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Notes on Bursera in South America, including a new species. Studies in Neotropical Burseraceae VII

Douglas C. Daly

Daly, Douglas C. (New York Botanical Garden, Bronx, NY 10458-5126, U.S.A.). Notes on *Bursera* in South America, including a new species. Studies in Neotropical Burseraceae VII. Brittonia 45: 240–246. 1993.—**Bursera inversa** is the first new species of the genus to be described from South America in 90 years. The ecology of this species is remarkable because it is a large (to 25 m × 40 cm or greater) canopy tree of primary moist to wet lowland forest. It is easily distinguished from its congeners by its large, obovoid fruits and bony pyrene. A key to the South American species of *Bursera* is provided.

Key words: Burseraceae, Bursera, South American flora.

Bursera Jacq. is a New World genus of some 100 species (Rzedowski & Guevara-Féfer, 1992). Like most of the tribe Bursereae, this group is characteristically found in semi-humid and (semi-)arid habitats. About 70 species of Bursera are endemic to Mexico, where it dominates much of the tropical deciduous forests, not only in terms of relative density but also of relative diversity (Rzedowski, 1986). Four or five of the 13odd Central American species are also found in Mexico. Another secondary center of diversity and endemism is the West Indies, where perhaps all but two of the approximately 14 species occurring there are endemic.

The family Burseraceae as a whole presents several challenges to the systematist. Most of the taxa are dioecious; the small, actinomorphic, usually green flowers often differ only subtly among species of a given genus; and flowering material is scarce or lacking for many taxa because the flowers are difficult to see in the larger trees. In several genera, sympatry of closely related species frequently occurs. Chromosome counts are hard to obtain because there is resin in the developing anthers and because the seeds have short viability, making it difficult to collect them for germination and make subsequent counts from roots.

The genus Bursera L. heaps additional complicating factors on top of these. Bark characters can be taxonomically useful, but bark material is rarely collected and even observations on bark characters are infrequently noted on herbarium labels. Most if not all species of this group are deciduous, and typically they flower in the leafless state. thus making it extraordinarily difficult to match flowering and fruiting material. Flowers may be hermaphrodite or functionally staminate or pistillate, and the number of flower parts can differ depending on the gender of the flower as well as the subgenus to which the species belongs. The form of the fleshy, brightly-colored arillate structure that partially or completely envelops the pyrene is taxonomically useful, but the pseudaril is at least as attractive to animals as it is to taxonomists, thus it is difficult to obtain specimens with mature fruits as well as intact pseudarils. Thereafter, ants and herbarium pests are inclined to eat the pseudarils as well. Hybridization appears to be frequent in Bursera (e.g., Bullock, 1936; McVaugh & Rzedowski, 1965), in some cases producing species of hybrid origin (e.g., Rzedowski & Ortíz, 1988). The two taxa in the genus most recently described from South America were B. graveolens (Jacq.) Triana & Planch. var. villosula

Cuatrec. and *B. tomentosa* (Jacq.) Triana & Planch. var. *pubescens* Cuatrec., both of which Cuatrecasas (1957) believed to have arisen from hybridization between *B. graveolens* and *B. tomentosa*.

Adequate study of Bursera requires collections of the species throughout their ranges and a great deal of fieldwork, including repeated visits to individuals as well as intensive studies of populations. A thorough understanding of the genus is attainable thanks principally to the numerous Mexican collections of George Hinton, the fine earlier efforts of Rose (1911) and Bullock (e.g., 1936) that laid the foundation for the more detailed work of McVaugh and Rzedowski (1965), and subsequent research by Rzedowski and other excellent Mexican botanists (e.g., Rzedowski & Kruse, 1979; Rzedowski & Guevara-Féfer, 1992; Toledo, 1984). Gillett (1980), through his comprehensive knowledge of the closely allied genus Commiphora, clarified the generic and subgeneric limits of Bursera.

