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Modern pollen rain in savanna and forest ecosystems of Gabon and Cameroon, Central Atlantic Africa

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ABSTRACT

Eighty modern soil surface and litter samples from southern Cameroon and Gabon, Central Atlantic Africa (5°N–4°S, 10°–15°W), were analysed for pollen content. The samples are distributed among two main vegetation types: savanna (8 samples) and forest (71 samples). The aim of this study is to provide new data on the modern pollen rain in the Guineo-Congolian phytogeographical region, mainly in forest communities (secondary and mature forests on well drained soils, and hygrophilous forests) and to interpret these data using diagrams of pollen percentages and numerical analyses. The savannas are well identified by high frequencies of non-arboreal pollen with as pollen marker the Poaceae, and the forests by high frequencies of arboreal pollen with as important families the Burseraceae, Caesalpiniaceae, Mimosaceae, Euphorbiaceae and Sapindaceae. Within the forest ecosystem, secondary and mature forests on well drained soils can be differentiated on the basis of distinct assemblages of tree pollen taxa such as *Zanthoxylum*, *Phyllanthus*, *Tetrorchidium*, *Margaritaria discoidea* in secondary forest spectra and abundance of Burseraceae, Caesalpiniaceae, Sapindaceae in mature forest ones. In addition, hygrophilous forests are well identified by the presence of high pollen contributors such as *Uapaca*, *Nauclea*, *Macaranga* and *Raphia*. This work shows that the major vegetation communities occurring today in Cameroon and Gabon can be well differentiated by their pollen assemblages.

1. Introduction

The Guineo-Congolian phytogeographical region (White, 1983) is today probably one of the least known of the African continent. Little is known about its floristic composition and biodiversity as well as its environmental history. This region occupies a large area of 2 800 000 km^2, the greater part of which is covered by rain forest more or less degraded by human activities (Schnell, 1976). As with many tropical humid areas in the world, the African tropical region plays a key role in the global climate. Indeed, it is a large source of heat and water vapour for Hadley circulation system and so it drives climatic changes of global impact (Zebiak and Cane, 1987). Presently, the ecosystems of this region are threatened by increasing human activities and ongoing climate change (IPCC, 2007). Several palaeoecological works have demonstrated the sensitivity of the Guineo-Congolian forest to climate changes in the past (Elenga et al., 2004; Bonnefille, 2007). For example, they have shown that ca. 3000–2500 years BP, a drier climate set in has induced forest disappearance in some areas such as in the Niari valley, Congo (Vincens et al., 1998, 1999), the extension of enclosed savannas into the Mayombe forest, Congo (Elenga et al., 1996) and secondary forest formation development in the rain forest of Cameroon (Reynaud-Farrera et al., 1996; Maley and Brenac, 1998). High time-resolution studies of the last 1500 years (resolution of ~20 to 30 years) have additionally shown that shorter climatic fluctuations, such as the "Medieval Warm Period" and the "Little Ice Age", well defined in the northern hemisphere, were registered in tropical humid Africa (Ngomanda, 2005; Ngomanda et al., 2007).

The qualitative and more recently quantitative (biome reconstructions and rainfall estimates, Ngomanda, 2005) interpretations of the continuous fossil pollen sequences from Central Atlantic Africa, and biome reconstructions of key periods (0 and 6000 BP, Jolly et al., 1998; 18,000 BP, Elenga et al., 2000a) have been made in the light of studies carried out on the modern relationship between vegetation and pollen rain using surface soil or litter samples (Gabon: Jolly et al., 1996; Congo: Elenga et al., 2000b; Cameroon: Reynaud-Farrera, 1995;

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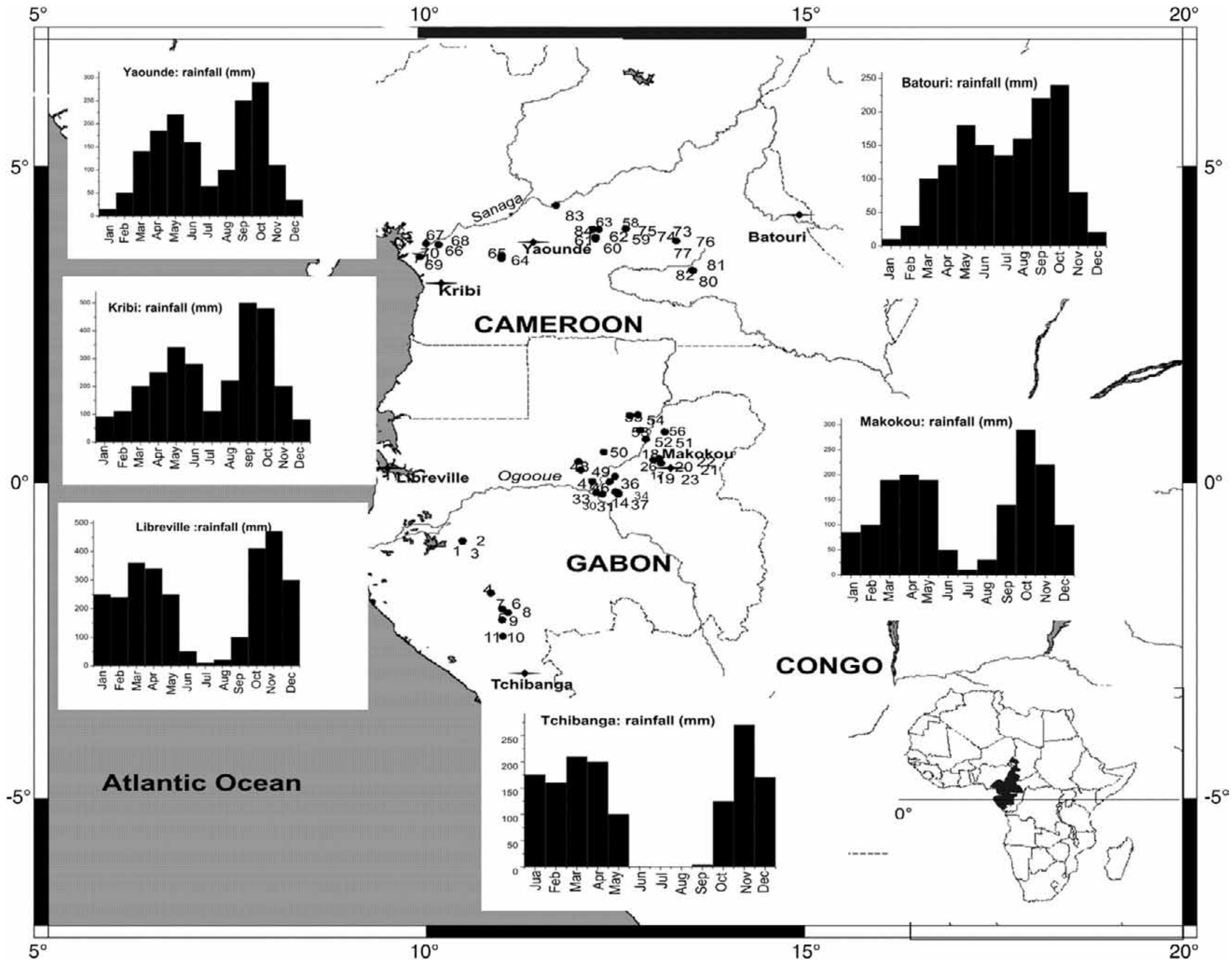

Fig. 1. Map of Central Atlantic Africa showing monthly precipitation patterns and the location of the 80 modern surface soil and litter pollen samples in Cameroon and Gabon. The numbers refer to the sites as numbered in Table 1.

