

Biosystematic Studies of *Vaccinium* Section *Macropelma* (Ericaceae) in Hawaii¹

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ABSTRACT: A survey of seed and seedling morphology of the three Hawaiian species of *Vaccinium* sect. *Macropelma* (*V. calycinum* Smith, *V. dentatum* Smith, and *V. reticulatum* Smith) revealed that seed shape, size, and seed coat sculpture showed little interspecific variation and that the primary shoots bore similar, thick, coarsely serrate, dorsally glandular green leaves. In certain populations of *V. reticulatum* subsequent ephylls may retain such leaves for the life of the plant. Selfing and crossing experiments demonstrated that each of the three species is self-compatible, especially *V. calycinum*, where selfing produces more seeds than outcrossing. Cleistogamous flowers have also been observed in *V. calycinum*. Interspecific hybrids are viable and resemble two taxa described by Skottsberg.

RECENTLY I ARGUED (Vander Kloet 1990a) that the morphological variation observed in *Vaccinium* sect. *Macropelma* Klotzsch growing on the Hawaiian Islands could be more readily accommodated in three species (*V. calycinum* Smith, *V. dentatum* Smith, and *V. reticulatum* Smith) than in six as proposed by Skottsberg (1927). In my taxonomic treatment, more emphasis was put on calyx lobe development, leaf persistence, and size of blade and less emphasis on the nature of the leaf margin or blade color and indumentum. The latter features were espoused by Skottsberg (1927, 1937, 1944) and by Degener (1940), both of whom described every nuance of the leaf margin and blade size; the former features were used by Smith (1817) and Hillebrand (1888).

Thus, in defining those taxa with small reticulate leaves, Skottsberg (1927) used the following descriptors: (1) leaf margin pectinate with long \pm double teeth or marginal teeth small or margin entire; (2) blades hirsute or glabrous; (3) blades green or glaucous; (4) leaf shape elliptical or ovate or suborbicular; (4) leaf base cuneate-truncate or truncate-

cordate. Quantitative characters given in conjunction with these qualitative features are continuous, with no obvious gaps in the range of measurements (e.g., calyx lobes 1–3 mm long or calyx lobes 3–5 mm long or longer).

My observations from 1981 until 1990 on seed and seedling development, shoot and foliage development, and floral development in conjunction with selfing and outcross trials tend to corroborate the taxonomy proposed by Smith (1817), Hillebrand (1888), and Vander Kloet (1990a) rather than that by Skottsberg (1927) and Degener (1940).

MATERIALS AND METHODS

At least six ripe berries were collected from each of 41 shrubs referable to *V. calycinum* (11), to *V. dentatum* (6), or to *V. reticulatum* s.l. (15); the remaining (9) were from forms or varieties described by Degener (1940) or Skottsberg (1927). Vouchers are in the E. C. Smith Herbarium at Acadia University, Wolfville, Nova Scotia (ACAD).

Provenance of Seeds

Collection numbers are mine unless indicated otherwise.

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Vaccinium calycinum Smith

Hawaii: Kauai, Alakai Swamp, 1170 msm, 711085, 811085, and 1111085. Oahu, Laie, Koolauloa Trail, 600 msm, 530886, 630886, and 730886. Hawaii, Hawaii Volcanoes National Park, Waldron Ledge, 1190 msm, *T. Flynn* 1A85, 2A85, 1C85; Byron Ledge, 1200 msm, 61390 and 81390.

Vaccinium dentatum Smith

Hawaii: Kauai, Alakai Swamp, 1130–1170 msm, 111085, 611085, 911085, and 1011085. Maui, Haleakala National Park, Hosmer Grove, 2040 msm, 624291 and 724291.

Vaccinium reticulatum Smith

Hawaii: Maui, Haleakala National Park, Route 378, 1650–2850 msm, 124291, 224291, 324291, 424291, and 524291. Hawaii, Hawaii Volcanoes National Park, Mauna Loa Road, 1950–1200 msm, 11390, 21390, and 31390; Halemaumau Crater, 1243 msm, 41390, 51390, *T. Flynn* 3A85, 3B85, and *Galletta* 81, 82, and 83.

Incertis sedis: *Vaccinium* aff. *dentatum*

Hawaii: Kauai, Alakai Swamp, 1170 msm, 211085, 311085, 411085, and 511085.

Incertis sedis: *Vaccinium* × *pahalae*

Skottsberg

Hawaii: Hawaii, Hawaii Volcanoes National Park, Byron Ledge, 1200 msm, 71390, *T. Flynn* 1C85 (3 collections).

Incertis sedis: *Vaccinium* × *berberidifolium*

Skottsberg

Hawaii: Maui, Haleakala National Park, Hosmer Grove, 1800 msm, 824291, 924291, and 1024291.

