

A taxonomic revision of the genus *Agave* (Agavaceae) in the Lesser Antilles, with an ethnobotanical hypothesis

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Rogers, G. K. (University of the West Indies, Dept. of Biological and Chemical Sciences, Cave Hill, St. Michael, Barbados). A taxonomic revision of the genus *Agave* (Agavaceae) in the Lesser Antilles, with an ethnobotanical hypothesis. *Brittonia* 52: 218–233. 2000.—The genus *Agave* (Agavaceae) is revised taxonomically for the Lesser Antilles. All 12 previously recognized species are placed into synonymy under *Agave karatto* Miller. A neotype is selected for the name *Agave karatto*, and lectotypes are designated for *A. barbadensis* Trel., *A. medioxima* Trel., *A. obducta* Trel., *A. vangrolae* Trel., and *A. ventum-versa* Trel. Specimens are cited for most of the Lesser Antillean islands. That the Caribbean agaves are similar to the Mexican *Agave nayaritensis* Gentry is supported. The hypothesis that the pattern of partial sterility, clonality, and minimal morphological differentiation of the Lesser Antillean agaves is related to prehistoric human activity is developed based on similar patterns among mainland agaves and historical information. Uses for the archaeological “Barbados shell tool” may have included decorticating agave leaves for fiber extraction.

Key words: Agavaceae, *Agave*, Antilles, Caribbean, taxonomic revision, shell tool.

Agave L. is a genus usually estimated at around 300 species of large, rosette-forming, succulent, usually monocarpic, herbaceous perennials. The placement and generic affinities of *Agave* have long been unsettled and probably confused by a traditional emphasis on ovary position in the delimitation of plant families and by scarcity of herbarium materials. Bogler and Simpson (1995) found chloroplast DNA data to support affinities among *Agave*, *Beschorneria*, *Furcraea*, *Hesperaloe*, *Manfreda*, *Polianthes*, *Yucca*, and (more distantly) *Hosta* and perhaps *Xanthorrhoea*. Agaves generally inhabit arid or semiarid habitats in Mesoamerica, the southwestern United States, the Caribbean, and South America. They are well known to naturalists and gardeners as “century plants” for their generally monocarpic life cycle, producing a large flowering scape fueled by food reserves packed into massive leaves.

The abundant sugary sap, fibers, and thick cuticle gave agaves prominent ancient roles in human affairs in arid North America and Mesoamerica. The beverages aguamiel, pulque, mescal, and tequila come from agaves. So do sisal and henequen fibers. Many species are popular ornamental garden plants.

Taxonomic History and Species Concepts

Gentry’s (1982) monograph of the agaves of continental North America is the foundation for modern taxonomic work on the genus. Trelease monographed the Caribbean species in 1913. Berger’s (1915) treatment of the Lesser Antillean species is virtually a reprint of Trelease. Howard (1979) updated Trelease’s Lesser Antillean work, noting the need for continued efforts.

Trelease (1913) divided 47 Caribbean *Agave* species into two small-flowered

groups and into four groups with medium or large flowers. He sorted the small-flowered types into: 1) the "Inaguenses" in and near the Bahamas and 2) the "Antillares" in and near Cuba. The four medium-flowered/large-flowered assemblages are a) the "Antillanae" in the Greater Antilles, b) the "Bahamanae" of the Bahamas, c) the "Viviparae" of the Venezuelan mainland and neighboring islands, and d) the "Cariabaeae" of the Lesser Antilles.

I agree with subsequent authors who felt that Trelease (1913) recognized too many species. He created a dozen new Lesser Antillean "species" based on inadequate material. Five are based on single collections and four are based on just two collections. The remainder rest on little more. Given the clonality of these plants and their variability within island populations, species based on one or two collections are especially ill-advised. Trelease's Lesser Antillean species are only weakly separated using few, vague characters, primarily characteristics of the terminal spine and the marginal teeth along with floral and fruit characters in some cases. Trelease apparently was inclined to give island isolation more weight than morphological differentiation in defining species.

Gentry (1982) dismissed Trelease's various publications as "the apogee of *Agave* taxonomic flights" and "uninhibited in describing species." Howard (1979) consolidated Trelease's (1913) 12 Lesser Antillean "species" into six. The islands occupied by these broadened "species" are listed in Appendix I. There is an imperfect north-to-south progression in the sequence of "*Agave scheuermaniana*" Trel., "*A. vangrolae*" Trel., *A. karatto* Miller, and "*A. caribaeicola*" Trel., with "*A. barbadensis*" Trel. to the east in Barbados. "*Agave caribaeicola*" sensu Howard has the widest distribution, from Dominica to Grenada. Howard's (1979) *Flora of the Lesser Antilles* embraces hundreds of genera, so it was impossible to give one troublesome genus the undivided attention required to reevaluate Trelease's (1913) classification fully. Sampling difficulties may always be a factor with agaves due to their enormity, succulence, caustic sap, flowers borne high out of reach,

poor suitability as herbarium specimens, clonality, and occurrence in difficult places.

Continued accumulation of material engenders my present perception that even more aggressive consolidation is in order—that on a morphological basis there is only one species of indigenous *Agave* in the Lesser Antilles. The characteristics used to distinguish formerly recognized "species" are all undermined by various combinations of erroneous reporting, continuous variation, overlap and sporadic occurrence among "species," and inconsistency and broad variation within "species." These flaws afflict even the most salient variations encountered in the present study, such as the lengths of capsules and their stipes, the sizes of leaves, and the shapes of the terminal leaf spines.

A different component to the present question of species definition is island isolation. There are three problems with taking isolation as automatic support for specific distinctions between Lesser Antillean agaves: 1) Eons of isolation would ideally be expected to be revealed as morphological differentiation from island to island, but this is not the case. 2) The Lesser Antillean agaves are highly clonal. 3) The island populations may not all have been separated long in evolutionary time, and may show the influence of dispersal, artificial selection, and propagation by humans.

Methods

The study was conducted primarily in Barbados and based at the Barbados National Herbarium (BAR). Lesser Antillean, and in certain cases Mexican, specimens were examined from 10 herbaria (see Acknowledgments). The greatest concentration of Trelease material and types is at the Missouri Botanical Garden (MO), and all of the relevant specimens there were examined. Fieldwork took place on Antigua, Barbados, Nevis, St. Kitts, and St. Vincent. Figure 1 represents a summary of data collected, showing measurements for the quantifiable characters of greatest concern in the discussion. Each data point in that figure represents one measurement from one herbarium specimen or one vouchered field

