SYSTEMATIC BOTANY MONOGRAPHS

VOLUME 72

Monograph of Schiedea (Caryophyllaceae-Alsinoideae)

Warren L. Wagner
Stephen G. Weller
Ann Sakai

THE AMERICAN SOCIETY OF PLANT TAXONOMISTS
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Schiedea trinervis (H. Mann) Pax & K. Hoffmann

[Pen and ink illustration taken from Fig. 18 and colored in Photoshop 6.5 by Alice Tangerini. Colors matched to living material of *Perlman 5448* grown in the greenhouse of the University of California at Irvine.]

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MONOGRAPH OF SCHIEDEA
(CARYOPHYLLACEAE–ALSINOIDEAE)

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ABSTRACT. *Schiedea* (Caryophyllaceae subfam. Alsinoideae), endemic to the Hawaiian Islands, comprises deciduous perennials, sprawling subshrubs, shrubs, and rainforest vines exhibiting an extraordinary range of breeding system variation and habitat preference. Morphological and molecular phylogenetic analyses support the division of *Schiedea* into seven sections and 34 species (including two subspecies). In a majority of the species each floral nectary is either terminated by a tubular, straight structure (a shaft) that extrudes a drop of nectar at the tip, or in three species a recurved shaft that deposits a pool of nectar on the adaxial face of each sepal. In four species (sections *Alsinidendron* and *Nothoschiedea*, formerly treated as a separate genus, *Alsinidendron*) the nectary appendages are flap- or cup-like, and collect large quantities of black nectar. These hypodermic shafts and flap- or cup-like extensions of the floral nectaries are unique within the Caryophyllaceae, and serve as a key feature to delineate *Schiedea* as a monophyletic group resulting from a single colonization of the Hawaiian Islands. Species are hermaphroditic and insect- or bird-pollinated or autogamous, or dimorphic (dioecious, subdioecious, and gynodioecious) and wind-pollinated. Nearly all hermaphroditic species occur in mesic or wet forests, whereas all dimorphic species are found in dry, often windy habitats. The morphological changes associated with the evolution of wind pollination, including a shift to smaller flower size, abundant pollen production and high pollen/ovule ratios, smaller pollen grains, and upright, highly condensed inflorescences, have had profound effects on the morphological diversity found within this lineage. Two species (*S. amplexicaulis*, *S. implexa*) are considered extinct, and the others are greatly at risk. Three new combinations (*Schiedea* sect. *Alsinidendron*, *S. diffusa* subsp. *macraei*, *S. obovata*) are proposed, and five new sections (*S.* sect. *Alphaschiedea*, *S.* sect. *Anestioschiedea*, *S.* sect. *Leucocalyx*, *S.* sect. *Mononeura*, *S.* sect. *Polyneura*) and two new species (*S. laui*, *S. perlmanii*) are described. All species are illustrated and their ranges mapped.

INTRODUCTION

Schiedea (Caryophyllaceae-Alsinoideae), a genus endemic to the Hawaiian Islands, consists of 34 species, including two subspecies, exhibiting an extraordinary range of morphological diversity, breeding system variation, and habitat preference. *Schiedea* is one of the best examples of adaptive radiation in the Hawaiian Islands. Species include deciduous perennials in coastal habitats, sprawling subshrubs in mesic forests, woody shrubs in dry, mesic, and wet forest, rainforest vines, and small subalpine subshrubs (Table 1). *Schiedea* also exhibits the greatest diversity in breeding systems of any native Hawaiian angiosperm genus (Weller et al. 1990; Weller & Sakai 1990; Wagner et al. 1995; Weller et al. 1995; Sakai et al. 1997b), including species with cleistogamy, mixed mating systems, gynodioecy, subdioecy, and dioecy (Table 1).

Schiedea was described by Chamisso and Schlechtendal (1826), and subsequently

TABLE 1. Breeding system, growth form, habitat, and distribution of species of *Schiedea*. Assessments based on herbarium, greenhouse, and/or field observations.

Species	Breeding System	Habit	Habitat	Distribution
S. adamantis	gynodioecious	shrub	dry shrubland	O`ahu (Diamond Head)
S. amplexicaulis	hermaphroditic	probably subshrub	probably diverse mesic forest	Kaua`i (extinct)
S. apokremnos	gynodioecious	shrub	dry coastal cliffs	Kaua`i
S. attenuata	hermaphroditic	shrub	cliffs in diverse mesic forest fragment	Kaua`i (Kalalau Valley)
S. diffusa subsp. *diffusa*	hermaphroditic, facultative autogamy	vine	wet montane forest	East Maui, Moloka`i
S. diffusa subsp. *macraei*	hermaphroditic, obligate autogamy via cleistogamy	vine	wet montane forest	Hawai`i
S. globosa	subdioecious	subshrub	dry coastal cliffs	O`ahu, Maui, Moloka`i, Lana`i (extirpated), Hawai`i
S. haleakalensis	dioecious	shrub	dry subalpine cliffs	East Maui
S. hawaiiensis	hermaphroditic, facultative autogamy	vine	dry forest	Hawai`i
S. helleri	hermaphroditic	vine	wet montane forest	Kaua`i
S. hookeri	hermaphroditic	subshrub	diverse mesic forest	O`ahu, East Maui (extirpated)
S. implexa	hermaphroditic	subshrub	probably mesic forest, cliffs	Maui (extinct)
S. jacobii	hermaphroditic, facultative autogamy	perennial herb to subshrub	wet montane forest	East Maui
S. kaalae	hermaphroditic	perennial herb	diverse mesic forest, wet forest	O`ahu
S. kauaiensis	hermaphroditic	subshrub	diverse mesic forest	Kaua`i
S. kealiae	subdioecious	subshrub	dry forest	O`ahu (Wai`anae Mts.)
S. laui	hermaphroditic, obligate autogamy via cleistogamy	subshrub	wet montane forest	Moloka`i
S. ligustrina	dioecious	shrub	dry shrubland or forest, clifs, rock crevices	O`ahu (Wai`anae Mts.)

TABLE 1 continued.

Species	Breeding System	Habit	Habitat	Distribution
S. lychnoides	hermaphroditic, facultative autogamy	vine	wet montane forest	Kaua`i
S. lydgatei	hermaphroditic	shrub	dry shrubland	Moloka`i
S. mannii	subdioecious	shrub	dry ridges in diverse mesic forest	O`ahu (Wai`anae Mts.)
S. membranacea	hermaphroditic	perennial herb	diverse mesic forest	Kaua`i
S. menziesii	hermaphroditic	shrub	dry shrubland, cliffs and crevices	Lana`i and West Maui
S. nuttallii	hermaphroditic	subshrub	diverse mesic forest	O'ahu, Moloka`i (extirpated), West Maui (extirpated)
S. obovata	hermaphroditic, facultative autogamy	shrub	diverse mesic forest	O`ahu (Wai`anae Mts.)
S. pentandra	hermaphroditic	vine	diverse mesic forest	O`ahu (Wai`anae Mts.)
S. perlmanii	hermaphroditic	vine	mesic shrubland	Kaua`i (Ha` upu & Papa`a)
S. pubescens	hermaphroditic	vine	diverse mesic to wet forest	Moloka`i, Lana`i (extirpated), and Maui
S. salicaria	gynodioecious	shrub	dry shrubland, slope, and cliffs	West Maui
S. sarmentosa	gynodioecious	shrub	dry forest and shrubland, cliffs and rocky areas	Moloka`i
S. spergulina	dioecious	shrub	dry shrubland or forest, cliffs	Kaua`i
S. stellarioides	hermaphroditic	subshrub	diverse mesic forest	Kaua`i
S. trinervis	hermaphroditic, obligate autogamy via cleistogamy	shrub	wet montane forest	O`ahu (Wai`anae Mts.)
S. verticillata	hermaphroditic	perennial herb	soil pockets and cracks on dry coastal cliffs	Nihoa
S. viscosa	hermaphroditic, facultative autogamy	vine	diverse mesic or margins of wet forest	Kaua`i

treated comprehensively by Mann (1866), Hillebrand (1888), and Sherff (1945). The treatment by Wagner et al. (1990) clarified the taxonomy of *Schiedea* and the formerly segregated genus *Alsinidendron*, and made possible a study of breeding system variability. Because of the diverse array of dimorphic breeding systems within *Schiedea*, it appeared that the group would serve as a useful model system for the study of breeding system evolution. The wide range of habitats occupied by *Schiedea*, and the correlation of breeding system with habitat indicates that breeding systems may have evolved in response to habitat shifts during the course of adaptive radiation in the Hawaiian Islands. A phylogenetic context can be utilized to attempt to determine the frequency and sequence of habitat and breeding system changes, and thus infer causal relationships (Felsenstein 1985; Donoghue 1989).

Detailed field, greenhouse, and herbarium investigations of *Schiedea* have yielded sufficient new information to warrant the monographic study presented here. The synergistic combination of morphological, phylogenetic, and ecological approaches has resulted in an increased understanding of the evolution of this lineage. Additional field and greenhouse studies, in particular, allowed for recognition of new taxa and clarification of the taxonomic status of several poorly known entities. Breeding systems of a number of species were unknown prior to the field work underlying this study, and in several cases differences in breeding systems aided in the discernment of previously unrecognized taxa.

TAXONOMIC HISTORY

Chamisso and Schlechtendal (1826) published the genus *Schiedea* with a single species, *S. ligustrina*, based on a collection that Chamisso obtained on O`ahu in 1817 when he served as botanist aboard the *Rurik* during the second Romanzoff expedition. Yet, the earliest specimens of *Schiedea* were collected in 1792 and 1793 by Archibald Menzies, serving as surgeon and naturalist under Capt. George Vancouver on the voyage of the *Discovery*. Menzies’s gatherings were later assigned to five species: *S. hookeri* (type), *S. ligustrina,* and *S. nuttallii* from O`ahu, and *S. implexa* and *S. menziesii* (type) from West Maui.

In 1844, William J. Hooker described two species, *S. nuttallii*, based on a Nuttall collection of 1834 from O`ahu, and *S. menziesii*, based on one of the Menzies collections of 1793.

Asa Gray (1854) added three more species when he published on the collections of the United States Exploring Expedition of 1838 to 1842 led by Lieutenant Charles Wilkes; he recognized *S. spergulina* from Kaua`i and *S. diffusa* from Maui. He based a third species on a Menzies collection in Hooker’s possession that Hooker believed to represent *S. ligustrina*. Hooker sent Gray a fragment of the Menzies specimen and provided some details of its diagnostic features (the letter is enclosed in a packet on the sheet bearing the holotype of *S. hookeri*). Gray considered the Menzies collection to represent an undescribed species, which he named *S. hookeri.*

In 1866 Horace Mann, Jr., son of the great American educator, published the first detailed study of the genus. He had visited the Hawaiian Islands on a botanical collecting trip, together with William T. Brigham, in 1864 and 1865. Mann’s study of *Schiedea* was based partly on his own collections and partly upon the specimens at Harvard University (GH), especially those collected by Jules Rémy. Mann described five new species (*S. amplexicaulis, S. stellarioides, S. remyi, S. globosa,* and *S. viscosa*) and more than doubled the size of the genus, which now comprised 11 species; all are currently accepted, except *S. remyi* (=*S. globosa*). Mann began to consider relationships in the genus when he placed *S. viscosa* in its own section, *Nothoschiedea*, because of its larger flowers, greater number of styles, and shorter and entire "staminodes" (now known to be extensions of the nectaries). He also described a new related genus, *Alsinidendron*, for one species, *A. trinverve*, which differed further in lacking "staminodes" (or so he thought) and often having 4-merous flowers.

Wawra (1873) contributed three taxa to *Schiedea*, but only *S. kaalae* is still recognized. The other two names are now considered synonyms: *S. oahuensis* (=*S. nuttallii*) and *S. diffusa* var. *angustifolia* (=*S. diffusa* subsp. *diffusa*).

William Hillebrand (1888) in the first major work on Hawaiian plants, the outstanding *Flora of the Hawaiian Islands*, described five species (*S. pubescens*, *S. hawaiiensis*, *S. salicaria*, *S. lydgatei*, and *S. lychnoides*), all based on collections accumulated between 1851 and 1871. He also noted three named and three unnamed varieties. Only one of his varieties, *S. nuttallii* var. *implexa*, is currently recognized, as *S. implexa*. At the time of publication of Hillebrand's Flora, 19 of the currently recognized 34 species had been described.

Earl E. Sherff published several papers on new Hawaiian taxa, some in collaboration with Otto Degener, a then-new resident collector in Hawaii, in which he described four new species (*S. haleakalensis*, *S. helleri*, *S. sarmentosa*, and *Alsinidendron obovatum*) and a number of varieties. Sherff's work culminated in the first complete revision of the genus (1945). The effort was hampered by World War II; Sherff was unable to see specimens from many herbaria, especially those of the Bishop Museum (BISH), and for several species merely repeated descriptions from previous work without any analysis of them. In all, Sherff (1943, 1944, 1945, 1951) recognized 19 species of *Schiedea*. He also accepted Mann's segregate genus *Alsinidendron*; he added one new species and transferred three others from *Schiedea* to *Alsinidendron* (*A. lychnoides*, *A. verticillatum*, and *A. viscosum*), a move suggested earlier by Hillebrand (1888) and Heller (1897). Sherff's criteria for the transfers were the leaf characters in particular, but also the larger flowers. The two genera then comprised 23 species, including two species published by researchers at Bishop Museum, *S. verticillata* by F. Brown (in Christophersen & Caum 1931) and *S. kealiae* by Caum and Hosaka (1936).

Harold St. John published seven species and one variety (1970, 1972, 1984, 1988). Five of the species (*S. adamantis*, *S. apokremnos*, *S. kauaiensis*, *S. mannii*, and *S. membranacea*) are currently accepted. St. John's first paper on *Schiedea* (1970) is among the more significant studies of the genus, because he clarified the nature of the extensions of the nectaries, structures long referred to as "staminodes." He demonstrated that these structures are hollow shafts that are outgrowths of the nectary and extrude nectar from their tips. Chamisso and Schlechtendal (1826) regarded the five structures as petals, perhaps because they had erroneously observed these "petals" as alternating with the sepals. Fenzl (1833), however, considered *S. ligustrina* to be without petals and believed these structures to be parastemones, or staminodia. He correctly described the position of the structures as opposite the sepals, and also considered the staminodia to be derived from a primary series of stamens. Asa Gray (1854) and Sherff (e.g., 1945) accepted Fenzl's interpretation of both the structures and their derivation, as did all later authors until the publication of St. John's paper in 1970.

In the mid-1980's Ann Sakai and Stephen Weller initiated a project to study the factors underlying the evolution of dimorphic breeding systems in *Schiedea*. A complete revision of *Schiedea* and *Alsinidendron* was realized as part of the Hawaiian flora project at the Bishop Museum (Wagner et al. 1990). Wagner then joined the Weller-Sakai collaboration to study, in particular, the taxonomy and phylogeny of the lineage in order to place the evolutionary and ecological studies into a phylogenetic context. During our studies collections obtained by collaborators yielded four additional species: *S. attenuata* (Wagner et al. 1994), *S. jacobii* (Wagner et al. 1999a), and two described here, *S. laui* and *S. perlmanii*. Their independent status was confirmed by detailed study of plants grown in the greenhouse of the University of California at Irvine.

Alsinidendron has nearly universally been recognized as distinct from *Schiedea* since it was described in 1866 by Mann. The differentiation of the four species assigned to *Alsinidendron* appears to have resulted from a shift to bird pollination and, in the case of the O`ahu species, potential bird dispersal facilitated by the fleshy, purple calyx (Wagner et al. 1995; Weller et al. 1995). Sherff (1944) also included *S. verticillata* in *Alsinidendron* based on the leaf characters and larger flowers, despite the presence of shaft-like nectary extensions in this species. He thought the various differences in these structures were merely variations in shape of the staminodia. We also recognized *Alsinidendron* as distinct until the results of the most recent phylogenetic analyses indicated otherwise. The first phylogenetic studies (Wagner et al. 1995; Weller et al. 1995; see also phylogeny below), based solely on morphology, showed that *Alsinidendron* is a strongly supported monophyletic group within a paraphyletic *Schiedea*; however, we continued to recognize *Alsinidendron*, because the support for this topology was weak. A similar result was obtained in the first molecular phylogenetic study of the group (Soltis et al. 1997), albeit with a similarly weakly supported topology at the critical nodes. The most recent study described below adds ITS and ETS sequence data to a revised morphological data set and shows the *Alsinidendron* clade moderately supported as sister to *S. verticillata*, and the *Alsinidendron* + *S. verticillata* clade nested within *Schiedea* in all maximum parsimony topologies. We have therefore concluded that *Alsinidendron* should be subsumed into *Schiedea*. In this new classification all taxonomic groups are monophyletic, and the extraordinary pattern of adaptive radiation in *Schiedea* is more strikingly evident.

MORPHOLOGY

Habit. Habit ranges from herbs (e.g., Fig. 9) to small woody shrubs (e.g., Fig. 19) and large wet-forest vines (e.g., Fig. 7). Development of secondary wood sets *Schiedea* apart from most continental Caryophyllaceae (Carlquist 1995). Wood is best developed among species occurring in dry habitats, where several *Schiedea* species produce small, highly branched shrubs less than two meters in height. In some cases, the basal stem diameter can be several centimeters. In mesic or wet forest, shrubby species often produce somewhat succulent stems. Two species, *S. membranacea* and *S. verticillata*, are truly herbaceous, producing stems that die back to fleshy roots in the dry season. All other extant species of *Schiedea* produce fibrous roots. Most species are largely herbaceous, but die back to slightly woody bases during the dry season. *Schiedea kaalae* is nearly acaulescent, producing a rosette of fleshy leaves at the apex of short stems. *Schiedea lychnoides*, *S. viscosa*, *S. perlmanii*, *S. hawaiiensis*, *S. helleri*, *S. pentandra*, *S. pubescens*, and *S. diffusa* are vines. At least in *S. helleri* and *S. diffusa*, stems may be several meters long and trail over other vegetation. There are no special adaptations for climbing in any of the vining species. One species, *S. hookeri*, appears variable in habit; in some populations plants have ascending stems, whereas in other populations stems are scandent and may occasionally root at nodes.

Leaves. Leaves in *Schiedea* are diverse. They range from large (up to 24 cm long) to short, linear or linear-subulate, and are multi- to single-veined. Leaves are usually entire, although several basal species have unique laminar margins with minute teeth. Differences in leaves are strongly correlated with habitat. Broad-leaved species are normally found in mesic or wet habitats, whereas species with narrow leaves occur in dry habitats. Some leaves, especially those of species occurring near the ocean, are succulent, and in the case of *S. verticillata*, to 9 cm wide. Coriaceous leaves are characteristic of species found in wet forest and of many species of mesic forest. Membranous leaves are found among a few species growing in mesic forests and dry shrublands, as well as in *S. kealiae*, which occurs in dry forest. Some species with narrow leaves have only one central vein, whereas a number of others have one, three, or five veins, a characteristic apparently reflecting their phylogenetic history. Leaves of some broad-leaved species, particularly of sect. *Mononeura*, have a single vein, which suggests the possibility of secondary expansion of the blade during adaptation to moister environments. Leaves of several species of sect. *Schiedea* and in *S. attenuata* (sect. *Leucocalyx*) are moderately to strongly falcate.

Inflorescence. Inflorescences of *Schiedea* have a determinate cymoid structure (Weberling 1989) with lateral dichasia or monochasia by abortion; species vary greatly in the degree of elongation of internodes and pedicels, as well as in the orientation of the inflorescence and individual flowers. As a result, variation in the inflorescence is one of the most distinctive features differentiating species of *Schiedea*. Species occurring in mesic or wet forest have large inflorescences with elongate internodes and pedicels (e.g., *S. pubescens*). Inflorescences of vining species are pendent (e.g., Fig. 38). Individuals flowers are also pendent in these species. The orientation of the inflorescences and flowers of these species may be an adaptation to preventing loss and wetting of pollen in wet environments. In contrast, species of *Schiedea* occurring in dry habitats produce upright, often very congested inflorescences (e.g., *S. adamantis*, Fig. 62). Culmination of inflorescence condensation occurs in *S. globosa* (Fig. 52) and *S. apokremnos* (Fig. 19), where extreme suppression of the main and lateral branches of the inflorescence leads to dense globose inflorescences. Condensation of the inflorescence is found in species with dimorphic breeding systems and appears to represent an adaptation for wind pollination (see Pollination; Weller et al. 1998). Flowers in species with condensed inflorescences are borne laterally or upright, depending on their position in the inflorescence.

In all species of sect. *Nothoschiedea* (*S. lychnoides* and *S. viscosa*) and sect. *Alsinidendron* (*S. obovata* and *S. trinervis*) the main axis is nearly or completely suppressed. We have termed this a pseudolateral inflorescence. It develops when the lateral branch of the next node below the inflorescence elongates coincident with flowering and assumes subsequent vegetative growth. Variation in inflorescence structure of the four species with pseudolateral inflorescences results from the degree of suppression of the lateral branches, pedicel length, and the orientation of the inflorescences. *Schiedea lychnoides* and *S. viscosa* are vines producing moderately congested, pendent inflorescences. The inflorescences of the shrubby O`ahu species, *S. obovata* and *S. trinervis*, differ in the degree of pedicel elongation. The longer pedicels of *S. trinervis* result in pendent orientation of the flowers (Fig. 18). In contrast, the more tightly congested inflorescences of *S. obovata* have laterally oriented or pendent flowers (Fig. 16).

Flowers. All species of *Schiedea* have apetalous flowers, although in a few species (sections *Nothoschiedea*, *Alsinidendron*, and *Leucocalyx*) the sepals are somewhat to conspicuously petaloid. Ten stamens are usually present, except in *S. pentandra*, where the outer or alternisepalous whorl is vestigial (Wagner & Harris 2000). Anthers are typically yellow, but in *S. stellarioides*, and sections *Nothoschiedea* and *Alsinidendron*, anthers are coral-colored. Pollen is normally yellow, although in sections *Nothoschiedea* and *Alsinidendron* pollen is gray. Ovaries vary considerably in size. Species in sections *Nothoschiedea*, *Alsinidendron*, and *Polyneura* have the largest ovaries and the largest capsules (Fig. 1D–H). Style number is also variable, ranging from three in the species with the smallest flowers to 8–11 in the larger-flowered species.

Nectaries. The nectary structure of *Schiedea* is unique in the Caryophyllaceae (Wagner et al. 1995; Wagner & Harris 2000). The five nectaries arise from an antisepalous mound of cells, and each nectary has a shaft-like tubular extension that develops to varying extents. This nectary shaft is thin and translucent, and its apex is usually bifid or variously divided, sometimes irregularly so. Nectar fills the shaft and is extruded from the tip as a drop (Plate 1A) in species with elongate nectar shafts; it forms in a pool on the surface of the sepal in species with recurved nectaries (Plate 1B). In the species formerly referred to *Alsinidendron* (sections *Nothoschiedea* and *Alsinidendron*) the nectary is enlarged during development and forms a nearly contiguous ring of nectariferous tissue. The abaxial margin of each nectary has a flap-like extension rather than a shaft. These extensions are either distinct to the base, oblong, and apically 2–3-toothed (sect. *Nothoschiedea*; e.g., Fig. 15F, G), or connate at the base or for about half their length and forming a cup-like structure with an apex that is either entire or has inconspicuous teeth (sect. *Alsinidendron*; e.g., Fig. 18C). The black nectar produced in sections *Alsinidendron* and *Nothoschiedea* is usually copious and hexose-rich (Plate 1C; Weller et al. 1998). Nectaries tend to be reduced in size in wind-pollinated species (Plate 1D). Developmental studies indicate (Wagner et al. 1990) that the nectaries are homologous in all sections of *Schiedea* (Wagner et al. 1995).

Fruit and seed. All species of *Schiedea* have a loculicidal capsule, opening by as many valves as styles. The size and shape of the capsule is variable, ranging from oblong capsules less than 4 mm long to nearly spherical capsules more than 10 mm in diameter (Figs. 1, 2).

Seeds of species in the eight sections of *Schiedea* vary considerably in size, but show the reniform shape characteristic of the Caryophyllaceae (Figs. 3, 4). The largest seeds are found in *S. obovata* and *S. trinervis* (sect. *Alsinidendron*; Fig. 3I, J). Seeds of these species are characterized by flat cells with strongly undulate margins in the central portion of the seed surface. Micropapillae dominate the central portions of the cells. Surface cells are elongated into papillae at the margins of the seed, particularly along the margin opposite the point of attachment of the placenta. Seeds of *S. lychnoides* and *S. viscosa* (sect. *Nothoschiedea*) differ from those of sect. *Alsinidendron* in lacking papillae at the cell margins, and possessing slightly convex cells and channeled cell boundaries (Fig. 3G, H). Micropapillae of species in sect. *Nothoschiedea* are distributed evenly over the cell surfaces. Seeds of the species in sect. *Nothoschiedea* are considerably smaller than those of species in sect. *Alsinidendron*.

Seeds of species in the other five sections of *Schiedea* are usually smaller and show considerable variation in cell shape, the degree of undulation of the margin, the degree of

Plate 1. Images of flowers of *Schiedea*, showing the four types of nectar presentation resulting from modifications in breeding system and related changes in nectary extensions. A. *S. lydgatei* (3 March 1989, *Weller & Sakai s.n.* [cult. *Weller & Sakai 870*]), example of a typical hermaphroditic outcrossing species with straight or slightly arched nectary shafts that extrude drops of nectar for insect pollinators. B. *S. verticillata* (from U.S. Fish and Wildlife personnel & S. Conant, *Weller & Sakai 880* [cult. *Wagner & Shannon 6819*]), one of two hermaphroditic outcrossing species in which the nectary shaft arches to touch the sepal where nectar pools, perhaps a response to windy habitats. C. *S. obovata* (*Perlman & Obata 5800*), example of hermaphroditic species with presumed bird pollination syndrome showing flap-like nectary extensions and black nectar pooling at their bases. D. *S. adamantis* (*Weller & Sakai 847*), example of a dimorphic species; female flower of a gynodioecious species, with reduced nectary shafts and nectar production. Images A, C, and D taken by Nobumitsu Kawakubo in the greenhouse of the University of California at Irvine, June 2003; image B taken by W. L. Wagner, May 2001.

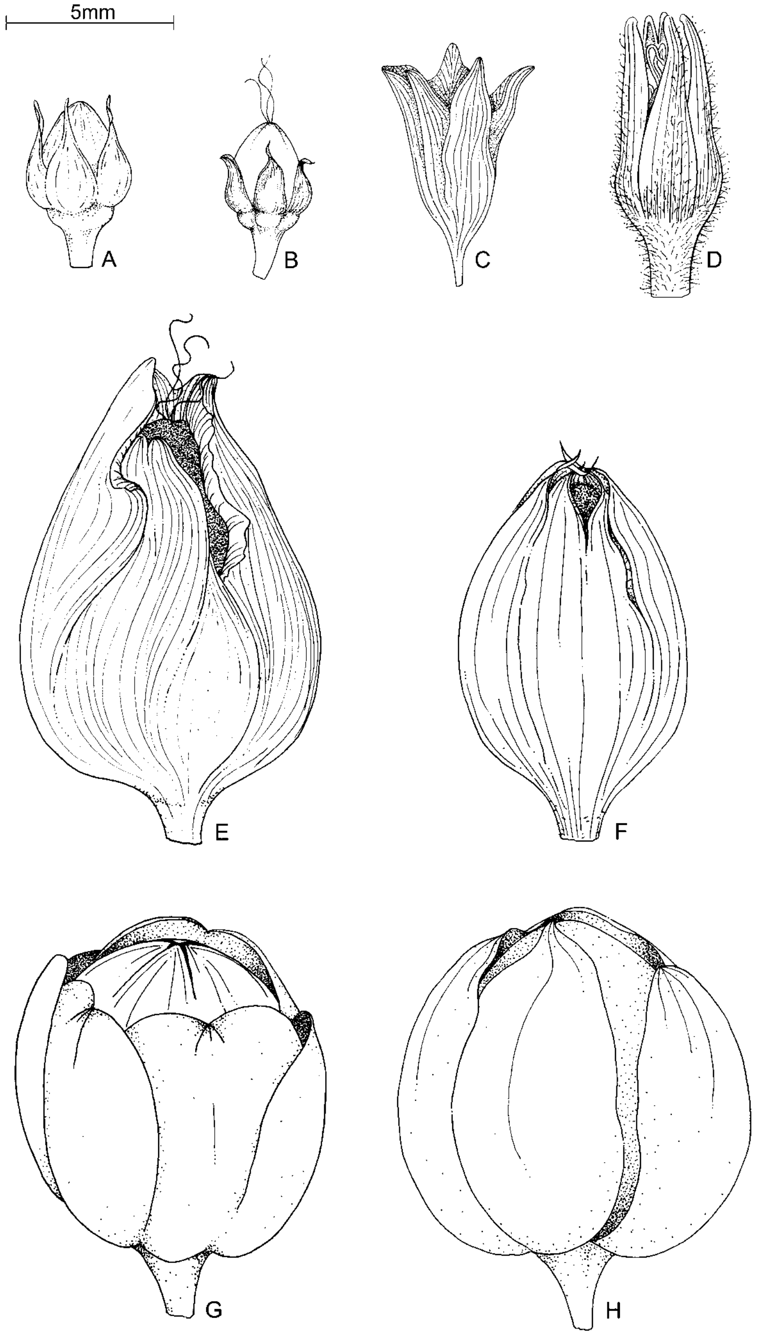

FIG. 1. Comparison of mature capsules with surrounding calyces of species of *Schiedea*, except the two extinct ones (*S. amplexicaulis* and *S. implexa*). A. *S. helleri* (*Perlman & Wood 13572* [cult. *Wagner & Shannon 6809*]). B. *S. membranacea* (March 1987, *Weller & Sakai s.n.* [cult. *Weller & Sakai 864*]). C. *S. attenuata* (*Wood 1394*) holotype. D. *S. verticillata* (from U.S. Fish and Wildlife personnel & S. Conant, *Weller & Sakai 880* [cult. *Wagner & Shannon 6819*]). E. *S. lychnoides* (1987, *Flynn s.n.* [cult. *Weller & Sakai 867*]). F. *S. viscosa* (*Flynn et al. 5031*). G. *S. obovata* (*Perlman & Obata 5800*). H. *S. trinervis* (*Weller & Sakai 908* [cult. *Wagner & Shannon 6853*]).

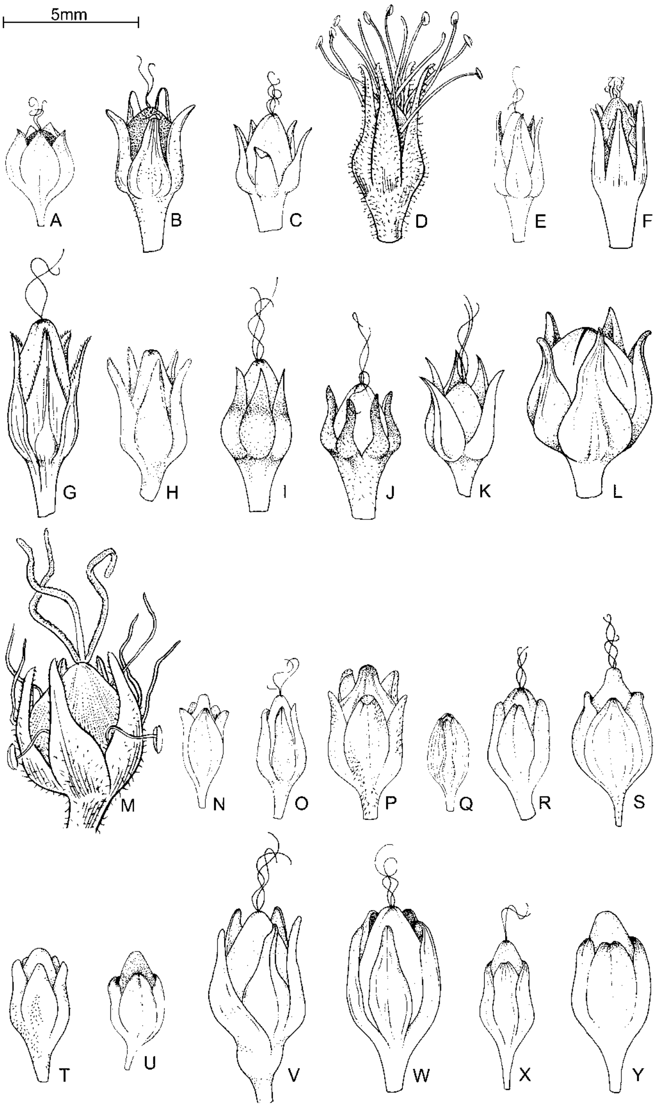

FIG. 2. Comparison of mature capsules with surrounding calyces of *Schiedea*, except the two extinct species (*S. amplexicaulis* and *S. implexa*). A. *S. apokremnos* (*Flynn et. al. 2219*). B. *S. stellarioides* (*Perlman & Wood 14651* [cult. *Wagner & Shannon 6855*]). C. *S. perlmanii* (*Perlman 12917*). D. *S. kauaiensis* (*Perlman 12074*). E. *S. nuttallii* (1 March 1987, *Weller & Sakai s.n.* [cult. *Weller & Sakai 861*]). F. *S. laui* (12 May 1998, *Lau s.n.*) type collection. G. *S. kaalae* (*Takeuchi 3587*). H. *S. jacobii* (*Perlman 14807*) type collection. I. *S. hawaiiensis* (s.d., *PTA personnel s.n.* [cult. *Weller & Sakai 932*). J. *S. pentandra* (cult. *Weller & Sakai 860*) no voucher. K. *S. pubescens* (*Perlman 14682*). L. *S. diffusa* subsp. *diffusa* (*Wagner et al. 5926*). M. *S. diffusa* subsp. *macraei* (*Perlman et.al. 14780* [cult. *Wagner & Shannon 6796*]). N. *S. kealiae* (*Weller & Sakai 791*). O. *S. hookeri* (29 July 1991, *Obata, Weller & Sakai s.n.* [cult. *Weller & Sakai 879*]). P. *S. menziesii* (27 January 1987, *Weller and Sakai s.n.* [cult. *Weller & Sakai 849*]). Q. *S. sarmentosa* ([cult. *Weller & Sakai 896*]) no voucher. R. *S. haleakalensis* (27 July 1991, *Weller & Sakai s.n.* [cult. *Weller & Sakai 851*]). S. *S. globosa* (March 1994, *Weller & Sakai s.n.* [cult. *Weller & Sakai 906*]). T. *S. spergulina* (*Weller & Sakai 863*). U. *S. mannii* (*Weller & Sakai 793*). V. *S. lydgatei* (3 March 1989, *Weller & Sakai s.n.* [cult. *Weller & Sakai 870*]). W. *S. salicaria* (*Weller & Sakai 842*). X. *S. ligustrina* (July 1985, *Obata & Perlman s.n.* [cult. *Weller & Sakai 846*]). Y. *S. adamantis* (*Weller & Sakai 847*).

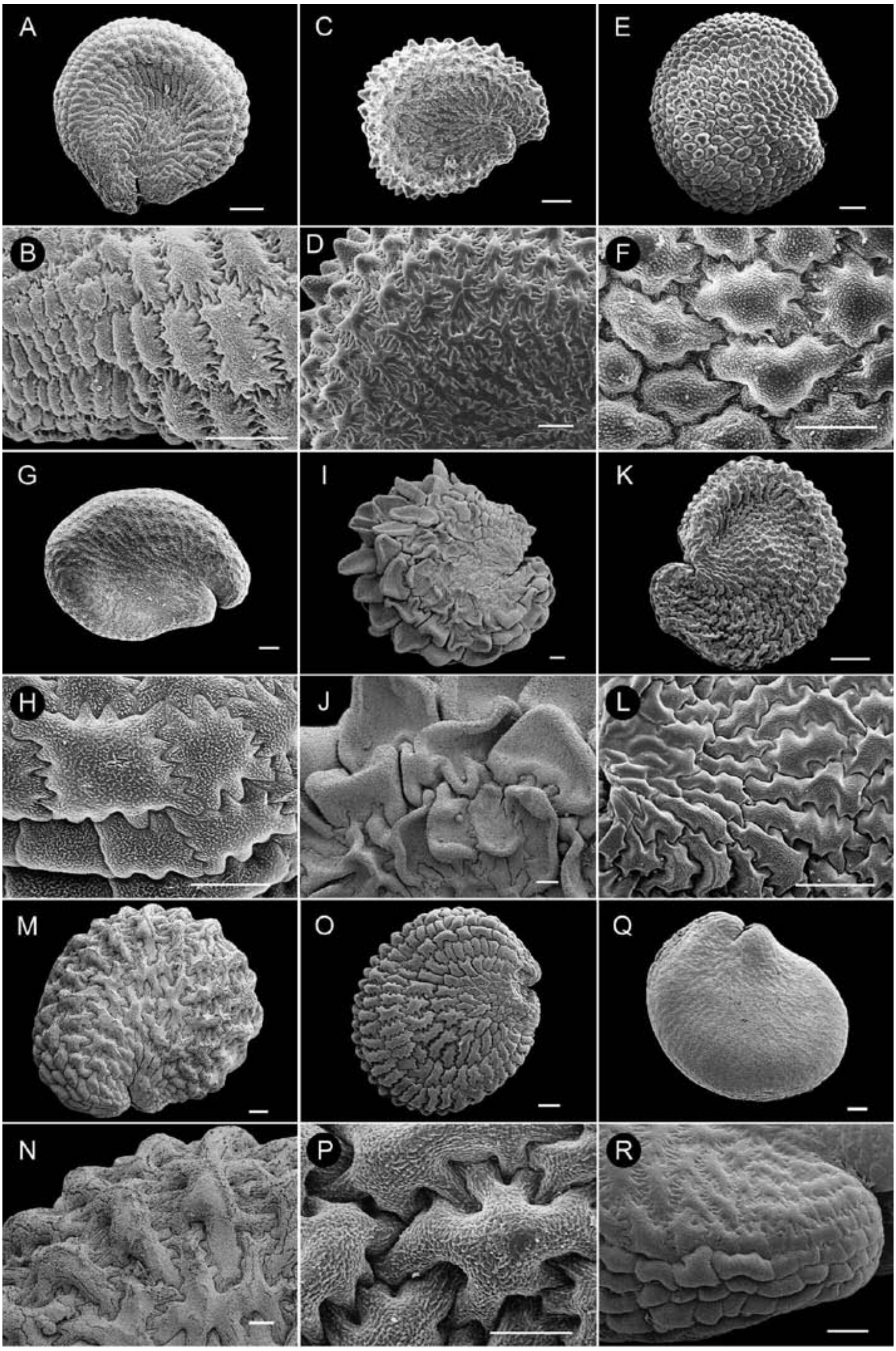

FIG. 3. Scanning electron micrographs of seeds of *Schiedea*. A, B. *S. membranacea* (*Flynn 1230*). C, D. *S. attenuata* (*Wood 1394*) holotype. E, F. *S. verticillata* (*Herbst 1401*). G, H. *S. lychnoides* (*Nagata 2123*). I, J. *S. obovata* (cult. from *Weller & Sakai 868*). K, L. *S. apokremnos* (1984, *Corn s.n.*). M, N. *S. hawaiiensis* (s.d., *PTA personnel s.n.* [cult. *Weller & Sakai 932*). O, P. *S. pentandra* (*Hutchinson et al. 7368*). Q, R. *S. diffusa* subsp. *diffusa* (cult. from *Weller & Sakai 848*). Scale bar: A, C, E, G, I, K, M, O, Q = 100 µm; B, D, F, H, J, L, N, P, R = 50 µm.

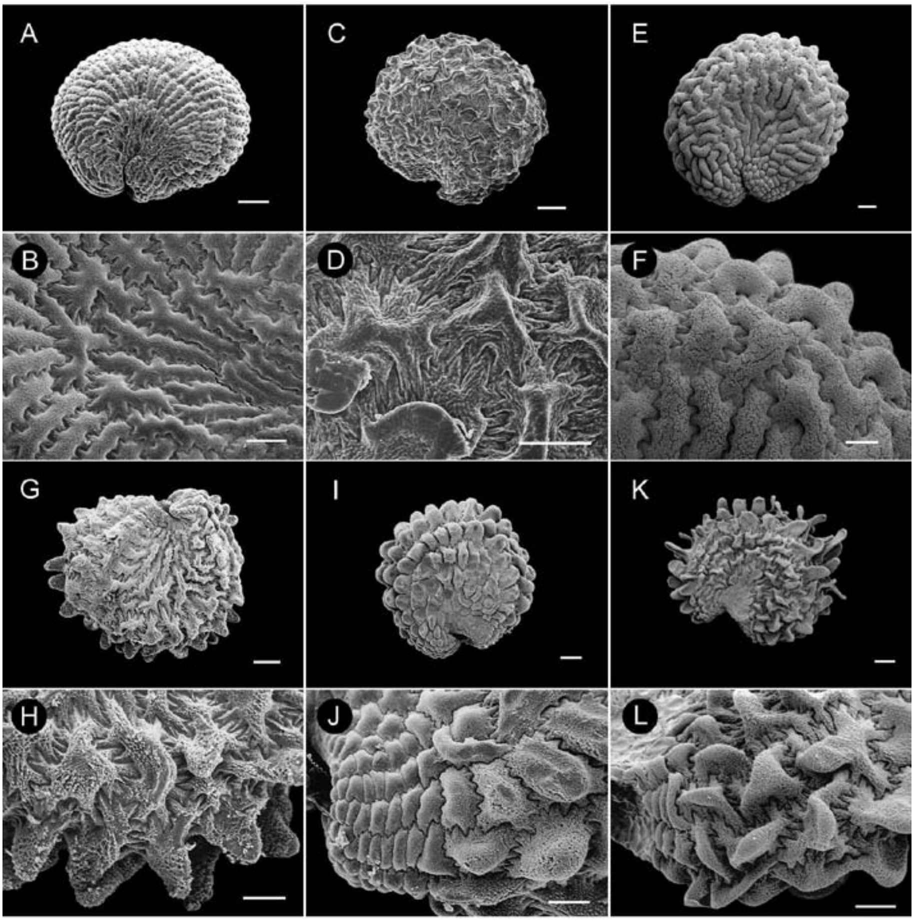

FIG. 4. Scanning electron micrographs of seeds of *Schiedea*. A, B. *S. kealiae* (*Weller & Sakai 791*). C, D. *S. haleakalensis* (27 July 1991, *Weller & Sakai s.n.* [cult. *Weller & Sakai 851*]). E, F. *S. globosa* (March 1994, *Weller & Sakai s.n.* [cult. *Weller & Sakai 906*]). G, H. *S. lydgatei* (*Stemmermann & Montgomery 3876*). I, J. *S. salicaria* (*Weller & Sakai 842*). K, L. *S. adamantis* (*Weller & Sakai 847*). Scale bar: A, C, E, G, I, K = 100 µm; B, D, F, H, J, L = 50 µm.

convexity, and the presence or absence of papillae along the cell margin. The simplest cell types are found in *S. verticillata*, which has uniformly micropapillate, isodiametric cells unique to this species (Fig. 3E, F). Cells are nearly uniform in size at the central and marginal portions of the seed surface. The moderately undulate cell boundaries are conspicuously channeled. Seeds are of intermediate size for the genus. In the remaining species of these five sections the surface cells are often elongated, and the elongated cells are arranged in rows near the outer margin of the seed in some species (Figs. 3, 4). The degree of elongation and regularity of cell shape varies markedly among the species.

In sect. *Schiedea*, *S. adamantis*, *S. haleakalensis*, *S. ligustrina*, *S. lydgatei*, and *S. salicaria* are characterized by papillate seeds with papillae on the seed margins (Fig. 4). Papillae are larger in *S. adamantis* and *S. lydgatei*, moderately developed on *S. haleakalensis* and *S. salicaria*, and variably developed on *S. ligustrina*. The papillae of these species resemble those of seeds of sections *Nothoschiedea* and *Alsinidendron*, although the habitats of the species are very different. Cell margins of *S. adamantis*, *S. ligustrina*, *S. lydgatei*, and *S. salicaria* are acutely lobed, in contrast to those of other species of *Schiedea*.

The effects of habitat differences on seed morphology in *Schiedea* are predicted in broad ecological surveys and more detailed studies of the adaptive significance of seed morphology (Baker 1972; Weller 1985; Baskin & Baskin 1998). Comparative studies indicate that selection favors large seed size in either shaded, usually moist environments or in xeric habitats. In these habitats, large seed size is adaptive because it permits establishment under conditions of rigorous competition or dry conditions. Expectations based on these correlations are borne out in most species of *Schiedea*. Mesic and wet forest species, including *S. lychnoides*, *S. viscosa*, *S. obovata*, *S. trinervis*, *S. diffusa*, and *S. kaalae*, have the largest seeds found in *Schiedea*. Large seeds are also found among those species occurring in the driest habitats, including *S. adamantis*, and *S. salicaria*. Not all species of *Schiedea* match expectations for seed size: *S. spergulina* and *S. apokremnos*, species of dry habitats on Kaua`i, have much smaller seeds than expected on the basis of habitat distribution.

Papillate margins are found in species occurring in ecologically extreme environments, such as the wet forests of the higher elevations of O`ahu (*S. trinervis*), and the very dry slopes of Diamond Head Crater (*S. adamantis*). One function of surface sculpturing may be to increase energy exchange and lead to greater cooling, as seeds cannot cool through transpiration (Barthlott 1981). This explanation may account for the papillae of species like *S. adamantis*, but it cannot account for the similar papillae of species occurring in mesic and wet areas.

Among species of *Schiedea*, retention of mature seeds on the placenta within open capsules is found only in *S. jacobii*. *Schiedea diffusa*, *S. lychnoides*, and *S. viscosa* retain seeds within closed capsules. Seedlings of *S. diffusa* have been observed germinating within disintegrating capsules still attached to the plant. This trait may provide an advantage during establishment in wet habitats. Whether precocious germination occurs in *S. jacobii* is unknown, although seeds eventually disperse from capsules under greenhouse conditions.

PHYLOGENY

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PREVIOUS ANALYSES

Phylogenetic relationships of *Schiedea* have been investigated using morphological, molecular, and biochemical characters in several previous studies, and we present additional data here from phylogenetic analyses of combined nuclear ribosomal ITS+ETS sequences and a revised morphological dataset. Earlier phylogenetic studies of *Schiedea* were carried out using morphological traits, and chloroplast and nuclear ribosomal DNA restriction site variation (Wagner et al. 1995; Weller et al. 1995; Soltis et al. 1997; Sakai et al. 1997b). Allozyme variation also was used for phylogenetic analysis by minimizing changes in allele frequency along branches (Swofford & Berlocher 1987; Weller et al. 1996). In these previous studies, morphological and molecular data were analyzed separately, and then combined to produce phylogenies to determine how geographic and ecological shifts affected the evolution of breeding systems.

Initial identification of a continental sister group for outgroup comparison proved difficult for *Schiedea*, because the Caryophyllaceae are largely temperate or boreal, with only a few tropical representatives (Pax & Hoffman 1934), and *Schiedea* species are morphologically divergent from continental representatives of the family. The difficulty in identification of the sister group was compounded by the lack of information on intergeneric relationships within the Alsinoideae. McNeill (1962) described *Schiedea* and *Alsinidendron* as aberrant members of the "*Arenaria* complex," but also suggested that these genera might be better placed in subfam. Paronychioideae. The presence of exstipulate leaves, capsules splitting into as many valves as styles, and distinct sepals clearly align *Schiedea* with the exstipulate Alsinoideae. Floral nectaries in *Schiedea* are very distinctive within the subfamily (see Morphology), and serve as the key feature delineating *Schiedea* as a monophyletic group. Nectaries in *Schiedea* were thought to be most similar to nectary extensions found in *Minuartia howellii* (S. Wats.) Mattf. and *M. douglasii* (Torr. & Gray) Mattf. (Wagner et al. 1995).

Forty-three morphological characters were used in previous phylogenetic reconstruction (Wagner et al. 1995; Weller et al. 1995). Outgroup comparison was used to determine the plesiomorphic state. Because of difficulties in specifying the most likely sister group for the morphological analysis, a generalized outgroup was used for all searches (Wagner et al. 1995; Weller et al. 1995). In addition to the morphological characters, forty-six cpDNA and three rDNA restriction site mutations were used for phylogenetic analysis (Soltis et al. 1997). *Moehringia lateriflora* (L.) Fenzl (Alsinoideae) and *Silene struthioloides* A. Gray (Caryophylloideae) were used as outgroups in these previous restriction site analyses.

In the previous analyses, using only those morphological characters presumed to be independent of the evolution of dioecy, six equally parsimonious trees with 132 steps were obtained using PAUP (Wagner et al. 1995; Weller et al. 1995); the strict consensus (Fig. 5) shows the presence of five distinct clades, four major clades (named for convenience), and one consisting only of the extinct *S. amplexicaulis*. Variation in topology occurred in the position of *S. amplexicaulis* and the degree of resolution within the *S. globosa* clade.

Analysis of morphological characters indicated the occurrence of a basal clade (the *S. membranacea* clade) consisting mostly of species bearing broad, multi-nerved leaves with ciliate or toothed margins (Fig. 5). Although bootstrap analysis of the morphological characters revealed no support for the basal clade as a whole, several lineages within the clade were strongly supported by morphological and molecular data (Fig. 5: Weller et al. 1995; Weller et al. 1996; Fig. 6: Soltis et al. 1997).

The *S. adamantis* clade (Fig. 5), with the exception of *S. apokremnos*, was weakly supported at the 52% level in the bootstrap analysis (Weller et al. 1995). Leaves broadest at or above the middle characterize species in the clade. Additional synapomorphies for all species, except *S. apokremnos*, were papillate seeds and acute margins on the epidermal cells of the seeds. The *S. adamantis* clade was delimited by a chloroplast restriction site mutation, and an additional restriction site mutation delimited the *S. lydgatei*–*S. salicaria* sister grouping (Soltis et al. 1997). Restriction site analysis weakly supported the inclusion of *S. kealiae* in the *S. adamantis* clade (Fig. 6), which in view of the distinctly different morphology of *S. kealiae* may indicate the occurrence of past hybridization.

The *S. nuttallii* clade (Fig. 5), delimited by the presence of fleshy stems in most species, large leaves with a single vein, and attenuate to caudate, strongly reflexed sepals,

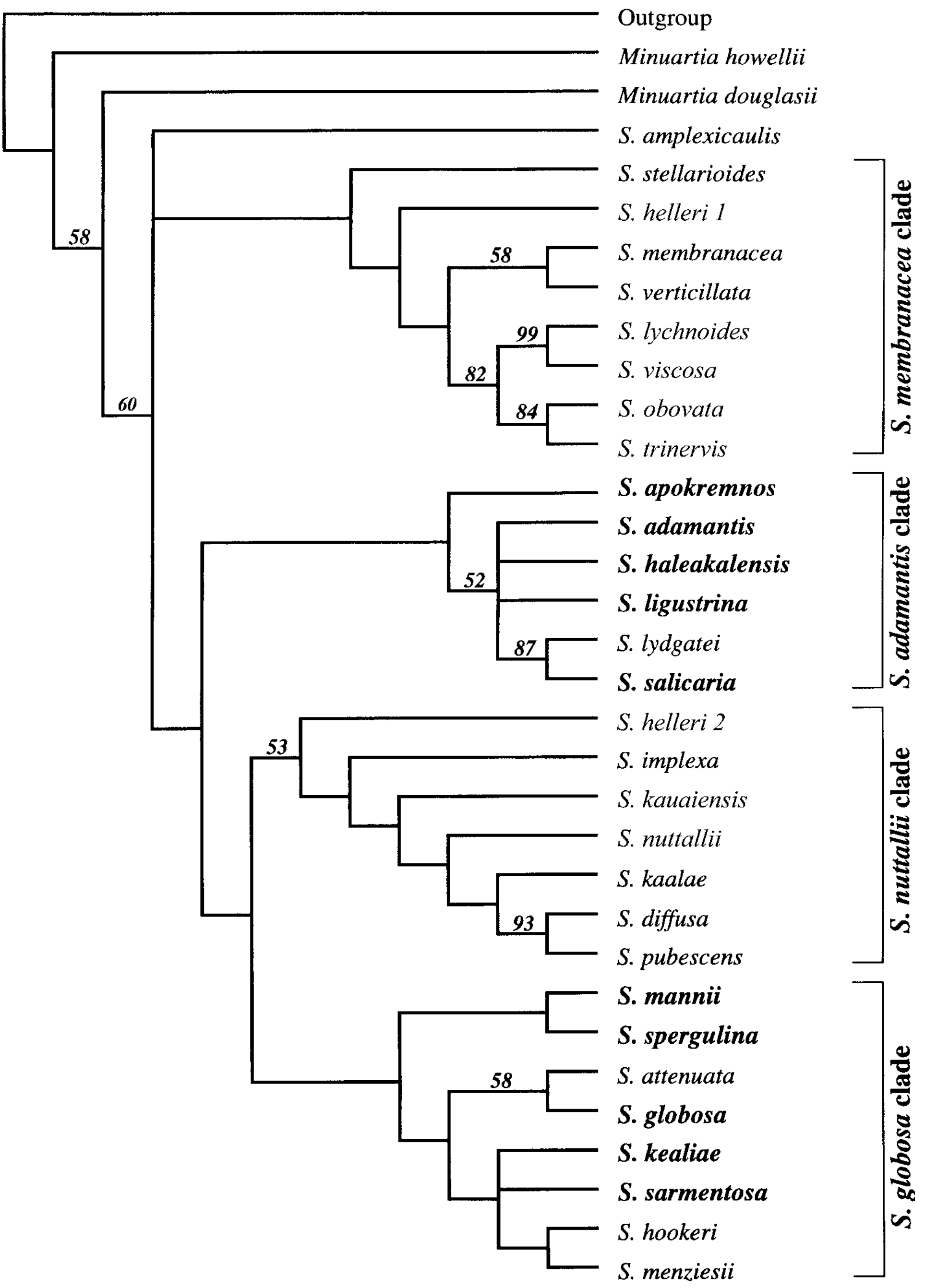

FIG. 5. Strict consensus of six equally parsimonious trees in morphological analyses showing presence of four major clades, named for convenience (Wagner et al. 1995; Weller et al. 1995). Names printed in boldface indicate species with dimorphic breeding systems.

was weakly supported using bootstrap analysis (53%). A single rDNA restriction site mutation delimited the *S. nuttallii* clade (Soltis et al. 1997). Analysis of allozyme variation provided additional support for this clade (Weller et al. 1996).

The *S. globosa* clade (Fig. 5) was delimited by a single morphological synapomorphy, the presence of long, attenuate leaf tips, but was not supported by bootstrap analysis. Two alternative trees involved different arrangements of *S. hookeri*, *S. menziesii*, *S. kealiae*, and *S. sarmentosa* (Wagner et al. 1995). No molecular characters were found that linked species in the *S. globosa* clade (Soltis et al. 1997).

CURRENT STUDY

Sampling. To examine relationships among the extant species of *Schiedea*, we performed an "ingroup" analysis including 32 accessions of *Schiedea*, representing 32 species (two extinct species, *S. amplexicaulis* and *S. implexa* were excluded) with seven taxa sampled as outgroups from among the most closely related groups identified in a global analysis of phylogenetic relationships within the Caryophyllaceae (Nepokroeff et al. unpubl.). Relationships among species of *Schiedea* were examined using nr ITS and ETS sequences and a revised dataset of 61 morphological characters. ETS sequences were not obtained for several outgroup species, including: *Geocarpon minimum* Mackenzie, *Minuartia rossii* (R. Br.) Graebr., *Minuartia moehringioides* (DC.) Mattf., *Scleranthus biflorus* Hook. f., *Wilhelmsia physodes* (Fisch ex DC.) McNeill, and *Honckenya peploides* (L.) Ehrh.-Oregon population. ETS sequences were also not available for two ingroup taxa, *Schiedea nuttallii* and *S. laui*. A more detailed analysis, addressing both the date of origin and diversification of *Schiedea*, and utilizing additional loci and methods, will be presented elsewhere.

Outgroups were previously determined using sequence analysis of *mat*K, *trn*L-F, and ITS and ETS genes (Nepokroeff et al. unpubl.). The extant sister group to *Schiedea* is a clade comprising *Honckenya peploides* and *Wilhelmsia physodes*, species with circumboreal and Alaskan to northeastern Asian distributions, respectively.

DNA extraction, amplification, and sequencing. DNA was extracted using one of three methods. Most ITS and ETS sequences were amplified from DNAs extracted according to Soltis et al. (1997). Several sequences were amplified from DNAs extracted using the DNeasy Plant Mini Extraction Kit (Qiagen, Inc., Valencia, CA), either at the Smithsonian Institution or the University of South Dakota: *Geocarpon minimum*, *Minuartia rossii*, *Minuartia moehringioides*, *Scleranthus biflorus*, *Wilhelmsia physodes*, *Honckenya peploides* (Oregon and Baffin Island populations), *Schiedea hawaiiensis*, S. *laui*, *S. viscosa*, *S. lychnoides*, *S. trinervis*, *S.adamantis*, *S. membranacea*, *S. salicaria*, *S. perlmanii*, *S. diffusa*, and *S. jacobii*. ITS sequences were generated using standard PCR protocols from the Soltis lab, with the exception of seven outgroup taxa and ten *Schiedea* accessions (*Schiedea trinervis*, *S. membranacea*, *S. globosa*, *S. salicaria*, *S. perlmanii*, *S. diffusa*-Maui, *S. jacobii*, *S. hawaiiensis*, and *S. laui*), which were generated either at the Smithsonian's Laboratory of Molecular Systematics or the University of South Dakota. ITS sequences generated at Smithsonian or the University of South Dakota facilities were amplified using protocols described in Nepokroeff et al. (2003); the primers LEU1 and ITS 4 were used for both amplification and sequencing in both directions. DNAs used for amplification of the ETS region were extracted in the Sakai-Weller lab at UC-Irvine using a modified CTAB protocol (Doyle & Doyle 1987). All ETS sequences were generated at the Smithsonian facility or the University of South Dakota using methods described in Nepokroeff et al. (2003). Long distance PCR was used to generate initial partial 3’ETS sequences from a fragment spanning the entire IGS region. Subsequently, a 5’primer specific to Hawaiian *Schiedea* (ETS Als2: ACC ACA CTA AAC GAA GCG) was designed and used together with 18s/etsR (Baldwin & Markos 1998) to amplify an approximately 525 bp fragment, using standard PCR, with either ProMega Taq or AmpliTaq. The region was amplified using the protocol described by Baldwin and Markos (1998). This 3’ETS region was sequenced for both strands using the amplification primers. Dideoxy sequencing was performed in a 10 ml final volume using the BigDye Terminator cycle sequencing kit (Perkin-Elmer, Applied Biosystems) or using Beckman sequencing reagents, following the manufacturer’s instructions. Sequencing reactions were cleaned by ethanol precipitation according to the manufacturer’s instructions. Sequences were analyzed at the Smithsonian facility on an ABI 377 Automated Sequencer, sent to Iowa State DNA Sequencing facility or analyzed on a Beckman CEQ 8000 Genetic Analyzer at the University of South Dakota. Sequence fragments were assembled and edited using Sequencher v. 4.1 software (GeneCodes Corp., Ann Arbor, MI). Alignment of sequences for the ITS and ETS regions was trivial due to low number of base substitutions and indels, and alignment was accomplished by hand. All sequences were deposited in GenBank (see Appendix 1 for GenBank Accession Numbers).

Morphological partition. Sixty-one morphological characters were scored (Appendix 2, 3), including 43 newly revised characters published in previous analyses (Wagner et al. 1995; Weller et. al. 1995). Several of the traits were used only for mapping the trait onto the phylogeny and are indicated as excluded in the character list (Appendix 2).

Phylogenetic Analysis. Maximum parsimony, maximum likelihood, and Bayesian inferences were conducted. Maximum parsimony analyses were performed using unweighted parsimony for both nucleotide (ITS and ETS regions) and morphology partitions, both separately and combined. Maximum likelihood searches on the molecular partition alone utilized an iterative approach (Sullivan et al. 1997) to evaluate models and then optimize model parameters for an initial set of trees resulting from parsimony analyses, after which analyses were conducted under the fully defined model parameters. ModelTest 3.0 (Posada & Crandall 1998) was used to evaluate models of DNA substitution that best fit the data, using the first MP tree to estimate starting parameters. Parameters were selected corresponding to the general time reversible corrected for among site rate variation using a discrete approximation of the gamma (GTR+ G). Estimated parameters were then fixed and a full heuristic ML search was conducted. MP and ML searches were implemented using PAUP* v. 4.0b10 (Swofford 2001). Bayesian analyses were conducted using MrBayes v. 3.0 (Huelsenbeck & Ronquist 2001) using both molecular and morphological partitions. The datatype was designated as “mixed” (both DNA and “standard”) and two default partitions were recognized. Only a single outgroup was used in Bayesian analyses due to missing data in other outgroup taxa. Likelihood settings for the molecular partition employed nst= 6 and rates=gamma (GTR+ G model as described above for likelihood searches), and a separate rate multiplier was specified for the morphological partition using ‘prset ratepr=variable’ for the morphological partition. Markov chain Monte Carlo (MCMC) runs used two analyses, the first of 150,000 generations and the second of 1 million. Four simultaneous Monte Carlo chains were run, saving trees every 100 generations, and trees found before stationarity of negative log likelihood scores was achieved (the first 1000 trees) were discarded as part of the burn-in period (Huelsenbeck & Ronquist 2001).

Results. Combining data sets of ITS+ETS sequence data and morphology resulted in 222 parsimony informative characters. The combined data analyzed together using equal weighting for all characters under the parsimony criterion resulted in 24 most parsimonious trees with a length of 613. The strict consensus of this tree is shown in Plate 2. Bootstrap values are indicated above branches. The combined ITS+ ETS partitions yielded a single best likelihood tree with a negative log likelihood score of -4852.35246 and a single Bayesian consensus tree was generated. Neither ML or Bayesian consensus trees are shown here. The ML and Bayesian consensus trees are congruent in topology (identical if hard polytomies recovered in the ML tree are compared with soft polytomies in the Bayesian consensus tree). The topology of the MP and ML/Bayesian trees are highly congruent and differ in only minor ways. First, the relative positions of *S. verticillata* (sect. *Polyneura*) and *S. attenuata* (sect. *Leucocalyx*) are reversed in the ML and Bayesian trees with respect to the MP trees, although the position of these two taxa in the MP analyses is not supported by MP bootstrap analyses. Second, although the composition of sect. *Mononeura* and sect. *Schiedea* is identical in both MP and ML/Bayesian analyses, the position of *S. apokremnos* as sister to the rest of the sect. *Mononeura* clade is not recovered in the ML/Bayesian consensus trees. Instead, the clade containing *S. stellarioides*, *S. perlmanii*, and *S. kauaiensis* is strongly supported with a posterior probability value of 98% as sister to the rest of sect. *Mononeura* in the Bayesian consensus tree, with *S. diffusa* (81% posterior probability) followed by *S. apokremnos* (98%) the next to branch off. The remaining taxa of sect. *Mononeura* are unresolved in a major polytomy in both the MP and the ML/Bayesian consensus trees, with the minor exception of *S. pubescens*, which is strongly associated with *S. pentandra* (95% bootstrap support) in the MP trees, but weakly associated (67% posterior probability) with *S. kaalae* in the ML/Bayesian trees.

The sect. *Schiedea* clade is identical in species composition in both MP and ML/Bayesian trees with only minor (unsupported) differences in topology of external tips. Hard polytomies in all MP, ML and Bayesian trees in this clade indicate extremely short or zero-length branches within members of this lineage. Only *S. salicaria*, *S. ligustrina*, *S. kealiae*, *S. adamantis*, and *S. spergulina* form a weakly supported clade, with identical topology in MP and ML/Bayesian analyses.

