NATURAL HISTORY OF NEOTROPICAL ERICACEAE, 1: *GONOCALYX PULCHER* (ERICACEAE: VACCINIEAE), A REDISCOVERED AND RETYPIFIED COLOMBIAN BLUEBERRY*

James L. Luteyn

The New York Botanical Garden
Bronx, New York 10458, U.S.A.
Current address:
32075 East Side Drive
Beaver Island, Michigan 49782, U.S.A.
jim.luteyn@gmail.com

Daniel Mauricio Díaz-Rueda

RENAZ - Red de Reservas Naturales de Zapatoca
GIMBBE - Grupo de Investigación sobre
Memoria Biocultural y Botánica Económica
ICN - Instituto de Ciencias Naturales
Universidad Nacional de Colombia
Current address:
Calle 20 N° 7-12, Zapatoca, Santander, COLOMBIA
damdiazru@unal.edu.co

ABSTRACT

Gonocalyx pulcher (Ericaceae: Vaccinieae) has been rediscovered in the northeastern Colombian Andes after a lapse of over 135 years. Recent collections herein reported represent the only collections made since the type gathering by Schlim in 1851. The history of collections, cultivation, taxonomy, and nomenclature is reviewed. Generic and species descriptions for *G. pulcher* are updated and photographic illustrations are provided. The vegetation in which *G. pulcher* occurs, a list of its commonly associated Ericaceae, and its conservation status are briefly described. A new second-step lectotypification is made and the associated type herbarium specimens are illustrated. A key to all 11 species of *Gonocalyx* is provided.

RESUMEN

Gonocalyx pulcher (Ericaceae: Vaccinieae) ha sido redescubierto en los Andes del noreste de Colombia después de un lapso de más de 135 años. Las colecciones recientes aquí reportadas representan las únicas colecciones realizadas desde la recolección de tipos por Schlim en 1851. Se revisa la historia de las colecciones, el cultivo, la taxonomía y la nomenclatura. Se actualizan las descripciones genéricas y de especies de *G. pulcher* y se proporcionan ilustraciones fotográficas. Se describe brevemente la vegetación en la que se encuentra *G. pulcher* y se incluye una lista de sus Ericaceae comúnmente asociadas y su estado de conservación. Se realiza una nueva lectotipificación de segundo paso y se ilustran las muestras de herbario de tipo asociadas. Se proporciona una clave para las 11 especies de *Gonocalyx*.

KEY WORDS: Neotropics, Andes, endemism, cultivation, nomenclature, lectotypification, key to species, conservation status

INTRODUCTION

In the Neotropics, Ericaceae are one of the keystone families of vascular plants in the montane cloud forest ecosystem with approximately 46 genera and 800 species (70% of the genera and ca. 95% of the species are native, with 27 of the native genera from the tribe Vaccinieae). They often dominate a vegetation type called the "Befaria" or "ericaceaous belt" or "cordón de ericáceas" (see also DAMA 2000). Their diversification has been both recent and rapid and most of them must be considered vulnerable with many in extreme danger of extinction (Churchill et al. 1995; Luteyn 2002, 2004; Kron & Luteyn 2005; Schwery et al. 2015). The most extensive radiation of neotropical Ericaceae has occurred in Colombia, where 284 species have been published to date (ca. 38% of all neotropical Ericaceae currently recognized) and of which 165 are endemic (ca. 58%). These species are mostly found as epiphytes in premontane to montane elevations between 900 to 3000 m, although many are terrestrial, and a few are climbers (Luteyn 2002; Luteyn & Pedraza-Peñalosa 2021; Pedraza-Peñalosa et al. 2015, 2016).

Neotropical Ericaceae are still poorly known due mainly to our lack of knowledge of the Andean species, where many species yet to be discovered and their basic taxonomy are still in need of detailed phylogenetic analyses. Unfortunately, the same anthropomorphic and climatic pressures that are impacting all plant and

***This is the first in a series of planned papers under the general title "Natural History of Neotropical Ericaceae" initiated by co-author JLL.**

J. Bot. Res. Inst. Texas 15(2): 377–392. 2021
https://doi.org/10.17348/jbrit.v15.i2.1156

animal populations throughout Latin America are also threatening Colombia's extraordinary Ericaceae plant diversity. Furbush et al. (2017) correctly noted that, "Low population density or species rarity can [also] lead to the false assumption that a species has gone extinct, but with comprehensive surveys such species sometimes can be rediscovered." They further noted that, "During a time when … extinctions are becoming more common, it is important to celebrate rediscoveries. … Although emerging conservation programs are present … these efforts could be more strategic if we knew the population status of … and understood the life history of this species. … Additional surveys will continue to improve our understanding of … and allow us to promote the importance of endemic … [plants and animals] to scientists, the … government, and local communities." Thus, this paper points out again how little we know about the distribution and biogeography of neotropical Ericaceae and points out the continued need for field studies along with the absolute need for conservation efforts.

Therefore, the overall purpose of this paper is an up-to-date review of the 11 species in the genus *Gonocalyx*, distributed from the Caribbean and southern Central American regions to northern Colombia, including a brief history of the known species, a revised generic description, a new key to the species, and an updated description and typification of the "rediscovered" type species, *G. pulcher*. The new collections herein documented for *G. pulcher* significantly expand our understanding of its geographical distribution and make knowledge of its presence available to a wider audience. We also note an increase in the range of morphological variation in the size of leaf blades, petioles, inflorescences, pedicels, bracts, bracteoles, several floral parts, as well as fruit characteristics for *G. pulcher* and, therefore, a revised description for this species is herein included. We hope this paper will be a stimulus for further field studies.

Throughout this paper, herbarium acronyms follow *Index Herbariorum* (Thiers 2020+); for those not in *IH*, the acronym and location are given in the Acknowledgments below. Author abbreviations follow Brummitt and Powell (1996).

Species of *Gonocalyx* and history of collecting

In 1845 Wm. Purdie made the first collections of a small vacciniaceous plant in "N. Granada" (Colombia)—the plant now known as *Gonocalyx pulcher*. Some of Purdie's living material, as well as herbarium collections, were sent to W.J. Hooker at the Royal Botanic Gardens, Kew (England) for cultivation and identification. In 1847 N. Funck and L.J. Schlim collected living plant material and herbarium specimens for cultivation and distribution in Europe under the sponsorship of J.J. Linden; they collected the same unknown plant as that of Purdie (i.e., *G. pulcher*) from "Prov. de Soccorro: Lajitas" (currently Santander or Norte de Santander departments, Colombia). Schlim made the third known collection of *G. pulcher* in 1851 from "Ocaña" (Colombia), sending living plant material (for cultivation) and dried herbarium specimens to Linden in Brussels (Belgium). The herbarium collections of Purdie at Kew and Funck and Schlim at the Muséum National d'Histoire Naturelle (Paris, France) were not identified until 1931, when a Ph.D. student from the New York Botanical Garden, A.C. Smith, annotated them as *G. pulcher* Planch. & Lind.—the first taxonomic usage of the name since validly published by Linden in his nursery catalogue of 1855.

In Smith's dissertation publication, "The American Species of Thibaudieae," he (Smith 1932:353) resurrected the genus *Gonocalyx* with three species—*G. pulcher* from Colombia and two previously described West Indian species *Thibaudia portoricensis* Urban from Puerto Rico [as *G. portoricensis* (Urban) A.C. Sm.] and *Vaccinium smilacifolium* Grisebach from Dominica [as *G. smilacifolius* (Griseb.) A.C. Sm.]—he cited the generic type as "*G. pulcher* Planch. & Lind." [Gard. Chron. 1856:152].

There was no further mention of the genus until Nevling (1970) described a fourth species, *G. concolor* Nevling, from Puerto Rico, followed by Liogier (1971) with a fifth species, *G. tetrapterus* Alain, from the Dominican Republic. Luteyn (1976a) recognized the genus as occurring in Central America when he transferred *Themistoclesia pterocarpa* J.D.Sm. into *Gonocalyx* [as *G. pterocarpus* (J.D.Sm.) Luteyn] and described the new species *G. costaricensis* Luteyn, both endemic to Costa Rica. Later that year, Luteyn (1976b) described *G. almedae* Luteyn, also from Costa Rica. In 1990, while sorting through material of Ericaceae for the *Flora*

Mesoamerica treatment (Luteyn et al. 2009), Luteyn uncovered the first collections of *Gonocalyx* from Panama (Prov. Chiriquí)—*G. almedae*, already known from adjacent Costa Rica, and another novelty, *G. amplexicaulis* Luteyn. In 2001, Luteyn transferred the Panamanian *Macleania megabracteolata* Wilbur & Luteyn (Wilbur & Luteyn 1981) into *Gonocalyx* [as *G. megabracteolatus* (Wilbur & Luteyn) Luteyn]. Rodríguez and J.F. Morales (2006) described *G. lilliae* Al. Rodr. & J.F.Morales from Costa Rica, bringing the total number of species in the genus to 11.

