



A new species of *Protium* (Burseraceae) from the Pacific Coast of Costa Rica

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Abstract

Protium santamariae is described and illustrated. The new species is restricted to the Pacific Coast of Costa Rica but shares morphological similarities with two South American species, *P. kleinii* and *P. krukoffii*. We provide a description, a distribution map, notes on its taxonomy, and a key to distinguish it from morphologically similar species.

Keywords: Biodiversity, Neotropics, Protieae, taxonomy

Introduction

The Burseraceae comprise approximately 750 species of trees and some shrubs in 17 genera in the tropics and subtropics (Daly *et al.* 2012, Daly & Fine 2018), and the family constitutes an important element in the structure and diversity of both humid and dry forests in tropical areas (Daly *et al.* 2012). In the Neotropics, the tribe Protieae stands out because of its high diversity as well as its abundance, and the group has been the focus of several studies that addressed questions regarding taxonomy, phylogenetics, ecology and evolution (Daly 1989, Fine *et al.* 2005, 2014, Daly *et al.* 2012, Daly & Fine 2018). Currently, this tribe consists of only one genus, *Protium* Burm. f. (1768: 88), which contains ca. 140 species (Daly 2017, 2018a, Daly & Fine 2018, Damasco *et al.* 2019) and nine sections, seven of which are exclusively Neotropical (Daly & Fine 2018).

The highest levels of species richness and abundance of *Protium* can be found in the Amazon (Fine *et al.* 2014, Daly 2018b), with secondary centers in the Guiana Shield, the Atlantic Forest of Brazil, and Central America. Central America harbors 21 species of *Protium*, which represents ca. 15% of its total species diversity. Three of these 21 species have been described in the past twelve years: *Protium pecuniosum* Daly (2007: 15–19), *P. aguilarii* D.Santam. in Santamaría-Aguilar & Lagomarsino (2017: 90–95), and *P. hammelii* D.Santam. in Santamaría-Aguilar & Lagomarsino (2017: 95–104). Furthermore, *P. brenesii* Standl. (1937: 583) D. Santam. in Santamaría-Aguilar & Lagomarsino (2017: 104–109) was only recently transferred to *Protium* from *Trichilia* P. Browne (1756: 278) (Meliaceae) (Standley 1937).

Two of these recently described species (*Protium aguilarii* and *P. pecuniosum*) are endemic to one of the most interesting biodiversity hotspots of Central America, the Osa peninsula in Costa Rica. This peninsula comprises a small area of ca. 1573 km² and harbors the last, large remnant of lowland rain forests on the Pacific Coast of Central America in Parque Nacional Corcovado. This wet forest is surrounded by much drier forests and is an important biodiversity refuge and center of endemism. In fact, 26% of the tree species diversity of the Osa peninsula is constituted by regional endemics to Central-South Mesoamerica (Costa Rica, Nicaragua, and Panama) (Cornejo *et al.* 2012).

On the other hand, many species from the Osa peninsula have broad geographic distributions and occur also in tropical South America (Cornejo *et al.* 2012). One of these widespread tree species was thought to be *Protium aracouchini* (Aublet 1775: 343–345) Marchand (1867: 51–52) (PASC hereafter), which is known to be part of a species complex of small trees that have distinctive fruits that when ripe are usually green below and red above (Daly *et al.* 2012). As currently circumscribed, PASC encompasses four species, *P. aracouchini*, *P. elegans* Engl. (1874: 273), *P. calanense* Cuatrec. (1952: 471), and *P. leptostachyum* Cuatrec. (1957: 391–392), and at least two undescribed species from Venezuelan Guayana. These were included in Daly (1997) as *Protium* sp. A and *Protium* sp. B. In phylogenetic

studies this species complex consistently appears as a clade with high support, nested within *P.* section *Icica* Aubl. (1775: 337) Swart (1942a: 266) (Fine *et al.* 2005, 2014).

The specimens collected in Costa Rica and identified as *P. aracouchini* suggested an unusual geographic distribution that caught our attention. The Costa Rican localities are separated from the collection localities of all other species in the PASC complex by a minimum of 1200 km and the Andes mountains. A careful examination of these specimens revealed that they actually represent an undescribed species. Here we recognize the Costa Rica populations previously referred to *P. aracouchini* as a new species: *P. santamariae* Perdiz, Daly & P.Fine. We provide a description, a distribution map, an illustration, notes on its taxonomy, and comparisons with other species that are most similar morphologically.

Material and methods

A total of 123 specimens deposited in the collections of ALCB, BM, CEPEC, CR, F, HURB, INPA, MO, NY, RB, S, U and US were examined in order to provide the taxonomic data presented here. Herbaria codes follow Thiers (2019). Barcode numbers, when available, are cited inside square brackets after the herbarium acronym. We used the software Fiji (Schindelin *et al.* 2012) to obtain measurements from digital images of the whole specimen or from specimen parts, such as flowers, fruits, and seeds. All morphological data were stored in the duckewiki platform (www.botanicaamazonica.wiki.br/botam/), a specimen-oriented online database to store and retrieve plant biological data. Taxonomic data presented here were generated through an aggregation of data for each of the species mentioned. Custom R scripts in conjunction with R function *tableToDescription* from the package *monographaR* (Reginato 2016) were used to generate the species description, and the function *phenoHist* was used to generate a phenology circular histogram (Fig. 1).