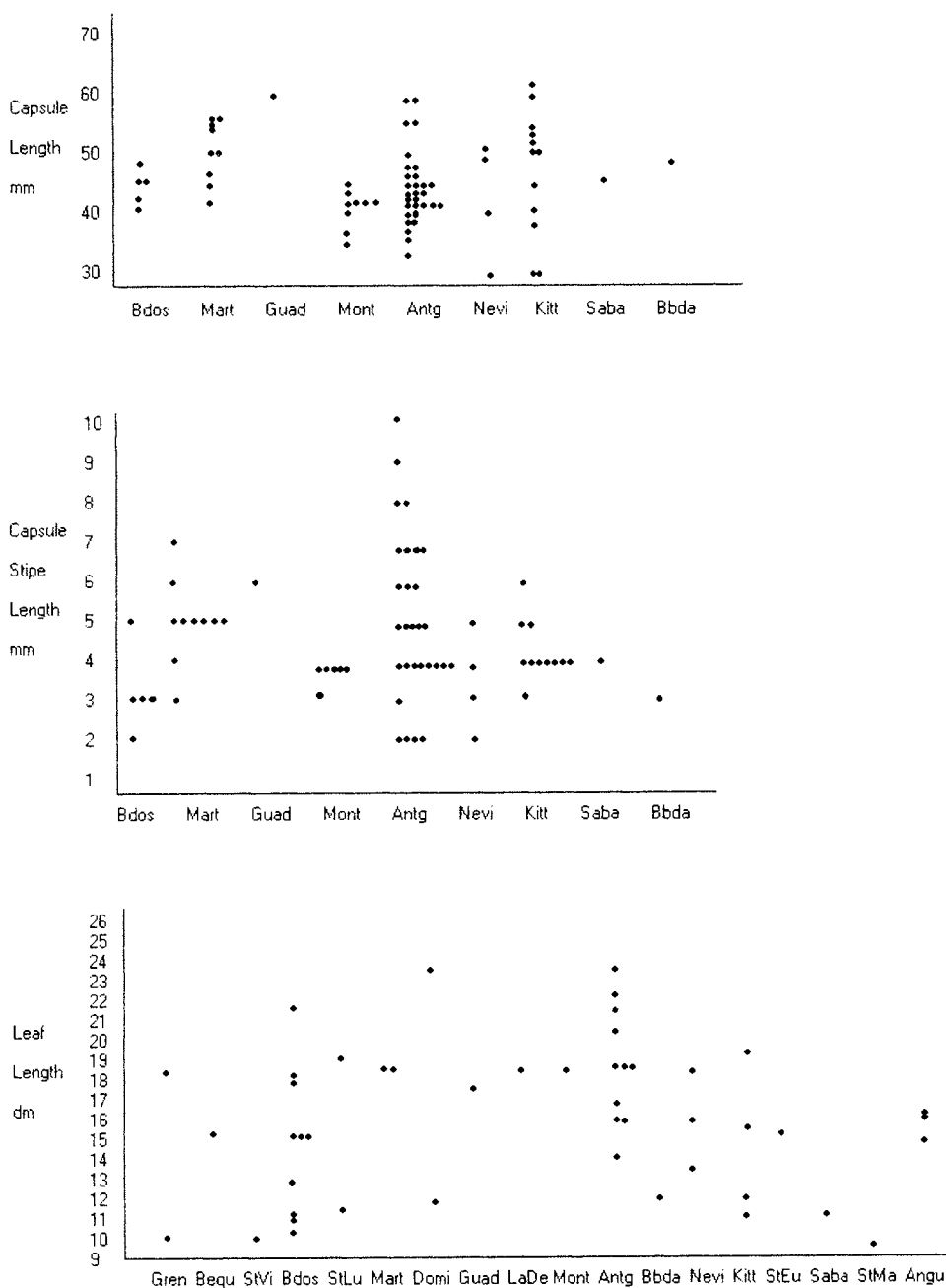


FIG. 1. Distributions of measurements for quantifiable characters showing the most salient variation among Lesser Antillean agaves: capsule length in mm, capsule stipe length in mm, and leaf length in dm. The horizontal axes list islands generally in order of increasing latitude, except that Barbados is almost due east of St. Vincent. Abbreviations: Gren, Grenada; Bequ, Bequia; StVi, St. Vincent; Bdos, Barbados; StLu, St. Lucia; Mart, Martinique; Domi, Dominica; Guad, Guadeloupe; LaDe, La Desirade; Mont, Montserrat; Antg, Antigua; Bbda, Barbuda; Nevi, Nevis; Kitt, St. Kitts; StEu, St. Eustatius; Saba, Saba; StMa, St. Martin; Angu, Anguilla.

measurement. Leaf widths in the field were measured by stretching a flexible tape measure across the widest point of the leaf. Leaf lengths were measured adaxially using the southernmost undamaged and readily measured leaf near the vertical middle of the rosette. In some cases, leaf length data came from herbarium labels. For measurements from herbarium specimens used in preparing Figure 1, the single mature, undamaged, readily measured representative of each organ closest to the right-hand edge of each specimen was recorded. Fruit lengths include the "stipe" (narrowed fruit base) but not the pedicel. Fibers were extracted by scraping with "Barbados shell tools" followed by retting for variable periods in fresh water and, finally, drying in the sun.

Typification

With the exception of *A. karatto*, all legitimate names applied to agaves in the Lesser Antilles have their protologues in Trelease (1913), whose typification practices create ambiguity in a modern context. It may help to outline the relationship between Trelease's (1913) typification practices, the actions taken in the present interpretation, and the current International Code of Botanical Nomenclature (Greuter et al., 1994, primarily Art. 9). Rather than designate a (holo-)type specimen, Trelease tended to list one or more collections or merely a collector's name and a time period as "type." Such materials are syntypes in the present interpretation. Trelease sometimes listed materials additional to his "types," and these are modern paratypes. Citation of one or more collection(s) as "type" creates the need to select a single lectotype specimen from among the syntypes. As a means of selecting one duplicate from a dispersed type collection, Rec. 9A.4 in Greuter et al. (1994) suggests taking the specimen housed in the author's home institution as holotype—the Missouri Botanical Garden (MO) for the Trelease names. I have examined all Lesser Antillean *Agave* material at that institution and find multiple duplicates of type collections housed there. Trelease often annotated one or more duplicates with

the word "type," and those have been given precedence in lectotypification in accordance with Rec. 9A.3 in Greuter et al. (1994).

The collection number typifying Trelease's "*Agave caribaeicola*," *Hahn 114*, pertains to materials gathered at two sites on different dates: "Case Pilote" 1868 (as on the BM and MO duplicates) and at Kew (K) labeled "Belle Fontaine" 1870. The duplicate at NY has no locality data and the date is unclear. For "*Agave vangrolae*" Trelease's (1913) type designation vaguely indicates collections made by Mrs. van Grol in 1909 and 1910. At the Missouri Botanical Garden there are several specimens from that collector labeled "Dec 1909," and one labeled "April 1910." The latter and one of the "Dec 1909" specimens were annotated by Trelease with the word "type." One "Dec 1909" specimen has been designated in the present work as lectotype. *Agave karatto* was described in 1768 by Philip Miller in the 8th Edition of his Gardeners Dictionary, with type material potentially residing at the British Museum. A search during the winter of 1998–1999 (see Acknowledgments), however, turned up no original material, hence a neotype has been designated. A lectotype has been selected for "*A. barbadensis*" from among three (syntype) collections Trelease (1913) listed with no designation of type.

Taxonomy

AGAVE KARATTO Miller, Gard. Dict. Ed. 8.
Agave No. 6. 1768. "Karat."

TYPE: St. Kitts, near Basse Terre, 2 Feb 1913, *Rose 3231* (NEOTYPE, here designated, NY; ISONEOTYPE, US).

