
Reinstatement of *Bonellia* (Theophrastaceae)

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ABSTRACT. Following the results of a recent phylogenetic study showing that the genus *Jacquinia* is paraphyletic, the following new combinations in the genus *Bonellia* are made (all by Ståhl & Källersjö): *B. albiflora* (Lundell), *B. brevifolia* (Urban), *B. flammea* (Millspaugh ex Mez), *B. frutescens* (Miller), *B. lippoldii* (Lepper), *B. longifolia* (Standley), *B. loeflingii* (Carrasquel), *B. macrocarpa* (Cavanilles), *B. macrocarpa* (Cavanilles) Ståhl & Källersjö subsp. *pungens* (A. Gray), *B. macrocarpa* (Cavanilles) Ståhl & Källersjö subsp. *panamensis* (Lundell), *B. montana* (Ståhl), *B. mucronata* (Roemer & Schultes), *B. nervosa* (Presl), *B. nitida* (Ståhl), *B. paludicola* (Standley), *B. pringlei* (Bartlett), *B. pauciflora* (Ståhl & F. Axelrod), *B. shaferi* (Urban), *B. seleriana* (Urban & Loesner ex Mez), *B. sprucei* (Mez), *B. stenophylla* (Urban), and *B. umbellata* (A. DC.). The genus *Bonellia* is distinguished from *Jacquinia* s. str. by its mostly orange flowers and alternate leaves, flattened seeds that are incompletely covered by placental tissue, and two-layered testa. A key to the genera of the Theophrastaceae is presented.

Key words: *Bonellia*, Theophrastaceae.

The Theophrastaceae form a small Neotropical family of about 100 species of shrubs and small trees. Recent phylogenetic research (Källersjö et al., 2000) has shown that *Samolus* L., a genus traditionally included in the Primulaceae, is sister group to the Theophrastaceae and therefore should be included within the latter family or recognized as a separate family.

The Theophrastaceae s. str. (excluding *Samolus*) were monographed by Mez (1903), who recognized four genera based mainly on floral morphology, viz. *Clavija*, *Jacquinia*, *Deherainia*, and *Theophrasta*. Votsch (1904), in a leaf anatomical work, transferred one of the species of *Deherainia* to a new genus, *Neomezia*, and during more recent taxonomic work (Ståhl, 1993), the genus *Votschia* was es-

tablished to accommodate a species previously included in *Jacquinia*.

Following a new analysis based on a combination of morphological and cpDNA data (Källersjö & Ståhl, 2003), it has become clear that the genus *Jacquinia* is not monophyletic and has to be divided into two genera. According to that analysis, *Jacquinia* s. str. should include species with pseudoverticillate leaves lacking or with a poorly developed mucro, lepidote young shoots, whitish flowers, globose seeds completely immersed in placental tissue, and sunken abaxial foliar sclerenchyma. This circumscription makes *Jacquinia* a chiefly Caribbean genus of 13 species. Only one of these species, *J. armillaris* Jacquin, occurs outside of the Caribbean islands, in northern coastal South America and eastern coastal Brazil (Ståhl, 1992, 1995). *Jacquinia arborea* Vahl, with a wide Caribbean distribution, has also been reported a few times from Mesoamerica, but then only from islands off the eastern coast of Mexico and Honduras.

The reinstated genus *Bonellia* is defined by alternate leaves with a well-developed mucro, glabrous or puberulous young shoots, mostly orange flowers, flattened seeds only partly immersed into placental tissue, and abaxial foliar sclerenchyma located adjacent to the lower epidermis. Two species, *B. longifolia* and *B. paludicola*, deviate by having whitish flowers, and it is therefore interesting to note that both appear at the base of the *Bonellia* clade in the phylogeny proposed by Källersjö and Ståhl (2003). Of these, *B. paludicola* is the most problematical species since it, like most members of *Jacquinia* s. str. (except *J. keyensis* Mez), has pseudoverticillate leaves. It should also be noted that one additional species, *B. albiflora*, has white flowers, but that species is morphologically very similar to *B. macrocarpa*, indicating a close relationship between these two taxa.