Vincens et al., 2000). Recently, Gajewski et al. (2002) and Watrin et al. (2007), using distribution of individual pollen taxa, presented maps of modern pollen from across Africa and suggested that there were sufficient data for large-scale analysis. We, however, think that modern pollen data are still scarce for quantifying relations between vegetation and climate at the scale of the Guineo-Congolian phytogeographical region. To fill this large gap in the pollen data network from Central Atlantic Africa and thereby allowing a more precise interpretation of fossil sequences, 80 new modern pollen samples, collected in southern Cameroon and Gabon are presented in this paper. This work aims to determine to what degree palynological methods allow to better identify the various ecosystems occurring today in the western part of the Guineo-Congolian region, especially the forested ones.

2. Environmental setting

The study area, covering the southern Cameroon and the Gabon, is located between latitude 5°N and 4°S and between longitude 10° and 15° E (Fig. 1). It is mainly occupied by lowlands, with an average altitude of 400 m.

The climate of this region is controlled primarily by the North-South movement of the Intertropical Convergence Zone (ITCZ) and the associated west African monsoon circulation, partly driven by sea surface temperature in the Gulf of Guinea and the tropical Atlantic Ocean (Leroux, 1983; Nicholson and Entekhabi, 1987; Leroux, 2001). In southern Cameroon, the mean annual rainfall is between 1200 and 1600 mm with a well-defined dry season of 3 months (December to February; $P<50$ mm/month according to Griffiths, 1972) (Suchel, 1988). In Gabon the mean annual rainfall is mostly between 1600 and 2000 mm with a dry season of 3 (4) months (June to August (September)) (Saint-Vil, 1977). Along the coast of Cameroon and Gabon, the mean annual rainfall is often more than 3000 mm, generally between 2000 and 3000 mm, with a very high atmospheric humidity throughout the year and without a dry season (Fig. 1). Mean monthly temperature is almost constant throughout the year, with mean annual temperatures of about 26 °C along the coast and of about 24 °C inland.

Gabon and southern Cameroon are floristically located in the Guineo-Congolian phytogeographical region of which the greater part is covered with rain forest on well-drained sites and swamp forest on hydromorphic soils (White, 1983). In this region, two main types of undisturbed forest are differentiated by this author:

- The *Guineo-Congolian "wet" rain forest*, which includes: (i) The coastal evergreen rain forest characterized by the presence of *Sacoglottis gabonensis* and *Lophira alata* in Cameroon (Letouzey, 1957; Tchouto Mbatchou, 2004), this latter tree being replaced by *Okoumea klaineana* in Gabon (Leroy Deval, 1973). This forest type is called "Atlantic littoral forest" by Letouzey (1968, 1985). Inland, this evergreen rain forest is replaced by a forest very rich in Caesalpiniaceae ("Biafran forest", Letouzey, 1968, 1985). (ii) The mixed moist semi-evergreen rain forest ("Congolian forest", Letouzey, 1968, 1985), well developed in southern Cameroon (Tchouto Mbatchou, 2004) and Central Gabon (Nicolas, 1977) and characterized by a mixture of evergreen and semi-deciduous formations.
- The *Guineo-Congolian "dry" rain forest*, or drier peripheral semi-evergreen rain forest ("semi-deciduous rain forest", Letouzey, 1968, 1985), in which more individuals of the common largest tree species are deciduous than in evergreen forest and lose their leaves during the dry season. It is well developed in southern Cameroon, north of the mixed moist semi-evergreen rain forest, and in southern Gabon.

Outside the forest reserves, much of the remaining Guineo-Congolian rain forest on well-drained soils occurs on land which has been formerly cultivated. It is therefore considered as secondary forest and corresponds to various stages of forest regrowth in which light-demanding species and pioneers are abundant (White, 1983). Moreover, inside these forests are found pockets of savannas such as in southern Cameroon, in coastal and inland Gabon; their occurrence is linked to past climatic changes and/or human impact (Clist, 1995).

3. Material and methods

Eighty surface soil and litter samples were collected in Gabon and Cameroon in 2004 and 2007 respectively. The sampling method follows the guidelines described by Wright (1967) and is widely used in African modern pollen studies (e.g. Lézine and Edorh, 1991; Vincens et al., 1997, 2000; Elenga et al., 2000b). In each site, about 20 sub-samples are randomly collected in a 200–400 m^2 area; these are then homogenized. This method was compared with other sampling procedures (along one or two diagonals crossing the plot or along two transverse sections) by Jolly et al. (1996) and appears to be the most adapted for tropical forested areas. The location of the study modern pollen samples is given on Fig. 1 and in Table 1. Samples were collected in savanna (8 samples), secondary forest (i.e. in disturbed evergreen and semi-evergreen forests; 17 samples) or mature forest (i.e. in undisturbed evergreen and semi-evergreen forests, and also probably, for some of them, in old secondary forest; 47 samples), and in swamp (1) or riverine (7) forests.

The chemical treatments of the samples followed standard methods (Faegri and Iversen, 1975). For each sample at least 350 pollen grains and spores were counted and the identification was achieved with the help of the reference collection of modern specimens of tropical Africa at ISE-M, published pollen atlases related to Central Africa (e.g. Sowunmi, 1973; A.P.L.F., 1974; Ybert, 1979; Salard-Cheboldaeff, 1980–1987, 1993; Sowunmi, 1995) and photographs available on the African Pollen Database web site. The nomenclature of the pollen taxa was standardized following Vincens et al. (2007) for tree and shrub pollen types. The preservation of pollen and spores was good, with few damaged (i.e. indeterminable) grains (less than 3%). On average 5% of the pollen grains in any one sample remain unidentified. The corresponding plant habit and habitat of pollen taxa was determined using West and Central African botanical literature (Table 2; e.g. Flore du Congo Belge et du Ruanda-Urundi, 1948-1963; Flore du Congo, du Rwanda et du Burundi, 1967-1971; Flore d'Afrique Centrale (Zaïre, Rwanda, Burundi), 1972-2004; Hutchinson and Dalziel, 1954-1972; Flore du Gabon, 1961-2004; Flore du Cameroun, 1963-2001; Letouzey, 1968, 1985; Lebrun and Stork, 2003, 2006; Tchouto Mbatchou, 2004).

The pollen data were then analysed using correspondence analysis (CA) (Benzécri, 1973). This method has been previously applied with success in Africa on modern pollen samples by Reynaud-Farrera (1995), Jolly et al. (1996), Bengo (1992), Vincens et al. (1997) and Elenga et al. (2000b). An important property of CA is that it can be applied to large abundance tables such as the modern pollen data described in this paper and that it produces a final factor space that simultaneously represents rows (individuals, here pollen spectra) and columns (variables, here pollen taxa) allowing their plotting together in the same scatter diagram (Lefèbvre, 1983). Two correspondence analyses, using Multivariate Statistical Package 3.1 software and without datatransformation of the percentage values, have been performed on the whole data set as well as on a consisting of the only samples from forests.

4. Results and discussion

After standardization of the nomenclature following Vincens et al. (2007), 121 pollen taxa have been identified in the 80 samples (Table 2).

