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A New Amazonian Section of *Protium* (Burseraceae) including both Edaphic Specialist and Generalist Taxa. Studies in Neotropical Burseraceae XVI.

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Abstract—*Protium* section *Papilloprotium* and *Protium alvarezianum* are described and a key to the four species of the section provided. The section is distinguished principally by its papillate abaxial leaflet surface, and the petals saccate at base and villous adaxially. The rather widespread edaphic generalist *P. ferrugineum* shares a common ancestor with two small clades, one containing two white-sand specialists (*P. reticulatum* and *P. alvarezianum*) that appear to have diverged from a common ancestor allopatrically via fragmentation of white-sand habitats, and the other exhibiting degrees of edaphic specialization among variants of *P. subserratum*. This scenario highlights the role of edaphic heterogeneity as a driver in the diversification of the Amazon flora.

Keywords—Amazonia, rain forest trees, South America, speciation, white-sand forests.

The Burseraceae comprise one of the most important tree families in the Amazon, and across the Andes in the Chocó biogeographic region, as has been made clear in numerous quantitative forest inventories (e.g. review by Daly et al. 2011). It is an excellent model system for studying biogeographic patterns of primary upland forests because it is usually not an important component of secondary forests (e.g. Lisboa 1989), nor of floodplain forests (e.g. Foster 1990; Campbell et al. 1992). Central Amazonia is where the family truly shines by all standard criteria (e.g. Matos and Amaral 1999; Lima Filho et al. 2001). For example, in an area of 70 ha inventoried prior to 1992 by the Biological Dynamics of Forest Fragments (BDFF) project near Manaus, Brazil, the family was one of the highest in relative density but also one of the most species rich. The Burseraceae placed second in relative diversity, with 49 species, and *Protium* Burm. f. was the most species-rich genus, with 35 species (Rankin-de-Merona et al. 1992). One species of *Protium* exhibited the highest relative density in the inventory.

Most Amazonian Burseraceae occur in upland forests on clay or sandy loam soils, but there is a significant number of habitat specialists as well, including the majority of the tribe Protieae (including the genera *Crepidosperrnum* Benth. & Hook. f., *Protium*, and *Tetragastris* Gaertn.) in the Peruvian Amazon. Almost three quarters of the thirty-five species encountered in the Peruvian Amazon by Fine et al. (2005) were restricted to only one of three edaphic habitats: white-sand forest, clay soil forest, or brown sand forest from eroded river terraces. Differences in soils and topography correlate with changes in species diversity, species composition, and forest structure; indeed, they often determine distinct forest types. In the mosaic of habitats one often encounters in regions of lowland humid forests, there are generalists in each component, but there are also edaphic specialists (e.g. Young and León 1989), and the compositional differences are often statistically significant (Guillaumet 1987; Tuomisto et al. 1995; Fine et al. 2010). The most extreme of the edaphic habitat types are white-sand forests, which are also known as campina, campinarana, varillal, or bana, among other local names (Fine et al. 2010). These low-canopy forests on partly exposed white sands occur sporadically throughout much of Amazonia as islands on the scale of hectares or square kilometers. White-sand forests have little

in common floristically with the surrounding tall forests on clay soils (Guillaumet 1987; Fine et al. 2010), and they function as habitat islands, with their floras showing a higher proportion of species adapted for relatively long-distance dispersal than surrounding forests on clay soils (Macedo 1977; Macedo and Prance 1978; Anderson 1981). White-sand forests are associated with a high degree of endemism, even including some endemic genera (e.g., Struwe et al. 1997).

Here we describe a new section of *Protium* from northern South America; the four species that comprise it include a new species from white-sand formations in northern and western Amazonia. The biogeographic and habitat preferences of these four species, together with their phylogenetic relationships, suggest an important role for the edaphic heterogeneity of the Amazon basin in the diversification of this new section.

MATERIALS AND METHODS

Morphological Studies—Both authors have observed and collected three of the four species in this new section in multiple localities, working with seedlings and saplings as well as sterile and fertile adult trees. We have also examined virtually all extant herbarium material of the group.

DNA Extractions—In Appendix I we list the collection numbers, herbaria where the specimens are deposited, geographic locality, and GenBank accession number for each of the samples included in our molecular analysis. The samples were either dried fresh in silica gel and stored at -80°C or taken from herbarium sheets. All leaf tissue was ground using BioSpec Products Inc. (Bartlesville, Oklahoma) mini beadbeater-16 with their 2.3 mm zirconia/silica beads. Extractions were carried out using the DNEasy plant mini kit (Qiagen, Valencia, California). The protocol for herbarium specimens was modified to include an additional step where 3–5 μ l of Proteinase K were added to the sample in the lysis buffer and incubated on a horizontal shaker at 42°C for 12–24 hr.

PCR - Five Loci—We sequenced the ribosomal ITS and external transcribed spacer (ETS), a single copy nuclear locus, *phytochrome C* (*phyC*), and two chloroplast loci, *rps16* and *trnL-F* to assess phylogenetic relationships within tribe *Papilloprotium*. The ITS region was broken into two regions, ITS1 and ITS2 (Table 1).

Polymerase Chain Reactions were carried out in 20 μ l volumes of 1.0 μ l 10⁻⁴ M primer, two to five μ l DNA, one μ l 100% DMSO and Bioneer's (Alameda, California) accupower standard or "high-fidelity TLA" PCR premix, which includes one U DNA polymerase, 250 μ l dNTPs and two μ l reaction buffer per 20 μ l PCR reaction. The amplification products were visualized with UV light on 1% TBE agarose gels and cleaned using exonuclease I and shrimp alkaline phosphatase (USB Corporation, Cleveland, Ohio).

TABLE 1. Sources of primers used in this study, and substitution model for each locus selected by MrModeltest 2.3. All model parameters were unlinked across loci.

Locus	Primer Name (Forward/Reverse)	Primer Sequence	Citation	Substitution Model selected by MrModeltest
ITS1	NY183 (F), NY109 (R)	CCTTATCATTAGAGGAAGGAG (F), GTGACGCCAGGCAGACGT (R)	K. Wurdack (Fine et al. 2005)	GTR + G
ITS 2	NY45 (F), NY 43 (R)	GCATCGATGAAGAACGTAGC (F), TATGCTTAAAYTCAGCGGCT (R)	K. Wurdack (Fine et al. 2005)	GTR + G
ETS	ETS-1(F), ETS 18S-IGS (R)	TTCGGTATCCTGTGTTGCTTAC (F), GAGACAAGCATATGACTACT GGCAGGATCAACCAG (R)	Weeks et al. 2005 (F), Baldwin and Markos 1998 (R)	HKY + G
<i>phyC</i>	<i>phyC</i> -smbF1, <i>phyC</i> -smbR1	GGCAYTGAARTCATAYAARCTTGC (F), CCRCCCCACTTGATCTGYTT (R)	Clayton et al. 2007	HKY + G
<i>rps16</i>	<i>rps16</i> (F), <i>rps16</i> (R)	GTGGTAGAAAGCAACGTGCGACTT (F), TCGGGATCGAACATCAATTGCAAC (R)	Oxelman et al. 1997	GTR + G
<i>TrnL-F</i>	<i>trnL</i> F-C, <i>trnL</i> F-F	CGAAATCGGTAGACGCTACG (F), ATTTGAACCTGGTGACACGAG (R)	Taberlet et al. 1991	GTR

Sequencing and Alignment—Amplification products were cycle-sequenced using 10 l reactions with the standard BigDye (Applied Biosystems, Foster City, California) protocol and afterwards cleaned again using an EDTA-ethanol precipitation step. Sequencing was performed on an ABI 3730 sequencer (Applied Biosystems). The resulting chromatograms were edited, and forward and reverse sequences were compiled using Geneious Pro 3.5.6 (BioMatters Ltd., Auckland, New Zealand). Initial sequence alignments were made using ClustalW (EMBL-EBI) with subsequent manual alignments in MacClade 4.05 (Maddison and Maddison 2002).

Taxon Sampling—For outgroup comparison we selected representatives from each of the named sections in the Protieae, which included the genera *Crepidosperrum* and *Tetragastris* (Fine et al. 2005). In Fine et al. (2005) the closest lineage to the *Papilloprotium* taxa was a clade including members of *Crepidosperrum*, *Tetragastris*, and sections *Pepeanthos* Daly, *Icicopsis* Engl., and *Sarcoprotium* Daly. Further analyses with more than 70 species of Protieae have identified Old World *Protium* (sections *Marignia* Swart and *Protium*) as comprising the outgroup to all New World Protieae (including *Protium*, *Crepidosperrum*, and *Tetragastris*) (P. Fine and D. Daly, unpublished data). Thus, we used *Protium madagascariense* Engl. from Madagascar as our outgroup taxon to root the clade. We added one other species to the outgroup, *Protium glaucescens* Urban, which in other preliminary analyses belonged to a large clade of *Protium* species that currently has no sectional assignment or status. We selected two individuals from *P. alvarezianum* (the new taxon), plus six individuals of *P. subserratum* (Engl.) Engl. representing each of the three morphotypes described below and five localities (French Guiana and Guyana, plus Iquitos/Nanay, Jenaro Herrera, and Río Blanco in Peru). These individuals were selected from a larger dataset of five individuals per population of nine populations of *Protium subserratum* (N = 45 individuals) and three populations of *Protium alvarezianum* (N = 15 individuals collected in Peru, French Guiana, and Guyana) (Fine et al. in press).

