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The Genus *Vaccinium* North America

The Genus *Vaccinium* in North America

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FOREWORD

One of the duties of the Biosystematics Research Centre of Agriculture Canada is the systematic clarification of Canadian crops. The genus *Vaccinium* provides Canada with its most important indigenous crops, the blueberries and cranberries, as well as other plants of pomological, ornamental, and wildlife interest. Toward the goal of clarifying systematic knowledge of this genus, a contract for the preparation of this monograph was issued to S.P. Vander Kloet, the recognized expert on *Vaccinium*. As the scientific authority responsible for this contract, I have enjoyed observing the synthesis of this important work.

Ernest Small

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All maps in this monograph are based on Goode's Series of Base Maps, numbers 102 and 202, originally prepared by Henry M. Leppard and published by the University of Chicago Press, reproduced by kind permission of the Committee on Geographical Studies at the University of Chicago. Fig. 22 originally appeared in *Canadian Journal of Botany* and appears by permission of the National Research Council of Canada.

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PREFACE

The impetus for this monograph stems from my failure to grasp, as a graduate student in plant ecology, that twigs from single colonies of lowbush blueberries growing on quartzite outcroppings in the Thousand Islands region of New York and Ontario, when fully exposed to sunlight, were sometimes referable to *Vaccinium brittonii* Porter; when partially shaded, to *V. angustifolium* Aiton; and when completely in the shade, to *V. lamarckii* Camp. This is patent nonsense. Any existing classification that gives such ambiguous answers to the honest efforts of naturalists, foresters, biologists, or general botanists brings taxonomy into disrepute. Consequently, I decided to approach the taxonomy of the blueberries with a view to providing a classification that was both biologically sound and taxonomically robust. This task, however laudable in concept, was somewhat more complex than I expected in 1967, and 17 years later my knowledge of the genus *Vaccinium* scarcely crosses the boundaries of North America.

Part 1

General discussion

The genus *Vaccinium* Linnaeus contains approximately 400 species of shrubs or small trees worldwide. About two-thirds of these species occur in Malaysia, 70 in southeast Asia, 19 in Japan, perhaps 5 in the Pacific area, 5 in Africa, 6 in Europe, 25 in South America, and 26 in North America. Several of the North American species have highly palatable fruit.

Plants may be terrestrial or epiphytic and are generally found on acidic, sandy, peaty, or organic soils. Disturbed or exposed areas are readily invaded by *Vaccinium* species.

Traditionally, the genus has been divided into sections. Sleumer (1941) and more recently Stevens (1969) have described the features that define these sections. A major problem confronting a student of *Vaccinium* is the delimitation of species. Camp (1942*a*, 1942*b*, 1944, 1945) was the first to describe population structure and possible biological species for the genus (i.e., groups separated by breeding barriers), but I could not substantiate many of the species he suggested (Vander Kloet 1972, 1977*a*, 1978*a*, 1980, 1983*a*, 1983*b*). Consequently I merged many, thereby drastically reducing the number of species that ought to be recognized in North America.

Casual usage

With the exception of *V. arboreum*, the berries produced by the genus are edible; their flavor varies from insipid to tart to sweet, but all are eaten by both birds and mammals. Martin et al. (1951) cite 53 species of wildlife that eat *Vaccinium*; indeed, blueberries form a substantial part of the diet of the black bear, chipmunk, tanager, Franklin grouse, and spruce grouse. Robins are considered a pest on the blueberry barrens of New Brunswick (Wood and Pearce 1977). Dale and Hughes (1977) reported that in Florida and Georgia *V. myrsinites* forms a major part of the diet of the ruffed grouse. Along the Pacific coast, grizzly and black bears eat large quantities of *V. ovalifolium* and *V. membranaceum* berries, climbing the mountain slopes to follow their ripening sequence (Scully 1970; Craighead et al. 1963). Deer, elk, hares, and rabbits browse on the twigs and leaves (Rogers 1974; Martin et al. 1951).

Vaccinium berries were also extensively eaten by North American aborigines. The Inuit preserved the berries of *V. uliginosum* in seal oil and blubber (Holm et al. 1912) or by gathering them into leather bags that were then stored in permafrost (Darrow and Camp 1945). Taylor (1974) has argued that cranberries (*V. oxycoccus*) were also an important food in the Inuit diet, because the berries keep well and contain enough acid to balance the almost exclusively meat diet of the Inuit. Hawkes (1916) reported that a mixture of salmon spawn, blueberries, and seal fat was a favorite dish of the Labrador Inuit.

According to Kalm (Benson 1966), Indians dried blueberries (*Vaccinium* sect. *Cyanococcus*) in the sun or by the fire in order to store them for winter, when the berries were baked in corn bread. The Flambeau and Pillager Ojibwa dried blueberries on "raised scaffolds of rush mats" for winter use in sweet bread or to cook with wild rice and venison or dried sweet corn and maple sugar (Smith 1932). In the Rocky Mountains, Indians gathered *V. ovalifolium* berries before they were fully ripe, pressed them into cakes, dried them, and then mixed them with cold water before use (Brown 1868).

In addition, Indians steeped *Vaccinium* leaves, flowers, and rhizomes in hot water; these teas, or infusions, were used to purify the blood (Smith 1932), to treat colic in infants, to induce labor, and as a diuretic (Black 1980).

The European settlers have a long history of casual usage (Hedrick 1919; Fernald and Kinsey 1943), but none were more assiduous consumers than those who settled in Newfoundland, where the location of the family's partridgeberry patch (*V. vitis-idaea*) is still a closely guarded secret. Indeed, Newfoundland is the only North American jurisdiction to have an act for the protection of the partridgeberry (Torrey 1914); only during open season may the berry be picked with impunity.

In addition to misapplying partridgeberry (the common name for *Mitchella repens*) to *V. vitis-idaea*, the Newfoundlanders also transposed the archaic West Country phrase "to go a-hurting" (i.e., berrying) to the substantive sweethurts, the common name for *V. boreale*, and groundhurts, the common name for *V. uliginosum*.

Cultivation

Vaccinium macrocarpon, the large or American cranberry, became the first species in the genus to be cultivated when Henry Hall of Dennis, Cape Cod, Mass., began to care for a few vines in about 1816. But not until 1845 was it established that the cranberry could be a marketable commodity (Hedrick 1919; Peterson et al. 1968). The crop is confined to cool, moist, natural or artificial bogs that can be flooded or drained as desired. These bogs may remain productive for many successive years; indeed, several bogs in New Jersey and Cape Cod have been productive for more than 75 years (McGregor 1976).

Moreover, cranberry culture minimally affects the peat deposit and causes far less disturbance to the peat-forming ecosystem than any other crop (Moore and Bellamy 1974).

Productivity is a function of pollinator density and ranges from 8000 kg to 11 000 kg/ha as reported by Hedrick (1919) and Hall (1978). The primary pollinators of the cranberry are bumblebees; these are gradually decreasing in New England and New Jersey and need to be supplemented by the addition of one colony per hectare of cranberry bog (McGregor 1976).

Although the centre of cranberry production and cultivation is still Massachusetts (Table 1), *V. macrocarpon* has been successfully introduced to the peatlands of British Columbia, Washington, and Oregon. The estimates of cranberry production presented in Table 1 are somewhat low since they do not include the harvest from wild populations, which are known to be exploited (Hall 1978).

The blueberry (*Vaccinium* sect. *Cyanococcus*) is the most recent major fruit crop to be brought under cultivation; improvement through breeding did not begin until 1909 (Galletta 1975; Camp et al. 1957). All early highbush (*V. corymbosum*) plantings consisted of shrubs transplanted from woods and swamps. Such plantings were first begun in northern Florida in about 1893 and were pursued with such vigor that by the late 1920s, 890 ha of rabbiteye (*V. corymbosum* f. *ashei*) were in cultivation (Mowry and Camp 1928).

The improvement of the wild highbush blueberry received much of its early impetus from Elizabeth White, who offered cash prizes for native highbush plants that produced the largest berries and thus was able to assemble large-fruited forms at her farm in Whitesbog, N.J. (Camp et al. 1957). Beginning in 1909, Coville and White made many crosses among these superior plants (Coville 1921), and selections made from those hybrids and their backcrosses are the foundation of today's extensive industry in cultivated highbush blueberries in New Jersey, North Carolina, and Michigan (Galletta 1975). The North American blueberry industry currently makes use of more than 10 000 ha of acid, badly drained soils that had been previously classed as agriculturally worthless. Table 2 gives the most recently available crop estimates.

During the 1930s the industry declined in the southern states, a result, at least in part, of the erratic fruit quality of the wild shrubs, which put them at a competitive disadvantage with blueberries produced in New Jersey and Michigan from clonally propagated cultivars (Coville 1937). Efforts to breed improved rabbiteye cultivars from wild *V. corymbosum* f. *ashei* began in 1940 in Tifton, Ga., and in 1948 in Gainesville, Fla. (Sharpe and Sherman 1971) and resulted in such highly successful cultivars as Tifblue and Homebell (Brightwell 1971).

Wild rabbiteye populations are resistant to stem canker (Lyrene and Sherman 1977), a disease that severely affects the North Carolina cultivars (Galletta 1975). Moreover, several severe winters have

Table 1 Cranberry production in North America, 1970–1979

	Area cultivated (ha)		Yield (tonnes)	
Place	1970	1979	1970	1979
Massachusetts	4 360	4 480	47 664	49 076
Wisconsin	2 280	2 840	24 925	40 953
New Jersey	1 240	1 200	13 556	11 495
British Columbia	475	480	5 900	6 577
Washington	400	440	4 373	6 680
Oregon	298	320	3 258	4 295
Quebec	40	–	320	–
Nova Scotia	10	22	80	18

Sources: McGregor 1976; Hall 1978; data on file, Statistics Canada, 1982; United States Department of Agriculture, Agricultural Statistics, 1980.

Table 2 Commercial highbush blueberry production in North America, 1968–1972

Region	Area (ha)	Yield (tonnes)
Michigan and Indiana	3 840	13 236
New Jersey	3 040	9 400
North Carolina	1 400	4 071
British Columbia	600	2 020
Washington	270	1 634
Oregon	130	444
Georgia and Florida	280	409
New England	140	409
Others	160	454
Total	10 370	32 077

Sources: Adapted from Galletta (1978); United States Department of Agriculture.

badly damaged the highbush blueberry plantings in Michigan. Finally, in New Jersey, where neither stem canker nor severe winters are a serious problem, the price of blueberry land has doubled from $2500/ha to $5000/ha; in Florida, however, it is still possible to buy blueberry land for about $1000/ha. All these factors have led to a renewed interest in the breeding program for *V. corymbosum* f. *ashei* at Gainesville.

In Canada, the principal centre for the highbush blueberry industry is British Columbia. On Lulu Island and the adjacent mainland, near the mouth of the Fraser River, several cultivars have been successfully introduced. Aside from these plantings, which yield 27 000 t annually, the industry is of minor importance in this country (Hall 1978). This stems from the fact that not only is *V. corymbosum* at the limit of its northern range in eastern Canada but also that the more than 45 highbush cultivars (Galletta 1975) are poorly adapted to withstand temperatures below −25°C to −30°C because they were developed from New Jersey and North Carolina wild stock (Craig 1967).

Currently, 348 seedlings (grown from open-pollinated seed collected from 12 apparently relatively hardy northern populations of *V. corymbosum*) have been set out for hardiness trials at Sheffield Mills, N.S. (Vander Kloet, unpublished data). The hardiest of these will be intercrossed with several popular cultivars, such as Earliblue, Blueray, and Berkeley, and selections will be made for fruit production and hardiness.

A valuable summary of blueberry genetics, breeding objectives, and breeding biology is given by Galletta (1975). Eck and Childers (1966) provide an excellent review of blueberry culture.

Vaccinium angustifolium is the only other taxon in *Vaccinium* sect. *Cyanococcus* from which cultivars have been selected through controlled crosses. This lowbush blueberry provides the best return per hectare to the grower in eastern Canada (Hall 1978) and in Maine, where Darrow and Moore (1962) reported more than 60 000 ha of lowbush blueberries. Statistics on area under cultivation, yield, and economic value grossly underestimate the actual harvest (McGregor 1976), because a major portion of the crop is gathered from managed wild stands. These are pruned by burning (burn-pruned) in late fall or early spring (Hall 1978) – a technique practiced by Indians (McGregor 1976).

In most regions, the wild harvest comes from a single species, *V. angustifolium*, but in areas that have been clear-cut, *V. myrtilloides* makes up a sizable proportion of the stand and crop (Hall and Aalders 1961).

In Canada, the major centres of lowbush blueberry production are all in the five easternmost provinces: the Avalon and Bonavista peninsulas of Newfoundland; Cumberland County, N.S.; the eastern and western extremities of Prince Edward Island; southern New Brunswick; and Abitibi County and the Lac-Saint-Jean region of Quebec (Hall 1978). In the United States, the centre for the lowbush blueberry industry is northeastern Maine, but extensive stands also occur in northern New Hampshire, West Virginia, and northern Michigan, Minnesota, and Wisconsin. In addition to these major production areas, substantial harvests come from numerous local stands, with scarcely any management.

Improvement of *V. angustifolium* was started in 1908 by Coville (1910, 1921), who selected Russell from wild New Hampshire populations. Currently, improvement trials are held at the University of Maine at Orono, Laval University in Quebec City, and the Kentville Research Station in Nova Scotia. Kender (1965) has listed the following desirable characteristics for lowbush blueberries: large fruit size; good blue color; fine flavor; heavy yield; self-fruitfullness – in wild populations, yield is a function of pollinator density (McGregor 1976) and self-incompatibility (Aalders and Hall 1961); late blooming; uniform ripening; disease resistance; vigorous rhizome growth; easy propagation; and upright, vigorous, tall stems.

Hall (1978), working in Kentville, N.S., collected more than 800 clones from the wild. After a large number of selections, three have been developed and registered as the cultivars Augusta, Brunswick, and Chignecto.

Although *V. macrocarpon*, *V. corymbosum*, and *V. angustifolium* are currently the only species of the genus to be improved through breeding, several others, among them *V. vitis-idaea*, are used extensively for jams and jellies in Newfoundland. Fernald and Kinsey (1943) reported that more than 395.6 t of partridgeberries were exported annually from Newfoundland to Minnesota. Indeed, Torrey (1914) advocated the selection and planting of superior clones in Newfoundland. But as Hall (1978) pointed out, this recommendation was neglected and the harvest has decreased in recent years to less than 100 t annually, with exports for 1976 amounting only to 27.8 t. Currently, Hall is crossing several superior Newfoundland clones with material from Finland, where other superior clones of the species have been developed (Lehmushovi and Säkö 1975). Other species have horticultural potential and are often used locally or sold at roadside stands. *Vaccinium pallidum*, the hillside blueberry, is harvested in Arkansas. *Vaccinium stamineum*, the deerberry, is usually considered to be unpalatable, although individual shrubs yield delicious fruit; this species is used in the Carolinas (Fernald and Kinsey 1943; Elliott 1821). *Vaccinium erythrocarpum*, the dingleberry, sometimes produces berries of excellent flavor, which are used locally for jellies; Uphof (1968) reports that this species has been recommended for cultivation. *Vaccinium ovatum*, the California blueberry, is often used as an ornamental plant (Camp 1945). Galletta (1975) maintains that *V. darrowii* has promise as an ornamental.

Distribution of the genus *Vaccinium* in North America

Although the physiography of North America has certain common features, I have chosen to treat the part of the continent that coincides with the biogeographic region known as the Nearctic (which includes all of Canada, Greenland, the continental United States, and northern Mexico). The Nearctic is linked to the Neotropical region (South America) by the Isthmus of Panama – a narrow land link that replaced an earlier water gap (Darlington 1957). A second barrier to species migration is provided by the arid regions in Mexico. Indeed, southern Mexico, Central America, and the Caribbean contain *Vaccinium* species that have strong Neotropical affinities, whereas the Nearctic is largely populated by endemic or circumboreal species.

Camp (1942*b*) has argued for a mid-Tertiary origin for the genus, but theories on its arrival and subsequent evolution on the North American continent are highly speculative (Vander Kloet 1983*b*; Vander Kloet and Hall 1981).

Not until the late Tertiary and Quaternary periods, when a series of ice sheets several kilometres thick covered the northern part of the continent, can we realistically try to reconstruct some of *Vaccinium*'s peregrinations. The ice sheets descended as far south as Seattle, Wash., and Brunswick, N.J., with a pronounced dip as far south as the 38th parallel in Illinois. Nevertheless, some unglaciated areas (refugia) remained in Alaska, the Yukon Valley, northern Greenland, and possibly a few other areas.

During the most recent, or Wisconsin, glacial episodes, all the *Vaccinium* populations north of this boundary were largely displaced, except for populations that could survive on the nunataks (Fernald 1925) and those occurring on the unglaciated areas in the Yukon and Alaska. Presumably, the eastern arctic and boreal populations migrated southward along a tundra belt that lay in front of the ice sheet on the Atlantic coast or migrated to the alpine tundra, which extended more than 300 km farther south down the Appalachian plateau (Maxwell and Davis 1972).

Vaccinium species from more temperate areas probably migrated southward as well. But according to Daubenmire (1978) plants also could have persisted in relatively small unglaciated refugia between ice lobes, which existed in southwestern Wisconsin and perhaps elsewhere. Periglacial climates may not have been extremely severe.

The species most affected by the advance of the Laurentian ice sheet was *V. boreale*. Its entire range currently lies north of the glacial boundary. Furthermore, the nunataks that Fernald (1925) described for this area are now thought to have been glaciated (Wynne-Edwards 1937). The eastern and now disjunct populations of *V. ovalifolium* and *V. membranaceum* were also displaced. But the transcontinental *V. myrtilloides*, *V. uliginosum*, *V. vitis-idaea*, *V. caespitosum*, and *V. oxycoccus* could have found refugia in several areas: the Alaska–Yukon area, the southern Rocky Mountains, and the Appalachian plateau. Except for the extreme northern fringe, Greenland was completely glaciated during the Wisconsin episode (Antevs 1929). Therefore, populations of *V. vitis-idaea*, *V. oxycoccus*, and *V. myrtillus* currently found in southwestern Greenland are thought to have migrated to the island since the glacial successions and probably came from Europe (Löve and Löve 1963). The notion that the sections of *Vaccinium* that currently occur north of the glacial boundary, because they are largely monotypic, underwent massive extinctions during the Pleistocene is contradicted by the observation that as many monotypic sections occur in unglaciated North America as in glaciated regions. Indeed the opposite theory – that the Pleistocene promoted evolution rather than extinction – might be more likely (Vander Kloet 1977*a*). Some of the sections are so distinct that they could be of mid-Tertiary age.

The 10 sections of *Vaccinium* that occur in North America are distributed in the following way:

- Section *Vitis-idaea* has one circumboreal arctic species that does not occur south of the glacial boundary in North America.
- Section *Vaccinium* has one circumboreal arctic species that does not occur south of the glacial boundary.
- Section *Oxycoccus* has two species. *Vaccinium macrocarpon* occurs only in eastern North America but has been successfully introduced along the Pacific coast; *V. oxycoccus* is circumboreal, although several populations, some of which are disjunct, occur south of the glacial boundary (Fig. 46).
- Section *Polycodium*, endemic in eastern North America and central Mexico, has one variable species.
- Section *Batodendron*, endemic in southeastern North America and Cuba, has two species. Only one, *V. arboreum*, occurs in North America. Camp (1945) claimed that this section is allied to several central Mexican species, but Sleumer (1941) maintained that this group is a distinct section and made no mention of Mexican affinities.
- Section *Herpothamnus* is monotypic, with one species, *V. crassifolium*, endemic in the Carolinas and the southeastern tip of Virginia.
- Section *Hugeria* has one species in the Appalachian highlands and a vicariad in China, Japan, and Korea (Camp 1945; Sleumer 1941).
- Section *Pyxothamnus*, endemic in the Pacific coast from British Columbia to the Andes, is represented by one species in North America.
- Section *Myrtillus* comprises ten species of which four occur in western North America only; one, *V. caespitosum*, is transcontinental. Three are disjunct: *V. myrtillus* in the Rockies, Greenland, and Eurasia; *V. ovalifolium* in a few localities in Newfoundland, Quebec, and Michigan, (Fig. 57), with a central range along the west coast of North America and disjunct populations in Japan and the U.S.S.R.; and *V. membranaceum*,

with one locality in northern Michigan and a central range along the west coast (Fig. 59). Two taxa are endemic in Japan.

- Section *Cyanococcus* includes nine species. All but the boreal *V. myrtilloides* are endemic in eastern North America.

Growth and development of *Vaccinium*

Fresh seed, sown on a 1:1 mixture of milled sphagnum and sand and placed in a lighted misting chamber, germinated quite readily. Radicles emerged in about 10 days for some taxa in sect. *Myrtillus* (Vander Kloet 1983*c*) and somewhat later for the other sections, depending on the weight of seeds (Crouch and Vander Kloet 1980), or, in the case of *V. uliginosum*, on the degree of cold stratification (Warr 1981). In sect. *Cyanococcus*, radicles emerge in 11–25 days, cotyledons emerge some 10–20 days later and the first true leaves develop in another 10–20 days, depending on temperature. Not until the primary shoot has reached 7–10 cm in height do the leaves begin to resemble those of the parents. At this time, several erect shoots emerge from the developing bole or root crown, that is, from the axils of the cotyledons or the first leaflets. These orthotropic shoots frequently overtop the primary shoot, which often becomes recurved. In the meantime, the radicle develops into a taproot (Hall 1957). In the greenhouse, plants attain their parental growth habit by their second or third year, but in the field this process may take up to 8 years.

The architecture of *V. corymbosum*, a member of sect. *Cyanococcus*, has been described in some detail by Hallé et al. (1978, pp. 233–235 and Fig. 2). In this crown-forming shrub, the shoots are initially erect, but during their first season of extension they curve down fairly abruptly and are certainly permanently recurved by the end of the second season. When disturbed, *V. corymbosum* may sucker (Camp 1945; Vander Kloet 1980); root shoots have also been reported (Vander Kloet 1982).

Many species produce rhizomes, and clones spread rapidly. Tillers or aerial shoots occur every 2–30 cm (depending on species) along a rhizome. Intact rhizomes up to 10 m long have been excavated from *V. angustifolium* colonies (Hall et al. 1979). In a detailed study of the age structure and dynamics of *V. myrtillus*, Flower-Ellis (1971) found that bilberry colonies expanded radially at a rate of about 7 cm per annum (the rate of rhizome growth may be greater), that aerial shoots had a maximum age of 15 years, and that the maximum age attained by rhizomes was 23–28 years. The largest colonies have been reported for *V. myrsinites* by Darrow and Camp (1945); they estimated a colony about 1 km across to be at least 1000 years old.

The Nearctic members of *Vaccinium* have a polymorphic growth habit. Several species form large bushes or small trees (examples of *V. arboreum* up to 10 m high have been reported) whereas others never exceed 10 cm in height (Table 7). Some species produce a few erect stems (e.g., *V. arboreum*), and others grow many erect stems from a common base or crown (e.g., *V. parvifolium*). Another group of species regularly form small compact colonies (e.g., *V. boreale*), and some species form extensive open colonies by means of rhizomes (e.g., *V. pallidum*). Still others are trailing shrubs (e.g., *V. crassifolium*).

Leaves are as variable as, or even more variable than, growth forms. Three sources of variation may be recognized: developmental, intraplant, and interplant. Developmental (ontological) differences include those such as in the size and shape of leaves along the length of twigs. For taxonomic analysis, this variation was controlled by taking samples at the midpoint of the twig. When a shoot emerges from a vegetative bud, the lowermost leaves are usually bractlike, becoming larger towards the distal portion of the shoot. In some species the largest leaf is at the apex, and in others the terminal leaflet is perhaps 10–25% smaller than those along the middle. At 27°N, vegetative bud break may occur throughout the year, especially in *V. corymbosum* populations; in contrast, vegetative bud break usually occurs twice between 40°N and 60°N but only once a season above 60°N. Furthermore, in all North American species shoot growth is determinate, being completed with the death of the apical meristem, which remains as a black tip; this process has been described in detail for *V. angustifolium* by Bell (1950). As the apical meristem dies, perennating buds form in the axils of the leaves. The color of the flush varies from species to species—quite red in some, bright green in others, and pale or glaucous in still others.

Intraplant differences occur in such features as persistence and thickness of the blade, size and shape of the leaf, indentation of the leaf margin, and indumentum. Glandular hairs may be present, sometimes with accompanying simple hairs on the leaf blade. There is a tendency for all types of pubescence to be concentrated on the veins of both the abaxial and adaxial surfaces. Should glandular hairs occur on the leaf blade, they may also be present on the stem but rarely elsewhere (except in *V. hirsutum*). When a leaf is serrate, each tooth is tipped with a glandular hair. In general, such characters of leaf variation have been used extensively for diagnostic features at the interspecific level (Table 7).

Interplant differences refer to those within a species. In *V. pallidum*, leaf pubescence and serration of the leaf margin often differ from plant to plant (Vander Kloet 1978*a*). Similarly, glaucescence varies in *V. angustifolium* (Vander Kloet 1978*b*) and glandular hairs vary in *V. corymbosum* (Vander Kloet 1980).

The anatomy of the leaves of species in all sections has been described by Stevens (1969), usually in terms of the lignification of the epidermis and mesophyll cells, presence or absence of hypodermis, midrib-to-petiole bundle configuration, and venation patterns.

The functions of the various leaf features cited above are largely unknown; however, Andersen et al. (1979) showed that glaucescence in several cultivars of the *V. corymbosum* complex was linked to water-loss resistance. The function of some of the features perhaps may be inferred from work done on other genera. For example, *V. darrowii*, *V. myrsinites*, *V. macrocarpon*, and *V. oxycoccus* have small, thick, recurved leaves, a feature usually classified as xeromorphic. Pubescence enhances the reflection of light (Ehlinger et al. 1976). Thick cuticles absorb damaging ultraviolet irradiation (Gausman et al. 1975). Lee and Lowry (1980) have shown that a red flush—that is, high levels of anthocyanins—also protects young leaves from ultraviolet light, which is stronger in tropical regions, at high elevations, and in northerly latitudes.

Reproduction

Flowers arise either singly (rarely in pairs) on pedicels from the axils of the lowermost leaves of the current flush, either at the elongation of the shoot or after the shoot is almost mature; or from a specialized bud on wood of the previous year, in short or long inflorescences that are pedunculate and racemose. North American species whose inflorescences arise from a specialized bud on wood of the previous year therefore have two types of perennating buds: floral and vegetative. In sect. *Cyanococcus* (blueberries) and sect. *Pyxothamnus*, these buds are dimorphic, with the flower bud at least twice the size of the vegetative. In the remaining sections with floral and vegetative buds, they can scarcely be distinguished except by dissection.

Flower development has been described in detail for *V. angustifolium* by Bell and Burchill (1955*a*). They found that in Nova Scotian plants bud primordia appear in June and floral parts appear in acropetal succession during July. The epigynous bud, in miniature, is formed by the beginning of August. The characteristic resting stage (Bell and Burchill 1955*b*) is assumed during the autumn. These observers noted that mitosis resumes in January and that cell differentiation starts in March. Active growth, including the initiation of meiosis, becomes general during April. Meiosis is completed in anthers during the first week of May and in ovules about a week later. The flower is mature by the last week in May.

In addition, Palser (1961) has given an excellent description not only of the number of parts and the organography of *V. angustifolium* flowers, but also of several other North American species. For example, she found that the number of ovules per carpel varied from a low of 5–8 for *V. arboreum* to a high of 40–50 for *V. ovalifolium*. The average appears to be 15–25 ovules per carpel or about 35–125 per pistil.

The stamens (twice as many as petals) are inserted at the base of the corolla. Shape and size of mature stamens vary markedly among the sections (Figs. 1, 2, 3). Moreover, tubal length and the absence of awns are good diagnostic characters at the section level. Indumentum of the filament is, however, extremely variable. The anthers usually

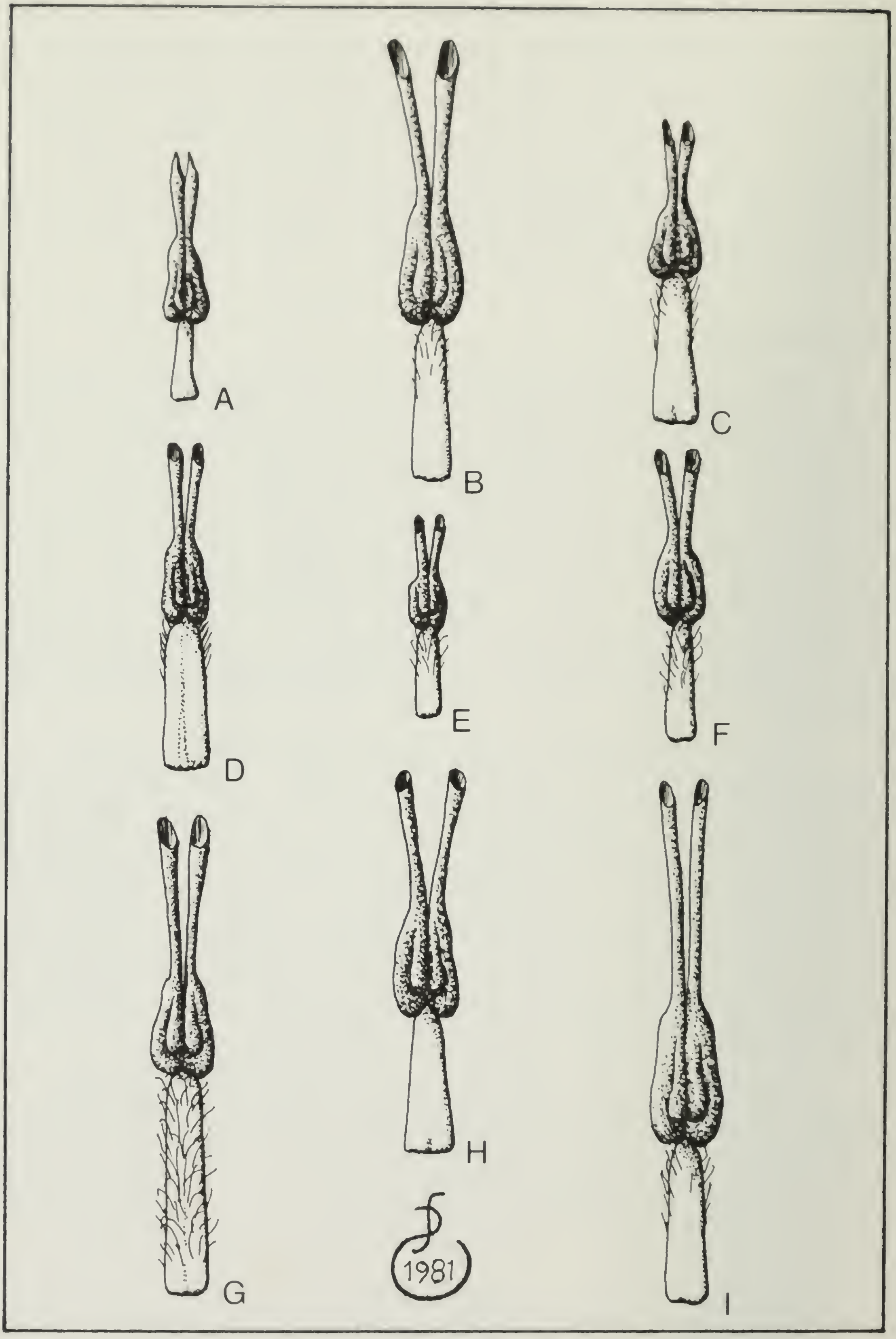

Fig. 1 Stamens from *Vaccinium* sect. *Cyanococcus*. (A) *V. darrowii;* (B) *V. angustifolium;* (C) *V. tenellum;* (D) *V. myrsinites;* (E) *V. boreale;* (F) *V. myrtilloides;* (G) *V. hirsutum;* (H) *V. pallidum;* (I) *V. corymbosum.*

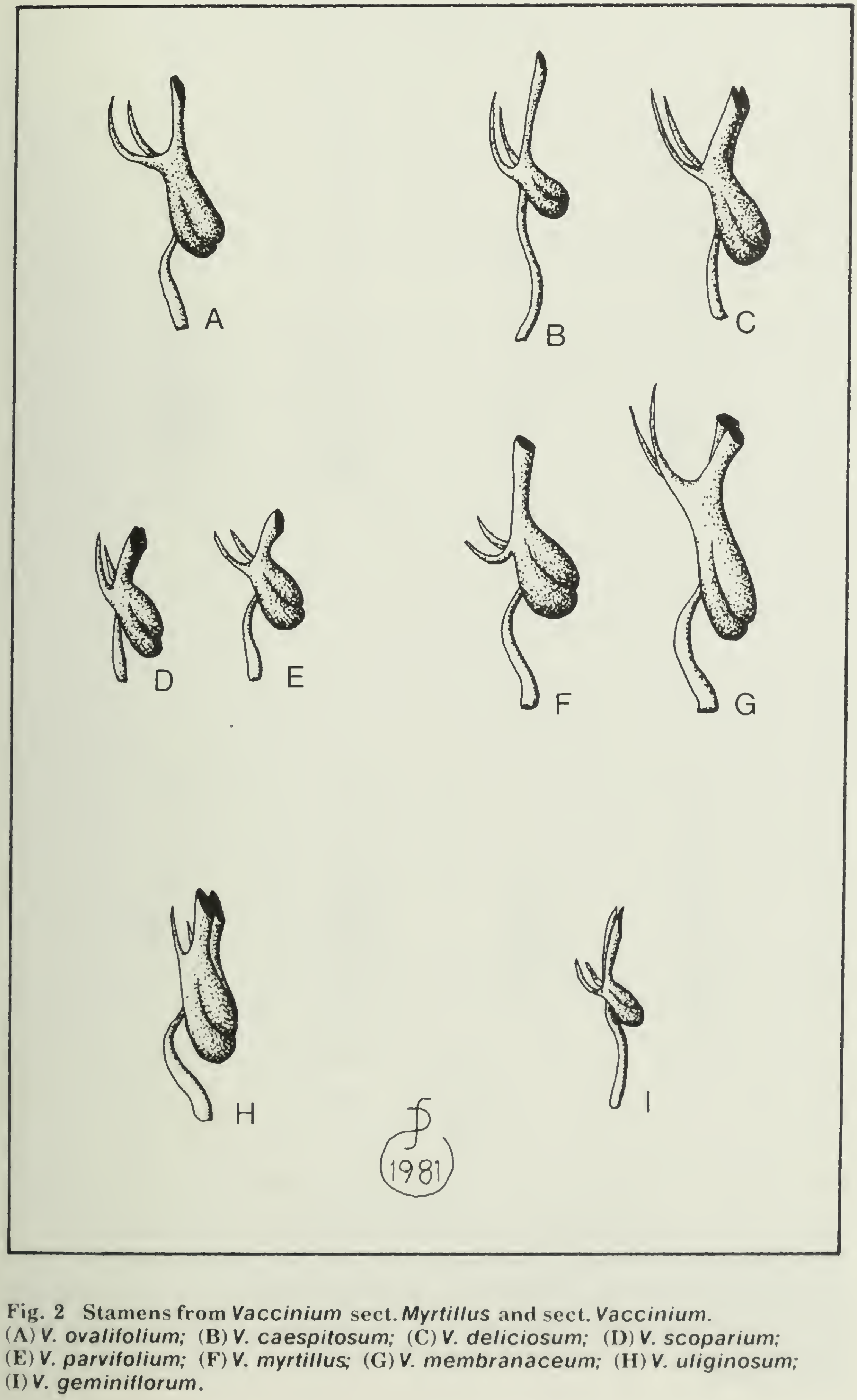

Fig. 2 Stamens from *Vaccinium* sect. *Myrtillus* and sect. *Vaccinium*.
(A) *V. ovalifolium;* (B) *V. caespitosum;* (C) *V. deliciosum;* (D) *V. scoparium;*
(E) *V. parvifolium;* (F) *V. myrtillus;* (G) *V. membranaceum;* (H) *V. uliginosum;*
(I) *V. geminiflorum.*

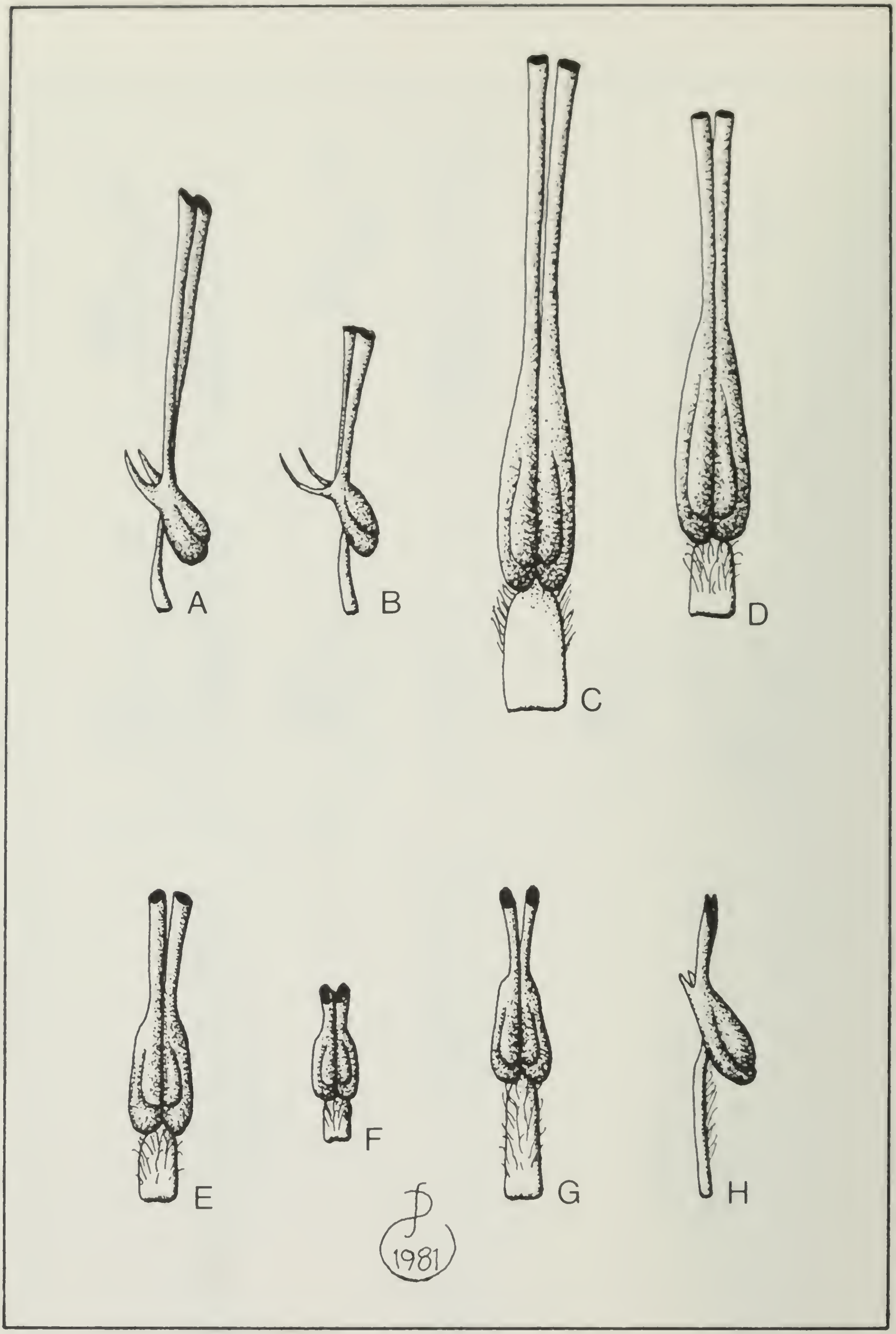

Fig. 3 Stamens from *Vaccinium* sect. *Batodendron*, sect. *Polycodium*, sect. *Vitis-idaea*, sect. *Oxycoccus*, sect. *Oxycoccoides*, sect. *Herpothamnus*, and sect. *Pyxothamnus*. (A) *V. stamineum* (sect. *Polycodium*); (B) *V. arboreum* (sect. *Batodendron*); (C) *V. erythrocarpum* (sect. *Oxycoccoides*); (D) *V. macrocarpon* (sect. *Oxycoccus*); (E) *V. oxycoccus* (sect. *Oxycoccus*); (F) *V. crassifolium* (sect. *Herpothamnus*); (G) *V. vitis-idaea* (sect. *Vitis-idaea*); (H) *V. ovatum* (sect. *Pyxothamnus*).

contain 100–300 pollen tetrads ranging in diameter from 30 to 70 µm (Fig. 4). This estimate agrees with Reader's (1977) count of 2400 ± 500 (mean ± standard deviation) pollen tetrads per flower for *V. myrtilloides*. However, species of hybrid origin have a large number of nonviable or partly viable pollen tetrads (Vander Kloet 1980). Villamil (1980) has described the development of deerberry (*V. stamineum*) stamens in some detail.

Vaccinium flowers are generally protandrous; the pollen is ready for dispersal a day or two before the stigma becomes receptive. This event is heralded by the presence of a creamy exudate on the surface of the stigma.

Pollen tetrads begin to germinate 2–3 h after deposit on the stigmatic surface and, depending on the compatibility of the style, the tubes will penetrate a 10-mm stylar column in 3–5 days. After syngamy, the ovule will mature in as few as 30 days in *V. uliginosum* and *V. scoparium* or will require up to 200 days for populations of *V. corymbosum*, *V. stamineum*, *V. ovatum*, and *V. arboreum*. Bell (1957) has described the development of the seed of *V. angustifolium* in considerable detail. He found that pollen tubes required about 4 days to grow from stigma to ovule. Many ovules did not develop. The average number of seeds per berry was 64, of which 50 (or 78%) were imperfect. He further reported that embryo development was of the solanad type, and that the mature seeds were "axile linear."

Perfect seeds are illustrated in Fig. 5. The inner and lateral walls of the cells of the single-layered seed coat are very heavily lignified; simple pits are numerous and conspicuous. Some sectional variation has been observed in the shape of these lignified cells (Vander Kloet 1983*b*). Peltrisot (1904), Bell (1957), and Brisson and Peterson (1976) have likewise described perfect seeds. According to Bell (1957), imperfect seeds were chiefly of two kinds: medium-sized and solid with the middle integumentary layers lignified or small and collapsed with all tissues inside the seed coat disintegrated. No imperfect seed had an embryo.

The number of perfect seeds per berry does not correlate with berry size unless the weight of the berry exceeds 1.78 g (Kushima and Austin 1979), a condition not met in wild populations but quite frequently seen in cultivars. Rather, the number of perfect seeds per berry is significantly correlated with pollen viability, especially when pollen viability is low (Vander Kloet 1983*c*). Seed weight does not correlate with the number of perfect seeds per berry but with latitude (Crouch and Vander Kloet 1980). Moreover, most species within sections have different seed weights, but only a few have a significantly different number of seeds per berry (e.g. *V. arboreum*, *V. stamineum*, and *V. scoparium*). As a rule, plants that occur above 45°N or above 2000 msm produce seeds that weigh less than 0.37 mg per 100 seeds and require more than 75 days to mature; and plants that grow below 45°N or below 2000 msm usually produce seeds that are heavier than 0.37 mg per 100 seeds and have a much more flexible maturation schedule.

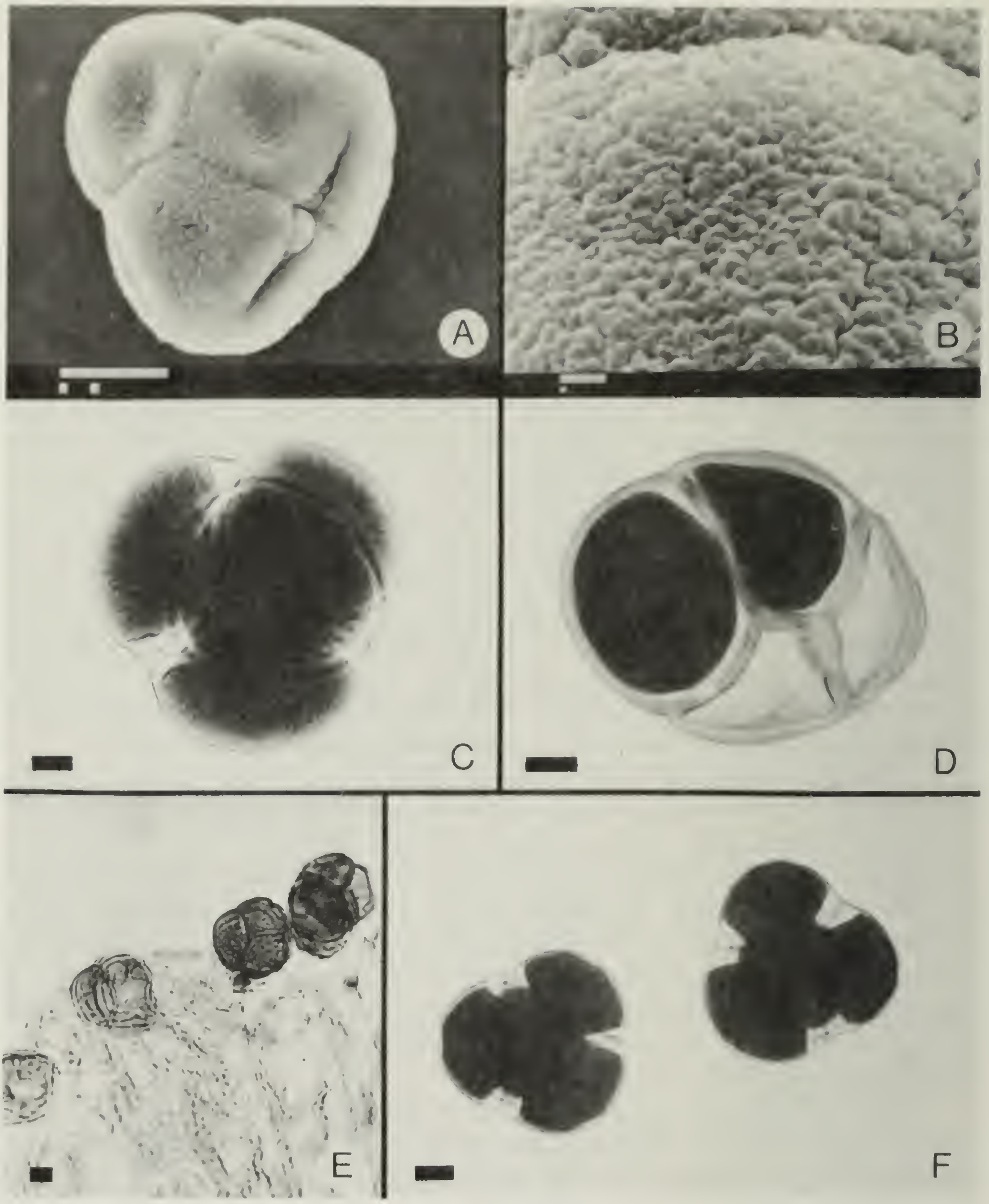

Fig. 4 Pollen tetrads from some North American species of *Vaccinium*. (A) Scanning electron micrograph of *V. stamineum* 220381 (scale bar: 10 µm); (B) Scanning electron micrograph of pollen extine sculpture of *V. stamineum* 220381 (scale bar: 0.1 µm); (C) Perfect pollen tetrad of *V. hirsutum* 83981 (scale bar: 7 µm); (D) Pollen tetrad of *V. corymbosum* 520675; this tetrad has two empty cells (scale bar: 6 µm); (E) Pollen tetrads of *V. corymbosum* 520675 on a stigma, tubes just beginning to emerge (scale bar: 11 µm); (F) Perfect pollen tetrads of *V. macrocarpon* 119781 (scale bar: 5 µm).

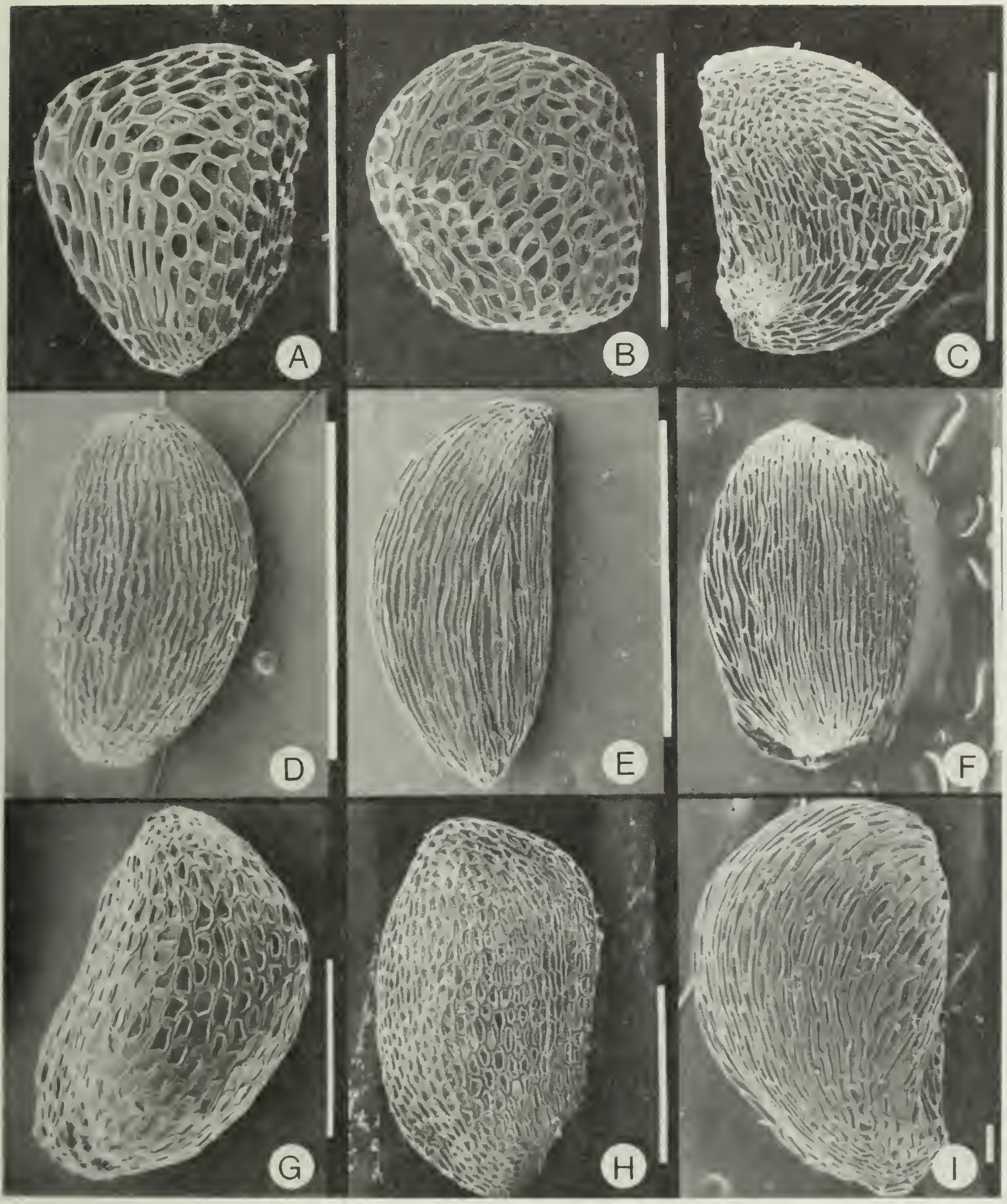

Fig. 5 Scanning electron micrographs of *Vaccinium* seeds. (A) Sect. *Cyanococcus, V. myrsinites* ABS–SW79; (B) Sect. *Cyanococcus, V. tenellum* 42679; (C) Sect. *Oxycoccoides, V. erythrocarpum* 134877; (D) Sect. *Vitis-idaea, V. vitis-idaea* 324979; (E) Sect. *Vaccinium, V. uliginosum* W1977; (F) Sect. *Myrtillus, V. membranaceum* 1329879; (G) Sect. *Batodendron, V. arboreum* 1221078; (H) Sect. *Polycodium, V. caespitosum* 133981; (I) Sect. *Myrtillus, V. caespitosum* 312881.
Scale bar: 1 mm, except for (I) in which scale bar is 0.1 mm.