Berries were measured to the nearest millimeter. Seeds were washed from the berries and air-dried; the large, plump, brown seeds were separated from the small, pale, or collapsed ones; and each batch was counted. From the plump seeds, 10 were randomly selected and weighed individually to 0.0001 g on an electronic balance (Cahn Model 4100). Means and standard deviations were

calculated for seeds from each accession number and expressed as mg/100 seeds.

A few of the plump seeds from each collection were attached to aluminum stubs with silver conductive paint and layered with gold in a vacuum evaporator. Specimens were observed with a scanning electron microscope (SEM) (JOEL JSM-255) and photographed with Polaroid P/N 55 film.

The remaining seeds of the 41 gatherings either were stored in sealed jars at 2°C for at least 6 months and then placed in pots on a 1:1 peat-sand mixture in a misting chamber in the greenhouse or were germinated fresh on a 1:1 peat-sand mixture in a misting chamber. To prevent damping-off, this soil mixture was treated with No-Damp® from Plant Products Co., Ltd., Bramalea, Ontario, Canada. Stored seeds were germinated under 14 hr of light at 28 ± 5°C and 10 hr of darkness at 13 ± 2°C. Fresh seeds were germinated under a similar regime. When the cotyledons emerged, pots were removed from the misting chamber, placed on greenhouse benches, and watered daily, if necessary. Days to emergence of radicles, cotyledons, and first leaves and percentage of germination were recorded for each pot. Three months after germination, five or more vigorous seedlings were removed from each pot. Each seedling was set out in a 10-cm clay pot and watered when necessary.

Seedling leaves and twigs were examined under a dissecting microscope, and several leaves were examined with the scanning electron microscope as well. Samples were prepared and air-dried according to Albrigo's (1972) procedures.

As soon as the plants began to bloom, selfing and reciprocal intra- and interspecific crosses were attempted. Flowers at anthesis either were selfed or the pollen was removed and applied to stigmata on emasculated flowers on different plants (which were subsequently tagged to follow ovule development) until at least 30 self or 30 reciprocal crosses were completed for each of the three species. In addition to the crosses within *Macropelma*, 81 reciprocal crosses were also attempted with diploid taxa from the following sections:

Myrtillus, *Hemimyrtilus*, *Oxycoccooides*, and *Cyanococcus*. Again seeds were separated, counted, and germinated as described above.

The NT-SYS package of multivariate statistical programs (Rohlf et al. 1981) was used for analysis of variance.

RESULTS AND DISCUSSION

Mature seeds of Hawaiian species of *Vaccinium* section *Macropelma* were very small, ranging from 0.7 to 1.2 mm long, and were light brown to reddish brown in color. Viable seeds were rounded, triangular, or elliptical in outline. The hilum was often quite pronounced. The seed coat morphology of these taxa was quite uniform (Figures 1–3). The reticula were pronounced, and the interstitial areas were long and narrow (Figure 4). These features are very similar to those found in sections *Myrtillus* and *Vaccinium* (Vander Kloet 1983, 1988).

Every berry also contained a number of small, pale seeds or collapsed seeds (Table 1). These seeds had either no embryos or poorly developed embryos. They did not germinate when sown in the misting chamber and thus were classified as inviable. *Vaccinium dentatum* berries contained the fewest of these inviable seeds, *V. reticulatum* berries contained the fewest viable seeds, and *V. caly-*

cinum had the largest number of viable seeds (Table 1). Indeed, the number of seeds per berry for these three taxa was on average much higher than that which has been reported for sections most closely related to section *Macropelma* (see Vander Kloet 1983, 1988). For example, berries from section *Myrtillus* contained 17 ± 7 large seeds (Vander Kloet 1983) compared to the usually more than 40 for berries from these Hawaiian taxa (Table 1).

Seeds freshly extracted from berries of all three taxa germinated en masse (Table 2), but all seedlings were susceptible to damping-off, with some pots losing up to 95%. *Vaccinium reticulatum* seeds began to germinate after about 18 days, but only about 77% of the seeds germinated. *Vaccinium calycinum* had the best germination rate but the slowest tempo of germination. Berries from plants of uncertain status or hybrids had very few viable seeds, and those few seeds that germinated produced seedlings that were extremely susceptible to damping-off. The four survivors did not flower.

Storage reduces the number of seeds that germinate, especially in *V. calycinum* where seeds germinated poorly and erratically (Table 3). The species with the heaviest seeds, *V. dentatum*, showed the least reduction in viability and in time required for germination. Again seedlings from stored seeds were prone

TABLE 1
COMPARISON OF FRUIT AND SEED FEATURES OF HAWAIIAN SPECIES OF *Vaccinium* SECTION *Macropelma*

TAXON	<i>n</i>	BERRY DIAM. ^a (mm)	LARGE SEEDS PER BERRY ^a (range)	SEED WT ^a (mg/100)	IMPERFECT SEEDS ^a
<i>V. reticulatum</i>	37	10 ± 2	43 ± 52 (1–202)	11 ± 3	89 ± 40
<i>V. dentatum</i>	43	8 ± 1	93 ± 51 (14–181)	14 ± 6	22 ± 17
<i>V. calycinum</i>	39	2 ± 1	190 ± 71 (79–315)	12 ± 4	60 ± 18

^aMeans ± SD.

