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ORIGINAL ARTICLE

Iron Age plant subsistence in the Inner Congo Basin (DR Congo)

Katharina Neumann[1] · **Barbara Eichhorn**[1] · **Hans-Peter Wotzka**[2]

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Abstract

Around 400 BC, pottery- and iron-producing populations immigrated into the Inner Congo Basin (ICB) and subsequently spread upstream some major tributaries of the Congo River. Until recently, their subsistence was almost completely unknown. We present an archaeobotanical study of three sites in the ICB covering parts of the Early Iron Age (ca. 400 BC-AD 650) and of the Late Iron Age (LIA) as well as subrecent times (ca. AD 1300–2000). We studied 82 flotated samples of botanical macroremains, and 68 soil phytolith samples, recovered from the *terra firme* sites Iyonda and Mbandaka, and the floodplain fishing camp site of Bolondo. The EIA assemblage from Iyonda yielded domesticated *Cenchrus americanus* (pearl millet), *Vigna unguiculata* (cowpea), *Canarium schweinfurthii*, *Elaeis guineensis* (oil palm), several wild plants, and parenchyma fragments tentatively attributed to *Dioscorea* sp. (yams). The exploitation of these plants originated in the savannas and forest-savanna ecotones of West Africa. The presence of *C. americanus* in LIA contexts at Bolondo and Mbandaka, dated to ca. AD 1350–1550, indicates that its cultivation is not dependent on a seasonal climate with a distinct dry season, contrary to previous views. The role of *C. americanus* as a staple is difficult to assess; it might have been used for special purposes, e.g. beer brewing. In spite of extensive screening, we did not detect any banana phytoliths in the EIA samples. *Musa* phytoliths were only present in LIA contexts after ca. AD 1400, leaving room for the possibility that the introduction and spread of *Musa* spp. AAB 'Plantain' in the ICB was a late phenomenon.

Keywords Archaeobotany · Central African rainforest · Human nutrition · *Musa* · *Cenchrus americanus* · *Vigna unguiculata* · Bantu expansion

Introduction

In comparison with other rainforests of the world, the Holocene prehistory of the Central African rainforest is still largely unknown. Some regions of the Central African rainforest have seen more intensive archaeological research, such as Cameroon, Gabon or the Central African Republic (Van Noten 1982; Clist 1989, 1995, 2005; Lanfranchi and Clist 1991; Essomba 1992; Oslisly 1993; Mbida Mindzie 1995/1996; Zangato 1999, 2000, 2007; Assoko Ndong 2002; Marliac 2006; Lavachery et al. 2010; Gouem Gouem 2011; de Saulieu et al. 2015; Eggert and Seidensticker 2016; Lupo et al. 2018). But the Inner Congo Basin (ICB) in the Democratic Republic of the Congo (DR Congo), covered by dense evergreen rainforest and swamp forest, counts among the most severely under-researched areas, not only within Central Africa but also in sub-Saharan Africa at large. This stands in marked contrast to the significance of the region for one of the most challenging topics of African culture history, the Bantu expansion (Nurse and Philippson 2003; Eggert 2005, 2012; de Maret 2013; Bostoen et al. 2015).

Earlier archaeological work in the ICB has revealed that probably Bantu speaking pottery- and iron-producing populations immigrated into the area in the second half of the first millennium BC (Eggert 1993; Wotzka 1995; Livingstone Smith et al. 2017) and subsequently spread upstream along some major tributaries of the Congo River. However, until recently, nothing was known about the subsistence of these

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Barbara Eichhorn—deceased.

✉ Katharina Neumann
k.neumann@em.uni-frankfurt.de

[1] Institute for Archaeological Sciences, Goethe University, Norbert-Wollheim-Platz 1, 60629 Frankfurt am Main, Germany

[2] Present Address: Institute for Prehistory, African Archaeology, Cologne University, Jennerstraße 8, 50823 Köln, Germany

immigrants. Were they farmers, i.e. did they mainly rely on domesticated plants and animals, as suggested by earlier, mainly linguistic-based studies (Vansina 1990; Phillipson 2002; Diamond and Bellwood 2003; Bostoen et al. 2013, 2015; Russell et al. 2014)? And to what extent did wild resources, likewise suggested as important by linguistic evidence (e.g. Bostoen et al. 2013; Bostoen 2014; Bostoen and Koni Muluwa 2017), contribute to their economies?

Similar questions concern the further development of Iron Age human subsistence and nutrition in the ICB. The earliest available historical source on staple foods in the area only dates back to the eve of European colonisation. We owe it to Curt von François (1888) who observed, in 1885, ubiquitous plantain (*Musa* spp. AAB 'Plantain') cultivation, supplemented only here and there by *Manihot esculenta* (manioc), *Zea mays* (maize) and *Saccharum officinarum* (sugar cane). From his detailed descriptions, it is clear that *Elaeis guineensis* (oil palm) and fish were likewise important, while domestic animals, hunting, and gathering were secondary. Of the staple foods consumed at the time none is indigenous to the Congo Basin, nor indeed to Africa. Also it is well attested that the New World crops *M. esculenta* and *Z. mays*, although principally available on the continent from around AD 1500, never gained importance in large parts of the ICB before the early 20th century (R Eggert 1987). When and how did plantains make their appearance, and what did equatorial rainforest economies look like before the introduction of *M. esculenta* and *Z. mays*? Above all, what did people principally eat before the late 19th century? So far, the evidence available on this question has been limited to piecemeal reports on a few individual finds of charred endocarps of oil palm or *Canarium schweinfurthii* (incense tree, Burseraceae) (e.g. MKH Eggert 1987; Wotzka 1995) and archaeozoological analysis of the very few terrestrial animal and fish bones found (Van Neer 1990, 1991, 2000).

The most accurate and meaningful evidence of ancient plant use comes from the remains of the plants themselves in archaeological sites. However, archaeobotanical studies focusing on plant exploitation in the Central African rainforest are still very rare. Besides charcoal and the endocarps of oil palm, ubiquitous in archaeological sites of the area (e.g. Oslisly and White 2007; Hubau et al. 2014, 2015; Kahlheber et al. 2014b; Morin-Rivat et al. 2016; Höhn and Neumann 2018), direct material evidence of other useful plants is scarce. It is therefore not surprising that each new archaeobotanical find, although not more than a needle in a haystack, entails far-reaching interpretations for the whole Central African rainforest. Especially relevant for the Bantu expansion are a handful of sites in southern Cameroon dating to the first millennium BC that yielded macro- and micro-remains of domesticated plants. The *Musa* phytoliths from Nkang (Mbida et al. 2000; Mbida Mindzie et al. 2001) seemed to support earlier claims that plantain, having originated in SE Asia, has been a staple crop in Central Africa for at least the past 3,000 years (De Langhe et al. 1994/1995). Unexpected finds of *Cenchrus americanus* (pearl millet) caryopses at the sites of Bwambé-Sommet and Abang Minko'o (Eggert et al. 2006; Kahlheber et al. 2009a) provoked the hypothesis that the savanna crop could only thrive in the Central African rainforest during the 'first millennium BC forest crisis', when the climate was drier and more seasonal than today. No less surprising was evidence for Early Iron Age (EIA) pearl millet cultivation found at Boso-Njafo in the ICB (DR Congo), dated around 400–200 BC (Kahlheber et al. 2014a).

We present here a detailed archaeobotanical study on the plant macroremains and phytoliths from three sites in the ICB (Fig. 1): Iyonda, Mbandaka, and Bolondo, covering the periods of ca. 400 BC-AD 650 (EIA), and Late Iron Age (LIA) and subrecent times (ca. AD 1300–2000). Our results challenge earlier hypotheses on prehistoric plant use in the Central African rainforest, especially regarding pearl millet, as well as previous assumptions about the nature of regional EIA subsistence.

The basic data for this study were generated by Barbara Eichhorn. Due to her tragic death on 7 February 2020, Barbara was not able to finish the manuscript and see publication of her results, which she had elaborated with great scrutiny. Barbara was an excellent archaeobotanist who had been working in many regions of Africa for more than 25 years. Her contribution to the progress of African archaeobotany cannot be overestimated. We greatly appreciate Barbara's work as participant of several international research groups, but mainly as a respected member of the archaeobotanical teams at the Universities of Frankfurt and Cologne. More detailed information about Barbara, her scientific work, and a publication list can be found in ESM 1.

The sites in their present-day ecological and economic settings

Ecological setting

All located within Köppen-Geiger zone Af, the sites of Mbandaka, Iyonda and Bolondo today have ecological conditions governed by Tropical Rainforest Climate (Peel et al. 2007), with approximate annual precipitation rates of between 1,675 (Mbandaka/Iyonda) to 2,077 mm (Boende). Rainfall seasonality across the year is only weakly pronounced, the driest month being July with > 70 mm rainfall at Mbandaka/Iyonda and > 130 mm at Boende. If this type of climate lacks any pronounced dry season, temperature variability is even more uniform, with maximal monthly average differences well below 2 °C and a long-term yearly average of 25.4 °C (https://en.climate-data.org/; retrieved

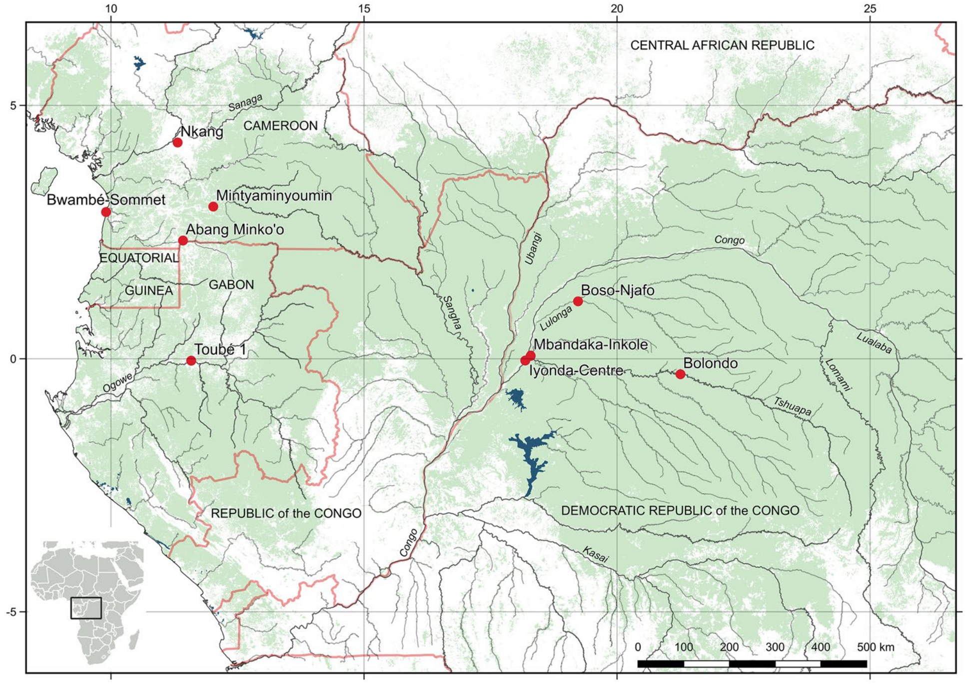

Fig. 1 Map of the Inner Congo Basin and adjacent areas with major archaeological sites mentioned in the text. Shading indicates the extent of tropical forests for the year 2001, extracted from MODIS Land Cover Type (MCD12Q1) Version 6 data (Friedl et al. 2019), Land Cover Type 1 (International Geosphere-Biosphere Programme), Class 2 (downloaded July 8, 2020, from NASA EARTHDATA; https://lpdaac.usgs.gov/products/mcd12q1v006/). With OpenStreetMap and other vector overlays provided by GEOFABRIK, RCMRD GeoPortal, GSHHG, and Natural Earth. Created using QGIS v3.10.10

August 2020; De Weerdt et al. 2016). Warm (annual temperature averages > 24.4 °C) and wet climates in our study area sustain permanently high air humidity.

Together, all these climatic parameters create typical settings for tropical rainforest, which is the dominant land cover type in the ICB and also around the three sites under discussion. The major vegetation types after the UNESCO/AETFAT/UNSO classification are Guineo-Congolian rainforest, riparian forest and swamp forest (White 1983). The formations on the *terra firme* include mature evergreen and, to a lesser degree, semi-evergreen forest, as well as pioneer and secondary forests. Periodically inundated forests (forêts périodiquement inondées) dominate on hygrophilous soils along river courses, and swamp forests (forêts marécageuses) occur where waterlogging prevents the complete decomposition of organic matter (Lebrun and Gilbert 1954; Vande Weghe 2004; De Weerdt et al. 2016).

There is considerable geographic diversity in species composition and appeareance of forest formations across the area, due among other things, to microclimatic, topographic, hydrographic, edaphic, and historical factors, both natural and anthropogenic. For instance, both evergreen rainforest and formations of the swamp forest type (with abundant *Uapaca heudelotii*) characterise much of the landscape just a few steps behind the fishing camp of Bolondo, while the terrain has been widely cleared and kept quite open by construction, urban activity and commercial mining in Mbandaka-Inkole, and by cattle grazing as well as regular mowing at Iyonda. Nevertheless, neither of these *terra firme* sites are far from the nearest patches of evergreen rainforest or swamp forest (< 1 km away).

Economy today

In terms of plant species grown and their respective importance, present-day subsistence farming in the study area is not much different from what it was in the late 19th century before European colonisation reached its full impact. *Manihot esculenta*, *Z. mays*, plantain, *Ipomoea batatas* (sweet potato), *Arachis hypogaea* (peanut), and *Saccharum officinarum* are the major crops, and oil palm exploitation is of paramount importance while *Dioscorea* sp. (yams) are of lesser significance (Omasombo Tshonda 2016, pp. 387–410). Many smallholders also cultivate a variety of fruit trees and keep some small livestock, chickens, geese, or ducks. In the vicinity of Iyonda and Mbandaka, the current agronomic system is a mixture of small-scale subsistence gardening and farming with intermediate commercial agriculture in which Asian wet rice cultivation and cattle herding likewise play a role. At Mabandaka-Inkole, urban subsistence gardening is widespread whereas extremely restricted space at fishing camps such as Bolondo usually allows only minor ancillary gardening on tiny plots of *M. esculenta*, plantain, *Z. mays* or *S. officinarum* as well as use of a few oil palms scattered between houses. Everywhere near rivers, fishing continues to be a major subsistence acitivity, which is becoming more and more economically important with the shipment of smoked or salted fish to urban centres. From an historical perspective, a common denominator

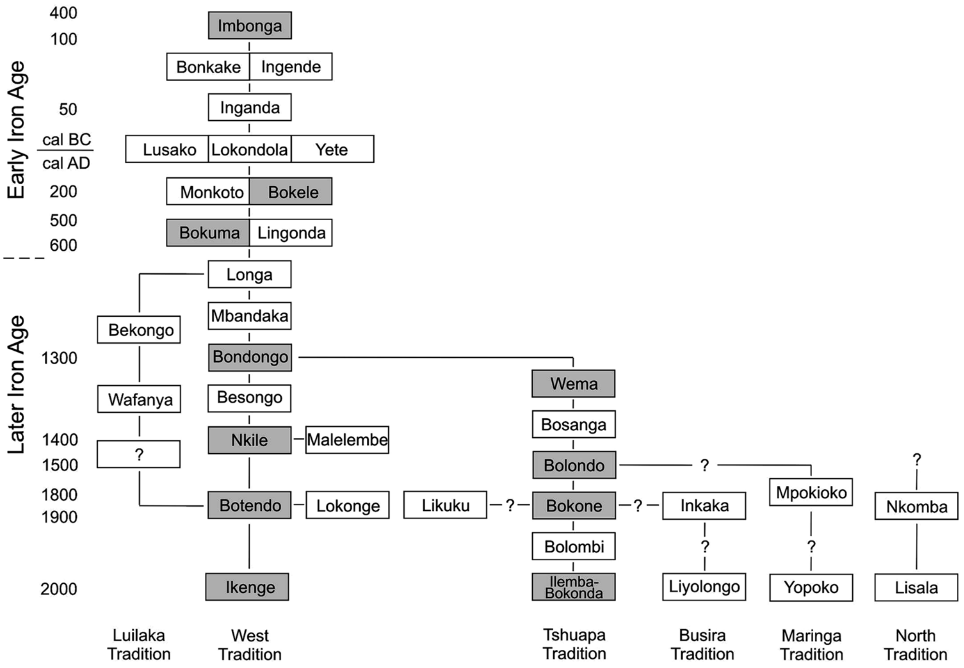

Fig. 2 Schematic Iron Age pottery sequence for the Inner Congo Basin with approximate absolute dates (modified after Wotzka 1995, p. 222, Fig. 4). Grey boxes show ceramic style groups relevant for the present study

of present-day plant subsistence in the study area is strong dependance on exotic species, i.e. domesticated plants that are not indigenous to Africa, first and foremost the Neotropical (New World) domesticates *M. esculenta* and *Z. mays* as well as Asian-derived plantain and *S. officinarum*.