Pollination

At anthesis, *Vaccinium* flowers are visited in large numbers by species of *Bombus* and *Andrena* and occasionally by *Apis mellifera* (Judd 1966; Dorr and Martin 1966; Boulanger et al. 1967; Vander Kloet 1972, 1976*b*; E. Small 1976; Kevan and Laberge 1978). These authors provide lists and numbers of pollinators visiting several species of *Vaccinium*. McGregor (1976) and Caron (1979) provide data on insects that remove both nectar and pollen. According to Reader (1977) the nectar volume of *V. myrtilloides* is 0.30 ± 0.11 μl per flower. Moreover, he found that 88% of the nectar is composed of dissolved solids, presumably simple sugars and histones. Pollen reward is also substantial, and several thousand grains may be dislodged from a freshly opened flower, each grain being rich in lipids (D. Fairbrothers, personal communication).

Pollen dispersal rarely exceeds 100 m, and dispersal appears to be non-random (Vander Kloet and Lyrene 1987). This observation supports Janzen's (1971) "trap-line" hypothesis rather than the "vagabond" hypothesis. That is, bees do not forage randomly but have a series of flowering plants that they visit consecutively.

Self-pollination is not spontaneous, and the reason for this failure was described in detail by Coville in 1910:

> In its natural position the flower [Figs. 6 and 7] is not erect but inverted, the narrow orifice of the corolla being lowermost, the nectar welling up from the surface of the disk between the base of the style and the base of the filaments. The ten stamens and the style hang downward within the corolla, the stamens being shorter than the style, the pollen when mature drops down from the two anther sacs through the two anther tubes which the stamens of the plants possess and out at the terminal pores.
>
> The pollen does not come out of the anthers readily on a cloudy, humid day, but on a warm, sunny dry day it accumulates in the tubes and when they are moved it runs out like grain from a grain chute....
>
> The pores of the anther tubes do not open squarely across the ends of the tubes, but they are set on a long bevel facing inward. The pollen when released would therefore fall upon the stigma were it not for a peculiarity of the structure of that organ. The sticky stigmatic surface, which the pollen must reach to effect pollination, is at the apex of the globular or top-shaped stigma, while the sides of the stigma as far up as the middle have a dry surface ending in a short collar a little wider, during the early maturity of the stigma, than the widest part of the stigmatic surface. In the inverted position of the flower the falling pollen strikes this dry surface, like the outside of an inverted funnel, and drops off the rim or remains on it, without reaching the stigmatic surface which lies protected beneath.

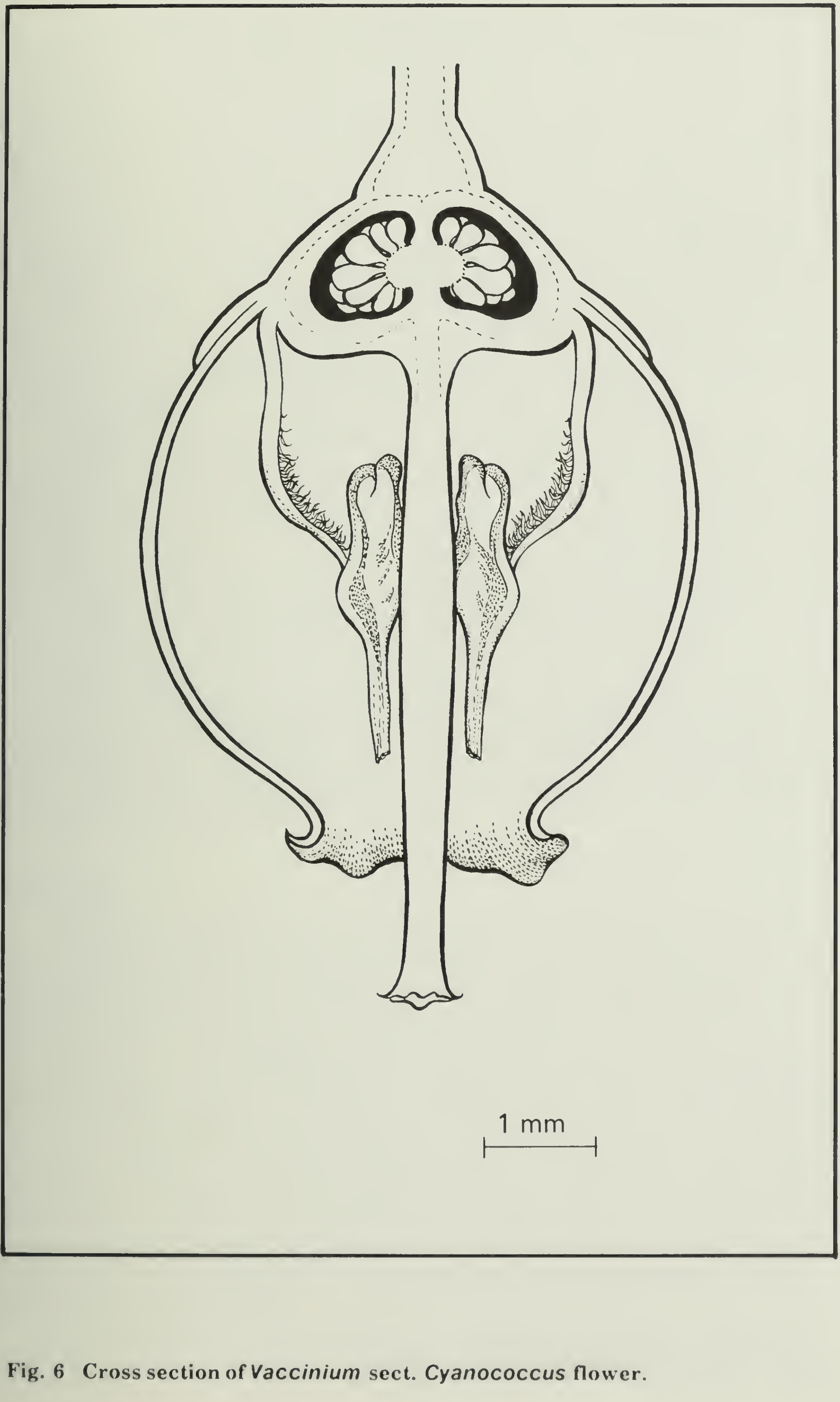

Fig. 6 Cross section of *Vaccinium* sect. *Cyanococcus* flower.

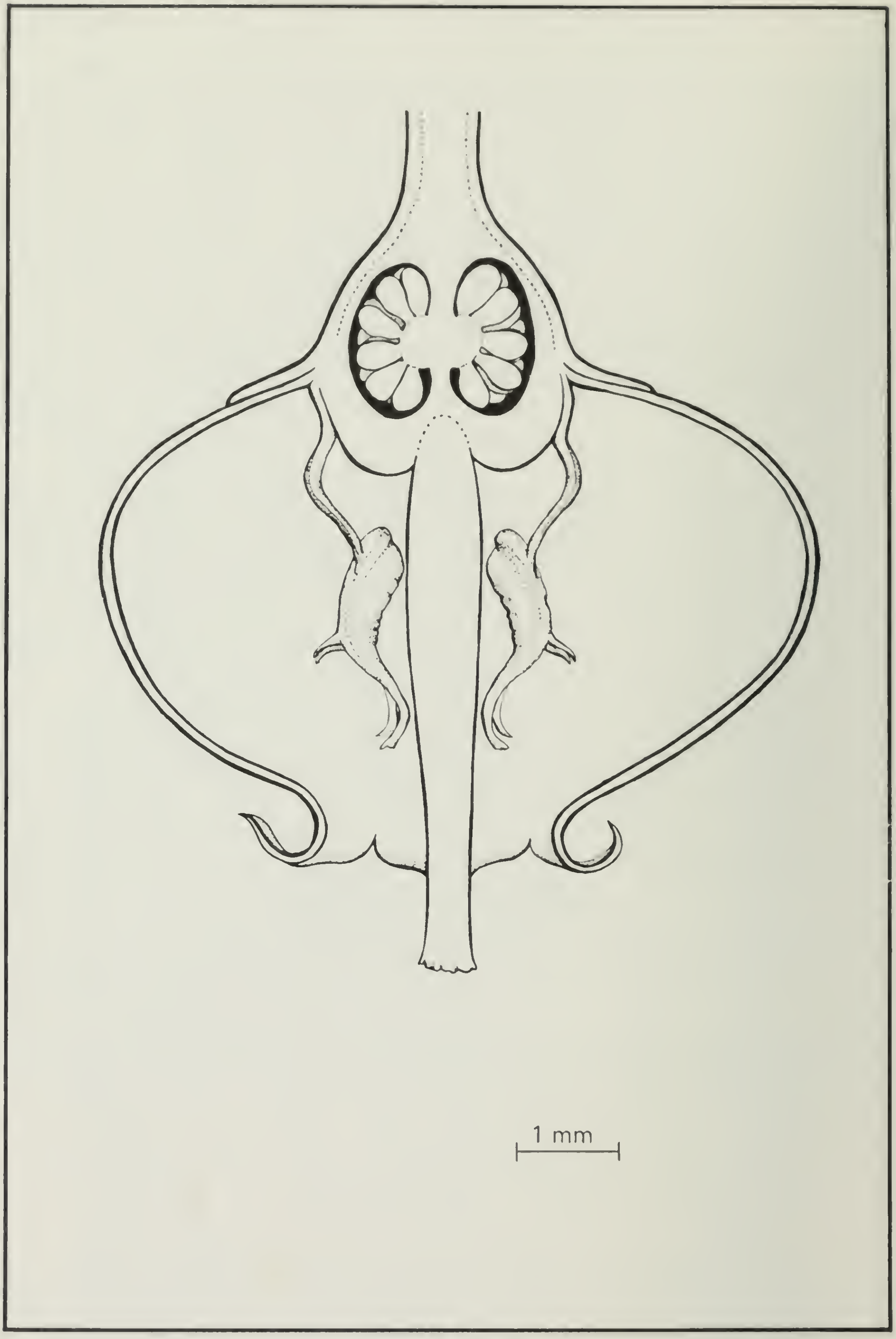

Fig. 7 Cross section of *Vaccinium* sect. *Myrtillus* flower.

Nevertheless, both Warming (1908) and Hagerup (1933) reported that in Greenland *V. uliginosum* was largely self-pollinating and by inference self-compatible. Furthermore, according to Cruden's (1977) outcrossing index, the pollen-to-ovule ratio for *Vaccinium* suggests that the genus is composed of obligate selfers. In a similar vein, Pojar's (1974) index of potential recombination (IPR) (which is based on generation length, basic chromosome number, relative chromosome length, level of ploidy, dichogamy, spatial separation of sexual organs, heterostyly, sexual reproduction, mode of pollination, cleistogamy, compatibility, geitonogamy, dispersibility, population size and structure, ecotypic variation, and hybridization) suggests that *V. deliciosum*, *V. scoparium*, *V. ovatum*, *V. oxycoccus*, and *V. vitis-idaea* ought to be moderately autogamous, because Pojar gave these species an average IPR value of 43 ± 2. (Strictly autogamous species score 40 or less, outcrossing species 50 or higher.)

These arguments are not, however, supported by carefully controlled, interflower crossing experiments. Aalders and Hall (1961), Vander Kloet (1976*b*, 1977*a*, 1978*a*), Ballington and Galletta (1978), Hall et al. (1979), and Vander Kloet and Hall (1981) have all shown that selfing is largely unsuccessful in *Vaccinium* sect. *Cyanococcus*. Not only is the seed set reduced, but plants resulting from self-fertilized lines have much lower vigor. Similarly, Vander Kloet (1977*b*) could not substantiate self-compatibility in experimental populations of *V. uliginosum*.

Field experiments purportedly indicating that selfing had occurred (Reader 1977; Whitton 1964; Merrill 1936) are suspect on two counts: clones are often intermingled (Vander Kloet and Hall 1981) and ants often contaminate even the best constructed enclosures (Kevan 1980).

Dispersal

Seeds are spread in the droppings of birds and mammals. On the basis of many reports, Martin et al. (1951) note that grouse, scarlet tanagers, bluebirds, thrushes, black bears, chipmunks, and white-footed mice consume large amounts of *Vaccinium* fruit. Similarly, Dale and Hughes (1977) state that in the southeastern United States, blueberries are the preferred summer food of wild turkeys, ruffed grouse, and quail. Indeed, about 19% of the quail's diet in July consists of blueberries. Songbirds such as scarlet tanagers, robins, cardinals, bluebirds, and thrushes also eat blueberries. Eaton (1956) found that the robin is a major seed disperser in southwestern New Brunswick because migratory flocks feed on the blueberry just before harvest by humans. Hall et al. (1979) have found seeds of *V. angustifolium* in the droppings of black bear, red fox, and raccoon.

Such animal dispersal implies a clumped dispersion pattern of seedlings. Indeed, random sampling of three abandoned meadows in

Pictou County, N.S., with 28 quadrats of 1 m^2 each, gave a mean of 1.1 ± 0.39 seedlings, a variance of 4.54, and a variance-to-mean ratio of 4.3:1, confirming that expectation (Vander Kloet 1976*c*; Hall et al. 1979). Except in the Maritimes and northern Maine, where *V. angustifolium* seedlings are common in abandoned fields, and in Washington and British Columbia, where *V. parvifolium* seedlings are common on rotting logs and coniferous stumps, *Vaccinium* seedlings are rarely encountered in North America.

Long-distance dispersal is a rare event at best because the dispersal agents cited above are often territorial. Even when fruit ripening coincides with migration of songbirds, as happens in Maine and the Maritimes, berry pulp is rarely retained in the gut of these cropless birds for more than 20 min. Birds with crops, such as wild turkeys, grouse, and quail, are not potential long-distance dispersers because their gizzards (which are capable of grinding seeds into a fine meal and which have a pH of 2–3) destroy a proportion of ingested seeds. Furthermore, these birds are also quite sedentary.

Krefting and Roe (1949) found that the germination of blueberry seeds was reduced by at least 15% when seed passed through the gut of bear, deer mouse, and chipmunk.

The energetics of dispersal are complex and as yet poorly understood. The principal components of *Vaccinium* berries are water, sugars, crude proteins, vitamins, fats (in seed), and fiber (Sheridan and Seeling 1973). Vander Kloet and Austin-Smith (1987) have calculated that a blueberry with a diameter of 7 mm has 85 calories (356 J) of which only about 40 calories or 167 J (from the pulp and the small, immature seeds) are available to the dispersal agent. However, populations from 27°N to 35°N produce berries with much larger seeds than those growing above 35°—especially those above 45°N (Crouch and Vander Kloet 1980)—and therefore the southern populations have a berry with somewhat less available energy. Northern populations with their smaller-seeded berries provide more available energy because the seed coat may be more easily broken down in the digestive tract (Vander Kloet and Austin-Smith 1987).

Both berry production per shrub and synchrony in ripening also vary markedly. At the Archbold Biological Station, Lake Placid, Fla. (27°N), I tagged 125 *V. corymbosum* shrubs in 1978 in order to follow phenological events for at least 10 years. The 1979 fruiting season showed scarcely any synchrony in ripening. Indeed, asynchrony in ripening might be a more apt description for this population. The first shrub began to disperse fruit on 18 March 1979, the last on 15 June 1979; several shrubs fruited sporadically for 3 months, ripening perhaps 2–3 berries a day, whereas others completed fruit set and dispersal in 2 weeks. Maximum berry production for this population occurred in the first week of May, during which time the entire group of 125 plants collectively produced about 300 ripe berries per day. No banner year has been observed for this species in southern Florida. Moreover, the vagaries of nature may severely limit fruit set; for example, a severe frost on 3 March 1980 destroyed all the developing berries on the early flowering shrubs and resulted in a 25% reduction in set.

In contrast, the Lake George, N.S. (44°N), population of *V. corymbosum* has one banner year out of every six. Moreover, the 50 tagged plants show some fruiting synchrony; berries on shrubs sharing the same habitat ripen at about the same time, although the yield per shrub is quite variable, for example from none to 3000, with an average of 200–400 berries per shrub in 1980. Furthermore, not only do *V. corymbosum* berries begin to ripen en masse during mid-August but so do those of *V. angustifolium* and *V. myrtilloides*. In short, the reward to birds and mammals foraging on blueberries in Nova Scotia is substantially larger and more predictable than in Florida.

Reproductive potential

I have calculated the seed set for both *V. parvifolium* (sect. *Myrtillus*) and *V. corymbosum* (sect. *Cyanococcus*). In the latter, a 2.5-m shrub at the Archbold Biological Station annually bears an average of 300 corymbs; each inflorescence has (5)7(11) flowers of which approximately 63% will set fruits; each ripe berry contains 16 ± 5 plump seeds of which 57% ± 29% germinate readily in an illuminated misting chamber. This germination rate will be at least 15% lower if the seed passes through the gut of birds or mammals before sowing. However, the reproductive potential of this species is much greater than its actual seed or seedling production. On the average, a 1.5-m shrub annually produces 231 000 ovules of which only about 11% develop into plump brown seeds and only about 5% may develop into vigorous seedlings.

Although *V. parvifolium* belongs to a different section (*Myrtillus*), with flowers borne singly in the axils of the lowermost leaves of the current flush, its reproductive potential is nevertheless very similar. Thus a 1.5-m shrub of *V. parvifolium* at 600 msm on Mount Seymour, North Vancouver, B.C. (49°N) produces about 1400 flowers annually of which 90% set fruit. Each berry contains 51 ± 11 seeds; out of this number 19 ± 8 are plump and perfect (Bell 1957), and, when placed in an illuminated misting chamber, approximately 25% of the plump seeds will germinate. The reproductive potential of this species also is much greater than its actual seed or seedling production. On average, a 1.5-m shrub produces 84 000 ovules annually; of this number 20% develop into plump brown seeds and 7% develop into vigorous seedlings.

A 1.5-m shrub of *V. corymbosum* produces about 2.75 times more ovules than a 1.5-m shrub of *V. parvifolium*, but wide variation in numbers of corymbs (0–1700) and set (0–8500 berries) was observed in all tagged populations. Of the 225 tagged plants, 45% contributed less than 1% each to the total seed production of the population, and two shrubs alone produced 21% of the total seeds.

Habitat

Vaccinium occurs throughout the Nearctic wherever the soil is acidic and the shade moderate (Camp 1942*a*, 1945). Above 75°N and along mountain summits of the Pacific coast, *Vaccinium* is absent from many of the exposed and acidic rock habitats partly because of extreme desiccation and the short growing season. Within these limitations, some of which were tested experimentally by 1910 (when Coville demonstrated the deleterious effect of liming on blueberry growth and development), *Vaccinium* occupies two major habitat types: stable sites and unstable sites. Stable sites include headlands, tundra, balds and slicks, subalpine shrubberies, alpine meadows, and rocky outcroppings; unstable sites involve a wide variety of successional communities such as burned-over areas, old fields, pine flatwoods, oak parklands, boreal forests, wet swales, bogs, and red maple swamps, as well as the margins of lakes, ponds, and streams. Recently disturbed ground, especially logging roads and the verges of railroad tracks, roadways, and ditches, is also rapidly invaded by *Vaccinium* species. Along the west coast, *V. parvifolium* is considered to be an indicator species of secondary succession in coniferous stands, since it establishes itself with high frequency on coniferous stumps and deadfall. The epiphytic habit so common in tropical montane forests has not been observed in *Vaccinium* in North America.

Species such as *V. angustifolium* and *V. myrtilloides* are most abundant in disturbance communities, which result from clear-cutting, forest fires, and the abandonment of agricultural land. Especially noteworthy in this regard are the Maritimes and New England, where many marginal farms were abandoned during the early part of the 20th century, leaving old fields for *V. angustifolium* and *V. myrtilloides* to colonize. Trevett (1956) reported that by the 1940s several of these fields were burn-pruned. This development, coupled with the introduction of frozen foods to the North American market, led to rapid exploitation and development of the barrens.

In natural communities or managed forests, the underground parts of *V. angustifolium*, *V. myrtilloides*, and *V. corymbosum* survive wild fire or controlled burning (Hall et al. 1979; Vander Kloet and Hall 1981; Flinn and Wein 1977; Ross 1978). Reestablishment occurs by bole and rhizome sprouting. Commercial stands are burn-pruned every second year; *V. angustifolium* tolerates this practice, but it is deleterious to *V. myrtilloides* (Vander Kloet and Hall 1981). Smith and Hilton (1971) found that the improved *V. angustifolium* performance in Ontario after burning stemmed from the stimulative effects of nutrients in the ash deposited on the surface of the soil.

Hitherto, seed bank data have been ambiguous. Milton (1935) estimated that soil cores collected in Wales during February–April 1933–1934 from dry slopes and oak woods contained up to 300 buried viable seeds of *V. myrtillus* per square metre. Furthermore, in a recent seed bank study of the Swedish taiga, Granström (1982) found 270 ± 200 seedlings of *V. myrtillus* per square metre but very few of either *V. vitis-idaea* or *V. uliginosum*. Oosting and Humphreys (1940), who collected soil samples during November 1936 from a series of successional communities and adjacent oak–hickory forests in the vicinity of Durham, N.C., found only one *Vaccinium* seed. Johnson (1975) took soil cores during June–August 1973 and 1974 in spruce–jack pine forests near Great Slave Lake, N.W.T. Although these stands had *V. vitis-idaea* and *V. uliginosum* as understory shrubs, only *V. vitis-idaea* seeds were uncovered, and these failed to germinate. Similarly McGraw (1980) collected soil samples on 12 August 1978 from cotton grass tundra at Eagle Creek, Alaska, but found no *Vaccinium* seeds, although both *V. vitis-idaea* and *V. uliginosum* were present in the stand.

Mycorrhiza

Mycorrhizal associations have been reported for the following species: *V. oxycoccus*, *V. macrocarpon*, *V. myrtillus* (Pearson and Reade 1973), *V. caespitosum*, *V. membranaceum*, *V. parvifolium*, *V. scoparium*, *V. uliginosum*, *V. ovatum* (Largent et al. 1980), and *V. angustifolium* (MacArthur 1955). Mycorrhizal fungi such as *Pezizella ericaea* Reade (Pearson and Reade 1973) or *Clavaria* spp. (Seviour et al. 1973) apparently infect only the unsuberized parts of the root (Pearson and Reade 1973) and increase the uptake of nitrogen (Stribley and Reade 1974) and phosphorus (Pearson and Reade 1973), thereby improving nutrient levels and growth rates of *Vaccinium* species, which invariably grow on acidic or peaty soils in which the natural rotting processes are slower. Bradley et al. (1982) have suggested that tolerance of heavy metals in *Vaccinium* may be a result of mycorrhizal infection.

Largent et al. (1980) found not only that 61% of *Vaccinium* plants examined had mycorrhizal systems present in the root tips but also that the degree of infection differed. The unsuberized roots of some plants were covered by a fungal mantle with intracellular penetration of fungal hyphae; others had their root tips covered by a fungal mantle, but no intracellular penetration was observed; still others had only intracellular penetration.

Evolution and genetic system

Hall and Galletta (1971), who have described the chromosome morphology of several diploid species in *Vaccinium*, found that the 12 chromosomes are small (1.5–2 μm long). The karyotype varies little from the ancestral group. Regular chromosome pairing and disjunction have been observed in many species (Longley 1927; Newcomer 1941; Rousi 1966; Stushnoff and Palser 1969; Cockerham 1972).

Only in the tetraploids ($2n = 4x = 48$) and hexaploids ($2n = 6x = 72$) have true multivalents or secondary associations of bivalents been observed (Galletta 1975). However, G. Rimmer (personal communication) has examined some 150 tetraploid biotypes of *V. corymbosum* from eastern Quebec and has found the multivalent incidence much lower than that reported by Jelenkovic and Harrington (1971). Such deviations from normal pairing may account for the reduced pollen viability observed in interspecific hybrids, hybrid species, or polyploid species in *Vaccinium* sect. *Cyanococcus* (Vander Kloet 1980, 1983*b*). The production of diploid (or unreduced) gametes may also stem from irregular pairing; the average occurrence of such diploid gametes is 1.4% for *Vaccinium* sect. *Cyanococcus*, but up to 6% has been reported for *V. darrowii* (Cockerham and Galletta 1976). In any case, the production of diploid gametes promotes the occasional occurrence of tetraploid or hexaploid plants.

Although large-scale selfing trials in *Vaccinium* sect. *Cyanococcus* have had some success (Ballington and Galletta 1978; Hall et al. 1979; Vander Kloet and Hall 1981) in the field, shrubs more than 800 m from a compatible neighbor do not produce viable seeds. Since 1972, I have observed three such isolated individuals of *V. corymbosum*: one at the Archbold Biological Station, Lake Placid, Highlands County, Fla.; another at Wells Island, Jefferson County, N.Y.; and the last on the shore of Lake Opinicon, Leeds County, Ont. All have flowered profusely and are visited by *Bombus* spp. but produce no viable seed unless compatible pollen is introduced.

Outcrossing, whether intraspecific or interspecific, is much more successful in *Vaccinium* sect. *Cyanococcus*, especially when the plants have the same chromosome number (homoploidy) (Ballington and Galletta 1978; Hall et al. 1979; Vander Kloet and Hall 1981; Vander Kloet 1980, 1983*b*). Therefore, whenever homoploid species are sympatric and occur in the same habitat, interspecific hybrids have frequently been observed (Camp 1942*a*, 1945; Hall and Aalders 1962; Mueller 1968; Vander Kloet 1977*b*, 1978*a*; Lyrene and Sherman 1980). If such interspecific hybrids are established in a population of one of the parental taxa, they are usually at a disadvantage, since these hybrids often display asynchronous flowering and have lower seed set and fewer viable offspring (Vander Kloet 1983*b*) and thus are selected against.

However, if by chance a few of these interspecific hybrids become established in a habitat previously unexploited by *Vaccinium* (Vander Kloet 1976*b*, 1980) they may be released from the constraint of natural selection and undergo a population flush. Details of this idea, with examples and references, are given by Carson (1968, 1971, 1973, 1975). According to this model, the major effect during the flush phase is that of genetic recombination within the population, followed by bizarre genetic variability.

This expansion is inevitably followed by a crash that may reduce the population to only a few novel forms. These plants constitute the nucleus of the next flush phase, which, if subject to habitat selection, may produce a new coadaptive gene pool. This, according to Carson, is the essence of the speciation process and may in a few generations result in reproductive isolation.

If the founder–flush concept is applied to the known distributions and morphological diversity of the putative hybrid species in *Vaccinium* sect. *Cyanococcus* (the lowbush tetraploids *V. myrsinites*, *V. hirsutum*, and *V. angustifolium* and the highbush *V. corymbosum*) then the following interpretation may be made: *V. angustifolium*, which is consistently tetraploid ($2n = 4x = 48$) and polymorphic, has large populations on barrens in Maine and the Maritime Provinces and has the largest geographical range despite its youth (Vander Kloet 1978*b*, 1977*a*). The original diploid hybrid swarm has apparently crashed completely, leaving only the tetraploid, which is currently in its flush phase. Conversely the monomorphic tetraploid *V. hirsutum* has only a few isolated populations in the Appalachians and is apparently going through a crash phase.

The tetraploid *V. myrsinites* is also morphologically quite uniform and is largely restricted to the coastal plain and the Gulf Coast of the southeastern United States. This species is presumed to be the oldest of the tetraploid species – individual plants have been dated at 1000 years (Darrow and Camp 1945) – and has gone through the crash phase at least once. Natural selection has left a xerophytic genotype which is strongly adapted to fire (Abrahamson 1980).

The hybrid species *V. corymbosum* presents a special case in that it contains diploid ($2n = 2x = 24$), tetraploid ($2n = 4x = 48$), and hexaploid ($2n = 6x = 72$) populations. Although these populations scarcely interbreed, I have yet to find even macroscopic characters that would consistently separate these gene pools in the field (Vander Kloet 1980) and therefore these gene pools, at the utmost, might be considered species *in statu nascendi*. Camp (1942*a*, 1945) was probably correct: before large-scale land clearing and disturbance occurred in eastern North America, the *V. corymbosum* complex had a very patchy and restricted distribution, and local populations may have diverged significantly owing to genetic drift (Wright 1969). Once clearing began, efficient dispersal would allow these relict populations to expand rapidly. Since no incompatibility system has developed within the homoploids, a large, open, and actively recombining system came into being. When faced with classifying such a wealth of variation, systematists can use various taxonomic methods. Some, like Camp (1945), create clusters of species, subspecies, ecotypes, or varieties, whereas others, like Vander Kloet (1980), use the same data to group the whole as a single variable species. Carson (1975) also argues that such entities would appear to be large species, with intact, closed, variability systems that have been able to resist change; indeed, such species have populations which are "incompetent" for speciation.

Ultimately, all the characters of *V. corymbosum* can apparently be traced back to its diploid ancestors: growth and evergreen habit, as well as some glaucescence, to *V. darrowii*; pubescence, glandular hairs, and dark, dull berries to *V. tenellum*; serration of the leaf margin, enlargement of the leaf blade, glaucescence, and blue berries to *V. pallidum*; and woolly pubescence, entire leaf margins, and short corollas to *V. myrtilloides*. Add a measure of hybrid vigor and intrademic crossability to hybrid swarms between these parental species and *V. corymbosum* results.

The acquisition of genetic information from sympatric lowbush taxa is almost certainly still taking place. Genes are probably being modified through selection and transmitted throughout the highbush populations. This revised and edited genetic code is not fed back through hybridization to its diploid ancestors. I have yet to discover the selection pressures responsible for that gene loss. *Vaccinium corymbosum* as it exists today nevertheless exhibits all the characteristics of a compilo species. It is "genetically aggressive, plundering related species of their heredities" (Harlan and de Wet 1963).

Ideas on the origin and evolution of the diploid ($n = 12$) lowbush blueberries of *Vaccinium* sect. *Cyanococcus* are somewhat more speculative. Camp (1942*a*) classified them as part of the basic diploid group that arose from phyletic divergence (as opposed to his "mere speciation"), which could occur whenever several diploid taxa introgress and could produce polyploid taxa through subsequent alloploidy.

Vander Kloet and Hall (1981) have postulated that *Vaccinium* sect. *Cyanococcus* originated in South America, in spite of the fact that no member of the section occurs or has been known to occur on that continent. Nevertheless, *V. darrowii*, an evergreen member of sect. *Cyanococcus*, has been crossed successfully with the evergreen *V. ovatum*, which belongs to the largely South American sect. *Pyxothamnus* (Darrow and Camp 1945). Like sect. *Cyanococcus*, this section has the inflorescences in racemes, the pedicel is articulated with the calyx, and the anthers rarely have awns or have very short ones. Sect. *Cyanococcus* differs in having berries that are pseudo 10-loculed and twigs that are verrucose. Except for *V. darrowii*, *V. myrsinites*, and a few southern plants of *V. corymbosum*, sect. *Cyanococcus* is also deciduous, and therefore the leaves are rarely as coriaceous as they are in sect. *Pyxothamnus*.

There are at present no members of *Vaccinium* sect. *Cyanococcus* growing on the isthmus between North and South America, in Mexico, in southwestern America, along the Pacific coast of the United States, or in the Caribbean. Vander Kloet (1983*a*) nevertheless favors the Caribbean as a route to North America, for the following reasons: the lowbush diploids are largely found in eastern North America (Fig. 8); the Greater Antilles have suitable habitats where several members of the Ericaceae occur including *V. racemosa* (Stearn 1972); and the Caribbean is a set of islands where the "taxon cycle" is known to operate (Ricklefs and Cox 1972), a fact that accounts for the rapid rate of extinction of species there.

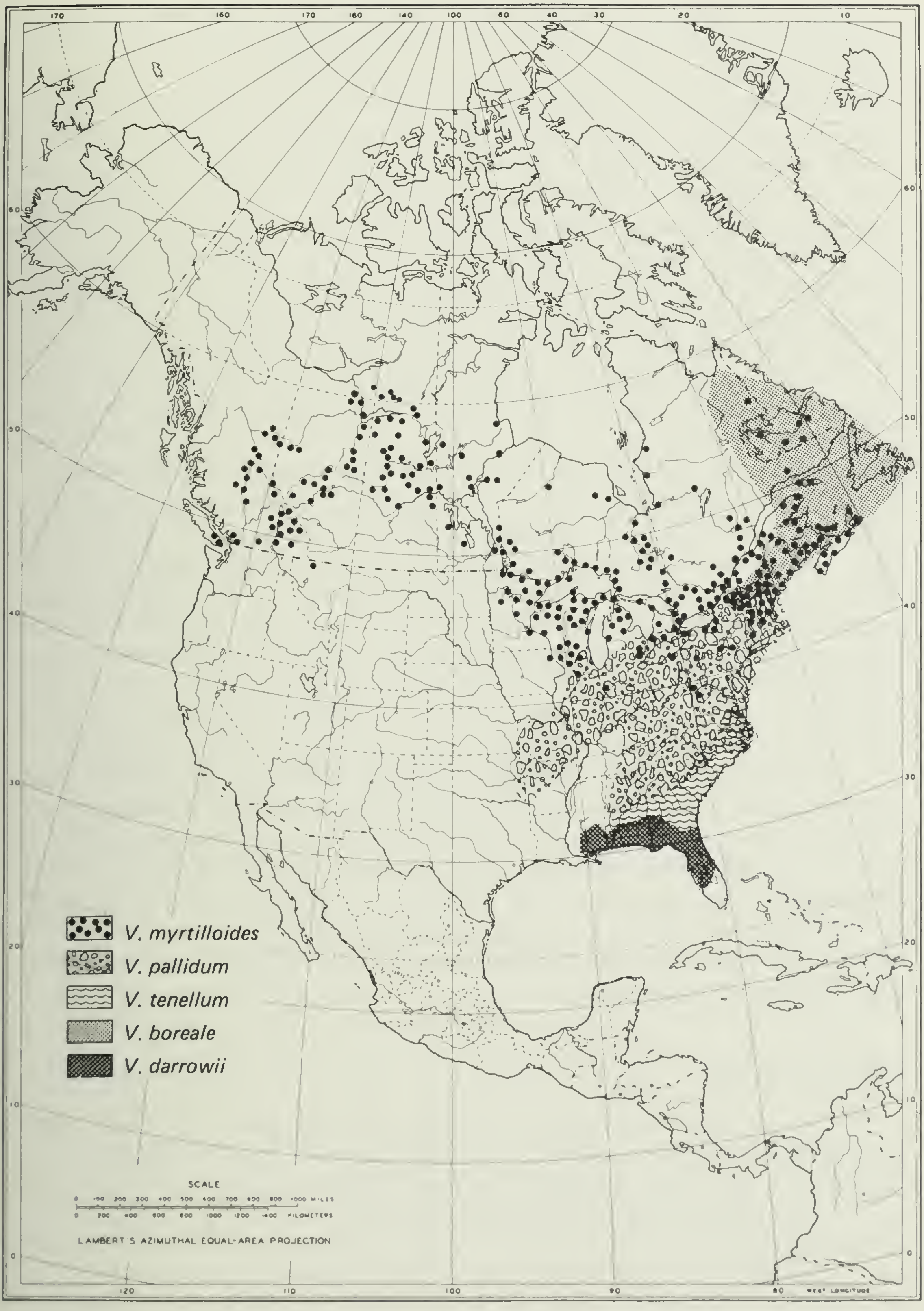

Fig. 8 Distribution of the diploid lowbush species in *Vaccinium* sect. *Cyanococcus*.

The following evolutionary history for *Vaccinium* sect. *Cyanococcus* is suggested. The ancestral *Cyanococcus* lowbush probably emigrated from South America to North America, using the Proto-Antilles (which later became the Greater Antilles) as stepping stones. As the North and South American continents drifted west-northwest at approximately 5 cm per year, the tongue of the crustal plate, which lies between them and on which the Greater Antilles were located, moved relatively eastward, bringing this chain of islands near Florida (Rosen 1975). During the Tertiary period, *Cyanococcus* invaded the sand dunes, relict sand dunes, and pine flatwoods of peninsular Florida, where the evergreen and diploid *V. darrowii* still thrives. At the periphery, populations diverged through parapatric speciation into sister groups. The trend has been to lose the evergreen and xeromorphic characters of the present-day *V. darrowii*, such as small, thick, glaucous, inrolled leaves (glaucescence has been shown to retard transpiration; see Andersen et al. 1979; Freeman et al. 1979), and to evolve more temperate deciduous plants with fewer xeromorphic characters, as in *V. tenellum*, or with larger leaf blades, as in *V. pallidum*. A concomitant decrease in seed weight (Crouch and Vander Kloet 1980) and pollen size has also been observed for the group. This reduction is most readily explained by the fact that the lowbush diploids occurred on a continent that was drifting 50–60 km west-northwest every million years into a more temperate or boreal climate, where the shorter season selected against larger leaf blades, heavier seeds, and larger pollen grains.

Whether the speciation process described for *Vaccinium* sect. *Cyanococcus* can be applied to the remaining sections of *Vaccinium* in North America is moot. Camp, in his papers on the biosystematics of *Vaccinium* sect. *Oxycoccus* (1944) and sect. *Euvaccinium* (1942*b*), presumed that they did, but evidence is scarce, especially for *Vaccinium* sect. *Myrtillus*, where the basic diploids do not form a tidy distributional cline of species like that shown in Fig. 8 for the lowbush diploids of sect. *Cyanococcus*.

Classification

The genus *Vaccinium* Linnaeus (Ericaceae: Vaccinoideae: Vaccinieae) is represented in North America by 10 sections and 26 species. Several of these sections were promoted to genera by J.K. Small (1933), but all were subsequently reduced to subgeneric or sectional level by Camp (1945). Sections, although arbitrary, seem to be more appropriate than genera for the following reasons: (*1*) Members from the different sections occasionally interbreed (Ritchie 1955; Darrow and Camp 1945; Vander Kloet 1977*c*; Ballington 1980). (*2*) Differences between sections are not always clear-cut. Taxa belonging to *Vaccinium* sect. *Oxycoccoides* have 4-merous flowers and have reflexed corolla lobes at anthesis, characters also found in *Vaccinium* sect. *Oxycoccus*, but the presence of solitary flowers in leaf axils and of bud scales suggests an affinity with *Vaccinium* sect. *Myrtillus*.

Indeed, it is possible to link all the inflorescence types found in *Vaccinium* (Fig. 9). A shoot with a single flower in a leaf axil (the sect. *Myrtillus* type) may be regarded as the most primitive in the series and a probable precursor both to the vegetative shoot and to more specialized inflorescences such as the leafy raceme of *Vaccinium* sect. *Polycodium*. The deerberry (sect. *Polycodium*) inflorescence differs from the bilberry type (sect. *Myrtillus*) by having a flower in every leaf axil, which increases the seed production potential of the shoot but also ensures its demise after dispersal. The remaining sections have a reduced version of either the bilberry type (e.g., sect. *Oxycoccus*) or the deerberry type (e.g., sect. *Batodendron*, sect. *Cyanococcus*, sect. *Vitis-idaea*, sect. *Pyxothamnus*, and sect. *Vaccinium*).

Taxonomists who have treated *Vaccinium* on a worldwide basis, for example, Sleumer (1941) and Stevens (1969, 1971), have employed sections in preference to other infrageneric categories as the simplest way to understand the complexity of the genus.

In addition to *Vaccinium*, the tribe Vaccinieae is represented in North America by *Gaylussacia* (huckleberries). *Gaylussacia* can be readily separated from *Vaccinium* by its fruit. The huckleberry contains 10 rather large bony seeds, whereas *Vaccinium* berries have a large number of small seeds.

The modern concept of the species in *Vaccinium* was first articulated by Camp (1941, 1942*a*, 1942*b*, 1944, 1945) in a series of biosystematic papers on *Gaylussacia* and *Vaccinium*. Before this assessment, attempts were made to describe formally every variant, especially by E.L. Greene, J.K. Small, and W.W. Ashe, who worked primarily in eastern North America. *Vaccinium* sect. *Polycodium* Rafinesque (deerberries) is a case in point.

Linnaeus (1753) described the first species of deerberry from material sent to him by Kalm; he placed it in his genus *Vaccinium* under the specific epithet of *stamineum*. Pursh (1813) and Nuttall (1843) added one species each, but around the turn of the century, Greene (1898, 1912), J.K. Small (1903, 1913, 1928, 1933), and Ashe (1925, 1927, 1931) not only described 19 new species for the section but also promoted several subspecific entities to species. Thus by 1933, 27 species were recognized in *Vaccinium* sect. *Polycodium*, which Greene (1898) had elevated to generic rank. Baker (1970) made an exhaustive and systematic study of the deerberries and found that his morphological and biological data were consistent with the concept of a single polymorphic species of deerberry in eastern North America, namely *V. stamineum* Linnaeus.

I have not adopted Camp's species concept for this monograph because in my view (Vander Kloet 1978*a*, 1980) he placed too much emphasis on chromosome number and the alleged ancient distributions of his evolutionary units. Camp favored a cladistic

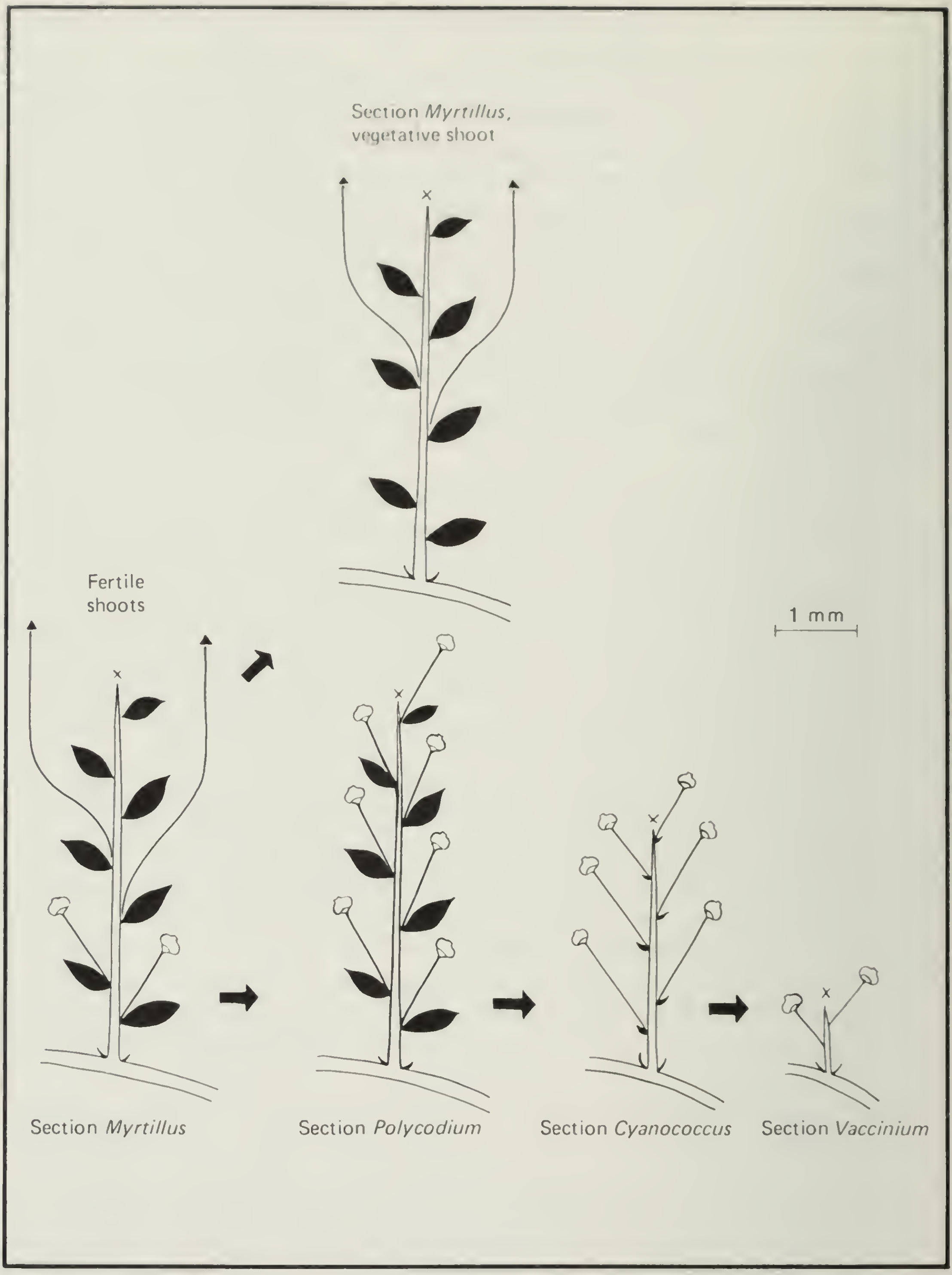

Fig. 9 **Possible evolution of inflorescence types in *Vaccinium*.**

approach, a point of view that holds that the most important information in a classification is the genealogy of the taxa it contains. I subscribe to the modern taxonomic practice of recognizing species on the basis of a combination of morphological, genetic, and distributional criteria that reflect useful and recognizable groupings. In short, I concur with E. Small (1979) who defined a species as a "distinct group of indistinct individuals." To make the recognition of species less arbitrary, I have adopted two criteria for placing a group in the species category: morphological discontinuity (the entity should be distinguishable from its sister group by at least three macroscopic morphological characters); and corroborative nonmorphological differentiation (the validity of the morphological group must be supported by ecological or biological data such as discrete distribution, different bloom periods, and presence of sterility barriers).

Whereas most species of *Vaccinium* can be neatly separated by one, two, or three morphological characters, some can be distinguished only by a generalized "family resemblance" – that is, on the basis of a suite of characters none of which alone is sufficient to differentiate them. In either case, the distinctiveness of species is maintained (even when populations are sympatric) by habitat selection (Vander Kloet 1983*a*) and by the failure to exchange genetic information. Thus, the separation of *Vaccinium* species is maintained by natural evolutionary processes. For example, *V. corymbosum* differs from *V. angustifolium* in habit, leaf dimensions, and corolla length. Although *Vaccinium* species are capable of free interbreeding, their habitat preference, phenology, plant height, corolla length, and pollinator frequency and constancy provide an efficient barrier to gene exchanges between the taxa and allow the species to remain distinct in areas of sympatry (Vander Kloet 1976*b*).

Highly compatible taxa (i.e., those that share the same chromosome number and belong to the same section) either overlap very little or, when they share the same area, show ecological specialization (Vander Kloet 1976*b*, 1983*b*).

Materials

This monograph is based largely on plants collected in nature and from permanently tagged shrubs; on plants grown at Acadia University, Wolfville, N.S., from open-pollinated seeds; on material derived from experimental crosses; and on borrowed herbarium material. Of course, previous literature has been carefully assessed.

Herbarium material

Although various herbaria have extensive *Vaccinium* collections, most of their specimens have serious shortcomings. Either the specimens often lack flowers, mature leaves, or berries, or information on plant height, growth habit, and habitat is not available. Moreover, herbarium specimens are usually neither collected at random nor representative of populations. Nevertheless, herbarium specimens are essential for nomenclatural purposes and have proved useful in supplementing field and experimental studies. Herbarium specimens were used extensively to substantiate distribution data. Specimens from North America were examined at or borrowed from some 34 herbaria. (For a list of these, see Appendix 1.)

The information presented on the growth and development of *Vaccinium* in North America is, to a considerable extent, based on over 1000 germination trials and on morphological and anatomical studies of seedlings, juveniles, and mature plants grown under uniform conditions in the Acadia Greenhouse, supplemented by herbarium material. For a list of the species studied and citations of representative specimens, see Vander Kloet (1972, 1977*a*, 1978*a*, 1978*b*, 1980). These original data have been supplemented by information from the literature. Developmental and anatomical data are taken mainly from Stevens (1969, 1971), Palser (1961), and Bell and his associates (Bell 1950, 1957; Bell and Burchill 1955*a*; and Bell and Giffin 1957).