Phylogenetic Analyses—A partition homogeneity test was performed as implemented in PAUP* 4.0b10 with 100 replicates to confirm the different genes sequenced could be combined for phylogenetic analysis (Farris et al. 1995). The likelihood-ratio test was used in MrModeltest 2.3 (Nylander 2004) using the AIC to select the best model of molecular evolution with the fewest parameters that fit the dataset. These parameter estimates were used in all subsequent Bayesian analyses. We combined the multilocus datasets, and using a mixed model analyzed the substitution parameters separately for each gene partition. Bayesian inference of phylogeny was performed using MRBAYES version 3.1.2 (Huelsenbeck and Ronquist 2001) with the following specifications: 1) assuming various models (see Table 1) of nucleotide substitution with estimated base frequencies, proportion of invariable sites, and rates for variable sites following a gamma distribution as selected by Mr Modeltest; and 2) running the Markov chain for 3×10^8 generations, sampling one tree every 300 generations for a total of 10,000 sampled trees. We analyzed two runs in parallel with four chains each (one cold and three heated), and assessed stationarity by examining the standard deviation of the split frequencies. At 3×10^8 generations, this value was below 0.003 and there was no trend in the log versus generation plot with sufficient mixing of the cold and heated chains. Thus, following the recommendations of Huelsenbeck and Ronquist (2001), we discarded the first 25% of all sampled trees as “burn in.” MrBayes computes a 50% majority-rule consensus tree of the retained trees. We also conducted a

maximum likelihood analysis on the partitioned data set using a randomized accelerated maximum likelihood (RAxML) program on the CIPRES cluster at the San Diego Supercomputing Center (Stamatakis et al. 2005). This analysis comes with a rapid bootstrap heuristic that automatically determines the point at which enough bootstrapping replicates have been produced (Stamatakis et al. 2008).

TAXONOMIC TREATMENT

Protium sect. **Papilloprotium** Daly & P. Fine, sect. nov.—
TYPE: *Protium subserratum* (Engl.) Engl.

Protium sect. *Icicopsis* Swart (1942), pro minima parte. *Icicopsis* Engl. in Mart., Fl. bras. 12(2): 255. 1874.

Turma naturalis a sectio *Pepeanthos* resina lactea plerumque sine pulvinulo laterali folioli venis sclereida ramosissimis terminans cotyledone plano-convexis simile sed a caeteris speciebus congeneribus his notulis differt: folioli pagina abaxialis plerumque dense papillata petali basis saccata et pagina adaxialis villosa antherae apex apiculatus.

Dioecious trees; outer bark thin, often rough due to raised lenticels, inner bark red; resin milky. Leaves usually lacking pulvinuli on lateral petiolules (present on *Protium ferrugineum*), present on terminal petiolule; leaflet margin (sub)serate or entire; abaxial surface densely papillate (Fig. 1). Leaflet architecture (Fig. 2) with secondary vein fabric festooned-brochidodromous; some intersecondaries usually present on most leaflets, parallel to secondaries and often nearly as long but slightly deflected (zig-zag); tertiaries alternate-percurrent with some composite admedials near midvein; same pattern found in quaternaries but these also occasionally freely ramify; perpendicular epimedial tertiaries usually present; freely ending veinlets (FEVs) proliferating into highly branched sclereids; when teeth present both the tooth and superjacent sinus vascularized by a principal vein. Inflorescences pseudospicate. Flowers 5-merous; calyx much taller than nectary disk; petals narrowly subulate, slightly saccate at base between calyx lobes, (sub)erect at anthesis, the adaxial surface villous, with dense whitish trichomes to 0.8 mm long; androecium pentadynamous, anthers apiculate (the connective extending beyond the thecae); pollen (from Harley and Daly 1996) 33–37 μ m, endoapertures very small (Endoaperture Shape Index-ENSI 4.9); shape subprolate or prolate, rarely prolate-spheroidal [ratio polar axis length to equatorial diameter-P/E (1.12–)1.14–1.68], P 22–40(–22.6–39.2), E 17.2–31.1(–16–34) μ m; angulaperturate; colpi narrow; costae pronounced; wall

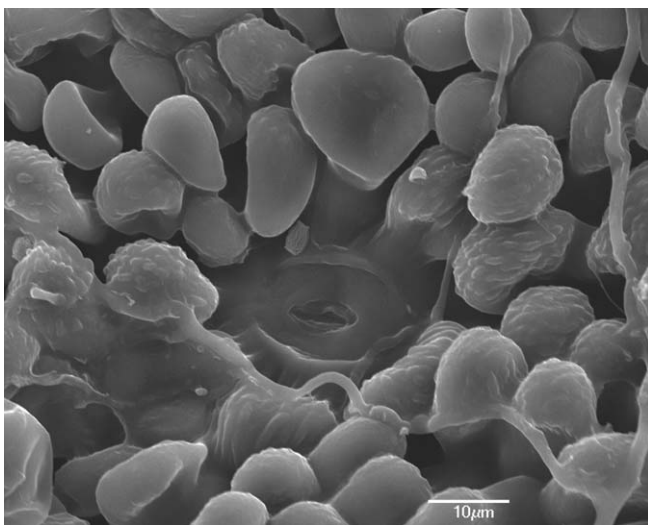


FIG. 1A. SEM images of abaxial leaflet surfaces of *Protium* sect. *Papilloprotium*. *Protium subserratum*, showing dense papillae crowded around a slightly sunken stoma; on most of the surface the stomata are obscured by papillae. From Clark 7190 (NY).

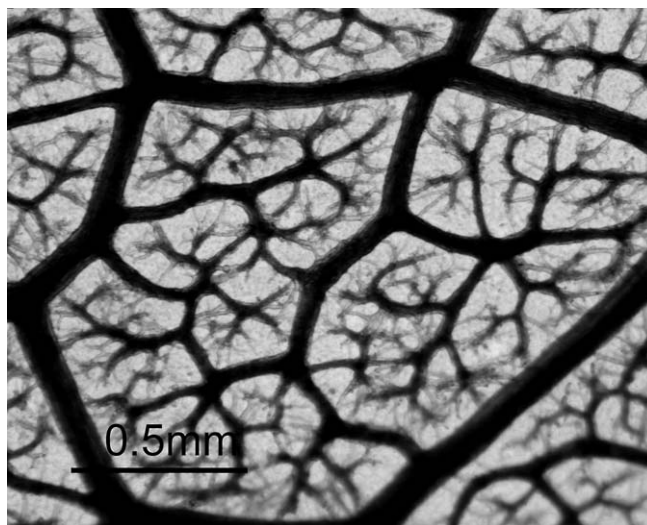


FIG. 2A. Leaf architecture of *Protium* sect. *Papilloprotium*. *Protium reticulatum*, showing the FEVs (freely ending veinlets) terminating in highly branched sclereids. From Acevedo et al. 10355 (NY).

thickness 1–2 mm; exine appears psilate; colpi with granular membranes; rarely (*P. ferrugineum*) the mesocolpium psilate and sparsely punctate and the apocolpium perforate; nectary disk surface pubescent (glabrous in *P. ferrugineum*, also rarely in *P. subserratum*); gynoeceum with style longer than ovary and unbranched, stigma surface smooth. Fruit red to orange; pyrene bony or rarely (*P. ferrugineum*) thinly cartilaginous, the funicular scar usually \leq halfway up ventral surface (3/4 in *P. ferrugineum*); cotyledons entire, plano-convex. Germination epigeal and cryptocotylar, seedlings with first eophylls opposite, 5–11-foliolate, serrate. Figures 1–4.

Distribution and Ecology—The distributions of the four species of sect. *Papilloprotium* range from rather widespread to regionally endemic (Fig. 3). *Protium subserratum* is widespread in Amazonia plus the Guianas, with a disjunct distribution

in Antioquia, Colombia; *P. ferrugineum* (Engl.) Engl. occurs in western Amazonia and is disjunct across the Andes in Valle, Colombia; *P. alvarezianum* is found in northern and western Amazonia; and *P. reticulatum* (Engl.) Engl. is known only from the upper Rio Negro basin (tributaries of the Rio Negro and Rio Uaupés) in Venezuela and Brazil. *Protium subserratum* has a broad edaphic distribution; it has been collected in clay soil, eroded river terrace soil (brown sand), and white-sand forests. *Protium ferrugineum* has similarly been collected in a variety of terra firme soil types, although it has never been found in extreme (low canopy) white-sand forests, famous for their stressful environments of extreme soil infertility and poor drainage due to a perched water table. In contrast, *Protium alvarezianum* and *P. reticulatum* are both restricted to these low-canopy white-sand areas, and have

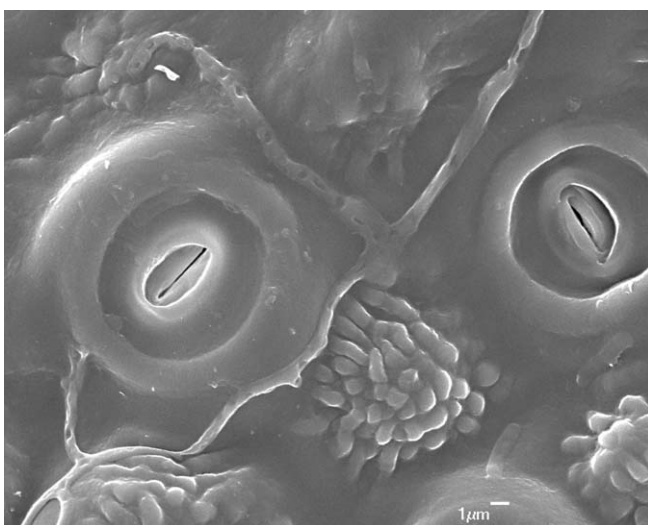


FIG. 1B. SEM images of abaxial leaflet surfaces of *Protium* sect. *Papilloprotium*. *Protium ferrugineum*, showing scattered clusters of small papillae interspersed among the stomata, which are recessed within a raised chamber. From Monsalve 1302 (NY).

