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Julien Engel, Jean-François Molino, Lucas C. Marinho. The maximum and the minimum: two new species of Tovomita Aubl. (Clusiaceae) from the Guiana Shield with an unusual number of stamens. Adansonia, 2022, 44 (16), pp.165-174. ⟨10.5252/adansonia2022v44a16⟩. ⟨hal-03699359⟩

HAL Id: hal-03699359

https://hal.inrae.fr/hal-03699359v1

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adansonia

2022 • 44 • 16

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art. 44 (16) — Published on 20 June 2022
www.adansonia.com

PUBLICATIONS SCIENTIFIQUES
MUSÉUM NAL HIST NATURELLE

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diff.pub@mnhn.fr / http://sciencepress.mnhn.fr

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ISSN (imprimé / *print*): 1280-8571/ ISSN (électronique / *electronic*): 1639-4798

The maximum and the minimum: two new species of *Tovomita* Aubl. (Clusiaceae) from the Guiana Shield with an unusual number of stamens

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Submitted on 25 May 2021 | accepted on 5 January 2022 | published on 20 June 2022

Engel J., Molino J.-F. & Marinho L. C. 2022. — The maximum and the minimum: two new species of *Tovomita* Aubl. (Clusiaceae) from the Guiana Shield with an unusual number of stamens. *Adansonia*, sér. 3, 44 (16): 165-174. https://doi.org/10.5252/adansonia2022v44a16. http://adansonia.com/44/16

ABSTRACT
Two new species of *Tovomita* Aubl. (Clusiaceae) from the Guiana Shield are described and illustrated. *Tovomita maxima* Molino & J.Engel, sp. nov., known from French Guiana, Guyana and Brazil, stands out by its large size (up to 30 m high), large leaves with eucamptodromous venation, calyptrate bracteoles and an unusual variation in the number of stamens (74-145). *Tovomita saulensis* J.Engel & Molino, sp. nov., probably endemic to central French Guiana, is an understory tree with small leaves with brochidodromous venation and flowers with few stamens (9-15). Illustrations, descriptions, photographs *in vivo*, a preliminary conservation status, distribution map and comments on the morphology of related species are provided.

KEY WORDS
Clusiaceae,
Guttiferae,
Clusieae,
French Guiana,
Guiana Shield,
new species.

RÉSUMÉ
Le maximum et le minimum : deux nouvelles espèces de Tovomita *Aubl. (Clusiaceae) du Plateau des Guyanes avec un nombre inhabituel d'étamines.*
Deux nouvelles espèces de *Tovomita* Aubl. (Clusiaceae) du Bouclier Guyanais sont décrites et illustrées. *Tovomita maxima* Molino & J.Engel, sp. nov., connue de Guyane française, du Guyana et du Brésil, se distingue par sa grande taille (jusqu'à 30 m de hauteur), ses grandes feuilles à nervation eucamptodrome, ses bractéoles calyptrées et une variation inhabituelle du nombre d'étamines (74-145). *Tovomita saulensis* J.Engel & Molino, sp. nov., apparemment endémique du centre de la Guyane française, est un arbre de sous-bois avec de petites feuilles à nervation brochidodrome et des fleurs avec peu d'étamines (9-15). Des illustrations, descriptions, photographies *in vivo*, un statut de conservation préliminaire, une carte de distribution et des commentaires sur la morphologie des espèces apparentées sont fournis.

MOTS CLÉS
Clusiaceae,
Guttiferae,
Clusieae,
Guyane française,
Plateau des Guyanes,
espèces nouvelles.

INTRODUCTION

The genus *Tovomita* Aubl. (Clusiaceae) comprises 54 Neotropical species that range from Central America and West Indies to the tropical zone of southeastern Brazil (Marinho *et al.* 2016c, 2020). These are dioecious trees (mainly medium-sized) or shrubs of Amazonian rainforest (Cuello 2003), but can also occur in seasonally drier environments such as the Brazilian Atlantic Forest (Marinho *et al.* 2016d). Flowers appear terminally in a simple or compound dichasium (rarely solitary flower). Staminate plants usually bear more flowers than pistillate ones. *Tovomita* is unique among the Clusiaceae in having a pair of sepals (usually fused at bud stage) that completely encloses the bud. Besides, floral bud shape is an important (and peculiar) taxonomic character for identifying *Tovomita* species (see illustration of floral bud shapes in Marinho 2018). When leaf morphology and venation pattern are also considered, this is usually sufficient to distinguish *Tovomita* species from each other (or at least to reduce the choice to 2-3 species). Fruits are distinctive fleshy capsules, exposing at maturity 4-7 seeds (one per locule) covered with a bright white, orange or reddish aril (Engels & Marinho 2018).

The relevance of the number of stamens in *Tovomita* had already been pointed out by Cuello (1999) when she described *T. stergiosii* Cuello, until now the species that had the lowest number of stamens (*c.* 20). Stamens and staminodes in *Tovomita* can be short (*c.* 2 mm long) to very long (up to 1 cm long), organized in two to five whorls, varying from dorsiventrally compressed, subclavate, terete or filiform-terete. In *T. clusiiflora* (Ducke) L.Marinho, the connective can even exceed the thecae (Marinho *et al.* 2018).