Collected material

To assess morphological variation and habitat specialization, 184 *Vaccinium* populations in North America were sampled between 1969 and 1981 as well as five European populations in 1975, 1976, and 1978 (Fig. 10; for details of geographical locations, see Appendix 1). Initially a minimum of 1 ha was systematically examined at each site, and a few mature twigs representing the range of variation of *Vaccinium* were collected and dried. Vouchers are at Acadia University. Soil samples were taken and habitat notes were made for each collection. In addition, about six ripe berries were harvested from each of at least three fruiting shrubs so that small populations could be reared under glass for later analysis of actual and potential gene exchange within and between the various morphological groups. This method is discussed in detail elsewhere (Vander Kloet 1976*a*).

If population density was quite high and the site was part of a nature preserve, park, or biological station, or if access to the stand was restricted, ensuring its relative safety, three or more 200-m grid lines were laid out in random directions. At every 10 m, the nearest *Vaccinium* bush was tagged and identified by number. For every 10 plants tagged, 3 were drawn at random and permanently tagged so that they could be revisited during the flowering and fruiting season for at least two reproductive seasons.

Fig. 10 Distribution of collection sites in North America.

If a species was known to be rare or local to a region (for example, *V. caespitosum*, *V. uliginosum*, *V. ovalifolium*, *V. boreale*, and *V. corymbosum* in Nova Scotia) all the shrubs encountered in an area would be tagged in order to overcome another serious shortcoming of herbarium material: flowering specimens from several deciduous species have either no leaves or immature ones at anthesis, whereas specimens collected with mature leaves usually are sterile or bear immature or ripe fruits. To collect adequate material for study, it is necessary to sample several developmental stages, preferably tagged plants in the field. Greenhouse-grown material is usually morphologically similar to plants in the wild, although leaves are usually at least 10% larger.

For gene exchange trials, small populations (3–17 plants) were grown from open-pollinated seed of a single shrub. A total of 344 such populations representing 21 taxa were grown in the greenhouse for at least 1 year. Afterwards, plants were transferred to cold frames in order to meet the dormancy and temperature requirements needed to initiate flowering.

After chilling, plants were moved into a greenhouse, where they began to flower in about 2–3 weeks. Every day, open corollas were removed from several plants, and the pollen was removed and applied once to receptive stigmata of either conspecific or congeneric relatives. The pollinated flowers were subsequently tagged in order to follow ovule development. A minimum of five reciprocal crosses were attempted among and within the species of a given taxonomic section.

Following successful pollination, seed number and seed viability for each reciprocal cross were assessed. Usually one-third of the mature seeds from each cross were immediately planted on top of a 1:1 peat–sand mixture and were placed in a lighted misting chamber until the cotyledons emerged, at which time the pots were moved to a greenhouse bench and watered when necessary. Days required for germination and for the establishment of viable seedlings and their numbers were recorded. The remaining seeds were air-dried and stored in a sealed jar at 2°C for 6 months or 1 year, after which they were sown using the procedure described above.

Young flower buds and rhizome tips were then fixed, stained, and squashed according to the procedure described by Hall and Galletta (1971) so that the chromosome number for each population might be ascertained.

Numerical taxonomic methods

Except for rare and local taxa, such as *V. hirsutum*, *V. myrtillus* (in North America), or *V. deliciosum*, at least 20 specimens were scored for each species for features arranged in three sets: continuous (Table 3); ordered multistate or binary characters (Table 4); and

Table 3 Continuous characters for North American species of *Vaccinium*

1. Plant height (cm)
2. Leaf width (mm)
3. Leaf length (mm)
4. Corolla width (mm)
5. Corolla length (mm)
6. Pollen diameter (µm)
7. Anther tubule length (mm)
8. Berry diameter (mm)
9. Large seeds per berry
10. Seed weight (mg/100)

Table 4 Ordered multistate or binary characters

1. Twigs of the current season
    - A. Glabrous
    - B. Pubescent in lines
    - C. Pubescent
    - D. Pilose

2. Leaves
    - A. Glaucous
    - B. Pale
    - C. Green beneath

3. Leaves
    - A. Glabrous
    - B. More or less pubescent
    - C. Pubescent beneath

4. Leaves
    - A. Glandular
    - B. More or less glandular
    - C. Eglandular beneath

5. Leaf margin
    - A. Entire
    - B. Intermediate
    - C. Serrate

6. Inflorescence type
    - A. Racemose
    - B. Singly in leaf axils

7. Corolla lobes
    - A. Fused
    - B. Free

8. Stamen filaments
    - A. Glabrous
    - B. Pubescent in lines
    - C. Pubescent

9. Length of hypocotyl
    - A. >1 cm
    - B. <1 cm

unordered multistate or binary characters (Table 5). Table 6 enumerates the samples scored for the continuous feature matrix.

In this study, the operational taxonomic unit (OTU) is the species. Treatments in the most recent taxonomic revisions have been adopted for the controversial cases (Baker 1970; Young 1970; Warr 1981; Vander Kloet 1977*a*, 1978*a*, 1980, 1983*b*). Where no recent revision exists, as in *Vaccinium* sect. *Myrtillus*, species were delimited by techniques described in Vander Kloet (1977*b*, 1978*a*, 1980, 1983*b*). For the 26 species, mean character scores for each of the 39 features were calculated and a character matrix created. Next, the similarity between each pair of species was computed and the resultant correlation coefficients were sorted by an unweighted pair–group method based on arithmetic averages (UPGMA).

For the actual processing, I used the numerical taxonomy system (NT–SYS), a program written by F.J. Rohlf, J. Kishpaugh, and D. Kirk (1974 version, State University of New York, Stony Brook, N.Y.).

Results

Three of the phenograms obtained from the sorting procedure are shown in Fig. 11. Phenogram I is based on the quantitative scores listed in Table 7 only. Initial separation occurred at a similarity coefficient of 0.23 and resulted in isolation of all the species except *V. geminiflorum* (OTU 25), *V. crassifolium* (OTU 12), and *V. caespitosum* (OTU 19) – all three species with short stature and small leaves. This sorting procedure, based on strictly quantitatively scored features, readily separates most species but consistently confounds sections. In phenogram I, for example, group IA contains members from sect. *Cyanococcus*, sect. *Myrtillus*, and sect. *Vaccinium*, and group IB contains members from sect. *Oxycoccus*, sect. *Cyanococcus*, sect. *Oxycoccoides*, and sect. *Polycodium*.

Conversely, in phenogram II, which is based on the qualitative or dichotomously scored characters listed in Tables 4 and 5, two taxonomic groups are formed. Initial separation occurred at a similarity coefficient of 0.43. Group IIA contains strictly 4-merous members – sect. *Oxycoccoides* (OTU 13), sect. *Vitis-idaea* (OTU 16), and sect. *Oxycoccus* (OTUs 14 and 15); group IIB contains members that, with one exception, are strictly 5-merous. The anomaly is OTU 17, sect. *Vaccinium*, which is usually 4-merous; specimens that are 3-, 5-, or 6-merous are present in any population. Indeed, close examination of 4-merous plants usually reveals several flowers which are either 3-, 5-, or 6-merous (Warr 1981).

Group IIB occupies an isolated position from the remaining 5-merous taxa and comprises sect. *Myrtillus*. Section *Cyanococcus* (group IIC) is, however, weakly linked to sect. *Pyxothamnus* (to which it may be related; see Vander Kloet 1982) and to sect. *Herpothamnus*

Table 5 Unordered multistate or binary characters

1. Habit
   A. Crown-forming
   B. Clumped
   C. Colonial
   D. Creeping

2. Twigs of the current season
   A. Terete
   B. Intermediate
   C. Angular

3. Twigs of the current season
   A. Verrucose
   B. Non-verrucose

4. Twigs of the current season
   A. Glandular
   B. Eglandular

5. Perennating bud scales
   A. 2
   B. >2

6. Perennating bud scales
   A. Obtuse
   B. Acute
   C. Piliferous at apex

7. Leaves
   A. Evergreen
   B. Intermediate
   C. Deciduous

8. Leaf margin
   A. Inrolled
   B. Flat

9. Inflorescence
   A. From specialized bud on old wood
   B. In leaf axils of current shoot

10. Flowering axis at anthesis
    A. Prominent bracts
    B. Few small or no bracts

11. Flowers
    A. Open aestivation
    B. Closed in bud

12. Corolla lobes
    A. 4
    B. 4–5
    C. 5

13. Corolla lobes at anthesis
    A. Reflexed
    B. Not reflexed

14. Corolla lobes
    A. Glandular
    B. Eglandular

15. Calyx and pedicel
    A. Continuous
    B. Articulated

16. Calyx lobes at anthesis
    A. Prominent
    B. Eroded

17. Calyx lobes
    A. 4
    B. 4–5
    C. 5

18. Stamens
    A. 8
    B. 8–10
    C. 10

19. Awns on anther sacs
    A. Present
    B. Absent

20. Berries
    A. Red
    B. Black
    C. Blue and glaucous
    D. Intermediate

Table 6 **Number of samples scored for the matrix of continuous features**

Taxa	Plant height	Leaf width	Leaf length	Corolla width	Corolla length
V. boreale	37	111	111	111	111
V. myrtilloides	122	366	366	366	366
V. angustifolium	736	2208	2208	430	430
V. corymbosum	496	1488	1488	1382	1382
V. pallidum	144	432	432	256	256
V. hirsutum	6	18	18	10	10
V. tenellum	22	66	66	50	50
V. myrsinites	154	462	462	60	60
V. darrowii	138	414	414	76	76
V. stamineum	30	90	90	130	130
V. arboreum	25	75	75	75	75
V. crassifolium	10	30	30	20	20
V. erythrocarpum	36	108	108	30	30
V. macrocarpon	31	93	93	93	93
V. oxycoccus	83	249	249	166	166
V. vitis-idaea	46	138	138	138	138
V. uliginosum	126	378	378	157	157
V. myrtillus	19	57	57	30	30
V. caespitosum	28	84	84	44	44
V. ovalifolium	39	108	108	38	38
V. membranaceum	23	69	69	15	15
V. deliciosum	15	45	45	33	33
V. parvifolium	47	141	141	122	122
V. scoparium	42	126	126	17	17
V. geminiflorum	12	36	36	15	15
V. ovatum	39	117	117	58	58

(*continued*)

Table 6 Number of samples scored for the matrix of continuous features (*concluded*)

Taxa	Pollen diameter	Anther tubule length	Berry diameter	Large seeds/ berry	Seed weight
V. boreale	200	111	70	70	500
V. myrtilloides	200	366	191	191	400
V. angustifolium	390	430	487	487	2700
V. corymbosum	2560	400	3582	3582	4900
V. pallidum	770	256	552	552	1000
V. hirsutum	100	10	12	12	30
V. tenellum	200	50	66	66	400
V. myrsinites	700	60	400	400	600
V. darrowii	308	76	400	400	550
V. stamineum	100	130	38	38	100
V. arboreum	100	75	17	17	25
V. crassifolium	100	20	8	8	20
V. erythrocarpum	100	30	159	159	220
V. macrocarpon	100	93	780	780	400
V. oxycoccus	100	166	552	552	600
V. vitis-idaea	100	138	140	140	100
V. uliginosum	500	157	280	280	330
V. myrtillus	100	30	29	29	40
V. caespitosum	100	44	43	43	120
V. ovalifolium	100	38	190	190	80
V. membranaceum	100	15	60	60	100
V. deliciosum	100	33	24	24	60
V. parvifolium	100	122	120	120	380
V. scoparium	100	17	48	48	80
V. geminiflorum	100	15	6	6	3
V. ovatum	100	58	64	64	120

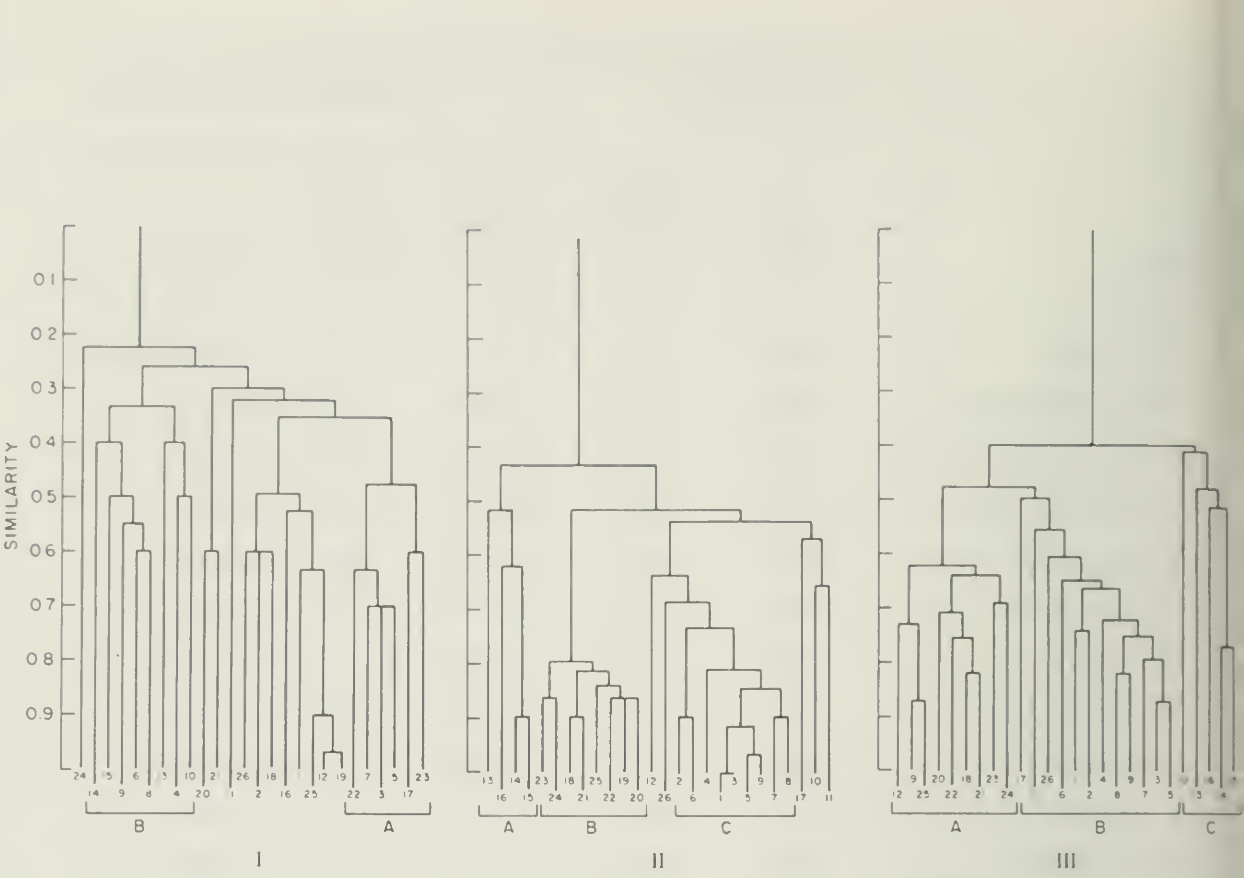

Fig. 11 Phenograms for the North American species of *Vaccinium*

Species number	Species name	Species number	Species name
1	*V. boreale* Hall & Aalders	15	*V. oxycoccus* Linnaeus
2	*V. myrtilloides* Michaux	16	*V. vitis-idaea* Linnaeus
3	*V. angustifolium* Aiton	17	*V. uliginosum* Linnaeus
4	*V. corymbosum* Linnaeus	18	*V. myrtillus* Linnaeus
5	*V. pallidum* Aiton	19	*V. caespitosum* Michaux
6	*V. hirsutum* Buckley	20	*V. ovalifolium* Small
7	*V. tenellum* Aiton	21	*V. membranaceum* Douglas ex Hooker
8	*V. myrsinites* Lamarck		
9	*V. darrowii* Camp	22	*V. deliciosum* Piper
10	*V. stamineum* Linnaeus	23	*V. parvifolium* Small
11	*V. arboreum* Marsh	24	*V. scoparium* Leiberg ex Coville
12	*V. crassifolium* Andrews	25	*V. geminiflorum* HBK
13	*V. erythrocarpum* Michaux	26	*V. ovatum* Pursh
14	*V. macrocarpon* Aiton		

Table 7 Comparison of several quantitative differences among North American species of *Vaccinium**

Taxa	Plant height (cm)	Leaf width (mm)	Leaf length (mm)	Corolla width (mm)
V. boreale	4 ± 2	4 ± 1.5	14 ± 3	4 ± 1
V. myrtilloides	35 ± 14	12 ± 4	29 ± 6	4 ± 1
V. angustifolium	18 ± 9	11 ± 5	26 ± 6	4 ± 1
V. corymbosum	230 ± 60	17 ± 4	46 ± 8	4 ± 1
V. pallidum	37 ± 14	17 ± 4	31 ± 6	4 ± 1
V. hirsutum	36 ± 5	20 ± 5	39 ± 10	4 ± 1
V. tenellum	30 ± 14	10 ± 2	25 ± 7	3 ± 1
V. myrsinites	27 ± 11	4 ± 1	7 ± 2	3 ± 1
V. darrowii	55 ± 39	4 ± 1	9 ± 2	4 ± 0.3
V. stamineum	98 ± 51	24 ± 5	46 ± 11	8 ± 2
V. arboreum	311 ± 102	16 ± 4	31 ± 9	4 ± 1
V. crassifolium	11 ± 7	5 ± 2	12 ± 3	4 ± 1
V. erythrocarpum	115 ± 34	23 ± 5	53 ± 10	2 ± 0.5
V. macrocarpon	6 ± 3	3 ± 1	8 ± 1	3 ± 1
V. oxycoccus	2 ± 1	2 ± 1	5 ± 2	2 ± 0.3
V. vitis-idaea	7 ± 3	6 ± 1	11 ± 2	5 ± 0.6
V. uliginosum	26 ± 14	5 ± 2	11 ± 3	4 ± 1
V. myrtillus	31 ± 14	9 ± 2	23 ± 4	6 ± 1
V. caespitosum	9 ± 4	9 ± 3	19 ± 7	3.5 ± 0.4
V. ovalifolium	84 ± 34	18 ± 2	32 ± 7	5 ± 0.6
V. membranaceum	79 ± 34	17 ± 6	38 ± 13	6 ± 1
V. deliciosum	17 ± 11	13 ± 4	26 ± 9	6 ± 1
V. parvifolium	192 ± 68	11 ± 3	19 ± 6	3 ± 1
V. scoparium	13 ± 6	5 ± 1	9 ± 2	3 ± 1
V. geminiflorum	10 ± 4	4 ± 1	13 ± 3	3 ± 0.4
V. ovatum	82 ± 42	10 ± 2	25 ± 4	4 ± 1

(*continued*)

Table 7 Comparison of several quantitative differences among North American species of *Vaccinium**

Taxa	Corolla length (mm)	Pollen diameter (µm)	Anther tubule length (mm)
V. boreale	4 ± 1	33 ± 3	1.6 ± 0.3
V. myrtilloides	4 ± 1	32 ± 3	2 ± 0.3
V. angustifolium	6 ± 2	38 ± 3	2 ± 0.5
V. corymbosum	8 ± 1	44 ± 2	4 ± 0.8
V. pallidum	7 ± 3	37 ± 2	2.6 ± 0.4
V. hirsutum	7 ± 1	41 ± 3	2.6 ± 0.5
V. tenellum	7 ± 2	36 ± 2	4 ± 0.3
V. myrsinites	6 ± 2	49 ± 2	3 ± 0.5
V. darrowii	5 ± 0.3	44 ± 2	3 ± 0.5
V. stamineum	6 ± 2	41 ± 2	5 ± 0.8
V. arboreum	4 ± 1	37 ± 2	3.6 ± 0.4
V. crassifolium	4 ± 1	33 ± 4	1 ± 0.3
V. erythrocarpum	9 ± 1	35 ± 2	4 ± 0.7
V. macrocarpon	7 ± 1	31 ± 2	6 ± 0.4
V. oxycoccus	4 ± 1	39 ± 2	2.2 ± 0.4
V. vitis-idaea	5 ± 0.5	30 ± 2	1.1 ± 0.3
V. uliginosum	6 ± 1	41 ± 3	0.9 ± 0.2
V. myrtillus	4 ± 1	36 ± 2	1 ± 0.4
V. caespitosum	4 ± 0.3	30 ± 3	1.3 ± 0.8
V. ovalifolium	5 ± 0.2	41 ± 8	1 ± 0.4
V. membranaceum	4 ± 1	38 ± 13	1.2 ± 0.3
V. deliciosum	5 ± 1	40 ± 3	1.1 ± 0.2
V. parvifolium	5 ± 1	34 ± 2	0.9 ± 0.3
V. scoparium	3 ± 1	27 ± 2	0.7 ± 0.4
V. geminiflorum	4 ± 1	31 ± 2	1.3 ± 0.4
V. ovatum	4 ± 1	33 ± 1	1.2 ± 0.3

(*continued*)

Table 7 Comparison of several quantitative differences among North American species of *Vaccinium** (*concluded*)

Taxa	Berry diameter (mm)	Large seeds/ berry	Seed weight (mg/100)
V. boreale	5 ± 2	21 ± 10	22 ± 2
V. myrtilloides	7 ± 1	25 ± 14	26 ± 7
V. angustifolium	8 ± 1	10 ± 7	31 ± 5
V. corymbosum	8 ± 1	16 ± 6	45 ± 8
V. pallidum	6 ± 1	12 ± 7	34 ± 6
V. hirsutum	8 ± 1	6 ± 3	98 ± 8
V. tenellum	7 ± 1	15 ± 9	39 ± 6
V. myrsinites	8 ± 1	9 ± 5	53 ± 9
V. darrowii	9 ± 1	14 ± 8	47 ± 8
V. stamineum	12 ± 2	11 ± 6	70 ± 19
V. arboreum	8 ± 1	5 ± 3	98 ± 30
V. crassifolium	7 ± 1	6 ± 3	29 ± 10
V. erythrocarpum	10 ± 1	10 ± 7	29 ± 10
V. macrocarpon	12 ± 2	17 ± 8	91 ± 28
V. oxycoccus	9 ± 2	8 ± 5	68 ± 17
V. vitis-idaea	9 ± 1	15 ± 6	28 ± 2
V. uliginosum	7 ± 1	12 ± 6	21 ± 6
V. myrtillus	8 ± 1	20 ± 11	25 ± 4
V. caespitosum	7 ± 1	8 ± 5	22 ± 2
V. ovalifolium	9 ± 1	26 ± 18	29 ± 15
V. membranaceum	10 ± 1	19 ± 9	30 ± 3
V. deliciosum	10 ± 1	20 ± 6	32 ± 4
V. parvifolium	8 ± 1	12 ± 12	33 ± 5
V. scoparium	5 ± 1	5 ± 4	13 ± 3
V. geminiflorum	6 ± 1	7 ± 4	20 ± 3
V. ovatum	7 ± 1	18 ± 6	33 ± 4

*Mean ± one standard deviation.

(OTU 12). Section *Polycodium* and sect. *Batodendron* are not closely linked either to each other or to the rest of the 5-merous groups. More importantly, perhaps, Sleumer's (1941) sect. *Pseudocyanococcus*, which differs from sect. *Cyanococcus* in that it is evergreen, does not occupy an isolated position in sect. *Cyanococcus*. Instead, OTU 8, *V. myrsinites*, is closely linked to *V. tenellum*, *V. darrowii*, and *V. corymbosum*, a fact that supports Camp's hypothesis that sect. *Pseudocyanococcus* and sect. *Cyanococcus* are interlocking parts of a common polyploid complex (see Ballington and Galletta 1978 and Vander Kloet 1978*b*, 1981 for details).

Phenogram III is based on both qualitative and quantitative character scores (listed in Tables 3, 4, and 5). Initial separation occurred at a similarity coefficient of 0.40 and resulted in the formation of two groups of well-separated species but a hodgepodge of sections. Thus, group IIIC has members that belong to sect. *Oxycoccus*, sect. *Vitis-idaea*, sect. *Oxycoccoides*, and sect. *Polycodium*. The other group comprises two smaller clusters, IIIA and IIIB, which separated at a similarity coefficient of 0.48. Groups IIIA and IIIB confound members that belong to sect. *Myrtillus* with sect. *Herpothamnus* and link them to the remainder of sect. *Myrtillus*. Group IIIB ties sect. *Cyanococcus* to sect. *Pyxothamnus*, then to sect. *Batodendron*, and finally to sect. *Vaccinium*. It might therefore seem that adding features that measure the dimensions of plants to suites of dimensionless features may confound and obscure sectional lines to some extent. Nonetheless, their addition promotes the separation of congeneric or sympatric species pairs such as *V. boreale* (OTU 1) and *V. angustifolium* (OTU 3), *V. pallidum* (OTU 5) and *V. darrowii* (OTU 9), or *V. oxycoccus* (OTU 15) and *V. macrocarpon* (OTU 14).

In addition to these phenetic differences between *Vaccinium* species, there are several biological differences as well. The considerable crossability data that have been gathered, especially for sect. *Cyanococcus*, suggest that homoploid species do not exchange genetic information freely, even under optimum experimental conditions, and that the interspecific hybrids produced fewer viable offspring than the intraspecific crosses (Vander Kloet 1978*a*, 1980, and 1983*b*; Ballington and Galletta 1978).

Similarly, the most compelling reasons for recognizing sections, aside from the rather marked morphological differences, are the conspicuous differences in crossing success between homoploid species belonging to the same section and those belonging to different sections (Ballington 1980; Ballington and Galletta 1978; Vander Kloet 1978*a*, 1980). Furthermore, it can be argued that the limited success of crosses between sections militates against promoting the various sections to generic level, as has been proposed by Greene (1898), Ashe (1931), and J.K. Small (1933) and to a lesser extent by Camp (1944), Seymour (1950), and Porsild (1937).

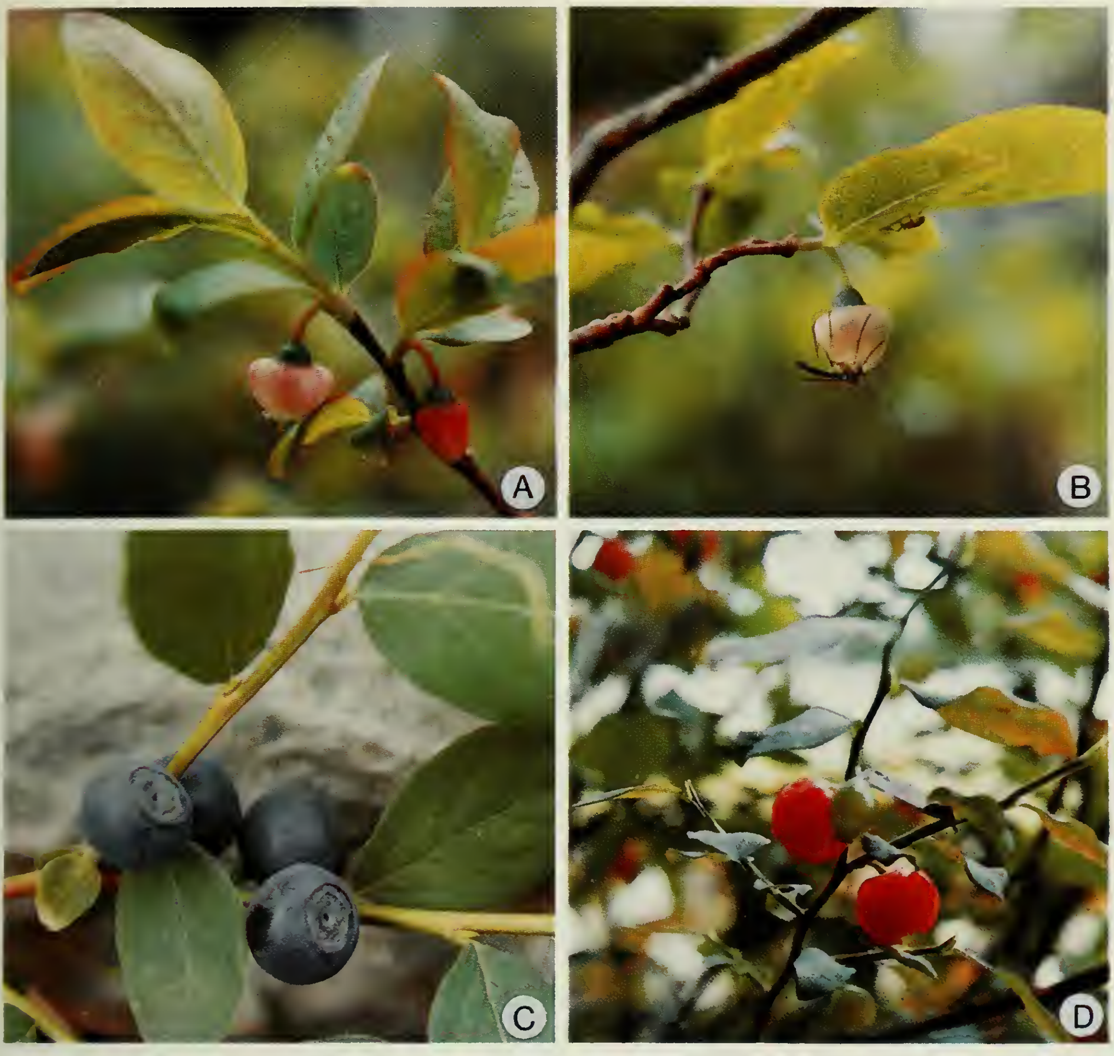

Fig. 12 *Vaccinium* sect. *Myrtillus* in flower and fruit, 21 July 1980, Mount Seymour, North Vancouver, B.C. (A), (B) *V. deliciosum* in flower, 1100 msm; (C) *V. ovalifolium* in fruit, 600 msm; (D) *V. parvifolium* in fruit, 600 msm. Photographs by Susan Fife.

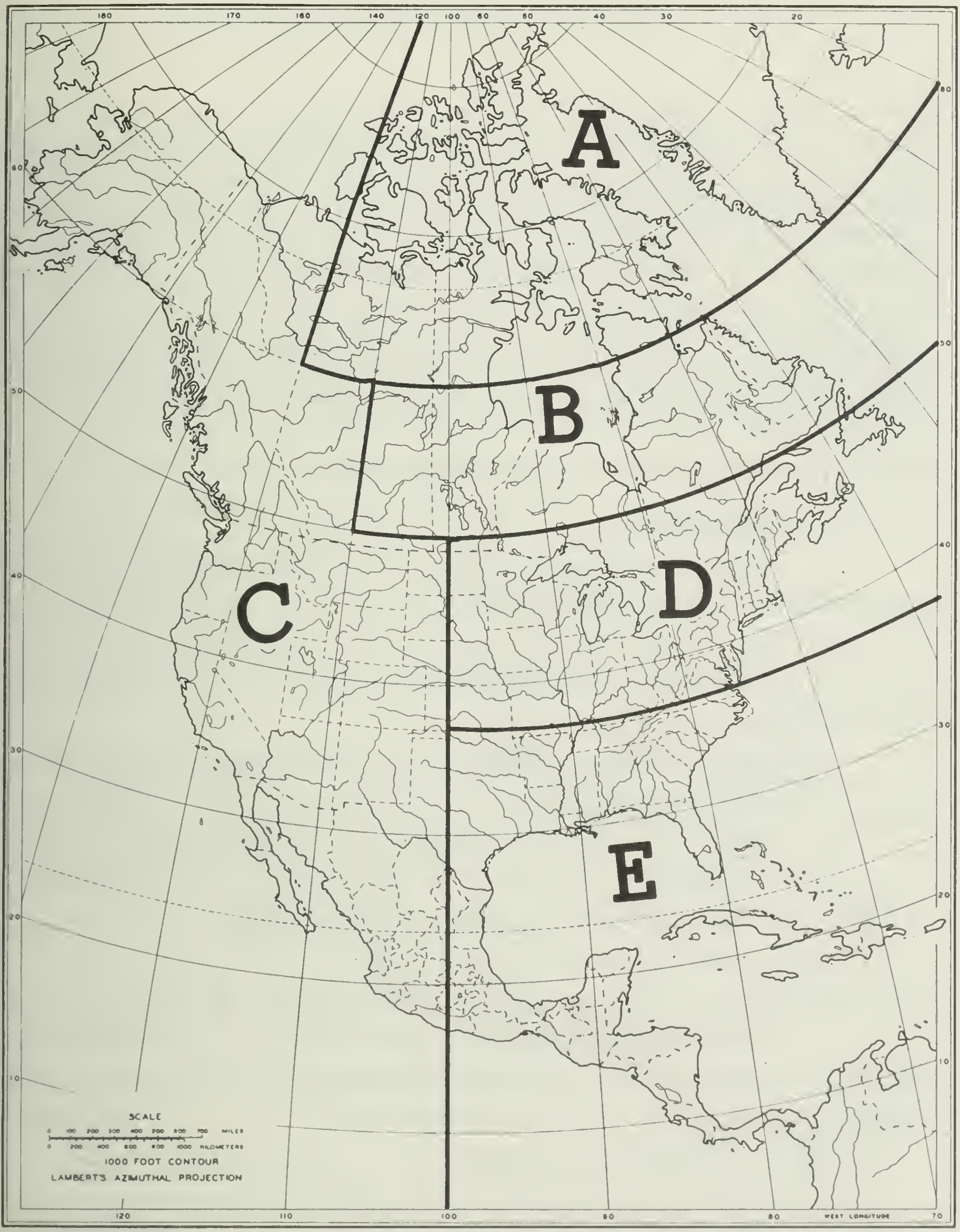

Fig. 13 Areas delineated by vegetative key; A–E correspond to the five sections listed in Key 2, p. 51.

Key 1 Key to sections of *Vaccinium* in North America

Note: These vegetative keys were designed for fresh material. Although drying does not significantly shrink the leaves, excessive heat (more than 40°C) or poor ventilation in the dryer turns the leaves brown, obscuring the presence of glaucescence. For optimum results, *Vaccinium* specimens should be dried at low heat and with good air circulation. Drying also increases the sharpness of the angles on twigs of the current season in *Vaccinium* sect. *Myrtillus*. In fresh material, only *V. myrtillus*, *V. parvifolium*, and *V. scoparium* have angular twigs. In dried material, however, this phenomenon has been observed in a few specimens of the other species in this section.

1\. Berry 4-celled; corolla 4- or 5-lobed

  2\. Leaves deciduous

    3\. Calyx continuous with pedicel; corolla deeply 4-cleft; anthers awnless . . . . *Oxycoccoides*

    3\. Calyx articulated with pedicel; corolla urceolate; 4-5(6)-merous; anthers awned . . . . *Vaccinium*

  2\. Leaves evergreen

    4\. Flowers on long pedicels; corolla deeply 4-cleft; lobes reflexed at anthesis . . . . *Oxycoccus*

    4\. Flowers on very short pedicels; corolla more or less campanulate, not deeply divided . . . . *Vitis-idaea*

1\. Berry 5-celled or pseudo 10-celled; corolla 5-lobed

  5\. Calyx continuous with pedicel

    6\. Flowers open in bud; stamens exerted at anthesis; bud scales more than 2 . . . . *Polycodium*

    6\. Flowers closed in bud; stamens enclosed at anthesis; bud scales 2 . . . . *Myrtillus*

  5\. Calyx articulated with pedicel

    7\. Anthers awned; plants often small trees sometimes up to 10 m high . . . . *Batodendron*

    7\. Anthers awnless; plants erect; shrubs colonial or creeping

      8\. Plants trailing, vine-like . . . . *Herpothamnus*

      8\. Plants erect, up to 4 m high, often rhizomatous

        9\. Twigs of the current season verrucose; berry pseudo 10-celled . . . . *Cyanococcus*

        9\. Twigs of the current season nonverrucose; berry 5-celled . . . . *Pyxothamnus*

Key 2 Vegetative key to the North American species of *Vaccinium*, by region

A. **Arctic** (east of 120° longitude and north of 60° latitude)
1. Leaves deciduous (present only on twigs of the current season)
2. Bud scales more than 2; twigs terete or verrucose, or both
3. Leaf margin entire
4. Leaves glaucous, glabrous, or minutely puberulent .... *V. uliginosum*
4. Leaves green, pilose, or densely pubescent .... *V. myrtilloides*
3. Leaf margin sharply serrate .... *V. boreale*
2. Bud scales 2; twigs angular .... *V. myrtillus*
1. Leaves persistent
5. Plants trailing; leaves glaucous and nonglandular beneath .... *V. oxycoccus*
5. Plants shrubby; leaves green and glandular beneath .... *V. vitis-idaea*

B. **Boreal** (east of 110° longitude and between 50° and 60°N)
1. Leaves deciduous (present only on twigs of the current season)
2. Bud scales more than 2
3. Twigs smooth .... *V. uliginosum*
3. Twigs verrucose
4. Leaf margin entire .... *V. myrtilloides*
4. Leaf margin sharply serrate
5. Plant height 2–6 cm .... *V. boreale*
5. Plant height 9–27 cm ... *V. angustifolium*
2. Bud scales 2
6. Plants less than 20 cm high .... *V. caespitosum*
6. Plants more than 40 cm high .... *V. ovalifolium*
1. Leaves persistent
7. Plants trailing; leaves glaucous and eglandular beneath .... *V. oxycoccus*
7. Plants shrubby, rhizomatous; leaves green and glandular beneath .... *V. vitis-idaea*

C. **Western North America** (west of 100° longitude at 50°N, west of 110° at 60°N, west of 120° latitude beyond the Arctic Circle)

1. Bud scales 2
    2. Shrubs less than 50 cm high, rhizomatous, forming colonies
        3. Twigs of the current season green and sharply angled
            4. Twigs slender; leaves 4–6 mm wide, more or less glabrous beneath .... *V. scoparium*
            4. Twigs stout; leaves 7–11 mm wide, more or less glandular beneath .... *V. myrtillus*
        3. Twigs of the current season glaucous, pale or yellow brown and not sharply angled
            5. Twigs glaucous, usually glabrous; leaves glaucous and eglandular .... *V. deliciosum*
            5. Twigs of the current season puberulent; leaves often green and eglandular
                6. Leaves persistent or tardily deciduous, 3–5 mm wide .... *V. geminiflorum*
                6. Leaves deciduous, 6–12 mm wide .... *V. caespitosum*
    2. Shrubs more than 50 cm high, usually crown-forming
        7. Twigs of the current season sharply angled, bright green .... *V. parvifolium*
        7. Twigs of the current season not sharply angled and not bright green
            8. Leaf margin sharply serrate *V. membranaceum*
            8. Leaf margin entire or nearly so *V. ovalifolium*
1. Bud scales more than 2
    9. Leaves persistent
        10. Vines or shrubs less than 50 cm high
            11. Plants shrubby; leaves glandular and green beneath .... *V. vitis-idaea*
            11. Plants trailing; leaves eglandular and glaucous beneath
                12. Leaves ovate; margin markedly inrolled .... *V. oxycoccus*

12. Leaves narrowly elliptical; margin scarcely inrolled (introduced) ..... *V. macrocarpon*

10. Shrubs more than 50 cm high .... *V. ovatum*

9. Leaves deciduous

13. Twigs of the current season verrucose

14. Shrubs rhizomatous, less than 100 cm high, forming colonies; twigs pilose .. *V. myrtilloides*

14. Shrubs crown-forming, more than 100 cm high; twigs puberulent (introduced) *V. corymbosum*

13. Twigs of the current season not verrucose

15. Shrubs less than 60 cm high; leaves usually less than 10 mm wide .... *V. uliginosum*

15. Shrubs more than 60 cm high; leaves usually more than 10 mm wide .... *V. stamineum*

D. **Northeastern North America** (east of 100° longitude and between 37° and 50° latitude)

1. Twigs of the current season verrucose

2. Shrubs crown-forming, usually more than 150 cm high .... *V. corymbosum*

2. Shrubs rhizomatous, forming colonies, usually less than 75 cm high

3. Leaves glandular beneath .... *V. tenellum*

3. Leaves eglandular beneath

4. Leaf margin sharply and uniformly serrate

5. Shrubs 2–6 cm high; leaf blades 2.5–5.5 mm wide .... *V. boreale*

5. Shrubs 9–27 cm high; leaf blades 6–16 mm wide .... *V. angustifolium*

4. Leaf margin entire, or irregularly more or less serrate

6. Leaves green, densely pubescent; twigs pilose .... *V. myrtilloides*

6. Leaves pale, mostly glabrous; twigs pubescent pubescent in lines .... *V. pallidum*

1. Twigs of the current season not verrucose
    7. Bud scales 2
        8. Shrubs less than 50 cm high .... *V. caespitosum*
        8. Shrubs more than 50 cm high
            9. Leaf margins more or less entire *V. ovalifolium*
            9. Leaf margins sharply serrate
                10. Plants of northern Michigan .... *V. membranaceum*
                10. Plants of the Appalachians from Tennessee to Virginia .... *V. erythrocarpon*
    7. Bud scales more than 2
        11. Leaves persistent
            12. Leaves puberulent above ...... *V. crassifolium*
            12. Leaves glabrous above
                13. Plants shrubby; leaves green and glandular beneath .... *V. vitis-idaea*
                13. Plants trailing; leaves glaucous and eglandular beneath
                    14. Leaves ovate or strongly inrolled .... *V. oxycoccus*
                    14. Leaves narrowly elliptical, not markedly inrolled .... *V. macrocarpon*
        11. Leaves deciduous
            15. Decumbent shrubs, less than 70 cm high .... *V. uliginosum*
            15. Tall shrub or small trees
                16. Shrubs usually 1–2 m high; mature leaves pale and glaucous, eglandular ... *V. stamineum*
                16. Shrubs or small trees, 3-5 m high; mature leaves usually green, glandular beneath .... *V. arboreum*

E. **Southeastern North America** (east of 100° longitude and south of 37° latitude)

1. Twigs verrucose
    2. Leaves persistent, less than 10 mm wide
        3. Flush glaucous, leaves eglandular beneath .... *V. darrowii*
        3. Flush green, leaves glandular beneath *V. myrsinites*
    2. Leaves usually deciduous, more than 10 mm wide
        4. Shrubs crown-forming, more than 100 cm high .... *V. corymbosum*
        4. Shrubs rhizomatous, forming colonies, less than 100 cm high
            5. Leaves glandular beneath .... *V. tenellum*
            5. Leaves eglandular beneath
                6. Foliage green and pilose ...... *V. hirsutum*
                6. Foliage pale, mostly glabrous *V. pallidum*
1. Twigs not verrucose
    7. Vines; leaves persistent
        8. Leaves narrowly elliptical, glabrous above; margin entire and eglandular .... *V. macrocarpon*
        8. Leaves elliptical, puberulent above; margin glandular, obscurely serrate .... *V. crassifolium*
    7. Shrubs or small trees; leaves more or less deciduous
        9. Bud scales 2
            10. Shrubs more than 50 cm high, usually crown-forming .... *V. erythrocarpum*
            10. Shrubs less than 50 cm high, colonial .... *V. geminiflorum*
        9. Bud scales more than 2
            11. Shrubs usually 1–2 m high; mature leaves pale and glaucous, eglandular .... *V. stamineum*
            11. Shrubs or small trees, 3–5 m high; mature leaves usually green, glandular beneath *V. arboreum*

In my opinion, generic membership can be defined on the basis of shared similarities (not on differences, as in the case of species) and on a common ancestor in the recent biota. The discovery by Hall and Galletta (1971) that sect. *Herpothamnus*, sect. *Oxycoccus*, and sect. *Cyanococcus* share a common diploid karyotype is indicative of common ancestry. This would explain the limited success that Ballington (1980), Darrow and Camp (1945), and Ritchie (1955) had in crossing taxa from various sections and in determining their occurrence (Ritchie 1954) and potential occurrence (Vander Kloet 1977*c*) in nature.

Part 2

Sections and species of *Vaccinium* in North America

Vaccinium sect. *Cyanococcus**

The North American taxa included in *Vaccinium* sect. *Cyanococcus* share the following morphological features: twigs of the current season are verrucose; in the leaf axils, two types of perennating buds develop, floral and vegetative; buds are covered with several (more than five) scales and are dimorphic, with the rotund floral bud at least twice the size of the vegetative; the inflorescence is corymbose; the pedicel is articulated with the calyx; the corolla is more or less urceolate or cylindrical; stamens are included and awnless; the berry is pseudo 10-loculed.

Gray (1859, 1860) argued for including, and Sleumer (1941) actually placed, several Japanese and northeastern Asian taxa (*V. smallii* Gray, *V. hirtum* Thunberg, and *V. usunoki* Nakai, among others) in sect. *Cyanococcus*, but I could not substantiate this (Vander Kloet 1972). The Japanese taxa have smooth or pitted twigs that bear, in the leaf axils, elongated perennating buds sheathed in two narrow bracts – a condition found in *Vaccinium* sect. *Myrtillus*. Likewise Stevens (1969) found that *V. hirtum* and *V. versicolor* (Koidz) Nakai had a 5-loculed berry instead of the pseudo 10-loculed fruit as suggested by Gray and Sleumer. He therefore removed these species from sect. *Cyanococcus* and placed them provisionally in sect. *Hemimyrtillus* Sleumer. I concur with this decision.

Sleumer (1941) also erected *Vaccinium* sect. *Pseudo-cyanococcus* to accommodate taxa that have all the features set out under sect. *Cyanococcus* but are evergreen – a judgment that Camp (1942*a*) found untenable, since all the members of *Vaccinium* sect. *Cyanococcus sensu* Gray "are interlocking parts of a common polyploid complex."

Indeed, Darrow and Camp (1945) found that the evergreen *V. myrsinites* Lamarck would cross successfully with *V. angustifolium* and with tetraploid populations of *V. corymbosum*. Similarly, Vander Kloet (1977*b*) and Ballington and Galletta (1978) produced ample evidence to show that the evergreen *V. darrowii* Camp will cross quite readily with *V. tenellum* Aiton and with various diploid populations of *V. corymbosum*.

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*For taxonomic synonyms, see Appendix 2.

In short, my concept of *Vaccinium* sect. *Cyanococcus* excludes the Japanese and northeastern Asian species but includes the taxa that Sleumer (1941) placed in sect. *Pseudocyanococcus* (Table 8). Indeed, of the nine species that constitute the section all but *V. myrtilloides*, which is transcontinental (Vander Kloet and Hall 1981), are restricted to eastern North America.

Five of the nine species are the diploid ($2n = 24$) lowbush blueberries, namely *V. darrowii* Camp, *V. tenellum* Aiton, *V. pallidum* Aiton, *V. myrtilloides* Michaux, and *V. boreale* Hall & Aalders. Although these species form a parapatric distribution pattern along the eastern seaboard from 27°N to 58°N, they nevertheless differ morphologically from each other in at least three characters (Table 9 and Key 3) and are distinct in terms of the time required for the seed set, seed germination, and seedling establishment (Vander Kloet 1983*b*).

The remaining species in this section are *V. myrsinites* Lamarck, *V. hirsutum* Buckley, and *V. angustifolium* Aiton, all lowbush tetraploids ($2n = 4x = 48$), which probably have a hybrid origin (Vander Kloet 1976*a*; Camp 1942*a*, 1945), and (last but not least) *V. corymbosum* Linnaeus, the highbush blueberry. This hybrid species presents a special case in that it contains diploid ($2n = 2x = 24$), tetraploid ($2n = 4x = 48$), and hexaploid ($2n = 6x = 72$) populations. Although these populations scarcely interbreed, I have yet to find macroscopic morphological characters to separate them (Vander Kloet 1980); they might be considered nascent species.

The putative origin, phylogeny, and speciation events of this section have been described by Camp (1942*a*, 1945) as well as by Vander Kloet (1977*a*, 1980, 1981, 1983*b*); these treatments are speculative and will not be repeated here.

