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Research article

Notes on cauliflory, sexual dimorphism and biogeography in *Drypetes* (Putranjivaceae, Malpighiales) and a taxonomic treatment for *D. gabonensis* and two new cauliflorous threatened species from Central Africa, *D. aphanes* sp. nov. and *D. cauta* sp. nov.

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Abstract. We present a preliminary discussion about cauliflory, sexual dimorphism and biogeographic patterns in *Drypetes* Vahl (Putranjivaceae Endl.), focused on Africa. We also present a taxonomic treatment for two new species of cauliflorous trees of this genus from the rainforests of western Central Africa, one endemic to Gabon and known from six gatherings, *D. aphanes* Quintanar, D.J.Harris & Barberá sp. nov., and the other distributed in Gabon and the Republic of the Congo, *D. cauta* D.J.Harris, Barberá & Quintanar sp. nov., also known from another six gatherings. They are presented along with *D. gabonensis* Pierre ex Hutch., known from 25 gatherings made throughout western Central Africa, a species with markedly dimorphic flowers between sexes compared to the rest of the species in the genus. Specimens of these two new species have been confused with *D. gabonensis* due to some morphological resemblances. This treatment includes the detailed descriptions of these three species, the typification of their names, a comparative table summarizing their main morphological differences, an identification key, an illustration and information about their habitat and distribution. A provisional IUCN Red List assessment shows that *D. gabonensis* and *D. cauta* sp. nov. are ‘Vulnerable’ species, and *D. aphanes* sp. nov. is ‘Endangered’. After the publication of these new species, *Drypetes* consists of 86 species in continental Africa and the Malagasy Region and 219 species for the whole world.

Keywords. Conservation, dioecy, Gabon, plant sexuality, Republic of the Congo, trunciflory.

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Introduction

Drypetes Vahl (Putranjivaceae Endl., Malpighiales) is a diverse pantropical genus of almost completely dioecious shrubs and trees, typically inhabitants of the understorey and the medium-low canopy of more or less humid, tropical and subtropical lowland forest formations. Some species also occur in woodland and savannah, as well as tropical montane forests and warm temperate areas. We currently recognise 217 species, of which 84 are known from continental Africa and the Malagasy Region after the description in recent years of several new species (Quintanar *et al.* 2020, 2021a, 2021b, 2022, 2023; Cheek *et al.* 2021). Putranjivaceae, consisting of *Drypetes* and the small Asiatic genus *Putranjiva* Wall. (4 spp.), is one of the 34 species-rich dioecious groups that represent 43% of all dioecious angiosperms (Renner 2014). The relatively high number of species classified in *Drypetes* seems to disprove the idea that dioecy is detrimental for species survival in plants (cf. Heilbuth 2000). This idea has been questioned in recent years (Käfer *et al.* 2014; Renner 2014; Muyle *et al.* 2020). Even though dioecy is by far the most common sexual system in *Drypetes*, both polygamo-dioecy and strict monoecy occur occasionally: unisexual and hermaphrodite flowers on the same plant were reported for *D. bipindensis* (Pax) Hutch. from Central Africa by Radcliffe-Smith (1987); only hermaphrodite flowers were reported for *D. subcubica* var. *hermaphrodita* Airy Shaw from Indonesia by Airy Shaw (1974), and both male and female unisexual flowers were noted on the same plant for both *D. comorensis* (Baill.) Pax & K. Hoffm from Comoros by Pax & Hoffmann (1922) and *D. usambarica* (Pax) Hutch. from East Africa by Radcliffe-Smith (1995). *Drypetes* can often be recognized in the field by its simple, alternate, rarely opposite, spirally arranged but sometimes appearing distichous, stipulate, petiolate and penninerved leaves without glands, leaf blades oblique to unequal-sided at the base, unisexual flowers, as well as often orthotropic trunks, plagiotropic branches and a more or less intense chemical smell, sometimes reminiscent of horseradish, that is often noticed in the cut bark of many but not all species. This smell is due to the sulphur-containing end products of the glucosinolate biochemical pathway. Relatively frequently, as it is recorded on herbarium labels, the flowers themselves also give off a smell, sometimes extremely pungent or even sickly sweet, that frequently reveals the presence of these plants. The flowers, more or less small and inconspicuous, are frequently found in the forest canopy up to 30 m in height, which can slow down the location and identification of *Drypetes* trees (Quintanar *et al.* 2021a). These flowers are apetalous and bear a nectariferous disk that in the male ones is surrounded or penetrated by stamens; likewise female flowers also bear a disk, typically cupulate or annular and more or less thick, and sessile or shortly stalked stigmas that may or may not remain on a single-to many-seeded drupe-like fruit. Flowers, and later fruits, of *Drypetes* appear solitary or clustered on the plant (much more rarely forming cymes), and are arranged on leafy or leafless axils along the branchlets and branches, older branches or main trunk. When on the main trunk, the flowers are typically crowded on fairly sturdy cushion-like excrescences of the bark. The inflorescences are habitually long-living and originate new flowers during the season every year.

Accurate information on the placement of the inflorescences of both sexes in *Drypetes* is often poor or lacking in the published descriptions of many species and many protologues are based on only one sex of flower or fruiting specimens. Inflorescence position is a taxonomically important character (cf. Radcliffe-Smith 1987, 1995) that shows variation between species and sometimes between sexes. Despite this information gap, only partially covered by our own observations of the available specimens and in the field, we recognize the following categories of inflorescences or flowers (if these are solitary) regarding their positions on the plant, here described in order from the base of the tree to the distal twigs: I) Inflorescences trunciflorous (Fig. 1c–d, f). We use this term to refer to inflorescences that occur on the main trunk of a tree. This position is often referred to as cauliflorous in tropical tree species, however this term refers to stems rather than trunks and occasionally it has been used for inflorescences on main branches, both in herbarium label descriptions and in literature (e.g., Radcliffe-Smith 1987). II) Inflorescences on main branches (Fig. 1e). This case could be referred to as ramiflorous, but we

choose not to use this term for flowers on the main branches because it could easily be used to refer to flowering on any branches. III) Inflorescences or flowers axillary on leafless branches (Fig. 1b, g). They occur on branches which have recently lost their leaves, on which the flowers are inserted in what were the axils of the fallen leaves. IV) Inflorescences or flowers axillary on leafy branches (Fig. 1a). We have observed or noted from the labels that mainly trunciflorous species can occasionally have flowers on the main branches. In those cases, we have described the species as “mainly trunciflorous and occasionally with flowers on the main branches” (categories I–II). The separation between flowers on main branches (category II) may overlap with flowers axillary on leafless branches (category III); however, those branches are very rarely the main branches in individual *Drypetes* trees that we have studied. The overlap between the last two categories is commoner, because the falling of the leaves results in a change from category IV to III.

The degree of sexual dimorphism in the flowers of *Drypetes* is usually very slight apart from the differences due to the absence or presence of male and female organs in unisexual flowers. In most species male and female flowers usually have similar dimensions, presentation and arrangement on the plant. There are, however, species whose dimorphism goes further and exhibit quite unequal flowers between sexes or even different locations of the inflorescences. During the preparation of the treatment of *Drypetes* for *Flore du Gabon* (Harris *et al.* 2021), we studied one of these sexually dimorphic species, *D. gabonensis* Pierre ex Hutch. This is a medium-sized or large tree up to 30(–35) m high which lives in the rainforests of western Central Africa and was classified in *D.* sect. *Oligandrae* Pax & K.Hoffm. in the monographic treatment of the genus published in *Das Pflanzenreich* (Pax & Hoffmann 1922), a section characterized by a low number of stamens, stigmas placed on short styles, 2–4-celled ovaries and deciduous stipules. Most of the representatives of this section bear different-sex flowers of similar sizes and small, 2-celled fruits. However, male flowers of *D. gabonensis* are noticeably much smaller and more gracile than the female ones. These male flowers also have slender pedicels and bear very few stamens and narrowly oval to oblong sepals, while female flowers have much more robust pedicels and bear larger, ovate to suborbiculate, sepals, as well as a 3(–4)-celled ovary. In addition, the position on the plant of the inflorescences of *D. gabonensis* also present differences related to their sex: male inflorescences are axillary on leafy or leafless branches (categories III and IV), while female ones are on leafless branches (category III) and eventually on older branches (category II), whereas most of the species of *D.* sect. *Oligandrae* have inflorescences of categories III–IV in both sexes.

Associated with the specimens of *D. gabonensis* in several herbaria, perhaps due to their overall similarity of the leaves and the female flowers and fruits, we found specimens that represent two different and new species of *Drypetes*, which we have named *D. aphanes* Quintanar, D.J.Harris & Barberá sp. nov. (endemic to Gabon) and *D. cauta* D.J.Harris, Barberá & Quintanar sp. nov. (Gabon and Republic of the Congo). These are two smaller species of tree with glabrous and mostly roundish, 3-celled ovaries similar to those of *D. gabonensis*, but without the special degree of floral dimorphism found in the latter. The inflorescences of the two new species are mostly found on cushion-like excrescences of the trunk bark and therefore belong to the category I. The general morphology of both species, particularly their deciduous stipules, numerous stamens surrounding the male disk, three-locular smooth ovaries and sessile or subsessile stigmas, makes it advisable to classify them in *D.* sect. *Sphragidia* (Thwaites) Pax & K.Hoffm. instead of *D.* sect. *Oligandrae*. Many of the representatives of *D.* sect. *Sphragidia* show plate-like flowers, grouped in crowded, many-flowered inflorescences (categories I and II), and bear 4–5(–6) sepals, the male ones with a quite high number of stamens. In these ways they also resemble those of *D. aphanes* and *D. cauta*. We present here complete morphological descriptions of *D. gabonensis*, *D. aphanes* and *D. cauta*, the typification and etymology of their names, diagnoses for the new species, illustrations that show their morphology, a table in which we summarize the main diagnostic characters, an identification key, a distribution map, lists of studied material, provisional IUCN Red List assessments, and all available information about their habitat and distribution.

Table 1 (continued on next page). Summary of diagnostic characters useful to distinguish *Drypetes gabonensis* Pierre ex Hutch., *D. aphanes* Quintanar, D.J.Harris & Barberá sp. nov. and *D. cauta* D.J.Harris, Barberá & Quintanar sp. nov.

	<i>D. gabonensis</i>	<i>D. aphanes</i>	<i>D. cauta</i>
Vegetative characters			
Bud scale (mm)	2–2.4 × ca 0.5	1.2–1.4 × 1–1.6	1.3–1.7 × 2.1–2.7
Bud scale shape	narrowly triangular	widely ovate	ovate-suborbicular
Bud scale indumentum	densely puberulous, not ciliate	glabrous, not ciliate	glabrous, minutely ciliate
Indumentum of young branchlets	glabrescent	glabrous	glabrous
Petiole length (mm)	(4.2–)7.7–9.6(–13.1)	(5.3–)7–8.1(–8.6)	(3.4–)5.8–7(–7.5)
Petiole surface	smooth, coarsely wrinkled and bullate when old	wrinkled, drying light-coloured	wrinkled, drying dark-coloured or blackish
Leaf blade base	markedly asymmetrical, rounded on one side, less often oblique	oblique	oblique
Leaf blade margin	subentire to shallowly and obscurely crenulate-serrulate	obscurely and shallowly crenulate-serrulate	obscurely and shallowly crenulate-serrulate
Leaf blade upperside	glossy	lustreless	lustreless
Angles of first order lateral veins to midrib	58–74°	(54–)58–81°	45–60°
First order lateral veins looping	near the margin	well within the margin	near the margin
Second order venation	slightly raised above and beneath	hardly raised above and very slightly beneath	slightly raised above and beneath
Males, reproductive characters			
Inflorescence category (disposition)	III–IV	I	I
Pedicel, length and diameter (mm)	(2.1–)4–5.3(–6.6) × 0.1–0.2	3.8–4.3(–5.2) × (0.6–)0.9–1.2(–1.4)	3.6–7.7 × 0.3–0.8
Sepals, number	(3–)4(–5)	5	5
Sepals, shape	ovate to slightly oblong, slightly cucullate towards the apex	widely ovate to slightly obovate, slightly cucullate	widely ovate, cucullate
Sepals, indumentum of outer surface	minutely and sparingly pubescent	glabrous	glabrous
Sepals, dimensions (mm)	(1.2–)1.9–2.3(–2.9) × (0.3–)1–1.8	(3.9–)4.4–5.2(–5.6) × (4.3–)4.6–5.2(–6.5)	4.2–5.3 × 4.1–4.7
Disk, diameter (mm)	(0.3–)0.5–0.8(–1.2)	3.4–4.6	3.1–3.3
Disk, characteristics	concave, cupular, thin, smooth, margin slightly lobed, glabrous, with a central conical projection to 0.1 mm, often absent	convex, very rugose	convex, strongly plicate

Table 1 (continued). Summary of diagnostic characters useful to distinguish *Drypetes gabonensis* Pierre ex Hutch., *D. aphanes* Quintanar, D.J.Harris & Barberá sp. nov. and *D. cauta* D.J.Harris, Barberá & Quintanar sp. nov.