Table 1
Location of modern pollen samples in Cameroon and Gabon

Site number	Samples	Latitude	Longitude	Altitude (m)	Country	Location	Local vegetation
1	Tchad1	0°56′30.7″S	10°28′26.7″E	148	Gabon	Lambaréné–Fougamou	Secondary forest
2	Tchad2	0°56′30.7″S	10°28′26.7″E	148	Gabon	Lambaréné–Fougamou	Secondary forest
3	Tchad3	0°56′30.7″S	10°28′26.7″E	148	Gabon	Lambaréné–Fougamou	Secondary forest
4	Doubou1	1°45′21.0″S	10°52′32.0″E	89	Gabon	Doubou	Savanna
5	Doubou2	1°45′21.0″S	10°52′32.0″E	89	Gabon	Doubou	Savanna
6	Doubou3	1°45′21.0″S	10°52′32.0″E	89	Gabon	Doubou	Ecotone savanna-forest
7	Doubou4	1°45′28.1″S	10°52′43.5″E	87	Gabon	Doubou	Swamp forest
8	Biendi1	2°4′2.1″S	11°5′13.3″E	139	Gabon	Biendi	Savanna
9	Sogadel_1	2°26′51.2″S	11°25′17.1″E	153	Gabon	Sogadel	Savanna
10	Massou_1	2°11′25.5″S	11°12′31.5″E	134	Gabon	Lake Massou	Savanna
11	Bengui_1	2°01′46.2″S	11°7′7.8″E	92	Gabon	Bengui	Secondary forest
12	Gabon-04_47	0°10′41.9″S	12°15′32.9″E	324	Gabon	Langoué road (Ivindo National Park)	Mature forest
13	Gabon-04_48	0°10′41.9″S	12°15′32.9″E	325	Gabon	Langoué road (Ivindo National Park)	Mature forest
14	Gabon-04_49	0°10′41.9″S	12°15′32.9″E	326	Gabon	Langoué road (Ivindo National Park)	Mature forest
15	Gabon04-50	0°10′41.9″S	12°15′32.9″E	327	Gabon	Langoué road (Ivindo National Park)	Mature forest
16	Gabon-04_51	0°10′51.6″S	12°32′40.1″E	327	Gabon	Ivindo (camp)	Mature forest
17	Gabon-04_65	0°11′16.6″S	12°32′43.8E	360	Gabon	Langoué bai	Mature forest
18	Gabon-04_69	0°11′22 S	12°33′35 E	360	Gabon	Langoué bai	Mature forest
19	Gabon-04_86	0°0′38.7″N	12°26′45.5″E	540	Gabon	Djjidji	Mature forest
20	Gabon-04_92	0°23′46″N	13°2′54.7″E	528	Gabon	Ntsiete	Mature forest
21	Gabon-04_96	0°48′50.8″N	12°53′11.9″E	457	Gabon	Aoua	Riverine forest
22	Gabon-04_110	0°22′45.7″N	12°12′47.4″E	442	Gabon	Makokou	Secondary forest
23	Gabon-04_111	0°20′4.9″N	12°3′25.2″E	413	Gabon	Ovan	Mature forest
24	Gabon-04_118	0°12′2.7″S	10°28′6.7″E	28	Gabon	Lake Nguene	Mature forest
25	Gabon-04_52	0°10′51.6″S	12°32′40.1″E	460	Gabon	Ivindo (camp)	Mature forest
27	Gabon-04_60	0°11′50″S	12°33′32″E	370	Gabon	Langoué bai	Mature forest
28	Gabon-04_61	0°11′8.7″S	12°33′28.6E	342	Gabon	Langoué bai	Mature forest
29	Gabon-04_62	0°11′5″S	12°33′32″E	350	Gabon	Langoué bai	Mature forest
30	Gabon-04_63	0°11′22.9S	12°33′16.2E	360	Gabon	Langoué bai	Mature forest
31	Gabon-04_64	0°10′41.4″S	12°32′22.6″E	495	Gabon	Langoué bai	Mature forest
32	Gabon-04_66	0°11′7.2″S	12°32′34.5″E	450	Gabon	Langoué bai	Mature forest
33	Gabon-04_67	0°10′51.6″S	12°32′40.1″E	460	Gabon	Langoué bai	Mature forest
34	Gabon-04_68	0°11′22.2″S	12°33′35.6″E	380	Gabon	Langoué bai	Mature forest
35	Gabon-04_70	0°10′43.6″S	12°32′31.6″E	468	Gabon	Langoué forest	Secondary forest
36	Gabon-04_71	0°10′29.9″S	12°32′12.3″E	515	Gabon	Langoué forest	Secondary forest
37	Gabon-04_72	0°10′14.5″S	12°31′49.8″E	500	Gabon	Langoué forest	Secondary forest
38	Gabon-04_73	0°10′41.4″S	12°32′22.6″E	495	Gabon	Langoué forest	Mature forest
39	Gabon-04_74	0°10′51.4″S	12°32′36.1″E	455	Gabon	Langoué forest	Mature forest
40	Gabon-04_75	0°10′52.8″S	12°32′26.0″E	460	Gabon	Langoué forest	Mature forest
41	Gabon-04_76	0°10′36.5″S	12°32′13.2″E	459	Gabon	Langoué forest	Mature forest
42	Gabon-04_81	0°10′47.3″S	12°32′55.3″E	463	Gabon	Langoué forest	Mature forest
43	Gabon-04_82	0°10′52.9″S	12°33′1.9″E	461	Gabon	Langoué forest	Mature forest
44	Gabon-04_83	0°10′14.5″S	12°31′49.8″E	500	Gabon	Ivindo National Park	Mature forest
45	Gabon-04_84	0°9′43.7″S	12°30′51.8″E	547	Gabon	Ivindo National Park	Mature forest
46	Gabon-04_87	0°0′38.7″N	12°26′45.5″E	540	Gabon	Djidji	Mature forest
47	Gabon-04_88	0°0′40.6″N	12°26′21.4″E	500	Gabon	Djidji	Mature forest
48	Gabon-04_89	0°1′37″N	12°24′21.8″E	420	Gabon	Djidji	Mature forest
49	Gabon-04_90	0°0′57.8″S	12°21′0.7″E	424	Gabon	Djidji	Mature forest
50	Gabon-04_91	0°29′4.9″N	13°5′3.7″E	501	Gabon	Ntsiete	Mature forest
51	Gabon-04_94	0°22′23.5″N	13°7′28.4″E	534	Gabon	Ntsiete	Mature forest
52	Gabon-04_95	0°19′48.5″N	13°10′41.1″E	554	Gabon	Ntsiete	Mature forest
53	Gabon-04_103	0°56′56.2″N	12°48′31.3″E	489	Gabon	Aoua	Riverine forest
54	Gabon-04_106	1°7′0.6″N	12°42′6.4″E	455	Gabon	Aoua	Riverine forest
55	Gabon-04_107	1°3′16.7″N	12°44′43.7″E	457	Gabon	Aoua	Riverine forest
56	Gabon-04_108	0°54′8.5″N	12°48′44.5″E	477	Gabon	Aoua	Riverine forest
57	Gabon-04_109	0°41′16.1″N	12°55′1.7″E	493	Gabon	Ivindo National Park	Riverine forest
58	CAM07002S	4°0′27.2″N	12°38′44.3″E	662	Cameroon	Nebodo	Mature forest
59	CAM07003S	3°59′13.5″N	12°16′56.6″E	695	Cameroon	Eyo	Riverine forest
60	CAM07007S	3°51′44.3″N	12°14′51.8″E	667	Cameroon	Biba	Secondary forest
61	CAM07008S	3°51′39.8″N	12°14′45.3″E	671	Cameroon	Biba	Secondary forest
62	CAM07009S	3°51′34.4″N	12°14′35.1″E	643	Cameroon	Biba	Secondary forest
63	CAM07010S	3°51′33.2″N	12°14′32.1″E	687	Cameroon	Biba	Secondary forest
66	CAM07038S	3°35′15.1″N	9°55′39.8″E	26	Cameroon	Tissongo	Mature forest
67	CAM07039S	3°35′9.7″N	9°55′40.3″E	14	Cameroon	Tissongo	Mature forest
68	CAM07040S	3°35′7.9″N	9°55′42.9″E	11	Cameroon	Tissongo	Mature forest
69	CAM07068S	3°33′53.5″N	9°46′30.3″E	17	Cameroon	Nsah	Mature forest
70	CAM07069S	3°33′50.9″N	9°46′30.7″E	19	Cameroon	Nsah	Mature forest
71	CAM07070S	3°33′48.2″N	9°46′30.6″E	19	Cameroon	Nsah	Mature forest
72	CAM07071S	3°33′36.3″N	9°46′28.9″E	15	Cameroon	Nsah	Mature forest
73	CAM07090S	3°21′17.8″N	13°32′22.3″E	710	Cameroon	Nkoul	Mature forest
74	CAM07091S	3°21′26.9″N	13°33′14.2″E	716	Cameroon	Nkoul	Mature forest
75	CAM07096S	3°49′17.4″N	13°19′1.9″E	668	Cameroon	Cyrie	Secondary forest
76	CAM07097S	3°49′17.9″N	13°19′10.4″E	678	Cameroon	Cyrie	Secondary forest
77	CAM07098S	3°49′18.8″N	13°19′23.8″E	684	Cameroon	Cyrie	Secondary forest