The genus *Bonellia* consists of 22 species distributed in Mesoamerica, northern and western

South America, and the Greater Antilles. Within the genus two morphologically and geographically distinct groups can be discerned. One of these comprises the South American species *B. mucronata* (northern Peru), *B. sprucei* (Ecuador), *B. frutescens* (northern Colombia–Venezuela), *B. loeflingii* (northern Venezuela), and the Mesoamerican *B. nervosa*. All species in this group have rather large, thick-walled and opaque fruits, comparatively flexible leaves (deciduous in *B. nervosa*), and whitened young shoots. The second group consists of species from Cuba, Hispaniola, and Puerto Rico (*B. brevifolia*, *B. lippoldii*, *B. pauciflora*, *B. stenophylla*, *B. umbellata*) with small or very small spine-tipped leaves, small, thin-walled fruits, and tiny flowers. The remaining, Mesoamerican species are more difficult to define as a natural group, although some species appear to be closely related (Ståhl, 1989; Källersjö & Ståhl, 2003).

The name *Bonellia* was published by Colla (1824) in a catalog of plants from his private garden. The name was evidently proposed by C. G. L. Bertero, whose material of a plant from Santa Martha in northern Colombia was distributed under the name of *Bonellia cavanillesii* to herbaria and botanical gardens in Europe. However, since Colla (1824) cited *Jacquinia macrocarpa* Cavanilles, a different Mesoamerican species, as a synonym, the name *B. cavanillesii* has to be treated as an obligate synonym of the latter species.

The name *Bonellia* honors the Italian zoologist Franco Andrea Bonelli (1784–1830), evidently a close friend of Bertero and Colla, but whose contribution to botany is obscure.

KEY TO THE GENERA OF THEOPHRASTACEAE S. STR.

- 1a. Unbranched or sparsely branched shrubs and trees; fully developed leaves 20–120 cm long, margins often serrate or serrulate.
 - 2a. Corolla rotate, tube smooth on inside; staminodes ovoid-gibbous; flowers often unisexual, male or functionally male flowers with stamen filaments fused into a permanent tube; anther not or inconspicuously produced at apex; leaf margins entire, serrulate, or serrate *Clavijsa* Ruiz & Pavón
 - 2b. Corolla campanulate or bowl-shaped, irregularly puckered on inside of tube; staminodes not obovoid; flowers bisexual, stamen filaments fused at base only; anther connective distinctly prolonged at apex; leaf margins usually spinose-dentate.
 - 3a. Plants erect, the stem spiny; corolla deeply campanulate, pale buff turning black upon drying; staminodes transversely oblong, inserted within the corolla tube *Theophrasta* L.
 - 3b. Plants semi-decumbent, the stem not spiny; corolla bowl-shaped, orange, not

- blackening upon drying; staminodes triangular, minute, inserted at the mouth of the corolla tube *Neomezia* Votsch
- 1b. Branched shrubs or small trees; leaves usually less than 20 cm long, margins entire.
 - 4a. Corolla green, > 2 cm diam. at anthesis; staminodes obtrullate to linear; fruits ovoid *Deherainia* Decaisne
 - 4b. Corolla orange, whitish, or pale yellow, < 2 cm diam. at anthesis; staminodes flattened, petaloid.
 - 5a. Corolla bowl-shaped, pale yellow; style shorter than the ovary; foliar sclerenchyma of the lower side arranged in a continuous or subcontinuous layer *Votschia* Ståhl
 - 5b. Corolla campanulate or urceolate, orange or whitish; style of the same length as the ovary; foliar sclerenchyma arranged in distinct bundles.
 - 6a. Young shoots ± lepidote from irregularly branched, thick-walled hairs; leaves mostly pseudovercillate (alternate in *J. keyensis*), without or with a poorly developed apical mucro; corolla white or whitish; seeds ± globose, covered by placental tissue; abaxial foliar sclerenchyma often somewhat immersed into the mesenchyma . . . *Jacquinia* L.
 - 6b. Young shoots puberulous from short uniseriate hairs or glabrous; leaves alternate (pseudovercillate in *B. paludicola*), usually distinctly mucronate; corolla orange, sometimes white or whitish; seeds flattened, incompletely covered by placental tissue; abaxial foliar sclerenchyma adjacent to lower epidermis *Bonellia* Colla

