

New Discoveries in the Canellaceae in the Antilles: How Phylogeny can Support Taxonomy

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Published online: 22 April 2008

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Abstract Six genera have been described in the family Canellaceae, four of them from the Neotropics and the other two from Africa and Madagascar. The Caribbean genera are *Canella*, *Pleodendron* and *Cinnamodendron*. *Canella* is a monotypic genus widespread in the region, and *Pleodendron* is present in the Greater Antilles and Costa Rica. *Cinnamodendron* occurs in the Greater Antilles (Cuba, Hispaniola, and Jamaica) as well as in South America. A recent phylogenetic analysis of the family shows that *Cinnamodendron* is not monophyletic because the South American species and the Antillean species are recovered in two different clades. The Antillean species formed a clade sister to *Pleodendron*. The synapomorphies of the Antillean species of *Cinnamodendron* are tetramerous flowers with eight petals, eight stamens, four carpels, and four placentae. Based on the results from the phylogenetic analysis major taxonomy changes are expected for the family.

Resumen Seis géneros han sido descritos en la familia Canellaceae, cuatro de estos para el neotrópico y los otros dos para Africa y Madagascar. En las Antillas se encuentran los géneros *Canella*, *Pleodendron* y *Cinamodendron*. *Canella* es un género monotípico de amplia distribución en la región del caribe y *pleodendron* se encuentra presente sólo en las antillas mayores y Costa Rica. *Cinnamodendron* ha sido dado tanto para las Antillas mayores como para America del Sur. Un análisis filogenético previo de la familia indica que el género *Cinnamodendron* no es monofilético. Existe una separación de las especies Sudamericanas y Antillanas en clados diferentes. Las especies de las Antillas forman un clado que es hermano de *Pleodendron*. Los caracteres sinapomórficos de las especies antillanas de *Cinnamodendron* son: flores tetrámeras con ocho pétalos, ocho estambres, cuatro carpelos y cuatro placentas. Basados en los resultados de la filogenia del grupo, se anticipan cambios taxonómicos para la familia.

Keywords Antilles · Canellaceae · *Canella* · *Cinnamodendron* · *Pleodendron* · Phylogeny

Taxonomic History

The Canellaceae are a small tropical plant family of aromatic trees, rarely treelets and shrubs, with a disjunct occurrence between tropical and subtropical America (the Caribbean Region, Costa Rica and South America) and Africa (Madagascar and Eastern Africa). Six genera and ca. 21 species have been traditionally recognized in this family (Cronquist, 1981; Takhtajan, 1997; Zanoni, 2004; Hammel & Zamora, 2005): *Canella* P. Browne (monotypic widespread Caribbean taxon), *Capsicodendron* Hoehne (a monotypic endemic taxon from Brazil), *Cinnamodendron* Endlicher (Greater Antilles and South America), *Pleodendron* Tieghem (Greater Antilles and Costa Rica), *Cinnamosma* Baillon (Madagascar) and *Warburgia* Engler (from Eastern and South Africa). The highest diversity of this family occurs in the Neotropics with four genera and approximately 13 species (Endlicher, 1842; Miers, 1858; van Tieghem, 1899; Urban, 1922, 1928; Uittien, 1926; Sleumer, 1936; Occhioni, 1943, 1947, 1948, 1949; Steyermark, 1952; Zanoni, 2004, Hammel & Zamora, 2005). The number of taxa has increased since new species have been discovered recently in Brazil and the Greater Antilles (Salazar, 2006). The Greater Antilles is a center of diversity and endemism for the family and has three genera (*Canella*, *Pleodendron* and *Cinnamodendron*) and seven species (Miers, 1858; van Tieghem, 1899; Urban, 1922, 1928; Fawcett & Rendle, 1926; Sleumer, 1936; León & Alain, 1953; Adams, 1972; Liogier, 1983, 1994; Bornstein, 1989; Liogier & Martorel, 2000; Zanoni, 2004).

Canellaceae species from the West Indies, specially the widespread *Canella winterana* Gaertn., are traditionally used for medicinal, fishing, aphrodisiac, ritualistic, and aromatic purposes (Salazar, 2006). Plant parts are mainly boiled for drinking and bathing, and more rarely consumed in alcohol. The bark is also grilled when used as a condiment.