(continued on next page)

Table 1 (*continued*)

Site number	Samples	Latitude	Longitude	Altitude (m)	Country	Location	Local vegetation
78	CAM07099S	3°49′21.4″N	13°19′28.7″E	681	Cameroon	Cyrie	Secondary forest
80	CAM07087S	3°21′58.1″N	13°31′30.1″E	697	Cameroon	Nkoul	Mature forest
81	CAM07088S	3°21′56.2″N	13°31′29.6″E	699	Cameroon	Nkoul	Secondary forest
82	CAM07089S	3°21′42.3″N	13°31′36.8″E	697	Cameroon	Nkoul	Mature forest
83	CAM070108	4°23′1.1″N	11°43′36.2″E	516	Cameroon	Ndokoua	Savanna
84	CAM07004	3°59′4.1″N	12°16′58.4″E	693	Cameroon	Nyek	Savanna

4.1. Pollen diagrams

4.1.1. Savanna pollen spectra

As expected, all the pollen spectra from savannas are characterized by an abundance of herbaceous taxa (NAP, >60%) among which the Poaceae undiff., characteristic of open habitats, are dominant (60 to 90%) (Figs. 2 and 3). These Poaceae are locally associated with some Asteraceae undiff. (<5%), Amaranthaceae undiff. (<2%) and Cyperaceae undiff. (<3%). Among the arboreal pollen (AP), *Albizia*-type (5%), a forest pioneer and *Trema*-type *orientalis* (30%), a marker of disturbed forest, are found in significant frequencies in savanna from Cameroon, and *Pycnanthus angolensis*-type (10%), a marker of old secondary forest, in savanna from Gabon. Locally Pteridophyta are abundant (30% in sample 8).

4.1.2. Secondary forest pollen spectra

Pollen assemblages from secondary forest ecosystems are characterized by low frequencies of NAP (maximum of 20%) and high frequencies of AP (70–80%) (Fig. 3). Among the AP, characteristic taxa of secondary forest such as *Piptadeniastrum*-type *africanum* (maximum of 20%), *Phyllanthus*-type and *Zanthoxylum*-type (maximum of 30%) register their highest frequencies in these pollen samples. They are locally associated with numerous pollen of Combretaceae undiff., *Pentaclethra macrophylla*, and more regularly with some Flacourtiaceae undiff., Moraceae undiff., Euphorbiaceae undiff., Sapindaceae undiff., Mimosaceae undiff. and Caesalpiniaceae undiff. Some pioneer taxa are locally present such as *Macaranga*-type, *Alchornea* and *Bridelia micrantha*-type (Fig. 2). No fundamental difference occurs between pollen spectra from Gabon and those from Cameroon, except for the presence in significant frequencies of *Aucoumea klaineana* exclusively in Gabon and of *Lophira alata*-type exclusively in Cameroon.

4.1.3. Mature forest pollen spectra

The pollen assemblages in this group come from samples collected in the undisturbed "wet" rain forest, but also probably from old secondary forest which is often difficult to differentiate from the former due to their locally very similar floristic composition (White, 1983). In these assemblages arboreal pollen grains (AP) are always very abundant (more than 70%), typically with the presence of the Sapindaceae undiff., Mimosaceae undiff. and Caesalpiniaceae undiff. in higher frequencies than those recorded in secondary forest pollen spectra (Figs. 2 and 3). Pollen of Burseraceae undiff., *Canarium*-type, *Dacryodes*-type, the Meliaceae undiff., Sapotaceae undiff. and *Diospyros* are abundant in the forest of Gabon, whereas *Coula edulis, Ceiba pentandra* and *Lophira alata*-type are well represented in the forest of Cameroon. Some pollen markers of secondary forest are present, such as *Zanthoxylum*-type, but in very low frequencies. NAP are scarce particularly the Poaceae undiff. (<2%). Locally Cyperaceae (<10%) and Pteridophyta (<20%) are present.

4.1.4. Hygrophilous forest

Two types of hygrophilous forest have been sampled: (i) Riverine forests whose pollen assemblages are dominated by arboreal pollen grains of *Uapaca* (20%) and *Nauclea*-type (2-5%) associated locally with some *Celtis*, *Macaranga*-type, Apocynaceae undiff., Sapindaceae undiff. and Mimosaceae undiff. NAP are scarce with some Asteraceae undiff.; (ii) A swamp forest in which the pollen assemblage is dominated by the *Raphia* palm (>30%) with significant frequencies of Pteridophya (30%) and Poaceae undiff. (15%), the latter probably from aquatic species.

4.2. Numerical analyses

4.2.1. Numerical analysis of all samples

A first CA was performed on 80 pollen spectra and 121 pollen taxa (Fig. 4).The first CA axis shows a clear separation of pollen spectra from forest formations from those from savanna. The most important taxa in savanna samples were Poaceae undiff., *Albizia*-type and *Trema*-type *orientalis*. The significance of this axis might be related to the stature of the sampled vegetation communities: closed canopy *versus* open formation.

The third CA axis separates pollen spectra from the forest of Gabon where important taxa include Sapotaceae undiff., *Klaineanthus gaboniae*, *Diospyros*, *Dacryodes*-type, *Canarium*-type, Sapindaceae undiff., Rutaceae undiff. , and those from the forest of Cameroon with *Lophira alata*-type, *Coula edulis*, *Ceiba pentandra*, Bombacaceae undiff., *Heliotropium indicum*-type and the Boraginaceae undiff. Inside this latter group, pollen spectra from the Cameroon coastal evergreen forest (67 to 72) can be differentiated from those from inland semi-evergreen forest (Fig. 4a), due to the relative importance of *Lophira alata*-type and *Coula edulis*. An intermediate group of spectra is present between the Gabon forest group and the Cameroon one. It consists of a mixture of spectra from these two countries with as important taxa Burseraceae undiff., Meliaceae undiff., Amaranthaceae undiff., Mimosaceae undiff., Caesalpiniaceae undiff. and *Cola*. In each group, all forest types (secondary, mature and hygrophilous) are represented.

