

分布尼泊尔至台湾的少齿越桔组 (越桔属)*

S. P. vander Kloet¹, T. A. Dickinson, W. Strickland^{2,3}

(1 Department of Biology Acadia University, Wolfville, Nova Scotia BOP 1X0, Canada; 2 Center for Biodiversity & Conservation Biology Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario M5S 2C6, Canada; 3 Department of Botany University of Toronto, 25 Willcocks Street, Toronto, Ontario M5S 3B2, Canada)

摘要: 对越桔属 *Vaccinium* 中曾经被认为属于越桔组 *sect. Vitis-idaea* 的种或与之相关的 76 个运算上的分类单位进行数值分析, 并记录了 44 个特征, 解析如下: *Vaccinium sect. Vitis-idaea* 应是局限于越桔 *V. vitis-idaea* 这个种而言; 5 个喜马拉雅的分类单位: *V. nummularia*, *V. paucicrenatum*, *V. delavayi*, *V. retusum*, *V. moupinense*, 有 2 个表面上类似 *V. vitis-idaea* 的分类单位, 运算上总是聚类在一起都被归入少齿越桔组 *sect. Aethopus*. 其余 20 个操作分类单位 (OTU) 包含 10 个分类单位, 每个都十分特殊, 但没有显著的片段的样式可分辨。

Airy-Shaw 于 1948 年建立 *Vaccinium sect. Aethopus* 时含有他的新种 *V. setipes*, 这是一个介于 *V. paucicrenatum* 和 *sect. Vitis-idaea* 间的居间泪群, 他将 *V. paucicrenatum* Sleumer 从 *sect. Vitis-idaea* 转隶至 *sect. Aethopus*, 他还论证了 *V. nummularia* Hook. f. 和 *sect. Aethopus* 有明显的关联, 因而推断 *sect. Aethopus* 对 *sect. Vitis-idaea* 来说是一对姐妹类群。

Sleumer (1941) 在他的属和组的修订中对 *sect. Vitis-idaea* 除保留了模式种外, 改变了这个组的内容, 例如把一些种改隶至 *sect. Herpothamnus* (Small) Sleumer, *sect. Pyxothamnus* 和 *sect. Eococcus* (Table 1)

对 *sect. Vitis-idaea* 的这一重组, Stevens (1969) 未予认可, 他认为除模式种外, 他的形态学论据支持全部种类或归属于 *sect. Conchophyllum* 或归属于 *Agapetes* D. Don, 他认为 *sect. Vitis-idaea* 是单型组。在对越桔属的分类处理中, 他未提及 *sect. Aethopus*, 而是把它作为 *Agapetes* D. Don 的部分。

因此我们的初衷是检验那些曾经置于 *sect. Vitis-idaea* 中的各个类群间形态变异的连贯性, 尤其是那些被 Airy-Shaw (1948) 置于他的 *sect. Aethopus* 中的喜马拉雅类群和那些被 Stevens (1969) 转隶到他的扩大了 *sect. Conchophyllum* 或 *Agapetes* 属的分类群。

结果根据聚类分析 (Cluster analysis), 主坐标分析 (Principal coordinates analysis), 分配分析 (Partitioning analysis), 我们相信对 *sect. Vitis-idaea* 和 *sect. Aethopus* 的修订是有根据的。

所有分析表明, *Vaccinium sect. Vitis-idaea* 形成了极为孤立的一群, 无疑支持 Stevens (1969) 的这个组的单型性位置的观点。遗憾的是, 我们的分析没能解决 *sect. Conchophyllum*, *sect. Galeopetalum* 和 *Agapetes* 之间的关系。还需要做更多的工作, 尤其是研究粘连的花药在这些分类群中的出现和分布。

Sleumer (1941) 置入 *sect. Vitis-idaea* 中的半数分类群和 Airy-Shaw 置入 *sect. Aethopus* 中的那些分类群总是聚类一起 (Fig. 2, 3), 这个聚类有以下特征: 植株通常有一些刚毛状硬毛, 有多数小而常绿的叶, 沿世界屋脊出现从尼泊尔至台湾, 海拔通常在 1 500 ~ 3 000 m 间 (Table 2, Fig. 8), 通常附生, 但在海拔稍高处严格地生或石生 (Fig. 7)。

对于 *sect. Aethopus* 而言, *Vaccinium vitis-idaea* 已被明确排除出这个类群, 因而其模式位

* 收稿日期: 2002-05-28, 2002-06-05 接受发表

置也必须被摒弃。

Airy-Shaw (1948) 首先提出了 *V. nummularia*, *V. chaetothrix*, *V. paucicrenatum* 和 *V. setipes* 之间的密切亲缘。这些分类群共同具有被刚毛的枝条 (Fig.2, V_A, V_B) 和聚类 V_C 及 V_D 不同, 后者植株即使有也只有很少的刚毛。运用随机扩增多态 DNA (RAPD), 本文和 Paterson (2000) 指出了 *V. retusum* 出自 group V_C, *V. nummularia* 出自 group V_B 具有一组共同的等位基因。简而言之, group V 的 A, B, C, D 形成一个我们认为在片段水平上的相干的分类单位。

关键词: 越桔属; 少齿越桔组; 数值分类; 分类

中图分类号: Q 949 文献标识码: A 文章编号: 0253-2700(2003)01-0001-24

From Nepal to Formosa, a Much Larger Foot Print for *Vaccinium* Sect. *Aëthopus*

S. P. vander Kloet¹, T. A. Dickinson, W. Strickland^{2,3}

(¹ Department of Biology Acadia University, Wolfville, Nova Scotia BOP 1X0, Canada; ² Center for Biodiversity & Conservation Biology Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario M5S 2C6, Canada;

³ Department of Botany University of Toronto, 25 Willcocks Street, Toronto, Ontario M5S 3B2, Canada)

Abstract: Numerical analyses of 76 operational taxonomic units alleged to belong to or be associated with *Vaccinium* sect. *Vitis-idaea* at one time or other, and scored for 44 features, resolved the following: *Vaccinium* sect. *Vitis-idaea* should be restricted to *V. vitis-idaea*; five Himalayan taxa, two of which superficially resembled *V. vitis-idaea*, consistently clustered together and are classified as *V. sect. Aëthopus*. The remaining 20 OTU's comprise 10 taxa, each quite distinct, but no obvious sectional pattern was discerned.

Key words: Genus *Vaccinium*; sect. *Aëthopus*; Numerical taxonomy; Taxonomy

Introduction

When Airy-Shaw (1948) erected *Vaccinium* sect. *Aëthopus* to accommodate his new species, *V. setipes* he also transferred *V. paucicrenatum* Sleumer from sect. *Vitis-idaea* to sect. *Aëthopus* on the grounds that *V. setipes* was an intermediate between *V. paucicrenatum* and *Vaccinium* sect. *Vitis-idaea*. Furthermore, he argued that *V. nummularia* Hook.f. and *V. chaetothrix* Sleumer were both clearly allied to his new section and thus by inference promoting his sect. *Aëthopus* as a sister taxon to sect. *Vitis-idaea*.

Sect. *Vitis-idaea* was first described by Dumortier in 1827 to accommodate those *Vaccinia* that possessed awnless stamens and campanulate corollas namely *V. vitis-idaea*. This meagre protologue was expanded by A. Gray in 1848 as follows: ovary 4-5 celled, corolla campanulate or globular, 4-5 lobed; anthers 8-10, awnless; filament hairy; flowers in short, bracteate, racemes, leaves evergreen; berries red or purple. Klotzsch (1851) modified this description slightly by adding that the locules contain no spurious septa; the corolla may be cylindrical; the anthers may be shortly awned; the racemes may be bracteate and these bracts may be coloured. All are shrubs with persis-

tent leaves growing in the Americas and Europe. In addition to the type, *V. vitis-idaea* L., which is usually reported as 4-merous with 8 stamens (Linnaeus, 1737; Camp, 1945; Palser, 1961; Vander Kloet, 1988), but where the occurrence of the 5 merous condition has been observed (Warmington, 1908), Klotzsch (1851) added 16 taxa from the Americas to this section (Table 1).

Table 1 List of species referred to *Vaccinium* sect. *Vitis-idaea* in previous taxonomic treatments.

Klotzsch (1851)	Sleumer (1941)	Stevens (1969)
<i>V. vitis-idaea</i> L.	<i>V. vitis-idaea</i> L.	<i>V. vitis-idaea</i> L.
<i>V. ovatum</i> Pursh	<i>V. sikkimense</i> Clarke	
<i>V. crassifolium</i> Andrews	<i>V. nummularia</i> Hook f. ****	
<i>V. thymifolium</i> Kl.	<i>V. monetarium</i> Sleumer	
<i>V. moztinia</i> Benth	<i>V. chaetothrix</i> Sleumer ****	
<i>V. confertum</i> HBK	<i>V. paucicrenatum</i> Sleumer ****	
<i>V. brachystachyum</i> Benth *	<i>V. chapaense</i> Merrill	
<i>V. mortizianum</i> Kl.	<i>V. pumilum</i> Kurz.	
<i>V. floribundum</i> HBK	<i>V. retusum</i> (Griff.) Hook f. ****	
<i>V. polystachyum</i> Benth **	<i>V. haitangense</i> Sleumer	
<i>V. montanum</i> Pohl.	<i>V. manipurensis</i> (Watt) Sleumer	
<i>V. scabrum</i> Pohl ****	<i>V. moupinense</i> Franchet ****	
<i>V. villosum</i> Smith	<i>V. dendrocharis</i> Handl.-Mazz. ****	
<i>V. consanguineum</i> Kl.	<i>V. delavayi</i> Franchet ****	
<i>V. densiflorum</i> Benth.	<i>V. merrillianum</i> Hayata ****	
<i>V. corymbodendron</i> D. Don.		
<i>V. caracasana</i> HBK		

* = *V. confertum*

** = *V. floribundum*

*** = *Gaylussacia pseudo-gaultheria*

**** = The hispid-setose cluster in Fig 3.

In his revision of the genus and its sections, Sleumer (1941) extended this description of *V. sect. Vitis-idaea* as follows: the inflorescences are pseudo-terminal, i.e., the flower buds are produced at, or near, the apex of the current shoots; the emerging raceme is few flowered; flowers are borne on short pedicels and these pedicels are articulated with the calyx tubes. Nonetheless, but for the type, he changed its entire contents, viz. *V. crassifolium* Andrews was transferred to *V. sect. Herpothamnus* (Small) Sleumer; *V. ovatum* Pursh, *V. confertum* Kunth, *V. floribundum* Kunth & *V. consanguineum* Klotzsch to his section *Pyxothamnus*; and the remaining taxa (Table 1) to his section *Eococcus*. In their stead, he included seventeen East Asian and Himalayan taxa (Table 1) most of which had been included by Clarke (1882), in section *Epigynium* (Klotzsch) J. D. Hooker.

This reconstitution of section *Vitis-idaea* was rejected by Stevens (1969) who argued that his morphological data supported the removal of all but the type species to either section *Conchophyllum* Sleumer or *Agapetes* D. Don. According to Stevens (1969), section *Vitis-idaea* is monotypic and *V. vitis-idaea* differs from all the species previously placed in this section in having campanulate, deeply lobed, 4-merous flowers; anthers dehiscing by terminal pores; marginal leaf fibres and a pericyclic phellogen. In his taxonomic treatment of *Vaccinium*, Stevens (1969) omitted any mention of section *Aëthopus* Airy-Shaw but dealt with it as part of *Agapetes* D. Don.

Nevertheless when the senior author saw the clonal mats of *V. dendrocharis* Handel-Mazzetti on the rocky summit of Fan Xi Pang at 3142 msm on 24 November 97, he was struck by their similarity to mats of *V. vitis-idaea* and he thought that this was either a case of habitat selection generating a similar

life form and physiognomy or , as Sleumer (1941) had surmised , a common ancestry .