Agave barbadensis Trel., Mem. Natl. Acad. Sci. 11: 28. 1913. Syntypes: "*Wright in Herb. Martii*" (n.v.); 1907, *Trelease 17* (MO), *18* (LECTOTYPE, here designated, MO; ISOLECTOTYPES, MO), *19* (n.v.); 1907, *Todd, Stockdale & Bovell s.n.* (n.v.).

Agave caribaeicola Trel., Mem. Natl. Acad. Sci. 11: 27. 1913. TYPE: Martinique, Case Pilote, *Hahn 114* (HOLOTYPE, MO; ISOTYPE, BM) (also with differing label data at K, and with vague label data at NY).

Agave dussiana Trel., Mem. Natl. Acad. Sci. 11: 26. 1913. TYPE: Guadeloupe, Port Louis, 22 Apr 1898, *Duss 3961* (HOLOTYPE, MO; ISOTYPE, NY).

Agave grenadina Trel., Mem. Natl. Acad. Sci. 11:

25. 1913. TYPE: Grenada, 6 Jun 1908, *Anstead C29* (HOLOTYPE, MO) [cultivated specimen].
- Agave medioxima* Trel., Mem. Natl. Acad. Sci. 11: 24. 1913. TYPE: Dominica, 1910, *Jones s.n.* (LECTOTYPE, here designated, MO; ISOLECTOTYPES, MO).
- Agave montserratensis* Trel., Mem. Natl. Acad. Sci. 11: 24. 1913. TYPE: Montserrat, 1909, *Robson 1* (HOLOTYPE, MO).
- Agave nevidis* Trel., Mem. Natl. Acad. Sci. 11: 24. 1913. TYPE: Nevis, 15 Mar 1910, *F. R. Shepherd, Maloney* (HOLOTYPE, MO).
- Agave obducta* Trel., Mem. Natl. Acad. Sci. 11: 25. 1913. TYPE: Antigua, "9/8/08," *Jackson s.n.* (LECTOTYPE, here designated, MO; ISOLECTOTYPES, MO).
- Agave scheuermaniana* Trel., Mem. Natl. Acad. Sci. 11: 25. 1913. TYPE: St. Martin, 1910, *Scheuerman s.n.* (n.v.). PARATYPES: Anguilla, 15 Mar 1910, *Shepherd (Owen) s.n.* (MO); 1911, *Owen s.n.* (MO).
- Agave unguiculata* Trel., Mem. Natl. Acad. Sci. 11: 29. 1913. TYPE: St. Lucia, Casembas, 25 Feb 1910, *Moore 1* (HOLOTYPE, MO).
- Agave vangrolae* Trel., Mem. Natl. Acad. Sci. 11: 24. 1913. TYPE: St. Eustatius, "1909, 1910," *Mrs. van Grol s.n.* (LECTOTYPE, here designated, "Dec 1909," MO; ISOLECTOTYPES, MO; SYNTYPE, "Apr 1910," MO).
- Agave ventum-versa* Trel., Mem. Natl. Acad. Sci. 11: 29. 1913. TYPE: St. Vincent, leeward cliffs, 1909, *Sands s.n.* (LECTOTYPE, here designated, MO; ISOLECTOTYPE, MO).

Large, monocarpic, rosette-forming succulent herbs sometimes producing basal suckers. Leaves ca. 100–220(–244) × (8–) 12–30(–40) cm, straight or curved outward, occasionally slightly twisted, green with light glaucescence, the marginal teeth (0.1–) 0.5–3(–5) mm long, highly variable, antrorse to retrorse, deltoid to acicular, usually more or less lens-based, usually dark-colored (or reddish when fresh), the terminal spine to (5–) 10–30(–45) mm long, 5–10 mm diam., comprised of hardened inrolled leaf margins, stout and sharp, recurved, or straight, or incurved, long-tapered to short and stubby, blackish. Inflorescence and stalk 3–8(–10) m tall, 8–16(–20) cm dbh, with up to 4(–5) orders of branching (excluding pedicels), the pedicels 7–25 mm long. Bulbils borne along the lower portion of the scape [Barbados, Dominica] and/or (more commonly) among the flowers. Flowers 5.5–10.5 cm long (when fully open and with filaments extended), often aborting before anthesis or shortly after opening, protandrous with the style elongating well

after anther dehiscence, golden-yellow, the tepals (14–) 20–25(–37) × 3–8(–12) mm, ligulate, united at the base into a broad-conical tube ca. (2–) 4–12(–15) mm long; filaments (2–) 2.5–6(–6.5) cm long, inserted at or very near the top of the floral tube; anthers 10–25 mm long, attached at or near the center; ovary (18–) 20–42(–48) mm long, fusiform and constricted apically beneath the floral tube, containing anatropous ovules [Barbados]; style (2.4–) 3.8–6.5 cm long, elongating late in anthesis (though sometimes protruding from bud prior to stamen elongation); stigma 3-lobed, with the lobes separating and becoming moist after style elongation [Barbados]. Loculicidal capsules 3–6(–6.2) cm long, ca. 2 cm diam. when closed, often failing to form, opening loculicidally to near the base, the valves usually elliptic or oblong, often beaked, divergent, the basal stipe 2–10 mm long, comprised of an unthickened portion of the ovary between the pedicel and the expanded portion of the capsule. Seeds 6.5–9 mm in the greatest dimension, D-shaped or irregularly polygonal, black (or white when infertile), wafer-thin.

The agaves in the island cluster of Nevis, St. Kitts, and St. Eustatius tend toward stubby (vs. longer, tapered) terminal spines. Although the stubby spines helped Trelease (1913) define his narrowly circumscribed *A. karatto*, in his view restricted to St. Kitts, some spines from St. Kitts and Nevis are tapered instead of stubby (*Rogers* 98–53, –54, –60; 1910, *Maloney s.n.*), and stubby spines turn up on other islands, such as Antigua (*Howard* 18493, *Rogers* 99–7), Barbados (*Trelease* 17, 18), Dominica (1910, *Jones s.n.*), Grenada (*Anstead* C29), Montserrat (*Robson* 1, 3), Redonda (*Howard* 19348), St. Lucia (*Moore* 1), and St. Vincent (1909, *Sands s.n.*). Moreover, in relatively well-studied Barbados, the spines are a mix of stubby, slender, recurved, upcurved, and straight. Complicating matters even further, the terminal spine is ill-defined morphologically. Where its base ends and where non-spine leaf tissue begins is not always clear: the two regions intergrade, and the age of the leaf influences the nature of the spine. Overall then, with individual spine shapes scattered among mul-

multiple islands, with single island populations showing multiple spine shapes, and with the definition of the spine vague to begin with, spine shape fails to support a narrowly defined *A. karatto*.

Miller's (1768) protologue of *Agave karatto* is based upon cultivated material tracing back to St. Kitts (Trelease, 1913; Howard, 1979). The protologue follows verbatim:

6. AGAVE (Karatto) foliis erectis laete virentibus, marginibus sulcis minime serratis. American Aloe with long deep green leaves, edged with brown, and very slightly sawed. This is called in America Karatto.

Discussion of *Agave karatto* Synonyms

Howard's (1979) interpretation is taken as the framework for the following discussion, with Trelease's (1913) earlier synonyms discussed under the names Howard accepted for them.

1. "AGAVE BARBADENSIS"

Island occupied by the species, as defined by Howard (1979): Barbados (type locality).