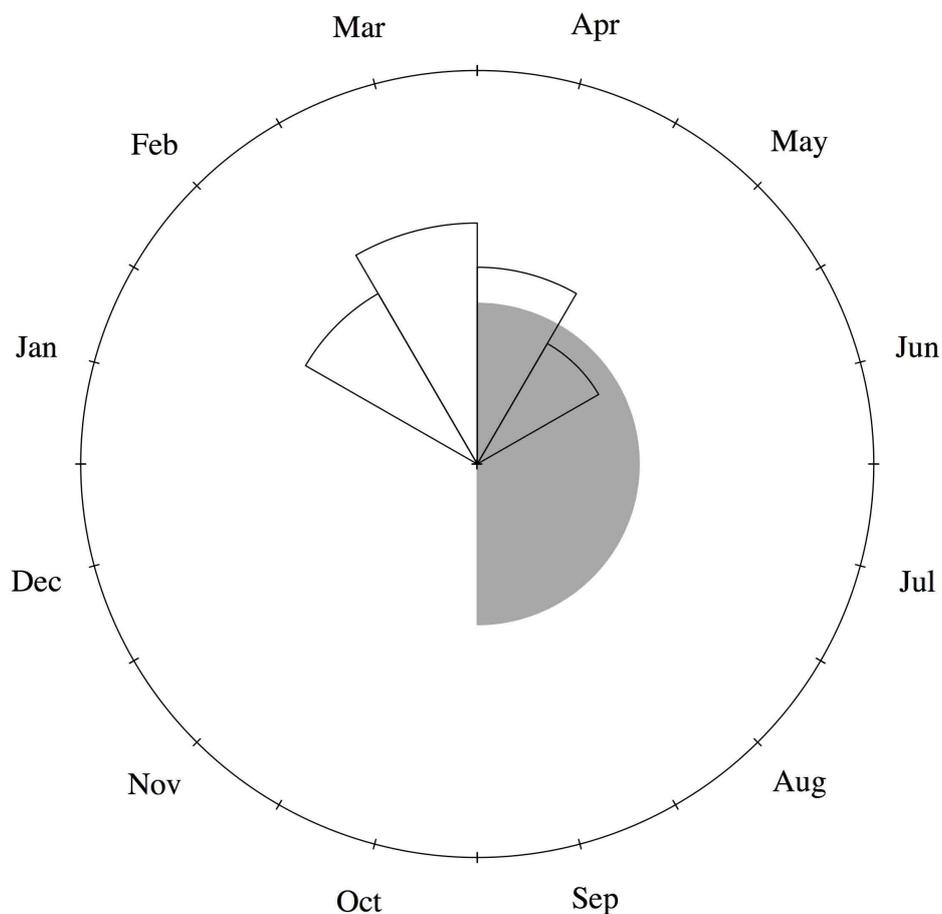


FIGURE 1. Phenology circular histogram of *Protium santamariae*, displaying flowers (white background) and fruits (grey background) frequencies per month.