Relationships in Schiedea. Using the ITS and ETS regions of the nuclear genome provides additional support for some of the earlier results based on previous molecular and morphological analyses. Direct comparisons of the two data sets are not always possible; although all taxa were used in the ITS/ETS study, fewer species were sampled for the cpDNA restriction site analysis (Soltis et al. 1997; Fig. 6). Relatively few strongly supported synapomorphies were detected using ITS and ETS sequences, but when combined with a revised and expanded morphological data set, a basal clade consisting of *S. helleri* and *S. membranacea* (sect. *Alphaschiedea*) is strongly supported, as is the monophyly of the genus (Plate 2). The new analysis also strongly supports sections *Nothoschiedea* and *Alsinidendron* and their relationship to each other. Weak support is seen for the clade consisting of sections *Nothoschiedea* and *Alsinidendron* plus *S. verticillata* (sect. *Polyneura*) and *S. attenuata* (sect. *Leucocalyx*). Moderate support is obtained for a basal clade in sect. *Mononeura* comprising the Kaua`i species *S. stellarioides*, *S. perlmanii*, and *S.*

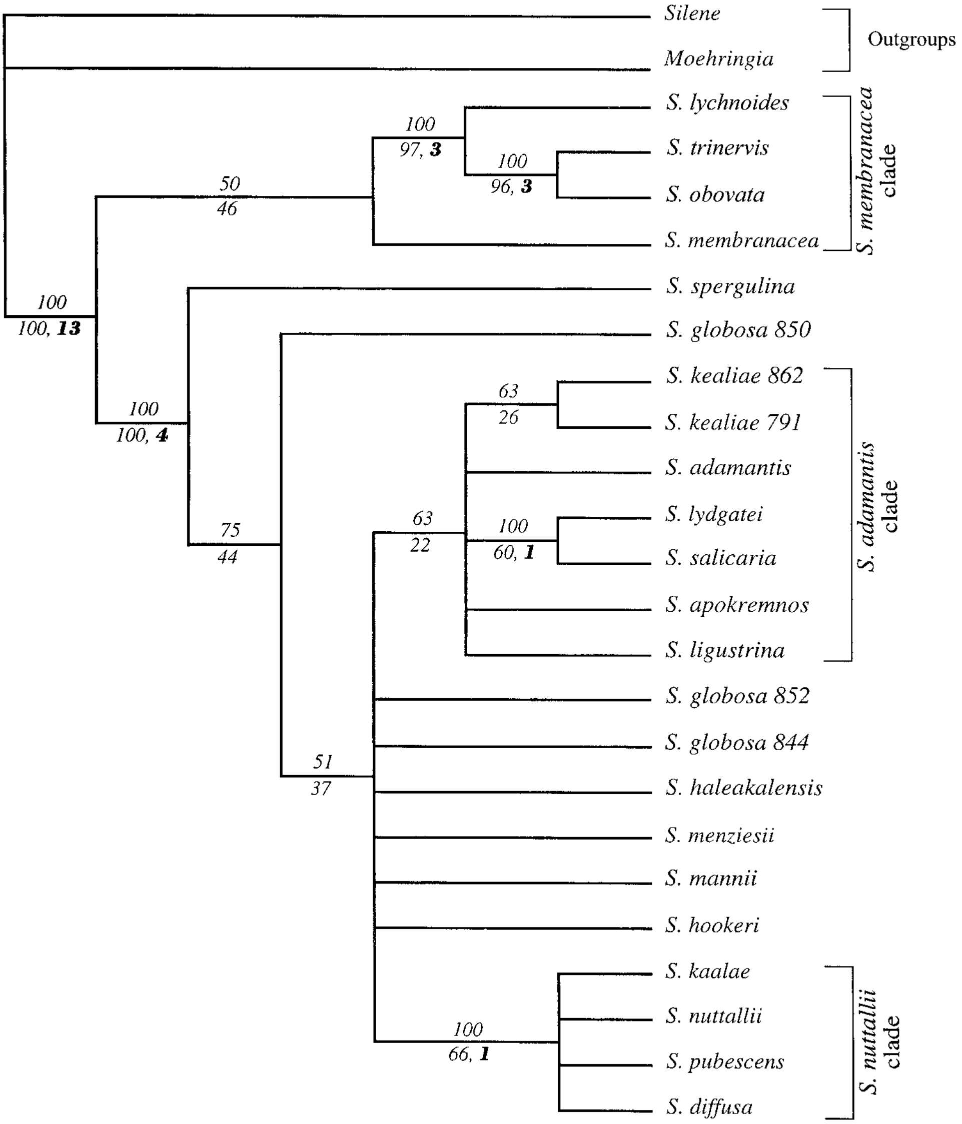

FIG. 6. Majority-rule consensus of 870 most parsimonious trees resulting from analysis of cpDNA and rDNA restriction site data. The analysis of cpDNA data alone produced the identical topology, except that the *Schiedea nuttallii* clade of Weller et al. (1995) is not recognized. Numbers above branches are the percentage of these 870 trees that support the branches; numbers below branches are bootstrap percentages and decay values (bold), respectively. Clades not present in all shortest trees have a decay value of 0. Adapted from Soltis et al. 1996.

kauaiensis. A sister relationship for *S. pubescens* and *S. pentandra* is also strongly supported in the MP analysis, but is not recovered in the ML/Bayesian analyses. Using ITS and ETS sequences, in combination with morphological data, there is moderate support for an expanded clade consisting of the previously delimited *S. adamantis* and *S. globosa* clades (Wagner et al. 1995; Weller et al. 1995; Sakai et al. 1997b), but not for the

S. membranacea and *S. nuttallii* clades of the earlier studies. The *S. nuttallii* clade (sect. *Mononeura* minus *S. stellarioides*) does appear in all 24 MP trees and ML/Bayesian trees, although boot strap values are below 50%.

TAXONOMIC CRITERIA

Sections. Sections are recognized for *Schiedea* because of the diversity in the lineage and the occurrence of clades consistently identified using diverse data sources. *Schiedea* represents a striking adaptive radiation and stands alone among Hawaiian angiosperms in the number of evolutionary shifts that have occurred in the course of its diversification. These shifts in breeding system, pollination mode, ecological adaptation, and geographic distribution are accompanied by substantial morphological discontinuities. Formal subdivision therefore seems desirable in order to give convenient names to these groups, which have taken such divergent evolutionary paths. Sectional names identify the most distinctive, but not all, of the subclades, which were discerned by a combination of either moderate to high bootstrap support (>60%) derived from morphological or molecular characters identified in the most recent and comprehensive phylogenetic study, or in some cases, by striking morphological discontinuity (in the absence of strong bootstrap support). Some clades do not have morphological support, although there is at least some molecular support. Application of this approach resulted in some unispecific sections (sections *Anestioschiedea*, *Leucocalyx*, and *Polyneura*) and two large sections (sections *Mononeura* and *Schiedea*). We did not group the highly distinctive species of sects. *Alsinidendron* and *Nothoschiedea* with *S. attenuata* (sect. *Leucocalyx*) and *S. verticillata* (sect. *Polyneura*), because such heterogeneous grouping would produce an assemblage lacking in morphological diagnostic characters. By contrast, it would seem desirable to subdivide species of section *Schiedea*, the largest of the sections, but this was not possible, because the members form a grade; the diagnosable subgroups (*globosa* and *adamantis* clades of earlier studies) are not recovered in analyses using molecular data. The end result of our approach is a series of recognizable monophyletic groups, which are sometimes robustly supported by the phylogenetic study and are not in any case at odds with the less robust portions of it.

Species. Species circumscriptions in *Schiedea* are based on all available evidence gathered in the herbarium and the field, and from experimental studies of breeding systems and phylogenetic analyses. We have tried to apply uniform criteria throughout our work on *Schiedea*. Herbarium, field, and experimental studies, including morphological, geographical, ecological, and cytological data have been taken into account. Our classification is especially influenced by the combination of diagnosable groups discerned from evidence from morphology, breeding systems, and current phylogenetic hypotheses, although our species concept remains largely based on both morphology and geography. Our field studies have been augmented by extensive assistance from Hawaiian field botanists, many of whom provided material used to propagate plants in the greenhouse. With the exception of two extinct species, all species descriptions and the key are based on living material grown in cultivation.

Species of *Schiedea* in this treatment are characterized by character complexes (e.g., correlated characters) with inherent discontinuities from other species. The degree and nature of the discontinuities of correlated morphological characters expressed in the Hawaiian flora are variable, with species distinctiveness varying among species in the same lineage, often in relation to island age (Wagner et al. 1990). In recognizing species we have emphasized changes in breeding systems correlated with discrete floral and vegetative characters. In all cases, changes in breeding system are also correlated with habitat and geographical discontinuities. Many species of *Schiedea*, especially those from older islands where extinction of intermediate forms may have occurred, are readily distinguished from all other species (e.g., *S. helleri*, *S. kaalae*, *S. stellarioides*, *S. trinervis*, and *S. verticillata*). Other species, especially those on younger islands, are less readily separated from their congeners. For example, in the *S. nuttallii* group, *S. laui* was initially viewed as a rediscovery of *S. nuttallii* on Moloka`i, albeit in a wetter habitat at higher elevations than is typical for *S. nuttallii* on O`ahu. Yet, plants grown in the greenhouse showed a number of morphological differences from *S. nuttallii*. Flowers of all plants were completely cleistogamous, whereas *S. nuttallii* on O`ahu has protandrous flowers and is primarily outcrossing. Initially, we planned to recognize *S. laui* as a subspecies of *S. nuttallii*, but it failed to group with *S. nuttallii* in phylogenetic analyses, and therefore we recognize *S. laui* as a distinct species. In a parallel situation, *S. jacobii* superficially resembles *S. nuttallii* but occurs allopatrically at higher elevations in very wet forests. *Schiedea jacobii* is autogamous and produces seeds that are retained in capsules, a characteristic feature of wet forest species of *Schiedea*. Similarly, *S. perlmanii* was initially grouped with *S. nuttallii*, but plants grown in the greenhouse uniformly differed from *S. nuttallii* in their vining (vs. erect) habit and in details of the inflorescence and flowers. The two species are also completely allopatric on different islands.

BIOGEOGRAPHY

Schiedea has colonized six of the eight main islands of the Hawaiian archipelago. Most species are restricted to a single island, but 6 of the 34 species occur on more than one island. Earlier phylogenetic analyses (Wagner et al. 1995; Weller et al. 1995) indicated a basal Kaua`i clade (4.7 Ma, based on Clague 1996), the oldest of the current major Hawaiian Islands. Similar patterns occur using the more comprehensive phylogenetic results presented here (Plate 3) with a reconstruction using MacClade 4.0 (Maddison & Maddison 2000). There is a basal *S. membranacea*-*S. helleri* clade (sect. *Alphaschiedea*) on Kaua`i, followed by the clade with *S. attenuata* (sect. *Leucocalyx)*, *S. verticillata* (sect. *Polyneura)*, and sections *Nothoschiedea* and *Alsinidendron* that also appears to originate on Kaua`i. *Schiedea obovata* and *S. trinervis* (sect. *Alsinidendron*), closely related species occurring in the Wai`anae Mountains (3.0 Ma, based on Clague 1996), represent a colonization to the younger island of O`ahu.

Schiedea stellarioides, *S. perlmanii*, and *S. kauaiensis*, basal species in sect. *Mononeura*, are found on Kaua`i, with more recently derived species of this section occurring on the younger Hawaiian Islands (Plate 3). One of the most widely distributed species in this clade, *S. nuttallii*, was once found on O`ahu, Moloka`i, and West Maui before the Moloka`i and West Maui populations were extirpated (Table 1). A Maui Nui origin is indicated for the base of the sect. *Schiedea* clade. Coding Moloka`i, Maui, and

Lana`i as a single island (Maui Nui, 1.2–2.0 Ma) is reasonable, because for long periods these islands were connected (Carson & Clague 1995; Clague 1996; Price & Elliott-Fisk 2004). If the base of the terminal sect. *Schiedea* clade originated on Maui Nui, back colonizations would be necessary to explain the occurrence of several species on O`ahu and Kaua`i. This senario is unlikely, given the general tendency for species to colonize from older to younger islands in Hawai`i (Wagner & Funk 1995), and allozyme data indicating that colonization by *S. globosa*, a member of this clade, has proceeded from older to younger islands (Weller et al. 1996). More robust data are needed to resolve this problem.

The known ages of the Hawaiian Islands, coupled with our hypothesized phylogeny of *Schiedea*, show how missing taxa, either because they are undiscovered or extinct, may obscure patterns of origin and colonization (Wagner et al. 1995). Basal clades (represented by sections *Alphaschiedea*, *Nothoschiedea*, *Alsinidendron*, *Leucocalyx*, *Polyneura*, and *Anestioschiedea*), are largely restricted to Kaua`i at present, but it seems likely that these lineages may have originated and diversified on islands older than Kaua`i, and subsequently experienced significant extinction of all but the relatively few species occurring on Nihoa and Kaua`i. If Kaua`i was colonized by only a few elements of each of several clades, subsequent extinction may have resulted in the grouping of the morphologically divergent surviving species into several diverse basal clades. These diverse clades have fewer species than either of the remaining two clades, which are more homogenous lineages found largely on younger islands, where presumably there has been less extinction. The hypothesized diversification of the basal lineage could have occurred on Necker and Nihoa between 7.3 and 11 Ma, when these islands were considerably larger (Carson & Clague 1995; Price & Clague 2002). Erosion and subsidence of Necker and Nihoa over the next several million years would have led to the extinction of all but the now relictual members of the basal clades, including *S. verticillata* on Nihoa, and those species in other basal clades that were able to colonize the then young island of Kaua`i. Only two species in the basal clades, *S. obovata* and *S. trinervis* (sect. *Alsinidendron*), have colonized younger islands beyond Kaua`i.

The pattern of diversification evident for sect. *Mononeura*, where basal species occur on Kaua`i and more recently derived species are found on islands younger than Kaua`i, may represent the typical evolutionary pattern in *Schiedea*, but one that is rarely evident in its entirety either because only remnants of a lineage remain on an old island (basal lineages represented by sections *Alphaschiedea*, *Leucocalyx*, *Polyneura*, *Alsinindendron*, *Nothoschiedea*, and *Anestioschiedea*), or alternatively, because a new lineage has evolved on a young island and is not yet fully diversified (sect. *Schiedea*). In comparisons of diverse lineages within the Hawaiian biota, parallel inter-island colonization to younger islands is followed by major diversification occurring during the post-eruptive, erosional stage (Wagner & Funk 1995).

HABITATS

Species of *Schiedea* occupy diverse habitats ranging from dry coastal cliffs to wet forests and subalpine cliffs. Nearly all species within the basal clades (sections *Alphaschiedea*, *Nothoschiedea*, *Alsinidendron*, and *Polyneura*) and species of sect. *Mononeura* prefer mesic or wet habitats, while species in sect. *Schiedea* are usually found in dry habitats. Regardless of habitat, individuals usually occupy steep north-facing slopes or cliffs. The only exception is *S. lydgatei*, which occurs in dry shrubland on south-facing slopes on Moloka`i. Restriction of species to these habitats may in part reflect the activity of alien herbivores, which consume or trample *Schiedea* in accessible habitat (Sakai et al. 1995b). Plants have not been observed on steep, south-facing slopes, however, which suggests that apparent habitat restriction results from true preference for shaded, cooler slopes. During periods of active growth during the winter rainy season, many of these north-facing slopes receive sunshine only for a limited portion of the day because of the low angle of the sun.

Species occurring in dry habitats are found in rock crevices and on steep slopes in grassland or shrubland. Some dryland species (*S. globosa* and *S. apokremnos*) may occur within a few meters of the ocean. In contrast, *S. haleakalensis* occurs at 1770 to 2400 m on the dry interior slopes of Haleakala Crater. The density of species occurring on cliffs or in shrubland can be very high, and under some conditions species of *Schiedea* become a dominant component of the vegetation (Norman 1994). Species occurring in mesic forest are usually found in lower density, often as scattered individuals throughout the forest. The role of alien herbivores and introduction of competing alien plant species in modifying population size is unknown, although our field observations and comments from Hawaiian field botanists indicate that declines in population size have occurred in recent years (Weller & Sakai unpubl.; J. Obata pers. comm.; see Conservation below). Species occupying wet forest also have low population densities. Although pigs are often present in wet forests, some wet forests are relatively undisturbed, and low density may be a natural feature of these populations.

Carlquist (1995) suggested that *Schiedea* was the woodiest genus in Caryophyllaceae, and that lack of rays may indicate that woodiness in *Schiedea* is secondarily derived. *Schiedea* wood anatomy shows less variation than expected based on the range of habitats occupied by the species. Even *S. trinervis*, which occurs in very wet forests, shows relatively little divergence from wood of *Schiedea* species collected from dry habitats (Carlquist 1995). Although wood in Caryophyllaceae is usually highly xeromorphic, Carlquist found that in general, insular species of woody Caryophyllaceae showed more mesomorphic features in their wood than continental species occurring in dry habitats.

Significant physiological differences among species of *Schiedea* are associated with habitat variation. When measured in a common greenhouse environment, species occurring in wet or mesic habitats have lower rates of photosynthesis (A), stomatal conductance to water vapor (g), and water-use efficiency (A/g) than species occurring in dry habitats (Dawson, Sakai, Weller & Culley, unpubl.; Mishio, Sakai, Weller & Kawakubo, unpubl.). In dry habitats higher water use efficiency and a reduced tendency toward cavitation are associated with narrow leaves and production of woody tissue. All species of *Schiedea*, including those found in dry habitats, have high rates of transpiration when actively growing (Dawson, Sakai, Weller & Culley, unpubl.), which suggests that species found in dry sites have not evolved adaptations typical of xerophytes. Hermaphrodites of subdioecious *S. globosa* occupy more mesic sites in a population on O`ahu, possibly because of increased water usage for individuals producing both seeds and pollen (Sakai & Weller 1991).

Significant differences in phenology are associated with habitat. Species occurring in dry habitats have pronounced dormant periods correlated with the summer dry season (June–September) when plants are essentially leafless. Active growth and emergence of seedlings begins shortly after fall rains, usually in November or December. Flowering and fruiting take place from January through June, with a peak in March and April. Species occurring on leeward O`ahu (*S. adamantis*) and Maui (*S. menziesii*) appear to respond to infrequent Kona storms, intense winter storms that deposit heavy rainfall in areas that often receive very little rainfall from any other source. As a result, these species have very unpredictable flowering and fruiting episodes. Drought that began with the 1997 El Niño has resulted in severe declines in species occurring in leeward areas of the Hawaiian Islands, including the near extinction of *S. adamantis* (see Conservation below and discussion under this species, no. 34).

Species of *Schiedea* occupying mesic habitats with peaks of flowering in April, May, and June appear to flower later in the season than species growing in dry habitats. Species found in very wet habitats appear to flower and fruit the year around, with little evidence of synchrony tied to environmental cues. All species of *Schiedea*, regardless of habitat, appear to produce seeds with some innate dormancy. Dormancy is probably adaptive; seeds are formed at the end of the winter wet season. The extended dormancy delays germination until heavy winter rains begin in November or December, at least among species occurring in drier habitats.

When habitats are mapped onto the current phylogeny for this lineage, occurrence in mesic environments appears to be the basal condition (Plate 4). Transitions to wet environments have occurred on at least four, and possibly five occasions (*S. helleri*, *S. trinervis* and *S. viscosa*, representing one or two transitions, the ancestor of *S. diffusa* subsp. *diffusa* and *S. diffusa* subsp. *macraei*, and the ancestor of *S. jacobii* and *S. laui*). Shifts to dry habitats have occurred for *S. verticillata*, *S. apokremnos*, *S. hawaiiensis*, and for most species in sect. *Schiedea*.

BREEDING SYSTEMS

Ten of the 34 species of *Schiedea* possess gynodioecious, subdioecious, or dioecious breeding systems, which are collectively termed dimorphic (Table 1). The remaining taxa are hermaphroditic, and are outcrossing to fully autogamous. In species with gynodioecious breeding systems, populations contain pistillate (female) and hermaphroditic individuals; in subdioecious species, populations contain pistillate and staminate individuals as well as a small number of polleniferous individuals that produce some hermaphroditic flowers. Only pistillate and staminate individuals are found in dioecious species. Male sterility is controlled by recessive nuclear genes in *Schiedea* (Weller & Sakai 1991). Once females have appeared in populations, loss of female function in hermaphrodites leads to evolution of individuals with increasingly male function. Significant quantitative genetic variation for allocation to female and male function has been detected in *S. salicaria* (Sakai, Weller, Culley & Campbell, unpubl.), and there is little evidence for significant genetic correlations that might impede the evolution of separate sexes.

Dimorphic breeding systems promote outcrossing to varying extents, depending on the frequency of hermaphroditic and pistillate individuals in populations, and the extent of biparental inbreeding (outcrossing among related individuals). Autogamy, which occurs in eight hermaphroditic species of *Schiedea*, is nearly as common as dimorphism. *Schiedea* is one of eight lineages in the Hawaiian Islands where outgroup analysis indicates that dimorphism has evolved from hermaphroditism in the Hawaiian Islands (Sakai et al. 1995a, 1995b). This interpretation was initially based on the assumption that hermaphroditic *Minuartia* L. was sister to the Hawaiian *Schiedea* (Wagner et al. 1995; Weller at al. 1995). More recent evidence indicating that a clade consisting of *Honckenya* Ehrh.

and *Wilhelmsia* Rchb. is sister to *Schiedea* does not change this interpretation. Although *Honckenya* is dioecious (Takahiro & Sugawara 1992), phylogenetic analysis suggests that the common ancestor of *Honckenya* and *Wilhelmsia* was hermaphroditic; *Wilhelmsia* and related outgroup taxa are hermaphroditic. Moreover, the first three clades in the current phylogenetic analysis within *Schiedea* (Plate 5) consist of hermaphroditic species, indicating that hermaphroditism was likely the basal condition for the entire lineage. Autochthonous evolution of dimorphism, coupled with the wide variety of breeding systems in *Schiedea*, suggests that these species may provide an excellent model system for study of those factors important in the evolution of dimorphism.

Approximately 6% of angiosperms are dioecious (Renner & Ricklefs 1995). The rarity of this breeding system relative to hermaphroditism has usually been attributed to the ability of hermaphroditic individuals to contribute gametes through ovules and pollen, whereas in dioecious species one sexual function is absent (Charlesworth & Charlesworth 1978; Geber et al. 1999; Sakai & Weller 1999). Presumed disadvantages to dimorphic breeding systems have led to concerted attempts to understand the causal basis for the evolution of separate sexes. Lewis (1941) first developed models showing that females should increase in frequency in populations only if they produced over twice as much seed as hermaphroditic individuals, if it is assumed that nuclear genes control expression of male sterility. Lloyd (1975) and Charlesworth and Charlesworth (1978) demonstrated that females could increase in populations if they produced more seed than hermaphrodites, or if the progeny of hermaphrodites produced through self-fertilization showed reduced fitness. The reduction in fitness associated with inbreeding is termed inbreeding depression. Conditions favoring the increase in frequency of females may be those where environmental changes, including a loss or shift in pollinators, result in a relatively sudden increase in the selfing rate, and the expression of inbreeding depression (Ganders 1978). Under such conditions, females producing outcrossed progeny would be likely to increase in frequency.

Primarily ecological factors have also been suggested as sufficient cause for the evolution of dioecy (Charnov 1982). For example, if unisexual individuals have higher fitness in certain microsites than hermaphroditic individuals, dioecy would be expected to evolve. The association between dioecy and small, generalist pollinators in the Hawaiian Islands and elsewhere (Sakai et al. 1995b) could be explained if larger, more specialized pollinators can discriminate against pistillate individuals that produce no pollen as a reward (Charlesworth 1993). Arguments stressing inbreeding depression and those emphasizing ecological factors in the evolution of dioecy may be complementary, and it is likely that several factors play a role in the evolution of dioecy.

To evaluate the theoretical basis for the evolution of dioecy in *Schiedea*, the magnitude of inbreeding depression, selfing rates, and the relative seed production of females and hermaphrodites must be known. This information is available for several dimorphic and monomorphic species of *Schiedea*. Very high inbreeding depression ($d >$ 0.6) is characteristic of most species of *Schiedea* that have been investigated, including *S. adamantis* (Sakai et al. 1997a), *S. globosa* (Sakai et al. 1989), *S. lydgatei* (Norman et al. 1995), *S. membranacea* (Culley et al. 1999), *S. menziesii* (Rankin et al. 2002), and *S. salicaria* (Sakai et al. 1989). Selfing rates, based on isozyme variation of progeny grown from field-collected seed and estimated using Ritland and Jain's (1981) maximum likelihood procedure, are low (usually $s << 0.3$) for subdioecious *S. globosa* (Sakai et al. 1997a), as well as *S. lydgatei* (Norman et al. 1997) and *S. membranacea* (Culley et al. 1999). Hermaphroditism may be stable in *S. lydgatei* and *S. membranacea*, because low rates of selfing prevent the expression of inbreeding depression. In contrast, selfing rates of hermaphrodites are substantially higher ($s = 0.5$) in *S. adamantis* (Sakai et al. 1997a), *S. menziesii* (Rankin et al. 2002), and *S. salicaria* (Weller & Sakai, in press). *Schiedea adamantis* and *S. salicaria* are gynodioecious, and the occurrence of high inbreeding depression and moderately high selfing rates in these species may explain the presence of females (Weller & Sakai 1990; Sakai & Westneat 2001). There is little evidence that shifts in resource allocation have promoted the initial increase in frequency of females in *S. salicaria*; in two populations where seed and fruit production have been investigated, there is no evidence for consistently higher reproductive output for females relative to hermaphrodites (Weller & Sakai 1992, in press). *Schiedea menziesii* is hermaphroditic, although females have appeared among progeny raised in the greenhouse. The failure of females to increase in frequency in the field may result from the absence of biotic pollen vectors or adaptations to wind pollination (Weller et al.1998; Rankin et al. 2002).

Eight species of *Schiedea* are facultatively or obligately autogamous (Table 1). Schemske and Lande (1985) suggested that highly self-fertilizing species should be purged of deleterious mutations causing inbreeding depression. More recent theoretical treatments indicate that a variety of factors may result in substantial inbreeding depression in highly selfing species (Charlesworth et al. 1990). Inbreeding depression has been detected in highly selfing *S. viscosa*, as predicted by recent theory (Weller, Sakai, Thai, Tom & Rankin, unpubl.). Autogamy is generally found in species occurring in wet habitats. Cleistogamy, which occurs in *S. laui, S. diffusa* subsp. *macraei*, and *S. trinervis*, is probably an adaptation to high elevation, very wet habitats. Our observations suggest that in very wet habitats, autogamy may limit exposure of pollen to rain, which may either wash pollen from flowers or cause pollen to burst. Additionally, visitation by insects capable of pollination may be rare in very wet habitats.

Striking differences in isozyme variation are associated with breeding systems (Weller et al. 1996). Dimorphic species and hermaphroditic species with outcrossing breeding systems are characterized by a high number of alleles per locus, a high percentage of polymorphic loci, and substantial heterozygosity. In contrast, isozyme loci of autogamous species are usually fixed for a single allele. Exceptions to these patterns result from founder effect and small population size. *Schiedea adamantis*, which possessed a gynodioecious breeding system and occurred in a single large population until recently, is nearly devoid of isozyme variation, presumably as a result of founder effect or population bottlenecks. A number of hermaphroditic species (*S. kaalae, S. nuttallii*, and *S. pentandra*) that require pollinators for fruit production also have low isozyme variability, probably because small population size has led to biparental inbreeding and loss of variability (Weller et al. 1996).

Phylogenetic analysis based on morphological characters and chloroplast restriction site variation (Figs. 5, 6; Wagner et al. 1995; Weller et al. 1995; Soltis et al. 1997; Sakai et al. 1997b) indicated that dimorphism has evolved on several occasions in *Schiedea*. Phylogenetic analysis based on ITS and ETS sequences, in combination with morphology (see Phylogeny), also indicates that dimorphism has evolved at least twice, although the sequence of evolutionary transitions is different (Plate 5). A reversal to hermaphroditism from a dimorphic ancestor may have occurred in *S. lydgatei* (Plate 5). When changes in habitat and breeding systems are compared (Plates 4, 5), phylogenetic evidence suggests that shifts to dry habitats are coincident with the evolution of dimorphism in *Schiedea*. At least two transitions to dry habitats, in *S. verticillata* and *S. hawaiiensis*, have occurred without the evolution of sexual dimorphism. The evolution of sexual dimorphism and a shift to dry habitats is coincident in *S. apokremnos*, while in sect. *Schiedea* a shift to dry habitats seems to have preceded the evolution of sexual dimorphism; *S. menziesii* in the sect. *Schiedea* clade is hermaphroditic, but occurs in dry habitats. A more strongly supported phylogenetic tree would be useful and might result in different interpretations.

POLLINATION

Field and greenhouse observations suggest that species of *Schiedea* are wind-pollinated, insect-pollinated, bird-pollinated, or autogamous. Dimorphic species are wind-pollinated; evidence has been obtained from wind tunnel studies and morphological correlates of wind pollination, including high pollen-ovule ratios, small pollen diameter, and often highly condensed inflorescences (Weller et al. 1998). Pollen-ovule ratios are well known indicators of pollination systems (Cruden 1977), and highly condensed inflorescences facilitate dispersal and receipt of pollen (Niklas 1985; Culley at al. 2002). Habitats of dimorphic species are often extremely windy with wind speeds of 30–50 kh^{-1}. Wind-pollinated species of *Schiedea* occur in dense populations, which is essential for successful wind pollination, because pollen transfer by wind is density-independent and drops sharply at short distances from the source (Levin & Kerster 1974; Culley et al. 2002).

In *Schiedea*, the degree of inflorescence condensation is positively correlated with the frequency of females in populations (Weller et al. 1998), suggesting that wind pollination may be poorly developed when females first appear in populations. For example, the inflorescences of gynodioecious *S. salicaria* are less condensed than the inflorescences of fully dioecious species. In addition, this species has larger pollen grains and a lower pollen-ovule ratio than species with higher frequencies of females. These observations indicate that *S. salicaria* is not as well adapted to wind pollination as a species like *S. globosa*, which has highly condensed, globose inflorescences, and smaller and more abundant pollen grains. Hermaphrodites of *S. salicaria* have high selfing because of wind pollination, which leads to the expression of inbreeding depression in the progeny of hermaphrodites, and contributes to the further advantage of outcrossing females in populations of this species. No native insects have been observed visiting any dimorphic species of *Schiedea* (Weller et al. 1990; Weller & Sakai, unpubl.), although occasional visits, primarily by introduced Syrphidae, have been noted.

Biotic pollination is another major mode of pollen transfer in *Schiedea*. Hermaphroditic species dependent on pollen vectors may rely on small insects for pollination, although observations are restricted to *S. lydgatei*. In this species field observations indicate that native Pyralidae moths are the most common visitors to this species; these moths also carry *S. lydgatei* pollen, which may indicate their role as pollinators (Norman et al. 1997). Pyralid moth larvae may also consume ovaries of *S. lydgatei*, as the larvae of species in this insect family are often flower herbivores (F. Howarth, pers. comm.). Emasculated flowers bagged with netting permeable to pollen but not insects produced some seed, although not as much as produced by unbagged, emasculated flowers (Norman et al. 1997). These results suggest that both wind and insects may play a role in pollination of *S. lydgatei*.

Pollination by nectarivorous birds (honeycreepers [Drepanidinae] or honeyeaters [incertae sedis]) may have occurred in sections *Nothoschiedea* and *Alsinidendron* (Weller et al. 1998). Bird pollination is most likely in *S. lychnoides* and *S. obovata*, which have more open, showier flowers than *S. viscosa* and *S. trinervis*. All four species produce abundant nectar, despite the occurrence of facultative or obligate autogamy. *Schiedea trinervis*, which produces cleistogamous flowers, had the highest standing nectar crops in a study of cultivated *Schiedea* (Weller et al. 1998). The combination of apparent adaptations for outcrossing with facultative or obligate autogamy may result from the very wet habitats occupied by some species in sections *Nothoschiedea* and *Alsinidendron*. The pendulous, enlarged calyces of these species may protect pollen from wetting and prevent dilution of nectar, and also promote selfing as a result of the close physical proximity of the anthers and stigmas within calyces. Unfortunately, rarity of honeycreepers and extinction of honeyeaters precludes field studies of the pollination biology of these species.

Adaptations to very wet environments appears to have resulted also in the evolution of facultative autogamy in *S. jacobii* and *S. diffusa* subsp. *diffusa* (Wagner et al. 1999a), and obligate autogamy via cleistogamy in *S. diffusa* subsp. *macraei* and *S. laui*. The occurrence of facultative autogamy in *S. hawaiiensis*, a species found in dry forests, may have evolved in response to pollinator limitation. In the greenhouse, self pollination of flowers of this species is facilitated by moderate to strong wind currents. Seed production in the field may also be dependent on wind; however, unlike sexually dimorphic species that exhibit adaptations to wind pollination, in *S. hawaiiensis* very little pollen is produced, and outcrossing, even to other flowers in the same inflorescence, is very low.

SEED DISPERSAL

There is little information indicating how species of *Schiedea* disperse seeds. For species occurring in dry or mesic sites, seeds are usually shaken loose from dehisced capsules; observations on the distribution of seedlings the following year indicate that seeds appear to fall near the plant that produced them (Sakai & Weller, unpubl.). *Schiedea diffusa*, *S. jacobii*, *S. lychnoides*, and *S. viscosa* are exceptional in producing seeds that remain in the capsule after maturation. In *S. diffusa*, seeds may germinate in the capsule, and eventually root as the capsule rots and falls to the ground. Seeds of *S. jacobii* are eventually dispersed from open capsules, whereas those of *S. lychnoides* and *S. viscosa* are released as the capsules gradually rot. *Schiedea obovata* and *S. trinervis* are unique in the Caryophyllaceae in producing fleshy sepals that contain a dark, purple juice at maturity. Although this fruit-like structure appears adapted for bird dispersal, there are no observations of dispersal for these species.

SYMPATRY AND HYBRIDIZATION

Species of *Schiedea* are capable of producing interspecific hybrids (Weller et al. 2001). Hybrids among dimorphic species typically produced highly fertile pollen, whereas hybrids among hermaphroditic species had high levels of pollen sterility. Interpretation of effects of breeding systems were complicated by the confounding association of dimorphism with large population size. It appears most likely that the production of fertile hybrids is related to genetic similarity among parental species, which in turn is a function of population size (Weller et al. 2001). Recent phylogenetic evidence indicating that sexually dimorphic species are for the most part placed in a single clade may explain the high fertility of hybrids among these species.

Under natural conditions, there are few instances of hybridization, in part because of limited sympatry (Table 2; Weller et al. 2001). One extensive case of hybridization occurs between *S. lydgatei* and *S. sarmentosa* on Moloka`i. *Schiedea sarmentosa* grows on steep

TABLE 2. Current sympatry or hypothesized past sympatry in *Schiedea*, and the extent of putative natural hybridization.

Sympatric species pair and breeding systems		Region of sympatry	Extent of hybridization	Method of detection
S. hookeri (hermaphroditic, outcrossing)	*S. mannii* (subdioecious, outcrossing)	Wai`anae Kai Forest Reserve, Waianae Mts., O`ahu	Minimal, two instances known	Morphological intermediacy
S. hookeri (hermaphroditic, outcrossing)	*S. pentandra* (hermaphroditic, outcrossing)	Pu`ukaua, Wai`anae Mts., O`ahu	Possible rare hybridization	Morphological intermediacy
S. kauaiensis (hermaphroditic, outcrossing)	*S. membranacea* (hermaphroditic, outcrossing)	Ku`ia Valley, Kaua`i	No hybrids detected	
S. ligustrina (dioecious, outcrossing)	*S. kealiae* (subdioecious, outcrossing)	Probably in Wai`anae Mts., O`ahu	Past hybridization followed by presumed introgression	cpDNA (Soltis et al. 1997)
S. ligustrina (dioecious, outcrossing)	*S. mannii* (subdioecious, outcrossing)	`Ohikilolo Ridge, W of Wai`anae Kai Forest Reserve, Wai`anae Mts.,O`ahu	Hybrids common in one locality with most individuals of *S. mannii* exhibiting influence of hybridization	Morphological intermediacy
S. lydgatei (hermaphroditic, outcrossing)	*S. sarmentosa* (gynodioecious, outcrossing)	Makolelau Gulch, Moloka`i	Hybrids present at interface of shrublands (*S. lydgatei* habitat) and cliffs (*S. sarmentosa* habitat)	Hybrids inferred from morphological intermediacy
S. menziesii (hermaphroditic, intermediate selfing rates)	*S. salicaria* (gynodioecious, females highly outcrossed, hermaphrodites with intermediate selfing rates)	Ridge between Pu`u Ula-ula and Pu`uko`ai, West Maui	Apparent hybrid swarm, very few parental types observed in population	Morphological intermediacy
S. nuttallii (hermaphroditic, outcrossing)	*S. obovata* (hermaphroditic, facultative selfer)	Two known instances of sympatry, Pahole Natural Area Reserve, Wai`anae Mts., O`ahu	No hybrids detected	
S. pentandra (hermaphroditic, outcrossing)	*S. trinervis* (hermaphroditic, cleistogamous)	One known instance of sympatry on slopes of Mt. Ka`ala, O`ahu	No hybrids detected	
S. spergulina (hermaphroditic, outcrossing)	*S. stellarioides* (hermaphroditic, outcrossing)	Wai`alae Valley, Kaua`i	No hybrids detected	
S. stellarioides (hermaphroditic, partially outcrossing)	*S. viscosa* (hermaphroditic, facultative autogamy)	Wai`alae Valley, Kaua`i	No hybrids detected	

cliffs and ledges, and *S. lydgatei* grows in xeric shrubland on slopes. Hybrids have been observed where populations of the two species come into contact. A second case of extensive hybridization occurs between *S. salicaria* and *S. menziesii* in the West Maui Mountains. *Schiedea salicaria* in found primarily on the east side of the West Maui Mountains at elevations below 305 m, and *S. menziesii* is limited to the west side of the West Maui Mountains, usually at elevations below ca. 610 m. Populations of *Schiedea* found at ca. 915 m elevation in the vicinity of `Ula`ula, on the southwest side of the West Maui Mountains where the geographical ranges of *S. salicaria* and *S. menziesii* overlap, appear to be morphologically intermediate between these species and may represent a hybrid swarm. Putative hybrids have also been observed between *S. mannii* and *S. ligustrina* on `Ohikilolo Ridge in the Wai`anae Mountains, O`ahu. Progeny raised from seed collected from *S. mannii* at Wai`anae Kai included an apparent F_1 hybrid with nearby *S. hookeri*, although no hybrids were observed in the field. In other cases of sympatry, differences in breeding systems or pollination biology may prevent formation of hybrid progeny. For example, *S. obovata* and *S. nuttallii* were observed growing within a few feet of one another on the north rim of Makua Canyon in the Wai`anae Mountains (until *S. obovata* became locally extinct), but no hybrids have been observed, possibly because of the high degree of autogamy in *S. obovata* or differences in pollinators determined by differences in floral morphology.

CYTOLOGY

Prior to our studies only two chromosome counts had been reported for the *Schiedea* lineage: 2n = 60 for *S. trinervis* (sect. *Alsinidendron*; Skottsberg 1953) and *S. verticillata* (sect. *Polyneura*; Carr 1985). To supplement these studies, the chromosome cytology of 20 of the 34 species of *Schiedea* was investigated (Appendix 4). Initial observations made by R. Oliver and W. L. Wagner at the Smithsonian Institution resulted in variable chromosome counts, sometimes even for the same population. The remainder of the work was carried out in collaboration with S. Lehner and M. Kiehn. Fixation of meristematic tissues (actively growing root tips or apices) for counts of mitotic chromosome numbers of plants cultivated in the University of California at Irvine was made in a freshly mixed 3:1 solution of ethanol(96%):glacial acetic acid. The fixed material was kept cool before staining with Giemsa (after hydrolysis in 5 N HCl for 50 min. at 20% C) or with Feulgen (see Kiehn & Lorence, 1996, for details). In cases of insufficient staining by these techniques, hot aceto-carmine (2% solution in 45 % acetic acid) was also added. In most cases, exact counts could not be achieved because of limited material, high chromosome numbers, and/or clumping of chromosomes, and thus, a range of chromosome numbers is given in those cases. Vouchers and chromosome determinations are provided in Appendix 4. Permanent slides for most counts are in the collection of M. Kiehn.

The results presented here are inconclusive. All determinations were high, ranging from 2n = 48 to 60, but none of them were definitive (Appendix 4), although 2n = 60 is the most frequent. The chromosomes of *Schiedea* are extremely small, usually < 1 µm in metaphase of mitosis. Chromosomes vary in size, with some chromosomes ≥ 2 µm. The same variation in chromosome numbers occurs within each of the four major clades and across six of the eight sections.

The cause for the variation in numbers and size of the chromosomes of *Schiedea* species is not presently clear. It is possible that b-chromosomes (supernumeraries) are

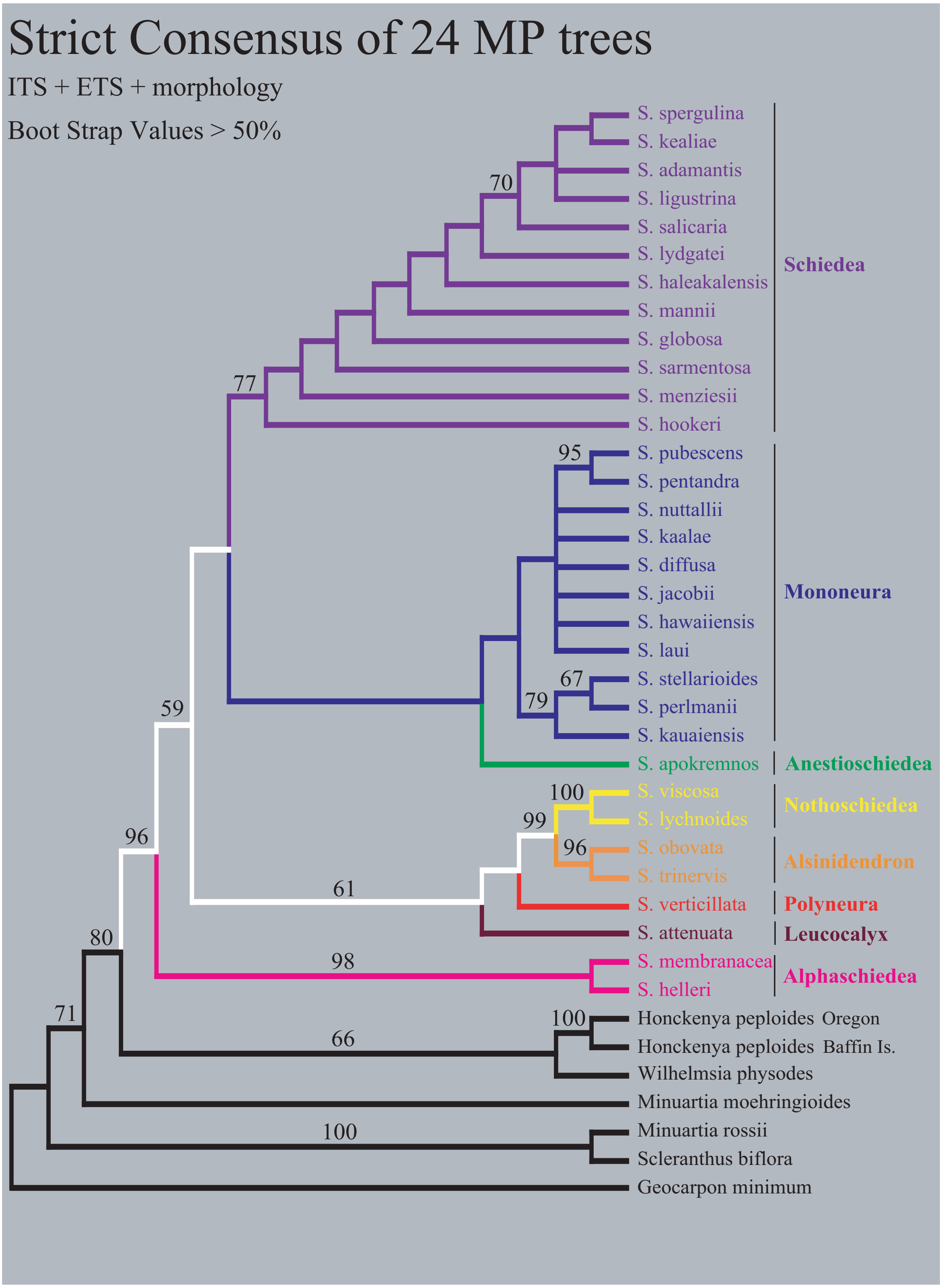

Plate 2. Strict Consensus tree of 24 MP trees. Two major partitions of data were analyzed comprising sequence data from nrDNA ITS and ETS regions and morphology. Sixty-one morphological characters were scored, including forty-three revised characters published in previous analyses (Weller et al. 1995; Wagner et al. 1995). The sections of the genus are shown to right of each clade. Two extinct species, *Schiedea amplexicaulis* and *S. implexa*, were omitted from the analyses.

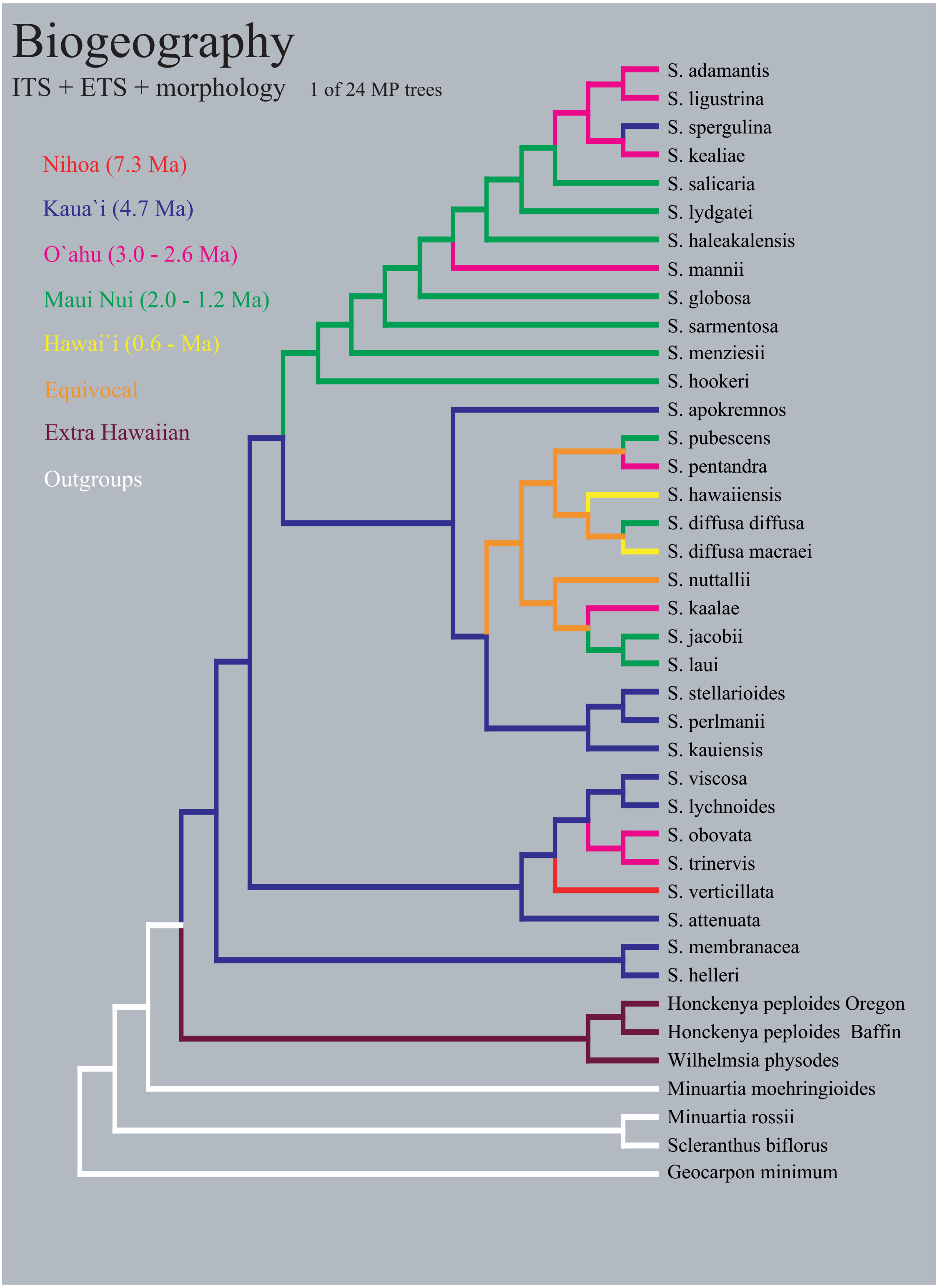

Plate 3. Biogeographic hypothesis for *Schiedea*; reconstructed with MacClade 4.0 (Maddison & Maddison 2000) and using one of 24 most parsimonious trees.

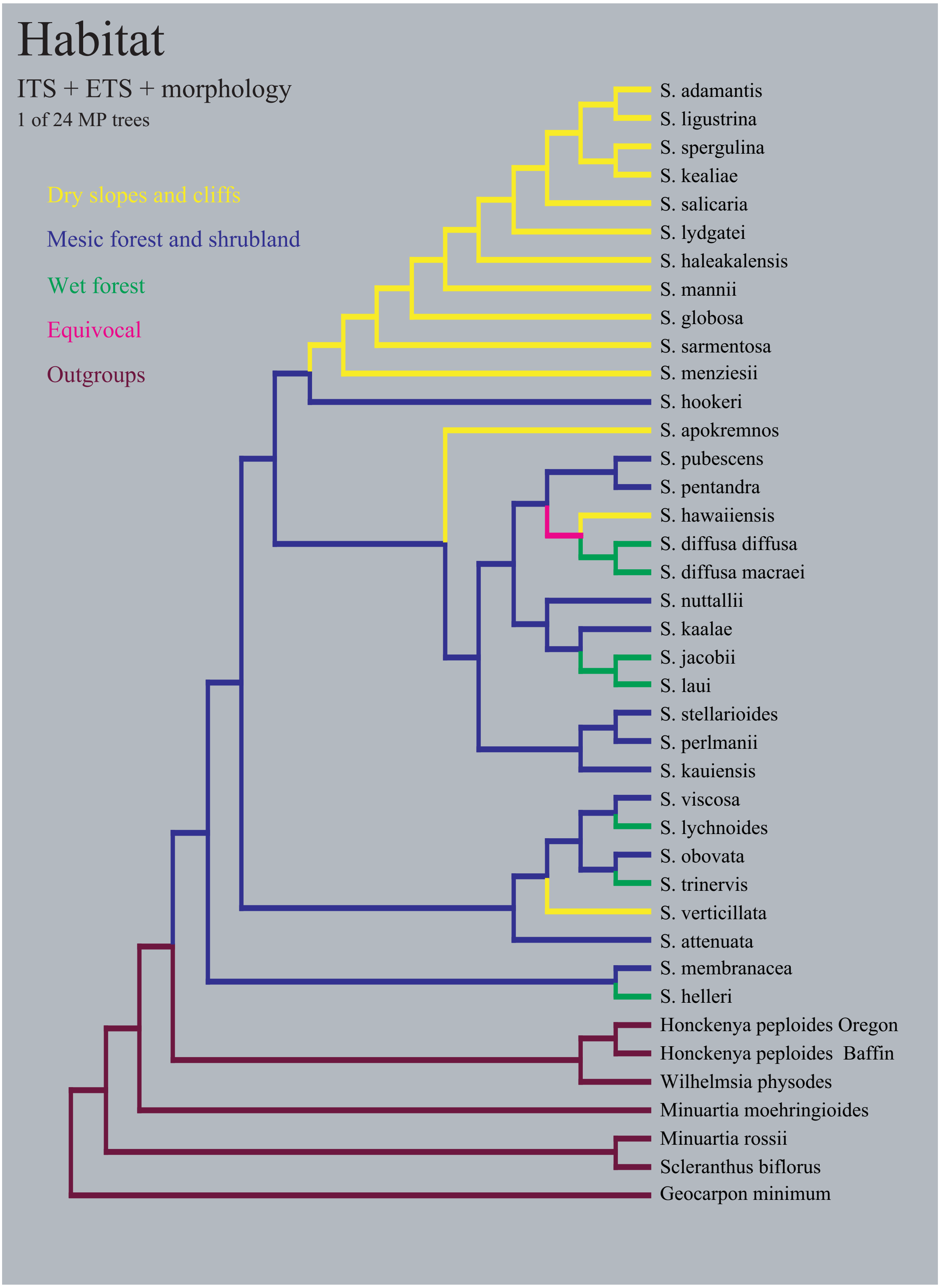

Plate 4. Habitat shift hypotheses for *Schiedea*; reconstructed with MacClade 4.0 (Maddison & Maddison 2000) and using one of 24 most parsimonious trees. *Schiedea kaalae* and *S. viscosa* are coded as mesic, although a few populations of both species occur in wet habitats.

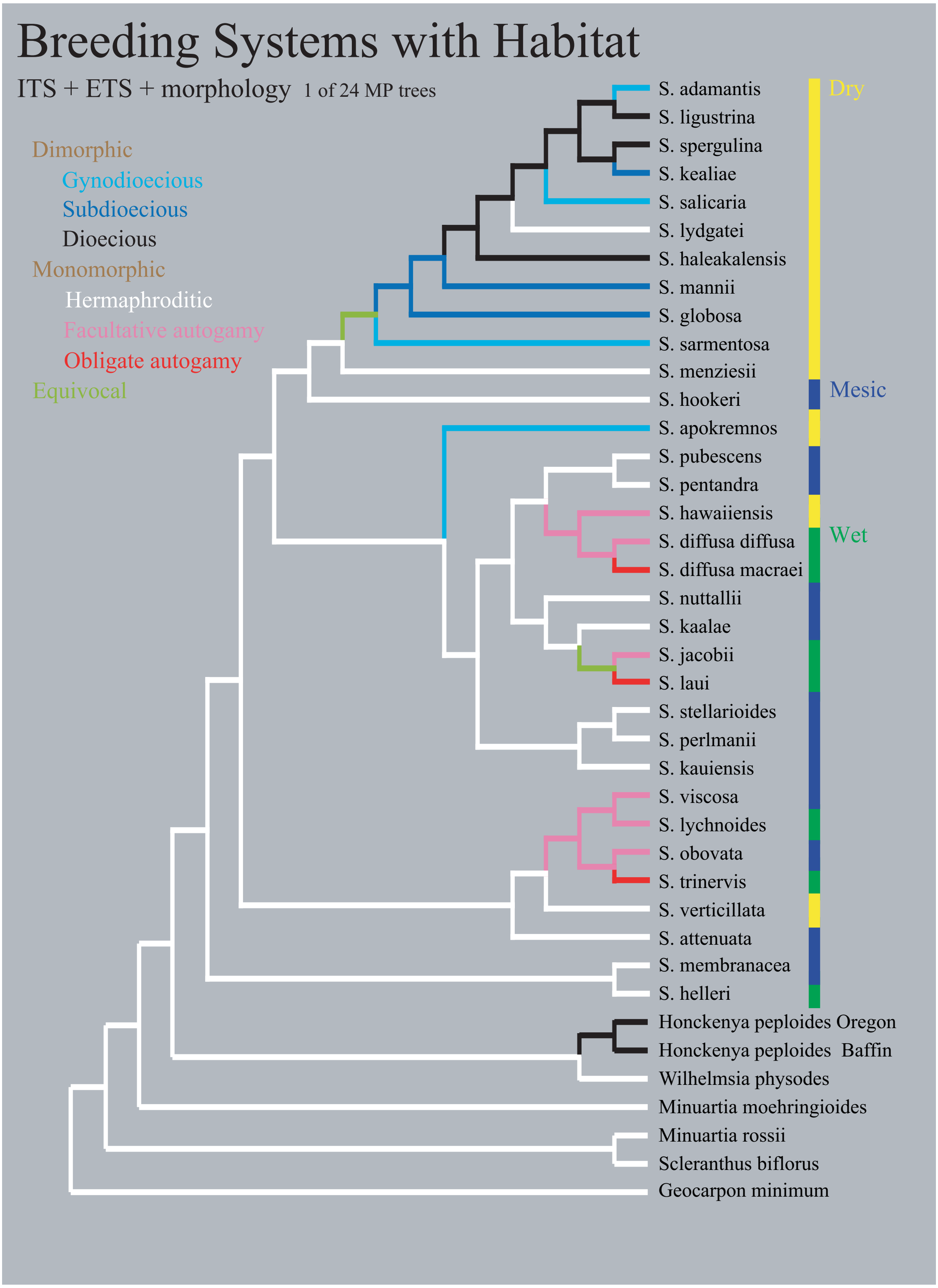

Plate 5. Breeding system evolution hypothesis for *Schiedea* with habitats shown on the right side of cladogram; reconstructed with MacClade 4.0 (Maddison & Maddison 2000) and using one of 24 most parsimonious trees.

common. Robertsonian fusion (Kiehn, pers. comm. in 1992) might explain the size differences, if fusion of two smaller acrocentric or telocentric chromosomes results in larger submetacentric to metacentric chromosomes. The apparent variability in chromosome numbers in *Schiedea* may be the result of the chromosomes sticking together; however, the presence of larger chromosomes in all cells of those taxa investigated supports the idea of Robertsonian fusion**.** Whether chromosomal variation can be attributed to b-chromosomes or possibly Robertsonian structural changes cannot been resolved by our preliminary investigations, although it seems clear that high chromosome numbers of around 2n = 60, probably resulting from polyploidy, are characteristic of *Schiedea*. It is interesting to note that the sister clade to *Schiedea* also has similar high chromosome numbers; *Honckenya peploides* has been reported as 2n = 66, 68, 70 and *Wilhelmsia physodes* as 2n = 50–60, 66, 70, 72, 100–110 (Murray & Kelso 1997).

CONSERVATION BIOLOGY

Fifteen taxa of *Schiedea* are currently listed as endangered or threatened by the United States Fish and Wildlife Service (E or T status). This is the highest proportion of endangered taxa for any species-rich lineage in the Hawaiian Islands. Causes of endangerment are usually competition from alien plant species, habitat degradation by feral pigs, browsing by feral goats or cattle, collection or trampling by humans, fire, the small number of remaining extant populations for the endangered taxa, and drought (Canfield 1991; Ellshoff et al. 1991; Sakai et al. 2002). Species from dry habitat are more adversely affected by goats than pigs, while in mesic to wet areas feral pigs appear to be the greater threat. Fire is a serious threat only in the drier habitats.

Detailed observations of populations of several species provide examples of the effects of alien plant competitors, fire, and alien herbivores in leading to rarity in *Schiedea*. *Schiedea adamantis*, which occurs in a single population on the north rim of Diamond Head Crater, was first surveyed in 1987, and completely mapped in 1989 (Sakai & Weller unpubl.). The species was most abundant in very rocky areas with little vegetative cover. Koa haole [*Leucaena leucocephala* (Lam.) de Wit], the most abundant alien species on this part of Diamond Head, is more common and reaches greater height in areas with better soil development. In 1987, areas dominated by koa haole had occasional adult individuals of *S. adamantis* in the understory, but there was little evidence of seedling establishment in these areas. In contrast, seedlings and juveniles were abundant in the open, rocky areas after winter rains. In 1990, koa haole suffered from severe dieback resulting from attack by the Caribbean psyllid (*Heteropsylla cubana*). The total population size of flowering plants of *S. adamantis* was 250, a far larger figure than previous estimates had indicated. Many large plants were discovered in areas that had been dominated by dense koa haole in the past. In 1994, 267 flowering plants were mapped. Although koa haole has recovered from the psyllid attack, it remains far less prevalent than before. The dieback initially appeared to have favored recruitment and growth of *S. adamantis* and indicates that control of koa haole should have been considered in plans for restoration of *S. adamantis*. Unfortunately, recent drought has resulted in severe mortality of *S. adamantis*, and only three individuals remained in 2003. Before invasive koa haole spread over Diamond Head Crater, *S. adamantis* may have been more widely distributed, and occurred in more mesic areas where it might have withstood drought conditions. In view of the severe decline of individuals in the natural population of *S. adamantis*, the recovery plan for

S. adamantis (U.S. Fish and Wildlife Service 1993) was implemented in 1997 with funding from U.S. Fish and Wildlife Service. Outplanting of seeds and seedlings on Diamond Head Crater failed due to drought, but plants of *S. adamantis* grown from seed produced in the greenhouse were established in botanical gardens and in garden-like settings in several areas of southeastern O`ahu, including Diamond Head Crater. Whether these populations will persist in the long term is uncertain.

Observations of *S. lydgatei* by Norman (1994) indicate that fire has resulted in degradation of native habitat and death of most *Schiedea* plants in burned areas. Populations of *S. lydgatei* were studied in an area unburned since at least 1971, and in a recently burned area where major fires occurred in 1988 and 1991. In 1993, 97% of the plant cover at the recently burned site consisted of introduced plants. In contrast, cover of introduced plants was 33% at the unburned site. Cover of *S. lydgatei* at the unburned site was 19% in 1993 compared to 0.5% at the burned site. Because there are no pre-burn surveys for either site, these data must be interpreted with caution. It appears, however, that fire is detrimental to both *S. lydgatei* and native Hawaiian plants in general.

A population of *S. mannii* on `Ohikilolo Ridge in the Wai`anae Mountains that was mapped and tagged in 1987 suffered severe herbivory by 1988. Most plants could not be relocated, but the bases of a number of plants, and the identifying tags in several cases, were found. Goats were common in the area, and probably responsible for the loss of plants. Marked populations of *S. salicaria* on West Maui were grazed extensively by cattle, to the extent that plants in more accessible areas gradually disappeared between 1987 and 1994. Inflorescences of *S. globosa* are frequently removed by rats in a population near Makapu`u, O`ahu. The lifespan of individual *S. globosa* plants appears to be short relative to other *Schiedea* species, indicating that removal of inflorescences is likely to affect recruitment and population size in this species.

Species of *Schiedea* that seem to have been affected most severely by direct or indirect effects of humans are those occurring in mesic and dry forests. These species are less likely to occur on steep cliffs, and appear highly susceptible to the activities of herbivores, in particular feral pigs and goats. Range restriction is especially evident in *S. nuttallii*, a species that formerly occurred on O`ahu, Moloka`i, and Maui. At present, there are no known extant populations on Moloka`i or Maui, and populations on O`ahu are restricted to several populations in the Wai`anae Mountains (Russell & Bruegmann 1996b). *Schiedea kaalae* was once distributed throughout the Wai`anae Mountains and the northern Ko`olau Mountains. At present, only five populations remain in the Wai`anae Mountains, and two in the Ko`olau Mountains (Ellshoff et al. 1991). These populations often consist of only one or two individuals. The total number of extant individuals is estimated to be fewer than 100. Clearly, minimal disturbance in any of these populations would result in local extinction. Feral pigs and goats are presumed to be the major herbivores of this species. *Schiedea obovata*, formerly distributed in mesic forest throughout the Wai`anae Mountains, is now restricted to a few populations in the northern part of the range. No single cause of rarity has been identified, although feral animals and competition from alien plant species are probably responsible (Ellshoff et al. 1991).

A high diversity of species of *Schiedea* (9 of 34 species) are found in the Wai`anae Mountains on O`ahu. The Wai`anae Mountains are perhaps more severely disturbed by human activities than any of the remaining natural areas in the Hawaiian Islands. Extensive military activities have resulted in numerous fires causing loss of native forest. The coincidental high diversity of *Schiedea* in this area has undoubtedly contributed disproportionately to endangerment in this genus.

Despite evidence that many species of *Schiedea* are severely endangered, recent exploration indicates that extinction has not occurred to the extent feared, and many species may be more common than anticipated before recent field studies were initiated. Recent investigations of the systematics and reproductive biology of *Schiedea* have spurred additional collecting by local botanists and resulted in discovery of many additional populations of the more common species, the rediscovery of species thought to be extinct, and the discovery of several new species. Five species (*S. amplexicaulis*, *S. helleri*, *S. implexa*, *S. stellarioides*, and *S. viscosa*) were thought to be extinct at the time of publication of the *Manual of Flowering Plants of Hawai`i* (Wagner et al. 1990). Subsequent collecting on Kaua`i resulted in the rediscovery of *S. helleri*, *S. stellarioides*, and *S. viscosa*, and the discovery of one new species, *S. attenuata*. *Schiedea jacobii* was discovered on East Maui by J. Jacobi and A. Medeiros, and *S. laui* was discovered by Joel Lau on Moloka`i. *Schiedea hawaiiensis*, which was thought to be conspecific with *S. diffusa* (Wagner et al. 1990), was rediscovered in 1996 and recognized as distinct. The discovery of new taxa on Kaua`i, Moloka`i, and Maui indicates that these islands have been investigated less extensively in the past than other islands, in part because of rugged terrain in areas where these species occur.

Protection of remaining populations of *Schiedea*, as well as restoration of habitats where these species occur, might result in preservation of the majority of species in this lineage. Species of *Schiedea* are amenable to cultivation, and reintroduction may be possible using plants produced in cultivation. Such approaches should be instituted as rapidly as possible, before selection on novel phenotypes expressed under cultivation produces races adapted for cultivated rather than field conditions. In any restoration process, reproductive systems will dictate appropriate population sizes as well as density (Weller 1994).

