

***Terminalia carinata* Sabatier & J.Engel, sp. nov. (Combretaceae), a new large tree species from the Guiana shield revealed by re-examination of material previously identified as *T. guyanensis* Eichler**

**Julien ENGEL
Daniel SABATIER**

AMAP, Université de Montpellier, IRD, CIRAD, CNRS, INRAE, Boulevard de la Lironde,
TA A-51/PS2, F-34398 Montpellier cedex 5 (France)
and AMAP, IRD, Herbar de Guyane, B.P. 90165, 97323 Cayenne, French Guiana (France)
julien.engel@ird.fr (corresponding author)

Submitted on 10 December 2019 | accepted on 13 May 2020 | published on 2 November 2020

Engel J. & Sabatier D. 2020. — *Terminalia carinata* Sabatier & J.Engel, sp. nov. (Combretaceae), a new large tree species from the Guiana shield revealed by re-examination of material previously identified as *T. guyanensis* Eichler. *Adansonia*, sér. 3, 42 (16): 261-271. <https://doi.org/10.5252/adansonia2020v42a16>. <http://adansonia.com/42/16>

ABSTRACT

A new species of *Terminalia* L. (Combretaceae) from the Guiana shield is described as *T. carinata* Sabatier & J.Engel, sp. nov. based on morphological evidences. This new species was often misidentified as *T. guyanensis* Eichler from which it differs, as well as from other neotropical *Terminalia*, by its leaf undersurface palish-gray and slightly pubescent, quite long petioles and fruits with two wings wider than the body that is distinctly keeled on one face and flat on the other. An updated description of *T. guyanensis* is provided and the conservation status of *T. carinata* Sabatier & J.Engel, sp. nov. and *T. guyanensis* is evaluated according to IUCN criteria and a status of Least Concern (LC) is proposed for these two species.

KEY WORDS

Guiana Shield,
French Guiana,
Combretaceae,
conservation assessment,
new species.

RÉSUMÉ

Terminalia carinata Sabatier & J.Engel, sp. nov. (Combretaceae), une nouvelle espèce de grand arbre du bouclier guyanais révélée par le réexamen de matériel précédemment identifié comme *T. guyanensis* Eichler. Une nouvelle espèce de *Terminalia* L. (Combretaceae) du bouclier guyanais est décrite comme *T. carinata* Sabatier & J.Engel, sp. nov. sur la base de caractères morphologiques. Cette nouvelle espèce a souvent été confondue avec *T. guyanensis* Eichler dont elle se distingue, ainsi que des autres *Terminalia* néotropicaux, par la face inférieure des feuilles gris pâle et légèrement pubescente, ses pétioles assez longs et ses fruits comportant deux ailes plus larges que le corps central qui est caréné d'un côté et plat de l'autre. Une description mise à jour de *T. guyanensis* est fournie et les statuts de conservation respectifs de *T. carinata* Sabatier & J.Engel, sp. nov. et *T. guyanensis* sont évalués selon les critères de l'IUCN. Un statut de préoccupation mineure (LC) est proposé pour ces deux espèces.

MOTS CLÉS

Plateau des Guyanes,
Guyane française,
Combretaceae,
statut de conservation,
espèce nouvelle.

INTRODUCTION

Terminalia L. is a genus of nearly 200 pantropical species occurring principally in Southeastern Asia (c. 90 species) (Stace 2010). According to recent molecular analyses (Maurin *et al.* 2010; Maurin *et al.* 2017), the genera *Anogeissus* (DC.) Guill. & Perr. (tropical West Africa to South East Asia), *Buchenavia* Eichler (tropical America) and *Pteleopsis* Engl. (tropical and southern Africa) should be included in *Terminalia*, and in this new circumscription it now comprises about 230-240 species. In the Neotropics, the genus *Terminalia* contains 54 species (including the 20 former *Buchenavia* species) mainly distributed in tropical South America. These are trees (or shrubs), often with a rhythmic growth leading to a characteristic pagoda-like habit with their horizontal lateral branches arranged in tiers (the so-called “Terminalia-branching”), the simple and alternate leaves usually clustered at ascending branchlet tips (Hallé *et al.* 1978; Bell 1991; Gentry 1993; Chomicki *et al.* 2017). The inflorescences are axillary compact to elongated spikes, often clustered at branchlet-ends. Flowers are small, actinomorphic and apetalous, with a distinctive lower hypanthium extended into a short “neck” surrounding the ovary that is clearly inferior. The upper hypanthium bears 4-5 distinct calyx lobes and 8 to 10 (rarely 4) well exerted stamens with versatile anthers; or calyx lobes are absent to poorly developed with 10 stamens only slightly exerted with basifixed anthers in former *Buchenavia* species (Stace 2010; Maurin *et al.* 2017). Outside these two categories, the flowers are quite similar from one species to another and classification of *Terminalia* thus relies more on fruits than on flowers. Indeed, fruit ample morphological variation (from 2-5-winged or -keeled to terete, dry to variably succulent) allows, combined with vegetative characters, the discrimination between species. The new species described here as *T. carinata* Sabatier & J.Engel, sp. nov. thus distinguished from many *Terminalia* by its fruits with two wings wider than the body that is distinctly keeled on one face and flat on the other, and is unique among neotropical *Terminalia* if also considering its leaf undersurface palish-gray and slightly pubescent, and its petioles mostly longer than 2 cm. In the last review of the genus *Terminalia* (Stace 2010), collections related to *T. carinata* Sabatier & J.Engel, sp. nov. were identified as *T. guyanensis* Eichler. In order to clarify the circumscription of *T. guyanensis*, a complete and updated description of this species, based on its isotype collections and newly collected specimens, is presented here in addition to the description of *T. carinata*, sp. nov.

MATERIAL AND METHODS

The physically studied material (cited with “!” following the barcode number) was received on loan from CAY or examined at P. Other materials, representing at least one accession of each neotropical *Terminalia* species, were studied from digitized herbarium sheets consulted online from various database portals, including the New York Botanical Garden (<http://sweetgum.nybg.org/science/vh/>), the Smithsonian National Museum of

Natural History (<http://collections.nmnh.si.edu/search/botany/>), the JSTOR Global Plants (<https://plants.jstor.org/>), the Naturalis Biodiversity Center (<https://bioportal.naturalis.nl/>), the Muséum national d’Histoire naturelle (https://science.mnhn.fr/institution/mnhn/collection/p/item/search/form?lang=en_US) the Fieldmuseum (<https://collections-botany.fieldmuseum.org/list>) and the Royal Botanic Gardens Kew (<http://apps.kew.org/herbcat/>). The terminology used for describing the type of pubescence is based on Harris & Harris (2001), those of the laminar shape and leaf venation follow Ellis *et al.* (1999). The conservation status was assessed using the IUCN Red List criteria (IUCN 2012); the extent of occurrence (EOO) and the area of occupancy (AOO) were calculated by using the online “GeoCAT” software (<http://geocat.kew.org>) with a cell width of 2 km (Bachman *et al.* 2011).