The interpretation of this axis is not easy. If a gradient of rainfall and seasonality could be proposed to separate two sub-groups inside the Cameroon pollen spectra group (coastal spectra representative of a forest area under high rainfall without dry season *versus* inland spectra representative of forest areas under less rainfall with a well defined dry season), such an interpretation cannot explain the difference between the Gabon and Cameroon forest inland spectra because at all pollen sites mean annual rainfall and dry season length are similar. However, we interpret this third CA axis in relation to particular features of the dry season ($P<50$ mm/month). In Gabon, pollen sites are located in areas of higher cloudy conditions, and so higher relative atmospheric humidity and lower potential evapotranspiration, during the dry season than the inland pollen sites from Cameroon (Leroux, 2001; FAO Web LocClim: http://www.fao.org/sd/locclim/srv/en/locclim.home). This feature is linked to monsoon influences from Gulf of Guinea in Gabon during June, July and August *versus* influences of continental trade winds (Harmattan) in Cameroon during December, January and February (Nicholson, 2000). Therefore, the relevance of this axis could be interpreted as a gradient of relative atmospheric humidity and of cloud cover during the dry season.

The only pollen spectrum from swamp forest is clearly separated from other samples due to a local high amount of *Raphia* pollen.

4.2.2. Numerical analysis of forest samples

This CA was performed on 72 samples and 121 pollen taxa excluding savanna spectra (Fig. 5). The second CA axis shows a clear

Table 2
List of identified taxa in the modern pollen spectra from Cameroon and Gabon (*Plant types*: H: herbs; T: trees; S: shrubs; L: lianas; P: palms; F: ferns)

Family	Taxa	Plant types	Vegetation types				
			sa	pif	sef	maf	swf
Acanthaceae	Acanthaceae undiff.	H/S/L	x	x	x	x	x
Amaranthaceae	Achyranthes-type aspera	H	x	x			
	Cyanthula-type	H	x	x	x	x	
	Amaranthaceae undiff.	H/L	x	x	x	x	x
Anacardiaceae	Anacardiaceae undiff.	S/T/L	x	x	x	x	x
	Lannea-type	S/T	x	x	x	x	
	Pseudospondias-type	S/T				x	x
	Trichoscypha-type	S/T/L				x	x
Apocynaceae	Apocynaceae undiff.	S/T/L	x	x	x	x	x
	Landolphia-type	L	x	x	x	x	x
	Rauvolfia	T			x	x	
Araliaceae	Polyscias fulva-type	T		x	x		
Asteraceae	Asteraceae undiff.	H/S	x				x
	Vernonieae undiff.	H/S/T	x	x	x		
Bombacaceae	Ceiba pentandra	T			x	x	
	Bombacaceae undiff.	T			x	x	x
Boraginaceae	Boraginaceae undiff.	H/S/T	x	x	x	x	
	Heliotropium indicum-type	H	x				
	Heliotropium steudneri-type	H	x				
Burseraceae	Aucoumea klaineana	T		x	x	x	
	Burseraceae undiff.	S/T	x		x	x	x
	Canarium-type	T			x	x	x
	Commiphora edulis-type	S/T	x				
	Dacryodes -type	T				x	x
Caesalpiniaceae	Anthonotha-type	T				x	x
	Caesalpiniaceae undiff.	S/T/L	x	x	x	x	x
	Copaifera-type	S/T				x	
	Detarium	T	x			x	
	Dialium	T	x			x	
	Gilbertiodendron-type	T				x	x
	Guibourtia demeusei-type	T				x	x
	Tessmania-type	T				x	
Capparidaceae	Capparidaceae undiff.	H/S/T/L	x	x	x	x	
Combretaceae	Combretaceae undiff.	S/T/L	x	x	x	x	x
	Terminalia-type	T	x		x	x	
Connaraceae	Cnestis	S/T/L		x	x	x	
Convolvulaceae	Convolvulaceae undiff.	H/L	x	x	x	x	x
Cucurbitaceae	Cucurbitaceae undiff.	H/L	x	x	x	x	
Cyperaceae	Cyperaceae undiff.	H/L	x	x	x		x
Dilleniaceae	Tetracera	S/L		x	x	x	x
Dracaenaceae	Dracaena	S/T	x	x	x	x	x
Ebenaceae	Diospyros	S/T				x	
Euphorbiaceae	Alchornea	S/T		x	x	x	x
	Anthostema-type	T				x	x
	Antidesma-type	S/T	x	x	x	x	x
	Bridelia micrantha-type	S/T	x	x	x	x	
	Discoglypremna caloneura	T			x	x	
	Drypetes-type	S/T				x	
	Euphorbia-type	H	x	x			
	Euphorbiaceae undiff.	H/S/T	x	x	x	x	x
	Klaineanthus gaboniae	T				x	x
	Macaranga-type	S/T		x	x	x	x
	Mallotus-type oppositifolius	S/T		x	x	x	
	Margaritaria discoidea	S/T		x	x	x	
	Martretia quadricornis	T				x	x
	Phyllanthus-type	H/S/T	x	x	x	x	x
	Plagiostyles-type africana	T			x	x	
	Tetrochidium	S/T		x	x	x	
	Uapaca	S/T			x	x	x
Fabaceae	Indigofera	H/S	x				
Flacourtiaceae	Caloncoba-type	S/T	x	x	x	x	x
	Flacourtiaceae undiff.	S/T	x	x	x	x	x
	Scottelia klaineana-type	T			x	x	
Hymenocardiaceae	Hymenocardia	S/T	x	x	x	x	
Hypericaceae	Vismia guineensis	S/T		x	x		x
Irvingiaceae	Irvingia-type gabonensis	T			x	x	x
Lamiaceae	Lamiaceae undiff.	H/S	x	x			
Loganiaceae	Anthocleista	T	x	x	x		x
Melastomataceae	Melastomataceae undiff.	H/S/T	x	x	x	x	x
Meliaceae	Khaya-type	T			x	x	
	Meliaceae undiff.	S/T		x	x	x	
	Trichilia-type	T			x	x	
Mimosaceae	Albizia-type	T	x	x	x		
	Calpocalyx-type letestui	T				x	
	Mimosaceae undiff.	T/L	x	x	x	x	x
	Pentaclethra macrophylla	T			x	x	x
	Piptadeniastrum-type africanum	T			x	x	
	Tetrapleura tetraptera-type	T		x	x	x	
Moraceae	Ficus	S/T	x	x	x	x	x
	Moraceae undiff.	S/T	x	x	x	x	x
	Musanga-type	T		x	x		
Myristicaceae	Pycnanthus angolensis-type	T			x	x	x
Myrtaceae	Syzygium-type	S/T	x	x	x	x	x
Ochnaceae	Lophira alata-type	T		x	x	x	x
Olacaceae	Coula edulis	T				x	
	Heisteria	S/T				x	
	Olax	S/T				x	x
	Strombosia	T				x	x
Palmae	Elaeis guineensis	P		x	x		
	Raphia	P					x
Poaceae	Poaceae undiff.	H	x	x			
Rubiaceae	Crossopteryx febrifuga	S/T	x	x			
	Hallea-type	T				x	x
	Keetia-type gueinzii	S/L	x			x	
	Morelia senegalensis	S/T	x				
	Morinda	S/T	x			x	
	Nauclea-type	T	x	x	x	x	x
	Pausinystalia-type macroceras	T				x	
	Rubiaceae undiff.	H/S/T	x	x	x	x	x
Rutaceae	Rutaceae undiff.	S/T		x	x	x	
	Zanthoxylum-type	S/T/L		x	x	x	
Sapindaceae	Allophylus	S/T/L	x	x	x	x	
	Aphania-type senegalensis	T				x	x
	Blighia	S/T	x			x	
	Dodonaea	S/T	x	x			
	Ganophyllum-type giganteum	T				x	
	Lecaniodiscus-type	S/T				x	x
	Sapindaceae undiff.	S/T/L	x	x	x	x	x
Sapotaceae	Sapotaceae undiff.	S/T				x	x
Sterculiaceae	Cola cordifolia-type	T			x		
	Mansonia altissima-type	T				x	
	Sterculia-type	T	x	x	x	x	x
	Sterculiaceae undiff.	S/T	x	x	x	x	x
Ulmaceae	Celtis	S/T			x	x	
	Chaetacme aristata	S/T		x	x	x	
	Holoptelea grandis	T			x	x	
	Trema-type orientalis	S/T		x	x	x	
	Ulmaceae undiff.	S/T		x	x	x	
Verbenaceae	Vitex-type	S/T/L	x	x	x	x	
Pterodophyta	Monoletes undiff.	F	x	x	x	x	x
	Triletes undiff.	F	x	x	x	x	x