The Barbados agaves are by far the most thoroughly studied of the Lesser Antillean populations. Their ecology, distribution, and reproductive biology are discussed in Rogers (1999). A brief synopsis follows: Spontaneous plants are almost entirely restricted to the northern, eastern, and southern coasts of Barbados, extending inland on exposed, steep, often rocky soils in the Scotland District of St. Andrew Parish. The sites are diverse but share the common attributes of being the most xeric portions of Barbados. The agaves are generally not found on inland sites characterized by thick clays and relatively high rainfall. One untended west coast population at Black Rock in the middle of suburban sprawl in St. Michael Parish may or may not be spontaneous. Flowering is primarily March or April through midsummer. A small minority continue to bloom later (e.g., Rogers 98-50, collected in September). Flowers sometimes form on short secondary flowering

stalks rising from bulbil clusters persisting on the main stalk of the scape long after the first flush of flowering (e.g., Rogers 98-69). The bulbil-borne flowers are sometimes deformed. The protandrous flowers are borne in large, complex panicles where the order of maturation is upward. Commonly observed floral visitors are hummingbirds, other birds, and bees. In a minority of the plants most or all of the flowers abort before opening. The flowers on most individuals open completely and have normal-looking floral organs, ovules, stigmas, and pollen grains. Artificial pollination on excised stigmas reveals pollen tubes entering stigmas. Although extremely rare, some individuals in St. Lucy Parish form capsules and seeds.

2. "AGAVE CARIBAEICOLA"

Islands occupied by the species, as defined by Howard (1979): Dominica, Grenada and the Grenadines, Martinique (type locality), St. Lucia, and St. Vincent.

Trelease "species" placed into synonymy by Howard (1979): *Agave grenadina*, *A. medioxima*, *A. unguiculata*, *A. ventum-versa*.

"*Agave caribaeicola*" sensu Howard comprises all populations in the southern Lesser Antilles from Dominica to Grenada, excluding Barbados, which lies to the east.

Howard (1979) distinguished "*A. caribaeicola*" from the geographically close "*A. barbadensis*" by the former's allegedly smaller leaves, bulbils produced in the inflorescence (as opposed to reportedly forming only on the rachis), twisted leaves, and a black spine rarely involute and with an unguiculate base. Contrary to earlier reports, and diminishing the site of bulbil production as a specific distinction, in Barbados and in other islands bulbils are often borne within the inflorescence. They are often borne on the main stalk as well, which is likewise recorded from Dominica (Webster 13171). I find nothing outstanding about the terminal spines in either of these two "species." The spines are diverse in shape and size in both. As shown in Figure 1, although there is great variation in leaf lengths, this character gives little basis for

recognition of different species on different islands. Detracting further from giving much taxonomic weight to the lengths of the leaves is a series of observations of environmental plasticity in plant size. (Because the plants are essentially acaulescent except for the flowering stalk, leaf size and plant size are closely related.) Trelease's Caribbean correspondents advised him of a strong environmental influence on plant growth: on 2 Sep 1909, St. Vincent Agricultural Superintendent C. W. Sands wrote in a letter that "this *Agave* [in St. Vincent] varies considerably in growth according to situation." The same sentiment is in a letter to Trelease dated 23 Mar 1910 from J. O. Maloney, Agricultural Instructor in Nevis. From living among agaves in Barbados and cultivating them 1996–1999, I perceive the statures of the plants to be influenced dramatically by their circumstances. The indigenous agaves have come into commercial horticulture in Barbados, with the result that the growth enhancement from favorable conditions has become especially obvious.

Trelease (1913) described "*Agave ventum-versa*" from St. Vincent as standing apart for having a "horny-based spine and nearly deltoid though not very thick prickles." With better sampling, neither the teeth (prickles) nor the spine bases distinguish St. Vincent material. As already discussed, the terminal spines are dubious taxonomic characters in the Lesser Antilles. The spines in St. Vincent do tend, inconsistently, to be narrow and gradually tapered. Narrow spines of the sort used to define "*A. ventum-versa*" occur in other "species," including the geographically distant "*A. scheuermaniana*," which Trelease (1913) likewise defined partially by its own narrow spines. Undercutting the narrow spines even further in defining *A. "ventum-versa*," stubby spines are known from the type collection itself (1909, *Sands s.n.*), and, as noted above, are scattered among several other islands.

The twisted leaves in St. Vincent are probably environmentally induced. Most of the agaves I have seen on that island occupy cliffs and steep rocky outcrops. Leaves on the downhill side of the tilted rosette express negative geotropism by

twisting toward an upright orientation. The St. Vincent plant represented by the collection *Rogers 98-65* grows on a horizontal terrace and has nontwisted leaves. Conversely, most specimens in comparatively flat Barbados have straight leaves, but an individual on an unusual vertical rock face near Cattle Wash, St. Joseph Parish, has twisted leaves. Similarly, in Antigua most agaves have straight leaves, but those on vertical limestone ruins have the "St. Vincent" morphology.

In Trelease's (1913) interpretation "*A. unguiculata*" (type locality St. Lucia) diverges along with "*A. ventum-versa*" by having the "spine solidly conical" as opposed to "spine with inrolled base." In every Lesser Antillean agave I have seen, however, including the types of these two species, the spines are consistently formed from inrolled margins. Trelease (1913) defined "*A. unguiculata*" partly on the basis of its recurved spines, and the spines from St. Lucia do have this tendency, yet even the type itself (*Moore 1*) has at least one straight spine, and recurved spines occur mixed with spines of other morphologies in Montserrat (1908, *Robson B*), Antigua (*Rogers 99-7*), and Barbados.

The Dominican collection *Webster 13171* is anomalous, having tepals described on the label as "greenish with yellowish margins" as opposed to the "yellow" or "golden-yellow" typical of other Lesser Antillean collections. The basal portion of the flowers is deformed, with the tube 35–40 mm long (vs. a fraction of that in non-deformed flowers). The flowers are not on well-defined pedicels but, rather, arise directly from the stem or nearly so on the remnants of a "mostly past fl." inflorescence, which bears developing bulbils. These teratological flowers are reminiscent of those on pre-detachment bulbil clusters in Barbados.

"*Agave grenadina*" is based on material from a single cultivated plant sent from Grenada Agricultural Superintendent Ralph Anstead to Trelease. Anstead related in a letter dated 19 Jul 1908 to Trelease a suspicion that the specimen was not indigenous to Grenada, and might have been imported from Antigua.

3. "AGAVE DUSSIANA"

Islands occupied by the species, as defined by Howard (1979): Antigua, Guadeloupe (type locality), Martinique, Montserrat (type locality of "*A. montserratensis*"), St. Barts.

Trelease "species" placed into synonymy by Howard (1979): *Agave montserratensis*.

The distinctions among "*Agave dussiana*," *A. karatto*, and "*A. obducta*" have a history of trouble, and recent fieldwork further diminishes their previously perceived differences. All three have been reported for Antigua. Howard (1979) justifiably placed "*A. obducta*" in synonymy with *A. karatto*, and distinguished *A. karatto* from "*A. dussiana*" on the basis of fruit stipes in *A. karatto* being 2–3 mm long vs. to 10 mm long. As data have accumulated, however, stipe length fails to support separation of species (Fig. 1).