TAXONOMIC TREATMENT

Terminalia carinata Sabatier & J.Engel, sp. nov.
(Figs 1, 2, 3, 4)

TYPE. — French Guiana. Montagnes Plomb, inv. code PG18-63A3, 355 m, 4°59’N, 52°59’W, fr., 18.X.2004, Sabatier *et al.* 4891 (holo-, CAY([CAY182887!]); iso-, P([P01155925!], K!)).

DIAGNOSIS. — The new species differs from other neotropical *Terminalia* by its papillose, palish-gray and slightly pubescent leaf undersurface, its quite long petioles (usually > 2 cm) and its 2-winged fruits with wings wider than fruits central body that is distinctly keeled on one face and flat on the other one.

ETYMOLOGY. — The specific epithet refers to the fruit central body which is keeled (or carinate) on one face and flat on the other one.

DISTRIBUTION. — Consulted specimens come mainly from French Guiana, only two from Suriname. One fruiting specimen, collected in the Brazilian state of Para by Kuhlmann and identified as *Terminalia* cf. *mameluco* Pickel by Stace in 2002, looks alike *T. carinata* Sabatier & J.Engel, sp. nov. However, the authors would need to physically study this herbarium sheet to be completely sure of the determination in *T. carinata* Sabatier & J.Engel, sp. nov.

HABITAT. — *T. carinata* Sabatier & J.Engel, sp. nov. occurs in terra-firme forest from sea-level to 630 m a.s.l. This species grows preferentially on well-drained soil in high, irregular canopy forests (Gond *et al.* 2011).

PHENOLOGY. — Mature flowers have been recorded in August during leafless stage, fruits in January, July, October and November.

CONSERVATION STATUS. — According to herbarium sheets and inventory data from GUYAFOR and GUYADIV networks (Engel 2015), *T. carinata* Sabatier & J.Engel, sp. nov. is known from 16 localities in French Guiana and two localities in Suriname. The extent of occurrence (EOO) calculated is 58 090 km² and the area of occupancy (AOO) 80 km², and the localities where this species is encountered are not threatened by human activities. According to the IUCN Red List criteria (IUCN 2012), *T. carinata* Sabatier & J.Engel, sp. nov. is thus classified as Least Concern (LC). However, and even if the number of individuals encountered in the GUYAFOR and GUYADIV plots is greater than those of *T. guyanensis* (52 vs 12), it remains an uncommon tree species with unknown ecological requirements and whose consequences of climate change on its regeneration cannot be predicted (Esquivel-Muelbert *et al.* 2018).



FIG. 1. — *Terminalia carinata* Sabatier & J.Engel, sp. nov.: **A**, stem with leaves; **B**, detail of abaxial leaf surface; **C**, inflorescences with a young shoot of leaves; **D**, flower; **E**, longitudinal section of flower; **F**, three views of stamens; **G**, fruits; **H**, transverse section of fruit; **A**, **B**, *Boom & Mori 2134* (CAY); **C**-**F**, *Mori & Gracie 18653* (CAY); **G**, **H**, *Mori & Boom 15121* (CAY). Drawn by Laurence Ramon. Scale bars: A, C, G, H, 1 cm; B, D, E, 1 mm; F, 0.5 mm.

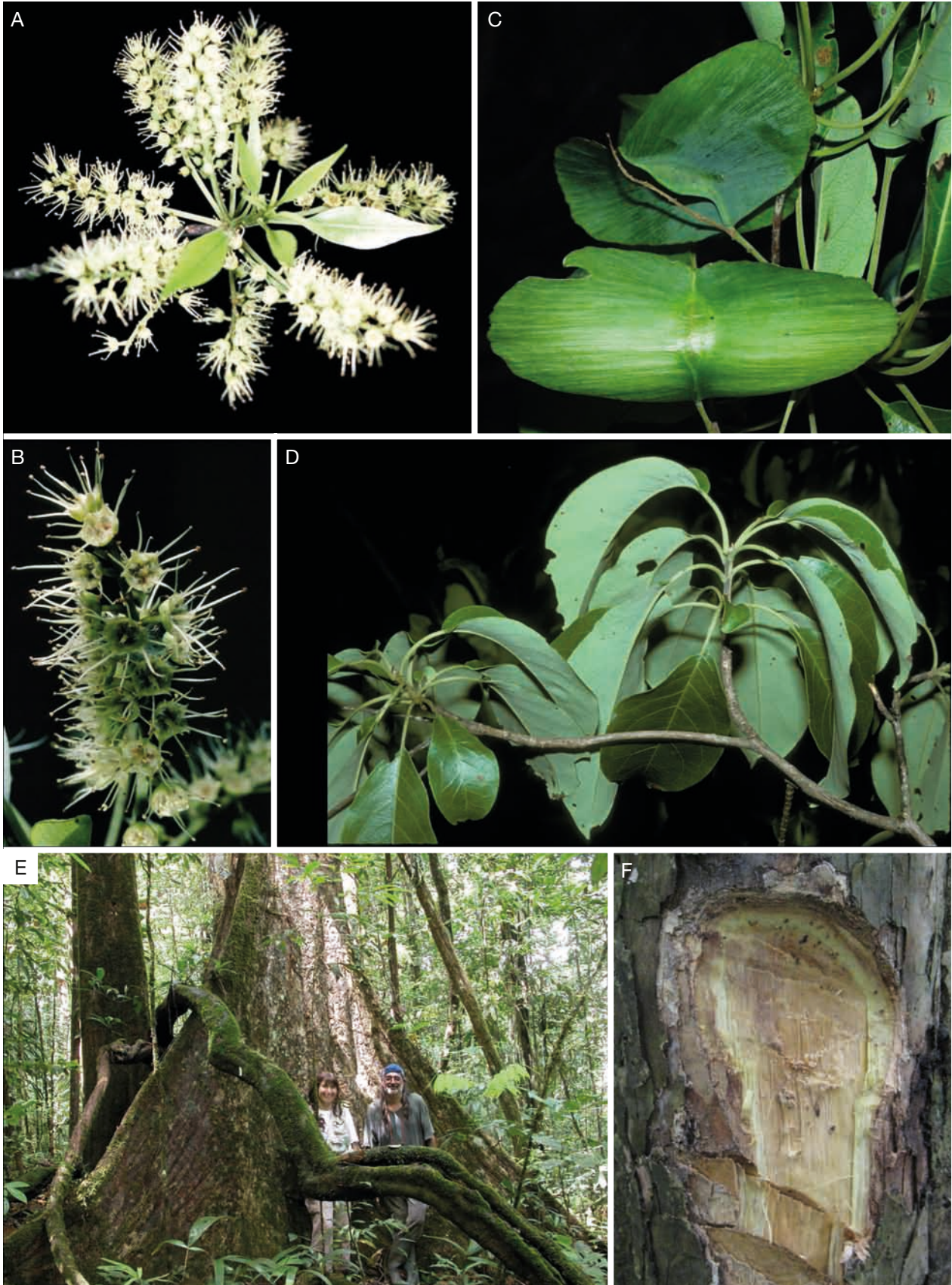


FIG. 2. — *Terminalia carinata* Sabatier & J.Engel, sp. nov.: **A, B**, inflorescences; **C**, fruiting branch (note fruit keeled on one side and flat on the other); **D**, stem with leaves; note: i) the typical *Terminalia* arrangement of leaves clustered at twig tips; and ii) the leaf margin revolute at very base; **E**, trunk; **F**, trunk slash; **A, B**, Mori & Gracie 18653; **C**, Sabatier et al. 4891 (type specimen); **D**, Sabatier 2309. **A, B**, Photographs by Carol Gracie; **C, D**, photographs by Daniel Sabatier; **E, F**, photographs by Julien Engel.

