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Research papers

Charcoal identification in species-rich biomes: A protocol for Central Africa optimised for the Mayumbe forest

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ABSTRACT

Direct evidence for Central African vegetation history is mostly derived from palynology and palaeolimnology. Although anthracology has proven worthwhile for palaeovegetation reconstructions in temperate regions and South America, charcoal analysis has hardly been applied for Central Africa. Moreover, a transparent charcoal identification procedure using large databases and well defined characters has never been developed. Therefore, we present a Central African charcoal identification protocol within an umbrella database of species names and metadata, compiled from an on-line database of wood-anatomical descriptions (InsideWood), the database of the world's largest reference collection of Central African wood specimens (RMCA, Tervuren, Belgium) and inventory and indicator species lists. The 2909 Central African woody species covered by this database represent a large fraction of the total woody species richness of Central Africa. The database enables a directed search taking into account metadata on (1) anatomical features, (2) availability of thin sections within the reference collection, (3) species distribution and (4) synonymy. The protocol starts with an anatomical query within this database, focussing on genus rather than species level, proceeds with automatic extension and reduction phases of the resulting species list and ends with a comparative microscopic study of wood reference thin sections and charcoal anatomy. In total, 76.2% of the Central African species in the database are taken into consideration, focussing on indicator and inventory species. The protocol has a large geographical applicability, as it can be optimised for every research area within Central Africa. Specifically, the protocol has been optimised for the Mayumbe region and applied to radiocarbon dated (2055–2205 ^{14}C yr BP) charcoal collections from a pedoanthracological excavation. The validity of the protocol has been proven by the mutual consistency of charcoal identification results and the consistency of these identification results with vegetation history based on phytogeographical and palynological research within and around the Mayumbe. As such, anthracology complements palynology and a combination of both can lead to stronger palaeobotanical reconstructions.

1. Introduction

African vegetation history is not yet fully understood. Indirect evidence is mostly based on phytogeographic and palaeolimnological research (Leal, 2004; Russell et al., 2009; Sosef, 1996; Tchouto et al., 2009; Verschuren et al., 2000). Direct evidence is mostly based on palynological research (Hessler et al., 2010; Maley, 1996, 2004; Ngomanda et al., 2009) while charcoal analysis has only sporadically been applied (Dechamps et al., 1988; Hart et al., 1996; Schwartz et al., 1990). Yet, soil macrocharcoal analysis (pedoanthracology) is spatially more precise than palynology because pollen is easily transported by wind over a long distance (Clark, 1988; Di Pasquale et al., 2008; Scott and Glasspool, 2007). Moreover, pollen types are rarely identifiable down to species level, which complicates interpretation of the results. Finally, species can be underrepresented (entomophilous taxa) or overrepresented (anemophilous taxa) in pollen diagrams (Elenga et al., 2000; Lebamba et al., 2009).

Charcoal is a chemically nearly inert material and extremely slowly affected by chemical weathering, thus remaining in soil profiles for a long period (Cope and Chaloner, 1980; Forbes et al., 2006; Scott and Glasspool, 2007; Skjemstad et al., 1996). Charcoal is especially valuable for palaeobotany and archaeology due to preservation of the anatomical structure during the charcoalification process. Thereby, it is

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Abbreviations: SEM, Scanning Electron Microscopy; RLM, Reflected Light Microscopy; TLM, Transmitted Light Microscopy; RMCA, Royal Museum for Central Africa (Tervuren, Belgium); UNESCO, United Nations Educational, Scientific and Cultural Organisation; IAWA, International Association of Wood Anatomists; FAO, Food and Agricultural Organisation of the United Nations; Tw(followed by a number), Tervuren wood specimen label; Tv, transversal direction (in wood); Tg, tangential direction (in wood); R, radial direction (in wood).

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feasible to identify charcoal using the same anatomical features as wood (Di Pasquale et al., 2008; Figueiral and Mosbrugger, 2000; Scheel-Ybert, 2000). Yet, absolute measurements have to be interpreted with caution as some features (e.g. vessel diameter) can change significantly due to heat shrinkage (Braadbaart and Poole, 2008; Prior and Gasson, 1993). Microscopic features for hardwood identification are thoroughly described and numbered by a Committee of the International Association of Wood Anatomists (IAWA Committee, 1989). Furthermore, the on-line search database 'InsideWood' archives photo-micrographs and wood anatomical descriptions applying these internationally accepted numbered features (InsideWood, 2011; Wheeler, 2011).

The most important challenge for Central African charcoal identification is coping with the extreme diversity of woody species. The species-richness in tropical regions such as Central Africa contrasts significantly with the relatively poor species diversity in temperate regions such as Europe or arid regions such as North Africa, where anthracology has been developed and applied regularly (FAO, 2005; Figueiral and Mosbrugger, 2000; Höhn and Neumann, 2012; Mutke and Barthlott, 2005). The few attempts for Central African pedoanthracology were based on personal expertise that did not make use of formal protocols, well defined characters and large wood anatomical databases (Dechamps et al., 1988; Hart et al., 1996; Schwartz et al., 1990). An identification protocol as used by Höhn and Neumann (2012) for the Sahara and the Sahel region and by Scheel-Ybert et al. (1998) for South America has never been developed for Central Africa to the knowledge of the authors.

Therefore, the main objective of this article is the development of a transparent and scientifically sound charcoal identification protocol taking into account a large number of Central African woody species. To do so, the authors compiled an umbrella database (Woody Species Database, WSD) composed of (1) the InsideWood database, (2) the digitized reference collection database of the xylarium of the RMCA (Royal Museum for Central Africa, Tervuren, Belgium) and (3) indicator species lists (Leal, 2004; Lebrun and Gilbert, 1954). In order to optimize the protocol for the study area, (4) species from inventory lists were added to the database. The protocol starts with a directed anatomical search in the WSD and ends with a comparative microscopic study of thin sections from the reference collection. A second objective of this article is the application, validation and evaluation of the protocol. To do so, charcoal fragments have been collected in a pedoanthracological excavation and analysed using the protocol.

2. Study area

Little is known on the evolution of species distribution patterns during the Pleistocene and Holocene in Africa. Senterre (2005) describes the phenomenon of choro-ecological transgressions. Particularly, certain species had a tendency to spread in several vegetation types and several geographical regions. On the other hand, due to e.g. forest regression phases, species disappear in certain regions (Senterre, 2005; Sosef, 1996). However, these tendencies are not yet fully mapped. Therefore, the protocol presented here does not take into account only those species currently occurring in the Mayumbe, but all species native to Central Africa.

The Central African forest complex can be divided into the Lower Guinean and Congolian forest regions, demarcated respectively as 'LG' and 'C' in Fig. 1 (Leal, 2004; Senterre, 2005; White, 1983). The Lower Guinean is separated from the Congolian forest by the marshes of the Congo and Ubangi rivers. The Congolian forest is separated from East Africa by the Albertine highland rift and Great Lakes (r&l). The Central African forest complex is surrounded by a transition zone of savanna types to the north (TN) and to the south (TS). The Lower Guinean forest is currently separated from the West African forest complex (WA) by savanna types in the 'Dahomey Gap' (dg) in Togo and Benin (Leal, 2004). Maley (1996) and Salzmann and Hoelzmann (2005) assume that this gap might have been overgrown by forest during the Holocene Maximum. As such, those West-African endemics are excluded and only species native to LG, C, TN and/or TS are taken into account for final identification.

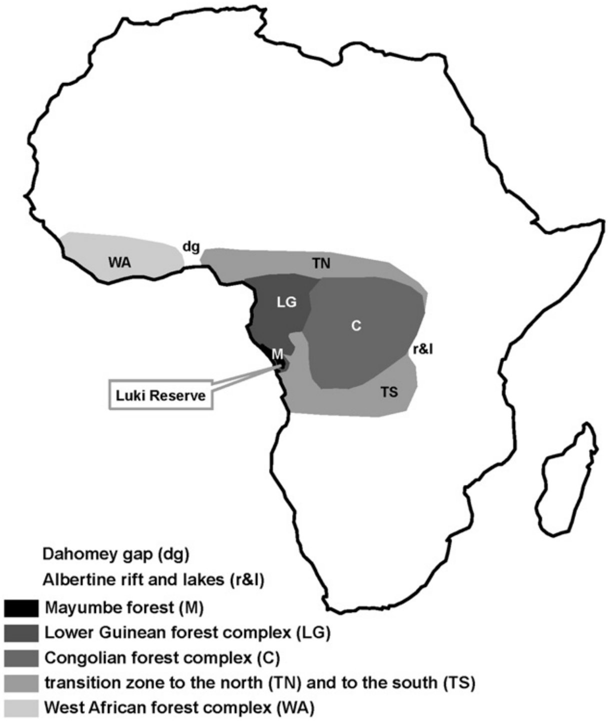


Fig. 1. Map of the Central and West African forest complexes; localisation of the Mayumbe forest and the Luki reserve.

The Mayumbe forest ('M' in Fig. 1) is part of the Lower Guinean forest complex. It is an assumed sub-mountainous glacial forest refuge located on the hills alongside the Atlantic coast, ranging from south Gabon down to the Luki reserve in the Bas-Congo, Democratic Republic of Congo (Maley, 1996; Sosef, 1996). The Luki reserve (indicated in Fig. 1) has been selected as research area because it shelters an important forest relic located on the southernmost Mayumbe forest edge. Pedoanthracological sampling was conducted in the well-documented experimental UH48 forest stand (Couralet, 2010; Donis, 1948; Donis and Maudoux, 1951).

3. Material and methods

3.1. Pedoanthracology

3.1.1. Sampling

In stand UH48, a relatively flat and dry area was chosen, which was probably not susceptible to human disturbance, erosion or deposition of colluvium, as recommended by Carcaillet and Thinon (1996). Next, prospection was conducted with an Edelmann auger, down to one metre. One pedoanthracological excavation (surface of 100 cm × 150 cm) was conducted on a spot where prospection yielded charcoal remains on a depth of at least 40 cm and where the soil was relatively dry and penetrable. Macro-charcoal fragments (largest width > 2 mm) were carefully collected by hand per interval of 10 cm. Specific anthracomass was calculated as described by Carcaillet and Thinon (1996). One kg of mixed disturbed soil was taken per two intervals for soil moisture content and organic matter content measurements (Ball, 1964). Also, thin sections were prepared from undisturbed soil samples embedded in polyester using standard procedures (Murphy, 1986) and micromorphological features were described applying polarisation microscopy, using the concepts and terminology of Stoops (2003). Finally, three charcoal fragments from different profile intervals were sent to the Poznán Radiocarbon Laboratory (Poland) for AMS ^{14}C measurement.

3.1.2. Detection of charcoal types and species-richness within the profile interval

For profile intervals with <50 charcoal fragments, all fragments were analysed using Reflected Light Microscopy (RLM) (e.g. Boutain et al., 2010; Scheel-Ybert, 2000). Based on microscopic features (IAWA Committee, 1989), most charcoal fragments were grouped in primary charcoal types, of which each type represents normally one species and sometimes several species. Some unidentifiable fragments originated from bark, juvenile wood or fruits. These might be originating from the same species represented by the primary types. Therefore, these fragments are grouped in secondary charcoal types which are not taken into account for further interpretation.

However, analysing all fragments is very time-consuming when charcoal fragments are numerous, e.g. >500 per layer. In our opinion, to retrieve the most important palaeobotanical data such as the total species-richness and species composition, there is no need to analyse all fragments as species-richness in a small pedoanthracological interval (<0.3 m³) is limited. The total number of charcoal types ($= c$) is considered to reach saturation after a certain number of analysed charcoal fragments ($= X$). Practically, the estimated total amount of charcoal types ($\hat{C}$) in the intervals was calculated with the CatchAll software (Bunge, 2011) for each record of X and c. Once $\hat{C}$ approximates c, saturation has been reached. From every layer, an arbitrary initial amount of 50 charcoal fragments was studied and more charcoal fragments were added until saturation.

3.1.3. Anatomical description of charcoal types

For each charcoal type, a large fragment containing all diagnostic features was mounted on a stub for Scanning Electron Microscopy (SEM). While studying SEM micrographs, charcoal types are described with the same numbered anatomical features as used on the on-line InsideWood database (IAWA Committee, 1989; InsideWood, 2011; Wheeler, 2011). The final result of the charcoal type description consists of two strings of numbered features. A first string represents primary features which are easily visible. A second string represents secondary features which are variable or unclear. Some anatomical features change during charcoalification, as illustrated by Bustin and Guo (1999) and Braadbaart and Poole (2008). Specifically, shrinkage has been taken into account while describing charcoal type anatomy (e.g. Prior and Gasson, 1993). According to Braadbaart and Poole (2008), tangential diameter shrinkage of vessels can amount to 50%. Moreover, also possible shrinkage of intervessel pits has been taken into account. Finally, some hardwood features are hard to see in charcoal. As such, following numbered IAWA features (IAWA Committee, 1989) are never used as primary features: growth rings (features 1–2), arrangement of intervessel pits (20–23), vestured pits (29), vessel-ray pitting (30–35), druses (144–148), other crystal types (149–158), and silica (159–163).