"*Agave dussiana*" tends also toward long capsules and long pedicels. Within the Lesser Antillean populations the capsule lengths range from about 30 mm long to about twice that. As with the stipes, there is no support in "capsule length" for species distinctions (Fig. 1). The type of "*A. dussiana*" (*Duss 3961*) from Guadeloupe is the only fruiting collection from that island, and the capsule is 59 mm long. Guadeloupe is close to Antigua, and the capsule lengths there are heterogeneous. The collection *Howard 18491*, from Shirley Heights, Antigua, has capsules 55–60 mm long, whereas my field measurements at the same locality (*Rogers 99-10*) and the collection *Howard 18493*, likewise from Shirley Heights, show capsules only 40–49 mm long. Shirley Heights occupies a southern hilltop in Antigua within view of Guadeloupe and within range of easily envisioned "contamination" by wind-borne seeds. Shifting to a broader geographic perspective, long capsules occur mixed with smaller ones on additional islands (Fig. 1). The variation is continuous, and the range even on single plants can be broad. For instance, on Martinique the collections *Duss 2136* and *Stehle 2507* have capsules 40–55 mm long; on St. Kitts they are 52–62 cm long

on *Rose 3231* and 38–51 mm long on *Rogers 98-52*. Pedicels as long as those of "*A. dussiana*" occur sporadically in the other "species," as is apparent even in Trelease's (1913) natural-size photographic plates.

4. "AGAVE SCHEUERMANIANA"

Islands occupied by the species, as defined by Howard (1979): St. Martin (type locality), Anguilla (paratype locality).

Trelease's (1913) key character for *A. scheuermaniana*, "spine very slenderly pointed, rather recurved," contradicts his plate 22, showing no recurved spines and a stubby one. The recent collections *Howard 18346* and *18377*, from the type locality, have straight spines. Moreover, slender spines are formed in other island populations, such as those in St. Vincent. The Anguilla and St. Martin agaves are not known to make fruits.

5. "AGAVE VANGROLAE"

Islands occupied by the species, as defined by Howard (1979): St. Eustatius (type locality), Nevis, St. Kitts.

Trelease "species" placed into synonymy by Howard (1979): *Agave nevidis*.

Howard (1979) distinguished "*A. vangrolae*" from "*A. karatto*" on the basis of the former allegedly having capsules <30 mm long (vs. >30 mm long). Trelease's protologue for "*A. vangrolae*," contradicting Howard's distinction, gives the capsules as "20 by 40 mm." Similarly, my fruiting collection from Nevis (*Rogers 98-61*) where "*A. vangrolae*" sensu Howard (including "*A. nevidis*") is the only agave recorded, agrees with Trelease's (1913) large dimensions, thus showing no difference from *A. karatto*.

Origins, Affinities, and Dispersal of Lesser Antillean Agaves

Trelease (1913) interpreted the distribution of the Caribbean agaves in terms of a Pleistocene "Antillean Bridge" from Mesoamerica across the Caribbean to Barbados and Venezuela. He believed that all the Caribbean species could be traced back to one or a few migration(s) from the mainland.

With the benefit of modern geology (e.g., Maury et al., 1990), land connections are set aside in favor of more plausible explanations for transoceanic agave dispersal. Flotation of bulbils or fruits is possible. Trelease (1913) reported this for cultivated *Agave americana* L. Also possible is wind dispersal of the wafer-thin seeds. *Agave* seedlings apparently from wind-borne seeds colonize coral stone ruins in Antigua. Beyond wind and waves, circumstantial evidence points to human-mediated dispersal as discussed below.

According to Gentry (1982: 507), the Caribbean agaves resemble his mainland Group Marmoratae. He noted similarity in the comparatively small terminal spines and in floral features. The Marmoratae and the Lesser Antillean species are mutually unusual by possessing short perianth tubes with the filaments inserted at or near their upper rims. The leaf photograph of *A. nayaritensis* Gentry (Gentry, 1982: 515) is very similar to the leaves seen in the Lesser Antilles. I have examined the following specimens of Mexican Marmoratae from the University of Michigan Herbarium: *A. nayaritensis* (Gentry & Gilly 10706) and *A. zebra* Gentry (Gentry 10205, 19899, 21207). The leaf of *Agave nayaritensis* conforms with "Lesser Antillean" morphology. In the Lesser Antilles most of the teeth are 1–4(–5) mm long; in *A. nayaritensis* the overall range of 1–4 mm is essentially the same, though the longer lengths predominate. The terminal spines in *A. nayaritensis*, consistent with Gentry's (1982) observation, are typical for the Lesser Antilles. *Agave zebra* has marginal teeth larger than the Lesser Antilles plants; some of its variable fruits agree morphologically with those the Lesser Antilles (Gentry 10205). The flowers in *A. zebra* (Gentry 10205) are a little smaller than normal for the Lesser Antilles and have the filaments inserted a little lower in the tube. Gentry's (1982) illustrations of floral dissections in other Marmoratae show filaments inserted near the top of the tube. Overall, Gentry's (1982) perception of similarity between his Marmoratae and Caribbean agaves is supported from a Lesser Antillean perspective.

Reproductive Biology

Of the 136 species recognized by Gentry (1982) for continental North America, 24 fail or nearly fail to form viable seeds and thus depend for propagation on suckers or bulbils (discussed by Szarek et al., 1996). In the Lesser Antilles bulbils appear to be the predominant form of reproduction. They are known from Anguilla, Antigua, Barbados (plants also sometimes form basal suckers), Barbuda, Bequia, Dominica, La Desirade, Martinique, Nevis, Saba, St. Eustatius, St. Kitts, St. Martin, and St. Vincent. The Lesser Antillean agaves are a mix of populations, with some able to produce seeds and others partially to completely sterile. The islands where capsules have been documented are Antigua (but some old inflorescences with no capsules), Barbados (capsules extremely rare), Barbuda, La Desirade, Guadeloupe, Martinique, Montserrat, Nevis, St. Eustatius, St. Kitts (apparently partly sterile), St. Lucia (probably unusual, but immature capsules seen), and St. Vincent (probably unusual, but immature capsules seen). Flowering collections but no fruiting collections have been made in Anguilla, Bequia, Dominica, Grenada, Redonda, and St. Martin.

One unsatisfying explanation for the partial sterility is self-incompatibility within clones. Undermining this notion is the observation that some fruitless agaves in Barbados abort their flowers prior to anthesis (Howard, 1979; Rogers, 1999) and thus prior to an opportunity for self-compatibility to show up. Hodgson and Slauson (1995) and Hodgson (1996) speculated that similar observations in Arizona may be due to ancient transportation of agaves by humans to areas with different precipitation patterns or away from critical pollinators. These possibilities apply to the West Indies, as does the possible loss of a pollinator. Yet another possibility is that the sterility may be genetic baggage left over from prehistoric cultivation. Polyploidy occurs in mainland agaves, indicating that cytological and/or molecular study of the Lesser Antillean island populations may be fertile ground for other researchers. Geneticist Dr. Lyndon Waterman and his students at the University

of the West Indies are initiating such investigations.

Ethnobotany

There appears to be a general correlation between cultivation and clonal reproduction for ancient New World cultigens. Referring to vegetatively propagated neotropical crops, Sauer (1972) remarked: "Because the planter was always concerned with vegetative propagation the plants that were thus fashioned in many cases lost the ability to reproduce themselves by seed. The forms of such sterility are various and still unstudied." Among the attributes of "domesticated or culturally selected" agaves, Hodgson et al. (1989) listed prolific bulbil production and seed-sterility.