FIGURES 1–6. 1–3, Scanning electron micrographs of *Vaccinium* section *Macropelma* seeds, ×41. 1, *V. reticulatum*, Vander Kloet 31390 (ACAD); 2, *V. calycinum*, Vander Kloet 61390 (ACAD); 3, *V. dentatum*, Vander Kloet 911085 (ACAD). 4, Seed coat sculpture of *V. calycinum*, ×255, Vander Kloet 630886 (ACAD). 5, Glandular hairs on lower surface of juvenile leaf of *V. reticulatum*, ×53, Vander Kloet 51390 (ACAD). 6, Unicellular hairs on lower surface of juvenile leaf of *V. reticulatum*, ×338, Vander Kloet 51390 (ACAD).

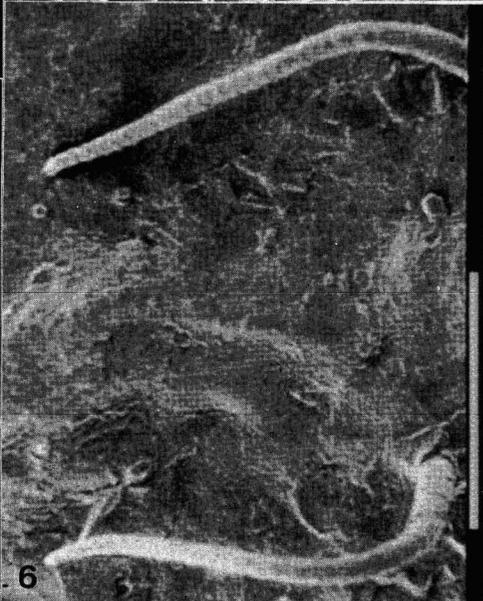
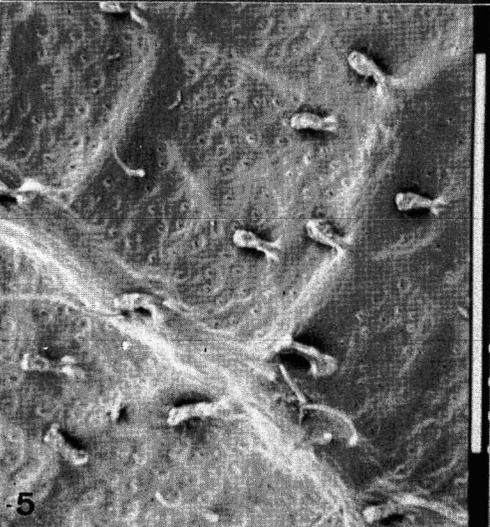
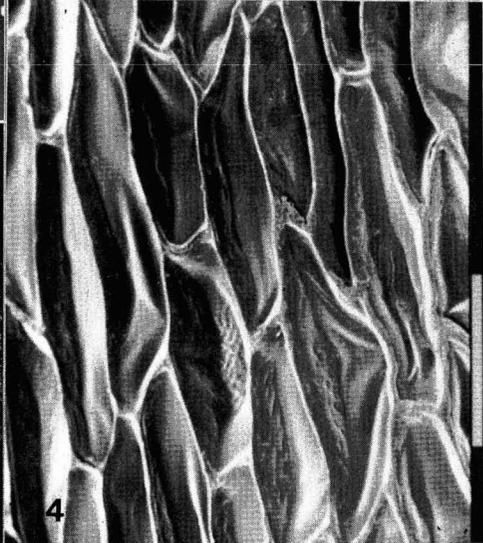
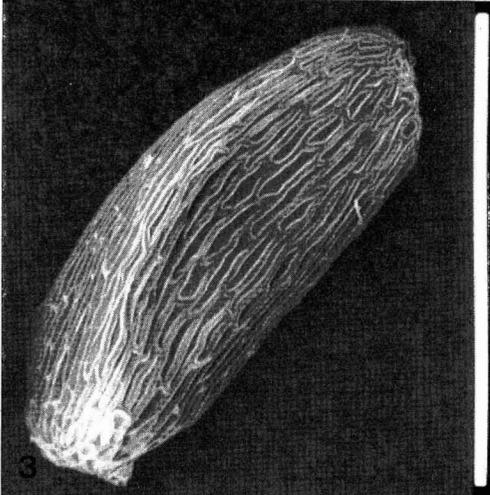
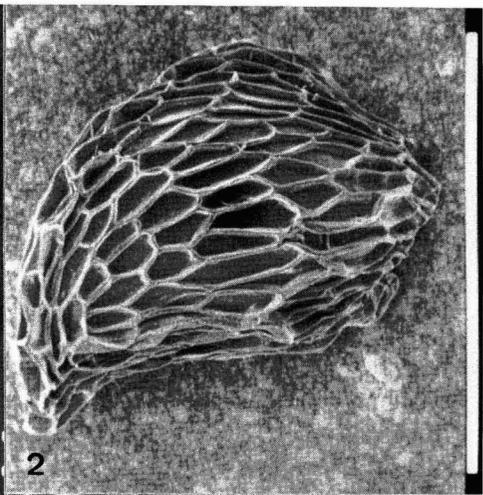
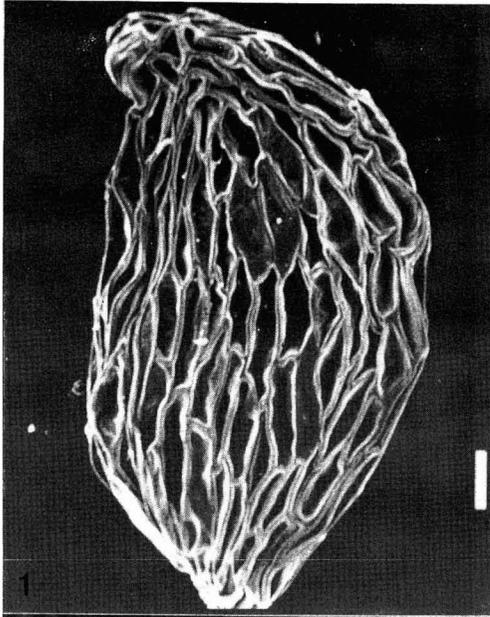