Key 3 Key to the species of *Vaccinium* sect. *Cyanococcus*

1. Shrubs usually more than 1.5 m tall; crown-forming; one to several main stems, branched many times; leaves usually more than 45 mm long .... *V. corymbosum*

1. Shrubs usually less than 75 cm tall; many shorter stems, branched less frequently; leaves usually less than 40 mm long

    2. Leaves persistent

        3. Leaves glandular beneath; flush bright green; berries black .... *V. myrsinites*

        3. Leaves eglandular beneath; flush glaucous; berries blue and glaucous .... *V. darrowii*

    2. Leaves deciduous

        4. Leaves glandular beneath .... *V. tenellum*

        4. Leaves eglandular beneath

            5. Leaf margin sharply and uniformly serrate

                6. Shrubs 2–6 cm high; leaf blades 3–5 mm wide .... *V. boreale*

                6. Shrubs 9–27 cm high; leaf blades 6–16 mm wide .... *V. angustifolium*

            5. Leaf margin entire or irregularly serrate

                7. Leaves green, densely pubescent; twigs pilose

                    8. Corolla and calyx glandular ... *V. hirsutum*

                    8. Corolla and calyx eglandular *V. myrtilloides*

                7. Leaves pale, mostly glabrous; twigs pubescent in lines .... *V. pallidum*

Table 8 Comparison of section names assigned to *Vaccinium* by various authorities

Sleumer (1941) sections	Camp (1945) "groups"	Stevens (1969) sections	Vander Kloet (present work) sections
Oxycoccus	*Oxycoccus*	*Oxycoccus*	*Oxycoccus*
Vitis-idaea	*Vitis-idaea*	*Vitis-idaea*	*Vitis-idaea*
Herpothamnus	*Herpothamnus*	*Herpothamnus*	*Herpothamnus*
Pseudocyanococcus	*Cyanococcus*	*Pseudocyanococcus*	*Cyanococcus*
Cyanococcus	*Cyanococcus*	*Cyanococcus*	*Cyanococcus*
Uliginosa	*V. uliginosum*	*Uliginosa*	*Vaccinium*
Batodendron	*Batodendron*	*Batodendron*	*Batodendron*
Polycodium	*Polycodium*	*Polycodium*	*Polycodium*
Pyxothamnus	*V. ovatum*	*Pyxothamnus*	*Pyxothamnus*
Myrtillus	*Euvaccinium*	*Myrtillus*	*Myrtillus*
Oxycoccoides	*Hugeria*	*Oxycoccoides*	*Oxycoccoides*

Table 9 Comparison of selected attributes of the nine species in *Vaccinium* sect. *Cyanococcus*

Taxon characters	*V. darrowii*	*V. tenellum*	*V. pallidum*	*V. myrtilloides*	*V. boreale*
Plant height (cm)	55 ± 39	30 ± 11	37 ± 14	35 ± 14	4 ± 2
Density (stems/m^2)	65 ± 33	168 ± 44	108 ± 30	246 ± 91	8366 ± 3157
Habit	evergreen	deciduous	deciduous	deciduous	deciduous
Lower leaf blade	glaucous glabrous	glandular pubescent	pale glabrous	green pubescent	green glabrous
Leaf width (mm)	4 ± 1	10 ± 2	17 ± 4	12 ± 4	4 ± 1.5
Leaf margin	entire	more or less entire	entire or serrate	entire	serrate
Corolla length (mm)	5 ± 2	7 ± 2	7 ± 3	4 ± 1	4 ± 1
Diameter of pollen tetrads (µm)	44 ± 2	36 ± 2	37 ± 2	32 ± 3	33 ± 3
Seed weight (mg/100 seeds)	47 ± 8	39 ± 6	34 ± 6	26 ± 7	22 ± 2
Chromosome number (n)	12	12	12 (rarely 24)	12	12
Habitat	pine flatwoods	pine flatwoods	open oak woods	taiga	headlands alpine–arctic tundra
Geographical range					
Latitude	27°N–32°N	30°N–37°N	33°N–44°N	39°N–61°N	44°N–58°N
Longitude	80°W–91°W	76°W–88°W	70°W–94°W	60°W–125°W	53°W–74°W

(continued)

Table 9 Comparison of selected attributes of the nine species in ***Vaccinium*** **sect.** ***Cyanococcus*** *(concluded)*

Taxon characters	*V. myrsinites*	*V. hirsutum*	*V. angustifolium*	*V. corymbosum*
Plant height (cm)	27 ± 11	43 ± 15	18 ± 9	220 ± 69
Density (stems/m^2)	35 ± 31	234 ± 118	278 ± 165	n/a*
Habit	evergreen	deciduous	deciduous	deciduous
Lower leaf blade	green glandular	green pubescent	green or glaucous glabrous or more or less pubescent	green or glaucous, more or less pubescent or glabrous, rarely glandular
Leaf width (mm)	4 ± 1	17 ± 4	11 ± 5	23 ± 5
Leaf margin	more or less serrate	entire	serrate	more or less entire
Corolla length (mm)	6 ± 2	8 ± 2	6 ± 2	8 ± 3
Diameter of pollen tetrads (µm)	49 ± 2	41 ± 3	38 ± 3	45 ± 10
Seed weight (mg/100 seeds)	53 ± 9	39 ± 11	31 ± 5	44 ± 8
Chromosome number (n)	24	24	24	12, 24, 48
Habitat	scrubby flatwoods	dry ridges "balds"	headlands, barrens, outcroppings	swamps or bogs, lake margins, river banks, upland meadows, "balds and slicks"
Geographical range				
Latitude	26°N–32°N	34°N–36°N	38°N–57°N	26°N–47°N
Longitude	80°W–86°W	83°W–86°W	53°W–98°W	66°W–95°W

*n/a not available

Vaccinium boreale Hall & Aalders

Description: Shrubs 1–9 cm high, in small dense colonies, with superficial rhizomes. Twigs green, verrucose, angular, delicate, intricately branched, pubescent along the grooves. Leaves narrowly elliptical, 2–6 mm wide, 8–21 mm long, bright green, glabrous or very rarely pubescent along the abaxial midvein; margin sharply serrate. Calyx and pedicel glaucous, glabrous, occasionally ciliate. Corolla cylindrical, 3–4 mm long, white to greenish white. Filaments ciliate along the margins; pollen tetrads 32–38(33) µm in diameter. Berry blue and glaucous, 3–5 mm in diameter; nutlet approximately 1.1 mm long. Chromosome number $2n = 24$ (Fig. 14).

Type locality: Avondale, Nfld. Type at DAO!*

Range: Northern Quebec, Labrador, Newfoundland, Cape Breton, and the Gaspé Peninsula, south to outlying stations on mountain summits in Maine, New Hampshire, Vermont, and New York (Fig. 15). This species has been reported from Ontario by D.W. Smith (1969), but his specimens should be referred to *V. angustifolium*. (See Vander Kloet 1977*b*, for details.)

Habitat: Forest–tundra, alpine meadows, and exposed coastal headlands, occasionally on open rocky uplands of Newfoundland.

Common name: Sweet hurts (Newfoundland).

Economic importance and use: Hall and Aalders (1961) have reported that *V. boreale* occurs in a few commercial blueberry fields in Newfoundland only. However, casual use, especially in northern Newfoundland, is extensive.

Vaccinium myrtilloides Michaux

Description: Shrubs (10)21–49(115) cm high, rhizomatous, with colonies usually small and open. Twigs green or brown, verrucose, terete, pubescent, or pilose. Leaves elliptical, 8–16 mm wide, 23–35 mm long, green, usually pubescent on both sides; margin entire. Calyx and pedicel green, glabrous; lobes occasionally ciliate. Corolla urceolate, 3–5 mm long, white to pink. Filaments often pubescent; pollen tetrads 29–35 µm in diameter. Berry blue and glaucous, 6–8 mm in diameter; nutlet approximately 1.1 mm long. Chromosome number $2n = 24$ (Fig. 16).

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*For herbarium abbreviations, see Appendix 1.

Fig. 14 *Vaccinium boreale*; habit, flower, and stamen.

Fig. 15 Distribution of *V. boreale* Hall & Aalders.

Fig. 16 *Vaccinium myrtilloides*; habit, flower, and stamen.

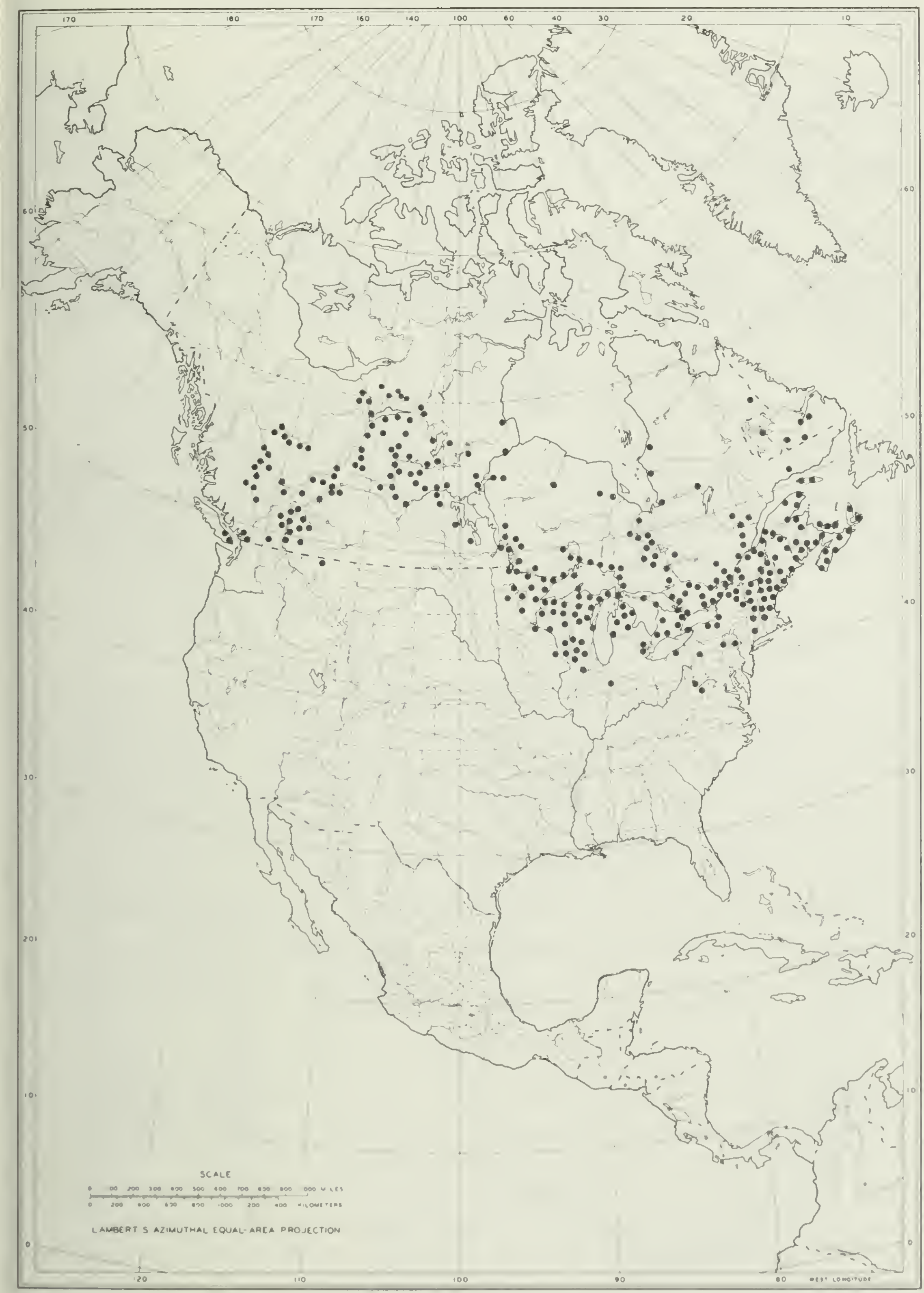

Fig. 17 Distribution of *V. myrtilloides* Michaux.

Type locality: Lake Mistassini, Que. (Camp 1945). Type at P!

Range: Central Labrador to Vancouver Island, from almost 61°N in the Northwest Territories, southeast to several isolated uplands in the Appalachian Mountains, to 39°N (Fig. 17). This species is apparently absent from the island of Newfoundland (Vander Kloet and Hall 1981).

Habitat: Disturbed sites in boreal forest, muskegs, bogs, barrens, headlands, outcrops, and mountain meadows. For a full description of habitat and ecological characteristics see Vander Kloet and Hall (1981).

Common names: Sour-top blueberry, velvet-leaf blueberry.

Economic importance and use: *V. myrtilloides* is a common component in the Maine and New Brunswick blueberry barrens (Hall et al. 1979; Vander Kloet and Hall 1981). The Cree Indians harvest the western populations.

Vaccinium angustifolium Aiton

Description: Shrubs (10)9–27(60) cm high, rhizomatous, forming dense, extensive colonies. Twigs of the current season green or glaucous, angular, verrucose, glabrous to pubescent. Leaves elliptical to narrowly elliptical, (5)6–16(20) mm wide, (15)20–32(41) mm long, green or blue green, glabrous, glaucous or pubescent beneath; margin sharply serrate, rarely entire. Calyx and pedicel glaucous or glabrous, rarely pubescent. Corolla cylindrical to urceolate, 4–6 mm long, white, occasionally with pink striping. Filaments ciliate along the margins, occasionally pubescent; style glabrous; pollen tetrads 35–41 µm in diameter. Berry blue and glaucous, dull black or shining black, rarely white, (3)7–9(12) mm in diameter; nutlet approximately 1.2 mm long. Chromosome number $2n = 48$ (Fig. 18).

Whether or not segments of this polymorphic species should be recognized at an infraspecific level remains moot (Vander Kloet 1976*a*, 1976*b*, 1978*b*). Apparently character sets are not constant from generation to generation, and novel recombinations occur from time to time. Moreover, Mosquin (1971) has argued that although descriptions are useful in drawing attention to such segments, the names more often than not turn out to be useless and, even worse, misleading and a burden on biological literature.

Range: Labrador and Newfoundland, west to southern Manitoba and Minnesota, south to northern Illinois, Pennsylvania, and Delaware, and in the mountains to Virginia and West Virginia (Fig. 19).

Fig. 18 *Vaccinium angustifolium*; habit, flower, and stamen.

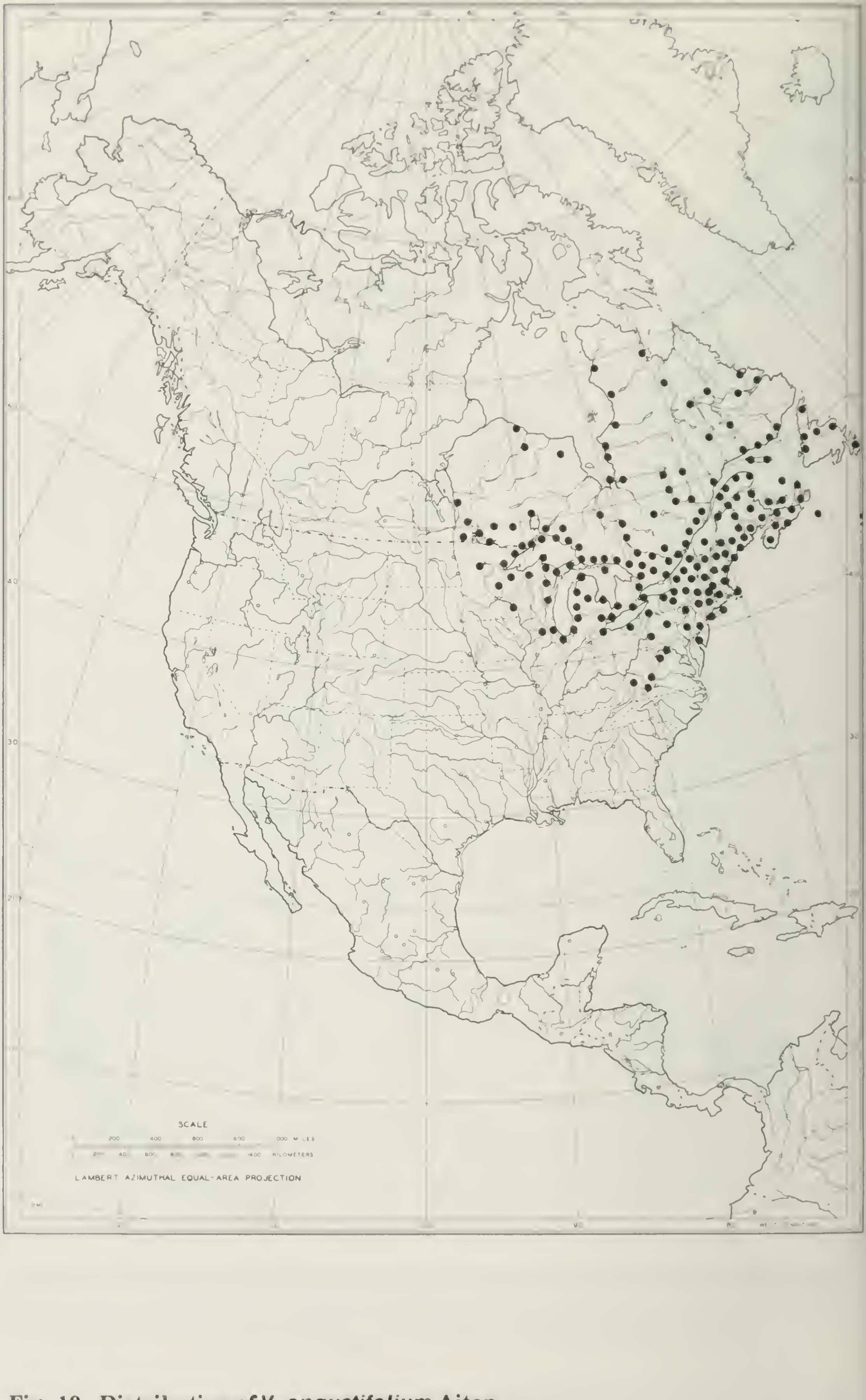

Fig. 19 Distribution of *V. angustifolium* Aiton.

Type locality: Native of Newfoundland and Labrador. Pouch Cove, Nfld., *fide* W.G. Dore (personal communication). Introduced at Kew in 1776 by Benjamin Bewick. Type at BM! As both *V. angustifolium* and *V. boreale* occur in Newfoundland and Labrador, there is some question as to whether the type, which was taken from material cultivated at Kew, is *V. angustifolium* or *V. boreale*. Using stomatal peels, Aalders and Hall (1962) showed that the type corresponded better to the tetraploid *V. angustifolium*.

Habitat: Headlands, high moors, dry sandy areas, peaty barrens, exposed rocky outcroppings of the Canadian Shield, jack pine barrens, pitch pine barrens, oak parklands, poplar regeneration forests, and (particularly in the Maritimes and New England) abandoned pastures and bogs. The natural habitats of *V. angustifolium* s.l. were described briefly by Camp (1945) and Vander Kloet (1977*a*) and in detail by Hall et al. (1979). It tolerates a wide range of temperature and frequent burning but not dense shade. Occurrence is restricted to acidic soils. The average pH for 60 soils in which it was found was 4.4, with a range of 2.8–6.6.

Common name: Sweet lowbush blueberry.

Economic importance and use: Although blueberry barrens occur throughout the range of the species, the highest density of managed barrens from which the fruit is harvested for commercial use occurs in Maine, New Brunswick, Nova Scotia, Newfoundland, and the Lac Saint-Jean region of Quebec (Hall and Aalders 1972). There is a great deal of casual usage elsewhere, and many recipes call for lowbush blueberries (Buszek 1979). In the past, Indians dried and pulverized blueberries for blending with meats (Hedrick 1919), and European settlers ate the berries raw and collected them for jams, jellies, and preserves (Hall et al. 1979).

Vaccinium corymbosum Linnaeus

Description: Shrubs (1)2–3(5) m high, crown-forming, occasionally suckering when disturbed or burnt, rarely reproducing by root sprouts 1–2 m from the parent; (1)2–5(12) stems from a single bole. Twigs angular to terete, green, yellow, or reddish, glaucous to densely pubescent, rarely glandular. Leaves ovate to narrowly elliptical, rarely spatulate, usually deciduous, (17)21(25) mm wide, (38)46(54) mm long; blades pubescent, glabrous, or glaucous beneath, rarely glandular; margins entire, subserrate, or sharply serrate. Pedicel green or glaucous, rarely finely pubescent. Calyx green or glaucous. Corolla cylindrical, rarely urceolate or campanulate, white, white tinged with pink, or pink, rarely red. Filaments ciliate along the margins, occasionally pubescent, rarely glabrous; pollen tetrads 42–46 μm in diameter. Berry dull black or blue and glaucous, occasionally shining black, (4)7–9(12) mm in diameter; nutlet approximately 1.2 mm long. Chromosome number $2n = 24, 48, 72$ (Figs. 20 and 21).

Type locality: North America; collected by Peter Kalm for Linnaeus. Type at LINN! The specimen LINN 497.6 has pubescent twigs and immature leaves that are pubescent along the veins and have entire margins. The corymbs bear cylindrical corollas 4–5 mm wide, 8–9 mm long.

Range: Northeastern Illinois, northern Indiana, and south central Michigan, northward along the St. Lawrence Valley to Quebec City, then east to southwestern Nova Scotia, south to Florida, and west to northeastern Texas and nearby Oklahoma (Fig. 22). Absent or very rare in Missouri, central Ohio, western Kentucky, western Tennessee, West Virginia, and central Pennsylvania. Introduced but not persisting near Tower Hill, N.B., collected by Hall in 1961 (DAO). Introduced, persisting, and possibly escaping in Adams County, Wisc., collected by Bigger s.n. in 1974 (WISC). Introduced and adventive on Lulu Island near Vancouver, B.C., collected by Holm in 1959 (UBC).

Habitat: Frequently encountered in open swamps and bogs and along sandy margins of lakes, ponds, and streams. It is locally common in flatwoods, gray birch scrub, pine barrens, mires, bayheads, upland ericaceous meadows, upland woods, ravines, and mountain summits. It is rare in xeric pine–oak woods and is adventive along ditch banks, low verges, cut-over pine savannas, and abandoned farmland. Details of habitat characteristics, preference, and relative abundance are given in Vander Kloet (1980).

Common names: Highbush blueberry, rabbiteye blueberry.

Economic importance and use: Extensively cultivated in New Jersey, Michigan, North Carolina, and Washington, and to a lesser extent in Georgia, Florida, Indiana, Ohio, Pennsylvania, New York, Massachusetts, British Columbia, Ontario, Quebec, and Nova Scotia. Since 1920, when the cultivars Pioneer, Cabot, and Katharine were released, more than 50 cultivars have been successfully developed and released (Eck and Childers 1966; Galletta 1978). Aboriginal use is also well documented. Peter Kalm, who traveled through eastern North America (1747–1751) stated that the Indians picked and dried highbush blueberries. When the Iroquois wished to treat him well, they would offer him fresh blueberry corn bread. Kalm found that European settlers also used the highbush blueberry extensively – cooked in tarts, dried, preserved in treacle, and raw with or without milk (Benson 1966).

Fig. 20 *Vaccinium corymbosum*; habit, flower, and stamen.

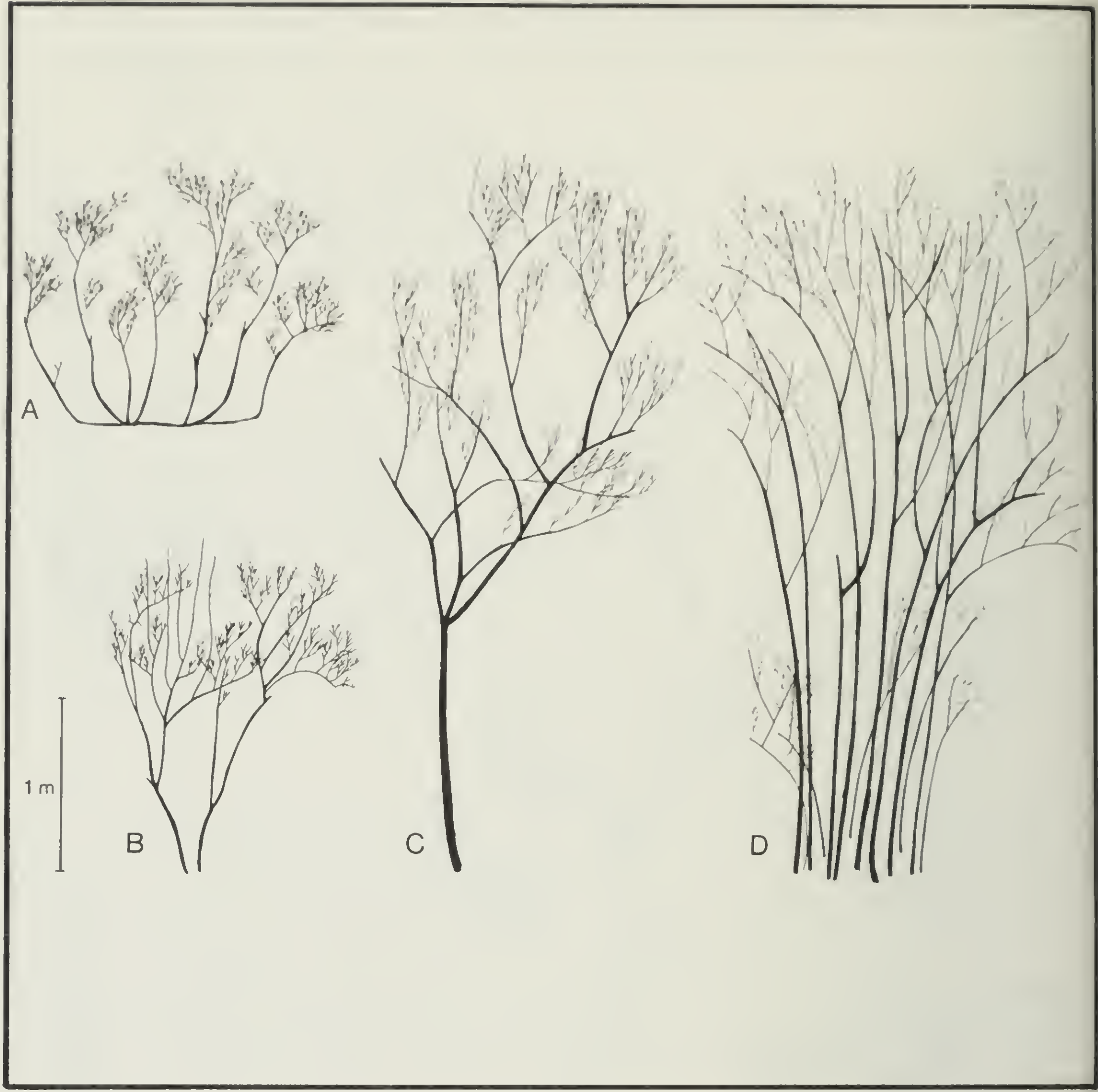

Fig. 21 Growth forms of *V. corymbosum*. (A) Layering, observed only in Quebec and Ontario; (B) Typical crown-forming; (C) Monopodial; (D) Suckering after disturbance.
Photograph by Sasan Fife.

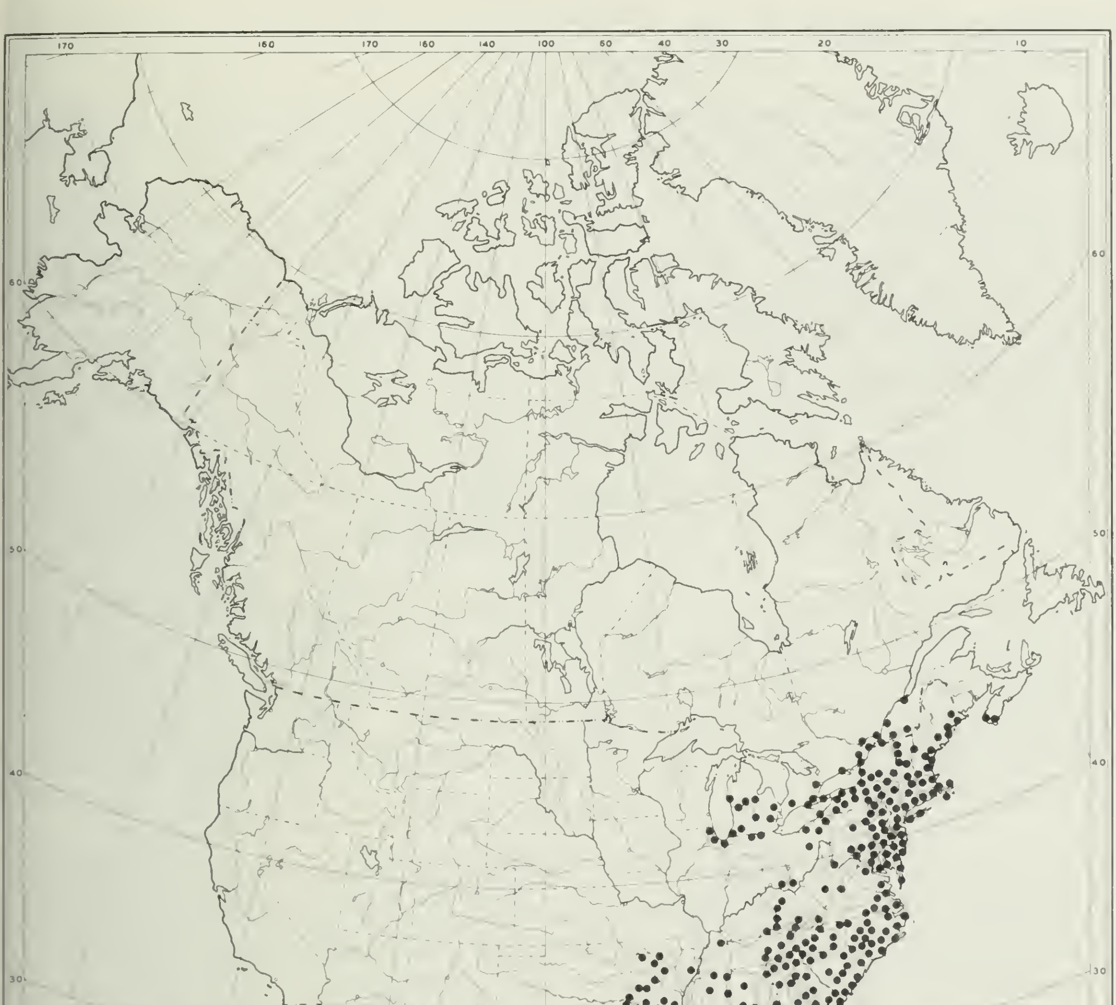

Fig. 22 Distribution of *V. corymbosum* Linnaeus.

Vaccinium pallidum Aiton

Description: Shrubs (8)23–51(100) cm high, rhizomatous, forming small to extensive open colonies. Twigs green, glaucous, or yellow, usually more or less angular, glabrous to pubescent. Leaves ovate to broadly elliptical, 13–22 mm wide, 25–38 mm long, pale green to dark blue green, glaucous or pubescent beneath; margin entire or serrate (occasionally both serrate and entire leaves may be found on the same plant). Calyx and pedicel glaucous, rarely finely pubescent. Corolla cylindro-urceolate, 4–10 mm long, greenish white with pink striping, occasionally white. Filaments glabrous to ciliate along the margins; pollen tetrads 35–39 μm in diameter. Berry blue and glaucous, or dull or rarely shining black, (4)6(8) mm in diameter; nutlet approximately 1 mm long. Chromosome number $2n = 24$, rarely 48 (Fig. 23).

Type locality: North America; introduced in 1772 at Kew by Samuel Martin, M.D. Type at BM! This specimen has variable leaf margins, usually serrate on the top third of the leaf, although one leaf may be almost entire and another obscurely serrate. Leaf size (21 mm by 34 mm) also falls well within the range of the species, and the leaves are pale beneath.

Range: Minnesota and southern Ontario to Maine, south to Georgia, Alabama, and Arkansas, as far west as eastern Oklahoma and southeastern Kansas (Fig. 24). Fernald (1921) reported the species for Nova Scotia, but the specimens at GH fit better in *V. angustifolium*. I carefully searched the Gavelton region of Yarmouth County, N.S., in 1974 and 1975 and could not find *V. pallidum*. The species is also absent from west central Ohio and central Indiana and is very rare in Wisconsin, Illinois, Kansas, and Oklahoma.

Habitat: Dry open oak or oak–hickory woods, open pine savannas or bushy areas, along rocky ledges, and in abandoned farmlands or cut-over deciduous forests. According to Moore (1965), the species resists drought. Additional details on life history characteristics are given in Vander Kloet (1978*a*).

Common name: Hillside blueberry.

Economic importance and use: According to Eck and Childers (1966), *V. pallidum* is harvested commercially in northeastern Alabama, northwestern Georgia, West Virginia, and western and northwestern Arkansas. Casual use is reported by both Strausbaugh and Core (1935) and Steyermark (1963).

Fig. 23 *Vaccinium pallidum*; habit, flower, and stamen.

Fig. 24 Distribution of *V. pallidum* Aiton.

Vaccinium hirsutum Buckley

Description: Shrubs (20)22–51(75) cm high, rhizomatous, in open colonies. Twigs green, verrucose, scarcely angular, pubescent. Leaves elliptical, (10)15–25(36) mm wide, (23)29–49(62) mm long, green, pubescent on both sides; margin entire. Calyx and pedicel green, glandular-pubescent. Corolla cylindrical, 5–9 mm long, white, glandular-pubescent. Filaments pubescent; pollen tetrads 38–44 µm in diameter. Berry black, glandular-pubescent rarely glabrous, 7–9 mm in diameter; nutlet approximately 1 mm long. Chromosome number $2n = 48$ (Fig. 25).

Range: Northern Georgia, southeastern Tennessee, and southwestern North Carolina (Fig. 26).

Type locality: Mountains of Cherokee County, N.C. Type at PH!

Habitat: Dry oak-pine ridges and mountain meadows, usually between 600 and 1500 msm.

Common names: Woolly berry, hairy-fruited blueberry.

Economic importance and use: None reported for this rare southern Appalachian endemic. Indeed, in 1886 C.S. Sargent led an expedition into North Carolina to rediscover the "hairy huckleberry", which had been described by Buckley in 1843 but had not been seen since. In Robbinsville, N.C., the party offered $5 reward for a specimen of this plant, an offer that "set all the boys in the county astir." In the following summer Sargent received at the Arnold Arboretum a box containing woolly berries, grafts, and seedlings. Some of these grafts and seedlings flowered at the arboretum in the summer of 1889. Although local inhabitants knew of this plant, they disregarded it, because the berries are gritty and insipid.

Vaccinium tenellum Aiton

Description: Shrubs (10)16–44(75) cm high, rhizomatous, forming extensive but open colonies. Twigs yellow green, scarcely angular, pubescent, verrucose. Leaves rarely persistent, spatulate to elliptical, (3)8–12(17) mm wide, (13)18–33(40) mm long, green, glandular beneath, pubescent especially when young, rarely fully glabrous even when mature; margin sharply to obscurely serrate. Calyx and pedicel usually pale, occasionally pubescent. Corolla cylindrical, 5–9 mm long, usually white tinged with pink to deep pink, rarely red. Filaments usually pubescent in lines; pollen tetrads 34–38 µm in diameter. Berry black and shining, rarely pubescent, 6–8 mm in diameter, usually of poor flavor and texture; nutlet approximately 1 mm long. Chromosome number $2n = 24$ (Fig. 27).

Fig. 25 *Vaccinium hirsutum*; habit, flower, and stamen.

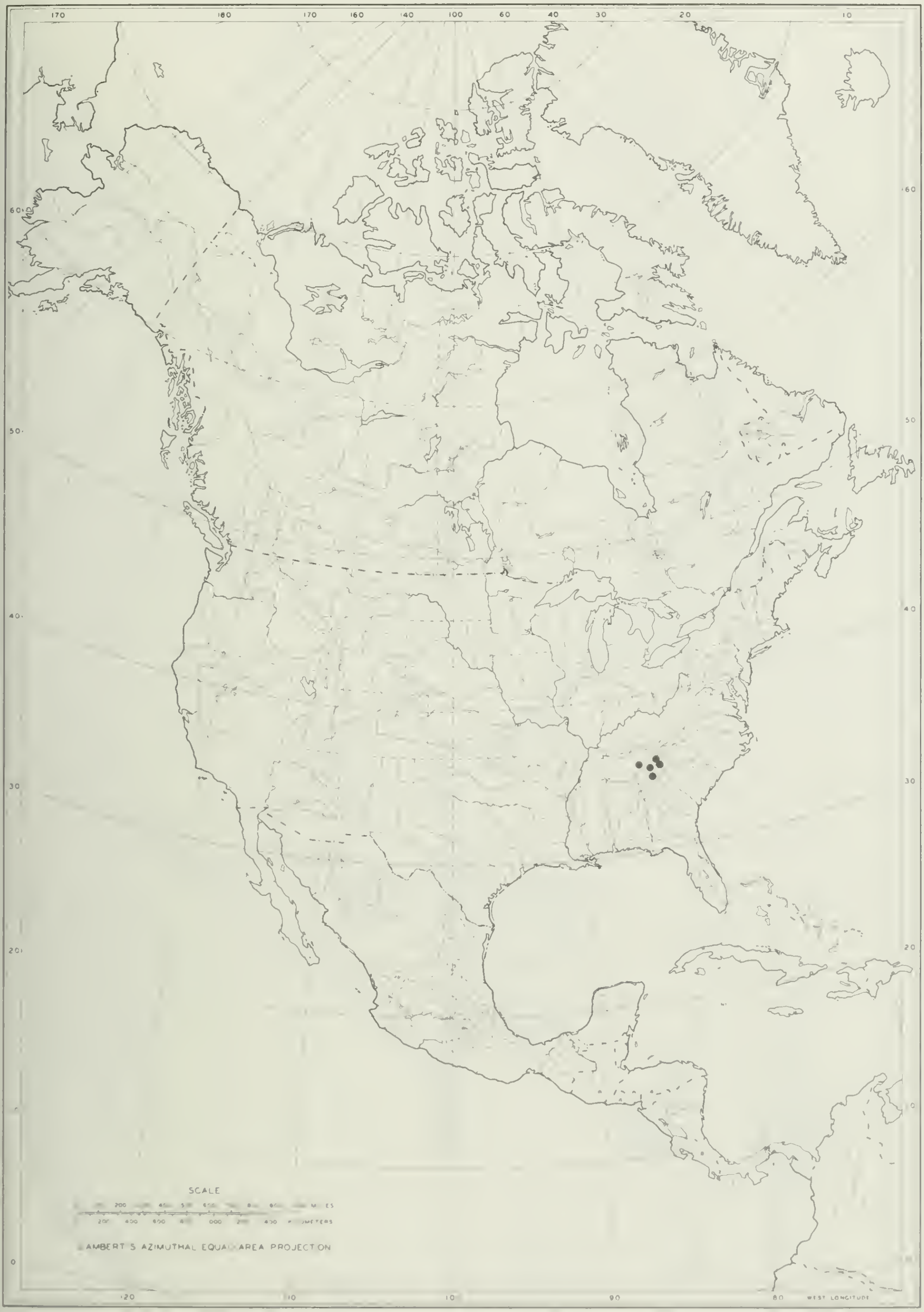

Fig. 26 Distribution of *V. hirsutum* Buckley.

Fig. 27 *Vaccinium tenellum*; habit, flower, and stamen.

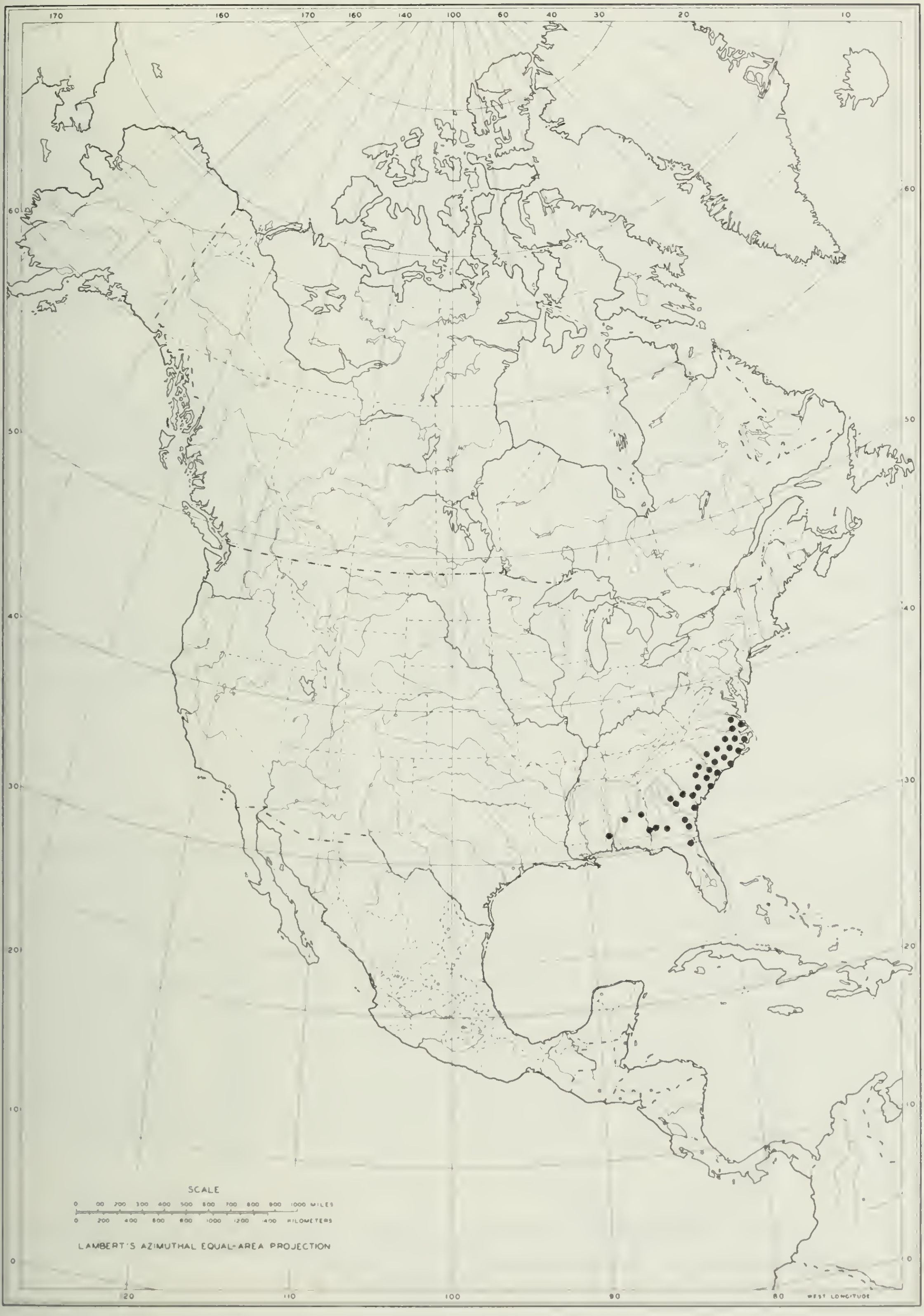

Fig. 28 Distribution of *V. tenellum* Aiton.

Type locality: North America, introduced in 1772 at Kew by William Young. Type at BM!

Range: Southeastern Virginia to southern Georgia then west to Alabama (Fig. 28). Ward (1974) has listed this species for northern Florida, but this report is based on a single 1943 collection from Penny Farms, Clay County. I carefully searched the area during May 1979 but could not find this colony. I am not aware of any other collections either for the region or for the state. Blauch (1970) has reported the species for Blount and Carter counties, Tenn., but his specimens correspond better to *V. hirsutum* Buckley.

Habitat: Flatwoods subjected to periodic burning, open oak–pine woods, pine barrens, scrubby oak woods, and dry meadows along the Coastal Plain; dry sand hills of the Fall-line from North Carolina to Alabama, as well as borders of xeric oak woods in the adjacent Piedmont region.

Common names: Small cluster blueberry, southern blueberry.

Economic importance and use: Aside from providing cover and food to ruffed grouse, this species has no economic value. Its poor flavor precludes extensive usage.

Vaccinium myrsinites **Lamarck**

Description: Shrubs (14)16–38(100) cm high, rhizomatous, forming extensive open colonies. Twigs green, verrucose, more or less angular, pubescent in lines; flush of the current season bright green. Leaves coriaceous, persisting for more than 1 year, elliptical, 3–5 mm wide, 5–9 mm long; lower surface glandular, rarely pubescent; margin usually inrolled and obscurely serrulate. Calyx and pedicel green. Corolla white, tinged with pink or red, urceolate to cylindrical, 4–8 mm long. Filaments ciliate along the margins; pollen tetrads 46–52 µm in diameter. Berry black and shiny, 7–9 mm in diameter; nutlet approximately 1 mm long. Chromosome number $2n = 48$ (Fig. 29).

Type locality: Roadsides and uncultivated places near St. Augustine, Fla. Collected by J. Lamarck in 1779. Type at P!

Range: Along the coastal plain from southeastern South Carolina to southern Florida, and west toward the Florida Panhandle. A few outlying stations in the Metamorphic Hills of Alabama have also been verified (Fig. 30). Other reports from western Florida, southern Alabama, and southern Louisiana are probably *V. darrowii*.

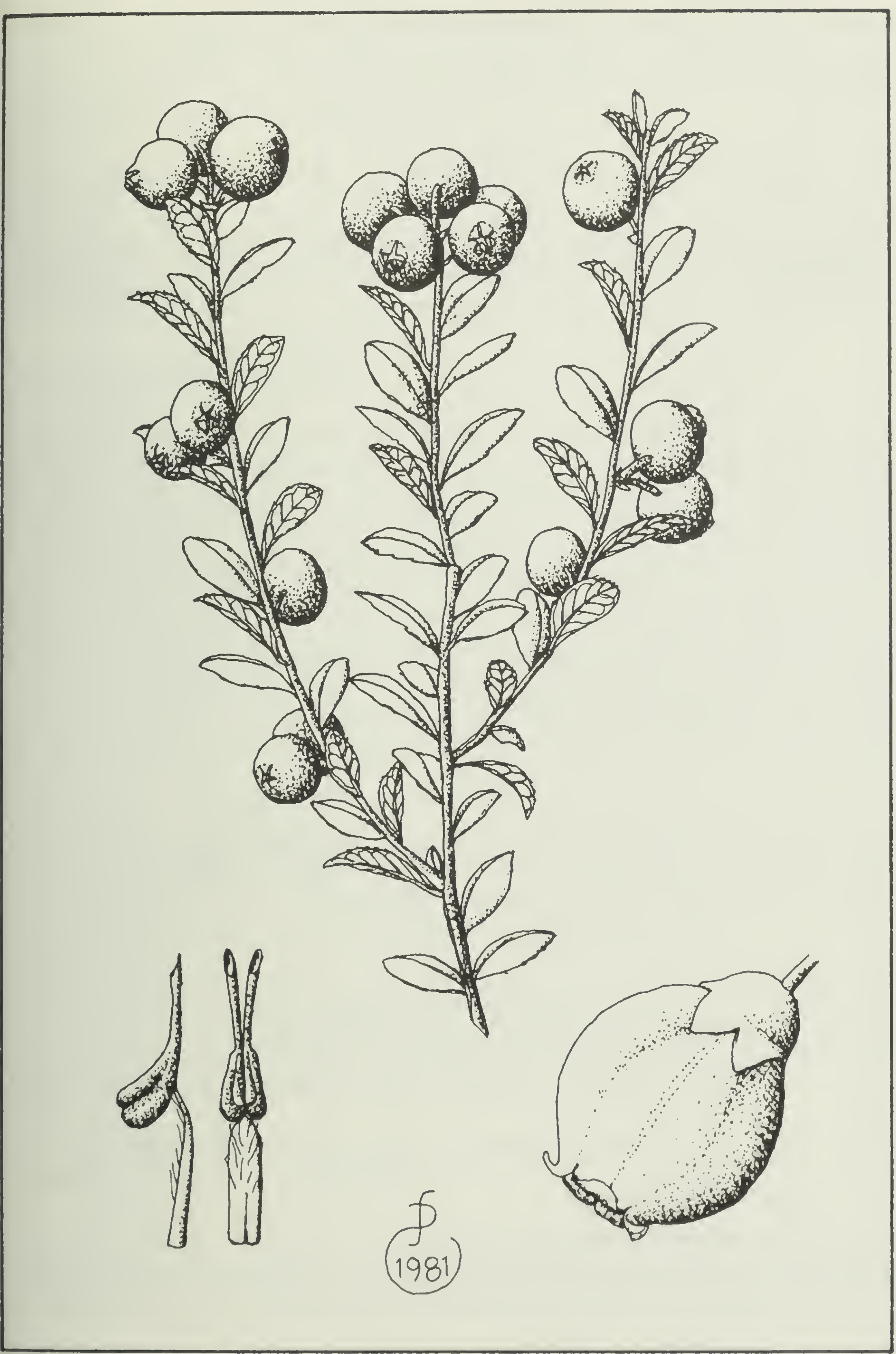

Fig. 29 *Vaccinium myrsinites*; habit, flower, and stamen.

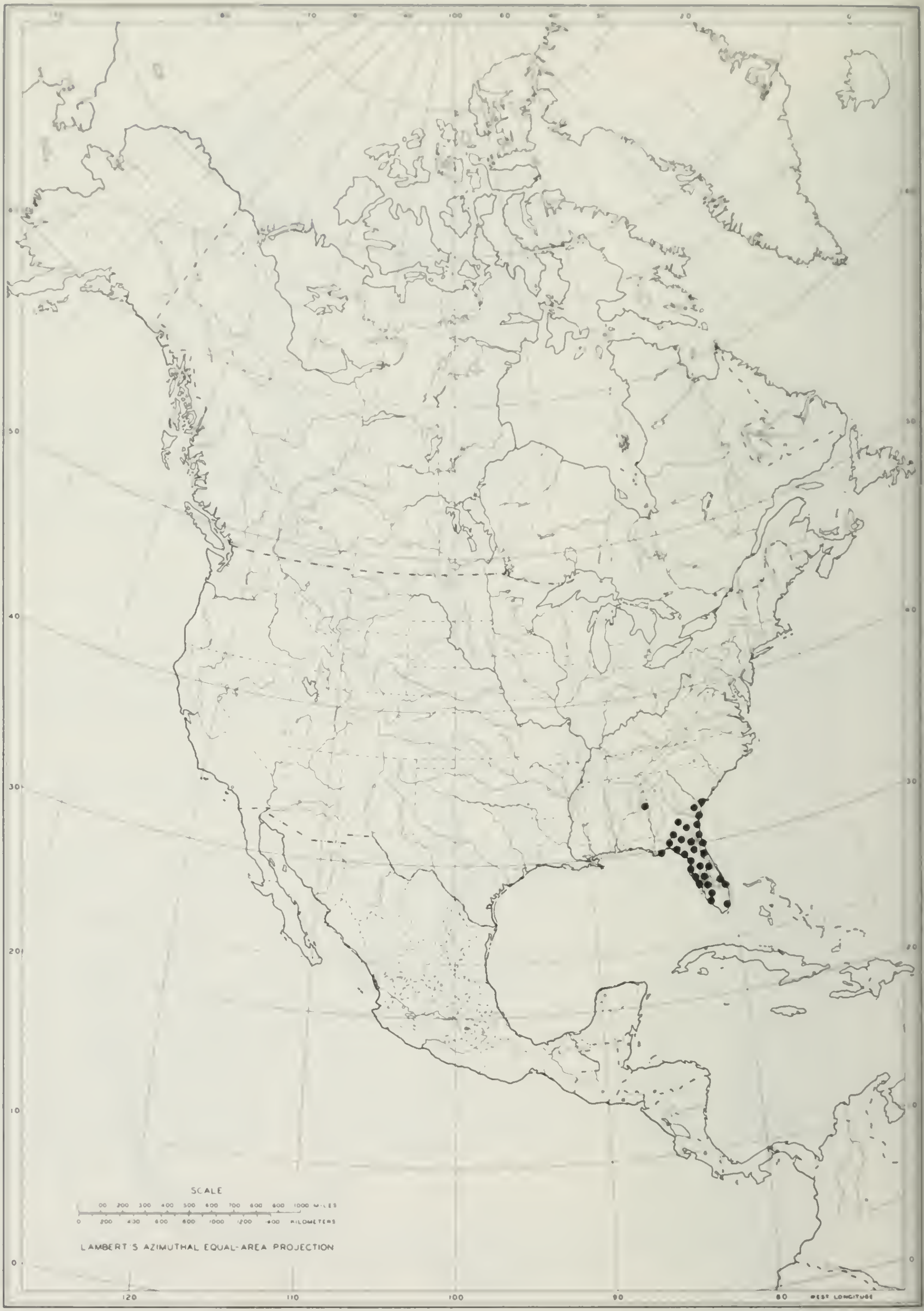

Fig. 30 Distribution of *V. myrsinites* Lamarck.

