
Redefinition of *Symbolanthus* to Include *Wurdackanthus* (Gentianaceae–Helieae)

Lena Struwe

Department of Ecology, Evolution, and Natural Resources, Rutgers University–Cook College,
237 Foran Hall, 59 Dudley Road, New Brunswick, New Jersey 08901-8551, U.S.A.
struwe@aesop.rutgers.edu

Katherine R. Gould

Department of Biology, Western Carolina University, 132 Natural Science Building,
Cullowhee, North Carolina 28723, U.S.A. kmathews@email.wcu.edu

ABSTRACT. The genus *Wurdackanthus* (Gentianaceae–Helieae) comprises two species restricted to northern South America. *Wurdackanthus argyreus* is a narrowly distributed species on tepuis of southern Venezuela and northern Brazil, and *W. frigidus* only occurs in the Lesser Antilles. Recent phylogenetic investigations have shown that *Wurdackanthus* is paraphyletic with respect to *Symbolanthus*, and that no clear morphological distinction exists between these two genera. These two genera share several unique morphological, anatomical, and molecular synapomorphies, such as (1) pollen released as tetrads and with a coarsely reticulated exine, especially in the equatorial zone (*Symbolanthus*-type pollen); (2) elongated dome-like seed testa cells; and (3) molecular characters from the *trnL* intron, *matK*, internal transgenic spacer (ITS), and 5S non-transcribed spacer (5S-NTS) DNA regions. Based on the concept of monophyly and the presence of structural support, we here include *Wurdackanthus* in *Symbolanthus* and provide new synonymy. The new combinations *Symbolanthus argyreus* (Maguire) Struwe & K. Gould and *S. frigidus* (Swartz) Struwe & K. Gould are made herein.

RESUMEN. El género *Wurdackanthus* (Gentianaceae–Helieae) comprende dos especies restringidas al norte de Sur América. *Wurdackanthus argyreus* se distribuye en los tepuis del sur de Venezuela y norte del Brasil y *W. frigidus* se encuentra únicamente en las Antillas menores. Investigaciones recientes sobre la filogenia del grupo han mostrado que *Wurdackanthus* es parafilético en relación a *Symbolanthus*, y que no existen tampoco diferencias morfológicas claras entre los dos géneros. Los dos géneros comparten varias sinapomorfías morfológicas, anatómicas y moleculares tales como (1) polen en tétradas y con exina abruptamente reticulada, especialmente en la zona ecuatorial (polen

del tipo *Symbolanthus*), (2) células de la cubierta seminal elongadas en forma de domo y (3) caracteres moleculares en las regiones de ADN del intron *trnL*, *matK*, del espaciador interno transgénico (ITS), y del espaciador no transcriptor 5S (5S-NTS). Con base en el concepto de monofilia y de la presencia de soporte estructural, incluimos *Wurdackanthus* en *Symbolanthus* y presentamos la nueva sinonimia. Se publican además las combinaciones nuevas *Symbolanthus argyreus* (Maguire) Struwe & K. Gould y *S. frigidus* (Swartz) Struwe & K. Gould.

Key words: Gentianaceae, Helieae, Neotropics, *Symbolanthus*, *Wurdackanthus*.

The genus *Wurdackanthus* Maguire comprises two species in the Neotropics and belongs to tribe Helieae in Gentianaceae (Maguire, 1985; Maguire & Boom, 1989; Struwe et al., 2002a). *Wurdackanthus argyreus*, the type species, is a narrowly distributed species occurring on two mountains in southern Venezuela and northern Brazil. The other species, *W. frigidus*, is present on the islands of Dominica, Guadeloupe, and St. Vincent in the Lesser Antilles. *Symbolanthus* G. Don is one of the most showy-flowered gentian genera in the American tropics with large and brightly colored corollas. The corollas are campanulate, trumpet- or funnel-shaped, and brightly pink, red, to purple (often with white stripes), or white, green, to yellow. *Symbolanthus* species occur from Costa Rica and Panama southward along the Andes in Colombia, Venezuela, Ecuador, Peru, and down to central Bolivia, as well as on the tepuis (table-top mountains) of the Guayana Highlands. The genus is currently being revised, and preliminary data suggest that it contains at least 30 species (Struwe et al., 2002a; Struwe, 2003a, b).