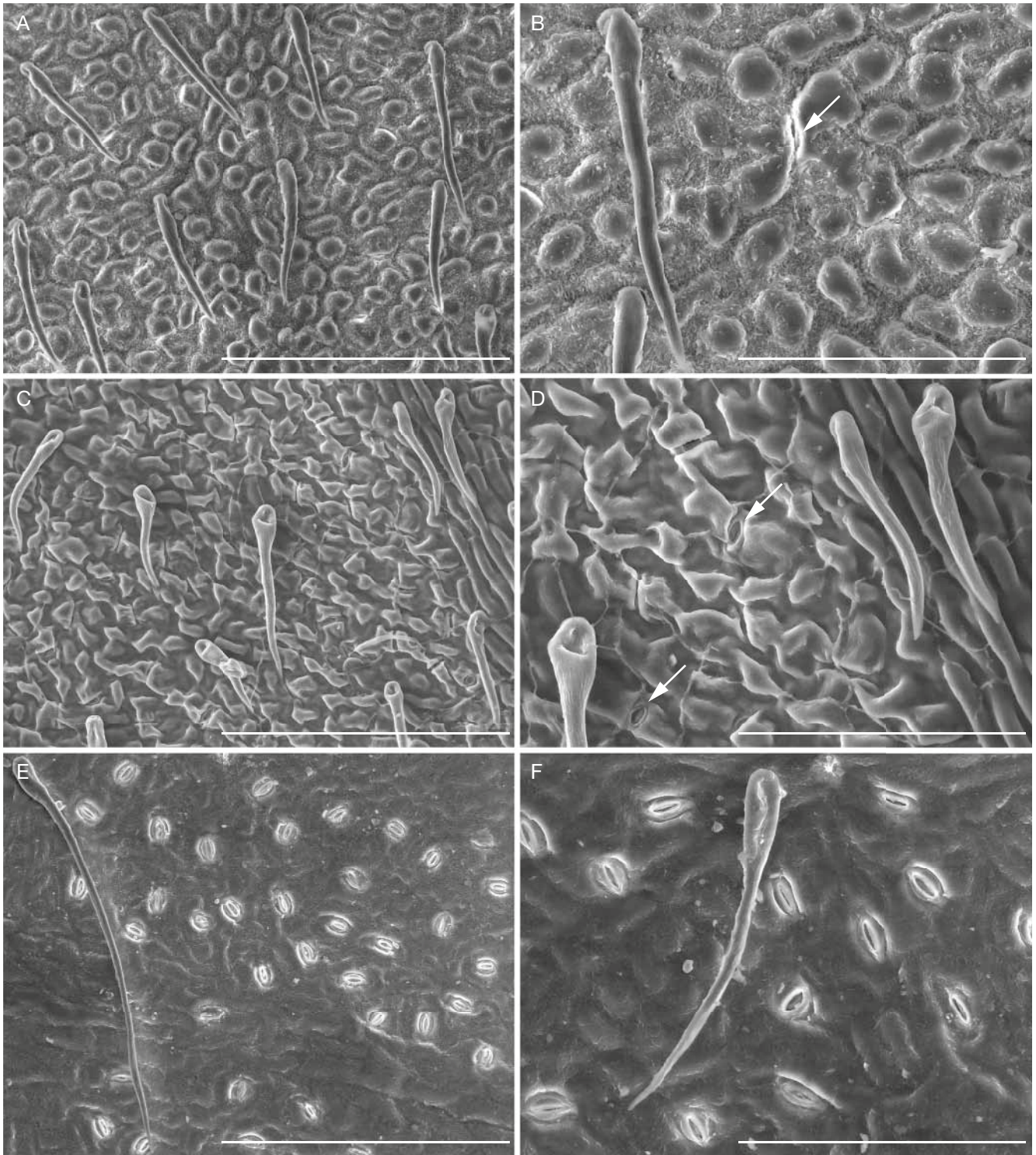


FIG. 3. — Leaf abaxial surface in SEM: **A-D**, *Terminalia carinata* Sabatier & J.Engel, sp. nov.; note the hidden stomata; **E, F**, *Terminalia guyanensis* Eichler; **A, B**, Sabatier et al. 4891; **D, E**, De Granville et al. 10958; **E, F**, Sabatier et al. 6018. Scale bars: A, C, E, 200 μ m; B, D, F, 100 μ m.

AFFINITIES. — Among other neotropical *Terminalia*, seven species have fruits with two wings longer than 1 cm and a body keeled or ridged on one side and flat on the other (*T. arbuscula* Sw., *T. bucidoides* Standl. & L.O. Williams, *T. chicharronia* C. Wright, *T. eriostachya* A. Rich., *T. mameluco* Pickel, *T. oblonga* (Ruiz & Pav.) Steud., and *T. valverdeae* A.H. Gentry). *Terminalia carinata* Sabatier & J.Engel, sp. nov. differs from these species by its leaf undersurface palish-gray and slightly pubescent, its venation weakly brochidodromous and its

petioles usually longer than 2 cm. Vegetatively, the leaves of *T. carinata* Sabatier & J.Engel, sp. nov. closely resemble those of *T. argentea* Mart. & Zucc., which is a small tree species typically found in savannah-like ecosystems like the Brazilian cerrado. But their fruits are different, those of *T. argentea* have a central body swollen on both sides and rounded (although sometimes with a slight ridge), whereas *T. carinata* Sabatier & J.Engel, sp. nov. fruits have a central body keeled on one side and flat on the other side with larger, more elongated wings.