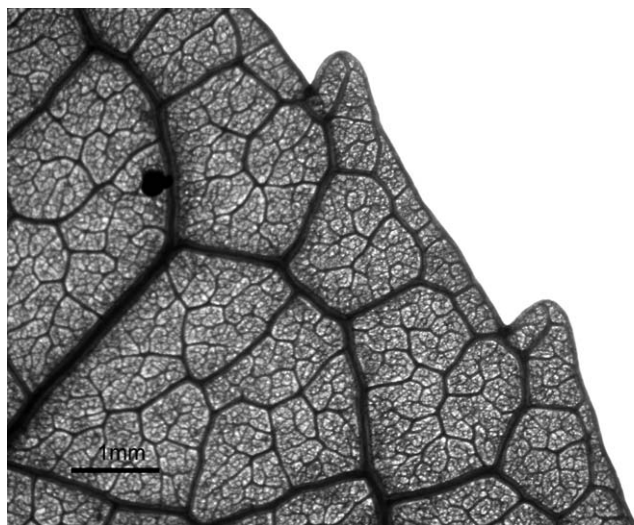


FIG. 2B. Leaf architecture of *Protium* sect. *Papilloprotium*. *Protium subserratum*, showing vascularization of the teeth. From Albuquerque 6724 (NY).

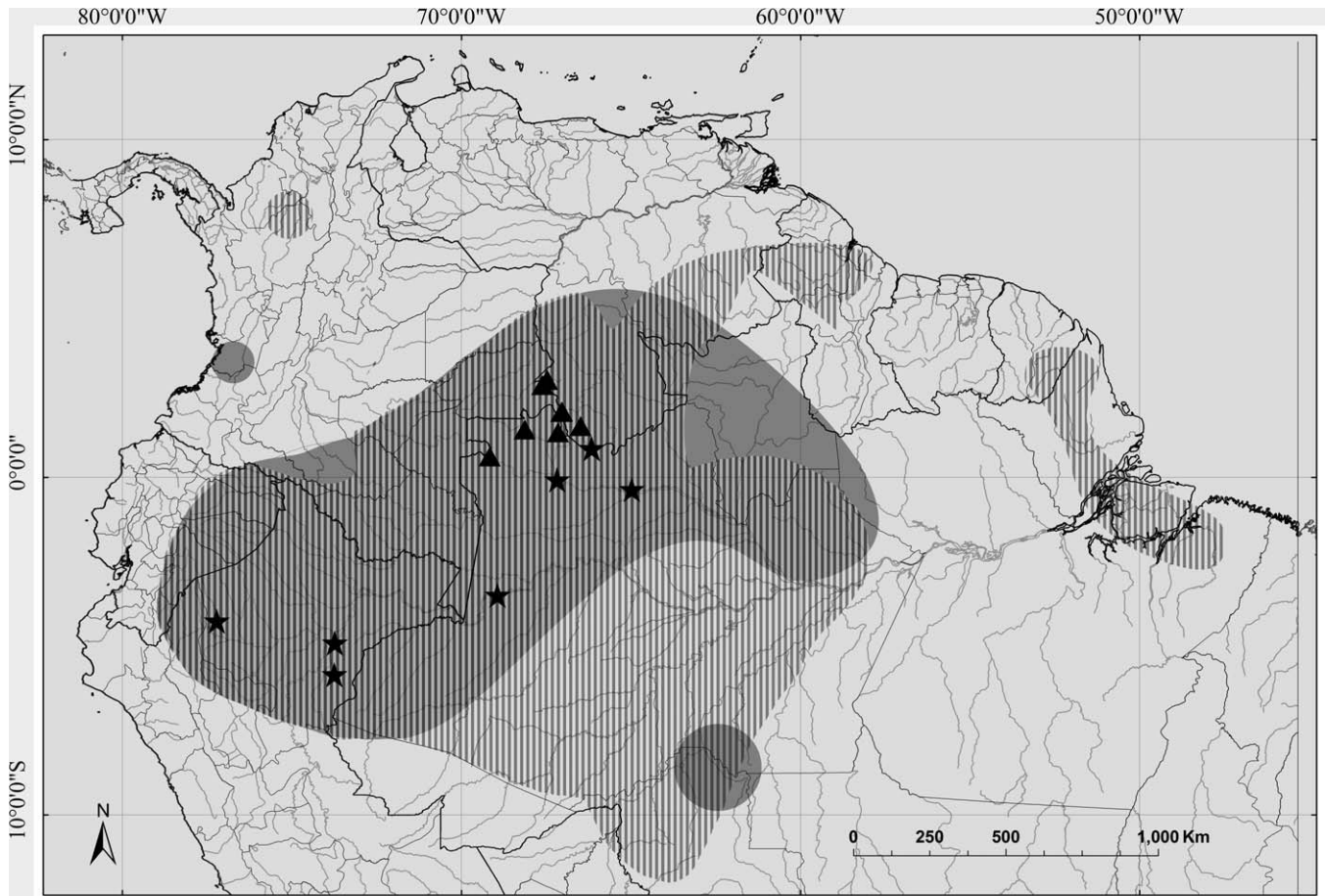


FIG. 3. Map showing distributions of the four species of *Protium* sect. *Papilloprotium*. Stars indicate collection localities for *Protium alvarezianum* and triangles indicate *Protium reticulatum* localities. All triangles and stars are located within white-sand forest habitat. Gray shading approximates the distribution of *Protium ferrugineum* and the vertical striped shading approximates the distribution of *Protium subserratum*.

not been collected on other, more common, edaphic habitat types.

Within *Protium*, section *Pepeanthos* could most easily be confused with sect. *Papilloprotium* because of the milky resin, the usual lack of conspicuous pulvinuli on lateral petiolules, leaflets with freely ending veinlets terminating in highly branched sclereids, and the cotyledons plano-convex. These similarities and salient differences between the two sections are summarized in Table 2.

Characteristics unique to sect. *Papilloprotium* in tribe Protieae are the papillate abaxial leaflet surface, the petals saccate at base and villous adaxially, and the anther apex apiculate. Other notable characteristics are found elsewhere in the genus: milky resin (also in sect. *Pepeanthos*), pseudospicate inflorescences (also in sect. *Icicopsis*), and the FEVs terminating in highly branched sclereids (also in *Tetragastris*, *Crepidospermum*, and *Protium* sect. *Pepeanthos*); the great majority of *Protium* species have the FEVs one- or two-branched.

Papillate leaf surfaces, usually on the abaxial side, are characteristic of understory plants in moist tropical forests, but they may serve distinct functions depending on their morphology and arrangement, as discussed in Rollet et al. (1990). Papillae significantly increase surface area, so thin-walled papillae may serve to increase cuticular evaporation; they

may also function as “collecting lenses” to enhance capture of diffuse understory light. On the other hand, thick-walled papillae that form a “wreath” around stomates create a calm air chamber above them, thereby reducing stomatal transpiration. The latter xeromorphic condition, with the papillae obscuring the stomates, is characteristic of *Protium subserratum* (Fig. 1A) except for an eastern Amazon variant (“morphotype 1”, see discussion below) that has a thick cuticle covering the whole surface other than the stomates. Meanwhile, *P. alvarezianum* and *P. ferrugineum* (Fig. 1B) have papillae that are mound-like or bulbous to subspherical, respectively, interspersed among stomates that are recessed within a raised chamber or collar. This xeromorphic condition fits logically with the high insolation and possible periodic water stress of white-sand habitats.

Protium ferrugineum stands apart in sect. *Papilloprotium* morphologically, and the molecular evidence indicates that it is sister to the common ancestor of the other three species. It is the only described species in the group that consistently has pulvinuli on the lateral leaflets, the pollen with the mesocolpium psilate and sparsely punctate and the apocolpium perforate, the nectary disk glabrous, the pyrene oblong to slightly obovoid (vs. ovoid), and the funicular scar three fourths (not < 50%) of the distance up the ventral face of the pyrene.