Phylogenetic analyses based on DNA sequences

Table 1. Overview of anatomical and morphological characteristics of *Symbolanthus* sensu stricto and the two species previously classified as *Wurdackanthus*, *S. argyreus*, and *S. frigidus*.

Character	<i>Symbolanthus</i> s. str.	<i>S. argyreus</i> (<i>Wurdackanthus a.</i>)	<i>S. frigidus</i> (<i>Wurdackanthus f.</i>)
Calyx size	16–45 mm	7–12 mm	7–12 mm
Calyx lobe length as percentage of total calyx length	80%–90%	80%–90%	60%–70%
Calyx lobe apex	acute, acuminate, obtuse	obtuse	obtuse
Corolla bud apex	tapering	tapering	obtuse
Corolla length	(23–)48–110 mm	40–55 mm	40–58 mm
Corolla color	white, pink, magenta, red, cream, green, yellow	pink, white, magenta	yellow, greenish yellow
Corolla lobe apex	acute or obtuse	obtuse	obtuse
Corona	present	absent	absent
Staminal gaps	present	absent	present
Pollen type	<i>Symbolanthus</i> -type	<i>Symbolanthus</i> -type	<i>Symbolanthus</i> -type
Pollen aggregation	tetrads	tetrads	tetrads
Exine (pollen)	coarsely reticulated, especially around equator	coarsely reticulate, especially around equator	coarsely reticulate, especially around equator
Testa (seed)	angular, not winged; testa cells rectangular, dome-like, sometimes with band-like thickenings	angular, not winged; testa cells rectangular, dome-like, sometimes with band-like thickenings	angular, not winged; testa cells rectangular, dome-like, sometimes with band-like thickenings
Number of flowers per inflorescence	1–4(–8)	1–3	5–7

of the *trnL* intron, *matK*, and internal transcribed spacer (ITS), all indicate a common origin of *Symbolanthus* and *Wurdackanthus* (Struwe et al., 2002a). *Wurdackanthus* is shown to be unresolved toward *Symbolanthus*, but together they form a strongly supported monophyletic group. The closest relatives appear to be tetrad-bearing species of *Chelonanthus* (e.g., *C. albus*). However, the ITS and *trnL* intron analyses showed no clear resolution within *Symbolanthus* and *Wurdackanthus* (Struwe et al., 2002a). Gould and Struwe (in press) present a detailed study of these two genera using DNA sequences from the 5S-NTS ribosomal region. This study also shows *Wurdackanthus* as being paraphyletic toward *Symbolanthus*. *Wurdackanthus frigidus* is positioned as the basalmost branch in the group, and the position of *W. argyreus* varies but is never together with *W. frigidus*, thereby never creating a monophyletic *Wurdackanthus* that is sister to *Symbolanthus* (Gould & Struwe, in press).

The floral and vegetative morphologies of *Symbolanthus* and *Wurdackanthus* are similar, and in fact no distinct apomorphic character can be used as a distinguishing trait between these two genera. Possible synapomorphies for *Symbolanthus* and

Wurdackanthus include pollen being released as tetrads and having a coarsely reticulated exine in the equatorial zone (a.k.a. pollen of the *Symbolanthus*-type; Nilsson, 1970, 2002). Both genera also have testa cells with elongated dome-like cells (Bouman et al., 2002). In conclusion, there is strong molecular and morphological support for a monophyletic *Symbolanthus*, which includes *Wurdackanthus*, but weak support for a *Symbolanthus* in the current stricter sense. Therefore, *Wurdackanthus* is here included in *Symbolanthus*. This new generic circumscription also extends the geographic range of *Symbolanthus* s.l. to the Lesser Antilles in the Caribbean. A generic description of *Symbolanthus* s.l. is provided below (see Table 1 for an overview).

TAXONOMIC TREATMENT

Symbolanthus G. Don, Gen. Syst. 4: 175. 1837. *Lisianthus* sect. *Symbolanthus* (G. Don) Benth., in Bentham & Hooker f., Gen. Pl. 2: 814. 1876. TYPE: *Symbolanthus anomalus* (Kunth) Gilg.