Beverages prepared with these plants are consumed to treat fever with *Canella winterana* (Roig, 1991), stomach problems with *Canella winterana* and *Cinnamodendron ekmanii* Sleumer from the Dominican Republic (Salazar, 2006), pain with *Canella winterana* (Ayensu, 1981), sexual diseases such as syphilis with *Canella winterana* (Ayensu, 1981), and as a post-partum beverage to “clean” the uterus (“matriz”) in the Dominican Republic with *Canella winterana* and *Cinnamodendron* sp (Salazar, 2006). Some species of Canellaceae are also used to catch octopus, *Cinnamodendron ekmanii* (Salazar, 2006), and fish, *Canella winterana* (Liogier, 2000). Their use as an aphrodisiac is a custom mainly in the West Indies, where *Canella winterana* (Liogier, 2000), *Cinnamodendron angustifolium* Sleumer (Liogier, 2000) and *C.* sp from Haiti (Salazar, 2006), *C. corticosum* Miers. from Jamaica (Salazar, 2006), and *C. ekmanii* from the Dominican Republic (Peguero et al., 1995) have been reported as having this use.

Teas are consumed as aromatic beverages, for e.g. *Canella winterana* (Duss, 1972), *Cinnamodendron ekmanii* and *C.* sp (Peguero et al., 1995; Salazar & Peguero, 1994). Furthermore, the bark of *C. corticosum* Miers in Jamaica is also used as a condiment (Hutchinson, 1964; Salazar, 2006).

Most of the Antillean species are regional or local endemics, very rare, and most of them can be considered as threatened (Salazar, 2006). According to the IUCN Red List 2007 three species are catalogued as threatened: *Cinnamodendron*

corticolum from Jamaica listed as vulnerable (Bellingham, 1998), *C. cubense* considered as endangered (Areces-Mallea, 1998), and *Pleodendron macranthum* Tiegh. from Puerto Rico listed as critically endangered (World Conservation Monitoring Centre, 1998). The others *Cinnamodendron* species from The West Indies are not listed, but status of their populations is unknown, for e.g. the Haitian *Cinnamodendron angustifolium* was collected only once from the type locality (Salazar, 2006).

The family Canellaceae was published in 1832 by Martius with *Canella* as described by Browne in 1756 as the sole genus. The taxonomy of the family has been confused and controversial since the type genus, *Canella*, was published. Members of this family were classified within the Winteraceae mainly because the bark of *Canella* and of *Drimys* J. R. Forster & G. Forster (Winteraceae) have similar therapeutic effects, and both have been known in folk medicine as “Cortex winteranus.” However, the most important reason for the taxonomic confusion between these two genera is that both were merged in a single taxon called *Winterania* by Linnaeus (1737), *Laurus winterana* (Linnaeus, 1754), and *Winterania canella* (Linnaeus, 1762–1763). Later Murray (1784) treated them as two different taxa, *Canella alba* Murray for the Caribbean species and *Wintera aromatica* Murray for the species that is today classified as Winteraceae.

Until relatively recently, the Canellaceae have been assigned either to the Parietales (Warburg, 1895; Gilg, 1925; Lawrence, 1951), Annonales (Dahlgren, 1983), or to the Magnoliales (Bonnet, 1876; Takhtajan, 1981; Cronquist, 1988). However, recent molecular and morphological analyses suggest that the family belongs to the magnoliid clade sensu APG II (2003), which includes several lineages that traditionally formed the sub-class Magnoliidae sensu Cronquist (1981). Within this group, the family has been assigned to the order Canellales (APG II, 2003; Cronquist, 1957) or Winterales (Doyle & Endress, 2000), and as sister taxon to Winteraceae (Doyle & Endress, 2000; Soltis et al., 2000; Judd et al., 2002; APG II, 2003; Bremer et al., 2003; Soltis & Soltis, 2004; Endress, 2004).

Members of the Canellaceae form a monophyletic group, which share several synapomorphies such as monadelphous stamens, parietal placentation, and campylotropous ovules (Salazar, 2006). In addition, plants of this family can be easily identified by their lenticels on the trunk and branches, aromatic bark and leaves with peppery taste, simple and alternate-distichous leaves, flowers with fleshy perianth, three sepals (rarely two) and berry fruit containing reniform seeds (Salazar, 2006).

