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Sam. P. vander Kloet
Acadia University

Jennifer L. Baltzer
Wilfrid Laurier University, jbaltzer@wlu.ca

Julia H. Appleby
University of Toronto

Rodger C. Evans
Acadia University

Donald T. Stewart
Acadia University

A re-examination of the taxonomic boundaries of *Symphysia* (Ericaceae)

Sam P. vander Kloet[1], Jennifer L. Baltzer[1,2], Julia H. Appleby[1,3], Rodger C. Evans[1] & Donald T. Stewart[1]

[1] *Department of Biology, Acadia University, Wolfville, Nova Scotia, B4P 2R6, Canada. sam.vanderkloet@acadiau.ca (author for correspondence); jennifer.baltzer@utoronto.ca; julie.appleby@utoronto.ca; rodger.evans@acadiau.ca; don.stewart@acadiau.ca*

[2] *Current Address: Faculty of Forestry, University of Toronto, Toronto, Ontario, M5S 3B3, Canada*

[3] *Current Address: Department of Molecular and Medical Genetics, University of Toronto, Toronto, Ontario, M5S 1A8, Canada*

DNA sequence data were generated for the nuclear ITS region for *Symphysia racemosa* and for 26 additional Vaccinieae representing 12 sections in the genus *Vaccinium* plus one species from each of five additional segregate genera. Our focus is on the placement of *S. racemosa* relative to *Vaccinium* sensu stricto and *Vaccinium* sect. *Oreades* (represented by *V. poasanum*). Maximum parsimony analysis of 608 bp of nrITS region suggests that *S. racemosa* and *V. poasanum* form a well-supported clade in spite of substantial morphological divergence. Furthermore, this clade is a sister group to a clade consisting of all segregate genera examined. These molecular results led us to undertake a morphological cladistic analysis of all of the other Central American green-flowered taxa. We suggest that the genus *Symphysia* should be expanded to encompass these 15 taxa, despite the lack of phylogenetic resolution within this group. This will necessitate eight new combinations, viz., *Symphysia almedae* (= *V. almedae*), *Symphysia costaricensis* (= *V. costaricense*), *Symphysia jefensis* (= *V. jefense*), *Symphysia orosiensis* (= *V. orosiense*), *Symphysia ovata* (= *Lateropora ovata*), *Symphysia perardua* (= *V. santafeënsis*), *Symphysia poasana* (= *Vaccinium poasanum*), *Symphysia santafeënsis* (= *L. santafeënsis*), and *Symphysia tubulifera* (= *L. tubulifera*).

KEYWORDS: Ericaceae, ITS, molecular phylogenetics, *Symphysia*, taxonomy, *Vaccinium*

INTRODUCTION

Symphysia racemosa (Vahl) Stearn was first recognised as a genus distinct from *Vaccinium* by Smith (1935). He cited a number of unique morphological features that defined this monotypic taxon including pleiomerous flowers, short carnose corollas, squat anthers, and anther tubules that dehisce by terminal pores (Fig. 1). Sleumer (1941) concurred with this segregation and noted that *Symphysia* flowers contain 10–14 stamens as well as a thick pedicel attached to a salver-shaped calyx tube.

In contrast to the above treatment, Stevens (1971) suggested that *Symphysia* "is no more different from *Vaccinium* sensu stricto than is *Vaccinium* § [sect.] *Oreades* Sleumer" and similarly, Luteyn & Wilbur (1978) argued that transferring *Symphysia* to *Vaccinium* "would not expand the limits of this extremely diverse genus". In the most recent review of the genus, vander Kloet (1985) concluded that adding *Symphysia* to *Vaccinium* is tantamount "to making the genus a dumping ground for taxa of uncertain affinity in the Vaccinieae..."

In this paper, we demonstrate that sequence data from the nuclear encoded ITS region clearly unites *S. racemosa* and *V. poasanum*. Given this result, we also undertook a morphological maximum parsimony analysis of 15 additional Central American green-flowered taxa to investigate their relationship to these two species.

MATERIALS AND METHODS

Molecular analysis. — Representative taxa were selected to include *S. racemosa*, *Vaccinium poasanum* sect. *Oreades* Sleumer, 20 other species of *Vaccinium* s.str. representing 11 sections, and five additional segregate genera in Ericaceae (Table 1). Sequences for two ericad outgroup taxa, *Kalmia cuneata* Michx. (U45905) and *Rhododendron alabamense* Rehder (AF091941) were obtained from the GenBank database.