Vegetation types: sa: savanna; pif: forest pioneer; sef: secondary forest; maf: mature forest; swf: swamp forest.

opposition between pollen spectra from forest on well-drained soils and those from hygrophilous forested formations (riverine forest), the latter having as highest contributor taxa *Uapaca* and *Macaranga*-type. The relevance of this axis might be related to local hygromorphic soil conditions, with a contrast between dry and humid edaphic environments. Such a feature was previously identified in pollen samples from forest regions of Congo (Elenga et al., 2000b).

The third CA axis shows a difference between a majority of pollen spectra from forests of secondary type, with as important taxa: *Tetrorchidium*, *Phyllanthus*-type, *Tetracera*, *Morelia senegalensis*, *Aucoumea klaineana* (exclusively found in Gabon), *Bridelia*, *Zanthoxylum*-type and Flacourtiaceae undiff., and a majority of spectra from mature forests, where Caesalpinaceae undiff., Apocynaceae undiff., Mimosaceae undiff., Sapindaceae undiff., Burseraceae undiff. and *Ceiba pentandra* are important. There is no differentiation between samples from Gabon or Cameroon forests. This axis might be an indication of the arboreal strata

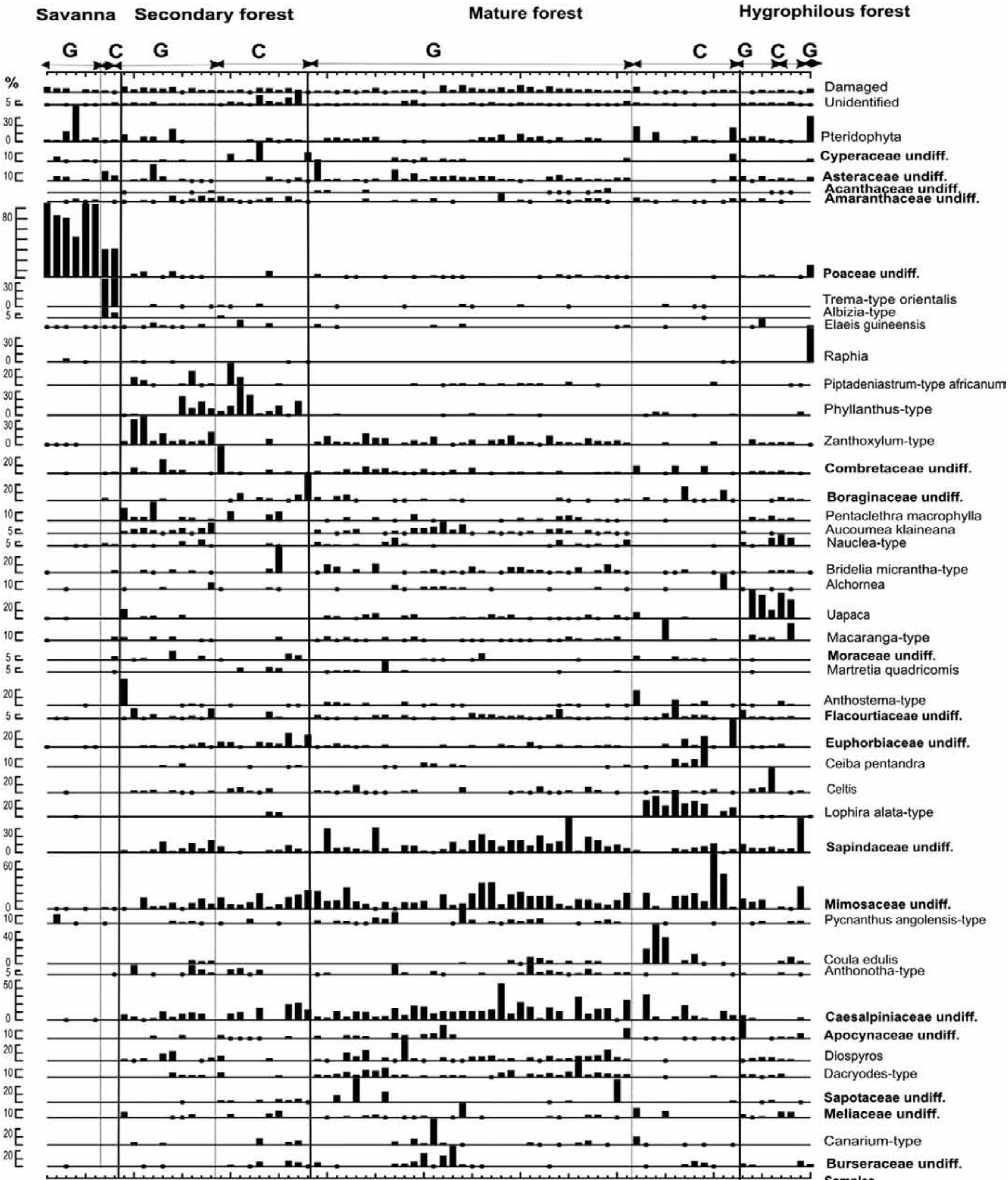

Fig. 2. Pollen diagram of modern spectra from Gabon and Cameroon showing histograms of percentages of the pollen taxa present in frequencies >1%. The pollen spectra have been grouped according to the local vegetation types as defined in the field, then, inside each group, a differentiation between the samples from Gabon (G) and from Cameroon (C) has been made. Data are expressed as pollen percentages of a sum excluding damaged grains.

stature of the two sampled forested communities: a low structured stature with many light-demanding dominants *versus* a densely structured stature with a high and closed canopy. Therefore, this axis may reflect the state of maturity of the two different forest types, a mature one *versus* a younger and regenerating one.

