Generic limits re-visited and an updated sectional classification for *Protium* (tribe Protieae). Studies in Neotropical Burseraceae XXV

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Abstract. In recent molecular phylogenetic work on tribe Protieae (Burseraceae) with thorough sampling, the major well-supported clades show remarkable congruence with infrageneric classifications based on morphology, but the results call for synonymizing *Crepidospermum* and *Tetragastris* with *Protium,* thereby making Protieae monophyletic and monogeneric under the name *Protium*. The necessary synonymies and a brief diagnosis for each of the eight sections of *Protium* are provided, and these new combinations are made: **Protium balsamiferum, P. catuaba, P. chagrense, P. herbertii, P. mucronatum, P. occhionii,** and **P. rhynchophyllum.**

Keywords: *Crepidospermum*, phylogeny, *Tetragastris*.

Although many parts of the infrafamilial classification of the Burseraceae are as yet unresolved, molecular phylogenetic investigations consistently show strong support for a monophyletic tribe Protieae (e.g., Weeks et al., 2005; Thulin et al., 2008; Weeks et al., 2014). In the last comprehensive assessment of generic limits in tribe Protieae (Daly, 1989), exceptions were found to most proposed apomorphies for *Crepidospermum* and *Tetragastris*, but *Crepidospermum* was maintained based on the presence of snail-shaped glands, and *Tetragastris* on anthers continuous with the filaments (Daly, 1989). Since then, however, snail-shaped glands have been observed in *Protium* s.s. (e.g. section *Pepeanthos*, Daly, 2007) and the presence in *Tetragastris* of staminodes with sagittate anthers calls into question the value of its stamen morphology as an apomorphy.

Molecular phylogenetic studies of the Protieae have shown consistently that the genera *Crepidospermum* and *Tetragastris* are embedded within the genus *Protium* (Fine et al., 2005, 2014). The most recent analysis (Fine et al., 2014) comprised multiple individuals of 102 taxa of tribe Protieae from throughout its biogeographic distribution. This sampling included five species of *Crepidospermum* and seven of *Tetragastris* (lacking only two published species of each genus), along with 90 species of *Protium*, representing all published sections (lacking 34 published species). Fine et al. (2014) sequenced three nuclear and two chloroplast genes and analyzed the aligned, concatenated sequences with Bayesian analysis, and found that *Tetragastris* and *Crepidospermum* were monophyletic groups that were sister to one another but nested within *Protium* (Fig. 1). These relationships were extremely strongly statistically supported, with 1.0 posterior probability. Furthermore, all published Neotropical Protieae sections had strong support with 1.0 posterior probability. The Asian section *Protium* also had 1.0 posterior probability but was embedded in a paraphyletic grade of taxa that included Section *Marignia,* which is native to Madagascar and Mauritius.

In order to establish a classification that better reflects the phylogeny, one option would be to recognize the published sections of *Protium* as distinct genera, but that would still leave a large number of unresolved species; more importantly, although the *Crepidospermum* and *Tetragastris* clades were strongly supported, they are clearly nested within *Protium*, thus rendering that genus

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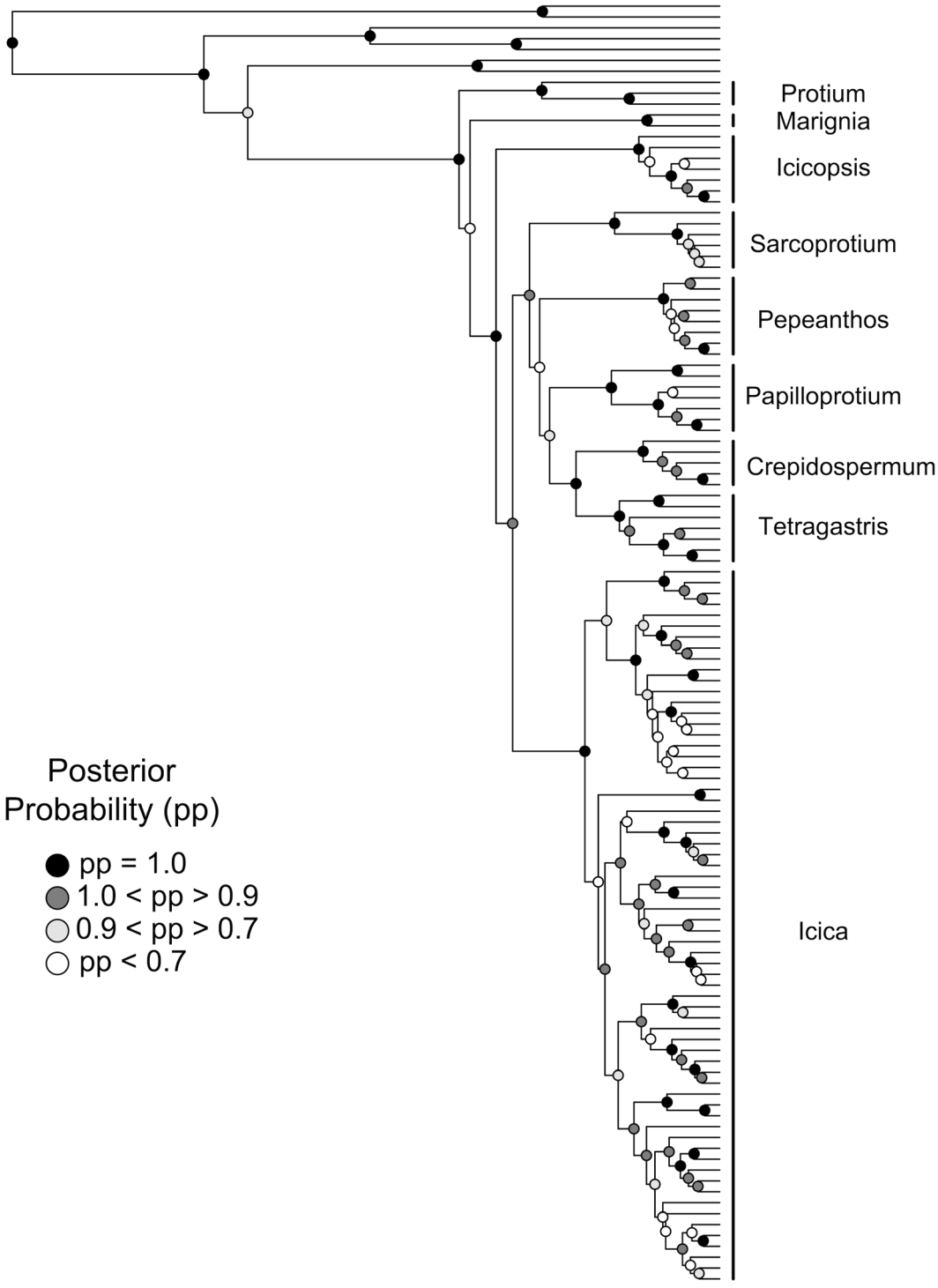