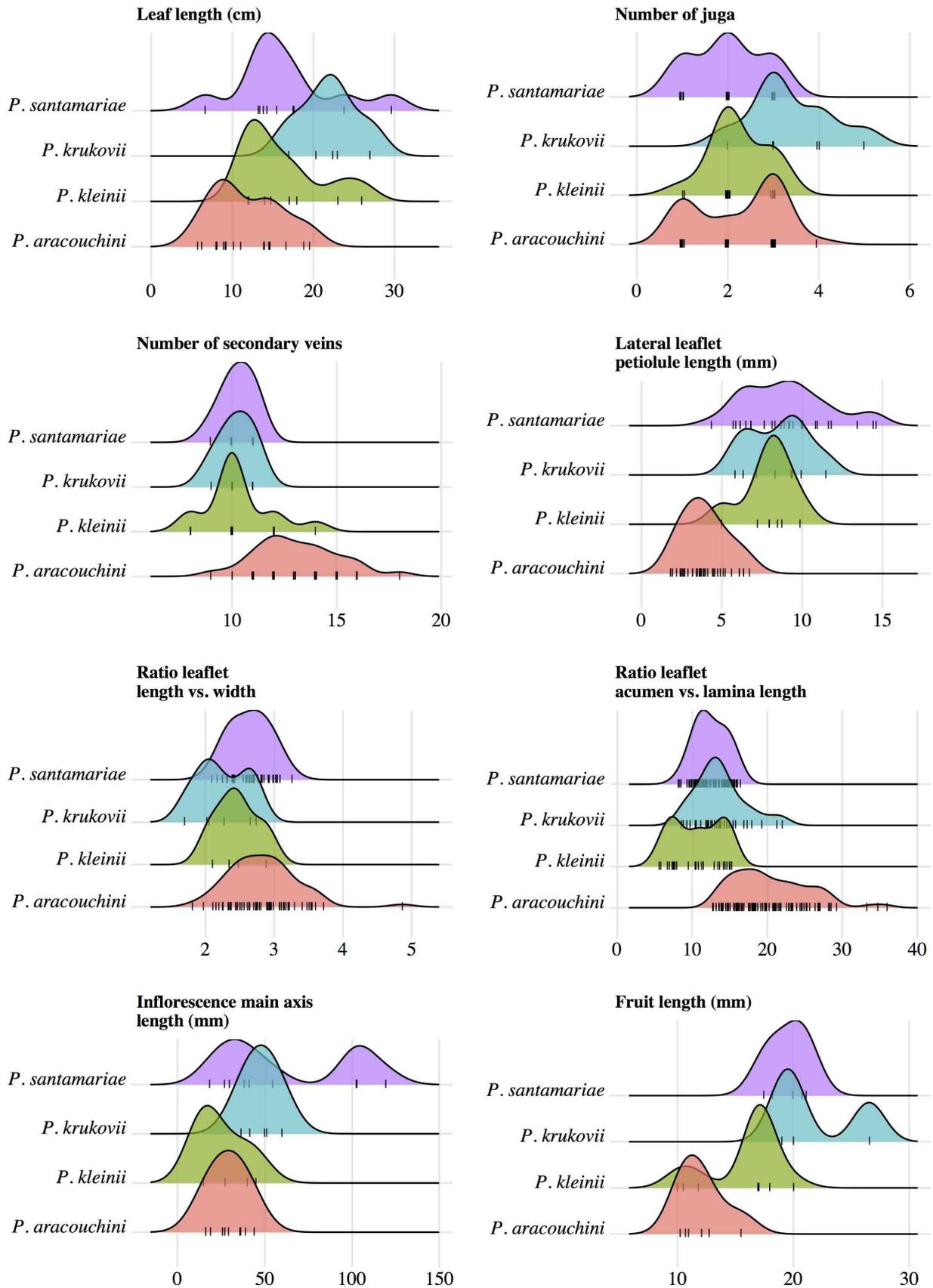


FIGURE 2. Density ridgeline plots displaying data distribution of some quantitative morphological variables of *Protium santamariae* and morphologically similar species. For each variable, plots are aligned to the same horizontal scale and presented with a slight overlap. Higher peaks mean more observations in that range, lower peaks mean less observations. Individual observations for each variable, from which these distributions were generated, can be seen as vertical traces at the base of each ridgeline.

We display quantitative data in the form “range [mean \pm standard deviation]” for each variable. Although unusual in traditional taxonomy, presenting mean and standard deviation along with the range provides a clearer picture of the distribution of values for each variable, allowing more refined comparisons between taxa. For semi-quantitative variables, such as number of juga and number of secondary veins, we chose as cutoff 10% of a value frequency to consider it as rarely encountered, and therefore placing it inside parentheses (for example, if we state in the description “(1–)2–3”, it means that the value 1 was observed in fewer than 10% of all the observations of that variable). We adopted the terminology of Ellis *et al.* (2009) for leaf characters. Data for leaflets and petiolules are presented in the description for each one of three positions: terminal, lateral distal (pair of leaflets closest to the terminal), and lateral proximal (pair of leaflets closer to the petiole) leaflets and petiolules. Data presented in Fig. 2 for variable lateral leaflet petiolule length is the combined data for lateral distal and proximal leaflet leaflet petiolule length. We included data of all leaflets for which we had data for both length and width in the variable “ratio of leaflet length per leaflet width” presented in Fig. 2.

Geographic data were extracted from specimen labels whenever available. We generated a map of geographic distribution for *P. santamariae* (Fig. 3), based on the stamen map terrain style raster image, accessed using the **OpenStreetMap** (www.openstreetmap.org) protocol through the R package OpenStreetMap (Fellows 2019). OpenStreetMap is available under the Open Database License. The R package OpenStreetMap makes use of Java library JMapViewr (Stotz 2019). Other R packages used for map production were prettymap (Dunnington 2017), ggsm (Santos Baquero 2017), rgdal (Bivand *et al.* 2018), sf (Pebesma 2018), and ggspatial (Dunnington 2018), inside the R environment (R Development Core Team 2018), version 3.5.1. The R package red (Cardoso 2018) was used to calculate the extent of occurrence (EOO) and area of occurrence (AOO) of the new species, in order to determine its conservation status based on IUCN criteria (IUCN 2012).

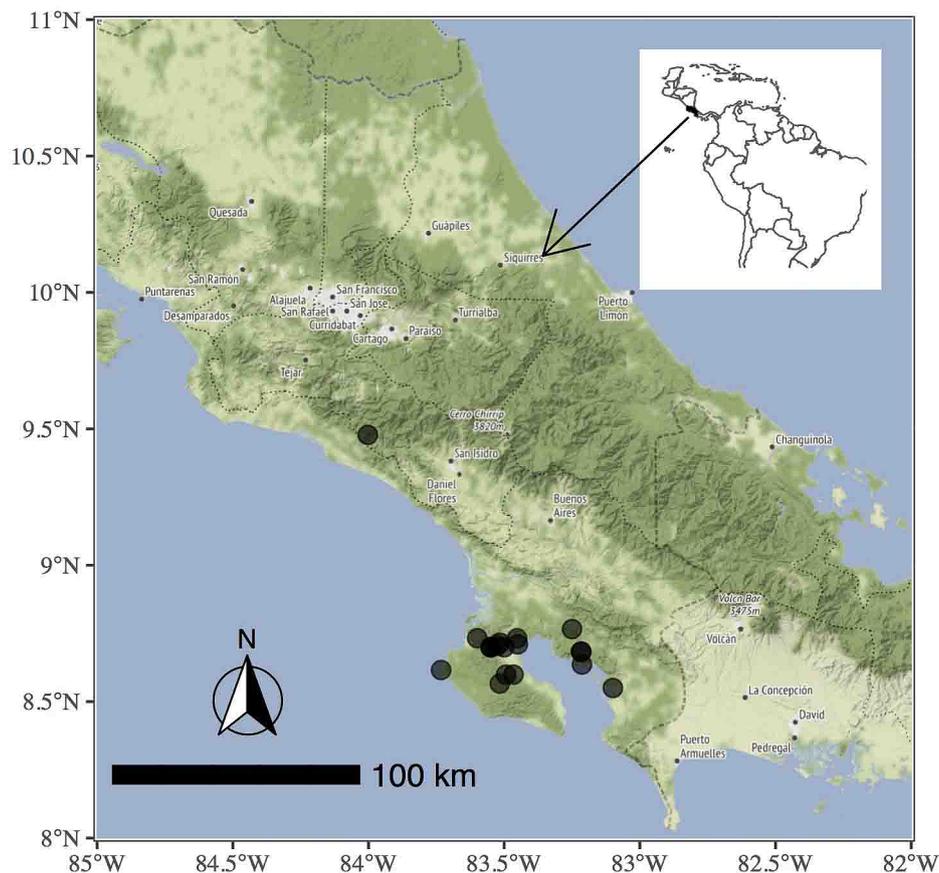


FIGURE 3. Distribution map of *Protium santamariae*. Raster image based on stamen maps, terrain style, accessed through OpenStreetMap protocol (www.openstreetmap.org) by R package OpenStreetMap.