Leiothamnus Grisebach, Gen. Sp. Gent. 205. 1839 [1838].

TYPE: *Leiothamnus anomalus* (Kunth) Grisebach.

Wurdackanthus Maguire, Phytologia 57: 312. 1985. TYPE: *Wurdackanthus argyreus* Maguire.

Herbs, subshrubs, shrubs to small *trees*, 0.3–5 m tall. *Leaves* opposite, decussate, petiolate to sessile, broadly ovate, obovate to elliptic, rarely linear or narrowly ovate, coriaceous to chartaceous, entire; interpetiolar line or raised ridge present. *Inflorescence* terminal, a 2- to 4(to 11)-flowered cyme (dichasial, sometimes with monochasial branches) or flowers solitary. *Flowers* 5-merous, erect, horizontal, to nodding, slightly zygomorphic; stamens and style slightly zygomorphic and gathered together in the lower side of the corolla mouth; *calyx* persistent and slightly enlarged in fruit (except *S. frigidus*), the lobes ovate to elliptic, imbricate in bud, with a dorsal glandular area on each lobe, sometimes dorsally keeled, hyaline-margined, the lobe apex acute, acuminate, or obtuse; *corolla* apex acute, acuminate, or obtuse, mucronate, the corolla bud apex tapering (obtuse in *S. frigidus*); *stamens* inserted in the lower quarter of corolla tube, with corona-like structure (absent in *S. argyreus* and *S. frigidus*) at the base of the filaments, with staminal pockets between the filaments and the corolla at the insertion point (absent in *S. argyreus*); *ovary* bilocular, superior, with a glandular disk at the base, the placentation axile to parietal with protruding, inrolled placentas; ovules numerous; style long, slender, at least partly persistent in fruit, flattened when dry and in fruit; stigma bilamellate, lobes oblong to ovate. *Capsule* globose to elliptic, leathery, slightly fleshy to woody, often glossy, sometimes nearly berry-like, medially dehiscent or sometimes possibly indehiscent, usually nodding.

Distribution. *Symbolanthus* contains at least 30 species, of which ca. 20 species are distributed in montane areas in Costa Rica and Panama as well as along the Andes in Colombia, Venezuela, Ecuador, Peru, and Bolivia. Eight additional species are known from montane habitats on the tepuis of the Guayana Shield in southern Venezuela, northern Brazil, and western Guyana. *Symbolanthus frigidus* is the only species occurring in the Caribbean and is restricted to the mountains of a few islands of the Lesser Antilles.

1. *Symbolanthus argyreus* (Maguire) Struwe & K. Gould, comb. nov. Basionym: *Wurdackanthus argyreus* Maguire, Phytologia 57: 312. 1985. TYPE: Venezuela. Amazonas: Cerro de la Neblina, Río Yatua, cumbre 5–18 km W of Cumbre Camp, 1–2 Dec. 1957, *B. Maguire, J. J. Wurdack, & C. K. Maguire 42260* (holotype,

NY; isotype, US). [Image available at (http://scisun.nybg.org:8890/searchdb/owa/wwwcatalog.detail_list?this_id=4441562)]

Symbolanthus aracamuniensis Steyermark, in Steyermark et al., Ann. Missouri Bot. Gard. 76: 958. 1989. TYPE: Venezuela. Amazonas: Dept. Río Negro, Cerro Aracamuni, summit, Popa Camp, savanna with small to large patches of forest and stream, 1550 m, 15 Oct. 1987, *R. Liesner & F. Delascio 21940* (holotype, MO; isotypes, NY, VEN not seen).

Distribution. *Symbolanthus argyreus* grows only in dwarf forest and savannas on tepui summits and slopes at altitudes of 1300 to 2200 m of the two tepuis Sierra de la Neblina (both on the Brazilian and Venezuelan sides) and Cerro Aracamuni (Venezuela: Amazonas; Struwe et al., 1999).