3.2. Development of the Woody Species Database (WSD)

3.2.1. A composed ‘umbrella’ database

Two databases and four species lists have been combined into a comprehensive excel file called ‘Woody Species Database’, further ‘WSD’. This WSD contains a list of species names followed by a wide range of metadata concerning the presence of thin sections in the RMCA, anatomical features, distribution area, ecology and synonymy. Within this umbrella database, a protocol has been developed using the excel column filter function and additional formulas.

First of all, the reference collection database of the xylarium of the RMCA has been used. This is one of the largest collections of wood specimens in the World and possibly the largest collection of Central African wood specimens (Lynch and Gasson, 2010). Large effort was put into digitizing all metadata of the species names and specimens, which resulted in (1) an on-line search database (Tervuren Xylarium Wood Database, 2011) and (2) an excel spreadsheet of species names with several columns of metadata. For every species name, this database provides metadata on the provenance of its specimens and the presence of thin sections in the RMCA collection.

A second database which has been used to create the WSD is the InsideWood search database, described by Wheeler (2011). On the 11th of July 2011, all 5910 modern wood descriptions have been downloaded from the InsideWood database in excel format. This database mentions, per species, the presence or absence of microscopic hardwood features (1–163) described by the IAWA Committee (1989, pp. 1–320). Furthermore, features 164–188 provide information on geographical species distribution (IAWA Committee, 1989, pp. 320–321).

Inventory species lists of the Mayumbe and, more specifically, the Luki reserve have been incorporated as well (Donis, 1948; Donis and Maudoux, 1951; Maudoux, 1954; Monteiro, 1962; Pendje, 1993; Couralet, 2010; Maloti Masongo, unpublished results). Inventories provide detailed information on current species composition of the research area. Finally, indicator species lists are incorporated. A first list contains indicator species for all Central African vegetation types described by Lebrun and Gilbert (1954). These vegetation types range from dense evergreen rainforest to sclerophyllous dry forest and edaphic and secondary forest types (see also Mayaux et al., 2000). A second list contains Caesalpinioideae which are indicators for old-growth rainforest in the Lower Guinean and the Congolian rainforest according to Leal (2004).

3.2.2. Synonymy, distribution area and species ecology

Each row in the WSD represents a unique species name, listed in the first column. Metadata of all combined databases are listed in subsequent columns. Next, large effort was put into the problem of synonymy. Within a group of synonyms, each species name has a certain name status: only one synonym is regarded as ‘accepted’ and the rest as ‘unaccepted’. When no consensus has been reached yet, name status is marked ‘uncertain’. Name status has been derived from the African Plants Database of The Conservatory and Botanical Gardens of the City of Geneva (African Plants Database, 2011).

Furthermore, the provenance area of reference collection specimens does not always fall within the native distribution area of the species, as species from all over the world have been introduced in Central Africa since the onset of Portuguese explorations in the 15th century and the foundation of coastal trade posts. Therefore, the distribution pattern of all species recorded as ‘Central African’ in the WSD has been verified by the information available on the African Plants Database (2011), the ‘Flore du Congo Belge et du Ruanda-Urundi’ (INEAC, 1948–1963), the ‘Flora of West Tropical Africa’ (Hutchinson and Dalziel, 1954–1972), the ‘Flora of Tropical Africa’ (Oliver, 1830–1916), and ‘The Useful Plants of West Tropical Africa’ (Burkill, 1985). Five separate columns have been added mentioning natural occurrence of the species in regions M, LG, C, TN, TS and/or WA, presented in Fig. 1. Finally, several columns have been added describing ecology, temperament and morphology for the Central African species.

3.2.3. Adding thin sections and descriptions to the WSD

New anatomical descriptions have been added to the WSD. These descriptions will also be added to the InsideWood database once they have been optimised. Specifically, those Central African species were selected from which the genus is not present on the InsideWood database and from which wood specimens are available at the RMCA. Additionally, thin sections have been prepared from those indicator and inventory species previously lacking thin sections at the RMCA.

3.3. The identification protocol

A flow-chart of the identification protocol is presented in Fig. 2. A first block presents the composition of the WSD. This database contains 163 columns representing all anatomical hardwood features, which are recorded as being ‘present’, ‘absent’ or ‘variable’ (InsideWood, 2011; Wheeler, 2011). The second block in Fig. 2 presents the anatomical query and a subsequent series of extension phases. A third block presents a series of reduction phases. The WSD and the protocol as such are not publicly available on the internet. However, the RMCA collection is on-line as the search platform Tervuren Xylarium Wood Database (2011) which provides direct links to micrographs of thin sections and to descriptions on the online InsideWood database. Those who are interested can contact the authors for access to the RMCA collection.

Table 1
Descriptions of anatomical hardwood features used during comparative microscopy and not described by the IAWA committee (1989).

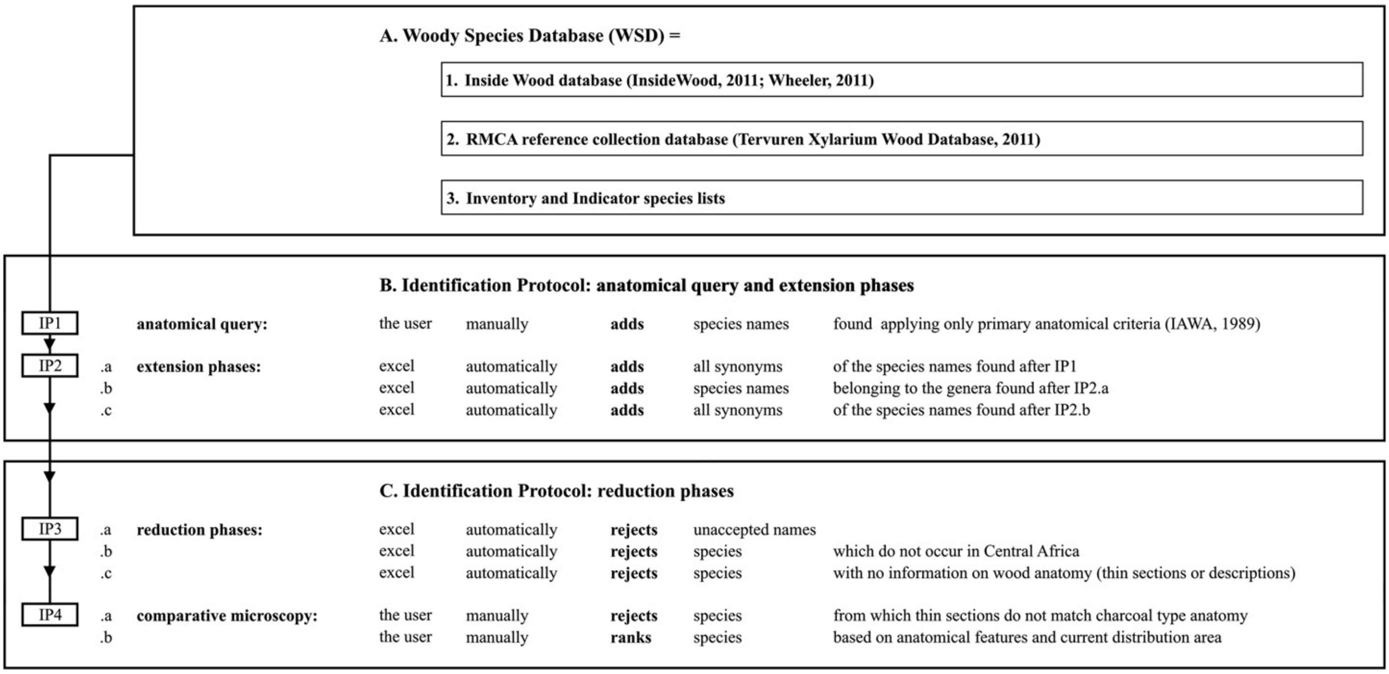
Non-IAWA anatomical feature	Description
Axial parenchyma difficult to recognise	Axial parenchyma could be diffuse, scanty paratracheal or vasicentric, but it is difficult to recognise due to charcoalification
Paratracheal axial parenchyma incomplete aliform	Aliform parenchyma forming wings on two opposite sides of a vessel without touching each other; fibres touch the vessel on 2 radially aligned sides
Ray cell lumina width << fibre lumina width	On Tg section
Ray cell lumina width = fibre lumina width	On Tg section
Ray cell lumina width >> fibre lumina width	On Tg section
Rays 100–80% uniseriate	A portion of 0–20% of the ray is 2-seriate
Rays 80–50% uniseriate	A portion of 20–50% of the ray is 2-seriate
Rays 50–0% uniseriate	A portion of 50–100% of the ray is 2-seriate
Presence of uniseriate rays	–
Presence of 2-seriate rays	–
Presence of 3-seriate rays	–
Presence of 4-seriate rays	–
Presence of 5-seriate rays	–
Presence of 6-seriate rays	–

3.3.1. Anatomical query and extension phases

The availability of a vast amount of reference thin sections in the RMCA collection offers the opportunity to consider much more species than only those present on the InsideWood search database. Based on morphological resemblances, including wood-anatomical resemblances of species, the science of plant taxonomy groups certain species into genera. Therefore, the first phase of the protocol (IP1 in Fig. 2) is designed to search genera, not species, on the InsideWood database, which is embedded in the WSD. Specifically, the excel filter function in the WSD is applied to the primary anatomical charcoal features. This query considers species from all over the world because some genera occur in several continents. The resulting species names are marked manually in a separate column (= results list) in the WSD. During a second identification phase, the resulting species name list is extended in three subsequent steps, for which the sequence is very important. In a first step, all synonyms of the species names found after the query, including the accepted names, are added to the results list applying an excel formula (IP2.a in Fig. 2). For certain species, synonyms belong to several genera. Next, excel adds all species belonging to the genera found after IP2.a (IP2.b). Finally, all synonyms of these species names are added to the results list (IP2.c). The resulting species name list is now at its maximum but covers many synonyms from species from all over the world. Moreover, some species lack reference material.

3.3.2. Reduction phases and comparative microscopy

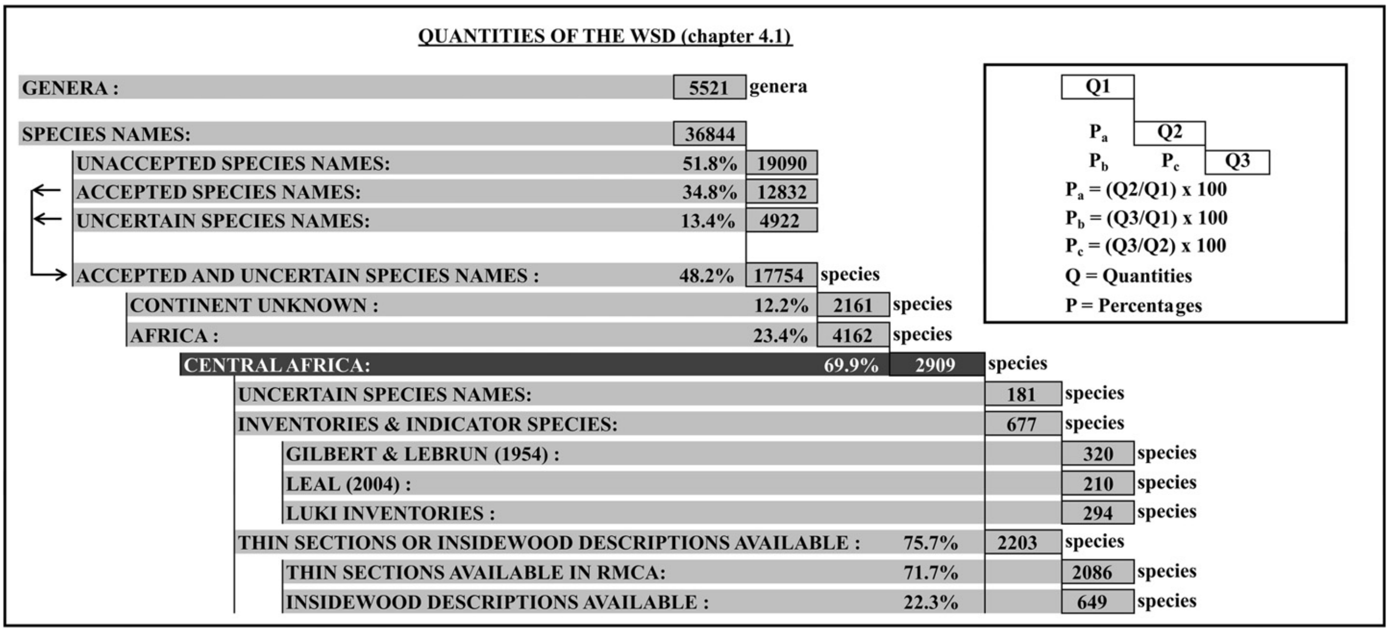
During a third identification phase (IP3 in Fig. 2) excel rejects all ‘unaccepted’ names (retaining only the ‘accepted’ or ‘uncertain’ name per species). Furthermore, all species which do not occur in Central Africa and all species without reference material or anatomical descriptions are rejected as well. Finally, thin sections of the species retained after IP3 are taken from the alphabetically ordered reference collection, stored in cupboards in the Laboratory for Wood Biology in the RMCA. Using Transmitted Light Microscopy (TLM) for


A. Woody Species Database (WSD) =
1. Inside Wood database (InsideWood, 2011; Wheeler, 2011)
2. RMCA reference collection database (Tervuren Xylarium Wood Database, 2011)
3. Inventory and Indicator species lists

B. Identification Protocol: anatomical query and extension phases
IP1 **anatomical query:** the user manually **adds** species names found applying only primary anatomical criteria (IAWA, 1989)
IP2 .a **extension phases:** excel automatically **adds** all synonyms of the species names found after IP1
.b excel automatically **adds** species names belonging to the genera found after IP2.a
.c excel automatically **adds** all synonyms of the species names found after IP2.b

C. Identification Protocol: reduction phases
IP3 .a **reduction phases:** excel automatically **rejects** unaccepted names
.b excel automatically **rejects** species which do not occur in Central Africa
.c excel automatically **rejects** species with no information on wood anatomy (thin sections or descriptions)
IP4 .a **comparative microscopy:** the user manually **rejects** species from which thin sections do not match charcoal type anatomy
.b the user manually **ranks** species based on anatomical features and current distribution area

Fig. 2. Flow-chart of the identification protocol; A: constitution of the anatomical search database; B: anatomical query and extension phases; and C: reduction phases.