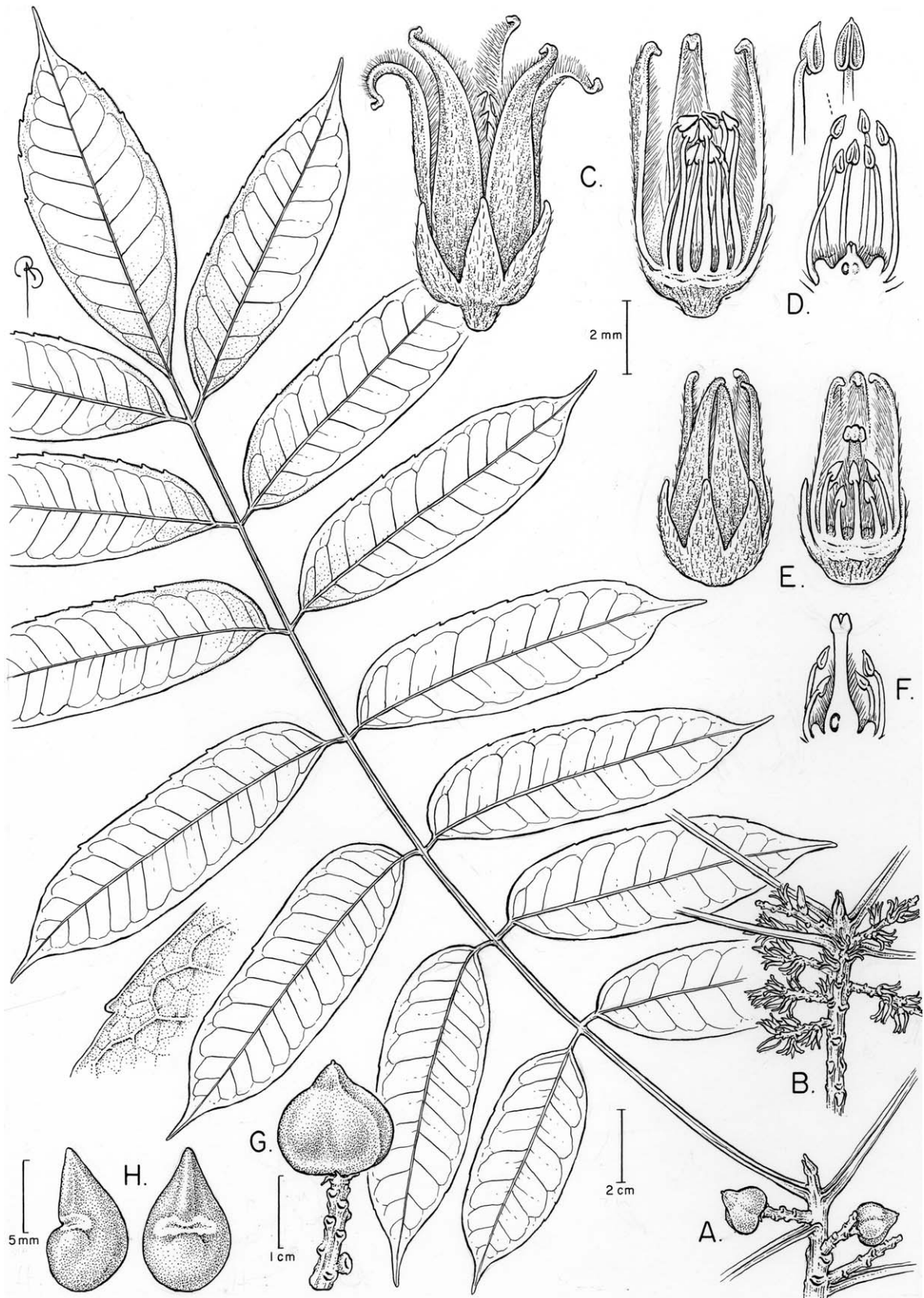


FIG. 4. *Protium alvarezianum* Daly & P. Fine. A. Fruiting branchlet, with inset showing detail of margin with tooth. B. Flowering branchlet, showing short subterminal inflorescences. C. Staminate flower, at right with calyx lobes and two petals removed. D. Longisection of staminate flower with perianth removed, showing pubescent nectary disk and pistillode with reduced locules and ovules; inset above showing antepetalous anther in lateral and ventral views. E. Pistillate flower, at right with calyx lobes and two petals removed. F. Longisection of pistillate flower with perianth removed, showing pubescent pistil with long style. G. Detail of infructescence, showing persistent bractole bases. H. Pyrene in lateral and ventral views, showing funicular scar less than halfway to apex. A from Vázquez & Soto 11891 (NY), B-D from Daly & Acevedo 5116 (NY), E-F from Boom & Weitzman 5381 (NY), G-H from Cid Ferreira 9336 (NY).

TABLE 2. Salient characters linking and separating sect. *Papilloprotium* and sect. *Pepeanthos*.

Character	sect. <i>Papilloprotium</i>	sect. <i>Pepeanthos</i>
Resin	milky	milky
Snail-shaped glands	absent	present
Lateral pulvinuli	absent or present	absent or inconspicuous
Leaflet margin	(sub)serrate or entire	entire
Leaflet abaxial surface	papillate (most taxa)	not papillate
FEVs (freely ending veinlets)	terminate in highly branched sclereids	terminate in highly branched sclereids
Inflorescences	pseudospicate (flowers (sub)sessile)	open-paniculate
Petal morphology	narrowly subulate, saccate at base between K lobes	not saccate at base
Petal adaxial surface	villous	glabrous
Petal orientation	(sub)erect at anthesis	(sub)erect at anthesis
Stamen series	dimorphic (pentadynamous)	sometimes pentadynamous
Antesepalous stamens	not reflexed	often reflexed between petals at anthesis
Anther apex	short-apiculate (extension of connective)	not apiculate
Pollen	polar outline angulaperturate	polar outline fossaperturate
Disk surface	usually pubescent	glabrous or pubescent
Style	at least as long as ovary, unbranched	shorter than ovary, with 5 short branches
Stigma surface	smooth	caudiculate and spiculate
Pyrene funicular scar	usually below halfway point on ventral surface	well above halfway point
Pyrene thickness	usually bony	usually cartilaginous
Cotyledons	entire, plano-convex	entire, plano-convex
Germination	epigeal, cryptocotylar	epigeal, phanerocotylar
First eophylls	opposite, 5–11-foliolate, serrate	opposite, simple, entire or distally serrulate

KEY TO THE SPECIES OF *PROTIUM* SECTION *PAPILLOPROTIUM*

1. Lateral petiolules 3–13 mm long, a distal pulvinulus usually visible; leaflets entire, rarely with a few scattered teeth 2
2. Lateral leaflets (broadly) elliptic to slightly (ob)lanceolate or slightly oblong-elliptic; antesepalous anthers often continuous with filaments (i.e. not sagittate); nectary disk glabrous; fruit apex acute or more often acuminate; pyrene thinly cartilaginous to almost chartaceous, oblong to oblong-(ob)ovate in dorsiventral view, funicular scar and cleft ca. 3/4 distance to apex *P. ferrugineum*
2. Lateral leaflets (oblong-)ovate to (oblong-)lanceolate; all anthers dorsifixed and sagittate; nectary disk pubescent; fruit apex retuse to slightly emarginate; pyrene bony, (broadly) ovate in dorsiventral view, funicular scar and cleft \leq halfway to apex *P. reticulatum*
1. Lateral petiolules 1–8 mm long, without a distal pulvinulus; leaflets entire or more often coarsely serrate or with at least a few scattered teeth 3
3. Leaflets coriaceous or less often chartaceous, the margin coarsely (sub)serrate or less often entire; pistillate inflorescences and infructescences 3.5–14 cm long; calyx lobes 0.7–1 mm long (staminate) or 1–1.3 mm long (pistillate, also often persistent and measurable on fruits); fruit (0.6–)1.1–1.4 cm wide (to 1.8 cm wide when >1 pyrene), apex acute or acuminate, base truncate *P. subserratum*
3. Leaflets thinly chartaceous, the margin entire or with a few scattered teeth; pistillate inflorescences and infructescences 2–3 cm long (–4.5 cm with fruits); calyx lobes 2.2–2.6 mm (staminate) or 1.5–2 mm long (pistillate, also often persistent and measurable on fruits); fruit 0.8–1 cm wide (to 1.4 cm wide when > 1 pyrene), apex narrowly and sharply short-acuminate, base cordate to truncate *P. alvarezianum*

Protium alvarezianum Daly & P. Fine, sp. nov.—TYPE: BRAZIL. Mun. São Paulo de Olivença, Estrada Bomfim, trail beyond road, ca. 6 km S of town center, 3°30'S, 68°57'W, 23 Nov 1986 (m fl), D. C. Daly, R. P. Lima, & V. S. Pinho 4414 (holotype: INPA!; isotypes: AAU!, C!, CAS!, DUKE!, NY!, PORT!, TUR!, W!).

Arbor 5–15 m usque altus in sylvis in arena alba Amazonia occidentalis ramuli graciles folioli parvi et chartacei margine (sub)integer ab affinis his notulis differt: inflorescentia constanter brevis (3 cm usque, 4.5 usque in fructu) calyx longior bracteae inflorescentiae tumidae base fructu persistens stamini et staminodii longiores fructus parvior basi cordata.

Sparsely branched tree 5–15 m \times 4–15 cm DBH. Inner bark red; sapwood white, 2–3 mm thick; heartwood reddish, soft without. Resin usually sparse, white, gummy and very thick (reportedly clear on *Thomas 3178*, "light latex" on *Gentry & Stein 46997*). Leaves 4–7-jugate, 30–54 cm long; petiole 7.3–15 cm long, interjuga 2.5–4.5 cm long, petiole and rachis with

dense, straight, ascending to appressed, golden hairs to 0.5 mm long, also sparse to dense, fine, erect, golden hairs to 0.25 mm long; lateral petiolules 0.1–0.7 cm long, without pulvinuli, basal pair of leaflets 5.6–10.8 \times 0.9–4.8 cm, lanceolate to ovate or elliptic, other laterals 6.2–16 \times 2.2–4.5 cm, oblong-elliptic to slightly oblong-(ob-)lanceolate, terminal petiolule 1.2–2 cm long, terminal leaflet 8–11 \times 2.9–4.3 cm, leaflets thinly chartaceous, drying dark greenish brown, apex abruptly to gradually and narrowly long-acuminate, the acumen (0.3) 0.7–2 cm long, base asymmetric, basiscopic side acute, acroscopic side truncate to obtuse, sometimes decurrent, margin entire or often some leaflets with a few scattered teeth, especially on the acumen; on abaxial surface the midvein prominent, the secondaries prominent to prominulous, the higher-order veins prominulous to flat, subglabrous or toward base provided with sparse to scattered, ascending to flexuous hairs to 0.5 mm long (sometimes all along midvein); on adaxial surface the midvein narrowly prominulous, the secondaries and higher-order veins narrowly prominulous