TAXONOMY

NOTES: Angle of sepal reflection is measured as the angle between the sepals and the pedicel when the sepals are maximally reflected. During anthesis the sepals change position from closed in bud to maximal reflection, eventually closing again during fruit development. Sepal length is easiest to measure in bud, just prior to opening. The basal bulge created by the strong reflection of the sepal at anthesis will cause an underestimation of the actual size of the sepal. Sepals can be measured during anthesis, but the measurement must be taken on the abaxial side from the tip to the base. Anthers should be measured before they dehisce, usually before the flower opens, as afterward they are significantly smaller. Unfortunately all anther measurements could not be made on anthers prior to dehiscence, and thus their full size may be underestimated and the variation in size overestimated. The island(s) on which a species occurs are given in the key at the end after the distinguishing morphological characters. The maps show localities for extant and presumably extirpated populations. Local extirpation was assumed if no collections were made after 1980, when attempts to locate *Schiedea* were intensified.

Schiedea Chamisso & Schlechtendal, Linnea 1: 46. 1826, non *Schiedea* A. Richard, 1830, nec *Schiedea* Bartling, 1830.—TYPE: *Schiedea ligustrina* Chamisso & Schlechtendal.

Alsinidendron H. Mann, Proc. Boston Soc. Nat. Hist. 10: 311. 1866. *Schiedea* sect. *Alsinidendron* (H. Mann) Pax & K. Hoffmann, Nat. Pflanzenfam., ed. 2, 16c:

326. 1934.—TYPE: *Alsinidendron trinerve* H. Mann [=*Schiedea trinervis* (H. Mann) Pax & K. Hoffmann].

Shrubs, subshrubs, or vines, stems terete, 4-angled or -ridged; lateral branches of primary stems usually elongating several or more nodes below the inflorescence; roots fibrous or fleshy and thickened (*S. membranacea* and *S. verticillata*). Leaves opposite or in one species occasionally in whorls of 3, with 1 or 3–12 principal longitudinal veins, margins entire and often slightly revolute or in basal sections with minute antrorse epidermal protuberances or serrulate, at least in the distal half, sometimes the teeth irregularly spaced and inconspicuous, petiolate, weakly to conspicuously connate around the stem, stipules absent. Inflorescence terminal, cymoid, flowers in dichasia (or monochasia by abortion) on the main and upper lateral branches, these forming panicle-like inflorescences, the internodes greatly elongated and inflorescence diffuse, or lateral internodes shorter and the inflorescence contracted, or in two species all internodes extremely reduced and the inflorescence head-like or sometimes (sections *Alsinidendron* and *Nothoschiedea*) the inflorescence appearing to have an axillary origin resulting from the main inflorescence axis completely suppressed, all but the terminal flower borne on lateral inflorescence branches, the flowers pendent, lateral vegetative branches of the next lower node elongating coincident with flowering or nearly so and one of them becoming dominant, assuming subsequent vegetative growth. Flowers hermaphroditic and chasmogamous, usually protandrous, a few species facultatively or obligately autogamous, adapted for insect pollination (in *S. menziesii* a pyralid moth), or unisexual (the plants dioecious, subdioecious, or gynodioecious) and adapted for wind pollination or in three species apparently with adaptations for bird pollination, and in *S. diffusa* subsp. *macraei*, *S. laui*, and *S. trinervis* cleistogamous. Sepals (4) 5, green, sometimes purple-tinged, imbricate or in several species broadly so, persistent, reflexed from base or spreading at anthesis, the adaxial face broadly to deeply concave, and weakly or strongly navicular, in some species becoming convex from about the middle to the base, apex acute to acuminate, white with a green tinge or the outermost ones green externally at least toward the base, completely white within, the outer ones ovate, rhombic, oblong or elliptic, the inner ones narrowly obovate to obovate or broadly elliptic, persistent, membranous, becoming papery and not changing color in fruit (sect. *Nothoschiedea*), or enlarging and becoming fleshy and dark purple (sect. *Alsinidendron*). Petals absent. Nectaries 5, arising from an antisepalous mound, usually yellowish green to dark yellow or orange, the apex of the nectary with a shaft-like tubular extension, thin and translucent, tip of shaft usually bifid or variously divided, sometimes irregularly so, the nectary base producing a transparent nectar that fills the shaft and is exuded from the tip as a drop or onto the surface of the sepal, or nectaries enlarged during development to form a nearly contiguous ring of nectariferous tissue, the abaxial margin of each nectary with a flap-like extension, the extensions either distinct to the base, oblong and apically 2–3-toothed (sect. *Nothoschiedea*), or connate at base or for about half their length forming a cup-like structure, the apex entire or with inconspicuous teeth (sect. *Alsinidendron*), producing usually copious amounts of hexose-rich black nectar (this sometimes pale), which collects on the extensions. Stamens (8–) 10 (–12), in 2 series, the antisepalous (inner) whorl inserted on the adaxial face of the nectary near the base or to about 3/4 of the way toward the apex, the other (outer) whorl inserted between the nectaries, or (sections *Nothoschiedea* and *Alsinidendron*) inserted on the adaxial margin of the nectaries, in dimorphic species all stamens sterile in pistillate flowers, these usually with empty anther sacs and smaller than fertile stamens; filaments greenish white to yellowish white; anthers yellow, rarely (sections *Nothoschiedea* and *Alsinidendron*, and *S. stellarioides*) pale reddish purple and then often changing to a darker reddish purple, oblong, attached in the lower 1/3 or just below the middle, pollen 25.7–38.5 µm, yellow to pale yellow or in a few species gray or pale purple. Ovary 1-celled, placentation free-central; styles usually 3, sometimes 4–5, or in a few species 7–11 and then sometimes variable in number within a single plant, filiform; stigma receptive completely around the distal half or rarely nearly throughout its length, slightly enlarged and papillose. Fruit an ovoid to subglobose capsule, enclosed by or exserted from the persistent dried calyx (in section *Alsinidendron* calyx fleshy and dark purple), dehiscing at maturity by 4–11 valves, or in some species failing to dehisce and seeds dispersing as capsule walls rot. Seeds relatively few to numerous, 0.6–1.8 mm long, the viable ones black or dark or light brown, the inviable ones usually reddish brown, orbicular-reniform, reniform, or rarely orbicular, usually laterally compressed, the surface rugose, papillose, or sometimes nearly smooth.

Schiedea is a genus of 34 species, all endemic to the Hawaiian Islands. *Schiedea* is here divided into eight sections based on the most recent phylogenetic analyses using molecular and morphological data (Plate 2). *Schiedea* appears to share a common ancestor with the morphologically divergent *Honckenya* and *Wilhelmsia*, circumboreal and north temperate unispecific genera, respectively. Fourteen of the species are U.S. Federally listed as Endangered, one is listed as Threatened, two have not been collected for nearly a century and are presumed extinct. The remaining species, while not given official status, are considered by us to be rare or endangered, with four, *S. globosa*, *S. ligustrina*, *S. mannii* and *S. menziesii*, considered vulnerable.

The genus is named in honor of Christian Julius Wilhelm Schiede (1798–1836), German physician and botanist, who resided in Mexico from 1828 until his death. Schlechtendal and Chamisso published on his plant collections, gathered in the company of the gardener Ferdinand Deppe (1794–1861).

KEY TO THE SECTIONS AND SPECIES OF SCHIEDEA

1. Leaves with 3–7 (–12) principal veins; leaf margin usually with weak epidermal protuberances or margin serrulate, the teeth or protuberances with small antrorsely curved hairs, or in *S. verticillata* margin entire and glabrous, and then margin very thick.
   2. Sepals ovate 1.7–3.1 mm long, oriented at 5° to 60° angle to the pedicel, sometimes the distal 1/2 curved outward at 90° angle; nectary shafts straight or gently recurved, nectar collecting as a drop at the tip (sect. *Alphaschiedea*).
      3. Evergreen vine; roots fibrous, not fleshy; leaves with 3 (–5) principal veins; Kaua`i. 1. *S. helleri*.
      3. Deciduous perennial; roots fleshy and thickened; leaves with 5–7 principal veins; Kaua`i. 2. *S. membranacea*.
   2. Sepals lanceolate, elliptic to obovate, or rhombic to oblong-rhombic, 8–12 mm long, in *S. lychnoides* enlarging up to 18 mm long, oriented at 80° to 90° angle to the pedicel or opening to form a campanulate calyx or not opening at all; nectary shaft recurved, tip touching sepal or highly modified into flaps or a cup-like structure.
      4. Nectaries distinct; nectary extensions forming a shaft-like, recurved tube; deciduous perennial; roots enlarged, fleshy; leaves thick, with 7–12 principal veins; inflorescence terminal; Nihoa (sect. *Polyneura*). 4. *S. verticillata*.
      4. Nectaries enlarged during development to form a nearly contiguous ring of nectariferous tissue; nectary extensions flap-like, distinct or connate at base or for about half their length; evergreen scandent vines or shrubs; roots not enlarged; leaves not especially thick, with 3–5 principal veins; inflorescence pseudolateral (lateral branch of the next node below inflorescence elongating coincident with flowering, and assuming subsequent vegetative growth).

5. Weakly climbing or sprawling vines; sepals puberulent externally, membranous, greenish white to white, at maturity becoming dry and papery; bracts foliaceous, gradually reduced in upper parts of the inflorescence; nectary extensions flap-like, distinct to the base (sect. *Nothoschiedea*).

6. Primary stems up to 30 dm long, with short lateral branches; flowers usually 10–21 per inflorescence; hairs on abaxial leaf surface more abundant on principal veins, antrorsely appressed or curved; sepals 9–12 long, 5–6 mm wide, enlarging up to 18 mm long in fruit; leaves ovate to elliptic, 1.5–3.8 cm wide; styles 8–11; Kaua`i. 5. *S. lychnoides*.

6. Primary stems up to 5 dm long, lateral branches well developed; flowers 3–11 per inflorescence; hairs on abaxial leaf surface only slightly more dense on the principal veins, antrorsely spreading to erect; sepals 6.5–9 mm long, 4–4.5 mm wide, enlarging up to ca. 12 mm long in fruit; leaves narrowly elliptic to narrowly ovate-elliptic, 0.8–1.8 cm wide; styles 5–7 (–8); Kaua`i. 6. *S. viscosa*.

5. Shrubs; sepals glabrous, thick, fleshy, white or green, becoming dark purple and fleshy as fruit matures, producing purple juice when broken; bracts greatly reduced in inflorescence, only the lowermost pair foliaceous; nectary extensions flap-like, connate, at least at the base (sect. *Alsinidendron*).

7. Sepals usually 5, sometimes 4 or 6, the number often variable on the same plant; petioles and youngest pair of leaves yellowish white, sometimes purple-tinged; peduncles (2–) 5–25 mm long at anthesis, not elongating much in fruit; inflorescences somewhat congested, the internodes of the lateral inflorescence branches 2–10 mm long; pedicels elongating just prior to anthesis; O`ahu. 7. *S. obovata*.

7. Sepals 4; petioles and youngest pair of leaves pale green; peduncles 16–30 mm long, elongating up to 50 mm long in fruit; inflorescences open, the internodes of the lateral inflorescence branches 20–30 mm long; pedicels elongating uniformly during inflorescence development; O`ahu. 8. *S. trinervis*.

1. Leaves with 1–3 (–5) principal veins; leaf margins entire or in *S. diffusa* with only 1 principal vein and margins with a few weak epidermal protuberances, these with small antrorsely curved hairs.

8. Sepals attenuate, usually strongly reflexed, the margins ciliate, in *S. stellarioides* inconspicuously so and only at the base, and then anthers pale reddish purple; leaves usually broadest toward the base or at the middle, with 1 principal vein; flowers all hermaphroditic (sect. *Mononeura*).

9. Leaves broadest near the base, weakly clasping the stem; leaf base ciliate; Kaua`i. 11. *S. amplexicaulis*.

9. Leaves tapering to the base, not clasping the stem; leaf base glabrous.

10. Anthers pale reddish purple; nectary base elongate, 1.6–2.6 mm long, dark yellow to orange, the nectary shaft 0.7–1.7 mm long; Kaua`i. 10. *S. stellarioides*.

10. Anthers yellow; nectary base not elongate, 0.4–1 (–1.2) mm long, usually pale yellow to yellow or orange, sometimes purple, the nectary shaft (1.4–) 1.8–6.5 mm long.

11. Erect or ascending subshrubs or perennial herbs; inflorescence erect to ascending.

12. Perennial herb; internodes greatly compressed, the leaves tufted toward apex of stem; O`ahu. 16. *S. kaalae*.

12. Subshrubs; internodes not compressed, the leaves distributed along the stem.

13. Stems flattened, not winged; seeds not persistent on the placenta, readily dispersing from the dehisced capsule; flowers chasmogamous or autogamous; sepals strongly reflexed, oriented at 5° to 80° angle to the pedicel, or scarcely spreading and flowers autogamous or cleistogamous.

14. Pedicels not filiform, 3–23 mm long; inflorescence sparsely to moderately flowered.

15. Sepals reflexed 40° to 80° angle to the pedicel; inflorescence 20–48 cm long, pubescent throughout; sepals 4.3–5.1 mm long; Kaua`i. 13. *S. kauaiensis*.

15. Sepals reflexed 5° to 30° angle to the pedicel, or flowers cleistogamous and not opening; inflorescence 17–25 (–32) cm long, glabrous or sometimes with a few hairs at the base of the internodes and bracts ciliate; sepals 3.5–4.5 mm long.

16. Sepals strongly reflexed, oriented at 5° to 30° angle to the pedicel; pedicel spreading at anthesis; nectary shaft 2.8–3.7 mm long; antisepalous staminal filaments 5.8–7.1 mm long; O`ahu, Moloka`i, West Maui. 14. *S. nuttallii*.

16. Sepals remaining closed at anthesis; pedicel appressed to inflorescence branch at anthesis; nectary shaft ca. 2.3 mm long; antisepalous staminal filaments 4.0–4.1 mm long; Moloka`i. 15. *S. laui*.

14. Pedicels filiform, 20–40 mm long; inflorescence densely flowered, diffuse; Maui. 17. *S. implexa*.

13. Stems conspicuously quadrangular, the angles weakly winged; seeds persistent on the placenta, not dispersing from capsule at dehiscence; flowers facultatively autogamous; sepals spreading, oriented at 90° to 135° angle to the pedicel; East Maui. 18. *S. jacobii*.

11. Vines; inflorescence pendent.

17. Inflorescence glabrous, or sometimes with a few translucent or whitish hairs.

18. Pedicel 13–15 mm long; sepals strongly reflexed, oriented at 5° to 30° angle to the pedicel, slightly twisted toward the apex, glabrous on adaxial face; Kaua`i. 12. *S. perlmanii*.

18. Pedicel 4–10 mm long; sepals spreading, oriented at 90° to the pedicel at base, later in anthesis abruptly curved upward in upper 2/3 at 130° to 160° angle to the pedicel, often strongly inrolled during late and post-anthesis, puberulent on adaxial face; Hawai`i. 19. *S. hawaiiensis*.

17. Inflorescence evenly pubescent with usually purple or purple-tinged hairs or sometimes white.

19. Fertile stamens 5 (antisepalous whorl), the alternate whorl minute and abortive; leaves 0.8–2.8 cm wide; O`ahu. 20. *S. pentandra*.

19. Fertile stamens 10; leaves (1.5–) 2.5–7.5 cm wide.

20. Sepals 2.8–3.5 mm long; seeds not persistent on placenta, dispersing from dehisced capsule; Moloka`i, Lana`i, Maui. 21. *S. pubescens*.

20. Sepals 4.2–7 mm long; seeds persistent on placenta, retained in the dehisced capsule.

21. Sepals strongly reflexed, oriented at 30° to 60° angle to the pedicel; flowers chasmogamous, facultatively autogamous; Moloka`i, East Maui. 22a. *S. diffusa* subsp. *diffusa*.

21. Sepals scarcely spreading at anthesis, rarely oriented at ca. 150° angle to the pedicel; flowers cleistogamous, obligately autogamous; Hawai`i. 22b. *S. diffusa* subsp. *macraei*.

8. Sepals obtuse, rounded, or weakly acuminate, glabrous or ciliate, or if attenuate and ciliate then anthers yellow; leaves broadest at base and with more than 1 principal vein, or if with 1 principal vein then broadest at middle or above the middle; flowers often unisexual, sometimes hermaphroditic (note: males often are morphologically very similar to hermaphroditic flowers at anthesis).

22. Styles 5–6 (–7); sepals greenish or yellowish white, somewhat petaloid; inflorescence diffuse; Kaua`i (sect. *Leucocalyx*). 3. *S. attenuata*.

22. Styles 2–4, or if up to 6, then the inflorescence vertically and laterally contracted, head-like; sepals green or purple-tinged, not petaloid; inflorescence diffuse or contracted.

23. Leaves dark green, glaucous, and weakly succulent, apex obtuse to acute; sepals broadly ovate; inflorescence laterally and vertically contracted; Kaua`i (sect. *Anestioschiedea*). 9. *S. apokremnos*.

23. Leaves yellowish green to green, coriaceous or membranous, not succulent or if so then falcate and apex long-attenuate, not or slightly glaucous; sepals lanceolate, narrowly ovate, rarely (*S. globosa*) ovate; inflorescence laterally contracted to relatively diffuse, or if laterally and vertically contracted then leaves falcate and leaf apex long-attenuate (sect. *Schiedea*).

24. Woody subshrubs or shrubs or perennial herbs, becoming woody at the base; usually pubescent, at least in the inflorescence, sometimes glabrous; leaves widest toward the base or linear, sometimes near the middle, often falcate; leaf apex long-attenuate or attenuate, or in *S. mannii* acute.

25. Inflorescence 2–15 cm long, open to laterally contracted, the internodes below inflorescence not conspicuously elongate.

26. Plants hermaphroditic, flowers perfect; sepals strongly reflexed, oriented at ca. 30° angle to the pedicel, 3.3–5 mm long.

27. Inflorescence 5–22 cm long, open and diffuse; sepals 3.3–4.5 mm long; leaves 0.4–2.4 cm wide; capsule 2.5–3 mm long; O`ahu. 24. *S. hookeri*.

27. Inflorescence 2–10 cm long, laterally contracted; sepals 4–5 mm long; leaves 0.15–1 cm wide; capsule 3–4.5 mm long; West Maui, Lana`i. 25. *S. menziesii*.

26. Plants sexually dimorphic, flowers male, female, or occasionally hermaphroditic (note: male flowers often are morphologically very similar to hermaphroditic flowers at anthesis); sepals spreading to slightly reflexed, oriented at 70° to 100° angle to the pedicel, 2.1–3.5 mm long.

28. Leaves sparsely to moderately densely puberulent with spreading to erect hairs, at least some of them glandular; nectary shaft with wide opening at apex, the margin laciniate; Moloka`i. 26. *S. sarmentosa*.

28. Leaves glabrous, or sometimes the upper ones sparsely glandular-puberulent or with erect or spreading non-glandular hairs; nectary shaft with narrow opening, margin notched or deeply slit, but not laciniate.

29. Leaves with 3 principal veins, (3–) 7–24 mm wide; inflorescence glandular-puberulent with minute hairs, the glands sessile giving surface a mealy appearance; O`ahu. 23. *S. kealiae*.

29. Leaves with 1 principal vein, 0.8–4 (–5) mm wide; inflorescence glabrous or pubescent with minute non-glandular hairs, or if hairs glandular then the gland clearly stalked.

30. Weakly erect to sprawling shrubs; leaves thin and membranous, reflexed or recurved becoming reflexed, often appearing fasciculate by short axillary stems; Kaua`i. 29. *S. spergulina*.

30. Erect to ascending shrubs; leaves somewhat thick and slightly fleshy, arched to slightly recurved, not appearing fasciculate by short axillary stems.

31. Inflorescence glabrous or puberulent with non-glandular hairs; East Maui. 27. *S. haleakalensis*.

31. Inflorescence sparsely puberulent with glandular hairs; O`ahu. 30. *S. mannii*.

25. Inflorescence 1–4 cm long, very congested and head-like, sometimes up to 15 cm with 1–2 pairs of additional lateral clusters at the next lower nodes, these somewhat smaller than the terminal dichasia, the 1–2 internodes below the inflorescence conspicuously elongated; O`ahu, Moloka`i, Maui, Hawai`i. 28. *S. globosa*.

24. Woody shrubs; glabrous throughout; leaves broader at or above the middle, not falcate; leaf apex acuminate to acute or mucronate.

32. Inflorescence relatively diffuse, (4–) 10–25 cm long; pedicel (5–) 7–18 (–20) mm long.

33. Sepals 4–4.7 mm long; breeding system hermaphroditic; leaves 3-nerved, the outer pair often less conspicuous than midrib; petioles 0.4–0.6 cm long; Moloka`i. 31. *S. lydgatei*.

33. Sepals 2.75–4.2 mm long; breeding system gynodioecious; leaves 1(3)-nerved; petioles 0–0.3 cm long; West Maui. 32. *S. salicaria*.

32. Inflorescence laterally contracted, 4–12 (–15) cm long; pedicel (1–) 3–10 (–12) mm long.

34. Plants dioecious; sepals of staminate flowers 2.2–2.7 mm long; sepals of pistillate flowers 2.1–2.3 mm long; capsules 2–3.5 mm long; O`ahu. 33. *S. ligustrina*.

34. Plants gynodioecious; sepals of perfect flowers 3.4–4.5 mm long; sepals of pistillate flowers 2.6–3.2 mm long; capsules 3.5–5 mm long; O`ahu. 34. *S. adamantis*.

I. **Schiedea** sect. **Alphaschiedea** W. L. Wagner & Weller, sect. nov.—TYPE: *Schiedea helleri* Sherff.

Folia venis principalibus 3, 5 vel 7, margine protuberationibus epidermalibus debilibus instructa vel serrulata. Flores hermaphroditi. Sepala ovata parva. Scapi nectariorum recti.

Deciduous perennial herbs or evergreen vine; roots fleshy and thickened or fibrous. Leaves broadly deltate-ovate or deltate-cordate to broadly elliptic, elliptic-ovate or lanceolate, coriaceous or membranous, with 3, 5, or 7 principal veins, margin with weak epidermal protuberances or margin serrulate, the teeth or protuberances with small antrorsely curved hairs. Inflorescence terminal. Flowers hermaphroditic. Sepals 5, ovate, small, oriented at 5° to 60° angle to the pedicel, sometimes the distal 1/2 curved outward at a 90° angle, glabrous or ciliate in proximal 1/2, apex attenuate. Nectary shafts straight. Styles 3–5 (–6).

Distribution. The two species of *Alphaschiedea* have narrowly restricted ranges on northwestern Kaua`i.

The species of *Alphaschiedea* share with other basal sections of *Schiedea* leaves with more than one principal nerve and are unique in their small flowers with ovate sepals. Despite the close similarity in leaf and especially flower morphology species of *Alphaschiedea* have divergent habits. *Schiedea helleri* is a large vine similar to the habit of a number of species in sect. *Mononeura,* and *S. membranacea* is a deciduous perennial herb with enlarged fleshy roots, a habit similar to that of *S. verticillata.*

The sectional name is formed from the first letter of the Greek alphabet, *alpha,* and *Schiedea* in reference to the basal position of this clade in *Schiedea.*

1. **Schiedea helleri** Sherff, Amer. J. Bot. 30: 607. 1943.—TYPE: HAWAIIAN ISLANDS. KAUA`I: on Kaholuamanu above Waimea, 11–16 Oct 1895, *A. A. Heller s.n.* (holotype: F-429310!, photos: F-2 sheets!).

Evergreen vines, at least to 20 dm long, arching over other vegetation or occasionally sprawling on ground, woody at base, glabrous, puberulent in the inflorescence; stems few-branched, terete; roots fibrous. Leaves opposite; blades 8–14 cm long, (3.3–) 4.5–6 cm wide, somewhat thickened and coriaceous, broadly deltate-ovate or deltate-cordate to lanceolate, usually somewhat undulate, adaxial surface dark green and glossy with a slight purple tinge, abaxial surface dull green conspicuously infused with purple, with 3 conspicuous principal veins, sometimes with an additional outer, somewhat irregular pair, sparsely puberulent along the adaxial midvein, the hairs 0.2–0.4 mm long, translucent to occasionally purple along the midvein, spreading to erect, margin entire, with scattered antrorsely curved hairs 0.1–0.2 mm long, each of these often associated with a weak epidermal protuberance, apex acute to acuminate with a short mucro, base cordate to truncate or sometimes broadly cuneate; petioles 1.3–2 cm long, strongly channeled, puberulent. Inflorescence terminal, with 30–164 flowers, branches 20–40 cm long, diffuse, lax, the lateral branches as long as or longer than central axis, puberulent, the hairs spreading to erect, straight to slightly crinkly, (0.15–) 0.3–0.6 mm long, on upper bracts hairs often restricted to the margins; bracts of central axis 40–80 mm long, leaf-like, deltate, those of branches and flowers 3–8 mm long, lanceolate; pedicels 7–25 mm long, terete. Flowers hermaphroditic. Sepals 1.7–3.1 mm long, ovate, green, usually purple toward the base, thin and somewhat translucent, strongly reflexed in the proximal 1/4, producing a

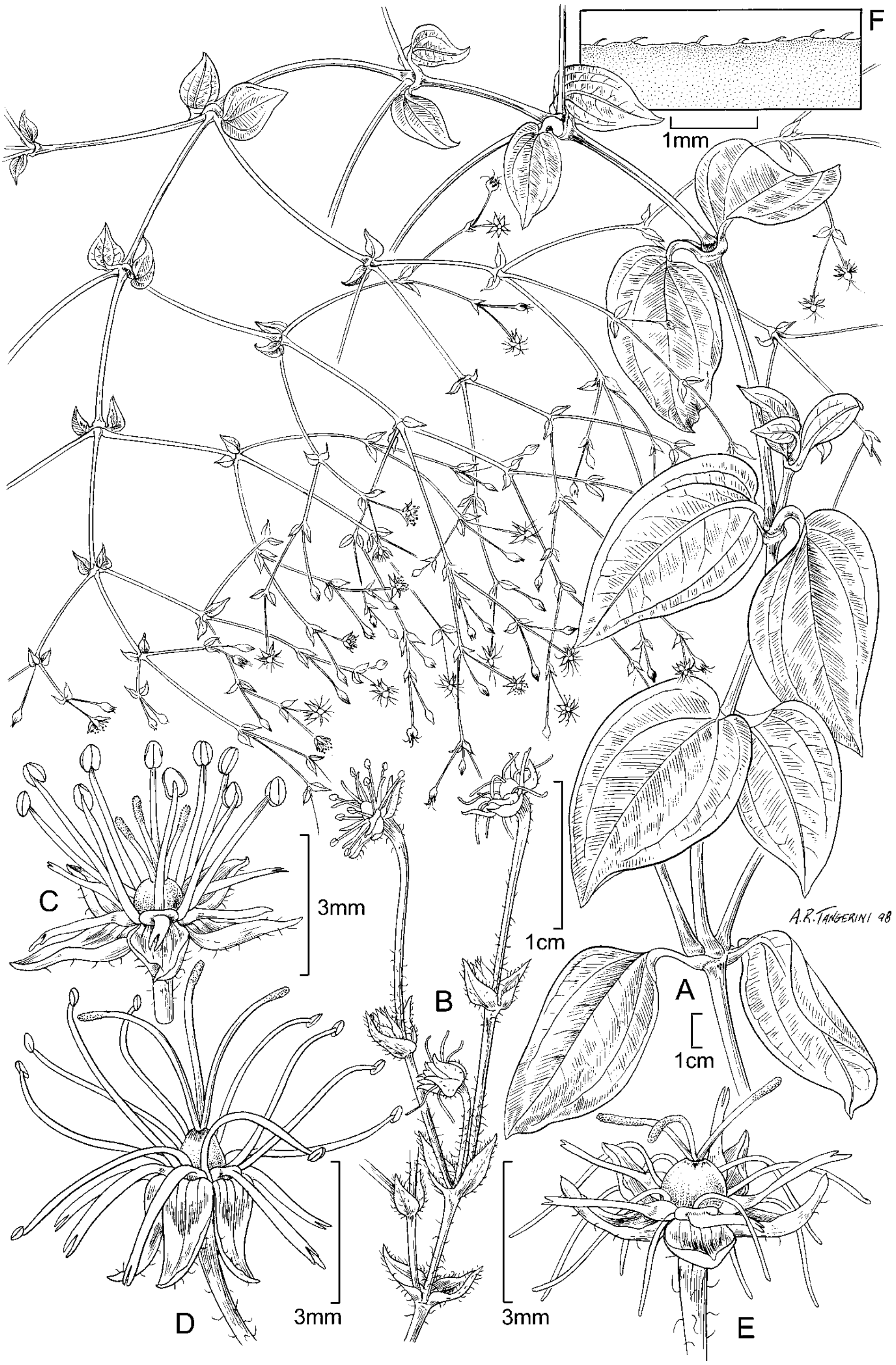

FIG. 7. *Schiedea helleri* (cult. from *Perlman 13572*). A. Habit. B. Portion of inflorescence. C. Flower in early anthesis, male stage. D. Flower in later anthesis, male stage. E. Flower in female stage. F. Detail of leaf margin.

transverse bulge, distal part strongly and deeply navicular and weakly inrolled in distal 1/2–2/3, oriented at 5° to 60° angle to the pedicel, sometimes the distal 1/2 curved outward at a 90° angle, very sparsely puberulent, occasionally some of the hairs glandular, margins scarious and sparsely ciliate in proximal 1/2, apex attenuate. Nectary base ca. 0.4 mm long, greenish yellow, the nectary shaft 3.5–4.2 mm long, straight or gently recurved, at 90° angle to axis, apex bifid, the sides subequal. Stamens 10; filaments dimorphic, the antisepalous whorl 4.5–5 mm long, the alternate whorl 4–4.5 mm long; anthers 0.9–1 mm long, subequal, pale yellow. Styles 3. Capsules 3–3.4 mm long, subglobose to broadly ovoid. Seeds 1.2–1.3 mm long, orbicular, compressed, transversely rugose. Chromosome number unknown. Figs. 1A, 7.

Distribution (Fig. 8). Kaua`i, the type from Kaholuamanu, rediscovered in 1993 along Mohihi Stream and in Nawaimaka Valley; in wet montane forest; 960–1180 m.

ADDITIONAL SPECIMENS EXAMINED. **Kaua`i.** Waimea District, Na Pali-Kona Forest Reserve, Kohua ridge, on slope to N of Mohihi-Wai`alae Tr., ca. 60 ft. below trail, about 1.25 mi in on Mohihi-Wai`alae trail, N facing slope of Mohihi Stream, [22°06′50.7″N, 159°35′0.1″W], *Flynn et. al. 5693* (BISH, US); Nawaimaka Valley, along banks of Nawaimaka Stream, to W of Wai`alae Valley ridge, *Perlman 14656* (PTBG, US); Nawaimaka stream, along stream banks, to W of Wai`alae Valley, [22°04′16.2″N, 159°36′4.3″W], *Perlman 14767* (BISH, K, NY, PTBG, US); Wai`alae Valley area but S of Wai`alae along Nawaimaka Stream on stream bank, *Perlman & Flynn 13448* (PTBG, US); Kohua ridge, Mohihi stream drainage, below Wai`alae-Wai`ale`ale tr., 10–20 m on steep slope, [22°07′1.4″N, 159°36′2.9″W], *Perlman & Wood 14777* (F, BISH, NY, US); Waimea canyon drainage, Nawaimaka valley, *Perlman et al. 17630* (PTBG); Mohihi Stream near trail head of Mohihi-Wai`alae, side gulch after second stream crossing, *Wood & Menard 10573* (PTBG); Waimea District, Mohihi Stream near gauging station, *Wood & Perlman 2543* (BISH, P, PTBG, US).

CULTIVATED. **Kaua`i.** Small side stream off Mohihi stream just past Wai`alae trail turnoff, *Perlman & Wood 13572* [cult. *Wagner & Shannon 6809*] (BISH, PTBG, US).

Schiedea helleri is closely related to *S. membranacea*, as reported by Wagner et al. (1990) and indicated in the most recent molecular-morphological analyses. It differs from *S. membranacea* in its vining habit, pendent inflorescence, thicker, 3-nerved leaves with a cordate or truncate base, which are broadest at the base, and much larger seeds. Plants in the population in Nawaimaka Valley exhibit a sprawling habit in the field, but have the same vining habit as the Mohihi population when grown in the greenhouse. Plants in the Nawaimaka population also have leaves somewhat narrower with the base truncate to cuneate, and inflorescences with denser puberulence.

Schiedea helleri was presumed extinct (Wagner et al. 1990; Weller et al. 1990), but was rediscovered in 1993 (Lorence et al. 1995). It was federally listed as endangered in 1996 (Russell & Bruegmann 1996a).

The specific epithet honors its discoverer, Amos A. Heller (1867–1944), who made extensive collections on O`ahu and Kaua`i in 1895. For details of his collection activity and itinerary see the account by Wagner and Shannon (1999).

2. Schiedea membranacea St. John, Pacific Sci. 26: 275. 1972.—TYPE: HAWAIIAN ISLANDS. KAUA`I: [Waimea District], Ku`ia Valley, 2000 ft [610 m], 3 Jul 1969, *R. D. Hobdy 130* (holotype, mounted on 2 sheets: BISH-501663! BISH-501664!; isotype: A!).

Deciduous perennial herbs dying back to enlarged fleshy roots in dry seasons, lower portions of stems glabrous, glabrous or occasionally sparsely puberulent in the inflorescence; stems 2–10 dm long, ascending to sprawling, usually multi-stemmed from the base,

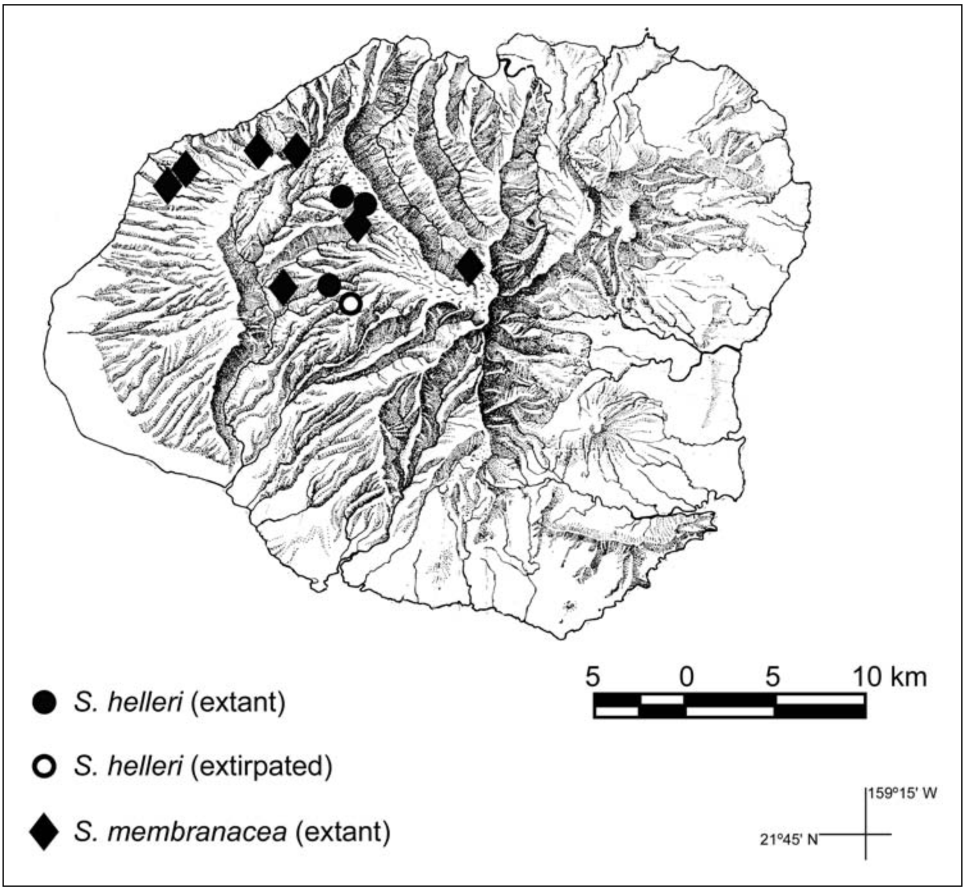

FIG. 8. Distribution of *Schiedea helleri* and *S. membranacea*.

often unbranched above, terete, internodes usually purple; roots fleshy, thickened. Leaves opposite; blades 7–22 cm long, 4–11 cm wide, thin or rarely slightly thickened, membranous, broadly elliptic to broadly elliptic-ovate, dull dark green, with 5–7 conspicuous principal veins, adaxial side glabrous, abaxial side sparsely puberulent, especially on the veins, the hairs 0.2– 0.6 mm long, mostly antrorsely curved to weakly appressed, slightly shorter on the surface, margin inconspicuously and irregularly serrulate, the teeth more prominent toward the apex, moderately covered with antrorsely curved or hooked hairs, 0.2–0.6 mm long, usually longer toward the leaf base, apex acuminate, base broadly obtuse to truncate and somewhat folded; petioles 0.3–2 cm long, weakly channeled, purple. Inflorescence terminal, with (28–) 100–205 flowers, ca. 25–57 cm long, large, diffuse; bracts green, broadly ovate to ovate or the smallest ones lanceolate, those of central axis 7–60 mm long, those of branches and flowers 2–18 mm long, usually purple, glabrous to ciliate toward the base; pedicels (10–) 20–35 mm long, elongating slightly in fruit, filiform, terete. Flowers hermaphroditic. Sepals 2–2.7 mm long, ovate, green turning purple above the base or in upper part near the apex, thin and somewhat translucent, strongly reflexed in the proximal 1/4, producing a large transverse bulge, distal part strongly and deeply navicular and becoming inrolled in distal 1/2, oriented at 5° to 60° angle to the

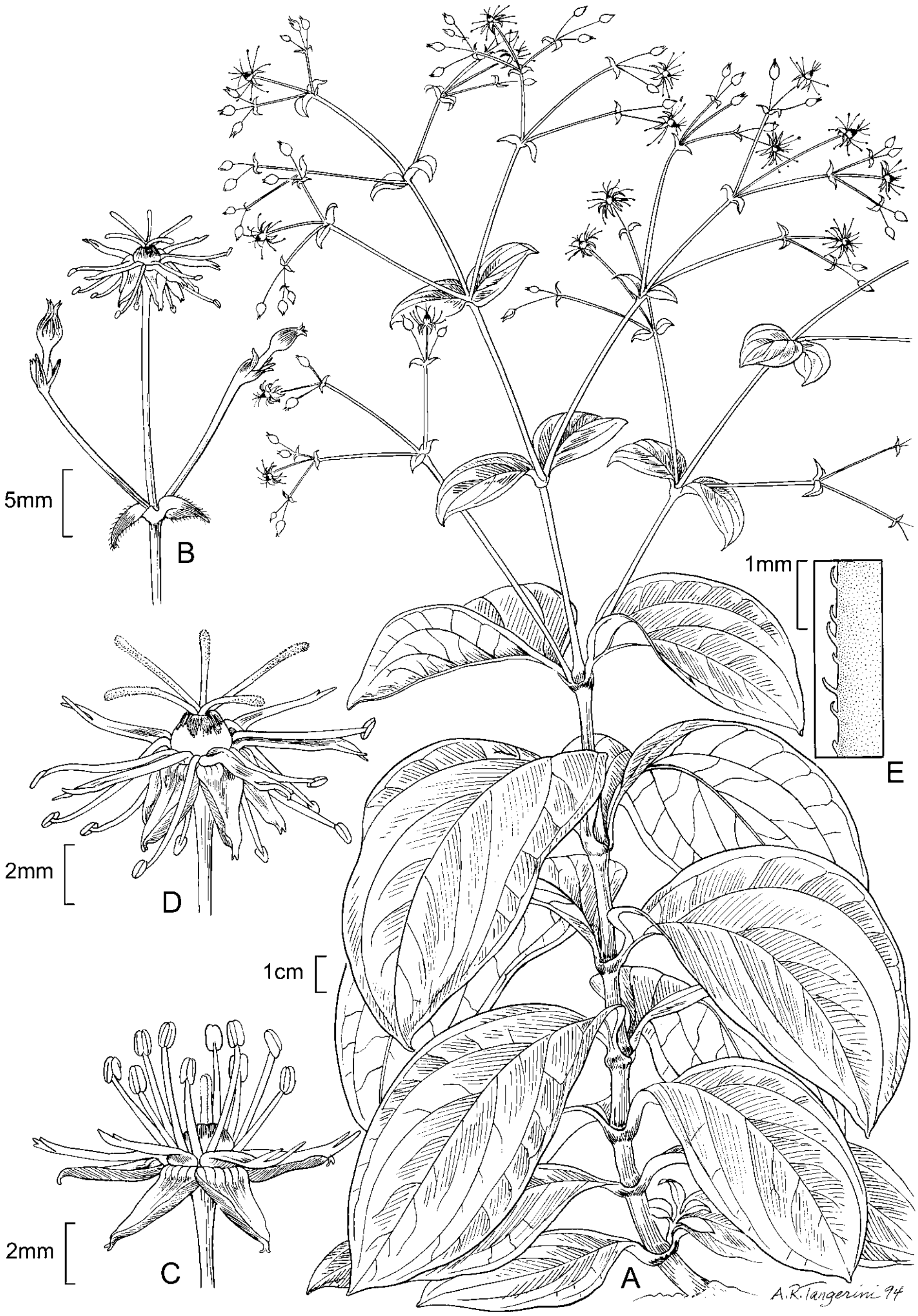

FIG. 9. *Schiedea membranacea* (cult. from *Weller & Sakai 864*). A. Habit. B. Portion of inflorescence. C. Flower in early anthesis, male stage. D. Flower in later anthesis, female stage. E. Detail of leaf margin.

pedicel, sometimes the distal 1/2 curved outward at a 90° angle, glabrous, margins scarious, apex attenuate. Nectary base 0.4–0.45 mm long, greenish yellow, the nectary shaft 4–5 mm long, pale green, straight or gently recurved, at 45–90° angle to axis, apex with usually (3–) 4 divisions, 2–3 of them much longer than the other(s). Stamens 10; filaments dimorphic, the antisepalous whorl 3.7–4.7 mm long, the alternate whorl 2.8–4 mm long; anthers of the antisepalous whorl 0.4–0.7 mm long, those of the alternate whorl 0.4–0.7 mm long, pale yellow. Styles 3–5 (–6), often variable in number on the same plant. Capsules 2.5–3 mm long, ovoid, apex purple. Seeds highly variable in number, (1–) 4–25 (–35) [average 12 per capsule], ca. 0.8–0.9 mm long, orbicular-reniform, compressed, the surface transversely rugose. Chromosome number unknown. Figs. 1B, 3A, B, 9.

Distribution (Fig. 8). Northern and western Kaua`i, including the northwestern exterior valleys of Mahanaloa and Ku`ia, Pa`aiki, the rim of Kalalau Valley, Nualolo Valley, Wainiha, and in the Waimea Canyon area from Wai`alae Ridge and upper Koai`e Canyon; rocky sites and bases of cliffs in mesic forest; 490–1160 m.

ADDITIONAL SPECIMENS EXAMINED. **Kaua`i.** Pa`aiki Valley, [22°08′016.5″N, 159°42′26.1″W], *Balgooy 4256* (BISH); Ku`ia Valley, *Christensen 134* (BISH [2]); Pu`uka Pele Forest Reserve, Mahanaloa Valley, *Fay 210* (A, BISH, F, NY, PTBG); Koke`e State Park, along Hwy 550 near mile 18.3, along W edge of ridge jutting into Kalalau Valley, *Flynn 1230* (BISH, PTBG); Waimea District, Napali-Kona Forest Reserve, Mahanaloa Valley, *Flynn et. al. 2087* (PTBG); Waimea District, Ku`ia Valley, one of the tributaries of the Miloli`i Valley, *Gustafson 1759* (RSA); Mahanaloa Valley, junction of Ku`ia and Mahanaloa valleys, *Herbst et. al. 2904* (BISH); without locality, 1982, *Lucas s.n.* (PTBG); Koke`e, Pu`uka Pele Forest Reserve, Mahanaloa Valley, [22°08′18″N, 159°42′6.2″W], *Plews 138* (PTBG [2]); Wainiha valley, back of valley, below Hinalele Falls, along stream on banks and in small side streams, [22°05′26.1″N, 159°30′57″W], *Perlman et. al. 13211* (PTBG, US); Koai`e Canyon, upper canyon, near waterfall where upstream travel is stopped, N facing slope, [22°06′29.4″N, 159°34′37.1″W], *Perlman & Wood 14360* (BISH, PTBG, US); Hanalei District, Kalalau Rim, N below Pu`uokila, [22°09′N, 159°38′4.8″W], *Wood 1033a* (PTBG, US); Ku`ia Natural Area Reserve, Nualolo Valley, *Wood & Perlman 1073* (PTBG); Waimae District, Wai`alae Ridge and N side of ridge above falls, steep basalt walls over falls, 18°N aspect, [22°04′28.9″N, 159°37′42.4″W], *Wood & Perlman 2376* (PTBG); Hanalei District, Kalalau Valley, below Pu`uokila, along wet W facing walls, *Wood & Perlman 2527* (PTBG); Ku`ia drainage, below confluence of N/S fork, *Wood & Query 8400* (PTBG, US); Hanalei District, Kalalau, Exocarpus Ridge, drainage west of Pu`uokila, *Wood & Sloan 874* (BISH, PTBG, US).

CULTIVATED. **Kaua`i.** Junction of Mahanaloa and Ku`ia Gulches, March 1987, *Weller & Sakai s.n.* [cult. *Weller & Sakai 864*] (BISH, US), *Weller & Sakai 864* [cult. *Wagner & Shannon 6794*] (BISH, PTBG, US).

Although the only members of a basal clade, *S. membranacea* and *S. helleri* are very distinctive; see discussion of *S. helleri* (no. 1).

Schiedea membranacea was federally listed as endangered in 1996 (Russell & Bruegmann 1996a). Introduced ungulate herbivores consume accessible plants. No regeneration from seeds has been observed, possibly because introduced mollusks destroy seeds and seedlings.

The specific epithet refers to the membranous leaf blades.

II. **Schiedea** sect. **Leucocalyx** W. L. Wagner & Weller, sect. nov.—TYPE: *Schiedea attenuata* W. L. Wagner, Weller & Sakai.

Frutex parce ramosus. Folia crassa firma aliquantum succulenta et nitida, nervis 1 vel 3. Flores hermaphroditi. Sepala adaxialiter viridi-alba vel flavido-alba. Scapi nectariorum recurvati et appressi ad sepala opposita.

Shrubs; stems few, sprawling, wood weakly developed; roots fibrous. Leaves linear-lanceolate or linear-elliptic, falcate, 1(–3)-nerved, thick, firm, somewhat succulent and glossy, margins entire. Inflorescence terminal. Flowers hermaphroditic. Sepals 5, lanceolate, greenish white or yellowish white adaxially, oriented at 90° to the pedicel at staminate stage and to 60° to the pedicel at the pistillate stage, glabrous, apex weakly acuminate. Nectary shafts recurved and appressed to the opposed sepal, directly releasing nectar onto the sepal. Styles 5–6 (–7).

Distribution. Known only from vertical cliffs of Kalalau Valley, Kaua`i.

The single species of sect. *Leucocalyx*, *S. attenuata*, was thought to be closely related to *S. globosa* (Wagner et al. 1994, 1995; Weller et al. 1995), which it resembles vegetatively. Yet, the most recent combined molecular and morphological analyses place it at the base of a clade with sections *Polyneura*, *Alsinidendron*, and *Nothoschiedea*, although this placement is very weakly supported. It is interesting that both *S. attenuata* and *S. verticillata* share the unique recurved nectary shafts that are appressed to the opposed sepal. A robust placement is elusive with current data. Based on current data a close relationship to *S. globosa*, however, seems unlikely.

The sectional name is formed from the Greek adjective *leukos* (“white”) and “calyx,” and refers to the whitish color of the adaxial surface of the calyx.

3. Schiedea attenuata W. L. Wagner, Weller & Sakai, Novon 4: 187. 1994.—TYPE: HAWAIIAN ISLANDS. KAUA`I: Hanalei District, Kalalau rim, Kalahu side below and W of first Kalalau lookout, 300 m E of plane crash [site], [22°08′N, 159°39′W, NW aspect], 790 m, 20 Nov 1991, *K. R. Wood 1394* (holotype: US-3238878!; isotype: PTBG!).

Erect, sparingly branched shrub to 7.5 dm tall (in cultivation forming massive hanging plants with stems to 10 dm long); stems compressed-terete, glabrous or very sparsely puberulent with minute ± purplish weakly hooked or curved hairs. Leaves opposite, 5.3–7 cm long (to 12 cm in cultivation), 5–7 mm wide (to 11 mm in cultivation), thick, firm and somewhat succulent, glossy, linear-lanceolate or linear-elliptic, falcate, 1(–3)-nerved, only the midrib prominent, strongly raised on abaxial surface and impressed on adaxial surface, margin slightly revolute, margin and abaxial surface very sparsely puberulent near base, apex long-attenuate, base narrowly acute, gradually tapering and weakly connate, sessile. Inflorescence terminal, with 14–66 flowers (up to 70 in cultivation), 4–9 cm long (up to 15 cm long in cultivation), diffuse, the branches and pedicels oriented to give a one-sided effect; bracts pale green to purple adaxially, the lowermost 11 mm long, 7–8 mm wide, those of the branches and flowers 2.3–5 mm long; internodes 3–28 mm long; pedicels 8–15 (–19) mm long. Flowers hermaphroditic. Sepals 4–5 mm long, lanceolate, greenish white or yellowish white adaxially, somewhat petaloid, often pale purple abaxially, margins conspicuously scarious, glabrous, strongly concave in upper half, shallowly navicular and usually inrolled in the upper 2/3, oriented at 90° to the pedicel at staminate stage and to 60° to the pedicel at the pistillate stage, apex weakly acuminate. Nectary base 0.7–0.8 mm long, dark greenish yellow, the nectary shaft ca. 3 mm long, recurved and appressed to the opposed sepal, the apex with an abaxial slit ca. 0.06–0.08 mm long, directly releasing nectar onto the sepal. Stamens 10; filaments dimorphic, the antisepalous whorl 4.7–4.8 mm long, the alternate whorl 4.2–4.5 mm long; anthers ca. 1 mm long, subequal, yellow. Styles 5–6 (–7). Capsules ca. 3.3–4.5 mm long, broadly ovoid. Seeds 0.6–0.7 mm long, orbicular-reniform, compressed, the faces transversely rugose, the margins papillose; margins of testa cells obtuse to rounded. Chromosome number unknown. Figs. 1C, 3C, D, 10.

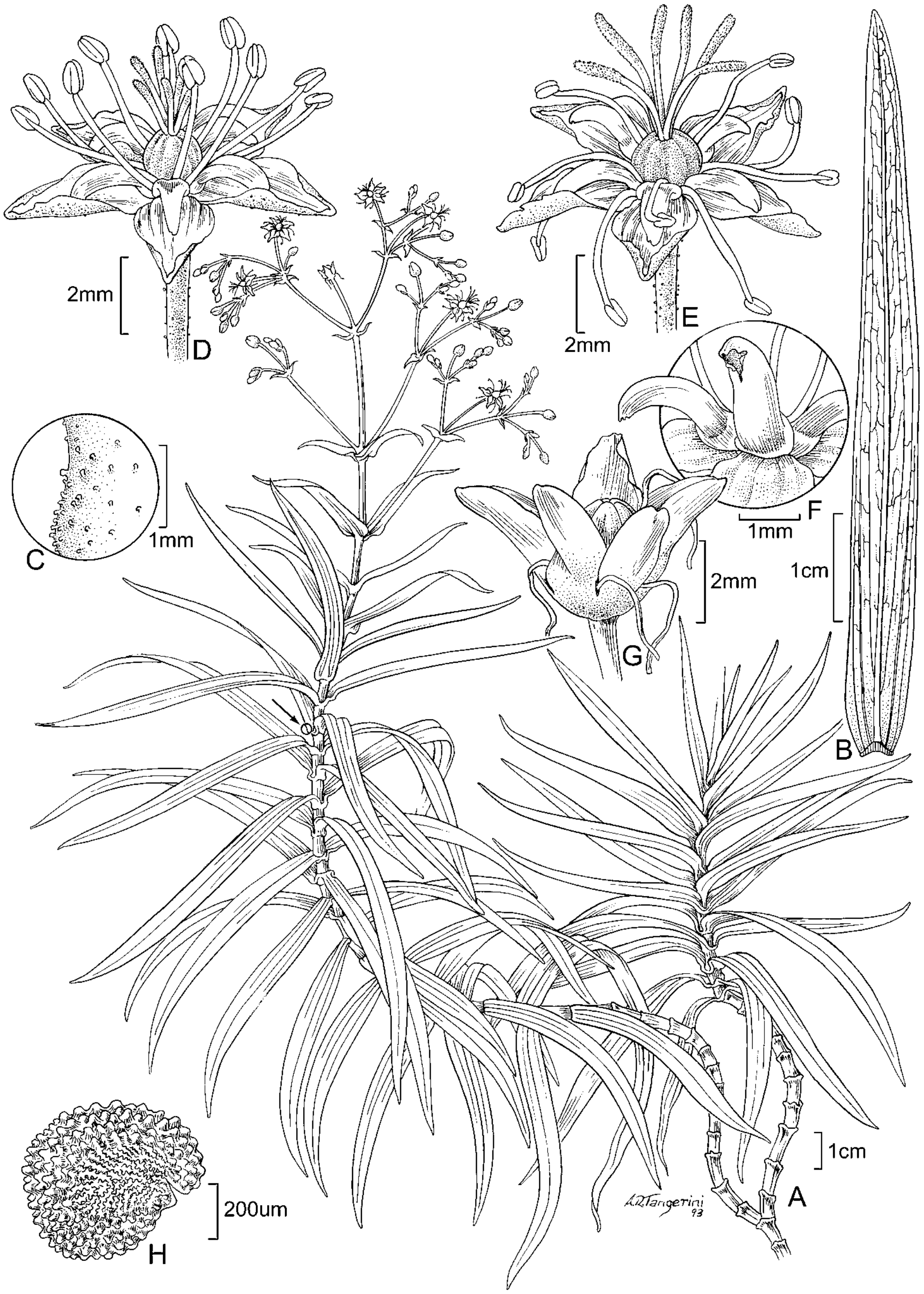

FIG. 10. *Schiedea attenuata* (cult. from *Wood 1394*). A. Habit. B. Leaf. C. Detail showing minute hairs on leaf abaxial surface near the base. D. Flower in early anthesis, male stage. E. Flower in later anthesis, female stage. F. Detail of flower showing nectary shaft; shaft raised to show apical opening. G. Early fruit stage. H. Seed.

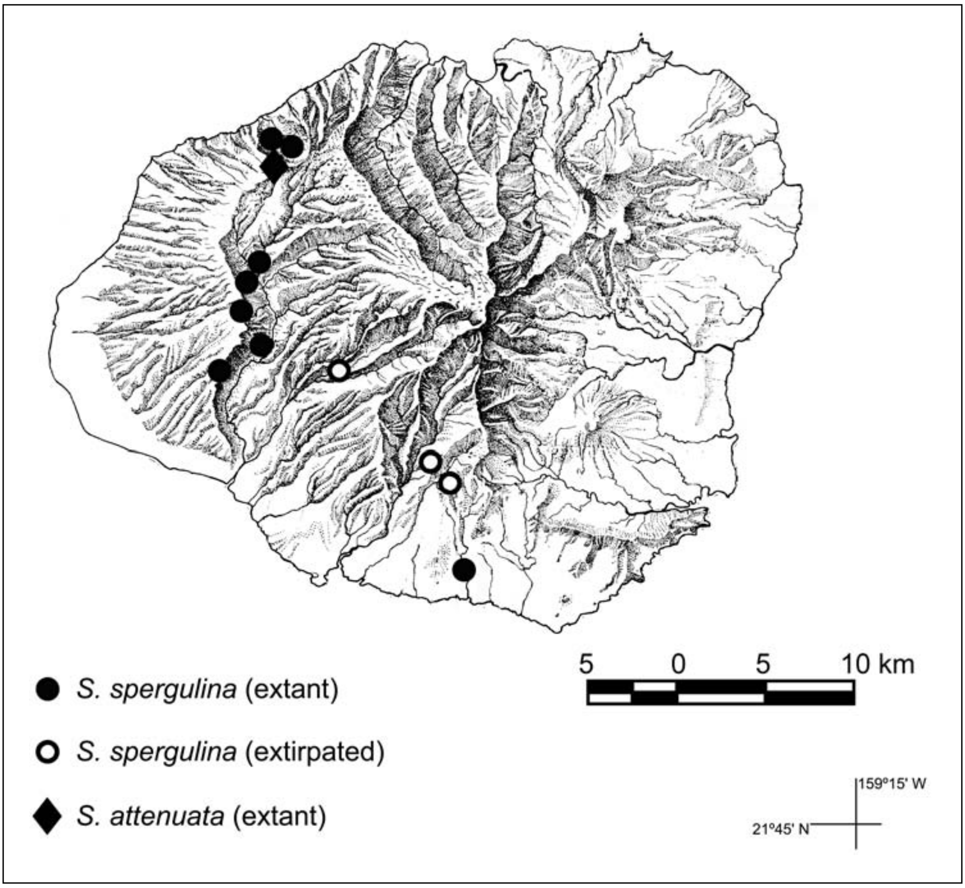

FIG. 11. Distribution of *Schiedea attenuata* and *S. spergulina*.

Distribution (Fig. 11). Kaua`i, a single population in Kalalau Valley, slopes of Kalahu; in diverse mesic forest on vertical cliffs; ca. 790 m.

ADDITIONAL SPECIMENS EXAMINED. **Kaua`i.** Hanalei District: Kalalau Rim, Kalahu side below and W of first Kalalau lookout, 300 m E of plane crash, [22°09′22″N, 159°38′45″W], *Wood 1423* (PTBG); Kalalau Valley, slopes of Kalahu, 300 m E of Navy plane crash, *Wood & Perlman 3382* (US).

Schiedea attenuata is characterized by a woody habit, glossy, succulent, long-attenuate leaves, a short, relatively open inflorescence, and hermaphroditic flowers with the sepals greenish or yellowish white adaxially, recurved nectary shafts, and 5–6 (–7) styles. It has been collected three times on rappels into Kalalau Valley in 1991 and 1994 on the Kalahu side below and west of the first, southwestern-most lookout. Fewer than 20 individuals of this new species were noted by Wood during his extensive investigations of diverse mesic forest patches on Kalalau Valley cliffs. The southwestern corner of the upper Kalalau Valley has habitats that may harbor additional populations of this rare species. It is currently a candidate for listing as endangered (Williams 2002).

The specific epithet refers to the long-attenuate leaves.

III. Schiedea sect. **Polyneura** W. L. Wagner & Weller, sect. nov.—TYPE: *Schiedea verticillata* F. Brown.

Herbae perennes et carnosae radicibus accrescentibus et carnosis. Folia opposita vel interdum ternata, venis principalibus 7–12. Flores hermaphroditi et grandes. Scapi nectariorum recurvati, unusquisque supra suum sepalum cum apice tantum sepalum contingenti.

Fleshy perennial herbs; roots enlarged, fleshy. Leaves opposite or sometimes ternate, broadly ovate to broadly elliptic, thick, with 7–12 principal veins, margins entire. Inflorescence terminal. Flowers hermaphroditic, large. Sepals 5, lanceolate, green to pale green, recurved from the base, proximal 1/3 flat, distal part very shallowly concave, usually slightly twisted toward apex, arching at a 80° to 90° angle to the pedicel, glandular-pilose, especially along the midrib, apex attenuate. Nectary shafts recurved, arching above sepal with only tip touching it, and nectary pooling directly onto the sepal. Styles 4–7.

Distribution. Known only from Nihoa in the Northwestern Hawaiian Islands.

Schiedea verticillata is in a weakly supported clade with sections *Alsinidendron, Nothoschiedea,* and *Leucocalyx.* The species of this clade produce the largest flowers in the genus. The specialized nectary shaft position in *S. verticillata* and large quantity of nectar provide no obvious clues to potential pollinators.

The sectional name is formed from the Greek adjective *polys* (“many”) and noun *neuron* (“nerve”) in reference to the 7–12-nerved leaves, the greatest number in the genus, and perhaps the Caryophyllaceae.

4. Schiedea verticillata F. Brown in Christophersen and Caum, Bernice P. Bishop Mus. Bull. 81: 29. 1931. *Alsinidendron verticillatum* (F. Brown) Sherff, Amer. J. Bot. 31: 157. 1944.—TYPE: HAWAIIAN ISLANDS. NIHOA: pockets in cliff wall, south side of beach, 30 m, Jun 1923, *E. L. Caum 70* (holotype: BISH-502024!; isotypes: BISH-2 sheets! GB! NY! P! UC! US!, photo of UC isotype: F!).

Perennial fleshy herbs dying back to enlarged fleshy roots in dry seasons, glabrous, except inflorescence and ± internode below it glandular-pilose; stems ascending, sprawling or sometimes pendent, 4–7 dm long, terete. Leaves opposite or sometimes ternate; blades 8–15 cm long, (4–) 7–9 cm wide, thick and succulent, often recurved from the base, broadly ovate to broadly elliptic, often somewhat undulate, pale or yellowish green, with 7–12 inconspicuous principal veins, glabrous, margins entire, thickened, apex acute to obtuse with a short mucro, sessile and slightly or prominently connate with other leaves at the node. Inflorescence terminal, with ca. 35 (–65) flowers, 17–25 (–30) cm long, weakly diffuse, densely glandular-pilose, the hairs (0.4–) 0.9–1.2 mm long; bracts pale green, opposite or whorled, lanceolate to broadly ovate, those of central axis 6–40 mm long, those of branches and flowers 3.5–7 mm long; pedicels 5–20 mm long, stout, terete. Flowers hermaphroditic. Sepals 8–10.5 mm long, lanceolate, green to pale green, opaque, recurved from the base, proximal 1/3 flat, distal part very shallowly concave, usually slightly twisted toward apex, arching at a 80° to 90° angle to the pedicel, glandular-pilose, especially along the midrib, the hairs 0.2–0.9 mm long, margin scarcely scarious, apex attenuate and minutely navicular. Nectary base 1.5 mm long, yellow with a slight green tinge, the nectary shaft 4.5–6 mm long, recurved, arching above sepal with only tip touching it, the nectar pooling directly onto the sepal. Stamens 10; filaments subequal, the antisepalous whorl ca. 10 mm long, the alternate whorl ca. 9.5 mm long; anthers 2.3–2.5 mm long, yellow. Styles 4–7. Capsules 7–9 mm long, narrowly ovoid. Seeds 0.7–0.8 mm long,

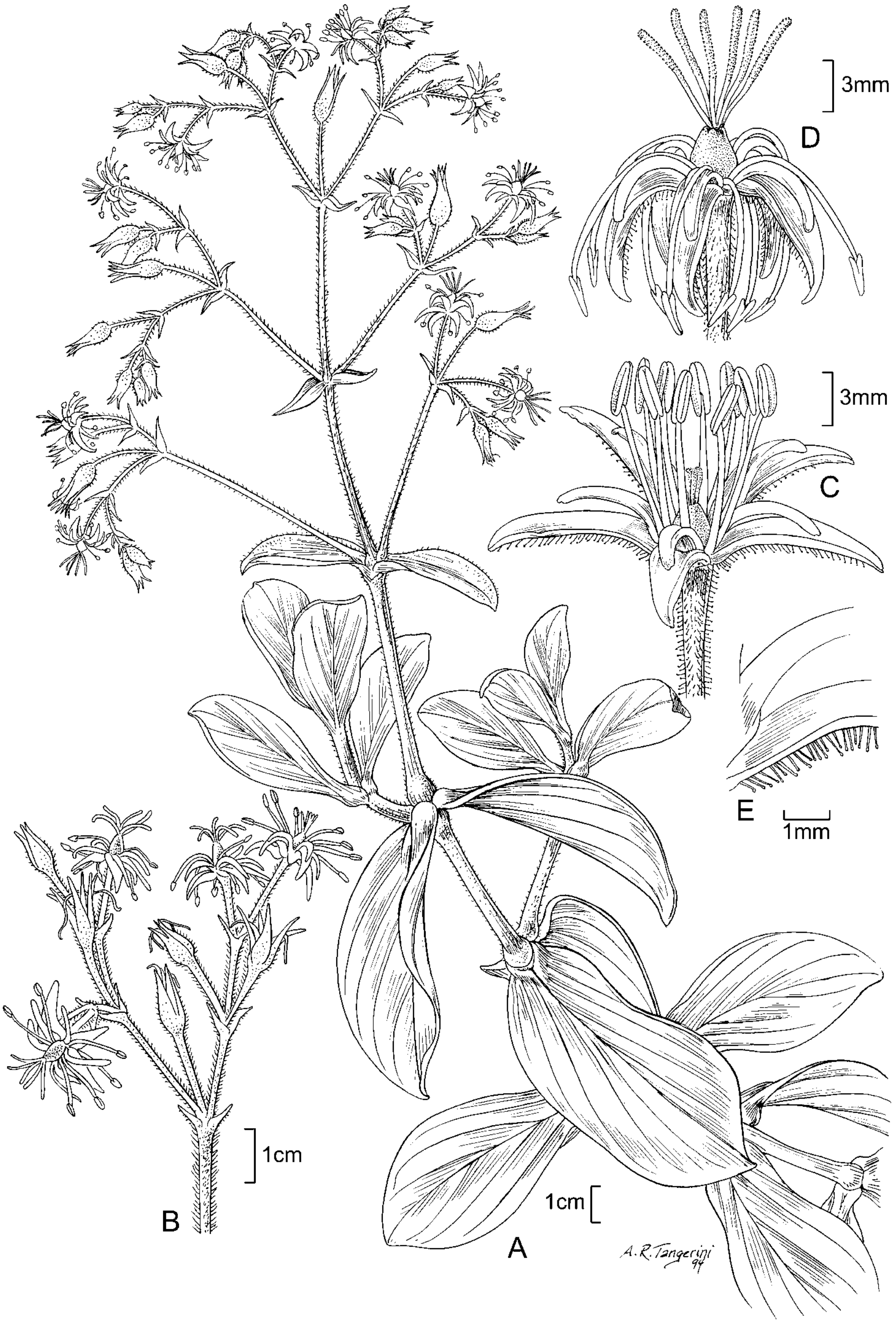

FIG. 12. *Schiedea verticillata* (cult. from *Weller & Sakai 880*). A. Habit. B. Portion of inflorescence. C. Flower in early anthesis, male stage. D. Flower in later anthesis, female stage. E. Detail showing minute hairs on leaf.

orbicular-reniform, slightly compressed, the surface evenly tuberculate. Chromosome number: 2n = probably 60 (Carr 1985). Plate 1B; Figs. 1D, 3E, F, 12.