Plant DNA was extracted from fresh eophylls and dried leaves from herbarium specimens using the DNeasy extraction kit (Qiagen). The manufacturer's extraction protocol was followed without modification. The nrITS region was PCR-amplified using the universal primers ITS-4 and ITS-5P of Möller & Cronk (1997). The PCR reaction conditions were as follows: initial

Table 1. Ericad nrITS sequences analysed. Voucher specimens corresponding to these sequences are deposited in the E.C. Smith Herbarium, Acadia University (ACAD). VDK = vander Kloet.

Genus, section, and species	Provenance	Ref. number	Genbank number
Segregate genera			
Cavendishia grandifolia Hoer.	Ecuador	8023	AY274558
Ceratostema peruviana Gmel.	Peru	5657	AY274559
Disterigma rimbachii (A.C. Smith) Luteyn	Ecuador	8011	AY274556
Macleania rupestris (H.B.K.) A.C. Smith	Costa Rica	VDK 513686	AY274557
Sphyrospermum buxifolium Poepp. & Endl.	Trinidad	VDK X123490	AY274555
Symphysia racemosa (Vahl) Stearn	Martinique	VDK 227274	AY27455
Vaccinium* sect. *Oreades			
Vaccinium poasanum	Costa Rica	VDK 1313686	AY274560
V.* sect. *Batodendron			
Vaccinium arboretum	Florida	VDK 49190	AY274569
V.* sect. *Bracteata			
Vaccinium acrobactracteatum	Papua-New Guinea	VDK 86875	AY274562
Vaccinium barandanum	Luzon	VDK 181092	AY274563
Vaccinium horizontale	Papua-New Guinea	VDK 530775	AY274561
Vaccinium varingiaefolium	Java	HS84-3	AY274564
V.* sect. *Conchophyllum			
Vaccinium nummularia	Nepal	VDK 1261092	AY274576
V.* sect. *Cyanococcus			
Vaccinium corymbosum	Florida	VDK ABS-5,6,7	AY274570
Vaccinium darrowii	Florida	VDK ABS8	AY274573
Vaccinium myrsinites	Georgia	VDK 422574	AY274572
Vaccinium tenellum	Georgia	VDK 133686	AY274571
V.* sect. *Eococcus			
Vaccinium fragile	Yunnan	VDK 12896	AY274580
V.* sect. *Galeopetalum			
Vaccinium gaultherifolium	Vietnam	VDK 1231197	AY274577
V.* sect. *Hemimyrtillus			
Vaccinium cylindraceum	Azores	VDK 1271097	AY274574
V.* sect. *Herpothamnus			
Vaccinium crassifolium	North Carolina	VDK 431881	AY274579
V.* sect. *Macropelma			
Vaccinium reticulatum	Hawaii	VDK 31390	AY274578
V.* sect. *Pyxothamnus			
Vaccinium consanguineum	Costa Rica	VDK 714686	AY274566
Vaccinium floribundum	Ecuador	*Ballington 14036* (ACAD)	AY274567
Vaccinium meridionale	Jamaica	VDK 10XII85	AY274565
Vaccinium ovatum	British Columbia	VDK 231879	AY274568
V.* sect. *Vaccinium			
Vaccinium uliginosum	New Hampshire	VDK 220895	AY274575
Outgroup:			
Kalmia cuneata			U48603
Rhododendron alabamense			AF072478

denaturation (95°C, 2 min), followed by 35 cycles of denaturation (95°C, 45 s), annealing (46°C, 45 s) and extension (72°C, 1 min 15 s), and concluding with a final extension (72°C, 4 min). PCR reactions were performed in 25 µl volumes containing 10× Amp buffer, 25 mM $MgCl_2$, 10 mM of each deoxynucleotide triphosphate, 1 µl of template DNA, 10 mg/ml bovine serum albumin and 5 U *Taq* polymerase.

A band corresponding to approximately 700 bp was excised from a 2% agarose gel in 1× TAE buffer and purified using a gel extraction kit (Qiagen). PCR products were cloned using a pGEM® T-easy vector system (Promega). A total of 500 ng of purified plasmid DNA was then sequenced in both directions on an Applied Biosystems 377 sequencer (University of Maine DNA sequencing facility). All sequences were submitted to GenBank.