OTHER MATERIAL STUDIED. — **French Guiana.** St-Élie, Réserve naturelle des Montagnes de la Trinité, Plateau Tabulaire, 400–630 m, 4°35'N, 53°21'W, fr., VII.1999, *Poncy & Crozier 1415* (CAY[CAY114758!]); Gobaya Soula, Bassin du Maroni, 230 m, 3°37'N, 53°58'W, fr., 31.I.1989, *De Granville et al. 10958* (B, CAY[CAY010133!], P, U, US[US00601847], NY); Saül, Mont la Fumée, 200–400 m, 3°37'N, 53°12'W, fr., 21.X.1982, *Mori & Boom 15121* (CAY[CAY170310!], LTR, NY, P[P04877940!]); Saül, Mont Galbao trail, between village and entrance to Grand Bœuf Mort trail, 200–250 m, fl., 6.VIII.87, *Mori & Gracie 18653* (CAY[CAY170302!], LTR, NY); Saül, Mont la Fumée, 200–400 m, 3°37'N, 53°12'W, st., 15.X.1982, *Boom & Mori 2134* (CAY[CAY170308!], LTR, NY); *ibid.*, 21.X.1982, *Boom & Mori 2237* (CAY[CAY170303!], LTR, NY); *ibid.*, 13.X.1982, *Boom & Mori 2028* (CAY[CAY170309!]); Saül and vicinity: Boeuf-Mort trail, less than 1 km from entrance at Route de Bélizon, st., 13.IX.1994, *Mori et al. 23905* (CAY[CAY170307!], NY[NY1365060]); Centre Orstom, Île de Cayenne, 5 m, 4°56'N, 52°19'W, st., 26.XI.1990, *De Granville 11158* (CAY[CAY170305, CAY170306!], K, P[P04717178!], U); Roche Dachine, st., 15.XII.1999, *Chareyre 1035* (CAY[CAY019647!]); Massif Dékou Dékou, région Paul Isnard, 300 m, 4°42'N, 53°56'W, st., 27.XI.2000, *Dutreve 608* (CAY[CAY046309!]); Montagne La Fumée, région de Saül, 3°38'N, 53°12'W, st., 21.XI.1988, *Sabatier 2298* (CAY[CAY010140!], LTR); Commune de Saül, 3°37'N, 53°13'W, st., 24.XI.1988, *Sabatier 2309* (CAY[CAY010139!], P, NY, MO, U); Plateau de la Douane, environ 3 km de Saül sur le tracé Carbet Maïs, st., 16.XII.1970, *Oldeman 3190* (CAY[CAY170311, CAY170312!], NY, P[P04878224], U[U0175056]); Saut Pararé, st., 29.IX.1983, *Sabatier 575* (CAY[CAY170313!]); Saut Pararé, riv. Arataye affluent Approuague, 70 km SW Régina, st., 9.III.1987, *Villiers 3833* (CAY[CAY070672!]); *ibid.*, 2.III.1988, *Villiers 4409* (CAY[CAY099763!]); *ibid.*, 11.III.1988, *Villiers 4505* (CAY[CAY099693!]); Camp Pararé, Station de l'Arataye, Bassin de l'Approuague, 200 m, st., 13.III.1983, *Barrier 2755* (CAY[CAY099694!]); *ibid.*, 7.IX.1983, *Barrier 4165* (B, CAY[CAY083661!], COL, IAN, K, MO, NY, U, US, VEN); station des Nouragues, Grand Plateau, inv. code NL110027, 4°45'N, 52°41'W, st., 30.XI.2007, *Baraloto 3067* (CAY[CAY182886!]); *ibid.*, inv. code NL110099, *Baraloto 3077* (CAY[CAY182885!]); Nouragues Nature Réserve, c. 100 km SSW of Cayenne and 40 km SW of Régina, Grand Plateau, 4°5'N, 52°41'W, st., 17.XI.2006, *Mori et al. 26498* (CAY[CAY080491!], NY); Saint-Georges, Régina, entre pk 30,6 et 31,85, st., 5.XI.1998, *Grenand 3065* (CAY[CAY000288!]). **Suriname.** Mts Bakhuis, concession BMS : zone 4, sud-ouest, 170 m, fr., 4.X.2005, *Bordenave et al. 8144* (BBS, CAY[CAY065001!]); Area of Kabalebo dam project, distr. Nickerie, c. 22 km SW of Avanavero dam site, fr., 15.XI.1976, *Heyde & Lindeman 89* (F[V0188958F], K, MO, NY, U[U0248638]).

DOUBTFUL SPECIMEN. — **Brazil.** Estado do Para: rodovia Belém-Brasília km 92, fr., 30.IX.1959, *Kuhlmann & Jimbo 318*, (US[US1891248]).

DESCRIPTION

Deciduous canopy tree up to 65 m tall, with large plank to thick buttresses to 2–6 m high. Diameter up to 120 cm. Bark brown-yellow, scaly, inner bark pale yellow-green. Twigs pubescent, becoming glabrous; terminal buds densely pubescent. Leaves alternate, spirally arranged, usually clustered at branchlet tips; blades chartaceous, elliptic-obovate to obovate, 5–12 × 2–6.5 cm; apex acuminate; base cuneate or attenuate-cuneate; margin entire, revolute at very base; densely pubescent-sericeous on both faces when young; mature with adaxial surface sparse-pubescent mainly along main veins, abaxial surface slightly pubescent, palish-gray (sometimes not obvious on dried material); lateral veins 6–8, uniformly pinnate, weakly brochidodromous, slightly raised on both

surfaces, lower venation random reticulate, visible on both surfaces; petioles 1.4–4 cm, slightly pubescent or glabrous, often with a pair of small glands toward apex (more obvious on fresh material).

Inflorescences axillary, clustered in about 10 spikes at mostly leafless branchlet-ends, c. 4–5 cm long, densely pubescent, c. 25–30-flowered; peduncle 0.7–1.7 cm long; bracts inconspicuous and caducous. Flowers bisexual, pale greenish, actinomorphic, 2.6–3.9 × 1.9–2.7 mm; lower hypanthium extended into a short “neck” surrounding the ovary, 1.2–1.9 mm long, densely pubescent, upper hypanthium cupuliform to campanulate, 1.5–1.9 mm long, pubescent on the external surface, densely lanate with much longer trichomes on the inner surface; calyx lobes 5, 0.8–1.2 mm long, pubescent on the external surface, lanate with much longer trichomes on the inner surface; petals 0; stamens 10, exserted, white, glabrous, 1.9–4.2 mm, anthers versatile, 0.4–0.5 mm long; intrastaminal disk lanate, 0.9–1.9 mm width; ovary inferior, unilocular, with two pendulous ovules, style exserted, 2.5–3.3 mm long, lanate over most of its length. Infructescence with 1–2 fruits, peduncle and rachis slightly pubescent to glabrous. Fruits 2-winged, dry, glabrous, dull green pruinose becoming shiny, 6.8–8.6 × 1.6–3.2 cm, apex flat to slightly emarginated, base obtuse; wings stiff, (sub)equal, 3.2–4 cm long, narrowly to very narrowly rounded; body c. 0.5–0.9 cm width, c. 4–5 mm high, keeled on one side and flat on the other.

NOTE

T. carinata Sabatier & J.Engel, sp. nov. was previously identified as *T. guyanensis* in CAY, while the ‘true’ *T. guyanensis*, as originally described by Eichler (Martius & Eichler 1867), was considered as an unknown morpho-species in CAY. This confusion is visible in Mori *et al.* (2005), where the illustration of *T. guyanensis* is in fact an illustration of *T. carinata* Sabatier & J.Engel, sp. nov. And in the last review of the genus *Terminalia* (Stace 2010), specimens of *T. carinata* Sabatier & J.Engel, sp. nov. and *T. guyanensis* were merged together as *T. guyanensis*. Here, we propose to revert to the original protologue of *T. guyanensis* by Eichler (Martius & Eichler 1867), and we introduce *T. carinata* Sabatier & J.Engel, sp. nov. as a new species according to the description above. The circumscription of *T. guyanensis* is therefore clarified and this species can be distinguished from *T. carinata* Sabatier & J.Engel, sp. nov. by its fruit central body bulging on both faces while *T. carinata* Sabatier & J.Engel, sp. nov. fruit central body is flat on one face and keeled on the other one. In addition, *T. guyanensis* leaves are glabrous whereas those of *T. carinata* Sabatier & J.Engel, sp. nov. are slightly pubescent and palish-gray abaxially with longer petioles (usually > 2 cm). In scanning electron microscope, we observe that this distinctive undersurface of *T. carinata* Sabatier & J.Engel, sp. nov. is made up of a very high density of papillae that are absent from the surface of the leaves of *T. guyanensis* (Fig. 3). Trichomes are similar in *T. carinata* Sabatier & J.Engel, sp. nov. and in *T. guyanensis*: pointed at base and widen at top to a rounded head with a cavity, but much less abundant in *T. guyanensis* whose lamina appears almost completely hairless at glance.