Archaeological background and site description

Our research ultimately goes back to pioneering fieldwork in the ICB by Manfred K.H. Eggert who directed a large-scale *River Reconnaissance Project* there and in regions adjoining to the west between 1977 and 1987 (Eggert 1983, 1993; Eggert and Misago 1987). Most of the banks of all major rivers in the ICB were surveyed in the course of this river-borne research project, and 190, almost exclusively Iron Age, archaeological sites identified and partly test-excavated. Wotzka (1995) provides a synthesis of all ceramic finds from Eggert's project. The resulting ICB Iron Age pottery sequence takes the form of a subregionally branching pottery tradition consisting of a total of 34 ceramic style groups of partially overlapping duration that together cover the time span from the earliest regional Iron Age (Imbonga Group, ca. 400–100 BC) up to a number of recent styles a few of which are still produced today (Fig. 2). This sequence, meanwhile strengthened by new radiocarbon dates and fresh insights confirming stylistic relationships, has formed the backbone of renewed fieldwork in the ICB since 2011. We also refer to that sequence below, treating ceramic style groups as representing chronological phases where appropriate. The sites excavated at Iyonda and Mbandaka are located on the western edge of the ICB, in Equator Province of Democratic Congo (Fig. 1). As part of the same extensive block of *terra firme* land to the south of the Ruki-Congo confluence, both are situated on flood-free terrain, some 5–7 m above mean river level, which is at ca. 305 m above MSL (SRTM height 304 m). However, the long-term maximum river level amplitude here reaches 4.7 m (Preuß 1986) and is the only readily perceptible seasonal feature of this landscape within a mere 6 km north (Mbandaka) and 4 km south (Iyonda) of the equator, with low water in July/August and high water in December/January. While the linear distance between the two sites is only 16 km, their present-day appearance is quite dissimilar, the former on the northeastern edge of the bustling Inkole quarter within the 1.2 million provincial capital of Mbandaka, the latter a quiet, mostly uninhabited special-purpose exclave of the rural village of Iyonda. As usual in the acidic soil *terra firme* environments of the ICB, neither of these sites has bone preservation, and organic materials have only survived in charred form.

The Mbandaka-Inkole site is located at 0.05730° N/18.29360° E, in a position overlooking a slope down into a swampy depression connected to the Ruki River, which presently passes about 1,500 m further north to reach its Congo mouth at about the same distance west. Commercial open-pit laterite quarrying active in 2011 had exposed in its vertical sections a local stratigraphy featuring an approximately 30 cm thick, dark and organic-rich colluvium, which was visually indistinguishable from the A horizon above but clearly sealed the basal remainders of two small Iron Age pits that had been cut into Pleistocene yellowish-brown loamy sands overlying a regionally ubiquitous, massive laterite crust. At one edge of the quarry, a subrectangular trench (MBA 11/1) of 9.11 m^2 surface area was excavated down to laterite level to allow archaeological and archaeobotanical sampling of both the colluvium and the pits. While the colluvium turned out to be composed of a mixture of LIA Bondongo (ca. AD 1200–1400) and Nkile (ca. AD 1300–1500) with a few EIA Bokele Phase ceramics (ca. AD 150–350), one of the pits (MBA 11/1/1) yielded a pure Bokele inventory, the other (MBA 11/1/2) contained Bondongo and Nkile pottery.

The site of Iyonda lies directly on the left bank of the Congo River, at 0.03467° S/18.18585° E. It is situated above a steep river shore, on an extensive, rather even and today mostly treeless plateau exceeding seven ha in area. There are oral and archaeological records of a former village at this place that had been abandoned some decades before modern clearing and construction of a diocesan convention centre began in the early 1980s. The latter, locally known as “Iyonda-Centre”, now comprises nine concrete buildings and a number of pavilions, the whole huge rest of the area being covered by grass, with a few fruit trees and palms planted long ago. A tiny brook originating immediately behind separates the site from a gentle slope up towards the hinterland before flowing into the Congo River less than four hundred metres away. As an archaeological site the place has been known since M. Eggert carried out rescue exavations there in 1981 after chance finds had been made during construction of a septic tank (Wotzka 1995, p. 302). Between 2012 and 2020, Iyonda-Centre was one major focus of archaeological and archaeobotanical research shared between the Universities of Cologne and Frankfurt. Multi-season systematic geomagnetic survey, coring, and excavations at selected spots revealed the presence, in yellowish loamy sands overlying the local laterite crust, of thousands of more or less eroded Iron Age pits spread over the entire surface of the riverside plateau. An extensive colluvium covers most of these, mixing finds from the entire regional Iron Age sequence, i.e. from EIA Imbonga to recent Ikenge Phase times (ca. 400 BC-20th century AD; Fig. 2); however, it has so far proved difficult to obtain well-dated pit inventories from the middle portions of this total time span.

Some 340 km as the crow flies further east, the site of Bolondo is located at the heart of the ICB, in western-central Tshuapa Province of DR Congo, at 0.305805° S/21.252809° E (Fig. 1). It is a floodplain site directly on the right bank of the Tshuapa River, within the zone of seasonal inundation, just over 40 km east of the provincial capital of Boende. Wrested from riparian inundated forest, the ~ 0.5 ha place is home to a tiny year-round fishing camp accomodating only a few families spread over 35-odd houses. Such camps, regionally referred to as *nganda*, represent a characteristic type of indigenous human floodplain settlement in the ICB. *Nganda* typically feature houses on stilts or on artifical mounds, frequently both. Like many *nganda* on the Tshuapa, Bolondo only has artificial house mounds. These are platforms that grow higher over time because each new, or newly used, house will have a ca. 20–40 cm thick floor of white river clay laid out on the ground or on top of previous levels. During the use of houses, floors are regularly swept clean, but during phases of temporary abandonment, any vacant house space will be used as rubbish dump, to the effect that a dark to black, organic- and artifact-rich refuse layer accumulates on the previous floor. To archaeologists this type of site offers at least partially waterlogged conditions, neat stratification of alternating white and black layers, and very good preservation of organics, including botanical remains, as well as human and animal bone, in particular a wealth of fish remains.

Bolondo is one of the very few *nganda* on the Tshuapa that have risen sufficiently over time to remain essentially dry even during the high water season, except in the case of exceptionally high flood events. If the river flooded to its present height in the past, occupations at heights no lower than ca. 1.5 m below the present surface would have remained dry. Most of the other regional fisher camps are liable to complete flooding at least once a year, and even at Bolondo it is hard to find spots more than about 120 cm above mean Tshuapa River level which is at around 335 m above MSL (SRTM elevation). According to ethnography (e.g. R Eggert 1987) traditional *nganda* are seasonally (low-water) inhabited special-function camps, each operated by a particular nearby *terra firme* village whence only a minute fraction of the total population would be present at the associated *nganda* during fishing (i.e. low water) seasons; only when recent population growth and food shortage at urban centres created new demands and sales chances for smoked or salted fish should some *nganda* have shifted from seasonal subsistence fishing to perennial inhabitation and increasingly market-oriented fishery. The terra firme hinterland backing Bolondo and to which the local population associates itself is at a distance of almost seven km and can be reached by dugout via a small watercourse that flows into the Tshuapa approximately 300 m upstream.

First surveys and test excavations were carried out in 1983 in the course of M. Eggert’s former River Reconnaissance Project (Eggert 1983, 1993; Eggert and Misago 1987; Wotzka 1995, pp. 369–389). New small-scale excavations as well as onsite and offsite pollen corings were undertaken in 2016 within the framework of our Cologne-Frankfurt twin projects. These investigations have provided rich stratigraphies, house remains, stake holes, and a number of human burials. Altogether these feature rich finds, including ceramics, a few iron objects, charcoal, charred and uncharred plant macroremains, phytoliths, human bone remains, as well as an abundance of fish, mammal, and bird bones. Faunal and human bone as well as food remains have recently been subjected to stable isotope analyses allowing for dietary

Table 1 Radiocarbon dates referred to in this study, sorted by laboratory number

Lab.code	^{14}C Age (BP ±1σ)	δ^{13}C (‰)	Sample material	Species	Site	Context code	Context-type	Depth below surface (cm)	Calibrated age (2σ)	Phase
Beta-428090	230 ± 30	-29.5	Charcoal	*Uapaca*	Iyonda	IYO 15/48/1-13	Iron smelting furnace	72	AD 1550–1870	Botendo
Beta-428091	120 ± 30	-28.1	Charcoal	*Uapaca*	Iyonda	IYO 15/48/2-4	Iron smelting furnace	102–114	AD 1600–2000	Botendo
Beta-441457	2,040 ± 30	-25.4	Charred endocarp	*Elaeis guineensis*	Iyonda	IYO 15/2/4-57	Pit	60–70	130 BC – AD 70	Imbonga
Beta-441458	2,110 ± 30	-24.0	Charcoal	*Lophira* spp.	Iyonda	IYO 15/2/4-197	Pit	71	220–20 BC	Imbonga
Beta-447441	410 ± 30	-25.6	Charred endocarp	*Elaeis guineensis*	Bolondo	BLD 16/5-72	Layer	102–123	AD 1390–1590	Wema/Bolondo
Beta-447442	520 ± 30	-24.5	Charred endocarp	*Elaeis guineensis*	Bolondo	BLD 16/5-76	Layer	125–153	AD 1370–1450	Wema
Beta-469857	420 ± 30	-9.4	Charred caryopsis	*Cenchrus americanus*	Bolondo	BLD 16/1-38	Layer	45–58	AD 1400–1520	Bolondo
Beta-469858	480 ± 30	-9.1	Charred caryopsis	*Cenchrus americanus*	Bolondo	BLD 16/1-39	Layer	58–60	AD 1390–1470	Bolondo
Beta-529832	950 ± 30	-33.3	Charred caryopsis	indet.	Iyonda	IYO 17/1-20	Colluvium	17–40	AD 990–1190	Mixed (Imbonga to modern)
Poz-48986	1,660 ± 35	nd	Charred endocarp	*Elaeis guineensis*	Mbandaka	MBA 11/1-10	Colluvium	8–22	AD 280–520	Mixed (Bondongo; Nkile; Bokele)
Poz-48988	2,160 ± 30	nd	Charcoal	indet.	Mbandka	MBA 11/1/1	Pit	40–60	420–60 BC	Bokele
Poz-48989	1,785 ± 30	nd	Charcoal	indet.	Mbandaka	MBA 11/1/1	Pit	40–60	AD 190–350	Bokele
Poz-48991	1,810 ± 30	nd	Charred endocarp	*Elaeis guineensis*	Mbandaka	MBA 11/1/1-37	Pit	40–60	AD 150–350	Bokele
Poz-48992	605 ± 30	nd	Charred endocarp	*Elaeis guineensis*	Mbandaka	MBA 11/1-22	Colluvium	12–25	AD 1260–1420	Mixed (Bondongo; Nkile; Bokele)
Poz-48993	1,745 ± 35	nd	Charred endocarp	*Elaeis guineensis*	Mbandaka	MBA 11/1/1-31	Pit	18–24	AD 210–410	Bokele
Poz-48995	1,835 ± 35	nd	Charred endocarp	*Elaeis guineensis*	Mbandaka	MBA 11/1/1-35	Pit	32–40	AD 100–300	Bokele
Poz-48996	470 ± 30	nd	Charred endocarp	*Elaeis guineensis*	Mbandaka	MBA 11/1-47	Colluvium	0–25	AD 1390–1470	Mixed (Bondongo; Nkile; Bokele)
Poz-55342	2,175 ± 30	nd	Charred endocarp	*Elaeis guineensis*	Iyonda	IYO 12/1/1-37	Pit	83–116	410–90 BC	Imbonga
Poz-55343	2,185 ± 30	nd	Charred endocarp	*Elaeis guineensis*	Iyonda	IYO 12/1/1-37	Pit	83–116	400–120 BC	Imbonga
Poz-55344	2,105 ± 30	nd	Charred endocarp	*Canarium*	Iyonda	IYO 12/1/1-37	Pit	83–116	210–10 BC	Imbonga
Poz-55345	2,135 ± 30	nd	Charred endocarp	*Canarium*	Iyonda	IYO 12/1/1-37	Pit	83–116	330–10 BC	Imbonga
Poz-72477	660 ± 30	nd	Charred caryopsis	*Cenchrus americanus*	Mbandaka	MBA 11/1/2-42	Pit	29–34	AD 1230–1430	Bondongo/Nkile
Poz-72478	630 ± 30	nd	Charred caryopsis	*Cenchrus americanus*	Mbandaka	MBA 11/1/2-42	Pit	29–34	AD 1260–1420	Bondongo/Nkile
Poz-74815	2,040 ± 60	nd	Charred caryopsis	*Cenchrus americanus*	Iyonda	IYO 12/1/1-25	Pit	62–65	220 BC – AD 140	Imbonga
Poz-74816	2,180 ± 50	nd	Charred caryopsis	*Cenchrus americanus*	Iyonda	IYO 12/1/1-27	Pit	69–82	420–60 BC	Imbonga
Poz-74817	1,960 ± 40	nd	Charred caryopsis	*Cenchrus americanus*	Iyonda	IYO 15/1/6-64	Pit	69–78	60 BC– AD 180	Mixed (Imbonga + Bokuma)
Poz-74880	115 ± 30	nd	Charcoal	cf. Phyllanthaceae	Iyonda	IYO 15/1/3-9	Pit	28–38	AD 1600–2000	Botendo
Poz-74881	2,155 ± 30	nd	Charred endocarp	*Canarium*	Iyonda	IYO 15/1/4-35	Pit	38–55	430–30 BC	Mixed (Imbonga + Bokuma)
Poz-74883	1,445 ± 30	nd	Charred endocarp	*Elaeis guineensis*	Iyonda	IYO 15/1/4-35	Pit	38–55	AD 550–670	Mixed (Imbonga + Bokuma)
Poz-74884	2,275 ± 30	nd	Charcoal	cf. Sapotaceae	Iyonda	IYO 15/1/6-59	Pit	55–69	450–170 BC	Mixed (Imbonga + Bokuma)
Poz-74885	2,290 ± 30	nd	Charred seed	*Vigna* cf. *unguiculata*	Iyonda	IYO 15/1/7-18	Pit	60-80	460–180 BC	Imbonga
Poz-74886	2,195 ± 30	nd	Charred seed	*Vigna* cf. *unguiculata*	Iyonda	IYO 15/1/7-26	Pit	52-85	410–130 BC	Imbonga