Alignment of approximately 600 bp of sequence for the 29 Ericaceae sequences was performed using ClustalW (Thompson & al., 1994). Sites with gaps were

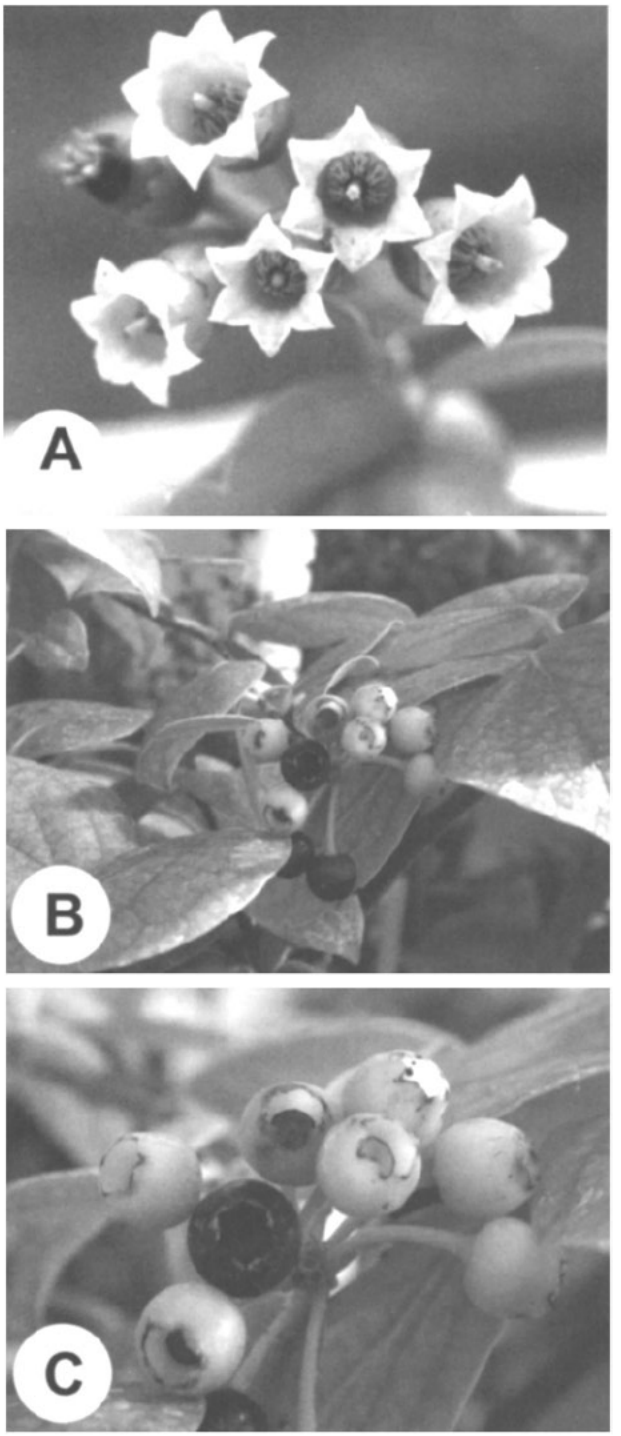

Fig. 1. Floral and fruit characteristics of *Symphysia racemosa* (Vahl) Stearn.

either excluded from the analysis or alternatively were treated as a fifth character-state. Maximum parsimony analysis was conducted in PAUP* (Swofford, 2000) using a Branch and Bound search routine. Support for each node was determined using heuristic bootstrapping (1000 replicates, each with 10 random addition sequences).

Table 2. Characters used in the maximum parsimony analysis of *Symphysia racemosa*, *Vaccinium poasanum*, and various other green-flowered taxa listed by Luteyn & Wilbur (1977).

	plesiomorphic - apomorphic
1.	Lignotuber absent - present
2.	Leaves conspicuously petiolate - subsessile
3.	Leaf base attenuate to rounded - cordate and/or amplexicaul
4.	Leaf venation pinnate - plinerved
5.	Secondary & tertiary veins neither strongly elevated nor forming a pronounced reticulum on the blade - secondary & tertiary veins strongly elevated beneath forming a coarse reticulum on the blade
6.	Floral axis development complete prior to anthesis - the axis continues to thicken until fruiting (i.e., becomes woody)
7.	flowers 5-merous - pleiomerous
8.	calyx tube obscure at anthesis - well developed at anthesis
9.	calyx tube terete at the base - lobed or angular at the base.
10.	calyx tube glabrous - hirsute or pubescent and/or glandular.
11.	calyx lobes obvious at anthesis - obscure (apiculate) at anthesis
12.	corolla lobes glabrous - floccose or glandular - hirsute on the inside
13.	corolla lobes much shorter than the tube (1:4) - ca. as long as the tube (1:1–1:3)
14.	corolla tube glabrous - hirsute, pubescent or glandular
15.	corolla not carnose (thin) - carnose and/or bistratose
16.	base of anther spurless - spurred
17.	anther sacs entire - split
18.	anther tubules well developed - rudimentary or absent
19.	anther tubule opening a pore - an introrse slit

