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

4 Author names and affiliations

- 5 Wannes Hubau^{1,2}, Jan Van den Bulcke¹, Peter Kitin², Florias Mees², Joris Van Acker¹, Hans
- 6 Beeckman²

7

11

- 8 ¹ Ghent University, Department of Forest and Water Management, Laboratory for Wood
- 9 Technology, Coupure Links 653, B- 9000 Gent, Belgium
- wannes.hubau@ugent.be,jan.vandenbulcke@ugent.be,joris.vanacker@ugent.be
- ² Royal Museum for Central Africa, Laboratory for Wood Biology, Leuvensesteenweg 13, B-3080
- 13 Tervuren, Belgium
- 14 florias.mees@africamuseum.be,peter.kitin@africamuseum.be,hans.beeckman@africamuseum.be

15 Corresponding author

- 16 Hubau Wannes
- 17 Ghent University
- 18 Department of Forest and Water Management
- 19 Laboratory for Wood Technology
- 20 Coupure Links 653
- 21 B-9000 Gent
- 22 Belgium

24 Tel: 0032 9 264 61 23

25 Gsm: 0032 485 44 59 84

26 Fax: 0032 9 264 90 92

27 E-mail: Wannes.Hubau@UGent.be

Abstract

47

48

49

50

51

52

53

54

55

56

57

58

59

60

61

62

63

64

65

66

67

68

69

70

71

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 ¹⁴C 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.

73 pedoanthracology; wood anatomy; charcoal analysis; Central Africa; vegetation history; 74 palaeoenvironment **Abbreviations** 75 76 SEM: Scanning Electron Microscopy 77 RLM: Reflected Light Microscopy 78 TLM: Transmitted Light Microscopy 79 RMCA: Royal Museum for Central Africa (Tervuren, Belgium) 80 UNESCO: United Nations Educational, Scientific and Cultural Organisation 81 IAWA: International Association of Wood Anatomists 82 FAO: Food and Agricultural Organisation of the United Nations 83 Tw(followed by a number): Tervuren wood specimen label 84 Tv: transversal direction (in wood) 85 Tg: tangential direction (in wood) 86 R: radial direction (in wood) 87 88 89 90 91 92

Keywords

1 Introduction

94	African vegetation history is not yet fully understood. Indirect evidence is mostly based on
95	phytogeographic and palaeolimnological research (Sosef, 1996; Verschuren et al., 2000; Leal, 2004
96	Russell et al., 2009; Tchouto et al., 2009). Direct evidence is mostly based on palynological
97	research (Maley, 1996, 2004; Ngomanda et al., 2009; Hessler et al., 2010) while charcoal analysis
98	has only sporadically been applied (Dechamps et al., 1988; Schwartz et al., 1990; Hart et al., 1996).
99	Yet, soil macrocharcoal analysis (pedoanthracology) is spatially more precise than palynology
100	because pollen are easily transported by wind over a long distance (Clark, 1988; Scott & Glasspool,
101	2007; Di Pasquale et al., 2008). Moreover, pollen types are rarely identifiable down to species level
102	which complicates interpretation of the results. Finally, species can be underrepresented
103	(entomophilous taxa) or overrepresented (anemophilous taxa) in pollen diagrams (Elenga et al.,
104	2000; Lebamba et al., 2009).
105	Charcoal is a chemically nearly inert material and extremely slowly affected by chemical
106	weathering, thus remaining in soil profiles for a long period (Cope & Chaloner, 1980; Skjemstad et
107	al., 1996; Forbes et al., 2006; Scott & Glasspool, 2007). Charcoal is especially valuable for
108	palaeobotany and archaeology due to preservation of the anatomical structure during the
109	charcoalification process. Thereby, it is feasible to identify charcoal using the same anatomical
110	features as wood (Figueiral & Mosbrugger, 2000; Scheel-Ybert, 2000; Di Pasquale et al., 2008).
111	Yet, absolute measurements have to be interpreted with caution as some features (e.g. vessel
112	diameter) can change significantly due to heat shrinkage (Prior & Gasson, 1993; Braadbaart &
113	Poole, 2008). Microscopic features for hardwood identification are thoroughly described and
114	numbered by a Committee of the International Association of Wood Anatomists (IAWA
115	Committee, 1989). Furthermore, the on-line search database 'InsideWood' archives photo-
116	micrographs and wood anatomical descriptions applying these internationally accepted numbered
117	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 (Figueiral & Mosbrugger, 2000; FAO, 2005; Mutke & Barthlott, 2005; Höhn & Neumann, 2011). 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; Schwartz et al., 1990; Hart et al., 1996). An identification protocol as used by Höhn & Neumann (2011) 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 (Lebrun & Gilbert, 1954; Leal, 2004). 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

118

119

120

121

122

123

124

125

126

127

128

129

130

131

132

133

134

135

136

137

138

139

140

141

143 geographical regions. On the other hand, due to e.g. forest regression phases, species disappear in 144 certain regions (Sosef, 1996; Senterre, 2005). However, these tendencies are not yet fully mapped. 145 Therefore, the protocol presented here does not take into account only those species currently 146 occurring in the Mayumbe, but all species native to Central Africa. 147 The Central African forest complex can be divided into the Lower Guinean and Congolian forest 148 regions, demarcated respectively as 'LG' and 'C' in Figure 1 (White, 1983; Leal, 2004; Senterre, 149 2005). The Lower Guinean is separated from the Congolian forest by the marshes of the Congo and 150 Ubangi rivers. The Congolian forest is separated from East Africa by the Albertine highland rift and 151 Great Lakes (r&l). The Central African forest complex is surrounded by a transition zone of 152 savanna types to the north (TN) and to the south (TS). The Lower Guinean forest is currently 153 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 & Hoelzmann (2005) assume that this 154 gap might have been overgrown by forest during the Holocene Maximum. As such, those West-155 156 African endemics are excluded and only species native to LG, C, TN and/or TS are taken into 157 account for final identification. 158 The Mayumbe forest ('M' in **Figure 1**) is part of the Lower Guinean forest complex. It is an 159 assumed sub-mountainous glacial forest refuge located on the hills alongside the Atlantic coast, 160 ranging from south Gabon down to the Luki reserve in the Bas-Congo, Democratic Republic of Congo (Sosef, 1996; Maley, 1996). The Luki reserve (indicated in **Figure 1**) has been selected as 161 162 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 163 164 UH48 forest stand (Donis, 1948; Donis & Maudoux, 1951; Couralet, 2010).

Figure 1 (TIFF file, one column wide = 8.9 cm)

165

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 & Thinon (1996). Next, prospection was conducted with an Edelmann auger, down to one meter. One pedoanthracological excavation (surface of 100 cm x 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 & 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 ¹⁴C 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. Scheel-Ybert, 2000; Boutain et al., 2010). 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 ($< 0.3 \text{ m}^3$) 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; Wheeler, 2011; InsideWood, 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 & Guo (1999) and Braadbaart & Poole (2008). Specifically, shrinkage has been taken into account while describing charcoal type anatomy (e.g. Prior & Gasson, 1993). According to Braadbaart & 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), silica (159-163).

3.2 Development of the Woody Species Database (WSD)

3.2.1 A composed 'umbrella' database

218	Two databases and four species lists have been combined into a comprehensive excel file called
219	'Woody Species Database', further 'WSD'. This WSD contains a list of species names followed by
220	a wide range of metadata concerning the presence of thin sections in the RMCA, anatomical
221	features, distribution area, ecology and synonymy. Within this umbrella database, a protocol has
222	been developed using the excel column filter function and additional formulas.
223	First of all, the reference collection database of the xylarium of the RMCA has been used. This is
224	one of the largest collections of wood specimens in the World and possibly the largest collection of
225	Central African wood specimens (Lynch & Gasson, 2010). Large effort was put into digitizing all
226	metadata of the species names and specimens, which resulted in (1) an on-line search database
227	(Tervuren Xylarium Wood Database, 2011) and (2) an excel spreadsheet of species names with
228	several columns of metadata. For every species name, this database provides metadata on the
229	provenance of its specimens and the presence of thin sections in the RMCA collection.
230	A second database which has been used to create the WSD is the InsideWood search database,
231	described by Wheeler (2011). On the 11 th of July 2011, all 5910 modern wood descriptions have
232	been downloaded from the InsideWood database in excel format. This database mentions, per
233	species, the presence or absence of microscopic hardwood features (1-163) described by the IAWA
234	Committee (1989, pp.1-320). Furthermore, features 164-188 provide information on geographical
235	species distribution (IAWA Committee, 1989, pp. 320-321).
236	Inventory species lists of the Mayumbe and, more specifically, the Luki reserve have been
237	incorporated as well (Donis, 1948; Donis & Maudoux, 1951; Maudoux, 1954; Monteiro, 1962;
238	Pendje, 1992; Couralet, 2010; Maloti Masongo, unpublished results). Inventories provide detailed
239	information on current species composition of the research area. Finally, indicator species lists are
240	incorporated. A first list contains indicator species for all Central African vegetation types described

216

by Lebrun & 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 & 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 **Figure 1**. Finally, several columns have been added describing ecology, temperament and morphology for the Central African species.