Our initial objective , therefore , was to examine the consistency of the morphological variation among the various taxa that have at one time or other been lodged in section *Vitis-idaea* , and in particular , those Himalayan taxa that Airy-Shaw (1948) placed in his section *Aëthopus* and those that Stevens (1969) transferred to his expanded section *Conchophyllum* or the genus *Agapetes* .

To that end , 76 OTU 's from 21 taxa (Table 2) were scored for the 44 characters described below (Table 3) . This is not a *de novo* list of characters and their states but rather a list of those utilized by the authors of the sectional classifications cited above in order to refute the allegation “ of course you could not recover my classification since you did not use my character suite ” . Only staminal characters 04STAM1 , 05STAM2 , 06ANTHD , and 28ANTHA require extensive explication here since the terminology of these features has been the subject of considerable dispute . Initially , as Table 4 shows , the anthers of *Vaccinium* were described as having *bicornes et aristis duabus* by Linnaeus in 1737 . Smith (1819) translated *aristae* as spurs or bristles , i. e. *calcar aut seta* . Wight (1850) described with illustrations various appendages on the anthers as well as partial fusion of the tubules . Klotzsch (1851) observed that stamens , or their parts , might differ in length within the same androecium , and , he also noted that filaments could be connate . Variation in anther dehiscence was elaborated by Smith in 1932 .

Table 2 Provenance of *Vaccinium* sect. *Vitis-idaea* specimens scored for the data matrix .

OTU	Taxon	Voucher No.	Provenance	MSM
01	<i>V. vitis-idaea</i>	625887 (ACAD)	Newfoundland ,	100
02	<i>V. vitis-idaea</i>	112989 (ACAD)	Scotland ,	900
03	<i>V. dendrocharis</i>	129796 (ACAD)	Yunnan ,	3200
04	<i>V. dendrocharis</i>	129796β (ACAD)	Yunnan ,	3200
05	<i>V. nummularia</i>	4241092 (ACAD)	Nepal ,	2300
06	<i>V. nummularia</i>	1261092 (ACAD)	Nepal ,	2200
07	<i>V. nummularia</i>	3251092 (ACAD)	Nepal ,	2840
08	<i>V. chapaense</i>	2231197 (ACAD)	No. Vietnam ,	2000
09	<i>V. chapaense</i>	6131197 (ACAD)	No. Vietnam ,	1900
10	<i>V. chapaense</i>	2241197 (ACAD)	No. Vietnam ,	2800
11	<i>V. retusum</i>	Ludlow 2973 (BM)	Bhutan ,	2100
12	<i>V. retusum</i>	Lister 62 (K)	Sikkim ,	2400
13	<i>V. retusum</i>	1251092 (ACAD)	Nepal ,	2840
14	<i>V. retusum</i>	2261092 (ACAD)	Nepal ,	2300
15	<i>V. retusum</i>	1271092 (ACAD)	Nepal ,	2300
16	<i>V. retusum</i>	5261092 (ACAD)	Nepal ,	2300
17	<i>V. retusum</i>	2271092 (ACAD)	Nepal ,	1952
18	<i>V. chaetothrix</i>	Kingdon-Ward 13223 (BM)	No. Burma ,	2850
19	<i>V. triflorum</i>	1131197 (ACAD)	No. Vietnam ,	1700
20	<i>V. glauco-album</i>	Beer <i>et al</i> 12331 (BM)	Nepal ,	2830
21	<i>V. glauco-album</i>	Kingdon-Ward 11548 (BM)	Assam ,	2700
22	<i>V. glauco-album</i>	Ludlow <i>et al</i> 17386 (BM)	Bhutan ,	3000
23	<i>V. sikkimense</i>	Beer 25475 (BM)	Nepal ,	3540
24	<i>V. sikkimense</i>	Stainton 8312 (BM)	Nepal ,	3750
25	<i>V. sikkimense</i>	Li 2304 (KUN)		2900
26	<i>V. moupinense</i>	Wu 57483 (KUN)	Szechuan ,	1900
27	<i>V. sciaphilum</i>	Wu 53569 (KUN)	Yunnan ,	2800
28	<i>V. sciaphilum</i>	Sun <i>et al</i> 678 (KUN)	Tibet ,	2400
29	<i>V. delavayi</i>	Su <i>et al</i> 628 (KUN)	Yunnan ,	3000
30	<i>V. delavayi</i>	Kingdon-Ward 20259 (BM)	Assam ,	3150
31	<i>V. delavayi</i>	Su <i>et al</i> 762 (KUN)	Yunnan ,	2800
32	<i>V. delavayi</i>	Guang <i>et al</i> 642 (KUN)	Guangxi ,	2018

Table 2 continued

OTU	Taxon	Voucher No.	Provenance	MSM
33	<i>V. delavayi</i>	51.576 (KUN)	Szechuan ,	2200
34	<i>V. delavayi</i>	1241196 (ACAD)	No. Vietnam ,	3142
35	<i>V. delavayi</i>	04454 (BM)	Tibet ,	2500
36	<i>V. delavayi</i>	Wu 7432 (KUN)	Yunnan ,	1810
37	<i>V. glauco-globosum</i>	Wu 64 – 0104 (KUN)	Yunnan ,	1600
38	<i>V. gauthierifolium</i>	Stainton 6844 (BM)	Nepal ,	2250
39	<i>V. gauthierifolium</i>	Ghashi <i>et al</i> 775316 (BM)	Nepal ,	2000
40	<i>V. gauthierifolium</i>	1231197 (ACAD)	No. Vietnam ,	2200
41	<i>V. tonkinense</i>	3241197 (ACAD)	No. Vietnam ,	2800
42	<i>V. ovatum</i>	8131182 (ACAD)	British Columbia ,	15
43	<i>V. consanguineum</i>	413886 (ACAD)	Costa Rica	3200
44	<i>V. crassifolium</i>	431881 (ACAD)	North Carolina	20
45	<i>V. dendrocharis</i>	Wu 8690 (KUN)	Yunnan	3200
46	<i>V. dendrocharis</i>	Wu 8156 (KUN)	Yunnan	2800
47	<i>V. dendrocharis</i>	Nujiang 79 – 0073 (KUN)	Yunnan	2600
48	<i>V. dendrocharis</i>	Kingdom-Ward 13052 (BM)	Burma	2400
49	<i>V. dendrocharis</i>	Lee <i>et al</i> 05159 (KUN)	Tibet	2500
50	<i>V. dendrocharis</i>	Wang 70459 (GH)	Yunnan	2300
51	<i>V. delavayi</i>	Rock 22483 (GH)	Tibet	3000
52	<i>V. delavayi</i>	Kingdom-Ward 6797 (K)	Tibet	2850
53	<i>V. delavayi</i>	Rock 22057 (GH)	Tibet	3000
54	<i>V. moupinense</i>	Lee 6514 (KUN)	Shichuang	2000
55	<i>V. chaetothrix</i>	Yü 12 (KUN)	Yunnan	2500
56	<i>V. chaetothrix</i>	inhai-Tibet Team 3983 (KUN)	Tibet	2600
57	<i>V. chaetothrix</i>	Sun <i>et al</i> 4054 (KUN)	Tibet	2700
58	<i>V. nummularia</i>	Agnes 22 (K)	Sikkim	3000
59	<i>V. nummularia</i>	Durongjiang Team 6930 (KUN)	Yunnan	2900
60	<i>V. delavayi</i>	Sino Brit expt in 1981 (GH)	Yunnan	2700
61	<i>V. delavayi</i>	Ching 21543 (GH)	Yunnan	2800
62	<i>V. delavayi</i>	Forrest 17597 (GH)	Yunnan	2900
63	<i>V. delavayi</i>	McLaren 35 (GH)	Yunnan	2850
64	<i>V. delavayi</i>	Yü 16728 (GH)	Yunnan	2700
65	<i>V. delavayi</i>	Fang 0201 (KUN)	Yunnan	2900
66	<i>V. delavayi</i>	Fang 65 – 0627 (KUN)	Yunnan	3200
67	<i>V. delavayi</i>	Bot . Team 0669 (KUN)	Yunnan	2850
68	<i>V. vitis-idaea</i>	227694 (ACAD)	New Hampshire	1078
69	<i>V. vitis-idaea</i>	921890 (ACAD)	Quebec	1083
70	<i>V. vitis-idaea</i>	83979 (ACAD)	Alberta	1875
71	<i>V. vitis-idaea</i>	14979 (ACAD)	Alberta	755
72	<i>V. vitis-idaea</i>	1119886 (ACAD)	Hinshu	2800
73	<i>V. moupinense</i>	David sn in 1869 (P)	Szechuan	2500
74	<i>V. paucirenatum</i>	Kingdom-Ward 9124 (GH)	Tibet	1200
75	<i>V. setipes</i>	Burkill 36976 (K)	Assam	1650
76	<i>V. merrillianum</i>	Lu 15951 (GH)	Taiwan	3110

Column I : Operational taxonomic units (OTU) ; Column II : Species designation according to the original determination on specimen label ; Column III : Herbarium Acronym ; For those specimens borrowed , the acronym of the lending herbarium follows the collector (s) and his collection number ; Column IV : Region and elevation in *metres supra mare* (msm)

In short , four terms , *viz.* *arista* , *seta* , *calcar* , *et cornu* have been used to describe appendages on the anther (28ANTHA) ; unfortunately they have not been at all consistently used throughout the centuries . *Cornu* has been confounded the least : only Dop (1922) & Copeland (1930) applied this term to the appendages that are either extensions of the filament or apparently arise directly from the anther , the remaining authors cited on table 4 use this term to refer to the extensions of the anther cells i.e. the tubule through which the pollen tetrads are dispersed (Fig.1 : A).

Table 3 Characters used in the numerical analyses

Binary characters :

01LIGNO	lignotuber : (0) present , (1) absent
02LEAFR	leaf margin : (0) in rolled , (1) appplanatus
03LEAFS	leaf surface : (0) top rugose when dry , (1) wrinkle free when dry
04STAM1	stamens : (0) \pm isomorphic , (1) \pm dimorphic
05STAM2	anthers : (0) free , (1) \pm fused
06ANTHD	anther tubules dehiscent by : (0) terminal pores , (1) slits
07TESTA	testa : (0) lax and thin , (1) tight and well-developed
08EMBRY	embryo : (0) white , (1) green

Multistate qualitative characters :

09HABIT	plant habit : (1) epiphytic , (2) epipetric , (3) terrestrial , (4) on rotting wood (nurse logs)
10GROWH	growth habit : (1) rhizomatous , (2) trailing vine , (3) sprawling shrub , (4) erect shrub
11PHELL	position of phellogen in aerial stems at least 3 years old : (1) absent , (2) deep-seated , (3) hypodermal
12TWIGI	twig indumentum : (1) glabrous/glaucous , (2) puberulent , (3) pubescent , (4) pilose , (5) hispid , (6) any combination of the above
13LEAFA	leaf apex : (1) retuse , (2) obtuse , (3) mucronulate , (4) acute , (5) cuspidate
14LEAFG	leaf glandularity (abaxial) : (1) none , (2) glands impressed in blade , (3) glandular hairs on veins and margin , (4) glandular hairs ubiquitous
15GLAND	sessile marginal glands : (1) restricted to base of leaf (usually a pair) , (2) scattered along the leaf margin , (3) absent
16INFLO	position of inflorescence : (1) apex of current shoots , from specialized buds , (2) in leaf axils of current shoots , (3) from primordia or perennating buds on old wood
17RACHB	rachis bracts : (1) absent , (2) present , but caducous prior to anthesis , (3) persisting , often until fruiting
18RACHI	rachis indumentum : (1) glabrous , (2) pubescent , (3) pilose , (4) glandular , (5) any combination of the above
19KLOBE	calyx lobes : (1) glabrous , (2) pubescent , (3) glandular
20KTUBE	calyx tube : (1) glabrous , (2) pubescent , (3) glandular , (4) pubescent & glandular
21CSHAP	corolla shape : (1) urceolate , (2) cylindrical , (3) campanulate
22CINDU	corolla indumentum : (1) glabrous inside , (2) pubescent inside , (3) pubescent inside at the throat only , (4) pilose inside
23LOCUL	locule number : (1) 4 , (2) 5 , (3) pseudo-10
24FRCOL	berry color : (1) blue , (2) black , (3) red , (4) pink