Distribution. Nihoa; in coastal soil pockets and cracks in cliff faces; 30–280 m.—Four new populations of this species were found in 1996, making a total of 10 known locations with an estimated 360 plants according to a U.S. Fish and Wildlife Services survey. The populations are primarily located on the western half of the island, but two populations are on the north cliffs of the island.

ADDITIONAL SPECIMENS EXAMINED. **Nihoa.** *Bryan 2* (BISH); cliff S of beach, *Christophersen 3* (BISH); Devil's Slide, *Conant 115* (BISH, US); S face of Dog's Head (W end) cliff adjacent to Emory's site 2, *Yen 1005* (BISH [2], US).

CULTIVATED. **Nihoa.** Devil's Slide, about half way down, 26 Aug 1968, *Kridler & Sincock s.n.* [cult. *Herbst 1401*] (BISH [3]); Devil's Slide and Dog's Head (plants and seed from U.S. Fish and Wildlife personnel and S. Conant), *Weller & Sakai 880* [cult. *Wagner & Shannon 6819*] (BISH, PTBG, US).

Schiedea verticillata dies back to its enlarged fleshy roots during the dry season. Nectar is deposited in relatively large quantities on the sepals by recurved nectary shafts (Weller et al. 1990; Weller et al. 1998), suggesting the possibility of biotic pollination. The species is apparently outcrossing; Weller et al. (1996) reported a very high level of isozyme variability. *Schiedea verticillata* was federally listed as endangered in 1996 (Bruegmann & Ellshoff 1996).

The specific epithet refers to the whorled leaves present on the type specimen; however, whorled leaves occur less frequently than opposite leaves in this species.

IV. **Schiedea** sect. **Nothoschiedea** H. Mann, Proc. Boston Soc. Nat. Hist. 10: 310. 1866.—TYPE: *Schiedea viscosa* H. Mann.

Sprawling or weakly climbing vines. Leaves ovate, narrowly ovate-elliptic to narrowly elliptic or elliptic, with (3) 5 principal veins, thin and membranous, margins with minute often antrorse epidermal protuberances, especially in the distal part, and ciliate with thin antrorsely curved or spreading hairs. Inflorescence pseudolateral (lateral branch of the next node below inflorescence elongating coincident with flowering and assuming subsequent vegetative growth). Flowers hermaphroditic, pendent. Sepals (4) 5, membranous, greenish white, remaining white or pale and becoming dry and papery as fruit matures, puberulent externally. Nectary shafts modified into distinct flaps separated to the base; nectar black. Styles 5–11. Seeds persistent on placenta, capsules gradually rotting to release seeds rather than dehiscing.

Distribution. The two species of *Schiedea* sect. *Nothoschiedea* are restricted and rare in wet or mesic forests in the western part of Kaua`i.

These species were treated by us in previous publications and by Wagner et al. (1990) as *Alsinidendron*, because they have large petaloid calyces, enlarged specialized nectaries, which produce copious black nectar held by the modified flap-type nectary extensions, and pseudoaxillary inflorescences. Phylogenetic analyses clearly show that this group was derived within *Schiedea*; therefore, we revert here to the earlier concept for these species by treating them as a distinctive section in *Schiedea* (Mann 1866, 1867; Hillebrand 1888).

The sectional name is formed from the Greek adjective *nothos* ("false, spurious") and *Schiedea* in reference to distinction of this section from the remainder of *Schiedea*.

5. Schiedea lychnoides Hillebrand, Fl. Hawaiian Isl. 36. 1888. *Alsinidendron lychnoides* (Hillebrand) Sherff, Amer. J. Bot. 31: 157. 1944.—TYPE: HAWAIIAN ISLANDS. KAUA`I: above Waimea, 1853–1871, *V. Knudsen 89* (holotype B, destroyed, photo: BISH!).—KAUA`I: on Kaholuamanu, above Waimea, 2–9 Sep 1895, *A. A. Heller 2796* (neotype, here designated: US-265557!; isoneotypes: F! G-2 sheets! GH! MO! NY! UC!; photo of F isoneotype: F!)

Weakly climbing or sprawling vines, primary stems to 30 dm long, with short lateral branches. Leaves opposite; blades 4.5–6.5 cm long, 1.8–3.8 cm wide, thin and membranous, dark green with a purple tinge, ovate to elliptic, with (3) 5 principal veins, the outer pair of veins usually only weakly developed, both surfaces sparsely puberulent, the hairs erect to somewhat antrorsely appressed, translucent with a purple tinge, those of the principal veins on abaxial side and margin coarser and more appressed, 0.25–0.5 mm long, margin inconspicuously serrulate, at least in the distal half, apex mucronate; petioles 0.2–0.7 cm long. Inflorescence pseudoaxillary, with usually 3–17 (–21) flowers, all parts densely glandular-puberulent throughout, the hairs translucent with a purple tinge, 0.25–0.5 mm long; bracts 14–24 mm long, foliaceous; peduncles 18–25 mm long, the internodes of the lateral inflorescence branches 2–14 mm long; pedicels thinner, 7–18 mm long. Flowers apparently adapted for bird pollination, pendent. Sepals 5, 9–12 mm long, 5–6.5 mm wide, enlarging to 12–18 mm long and 7–9 mm wide in fruit, the outer ones larger, rhombic, the inner ones oblong-rhombic, greenish white, thin and membranous, dry at maturity, becoming slightly recurved along the margin of the upper half of the outer pair, especially as fruit develops, apex obtuse and mucronulate, abaxially densely glandular-puberulent throughout, glabrous adaxially. Stamens 10–13; filaments 5.5–6.3 mm long, the antisepalous ones slightly longer to subequal; anthers 0.8–1.3 mm long, pale reddish purple at anthesis, changing to a darker reddish purple, the pollen pale gray. Nectary ring bright green, the flap-like extensions thin, translucent, 1.7–3.5 mm long and nearly as wide or sometimes wider, irregularly shallowly 2–3-toothed. Styles 8–11, often the number variable on the same plant. Capsules 9–12 mm long, ovoid. Seeds 0.8–1.0 mm long, black, persistent on placenta, released as the capsule gradually rots, the margins of the cells of the testa slightly convex, the raised cells forming low transverse ridges across the seed surface. Chromosome number: 2n = possibly 60 (*Weller & Sakai 867*). Figs. 1E, 3G, H, 13.

Distribution (Fig. 14). Kaua`i, known only from the southern margin of the Alaka`i Swamp from Ke`aku Cave near Mount Wai`ale`ale to Pihea Trail along the rim of Kalalau Valley; in wet forest, often along streams, trailing on the ground or sprawling over other vegetation, in forests dominated by *Metrosideros polymorpha* Gaudich. and *Cheirodendron* spp. with understory commonly of *Broussaisia arguta* Gaudich., *Hedyotis*, *Vaccinium*, *Myrsine*, *Labordia*, *Cyanea*, *Melicope*, and pteridophytes such as *Athyrium microphyllum* (Sm.) Alston, *Dicranopteris linearis* (Burm. f.) Underw., *Dryopteris glabra* (Brack.) Kuntze, *Nephrolepis cordifolia* (L.) C. Presl, and *Sticherus owhyhensis* (Hook.) Ching; 1090–1320 m.

ADDITIONAL SPECIMENS EXAMINED. **Kaua`i.** Koke`e, Waineke swamp, [22°07′32.7″N, 159°39′12.6″W], *Degener 5950* (B, F, G, GH, K, MIN, NY, P, US); Koke`e, NW of Lehua Makanoi, *Degener et. al. 23942* (B, BISH, NY, W); on the trail between Kawaikoi Stream and Lehua Makanoi, *Fagerlind & Skottsberg 6584* (S); Waimea, *Faurie 1097* (P); Napali-Kona Forest Reserve, Alaka`i Swamp and Pihea trails, [22°08′54.1″N, 159°36′57.8″W], *Flynn et. al. 2825* (PTBG); Kaholuamanu, above Waimea, *Forbes 342.K* (BISH, MO, NY, UC, US); Waimea drainage basin, W side, *Forbes 886.K* (BH, BISH, M, P, US), *1150.K* (BISH, GH); Kaholuamanu,

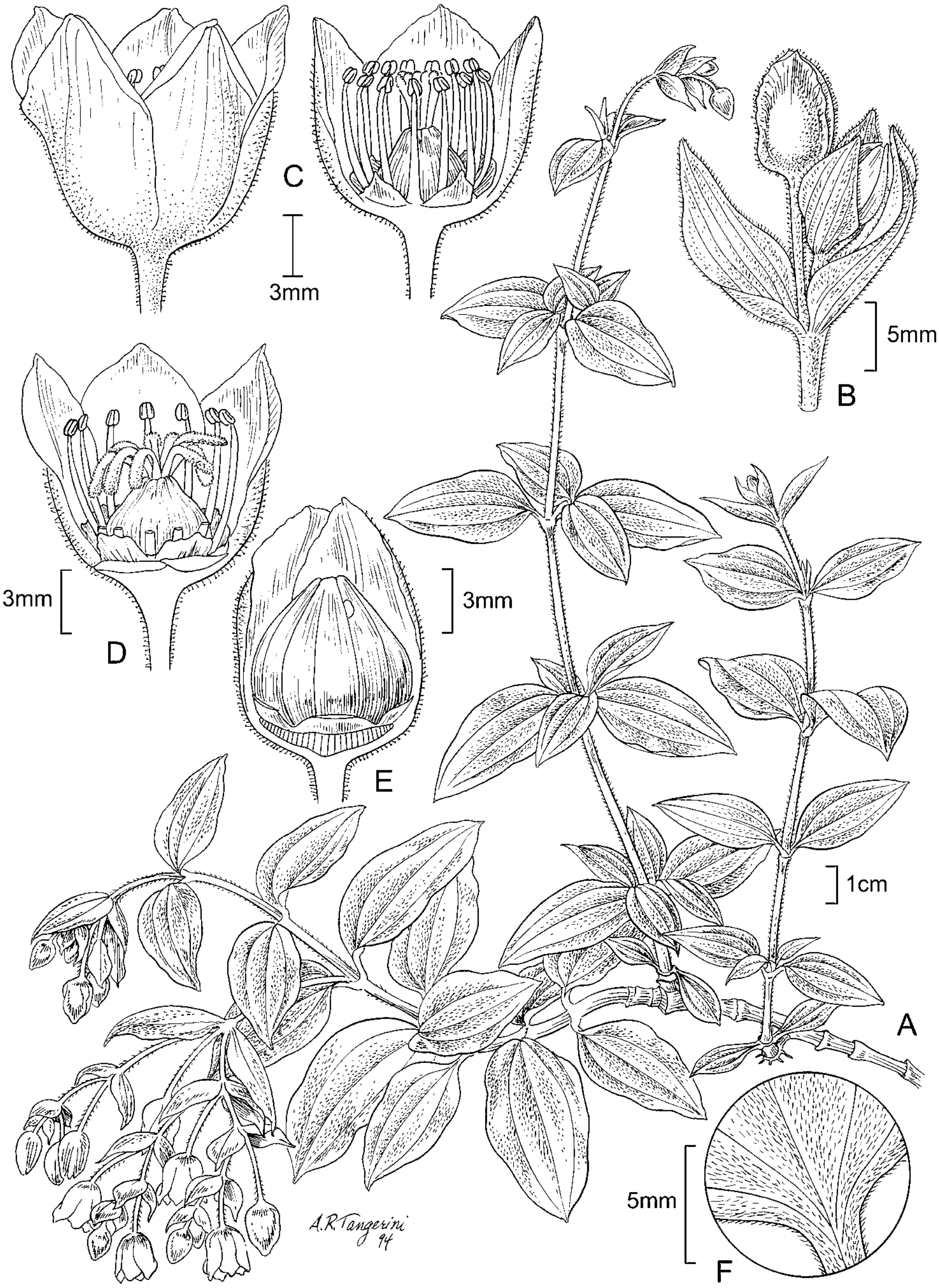

FIG. 13. *Schiedea lychnoides* (cult. from *Weller & Sakai 867*). A. Habit. B. Portion of young inflorescence. C. Flowers in early anthesis, male stage, flower on right with sepals removed to show stamens. D. Flower in later anthesis, female stage. E. Longitudinal section showing capsule. F. Detail showing minute hairs on leaf.

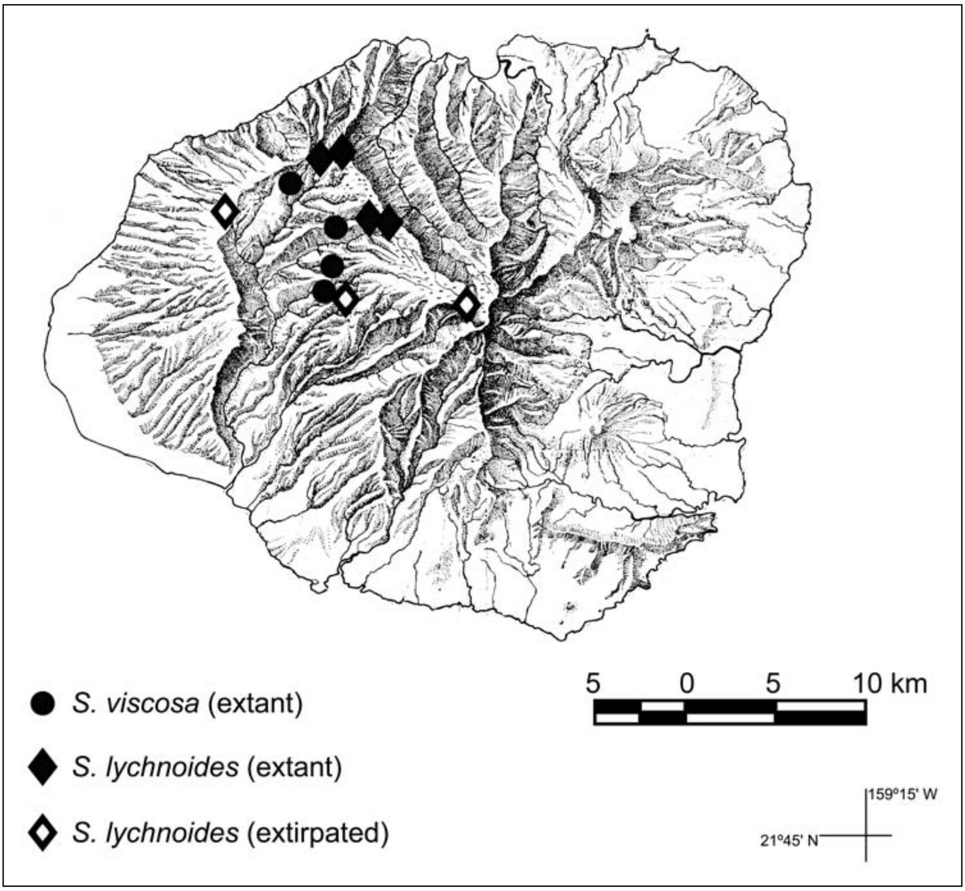

FIG. 14. Distribution of *Schiedea lychnoides* and *S. viscosa*.

Hitchcock 15415 (US); Kaholuamanu, s.d., *Lydgate s.n.* (BISH [3]); on trail above Koai`e Camp, upper Waimea plateau, [22°06′53.2″N, 159°33′43.7″W], *Medeiros 201* (BISH); Alaka`i Wilderness, *Nagata 2123* (BISH); Koke`e State Park, on Pihea Trail about 0.25 mi N of Alaka`i Trail, at top of vertical cliff dropping into Kawaikoi Valley, 2 May 1987, *Plews s.n.* (PTBG); woods of Kaholuamanu above Makaweli, *Rock 2638* (BISH [2]); Kaluiti stream, back of central plateau, *Rock 4876* (BISH); banks of Kaluiti stream, Wai`ale`ale, near Ke`aku Cave, [22°04′15.9″N, 159°31′3.6″W], *Rock 4877* (BISH); back of Kaholuamanu, [22°03′53.6″N, 159°35′55.9″W], *Rock 5459* (BISH), *Rock 5460* (A), *Rock 5461* (GH, NY); Kaholuamanu, *Rock 5907* (BISH); Kaholuamanu, *Rock 17105* (BISH); without locality, Oct 1916, *Rock s.n.* (BISH [2]); Pihea Trail, *Wagner et. al. 6031* (BISH); Waimea District, Mohihi-Wai`alae trail 2.75 mi in and drop into upper Mohihi drainage to N, [22°06′50.4″N, 159°34′19.5″W], *Wood 3861* (US); Hanalei District, Alaka`i, 30° NE to drainage from second bog, on vertical walls of stream where it dog-legs, 120° SE aspect, *Wood & Wood 2012* (US).

CULTIVATED. **Kaua`i.** Napali-Kona Forest Reserve, Alaka`i Swamp and Pihea trails, 1987, *T. Flynn s.n.* [cult. *Weller & Sakai 867*] (US).

Schiedea lychnoides is closely related to *S. viscosa*, which differs primarily in having narrower smaller leaves, and fewer, smaller flowers and capsules. They are well separated ecologically; *S. lychnoides* grows in wet forest, whereas *S. viscosa* occurs in diverse mesic forest or at margins of wet forest. Flowers of *S. lychnoides* produce as much as 50 µl of nectar at a time, which suggests adaptation for bird pollination, perhaps by species of

Hawaiian honeycreepers or now-extinct honeyeaters. Under greenhouse conditions seeds are produced autogamously, which may indicate that in the absence of pollinators seeds are produced autogamously in the field as well.

Although *S. lychnoides* has been collected a fair number of times historically, it has now a very restricted distribution in high-elevation wetter areas of Kaua`i. Because of its current rarity, clear threats to extant populations, and degradation of the overall habitat, *S. lychnoides* was federally listed as endangered in 1996 (Russell & Bruegmann 1996a).

The specific epithet refers to a resemblance to the genus *Lychnis*, particularly to the similarly viscid pubescence found in the inflorescences of *L. alba* Mill.

6. Schiedea viscosa H. Mann, Proc. Boston Soc. Nat. Hist. 10: 311. 1866. *Alsinidendron viscosum* (H. Mann) Sherff, Amer. J. Bot. 31: 155. 1944.—TYPE: HAWAIIAN ISLANDS. KAUA`I: mountains of Waimea, 2000–3000 ft [610–915 m], 1864–1865, *H. Mann & W. T. Brigham 579* (holotype: GH!, photos: BISH! F-2 sheets! G! GB!; isotypes: BISH! BM! CU! F! G! K! NY! UC! US!, photo of F isotype: F!).

Alsinidendron viscosum var. *laeve* Sherff, Amer. J. Bot. 31: 157. 1944. *Schiedea viscosa* var. *laevis* (Sherff) St. John, Pacific Trop. Bot. Gard. Mem. 1: 159. 1973.—TYPE: HAWAIIAN ISLANDS. KAUA`I: Kaholuamanu, s.d., *J. M. Lydgate s.n.* (holotype: NY!, photo: F!; isotype: BISH!).

Weakly climbing or sprawling vines, primary stems to 5 dm long, the lateral branches almost as well developed. Leaves opposite; the blades 2.5–5 cm long, 0.8–1.8 cm wide, thin and membranous, dark green with a purple tinge, narrowly elliptic to narrowly ovate-elliptic, with 3 principal veins, both surfaces moderately puberulent, the hairs gland-tipped (and the plant viscid) or not, erect to antrorsely spreading, those of the abaxial principal veins slightly coarser and erect or spreading, those along the margin more deeply infused with purple and antrorsely curved, (0.2–) 0.3–0.5 (–0.8) mm long, margin inconspicuously serrulate, at least in the distal half, apex mucronate, petioles 0.4–0.8 cm long. Inflorescence pseudoaxillary, with usually (1–) 6–11 flowers, all parts moderately puberulent, the hairs gland-tipped or not, translucent, rarely with a purple tinge, 0.3–0.7 (–0.8) mm long; bracts 7–18 (–20) mm long, foliaceous; peduncles 13–35 mm long, the internodes of the lateral inflorescence branches 2–7.4 mm long; pedicels thinner, 4–15 mm long. Flowers apparently adapted for bird pollination, pendent. Sepals (4) 5, 6.5–9 mm long, 4–4.5 mm wide, enlarging to ca. 12 mm long and 5–5.5 mm wide in fruit, the outer ones oblong-obovate, greenish white, becoming green toward the base, the inner ones oblong-elliptic to elliptic, white with greenish tinge, becoming green toward the base, thin and membranous, dry at maturity, apex obtuse and mucronulate, abaxially moderately puberulent, the hairs gland-tipped or not, glabrous adaxially. Stamens 10–13; filaments 4.2–5 mm long, the antisepalous one slightly longer; anthers 0.8–1.4 mm long, pale reddish purple at anthesis, changing to a darker reddish purple, the pollen pale gray. Nectary ring bright green, the flap-like extensions thin, translucent, 2–2.5 mm long, ca. 1 mm wide, apex irregularly toothed, often deeply 2-toothed, or sometimes with an additional smaller or larger central tooth. Styles 5–7 (–8), often variable in number on the same plant. Capsules 8–12 mm long, narrowly ovoid. Seeds 0.7–0.9 mm long, black, persistent on placenta, released as capsule gradually rots, the margins of the cells of the testa slightly convex, the slightly raised cells forming indistinct irregular transverse ridges across the seed surface. Chromosome number: 2n = 52–56 (*Perlman 11904*). Figs. 1F, 15.

Distribution (Fig. 14). Western Kaua`i, in and around Mohihi-Wai`alae Trail and

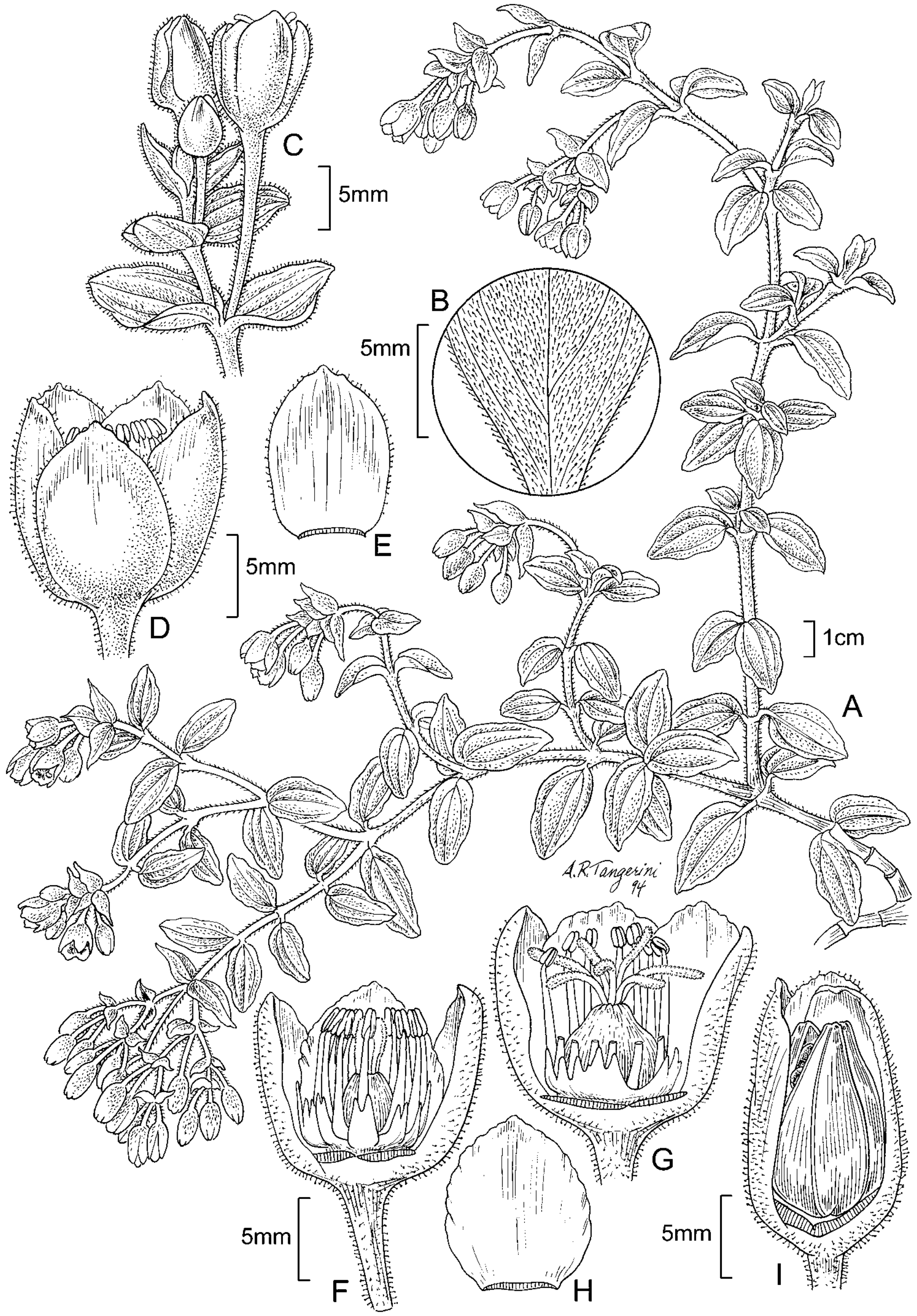

FIG. 15. *Schiedea viscosa* (cult. from *Perlman 11904*). A. Habit. B. Detail showing minute hairs on leaf. C. Portion of inflorescence. D. Flower at anthesis. E. Interior sepal. F. Longitudinal section of flower, sepals removed to show nectary extensions and stamens, early male stage of anthesis. G. Longitudinal section of flower, later female stage of anthesis. H. Exterior sepal. I. Sepal removed to show mature capsule.

Wai`alae and Nawaimaka valleys; in diverse mesic forest or margins of wet forest, dominated by *Acacia koa* and *Metrosideros polymorpha* with *Alyxia stellata* (J. R. Forst. & G. Forst.) Roem. & Schult., *Bobea*, *Dodonaea viscosa* Jacq., *Ilex anomala* Hook. & Arn., *Psychotria*, *Melicope*, and *Pleomele*; (610–) 820–1150 m.

ADDITIONAL SPECIMENS EXAMINED. **Kaua`i.** Waimea, *Faurie 1096* (P); Waimea District, Na Pali-Kona Forest Reserve, Mohihi-Wai`alae trail from Camp 10 road, *Flynn et. al. 5031* (PTBG); Waimea District, Na-Pali Kona Forest Reserve, on spur off of the Ditch trail on a ridge just above Kauikinana Valley, [22°07′53″N, 159°37′50.1″W], *Flynn et. al. 5963* (BISH). Waimea drainage basin, W side, trail, grade on mauka side away from Kawaikinana, *Forbes 1058.K* (BISH [2]); without locality, s.d., *Knudsen s.n.* (BISH); Wai`alae, ridge between Wai`alae and Nawaimaka stream, on ridge top, [22°04′21.3″N, 159°36′14.8″W], *Perlman 14657* (US [2]); Kohua ridge, Mohihi drainage, below Wai`alae-Wai`ale`ale trail, about 10–30 m below trail, N facing slope, [22°06′34.7″N, 159°35′36″W], *Perlman & Wood 14643* (US); Wai`alae Valley, on N facing slopes above Wai`alae Falls, on N side of ridge between Wai`alae and Nawaimaka, [22°04′21.3″N, 159°36′16.7″W], *Perlman & Wood 14650* (BISH, US); Kohua ridge, Mohihi stream drainage, below Wai`alae-Wai`ale`ale tr., 10–20 m on steep slope, *Perlman & Wood 14776* (RSA, US); Kawai`iki, off Kaluakaula ridge, upper forest and drainage to the S of Koai`e and N of Wai`alae, *Wood 8639* (PTBG); Waimea District, Nawaimaka drainage above stream, [22°04′14.9″N, 159°36′4.3″W], *Wood & Perlman 3998* (RSA), *Wood & Perlman 3999* (US), *Wood & Perlman 4000* (UC), *Wood & Perlman 4001* (US), *Wood & Perlman 4002* (BISH), *Wood & Perlman 4003* (US), *Wood & Perlman 4004* (NY), *Wood & Perlman 4005* (US), *Wood & Perlman 4006* (PTBG); Waimea District, Nawaimaka drainage above stream, 320 NW aspect, *Wood & Perlman 4007* (US [2]); Kawai`iki, off Kaluakaula ridge, upper forest and drainage to the S of Koai`e and N of Wai`alae, *Wood & Perlman 8611A-C* (PTBG); Waimea District, Wai`alae valley, ridge between Wai`alae and Nawaimaka valleys, above Wai`alae falls, northern aspect, *Wood et. al. 842* (US); Waimea District, Nawaimaka Stream, steep forested area above stream, N aspect, *Wood et. al. 2438* (BISH, PTBG, US); Waimea District, Mohihi-Wai`alae trail, just below bench overlooking Koai'e, *Wood et. al. 3980* (US).

CULTIVATED. **Kaua`i.** Nawaimaka valley, along banks of Nawaimaka stream, to W of Wai`alae valley ridge, *Perlman 14654* [cult. *Wagner & Shannon 6814*] (BISH, PTBG, US); Wai`alae Valley, *Perlman 11904* [cult. *Wagner & Shannon 6811*] (BISH, PTBG, US); Waimea District, Na Pali-Kona Forest Reserve, Mohihi-Wai`alae trail from Camp 10 road, *Flynn et.al. 5031* [cult. *Wagner & Shannon 6810*] (BISH, PTBG, US).

Schiedea viscosa differs from *S. lychnoides* in its slightly greener and smaller sepals and makes far less nectar, which is consistent with production of seeds usually by autogamy. For a comparison with *S. lychnoides* see that species (no. 5).

Schiedea viscosa was considered extinct (Wagner et al. 1990; Weller et al. 1990), but was rediscovered in 1991, 75 years after it was last collected (Lorence et al. 1995). The several populations now known result from the collecting activity of the botanists at the National Tropical Botanical Garden. *Schiedea viscosa* was federally listed as endangered in 1996 (Russell & Bruegmann, 1996a). In cultivation seeds are produced autogamously.

The specific epithet refers to the viscid pubescence of the inflorescence in this species.

V. **Schiedea** sect. **Alsinidendron** (H. Mann) Pax & K. Hoffmann, Nat. Pflanzenfam., ed. 2, 16c: 326. 1934. *Alsinidendron* H. Mann, Proc. Boston Soc. Nat. Hist. 10: 311. 1866.—TYPE: *Schiedea trinervis* (H. Mann) Pax & K. Hoffmann.

Shrubs; roots fibrous. Leaves elliptic-ovate, elliptic to broadly elliptic, sometimes obovate or oblanceolate, with 3 principal veins, coriaceous, margins serrulate, the teeth with short, antrorsely hooked hairs. Inflorescence pseudolateral (lateral branch of the next node below inflorescence elongating coincident with flowering and assuming subsequent vegetative growth). Flowers hermaphroditic, pendent. Sepals 4–5 (–6), thick, fleshy, white or green, becoming dark purple and fleshy as fruit matures, glabrous. Nectary shafts modified into distinct flaps connate only at the base or for about half their length; nectar black. Styles 4–7 (–8).

Distribution. The two species of sect. *Alsinidendron* are restricted and rare in mesic and wet forests in the Wai`anae Mountains, O`ahu.

The fleshy dark purple sepals surrounding the mature capsules of the two species are unique in the Caryophyllaceae and may have attracted birds as dispersal agents.

The sectional name is formed from the generic name *Alsine* L. and the Greek noun *dendron* ("tree") in reference to the shrubby habit of these species.

7. Schiedea obovata (Sherff) W. L. Wagner & Weller, comb. nov. *Alsinidendron obovatum* Sherff, Bot. Leafl. 3: 2. 1951.—TYPE: HAWAIIAN ISLANDS. O`AHU: Wai`anae Range, Palehua [21°24'N, 158°06'W], 1–4 Apr 1911, *C. N. Forbes 1680.O* (holotype: F-485280!, photos: B! BISH-3 sheets! F-2 sheets! GB!; isotypes: B! BISH! NY! UC!).

Alsinidendron obovatum var. *parvifolium* Degener & Sherff in Sherff, Bot. Leafl. 3: 3. 1951.—TYPE: HAWAIIAN ISLANDS. O`AHU: southwestern O`ahu, summit ridge between Pu`u Manawahua and Mauna Kapu, in shrubby tangle, 2500 ft [760 m], 28 Jun 1950, *O. Degener, A. B. Greenwell, W. H. Hatheway & Caindec 20675* (holotype: F-1449133!, photo: BISH!; isotypes: B! BISH! F! G! M! MASS! MICH MIN! MO! NY! PH! UC! W-3 sheets!). [Part of holotype is missing; see the photo at BISH.]

Suberect or ascending, branched shrubs 3–10 dm tall, glabrous throughout except for the leaf margins. Leaves opposite; blades 4–11 cm long, (1.5–) 2.5–5 (–6.8) cm wide, thick and somewhat fleshy, light green becoming yellowish white toward the base and at the apex (youngest yellowish white, sometimes purple tinged), elliptic to broadly elliptic, sometimes obovate or oblanceolate, with 3 principal veins, sometimes also with an inconspicuous looping pair of veins near the margins, margins serrulate, the teeth with antrorsely hooked hairs ca. 0.1–0.2 mm long, apex mucronate; petioles 1–3 (–3.8) cm long, yellowish white. Inflorescence pseudoaxillary, with 22–33 flowers, somewhat congested; bracts much smaller than uppermost leaves, usually curled and twisted, lowest pair to 1.4 cm long; peduncles (2–) 5–25 mm long, not elongating much in fruit, the internodes of the lateral inflorescence branches 2–10 mm long; pedicels thinner, 15–30 mm long, elongating mostly just prior to anthesis. Flowers apparently adapted for bird pollination, pendent. Sepals (4–) 5 (–6), often variable on the same plant, 7–8.4 mm long, 5.5–6 mm wide, enlarging to 9–12 mm long and 8–9 mm wide in fruit, white adaxially, the outer ones oblong-elliptic, pale green abaxially, inner ones elliptic to obovate, greenish white with a green midrib, the apex broadly obtuse and usually retuse, the outer ones sometimes with a subapical minute mucro, becoming dark purple and fleshy as fruit matures. Stamens (8–) 10 (–12); filaments 4.4–5 mm long, subequal; anthers 1.9–2.65 mm long, pale reddish purple at anthesis, changing to a darker reddish purple, the pollen gray. Nectary ring bright green, the flap-like extensions weakly connate at the base, thin, translucent, 2.2–2.5 mm long, irregularly 2-toothed to subentire. Styles (4–) 6–7 (–8), often variable in number on the same plant. Capsules 9–12 mm long, ovoid to subglobose. Seeds 1.2–1.5 mm long. Chromosome number: 2n = 48–50 (*Weller & Sakai 868*). Plate 1C; Figs. 1G, 3I, J, 16.

Distribution (Fig. 17). O`ahu, formerly nearly throughout the Wai`anae Mountains, now restricted to the north end of the Wai`anae Mountains; rare and scattered on ridges and slopes in diverse mesic forest; 550–800 m.

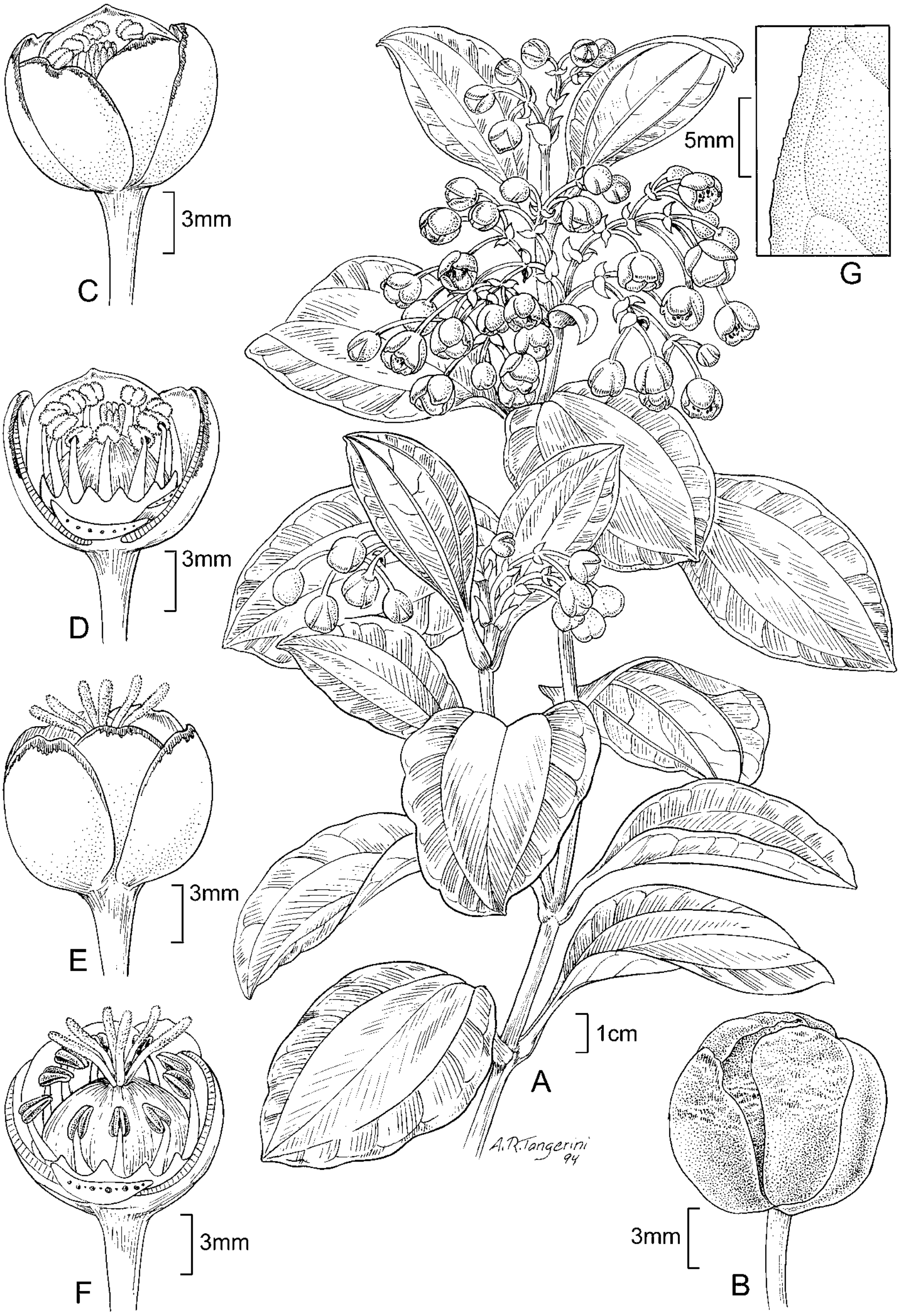

FIG. 16. *Schiedea obovata* (cult. from *Weller & Sakai 868*). A. Habit. B. Early Fruit. C. Flower in early anthesis, male stage. D. Longitudinal section of flower showing early anthesis, male stage. E. Flower in later anthesis, female stage. F. Longitudinal section of flower showing later anthesis, female stage. G. Detail of leaf margin.

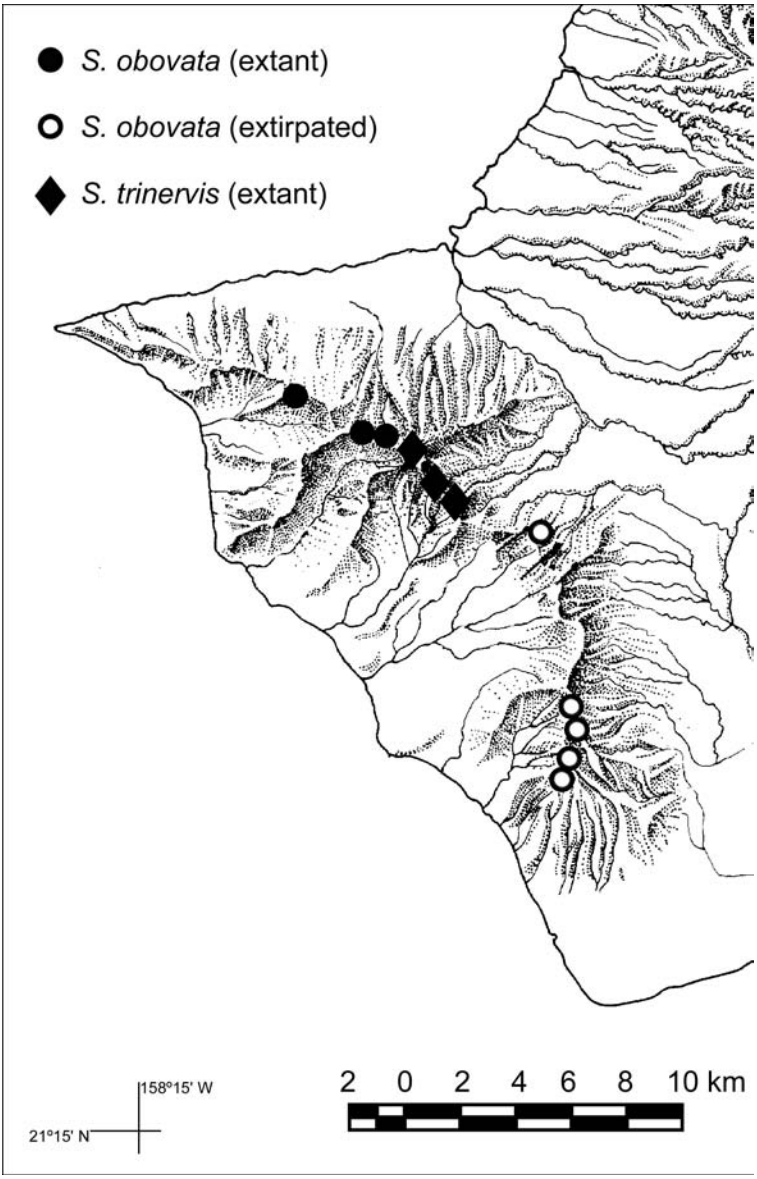

FIG. 17. Distribution of *Schiedea obovata* and *S. trinervis.*

ADDITIONAL SPECIMENS EXAMINED. **O`ahu.** Ridge trail to Palikea, Honouliuli, [21°024′46″N, 158°6′2.4″W], *Cowan 806* (G, NY [2]); Mokule`ia Forest Preserve, Pahole Gulch and Makua Ridge, *Darwin 1022* (US); along summit ridge near Palehua, [21°23′46.4″N, 158°6′6″W], *Degener & Horner 5930* (B, BISH, CU, K, MASS, MO, NY, US); between Pu`umanawahua and Palikea, *Degener & Park 5928* (B, BISH [2], K, MASS, NY [2], US); summit ridge N of Makua Valley, *Degener et. al. 5945* (BISH, NY); Mokule`ia, slopes of Ka`ala, *Forbes 1833.O* (BISH); Honouliuli-Nanakuli divide, Palehua, *Fosberg & Fosberg 13807* (US); Mt. Ka`ala, ridge 0.25 mi W of W branch of Makaleha Gulch, [21°31′13″N, 158°10′11.7″W], 17 September 1978, *Gagné & Gagné s.n.* (BISH); Wai`anae Range: between Maunakapu and Pu`umanawahua, *Hatheway et. al. 87* (B, BISH); Pahole Gulch, *Herbst & Obata 5360* (BISH, US); Honouliuli, near Manawahua, [21°23′16.5″N, 158°06′12.8″W], Jun 1933, *Judd s.n.* (BISH); Palehua, *Kerr 37-1* (BISH); Mokule`ia Forest Reserve, head of

Kukuiala Gulch, *Morley 100* (BH, NY, W); Pahole Gulch, along pig trail near crest of small gully, W section, between missile site and plateau., *Nagata & Obata 1167* (BISH); Mokule`ia Forest Reserve, Piko Trail, 4 Feb 1934, *Onouye s.n.* (BISH); Ka`aikukae, [21°24′32″N, 158°05′52.3″W], Oct 1929, *Russ s.n.* (BISH); Palehua, Honouliuli, 18 May 1933, *Russ s.n.* (BISH, K); ridge of Pu`umanawahua, *St. John 9888* (BISH); Mokule`ia, Kukuiala Gulch, *St. John 14083* (BISH, P); Palehua, *Skottsberg 335* (GB); Honouliuli, moist subgulch near Pu`uhapapa, [21°27′55″N, 158°06′12″W], 1978, *Takeuchi & Takeuchi s.n.* (BISH); Pahole Gulch, rim between Makua Valley and Pahole, on Pahole side, N facing slope, in washout area, [21°32′4.8″N, 158°11′17.5″W], *Perlman et. al. 6472* (BISH [3], PTBG, US); rim of Makua Valley and Pahole Gulch, Pahole side, W of washout, 0.5 mile W of Peacock Flats Trail and Makua Rim jct., *Perlman & Obata 5800* (BISH, MO, PTBG); Palehua, Honouliuli Forest Reserve, 22 July 1934, *Wilder s.n.* (BISH).

CULTIVATED. **O`ahu.** *Rock 496-61* [cult. *Cult. Kew H4341/60a*] (K), *Rock E.N.496/61* [cult. *Cult. Kew H4341/60b*] (K), *Rock E.N.496.61* [cult. *Cult. Kew H4341/60c*] (K); Wai`anae Range: E side of Pahole Gulch (seed from P. Welton), *Weller & Sakai 893* [cult. *Wagner & Shannon 6803*] (BISH, PTBG, US); N rim of Makua Gulch, *Weller & Sakai 868* [cult. *Wagner & Shannon 6808*] (BISH, PTBG, US), *Perlman & Obata 5800* [cult. *Weller & Sakai 868*] (US); Pahole Natural Area Reserve, Keawapilau Gulch (seed from P. Welton), *Weller & Sakai 897* [cult. *Wagner & Shannon 6815*] (BISH, PTBG, US).

Schiedea obovata is differentiated from the closely related *S. trinervis* by its more congested inflorescence, flowers that open fully during anthesis and have greater nectar production, and thicker leaves, the young ones whitish green. It grows in mesic forests at lower elevations than *S. trinervis*. The congestion in the inflorescence of *S. obovata* appears to be primarily due to the reduction of the internodes of the lateral inflorescence branches and to the delayed elongation of the pedicels until just prior to anthesis.

Schiedea obovata was federally listed as endangered in 1991 (Ellshoff et al. 1991). Plants raised from seeds collected by Joseph Rock in 1960, and the progeny of these plants, have been in cultivation at Kew Gardens, England, for over 44 years.

The specific epithet refers to the leaf shape of some individuals of this species.

8. Schiedea trinervis (H. Mann) Pax & K. Hoffmann, Nat. Pflanzenfam., ed. 2, 16c: 326. 1934. *Alsinidendron trinerve* H. Mann, Boston Soc. Nat. Hist. 10: 312. 1866.—TYPE: HAWAIIAN ISLANDS. O`AHU: Ka`ala Mountains, 2000 ft [610 m], 1864–1865, *H. Mann & W. T. Brigham 582* (holotype: GH!; isotypes: BISH-3 sheets! CU! F!G-2 sheets! K! MASS! MO! NY-2 sheets! UC, US! W!, photos of F and W isotypes: F!).

Erect or strongly ascending, branched shrubs 3–8 (–18) dm tall, glabrous throughout except for the leaf margins. Leaves opposite; blades 6–12.5 cm long, 2.3–6 (–6.8) cm wide, thick, chartaceous at least when dry, green throughout, elliptic-ovate or sometimes oblanceolate, with 3 principal veins, sometimes also with an inconspicuous looping pair of veins near the margins, margins serrulate, the teeth with antrorsely hooked hairs ca. 0.1–0.15 mm long, apex weakly mucronate; petioles 1.5–3 (–3.8) cm long, pale green. Inflorescence pseudoaxillary, with (2–) 18–34 flowers; bracts much smaller than the uppermost leaves, recurved, the lowest pair to 1.4 cm long; peduncles 16–30 mm long, elongating to 50 mm long in fruit, secondary and tertiary internodes of the lateral inflorescence branches 20–30 mm long; pedicels thinner, 10–20 mm long, elongating uniformly during inflorescence development. Flowers cleistogamous, pendent. Calyx not or only slightly opening at anthesis; sepals 4 (5), 6–8 mm long, enlarging to 9–10 mm long and the inner ones to 10 mm wide and the outer ones to 14 mm wide in fruit, greenish white within, outer ones green externally, inner ones white, green toward midrib, elliptic to broadly elliptic, apex obtuse and retuse, or truncate, becoming dark purple and fleshy as fruit matures. Stamens 10 (–11); filaments ca. 4.5 mm long, subequal; anthers 2.2–2.5 mm long, pale reddish purple at anthesis, changing to a darker reddish purple, the pollen gray. Nectary ring bright green, the flap-like extensions connate about half their length, thin, translucent, ca. 1–1.5 mm long, margin irregularly toothed. Styles 4–6 (–7), sometimes variable in number on the same plant. Capsules 8–12 mm long, ovoid to subglobose. Seeds 1.4–1.8 mm long. Chromosome number: 2n = 50–54 (*Perlman 5448*), 2n = 60 (Skottsberg 1953). Frontispiece; Figs. 1H, 18.

Distribution (Fig. 17). O`ahu, restricted to Mount Ka`ala from Pu`ukalena, Pu`ukawiwi, and Makaha Valley, northern Wai`anae Mountains; rare on slopes in wet forest; (600–) 900–1230 m.

Additional Specimens Examined. **O`ahu.** Ka`ala, N side, 11 Feb 1928, *Bergman s.n.* (BH, BISH, P, NY, UC, US [2]); Pu`uka`ala, Wai`anaeuka, by side of ridge-trail, [21°30′27.6″N, 158°08′27.4″W], 5 Nov 1933, *Bucknell s.n.* (BISH); summit of Mt. Ka`ala, *Carlquist 2352* (RSA); top of Ka`ala, *Christophersen et. al. 1704* (A, BISH, US), *Christophersen et. al. 1769* (A, BISH); Pu`uka`ala, *Cowan 342* (BISH, NY); Pu`uka`ala, Wai`anaeuka, 8 Jan 1933, *Davis s.n.* (BISH); Mt. Ka`ala, [21°30′32″N, 158°08′53.2″W], *Degener 5942* (B, BISH, GH, K, NY), *Degener 5970* (coll. K. Nitta) (BISH); S Hale`au`au Valley below Ka`ala summit cliffs, *Degener et. al. 21266* (NY, W); Pu`uka`ala, E side trail, *Douglas et. al. 463* (BISH, CU); [Mt.] Ka`ala, [21°30′25.6″N, 158°08′30.6″W], *Fagerlind 6877* (S); Ko`olau Range: Makaha Valley, 12 Feb 1909, *Forbes s.n.* (A, B, BISH [2], NY, P, UC, US); Pu`uka`ala, Wai`anaeuka, E slope, *Fosberg 9073* (A, BISH, F); Pu`ukawiwi-Pu`uka`ala ridge, Makaha-Wai`anae Kai, [21°30′8″N, 158°09′0.3″W], *Fosberg 10861* (BISH, F); summit plateau, Mt. Ka`ala, N edge at top of cliffs, *Fosberg 12628* (BISH, F); Wai`anaeuka, E ridge of Pu`uka`ala, N side of Hale`au`au valley, *Fosberg 13661* (US); summit of Pu`uka`ala, E side, Wai`anaeuka, *Fosberg 13669* (US); Wai`anaeuka, steep slope of Pu`uka`ala, 8 Jan 1933, *Furmidge s.n.* (BISH); Mt. Ka`ala, 9 Jan 1933, *Furmidge s.n.* (BISH [2]); Mt. Kalena, summit, [21°29′20.59″N, 158°07′55.8″W], *Grant 7413* (BISH, MO); Mt. Ka`ala, *Grant 7470* (BISH, MO); [Mt.] Ka`ala, [21°30′49.7″N, 158°08′43.1″W], s.d., *Hillebrand s.n.* (BISH, MEL, US); Mt. Ka`ala, *Hillebrand 182 p.p.* (K), 1860, *Hillebrand s.n. p.p.* (K); Mt. Ka`ala, summit, 1869, *Hillebrand s.n.* (GH); Wai`anaeuka, Pu`uka`ala, 30 Nov 1930, *Ho s.n.* (BISH); Mt. Ka`ala, Wai`anaeuka, *Hosaka 133* (BISH), *Hosaka 229* (BISH), *Hosaka 351* (BISH); Pu`uka`ala, Wai`anaeuka, 2 Feb 1930, *Hosaka s.n.* (BISH); Pu`uka`ala, Wai`anaeuka, 30 Nov 1930, *Inafuku s.n.* (BISH); Mt. Ka`ala, *Kerr 1* (A, BISH); Pu`uka`ala, Wai`anaeuka, 8 Jan 1933, *Krauss s.n.* (BISH); slope of Ka`ala, *Lyon 1129* (GB, S); Ka`ala, 7 Sep 1913, *Lyon s.n.* (BISH); Mt. Ka`ala, *MacDaniels 934* (BH, BISH); Ka`ala, *Meebold 8607* (M); Pu`uka`ala, Wai`anaeuka, *Morley 91* (MIN); between Pu`ukalena and Mt. Ka`ala, ridge trail, on ridge between Kanewai Gulch and Hale`au`au Gulch, *Perlman 4910* (BISH); 0.5 mile N of Pu`ukalena, ridge between Kalena and Mt. Ka`ala, [21°29′35.3″N, 158°08′17.4″W], *Perlman 5448* (BISH, PTBG); Wai`anae Range: Kuala [Ka`ala], Makaha, 17 Nov 1946, *Rogers s.n.* (NY); Mt. Ka`ala, back of Makaleha Gulch, E branch, below Ka`ala road and gulch just W of DuPont trail, below cliffs, *Perlman et. al. 15564* (PTBG, US); Wai'anaeuka, Pu`uka`ala, E slope, *St. John 10060* (A, BISH, M); Wai`anaeuka, Pu`uka`ala, *St. John 10645* (B, BISH, M, NY, P [2], UC, US); Wai'anaeuka, E ridge of Pu`uka`ala, main trail, *St. John 17553* (BISH); Pu`uka`ala, Wai`anaeuka, *St. John 19970* (BISH, UC, US); slope of Ka`ala, *Selling 3590* (GB, S); Pu`uka`ala, 8 Jan 1933, *Suehiro s.n.* (BISH), *Suehiro 87* (BISH [3]); Wahiawa District, Mt. Ka`ala, below facility, 70°N aspect, *Wood 2911* (PTBG, US); Ka`ala Summit, steep E face below facility, just N of tram ridge, *Wood & Lau 5900* (PTBG, US).

Cultivated. **O`ahu.** Wai`anae Range: 0.5 mile N of Pu`ukalena, ridge between Kalena and Mt. Ka`ala, *Perlman 5448* [cult. 1987, *Weller & Sakai s.n.*] (US), *Perlman 5448* [cult. *Wagner & Shannon 6807*] (BISH, PTBG, US); Mt. Ka`ala at Natural Area Reserve boundary N of radar dome, Hale`au`au drainage, *Weller & Sakai 908* [cult. *Wagner & Shannon 6853*] (BISH, PTBG, US).

Schiedea trinervis is most similar to *S. obovata*; see that species (no. 7). Like several other wet-forest species of *Schiedea*, it produces cleistogamous flowers.

At least three populations of *S. trinervis* are still extant, two on ridges just below the summit of Mount Ka`ala, and a third population on the north slope of Pu`ukalena. The species is threatened by feral goats and subsequent invasion by *Rubus argutus* Link. It was federally listed as endangered in 1991 (Ellshoff et al. 1991).

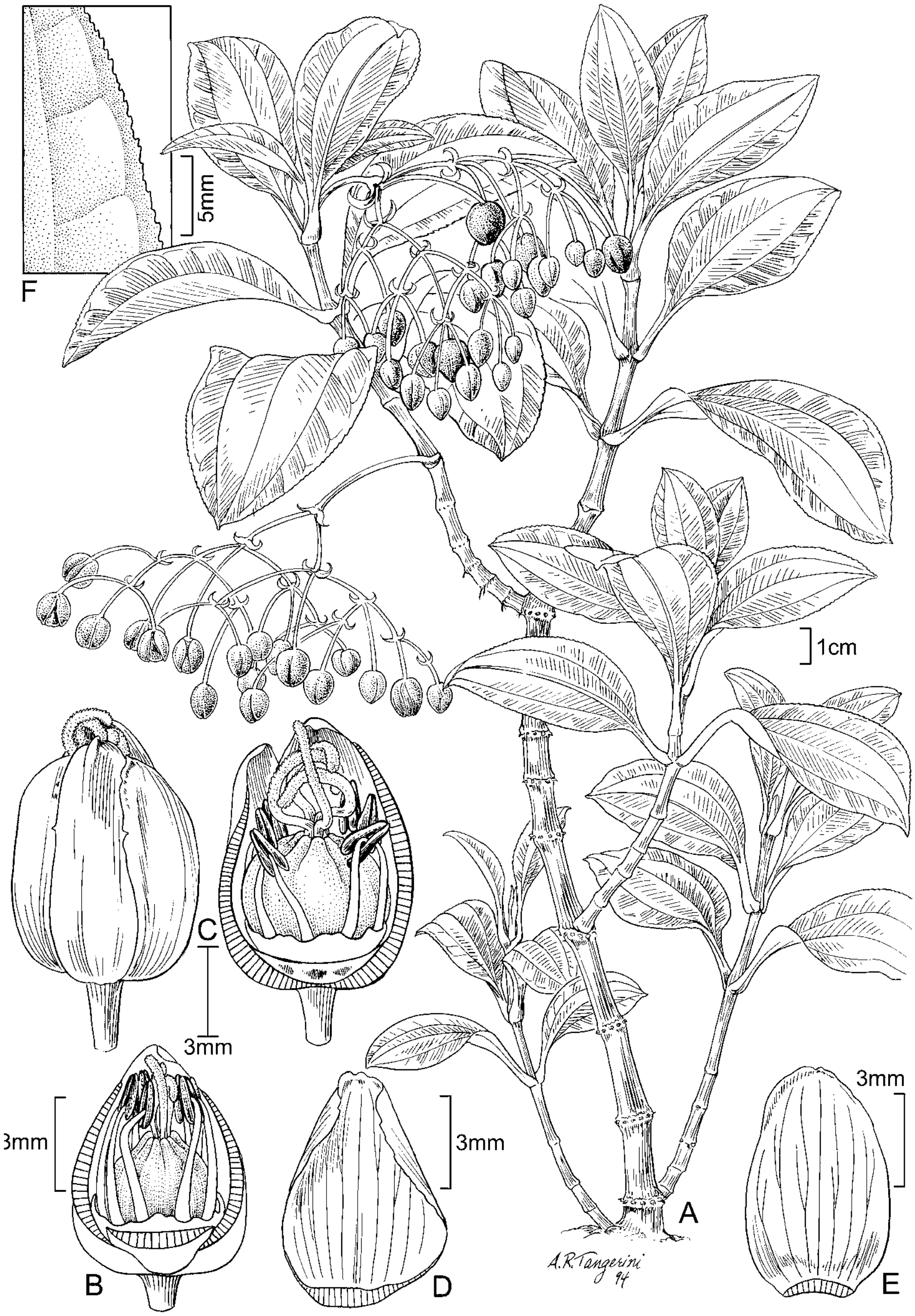

FIG. 18. *Schiedea trinervis* (cult. from *Perlman 5448*). A. Habit. B. Bud before anther dehiscence. C. Anthesis, flower at right in longitudinal section showing receptive stigmas in contact with dehiscing anthers. D. Outer sepal. E. Inner sepal. F. Detail of leaf margin.

Schiedea trinervis was selected for the frontispiece to show the extent of the divergence of *Schiedea* from continental shared ancestors, including evolutionary shifts to pseudoaxillary inflorescences, fleshy dark calyces for (presumed) bird dispersal, and cleistogamous flowers.

The specific epithet refers to the 3-nerved leaves of this species.

VI. **Schiedea** sect. **Anestioschiedea** W. L. Wagner & Weller, sect. nov.—TYPE: *Schiedea apokremnos* St. John.

Frutices gynodioecii. Folia infirme succulenta et maturitate glaucescentia oblanceolata vel elliptico-oblanceolata, nervo medio tantum evidenti. Inflorescentiae contractae verticaliter et lateraliter, saepe congestae et capitulo similes vel apertiores et leviter contractae.

Gynodioecious shrubs. Leaves weakly succulent and at least the mature ones glaucous, oblanceolate or elliptic-oblanceolate, with only the midvein evident, margins entire. Inflorescence terminal, contracted vertically and laterally, often congested and head-like or more open and only somewhat contracted. Sepals 5, broadly ovate, oriented at ca. 110° angle to the pedicel, glabrous, apex obtuse. Nectary shaft held above sepal surface, sometimes vestigial. Styles 3 (–4).

Distribution. *Schiedea apokremnos* is known only from leeward cliff crevices, Kaua`i.

The sectional name is formed from the Greek adjective *anestios* (“without home, homeless”) and *Schiedea* in reference to very weak placement of *S. apokremnos* anywhere on phylogenetic trees. The species was previously considered to be an atypical member of the *S. adamantis* clade (Wagner et al. 1995; Weller et al. 1995; Soltis et al. 1997), albeit similarly weakly supported.

9. **Schiedea apokremnos** St. John, Pacific Sci. 24: 250. 1970.—TYPE: HAWAIIAN ISLANDS. KAUA`I: Waimea District, Nu`alolo Kai, crevices in cliffs, 200 ft [60 m], 23 Apr 1965, *H. St. John 26688* (holotype: BISH-501284!; isotypes: GH! K, P! UC!).