Gentry (1982) extended the general correlation of sterility, clonality, and ancient cultivation specifically to agaves by documenting the phenomenon in his groups *Americanae*, *Ditepalae*, *Rigidae*, and *Sisilanae*, all of which are believed to have been cultivated in prehistory. Gentry's (1982: 551) comments on the *Rigidae* bear repeating: "Other groups [of agaves] that are difficult to separate and define as species are the cultivated groups (fiber and beverage), most of which are clones and some are sterile hybrids." Hodgson and Slauson (1995) and Hodgson (1996) interpreted *Agave murpheyi* Gibson and *A. delamateri* Hodgson & Slauson (which forms no capsules) as ancient asexually propagated cultigens in Arizona.

That agaves would be significant in prehistoric Caribbean cultures might be predicted from the mainland symbiosis between agaves and ancient cultures richly documented by Gentry (1982), Hodgson et al. (1989), Hodgson and Slauson (1995), and Hodgson (1996). Agave remains go back millennia in Mesoamerican coprolites. Agaves served the ancient mainlanders as sources of food, food wrappers, beverages, and fibers. Their obvious utility would be enhanced on islands where resources are limited. Human settlements in the Greater Antilles date back more than 7000 years (Cassa, 1992), and in the Lesser Antilles at least 3600 years (Drewett, 1991). Although

the Caribs and Tainos entered the Antilles from South America, they experienced Mesoamerican influences (e.g., Goyco, 1984).

The Caribs and Tainos were accomplished horticulturists adept with vegetative propagation (Sauer, 1966; Chanca, 1493). Agave bulbils are easy to transport, store, and cultivate. Szarek et al. (1996) found them to remain viable for at least three years after detachment. Hodgson and Slauson (1995) and Hodgson (1996) discussed probable ancient relocation of Arizona agaves by humans. Cassa (1992) discussed inter-island travel in the pre-Columbian Antilles.

In Barbados, agaves and prehistoric peoples lived in close proximity. The Barbadian agaves are virtually restricted to the thin coastal strip from the south coast up along the east coast and across the northern shores. Drewett (1991) recorded 56 prehistoric settlement sites for Barbados. Thirty-five of these are within the "agave strip." The greatest concentration of agaves occupies a narrow coastal ribbon in St. Lucy Parish extending about 9 km from Archers Bay to approximately Pico Teneriffe. The same small area has almost half (21) of the Barbadian ancient settlement sites. Whether or not this is a causal relationship, it demonstrates proximity between plants and people. Agaves are the dominant plants of northeastern Barbados. That they are useful and easily grown would have been difficult to overlook.

As Gentry (1982) described, agaves are outstanding sources of fibers. I have isolated abundant, strong, pleasing fibers from the Barbados agave by decorticating the fresh leaves, retting them for several days in water, washing the fibers, and drying them in the sun (Fig. 2). The heavy cuticle makes decortication necessary. Perhaps applied to this purpose, an abundant archaeological artifact in Barbados is a class of scraping instruments made of conch shells and called "Barbados shell tools" or "Barbados adzes" (Figs. 3, 4). (See Cartwright et al., 1991 for an illustrated discussion of these.) The purposes of the shoehorn-shaped implements have been the subjects of conjecture. Among the possibilities are



FIG. 2. Fibers from *Agave karatto* in Barbados.

horticulture, cleaning fish, and processing wood.

I have found the tools ideal for removing the cuticle and underlying parenchymatous tissue from agave leaves. Their curved shape fits the ridges and hollows of the leaves. The shell tools are similar to the "mescal knife," illustrated by Hodgson et al. (1989), recovered near a persistent ancient cultigen in Arizona and accepted by those authors as serving to process agave leaves.

There exists direct evidence of agave use by Caribbean Amerindians. In his *Natural History of the West Indies*, Gonzalo Fernandez de Oviedo (1526) described the use of agave fibers in the northern Caribbean for hammocks and for cutting iron. Sauer (1966) suspected Caribbean agaves to have been cultivated to make hammocks and fishing gear.

In sum, the weak morphological differentiation of the Lesser Antillean agaves raises the possibility of relatively recent

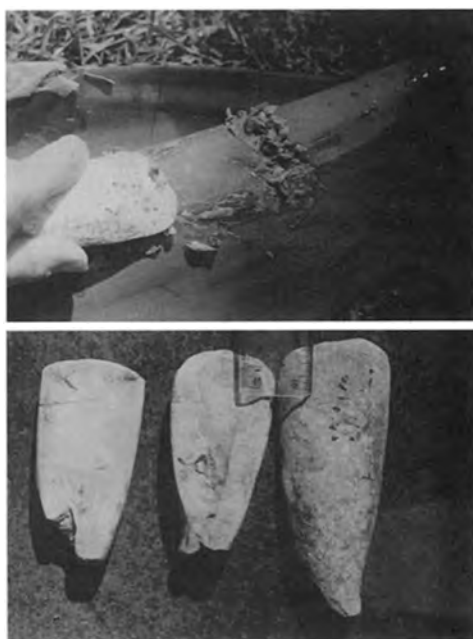


FIG. 3. Shell tool used to decorticate an *Agave karatto* leaf in Barbados.

FIG. 4. Barbados shell tools, from Andromeda Botanic Gardens, Bathsheba, Barbados.

geographic dispersal, although partial sterility and clonality could have dampened evolutionary diversification. The feeble differentiation, geographic intermixing of variations, and clonality are consistent with interpreting the Lesser Antillean agaves as minor variants, possibly human-dispersed cultivars, of a single species. Multiple clusters of ancient mainland *Agave* cultivars feature similar tendencies toward sterility and weak differentiation. There is no reason for the mainland human-agave symbiosis to have sidestepped the Caribbean, especially since pre-Columbian Caribbean peoples were gardeners and mariners, were in contact with the mainland, were recorded shortly post-contact to use agaves, were sometimes living among agaves, and were equipped with tools well suited to processing agave leaves.

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Appendix: Additional Specimens Examined and Island Notes

ANGUILLA

Previously reported “species”: *S. scheuermaniana* (Howard, Trelease).

15 Mar 1910, *F. R. Shepherd, Owen s.n.* (paratype collection of *A. scheuermaniana*) (MO); Dec 1911, *Owen s.n.* (paratype collection of *A. scheuermaniana*) (MO).