	<i>D. gabonensis</i>	<i>D. aphanes</i>	<i>D. cauta</i>
Stamens, arrangement	one-whorled, surrounding the disk and hardly entangled by the disk marginal lobes	apparently one-whorled surrounding the disk, more or less entangled by the disk marginal lobes	obscurely whorled, mainly surrounding the disk, entangled by the disk marginal lobes, some penetrating
Stamens, number	3	(11–)14–15	16–17
Females, reproductive characters			
Inflorescence category (disposition)	II–III	I (–II)	I
Pedicele, length and diameter (mm)	1.9–3.2 × 0.9–1	2.9–3.2 × 1–1.1	7.5–10.9 × 0.7–0.9
Sepals, dimensions (mm)	2.9–3.9 × 2.5–3.1	3.4–4.1 × 3.9–4	4.1–4.7 × 4.2–4.8
Disk, diameter (mm)	2.8–3.3	3–3.2	4.1–4.3
Style, length (mm)	0.6–1.1	to 0.1 mm	0.4–0.6
Style, branching	3(–4)-branched	unbranched	unbranched
Stigma, shape	spathulate to obdeltoid	obdeltoid	obdeltoid
Fruiting pedicel, length (mm)	2–4.6(–8) × 2.3–2.5	(6.7–)9–12.6(–13) × 1.3–2.3(–2.9)	11.3–12.2 × 0.8–1.1
Fruit, length and diameter (mm)	19–20.7(–30) × 20–23.4(–30)	(18.2–)18.8–22.6 × (15.7–)18–23.1(–23.4)	15–16.8 × 12.1–15.4
Fruit, shape	subglobose	subglobose	widely elliptic
Fruit, surface	uneven	uneven	even

Material and methods

Classical methods of herbarium taxonomy were followed. The descriptions presented here, as well as all the information about the habitat and distribution, are based on the revision of 25 gatherings of *D. gabonensis*, six of *D. aphanes* sp. nov. and six of *D. cauta* sp. nov. (see the list of associated specimens in the taxonomic treatment, below each species) from the following herbaria: BM, BR, BRLU, COI, IEC, K, LBV, LISC, LISU, M, MA, MO, PRE, WAG and YA (Thiers 2020, continuously updated), all of them collected in Central Africa (abbreviations: fl., flowering specimen; fr., fruiting specimen; veg., vegetative specimen). Measurements were carried out using a Mitutoyo CD-15CD digital caliper and a manual scale with precision of 0.1 mm to record quantitative morphological characters, to build up the new species' description, and for comparative purposes as well. The descriptive terminology follows that used in Stearn (1973), Harris & Harris (1994), and Pole (1991) for venation. Most of the specimens included in this work have been studied in situ by the authors; in for those that could not be examined we add “n.v.”, i.e., non vidi. Table 1 introduces the main diagnostic characters to distinguish *D. gabonensis* from *D. aphanes* and *D. cauta* and supplements the information offered in our taxonomic notes. Table 2 shows the number of African species of *Drypetes* by inflorescence category (see Introduction), as well as an alphabetical list of the species with either male or female inflorescences attributable to categories I and II. Table 3 accounts for the total number of *Drypetes* species of the world accepted to date by us, alphabetically listed and grouped according to their distribution in geographical areas. The compilation of the American and Asian species has followed *Plants of the World Online* (<http://www.plantsoftheworldonline.org/>; cf. Govaerts R.H.A. World Checklist of Selected Plant Families Database in ACCESS: 1 -216203. The Board of Trustees of

the Royal Botanic Gardens, Kew). Figure 1 is made of photographs that show different placements of the inflorescences in some African species of *Drypetes* and their corresponding categories. Figure 2 shows the morphology of *D. gabonensis* and is a modification of an original engraving by E. Delpy in 1908 that is preserved in the herbarium P and that we previously used to illustrate the species in *Flore du Gabon*. A new original plate, Figure 3, has likewise been drawn to illustrate the morphology of the new species. The information about the habitat of the involved species, as well as their phenology, and chorology is based on collection data from herbarium labels. Geographical data were used to construct Figure 4, a distribution map for all the studied species with ArcView GIS ver. 3.2 for Windows (ESRI 2000). The coordinates that were not indicated on herbarium labels were determined a posteriori and are presented here between square brackets. A preliminary assessment of conservation status using the IUCN categories and criteria (IUCN Standards and Petitions Committee 2022) is provided for all of them as well. The geographical parameters of Area of Occupancy (AOO), estimated using a 2 × 2 km grid, and Extent of Occurrence (EOO), were calculated using GeoCAT (Bachman *et al.* 2011).

Results

Taxonomy

Order Malpighiales Juss. ex Bercht. & J.Presl
Family Putranjivaceae Endl.
Genus *Drypetes* Vahl

Drypetes sect. *Oligandrae* Pax & K.Hoffm.

Das Pflanzenreich 147, 15 (Heft 81): 234, 251 (Pax & Hoffmann 1922) – Type: not designated.

Drypetes gabonensis Pierre ex Hutch.

Fig. 2

Flora of tropical Africa 6 (1): 680 (Hutchinson 1912). – Type: GABON • [Estuaire, environs de Libreville]; [0°25'N 9°27'E]; 18 Jul. 1898; *T.J. Klaine 1278*; fr.; lectotype, here designated: P[P04707398]; isoelectotypes: BR[BR0000006238124, BR0000006238452, BR0000006238780 (BR-S.P. 623 878)], K[K000406326], P[P04707401].

Etymology

The specific epithet is the Neolatin adjective ‘*gabonensis*’, which refers to Gabon, the country in which the first gatherings of this species were made and therefore from which it was originally known.

Material examined

ANGOLA – **Cabinda** • Along the river Lufo, Hombe region, Maiombe, area de Belize; [4°46' S, 12°36' E]; Mar. 1919; *J. Gossweiler 8227*; fl. ♂; BM, BR[BR0000015778390, BR0000015778406, BR0000015778413], COI[COI00033993], K, LISC[LISC053291, LISC053294], LISU[LISU 60111, LISU 60112] • Near Caio, Hombe region, Rio Lufo; [4°46' S, 12°36' E]; 26 Feb. 1919; *J. Gossweiler 7859*; fl. ♂; BM, COI[COI00033992], LISC[LISC053287, LISC053306, LISC053307, LISC053308], LISU[LISU 60106, LISU 60113] • Near the village Caio, Hombe region, Río Lufo, Maiombe; [4°46'S12°36'E] 8 Apr. 1919; *J. Gossweiler 7985*; fr.; BM, COI[COI00033990], LISU[LISU 60109, LISU 60108] • Río Lufo, Caio, Hombe region, Maiombe; [4°46' S, 12°36' E]; 27 Mar. 1919; *J. Gossweiler 7956*; fl. ♂; BM, COI[COI00033991], LISC[LISC053298, LISC053299, LISC0532301,

Table 2. Species number of *Drypetes* Vahl in Africa and the Malagasy region according to their inflorescence category and sex.

Category range	I	I-II	II	II-III	II-IV	III	III-IV	IV	Unknown
Males	5	10	3	0	3	0	48	13	3
Females	6	9	3	2	2	3	45	11	4
Category I	<i>D. aphanes</i> Quintanar, D.J.Harris & Barberá sp. nov., <i>D. cauta</i> D.J.Harris, Barberá & Quintanar sp. nov., <i>D. preussii</i> (Pax) Hutch., <i>D. staudtii</i> (Pax) Hutch., <i>D. stipularis</i> (Müll. Arg.) Hutch. (♀), <i>D. verrucosa</i> Pierre ex Hutch.								
Categories I-II	<i>D. afzelii</i> (Pax) Hutch., <i>D. comorensis</i> (Baill.) Pax & K. Hoffm., <i>D. floribunda</i> (Müll. Arg.) Hutch., <i>D. ivorensis</i> Hutch. & Dalziel, <i>D. natalensis</i> (Harv.) Hutch., <i>D. polyantha</i> Pax & K.Hoffm., <i>D. stevartii</i> Sonké & Quintanar, <i>D. stipularis</i> (Müll.Arg.) Hutch. (♂), <i>D. ugandensis</i> (Rendle) Hutch., <i>D. usambarica</i> (Pax) Hutch.								
Category II	<i>D. bathiei</i> Capuron & Leandri, <i>D. obanensis</i> S.Moore (♂), <i>D. spinosodentata</i> (Pax) Hutch., <i>D. stipulacea</i> Leandri (♀)								
Categories II-III	<i>D. gabonensis</i> Pierre ex Hutch. (♀), <i>D. gossweileri</i> S.Moore (♀)								
Categories II-IV	<i>D. capuronii</i> Leandri, <i>D. gossweileri</i> S.Moore (♂), <i>D. pleioneura</i> (Radel.-Sm.) Christenh. & Byng								

LISC0532302, LISC0532305], LISU[LISU 60107, LISU 60110] • Portuguese Maiombe, Chiloango; [5°1'S, 12°25'E]; 1919; *J. Gossweiler s.n.*; fl. ♂; K.

CAMEROON – **East Region** • Bertoua, near catholic mission; [4°35'N, 13°40'E]; 15 Dec. 1960; *F.J. Breteler* 829; fl. ♂; A n.v., BR[BR0000015788429], BRLU[BRLU0000145], FI n.v., K, M[M 257127], P[P04707288], WAG[WAG.1563830, WAG.1563831], YA[YA 29609] • Bertoua, near catholic mission; [4°35'N, 13°40'E]; 7 Sep. 1961; *F.J. Breteler* 1897; fr.; BRLU[BRLU0000144], WAG[WAG.1563827, WAG.1563829, WAG.1563828]. – **South Region** • About 7 km NE of Ebom, plot 19, subplot 47, tree 2; 3°7' N, 10°45' E; Aug. 1996; *M.P.E. Parren* 268; veg.; KRIBI, WAG[WAG.1564719] • ibid., plot 19, subplot 59, tree 5; 3°7' N, 10°45' E; Aug. 1996; *M.P.E. Parren* 277; veg.; KRIBI, WAG[WAG.1564749, WAG.1564750] • ibid., plot 9, subplot 69, tree 5; 3°7' N, 10°45' E; Aug. 1996; *M.P.E. Parren* 122; veg.; KRIBI, WAG[WAG.1564714, WAG.1564715, WAG.1255335] • ibid., plot 9, subplot 89, tree 5; 3°7' N, 10°45' E; Aug. 1996; *M.P.E. Parren* 141; veg.; KRIBI, WAG[WAG.1564712, WAG.1564713] • Ebolowa-Jaunde [südl. des Njong, Amugebane-Nkolemajang]; [3°15' N, 10°59' E]; Jan. 1914; *G.W.J. Mildbraed* 7672; fl. ♂; BR[BR0000015785268, BR0000006576394 (BR-S.P. 657 639)], K[K000406365].

EQUATORIAL GUINEA – **Centro-Sur** • Parc National de Monte Alén, transect de Monte Chocolate; 1°39'N10°19'E; 14 Jul. 1995; *J. Lejoly* 95T/L3.647; veg.; BRLU.

GABON – **Estuaire** • *T.J. Klaine* 1278 (type, see above) • Environs de Libreville; [0°25'N9°27'E]; Jul. 1897; *T.J. Klaine* 690; fr.; BM, P[P04707286, P04707289], WAG n.v.) • Environs de Libreville; [0°25' N, 9°27' E]; 18 Jul. 1898; *T.J. Klaine* 1034; fl. ♂, ♀, fr.; K[K000406329, K000406330], P[P04707273, P04707274, P04707275], WAG n.v. • Environs de Libreville; [0°25' N, 9°27' E]; 18 Jul. 1898; *T.J. Klaine* 182; fl. ♀; K, P[P04707843, P04707845, P04707847] • Environs de Libreville; [0°25' N, 9°27' E]; 20 Jul. 1901; *T.J. Klaine* 437; fl. ♂, fr.; P[P04777141, P04777142], WAG n.v. • Environs de Libreville; [0°25' N, 9°27' E]; 18 Jul. 1898; *T.J. Klaine* 1034bis; fl. ♂; BR[BR0000006239091], K[K000406327, K000406328], P[P04707402, P04707403, P04707404] • Environs de Libreville; [0°25' N, 9°27' E]; 17 Dec. 1902; *T.J. Klaine* 3188; fr.; P[P04707399], WAG n.v. • Environs de Libreville; [0°25'N, 9°27' E]; 26 Aug. 1896; *T.J. Klaine* 551; fr.; P[P04707278, P04707279, P04707280, P04707282, P04707283], WAG

n.v. – **Ogooué-Ivindo** • Forêt des Abeilles, 7 km SE of confluence Ogooué-Ivindo; 0°13' S, 12°14' E; 7 Aug. 1993; *J. Dibata 1174*; fl. ♀; BR[BR0000016221437], MA[MA 579857], MO[MO 05016606], WAG[WAG.1255159] – **Ogooué-Lolo** • Région de Lastoursville, Mouila (Poubi); [1°19'S12°11'E]; 2 Aug. 1930; *G.M.P.C. Le Testu 8214*; fl. ♂; G n.v., K, MO[MO 5709020], P[P04707816, P04707817], WAG[WAG.1579080, WAG.1579081].