Fig. 1. Molecular phylogeny of the Protieae, showing the relationships of the sections of *Protium*, based on a Bayesian analysis of three nuclear and two chloroplast genes. Each tip of the phylogenetic tree represents a taxon. For more details see Fine et al. (2014).

paraphyletic. The solution adopted here is to synonymize *Crepidospermum* and *Tetragastris* under *Protium*, thereby forming a rather large and monogeneric – and monophyletic – tribe Protieae.

Protium Burm.f., Fl. Ind. (N. L. Burman): 88. 1768. Type species: *P. javanicum* Burm.f.

Icica Aubl., Hist. Pl. Guiane 1: 337. 1775. Type species, **here designated**: *I. heptaphylla* Aubl.

Hedwigia Sw., Prodr. [O. P. Swartz]: 62. 1788. Type species: *H. balsamifera* Sw.

Dammara Gaertn., Fruct. Sem. Pl. 2: 100. 1802. Type species: *D. graveolens* Gaertn.

Tetragastris Gaertn., Fruct. Sem. Pl. 2: 130. 1802. Type species: *T. ossea* Gaertn. ≡ *Protium balsamiferum* (Sw.) Daly & P. Fine.

Marignia Comm. ex Kunth, Ann. Sci. Nat., Bot., Sér. 1, 2: 352. 1824. Type species: *M. obtusifolia* (Lam.) DC. ≡ *Protium obtusifolium* (Lam.) Marchand. *Protium* section *Marignia* (Comm. ex Kunth) Hook.f. in Gen. P1. [Bentham & Hooker f.] 1(1): 324. 1862.

Knorrea Moc. & Sessé, Fl. Mexic., icon. ined. ex DC. in Prodr. [A. P. de Candolle] 2: 80. 1825. Type species: *K. mexicana* Moc. & Sessé. [doubtful species].

Caproxylon Tussac, Fl. Antill. 4: 87: 1827. Type species: *C. hedwigii* Tussac.

Schwägrichenia Rchb., Consp. Regn. Veg. [H. G. L. Reichenbach]: 147. 1828, non Spreng., Pl. Min. Cogn. Pug. 2: 58. 1815, nom. illegit.

Crepidospermum Hook.f. in Gen. P1. [Bentham & Hooker f.] 1(1): 325. 1862. Type species: *C. sprucei* Hook.f., nom. illegit. ≡ *C. goudotianum* (Tul.) Triana & Planch., Ann. Sci. Nat., Bot., sér. 5, 14: 300. 1872.

Icicopsis Engl., Mart. Fl. bras. 12(2): 254. 1874. Type species, **here designated**: *I. tenuifolia* Engl.

Tingulonga altissima (Aubl.) Kuntze, Revis. Gen. Pl. 1: 108. 1891, nom. illegit.

Hemicrepidospermum Swart, Recueil Trav. Bot. Néerl. 39: 205. 1942. Type species: *H. rhoifolium* (Benth.) Swart. *Crepidospermum* sect. *Hemicrepidospermum* (Swart) Daly, Brittonia 39: 55. 1987.

Paraprotium Cuatrec., Revista Acad. Colomb. Ci. Exact. 8: 472. 1952. Type species: *P. vestitum* Cuatrec.

The sections of *Protium*

Please note that all the species of Protieae accepted here are listed in Appendix 1 with the sectional assignment of each.

Protium* section *Protium Burm.f., Fl. Ind.: 88. 1768, nom. conserv. Type species: *P. javanicum* Burm.f.

This was published as section *Eu-Protium* by Swart (1942). Fissuring in bark sparse, irregular, and deep, the outer bark thick and shed in large irregular plates; resin clear; pulvinuli on lateral leaflets usually present; leaflet margin sometimes serrate; leaflet secondary vein framework brochidodromous, tertiary vein fabric irregular-reticulate, freely ending veinlets 2–4+-branched; inflorescence thyrsoid; petals free; stamens in two subequal series, the anthers sagittate; in staminate flowers the annular disk and pistillode distinct; pseudaril grayish and translucent, pyrene rather bony; cotyledons palmately lobed; germination epigeal, phanerocotylar, first eophylls alternate, simple. Four published species recognized here, Tropical Asia.

Included species.—Protium connarifolium (Perk.) Merr., *P. javanicum* Burm.f., *P. macgregorii* (F. M. Bailey) Leenh. & Steenis, *P. serratum* (Wall. ex Colebr.) Engl.