QUANTITIES OF THE WSD (chapter 4.1)

GENERA : 5521 genera

SPECIES NAMES: 36844

UNACCEPTED SPECIES NAMES: 51.8% 19090

ACCEPTED SPECIES NAMES: 34.8% 12832

UNCERTAIN SPECIES NAMES: 13.4% 4922

ACCEPTED AND UNCERTAIN SPECIES NAMES : 48.2% 17754 species

CONTINENT UNKNOWN : 12.2% 2161 species

AFRICA : 23.4% 4162 species

CENTRAL AFRICA: 69.9% 2909 species

UNCERTAIN SPECIES NAMES: 181 species

INVENTORIES & INDICATOR SPECIES: 677 species

GILBERT & LEBRUN (1954) : 320 species

LEAL (2004) : 210 species

LUKI INVENTORIES : 294 species

THIN SECTIONS OR INSIDEWOOD DESCRIPTIONS AVAILABLE : 75.7% 2203 species

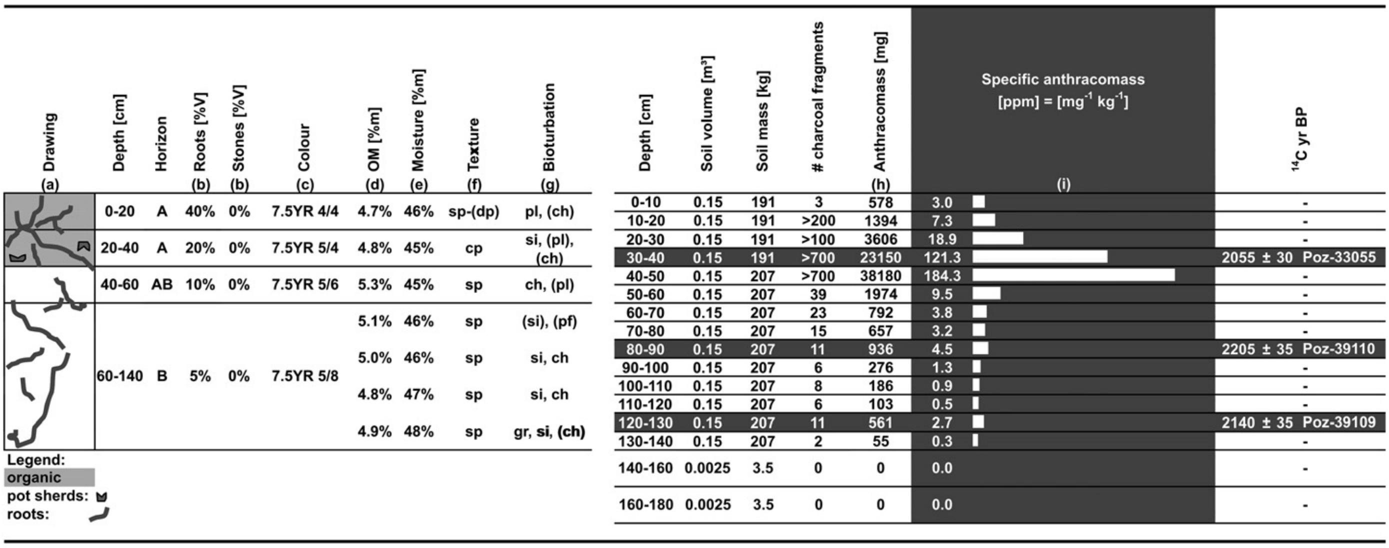
THIN SECTIONS AVAILABLE IN RMCA: 71.7% 2086 species

INSIDEWOOD DESCRIPTIONS AVAILABLE : 22.3% 649 species

P_a = (Q2/Q1) x 100
P_b = (Q3/Q1) x 100
P_c = (Q3/Q2) x 100
Q = Quantities
P = Percentages

Fig. 3. Quantities of the Woody Species Database.

the thin sections and SEM and RLM for the charcoal, wood anatomy is compared to the charcoal type anatomy. During this phase (IP4), species are rejected based on the secondary and tertiary charcoal anatomy features. Furthermore, this in-depth comparative microscopic phase offers the possibility to take into account anatomical features which are not described by the IAWA Committee (1989). These features are listed and described in Table 1. The final result of the charcoal identification protocol is a small group of species, which are all given a probability ranking. Specifically, a 10-point grading system, subject to the user's opinion, is used. Half of the points of the ranking system consider primary and secondary anatomical features as well as features described in Table 1: if a species resembles the charcoal anatomy perfectly, 5 points should be attributed. The other 5 points of the ranking system consider the distribution area (Fig. 1): occurrence in 'M' = 5 points; 'LG' = 4 points; 'C' = 3 points; 'TS' = 2 points; 'TN' = 1 point. The charcoal type gets a 9-character label consisting of the three first letters of respectively family, genus and species name of the best ranked species.



Depth [cm]	Horizon	Roots [%V] (b)	Stones [%V] (b)	Colour (c)	OM [%m] (d)	Moisture [%m] (e)	Texture (f)	Bioturbation (g)
0-20	A	40%	0%	7.5YR 4/4	4.7%	46%	sp-(dp)	pl, (ch)
20-40	A	20%	0%	7.5YR 5/4	4.8%	45%	cp	si, (pl), (ch)
40-60	AB	10%	0%	7.5YR 5/6	5.3%	45%	sp	ch, (pl)
60-140	B	5%	0%	7.5YR 5/8	5.1%	46%	sp	(si), (pf)
					5.0%	46%	sp	si, ch
					4.8%	47%	sp	si, ch
					4.9%	48%	sp	gr, si, (ch)

Depth [cm]	Soil volume [m³]	Soil mass [kg]	# charcoal fragments	Anthracomass [mg] (h)	Specific anthracomass [ppm] = [mg⁻¹ kg⁻¹] (i)	¹⁴C yr BP
0-10	0.15	191	3	578	3.0	-
10-20	0.15	191	>200	1394	7.3	-
20-30	0.15	191	>100	3606	18.9	-
30-40	0.15	191	>700	23150	121.3	2055 ± 30 Poz-33055
40-50	0.15	207	>700	38180	184.3	-
50-60	0.15	207	39	1974	9.5	-
60-70	0.15	207	23	792	3.8	-
70-80	0.15	207	15	657	3.2	-
80-90	0.15	207	11	936	4.5	2205 ± 35 Poz-39110
90-100	0.15	207	6	276	1.3	-
100-110	0.15	207	8	186	0.9	-
110-120	0.15	207	6	103	0.5	-
120-130	0.15	207	11	561	2.7	2140 ± 35 Poz-39109
130-140	0.15	207	2	55	0.3	-
140-160	0.0025	3.5	0	0	0.0	-
160-180	0.0025	3.5	0	0	0.0	-

(a) drawing of the profile; legend is given under the figure
(b) percent (Volume%) stones and roots in total interval volume
(c) soil color based on Munsell Soil Color Chart
(d) total soil Organic Matter (OM), based on Loss On Ignition (LOI) method (mass %)
(e) total soil moisture content (mass %)
(f) microscopic features related to groundmass texture (c/f related distribution pattern) - sp = single spaced porphyric, dp = double spaced porphyric, cp = close porphyric
(g) microscopic features recording bioturbation - ch = channels, gr = granular structure, pl = pellet structure, si = sediment infillings
(h) $m_{char,o75}$ = oven-dry anthracomass [mg] (cf. Carcaillet & Thinon, 1996): charcoal dried at 75°C for 48h
(i) $\rho_{char,o75}$ = oven-dry specific anthracomass [ppm = mg-1 kg-1] (cf. Carcaillet & Thinon, 1996): charcoal dried at 75°C for 48h

Fig. 4. Profile in UH48 (Luki reserve); visual representation of pit structure, profile description and anthracomass per soil layer.

4. Results

4.1. Woody Species Database: quantities

Quantities of the WSD are presented in Fig. 3. In total, the list covers 5521 genus names and 36844 species names. 19090 (= 51.8%) of these are unaccepted names, as synonyms of 12832 (= 34.8%) accepted names. The 4922 uncertain names are treated as accepted names. As there is only one accepted or uncertain name per species, quantities of accepted and uncertain names are equivalent to quantities of species. For the accepted names, metadata of all synonyms has been taken into account.

The database contains 4162 African species, from which the identification protocol presented in this article considers the 2909 Central African species. Inventory and indicator species lists cover 677 species. Specifically, 320 of these are indicator species mentioned by Lebrun and Gilbert (1954), 210 species are indicator Caesalpinioideae mentioned by Leal (2004) and 294 species were listed during inventories in the Mayumbe.

Furthermore, for 2086 (= 71.7%) of all Central African species, at least one transversal thin section has been produced and stored in the xylarium of the RMCA and for 649 (= 22.3%) of all Central African species, a wood anatomical description is available on InsideWood.

4.2. Sampling results

In the UH48 block within the Luki reserve, one pedoanthracological profile has been excavated on a spot where prospection (Edelmann auger) yielded charcoal fragments down to 100 cm. Pedological and anthracological results are presented in Fig. 4. Roots become less abundant from top to bottom of the profile. Stones are absent. Few horizons are distinguishable. This is confirmed by the study of micromorphological features (cf. Stoops et al., 2010), including a darker micromass in the 0–40 cm interval above a transitional zone (40–60 cm), and indications for the presence of lithological discontinuities around 20 and 40 cm depth. Throughout the profile, the soil shows various features related to bioturbation, in varying abundance.

Fig. 4 also presents the total number of charcoal fragments and absolute and specific anthracomass (cf. Carcaillet and Thinon, 1996). Only the four intervals between 10 and 50 cm contain more than 100 fragments. The two intervals between 30 and 50 cm contain more than 700 fragments. Small pottery fragments were found in the 30–40 cm interval, which is the second most charcoal-rich: 23.15 g charcoal in 0.15 m³ (= 121 ppm). Radiocarbon dating yielded radiocarbon ages of 2055 ± 30 ^{14}C yr BP for the 30–40 cm interval, 2205 ± 35 ^{14}C yr BP for the 80–90 cm interval and 2140 ± 35 ^{14}C yr BP for the 120–130 cm interval. As these dates are very close, the

Table 2

Number of studied fragments per profile interval per charcoal type; number of species (names) per identification phase per charcoal type.