REPUBLIC OF THE CONGO – **Lékoumou** • Chantier forestier de M. Fouet, Moussoumou, 35 km E of Sibiti; 3°45'S13°35'E; 18 Aug. 1965; *C. Farron 4469*; fl. ♂; MO[MO 5558745], P[P04707281, P04707284, P04707285] – **Sangha** • [Ouéssou] Layon 2252-piquet 223; unknown coordinates; 7 Jan. 1970; *Ledreau 55*; veg.; P[P04707758].

Description

Tree to 30(–35) m, with plagiotropic branches and a dense crown, dioecious; trunk to 50 cm in diameter, upright or leaning, more or less cylindrical at the base, bark smooth, pale greenish-brown to pale greyish-brown, branchlets terete to slightly flattened, sulcate, glabrescent, with few scattered trichomes to 0.1 mm; apical buds scaly, scales 2–2.4 × ca 0.5 mm, narrowly triangular, densely and minutely pubescent outside, trichomes to 0.1 mm. Leaves simple, alternate, glossy and dark-medium green above, dull and paler beneath; stipules ca 1.8(–3) × 0.4 mm, ovate, deciduous, falling very early, densely and minutely pubescent outside, glabrous inside, trichomes to 0.1 mm; petiole (4.2–)7.7–9.6(–13.1) mm long, (1.1–)1.4–1.8(–2.3) mm in diameter, smooth, becoming coarsely wrinkled and bullate when old, channeled above, drying blackish, glabrous, exceptionally sparingly and minutely pubescent, trichomes to 0.1 mm; blade (10.3–)12.8–17.8(–21.7) × (3.4–)4.4–5.8(–8.9) cm, narrowly to widely elliptic or oblong, sometimes wider at distal half, coriaceous, shortly and abruptly acuminate, frequently cuspidate, apex (5–)8.3–11.1(–12) mm, base acute to slightly obtuse, markedly asymmetrical, rounded on one side, less often oblique, basal sides often meeting the petiole at different points up to 1.6 mm apart, margin subentire to shallowly and obscurely crenulate-serrulate, mostly towards the leaf apex, crenulae to 0.3 mm, flat to slightly recurved, frequently undulate, underside of the lamina glabrous; midrib longitudinally slightly wrinkled when dry, glabrous, first order lateral veins 6–8(–9) pairs, ascending, more or less regularly spaced, slightly depressed above, prominent beneath, obscurely diminishing and anastomosing near the margin, forming angles of 58–74° to the midrib, glabrous, second order venation slightly raised above and beneath. Male inflorescence clusters borne axillary on leaf and leafless branches (categories III and IV), to ca 25(–50) flowers, often in much smaller numbers; bracts 0.2–0.4(–1.3) × 0.3–0.5(–0.7) mm, ovate, densely and minutely pubescent outside, glabrous inside, trichomes to 0.1 mm. Male flowers not plate-like at anthesis, yellowish to bright yellow or reddish orange, remarkably scented; pedicel (2.1–)4–5.3(–6.6) mm long, 0.1–0.2 mm in diameter, slender, minutely and sparingly pubescent, trichomes to 0.1 mm; sepals (3–)4(–5), (1.2–)1.9–2.3(–2.9) × (0.3–)1–1.8 mm, ovate to slightly oblong, obtuse, imbricate, slightly cucullate towards the apex, minutely pubescent outside, trichomes to 0.1 mm, glabrous inside, minutely ciliate, cilia to 0.2 mm; stamens 3, one-whorled, surrounding the disk and hardly enveloped by the marginal lobes of the disk, filaments (0.8–)1.5–3.4(–4.2) mm long, white, anthers (0.4–)1–1.1(–1.4) mm long, 0.5–1 mm in diameter, ovate-elliptic, subbasifixed to dorsifixed, introrse, yellow, glabrous; disk (0.3–)0.5–0.8(–1.2) mm in diameter, 0.1–0.4 mm high, concave, cupular, thin, smooth, margin slightly lobed, glabrous, sometimes with a central conical projection to 0.1 mm. Female inflorescence clusters borne axillary on leafless branches (category III), sometimes on main branches (category II), to ca 7 flowers; bracts 0.6–0.9 × 0.7–1.2 mm, ovate, densely and minutely pubescent outside, glabrous inside, trichomes to 0.1 mm. Female flowers plate-like at anthesis, with pedicel 1.9–3.2 mm long, 0.9–1 mm in diameter, more robust than in male flowers, minutely pubescent, trichomes to 0.1 mm; sepals 4–5, 2.9–3.9 × 2.5–3.1 mm, ovate, imbricate, cucullate, minutely and sparingly pubescent outside, trichomes to 0.1 mm, glabrous inside, minutely ciliate at margin, cilia to 0.1 mm; disk 2.8–3.3 mm in diameter, 0.3–0.4 mm high, cupulate, fleshy, glabrous; style 1, 0.6–1.1 mm long, not noticeably hollow, 3(–4)-branched, basally united to 0.3–0.5 mm; stigmas 3(–4), each arm

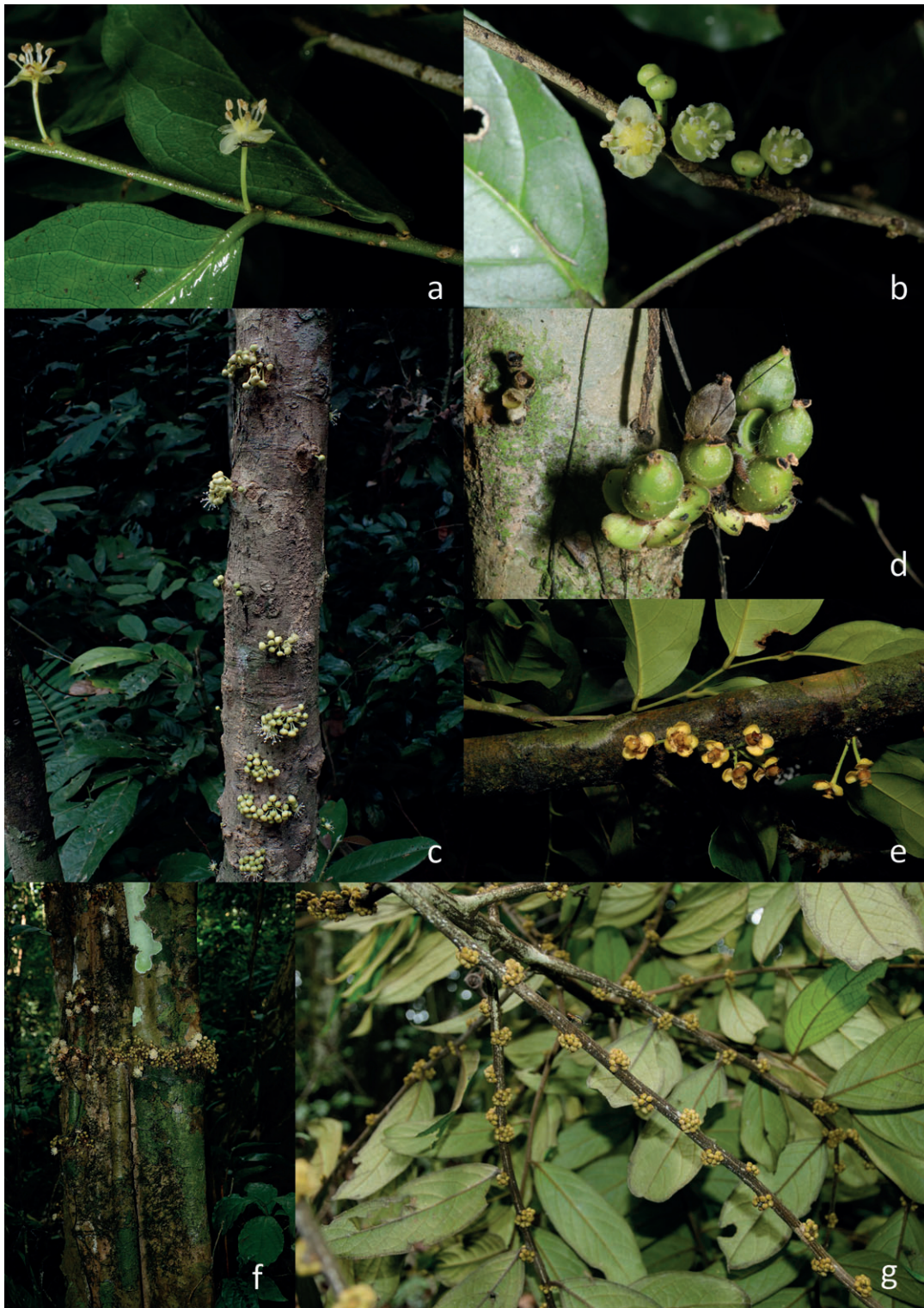


Fig. 1. Different placements of the inflorescences in some African species of *Drypetes* Vahl: **a–b.** *D. gilgiana* (Pax) Pax & K.Hoffm. (categories IV and III, respectively). **c.** *D. preussii* (Pax) Hutch. (category I). **d.** *D. stipularis* (Müll.Arg.) Hutch. (category I). **e.** *D. polyantha* Pax & K.Hoffm. (category II). **f.** *D. verrucosa* Pierre ex Hutch. (category I). **g.** *D. laciniata* (Pax) Hutch. (category III) (a. *E. Bidault* 5644. b. *E. Bidault* 4844. c. *A.H. Paradis* 332. d. *E. Bidault* 2258. e. *D.J. Harris* 9761. f. *E. Bidault* 1861. g. *E. Bidault* 2245.) Photographs taken by the collectors.

0.8–1 mm long, stigmatic surface 1–1.7 mm wide, spatulate to obdeltoid; ovary 1.7–2.1 mm long, 2.4–2.7 mm in diameter, globose, apex depressed, 3(–4)-celled, glabrous. Fruits 19–20.7(–30) mm long, 20–23.4(–30) mm in diameter, subglobose, apically slightly depressed, surface smooth, uneven, reddish brown when young, then red, glabrous, sepals deciduous, style and stigmas deciduous, 3(–4)-celled, (1–)2–3(–4)-seeded, seeds ca 16.9 mm long, ca 9.7 mm in diameter; fruiting pedicel 2–4.6(–8) mm long, 2.3–2.5 mm in diameter, glabrous.

Distribution and habitat

Central Africa: Angola (Cabinda), Cameroon (East Region and South Region), Equatorial Guinea (Centro Sur), Gabon (Estuaire, Ogooué-Ivindo and Ogooué-Lolo) and Republic of the Congo (Lékoumou and Sangha, not mapped) (Fig. 4). Primary and secondary wet evergreen forests, gallery forests; 50–650 m a.s.l.

Phenology

Flowering specimens were collected from December to August, fruiting specimens from April to December.

Notes

Most gatherings of *D. gabonensis* available to us were made from male individuals, and we have only been able to study a few fruiting specimens and only two with female flowers. Herbarium labels inform us about many relevant features of the species, apart from those used to elaborate the description, such as the wood, brownish at first, turning white by exposure and soon destroyed by insects, the scarlet-red extremities of its twigs, and that male flowers are frequented by bees. Female inflorescences of *D. gabonensis* are mostly axillary on leafless branches (category III), although they are also observed on older wood along branches (which could eventually fall within category II), unlike male ones, which are constantly axillary on leaf or leafless branches (categories III and IV). In addition, the protologue of *D. gabonensis* stated that male inflorescences were yet “rarely on the older wood” (the position of female ones is not described), without enabling us to know whether this refers merely to the leafless portions of the branchlets immediately under the leaves or also to the older wood of main branches, as seems to be possible for females. Only future field observations can help to describe the exact distribution of the inflorescences located on the branches of both sexes of *D. gabonensis*.