241

242

243

244

245

246

247

248

249

250

251

252

253

254

255

256

257

258

259

260

261

262

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 **Figure 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 Figure 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 online as the search platform Tervuren Xylarium Wood Database (2011) which provides direct links to micrographs of thin sections and to descriptions on the on-line InsideWood database. Those who are interested can contact the authors for access to the RMCA collection.

Figure 2 (TIFF file, 2 columns wide = 18.4 cm)

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 **Figure 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 **Figure 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 **Figure 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 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 (**Figure 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.

318

319

320

321

313

314

315

316

317

Table 1 (XLS file, 1 column wide = 8.9 cm)

4 Results

4.1 Woody Species Database: quantities

322 Quantities of the WSD are presented in Figure 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 (= 323 324 34.8%) accepted names. The 4922 uncertain names are treated as accepted names. As there is only 325 one accepted or uncertain name per species, quantities of accepted and uncertain names are 326 equivalent to quantities of species. For the accepted names, metadata of all synonyms has been 327 taken into account. The database contains 4162 African species, from which the identification protocol presented in this 328 article considers the 2909 Central African species. Inventory and indicator species lists cover 677 329 330 species. Specifically, 320 of these are indicator species mentioned by Lebrun & Gilbert (1954), 210 species are indicator Caesalpinioideae mentioned by Leal (2004) and 294 species were listed during 331 332 inventories in the Mayumbe. 333 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 334 335 African species, a wood anatomical description is available on InsideWood.

336

337

Figure 3 (TIFF file, 2 columns wide = 18.4 cm)

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 **Figure 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. **Figure 4** also presents the total number of charcoal fragments and absolute and specific anthracomass (cf. Carcaillet & Thinon, 1996). Only the four intervals between 10-50 cm contain more than 100 fragments. The two intervals between 30-50 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 ¹⁴C yr BP for the 30-40 cm interval, 2205 ± 35 ¹⁴C yr BP for the 80-90 cm interval and 2140 ± 35 ¹⁴C yr BP for the 120-130 cm interval. As these dates are very close, the charcoal

Figure 4 (TIFF file, 2 columns wide = 18.4 cm)

4.3 Charcoal types and identification results

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

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 **Figure 2** and **Table 2**), but is reduced drastically during subsequent extension 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 woodderived 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. **Figure** 1), species ecology, temperament and morphology for every species (Oliver, 1830-1916; INEAC, 1948-1963; Hutchinson & Dalziel, 1954-1972; Burkill, 1985; African Plants Database, 2011). 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 the relative abundance of the pollen type in the pollen record of Elenga et al. (2000).

Table 2 (XLS file, 2 columns wide = 18.4 cm)

363

364

365

366

367

368

369

370

371

372

373

374

375

376

377

378

379

380

381

382

383

384

385

386

Table 3 (XLS file, 2 columns wide = 18.4 cm). This table should probably be splitted into "Table 3" and "Table 3 (continued)", in order to fit on the pages. Please, repeat column headings if splitted.

4.4 Estimation of species-richness

388

389

390

391

392

393

394

395

396

397

398

399

400

401

402

403

404

405

406

407

408

409

410

411

412

Figure 5 is an example of a charcoal type saturation curve. It presents the evolution of the number of studied charcoal types (= \hat{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 impedes 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.

Figure 5 (TIFF file, 1 column wide = 8.9 cm)

4.5 Refining identification results: probability ranking

4.5.1 IRV IRV SMI

413

414

415

416

417

418

419

420

421

422

423

424

425

426

427

428

429

430

431

432

433

434

435

436

437

Charcoal type IRV IRV SMI has clear parenchyma bands of more than 3 cells wide, wood rays with mostly procumbent ray cells (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 Figure 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*. I. smithii is mentioned by Lebrun & Gilbert (1954) as an indicator species for riverine rainforest and gallery forest. It is a relatively high and light-demanding tree. On the contrary, *I. 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**).

Plate I (TIFF file, 2 columns wide = 18.4 cm)

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 $40 \pm 5 \mu m$ wide (Tg diameter on Tv section in PLATE II.1 and II.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

PLATE II (TIFF file, 2 columns wide = 18.4 cm)

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 (**Tables 3** and **4**). 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 (0-20m) or large (>20m) 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 ¹⁴C 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 *E. 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 & Giresse, 1998, Maley & Chepstow-Lusty, 2001). *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 & Brenac, 1998; Maley & Giresse, 1998; Maley & Chepstow-Lusty, 2001). 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. (2011) 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 ¹⁴C 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 ¹⁴C yr BP (Schwartz et al., 1990; Maley & Brenac, 1998; Vincens et al., 1998; Leal, 2004; Ngomanda et al., 2009). 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; Schwartz et al., 1990; Hart et al., 1996). 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 (Figure 1) covers 5 countries completely (DRC, Congo, Cameroon, Gabon, Equatorial Guinea) and 3 countries partly (Nigeria, Central African Republic, Angola). According to Figure 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 & 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 10000 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 (**Figure 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 (**Figure 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 (**Figure 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 (**Figure 6**). This is substantial compared to charcoal identification protocols for other research areas.

Figure 6 (TIFF file, 2 columns wide = 18.4 cm)

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 et al., 1998; Scheel-Ybert, 2000). 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 & Thinon, 1996; Figueiral & Mosbrugger, 2000; Théry-Parisot et al., 2010). FAO (2005) reports a maximum of only 280 native tree species 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 & 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 **Figure 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 (**Figure 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

607

608

609

610

611

612

613

614

615

616

617

618

619

620

621

622

623

624

625

626

627

628

629

630

631

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 ¹⁴C 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.

7 Acknowledgements

This paper is dedicated to Kembo, one of the WWF-eco-guards in the Luki reserve who has regretfully perished performing a dangerous but indispensable job. We are indebted to the Special Research Fund of Ghent University for financing the PhD project of Wannes Hubau. We thank the Commission for Scientific Research (Faculty of Bioscience Engineering, Ghent University) and the King Leopold III Fund for financially supporting the fieldwork. Furthermore, we thank the World Wide Fund for Nature (WWF), the École Régionale post-universitaire d'Aménagement et de gestion Intégrés des Forêts et Territoires tropicaux (ERAIFT, DRCongo) and the Institut National pour l'Étude et la Recherche Agronomique (INERA, DRCongo) for organisational and logistic support. Specifically, we thank Geert Lejeune, Bruno Pérodeau and Laurent Nsenga (WWF) for their services and discussions in the field and all WWF-eco-guards who guided us through the Luki reserve. We thank the Royal Museum for Central Africa (Tervuren, Belgium) for financing radiocarbon dating and for organising the SEM sessions. We are indebted to Prof. Dr. Dirk Verschuren (Ghent University) for proof-reading, to Wim Tavernier (RMCA) for organising and digitizing the reference collection and to Piet Dekeyser (Ghent University) for preparing the thin

- sections. The authors also wish to thank the Fund for Scientific Research-Flanders (FWO-Belgium)
- 657 for the postdoctoral funding granted to Jan Van den Bulcke.