ANTIGUA

Previously reported “species”: *A. dussiana* (Howard), *A. karatto* (Howard), *A. obducta* Trelease (type locality)

28 Jul 1908, *Archer s.n.* (paratype of *A. obducta*) (MO); Old Rd., dry rocky country throughout the island, abundant, 29 May 1938, *Box 1463* (A, BM, US); bord de mer,

Dec 1902, *Duss 53* (MO, NY); Shirley Heights, 26 Jul 1977, *Howard 18491, 18493* (A); Kick's Hill, 26 Jul 1977, *Howard 18486* (A); "9/8/08," *Jackson s.n.* (type collection of *A. obducta*) (MO); 1903, *Officers of the Botanic Station s.n.* (paratype collection of *A. obducta*) (MO) [a note affixed to a MO duplicate of this collection bears the date "12/17/03"]; just S of Chalky Hill (near Falmouth Harbour), in dry rocky pasture, bearing fruits and bulbils within inflorescence, 6 Jan 1999, *Rogers 99-1* (BAR); same locality and date, different fruiting plant, *Rogers 99-2* (BAR); Emerald Cove (just inland from Long Bay Beach), thorn-scrub inland hillside on coral rock, fruiting, 6 Jan 1999, *Rogers 99-3* (BAR); along rd. on rocky hill overlooking Falmouth Bay, just uphill from Falmouth Bay Beach Apartments, with young flower stalk, 6 Jan 1999, *Rogers 99-4* (BAR); Morris Bay (just W of Fig Tree rain forest), sterile plant, rocky pasture by sea, thorn-scrub, 7 Jan 1999, *Rogers 99-5* (BAR); same locality and date, with fruits and with bulbils in inflorescence, *Rogers 99-6* (BAR); Chalky Hill, steep rocky hill with full exposure, sterile plant, leaf tips in this population varying from stubby to narrowly conical and straight or recurved, 7 Jan 1999, *Rogers 99-7* (BAR); Shirley Heights, assorted leaf fragments from same population, 8 Jan 1999, each plant assigned a different collection number: *Rogers 99-8, 99-9, 99-10* (BAR); near St. John, 4[5?]-16 Feb 1913, *Rose 3282* (GH, NY); English Harbour, sea level to 10 m, thorn bush, frequent, 4 Apr 1956, *Smith 10435* (NY, US).

BARBADOS

Previously reported "species": *Agave barbadensis* (Howard, Trelease, only locality).

No locality data: "2/5/07," *Trelease 17* (syntype collection of "*A. barbadensis*") (MO); "2/6/07," *Trelease 18* (lectotype collection of *A. barbadensis*) (MO); "7/29/08," *Trelease 85/08/1* (MO). **Christ Church:** Inch Marlow, clump of 2 plants growing on thin soil and exposed rock, 14 Jul 1998, *Burnett 98-8* (BAR); on rocks rising out of Chancery Lane Swamp, mid-Jul

1998, *Burnett 98-11* (BAR); South Point, buds not yet opened, plant near cliff overlooking sea, 1998, *Burnett 98-7* (BAR); same plant, in full bloom, 20 Sep 1998, *Rogers 98-50* (BAR). **St. Andrew:** Eroded hillside above sea between Belleplaine and Barclay's Park, 29 Apr 1998, *Rogers 98-32* (BAR); eroded hills above sea, Belleplaine to Bathsheba, just S of high white ragged rock formation, 22 May 1998, *Rogers 98-36* (BAR); first hill S of Cherry Tree Hill, 6 Apr 1998, *Rogers 98-23* (BAR); Chalky Mtn., aborted flowers collected from ground, 29 Apr 1998, *Rogers 98-30* (BAR). **St. John:** Conset Bay, shaded area close to stream, 24 Jul 1998, *Burnett 98-19* (BAR); Glenburne, large population of plants near sea, 24 Jul 1998, *Burnett 98-18* (BAR); Palmer's, rocky dry soil, Mar 1941, *Gooding 611* (BAR); same locality and number, Feb 1941, *Gooding 611* (BAR); same locality, Apr 1942, *Gooding 676* (BAR); Martins Bay, on slope just above sea, in bud, ovules appear normal, more or less anatropous, 2 Apr 1998, *Rogers 98-20* (BAR). **St. Joseph:** Malvern Lodge Ledge, 27 Sep 1902, *Freeman & Bovell s.n.* (BAR); on rocks just above sea, Bathsheba, just S of NCC park, inflorescence with buds only (one open flower), 30 Mar 1998, *Rogers 98-19* (BAR); same locality, inflorescence with buds only, 6 Apr 1998, *Rogers 98-22* (BAR); same locality, 20 Apr 1998, *Rogers 98-29* (BAR); hill above Cattlewash, 2 Apr 1998, *Rogers 98-21* (BAR); on hill above Cattlewash, buds aborting before opening in this clump, collected on plant, 24 Apr 1998, *Rogers 98-34* (BAR); on hill (burned area) above stretch of rd. between Barclays Park and Cattlewash, 20 May 1998, *Rogers 98-35* (BAR); Bathsheba, sands and limestone rocks, seashore, 8 Apr 1937, *Stehle 1646* (NY). **St. Lucy:** Graveyard [on rocky bluff overlooking the sea], clump producing fruits and seeds, 22 Jul 1998, *Burnett 98-16* (BAR); Animal Flower Cave, 15 Jul 1998, *Burnett 98-10* (BAR); rocky bluff overlooking sea at Graveyard near Boscobel (very near site of *Burnett 98-16*), with fruit, 26 Nov 1998, *Rogers 98-71* (BAR); Rockfield, 9 Apr 1998, *Rogers 98-24* (BAR); same locality but different clump, this specimen a small flowering

stalk borne branchlike on the scape at eye level, 9 Apr 1998, *Rogers 98-25* (BAR); North Point between Animal Flower Cave and Roaches, flat plain overlooking sea, flowers at different stages of maturity, 30 Apr 1998, *Rogers 98-33* (BAR); meadow at River Bay, anomalous flowering stalk coming from bulbil cluster on side of main inflorescence stalk, 26 Nov 1998, *Rogers 98-69* (BAR). **St. Michael:** Along ABC hwy. between UWI campus and Warrens, several individuals scattered in this area, exposed rock mixed with thin patches of soil dominated by clay, 18 May 1998, *Rogers 98-47* (BAR). **St. Philip:** Four Roads, sole plant near abandoned house, 17 Jul 1998, *Burnett 98-13* (BAR); Johnson Development, very large flowers seen, 17 Jul 1998, *Burnett 98-12* (BAR).

BARBUDA

Previously reported "species": *A. karatto* (Howard annotation).

Round Hill area, 28 Jul 1977, *Howard 18516* (A).

DOMINICA

Previously reported "species": *A. caribaeicola* (Howard), *A. medioxima* (Trelease, type locality).

Colihant, 100 m S of town, 45 m, 29 Jun 1992, *Beck 1700* (NY); 31 Mar 1910, *Botanical Gardens 1* (MO); dry forest over volcanic rock, thin soil, Morne Raquette to Au Piton Rd., 18 Dec 1993, *Hill 25524* (NY); Grand Savannah, Jan 1910, *Jones s.n.* (with the number "1" on the label but apparently not as a conventional collection number) (type collection of "*A. medioxima*") (MO); 18 May 1940, *Hodge 3817* (GH); lava ridges above S bank of Batali River, S of Morne Raquette, 200–300 ft, 30 May 1965, *Webster 13171* (US); hillside near Coulibistri, 4 Apr 1987, *Whitefoord 5760* (A, BM).

GRENADA AND THE GRENADINES

Previously reported "species": *A. caribaeicola* (Howard), *A. grenadina* (Trelease, type locality).