Since its valid publication in 1855, no further herbarium collections of *Gonocalyx pulcher* were made despite many surveys in the same general areas of its original discovery ("Lajitas" and "prov. de Ocaña"), and all attempts to find *G. pulcher* (by the first author) in the Cordillera Oriental (Colombia) and Cordillera de Mérida (western Venezuela) failed. However, in 1984, one plant collection of this species (although unidentified) was made in the Serranía de Los Yariguíes (Dept. Santander) by R. Ardila (no. *255*). Later, between 2002–2005, three additional collections of *G. pulcher* were made (but still undetermined) in Dept. Norte de Santander by R. Galindo (no. *874*), J. Betancur (no. *11452*), and L.R. Sánchez (no. *9463*). In 2004, the *Galindo 874* and *Betancur 11452* collections (both at COL) were determined as *G. pulcher* by N. Salinas. At that time Salinas did not recognize the historical importance of these collections and the fruits remained unknown. Since 2012, the species has been collected several times in the Reserva Natural La Montaña Mágica - El Poleo near the village of Zapatoca (Dept. Santander) by co-author D. Díaz-Rueda (see all specimen citations below).

Authorship and typification of *Gonocalyx pulcher*

Since it was first mentioned by Linden (1854) and described by him (Linden 1855), the authorship, place of publication, and type of *Gonocalyx pulcher* (at both genus and species' levels) have been misunderstood, misinterpreted, and incorrectly cited. The following discussion clarifies these mistakes.

It took a few years for Schlim's living plant material to flower after he sent it to Linden in Brussels, but in his companies' nursery *Catalogue* no. 9, "Printemps et Été 1854" (Linden 1854:2), Linden mentioned (in passing) that several plants of "grand merite," such as "*Gonocalyx pulcher*," would soon be available for sale and distribution—that was the first ever mention of the generic name "*Gonocalyx*" (although not validly published therein). Linden's original 1854 (*Catalogue* 9) discussion follows:

> "… en compagnie d'autres arbustes de grand merite, que nous sommes heureux de posseder egalement a l'etat vivant et dont nous aurons prochainement occasion de parler. Ce sont … le *Gonocalyx pulcher*, charmant petit arubste a feuilles epaisses charnues, presque orbiculaires et a nombreuses fleurs tubuleuses d'un rouge vif; …"

The following year, in *Catalogue* 10 "Printemps, Été et Automne de 1855," on pages 5–6 under the section "Introductions de 1855," Linden formally and validly published "Gonocalyx pulcher, Pl. et Lind." (authorship of Planchon and Linden), therein also giving the first formal (valid) combined generic-specific description for *Gonocalyx*. It was offered for sale for 25 francs. According to Nevling (1970:227), "Planchon collaborated with Linden and it was he [Planchon] who did the technical botanical aspects of their joint efforts. … Linden would have sought Planchon's critical opinion prior to any decision to publish, particularly with such an interesting plant in a difficult family." Nevling (1970:226) also implied that *Catalogue* 10 of 1855 "contains a fine colored plate…"—but it does not. The colored plate appeared in *Catalogue* 11 issued in 1856 (see below). Linden's original 1855 (*Catalogue* 10) description follows:

> "Gonocalyx pulcher, Pl. et Lind. Charmante Vacciniée fructescente, à rameaux touffus, dressés, garnis d'un feuillage dense, et ca et là, parmi les feuilles, de jolies fleurs tubuleuses d'un rouge vif. Les feuilles sont petites, presqu'orbieulaires et ressemblent un peu à celles de l'Alaterne (*Rhamnus Alaternus*). Les jeunes pousses de méme que les nouvelles feuilles se colorent d'un beau rose pourpré. Découvert par M. Schlim, en compagnie du *Calyptraria haemantha*, etc., dans les provinces de Pamplona et d'Ocaña, où cet arbuste croit à un altitude de 7,000 pieds. …….. fr. 25"

The description of *Gonocalyx pulcher* was repeated in Linden's *Catalogue* 11 "Printemps, Été et Automne de

1856," virtually the same as that given in *Catalogue* 10 (quoted above), but was listed under "Plantes Nouvelles" and "Livrables Pour La Première Fois En 1856." At the end of *Catalogue* 11, Linden also provided an excellent color plate (illustration) of "*Gonocalyx pulcher* Planch. et Lind.—*Nouvelle Grenade*" (herein reproduced as Fig. 1A). Aside from Linden's nursery catalogues, *G. pulcher* (as genus and species) went uncollected and was unmentioned, seemingly forgotten, even in the important monographic works of Bentham and Hooker (1876) and Hoerold (1909). Nevling (1970:226) felt that the illustration was originally prepared for publication in the Belgian periodical *Flore des Serres* (ed. Ch. Lemaire), but it was never used—the reason for Nevling's opinion was not given. We feel that it is also possible that the description and illustration were intended for publication in Linden and Planchon's *Plantae columbianae* (1863, *Fl. Columb.* ined.).

Linden also promoted the sale of his new plant when he sent the color illustration and a brief description of "Gonocalyx pulcher. *Planchon and Linden Fl. Columb. ined.*" to John Lindley for publication in his *Gardeners' Chronicle* (1856:152). Lindley's note on the new introduction was translated as follows:

> "A charming (greenhouse) shrub, related to *Vaccinium*, with close upright branches, clothed with dense foliage, among which appear here and there pretty tubular flowers of a brilliant rose. The leaves are small, almost orbicular, and not very unlike those of an *Alaternus*. The young shoots and new leaves are of a bright rosy purple colour. It was found by Schlim in company with *Calyptraria haemantha* (a glorious shrub, noticed in our volume for 1854, p. 556) in the provinces of Pamplona and Ocaña at the elevation of 7000 feet above the sea."

The description and illustration of *Gonocalyx pulcher* from Lindley's *Gardeners' Chronicle* (Lindley 1856; the left-hand flowering branchlet from the *Catalogue* printed without color and in reverse, not the three flowering branches with several vegetative ones of the original *Catalogue* 11 plate), in turn, was picked up and re-used in the *Floricultural Cabinet* (vol. 24: 57, March 1856, where the illustration consisted of only the central flowering branchlet from the original *Catalogue* 11), and was again repeated and translated in both the *Belgique Horticole* (Morren 1856) and the *Revue Horticole* (Martins 1856).

Basically, all modern indices and online references are incorrect in their citations of the authors, place of publication, and/or date of publication and all need to be updated with the information herein provided. For example: 1) *Index Kewensis* (Jackson & Hooker 1893, vol. 1, pt. 2: 1054) cited the authorities of *Gonocalyx* as "Planch. & Linden," but incorrectly cited the *Gardeners' Chronicle* as the place of publication, an opinion which was accepted by A.C. Smith and H. Sleumer, the two world's "ericologists" of the 1920s–1960s; 2) the "Supplement 13" of *Index Kewensis* (Taylor 1966: 62) attributed authorship to "Planchon & Linden ex A.C. Smith" with Smith's (1932:352) publication of "The American Species of Thibaudieae" as the place of publication, and through its "*Supplement 21*" (Davies 2002) this citation was never corrected; 3) after "*Supplement 21*" (1996–2000), the last "*Supplement*" published in book-form, the entire *Index Kewensis* dataset including the "*Supplement*" series ceased to exist in book-form and became part of the *International Plant Names Index* (IPNI), which is now available online at www.ipni.org; 4) the *International Plant Names Index* (IPNI) (online ver. seen 14 May 2021) gives the generic authority and place of publication of *Gonocalyx* as "Planch. & Linden, Gard. Chron. 1856: 152"—it also gives two choices for the species *G. pulcher*, the first "Planch. & Linden ex A.C. Sm., Contr. U.S. Natl. Herb. xxviii. 353 (1932)" and the second "Planch. & Linden, Gard. Chron. 1856: 152 (1856)"; 5) the online version of *Index Nominum Genericorum* (ING, Farr et al. 1979; update for the *Gonocalyx* record was 9 Feb 1996) has corrected the authority, but the place of publication is still listed as "Gard. Chron. 1856"; as does 6) *Tropicos* (online ver. seen 14 May 2021), which gives the correct authority as "Planch. & Linden," but still attributes the place of publication to the *Gardeners' Chronicle*.

Second-step lectotypification of *Gonocalyx pulcher*

In following *Index Kewensis* A.C. Smith (1932:353) incorrectly cited the place of publication of *Gonocalyx pulcher* as "Gard. Chron. 1856: 152. 1856"—he also stated that the type was a "Cultivated Plant: (K, type, raised from original)." The plant may have been cultivated at Kew from original material of a Schlim collection that