658 **8 References**

- African Plants Database, 2011. African Plants Database Version 3.3.3, Conservatoire et Jardin
- botaniques de la Ville de Genève and South African National Biodiversity Institute, Pretoria.
- Published on the internet [accessed 10th January 2011 26th July 2011], from http://www.ville-nternet
- ge.ch/musinfo/bd/cjb/africa/>.
- Ball, D.F., 1964. Loss-On-Ignition as an estimate of organic matter and organic carbon in non-
- calcareous soils. European Journal of Soil Science, 15, 84-92.
- Boutain, J.R., Brown, A.R., Webb, D.T., Toyofuku, B.H., 2010. Simplified procedure for hand
- fracturing, identifying, and curating small macrocharcoal remains. IAWA Bull. n.s., 31, 139-147.
- Braadbaart, F., Poole, I., 2008. Morphological, chemical and physical changes during
- charcoalification of wood and its relevance to archaeological contexts. Journal of Archaeological
- 669 Science, 35, 2434-2445.
- Bunge, J., 2011. Estimating the number of species with CatchAll. In: Proceedings of the Pacific
- 671 Symposium on Biocomputing. World Scientific Publishing Company, Hawaii, pp. 121-130.
- Burkill, H.M., 1985. The Useful Plants of West Tropical Africa. Royal Botanic Gardens, Kew. 1st
- edition, 6 Volumes.
- Bustin, R.M., Guo, Y., 1999. Abrupt changes (jumps) in reflectance values and chemical
- compsitions of artificial charcoals and inertinite in coals. International Journal of Coal geology, 38,
- 676 237-260.
- 677 Carcaillet, C., Thinon, M., 1996. Pedoanthracological contribution to the study of the evolution of
- the upper treeline in the Maurienne Valley (North French Alps): methodology and preliminary data.
- Review of Palaeobotany and Palynology, 91, 399-416.

- 680 Clark, J.S., 1988. Particle motion and the theory of charcoal analysis: source area, transport,
- deposition and sampling. Quaternary Research, 30, 67–80.
- 682 Cope, M.J., Chaloner, W.G., 1980. Fossil charcoal as evidence of past atmospheric composition.
- 683 Nature, 283, 647–649.
- 684 Couralet, C., 2010. Community dynamics, phenology and growth of tropical trees in the rain forest
- reserve of Luki, Democratic Republic of Congo. PhD Thesis. Faculty of Bioscience Engineering,
- 686 Ghent University, 173 pp.
- Dechamps, R., Lanfranchi, R., Le Cocq, A., Schwartz, D., 1988. Reconstruction d'environnements
- quaternaires par l'étude de macrorestes vegetaux (Pays Bateke, R.P. du Congo). Palaeogeography,
- Palaeoclimatology, Palaeoecology, 66, 33-44.
- 690 Di Pasquale, G., Marziano, M., Impagliazzo, S., Lubritto, C., De Natale, A., Bader, M.Y., 2008. The
- Holocene tree line in the northern Andes (Ecuador): First evidence from soil charcoal.
- 692 Palaeogeography, Palaeoclimatology, Palaeoecology, 259, 17-34.
- 693 Donis, C., 1948. Essai d'économie forestière au Mayumbe. Publications de l'Institut National pour
- 694 l'Etude Agronomique du Congo Belge (INEAC), Bruxelles, Belgique. Série scientifique, 37, 92 pp.
- 695 Donis, C., Maudoux, E., 1951. Sur l'uniformisation par le haut Une méthode de conversion des
- 696 forêts sauvages. Publications de l'Institut National pour l'Etude Agronomique du Congo Belge
- 697 (INEAC), Bruxelles, Belgique. Série scientifique, 51, 77 pp.
- 698 Elenga, H., de Namur, C., Vincens, A., Roux, M., Schwartz, D., 2000. Use of plots to define pollen-
- 699 vegetation relationships in densely forested ecosystems of Tropical Africa. Review of Palaeobotany
- 700 and Palynology, 112, 79-96.
- 701 FAO, 2005. Global Forest Resources Assessment 2005: main report. FAO Forest Paper 147, FAO,
- 702 Rome, 350 pp.
- Figueiral, I., Mosbrugger, V., 2000. A review of charcoal analysis as a tool for assessing Quaternary
- and Tertiary environments: achievements and limits. Palaeogeography, Palaeoclimatology,
- 705 Palaeoecology, 164, 397-407.

- Forbes, M.S., Raison, R.J., Skjemstad, J.O., 2006. Formation, transformation and transport of black
- carbon (charcoal) in terrestrial and aquatic ecosystems. Science of the Total Environment, 370, 190-
- 708 206.
- 709 Hart, T.B., Hart, J.A., Dechamps, R., Fournier, M., Ataholo, M., 1996. Changes in forest
- 710 composition over the last 4000 years in the Ituri basin, Zaire. In: van der Maesen, L.J.G., van der
- Burgt, X.M., van Medenbach de Rooy, J.M. (Eds.), The Biodiversity of African plants. Kluwer
- Academic Publishers, The Netherlands, pp. 545-563.
- 713 Hessler, I., Dupont, L., Bonnefille, R., Behling, H., González, C., Helmens, K.F., Hooghiemstra, H.,
- Lebamba, J., Ledru, M.,-P., Lézine, A.,-M., Maley, J., Marret, F., Vincens, A., 2010. Millennial-
- scale changes in vegetation records from tropical Africa and South America during the last glacial.
- 716 Quaternary Science Reviews, 29, 2882-2899.
- Höhn, A., Neumann, K., 2011. Shifting cultivation and the development of a cultural landscape
- during the Iron Age (0-1500 AD) in the northern Sahel of Burkina Faso, West Africa: Insights from
- 719 archaeological charcoal. Quaternary International, In Press.
- Hutchinson, J., Dalziel, J.M., 1954-1972. Flora of West Tropical Africa. Crown agents for oversea
- 721 governments and administrations, London. 2nd edition, 3 Volumes.
- 722 IAWA Committee, 1989. IAWA list of microscopic features for hardwood identification. IAWA
- 723 Bull. n.s., 10, 219–332.
- 724 INEAC, 1948-1963. Flore du Congo Belge et du Ruanda-Urundi. Spermatophytes. Publications de
- 1'Institut National pour l'Etude Agronomique du Congo Belge (INEAC), Bruxelles, Belgique. 1st
- 726 edition, 10 Volumes.
- 727 InsideWood, 2011. The InsideWood Working Group (IWG), 2004-onwards. Published on the
- 728 Internet [accessed 11th July 2011, 14:30 GMT], from http://insidewood.lib.ncsu.edu/search
- 729 Leal, M.E., 2004. The African rain forest during the Last Glacial Maximum, an archipelago of
- forests in a sea of grass. PhD Thesis. Wageningen University, Wageningen, 96 pp.

- T31 Lebamba, J., Ngomanda, A., Vincens, A., Jolly, D., Favier, C., Elenga, H., Bentaleb, I., 2009.
- 732 Central African biomes and forest succession stages derived from modern pollen data and
- functional plant types. Climate of the Past, 5, 403-429.
- 734 Lebrun, J. & Gilbert, G., 1954. Une classification écologique des forêts du Congo. Publications de
- 1'Institut National pour l'Etude Agronomique du Congo Belge (INEAC), Bruxelles, Belgique. Série
- scientifique 63, 89 pp.
- 737 Lynch, A.H., Gasson, P.E., 2010. Index Xylariorum Edition 4. Royal Botanic Gardens, Kew.
- Published on the internet [accessed 26th July 2011, 14:30 GMT], from
- 739 http://www.kew.org/collections/wood-index/Index_Xylariorum4.htm
- 740 Maley, J., 1996. Le cadre paléoenvironnemental des refuges forestiers africains: quelques données et
- hypothèses. In: van der Maesen, L.J.G., van der Burgt, X.M., van Medenbach de Rooy, J.M. (Eds.),
- The Biodiversity of African plants. Kluwer Academic Publishers, The Netherlands, pp. 519-535.
- Maley, J., 2004. Les variations de la végétation et des paléoenvironnements du domaine forestier
- africain au cours du Quaternaire récent. In: Renault-Miskovsky, J., Semah, A.M. (Eds.), Guide de la
- préhistoire mondiale. Artcom/Errance, Paris, pp. 143-178.
- Maley, J., Brenac, P., 1998. Vegetation dynamics, palaeoenvironments and climatic changes in the
- forests of western Cameroon during the last 28,000 years B.P. Review of Palaeobotany and
- 748 Palynology, 99, 157-187.
- 749 Maley, J., Chepstow-Lusty, A., 2001. *Elaeis guineensis* Jacq. (oil palm) fluctuations in central Africa
- during the late Holocene: climate or human driving forces for this pioneering species? Vegetation
- History and Archaeobotany, 10, 117-120.
- 752 Maley, J., Giresse, P., 1998. Etude d'un niveau argileux organique du Mayombe (Congo occidental)
- riche en pollens d'Elaeis guineensis et daté d'environ 2800 ans BP. Implications pour les
- 754 paléoenvironnements de l'Afrique Centrale. In: Vicat, J.P., Bilong, P. (Eds). Géosciences au
- 755 Cameroun. Publication occas GEOCAM n°1, Presses Universitaires, Yaoundé, pp. 77-84.