Morphological analysis. — Based on the results of the molecular analysis that grouped *V. poasanum* with *S. racemosa* (see below), we decided to examine relationships among a number of additional Caribbean and Central American green-flowered Vaccinieae of uncertain affinity using the protologues and examining the specimens cited by Luteyn & Wilbur (1977), Wilbur & Luteyn (1978) and Wilbur (unpubl.) at the New York Botanical Garden. A total of 19 morphological characters (Table 2) was examined. Character states were coded using representatives of *Vaccinium* s.str. (namely *V. corymbosum* L. and *V. ovatum* Pursh) as the outgroup (Table 3). Phylogenetic relationships among these taxa were reconstructed using a Branch and Bound search routine in PAUP* (Swofford, 2000).

RESULTS AND DISCUSSION

Results from the phylogenetic analysis of nrITS sequences clearly demonstrate a close relationship between *Symphysia racemosa* and *Vaccinium poasanum* (Fig. 2). Although the ITS sequence data are clearly not

Table 3. Character states for the 19 morphological characters given in Table 2 coded with respect to the outgroup, represented by *Vaccinium corymbosum* and *V. ovatum*. New combinations and provenance of these taxa are provided in the text.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Lateropora ovata	0	0	0	0	0	1	0	1	0	0	0	1	1	1	1	1	1	1	0
Lateropora santafeënsis	0	0	0	0	0	1	0	1	0	0	0	1	1	1	0	1	1	1	1
Lateropora tubulifera	0	0	0	0	0	1	0	1	1	0	1	1	1	1	0	1	1	1	1
Vaccinium corymbosum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vaccinium costaricense	0	1	0	1	1	1	0	1	0	1	1	1	1	1	1	1	0	0	0
Vaccinium jefense	0	0	0	0	0	1	0	1	0	1	0	1	1	1	0	1	0	0	1
Vaccinium orosiense	0	1	1	1	0	1	0	1	0	0	1	1	0	1	0	1	0	0	0
Vaccinium ovatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vaccinium poasanum	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0
Vaccinium santafeënsis	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0	1
Symphysia flocosum	0	0	0	1	0	1	0	1	0	0	0	1	1	1	0	1	0	1	0
Symphysia racemosa	0	0	0	1	0	1	1	1	0	0	1	0	1	0	1	0	0	0	0
species nov. I	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1
species nov. II	0	0	0	0	1	1	0	1	0	1	0	0	1	1	0	1	0	0	1
species nov. III	0	0	0	0	0	1	0	1	1	0	1	1	1	1	1	0	0	0	0
species nov. IV	0	0	0	0	0	1	0	1	0	1	0	1	1	1	1	0	0	0	0
species nov. V	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0

able to resolve relationships among many of the sections of *Vaccinium* represented here, *S. racemosa* and *V. poasanum* are united with 76 and 88% bootstrap support (with gaps treated as missing data or as an additional character state, respectively). When gaps are treated as a new character, there is considerable bootstrap support (92%) for *S. racemosa* and *V. poasanum* grouping with the segregate genera. However, when these sites are eliminated from the analysis, support for this relationship drops to 54%.

These phylogenetic patterns are corroborated by Kron & al. (2002) and Kron (unpubl.), who not only found that *V. poasanum* and *V. luteynii* Wilbur are consistently linked with *Symphysia*, but also that this trilogy is a consistent subset within the Meso-American clade that comprises such South American segregate genera as *Cavendishia* Lindley, *Macleania* Hooker, *Siphonandra* Klotzsch and *Psammisia* Klotzsch. This Meso-American clade of segregate genera, which, according to Kron & al (2002) has 93% bootstrap support, is linked to the Andean clade of segregates such as *Satyria* Klotzsch and *Diogenesia* Sleumer.

The taxonomic choices available are as follows. Either transfer all these segregate genera to *Vaccinium* or just transfer *V. poasanum* and *V. luteynii* to *Symphysia*. Before advocating the latter, we felt that taxa associated with this pair by Luteyn and Wilbur (1977), Wilbur & Luteyn (1978) and Wilbur (unpubl.) and referred to as plants with "short, racemose, umbellate to subcorymbose inflorescences with green or yellowish corollas" ought to be examined. Furthermore, *Lateropora* A.C. Smith should be examined as it differs from these taxa only by two obvious characters: rudimentary antherial tubules and rupturing thecae.