TAXONOMY AND NEW COMBINATIONS

- Bonellia** Colla, Hortus Ripul. 21. 1824. TYPE: *Bonellia cavanillesii* Bertero ex Colla (≡ *Jacquinia macrocarpa* Cavanilles).
- Bonellia albiflora** (Lundell) Ståhl & Källersjö, comb. nov. Basionym: *Jacquinia albiflora* Lundell, Wrightia 2: 60. 1960. TYPE: Guatemala. Petén: Tikal, 29 July 1959, Contreras 45 (holotype, LL; isotypes, S, TEX, US).
- Bonellia brevifolia** (Urban) Ståhl & Källersjö, comb. nov. Basionym: *Jacquinia brevifolia* Urban, Symb. Antill. 1: 379. 1899. TYPE: Cuba. Sine loco, Wright 2913 (lectotype, designated in Ståhl (1995), GH; isotypes, G, GOET, M).
- Bonellia flammea** (Millspaugh ex Mez) Ståhl & Källersjö, comb. nov. Basionym: *Jacquinia flammea* Millspaugh ex Mez, Pflanzenr. IV. 236a: 40. 1903. TYPE: Mexico. Yucatán: Silam, Gaumer 531 (lectotype, designated in Ståhl (1989), G; isotypes, A, BM, BR, C, CAS, DS, E, F, FHO, GH, K, LE, MO, NY, UPS, US, W).