In order to compare the new species with the morphologically similar *P. kleinii* Cuatrecasas (1961: 261–263), *P. krukoffii* Swart (1942b: 13) and *P. aracouchini*, we extracted and tabulated morphological data from the protologues of all these species, as well from published taxonomic works (Porter 1970, Lima & Pirani 2005), and herbarium specimens (see list of additional specimens examined in supplementary files). A comparison table (Table 1) was made to summarize the main characters used to distinguish the new species from the others. To facilitate visualization of some diagnostic characters and of the distribution of the raw data for each variable, we generated a ridgeline plot (Fig. 2) using R packages ggplot2 (Wickham 2009) and ggridges (Wilke 2018).

We adopted the general lineage species concept (de Queiroz 2007) for species delimitation. This way, any single source of evidence, or a combination of sources, such as morphological, ecological, or phylogenetic data, can be used to delimit a new species. In this case, we propose this new species based on morphological and geographical evidence.

TABLE 1. Morphological variables that distinguish *Protium santamariae* from morphologically similar species (salient features in bold).

Character	<i>P. santamariae</i>	<i>P. kleinii</i>	<i>P. krukoffii</i>	<i>P. aracouchini</i>
Number of juga	1–3	(1–)2–3	2–5	1–3(–4)
Callus around the petiole base	Present	Present	Present	Absent
Number of secondary veins	9–11	8–12(–14)	9–11	(9–)11–14(–18)
Inflorescence main axis length relative to petiole	Longer	Shorter	Longer	Longer
Floral parts	4	5	4	4
Calyx height relative to nectary disk	Taller	Taller	Shorter	Shorter
Pistil/pistillode pubescence	Glabrous	Pilose	Glabrous	Glabrous
Fruit apex	Short-acuminate	Rounded to acuminate	Sharply acuminate	Short-acuminate
Mature fruit color	Light-red	Dark-red	Green	Bicolored, green below, red above

Taxonomy

Protium santamariae Perdiz, Daly & P.Fine, *sp. nov.* (Fig. 4).

Type: COSTA RICA. Puntarenas: Golfito, Reserva Forestal Golfo Dulce, between Rincón de Osa and entrance to Parque Nacional Corcovado, along new lumber road on red clay soil ridge in primary forest ca. 5 km NE of Los Patos, 8°36'0"N 83°28'0"W, 200 m, 1 April 1988, B. Hammel & M. Bozzoli 16626 (fl.) (holotype MO [805791]!, isotypes CR, F!, NY!).

Diagnosis:—*Protium santamariae* resembles *P. kleinii* and *P. krukoffii* in the presence of a prominent callus around the petiole base, but it differs from them in its generally longer inflorescences (18.5–119.3 [63.7 ± 38.6] mm long vs. 15–45 [24.6 ± 13.1] mm long in *P. kleinii* and 36.6–60 [47.8 ± 9.1] mm long in *P. krukoffii*) and fruit apex (short-acuminate vs. rounded to acuminate in *P. kleinii* and sharply acuminate in *P. krukoffii*). In addition, it differs from *P. kleinii* by the inflorescence main axis length relative to petiole (longer vs. shorter in *P. kleinii*), by the merosity of flowers (tetramerous flowers vs. pentamerous flowers in *P. kleinii*), by the pubescence on pistil and pistillodes (glabrous vs. pilose in *P. kleinii*), by mature fruit color (light-red vs. dark-red in *P. kleinii*). It also differs from *P. krukoffii* in the calyx height relative to nectary disk (taller vs. shorter in *P. krukoffii*) and by the mature fruit color (light-red vs. green in *P. krukoffii*).

Trees, or shrubs, reproductive size 5–20 [11.5 ± 4.8] m tall; trunk 4–30 [15.2 ± 8.2] cm diam., cylindrical, with well-developed plank buttresses, outer bark light brown, with longitudinally oriented brownish lenticels, inner bark light brown to light yellow; resin translucent and runny when fresh, drying as a white powder, very aromatic, with strong odor of kerosene. Trichomes throughout the vegetative and reproductive parts consisting of appressed hairs,