Despite the superficial resemblances that one might find between specimens of *D. gabonensis* and the two species treated below, as they all have leaves of similar dimensions with subentire margins (*D. gabonensis*) to shallowly and obscurely crenulate-serrulate (all three species) and glabrous fruits, there are numerous useful diagnostic characters, both vegetative and reproductive, that can be used to separate them (see Table 1 for a summary of diagnostic characters). From *D. aphanes* sp. nov. and *D. cauta* sp. nov., we can distinguish *D. gabonensis*, first of all, because the first two are mostly trunciflorous (category I). Bud scales are larger in *D. gabonensis* than in *D. aphanes* and *D. cauta* and have different shapes, narrowly triangular in *D. gabonensis* and more or less ovate in the others. Twigs and branchlets are completely glabrous in *D. aphanes* and *D. cauta*, while they are glabrescent in *D. gabonensis*, often with few scattered trichomes to 0.1 mm. The petiole of *D. gabonensis* is usually longer than those of the other two species ((4.2–)7.7–9.6(–13.1) vs (3.4–)5.8–8.1(–8.6) mm) and its surface is different, smooth and coarsely wrinkled and appearing blistered on dried mature material of *D. gabonensis*, while the petioles of *D. aphanes* and *D. cauta* are finely and densely wrinkled. The leaves of *D. gabonensis* are distinctively glossy above and frequently cuspidate, as well as they frequently have markedly asymmetrical bases, while *D. aphanes* and *D. cauta* are much more lusterless above and, although they are also acuminate, the apex diminishes much more smoothly and the base is oblique.

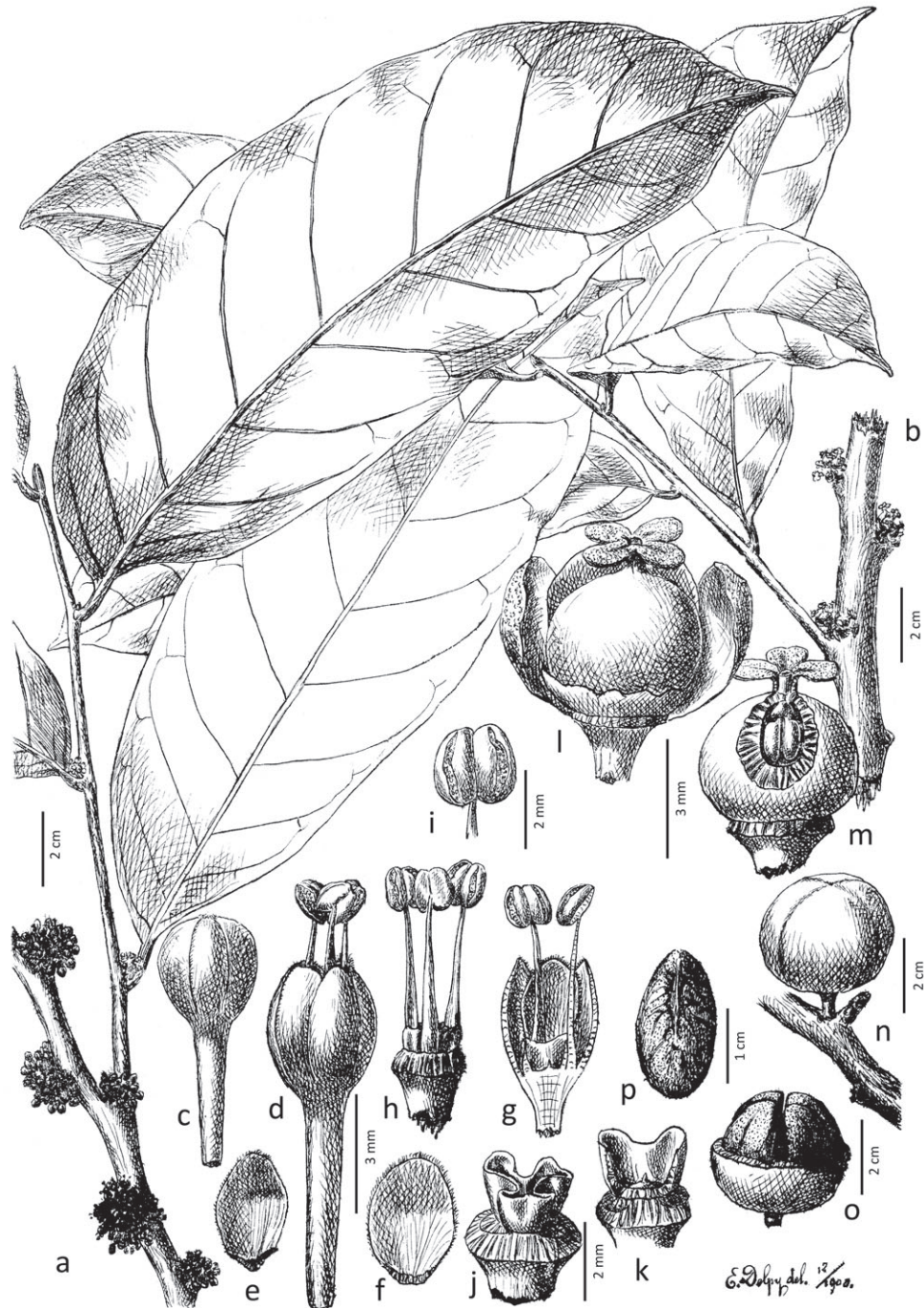


Fig. 2. *Drypetes gabonensis* Pierre ex Hutch. **a.** Branch, leaves, male inflorescences. **b.** Branch, leaves, female inflorescences. **c.** Male flower before anthesis. **d.** Male flower. **e–f.** Sepals of male flower. **g.** Longitudinal section of male flower. **h.** Male flower without sepals. **i.** Ventral view of anther. **j.** Disk of male flower. **k.** Longitudinal section of the disk of the male flower, showing the central conical projection. **l.** Female flower without a sepal. **m.** Opened ovary showing the ovules and transverse section of the ovary. **n.** Fruit. **o.** Opened fruit showing the seeds. **p.** Seed. [a–p, *Klaine* 551, 690, 1034, 1278 (many specimens, see list of studied material).] Details c–h share the scale of 3 mm placed in d. Details j and k share the scale of 2 mm placed in j. details l and m the scale of 3 mm placed in m. Illustration by E. Delpy, modified for its publication in *Flore du Gabon* (Harris *et al.* 2021).

Apart from the different placement of inflorescences, the comparatively small and reduced male flower of *D. gabonensis* is quite different from those of *D. aphanes* sp. nov. and *D. cauta* sp. nov.: fewer sepals (usually 4, vs 5) and stamens (3, vs 11–17), and a much smaller disk ((0.3–)0.5–0.8(–1.2) vs 3.1–4.6 mm in diameter). The male disk of *D. gabonensis* is concave and more or less thin, often with a central conical projection, while in the other two species it is convex and more developed. Other diagnostic characters are the slender pedicels of the male flowers of *D. gabonensis* (in the other two species they are much more robust and usually shorter) and the indumentum of the sepals because that of *D. gabonensis* is sparingly and minutely pubescent, while those of *D. aphanes* and *D. cauta* are glabrous (with the exception of short marginal cilia). Finally, a somewhat longer and branched style and spatulate to obdeltoid stigmas are also useful to distinguish *D. gabonensis* from the other two species, which have much shorter, not branched, styles and consistently obdeltoid stigmas.

The characters linked to flowers and inflorescences of *D. gabonensis*, as well as its large 3(–4)-celled fruits, may make its classification within *D. sect. Oligandrae* problematic in our opinion (most of the representatives of this section bear different-sex flowers of similar appearance (that is, not dimorphic) and small, 2-celled fruits). However, for the moment we leave *D. gabonensis* classified within its traditional section until the typification and amendment of the sections of the genus will be carried out in the near future in conjunction with molecular phylogenies.

Nomenclature

We choose as lectotype of *D. gabonensis* the specimen P04707398 of the gathering *Klaine 1278*, since we consider it to be the most suitable specimen located among the syntypes cited in the protologue: “Lower Guinea. Gaboon: Libreville, Klaine, 551! 690! 1034! 1278! 3188!” (Hutchinson 1912). Hutchinson described *D. gabonensis* on the basis of several gatherings made by T.J. Klaine in the surroundings of Libreville (Gabon) between the years 1896 and 1902, as well as on an unnumbered illustration with analysis drawn by E. Delpy in 1908 (Fig. 2, modified) and based on a part of these gatherings. This illustration belongs to the *Tabulae herbarii* L. Pierre (Delpy 18??–19??) opera utique rej., a suppressed work (Rijckevorsel 2011; Turland *et al.* 2018, Appendix I) and, consequently, the designation “*Cyclostemon gabonense* Pierre” that appears on it (and also cited in the protologue of *D. gabonensis*) was not validly published.

The gathering *Mildbraed 7672* was cited by Pax & Hoffmann (1922) as a part of the original material associated to *D. calvescens* Pax & K.Hoffm., a different species that also inhabits Central Africa, but it is actually conspecific with *D. gabonensis* (Quintanar *et al.* 2022) and we have therefore classified it here as such (see below the list of studied specimens).

IUCN Red List preliminary status

The species is known from 30 gatherings made between 1896 (*Klaine 551*) and 2021 (transects made by MBG team). The geographical information for *Ledreau 55* is imprecise and is therefore not considered for this evaluation. We consider two occurrences as extirpated because of the loss of forest cover due to urbanization at the surroundings of Libreville (*Klaine 182, 437, 551, 690, 1034, 1034bis, 1278*) in Gabon and Bertoua (*Breteler 829*) in Cameroon. The 29 remaining gatherings represent 13 occurrences representing 8–9 subpopulations. The extent of occurrence (EOO) of *D. gabonensis* is estimated to be 162 814 km², exceeding the upper threshold for ‘Vulnerable’ status under subcriterion B1, whereas its area of occupancy (AOO) is estimated to be 52 km², which falls within the limits for ‘Endangered’ status under the subcriterion B2. In Cameroon, the two occurrences are threatened by wood harvesting (two locations). The occurrence from Equatorial Guinea is located within a protected area (Monte Alén National Park). In Gabon, one occurrence is located within a protected area (Forêt des Abeilles); four occurrences are located within two different logging concessions, and are threatened by logging (two

locations); the other two are threatened by shifting agriculture and wood harvesting (two locations). In the Republic of the Congo, the occurrence is located within a logging concession and threatened by logging (one location). In Cabinda (Angola), the three occurrences are threatened by shifting agriculture and wood harvesting (three locations). All activities induce a decline in the quality and extent of the habitat of this species. As a consequence, these 13 occurrences represent 10 locations (cf. IUCN Standards and Petitions Committee 2022), with regard to the most serious plausible threat (urbanization), within the limits for ‘Vulnerable’ status. We infer a past, current, and future continuous decline in the extent of occurrence, area of occupancy, number of locations, and number of mature individuals. *Drypetes gabonensis* is therefore assigned a preliminary status of ‘Vulnerable’ [VU B2ab(i,ii,iii,iv,v)].

Drypetes sect. *Sphragidia* (Thwaites) Pax & K.Hoffm.

Das Pflanzenreich 147, 15 (Heft 81): 234 (Pax & Hoffmann 1922).

Basionym

Sphragidia Thwaites, *Hooker’s journal of botany and Kew garden miscellany* 7: 269 (Thwaites 1855).
– Type: *Sphragidia zeylanica* Thwaites (*D. longifolia* (Blume) Pax & K.Hoffm.).

Drypetes aphanes Quintanar, D.J.Harris & Barberá sp. nov.

urn:lsid:ipni.org:names:77319368-1

Fig. 3a–g

Type

GABON • **Estuaire** – ± 26 km before Mbé River on Kango road; 0°21'N 9°58'E; 22 Oct. 2000; *F.J. Breteler* 15662; fr.; holotype: MO[MO 6683078]; isotypes: WAG[WAG.1564809], LBV[LBV0002377].

Diagnosis

Haec species a Drypete gabonensi ramulis junioribus omnino glabris, cortice ramulorum tessellato, petiolis (5.3–)7–8.1(–8.6) mm longis, confertim rugosis, in sicco saepe pallidis, foliis ad basim plerumque obliquis, inflorescentiis in corticem veterem truncumque positis, sepalis masculinis 5, (3.9–)4.4–5.2(–5.6) × (4.3–)4.6–5.2(–6.5) mm, late ovatis, ac abaxialiter glabratis, disco convexo, in diam. 3.4–4.6 mm, staminibus (11 ad)14 vel 15, stylis eramosis, ca 0.1 mm longis, atque stigmatibus obdeltoideis differt.