		Primary charcoal types																Secondary types									
		ANN XYL AUR	ARE ELA GUI	CAE GIL MAY	CAE TET BIF	HUA HUA GAB	IRV IRV SMI	IRV KLA GAB	MEL GUA CED	MYR COE BOT	MYR SYZ GUI	RUB COR PAN	APO TAB IBO	DIC DIC MAD	ULM HOL GRA	unidentifiable - monocotyl	unidentifiable - mature wood	unidentifiable - bark	unidentifiable - juvenile wood	unidentifiable - fruit	# fragments belonging to primary types	# fragments belonging to secondary types	total # studied fragments	total # available fragments	# primary charcoal types	# secondary charcoal types	total # types
Profile interval depth [cm]	14C yr BP	# studied fragments in profile intervals per charcoal type																									
0–10	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	3	3	3	0	1	1
10–20	–	2	0	0	0	0	0	4	1	13	12	0	2	1	3	8	2	2	0	0	48	2	50	>200	10	1	11
20–30	–	0	6	1	6	1	2	1	0	0	30	0	0	0	2	1	0	0	0	0	50	0	50	>100	9	0	9
30–40	**2055 ± 30**	2	7	19	0	8	30	13	11	0	1	0	1	6	0	0	0	0	2	0	98	2	100	>700	10	1	11
40–50	–	1	8	22	0	0	7	5	7	0	0	0	0	0	0	0	0	0	0	0	50	0	50	>700	6	0	6
50–60	–	0	1	4	3	2	7	5	4	0	2	8	0	2	0	1	0	0	0	0	39	0	39	39	11	0	11
60–70	–	0	1	3	1	3	4	0	11	0	0	0	0	0	0	0	0	0	0	0	23	0	23	23	6	0	6
70–80	–	0	0	0	0	0	1	0	12	0	2	0	0	0	0	0	0	0	0	0	15	0	15	15	3	0	3
80–90	**2205 ± 35**	0	0	0	0	0	0	3	7	0	0	0	0	1	0	0	0	0	0	0	11	0	11	11	3	0	3
90–100	–	0	0	2	0	0	1	0	2	0	1	0	0	0	0	0	0	0	0	0	6	0	6	6	4	0	4
100–110	–	0	1	0	0	0	2	0	5	0	0	0	0	0	0	0	0	0	0	0	8	0	8	8	3	0	3
110–120	–	0	0	1	0	0	1	0	4	0	0	0	0	0	0	0	0	0	0	0	6	0	6	6	3	0	3
120–130	**2140 ± 35**	0	1	2	2	0	0	0	3	0	2	0	0	1	0	0	0	0	0	0	11	0	11	11	6	0	6
130–140		0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	2	2	1	1	2
All profile layers		5	25	54	12	14	55	31	68	13	50	8	3	11	5	10	2	5	2	1	361	8	**374**	>1800	15	3	**18**
Identification phase		# species (names) throughout the Identification phases																									
IP1 (anatomical query)		31	–	71	108	23	58	104	41	124	91	50	132	107	47	–	–	–	–	–	species names						
IP2.a (extension phase)		72	–	166	273	71	131	208	133	255	222	91	334	243	98	–	–	–	–	–	species names						
IP2.b (extension phase)		442	–	2149	2430	440	1781	2765	1443	1906	2614	453	2006	2402	1833	–	–	–	–	–	species names						
IP2.c (extension phase)		615	–	2880	2974	640	2709	4000	2329	2547	3806	622	2768	3478	2552	–	–	–	–	–	species names						
IP3.a (reduction phase)		230	–	1063	1127	231	832	1245	613	1164	1260	269	1037	1312	934	–	–	–	–	–	species						
IP3.b (reduction phase)		64	–	221	240	81	124	227	83	149	115	67	163	228	92	–	–	–	–	–	species						
IP3.c (reduction phase)		55	–	169	183	68	103	185	67	127	99	50	130	181	75	–	–	–	–	–	species						
IP4.a (microscopy)		10	–	11	9	7	9	8	5	8	12	11	9	8	6	–	–	–	–	–	species						
IP4.b (ranking)		4	–	2	1	1	2	1	2	2	2	3	1	1	5	–	–	–	–	–	best matching species						

charcoal fragments could be considered to be the result of the same fire event.

4.3. Charcoal types and identification results

A total amount of 374 charcoal fragments are grouped into 19 charcoal types. Table 2 presents the number of fragments per type and the number of species (names) retained after each phase of the protocol. The number of species names in the results list is always at its maximum at the end of the extension phase (IP2.c in Fig. 2 and Table 2), but is reduced drastically during subsequent reduction phases (IP3.a-IP3.c).

Three unidentifiable types consist of bark, fruit or juvenile wood, which might belong to one of the identifiable types. These 3 types are therefore classified as secondary charcoal types. The 2 other unidentifiable types consist of monocotyl wood and mature hardwood and are clearly different from the 14 identifiable types. As a result, the overall interval is composed of 16 primary charcoal types which belong to at least 16 different species. The charcoal types are randomly spread in all profile intervals, confirming the presumption that all charcoal fragments in all intervals have been formed during the same fire event.

One charcoal type, represented by a large number of fragments, is clearly derived from oil palm nut shells (*Elaeis guineensis* Jacq.). All other 13 primary identifiable charcoal types are clearly wood-derived and identified applying the protocol. For each charcoal type, the group of species retained after application of the protocol is presented in Table 3, which specifies whether identification was very successful or not. Less successful identification can be due to a low amount of available charcoal (ULM HOL GRA and APO TAB IBO) or due to unclear charcoal anatomy (DIC DIC MAD). Species names are accepted according to the African Plants Database (2011). Probability ranking is given in a separate column. Table 3 also provides information on distribution (cf. Fig. 1), species ecology, temperament and morphology for every species (African Plants Database, 2011; Burkill, 1985; Hutchinson and Dalziel, 1954–1972; INEAC, 1948–1963; Oliver, 1830–1916).

Finally, Table 3 also presents the taxonomic level down to which Elenga et al. (2000) and Lebamba et al. (2009) identified pollen from modern soil samples. Data of Elenga et al. (2000) is derived from study sites in the Mayumbe and those of Lebamba et al. (2009) from sites all over the Lower Guinea. Also, Table 3 presents

Table 3
identification results of very successful and less successful charcoal types. Species retained after application of the protocol, per charcoal type found in the UH48 profile. Best ranked species are marked in grey for each charcoal type.

			Ranking			Distribution					Ecology							Temperament				Morphology				Databases & lists						Pollen		
CHARCOAL TYPE	Family	Species	Distribution ranking (/5)	Anatomy ranking (/5)	Ranking (/10)	Mayumbe (M)	Lower Guinea (LG)	Congolia (C)	Transition South (TS)	Transition North (TN)	Moist evergreen forest	Moist semi-deciduous forest	Dry deciduous forest	Margin forest-savanna	Woodland savanna	Tree savanna	Shrub savanna	Pioneer species	Light demanding	Light/shade tolerant	Shade bearing	High tree (>20m)	Small tree (5-20m)	Shrub (0-5m)	Lianescent	RMCA wood sample	RMCA thin sections	Inside Wood Database	Invenory lists Luki	Indicator old forest	Indicator forest type	Relative abundance	Taxonomic level	Taxonomic level
						(a)					(b)							(b)				(b)				(c)	(d)	(e)	(f)	(g)	(h)	(i)	(j)	(k)
											Very succesful identification																							
ANN XYL AUR	Annonaceae	*Xylopia parviflora* (A. Rich.) Benth.	5	4	9	p	p	p	p	p	a	a	p	p	p	p	p	a	a	?	?	a	p	p	a	p	a	p	p	a	a	–	f	f
	Annonaceae	*Xylopia villosa* Chipp.	5	4	9	p	p	a	a	a	p	p	a	a	a	a	a	a	a	?	p	a	p	a	a	p	p	a	p	a	a	–	f	f
	Annonaceae	*Xylopia aurantiiodora* De Wild. & T. Durand	4	4	8	?	p	p	p	?	p	p	a	a	a	a	a	a	a	?	p	p	p	a	a	p	p	a	a	a	a	–	f	f
	Annonaceae	*Xylopia gilbertii* Boutique	4	4	8	?	p	p	?	?	p	p	a	a	a	a	a	a	a	?	p	p	a	a	a	p	p	a	a	a	a	–	f	f
	Annonaceae	*Piptostigma fasciculatum* (De Wild.) Boutique ex R.E. Fr.	5	3	8	p	p	p	a	?	p	p	p	?	?	a	a	a	a	?	p	a	p	a	a	p	p	p	a	a	a	–	f	f
	Annonaceae	*Polyceratocarpus gossweileri* (Exell) Paiva	5	2	7	p	p	p	p	?	p	p	p	a	a	a	a	a	a	?	p	a	a	p	p	p	p	a	a	a	a	–	f	f
	Annonaceae	*Exellia scammopetala* (Exell) Boutique	5	1	6	p	p	p	p	a	p	p	?	a	a	a	a	?	?	?	?	a	a	a	p	p	p	a	a	a	a	–	f	f
	Annonaceae	*Friesodielsia obovata* (Benth.) Verdc.	2	4	6	a	a	a	p	a	a	a	a	a	p	p	p	a	?	?	a	a	p	p	a	p	p	a	a	a	a	–	f	f
	Annonaceae	*Monanthotaxis schweinfurthii* (Engl. & Diels) Verdc.	5	1	6	p	p	p	p	p	p	p	p	a	a	a	a	a	a	?	p	a	a	p	p	p	p	a	a	a	a	–	f	f
	Annonaceae	*Xylopia tomentosa* Exell	2	4	6	?	?	?	p	a	a	a	a	a	p	p	p	a	a	p	a	a	a	p	a	p	p	a	a	a	a	–	f	f
	Arecaceae	*Elaeis guineensis* Jacq.	5	5	10	p	p	p	p	p	p	p	p	p	p	p	a	p	p	a	a	a	p	a	a	p	p	a	p	a	p	++	s	s
CAE GIL MAY	Caesalpinioideae	*Gilbertiodendron grandistipulatum* (De Wild.) J. Léonard	5	4	9	p	p	?	a	a	p	p	p	a	a	a	a	a	a	?	p	a	p	a	a	p	p	a	a	p	a	–	f	g
	Caesalpinioideae	*Gilbertiodendron mayombense* (Pellegr.) J. Léonard	5	4	9	p	p	?	a	a	p	p	p	a	a	a	a	a	a	?	p	a	p	a	a	p	p	a	p	p	a	–	f	g
	Caesalpinioideae	*Anthonotha brieyi* (De Wild.) J. Léonard	5	3	8	p	p	?	a	a	p	p	p	?	a	a	a	?	?	?	?	?	?	?	?	p	p	a	a	a	a	–	f	g
	Caesalpinioideae	*Anthonotha macrophylla* P. Beauv.	5	3	8	p	p	p	p	p	a	a	p	p	a	a	a	a	a	p	p	a	a	p	a	p	p	a	p	p	a	–	f	g
	Caesalpinioideae	*Anthonotha pynaertii* (De Wild.) Exell & Hillc.	5	3	8	p	p	p	p	p	a	p	p	p	a	a	a	a	a	p	p	a	p	p	a	p	p	a	p	p	a	–	f	g
	Caesalpinioideae	*Berlinia grandiflora* (Vahl) Hutch. & Dalziel	5	3	8	p	p	p	p	p	p	p	a	p	a	a	a	a	p	a	a	a	p	p	a	p	p	p	p	p	p	++	g	g
	Caesalpinioideae	*Brachystegia zenkeri* Harms	5	2	7	p	p	a	a	a	p	p	p	a	a	a	a	a	?	?	?	p	a	a	a	p	p	a	a	p	a	–	f	f
	Caesalpinioideae	*Brachystegia laurentii* (De Wild.) Louis ex Hoyle	4	2	6	?	p	p	a	a	p	p	p	a	a	a	a	a	a	p	p	p	a	a	a	p	p	p	a	p	p	–	f	f
	Caesalpinioideae	*Julbernardia gossweileri* (Baker f.) Torre & Hillc.	2	4	6	a	a	a	p	a	a	a	a	p	p	p	p	?	?	?	a	a	a	p	a	p	p	a	a	a	a	–	f	f
	Mimosoideae	*Tetrapleura tetraptera* (Schumach. & Thonn.) Taub.	5	1	6	p	p	p	p	p	p	p	p	p	a	a	a	a	p	p	a	p	p	a	a	p	p	p	p	a	a	—	–	s
	Caesalpinioideae	*Pachyelasma tessmannii* (Harms) Harms	4	1	5	?	p	p	a	a	p	p	?	a	a	a	a	a	a	p	p	p	a	a	a	p	p	p	a	p	a	–	f	f
CAE TET BIF	Caesalpinioideae	*Tetraberlinia bifoliolata* (Harms) Hauman	5	4	9	p	p	a	?	?	p	p	p	a	a	a	a	a	a	?	?	p	a	a	a	p	p	p	a	p	a	–	f	f
	Caesalpinioideae	*Aphanocalyx microphyllus* (Harms) Wieringa	5	3	8	p	p	p	p	p	p	p	p	p	a	a	a	a	?	?	?	p	a	a	a	p	p	a	a	p	a	–	f	f
	Mimosoideae	*Newtonia duparquetiana* (Baill.) Keay	5	3	8	p	p	?	a	p	p	p	p	a	a	a	a	a	a	?	?	p	a	a	a	p	p	a	a	a	a	—	–	f
	Mimosoideae	*Pentaclethra eetveldeana* De Wild. & T. Durand	5	3	8	p	p	p	?	?	p	p	p	?	a	a	a	p	p	a	a	p	p	a	a	p	p	a	p	a	p	++	s	s
	Caesalpinioideae	*Aphanocalyx heitzii* (Pellegr.) Wieringa	4	3	7	?	p	p	a	?	p	p	p	p	a	a	a	a	?	?	?	p	a	a	a	p	p	p	a	p	a	–	f	f
	Combretaceae	*Terminalia superba* Engl. & Diels	5	1	6	p	p	p	p	p	p	p	p	p	p	a	a	p	p	a	a	p	a	a	a	p	p	p	p	a	p	—	–	g
	Caesalpinioideae	*Tetraberlinia tubmaniana* J. Léonard	2	1	3	a	a	a	a	p	a	p	p	a	a	a	a	a	a	?	?	p	p	a	a	p	p	p	a	a	a	—	–	f
	Caesalpinioideae	*Didelotia idae* J. Leonard, Oldeman & de Wit	2	0	2	a	a	a	a	p	p	p	?	a	a	a	a	a	a	?	?	p	p	a	a	p	p	p	a	a	a	–	f	f
	Mimosoideae	*Newtonia aubrevillei* (Pellegr.) Keay	1	1	2	?	?	?	p	?	p	p	p	a	a	a	a	a	a	?	?	p	a	a	a	p	p	a	a	a	a	—	–	f
HUA HUA GAB	Huaceae	*Hua gabonii* Pierre ex De Wild.	5	4	9	p	p	p	a	a	p	p	p	a	a	a	a	a	a	?	p	a	p	a	a	p	p	a	p	a	a	—	–	–
	Caesalpinioideae	*Airyantha schweinfurthii* (Taub.) Brummitt	4	4	8	a	p	p	a	p	p	p	p	?	a	a	a	a	?	?	a	a	a	a	p	p	p	a	a	a	a	+	f	f
	Icacinaceae	*Desmostachys brevipes* (Engl.) Sleumer	4	3	7	?	p	a	a	?	p	p	a	a	a	a	a	?	?	?	?	a	a	a	p	p	p	a	a	a	a	—	–	f
	Icacinaceae	*Desmostachys vogelii* (Miers) Stapf	4	3	7	?	p	a	a	?	p	p	p	a	a	a	a	a	a	?	p	a	a	p	p	p	p	p	a	a	a	—	–	f
	Annonaceae	*Isolona campanulata* Engl. & Diels	5	2	7	p	p	a	a	?	p	p	p	a	a	a	a	a	a	?	p	a	p	a	a	p	a	p	a	a	a	–	f	f
	Clusiaceae	*Allanblackia parviflora* A. Chev.	4	2	6	a	p	p	a	p	p	p	a	a	a	a	a	a	a	p	p	p	p	a	a	p	p	p	a	a	a	+	g	g
	Annonaceae	*Monanthotaxis poggei* Engl. & Diels	4	1	5	?	p	p	p	?	p	p	?	a	a	a	a	a	a	?	?	a	a	a	p	p	p	a	a	a	a	–	f	f
IRV IRV SMI	Irvingiaceae	*Irvingia robur* Mildbr.	5	4	9	p	p	p	p	p	p	p	a	a	a	a	a	a	a	?	p	p	a	a	a	p	p	a	p	a	a	++	g	–
	Irvingiaceae	*Irvingia smithii* Hook. f.	5	4	9	p	p	p	p	p	p	p	p	p	a	a	a	p	p	a	a	p	p	a	a	p	p	a	p	a	p	++	g	–
	Meliaceae	*Guarea cedrata* (A. Chev.) Pellegr.	5	3	8	p	p	p	p	p	p	p	a	a	a	a	a	a	a	p	p	p	a	a	a	p	p	p	p	a	p	—	–	f
	Caesalpinioideae	*Caesalpinia welwitschiana* (Oliv.) Brenan	5	2	7	p	p	p	p	p	p	p	p	p	a	a	a	?	?	?	?	a	a	a	p	p	p	a	a	p	a	–	f	f
	Caesalpinioideae	*Schefflerodendron adenopetalum* (Taub.) Harms	5	2	7	p	p	a	p	a	?	?	p	p	p	?	a	a	?	?	a	a	p	a	a	p	p	a	a	a	a	+	f	f
	Rhamnaceae	*Quassia undulata* (Guill. & Perr.) D. Dietr.	4	2	6	?	p	?	a	p	a	a	a	p	p	p	?	a	a	p	p	a	p	p	a	p	p	p	p	a	a	—	–	–
	Caesalpinioideae	*Schefflerodendron gilbertianum* J. Leonard & Latour	4	2	6	?	p	p	a	a	p	p	p	a	a	a	a	a	?	?	?	p	a	a	a	p	p	a	a	a	a	+	f	f
	Caesalpinioideae	*Bauhinia petersiana* Bolle	2	1	3	a	a	?	p	a	a	a	a	a	p	p	p	?	?	?	a	a	p	p	a	p	p	a	a	a	a	–	f	f
	Caesalpinioideae	*Bauhinia rufescens* Lam.	1	1	2	a	a	a	a	p	a	a	a	a	p	p	p	a	?	?	a	a	p	p	a	p	p	p	a	a	a	–	f	f