TABLE 2
GERMINATION CHARACTERISTICS OF HAWAIIAN TAXA OF *Vaccinium* SECTION *Macropelma*

TAXON ^a	NO. OF SEEDS SOWN	% GERMINATION	DAYS TO FIRST RADICLE EMERGENCE ^b	DAYS TO FIRST COTYLEDON ^b	DAYS TO FIRST TRUE LEAF ^b
<i>V. reticulatum</i> (15)	370	77	18 ± 2	25 ± 4	42 ± 5
<i>V. dentatum</i> (6)	1,602	81	31 ± 10	38 ± 9	55 ± 11
<i>V. calycinum</i> (11)	1,257	92	29 ± 7	39 ± 14	57 ± 17

NOTE: Seeds freshly extracted from berries and sown under a regime of 14 hr light at 28 ± 5°C and 10 hr darkness at 13 ± 2°C.

^aNumber of seed collections sown for each species in parentheses.

^b ± 1 SD.

TABLE 3
GERMINATION CHARACTERISTICS OF HAWAIIAN TAXA OF *Vaccinium* SECTION *Macropelma*

TAXON ^a	NO. OF SEEDS SOWN	% GERMINATION	DAYS TO FIRST RADICLE EMERGENCE ^b	DAYS TO FIRST COTYLEDON ^b	DAYS TO FIRST TRUE LEAF ^b
<i>V. reticulatum</i> (15)	250	58	20 ± 5	29 ± 6	45 ± 4
<i>V. dentatum</i> (6)	567	76	27 ± 10	38 ± 7	55 ± 12
<i>V. calycinum</i> (11)	610	20	35 ± 18	47 ± 20	67 ± 29

NOTE: Seeds dried and stored at 2°C for 6 to 12 months, then sown under a regime of 14 hr light at 28 ± 5°C and 10 hr darkness at 13 ± 2°C.

^aNumber of seed collections sown for each species in parentheses.

^b ± 1 SD.

to massive dieback due to damping-off unless the soil was treated with a double dose of No-Damp[®] before sowing.

These germination data suggest that these Hawaiian taxa have the capacity to become established immediately after dispersal, which in some populations may continue throughout the year.

In all three taxa, young emerging shoots bore green, ± broadly elliptical, thick leaves whose margins were coarsely serrate and whose blades were glandular and ± pubescent beneath (Figures 5 and 6; Figure 7, column A). In both *V. dentatum* and *V. calycinum*, the transition from juvenile leaves to mature foliage was rapid; the process began about halfway along the first primary shoot and in all subsequent ephylls only mature foliage was expressed. However, in *V. reticulatum* the transition from juvenile to mature foliage was much more gradual, if it occurred at all, and only the topmost leaves of the primary shoot expressed the mature state. In some few seedlings the mature leaves were merely somewhat

larger and more pubescent than the juveniles (Figure 7); in others the serrations gradually disappeared and the blades became glabrous or glaucous or both. Subsequent ephylls in *V. reticulatum* only expressed the mature state, but shoots that arose either from the bole or rhizome reiterated the juvenile state before developing the mature foliage at the apex of the shoot.