Etymology

The specific epithet of this new species is the Neolatin adjective ‘*aphanes*’ (from Gr. ἀφάνης), which means unseen, invisible, unnoticed, not manifest, unknown, etc. Because of the low number of gatherings of *D. aphanes* sp. nov. made to date and the recent collection dates of all of them.

Material examined

GABON – **Estuaire** • *F.J. Breteler* 15662 (type, see above) • ca 3 km on Kougouleu-Médouneu road; 0°25' N, 9°55' E; 14 Oct. 1997; *F.J. Breteler* 14274, *M.E. Leal*, *J.M. Moussavou* & *G. Nang*; fl. ♂; BR[BR0000015777454], BRLU, LBV[LBV0030849], MO[MO 6561417], WAG[WAG.1564805]
– **Ogooué-Lolo** • ca 30 km E of Lastoursville; 0°40' S, 13°0' E; 18 Nov. 1991; *F.J. Breteler* 10545 & *C.C.H. Jongkind*; fr.; LBV, WAG[WAG.1564829] • East of Lastoursville, near Bambidie, C.E.B. chantier; 0°45'S13°3'E; 25 Sep. 1996; *G.D. McPherson* 16690; fl. ♂; LBV[LBV0008192], MO[MO 6343501], WAG n.v. • ibid.; 0°46'S13°3'E; 23 Sep. 1996; *G.D. McPherson* 16666; fl. ♀; LBV[LBV0008194], MO[MO 6343499, MO 6343500], WAG n.v. • Makande surroundings, c. 65 km

SSW of Booué; 0°41'S11°55'E; 26 Jan. 1999; *F.J. Breteler 14796, G. Caballé, Y.A. Issembé, J.J. Moussavou & O. Pascal*; fr.; BR[BR0000015777386], FHO n.v., HUI n.v., K, LBV[LBV0030870], MO[MO 6561411], NY n.v., P n.v., PE n.v., WAG[WAG.1564806, WAG.1564807, WAG.1564808], YA n.v.

Description

Tree to 15 m high, dioecious; trunk to 20 cm in diameter, slightly fluted at the base, bark very finely tessellated, light-coloured; branchlets terete to slightly sulcate, glabrous; apical buds scaly, scales 1.2–1.4 × 1–1.6 mm, widely ovate, glabrous. Leaves simple, alternate, lustreless and dark-medium green above, much paler beneath; stipules not seen, deciduous, very soon falling; petiole (5.3–)7–8.1(–8.6) mm long, (1.1–)1.7–2.1(–2.3) mm in diameter, finely and densely wrinkled, channelled above, drying light-coloured, glabrous; leaf blade (12.5–)14.3–16.4(–18.8) × (4.2–)5.1–6.1(–7.4) cm, widely to narrowly elliptic, subcoriaceous or stiffly chartaceous, acuminate, apex (6–)8–15(–18) mm, base acute to slightly obtuse, oblique, margin obscurely and shallowly crenulate-serrulate, crenulae to 0.2 mm, flat to slightly recurved near the blade base, underside of the lamina glabrous; midrib longitudinally wrinkled, glabrous, first order lateral veins 7–9, ascending, regularly spaced, slightly depressed above, slightly prominent beneath, noticeably curved and anastomosing well within the margin, forming angles of (54–)58–81° to the midrib, glabrous, second order venation hardly raised above and very slightly beneath. Male inflorescence trunciflorous (category I), many-flowered clusters; bracts 0.7–0.9 × 0.8–1 mm, ovate to obovate, quite irregular in shape, glabrous, minutely ciliate at margin, cilia to 0.1 mm. Male flowers plate-like at anthesis, white, pedicel 3.8–4.3(–5.2) mm long, (0.6–)0.9–1.2(–1.4) mm in diameter, robust, glabrous; sepals 5, (3.9–)4.4–5.2(–5.6) × (4.3–)4.6–5.2(–6.5) mm, widely ovate to slightly obovate, imbricate, slightly cucullate, obtuse, glabrous outside and inside, sometimes minutely ciliate, cilia to 0.1 mm; stamens (11–)14–15, apparently one-whorled, surrounding the disk, more or less enveloped by its marginal folds, filaments (3.4–)4–6(–6.3) mm long, anthers 1.6–1.9 mm long, 0.7–1.1 mm in diameter, ovate-elliptic, dorsifixed, introrse, yellow, glabrous; disk 3.4–4.6 mm in diameter, 0.3–0.5 mm high, convex, very rugose, glabrous. Female inflorescence trunciflorous (category I) from the base up or nearly so to ca 10 m height, occasionally on old wood of branches (category II), many-flowered clusters; bracts 0.9–1.5 × 0.7–1.2 mm, as the male ones. Female flowers plate-like at anthesis, white; pedicel 2.9–3.2 mm long, 1–1.1 mm in diameter, robust, glabrous; sepals 5, 3.4–4.1 × 3.9–4 mm, widely ovate to slightly obovate, imbricate, slightly cucullate, glabrous outside and inside, without cilia; disk 3–3.2 mm in diameter, 1.1–1.3 mm high, cupulate, fleshy, glabrous; style 1, to 0.1 mm, hollow, unbranched; stigmas 3, each arm 0.6–0.8 mm long, stigmatic surface 1–1.3 mm wide, obdeltoid; ovary 1.4–1.5 mm long, 2.2–2.4 mm in diameter, subglobose, apex slightly depressed, 3-celled, glabrous. Fruits (18.2–)18.8–22.6 mm long, (15.7–)18–23.1(–23.4) mm in diameter, subglobose, apex slightly depressed, surface smooth, uneven, green, glabrous, without persistent sepals or stigmas, 3-celled, (2–)3-seeded, seeds (11.5–)12.1–16.1(–16.4) mm long, (4.8–)5.9–6.4(–6.7) mm in diameter; fruiting pedicel (6.7–)9–12.6(–13) mm long, 1.3–2.3(–2.9) mm in diameter, glabrous.

Distribution and habitat

Central Africa. Endemic to Gabon (Estuaire and Ogooué-Lolo) (Fig. 4). Primary and secondary evergreen forests; 30–660 m a.s.l.

Phenology

Flowering specimens were collected from September to October, fruiting specimens from October to January.

Notes

The inflorescences of this new species of medium-sized tree, according to the information supplied by herbarium labels, belong to category I, although in *Breteler 14796* we have found a fruit on the old wood of a branch, which may imply the existence of inflorescences of category II. As for *D. gabonensis*, only future field observations can help to assess the frequency with which inflorescences can be found on the main branches of *D. aphanes* sp. nov. The overall morphology of *D. aphanes* let us classify it in *D.* sect. *Sphragidia*, i.e., deciduous stipules, high number of stamens, 3-celled smooth ovaries and subsessile stigmas.

The fruits, subglobose with slightly depressed apex and uneven surface, recall those of *D. gabonensis*, a species from which, as we have commented above, it differs by a series of vegetative and reproductive characters (see above the notes under *D. gabonensis*, as well as Table 1 for a summary of diagnostic characters). No colour except green has been recorded for these fruits and fruit colour may have diagnostic value (*D. gabonensis* bears red ripe fruits), it will be necessary to wait for new gatherings of this species to find out if they remain green in a mature state. *Drypetes aphanes* sp. nov. also differs from *D. gabonensis* by the leaf nervation, because the courses of the first order lateral veins are strongly arched and loop clearly well within the margin, while those of this later species and *D. cauta* sp. nov. are not so strongly arched and loop obscurely near the margin; as well, the petiole of *D. aphanes* often dries light-coloured in herbarium specimens, while those of the others dry dark-coloured or even blackish.

Both *D. aphanes* sp. nov. and *D. cauta* sp. nov. present inflorescences mostly from category I. However, the petiole of *D. aphanes* is often longer than that of *D. cauta* ((5.3–)7–8.1(–8.6) vs (3.4–)5.8–7(–7.5) mm) and the courses of the first order lateral veins run at greater angles to the midrib ((54–)58–81° vs 45–60°). Neither of these species shows the high degree of morphologic dimorphism of *D. gabonensis* regarding their flowers and the flowers of different sexes in these two species have corresponding dimensions and characteristics. In both species the flowers are shortly stalked, glabrous, sometimes with minute marginal cilia, and plate-like when fully open during anthesis. The number of stamens is lower in *D. aphanes* ((11)14–15 vs 16–17) and their arrangement also differs: while those of this species surround the disk and are more or less enveloped by the disk marginal lobes, in *D. cauta* they show a similar disposition, but are quite obscurely whorled and some of them penetrate within a different, very plicate and convolute disk, while the male disk of *D. aphanes* is just rugose. Female flowers and fruits of these species also offer diagnostic characters, such as shorter pedicels (2.9–3.2 × 1–1.1 vs 7.5–10.9 × 0.7–0.9 mm, flower) which are much thicker in the fruit of *D. aphanes* (1.3–2.3(–2.9) vs 0.8–1.1 mm wide), and shorter styles (to 0.1 vs 0.4–0.6 mm), which are quite persistent in *D. cauta* sp. nov. and not observed in any fruit of *D. aphanes*. Finally, the fruit body of *D. aphanes* sp. nov., as well as that of *D. gabonensis*, is bigger than the fruit of *D. cauta* ((18.2–)18.8–22.6 × (15.7–)18–23.1(–23.4) vs 15–16.8 × 12.1–15.4 mm) and also differs by its shape (subglobose vs widely elliptic) and surface (uneven vs even).

IUCN Red List preliminary status

The extent of occurrence (EOO) of *D. aphanes* sp. nov. is estimated to be 8 756 km², which falls within the limits for ‘Vulnerable’ status under the subcriterion B1, whereas its area of occupancy (AOO) is estimated to be 24 km², which falls within the limits for ‘Endangered’ status under the subcriterion B2. The species is known from six gatherings representing six occurrences, all made between 1991 and 2000, and three subpopulations. All of the occurrences are located outside of protected areas. The two occurrences in Estuaire province are threatened by shifting agriculture and wood harvesting (two locations). The three occurrences in Ogooué-Lolo province are located within two different forest concessions, and are, therefore, threatened by logging (two locations). All activities induce a decline in the extent and quality of the habitat of this species. As a consequence, these six occurrences

represent four locations (cf. IUCN Standards and Petitions Committee 2022) with regard to the most serious plausible threat (logging). *Drypetes aphanes* is therefore assigned a preliminary status of ‘Endangered’ [EN B2ab(iii)].

Drypetes cauta D.J.Harris, Barberá & Quintanar sp. nov.

urn:lsid:ipni.org:names:77319369-1

Fig. 3h–n

Type

GABON • **Ngounié** – Boudyanguila, Pays itsogles; [1°56'S 11°30'E]; 21 Sep. 1925; *G.M.P.C. Le Testu 5512*; fl. ♀; holotype: P[P04707049]; isotypes: BM, BR[BR0000015777379], P[P04707045, P04707048].

Diagnosis

Haec species a Drypete gabonensi ramulis junioribus omnino glabris, cortice ramulorum tessellato, petiolis (3.4–)5.8–7(–7.5) mm longis, confertim rugosis, in sicco saepe fuscatis, foliis ad basim plerumque obliquis, inflorescentiis in truncum positis, sepalis masculinis 5, 4.2–5.3 × 4.1–4.7 mm, late ovatis, ac abaxialiter glabratis, disco convexo, in diam. 3.1–3.3 mm, staminibus 16 vel 17, stylis eramosis 0.4–0.6 mm longis, atque stigmatibus obdeltoideis differt.

Etymology

The specific epithet of this new species is the nominative feminine singular of the Latin adjective ‘cautus’, which means ‘cautious, careful, prudent, etc.’ The cautious character of *D. cauta* sp. nov. seems to be apparent after having spent a long time hidden in herbaria, after the first gatherings made by Le Testu during the first half of the past century, until its description today.

Material examined

GABON – **Estuaire** • Concession Sud Estuaire, rivière Remboué; 0°7'S9° 51'E; 26 Jun. 2021; *MBG transect 7194* (*J. Klein, E. Akouangou, J.D. Kaparidi, L.C. Mougoudy & C.D. Kombil*; veg.; BRLU – **Ngounié** • *G.M.P.C. Le Testu 5512* (type, see above) – **Ogooué-Ivindo** • SE of Boooué, in Lutexfo timber concession; 0°21'S12°14'E; 23 Nov. 1993; *G.D. McPherson 16249*; fr.; K, LBV[LBV0008206], MO[MO 4647294], PRE, WAG[WAG.1563832] – **Ogooué-Lolo** • Région de Lastoursville, Iméno; [1°30'S12°19'E]; 10 Sep. 1930; *G.M.P.C. Le Testu 8327*; fl. ♂; BM, BR[BR0000015777188], P[P04707811, P04707812], WAG n.v. – **Woleu-Ntem** • Concession Rougier du Haut-Abanga, Sud-Est de Mikongo, partie Nord des montagnes Mekié; [0°25'N11°13'E]; 17 Jul. 2008; *G. Dauby 1022, D. Nguema, E. Mounoumoulossi & P. Bissiemou*; fr.; BRLU, MO[MO 6358905].