Table 3 (*continued*)

			Ranking			Distribution					Ecology							Temperament				Morphology				Databases & lists						Pollen		
CHARCOAL TYPE	**Family**	**Species**	**Distribution ranking (/5)**	**Anatomy ranking (/5)**	**Ranking (/10)**	**Mayumbe (M)**	**Lower Guinea (LG)**	**Congolia (C)**	**Transition South (TS)**	**Transition North (TN)**	**Moist evergreen forest**	**Moist semi-deciduous forest**	**Dry deciduous forest**	**Margin forest-savanna**	**Woodland savanna**	**Tree savanna**	**Shrub savanna**	**Pioneer species**	**Light demanding**	**Light/shade tolerant**	**Shade bearing**	**High tree (>20m)**	**Small tree (5-20m)**	**Shrub (0-5m)**	**Lianescent**	**RMCA wood sample**	**RMCA thin sections**	**Inside Wood Database**	**Invenory lists Luki**	**Indicator old forest**	**Indicator forest type**	**Relative abundance**	**Taxonomic level**	**Taxonomic level**
						(a)					(b)							(b)				(b)				(c)	(d)	(e)	(f)	(g)	(h)	(i)	(j)	(k)
		Very succesful identification																																
IRV KLA GAB	Irvingiaceae	*Klainedoxa gabonensis* Pierre ex Engl.	5	4	9	p	p	p	p	p	p	p	p	p	p	a	a	a	p	a	a	p	a	a	a	p	p	p	p	a	p	––	-	-
		Cynometra mannii Oliv.	5	3	8	p	p	a	a	a	p	p	a	a	a	a	a	a	p	p	a	a	p	a	a	p	p	a	a	p	a	–	f	f
	Irvingiaceae	*Irvingia gabonensis* (Aubry-Lecomte ex O'Rorke) Baill.	5	2	7	p	p	p	a	p	p	p	p	a	a	a	a	a	a	?	p	p	a	a	a	p	p	p	p	a	a	++	g	s
	Irvingiaceae	*Irvingia grandifolia* (Engl.) Engl.	5	2	7	p	p	p	a	p	a	p	p	a	a	a	a	a	a	?	p	p	a	a	a	p	p	p	p	a	a	++	g	–
	Irvingiaceae	*Irvingia wombolu* Vermoesen	4	3	7	a	p	p	p	p	p	p	a	a	a	a	a	a	a	?	p	p	p	a	a	p	p	a	a	a	a	++	g	–
	Caesalpinioideae	*Scorodophloeus zenkeri* Harms	5	2	7	p	p	p	p	a	p	a	a	a	a	a	a	a	a	p	p	p	p	a	a	p	p	p	p	p	p	–	f	f
	Moraceae	*Ficus thonningii* Blume	4	2	6	a	p	p	p	a	a	a	a	a	p	p	p	a	p	a	a	a	p	p	a	p	p	a	a	a	a	+	g	g
	Rhamnaceae	*Pseudolachnostylis maprouneifolia* Pax	2	3	5	a	a	a	p	a	a	a	?	?	p	p	?	?	?	?	a	a	p	p	a	p	p	p	a	a	a	–	f	f
MEL GUA CED	Meliaceae	*Guarea cedrata* (A. Chev.) Pellegr.	5	4	9	p	p	p	p	p	p	p	a	a	a	a	a	a	a	a	p	p	a	a	a	p	p	p	p	a	p	––	–	f
	Meliaceae	*Guarea laurentii* De Wild.	4	4	8	?	p	p	a	a	p	p	a	a	a	a	a	a	a	a	p	p	a	a	a	p	p	p	a	a	p	––	–	f
	Meliaceae	*Guarea thompsonii* Sprague & Hutch.	5	3	8	p	p	p	p	p	p	p	a	a	a	a	a	a	a	a	p	p	a	a	a	p	p	p	p	a	p	––	–	f
	Simaroubaceae	*Quassia undulata* (Guill. & Perr.) D. Dietr.	4	3	7	?	p	?	a	p	a	a	a	p	p	p	?	a	a	p	p	a	p	p	a	p	p	p	p	a	a	––	–	–
	Sapindaceae	*Zanha golungensis* Hiern	5	1	6	p	p	p	p	p	a	p	p	p	p	?	a	a	?	?	a	p	p	a	a	p	p	a	p	a	a	––	–	f
MYR COE BOT	Myristicaceae	*Coelocaryon botryoides* Vermoesen	5	4	9	p	p	p	p	?	p	p	p	a	a	a	a	a	a	p	?	p	a	a	a	p	p	a	p	a	p	+	g	g
	Myristicaceae	*Coelocaryon preussii* Warb.	5	4	9	p	p	p	p	p	p	p	p	a	a	a	a	a	a	?	?	p	a	a	a	p	p	p	p	a	a	+	g	g
	Flacourtiaceae	*Oncoba gilgiana* Sprague	4	4	8	a	p	a	p	a	a	p	p	p	?	a	a	?	?	?	a	a	a	p	a	p	p	a	a	a	a	––	-	f
	Euphorbiaceae	*Antidesma laciniatum* Müll. Arg.	5	2	7	p	p	p	p	p	p	p	p	p	a	a	a	a	?	?	?	a	p	p	a	p	p	a	a	a	a	–	f	g
	Euphorbiaceae	*Antidesma vogelianum* Müll. Arg.	5	2	7	p	p	p	p	p	p	p	p	?	a	a	a	a	?	?	?	a	p	p	a	p	p	p	a	a	a	–	f	g
	Flacourtiaceae	*Oncoba crepiniana* De Wild. & T.Durand	3	4	7	a	?	p	p	a	a	a	?	p	p	?	a	?	?	?	a	p	p	?	a	p	p	a	a	a	a	––	–	f
	Flacourtiaceae	*Oncoba subtomentosa* (Gilg) S. Hul & Breteler	3	3	6	a	a	p	p	p	p	p	p	p	a	a	a	?	?	?	a	a	p	a	a	p	p	a	a	a	a	––	–	f
	Euphorbiaceae	*Flueggea virosa* (Roxb. ex Willd.) Voigt	2	2	4	a	a	a	p	p	a	a	a	p	p	p	p	a	p	a	a	a	a	p	p	p	p	a	a	a	p	–	f	f
MYR SYZ GUI	Myrtaceae	*Syzygium guineense* (Willd.) DC.	5	4	9	p	p	p	p	p	p	p	p	p	p	p	?	a	p	p	p	p	p	p	a	p	p	p	a	a	p	++	g	g
	Myrtaceae	*Syzygium staudtii* (Engl.) Mildbr.	5	4	9	p	p	p	p	p	?	p	p	p	p	p	?	a	?	?	?	a	p	p	a	p	p	a	a	a	a	++	g	g
	Moraceae	*Ficus louisii* Lebrun & Boutique ex Boutique & J.Léonard	4	4	8	?	p	p	a	p	p	p	p	a	a	a	a	a	a	?	?	p	a	a	a	p	p	a	a	a	a	+	g	g
	Moraceae	*Ficus lutea* Vahl	5	3	8	p	p	p	p	p	p	p	p	p	p	p	a	a	?	?	?	p	p	a	a	p	p	p	a	a	a	+	g	g
	Moraceae	*Ficus ovata* Vahl	5	3	8	p	p	p	p	p	p	p	p	p	p	?	a	a	?	?	?	p	p	a	a	p	p	a	a	a	a	+	g	g
	Hypericaceae	*Vismia affinis* Oliv.	5	2	7	p	p	a	p	a	a	?	p	p	p	?	a	a	?	?	?	a	p	p	a	p	p	a	a	a	a	––	–	–
	Ulmaceae	*Celtis gomphophylla* Baker	5	1	6	p	p	p	p	p	p	p	a	a	a	a	a	a	a	p	a	p	a	a	a	p	p	p	p	a	p	+	g	g
	Ulmaceae	*Celtis mildbraedii* Engl.	5	1	6	p	p	p	p	p	p	p	a	a	a	a	a	a	a	p	a	p	a	a	a	p	p	p	p	a	p	+	g	g
	Moraceae	*Ficus cordata* Thunb.	2	4	6	a	a	a	p	p	a	a	a	a	?	p	p	?	?	a	a	a	a	p	a	p	p	p	a	a	a	+	g	g
	Moraceae	*Morus mesozygia* Stapf	5	1	6	p	p	p	p	p	p	p	p	p	?	a	a	a	a	p	a	a	p	a	a	p	p	p	a	a	p	––	–	f
	Moraceae	*Trilepisium madagascariense* Thouars ex DC.	5	1	6	p	p	p	p	p	p	p	p	p	?	a	a	a	p	a	a	p	p	a	a	p	p	p	p	a	p	––	–	f
	Sapotaceae	*Inhambanella guereensis* (Aubrév. & Pellegr.) T.D. Penn.	1	3	4	a	a	a	a	p	p	p	a	a	a	a	a	a	a	?	?	p	a	a	a	p	p	a	a	a	a	+	f	f
RUB COR PAN	Rubiaceae	*Corynanthe pachyceras* K. Schum.	5	4	9	p	p	?	?	p	p	p	p	a	a	a	a	a	a	?	?	a	p	a	a	p	p	p	a	a	a	––	–	f
	Rubiaceae	*Corynanthe paniculata* Welw.	5	4	9	p	p	?	?	p	a	p	p	a	a	a	a	a	a	?	?	p	p	a	a	p	p	a	p	a	a	––	–	f
	Rubiaceae	*Pausinystalia johimbe* Pierre ex Beille	5	4	9	p	p	?	p	a	p	p	p	a	a	a	a	a	?	?	?	p	a	a	a	p	p	a	p	a	a	+	g	f
	Rubiaceae	*Pausinystalia talbotii* Wernham	4	4	8	a	p	?	p	a	p	p	p	a	a	a	a	a	a	p	a	p	a	a	a	p	p	p	a	a	p	+	g	f
	Rubiaceae	*Pausinystalia zenkeri* W. Brandt	4	4	8	a	p	?	p	a	p	p	p	a	a	a	a	a	?	?	?	p	a	a	a	p	p	a	a	a	a	+	g	f
	Rubiaceae	*Crossopteryx febrifuga* (Afzel. ex G. Don) Benth.	4	3	7	?	p	p	p	?	a	a	a	a	p	p	p	?	p	a	a	a	a	p	a	p	p	p	a	a	p	––	–	s
	Rubiaceae	*Mitragyna inermis* (Willd.) Kuntze	4	3	7	a	p	p	p	a	a	a	p	p	p	p	a	a	?	?	?	a	p	a	a	p	p	p	a	a	a	––	–	f
	Rubiaceae	*Craterispermum triflora* (K.Schum.) Thonn.	2	4	6	a	?	a	a	p	a	a	?	?	?	?	?	?	?	?	?	?	?	?	?	p	p	a	a	a	a	––	–	f
	Rubiaceae	*Hallea rubrostipulata* (K. Schum.) J.-F. Leroy	1	4	5	a	a	?	p	a	a	a	p	p	p	a	a	a	p	a	a	a	p	p	a	p	p	p	a	a	p	+	g	s
	Rubiaceae	*Gardenia imperialis* K. Schum.	1	3	4	a	?	?	p	a	a	a	a	p	p	a	a	a	?	?	a	a	a	p	a	p	p	a	a	a	a	––	–	f
	Rubiaceae	*Gardenia ternifolia* Schumach. & Thonn.	1	3	4	a	?	?	p	a	a	a	a	a	p	p	p	?	p	a	a	a	p	p	a	p	p	a	a	a	p	––	–	f