Protium* section *Crepidospermum (Hook.f.) Daly & P. Fine, **comb. nov.**

Icica Aubl., Hist. P1. Gui. Fr. 1: 337. 1775, ex parte quoad *I. goudotiana* Tul.

Hedwigia Sw., Prodr. Veg. Ind. Occ. 62. 1788, ex parte quoad *H. rhoifolia* Benth.

Crepidospermum Hook.f. in Gen. P1. [Bentham & Hooker f.] 1(1): 325. 1862. Type species: *C. sprucei* Hook.f., nom. illegit. ≡ *C. goudotianum* (Tul.) Triana & Planch., Ann. Sci. Nat., Bot., sér. 5, 14: 300. 1872.

Hemicrepidospermum Swart, Recueil Trav. Bot. Néerl. 39: 205. 1942. Type species: *H. rhoifolium* (Benth.) Swart. *Crepidospermum* sect. *Hemicrepidospermum* (Swart) Daly, Brittonia 39: 55. 1987.

Bark thin and rather smooth; resin clear; pulvinuli absent; leaflet margin consistently serrate; snail-shaped glands present; leaflet secondary vein framework semi-craspedodromous, tertiary vein fabric often alternate-percurrent, freely ending veinlets usually highly branched; inflorescences thyrsoid; petals free; stamen series sometimes pentadynamous, in staminate flowers the stamens 5 or 10, the anthers sagittate; in staminate flowers the pistillode either containing locules and reduced ovules or sometimes reduced to a parenchymatous cylinder; pseudaril white, pyrene cartilaginous; cotyledons plano-convex and J- or U-shaped; germination unknown. Six published species accepted here, Neotropics.

Included species.—Protium atlanticum (Daly) Byng & Christenh., *P. cuneifolium* (Cuatrec.) Byng & Christenh., *P. goudotianum* (Tul.) Byng & Christenh., *P. multijugum* (Swart) Byng & Christenh., *P. prancei* (Daly) Byng & Christenh., *P. rhoifolium* (Benth.) Byng & Christenh.

Protium* section *Icica (Aubl.) Swart, A monograph of the genus *Protium* and some allied genera (Burseraceae): 266. 1942 (published as *Eu-Icica*).

Bark variable; resin usually clear; pulvinuli on lateral leaflets usually present; leaflet margin entire or distally sparsely serrulate; leaflet secondary framework (festooned) brochidodromous, tertiary vein fabric percurrent or irregular-reticulate, freely ending veinlets diverse; inflorescences thyrsoid; petals distinct or irregularly fused less than 1/2 their length; stamens in two subequal series (rarely flowers haplostemonous), anthers usually sagittate; annular disk and pistillode distinct; pseudaril white (very rarely red), pyrenes bony to papery; cotyledons lobed and contortuplicate or entire and plano-convex; germination variable. Eighty-six published species recognized here, Neotropics.

Included species.—Protium aguilarii D. Santam., *P. aidanianum* Daly, *P. altsonii* Sandwith, *P. amplum* Cuatrec., *P. angustifolium* Swart, *P. aracouchini* (Aubl.) Marchand, *P. araguense* Cuatrec., *P. attenuatum* (Rose) Urb., *P. bahianum* Daly, *P. boomii* Daly, *P. brasiliense* (Spreng.) Engl., *P. brenesii* (Standl.) D. Santam., *P. buenaventurense* Cuatrec., *P. calanense* Cuatrec., *P. carolense* Daly, *P. colombianum* Cuatrec., *P. confusum* (Rose) Pittier, *P. copal* (Schtldl. & Cham.) Engl., *P. correae* D. M. Porter, *P. costaricense* (Rose) Engl., *P. cranipyrenum* Cuatrec., *P. crenatum* Sandwith, *P. cubense* (Rose) Urb., *P. cundinamarcense* Cuatrec., *P. cuneatum* Swart, *P. dawsonii* Cuatrec., *P. decandrum* (Aubl.) Marchand, *P. demerarense* Swart, *P. divaricatum* Engl., *P. ecuadorense* Benoist, *P. elegans* Engl., *P. gallicum* Daly, *P. giganteum* Engl., *P. glabrescens* Swart, *P. glabrum* (Rose) Engl., *P. glaucescens* Urb., *P. glaucum* J. F. Macbr., *P. glaziovii* Swart, *P. glomerulosum* Cuatrec., *P. grandifolium* Engl., *P. guacayanum* Cuatrec., *P. guianense* (Aubl.) Marchand, *P. hammelii* D. Santam., *P. hebetatum* Daly, *P. heptaphyllum* (Aubl.) Marchand, *P. icicariba* (DC.) Marchand, *P. inconforme* Pittier, *P. inodorum* Daly, *P. kleinii* Cuatrec., *P. klugii* J. F. Macbr., *P. krukovii* Swart, *P. laxiflorum* Engl., *P. leptostachyum* Cuatrec., *P. llanorum* Cuatrec., *P. macrophyllum* (Kunth) Engl., *P. macrosepalum* Swart, *P. maestrense* Bisse, *P. melinonis* Engl., *P. meridionale* Swart, *P. montanum* Swart, *P. morii* Daly, *P. multiramiflorum* Lundell, *P. nervosum* Cuatrec., *P. nodulosum* Swart, *P. occultum* Daly, *P. opacum* Swart, *P. ovatum* Engl., *P. pallidum* Daly, *P. panamense* (Rose) I. M. Johnst., *P. paniculatum* Engl., *P. pilosellum* Swart, *P. pilosissimum* Engl., *P. pilosum* (Cuatrec.) Daly, *P. pittieri* (Rose) Engl., P. *poeppigianum* Swart, *P. ptarianum* Steyerm., *P. puncticulatum* J. F. Macbr., *P. ravenii* D. M. Porter, *P. spruceanum* (Benth.) Engl., *P. strumosum* Daly, *P. tovarense* Pittier, *P. trifoliolatum* Engl., *P. unifoliolatum* Engl., *P. veneralense* Cuatrec., *P. vestitum* (Cuatrec.) Daly, *P. widgrenii* Engl.