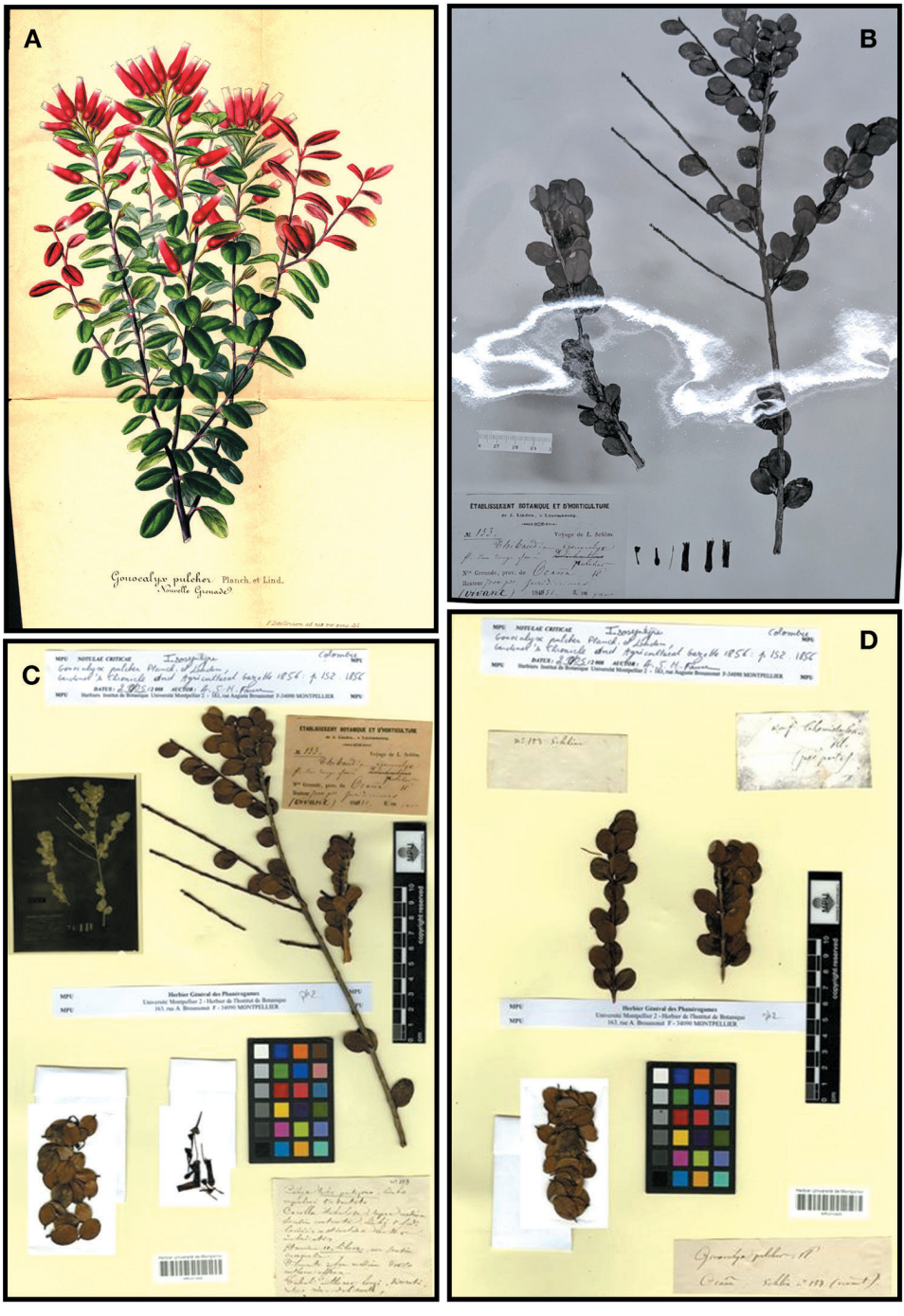

Fig. 1. *Gonocalyx pulcher.* **A.** original plate from Linden's (1856) "Catalogue des plantes exotiques" (reproduced from The New York Botanical Garden, LuEsther T. Mertz Library's copy of Linden's Cat. 11). **B.** photograph from MPU of the original *Schlim 153* material used by Nevling (1970) for his lectotype (photo currently mounted on a herbarium sheet at the Arnold Arboretum of Harvard University (A), kindly made available to JLL by David Boufford). **C.** re-mounted "syntype" at MPU (MPU012422) herein designated as the new, second-step lectotype (image downloaded from JSTOR's Global Plants). **D.** re-mounted "syntype" (=isolectotype) at MPU (MPU012423) (image downloaded from JSTOR's Global Plants).

was sent to W.J. Hooker by Linden, but the Kew herbarium specimen (K000370583) was incorrectly cited by Smith as the "type." There was no collection number given on the Kew specimen, but Nevling (1970:226) stated that it "bears the *Gardeners' Chronicle* reference and it is possible, if not probable, that the specimen had its origin from Linden's original sale offering. The important questions are when, where, and by whom the original gathering was made. On the basis of the information supplied by Linden, the original discovery was made by Schlim … at Ocaña …" [Colombia].

Sometime around 1970, while working on the ecology of an elfin forest in Puerto Rico, Larry Nevling was sent a photograph from the herbarium MPU in Montpellier, France of a plant specimen collected by Schlim in 1851 (i.e., *Schlim 153;* see Fig. 1B; photo negative currently at MPU; photo print mounted at A). The collection label from that material (see Fig. 2A) was a printed label and stated "ÉTABLISSEMENT BOTANIQUE ET D'HORTICULTURE de J. Linden, à Luxembourg" for the "Voyage de L. Schlim." It showed a hand-written determination of "Thibaudia - Gonocalyx pulcher Pl." [JLL feels that this handwriting compares favorably with that of Planchon as illustrated in Steinberg (1977:14)], also the collection date as 1851 and the collection locality as "N^{lle} Grenade, prov. de Ocaña," and the notation "(vivant)" indicating that living material had been collected—all corresponding to the information given by Linden (1855) for his newly cultivated plant *Gonocalyx pulcher.* With this photograph in hand, along with the information given on the labels seen in the photograph, Nevling (1970:227) recognized that the specimen of *Schlim 153* at MPU was original material of *G. pulcher* Planchon & Linden. He also stated, "It is apparent that the *Schlim 153* (MPU) is the holotype … of *G. pulcher* Planchon & Linden and that Smith's [1932:353] typification was in error." Thus, the photograph of the specimen at MPU (see Fig. 1B) that was sent to Nevling was what he used as the basis for stating the "specimen" at MPU was the "holotype" (actually lectotype) of *Gonocalyx pulcher.* Nevling worked only from the photograph sent to him by MPU, because he himself never actually annotated any material at MPU, or at least there are no annotation labels with his name on any specimens of *G. pulcher* at MPU.

Since 1970, the specimen that Nevling saw in the photograph from MPU (Fig. 1B), and upon which he based his lectotype, has been broken up, re-arranged, and now mounted onto two syntype sheets (see Fig. 1C and 1D herein, and JSTOR Global Plants). This may be confirmed by a closer look at the actual photograph of the MPU herbarium material of *Schlim 153* that was subsequently sent to Nevling. It reveals (to us) that the plant material was actually unmounted and still in newspaper at the time the photograph was taken. We may assume this because of the way the current two syntype sheets are re-arranged and now mounted, each sheet with different plant fragments and labels from what is shown in the original MPU photograph; it is also obvious that in some cases pieces of the plants shown in the photograph were further broken up and re-mounted on different sheets!

Since there are currently two syntype sheets of *Gonocalyx pulcher*, *Schlim 153* at MPU, neither of them corresponding to the MPU photograph that was used by Nevling (1970) to establish the lectotype, a new typification is needed. We are herein designating as a second-step lectotypification (as per the *Code*, Art. 9.17 Ex. 12, Turland et al. 2018) the sheet at MPU (with barcode MPU012422), which is a specimen from the original material most likely used by Planchon and which is the best sheet of the two syntypes.

From our newly designated lectotype specimen at MPU (see Fig. 1C herein and shown on JSTOR's Global Plants), it can be seen that the sheet has mounted on it: 1) a large, upper sterile portion of a branch and a smaller fertile portion of a branch bearing one partially-covered flower, 2) the original printed label "ÉTABLISSEMENT BOTANIQUE ET D'HORTICULTURE, de J. Linden, à Luxembourg" for the "Voyage de L. Schlim." (Fig. 2A) in the upper right-hand corner that gives the collection date of 1851 and the collection locality of "Nlle. Grenade, prov. de Ocaña," and the notation "(vivant)," 3) an original, hand-written label (in the hand of Planchon) in the lower right-hand corner that bears abundant notes on the flower morphology (Fig. 2B), 4) two packets with loose leaves and flowers in the lower left-hand side of the sheet, 5) a glassine packet in the upper left-hand side containing the photo negative of the "type" specimen seen and used by Nevling (1970), and 6) at the top of the sheet an MPU annotation label dated 20 May 2008 with the determination "Gonocalyx pulcher Planch. et Linden, Gardeners' Chronicle. …" and "Isosyntype" by A.J.M. Faure.