Table 1 (continued)

Lab.code	14C Age (BP ±1σ)	δ13C (‰)	Sample material	Species	Site	Context code	Context-type	Depth below surface (cm)	Calibrated age (2σ)	Phase
Poz-74887	2,230 ± 30	nd	Charcoal	*Crudia* type	Iyonda	IYO 15/1/8-25	Pit	111–128	410–170 BC	Imbonga
Poz-74888	2,170 ± 30	nd	Charcoal	Fabaceae	Iyonda	IYO 15/1/8-25	Pit	111–128	410–90 BC	Imbonga
Poz-74889	2,140 ± 30	nd	Charred endocarp	cf. *Canarium*	Iyonda	IYO 15/1/9-38	Pit	89	400–0 BC	Imbonga
Poz-74890	2120 ± 30	nd	Charred endocarp	*Elaeis guineensis*	Iyonda	IYO 15/1/9-38	Pit	89	230–30 BC	Imbonga
Poz-74893	1,475 ± 30	nd	Charcoal	Phyllanthaceae	Iyonda	IYO 15/1/13-25	Pit	58–137	AD 530–650	Bokuma
Poz-74894	1,395 ± 30	nd	Charcoal	Phyllanthaceae	Iyonda	IYO 15/1/13-25	Pit	58–137	AD 570–690	Bokuma
Poz-74895	2,080 ± 30	nd	Charred endocarp	*Elaeis guineensis*	Iyonda	IYO 15/1/14-5	Pit	64–74	190 BC – AD 10	Imbonga
Poz-74896	2,100 ± 30	nd	Charred endocarp	*Elaeis guineensis*	Iyonda	IYO 15/1/14-5	Pit	64–74	210–10 BC	Imbonga
Poz-74897	2,220 ± 30	nd	Charcoal	Phyllanthaceae	Iyonda	IYO 15/1/15-9	Pit	100	400–160 BC	Imbonga (+ contact finds)
Poz-74898	2,235 ± 30	nd	Charcoal	cf. *Uapaca*	Iyonda	IYO 15/1/15-9	Pit	100	430–150 BC	Imbonga (+ contact finds)
Poz-74899	2,200 ± 30	nd	Charred endocarp	indet.	Iyonda	IYO 15/2/4-125	Pit	118	410–130 BC	Imbonga
Poz-74918	2,180 ± 30	nd	Charred endocarp	indet.	Iyonda	IYO 15/2/4-184	Pit	200–207	420–100 BC	Imbonga
Poz-74919	2,185 ± 30	nd	Charcoal	cf. *Lophira*	Iyonda	IYO 15/2/4-269	Pit	283	400–120 BC	Imbonga
Poz-74979	2,210 ± 30	nd	Charred endocarp	indet.	Iyonda	IYO 15/2/4-245	Pit	250–263	400–160 BC	Imbonga
Poz-75080	40 ± 30	nd	Charred endocarp	*Elaeis guineensis*	Iyonda	IYO 15/1/3-9	Pit	28–38	AD 1820–2020	Botendo
Poz-79288	645 ± 30	nd	Charred endocarp	*Elaeis guineensis*	Iyonda	IYO 15/19/1-24	Pit	30–60	AD 1250–1410	Bondongo? (no ceramic finds)
Poz-79289	150 ± 30	nd	Charcoal	Araliaceae	Iyonda	IYO 15/19/6-46	Pit	35–50	AD 1600–2000	Ikenge
Poz-79290	120 ± 30	nd	Charred endocarp	*Elaeis guineensis*	Iyonda	IYO 15/19-43	A-horizon	10–14	AD 1600–2000	Mixed (Bokuma; Botendo/Ikenge; Imbonga)
Poz-79291	2,165 ± 30	nd	Charred endocarp	*Elaeis guineensis*	Iyonda	IYO 15/42/4-27	Pit	53–73	420–60 BC	Bokuma (+ slight Imbonga admix.)
Poz-79295	490 ± 30	nd	Charred endocarp	*Elaeis guineensis*	Iyonda	IYO 15/63/3-32	Pit	40–60	AD 1380–1460	Nkile
Poz-79296	495 ± 30	nd	Charred endocarp	*Elaeis guineensis*	Iyonda	IYO 15/63/3-64	Pit	30–45	AD 1380–1460	Nkile
Poz-79297	545 ± 30	nd	Charred endocarp	*Elaeis guineensis*	Iyonda	IYO 15/63/4-47	Pit	40–47	AD 1290–1450	Bondongo/Nkile
Poz-79298	535 ± 30	nd	Charred endocarp	*Elaeis guineensis*	Iyonda	IYO 15/63/5-67	Pit	22–40	AD 1300–1460	Imbonga
Poz-79299	535 ± 30	nd	Charred endocarp	*Elaeis guineensis*	Iyonda	IYO 15/64/2-3	Pit	23–27	AD 1300–1460	Nkile
Poz-79300	500 ± 30	nd	Charred endocarp	*Elaeis guineensis*	Iyonda	IYO 15/64/2-7	Pit	18–27	AD 1380–1460	Nkile
Poz-79301	115 ± 30	nd	Charred endocarp	*Elaeis guineensis*	Iyonda	IYO 15/65-3	Pit?	15–24	AD 1600–2000	Botendo
Poz-79304	2,325 ± 35	nd	Charred caryopsis	*Cenchrus americanus*	Iyonda	IYO 15/1/6-73	Pit	92–107	450–330 BC	Mixed (Imbonga + Bokuma)
Poz-79306	290 ± 30	nd	Charred matter	indet.	Mbandaka	MBA 11/1-46	Colluvium	5	AD 1460–1700	Mixed (Bondongo; Nkile; Bokele)
Poz-79307	2,100 ± 30	nd	Charred	indet.	Iyonda	IYO 12/1/1-25	Pit	62–65	210–10 BC	Imbonga
Poz-93614	565 ± 30	nd	Charcoal	indet.	Bolondo	BLD1.02	Pollen core	96	AD 1280–1440	Bondongo/Wema? (no ceramic finds)
Poz-98058	334 ± 30	nd	Charred	*Cenchrus americanus*	Bolondo	BLD 16/5-61	Layer	86–91	AD 1430–1670	Bolondo
Poz-98264	460 ± 30	nd	Animal bone	*Capra hircus*	Bolondo	BLD 16/5-35	Layer	115–118	AD 1390–1470	Wema/Bolondo
Poz-98311	365 ± 30	nd	Charred	*Cenchrus americanus*	Bolondo	BLD 16/5-59	Layer	75–86	AD 1400–1680	Bolondo

Calibrations were calculated with CalPal v. 2020.8 (Weninger and Jöris 2008) using the IntCal20 Northern Hemisphere Radiocarbon Age Calibration Curve (Reimer et al. 2020). Southern Hemisphere Correction was not applied in view of all sites' very close proximity to the equator

Table 2 Overview of fruits and seeds, parenchyma, and food processing remains from Iyonda, Bolondo and Mbandaka (for detailed list of individual archaeobotany samples and ^{14}C dates see ESM 2 Table 1)

Site	Context	Number of samples	Depth below surface (cm)	Phase + context type	Approx. date [estimated]	*Cenchrus americanus*	cf. *C. americanus*	cf. *C. americanus* fragm.	*Vigna* cf. *unguiculata*	*V.* cf. *unguiculata*, cotyl.	cf. *Vigna*, fragm.	*Musanga cecropioides*	*Nauclea/Sarcocephalus*-type	Paniceae indet, corroded	cf. *Setaria/Brachiaria*	*Eleusine indica*	*Digitaria* sp.	*Cleome* sp.	cf. *Portulaca*	*Scleria* sp.	Parenchyma charred fragm.	*Raphia* endosperm fragm.	Charred food fragm.	*Canarium schweinfurthii* (g/l)	*Elaeis guineensis* (g/l)
Bolondo	BLD 16/5	2	123–153	Wema layers	~AD 1350–1500																		38		xxx
Bolondo	BLD 16/5	1	102–123	Wema/Bolondo layer	~AD 1450																		23		xxx
Bolondo	BLD 16/1	7	0–80	Bolondo layers	~AD 1400–1600	11		100												1	9	1	298		xxx
Bolondo	BLD 16/5	9	56–102	Bolondo layers	~AD 1400–1600	4		16												2	7		206		xx
Bolondo	BLD 16/5	3	13–56	Bokone layers	~AD 1600–1900																7		7		xx
Bolondo	BLD 16/5	1	0–13	Ilemba-Bokonda layer	~AD 1900–present																1		5		x
Iyonda	IYO 15/1/7	3	57–85	Imbonga pit	~350–250 BC	3	1		11	80	67		1								27			x	xxx
Iyonda	IYO 15/2/4	3	117–263	Imbonga pit	~300–100 BC		1						2								11			x	xxx
Iyonda	IYO 12/1/1	5	53–116	Imbonga pit	~200–100 BC	3							109	12		59	2				25			xx	xxx
Iyonda	IYO 12/1	1	44–51	Imbonga pit (+ slight Bokuma admixture + 1 contact find)	~200–100 BC (~500–AD 650)																			x	xxx
Iyonda	IYO 15/1/9	1	89	Imbonga pit	~200–100 BC																			x	xxx
Iyonda	IYO 15/5-8	1	46–64	Imbonga pit	[~400–100 BC]																			x	xxx
Iyonda	IYO 15/17/1	1	33–47	Imbonga pit	[~400–100 BC]																				xxx
Iyonda	IYO 15/30/1	1	0–45	Imbonga pit	[~400–100 BC]													1			1				xxx
Iyonda	IYO 16/1/5	1	49–59	Imbonga pit	[~400–100 BC]																	3			xxx
Iyonda	IYO 15/63/5	1	22–35	Imbonga grave(?), intersected by Nkile pit	[~400–100 BC] ~AD 1350–1450												1								
Iyonda	IYO 15/1/6	4	69–107	Mixed, intersecting pits (Imbonga + Bokuma)	~400 BC–AD 70 [~AD 500–650]	11	6		36	66	2	1											x		xxx
Iyonda	IYO 15/1/13	2	59–69	Bokuma pit	~AD 600–650						6											25		x	xx
Iyonda	IYO 17/2/1	5	60–105	Bokuma pit	[~AD 500–650]		1	1				26							2		9				xxx
Iyonda	IYO 16/1/6	1	48–59	Bokuma pit	[~AD 500–650]																				xx
Iyonda	IYO 15/42/4	1	40–65	Bokuma pit (+ slight Imbonga admixture)	[~AD 500–650] (~400–100 BC)							3													xxx
Iyonda	IYO 16/1/3	1	36–52	Bokuma pit (+ slight Imbonga admixture)	[~AD 500–650]																	2			xxx
Iyonda	IYO 15/19/1	1	30–60	Bondongo(?) posthole (no ceramic finds)	~AD 1300–1400						1														xx
Iyonda	IYO 15/63/4	1	40–47	Bondongo/Nkile pit	~AD 1350							4				1					3				xxx
Iyonda	IYO 15/63/3	2	30–60	Nkile pit	~AD 1400–1450								1		2						5				xxx
Iyonda	IYO 15/1/3	1	28–38	Botendo pit	~AD 1700–1900																8				xx
Iyonda	IYO 15/48/1	1	21–32	Botendo iron smelting furnace	~AD 1700–1900							6									1				x
Iyonda	IYO 15/65-3	1	15–24	Botendo pit(?)	~AD 1700–1900																9				xxx
Iyonda	IYO 15/19/6	2	15–50	Ikenge posthole	~AD 1900–present																22				xxx
Iyonda	IYO 12/1	1	30–43	Mixed colluvium + pit (Imbonga?; Bokuma; contact finds)	[~400 BC–AD 650]								1												xxx
Iyonda	IYO 17/1	2	10–40	Colluvium (Imbonga to modern)	[~400 BC–present] ~AD 1000–1200							31													xxx
Iyonda	IYO 15/19	1	10–14	Mixed A-horizon (Bokuma; Botendo/Ikenge; Imbonga)	[~400 BC–present] ~AD 1700–1900						1										24				xx
Iyonda	IYO 16/2	8	0–32	Mixed colluvium (Bondongo to modern)	[~AD 1250–present]							105									5				xxx
Mbandaka	MBA 11/1/1	2	18–40	Bokele pit	~AD 200–300							127							74						xx
Mbandaka	MBA 11/1/2	1	29–34	Bondongo/Nkile pit	~AD 1350	3						51							1						xx
Mbandaka	MBA 11/1	3	8–25	Mixed colluvium (Bondongo; Nkile; Bokele)	~AD 200–1600							65	1						3		6				xx

Associated radiocarbon dates (see Table 1 for details) are given as interpretive approximate values. For undated contexts, age estimates are provided [in square brackets]. Semi-quantitative values: x = < 0.1 g/l, xx = 0.1–1.0 g/l, xxx = >1.0 g/l

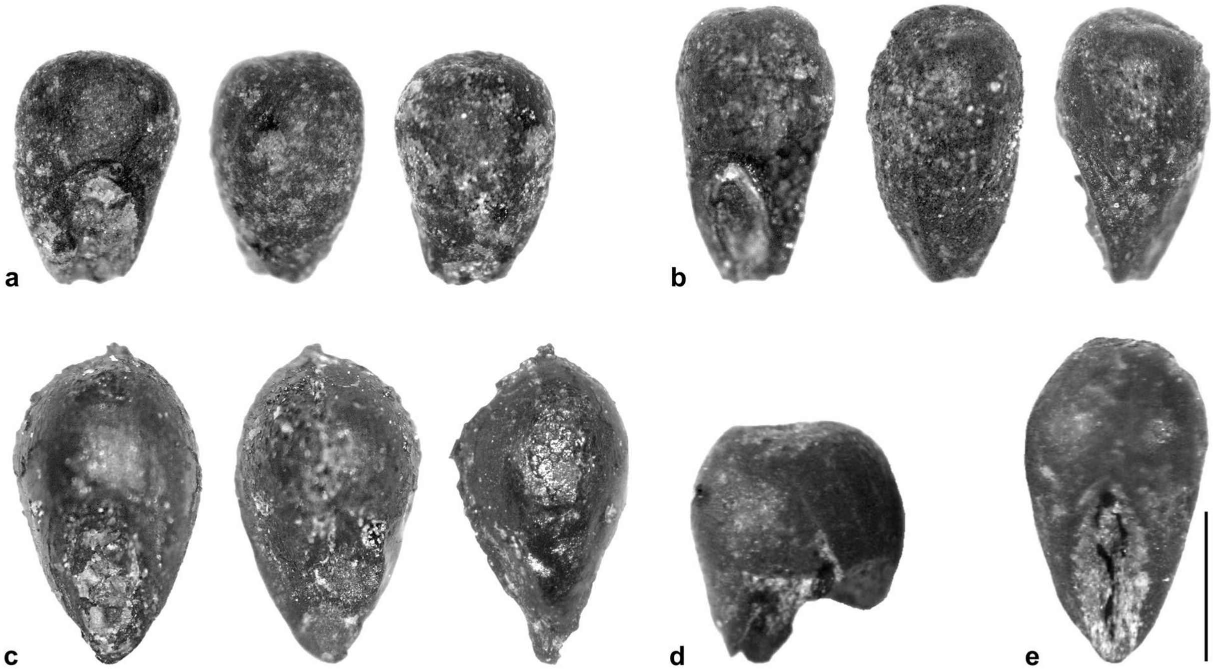

Fig. 3 Charred archaeological *Cenchrus americanus* (pearl millet) caryopses from ICB sites; **a**–**c** in dorsal, ventral and lateral view, **d**, **e** in dorsal view: **a**, **b** two specimens from Iyonda, Imbonga Phase (ca. 400–200 BC); **c** Bolondo, Bolondo Phase (ca. AD 1450–1550); **d**, **e** caryopses with germination features, Mbandaka, Bondongo/Nkile Phase (ca. AD 1350); scale bar = 1 mm

and ecological inferences (Bleasdale et al. 2020). Founded around the mid-14th century AD (Poz-93614; Table 1) during the LIA Wema Phase, Bolondo has featured repeatedly raised house platforms from the beginning; these have fused over time to form an artificial island. Together with evidence for on-site potting and iron metallurgy (exogenous laterite iron ore; slagged tuyère finds) this points to a long tradition of year-round habitation, contrary to ethnographic accounts. The local archaeological sequence embraces all regionally known Iron Age ceramic styles, from Wema up to the recent Ilemba-Bokonda Group (Fig. 2).