Habitat: Xeric flatwoods, sand pine scrub, oak–palmetto scrub, scrubby flatwoods, and rosemary balds – in general, dry sandy areas with full sunlight. Abrahamson (1980) has shown that *V. myrsinites* is adapted to periodic burning.

Common names: Florida evergreen blueberry, ground blueberry.

Economic importance and use: The berries are eaten in large numbers by such game birds as quail, ruffed grouse, and wild turkeys (Halls 1977).

Vaccinium darrowii Camp

Description: Shrubs (10)16–94(150) cm high, rhizomatous, forming extensive open colonies, rarely monopodial. Twigs pale, verrucose, scarcely angular, minutely puberulent, rarely pubescent; flush of the current season glaucous. Leaves coriaceous, persistent for more than 1 year, elliptical, occasionally spatulate, 3–5 mm wide, 7–11 mm long, pale, glabrous beneath, or rarely with minute puberulence along midvein; margin inrolled and entire. Calyx and pedicel glaucous. Corolla urceolate to cylindrical, 4–6 mm long, white, white tinged with pink, or red. Filaments ciliate along the margins; pollen tetrads 42–46 µm in diameter. Berry blue and glaucous, 8–10 mm in diameter; nutlet approximately 1 mm long. Chromosome number $2n = 24$ (Fig. 31).

Type locality: Alabama. Type at GH. Chosen in 1982 from a collection of four specimens on a single sheet from A. Gray's herbarium. On this sheet, he wrote "*Vaccinium myrsinites* var. *glaucum*." I have designated the specimen on the bottom right as the type.

Range: Florida, southwestern Georgia, southern Alabama, and southeastern Louisiana (Fig. 32). Correll and Johnston (1970) list this species for Texas, but the voucher specimen SMU 307153 is in fact a variant of *V. corymbosum*, namely *V. virgatum* Aiton.

Habitat: Low flatwoods, scrubby flatwoods, fetterbush–oak scrub, palmetto–oak scrub, and swales.

Common name: Darrow's evergreen blueberry; named in honor of G.M. Darrow, who first recognized the specific nature of this plant and brought it into cultivation at Beltsville, Md., in 1940 (Camp 1942*a*).

Economic importance and use: No use has been reported, but the species shows some promise as a hedge plant (Galletta 1975). It also has several desirable characters of potential value in any blueberry breeding program, such as low chilling requirements, heat and drought resistance, and light blue fruit color (Moore 1965).

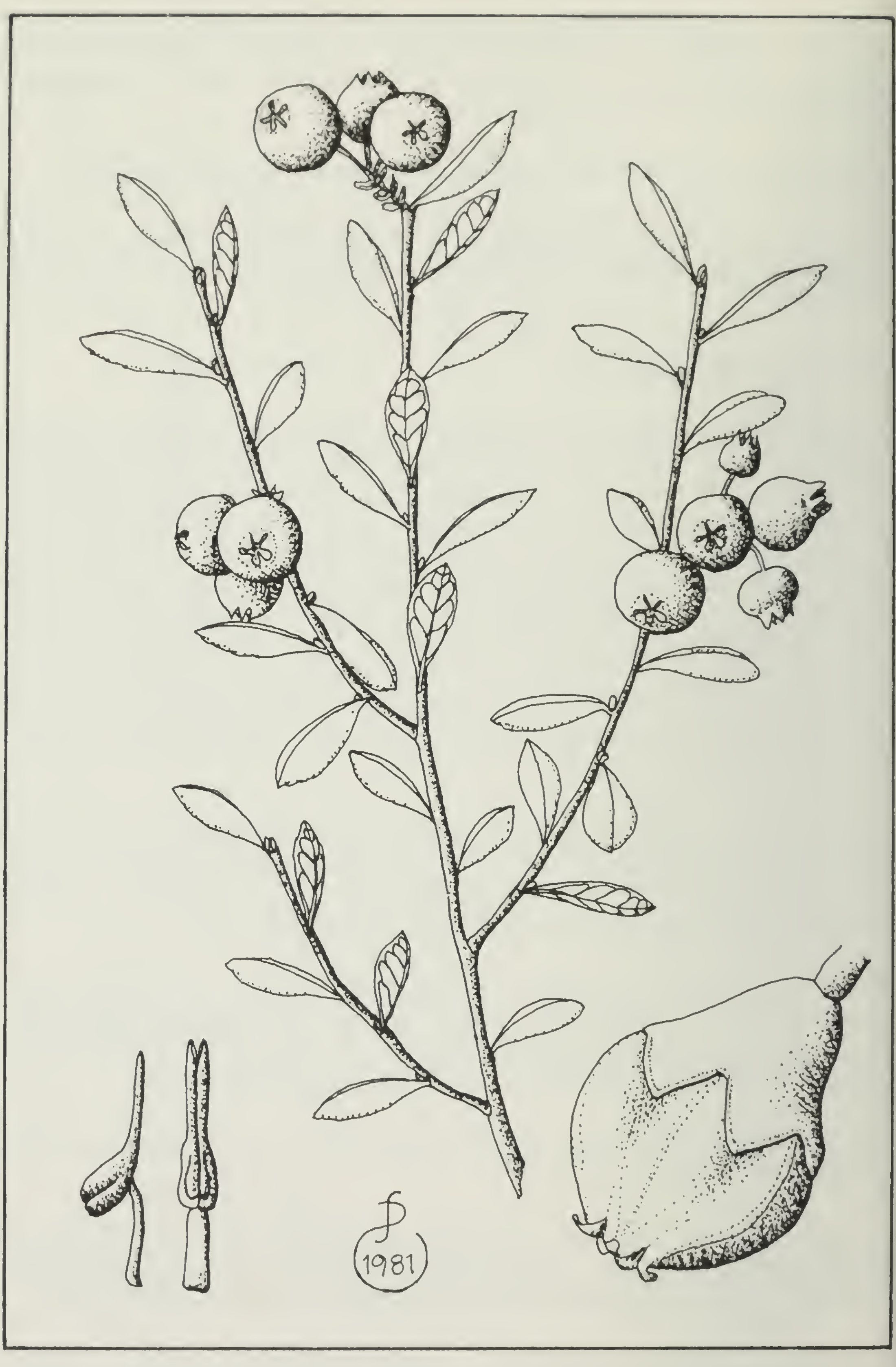

Fig. 31 *Vaccinium darrowii*; habit, flower, and stamen.

Fig. 32 Distribution of *V. darrowii* Camp.

Shrubs in the monotypic section *Polycodium* possess the following features: flowers are open in bud (open aestivation); mature flowers, borne on specialized lateral branches, are campanulate and occur singly in the axils of the leafy raceme. Stamens are awned; the sacs have long tubules, with lacinate terminal pores that are exposed at anthesis. The calyx tube is continuous with the pedicel. The berry is pseudo 10-loculed. Each carpel contains 8–10 ovules.

Although both Palser (1961) and Baker (1970) state that the calyx tube is articulated with the pedicel, I have not been able to verify this observation. Indeed, the 760 specimens I have thus far examined have all had the calyx tube continuous with the pedicel. Likewise, Rehder (1927), Sleumer (1941), and P.F. Stevens (1969) categorically state that in sect. *Polycodium* the calyx tube is continuous with the pedicel.

The number of species that ought to be recognized in sect. *Polycodium* has been the source of considerable controversy. Ashe (1931) divided *Polycodium* into 6 sections and 21 species. However, Ashe's "species" do not breed true. Seeds from a glaucous and glabrous plant ("*V. neglectum*") yield some seedlings that mature into glaucous and glabrous plants but also some that become glaucous and pubescent ("*V. stamineum*"), pale and pubescent ("*V. interius*"), and pale and pilose (tending toward "*V. melanocarpum*") (Eck and Childers 1966, p. 47; Ballington 1980). By contrast, Camp (1945) has argued that the tetraploid *V. hirsutum*, currently placed in sect. *Cyanococcus*, is in fact a hybrid resulting from a cross between two scarcely compatible species, *V. pallidum* (sect. *Cyanococcus*) and *V. stamineum* (sect. *Polycodium*), followed by inbreeding and selection for a stabilized recombinant. As an indication of this hypothesis, the corymbose inflorescence of *V. hirsutum* is typical of sect. *Cyanococcus*, but its woolly berries with few large seeds are characteristic of sect. *Polycodium*. However, Ballinger et al. (1981) found that deerberries resemble cranberries (sect. *Oxycoccus*) more than blueberries (sect. *Cyanococcus*), not only in fresh market and culinary quality but also in anthocyanin and flavonol content.

Section *Polycodium* is endemic in North America and is found primarily in eastern North America from southwestern Ontario to central Florida and west to eastern Texas. A few outlying populations occur in central Mexico and were correctly assigned by Humboldt, Bonpland, and Kunth (1818) to *V. stamineum*; the variation encountered in the Mexican plants is the same as that observed along the Gulf Coast from Florida to Texas. Section *Polycodium* has no close affinity to Neotropical members of *Vaccinium* (Baker 1970), to sections found in old world tropics (Stevens 1969), or to the North American sections.

Some biological aspects of the section are interesting as well. At anthesis, when the corolla lobes are markedly reflexed, the exposed stamens are "buzz-pollinated" by the oligolectic bee *Melitta americana* (Cane et al. 1985). Plants are capable of maturing full crops of fruit even under xeric conditions (Sharpe and Sherman 1971). Dispersal is also unique; the berry (including pedicel) drops to the ground as soon as it ripens. There it is eagerly sought after by quail, who come along and harvest the berries on the ground by neatly incising the tough, bitter hull and removing the sap, pulp, and seeds. As in sect. *Cyanococcus*, seeds from sect. *Polycodium* germinate best when freshly extracted from the berries (Baker 1970).

Vaccinium stamineum **Linnaeus**

Description: Shrubs (20)47–149(500) cm high, frequently crown-forming, suckering when disturbed, forming either clumps or colonies. Twigs of the current season glaucous, green, yellow green, or light brown, terete, glabrous to densely pubescent, occasionally pilose or glandular. Leaves usually deciduous, occasionally more or less persistent in southern populations, elliptical, (9)18–29(32) mm wide, (20)35–57(80) mm long, usually pale or glaucous beneath, glabrous to densely pubescent, rarely glandular; margin usually entire, inrolled on the more coriaceous blades, rarely obscurely serrate. Calyx and pedicel continuous; pedicel subtended by a persistent leaf-like bract; bract usually somewhat smaller than the leaves on sterile shoots, glaucous, glabrous, or pubescent, occasionally glandular; lobes 5. Corolla open in bud, campanulate, 4–8 mm long, lobes 5, reflexed at anthesis, white to greenish white, veins occasionally purple. Stamens 10; filaments glabrous to pubescent; sacs awned, glabrous to pubescent; tubules up to 6 mm long; pollen tetrads (28)39–42(53) µm in diameter. Berry green, yellow, purple, or black, frequently with light bloom, occasionally pubescent and sparsely glandular, (7)10–14(18) mm in diameter; nutlet approximately 2 mm long. Chromosome number $2n = 24$. (Figs. 33 and 34).

Type locality: "Northern America," collected by Peter Kalm for Linnaeus. Type at LINN! The specimen LINN 497.2 has immature leaves and bears leafy racemes and flowers that are nearly at anthesis. LINN 497.22 is also *V. stamineum*, but is a vegetative twig with mature leaves and bears the annotation "K."

Range: From southeastern Ontario, south to central Florida, and west to eastern Texas, extreme eastern Oklahoma, and extreme southeastern Kansas. The species is apparently absent in northern Missouri, Illinois, and northern and northwestern Indiana. However, a few isolated stations occur in central Mexico (Fig. 35).

Fig. 33 *Vaccinium stamineum*; habit, flower, and stamen.

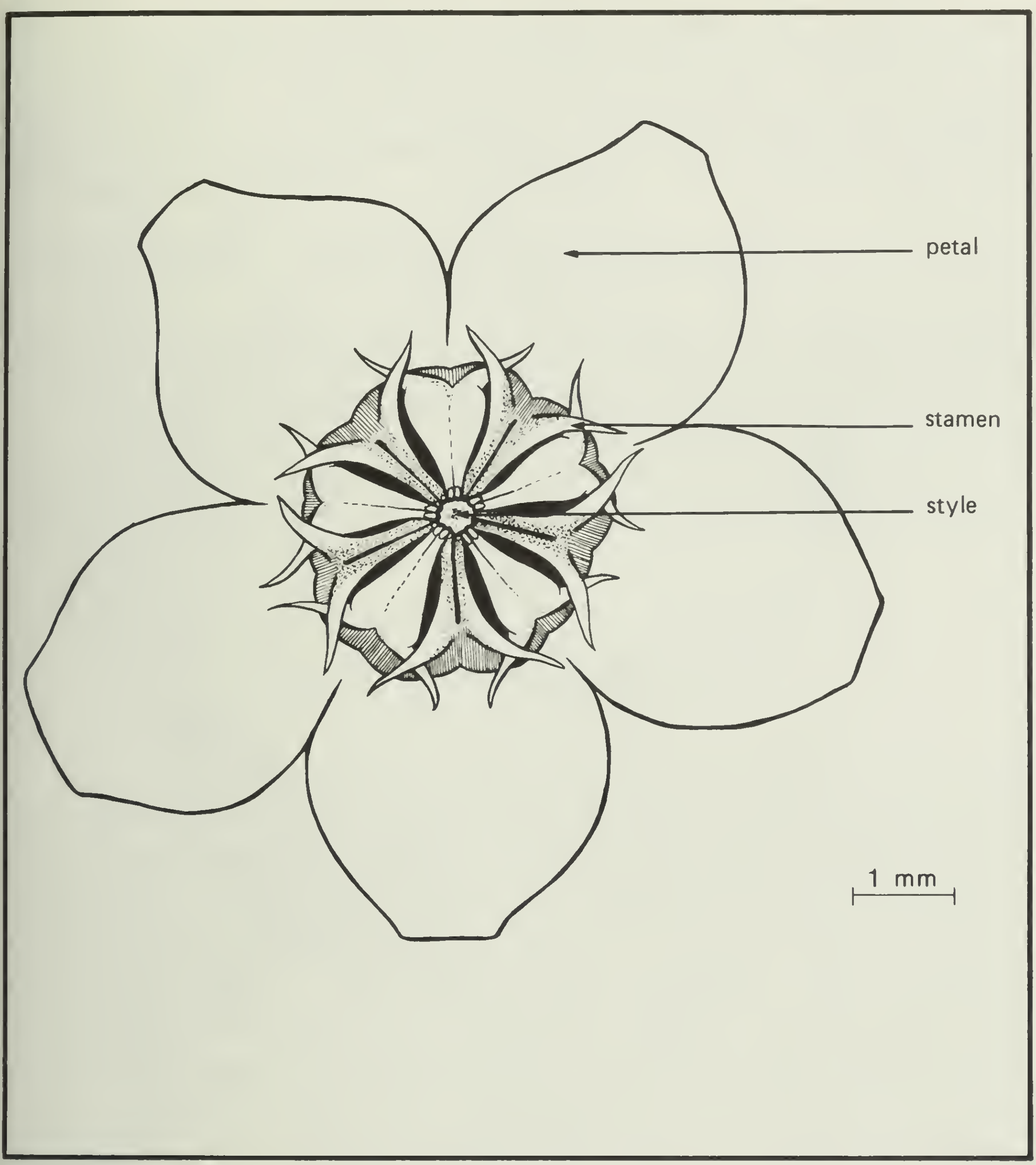

Fig. 34 **Details of the floral architecture of *V. stamineum*.**

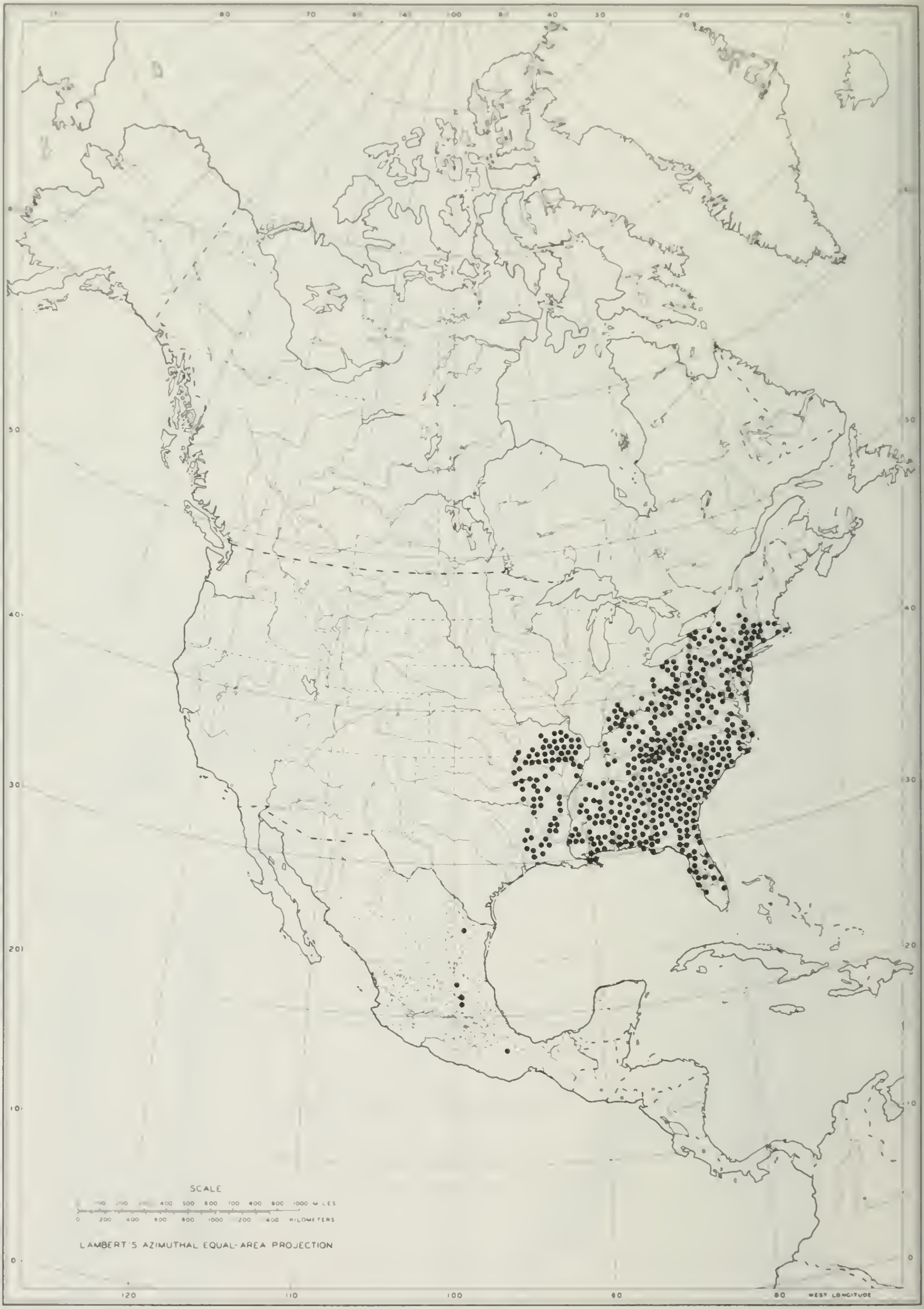

Fig. 35 Distribution of *V. stamineum* Linnaeus.

Habitat: Sandy, well-drained soils, from sea level to 1700 msm. *V. stamineum* is frequently encountered in xeric communities such as dry oak woods, sandy pine–oak flatwoods, sandy flatwoods, pine barrens, sandy hummocks, low flat woods, savannas, longleaf pine flatwoods, dry longleaf pine ridges, sparsely wooded bluffs, sandhills, thickets, and clearings.

Common names: Deerberry, southern gooseberry.

Economic importance and use: Throughout the southern Appalachian highlands the berries are used in making excellent pies, jams, and jellies (Strausbaugh and Core 1958; Stupka 1964; and Ballinger et al. 1980). Indeed, the latter argue that *V. stamineum* has considerable horticultural potential, since it has large fruit, is adapted to upland habitats, and has shown considerable tolerance for drought.

Vaccinium sect. *Batodendron*

Taxa included in sect. *Batodendron* share the following features: the epidermis and cuticles of the current twigs die after about 1 year but persist for several years, giving the older twigs a distinct gray or whitish hue. Flowers are borne on specialized lateral branches. Inflorescence is racemose. The calyx tube is articulated with the slender pedicel, which is subtended by a more or less persistent foliaceous bract; the calyx has five prominent lobes. The corolla has 5 lobes and is campanulate to urceolate; stamens 10, included, sacs awned. The berry is pseudo 10-loculed, but each carpel contains only 5–8 ovules, and usually fewer than 10 mature nutlets are found in a berry; the berry usually persists for a considerable time after ripening.

Asa Gray (1846) placed *V. stamineum* in his sect. *Batodendron*, but it was removed by Rehder (1927), and rightly so, since this species has open aestivation, the calyx is continuous with the pedicel, the stamens are exerted, and the corolla is rotate at anthesis. Section *Batodendron* differs from sect. *Cyanococcus*, another pseudo 10-loculed section, by having more or less leafy racemes, awned anthers, more or less persistent coriaceous leaves, and nonverrucose twigs.

Section *Batodendron* is represented in North America by *V. arboreum* Marsh, the only known deciduous member of this section. It differs from the remainder in that it has campanulate corollas, whereas the others have urceolate corollas. Two evergreen taxa have been assigned to this section by Sleumer (1941): the Caribbean *V. cubense* (A. Rich) Grisebach and the Mexican *V. stenophyllum* Steudel. Several poorly known taxa from Central

America and the Panamanian isthmus possibly belong here also. A thorough taxonomic study of these is required.

Vaccinium arboreum Marshall

Description: Shrubs or small trees (2)3–5(10) m high, trunks up to 35 cm diameter at breast height. Twigs of the current season reddish green, terete, glaucous, glabrous, or glandular-pubescent. Leaves coriaceous and tardily deciduous, obovate to oblong, 12–20 mm wide, 22–40 mm long, glabrous and lustrous above, glaucous, pale, glabrous or glandular-pubescent beneath; margin entire or obscurely dentriculate. Calyx articulated with pedicel; lobes 5, ciliate; pedicel 8–12 mm long, slender, often pubescent in lines, subtended by subpersistent leafy bracts 7–13 mm wide, 21–29 mm long, frequently glandular beneath. Corolla campanulate, 3–5 mm long, white; lobes 5, prominent. Filaments ciliate along the margins; anther sacs awned; pollen tetrads 35–39 µm in diameter. Berry black and shiny, 7–9 mm in diameter; nutlet approximately 2 mm long. Chromosome number $2n = 24$ (Fig. 36).

Type locality: "Grows naturally in Carolina." Type at GH!

Range: From southern Virginia to central Florida, west to eastern Texas, central Oklahoma, and southeastern Missouri. *V. arboreum* is rare and local in Illinois, Indiana, Kentucky, and Virginia (Fig. 37).

Habitat: Sandy or rocky sites, usually xeric woodlands, from sea level to 800 msm in the Appalachians. Along the Gulf coast, the species also occurs in hammocks and bottomland forests. Although it is restricted to dry sites such as granite outcroppings, sand dunes, pine scrub, and barren siliceous soils, Phillips (1981) has found that the species succumbs during periods of extreme drought. Moreover, Gleason (1923) observed that in the Midwest, *V. arboreum* has failed to utilize extensive rocky bluffs north of the Ozark plateau and did not migrate into glaciated regions.

Common names: Farkleberry, sparkleberry.

Economic importance and use: None; the berries are inedible.

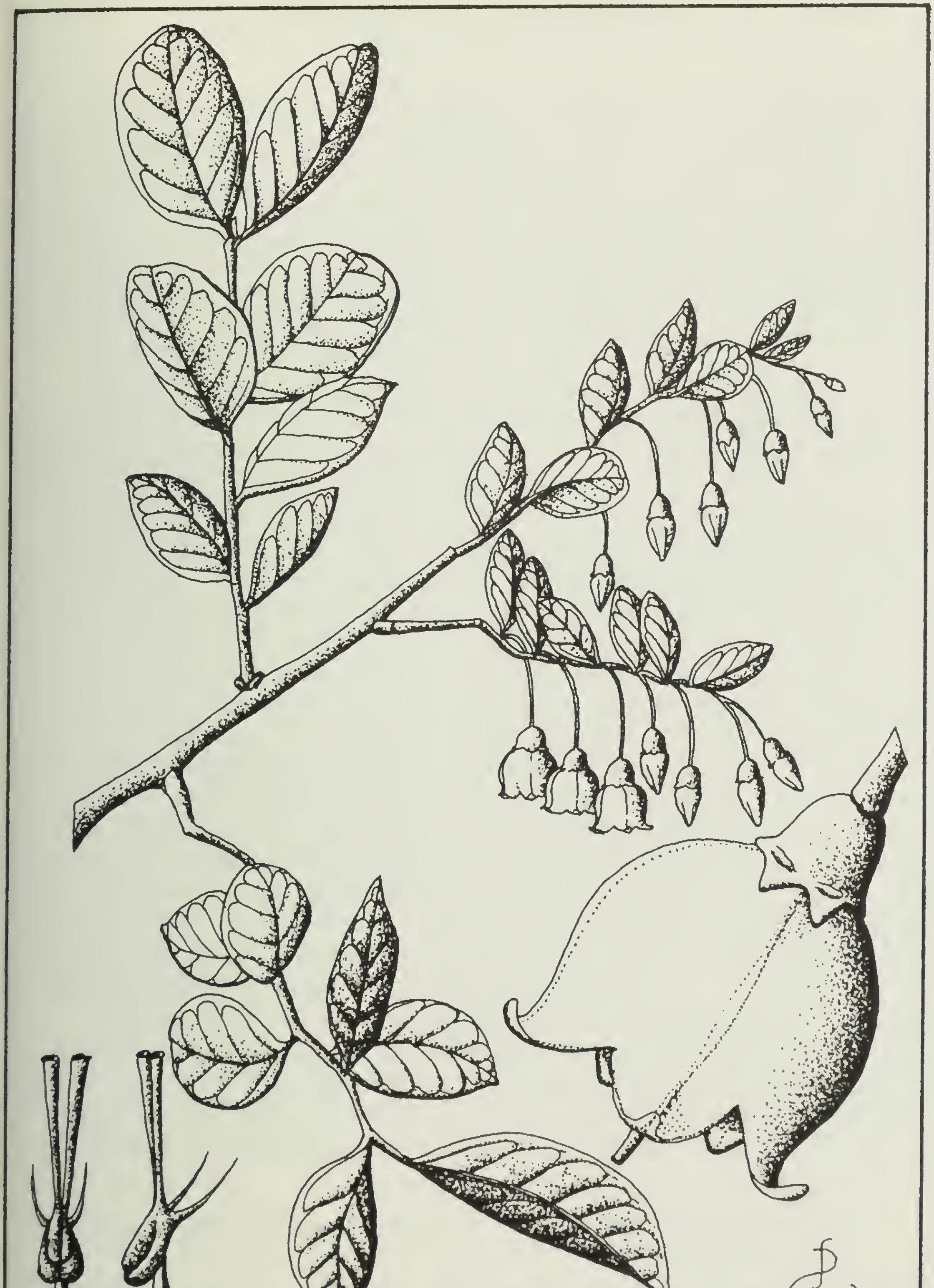

Fig. 36 *Vaccinium arboreum*; habit, flower, and stamen.

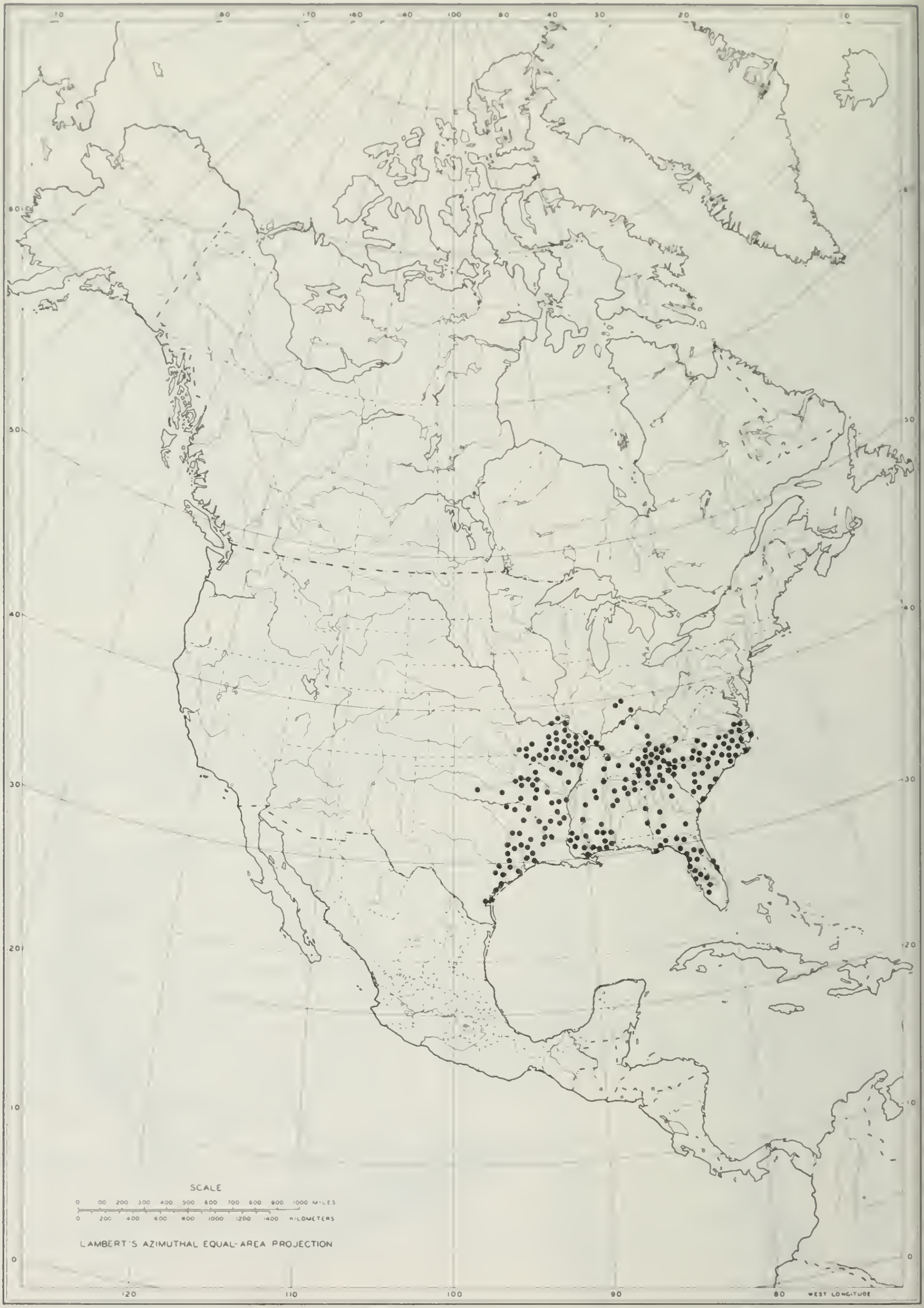

Fig. 37 Distribution of *V. arboreum* Marshall.

Vaccinium sect. *Herpothamnus*

This monotypic section, largely restricted to the Carolinas, is characterized by trailing evergreen vines. The flowers (5-merous) are disposed in lateral clusters or in small racemes in axils of leaves in the growth of the preceding year. The calyx is articulated with the pedicel; the corolla is not deeply divided, and the anthers are not awned. The berry is 5-loculed; each locule contains 15–20 ovules of which only 1 or 2 mature. According to Stevens (1969), plants in sect. *Herpothamnus* also have a lignified epidermis, and the spongy mesophyll has moderately thickened walls.

Three additional features, while not diagnostic, are nevertheless worthy of note: the roots are thickened or even nodulated; vegetative reproduction occurs by layering; and berry maturation is slow, fruiting beginning 110–140 days after anthesis.

Camp (1945) has argued that the trailing vine and nodulated roots found in sect. *Herpothamnus* suggest a possible link to South America and perhaps an epiphytic ancestry, since *Vaccinium* species with such growth habits frequently occur in the highlands of Ecuador. However, on the basis of overall similarity, sect. *Herpothamnus* is linked to both sect. *Cyanococcus* and sect. *Pyxothamnus*, from which it differs in growth habit, locular structure, and stamen morphology. Section *Cyanococcus* has a pseudo 10-loculed ovary and well-developed tubules on the anther sacs, whereas sect. *Herpothamnus* has a 5-loculed ovary and very much reduced anther sac tubules. Section *Pyxothamnus* has short awns on the anther sacs (which are sometimes very much reduced and even absent) and the spongy mesophyll is thick-walled, rigid, and lignified (Stevens 1969). In addition Hall and Galletta (1971) found that the distribution of chromosome lengths and centromere positions in sect. *Herpothamnus* and sect. *Cyanococcus* did not differ significantly.

Recently Rayner and Henderson (1980) recognized a second species in sect. *Herpothamnus*, *V. sempervirens*. But Ballington et al. (1980) regard *V. sempervirens* as merely a coarse variant of *V. crassifolium*. Having examined their herbarium collections and their greenhouse material, I am inclined to agree.

Vaccinium crassifolium Andrews

Description: Shrubs with trailing, woody vines, with erect branches from lateral buds (5)7–18(30) cm high, rooting at the nodes and forming extensive mats. Twigs of the current year, reddish green, finely pubescent, and terete. Leaves coriaceous, persistent, elliptical to obovate, (4)5–7(24) mm wide, (10)12–15(39) mm long; upper surface green and very short pubescent, becoming glabrous with age; lower surface pale and glabrous; margin entire to markedly serrate. Calyx

Fig. 38 *Vaccinium crassifolium*; habit, flower, and stamen.

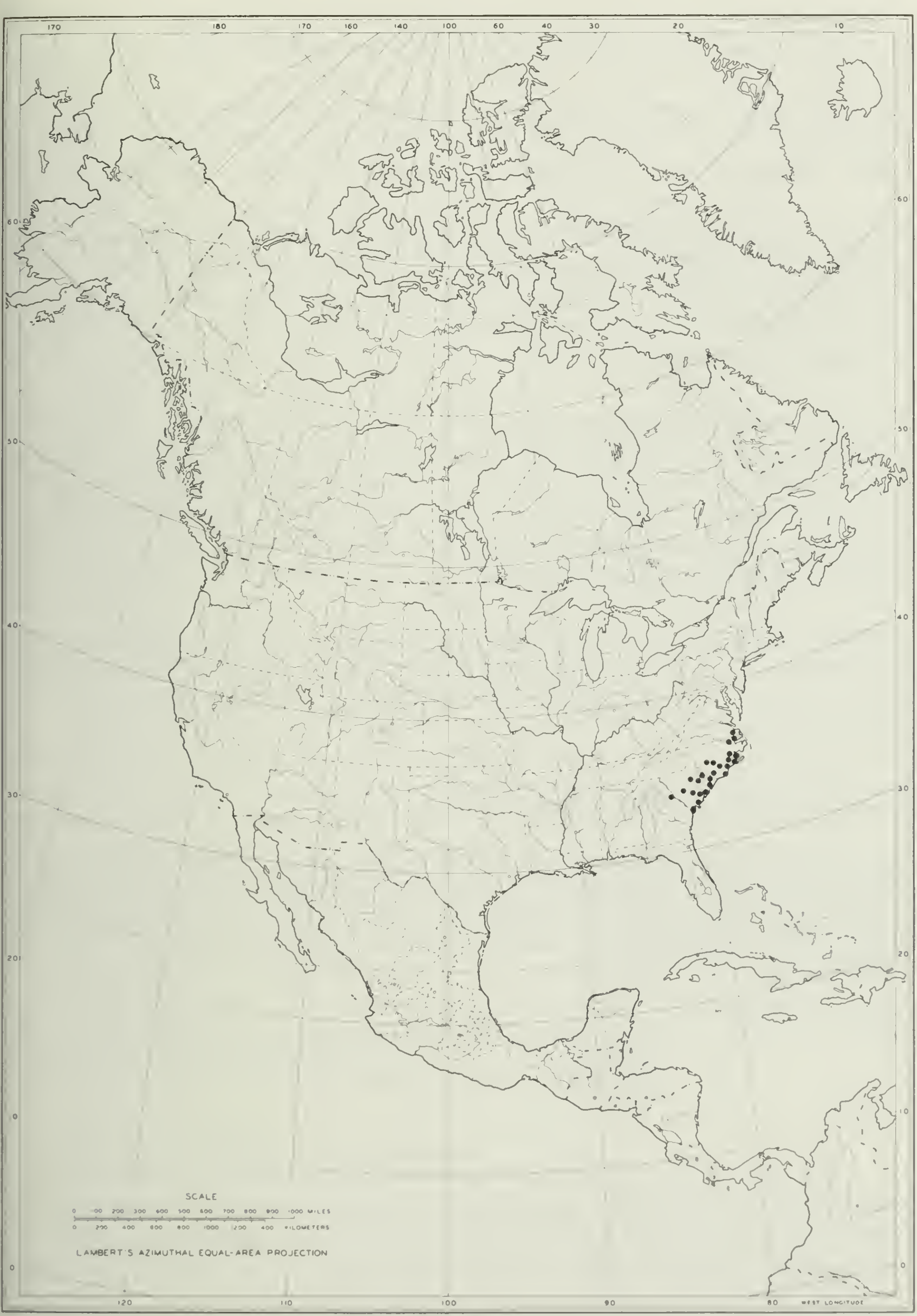

Fig. 39 Distribution of *V. crassifolium* Andrews.

and pedicel articulated, green and glabrous; calyx lobes 5, distinct. Corolla urceolate, 3–5 mm long, white, occasionally with pink striping; 5 small lobes. Stamens 10; filaments ciliate along the margins; sacs awnless with short tubules; pollen tetrads 29–37 μm in diameter. Berry black, 6–8 mm in diameter, insipid; nutlet approximately 1 mm long. Chromosome number $2n = 24$ (Fig. 38).

Type locality: "Carolina"; introduced to the United Kingdom about 1794 by J. Fraser. Type specimen: in Andrews (1800), *Pl.* 105. According to W.T. Stearn (personal communication), Andrews sketched plants in gardens throughout England but refrained from making herbarium collections.

Range: From southeastern Virginia to Savannah, Ga., and southeastern South Carolina (Fig. 39). Blauch (1970) reported a collection from Knox County, Tenn., but none of the institutions he consulted has a supporting specimen, nor have I seen a Tennessee collection in the herbaria I consulted. Therefore I have omitted this location from the distribution map.

Habitat: Open pine flatwoods, pine barrens, pocosin ecotones, and especially road cuts, fire trails, or mown verges through these communities. Ballington et al. (1980) report that the species is adapted to fire.

Common name: Creeping blueberry.

Economic importance and use: Ballington et al. (1980) suggest that *V. crassifolium* has potential as an evergreen groundcover, and cultivation trials have been laid out at Raleigh, N.C., in order to test the species.

Vaccinium sect. *Oxycoccoides*

Shrubs in this section have perennating buds composed of two partly fused scales; deciduous leaves; and flowers that are solitary in leaf axils and are set on nodding pedicels that are continuous with the calyx tube. The corolla is deeply cleft and is 4-merous. Stamens number 8; they are awnless with long anther sac tubules, exposed at anthesis. The berry is 4-loculed, with each locule containing 20–25 ovules.

Rehder (1927) has reported that in sect. *Oxycoccoides* the calyx tube is articulated with the pedicel; Sleumer (1941) observed that the berry is 5-loculed and the corolla 5-merous; Palser (1961) has stated that the stamens have short awns. I have been unable to verify any of these observations in the specimens I have collected or have seen at GH and NY.

Stevens (1969) has observed that sect. *Oxycoccoides* shows extensive lignification around the midrib bundle, that flowers are borne toward the ends of the shoots of the same season, and that the main growth of the plant is carried out by nonflowering shoots.

This section has a southeastern North American and eastern Asian distribution, a pattern first detected and described by A. Gray in 1860 for some 150 taxa of flowering plants. The distribution is usually explained in terms of a former continuous distribution disrupted by the shifting crustal plates. This section may be regarded as morphologically intermediate between sect. *Myrtillus* and sect. *Oxycoccus*. Section *Myrtillus* has similar perennating buds and bears single flowers in the axils of the lower leaves on the vegetative shoots, and the calyx tube is continuous with the pedicel; but it differs from sect. *Oxycoccoides* in that the flowers are 5-merous and have 10 awned stamens, and the corolla lobes are not reflexed at anthesis. Section *Oxycoccus* has a 4-merous flower, 8 awnless stamens, and corolla lobes deeply cleft at anthesis; but it differs from sect. *Oxycoccoides* in that the calyx tube is articulated with the pedicel, the pedicels bear bracts, and the inflorescence is frequently reduced to a pseudo-raceme, especially in *V. oxycoccus* (Vander Kloet 1983*b*).

Traditionally, two species have been referred to sect. *Oxycoccoides*: plants from the Appalachians have been placed in *V. erythrococcum* Michaux, whereas the east Asian material has generally been accommodated in *V. japonicum* Miguel. However, as Table 10 shows, the only morphological difference between these disjuncts is that the Appalachian material is usually more glandular and pubescent than the Japanese. These differences are scarcely enough to warrant specific status, especially when one considers that *V. japonicum* var. *ciliare* Matsun was established to accommodate the more glandular and pubescent Japanese material. Before combining these highly disjunct populations into a single species, their biology and ecology ought to be studied.

Vaccinium erythrocarpum Michaux

Description: Shrubs (60)80–150(300) cm high, crown-forming; suckering or rhizomatous when injured. Twigs of the current season smooth, more or less terete, pubescent in lines. Leaves elliptical, ovate to oblong-lanceolate, deciduous, membranaceous, 18–29 mm wide, 43–63 mm long, glandular-pubescent beneath, green on both sides; margin serrulate. Calyx and pedicel continuous, usually glabrous; calyx lobes 4, small; pedicel up to 1.5 cm long. Corolla lobes 4, deeply reflexed at anthesis, white, pink, rarely red. Filaments pilose; anther sacs awnless; tubules 3–5 mm long; pollen tetrads

Table 10 Morphological comparison of selected attributes of the North American *Vaccinium erythrocarpum* and the Asian *Vaccinium japonicum*

Character	*V. erythrocarpum*	*V. japonicum*
Twigs	more or less terete	more or less terete
Twig indumentum	pubescent in lines	more or less glabrous
Leaf width (mm)	23 ± 5	19 ± 3
Leaf length (mm)	53 ± 10	41 ± 9
Leaf margin	serrate	serrate
Leaf blade	glandular beneath	more or less eglandular beneath
Corolla lobes	reflexed at anthesis	reflexed at anthesis
Filaments	pilose	pilose
Anther sac tubules, length (mm)	4 ± 1	4 ± 1
Pedicel length (mm)	8–15	10–20
Berry color	red, deep purple, black	red

33–37 μm in diameter. Berry red, deep purple, or black, (6)9–11(15) mm in diameter; nutlet approximately 1 mm long. Chromosome number $2n = 24$ (Fig. 40).

Type locality: High mountains in northern Carolina. Type at P!

Range: At high elevations from West Virginia to northern Georgia. Several outlying populations occur in central Tennessee (Fig. 41).

Habitat: Wooded slopes, subalpine shrubbery, boggy areas, rocky slopes, and thickets from (600)1000–1950 msm. In the southern Appalachians, *V. erythrocarpum* frequently occurs in virgin spruce–fir forests, where it is associated with *Viburnum alnifolium*, *Rubus canadensis*, and *Sambucus pubens* (Oosting and Billings 1951).

Common names: Southern mountain cranberry, bearberry.

Economic importance and use: None; the berries are usually insipid, rarely sweet or tart.

Fig. 40 *Vaccinium erythrocarpum*; habit, flower, and stamen.

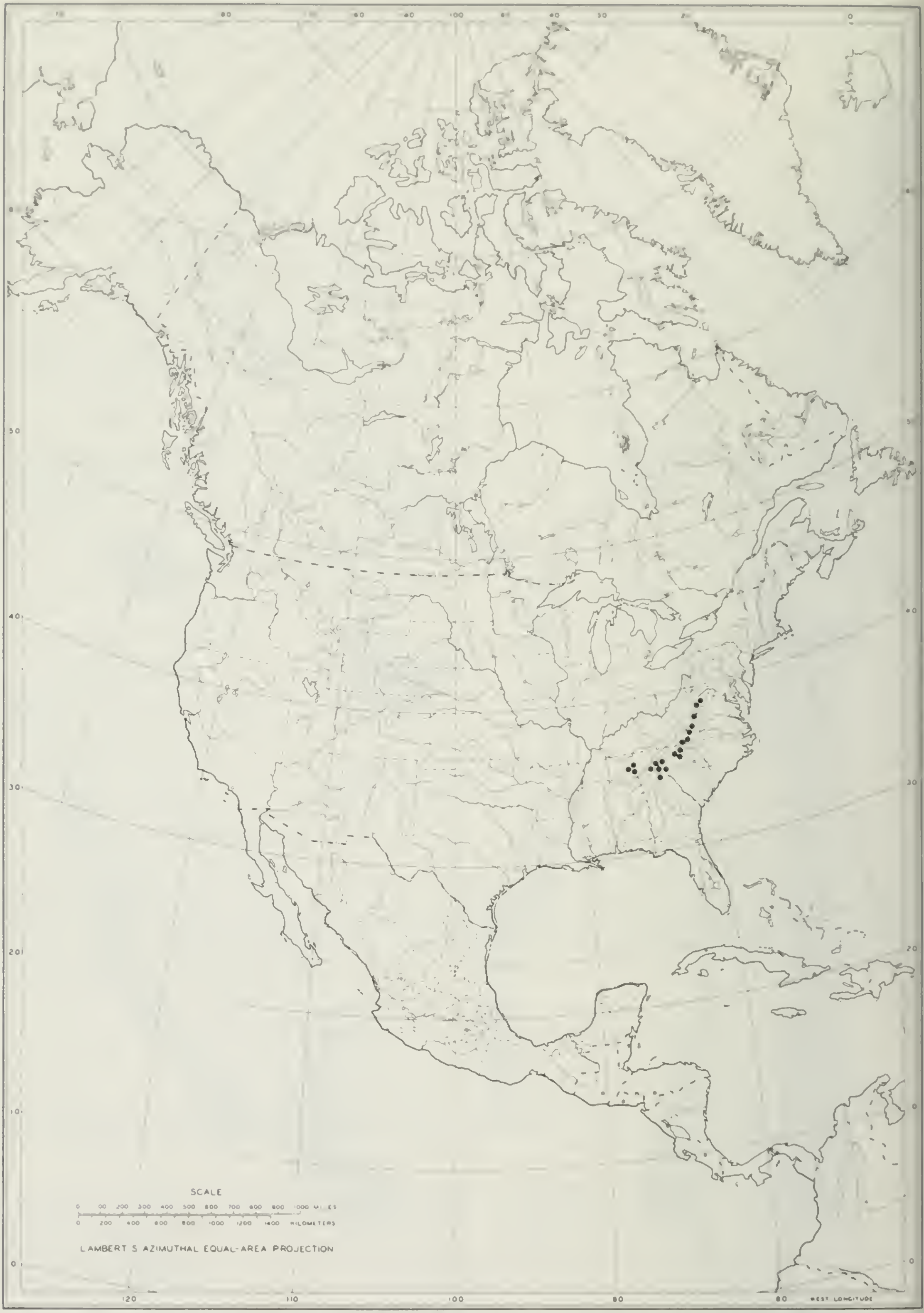

Fig. 41 **Distribution of *V. erythrocarpum* Michaux.**

Vaccinium sect. *Oxycoccus*

Trailing vines; branches woody, slender, flexible, terete, and glabrous or pubescent. Leaves persistent; margin entire. Flowers 4-merous, solitary or in small clusters, axillary or apparently terminal, nodding on long slender pedicels. Calyx tube articulated with pedicel. Corolla white to dark pink; lobes cleft nearly to the base, strongly recurved at anthesis; anthers 8, awnless but with long slender tubules. Ovary 4-celled. Berry red with several seeds.

Recently I have argued (Vander Kloet 1983*b*) that the morphological and biological evidence supports the division of sect. *Oxycoccus* into only two species: *V. macrocarpon*, an eastern North American endemic, and the circumboreal *V. oxycoccus*. Furthermore, Stevens (1969) contended that the differences in testa and corolla stomata between these two species are of the same order as sectional differences elsewhere in the genus. As Fig. 42 shows, however, the difference in testa is a matter of degree only; the outer integument of *V. macrocarpon* contains several more layers of large thin-walled cells than *V. oxycoccus*.

According to Camp (1944), the southern diploid ($2n = 24$) *V. macrocarpon* is the more primitive, and the circumboreal *V. oxycoccus* is the derived species and was initially entirely diploid. Through autopolyploidy, *V. oxycoccus* became locally a tetraploid ($2n = 4x = 48$) or a hexaploid ($2n = 6x = 72$). Also, interspecific hybridization could have occurred in eastern North America when the diploid populations of *V. oxycoccus* migrated southward, following the onset of Pleistocene glaciation, and came into contact with *V. macrocarpon*. A few plants in the resultant hybrid swarms might have become tetraploids through the production of unreduced gametes and thus were effectively isolated from both parental species. Camp (1944) argued that these polyploids, whatever their origin, gradually supplanted the diploids everywhere but in the Northwest Territories and the Yukon.