The first taxon described in this family was the Caribbean species *Canella winterana* Gaertn. Although this name was published by Browne in, 1756, the species was well known prior to its taxonomic description because of its medicinal use. The bark of *Canella* was introduced into Europe between the late 16th and early 17th centuries, and it was known as “Canelle blanche” (Bonnet, 1876). However, it is likely that by then this plant was already known to Europeans because Dr. Diego Alvarez Chanca, who accompanied Columbus on his second voyage (Dalby, 2001; Gerbi, 1978), reported the presence of a cinnamon (=“cana” in Spanish), which was different from the one that was known in Europe. It is believed that this account refers to *Canella winterana* (Gerbi, 1978).

The Endemic Species of *Cinnamodendron* and *Pleodendron*

Cinnamodendron was published by Endlicher (1840). The first published species of this genus, the Brazilian *C. axillare* Endl. ex Walp., was originally described as *Canella axillaris* (Nees & von Martius, 1824). Two additional Brazilian species have been described: *Cinnamodendron dinisii* Schwacke (Schwacke, 1898) and *C. sampaioanum* Occhioni (Occhioni, 1948). The other South American taxa are: *C. tenuifolium* Uittien based on material collected in Surinam in 1921 (Uittien, 1926), and *C. venezuelense*, a Venezuelan endemic published by Steyermark (1952).

Four species of *Cinnamodendron* are recognized in the Caribbean Islands, and they are all confined to the Greater Antilles: *Cinnamodendron angustifolium* Sleumer from Hispaniola, *C. corticosum* Miers from Jamaica, *C. cubense* Urb. from Cuba, and *C. ekmanii* Sleumer from Hispaniola (Miers, 1858; Urban, 1922; Sleumer, 1936).

The first species of this genus described for the region was the Jamaican *C. corticosum* (Miers, 1858). Also, the same taxon was described as *C. rubrum* by Grisebach (1864). Bonnet (1876) suggested that the Jamaican species, described by Sloane (1686–1692, 1725) as *Arbor baccifera laurifolia, aromatica, Fructu viridi calyculato, racemoso* refers to *C. corticosum*, but the illustration and description of the plant, including characters such as terminal inflorescences and fruit with gelatinous pulp, clearly suggest that this species corresponds to *Canella winterana* (Salazar, 2006).

Cinnamodendron macranthum Baill. was described as an endemic species from Puerto Rico (Baillon, 1882). Later *Pleodendron* was erected based on *C. macranthum*, and the combination *P. macranthum* Tiegh. was made (van Tieghem, 1899). This genus has been reported for two islands in the Greater Antilles: Hispaniola (*P. ekmanii* (Urban, 1928; Liogier, 1983)) and Puerto Rico (*P. macranthum* (van Tieghem, 1899; Liogier, 1994; Liogier & Martorel, 2000)). *Pleodendron* was considered as a genus endemic to the Greater Antilles until an additional species, *P. costaricense* N. Zamora, Hammel & R. Aguilar, was described recently from Costa Rica (Hammel & Zamora, 2005).

Recent Discoveries

Four of the Greater Antilles endemics have been traditionally placed in *Cinnamodendron*: *C. angustifolium*, *C. corticosum*, *C. cubense*, and *C. ekmanii*. However, a recent molecular cladistic analysis of the Canellaceae based on ITS, *matK*, *trnL-trnF*, *trnD^{GUC}-trnT^{GGU}* and *rbcL* DNA regions from the nuclear and chloroplast genome places these taxa in a distinct clade that does not include the five South American species of this genus, *C. axillare*, *C. dinisii*, *C. sampaioanum*, *C. tenuifolium*, and *C. venezuelense* (Salazar, 2006) (Fig. 1). Indeed, the clade with the species from the Greater Antilles is sister to a group composed exclusively by taxa belonging to *Pleodendron* (Fig. 1). The same study found that the South American species of *Cinnamodendron* and the Brazilian genus *Capsicodendron* form a monophyletic group that is part of a clade containing the Old World genera, *Warburgia* and *Cinnamosma* (Salazar, 2006) (Fig. 1).

