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Re-evaluation of the genus *Englerodendron* (Leguminosae–Detarioideae), including *Isomacrolobium* and *Pseudomacrolobium*

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Abstract. On the basis of a new phylogeny of the Detarioideae, with a particular focus on *Englerodendron* Harms, *Anthonotha* P.Beauv. and related genera, the possible options for delimiting monophyletic genera are discussed. As a result, *Isomacrolobium* Aubrév. & Pellegr. and *Pseudomacrolobium* Hauman are synonymised under *Englerodendron*. The following 12 new combinations are formed within the expanded *Englerodendron: E. brachyrhachis* (Breteler) Estrella & Ojeda, *E. explicans* (Baill.) Estrella & Ojeda, *E. graciliflorum* (Harms) Estrella & Ojeda, *E. hallei* (Aubrév.) Estrella & Ojeda, *E. isopetalum* (Harms) Breteler & Wieringa, *E. lebrunii* (J.Léonard) Estrella & Ojeda, *E. leptorrhachis* (Harms) Estrella & Ojeda, *E. mengei* (De Wild.) Estrella & Ojeda, *E. nigericum* (Baker f.) Estrella & Ojeda, *E. obanense* (Baker f.) Estrella & Ojeda, *E. triplisomere* (Pellegr.) Estrella & Ojeda and *E. vignei* (Hoyle) Estrella & Ojeda. A key to identification of the 17 species now recognised within *Englerodendron* is presented.

Additional keywords: Africa, *Anthonotha*, classification, generic delimitation, *Macrolobium*, monophyly.

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Introduction

The tribe Amherstieae Benth. is the most diverse group within subfamily Detarioideae of the Leguminosae, with 50 genera and ~570 species being currently recognised (Legume Phylogeny Working Group 2013, 2017; de la Estrella *et al*. 2018). Within this tribe, floral morphology is extremely variable and, in many taxa, highly modified, making classification of the group very challenging (Mackinder 2005; de la Estrella *et al*. 2018). Flowers vary from bilaterally to radially symmetrical, with sepals sometimes entirely lacking but most commonly having 4–5 (rarely up to 10) sepals. Petal number is also extremely variable. Five petals are found in many species and this seems to be the ancestral state (Ojeda *et al*. 2019); however, several reduction series exist, often resulting in one large adaxial petal with the other four being reduced or absent. In a few genera, all petals have disappeared. In *Englerodendron usambarense* Harms, an additional one or two petals are present, resulting in six- or seven-merous flowers (Breteler 2008). Stamen numbers in tribe Amherstieae follow trends similar to those seen in the petal number. The ancestral value is likely to be 10, which is reduced in several lineages, often resulting in three fertile stamens and several staminodes, but these staminodes may disappear in a later step (Ojeda *et al*. 2019). In some cases, the stamen number is increased, being, for example, ~20 in some species of *Hymenostegia* Harms, and up to 80 in *Maniltoa* Scheff. Reduction in stamen number, including transformation to staminodes as an intermediate step towards complete loss, appears to be a general trend observed in several groups (Bruneau *et al*. 2014), potentially being correlated with flower size. Indeed, members of the genus with the largest flowers in the Amherstieae (*Berlinia* Sol. ex Hook.f.) have 10 stamens and no or partial reduction in the numbers of sepals and petals. However, not all lineages with small flowers have a reduced stamen number. Some genera with small flowers, such as *Michelsonia* Hauman, *Bikinia* Wieringa and *Zenkerella* Taub., have 10 stamens (Cowan and Polhill 1981; Wieringa 1999). One consequence of this variability is that the number of stamens and staminodes appears to be highly homoplasious and does not provide a good basis for classification. Some of the most extreme variation in floral traits within Amherstieae is found within the Berlinia clade (*sensu* Bruneau *et al*. 2008), where great plasticity in the number of petals is observed within the same species and among flowers of the same individual (Breteler 2006, 2008, 2010, 2011; Ojeda *et al*. 2019). For example, Breteler (2008) observed that the corolla in *Isomacrolobium* Aubrév. & Pellegr. is extremely labile, which hampered any attempt to structure the

observed variability into distinct taxonomic entities. The only distinction Breteler (*l.c.*) could make was between an actinomorphic and a zygomorphic corolla.

The Berlinia clade was first described by Bruneau *et al*. (2000, 2001) as the 'Macrolobieae' clade, and further delimited to include 18 exclusively African genera (Bruneau *et al*. 2008). The ancestral biome of this clade was reconstructed as primary evergreen rainforest in tropical Africa (de la Estrella *et al*. 2017), where Detarioideae, and especially members of the Berlinia clade, form the most dominant group of trees in western central Africa (Wieringa 1999; Newbery *et al*. 2013).