These homogeneous juvenile leaf features found in all Hawaiian plants of section *Macropelma*, in conjunction with little variation in seed size, shape, and sculpture, suggest a rather homogeneous group of plants of recent origin. Indeed, these juvenile leaves scarcely differ from the juvenile leaves found in *Vaccinium* section *Myrtilus* (cf. fig. 13 in Vander Kloet 1983), whose seeds, although somewhat larger than those in section *Macropelma*, nevertheless have the same seed shape and sculpture as those in section *Macropelma*. Moreover, both section *Myrtilus* and section *Macropelma* have 5 merous flowers and similar inflorescences (Sleumer 1941). It seems

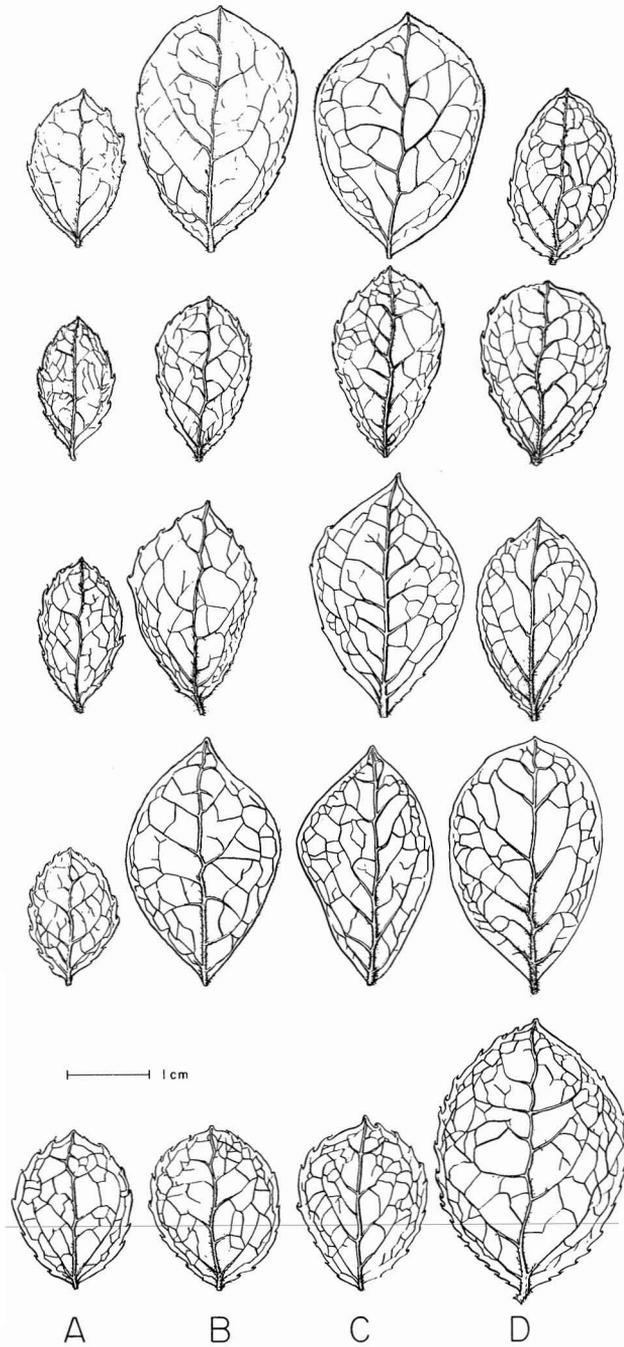


FIGURE 7. Leaf transformation from juvenile to mature foliage on primary shoots of *V. reticulatum*: Column A, juvenile leaves 3 cm from the base of the cotyledons; column B, leaves 8 cm from base of the cotyledons; column C, mature foliage at the apex of the primary shoot. For comparison, column D is a series of leaves from the seed parents collected on 1 March 1990 in Hawaii Volcanoes National Park along an altitudinal gradient from 1950 msm (top row) to 1243 msm (bottom row). Vouchers are at ACAD.

likely, therefore, that these two sections are not only vicariads but also, and more important perhaps, sister taxa.

The foliage of both *V. reticulatum* and *V. calycinum* is susceptible to powdery mildew, but that of *V. dentatum* is not. When protected with ultraviolet light for about 1 hr a day, *V. calycinum* retains its leaves for about 9–12 months, losing most if not all before flushing. Under those conditions, *V. reticulatum* holds its leaves for about 12–16 months, usually flushing before losing its older leaves; *V. dentatum* retains its leaves for at least 3 or 4 yr.

When plants are about 3 yr old, rhizome development may occur, invariably in *V. reticulatum*, but only in about one-third of *V. calycinum* and *V. dentatum*.