Protium* section *Icicopsis (Engl.) Swart, J. J., A monograph of the genus *Protium* and some allied genera (Burseraceae): 368. 1942.

Icicopsis Engl. in Mart. Fl. bras. 12(2): 254. 1874.

This section was originally published as a distinct genus by Engler (1874). Bark sometimes thick and fissured; resin translucent; pulvinuli on lateral leaflets present; leaflet margin entire; leaflet secondary framework (festooned) brochidodromous, tertiary vein fabric usually mixed opposite-alternate percurrent, freely ending veinlets 2–4+-branched; inflorescences pseudospicate and often pseudoterminal; petals free, sometimes carinate; stamen series pentadynamous or staminodes 5 in a few species, the anthers sagittate; disk and pistillode replaced by a discoid to conical, densely pubescent, parenchymatous "ovariodisk"; pseudaril white, pyrenes cartilaginous, attachment of funicle near or below halfway point; cotyledons entire, transversely twice folded, germination epigeal and phanerocotylar; first eophylls alternate, simple, entire. Twelve published species recognized here, Neotropics.

Included species.—Protium chagrense (Pittier) Daly & P. Fine, *P. fragrans* (Rose) Urb., *P. herbertii* (Cuatrec.) Daly & P. Fine, *P. insigne* (Triana & Planch.) Engl., *P. mcleodii* I. M. Johnst., *P. neglectum* Swart, *P. rhynchophyllum* (Rusby) Daly & P. Fine, *P. robustum* (Swart) D. M. Porter, *P. sagotianum* Marchand,

P. sessiliflorum (Rose) Standl., *P. tenuifolium* (Engl.) Engl., *P. warmingianum* Marchand.

Protium* section *Marignia (Comm. ex Kunth) Hook.f. in Gen. Pl. [Bentham & Hooker f.] 1(1): 324. 1862. *Marignia* Comm. ex Kunth, Ann. Sc. Nat., ser. 1, 2: 351. 1824. Type species: *M. obtusifolia* (Lam.) DC. ≡ *Protium obtusifolium* (Lam.) Marchand.

Bark gray, thickening and irregularly fissured with age, inner bark red; resin translucent; pulvinuli on lateral leaflets absent; leaflet secondary framework festooned brochidodromous, tertiary fabric irregular reticulate and markedly admedially branched, freely ending veinlets 2–3-branched; inflorescences thyrsoid; petals free; stamens in two subequal series, the anthers sagittate; in staminate flowers the annular disk and pistillode distinct; pseudaril red, pyrenes cartilaginous; cotyledons lobed and contortuplicate, germination phanerocotylar, first eophylls alternate and simple. Two published species accepted here, one each in Madagascar and Mauritius.

Included species.—Protium madagascariense Engl., *P. obtusifolium* (Lam.) Marchand.

Protium* section *Papilloprotium Daly & P. Fine, Systematic Botany 36: 139–149. 2011. Type species: *P. subserratum* (Engl.) Engl.

Bark thin, often rough due to raised lenticels; resin milky; pulvinuli on lateral leaflets usually lacking; leaflet margin (sub)serrate or entire, abaxial leaflet surface papillate; leaflet secondary framework festooned brochidodromous, tertiary vein fabric irregular-reticulate, freely ending veinlets 4+-branched, terminating in highly branched sclereids; inflorescences pseudospicate; petals free, saccate at base and villous adaxially, (sub)erect at anthesis; stamen series pentadynamous, anthers sagittate, the apex apiculate; in staminate flowers the annular disk and pistillode distinct; style at least as long as ovary, unbranched; pseudaril white, pyrenes thinly cartilaginous; cotyledons entire and plano-convex; germination epigeal, cryptocotylar, first eophylls opposite, 5–11-foliolate, serrate. Five published species recognized here, Neotropics.

Included species.—Protium alvarezianum Daly & P. Fine, *P. ferrugineum* (Engl.) Engl., *P. pristifolium* Daly, *P. reticulatum* (Engl.) Engl., *P. subserratum* (Engl.) Engl.

Protium* section *Pepeanthos Daly, Brittonia 59: 1–24. 2007. Type species: *P. amazonicum* (Cuatrec.) Daly.

Bark smooth or striate, powdery or less often shed in small plates or granules; resin milky; snail-shaped glands present; pulvinuli on lateral leaflets absent, or present but inconspicuous; leaflet margin entire; freely ending veinlets 4+-branched and terminating in highly branched sclereids; inflorescences thyrsoid; petals free, (sub)erect at anthesis; stamen series sometimes pentadynamous and the antesepalous stamens often reflexed between petals at anthesis; in staminate flowers the annular disk and pistillode distinct, the disk glabrous or pubescent; stigmas caudiculate and spiculate; pseudaril white (red in *P. apiculatum* Swart), pyrenes usually cartilaginous, attachment of funicle well above halfway point, cotyledons entire and plano-convex; germination epigeal, phanerocotylar; first eophylls opposite, simple, entire or distally serrulate. Nine published species recognized here, Neotropics.