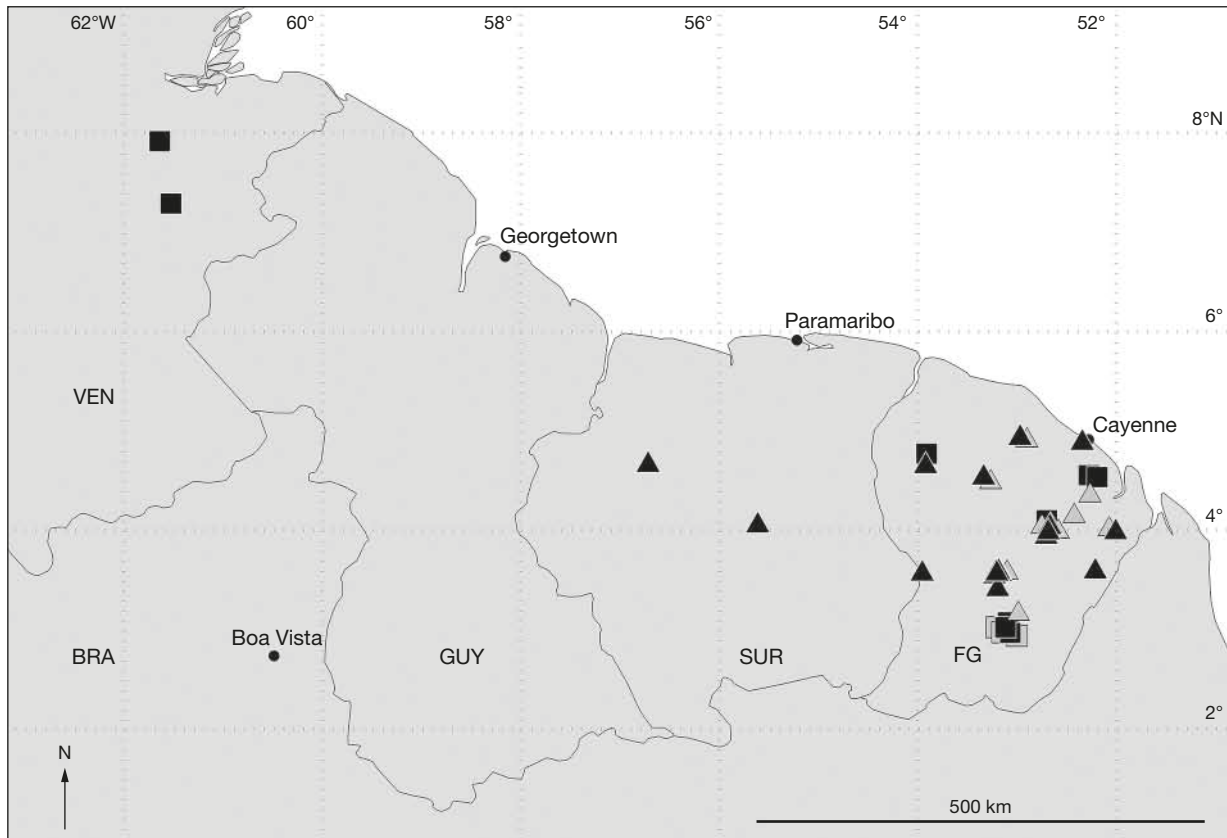


FIG. 4. — Distribution of *Terminalia guyanensis* Eichler and *Terminalia carinata* Sabatier & J.Engel, sp. nov.: (■) *T. guyanensis* and (▲) *T. carinata* Sabatier & J.Engel, sp. nov., herbarium specimens; (□) *T. guyanensis* and (△) *T. carinata* Sabatier & J.Engel, sp. nov., observations (no voucher) from the GUYADIV and GUYAFOR networks (Engel 2015).

Terminalia guyanensis Eichler in Mart.
(Figs 3, 4, 5, 6)

Flora Brasiliensis 14 (2): 88 (1867). — *Myrobalanus eichleriana* Kuntze, *Revisio Generum Plantarum* 1: 237 (1891), nom. nov. pro *Terminalia guyanensis* Eichler, non *Myrobalanus guianensis* Kuntze (1891), nec. *Terminalia eichleriana* Alwan & Stace (1989). — Typus: French Guiana. 1817-1822, Poiteau s.n. (holo-, B, destroyed, photograph at FI; iso-, K[K000640657], P[P01901252, P01901253, P01901254]!, U[U0001197], W[W-Rchb. 1889-0125487]); No collector (probable iso-, A/GH[GH00068628]).

DISTRIBUTION. — The specimens consulted were collected in Venezuela and French Guiana. It is very likely that *T. guyanensis* also occurs in the region between these two countries, which would include Guyana, Suriname and adjacent areas in Brazil.

HABITAT. — According to herbarium sheets and inventory data from the GUYADIV and GUYAFOR networks (Engel 2015), *T. guyanensis* is encountered in *terra-firme* forest between 100 to 810 m elevation. Its privileged habitat seems to be cloud forest and very rainy forest receiving more than 3500 mm of precipitation per year.

PHENOLOGY. — Flowers were collected in November during leafless stage, fruits in March and May.

CONSERVATION STATUS. — Based on the herbarium sheets consulted, *T. guyanensis* is known from five localities in French Guiana and two localities in Venezuela. Outside one site in French Guiana (Mont Iroupé) where *T. guyanensis* is relatively common, the authors rarely

encountered this species during the inventory work carried out as part of the GUYAFOR and GUYADIV networks. More precisely, out of the almost 180 000 trees inventoried in these two networks, only 12 were identified as *T. guyanensis*. The calculated AOO is 32 km², the calculated EOO is 138 589 km² which is very high as this species has been collected in Venezuela and French Guiana and is thus very likely to also occur in Guyana and Suriname. In countries where *T. guyanensis* has been collected, as well as in countries where this species is probably present, the forest massif is generally (still) preserved. *Terminalia guyanensis* is thus classified as Least Concern (LC) following the IUCN Red List criteria (IUCN 2012). However, even if the forest massif is not directly threatened by human activities, *T. guyanensis* is one of the many rare Amazonian tree species with low densities and unknown ecological requirements and whose regeneration could potentially be affected by climate change (ter Steege *et al.* 2013; Esquivel-Muelbert *et al.* 2018).