to flat, surface glabrous. Inflorescences conferted at branchlet apices, robust, staminate ones to 9 cm long, pistillate inflorescences and infructescences 2–3 cm long (–4.5 cm with fruits), pseudospicate; axes with dense, appressed to ascending, golden hairs to 0.3 mm long; bracts on primary axes 1.5–2 mm long, subulate to lanceolate, fleshy and persistent, bractlets 0.5–1.3 mm long, very broadly ovate and sharply acuminate, the base semiclasping and swollen. Flowers congested along axes, calyx 2.5–3 × 2.8–3.6 mm overall, taller than the nectary disk, with dense to sparse hairs as on axes; in staminate flowers the lobes 2.2–2.6 mm long, (narrowly) triangular and slightly acuminate; petals 4.8–6 × 1.3–1.4 mm, green without, subulate, distally spreading to reflexed, with an inflexed apiculum 0.35–0.5 mm long, slightly saccate at base, abaxial surface with pubescence as on calyx (rarely scattered), adaxial surface with dense, ascending to flexuous, white hairs to 0.8 mm long; antesealous stamens 3.6–4 mm long with lanceolate anthers 0.6–0.75 mm long, the antepetalous ones 2.8–3.6 mm long with ovate anthers 0.4–0.5 mm long, filaments slightly compressed; nectary disk 0.3–0.5 mm tall and 0.2–0.5 mm thick, with dense, ascending hairs to 0.3 mm long; pistillode 0.35 long × 0.5 mm wide, slightly taller than nectary disk, depressed-ovoid, with dense, ascending hairs to 0.4 mm long, provided with reduced locules and ovules, the style 0.2–0.35 mm long; pistillate flowers with calyx lobes 1.5–2 mm long; petals 4.4–5.5 × 1.4–1.85 mm, suberect at anthesis; antesealous staminodes 2.2–2.8 mm long with lanceolate anthers 0.4–0.6 mm long, the antepetalous ones 1.4–1.85 mm long with ovate anthers 0.4–0.45 mm long; nectary disk 0.2–0.4 mm tall and 0.3–0.4 mm thick; pistil 3.2 × 1.2–1.4 mm, with dense, ascending hairs to 0.4 mm long, ovary ovoid, style 1.6 mm long, the stigmas 0.4 mm tall, laterally depressed-globose. Fruit maturing dark red, 1.4–1.6 × 0.8–1 cm (to 1.4 cm wide when > 1 pyrene), obliquely ovoid, the apex narrowly and sharply short-acuminate, the base cordate to truncate, not stipitate, surface with sparse to scattered, flexuous hairs to 0.5 (–0.6) mm long, sometimes these persisting only at base and apex; on dehiscence the valves pink within; pseudaril white; pyrene 1.05–1.2 × 0.6–0.8 cm, in dorsiventral view ovate with acute to slightly acuminate apex and rounded base, in lateral view ovate with a shallow cleft slightly less than halfway to the apex corresponding to the funicular scar, the scar laterally oblong and covering ca. 20% of the anterior face, the surface glabrous and smooth. Cotyledons unknown, on seedlings the first eophylls 11-foliolate (Fine *et al.* 823, NY). Figure 4.

Common Names, Uses, Etymology—Brazil: “lacre” (Daly *et al.* 5116); Peru: “copal” (Vásquez & Soto 11891). It should be noted that these names are by no means species-specific; rather the Brazilian name is applied to various taxa having a milky resin, and the Peruvian name is applied to most Amazonian Burseraceae. No uses reported. The specific epithet acknowledges José Álvarez Alonso, conservation biologist, ornithologist, journalist, discoverer of and champion for white-sand forests in the Peruvian Amazon. He was the driving force behind the creation of the first reserve in Peru that protects white-sand forests, the Reserva Nacional Allpahuayo-Mishana.

Distribution and Ecology—The known distribution of the new species consists of four apparent disjunctions: (1) the upper Río Negro basin, in southern Amazonas department in Venezuela and contiguous Amazonas, Brazil; (2) the Japurá basin in NW Brazil; (3) the middle Ucayali basin in Loreto, Peru; and 4) the Morona basin north of the Marañon River in

Loreto, Peru. This is clearly a white-sand specialist, growing in sandy ultisols or podzols. It has been recorded from two similar vegetation types in Brazil and Peru (Fig. 3):

1. chamisal / low campinarana / low bana — Dense poles, few exceeding 4–5 m, in soil with ca. 20 cm of litter/humus overlying ca. 30 cm of impermeable concretion overlying sand (e.g. Peru, Daly & Acevedo 5116, 5118).

2. varillal / Amazonian caatinga / campinarana or campina forest / tall bana, in white-sand on undulating terrain, the canopy discontinuous with occasional trees to 15 m tall, layer of litter and humus 10–30 cm deep (Peru, Dávila *et al.* 1171), or in caatinga alta, the canopy ca. 15 m tall and few emergents to 35 m (Brazil, Cid Ferreira 9336, Daly *et al.* 4414).

This species has been collected flowering Nov–Apr, and fruiting Feb–Jul (Oct).

Additional Specimens Examined—VENEZUELA. Amazonas: Depto. Río Negro, Neblina Base Camp, Río Mawarinuma, 00°50'N, 66°10'W, 140 m, 27 Jan 1985 (f fl), Boom & Weitzman 5381 (AAU, AMAZ, MO, NY), 23 Feb 1985 (immat. fr), Boom & Weitzman 5948 (AAU, COL, MICH, MO, NY, US, W), 4–5 Jul 1984 (fr), Davids & Miller 26997 (NY), 22 Apr 1984 (immat. fr), Gentry & Stein 46874 (NY), 27 Apr 1984 (immat. fr), Gentry & Stein 46997 (NY), 20 Mar 1984 (immat. fr), Liesner 16846 (NY); S side of Río Mawarinuma (= Río Baria), 00°49'50"N, 66°09'40"W, 23 Feb 1985 (immat. fr), Nee 31066 (NY, 2 sheets), near base camp, 00°50'N, 66°10'W, 23 Apr 1984 (immat. fr), Thomas 3178 (NY).

PERU. Loreto: Prov. Requena, Dto. Sapuena, Centro de Investigaciones Jenaro Herrera, ca. 5 km E of Río Ucayali, 4°55'S, 73°45'W, 21 Apr 1987 (m fl), Daly & Acevedo 5116 (NY), 21 Apr 1987 (immat. fr), Daly & Acevedo 5118 (NY); Prov. Requena, Dto. Curinga, near Ungurahuillo, Río Blanco, 5°51'S, 73°46'W, 1 Nov 2004 (fl), Dávila *et al.* 1171 (NY); Prov. Datem de Marañon, Dto. San Lorenzo, near community of Tierra Blanca, Río Morona, 4°16'S, 77°14'W, 24 Apr 2002 (seedling), Fine *et al.* 823 (NY), 24 Apr 2002 (fr), Fine *et al.* 832 (UC), 24 Apr 2002 (juvenile), Fine *et al.* 844 (AMAZ, MO, NY, UC), 5 Dec 2006 (fr), Mesones 1312 (NY, UC), 5 Dec 2006 (fl), Mesones 1316 (NY, UC); Jenaro Herrera, 4°55'S, 73°45'W, 130 m, 13 Mar 1989 (immat. fr), Vásquez & Soto 11891 (NY).

BRAZIL. Amazonas: Río Negro, right bank, 4 Jul 1976 (immat. fr), L. Coêlho 551 (INPA); Mun. Santa Izabel do Rio Negro, 7 km behind town of Sta. Izabel, near old airport, 0°22'S, 64°59'W, 10 Oct 1987 (immat. fr), Cid Ferreira 9336 (NY); subbase Proj. RADAM Ponto 02-A, 1 Jun 1976 (fr), Marinho 370 (IAN); Rio Japurá, 0°05'S, 67°11'W, 18 Apr 1975 (immat. fr), Nascimento *et al.* 155 (IAN, MG, 2 sheets).

In comparison to other species in sect. *Papilloprotium*, *P. alvarezianum* is distinctive because of its slender branchlets; the leaflets are small and thinly chartaceous, with (sub)entire margin; the pistillate inflorescences are consistently short (to 3 cm long, 4.5 cm with fruits); the calyx is longer; the inflorescence bracts are swollen and at least the base persists in fruit; the stamens and staminodes are longer; and the fruits are smaller with a cordate or less often truncate base.

PROTIUM FERRUGINEUM (Engl.) Engl. in DC., Monogr. phan. 4: 79. 1883. *Icicopsis ferruginea* Engl. in Mart., Fl. bras. 12(2): 258. 1874. *Tingulonga ferruginea* (Engl.) Kuntze, Rev. Gen. Pl. 1: 108. 1891. *Paraprotium ferrugineum* (Engl.) Cuatrec., Webbia 12(2): 411. 1957.—TYPE: VENEZUELA. Amazonas: Río Negro, near San Carlos, May 1854 (fr), Spruce 3494 (lectotype, designated by Swart 1942: 388, P!; isotypes: BM!, BR!, C!, G!, K!, LE, NY!, W!).

Distribution and Ecology—*Protium ferrugineum* is widespread in Amazonia north of the Río Amazonas, with a trans-Andean disjunction in Valle, Colombia and an apparent disjunction to the south in Humaitá, Amazonas, Brazil. It is also versatile ecologically, reported from tall moist forest in clay or sandy clay or white-sand soil; high caatinga, forest seasonally flooded by black-water rivers; and dwarf forest in quartzite deposits. The species occurs in two distinct habitats in the Ducke Reserve outside of Manaus, Brazil: baixio or

forest on low-lying terrain in sandy soil with poor drainage, and vertente or well-drained slope forest in clay soil. In Peru, *P. ferrugineum* is not associated with low-canopy white-sand forest, although there are a few collections of juvenile individuals from high canopy white-sand forest (Fine et al. 2005).