Gynodioecious shrubs; stems 2–4 (–5) dm long, branching, the lowermost ascending or decumbent, the flowering branches strongly ascending, glabrous, internodes 0.3–0.9 (–1.3) cm long, green or purple. Leaves opposite; blades (1.5–) 3–5.5 (–8.3) cm long, (0.3–) 0.6–1.4 cm wide, weakly succulent and at least the mature ones glaucous, oblanceolate or elliptic-oblanceolate, with only the midvein evident, margins entire, slightly thickened, apex acute to obtuse, base attenuate; petioles 0–0.4 cm long. Inflorescence terminal, 0.3–6 cm long, contracted vertically and laterally, often congested and head-like or more open and only somewhat contracted; hermaphroditic inflorescences 1.5–4.8 cm long, with 26–93 flowers, less congested and broader than the pistillate inflorescences; pistillate inflorescence 0.3–6 cm long, with 39–140 flowers; bracts of central axis 2–3.5 mm long, those of branches and flowers 1–1.5 mm long, linear to subulate, green or purple-tinged. Flowers hermaphroditic or pistillate. Hermaphroditic flowers: pedicels 2–5 mm long, somewhat flattened; sepals 2–2.85 mm long, broadly ovate, broadly and very shallowly navicular, oriented at ca. 110° angle to the pedicel, green or tinged purple toward the apex, opaque, reflexed and convex at the base, producing a small transverse bulge, glabrous, margins scarious, glabrous, apex obtuse; nectary base 0.4–0.7 mm long, spreading at 70° to 80° to the axis, dark yellow, the nectary shaft held above sepal surface, sometimes vestigial, 0.25–1.25 mm long, apex deeply notched, more variable when vestigial, the abaxial side not developing, adaxial side apex irregularly divided to nearly entire, or the abaxial side developing and the nectary shaft deeply divided on only the abaxial side or both sides nearly to the base of the shaft; stamens (9–) 10, the filaments very slightly dimorphic to subequal, white, the antisepalous whorl 3.6–4.8 mm long, the alternate whorl 3.4–5.75 mm long, anthers 0.75–0.9 mm long, yellow or pale reddish purple; styles 3 (–4), green. Pistillate flowers: pedicels 2–4.25 mm long, somewhat flattened; sepals 2.05–3.1 mm long, broadly ovate, green or tinged purple, opaque, reflexed and convex at the base, producing a small transverse bulge, broadly and very shallowly navicular, oriented at ca. 140° angle to the pedicel, margins scarious, entire, glabrous, apex obtuse; nectary base 0.5–0.6 mm long, spreading at 70° to 80° to the axis, green to pale yellow, the nectary shaft held above the sepal surface, vestigial, 0.1–0.5 mm long, abaxial side not developing, adaxial side apex irregularly divided to nearly entire or toothed, sometimes the abaxial side developing and the shaft deeply divided on only the abaxial side or both sides nearly to the base of the shaft; stamens 10, vestigial, filaments unequal, the antisepalous whorl 0.5–0.85 mm long, the alternate whorl 0.2–0.6 mm long, white, anthers 0.35–0.45 mm long, white to pale yellow, not producing pollen; styles 3 (–4), pale greenish white. Capsules 1.5–2.5 mm long, broadly ovoid. Seeds 0.6–0.8 mm long, orbicular-reniform, compressed, the surface papillose. Chromosome number: 2n = possibly 48 (*Weller & Sakai 865*). Figs. 2A, 3K, L, 19.

Distribution (Fig. 20). Kaua`i: Nu`alolo Kai, Ka`aweiki Ridge Ha`ele`ele Ridge, Nakeikionaiwi Valley, Pohakuao, Ka`a`alahina ridge Miloli`i Valley, and Kalalau Valley on the Napali Coast; in leeward cliff crevices of seacliff shrublands with such species as *Artemisia australis*, *Myoporum sandwicense*, and *Eragrostis variabilis* (Gaudich.) Steud., as well as *Lobelia niihauensis* H. St. John, *Dodonaea viscosa*, *Wilkesia hobdyi*, *Peucedanum sandwicense* Hillebr., *Bidens sandwicensis*, *Lipochaeta connata*, *Munroidendron racemosa*, *Lepidium serra*, *Sida fallax*, *Chamaesyce celastroides*, *Nototrichium sandwicensis*, *Lipochaeta succulenta*, *Hibiscus kokio* subsp. *saintjohnianus*, and *Carex meyenii*; 60–400 (–610) m.

ADDITIONAL SPECIMENS EXAMINED. **Kaua`i.** Napali Coast, Miloli`i Valley, [22°8′51.3″N, 159°43′20.3″W], 16 July 1984, *Corn s.n.* (BISH); Pu`uka Pele Forest Reserve, Ka`aweiki Ridge, [22°06′21.3″N, 159°44′18.6″W], *Flynn et. al. 2219* (PTBG); Ha`ena-Kalalau Valley, cliff face by valley trail, almost 9.5 mi from Ha`ena, [22°10′51.2″N, 159°38′22.6″W], *Herbst 1062* (BISH); Kalalau, [22°10′17.2″N, 159°39′35.4″W], *Hobdy 1657* (BISH); on pali at lower part of Ha`ele`ele Ridge, *Lamoureux 2321* (HAW); without locality, s.d., *Lydgate s.n.* (BISH); Napali Coast State Park, Pohakauo Transect, Survey Supp. Sta. D, left side subgulch above Kalalau trail where trail passes by small waterfall, on cliff on dividing ridge, *Perlman 10372* (PTBG [2], US); Ha`ele`ele Valley, behind Polihale State Park, on cliffs on N facing side of ridge, *Perlman 14775* (BISH, UC, US [2]); Nakeikionaiwi Valley, back of valley, on cliff walls in back of gulches, *Perlman & Wood 14726* (US [3]), *Wood & Perlman 5306* (PTBG, US); Napali Coast, Pohakuao, mid-valley, above trail in steep gulches, on cliff walls, basalt rock, *Perlman & Wood 14728* (US); Napali Coast, Kalalau, Kanakou pop., near 9 mile marker, *Perlman & Wood 14732* (US), *Wood & Fay 7869, 7870* (PTBG); Napali Coast, Kalalau, Red Hill pop., above Kalalau tr. *Perlman & Wood 14733* (US [2]); Napali Survey Transect 7, Kalalau Trail, Pohakuao to Kanakou along Ka`a`alahina Ridge, [22°10′42.3″N, 159°38′28.8″W], *Perlman et. al. 10375* (PTBG); Pohakuao, Napali Survey Transect Supp. Sta. D, *Perlman et. al. 10389* (PTBG, US); Ha`ele`ele Valley, above Polihale State Park, ridge SW of Ha`ele`ele valley, N facing cliff, [22°5′32.5″N, 159°44′40.4″W], *Perlman et. al. 12797* (PTBG); Hanalei District, Pohakuao, up stream to cliff facing directly W, [22°11′3.3″N, 159°38′W], *Wood et. al. 361* (BISH, PTBG, US); Pohakuao, up stream to cliff facing directly W, *Wood et. al. 362* (PTBG), *Wood et. al. 363* (PTBG); between Pohakuao and Red Hill along Napali Coast Trail, growing on N facing cliff, *Wood et. al. 366* (PTBG); Waimea District, cliffs above Polihale State Park, Ha`ele`ele Valley, N facing slope of Ha`ele`ele Ridge, *Wood et. al. 1946* (BISH, PTBG, US).

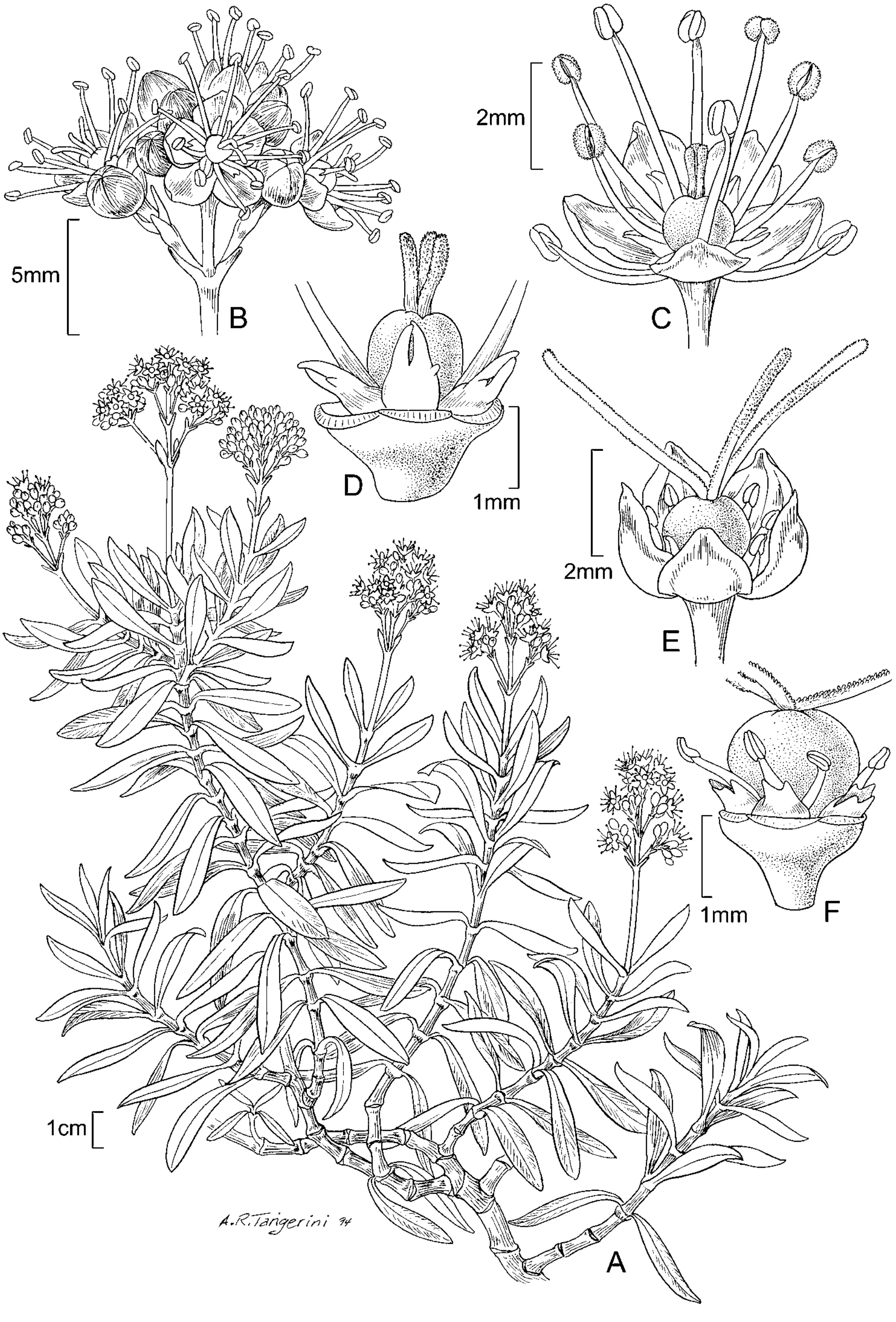

FIG. 19. *Schiedea apokremnos* (cult. from *Weller & Sakai 865*). A. Habit. B. Inflorescence of hermaphroditic plant. C. Hermaphroditic flower. D. Detail of hermaphroditic flower. E. Female flower. F. Detail of female flower, sepals removed to show vestigial stamens and nectary shafts.

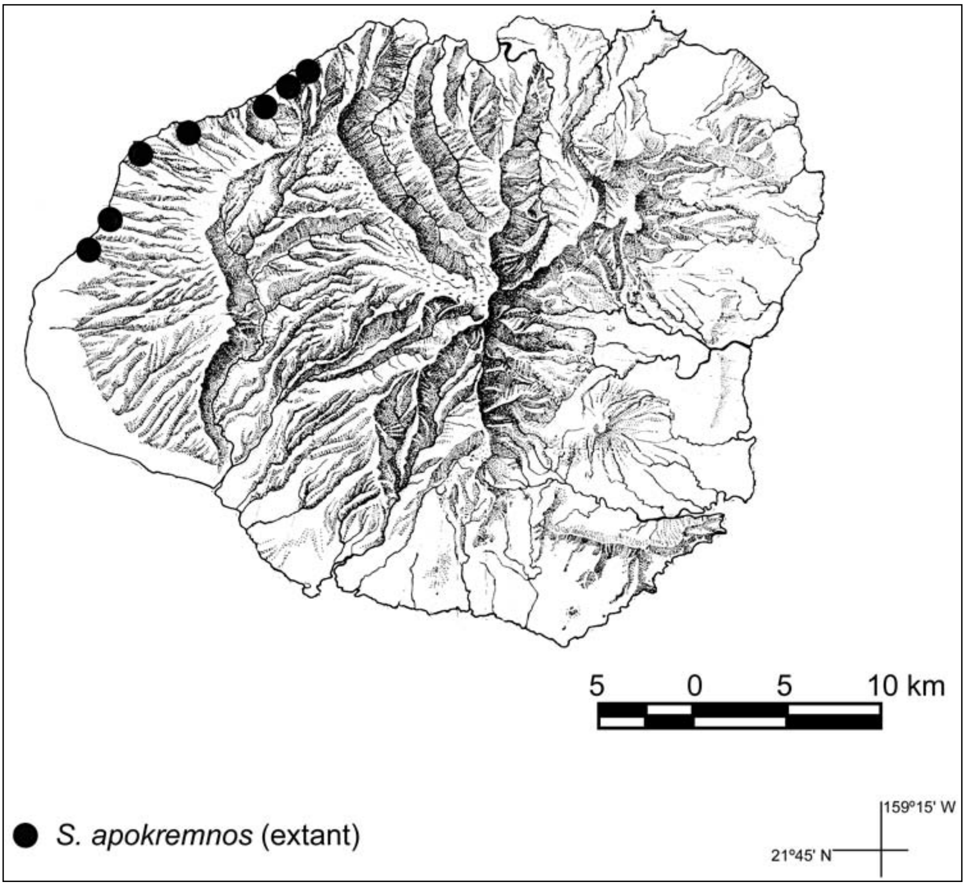

FIG. 20. Distribution of *Schiedea apokremnos*.

CULTIVATED. **Kaua`i.** Napali cliffs, S end, Ka`aweiki Ridge, *Flynn et. al. 2219* [cult. *Weller & Sakai 865*] (BISH, US); Napali cliffs, s.d., *Perlman s.n.* [cult. *Weller & Sakai 889*] (US).

Schiedea apokremnos is polymorphic in the extent of inflorescence condensation, apparently even within populations, although there is a weak trend for more condensed inflorescences in populations toward the south end of the range. Flower size (at least on hermaproditic plants), however, reaches extreme ends of the spectrum in populations from Ka`aweiki Ridge and two ridges north at Ha`ele`ele Ridge.

Schiedea apokremnos was listed as endangered in 1991 (Canfield 1991).

The specific epithet, the Greek adjective *apokremnos* (“precipitous”), refers to the steep cliffs and slopes on which this species occurs.

VII. **Schiedea** sect. **Mononeura** W. L. Wagner & Weller, sect. nov.—TYPE: *Schiedea nuttallii* Hook.

Subfrutices infirme erecti usque ad effusi vel reclinati. Folia grandia uninervata. Inflorescentiae apertae magnae et diffusae. Sepala reflexa leviter torta ciliata apice attenuato.

Subshrubs to vines; stems weakly erect to sprawling; roots fibrous. Leaves large, narrowly lanceolate, ovate, broadly ovate to elliptic or oblong-elliptic, 1-nerved, sometimes slightly falcate, margins entire or in one species with a few scattered minute excrescences, each usually with a retrorsely hooked hair. Inflorescence terminal, open, large and diffuse. Flowers hermaphroditic. Sepals 5, lanceolate or rarely ovate, strongly reflexed and convex in the proximal 1/4, producing a conspicuous transverse bulge, the distal part broadly navicular, usually oriented at 0° to 80° angle to the pedicel (in three species not opening or only slightly in anthesis), margins ciliate, apex attenuate, inconspicuously slightly twisted. Nectary shafts gently recurved or straight (in one species the shaft appressed to the sepal surface and following its contour) or raised above the surface and sigmoid with the distal 2/3 curving upward. Styles 3 (4–5).

Distribution. Twelve of the thirteen species of sect. *Mononeura* occur in mesic to wet forest, and one species (*S. hawaiiensis*) in dry forest. Members of sect. *Mononeura* occur on six of the main Hawaiian Islands: five species on Maui, four species on Kaua`i and Moloka`i, three on O`ahu, two on Hawai`i, and one on Lana`i. This section also includes half of the species in the genus that occur on more than one island (*S. nuttallii*, *S. pubescens*, and *S. diffusa*).

All of the species are hermaphroditic, and autogamy has evolved in four species (*S. diffusa*, *S. hawaiiensis*, *S. jacobii*, and *S. laui*). Two of the species, *S. amplexicaulis* and *S. implexa*, are presumed extinct.

The sectional name is formed from the Greek adjective *monos* (“one”) and the noun *neuron* (“nerve”) in reference to the large leaves with only the midrib prominent.

10. Schiedea stellarioides H. Mann, Proc. Boston Soc. Nat. Hist. 10: 310. 1866.—TYPE: HAWAIIAN ISLANDS. KAUA`I: Waimea, 2000–3000 ft [610–915 m], 1864–1865, *H. Mann & W. T. Brigham 595* (holotype: GH!; isotypes: BISH-2 sheets! BM! CU! K! MO! NY! UC! US!; photo of CU isotype: F!).

Schiedea stellarioides var. *hillebrandii* Hochreutiner, Candollea 2: 360. 1925.—TYPE: HAWAIIAN ISLANDS. KAUA`I: mountains of Waimea, 1853–1871, *V. Knudsen 52* (holotype: B, destroyed, photo: BISH!; isotype: BISH-46621!).

Schiedea stellarioides var. *longifolia* Sherff, Amer. J. Bot. 30: 606. 1943.—TYPE: HAWAIIAN ISLANDS. KAUA`I: on Kaholuamanu above Waimea, 4000 ft [1220 m], 30 Aug 1895, *A. A. Heller 2766 p.p.* (holotype: PH!; isotypes: CU! F! G! GH! K! MIN! MO! NY! P! UC! US!, photo of F isotype: F!).

Schiedea stellarioides var. *implexoides* Sherff, Bot. Leafl. 9: 4. 1954.—TYPE: HAWAIIAN ISLANDS. KAUA`I: northwesternmost Kaua`i, sea cliffs of Hanakapi`ai beach, Sep 1913, *C. N. Forbes & H. J. Forbes 463.K* (holotype: BISH-502023!, photo: F!).

Weakly erect to sprawling subshrubs 3–6 dm tall, multi-stemmed from the base, often forming a dense clump; stems branched, green, conspicuously 4-ridged, compressed (at least the younger ones), moderately puberulent on younger stems, the hairs crinkly to curved, 0.1–0.3 mm long, and a few of them to 0.5 mm long on the angles, becoming sparsely puberulent on older stems. Leaves opposite, 2.5–8.2 cm long, 0.2–1.3 cm wide, slightly thickened and membranous, linear to oblong-elliptic, with only the midvein evident, puberulent toward and on margins on adaxial side and on the midvein on abaxial side, otherwise glabrate, margins entire, slightly revolute, apex acute to acuminate, base gradually tapering, sessile. Inflorescence terminal, with 17–85 flowers, 15–32 cm long, diffuse, weakly erect, the tertiary and higher-order internodes and pedicels ascending to weakly spreading, glabrous to puberulent, the hairs similar to those of the leaves; bracts green, filiform to subulate, those of central axis 5–10 mm long, those of branches and flowers 2–3 mm long; pedicels 7–15 mm long, 4-angled and somewhat compressed. Flowers hermaphroditic, usually pendent. Sepals 2.8–3.6 mm long, lanceolate, green, tinged purple at apex, along the midrib, and toward the base, strongly reflexed at the base, producing a small bulge, deeply navicular and inrolled in the distal 1/2, oriented at 60° to 80° to the pedicel but curved throughout so that the proximal 1/2 curved upward, abaxial side keeled, glabrous to sparsely puberulent, margin scarious, glabrous or ciliate, especially toward the base, apex attenuate. Nectary base elongate, 1.6–2.6 mm long, dark yellow to orange, the nectary shaft 0.7–1.7 mm long (forming an overall structure 2.9–3.7 mm long), appressed to the sepal surface and following its contour or raised above the surface and sigmoid with the distal 2/3 curving upward, apex bifid, the abaxial side longer. Stamens 10 (–11); filaments strongly dimorphic, in staminate phase the antisepalous whorl strongly ascending and the alternate whorl spreading, the antisepalous whorl 3.5–4.7 mm long, the alternate whorl 2–2.9 mm long; anthers of the antisepalous stamens 0.6–1 mm long, those of the alternate whorl 0.5–0.6 mm long, pale reddish purple. Styles 3 (–4). Capsules 2.4–3 mm long, ovoid. Seeds 0.8–1.1 mm long, orbicular-reniform, the surface slightly rugose. Chromosome number: 2n = 56–60 (*Perlman11903*). Figs. 2D, 21.

Distribution (Fig. 22). Kaua`i, western side of island from Waimea, `Opaewela, Kaholuamanu, and above Hanakapi`ai Beach, a single collection from Ha`upu Ridge; in open, dry sites on cliffs and mesic forest; 300–1220 m.

ADDITIONAL SPECIMENS EXAMINED. **Kaua`i.** Waimea, *Faurie 1089* (BISH, BM, G, P), *Faurie 1090* (BM, G [2], P); Kaholuamanu, *Forbes 380.K* (A, BISH, M, MO, NY, P, UC, US); Ha`upu, rocky cliffs, [22°55′32″N, 159°24′3.6″W], *Forbes 758.K* (BISH); on Kaholuamanu above Waimea, 2–9 Sep 1895, *Heller 2766 p.p.* (BISH-2 sheets, K, NY); Kaholuamanu, *Hitchcock 15387* (US); in vicinity of Kaholuamanu, [22°03′53.6″N, 159°35′55.9″W], *Hitchcock 15539* (US); Waimea, près du cottage Gay, foret de Lihu`e et buisson et Koa, *Laulikiliki 3596* (G); Kaholuamanu, s.d., *Lydgate s.n.* (BISH); Wai`alae Valley, steep slopes on S side of main Wai`alae falls, across gulch from goat fence exclosure, N facing slopes, [22°4′25.6″N, 159°36′19.4″W], *Perlman & Wood 13325* (BISH, MO, NY, PTBG, US); Wai`alae valley, S ridge of valley, above Wai`alae falls, *Perlman & Wood 16417* (PTBG); Waimea canyon, Kawai`iki valley, N of Kaluahaulu ridge, [22°05′7.9″N, 159°35′54.6″W], *Perlman & Wood 17606* (MO, NY, PTBG, US); Koai`e canyon drainages, above "Twin Falls," N of Kawai`iki ridge, *Perlman & Wood 17689* (PTBG); along the trail to `Opaewela, *Rock 27(5468)* (BH, NY), *Rock 27(5471)* (BISH), *Rock 27(5473)* (BISH); mountains of Waimea, *Rock 27(5934)* (BISH); woods of Kaholuamanu, *Rock 27(5935)* (BISH); along the trail to `Opaewela, *Rock 5464* (GH); Kaholuamanu, *Rock 5474* (BISH); along the trail to `Opaewela, *Rock 5475* (GH); Kaholuamanu, *Rock 17095* (BISH); `Opaewela, [22°03′30.3″N, 159°35′33.9″W], Sep 1909, *Rock s.n.* (NY); Ha`upu, rocky cliffs, [22°55′32″N, 159°24′3.6″W], Oct 1916, *Rock s.n.* (BISH, K); Wai`alae Canyon, below falls along drainage, *Wood 6015* (PTBG); Waimea District, Wai`alae ridge and N side of ridge above falls, [22°04′21.3″N, 159°36′14.8″W], *Wood & Perlman 2846* (PTBG), *Wood & Perlman 2847* (AD, BISH, F, K, MO, NY, PTBG, US); Wai`alae ridge E of falls, *Wood & Perlman 3983* (US), *Wood & Perlman 3984* (US), *Wood & Perlman 3985* (BISH, US), *Wood & Perlman 3986* (K, PTBG, US [2]), *Wood & Perlman 3987* (NY, US), *Wood & Perlman 3989* (K, MO, US), *Wood & Perlman 3990* (BISH, PTBG, US), *Wood & Perlman 3991* (PTBG, US), *Wood & Perlman 3992* (BISH, CHR, RSA, US); Waimea District, Nawaimaka drainage, [22°4′14.9″N, 159°36′4.3″W], *Wood & Perlman 4009* (BISH, US); Kawai`iki, off Kaluahaula ridge, upper forest and drainage to the S of Koai`e and N of Wai`alae, *Wood & Perlman 8620* (PTBG); Waimea District, cross first stream SW of Wai`alae cabin, go up hillside and head W along N facing ridge, *Wood et. al. 659* (PTBG [2], US); Waimea District, Wai`alae valley, ridge between Wai`alae and Nawaimaka valleys, above Wai`alae falls, N aspect on steep upper slope, *Wood et. al. 841* (BISH, PTBG, US).

CULTIVATED. **Kaua`i.** Wai`alae Valley, *Perlman 14765* [cult. *Wagner & Shannon 6854*] (BISH, PTBG, US); on N facing slopes above Wai`alae Falls, on N side of ridge between Wai`alae and Nawaimaka, *Perlman & Wood 14651* [cult. *Wagner & Shannon 6855*] (BISH, PTBG, US); Nawaimaka stream, *Perlman & Wood 14658* [cult. *Wagner & Shannon 6800*] (BISH, PTBG, US); ridge between Wai`alae and Nawaimaka valleys,

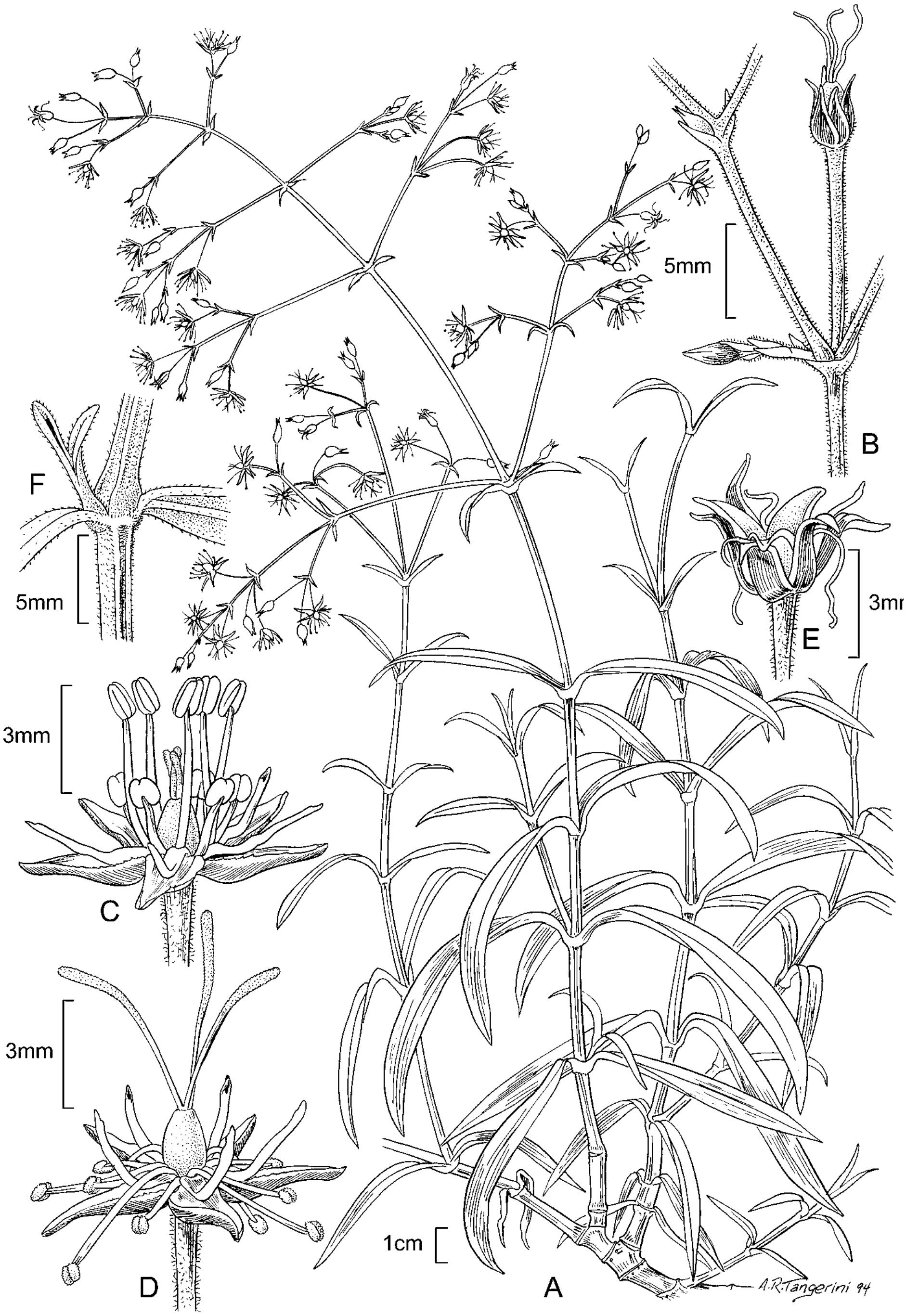

FIG. 21. *Schiedea stellarioides* (cult. from *Perlman 11903*). A. Habit. B. Portion of inflorescence. C. Flower in early anthesis, male stage. D. Flower in later anthesis, female stage. E. Dehisced capsule. F. Internode, showing quadrangular stem.

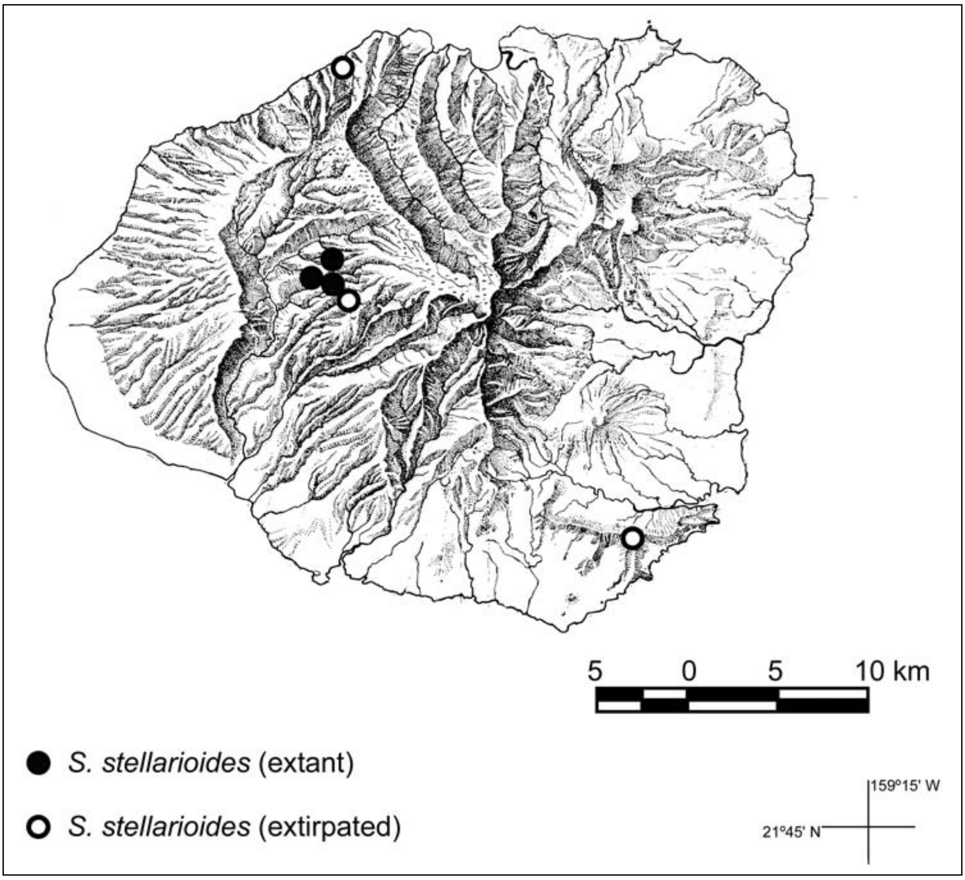

FIG. 22. Distribution of *Schiedea stellarioides*.

above Wai`alae Falls, *Perlman 11903* [cult. *Wagner & Shannon 6812*] (BISH, PTBG, US), *Perlman 11903* [cult. 1991, *Weller & Sakai s.n.*] (BISH, US).

Schiedea stellarioides is highly variable in leaf shape and size. One collection from cliffs above Hanakapi`ai Beach has leaves to 1.3 cm wide, broader than all other collections. Sherff (1945) in his revision of *Schiedea* recognized three varieties of *S. stellarioides* based on the leaf variation. The extinction of many populations has hindered a more detailed investigation of variation in this species. Other than perhaps in the Hanakapi`ai collections, however, variation appears to occur within populations. Plants cultivated from seed collected at Wai`alae (*Perlman 11903*) have variable leaf size and shape, which suggests that leaf variation would be unreliable for describing infraspecific taxa of this species. Unfortunately, we have not been able to re-collect this species from Hanakapi`ai and cannot evaluate the apparent distinctness of this population.

Schiedea stellarioides has a number of unusual traits, including 4-ridged stems, elongate nectary bases, nectary shafts that are appressed to and follow the contour of the sepal during anthesis, and pale reddish purple anthers (otherwise known elsewhere in *Schiedea* only in sections *Nothoschiedea* and *Alsinidendron*).

Because *S. stellarioides* had not been collected since 1916, it was thought to be extinct (Wagner et al. 1990; Weller et al. 1990); however, a population was discovered near Wai`alae in 1991 (Lorence et al. 1995), and it is now known from two populations. It was federally listed as endangered in 1996 (Russell & Bruegmann 1996a).

The specific epithet refers to a resemblance to the genus *Stellaria* L.

11. Schiedea amplexicaulis H. Mann, Proc. Boston Soc. Nat. Hist. 10: 310. 1866.—TYPE: HAWAIIAN ISLANDS. KAUA`I or NI`IHAU: 1851–1855, *J. Rémy 548bis* (holotype: GH!, photo: F!; isotype: P-4 sheets!). [The label of one sheet at P indicates only Kaua`i, whereas the other three labels list both Kaua`i and Ni`ihau.]

Probably suffrutescent, habit and height unknown, but apparently stems weakly erect to sprawling; stems at least to 6 dm long, 4-angled in cross section, internodes 2–3 cm long. Leaves opposite, 4–5.3 cm long, 0.5–1.7 cm wide, membranous, narrowly lanceolate to oblong-lanceolate, with only the midvein evident, glandular-puberulent throughout or glabrous, margins entire, slightly thickened and often revolute, with scattered antrorse hooked hairs near the base, apex obtuse, mucronate, the broader sessile base weakly clasping the stem and ciliate. Inflorescence terminal, with 21–140 flowers, 10–30 cm long, diffuse, younger portions glandular-puberulent; bracts green, lanceolate to ovate, those of central axis 3–8 mm long, those of branches and flowers 2–3.5 mm long; pedicels 8–22 mm long. Flowers probably hermaphroditic. Sepals ca. 3–3.5 mm long, enlarging to 4–4.5 mm long in fruit, green, lanceolate, glandular-puberulent, margins scarious, apex attenuate. Nectary shafts 3–3.5 mm long, apex bifid. Stamens 10; filaments dimorphic, ca. 4 mm long; anther size unknown, yellow, pollen yellow. Styles 3. Capsules 3–3.5 mm long, ovoid. Seeds ca. 0.9–1 mm long, the surface of nearly mature seeds smooth. Chromosome number unknown. Fig. 23.

ADDITIONAL SPECIMENS EXAMINED. **Kaua`i.** Without locality, *Lydgate A* (BISH [2]).

The range (Fig. 24) of *S. amplexicaulis* is largely unknown. The habitat and specific locality were not given on the only two collections from Kaua`i. The most recent collection is that of John Lydgate, who collected primarily in the late 1800's and early 1900's. The relatively broad leaves and placement in sect. *Mononeura* suggest that the habitat may have been mesic or wet forest.

The specific epithet refers to the weakly clasping leaves, which characterize this species.

12. Schiedea perlmanii W. L. Wagner & Weller, sp. nov.—TYPE: HAWAIIAN ISLANDS. KAUA`I: Mt. Haupu, near Queen Victoria's profile, W of head of Victoria, *Diospyros-Metrosideros* lowland mesic forest, 1700–1950 m, 27 Feb 1992, *S. Perlman 12614* (holotype: US-3252201!; isotypes: BISH! PTBG!).

Schiedea nuttallii var. *pauciflora* Degener & Sherff in Sherff, Bot. Leafl. 7: 6. 1952.—TYPE: HAWAIIAN ISLANDS. KAUA`I: Moloa`a Forest Reserve, ridge behind Papa`a, 16 Jan 1952, *O. Degener & A. B. Greenwell s.n.* (holotype: F-1451309, F-1451310, originally mounted on a single sheet [photo: F!], but now on 2 sheets [photos: F!]; isotypes: B! BISH-2 sheets!, F! K, NY-2 sheets!, PH-2 sheets!, US-2 sheets!).

Schiedea nuttallii var. *lihuensis* Sherff, Bot. Leafl. 9: 3. 1954.—TYPE: HAWAIIAN ISLANDS. KAUA`I: [southeastern Kaua`i] "mauka of Gap?, near Lihue," 1911, *J. M. Lydgate s.n.* (holotype: BISH-501710!, photo: F!, isotypes: BISH-2 sheets!).

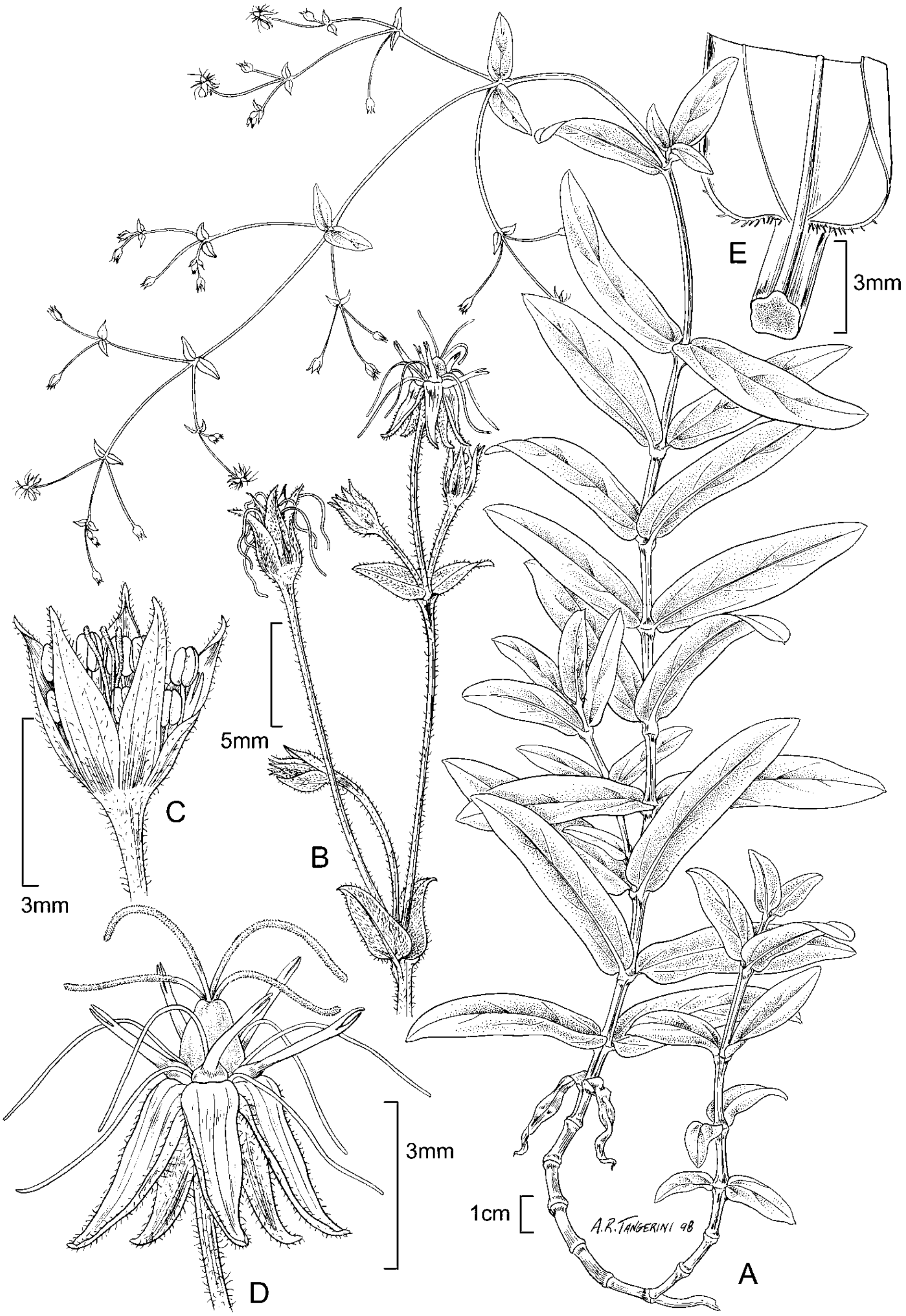

FIG. 23. *Schiedea amplexicaulis* (*Rémy 548bis*, isotype, P). A. Habit. B. Inflorescence. C. Flower in early anthesis, male stage. D. Flower in later anthesis, female stage. E. Leaf base.

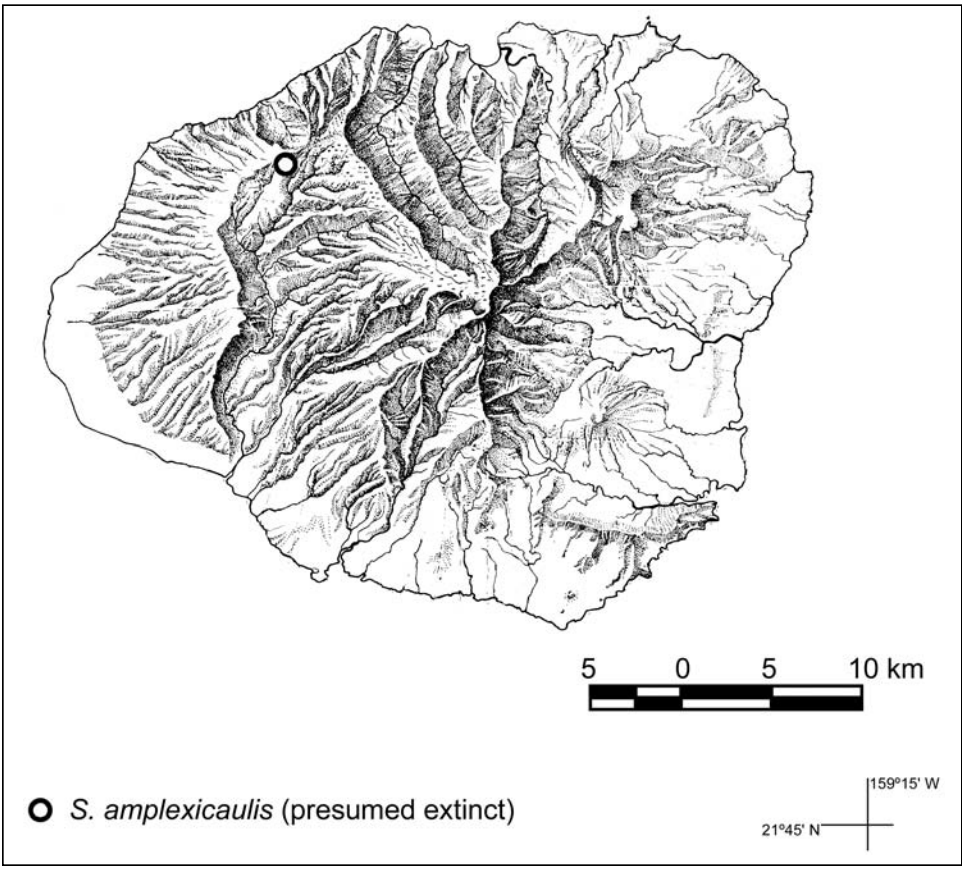

FIG. 24. Distribution of *Schiedea amplexicaulis* (known from only two collections; the locality is approximate).

Differt a S. nuttallii habitu scandenti caulibus usque ad 12 dm longis, inflorescentia patenti vel pendenti, pedicellis vel internodiis leniter effusis, superficiebus bractearum puberulis, pedicellis 13–15 mm longis.

Vine; stems 6–12 dm long (in cultivation eventually to 15 dm or more long), sprawling when young to reclining when longer, at least sparingly branched, internodes deep purple or purplish green, glabrous throughout, except bracts, sepals, and sometimes the pedicel. Leaves opposite; blades 6.5–11.5 cm long, 2–2.8 cm wide, narrowly ovate or lanceolate to elliptic-lanceolate, weakly glossy, green or yellowish green, sometimes purple-tinged, especially on lower surface, weakly coriaceous and rubbery, chartaceous when dry, with only the midvein evident, the midvein ± slightly excentric, usually reddish purple, margin entire, slightly thickened becoming revolute toward the base, apex acute to acuminate; petioles 0.8–0.9 cm long, purple, weakly ± grooved. Inflorescence terminal, with 40–60 flowers, 20–35 cm long and nearly as wide, diffuse, laterally-directed or pendent, the tertiary and higher level internodes or pedicels weakly spreading; bracts subulate, the lowermost of central axis narrowly elliptic, falcate, green and purple-tinged or purple, the lowermost ones 2–17 mm long, those of branches and flowers 1.5–4.5 mm long, purple, the adaxial surface puberulent; pedicels 13–15 mm long at anthesis, weakly flattened, very weakly angled just below the flower and often with a few hairs. Flowers hermaphroditic, usually pendent. Sepals 2.2–3 mm long, elongating to 4 mm long in fruit, ovate, green, sometimes purple-tinged toward apex or irregularly purple throughout, opaque, strongly reflexed and convex in the proximal 1/4, producing a conspicuous transverse bulge, the distal part broadly navicular, oriented at 5° to 30° angle to the pedicel, abaxial side sparsely puberulent toward the base, the adaxial side puberulent, primarily near the midrib, margins conspicuously scarious, ciliate, apex attenuate, inconspicuously slightly twisted. Nectary base 0.7–0.9 mm long, yellow, the nectary shaft 4.5 mm long, gently recurved, at 90° angle to the axis, apex deeply bifid to ca. 1/2 their length. Stamens 10; filaments dimorphic, the antisepalous whorl 6.2–6.3 mm long, the alternate whorl 5 mm long; anthers 0.75–0.8 mm long, subequal, pale yellow. Styles 3, white. Capsules 2.5–2.7 mm long, ovoid. Seeds ca. 1.2 mm long, orbicular-reniform, compressed, the surface rugose. Chromosome number unknown. Figs. 2C, 25.

Distribution (Fig. 26). Kaua`i, known from only three collections from mesic shrubland near the summit of the Hoary Head Mountains (Ha`upu), where it is still extant, and from a single collection from above Papa`a made over 50 years ago; ca. 410–570 m.

ADDITIONAL SPECIMENS EXAMINED. **Kaua`i.** Ha`upu summit, slopes of N facing side near top, [21°55′33.6″N, 159°24′1.9″W], *Perlman et. al. 12917* (PTBG); Mt. Ha`upu, N facing cliffs above Kipu, between Queen Victoria's Profile and Mt. Ha`upu summit, *Perlman 17563* (BISH, NY, PTBG, US); Mt. Ha`upu, slopes above Kipu ranch, to W of Queen Victoria's Profile, *Perlman 17439, 17449* (PTBG); windward Ha`upu, just E of Ha`upu Peak, Kipu, below "Queen Elizabeth's [Queen Victoria's] Profile," *Warshauer 1184* (BISH).

CULTIVATED. **Kaua`i.** Ha`upu summit, slopes of N facing side near top, *Perlman et.al. 12917* [cult. *Wagner & Shannon 6795*] (BISH, GH, NY, PTBG, US).

Wagner et al. (1990) included in *S. nuttallii* specimens now assigned to *S. perlmanii* as well as the types of *S. nuttallii* var. *pauciflora* and var. *lihuensis*. Observations of greenhouse-grown plants of *S. perlmanii* revealed the unique characters distinguishing *S. perlmanii* from both *S. nuttallii* and *S. kauaiensis*, such as the vining habit and smaller, pendent flowers. Sherff (1952) described this taxon as a variety of *S. nuttallii* based on the ample collection of Otto Degener.

Schiedea perlmanii was considered by Wagner et al. (1999b) to be endangered, because the only known extant populations occur in a small area on Ha`upu.

The specific epithet honors Steven Perlman (b. 1948), one of the foremost Hawaiian field botanists and explorers, who helped us extensively with the *Schiedea* project.

13. Schiedea kauaiensis St. John, Phytologia 64: 177. 1988.—TYPE: HAWAIIAN ISLANDS. KAUA`I: Wainiha-Manoa ridge, wet forest near edge of pali, 2000 ft [610 m], 30 Jul 1977, *C. Christensen 290* (holotype: BISH-522854!).

Schiedea wichmanii St. John, Phytologia 64: 178. 1988.—TYPE: HAWAIIAN ISLANDS. KAUA`I: Limahuli Valley, E wall, 60° slope, locality on dark soil and loose rock with remnant `Ohi`a, *Eugenia*, Uluhe, *Santalum* [*freycinetianum* var. *pyrularium* (A. Gray) Stemmerm.], *Diospyros*, *Psychotria*, and *Hibiscus*, 1300 ft [395 m], 13 Sep 1978, *S. Perlman & C. Wichman, Jr. 219* (holotype: BISH-522858!; isotype: BISH! PTBG!). [Sterile specimens, flowers liquid-preserved.]

Erect to ascending subshrubs 3–10 dm tall; stems few-branched, glabrous, becoming sparsely then moderately glandular-puberulent in the inflorescence, the internodes purple. Leaves opposite; blades 7.5–15 cm long, 1.8–4.1 cm wide, oblong-elliptic, light green or

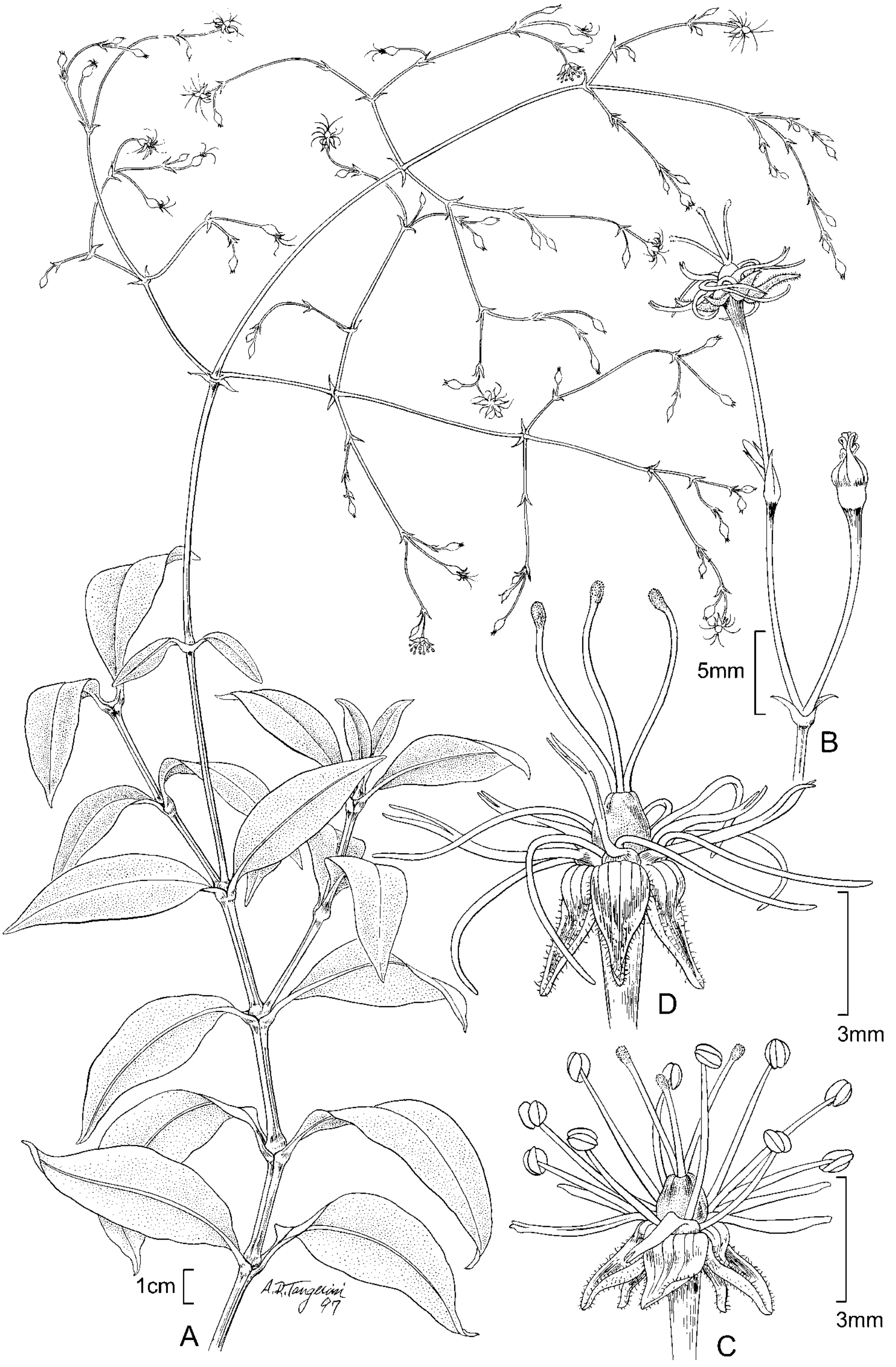

FIG. 25. *Schiedea perlmanii* (cult. from *Perlman 12917*). A. Habit. B. Portion of inflorescence. C. Flower in early anthesis, male stage. D. Flower in later anthesis, female stage.

yellowish green, adaxial surface slightly glossy, the abaxial surface glossy, slightly thickened and rubbery, chartaceous when dry, usually slightly undulate, with only the midvein evident or sometimes with an additional pair of inconspicuous, smaller, looping veins, the midvein ± slightly excentric, margin entire, slightly thickened and weakly revolute, especially toward the base, apex acute to weakly acuminate, base gradually attenuate; petioles 0.5–1.1 cm long, pale green, purple toward the base, weakly ± grooved. Inflorescence terminal, with 27–70 flowers, 20–48 cm long, diffuse, flowers widely spaced, branches spreading, progressively more densely puberulent to apex, the hairs straight, erect, 0.1–0.35 mm long; bracts subulate, the lowermost of the central axis elliptic-lanceolate, as green as the leaves, recurved and often twisted, the lower ones 30–45 mm long, those of the branches and flowers 5–18 mm long; pedicels (7–) 10–23 mm long, elongating slightly in fruit, slightly asymmetrically flattened. Flowers hermaphroditic. Sepals 4.3–5.1 mm long, lanceolate, green, opaque, strongly reflexed and convex in the proximal 1/4, producing a small transverse bulge, the distal part shallowly concave, oriented ca. 40° to 80° angle to the pedicel, glandular-puberulent, a few of the hairs non-glandular, margins scarious, ciliate, apex long-attenuate. Nectary base 0.6–0.9 mm long, dark yellow, the

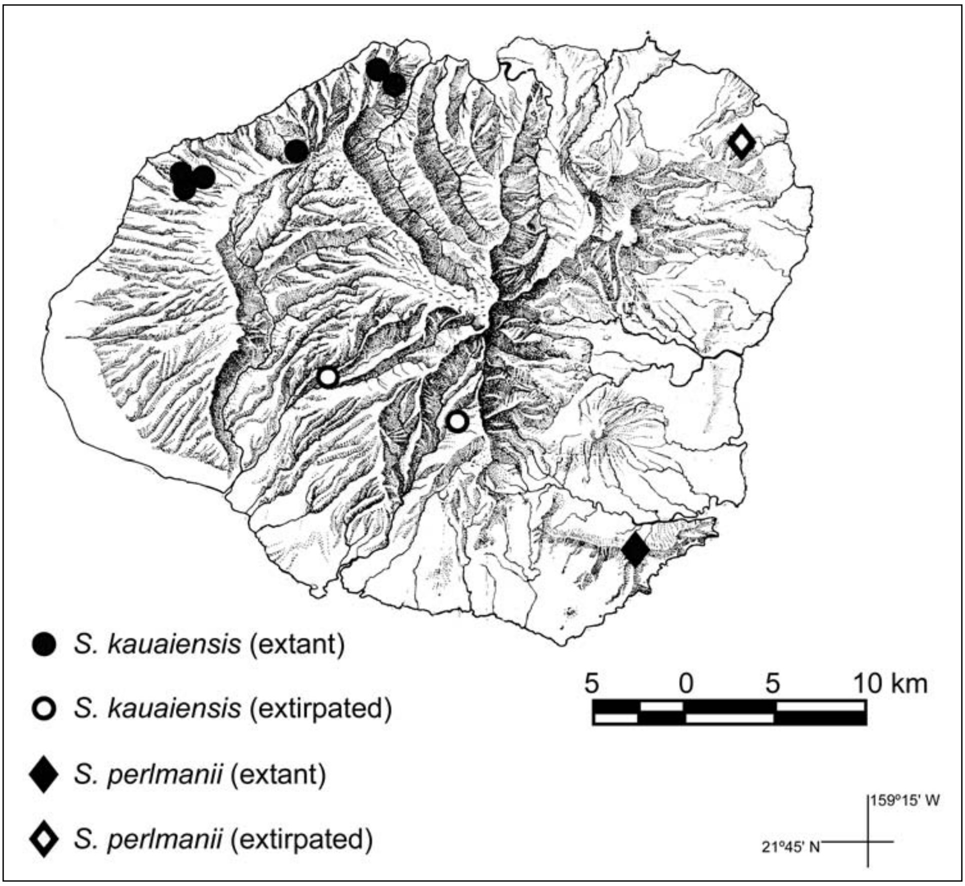

FIG. 26. Distribution of *Schiedea perlmanii* and *S. kauaiensis*. (The localities indicated for older collections of *S. kauaiensis* from Olokele Canyon and Hi`i Mountains are approximate.)

nectary shaft 3–4.5 mm long, gently recurved, at 90° to the axis, apex deeply bifid, sometimes divided nearly to the base. Stamens 10; filaments dimorphic, the antisepalous whorl 7.5 mm long, the alternate whorl 5.3–5.8 mm long; anthers 0.75–0.85 mm long, subequal, pale yellow. Styles 3. Capsules 3.1–3.5 mm long, ovoid. Seeds ca. 1.3 mm long, orbicular-reniform, compressed, the surface rugose. Chromosome number unknown. Figs. 2D, 27.

Distribution (Fig. 26). Kaua`i, in the Wainiha, Kalalau, and Mahanaloa valleys on the northern to western side, and Olokele Valley and the Wahiawa Mountains in the central region; in open areas of diverse mesic forest; 395–800 m.

ADDITIONAL SPECIMENS EXAMINED. **Kaua`i.** Wainiha valley, on ridge 1300 ft. S of Kulanaililia, top of ridge, [22°12′20.5″N, 159°34′5.1″W], *Christensen 317* (BISH); Kopiwai, Ku`ia Valley, [22°08′9.6″N, 159°41′32.7″W], *Hobdy 200* (BISH, US); Waimea District, Ku`ia Natural Area Reserve, in Mahanaloa Valley, N facing slope of valley N of Milolii Ridge, above confluence with Pa`aiki Valley, [22°08′1.4″N, 159°41′48.5″W], *Lorence & Wood 7620* (BISH [2], MO, PTBG); Olokeke Valley, *Lydgate 12* (BM); Hi`i Mts., s.d., *Lydgate s.n.* (BISH); Ku`ia Valley, a tributary of Mahanaloa Valley, 200 ft inside Ku`ia, right side slope, [22°8′17.2″N, 159°42′3″W], *Perlman 472* (BISH, US); Lower Limahuli valley, up subgulch on W side of valley, *Perlman & Bender 17370* (PTBG); Mahanaloa Valley, up valley from old horse trail, S side of valley, [22°12′35.6″N, 159°34′27.2″W], *Perlman & Obata 12074* (BISH, PTBG, US); Hanalei District, Kalalau Valley, in back of valley, native cliffs and ridges, along ridge, [22°09′7.2″N, 159°37′42.8″W], *Wood et. al. 1973* (PTBG, US).

CULTIVATED. **Kaua`i.** Mahanaloa Valley, up valley from old horse trail, S side of valley, *Perlman & Obata 12074* [cult. *Wagner & Shannon 6805*] (BISH, PTBG, US), *Perlman & Obata 12074* [cult. 1991, *Weller & Sakai s.n.*] (US).

Schiedea kauaiensis was first noted as distinct by Hillebrand (1888, p. 31) in a comment on a Kaua`i specimen (K) he included under *S. nuttallii*: "leaves obovate-oblong; panicle smaller, with fewer divisions, the flower larger, approaching those of *S. diffusa*; immature seeds only rugose."

St. John discerned two elements among material collected in the 1970's, which he described as *S. kauaiensis* and *S. wichmanii*, although the types show overlapping differences in the size of the leaves, inflorescence dimensions, pedicel length, and sepal length. Wagner et al. (1990) included all of these collections in *S. nuttallii*, but noted that they differed at least in pubescence of the inflorescence. During our study we noted that this taxon is distinguishable from *S. nuttallii* by a considerable number of characteristics, including the larger leaves and fewer, widely spaced, larger flowers borne in a puberulent inflorescence, has a distinct geographical range, and does not share a unique synapomorphy with *S. nuttallii* in our phylogenetic analysis. Therefore, we also recognize it at the species level.

The specific epithet refers to Kaua`i, where this species is endemic.

14. Schiedea nuttallii Hooker, Hooker's Icon. Pl. 7: t. 649, 650. 1844.—TYPE: HAWAIIAN ISLANDS. O`AHU: on rocks of the Parri [Ko`olau Mts., Nu`uanu Pali (?)], Dec 1834, *T. Nuttall s.n.* (holotype: K!; isotypes: BM! GH! K! MO! PH, photo of PH isotype: F!).

Schiedea oahuensis Wawra, Flora 56: 175. 1873.—TYPE: HAWAIIAN ISLANDS. O`AHU: [1–30 Apr 1870,] *H. Wawra 2280* (holotype: W, destroyed; isotypes not located).

Schiedea nuttallii var. *intermedia* Hillebrand, Fl. Hawaiian Isl. 31. 1888.—TYPE: HAWAIIAN ISLANDS. MOLOKA`I: "western end" [but presumably he meant eastern end], 1851–1871, *W. Hillebrand s.n.* (holotype: B, destroyed, photo BISH!).

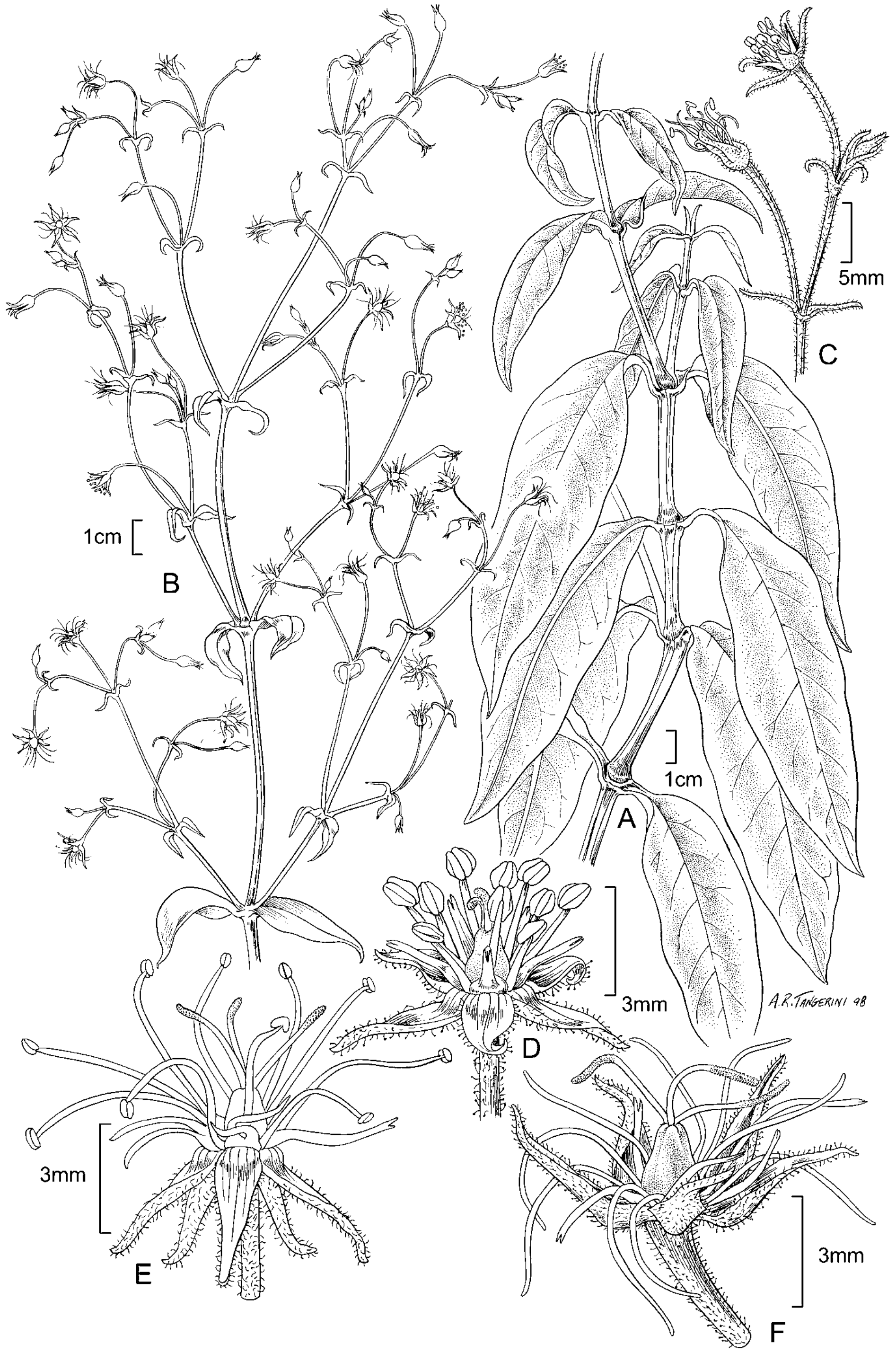

FIG. 27. *Schiedea kauaiensis* (cult. from *Perlman 12074*). A. Vegetative habit. B. Inflorescence. C. Portion of inflorescence. D. Flower in early anthesis, male stage. E. Flower in later anthesis, male stage. F. Flower in female stage.