AFFINITIES. — Like 14 other neotropical *Terminalia*, *T. guyanensis* has 2-winged fruits, each wing > 1 cm long. But only *T. argentea* Mart. & Zucc., *T. januarensis* DC. and *T. phaeocarpa* Eichler have quite similar fruit body, bulging on both faces, although often with a slight ridge or slightly wavy while the surface of *T. guyanensis* fruit body is rounded and smooth. Vegetatively, these three species can be distinguished from *T. guyanensis* by their pubescent or subglabrous leaves (but at least they are pubescent on main veins abaxially) while *T. guyanensis* leaves are glabrous. If we consider more specifically the 15 species of *Terminalia* found in French Guiana (including *T. carinata* Sabatier & J.Engel, sp. nov.), five are immediately distinguishable by the size of their leaves, which are clearly larger (*T. aubletii* Gere & Boatwr., *T. macrophylla* (Eichl.) Gere &

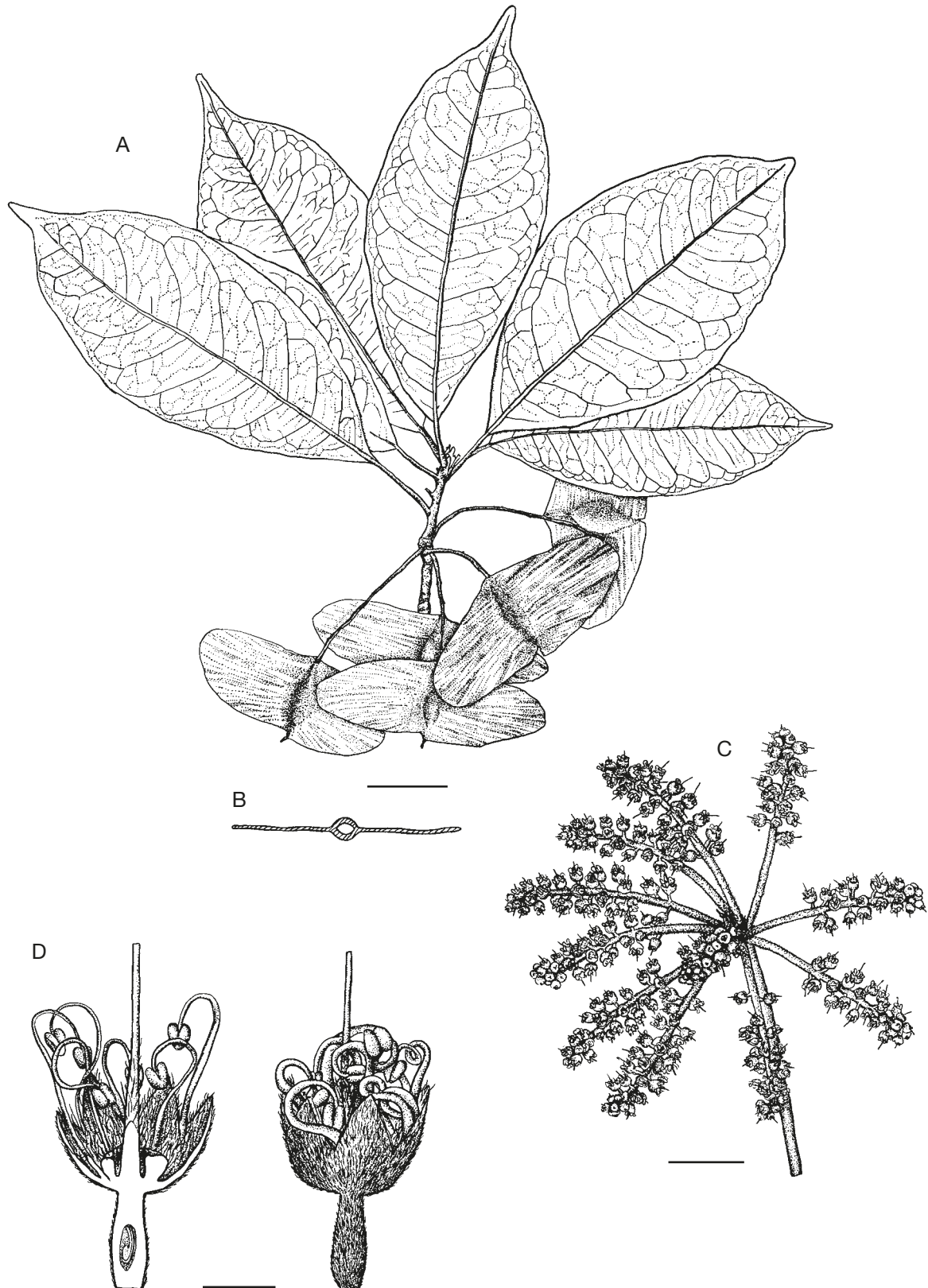


FIG. 5. — *Terminalia guyanensis* Eichler: **A**, fruiting branch; **B**, transverse section of fruit; **C**, inflorescences; **D**, longitudinal section (**left**) and lateral view (**right**) of flower; **A, B**, Sabatier 6331 (CAY); **C, D**, Sabatier & al. 6018 (P). Drawn by Laurence Ramon. Scale bars: A, B, 2 cm; C, 1 cm; D, 1 mm.