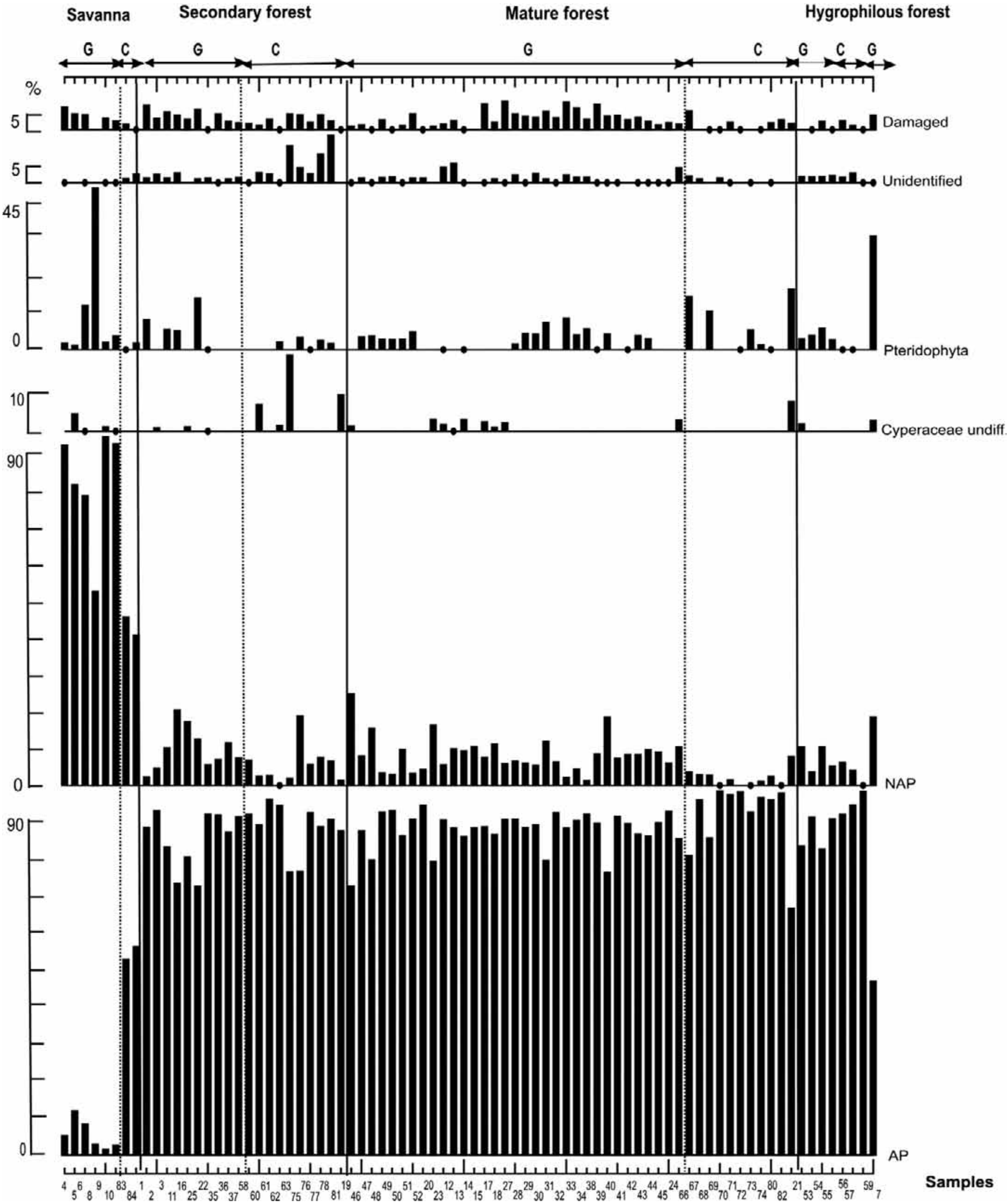

Fig. 3. Synthetic diagram of modern surface soil and litter pollen spectra from Gabon and Cameroon, showing the main groups of taxa amalgamated according to the plant types.

One pollen spectrum from secondary forest is found inside the mature forest group (77) and conversely (18 and 20). Also,, one spectrum from riverine forest (59) is found in the mature forest group (Fig. 5a). This could be explained by an erroneous definition of the sampled vegetation type at these sites since old secondary forest is not always easy to differentiate from mature forest.

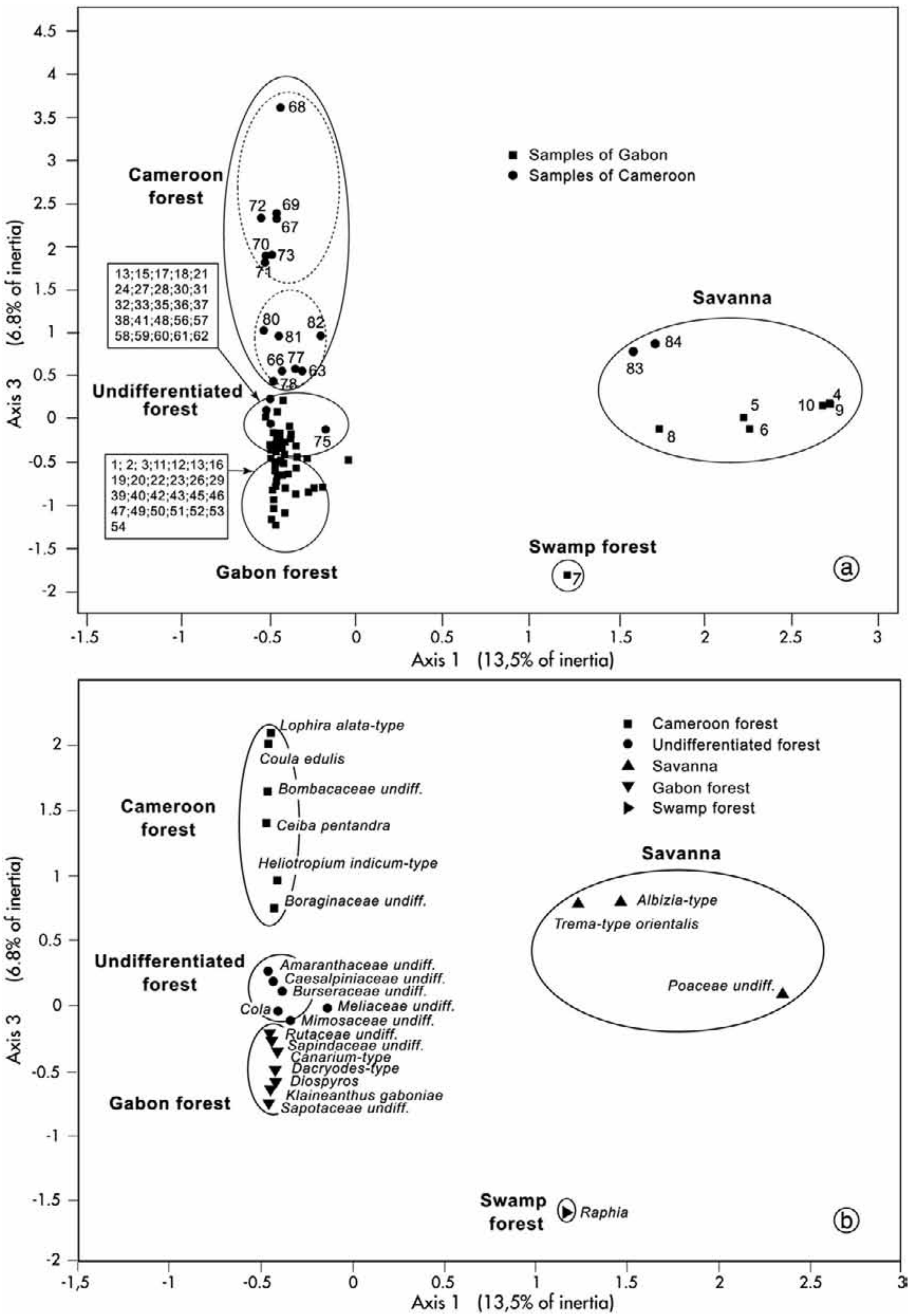

Fig. 4. Correspondence analysis with respect to CA axes 1 and 3: (a) of all modern pollen spectra (80); (b) showing the most abundant pollen taxa identified in all modern spectra.