Within the Berlinia clade, several genera have been the focus of recent taxonomic treatments, increasing our knowledge of their diversity and morphological complexity (Wieringa 1999; Mackinder and Pennington 2011; de la Estrella *et al*. 2012*a*, 2012*b*; de la Estrella and Devesa 2014; van der Burgt *et al*. 2015). *Anthonotha* P.Beauv., *Isomacrolobium* and *Englerodendron* Harms, which show particularly complex floral ontogeny, were recently revised by Breteler (2006, 2008, 2010, 2011).

Anthonotha was first described by Palisot de Beauvois (1806) to accommodate a new species from West Africa, but subsequently described African taxa were initially placed within a pantropical *Macrolobium* Schreb. (see de la Estrella and Devesa (2014), for a history review of the group). Although it is the most speciose genus within Detarioideae and was previously posited as being non-monophyletic (Mackinder 2005), *Macrolobium*, as currently circumscribed, is an American genus recently demonstrated to be monophyletic (Murphy *et al*. 2018). The African taxa previously treated under *Macrolobium* had already been accommodated by Léonard (1952, 1954, 1955) within a reinstated *Anthonotha* and the newly published *Gilbertiodendron* J.Léonard, *Paramacrolobium* J.Léonard and *Pellegriniodendron* J. Léonard. *Isomacrolobium* and *Triplisomeris* Aubrév. & Pellegr. were subsequently split off from *Anthonotha* (Aubréville and Pellegrin 1958 and Aubréville 1959 respectively) and Aubréville (1968) added a further segregate genus, namely, *Leonardendron* Aubrév. Breteler (2006, 2008, 2010, 2011), accepted *Anthonotha sensu* Aubréville & Pellegrin (Aubréville 1959) but rearranged the other species into *Isomacrolobium* (zygomorphic flowers) and *Englerodendron* (non-zygomorphic flowers). *Gilbertiodendron* and related genera have been the subject of further taxonomic and phylogenetic studies (de la Estrella *et al*. 2012*a*, 2014), but relationships among other Berlinia clade genera, especially those of *Anthonotha* and related genera, have remained obscure (de la Estrella *et al*. 2017, 2018).

The new phylogenomic framework

With the aim to resolve relationships within Detarioideae, Ojeda *et al*. (2019) developed a target capture-sequence bait set for the subfamily, by selecting orthologues shared among four representative transcriptomes from the group. Target capture sequence (Hybseq) has proven to be an effective strategy for phylogenetic reconstruction across different taxonomic levels (Vatanparast *et al*. 2018; Villaverde *et al*. 2018). With this Detarioideae bait set (ver. 1.0, MYbaits, Arbor Biosciences, Ann Arbor, MI, USA), Ojeda *et al*. (2019) reconstructed a phylogeny for *Anthonotha* and closely related genera, which included near-complete species sampling of *Anthonotha*, *Isomacrolobium* (except *I. sargosii* (Pellegr.) Aubrév. & Pellegr. and *I. hallei* Aubrév.) and *Englerodendron*, the three genera that had been previously recognised within the group (Bruneau *et al*. 2000, 2001, 2008; de la Estrella *et al*. 2018). With near-complete genus-level sampling across the subfamily, the previously unplaced *Pseudomacrolobium* Hauman, a monospecific African endemic genus from Congo (Kinshasa), was shown to be closely related to *Englerodendron* and *Isomacrolobium* (Ojeda *et al*. 2019). The Ojeda *et al*. (2019) phylogeny (Fig. 1) shows more robust support across the clades than does any previous study. Two main clades are resolved, one including all *Anthonotha* species and the other containing the three remaining genera of *Englerodendron*, *Isomacrolobium* and *Pseudomacrolobium*. However, neither *Englerodendron* nor *Isomacrolobium* is monophyletic in this phylogeny (Fig. 1), leaving several options for generic re-delimitation.

Generic circumscription

The Englerodendron clade as shown in Fig. 1 could be split into different recircumscribed genera (*Englerodendron, Isomacrolobium*, *Pseudomacrolobium*); however, this would require reinstatement of genera currently placed in synonymy under *Isomacrolobium*, and the resulting genera would not be diagnosable morphologically. Breteler (2006, 2008, 2011) previously recognised that the members of this group exhibit extensive floral variation, and the phylogenetic evidence (Fig. 1) supports the option, chosen here, of combining these three genera within an enlarged *Englerodendron* (Ojeda *et al*. 2019).