- Bonellia frutescens** (Miller) Ståhl & Källersjö, comb. nov. Basionym: *Ruscus frutescens* Miller, Gard. Dict. ed. 8: unpaginated (species no. 8 under *Ruscus*). 1768. TYPE: Colombia. Bolívar: vic. of Cartagena, no date, *Heriberto* 279 (neotype, designated in Ståhl (1995), US).
- Bonellia lippoldii** (Lepper) Ståhl & Källersjö, comb. nov. Basionym: *Jacquinia lippoldii* Lepper, Wiss. Z. Friedrich-Schiller-Univ. Jena, Math.-Naturwiss. Reihe 32: 876. 1983. TYPE: Cuba. Guantánamo: San Antonio del Sur, Abra de Mariana, E of Abra, 100–400 m alt., 9 Feb. 1979, *Bisse et al. s.n.* (holo- and isotype, HAJB no. 39068).
- Bonellia loeflingii** (Carrasquel) Ståhl & Källersjö, comb. nov. Basionym: *Jacquinia loeflingii* Carrasquel, Acta Bot. Venez. 4: 348. 1970. TYPE: Venezuela. Anzoátegui: about 10 km from Píritu on road to Clarines, Jan. 1968, *Aristeguieta et al. 6524* (holotype, VEN).
- Bonellia longifolia** (Standley) Ståhl & Källersjö, comb. nov. Basionym: *Jacquinia longifolia* Standley, J. Wash. Acad. Sci. 14: 241. 1924. TYPE: El Salvador. San Vicente: vic. of San Vicente, alt. 350–500 m, 2–11 Mar. 1922, *Standley 21159* (holotype, US; isotypes, F, G, GH, K, NY).
- Bonellia macrocarpa** (Cavanilles) Ståhl & Källersjö, comb. nov. Basionym: *Jacquinia macrocarpa* Cavanilles, Icon. 5: 55, tab. 483. 1799. TYPE: Mexico. Acapulco, Feb. 1791, *Neé s.n.* (lectotype, designated in D'Arcy (1980), B-WILLD; isotypes, HBG, MA).
- Bonellia macrocarpa** (Cavanilles) Ståhl & Källersjö subsp. **pungens** (A. Gray) Ståhl & Källersjö, comb. nov. Basionym: *Jacquinia pungens* A. Gray, Proc. Amer. Acad. Arts 5: 325. 1854. TYPE: Mexico. Sonora: hills between Rayón and Ures, 10 Oct. 1851, *Thurber 903* (lectotype, designated in Ståhl (1989), GH; isotypes, GH, NY).
- Bonellia macrocarpa** (Cavanilles) Ståhl & Källersjö subsp. **panamensis** (Lundell) Ståhl & Källersjö, comb. nov. Basionym: *Jacquinia panamensis* Lundell, in Woodson & Schery, Ann. Missouri Bot. Gard. 27: 329. 1940. TYPE: Panama. Panamá: vic. of Bejuco, 18 Oct. 1938, *Allen 985* (holotype, MICH; isotypes, GH, MO, US).
- Bonellia montana** (Ståhl) Ståhl & Källersjö, comb. nov. Basionym: *Jacquinia montana* Ståhl, Nordic J. Bot. 9: 27. 1989. TYPE: Nicaragua. Jinotega: Cerro de la Cruz and vic., W of Jinotega, alt. 1200–1400 m, 7 July 1947, *Standley 10968* (holotype, F).
- Bonellia mucronata** (Roemer & Schultes) Ståhl & Källersjö, comb. nov. Basionym: *Jacquinia mucronata* Roemer & Schultes, Syst. Veg. 4: 802. 1819. TYPE: Peru. Colasay, *Humboldt 3581* (holotype, B-WILLD, seen on microfiche; isotypes, HAL, P).
- Bonellia nervosa** (Presl) Ståhl & Källersjö, comb. nov. Basionym: *Jacquinia nervosa* Presl, Reliq. Haenk. 2: 67. 1835. TYPE: Mexico. Sine loco, *Haenke s.n.* (holotype, PR).
- Bonellia nitida** (Ståhl) Ståhl & Källersjö, comb. nov. Basionym: *Jacquinia nitida* Ståhl, Nordic J. Bot. 9: 24. 1989. TYPE: Honduras. Comayagua: vic. of Comayagua, alt. 600 m, 12–13 Mar. 1947, *Standley & Chacón 6025* (holotype, F).
- Bonellia paludicola** (Standley) Ståhl & Källersjö, comb. nov. Basionym: *Jacquinia paludicola* Standley, Field Mus. Nat. Hist., Bot. Ser. 11: 138. 1932. TYPE: Belize. Punta Gorda, "Forest Home," alt. 60 m, 11 Sep. 1932, *Schipp 1028* (holotype, F; isotypes, A, BM, G, GH, K, MICH, MO, NY, S).
- Bonellia pauciflora** (Ståhl & F. Axelrod) Ståhl & Källersjö, comb. nov. Basionym: *Jacquinia pauciflora* Ståhl & F. Axelrod, Brittonia 50: 1. 1998. TYPE: Puerto Rico. Municipio Quebradillas, Barrio Charcas, 0.7 km SSE of Charcas, 200–350 m alt., 23 June 1994, *Proctor et al. 49406* (holotype, SJ; isotypes, GB, NY).
- Bonellia pringlei** (Bartlett) Ståhl & Källersjö, comb. nov. Basionym: *Jacquinia pringlei* Bartlett, Proc. Amer. Acad. Arts 44: 630. 1909. TYPE: Mexico. Guerrero: Iguala Canyon, 8 Oct. 1908, *Pringle 10337* (holotype, GH; isotypes, BH, BM, C, CM, E, F, G, GOET, HBG, K, L, LE, M, MICH, MO, MSC, NY, P, PH, PR, US, VT, W).
- Bonellia seleriana** (Urban & Loesner ex Mez) Ståhl & Källersjö, comb. nov. Basionym: *Jacquinia seleriana* Urban & Loesner ex Mez, Pflanzenr. IV. 236a: 43. 1903. TYPE: Mexico. Oaxaca: above San Carlos Yauhatepec, 5 Jan. 1896, *Seler & Seler 1759* (lectotype, designated in Ståhl (1989), GH; isotypes, A, NY).
- Bonellia shaferi** (Urban) Ståhl & Källersjö, comb. nov. Basionym: *Jacquinia shaferi* Urban, Symb. Antill. 7: 320. 1912. TYPE: Cuba. Holguín: vic. of Holguín, 7 Apr. 1909, *Shafer 1231* (lectotype, designated in Ståhl (1995), NY; isotypes, A, F, GH, HAC, K, MO, US).
- Bonellia sprucei** (Mez) Ståhl & Källersjö, comb. nov. Basionym: *Jacquinia sprucei* Mez, Pflanzenr. IV. 236a: 43. 1903. TYPE: Ecuador. Guayas: Chanduy, *Spruce 6478* (lectotype, designated in Ståhl (1990), K; isotypes, BM, BP, CGE, G, LE, OXF, P, W).

Bonellia stenophylla (Urban) Ståhl & Källersjö, comb. nov. Basionym: *Jacquinia stenophylla* Urban, Symb. Antill. 1: 378. 1899. TYPE: Cuba. "Cuba Occ.," 1865, *Wright 2912 p.p.* (lectotype, designated in Ståhl (1995), G; isotypes, BM, GH, GOET, HAC, LE, M, NY, S, US, W). [See Ståhl (1995) for comments.]

Bonellia umbellata (A. DC.) Ståhl & Källersjö, comb. nov. Basionym: *Jacquinia umbellata* A. DC., Prodr. 8: 150. 1844. TYPE: Puerto Rico. Sine loco, *Bertero s.n.* (holotype, G-DC, seen on microfiche; isotypes, H, MEL, MO, P).

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