Vaccinium calycinum plants grown from seed may begin to bloom when 9 months old, and then sporadically about twice a year thereafter. *Vaccinium dentatum* plants require about 2–3 yr after germination to begin to bloom, and then continue to fruit and flower simultaneously throughout the year. Five years are needed to bring *V. reticulatum* into bloom after germination, and plants usually bloom twice a year thereafter.

The results of the crossing trials are given

in Tables 4, 5, and 6; these data show that, except for *V. dentatum*, selfing was as successful as intraspecific outcrossing in terms of berry set. Even interspecific crosses yielded a high berry set (Table 4). The time required from pollination until the berries were fully ripe was, however, significantly different for all three species (Table 6). *Vaccinium calycinum* needed the fewest days for berry development: 45 ± 1 days whether selfed or outcrossed. *Vaccinium dentatum* required the most days to produce a ripe berry (60 ± 2 days). Only in *V. dentatum*, where selfing failed 52% of the time because of abortion of the developing calyx tube, was berry ripening somewhat quicker after selfing (56 ± 2 days) than after outcrossing (62 ± 2 days). However, seed set per berry in selfs and intraspecific crosses showed some rather surprising but nonetheless significant differences (Table 5). Selfing resulted in significantly fewer seeds per berry in both *V. reticulatum* and *V. dentatum* than did intraspecific crosses. Berries produced by selfing in *V. reticulatum* contained 10 ± 1 seeds, but outcrossing resulted in 93 ± 10 seeds per berry. Similarly, *V. dentatum* flowers that were selfed produced berries that contained 39 ± 12 seeds versus

TABLE 4

BERRY MATURATION IN DAYS FROM GEITOGAMOUS POLLINATION AND CROSS-POLLINATION AMONG AND BETWEEN HAWAIIAN TAXA OF *Vaccinium* SECTION *Macropelma*

TAXON	SELF-POLLINATION ^a	INTRASPECIFIC POLLINATION ^a	INTERSPECIFIC ^a	F	P
<i>V. dentatum</i>	56 ± 2 (48)	62 ± 2 (100)	60 ± 2 (71)	1.722	ns
<i>V. calycinum</i>	45 ± 1 (100)	45 ± 1 (100)	51 ± 3 (100)	4.783	0.002
<i>V. reticulatum</i>	51 ± 2 (100)	51 ± 2 (100)	53 ± 3 (93)	1.041	ns

^aMean \pm SE; percentage berry set in parentheses.

TABLE 5

DIFFERENCES IN SEED SET BETWEEN *Vaccinium* SECTION *Macropelma* PLANTS SELFED AND OUTCROSSED

TAXON	SELF-POLLINATED ^a	INTRASPECIFIC OUTCROSS ^a	F	P
<i>V. reticulatum</i>	10 ± 1 seeds per berry	93 ± 10 seeds per berry	116.547	<0.0001
<i>V. dentatum</i>	39 ± 12 seeds per berry	97 ± 8 seeds per berry	9.552	<0.005
<i>V. calycinum</i>	104 ± 19 seeds per berry	64 ± 18 seeds per berry	2.853	0.02

^aMean \pm SE.

TABLE 6
CROSSABILITY OF *Vaccinium* SECTION *Macropelma*

TYPE OF CROSS	NO. OF CROSSES ATTEMPTED	% SUCCESS	BERRY MATURATION ^{a,*} (days)	SEEDS PER BERRY ^{a,**}	SEED GERMINATION (days)				% GERMINATION
					RADICLE EMERGES ^b	COTYLEDONS ^b	TRUE LEAVES ^b		
Intraspecific	52	100	53 ± 1	54 ± 7	27 ± 13	38 ± 15	61 ± 20	78	
Interspecific	41	88	54 ± 1	61 ± 7	20 ± 6	32 ± 10	48 ± 7	94	
Intersectional ♀	22	100	63 ± 3	18 ± 7	30 ± 13	40 ± 18	55 ± 21	25	
Intersectional ♂	59	36	109 ± 5	13 ± 4	36 ± 21	75 ± 69	87 ± 66	6	

^a Means ± SE; columns 3 and 4.

^b Means ± SD; columns 5, 6, and 7.

* $F = 111.69$; $df = 3, 123$; $P = < 0.0001$.

** $F = 24.01$; $df = 3, 134$; $P = < 0.0001$.

97 ± 8 seeds for berries that were outcrossed. Only in *V. calycinum* did selfing give a significantly higher seed set than in outcrossing (104 ± 19 versus 64 ± 18 seeds per berry). Indeed, about 19% of plants grown from seed collected on Oahu had cleistogamous flowers, a condition not observed in *V. calycinum* from Hawaii or Kauai. In short, selfing, which is rare elsewhere in *Vaccinium* (Vander Kloet and Lyrene 1987, Vander Kloet 1988), is well established in these island populations but is expressed differently in each species. Selfed flowers of *V. reticulatum* invariably set fruit but each berry contained only 10 ± 1 seeds (cf. 93 ± 10 seeds for outcrossed berries). Field data (Table 1) suggested that some selfing occurred in wild populations because seed set was extremely variable, ranging from 1 to 202 seeds per berry. But in *V. dentatum* 52% of the developing calyx tubes aborted about 30 days after self-pollination; those that did not abort contained about 40 seeds. In short, the self-compatible gene is not yet fixed in the entire population of *V. dentatum*. Conversely, in *V. calycinum*, self-compatibility is widespread and successful.