Most of the morphological differences given by Breteler (2008) to differentiate *Anthonotha* from *Isomacrolobium* apply equally to the newly circumscribed *Englerodendron*, even though, in that paper, Breteler did not consider *Englerodendron* because he assumed it to be more closely related to *Oddoniodendron* De Wild. and *Isoberlinia* Craib & Stapf ex Holland (Breteler 2006). However, these characters apply to his *Englerodendron* species as well, just as they do for *Pseudomacrolobium*, which, because of its many stamens (10–13), has never previously been considered as being related to this clade. *Anthonotha* is characterised by the presence of a single large petal in the adaxial position, which has a well-developed, inrolled, gutter-shaped claw that is at least half as long as the lamina and the lamina is always bilobed or divided into two. The other four petals may be reduced in various stages, or absent. *Englerodendron* in this new circumscription has (1–)2–5 large petals, whereas the other petals may be reduced in various stages or be absent. Where only a single petal remains (possible in *E. vignei* (Hoyle) Estrella & Ojeda), it is not located in the adaxial position. Petals may be clawed, but the claw is often short and not inrolled into a solid support for the laminae, and the lamina of the adaxial petal may be lobed or split, although not as strongly as it is in *Anthonotha*. In addition to these floral differences, *Anthonotha* can be distinguished by its dense, usually persistent (except in *A. trunciflora* (Harms) J.Léonard), appressed indumentum on the lower leaflet surfaces, whereas the leaflets of *Englerodendron* are sparsely hairy to glabrous, the indumentum not obscuring the lower leaflet surfaces.