Zooarchaeological analysis of the Bolondo faunal finds by Veerle Linseele (then University of Leuven, Belgium) produced a preliminary list of more than 20 identified taxa, including a number of fishes, crocodile, monkeys, antelope and other wild species. The bulk of the faunal material still awaits detailed scrutiny and publication. However, the fish bones were studied in the course of an MSc thesis at Brussels University which resulted in a publication (Nieblas Ramirez et al. in press). A few mammal bones were identified as from domestic goat; these were found in the earlier settlement layers and have been directly dated by two radiocarbon dates to ca. AD 1450, the oldest evidence of precolonial animal husbandry discovered so far in the ICB.

Material and methods

Archaeobotanical sampling

Between 2011 and 2020, 11 archaeological field seasons in the ICB were devoted to survey and excavation with one major aim being the collection of botanical remains in a systematic manner and from as great a diversity of properly controlled contexts as possible. The basis of the present study are 82 flotated botanical samples and 68 soil phytolith samples taken in this framework from 2011 to 2017. During archaeological excavations at the sites of Iyonda, Mbandaka and Bolondo, sediment samples were subjected to systematic flotation and wet sieving for botanical macroremains, using a sieve set with mesh widths of 1.0 mm and 2.5 mm at Bolondo, and 0.5, 1.0 and 2.5 mm at the other sites. In the majority of cases, 10 l sediment samples were processed. Smaller flotation samples were taken when less sediment volume was available per archaeological context, e.g. vessel fills and post holes. Small sediment samples of 10–20 g were retrieved in parallel for phytolith analysis.

Sample processing and identification

Samples were further processed in the archaeobotany laboratory at Goethe University Frankfurt, Institute of Archaeological Sciences. The macroremains were sorted under a binocular microscope with magnifications ranging from ×6.3 to ×10 and later identified using the African fruit and seed reference collection, as well as published archaeobotanical literature for West and Central Africa (e.g. D'Andrea et al. 2006; Neumann et al. 2012; Kahlheber et al. 2014a, b; Oas et al. 2015). Seeds and fruits and their corresponding fragments were counted. The fragmented endocarp remains of *Elaeis* and *Canarium* were weighed and their density calculated as g/l sediment.

Phytoliths were extracted from the sediment samples in the laboratory of the Senckenberg Research Institute, Frankfurt, using a modified protocol after Madella et al. (1998) and Piperno (2006, pp. 90–93): (1) Deflocculation with EDTA; (2) Sieving in order to remove coarse sediment and plant remains; (3) Clay removal with Stoke's Law gravity separation; (4) Carbonate destruction with HCl; (5) Organic matter removal with HNO_3 and $KClO_3$; (6) Heavy liquid separation with sodium polytungstate. The phytolith samples were mounted on micro-slides in immersion oil allowing for rotation and 3-dimensional investigation of the encountered phytolith morphotypes. 68 samples from the three sites Mbandaka, Iyonda and Bolondo, covering all represented phases, were completely screened with a special focus on finding *Musa* phytoliths.

In addition, 18 phytolith samples from former excavations by M. Eggert and C. Meister in Cameroon which had been counted but not fully published (Eggert et al. 2006) are considered here in regard to the presence/absence of *Musa* phytoliths. The samples come from the sites of Bwambé-Sommet (n = 3), Abang Minko'o (n = 7), Minyin (n = 5) and Akonétye (n = 3). 300–400 diagnostic phytoliths were counted for each sample, and the remainder of each slide was screened for *Musa* phytoliths. Nomenclature of the morphotypes follows ICPT (2019).

Results: the archaeobotanical remains

A high amount of the retrieved archaeobotanical material was heavily corroded and fragmented and did not allow a secure botanical identification. A large number of flotated samples only contained fragmented *E. guineensis* endocarps and/or wood charcoal. These samples are not considered in our analysis. 82 flotated samples yielded identifiable fruits, seeds, parenchyma and/or food processing remains: Bolondo (23), Mbandaka (6), Iyonda (53) (Table 2; ESM 2 Table 1).

Cenchrus americanus, syn. *Pennisetum glaucum*

Unequivocal *C. americanus* processing remains (such as bristles, involucri) are absent in the archaeobotanical assemblages. The attribution to domesticated *C. americanus* must therefore be based on caryopsis morphology alone. In general, the charred pearl millet caryopses are distinctly club-shaped, but very small (Fig. 3; ESM 2 Table 2). Often the basal part is missing or the embryonic area is modified.

At Iyonda, a total of 8 charred pearl millet caryopses were found in three Imbonga Phase pits: Pit 12/1/1 (n = 3); Pit 15/1/7 (n = 4); Pit 15/2/4 (n = 1). Two specimens from Pit 12/1/1 were AMS dated and gave ages (2σ) between ca. 420 BC and AD 140 (Table 1). More early evidence comes from the mixed Imbonga + Bokuma Phase Pit 15/1/6 (n = 17), directly dated to between ca. 450 BC and AD 180 (Table 1), and from the Bokuma Phase Pit 17/2/1 (n = 1; undated). No pearl millet was detected in any of the younger contexts of Iyonda. With length values of 1.1–2 mm (ESM 2 Table 2), the caryopses identified at Iyonda are in the size range of domesticated *C. americanus* from Iron Age contexts in Burkina Faso (ESM 3; Kahlheber 2004, catalogue: Table 3).

At Mbandaka, three charred caryopses were found in the LIA Pit 11/1/2 which contained Bondongo/Nkile ceramics. Direct AMS radiocarbon dates between ca. AD 1230–1430 (2σ) were obtained on two of these caryopses (Table 1). Two of the three individuals display distinct morphological modifications: Caryopsis 1 had its base broken off, and the remainder of the dorsal side is concave (Fig. 3d). Caryopsis 2 has a concave dorsal side and a distinct groove-like channel; coleoptile and coleorhiza remnants are visible (Fig. 3e). These modifications are indications for sprouting.

At the LIA site of Bolondo, complete *C. americanus* caryopses are present in low numbers (n = 15; Table 2; Fig. 3c), while fragments are more numerous (n = 116). Four caryopses were directly dated, ranging between ca. AD 1390 and 1680 (2σ). In two contexts, the caryopses occur in conglomerates, representing charred food fragments (see "Charred food fragments" section below).

Earlier identifications of archaeobotanical *C. americanus* specimens in sub-Saharan West Africa were primarily based on caryopsis shape. This feature has been suggested as a more effective criterion than overall grain size for the identification of archaeological pearl millet (Neumann et al. 1996; D'Andrea et al. 2001). Archaeological specimens are often distinctly smaller than extant *C. americanus*, but in contrast to the wild progenitor and hybrids of both species, their shape is obovate (= club-shaped), and terete, i.e. almost circular in transverse section. For the EIA ICB site of Boso-Njafo on the Lulonga River, Kahlheber et al. (2014a) stressed that confusion of domesticated *C. americanus* caryopses with any other species of the same genus is unlikely.

To further validate the identification and domestication status of the *C. americanus* caryopses from Mbandaka, Bolondo and Iyonda, we conducted a differential diagnosis. We compared shape and size of the finds with available information on seven related *Cenchrus* species and hybrids, and *S. officinarum*, which is currently cultivated in the ICB (ESM 4). In contrast to the characteristic club-shape of *C.*

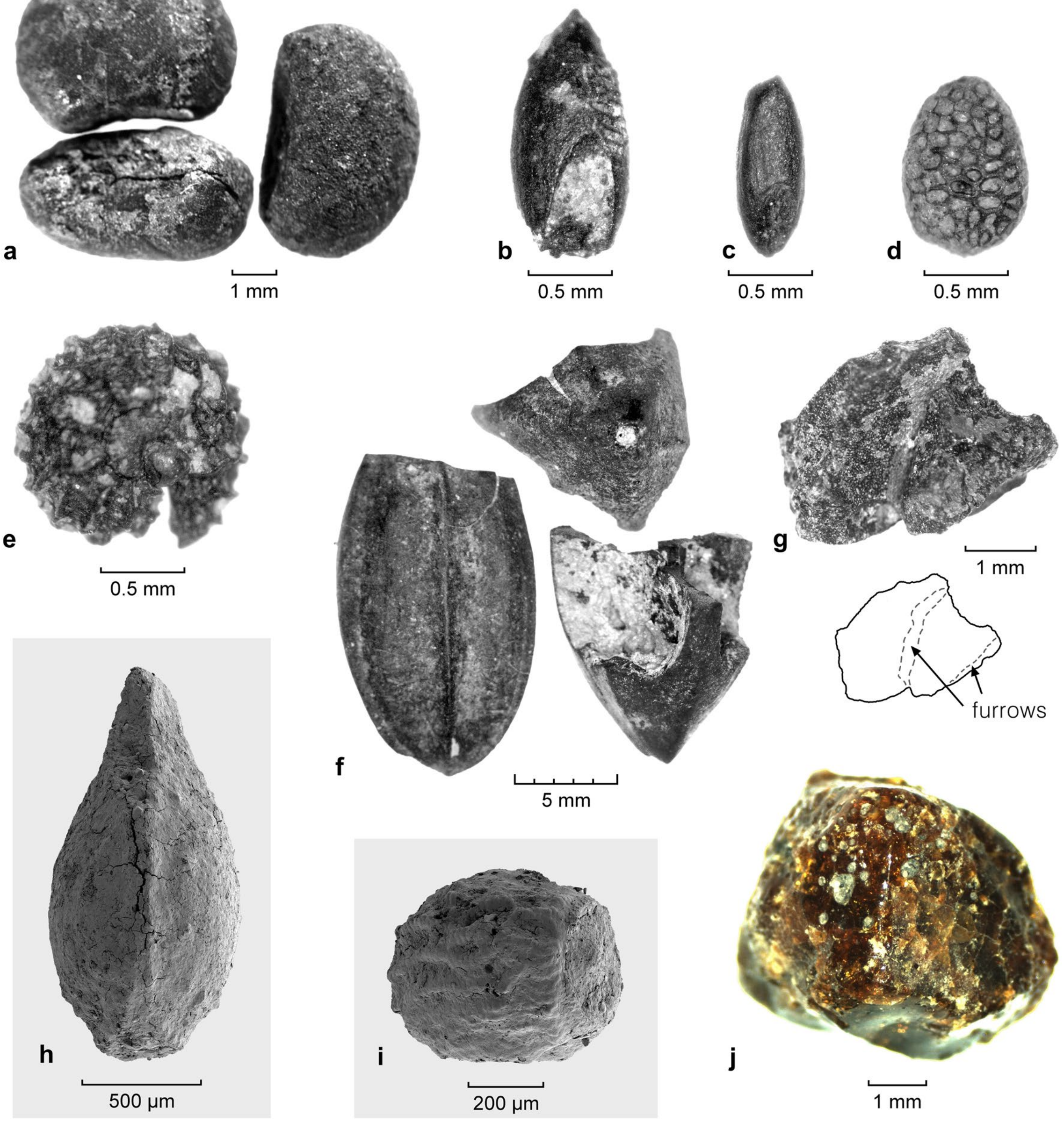

Fig. 4 Archaeobotanical finds from ICB sites: **a** *Vigna unguiculata*, seeds; **b** *Setaria/Brachiaria* type, caryopsis; **c** *Digitaria* sp., caryopsis; **d** *Nauclea/Sarcocephalus* type, seed; **e** *Cleome* sp., seed; **f** *Canarium schweinfurthii*, endocarp; **g** *Raphia* sp., ruminated endosperm; **h** *Musanga cecropioides*, diaspores; **i** cf. *Portulaca*, seed; **j** copal

Table 3 Size ranges of *Vigna unguiculata* seeds from Iyonda in comparison with archaeobotanical *Vigna* finds from Ghana and Burkina Faso

	Iyonda	Kintampo B-sites, Ghana (D'Andrea et al. 2007)	Burkina Faso, Iron Age sites (Kahlheber 2004)
Length (mm)	4.1–5.9	5.0–6.3	3.7–9.7
Breadth (mm)	4.2–5.3	3.6–4.6	2.4–6.6
Height (mm)	3.2–4.3	3.4–4.2	3.0–6.1
Length/Height	1.2–1.9	1.5–1.6	0.9–2.1
Breadth/Height	1.0–1.4	0.9–1.1	0.7–1.4
Length/Breadth	0.9–1.4	1.4–1.8	1.0–2.3

americanus, all other species have caryopses with either elliptic, lanceolate or ovate shapes.

In addition, we conducted detailed morphometric measurements of L = Length, B = Breadth, and T = Thickness (after van Zeist and Bakker-Heeres 1984, and their corresponding ratios) for 40 charred archaeobotanical caryopses in comparison to modern domesticated *C. americanus*, *C. purpureus, Sorghum bicolor* ssp. *verticilliflorum* (wild sorghum) and domesticated *S. bicolor* ssp. *bicolor* (ESM 2 Table 3). The caryopses of the modern domesticate are highly variable in length, with mean values of 1.7–4.0 mm. In contrast, the B/T ratio varies consistently around 1.0, reflecting terete shape of the caryopsis. This is the most robust criterion to differentiate domesticates from both closely related *Cenchrus* species and *Saccharum* as well as, potentially, from extraordinarily small *Sorghum* caryopses. The 40 measured archaeological specimens also have B/T ratios around 1.0, confirming the identification (ESM 2 Table 2).

Vigna cf. *unguiculata,* Fabaceae

Charred finds of *V.* cf. *unguiculata* (cowpea) occur in EIA contexts of Iyonda (IYO 15/1/6; 15/1/7), either as whole seeds, mostly without testa (n = 47; Fig. 4a) and charred cotyledons (n = 146). Two seeds were directly dated to ca. 460–130 BC (Table 1). Cotyledon fragments are only classified as cf. *Vigna*. In the case of IYO 15/1/6 (n = 2) and 15/1/7 (n = 66), the fragments can be attributed to *V.* cf. *unguiculata* with reasonable certainty. The few cf. *Vigna* fragments occurring in later contexts of Iyonda do not allow the conclusion that *V. unguiculata* was present.

With mean length values of about 5 mm and mean height values of 3.7 mm the seeds are at the lower end of the known range of archaeological *V. unguiculata* specimens from Burkina Faso and the Kintampo B-sites of Ghana (ESM 3; Table 3). According to D'Andrea et al. (2007) a length of 5 mm falls within the range of modern domesticated *V. unguiculata* landraces. All ratios (Length/Height; Breadth/Height; Length/Breadth) are similarly within the range of archaeobotanical finds from Burkina Faso and Ghana.