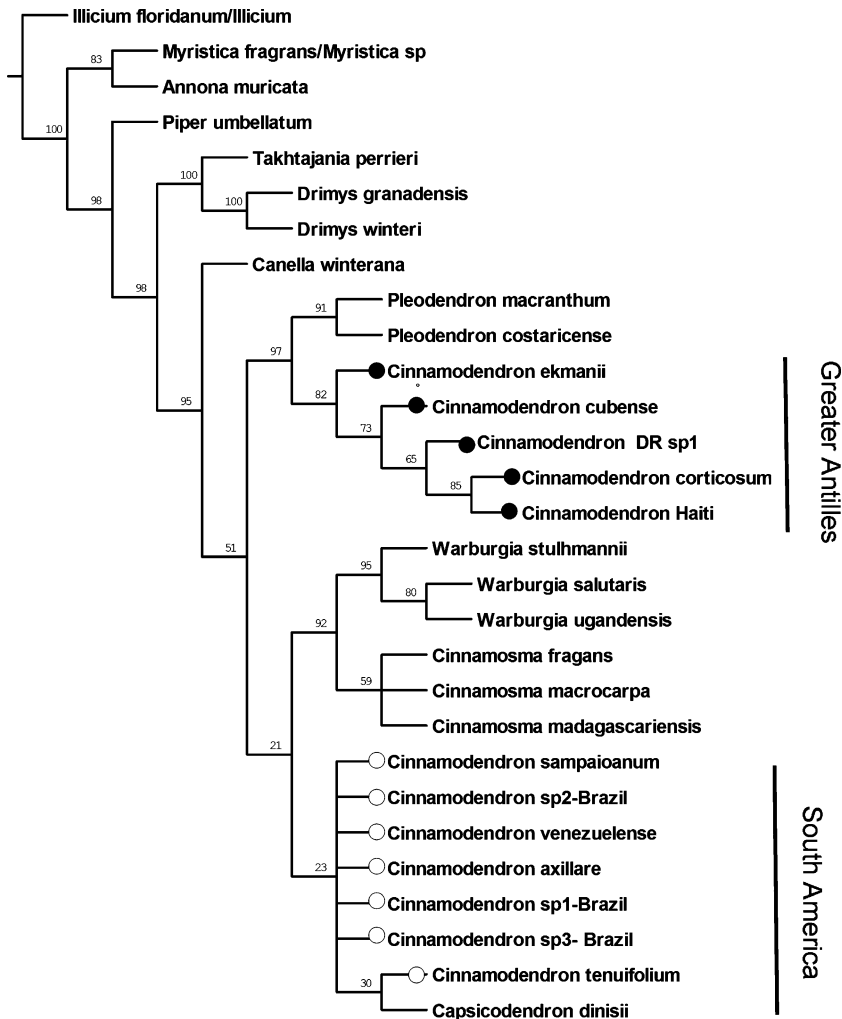


Fig. 1 Strict consensus of 42 most parsimonious trees from the combined analysis of ITS, *matK*, *trnL-trnF*, *trnD-trnT* and *rbcL* and 49 informative morphological characters by 29 taxa: 22 Canellaceae and seven outgroups. Bootstrap support values above branches (Salazar, 2006). Lineages of *Cinnamodendron* from the Antilles are indicated with solid circles and lineages of *Cinnamodendron* from South America are indicated with open circles

The sister relationship between *Pleodendron* and the Antillean species of *Cinnamodendron* is also well supported by cladistic analyses of morphological characters and of a combined DNA and morphology data sets (Salazar, 2006). Morphological synapomorphies supporting these two groups are the presence of many-seeded fruits with fibrous pulp. The two groups of this clade are easily distinguished because *Pleodendron* possess hexamerous flowers (12 petals, 12 stamens, 6 carpels, and 6 placentae). In contrast, the Antillean *Cinnamodendron* species have tetramerous flowers (8 petals, 8 stamens, 4 carpels, and 4 placentae).

The South American species of *Cinnamodendron* do not form a monophyletic group because the Brazilian genus *Capsicodendron* is nested within this group. The synapomorphies of the *Cinnamodendron*-*Capsicodendron* clade are a stipe in the fruit and the presence of a connective projection above the anther (Salazar, 2006).