Representative specimens. BRAZIL. **Amazonas:** Rio Negro, Rio Cauaburi, Rio Maturacá, Serra Pirapucú, 1300–1700 m, *Silva & Brazão 60928* (NY). VENEZUELA. **Amazonas:** NW tepui of Cerro Neblina massif, 1800 m, *Gentry & Stein 46653* (MO); Río Negro, Camp III, Neblina & Massif, NW Plateau (Arm) 13.5 km ENE of Cerro de La Neblina Base Camp, 1750–1850 m, *Liesner 15997* (MO); Cerro de la Neblina, Río Yatua, W headland, 1700–2000 m, *Maguire et al. 37117* (NY); Cerro de la Neblina, 6.5 km SSE of base camp, 1600 m, *Stein et al. 1617* (NY, U); Cerro de la Neblina, headwaters of Caño Grande, SE portion, 1900 m, *Steyermark 103979* (NY, VEN).

2. *Symbolanthus frigidus* (Swartz) Struwe & K. Gould, comb. nov. Basionym: *Lisianthus frigidus* Swartz, Prodr. Nov. Gen. & Sp. Pl. Veg. Ind. Occ.: 40. 1788. *Lisianthus frigidus* (Swartz) Grisebach, Gen. Sp. Gent.: 177. 1839 [1838]. *Helia frigida* (Swartz) Kuntze, Rev. Gen. 2: 428. 1891. *Calolisianthus frigidus* (Swartz) Gilg, Nat. Pflanzenfam. 4(2): 101. 1895. *Chelonanthus frigidus* (Swartz) Urban, Symb. Antill. 3: 334. 1902. *Irlbachia frigida* (Swartz) Maas, Proc. Kon. Ned. Akad. Wetensch. Ser. C. 88(4): 410. 1985. *Wurdackanthus frigidus* (Swartz) Maguire & Boom, Mem. New York Bot. Gard. 51: 9. 1989. TYPE: DOMINICA. “Incolit regionem muscosam montis la Soufriere Insulae Dominicae, [date unknown], *Ponthieu* (holotype, BM; isotype, S not seen). Figure 1.

Lisianthus acuminatus Desrousseaux, in Lamarek, Encycl. 3: 660. 1789, non *Lisianthus acuminatus* Perkins, Engl. Jahrb. 31: 493. 1902. TYPE: Guadeloupe. [Date unknown], *De Badier* (P not seen).

Distribution. *Symbolanthus frigidus* is endemic to montane areas of the high cinder volcano areas of the islands of Dominica, Guadeloupe, and St. Vincent of the Lesser Antilles (Howard, 1989).