PROTIUM RETICULATUM (Engl.) Engl. in DC., Monogr. phan. 4: 79. 1883. *Icicopsis reticulata* Engl. in Mart., Fl. bras. 12(2): 258, t. 51. 1874.—TYPE: VENEZUELA. Amazonas: Río Negro, near San Carlos, Apr 1854 (fr), *Spruce 3476* (lectotype, designated by Swart 1942: 389, P!; isotypes: BM!, BR!, G!, K!, LE, NY!, W!).

Distribution and Ecology—This species has the most restricted distribution of the section, to date known only from the upper Río Negro basin in Venezuela and Brazil, but expected in contiguous Colombia. It is usually a small tree, 4–16(–25) m × 5–30 cm DBH, reported explicitly from bana (= campina) vegetation and descriptively from low forests on poorly drained soils overlain by white sand, with one report from caatinga pedregosa or rocky caatinga at Tunuí on the Rio Uaupés; this is likely an analogous formation with granitic outcrops.

PROTIUM SUBSERRATUM (Engl.) Engl. in DC., Monogr. phan. 4: 89. 1883. *Icicopsis subserrata* Engl. in Mart., Fl. bras. 12(2): 259. 1874. *Tingulonga subserrata* (Engl.) Kuntze, Rev. Gen. Pl. 1: 108. 1891.—TYPE: BRAZIL. Amazonas: Rio Uaupés, near Panuré, Oct. 1852 (f fl and young fr), *Spruce 2620* (lectotype, designated by Swart 1942: 387, P!; isotypes: BM!, BR!, C!, G!, GH!, K!, LE, MO!, NY!, W!).

Distribution and Ecology—This is by far the most broadly distributed species of the section, widespread in Amazonia, extending into Guyana and French Guiana, and disjunct in Antioquia, Colombia. In Amazonia the species is known from Brazil (Acre, Amapá, Amazonas, Maranhão, Pará, Rondônia), Colombia (Amazonas), Ecuador (Napo, Santiago-Zamora), Peru (Loreto), and Venezuela (Amazonas). It occurs in a range of habitats like that of *P. ferrugineum*.

Protium subserratum shows pronounced geographic variation, but thus far the species is considered to be a widespread and variable taxon. Any future assessment of the infraspecific taxonomy must take into consideration the variation that can be observed even within a single collection. For example, on the several duplicates of *Krukoff 7063* (seen at BM, GH, K, NY), collected in the Rio Madeira basin, the leaflet size varies

greatly from one specimen to another and the leaflet margin ranges from markedly serrate to completely entire. The morphological variants (morphotypes) of *P. subserratum* and their geographic distributions are presented in Table 3 and their putative relationships are shown in Fig. 5.

RESULTS

The Bayesian posterior probabilities were mapped onto a majority rule consensus of all 7,500 post burn-in trees (Fig. 5). The topology of this consensus tree for the ingroup (sect. *Papilloprotium*) exactly matched the best tree produced by maximum likelihood (RAxML). Both the Bayesian and maximum likelihood analyses suggest strong support (1.00 posterior probability, 100% bootstrap) for the monophyly of sect. *Papilloprotium*. Trees have been submitted to TreeBASE (study number S11442). *Protium ferrugineum*, the most divergent of the four taxa within sect. *Papilloprotium*, is sister to the other three species. The two taxa restricted to low-canopy white-sand forests, *P. reticulatum* and the new *P. alvarezianum*, are sister to each other, and their common ancestor is sister to *P. subserratum*. Within *P. subserratum*, Peruvian Amazonian specimens are sister to the clade that is composed of the eastern specimens collected in French Guiana and Guyana, showing some amount of phylogeographic structure among populations across the continent. However, individuals from “morphotype 1” are nested within a grouping that includes individuals categorized as “morphotype 2” and “morphotype 3.” Therefore, these three morphotypes do not form monophyletic clades, consistent with the hypothesis that they do not warrant taxonomic status without more comprehensive sampling.

DISCUSSION

Intrafamilial classification of the Burseraceae is approaching resolution (e.g. Thulin et al. 2008), although some groupings of genera based on molecular phylogenies obtained to date are difficult to justify on morphological grounds (Daly et al. 2011). Tribe Protieae (*Protium*, *Tetragastris*, *Crepidospermum*; e.g. Daly 1989) has survived intact despite rather drastic realignments in the rest of the family (e.g. Weeks et al. 2005), but it is clear that final resolution of generic limits in Protieae will require accessing DNA material of several as yet unsampled lineages. Still, it is remarkable that a number of

TABLE 3. Morphological variants of *Protium subserratum* and their geographic distributions.

Character	morphotype 1	morphotype 2	morphotype 3	morphotype 4
Leaflet texture	chartaceous	coriaceous	coriaceous	markedly coriaceous
Leaflet margin	entire	teeth usually present	entire	entire
Abaxial tertiaries	impressed	raised	raised	raised
Abaxial color	(greenish) brown	usually brown	usually whitish, less often reddish	reddish
Adaxial surface	often glossy	dull	dull	dull
Inflorescence secondary axes	often well-developed	sometimes well-developed	poorly-developed	well-developed
Fruit apex	acuminate	acuminate	acute to acuminate	rounded or rounded-acuminate
Distribution	Brazil: Amapá, Maranhão, N Pará (except Rio Trombetas) French Guiana	Brazil: Acre, Amazonas (most), Rondônia; Colombia: Antioquia Ecuador: Napo, Santiago-Zamora Guyana Peru: Maynas, San Martín	Brazil: N Amazonas Colombia: Amazonas Peru: Loreto, Ucayali Venezuela: Amazonas	Colombia: Amazonas, Caquetá
Voucher	<i>Daly et al. 3764</i> (MG, NY)	<i>Palacios et al. 999</i> (MO, NY)	<i>Clark 6672</i> (MO, NY)	<i>Restrepo & Matapi 365</i> (COAH, NY)

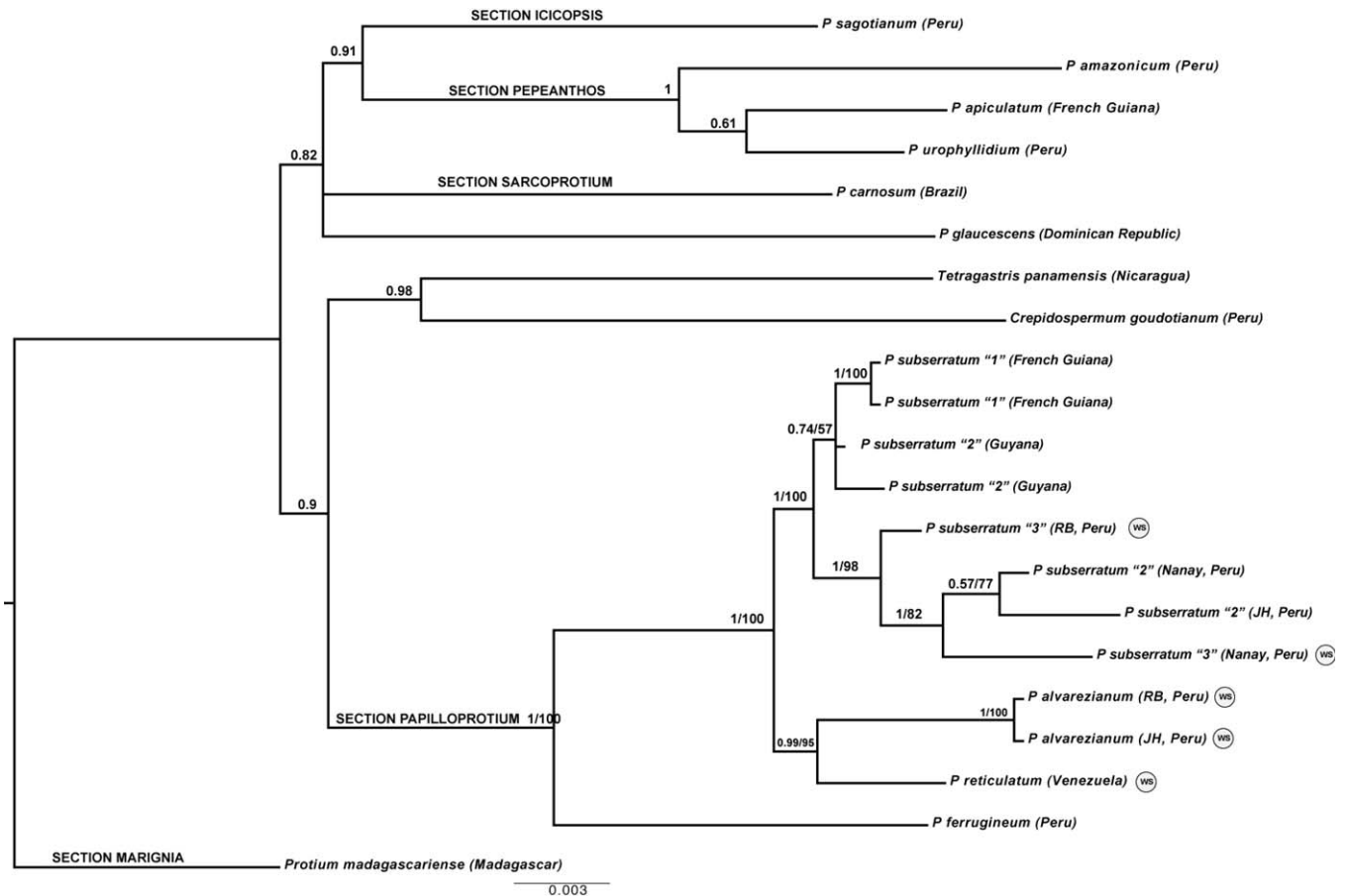


FIG. 5. Phylogeny of *Protium* sect. *Papilloprotium* based on two chloroplast and three nuclear genes. Numbers at nodes correspond to Bayesian posterior probabilities/RAxML bootstrap support. RAxML topology of outgroups was slightly different than the Bayesian tree, so only Bayesian posterior probabilities are listed for the outgroup relationships. Scale bar represents number of substitutions per site. Taxa from white-sand forest habitat are indicated by "ws" inside the shaded circles. JH = Jenaro Herrera, RB = Río Blanco, Nanay = Nanay River basin. See Appendix 1 for more detailed locality information.

groups within *Protium* proposed as "natural" based on morphological evidence have been well-supported in molecular phylogenies (Fine et al. 2005); these include the neotropical sections *Icicopsis* (Daly 1989), *Sarcoprotium* (Daly 1992), and *Pepeanthos* (Daly 2007), plus African *Marignia*, and Asian *Protium* (Harley and Daly 1996), and now *Papilloprotium*.