- 756 Maudoux, E., 1954. La Régénération naturelle dans les Forêts remaniées du Mayumbe. Extrait du
- 757 Bulletin agricole du Congo Belge, 45, 403-422.
- 758 Mayaux, P., De Grandi, G., Malingreau, J.-P., 2000. Central African Forest Cover Revisited : A
- 759 Multisatellite Analysis. Remote Sensing of Environment, 71, 183-196.
- 760 Mitchener, W.K., Brunt, J.W., Helly, J.J., Kirchner, T.B., Stafford, S.G., 1997. Nongeospatial
- metadata for the ecological sciences. Journal of Applied Ecology, 7, 330-342.
- 762 Monteiro, R.F.R., 1962. Le massif forestier du Mayumbe angolais. Bois et Forêts des Tropiques, 82,
- 763 3-17.
- Murphy, C.P., 1986. Thin Section Preparation of Soils and Sediments. AB Academic Publishers,
- 765 Berkhamsted, U.K., 149 pp.
- 766 Mutke, J., Barthlott, W., 2005. Patterns of vascular plant diversity at continental to global scales.
- 767 Biologiske Skrifter, 55, 521-531.
- Neumann, K., Bostoen, K., Höhn, A., Kahlheber, S., Ngomanda, A., Tchiengué, B., 2011. First
- 769 farmers in the Central African rainforest: A view from southern Cameroon. Quaternary
- 770 International, In Press.
- 771 Ngomanda, A., Chepstow-Lusty, A., Makaya, M., Favier, C., Schevin, P., Maley, J., Fontugne, M.,
- Oslisly, R., Jolly, D., 2009. Western equatorial African forest-savanna mosaics: a legacy of late
- Holocene climatic change? Climate of the Past, 5, 647–659.
- Oliver, D., 1830-1916. Flora of Tropical Africa. L. Reeve and Co., London. 1st edition, 8 Volumes.
- Pendje, G., 1993. Croissance et productivité de deux essences forestières plantées au Mayombe,
- 776 Zaïre: le limba (*Terminalia superba* Eng. et Diels) et le bilinga (*Nauclea diderrichii* (De Wild)
- Merrill). International journal of tropical geology, geography and ecology, 17, 101-120.
- Prior, J. & Gasson, P., 1993. Anatomical changes on charring six African hardwoods. IAWA Bull.
- 779 n.s., 14, 77-86.

- Russell, J.M., McCoy, S.J., Verschuren, D., Bessems, I., Huang, Y., 2009. Human impacts, climate
- change, and aquatic ecosystem response during the past 2000 yr at Lake Wandakara, Uganda.
- 782 Quaternary Research, 72, 315-324.
- 783 Salzmann, U., Hoelzmann, P., 2005. The Holocene History of the Dahomey Gap: A climatic induced
- fragmentation of the West African Rainforest. The Holocene, 15, 190-199.
- 785 Scheel-Ybert, R., 2000. Vegetation stability in the Southeastern Brazilian coastal area from 5500 to
- 786 1400 14C yr BP deduced from charcoal analysis. Review of Paleobotany and Palynology, 110, 111-
- 787 138.
- 788 Scheel-Ybert, R., Scheel, M., Ybert, J.-P., 1998. Atlas Brasil Databank for Charcoal Analysis and
- 789 Computerized Key to Charcoal Determination. Version 1.8. CD-ROM, in Portuguese, English and
- 790 French, 1500 entries.
- 791 Schwartz, D., de Foresta, H., Dechamps, R., Lanfranchi, R., 1990. Découverte d'un premier site de
- 792 l'âge du fer ancien (2110 B.P.) dans le Mayombe congolais. Implications paléobotaniques et
- 793 pédologiques. Comptes Rendus de l'Académie des Sciences, Paris, série II, 310, 1293-1298.
- 794 Scott, A.C., Glasspool, I.J., 2007. Observations and experiments on the origin and formation of
- inertinite group macerals. International Journal of Coal Geology, 70, 53-66.
- 796 Senterre, B., 2005. Recherches méthodologiques pour la typologie de la végétation et la
- 797 phytogéographie des forêts denses d'Afrique tropicale. Thèse de doctorat, Université Libre de
- 798 Bruxelles, 345 pp.
- 799 Skjemstad, J.O., Clarke, P.J., Taylor, A., Oades, J.M., McClure, S.G., 1996. The chemistry and
- nature of protected carbon in soil. Australian Journal of Soil Research, 34, 251-271.
- 801 Sosef, M.S.M., 1996. Begonias and African rain forest refuges: general aspects and recent progress.
- In: van der Maesen, L.J.G., van der Burgt, X.M., van Medenbach de Rooy, J.M. (Eds.), The
- Biodiversity of African plants. Kluwer Academic Publishers, The Netherlands, pp. 602-611.
- 804 Stoops, G., 2003. Guidelines for Analysis and Description of Soil and Regolith Thin Sections. Soil
- Science Society of America, Madison, WI, 184 pp.

- 806 Stoops, G., Marcelino, V., Mees, F., 2010. Interpretation of Micromorphological Features of Soils
- and Regoliths. Elsevier, 752 pp.
- 808 Tchouto, M.G.P., de Wilde, J.J.F.E., de Boer, W.F., van der Maesen, L.J.G., Cleef, A.M., 2009. Bio-
- indicator species and Central African rain forest refuges in the Campo-Ma'an area, Cameroon.
- 810 Systematics and Biodiversity, 7, 21-31.
- 811 Tervuren Xylarium Wood Database, 2011. Tervuren Wood Collection database of the Royal
- Museum for Central Africa. RMCA, Tervuren, Belgium. Published on the internet [accessed 10th
- 813 January 2011 26th July 2011], from
- $\verb| 814 | < http://www.africamuseum.be/collections/browsecollections/naturalsciences/earth/xylarium>. \\$
- 815 Théry-Parisot, I., Chabal, L., Chrzavzez, J., 2010. Anthracology and taphonomy, from wood
- gathering to charcoal analysis. A review of the taphonomic processes modifying charcoal
- assemblages, in archaeological contexts. Palaeogeography, Palaeoclimatology, Palaeoecology, 291,
- 818 142-153.
- 819 Verschuren, D., Laird, K.R., Cumming, B.F., 2000. Rainfall and drought in equatorial east Africa
- 820 during the past 1,100 years. Nature, 403, 410-414.
- Vincens, A., Schwartz, D., Bertaux, J., Elenga, H., de Namur, C., 1998. Late Holocene Climatic
- 822 Changes in Western Equatorial Africa Inferred from Pollen from Lake Sinnda, Southern Congo.
- 823 Quaternary Research, 50, 34-45.
- Wheeler, E.A., 2011. InsideWood a web resource for hardwood anatomy. IAWA Bull. n.s., 32,
- 825 199-211.
- White, F., 1983. The vegetation of Africa, a descriptive memoir to accompany the
- 827 UNESCO/AETFAT/UNSO vegetation map of Africa. UNESCO, Natural Resources Research, 20,
- 828 1-356.

Captions 829 830 Figure 1: map of the Central and West African forest complexes; localisation of the Mayumbe 831 forest and the Luki reserve. 832 833 Figure 2: flow-chart of the identification protocol; A: constitution of the anatomical search 834 database; **B:** anatomical query and extension phases; **C:** reduction phases. 835 836 Figure 3: quantities of the Woody Species Database. 837 838 Figure 4: profile in UH48 (Luki reserve); visual representation of pit structure, profile description 839 and anthracomass per soil layer. 840 Figure 5: charcoal type saturation curve; comparison between the amount of observed charcoal 841 types (c) and estimated total amount of charcoal types (\hat{C}) in the interval, in function of the number 842 of observed charcoal fragments (X) for the interval between 30 and 40 cm depth: c=f(X) and 843 844 $\hat{C}=f(X)$. For every X<22, the total amount of analysed fragments was too small for reliable species-845 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 846 847 proposed by the CatchAll software was used. 848 **Figure 6:** power of the identification protocol. 849 850 851 **Table 1:** descriptions of anatomical hardwood features used during comparative microscopy and 852 not described by the IAWA committee (1989).

Table 2: number of studied fragments per profile interval per charcoal type; number of species
 (names) per identification phase per charcoal type.

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.