(a)	Distribution:	cf. Figure 1, data are derived from African Plants Database (2011), INEAC (1948-1963), Hutchinson & Dalziel (1954-1972), Oliver (1830-1916), Burkill (1985)
(b)	Ecol., temp., morph.:	Data are derived from African Plants Database (2011), INEAC (1948-1963), Hutchinson & Dalziel (1954-1972), Oliver (1830-1916), Burkill (1985)
(c)	RMCA wood sample:	Presence (p) or absence (a) of a wood sample of this species in the xylarium of the Royal Museum for Central Africa in Tervuren, Belgium (Tervuren Xylarium Wood Database, 2011)
(d)	RMCA thin sections:	Presence (p) or absence (a) of thin sections (Tv, Tg and R) of this species in the xylarium of the Royal Museum for Central Africa in Tervuren, Belgium (Tervuren Xylarium Wood Database, 2011)
(e)	Inside Wood Database:	Presence (p) or absence (a) of a wood anatomical description of this species on the on-line Inside Wood Database (july, 2011)
(f)	Inventory lists Luki:	Presence (p) or absence (a) of this species in one (or several) of the lists resulting from inventories in or around the Luki reserve
(g)	Indicator old forest:	Indicates whether this species is (p) or is not (a) one of the Caesalpinioideae considered as indicator species for old-growth rainforest by Leal (2004)
(h)	Indicator forest type:	Indicates whether this species is (p) or is not (a) one of the indicator species for a certain Central african forest type described by Lebrun & Gilbert (1954)
(i)	Relative abundance	Relative abundance of pollen type in modern soil samples (Elenga et al., 2000): "--"= not detected; "-": detected but very scarce; "+"= detected in moderate quantities; "++"= abundant
(j)	Taxonomic level:	Taxonomic level of pollen identification (Elenga et al., 2000): "f"= family level; "g"= genus level; "s"= species level; "-"= no defined pollen type available
(k)	Taxonomic level:	Taxonomic level of pollen identification (Lebamba et al., 2009): "f"= family level; "g"= genus level; "s"= species level; "-"= no defined pollen type available

the relative abundance of the pollen type in the pollen record of Elenga et al. (2000).

4.4. Estimation of species-richness

Fig. 5 is an example of a charcoal type saturation curve. It presents the evolution of the number of studied charcoal types (= c) and the estimated total amount of charcoal types (= $\hat{C}$) in the 30–40 cm profile interval. $\hat{C}$ approached c very closely when 40 charcoal fragments were analysed. However, as saturation was not yet fully reached, 50 additional fragments from this 30–40 cm interval were analysed. Only 2 new types were found, resulting in a total number of 11 charcoal types in the interval. Furthermore, the estimated total amount of charcoal fragments did not change significantly over the last 25 fragments. Specifically, after 100 charcoal fragments, CatchAll predicted the presence of slightly more than 1 charcoal type left to find in the interval: an estimated amount of 12.4 types versus an observed amount of 11 types. Theoretically, there is a chance that another type can be present in the 30–40 cm interval. Indeed, 6 out of the 16 primary types in the overall profile were not recorded in the 30–40 cm interval. 2 of these types are very rare in the profile. These rare types are represented by few (<6) and very small fragments, which impede proper visualisation and identification.

If the 366 charcoal fragments belonging to the 16 primary charcoal types in the overall profile are considered, the CatchAll software estimates a total species-richness of 16.7 species in the overall profile. Based on these CatchAll estimates, the chance that a new charcoal type can be found by analysing more charcoal fragments is considered small enough to stop adding fragments, both for the 30–40 cm interval as for the overall profile. The same conclusion could have been drawn after analysis of the first 50 charcoal fragments in the 30–40 cm interval.

4.5. Refining identification results: probability ranking

4.5.1. IRV IRV SMI

Charcoal type IRV IRV SMI has clear parenchyma bands of more than 3 cells wide, wood rays with mostly procumbent ray cells

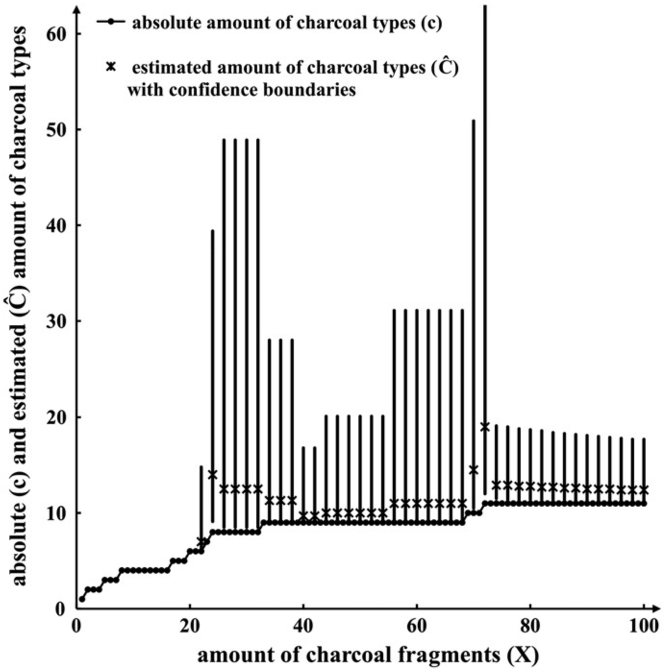


Fig. 5. Charcoal type saturation curve; comparison between the amount of observed charcoal types (c) and estimated total amount of charcoal types ($\hat{C}$) in the interval, in function of the number of observed charcoal fragments (X) for the interval between 30 and 40 cm depth: $c = f(X)$ and $\hat{C} = f(X)$. For every $X<22$, the total amount of analysed fragments was too small for reliable species-richness estimation with the CatchAll software. For every $22<X<72$, the non-parametric model Chao1 has been selected for calculation of $\hat{C}$ (Bunge, 2011). Finally, for every $X>72$, the best model proposed by the CatchAll software was used.

(sporadically a row of square top cells), rays of 2 or 3 cells wide and medium sized intervessel pits (Plate I). Species retained after application of the protocol are presented in Table 3. *Bauhinia rufescens* Lam., *Bauhinia petersiana* Bolle and *Caesalpinia welwitschiana* (Oliv.) Brenan are ranked lowest because their rays are regularly unicellular with rather large and irregular ray cell width. Furthermore, both *Bauhinia* spp. occur only in the margins of the Central African forest complex (region TS in Fig. 1). Next, *Schefflerodendron gilbertianum* J. Leonard & Latour, *Schefflerodendron adenopetalum* (Taub.) Harms and *Quassia undulata* (Guill. & Perr.) D. Dietr. are ranked low because their intervessel pits and their vessels seem to be too small and because they do not exhibit radial vessel groupings (up to 3) regularly. *Guarea cedrata* (A. Chev.) Pellegr. resembles the charcoal type anatomy very well, but its fibre lumina seem to be too wide, the parenchyma bands too narrow and there are too many upright marginal ray cells. Finally, there is no anatomical feature which is sufficiently diagnostic to distinguish *Irvingia smithii* Hook. f. from *Irvingia robur* Mildbr. Both are ranked highest and resemble the charcoal type anatomy almost perfectly. As an illustration of the agreement between the charcoal type anatomy and the wood anatomy, Plate I presents SEM images of charcoal type IRV IRV SMI, compared to TLM images of a wood specimen of *I. smithii*.

Irvingia smithii is mentioned by Lebrun and Gilbert (1954) as an indicator species for riverine rainforest and gallery forest. It is a relatively high and light-demanding tree. On the contrary, *Irvingia robur* is described by the African Plants Database (2011) as a rainforest tree on dry land. Both species occur in the Mayumbe and more specifically in the Luki reserve according to several inventories (Table 3).

4.5.2. DIC DIC MAD

Charcoal type DIC DIC MAD is very unclear, as illustrated by the SEM images in Plate II. Growth rings are not discernible on the charcoal fragments. The few vessels which are measurable are 40 ± 5 μm wide (Tg diameter on Tv section in Plate II.1 and 2), but the number of vessels mm^{-2} is unknown as most of the vessels are very small and difficult to distinguish from parenchyma cells on the Tv section. Vessels seem to be rare and mostly solitary; sometimes they occur as radially aligned couples. Perforation plates seem to be exclusively simple (Tg and R). Intervessel pits and vessel-ray pits are not discernible. Parenchyma is very unclear but seems to be scanty paratracheal or vasicentric. Possibly it is diffuse or banded (up to 3 rows). It is certainly not lozenge aliform. Rays are mostly 3 or 4 cells wide, not very high (up to 1 cm) and not storied. Body ray cells are procumbent or square and up to 2 rows of upright marginal ray cells are discernible. Ray cells are wider than fibre lumina. Fibres are very thick-walled. Canals are not discernible.