Representative specimens. DOMINICA. Upper rainfo-

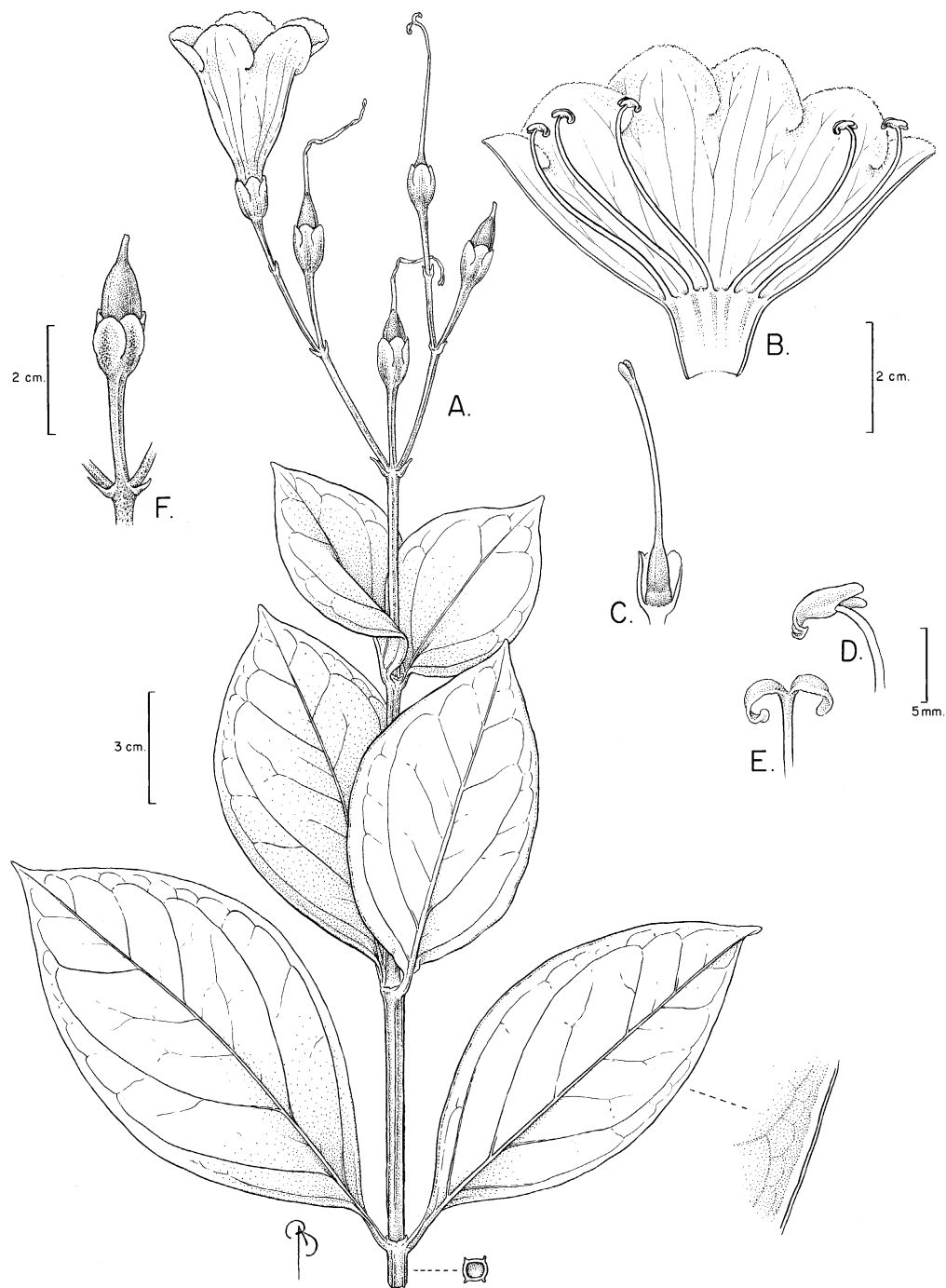


Figure 1. *Symbolanthus frigidus* (Swartz) Struwe & K. Gould. —A. Habit of flowering stem. —B. Opened corolla with stamens with bent filaments. —C. Opened calyx with gynoecium (note glandular base of ovary). —D. Sagittate, slightly recurved anther at anthesis. —E. Bilobed stigma with nearly linear stigma lobes. —F. Part of infructescence showing erect capsular fruit with small persistent style base. Drawing by Bobbi Angell. A–E, *Cooley 8211* (GH, S); F, *Beard 1339* (S).

rest-clad slopes, 3750 ft., Morne Anglais, *Fennah 16* (GH); Valley of Desolation, *Honychurch s.n.* (A); Morne Diablotins, elfin woodland, *Whitefoord 5315* (A). GUADELOUPE. Cone de la Soufriere, 1000–1480 m, *Duss 2306* (NY); Basse Terre, Savans-aux-Ananas, ca. 1000 m, *Proctor 20339* (A); Basse Terre, Mamelle Petit-Bourg, sommet, su vent, 715 m, *Sastre et al. 1916* (A); bois chemus Savane aua, 1050 m, *Stehlé 867* (NY). ST. VINCENT. Summit of Soufriere, *Beard 17* (S); Mt. St. Andrew, elfin woodland, *Beard 1339* (GH, NY, S); Charlotte Parish, on W slope of Soufriere Mtn., *Cooley 8211* (NY, S); ad Soufriere, *Egger 6909* (NY); summit of Soufriere crater, 3000 ft., *Howard 11195* (GH); top of Mt. Soufriere (volcano), *Smith & Smith 18* (NY, GH); Richmond Peak, Morne Garou Mtns., 900–1050 m, *Morton 4949* (GH); St. David Parish, upper outer slopes & rim of Soufriere crater, *Proctor 26007* (GH).