860

861

862

863

864

865

866

857

858

Plate I. LEFT: Scanning Electron Micrographs (SEM) of charcoal type IRV IRV SMI; 1:

Transversal direction (scale bar = $100\mu m$); 2: Radial direction (scale bar = $100\mu m$); 3: Tangential

direction (scale bar = $100\mu m$); **4:** Tangential detail of intervessel pits (scale bar = $10\mu m$); RIGHT:

Transmitted Light Micrographs (TLM) of *Irvingia smithii* Hook. f. (Tw 13339); **5:** Transversal

direction (scale bar = 200µm); 6: Radial direction (scale bar = 200µm); 7: Tangential direction

(scale bar = $200\mu m$); **8:** Tangential detail of intervessel pits (scale bar = $50\mu m$).

867

868

869

870

871

872

873

Plate II. LEFT: Scanning Electron Micrographs (SEM) of charcoal type DIC DIC MAD; 1:

Transversal direction (scale bar = 200µm); 2: Transversal detail of vessel and parenchyma (scale

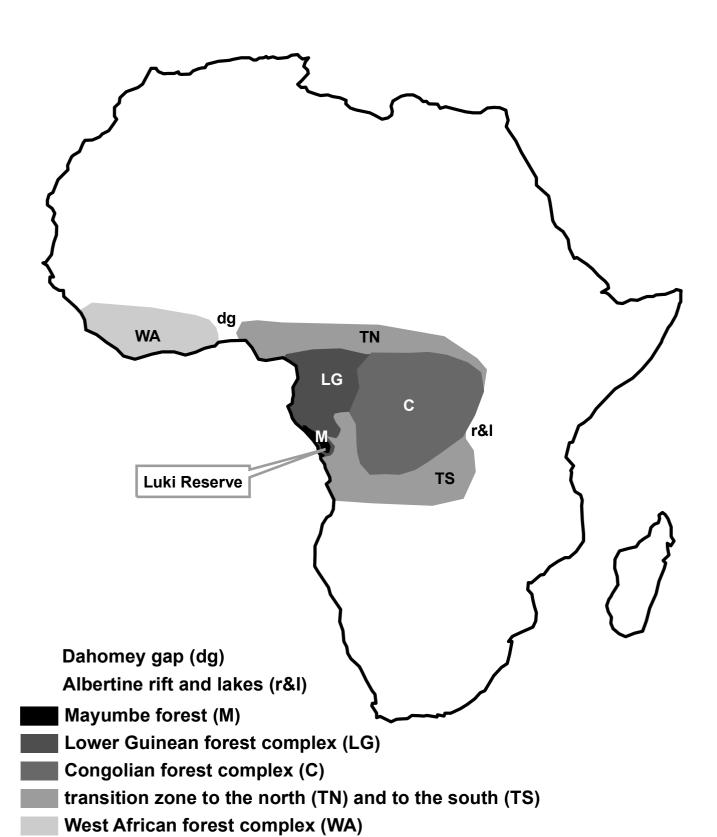
bar = $20\mu m$); **3:** Radial direction (scale bar = $200\mu m$); **4:** Tangential direction (scale bar = $200\mu m$);

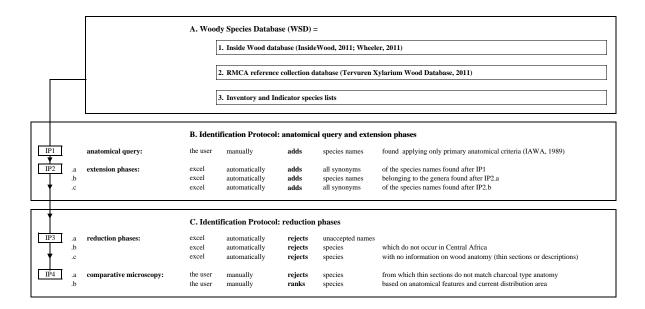
RIGHT: Transmitted Light Micrographs (TLM) of Dichapetalum madagascariense Poir. (Tw

32792); **5:** Transversal direction (scale bar = 250µm); **6:** Transversal detail of vessel and

parenchyma (scale bar = 50µm) 7: Radial direction (scale bar = 250µm); 8: Tangential direction

874 (scale bar = $250\mu m$).

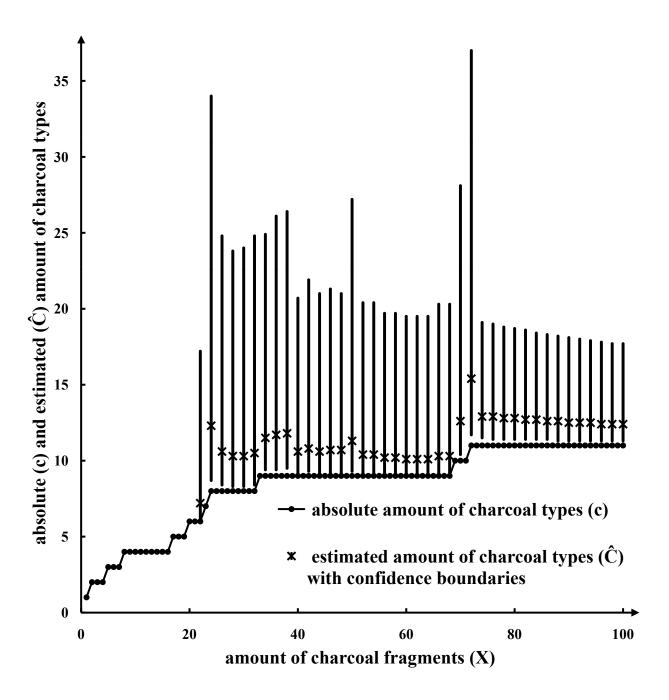


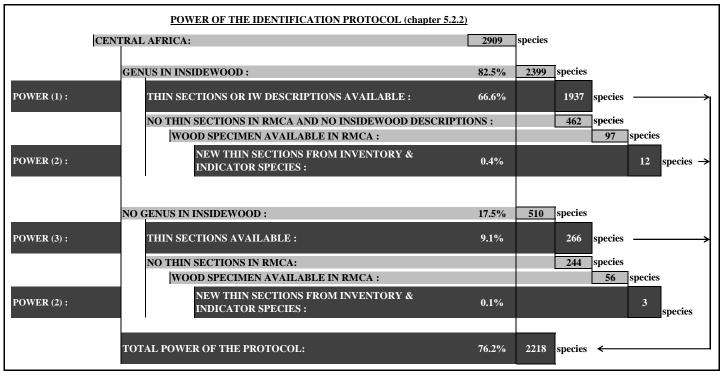


QUANTITIES OF THE WS	SD (chapter 4.1)
GENERA:	5521 genera Q1
SPECIES NAMES:	36844 P _a Q2
UNACCEPTED SPECIES NAMES:	51.8% 19090 P _b P _c Q3
← ACCEPTED SPECIES NAMES:	34.8% 12832 $P_a = (Q2/Q1) \times 100$
← UNCERTAIN SPECIES NAMES:	13.4% 4922 $P_b = (Q3/Q1) \times 100$
	$P_c = (Q3/Q2) \times 100$
→ ACCEPTED AND UNCERTAIN SPECIES NAMES :	48.2% 17754 species Q = Quantities
CONTINENT UNKNOWN:	12.2% 2161 species P = Percentages
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 DESCRIP	PTIONS AVAILABLE: 75.7% 2203 species
THIN SECTIONS AVAILABLE IN RMCA	A: 71.7% 2086 species
INSIDEWOOD DESCRIPTIONS AVAILA	ABLE: 22.3% 649 species