Table 6 presents an overview of potential crossability data, abstracted from Tables 4 and 5 and in part from Vander Kloet (1990b), which demonstrate not only that intra- and interspecific crosses are quite successful but also that intersectional crosses can be accomplished with relative ease especially when section *Macropelma* is the seed parent. Intra-sectional crosses are, however, significantly more successful than intersectional crosses. Although no barrier to potential gene exchange in section *Macropelma* was demonstrated, the 22 intersectional hybrids that survived produced very few flowers. Only eight plants flowered and all these flowers contained malformed stamens either without pollen (six plants) or with very little collapsed pollen (two plants). Moreover, all crosses attempted, even with viable pollen from *Macropelma*, failed to set seed. But interspecific hybrids within section *Macropelma* produced fertile flowers, selfed readily, and produced ample seed on outcrossing. Whether these hybrids will breed true or self remains to be tested. Indeed, hybrids from crossing

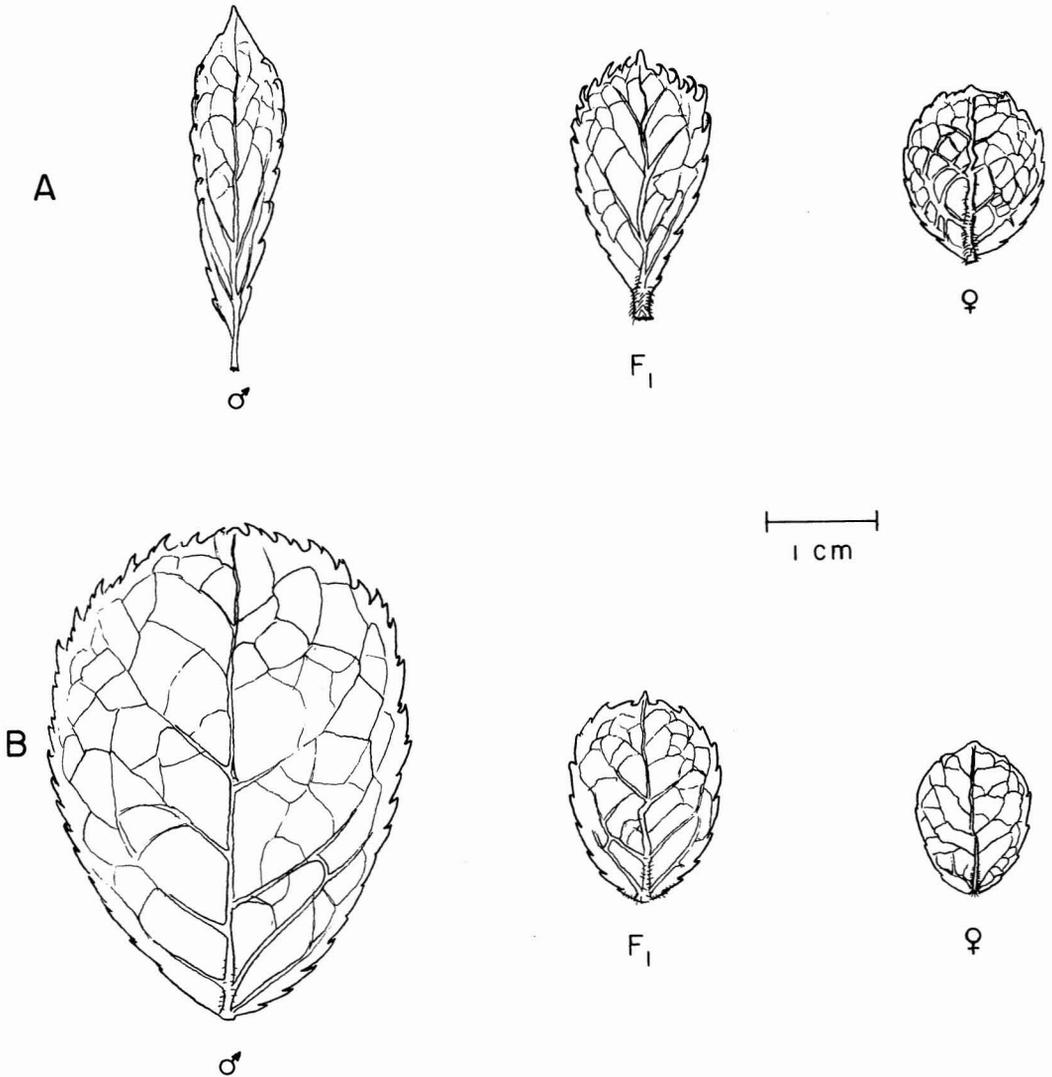


FIGURE 8. Comparison of leaf shape, venation, and margin of interspecific hybrids with that of the parents: *A* (left), pollen donor *V. dentatum*, 611085; (center), interspecific hybrid \times 34488; (right), seed parent *V. reticulatum* Galletta 82. *B* (left), pollen donor *V. calycinum* Flynn 2H85; (center), interspecific hybrid \times 129488; (right) seed parent *V. reticulatum* Galletta 81. Vouchers are at ACAD.

V. dentatum with *V. reticulatum* resemble *V. berberidifolium* Skottsberg (Figure 8A), while hybrids from crossing *V. reticulatum* with *V. calycinum* are similar to *V. pahalae* Skottsberg (Figure 8B and Vander Kloet 1990b). The blade shape and size are that of *V. reticulatum* but the texture is that of *V. calycinum*. Fur-

thermore, in habit this hybrid also resembles *V. calycinum*.

Differences in growth and development, in berry maturation and seed set, in crossability, and in self-compatibility systems in these three Hawaiian taxa belonging in *Vaccinium* section *Macropelma* suggest that the species