In recent years, many new species of *Tovomita* have been described (Poncy & Offroy 2006; Marinho *et al.* 2015, 2016a, b, c, 2019, 2020; Marinho 2018). While preparing a checklist of the tree species of French Guiana, the first two authors found material that did not match any known *Tovomita* species. It corresponds to two new species that we describe here. The first one, *Tovomita maxima* Molino & J.Engel, sp. nov. is found in French Guiana, Guyana and the Brazilian state of Amazonas; the second one, *Tovomita saulensis* J.Engel & Molino, sp. nov., is possibly endemic to central French Guiana.

MATERIAL AND METHODS

All physically studied material was examined at CAY, and part of it was received on loan at MPU for detailed analysis. This includes eight fertile specimens of *Tovomita maxima* sp. nov. (four with staminate flowers and/or staminate floral buds, one with a pistillate flower and three with fruits), and three fertile specimens of *Tovomita saulensis* sp. nov. (two with staminate floral buds and one with immature fruits). Digitized specimens (including type material) of other *Tovomita* species were consulted online on several websites, including those of the Herbier IRD de Guyane (CAY), the Field Museum (F), the Conservatoire et Jardin Botaniques de la ville de Genève (G), the Meise Botanic Garden (BR), the Naturalis Biodiversity Center (L [and AMD, U, WAG]), the New York Botanical Garden (NY), the Muséum national d'Histoire naturelle de Paris (P), the Royal Botanic Gardens Kew (K), the Smithsonian National Museum of Natural History (US), JSTOR Global Plants, iDigBio and e-Recolnat (abbreviations according to Thiers 2021). Measurements and photographs of the floral parts were made with Keyence VHX-7000/7020 digital microscope. Floral bud shapes terminology is based on Marinho (2018). The conservation status was evaluated according to 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

Family Clusiaceae Lindl.
Genus *Tovomita* Aubl.

Tovomita maxima Molino & J.Engel, sp. nov.
(Figs 1; 2; 3; 4)

Tovomita maxima sp. nov. is similar to *T. speciosa* Ducke by the large and coriaceous leaves and large floral buds. The species can be distinguished by the floral bud and outer pair of sepals apiculate (vs rounded in *T. speciosa*), the presence of bracteoles forming a calyptra around the floral bud or dichasium (vs absent in *T. speciosa*); and higher number of stamens in *T. maxima* (74-many vs *c.* 50 stamens in *T. speciosa*). Regarding staminate flowers, *T. maxima* sp. nov. is unique in the genus both by its exceptionally large (145), and unusually variable number of stamens (74-145).

Typus. — **French Guiana**. Montagne des Chevaux, parcelle SPP, tree SPP-624, 4°41'N, 52°22'W, ♂ fl., 11.XI.2009, *Sabatier & Fonty 5595* (holo-, CAY[CAY112114!]).

Etymology . — The specific epithet refers to the large size of this species, as well as its high number of stamens.

Distribution. — *T. maxima* sp. nov. was collected in northern and southern French Guiana, in southern Guyana and in the Brazilian state of Amazonas in upper Solimões River.

Habitat. — The new species was found in *terra firme* forest from sea level to around 1000 m a.s.l. Precipitations on the different localities vary from 2000 mm in southern French Guiana to 4000 mm for the most rainy localities in northern French Guiana, which makes *T. maxima* sp. nov. a fairly ubiquitous species in terms of water requirements.

Phenology. — Staminate flowers have been observed in October and November, staminate floral buds in August and December, (one) pistillate flower in April. Fruits were collected in January and March.

Conservation status. — The studied specimens come from twelve different localities, eight in French Guiana, three in southern Guyana and one in the Brazilian state of Amazonas in upper Solimões River. Based on these collections, the estimated extent of occurrence (EOO) is 228 815 km² and the area of occupancy (AOO) is 44 km². Among the 94 000 trees censused in the GUYADIV