REPUBLIC OF THE CONGO – **Kouilou** • Mayombe hills, near Niari River; 4°2'S12°9'E; 18 Oct. 2010; *R. M'Boungou 462, X. M. van der Burgt & F. Gislain*; fl. ♀; IEC[IEC025751], K[K000683528].

Description

Treelet to 8 m high, dioecious; trunk to ca 15 cm in diameter, bark finely tessellated, somewhat flaky, dark-coloured; branchlets terete or slightly flattened, sulcate, glabrous; apical buds scaly, scales 1.3–1.7 × 2.1–2.7 mm, ovate-suborbicular, strongly cucullate, glabrous, minutely ciliate, cilia to 0.1 mm. Leaves simple, alternate, lustreless above and beneath; stipules 1.4–1.6 × 0.2–0.4 mm, narrowly triangular, deciduous, very soon falling, glabrous, ciliate at the margin, trichomes to 0.2 mm; petiole (3.4–)5.8–7(–7.5) mm long, 1.4–2 mm in diameter, finely and densely wrinkled, channeled above, drying dark-coloured or blackish, glabrous; leaf blade (10.5–)12.6–15.6(–19.2) ×



Fig. 3. *Drypetes aphanes* Quintanar, D.J. Harris & Barberá sp. nov. **a.** Branch and leaves. **b.** Petiole and leaf base, adaxial view. **c.** Female inflorescence. **d.** Female flower. **e.** Female sepal, abaxial view. **f.** Male flower. **g.** Fruit. – **h–n.** *D. cauta* D.J.Harris, Barberá & Quintanar sp. nov. **h.** Branch and leaves. **i.** Petiole and leaf base, adaxial view. **j.** Terminal bud and stipules. **k.** Female flower. **l.** Female sepal, abaxial view. **m.** Male flower. **n.** Fruit [a–c, g. *Breteler* 14796 (MO 6561411). d–e. *McPherson* 16666 (MO 6343500). f. *McPherson* 16690 (MO 6343501). h–i, m. *Le Testu* 5512 (P04707049). j. *M'Boungou*462 (K). k–l. *Le Testu* 8327 (P04707812). n. *McPherson* 16249 (MO 04647294)]. Illustration by Román García Mora.

(2.4–)3.8–5.2(–6.2) cm, narrowly elliptic, subcoriaceous, acuminate, apex (4–)8.1–11.2(–17) mm, base acute to slightly obtuse, oblique, margin obscurely and shallowly crenulate-serrulate, crenulae to 0.2 mm, flat to slightly recurved near the blade base, underside of the lamina glabrous; midrib longitudinally wrinkled, glabrous, first order lateral veins (6–)8(–10) pairs, ascending, somewhat irregularly spaced, depressed above, prominent beneath, obscurely diminishing and anastomosing near the margin, forming angles of 45–60° to the midrib, glabrous, second order venation hardly raised above and very slightly beneath. Male inflorescence trunciflorous (category I), many-flowered clusters; bracts 1.2–1.5 × 1.3–1.6 mm, ovate to obovate, quite irregular, glabrous, minutely ciliate at margin, cilia to 0.2 mm. Male flowers plate-like at anthesis, yellow, pedicel 3.6–7.7 mm long, 0.3–0.8 mm in diameter, more or less robust, glabrous; sepals 5, 4.2–5.3 × 4.1–4.7 mm, widely ovate, obtuse, imbricate, cucullate, glabrous outside and inside, minutely ciliate at margin, cilia to 0.1 mm; stamens 16–17, obscurely whorled, mainly surrounding the disk and enveloped by its marginal folds, some of them (2 or 3) penetrating, filaments 2.2–2.3 mm long, anthers 1.4–1.5 mm long, 0.6–0.7 mm in diameter, ovate-elliptic, dorsifixed, introrse, glabrous; disk 3.1–3.3 mm in diameter, ca 0.4 mm high, convex, strongly plicate, convolute, glabrous. Female inflorescence trunciflorous (category I) from the base up or nearly so to ca 4 m height, many-flowered clusters; bracts 1–1.9 × 1.3–1.6 mm, as the male ones. Female flowers plate-like at anthesis, with pedicel 7.5–10.9 mm long, 0.7–0.9 mm in diameter, more or less robust, glabrous; sepals (4–)5, 4.1–4.7 × 4.2–4.8 mm, widely ovate, imbricate, cucullate, glabrous outside and inside, minutely ciliate at margin, cilia to 0.1 mm; disk 4.1–4.3 mm in diameter, 0.3–0.8 mm high, cupulate, fleshy, glabrous; style 1, 0.4–0.6 mm long, hollow, unbranched; stigmas 3, each arm 0.8–1.1 mm long, stigmatic surface 1.5–2.3 mm wide, obdeltoid; ovary 2.5–2.8 mm long, 4.1–3.9 mm in diameter, globose, longitudinally flattened, apex depressed, 3-celled, glabrous. Fruit 15–16.8 mm long, 12.1–15.4 mm in diameter, widely elliptic, apex depressed, surface smooth, even, green, glabrous, without sepals, stigmas subpersistent, 3-celled, 2(–3)-seeded, seeds ca 9 mm long, ca 2.2 mm in diameter; fruiting pedicel 11.3–12.2 mm long, 0.8–1.1 mm in diameter, glabrous.

Distribution and habitat

Central Africa. Gabon (Estuaire, Ngounié, Ogooué-Ivindo, Ogooué-Lolo and Woleu-Ntem) and Republic of the Congo (Kouilou) (Fig. 4). Primary evergreen forests; 400–650 m a.s.l.

Phenology

Flowering specimens were collected from September to October, fruiting specimens from July to November.

Notes

This new treelet to 8 m high from the rainforests of Gabon and Republic of the Congo also shows the inflorescences placed on the trunk, like *D. aphanes* sp. nov. As for *D. aphanes*, the overall morphological characteristics of *D. cauta* sp. nov. let us classify it in *D. sect. Sphragidia*, due to its deciduous stipules, high number of stamens, 3-locular smooth ovaries and subsessile stigmas.

Drypetes cauta sp. nov. differs from the species treated above by a series of vegetative and reproductive characters (see above the notes under *D. gabonensis* and *D. aphanes* sp. nov., as well as Table 1 for a summary of diagnostic characters). The petiole of *D. cauta* is often shorter than that of *D. aphanes* ((3.4–)5.8–7(–7.5) vs (5.3–)7–8.1(–8.6) mm) and the courses of the first order lateral veins form lower angles to the midrib (45–60° vs (54–)58–81°). The number of stamens is lower in *D. cauta* (16–17 vs (11)14–15) and they are obscurely whorled, some of them (2–3) penetrating within a very plicate and convolute disk of complex structure, while in *D. aphanes* the stamens do not penetrate a rugose disk. *Drypetes cauta* additionally has longer female pedicels (7.5–10.9 vs 2.9–3.2 mm), which are much thinner in the fruit than those of *D. aphanes* (0.8–1.1 vs 1.3–2.3(–2.9) mm); it also bears

longer styles (0.4–0.6 vs to 0.1 mm) that remain, along with the stigmas, for a long period of time on the fruit than those of *D. aphanes*. As we have mentioned, the fruit of *D. cauta* is different and not to be confused with that of the previous species, smaller (15–16.8 × 12.1–15.4 vs (18.2–)18.8–22.6 × (15.7–)18–23.1(–23.4) mm) and widely elliptic with a quite even surface, while the fruit of *D. aphanes* is subglobose and its surface is uneven.

IUCN Red List preliminary status

The extent of occurrence (EOO) of *D. cauta* sp. nov. is estimated to be 66 594 km², exceeding the upper threshold for ‘Vulnerable’ status under subcriterion B1, whereas its area of occupancy (AOO) is estimated to be 24 km², which falls within the limits for ‘Endangered’ status under the subcriterion B2. The species is known from six gatherings, representing six occurrences, all made between 1925 and 2021, and six subpopulations. Considering the forest cover, which is still significant in these countries, we do not regard any of these occurrences as extirpated. All of the occurrences are located outside of protected areas. The five occurrences in the different provinces of Gabon and the one in the Republic of the Congo are located within six different forest concessions, and are, therefore, threatened by logging. This activity presumably induces a decline in the extent and quality of the habitat of this species. As a consequence, these six occurrences represent six locations (cf. IUCN Standards and Petitions Committee 2022) with regard to the most serious plausible threat (logging). *Drypetes cauta* is therefore assigned a preliminary status of ‘Vulnerable’ [VU B2ab(iii)].

Identification key

1. Young branchlets glabrescent; bark smooth; petiole surface smooth, coarsely wrinkled and bullate when old, often drying dark-coloured or blackish; leaf blade subentire to shallowly and obscurely crenulate-serrulate, shortly and abruptly acuminate, frequently cuspidate, glossy above; leaf blade base markedly asymmetrical, sometimes oblique; male inflorescence in leafy and leafless axils along the branchlets; male pedicel slender, pubescent; male sepals (3–)4(–5), (1.2–)1.9–2.3(–2.9) mm long, ovate to slightly oblong, minutely and sparingly pubescent outside; disk (0.3–)0.5–0.8(–1.2) mm in diameter, concave; stamens 3; style 0.6–1.1 mm long, branched; stigmas obspathulate *D. gabonensis* Pierre ex Hutch.
- Young branchlets glabrous; bark tessellated; petiole surface finely and densely wrinkled, drying light or dark-coloured; leaf blade shallowly and obscurely crenulate-serrulate, acuminate, lustreless above; leaf blade base oblique; male inflorescence on cushion-like excrescences of the trunk bark; male pedicel more or less robust, glabrous; male sepals 5, 3.9–5.6 mm long, widely ovate, glabrous outside; disk 3.1–4.6 mm in diameter, convex; stamens 11–17; style to 0.6 mm long, unbranched; stigmas obdeltoid 2
2. Petiole (5.3–)7–8.1(–8.6) mm, often drying light-coloured; first order lateral veins forming angles (54–)58–81° to midrib, strongly arched and looping clearly well within the margin; male pedicel 3.8–4.3(–5.2) × (0.6–)0.9–1.2(–1.4) mm; stamens (11)14–15, surrounding the disk and more or less enveloped by the disk marginal lobes; male disk very rugose; female pedicel 2.9–3.2 × 1–1.1 mm; style to 0.1 mm, not persistent on fruit; fruit pedicel 1.3–2.3(–2.9) mm wide; fruit (18.2–)18.8–22.6 × (15.7–)18–23.1(–23.4) mm, subglobose, surface uneven..... *D. aphanes* Quintanar, D.J.Harris & Barberá sp. nov.
- Petiole (3.4–)5.8–7(–7.5) mm, often drying dark-coloured; first order lateral veins forming angles 45–60° to midrib, not strongly arched and looping obscurely near the margin; male pedicel 3.6–7.7 × 0.3–0.8 mm; stamens 16–17, surrounding the disk and enveloped by the disk marginal lobes, some penetrating; male disk strongly plicate; female pedicel 7.5–10.9 × 0.7–0.9 mm; style 0.4–0.6 mm, often persistent on fruit; fruit pedicel 0.8–1.1 mm wide; fruit 15–16.8 × 12.1–15.4 mm, widely elliptic, surface even *D. cauta* D.J.Harris, Barberá & Quintanar sp. nov.