Schiedea nuttallii var. *molokaiensis* Sherff, Bot. Leafl. 9: 3. 1954.—TYPE: HAWAIIAN ISLANDS. MOLOKA`I: Kalawao Valley, 1851–1871, *W. Hillebrand s.n.* (holotype: BISH-501712!, photo: F]).

Erect to strongly ascending subshrubs 10–15 (–19) dm tall; stems many-branched, glabrous throughout, except bracts and sepals, internodes purple-tinged. Leaves opposite; blades 5–13 cm long, 1.4–3.5 cm wide, narrowly ovate or lanceolate to narrowly or broadly elliptic, dull green, sometimes purple-tinged, slightly thickened and rubbery, chartaceous when dry, with only the midvein evident, the midvein ± slightly excentric, margin entire, slightly thickened becoming revolute toward the base, apex acute to acuminate; petioles 0.3–1 cm long, weakly ± grooved. Inflorescence terminal, with 50–240 flowers, 20–25 (–32) cm long, diffuse, erect, the tertiary and higher level internodes or pedicels usually ascending or appressed, but pedicels usually spreading at anthesis, sometimes with a few hairs toward the base of the internodes; bracts subulate, the lowermost of central axis elliptic, green and purple-tinged or purple, margins ciliate, the lower ones 2–60 mm long, those of branches and flowers 1.5–2 mm long; pedicels 6–12 mm long at anthesis, elongating to 10–20 mm long in fruit, conspicuously asymmetrically flattened and weakly quadrangular, sometimes with a few hairs toward the base on the angles. Flowers hermaphroditic. Sepals 3.5–4.5 mm long, lanceolate, green, sometimes purple-tinged or nearly purple throughout, opaque, strongly reflexed and convex in the proximal 1/4, producing a small transverse bulge, the distal part concave or shallowly navicular, oriented at 5° to 30° angle to the pedicel, abaxial side glabrous, margins conspicuously scarious, ciliate, apex attenuate, often slightly twisted. Nectary base 0.7–1 mm long, yellow, the nectary shaft 2.8–3.7 mm long, gently recurved, at 90° angle to the axis, apex deeply bifid to ca. 1/2 their length. Stamens 10; filaments dimorphic, the antisepalous whorl 5.8–7.1 mm long, the alternate whorl 4.8–5.5 mm long; anthers 0.7–1.1 mm long, subequal, pale yellow. Styles 3. Capsules 2.5–3.5 mm long, narrowly ovoid. Seeds 0.9–1 mm long, orbicular-reniform, compressed, the surface rugose. Chromosome number: 2n = 56 (*Weller & Sakai 861*). Figs. 2E, 28.

Distribution (Fig. 29). O`ahu (in Wai`anae from `Ekahanui Gulch to Mokule`ia and Ko`olau ranges; also formerly from Nu`uanu pali, and Manoa and Niu Valleys, but not collected since 1922), Moloka`i (Kala`e and Kamalo, not collected since 1910), and Maui (probably West Maui, not collected since 1792 [1793]); in diverse mesic forest; 350–760 m.

ADDITIONAL SPECIMENS EXAMINED. **Maui.** [West Maui], *Menzies 3* (MO). **Moloka`i.** Kala`e, 1870, *Hillebrand s.n.* (BISH, BM, S); Kamolo [Kamalo?], *Faurie 1092* (G [2]. P). **O`ahu.** Honolulu, pa'bergen, 1852, *Andersson s.n.* (S [4]); Pauoa Valley, *Brigham 370* (BISH); Hale`au`au Valley, *Bryan, Jr. 851* (BISH); Honouliuli Forest Reserve, Pu`ukanehoa, [21°27′16.1″N, 158°05′45.2″W], *Cowan 1038* (BISH, K); E slope of Pu`ukaua, *Degener 17493* (G, GH, NY); Ko`olau Range: NE slope of Pu`uku Makali`i, *Degener 17494* (BH, G, GH [2], K, MO, NY [2], P, PH [2]); Ka`ala, near top, *Degener 17694* (K [2], NY, US); N rim of head of Kahanahaiki Valley, [21°32′53.5″N, 158°12′27.7″W], *Degener & Hosaka 12105* (B, CU, F [2], GB, GH, K, M [2], MIN, MO, NY [2], P, PH, UC, US); Makua Valley, *Degener 21988* (M); on summit ridge N of Makua Valley, *Degener et. al. 5918* (A, CU, G, GH, K, M, MIN, MO, NY, PH, UC, W); ridge on right side of head of Makua Valley, *Degener et. al. 5921* (F, NY); middle ridge E of Pu`ukanehoa, *Degener et. al. 12799* (A, B, BH, BISH [2], BM, CU, F [2], G, GH [2], K, M, MIN, MO, NY [2], P, PH [2], UC [2], US [2]); Mokule`ia mauka, *Degener et. al. 19586* (B, BISH [2], BM, F, G, K, NY [2], P, S, UC, W); N rim of Makua Valley, [21°32′2.8″N, 158°11′1.8″W], *Degener et. al. 27959* (A, B, BH, BISH, F [2], G, K, MASS, MEL, MIN, MO, NY, US, W); Wai`anae, *Faurie 1083* (A, BM, G, P); Nu`uanu pali, [21°22′3.9″N, 157°47′38″W], *Faurie 1091* (BM, G, P); Mokule`ia, slopes of Ka`ala, *Forbes 1781.O* (A, BISH, BM, G, MO, NY [2], S, UC), *Forbes 1781b.O* (BISH);

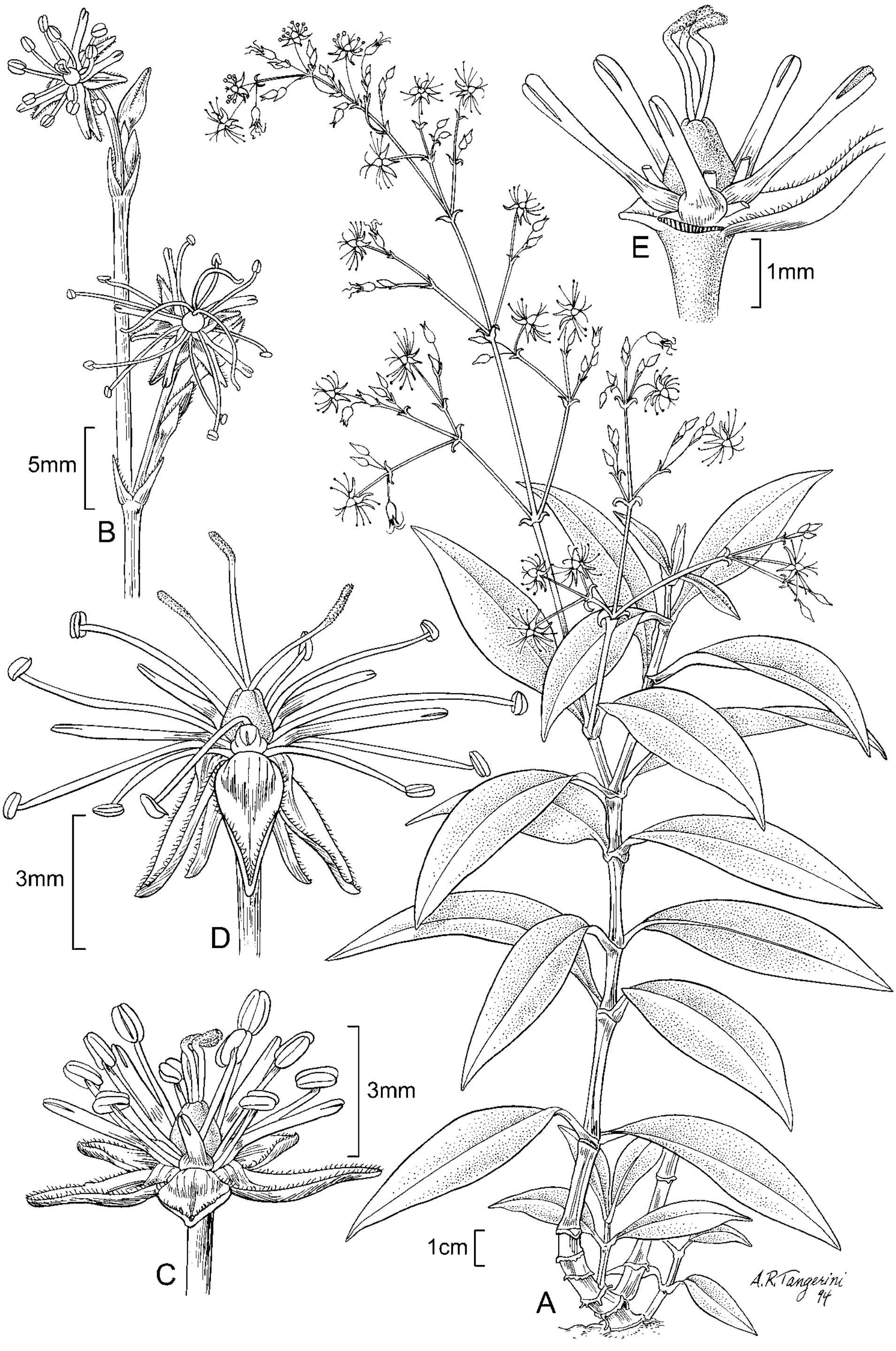

FIG. 28. *Schiedea nuttallii* (cult. from *Weller & Sakai 861*). A. Habit. B. Portion of inflorescence. C. Flowers in early anthesis, male stage D. Flower in later anthesis, female stage. E. Flower, sepals removed to show nectary shafts.

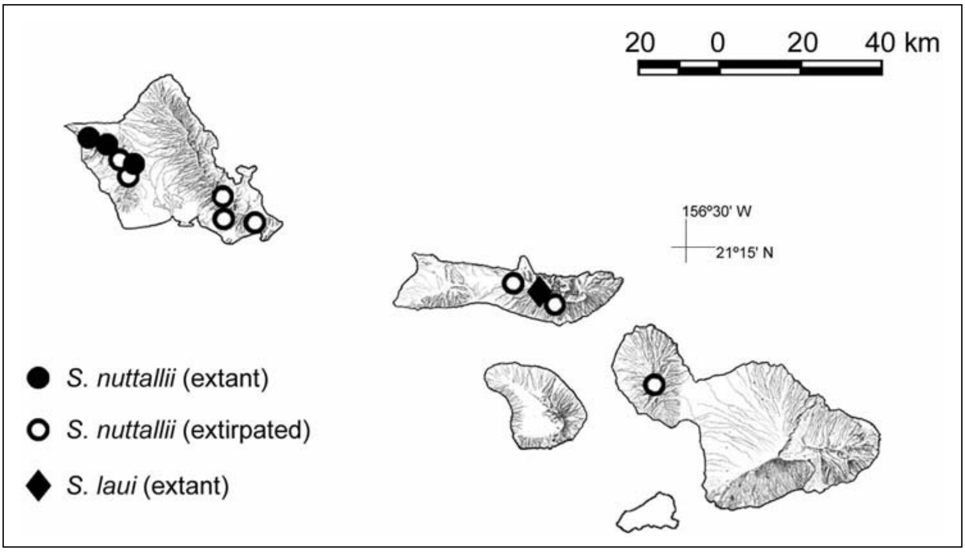

FIG. 29. Distribution of *Schiedea nuttallii* and *S. laui*. (The West Maui locality for *S. nuttallii* is approximate.)

Waianaeuka, N ridge of Pu`ukumakali`i, [21°28′58.3″N, 158°7′15.1″W], *Fosberg 13644* (US); Kaua slope of Ekakaku [`Ekahanui?] gulch, [21°26′35.2″N, 158°5′46.9″W], *Funk & Lowrey 130* (HAW [2]); Ekahaka [`Ekahanui?] Gulch, *Funk & et al. 78* (BISH); without locality, *Galathea Expedition 3545* (BISH, US); Peacock Flats, Pahole Gulch, *Herbst 3083* (BISH, MO, US); Pahole Gulch, middle elevation, *Herbst 4055* (BISH [2], HAW, US); without locality, *Hillebrand 429* (K), 1851–1871, *Hillebrand s.n.* (US); Niu, [21°19′18.4″N, 157°44′30.8″W], Jun 1867, *Hillebrand & Lydgate s.n.* (BISH [2], MEL); Wai`anae District, Kahanahaiki, *Lau 830* (BISH); Makaleha, [21°31′38.2″N, 158°9′54.6″W], Dec 1870, *Lydgate s.n.* (BISH); Ins. Owhyhee, ad montem Kaah [Mount Ka`ala], Jun 1825, *Macrae s.n.* (K); Wai`anae, *Meebold 8540* (M); `Ekahanui Gulch, northernmost subgulch of ridge top on N face, [21°26′30.5″N, 158°5′2.9″W], *Obata et. al. 402* (BISH); Pahole Gulch crest, *Obata et. al. 442* (BISH, PTBG); Pahole Gulch, below back rim of Makua Valley, *Perlman & Obata 5279* (BISH, MO, PTBG [2]); Pahole gulch, rim between Pahole and Makua Valley, *Perlman et. al. 10931* (PTBG); without locality, *Rémy 547* (GH, P [10]); Makaleha Valley, *Rock 17004* (A, BISH [2], K, P, UC, US); Huliwai, W slope, 8 May 1933, *Russ s.n.* (BISH); Wai`anaeuka, Pu`uka`ala, lower woods, *St. John 11096* (BISH); Mokule`ia, Kukuiala Gulch, *St. John 14082* (BISH); Pu`ukaua, S branch of N fork of `Ekahanui Gulch, *St. John 21536* (BISH); Mokule`ia Forest Reserve, Makaleha Trail, [21°31′15.8″N, 158°9′14.3″W], 13 Jul 1947, *Sakimura et. al. s.n.* (BISH); without locality, *Seemann 2271* (K); Ka`ala, NE slope of Pu`ukalena, along the trail to Ka`ala, [21°29′30.7″N, 158°8′12.2″W], *Selling 3608* (BISH, GB, K, S); Mokule`ia Forest Reserve, Makaleha Trail, [21°31′15.8″N, 158°9′14.3″W], 13 Jul 1947, *Sakimura et. al. s.n.* (BISH); Ko`olau, Manoa Valley, [21°20′14.2″N, 157°47′22″W], *Skottsberg 251* (GB); Ka`ala range, *Swezey 12770* (BISH); on rocks near Honolulu, 1838, *U.S. Expl. Exped. s.n.* (GH, US); Honoliuli, Pu`ukanehoa, *Webster 1644* (US); Pahole drainage #3, *Welton 768* (BISH); Keawapilau Gulch, [21°31′52.9″N, 158°10′39.2″W], *Welton & Haus 632* (BISH); Kanehoa, Honouliuli Forest Reserve, *Wilbur 783* (UC); Wai`anae Range: base of Mt. Ka`ala, 19 Apr 1931, *Williams s.n.* (BISH); Ka`ala, 3 Jan 1932, *Williams s.n.* (BISH). ISLAND UNKNOWN: *Hillebrand 432 bis* (K), *Hillebrand 433* (K), s.d., *Hillebrand s.n.* (B), *Hillebrand s.n.* (P).

CULTIVATED. **O`ahu.** Wai`anae Range, N rim of Makua Gulch, [21°32′2.8″N, 158°11′1.8″W], *Perlman 11046* [cult. *Wagner & Shannon 6806*] (BISH, PTBG, US), 1 Mar 1987, *Weller & Sakai s.n.* [cult. *Weller & Sakai 861*] (BISH, US), *Weller & Sakai 861* [cult. *Wagner & Shannon 6793*] (BISH, PTBG, US); Pahole Natural Area Reserve, Keawapilau Gulch, 23 Apr 1993, *Weller & Sakai s.n.* [cult. *Weller & Sakai 903*] (BISH, PTBG, US), *Weller & Sakai 903* [cult. *Wagner & Shannon 6792*] (BISH, PTBG, US).

Schiedea nuttallii is morphologically similar to *S. kauaiensis, S. laui, S. jacobii,* and *S. implexa*. These four species share an erect habit, but differ primarily in the size of the inflorescence and flower. *Schiedea kauaiensis* differs from *S. nuttallii* in its fewer-flowered, open, sparsely to moderately puberulent inflorescences, and larger flowers and leaves, whereas *S. implexa* is characterized by numerous small flowers, a glabrous or puberulent inflorescence, and narrow leaves. *Schiedea jacobii* has smaller, facultatively autogamous flowers; the seeds are retained in capsules. *Schiedea laui* differs primarily in having cleistogamous flowers.

Schiedea nuttallii formerly had one of the widest geographical ranges in the genus, but it is now restricted to a few populations in the northern Wai`anae Mountains. It was federally listed as endangered in 1996 (Russell & Bruegmann 1996b).

The specific epithet honors Thomas Nuttall (1786–1859), a British naturalist, who explored much of North America, as a botanist, ornithologist, and malacologist (1808–1841). He made two trips to the Hawaiian Islands (4 January to 26 March 1835; October 1835 to January 1836), where he collected primarily on O`ahu, but also visited at least Kaua`i and Hawai`i.

15. Schiedea laui W. L. Wagner & Weller, sp. nov.—TYPE: HAWAIIAN ISLANDS. MOLOKA`I: Kamakou Preserve, Waikolu drainage, Hanalilolilo pipeline trail, about 0.8 km NW of Pepe`opae Bog [approximately between 21°07′19″N, 156°54′12.4″W and 21°07′25.2″N, 156°54′25.8″W], 1146 m, in streamside grotto formed by overhang, wet *Metrosideros polymorpha/Cheirodendron trigynum* forest, 12 May 1998, *J. Lau & S. Loo 3951* (holotype: US-3376195!).

Differt a *S. nuttallii* pedicellis appressis ad ramum inflorescentiae in anthese, floribus cleistogamis, sepalis clausis remanentibus per anthesin scapis nectariorum 2.3 mm longis, filamentis staminum ante sepala 4.0–4.1 mm longis.

Erect to strongly ascending subshrubs 5–15 dm tall; stems many-branched, glabrous throughout, except bracts and sepals, internodes lightly purple-tinged. Leaves opposite; blades 6.5–13 cm long, 1.5–2.8 cm wide, narrowly ovate or lanceolate to narrowly or broadly elliptic, dull green, sometimes purple-tinged, slightly thickened and rubbery, chartaceous when dry, with only the midvein evident, the midvein ± slightly excentric, margin entire, slightly thickened becoming revolute toward the base, apex acute to acuminate, base gradually attenuate; petioles 0.5–1.1 cm long, weakly ± grooved. Inflorescence terminal, with 10–18 flowers, 17–26 cm long, diffuse, erect, the tertiary and higher-level internodes usually ascending or appressed, and pedicels appressed at anthesis, sometimes with a few hairs toward the base of the internodes; bracts subulate, the lowermost of central axis elliptic, green and purple-tinged or purple, margins ciliate, the lower ones 10–45 mm long, those of branches and flowers 3–8 mm long; pedicels 3–11 mm long at anthesis, elongating to 10–15 mm long in fruit, conspicuously asymmetrically flattened and weakly quadrangular, sometimes with a few hairs toward the base on the angles. Flowers hermaphroditic, cleistogamous. Sepals 4.0–4.5 mm long, narrowly lanceolate, green, sometimes purple-tinged or nearly purple throughout, opaque, abaxial side glabrous, margins scarious, weakly ciliate, apex attenuate, often slightly twisted. Nectary base obsolete, the nectary shaft ca. 2.3 mm long, apex deeply bifid to ca. 1/2 of its length. Stamens 10; filaments dimorphic, the antisepalous whorl 4.0–4.1 mm long, the alternate whorl ca. 3.5 mm long; anthers ca. 0.3–0.4 mm long, subequal, pale yellow. Styles 3–4. Capsules ca. 4.0–4.5 mm long, narrowly ovoid. Seeds ca. 1 mm long, orbicular-reniform, compressed, the surface rugose. Chromosome number unknown. Figs. 2F, 30.

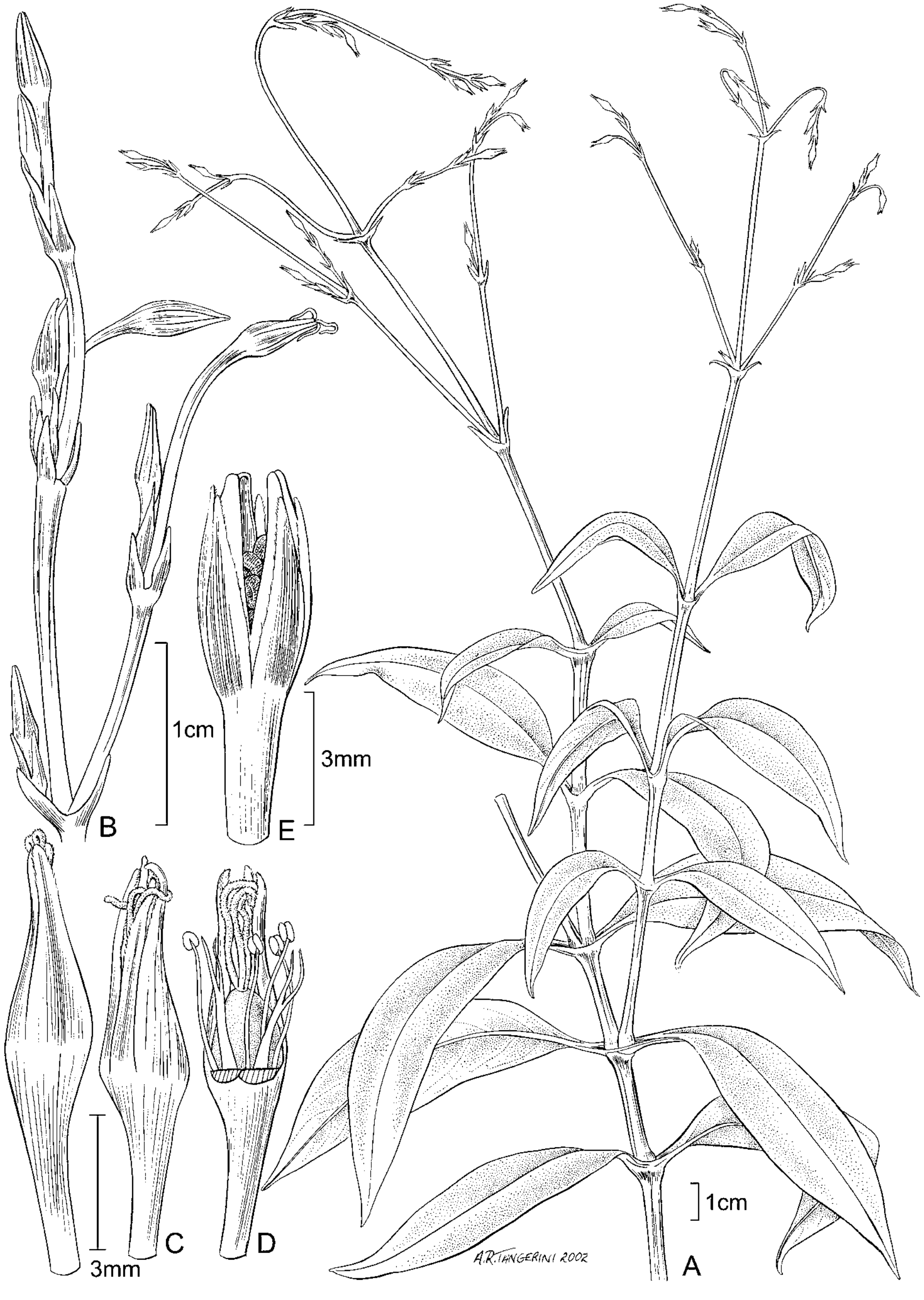

FIG. 30. *Schiedea laui* (cult. from *Weller & Sakai 952*). A. Habit. B. Portion of inflorescence. C. Flowers in anthesis. D. Flower, sepals removed to show stamens and nectary shafts. E. Dehisced capsule surrounded by sepals.

Distribution (Fig. 29). Moloka`i, known from a single collection from the base of a waterfall in Kamakou Preserve, upper Waikolu drainage, Moloka`i; 1100–1146 m.

PARATYPES. **Moloka`i.** Kamakou preserve, Hanalilolilo drainage, along pipeline trail past tunnel, below trail in cave on stream, 21°07′N, 156°53′W, *Perlman 18155* (PTBG, US).

Schiedea laui differs from *S. nuttallii* by the cleistogamous flowers and occurs at higher elevations in wet, rather than mesic, forest. It is here recognized as a new species because of its distinctive morphology relating to its autogamy (tertiary and higher level internodes usually ascending or appressed as are the pedicels, flowers not opening, nectaries nearly obsolete); it does not share any unique synapomorphies with *S. nuttallii* to which it is morphologically most similar.

When *S. laui* was first discovered in 1998, 16 mature plants were found. Apparently as the result of prolonged drought, only nine mature plants and several additional immature plants and seedlings were found in 2000 (J. Lau, pers. com. in 2003). The population occurs in a streamside grotto formed by an overhang. Some individuals grow in the outer portion of the grotto, which is constantly wet from dripping water, and others are located further within where it is drier. Associated species in order of abundance within the grotto are: *Asplenium lobulatum*, *Asplenium macraei*, *Thelypteris sandwicensis*, *Vandenboschia davallioides*, *Cyrtandra hawaiiensis*, *Asplenium unilaterale*. The flowers are completely cleistogamous, a breeding system characteristic of wet forest species.

The specific epithet honors the discoverer of this novelty, Joel Q. C. Lau of the Hawaii Natural Heritage Program, who is one of the most knowledgeable botanists of the Hawaiian flora.

16. Schiedea kaalae Wawra, Flora 56: 175. 1873.—TYPE: HAWAIIAN ISLANDS. O`AHU: Ka`ala, [1–30 Apr 1870,] *H. Wawra 2220* (W, destroyed).—O`AHU: Wai`anae Mts., Pu`ukaua, `Ekahanui, in subgulch on S side of `Ekahanui, diverse mesic forest with *Alectryon*, *Elaeocarpus*, *Pouteria*, *Antidesma*, *Pisonia*, *Charpentiera*, *Melicope*, *Freycinetia*, *Claoxylon*, *Hibiscus*, *Pipturus*, *Passiflora*, *Labordia*, *Platydesma*, *Athyrium*, *Neraudia*, 2200 ft [670 m], 28 Jun 1987, *S. Perlman & J. Obata 6107* (neotype, here designated: PTBG-015093!; isoneotypes: MO, US!).

Schiedea kaalae var. *acutifolia* Sherff, Amer. J. Bot. 30: 607. 1943.—TYPE: HAWAIIAN ISLANDS. O`AHU: [Ko`olau Mountains] Hau`ula Valley, on wet precipice at water fall, 10 Apr 1927, *O. Degener & W. Bush 5931* (holotype: CU!, photo: F; isotypes: F! G! GH! MICH NY! P! US!).

Coarse herb from a woody caudex; stems, 0.2–1.2 (–5) dm long, thick and somewhat fleshy, purple, ± ascending, unbranched, tortuous, internodes greatly compressed, leaves tufted at apex, glabrous. Leaves opposite; blades (8–) 14–24 cm long, (1.5–) 2–5 (–6) cm wide, thick and coriaceous, usually somewhat irregular, either curved or concave, elliptic-oblanceolate to nearly spatulate, with only the midvein evident, the midvein ± excentric, glabrous, margin entire, apex acuminate, acute, or obtuse with a mucronate tip, base long-attenuate; petioles 0–3 cm long, purple, at least near the stem. Inflorescence terminal, with 20–300 flowers, 20–40 (–60) cm long, diffuse, erect, the tertiary and higher order internodes ascending or appressed; bracts subulate, purple, ciliate at least toward base, those of central axis 2–4 mm long, those of branches and flowers 1.5–3 mm long; pedicels 7–10 mm long, elongating to 15 mm long in fruit, conspicuously asymmetrically flattened. Flowers hermaphroditic. Sepals 3.5–4.1 mm long, lanceolate, purple, opaque, completely reflexed, the proximal 1/2 convex, producing an elongate low bulge, the distal part concave to shallowly navicular, usually slightly twisted, abaxial side glabrous, margin scarious, sparsely ciliate, especially toward the apex, apex attenuate. Nectary base 1–1.2 mm long, whitish purple to pale yellow, the nectary shaft 2.3–3.2 mm long, straight to gently recurved, at 90° angle to the axis, apex bifid to slit on the abaxial side. Stamens 10; filaments dimorphic, the antisepalous whorl 4.3–4.5 mm long, the alternate whorl 3.7–4 mm long; anthers 0.7–0.95 mm long, subequal, yellow. Styles 3 (–4). Capsules ca. 3.5–5 mm long, ca. 1.6–2.2 mm in diameter, narrowly ovoid. Seeds 1.0–1.1 mm long, orbicular-reniform, slightly compressed, transversely rugose. Chromosome number: 2n = probably 60 (*Takeuchi 3587*). Figs. 2G, 31.

Distribution (Fig. 32). O`ahu, Punalu`u and Kaipapa`u, Ko`olau Mountains, and Makaleha, Pahole Gulch, Mokule`ia, Pu`uhapapa, and Huliwai, Wai`anae Mountains; diverse mesic forest to perhaps wet forest on steep slopes in shaded sites; 410–730 m.

ADDITIONAL SPECIMENS EXAMINED. **O`ahu.** Ko`olau Range, *Degener 5966* (coll. W. Bush) (BISH); Mauka of Peacock Flats, Mokule`ia, *Degener & Degener 27924* (F); Kaipapa`u Valley, *Degener et. al. 4153* (BISH [2], NY); along Kaipapa`u stream, [21°35′40″N, 157°56′5.1″W], *Degener et. al. 5925* (F, GH, MO, NY, P, S, US); Mokule`ia, slopes of Ka`ala, *Forbes 1771.O* (BISH [2], MO, NY); Mt. Ka`ala, N slope, 1871, *Hillebrand s.n.* (GH); Kalua`a Gulch, (Lihue), above Schofield, between Pu`ukanehoa and Hapapa, [21°27′54.6″N, 158°6′6.9″W], *Hutchison et. al. 7368a* (UC); Ko`olauloa District, Makaua (Olona) Stream, *Lau 850* (BISH); Makaleha, [21°31′20.5″N, 158°10′16.6″W], *Lydgate s.n.* (BISH); Pahole Gulch, Mokule`ia Forest Reserve, first sub-gulch to the E, near gully floor on steep rock face, [21°32′41.3″N, 158°11′17.1″W], *Obata et. al. 344* (BISH); Hidden Valley, main fork of valley under Kukui tree, *Perlman & Obata 5419* (BISH, PTBG); Hidden Valley, 200 yards up S fork from main stream, [21°35′3.8″N, 157°55′28.6″W], *Perlman & Obata 5421* (PTBG); northernmost subgulch of Kalua`a Gulch below Pu`uhapapa, *Perlman & Obata 5812* (BISH, PTBG); Huliwai, W slope, [21°27′10.8″N, 158°5′39.3″W], 8 May 1933, *Russ s.n.* (BISH); Punalu`u, 26 March 1933, *Swezey s.n.* (BISH); near Pohakea, along rock face in dense shade, [21°25′32.2″N, 158°5′32.5″W], *Takeuchi 3417* (BISH); near Pu`umaialau, [21°26′8.7″N, 158°5′25.3″W], *Takeuchi 3587* (BISH); Kaua, *Takeuchi & Paquin 3438* (BISH [2]), *Takeuchi & Paquin 3442* (BISH); Wai`anae Range: Honouliuli contour, Mauka slopes in general vicinity of Gunsight Pass, *Takeuchi & Tate 3574* (BISH [2]), *Takeuchi & Tate 3575* (BISH); gulch SE of [Pu`u] Hapapa, [21°27′57.7″N, 158°6′13.3″W], *Warshauer 1056* (BISH).

CULTIVATED. **O`ahu.** Ko`olau Range: Hidden Valley, Mar 1990, *Obata s.n.* [cult. *Weller & Sakai 881*] (US), *Weller & Sakai 881* [cult. *Wagner & Shannon 6801*] (BISH, PTBG, US); Wai`anae Range: E of Pu`ukaua, near Pu`umaialau, *Takeuchi 3587* [cult. 1987, *Weller & Sakai s.n.*] (US); Kalua`a Gulch, S of Pu`uhapapa, 29 Jul 1991, *Weller & Sakai s.n.* [cult. *Weller & Sakai 892*] (US); Pahole Natural Area Reserve, *Weller & Sakai 904* [cult. *Wagner & Shannon 6804*] (BISH, PTBG, US).

Schiedea kaalae is distinctive in its habit, a perennial herb with greatly compressed internodes. Sherff recognized two varieties: var. *kaalae*, the leaves 3–6.5 cm wide, the apex rounded and with a mucronate tip, and sepals ca. 4 mm long; and var. *acutifolia*, the leaves narrower, with an acute apex, and sepals ca. 3 mm long. Several populations are now known where both variants are represented, and thus they are not given formal recognition here (also in Wagner et al. 1990).

Fewer than 100 individuals are now known of *S. kaalae*, which appears to be especially susceptible to habitat degradation by feral goats and pigs. It was federally listed as endangered in 1991 (Ellshoff et al. 1991).

The specific epithet refers to Wawra’s type locality, Mt. Ka`ala.

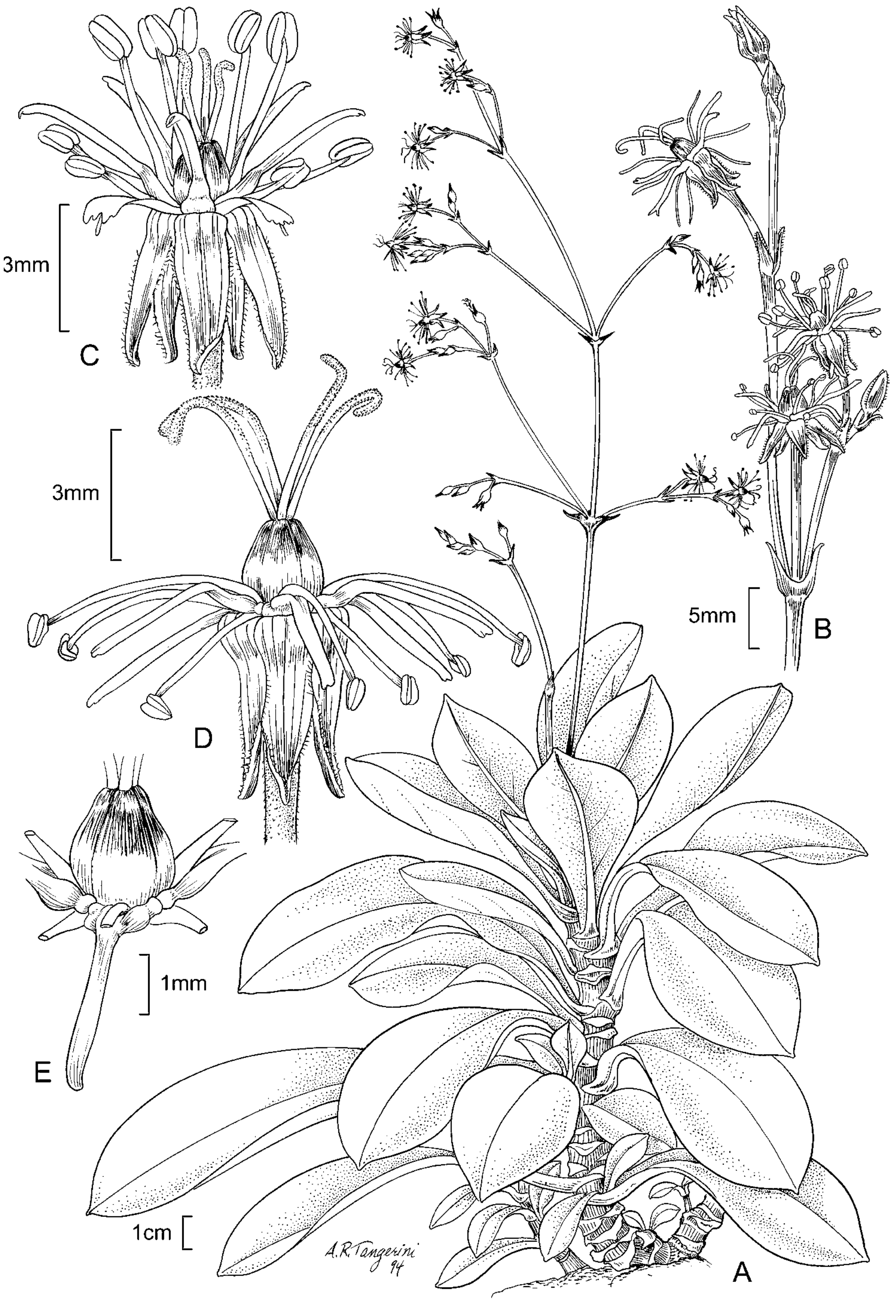

FIG. 31. *Schiedea kaalae* (cult. from *Takenchi 3587*). A. Habit. B. Portion of inflorescence. C. Flower in early anthesis, male stage; this flower shows the rare expression of small petals (at least in cultivation). D. Flower in later anthesis, female stage. E. Flower, sepals removed to show nectary shafts.

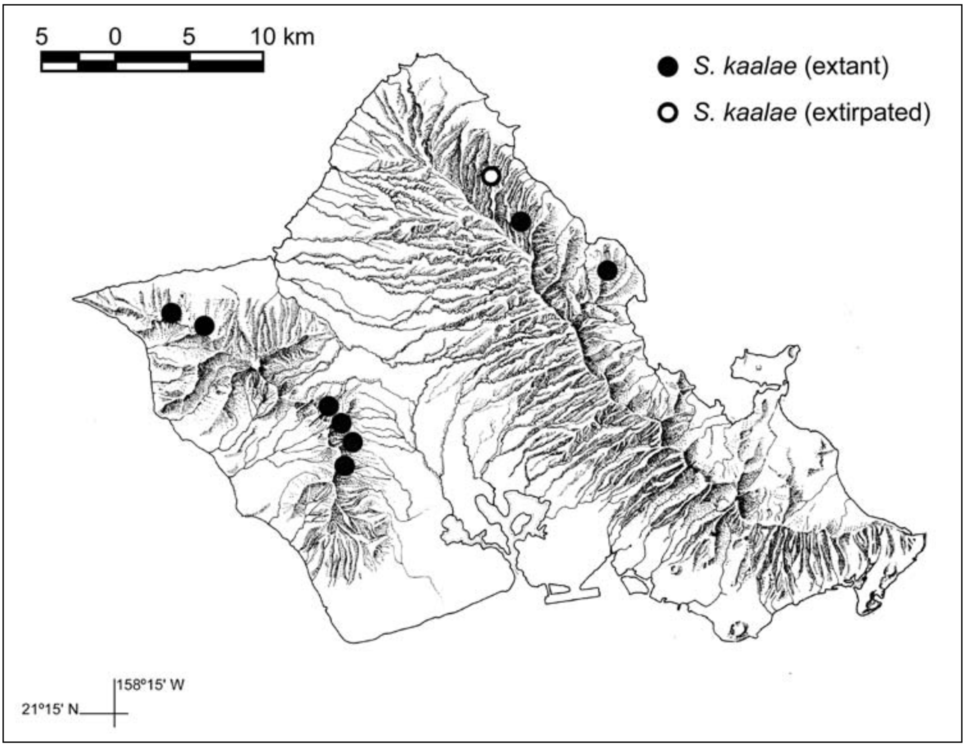

FIG. 32. Distribution of *Schiedea kaalae*.

17. Schiedea implexa (Hillebrand) Sherff, Amer. J. Bot. 30: 607. 1943. *Schiedea nuttallii* var. *implexa* Hillebrand, Fl. Hawaiian Isl. 31. 1888.—TYPE: HAWAIIAN ISLANDS. MAUI: West Maui, *E. Bishop s.n. p.p.* (lectotype, here designated: K!; see discussion below).

Subshrubs ca. 3–6 dm tall; stems probably erect or ascending, branched, glabrous except sometimes in the inflorescence. Leaves opposite; blades 10–18 cm long, 0.8–2 cm wide, narrowly lanceolate, the uppermost linear, chartaceous when dry, with only the midvein evident, the midvein ± slightly excentric, apex attenuate; petioles 0–0.3 cm long. Inflorescence terminal, with 20–150 flowers, ca. 20–27 cm long, diffuse, glabrous or sparsely puberulent; bracts green, oblong-lanceolate to subulate, those of central axis 2–70 mm long, those of branches and flowers 1–2 mm long; pedicels 20–40 mm long, filiform. Flowers apparently hermaphroditic. Sepals 2–3 mm long, narrowly lanceolate, apparently purple, probably strongly reflexed and convex in the proximal 1/4, the distal part concave or shallowly navicular, oriented at 5° to 30° angle to the pedicel, abaxial side glabrous, margins conspicuously scarious, ciliate, apex attenuate. Nectary base 3.5–4 mm long, apex bifid. Stamens apparently 10; filaments ca. 6–7 mm long; anthers unknown. Styles 3. Capsules ca. 4 mm long, oblong-ovoid, sometimes strongly exserted from calyx. Seeds unknown. Chromosome number unknown. Fig. 33.

Distribution (Fig. 34). East Maui, known from only five collections from `Auwahi to

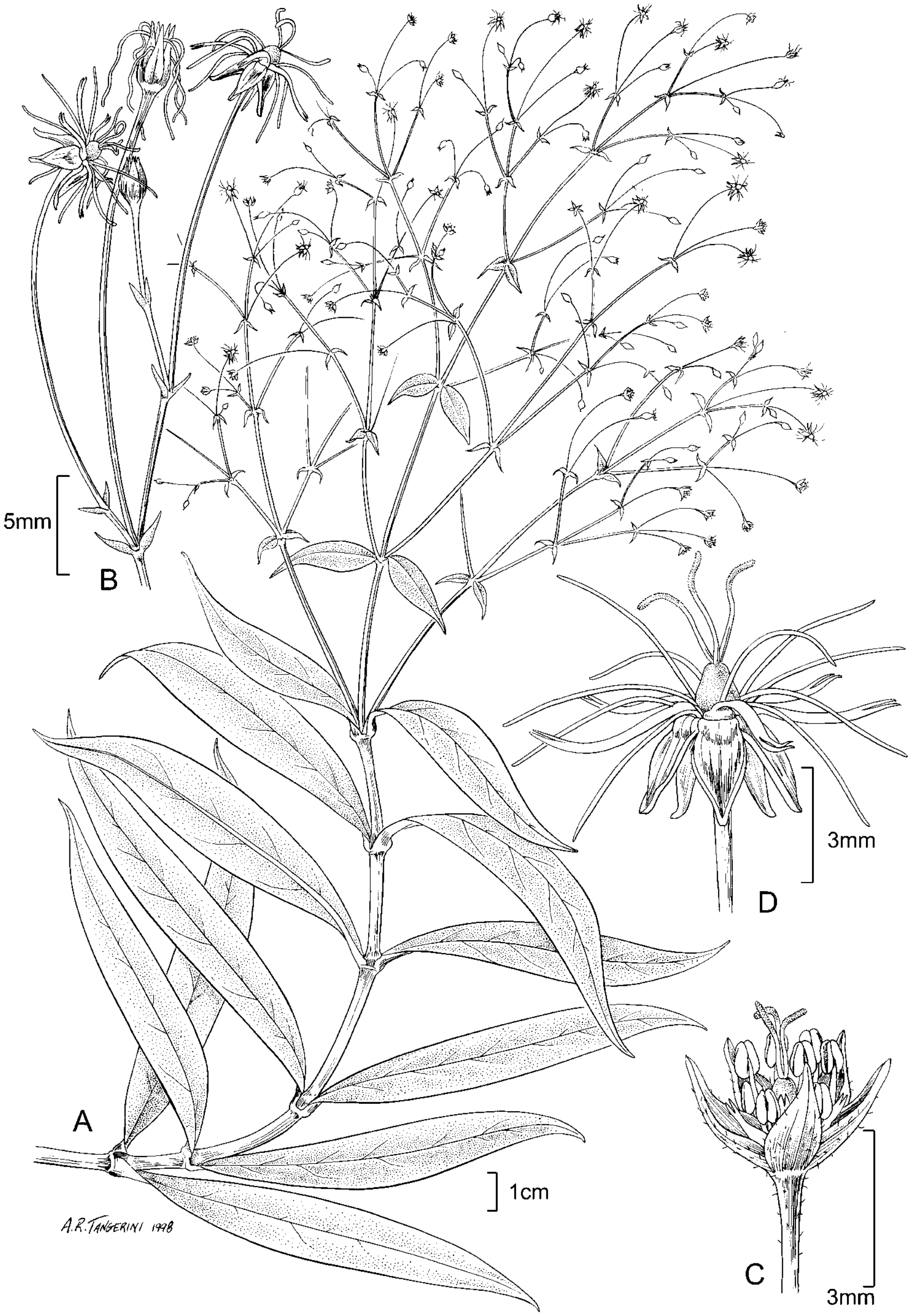

FIG. 33. *Schiedea implexa* A. Habit. B. Inflorescence. C. Flower in early anthesis, male stage. D. Flower in later anthesis, female stage. (Based on: A, *Hillebrand s.n.* [K]; B, *Rock 8643* [GH, sheet 2]; C, D, *Rock 8643* [BISH].)

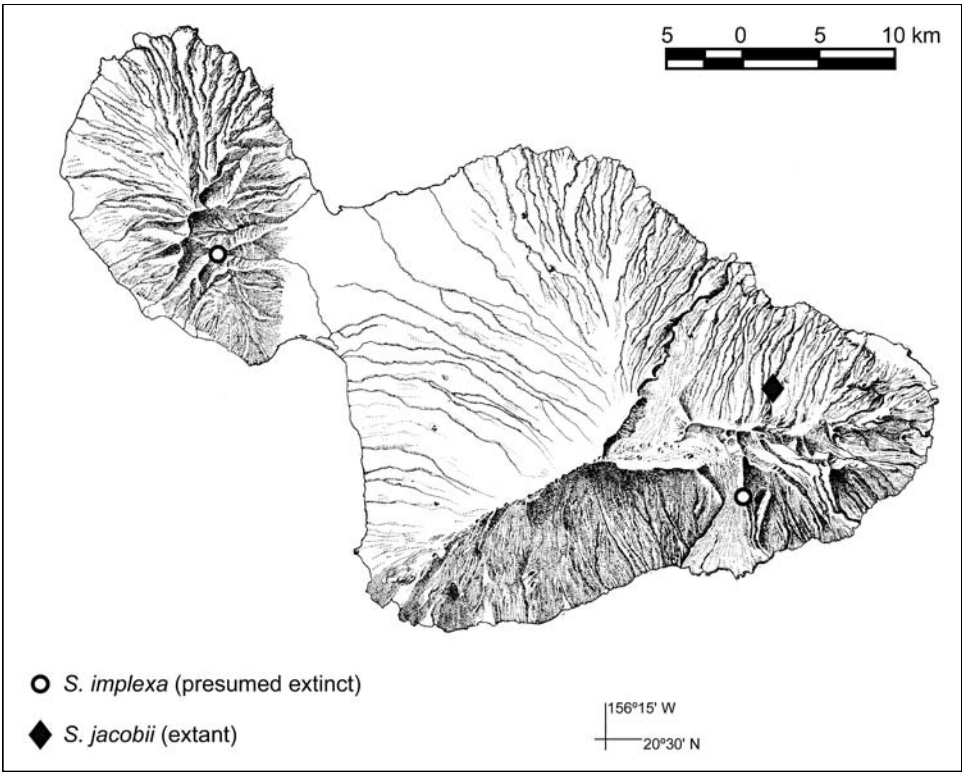

FIG. 34. Distributions of *Schiedea implexa* and *Schiedea jacobii*. (The West Maui locality for *S. implexa* is based on a single collection without precise locality information.)

Kaupo Gap; on cliff walls, probably in mesic forest; a single collection from somewhere on West Maui (lectotype); from ca. 1525 m.

ADDITIONAL SPECIMENS EXAMINED. **Maui.** S Haleakala, *Hillebrand 432* (K); *Menzies 3* (MO); Haleakala, Kaupo, [20°41′43.9″N, 156°8′17.2″W], *Rock 8643* (BISH [3], GH [2], NY); East Maui, Haleakala, Nov 1910, *Rock s.n.* (NY); 1838, *U.S. Explor. Exped. s.n.* (US).

Schiedea implexa is distinctive in its terminal inflorescences, which bear the many flowers on filiform pedicels.

The species was last collected in 1910 (*Rock 8643*) and is presumed to be extinct (Wagner et al. 1990; Wagner et al. 1999b), but it may still be extant, because its specific habitat has not been searched in recent decades. Steve Perlman and Ken Wood looked for this species in 1995 without success; however, recent study of all of the notes made by Joseph Rock suggest that *S. implexa* may be restricted entirely to vertical cliffs, which are nearly impossible to search thoroughly.

Hillebrand cited both East and West Maui collections, and a photo of a sheet at B, now destroyed, shows both a Hillebrand collection from East Maui and a Bishop collection from West Maui mounted together. Sherff (Brittonia 5: 315. 1945) indicated that the B sheet likely is the type, but he only saw a US sheet, which is a duplicate of the Hillebrand collection only. We have selected the best extant material as the lectotype; it is the pubescent specimen mentioned by Hillebrand as obtained from West Maui. Unfortunately, it seems that when both collections were sent to Kew, a label for the Bishop collection from West Maui was omitted or lost. The label on the K sheet is associated only with the small, glabrous inflorescence in the upper right-hand corner of the sheet; it reads "[East Maui,] Haleakala South, Aug. 1858, *Hillebrand s.n.*" Additional small branches of the Hillebrand syntype from East Maui are known (fragment BISH-501313! BM! K-pro parte! US!, photo of US syntype: F!).

The specific epithet is taken from the Latin adjective *implexus* ("entwined," "interwoven") and refers to the delicate intertwined flowers of the inflorescence of this species.

18. Schiedea jacobii W. L. Wagner, Weller & Medeiros in W. L. Wagner et al., Novon 9: 284. 1999.—TYPE: Specimens taken from plants cultivated from seeds at the greenhouse of the University of California at Irvine, 1997, *S. Perlman, K. Wood, A. Medeiros, R. Hobdy, & B. Evanson 14807[cult]* (holotype: US-3351775!; isotypes: BISH! CANB! CHR! K! MO! NY! PTBG!). [Source of seed: Hawaiian Islands, East Maui, Hanawi, Kuhiwa unit, east of Hanawi Stream, between Hanawai stream and Kuhiwa drainage [20°45′N, 156°07′40″W], 6340 ft [1930 m], east-facing slope, ca. 20 ft below ridge top, in *Metrosideros* montane wet forest, 22 Jun 1995, *S. Perlman, K. Wood, A. Medeiros, R. Hobdy, & B. Evanson 14807*.]

Perennial herbs or subshrubs, pale yellowish green throughout (at least in cultivation); stems 4–7.6 dm long, ascending to sprawling when longer, conspicuously quadrangular, the angles weakly winged, glabrous throughout. Leaves opposite; blades 4.5–10.5 cm long, 1.4–2.6 cm wide, coriaceous, lanceolate to oblong-elliptic, with only the midvein evident, the midvein ± slightly excentric, margin slightly thickened and weakly revolute, apex acute to attenuate, base acute to obtuse; petioles 0.4–0.8 cm long, the base often flared at juncture with stem and the leaf pair slightly connate. Inflorescence terminal, with 10–70 flowers, 40–50 cm long, weakly diffuse, the lateral branches 11–18 cm long, ascending, each with 25–35 flowers; bracts yellowish green, foliaceous, and nearly as large as the leaves in the lower portions of the central axis and the lateral branches, those in the upper part of the inflorescence and subtending the flower narrowly lanceolate to subulate, 3–11 mm long; pedicels 3–8 mm long at anthesis, elongating slightly in fruit, but none over 9 mm long, conspicuously asymmetrically flattened. Flowers hermaphroditic, facultatively autogamous. Sepals 3.9–4.2 mm long, lanceolate, dull yellowish green, greener toward the center, sometimes with purple toward the apex, thick and opaque, ascending and concave to shallowly navicular toward the apex, oriented at 90° to 135°angle to the pedicel, abaxial side smooth and rounded, glabrous, margins weakly scarious, sparsely ciliate, apex attenuate. Nectary base 0.4–0.5 mm long, somewhat broadened and flattened at base, dark yellow, the nectary shaft 1.4–1.8 mm long, apex deeply bifid. Stamens 10; filaments weakly dimorphic, the antisepalous whorl 3.2–3.5 mm long, the alternate whorl 2.8–3.0 mm long; anthers 0.3–0.4 mm long, subequal, yellow, dehiscing after flower opens. Styles (3–) 4–5, stigmas receptive when flower opens. Capsules 3.7–4.2 mm long, ovoid. Seeds ca. 16–22 per capsule, 0.7–0.9 mm long, suborbicular, asymmetrical, compressed brown, remaining coherent as a unit and persistent on the placenta after dehiscence of capsule, seeds eventually dispersing (or perhaps germinating *in situ* in the wild), the surface rugose. Chromosome number unknown. Figs. 2H, 35.

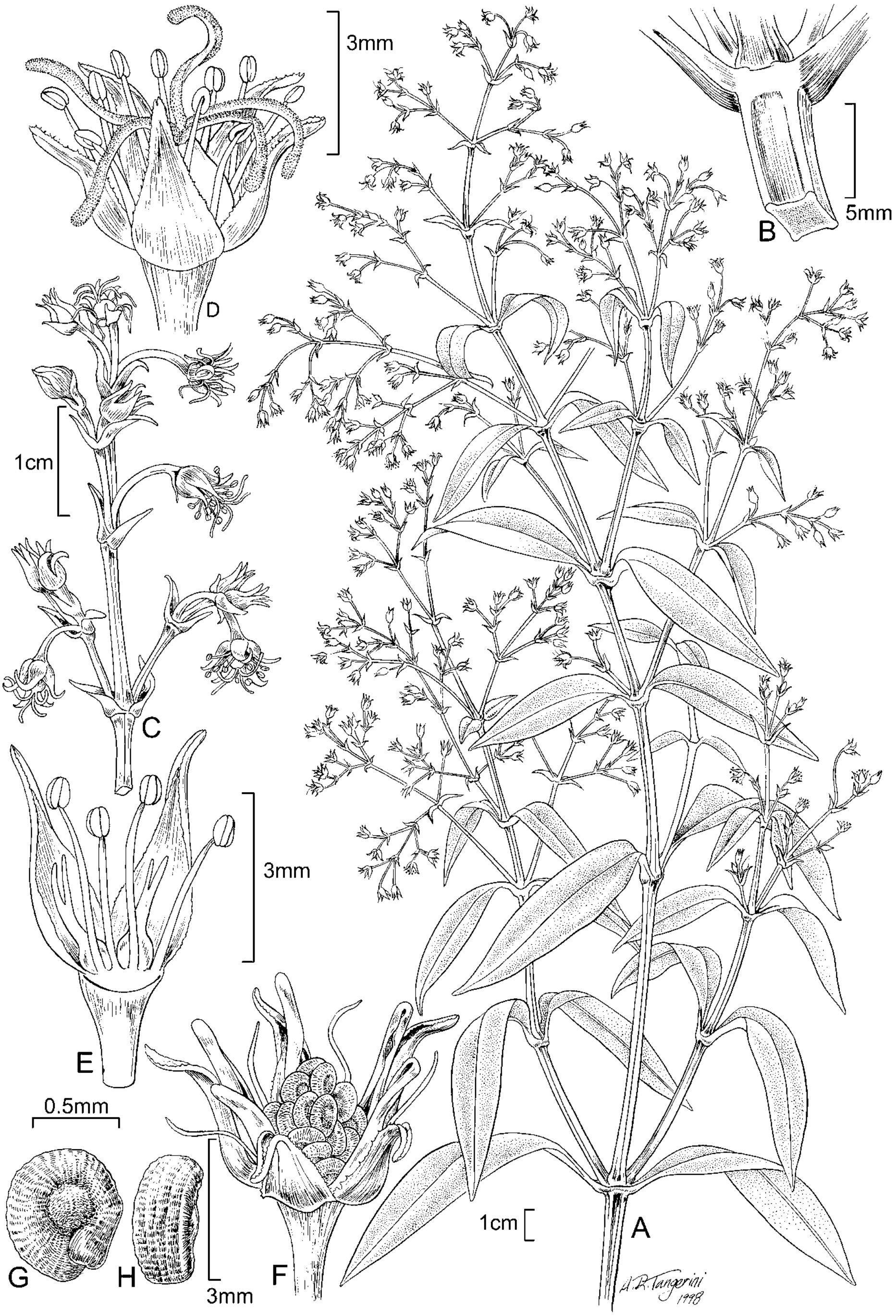

FIG. 35. *Schiedea jacobii* (cult. from *Perlman et al. 14807*). A. Flowering stem. B. Cross section of stem. C. Portion of inflorescence. D. Flower, showing stamens ready to dehisce and styles elongated and receptive. E. Flower, adaxial view of sepals with nectaries and stamens. F. Dehisced capsule exposing the mass of persistent seeds, surrounded by the sepals. G, H. Seeds.

Distribution (Fig. 34). East Maui, known only from the wet cliffs of Hanawi, Kuhiwa unit, east of Hanawi stream, between Hanawai stream and Kuhiwa drainage at 1930 m.

ADDITIONAL SPECIMENS EXAMINED. **Maui.** East Maui, Hanawi, Horseshoe Ridge, off east unit, [20°45′N, 156°07′40″W], 6340 ft, on rock face, *Medeiros & Jacobi 798* (BISH, US).

Schiedea jacobii, with its fleshy stems, large leaves with one principal vein, open inflorescence, and attenuate sepal apex, is morphologically most similar to *S. nuttallii* and *S. laui*; however, current molecular analyses do not resolve this group (Plate 2). It differs from *S. nuttallii* most conspicuously in characters related to the breeding system, especially those associated with autogamy. *Schiedea jacobii* differs from *S. laui* in producing chasmogamous rather than cleistogamous flowers and in retaining seeds on the placenta after capsule dehiscence. Several characters of *S. jacobii* are the same as in *S. diffusa*, but seem to be homoplasious and based on the evolution of autogamy in a wet forest environment. Support for this homoplasy hypothesis comes most strongly from seed morphology; seeds of *S. diffusa* are large and smooth, while those of *S. jacobii* are similar to those of many other species of *Schiedea* in their smaller size and rugose surface. *Schiedea diffusa* is a large vine, but *S. jacobii* is a small, upright or sprawling shrub.

Experimental crosses in the greenhouse and observations of pollen tube growth in styles indicate that *S. jacobii* is autogamous. Emasculated flowers failed to produce capsules. In unmanipulated flowers numerous pollen tubes were observed in the styles (Wagner et al. 1999a). Interspecific hybrids of *S. jacobii* were obtained, showing that this species is sexual. Together these results indicate that the abundant capsule production of this species in the absence of cross-pollination is likely to result from self-fertilization rather than apomixis. Autogamy is facilitated by the synchrony of pollen dispersal and stigma receptivity, a feature unusual in outcrossing species of *Schiedea*, which are usually strongly protandrous. *Schiedea diffusa*, which occurs in very wet forests, is also autogamous.

The type locality is within a protected Hawaii State Natural Area Reserve. The habitat is a montane wet *Metrosideros* forest. The only known population consisted of nine plants when first discovered in 1992, but in 1995 shoots representing only two to four plants could be located. All of the living plants in 1995 were confined to one small area; a separate population downhill noted in 1992 was not relocated. Other populations may occur in this rugged, largely inaccessible region of East Maui, especially on wet cliffs. Degradation of forests in the Hanawi area by alien animals appears to be the major threat to *Schiedea jacobii*; the species is considered to be endangered by Wagner et al. (1999b).

The specific epithet honors the discoverer of the species, James D. Jacobi, Biological Resources Division, Pacific Islands Science Center, who has made significant contributions in vegetation ecology and alien plant management in the Hawaiian Islands.

19. Schiedea hawaiiensis Hillebrand, Fl. Hawaiian Isl. 33. 1888.—TYPE: HAWAIIAN ISLANDS. HAWAI`I: Waimea, *Lydgate s.n.* (holotype: B, destroyed).—HAWAI`I: Pohakaloa Training Area, W side along MPRC access rd at power pole #402, *Metrosideros [polymorpha]* forest with *Zanthoxylum hawaiiense*, *Dodonaea [viscosa]*, and *Tetramolopium consanguineum*, 1200 yr old pahoehoe lava, 1640 m, 3 Dec 1996, *Gon III & Tierney s.n.* (neotype, designated by Herbst & Wagner, 1999: US-3335666!).

Reclining or sprawling vines; stems 3–7 dm long (in cultivation eventually to 15 dm or more long), conspicuously compressed-quadrangular, the angles weakly winged, pale yellowish green throughout or stems purple-tinged in lower portion of the plant (at least in cultivation), glabrous throughout, except sparsely puberulent at the base of the internodes of the inflorescence and on the margins and adaxial surface and margins of bracts and sepals. Leaves opposite; blades 4–7.8 cm long, 1.7–3 cm wide, thinly coriaceous, ovate to elliptic-ovate, with only the midvein evident, the midvein ± slightly excentric, purple on lower leaves, margin very slightly thickened, apex acuminate to acute, base acute to obtuse; petioles 0.5–0.7 cm long, the base often slightly flared at juncture with stem and the leaf pair slightly connate. Inflorescence terminal, with 12–50 flowers, 20–40 cm long, diffuse, the branches 8–20 cm long, each branch with 5–12 flowers, sparsely puberulent with translucent to whitish hairs 0.3–0.5 mm long at the base of the internodes of the inflorescence; bracts yellowish green, foliaceous, the lower ones foliaceous and nearly as large as the leaves, those in the upper part of the inflorescence and subtending the flower narrowly subulate, 3–5 mm long, ciliate and puberulent on the adaxial surface with hairs 0.1–0.2 mm long; pedicels 4–10 mm long at anthesis, elongating slightly in fruit, conspicuously asymmetrically flattened. Flowers hermaphroditic, usually pendent, apparently facultatively autogamous. Sepals 3–4 mm long, lanceolate, dull yellowish green, purple-tinged, or purple, opaque, concave to shallowly navicular toward the apex, oriented at 90° to the pedicel at base, later in anthesis abruptly curved upward in upper 2/3 at 130° to 160° angle to the pedicel, often strongly inrolled during late- and post-anthesis, abaxially smooth and rounded, puberulent toward base, usually with scattered hairs primarily toward the margin, also adaxially moderately puberulent with hairs 0.1–0.2 mm long, margins weakly scarious, ciliate, apex attenuate. Nectary base 0.7 mm long, broadened and flattened at base, dark yellow, the nectary shaft 1.8–2.25 mm long, apex deeply bifid. Stamens 10; filaments dimorphic, the antisepalous whorl 3.5–4 mm long, the alternate whorl 2.4–2.8 mm long; anthers subequal, those of the antisepalous whorl 0.65 mm long, of the alternate whorl 0.55 mm long, yellow. Styles 3–4, the stigmatic area extending nearly the full length of the style. Capsules 3.5–4 mm long, ovoid. Seeds 9–20 per capsule, 1–1.3 mm long, reniform-suborbicular, compressed pale brown, the margins of the cells of the testa slightly convex, the raised cells forming low transverse ridges across the seed surface. Chromosome number unknown. Figs. 2I, 3M, N, 36.