The Bursera simaruba Complex

Three groups of species in Bursera have thwarted traditional alpha-taxonomic approaches and need special attention (Rzedowski, pers. comm.). The Bursera fagaroides (H.B.K.) Engl. and B. excelsa (H.B.K.) Engl. complexes are prone to hybridize, and they present a series of localized taxonomic problems in Mexico. The B. simaruba (L.) Sarg. complex is far more widespread, ranging from Mexico through Central America into northern South America and throughout the Antilles. Many of the taxa in this complex are seriously under-collected, and the existing collections (usually incomplete) are scattered among herbaria in Mexico, Europe, and the United States. The type of B. simaruba (plate 199 of Sloane's catalog at BM) is from Jamaica.

The species that appear to belong in the *B. simaruba* complex are listed in Appendix I, along with their overall distributions and principal synonymies. These species belong to subgenus *Bursera* because they have threevalved fruits and a red, brown, or yellowish outer bark that is shed in thin, papery plates.

The complex in question consists essentially of those species with relatively large (>5 cm long), ovate to broadly elliptic, entire leaflets. It does not include a group of closely-related Greater Antillean species exemplified by *B. inaguensis* Britton that is characterized by leaflets that are coriaceous, usually glaucous, narrowly elliptic to narrowly lanceolate and usually less than 5 cm long.

In addition to the geographic considerations that have made it difficult for the Mexican specialists in the genus to resolve the taxonomy of the B. simaruba complex, many of the characters previously used to distinguish the component species can be unreliable. Virtually all of the literature overemphasizes the amount of pubescence on the leaf rachis and leaflet blades. Other characters that are often inconsistent include shape of the leaflet apex; prominence of venation; and leaflet base shape. Fruit shape and size, which can vary somewhat, can be diagnostic in just a few cases. Pubescence on the ovary and fruit serves to distinguish only B. grandifolia Engl. from the rest of the complex (assuming it includes B. permollis Standl. & Steverm.). Bark color appears to be a useful character, but it is described infrequently on herbarium labels. The length of the lateral petiolules is often rather variable in the B. simaruba complex, and even in B. grandifolia, for which subsessile lateral leaflets was used as a diagnostic character (e.g., McVaugh & Rzedowski, 1965). The range of the number of leaflets can help separate species, but it must be based on a large sample. This is also true of the range of petiol(ul)e and inflorescence lengths.

Species concepts in this complex have diverged greatly among taxonomic treatments. For example, Standley (1923) considered Terebinthus acuminata Rose, Bursera arborea (Rose) Riley, B. attenuata (Rose) Riley, and B. ovalifolia Engl. to be synonyms of B. simaruba (as Elaphrium, which has priority although Bursera is conserved). Bullock (1936) maintained B. arborea, considered B. attenuata a species dubia due to poor type material, and placed T. acuminata under B. ovalifolia while noting that the latter differs from B. simaruba

by only minor characters. McVaugh and Rzedowski (1965) maintained B. arborea and tentatively placed T. acuminata under B. attenuata; they concluded that although B. attenuata was probably conspecific with B. ovalifolia, the evidence of the latter's identity (a type in Berlin seen by Bullock but later destroyed) was probably not adequate to maintain the name. They referred a number of specimens of 10-20 m trees from "barranca" forests of the Mexican Pacific lowlands to "B. aff. simarubae," although they remarked that some of the Mexican populations differ from typical West Indian B. simaruba by only trivial characters.

During an expedition to northern Antioquia, Colombia, I encountered a single population of several individuals of an unusually tall Bursera with large, obovoid fruits. Subsequent work at NY confirmed that this is a new species and revealed two additional collections, one with poor locality data and one in a region that apparently has since been deforested. Because it has not been possible to re-visit the type locality due to political unrest in the region, the new species is described here from fruiting material only. I am giving provisional recognition to B. malacophylla B. L. Robinson, described in 1902 from Galápagos Islands, as distinct from B. graveolens in this paper. Bursera howellii Standl. & Steyerm. was published more recently, but is clearly a taxonomic synonym of B. glabra (Jacq.) Tr. & Pl. The species described below, therefore, is the first new species of Bursera from South America in more than 90 years.