Discussion

From our categorization of the inflorescence types of all African species of *Drypetes* (Table 2), we note that the position of the inflorescence it is usually congruent between males and females. If they differ, they are found in adjacent areas of the plant, the female ones always displaced from distal to basal parts with respect to the male ones. A good example of remarkable sexual dimorphism is the species *D. gabonensis*, whose taxonomic treatment we present above, with male inflorescences belonging to categories III and IV and female ones to categories III and II. Most of the African species of *Drypetes* belong to categories III and IV (axillary inflorescences, 61 spp. for males and 59 spp. for females), while 21 spp. for males and 22 spp. for females account for categories I and II, after including the new species here described, *D. aphanes* sp. nov. and *D. cauta* sp. nov. This represents approximately a quarter of the whole African species set. Most of the species of the categories I and II are currently classified in *D.* sect. *Sphragidia*, with exceptions such as *D. stipularis* (Müll.Arg.) Hutch. and *D. verrucosa* Pierre ex Hutch., both in *D.* sect. *Stipulares* Pax & K.Hoffm. and from Central Africa, *D. staudtii* (Pax) Hutch., also from Central Africa but classified in *D.* sect. *Stenogynium* (Müll.Arg.) Pax & K.Hoffm., or *D. comorensis* (Baill.) Pax & K.Hoffm. from the Comoro Islands (Mayotte) and *D. polyantha* Pax & K.Hoffm. from Central Africa, both classified in *D.* sect. *Humblotia* (Baill.) Pax & K.Hoffm. Moreover, categories I and II occur throughout the entire distribution area of this genus in Africa, from the northernmost (e.g., *D. floribunda* (Müll.Arg.) Hutch. in Senegal) to the southernmost (e.g., *D. natalensis* (Harv.) Hutch. in South Africa), and with no shortage in the Malagasy Region (e.g., *D. bathiei* Capuron & Leandri in Madagascar). Nor does it seem that this reproductive strategy is associated with certain types of habitat since, in the same way, there are cauliflorous species both in those formations that receive less rainfall (e.g., *D. floribunda* and *D. natalensis*), as well as in areas with some of the highest rainfall in Africa (e.g., *D. staudtii* and *D. spinosodentata* (Pax) Hutch., both from Central Africa or, again, *D. aphanes* sp. nov. and *D. cauta* sp. nov.). It is remarkable that we have been able to find to date few species of *Drypetes* from out of Africa whose inflorescences could be classified in categories I or II, all of them from southern and southeastern Asia, although again the lack of a concise description of their location in the plant prevents us from assigning them in a certain category yet. They are *D. longifolia* (Blume) Pax & K.Hoffm., widely distributed in southeastern Asia and “ramiflorous on older twigs and branches” (Phuphathanaphong & Chayamarit 2005), and the Indian *D. confertiflora* (Hook.f.) Pax & K.Hoffm., *D. malabarica* (Bedd.) Airy Shaw and *D. oblongifolia* (Bedd.) Airy Shaw, of which we know that their flowers are “all or mostly from the old wood” (Hooker 1887; Chakrabarty *et al.* 1997). Of the checked material of these species by our team so far, only two specimens collected in northern Borneo (*Primack S42434* and *Coode & al. 7244*), both attributed to *D. longifolia*, have inflorescences placed on the trunk and can be clearly attributed to category I. In light of this and pending further research to expand the information available on the accurate arrangement of inflorescences of many species of *Drypetes*, we note, for the moment, that the role of cauliflory in speciation may have been more important in Africa than in the rest of the world.

Furthermore, after the publication of *D. aphanes* sp. nov. and *D. cauta* sp. nov., *Drypetes* now consists of 86 species in continental Africa and the Malagasy Region and 219 species in the world (Table 3). There is a clear pattern across tropical angiosperms that many groups contain more species in the Americas or Asia compared to Africa (Richards 1973; Parmentier *et al.* 2007; Couvreur 2015), which has sometimes been referred to colloquially as continental Africa being the “odd man out” for the species diversity of these plants. There are, however, exceptions such as the monophyletic subfamily of the Fabaceae Lindl. (Fabales), the Detarioideae Burmeist., that have more species in Africa (De la Estrella *et al.* 2017). Our species counts show that *Drypetes* is another such exception, since the species number of *Drypetes* is much higher in the tropical forests of Africa than in those of America (20 spp., see Table 3), as well as just moderately lower than in those of Asia (113 spp.). There are no common species among these continental areas. The difference in figures between Asia and Africa

is only 27 species and we expect this figure to decrease as the number of species from Africa will continue to grow, further emphasising the particular nature of the distribution of species in this genus compared to the more general pattern.

When considering possible explanations for *Drypetes* being more species rich than the norm on continental Africa, we examined the following: the range of habitat of *Drypetes* from savannah to high rainfall forest; dioecy; the size of the individuals; infructescence traits and fruit dispersal mechanisms. We note that many species of *Drypetes* occur in the rainforest with 1–3 dry months per year as well as in the higher rainfall savannas. The continued presence of *Drypetes* species throughout this intermediate band between high rainfall forest and the arid savannas suggests, as in the case of the Detarioideae, that the genetic plasticity in *Drypetes* has facilitated either the persistence or speciation within the genus over the fluctuating drier and wetter periods that have taken place in Africa since the Eocene. In addition to some narrow endemics, *Drypetes* has numerous species in Africa with both a wide distribution area and range of habitat and morphological variation, such as *D. laciniata* (Pax) Hutch. and *D. diopa* (Hiern) Brenan, that suggest that these species have been actively involved in the successive processes of recolonization of new forested areas that have taken place during the Quaternary in Africa (Maley 1996, 2002). Dioecy is another species character that could explain species richness, however, since almost all *Drypetes* species are dioecious, this does not help to explain the continental differences. The commonest size of *Drypetes* species and individuals is trees 5–20 m tall with no herbs or climbers. We note the similarity to the example of the Detariodieae, and suggest that the exceptions to Africa being the “odd man out”, may be more common in trees. The fruit of *Drypetes* that we have examined in Africa all appear to be dispersed by vertebrates, such as monkeys to elephants (direct observations; Gautier-Hion *et al.* 1985; Dowsett-Lemaire 1988). In addition, we have observed that several morphologically similar species, such as *D. diopa*, *D. gilgiana* (Pax) Pax &

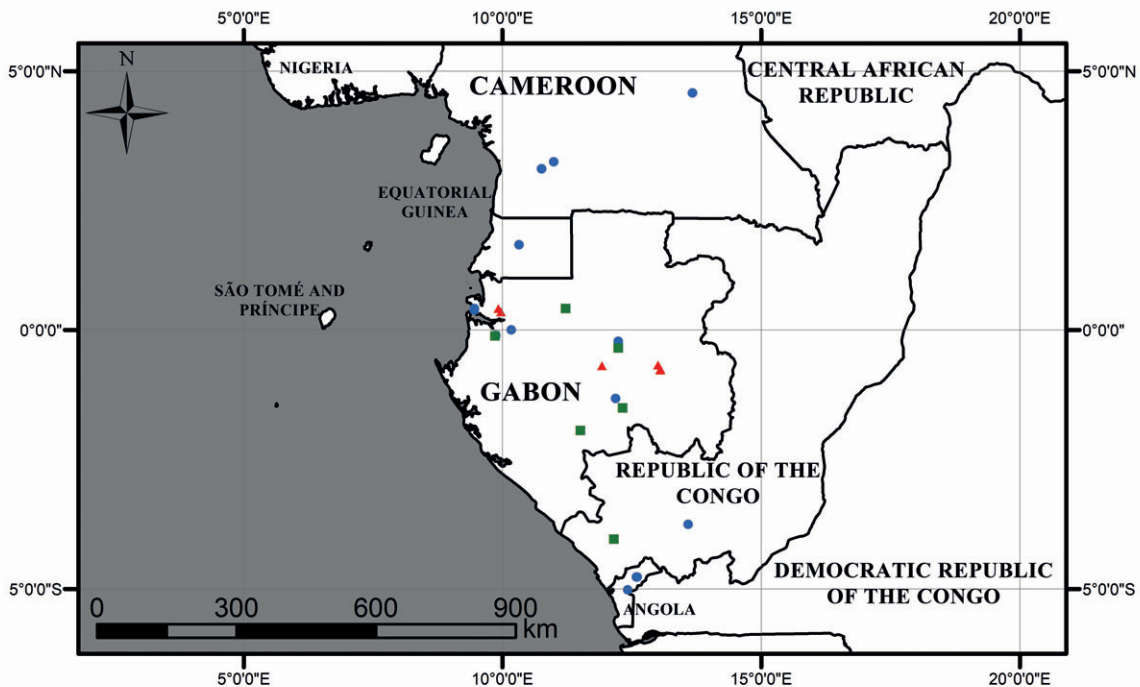


Fig. 4. Distribution of *Drypetes gabonensis* Pierre ex Hutch. (blue circles), *Drypetes aphanes* Quintanar, D.J.Harris & Barberá sp. nov. (red triangles) and *D. cauta* D.J.Harris, Barberá & Quintanar sp. nov. (green squares).

Table 3 (continued on the next 2 pages). Species of *Drypetes* Vahl over large areas of the world at the sub-continental level rather than country level, names and figures. Species with either male or female inflorescences attributable to categories I and II are marked with an asterisk.

Africa		
86 spp.	Central Africa	40 spp.
	<i>D. aphanes</i> Quintanar, D.J.Harris & Barberá sp. nov.*, <i>D. arborescens</i> (Oliv.) Hutch., <i>D. bakembei</i> D.J.Harris & Wortley, <i>D. burnleyae</i> Cheek, <i>D. capillipes</i> (Pax) Pax & K.Hoffm., <i>D. cauta</i> D.J.Harris, Barberá & Quintanar sp. nov.*, <i>D. celastrinea</i> Pax & K.Hoffm., <i>D. cinnabarina</i> Pax & K.Hoffm., <i>D. darimontiana</i> J.Léonard, <i>D. dinklagei</i> (Pax) Hutch., <i>D. diopa</i> (Hiern) Brenan, <i>D. euryodes</i> (Hiern) Hutch., <i>D. fallax</i> Pax & K.Hoffm., <i>D. fernandopoana</i> Brenan, <i>D. gabonensis</i> Pierre ex Hutch.*, <i>D. glabra</i> (Pax) Hutch., <i>D. gossweileri</i> S.Moore*, <i>D. gracilis</i> Pax & K.Hoffm., <i>D. henriquesii</i> (Pax) Hutch., <i>D. ituriensis</i> Pax & K.Hoffm., <i>D. kamerunica</i> Pax & K.Hoffm., <i>D. magnistipula</i> (Pax) Hutch., <i>D. moliwensis</i> Cheek & Radcl.-Sm., <i>D. morocarpa</i> J.Léonard ex D.J.Harris & Quintanar, <i>D. occidentalis</i> (Müll.Arg.) Hutch., <i>D. palustris</i> D.J.Harris, Barberá & Quintanar, <i>D. paxii</i> Hutch., <i>D. polyantha</i> Pax & K.Hoffm.*, <i>D. preussii</i> (Pax) Hutch.*, <i>D. rubriflora</i> Pax & K.Hoffm., <i>D. similis</i> Hutch., <i>D. spinosodontata</i> (Pax) Hutch.*, <i>D. staudtii</i> (Pax) Hutch.*, <i>D. stevartii</i> Sonké & Quintanar, <i>D. stipularis</i> (Müll.Arg.) Hutch.*, <i>D. tessmanniana</i> (Pax) Pax & K.Hoffm., <i>D. umbricola</i> D.J.Harris & Quintanar, <i>D. urophylla</i> Pax & K.Hoffm., <i>D. verrucosa</i> Pierre ex Hutch.*, <i>D. vilhenae</i> Cavaco	
	Central and East Africa	2 spp.
	<i>D. bipindensis</i> (Pax) Hutch., <i>D. calvescens</i> Pax & K.Hoffm.	
	Central, East and West Africa	1 sp.
	<i>D. parvifolia</i> (Müll.Arg.) Pax & K.Hoffm.	
	East and South Africa	11 spp.
	<i>D. arguta</i> (Müll.Arg.) Hutch., <i>D. gerrardii</i> Hutch., <i>D. gerrardinoides</i> Radcl.-Sm., <i>D. mossambicensis</i> Hutch., <i>D. natalensis</i> (Harv.) Hutch.*, <i>D. pleioneura</i> (Radcl.-Sm.) Christenh. & Byng*, <i>D. taylorii</i> S. Moore, <i>D. reticulata</i> Pax, <i>D. sclerophylla</i> Mildbr., <i>D. ugandensis</i> (Rendle) Hutch.*, <i>D. usambarica</i> (Pax) Hutch.*	
	Malagasy Region	15 spp.
	<i>D. ambigua</i> Leandri, <i>D. bathiei</i> Capuron & Leandri*, <i>D. birkinshawii</i> McPherson, <i>D. capuronii</i> Leandri*, <i>D. caustica</i> (Frapp. ex Cordem.) Airy Shaw, <i>D. chevalieri</i> Beille, <i>D. comorensis</i> (Baill.) Pax & K.Hoffm.*, <i>D. darcyana</i> McPherson, <i>D. madagascariensis</i> (Lam.) Humbert & Leandri, <i>D. oppositifolia</i> Leandri, <i>D. perrieri</i> Leandri ex Humbert, <i>D. riseleyi</i> Airy Shaw, <i>D. stipulacea</i> Leandri*, <i>D. thouarsiana</i> (Baill.) Capuron, <i>D. thouarsii</i> (Baill.) Leandri	
	West Africa	9 spp.
	<i>D. afzelii</i> (Pax) Hutch.*, <i>D. aubrevillei</i> Leandri, <i>D. floribunda</i> (Müll.Arg.) Hutch.*, <i>D. leonensis</i> Pax, <i>D. liberica</i> Quintanar & D.J.Harris, <i>D. obanensis</i> S.Moore*, <i>D. pellegrinii</i> Leandri, <i>D. rowlandii</i> Pax, <i>D. singroboensis</i> Aké Assi	
	West and Central Africa	8 spp.
	<i>D. aframensis</i> Hutch., <i>D. aylmeri</i> Hutch. & Dalziel, <i>D. gilgiana</i> (Pax) Pax & K.Hoffm., <i>D. inaequalis</i> Hutch., <i>D. ivorensis</i> Hutch. & Dalziel*, <i>D. klainei</i> Pierre ex Pax, <i>D. laciniata</i> (Pax) Hutch., <i>D. principum</i> (Müll.Arg.) Hutch.	