Distribution (Fig. 37). Hawai`i, originally known only from the type collected near Waimea; a single individual was discovered in 1996 in the Pohakaloa Training area on the western side of the island in a montane dry *Metrosideros polymorpha* forest with *Zanthoxylum hawaiiense*, *Dodonaea viscosa*, and *Tetramolopium consanguineum* on a pahoehoe lava flow about 1200 years old at 1640 m.

CULTIVATED. **Hawai`i.** Pahakuloa Training Area, s.d., *PTA personnel s.n.* [cult. *Weller & Sakai 932*] (BISH, F, GH, K, MO, NY, PTBG, US).

Schiedea hawaiiensis was known only from the type, collected by Hillebrand near Waimea, Hawai`i, and deposited at B but now destroyed. Without any material to examine, and despite the discrepancies in Hillebrand's description of *S. hawaiiensis* and characters of *S. diffusa*, notably the habit, leaf shape, inflorescence, and seed surface morphology, Wagner et al. (1990) considered *S. hawaiiensis* and *S. diffusa* conspecific. In part because there were no taxa other than *S. diffusa* then known from the island of Hawai`i, Hillebrand's description was assumed to be inaccurate. When we examined the 1996

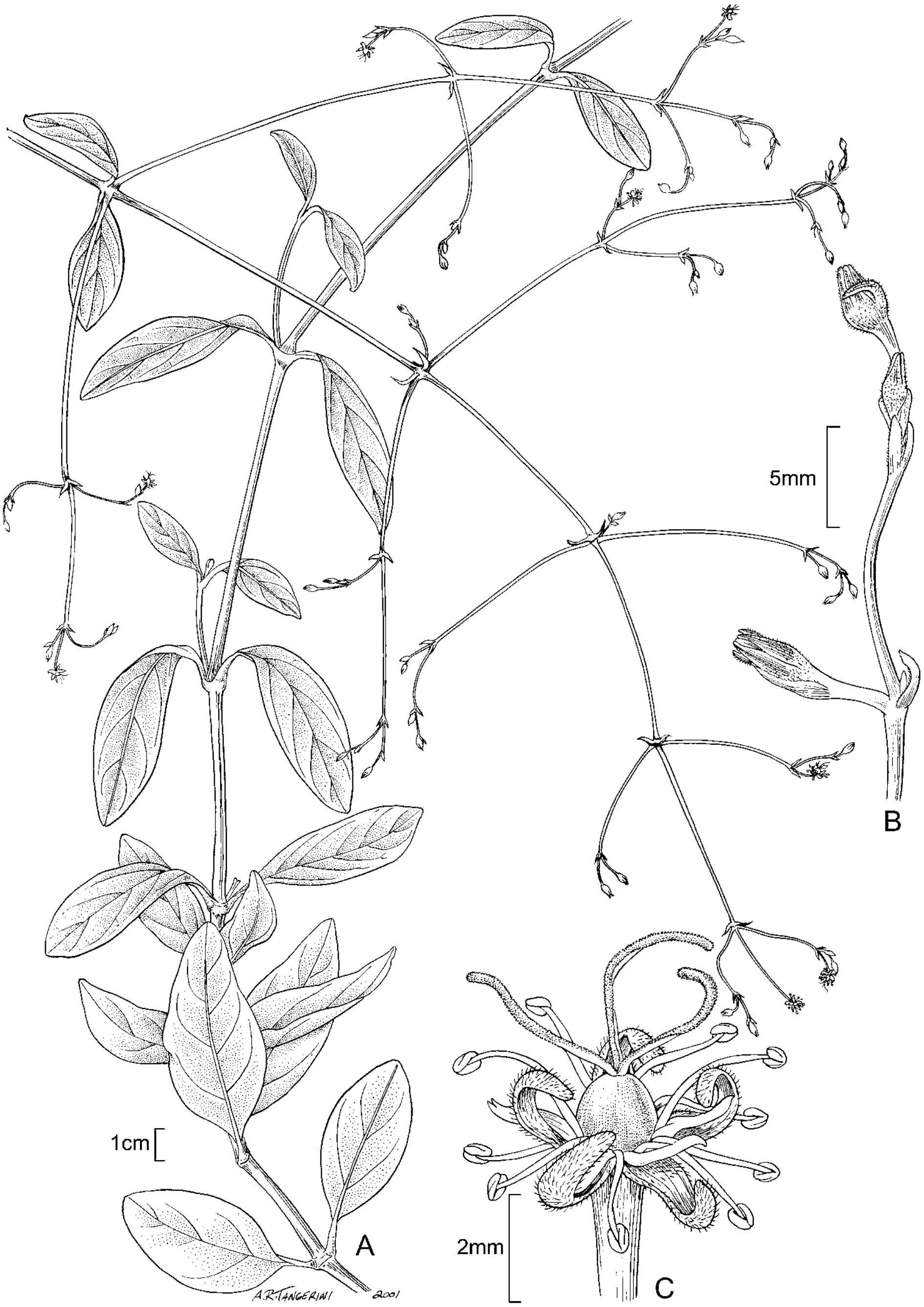

FIG. 36. *Schiedea hawaiiensis* (cult. from *Weller & Sakai 932*). A. Habit. B. Portion of inflorescence. C. Flower, early anthesis, showing receptive stigmas and anthers ready to dehisce.

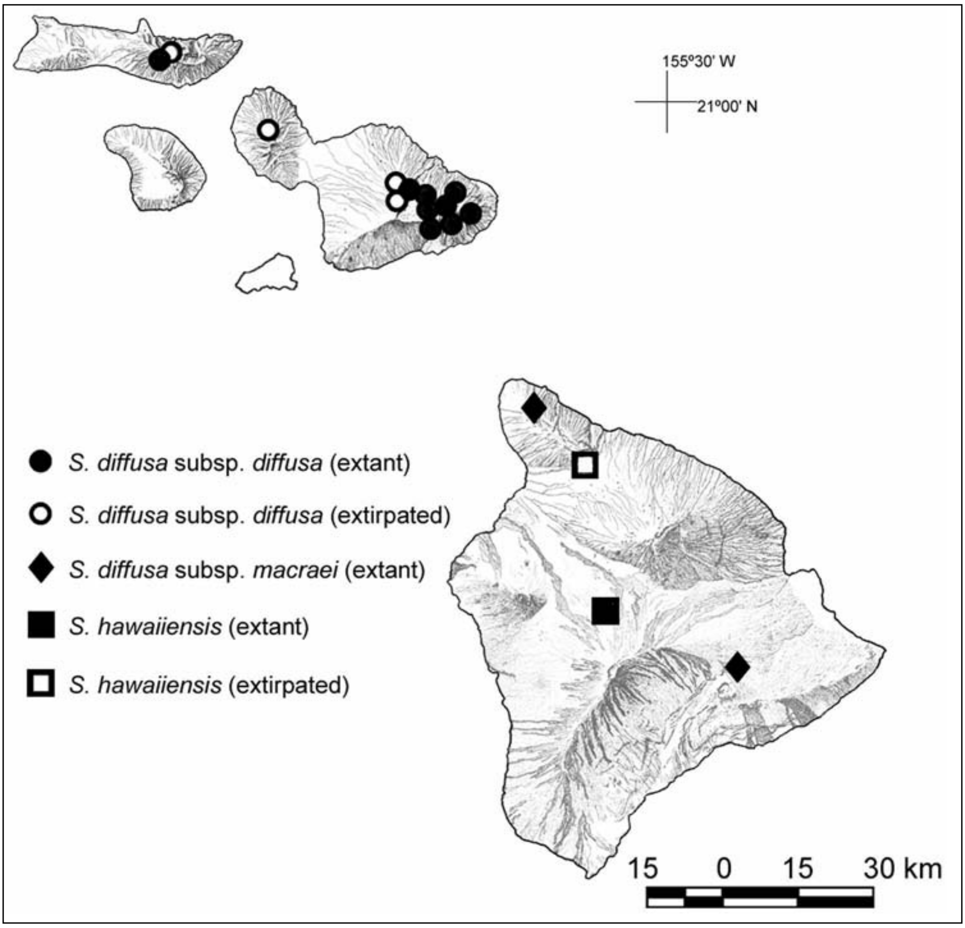

FIG. 37. Distribution of *Schiedea diffusa* and *S. hawaiiensis.* (The approximate location of the extinct population of *S. hawaiiensis* is based on Lydgate's collection from Waimea.)

collection from the Pohakaloa Training area, we thought it represented a new island record for *S. pubescens*, albeit a depauperate specimen. When plants cultivated from seeds from this collection were grown, it was clear as soon as the first few sets of leaves appeared that the collection did not represent *S. pubescens*. The plants had narrower leaves and grew much more quickly to flowering stage than any individuals of *S. pubescens*, which typically grow vegetatively for a long period before flowering. When the plants flowered, it was apparent that Hillebrand's original description of *S. hawaiiensis* fit this new collection exactly. Herbst and Wagner (1999) designated the new collection a neotype for the name *S. hawaiiensis*.

Flowers of greenhouse-grown plants of *S. hawaiiensis* often produce odd mutations, such as styles arising from anthers, extra nectaries and stamens, completely divided nectary shafts, atypically formed nectaries, and an extra small ovary with a single style growing laterally from the base of the main ovary. Abnormalities may be associated with inbreeding related to the small population size.

Schiedea hawaiiensis is the only dry-site species with an autogamous breeding system. Selfing is facilitated by wind; when pollen is shaken from the anthers, it is deposited on the stigma. The species is apparently not adapted to cross-pollination via wind, because there are so few pollen grains per flower. Most species of *Schiedea* occurring in dry habitats have evolved sexual dimorphism rather than autogamy. Mutations to male sterility may not have occurred in *S. hawaiiensis*; sexual dimorphism does not occur in any closely related species.

Because only one individual is now known to occur in the wild, *S. hawaiiensis* is clearly extremely endangered, and will probably go extinct in a relatively short time in the wild.

The specific epithet refers the island of Hawai`i, where the species is endemic.

20. Schiedea pentandra W. L. Wagner & E. Harris, Amer. J. Bot. 87: 159. 2000.—TYPE: HAWAIIAN ISLANDS. O`AHU: Wai`anae Mountains, Huliwai-Kalua`a Ridge, near summit of Kanehoa, 2600 ft [790 m], 21 Jun 1985, *S. G. Weller & A. Sakai 796* (holotype: US-3218732!).

Reclining vines, primary stems 10–60 dm long, apparently occasionally rooting at the nodes, purple or green with a purple tinge, glabrous proximally, puberulent in the inflorescence. Leaves opposite; blades 4.5–11 cm long, (0.8–) 1–2.8 cm wide, coriaceous, narrowly lanceolate, usually somewhat falcate, purple-tinged, especially along the midrib, with only the midvein evident, the midvein excentric, ± purple, occasionally with a few scattered hairs on abaxial side, margin slightly thickened and usually slightly scarious, occasionally with a few scattered hooked hairs ca. 0.1 mm long, apex attenuate to long-acuminate, base cuneate; petioles 0.2–0.9 cm long. Inflorescence terminal, with 26–204 flowers, 30–50 (–150) cm long, diffuse, pendent, moderately to densely puberulent, the hairs purple or purple-tinged, 0.05–0.15 mm long; bracts green, purple-tinged, narrowly lanceolate to subulate, those of central axis 2.5–11 mm long, those of branches and flowers 1.5–3 mm long; pedicels 6–18 mm long. Flowers hermaphroditic. Sepals 2.3–3 mm long, lanceolate, purple, or green with a purple midvein, opaque, strongly reflexed in the proximal 1/4, producing a large transverse bulge, distal part strongly navicular and weakly inrolled toward the apex, oriented at 10° to 30° angle to the pedicel, densely puberulent, margins scarious and densely ciliate, apex long-attenuate. Nectary base 0.5–0.6 mm long, dark yellowish orange or purple-tinged, the nectary shaft 2.25–2.5 mm long, at 90° angle to the axis, apex usually not divided, less developed on one side. Stamens 5, the antisepalous whorl developed and fertile, usually erect at anthesis, the alternate whorl minute and abortive; filaments of fertile stamens 3–3.2 mm long, those of the abortive whorl ca. 0.5 mm long, rarely one developing; anthers 0.5 mm long, yellow, those of the abortive whorl 0.35 mm long, not producing pollen. Styles 3 (–4). Capsules 2.5–3 mm long, ovoid. Seeds 0.9–1.1 mm long, orbicular-reniform, compressed, the surface transversely rugose. Chromosome number unknown. Figs. 2J, 3O, P, 38.

Distribution (Fig. 39). O`ahu, Maunakapu to Mount Ka`ala, Wai`anae Mountains; scattered in diverse mesic forest; 600–920 m.

ADDITIONAL SPECIMENS EXAMINED.**O`ahu.** Palehua-Palikea Trail, [21°24′6.2″N, 158°5′52.7″W], *Bennett & Linney PRC 192* (BISH); Wai`anae District, Palikea, Pu`ukapu, [21°24′17.4″N, 158°5′50.6″W], *Christophersen et. al. 1572* (BISH); probably Wai`anae Range, *Degener 5971* (F); between Wai`anae Valley and summit of Mt. Ka`ala, [21°30′N, 158°9′5.5″W], *Degener & Park 5919* (F); E of Palikea, [21°24′54.1″N, 158°5′5.3″W], *Degener & Park 5922* (F, NY); SE slope of Pu`uhapapa, *Degener et. al. 12361* (B, CU, F, GH, K [2], MIN, MO, NY, P, PH, UC, US); summit ridge NW of Pu`ukanehoa, *Degener et. al. 12736* (B, CU, F, G,

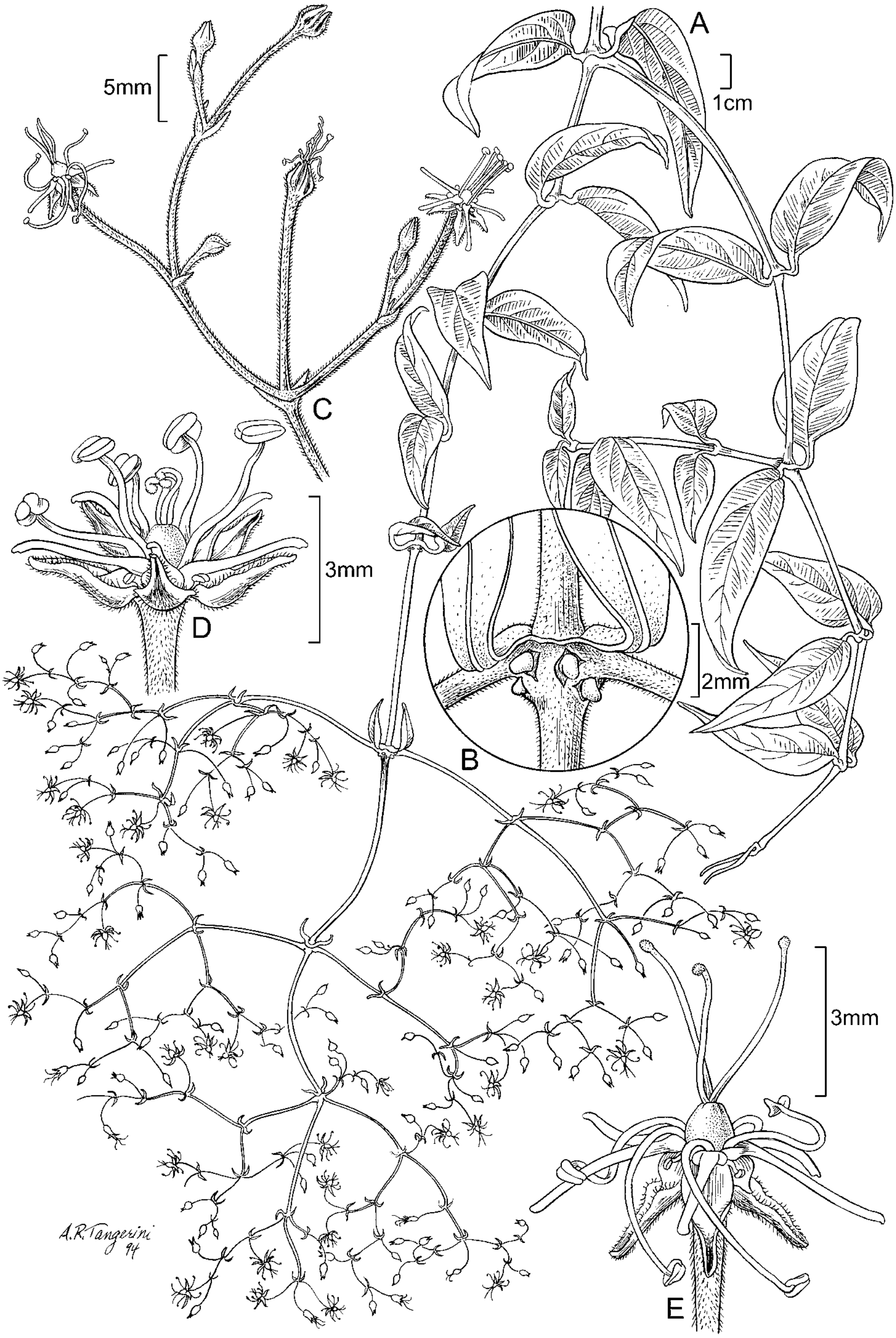

FIG. 38. *Schiedea pentandra* (cult. from *Weller & Sakai 796*). A. Habit. B. Detail of node, showing origin of adventitious roots. C. Detail of inflorescence. D. Flower in early anthesis, male stage. E. Flower in later anthesis, female stage.

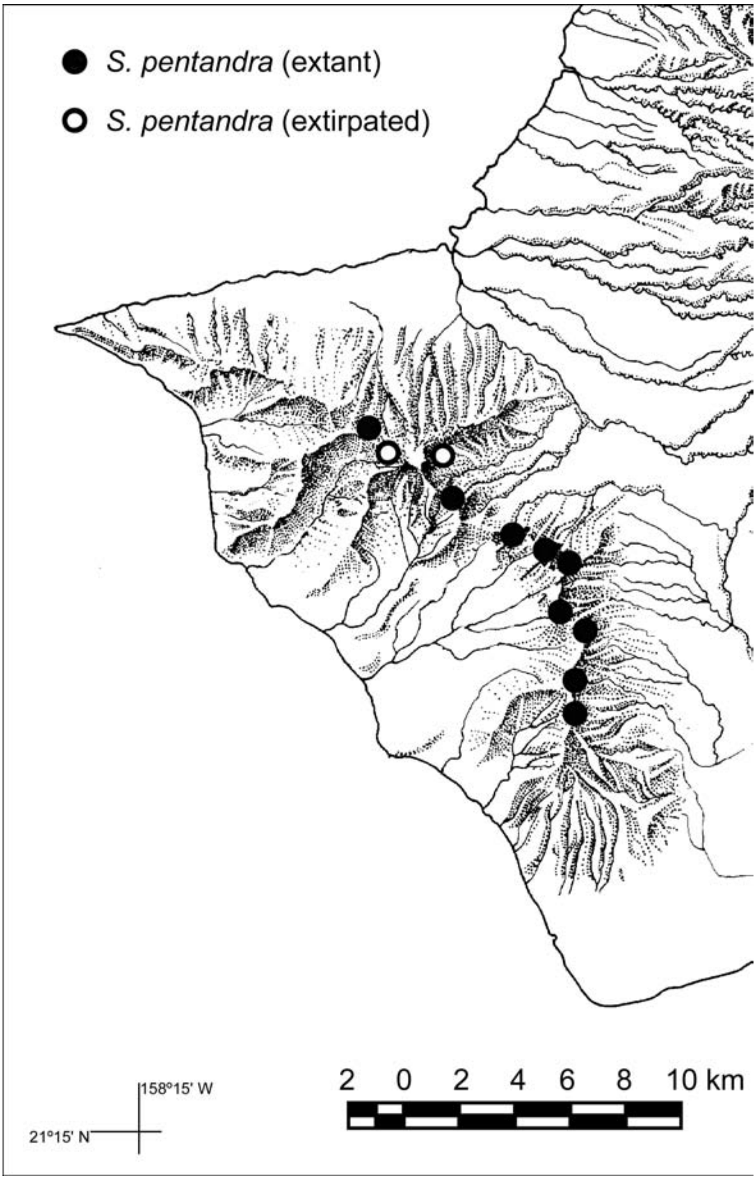

FIG. 39. Distribution of *Schiedea pentandra*. (The northwestern-most locality in East Makaleha Gulch is based on recent field observations of Joel Lau, pers. comm.)

GH, K, MIN, MO, NY, UC, US); summit ridge N of Pu`ukanehoa, [21°27′2.7″N, 158°5′49.7″W], *Degener et. al. 12756* (B, F, GH, K, MO, PH); Palikea, *Fagerlind 6448* (S); Pu`ukaua, summit trail, [21°26′31.2″N, 158°5′55.9″W], *Funk 9* (BISH, HAW [4], PTBG); Maunakapu, *Gillett 1867* (BISH, HAW); from Kuhio Trail (Kanehoa-Hapapa) summit of trail at crest of range, *Gillett 2065* (BISH); Wai`anae District, Pu`ukaua, along the knife-edge trail that leads to the summit, *Gustafson 1318* (BISH, RSA); SE slope of Mt. Ka`ala (Schofield fire-break trail), *Hatheway et. al. 216* (BISH); S fork of central Kalua`a Gulch, on ridge above Joinvillea gully, *Herbst 1133* (BISH); without locality, 1851-1871, *Hillebrand s.n.* (US); Wai`anae Range: below Maunakapu, *Hume 399* (BISH); Schofield Trail to Ka`ala, *Hume 562* (BISH); Kalua`a Gulch (Lihue), above Schofield, between Pu`ukanehoa and Pu`uhapapa, *Hutchison et. al. 7368* (BISH, NY, UC); Pu`uhapapa, [21°27′57.7″N, 158°6′13.3″W], *Krajina 620401125* (BISH); trail to unnamed peak between Pu`uhapapa and Pu`ukanehoa, *Mihata 71* (HAW); Honouliuli Forest Reserve, ridge to Pu`ukaua, [21°26′20.9″N, 158°54′2.7″W], *Nagata 1154* (BISH [2]); `Ekahanui Gulch, on ridge top radiating east from summit of Pu`ukaua, [21°26′24.2″N, 158°5′49.7″W], *Obata et. al. 414* (BISH, PTBG); on ridge top, S Pu`ukaua summit, *Obata et. al. JO(84)-442* (BISH, US); trail between Pu`ukanehoa and Pu`uhapapa leading to top of Pu`uhapapa, *Ochikubo 68* (HAW); Pu`uhapapa, ridge to left of and above Schofield firing range, *Pearsall 515* (A, BISH, P, UC, US); Pu`ali Gulch near Pohakea Pass, 0.25 mi. below summit trail, *Perlman 5456* (BISH, MO, PTBG, UC); S side of Palikea Peak, along trail to Palikea, *Perlman & Obata 5670* (BISH, MO, PTBG [2]); Palikea peak, Lualualei, ridge between Lualualei and Nanakuli, *Perlman & Wood 14057* (PTBG, US); Wai`anae Mts., summit of Pu`ukaua, Lualualei, N of Pu`uukaua, NW-facing cliffs, *Perlman & Wood 14074* (PTBG); Makaha valley, Wai`anae Kai, spur into Makaha valley N of Pu`ukawiwi, off Kamaileunu ridge, *Perlman & Wood 16629* (PTBG); Pualii gulch, TNC Honouliuli Preserve, *Perlman et al. 16496* (PTBG); Hapapa Gulch, April 1930, *Russ s.n.* (BISH); trail to unnamed peak between Pu`uhapapa and Pu`ukanehoa, *Sakai 134A* (HAW); Honouliuli District, E side, Kunia-Pu`ukanehoa Trail, [21°27′54.6″N, 158°6′6.9″W], *Thorne 33338* (RSA); Honouliuli, South Palawai Gulch, *Webster 1442* (BISH), *Webster 1470* (K); S of Honouliuli, Pu`ukanehoa, *Webster 1632* (BISH); South Palawai Gulch, *Wilbur 625* (UC); Kanehoa, Honouliuli Forest Reserve, *Wilbur 767* (US); Lualualei, across via Kolekole contour trail, *Wood & Lau 10586* (PTBG); Wai`anae District, Palikea, ridge between Nanakuli and Lualualei, below Palikea, *Wood et. al. 1936* (PTBG, US); Wai`anae Mts., Pu`ukaua, *Wood et al. 3075* (MO, NY, PTBG, US).

CULTIVATED. **O`ahu.** Wai`anae Range, ridge separating Huliwai and Kalua`a Valleys, near summit of [Pu`u] Kanehoa (type), *Weller & Sakai 796* [cult. 1985, *Weller & Sakai s.n.*] (US).

Schiedea pentandra is unique in the genus in producing only five fertile stamens owing to partial suppression of one whorl during development. The taxon has been known as *S. pubescens* var. *purpurascens*; however, that name was not validly published, because Sherff (1943) failed to provide a Latin description.

Schiedea pentandra is considered to be rare by Wagner et al. (1999b).

The specific epithet is formed from the Greek compound word forms *penta-* (“five-”) and *-andrus* (“male”), and refers to the presence of only five fertile stamens per flower.

21. Schiedea pubescens Hillebrand, Fl. Hawaiian Isl. 31. 1888.—TYPE: HAWAIIAN ISLANDS. MAUI: East Maui, Hamakua, *Hillebrand s.n.* (lectotype, designated by Sherff, 1945: B, destroyed).—MOLOKA`I: Kala`e, 1870, *Hillebrand s.n.* (lectotype, here designated: GH!, photo: F!; isolectotypes: B-destroyed, BM! F!, photo of B isolectotype: BISH!, photo of F isolectotype: F!).

Schiedea pubescens var. *lanaiensis* Sherff, Amer. J. Bot. 30: 606. 1943.—TYPE: HAWAIIAN ISLANDS. LANA`I. Waikeakua [Waiakeakua] by Waiopaa! [Waiapaa], 11 Mar 1922, *G. C. Munro s.n.* (holotype: NY!, photo: F; isotypes: BISH! UC! US!).

Schiedea pubescens var. *degeneri* Sherff, Amer. J. Bot. 30: 607. 1943.—TYPE: HAWAIIAN ISLANDS. MOLOKA`I: branch of Mapulehu Valley, 27 Jul 1928, *O. Degener 5948* (holotype: F-1142023!, photo: F!; isotypes: B! CU! F! GH! MIN! NY-2 sheets! P! PH, UC!, photo of F isotype: F!).

Reclining or weakly climbing vines, primary stems 10–60 dm long, green with a purple tinge or purple-spotted, glabrous proximally, puberulent or glabrate in the inflorescence. Leaves opposite; blades 6–18.7 cm long, 3–7.5 cm wide, coriaceous, lanceolate to ovate or broadly ovate, usually inconspicuously falcate, purple-tinged or purple-spotted, especially along the midrib, with only the midvein evident, the midvein excentric, ± purple, occasionally with a few scattered hairs on abaxial side of the younger leaves, margin slightly thickened, occasionally with a few scattered antrorsely hooked hairs 0.1–0.15 mm long, apex acute to acuminate or sometimes obtuse with a small mucronate tip, base cuneate to broadly obtuse; petioles 0.5–3.1 cm long. Flowers hermaphroditic. Inflorescence terminal, with 30–88 flowers, 30–50 (–150) cm long, open, diffuse, sparsely to densely puberulent in the inflorescence, the hairs purple, 0.15–0.3 mm long; bracts green, purple-tinged or purple-spotted, lanceolate to narrowly lanceolate or the smallest ones subulate, those of central axis 2.5–11 mm long, those of branches and flowers 1.5–3 mm long; pedicels 6–18 mm long. Sepals 2.8–3.5 mm long, lanceolate, purple, or green with a purple midvein, opaque, strongly reflexed in the proximal 1/4, producing a large transverse bulge, distal part deeply navicular and usually weakly inrolled toward the apex, oriented at 0° to 10° angle to the pedicel, sparsely to densely puberulent, margins scarious and densely ciliate, apex long-attenuate. Nectary base 1–1.05 mm long, dark orange, the nectary shaft 2.55–3.15 mm long, at 90° angle to the axis, apex usually not divided, less developed on one side. Stamens 10; filaments strongly dimorphic, the antisepalous whorl usually erect, 4.5–5.5 mm long, the alternate greatly reduced, 0.6–1.3 mm long; anthers dimorphic, those of the antisepalous stamens 0.8–0.9 mm long, those of the alternate stamens 0.55–0.6 mm long, yellow. Styles 3 (–4). Capsules 2.5–3 mm long, ovoid. Seeds 0.9–1.1 mm long, orbicular-reniform, compressed, the surface transversely rugose. Chromosome number unknown. Figs. 2K, 40.

Distribution (Fig. 41). Moloka`i (Pelekunu to Kala`e), Lana`i (southern half of Lana`ihale), and Maui (Makawao, Hamakua, Olowalu Valley, and Ka`anapali); rare, in mesic to wet forest; 640–1220 m.

Additional Specimens Examined. **Lana`i.** Mountains, E end, *Forbes 270.L* (BISH [2]); without locality, *Forbes 341.L* (BISH); Kawaiakahu, *Munro 535* (BISH); in a small valley Kanahau near Waiopaa [Wai`opa] W side of main ridge, [20°49′7.8″N, 156°51′22.8″W], *Munro 695* (BISH). **Maui.** East Maui: woods E of Makawao, [20°51′15.6″N, 156°17′44.4″W], *Forbes 230.M* (BISH, MO).—West Maui: central ridge of Olowalu Valley, *Forbes 2328.M* (BISH); Lihau, [20°51′5.6″N, 156°35′53.3″W], *Hobdy & Medeiros 3295* (BISH [3]), *Welton & Haus 1569* (BISH [2]); `Iao Valley, Kapilau ridge, Pu`ulio, *Oppenheimer & Duval H59914* (PTBG[2]); `Iao Valley, Nakalaloa Gulch, along streambed on steep cliffs, [20°52′24.7″N, 156°34′38.8″W], *Perlman & Marr 11977* (BISH, PTBG, US); below and W of Helu, rim of Kauaula, *Wood 5970* (PTBG); Ukumehame, prominent ridge W of reservoir near Hana`ula and down ridge, *Wood et al. 7319-A* (PTBG). **Moloka`i.** Head of Waikolu Valley, [21°7′45.2″N, 156°54′35.2″W], *Degener & Degener 23745* (BISH, NY); Kala`e, *Forbes 34.Mo* (BISH [2]); Pelekunu Trail, [21°6′32.6″N, 156°52′41.3″W], *Forbes 237.Mo* (BISH); Puko`o Ridge, [21°5′58.8″N, 156°49′18.4″W], *Forbes 424.Mo* (BISH, BM, MO); Waianui gulch, N branch, along banks of stream, *Perlman 14682* (BISH, US); Kalawao District, Waianui, upper S gulch, on saturated, vertical, basalt walls of S gulch, [21°9′35″N, 156°58′10.6″W], *Wood & Perlman 4087* (US).

Schiedea pubescens is morphologically similar to *S. pentandra* and *S. diffusa*, and is the sister species of *S. pentandra* in the phylogenetic analyses. It differs from *S. pentandra* in its larger and broader leaves, subglabrous inflorescence, and 10 fertile stamens. The two whorls of stamens are strongly differentiated in length; the anthers of the shorter whorl are smaller and have lower pollen production.

There are no recent collections of this species from Lana`i and East Maui, and only a single extant population is known on Moloka`i. *Schiedea pubescens* is currently a candidate for listing as endangered (Williams 2002).

Hillebrand cited five of his collections in the protologue. He listed the first three as “East and West Maui! Hamakua, Waihe`e, Ka`anapali,” followed by one more each under unnamed varieties: β (Moloka`i) and γ (O`ahu, Mt. Ka`ala). Of these five collections, we have seen the following: 1) West Maui, Waihe`e, Aug. 1870, *Hillebrand s.n.* [photo of B sheet (now destroyed), BISH]; 2) West Maui, Ka`anapali, Aug. 1870, *Hillebrand s.n.*

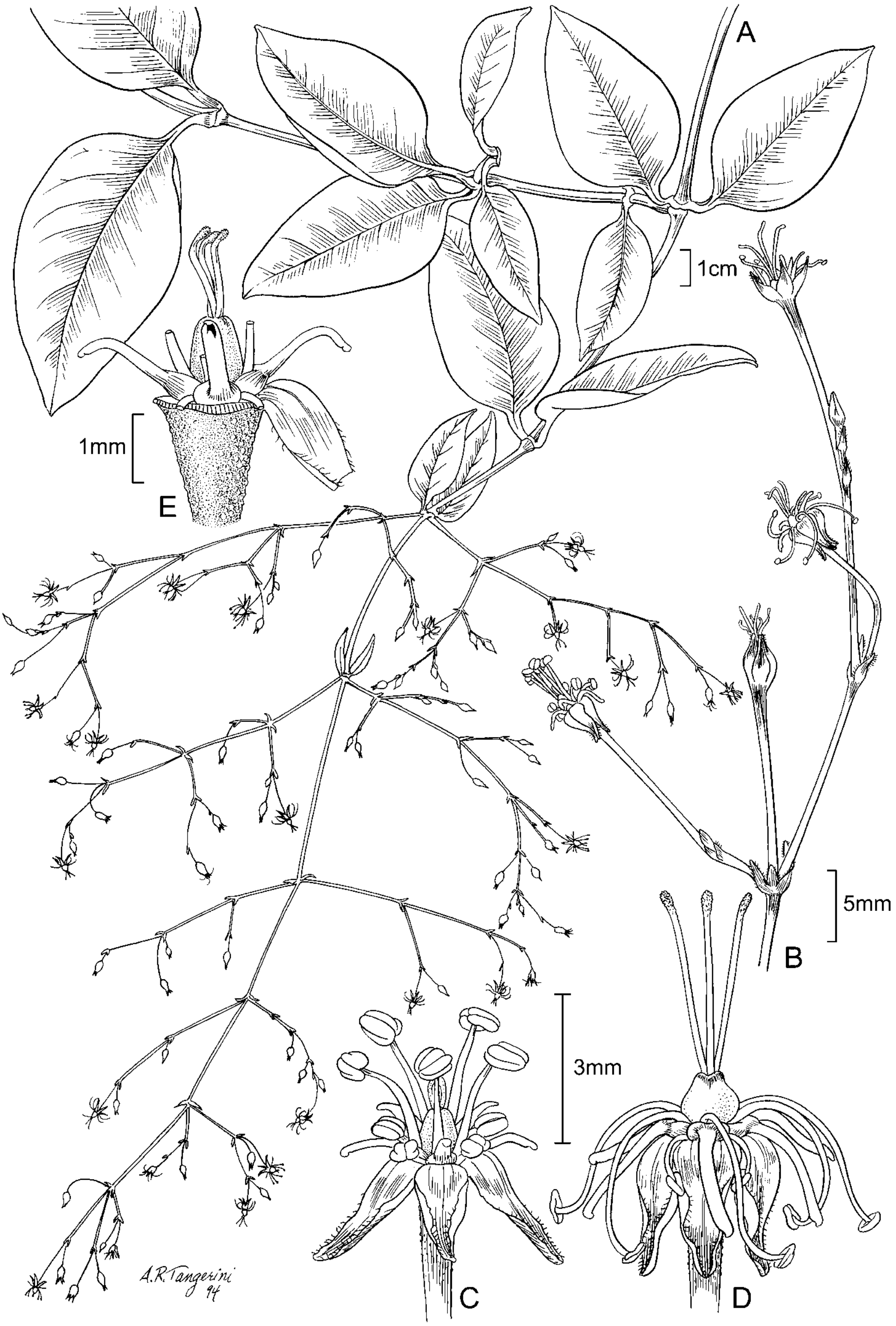

FIG. 40. *Schiedea pubescens* (cult. from *Perlman 11977*). A. Habit. B. Portion of inflorescence. C. Flower in early anthesis, male stage showing difference in size between anther whorls. D. Flower in later anthesis, female stage. E. Flower, with sepals and stamens removed to show nectary shafts.

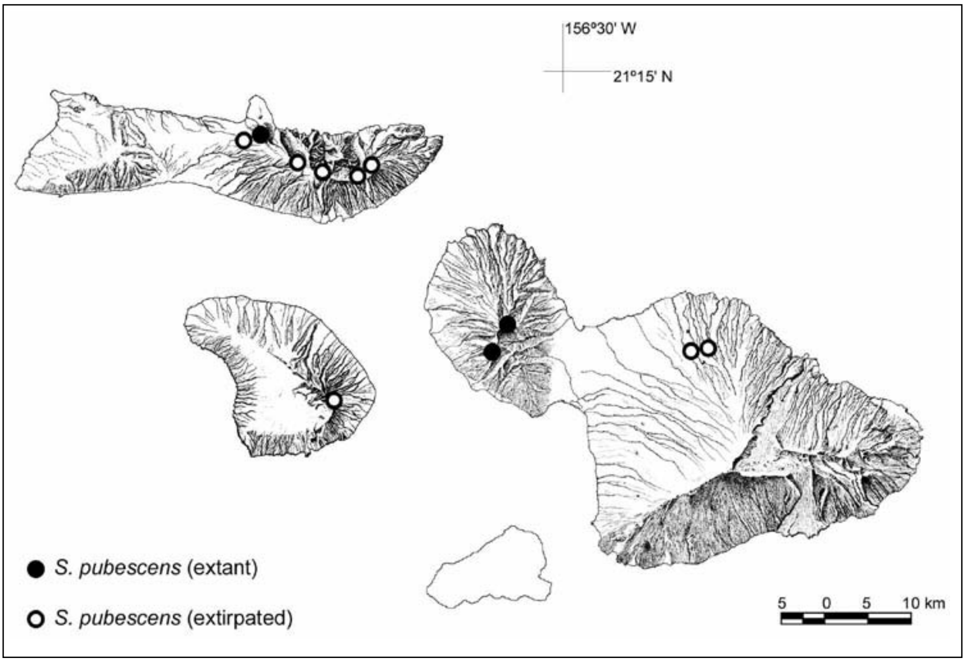

FIG. 41. Distribution of *Schiedea pubescens*.

[MEL 2 sheets]; 3) East Maui, Hamakua [presumably above Hamakua Poko], [BISH]; 4) Moloka`i, Kala`e, 1870, *Hillebrand s.n.* [B (now destroyed), photos: BISH, BM, F, GH); 5) O`ahu, Wai`anae Mts., July 1860, *Hillebrand 430* [B (now destroyed), photos: BISH, US]. Sherff (1945) selected the Hillebrand collection from Hamakua as the lectotype of *S. pubescens*, although he did not see the specimen, which was deposited at B (destroyed). The best extant material with the most duplicates is the Moloka`i collection, from which we here select a new lectotype. Sherff also (1943) provided names for Hillebrand's varieties, but the names were not validly published because he did not he provide Latin diagnoses. Hillebrand's variety γ of O`ahu was published as *S. pentandra*.

The specific epithet is formed from the Latin adjective *pubescens* ("hairy") and refers to the often densely puberulent inflorescences of this species.

22. Schiedea diffusa A. Gray, U.S. Expl. Exped., Phan. 138. 1854; U.S. Expl. Exped., Atlas Phan. pl. 11b. 1856.—TYPE: HAWAIIAN ISLANDS. MAUI: "Mountains of the west side of the island," 1841, *U.S. Expl. Exped. s.n.* (lectotype, designated by Sherff, 1945: US-10253!; see discussion below).

Reclining or weakly climbing vines, primary stems 30–60 (–100) dm long, glabrous or nearly so below, antrorsely puberulent in the inflorescence, the hairs usually reddish purple, 0.1–0.4 mm long. Leaves opposite; blades 4–12 cm long, 1.5–4 cm wide, coriaceous, green to yellowish green, lanceolate to ovate or oblong-elliptic, with only the midvein evident, the midvein ± slightly excentric, usually a weakly looping vein near the margins, margin slightly thickened, with a few scattered minute excrescences, each usually with a retrorsely hooked hair 0.01–0.15 mm long, apex acute to attenuate, base acute to broadly obtuse; petioles 0.2–0.7 cm long. Inflorescence terminal, with 20–92 flowers, 10–50 cm long, pendent, diffuse, the internodes and pedicels often purple or purple-tinged; bracts green, sometimes purple-tinged, subulate, the lowermost of the central axis sometimes ovate to elliptic, 5–15 mm long, those of branches and flowers 3–8 mm long; pedicels 8–24 mm long at anthesis, elongating to 20–40 (–50) mm long in fruit, conspicuously asymmetrically flattened. Flowers hermaphroditic. Sepals 4.2–7 mm long, ovate, green purple toward base and apex, thick and opaque, strongly reflexed and convex in proximal 1/4, producing transverse bulge, the distal part shallowly concave to shallowly navicular, oriented at ca. 30° to 60° angle or ca. 150° angle to the pedicel, abaxial side slightly keeled, glabrate to sparsely puberulent with reddish purple hairs 0.1–0.25 mm long, especially toward the base, margins weakly scarious, ciliate, apex abruptly attenuate. Nectary base somewhat broadened and flattened at base but functional, 0.4–0.75 mm long or divided into two flattened non-functional segments, 0.7–1.1 mm long, dark yellow or yellow to pale greenish yellow, the nectary shaft 3.6–6.5 mm long, apex bifid. Stamens 10; filaments dimorphic, the antisepalous whorl 6.4–9 mm long, the alternate whorl 5–7.5 mm long; anthers subequal, those of the antisepalous whorl 1.15–1.25 mm long, of the alternate whorl 1 mm long, yellow. Styles 3–6. Capsules 4.5–7 mm long, very broadly ovoid or ovoid-globose. Seeds numerous, 1–1.2 mm long, suborbicular, asymmetrical, compressed, the surface smooth, under high magnification with minute depressions, persistent on the placenta, and retained in the undehisced capsule. Figs. 2L, M, 3Q, R, 42.

Schiedea diffusa is unique in the genus in producing seeds that remain attached to the placenta at maturity and eventually may germinate on the plant. In cultivation, this species is autogamous. *Schiedea diffusa* is here divided into two subspecies, subsp. *diffusa* on Maui and Moloka`i, and subsp. *macraei* on Hawai`i. Subspecies *macraei* has cleistogamous flowers, which open only slightly at the time when pollen is shed. Pollen is shed directly onto the receptive stigmas. Subspecies *diffusa* has chasmogamous flowers. Leaves of subsp. *macraei* are smaller and narrower than those of subsp. *diffusa*.

Gray mentioned several localities in the protologue: “Sandwich Islands; in the forests of Mouna Loa and Mouna Kea. Also in mountains of the west side of the island of Maui.” Sherff (Brittonia 5: 315. 1945) indicated the US sheet as the type without seeing it and cited the locality as “forests of Mauna Kea and Mauna Loa.” St. John (1985) accepted this as a lectotypification. Yet, we did not find any specimen collected by U.S. Exploring Expedition from the island of Hawai`i at US. The collection from Maui, here chosen as lectotype, is the only US sheet from the Hawaiian Islands of this species, and the one used for the plate in the *Atla*s. The other three specimens of *S. diffusa* collected by the U.S. Exploring Expedition (GH! NY! P!) have no specific locality on the label; because Gray listed several localities we cannot determine whether these were collected on Maui or Hawai`i.

The specific epithet refers to the large open inflorescences that characterize this species.

22a. Schiedea diffusa subsp. **diffusa.**

Schiedea diffusa var. *angustifolia* Wawra, Flora 56: 175. 1873.—TYPE: HAWAIIAN ISLANDS. “Kaua`i” [WEST MAUI]: Wailuku Valley, [27 Jan–12 Feb 1870,] *H. Wawra 1825* (holotype: W, destroyed).

Leaf blades 4–12 cm long, 1.5–4 cm wide, lanceolate to ovate or oblong-elliptic; petioles 0.2–0.7 cm long. Inflorescence with 20–92 flowers, 10–50 cm long, the internodes

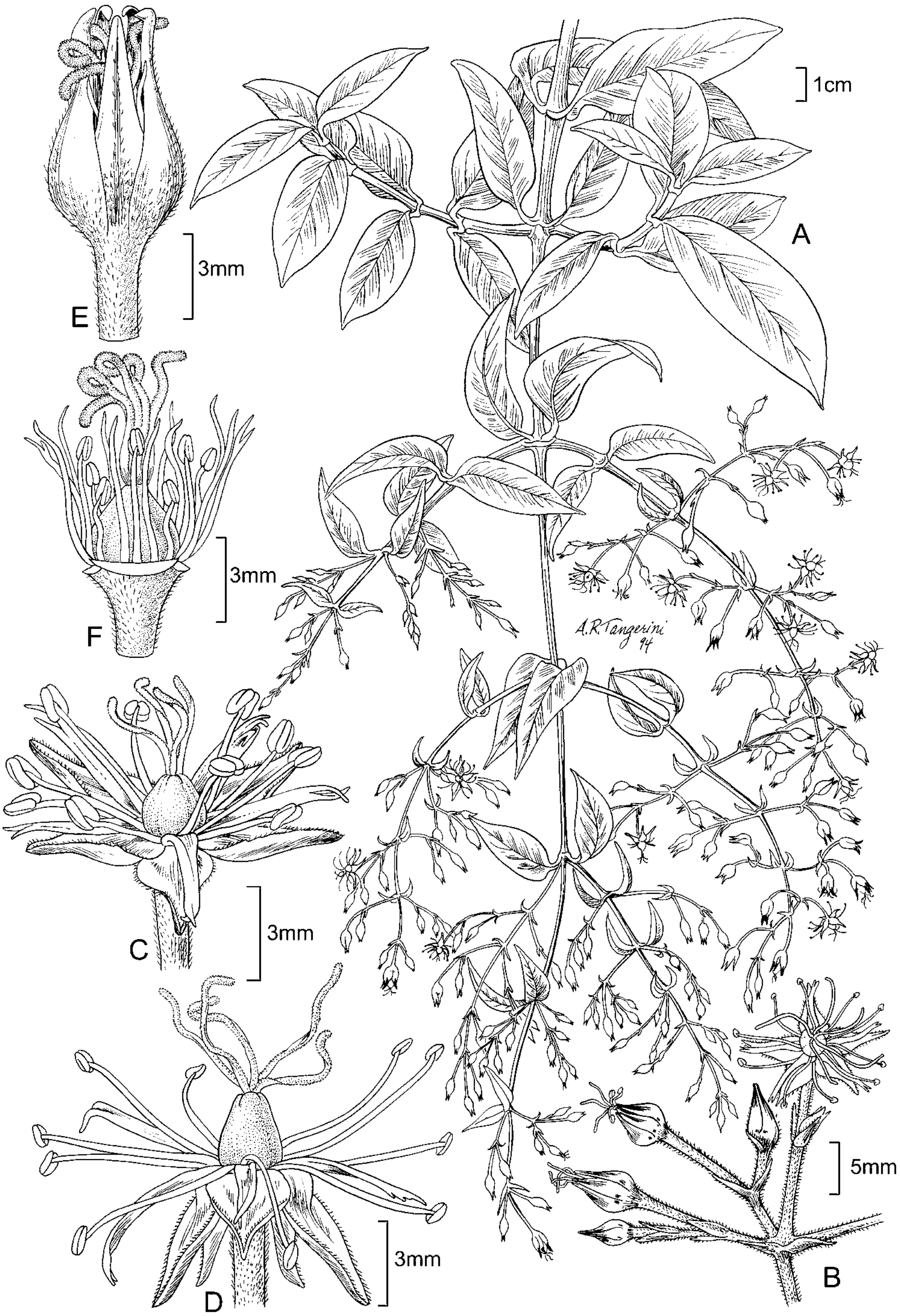

FIG. 42. *Schiedea diffusa*. A–D, *S. diffusa* subsp. *diffusa* (cult. from *Weller & Sakai 848*). A. Habit. B. Portion of inflorescence. C. Flower in anthesis, male stage. D. Flower in later anthesis, female stage. E, F. *S. diffusa* subsp. *macraei* (cult. from *Perlman 14780*). E. Flower at anthesis, showing partially emerged stigmas. F. Flower, sepals removed to show anthers and vestigial nectaries.

and pedicels often purple or purple-tinged; pedicels 8–20 mm long at anthesis, elongating to 20–40 (–50) mm long in fruit. Flowers potentially outcrossing, protandrous. Sepals (4.2–) 5–7 mm long, strongly reflexed and convex in proximal 1/4, producing transverse bulge, the distal part shallowly concave to shallowly navicular, oriented at ca. 30° to 60° angle to the pedicel. Nectary base somewhat broadened and flattened at base but functional, 0.4–0.75 mm long, dark yellow, the nectary shaft 3.6–6.5 mm long, apex bifid. Staminal filaments dimorphic, the antisepalous whorl 6.4–9 mm long, the alternate whorl 5–7.5 mm long. Styles 3–5. Capsules 5–7 mm long, very broadly ovoid. Chromosome number: 2n = possibly 54 (*Weller & Sakai 848*). Figs. 2L, 42A–D.

Distribution (Fig. 37). Eastern Moloka`i (Kawela to Waikolu valleys, to 1160 m) and Maui (to 2050 m); scattered in wet forest.

Additional Specimens Examined. **Maui.** East Maui: Olinda pipeline trail, [20°48′13.6″N, 156°13′15.1″W], *Degener 2355* (B, F, NY, NY, P), *Degener & Topping 5934* (BISH, F, NY); woods near Ukulele above Olinda, [20°47′36.7″N, 156°15′3.5″W], *Forbes 163.M* (BH, BISH, M, NY); Nahiku, *Forbes 246.M* (BISH, F, MO, NY, P, UC, US); N slope of Haleakala, *Forbes 1138.M* (BH, F, M, P, UC, US); ridge at side of Kipahulu, *Forbes 1665.M* (BISH, NY, NY); W bank of Honomanu Gulch, *Forbes 2576.M* (BISH); NW slopes Haleakala, Ha`iku Uka, W of Waikamoi Gulch, Headwaters of Kailua Stream, *Fosberg 41520a* (POM); Makawao District, Haleakala, Haiku-Uka trail, [20°48′46.7″N, 156°14′36.9″W], *Fosberg 9854* (PTBG, US); Waiho`i Valley, [20°42′29″N, 156°02′52.3″W], *Harrison 23* (BISH); Waiho`i Valley, Pu`u Ho`olio, *Harrison 99* (BISH); Waiho`i Valley, Pu`uho`olio, *Harrison & Herbst 2522* (BISH); Hana Forest Reserve, ridge above N rim of Kipahulu, [20°44′2.5″N, 156°06′58.6″W], *Harrison 590* (A, BISH); Hana District, Tr 9(30), N slope of Haleakala, Ko`olau FR, on ridge E of Kuhiwa Valley, [20°45′55.1″N, 156°06′26.6″W], *Higashino & Holt 9162* (BISH); Hana District, Tr 16(24/25), along ridge in central Kipahulu Valley, *Higashino & Holt 9409* (BISH); Waikamoi Gulch, head of flume, 12 October 1981, *Kores & Touw s.n.* (BISH); Waiho`i Valley, Pu`uho`olio, *Nagata et. al. 1052* (BISH); Waikamoi flume trail, at end of flume in Haipuaena stream, 0.25 mile downstream, *Perlman 14677* (PTBG, US); Pu`uokaka`e, N side of pu`u in small gulch, [20°48′2.5″N, 156°14′34.7″W], *Perlman et. al. 16068* (BISH, PTBG, US); Hamakua, NW slope of Haleakala, *Rock 8544* (A, BISH, F, GH, NY, P, UC, US); Kailua ditch trail, *Rock 12932* (BISH); Waikamoi, Oct 1910, *Rock s.n.* (NY); Nahiku, Kuhiwa trail, Ko`olau Forest Reserve, *St. John & Catto 17960* (BISH); Haleakala, Kula pipeline, *Skottsberg 855* (BISH, GB, S); end of Waikamoi flume trail, [20°48′13.6″N, 156°15′3.5″W], *Wagner et. al. 4802* (BISH); Hana District, Tr 18(16/17), Kipahulu Valley, lower dogleg, [20°42′20.6″N, 156°4′35.6″W], *Wagner et. al. 5926* (BISH, US [3]); Hana District, Tr 17(50), Pu`uahulili, E of Niniao Pali, across small stream and gully, [20°41′5.9″N, 156°6′53.1″W], *Warshauer & McEldowney 3020* (BISH); SW Kipahulu Valley, along Koukouai Gulch, [20°41′36.5″N, 156°5′44.3″W], *Warshauer 2864* (BISH); Hana District, Tr 10(6), NE slope of Haleakala, Hana Forest Reserve, along Kalapawili ridge, [20°43′48.9″N, 156°08′28.2″W], *Warshauer & et al. 2546* (BISH); Kipahulu valley, National Park lands between Kaupo Gap and Kipahulu valley, Kekuewa Camp, *Wood et al. 6670* (MO, NY, PTBG, US); Pi`ina`au Stream region, Haiku Uka, Ko`olau Forest Reserve, *Wood et al. 10611* (PTBG); Kipahulu Valley, just S of Palikea Stream, [20°42′46.2″N, 156°5′32.5″W], *Yoshinaga 334* (BISH).—West Maui: on ridge from Nakalaloa to Pu`ukukui, [20°53′13″N, 156°35′23.1″W], *Cranwell et. al. 2679* (GB, K, S). **Moloka`i.** E highland, head of Waikolu valley along Pipeline Trail, *Cranwell & Skottsberg 2595* (BISH, GB, S); gullied region between Waikolu Valley and probably N base Pu`uali`i, *Degener 5954* (F, NY); Nu`alele Valley, E of Waikolu, *Degener 22030* (BISH, F, NY, US); end of Hanalilolilo Pipeline trail, [21°7′29.5″N, 156°5′32.5″W], *Degener 5944* (B, BM, F, GH, K, M, MIN, NY, P, PH, UC); without locality, *Degener 10867* (coll. L. Whitney) (F); upper Kawela Gulch, [21°6′32.7″N, 156°54′45.9″W], 7 January 1981, *Gagné s.n.* (BISH); pipeline trail, steep bank, head of Waikolu Valley, Hanalilolilo, *St. John et. al. 12393* (BISH, NY); pali above ditch trail, head of Waikolu Valley, Hanalilolilo, *St. John et. al. 12615* (BISH, NY); ditch trail, Hanalilolilo, head of Waikolu, [21°7′29.5″N, 156°54′33.8″W], *St. John 25224* (BISH, K, RSA).

Cultivated. **Maui**. East Maui: end of Waikamoi flume, Dec 1984, *Weller & Sakai s.n.* [cult. *Weller & Sakai 848*] (BISH, PTBG, US); Kipahulu Valley, steep slopes above Koukoui Stream, 22 Sep 1992, *Welton s.n.* [cult. *Weller & Sakai 898*] (US); lower shelf of Kipahulu Valley, *Weller & Sakai 914* [cult. *Wagner & Shannon 6797*] (BISH, PTBG, US); Waiho`i Valley, *Herbst & Gagné 2612* [cult. *Herbst 4019*] (BISH); Waikamoi Reserve, Ko`olau Gap, Halehaku Lake, 1994, *Hughes s.n.* [cult. *Weller & Sakai 910*] (BISH, US).

Schiedea diffusa subsp. *diffusa* is most common on East Maui, but previously occurred on West Maui. It has not been collected on Moloka`i since 1981 (*Gagné s.n.*). The type of *Schiedea diffusa* var. *angustifolia* was almost certainly collected on West Maui; there is no Wailuku Valley known to us on Kaua`i.

22b. Schiedea diffusa subsp. **macraei** (Sherff) W. L. Wagner & Weller, comb. et stat. nov. *Schiedea diffusa* var. *macraei* Sherff, Amer. J. Bot. 30: 606. 1943.—TYPE: HAWAIIAN ISLANDS. [HAWAI`I:] "Ins. Owhyhee, ad montem kaah" [on Mauna Kea], Jun 1825, *J. Macrae s.n.* (holotype: GH!, photo: F!).

Leaf blades 6.5–8.9 cm long, 1.5–2.5 cm wide, lanceolate to narrowly ovate or sometimes oblong-elliptic; petioles 0.4–1 cm long. Inflorescence with 65–73 flowers, 10–50 cm long, internodes and pedicels yellowish green; pedicels 14–24 mm long at anthesis, elongating slightly in fruit. Flowers cleistogamous. Sepals 4.3–4.7 mm long, shallowly concave to shallowly navicular, scarely spreading, oriented at ca. 150° to the pedicel, quickly closing. Nectary base divided into two flattened segments, non-functional, 0.7–1.1 mm long, yellow to pale greenish yellow, the nectary shaft 3.6–3.75 mm long, apex bifid. Staminal filaments dimorphic, the antisepalous whorl 5.25–6.25 mm long, the alternate whorl 5.5–6.1 mm long. Styles 5–6, stigmas receptive when flower opens. Capsules 4.5–5 mm long, ovoid-globose. Chromosome number unknown. Figs. 2M, 42E, F.

Distribution (Fig. 37). Hawai`i, on windward slopes of Mauna Loa (Ola`a) and Kohala Mountains, where it has been collected in 1911 (*Forbes 484.H*) and 2001 (*Perlman et al. 17808*), and twice in Hawai`i Volcanoes National Park in the `Ola`a Tract, once in 1987 (*Katahira & Taylor s.n.*) and again for us in 1995 (*Perlman et al. 14780*); 1000–1220 m.

ADDITIONAL SPECIMENS EXAMINED. **Hawai`i.** Waimea, [20°06′52″N, 155°43′1″W], *Forbes 484.H* (BISH, BH, GH, MO, NY, P, UC, US [2]); Puna District, Volcanoes Nat'l Park, `Ola`a Tract, [19°28′47.7″N, 155°14′21.1″W], 24 Feb 1987, *Katahira & Taylor s.n.* (BISH); Waimea, Jan 1873, *Lydgate s.n.* (BISH); Kohala [Mts.], s.d., *Lydgate s.n.* (BISH); Ola`a Tract, Ag Unit, transect 7, 810 meter mark, 20 m from fence, *Perlman et al. 14780* (PTBG); slopes of `Eke, near transect 6, between transects 6 and 7, *Perlman et al. 17808* (PTBG); without locality, *Rémy 546* (GH [mounted on same sheet as type of *S. diffusa*], P [7]); Kohala [Mts.] *Rock 8360* (BISH, GH, K, NY, UC, US), Jun 1910, *Rock s.n.* (F, NY).

CULTIVATED. **Hawai`i.** Ola`a Tract, Ag Unit, Transect 7, 810 meter mark, 20 m from fence, *Perlman et al. 14780* [cult. *Wagner & Shannon 6796*] (BISH, GH, NY, PTBG, US).

The specific epithet honors James Macrae (?–1830), a British botanist for the Royal Horticultural Society, who traveled on the British warship *HMS Blonde* under Captain George Anson (Lord) Byron. The purpose of the trip to the Hawaiian Islands (May to July 1825) was the repatriation of the remains of the young King Liholiho (Kamehameha II) and queen Kamamalu of Hawai`i, who had died tragically in 1824 of measles during a visit to England.

VIII. Schiedea sect. Schiedea.

Shrubs with well-developed wood or subshrubs with weakly developed wood; stems 1–many, erect to sprawling; roots fibrous. Leaves either coriaceous and elliptic-oblanceolate or oblanceolate, occasionally elliptic, 1(–3)-nerved, or succulent-coriaceous to thin and membranous, linear, linear-elliptic to lanceolate, 1–3(–5)-nerved with an attenuate and usually falcate apex, margins entire. Inflorescence terminal. Flowers hermaphroditic or unisexual. Sepals 5, ovate to occasionally lanceolate, oriented at 30° to 120° angle to the pedicel, margin glabrous to ciliate. Nectary shafts straight to recurved. Styles (2–) 3–4 (–6).

Schiedea sect. *Schiedea* includes fourteen species, which have been divided, based on morphological phylogenetic analysis, into two clades, referred to as the "globosa" and "adamantis" clades (Wagner et al. 1995; Weller et al. 1995), which correspond to the two leaf types noted in the sectional description. More recent molecular and morphological analyses do not support this division; rather, most of the species of the "globosa" group form a grade at the base of the clade, whereas species of the "adamantis" group are placed at the terminal end of the clade. Thus we broadly circumscribe this section by including both groups. Section *Schiedea* includes all of the species with dimorphic breeding systems (gynodioecy, subdioecy, or dioecy), except for *S. apokremnos* (sect. *Anestioschiedea*).

23. Schiedea kealiae Caum & Hosaka, Occas. Pap. Bernice P. Bishop Mus. 11(23): 3. 1936.—TYPE: HAWAIIAN ISLANDS. O`AHU: Kealia, Wai`anae Mountains, 500 ft [150 m], 2 Feb 1936, *E. Y. Hosaka 1320* (holotype: BISH-501314!; isotypes: BISH-2 sheets! M! P! UC! US!).

Subdioecious weakly erect to sprawling softly woody shrubs; stems 2–10 dm long, few- to many-stemmed from the base, forming loose clumps, the primary stems few-branched, weakly ascending to sprawling, internodes 0.3–4.5 cm long, pale green, glabrous below, minutely glandular-puberulent on the upper stems and inflorescence, sometimes glabrate. Leaves opposite, often appearing fasciculate on short axillary stems, recurved, becoming more so in age; blades 3–11 cm long, (0.3–) 0.7–1.2 (–2.4) cm wide, thin and membranous, lanceolate to elliptic-lanceolate, conspicuously falcate and usually slightly twisted, weakly v-shaped in cross section toward the apex and especially toward the base, with 3 principal veins, these pale and somewhat translucent, the midvein slightly excentric, young leaves and upper ones sparsely minutely glandular-puberulent, especially on the lower surface, the hairs sessile, 0.05–0.1 mm long, erect, white-opaque, margins weakly revolute, apex attenuate and often slightly curved, base tapered; petioles 0–0.5 cm long. Inflorescence terminal, with 55–534 flowers, 3–11 cm long, laterally contracted and congested, lateral branches short, the branches and pedicels ascending, puberulent with hairs like those of the leaves; bracts green, linear-subulate, recurved, those of central axis 2–20 mm long, those of branches and flowers 0.5–2 mm long. Staminate flowers: pedicels 5–8 mm long, slender, inconspicuously flattened, those of the central flower usually longer; sepals subequal, 2.5–3.4 mm long, narrowly ovate, yellowish green, yellow toward the base, opaque, reflexed and convex at the base, producing a small transverse bulge, the middle part concave, curved upward and broadly navicular to nearly flat in the distal 1/3, sometimes irregularly inrolled toward the apex, oriented at 90° to 100° angle to the pedicel, sparsely minutely glandular-puberulent, the glands almost sessile, margins scarious, apex obtuse; nectary base 0.5 mm long, spreading at ca. 70° to the axis, yellow, the nectary shaft held well above the sepal surface, 0.9 mm long, apex notched, more deeply so on the abaxial side; stamens 10, the filaments dimorphic, the antisepalous whorl 3.5–3.8 mm long, the alternate whorl 3.0 mm long, anthers ca. 0.6 mm long, pale yellow; styles 2–3, greenish yellow, weakly elongating, non-functional. Hermaphroditic flowers occurring occasionally intermixed in staminate inflorescences, numbers varying with site and moisture, similar to staminate flowers except ovary and styles functional. Pistillate flowers: pedicels 4–6 mm long, slender, inconspicuously flattened, those of the central flower usually longer; sepals subequal, 2.1–2.5 mm long, narrowly ovate, yellowish green, opaque, convex at the base, producing a small transverse bulge, the middle part concave, nearly flat in the distal 1/2, inrolled at apex, oriented at 90° to 100° angle to the pedicel, sparsely minutely glandular-puberulent, the glands nearly sessile, margins scarious, apex obtuse; nectary base 0.3–0.4 mm long, spreading at 60° to the axis, yellowish green, the nectary shaft held well above the sepal surface, 0.5–0.7 mm long, apex deeply slit on adaxial side, notched or slit on abaxial side, apparently non-functional; stamens 10, vestigial, the filaments subequal, the antisepalous whorl 0.4–0.55 mm long, the alternate whorl 0.3–0.4 mm long, anthers ca. 0.15 mm long, yellowish white, not producing pollen; styles (2–) 3–4. Capsules 2–2.5 mm long, narrowly ovoid. Seeds relatively few, ca. 0.6 mm long, orbicular-reniform, compressed, the faces depressed, the surface transversely rugose. Chromosome number: 2n = possibly 60 (*Weller & Sakai 791*). Figs. 2N, 4A, B, 43.

Distribution (Fig. 44). O`ahu, northern Wai`anae Mountains; in remnant *Sapindus oahuensis* dry forest now mixed with *Leucaena*, on steep slopes and exposed ledges; 60–305 m.