Despite numerous attempts, we have not been able to successfully isolate and/or amplify DNA from the leaves of numerous herbarium specimens. Samples have historically been treated with alcohol and bromine to prevent rot that may render them useless for DNA analysis. Ideally, fresh *ex situ*, garden grown, or frozen material or possibly material stored in one of a number of field storage buffers (e.g., saturated NaCl/CTAB; see Štorchová & al., 2000) should be used as a source of DNA. Furthermore, obtaining fresh flush from the field in the near future for these various green-flowered species is highly unlikely. Aside from *V. poasanum* and *S. racemosa*, all the taxa listed by Luteyn & Wilbur (1977), Wilbur & Luteyn (1978) and Wilbur (unpubl.) are rare local endemics. Indeed, eleven out of the fifteen taxa under consideration are only known from the type or type locality (see taxonomy below).

Given that molecular work was not feasible, we attempted a morphological maximum parsimony analysis for these taxa. Twelve equally parsimonious trees were generated (not shown). If we accept the 50% majority rule consensus tree (Fig. 3), then the Central American *V. poasanum* is an obvious outlier, but the Caribbean *S. racemosa* is linked with a group of species endemic to the Chiriqui Region of Panama and adjacent Costa Rica. Indeed, in all the morphological cladograms these two taxa are consistently separated but are in fact genetically very similar (only differing by ~1% uncorrected sequence divergence). Note also that the only other species traditionally assigned to *Symphysia* (i.e., *S. floccosa*) is invariably placed in the same grade as the genus *Lateropora*.