The majority of modern West and Central African *V. unguiculata* are distinctly larger than the EIA archaeobotanical finds from Iyonda. One reason for this might be the reduction in size during charring. In experimental furnace charring, the length of pulse seeds is reduced by 10–20% or slightly more, the width by about 10% (Fuller and Harvey 2006, and references therein). In open fires, after destruction of the seed coat, shrinkage rates strongly increase. Fuller and Harvey (2006) therefore suggest adjusting modern length and width by -20% for comparison with measured charred archaeological specimens. Taking account of shrinkage during charring and the absence of the testa in most of the finds from Iyonda, the specimens are in the size range of small modern landraces.

Most wild West and Central African *Vigna* species from the Frankfurt reference collection measured for comparison are smaller than the archaeobotanical specimens from Iyonda. Only if disregarding shrinkage of the archaeobotanical specimens, the wild species *V. luteola* and *V. ambacensis,* and some wild *V. unguiculata* accessions as well, would approximate our charred finds in size. The seeds of *V. luteola* are hollow inside, which allows them to float on water for dispersal, a fact expressed morphologically by strongly concave cotyledons (own observations on reference specimens). This special character was not observed in the archaeobotanical material. *V. ambacensis* has an extremely lateral position of the hilum while the archaeobotanical specimens, whenever still visible, display a central to slightly lateral hilum position. *V. oblongifolia* from Congo is much smaller than the Iyonda specimens while material from Kenya is closer in length and breadth, but not in height. The hilum of this species has a distinctly lateral position and the form of the seeds is oblique. Therefore, it can also be ruled out as a likely candidate for the archaeobotanical specimens.

Elaeis guineensis, Arecaceae, and *Canarium schweinfurthii,* Burseraceae

The archaeobotanical samples from all sites and phases are characterised by the dominance of mostly small *E. guineensis* endocarp fragments (Table 2; ESM 2 Table 1), with the exception of surface and near-surface layers at Bolondo and Iyonda, where entire or almost entire kernels were also retrieved. Identification of *Elaeis* endocarps and their separation from *C. schweinfurthii* follows the criteria of D'Andrea et al. (2006). The density of *Elaeis* varies between 0.03 and 6 g/l, with > 1 g/l in ca. 50% of the samples. By contrast, the density of *Canarium* is always lower than 1 g/l.

The few *C. schweinfurthii* endocarp fragments, big enough for secure identification are restricted to EIA contexts at Iyonda (Fig. 4f). All four directly AMS-dated fragments of *C. schweinfurthii* have yielded radiocarbon dates between ca. 430-1 BC (2σ; Table 1), contemporaneous with Imbonga pottery, the earliest regional Iron Age ceramic style group (Wotzka 1995, 2006). Three of these come from Imbonga Phase contexts while the fourth stems from the mixed Imbonga + Bokuma Phase Pit IYO 15/1/4 where it had been associated with an *E. guineensis* fragment that was directly dated to ca. AD 550–670 (2σ, Poz-74883; Table 1) and thus undoubtedly represents the Bokuma Phase portion of the infill. Incidentally, the latter is the period of our most recent *Canarium* specimens, found in Bokuma Phase Pit IYO 15/1/13 and indirectly dated to ca. AD 580–660 (2σ weighted average of Poz-74893 and Poz-74894; Table 1).

Other carpological finds

Cleome sp. (Capparaceae): The single charred seed found in an EIA (Imbonga Phase) context at Iyonda is 1.4 mm in diameter, circular and forming a spiral. The surface is distinctly vestured, reticulate, with some echinate protuberances, and only faintly radially ridged (Fig. 4e). The closest species with regard to both size and surface vesturing available in the reference collection are some of the samples identified as *C. gynandra* (syn. *Gynandropsis gynandra*) and *C. monophylla.* The available reference samples of the first species are very heterogeneous in their surface vesturing. Some of them display a reticulate pattern without further vesturing or ridges as described in Zach and Klee (2003) while others are quite similar to our archaeobotanical specimen. *Cleome monophylla* seeds have better defined radial ridges. There are, however, a number of Central African *Cleome* species which are not represented in the reference collection.

Scleria sp. (Cyperaceae): The three achenes of *Scleria* sp., solely identified at Bolondo, are mineralised and in two cases distinctly darkened due to contact with fire. The only entirely preserved achene is 3.6 mm long and 2.6 mm wide. The hypogynium is trilobulate, the style persistent. The surface of the achenes has verrucate to tuberculate protrusions. The attribution to the genus is secure, although there are no perfectly matching species in the reference collection.

Eleusine indica (Poaceae): The caryopses of *E. indica*, found at Iyonda in both EIA (IYO 12/1/1; n = 59) and LIA contexts (IYO 15/63/4; n = 1), are ca. 1 mm long and 0.5 mm wide. Their shape is ovoid to nearly triangular and in cross-section they are likewise almost triangular. The circular hilum is basal while the scutellum, measuring slightly less than one third of the caryopsis' length, has a triangular shape. The surface of the caryopses is vestured (verrucate) with the small protrusions linearly arranged on ridges running radially over the lateral surfaces (cf. Zach and Klee 2003; Kahlheber et al. 2014a).

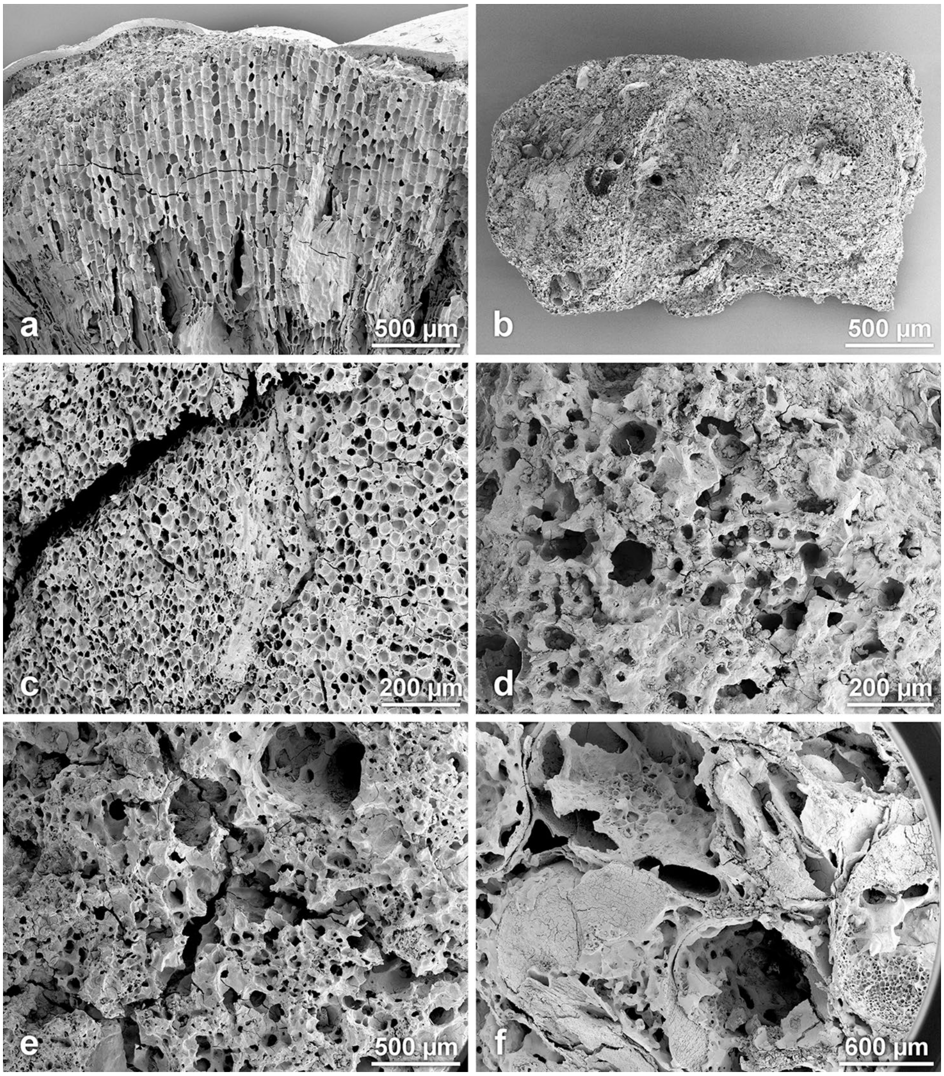

Fig. 5 Charred tuber parenchyma and food fragments from ICB sites (SEM): **a** tuber fragment with wavy cortex, Bolondo, Bokone Phase; **b**, **c** tuber parenchyma fragment with vascular bundles, Iyonda, Imbonga Phase; **d**, **e** charred food fragments, Bolondo, Bolondo Phase; **f** charred fragment of food residue (gruel) with outlines of *Cenchrus americanus* caryopses, Bolondo, Bolondo Phase

cf. *Digitaria* (Poaceae): The three charred caryopses from EIA contexts at Iyonda, probably attributable to the genus *Digitaria*, are narrowly oblong with a length of 1.1 mm, a width of 0.4 mm, and a height of 0.3 mm (Fig. 4c). The scutellum does not reach half of the length of the caryopsis. They are similar in shape to the type *Digitaria* sp. described in Zach and Klee (2003) but smaller (less broad and less high). The dimensions are, however, similar to those of the *Digitaria* sp., type 2, described by Kahlheber (2004, Catalogue, p. 165), attributable either to small-grained *Digitaria* species or unripe caryopses of many species of the genus.

Setaria/Brachiaria-type (Poaceae): Two charred caryopses of this type, found at Iyonda in an EIA pit (IYO 12/1/1), are recognisable by small remnants of glumes with distinct horizontal wrinkles (Fig. 4b). Slightly asymmetrical papillae are rarely preserved and damaged. The scutellum reaches more than half of the caryopses' length. The caryopses mostly lack their basal part and are 1.2 to 1.5 mm long and less than 1 mm wide. A number of caryopses are strongly damaged and lack distinct wrinkles but otherwise resemble the above-described type in shape and, if preserved, scutellum form and size. They have been tentatively ascribed to the same type.

Nauclea/Sarcocephalus-type (Rubiaceae): Seed macro remains attributed to this type are especially common in EIA assemblages from Iyonda. They are about 0.7–1.0 mm long, 0.5–0.6 mm wide, ellipsoid to almost rectangular and characterised by a reticulate surface pattern (Fig. 4d). They match the seeds of the woodland shrub or tree *Nauclea latifolia* (African peach, syn. *Sarcocephalus latifolius*) in the Frankfurt reference collection. A similar description is given for the seeds of the forest tree *N. diderrichii* (syn. *Sarcocephalus diderrichii*) which is not represented in the Frankfurt reference collection (Opuni-Frimpong and Opuni-Frimpong 2012). Only at the first cursory glance, confusion of the archaeobotanical finds might be possible with the seeds of *Bergia capensis* (Elatinaceae), which similarly show a reticulate surface pattern (Oas et al. 2015). The seeds of *B. capensis* are, however, smaller than the seeds of *Nauclea latifolia* and the archaeobotanical material, and their shape is narrowly reniform. The African Plant Database does not record *B. capensis* for the DR Congo. Most of the archaeobotanical specimens have a strongly corroded surface blurring the reticulate pattern but are similar in size and shape. They have tentatively been attributed to the same type.

Musanga cecropioides (Urticaceae): Charred diaspores of *Musanga cecropioides* are particularly common in LIA contexts from Mbandaka (n = 243) and Iyonda (n = 149) while they were only occasionally identified in EIA contexts. *M. cecropioides* yields edible fruits and is indicative of open pioneer vegetation. The diaspores of *M. cecropiodes* at both sites vary in size from 1.3–1.9 mm × 0.7–1 mm. They have a keel-like ridge, their tip is acute and the basis rounded to

Table 4 Counts of identified *Musa* phytoliths from archaeological sites Iyonda, Bolondo and Mbandaka

Sample ID	Phytolith extraction ser. No.	No. of *Musa* phytoliths	Counted phytoliths	Site	Context	Depth below surface (cm)	Archaeological phase	^{14}C date (BP)	Lab.code
356	794	10	>300, screened	Iyonda, Catholic Mission	IYO 15/68-1	Surface	Under modern sweet banana		
358	795	2	>300, screened	Iyonda, Catholic Mission	IYO 15/69-1	Surface	Under modern plantain		
360	796	6	>300, screened	Iyonda, Catholic Mission	IYO 15/70-1	Surface	Under modern banana (sweet or plantain)		
296	790	1	>300, screened	Iyonda	IYO 15/19-43	10–14	Botendo	120 ± 30	Poz-79290
30	720	2	>300, screened	Mbandaka	MBA 11/1-46	4–6	From colluvium containing Nkile, Bondongo and Bokele ceramics - ^{14}C date matches Nkile	290 ± 30	Poz-79306
364	805	1	383	Bolondo	BLD 16/1-35	9–18	Bolondo		
386	797	1	290	Bolondo	BLD 16/5-49	20–35	Bolondo		
370	806	2	153	Bolondo	BLD 16/1-38	45–58	Bolondo	420 ± 30	Beta-469857
372	864	3	386	Bolondo	BLD 16/1-39	58–60	Bolondo	480 ± 30	Beta-469858
374	842	1	243	Bolondo	BLD 16/1-40	66–71	Bolondo		
376	807	2	422	Bolondo	BLD 16/1-41	71–80	Bolondo		
397	799	1	338	Bolondo	BLD 16/5-57	71–75	Bolondo		
413	803	4	>300, screened	Bolondo	BLD 16/5-72	102–123	Wema/Bolondo	410 ± 30	Beta-447441
417	804	2	419	Bolondo	BLD 16/5-76	125–153	Wema	520 ± 30	Beta-447442