) Drawing	Depth [cm]	Horizon	Roots [%V]	Stones [%V]	Colour	OM [%m]	Moisture [%m]) Texture) Bioturbation	Depth [cm]	Soil volume [m³]	Soil mass [kg]	# charcoal fragments	Anthracomass [mg]		Specific anthracomass [ppm] = [mg ⁻¹ kg ⁻¹]	14 C yr B P
(a)	_		(b)	(b)	(c)	(d)	(e)	(1)	(g)	0.40	0.15	191	_	(h)		(i)	
120	0-20	Α	40%	0%	7.5YR 4/4	4.7%	46%	sp-(dp)	pl, (ch)	0-10 10-20	0.15	191	>200	578	3.0		-
	_													1394 3606	7.3		
	20-40	Α	20%	0%	7.5YR 5/4	4.8%	45%	ср	si, (pl),	20-30 30-40	0.15	191 191	>100		18.9 121.3		2055 ± 30 Poz-33055
								sp-(dp) sp sp sp sp sp sp	(ch)	40-50	0.15 0.15	207	>700	23150 38180	184.3		2055 ± 30 F02-33055
١ ٦	40-60	AB	10%	0%	7.5YR 5/6	5.3%	45%	sp	ch, (pl)	50-60	0.15	207	39	1974	9.5		
(- July -										60-70	0.15	207	23	792	3.8		
7						5.1%	46%	sp	(si), (pf)	70-80	0.15	207	15	657	3.2		
										80-90	0.15	207	11	936	4.5		2205 ± 35 Poz-39110
	60-140	В			7 FVD F40	5.0%	46%	sp	si, ch	90-100	0.15	207	6	276	1.3		-
111	60-140	В	5%	0%	7.5YR 5/8	4.8%	470/		al ab	100-110	0.15	207	8	186	0.9		-
`/						4.0%	41 70	sp	si, ch	110-120	0.15	207	6	103	0.5		-
1. /						4.9%	48%	en	gr, si, (ch)	120-130	0.15	207	11	561	2.7		2140 ± 35 Poz-39109
V						4.5 /0	40 /0	эþ	gr, sr, (cm)	130-140	0.15	207	2	55	0.3		-
Legend: organic										140-160	0.0025	3.5	0	0	0.0		-
pot sherds: roots:	لاً ر									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





POWER (1): combined power of InsideWood & xylarium of the RMCA (Tervuren, Belgium)

POWER (2): added power by OWN anatomical descriptions on OWN thin sections from Inventory and Indicator species

POWER (3): added power by OWN anatomical descriptions on EXISTING thin sections

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 whithout 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	-

									Prim	ary ch	arcoal	types							Secon	ndary	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	s belonging to secondary types	# studied fragments	total # available fragments	primary charcoal types	secondary charcoal types	S
Profile interval depth [cm]	14C	yr BP						# stu	ıdied fı	ragmer	ıts in p	rofile i	nterva	ls per c	harcoa	ıl type						# fragment	# fragments	total # stuc	total # avai	# primary	# secondar	total # types
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 50-60		-	0	8	22 4	0	0	7	5	7 4	0	0	0 8	0	0	0	0	0	0	0	0	50 39	0	50 39	>700 39	6 11	0	6 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									pecies (names) throu	ghout	the Ide	entifica	tion ph	ases												
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 (after comparative i	microsc	onv)	10		11	9	7	9	8	5	8	12	11	9	8	6					_	species						
IP4.b (ranking)		·PJ)	4		2	1	1	2	1	2	2	2	3	1	1	5			-			best ma	tching	nacies				
11 4.0 (ranking)			4	-	-	1	1	-	1	-	-	-	3	1	1	J	-	-	-	-	-	oest ma	cinng:	species				