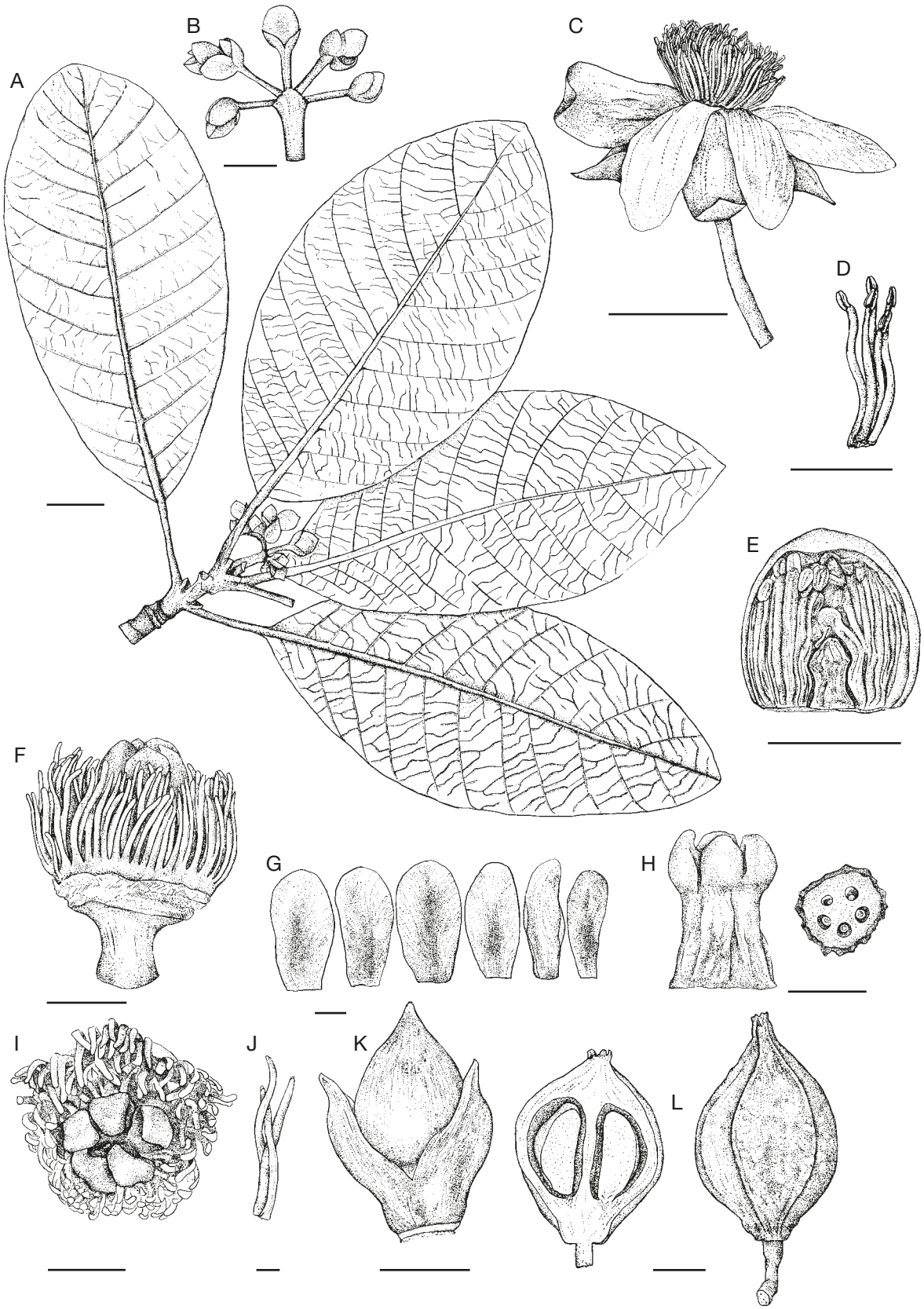

Fig. 1. — *Tovomita maxima* Molino & J.Engel, sp. nov.: **A**, stem with male inflorescence; **B**, part of male inflorescence; **C**, staminate flower; **D**, detail of stamens; **E**, staminate floral bud longitudinal section (note the pistillode in the middle); **F**, pistillate flower (perianth missing); **G**, petals (from dissected bud); **H**, gynoecium (left), ovary transverse section (right); **I**, pistillate flower apical view; **J**, detail of staminodes; **K**; staminate floral bud (note calyptrate bracteoles); **L**, fruit medial section (left), fruit lateral view (right); **A**, **B**, *Sabatier & Fonty 5595*; **C**-**E**, **K**, *Tostain et al. 2488*; **F**, **H**-**J**, *Larpin 1057*; **G**, *Sabatier & Molino 5153*; **L**, *Granville & Crozier 13646* (left), *Henkel 4994* (right). Drawn by Laurence Ramon. Scale bars: A, B, I, 2 cm; C, 1 cm; D-I, K, 5 mm; J, 1 mm.