Moreover, some spectra appear to be poorly ordinated. Such a position can be explained by the presence in the pollen assemblages of dominant taxa not present in the other assemblages or only in very low percentages: *Anthostema*-type in the sample 1, *Canarium*-type in the sample 14, Cyperaceae undiff. in the sample 63, *Coula edulis* in the samples 68 and 69, and Boraginaceae undiff. in the sample 81. But no explanation can be given for the mature forest spectra 50.

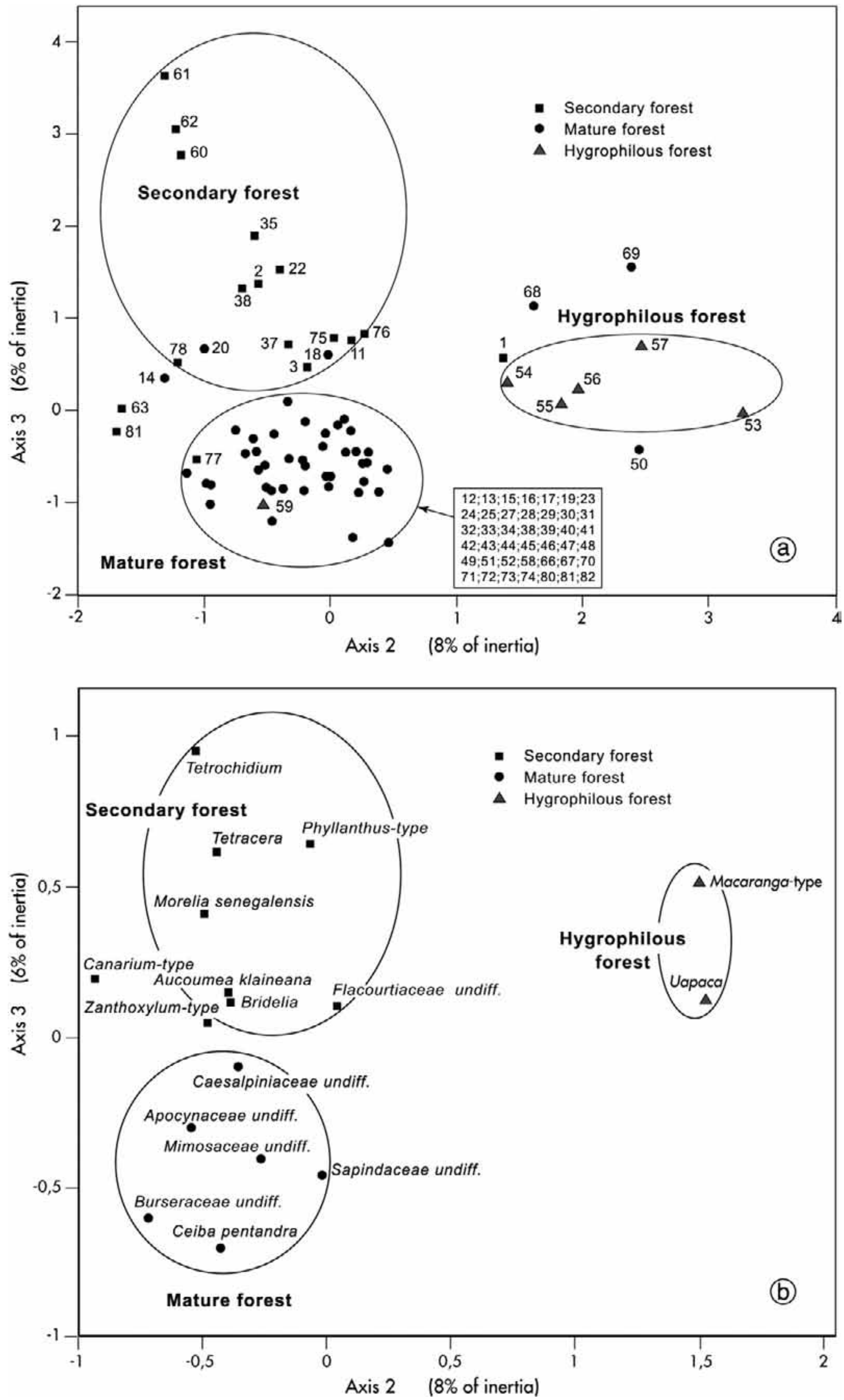

Fig. 5. Correspondence analysis with respect to CA axes 2 and 3: (a) of the modern pollen spectra from forest vegetation (72); (b) showing the most abundant pollen taxa identified in the modern spectra from forest vegetation.

5. Conclusions

The new modern pollen data set presented in this paper complements the data today available and published in Central Atlantic Africa, particularly concerning forested environments, covering a larger sampled area compared to the scarce sites previously investigated (Makokou and Belinga, Gabon, Jolly et al., 1996; Mayombe massif, Congo, Elenga et al., 2000b; Kandara, Cameroon, Vincens et al., 2000).

This work shows that major vegetation types occurring today in Cameroon and Gabon can be differentiated qualitatively (pollen diagrams) and numerically (using Correspondence Analysis) by the values of their pollen percentages. The savanna is easily identified by high frequencies of non-arboreal taxa, mainly the Poaceae undiff., and the forests by high arboreal taxa, a feature now well known in many regions of Africa (i.e. Vincens et al., 1997; Lézine et al., submitted). In addition, secondary and mature forests can be differentiated, as well as forest on well drained soils and hygrophilous ones on the basis of the presence of pollen markers of these vegetation types. In that way, pollen analysis appears to be a more robust and precise method to discriminate the maturity, structure and floristic composition of Central Atlantic African forests compared to other methods such as phytoliths analysis (Bremond et al., 2005), isotopic analysis (Guillet et al., 2001) or Leaf Area Index (Cournac et al., 2002) whose results are interpreted essentially in terms of tree cover density of the vegetation (forest *versus* grassland).

Our study suggests that in the Guineo-Congolian region, in forested areas with similar mean annual rainfall and dry season length, the cloud cover and therefore the relative atmospheric humidity during the dry season could play a prominent part in the phenology of plants and thus in the floristic composition of the forests north and south of the meteorological equator. This hypothesis may be confirmed using statistical analysis on a larger pollen data set including all available Central African modern pollen data.

Finally, this work was focused on the study of modern pollen rain in ecosystems that appear little disturbed by man. Future palynological research should be extended to include recently disturbed habitats such as croplands or regrowths in anthropogenic clearings, preferentially along transects across areas of varying degree of human disturbance to find, if possible, pioneer and anthropogenic pollen markers.

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