Ordered multistate characters

25LEAFI	leaf indumentum (abaxial) : (1) glabrous , (2) pubescent veins , (3) pubescent , (4) pilose
26KTUBE	at anthesis , calyx tube : (1) as long as the calyx lobes , (2) shorter than the calyx lobes , (3) longer than the calyx lobes
27CLOBE	corolla lobes : (1) < 1 mm long , (2) > 1 mm long
28ANTHA	anthers : (1) hornless , (2) with rudimentary horns , (3) horned
29FILAM	filament : (1) glabrous , (2) puberulent , (3) pubescent , (4) pilose
30STYLE	style : (1) glabrous , (2) pubescent , (3) pilose

Quantitative characters :

31LEAFL	leaf blade length in mm
32LEAFW	leaf blade length in mm
33LEAFM	leaf margin (serrations per cm)
34PETIL	petiole length in mm
35CLENG	corolla length in mm
36CLNUM	number of corolla lobes
37STNUM	number of stamens
38STAML	stamen length in mm
39FILAL	free filament length in mm
40FRACL	length of rachis at fruiting in mm
41RBRAL	length of rachis bracts at fruiting in mm
42PEDIL	length of pedicel at fruiting in mm
43FRDIA	berry diameter in mm
44SEEDL	mature seed length in 0.1 mm

Table 4 Stamen descriptions for *Vaccinium* since 1737

author	filament	anther-theca	tubules
Linne (1737)	Octo	bicornes	
Linne (1737)	Simplicia	aristis duabus	apice dehiscentes
Smith (1819)	8 , simple	two-horned	bursting at summits
Smith (1819)		two spreading spurs or bristles	
Wight (1850)	± cohering	Adnate	tube open at apex
Wight (1850)	Short/long	two-celled , short or long	cohering tubes
Wight (1850)	Pilose	2-bristled or not	filiformis tubes
Wight (1850)	Pubescent	rough/ glabrous	dilated at apex
Wight (1850)	Slender	Bifid	thick tubes
Wight (1850)	Subulate	Pubescent	long tubes
Wight (1850)	Broad	calcarate at base	
Wight (1850)		horns with 2 retrorse bristles	
Wight (1850)		cells united at base forming spur	
Wight (1850)	Setigerous		
Klotsch (1851)	connata aut distincta	bilocularis aut unilocularis	ad apicem
Klotsch (1851)		alternatim inaequilonga	poris dehiscentes
Klotsch (1851)	Alternatim inaequilonga	Aequilonga	foraminibus dehiscentes
Klotsch (1851)	Aequilonga		
Dop (1922)	filets libres	Munies de 2 cornes aut non	deux tubes apicaux
Copeland (1930)	Pubescent	Without or with horns	with tubes
Copeland (1930)		Rudimentary horns	attenuate
Smith (1932)			long & straight
Smith (1932)		Smooth	broad
Smith (1932)			flexible
Smith (1932)			dehiscent
Smith (1932)			introrse clefts
Sleumer (1941)	Hirta	Ecalcaratae	tubuli thecis aequilongi
Sleumer (1941)	Pilosula	Bicalcaratae	rima brevi introrsa
Sleumer (1941)	Pilosa	Appendiculata	dehiscentes
Sleumer (1941)	Glabra		erecti longiusculi
Sleumer (1941)			forma longitudineque
Sleumer (1941)			valde varii
Macbride (1944)	unequal or not	unequal or not	orifice pore like
Macbride (1944)		Granular	orifice narrow & long
Macbride (1944)			
Camp (1945)		awned/awnless	
Camp (1945)		reduced to papillae	
Palser (1961)		spur long/short	awns apical
Palser (1961)		basal extension/or not	tube
Palser (1961)			2/anther (temperate)
Palser (1961)			1/anther (tropical)
Palser (1961)			pore or slit
Wilbur & Luteyn (1978)		Awnless	tapering into tubules
		spurs or not	terminal pore or obliquely cleft
Fang (1985)	Separated	2-spurs or not	erect
Fang (1985)	Pubescent		long/short tubes
Fang (1985)	Glabrous		pore dehiscent
Fang (1985)			crack dehiscent
Stevens (1996)	short to long	with spurs	short/long
Stevens (1996)		Spurless	broad/slender
Stevens (1996)		cells smooth	
Stevens (1996)		or papillate	

The term *calcar* , first used by Smith (1819) was restricted by Wight (1850) to that projection formed whenever the bases of anthers are fused into a spur (Fig. 1 : C).

The two appendages that are either extensions of the filament (Fig.1 : E) or apparently arise directly from the anther or tubule (Fig.1 : B) have been called *arista* by Linné (1737) and Camp (1945), *seta* by Smith (1819) & Wight (1850), or *calcar* by Smith (1819), Sleumer (1941), Palser (1961), Fang (1985) & Stevens (1996).

Stamen developmental data adduced by Hermann and Palser (2000) clearly demonstrates however that the anther tubules in *Vaccinium* are actually modified ericad awns (aristae). Our modest proposal (Table 5) would restrict usage as follows : *arista* for tubules ; *calcar* for a basal extension of the anther ; *cornu* for a horn-like projection from the anther/tubule ; and *seta* for an extension of the filament .

Table 5 Proposed nomenclature for stamen appendages in *Vaccinium*

Latin	English	Origin	Illustration
Cornu	horn (tubule)	extension of anther cells	Fig.1 : A
Arista	Awn	anther/tubule	Fig.1 : B
Calcar	Spur	base of anther	Fig.1 : C
Seta	Bristle	Filament	Fig.1 : E

In nature all stamens form a ring surrounding the style , with each section displaying a distinct architectural pattern , presumably depending on pollination syndrome (Fig.1 : D). Usually the stamens are free , but in a few cases , the filaments (Klotzsch , 1851) or tubules (Wight , 1850) are

connate . Reports of the connation of anthers are poorly documented , although Airy-Shaw (1935) observed some coherence among anthers in species *Agapetes* . We have found connation of anthers in *Vaccinium* sect. *Galeopetalum* (Fig.1 : D), so that the anthers must be ripped apart for dissection (05STAM2).

Inequality among the stamens in the androecium has also been observed (Klotzsch , 1851) for filament length , anther length & tubule arrangement (Fig.1 : F ex vander Kloet , 1977) or horn display (Fig.1 : D).

Materials and Methods

Data were collected for 30 qualitative descriptors (eight binary , 16 unordered multistate , and six ordered multistate) and 14 quantitative ones (Table 3). Initially only data from living collections grown from open-pollinated seed at ACAD or from material collected by the senior author (vouchers at ACAD) for 16 putative taxa , represented by OTUs one through 44 (Table 2), were analyzed . These results demonstrated substantial structure (not shown , but similar to that in Fig.2) that encouraged us to add data from 32 more herbarium specimens (Table 2) so as to confirm the relative position of *V. vitis-idaea* and to explore the structure of the most compact cluster . Herbaria consulted are listed in the acknowledgements .

Unfortunately using even the very best herbarium specimens as OTUs has one serious shortcoming : they can rarely be scored for the entire character list in that flowers and fruits are rarely if ever present on a single sheet . Rather than ignore such collections , especially when the taxon has been but rarely collected , judicious use of the protologue and material collected from the same locality was used to fill in the gaps . However such infilling was never allowed to exceed 18% of the total character suite .

Resemblances between OTUs were quantified using a modification of the dissimilarity form of Gower 's coefficient for mixed data (Gower , 1971) as implemented by the S-Plus function ' daisy ' (Kaufman and Rousseeuw , 1990 ; MathSoft , 1999) and the program SYN-TAX 2000 (Podani , 2001). As described by Kaufman and Rousseeuw (1990) and by Podani (1999), Gower 's coefficient can be usefully extended so as to incorporate information from ordered , as well as un-ordered , multistate descriptors .

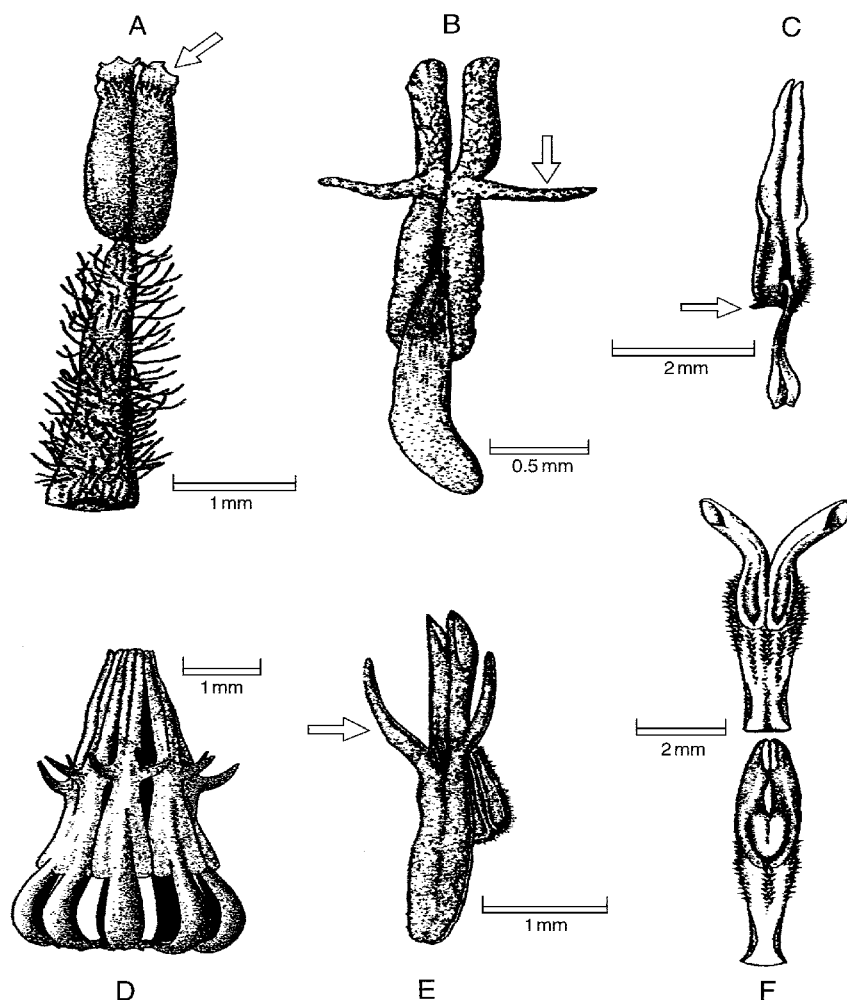


Fig. 1 Stamen appendages in *Vaccinium* (see Table 5 for details). A = awn (tubule); B = horn; C = spur; D = fused anthers; E = bristle; F = dimorphic tubules. (c. f. arrows in figure)

Between-OTU resemblances were summarized graphically by means of single-, average-, and complete-linkage clustering (Legendre and Legendre, 1998). Because we are interested in the validity of partitioning our sample into groups of OTUs corresponding to possible taxa (more so than in the hierarchical relationships between OTUs depicted in a dendrogram) we used two further approaches based on the resemblance matrix to examine the distinctness of these groups: (1) principal coordinates analysis (PCoA; Gower, 1966) and (2) partitioning around medoids ('pam'; MathSoft, 1999) and silhouette plots (Rousseeuw, 1987). Medoids are to centroids, for multivariate data, as medians are to means for univariate data. These analyses were interpreted by referring to boxplots and frequency histograms for individual descriptors, as well as to the correlations between 11 measurement descriptors (Table 6) and the scores on the PCoA axes. A classification tree (Clark & Pregibon, 1992; MathSoft, 1999) was constructed in order to look for alternative descriptors for use in keys. PCoA was carried out using SYN-TAX 2000 and NISYSpc 2.0 (Rohlf, 1997); all other data analyses and graphics were done using S-Plus 2000 (MathSoft, 1999).