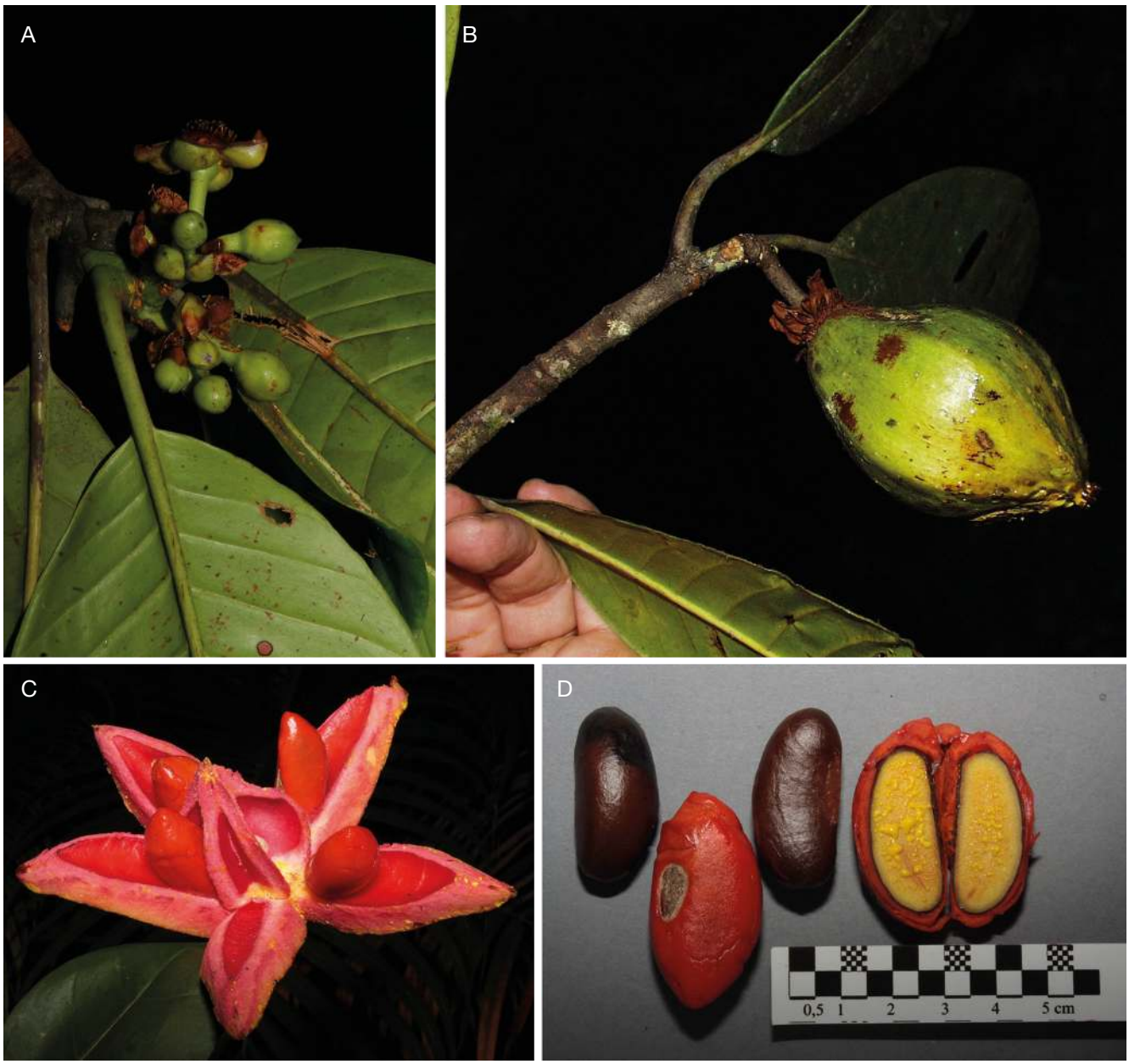

Fig. 2. — *Tovomita maxima* Molino & J.Engel, sp. nov.: **A**, male inflorescence; **B**, fruit; **C**, open fruit showing four seeds (one seed missing); **D**, seeds (two with the red aril removed, one in longitudinal section); **A**, *Sabatier & Fonty 5595*; **B**-**D**, no voucher. **A**-**D**, Photographs by Daniel Sabatier.

network (Engel 2015), 65 individuals were identified as *T. maxima* sp. nov. The localities where this new species has been collected or identified in the field are not directly threatened by human activities. *Tovomita maxima* sp. nov. is thus classified as Least Concern (LC) according to IUCN Red List criteria (IUCN 2012). However, this status must be considered with caution as it is a rare species whose survival and regeneration capacities could be affected by ongoing climate changes (Phillips *et al.* 2008; Esquivel-Muelbert *et al.* 2018; Gomes *et al.* 2019).

Affinities. — In *Tovomita maxima* sp. nov., large leaves resemble those of *T. speciosa*, a species known from the Brazilian states of Pará and Amapá (Marinho 2020). However, the leaves of *T. maxima* sp. nov. have a longer petiole and the base of the lamina is attenuate vs cuneate in *T. speciosa*. Floral buds and outer pair of sepals are apiculate (vs rounded in *T. speciosa*), the bracteoles form a calyptra while they are absent in *T. speciosa*; and the stamens are much more numerous (74-many vs *c.* 50 in *T. speciosa*). In French Guiana, *T. gazelii* Poncy & Offroy is the most similar species with its large, long-petioled leaves, its apiculate floral buds and its numerous stamens (90-100). However, this species is easily distinguished by its fruit covered with woody protrusions (a unique feature in *Tovomita*), its chartaceous leaves (vs coriaceous in *T. maxima* sp. nov.) and its remarkable cone of prop roots that can reach 3 m high.

Other material studied. — **French Guiana**. Montagnes de la Trinité, zone sud, Bassin de la Mana, 400 m, 4°34'N, 53°21'W, fr., 15.I.1998, *Granville & Crozier 13646* (B, BRIT, CAY[CAY004734!, CAY004735!], P[P05061603]); Montagnes des Nouragues, bassin de l'Approuague, Arataye, 180 m, 4°3'N, 52°42'W, ♀ fl., 20.IV.1992, *Larpin 1057* (CAY[CAY167622!]); New road to Brazil (Route de l'Est), 7 kms S of the bridge over the Comté River, *c.* 52 km S of Cayenne,

Fig. 3. — *Tovomita maxima* Molino & J.Engel, sp. nov.: **A**, gynoecium; **B**, pistillate flower (perianth missing); **C**, outer sepals; **D**, staminate floral buds (note calyptrate bracteoles); **E**; two inner sepals (top left) and seven petals; **F**, androecium; **C**, **E**, **F**, from dissected staminate floral bud; **A**, **B**, *Larpin 1057*; **C**, **E**, **F**, *Clarke 7145*; **D**, *Tostain et al. 2488.* Photographs by Julien Engel. Scale bars: A-E, 5 mm; F, 2 mm.