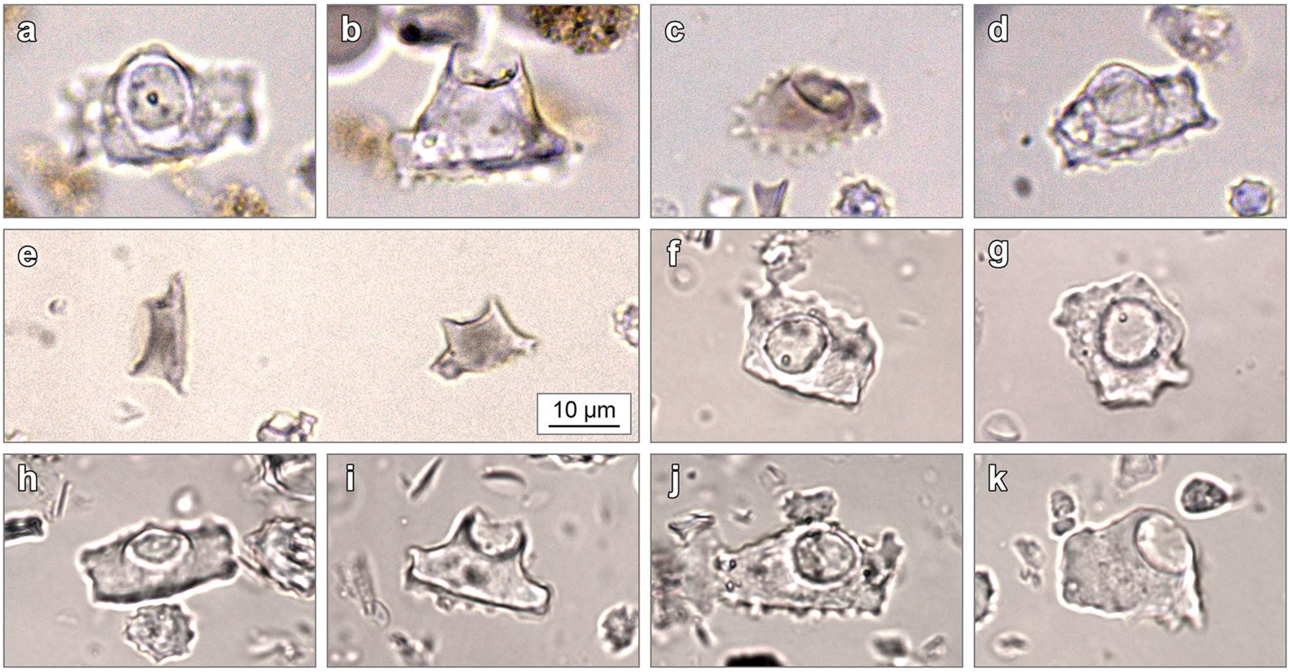

Fig. 6 Phytoliths of *Musa* sp. in LIA ICB sites: **a**, **b** specimen 1 in top and side view, Bolondo, Wema Phase (ca. AD 1300–1500), soil sample ID 417; **c** Bolondo, Bolondo Phase, soil sample ID 376; **d** specimen 2, Bolondo, Wema Phase (ca. AD 1300–1500), soil sample ID 417; **e** two specimens in side view, Mbandaka, Nkile Phase (ca. AD 1500–1700), soil sample ID 30; **f–k** modern Musa phytoliths from surface soil sample under *M.* x *paradisiaca*, Iyonda, soil sample ID 356

truncate (Fig. 4h). The surface is vestured with small wart-like protuberances. *M. cecropioides* diaspore finds from Boso-Njafo have been described and illustrated by Kahlheber et al. (2014a).

cf. *Portulaca* (Portulacaceae): The 78 seeds come from both EIA and LIA contexts at Mbandaka. They are similar in shape and size to small-seeded *Portulaca* species, e.g. *P. oleracea*. The roundish seeds are ca. 0.5 mm in diameter and the surface is vestured. The surface of the specimens is, however, strongly corroded, leaving small holes where the vesturing is destroyed, not allowing for a lower taxonomic level identification (Fig. 4i). Seeds of other Portulacaceae (e.g. *Talinum* spp.) can be excluded mainly due to their larger size.

Raphia sp.: 25 fragments of *Raphia* endosperm have been found in the EIA (Bokuma Phase) context of IYO 15/1/13 at Iyonda (Fig. 4g). In later contexts of Iyonda and at Bolondo only single fragments occur. Identification of the fragments was possible by comparison with the finds from Boso-Njafo (Kahlheber et al. 2014a). The fragments consist of a tissue with small isodiametric cells, crossed by furrows representing the casts of endosperm ruminations (Bayer and Appel 1996).

Charred parenchyma fragments

Small charred parenchyma fragments occur regularly in all sites and phases, revealed by routine flotation. We consider them as possible remnants of tuber preparation for food. The potential of parenchyma fragments for the identification of underground storage organs such as tubers in general, and for tropical archaeology in particular has been shown by the seminal works of Hather (1994, 2000). In island Southeast Asia, charred parenchyma fragments were attributed to roots and, among others, tentatively identified as wild and domesticated *Dioscorea* spp. (Paz 2005; Barker and Richards 2013). Similar to these, the fragments of the ICB sites consist of charred parenchyma tissue with mostly isodiametric cells and vascular bundle traces (Fig. 5b, c), but without further diagnostic features such as mineral inclusions, e.g. calcium oxalate raphides, which might point to *Dioscorea* tubers. Their small size precludes a more precise botanical identification. Only in one single case was a LIA parenchyma fragment still covered on one side by a corrugated (wavy) cortex, possibly allowing for future taxon identification (Fig. 5a; context BLD 16/5-47).

Charred food fragments

Potential small charred food preparation remains, mostly with a vesicular texture, occur abundantly in the LIA archaeobotanical record of Bolondo. They were, similarly to the rare parenchyma fragments, revealed by routine flotation. Most fragments have an amorphous, irregularly porous appearance (Fig. 5d), probably due to agglutination of gelatinised starch grains (Crowther 2012). Some fragments still show the irregular cellular structure (Fig. 5e). In some cases, club-shaped *C. americanus* caryopses or their outlines are visible, pointing to the processing of gruel from complete pearl millet grains (Fig. 5f).

Stable isotope studies by Amy Styring (Bleasdale et al. 2020) on seven charred potential food fragments from Bolondo have revealed a signature of C_3 plants or aquatic resources in five cases ($\delta^{13}C$ between − 27‰ and − 24‰) and a C_4-signature ($\delta^{13}C$ around − 9‰) in two cases. These values are in line with the origin of the food remains from different sources, including *C. americanus* and tubers, possibly *Dioscorea* spp.

Copal

Small chunks of fossil plant resin (copal) are found widely (although in small quantities) in nonarchaeological sediments as well as archaeological contexts of the Inner Congo Basin and its margins (e.g. Lepersonne 1937, pp. 31, 43, 49; Bouillenne et al. 1955, p. 20; Wotzka 1995). While both EIA and LIA contexts of Iyonda did provide a number of specimens, hardened copal lumps were much more steadily represented in the exclusively LIA levels of Bolondo (ESM 2 Table 1), there occurring either uncharred or darkened by partial charring (Fig. 4j). No associations with specific site features can be established, but ethnographic and historical evidence points to a range of indigenous uses of copal, including as torches (R Eggert 1987, pp. 280–281, note 1; Denbow 2013, p. 118), for ceramic vessel coatings (Coart and de Hauleville 1907, p. 153; Wotzka 1995, pp. 207, 210), or for sealing leaky dugout canoes (Ney 1887, p. 38). In earlier colonial times, copal was among the most sought-after rainforest resources, for example, for varnishes and paints, and the Belgian colonial powers forced Congo Basin inhabitants to collect it on a large scale (e.g. Payeur-Didelot 1899, p. 309; R Eggert 1987, p. 301, note 2; Omasombo Tshonda 2016, p. 148).

Phytoliths

65 sediment samples from all sites were screened for the presence of Musaceae phytoliths (Table 4; ESM 2 Table 4). For comparison, three soil surface samples taken at Iyonda in a garden area, which has been under plantain and sweet banana cultivation for many years, were also screened. The modern surface samples contained a small number of conspicuous Musaceae phytoliths (Fig. 6f–k), while the dominant morphotypes in these samples are Spheroid ornate, Spheroid echinate (nomenclature after ICPT 2019) and grass short cell phytoliths. Despite intensive screening of 27 sediment samples from EIA Iyonda, dated between ca. 460–180 BC (Poz-74885) and AD 570–690 (Poz-74894; both at 2σ) no Musaceae phytoliths could be detected.

Musaceae phytoliths were only identified in the LIA archaeological sediments excavated at all three sites (Fig. 6a–e); at Iyonda they were restricted to near-surface layers. A selection of these phytoliths could be indirectly dated by associated pottery and organic materials: Bolondo (ca. AD 1370–1590; Beta-447442; Beta-469858; Beta-469857; Beta-447441); Mbandaka (ca. AD 1460–1700; Poz-79306); and Iyonda (ca. AD 1600–2000; Poz-79290; all at 2σ). Whenever detected, the LIA Musaceae phytoliths occur in only very small numbers.

With a high certainty these phytoliths can be attributed to bananas (*Musa* spp.). Differential diagnosis allows us to distinguish some of the morphotypes (Mbandaka) from morphologically somewhat similar Commelinaceae seed phytoliths (*Cyanotis* spp. and *Commelina subulata*; Eichhorn et al. 2010, Figs. 2c–f, 3l–r). The differentiation from *Cyanotis* is first of all based on the character of the central cone (*Cyanotis*: truncated; *Musa*: 'crateriform' = distinctly concave), and on surface vesturing in the case of *C. subulata* (basal part distinctly scrobiculate = pitted; *Musa*: surface psilate = smooth).

The genus *Ensete*, like *Musa* spp. belonging to the Musaceae family, comprises three species in Africa (*E. livingstonianum*, syn. *E. gilletii*; *E. homblei*; *E. ventricosum*). Their distribution is restricted to areas outside the lowlands of the Inner Congo Basin (African Plant Database 2012a), where they thrive at elevations above 900 m a.s.l. (see species information for the three species, African Plant Database 2012b, c, d). *Ensete* species can therefore already be excluded on a phytogeographic basis as potential producers of the identified ICB Musaceae phytoliths. Furthermore, the ICB site morphotypes display the characters considered as useful for the distinction of *Musa* from *Ensete* by Perrier et al. (2011, Table S3): smooth surface; concave top of cone = crater; thin cone rims and abundant and well-defined processes at the base of the phytolith. They are morphologically similar to the *Musa* spp. phytoliths in our reference collection and the Musaceae morphotypes found in modern soil samples under plantain at Iyonda.

The 18 phytolith samples from the Cameroonian sites Bwambé Sommet, Abang Minko'o, Akonétye and Minyin are dominated by Spheroid ornate (from woody plants) and Spheroid echinate (from palms), while other morphotypes, including grass short cell phytoliths, are less common. No *Musa* phytoliths were detected.

Changes through time

Two phases are visible in the archaeobotanical samples, reflecting differences in plant use through time. The EIA, present at the sites of Iyonda and Mbandaka, includes material from the ceramic phases Imbonga, Bokele and Bokuma, dated between ~ 400 BC and ~ AD 650 (Fig. 2). Most remarkable for this period is the combination of *C. americanus* and *V.* cf. *unguiculata*, especially at the site of Iyonda. Whether these two species really remained in use over the entire EIA span covered here will require further confirmatory evidence. The most recent direct dates currently available on *C. americanus* and *V.* cf. *unguiculata* have calibrated 2σ intervals of ~ 60 BC-AD 180 and ~ 410–130 BC, respectively (Table 1: Poz-74817 and Poz-74886). Disregarding mixed associations, the only more recent EIA finds currently at hand are a single cf. *C. americanus* specimen from the Bokuma Phase pit IYO 17/2/1 and six cf. *Vigna* fragments from the Bokuma pit IYO 15/1/13, for which two coherent charcoal dates give a calibrated 2σ mean of ~ AD 580–660 (Table 1: Poz-74893 and Poz-74894; Table 2). Furthermore, charred parenchyma fragments (possibly *Dioscorea* spp.), *Canarium schweinfurthii*, *E. guineensis*, and various other wild plants are present in our EIA contexts, whereas *Musa* phytoliths are absent.

After a large chronological gap in the later first and earlier second millennium AD, plant remains from the LIA and subrecent times have been found at all three sites, corresponding to eight ceramic groups (Bondongo; Nkile; Botendo; Ikenge; Wema; Bolondo; Bokone; Ilemba-Bokonda), dated from ~ AD 1300 to the present (Fig. 2). In regard to pearl millet, charred parenchyma fragments, oil palm and wild plants, the assemblages are similar to those from the EIA, although wild plants, except for oil palm, are less numerous. The major difference in comparison with the EIA is the absence of *V. unguiculata* and *Canarium*, and the appearance of *Musa* phytoliths. The numerous charred food fragments at Bolondo are unique and indicate food preparation directly on the site.

Discussion

The arrival of a 'West African package': pearl millet and cowpea

The EIA finds of domesticated *C. americanus* at Iyonda, dated between ca. 400 BC and AD 50, indicate that the appearance of this crop in the Central African rainforest in the second half of the first millennium BC was a supra-regional phenomenon. Iyonda is the fifth site at which the presence of pearl millet for this time period has been attested, after Abang Minko'o, Bwambé-Sommet and Mintyaminyoumin in southern Cameroon, and Boso-Njafo in DR Congo (Eggert et al. 2006; Kahlheber et al. 2009a, 2014a). Boso-Njafo and EIA Iyonda are both attributed to the Imbonga Group, the oldest ceramic style group in the ICB. The pearl millet finds suggest that the people who had migrated into the ICB from a still unknown area of origin, introduced the crop together with Imbonga pottery and other constituents of their culture.

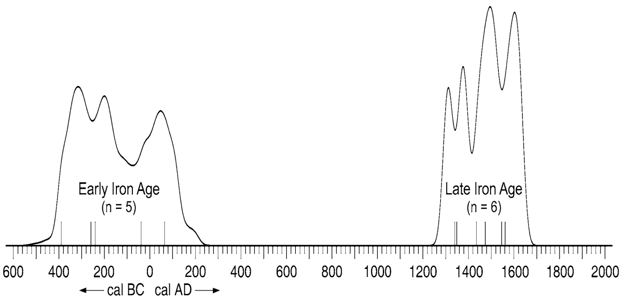

Fig. 7 Direct *Cenchrus americanus* AMS ^{14}C dates from Inner Congo Basin sites (n = 11): Cumulative dating probabilities, calibrated with CalPal v. 2020.8 (Weninger and Jöris 2008) using the IntCal20 Northern Hemisphere Radiocarbon Age Calibration Curve (Reimer et al. 2020). Southern Hemisphere Correction was not applied in view of all sample locations' close proximity to the equator. Ticks on the horizontal axis denote means of individual calibrated dates. The second oldest date (Erl-17763: 2,201 ± 52 BP) is from the site of Boso-Njafo (Kahlheber et al. 2014a, p. 500, Table 4). For details of all other dates, see Table 1

A newly discovered element is the *Vigna* cf. *unguiculata* found in Imbonga Phase pits of Iyonda. Iyonda is the first site in the Central African rainforest for which domesticated *V. unguiculata* is attested. Charred cowpea seeds are usually underrepresented in archaeological sites because they do not preserve well, and identification to species level and separation from wild *Vigna* species is difficult. Between ca. 800–400 BC, cowpea was present together with pearl millet at Nok sites in central Nigeria (ESM 3; Kahlheber et al. 2009b; Höhn and Neumann 2014, 2016), at Zilum in the Chad Basin (Breunig et al. 2006), and at Alibori and Dendi in Benin (Champion and Fuller 2018; Champion 2019).

Both pearl millet and cowpea are savanna crops that can deal with low and irregular rainfall (Andrews and Kumar 2006; Madamba et al. 2006). *C. americanus* was domesticated in the third millennium BC at the southwestern margin of the Sahara (ESM 3; Manning et al. 2011; Burgarella et al. 2018; Fuller et al 2021) from where it subsequently spread through West Africa, the Eastern Sahel and to India (Ozainne et al. 2009, 2014; Winchell et al. 2018). For *V. unguiculata*, genetic studies suggest a single origin of domestication, but the exact area could not yet be determined (Ba et al. 2004; D'Andrea et al. 2007 and references therein). Earliest evidence for domesticated *V. unguiculata* comes from the Kintampo B-sites in Ghana (AMS date of 1830–1595 BC; D'Andrea et al. 2007), lending support to a West African origin of the crop (ESM 3). The joint occurrence of the two crops at West African first millennium BC sites in the savanna and savanna/forest ecotone justify speaking of a 'West African package'. The 'package' implies a certain intensification of agricultural production, as elsewhere in the world where legumes and cereals have been cultivated together or in intercropping systems. It is reasonable to assume that this package would have remained an integral part of the agricultural repertoire of pottery-producing populations who migrated from the West African open grasslands and woodlands during the first millennium BC. However, archaeological proof of such migrations has been lacking until now.