Bursera (subgenus Bursera) **inversa** Daly, sp. nov. (Fig. 1)

Type: COLOMBIA. Antioquia: Mun. Carepa, 45 km S of Turbo on Turbo-Mutatá road, Reserva Forestal Tulenapa (ICA), 7°50'N, 77°40'W, 31 Jul 1987 (fr), D. C. Daly, R. Callejas P., W. Thomas, J. Betancur & O. Marulandia 5414 (HOLOTYPE: NY; ISOTYPES, AAU, COL, HUA, IEB, K, MEXU, MO, US, VEN).

Arbor rarior silvis humidis prope oras Caribaeas Venezuelae Colombiae et Panamae incola; a caeteris con-

generibus fructu grandi obovoideo et pyrena crassa ossea facile distinguitur.

Canopy tree, reproductive height to at least 25 m \times 40 cm, with low plank buttresses. Bark green tinged with red, thin, smooth, shed in papery sheets or thin plates, inner bark off-white, spongy, fibrous. Sap watery (although milky resin present in fruits). Trichomes: slender, multicellular, curly to suberect, 0.1–0.4 mm long. Branchlets robust. Leaves 3-6-jugate, 12-40 cm long; petiole terete, 5.1–14.5 cm long, longer than interjuga, these 2.7-4.3 cm long and not winged; petiolules 1-canaliculate, relatively short and robust, 1-6 mm long, petiol(ul)es and interjuga densely pubescent; leaflets chartaceous, drying blackish-brown above, brown beneath, the basal ones obliquely ovate, $7.6-8 \times 3.5-3.9$ cm, the other laterals lanceolate to obliquely oblong, $9.5-12.8 \times 3.8-4.2$ cm, all laterals with asymmetric base, with proximal side acute and distal side truncate to slightly cordate. the terminal leaflet (broadly) elliptic, 9–10 \times 4.1–4.5 cm, drying almost black, acute at base, all leaflets with entire margin and contracted at apex to a relatively long and narrow acumen 1-1.8 cm long, on both surfaces the midvein pubescence dense, becoming sparse to scattered on higher-order veins, the veins prominent to prominulous abaxially, prominulous adaxially. *Inflores*cences solitary, paniculate, $4-13 \text{ cm} \times 1.7-$ 2.8 mm, sometimes reaching basal leaflet, the secondary axes poorly developed, all axes densely pubescent, the bracts and bracteoles semi-clasping. Flowers unknown except staminodes (persistent at some fruit bases of Daly et al. 5314) 1.15 mm long, the rudimentary anthers essentially lanceolate with lobulate base and truncate apex, dorsifixed, 0.8 mm long. Fruiting pedicel terete, 2–6 mm \times 1.6–2.5 mm; *fruit* dark green to brown at maturity, $1.5-1.7 \times 1-1.2$ cm, obliquely obovoid with three shallow vertical sulci when fresh, the ovary sessile (not stipitate), at base obtuse to acute, at apex obtuse to rounded, surface smooth, glabrous, drying wrinkled; pseudaril (arillate structure on pyrene) thin, red; pyrene obliquely obovoid, $1.3-1.4 \times 1-1.1$ cm, vertically striate and somewhat pitted on surface, very thick and

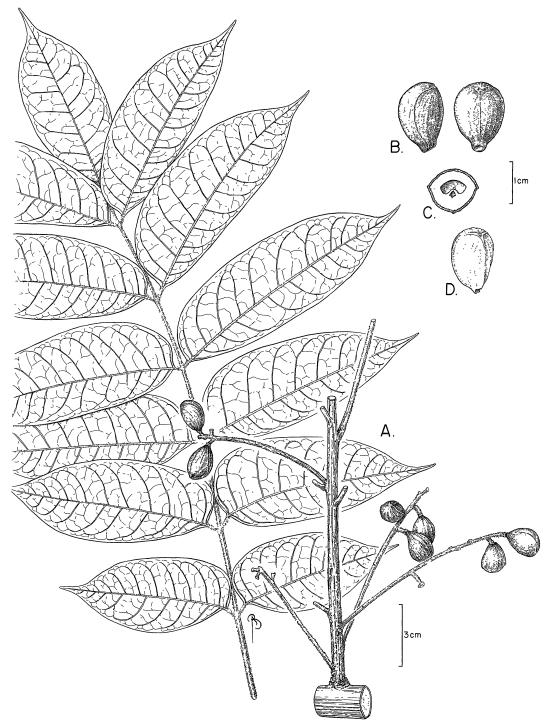


Fig. 1. Bursera inversa Daly (Daly et al. 5314). A. Fruiting branchlet. B. Fruit in lateral and in dorsiventral view, showing obovate shape and the sulci defining the three valves. C. Transverse section of fruit, showing bony pyrene and one of two aborted locules. D. Pyrene, showing pitted surface.

bony, 3-locular but only one locule developing; mature *seeds* unknown.