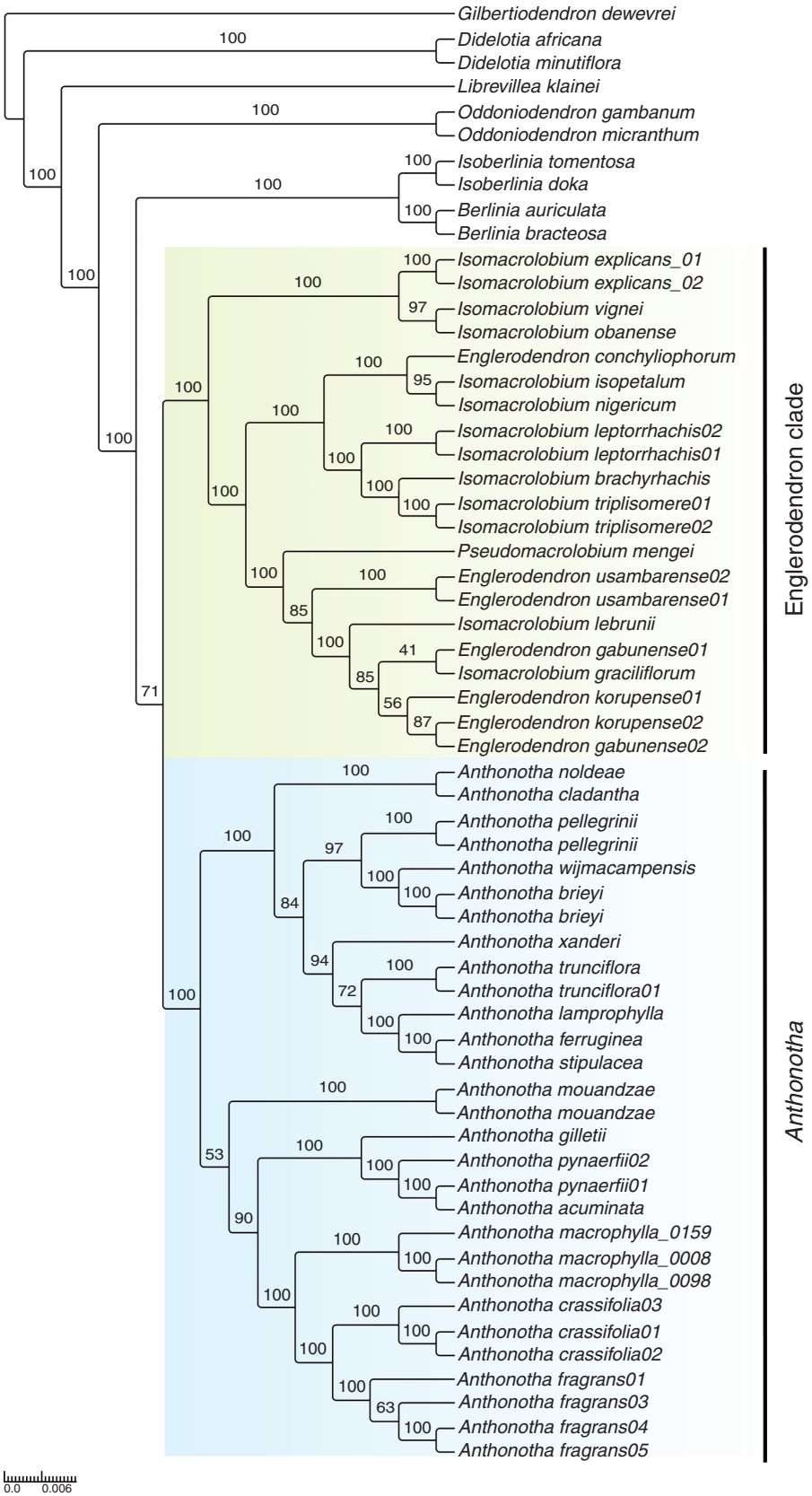

Fig. 1. Phylogeny of the Berlinia clade, showing the monophyly of *Anthonotha sensu stricto* and of Englerodendron *sensu lato*. This tree was obtained from Ojeda *et al*. (2019), and is based on a concatenated analyses of 922 exonic regions (clusters) and a matrix size of 239 334 base pairs (74.06% taxon occupancy) using maximum likelihood (RAxML, ver. 8.2.9, https://github.com/stamatak/standard-RAxML, the GTRCAT model, 1000 bootstrap replicates and default settings, Stamatakis 2014). Full analytical details are available in Ojeda *et al*. (2019). Values above branches are bootstrap values.

Taxonomic treatment

Englerodendron Harms, *Bot. Jahrb. Syst.* 40(1): 27–30, fig. 2 (1907)

Type species: Englerodendron usambarense Harms.

Pseudomacrolobium Hauman, *Bull. Séances Inst. Roy. Colon. Belge* 23: 477 (1952), *syn. nov.*

Type species: Pseudomacrolobium mengei (De Wild.) Hauman.

Isomacrolobium Aubrév. & Pellegr., *Bull. Soc. Bot. France* 104: 497 (1958), *syn. nov.*

Type species: Isomacrolobium leptorrhachis (Harms) Aubrév. & Pellegr.

Triplisomeris Aubrév. & Pellegr., *Bull. Soc. Bot. France* 104: 497 (1958), *syn. nov.* [previously synonymised under *Isomacrolobium* Aubrév. & Pellegr. (Breteler 2008)].

Type species: Triplisomeris explicans (Baill.) Aubrév. & Pellegr.

Leonardendron Aubrév., *Adansonia* sér. 2, 8: 167 (1968).

Type species: Leonardendron gabunense (J.Léonard) Aubrév.

Trees or shrubs, up to 36 m tall and 85-cm diameter at breast height. Stipules free or united at base. Leaves paripinnate, 1–7-jugate, leaflets opposite to subopposite, glabrous to sparsely hairy below. Inflorescence of most species a compound raceme up to 1.25 m long, but, in some species, shorter and not pendulous. Bracteoles covering the flower in bud. Flowers 5-merous (6- or 7-merous in *E. usambarense*). Sepals 5(–7), or 4 when the two adaxial ones are united. Petals (1–)2–5(–7), base often narrowed into a claw, but claw not stiff or inrolled. Fertile stamens 3–7 or 10(–13), supplemented by up to 7 staminodes. Ovary 2–8 ovulate. Pods leathery to woody, (explosively) dehiscent or only dehiscent once on the forest floor, laterally flattened, in general oblong, depauperate pods also (ob)ovate.

Seventeen species, distributed in rain forest of tropical Africa from Guinea to Congo (Kinshasa) and one disjunct species in the Usambara Mountains of Tanzania (*Englerodendron usambarense*) (Robyns 1952; Breteler 2006, 2008, 2011; van der Burgt *et al*. 2007).

1. *Englerodendron brachyrhachis* (Breteler) Estrella & Ojeda, *comb. nov.*

Isomacrolobium brachyrhachis Breteler, *Pl. Ecol. Evol.* 144 (1): 66 (2011).

Type: Gabon, 50 km south-east of Achouka, *A.M.Louis, Breteler & de Bruijn 729* (holo: WAG [3 sheets]!; iso: BR!, K!, LBV!, MA!, MO!, P!, PRE!).

2. *Englerodendron conchyliophorum* (Pellegr.) Breteler, *Adansonia* 28(1): 109 (2006)

Macrolobium conchyliophorum Pellegr., *Bull. Soc. Bot. France* 88: 503 (1941); *Anthonotha conchyliophora* (Pellegr.) J.Léonard, *Mém. Cl. Sci. Acad. Roy. Sci. Belgique (8vo)* sér. 2, 30(2): 223 (1957); *Isomacrolobium conchyliophorum* (Pellegr.) Aubrév. & Pellegr., *Bull. Soc. Bot. France* 104: 498 (1958).

Type: Gabon, near Lastoursville, Micouma, 23 Nov. 1929, *M. G. Le Testu 7680* (lecto: P[2 sheets]!; isolecto: BM, BR [2 sheets]!, WAG [3 sheets]!), *fide* F.Pellegrin, *Mém. Inst. Étud. Centrafr.* 1: 45 (1949) and, subsequently, J.Léonard, *Mém. Cl. Sci. Acad. Roy. Sci. Belgique (8vo)* sér. 2, 30(2): 224 (1957)).