Included species.—Protium amazonicum (Cuatrec.) Daly, *P. apiculatum* Swart, *P. calendulinum* Daly, *P. gallosum* Daly, *P. minutiflorum* Cuatrec., *P. nitidifolium* (Cuatrec.) Daly, *P. pecuniosum* Daly, *P. retusum* Daly, *P. urophyllidium* Daly.

Protium* section *Sarcoprotium Daly, Brittonia 44: 280–283. 1992. Type species: *P. carnosum* A.C. Sm.

Bark thin, brittle; resin translucent; pulvinuli on lateral leaflets present; leaflet margin entire; leaflet secondary framework festooned-brochidodromous, tertiary vein fabric irregular-reticulate, intersecondary veins often present, freely ending veinlets 2–3-branched; inflorescences thyrsoid, staminate flowers usually 3-merous, the petals free, usually with a fleshy apical extension and clawed base; stamens in two subequal series, the anthers sagittate, the thecae separated by the connective, the filaments stout and cylindrical, staminodes taller than pistil; in staminate flowers the annular disk and cylindrical pistillode distinct; style with 5 short branches, stigmas caudiculate and spiculate; pseudaril white, pyrenes bony or cartilaginous; cotyledons lobed and contortuplicate; germination hypogeal and cryptocotylar; first eophylls

opposite, simple, entire. Eight published species recognized here, Neotropics.

Included species.—P. carnosum A. C. Sm., *P. crassipetalum* Cuatrec., *P. macrocarpum* Cuatrec., *P. pedicellatum* Swart, *P. plagiocarpium* Benoist, *P. polybotryum* (Turcz.) Engl., *P. rubrum* Cuatrec., *P. tonyanum* Daly.

Protium* section *Tetragastris (Gaertn.) Daly & P. Fine, **comb. nov.**

Tetragastris Gaertn., Fruct. Sem. Pl. 2: 130. 1802. Type species: *T. balsamifera* (Sw.) Kuntze ≡ *Protium balsamifer*um (Sw.) Daly & P. Fine (syn.: *Hedwigia balsamifera* Sw.).

Outer bark thick and fissured; resin clear; pulvinuli on lateral leaflets absent; leaflet margin entire; leaflet secondary vein framework (festooned) brochidodromous, tertiary vein fabric usually alternate-percurrent, freely ending veinlets 4+-branched and terminating in highly branched sclereids; inflorescences thyrsoid; petals connate at least 1/2 their length; stamens in two subequal series, in staminate flowers the anthers continuous with the filaments; disk and pistillode replaced by a conical, parenchymatous "ovariodisk"; pseudaril white, pyrenes cartilaginous; cotyledons entire, plano-convex and straight; germination epigeal and phanerocotylar, the first eophylls opposite and simple. Ten published species recognized here, Neotropics.

Included species.—Protium altissimum (Aubl.) Marchand, *P. balsamiferum* (Sw.) Daly & P. Fine, *P. breviacuminatum* (Swart) Byng & Christenh., *P. catuaba* (Soares da Cunha) Daly & P. Fine, *P. mucronatum* Rusby, *P. occhionii* Rizzini, *P. picramnioides* Byng & Christenh., *P. surinamense* Byng & Christenh., *P. varians* (Little) Byng & Christenh.

New names and combinations, and newly accepted names, in tribe Protieae

The following includes taxa published in *Protium* that were long out of use but are now recognized once again, as well as several new combinations, some not essential to the generic limits but that help to simplify the lists of accepted names by section. It also includes some recent combinations made by other authors, in order to clarify the taxonomic history.

Protium altissimum (Aubl.) Marchand, Adansonia 8: 51. 1867–1868. *Icica altissima* Aubl., Hist. Pl. Guiane 1: 342, t. 132. 1775. *Amyris altissima* Willd. in Linn. Sp. pl., ed. 4 [Willdenow], 2: 336. 1799. *Elaphrium altissimum* (Aubl.) Spreng. ex Dietr., Syn. Pl. [D. Dietrich] 2: 1273. 1840. *Bursera altissima* (Aubl.) Baill., Hist. Pl. [Baillon] 5: 296. 1874. *Tingulonga altissima* (Aubl.) Kuntze, Revis. Gen. Pl. 1: 108. 1891. *Tetragastris altissima* (Aubl.) Swart, A monograph of the genus *Protium* and some allied genera (Burseraceae): 413–416. 1942. *Protium excelsior* Byng & Christenh., Plant Gateway's the global flora: A practical flora to vascular plant species of the world: 140. 2018, nom. illegit. Lectotype, designated by Swart (1942: 415): French Guiana, (without date), *J. B. C. F. Aublet s.n.* (BM).

Tetragastris phanerosepala Sandwith, Kew Bulletin 5: 209. 1932. Type: Guyana. Demerara River, May 1880, *G. S. Jenman 4928* (lectotype, **here designated**: K-K000530960; isolectotype K-K000530961).

Swart (1942: 415) lectotypified the BM specimen and clearly annotated it as the type collection, so contrary to Christenhuz et al. (2018), there is no need for inventing a new name for this very common and well-known taxon.

Protium balsamiferum (Sw.) Daly & P. Fine, **comb. nov.** *Hedwigia balsamifera* Sw., Prodr. [O. P. Swartz]: 62. 1788. *Bursera balsamifera* (Sw.) Pers., Syn. Pl. [Persoon] 1: 414. 1805. *Tetragastris balsamifera* (Sw.) Oken, Allg. Naturgesch. 3(3): 875. 1841 [often cited as the later combination *T. balsamifera* (Sw.) Kuntze, Revis. Gen. Pl. 1: 106. 1891.]. Type: Dominican Republic, (without date), *O. P. Swartz s.n.* (lectotype: M; isotypes: C, S-R-2761).