Distribution and ecology: Colombia (N Antioquia); Panama (Darién); Venezuela (W Zulia). Although the three known collections of this species are from three different countries, its distribution is somewhat restricted in the northwest corner of South America, including the Darién Peninsula of Panama. Ecologically, it is interesting to see that Bursera, which characteristically is a genus of small trees or even shrubs through most of its range, has adapted to several habitats with abundant available water. Bursera standleyana L. O. Wms. & Cuatrec. is an epiphytic tree in lower montane vegetation of the Osa Peninsula of Costa Rica (Williams & Cuatrecasas, 1959), while B. *inversa* is a canopy tree of primary moist to wet lowland forest in a few discrete subcoastal areas of South America near the Caribbean.

Other specimens examined: PANAMA. Darién: Rio Pirre, near town of Pirre, 27 Dec 1972, Gentry & A. Clewell 6915 (NY).

VENEZUELA. **Zulia**: Hacienda Raizudo (Hda. San Benito), approx. 1 km S of Concha, 14 Dec 1967, *Bunting 2785* (F).

Bursera inversa is easily distinguished within the genus by its large, obovate fruits; thick, bony pyrene; and pitted pyrene surface. All of its congeners have ellipsoid to ovoid fruits and thinner, smooth-surfaced pyrenes.

Bursera in South America

Seven species of *Bursera*, including representatives of both subgenera, are recognized here to occur in South America. All of them are found north of the Rio Amazonas (see Appendix II) and, with the exception of *B. inversa*, in (semi-)deciduous vegetation and seasonally very dry climates. Three other species accepted by Engler—*B. leptophloeos* Mart., *B. orinocensis* Engl., and *B. martiana* Engl.—are excluded because the former has been transferred to *Commiphora* (Gillett, 1980) and the other two are treated here as taxonomic synonyms of *C. leptophloeos* (Mart.) Gillett.

I have not seen enough material of B. malacophylla to determine whether it is distinct from B. graveolens, so it is maintained here and I have borrowed from Porter's (1971) work that couplet in the key below. The characters that he used to separate these two species are not strong, and I am uncertain as to what constitutes a "pubescent aril," which is not apparent on the few fruiting specimens I have seen (e.g., Wheeler et al. 64, determined by Porter). I am not aware of such a character elsewhere in the Burseraceae. The endocarp of a number of Protium species is provided with a dense hygroscopic layer of fibers that is overlain by the pseudaril (Daly, 1987, 1989), but this character is not homologous to a pubescent aril.

Key to the species of *Bursera* in South America

1 Outer bark papery and peeling; leaf rachis exalate; leaflets entire; flowers glabrous; fruits tri-valved (subgen. Bursera). 2 Leaves 0-1 (2)-jugate, the lateral petiolules 0-2 (3) mm long, the leaflets broadly ovate, the apex obtuse to very broadly short-acuminate; fruiting pedicels usually recurved _______B. karsteniana Engl. 2 Leaves (1) 2-6-jugate, the lateral petiolules (2) 3-8 mm long, the leaflets lanceolate to ovate, the apex acuminate; fruiting pedicels straight. 3 Fruits ovoid to ellipsoid, 10-13 mm long, the pyrene cartilaginous _______B. simaruba (L.) Sarg. 3 Fruits obovoid, 15-17 mm long, the pyrene bony 1 Outer bark close (not papery or peeling); leaf rachis alate; leaflets crenate or serrate; at least some part of flower pubescent; fruits bivalved (subgen. *Elaphrium*). 4 Leaves 3-11 cm long, the leaflet margin 2-4-lobulate on each side only on distal half. B. glabra (Jacq.) Triana & Planch. 4 Leaves 5-25 cm long, the leaflet margin rounded- or acute-dentate from base to apex. 5 Leaves 2-6-jugate; sepals lanceolate to linear, more than half the length of the petals; fruit 6-10 B. tomentosa (Jacq.) Triana & Planch. 5 Leaves (1) 2-3-jugate; sepals deltate to triangular, less than half the length of the petals; fruit 8-12 mm

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Appendix I

DISTRIBUTIONS OF THE Bursera simaruba Complex

Bursera ovalifolia Engl. [syn.: Terebinthus acuminata Rose?]. MEXICO: Jalisco, México, Michoacán, Nayarit, Zacatecas.