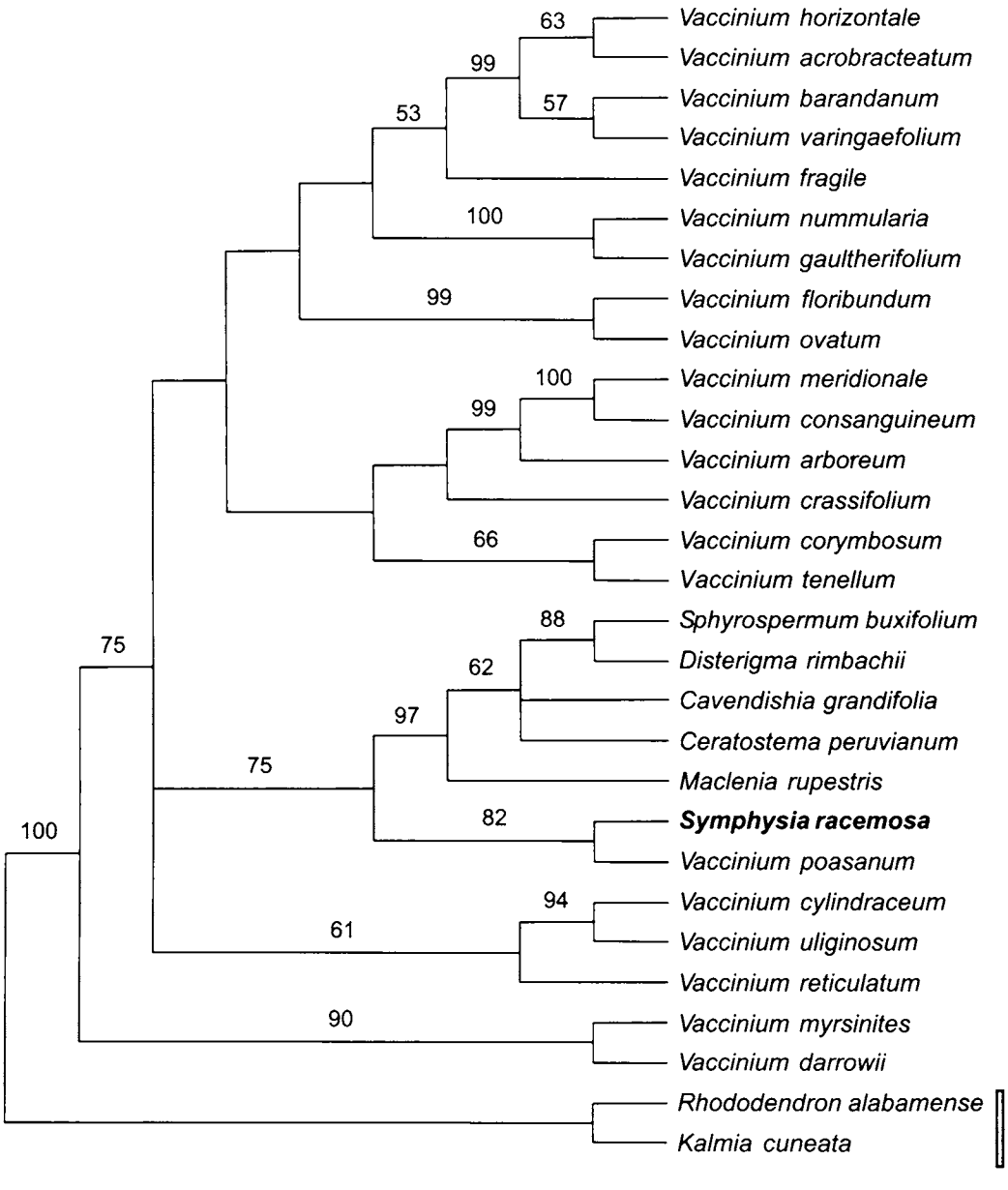

Fig. 2. Strict consensus Branch and Bound tree based on 608 bp of nrITS sequence data for 21 *Vaccinium* species, *Symphysia racemosa*, and five additional segregate genera. *Rhododendron alabamense* and *Kalmia cuneata* were included as outgroup taxa. Branch and bound analyses yielded six trees of length 360 steps (retention index = 0.726; consistency index = 0.617, excluding autapomorphies). Numbers above the lines are bootstrap values obtained using a heuristic search.

These results, both molecular and morphological, suggest that *V. poasanum* is misplaced in *Vaccinium* and should be transferred to an expanded *Symphysia* defined by the following synapomorphies: (1) a short rachis that continues to thicken until fruiting, i.e., becomes woody; and (2) the pedicels continue to lengthen and thicken distally until fruiting. These flaring pedicels often bear a corona of 5–12 caducous pili around the margin of the cup, where it articulates with the calyx tube (see vander Kloet, 1985, figs. 7 & 9). Furthermore, flowers of this group have greenish-white to greenish-pink corollas often with floccose lobes, and stamens or parts thereof that are often reduced, may have short, squat filaments, an anther sac base which is often contracted into a spur, anther tubules that are often rudimentary or absent; and thecae that may rupture; the latter allowing for a novel way for pollen dispersal.