Caproxylon hedwigii Tussac, Fl. Antill. 4: 87, t. 30. 1827. *Hedwigia tussacii* Walp., Repert. Bot. Syst. (Walpers) 1: 559. 1842, nom. illegit. (cited as synonym of *C. hedwigii*).

Icica hedwigia A. Rich., Hist. Phys. Cuba, Pl. Vasc. 388. 1842. Type not located.

Amyris toxifera Willd. in Sp. pl., ed. 4 [Willdenow], 2: 336. 1799. Type. Puerto Rico: Carolina, *herb. Willd. 7290* (B).

Tetragastris ossea Gaertn., Fruct. Sem. Pl. 2: 130, t. 109, f. 5. 1791. Protium osseum Byng & Christenh., Plant Gateway's the global flora: A practical flora to vascular plant species of the world: 140. 2018. Type not located.

Tetragastris balsamifera (Sw.) Kuntze var. *lanceifolia* [sic] Swart, Recueil Trav. Bot. néerl. 39: 206. 1942. Type:

Puerto Rico, near Utuado, Mt. Pellejas, 1886, Jun 1886, *H. Sintensis 4486* (lectotype**, here designated**: BM; isotype: K).

Kuntze (Revis. Gen. Pl. 1: 107. 1891.) called attention to the fact that the moss genus *Hedwigia* P. Beauv. has priority over *Hedwigia* Sw., and he pointed out the synonymy of *T. ossea* Gaertn. with *Hedwigia balsamifera* Sw. ≡ *Tetragastris balsamifera* (Sw.) Kuntze, now transferred to *Protium*. Christenhuz et al. (2018) neglected to note that the epithet *balsamiferum* has priority.

Protium catuaba (Soares da Cunha) Daly & P. Fine, **comb. nov.** *Tetragastris catuaba* Soares da Cunha, Tribuna Farm. 7(3): 45–52. 1939. Type: Brazil. Bahia: Estacão Experimental de Belmonte/CEPLAC, 16 Sept. 1970, *T. S. dos Santos 1102* (neotype, designated by Daly, Kew Bull. 45: 188. 1990: CEPEC; isoneotypes: K, NY-345724, SP-003587, UEC).

Protium chagrense (Pittier) Daly & P. Fine, **comb. nov.** *Tapirira chagrensis* Pittier, Contr. U.S. Natl. Herb. 18: 158. 1916. Type: Panama. Prov. Panama, Canal Zone, around Alhajuela, Chagres Valley, 30–100 m, 12–15 May 1911, *H. Pittier 3503* (holotype: US- 00095684; isotype: NY-00345690).

Protium neglectum var. *panamensis* Swart, Recueil Trav. Bot. Néerl. 39: 205. 1942. Type: Panama. Canal Zone: Barro Colorado Island, 22 Jun 1931, *L. H. Bailey & E. Z. Bailey 294* (holotype: F-643071).

Protium herbertii (Cuatrec.) Daly & P. Fine, **comb. & nom. nov.** *Protium neglectum* Swart var. *tenuifolium* Swart, Recueil Trav. Bot. Néerl. 39: 204. 1942. *Protium tenuifolium* Engl. var. *herbertii* Cuatrec., Webbia 12: 407. 1957, nom. illegit. *Protium tenuifolium* Engl. subsp. *herbertii* (Cuatrec.) D.M. Porter, Ann. Missouri Bot. Gard. 56: 475. 1970, nom. illegit. Type: Colombia. Región de Santa Marta, cerca de la plantación Maria Teresa, 1150 m, 19 Jan 1899, *H. H. Smith 1741* (holotype: U; isotypes: A, BM-000797126, BR-0000006955090, COL-000001888, E-00326228, F-138607, GH-00273073, GH-00273074, MPU-020455, NY, P-00482319, S-08-11,961, US-533713).

Cuatrecasas (1957: 407.) suggested that *P. neglectum* var. *tenuifolium* is a superfluous name because the complex of varieties of *P. neglectum* cannot be separated from that associated with *P. tenuifolium*, nonetheless, Swart's name is legitimate if confusing, so the homotypic synonyms are illegitimate. This taxon is recognized here as a species, but the varietal epithet *tenuifolium* is occupied at species rank, so we have chosen to adopt Cuatrecasas' varietal name *herbertii* as the specific epithet.

Protium mucronatum Rusby, Descr. S. Amer. Pl.: 34. 1920. *Tetragastris mucronata* (Rusby) Swart, A monograph of the genus *Protium* and some allied genera (Burseraceae): 406–407. 1942. Type: Colombia. Santa Marta: Don Diego, 21 May 1899, *H. H. Smith 2743* (holotype: NY [2 sheets, NY-345720, 345,721]; isotypes: B [destroyed], F, G, K, MICH, MO-216126, U, US).

Protium occhionii Rizzini, Leandra 4–5 (ano 3–4): 15. 1974. Type: Brazil. Bahia: Salvador, restinga on dunes, 5 Dec 1973, *A. Duarte s.n.* (holotype: RB-170553 [2 sheets]). *Tetragastris occhionii* (Rizzini) Daly, Brittonia 41: 23. 1989.

Protium picramnioides Byng & Christenh., Plant Gateway's the global flora: A practical flora to vascular plant species of the world: 140. 2018. *Hedwigia panamensis* Engl., Bot. Jahrb. Syst. 1: 42. 1881. *Tetragastris panamensis* (Engl.) Kuntze, Revis. Gen. Pl. 1: 106. 1891. Type: Panama. Near Panama City, Jun 1861, *S. Hayes 342* (lectotype, designated by Swart, A monograph of the genus *Protium* and some allied genera [Burseraceae]: 418. 1942: BR-0000006954796; isolectotypes: BM, K-000530955, P, W).