3. *Englerodendron explicans* (Baill.) Estrella & Ojeda, *comb. nov.*

Vouapa explicans Baill., *Adansonia* 6: 181, adnot. (oct. 1865); *Macrolobium explicans* (Baill.) Keay, *Kew Bull.* 8(4): 490 (1953); *Anthonotha explicans* (Baill.) J.Léonard, *Bull. Jard. Bot. État. Bruxelles* 25: 202 (1955); *Triplisomeris explicans* (Baill.) Aubrév. & Pellegr., *Bull. Soc. Bot. France* 104: 497 (1958); *Isomacrolobium explicans* (Baill.) Breteler, *Syst. & Geogr. Pl.* 78(2): 143 (2008).

Type: Guinea, Fouta Djallon, 1837, *Heudelot 738* (holo: P [3 sheets]!; iso: BM!, BR!, HBG, K [2 sheets]!, OXF!, WAG [2 sheets]!).

Note

In the first part of his paper (*Adansonia* 5: 361), Baillon stated that he was studying the herbarium of the 'Musée des Colonies Françaises'; this herbarium is now part of P.

Macrolobium heudelotii Benth., *Trans. Linn. Soc.* 25: 308. (Nov. 1865) *nom. superfl.*

Type: Guinea, Fouta Djallon, 1837, *Heudelot 738* (syn-: BM!, BR!, K [2 sheets]!, P [3 sheets]!, OXF!, WAG [2 sheets]!).

Note

Bentham referred to the sheet in the Hooker herbarium (then still private, now part of K), but another sheet was part of his own herbarium that was incorporated in K before publication. Both got annotated with observations and were clearly used for the description; hence, all *Heudelot 738* sheets should be regarded as syntypes.

4. *Englerodendron gabunense* (J.Léonard) Breteler, *Adansonia* 28(1): 109 (2006)

Anthonotha gabunensis J.Léonard, *Mém. Cl. Sci. Acad. Roy. Sci. Belgique (8vo)* sér. 2, 30(2): 224 (1957); *Isomacrolobium gabunense* (J.Léonard) Aubrév. & Pellegr., *Bull. Soc. Bot. France* 104: 498 (1958); *Leonardendron gabunense* (J.Léonard) Aubrév., *Adansonia* sér. 2, 8: 167 (1968).

Type: Gabon, Roungassa, 21 Dec.1929, *G.M.P.C. Le Testu 7808* (holo: BR!; iso: BM, BR!, K, LISC, P!, WAG!). The isotype at BR arrived in BR only after publication of the basionym; hence, the other BR sheet is the holotype as indicated in the protologue.

5. *Englerodendron graciliflorum* (Harms) Estrella & Ojeda, *comb. nov.*

Macrolobium graciliflorum Harms, *Bot. Jahrb. Syst.* 45(2): 302 (1910); *Anthonotha graciliflora* (Harms) J.Léonard, *Bull. Jard. Bot. État. Bruxelles* 25: 202 (1955); *Isomacrolobium graciliflorum* (Harms) Aubrév. & Pellegr., *Bull. Soc. Bot. France* 104: 498. 1958.

Type: Equatorial Guinea, Nkolentangan, Dec. 1907, *Tessmann B.57* (lecto: K, isolecto: BR (fragment from K), B (destroyed) *fide* F.J.Breteler, *Pl. Ecol. Evol.* 144 (1): 71 (2011)).

6. *Englerodendron hallei* (Aubrév.) Estrella & Ojeda, *comb. nov*.

Isomacrolobium hallei Aubrév., *Fl. Gabon* 15: 362 (1968); *Anthonotha hallei* (Aubrév.) J.Léonard in L.J.G. van der Maesen *et al*. (eds), *Biodiversity Afr. Pl. (Proc. XIV AETFAT Congr.)* 446 (1996).

Type: Gabon, Abanga, chantier C.E.F.A., bord riv. Lano, Jun. 1963, *N.Hallé 2195* (holo: P!).

7. *Englerodendron isopetalum* (Harms) Breteler & Wieringa, *comb. nov*.

Macrolobium isopetalum Harms, *Bot. Jahrb. Syst.* 40(1): 25–26 (1907); *Anthonotha isopetala* (Harms) J.Léonard, *Bull. Jard. Bot. État. Bruxelles* 25: 202 (1955); *Isomacrolobium isopetalum* (Harms) Aubrév. & Pellegr., *Bull. Soc. Bot. France* 104: 498 (1958).

Type: Cameroon, Bipindi, 1905, *G.Zenker 3384* (lecto: BR!; isolecto: BM!, E, G!, HBG, GOET, K, L!, M, MO!, P!, S, US,*fide* J.Léonard, *Mém. Cl. Sci. Acad. Roy. Sci. Belgique (8vo)* sér. 2, 30 (2): 224 (1957)).