initially described by Smith (1817) and tested by phenetic analysis by Vander Kloet (1990a) have a sound biological basis. Indeed Skottsberg (1927) was quite right when he inferred from herbarium collections and field observations that both *V. pahalae* and *V. berberidifolium* were hybrids. Nonetheless this hypothesis did not prevent him from describing these hybrids as new species! Of course, massive numbers of interspecific hybrids can be produced from controlled crosses, and some have been reported from nature (Skottsberg 1927, Degener 1940), but as these populations become more self-compatible and cleistogamy becomes more widespread such hybridization events will become less common and a concomitant decline in the description of novelties will ensue.

LITERATURE CITED

- ALBRIGO, L. G. 1972. Distribution of stomata and epicuticular wax on oranges as related to stem and rind breakdown and water loss. *J. Am. Soc. Hort. Sci.* 97:220–223.
- DEGENER, O. 1940. *Flora Hawaiiensis*, fam. 287. *Vaccinium pahalae*. Published privately, 2 pp. Reprinted, 1946.
- HILLEBRAND, W. 1888. *Flora of the Hawaiian Islands*. Carl Winter, Heidelberg, Germany.
- HOLMGREN, P. K., and W. KEUKEN. 1974. *Index herbariorum*. Part I. The herbaria of the world, 6th ed. Oosthoek, Scheltema, and Hoilkema, Utrecht, Netherlands.
- ROHLF, F. J., J. KISHPAUGH, and D. KIRK 1981. NT-SYS. Numerical taxonomy systems of multivariate statistical programs. State University of New York, Stony Brook, N.Y.
- SKOTTSBERG, C. 1927. *Artemisia*, *Scaevola*, *Santalum* and *Vaccinium* of Hawaii. *Bernice P. Bishop Mus. Bull.* 43:1–89.
- . 1937. Further notes on *Vaccinium* of Hawaii. *Acta Hort. Gothb.* 12:145–151.
- . 1944. Vascular plants from the Hawaiian Islands. IV. Phanerogams collected during the Hawaiian Bog Survey 1938. *Acta Hort. Gothb.* 15:275–531.
- SLEUMER, H. 1941. *Vaccinioideen studien*. *Bot. Jahrb.* 71:375–510.
- SMITH, J. E. 1817. *Vaccinium*. in *Rees's Cyclopaedia*, vol. 36. Longman, Hurts, Rees, Orme, and Bronn, London.
- VANDER KLOET, S. P. 1983. Seed and seedling characters in *Vaccinium* § *Myrtillus*. *Nat. Can.* 110:285–292.
- . 1988. The genus *Vaccinium* in North America. *Agric. Can. Publ.* 1828. Ottawa, Ontario.
- . 1990a. Ericaceae, pages 591–595 in W. L. Wagner, D. R. Herbst, and S. H. Sohmer, eds. *Manual of the flowering plants of Hawai'i*. Bishop Mus. Spec. Publ. 83. University of Hawaii Press, Honolulu.
- . 1990b. Origin, speciation and self-compatibility in *Vaccinium* § *Macropelma*, in *Abstracts of the Fourth International Congress of Systematic and Evolutionary Biology*, University of Maryland, College Park, Maryland.
- VANDER KLOET, S. P., and P. M. LYRENE. 1987. Self-incompatibility in diploid, tetraploid and hexaploid *Vaccinium corymbosum*. *Can. J. Bot.* 65:660–665.