Tetragastris and *Crepidospermum* are supported as distinct clades, although current evidence indicates they are nested within *Protium* (Fine et al. 2005; see Fig. 5). Characters almost unique to *Tetragastris* in Proteieae include petals fused at least half their length and the anther base entire (not sagittate) in staminate flowers; the lack of lateral pulvinuli is unusual but not unique. The only character state unique to *Crepidospermum* in the tribe is the total lack of pulvinuli; characteristics rare elsewhere in the tribe include the presence of snail-shaped glands on most surfaces, flowers sometimes haplostemonous, and the cotyledons plano-convex and U- or J-shaped. Further analysis will be required to determine if these two genera should be subsumed within a more broadly defined *Protium*, perhaps as distinct sections.

Edaphic specialization has been implicated as a major contributor to the Neotropical flora (Gentry 1989). Fine et al. (2005) found that a great majority of Proteieae in the Peruvian Amazon were restricted to a subset of edaphic habitats available in the region. Two of the four species in section *Papilloprotium*, *P. alvarezianum* and *P. reticulatum*, are restricted

to rare, physiologically stressful, white-sand habitats on sites that are extremely nutrient-poor and often poorly drained due to a perched water table. Moreover, these are commonly small habitat islands often separated from similar habitats by hundreds (sometimes many hundreds) of kilometers.

The phylogenetic results, which indicate that *P. alvarezianum* and *P. reticulatum* are closest relatives, suggest that in the past the common ancestors became separated geographically, likely somewhere close to the vertex of Venezuela, Brazil, and Colombia in the upper Río Negro basin (Fig. 3). *Protium reticulatum* is found only in this area, while *P. alvarezianum* has a distribution ranging into Brazil and into Peru as far west as the Río Morona, but always in white-sand forests. Possible vicariant fragmentation of white-sand habitats in the last several million years in the western Amazon (Frasier et al. 2008) may have separated ancestors of *P. alvarezianum* and *P. reticulatum*, leading to an instance of allopatric speciation between white-sand islands. An alternative to this latter scenario is a long-distance dispersal event by ancestors of *P. alvarezianum* to white-sand forests to the west, initiating the speciation process that split this lineage within section *Papilloprotium*.

The other two species, *P. ferrugineum* and *P. subserratum*, have been collected in a variety of edaphic habitat types. As noted above, *P. subserratum* includes four main morphotypes, one of which is found only in white-sand forests. Interestingly, the phylogenetic results indicate that this

white-sand morphotype does not derive from the most basal nodes within the taxon, but instead appears to be derived from common ancestors that likely inhabited clay or brown-sand forests. Additional sampling is needed to further investigate the role of edaphic heterogeneity in driving morphological evolution within this species.

It is striking that colonization of white-sand forests has occurred at least twice in this small clade of four species: once in the common ancestor of *P. alvarezianum* and *P. reticulatum*, and again within *P. subserratum*. It is interesting to note that *P. ferrugineum* is only rarely found in white-sand forests, being much more common in clay or brown sand soils, even though it is sister to the other three species of the section. This suggests that colonization of white-sand forests has been a recent phenomenon for this section relative to the long history of the Proteieae in the Amazon basin. This is curious, given the ancient presence of white sands in the region (Räsänen et al. 1987; Hoorn 1993; Hoorn 1994; Huber 1995; Struwe et al. 1997). Phylogenetic studies of other Amazonian angiosperm clades that include white-sand specialists have found the reverse pattern, with white-sand specialists appearing at a basal position within a clade and therefore likely representing the most ancient species, as in *Potalia* (Gentianaceae; Frasier et al. 2008).

The phylogenetic results suggest that diversification within this part of tribe Proteieae has been promoted in two ways: vicariance or long-distance dispersal, and habitat shifts. First, the likely fragmentation of white-sand habitats in the last several million years in the western Amazon would have increased the chances for allopatric speciation to occur between white-sand islands, sundering *P. reticulatum* from *P. alvarezianum*. Second, coupled with the tribe's remarkable tolerance of a variety of different substrates is a proclivity for subsequent edaphic specialization, as it appears has happened two times just in this small group of four species, notably within *P. subserratum*. Such examples highlight the importance of the edaphic heterogeneity of the Amazon in the diversification processes of its extraordinarily diverse flora.

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LITERATURE CITED

- Anderson, A. B. 1981. White-sand vegetation of Brazilian Amazonia. *Biotropica* 13: 199–210.
- Baldwin, B. G. and S. Markos. 1998. Phylogenetic utility of the external transcribed spacer (ETS) of 18S-26S rDNA: congruence of ETS and ITS trees of *Calycadenia* (Compositae). *Molecular Phylogenetics and Evolution* 10: 449–463.
- Campbell, D. G., J. L. Stone, and A. Rosas Jr. 1992. A comparison of the phytosociology and dynamics of three floodplain (*várzea*) forests of known ages, Rio Juruá, western Brazilian Amazon. *Botanical Journal of the Linnean Society* 108: 213–237.
- Clayton, J. W., E. S. Fernando, P. S. Soltis, and D. E. Soltis. 2007. Molecular phylogeny of the tree-of-heaven family (Simaroubaceae) based on chloroplast and nuclear markers. *International Journal of Plant Sciences* 168: 1325–1339.
- Daly, D. C. 1989. Studies in Neotropical Burseraceae II. Generic limits in Neotropical Proteieae and Canarieae. *Brittonia* 41: 17–27.
- Daly, D. C. 1992. New taxa and combinations in *Protium* Burm. f. Studies in Neotropical Burseraceae VI. *Brittonia* 44: 280–299.
- Daly, D. C. 2007. A new section of *Protium* Burm. f. from the Neotropics. Studies in Neotropical Burseraceae XIV. *Brittonia* 59: 1–24.
- Daly, D. C., M. C. Martínez-Habibe, A. Weeks, and M. M. Harley. 2011. Burseraceae. Pp. 76–104 in *The families and genera of vascular plants*, ed. K. Kubitzki. New York: Springer-Verlag.
- Farris, J. S., M. Källersjö, A. G. Kluge, and C. Bult. 1995. Testing significance of incongruence. *Cladistics* 10: 315–319.
- Fine, P. V. A., D. C. Daly, F. G. Villa M., I. Mesones A., and K. M. Cameron. 2005. The contribution of edaphic heterogeneity to the evolution and diversity of Burseraceae trees in the Western Amazon. *Evolution* 29: 1464–1478.
- Fine, P. V. A., F. Zapata, D. C. Daly, T. M. Misiewicz, I. Mesones, H. F. Cooper, and C. E. A. Barbosa. In press. The importance of environmental heterogeneity and spatial distance in generating phylogeographic structure in edaphic specialist and generalist species of *Protium* (Burseraceae) across the Amazon basin. *Journal of Biogeography*.
- Fine, P. V. A., R. García-Villacorta, N. C. A. Pitman, I. Mesones, and S. W. Kembel. 2010. A floristic study of the white-sand forests of Peru. *Annals of the Missouri Botanical Garden* 97: 283–305.
- Foster, R. B. 1990. The floristic composition of the Río Manu floodplain forest. Pp. 99–111 in *Four Neotropical rainforests*, ed. A. H. Gentry. New Haven: Yale University Press.
- Frasier, C. L., V. A. Albert, and L. Struwe. 2008. Amazonian lowland, white sand areas as ancestral regions for South American biodiversity: biogeographic and phylogenetic patterns in *Potalia* (Angiospermae: Gentianaceae). *Organisms, Diversity & Evolution* 8: 44–57.
- Gentry, A. H. 1989. Speciation in tropical forests. Pp. 113–134 in *Tropical forests: botanical dynamics, speciation, and diversity*, eds. L. Holm-Nielsen and H. Balslev. London: Academic Press.
- Guillaumet, J.-L. 1987. Some structural and floristic aspects of the forest. *Experientia* 43: 241–251.
- Harley, M. M. and D. C. Daly. 1996. Burseraceae-Proteieae. *World Pollen and Spore Flora* 20: 1–44.
- Hoorn, C. 1993. Marine incursions and the influence of Andean tectonics on the Miocene depositional history of northwestern Amazonia: results of a palynostratigraphic study. *Palaeogeography, Palaeoclimatology, Palaeoecology* 105: 267–309.
- Hoorn, C. 1994. An environmental reconstruction of the palaeo-Amazon river system (Middle-Late Miocene, NW Amazonia). *Palaeogeography, Palaeoclimatology, Palaeoecology* 112: 187–238.
- Huber, O. 1995. Geographical and physical features. Pp. 1–61 in *Flora of the Venezuelan Guayana vol. 1*, eds. P. E. Berry, B. K. Holst, and K. Yatskiyevich. St. Louis and Portland: Missouri Botanical Garden Press and Timber Press.
- Huelsenbeck, J. and F. R. Ronquist. 2001. MRBAYES: bayesian inference of phylogenetic trees. *Bioinformatics* 17: 745–755.
- Lima Filho, D. A., F. D. A. Matos, I. L. Amaral, J. Revilla, L. S. Coêlho, J. F. Ramos, and J. L. Santos. 2001. Inventário florístico de floresta ombrófila densa de terra firme, na região do Rio Urucu-Amazonas, Brasil. *Acta Amazonica* 31: 565–579.
- Lisboa, P. L. B. 1989. Estudo florístico da vegetação arbórea de uma floresta secundária, em Rondônia. *Boletim do Museu Paraense Emílio Goeldi. Botânica* 5: 145–162.
- Macedo, M. 1977. Dispersão de plantas lenhosas de uma campina Amazônica. *Acta Amazonica* 7 Suplemento: 1–69.
- Macedo, M. and G. T. Prance. 1978. Notes on the vegetation of Amazonia II. The dispersal of plants in Amazonian white sand campinas: the campinas as functional islands. *Brittonia* 30: 203–215.
- Maddison, D. R. and W. P. Maddison. 2002. MacClade 4.05: Analysis of phylogeny and character evolution. Version 4.05. Sunderland: Sinauer.
- Matos, F. D. A. and I. L. Amaral. 1999. Análise ecológica de um hectare em floresta ombrófila densa de terra-firme, Estrada da Várzea, Amazonas, Brasil. *Acta Amazonica* 29: 365–379.
- Nylander, J. A. A. 2004. MrModeltest v2. Uppsala: Program distributed by the author. Evolutionary Biology Centre, Uppsala University.
- Oxelman, B., M. Liden, and D. Berglund. 1997. Chloroplast *rps16* intron phylogeny of the tribe Sileneae (Caryophyllaceae). *Plant Systematics and Evolution* 206: 393–410.
- Rankin-de-Merona, J. M., G. T. Prance, R. W. Hutching, M. F. Silva, W. A. Rodrigues, and M. E. Uehling. 1992. Preliminary results of a large-scale tree inventory of upland rain forest in the central Amazon. *Acta Amazonica* 22: 493–534.
- Räsänen, M. E., J. Salo, and R. J. Kalliola. 1987. Fluvial perturbation in the Western Amazon basin: regulation by long-term sub-Andean tectonics. *Science* 238: 1398–1401.