The 'West African package' hypothesis is in line with linguistic data for the Bantu languages. From a detailed linguistic study on terms for pearl millet, Bostoen (2010) and Kahlheber et al. (2009a) concluded that pearl millet was an element of agricultural traditions of early Bantu speakers and was distributed together with the term **-cáŋgʊ́* in the western half of the Bantu area. Blench (2006, p. 240) considers cowpea as one of the few crops that reconstruct unambiguously to Proto-Bantu while Bostoen and Koni Muluwa (2017) more cautiously speak of a possibility. However, at least from a somewhat later stage of Western Bantu diversification, pearl millet and cowpea seem to have been in combined use. Comparative lexical data for the tentative reconstruction of Proto-West Coastal Bantu indicate that both crops were part of an inventory known to Bantu speakers before they left the West-Coastal Bantu Homeland, tentatively situated south of the rainforest, i.e. between the Bateke Plateau and Bandundu (ESM 3; Bostoen and Koni Muluwa 2017).

The persistence of *C. americanus* in the Central African rainforest

Pearl millet and seasonality

Cenchrus americanus originated in drier areas of West Africa with a seasonal climate. Seasonality does not automatically imply low total precipitation, but is characterised by the annual alternation of a humid and a dry period. At present, pearl millet is mainly, but not exclusively grown in areas with a distinct dry season during which the crop ripens and is harvested and stored (e.g. National Research Council 1996; Upadhyaya et al. 2017). In the ICB, the major areas with pearl millet cultivation are savannas and savanna/forest transition zones (Miracle 1967; Kahlheber et al. 2014a and references therein for the DR Congo). Thus, the first archaeobotanical *C. americanus* finds of Bwambé-Sommet and Abang Minko'o (Cameroon), and later the ones from Boso-Njafo (DR Congo) were interpreted as indicators for a seasonal climate in the second half of the first millennium BC, regarded as indispensable for the successful cultivation of the crop (Eggert et al. 2006; Kahlheber et al. 2009a, 2014a; Neumann et al. 2012). The seasonality hypothesis was corroborated by the palynological data from Nyabessan (ESM 3), showing a rapid partial breakdown of mature evergreen and swamp forests and development of pioneer vegetation between ca. 500–200 BC, indicative of rainforest disturbance and its replacement by secondary formations with semi-evergreen species (Ngomanda et al. 2009a). The pearl millet finds fitted into the scenario of the '3rd millennium BP rainforest crisis', first formulated by Schwartz (1992) and Maley (1992), and visible in several pollen diagrams from Central Africa (e.g. Elenga et al. 1996, 2004; Reynaud-Farrera et al. 1996; Maley and Brenac 1998; Vincens et al. 1998; Brncic et al. 2007, 2009; Ngomanda et al. 2009a, b; Maley et al. 2018). Kahlheber et al. (2009a, 2014a) and Neumann et al. (2012) concluded that pearl millet cultivation in the rainforest zone was a short interlude of a few hundred years in the second half of the first millennium BC, under the basic assumption that the crop would only thrive under climatic conditions with a clear dry season. Ever since then, the idea of pearl millet as a seasonality indicator has found its way into the secondary literature (e.g. Bostoen et al. 2013, 2015).

The LIA pearl millet finds at Mbandaka and Bolondo, dated between ca. AD 1300–1700 (Fig. 7), are not consistent with this hypothesis and suggest that pearl millet cultivation was not restricted to a short period in the second half of the first millennium BC. Palynological and other palaeoenvironmental data from key sites in Central Africa show forest regeneration and generally wet climatic conditions at least for the last 400–600 years (Elenga et al. 1996, 2004; Reynaud-Farrera et al. 1996; Brncic et al. 2007, 2009; Ngomanda et al. 2009b). This implies that pearl millet was cultivated between ca. AD 1300 and 1700 under climatic conditions with permanent rainfall all the year round. At Iyonda, Wotzka (2019a) conducted a cultivation experiment with pearl millet, showing that the crop can be successfully grown at the very heart of the evergreen rainforest (ESM 5). The cultivation experiment as well as a careful reconsideration of historic and agronomic sources (Wotzka 2019b) show convincingly that pearl millet cultivation, even though it has almost completely disappeared from ICB rainforests today, is not dependent on a seasonal climate with a distinct dry season. In contrast, they indicate that pearl millet cultivation is well possible under the presently prevailing all-year-round humid climate, in particular if simple horticultural measures such as the creation of open, sun-exposed spaces are applied. The new *C. americanus* finds from Mbandaka and Bolondo support the alternative hypothesis by Wotzka (2019b) that pearl millet cultivation may have been continuously practised in the ICB until at least the 16th century AD.

Staple or special food?

Although the planting and harvesting experiments at Iyonda have provided unequivocal evidence that pearl millet cultivation in the area is feasible and may provide a considerable harvest, grain storage could still have posed problems in the past. Mold may quickly attack the grains under permanent humid conditions (Williams and McDonald 1983). In all Central African sites where pearl millet caryopses have been found, they are only represented by small numbers, in comparison to the ubiquity and strong abundance of charred pearl millet remains at West African savanna sites (e.g. D'Andrea et al. 2001; Kahlheber 2004; Kahlheber and Neumann 2007; Neumann 2018; Champion 2019). Taking all information together, pearl millet in the rainforest should therefore be regarded as a marginal crop. This raises the question of which role it played in the diet and subsistence of regional Iron Age populations.

The use of pearl millet for special uses, such as brewing beer, may provide an explanation for its persistence at a low level in the Central African sites far beyond the rainforest crisis of the late first millennium BC. In Africa, the acidic traditional beer brewed from malted millets (e.g. *C. americanus*, *Eleusine indica*), or *Sorghum* (Hornsey 2003; Kubo 2016) is not only important as a nutritious and intoxicating drink, but is also of outstanding cultural and ritual significance (Arthur 2003). Intentional germination of cereals for malting renders the grains brittle, leading to bad preservation when they are charred (Stika 1996; Bouby et al. 2011; Eichhorn 2019; Fig. 4 in Larsson et al. 2019). This is in line with our observation of damaged archaeobotanical pearl millet caryopses, particularly corroded in their embryonic area.

That pearl millet may have been put to special use, is also indirectly suggested by a study on stable isotopes in human and animal bone collagen and tooth enamel from four Central African Iron Age rainforest sites, including Bolondo and Imbonga (Bleasdale et al. 2020). Bone collagen samples from LIA Bolondo humans show δ^{13}C values between – 21.0 and – 16.3‰, consistently higher than those of the wild fauna and fishes from the same site; this points to a mainly C_3-based human diet with some C_4 component, possibly pearl millet. By contrast, the human tooth enamel samples from Bolondo (LIA) and Imbonga (EIA) show distinct C_3 signals (– 14.7‰ to – 10.8‰), overlapping with the local fish value range. Considering that enamel ^{13}C isotopy represents mid-late childhood while collagen measurements are informative of nutrition during adulthood, an age-dependent disparity is in evidence, confirmed by discrepant values in some individuals for which both values are available. One possible explanation for this observation is that C_4-based resources, including millet beer, may have made somewhat greater contributions to adult diet in comparison to that of children. Hence, both the pearl millet macroremains and the stable isotope results do lend some support to the interpretation that the major use of pearl millet was for the production of beer. This does not, however, exclude the possibility that the cereal was also consumed for food, for example as gruel, but its role as a staple is questionable.

Cultivation or import?

For the sparse EIA pearl millet finds, we assume that the crop was locally cultivated. From an archaeological point of view, there is no indication of trade or imports during that period. Concerning the LIA pearl millet finds, local cultivation is also much more likely than import. In the study area, ancient transport of millets over hundreds of kilometers, e.g. by boat, is possible, but unlikely. Even beyond, traditional plant food production in Africa was mainly at a subsistence level and if traded or bartered at all, crops were rather offered on local markets than transported very far. At present, the bulk of daily plant food consumed at fisher camps comes from the surrounding *terra firme* villages whereas fish is transported inland in exchange. A similar subsistence pattern may have already persisted during the past 500 years.

The role of tuber plants

The small parenchyma fragments regularly present in all sites and phases are indicators of tuber use. The tubers could have been either roasted in hot ash or cooked in pots and subsequently pounded in mortars. The finds of charred parenchyma point to the first method. Potential evidence for cooking of the tubers in pots is provided by the charred food remains with amorphous structure, and the isotopic C_3 signature of some food remains from Bolondo (Bleasdale et al. 2020).

The parenchyma fragments lack diagnostic features which might allow a confident taxon identification and could therefore potentially be attributed to any of the 12 plant families distributed in the Central African rainforest that produce underground storage organs (Hladik et al. 1984). However, among those, wild yams (*Dioscorea* spp.) are the most important ones in regard to diversity, productivity, and edibility (Hladik and Dounias 1993). Burkill (1939) described 23 *Dioscorea* spp. for DR Congo (formerly Belgian Congo), while Hladik and Dounias (1993) reported 15–17 species from the Central African rainforest most of which are edible. In contrast to a widespread view, many wild yam species can grow in dense forest, but they usually thrive best in either natural or man-made clearings, and they are more common in semi-deciduous than in humid evergreen forests (Hladik and Dounias 1993). In the dense evergreen forests dominant in the research area, wild yam species might have taken advantage of the open habitation spaces and pearl millet fields or gardens created by the Imbonga Phase settlers and later sedentary groups.

The presence of parenchyma, possibly of yams, in the archaeological sites does by no means imply that the plants were cultivated or even domesticated. The fragments could also originate from wild *Dioscorea* spp. Ethnographic studies among the Baka and Aka pygmies in Cameroon, DR Congo and the Central African Republic show that several wild *Dioscorea* spp. are collected as staples. The distribution of wild *Dioscorea* in different rainforest types is highly variable, but the density of the plants in the forest is usually sufficient to cover the carbohydrate needs of the forager populations (Hladik and Dounias 1993; Sato 2001; Yasuoka 2013).

However, the Baka and Aka are mobile foragers, and extensive movements in the forest are necessary to harvest the individual *Dioscorea* plants which usually show a dispersed distribution pattern. By contrast, the ICB pottery-producing populations were sedentary, as can be inferred from their large-scale, often multi-phase settlement sites featuring dozens to hundreds of refuse pits and pit deposits each (Wotzka 1995). In such settings, some kind of management of the tuber plants has to be assumed. This could have been some form of ‘paracultivation’, i.e. human activities to increase the yield of non-domesticated plants. Paracultivation, as practised by the Baka (Dounias 1993, 2001), designates a special method in which parts of the tuber remain in the ground during harvest, and afterwards the growth of new tubers is favoured in the soil with a less dense texture due to the digging. The Baka and Aka use specific wooden augers for digging up the tubers (Dounias 2001). Similar harvesting tools that were not archaeologically preserved, might have been used by the ICB settlers for tuber harvesting. Another form of paracultivation is common among yam farmers of West Africa and the Sheko in SW Ethiopia who regularly transplant wild *Dioscorea* individuals to their fields and gardens in addition to their domesticated varieties (Mignouna and Dansi 2003; Vernier et al. 2003; Hildebrand 2007).

Recent genetic research has identified *D. praehensilis*, a forest species, as the most probable ancestor of the domesticated West African *D. rotundata* (Scarcelli et al. 2019). Today, *D. praehensilis* has a very wide sub-Saharan distribution across savanna and forest zones, including the Central African rainforests; it mostly occurs in disturbed forests and cultivated areas (African Plant Database 2012e). It is quite probable that the immigrants settling the ICB rainforest during the second half of the first millennium BC were aware of the nutritional value of *D. praehensilis*. This hypothesis is in line with linguistically reconstructed vocabulary suggesting that yams, either wild or domesticated, had already been part of the diet of Proto-Bantu speakers (Philippson and Bahuchet 1994/1995; Blench 2006; Bostoen and Koni Muluwa 2017).

The banana enigma

Plantain bananas of the AAB genomic type are the most important staple crop all over the African equatorial rainforest, with more than 120 regional varieties estimated (De Langhe et al. 1994/1995). The plantains are triploid hybrids from *Musa balbisiana* and *M. acuminata*, originating in SE Asia, and introduced at an unknown date into Africa (Simmonds 1962; Perrier et al. 2011). Because direct material evidence for the initial introduction of plantains is still not available, it is not clear where and when they reached the continent and how they diffused into the equatorial rainforest. The scenarios for the spread of plantains from the East African coast to the interior of the continent are hypothetical (e.g. De Langhe et al. 1994/1995), and the claim of banana phytoliths in Uganda, dated to the fourth millennium BC (Lejju et al. 2005) has not found acceptance (Neumann and Hildebrand 2009).

Because plantains are parthenocarpic and vegetatively propagated, diversification can only occur through somatic mutation, also called ‘somaclonal variation’. De Langhe et al. (1994/1995) have calculated a time span of more than 1,500 years for the development and diversification into such a large number of varieties in Central Africa. Most linguistic studies, e.g. Philippson and Bahuchet (1994/1995), Vansina (1990), Blench (2009) and Bostoen and Koni Muluwa (2017), associate the spread of plantain in Central Africa with the Bantu expansion and estimate the arrival of plantains in the equatorial rainforest between > 3000–2000 years ago. The finds of *Musa* phytoliths in two pits at Nkang (central Cameroon), dated to ca. 800–150 BC (Mbida et al. 2000; Mbida Mindzie et al. 2001; Perrier et al. 2011) seemed to fit into this time frame and are often cited as confirmation of the linguistic scenarios.

However, notwithstanding intensive efforts, there is still no evidence for an EIA presence of *Musa* phytoliths in other archaeological sites of the Central African rainforest. Among 65 sediment samples taken at the sites of Iyonda, Mbandaka and Bolondo, only 10 yielded *Musa* phytoliths, in very small numbers and exclusively from LIA contexts. Equally, all attempts failed to find *Musa* phytoliths in the southern Cameroonian EIA sites of Bwambé Sommet, Abang Minko’o, Minyin, and Akonétye, dated between 400 BC and AD 400 (Eggert et al. 2006), despite laborious screening of 19 sediment samples.

Plantains are the only present-day staple crop in the ICB with a Central African history apparently beginning before the introduction of *M. esculenta* and *Z. mays*. The crop is easy to propagate, yields are high, and the fruits can be continuously harvested. Given the equivocal dietary role of tuber plants and pearl millet, and considering the historical linguistic evidence for *Musa* in Africa, how can the absence of *Musa* phytoliths in EIA pits in southern Cameroon and DR Congo be explained?

One possible answer is that plantains might have been present in the Central African rainforest during the first millennium BC, but not everywhere, and that their diffusion might have been slow. The presence of *Musa* phytoliths at central Cameroonian Nkang (Fig. 1) and their absence from Imbonga Phase contexts at Iyonda would then mirror scattered use of the crop during the earliest Iron Age. On the premise that the Imbonga Phase does indeed represent the first wave of Bantu immigration into the ICB, as has been tentatively suggested by Wotzka (1995, p. 248), the absence of *Musa* phytoliths at EIA Iyonda would mean at the same time that plantains were not part of the useful plants inventory of the (Bantu-speaking?) pioneer ICB immigrants.

However, *Musa* phytoliths are also absent from the well-studied southern Cameroonian sites of Abang Minko'o and Bwambé-Sommet, which are likewise more or less contemporaneous with Nkang and located only ca. 200 km further south. This renders the *Musa* phytoliths of Nkang even more isolated. Possibly, plantains were much rarer and more patchily distributed in the first millennium BC than has so far been assumed; their wide innovation as a staple food across Central African rainforest landscapes would then have happened at much later dates and would probably have had origins outside the wider region of present-day Yaoundé where Nkang is located.