It is clear that the Greater Antillean and South American species traditionally classified within *Cinnamodendron* belong to two distinct phylogenetic clades, which are distantly related (Kubitzki, 1993; Zanoni, 2004). These two groups present very well defined morphological synapomorphies that support the separation of the *Cinnamodendron* species into two distinct genera, as it has been suggested by Salazar (2006). *Cinnamodendron* taxa from South America are characterized by having flowers with 6–10 petals, generally 10; 8–10 stamens, commonly 10; bicarpellate or tricarpellate, few ovules (4–6); stipite, a few seeded fruit (4 or less) with a gelatinous pulp; big seeds (up to 12 mm long). In contrast, the Antillean clade of “*Cinnamodendron*” is characterized by having tetramerous flowers (8 petals, 8 stamens, 4 carpels; ovary with 4 placentae), many ovules (more than 14); not stipitate, many seeded fruit (more than 8) with a non-gelatinous pulp; small seeds (up to 3 mm long) (Fig. 2).

In summary, the phylogenetic analysis of Canellaceae in combination with morphological characters has clarified the taxonomy of the genus *Cinnamodendron*, which has been traditionally reported for South America as well as the Greater Antilles. The Antillean species of *Cinnamodendron* must be placed in a genus different from the *Cinnamodendron* species from South America, because the type for the genus *Cinnamodendron* is *C. axillare* from Brazil (Salazar, 2006). A formal description of this new genus will be published in a separate study.

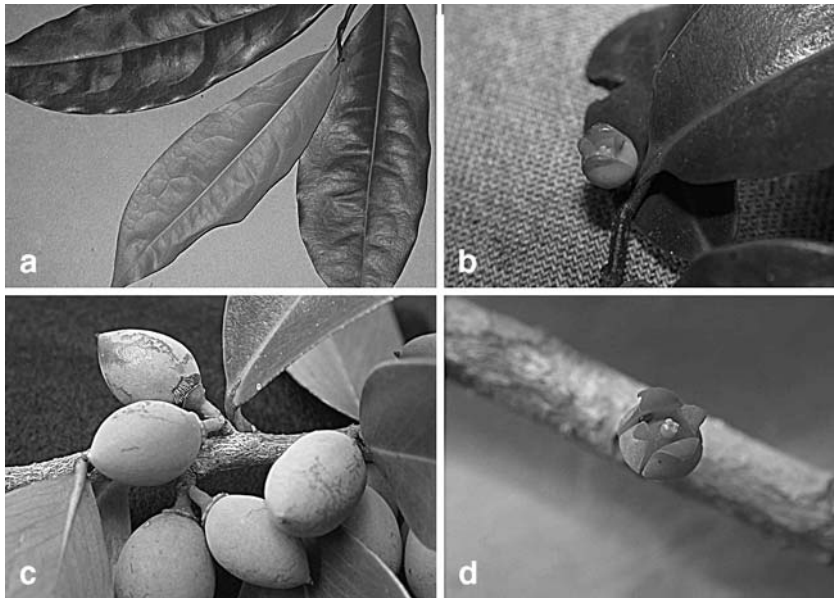


Fig. 2 Species of *Cinnamodendron* reported in the Greater Antilles. *Cinnamodendron corticosum* (a), *Cinnamodendron cubense* (b), *Cinnamodendron ekmanii* (c, d)

Acknowledgements We thank the staff at the following herbaria for facilitating specimens: K, S,U, MO, NY, HUH, UPR, CICY, FLAS, BM, US, MU, MEXU, G, IJ, SJ, UPRRP, HAC, HAJB, RB, HB, SP, MBM, USP, UFSC, UPCB, HBR, FLOR, UEC, BM, BH, and INB. Alberto Veloz, Brígido Peguero, e Idelfonso de los Angeles from the Botanical Garden of Santo Domingo provided assistance in the field. George Proctor and Keron Campbell (Museum of Natural History of Jamaica) facilitated the work in Jamaica. Hilaire Vilmond made possible the work in Haiti. Eugenio Santiago-Valentin, Marcos Caraballo, and Tomas Carlos supported the work in Puerto Rico. Rosalina Berazzain from Jardín Botánico de La Habana made possible the work in Cuba.

We appreciate the comments and suggestions done by Dennis Stevenson, Eugenio Santiago-Valentin, and Javier Francisco-Ortega.

Funding for Jackeline Salazar was provided by Cornell University (Harold E. Moore Jr. Endowment Fund, The Mario Einaudi Center for International Studies: LASP/Tinker Graduate Student Field Research Grants, Department of Plant Biology), Botanical Society of America, American Society of Plant Taxonomists, International Association for Plant Taxonomy, The Linnean Society of London, and the Botanical Garden of Santo Domingo.

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