Table 6 Percent contributions of the first five eigenvalues of the resemblance matrix analyzed by means of Principal Coordinates Analysis (PCoA ; Fig.3) , percent contribution expected under the broken-stick model , and correlations between 11 log-transformed measurements (Table 3) and scores on the first five principal coordinate axes .

PCoA dimension	1	2	3	4	5
Eigenvalue (%)	21.9	19.4	9.4	7.2	6.3
Broken-stick (%)	6.5	5.2	4.5	4.1	3.7
31LEAFL	-0.06	0.78	0.29	0.06	-0.02
32LEAFW	-0.05	0.83	0.21	0.14	0.01
34PETIL	0.02	0.51	0.18	0.04	-0.05
35CLENG	-0.15	0.61	-0.27	0.30	-0.14
38STAML	-0.07	0.65	-0.29	0.47	-0.07
39FILAL	0.16	0.71	-0.28	0.23	-0.11
40FRACL	-0.25	0.15	0.41	-0.39	-0.44
41RBRAL	0.13	0.33	-0.65	0.09	-0.24
42PEDIL	-0.47	0.25	0.52	0.04	0.06
43FRDIA	0.23	0.64	0.03	0.42	-0.08
44SEEDL	-0.18	0.24	0.03	0.22	0.21

Results

Cluster Analysis

Average linkage clustering of the 76 OTUs based on resemblance matrices calculated with and without log-transformation of measurement descriptors (Table 3) produced six groups (I-VI , Fig.2). Of these , group V is the largest , and readily breaks down into five sub-groups (A-C , D1 , D2) , with three OTUs (30 , 34 , 54) remaining as outliers (Fig.2). Taxonomic interpretation of these groups follows descriptions of their distinctness .

The similarity between dendrograms calculated from raw (Fig.2) and from log-transformed (not shown) measurement data (Table 3) suggests that plant and plant-part size differences do not play a major part in distinguishing these taxa from each other . In each of the analyses the same groups appeared , in the same topological relationships to each other . Group IV comprised three OTUs (Fig.2) or was dismembered so that OTU 44 joined group VI (not shown). The only difference within group V was in the composition of the two D sub-clusters , where OTUs 65 and 48 switched between D1 and D2 , and OTU 34 was an outlier (Fig.2) or was included in B (not shown).

The effect of treating the states of six of the qualitative descriptors as ordered (Table 3) was small but detectable , most notably in the difference seen in Fig.2 between OTUs scored from fresh material collected from plants growing in an experimental garden at ACAD (OTUs 01 , 02) and those scored from herbarium collections (OTUs 68 - 72). This difference disappeared when the states of these six descriptors were treated as if unordered . Similarly , the outlier status of OTU 's 34 , 30 , and 54 also diminished when the states of these six descriptors were treated as if unordered .

The effect of sorting algorithm (Legendre and Legendre , 1998) was examined by comparing the average-linkage dendrograms with those obtained using space-contracting and space-dilating algorithms (complete- and single-linkage sorting , respectively ; not shown). With both raw (Fig.2) and log-transformed data (not shown) the effect of complete linkage was small . All groups remained distinct , although a few OTUs changed their affiliation (e.g. OTUs 37 , 23-25 , with the raw but not the log-transformed data). Also , subgroups C , D1 , and D2 in group V exchanged OTUs . The effect of sin-

gle-linkage clustering was much more dramatic because of frequent chaining, and only groups I, II, and subgroups A and B (and to a lesser extent D1 and D2) in group V remained distinct.

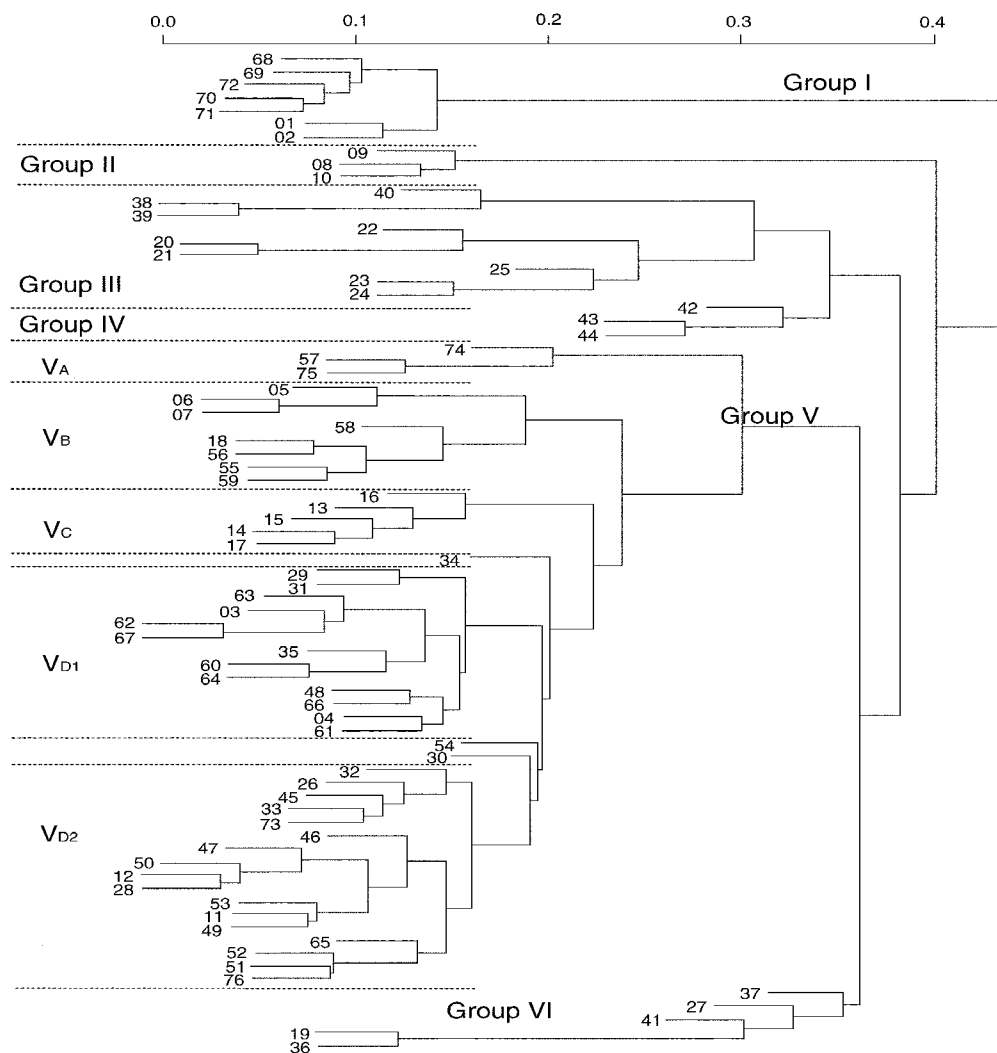


Fig. 2 Average-linkage dendrogram calculated from raw data (Table 3) for 76 *Vaccinium* OTUs summarized using the dissimilarity form of Gower's coefficient for mixed data (Gower, 1971) as modified to incorporate information about ordered descriptor states. OTUs numbered as in Table 2.

In two descriptors (12TWIGI, 18RACHI) within-specimen variability was coded for with an additional state (Table 3; Fig. 4). Recalculating the average-linkage dendrogram without these two descriptors demonstrated that they have no effect on overall group structure (group IV loses OTU 44 to group III, OTU 54 joins D1, and OTU 30 and OTU 34 join D2) other than to contribute to the differentiation of three OTUs from groups D1 and D2.

Principal Coordinates Analysis

Plots of just the first four PCoA axes (Fig.3) are sufficient to demonstrate the group structure indicated in the average-linkage cluster analyses(Fig.2). In fact , all of the first 11 axes are associated with eigenvalues that account for larger proportions of the total sample variance than would be expected from random partitions of that variance under the broken-stick model(Table 6 ; Frontier , 1976 ; Legendre & Legendre , 1998). We note that although the broken-stick model is most commonly applied to evaluating the dimensionality of principal components analyses (PCA), it is applicable here as well since the PCoA eigenvalues are equivalent to those from PCA of the same data , inflated by a scaling factor(Legendre & Legendre , 1998). In other words , the first four eigenvalues in Table 6 refer to four dimensions in which the scatter of OTUs described by the Gower coefficient dissimilarities departs from hypersphericity. The first 11 dimensions should correspond(Lefkovich , 1976) to the last 11 fusions in the dendrogram(Fig.2). By this criterion groups I-V are all distinct , as is subgroup A in but Group VI is artificial , since OTUs 27 , 37 , and 41 would all be outlier singletons. Frequency histograms (Fig.4) , boxplots (Fig.5) and correlations between scores on the first five PCoA axes and 11 log-transformed measurement descriptors(Table 6) indicate the way in which these descriptors contribute to the scatter of OTUs on these axes. Descriptors (Table 3) strongly associated with the first PCoA axis (PCo1) include 11PHELL , 15GLAND , 21CSHAP (Fig.4) , 23LOCUL , 28ANTHA , 36CLNUM , 37STNUM , 40FRACL(Fig.5 , Table 6) , and 42PEDIL (Fig.5 , Table 6). Descriptors (Table 3) strongly associated with PCo2 include 02LEAFR , 03LEAFS (Fig.4) , 13LEAFA , 32LEAFW(Fig.5 , Table 6) , 35CLENG (Table 6) , 38STAML (Table 6) , 39FILAL (Table 6) , and 43FRDIA (Table 6). Descriptors (Table 3) strongly associated PCo3 include 12TWIGI(Fig.4) ,

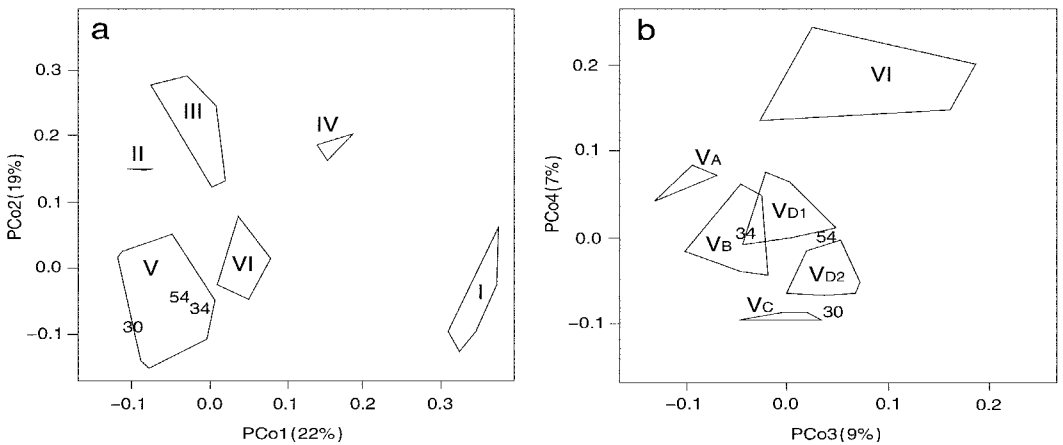


Fig. 3 The first four axes of a principal coordinates analysis (PCoA) of data (Table 3) for 76 *Vaccinium* OTUs summarized using Gower's coefficient for mixed data (Gower , 1971) as modified to incorporate information about ordered descriptor states. Eleven continuous descriptors (Table 6) log-transformed. Convex hulls enclose the OTUs in the ten groups seen in Fig. 2 ; note the outlier OTUs 30 , 34 , and 54. For PCo3 and PCo4 (b) , only the details of groups V and VI are shown. See Table 6 for information about the relative magnitude of the eigenvalues corresponding to these axes.