After application of the identification protocol, 8 species have been retained and presented in Table 3. *Leptactina arnoldiana* De Wild. and *Erythrococca bongensis* Pax are ranked lowest because their rays are not large enough. Furthermore, *E. bongensis* does not occur in the Lower Guinea. Both *Aulacocalyx* spp. and *Schumanniophyton magnificum* (K. Schum.) Harms are ranked low because they exhibit too many (>10) upright marginal ray cells. *Euadenia eminens* Hook.f. resembles well, but its rays are too high. Also, *Cassipourea gummiflua* Tul. resembles well but its parenchyma seems to be too abundant compared to the absence of a clear parenchyma pattern in the charcoal. Finally, *Dichapetalum madagascariense* Poir. is the best match, although its rays seem to be slightly too high. *D. madagascariense* is a lianescent shrub and occurs all over Central Africa in a large range of habitats.

5. Discussion

5.1. Protocol validation: identification results vs. forest history

5.1.1. Mutual consistency of identification results

For most charcoal types, the species retained and ranked during the last identification phase belong to several vegetation types (Table 3). The best ranked species for charcoal types RUB COR PAN, CAE TET BIF, MYR COE BOT, CAE GIL MAY, MEL GUA CED, ANN XYL AUR, HUA HUA GAB and APO TAB IBO occur only in rainforest environments. All these species are small (0–20 m) or large (>20 m) shade-bearing or light-tolerant trees (Table 3). For charcoal type ULM HOL GRA, 5 species were retained, which all occur in a rainforest environment (Table 3). Moreover, nearly all species retained for charcoal type CAE GIL MAY and the best ranked species of CAE TET BIF belong to the family of Caesalpinoideae and are typical old-growth rainforest species according to Leal (2004), including the best ranked species, *Gilbertiodendron mayumbense* (Pellegr.) J. Léonard. Also, *I. robur* is a rainforest species and one of the best ranked species for type IRV IRV SMI. The best ranked species for IRV KLA GAB, MYR SYZ GUI and DIC DIC MAD are characterised by a large ecological amplitude, which also comprises rainforest. As a conclusion, identification results suggest a rainforest environment in the southern Mayumbe around 2055–2205 ^{14}C yr BP. The results seem to be consistent, confirming the validity of the identification protocol.

5.1.2. The presence of oil palm as a bottleneck?

Only the presence of *Elaeis guineensis* seems contradicting the other identifications as the oil palm is an important pioneer species which is thought to play a major role in recolonisation of savanna (Maley and Chepstow-Lusty, 2001; Maley and Giresse, 1998). *E. guineensis* has been detected in several palynological records from the Lower Guinea (including the Mayumbe), indicating arid and cool palaeoclimatic phases characterised by forest regression. These records date back to the Eocene and the Miocene, indicating the indigenous nature of the species in the area (e.g. Maley and Brenac, 1998; Maley and Chepstow-Lusty, 2001; Maley and Giresse, 1998). However, only nut shell fragments have been found in the interval. Furthermore, the charcoal fragments in the profile interval were associated with pottery sherds, indicating human influence. Also, Neumann et al. (2012) mention a long tradition in the use of oil palm nuts by humans. This indicates that the fire which produced the charcoal fragments could have been a result of human activity and was either a wild-burning fire or a bonfire.

5.1.3. The Mayumbe during the Holocene cool period

By comparing ages of different Early Iron Age sites from Cameroon and Congo, Schwartz et al. (1990) found that iron smelting and thus human occupation spread relatively fast, down to the southern Mayumbe at the end of the Holocene cool period, between 2200 and 2100 ^{14}C yr BP. This may have been due to a greater extension of savanna. More specifically, archaeological, palynological and phytogeographical results suggest the existence of a complex and shifting forest-savanna mosaic pattern in the southern Mayumbe during the Holocene Cool period between 2500 and 2000 ^{14}C yr BP (Leal, 2004; Maley and Brenac, 1998; Ngomanda et al., 2009; Schwartz et al., 1990; Vincens et al., 1998). This mosaic pattern was characterised by a complex mixture of savanna, pioneer forest, secondary forest, primary rainforest and a broad range of intermediate phases within the forest succession cycle. As such, it is possible that the humans entering the primary rainforest brought along pots and oil palm nuts from nearby regenerating forest. Hence, the consistency of the identification results with forest history seems to confirm the validity of the identification protocol.

5.2. Protocol evaluation

The ultimate goal of search databases such as InsideWood (2011) and an umbrella database with an identification protocol as presented here, is to standardize identification of charcoal fragments between different analysts (e.g. Mitchener et al., 1997). Previous charcoal identification attempts for Central Africa were based upon the experience of individuals and did not address the complexity of species-richness, synonymy, or the limitation of the reference collection capacity (Dechamps et al., 1988; Hart et al., 1996; Schwartz et al., 1990). To the knowledge of the authors, this article presents the first attempt to quantify the possibilities and limitations of charcoal identification in Central Africa.

5.2.1. Species-richness of the Woody Species Database

Central Africa as presented by regions LG, C, TN and TS (Fig. 1) covers 5 countries completely (DRC, Congo, Cameroon, Gabon, Equatorial Guinea) and 3 countries partly (Nigeria, Central African Republic, Angola). According to Fig. 3, the WSD contains 2909 species from these countries. Data of the Food and Agricultural Organisation of the United Nations can serve as a good comparison. FAO (2005) has been monitoring the world's forests at 5 to 10 year intervals since 1946. Furthermore, FAO (2005) uses a broad definition of 'tree', including bamboo, palm and other woody species. Specifically, countries from West and Central Africa reported a maximum of 2243 native woody species per country. Assuming that there is a very large overlap in woody species composition between neighbouring countries, the total woody species diversity in Central Africa will probably not exceed multiples of this number. As such, the WSD presented here covers already a large percentage of the total Central African woody species-richness. Furthermore, the highest tree species diversity is recorded for South America, where Brazil reports more than 7880 native tree species (FAO, 2005). Indeed, Mutke and Barthlott (2005) confirm that the African continent is less diverse than South America and South-East Asia, although numbers go up to 4000 vascular plant species per 10,000 km² in the Lower Guinea.

5.2.2. Power of the identification protocol

By searching on genus level in the InsideWood database, the protocol takes into account 2399 (= 82.5%) of the Central African species recorded in the WSD (Fig. 6). However, reference material, being anatomical descriptions and/or thin sections, is needed for further consideration of these species during comparative microscopy. This is the case for 1937 (= 66.6%) of the Central African species. These species represent the combined power of InsideWood and the RMCA reference collection (Fig. 6). Furthermore, for 266 (= 9.1%) of the Central African species, the genus is not present on the InsideWood database, although thin sections are available at the RMCA (Fig. 6). Additionally, for 15 inventory and indicator species, thin sections had to be prepared from wood samples available in the RMCA. For these 281 species, anatomical descriptions have been added to the WSD. Finally, the total power of the protocol accounts for 76.2% of the 2909 Central African species in the WSD (Fig. 6). This is substantial compared to charcoal identification protocols for other research areas.

As a comparison, a computer-aided key to charcoal identification for a southern Brazilian coastal research area takes into account more than 900 species (Scheel-Ybert, 2000; Scheel-Ybert et al., 1998). Another example is the identification protocol for the upper northern Andes developed by Di Pasquale et al. (2008), which takes into account only 32 species described for the first time by the authors. The species composition in the upper Andes is well-defined and limited, in contrast to the complexity inherent in species composition in the Central African rainforest. Finally, pedoanthracology has been developed and since long been applied in Europe (Carcaillet and Thinon, 1996; Figueiral and Mosbrugger, 2000; Théry-Parisot et al., 2010). FAO (2005) reports a maximum of only 280 native tree species

Plate I. LEFT: Scanning Electron Micrographs (SEM) of charcoal type IRV IRV SMI;

1: Transversal direction (scale bar = 100 μm);
2: Radial direction (scale bar = 100 μm);
3: Tangential direction (scale bar = 100 μm);
4: Tangential detail of intervessel pits (scale bar = 10 μm);
RIGHT: Transmitted Light Micrographs (TLM) of *Irvingia smithii* Hook. f. (Tw 13339);
5: Transversal direction (scale bar = 200 μm);
6: Radial direction (scale bar = 200 μm);
7: Tangential direction (scale bar = 200 μm);
8: Tangential detail of intervessel pits (scale bar = 50 μm).

Plate II. LEFT: Scanning Electron Micrographs (SEM) of charcoal type DIC DIC MAD; (see on page 12)

1: Transversal direction (scale bar = 200 μm);
2: Transversal detail of vessel and parenchyma (scale bar = 20 μm);
3: Radial direction (scale bar = 200 μm);
4: Tangential direction (scale bar = 200 μm);
RIGHT: Transmitted Light Micrographs (TLM) of *Dichapetalum madagascariense* Poir. (Tw 32792);
5: Transversal direction (scale bar = 250 μm);
6: Transversal detail of vessel and parenchyma (scale bar = 50 μm)
7: Radial direction (scale bar = 250 μm);
8: Tangential direction (scale bar = 250 μm).