st., 12.I.1977, *Mori 8898* (P[P04727131]); Régina, Savane-roche Virginie, parcelle SRV3, tree SRV3-103, 4°11'3"N, 52°8'50"W, st., 9.X.2007, *Prévost et al. 5017* (CAY!, MO); Piste de Saint-Elie, interfluve Sinnamary-Counamama, 5°20'N, 53°W, fr., 16.I.1991, *Prévost & Sabatier 2995* (CAY[CAY167615!], P[P01155523!]); Rivière Arataye, Saut Pararé – Bassin de l'Approuague, 4°2'N, 52°42'W, st., 17.X.1986, *Sabatier 1449* (CAY[CAY167620, CAY167621!], P[P01155524!]); Petit Saut – Bassin du Sinnamary, 5°3'50"N, 53°3'17"W, st., 3.VII.1997, *Sabatier et al. 4394* (CAY[CAY167616!], P[P01155525!]); France-Brazil border, Borne Frontière N°1, parcelle BOU3, tree BOU3-586, 300 m, 2°12'43"N, 54°25'28"W, ♂ fl., 15.X.2006, *Sabatier & Molino 5153* (CAY[CAY109336!], MO); Montagne des Chevaux, carrière SCC., 28 m, 4°44'34"N, 52°26'12"W, ♂fl., 23.XII.2008, *Tostain et al. 2488* (CAY[CAY111776!], NY, MO, P, U, US).
Guyana. Upper Takutu-Upper Essequibo, Acarai Mts, ridge ascending to summit of unnamed peak, 6 km S of Sipu River, 700 m, 1°22'N, 58°56'W, ♂ fl. b., 26.VIII.1998, *Clarke 7145* (CAY[CAY167617!], US[US00708843]); Acarai Mts, summit and adjacent slopes of Tinarmau Peak, 975 to 1000 m, 1°16'N, 58°35'W, fr., 6.III.1994, *Henkel 4994* (CAY[CAY167618, CAY167619!], US[US00587954]); Akarai Mountains: height of land between drainage of Rio Mapuera (Trombetas tributary) and Shodikar Creek (Essequibo tributary), 600-800m, st., 19.I.1938, *Smith 3000* (NY[NY01416670]).
Brazil. Estado de Amazonas – Upper Rio Solimões, Mun. São Paulo de Olivença, Estrada Bomfim, trail beyond road, 6 km S of town center, 3°30'S, 68°57'W, ♂ fl., 25.XI.1986, *Daly 4430* (NY[NY01417001], US[US01882507]).

Description

Dioecious trees up to 30 m tall and 90 cm in diameter, prop roots up to 3 m high. Bark grey, exsudate yellow, abundant. All plant glabrous, including flower and fruit.

Leaves

Opposite; petioles 2.6-6.5 cm long, with an adaxial margined pit; leaf blades coriaceous, mostly broadly elliptic, 12.2-33 × 7.1-16.6 cm; apex slightly acuminate to rounded, rarely retuse; base attenuate; margin entire; midvein prominent abaxially and slightly raised adaxially; secondary veins in 9-15 pairs, 0.7-2.5 cm distant from each other, eucamptodromous, prominent abaxially and slightly raised adaxially; intersecondary veins usually absent or inconspicuous (sometimes visible in last third of the leaves); tertiary veins visible on both surfaces of young leaves but barely visible on mature leaves.

Inflorescences

Terminal. Male inflorescence a compact to ample compound dichasium, 3.5-12 cm long with up to 20 flowers; bracts not seen; bracteoles 7-11 × 3-9 mm, connate, forming a calyptra, often caducous; pedicels 9-34 × 1.5-3.5 mm. Female inflorescence reduced to a single flower.

Staminate flowers

Buds 8-18 × 6-15 mm, ovoid with a mucronate apex to spheroid with an apiculate apex, pale green. Flowers 1-2 cm diam.; sepals 4: two outer sepals 10-17 × 7-16 mm, fleshy, greenish, broadly ovate (to almost orbicular in buds), concave (cymbiform in buds), apex mucronate, and two inner sepals 6-15 × 5-11 mm, fleshy (although less than the inner sepals), greenish, broadly ovate, concave, apex mucronate; petals 4-7, 5-20 × 3-11 mm, linear to oblong to broadly ovate, apex rounded to acute; stamens 74-145, filaments 4-12 mm long, terete; anthers *c.* 1 mm long; pistillode 2-2.5 mm high × 1-2 mm large, stigmas 5.

Pistillate flowers

Pedicels *c.* 6 × 3 mm; receptacle *c.* 1.5 cm diam.; perianth not seen; staminodes 109, 5-8 mm long, terete; gynoecium 10 mm high × 5-7 mm large; ovary *c.* 3 × 6 mm, 5-locular, 1 ovule per locule; style *c.* 3 × 5 mm; stigmatic area *c.* 3 × 7 mm, stigmas 5, *c.* 2-3 mm wide, free from each other, sessile.

Fruit

A fleshy capsule, 5-6.8 × 3-4.6 cm, pericarp splitting septifragally into 5 valves, fragments of sepals, petals and staminodes persistent; epicarp smooth, greenish; mesocarp pinkish; endocarp orange-red; seeds 5, 2.8-3.4 × 1.3-1.7 cm, reniform, brown, covered with a bright orange-red aril.