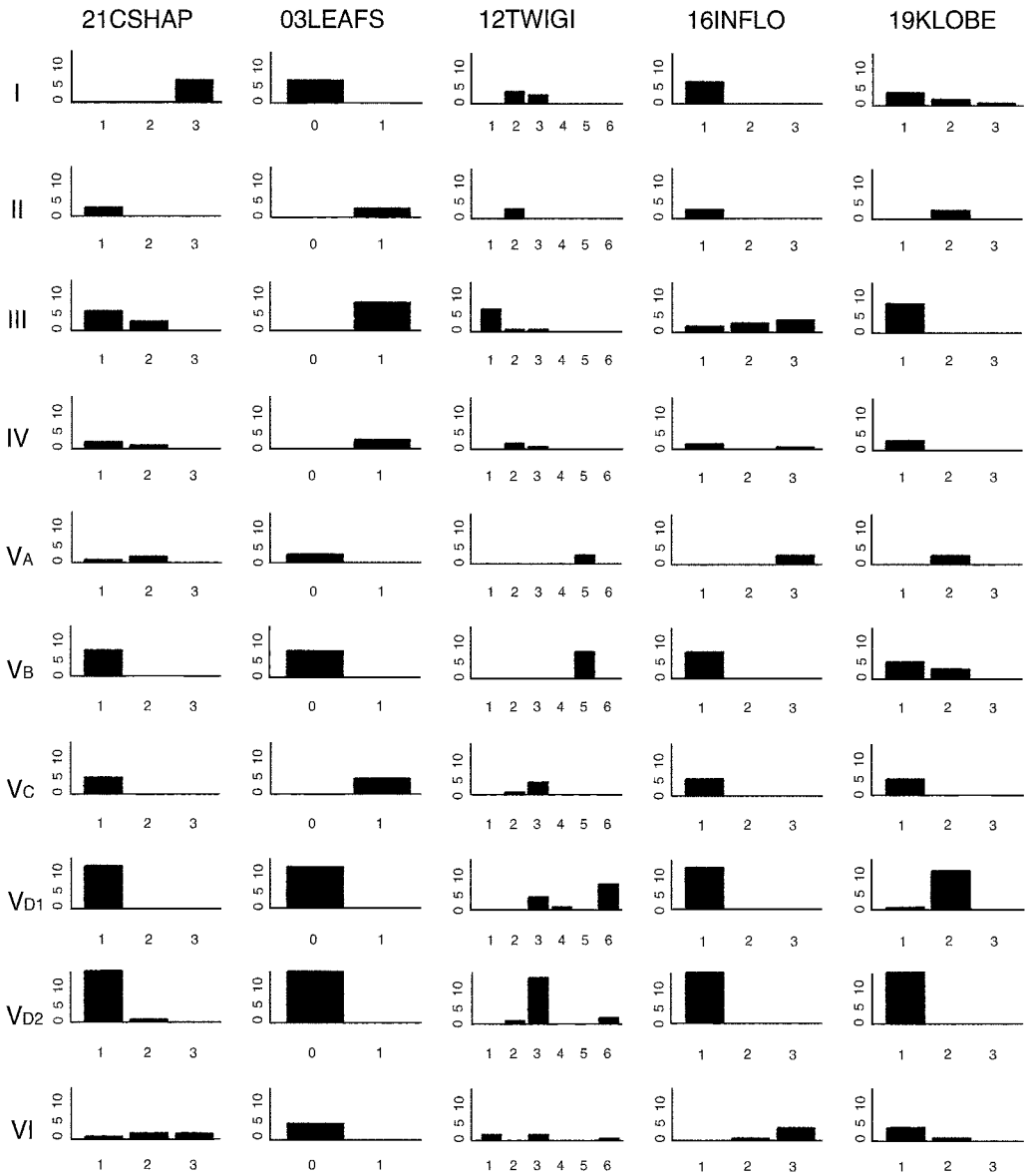


Fig. 4 Frequency histograms comparing the ten groups of *Vaccinium* OTUs (Fig. 2) with respect to five unordered multistate descriptors 21CSHAP, 03LEAFS, 12TWIGI, 16INFLO, and 19KLOBE (Table 3) that are strongly associated with PCoA axes 1, 2, 3, and 4 respectively (Fig. 3a, b).

41RBRAL (Fig.5, Table 6), and 42PEDIL (Table 6). The only descriptors strongly associated with PCo4 are 16INFLO and 19KLOBE (Fig.4), 38STAML (Table 6), 40FRACL (Table 6), and 43-FRDIA (Table 6). Classification tree analysis demonstrated the utility of 19KLOBE for distinguishing groups D1 and D2 (Fig.4). Four of the descriptors were virtually invariant in our sample and so contribute nothing to the group structure observed (04STAM1, 08EMBRYO, 25LEAFI, 30STYLE).

PCoA of just the group V OTUs (not shown) corroborated the distinctness of the five subgroups, with A and B being most distinct, and D1 and D2 showing some overlap.

Partitioning Analysis

The success of partitioning a sample into varying numbers of groups (in terms of the discreteness of those groups) can be evaluated as the ratio of the distance of an OTU to the nearest group to which it does not belong, less the average within-group distance in its group, to the maximum of these two distances (MathSoft, 1999). This ratio will vary from -1 (the OTU is poorly classified) through zero (the OTU lies between the two groups) to $+1$ (the OTU is clearly within a well-defined group). A silhouette plot displays values of this ratio for the members of each group in turn, in rank order within each group from largest to smallest. Each group can be described in terms of its average silhouette width, and the partition as a whole in terms of the average over all groups. In our study (Fig. 6),

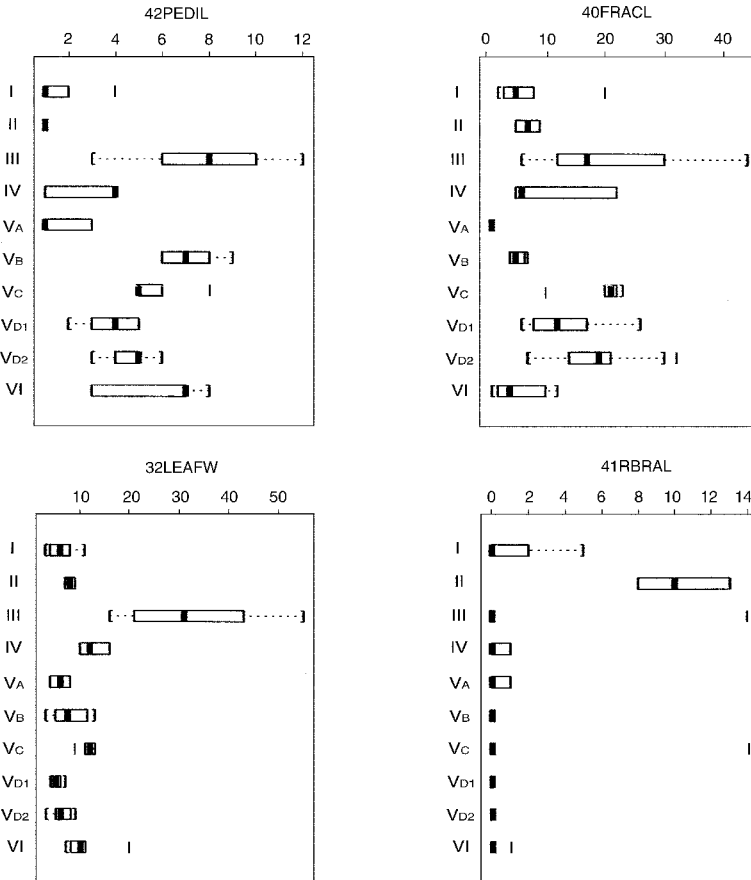


Fig. 5 Boxplots comparing the ten groups of *Vaccinium* OTUs (Fig. 2) with respect to four log-transformed measurement descriptors 42PEDIL, 40FRACL, 32LEAFW, AND 41RBRAL (Table 3) that are strongly correlated with PCo1, PCo1, PCo2, and PCo3, respectively (Table 6). The dotted 'whiskers' represent the spread of values within 1.5 times the interquartile range, the boxes represent the second and third quartiles, and the heavy line within each of the boxes represents the median. Outliers (beyond 1.5 times the interquartile range) are identified with thin lines.

average silhouette width for the entire sample reached maxima with two (0.369), three (0.370), and 10 groups (0.341). In each case group I was distinguished from the rest of the sample. The 10 groups were found to correspond largely to those found by average-linkage clustering, with groups I, II, and part of III being recognized as most distinct.

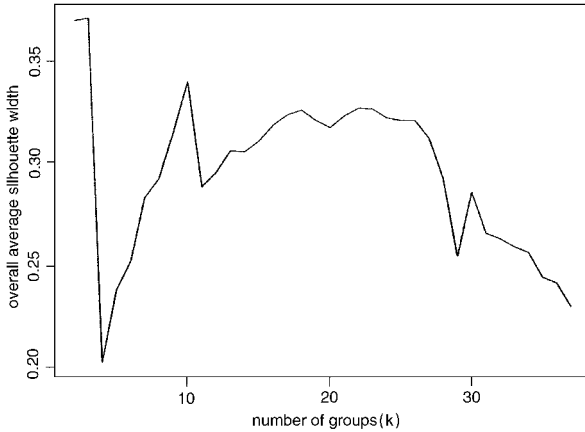


Fig. 6 Overall average silhouette width plotted against number of groups for data (Table 3) for 76 *Vaccinium* OTUs summarized using Gower's coefficient for mixed data (Gower, 1971) as modified to incorporate information about ordered descriptor states. Groups produced by partitioning OTUs around group medoids ('pam'; MathSoft, 1999).

at anthesis; corolla campanulate, glabrous throughout, 5 ± 1 mm long, lobes four ca. 1 mm long; stamens 8, isomorphic, 4 ± 1 mm long, filaments free, 2 ± 1 mm long, usually pubescent, anthers free and hornless, tubules dehiscing by a terminal pore; style glabrous; locules four, rarely five; berries red, 7 ± 2 mm in diameter, seeds about 1 mm long, testa well developed, embryo white. The dichotomy observed in this cluster reflects the difference between scoring fresh material (OTU 1 & 2) collected from plants growing in an experimental garden at ACAD and scoring herbarium collections (OTU 68–72). Nonetheless this entire group fits *Vaccinium vitis-idaea* (Gray, 1848).