DISCUSSION

Wurdackanthus was not described until 1985 and was typified with *W. argyreus* Maguire (here *Symbolanthus argyreus*) from Sierra de la Neblina in southern Venezuela and northern Brazil (Maguire, 1985). Four years later, Steyermark (1989) described *Symbolanthus aracamuniensis* from Cerro Aracamuni, also in southern Venezuela, which is conspecific with *W. argyreus*, but found on a different mountain (Struwe et al., 1999). *Symbolanthus argyreus* is the only species of *Symbolanthus* investigated so far that appears to lack a corona or corona-like structure in the corolla tube as well as staminal pockets between the corolla tube and the base of the filaments (Struwe et al., 2002b). *Symbolanthus frigidus* is lacking the corona but has the staminal pockets.

NOMENCLATURE AND CLASSIFICATION OF *SYMBOLANTHUS FRIGIDUS*

The problematic taxonomy of *Symbolanthus frigidus* is reflected in its having been transferred among genera more than any other Helieae taxon. Swartz (1788) originally described it as *Lisianthus frigidus*. Grisebach (1839) included *S. frigidus* in his *Lisyanthus* in the classic work *Genera et Species Gentianearum*, and Kuntze (1891) moved the species to his exceptionally broadly circumscribed *Helia*. Not long thereafter, Gilg (1895) split up *Helia* and included *S. frigidus* in his new genus *Calolisianthus*. Only seven years after this, Urban (1902) transferred *S. frigidus* to another of Gilg's segregate genera, *Chelonanthus*, a view that was not commonly accepted in subsequent treatments. Based on palynological data, Nilsson (1970: 31) suggested that *S. frigidus* (as *Calolisianthus frigidus*) should be transferred to *Symbolanthus*, since it had pollen of the distinct *Symbolanthus*-type. Indeed, *S. frigidus* was soon moved again, this time by Maas

(1985), but not to *Symbolanthus*. It was instead transferred to *Irlbachia*, a genus that is now restricted to species with spinose pollen polyads. A few years later, *S. frigidus* was included in the newly described genus *Wurdackanthus* (Maguire & Boom, 1989). In fact, *S. frigidus* has previously been placed in all major tetrad-bearing genera of the tribe Helieae, except for *Symbolanthus* itself, a genus to which Nilsson (1970) suggested this species should belong. With its inclusion in *Symbolanthus*, *S. frigidus* becomes historically the first described *Symbolanthus* species. It predates the previously oldest-known species, *S. calygonus*, by 11 years (Ruiz & Pavon, 1799).

CLASSIFICATION OF *WURDACKANTHUS*–*SYMBOLANTHUS*

The alternatives to including *Wurdackanthus* in *Symbolanthus* are (1) to create a new genus for *W. frigidus* and restrict *Wurdackanthus* to *W. argyreus* only, or (2) to create a new genus for *W. frigidus* and include *W. argyreus* in *Symbolanthus*, since *W. argyreus* is the type of the genus *Wurdackanthus*. However, the molecular support for the clade consisting of *Symbolanthus* s. str., excluding *Wurdackanthus*, is weak (Gould & Struwe, in prep.). Morphological differences between *Symbolanthus* and *Wurdackanthus* are also few, mainly being the absence of a corona and the presence of smaller and less deeply divided calyces in *Wurdackanthus*. Rather, a more broadly circumscribed genus that includes both *Symbolanthus* and *Wurdackanthus* as advocated here, forms a well-supported unit by all available data. Instead of having one or two monotypic genera based on no unique characters and a poorly supported *Symbolanthus* s. str., we prefer a widely circumscribed *Symbolanthus* that is morphologically and molecularly well supported. *Symbolanthus* s.l. is supported by characters such as tetrad pollen of the *Symbolanthus*-type (unique to this group), staminal pockets (except *W. argyreus*), coronas (unique to this group, found in all species except *W. argyreus* and *W. frigidus*), and relatively large corollas (ca. 40–100 mm long) and fruits (ca. 20–40 mm long) as compared to sister taxa in *Chelonanthus* (Gould & Struwe, in press).

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We dedicate this paper in memory of the late Siwert Nilsson (1933–2002), prominent palynologist and gentian specialist from Stockholm, Sweden. Nilsson suggested the transfer of *Wurdackanthus frigidus* to *Symbolanthus* over 30 years ago based on pollen data, a transfer that is officially made here.

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