Tovomita saulensis J.Engel & Molino, sp. nov.
(Figs 4; 5; 6)

Tovomita saulensis sp. nov. is similar to *T. mangle* G.Mariz especially in its mucronulate and oblong floral bud. The species can be distinguished by the combination of small leaves (4-7 cm on average) and a low number of stamens (9-15 vs 35-45 in *T. mangle*). To date, the species has the lowest number of stamens in the genus.

Typus. — **French Guiana**. Saül and vicinity: Route de Bélizon, 0-2 km S of Eaux Claires, 230-300 m, 3°37'N, 53°12'W, ♂ fl. b., 22.IX.1994, *Mori et al. 24002* (holo-, CAY[CAY167624!]; iso-, P[P04897763], NY[NY04204154], U[U0181523], US[US00872988]).

Etymology . — The specific epithet refers to the type locality Saül.

Distribution. — *Tovomita saulensis* sp. nov. is presently known only from Central French Guiana, near the village of Saül. Therefore it could be considered as endemic of this area, pending additional records.

Habitat. — According to the three specimens studied, *T. saulensis* sp. nov. occurs in *terra firme* forest between 200-400 m a.s.l and receiving about 2500 mm of annual rainfall.

Phenology. — Staminate floral buds were collected in September, immature fruits in April.

Conservation status. — *Tovomita saulensis* sp. nov. is too poorly known (three specimens) to assess its protection status. Following the procedures adopted by Marinho & Beeck (2019), a DD (Deficient Data) status is therefore suggested.

Affinities. — *Tovomita saulensis* sp. nov. has small leaves and oblong floral buds with a mucronulate apex. These characters are found in two other *Tovomita* species, *T. divaricata* Maguire from Guyana, and *T. nebulosa* L. Marinho & Luján from Cerro de la Neblina in Venezuela. But the leaf venation of these two species is not distinctly brochidodromous as in *T. saulensis*. Specimens of *T. saulensis* were initially identified by Marinho (2019) as *T. mangle*, a species widely distributed in Brazil and also occurring in French Guiana, especially due to the shape of the floral buds (oblong with mucronulate apex) and the brochidodromous leaf venation. The species can be distinguished by the smaller aspect of *T. saulensis*, its smaller leaves (4.3-7.5(9) × 1.2-3.2 cm vs 9-21 × 3.4-9.7 cm in *T. mangle*), smaller floral buds (3-6 vs 6-11 mm in *T. mangle*) and smaller number of stamens (9-15 vs 35-45 in *T. mangle*).