Group II (OTUs, 8, 9, 10), epiphytic or epipetric sprawling shrub; [Although the hypocotyl is not swollen into a tuber, there are nevertheless in greenhouse grown plants small tubercles scattered along the roots.] stems with hypodermal phellogen; twigs of the current season puberulent; leaves 13 ± 2 mm long, 8 ± 1 mm wide, apices obtuse, margins coarsely serrate, applanate, sessile marginal glands usually restricted to a pair at the base, upper surface smooth, abaxial surface eglandular and glabrous, petioles 2 ± 1 mm long; inflorescence buds at apex of current shoots; rachis 6 ± 1 mm long at fruiting; pubescent to glabrous, bracts persisting until fruiting, 11 ± 2 mm long; pedicel ca 1 mm long, calyx lobes pubescent, longer than the tube at anthesis; corolla urceolate, pilose inside, glabrous outside, 10 ± 1 mm long, lobes five, < 1 mm long; stamens 10, somewhat dimorphic, 10 ± 1 mm long, lobes five, filaments free, 6 ± 1 mm long, pilose, anther \pm fused, horned, tubules dehiscing by an introrse slit, style glabrous; locules pseudo-10; berries red or pink, 8 ± 1

Group I (OTUs, 1, 2, 68–72): terrestrial, rhizomatous shrubs with slender rhizomes; aerial shoots slender, short lived, hence phellogen position could not be determined; twigs of the current season puberulent or pubescent; leaves 12 ± 4 mm long, 6 ± 2 mm wide, apices retuse, margins entire, inrolled, sessile marginal glands absent, upper surface rugose, abaxial impressed with glandular hairs; petioles 2 ± 1 mm long; inflorescence buds at the apex of current shoots; rachis pubescent, bracts present but caducous prior to anthesis, 7 ± 6 mm long at fruiting; pedicel 2 ± 1 mm long; calyx lobes glabrous, usually as long as or longer than the tube

mm in diameter, seeds about 1.5 mm long, testa well developed, embryo white. This group fits the concept of *V. chapanese* Merrill sensu Sleumer (1941) but reclassified as *Agapetes rubrocinctus* by Huang in 1983.

Group III (OTUs 20 – 25, and 38 – 40) terrestrial, usually erect shrubs; lignotubers are absent; stems with hypodermal phellogen; twigs of the current season usually glabrous; leaves 67 ± 35 mm long, 33 ± 13 mm wide, apices various but not retuse, margins entire or obscurely serrate, applanate, sessile marginal glands usually restricted to a pair at the base, upper surface smooth, abaxial surface glabrous but a few glandular hairs may be found on the midvein and margins, petioles 4 ± 3 mm long; inflorescence buds scattered along both old and new stems; rachis 21 ± 12 mm long at fruiting, glabrous, rachis bracts usually present but often caducous prior to anthesis; pedicel 8 ± 3 mm long; calyx lobes glabrous and shorter than the tube at anthesis; corolla urceolate or cylindrical, usually glabrous on both sides, 7 ± 1 mm long, lobes five < 1 mm long; stamens 10, isomorphic, 6 ± 1 mm long, filaments free, 3 ± 1 mm long, pubescent or pilose, anthers free or \pm fused, horned, tubules usually dehiscing by a terminal pore; style glabrous; locules pseudo-10; berries usually black, 9 ± 1 mm in diameter, seeds ca 1.5 mm long, testa well developed, embryo white. This group fits *Vaccinium* ξ *Galeopetalum* J. J. S. sensu Sleumer (1941) but not Stevens (1969) who regarded this section as a dump cluster.

Group IV (OTUs 42, 43 and 44) is a heterogenous assembly of terrestrial shrubs from the Americas that share but 33% of the character suite. Identified as *V. crassifolium* Andrews, *V. ovatum* Pursh and *V. consanguineum* Klotzsch and assigned by the latter to section *Vitis-idaea* (Table 1) but transferred by Sleumer (1941) to sections *Herpothamnus* (Small) Sleumer, and *Pyxothamnus* Sleumer respectively.

Group V_A (OTUs 57, 74, 75): usually epiphytic trailing vines; swollen hypocotyls (tubers) not observed; phellogen in older shoots hypodermal; twigs of the current season hispid (Fig. 4); leaves 12 ± 3 mm long, 6 ± 2 mm wide, apices acute or mucronulate, margins coarsely serrate, inrolled, sessile glands scattered along the leaf margin, upper surface rugose, abaxial surface usually glabrous and eglandular; petioles ca. 1 mm long; in florescence buds scattered in leaf axils on loder wood; rachis pilose, bracts usually absent, ca. 1 mm long at fruiting; pedicel 1 – 3 mm long, calyx lobes pubescent, as long as the tube of abthesis; corolla usually cylindrical, often pubescent at the throat, glabrous outside, 5 ± 1 mm long, lobes five, < 1 mm long; stamens 10, isomorphic, 4 ± 1 mm long, filaments free, ca 1 mm long, pilose, anthers free and usually horned, tubules dehiscing by an introrse slit; style glabrous, locules pseudo-10, berries black, 6 ± 1 mm in diameter, seeds about 1 mm long, testa well developed, embryo white. This group fits both *V. paucicrenatum* Sleumer and *V. setipes* Airy-Shaw.

Group V_B (OTUs 5 – 7; 18; 55 – 56; 58 – 59): usually epiphytic trailing vines; swollen hypocotyls (tubers) not observed; phellogen in older shoots hypodermal; twigs of the current season hispid (Fig. 4); leaves 13 ± 7 mm long, 8 ± 4 mm wide, apices usually obtuse, margins usually entire, inrolled, sessile marginal glands usually restricted to the base often as a pair, upper surface

rugose, abaxial surface with a few glandular hairs on midvein, often glabrous on the blade; petioles ca 1 mm long; inflorescence buds at the apex of current shoots; rachis usually pubescent, bracts often absent, but if present, caducous prior to anthesis, 5 ± 1 mm long at fruiting; pedicel 7 ± 1 mm long, calyx lobes usually glabrous, and usually shorter than the tube at anthesis; corolla urceolate glabrous outside, but often somewhat pubescent inside, 6 ± 1 mm long, lobes five < 1 mm long; stamens 10, isomorphic, 4 ± 1 mm long, filaments free 2 ± 1 mm long, pubescent or pilose, anthers free and horned, tubules dehiscing by an introrse slit; style glabrous; locules pseudo-10; berries black, 6 ± 1 mm in diameter, seeds about 2 mm long, testa well developed, embryo white. As in group I, the dichotomy observed in this cluster reflects the difference in scoring fresh material (OTUs 5, 6 & 7) and scoring herbarium collections. Nonetheless this group fits both *Vaccinium nummularia* Hooker and *V. chaetothrix* Sleumer.

Group V_C (OTUs 13 – 17): usually epiphytic sprawling shrubs with a well developed lignotuber; phellogen in older stems hypodermal; twigs of the current season puberulent or pubescent (Fig. 4); leaves 25 ± 3 mm long, 11 ± 2 mm wide, apices retuse, margins entire, sessile marginal restricted to a pair at the base, upper surface smooth, abaxial surface glabrous and eglandular; petioles 2 ± 1 mm long; inflorescence buds at the apex of current shoots; rachis pubescent or pilose, bracts present but usually caducous prior to anthesis, 19 ± 5 mm long at fruiting; pedicel 6 ± 1 mm long, calyx lobes glabrous, shorter than the tube at anthesis; corolla urceolate, glabrous on the outside, pubescent inside at the throat only, 5 ± 1 mm long, lobes five, < 1 mm long; stamens 10, isomorphic, ca. 3 mm long, filaments free, ca. 1 mm long, puberulent or pubescent, anthers free and horned, tubules dehiscing by an introrse slit; style glabrous but verrucose; locules pseudo-10; berries usually black, 5 ± 1 mm in diameter; seeds ca 1.5 mm long, testa well developed, embryo white. This group fits *Vaccinium retusum* (Griffith) J. D. Hooker.

Group V_{DI} (OTUs 3, 4, 29, 31, 35, 48, 60 – 64, 66, 67): usually epipetric or terrestrially sprawling shrubs; swollen hypocotyls (tubers) not observed; phellogen in older shoots hypodermal; twigs of the current season usually pubescent or pilose with a few long glandular hairs scattered among this indumentum (Fig. 4); leaves 11 ± 3 mm long, 5 ± 1 mm wide, apices usually retuse, margins entire, inrolled, sessile marginal glands restricted to a pair at the base, upper surface rugose, abaxial surface glabrous and usually eglandular; petioles 2 ± 1 mm long; inflorescence buds at the apex of current shoots; rachis usually glandular and pubescent, bracts present but caducous prior to anthesis, 14 ± 7 mm long at fruiting; pedicel 4 ± 1 mm long, calyx lobes usually pubescent, as long as or shorter or longer than the calyx tube at anthesis; corolla urceolate, glabrous outside, but often somewhat pilose inside, 5 ± 1 mm long; lobes five, < 1 mm long; stamens 10, isomorphic, 3 ± 1 mm long, filaments free, about 1 mm long and usually glabrous, anthers free and horned, tubules dehiscing by an introrse slit, style glabrous; locules pseudo-10; berries black or blue, 6 ± 1 mm in diameter, seeds about 1 mm long, testa well developed, embryo white. This group fits *Vaccinium delavayi* Franchet.

Group V_{D2} (OTUs 11, 12, 26, 28, 32, 33, 45 – 47, 49 – 53, 65, 73, 76): epiphytic

or terrestrial shrubs ; swollen hypocotyls(tubers) not observed ; phellogen in older shoots hypodermal ; twigs of the current season usually pubescent(Fig.4) ; leaves 25 ± 3 mm long , 11 ± 2 mm wide , apices usually retuse , margins entire , inrolled , sessile marginal glands restricted as a pair to the base , upper surface rugose , abaxial surface glabrous and eglandular ; petioles 2 ± 1 mm long ; inflorescence buds at the apex of current shoots ; rachis glabrous or pubescent , bracts present but caducous prior to anthesis , 18 ± 7 mm long at fruiting ; pedicel 5 ± 1 mm long , lobes five , < 1 mm long ; stamens 10 , isomorphic , 3 ± 1 mm long , filaments free ca. 1 mm long , glabrous to pubescent , anthers free and horned , tubules dehiscing by an introrse slit ; style usually glabrous ; locules pseudo-10 ; berries black , 6 ± 1 mm in diameter ; seeds about 1 mm long , testa well developed , embryo white. This group fits *Vaccinium dendrocharis* Handel-Mazzetti , *V. moupinense* Franchet and *V. merrillianum* Hayata. Obvious outliers in group V_D are OTUs 30 , 34 and 54 ; OTU 34 is from a disjunct population from Fan Xi Pan(Fig.8) that combines both features from subgroup D_1 and D_2 whilst OTU 30 and 54 , although associated with subgroup D_2 , are also intermediates and may indeed represent hybrids between these taxa.

Group VI (OTUs 19 , 27 , 36 , 37 , 41) epiphytic or epipetric shrubs with a variable growth habit ; lignotuber may be present or absent ; stems with hypodermal phellogen ; twigs of the current season may be glabrous or pubescent ; leaves 22 ± 10 mm long , 11 ± 5 mm wide , apices usually retuse , margins entire , in rolled , sessile marginal glands usually restricted to a pair at the base , upper surface rugose , abaxial surface either glabrous or with a few glands impressed into the blade ; petiole 2 ± 1 mm long ; inflorescence buds usually from primordia on old wood ; rachis 6 ± 4 mm long at fruiting , usually pubescent ; rachis bracts present but usually caducous prior to anthesis ; pedicel 6 ± 2 mm long ; calyx lobes usually glabrous , 5 ± 1 mm long , lobes five > 1 mm long ; stamens 10 , isomorphic 5 ± 1 mm long , filaments free 2 ± 1 mm long , glabrous , puberulent or pilose , anthers usually free and horned , tubules usually dehiscing by a terminal pore ; style glabrous ; locules pseudo-10 ; berries usually pink , 9 ± 1 mm in diameter ; seeds almost 2 mm long , testa lax and thin with green embryo (OTUs 19 and 36) or tight and well developed with embryos white (OTUs 27 , 37 , 41). This group is heterogenous and its members do not fit easily into any of the sections described by either Sleumer(1941) or Stevens(1969). It has several features such as campanulate corollas with lobes ca 1/3 of the total length of the corolla , a tendency towards fused anthers and seeds with lax and thin testa containing green embryos : features that Stevens (1969 & 1974) associated with section *Conchophyllum* which he claims lies between *Vaccinium* and *Agapetes* .