Cultural practice and taphonomy also need to be considered. Even in our modern soil samples from a garden plot under cultivated plantains the number of *Musa* phytoliths is astonishingly low. In modern ICB villages, the remains of the plants, namely leaves and pseudostems which produce the conspicuous volcaniform phytoliths (Lentfer 2009), are usually not disposed in pits after fruit harvest, but are left to rot on in-situ open-air middens. Similar discard behaviour would have reduced the probability for *Musa* phytoliths to end up in pits. This could explain their rarity even in the more recent ICB contexts after ca. AD 1400.

The importance of *Elaeis* and *Canarium*

At the ICB sites, oil palm endocarp fragments occur with a high ubiquity and in high amounts compared to other macroremains. Because the Central African rainforests are relatively poor in plant foods, particularly in carbohydrate-rich resources, and the available game is low in fat, oil palm as a secure fat supplier can efficiently replace or supplement other sources of energy for the human metabolism. *Elaeis guineensis* has the highest yield of all oil crops (Corley and Tinker 2016, p. 11).

During the production of palm kernel oil, the endocarp is crushed to release the oil-rich endosperm. In contrast, oil extraction from the mesocarp mainly leaves entire endocarps. The predominance of small charred fragments in the ICB sites thus points to the production of palm kernel oil, probably in combination with oil exploitation from the mesocarp (D'Andrea et al. 2006).

Remains of oil palm endocarps are a common element of many West and Central African archaeological sites in the rainforest or forest–savanna ecotone, reported from 6,000 BP onwards (D'Andrea et al. 2006, and references therein). In traditional African agricultural systems, oil palm is neither domesticated nor deliberately planted (Zeven 1972). Oil palm seedlings easily establish themselves in clearings within the forest, such as settlements or fields. Sowunmi (1999) proposed that the increase of *Elaeis* pollen in West and Central African pollen diagrams after 3,000 BP would indicate plant cultivation. However, because *Elaeis* is a heliophile coloniser of open ground, it also successfully grows in natural openings of the forest (Maley and Chepstow-Lusty 2001). At the ICB sites for which we assume small-scale cultivation of pearl millet, cowpea and, later at least, plantain, open spaces were present due to settlement and cultivation activities. On these open grounds, oil palm groves could have developed without much human effort. Given the importance of palm oil in the diet, it is quite possible that people actively tended and managed their oil palms, as has been suggested for Kintampo contexts in Ghana (ESM 3; D'Andrea et al. 2006; Logan and D'Andrea 2012).

In the ICB samples, fragments of *Canarium schweinfurthii* appear in much smaller frequency and ubiquity than *E. guineensis* remains. In fact, the species has so far only been found at Iyonda, and is there exclusively restricted to EIA inventories, with only one of 13 relevant contexts definitely post-dating the Imbonga Phase (Table 2; ESM 2 Table 1). The general rarity of *Canarium* might be influenced by the high fragmentation rate of the endocarps, which makes identification of the small fragments difficult and results in a bias towards *E. guineensis* (D'Andrea et al. 2006). Although the absence of *Canarium* in later contexts might also be due to its ecological requirements (see 'Ecological implications' below), its low representation at Iyonda in comparison to *E. guineensis* rather reflects its minor role in the subsistence. *Canarium* endocarp fragments are common in West and Central African sites from the early Holocene onwards (Mercader et al. 2003; Oas et al. 2015 and references therein; Lupo et al 2021). In the Late Stone Age sites of Bosumpra and Shum Laka (ESM 3), *Canarium* dominates over *E. guineensis* (Lavachery 2001; Oas et al. 2015), suggesting that the incense tree was an important element of forager subsistence in West Africa. By contrast, in the Kintampo B-sites, the abundance and density of *Canarium* fragments is very low in comparison to oil palm which is interpreted as a shift to a more productive food-producing economy of the Kintampo populations (D'Andrea et al. 2006; Logan and d'Andrea 2012; Oas et al. 2015). Similarly, it seems that, in the ICB, oil palm was already a staple during the Imbonga Phase, while the role of *Canarium* is difficult to assess. Linguistic evidence points in the same direction. Although Bantu terms for *Canarium* are reconstructed to great time depth, their distribution is scattered, and Bostoen et al. (2013) conclude that *Canarium* was of lesser economic importance than oil palm.

Ecological implications

The small-seeded grasses (e.g. *Eleusine indica, Setaria/Brachiaria, Digitaria*) and small-seeded herbs *(Cleome,* cf. *Portulaca*) occasionally present in the samples may have potentially served for human nutrition, but first of all, they are weedy taxa of the ruderal flora of settlements and cultivated fields. Together with the ubiquitous *E. guineensis*, they indicate disturbed ground at the sites and in their vicinity. At Bolondo, small-seeded herbs and grasses (except for *Scleria*, growing in wet places and swamps) are absent, which is due to the function of the site as a fisher camp, without any cultivated plots in the surroundings and only minute gardening areas within. But even at Bolondo, *E. guineensis* is well represented, pointing to local, probably human-induced disturbance of the forest nearby.

At Iyonda the occurrence of *Canarium schweinfurthii* is chronologically complementary with *Musanga cecropioides*. *Canarium* is continuously present in Imbonga Phase pits dating to the late first millennium BC, but very rare in younger contexts and completely absent in the soil and colluvium samples of the last 700 years. By contrast, *Musanga* is absent from pure Imbonga Phase contexts, but well represented in post-Christian pits and colluvia. For instance, at Mbandaka *Musanga* is present from the Bokele Phase, ca. AD 100–300 (2σ; Poz-48995; Table 1).

C. schweinfurthii has a very wide distribution (African Plant database 2012f), mostly in semi-evergreen forests. Detailed data about its ecology are scarce. In the ICB, the deciduous tree is restricted to old secondary formations (Lebrun and Gilbert 1954, p. 61), especially in drier areas with semi-evergreen forest as potential natural vegetation (Vande Weghe 2004, p. 103; White 1983, pp. 78, 81). A possible explanation for its continuous presence during Imbonga times is that the species took advantage of drier climatic conditions (with seasonal rainfall?) in the late first millennium BC. The '3rd millennium cal BP rain forest crisis' might have favoured the distribution of semi-deciduous tree species which later disappeared. *Canarium* endocarps have also been found in southern Cameroonian EIA sites dated to between 400 BC and AD 400 (Eggert et al. 2006). In the Lopé area in Gabon (ESM 3), *Canarium* is restricted to EIA archaeological sites with similar dates (Oslisly and White 2007). As Oslisly and White (2007) suggest, *Canarium* was an appreciated useful tree for the EIA settlers, and its wide distribution probably results from a combination of ecological plasticity and human management practices. As mentioned in section '*Elaeis guineensis,* Arecaceae, and *Canarium schweinfurthii,* Burseraceae' above, the most recent specimens of *C. schweinfurthii* presently known from the ICB were found in an advanced EIA context of Iyonda, dated to around AD 600. Climatic factors might have played a role in the disappearance of *Canarium* from the regional archaeological record after this date, but a change in human preferences, with a shift from *Canarium* to more *E. guineensis*, is also conceivable.

Musanga cecropioides is today the most common pioneer species in the humid evergreen rainforest, but it does not occur in the semi-deciduous forest zone with a pronounced dry season (Coombe and Hadfield 1962). In the pollen profile of Nyabessan (ESM 3), *Musanga* is dominant in the modern pollen precipitation, but replaced by *Trema* as pioneer during the period with increased seasonality after ca. 450 cal BC (Ngomanda et al. 2009a). We therefore interpret the strong ubiquity of *Musanga* in contexts after ca. AD 100 in the ICB as an indicator of climatic conditions with year-round precipitation, comparable to today. The absence of *Musanga* at Bolondo is consistent with this interpretation because the riverbank location of the site, surrounded by swamp forest, does not allow cultivation, so that no or only a few open spaces are available for the establishment of pioneer trees.

Conclusions

Our research in the Interior Congo Basin (ICB) adds a further piece to the puzzle of early agricultural communities in the Central African rainforest. The sequence of our study covers the periods of ca. 400 BC to AD 650, and ca. AD 1300–2000, with a large chronological gap of some 650 years. The subsistence of the first sedentary populations in the ICB Basin after ca. 400 BC (Imbonga Phase) was based on *Cenchrus americanus*, *Vigna unguiculata*, *Elaeis guineensis*, *Canarium schweinfurthii* and tubers, possibly *Dioscorea*. Despite a taphonomy-related lack of direct evidence for this early period, there can be no doubt that fish also made a significant contribution to contemporary human diets in the region. Hunting and small livestock husbandry could likewise have been part of this initial EIA rainforest economy as is suggested, for instance, by roughly coeval faunal remains from Nkang in south-central Cameroon (Mbida et al. 2000) and Toubé 1 in north-central Gabon (Fig. 1; Assoko Ndong 2002). The set of vegetable resources central to this subsistence mode represents a combination reminiscent of similar, yet much earlier polythetic selections from the same plant resource pool which are known to have been practised by a number of culturally diverse societies in West Africa from the second millennium BC onwards (Neumann 2018; Kay et al. 2019). Prominent examples include the Kintampo Tradition of Ghana (D'Andrea et al. 2001, 2006, 2007) and Nigeria's Nok Culture (ESM 3; Kahlheber et al. 2009b; Höhn and Neumann 2014, 2016; Franke et al. 2020). The attested species are somewhat variable for cultural and taphonomic reasons. For instance, Nok Culture subsistence manifestly excluded use of oil palm and cannot as yet be firmly associated with animal husbandry while there is proof that an essentially similar Kintampo plant food regime included oil palm and was supplemented by small livestock and fish (Gautier and Van Neer 2005). Notwithstanding variable appearance across space and time, there can be no doubt that the conceptual origins of this basic mode of subsistence lie in the West African forest-savanna transition zone.

The first Iron Age immigrants into the ICB brought their specific variation on this basic economic theme with them as a ready-made kit forming the subsistence module within a comprehensive cultural package that had been assembled elsewhere; this package was well adapted to a settled lifestyle in tropical rainforest milieu and furthermore included pottery and iron metallurgy. As there is no evidence for Stone Age farming or agricultural innovation or acculturation in Stone Age populations, nor even evidence for any substantial presence of pre-Imbonga indigenous hunter-gatherer-fisher populations in the ICB at all (Wotzka 1995), all early exploitation practices associated with domesticated species must also have been introduced by the EIA immigrants (cf. Eggert 2014, p. 190). This concerns the cultivation techniques for *C. americanus* and *V. unguiculata*, but also the management of wild or semi-wild resources, such as *Dioscorea*, *Canarium* or *Elaeis*, and their associated tools and equipment.

A detailed consideration of the ICB archaeological record against the state of research in Historical Linguistics at the time led to the tentative conclusion that these first sedentary societies establishing themselves at the heart of the Central African rainforest during the Imbonga Phase might have been Bantu speakers who had taken part in the much studied expansion of that language family from its original homeland (Wotzka 1995). Thanks to Historical Linguistics, the location of this homeland may be safely assumed to have been in the savanna-forest mosaic landscapes linking West and Central Africa across the present-day Cameroon-Nigeria borderland. It may count as a rough yet significant match that the archaeobotanically inferred history of the ICB subsistence tradition points in the same direction. Moreover, lexical reconstructions of *C. americanus* and *V. unguiculata* as ingredients of early Bantu speakers' foodways agree with our findings.

The first occupation of the ICB took place during a period of increased seasonality in the second half of the first millennium BC. Both natural rainforest disturbance and human clearing for pearl millet and cowpea fields will have created favourable conditions for pioneer and secondary forest formations where *Canarium*, wild *Dioscorea* and oil palm could flourish. However, the former hypothesis that pearl millet could only be cultivated during a short time period in the late first millennium BC due to a more seasonal climate, is falsified by our new pearl millet finds from Mbandaka and Bolondo, dated to between the 14th and 16th centuries AD. Moreover, our cultivation experiment with modern landraces has shown that the crop can be grown under year-round rainfall. Pearl millet cultivation might have persisted in the area throughout the first and early second millennium AD, but there are no data yet between the mid-1st and mid-14th centuries AD. However, the role of pearl millet as a staple remains doubtful, because pearl millet caryopses occur only in small numbers in all sites and phases. Indications for sprouting on some of the caryopses, the marginal role of the crop in the rainforest today, and the isotope data from Bolondo may suggest that pearl millet played a special role in the diet. For instance, use of pearl millet for beer production in specific cultural contexts might explain its persistence until the recent past.

The role of *Musa* for the first EIA populations is still unclear. A combination of *C. americanus*, *V. unguiculata*, *Dioscorea* spp., *E. guineensis*, *Canarium*, fish, some caprines and wild game would surely have been sufficient to supply the basic nutritional needs of the small EIA village communities. In this scenario, it is not necessary to claim plantain as an indispensable crop. The lack of *Musa* phytoliths from the well-studied EIA sites in both the ICB and southern Cameroon might indeed be evidence of absence. It is conceivable that *Musa*, although present at Nkang by the middle of the first millennium BC, was still unknown in larger areas of the Central African rainforest at that time and that their diffusion as an introduced crop was very slow. In the ICB, *Musa* has been present since at least around AD 1400, a time when pearl millet still persisted. The combination of *C. americanus*, *Musa*, *E. guineensis*, possibly *Dioscorea*, and fish was the base of subsistence for LIA populations in the ICB during the 15th and 16th centuries AD. Afterwards, the indigenous crops were replaced by the Neotropical domesticates *Manihot esculenta* and *Zea mays*, while plantain still remained a basic staple.

The development of agriculture in the Central African rainforest is historically unique and dissimilar from corresponding processes in other tropical rainforests of the world. In rainforests of SE Asia, New Guinea and South America indigenous agriculture was based on long-term resource exploitation by hunter-gatherers, deeply rooted from back in the Early Holocene and even sometimes the Pleistocene (e.g. Denham et al. 2009; Piperno 2011; Clement et al. 2015; Roberts and Petraglia 2015; Barker et al. 2017; Roberts 2019). Traditional agriculture in these areas is still mainly based on indigenous domesticates (e.g. *Manihot* and other root crops in Amazonia; *Dioscorea*, *Colocasia esculenta* (taro), and fruit trees including *Metroxylon sagu* (sago palm) in SE Asia). All these areas had an indigenous stock of highly productive wild starch plants—which is not the case in the Central African rainforest. There, it seems, not too long after their introduction to West-Central Africa and subsequent spread into the interior during Early Modern times, the much more productive American crops of *M. esculenta* and *Z. mays* became more attractive alternatives to African *Dioscorea* spp. and *C. americanus*, which they had outcompeted, or even consigned to oblivion, by the 1880s (R Eggert 1987, pp. 7–18; Wotzka 2019b, pp. 424–425).

The diversity of Central African rainforest subsistence in the past remains to be explored. The picture is still patchy and incomplete, based on a very small number of sites with in-depth archaeobotanical studies. Many more sites have to be studied for their inventory of plant and animal resources. Systematic archaeological fieldwork and analysis open to the integration of results from all relevant disciplines yet free of excessive linguistic, biogeographic, climatic, vegetational or cultural preconceptions will have to play the main role for a long time to come.

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Authors contributions BE identified the plant macroremains and the phytoliths from the ICB, described the finds and did the comparative studies on modern plant material. KN studied the phytoliths from Cameroon. KN prepared the archaeobotanical data for publication. HPW assembled the archaeological data. KN and HPW wrote the manuscript.

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Data availability All basic data of this publication are available in the Electronic Supplementary Materials (ESM) provided.

Declarations

Conflict of interest The authors declare that they have no competing interest.

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