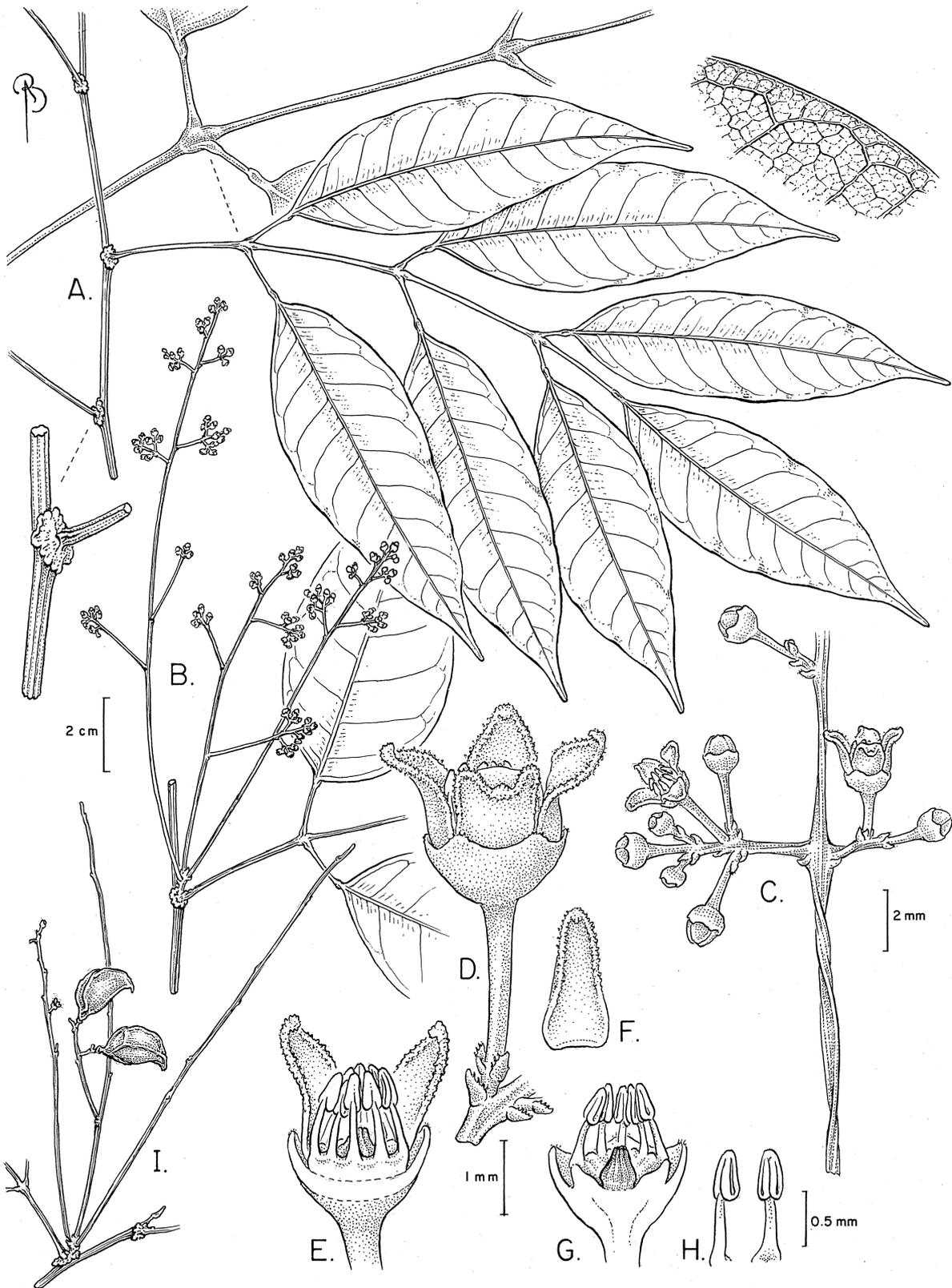


FIGURE 4. *Protium santamariae*. **A.** Sterile branch with detail of a callus around petiole base (inset middle left) and of leaflet venation (inset above right). **B.** Flowering branchlet. **C.** Portion of inflorescence, displaying the twisted main inflorescence axis. **D.** Detail of inflorescence with flower. **E.** Staminate flower, with two petals removed. **F.** Adaxial view of petal. **G.** Longitudinal section of staminate flower. **H.** Lateral and adaxial views of stamen. **I.** Fruiting branch. **A:** Drawn from *Aguilar 3342*; **B:** Drawn from *Thomsen 283* **C–H:** Drawn from *Hammel et al. 18174* **I:** Drawn from *Aguilar 193*. Illustration by Bobbi Angell.