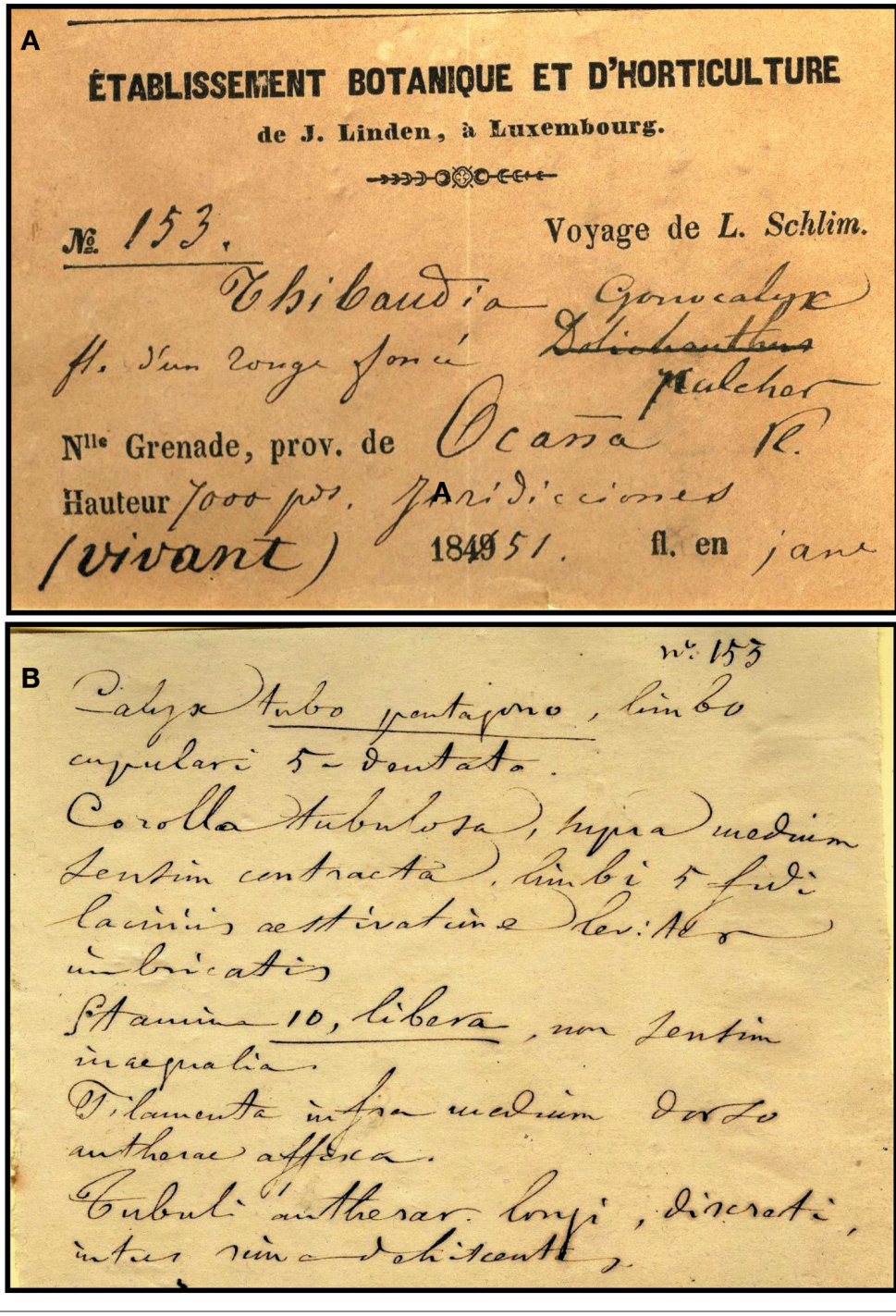

Fig. 2. *Gonocalyx pulcher*. **A.** original label from *Schlim 153* mounted on lectotype sheet MPU012422 (image downloaded from JSTOR Global Plants). The characters "Vr" to the right of Ocaña and the word "Jurisdicciones" below Ocaña seemingly indicate the more exact locality, possibly "páramo de Jurisdicciones" in Ábrego municipality. **B.** original description of *G. pulcher* mounted on lectotype sheet MPU012422 (image downloaded from JSTOR Global Plants).

The second syntype (now isolectotype) sheet at MPU (MPU012423; see Fig. 1D herein and JSTOR's Global Plants) has mounted on it: 1) in the center of the sheet, two sterile twig fragments with numerous leaves (seen in the original MPU photograph), 2) in the lower right-hand corner, a hand-written label (I believe in Planchon's hand!) stating "Gonocalyx pulcher, Pl. Ocaña . Schlim n. 153 (vivant)" (also seen in the original MPU photograph), 3) near the top of the sheet, a small unopened packet bearing an unrecognized hand-written "No. 153 Schlim", 4) in the upper right-hand side of the sheet, another small unrecognized hand-written label reading "conf. Themistoclesia Kl. (pro parte)", 5) in the lower left-hand portion of the sheet, another small packet bearing loose leaves, and 6) at the top of the sheet an MPU annotation label also dated 20 May 2008 with the determination "Gonocalyx pulcher Planch. et Linden, Gardeners' Chronicle …." and "Isosyntype" by A.J.M. Faure.

Updated generic description of *Gonocalyx*

Small, compact terrestrial or usually epiphytic shrubs. Leaves alternate, coriaceous, sessile or petiolate, the lamina orbicular, elliptic to ovate, flat to revolute, the apices acute to acuminate, obtuse, or retuse, the margin entire or crenate; venation obscurely plinerved. Inflorescence axillary, flowers solitary, in pairs, or in loose few-flowered racemes; floral bract 1, usually small but in *G. lilliae* 5–20 mm long and foliaceous (*fide* protologue), persistent; bracteoles 2, usually basal (but apical and just below calyx in *G. megabracteolatus*), aristate, ovate to elliptic, acuminate, 1–16 mm long, deciduous in *G. lilliae*. Flowers perfect, 5-merous (4-merous in *G. tetrapterus*), aestivation valvate; calyx articulate with pedicel, somewhat obprismatic, the tube terete, bluntly angled or narrowly winged alternately with the lobes, the limb erect, 4–5-lobed, the lobes triangular, apiculate; corolla tubular, subcylindric, cylindric-campanulate, or globose-urceolate, carnose, glabrous within, 5-lobed, the lobes triangular, subacute, erect to spreading; stamens 8–10, isomorphic, equal, inserted on a fleshy, 10-lobed nectariferous disc, nearly as long as corolla, without disintegration tissue; filaments distinct or connate, basifixed, the thecae granular, the tubules thinner and (2–)3–5 times longer than thecae, dehiscing by minute, subterminal, introrse, oblique pores or short slits; pollen in tetrahedral tetrads, viscin threads absent; ovary inferior, 5-locular, the placentation axile, the ovules numerous, the style filiform about as long as corolla, or the truncate stigma slightly exserted. Fruit a spherical to depressed-globose berry (possibly winged in *G. tetrapterus fide* protologue), the mature color white or red in *G. portoricensis*, possibly red in *G. tetrapterus*, dark purple to blue-black in *G. pterocarpus* and *G. pulcher*, unknown in all other species).

Distribution.—Costa Rica, Panama, Colombia, Caribbean (Dominican Republic, Puerto Rico, Dominica, Guadeloupe). *Gonocalyx* is generally poorly collected and additional fieldwork is needed because the species are usually known from only a few gatherings.

Generic Characterization.—A.C. Smith (1932) characterized *Gonocalyx* by the *combination* of calyx articulate (not continuous) with the pedicel, corollas tubular-cylindric with short lobes, stamens isomorphic (not dimorphic) and twice as many as the calyx (not equal in number), staminal filaments distinct, anthers with rigid, elongated (long), slender tubules (2–5 times longer than and ca. half diam. as the thecae) that open by introrse oblique pores. Smith (1932), Sleumer (1941), and Luteyn (1976a,b, 1990) have all continued to emphasize the length of the corolla lobes (i.e., shorter than and in comparison with *Ceratostema*) and the anther tubules (much longer in proportion with the thecae) as the characters most important to the generic recognition of *Gonocalyx*. At this time, however, several of these morphological features are seen to vary—for example, both connate and distinct staminal filaments occur in *Ceratostema*, *Semiramisia*, *Oreanthes*, *Macleania*, *Psammisia*, and *Thibaudia*, whereas both articulate and continuous calyces with regard to their pedicels occur in *Vaccinium*, *Ceratostema*, *Themistoclesia*, *Thibaudia*, etc.—and perhaps should not be considered of primary taxonomic importance in generic delimitation—most are not synapomorphic, sometimes not even in combinations.

Phylogenetic studies by Kron et al. (2002b) demonstrated the Vaccinieae as a monophyletic tribe within the Ericaceae: Vaccinioideae and molecular studies by Kron et al. (2002a) of the neotropical genera of Vaccinieae have further shown that *Gonocalyx* is part of a well-supported Meso-American/Caribbean clade, of Mesoamerican origin, and sister to an Andean clade of South American genera. Unfortunately, the Kron et al.

(2002a) study sampled only two of the 11 species of *Gonocalyx*, both from Costa Rica-Panama and viz., *G. costaricensis* and *G. megabracteolatus*. The most recent and only other phylogenetic (molecular) study of neotropical Vaccinieae by Pedraza-Peñalosa et al. (2015), nearly doubled the number of species sampled compared to the studies of Kron et al. (2002a,b), although no additional species of *Gonocalyx* were included. It did, however, confirm that those two species of *Gonocalyx* were a monophyletic group and were sister to each other in a Meso-American/Caribbean Clade of Mesoamerican origin. It would now be interesting to sample additional species of *Gonocalyx* to see where the South American *G. pulcher* fits into this scheme and if a Mesoamerican origin is still upheld. Pedraza-Peñalosa et al. (2015) concluded, "Clearly, more exhaustive analyses are necessary to fully resolve intergeneric relationships, and even the monophyletic groups here discerned … need better representation," such as *Gonocalyx*. Because the results of Pedraza-Peñalosa et al. (2015) also showed evidence of multiple dispersals of Andean Vaccinieae to Central America, they concluded that it would also be important to increase the representation of Central American species to further explore diversification and colonization of that region. It is possible that a radiation within the Central America/Caribbean region of a genus of Andean origin such as *Gonocalyx* may have occurred to produce the seven species in Costa Rica-adjacent Panama, the four species in the Caribbean West Indies (Dominican Republic-Puerto Rico-Dominica/Guadeloupe), and *G. pulcher* the only species in South America (Colombia).

In summary, *Gonocalyx* is difficult to circumscribe. The species are distinct, but the morphological characters that have been used traditionally to define the genus are also found in several other genera of neotropical Vaccinieae—see Smith (1936), Macbride (1959), Stevens (1971), and the various Luteyn papers cited herein for morphologically-oriented taxonomic opinions. Current molecular phylogenetic work indicates that not only are there problems of generic circumscription in neotropical Vaccinieae in general, but that various genera are monophyletic or paraphyletic and that, for example, *Macleania* is derived from within *Psammisia* (see Kron et al. 2002a,b; Powell & Kron 2003, although *Gonocalyx* was not included in this study, and Pedraza-Peñalosa et al. 2015 for molecular-oriented opinions). So clearly, further generic realignments will be necessary. Based on extremely limited molecular data, the genus *Gonocalyx* is monophyletic as currently circumscribed (see Kron et al. 2002a; Pedraza-Peñalosa et al. 2015). In general and taking into account current molecular phylogenetic work, generic limits in neotropical Vaccinieae need to be reassessed and it is almost certain that further generic realignments will be necessary.