8. *Englerodendron korupense* Burgt, *Adansonia* 29 (1): 60 (2007)

Type: Cameroon, South-west Province, Korup National Park, north-western plot near P transect, Subplot 44LN, 6 Apr. 2005, *X. M. van der Burgt 741* (holo: WAG!; iso: BR, G, K!, MO, P, SCA, WAG!, YA).

9. *Englerodendron lebrunii* (J.Léonard) Estrella & Ojeda, *comb. nov*.

Macrolobium lebrunii J.Léonard, *Bull. Jard. Bot. État. Bruxelles* 22: 186 (1952); *Anthonotha lebrunii* (J.Léonard) J.Léonard, *Mém. Cl. Sci. Acad. Roy. Sci. Belgique (8vo)* sér. 2, 30(2): 226 (1957); *Isomacrolobium lebrunii* (J.Léonard) Aubrév. & Pellegr. ex Breteler, *Syst. & Geogr. Pl.* 78 (2): 143 (2008).

Type: D.R.Congo, between Dekese and Bumbuli, Oct. 1932, *J-P.A.Lebrun 6497* (holo: BR[3 sheets]!; iso: K!, WAG!, YBI).

10. *Englerodendron leptorrhachis* (Harms) Estrella & Ojeda, *comb. nov*.

Macrolobium leptorrhachis Harms, *Bot. Jahrb. Syst.* 33(1): 157 (1902); *Anthonotha leptorrhachis* (Harms) J.Léonard, *Bull. Jard. Bot. État. Bruxelles* 25: 202 (1955); *Isomacrolobium leptorrhachis* (Harms) Aubrév. & Pellegr., *Bull. Soc. Bot. France* 104: 498 (1958).

Type: Cameroon, Bipindi, Sep. 1901, *G.A,Zenker 2445* (lecto: P!; isolecto: B (destroyed), BR!, G!, GOET, K!, L!, MO!, WAG!, *fide* F.J.Breteler, *Pl. Ecol. Evol.* 144 (1): 73 (2011)).

11. *Englerodendron mengei* (De Wild.) Estrella & Ojeda, *comb. nov*.

Berlinia mengei De Wild., *Pl. Bequaert.* 3(1): 143 (1925); *Pseudomacrolobium mengei* (De Wild.) Hauman, *Bull. Séances Inst. Roy. Colon. Belge* 23: 477 (1952).

Type: Congo (Kinshasa), Djombo, 5 Mar. 1913, *A.Mengé 88* (holo: BR).

12. *Englerodendron nigericum* (Baker f.) Estrella & Ojeda, *comb. nov*.

Macrolobium leptorrhachis var. *nigericum* Baker f., in A.B.Rendle, E.G.Baker, H.F.Wernham and S.Moore, *Cat. Pl. Oban* 29 (1913); *Macrolobium nigericum* (Baker f.) J.Léonard, *Fl. Congo Belge & Ruanda–Urundi* 3: 416 (1952); *Anthonotha nigerica* (Baker f.) J.Léonard, *Bull. Jard. Bot. État. Bruxelles* 25: 202 (1955); *Isomacrolobium nigericum* (Baker f.) Aubrév. & Pellegr., *Bull. Soc. Bot. France* 104: 498 (1958).

Type: Nigeria, Oban, 1911, *Talbot 582* (lecto: BM[2 sheets]!; isolecto: K!), *fide* F.Pellegrin, *Bull. Soc. Bot. France* 104: 498 (1958))

13. *Englerodendron obanense* (Baker f.) Estrella & Ojeda, *comb. nov*.

Macrolobium obanense Baker f. in A.B.Rendle, E.G.Baker, H.F. Wernham and S.Moore, *Cat. Pl. Oban* 28 (1913); *Anthonotha obanensis* (Baker f.) J.Léonard, *Bull. Jard. Bot. État. Bruxelles* 25: 203 (1955); *Isomacrolobium obanense* (Baker f.) Aubrév. & Pellegr., *Bull. Soc. Bot. France* 104: 498 (1958).

Type: Nigeria, Oban, 1911–1912, *Mr. & Mrs. Talbot 1428* (lecto-: BM!,; isolecto- BR! (fragment), K!) *fide* F.Pellegrin, *Bull. Soc. Bot. France* 104: 498 (1958)).

Macrolobium elongatum Hutch., *Bull. Misc. Inform. Kew* 1916(9): 229 (1916); *Anthonotha elongata* (Hutch.) J.Léonard, *Bull. Jard. Bot. État. Bruxelles* 25: 202 (1955); *Isomacrolobium elongatum* (Hutch.) Aubrév. & Pellegr., *Bull. Soc. Bot. France* 104: 498 (1958).

Type: Sierra Leone, Pujehun, 16 Feb. 1914, *C.E.Lane-Poole 161* (holo: K[2 sheets]!; iso: BR).