erect hairs, glandular trichomes, and short (< 0.03 mm long) or long (> 0.04 mm long) papillae. Leaves 1–3-jugate, 6.7–29.6 [16.6 ± 6.3] cm long; petiole 14.8–37.8 [26.7 ± 6.2] mm long, conspicuous callus visible around the petiole base, petiole and rachis with sparse short appressed hairs covering the surface; rachis 20.4–108.1 [54.7 ± 26.3] mm long, interjuga 20.4–59.8 [39.6 ± 10.1] mm long; petiolules semiterete, sometimes keeled in the middle, proximal lateral petiolules 7.6–14.6 [10.4 ± 2.4] mm long, distal laterals 4.3–13.4 [8.1 ± 2.5] mm long, terminal one 18.1–40.1 [25.7 ± 7.1] mm long, pulvinuli usually sulcate, conspicuous at both ends of a petiolule; leaflets membranaceous, drying light brown, both sides dull, proximal lateral leaflets elliptic, lanceolate or ovate, 66.2–132.9 [93.1 ± 19.4] × 24.1–47.7 [36.1 ± 7.6] mm, distal laterals elliptic, lanceolate or ovate, 70.2–122.9 [88.4 ± 15.2] × 24.2–40.4 [31.6 ± 4.8] mm, terminal leaflet elliptic or ovate, 71.7–129.2 [89.6 ± 18] × 29.7–45.8 [35.6 ± 4.7] mm; leaflet apex angle acute, the shape acuminate, acumen 8.3–19.7 [12.7 ± 3.7] mm long, apex teeth absent, base angle acute or obtuse, and shape rounded, convex, cuneate or decurrent, leaflets medially symmetrical or asymmetrical, basal insertion asymmetrical, base shape symmetrical or asymmetrical; secondary vein framework weakly festooned brochidodromous, secondaries in 9–11 pairs, nearly straight to weakly arcuate, spacing irregular, angle somewhat irregular; intersecondaries absent; usually 1 epimedial tertiary vein per intercostal space, perpendicular to the midvein; tertiary vein fabric alternate percurrent and irregular reticulate, quaternary fabric irregular reticulate, quinary fabric irregular polygonal, on abaxial side the midvein narrowly prominulous but sunk in a groove, rest narrowly prominulous, surface glabrous, on adaxial side the midvein narrowly prominulous, secondaries nearly flat, rest of veins narrowly prominulous; leaflet surface glabrous or with sparse appressed simple trichomes. Inflorescences axillary, axes twisted and branching up to the third order, main axes 18.5–119.3 [63.7 ± 38.6] mm long, secondary axes 3.5–27.4 [12.9 ± 8.6] mm long, axes with scattered simple appressed hairs, hairs ca. 0.1 mm long, bracts subtending inflorescences 0.5–0.6 [0.6 ± 0.1] mm long, those on primary and secondary axes 0.4–0.5 [0.4 ± 0.1] mm long, bracteoles subtending flowers 0.2–0.4 [0.3 ± 0.1] mm long; all bracts broadly ovate, often apiculate, with sparse to dense appressed simple trichomes, margin densely ciliate with erect simple hairs, ca. 0.1 mm long, pedicel 1–3 [1.9 ± 0.6] mm long, cylindrical to clavate, glabrous or with scattered glandular trichomes. Flowers 4-merous, 3–4 [3.5 ± 0.3] mm long at anthesis; in staminate flowers calyx lobes cupular, ca. 0.3 × ca. 0.6 mm, taller than the nectary disk, lobes slightly deltate, usually separated by a flat sinus, surface with sparse to scattered appressed hairs; petals yellowish-green, orangish, cream, or white, 1.3–1.9 [1.7 ± 0.2] × 0.8–1.1 [1 ± 0.1] mm, ovate, with an inflexed apiculum 0.1–1.6 [0.5 ± 0.6] mm long, membranaceous, spreading at anthesis, abaxial surface glabrous but densely long-papillate at margin, the papillae ca. 0.06 mm long, densely short-papillate on the surface and long-papillate along the margin, stamens 8, antesealous stamens 0.8–1.3 [1.1 ± 0.3], antepetalous stamens 0.8–1 [0.9 ± 0.1] mm long, the filaments strap-shaped, with sparse glandular trichomes, the anthers 0.4–0.6 [0.4 ± 0.1] mm long, yellowish-green, in dorsiventral view lanceolate, in lateral view elliptical, sparsely to densely short-papillate; annular disk ca. 0.3 mm tall, ca. 0.3 mm thick, yellowish-green, with sparse to scattered glandular trichomes; pistillode depressed-ovoid, glabrous or with scattered glandular trichomes, yellowish-green. Pistillate flowers not seen. Fruiting pedicel 2.3–2.7 [2.4 ± 0.3] × 0.7–1.2 [1 ± 0.3] mm, slightly clavate; fruits reddish, broadly and slightly obliquely ovoid (broadly ellipsoid when more than one pyrene develops), 17.5–21.1 [19.5 ± 1.6] × 13–22.3 [17.9 ± 4.3] mm, smooth, glabrous, short acuminate at apex, base stipitate, the stipe 1.5–2 [1.8 ± 0.3] mm long, truncate above constriction; pyrene 13–14.5 [13.9 ± 0.8] × 9.6–12.4 [10.8 ± 1.4] mm, in dorsiventral view broadly ovate with apex acute and base truncate, in lateral view semi-ovate on posterior side, with a distal cleft at the site of the funicle 50% the distance from apex to base, glabrous, cartilaginous, wall ca. 0.3 mm thick. Seed ca. 10.5 × ca. 8 mm, smooth, cotyledons plano-convex.

Distribution and ecology:—*Protium santamariae* is endemic to the Pacific Coast of Costa Rica, mainly inhabiting the Osa Peninsula, but disjunct further north in the province of San José (Fig. 3). It is always found in wet forests on clay soils. According to notes on *Thomsen 793*, *P. santamariae* grows sympatrically with *Symphonia* L. f (1782: 49), *Carapa* Aubl. (1775: 32), *Brosimum utile* (Kunth in H.B.K. (1825: 163)) Oken (1841: 1571), *Qualea* Aubl. (1775: 5), *Otoba* (de Candolle (1855: 22, 30)) Karsten (1882: 578), *Iriarteia* Ruiz & Pavon (1794: 149), and *Vantanea* Aubl. (1775: 572). Notes on *Santamaría & Aguilar 9836* indicate that flowers are visited by *Trigona* spp. bees during the morning. The new species has been found at 20–700 m elevation.

Phenology:—*Protium santamariae* has been collected with flowers from February to May, with a peak in March, mostly during the dry season, and it has been collected with fruits from April to September during the rainy season. (Fig. 1).

Etymology:—The specific epithet honors Daniel Santamaría-Aguilar, a very talented Costa Rican botanist with an extensive knowledge of the Neotropical flora, having described several new species of different angiosperm families (e.g., Santamaría-Aguilar 2015, Santamaría-Aguilar & Ortiz 2016, Santamaría-Aguilar & Aguilar 2017, Santamaría-Aguilar & Lagomarsino 2017). He is also working on the taxonomic treatment of Burseraceae for the Flora of Costa

Rica, and collected one of the paratypes (*Santamaría & Aguilar 9836*) of this new species that is the source for many of the field observations presented here.

Common names:—Canfincillo (“little gasoline”, *Aguilar 193*).

Conservation status:—According to IUCN criteria B1 and B2 (IUCN 2012), this species is categorized as Endangered, with an EOO of 3654 km², and AOO of 64 km², despite its occurrence in protected areas (e.g., the Reserva Forestal Golfo Dulce, Corcovado National Park, and Piedras Blancas National Park).

Taxonomic discussion:—Despite being a relatively well-sampled species, like many other Neotropical species, *P. santamariae* is described here more than 30 years after the first collections were made. In this case, field observations made by Dr. Santamaría were essential to recognize this new species. The presence of a callus around the petiole base is a rare character among Neotropical *Protium*. Its presence in a combination with additional features of *P. santamariae* distinguish this species from all other species of this genus.