KEY TO THE SPECIES OF *GONOCALYX*

1. Flowers in racemes.
   2. Bracteoles large, 13–16 mm long, borne at apex of pedicel _____ **G. megabracteolatus** (Wilbur & Luteyn) Luteyn
   2. Bracteoles small, 1–2 mm long, borne at base of pedicel.
      3. Leaves 7–10 cm long; pedicels 16–29 mm long; calyx narrowly winged, the lobes less than 1 mm long; corolla 6–11 mm long; anther tubules 2.5–6 mm long; Panama and Caribbean.
         4. Leaves sessile, amplexicaul, broadly ovate to rotund; racemes 3–4-flowered; pedicels 16–20 mm long; calyx sinuses glabrous; corolla ca. 11 mm long; Panama _____ **G. amplexicaulis** Luteyn
         4. Leaves petiolate, not amplexicaul, ovate to ovate-lanceolate; racemes 4–8-flowered; pedicels 20–29 mm long; calyx sinuses ciliate; corolla 6–8 mm long; Dominica and Guadeloupe _____ **G. smilacifolius** (Grisb.) A.C. Sm.
      3. Leaves 1.9–6 cm long; pedicels 4–11 mm long; calyx not winged, the lobes 1–2 mm long; corolla 12–17 mm long; anther tubules 7–8 mm long; Costa Rica.
         5. Branches, rachises, pedicels, calyx tubes, corollas, and fruits short-pilose; floral bracts 5–20 mm long; staminal filaments connate _____ **G. lilliae** Al. Rodr. & J.F. Morales
         5. Branches, rachises, pedicels, calyx tubes, corollas, and fruits glabrous to glabrescent; floral bracts ca. 1 mm long; staminal filaments distinct _____ **G. costaricensis** Luteyn
1. Flowers solitary or in pairs.
   6. Flowers tetramerous; Dominican Republic _____ **G. tetrapterus** Alain
   6. Flowers pentamerous; Puerto Rico, Central and South America.
      7. Staminal filaments connate; Costa Rica and Panama _____ **G. almedae** Luteyn
      7. Staminal filaments distinct; Puerto Rico, Costa Rica, and Colombia.
         8. Staminal dehiscence by subterminal, elliptical pores 0.5–0.75 mm long; corolla 13–15 mm long, glabrous within; Puerto Rico.
            9. Leaves ovate, ovate-elliptic, or rarely nearly orbicular, the margins obscurely crenate distally and nearly flat, the apices acute or obtuse _____ **G. concolor** Nevling

9. Leaves orbicular or broadly elliptic, the margins entire and strongly revolute, the apices rounded _____ **G. portoricensis** (Urb.) A.C. Sm.

8. Staminal dehiscence by lateral slits 2–4 mm long; corolla 15–23 mm long, densely white-pubescent distally within; Colombia and Costa Rica.

10. Leaf margins remotely but conspicuously crenate; pedicels (9–)15–18 mm long, glabrous; calyx ca. 5 mm long; filaments glabrous or sparsely pubescent at margins; Colombia _____ **G. pulcher** Planch. & Linden

10. Leaf margins entire or remotely crenate distally; pedicels 5–9(–13) mm long, glabrous; calyx 3–4.5 mm long; filaments glabrous; Costa Rica _____ **G. pterocarpus** (Donn. Sm.) Luteyn

Updated species description of *Gonocalyx pulcher*

Gonocalyx pulcher Planch. & Linden, Établ. Linden, prix-courant 10:5–6. 1855. TYPE. "N^{lle} Grenade, prov. de Ocaña" [Colombia: Norte de Santander], 2150 m, 1851, *Schlim 153* [LECTOTYPE: first-step designated by L. Nevling (1970:227), MPU (photo A); second-step lectotypification (as per ICN, Art. 9.17 Ex. 12), **here designated,** MPU (MPU012422, online image!); ISOLECTOTYPE: MPU (MPU012423 online image!).] No other material of this collection number has been seen or located by us.

Terrestrial **shrub** 1.5–5 m tall, sometimes scandent, much-branched from the base, seemingly without lignotuber (Fig. 3A); young branchlets angled or slightly ribbed and purplish, becoming subterete and reddish-brown when mature, drying brown, glabrous; axillary buds with prophylls 2, inconspicuous, valvate, lanceolate-acuminate, 1.5–1.7 mm long. **Leaves** with mature blades oriented more-or-less perpendicular to the stem, elliptic to ovate-elliptic, 14–27 × 10–18 mm, apically rounded, apiculate and tipped with a tiny, blunt, glandular-mucro, basally cuneate to rounded, marginally remotely but conspicuously bluntly crenate, glabrous, but with few, scattered, reddish glandular-fimbriae on both surfaces, the juvenile leaves red (Fig. 3B), the mature leaves discolorous, lighter colored beneath; 5(–7)- plinerved, the secondary nerves oriented from base or slightly above, ascending and along with the midnerve slightly raised above, obscure to plane or slightly raised beneath, the reticulate veinlets slightly raised above, but obscure beneath; **petioles** subterete, flat above, 1–4 mm long, puberulous with unicellular hairs or glabrous, red. **Inflorescences** axillary, toward ends of branchlets, of solitary or paired flowers, these surrounded at base by a few imbricate ovate, acute bractlets to 2 mm long; floral bract 1, ovate, acute, ca. 1-1.5 mm long, glabrous; **pedicels** terete to weakly ribbed, (9–)15–18 mm long, glabrous, red, apically bearing a few minute deciduous cartilaginous teeth; **bracteoles** 2, basal, similar to floral bracts but ca. 0.8–1.3 mm long. **Flowers** 5-merous; **calyx** articulate with pedicel, 4–7 mm long, glabrous, the tube subcylindric, 2–4 mm long, ca. 3.5 mm diam., pentagonal to slightly and bluntly 5-angled to sinuses, glabrous, green in bud, reddish-green at anthesis, the limb erect, campanulate, 2–3 mm. long including lobes, the lobes ovate, acuminate ca. 1–1.3 mm long, persistent and connivent over the ovary in fruit, the sinuses acute; **corolla** (Fig. 3C) carnose, tubular, cylindric and seemingly slightly curved at maturity, broadening distally, 17–20 mm long, 3–3.5 mm diam., red, glabrous without, white-tomentose distally within, the lobes spreading, oblong, obtuse, sometimes drying acute, 1–3 mm long; **stamens** 10, equal, ca. 14 mm long, yellow, the filaments equal, distinct, ca. 3–3.5 mm long, glabrous or sparsely pubescent at margins, the anthers equal, ca. 12–13 mm long, the thecae incurved at base, smooth to slightly papillose, ca. 4–5.2 mm long, the tubules slender, ca. 7.5–11 mm long, dehiscing by short distal clefts ca. 1–2 mm long; **style** equal to corolla or slightly exserted, the stigma truncate; nectariferous disc pulvinate, glabrous. **Fruit** a spherical berry (Fig. 3D), 10–14 mm diam., green when immature, turning whitish ("blanco") to purplish ("morados"), maturing nitid and dark purple or blue-black ("morado oscuro" to "rojizos"); seeds brown to orange, the embryo white.

Distribution and Ecology.—*Gonocalyx pulcher* is a showy, ornamental plant locally distributed in the Cordillera Oriental of northeastern Colombia. Since about 2005, co-author Díaz-Rueda has been studying montane forests in the Reserva Natural La Montaña Mágica - El Poleo and the Reserva Natural El Páramo - La Floresta in Santander department, where the species is found especially in semi-shade to open forest edges, to shrubby subpáramo sites, on rocky slopes, and generally humid to dry or semi-dry areas, at elevations of 1300–2700 m. It is found in association with Andean high-elevation forest species such as oak (*Quercus humboldtii* Bonpl., Fagaceae), wax palm [*Ceroxylon quindiuense* (H.Karst.) H.Wedl., Arecaceae], *Alfaroa williamsii* Ant.Molina (Juglandaceae), *Billia rosea* (Planch. & Linden) C.Ulloa & P.Jørg. (Sapindaceae),

Fig. 3. *Gonocalyx pulcher.* **A.** habit of terminal branches (*D. Díaz-R. et al. 1528,* MEDEL). **B.** new foliage (*D. Díaz-R. 1418,* MEDEL). **C.** branch tip showing mature leaves and flowers (*D. Díaz-R. et al. 1528,* MEDEL). **D.** branch tip showing mature berries (*D. Díaz-R. et al. 1528,* MEDEL). Photos: D.M. Díaz-Rueda.