Table 3 (continued). Species of *Drypetes* Vahl over large areas of the world at the sub-continental level rather than country level, names and figures. Species with either male or female inflorescences attributable to categories I and II are marked with an asterisk.

America		
20 spp.	Central and South America	1 sp.
	<i>D. standleyi</i> G.L.Webster	
	North and Central America (incl. Florida, the Antilles and Bahamas)	12 spp.
	<i>D. alba</i> Poit., <i>D. asymmetricarpa</i> G.A.Levin, <i>D. brownii</i> Standl., <i>D. diversifolia</i> Krug & Urb., <i>D. dussii</i> Krug & Urb., <i>D. gentryi</i> Monach., <i>D. glauca</i> Vahl, <i>D. guatemalensis</i> Lundell, <i>D. ilicifolia</i> (DC.) Krug & Urb., <i>D. mucronata</i> C.Wright ex Griseb., <i>D. lateriflora</i> (Sw.) Krug & Urb., <i>D. picardae</i> Krug & Urb.	
South America	7 spp.	
<i>D. amazonica</i> Steyerl., <i>D. azulensis</i> Vásquez & Soto-Shareva, <i>D. brevipedicellata</i> Zent.-Ruíz & A.Fuentes, <i>D. fanshawei</i> Sandwith, <i>D. gentryana</i> Vásquez, <i>D. sessiliflora</i> Allemão, <i>D. variabilis</i> Uittien		
Asia		
113 spp.	Australasia (incl. Melanesia), Micronesia (incl. Bonin and Volcano Islands) and Polynesia	14 spp.
	<i>D. acuminata</i> P.I.Forst., <i>D. carolinensis</i> Kaneh., <i>D. deplanchei</i> (Brongn. & Gris) Merr., <i>D. dolichocarpa</i> Kaneh., <i>D. glaberrima</i> Airy Shaw, <i>D. integerrima</i> (Koidz.) Hosok., <i>D. iodoformis</i> L.S.Sm. ex P.I.Forst., <i>D. lasiogynoides</i> Pax & K.Hoffm., <i>D. nitida</i> Kaneh., <i>D. pacifica</i> (I.W.Bailey & A.C.Sm.) A.C.Sm., <i>D. sherffii</i> Govaerts & Radcl.-Sm., <i>D. vernicosa</i> P.I.Forst., <i>D. vitiensis</i> Croizat, <i>D. yapensis</i> Tuyama	
	China	4 spp.
	<i>D. integrifolia</i> Merr. & Chun, <i>D. kwangtungensis</i> F.W.Xing, X.S.Qin & H.F.Chen, <i>D. longistipitata</i> P.T.Li, <i>D. nienkui</i> Merr. & Chun	
	China and Indochina	5 spp.
	<i>D. arcuatineruvia</i> Merr. & Chun, <i>D. hoensis</i> Gagnep., <i>D. salicifolia</i> Gagnep., <i>D. obtusa</i> Merr. & Chun, <i>D. perreticulata</i> Gagnep.	
	China and Malesia	3 spp.
	<i>D. congestiflora</i> Chun & T.C.Chen, <i>D. cumingii</i> (Baill.) Pax & K.Hoffm., <i>D. littoralis</i> (C.B.Rob.) Merr.	
	India	10 spp.
	<i>D. confertiflora</i> (Hook.f.) Pax & K.Hoffm. (*?), <i>D. gardneri</i> (Thwaites) Pax & K.Hoffm., <i>D. jaintensis</i> (C.B.Clarke) Pax & K.Hoffm., <i>D. kalamii</i> G.Krishna, Karthig., Arisdason & Chakrab., <i>D. malabarica</i> (Bedd.) Airy Shaw (*?), <i>D. oblongifolia</i> (Bedd.) Airy Shaw (*?), <i>D. porteri</i> (Gamble) Pax & K.Hoffm., <i>D. sepiaria</i> (Wight & Arn.) Pax & K.Hoffm., <i>D. venusta</i> (Wight) Pax & K.Hoffm., <i>D. wightii</i> (Hook.f.) Pax & K.Hoffm.	
	India and Indochina	4 spp.
	<i>D. assamica</i> (Hook.f.) Pax & K.Hoffm., <i>D. balakrishnanii</i> Chakrab. & M.Gangop., <i>D. eglandulosa</i> (Roxb.) Pax & K.Hoffm., <i>D. subsessilis</i> (Kurz) Pax & K.Hoffm.	
	India, Indochina and Malesia	1 sp.
	<i>D. sumatrana</i> (Miq.) Pax & K.Hoffm.	
	India, Indochina and China	1 sp.
	<i>D. indica</i> (Müll.Arg.) Pax & K.Hoffm.	
India, Indochina, Malesia and Australasia	1 sp.	
<i>D. longifolia</i> (Blume) Pax & K.Hoffm. (*?)		

Table 3 (continued). Species of *Drypetes* Vahl over large areas of the world at the sub-continental level rather than country level, names and figures. Species with either male or female inflorescences attributable to categories I and II are marked with an asterisk.

Indochina (excl. Peninsular Malaysia)	11 spp.
<i>D. andamanica</i> (Kurz) Pax & K.Hoffm., <i>D. bisacuta</i> Gagnep., <i>D. bhattacharyae</i> Chakrab., <i>D. cambodica</i> Gagnep., <i>D. dasycarpa</i> (Airy Shaw) Phuph. & Chayam., <i>D. elliptica</i> (Hook.f.) Pax & K.Hoffm., <i>D. harmandii</i> Pierre ex Gagnep., <i>D. helferi</i> (Hook.f.) Pax & K.Hoffm., <i>D. leiocarpa</i> (Kurz) Pax & K.Hoffm., <i>D. poilanei</i> Gagnep., <i>D. thorelii</i> Gagnep.	
Indochina and Malesia	5 sp.
<i>D. curtisii</i> (Hook.f.) Pax & K.Hoffm., <i>D. hainanensis</i> Merr., <i>D. ochrothrix</i> Airy Shaw, <i>D. pendula</i> Ridl., <i>D. viridis</i> Airy Shaw	
Malesia (excl. Melanesia)	53 spp.
<i>D. aetoxylodes</i> Airy Shaw, <i>D. bawanii</i> (Merr.) Airy Shaw, <i>D. caesia</i> Airy Shaw, <i>D. calyptosepala</i> Airy Shaw, <i>D. castilloi</i> (Merr.) Merr., <i>D. convoluta</i> Airy Shaw, <i>D. crassipes</i> Pax & K.Hoffm., <i>D. cockburnii</i> Airy Shaw, <i>D. dasyneura</i> Airy Shaw, <i>D. deterrentis</i> Airy Shaw, <i>D. dewildei</i> Airy Shaw, <i>D. ellipsoidea</i> (Merr.) Pax & K.Hoffm., <i>D. eriocarpa</i> Airy Shaw, <i>D. falcata</i> (Merr.) Pax & K.Hoffm., <i>D. forbesii</i> Pax & K.Hoffm., <i>D. fusiformis</i> Airy Shaw, <i>D. gitingensis</i> (Elmer) Pax & K.Hoffm., <i>D. glabridiscus</i> J.J.Sm., <i>D. iliae</i> Airy Shaw, <i>D. globosa</i> (Merr.) Pax & K.Hoffm., <i>D. grandifolia</i> (C.B.Rob.) Pax & K.Hoffm., <i>D. heptandra</i> Pax & K.Hoffm., <i>D. impressinervis</i> Airy Shaw, <i>D. kikir</i> Airy Shaw, <i>D. laevis</i> (Miq.) Pax & K.Hoffm., <i>D. macrostigma</i> J.J.Sm., <i>D. maquilingensis</i> (Merr.) Pax & K.Hoffm., <i>D. microphylla</i> (Merr.) Pax & K.Hoffm., <i>D. microphyllodes</i> S.Moore, <i>D. minahassae</i> (Boerl. & Koord.) Pax & K.Hoffm., <i>D. monosperma</i> (Merr.) Pax & K.Hoffm., <i>D. neglecta</i> (Koord.) Pax & K.Hoffm., <i>D. nervosa</i> (Hook.f.) Pax & K.Hoffm., <i>D. ochrodasya</i> Airy Shaw, <i>D. ovalis</i> (J.J.Sm. ex KoorD. & Valetton) Pax & K.Hoffm., <i>D. oxyodonta</i> Airy Shaw, <i>D. pachycarpa</i> Airy Shaw, <i>D. perakensis</i> Gage, <i>D. polyalthioides</i> Airy Shaw, <i>D. polyneura</i> Airy Shaw, <i>D. prunifera</i> Airy Shaw, <i>D. rhakodiskos</i> (Hassk.) Bakh.f., <i>D. riparia</i> Ridl., <i>D. sibuyanensis</i> (Elmer) Pax & K.Hoffm., <i>D. simalurensis</i> J.J.Sm., <i>D. stylosa</i> Airy Shaw, <i>D. subcrenata</i> (Merr.) Pax & K.Hoffm., <i>D. subcubica</i> (J.J.Sm.) Pax & K.Hoffm., <i>D. subsymmetrica</i> J.J.Sm., <i>D. talamauensis</i> J.J.Sm., <i>D. teysmannii</i> (Hassk.) Bakh.f. & Steenis, <i>D. tomentella</i> Pax & K.Hoffm., <i>D. xanthophylloides</i> Airy Shaw	
Malesia and Australasia	1 sp.
<i>D. celebica</i> (Boerl. & Koord.) Pax & K.Hoffm.	

K.Hoffm. and *D. gerrardinoides* Radcl.-Sm., are easily separated by ripe fruits. In *D. usambarica* (Pax.) Hutch., the varieties were described by differ mostly in ripe fruit characters. In other species pairs, such as *D. floribunda* (Müll.Arg.) Hutch. and *D. ivorensis* Hutch. & Dalziel, the size of the fruit and the woodiness of the mesocarp appears as if it would attract different sized vertebrates. Fruit characters are particularly important in the taxonomy of *D. littoralis* (C.B.Rob.) Merr. and close species in Southeast Asia (Airy Shaw 1975). We put forward the hypothesis that competition for vertebrate dispersers should be considered as a potential driver for speciation in *Drypetes* in Africa.

After the taxonomic treatment here offered for *D. gabonensis*, *D. aphanes* sp. nov. and *D. cauta* sp. nov., these three species will be included in a wider systematic survey in which the comparative study of their morphology in a phylogenetic context in order to confirm or find out their position in an updated infra-generic classification of *Drypetes*. There is a need to understand their evolutionary relationships with other cauliflorous species from the rest of the continent, and to evaluate the taxonomic value of many of the morphologic characters here presented and, particularly, those with diagnostic value or linked to their reproductive biology. Until we complete this study, we have decided to assign both *D. aphanes*

and *D. cauta* to *D. sect. Sphragidia* and to retain *D. gabonensis* in the section where it has traditionally been placed, *D. sect. Oligandrae*. Likewise, we also consider it prudent to wait for this future income of phylogenetic information to carry out the lectotypification of *D. sect. Oligandrae* satisfactorily. We think that the species of *Drypetes* deserve a special attention in conservation policies due to both their ecological value (the presence of these species has been suggested as an indicator of good-quality, undisturbed forests, cf. Cheek *et al.* 2021) and their reproductive singularities. They belong to a family, the Putranjivaceae, that is regarded as potentially enriched in species at risk since dioecy is considered itself to be an indicator of high level of extinction in groups of tropical plants under the current conditions (Vamosi & Vamosi 2005, 2008). In line with this, our preliminary IUCN assessments of the conservation status for these species show that *D. gabonensis* and *D. cauta* are ‘Vulnerable’ species, and *D. aphanes* is an ‘Endangered’ species. We hope that this article will facilitate a deeper future study of the reproductive traits of these species in Africa, and particularly promote their conservation.

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