The long-standing attribution of the name *P. aracouchini* to specimens here included in *P. santamariae* may be understood in light of a superficial resemblance between the first collections (staminate flowering) of the latter, gathered between 1990 and 1998, to those of *P. aracouchini* from the Amazon. These early specimens share some morphological similarities with *P. aracouchini*, such as leaflets of similar length, leaflet venation narrowly prominulous to almost flat on both surfaces, main axis of the inflorescence longer than the petiole, and flowers with glabrous pistillodes. However, a closer look revealed many differences that are diagnostic for *P. santamariae*. It differs further from *P. aracouchini* by the presence (vs. absence) of a callus near the petiole base; leaflets with lateral leaflet petiolule 4.3–14.6 [9 ± 2.7] mm (vs. 1.8–6.8 [3.9 ± 1.4] mm) long; secondary veins in 9–11 pairs (vs. (9–)11–14(–18) pairs); calyx taller than (vs. shorter than) the nectary disk; fruits 17.5–21.1 [19.5 ± 1.6] mm (vs. 10.2–15.5 [12 ± 1.9] mm) long, light-red (vs. bicolored, green below and red above) when mature (see Table 1, Fig. 2), and broadly and slightly obliquely ovoid or broadly ellipsoid when more than one pyrene develops (vs. narrowly oblique-ovoid), and inflorescence usually ramified to the third (vs. the second) order (see pictures of *P. santamariae* in Santamaría-Aguilar & Lagomarsino (2017), Fig. 6G–J, cited as *P. aracouchini*).

Protium santamariae resembles *P. kleinii*, which is endemic to lowland and submontane forests in the southern Atlantic Forest of Brazil, and *P. krukoffii*, which is widely distributed if not common in várzea forests (and occasionally in terra firme forests) in the Amazon basin. These three species share the most distinctive feature of this new species, which is the presence of a callus around the petiole base, sometimes with a large deposition of resin on it (“copious resin in the petiole base” in *Valverde 1084*). Of these two species, *Protium santamariae* is most similar to *P. krukoffii*, with which it shares leaflets with a similar number of secondary veins, an inflorescence axis longer than the petiole, 4-merous flowers, and glabrous pistil and pistillode (Table 1). However, *P. santamariae* differs from *P. krukoffii* not only by characters summarized in Table 1, but also by the leaflet venation of all ranks narrowly prominulous to almost flat on both surfaces (vs. midvein, secondaries and tertiaries prominulous to prominent and the higher orders flat on both surfaces). Leaflet venation is also useful for distinguishing *Protium santamariae* from *P. kleinii*, mainly by leaflet secondary veins course (nearly straight to weakly arcuate vs. straight in *P. kleinii*).

In Costa Rica, *Protium santamariae* can be readily distinguished from all other species of *Protium* by the combination of a prominent callus at the petiole base and glabrous leaflets. This combination sets *P. santamariae* apart from all other *Protium* species in Costa Rica whose leaves are pubescent abaxially (*P. aguilarii* D.Santam. in (Santamaría-Aguilar & Lagomarsino 2017: 90–95), *P. brenesii*, *P. costaricense* (Rose 1911: 259–260) Engler (1931: 414), *P. glabrum* (Rose 1911: 259) Engl. (1931: 414), *P. pecuniosum*, *P. pittieri* (Rose 1911: 260) Engl. (1931: 414), *P. ravenii* D.M. Porter (1972: 263–265)), also from the species with glabrous leaflets (*P. hammelii* D.Santam. in Santamaría-Aguilar & Lagomarsino (2017: 95–104), *P. multiramiflorum* Lundell (1937: 11), *P. panamense* (Rose 1911: 260–261) I.M. Johnst. (1924: 72), *P. sessiliflorum* (Rose 1911: 259) Standley (1925: 459), *P. tenuifolium* Engl. (1874: 255–256) Engl. (1883: 76–77)).

Protium santamariae fits into *Protium* section *Icica* because of a combination of characters: translucent fresh resin, abaxial surface of leaflets lacking papilla, lateral leaflets with pulvinuli, inflorescence thyrsoid, flowers 4-merous, annular disk and pistillode distinct, and cotyledons plano-convex. This section is monophyletic according to a molecular phylogeny published by Fine *et al.* (2014) and is the largest section of *Protium*, encompassing 86 published species (Daly & Fine 2018). *Protium* section *Icica* includes *P. kleinii* and *P. krukoffii*, and as shown in Fine *et al.* (2014), these two species are distantly located from each other in a large clade that embraces ca. 16 species and is subdivided in two subclades. Within this large clade, *P. krukoffii* appears in one of the subclades as a sister species of the *P. heptaphyllum* Aubl. (1775: 337) Marchand (1873: 54) complex clade and it is composed mainly of taxa from the Amazon and Guianas, with few species reaching the Atlantic Forest and the Brazilian Cerrado. *Protium kleinii*, however, is nested within the other subclade and includes primarily species restricted to the Brazilian Atlantic

Forest, of which one (*P. brasiliense* (Sprengel 1825: 217) Engler (1874: 268)) reaches the Brazilian Cerrado, also *P. unifoliolatum* Engl. (1874: 262), which is restricted to the Amazon. *Protium aracouchini* (with which early collections of *P. santamariae* were confused) appears in the clade that is sister to the large clade of 16 species that embraces both *P. kleinii* and *P. krukoffii*, suggesting that *P. santamariae* is not closely related to *P. aracouchini*. Considering morphological and geographical data, we expect *P. santamariae* to be more closely related phylogenetically to *P. krukoffii* than to *P. kleinii* because of their geographical ranges and higher number of morphological similarities.