Although sizeable gaps remain in this cladogram and

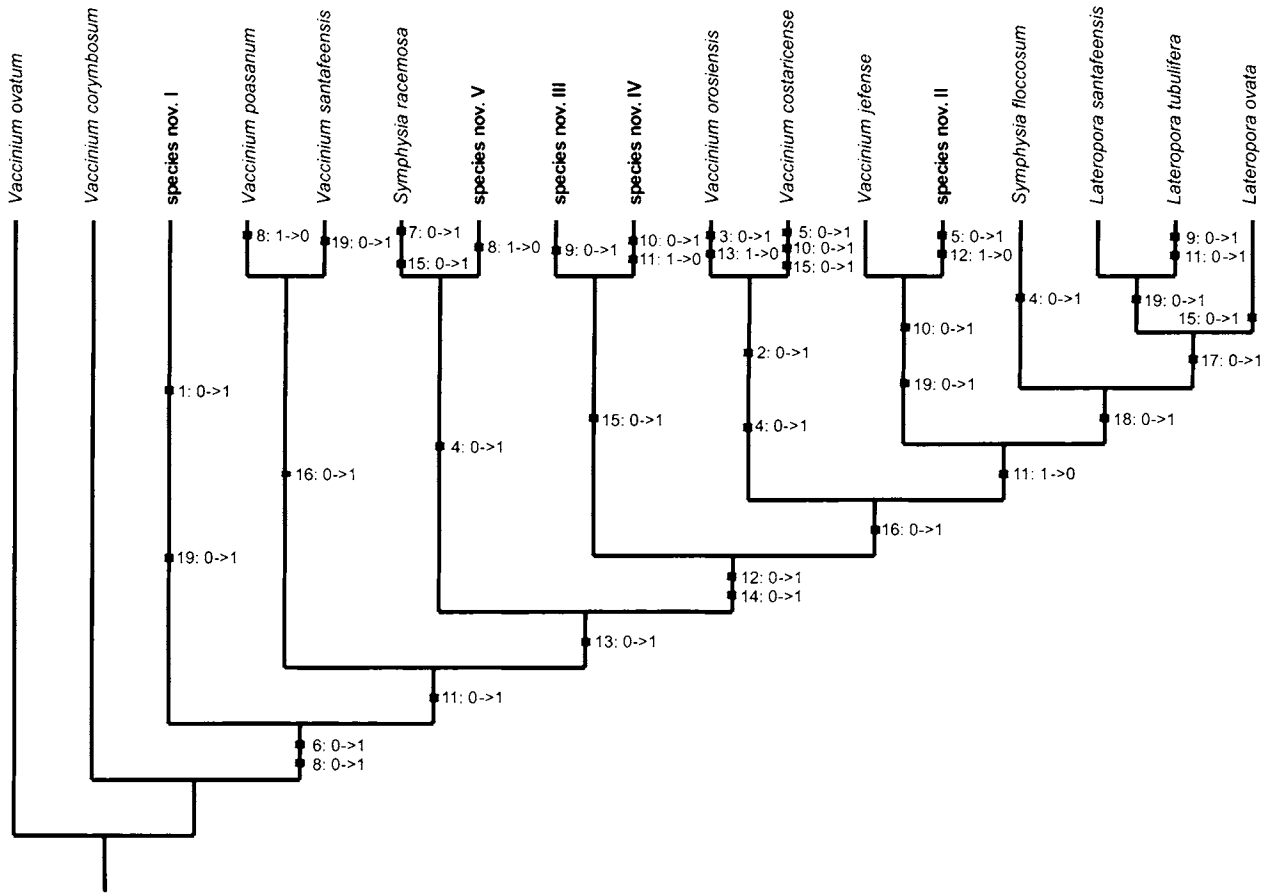

Fig. 3. One of 12 most parsimonious trees obtained from analysis of 19 morphological characters (see tables 2 and 3 for character state information). Branch and Bound analysis yielded trees of length 39 steps (retention index = 0.661; consistency index = 0.444, excluding autapomorphies).

others of the *Vaccinia* (see, for example, Kron & al., 1999, and vander Kloet & Patterson, 2000), revelation will come slowly as 90% of the 500 species in *Vaccinium* (Sleumer, 1941) are tropical or subtropical epiphytes, represented in the world's herbaria by only a few specimens.

TAXONOMY

Symphysia C.B. Presl, Epist. *Symphysia* (1827)

Type species: *Hornemannia racemosa* Vahl (1810) ≡ *Symphysia racemosa* (Vahl) Stearn (1972).

Hornemannia Vahl in Skrivter Nat.-Selsk. Kiøben havnb: 120 (1810); non *Hornemannia* Willd. (1809)

Vaccinium § *Oreades* Sleumer, Bot. Jahrb. 71: 417 (1941)

Straggly to compact and erect, epiphytic or terrestrial shrubs. Leaves alternate, short petiolate, coriaceous, pinnately veined or plinerved. Inflorescence axillary or terminal, subfasciculate or racemose with many flowers on long pedicels. Flowers with the calyx tube articulate with the pedicel, calyx tube often expanding prior to anthesis, calyx lobes 5–7, often rudimentary; corolla usually campanulate, often sub-carnose, greenish white to greenish pink, 5–8 lobed, lobes often floccose; stamens 10–12 (14) equal, usually 2/3 the length of the corolla, the filaments ± distinct, dorsally attached to the anthers near their midpoint, the anthers stout with granular thecae whose bases often end in a spur, the tubules rarely rudimentary but if present opening with a terminal pore or an introrse slit; style filiform and about as long as the corolla tube; the ovary inferior. Fruit a white, pink, purple or black berry with numerous tiny seeds.

The genus *Symphysia* contains approximately 15 species in Central America and the Caribbean with its center of diversity in the Chiriqui Region of Panama and adjacent Costa Rica.

Key to the species:

1. Flowers pleiomerous; corollas bistratose and carnose ..... *S. racemosa*
1. Flowers usually 5-merous; corollas subcarnose or