Tetragastris stevensonii Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 4, 8: 216. 1929. Type: British Honduras [Belize], (without locality), 14 Sep 1928 [may be date of identification], *N. S. Stevenson 9* (holotype: US-1491623; isotypes F-0052837F, WIS-00000558MAD).

Tetragastris panamensis (Engl.) Kuntze var. *hirtella* Swart, Recueil Trav. Bot. Néerl. 39: 207. 1942. Type: Surinam. Saramacca River, Boschreservaat Sectie O, 8 Nov 1920, *BW (Bureau Boschwezen) 4777* (holotype: U; isotypes: BR-0000006955120, NY-00345718).

Tetragastris paraensis Cuatrec., Bol. Mus. Paraense "Emilio Goeldi," n.s., Bot. 11: 7. 1961. Type: Brazil. Pará. Mata da Cia. Pirelli, Fazenda Uriboca, Jun 1958, *J. M. Pires 6827* (holotype: US-2340359; isotypes: RB-114136, U-0000921).

Tetragastris panamensis (Engl.) Kuntze var. *grandifolia* Swart, Acta Bot. Neerl. 15: 56. 1966. Type: Suriname. Mapane Creek area (Suriname River), 5 Nov 1953, *J. C. Lindeman 5052* (holotype: U; isotype: NY-00345723).

We note that the epithet of *Protium panamense* (Rose) I. M. Johnst. had priority, thereby necessitating a new epithet for the transfer of this taxon to *Protium*.

Engler [in Fl. bras. (Martius) 12(2): 285: 1874] cited *Hedwigia balsamifera* Sw. [≡*Tetragastris balsamifera* (Sw.) Oken, here transferred to *Protium balsamiferum* (Sw.) Daly & P. Fine] as occurring in Brazil, and he included *Caproxylon hedwigii* Tussac as a synonym, but later (Bot. Jahrb. Syst. 1: 42. 1881.), he published *Hedwigia panamensis* Engl., and indicated that the description and illustration he had provided for *H. balsamifera* in *Flora brasiliensis* should be applied to his new species. It should be pointed out that in the latter publication the collection he cited for *H. balsamifera* Sw. was *Hayes 343,* while the one cited for *H. panamensis* in 1881 was *Hayes 342.*

Protium rhynchophyllum (Rusby) Daly & P. Fine, **comb. nov.** *Icica rhynchophylla* Rusby, Mem. New York Bot. Gard. 7: 278. 1927. Type: Bolivia. [Beni:] Rurrenabaque, 1000 ft., 8 Oct 1921, *H. H. Rusby 1592* (lectotype, **here designated**: NY; isotype: BKL).

Protium surinamense Byng & Christenh. *Hedwigia hostmannii* Engl., Monogr. Phan. [A.DC. & C.DC.] 4: 97. 1883. *Tetragastris hostmannii* (Engl.) Kuntze, Revis. Gen. Pl. 1: 107. 1891. Type: Suriname. [without locality], *F. W. R. Hostmann 1161* (holotype: K-000530958; isotypes: B, G-00236494, NY-01746447, U-0000919, W).

Given that the specific epithet *hostmannii* was already occupied in *Protium* [*P. hostmannii* (Miq.) Engl. ≡ *P. guianense* (Aubl.) Marchand], a new name had to be designated. Christenhuz et al. (2018) erroneously asserted that *P. surinamense* is endemic to Suriname, whereas it also occurs in French Guiana, Guyana, Venezuela (Bolívar), and Brazil (Amapá, Pará, Roraima).

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Appendix 1. Sectional placements of the species of *Protium*. Numbers following species names indicate the following sections: **1.** *Protium* section *Protium* Burm.f.; **2.** *Protium* section *Crepidospermum* (Hook.f.) Daly & P. Fine; **3.** *Protium* section *Icica* (Aubl.) Swart; **4.** *Protium* section *Icicopsis* (Engl.) Swart; **5.** *Protium* section *Marignia* (Comm. ex Kunth) Hook.f.; **6.** *Protium* section *Papilloprotium* Daly & P. Fine; **7.** *Protium* section *Pepeanthos* Daly; **8.** *Protium* section *Sarcoprotium* Daly; **9.** *Protium* section *Tetragastris* (Gaertn.) Daly & P. Fine.

Protium aguilarii D. Santam. (3), *P. aidanianum* Daly (3), *P. altsonii* Sandwith (3), *Protium altissimum* (Aublet)