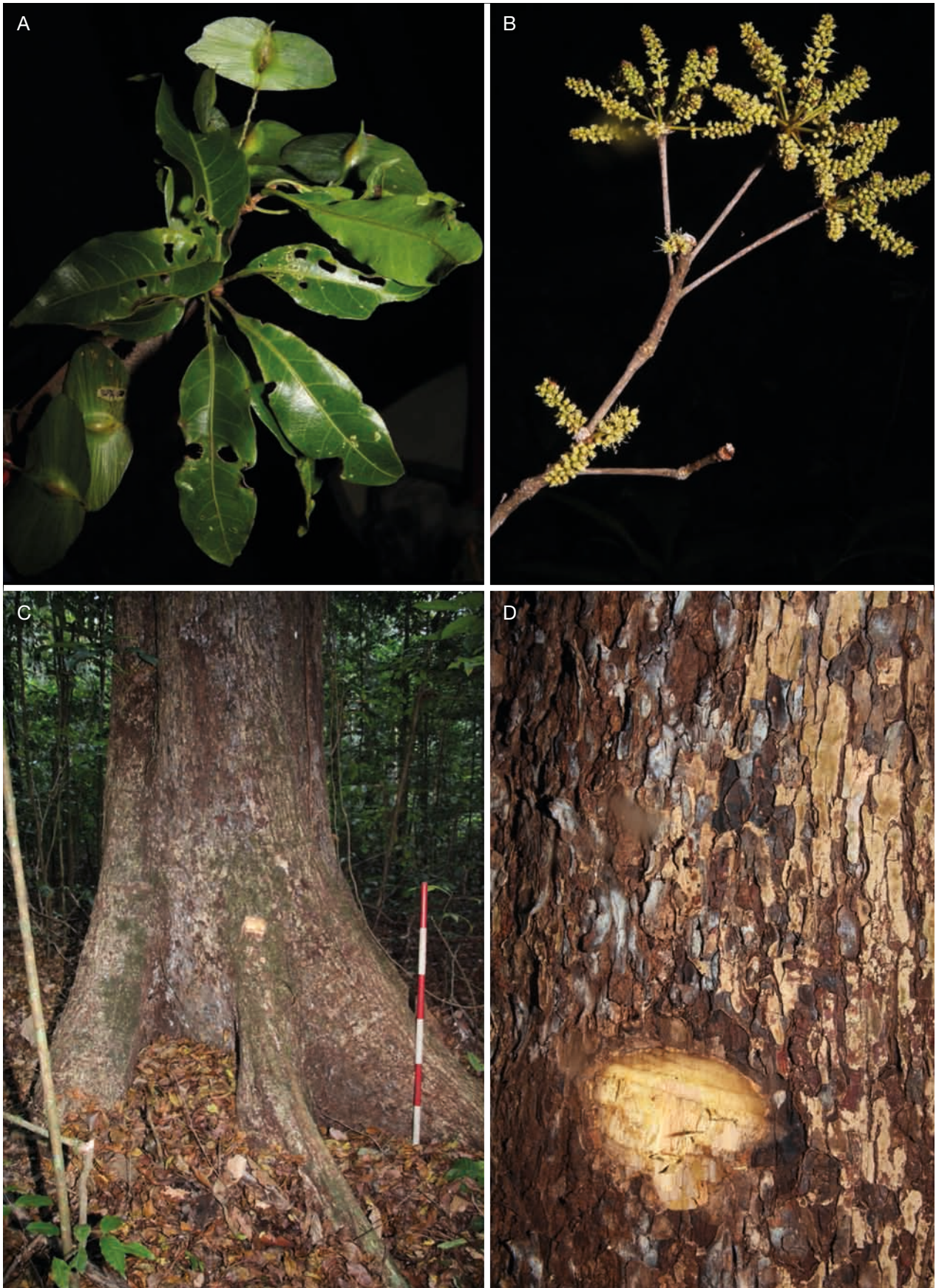


FIG. 6. — *Terminalia guyanensis* Eichler: **A**, fruiting branch; **B**, inflorescences; **C**, trunk; **D**, bark with a machete slash; **A**, Sabatier & Molino 5682 (CAY); **B-D**, Sabatier et al. 6018 (P). **A-D**, Photographs by Daniel Sabatier.

Boatwr., *T. megalophylla* (Van Heurck & Müll.) Gere & Boatwr. and *T. nitidissima* Rich.), or smaller (*T. parvifolia* (Ducke) Gere & Boatwr.) than those of *T. guyanensis*. And none of the other species has glabrous leaves with such brochidodromous veins with one or two sets of loops outside of the main brochidodromous loop.

OTHER MATERIAL STUDIED. — French Guiana. Mont Itoupé, 430 m, 3°1'21"N, 53°6'29"W, fl., 17.XI.2014, Sabatier et al. 6018 (CAY[CAY182882!], P[P01155923!]); Mont Itoupé, inv. code ITO1-K4, 600 m, 3°1'20"N, 53°5'29"W, fr., 12.III.2010, Sabatier & Molino 5682 (CAY[CAY103783!]); Mont Itoupé, 433 m, 3°2'22"N, 53°6'19"W, fr., 13.III.2017, Sabatier 6331 (CAY[CAY182884!], P[P01155924!]); Mont Itoupé, inv. code ITOW8-5, 328 m, 3°3'18"N, 53°6'34"W, st., 12.XI.2014, Sabatier et al. 6051 (CAY[CAY182883!]); Mont Itoupé, 3°1'18"N, 53°7'10"W, 200 m, st., 20.III.2010, Molino & Sabatier 2794 (CAY[CAY104624!], MPU); Réserve Trésor, inv. code T10380, 235 m, 4°34'12"N, 52°17'24"W, st., 1.IX.2008, Engel et al. 16 (CAY[CAY182881!]); Massif Lucifer, plateau Tabulaire, 530 m, 4°47'11"N, 53°55'23"W, st., 15.XI.1999, Dutreue 355 (CAY[CAY046077!]); Station des Nouragues, Bassin de l'Arataye, inv. code NOU3-146, 4°3'N, 52°42'W, st., 7.VII.1989, Sabatier & Prévost 2627 (CAY[CAY010136!], LTR); Montagne de Kaw, st., 16.IX.1969, Petrov 203 (CAY[CAY170282!], P[P04717175!]); *ibid.*, 17.IX.1969, Petrov 208 (CAY[CAY182888!], P[P04717176!]). Venezuela. Territorio federal, delta Amacuro: bosque pluvial, Este de Río Grande. Este-Noreste de El Palmar, cerca de los límites del Estado Bolívar, fr., 23.V.1964, Marcano Berti 187 (A/GH, BM, F[V0397201F], MG, US[US00766632], VEN); East of Cerro El Picacho, near Las Nieves & Las Chicharras, 45 km North of Tumeremo, 600-650 m, st., 5-8.II.1961, Steyermark 89070 (A/GH, P[P04717179!], S, VEN).

DESCRIPTION

Deciduous canopy tree up to 60 m tall, with thick, rounded buttresses to 1–2 m high. Diameter up to 105 cm. Bark brown-yellow, densely scaly, inner bark pale yellow. Twigs pubescent, becoming glabrous; terminal buds densely pubescent. Leaves alternate, spirally arranged, usually clustered at branchlet tips; blades chartaceous, elliptic-oblong to elliptic, 5–13 × 2–5 cm; apex acuminate; base cuneate or attenuate-cuneate; margin entire; both surfaces glabrous, except rarely a tuft of hairs in axils of secondary veins abaxially; lateral veins 7–10, uniformly pinnate, intersecondary veins often present, brochidodromous, with one or two sets of loops outside of the main brochidodromous loop, slightly raised on both surfaces, lower venation randomly reticulate, visible on both surfaces; petioles 0.8–2 cm, slightly pubescent or usually glabrous, often with a pair of small glands toward apex.

Inflorescences axillary, clustered in *c.* 6–13 spikes at leafless branchlet-ends, 1.5–3 cm long, covered by lanate trichomes, *c.* 25–40-flowered; peduncle 0.4–1.1 cm long; bracts inconspicuous and caducous. Flowers bisexual, pale yellowish, actinomorphic, 1.6–3 × 1.5–2.3 mm; lower hypanthium extended into a short “neck” surrounding the ovary, 0.8–1.5 mm long, densely pubescent, upper hypanthium cupuliform to campanulate, 0.8–1.6 mm long, pubescent on the external surface, lanate with much longer trichomes on the inner surface; calyx lobes 5, 0.6–1 mm long, pubescent on the external surface, lanate with much longer trichomes on the inner surface; petals 0; stamens 10, white, glabrous, 2.1–2.8 mm, anthers versatile, *c.* 0.3 mm long; intrastaminal disk *c.* 1.2 mm width, slightly lanate; ovary inferior, unilocular, style exerted, 2.4–3.7 mm

long, slightly lanate over about a third of its lower part. Inflorescence with 1–2 fruits, peduncle and rachis slightly pubescent or usually glabrous. Fruits 2-winged, dry, glabrous and shiny, 4.9–6.3 × 1.8–2.4 cm, apex shortly acuminate, flat or slightly emarginate, base obtuse; wings stiff, green, (sub) equal, 2–2.8 cm long, rounded to narrowly rounded; body *c.* 0.5–0.7 cm wide, *c.* 4 mm high, bulging on both faces.