thinner, not bistratose 2
2. Corollas 12–14 mm in diameter; tubules as long as or longer than the rest of the stamen 3
2. Corollas < 11 mm in diameter, tubules shorter than the rest of the stamen 4
3. Calyx lobes ca. 0.5 mm long or less; calyx tube ca. 3 mm long at anthesis . . . . . *S. poasana*
3. Calyx lobes 3–4 mm long; calyx tube 5–7 mm long at anthesis . . . . . species nov. I [Based on material collected by J. L. Luteyn (NY) prior to 1990. Protologues are to be written by R. L. Wilbur.]
4. Anther tubules absent or rudimentary; thecae usually split 5
4. Anther tubules present, usually 1–4 mm long; thecae usually entire 6
5. Petioles > 5 mm long; calyx lobes 4–5 mm wide . . . . . *S. ovata*
5. Petioles < 5 mm long; calyx lobes ca. 2 mm wide . . . . . *S. santefeënsis*
6. Secondary and tertiary veins strongly elevated beneath forming a coarse reticulum on the blade. . 7
6. Secondary and tertiary veins neither strongly elevated nor forming a pronounced reticulum on the blade 8
7. Petioles 5–9 mm long; calyx lobes 5–6 mm long . . . . . *S. jefensis*
7. Petioles 2–4 mm long; calyx lobes < 2 mm long. . . . . species nov. II
8. Calyx tube angular or lobed at anthesis. 9
8. Calyx tube terete at anthesis 10
9. Calyx tube 10-lobed at the base . . . species nov. III
9. Calyx tube 5-angled at the base . . . . . *S. tubulifera*
10. Calyx lobes 2–5 mm long 11
10. Calyx lobes < 2 mm long or rudimentary 12
11. Calyx tube and lobes pilosulose . . . species nov. IV
11. Calyx tube and lobes glabrous . . . . . *S. floccosa*
12. Corolla glabrous on the inside. 13
12. Corolla ± pilose on the inside 14
13. Leaf venation 3, 5-plinerved; calyx lobes rudimentary . . . . . species nov. V
13. Venation pinnate; calyx lobes > 0.5 mm long . . . . . *S. perardua*
14. Calyx lobes rudimentary. . . . . *S. costaricensis*
14. Calyx lobes ca. 1 mm long; leaves usually amplexicaule or cordate. . . . . *S. orosiensis*

Synonymy:

Symphysia costaricensis (Wilbur & Luteyn) vander Kloet, **comb. nov.** ≡ *Vaccinium costaricense* Wilbur & Luteyn, Brittonia 29: 270. 1977.

Known from isolated collections from Heredia and San José, Costa Rica as well as adjacent Panama.

Symphysia floccosa (L.O. Williams) L.O. Williams, Phytologia 24: 158. 1972. ≡ *Hornemannia floccosa* L.O. Williams, Brittonia 18: 248. 1966 ≡ *Vaccinium floccosum* (L.O. Williams) Wilbur and Luteyn, Brittonia 29: 272. 1977.

Endemic to the Chiriquí region of Panama.

Symphysia jefensis (Luteyn & Wilbur) vander Kloet, **comb. nov.** ≡ *Vaccinium jefense* Luteyn & Wilbur, Brittonia, 29: 272. 1977.

Known only from a few localities in Panama.

Symphysia orosiensis (Wilbur & Luteyn) vander Kloet, **comb. nov.** ≡ *Vaccinium orosiense* Wilbur & Luteyn, Brittonia 29: 275. 1977.

Known only from the type locality, Tapanti, Cartago, Costa Rica.

Symphysia ovata (A.C. Smith) vander Kloet, **comb. nov.** ≡ *Lateropora ovata* A.C. Smith, Contrib. U.S. Natl. Herb. 28: 334. 1932.

Known only from a few collections from Cerro de la Horqueta, Chiriquí, Panama

Symphysia perardua vander Kloet, **nom. nov.** ≡ *Vaccinium santafeënse* Wilbur & Luteyn, Am. Mo. Bot. Gard. 65: 140. 1978.

This epithet is preoccupied by *Lateropora santafeënsis*, see below.

Known only from Cerro Tute, Veraguas, Panama.

Symphysia poasana (Donnell Smith) vander Kloet, **comb. nov.** ≡ *Vaccinium poasanum* Donnell Smith, Bot. Gaz. 24: 395. 1897.

Description and distribution of this Central American endemic in Wilbur and Luteyn (1978).

Symphysia racemosa (Vahl) Stearn, Taxon 21: 111. 1972. ≡ *Vaccinium racemosum* (Vahl) Wilbur & Luteyn, Brittonia 29: 275. 1977.

Description, distribution and synonomy of this much described West Indian species can be found in Smith (1935), Stearn (1972) and vander Kloet (1985).

Symphysia santafeënsis (Wilbur & Luteyn) vander Kloet, **comb. nov.** ≡ *Lateropora santafeënsis* Wilbur & Luteyn, Brittonia 29: 261. 1977.

Known only from the type collected near Santa Fé, Veraguas, Panama.

Symphysia tubulifera (Wilbur & Luteyn) vander Kloet, **comb. nov.** ≡ *Lateropora tubulifera* Wilbur & Luteyn, Ann. Miss. Bot. Gard. 68: 162. 1981.

Known only from the type locality, Cerro Hornito, Chiriquí, Panama.

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