Discussion

The results presented here demonstrate the constraints imposed on data analysis by limited sample sizes. Unlike studies of larger samples in which groups discovered by clustering were evaluated using canonical variates analysis(Vander Kloet & Dickinson , 1999) , the small sample available here only supports descriptive analyses. Nevertheless , results from these analyses are sufficiently unambiguous that we believe revision of sect. *Vitis-idaea* and *Aëthopus* as described below is warranted.

In all analyses, *Vaccinium vitis-idaea* formed the most isolated cluster, which certainly supports Stevens (1969) monotypic status for this section. Indeed American taxa that Klotzsch (1851) had transferred to sect. *Vitis-idaea* had more in common with Himalayan taxa than they had with sect. *Vitis-idaea*.

Nor did any of the analyses support the transfer of the taxa remaining in sect. *Vitis-idaea sensu* Sleumer (Table 1) into a single taxon or two, as done by Stevens (1969) who transferred these species from sect. *Vitis-idaea sensu* Sleumer to either his concept of *Vaccinium* ξ *Conchophyllum* or the segregate genus *Agapetes*. We found that *V. sikkimense* tends to cluster with *V. gaultheriifolium* and *V. glauco-album* as predicted by Stevens (1969), but also that this glaucous group of plants has very little in common with the hispid-setose group (marked with four asterisks on table 1). the *V. chapaense* cluster, or with the *V. triflorum* complex. The two latter have recently been reclassified as *Agapetes* by Huang (1983) and Stevens (1985). Unfortunately, our analyses do not resolve the relationship between sect. *Conchophyllum*, sect. *Galeopetalum*, and the genus *Agapetes*. Much more work is necessary, especially, on occurrence and distribution of fused anthers in these taxa.

Nevertheless half the taxa that Sleumer (1941) placed in sect. *Vitis-idaea* consistently cluster together (Figs 2 & 3) with those that Airy-Shaw (1948) placed in his sect. *Aëthopus*. This cluster has the following characteristics: plants usually have some hispid-setose hairs, numerous small persistent leaves, and occur along the roof of the world from Nepal to Formosa usually between 1500 – 3000 msm (Table 2 & Fig 8), frequently epiphytic but at higher elevations strictly terrestrial or epipetric (Fig. 7).

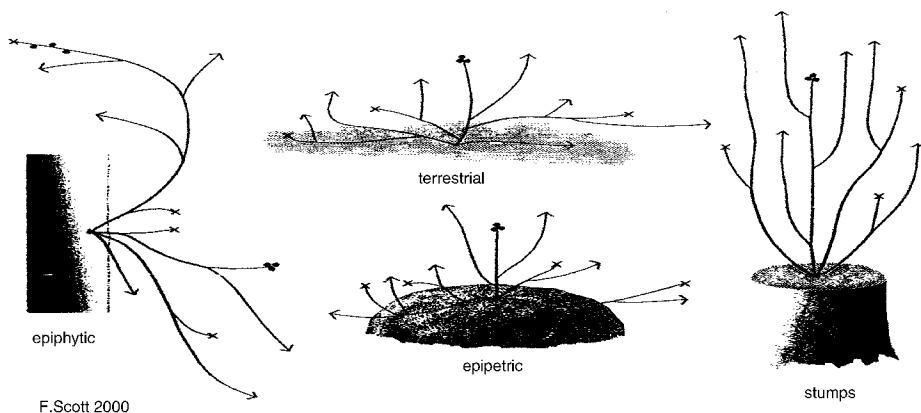


Fig. 7 Pattern of growth and plant habit of *Vaccinium* sect. *Aëthopus*.

Unfortunately, since *V. vitis-idaea* is decisively excluded from this group, *ipso facto*, its name and type status must be forsaken for the next available name which is sect. *Aëthopus* Airy-Shaw. This is eminently suitable since Airy-Shaw (1948) was the first to propose a close alliance between *V. nummularia*, *V. chaetothrix*, *V. paucicrenatum* and *V. setipes*. These taxa share setose twigs (clusters V_A & V_B in figure 2) and are quite distinct from cluster V_C & V_D where the plants have fewer, if any,

setose hairs. Nonetheless, using random amplified polymorphic DNA (RAPD), Vander Kloet and Paterson (2000) have shown that *V. retusum* from group V_C and *V. nummularia* from group V_B share a suite of common alleles. In short, clusters A, B, C & D in group V form a coherent taxon that we recognize at the sectional level.

Taxonomy

Vaccinium sect. *Aëthopus* Airy-Shaw

Vaccinium sect. *Aëthopus* Airy-Shaw, Kew Bull. 3:254. 1948. *V.* sect. *Vitis-idaea* sensu Sleumer, Bot. Jahr 671:413. 1941 [in parte]. Type species: *Vaccinium paucicrenatum* Sleumer. Typified by Airy-Shaw (1948).

Epiphytic, epipetric or terrestrial shrubs, rhizomatous or not; twigs terete covered with short brownish hairs and/or hispid-setose hairs; buds strongly dimorphic; leaves persistent and small, usually < 1 cm wide and < 2 cm long; flowers usually on short racemes borne near the tips of branches; calyx articulated with the pedicel; corolla 3–5 mm long, usually urceolate, shallowly 5-lobed; ovary pseudo-10-loculed, berry reddish-black or blue black, the seeds few, testa well developed.

All the species belonging to *Vaccinium* sect. *Aëthopus* as circumscribed are primarily Himalayan in distribution between 28° & 29° N and 82° & 104° E; disjunct populations occur on Fan Xi Pan, North Vietnam and on Taiwan (Formosa). The section occupies three distinct altitudinal belts between 1800 and 4000 msm. At lower elevations, it is usually epiphytic in mesic, mixed forests, especially on *Rhododendron*, *Tsuga*, *Quercus* and *Acer* spp. Two taxa epiphytic on a single tree or more than two plants on a single tree are rarely seen. Indeed at 2100 msm near Annapurna, Nepal, fewer than 7% of trees with dbh greater than 120 cm had any epiphytic *Vaccinia* on them. Between 2500 and 3500 msm, the taxa occupy a wider array of habitats: not only are they epiphytic, but also occur on large boulders, a variety of rotting logs and stumps and in rare instances as rhizomatous terrestrial shrubs. Above 3500 msm, they are strictly terrestrial or epipetric not as massed stands but only as scattered individual plants. The various growth forms and habits are depicted in Figure 6.

The evolution and phylogeny of this section remains elusive: using random amplified polymorphic DNA, vander Kloet & Paterson (2000) could not, with any confidence, link section *Aëthopus* to any other SE Asian taxa sampled; nor did this morphological analyses reveal any unique characters that it shares with sections in this region. Currently we are about to sequence DNA from *V. vitis-idaea* as well as several other boreal-arctic taxa on the assumption that the Himalayan tundra *Vaccinia* are the precursors of those found throughout the Arctic tundra.

Three taxa listed by Sleumer (1941) as belonging to *V.* sect. *Vitis-idaea* (Table 1) were omitted from, the analyses due to a paucity of material in the herbaria consulted. *V. haitangense* Sleumer: no material seen and presumably destroyed. *V. pumilum* Kurz, no material seen but Stevens (1969) placed it with *V. gaultheriifolium* on the basis of floral characters. *V. manipurensis* (Watt) Sleumer: from the little material seen, its transfer by Stevens (1969) to *Agapetes* cannot be gainsaid.

Keys to the Species

- A. Twigs of the current season setose with dark-reddish bristles ; leaves almost sessile , apices obtuse , acute or cuspidate.
- B. Flowers on rachides , 5 – 15 mm long , emerging from large buds near the apex of shoots
..... *V. nummularia*
- BB. Flowers on very short rachides , less than 2 mm long as if single flowers in leaf axils along the entire shoot..... *V. paucicrenatum*
- AA. Twigs of the current season pilose , pubescent or puberulent , rarely glabrous (dark reddish bristles may or may not be present) ; leaves obviously petiolate , apices retuse or emarginate.
- C. Dark-reddish bristles present on current twigs and racemes..... *V. delavayi*
- CC. Dark-reddish bristles absent on current twigs and racemes
- D. Leaves usually > 1 cm wide and/or > 2 cm long..... *V. retusum*
- DD. Leaves usually < 1 cm wide and/or < 2 cm long..... *V. moupinense*

V. nummularia J. D. Hooker et Thomson ex Clarke in Hooker f. , Fl. Brit Ind. 3 : 451 (1882). Type : Bhutan sine loco ; Griffith 2264 (Lectotype : K !) Lectotypified by Sleumer in 1941.

V. chaetothrix Sleumer , Bot. Jahrb. 71 : 432 (1941)

Trailing , prostrate usually epiphytic shrub ; twigs of the current season densely hispid-setose ; leaves elliptical , 6 – 14 mm wide , 9 – 22 mm long , blade glaucous beneath , setose when young , the margin entire , the apex obtuse ; flower buds aggregated near the tip of shoots ; racemes 3 – 16 flowered , the corolla whitish-pink , usually urceolate , 5-lobed , 4 – 6 mm long ; stamens 10 , the filaments pilose , the anthers horned , the tubule opening a slit ; berries usually black , 5 – 8 mm in diameter , the seeds few , the testa brown , usually 1 – 2 mm long.

Distribution : Nepal , Sikkim , Bhutan , Assam , Burma-Tibet Frontier , Szechuan , and Yunnan (Fig.8). Epiphytic on *Rhododendron* , *Quercus* & *Tsuga* ; occasionally epipetric ; 2200 – 4000 msm.

An attenuated and diminutive form of this taxon has been described as *V. chaetothrix* .

Vaccinium paucicrenatum Sleumer , Bot. Jahrb. 71 : 432 – 433 (1941). Type : Burma , Nam Tamai Valley , 27°45' N , 97°30' E , 1600 msm ; Ward 13560 (Holotype : BM !)

V. setipes Airy-Shaw , Kew Bull. 3 : 245 – 246 (1948)

Trailing , prostrate , epiphytic shrub ; twigs of the current season densely hispid-setose ; leaves elliptical to ovate , 4 – 7 mm wide , 8 – 18 mm long , the margin serrate , the apex acute ; flower buds scattered along the shoots ; racemes much reduced or absent ; pedicels 1 – 4 mm long , setose ; calyx tube glabrous to setose ; corolla 4 – 6 mm long ; whitish-pink , urceolate , 5-lobed ; stamens 10 , the filaments pilose , the anthers horned or hornless , the tubule opening a slit ; berries usually black , 4 – 7 mm in diameter , the seeds few , the testa brown , usually 1 – 2 mm long.

Distribution : Assam , Burma-Tibet Frontier & SE Tibet (Fig.8). Epiphyte on the higher branches in the canopy ; 900 – 2000 msm.

The only difference between these taxa is the density of setose hairs on the pedicel and calyx tube .

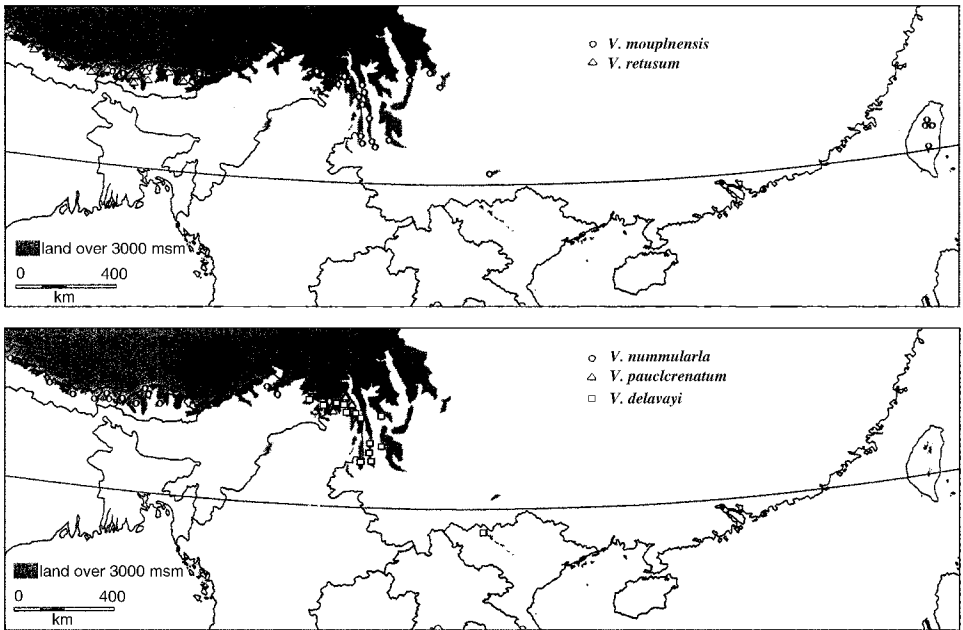


Fig. 8 Distribution of *Vaccinium* sect. *Aethopus*.