NOTE

We have previously discussed the confusion between *T. guyanensis* and *T. carinata* Sabatier & J.Engel, sp. nov. Sterile specimens of *T. guyanensis* have sometimes also been confused with *T. dichotoma* G. Mey. Thus, three specimens studied by the authors (Sabatier & Prévost 2627, Petrov 203 and Petrov 208) and cited in the present study are recorded as *T. dichotoma* in Stace (2010). These two species can be distinguished from each other by their venation pattern: *T. guyanensis* veins are more brochidodromous with one or two sets of loops (absent in *T. dichotoma*) outside of the main brochidodromous loop.

Acknowledgements

We thank Laurence Ramon for the beautiful illustration, Sophie Gonzalez and Chantal Geniez (CAY) and Caroline Loup (MPU) for providing loan material and access to specimens. We also thank the MEA platform, University of Montpellier, for electronic microscope images, and Carole Gracie and Scott Mori for the photos of fresh material. Finally, we are grateful to the reviewers (Dr Odile Poncy, Dr Clive A. Stace and Dr Thierry Deroin) for their detailed and helpful comments. This study was carried out as part of the DynForDiv project (IRD and “Parc amazonien de Guyane” partnership) supported by a BGF grant from the French Ministry of Ecology (MEDDE) and an “Investissement d’Avenir” grant managed by Agence nationale de la Recherche (CEBA, ref. ANR-10-LABX-0025). The MNHN gives access to the collections in the framework of the RECOLNAT national Research Infrastructure.

REFERENCES

- ALWAN A. R. A & STACE C. A. 1989. — New Species, Names, and Combinations in American Combretaceae. *Annals of the Missouri Botanical Garden* 76: 1125. <https://doi.org/10.2307/2399697>
- BACHMAN S., MOAT J., HILL A., TORRE J. DE LA & SCOTT B. 2011. — Supporting Red List threat assessments with GeoCAT: geospatial conservation assessment tool, in SMITH V. & PENEV L. (eds), e-Infrastructures for data publishing in biodiversity science. *ZooKeys* 150: 117–126. <https://doi.org/10.3897/zookeys.150.2109>
- BELL A. D. 1991. — *Plant Form. An Illustrated Guide to Flowering Plant Morphology*. Oxford University Press, Oxford, 341 p.
- CHOMICKI G., COIRO M. & RENNER S. 2017. — Evolution and ecology of plant architecture: Integrating insights from the fossil record, extant morphology, developmental genetics and phylogenies. *Annals of Botany* 120: 855–891. <https://doi.org/10.1093/aob/mcx113>
- ELLIS B., ASH A., HICKEY L. J., JOHNSON K., WILF P. & WING S. 1999. — *Manual of Leaf Architecture – Morphological Description and Categorization of Dicotyledonous and Net-Veined Monocotyledonous Angiosperms*. Smithsonian Institution, Washington, 65 p.

- ENGEL J. 2015. — ATDN tree morphospecies website. <http://atdn-morphospecies.myspecies.info/node/781> [accessed 09/12/2019].
- ESQUIVEL-MUELBERT A., BAKER T. R., DEXTER K. G., LEWIS S. L., BRIENEN R. J. W., FELDPAUSCH T. R., ... PHILLIPS O. L. 2018. — Compositional response of Amazon forests to climate change. *Global Change Biology* 25: 39-56. <https://doi.org/10.1111/gcb.14413>
- GENTRY A. H. 1993. — *A field Guide to the Families and Genera of Woody Plants of Northwest South America (Colombia, Ecuador, Peru), with Supplementary Notes on Herbaceous Taxa*. Conservation International, Washington DC, 920 p.
- GOND V., FREYCON V., MOLINO J.-F., BRUNAUX O., INGRASSIA F., JOUBERT P., ... SABATIER D. 2011. — Broad-scale spatial pattern of forest landscape types in the Guiana Shield. *International Journal of Applied Earth Observation and Geoinformation* 13: 357-367. <https://doi.org/10.1016/j.jag.2011.01.004>
- HALLÉ F., OLDEMAN R. A. A. & TOMLINSON P. B. 1978. — *Tropical Trees and Forests : An Architectural Analysis*. Springer-Verlag, Berlin-Heidelberg-New York, 441 p. <https://doi.org/10.1007/978-3-642-81190-6>
- HARRIS J. G. & HARRIS M. W. 2001. — *Plant Identification Terminology: An Illustrated Glossary (Second edition)*. Spring Lake Pub., Utah, 206 p.
- IUCN 2012. — *IUCN Red List Categories and Criteria: Version 3.1. Second edition*. IUCN, Gland, Switzerland and Cambridge, UK, 32 p.
- KUNTZE C. E. O. 1891. — *Revisio Generum Plantarum*. Felix, Leipzig, 374 p. <https://bibdigital.rjb.csic.es/idurl/1/14269>
- MARTIUS C. F. P. V. & EICHLER A. W. 1867. — *Flora Brasiliensis*. Fleischer, München & Leipzig, 418 p., 91 pls.
- MAURIN O., CHASE M. W., JORDAAN M. & VAN DER BANK M. 2010. — Phylogenetic relationships of Combretaceae inferred from nuclear and plastid DNA sequence data: implications for generic classification. *Botanical Journal of the Linnean Society* 162: 453-476. <https://doi.org/10.1111/j.1095-8339.2010.01027.x>
- MAURIN O., GERE J., VAN DER BANK M. & BOATWRIGHT J. S. 2017. — The inclusion of Anogeissus, Buchenavia and Pteleopsis in Terminalia (Combretaceae: Terminaliinae). *Botanical Journal of the Linnean Society* 184: 312-325. <https://doi.org/10.1093/botlinnean/box029>
- MORI S. A., CREMERS G., GRACIE C. A., DE GRANVILLE J. J., HEALD S. V., HOFF M. & MITCHELL J. D. 2005. — *Guide to the Vascular Plants of Central French Guiana. Part 2. Dicotyledons*. New York Botanical Garden, New York, 944 p.
- STACE C. A. 2010. — *Flora Neotropica*. Vol. 107. *Combretaceae*. New York Botanical Garden Press, Organization for Flora Neotropica, 369 p.
- TER STEEGE H., PITMAN N. C. A., SABATIER D., BARALOTO C., SALOMÃO R. P., GUEVARA J. E., ... SILMAN M. R. 2013. — Hyperdominance in the Amazonian tree flora. *Science* 342. <https://doi.org/10.1126/science.1243092>

Submitted on 10 December 2019;
accepted on 13 May 2020;
published on 2 November 2020.