Key to the species

1. Leaves narrowly elliptical, largest usually more than 1 cm long; pedicels with leaf-like bracts more than 1 mm wide .... *V. macrocarpon*

1. Leaves ovate, largest usually less than 1 cm long, margin often inrolled; pedicels with red scale-like bracts, less than 1 mm wide, sometimes absent .... *V. oxycoccus*

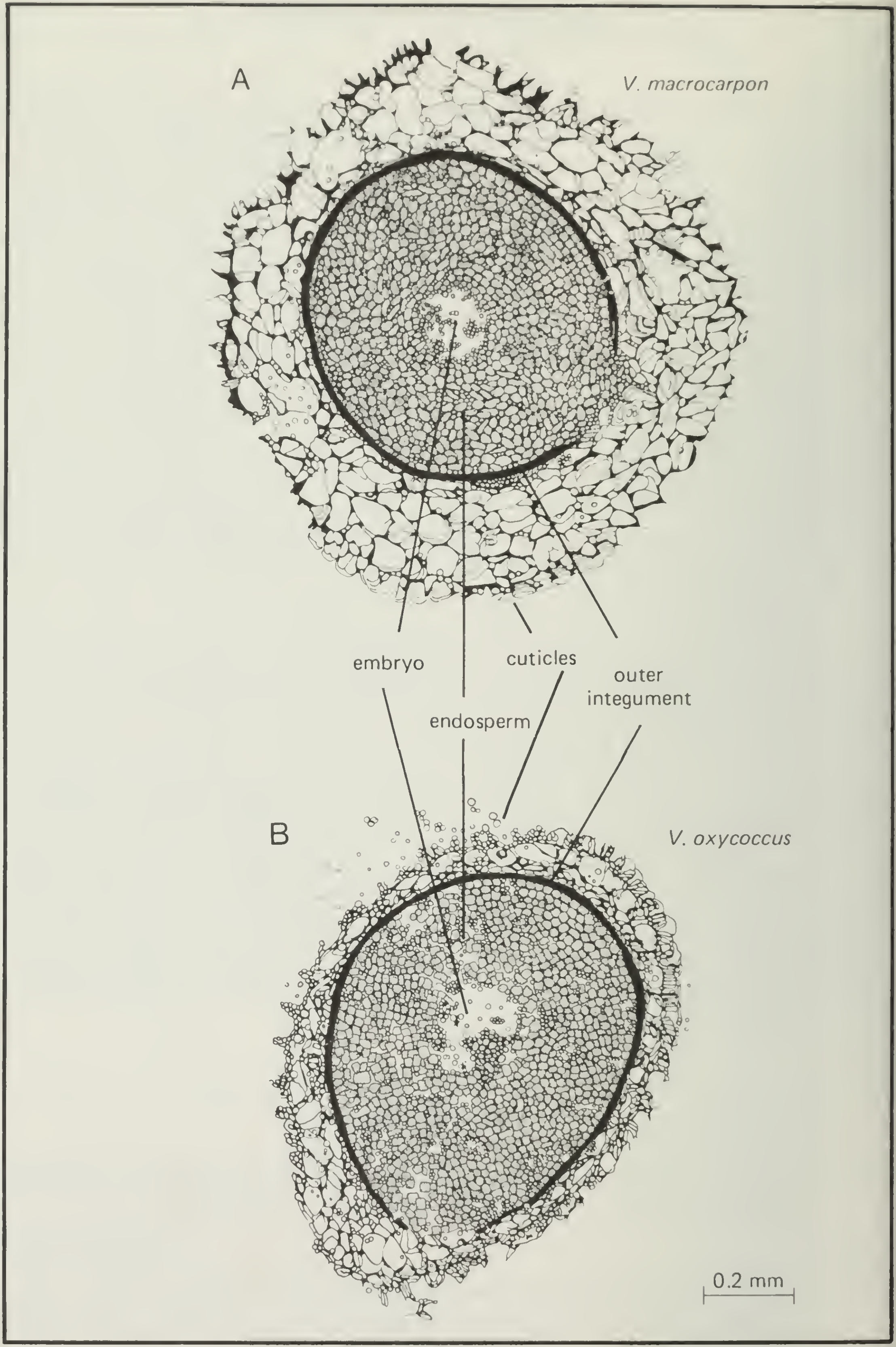

Fig. 42 Cross sections of *Vaccinium* sect. *Oxycoccus* seeds. (A) *V. macrocarpon;* (B) *V. oxycoccus.*

Vaccinium macrocarpon Aiton

Description: Vine trailing, woody; shoots from axillary buds, frequently erect or ascending, 4–15 cm high. Twigs of the current season terete, golden brown, glabrous, rarely pubescent. Leaves persistent, narrowly elliptical, elliptical, or rarely oblong, (2)3–4(5) mm wide, (5)7–10(18) mm long, green above, glaucous beneath with the wax so thick that it frequently obscures the stomata; margin entire, scarcely revolute. Flowers borne singly in the axils of reduced leaves at the base of current shoots. Pedicels slender, 2–3 cm long, glabrous or pubescent, bearing a pair of green bracts 1–2 mm wide. Calyx lobes 4, very small. Corolla lobes 4, white to pink, strongly reflexed at anthesis. Stamens 8; filaments usually stiffly pubescent along the margins, rarely entirely pubescent or glabrous; anther sacs awnless; tubules long, slender, 1–2 mm long; pollen tetrads 32–37 µm in diameter; locules 4. Berry red, 9–14 mm in diameter; nutlet approximately 2 mm long. Chromosome number $2n = 24$ (Fig. 43).

Type locality: Native of North America. Introduced at Kew in 1760 by Mr. James Gordon. Type at BM!

Range: Newfoundland, west to central Minnesota, south to northern Illinois, northern Ohio and central Indiana, and in the Appalachian Mountains to Tennessee and North Carolina. Its main distribution lies between 40°N and 50°N and 70°W and 80°W (Fig. 44). The only report of *V. macrocarpon* occurring north of 50° latitude comes from Sir Joseph Banks, Nfld. However, Lysaght (1971, pp. 69, 341) has argued that Banks's specimen came from the Bay of Isles (near Corner Brook) via Wilkinson from James Cook in 1767 rather than from "The Illettes" near Hare Bay in the vicinity of St. Anthony. Aside from the dubious Banks record, there are no other specimens in the herbaria I consulted to support this claim; furthermore, I searched the headlands near St. Anthony for 2 days without finding the species.

The species is now quite rare, if indeed not extirpated, in Illinois, Ohio, Maryland, North Carolina, and Tennessee. *V. macrocarpon* has been introduced and is adventive along the eastern shore of Maryland (Brown and Brown 1972) as well as on Lulu Island near Vancouver, B.C., and at several localities in Washington and Oregon. The species has also been introduced in Europe and thrives as an escape in Britain, Germany, Switzerland, and the Netherlands (Popova 1972).

Habitat: Open bogs, swamps, mires, wet shores, and headlands, and occasionally poorly drained upland meadows. Occurrence is restricted to acidic soils and peat. The pH for 27 soils and peaty substrates tested ranged from a low of 4.8 in bogs to a high of 6.1 in old fields. A more detailed description of habitat is given by Vander Kloet (1983*b*).

Common names: Large cranberry, American cranberry.

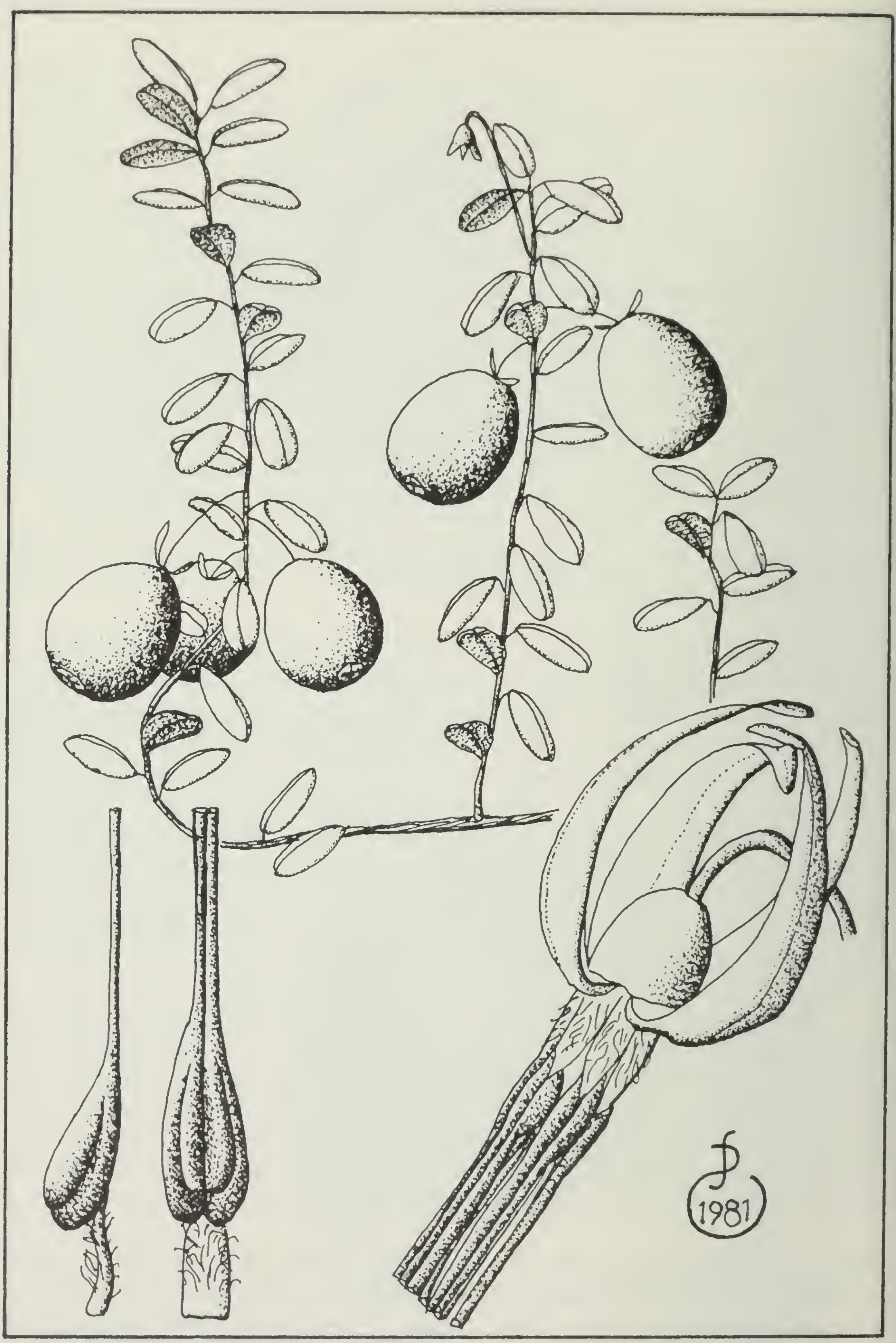

Fig. 43 *Vaccinium macrocarpon*; habit, flower, and stamen.

Fig. 44 Distribution of *V. macrocarpon* Aiton.

Economic importance and use: *V. macrocarpon* is highly exploited in Massachusetts, New Jersey, Wisconsin, Oregon, and Washington; in 1981 some 119 000 t were harvested in the United States. Indeed, throughout the range of the species, casual usage by the Indians and later by the European settlers has been documented (see Part 1 for details and references).

Vaccinium oxycoccus Linnaeus

Description: Vines trailing, wiry, woody; shoots from axillary buds, often ascending, 1–3 cm high. Twigs of the current season terete, very slender, dark brown to red, glabrous to pubescent. Leaves persistent, ovate, occasionally elliptical, (1)2–3(5) mm wide, (3)5–6(10) mm long; green above, glaucous beneath with wax so thick that it frequently obscures the stomata (Vander Kloet 1983*b*); margin entire, frequently revolute and often strongly so. Flowers borne singly in the axils of reduced leaves at the base of current shoots, but on most vines (especially north of 50° latitude) the leafy portion of the fertile shoot does not develop, giving the illusion that *V. oxycoccus* has an inflorescence comprised of a short rachis bearing 1–4 flowers on long slender pedicels. Pedicels slender, 2–3 cm long, glabrous to pubescent, bearing (0)2(5) reddish scaly bracts less than 1 mm wide. Calyx lobes 4, very small. Corolla lobes 4, white to deep pink, strongly reflexed at anthesis. Stamens 8; filaments usually stiffly pubescent along the margins, occasionally pubescent, rarely glabrous; anther sacs awnless; tubules slender, 1 mm long; pollen tetrads 34–46 μm in diameter. Berry at first punctate, later turning deep red, 6–12 mm in diameter; locules 4; nutlet approximately 1 mm long. Chromosome number $2n = 24, 48, 72$ (Fig. 45).

Type locality: Sweden. Type at LINN! Specimen no. 497.18.

Range: Circumboreal (but absent from the Arctic archipelago, including Baffin Island) and southward to central Oregon in the Cascades and to Virginia in the Appalachians (Fig. 46).

Habitat: Half buried in sphagnum hummocks of bogs, muskegs of taiga, and low arctic tundra. This habitat is oligotrophic, with low pH (2.9–3.8), few exchangeable cations (Grandtner 1960), and little available nitrogen and phosphorus (E. Small 1972).

Common names: Small cranberry, atocas.

Economic importance and use: Since berries are quite small compared with *V. macrocarpon* and fruiting is usually sparse, *V. oxycoccus* is little exploited in the eastern part of the continent. In

Fig. 45 *Vaccinium oxycoccus*; habit, flower, and stamen.

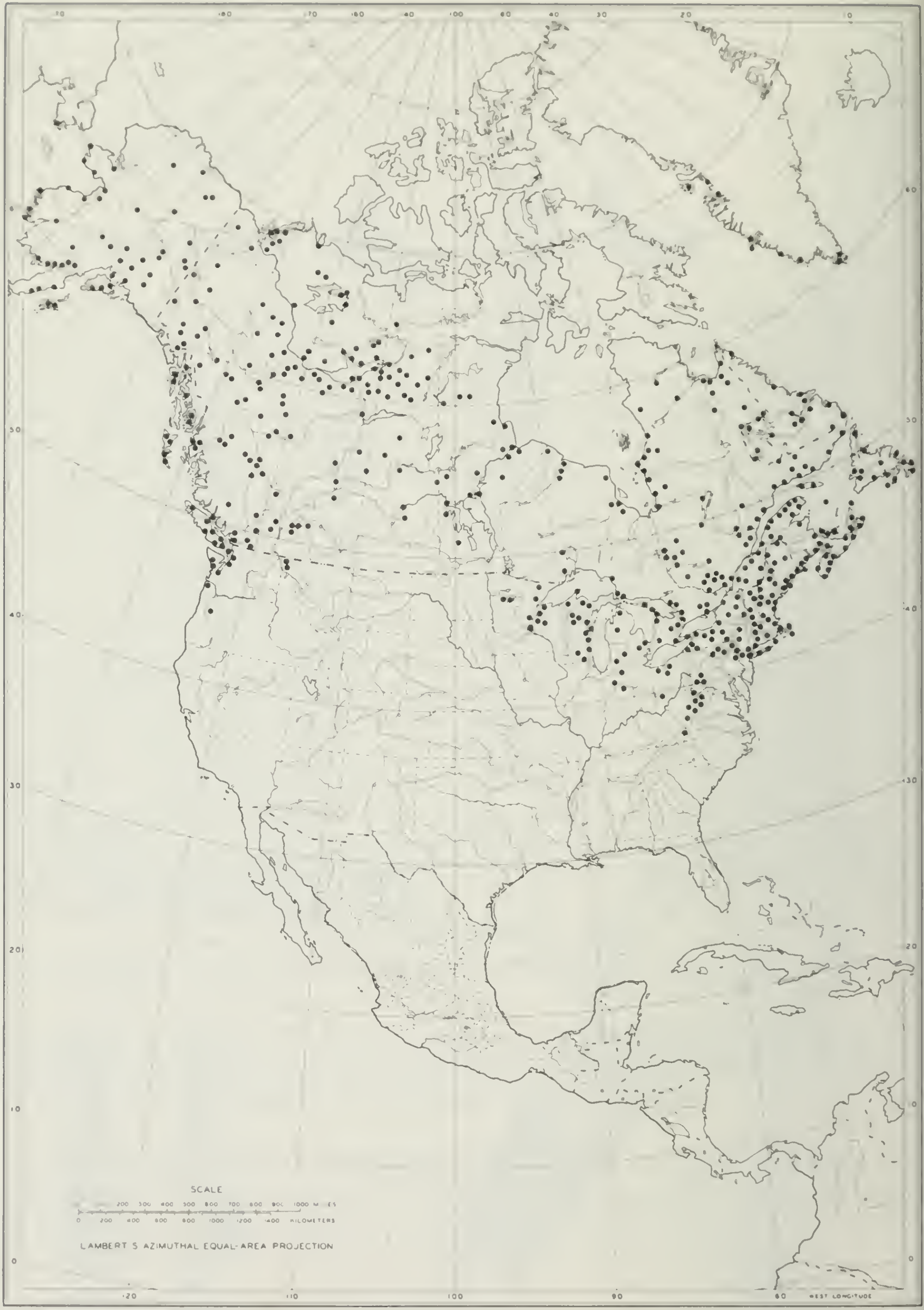

Fig. 46 North American distribution of *V. oxycoccus* Linnaeus.

Washington, British Columbia, and Alaska, Indians have an extensive record of casual usage. Turner (1975, 1978) has provided an excellent account of Indian usage in British Columbia.

Vaccinium sect. *Vitis-idaea*

This monotypic section of circumboreal evergreen dwarf shrubs has the following features: twigs of the current season are terete and puberulent. In the leaf axils two types of perennating buds develop, floral and vegetative. These buds are covered with several small scales and are dimorphic; the rotund floral bud is usually pseudo-terminal and at least three times the size of the vegetative. The inflorescence is a few-flowered raceme. The pedicels are short, articulated with the calyx tube; the calyx has four small lobes; the corollas are campanulate, deeply lobed, 4-merous; stamens 8, included and awnless; the berry is 4-loculed.

Stevens (1969) found marginal leaf fibers, pericyclic phellogen, and thick-walled but unlignified spongy mesophyll in *V. vitis-idaea*. These anatomical characteristics suggest that sect. *Vitis-idaea* has stronger affinities with American sections such as sect. *Pyxothamnus* than with southeastern Asian sections. Therefore Stevens (1969) removed those taxa which were 5-merous and had urceolate corollas, awned stamens, hypodermal phellogen, and no marginal leaf fibers from Sleumer's (1941) concept of sect. *Vitis-idaea* and placed them in sect. *Conchophyllum* Sleumer.

Conversely, both Howell (1897) and Rehder (1927) accommodated *V. ovatum* Pursh in sect. *Vitis-idaea* sensu Gray (1848), which was characterized as follows: "Ovary 4–5 celled: corolla bell-shaped or globular, 4–5 lobed; anthers 8–10, awnless; filaments hairy; flowers in short bracted racemes; leaves evergreen; berries red or purple." This concept of sect. *Vitis-idaea* was erroneously attributed by Gray to Tournefort. The latter's sect. *Vitis-idaea* is synonymous with Linnaeus's (1737) generic concept of *Vaccinium*; it is a far cry from Koch's (1837) laconic description: "anthers awnless, corolla campanulate." *Vaccinium ovatum* has anthers with short or rudimentary awns (Camp 1945). Sleumer (1941) was justified according to Stevens (1969) in transferring *V. ovatum* to his sect. *Pyxothamnus*, a section with neotropical affinities.

I have adopted Stevens's (1969) concept of sect. *Vitis-idaea*. I also agree with his proposal that this section is allied to the Neotropical sect. *Pyxothamnus*, in spite of the fact that sect. *Vitis-idaea* naturally interbreeds with sect. *Myrtillus* (Ritchie 1954, 1955). The occurrence of this natural hybrid (which has been described as *V. intermedium* Ruthe) indicates that the 4-merous condition is not fundamentally different from the 5-merous, and suggests that 4-merous taxa ought not be excluded from 5-merous taxa on only those grounds. I agree with Stevens that although the 4-merous condition is derived from the 5-merous, it has evolved independently at least several times. Furthermore, sect. *Vaccinium* shows this transition in development; most of the flowers on any one shrub of *V. uliginosum* are 4-merous, but a few 5-merous flowers can always be found (Warr 1981).

Vaccinium vitis-idaea Linnaeus

Description: Sub-shrub (1)4–10(35) cm high, in dense rhizomatous colonies, frequently forming mats. Twigs of the current season green, terete, and puberulent. Leaves persistent, elliptical to obovate, (3)5–7(9) mm wide, (5)9–13(18) mm long, bright green above, pale and glandular beneath; margins entire, slightly revolute. Calyx articulated with pedicel; lobes 4, small, occasionally ciliate. Corolla campanulate; lobes 4, up to 3 mm long, pinkish white. Stamens 8; filaments pubescent; sacs awnless; tubules short; pollen tetrads 28–32 µm in diameter. Berry 4-celled, red, 8–10 mm in diameter; nutlet approximately 1 mm long. Chromosome number $2n = 24$ (Fig. 47).

Type locality: Sweden. Type at LINN! Specimen No. 497.17.

Range: In North America, from northwestern Greenland at 77°N, south to Connecticut at 42°N, and from 45°W longitude (the southern tip of Greenland) west to 170°W longitude (the Aleutian Islands) (Fig. 48). The species is quite rare in Vermont, Massachusetts, Connecticut, and Wisconsin and has not been found in the Adirondacks. See Hall and Shay (1981) for a complete list of published distribution maps for this species.

Habitat: In the boreal taiga, *V. vitis-idaea* is found in jack pine stands, muskegs, raised bogs, dry rocky barrens, and lichen woodlands; elsewhere, the species occupies a wide range of exposed habitats such as heaths, high moors, headlands, tundra, cliffs, and mountain summits. For a comprehensive list of habitats, soil types, and community associates see Ritchie (1955) and Hall and Shay (1981).

Common names: Foxberry, cowberry, mountain cranberry, partridgeberry (Newfoundland), dry ground cranberry, rock cranberry, ling berry, lingonberry, redberries.

Economic importance and use: This species is exploited commercially only in Newfoundland (see Part 1; see also Torrey 1914; Hall and Shay 1981). Casual use by Indians, Inuit, and Europeans has

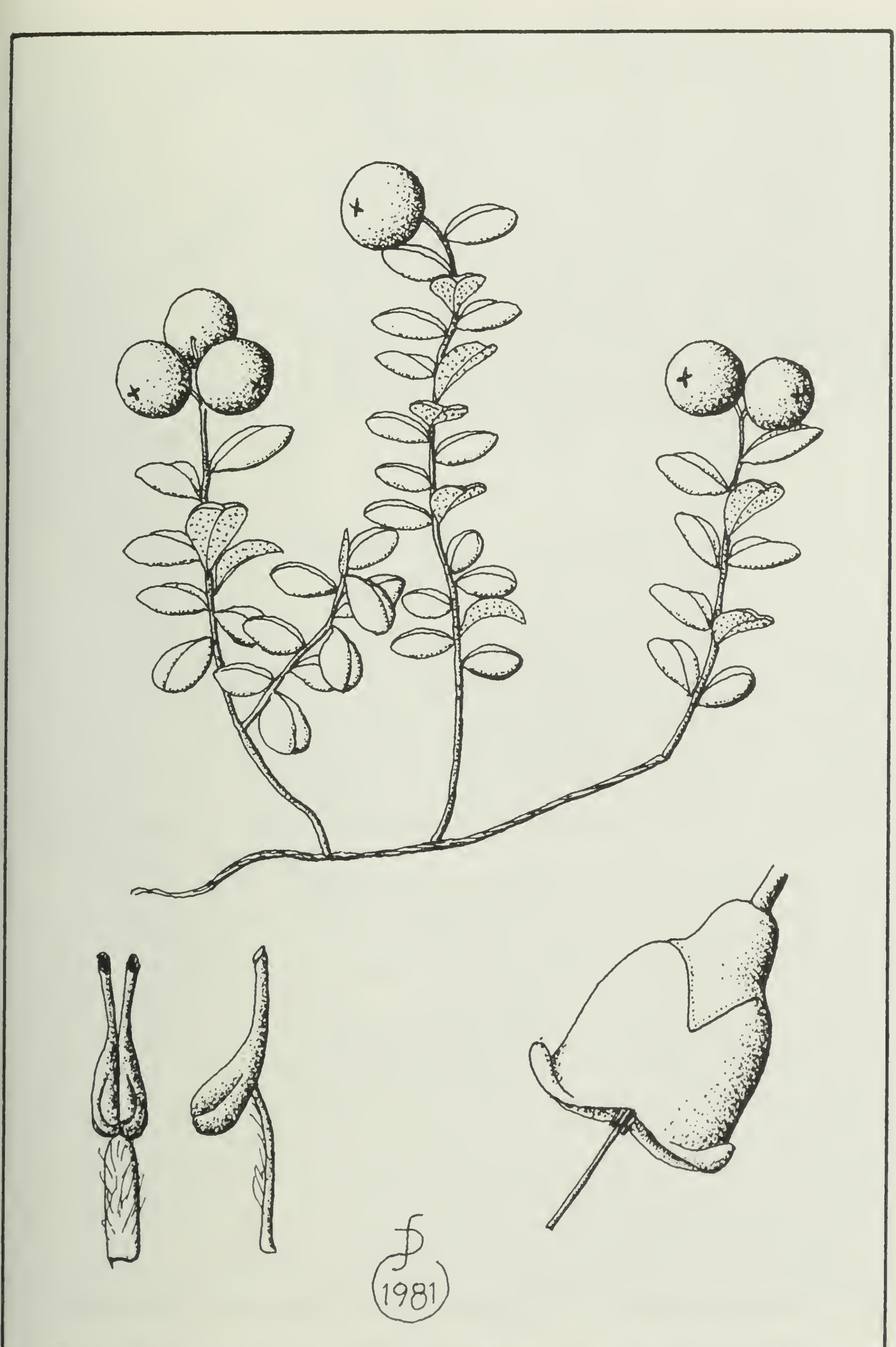

Fig. 47 *Vaccinium vitis-idaea*; habit, flower, and stamen.

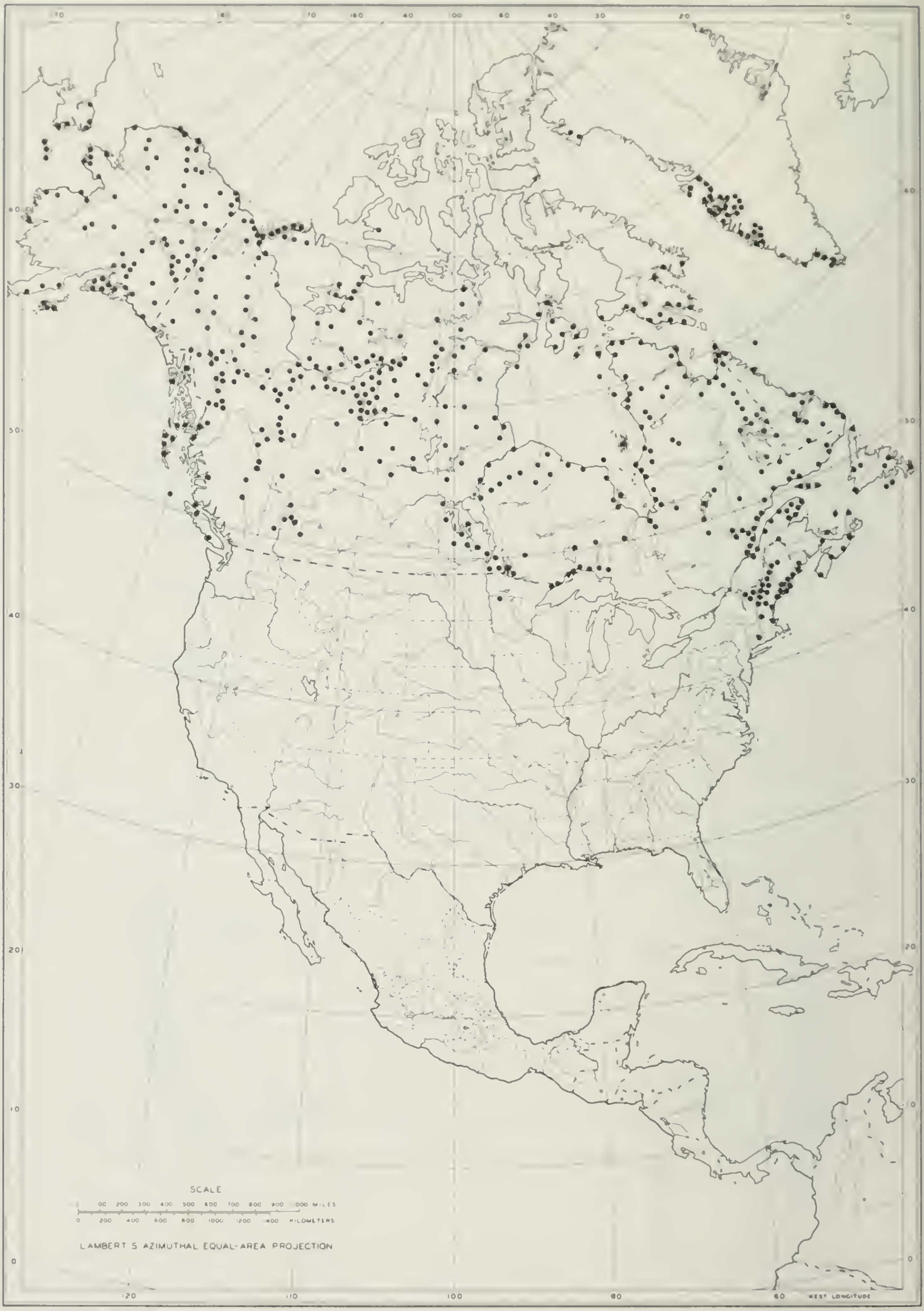

Fig. 48 North American distribution of *V. vitis-idaea* Linnaeus.

been documented extensively. Smith (in Rees's *Cyclopedia* 1817) stated that cowberries made an excellent jelly, both for colds and sore throats and for eating with roast beef, as the Swedes still do. According to Low (1896) the cowberry is the most important berry in northern Labrador, especially about the Hamilton and Big rivers, where it is plentiful. Indians gather it in large quantities after a sharp frost for use during the long winter, throughout which the berries keep perfectly and help counteract the ill effects of the constant meat diet. Porsild (1937) regarded *V. vitis-idaea* as a valuable antiscorbutic because of its high vitamin C content. Turner (1978) reported that the Niska and probably the Slave and Athabaska Indians gathered the berries, boiled them, and mixed them with oil for storage. For additional references and information on use, see Hall and Shay (1981).

Vaccinium sect. *Vaccinium*

This monotypic section includes circumboreal and arctic or alpine shrubs that possess the following features: twigs of the current season pale green and terete; leaves deciduous; flowers in small clusters of 2–3, often reduced to a single flower, but always from a scaly bud on wood of the previous season; calyx more or less articulated with pedicel; calyx lobes usually 4; corolla urceolate, usually 4-merous; stamens usually 8; filaments glabrous; sacs awned; ovary usually 4-celled.

Traditionally, sect. *Vaccinium* has been included in sect. *Myrtillus* sensu Koch (1837) or Dumortier (1827) or sect. *Euvaccinium* A. Gray (1848). However, more recent students of the Ericaceae, such as Sleumer (1941), Camp (1944, 1945), and Stevens (1969), have found this arrangement untenable because sect. *Myrtillus* s.s. is strictly 5-merous and has 10 stamens; the calyx is continuous with the pedicel, and (more importantly) the plant bears solitary flowers in the axils of leaves on branches of the current season. Indeed, Stevens (1969) has argued that sect. *Vaccinium* is superficially similar to sect. *Cyanococcus*, although in the former the ovary is 5-loculed, anthers are awned, leaves have well-developed lignification of the midrib bundle, and the corolla has no stomata. Nevertheless, tetraploid plants of *V. uliginosum* cross successfully with *V. angustifolium* (Vander Kloet 1977*c*) and with *V. corymbosum* (United States Department of Agriculture, unpublished data) both members of sect. *Cyanococcus*.

Both Sleumer (1941) and Stevens (1969) state that sect. *Vaccinium* is 5-merous. But Palser (1961) and more recently Warr (1981) have found that most of the North American material is 4-merous. A few 3-merous, 5-merous, or even 6-merous flowers may be found on 4-merous plants, but on the whole the so-called 5-merous plants possess most of this variation. It is exceedingly difficult to find a strictly 5-merous plant (i.e., one with 5 calyx lobes, 5 corolla lobes, 10 stamens and an ovary with 5 locules); usually one of the whorls has one less or one more segment (Warr 1981).

As in sect. *Cyanococcus*, sect. *Polycodium*, and sect. *Oxycoccus*, so also in sect. *Vaccinium*: the number of species that ought to be included in the section has been the source of considerable taxonomic dispute. Löve and Löve (1965, 1966) and Löve and Boscaiu (1966) have consistently argued that at the very least the different ploidy levels ought to be given specific rank. However, Young (1970) found that, on a worldwide basis, there seems to be no clear-cut morphological discontinuity among the races of *V. uliginosum*; because there were not enough chromosome data on which to base these correlations, he treated the various morphological races as subspecies. Subsequently, Warr (1981) found that there was no correlation between floral features and the vegetative features on which Young's (1970) subspecies are primarily based, and he could not link the number of floral segments with ploidy level. Warr therefore concluded that his data supported the concept of a single polymorphic species comprising diploid, tetraploid, and probably several hexaploid populations. In eastern North America, known diploids intermingle with the tetraploids at the lower latitudes. Above 60°N the diploids are encountered much more frequently, and above 70°N tetraploids appear to be very rare. However, along the Pacific coast, Young (1970) found the ploidy level to be quite variable, with the diploids ($n = 12$) being rare.

In order to bring the nomenclatural type of the genus in line with the Linnaean concept of *Vaccinium*, I recently proposed a change of lectotype from *V. myrtillus* to *V. uliginosum* (Vander Kloet 1981).

Vaccinium uliginosum Linnaeus

Description: Shrubs (3)12–40(70) cm high, procumbent to rhizomatous and erect, forming dense mats or open extensive colonies. Twigs of the current season pale green, glabrous or very short pubescent. Leaves deciduous, orbicular, ovate, obovate to narrowly elliptical, 3–7 mm wide, 8–14 mm long, green above, pale or glaucous beneath, glabrous, puberulent or short pubescent throughout; margin entire. Calyx and pedicel pale green; lobes 4(5,6) usually distinct, glabrous. Corolla cylindrical, 3–4 mm long, white or pink; lobes 4(5,6,7). Stamens 8(10); filaments glabrous; anther sacs awned; pollen tetrads 38–44 µm in diameter. Berry (3)4(5,6)-loculed, blue and glaucous, 6–8 mm in diameter; nutlet approximately 1 mm long. Chromosome numbers $2n = 24, 48, 72$, and possibly 36 (Young 1970) (Fig. 49).

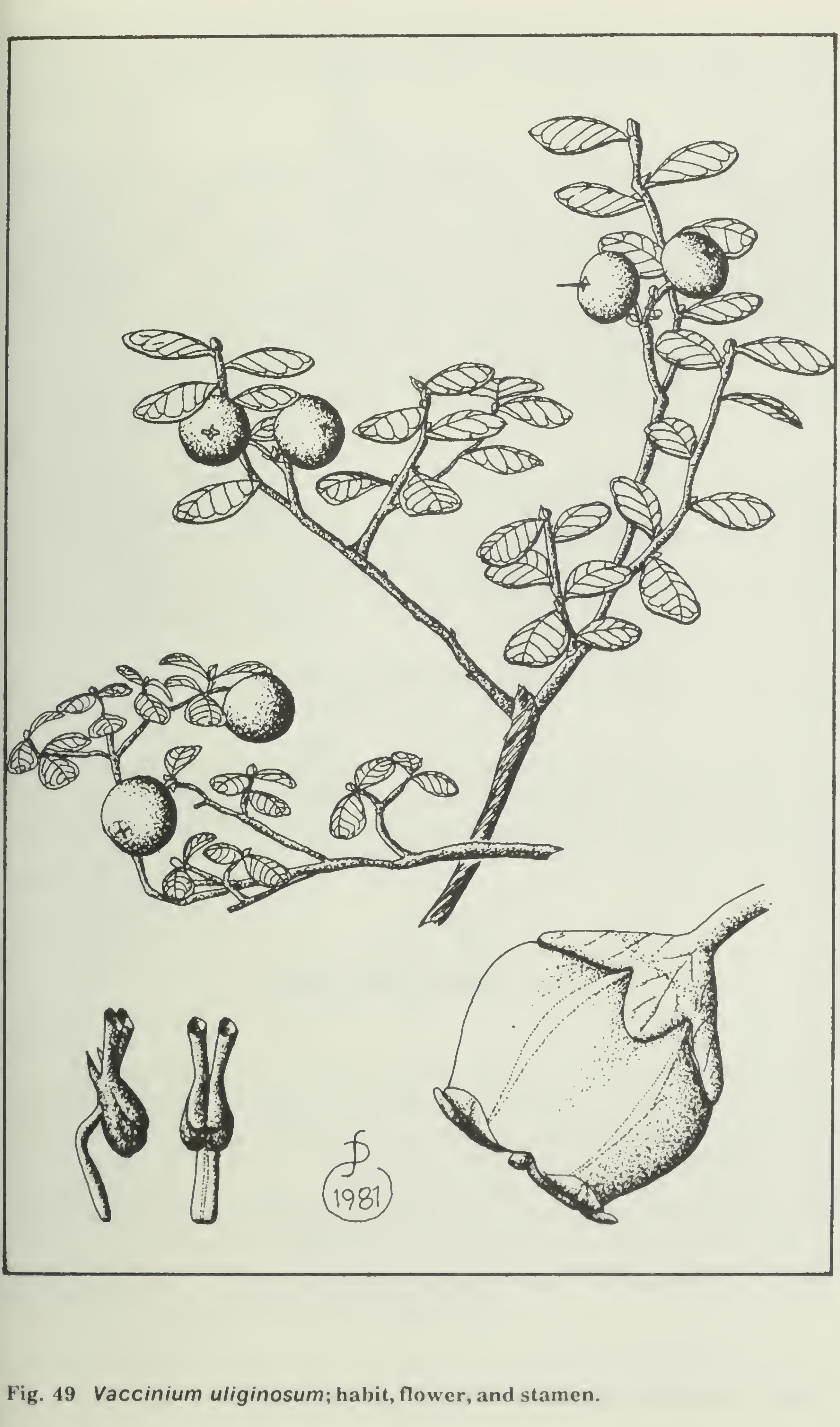

Fig. 49 *Vaccinium uliginosum*; habit, flower, and stamen.

Fig. 50 North American distribution of *V. uliginosum* Linnaeus.

Type locality: Sweden. Type at LINN! This specimen, No. 497.3, has flowers which are apparently 4-merous and are borne on very short racemes.

Range: In North America, *V. uliginosum* is transcontinental between 60°N and 70°N latitude; further north, however, the species is quite rare, especially in the Queen Elizabeth Islands. To the southwest, the species is found as far as northern California and northeastern Utah. The summits of the White Mountains of New Hampshire form its southernmost limit (Fig. 50). Ashley (1972), Miller and Thompson (1979) as well as Miller and Benninghoff (1969) present fossil evidence that *V. uliginosum* occurred at lower elevations or slightly to the south of its current range during the later stages of the Pleistocene.

Habitat: *V. uliginosum* occurs in acidic soils (pH 3.5–6.2 in 25 soils tested), dry or wet, organic or inorganic. Habitats include open alpine shrubberies, talus slopes, exposed outcroppings, eskers, moraines, headlands, high moors, muskegs, bogs, lichen woodlots, and low tundra. The species is also tolerant of high copper concentrations (DiLabio and Rencz 1980).

Common names: Ground hurts (Newfoundland), bilberry, tundra bilberry, alpine bilberry, bog bilberry.

Economic importance and use: Casual usage by the Inuit, who ate the fruit raw or stored it frozen or in seal oil, has been documented extensively (see Part 1). Genes for coldhardiness and resistance to stem diseases may make the species useful for horticultural breeding experiments (Moore 1965).

Vaccinium sect. *Myrtillus*

Species referred to this section share a number of features. Flowers are borne singly in the axils of the lowermost leaves of the vegetative shoot. The pedicel is continuous with the calyx tubes; the calyx has 5 lobes, often very poorly developed or even sinuate. The corolla is globose, lobes 5, very small. The flowers have 10 stamens; the filaments are glabrous, and the anther sacs bear long dorsal awns. The berry is 5-loculed. Perennating buds have 2 scales that are partly fused. Stomata tend to occur on both sides of the leaves, which scarcely if ever persist for more than 1 year.

The 10 species that comprise sect. *Myrtillus* share several juvenile foliage characteristics: the first shoots that arise from between the cotyledons have thick, persistent leaves with serrated margins and are glandular beneath (see for example Fig. 51). Apart from *V. geminiflorum*, the deciduous habit and mature foliage does not appear until the second or third set of eophylls is produced (Vander Kloet 1983*d*). Indeed, in *V. parvifolium* the mature leaf form may not be expressed until the plant is 3–4 years old and up to 50 cm high. Both Camp (1942*b*) and Szczawinski (1962) were aware of this phenomenon in *V. parvifolium*, and the latter made allowances for it in his key to the species of sect. *Myrtillus*.

These juvenile features, in conjunction with strong similarities in flower shape and structure and the lack of morphological differentiation in sibling species in the "caespitosa" and the "myrtillus" complex (Camp 1942*b*) might suggest a homogeneous group of rather recent origin. But the distributional data argue against it. Table 11, which lists the ranges of the 10 species, shows that several species are almost circumboreal, several comprise disjunct populations (the remnants of a former circumboreal range), and the rest are rather narrowly distributed endemics. The distributional data suggest an ancient group undergoing secondary radiation along the Pacific Rim. It could be argued that the way in which the flowers are disposed (singly in the axils of the lowermost leaves of the shoot) represents the primitive floral condition in the genus. From this primitive arrangement, the racemose inflorescences are derived (Fig. 9).

The mode of speciation for the North American taxa of sect. *Myrtillus* has been described by Camp (1942*b*), but his view is highly speculative and will not be repeated here. Viable experimental hybrids between species in this section can be produced readily and hybrids have been found in the wild. *V. nubigenum* Fernald refers to a series of F_1 and F_2 hybrids between *V. caespitosum* Michaux and *V. ovalifolium* Smith, as well as their backcrosses. For a detailed discussion of this hybrid, see Camp (1942*b*, pp. 229–231).

Both Mount Seymour in North Vancouver and the Forbidden Plateau on Vancouver Island exhibit diverse hybrids. At the latter site, hybridization among *V. deliciosum*, *V. ovalifolium*, and *V. caespitosum* has produced interesting plants. The former site has hybrids whose parentage is a curious mixture of *V. deliciosum*, *V. ovalifolium*, and *V. membranaceum*. However, two random samples, taken at 1100 msm on Mount Seymour in July 1980, showed that the hybrids occur only at a rate of 6%. Hybrids were not encountered among the plants sampled at 900 and 1000 msm.

A conservative taxonomic treatment for the North American members of sect. *Myrtillus* (Keys 4 and 5; Table 12) is warranted until such time as the Japanese populations can be assessed and additional experimental data on the North American species can be gathered.

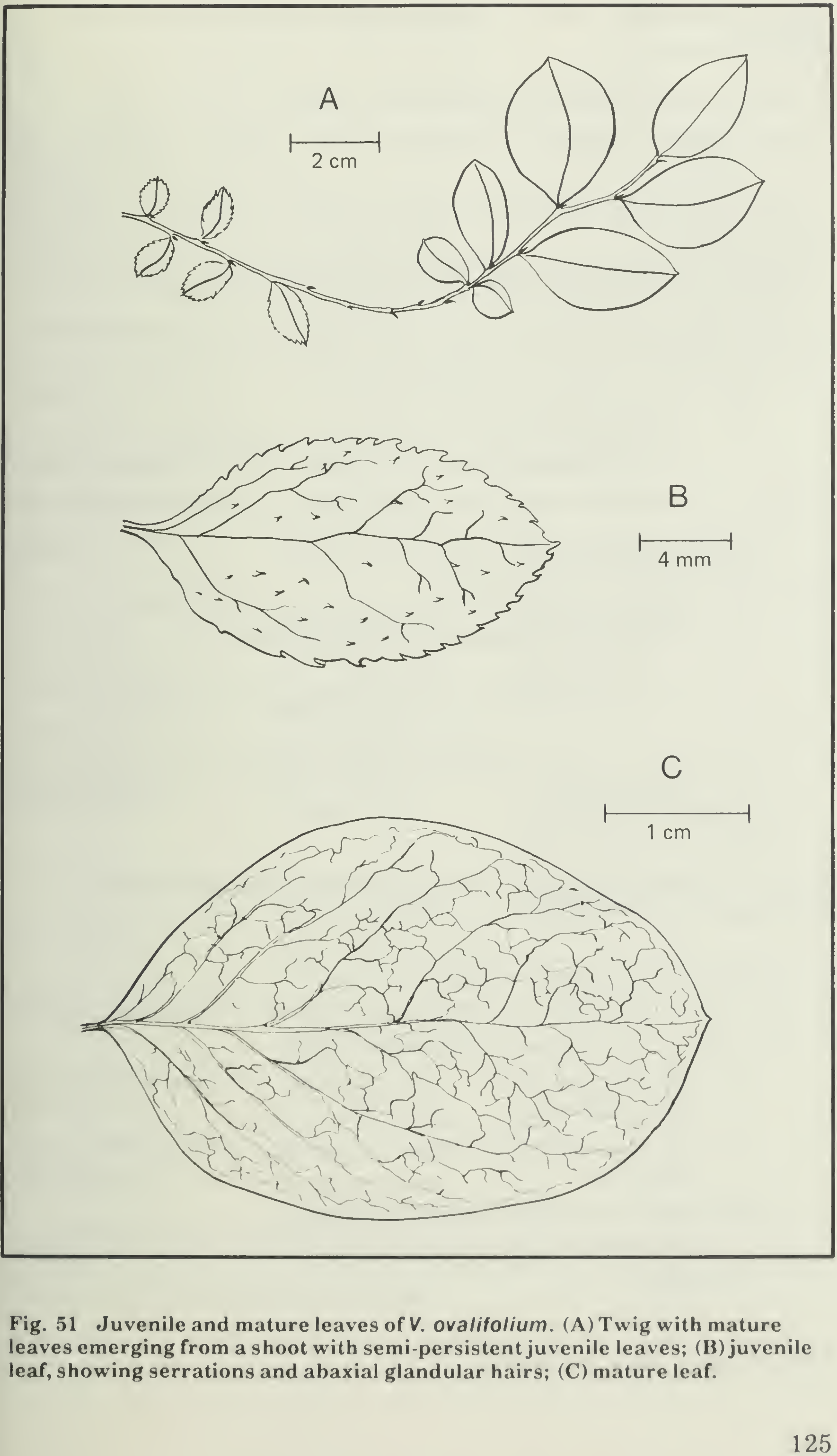

Fig. 51 Juvenile and mature leaves of *V. ovalifolium*. (A) Twig with mature leaves emerging from a shoot with semi-persistent juvenile leaves; (B) juvenile leaf, showing serrations and abaxial glandular hairs; (C) mature leaf.

Key 4 Key to the North American species of *Vaccinium* sect. *Myrtillus**

1. Berries red; young twigs green and angular
    2. Shrubs colonial, 7–20 cm high; berries 4–6 mm in diameter .... *V. scoparium*
    2. Shrubs crown-forming, 1–3 m high; berries 7–9 mm in diameter .... *V. parvifolium*
1. Berries black, dull black, or blue and glaucous; young twigs more or less terete, infrequently green (except for *V. myrtillus*)
    3. Leaf margins sharply serrate throughout; blade glandular beneath
        4. Young twigs green and angular .... *V. myrtillus*
        4. Young twigs not green and more or less terete
            5. Leaves less than 10 mm wide .... *V. geminiflorum*
            5. Leaves more than 10 mm wide ... *V. membranaceum*
    3. Leaf margins entire or partially serrate; blade usually eglandular beneath
        6. Shrubs 3–50 cm high, forming extensive colonies
            7. Plants glaucous; twigs usually glabrous .... *V. deliciosum*
            7. Plants green or pale green; twigs puberulent .... *V. caespitosum*
        6. Shrubs more than 50 cm high, forming small clumps, or monopodial .... *V. ovalifolium*

Key 5 Alternative key to the North American species of *Vaccinium* sect. *Myrtillus**

1. Young twigs angular and green
    2. Leaves glandular beneath; berries black or blue *V. myrtillus*
    2. Leaves eglandular beneath; berries red
        3. Shrubs colonial, 7–20 cm high; berries 4–6 mm in diameter .... *V. scoparium*
        3. Shrubs crown-forming, 1–3 m high; berries 7–9 mm in diameter .... *V. parvifolium*
1. Young twigs more or less terete, not green
    4. Leaf margins sharply serrate throughout; blade glandular beneath

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*For best results, use fresh material.

    5. Leaves less than 10 mm wide .... *V. geminiflorum*
    5. Leaves more than 10 mm wide .... *V. membranaceum*
4. Leaf margins entire or partly serrate; blade usually eglandular beneath
    6. Shrubs 3–50 cm high, forming extensive colonies; leaves 6–17 mm wide
        7. Plants glaucous; twigs usually glabrous; berries 9–11 mm in diameter .... *V. deliciosum*
        7. Plants green or pale green; twigs puberulent; berries 6–8 mm in diameter .... *V caespitosum*
    6. Shrubs more than 50 cm high, crown-forming or in small clumps; leaves 16–24 mm wide .... *V. ovalifolium*

Table 11 Distribution of *Vaccinium* sect. *Myrtillus*

Taxon	Approximate continuous range	Disjunct populations
V. myrtillus	circumboreal (Europe–Asia)	interior Rocky Mountains*
V. caespitosum	circumboreal (N America–Rocky Mountains)	Mexico
V. ovalifolium	Pacific Rim (Japan–Ore.)	S. Dak., shore of Lake Superior, NE Que., Cape Breton, and Nfld.
V. membranaceum	Rocky Mountains (N.W.T.–Utah)	Lake Superior (N Mich.)
V. scoparium	Rocky Mountains (B.C.–Colo.)	–
V. parvifolium	Pacific Coast (Alaska–N Calif.)	–
V. deliciosum	Pacific Coast (B.C.–N Calif.)	interior Rocky Mountains
V. geminiflorum	Central America	–
V. yatabei	Central Japan	–
V. shikokianum	N.–central Japan	–

*Greenland population an ancient introduction.