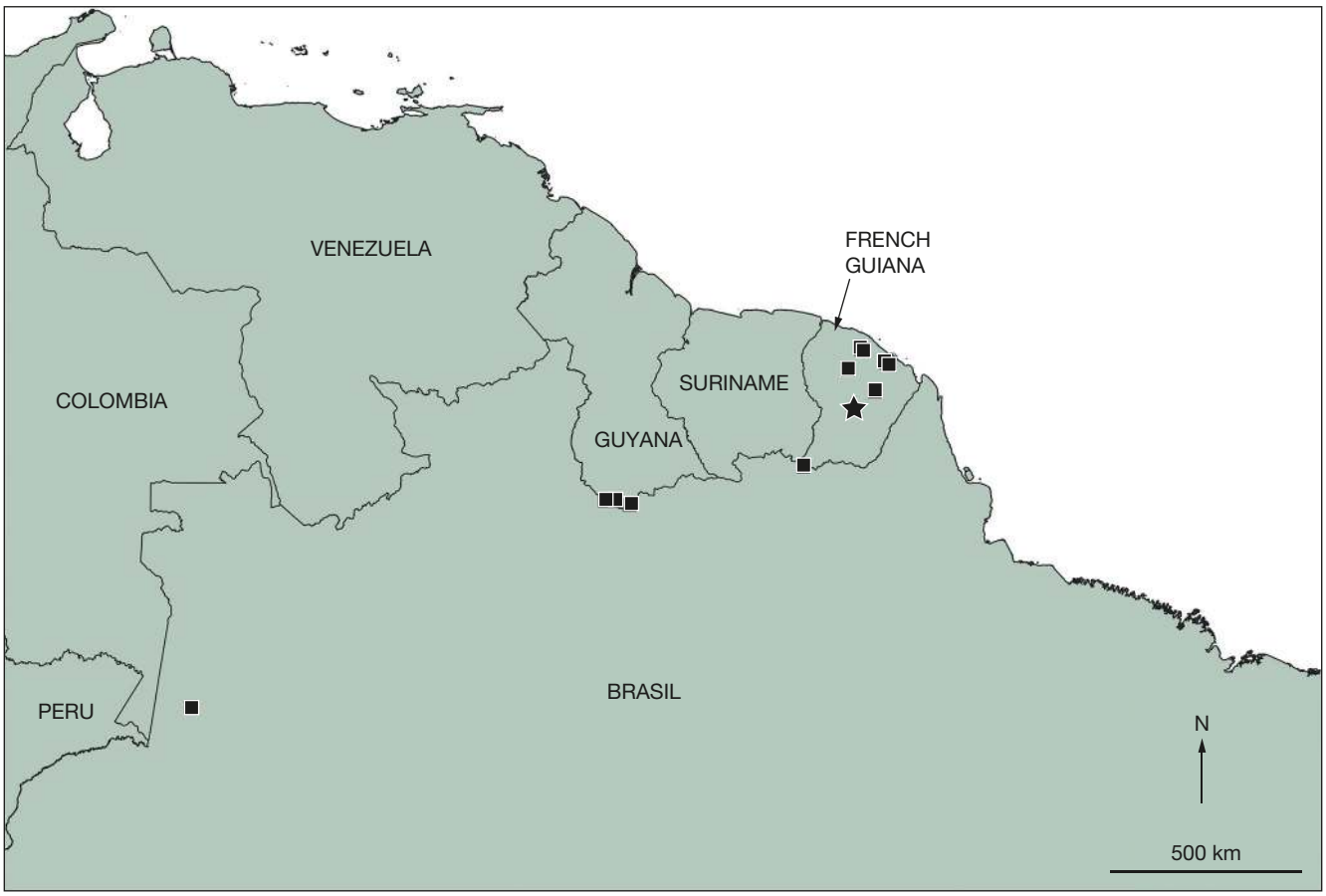

Fig. 4. — Distribution of *Tovomita maxima* Molino & J.Engel, sp. nov. (■) and *Tovomita saulensis* J.Engel & Molino, sp. nov. (★).

Other material studied. — **French Guiana**. Saül, La Fumée Ouest, 200-400 m, 3°37'N, 53°12'W, fr., 8.IV.1983, *Mori & Pipoly 15551* (CAY[CAY167625!], US[US00873003]); Saül, La Fumée Ouest, 200-400 m, 3°37'N, 53°12'W, st., 26.IV.1983, *Mori & Pipoly 15674* (P[P04897837]); Saül, Along botany trail northeast of Les Eaux Claires, 270 m, 4°42'N, 52°25'W, ♂ fl. b., 24.IX.1995, *Phillippe et al. 26984* (CAY[CAY167623!], ILLS).

Description

Dioecious small trees up to 6 m and 12 cm in diameter, trunks without prop roots, exsudate sparse. All plant glabrous, including flower and fruit.

Leaves

Opposite; petioles 4-12 × *c.* 1 mm, with an adaxial margined pit; leaf blades chartaceous, narrowly elliptic to elliptic, 4.3-7.5(9) × 1.2-3.2 cm; apex long-attenuate to acuminate; base acute and slightly decurrent; margin entire; midvein slightly raised on both surfaces; secondary veins in 6-10 pairs, 0.5-1 cm distant from each other, brochidodromous, slightly raised on both surfaces; intersecondary veins present; tertiary veins visible on both surfaces.

Inflorescences

Terminal. Male inflorescences a compound dichasium, 1.5-3 cm long with up to 20 flowers; bracts not seen; bracteoles triangular, *c.* 0.5 mm, caducous; pedicels 2-5 mm long.

Staminate flowers

Buds 3-6 × 1-2.5 mm, oblong with a mucronulate apex, green. Flowers known only from buds; sepals 2, *c.* 5 × 1-2 mm, oblong to ovate, apex acuminate (with rounded tip); petals 4, 3-4 × 1-2 mm, linear to oblong, apex acuminate; stamens 9-15, filaments 2-3 mm long, white; anthers *c.* 0.5 mm long; pistillode *c.* 0.5 mm high × 1 mm large, stigmas 4.

Pistillate flowers

Not seen.

Fruit

Known only immature. Fleshy capsule *c.* 2.5 × 1 cm, with apical rostrum *c.* 1 × 0.3 cm; epicarp smooth; seeds 2-4, *c.* 1.2 × 0.5 cm.

Note

Tovomita saulensis sp. nov. has long been misidentified in CAY herbarium as *T. fructipendula* (Ruiz & Pav.) Cambess. (syn. of *T. brasiliensis* (Mart.) Walp.; see Marinho *et al.* 2016d). This is also the case in the *Guide to the Vascular Plants of Central French Guiana* (Mori *et al.* 2002) where the illustration of *T. fructipendula* is based on at least two specimens of *T. saulensis* sp. nov. (*Mori & Pipoly 15551*,