Bequia (Grenadines): "1/17/90," *Eggers 7057* (MO); 20 Mar 1977, *Howard*

18244, 18246 (A). **Grenada:** From a plant cultivated at the Botanic Station, *Anstead C29*, (type collection of *A. grenadina*) (MO); cultivated, 6 Jun 1908, *Anstead C29*, 16 Jul 1908 (MO); St. David's Point, 31 Mar 1977, *Howard 18336* (A); "from our number 205/06," 1906, collector not clear (MO). **Isle of Ronde (Grenadines):** Plants of windward coast, windswept area, inflorescence to 15 ft tall, flowers yellow, 7–25 Mar 1950, *Howard 10718* (BM).

GUADELOUPE

Previously reported "species": *A. dussiana* (Howard, Trelease, type locality).

Port-Louis, 22 Apr 1898, *Duss 3961* (type collection of *A. dussiana*) (MO, NY); Basse Terre, *Mme. Carrere*, "rec'd. 8/5/11" (paratype of *A. dussiana*) (MO); Massécoux, 27 Feb 1978, *Howard 18592* (NY).

LA DESIRADE

Previously reported "species": *A. karatto* (Howard).

Grande Anse area, in new or old fence rows, bulbil-forming, 28 Feb 1978, *Howard 18615* (BM, NY); vic. of Grande Anse, 1–10 m, 12 Jun 1960, *Proctor 21307* (A, BM, US); 70 m, 16 May 1935, *Stehle 2076* (US).

MARTINIQUE

Previously reported "species": *A. caribaeicola* (Howard, Trelease, type locality), *A. dussiana* (Howard).

Caravelle, Case-Pilote, 16 Apr 1885 (or Apr–May 1885), *Duss 2136* (MO, NY, with a second sheet at NY labeled "cresgn'île de la Caravelle," 1884; *Duss 2136* and one packet at MO labeled *Caravelle, 1884*; *Hahn 114* (type collection of *A. caribaeicola*) (BM, K, MO, NY) [differing information on labels under the collection number *Hahn 114*: the MO and BM specimens give Case Pilote, 1868, whereas "Belle Fontaine, Apr 1870" appears at K, and the NY specimen gives no locality data and the date as 1867–1870]; dry hillside at La Du-prey, 6 Mar 1978, *Howard 18664* (BM, NY); Fond Capot near La Carbet, dry hillside, 8 Mar 1978, *Howard 18685* (NY); St. Luce, littoral sec, 3 Sep 1937, *Stehle 2507* (NY).

MONTSERRAT

Previously reported "species": *A. dussiana* (Howard), *A. karatto* (Howard), *A. montserratensis* (Trelease, type locality).

St. John's Village, 23 Apr 1977, *Adams M19* (A); S slopes, May 1972, *Adams M21* (A); St. John's Village, 19 Mar–16 Apr 1979, *Howard 19289* (NY, BM, US); 1909, *Robson 1* (type collection of *A. montserratensis*); Apr 1908, *Robson s.n.* "A" (MO), "B" (MO), and "C" (MO) (paratype collections of *A. montserratensis*); 1909, *Robson 2, 3* (paratype collections of *A. montserratensis*) (MO).

NEVIS

Species reported: *S. nevidis* (Trelease, type locality), *A. vangrolae* (Howard).

Dry area S of Charlestown, 23 Jul 1977, *Howard 18470* (A); inland hillside along Hanley's Rd., 24 Oct 1998, *Rogers 98-57* (BAR); same locality and same date, *Rogers 98-58* (BAR); just E of Charlestown, scrubby hillside overlooking sea, 24 Oct 1998, *Rogers 98-59* (BAR); along rd. (probably planted) near airport, 24 Oct 1998, *Rogers 98-60* (BAR); E coast at edge of pasture, bearing fruits and bulbils, 24 Oct 1998, *Rogers 98-61* (BAR); 15 Mar 1910, *F. R. Shepherd, Maloney s.n.* (type collection of *A. nevidis*) (MO).

REDONDA

Previously reported "species": *A. karatto* (annotation).

Apr 1979, *Howard 19348* (A, NY).

SABA

Previously reported "species": *A. karatto* (annotation).

Upper level of Mt. Scenery, 15 Jul 1977, *Howard 18409* (A).

ST. EUSTATIUS

Previously reported "species": *A. vangrolae* (type locality).

Signal Hill, 17 Jul 1977, *Howard 18437* (A); Dec 1909, *van Grol s.n.* (lectotype collection of "*A. vangrolae*") (MO); Apr 1910, *van Grol s.n.* (syntype collection of "*A. vangrolae*") (MO); May 1912, *van Grol s.n.* (MO).

ST. KITTS

Previously reported "species": *A. karatto* (type locality), *A. vangrolae* (Howard).

Cultivated at NY from a St. Kitts plant collected by N. L. Britton in 1901 (#344), 1904, *NYBG #01986* (MO); Timothy Hill, coastal cliffs, 19 Jul 1977, *Howard 18447* (A); Friar's Bay, seashore behind beach, with fruits, 23 Oct 1998, *Rogers 98-52* (BAR); same locality and date, *Rogers 98-55* (BAR); S St. Kitts, immediately N of the S Peninsula, on rocky hillside overlooking sea, 23 Oct 1998, *Rogers 98-53* (BAR); same locality and date, *Rogers 98-54* (BAR); Major's Bay, seashore, 23 Oct 1998, *Rogers 98-56* (BAR); near Basse Terre, 2 Feb 1913, *Rose 3231* (NY–neotype, US); 1 Oct 1908, *F. R. Shepherd s.n.* (MO); 5 Oct 1910, *Shepherd s.n.* (MO).

ST. LUCIA

Previously reported "species": *A. caribaeicola* (Howard), *A. unguiculata* (Trelease, type locality).

Casembas, 1910, *Moore 1* (type collection of *A. unguiculata*) (MO); Esperance, 16 May 1985, *Pierre 149* (A); volcanic sea-cliffs at Marquis Bay, 20–200 ft, inflorescence slender, 3.5 m tall, 4 Apr–12 Jun 1958, *Proctor 17547* (A, BM); Grande Anse, Apr 1968, *Sturrock 476* (A).

ST. MARTIN

Previously reported "species": *A. scheuermaniana* (Howard, Trelease, type locality).

Fort Amsterdam, 11 Jul 1977, *Howard 18346* (A); Poiné Blanche, 12 Jul 1977, *Howard 18377* (A).

ST. VINCENT

Previously reported "species": *A. caribaeicola* (Howard), *A. ventum-versa* (Trelease, type locality).

Peter's Hope, 21 Mar 1977, *Howard 18252* (A); just S of Barrouallie, rocky bluffs overlooking sea, along W coast of St. Vincent this species scattered and uncommon, on usually vertical rocky outcrops, these often in otherwise dense forest, from seaside splash zone to high elevations, 17 Nov 1998, *Rogers 98-65, 98-66* (BAR); S

of Barrouallie, top of sea cliff, with young fruits, 28 Feb 1965, *Proctor 26018* (GH); 1909, *Sands s.n.* (type collection of *A. ventum-versa*) (MO); Mar 1890, *H. H. & G. W. Smith* (NY) (probably a differently labeled duplicate of the following collection); no data, *H. H. & G. W. Smith 1705* (paratype collection of *A. ventum-versa*) (MO, NY); dry cliffs and ridges near leeward coast and S end of island, near sea level to 800 ft, "Jan-Apr" (no year specified but probably 1890), *Smith & Smith 1704* (K).