			ranking	distribution	ecology	temperament	morphology	databases & lists	pollen
CHARCOAL TYPE	Family	Species	distribution ranking (75) anatomy ranking (75) Ranking (740)	May umbe (M) Lower Guinea (LG) Congodia (C) Transition South (TS) Transition North (TN)	moist evergreen forest moist semi-deciduous forest dry deciduous forest wordhard savama tree savama shrub savama	pioneer specks light den anding light/shade tokrant shade bearing	high tree (>20m) small tree (5.20m) shaub (0.5m) Lamescent	RMCA wood sample RMCA thin sections Inside Wood Database Invenory lists Luki Indicator fold forest Indicator forest type	relative abundance taxonomic level
			VERY	SUCCESFUL IDENTIFICA	***	(b)	(b)	(c) (d) (e) (f) (g) (h)	(i) (j)
ANN XYL AUR	Аппопассае Аппопассае Аппопассае Аппопассае Аппопассае Аппопассае Аппопассае Аппопассае Аппопассае	Aylopus parviflora (A. Rich.) Benth. Aylopus uritine Cupp. Aylopus announcidora De Wild, R. T. Durand Aylopus announcidora De Wild, R. T. Durand Aylopus announcidora (P. Wild). Bontique ex R. E. Fr. Poportunicas parasveleri (Euchl) Bontique Friendelia domain (Benth) Verte. Friendelia domain (Benth) Verte. Monumbonatis schwediprishi (Engl. & Diels) Verde. Astopia montronat Eurll	5 4 9 5 4 9 4 4 8 4 4 8 5 3 8 5 2 7 5 1 6 2 4 6 5 1 6	P P P P P P P P P P P P P P P P P P P	a a p p p p p p p p p p p p a a a a a a	a a ? ? p a a ? p a a ? p a a ? p a a ? p a a ? p a a ? p a a ? p 2 ? ? ? ? a a ? p	a p p a a p a a p a a a a a p a a a a p a a a a a p a	p a p p a a p p a a a p p a a a a a a a	- f - f - f - f - f - f - f - f - f - f
CAE TET BIF CAE GIL MAY	Arrescene (Cascalprinistere Cascalprinistere Mimonidere Huscose	East is guinemic Jacq. Gilbertisched 1909. milestudie (Ok. Wild.) J. Léonard Gilbertisched 1909. missenscheus (Pellege.) J. Leonard Gilbertisched 1909. missenscheus (Pellege.) J. Leonard Gilbertisched 1909. missenscheus (Pellege.) J. Leonard Gilbertisched 1909. missenscheus (Pellege.) Leonard Anthonorda proserti (De Wild.) Exelt & Hillic. Berindig parallel (Vid.) Hinch. & Dalziel Brachystegia carelor i Harms Brachystegia carelor i Harms Brachystegia carelor i Harms Brachystegia carelor i Harms Brachystegia (Pellege.) Leonaria, E. Berna, Tiada Julierantia genvieller (Schunch, & Teonaria) Julierantia genvieller (Schunch) Julierantia genvieller (Schunc	5 5 10 5 4 9 5 3 8 5 3 8 5 3 8 5 3 8 5 3 8 5 2 7 4 2 6 5 1 6 5 1 6 5 1 7 5 4 9 5 3 8 5 3 8 6 5 3 8 7 7 8 7 9 8 7 9 9	P	P P P P P P P P P P	P	a p a a a p a a a p a a	P P A P A P P A P A P P A P P P A P P P A P P P P P P P P P	+++ s - f - f - f - f - f - f - f - f - f - f
HUA HUA GAB	Caesalpinoideae Icacinaceae Icacinaceae Icacinaceae Annonaceae Clusiaceae Annonaceae Irvingiaceae	Hus qualwait Neuries Ch (Vals.) Brummit De monatorly brevipes (Hag.) Sleumer De monatorly brevipes (Hag.) Sleumer De monatorly specific (Miers) Starf Isolona companulate Engl. & Diels Allandhackia partylirar A. Chev. Monanthackia progger Engl. & Diels Tevrigis robust Milder.	4 4 8 4 3 7 4 3 7 5 2 7 4 2 6 4 1 5	a p p a p ? ? p a a ? ? p a a ? p p a a ? p p a a ? a p p a a ? a p p a p ?	p p p ? a a a a p p p a a a a a p p p a a a a	a ? ? a ? ? a ? ? ? a a ? p a a ? p a a ? p a a ? ?	a a a p a a a p a a p p a p a a p p a a a a a p	p p a a a a a p p a a a a a p p p a a a a a a p p p a a a a a p p p a a a a p p p a a a a p p p a	+ f f + g - f
IRV IRV SMI	Irvingiaceae Meliaceae Caesalpinioideae Caesalpinioideae Rhamnaceae Caesalpinioideae Caesalpinioideae Caesalpinioideae	Irvingia suithi Hook. f. Guarca cedrata (A. Chev.) Pellegr. Gastaphinia webritzchiana (Oliv.) Bruan Schefftersdemran aelsopealum (Taub) Harms Quassia undulan (Guil. & Perr.) D. Dietr. Schefftersdemran giberrianum J. Leonard & Latour Bauthinia petersianum Bolle Bauthinia petersianum Bolle Bauthinia refecent Iam.	5 4 9 5 3 8 5 2 7 5 2 7 4 2 6 4 2 6 2 1 3 1 1 2	P P P P P P P P P P P P P P P P P P P	p p p a a a a a a a a a a a a a a a a a	a a p p a a a a p p ? ? ? ? ? a a a a p p a a a a	p a a a a p a a a a a a a a a a a a a a	p p a p a p p p a p p p a p p p p a a p a p p p p a a a a a p p p p a a a a a p p p a a a a a p p p a a a a a p p p a a a a a p p p a a a a a p p p a a a a a p p p a a a a a p p p a a a a a a p p p a	++ g f f f f f
IRV KLA GAB	Irvingiaceae Caesalpinioideae Irvingiaceae Irvingiaceae Irvingiaceae Irvingiaceae Caesalpinioideae Moraceae Rhammaceae	Maintodaus gubornensis Patrice R. Bagl. Cymontern manni Oliv. Irvingis gubornensis (Aubry-Lecomte et O'Rorke) Balll. Irvingis gundiolis (Engl.) Engl. Irvingis vombola (Engl.) Engl. Irvingis vombola Vermoscen Scorrdopholoros zuderi Harms Ficus hononingii Blume Perudaloi.monytri margrounejiolis Pax	5 4 9 5 3 8 5 2 7 5 2 7 4 3 7 5 2 7 4 2 6	p p p p p p p p p p p a a a a p p p a a p a p p p a a a a p p p p a a a p p p p a a a p p p a a a p p p a a a p p p a a a p p p a a a p p p a a a a p p p a a a a p p p a a a a p p p a a a a p p p a	p p p p p a a a p p p a a a a a a a a a	a p a a a a a a a a a ? p a a a ? p a a a ? p a a a p a a a p a a a p a a a p a a a p a a a p a a a p a a a p a a a p a a a p a a a a p a a a a p a a a a p a a a a p a	p a a a a a a a a a a a a a a a a a a a	p p p p a p p p p p p a a p a p p p p p	- f ++ g ++ g ++ g - f + g
MEL GUA	Meliaceae Meliaceae Meliaceae Simaroubaceae	Pseudolachnostylis maproaneifolia Pax Gaurae cedrata (A. Chev.) Pellegr. Gaurae laurenti ibe Wild. Gaurae thomponii Sprague & Hutch. Quassia undulata (Guill. & Perr.) D. Dietr. Zamha golungensis Hierm	5 4 9 4 4 8 5 3 8 4 3 7	p p p p p p p p p p p p p p p p p p p	p p a a a a a a p p p a a a a a a a a a	a a a p a a a p a a a p a a a p	paaa paaa paaa ppaa	p p p a a a p p p p a a p p p p a a p p p p a a p p p a a p p p a a a p p p p a a a a a p p p p p a	
MYR COE BOT	Myristicaceae Myristicaceae Flacourtiaceae Euphorbiaceae Euphorbiaceae Flacourtiaceae Flacourtiaceae Euphorbiaceae Euphorbiaceae	Coelocaryon botryoides Vermosen Coelocaryon preussii Warh. Oncodu gilgiuma Sprague Antidewan lacinintum Mill. Arg. Antidewan ogocilanum Mull. Arg. Oncodu crepinintu De Wild. & T. Durand Oncodu crepinintu De Wild. & T. Durand Oncodu cridomatrase (Cilis) S. Mul & Entabler	5 4 9 5 4 9 4 4 8 5 2 7 5 2 7 3 4 7 3 3 6	P P P P P P P P P P P P P P P P P P P	p p p a a a a a p p p p a a a a a p p p p a a a a a p p p p a a a a a p p p p a a a a a p p p p p a a a a a 2 p p a a a a	a a p ? a a ? ? ? ? a a a ? ? a a ? ? a a ? ? a ? ? a ? ? a ? ? a ? ? a ? ? a ? a a ? a	p a a a a a a a a a a a a a a a a a a a	p p a p a p p p p a a a a a a p p a a a a a a a p p a a a a a a a p p a	+ g + g - f - f
MYR SYZ GUI	Myrtaceae Myrtaceae Myrtaceae Moraceae Moraceae Moraceae Hypericaceae Ulmaceae Ulmaceae Moraceae Moraceae Moraceae	Flargen strone (Walk) Voge Syrgian galacene (Walk) LiCe Syrgian sambet (Fine) Malhe Flara Institut Hand) Malhe Flara Institut Hand) Malhe Flara Institut Hand Bensique ex Bontique & Ji. éonard Flara Institut Vall Vinniu affisite Üliv. Celtis gomphosphila Baker Celtis mildhreadii Engl. Flara cordata Thunh Mora menceygia Stapf Trilopinium madagacardinas Thomare ex DC.	5 4 9 5 4 9 4 4 8 5 3 8 5 3 8 5 2 7 5 1 6 5 1 6 5 1 6 5 1 6	P P P P P P P P P P P P P P P P P P P	P P P P P P P P ? ? P P P P P P P ? ? P P P P	a p p p p a 2 ? ? ? a a ? ? ? ? a a ? ? ? ? a a a p a a a a	p p p a a a p p a a a p p a a a a p p a a a a a a p a a a a p a a a a p a a a p p a a a a p p a a a a p p a a a a p p a a a a p p a a a a p a a a a p a a a a p a a a a p a a a a p a a a a p a a a a p a a a a p a a a a a p a a a a a p a a a a a p a a a a a p a a a a a a p a		++ 8 8 + 6 6 6 + 6 6 6 6 6 6 6 6 6 6 6 6
RUB COR PAN	Sapotaceae Rubiaceae	Inhambanda guerrenis (Anbrés, & Pellegs,) T.D. Penn. Cenyamile pasicycari. K. Schum. Cenyamile pasicycari. K. Schum. Cenyamile pasicycari. K. Schum. Pansinystala jatholie Perne en Beille Pansinystala satholie Perne en Beille Pansinystala satholie Perne en Beille Pansinystala carior. W. Berla et et G. Doni Benth. Miragapa farenis (Willd. Kastare Cincitigenem artiforio. (K. Schum.) Thom. Hallet arthoristydatus (K. Schum.) J.F. Leroy Gardnein imperials K. Schum.	1 3 4 5 4 9 5 4 9 5 4 9 4 4 8 4 3 7 4 3 7 2 4 6 1 4 5 1 3 4	a a a a p p p ? ? p p p ? ? p p p ? ? p a p ? p a a p ? p a a p ? p a a p ? p a a p ? a p p a p p a a 2 a p a a 2 a p a a ? p a a ? p a a ? p p	P	a a ? ? a a ? ? a a ? ? a a ? ? a a ? ? a a ? ? a a ? ? ? a a p a a ? ? ? ? p a a a ? ? ? ? ? ? a p a a a ? ? ? ?	p a a a a p a a a p a a a a a a a a a a	p p a a a p p a a a p p a p a a p p a p a a p p a a p p a a p p a a p p a a p p a a a p p a a a a p p a a a a p p a a a p p a a a p p a a a p p a a p p a a a a p p a a a a a a p p a a a a a a a a a a a a a a	+ f
(a) (b) (c) (d) (e) (f) (g) (h) (i) (j) (k)	Rubiaceae distribution: ecol, temp, morph.: RMCA wood sample: RMCA thin sections: Inside Wood Database: Inventory lists Luki: Indicator forest type: relative abundance taxonomic level: taxonomic level:	Gardenius tratifolia Schumach. & Thom. of Figure 1, data are derived from African Plusts Database (2011), NEAC data are derived from African Plusts Database (2011), NEAC (1984-8), data data are derived from African Plusts Database (2011), NEAC (1984-8), desired persence (p) or abmence (a) or a found annotation description on the system presence (p) or abmence (a) or a finis sections (Tv. Tg. and RJ) of this species presence (p) or abmence (a) or a finis species in one (or several) of the list no indicates whether this species is (p) or is not (a) one or the Caralaphinide indicates whether this species is (p) or is not (a) one or the Caralaphinide indicates whether this species is (p) or is not (a) one or the Caralaphinide indicates whether for pollent species indicates on sit unples (Hingua) 1, taxonomic level of pollen indenfication (Hengue et al., 2000): "F = finish interaction level of pollen indenfication (Hengue et al., 2000): "F = finish interactions (a) of the indication (Hengue et al., 2000): "F = finish interaction (b) of their indication (Hengue et al., 2000): "F = finish interaction (b) of their indication (Hengue et al., 2000): "F = finish interaction (b) of their indication (Hengue et al., 2000): "F = finish interaction (b) of their indication (Hengue et al., 2000): "F = finish interaction (b) of their indication (Hengue et al., 2000): "F = finish interaction (b) of the indication (Hengue et al., 2000): "F = finish interaction (b) of their indication (Hengue et al., 2000): "F = finish interaction (b) of their indication (Hengue et al., 2000): "F = finish interaction (b) of their indication (Hengue et al., 2000): "F = finish interaction (b) of their indication (Hengue et al., 2000): "F = finish interaction (b) of their indication (Hengue et al., 2000): "F = finish interaction (b) of their indication (Hengue et al., 2000): "F = finish interaction (b) of their indication (Hengue et al., 2000): "F = finish interaction (b) of their indication (Hengue et al., 2000): "F = finish interaction (B) of their	3), Hutchinson & Dalzi am of the Royal Museur in the xylarium of the I es on the on-line Inside esulting from inventorie are considered as indica- es for a certain Central	iel (1954-1972), Oliver (1830 m for Central Africa in Tervus Royal Museum for Central Af Wood Database (july, 2011) set to around the Luki resev- tor species for old-growth rai african forest type described!	a a a p p p Oliver (1830-1916), Burkill (1985) -1916), Burkill (1985) ren, Belgium (Tervuren Xylarium Woos rica in Tervuren, Belgium (Tervuren X; ve nforest by Leal (2004) by Lebrun & Gilbert (1954)		a p p a	<u>ppaaap</u>	