Table 12 Comparison of selected attributes of the eight North American species of *Vaccinium* sect. *Myrtillus*

Taxon characteristics	*V. myrtillus*	*V. caespitosum*	*V. ovalifolium*	*V. membranaceum*
Plant height (cm)	31 ± 14	9 ± 4	84 ± 34	79 ± 34
Growth habit	colonial	colonial	clumped (crown-forming)	clumps, colonial (crown-forming)
Angularity of twigs of the current season	angular	more or less terete	more or less terete	more or less terete
Abaxial leaf blade				
Color	green	green or pale	pale or glaucous	green
Pubescence	glandular	more or less eglandular	more or less glabrous	glandular
Leaf width (mm)	9 ± 2	9 ± 3	18 ± 2	17 ± 6
Leaf margin	serrate	more or less serrate	more or less entire	serrate
Berry color	black	blue and glaucous; dull black	blue and glaucous; dull black	black
Berry diameter (mm)	8 ± 1	7 ± 1	9 ± 1	10 ± 1
Seed weight(mg/100 seeds)	25 ± 4	22 ± 4	29 ± 15	30 ± 3

(continued)

Table 12 Comparison of selected attributes of the eight North American species of *Vaccinium* sect. *Myrtillus* (*concluded*)

Taxon characteristics	*V. deliciosum*	*V. parvifolium*	*V. scoparium*	*V. geminiflorum*
Plant height (cm)	17 ± 11	192 ± 68	13 ± 6	10 ± 4
Growth habit	colonial	crown-forming	colonial	colonial
Angularity of twigs of the current season	more or less terete	angular	angular	more or less terete
Abaxial leaf blade				
Color	glaucous	pale	pale	green
Pubescence	more or less glabrous	very short pubescence	glabrous	glabrous
Leaf width (mm)	13 ± 4	11 ± 3	5 ± 1	4 ± 1
Leaf margin	more or less serrate	entire	finely serrate	serrate
Berry color	blue and glaucous	red	red	dull black
Berry diameter (mm)	10 ± 1	8 ± 1	5 ± 1	6 ± 1
Seed weight (mg/100 seeds)	32 ± 4	33 ± 5	13 ± 3	20 ± 3

Vaccinium myrtillus Linnaeus

Description: Shrubs (10)17–45(60) cm high, rhizomatous, forming open colonies. Twigs green, conspicuously 3-angled, glabrous. Leaves broadly elliptical or ovate, 7–11 mm wide, 19–27 mm long, green, laxly glandular beneath; margin serrate. Calyx continuous with pedicel, green and glabrous; lobes very small or even absent; margin of the calyx tube merely sinuate. Corolla globose, pink, cream, or greenish white, 5–7 mm wide, 3–5 mm long; lobes very small. Filaments glabrous; anther sacs awned; pollen tetrads 34–38 µm in diameter. Berry purple black, usually not glaucous, 7–9 mm in diameter; nutlet approximately 1 mm long. Chromosome number $2n = 24$ (Fig. 52).

Type locality: Sweden. Type at LINN! Specimen No. 497.1.

Range: Europe and Asia (Popova 1972; Bush and Bobrov 1967). In North America, the species occupies two areas in the Rocky Mountains: one in southeastern British Columbia to central Oregon; the other in central Colorado, adjacent Utah, north-central New Mexico, and southern Arizona (Fig. 53). The Greenland populations are thought to be ancient European introductions (Löve and Löve 1963).

Habitat: Open, moist coniferous woods such as lodgepole pine woods, hummocky seepage slopes, and moraines above 1600 msm in the Rocky Mountains and Cascades. The biology of the European populations has been described by Ritchie (1955) and Flower-Ellis (1971).

Common names: Whortleberry, mountain bilberry, dwarf bilberry.

Economic importance and use: In North America the berries were used extensively by the Kootenay, Carrier, and Shuswap Indian tribes (Turner 1978). Throughout northern Europe and Siberia, the berries are gathered in large quantities for jellies, pie fillings, and jams (Smith 1817; Bush and Bobrov 1967).

Vaccinium caespitosum Michaux

Description: Shrubs (3)5–13(60) cm high, forming mats from superficial rhizomes. Twigs somewhat angled to terete, yellow green, reddish green, or rarely brown, finely pubescent or rarely glabrous. Leaves usually oblanceolate, sometimes obovate or even narrowly elliptical, 6–12 mm wide, 12–26 mm long, green, usually glabrous

Fig. 52 *Vaccinium myrtillus*; habit, flower, and stamen.

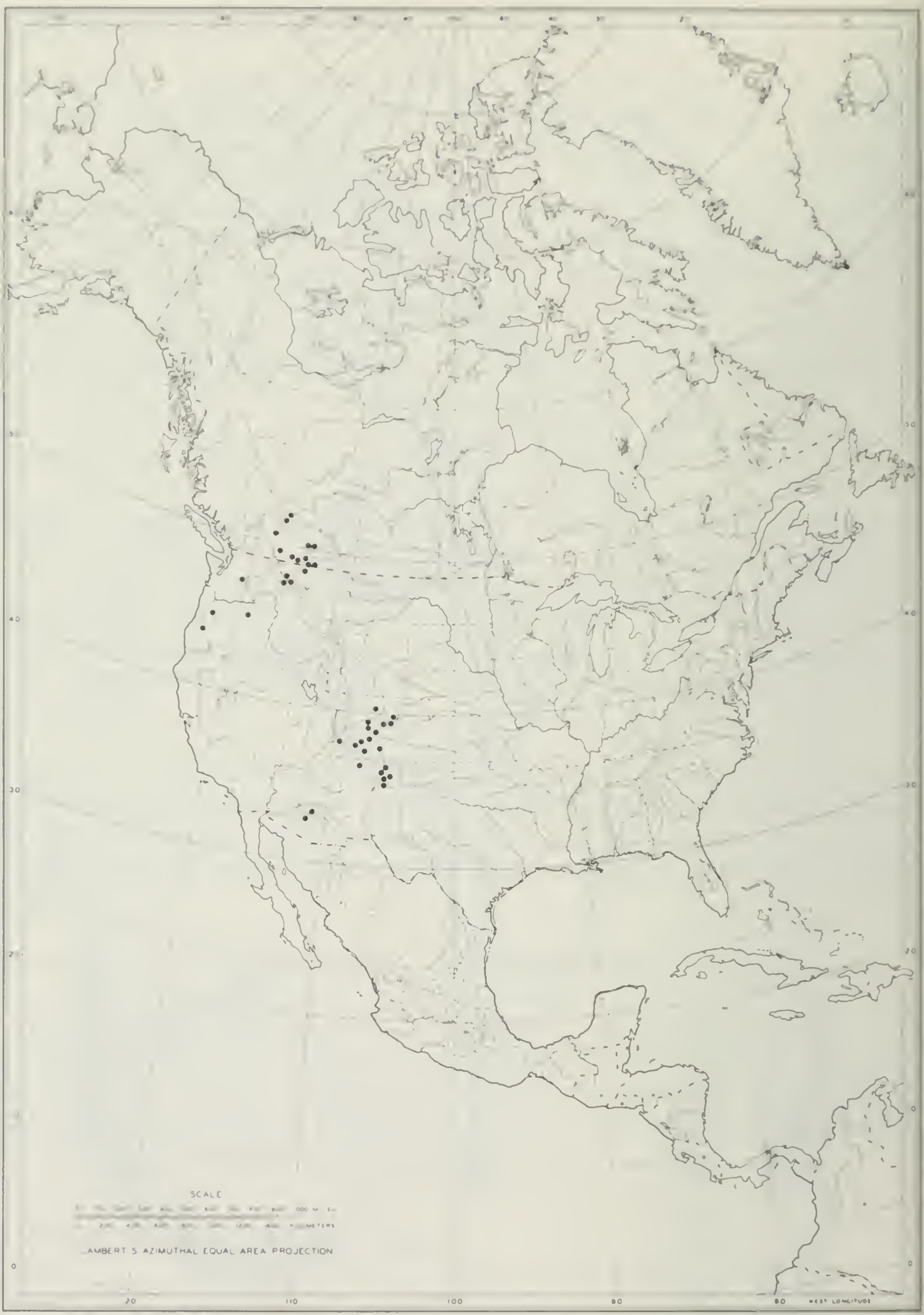

Fig. 53 North American distribution of *V. myrtillus* Linnaeus

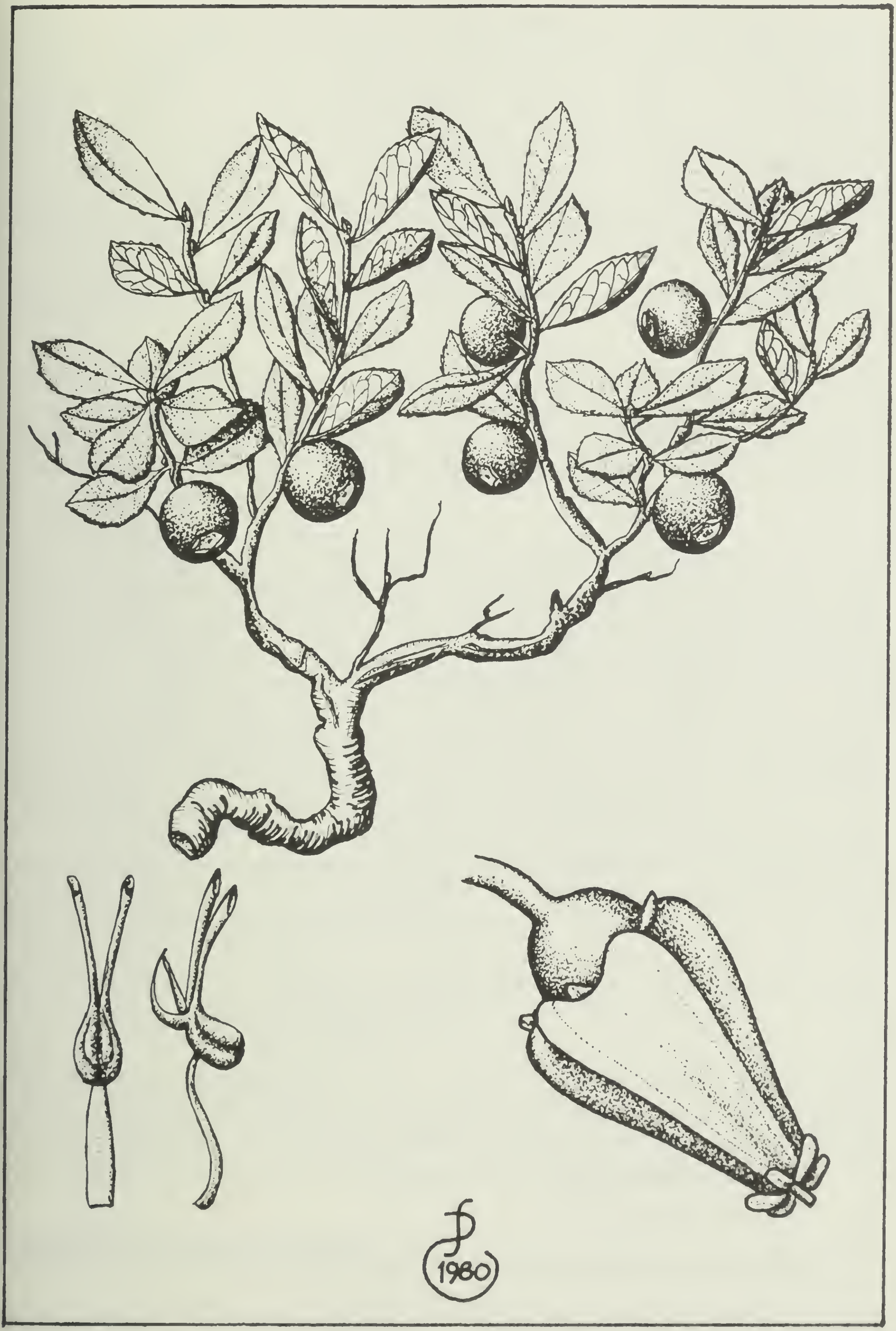

Fig. 54 *Vaccinium caespitosum*; habit, flower, and stamen.

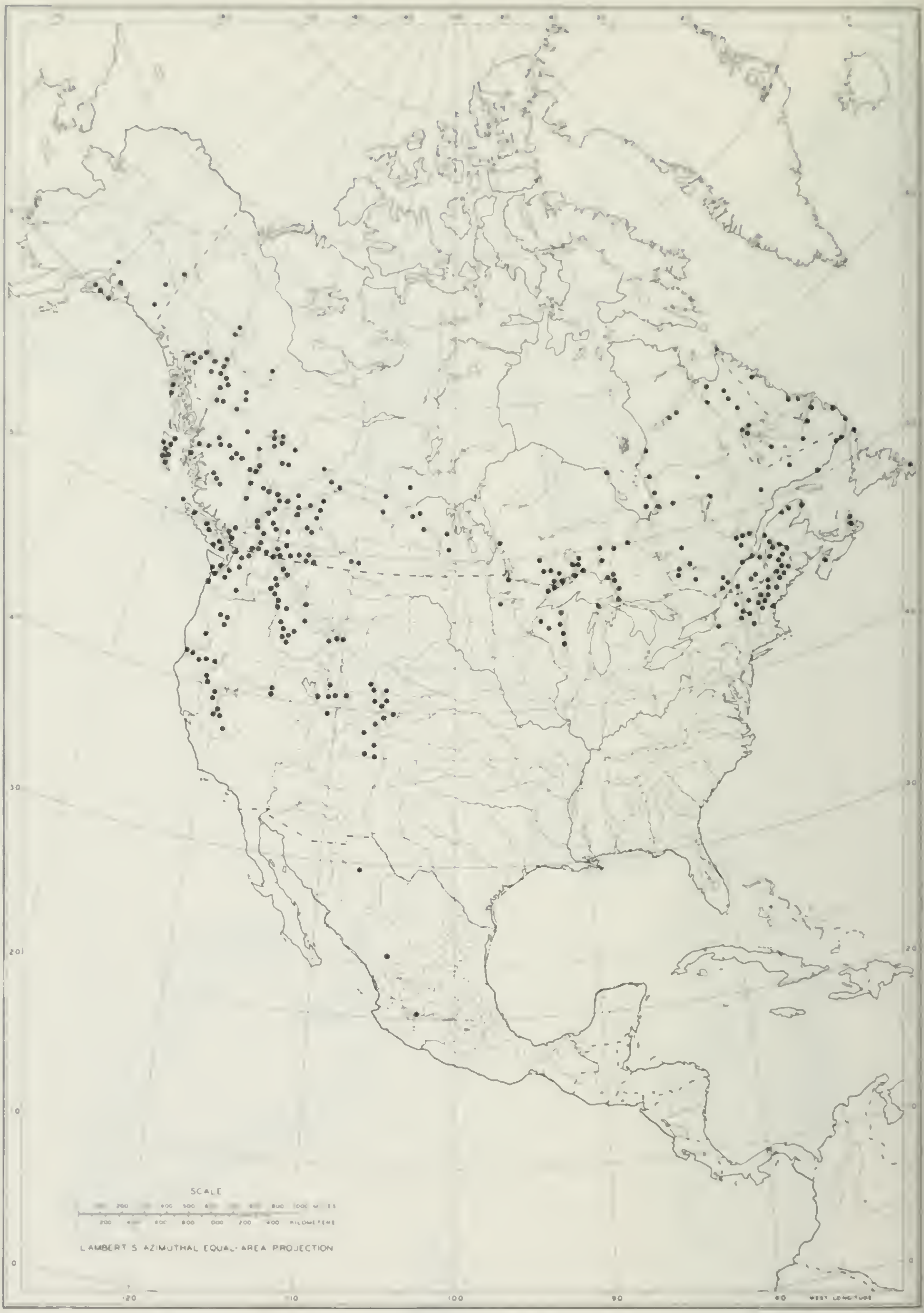

Fig. 55 Distribution of *V. caespitosum* Michaux.

above, paler and usually somewhat glandular beneath; margin usually serrulate from the apex to at least the middle of the blade. Calyx continuous with pedicel, pale green and glabrous; lobes very small. Corolla cylindrical to globose, 3–5 mm wide, 4–7 mm long, white, white with pink striping, or pink. Filaments glabrous; anther sacs awned; pollen tetrads 27–33 μm in diameter. Berry usually blue and glaucous, rarely dull black, 5–9 mm in diameter; nutlet approximately 1 mm long. Chromosome number $2n = 24$ (Fig. 54).

Type locality: In northern America, chiefly around Hudson Bay. Type at P!

Range: Alaska to Newfoundland, southward along the Atlantic Seaboard to southern Maine and southern Vermont; in the west, south to the Colorado–New Mexico border; in the coastal mountains to central California. One disjunct population occurs in central Mexico at approximately 20°N (Fig. 55).

Habitat: Dry or wet acidic sites from sea level to 3800 msm. In mountainous regions, it has been found along rocky ledges, subalpine talus slopes, wet meadows, edges of valley glaciers, alpine sedge meadows, alpine herb mats, edges of coniferous forests, subalpine heaths, and open pine woods. Elsewhere it has been found along rocky or sandy lakeshores, rocky, gravelly, or sandy river banks, gravel terraces, headlands, low arctic tundra, jack pine outcroppings, open spruce woods, barrens, dry oak woods, dry pine woods, poplar regeneration forests, road cuts, and railway rights of way.

Fernald (1900) was the first to record the dichotomy in habitat preference of *V. caespitosum* when he found this species not only on the highest alpine summits in New England, Maine, and eastern Canada but also at several lowland sites.

Common names: Dwarf blueberry, dwarf bilberry, dwarf whortleberry, dwarf huckleberry.

Economic importance and use: According to Turner (1978) the Indians of interior British Columbia extensively harvested these rather small but sweet berries; the berries were commonly traded near Quesnel during the early days of European settlement.

Vaccinium ovalifolium Smith

Description: Shrubs (30)50–90(400) cm high, crown-forming, suckering when injured, forming small clumps, rarely forming extensive colonies. Twigs yellow green or golden brown, terete to conspicuously angled, glaucous and glabrous to pubescent in lines.

Leaves ovate to elliptical, rarely obovate, 16–20 mm wide, 25–39 mm long; upper surface pale green and usually glabrous; lower surface paler or glaucous, usually glabrous, occasionally pubescent or glandular, or both, especially along the abaxial midvein; margin entire to obscurely serrate. Calyx continuous with pedicel, pale green, glabrous; calyx lobes very small or absent. Corolla globose, occasionally urceolate, 4–5 mm wide, 5–7 mm long, pink, bronzy pink, or greenish white; lobes 5, small. Filaments glabrous; anther sacs awned; pollen tetrads 33–49 µm in diameter. Berry blue and glaucous, dull purplish black or black, 8–10 mm in diameter; nutlet approximately 1 mm long. Chromosome number $2n = 24, 48$ (Fig. 56).

Type locality: West coast of North America. Type at BM, chosen by Vander Kloet in 1981. Type is No. 78, collected by Menzies and annotated by him as "*Vaccinium* fruct. nigrum, frequent on the west coast of N. America 1787–1788." This sheet is a collection of three twigs, two of which have neither leaves nor flowers; the third has only pale, glabrous, eglandular leaves, 24–32 mm wide, 40–50 mm long, with entire margins. There are additional specimens of *V. ovalifolium*, sent by Menzies to Banks, both at the BM and in the Smithian collection at LINN; the latter (Nos. 678.4, 678.10, and 678.11) consist of a number of twigs from the Menzies collections given to Smith by Banks. Although Smith's description of *V. ovalifolium* is based on all these collections, these specimens probably should not be the type, since Smith stated that *V. ovalifolium* was "brought by Mr. Menzies from the west coast of North America," and the only sheet that contains that information in Menzies's own hand is at BM. Sir Joseph Banks's specimens of *V. ovalifolium*, collected in 1766 at Croque, Nfld., and drawn by G.D. Ehret, should not qualify as the lectotype since they are not cited by Smith nor are they incorporated in his description of the taxon.

Range: In North America, from the Aleutian Islands, south along the Pacific coast to south central Oregon and inland to northern Idaho. Disjunct populations occur in the Black Hills region of South Dakota, on the shores of Lake Superior, in the Gaspé Peninsula, on the north shore of the St. Lawrence River, on Cape Breton Island, and on the island of Newfoundland (Fig. 57).

Habitat: Moist or mesic coniferous woods from sea level to 2100 msm; also a large number of transitional habitats adjacent to these coniferous stands, such as cut-over coniferous woods, verges of road cuts, margins of coniferous woods, and peaty slopes. In the mountains, *V. ovalifolium* is also encountered in subalpine shrubberies and ravines. Inland, the species is usually found in somewhat drier and more open habitats than along the coast.

Fig. 56 *Vaccinium ovalifolium*; habit, flower, and stamen.

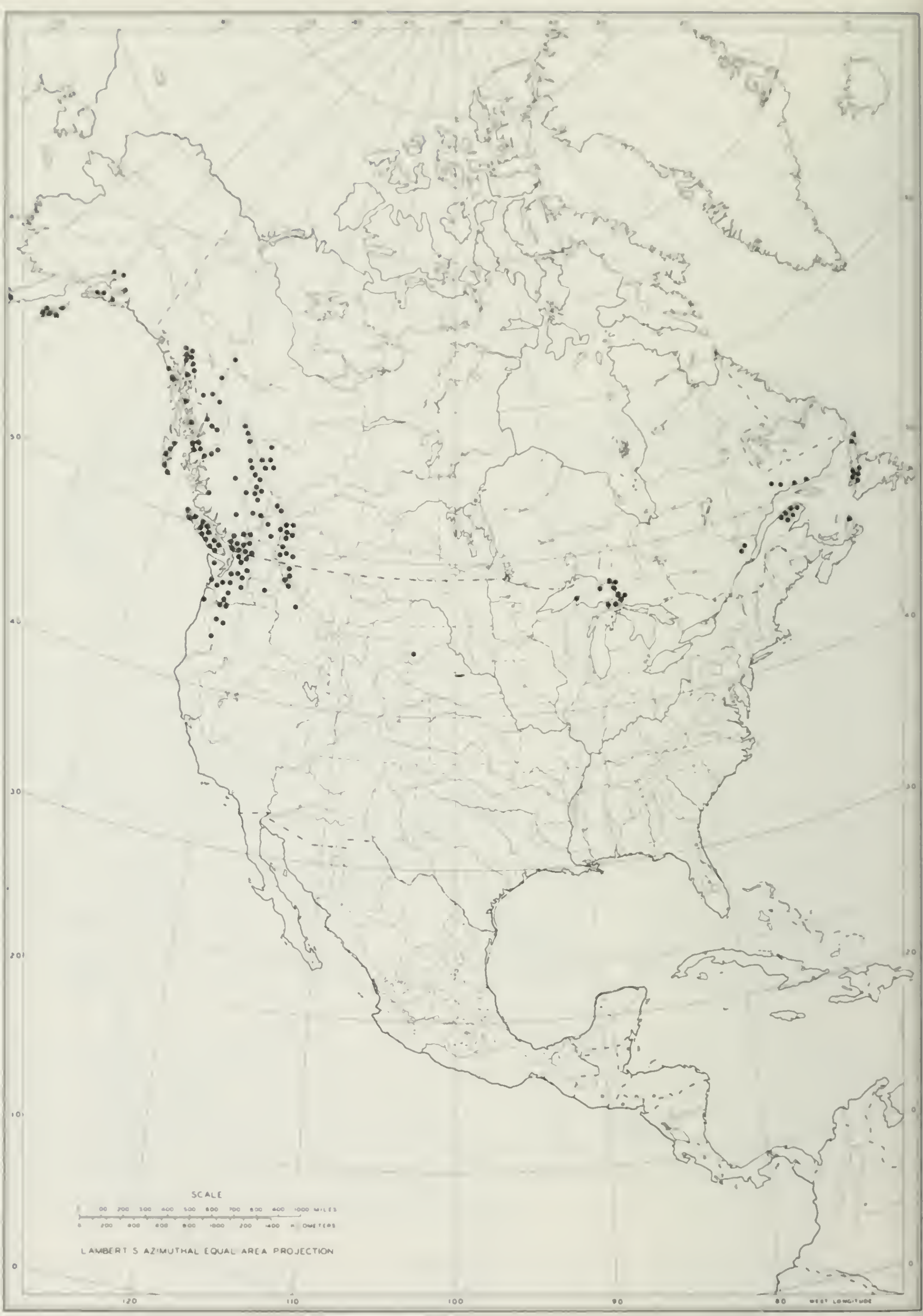

Fig. 57 Distribution of *V. ovalifolium* Small.

Common names: Oval-leaved bilberry, oval-leaved blueberry, highbush blueberry (Nfld.), Alaska blueberry.

Economic importance and use: Indian tribes of both interior and coastal British Columbia used the berries of *V. ovalifolium*, but since the berries are gritty and tend to rot easily, they were in general not as popular as those of the other species in sect. *Myrtillus*.

Vaccinium membranaceum Douglas ex Hooker

Description: Shrub (20)45–110(300) cm high, forming small to extensive clumps, rarely crown-forming. Twigs of the current season yellow green or reddish green, terete to slightly angled, glabrous to pubescent in lines. Leaves broadly elliptical to ovate, 11–23 mm wide, 25–50 mm long, usually green on both sides, glandular beneath; margin sharply serrate. Calyx continuous with pedicel, green and glabrous; calyx obscurely lobed. Corolla globose to urceolate, 5–7 mm wide, 3–5 mm long, white to creamy or yellowish pink. Filaments glabrous; anther sacs awned; pollen tetrads 36–40 µm in diameter. Berry shining black, dull black, or deep purple, 9–11 mm in diameter; nutlet approximately 1 mm long. Chromosome number $2n = 48$ (Fig. 58).

Type locality: Summit of the high mountains of the Grand Rapids and valleys on the west side of the Rocky Mountains. Type at K, chosen by Vander Kloet in 1981. The type specimen is on a sheet marked "Herb. Hook. 1867" (which holds fragments of six twigs belonging to four taxa) and is located on the top right. This small branch has leaves about 16 mm wide and 33 mm long, glandular beneath, with sharply serrate margins. This shoot bears dark purple fruit and the twigs of the current season are more or less angular and glabrous. To the left of this twig is an annotation in Douglas's hand: "*Vaccinium membranaceum* D.D. (on the summits of the high mountains of the grand rapids and valleys of the Rocky Mountains); fruit common, large brown and is greatly esteemed by the natives."

Range: Rocky Mountains from southwestern Northwest Territories south to northern California and northern Utah. Disjunct populations occur in northern Michigan and central Arizona (Fig. 59).

Habitat: Coniferous woods, especially cut-over stands, talus slopes, subalpine fir forests, and alpine heaths from 900 to 3500 msm.

Common names: Mountain bilberry, mountain huckleberry, twin-leaved huckleberry.

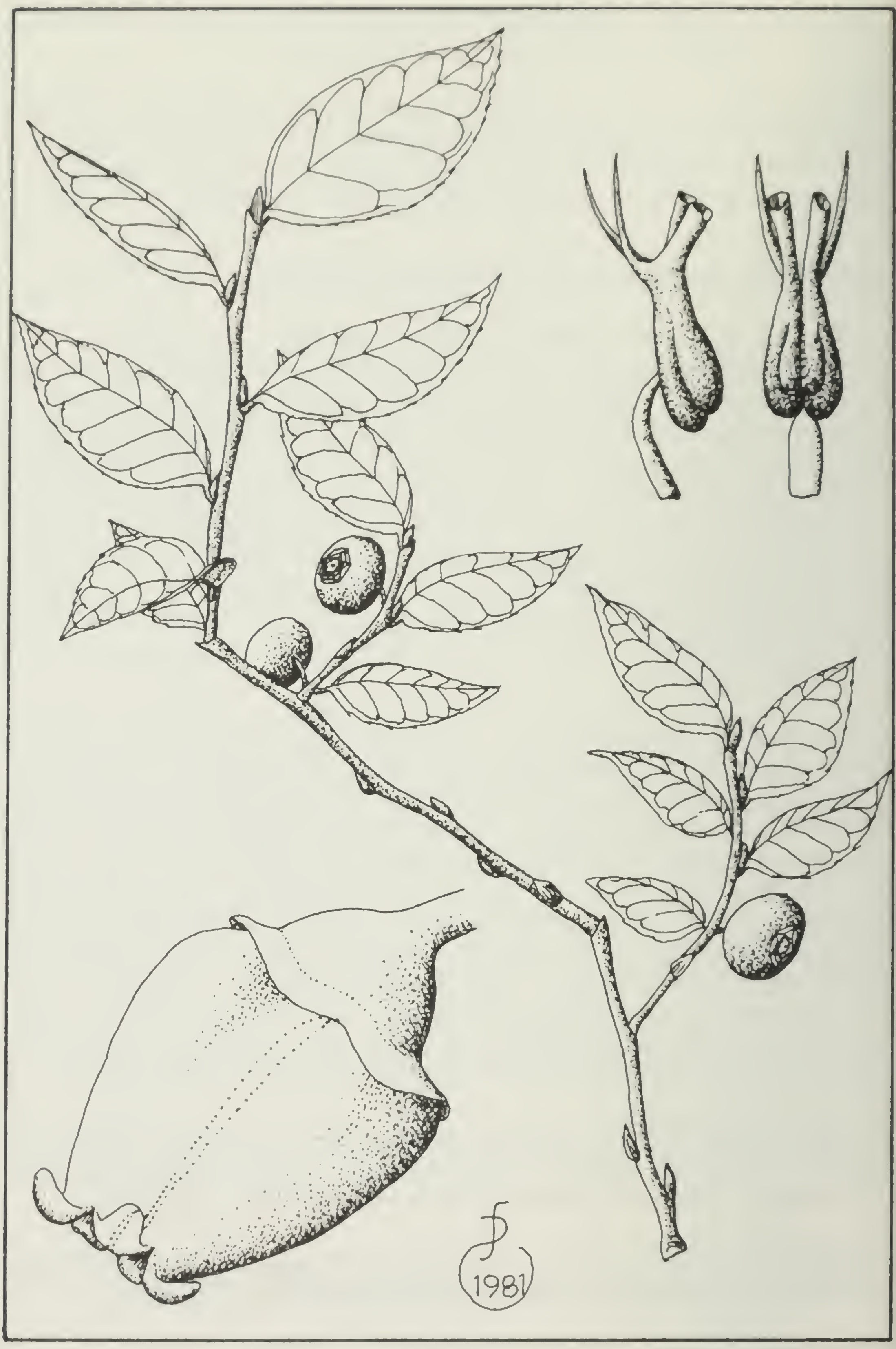

Fig. 58 *Vaccinium membranaceum*; habit, flower, and stamen.

Fig. 59 **Distribution of** ***V. membranaceum*** **Douglas ex Hooker.**

Economic importance and use: Early collectors such as Douglas (BM, MSS 1825) and Tolmie (BM, MSS 1836), as well as modern compilers such as Turner (1975, 1978), have all reported that Indians of both the coast and interior of the Pacific region harvested large quantities of mountain bilberries. The berries ripened from July to September, depending on elevation, and as the season progressed women would venture higher into the mountains to pick them. Formerly the berries were eaten raw or dried for future use; currently they are canned, frozen, or made into jam, but only on a limited basis. The Okanagan tribe used to sell them to the European settlers.

Vaccinium deliciosum Piper

Description: Shrubs (3)7–28(60) cm high, rhizomatous, forming mats and extensive open colonies. Twigs glaucous, occasionally green, more or less terete, rarely angled, glabrous, or rarely pubescent in lines, or puberulent. Leaves obovate, oblanceolate, or rarely elliptical, 9–17 mm wide, 17–35 mm long, usually glaucous and glabrous; margin usually serrate for at least the upper two-thirds of the leaf. Calyx continuous with pedicel, glaucous and glabrous; lobes indistinct or shallowly 5-lobed. Corolla globose to globular–urceolate, 5–7 mm wide, 4–6 mm long, pink or creamy pink. Filaments glabrous; anther sacs awned; pollen tetrads 37–43 µm in diameter. Berry blue and glaucous, rarely dull black, 9–11 mm in diameter; nutlet approximately 1 mm long. Chromosome number $2n = 48$ (Fig. 60).

Type locality: Mount Rainier, Wash. Type at GH! Allen 17 in 1896.

Range: Pacific coastal mountain ranges from southern British Columbia to central Oregon. Isolated stations occur in northern and eastern British Columbia, eastern Idaho, and northern California (Fig. 61).

Habitat: Alpine meadows, subalpine coniferous woods, and talus slopes along the coast from 600 to 2000 msm. Pojar (1974) has described the biology of the species in some detail.

Common names: Cascade bilberry, blue huckleberry.

Economic importance and use: None reported, possibly because this species is often confused with *V. caespitosum*. Its large, very palatable berry would certainly have been gathered by those Indian women who followed the seasonal progression of *V. membranaceum*.

Fig. 60 *Vaccinium deliciosum*; habit, flower, and stamen.

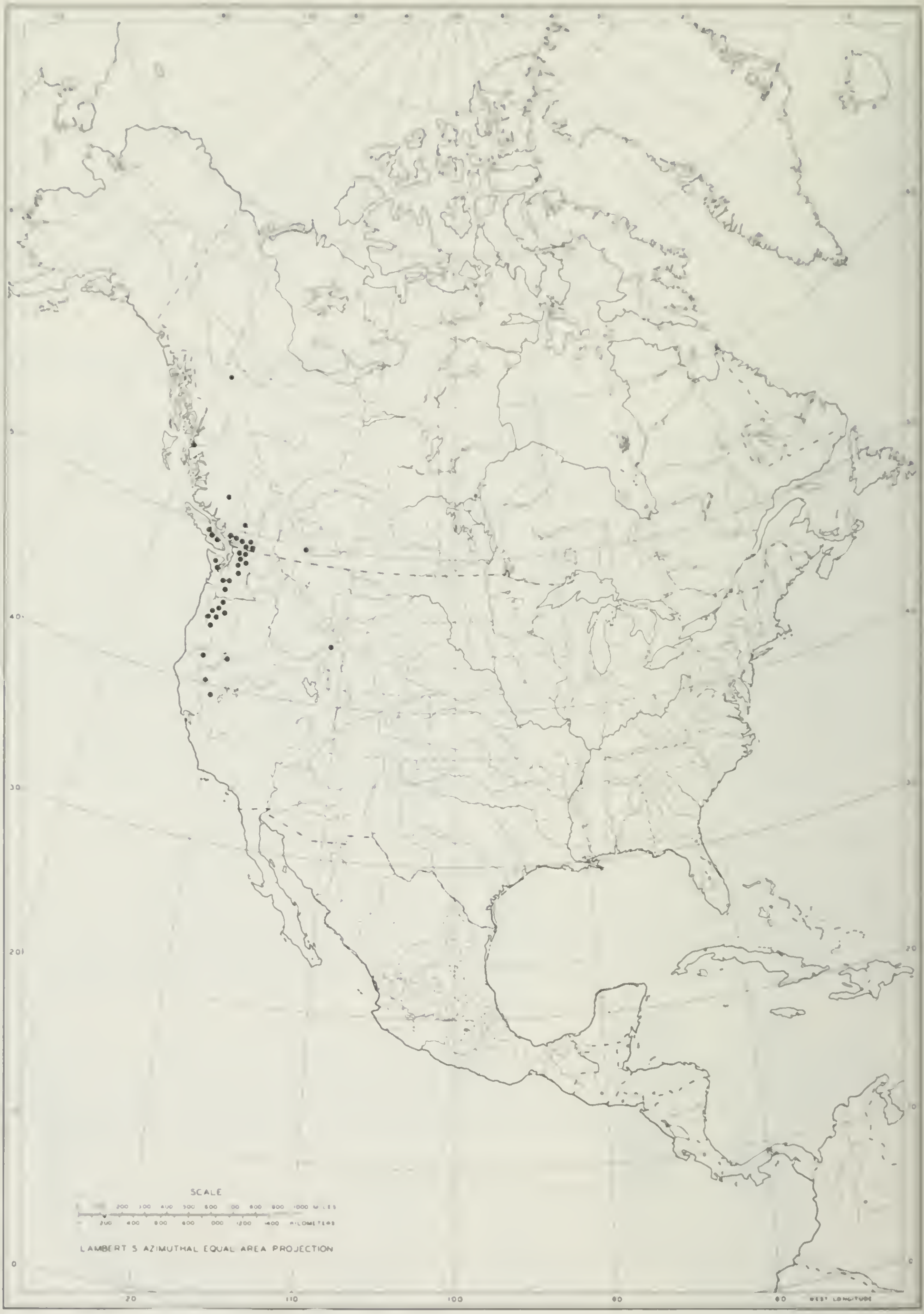

Fig. 61 Distribution of *V. deliciosum* Piper.

Vaccinium parvifolium Smith

Description: Shrubs (100)124–260(700) cm high, crown-forming, occasionally suckering when injured. Twigs of the current season green, sharply angled, glabrous or minutely puberulent in lines. Leaves oval to oblong–elliptical, 8–14 mm wide, 13–25 mm long, usually glabrous above and very short pubescent below; margin entire. Calyx continuous with the pedicel, pale green and glabrous; lobes 5, distinct and rather broad. Corolla globose to urceolate, 3–4 mm wide, 4–6 mm long, waxy, pink to yellowish green. Filaments glabrous; anther sacs awned; pollen tetrads 32–36 µm in diameter. Berry red, occasionally faintly glaucous, 7–9 mm in diameter; nutlet approximately 1 mm long. Chromosome number $2n = 24$ (Fig. 62).

Type locality: Nootka, west coast of North America. Type at BM. Chosen by Vander Kloet in 1981; annotation reads "A. Menzies 79, in 1787." This sheet has six twigs from three different shrubs of *V. parvifolium*, and I have designated twig number 5 as the nomenclatural type. This specimen has angular twigs; leaves pale, 7–9 mm wide, 12–18 mm long, glabrous above, very short pubescent beneath; margins entire. Sheet number 79 was annotated by Menzies as "*Vaccinium*, grows to 8 or 10 feet high; this plant produces red fruit of a pleasing acid taste which makes excellent tarts. Preferable in my opinion to the well known cranberries." The reason for choosing a BM specimen as type rather than the Smith collection at LINN is the same as that presented for *V. ovalifolium*.

Range: Pacific coast from 60°N, 140°W (Alaska) to northern California, inland to southeastern British Columbia (Fig. 63).

Habitat: Coniferous woods, especially along the edges of clearings, and lumber trail verges in cut-over coniferous woods. Rotting trunks and stumps in these coniferous woods are invariably occupied by either *Gaultheria shallon* Pursh or *V. parvifolium*, or both, from sea level up to 400 msm near the coast, and in drier coniferous woods up to 1100 msm in the interior.

Common names: Red huckleberry, red bilberry.

Economic importance and use: *Vaccinium parvifolium* has some potential as an ornamental shrub. Ripe berries tend to persist on the shrub for at least 2 months, and some of its leaves turn a brilliant red in late autumn, contrasting with the light green branches. The berries may persist well into winter, when they are ruined by repeated heavy frosts. According to Turner (1975) all the coastal Indian tribes used and continue to use the berries of *V. parvifolium* in jams and preserves, often undertaking long expeditions to harvest them.

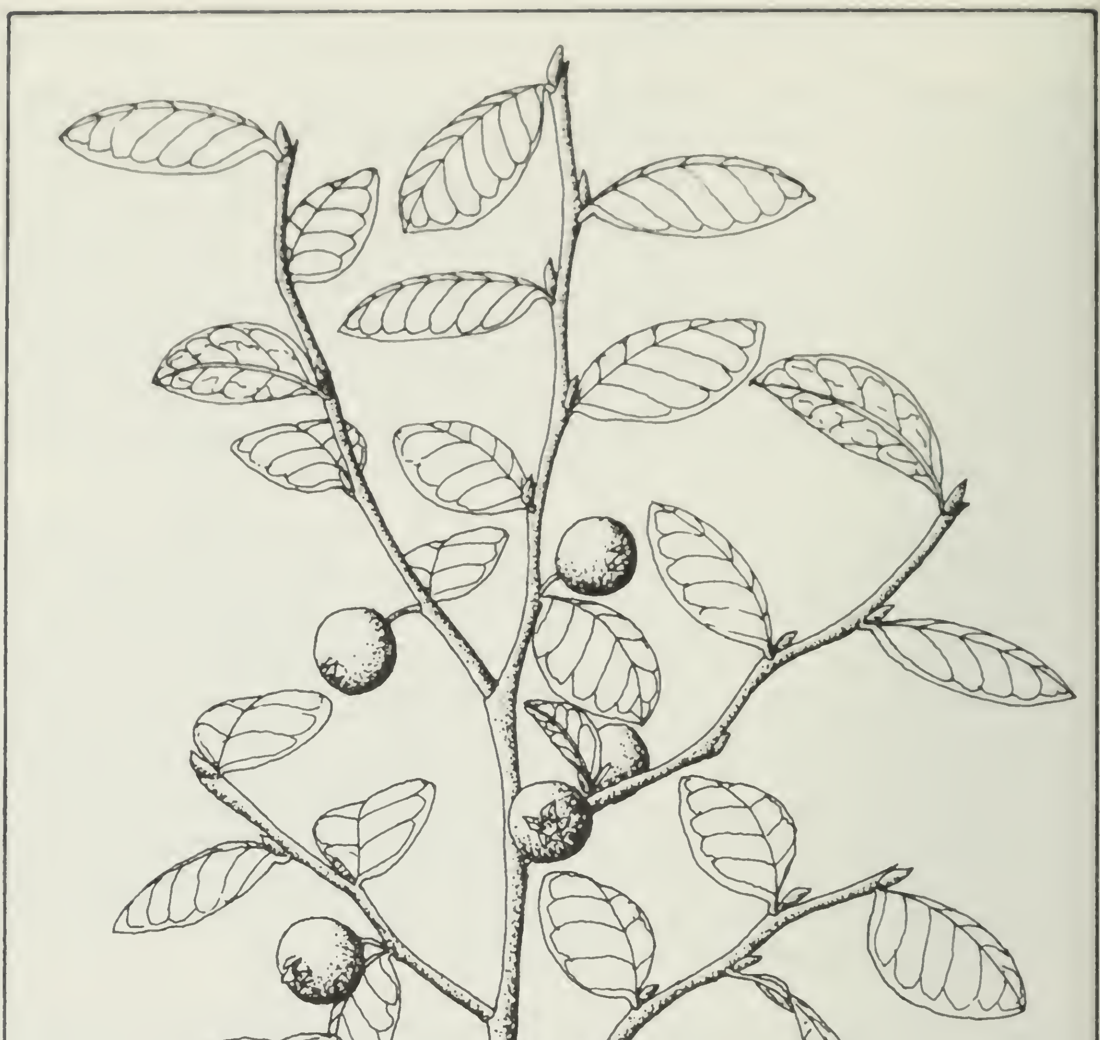

Fig. 62 *Vaccinium parvifolium*; habit, flower, and stamen.

Fig. 63 Distribution of *V. parvifolium* Small.

Vaccinium scoparium Leiberg ex Coville

Description: Shrubs (4)7–20(30) cm high, rhizomatous, forming extensive colonies. Twigs green, glabrous, angular; ultimate branches compact, often forming "broom-like" clumps or tufts. Leaves elliptical, lanceolate, or ovate–lanceolate, 4–6 mm wide, 7–11 mm long, pale green and glabrous beneath; margin finely serrulate. Calyx continuous with pedicel, pale green and glabrous; lobes obsolete. Corolla globose to urceolate, 3–4 mm wide, 3–4 mm long, pink. Filaments glabrous; anther sacs awned; pollen tetrads 25–29 µm in diameter. Berry red, 4–6 mm in diameter; nutlet approximately 1 mm long. Chromosome number $2n = 24$ (Fig. 64).

Type locality: Alpine woods near the Height of Land and Columbia Portage. Collected by Drummond. Type at K! In Herbarium Hooker.

Range: Southeastern British Columbia and adjacent Alberta, east to the Black Hills of South Dakota, and south to southwestern Colorado (Fig. 65). Calder and Taylor (1968) list this species for the Queen Charlotte Islands, but the specimens cited are sect. *Myrtillus* hybrids.

Habitat: Alpine and subalpine meadows, heaths, talus slopes, and moraines, as well as edges of subalpine coniferous forests at (780)1500–2400(3000) msm. The biology of *V. scoparium* has been described by Pojar (1974).

Common names: Grouseberry, dwarf red whortleberry, red alpine blueberry, small-leaved huckleberry.

Economic importance and use: The tiny red berries were gathered and eaten raw by the Kootenay, Okanagan, and Shuswap Indians (Turner 1978).

Vaccinium geminiflorum Humboldt, Bonpland, & Kunth

Description: Shrubs (3)6–14(17) cm high, rhizomatous, forming mats or colonies. Twigs purple green, scarcely angular, puberulent. Leaves more or less persistent, narrowly elliptical, 3–5 mm wide, 10–16 mm long, green, often sparsely glandular beneath; margin sharply serrate. Calyx continuous with pedicel, glabrous; lobes obsolete. Corolla globose–urceolate, occasionally cylindrical, 3–4 mm wide, 4–5 mm long, white to pink. Filaments glabrous; anther sacs awned; pollen tetrads 29–33 µm in diameter. Berry dull black, 5–7 mm in diameter; nutlet approximately 1 mm long. Chromosome number not known (Fig. 66).

Fig. 64 *Vaccinium scoparium*; habit, flower, and stamen.

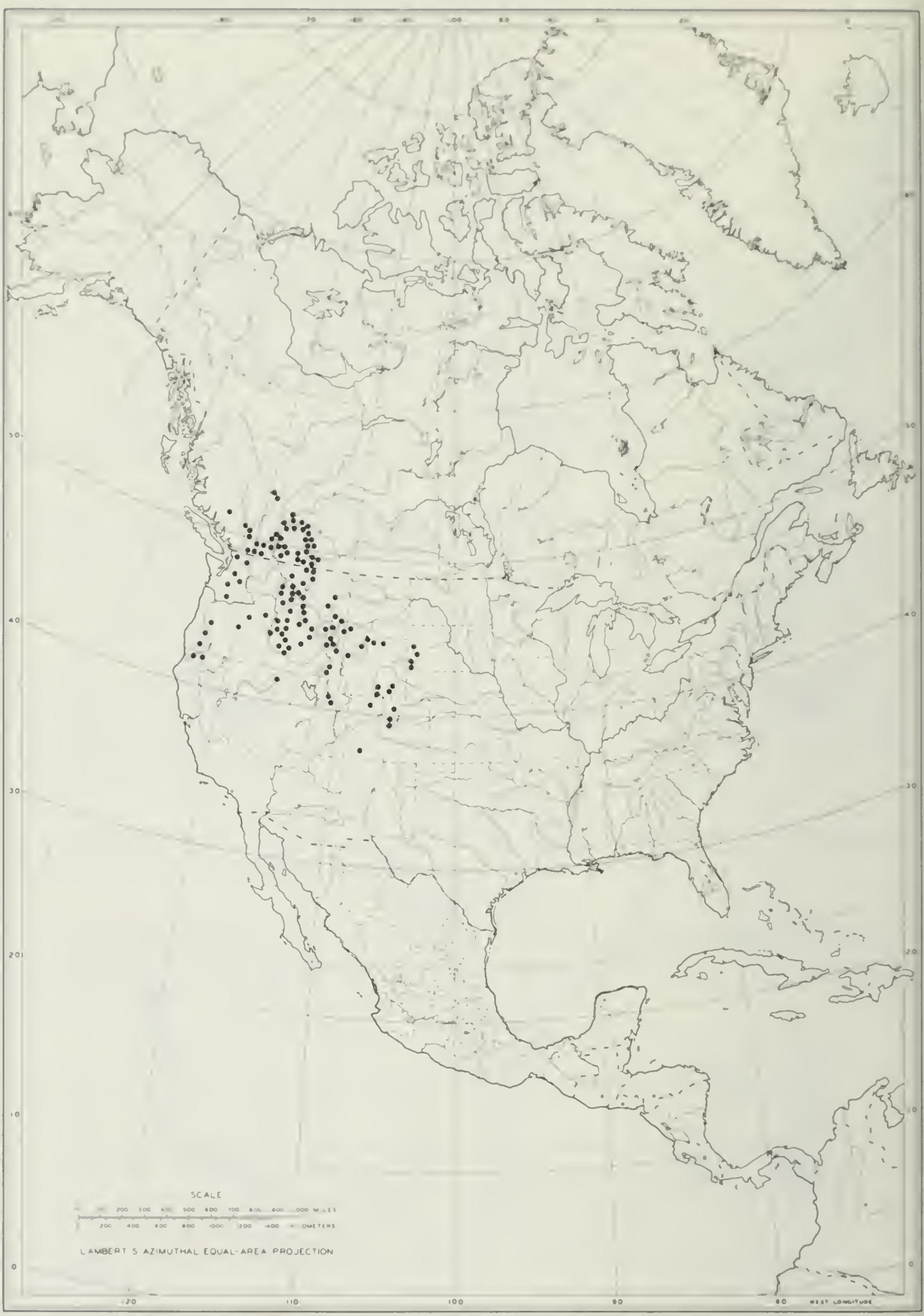

Fig. 65 Distribution of *V. scoparium* Leiberg ex Coville.