Calycolpus moritzianus (O.Berg) Burret (Myrtaceae), *Clusia* spp. (Clusiaceae), *Myrsine latifolia* (Ruiz & Pav.) Spreng. (Primulaceae), *Sloanea* sp. (Elaeocarpaceae), *Symplocos crassulacea* B.Ståhl (Symplocaceae), *Viburnum glabratum* Kunth (Viburnaceae), and *Vismia baccifera* (L.) Triana & Planch. (Hypericaceae). In more open and drier areas it is found with species such as *Baccharis nitida* (Ruiz & Pav.) Pers. (Asteraceae), *Byrsonima crassifolia* (L.) Kunth (Malpighiaceae), *Calea trianae* Hieron. (Asteraceae), *Epidendrum arachnoglossum* Rchb.f. ex André (Orchidaceae), *Freziera candicans* Tul. (Pentaphylacaceae), *Ilex* cf. *nervosa* Triana (Aquifoliaceae), *Miconia rubiginosa* (Bonpl.) DC. (Melastomataceae), *Polygala paniculata* L. (Polygalaceae), *Psychotria erythrocephala* (K.Schum. & K.Krause) Standl. (Rubiaceae), *Pteridium arachnoideum* (Kaulf.) Maxon (Dennstaedtiaceae), *Siphocampylus glareosus* Zahlbr. (Campanulaceae), and *Turnera lineata* Urb. (Passifloraceae). In subpáramo

habitats it is generally found with species such as *Puya nitida* L.B.Sm. & Read (Bromeliaceae) and *Tamania chardonii* (A.C. Sm.) Cuartrec. (Asteraceae). It may even be found in disturbed areas along the edges of *Pinus* spp. (Pinaceae) plantations.

At the Reserva Natural La Montaña Mágica - El Poleo, *Gonocalyx pulcher* is associated with eight other species of Ericaceae—*Bejaria aestuans* L.f. (locally known as "morcate"), *Cavendishia bracteata* (Ruiz & Pav. ex J. St.-Hil.) Hoer., *Gaultheria erecta* Vent., *Monotropa uniflora* L., *Sphyrospermum buxifolium* Poepp. & Endl., *Orthaea cavendishioides* A.C. Sm., *Psammisia penduliflora* (Dunal) Klotzsch, and *P. pauciflora* [now *P. urichiana* (Britton) A.C. Sm., see Luteyn 2019]; whereas, in the Reserva Natural El Páramo - La Floresta, with low páramo vegetation in open areas and oak forests, it is associated with the Ericaceae—*Bejaria aestuans*, *B. resinosa* Mutis ex L.f., *Cavendishia bracteata*, *C. guatapeensis* Mansf., *C.* sp. subgen. *Chlamydantha* Luteyn, *Disterigma noyesiae* Luteyn, *D. staphelioides* (Planch. ex Wedd.) Nied., *Gaylussacia buxifolia* Kunth, *Gaultheria anastomosans* (L.f.) Kunth, *G. erecta, Monotropa uniflora*, *Psammisia penduliflora*, *Satyria* cf. *warscewiczii* Klotzsch, and *Sphyrospermum buxifolium*. [**Note**: The extremely rare *Orthaea cavendishioides* A.C. Sm., known only from the type collection made in 1927, has also been tentatively identified (by N.R. Salinas, COL) from both of these reserve areas.]

Gonocalyx pulcher has been collected in flower in the months of January, February, March, April, May, June, July, and October, and in fruit in January, February, September, and October. The fruits "didn´t taste very sweet to me" (Díaz-Rueda, pers. obs.).

Ecological studies of hummingbirds at Reserva Natural La Montaña Mágica - El Poleo by biologist M.A. Contreras-Vásquez have identified at least two hummingbird species, *Chlorostilbon poortmani* ["Short-tailed Emerald"] and *Amazilia franciae* ["Andean Emerald"], visiting the flowers of *Gonocalyx pulcher* (Contreras-Vásquez 2017, 2019 pers. comm.). Other personal observations by co-author D. Díaz-Rueda at Reserva Natural El Páramo - La Floresta, ca. 2500 m, include the hummingbirds *Colibri coruscans* ["Sparkling Violetear"], *Ocreatus underwoodii* ["Booted Racket-tail"], and *Chlorostilbon* sp., and the nectar-robber *Diglossa albilatera* ["White-sided Flowerpiercer"], along with the africanized european honeybee *Apis mellifera*. He has also observed there in the open, low páramos partially eaten fruits in the feces of the locally known "dog fox" (*Cerdocyon thous*), a medium-sized canid.

Preliminary Conservation Status.—*Gonocalyx pulcher* is endemic to montane areas in the Cordillera Oriental of northeastern Colombia (Santander and Norte de Santander departments), a region historically and currently under severe degradation from human activities, such as agriculture, logging, and livestock grazing (pers. obs.), which makes habitat destruction a potential threat. This is a poorly known species in ecological aspects that requires further collection and study. Unfortunately, there is little known about its population quantifications. Although this species has an EOO of 6,269.521 km^2, calculated with GeoCAT (http://geocat.kew.org/editor) according to our known coordinate collections and suggesting it as "Vulnerable" in accordance with the IUCN Red List Criteria (IUCN Standards and Petitions Subcommittee 2019), and an AOO of 36.000 km^2 suggesting it as "Endangered", our observations *in situ* and studied collections suggest that at least 10 healthy populations exist (and perhaps more), which apparently are not being reduced in extension, area or quality of habitat, conditions that would suggest that it is not in any category of threat (see also Bachman et al. 2011).

Although populations of *Gonocalyx pulcher* are found within areas dedicated to activities such as agriculture and livestock and so represent fragmented areas of continuous deforestation and human disturbances, most of the known localities of this species do have the protection of occurring in at least two national parks, the Área Natural Única Los Estoraques (near Ocaña and Playa de Belén, Dept. Norte de Santander) and the Serranía de Los Yariguíes (near San Vicente de Chucurí, Dept. Santander), as well as in all eight of the nature reserves of RENAZ (Red de Reservas Naturales de Zapatoca) (Dept. Santander), viz., El Páramo - La Floresta, La Montaña Mágica - El Poleo, Nirvana - Clavellinas, El Refugio del Oso, Mamá Bertha, El Naranjito - Nacumal, Traganubes, and Altagracia, with the largest and healthiest populations being found in the first two nature reserves. For those reasons, we categorize *G. pulcher* under the category called "Least Concern" (LC),

because it is unlikely to become extinct in the near future, but likely to be vulnerable due to large-scale forest destruction at higher elevations, even though some populations are in national parks." Currently the presence of *G. pulcher* in two national parks and eight civil society nature reserves should allow its long-term conservation.

All Specimens Known and Examined of *Gonocalyx pulcher.*—COLOMBIA: "Prov. de Socorro: Lajitas, 6000 ft, Jan 1847," (probably south of Socorro) (fl), *Funck & Schlim 1418*, P (P 00649617 on line!; no other herbarium material of this collection have been found and it is not a type of any sort as implied by H.O. Sleumer's annotations of 1959). **Santander**. San Vicente de Chucurí, Yariguíes, 1984 (st), *R. Ardila 255* (currently in the old INDERENA herbarium soon to be incorporated into FMB); Vereda La Cacica, nr. Zapatoca, Reserva Natural La Montaña Mágica - El Poleo, ca. 6°50'N, 73°18'W, 1800–2400 m, 2 Jul 2012 (fl), *D. Díaz-Rueda et al. 70* (MEDEL), alrededores de la casa y parte baja del sendero, 1800–1950 m, 12 Jan 2014 (fl, fr), *D. Díaz-Rueda et al. 539* (MEDEL), 2200–2300 m, 6 Oct 2017 (fl, fr), *D. Díaz-Rueda et al. 1418* (COL, MEDEL), 2100–2300 m, 2 Oct 2018 (fl, fr), *D. Díaz-Rueda et al. 1528* (MEDEL); Vereda Bellavista, nr. Zapatoca, Reserva Natural El Páramo - La Floresta, nr. bosque de La Herradura, ca. 6°49'N, 73°19'W, 2500–2700 m, 6 Jan 2015 (fl, fr), *D. Díaz-Rueda et al. 869* (MEDEL); Vereda Santa Rita, Reserva Natural Altagracia, junto a la vía que conduce a la escuela de la Vereda Santa Rita, 6°51'N, 73°18'W, 2000–2100 m, 27 Feb 2021 (fl, fr), *D. Díaz-Rueda et al. 2203* (CDMB, COL, HJJT, JAUM); Vereda Centro, Betulia, camino de Lengerke, desde el casco urbano de Betulia hacia la hacienda El Florito, 6°54'N, 73°17'W, 1900–2000 m, 3 Jan 2021 (fl, fr), *D. Díaz-Rueda et al. 2185* (CDMB, COL); Vereda Santa Bárbara, Betulia, camino de Lengerke, desde el casco urbano de Betulia hacia la hacienda El Florito, 6°55'N, 73°17'W, 2000–2100 m, 2 Jan 2021 (fl, fr), *D. Díaz-Rueda et al. 2188* (COL, JBB); Vereda Chanchón, San Vicente de Chucurí, Serranía de Los Yariguíes, cerro de Santa Lucía, camino de Lengerke entre Zapatoca y San Vicente de Chucurí, 6°51'N, 73°20'W, 2400–2500 m, 3 Feb 2021 (fl, fr), *D. Díaz-Rueda et al. 2195* (CDMB, COL, HJJT, JBB). **Norte de Santander**. "N^{lle} Grenade, prov. de Ocaña," 2150 m, 1851, *Schlim 153* (lectotype, here designated, see above, MPU; isolectotype, MPU); La Playa de Belén, Área Natural Única Los Estoraques, bosque de Piritama, 1800 m, 1 Jul 2002 (fl), *R. Galindo et al. 874* (COL), same area, 8°15'N, 73°15'W, 1700–1850 m, 23 Mar 2005 (fl), *J. Betancur et al. 11452* (COL, HUA); Vereda La Unión, Bochalema, montañas al noroccidente de la escuela, 7°35'N, 72°39'W, 1300–1500 m, 7 Jun. 2005 (fl), *L. Sánchez et al. 9463* (HECASA). **Other specimens examined.** Colombia: "New Granada," ex Hooker 1849, *Purdie s.n.* (GH), "N. Granada," *Purdie s.n.* (K), "N. Granada" *Purdie bis* (K); Cultivated plants, 1845, *Purdie s.n. "seed 248"* (K); "Hort. Kew" October 1879 (K).