- Rollet, B., C. Högermann, and I. Roth. 1990. *Stratification of tropical forests as seen in leaf structure*. Dordrecht/Boston/London: Kluwer Academic Publishers.
- Stamatakis, A., M. Ott, and T. Ludwig. 2005. RAxML-OMP: an efficient program for phylogenetic inference on SMPs'. In Proceedings of 8th International Conference on Parallel Computing Technologies (PaCT2005). *Lecture Notes in Computer Science* 3506: 288–302.
- Stamatakis, A., P. Hoover, and J. Rougemont. 2008. A fast bootstrapping algorithm for the RAxML Web-servers. *Systematic Biology* 57: 758–771.
- Struwe, L., P. Maas, and V. Albert. 1997. *Aripuana cullmaniorum*, a new genus and species of Gentianaceae from white sands of southeastern Amazonas, Brazil. *Harvard Papers in Botany* 2: 235–253.
- Swart, J. J. 1942. *A monograph of the genus Protium and some allied genera (Burseraceae)*. Gouda: Drukkerij Koch en Knuttel.
- Taberlet, P., L. Gielly, G. Pautou, and J. Bouvet. 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. *Plant Molecular Biology* 17: 1105–1109.
- Thulin, M., B. A. Beier, S. G. Razafimandimbison, and H. I. Banks. 2008. *Ambilobeia*, a new genus from Madagascar, the position of *Aucoumea*, and comments on the tribal classification of the frankincense and myrrh family. *Nordic Journal of Botany* 26: 218–229.
- Tuomisto, H., K. Ruokolainen, R. Kalliola, A. Linna, W. Danjoy, and Z. Rodriguez. 1995. Dissecting Amazonian biodiversity. *Science* 269: 63–66.
- Weeks, A., D. C. Daly, and B. B. Simpson. 2005. The phylogenetic history and historical biogeography of the frankincense and myrrh family (Burseraceae) based on nuclear and chloroplast sequence data. *Molecular Phylogenetics and Evolution* 35: 85–101.
- Young, K. R. and B. León. 1989. Pteridophyte species diversity in the central Peruvian Amazon: importance of edaphic specialization. *Brittonia* 41: 388–395.
- APPENDIX 1. Information concerning voucher specimens used for molecular phylogenetic analyses, presented in the following sequence: taxon (arranged alphabetically), collector and collection number, (herbarium where voucher is housed using standard acronyms of Index Herbariorum), date collected, locality and GenBank accession numbers (ETS, ITS1, ITS2, *rps16*, *trnL-F*, and *phyC*). “—” indicates a missing sequence.
- Crepidospermum goudotianum* (Tul.) Triana & Planch., *Fine et al.* 959 (NY), June 2002, Allpahuayo-Mishana National Reserve, Peru: HQ65568, HQ655703, HQ655723, HQ655762, HQ655775, HQ655784.
- Protium alvarezianum* Daly & P. Fine, *Fine et al.* 1207 (UC), May 2005, near Ungurahuillo, Río Blanco, Dist. Curinga, Requena, Loreto, Peru: HQ655690, HQ655714, HQ655726, HQ655751, HQ655766, HQ655786; *Dávila* 5949 (UC), 11 Nov 2006, white-sand forest along carretera near the Centro de Investigación Jenaro Herrera, Peru: HQ655689, HQ655713, HQ655725, HQ655752, HQ655765, HQ655785. *Protium amazonicum* (Cuatrec.) Daly, *Daly* 10960 (NY), Brazil: HQ655684, HQ655707, HQ655737, HQ655749, HQ655778, HQ655787. *Protium apiculatum* Swart, *Fine* 1368 (UC), 11 Jul 2006, Paracou, French Guiana: HQ655685, HQ655709, HQ655738, HQ655748, HQ655779, HQ655788. *Protium carnosum* A. C. Sm., *Daly* 12811 (NY), 23 Mar 2005, Acre, Brazil: HQ655701, HQ655705, HQ655736, HQ655760, HQ655782, HQ655789. *Protium ferrugineum* (Engl.) Engl., *Fine et al.* 953 (NY), June 2002, Allpahuayo-Mishana National Reserve, Peru: HQ655688, HQ655711, HQ655724, HQ655746, HQ655764, HQ655790. *Protium glaucescens* Urban, *Martínez* 2292 (NY), 13 Sep 2008, Sierra del Batoruco, Sección La Filipina, Municipio La Ciénaga, Provincia Barahona, Dominican Republic: HQ655682, HQ655708, HQ655741, HQ655761, HQ655783, HQ655791. *Protium madagascariense* Engl., *Daly* 12982 (NY), 12 Jan 2006, Madagascar: HQ655700, HQ655704, HQ655716, HQ655731, HQ655776, HQ655792. *Protium reticulatum* (Engl.) Engl., *Clark* 6871 (NY), 8 Oct 1978, San Carlos del Río Negro, Venezuela: HQ655691, HQ655712, —, HQ655750, —, HQ655794. *Protium sagotianum* Marchand, *Daly* 12163 (NY), 10 Apr 2003, Brazil: HQ655687, HQ655702, HQ655716, HQ655758, HQ655780, HQ655793. *Protium subserratum* (Engl.) Engl., “morphotype 1”, *Fine* 1378 (UC), 11 July 2006, Paracou, French Guiana: HQ655694, HQ655715, HQ655730, HQ655753, HQ655767, HQ655795; *Fine* 1380 (UC), 12 July 2006, Paracou, French Guiana: HQ655695, HQ655716, HQ655731, HQ655754, HQ655768, HQ655796. *Protium subserratum*, “morphotype 2”, *Fine* 1272 (UC), July 2005, Ireng River, Guyana: HQ655696, HQ655717, HQ655733, HQ655755, HQ655770, HQ655799; *Fine* 1275 (UC), July 2005, Ireng River, Guyana: HQ655697, HQ655718, HQ655727, HQ655756, HQ655771, HQ655800; *Mesones* 1066 (UC), October 2006, near the community of Lagunas, Río Nanay, Peru: HQ655693, HQ655720, HQ655732, HQ655759, HQ655772, HQ655798; *Dávila* 5960 (UC), 28 Nov 2006, Arboretum, Centro de Investigación Jenaro Herrera, Peru: HQ655692, HQ655719, HQ655728, HQ655744, HQ655769, HQ655797. *Protium subserratum*, “morphotype 3”, *Fine et al.* 1207 (UC), Ungurahuillo, Río Blanco, Dist. Curinga, Loreto, Peru: HQ655698, HQ655721, HQ655729, HQ655757, HQ655773, HQ655801; *Mesones* 1014 (UC), June 2006, Allpahuayo-Mishana National Reserve, Peru: HQ655699, HQ655722, HQ655734, HQ655743, HQ655774, HQ655802. *Protium urophyllidium* Daly, *Dávila et al.* 958 (NY), October 2004, Matsés National Reserve, Peru: HQ655683, HQ655710, HQ655739, HQ655747, HQ655777, HQ655803.
- Tetragastris panamensis* (Engl.) Kuntze, *de la Cerda et al.* 4523 (UC), Río Kukra, Bluefields, Nicaragua: HQ655681, HQ655706, HQ655735, HQ655745, HQ655781, HQ655804.