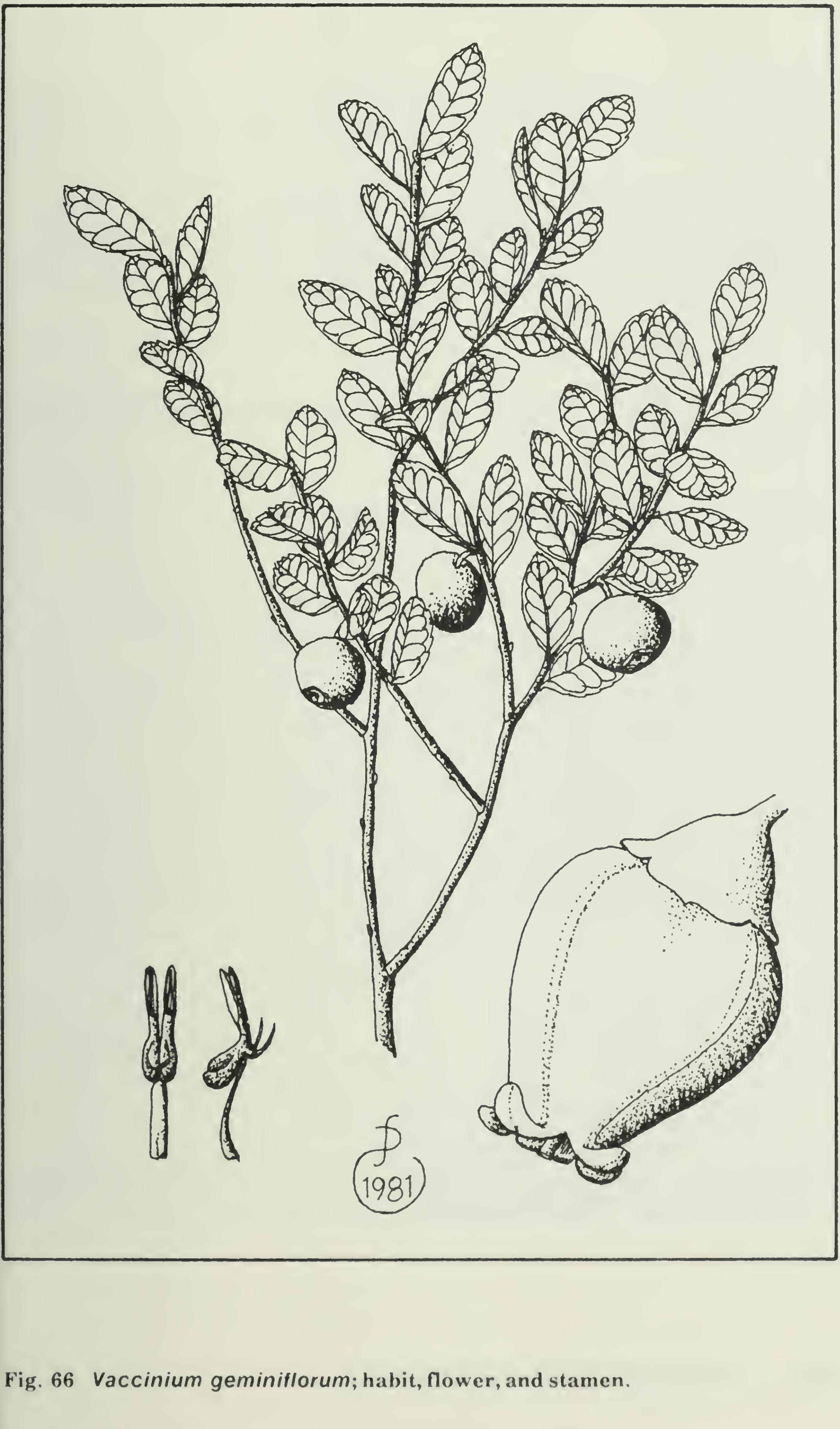

Fig. 66 *Vaccinium geminiflorum*; habit, flower, and stamen.

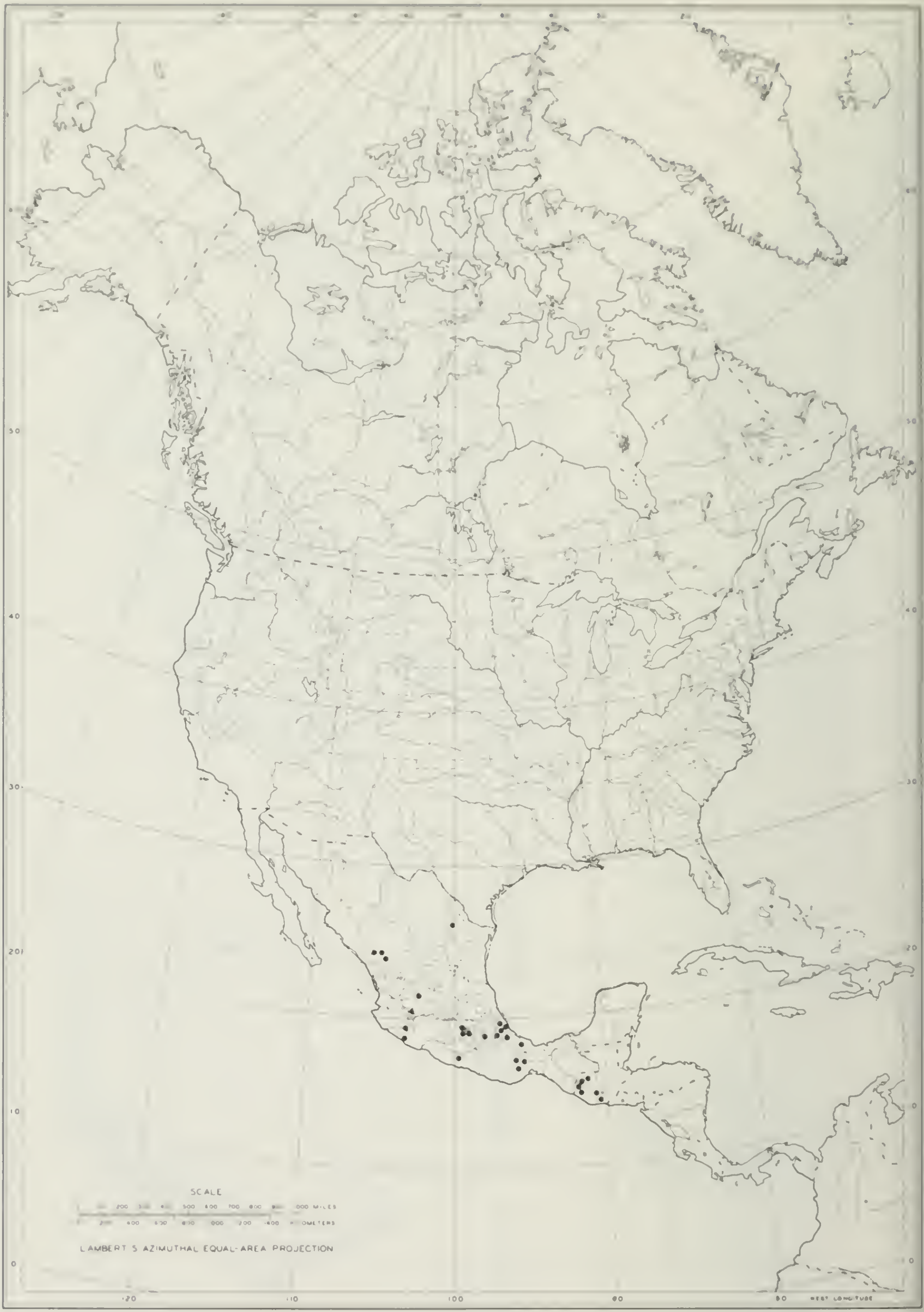

Fig. 67 Distribution of *V. geminiflorum* HBK.

Type locality: At 2500 msm, between Omitlan and Moran, Hidalgo, Mexico. Type at P!

Range: Central Mexico to the western highlands of Guatemala (Fig. 67). Camp (1942*b*) cited a specimen from Arizona, but it should be referred to *V. caespitosum*.

Habitat: Summits, rocky ledges, volcanic ash, crater rims, talus slopes, alpine meadows, and open pine woods from 1700 to 4500 msm. According to Camp (1942), below 3000 msm the leaves are persistent, whereas above 3000 msm they are deciduous.

Common name: Unknown.

Economic importance and use: None reported.

Vaccinium sect. *Pyxothamnus*

Vaccinium sect. *Pyxothamnus* is a Neotropical or subtropical section of evergreen shrubs that share several features. In the leaf axils, two types of perennating buds develop, floral and vegetative. These buds are covered with several scales and are dimorphic; the rotund floral bud is at least twice the size of the vegetative bud, and the flower buds are usually near the tip of the shoot. The inflorescence is racemose. Bracts are not persistent. The pedicel is articulated with the calyx. The corolla is 5-lobed and more or less urceolate. There are 8–10 stamens. The anther sacs may have short awns, which are sometimes reduced to papillae or even absent. The berry is 5-loculed. Stevens (1969) found that several species of sect. *Pyxothamnus* have spongy mesophyll that is thick walled, rigid, and lignified.

Aside from the North American *V. ovatum* Pursh, which has from time to time been put in sect. *Vitis-idaea* (see Rehder 1927), Sleumer (1941) placed three Central American species (*V. confertum* HBK, *V. consanguineum* Klotzsch, and *V. selerianum* [Loesen] Sleumer) and one Andean species (*V. floribundum* HBK) in his section *Pyxothamnus*. Since the distribution and biology of the last species are poorly known, both the classification and the evolution of sect. *Pyxothamnus* require more data. The possible relationship of sect. *Pyxothamnus* to sect. *Cyanococcus* has been discussed under the latter.

Vaccinium ovatum Pursh

Description: Shrubs (30)40–120(400) cm high, forming small clumps, rarely crown-forming or colonial. Twigs more or less terete, pilose (including the outer scales of the perennating scales when young). Leaves persistent, narrowly ovate, 8–12 mm wide, 21–29 mm long, dark green and lustrous above, pale and glandular beneath; margin sharply serrate. Calyx articulated with pedicel, pale and glabrous; lobes prominent. Corolla cylindrical or urceolate, 3–5 mm long, pinkish; lobes distinct. Filaments pubescent; anther sacs awnless or with short awns; pollen tetrads 32–34 μm in diameter. Berry blue and glaucous to dull black, 6–8 mm in diameter; nutlet approximately 1 mm long. Chromosome number $2n = 24$ (Fig. 68).

Type locality: West coast of North America. Type at LINN! Smithsonian collection 678.12.

Range: Along the Pacific coast from central British Columbia south to central California (Fig. 69).

Habitat: Coniferous forests along the coast, especially edges, clearings, and roadsides therein. Pojar (1974) has described the floral biology for this species in some detail.

Common names: Evergreen huckleberry, shot huckleberry, blackwinter huckleberry.

Economic importance and use: This shrub is often used as an ornamental and as ground cover in rhododendron plantings; in addition florists extensively use *V. ovatum* twigs in floral arrangements (Camp 1945). Coastal Indians picked the berries in late fall and even during December, when all other fresh fruit had disappeared (Turner 1975). The berries of *V. ovatum* tend to develop sporadically and when ripe tend to persist for a month or longer.

Fig. 68 *Vaccinium ovatum*; habit, flower, and stamen.

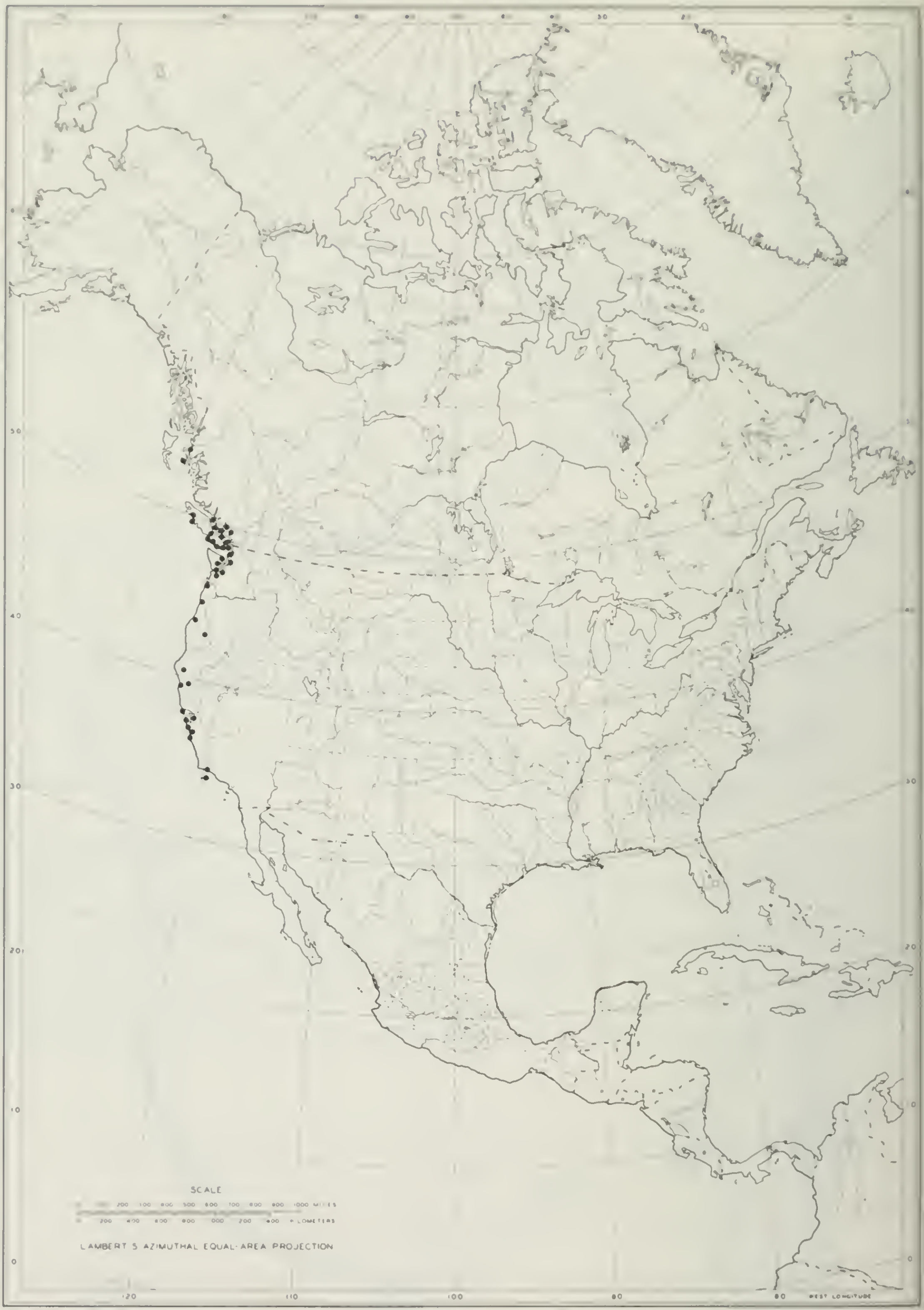

Fig. 69 Distribution of *V. ovatum* Pursh.

APPENDIX 1 Herbaria and collection sites

List of herbaria consulted

A	Arnold Arboretum, Harvard University, Cambridge, Mass.
ACAD	E.C. Smith Herbarium, Department of Biology, Acadia University, Wolfville, N.S.
ALTA	Herbarium, Department of Botany, University of Alberta, Edmonton, Alta.
BM	Herbarium, British Museum, London, U.K.
CAN	National Herbarium of Canada, National Museum of Natural Sciences, Ottawa, Ont.
DAO	Vascular Plant Herbarium, Biosystematics Research Centre, Agriculture Canada, Ottawa, Ont.
FLAS	Herbarium, Department of Botany, University of Florida, Gainesville, Fla.
GA	Herbarium, Botany Department, University of Georgia, Athens, Ga.
GH	Gray Herbarium, Harvard University, Cambridge, Mass.
K	Herbarium, Kew Gardens, London, U.K.
L	Rijksherbarium, Leiden, the Netherlands
LINN	Linnaean Society of London, Burlington House, London, U.K.
LL	Lundell Herbarium, Texas Research Foundation, Renner, Tex.
MICH	Herbarium, University of Michigan, Ann Arbor, Mich.
MIN	Herbarium, University of Minnesota, St. Paul, Minn.
MTMG	McGill University Herbarium, Macdonald College, Sainte-Anne-de-Bellevue, Que.
NCSC	Herbarium, Department of Botany, North Carolina State University, Raleigh, N.C.
NCU	Herbarium, Department of Botany, University of North Carolina, Chapel Hill, N.C.
NEBC	Herbarium, New England Botanical Club, Cambridge, Mass.
NY	Herbarium, New York Botanical Gardens, New York, N.Y.
NYS	Herbarium, New York State Museum and Biological Survey, Albany, N.Y.
OAC	Herbarium, Department of Botany and Genetics, University of Guelph, Guelph, Ont.
P	Laboratoire de Phanérogamie, Musée national d'histoire naturelle, Paris, France
PH	Herbarium, Academy of Natural Sciences of Philadelphia, Philadelphia, Pa.

QFA	Herbier Louis-Marie, Faculté des sciences de l'agriculture et de l'alimentation, Laval University, Sainte-Foy, Que.
QK	Fowler Herbarium, Biology Department, Queen's University, Kingston, Ont.
SFS	Herbier Rolland-Germain, Département de biologie, University of Sherbrooke, Sherbrooke, Que.
SMU	Herbarium, Southern Methodist University, Dallas, Tex.
TEX	Herbarium, Department of Botany, University of Texas, Austin, Tex.
TRT	Vascular Plant Herbarium, Department of Botany, University of Toronto, Toronto, Ont.
UAC	Herbarium, Department of Biology, University of Calgary, Calgary, Alta.
UBC	Herbarium, Department of Botany, University of British Columbia, Vancouver, B.C.
US	United States National Herbarium, Department of Botany, Smithsonian Institution, Washington, D.C.
V	Herbarium, Botany Division, British Columbia Provincial Museum, Victoria, B.C.
WIS	Herbarium, Department of Botany, University of Wisconsin, Madison, Wisc.

Geographical locations of sampling sites

Canada

Alberta

Banff National Park, Mirror Lake–Lake Agnes environs, 1800–2000 msm, Lake Louise area, talus slopes–open coniferous forests. Spp. *V. scoparium, V. myrtillus.*

Banff National Park, trail toward Larch Valley, 1857–1950 msm, Moraine Lake, boggy coniferous woods. Spp. *V. myrtillus, V. scoparium.*

Jasper, Whistler Mountain, 1530–2250 msm, steep heath slopes. Spp. *V. vitis-idaea, V. membranaceum, V. scoparium, V. caespitosum.*

Seebe, along Hwy 1, 22.3 km E of jct with Hwy 40, 1200 msm, poplar-spruce regeneration woods behind abandoned service centre. Sp. *V. caespitosum.*

Wabanum–Edmonton Beach, along Hwy 16 (Jasper Hwy), 1 km W of jct with Hwy 43, poplar regeneration forest. Spp. *V. vitis-idaea, V. myrtilloides.*

British Columbia

Blue River, 1000 msm, along Hwy 5, abandoned gravel bars and badly disturbed woods behind Sandman Motel. Spp. *V. myrtilloides, V. caespitosum, V. ovalifolium, V. membranaceum.*

Burns Bog on the Fraser River Delta, near Delta, 49°08'N/123°W, heathland. Spp. *V. uliginosum, V. myrtilloides, V. oxycoccus.*

Eagle Pass, 1200 msm, Hwy 1, 100 m W of the Craigellachie Historic Marker (CPR), coniferous woods. Spp. *V. myrtilloides, V. parvifolium, V. caespitosum, V. membranaceum.*

Lulu Island, Fraser River Delta at Richmond Rd. No. 5 and the CNR right-of-way, disturbed raised bog. Sp. *V. macrocarpon.*

Manning Park, near Blackwell Peak, subalpine meadows at 1800 msm. Spp. *V. deliciosum, V. scoparium.*

North Vancouver, Mount Seymour Park; upper slopes 800–1100 msm, open coniferous woods. Spp. *V deliciosum, V. ovalifolium, V. membranaceum, V. parvifolium.*

Rogers Pass, Glacier National Park, Hwy 1, 1320 msm, spruce woods. Spp. *V. membranaceum, V. ovalifolium.*

Valemount, along Hwy 4, 5.6 km S of jct Hwys 5 and 16, 1200 msm, lodgepole pine parkland on ancient dune system. Spp. *V. caespitosum, V. myrtilloides.*

Vancouver, University of British Columbia, Forest Lands, disturbed coniferous woods. Sp. *V. parvifolium.*

Vancouver Island, vicinity of Horne Lake, open coniferous woods along newly cut logging road. Sp. *V. parvifolium.*

Vancouver Island, Block 70, Muir Creek Logging Company, Shirley District, along Hwy 14, 10 km S of Point-No-Point, open coniferous woods. Spp. *V. ovatum, V. parvifolium.*

Vancouver Island, Paradise Meadows, 1590 msm, Forbidden Plateau, vicinity of Strathcona Provincial Park. Spp. *V. caespitosum, V. uliginosum, V. deliciosum, V. membranaceum, V. ovalifolium, V. parvifolium.*

Vancouver Island, 4.1 km NW of River Jordan, creek bed through mixed coniferous woods. Sp. *V. parvifolium.*

Manitoba

8 km E of Churchill, 58°46'N/94°01'W, headlands. Spp. *V. uliginosum, V. vitis-idaea.*

New Brunswick

Charlotte County, Deer Island, outcropping. Spp. *V. angustifolium*, *V. vitis-idaea*.

Charlotte County, Glebe Rd at Chamcook, edge of spruce woods. Spp. *V. myrtilloides*, *V. angustifolium*, *V. vitis-idaea*.

Charlotte County, St. Davids Ridge Rd, blueberry barrens. Spp. *V. angustifolium*, *V. myrtilloides*, *V. caespitosum*.

Charlotte County, Tower Hill along Hwy 755, blueberry barrens. Spp. *V. myrtilloides*, *V. angustifolium*.

Saint John County, along Hwy 1, 16 km W of Saint John, granite outcropping. Spp. *V. angustifolium*, *V. myrtilloides*.

Sunbury County, CFB Gagetown, 8 km S of Geary along Hwy 7, open aspen grove. Spp. *V. myrtilloides*, *V. angustifolium*.

York County, 3.2 km N of Upper Brockway, along Rte 3, blueberry barrens. Spp. *V. myrtilloides*, *V. angustifolium*.

Newfoundland

Avalon Peninsula, Cape Spear, massive rocky outcropping. Spp. *V. boreale*, *V. uliginosum*, *V. angustifolium*, *V. vitis-idaea*.

Bonavista, 48°38'N/53°08'W, headlands. Spp. *V. boreale*, *V. angustifolium*, *V. uliginosum*, *V. oxycoccus*, *V. vitis-idaea*.

Harbour Main, Avondale, Ballyhack, granite outcropping. Spp. *V. angustifolium*, *V. boreale*.

Humber East, Mount Sykes, Birchy Bay, gravel slopes. Spp. *V. boreale*, *V. angustifolium*.

Humber West, Blomidon Mountain, spruce tangle, talus slopes, gravelly slopes. Spp. *V. boreale*, *V. angustifolium*, *V. ovalifolium*.

Labrador, West St. Modeste, 51°36'N/56°45'W, sandstone outcropping. Spp. *V. boreale*, *V. uliginosum*.

Lower Cove, 51°32'N/56°04'W, sandstone pavement. Spp. *V. boreale*, *V. vitis-idaea*, *V. uliginosum*.

St. Anthony, Mad Moll Rock, 51°21'N/55°34'W, headlands, spruce tangles, outcroppings. Spp. *V. ovalifolium*, *V. caespitosum*, *V. boreale*, *V. uliginosum*, *V. vitis-idaea*.

St. John's North, Pouch Cove, headlands. Sp. *V. angustifolium*.

Northwest Territories

Baffin Island, Frobisher Bay, 1.4 km SW of the airfield, 63°44'N/68°34'W, granite–gneiss outcroppings along the Sylvia Grinnell River. Spp. *V. uliginosum*, *V. vitis-idaea*.

Baffin Island, 6 km SW of Pangnirtung, 66°08'N/65°48'W, granite–gneiss plateau, 600 msm. Sp. *V. uliginosum.*

Baffin Island, 11 km S of Pond Inlet, 72°38'N/77°50W', gravel ridges and hummocks. Sp. *V. uliginosum.*

Devon Island, Dundas Harbour, 74°31'N/82°57'W, granite–gneiss outcroppings. Sp. *V. uliginosum.*

District of Keewatin, 17 km W of Eskimo Point, 61°07'N/94°13'W, low gravel ridges and hummocky terrain. Spp. *V. uliginosum, V. vitis-idaea.*

Ellesmere Island, Grise Fiord, 76°26'N/82°55'W, granite–gneiss outcropping at 510 msm. *Vaccinium* spp. absent.

Resolution Island, Brewer Bay, 62°35'N/64°39'W, headlands. Spp. *V. uliginosum, V. vitis-idaea.*

Nova Scotia

Antigonish County, along Copper Lake Rd, 2 km E of Hwy 7 at Middleton, barrens. Spp. *V. angustifolium, V. myrtilloides.*

Antigonish County, Merland, abandoned pasture. Spp. *V. angustifolium, V. myrtilloides.*

Cape Breton County, Kennington Cove, raised bog. Spp. *V. boreale, V. angustifolium, V. oxycoccus;* headlands, *V. macrocarpon, V. vitis-idaea, V. angustifolium, V. myrtilloides.*

Cape Breton County, Little Lorraine, Wild Cove, rocky headlands. Spp. *V. uliginosum, V. macrocarpon, V. angustifolium, V. vitis-idaea.*

Digby County, Brier Island, boggy barrens; headlands. Spp. *V. vitis-idaea, V. macrocarpon, V. oxycoccus, V. myrtilloides, V. angustifolium.*

Guysborough County, N edge of Boylston along Hwy 16, blueberry barrens. Spp. *V. angustifolium, V. myrtilloides, V. vitis-idaea.*

Halifax County, Portuguese Cove, headlands. Spp. *V. uliginosum, V. vitis-idaea, V. angustifolium, V. macrocarpon, V. oxycoccus.*

Halifax County, 1.5 km N of West Dover along Hwy 333, boggy barrens. Spp. *V. oxycoccus, V. vitis-idaea, V. angustifolium.*

Inverness County, Cape Breton Highlands, French Mountain, extensive high moor. Spp. *V. oxycoccus, V. boreale, V. angustifolium.*

Inverness County, Frizzleton, Margaree Municipal Airport, blueberry barrens. Spp. *V. boreale, V. myrtilloides, V. angustifolium.*

Kings County, 4 km E of Kingston along Hwy 1, *Corema* barrens and boggy depressions. Spp. *V. angustifolium, V. macrocarpon.*

Kings County, Mud Lake, 1 km W of Black River Lake, bog. Spp. *V. oxycoccus*, *V. macrocarpon*.

Lunenburg County, Hwy 103 interchange to Mahone Bay, poplar regeneration forest. Spp. *V. myrtilloides*, *V. angustifolium*.

Lunenburg County, 2 km S of New Ross along Hwy 12, red oak–red maple regeneration forest over Acadian granite. Spp. *V. myrtilloides*, *V. angustifolium*.

Pictou County, 3.2 km W of West Branch, poverty-grass meadows. Spp. *V. myrtilloides*, *V. angustifolium*, *V. macrocarpon*.

Queens County, Liverpool, Western Head adjacent to Victoria Lake, rocky barrens. Spp. *V. angustifolium*, *V. myrtilloides*, *V. vitis-idaea*.

Richmond County, Cape Breton Island, Hwy 104, 5 km N of exit 46, raised bog. Spp. *V. angustifolium*, *V. oxycoccus*.

Shelburne County, 8 km W of Birchtown along Hwy 3, raised bog and boggy barrens. Sp. *V. oxycoccus*.

Victoria County, Middle River, along Cabot Trail, 4 km S of the Inverness County line, abandoned pasture. Spp. *V. myrtilloides*, *V. angustifolium*, *V. boreale*.

Victoria County, South Point at Black Brook Cove, jack pine headlands. Spp. *V. vitis-idaea*, *V. angustifolium*, *V. myrtilloides*.

Yarmouth County, Gavelton, rocky lake margin. Sp. *V. angustifolium*.

Yarmouth County, Lake George, lake margin. Spp. *V. corymbosum*, *V. myrtilloides*.

Yarmouth County, Port Maitland, Leap Frog Lake, boggy margin, spruce woods. Spp. *V. corymbosum*, *V. oxycoccus*.

Yarmouth County, Red Head, Port Maitland, mire. Sp. *V. oxycoccus*; headlands, *V. macrocarpon*.

Ontario

Carleton County, Mer Bleue, beyond Borthwick Road, raised bog. Spp. *V. oxycoccus*, *V. macrocarpon*.

Elgin County, Springwater Conservation Area, 1.5 km N of Jaffa, Malahide Township, lake margin. Sp. *V. corymbosum*.

Frontenac County, Hebert Bog, Upper Rock Lake, bog. Spp. *V. oxycoccus* ($n = 24$), six plants; *V. macrocarpon* ($n = 12$), four plants; *V. corymbosum* ($n = 24$), eight plants.

Frontenac County, Washburn, outcropping. Spp. *V. angustifolium*, *V. myrtilloides*.

Lambton County, Pinery, Port Franks, pine woods. Sp. *V. angustifolium.*

Leeds County, Blue Mountain, Charleston Lake, near Lansdowne, outcroppings. Spp. *V. angustifolium, V. corymbosum.*

Leeds County, 4 km S of Delta, 2.4-ha quartzite outcroppings. Sp. *V. angustifolium.*

Leeds County, Hill Island, quartzite outcropping. Spp. *V. corymbosum, V. pallidum, V. angustifolium.*

Leeds County, Lake Opinicon, Chaffey's Locks, lake margin. Spp. *V. angustifolium, V. corymbosum.*

Leeds County, Mount Fitzsimmons, near Ivy Lea, outcropping. Spp. *V. angustifolium, V. myrtilloides, V. corymbosum.*

Leeds County, Red Horse Lake, near Lansdowne, outcroppings. Sp. *V. angustifolium.*

Leeds County, Ring Bog, Crow Lake, bog. Sp. *V. corymbosum.*

Leeds County, Rock Dunder, 3 km SW of Morton, outcroppings. Sp. *V. angustifolium.*

Leeds County, Westport Bog, 4 km NE of Westport, bog. Spp. *V. oxycoccus, V. macrocarpon.*

Lennox and Addington County, 0.5 km N of Kaladar, 1.7 ha granite–gneiss outcropping. Sp. *V. angustifolium.*

Middlesex County, Byron Bog, suburban London, bog. Spp. *V. oxycoccus* ($n = 24$), three plants; *V. macrocarpon* ($n = 12$), one plant; *V. corymbosum.*

Norfolk County, Turkey Point, oak woods. Sp. *V. pallidum.*

Peel County, 1 km W of Heart Lake, near Snelgrove, bog. Spp. *V. macrocarpon, V. corymbosum.*

Wellington County, Puslinch Township, Oilwell Swamp, lots 6, 7, 8, and 9, concessions 3 and 4, red maple swamp–bog transition. Spp. *V. corymbosum, V. macrocarpon.*

York County, High Park, Toronto, Rte 130, oak woods. Sp. *V. pallidum.*

Prince Edward Island

Queens County, along the Trans-Canada Hwy, 1 km S of Flat River, open white spruce regeneration forest. Sp. *V. angustifolium.*

Queens County, North River, edge of spruce woods. Sp. *V. myrtilloides.*

Queens County, Point Deroche, dunes. Sp. *V. angustifolium.*

Quebec

Argenteuil County, Lake Bevan, near Arundel, outcroppings along the lakeshore. Spp. *V. myrtilloides*, *V. caespitosum*.

Kamouraska County, Rte 20, rest centre 11.3 km NE of the St. Pacoma exit, granite outcropping. Spp. *V. vitis-idaea*, *V. myrtilloides*, *V. angustifolium*.

Lotbinière County, Rte 20, exit 158, Villeroy, raised bog and birch woods. Spp. *V. corymbosum*, *V. macrocarpon*, *V. myrtilloides*, *V. angustifolium*.

Missisquoi County, 1.2 km S of Farnham, poplar–birch regeneration forest. Sp. *V. corymbosum*.

Rivière-du-Loup County, along Rte 185, 3.2 km E of Rivière-du-Loup, raised peat bog. Spp. *V. angustifolium*, *V. myrtilloides*, *V. oxycoccus*.

Témiscouata County, Rte 185 at Que.–N.B. border, spruce woods and extensive bogs. Spp. *V. myrtilloides*, *V. angustifolium*, *V. oxycoccus*.

The Netherlands

Friesland, Zevenwouden, 1 km E of Orangewood, fern. Sp. *V. myrtillus*.

Spain

Navarre, Puerto de Velate at Valle del Baztan on Hwy N 121, open beech–pine woods on moderate slope. Sp. *V. myrtillus*.

United Kingdom

Scotland, Inverness-shire, Aviemore talus slope, 45–50°. Spp. *V. myrtillus*, *V. vitis-idaea*.

Scotland, Perthshire, Pitlochry margin of Loch Faskally, open oak wood. Sp. *V. myrtillus*.

Wales, County Gwynedd, Carnedd Moel-siabad, Glyder Fawr, 350 msm, degraded sedge meadow. Sp. *V. myrtillus*.

United States

Alabama

Baldwin County, 1 km N of exit 38, I-10, 11 km W of Loxley, recently burned slash pine stand. Spp. *V. corymbosum*, *V. darrowii*.

Connecticut

Fairfield County, North Stamford, Merritt Parkway, rocky hillside. Sp. *V. corymbosum.*

Delaware

New Castle County, rest area, I-95, red maple swamp. Spp. *V. corymbosum, V. pallidum* (edge of white pine thicket), *V. stamineum.*

Florida

Alachua County, Santa Fe River at New Hope Church, river bank. Spp. *V. corymbosum, V. arboreum, V. stamineum.*

Alachua County, Fla. 225, 1.5 km S of the Beef Research Unit, University of Florida, disturbed flatwoods. Sp. *V. corymbosum.*

Baker County, Osceola National Forest, I-10, just W of rest area, slash pine flatwoods. Spp. *V. corymbosum, V. darrowii, V. myrsinites.*

Bradford County, Rte 16, Clay–Bradford county line, oak parkland. Spp. *V. stamineum, V. myrsinites, V. arboreum.*

Escambia County, welcome center, I-10, pine–oak woods. Sp. *V. corymbosum.*

Highlands County, jct U.S. 27 and Fla. 70, Archbold Biological Station, pine flatwoods, oak scrub, bayheads, and swales. Spp. *V. corymbosum, V. darrowii, V. myrsinites.*

Highlands County, Highlands Hammock State Park, Sebring, red maple swamp. Sp. *V. corymbosum.*

Lake County, SW boundary of Leesburg, disturbed pine flatwoods. Spp. *V. darrowii, V. myrsinites, V. stamineum, V. arboreum, V. corymbosum.*

St. Johns County, St. Augustine, Anastasia State Park, disturbed dunes. Spp. *V. myrsinites, V. stamineum, V. arboreum.*

Santa Rosa County, U.S. 90, 10 km E of Milton, slash pine–oak woods. Spp. *V. corymbosum, V. darrowii.*

Georgia

Appling County, Pine Grove, 8 km W of Baxley, 31°N, pine flatwoods. Spp. *V. myrsinites, V. corymbosum.*

Bryan County, Richmond Hill, I-95 and U.S. 17, edges of deciduous woods. Spp. *V. corymbosum, V. tenellum, V. myrsinites.*

Clark County, R.B. Russell Field Station (USDA), Athens, pine woods. Sp. *V. corymbosum.*

Clinch County, 6 km E of Dupont, sandy roadside. Spp. *V. corymbosum, V. myrsinites.*

Coffee County, Ga. 32, 12.5 km W of Alma, near Nicholls, pine flatwoods. Spp. *V. corymbosum, V. myrsinites, V. tenellum.*

De Kalb County, Stone Mountain Park, deciduous woods. Spp. *V. arboreum, V. stamineum, V. pallidum.*

Lumpkin County, Dahlonega, edge of gravel pit. Sp. *V. pallidum.*

Lumpkin–Union County Line, Appalachian Trail, wooded slopes. Spp. *V. pallidum, V. corymbosum, V. stamineum.*

White County, 11 km N of Helen on Hwy 17, Ga. 128, oak woods. Sp. *V. pallidum.*

Louisiana

Tammany Parish, Pearl River, along I-59, 6.5 km N of Slidell, pine flatwoods. Spp. *V. corymbosum, V. darrowii, V. arboreum, V. stamineum.*

Maine

Cumberland County, I-95, 9 km N of exit 10, edge of birch–pine regeneration forest. Spp. *V. angustifolium, V. corymbosum, V. myrtilloides.*

Waldo County, 8 km W of Liberty along Hwy 3, old field. Spp. *V. angustifolium, V. myrtilloides.*

Washington County, Quoddy Head, hummocks on high moor. Spp. *V. boreale, V. angustifolium, V. oxycoccus, V. vitis-idaea.*

Washington County, Rte 9 at Wesley, abandoned gravel pit. Spp. *V. myrtilloides, V. angustifolium.*

York County, Drake Island, Rachel Carson Wildlife Refuge, red maple swamp. Spp. *V. corymbosum, V. macrocarpon.*

York County, I-95, exit 3, Kennebunk, edge of *Typha* marsh. Sp. *V. corymbosum.*

Massachusetts

Middlesex County, Reservoir System, Framingham, lake margin. Sp. *V. corymbosum.*

Worcester County, I-86 rest area, Sturbridge, oak woods. Sp. *V. pallidum.*

Michigan

Washtenaw County, Ann Arbor, Sister Lakes, oak woods. Sp. *V. pallidum.*

Mississippi

Forrest County, De Soto National Forest, jct U.S. 49 and Miss. 13, cut-over pine woods; oak scrub understory. Sp. *V. corymbosum.*

Hancock County, 5 km W of the Bay St. Louis interchange along I-10, pine flatwoods. Sp. *V. corymbosum.*

Harrison County, De Soto National Forest, 8 km S of Saucier, on U.S. 49, pine forests. Spp. *V. darrowii, V. corymbosum.*

Harrison County, railway spur through an undeveloped industrial park, 22 km NW of Biloxi, 0.6 km S of I-10, slash pine flatwoods. Sp. *V. corymbosum.*

Jackson County, Orange Grove, along U.S. 90, 3.5 km W of the Alabama state line, open slash pine flatwoods. Spp. *V. darrowii, V. corymbosum.*

Missouri

Stone County, Table Rock, 64 km S of Springfield, oak woods. Sp. *V. pallidum.*

New Hampshire

Coos County, Mount Washington, White Mountains, summit, alpine meadow. Spp. *V. uliginosum, V. boreale, V. vitis-idaea, V. caespitosum*; lower slopes, *V. angustifolium, V. myrtilloides.*

Strafford County, Mast Way, Lee, bog. Spp. *V. corymbosum, V. oxycoccus* ($n = 24$), 2 plants.

Strafford County, Wheelwright Pond at Lee, oak–hickory forest. Spp. *V. pallidum, V. angustifolium.*

New Jersey

Atlantic County, Rte 559, 1.61 km N of Weymouth, Atlantic Blueberry Co., sandy ridge. Spp. *V. pallidum, V. corymbosum.*

Burlington County, Lebanon State Forest, jct Hwys 70 and 72, pine–oak woods. Sp. *V. pallidum.*

Ocean County, jct of Webbs Mill Brook and N. J. 539, mire. Spp. *V. macrocarpon, V. corymbosum.*

New York

Albany County, I-87, McKownville, Albany, pitch pine barrens. Sp. *V. pallidum.*

Essex County, Whiteface Mt., (summit: 1405–1484 msm) spruce–fir Krumholz. Spp. *V. uliginosum, V. boreale, V. myrtilloides.*

Jefferson County, Butterfield Lake, outcropping. Sp. *V. pallidum.*

Jefferson County, Wells Island, oak–pitch pine outcroppings. Spp. *V. pallidum, V. angustifolium, V. stamineum, V. corymbosum.*

Oneida County, Sylvan Beach, birch woods. Spp. *V. corymbosum, V. angustifolium, V. myrtilloides.*

Orange County, I-84, look-off, 390 msm, granite outcropping. Spp. *V. pallidum, V. stamineum.*

St. Lawrence County, jct of N.Y. 3 and N.Y. 56, P.O. Childwold, sand hills and thin woods. Spp. *V. myrtilloides, V. angustifolium.*

St. Lawrence County, along Hwy 3 at Sevey, poverty-grass meadow on gravelly slopes, 480 msm. Spp. *V. angustifolium, V. myrtilloides.*

Suffolk County, Sag Harbour, Long Island, oak woods. Spp. *V. corymbosum, V. angustifolium, V. pallidum.*

Warren County, along N.Y. 8 at Graphite, lake margin. Sp. *V. macrocarpon.*

North Carolina

Avery County, Grandfather Mountain, Linville, rhododendron shrubbery at summit. Sp. *V. corymbosum.*

Caldwell County, Blowing Rock, Linville, steep slopes, oak woods. Spp. *V. pallidum, V. corymbosum.*

Davidson County, Thomasville, N.C. 827, oak woods. Spp. *V. pallidum, V. stamineum.*

Franklin County, along U.S. 401, 11 km S of Louisburg, deciduous woods. Spp. *V. pallidum, V. corymbosum, V. stamineum, V. tenellum.*

Halifax County, jct of Hwys 561 and 4, N.C. 622, oak–pine woods. Spp. *V. tenellum, V. pallidum, V. corymbosum.*

Haywood County, Blue Ridge Parkway, mile 420.2, Gaylord Stoney Tennent Mountain, 1841 msm. Spp. *V. erythrocarpum, V. corymbosum, V. pallidum.*

Haywood County, Blue Ridge Parkway, Richland Balsam Fir Forest, 1844 msm. Spp. *V. corymbosum, V. erythrocarpum.*

Haywood County, Blue Ridge Parkway, Water-rock Knoll, 1783 msm. Sp. *V. erythrocarpum.*

Johnston County, 6.5 km N of Newton Grove, N.C. 127, oak–pine woods. Spp. *V. pallidum, V. stamineum.*

Robeson County, Rte 301, 3 km N of Rowland, pine flatwoods. Spp. *V. corymbosum, V. tenellum.*

Sampson County, along U.S. 421, 8 km S of Clinton, N.C. 141, pine flatwoods. Spp. *V. crassifolium, V. tenellum, V. corymbosum, V. arboreum.*

Sampson County, along U.S. 421, 3 km from the Pender County line, pine flatwoods. Spp. *V. corymbosum, V. crassifolium.*

Transylvania County, Eco-Village, King Rd, between Brevard and Hendersonville, along U.S. 64, oak woods. Spp. *V. stamineum, V. pallidum, V. corymbosum.*

Wake County, Umstead Park, Reedy Creek Section, deciduous woods. Spp. *V. corymbosum, V. pallidum, V. stamineum, V. arboreum.*

Warren County, 5 km E of Macon, along Hwy 158, edges of pine forests. Spp. *V. pallidum, V. tenellum.*

Watauga County, Deep Gap, deciduous forests. Sp. *V. corymbosum.*

Wilkes County, 5 km W of Ferguson, oak woods. Sp. *V. pallidum.*

Ohio

Fairfield County, 1 km E of Sugar Grove, oak woods. Sp. *V. pallidum.*

Pennsylvania

Centre County, Scotia Barrens, State Game Lands, No. 176. Spp. *V. pallidum, V. angustifolium, V. stamineum, V. macrocarpon, V. corymbosum.*

Monroe County, Pocono Summit, I-380, jct with Pa. 940, boggy depression. Spp. *V. corymbosum, V. myrtilloides, V. angustifolium.*

Montour County, 14.5 km E of Milton, rest centre on I-80, oak woods. Spp. *V. pallidum, V. stamineum.*

Schuylkill County, Pine Grove, oak woods. Sp. *V. pallidum.*

Wayne County, Gouldsboro, Rte 507, E edge of town, 654 msm, red maple–birch regeneration forest. Spp. *V. myrtilloides, V. corymbosum.*

South Carolina

Colleton County, jct I-95 and S.C. 61, Walterboro, pine flatwoods. Spp. *V. corymbosum*, *V. tenellum.*

Horry County, Hwy 17, 1 km N of Myrtle Beach, pine–oak forest. Spp. *V. tenellum*, *V. crassifolium*, *V. arboreum.*

Sumter County, I-95, exit 141, pine flatwoods. Spp. *V. corymbosum*, *V. tenellum.*

Tennessee

Blount County, Cades Cove, pine–oak ridge. Spp. *V. hirsutum*, *V. stamineum*, *V. pallidum.*

Texas

Hardin County, Big Thicket National Preserve, Roy E. Larsen Sandyland Sanctuary, Silsbee, oak scrub. Spp. *V. arboreum*, *V. corymbosum*, *V. stamineum.*

Virginia

Caroline County, U.S. 301 and Va. 521, Lorne, roadsides and edges of pine–oak woods. Spp. *V. pallidum*, *V. corymbosum*, *V. stamineum.*

Greensville–Sussex County line, 8 km N of Emporia, along U.S. 301, pine flatwoods. Spp. *V. corymbosum*, *V. pallidum*, *V. tenellum*, *V. stamineum.*

Rappahannock County, Jeremy Run, Skyline Drive, Shenandoah National Park, oak scrub. Sp. *V. pallidum.*

Washington

Island County, Whidby Island, 5 km N of Oak Harbor along Wash. 525, coniferous woodlot. Spp. *V. ovatum*, *V. parvifolium.*

King County, North Bend, Mount Si, 300–1100 msm, open coniferous woods and steep slopes. Spp. *V. parvifolium*, *V. membranaceum*, *V. ovalifolium.*

Pacific County, South Bend, stumps and rotting logs at edge of town. Sp. *V. parvifolium.*

Thurston County, Summit Lake, rest centre along Wash. 8, second growth coniferous woods. Spp. *V. parvifolium*, *V. ovatum.*

APPENDIX 2 List of synonyms for species names

Vaccinium sect. *Cyanococcus*

Vaccinium* sect. *Cyanococcus A. Gray, Chlor. Bor. Am. 52. 1846.
  Vaccinium sect. *Pseudocyanococcus* Sleumer, Bot. Jahrb. Syst. 414. 1941.

Vaccinium boreale Hall & Aalders, Am. J. Bot. 48:200. 1961.
  V. pensylvanicum var. *angustifolium* (Aiton) A. Gray, Man. Bot. 1st ed. 261. 1848.
  V. pensylvanicum var. *alpinum* Wood, Class Book. 1861 ed. 483. 1861.

Vaccinium myrtilloides Michaux, Fl. Bor. Am. 1:234. 1803.
  V. canadense Richardson, in J. Franklin, Journal, 736. 1823.
  V. pensylvanicum var. *myrtilloides* (Michaux) Fernald, Rhodora 10:148. 1908.
  V. angustifolium var. *myrtilloides* (Michaux) House, N.Y. State Mus. Bull. 243–244:61. 1923.
  V. angustifolium var. *integrifolium* Lepage, Nat. Can. 78:341. 1951.

Vaccinium angustifolium Aiton, Hort. Kew. 1st ed. 2:11. 1789.
  V. pensylvanicum Lamarck, Encycl. 1:74. 1783; non *V. pensylvanicum* Miller, Gard. Dict. 8th ed. 1768 = *Royena glabra*; nec *V. pensylvanicum* var. *angustifolium* (Aiton) A. Gray, Man. Bot. 1st ed. 261. 1848; misapplied to *V. boreale* Hall & Aalders.
  V. pensylvanicum var *nigrum* Wood, Class Book. 1861 ed. 252. 1861.
  V. nigrum (Wood) Britton, Mem. Torrey Bot. Club 5:252. 1894.
  V. pensylvanicum f. *leucocarpum* Deane, Rhodora 3:264. 1901.
  V. brittonii Porter ex Bicknell, Bull. Torrey Bot. Club 41:420. 1914.
  V. angustifolium var *laevifolium* House, N.Y. State Mus. Bull. 243–244:61. 1923.
  V. angustifolium var. *nigrum* (Wood) Dole, Fl. Vt. 3rd ed. 210. 1937.
  V. lamarckii Camp, Bull. Torrey Bot. Club 71:180. 1943.
  V. angustifolium var. *hypolasium* Fernald, Rhodora 51:104. 1949.
  V. angustifolium f. *nigrum* (Wood) Boivin, Nat. Can. 93:437. 1966.
  Cyanococcus angustifolium (Aiton) Rydberg, Brittonia 1:94. 1931.

Vaccinium corymbosum Linnaeus, Sp. Pl. 1:350. 1753.

- *V. amoenum* Aiton, Hort. Kew. 1st ed. 2:12. 1789.
- *V. fuscatum* Aiton, Hort. Kew. 1st ed. 2:11. 1789.
- *V. virgatum* Aiton, Hort. Kew. 1st ed. 2:12. 1789.
- *V. formosum* Andrews, Bot. Repos. 2:*Pl.*97. 1800.
- *V. disomorphum* Michaux, Fl. Bor. Am. 1:231. 1803.
- *V. ligustrinum* Pursh, Fl. Am. Sept. 1:288. 1814.
- *V. myrtilloides* Elliott, Sketch. 1:500. 1821.
- *V. elongatum* Watson, Dendrol. Br. *Pl.*125. 1824.
- *V. grandiflorum* Watson, Dendrol. Br. *Pl.*125. 1824.
- *V. marianum* Watson, Dendrol. Br. *Pl.*124. 1824.
- *V. albiflorum* Hooker, Bot. Mag. 9:*Pl.*3428. 1835.
- *V. corymbosum* var. *fuscatum* (Aiton) Hooker, Bot. Mag. 62:*Pl.*3433. 1835.
- *V. discocarpum* Bigelow, Boston Fl. 2nd ed. 2:151. 1840.
- *V. constablaei*, A. Gray, Am. J. Sci. I. 42:42. 1842.
- *V. corymbosum* var. *amoenum* (Aiton) A. Gray, Man. Bot. 2nd ed. 250. 1856.
- *V. corymbosum* var. *glabrum* A. Gray, Man. Bot. 2nd ed. 250. 1856.
- *V. corymbosum* var. *atrococcum* A. Gray, Man. Bot. 2nd ed. (rev.) 250. 1857.
- *V. elliottii* Chapman, Fl. S U.S. 260. 1860.
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INDEX TO *VACCINIUM* SPECIES

Accepted names are set in roman type, synonyms in italics.

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