects on plant growth of lower atmospheric CO_2 (e.g., Cowling, 1999). The decrease in phytolith occurrence per unit of a silt fraction suggests fewer occupation episodes or scarcer use of plants by Pleistocene foragers. The variability in the Holocene phytolith assemblages, on the other hand, may reflect food gathering and processing at the rock shelters, changing spatial distribution of plant resources in this part of the Ituri region, or changes in forest composition due to climatic factors that altered the abundance and distribution of plant resources available for exploitation. Tropical forest communities were not stable even after the vegetational rearrangements that marked the close of the Pleistocene. In fact, modern climate and vegetation patterns in central Africa were established only after 3,000 ^{14}C yr B.P. (Elenga *et al.,* 1994; Hart *et al.,* 1996; Jolly *et al.,* 1998; Maley and Brenac, 1998), perhaps even centuries ago (Alexandre *et al.,* 1997, p. 226).

Our phytolith analysis also suggests that the spatial boundaries between forest and grasslands, as shown in the paleogeographical depiction of the northeastern Congo "refugium" or "core area" (Hamilton, 1972), should be reconsidered. During the LGM the core area may have consisted of heterogenous vegetational formations, including forests (Ituri), mosaics of forests and grasslands (Matupi Cave: Van Noten, 1977; Brook *et al.,* 1990), and, perhaps, parkland environments (Runge, 1995), rather than a homogenous forest block. This diversity implies that proposed areas of forest refugia probably should not be depicted as monolithic havens in space and time, or as stable zones unaffected by a dryer and cooler late glacial maximum.

As for the antiquity of human colonization in Ituri, phytolith and archaeological data indicate that Later Stone Age African foragers lived in and exploited plant resources of the tropical forest (Mercader, 1997) by perhaps 19,000 ^{14}C yr B.P.

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