Other specimens examined:—COSTA RICA. Puntarenas: Golfito, R.F. Golfo Dulce, Cantón de Osa, Fila Ganado hasta Guerra, 300 m, 8°43'57"N, 83°35'57"W, 28 March 1991, fl., *B.E. Hammel et al. 18174* (CR!, F!, MO [barcode 805789]!, NY [barcode 0399607]!); Golfito, Reserva Forestal Golfo Dulce Aguabuena, Golfito, 50–150 m, 8°42'18"N, 83°31'30"W, 5 August 1991, fr., *R. Aguilar 193* (CR!, F!, MO [barcode 805793]!, NY [barcode 03996605]!); Fila before Rancho Quemado, near Rincón, Osa Peninsula, Transect 1, 300 m, 8°41'57"N, 83°32'57"W, 11 January 1993, st., *A.H. Gentry et al. 78648* (MO!); Fila before Rancho Quemada, near Rincón, Osa Peninsula, transect 6, 300 m, 8°41'58"N, 83°32'58"W, 12 January 1993, st., *A.H. Gentry et al. 78737* (MO!); Fila before Rancho Quemada, near Rincón, Osa Peninsula, Transect 9, 300 m, 8°41'59"N, 83°32'59"W, 13 January 1993, st., *A.H. Gentry 78772* (MO!); Aguabuena, 3 km W of Rincón, well drained, sloping terrain on farm land of Henry Monge, Selectively logged forest along timber trail, 100 m, 8°41'56"N, 83°30'0"W, 28 March 1993, bud, *K. Thomsen 283* (C, CR!, NY [barcode 00608665]!); Aguabuena, 3.5 km W of Rincón, Four-hectare permanent sample plot 1 km N of BOSCOA station in well drained undulating terrain with slopes of 15–35°, 350 m, 8°42'58"N, 83°30'58"W, 17 June 1993, st., *K. Thomsen 793* (CR!); Golfito, P.N. Corcovado, Península de Osa, Estación San Pedrillo, sendero que va al límite, 100 m, 8°36'57"N, 83°43'57"W, 21 September 1993, fr., *R. Aguilar 2384* (CR, MO!, NY!); Golfito, Refugio de Vida Silvestre Golfito, Sendero Los Naranjales, 20 m, 8°38'9"N, 83°12'49"W, 6 March 1994, bud, *J. Hoomans 29* (CR!); Golfito, Refugio de fauna silvestre Golfito, Material proyecto Edgar Gutiérrez, 300 m, 8°33'0"N, 83°5'58"W, 1 April 1994, fr., *G. Rivera & G. Herrera 2351* (CR!); Golfito, P.N. Corcovado, Valle de Coto Colorado, Sección Esquinas, orilla Quebrada Arenas Bosque Esquinas, 100 m, 8°45'57"N, 83°15'0"W, 15 April 1994, fl., *F.J. Quesada 894* (CR!, MO!, NY!); Golfito, Estacion Los Patos, Cerro Degra, 200 m, 8°33'58"N, 83°30'58"W, 5 June 1994, fr., *R. Aguilar 3342* (CR!, MO [barcode 805794]!, NY [barcode 03996603]!); Golfito, R.F. Golfo Dulce, Cuenca Térraba-Sierpe. Bahía Chal, La Parcela, 150 m, 8°42'36"N, 83°27'0"W, 18 July 1996, st., *R. Aguilar 4576* (CR!, MO!); Golfito, Seccion 'Bosque de los Austriacos' gap near the research plot Esquinas, 300 m, 8°40'58"N, 83°12'58"W, 6 May 1997, fl., *W. Huber & A. Weissenhofer 620* (CR!); Golfito, P.N. Piedras Blancas, bosque Esquinas, Sendero Ozelot, forest in a gorge (near Esquinas Rainforest Lodge), 100 m, 8°40'60"N, 83°12'60"W, 16 February 2002, bud, *E.G.A. Suarez 3459* (WU, CR!, LI); Golfito, Orillas del camino sobre trocha La Tarde, Orillas de bosque, 152 m, 8°35'56"N, 83°29'35"W, 27 February 2016, fl., *D. Santamaría & R. Aguilar 9836* (CR); Golfito, Reserva Forestal Golfo Dulce. Bahía Chal. Finca El Eden, 174 m, 8°43'56"N, 83°27'9"W, 10 May 2017, fr., *D. Santamaría & R. Aguilar 9857* (CR). San José: San Isidro, Dota, Camino a rio Saavegre, Faldas de Cerro Nara, 600–700 m, 9°28'40"N, 84°0'10"W, 21 July 1998, fr., *O. Valverde 1084* (CR!, NY!).

Identification key for *Protium santamariae* and morphologically similar species

1. Leaves with a callus around petiole base, lateral petiolules 4.3–14.6 [8.7 ± 2.4] mm long, fruits 10–26.5 [17.6 ± 3.6] mm long, when mature light-red, dark-red, or green, never bicolored.....2.
- Leaves without a callus around petiole base, lateral petiolules 1.8–6.8 [3.9 ± 1.4] mm long, fruits 10.2–15.5 [12 ± 1.9] mm long, when mature bicolored, red above and green below*Protium aracouchini*
2. Leaflet secondary veins straight, main inflorescence axes shorter than petiole, flowers 5-merous.....*P. kleinii*
- Leaflets with secondary veins nearly straight to weakly arcuate or arcuate, main inflorescence axes longer than petiole, flowers 4-merous.....3.
3. Leaflets with secondary veins arcuate, petals 1.9–2 [1.9 ± 0] mm long, mature fruits green, inhabiting várzea forests or occasionally terra firme forests in the Amazon basin.....*P. krukoffii*
- Leaflets with secondary veins nearly straight to weakly arcuate, petals 1.3–1.9 [1.7 ± 0.2] mm long, mature fruits light-red, inhabiting lowland to premontane non-flooded forests in Costa Rica*P. santamariae*

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