Vaccinium retusum (Griffith) J. D. Hooker ex Clarke in Hooker f., Fl. Brit. Ind. 3: 451 (1882). Type: Bhutan, *sine loco*; Griffith 3457 (Lectotype: K!) Lectotypified by Sleumer in 1941.

Thibaudia retusa Griffith, Notulae 4: 200, Icones Pl. Asiat. t. 509 (1854)

V. haitangense Sleumer, Bot. Jahrb. 71: 434–435 (1941). [N. B. no material seen, type at B, presumably destroyed by Allied bombs during WW II but protologue suggests a minor variant of *V. retusum*]

Sprawling, weakly rhizomatous shrubs, 80–200 cm high, usually epiphytic; twigs of the current season densely pubescent or puberulent; leaves usually obovate, 7–13 mm wide, 15–30 mm long, the blades pale beneath, the margin entire, the apex retuse, the base attenuates into the petiole 1–3 mm long; flower buds aggregated near the tip of the shoots; racemes 7–20 flowered, the corolla whitish-pink, usually urceolate, 5-lobed, 4–7 mm long; stamens 10, the filament pubescent, the anthers horned, the tubule opening a slit; berries usually blue-black, 4–6 mm in diameter, the seeds usually 10–30, the testa blackish, usually ca. 1 mm long.

Distribution: Nepal, Sikkim, Bhutan, Assam, Burma-Tibet Frontier and Szechuan (Fig. 8). Epiphytic especially on *Rhododendron*, *Quercus* & *Acer* spp., rarely epipetric, in a broad range of forests from 1900 to 3000 msm.

V. moupinense Franchet, Nouv. Arch. Mus. Paris, 2nd series, 10: 43 (1888) Type: China, Szechuan, Moupin, 2300–2800 msm; David s.n. in 1869 (Holotype: P!)

V. dendrocharis Handel-Mazzetti, Anz. Acad. Wiss. Wien 42: 132 (1925). — *V. merrillianum* Hayata, J. Coll. Sci. Tokyo 25 Srt. 19 (1908). *Agapetes merrilliana* (Hayata) Nakai, J. Jap. Bot. 12: 377 (1936).

Rhizomatous shrubs 30 – 70 cm high, epiphytic, epipetric or terrestrial; twigs of the current season pubescent, rarely glandular or pilose; leaves frequently obovate, 5 – 8 mm wide, 10 – 16 mm long, the blades pale beneath, the margin entire, the apex retuse, and the base attenuates into the petiole 1 – 3 mm long; flower buds aggregated near the tip of the shoots; racemes 3 – 20 flowered, the corolla whitish-pink, usually urceolate, 5-lobed, 4 – 7 mm long; stamens 10, the filament glabrous to pilose, the anthers horned, the tubule opening a slit; berries usually reddish-black, 4 – 6 mm in diameter, the seeds few, the testa dark-brown, usually ca. 1 mm long.

Distribution: Sikkim, Bhutan, Assam, Burma-Tibet Frontier, SE Tibet, Szechuan & Yunnan; disjunct populations occur on Fan Xi Pang in North Vietnam & on Formosa (Fig. 8). Epiphytic or epipetric in a broad range of forests at lower elevations but above 3000 msm usually terrestrial; 1900 – 3500 msm.

Although all plants in this taxon have ample pubescence on recent innovations and on expanding inflorescences, its persistence varies markedly: those plants referred to *V. merrilianum* are often quite glabrous at maturity whilst those referred to *V. moupinense* usually retain their indumentum.

Vaccinium delavayi Franchet, J. Bot. 9 :367 (1895). Type: China, Yunnan, Tali, 2800 – 3350 msm; *Delavay* 325 (Holotype P!).

Prostrate weakly rhizomatous, usually terrestrial; twigs of the current season usually pubescent or pilose, as well as bearing a few dark-reddish bristles; leaves obovate, 4 – 6 mm wide, 8 – 14 mm long, the margin entire, the apex retuse, the base attenuates into a petiole 1 – 3 mm long; flower buds aggregated near the tip of shoots, the racemes hispid-setose, ± pubescent, 3 – 15 flowered, the corolla whitish-pink, usually urceolate, 5-lobed, 4 – 7 mm long; stamens 10, the filament glabrous to pilose, the anthers horned, the tubule opening a slit; berries usually reddish-black, 4 – 7 mm in diameter, the seeds few, the testa brown, usually 1 – 2 mm long.

Distribution: Burma-Tibet Frontier, SE Tibet, Szechuan & Yunnan (Fig 8). Usually terrestrial especially at higher elevations, occasionally epipetric or epiphytic; 2400 – 4000 msm.

Acknowledgements: This research was supported by NSERC operating grants A9559 to (SPVDK) and A3430 to (TAD). We wish to thank János Podani, Eötvös University, Budapest for allowing us to use a pre-release version of SYN-TAX 2000 and P. F. Stevens for his critical reading of the MS. We also wish to thank the curators at E, BM, K, L, P, GH & KUN for permission to study their holdings of Himalayan *Vaccinia*.

References:

- Airy-Shaw HK, 1935. Studies in the Ericales I: New and less known species of *Agapetes* [J]. *Kew Bulletin*, 1: 24–53
- Airy-Shaw HK, 1948. Studies in the Ericales VIII: A new section of *Vaccinium* from eastern Himalayas [J]. *Kew Bulletin*, 3: 244–247
- Camp WH, 1945. The North American Blueberries with notes on other groups of Vacciniaceae [J]. *Brittonia*, 5: 203–275
- Clark LA, Pregibon D, 1992. Tree-based Models. In: Chambers JM, Hastie TJ, editors. Statistical models in S. Wadsworth and Brooks/Cole [M], Pacific Grove CA
- Clarke CB, 1882. Vacciniaceae. in J. D. Hooker. Flora of India [M]. London: Reeve & Co
- Copeland HF, 1930. Phillipine Ericaceae III: Taxonomic revision [J]. *Philippine Journal of Science*, 42: 537–604

- Dop P, 1922. Flora Gén-Indo Chine III " Vacciniacees " [M]. Masson, Paris : H. Lecomte, redacteur, 698—714
- Dumortier BCJ, 1827. Florula Belgica [M]. Tournay : J. Casterman, 172
- Fang RC, 1986. Studies on Chinese *Vaccinium* [J]. *Acta Bot Yunnan* (云南植物研究), 8 : 239—258
- Frontier S, 1976. Étude de la décroissance des valeurs propres dans une analyses en composantes principales : comparaison avec le modèle du bâton brisé [J]. *J exp mar Biol Ecol*, 25 : 67—75
- Gower JC, 1966. Some distance properties of latent root and vector methods used in multivariate analysis [J]. *Biometrika*, 53 : 325—338
- Gower JC, 1971. A general coefficient of similarity and some of its properties [J]. *Biometrics*, 27 : 857—871
- Gray A, 1848. Manual of Botany [M]. Mass : James Munroe & Co. Boston & Cambridge
- Huang SH, 1983. A preliminary study of the genus *Agapetes* from Yunnan [M]. *Acta Bot Yunnan* (云南植物研究), 5 : 141—151
- Kaufman L, Rousseeuw PJ, 1990. Finding groups in data : an introduction to cluster analysis [M]. New York : Wiley
- Klotzsch JF, 1851. Studien uber die naturliche Klasse Bicomes Linne [J]. *Linnaea*, 24 : 1—85
- Legendre P, Legendre L, 1998. Numerical Ecology, 2nd ed. Amsterdam : Elsevier Scientific Publishing Company
- Lefkovich LP, 1976. Hierarchical clustering from principal coordinates : an efficient method for small to very large numbers of objects [J]. *Math Biosci*, 31 : 157—174
- Linnaeus C, 1737. Flora Lapponica [M]. Amsterdam
- MathSoft, 1999. S-Plus 2000-Guide to statistics, Volume 2 [R]. Seattle WA, Data Analysis Products Division, MathSoft
- Palser BF, 1961. Studies of floral morphology in the Ericales. V. Organography and vascular anatomy in several United States species of the Vacciniaceae [J]. *Botanical Gazette*, 123 : 79—111
- Podani J, 1999. Extending Gower 's general coefficient of similarity to ordinal characters [J]. *Taxon*, 48 : 331—340
- Podani J, 2001. SYN-TAX 2000-Computer Programs for Data Analysis in Ecology and Systematics-User 's Manual [R]. Budapest, J. Podani
- Rohlf FJ, 1997. NTSYSpc-Numerical Taxonomy and Multivariate Analysis System version 2.00-user 's Guide [R]. Setauket NY, Exeter Software
- Rousseeuw PJ, 1987. Silhouettes : A graphical aid to the interpretation and validation of cluster analysis [J]. *J Comput Appl Math*, 20 : 53—65
- Sleumer H, 1941. Vacciniodeen studien [J]. *Bot Jahr*, 71 : 375—510
- Smith AC, 1932. The American species of *Thibaudiaea* [J]. *Contributions from the U. S Natural Herbarium*, 28 : 311—547
- Smith JE, 1817. " *Vaccinium* " Rees Cyclopedia [M], Vol 36. London : Longman, Hurts, Rees, Grme & Brown
- Stevens PF, 1969. Taxonomic Studies in the Ericaceae [M]. Edinburgh, Scotland, Ph. D. thesis
- Stevens PF, 1985. Notes on *Vaccinium* and *Agapetes* (Ericaceae) in Southeast Asia [J]. *Journal of the Arnold Arboretum*, 66 : 471—490
- Stevens PF, 1995. Familial and interfamilial relationship. In Luteyn, J. L. (ed.) Flora Neotropica. Monograph 66, Ericaceae Part II, the Superior-ovariad Genera [M]. New York : New York Botanical Garde, 1—12
- vander Kloet SP, 1977. Contributions to the Papuasian Flora : Notes on the ecology and taxonomy of the Vaccinioideae of PNG [J]. *Proc N S Inst Sci*, 28 : 105—117
- vander Kloet SP, 1988. The genus *Vaccinium* in North America [R]. Agric. Can. Pulb. No. 1828. Ottawa, ONT. 201
- vander Kloet SP, Paterson IG, 2000. PAPD assessment of novelities resulting in a new species of *Vaccinium* L. (Ericaceae) from Vietnam [J]. *Botanical Journal of the Linnean Society*, 133 : 575—586
- vander kloet SP, Dickinson TA, 1999. The taxonomy of *Vaccinium*. sect *Myrtilus* (Ericaceae) [J]. *Brittonia*, 51 : 231—254
- Warming E, 1908. The Structure of biology of Arctic flowering plants. I. Ericaceae : Morphology and Biology [J]. *Canadian Field-Naturalist*, 94 : 23
- Wight R, 1850. Icones Plantae Indica Orientalis IV : 3 - 5 and t [R]. J. B. Pharaoh, Madras, 1180—1203