			п	nkin	g		distri	butior	1			•	cology				tem	peran	nent		me	rphol	gy		da	atabase	es & li	sts		polle	1
CHARCOAL TYPE	Family	Species	distribution ranking (75)	anatomy ranking (75)	Ranking (/10)	Mayumbe (M)	Lower Guinea (LG)	Transition	Transition North (TN)	moist evergreen forest	moist semi-deciduous forest	dry deciduous forest	emargin forest-savanna	woodland savanna	tree savanna shrub savanna		pioneer species	light demanding	light/shade tolerant shade hearing		ž	enall tree (5-20m)	Lianescent	RMCA wood sample	RMCA thin s	Inside Wood	Invenory	Indicator old forest Indicator forest tens		relative abundance taxonomic level	taxonomic kvd
				-				_					(D)					(D)				(D)		(c) (d)	. (e)	(f)	(g) (ł	1)	(i) (j)	(k)
					ESS :	succi	ESFUL	IDEA	NTIFIC	ATIO	N																				
	Apocynaceae	Tabernanthe iboga Baill.	4	3	7	?	p :	2	? ?	p	P	P	2	a	a a		a	?	p 1		a	P F	a	P	P	2	2	3 2	1		f
_	Rubiaceae	Antidesma membranaceum Müll. Arg.	5	2	7	P	P	P F	P	P	P	P	P	P	p a		a	P	p a	1	a	P I	a	P	, p	P	a	a a	1	- f	g
100	Rubiaceae	Antidesma vogelianum Müll. Arg.	5	2	7	P	P	· F	p p	P	P	P	?	a	a a		a	?	? ?		a	P I	a	P	P	P	a	a 2	1	- f	g
- F	Rubiaceae	Polysphaeria pedunculata K. Schum. ex De Wild.	3	3	6	a	?	, ?	? ?	a	a	a	?	P	? ?		?	?	? ?		?	? :	?	P	P	a	a	a 2	1		f
Ε.	Flacourtiaceae	Homalium letestui Pellegr.	5	1	6	P	P	, ?	? P	P	P	P	?	a	a a		a	?	? ?		P	p a	a	P	P	P	a	a 2	1		g
0	Flacourtiaceae	Homalium longistylum Mast.	5	1	6	P	P	P F	p p	P	P	P	P	P	a a		a	?	? ?		P	a a	a	P	, p	P	a	a a	1		g
2	Rubiaceae	Ancylanthos rubiginosus Desf.	2	3	5	a	a	1 F	a a	a	a	a	a	P	p p		a	?	? 2	1	a	a p	a	P	P	a	a	a 2	1		f
	Flacourtiaceae	Casearia stipitata Mast.	4	1	5	?	P	P F	p p	P	P	P	a	a	a a		a	?	? ?		a	р :	a	P	, p	2	a	a a	1		g
	Verbenaceae	Vitex congolensis De Wild. & Durand	3	1	4	_ ?	?	2	? ?	a	P	P	a	a	a a		a	Р	p a		?	? :	a	P	, p	_ a	a	a p	,		g
	Dichapetalaceae	Dichapetalum madagascariense Poir.	5	3	8	P	P) F	p p	P	P	P	P	P	p p		a	?	? ?		a	P F	P	P	P	2	a	a 2	1		
e.	Rhizophoraceae	Cassipourea gummiflua Tul.	4	3	7	?	P	, E	?	a	a	P	a	a	a a		a	?	? ?		P	р :	a	P	, b	P	2	a 2	1		
NA.	Capparaceae	Euadenia eminens Hook.f.	5	2	7	P	P	, ?	? ?	P	P	?	?	a	a a		a	?	? ?		a	a p	a	P	P	a	a	a 2	1		f
olc:	Rubiaceae	Aulacocalyx jasminiflora Hook. f.	5	0	5	P	P	1 F	?	P	P	P	?	a	a a		a	a	P F	•	а	P I	a	P	, b	2	a	a 2	1		f
	Rubiaceae	Schumanniophyton magnificum (K. Schum.) Harms	4	1	5	?	P	? ?	? ?	P	P	P	?	a	a a		a	a	? ?		a	a p	a	P	P	a	a	a 2	1		f
DIC	Rubiaceae	Aulacocalyx talbotii (Wernham) Keay	4	0	4	?	P	? ?	? ?	P	P	P	?	a	a a		a	2	P F	,	a	P F	a	P	, b	2	2	a 2	1		f
-	Euphorbiaceae	Erythrococca bongensis Pax	3	1	4	a	a	, ?	? P	a	a	a	a	P	p p		a	a	p 2	1	a	a p	a	P	P	a	a	a p	,	- f	f
	Rubiaceae	Leptactina arnoldiana De Wild.	3	0	3	_ ?_	?	, :	? ?	- ?	?	?	?	?	? ?		?	?	? ?		?	? :	' ?	P	, p	_ a	a	a a	1		f
SE SE	Ulmaceae	Celtis mildbraedii Engl.	5	3	8	P	P	P F	p p	P	P	a	a	a	a a		a	a	p 2	1	P	a :	a	P	P	P	p	a p	,	+ g	g
9	Ulmaceae	Celtis philippensis Blanco	5	3	8	P	P :	, L	p p	P	P	P	P	P	a a		a	2	? ?		P	a :	a	P	P	P	2	a 2	1	+ g	8
HOL	Ulmaceae	Celtis prantlii Priemer ex Engl.	5	3	8	P	P) F	p p	a	P	P	P	P	a a		a	?	? 1		a	p =		P	P	P	2	2 2	1	+ g	8
Ξ	Ulmaceae	Celtis tessmannii Rendle	5	3	8	P	P) F	P	P	P	a	a	a	a a		a	a	7 3		P	a :	a	P	P	P	P	a F	,	+ g	g
ULM	Ulmaceae	Holoptelea grandis (Hutch.) Mildbr.	5	3	8	P	P) F	?	a	P	P	P	a	a a		a	P	a 2		P	2 2	a	P	P	P	P	a p	,		5
	Boraginaceae	Cordia subcordata Lam.	2		5	a	a	1 3	р	a	a	a	a	a	p p		?	?	? ?	'	a	a p	a	P	, p	P	a	a 2	1		f
(a)	distribution:	cf. Figure 1, data are derived from African Plants Database (2011), INE/												rkıll (1985)																
(b)	ecol., temp., morph.:	data are derived from African Plants Database (2011), INEAC (1948-196																													
(c)	RMCA wood sample:	presence (p) or absence (a) of a wood sample of this species in the xylari																													
(d)	RMCA thin sections:	presence (p) or absence (a) of thin sections (Tv, Tg and R) of this species									Terv	uren,	Belgiu	ım (Te	ervuren :	Xylar	um W	rood l	Jatabas	se, 20	11)										
(e)	Inside Wood Database:	presence (p) or absence (a) of a wood anatomical description of this spec																													
(f)	Inventory lists Luki:	presence (p) or absence (a) of this species in one (or several) of the lists i																													
(g)	Indicator old forest:	indicates whether this species is (p) or is not (a) one of the Caesalpinioid																													
(h)	Indicator forest type:	indicates whether this species is (p) or is not (a) one of the indicator spec																													
(i)	relative abundance	relative abundance of pollen type in modern soil samples (Elenga et al., 2													quantitie	s; "++	"= ab	undar	t												
(j)	taxonomic level:	taxonomic level of pollen identification (Elenga et al., 2000): "f"= family																													
(k)	taxonomic level:	taxonomic level of pollen identification (Lebamba et al., 2009): "f"= fam	ily level; "g	'= ger	nus lev	el; "s":	= specie	s leve	d; "-"= n	o defi	ied po	llen ty	pe ava	ailable	e																