ACKNOWLEDGMENTS

We wish to thank the staff and directors of the following herbaria for making specimens available for our study: CDMB (Corporación para la Defensa de la Meseta de Bucaramanga, Floridablanca, Santander), COL, FMB, HECASA, HJJT, HUA, JAUM, JBB, MEDEL, UDBC, and UIS. A sincere note of thanks goes to Esther Jackson and Don Wheeler, both retired, and Samantha D'Acunto (all from the LuEsther T. Mertz Library of The New York Botanical Garden) and Pedro Acevedo and Larry Dorr (both US) for their continued help with library resources. Thanks are due to Pierre Boillat (G), Craig Brough (K), Nicole Schuermans Ceulemans (the great-great-granddaughter of J.J. Linden!), Stefan Dressler (FR), Robbert Gradstein (GOET), Nicole Hanquart (Meise Botanic Garden), Caroline Loup (MPU), Pete Lowry (MO), Liesbeth Missel (Wageningen University & Research - Library), Walter Till (WU) and Matthias Svojtka (Library of the Institute of Botany and Biodiversity Research, University of Vienna), Jovita C. Yesilyurt and Jon Earle (both BM), and to the European Botanical and Horticultural Libraries Group (EBHL) for helping to locate rare copies of J.J. Linden's nursery catalogues (*Établ. Linden, prix-courant*). Special thanks are also extended to Clemens A. Wimmer (Deutsche Gartenbaubibliothek, Berlin) and the "European Nursery Catalogues" project for making available scans of Linden "Catalogues" on their website hosted by Internet Archive (https://archive.org/details/europeannurserycatalogues). We thank Cristina López-Gallego and Juan Daniel Vásquez-Restrepo for their collaboration with regard to determining the IUCN threat categorization of *G. pulcher*. We also thank Carmen Galdames (SCZ, retired) for reviewing the manuscript at various stages and for preparing the figures. We acknowledge the JSTOR Global Plants website as an extremely valuable repository of herbarium specimen images. Co-author JLL thanks Monique Boekhout for help translating French papers, and Sue Zmarzty (K) and Dave Boufford (A) for their efforts in sending images of herbarium sheets at Kew and the Harvard University Herbaria, respectively. Co-author DMD-R wishes to thank his family and the authorities at the Reserva "La Montaña Mágica-El Poleo" for permission to study and collect the plants there, and the RENAZ community, especially Milton Rueda Serrano, Reynaldo Díaz Rueda, Armando Gómez Rincón, Björn Reu, and Juan Fernando Martínez Contreras for permission and support to study and collect plants in nature reserves, and to biologists María Angélica Contreras-Vásquez and Daniel Eduardo Badillo-Mojica for hummingbird

determinations. We also wish to thank Walt Judd, "Chico" Morales, and one other anonymous reviewer for their helpful comments. In the end all decisions are ours and any comments/criticisms or differences of opinion concerning them are welcome.

REFERENCES

Bachman, S., J. Moat, A.W. Hill, J. de la Torre, & B. Scott. 2011. Supporting Red List threat assessments with GeoCAT: Geospatial conservation assessment tool. ZooKeys 150:117–126. doi: 10.3897/zookeys.150.2109

Bentham, G. & J.D. Hooker f. 1876. Genera plantarum ad exemplaria imprimis in Herbariis Kewensibus servata definita. 3 vols. Reeve, Williams & Norgate, London. [Vacciniaceae 2:564–577]

Brummitt, R.K. & C.E. Powell. 1992. Authors of plant names. Royal Botanic Gardens, Kew, UK.

Ceulemans, N.S. 2006. Jean Linden. Explorer - Master of the Orchids. Fonds Mercator, Brussels, Belgiium. [website: jean-linden.com]

Churchill, S.P., H. Balslev, E. Forero, & J.L. Luteyn, eds. 1995. Biodiversity and conservation of neotropical montane forests. New York Botanical Garden, Bronx, NY, U.S.A.

Contreras-Vásquez, M.A. 2017. Caracterización de los recursos florales utilizados por los colibríes en la RNSC "La Montaña Mágica - El Poleo," Zapatoca, Santander. Trabajo de grado presentado para optar al título de Bióloga. Universidad Nacional de Colombia – Sede Bogotá, Colombia.

Contreras-Vázquez, M.A. 2019. Interacciones entre colibríes y flores en la Reserva Natural de la Sociedad Civil "La Montaña Mágica - El Poleo," Zapatoca, Santander (Colombia). Ponencia oral presentada en el XI Congreso de Ornitología Neotropical, San José, Costa Rica.

DAMA (Departamento Técnico Administrativo Medio Ambiente). 2000. Protocolo distrital de restauración ecológica: Guía para la restauración de ecosistemas nativos en las áreas rurales de Santa Fé de Bogotá. Departamento Técnico Administrativo Medio Ambiente (DAMA), Alcaldía Mayor de Santa Fé de Bogotá, Bachaqueros, Fundación Estación Biológica. Santa Fé de Bogotá, Colombia.

Davies, R.A., ed. 2002. Index Kewensis Supplement 21. Royal Botanic Gardens, Kew, UK.

Farr, E.R., J.A. Leussink, & F.A. Stafleu, eds. 1979. Index Nominum Genericorum (Plantarum). Regnum Veg. 100–102:1–1896. Bohn, Scheltema & Holkema, Utrecht, Netherlands.

Farr, E.R., J.A. Leussink, & G. Zijlstra, eds. 1986. Index Nominum Genericorum (Plantarum) Supplementum I. Regnum Veg. 113:1–126. Bohn, Scheltema & Holkema, Utrecht, Netherlands.

Floricultural Cabinet. 1856 (March). [*Gonocalyx pulcher* Pl. & Lind.] 24:57, illustr.

Furbush, R., I.W. Caviedes-Solis, F.R. Méndez-de la Cruz, & A.D. Leaché. 2017. Missing in action for nearly 50 years: Rediscovery of the Mexican treefrog *Duellmanohyla ignicolor* (Anura: Hylidae). Mesoamerican Herpetology 4:120–127.

Hoerold, R. 1909. Systematische Gliederung und geographische Verbreitung der amerikanischen Thibaudieen. Bot. Jahrb. Syst. 42:251–334.

Index Nominum Genericorum (ING). 1954 (printed cards) and 1979 (book form, Farr et al. 1979). A compilation of generic names published for organisms covered by the ICN: International code of nomenclature for algae, fungi, and plants. [Supplement: Farr et al. 1986; online at https://naturalhistory2.si.edu/botany/ing/]

IUCN Standards and Petitions Subcommittee. 2019. Guidelines for using the IUCN Red List categories and criteria. Version 14. Prepared by the Standards and Petitions Subcommittee of the IUCN Species Survival Commission. Available at iucnredlist.org/documents/RedListGuidelines.pdf. [Accessed Aug. 2021]

Jackson, B.D. & J.D. Hooker, eds. [1893]–1895. Index Kewensis plantarum phanerogamarum: nomina et synonym omnium generum et specierum a linnaeo usque as annum MDCCCLXXXV complectans nomine recepro auctore patria unicuique planta subjectis: sumptibus beati Caroli Roberti Darwin ductu et consilio Josephi D. Hooker. Tomus 1–22 [Index Kewensis: an enumeration of the genera and species of flowering plants from the time of Linnaeus to the year 1885 inclusive together with their authors names, the works in which they were first published, their native countries and their synonyms: compiled at the expense of the late Charles Robert Darwin under the direction of Joseph D. Hooker. 2 vols.]. Clarendon Press, Oxford. doi: https://doi.org/10.5962/bhl.title.66720

JSTOR-Plants. 2018. JSTOR global plants. http://plants.jstor.org/

Judd, W.S. & J.L. Luteyn. 2006. Rediscovery of *Agarista bracamorensis* (Ericaceae: Vaccinioideae). Rhodora 108:97–102. http://www.jstor.org/stable/23313707

Kron, K.A. & J.L. Luteyn. 2005. Origins and biogeographic patterns in Ericaceae: New insights from recent phylogenetic analyses. Biol. Skr. 55:479–500.

Kron, K.A., E.A. Powell, & J.L. Luteyn. 2002a. Phylogenetic relationships within the blueberry tribe (Vaccinieae, Ericaceae) based on sequence data from *matK* and nuclear ribosomal ITS regions, with comments on the placement of *Satyria*. Amer. J. Bot. 89:327–336. doi: 10.3732/ajb.89.2.327

Kron, K.A., W.S. Judd, P.F. Stevens, D.M. Crayn, A.A. Anderberg, P.A. Gadek, C.J. Quinn, & J.L. Luteyn. 2002b. Phylogenetic classification of Ericaceae: Molecular and morphological evidence. Bot. Rev. 68(3):335–423.