Macrolobium ernae Dinkl., *Repert. Spec. Nov. Regni Veg.* 42: 157 (1937); *Anthonotha ernae* (Dinkl.) J.Léonard, *Bull. Jard. Bot. État. Bruxelles* 25: 202 (1955); *Triplisomeris ernae* (Dinkl.) Aubrév. & Pellegr., *Bull. Soc. Bot. France* 104: 497 (1958).

Type: Liberia, Monrovia, 5 Feb. 1922, *Dinklage 2805* (syn-: B (destroyed), HBG, P! [two sheets]). Breteler (2011) selected a neotype (*Jongkind 5706,* WAG), only to discover later that some isotypes were extant.

14. *Englerodendron sargosii* Pellegr., *Bull. Soc. Bot. France* 68: 11 (1921)

Macrolobium sargosii (Pellegr.) Pellegr., *Bull. Soc. Bot. France* 77: 666 (1931); *Anthonotha sargosii* (Pellegr.) J.Léonard, *Mém. Cl. Sci. Acad. Roy. Sci. Belgique (8vo)* sér. 2, 30(2): 225 (1957); *Isomacrolobium sargosii* (Pellegr.) Aubrév. & Pellegr., *Bull. Soc. Bot. France* 104: 498 (1958).

Type: D.R. Congo, Kouilou River, *R.Sargos 101* (holo: P!; iso: BR!, WAG!). Both BR and WAG are fragments from the holotype obtained after the publication of the protologue.

15. *Englerodendron triplisomere* (Pellegr.) Estrella & Ojeda, *comb. nov*.

Macrolobium triplisomere Pellegr., *Bull. Soc. Bot. France* 88: 508 (1941); *Anthonotha triplisomeris* (Pellegr.) J.Léonard, *Mém. Cl. Sci. Acad. Roy. Sci. Belgique (8vo)* sér. 2, 30(2): 226 (1957); *Triplisomeris triplisomeris* Aubrév. & Pellegr., *Bull. Soc. Bot. France* 104: 497 (1958), *nom. inval.* [tautonym]; *Isomacrolobium triplisomere* (Pellegr.) Breteler, *Syst. & Geogr. Pl.* 78(2): 143 (2008).

Type: Gabon, Nyanga Mount, between l'Onoij and Mouila, 26 Nov. 1925, *G.M.P.C. Le Testu 5792* (lecto-: P!; isolecto: BM!, WAG!), *fide* J.Léonard, *Mém. Cl. Sci. Acad. Roy. Sci. Belgique (8vo)* sér. 2, 30(2): 226 (1957)).

16. *Englerodendron usambarense* Harms, *Bot. Jahrb. Syst.* 40(1): 28 (1907)

Type: Tanzania, Lushoto District, between Amani and Bomole, Oct. 1905, *H.G.A.Engler 3436* (syn- B(destroyed), B! [in Herb. A.Peter 48011, photo: K!]). Harms also mentioned a second gathering (*W. Busse 2210*) that is assigned to the species with doubt ('Offenbar'), rendering it unclear whether this should be considered syntype material as well.

17. *Englerodendron vignei* (Hoyle) Estrella & Ojeda, *comb. nov.*

Macrolobium vignei Hoyle, *Bull. Misc. Inform. Kew* 1933(4): 171 (1933); *Anthonotha vignei* (Hoyle) J.Léonard, *Bull. Jard. Bot. État. Bruxelles* 25: 203 (1955); *Isomacrolobium vignei* (Hoyle) Aubrév. & Pellegr., *Bull. Soc. Bot. France* 104: 498 (1958).

Type: Ghana, Dompim, May 1930, *C.Vigne 1968* (lecto-: K!; isolecto: BR, FHO!, WIS). *fide* A.Aubréville & F.Pellegrin, *Bull. Soc. Bot. France* 104: 498 (1958)). Although Hoyle marked the K sheet as holotype, the protologue cites both Kew and Oxford, rendering them syntypes.

Key to the species of *Englerodendron*

Adapted from previous treatments for the included genera (Cowan and Polhill 1981; Breteler 2006, 2008, 2010, 2011; van der Burgt *et al*. 2007).