Bursera aromatica Proctor. JAMAICA.

Bursera arborea (Rose) Riley. MEXICO: Colima, Durango, Michoacán, Nayarit, Oaxaca, Sinaloa.

Bursera attenuata (Rose) Riley. MEXICO: México, Nayarit, Sinaloa.

Bursera grandifolia (Schlecht.) Engl. [incl. B. cinerea Engl., B. occidentalis (Rose) Riley, ?B. permollis Standl. & Steyerm.]. MEXICO: Chiapas, Guerrero, Jalisco, México, Michoacán, Morelos, Nayarit, Oaxaca, Sinaloa, Sonora. COSTA RICA. GUATEMALA. HONDURAS. NICARAGUA.

Bursera hollickii Fawc. & Rendle. JAMAICA.

Bursera inversa Daly. PANAMA: Darién. COLOM-BIA: Antioquia. VENEZUELA: Zulia.

Bursera longipes Standl. MEXICO: Guerrero, México, Morelos, Puebla, Oaxaca.

Bursera malacophylla B. L. Robinson. ECUADOR: Galápagos.

Bursera simaruba (L.) Sarg. [incl. B. bonairensis Boldingh, B. gummifera L., B. subpubescens Engl.]. UNITED STATES: Florida. MEXICO (most states from Sinaloa and Tamaulipas south). BELIZE. COSTA RICA. EL SALVADOR. GUATEMALA. HONDURAS. NICARAGUA. PANAMA. ANTILLES (most if not all). BRAZIL: Amazonas, Roraima. COLOMBIA: Antioquia, Bolívar, Vichada, Magdalena. GUYANA. TRINIDAD. VENEZUELA: Bolívar, Zulia, Aragua, Atures, Margarita, Mérida, Falcón.

Bursera standleyana L. O. Wms. & Cuatrec. COSTA RICA.

Appendix II

DISTRIBUTIONS OF THE Bursera SPECIES KNOWN IN SOUTH AMERICA

Bursera glabra (Jacq.) Tr. & Pl. [incl. B. howellii Standl.]. COLOMBIA: Bolívar, Sta. Marta, Magdalena, Guajira. VENEZUELA: Mérida, Zulia.

Bursera graveolens (Jacq.) Tr. & Pl. [=B. penicillata (Sessé & Moc. ex DC.) Engl.?]. COSTA RICA. EL SALVADOR. GUATEMALA. HONDURAS. MEXICO: Chiapas, Tabasco, Veracruz, Yucatán. NICARAGUA. COLOMBIA: Sta. Marta, Huila, Antioquia, Magdalena, Cundinamarca. ECUADOR: Galápagos, Guayas, Loja, Manabi. PERU:

Tumbes, Cajamarca, Lambayeque, Piura. VENE-ZUELA: Mérida.

Bursera inversa Daly. PANAMA: Darién. COLOM-BIA: Antioquia. VENEZUELA: Zulia.

Bursera karsteniana Engl. CURAÇAO. COLOMBIA: Guajira. TRINIDAD. VENEZUELA: Distrito Federal, Falcón, Miranda, Sucre, Anzoátegui.

Bursera malacophylla B. L. Robinson. ECUADOR: Galápagos.

Bursera simaruba (L.) Sargent. [see Appendix I] Bursera tomentosa (Jacq.) Tr. & Pl. COSTA RICA. GUATEMALA. MEXICO: Chiapas. NICARA-GUA. BONAIRE. CURAÇAO. BRAZIL: Roraima. COLOMBIA: Boyacá, Huila, Antioquia, César, Santa Marta