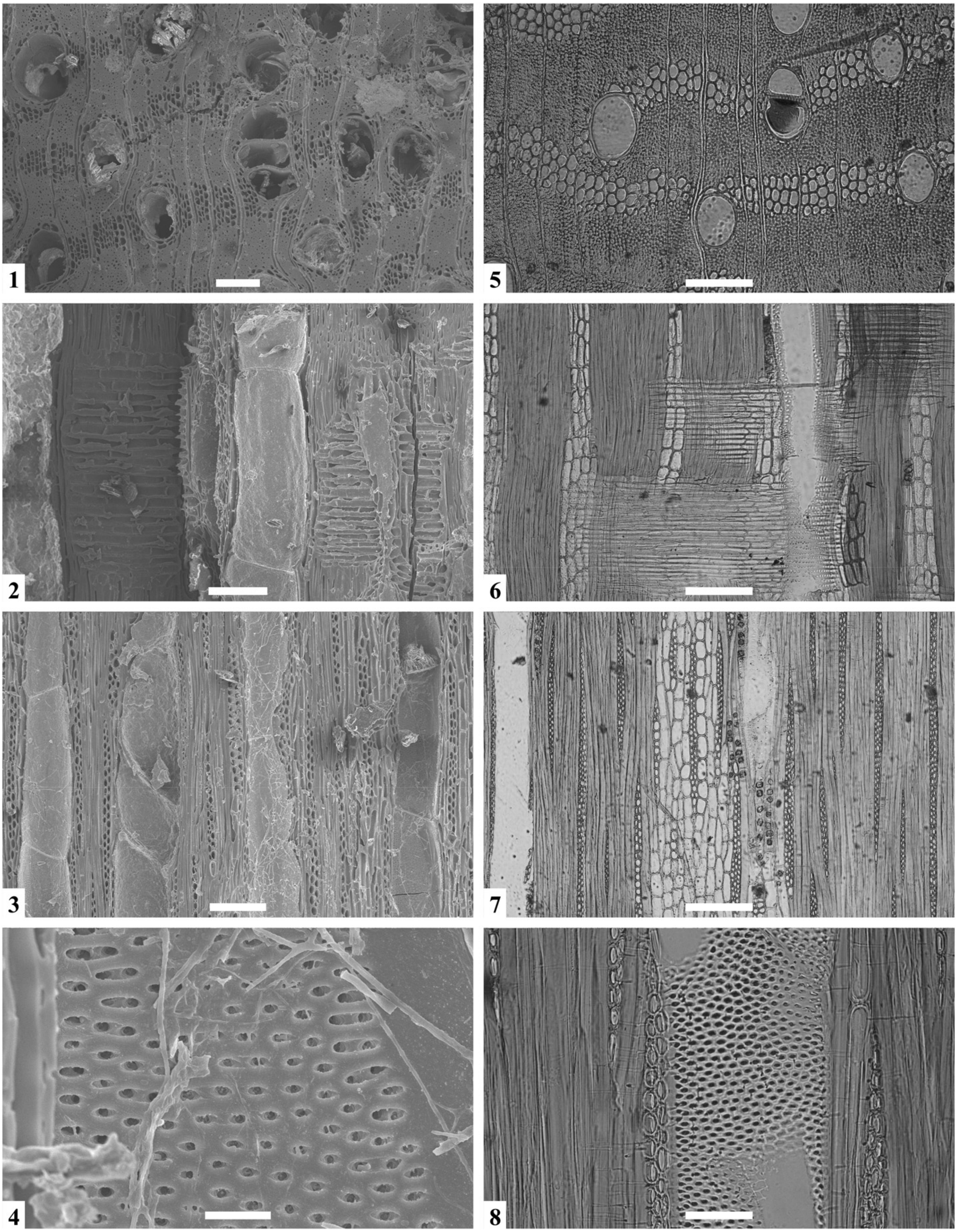


Plate I

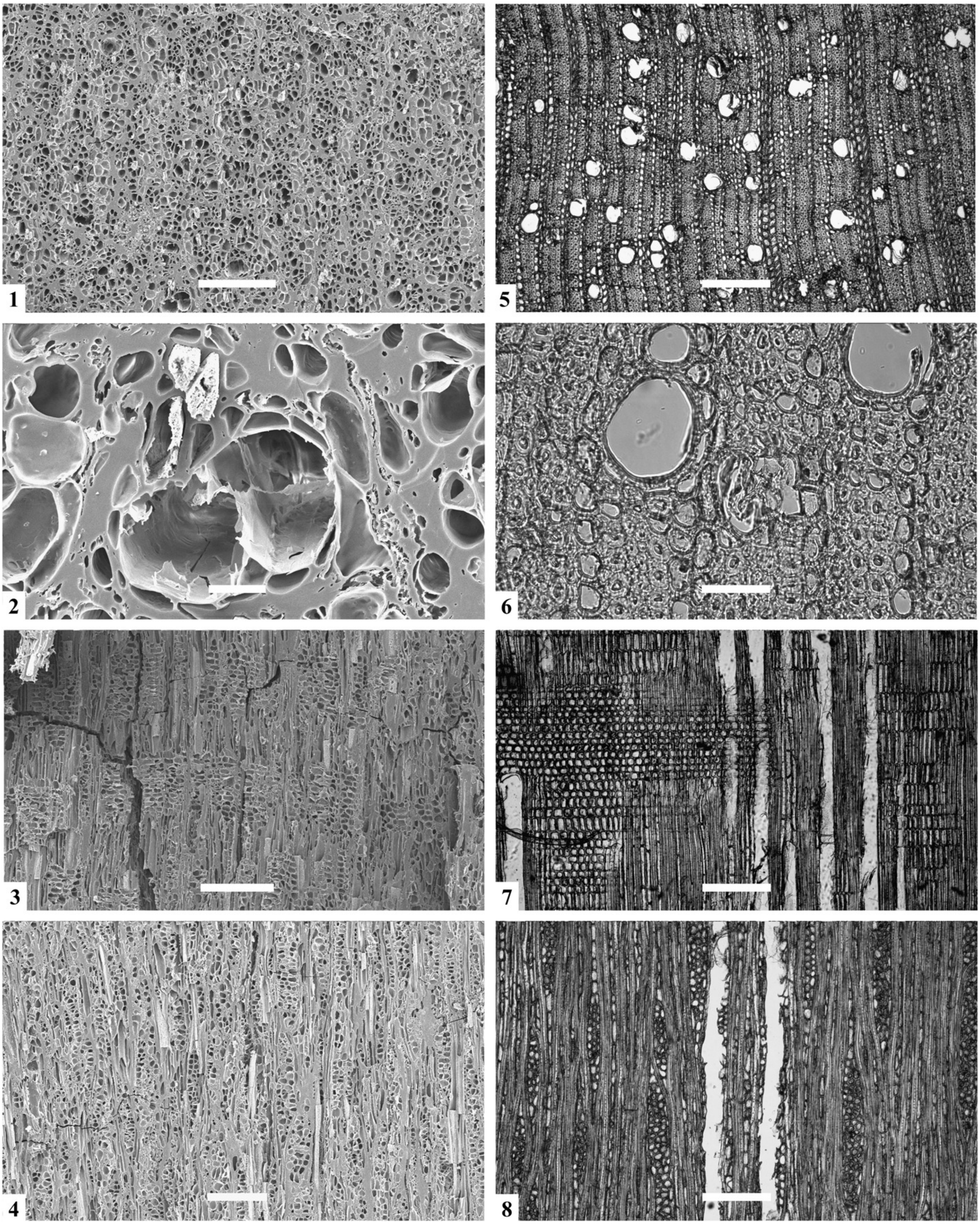


Plate II *(caption on page 10).*

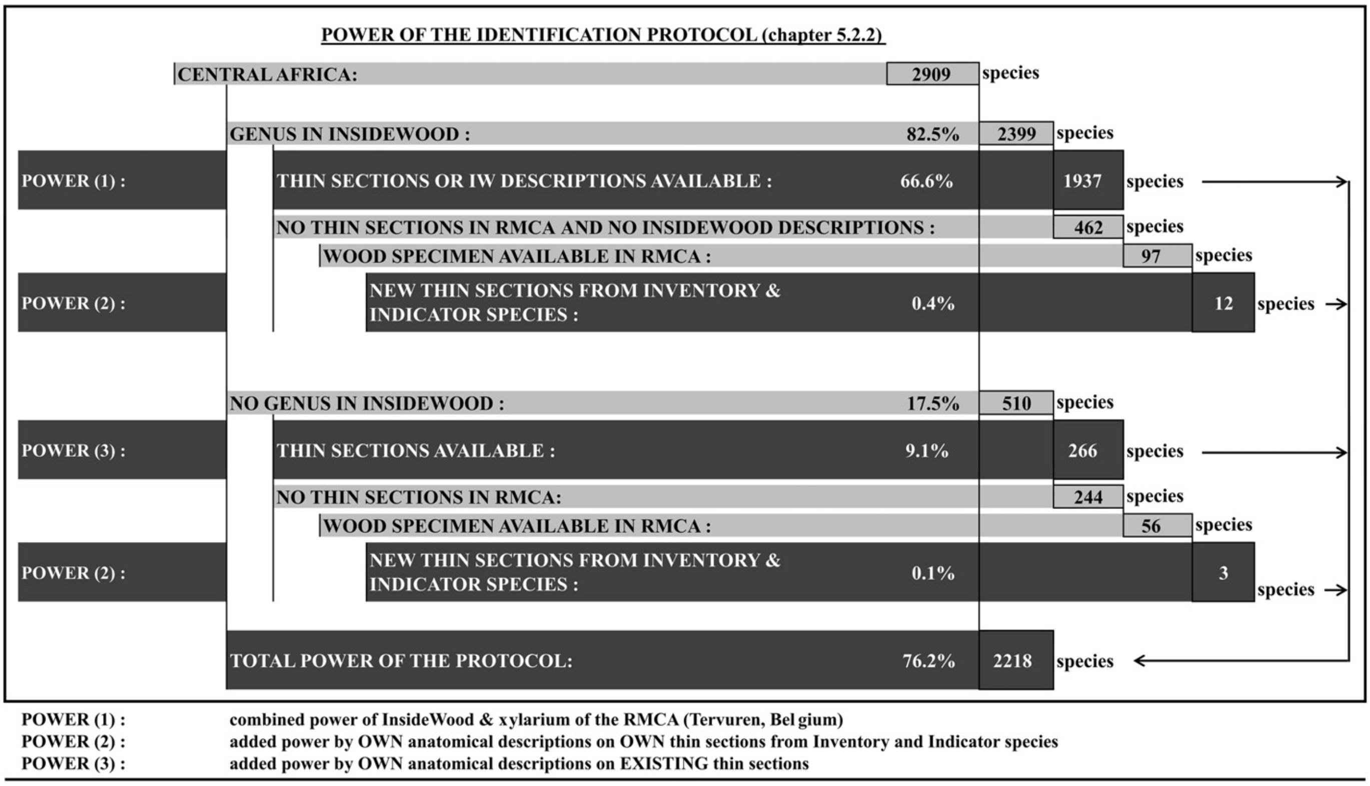


Fig. 6. Power of the identification protocol.

per country in Europe, indicating the convenience of European anthracology relative to Central African anthracology.

5.2.3. Flexibility

Another important advantage is the flexibility of the WSD. First of all, the quantities presented in this article are growing constantly, as wood descriptions are regularly added to the InsideWood database (Wheeler, 2011) and thin sections are regularly prepared and added to the RMCA reference collection. Secondly, an important advantage is the applicability of the protocol within a large geographical context. If a small amount of information is added to the excel spreadsheet in the form of inventory or indicator species lists, the protocol can be optimised for specific research areas all over Central Africa. As an illustration of the importance of inventory and indicator lists, the best ranked species for charcoal type HUA HUA GAB is a Luki inventory species which has been described by the authors for the first time. Moreover, a lot of the retained species (Table 3) occur in the indicator list of Lebrun and Gilbert (1954) and nearly all retained species for charcoal type CAE GIL MAY occur in the indicator list of Leal (2004).

5.2.4. Uncertainty

The WSD is not complete in terms of species. Moreover, there are significant gaps in the metadata of the species names. These gaps are sources of uncertainty in the identification protocol. As presented in Fig. 3, for 2161 (= 12.2%) accepted and uncertain species names recorded in the WSD no provenance continent has been registered. Therefore, these species are excluded. Furthermore, name status is still registered as ‘uncertain’ for 182 (= 6.2%) of the Central African species names. Next, a third source of uncertainty is the lack of thin sections or anatomical descriptions (Fig. 6).

Next to these quantifiable sources of uncertainty, a more complex problem is linked to the ‘readability’ of charcoal anatomy. After the last identification phase (comparative microscopy), a group of species is selected for which anatomy matches the charcoal fragment. Sometimes, it is very difficult to distinguish the best matching species, as illustrated for charcoal types ULM HOL GRA, APO TAB IBO and DIC DIC MAD in Table 3 and Plate II. Furthermore, one mature hardwood type was not identifiable at all (Table 2) and a secondary charcoal type originated from very young (juvenile) wood, which may exhibit different characteristics than mature wood. However, 10 wood-derived charcoal types have a very distinct and legible anatomy and clearly originated from mature wood, as illustrated for IRV IRV SMI on Plate I.

A third source of uncertainty is inherent in categorizing and coding naturally variable features. Categories are not always compatible with the wide range of varieties nature may produce. Moreover, individuals may code the same characters differently. These problems are partly solved by the manual comparative microscopy in the end where wrongly included taxa are eliminated. However, it is well possible that matching taxa do not enter the protocol because they are coded in a way that they do not appear during the search, even though they have a matching anatomy. A final source of uncertainty is due to imperfections in metadata of RMCA specimens and in descriptions on InsideWood (e.g. Wheeler, 2011).

5.2.5. Compatibility of anthracology and palynology

For most species presented in Table 3, the pollen type is only identifiable down to family level or is not defined at all by Elenga et al. (2000) and Lebamba et al. (2009). Only few species are identifiable down to genus level and very few down to species level. Also, charcoal types cannot always be attributed to one single species. However, charcoal identification down to genus level is mostly feasible as the best ranked species mostly belong to the same genus. Therefore, charcoal identification is often taxonomically more precise than pollen identification.

An advantage of palynology is the fact that pollen abundance is a good indication for the actual abundance of that taxon in the surrounding vegetation. However, a lot of the species presented in Table 3 belong to the families of Annonaceae and Caesalpiniodeae. Those are insect-pollinated plants which are mostly underrepresented or not represented at all in pollen spectra (Elenga et al., 2000). In contrast, all woody species are detectable by anthracology, although some light and porous woods might burn mainly to ashes. On the other hand, the pollen type *Syzygium* is prominently present in the pollen diagram of Elenga et al. (2000), although *Syzygium* spp. were not represented massively in accompanying floristic inventories. One of the reasons is the fact that *Syzygium* spp. produce a massive amount of pollen compared to other (e.g. entomophilous) species. The species composition of charcoal collections from several pits all over a research area may specify the relative abundance of taxa detected in pollen spectra. As such, anthracology and palynology are highly compatible.

6. Conclusion

The WSD enables a directed search taking into account metadata on (1) anatomical features, (2) availability of thin sections within the reference collection of the RMCA, (3) species distribution and (4) synonymy. Numbers reported by FAO (2005) indicate that the 2909 Central African woody species covered by this database are a substantial percentage of the total woody species richness of Central Africa. The Central African charcoal identification protocol presented here starts with an anatomical query within the WSD, proceeds with automatic extension and reduction phases of the resulting species list and ends with a comparative microscopic study of wood reference thin sections and charcoal anatomy.

2218 (= 76.2%) of the 2909 Central African species are considered by the identification protocol. This is substantial compared to existing identification protocols for South America and Europe. Additionally, the protocol has a large geographical applicability, as it can be optimised for every research area within Central Africa if inventory and indicator species lists are available. Moreover, as the reference collection and InsideWood databases are growing on a regular basis, the power of the protocol is still increasing. Finally, anthracology could confirm the presence of taxa which are underrepresented in pollen spectra and specify the abundance of overrepresented taxa. As such, a combination of both disciplines can produce stronger palaeobotanical reconstructions.

The protocol has been optimised for the Mayumbe (DRCongo) and applied on charcoal from a radiocarbon dated (2055–2205 ^{14}C yr BP) soil profile in the Luki reserve. 13 out of 16 charcoal types originated clearly from mature hardwood and could be identified. All best ranked species occur in rainforest and the best ranked species of one type, *Gilbertiodendron mayombense*, is an indicator species for old-growth rainforest. This is a consistent result and a first evidence for the validity of the protocol. Furthermore, the presence of nut shells of the pioneer species *Elaeis guineensis* in the same profile can be explained by the presence of humans that used those nuts. The presence of humans is confirmed by the finding of pottery sherds. Probably, humans entered the rainforest carrying pots and oil palm nuts from regenerating forest located nearby. This also seems to confirm the existence of a complex and shifting forest-savanna mosaic pattern in the southern Mayumbe, as proposed by several authors.

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