1. Stamens 10(–13), fertile and uniform; free sepals subcordate, adaxial sepals largely joined, bifid; 3 petals well developed, 2 minute; pod compartmented within ..... ***E. mengei*** (D.R. Congo)
1: Fertile stamens 3–7, in addition 0–7 staminodes; 4 or 5 sepals equal to narrowed at base; petals (2–)5–7, variable in shape and size; pod ±continuous inside 2
2. Fertile stamens 5–7, 0–6 minute staminodes; flowers more or less actinomorphic, 5 sepals little narrowed at base, adaxial sepals partly united; petals 5–7, subequal 3
3. Stipules 10–45 mm long, enveloping the leaf axis; bracteoles 15–20 mm long; petals ±as long as the fertile stamens .... ***E. conchyliophorum*** (Nigeria to Gabon)
3: Stipules 1–7 mm long, not enveloping the leaf axis; bracteoles 5–12 mm long; petals shorter than the fertile stamens 4
4. Flowers 6- or 7-merous; largest leaflets 10.8(–12.5) cm long; inflorescences 9–13 cm long ..... ***E. usambarense*** (Tanzania)
4: Flowers 5-merous; largest leaflets up to 19(–27) cm long; inflorescences 18–78 cm long 5
5. Petiole 2–4 mm long; lowest leaflet pair subsessile, cordiform, 1.2–4 cm long; bracteoles 5–7 mm long; staminodes 0–2 ..... ***E. gabunense*** (Cameroon to Gabon)
5: Petiole 4–13 mm long; lowest leaflet pair petiolulate, ovate, (3–)6–9(–13) cm long; bracteoles 9–12 mm long; staminodes 5 ..... ***E. korupense*** (Cameroon)
2: Fertile stamens 3, 0–7 staminodes; flowers zygomorphic, 4 sepals (adaxial sepals more or less united), equal to slightly unequal; petals 1–5, usually very variable in size and shape 6
6. Leaf rachis winged, at least below the attachment of each leaflet pair ..... ***E. leptorrhachis*** (Cameroon)
6: Leaf rachis not winged, usually terete to somewhat grooved 7
7. Leaves 1-jugate ..... ***E. hallei*** (Gabon)
7: Leaves 2–7-jugate, exceptionally 1-jugate, but then leaves with at least two pairs of leaflets present as well 8
8. Leaves 5–7-jugate ..... ***E. lebrunii*** (D.R. Congo)
8: Leaves 2–4-jugate, rarely 1-jugate leaves may be present as well 9
9. Flowers sessile (or nearly so); bracts (5–)6–9 mm long, ±as long as the mature bracteoles..... ..... ***E. vignei*** (Guinea to Ghana)
9: Flowers distinctly pedicellate; bracts up to 2 mm long, much shorter than the mature bracteoles 10
10. Leaves 2-jugate; leaf rachis (5–)8–10(–18) mm long, petiole (1–)2–3(–4) mm long; leaflets of the upper pair 1.5–2(–2.5) times as long as those of the lower pair ..... ***E. brachyrhachis*** (Gabon)
10: Leaves (1–)2–4-jugate; differing from above leaf characters, the petiole or the rachis longer, or with more than 4 leaflets or apical leaflets relatively smaller than the lower leaflets 11
11. Leaves 2-jugate, rarely 1-jugate or unifoliolate, but then 2-jugate leaves also present; sepals with ciliate apex ..... ***E. triplisomere*** (Gabon)
11: Leaves 2–4-jugate, sometimes 1-jugate leaves may be present as well, sepals glabrous..... 12
12. Inflorescence up to 20 cm long, ±stiff, not pendulous; sepals and petals subequal in length, the petals equal in size and shape... 13
13. Branchlets glabrous; leaves glabrous; pedicel (1.5–)2–3(–4) mm long; petals and stamens glabrous.... ***E. isopetalum*** (Cameroon to Gabon)
13: Branchlets sparsely pubescent, glabrescent; leaves sparsely pubescent; pedicel 5 mm long; petals and stamens densely villous at base..... ***E. sargosii*** (Gabon to Congo)
12: Inflorescence slender, pendulous, up to ~1 (–1.25) m long; petals unequal, the adaxial one(s) bigger 14
14. Leaves 2-jugate, leaflets with 12–15 pairs of main lateral veins ..... ***E. nigericum*** (Nigeria to Cameroon (cf. D.R. Congo))
14: Leaves (1–)2–4-jugate, leaflets with (4–)5–9(–11) pairs of main lateral veins.... 15
15. Bracteoles 8–10(–13) × 4–7 mm, firm, stiff, veins not visible..... ..... ***E. obanense*** (Liberia to Ivory Coast; Nigeria to D.R. Congo)
15: Bracteoles (4–)5–6(–7) × 2–5 mm, thin, ±flexible, almost transparent, veins visible 16
16. Petiole 1–4 cm long; petals 5 (rarely a small petal missing), 3 large, subequal, 6–8 × 3–5 mm, 2 small, ligulate to ovate–elliptic, 1–4 mm..... ..... ***E. explicans*** (Guinea to Liberia)
16: Petiole (1–)2–4(–6) mm long; petals 2–5, subequal, narrowly spathulate, 3–3.5 mm long..... ..... ***E. graciliflorum*** (Cameroon to D.R. Congo)

Conflicts of interest

The authors declare that they have no conflicts of interest.

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