Marchand (9), *Protium alvarezianum* Daly & P. Fine (6), *P. amazonicum* (Cuatrec.) Daly (7), *P. amplum* Cuatrec. (3), *P. angustifolium* Swart (3), *P. apiculatum* Swart (7), *P. aracouchini* (Aubl.) Marchand (3), *P. araguense* Cuatrec. (3), *P. atlanticum* (Daly) Byng & Christenh. (2), *P. attenuatum* (Rose) Urb. (3), *P. bahianum* Daly (3), *P. balsamiferum* (Sw.) Daly & P. Fine (9), *P. boomii* Daly (3), *P. brasiliense* (Spreng.) Engl. (3), *P. brenesii* (Standl.) D. Santam. (3), *P. balsamiferum* (Sw.) Daly & P. Fine (9), *P. breviacuminatum* (Swart) Byng & Christenh. (9), *P. buenaventurense* Cuatrec. (3), *P. calanense* Cuatrec. (3), *P. carolense* Daly (3), *P. carnosum* A.C. Sm. (8), *P. catuaba* (Soares da Cunha) Daly & P. Fine (9), *Protium chagrense* (Pittier) Daly & P. Fine (4), *P. colombianum* Cuatrec. (3), *P. confusum* (Rose) Pittier (3), *P. connarifolium* (Perk.) Merr. (1), *P. copal* (Schtldl. & Cham.) Engl. (3), *P. correae* D.M. Porter (3), *P. costaricense* (Rose) Engl. (3), *P. cranipyrenum* Cuatrec. (3), *P. calendulinum* Daly (7), *P. crassipetalum* Cuatrec. (8), *P. crenatum* Sandwith (3), *P. cubense* (Rose) Urb. (3), *P. cundinamarcense* Cuatrec. (3), *P. cuneatum* Swart (3), *P. cuneifolium* (Cuatrec.) Byng & Christenh. (2), *P. dawsonii* Cuatrec. (3), *P. decandrum* (Aubl.) Marchand (3), *P. demerarense* Swart (3), *P. divaricatum* Engl. (3), *P. ecuadorense* Benoist (3), *P. elegans* Engl. (3), *P. ferrugineum* (Engl.) Engl. (6), *P. fragrans* (Rose) Urb. (4), *P. gallicum* Daly (3), *P. gallosum* Daly (7), *P. giganteum* Engl. (3), *P. glabrescens* Swart (3), *P. glabrum* (Rose) Engl. (3), *P. glaucescens* Urb. (3), *P. glaucum* J.F. Macbr. (3), *P. glaziovii* Swart (3), *P. glomerulosum* Cuatrec. (3), *P. goudotianum* (Tul.) Byng & Christenh. (2), *P. grandifolium* Engl. (3), *P. guacayanum* Cuatrec. (3), *P. guianense* (Aubl.) Marchand (3), *P. hammelii* D. Santam. (3), *P. hebetatum* Daly (3), *P. heptaphyllum* (Aubl.) Marchand (3), *P. herbertii* (Cuatrec.) Daly & P. Fine (4), *P. icicariba* (DC.) Marchand (3), *P. inconforme* Pittier (3), *P. inodorum* Daly (3), *P. insigne* (Triana & Planch.) Engl. (4), *P. javanicum* Burm.f. (1), *P. kleinii* Cuatrec. (3), *P. klugii* J.F. Macbr. (3), *P. krukovii* Swart (3), *P. laxiflorum* Engl. (3), *P. leptostachyum* Cuatrec. (3), *P. llanorum* Cuatrec. (3), *P. macgregorii* (F.M. Bailey) Leenh. & Steenis (1), *P. macrocarpum* Cuatrec. (8), *P. macrophyllum* (Kunth) Engl. (3), *P. macrosepalum* Swart (3), *Protium madagascariense* Engl. (5), *P. maestrense* Bisse (3), *P. mcleodii* I.M. Johnst. (4), *P. melinonis* Engl. (3), *P. meridionale* Swart (3), *P. minutiflorum* Cuatrec. (7), *P. montanum* Swart (3), *P. morii* Daly (3), *P. mucronatum* Rusby (9), *P. multijugum* (Swart) Byng & Christenh. (2), *P. multiramiflorum* Lundell (3), *P. neglectum* Swart (4), *P. nervosum* Cuatrec. (3), *P. nitidifolium* (Cuatrec.) Daly (7), *P. nodulosum* Swart (3), *P. occultum* Daly (3), *P. obtusifolium* (Lam.) Marchand (6), *P. occhionii* Rizzini (9), *P. opacum* Swart (3), *P. ovatum* Engl. (3), *P. pallidum* Daly (3), *P. panamense* (Rose) I.M. Johnst. (3), *P. paniculatum* Engl. (3), *P. pecuniosum* Daly (7), *P. pedicellatum* Swart (8), *P. peruvianum* Swart (3), *P. picramnioides* Byng & Christenh. (9), *P. pilosellum* Swart (3), *P. pilosissimum* Engl. (3), *P. pilosum* (Cuatrec.) Daly (3), *P. pittieri* (Rose) Engl. (3), *P. plagiocarpium* Benoist (8), P. *poeppigianum* Swart (3), *P. polybotryum* (Turcz.) Engl. (8), *P. prancei* (Daly) Byng & Christenh. (2), *P. pristifolium* Daly (6), *P. puncticulatum* J.F. Macbr. (3), *P. reticulatum* (Engl.) Engl. (6), *P. retusum* Daly (7), *P. rhoifolium* (Benth.) Byng & Christenh. (2), *P. rhynchophyllum* (Rusby) Daly & P. Fine (4), *P. rubrum* Cuatrec. (8), *P. ravenii* D.M. Porter (3), *P. robustum* (Swart) D.M. Porter (4), *P. rubrum* Cuatrec. (8), *P. sagotianum* Marchand (4), *P. serratum* (Wall. ex Colebr.) Engl. (1), *P. sessiliflorum* (Rose) Standl. (4), *P. spruceanum* (Benth.) Engl. (3), *P. strumosum* Daly (3), *P. subserratum* (Engl.) Engl. (6), *P. surinamense* Byng & Christenh. (9), *P. tenuifolium* (Engl.) Engl. (4), *P. tonyanum* Daly (8), *P. tovarense* Pittier (3), *P. trifoliolatum* Engl. (3), *P. unifoliolatum* Engl. (3), *P. urophyllidium* Daly (7), *P. varians* (Little) Byng & Christenh. (9), *P. veneralense* Cuatrec. (3), *P. vestitum* (Cuatrec.) Daly (3), *P. warmingianum* Marchand (4), *P. widgrenii* Engl. (3).