Linden, J.J. 1853–1869. Jardin royal de zoologie et d'horticulture, de Bruxelles. Établissement d'introduction pour les plantes nouvelles, Catalogue des plantes exotiques, nouvelles et rares, cultivées dans les serres de J. Linden, … à Bruxelles. [TL-II abbrev.: *Cat. pl. exot.*] This overall title is given to Linden's nursery catalogues numbers 8–23 (1853–1869) since individual titles vary slightly, although older taxonomic literature still often refer to them simply as Linden's *Catalogue*, such as Lind. Cat. no. 10:5. 1855. [Examples of the title pages for the three catalogues mentioned in this paper are: *Catalogue* 9 "Établissement d'Introduction Pour les Plantes Nouvelles.—Printemps et Été 1854.—Supplément et Extrait du Prix Courant des Plantes Nouvelles et Rares, disponibles chez J. Linden, Horticulteur, au Jardin Royal de Zoologie et d'Horticulture, á Bruxelles"; for *Catalogue* 10 "Jardin Royal de Zoologie et d'Horticulture, de Bruxelles.—N° 10.—Établissement d'Introduction Pour les Plantes Nouvelles.—Catalogue des Plantes Exotiques, Nouvelles et Rares, Cultivées dans les Serres de J. Linden, …—A Bruxelles.—Printemps, Été et Automne de 1855"—Bruxelles."; and for *Catalogue* 11 "Établissement d'Introduction pour les Plantes Nouvelles. (Collections Botaniques et Zoologiques).—N° 11.—Supplément et Extrait du Catalogue des Plantes Exotiques, Nouvelles et Rares Cultivées dans les Serres de J. Linden, au Jardin Royal de Zoologie et d'Horticulture á Bruxelles.—Prix Courant pour Printemps, Été et Automne de 1856—Bruxelles."]

Linden, J.J. & J.E. Planchon. 1863. Plantae columbianae. Bruxelles. Reprint ed. 1977, Boerhaave Press, Leiden. [see "Avant-propos," p. i]

Lindley, J. 1856. New Plants. "164. Gonocalyx pulcher. *Planchon and Linden Fl. Columb. ined.*" Gard. Chron. 1856:152. [March 8, 1856]

Liogier, A.H. 1971. Novitates Antillanae. Mem. New York Bot. Gard. 21:107–157. [*Gonocalyx tetrapterus*, p. 140 and fig. 6A–E]

Luteyn J.L. 1976a. Notes on neotropical Vaccinieae (Ericaceae). I. *Gonocalyx*—a genus new to Central America. Brittonia 28:37–41. [*Gonocalyx pterocarpus*, p. 38, fig. 1; *G. costaricensis*, p. 40, fig. 2]

Luteyn J.L. 1976b. Notes on neotropical Vaccinieae (Ericaceae). III. New and noteworthy species from Mexico and Central America. Brittonia 28:400–406. [*Gonocalyx almedae*, p. 403, fig. 1]

Luteyn, J.L. 1987a. *Orthaea* (Ericaceae-Vaccinieae): New species and redefinition of the genus. Nord. J. Bot. 7(1):31–37.

Luteyn, J.L. 1987b. New species and notes on neotropical Ericaceae, Opera Bot. 92:109–130.

Luteyn J.L. 1990. *Gonocalyx amplexicaulis* (Ericaceae): A new Panamanian blueberry. Syst. Bot. 15:745–747. [*Gonocalyx amplexicaulis*, p. 745, fig. 1]

Luteyn, J.L. 2001. Two new species and two new combinations in Mesoamerican Ericaceae. Brittonia 53:437–446. [*Gonocalyx megabracteolatus*, p. 437]

Luteyn, J.L. 2002. Diversity, adaptation, and endemism in neotropical Ericaceae: Biogeographical patterns in the Vaccinieae. In: K. Young, C. Ulloa Ulloa, J.L. Luteyn & S. Knapp, co-authors & eds. Plant evolution and endemism in Andean South America. Bot. Rev. 68:55–87. doi10.1663/0006-8101(2002)068[0055:DAAEIN]2.0.CO;2

Luteyn, J.L. 2004. Ericaceae (Heath Family). Pp. 140–143. In: N. P. Smith, S.A. Mori, A. Henderson, D.W. Stevenson & S.V. Heald, eds. Flowering Plants of the Neotropics. Princeton University Press, Princeton, NJ, U.S.A.

Luteyn, J.L. 2019. Typification in and contributions to a revision of *Psammisia* (Ericaceae: Vaccinieae). J. Bot. Res. Inst. Texas 13:397–449.

Luteyn, J.L. & P. Pedraza-Peñalosa. 2021. Ericaceae. In: Acevedo-Rodríguez, P. et al. 2015-onwards. Lianas and climbing plants of the Neotropics. https://naturalhistory.si.edu/research/botany/research/lianas-and-climbing-plants-neotropics

Luteyn, J.L., R.L. Wilbur & L.B. Dorr. 2009. Ericaceae. Pp. 411–463. In: G. Davidse, M. Sousa S., S. Knapp, & F. Chiang, eds. Flora Mesoamericana: Cucurbitaceae a Polemoniaceae, Vol. 4(1). Mexico. [*Gonocalyx*, pp. 442–444]

Macbride, J.F. 1959. Ericaceae. In: J.F. Macbride, ed. Flora of Peru. Field Mus. Nat. Hist., Bot. Ser. 13(5):50–149.

Martins, Ch. 1856. Revue de l'Horticulture étrangère. Rev. Hort. IV. 5:162–165. [May 1856] https://www.biodiversitylibrary.org/item/196176 [—description of *Gonocalyx pulcher* taken from the *Gardeners' Chronicle* with French translation of the English]

Morren, ed. 1856. Plantes nouvelles de serre froide et tempérée: Mises pour la première fois dans le commerce, par M.J. Linden (Extrait du catalogue de M. Liden, *pour* 1856). Belgique Hort. 6:232 [*Gonocalyx pulcher* Planch. & Lind.].

https://www.biodiversitylibrary.org/item/27339 [*Gonocalyx pulcher* is listed, with text a near faithful reproduction of Linden's *Catalogue* 10 presentation, but without illustration]

Nevling, L.I., Jr. 1970. The ecology of an elfin forest in Puerto Rico, 12. A new species of *Gonocalyx* (Ericaceae). J. Arnold Arbor. 51:221–227. [*Gonocalyx concolor*, p. 222]

Pedraza-Peñalosa, P. 2015. *Themistoclesia diazii*, una especie neuva relacionada con los mortiños Colombianos (Ericaceae: Vaccinieae). Caldasia 37:99–105.

Pedraza-Peñalosa, P., J.L. Luteyn, & N.R. Salinas. 2016. Lista de Ericaceae de Colombia. Pp. 1188–1212. In: R. Bernal, S.R. Gradstein, & M. Celis. 2016. Catálogo de plantas y líquenes de Colombia, Vol I. Universidad Nacional de Colombia (Sede Bogotá), Colombia.

Pedraza-Peñalosa, P., N.R. Salinas, A.L.S. Virnig, & W.C. Wheeler. 2015. Preliminary phylogenetic analysis of the Andean clade and the placement of new Colombian blueberries (Ericaceae, Vaccinieae). PhytoKeys 49:13–31. doi: 10.3897/phytokeys.49.8622

Powell, E.A. & K.A. Kron. 2003. Molecular systematics of the northern Andean blueberries (Vaccinieae, Vaccinioideae, Ericaceae). Intern. J. Pl. Sci. 164(6):987–995. doi: 10.1086/378653

Rodríguez, Al. & J.F. Morales. 2006. El género *Gonocalyx* (Ericaceae) en Costa Rica, con una nueva especie. Novon 16:263–266. [*Gonocalyx lilliae*, p. 264]

Schwery O., R.E. Onstein, Y. Bouchenak-Khelladi, Y. Xing, R.J. Carter, & H.P. Linder. 2015. As old as the mountains: The radiations of the Ericaceae. New Phytologist 207:355–367.

Smith, A.C. 1932. The American species of Thibaudieae. Contr. U.S. Natl. Herb. 28:311–547. [*Gonocalyx*, pp. 329, 332, 352–355, *Gonocalyx smilacifolius*, p. 354, *Gonocalyx portoricensis*, p. 354 and plate 6]

Smith, A.C. 1936. Studies of South American plants, V. Additional notes on Thibaudieae. Bull. Torrey Bot. Club 63:307–316.

Stafleu, F.A. & R.S. Cowan. 1976–1988. Taxonomic literature: A selective guide to botanical publications and collections with dates, commentaries and types, TL-II. Ed. 2. Vols. I–VII. Bohn, Scheltema & Holkema, Utrecht, Netherlands.

Steinberg, C.H. 1977. The collectors and collections in the Herbarium Webb. Webbia 32:1–49.

Stevens, P.F. 1971. A classification of the Ericaceae: Subfamilies and tribes. J. Linn. Soc. Bot. 64:1–53.

Taylor, G. 1966. Index Kewensis plantarum phanerogamarum. Supplementum 13. Royal Botanic Gardens, Kew, UK.

Thiers, B. 2020+. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/science/ih/

Turland, N.J., J.H. Wiersema, F.R. Barrie, W. Greuter, D.L. Hawksworth, P.S. Herendeen, S. Knapp, W.-H. Kusber, D.-Z. Li, K. Marhold, T.W. May, J. McNeill, A.M. Monro, J. Prado, M.J. Price, & G.F. Smith, eds. 2018. International code of nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Veg. 159. Koeltz Botanical Books, Glashütten, Germany. https://doi.org/10.12705/Code.2018

Wilbur, R.L. & J.L. Luteyn. 1981. Additions to the Ericaceae of Panama. Ann. Missouri Bot. Gard. 68:154–166.