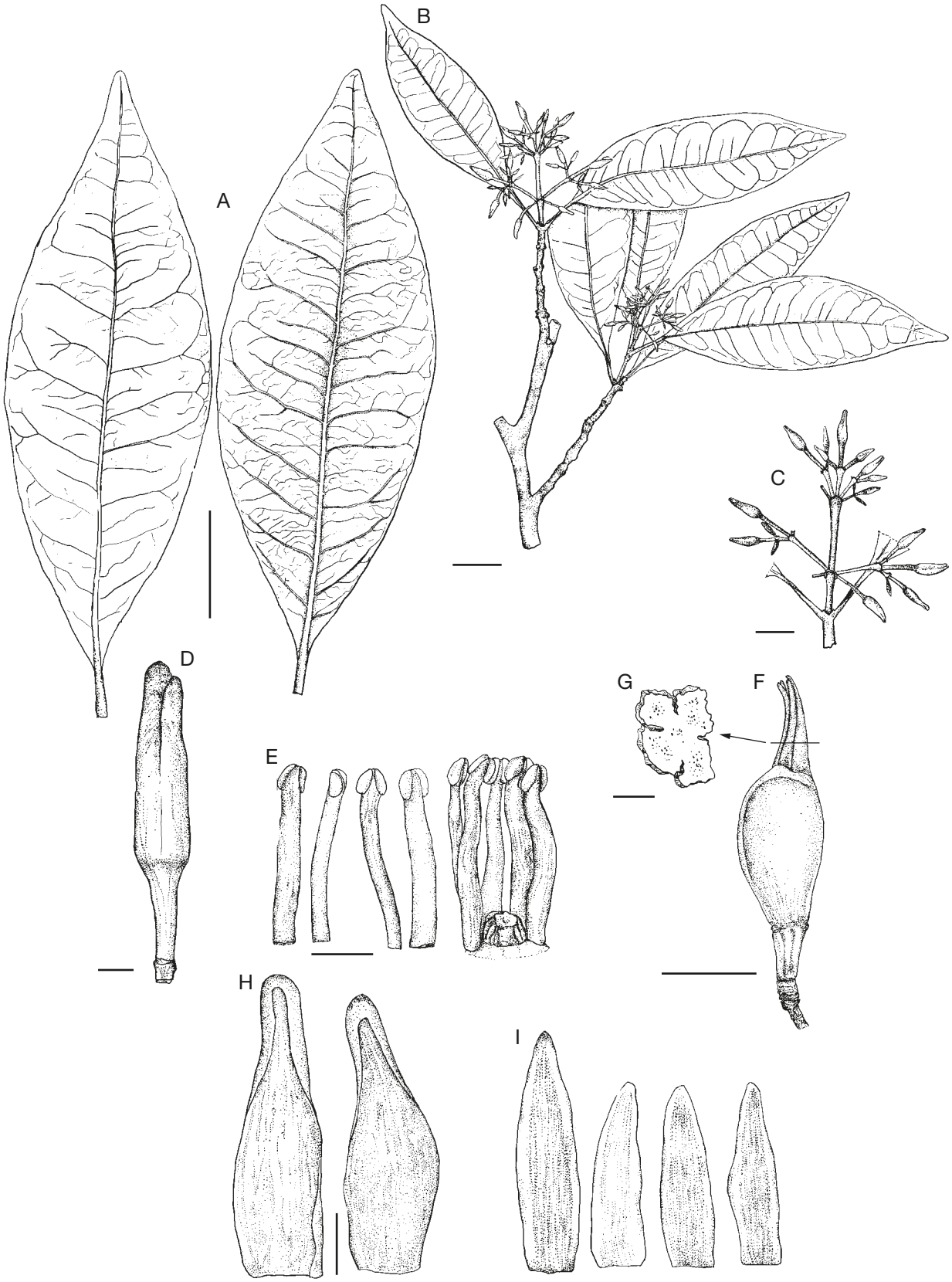

Fig. 5. — *Tovomita saulensis* J.Engel & Molino, sp. nov.: **A**, leaf adaxial surface (left), abaxial surface (right); **B**, stem with male inflorescence; **C**, part of male inflorescence; **D**, staminate floral bud; **E**, detail of stamens (left), detail of pistillode and stamens (right); **F**, immature fruits; **G**, transverse section of immature fruit apical rostrum (i.e., remaining styles and stigmas); **H**, sepals (from dissected bud); **I**, petals (from dissected bud); **A**, **D**, **E**, *Phillippe et al. 26984*; **B**, **C**, **H**, **I**, *Mori et al. 24002*; **F**, **G**, *Mori & Pipoly 15551*. Drawn by Laurence Ramon. Scale bars: A, B, F, 1 cm; C, 5 mm; D, E, G-I, 1 mm.

Fig. 6. — *Tovomita saulensis* J.Engel & Molino, sp. nov.: **A**, male inflorescence; **B**, staminate floral bud dissected: androecium (top left), sepals (top right), petals (bottom); **C**, detail of pistillode (red circle) and stamens; **D**, detail of leaf venation; **A**, *Mori et al. 24002*; **B**, **C**, **D**, *Phillippe et al. 26984*. Photographs by Julien Engel. Scale bars: A, D, 5 mm; B, C, 1 mm.

Mori et al. 24002). The drawing of the fruit is based on a third specimen (*Mori 22720*), not seen. Both species have leaves of about the same size (around 4-7 cm long) but those of *T. fructipendula* have more secondary veins, and these are not brochidodromous. Also, the floral bud apex is rounded in *T. fructipendula* (vs mucronulate in *T. saulensis*), and the fruit epicarp is asperous (vs smooth in *T. saulensis*). Field photos of *Mori et al. 24002* are visible at: http://sweetgum.nybg.org/science/vh/specimen-details/?irn=415530

Acknowledgements

We thank Laurence Ramon for the beautiful illustrations, Sophie Gonzalez and Chantal Geniez (CAY) for providing loan material and access to specimens, and Jean-Louis Smock (CAY) for scanning CAY herbarium sheets. We also thank the histology and biomechanics technical platform of UMR AMAP (Montpellier) for providing access (and training) to digital microscope Keyence, and Daniel Sabatier for the photos of fresh material. CAY specimens have been digitized thanks

to the "Investissement d'Avenir" program e-RECOLNAT managed by the Agence Nationale de la Recherche (RECOLNAT-ANR-11-INBS-0004). This work was supported by an "Investissement d'Avenir" grant, also managed by the ANR (Labex CEBA, ref. ANR-10-LABX-25-01). We are grateful to Odile Poncy and an anonymous referee for their useful comments on the manuscript.

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Submitted on 25 May 2021;
accepted on 5 January 2022;
published on 20 June 2022.