Additional Specimens Examined. **O`ahu.** Makua Trail, Apr 1939, *Baxter s.n.* (MO); Kealia Trail, *Bennett 242* (BISH); Kealia Pali, *Bryan, Jr. 786* (BISH [2]); Waialua District, Kealia Trail, Kawaihapai, *Carlson 3826* (F, PENN); Kealia Army Trail, 1 Apr 1942, *Caum s.n.* (BISH, P, UC, US); without locality, *Degener 5969* (F); Kawaihapai, [21°34′23.4″N, 158°12′38.2″W], *Degener 17159* (F, GH, K); Kealia Trail, Kawaihapai, *Degener & Degener 24067* (B, BM, G, K, M, MIN, MO, NY, US, W), *Degener & Degener 24110* (B, BH, BISH, CU, M, MIN); between end of Kawaihapai Road and Ka`ena Point, *Degener & Park 5923* (BISH, GH, MASS, NY, US); near summit of new CCC trail, Kawaihapai, *Degener et. al. 10484* (B, BISH, CU, G, GH, MO, NY, US); new CCC trail, Kawaihapai, *Degener et. al. 11036* (B, BISH, CU, G, GH, MASS, MO, NY, S [2], US); Kealia Trail, Kawaihapai, *Degener et. al. 20391* (B, G [2]); Wai`anae, *Faurie 1083* (G); Kealia Trail above Dillingham Airfield, *Flynn 787* (PTBG); Kawaihapai, [21°34′23.4″N, 158°12′38.2″W], *Forbes et. al. 1838.O* (BISH, MO, NY); Kealia, zig-zag trail up cliff, *Fosberg 12853* (US); Kealia-Kawaihapai gulches, *Gagné 644* (BISH [2], US); Wai`anae District, Kealia Trail above Dillingham Base, *Gustafson 2917* (RSA); Kealia trail, Ka`ena, *Hatheway 141* (B, BISH, BM, G, GB, K, NY, P, PH, UC, US), *Hatheway 300* (P, PH, W); Wai`anae Range: behind Ka`ena Point, on N side at base of cliffs, *Herbst & Bishop 1378* (HAW); Kealia, *Hosaka 1292* (NY, RSA); Kealia Trail, *Lamoureux 293* (HAW [2]), *Lamoureux 529* (HAW); without locality, Aug 1934, *Lyon s.n.* (BISH); Mokule`ia, hillside above Dillingham Airfield, W end of airstrip, above second paved bunkered area from the west, 80 m E of Kealia Trail, *Obata et. al. 422* (BISH, US); Palikea, 11 Jun 1954, *Pearsall s.n.* (BISH); valley E of Kealia Tr., behind Dillingham Airfield, E side slopes, valley behind old runway, *Perlman 5221* (BISH, MO, PTBG); Dillingham area, above Camp Erdman, [21°34′22.3″N, 158°13′27.9″W], *Perlman & Obata 7002* (BISH, PTBG, US [2]); Mts. behind Dillingham Military Reservation, steep slopes to east of Kealia trail, below old camp at [unnamed] peak at 1048 ft., *Perlman & Wood 15329* (NY, PTBG, US); Kealia Trail, *Selling 3844* (BISH, GB, K, S); Kealia Ridge behind Dillingham A.F.B., *Shigematsu et. al. 76.38* (HAW); Makua trail, *St. John 20028* (B, BISH, K, P); Kealia trail, upper section overlooking Dillingham Airfield, *Takeuchi Waianae 57* (BISH); Kealia Trail above Dillingham Airfield, *Takeuchi Waianae 68a* (BISH), *Takeuchi Waianae 68b* (P); Mokule`ia, grassy slopes, *Takeuchi & Paquin 3858* (BISH); Kealia Trail above Dillingham Airfield, *Wagner et. al. 5325* (BISH, US [2]); Kealia Tr. approx. 1–2 mi (5th switchback) from start of trail, departing S of Dillingham glider airstrip, *Weller & Sakai 791* (US); Kealia, 20 Nov 1960, *Wiemer s.n.* (HAW); Mokule`ia, Kealia Trail, s.d., *Wirawan s.n.* (HAW); Dillingham airfield mts., above Mokule`ia aspect 50° NE, *Wood & Perlman 5109* (PTBG, US).

Cultivated. **O`ahu.** Wai`anae Range: Kealia Tr., between 1 to 2 mi from start of trail, *Weller & Sakai 791* [cult. 1985, *Weller & Sakai s.n.*] (BISH, F, GH, K, NY, PTBG, US), 1985, *Weller & Sakai s.n.* [cult. *Wagner & Shannon 6858*] (BISH, PTBG, US), 1985, *Weller & Sakai s.n.* [cult. *Wagner & Shannon 6859*] (BISH, PTBG, US).

Schiedea kealiae is morphologically similar to *S. menziesii*, *S. sarmentosa*, and *S. hookeri*; it differs primarily in the subdioecious rather than hermaphroditic or

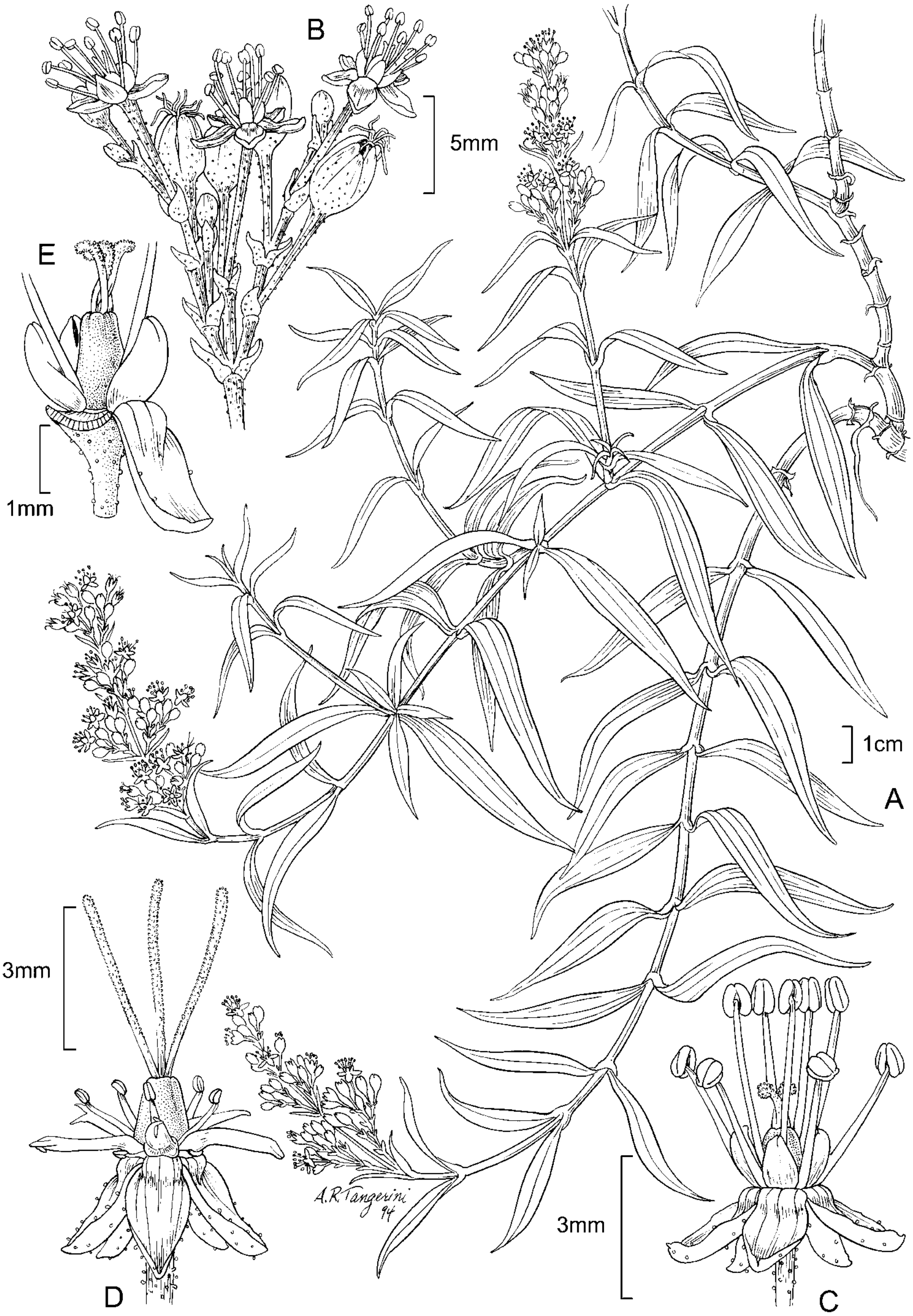

FIG. 43. *Schiedea kealiae* (cult. from *Weller & Sakai 791*). A. Habit. B. Inflorescence of male plant. C. Flower, male. D. Flower, female. E. Flower, one sepal and stamen removed to show nectary shafts.

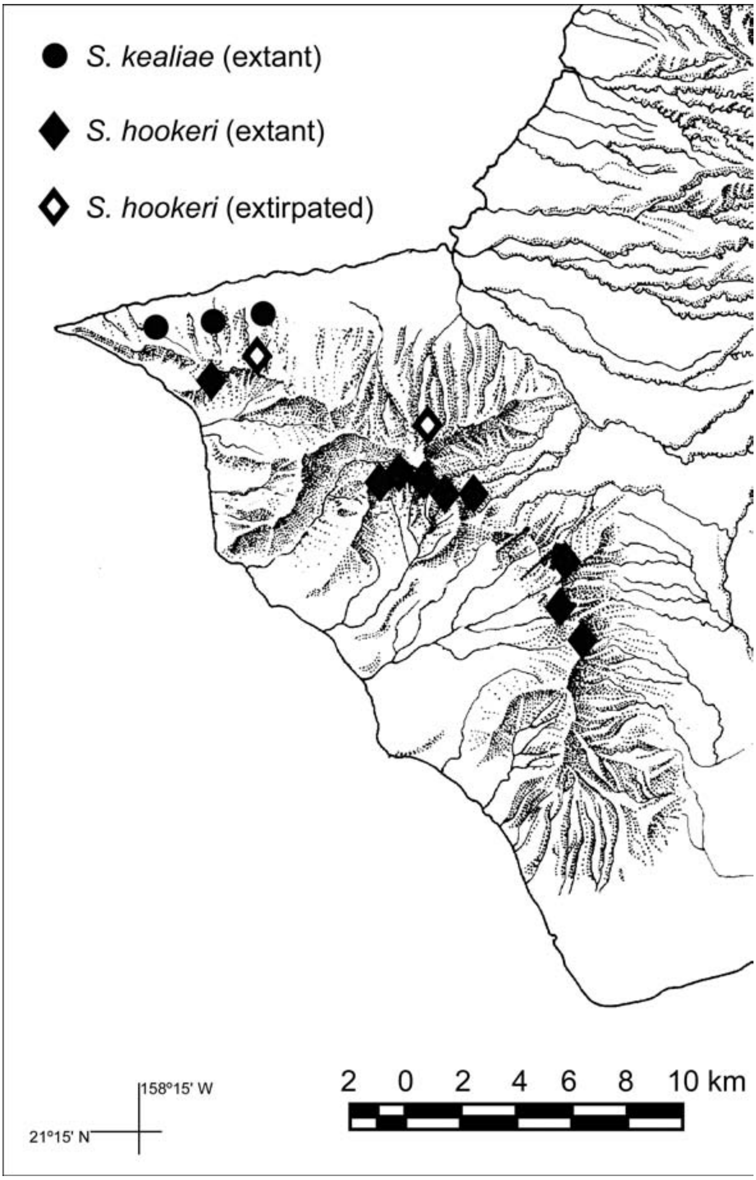

FIG. 44. Distribution of *Schiedea kealiae* and *S. hookeri*.

gynodioecious breeding system and in having denser inflorescences and smaller sepals. An apparently disjunct population (1954, *Pearsall s.n.*, BISH) from Palikea, southern end of the Wai`anae Mountains, has never been confirmed.

Schiedea kealiae was listed as endangered in 1996 (Russell & Bruegmann 1996c).

The specific epithet refers to Kealia, the type locality of this endemic of the Wai`anae Mountains.

24. Schiedea hookeri A. Gray, U.S. Expl. Exped., Phan. 133. 1854.—Type: Hawaiian Islands. [O`ahu: March 1792 or 19–24 March 1793], *A. Menzies s.n.* (holotype: GH!; isotypes: K!, photos of K isotype: BISH! NY! PH!).

Schiedea hookeri var. *acrisepala* Sherff, Amer. J. Bot. 31: 153. 1944.—Type: Hawaiian Islands. O`ahu: Wai`anae Mountains, Lualualei Valley, head of valley below Pu`ukanehoa, on grassy slopes, 600–700 m, 25 May 1932, *E. Christophersen 3658* (holotype: UC-504973!, photo: F; isotypes: BISH-2 sheets! P! US!).

Schiedea hookeri var. *intercedens* Sherff, Brittonia 5: 330. 1945.—Type: Hawaiian Islands. O`ahu: [Wai`anae Mountains], N slope of Mount Ka`ala, 1871, *W. Hillebrand s.n.* (holotype: GH!, photo: F]).

Sprawling perennial herbs, becoming woody toward base; stems 3–10 dm long, multi-stemmed from the base, the primary stems usually much branched, weakly ascending to nearly decumbent, producing matted clumps, pale purple, glabrate below, glandular-puberulent and somewhat viscid in the inflorescence. Leaves opposite; blades 3–8.8 cm long, 0.4–2.4 cm wide, thin and membranous, narrowly lanceolate to narrowly elliptic, falcate, with 3 principal veins, the midvein excentric, glandular-puberulent or glabrate, especially toward base, the hairs translucent, straight, ± erect, 0.05–0.15 mm long, margins weakly revolute, apex attenuate and ± recurved; petioles 0–0.3 (–0.6) cm long. Inflorescence terminal, with 18–149 flowers, 5–22 cm long, open, moderately to densely glandular-puberulent, the hairs 0.15–0.25 mm long; bracts green, narrowly linear-elliptic to subulate, falcate and often somewhat twisted, those of central axis 2–31 mm long, those of branches and flowers 1–12 mm long; pedicel filiform, 7–16 mm long, inconspicuously flattened. Flowers hermaphroditic. Sepals 3.3–4.5 mm long, lanceolate, green to purple, opaque, strongly reflexed and convex in the proximal 1/4, producing a small transverse bulge, the distal part concave, sometimes shallowly navicular at apex, oriented at ca. 30° angle to the pedicel, moderately to densely glandular-puberulent, the hairs 0.05–0.15 mm long, margins conspicuously scarious, ciliate, apex attenuate to subulate. Nectary base slightly broadened at base, 0.6 mm long, greenish yellow, the nectary shaft 4–5.75 mm long, at 90° to the axis, quickly recurving to 60°, apex bifid, but slit more deeply on abaxial side. Stamens 10; filaments dimorphic, the antisepalous whorl 4.5–5.8 mm long, the alternate whorl 4–5 mm long; anthers 0.85–1 mm long, yellow. Styles 3 (–4). Capsules ca. 2.5–3 mm long, narrowly ovoid. Seeds relatively few, ca. 0.6–0.7 mm long, suborbicular, compressed, the surface transversely rugose. Chromosome number: $2n$ = probably 60 (*Weller & Sakai 871*). Figs. 2O, 45.

Distribution (Fig. 44). O`ahu, northern and central Wai`anae Mountains; scattered and sometimes locally common in diverse mesic forest; 360–870 m.—A single specimen from East Maui (*Lydgate s.n.*, BISH) labeled Haleakala is this species and presumably represents a former wider distribution. *Nototrichium humile* Hillebr. (Amaranthaceae) exhibits a similar disjunct distribution.

Additional Specimens Examined. **Maui.** East Maui: Haleakala, s.d., *Lydgate s.n.* (BISH). **O`ahu.** Kaumokunui Gulch, *Degener & Kepaa 12735* (A [2], B [2], BH, CU [2], F, G, GB, GH, M, MIN, MO, NY [2], P [2], PH [2], UC, US [2]); Kamokuiki Valley, between Pu`uiki and Pu`ukamananui, [21°30′54.9″N, 158°08′26.6″W], *Degener & Park 5913* (B, CU, F, G, GB, GH, K, M, MIN, MO, NY, UC); Kaumokunui Gulch, *Degener et. al. 12107* (A, B, CU, F, G, GH, K, US); Mokule`ia, SW of Dillingham Ranch, *Degener et. al. 20618* (B, BISH, BM, F, G [2], MO, S, W); Wai`anae, *Faurie 1084* (A, BM, G, P); Wai`anae District, along main ridge separating Makaha and Wai`anae Kai Valleys, N of Pu`ukawiwi, *Gustafson 3316* (RSA); Kukui`ula, Mokule`ia, Forest Trail #20a, *Hatheway 162* (B, BISH, K, UC); Wai`anae District, Wai`anae Kai, ridge between Kalalua

FIG. 45. *Schiedea hookeri* (cult. plant from *Weller & Sakai 879*). A. Habit. B. Portion of inflorescence. C. Flower in early anthesis, male stage. D. Flower in later anthesis, female stage.

and Kanewai Streams, [21°29′32.2″N, 158°08′23.9″W], *Lau 1313.1* (BISH); Wai`anae Kai, below Ka`ala, 24 May 1992, *Obata s.n.* (PTBG); Wai`anae Kai, Makaha Ridge, slightly to the W of W branch of the loop trail, 17 May 1992, *Obata et al. s.n.* (PTBG); about 100 m (below) crest of Lualualei-Kalua`a ridge S of Pu`uhapapa, on a small side ridge, in Kalua`a Gulch, [21°27′52.3″N, 158°06′9.6″W], 17 Apr 1990, *Obata et. al. s.n.* (BISH [2]); off Makaha-Wai`anae Kai ridge, near two pinnacle rocks, *Obata & Perlman JO(85)546* (BISH); Wai`anae Kai, on Kamaile`unu slopes below Pinnacle Rocks, Wai`anae Valley side of Saddle Ridge, *Perlman 5484* (BISH, MO, PTBG [2]); Wai`anae Mts., ridge between Pu`ukalena and Mt. Ka`ala, *Perlman & Garnett 16697* (NY, PTBG, US); Lualualei, slopes of Pu`uhapapa, N-facing cliffs, [21°26′39.6″N, 158°05′57.4″W], *Perlman et. al. 14065* (NY, PTBG, US, WU); summit of Pu`ukaua, Lualualei, N of Pu`ukaua, NW facing cliffs, *Perlman & Wood 14072* (BISH, MO, PTBG, US); Wai`anae Valley, Hiu, 22 Jun 1933, *Russ s.n.* (BISH); Wai`anae Kai Forest Reserve, crestline near Pu`ukawiwi, *Takeuchi et. al. Waianae 106* (BISH); Kamaile`unu near Pinnacle Rock, [21°30′4.9″N, 158°09′43.2″W], *Takeuchi et. al. 2112* (BISH [2], GB, NY); Hapapa, near rim, *Welton & Fenstermacher 319* (BISH); Wai`anae Kai, Makaha rim, *Welton & Marr 705* (BISH); Kaluakauila Gulch, [21°33′5″N, 158°13′22.6″W], *Welton et. al. 164* (BISH); Wai`anae kai, up ridge toward Ka`ala, NW ridge from Gouania vitifolia, *Wood 3438* (NY, PTBG, US); Wai`anae Range, Makaha side of dividing ridge, W of Wai`anae Kai N of Pu`u Kawiwi, S of pinnacle peaks, *Wood 7831* (PTBG, US); Pu`ukaua Region, Laulualei, N-facing cliff along ridge just N of Kaua, *Wood 10640* (PTBG); Lualualei, across via Kolekole contour trail, *Wood & Lau 10585* (PTBG); Pu`ukaua Region, Lualualei, steep ridge just to S of Kaua, *Wood & Lau 10633, 10634* (PTBG); Wai`anae Range: central, `Ewa district, Honouliuli Forest Reserve, *Wood et. al. 304* (BISH, PTBG, US); Wahiawa District, forest below Kumukalii and Kalena, [21°29′1.2″N, 158°7′35.3″W], *Wood et. al. 1907* (PTBG, US); Wai`anae District, Lualualei, ridge W of Pohakea Pass, NW of Palikea, *Wood et al. 3053* (PTBG); Wai`anae Mts., Pu`ukaua, *Wood et al. 3076* (BISH, MO, NY, PTBG, US).

CULTIVATED. **O`ahu.** Wai`anae Range: Kalua`a Gulch, S of Pu`uhapapa, 29 Jul 1991, *Obata et. al. s.n.* [cult. *Weller & Sakai 879*] (BISH, US), *Weller & Sakai 879* [cult. *Wagner & Shannon 6839*] (BISH, PTBG, US); Kaluakauila Gulch, March 1987, *Wagner s.n.* [cult. *Weller & Sakai 862*] (US); on ridge separating Makua and Wai`anae Valleys, ca. 1.3 km W of junction of trail up Wai`anae Valley and crest trail, 1987, *Obata s.n.* [cult. *Weller & Sakai 866*] (US), *Weller & Sakai 866* [cult. *Wagner & Shannon 6841*] (BISH, PTBG, US); ridge separating Wai`anae Kai and Makaha Valley, 20 June 1985, *Weller & Sakai s.n.* [cult. *Weller & Sakai 794*] (BISH, NY, PTBG, US), *Weller & Sakai 794* [cult. *Wagner & Shannon 6842*] (BISH, PTBG, US); Wai`anae Kai, below Ka`ala (cuttings from J. Obata), *Weller & Sakai 891* [cult. *Wagner & Shannon 6851*] (BISH, PTBG, US); Wai`anae Kai, gulch between the Makaha-Wai`anae ridge and Pu`ukalena, 1992, *Obata s.n.* [cult. *Weller & Sakai 899*] (US), *Weller & Sakai 899* [cult. *Wagner & Shannon 6840*] (BISH, PTBG, US); Keawa`ula, Kaluakauila Gulch, [21°33′5″N, 158°13′22.6″W], *Lau 2394* (BISH).

Schiedea hookeri is related to *S. menziesii* and *S. sarmentosa* but differs in its looser, fewer-flowered inflorescences, occurrence in mesic forest, and from *S. sarmentosa* in being hermaphroditic. *Schiedea hookeri* hybridizes with *S. mannii* (see discussion under *S. mannii*, no. 30). *Schiedea hookeri* was listed as endangered in 1996 (Russell & Bruegmann 1996b).

Table 8 in Wagner et al. (1990) was used for reconstruction of the collection date of the type. The K sheet of the Menzies collection, long assumed to represent the holotype (e.g., Sherff 1945), cannot be because Asa Gray never saw it, nor did he mention it in the protologue. This is clear from correspondence from W. J. Hooker to Gray about this collection (enclosed along with the fragment from the K specimen) mounted on a herbarium sheet at GH. In his letter, Hooker describes the Menzies collection at K in some detail (although concluding that it represented *S. ligustrina*). Much of Gray's description comes from study of the fragment from the K sheet sent with Hooker's letter, which consists of part of an inflorescence and two crumpled leaves, but he also used the details in Hooker's letter.

The specific epithet honors William J. Hooker (1785–1865), British botanist and Director of Royal Botanic Gardens, Kew, who described two species of *Schiedea* and corresponded with Asa Gray about this one.

25. Schiedea menziesii Hooker, Hooker's Icon. Pl. 7: t. 649, 650. 1844.—TYPE: HAWAIIAN ISLANDS. [MAUI: West Maui,] "Mowee" [11–18 Mar 1793], *A. Menzies s.n.* (holotype: K! [photos BISH, NY, PENN]; isotype: MO!).

Schiedea menziesii var. *spergulacea* Hillebrand, Fl. Hawaiian Isl. 35. 1888.—TYPE: HAWAIIAN ISLANDS. LANA`I: 1864–1865, *H. Mann & W. T. Brigham 342* (holotype: B, destroyed, photo: BISH; isotypes: BISH-4 sheets! F-2 sheets! BM! GH! MASS! MO! NY! UC! US!, photo of F isotype: F!).

Schiedea menziesii var. *forbesii* Sherff, Amer. J. Bot. 31: 155. 1944.—TYPE: HAWAIIAN ISLANDS. MAUI: West Maui, Lahaina Luna Gulch, Aug 1910, *C. N. Forbes 311.M* (holotype: NY, photo: F!; isotypes: BISH-2 sheets!).

Schiedea menziesii var. *lihauensis* St. John, Bull. Torrey Bot. Club 111: 479. 1984.—TYPE: HAWAIIAN ISLANDS. MAUI: West Maui, foothills of Lihau Peak, on open ridge, 2500 ft [760 m], 2 May 1979, *R. D. Hobdy 511* (holotype: BISH-497527!).

Sprawling perennial herbs, becoming woody toward base; stems 3–10 dm long, multi-stemmed from the base, forming clumps, the primary stems many-branched, weakly ascending to sprawling, green or purple-tinged, glabrous below, puberulent, usually densely so in the upper stems and inflorescence. Leaves opposite, 2–9 cm long, 0.15–1 cm wide, thin and membranous, linear to linear-lanceolate or linear-elliptic, falcate, with 1 or 3 principal veins, the midvein excentric, glabrous except puberulent along adaxial midvein, margin and toward the base, the hairs translucent, spreading to somewhat appressed, 0.1–0.2 mm long, margins slightly revolute, especially toward the base, apex attenuate and often recurved, gradually tapering to base. Inflorescence terminal, with 8–100 flowers, 2–8 (–10) cm long, laterally contracted, the branches and pedicels ascending to somewhat appressed, moderately puberulent with whitish retrorsely spreading to erect hairs 0.05–0.4 mm long; bracts green, linear to subulate, those of central axis 2–30 mm long, those of branches and flowers 1–1.5 mm long; pedicels 3–9 mm long, slender, inconspicuously flattened. Flowers hermaphroditic. Sepals 4–5 mm long, narrowly lanceolate and usually undulate, green, opaque, strongly reflexed and convex in the proximal 1/3, producing a small transverse bulge, the distal part concave, becoming navicular in the distal 1/4, often recurved toward the apex, oriented at ca. 30° angle to the pedicel, moderately puberulent, the hairs 0.05–0.25 mm long, margins conspicuously scarious, ciliate, apex acute to obtuse. Nectary base 0.75–1 mm long, dull yellow, the nectary shaft 3.7–4.3 mm long, at 90° to the axis, apex bifid. Stamens 10; filaments subequal, 10 mm long; anthers 0.9–1 mm long, yellow. Styles 3 (–4). Capsules 3–4.5 mm long, ovoid. Seeds ca. 0.8 mm long, orbicular-reniform, compressed, the surface transversely rugose. Chromosome number: $2n$ = possibly 50–52 (*Weller & Sakai 849*). Figs. 2P, 46.

Distribution (Fig. 47). Lana`i (Maunalei Valley) and West Maui (Hahakea, above Lahaina, Lahaina Luna Gulch, Lihau, and Ma`alaea); uncommon on ledges and cliffs in shrubland, in scattered localities; 30–670 m.

ADDITIONAL SPECIMENS EXAMINED. **Lana`i.** Maunalei Gulch, mauka of pump house, *Degener et. al. 28390* (B, BISH, F, K, NY); without locality, 1870, *Hillebrand s.n.* (K); 1870, *[Hillebrand] s.n.* (BISH); Maunalei Valley, 21 Apr, *Munro s.n.* (BISH), *Munro 131* (BISH), *Munro 508* (BISH), *Munro 933* (BISH, GH, P); Maunalei, in cliff near head of valley, *Munro 328* (BISH). **Maui.** WEST MAUI: Ma`alaea, *Hillebrand & Lydgate 130* (BISH); Lahaina, *Hillebrand & Lydgate 131* (BISH); Ukumehame, Makiwa Gulch [20°49′07″N, 156°34′34″W], *Oppenheimer H110150* (PTBG); Lihau Peak, ridgetop, 1 May 1979, *Perlman s.n.* (BISH); Lihau Peak, 3 May 1979, *Perlman s.n.* (BISH, PTBG); Lihau N.A.R., T.N.C. survey transect 4, *Perlman et. al. 8442*

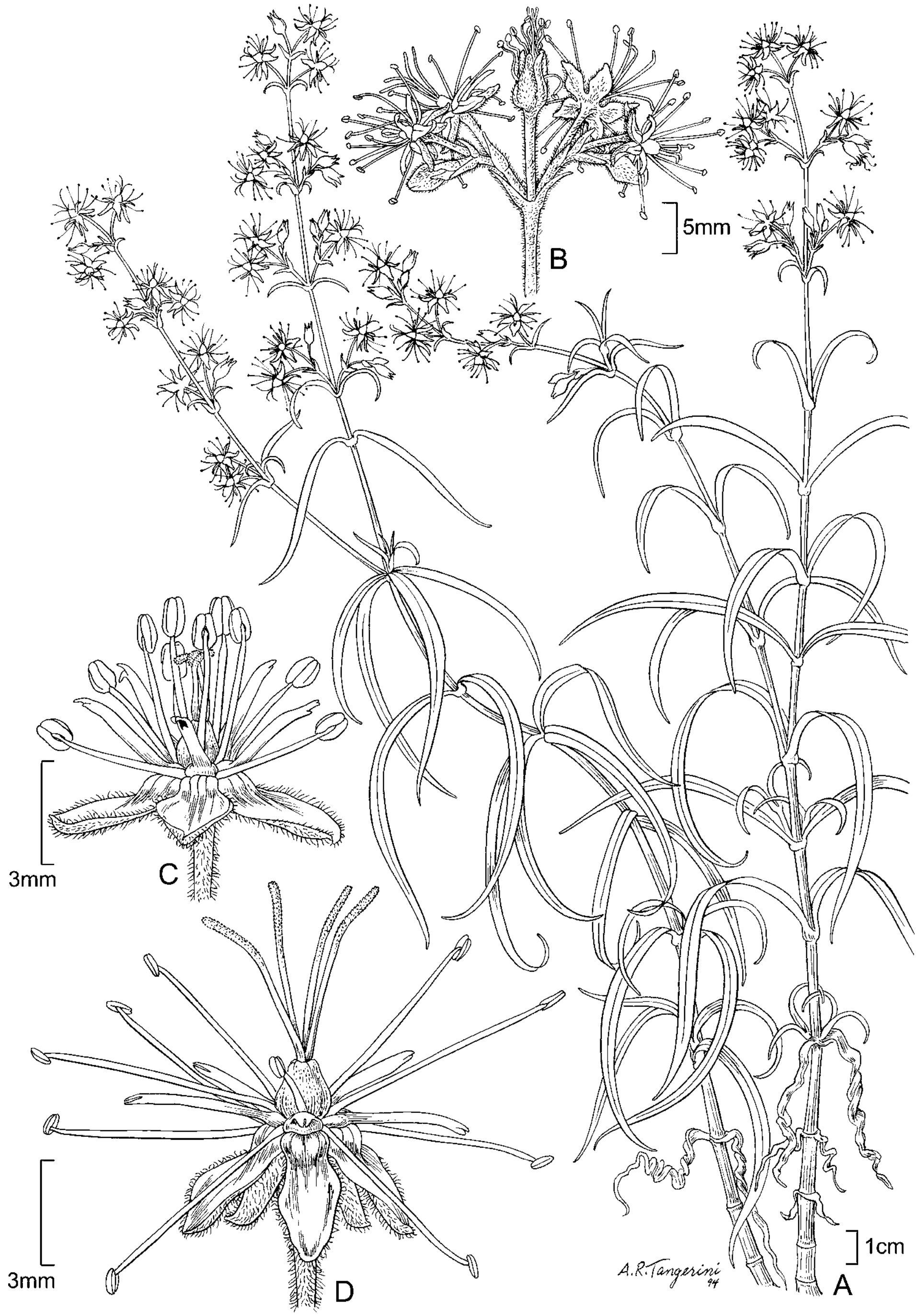

FIG. 46. *Schiedea menziesii* (cult. from *Weller & Sakai 849*). A. Habit. B. Portion of inflorescence. C. Flower in early anthesis, male stage. D. Flower in later anthesis, female stage.

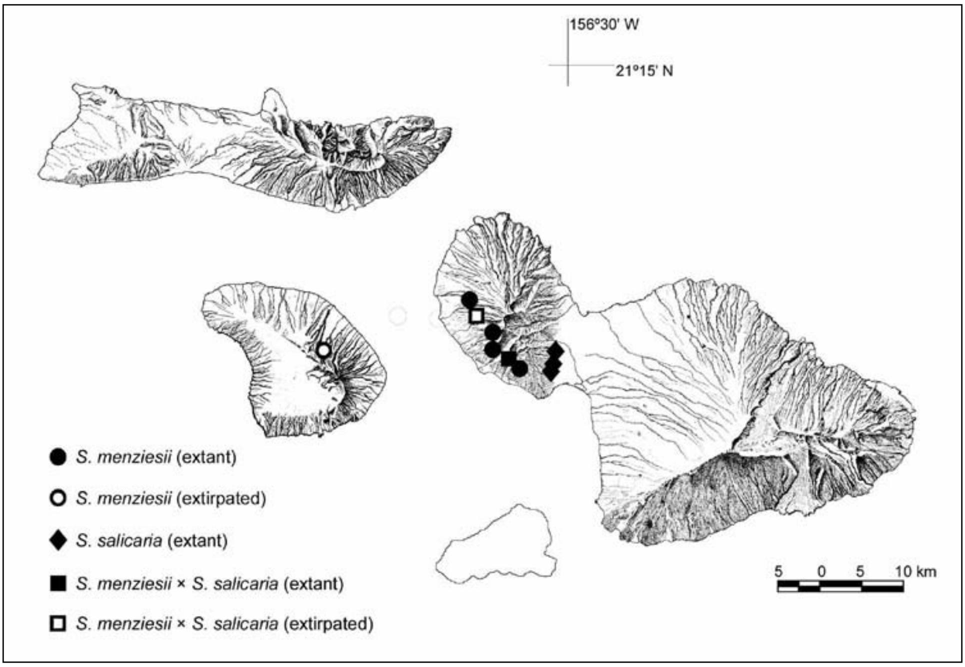

FIG. 47. Distribution of *Schiedea menziesii*, *S. salicaria*, and putative hybrids of *S. menziesii* and *S. salicaria*. (The locality of the more northern putative hybrid population is based on Hillebrand's collections and thus approximate.)

(PTBG, US); Lihau, [20°50′21.2″N, 156°36′40.1″W], *Welton & Haus 1118* (BISH); Lahaina District, Lihau between Olowalu and Launiupoko, on N facing hillside and rock faces, *Wood & Perlman 330* (BISH, PTBG, US).

CULTIVATED. **Maui.** WEST MAUI: Lihau ridge, 27 Jan1987, *Weller & Sakai s.n.* [cult. *Weller & Sakai 849*] (BISH, NY, PTBG, US), *Weller & Sakai 849* [cult. *Wagner & Shannon 6787*] (BISH, US), *Weller & Sakai 849* [cult. *Wagner & Shannon 6823*] (US).

Schiedea menziesii hybridizes with *S. salicaria* (see discussion under *S. salicaria,* no. 32). Occasional pistillate plants have been detected in progeny of *S. menziesii* raised in the greenhouse, and more extensive field surveys may reveal the occurrence of infrequent pistillate plants (Rankin et al. 2002).

The only place that Menzies collected that is within the known range of *S. menziesii* is West Maui (Wagner et al. 1990, p. 117). The collection date was reconstructed using Table 8 in Wagner et al. (1990).

The specific epithet honors Archibald Menzies (1754–1842), who was among the first to explore the Hawaiian Islands after European discovery. He collected most of the main islands in 1792, 1793, and 1794 while serving as surgeon and naturalist on the *Discovery* under the command of Capt. George Vancouver.

26. Schiedea sarmentosa Degener & Sherff in Sherff, Amer. J. Bot. 33: 504. 1946.—TYPE: HAWAIIAN ISLANDS. MOLOKA`I: southeastern Moloka`i, East Fork of Kawela Gulch, on very dry, sunny, rocky slope, 11 Jun 1928, *O. Degener 5947* (holotype: F-1176576!, photos: F-2 sheets! PH!; isotypes: B! BM! F! G! GB-2 sheets! GH! LE M! NY! P! PENN! US! W!, photo of F isotype: F!).

Schiedea menziesii Hook. var. *molokaiensis* Sherff, Amer. J. Bot. 31: 155. 1944.—TYPE: HAWAIIAN ISLANDS. MOLOKA`I: on slopes below Pu`ukolekole, Jul 1912, *C. N. Forbes 133.Mo* (holotype: NY!, photo: F!; isotypes: BISH-3 sheets! MO! UC! US!).

Gynodioecious, sprawling perennial herbs, becoming woody toward base; stems 1.5–5 dm long, multi-stemmed from the base, forming dense tangled clumps, the primary stems many-branched, weakly ascending to sprawling, internodes (1.4–) 2.5–5 (–5.7) cm long, green or purple-tinged, glabrous below, puberulent, usually densely so, on the upper stems and inflorescence. Leaves opposite, usually spreading or reflexed, 3–5 (–7) cm long, 0.15–0.5 cm wide, thin and membranous, linear or linear-elliptic, falcate, with 1 or 3 principal veins, the midvein excentric, sparsely to moderately puberulent, especially along adaxial vein and near the margins, the hairs 0.05–0.1 (–0.2) mm long, spreading to nearly erect, the hairs white-opaque, at least some of the hairs gland-tipped, margins slightly revolute, especially toward the base, apex attenuate and often slightly curved, gradually tapering to base. Inflorescence terminal, with 13–35 flowers, 8–12 cm long, laterally contracted, lateral branches short, the branches and pedicels ascending to somewhat spreading, moderately puberulent with hairs like those of the leaves, the hairs retrorsely appressed, spreading to erect; bracts green, linear to subulate, those of central axis 5–35 mm long, those of branches and flowers 1–1.5 mm long; pedicels 3–6 mm long, slender, inconspicuously flattened. Flowers hermaphroditic or pistillate. Hermaphroditic flowers: Sepals 2.8–3.5 mm long, narrowly ovate, green or tinged purple toward the apex, opaque, strongly reflexed and convex at the base, producing a small transverse bulge, the distal part concave, deeply navicular in the distal 1/2, often inrolled at the apex, oriented at 70° to 80° angle to the pedicel, moderately puberulent, the hairs 0.05–0.25 mm long, some of them gland-tipped, margins conspicuously scarious, weakly lacerate, ciliate at the base, apex obtuse; nectary base 0.35–0.55 mm long, dull yellow, the nectary shaft 0.5–1.5 mm long, at 60° to the axis, apex laciniate; stamens 10, filaments subequal, 3.4–4.1 mm long, anthers 0.75–0.9 mm long, yellow; styles 3 (–4). Pistillate flowers: Sepals 2.1–2.8 mm long, narrowly ovate, green or tinged purple toward the apex, opaque, strongly reflexed and convex at the base, producing a small transverse bulge, the distal part concave, broadly and deeply navicular in the distal 1/2, often involute at the apex, oriented at 70° to 80° angle to the pedicel, moderately puberulent, the hairs 0.05–0.25 mm long, some of them gland-tipped, margins conspicuously scarious, ciliate at the base, apex obtuse; nectary base 0.3–0.4 mm long, dull yellow, the nectary shaft 0.7–0.9 mm long, at 60° to the axis, apex laciniate; stamens 10, vestigial, the filaments subequal, 0.4–0.9 mm long, anthers ca. 0.25 mm long, yellow, not producing pollen; styles 3 (–4). Capsules 2.3–2.7 mm long, narrowly ovoid. Seeds 0.6–0.8 mm long, orbicular-reniform, compressed, the surface transversely rugose. Chromosome number: 2n = 55–60 (*Wagner et al. 6675, 6681*). Figs. 2Q, 48.

Distribution (Fig. 49). Leeward Moloka`i, Pu`ukolekole, Kamalo, and Kawela gulches; on steep rocky cliffs and ledges; 500–1000 m.

ADDITIONAL SPECIMENS EXAMINED. **Moloka`i.** `Onini Gulch, on bluff on E slope, [21°06′7.9″N, 156°57′11.8″W], *Bishop 1700* (HAW); Moloka`i Project-Transect 6, upper slopes of large gulley, NW of jeep trail, E Kamiloloa, [21°06′21.3″N, 156°57′3.2″W], *Char et. al. 82.038* (BISH, HAW); Kamolo [Kamalo], [21°05′58.7″N, 156°53′41.1″W], *Faurie 1085* (BISH, P); land of Makakupa`ia `Onini Gulch, S slope, [21°06′30″N, 156°56′58″W], *Lau 2870* (BISH), *Lau 2871* (BISH); Makolelau, bottom of gulch of W facing slopes, 18 Mar 1992, *Norman s.n.* (US); Makolelau Gulch, below Pu`ukolekole, TNC survey, [21°05′15.8″N,

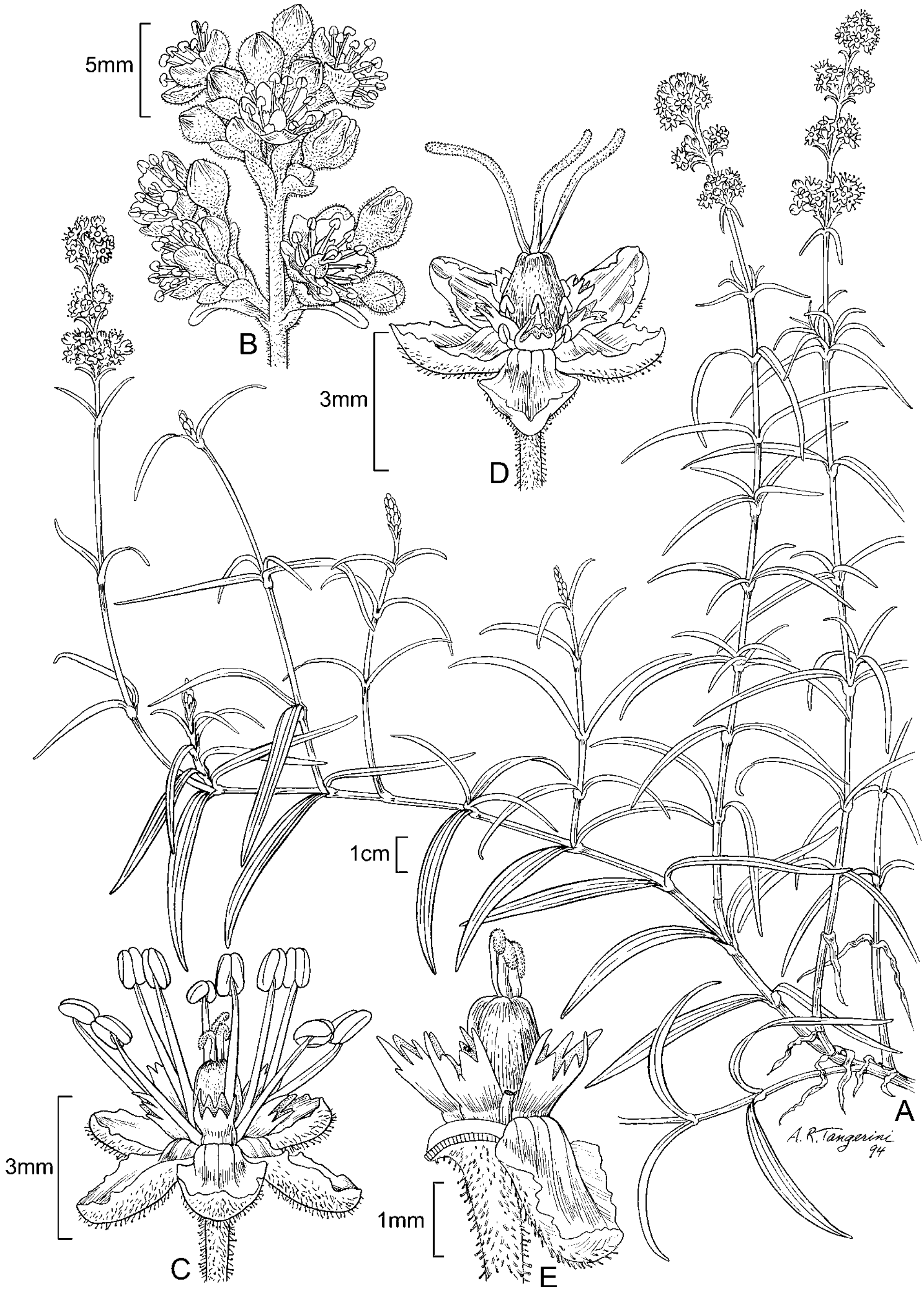

FIG. 48. *Schiedea sarmentosa* (cult. from *Weller & Sakai 896*). A. Habit. B. Portion of hermaphroditic inflorescence. C. Flower, hermaphroditic, show in male stage. D. Flower, female. E. Flower, one sepal and stamens removed to show nectary shafts.

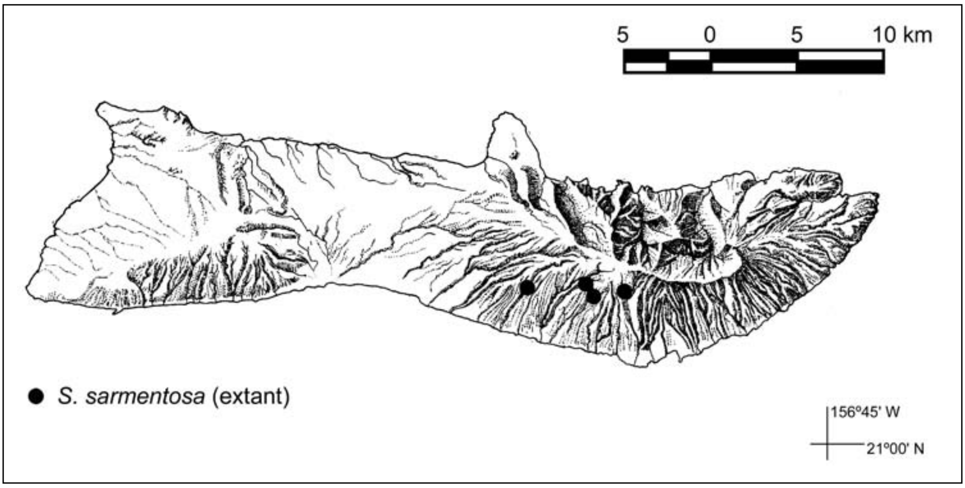

FIG. 49. Distribution of *Schiedea sarmentosa*.

156°54′45″W], *Perlman 6676* (BISH [2], PTBG, US); Makolelau Gulch, on cliffs near streambed by trail to Springs, *Perlman 16565* (PTBG); Makolelau Gulch, below Pu`ukolekole, [21°5′58.9″N, 156°54′57.3W], *Perlman & Burt 17514* (NY, PTBG, US); Makolelau Gulch, [21°05′31.1″N, 156°54′34.1″W], *Perlman & Marr 11988* (PTBG, US); Makolelau, Gulch W of Makolelau gulch, below Pu`ukolekole, *Perlman & Wood 12863* (PTBG); without locality, *Rémy 591* (P); Moloka`i District, Makolelau, first major gulch W of Makolelau, [21°6′N, 156°55′W], *Wagner et. al. 6740* (US); Moloka`i District, Land of Makolelau, old jeep road (adjacent to E side of area) leading to Pu`ukolekole, [21°05′N, 156°55′W], *Wagner et. al. 6681* (US [3]); Makolelau, below and W of Pu`ukolekole, 2nd drainage to E of nearby contour road, *Wood 6038* (PTBG); East Kawela, *Wood & Lau 2893* (PTBG); below Pu`ukolekole, W of Makolelau, [21°05′31″N, 156°54′43.5″W], *Wood & Perlman 1994* (PTBG, US), *Wood & Perlman 2003* (PTBG, US).

Cultivated. **Moloka`i.** Moloka`i District, Land of Makakupaia, `Onini Gulch, [21°06′29.1″N, 156°56′58″W], *Wagner et. al. 6675* (US).

Schiedea sarmentosa differs from *S. menziesii* in its smaller flowers and gynodioecious breeding system. It was included in *S. menziesii* by Wagner et al. (1990) based on examination of the type. When new collections were made after 1990, it was clear that they were from a quite distinct species, although appearing to be closely related. *Schiedea sarmentosa* is known to hybridize with the sympatric *S. lydgatei* at Makolelau Gulch. Recent fires and browsing by goats have eliminated many individuals of *S. sarmentosa,* which was listed as endangered in 1996 (Bruegmann 1996).

The specific epithet refers to the highly branched stems of this species. In classical Latin the adjective *sarmentosus* means “full of twigs” (in botanical Latin *sarmentosus* has come to mean “producing long runners”).

27. Schiedea haleakalensis Degener & Sherff in Sherff, Amer. J. Bot. 29: 332. 1942.—Type: Hawaiian Islands. Maui: East Maui, Mount Haleakala cliffs on W side of Kaupo Gap, 11 Aug 1939, *O. Degener, E. Ordoñez, F. C. Salucop 12695* (holotype: F-1142022!, photos: F-2 sheets!; isotypes: A-3 sheets! BISH! M! MICH MIN! MO! NY-2 sheets! US!; an unnumbered sheet at NA maybe an additional isotype).

Dioecious shrubs 2–6 dm tall; stems numerous from the base ascending to erect, glabrous, internodes 0.5–2.3 long, deep yellowish green. Leaves opposite; blades 4–6 (–8) cm long, 0.18–0.25 cm wide, slightly fleshy, narrowly linear to linear-subulate, weakly falcate, arched to recurved, bright yellowish green, glabrous, with only the midvein evident, the midvein impressed on upper surface, margins thickened and weakly revolute, apex attenuate, base slightly tapering, sessile. Inflorescence terminal, with 8–60 flowers, 2.5–5 cm long, laterally contracted, flowers congested, glabrous or densely puberulent with crinkly hairs to 0.25 mm long; bracts green, linear to subulate, those of central axis 5–20 mm long, those of branches and flowers 1.5–2 mm long; pedicels weakly quadrangular, slightly compressed. Staminate flowers: pedicels 3–6 mm long; sepals 2.5–3 mm long, ovate to broadly navicular, subequal, convex at the base, oriented at 80°to 100° angle to the pedicel, green, yellowish green toward the base, often purple toward the apex, opaque, glabrous or puberulent toward the base and margin, margin scarious and usually with a few lacerations toward the apex, apex obtuse; nectary base 0.5–0.55 mm long, bright yellow, the nectary shaft 1.6–1.9 mm long, arched with the apex touching the subtending sepal and nectar pooling on the sepal, white, apex on the adaxial side with a small notch and on the abaxial side with a deep slit 1/2–2/3 of the way to the base, the slit wider toward the apex; stamens 10, the filaments dimorphic, white, the antisepalous whorl 4.2–4.8 mm long, the alternate whorl 3.9–4.5 mm long, anthers 0.5–0.65 mm long, yellow; styles 3 (–4), short and non-functional. Pistillate flowers: pedicels 3.5–7.5 mm long; sepals 2.3–2.8 mm long, ovate to broadly navicular, subequal, the apex often inrolled, convex at the base, oriented at 90° to 110° angle to the pedicel, green, yellowish green toward the base, often purple toward apex, opaque, glabrous or puberulent toward the base and margin, margin scarious and usually with a few lacerations toward the apex, apex obtuse; nectary base 0.55–0.6 mm long, bright yellow, the nectary shaft 1.25–1.35 mm long, arched with the apex touching the subtending sepal and nectar pooling on the sepal, greenish white, apex on the adaxial side with a small notch and on the abaxial side with a deep slit 1/2–2/3 of the way to the base, the slit wider toward the apex; stamens (9–) 10, the filaments weakly dimorphic, the antisepalous whorl 0.5–0.8 mm long, the alternate whorl 0.4–0.5 mm long, anthers 0.15–0.35 mm long, yellow, not producing pollen; styles 3 (–4). Capsules 3–4 mm long, narrowly ovoid. Seeds 0.7–0.8 mm long, orbicular-reniform, compressed, the surface transversely rugose. Chromosome number unknown. Figs. 2R, 4C, D, 50.

Distribution (Fig. 51). East Maui, west side of Kaupo Gap and Holua Cabin near Ko`olau Gap; extremely rare, known only from sheer arid cliffs; 1770–2440 m.—This species should be sought on north-facing cliffs within the crater.

ADDITIONAL SPECIMENS EXAMINED. **Maui.** EAST MAUI: Haleakala crater, below Haleakala Peak, West Kaupo, [20°42′15.2″N, 156°10′14.4″W], *Medeiros 575* (BISH); cliffs below Wailani head below Haleakala Peak, *Medeiros 576* (BISH); Haleakala Natl. Park, upper W Kaupo Gap, *Stemmermann 1004* (HAW).

CULTIVATED. **Maui.** EAST MAUI: Haleakala National Park, ca. 0.5 mi SW of Holua Cabin, 27 Jul 1991, *Weller & Sakai s.n.* [cult. *Weller & Sakai 851*] (BISH, NY, PTBG, US).

Schiedea haleakalensis is a dioecious, woody shrub characterized by its short, narrow leaves, and glabrous or puberulent inflorescence.

Flowers were described as “perfect(?)” by Wagner et al. (1990) and assumed to be hermaphroditic (Weller & Sakai 1990; Weller et al. 1990); only a few herbarium collections were available for study at that time. Subsequent field work in 1992 and greenhouse studies showed that the species is dioecious (Wagner et al. 1995; Weller et al. 1995).

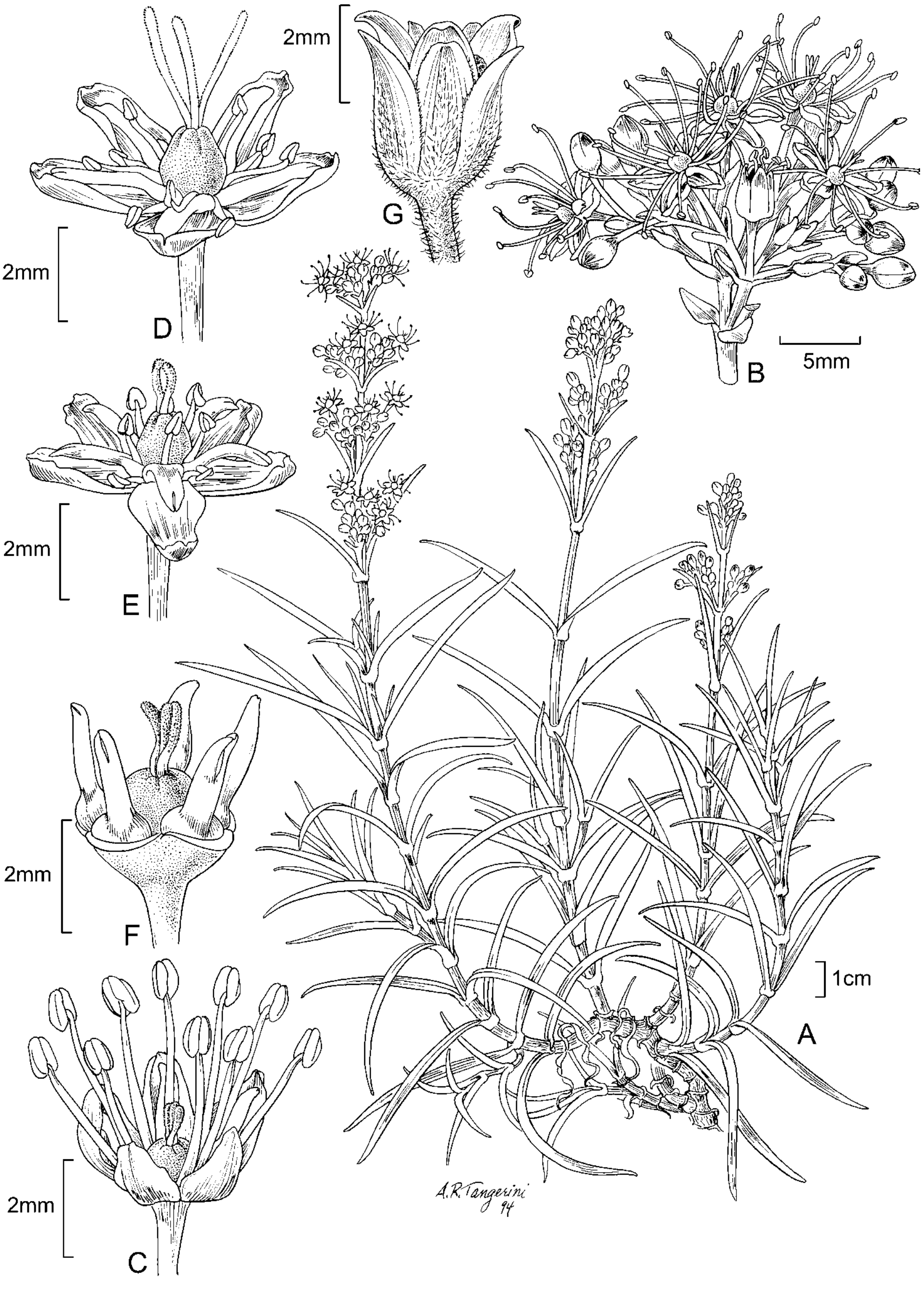

FIG. 50. *Schiedea haleakalensis*. A. Habit. B. Portion of male inflorescence. C. Flower, male. D. Flower in late anthesis, female. E. Flower in early anthesis, female. F. Flower, sepals and stamens removed to show nectary shafts. G. Sepals enclosing capsule from pubescent population. (Based on: A–F, cult. from *Weller & Sakai 851*; G, *Degener et al. 12695* [A].)

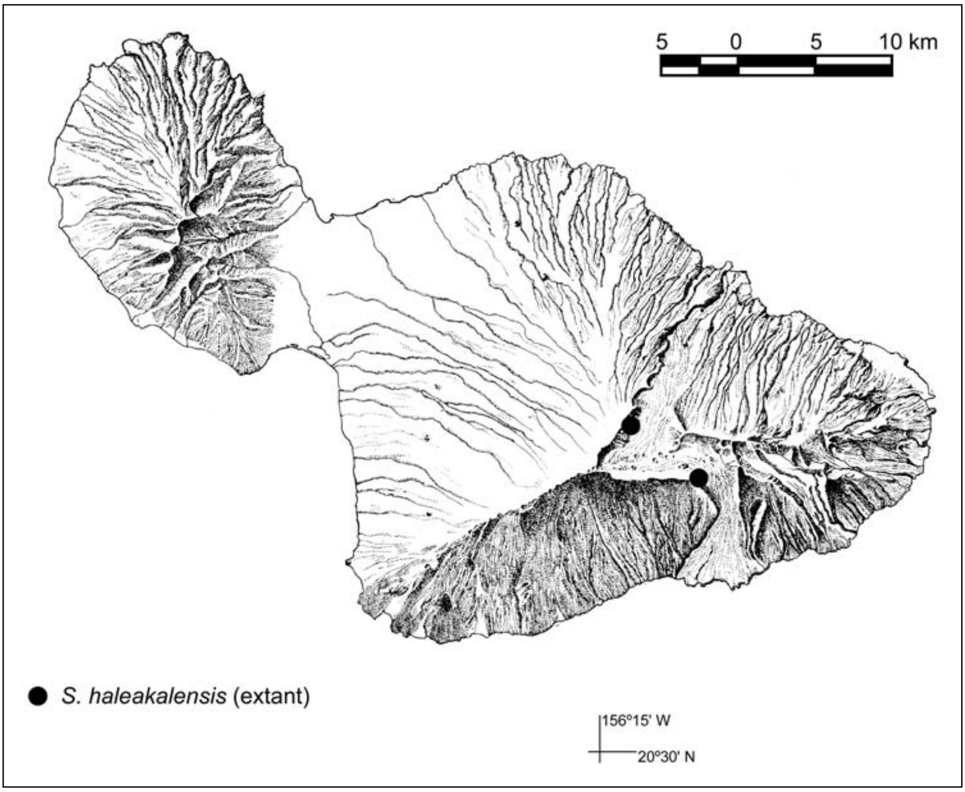

FIG. 51. Distribution of *Schiedea haleakalensis*.

Flowering appears to occur primarily during the summer, unlike in other species of *Schiedea* occurring in dry habitats, and may be a response to the cold winter temperatures at the high elevation where *S. haleakalensis* grows.

Schiedea haleakalensis was federally listed as endangered in 1992 (Herbst et al. 1992a).

In the protologue, Sherff indicated that the "type" was to be at NY and that additional material was to be distributed. Yet, examination of the specimens of the entire type collection shows that the labels are unequivocal in indicating that the holotype is at F, the first duplicate is at NY, and additonal duplicates were sent to other institutions

The specific epithet refers to the occurrence of this species on Haleakala, East Maui.

28. Schiedea globosa H. Mann, Proc. Boston Soc. Nat. Hist. 10: 311. 1866.—TYPE: HAWAIIAN ISLANDS. O`AHU: Makapu`u or Koko Point, 1864–1865, *H. Mann & W. T. Brigham 580* (lectotype, here designated: GH!, photos: F!; isolectotypes: BISH! CU! G! K! MO! NY!, photos of CU isotype: BISH-2 sheets! F!).

Schiedea remyi H. Mann, Proc. Boston Soc. Nat. Hist. 10: 310. 1866.—TYPE: HAWAIIAN ISLANDS. MOLOKA`I: 1851–1855, *J. Rémy 551* (holotype: GH!, photo: F!; isotypes: P-2 sheets!).

Schiedea remyi var. *foliosa* Sherff, Amer. J. Bot. 31: 153. 1944.—TYPE: HAWAIIAN ISLANDS. MOLOKA`I: Halawa Valley, Apr 1910, *J. F. Rock 7008* (holotype: NY!, photo: F!; isotypes: BISH-3 sheets! GH! K, NY! UC!, photo of NY isotype: F!, photos of UC isotype: BISH-2 sheets! F!).

Schiedea globosa var. *graminifolia* Degener & Sherff in Sherff, Amer. J. Bot. 31: 155. 1944.—TYPE: HAWAIIAN ISLANDS. O`AHU: in crevices of cliffs SW of Waimanalo Landing, 10 Apr 1936, *O. Degener 17492* (holotype: F, not located, photo: F!; isotypes: GH! P!).

Schiedea remyi var. *multinervia* Sherff, Bot. Leafl. 9: 5. 1954.—TYPE: HAWAIIAN ISLANDS. MAUI: East Maui, Hana, rocks by the ocean, Sep 1909, *U. Faurie 1094* (holotype: BISH-501736!, photo: F!; isotypes: G-2 sheets! P!).

Schiedea globosa var. *foliosior* Degener & Sherff in Sherff, Brittonia 12: 171. 1960.—TYPE: HAWAIIAN ISLANDS. MAUI: West Maui, Pohakupule, coastal clay ledges, 30 Mar 1959, *O. Degener, I. Degener, W. Fleming 25047* (holotype: F-1537156!, photo: F!; isotypes: B! BISH! G-2 sheets! GH! K, MO! NY! US! W!).

Subdioecious subshrubs, weakly woody only at base; stems 0.5–3 (–10) dm long, usually thick and somewhat succulent, prostrate to ascending, forming clumps, internodes 0.3–2 (–7) cm long, the 1 or 2 below inflorescence elongated to 7–10.5 cm long, yellowish green, glabrous proximally, puberulent or glandular-puberulent on the distal stems and inflorescence; roots fibrous. Leaves opposite, 3–14 (–16) cm long, 0.3–1.5 (–2.5) cm wide, recurved, succulent-coriaceous, glossy, linear or linear-elliptic to linear-subulate, occasionally elliptic-oblanceolate, falcate, 1- or 3- or 5-nerved, the midrib more prominent than lateral veins when present, glabrous, margins entire and inconspicuously revolute, apex long-attenuate, base tapering and connate at the node. Inflorescence terminal, with 69–460 flowers, 1–4 cm long, very congested, head-like, sometimes to 15 cm with 1–2 pairs of additional lateral clusters at the next lower nodes, these somewhat smaller than the terminal dichasia, the staminate inflorescence (occasionally with some hermaphroditic flowers intermixed) less congested and fewer-flowered than the pistillate inflorescence, moderately puberulent or in some populations glandular-puberulent throughout, the hairs erect, translucent, 0.15–0.25 mm long, with or without a small glandular apex; bracts of central axis 2–10 (–30) mm long, those of branches and flowers 1–3 mm long, pedicels 3–9 (–11) mm long, those of staminate (and hermaphroditic) flowers longer than those of pistillate ones, slightly flattened. Staminate flowers: Sepals 2.5–3.3 mm long, ovate, green or tinged purple toward the apex, opaque, reflexed and convex at the base, producing a small transverse bulge, broadly navicular oriented at 100° to 120° angle to the pedicel, moderately puberulent or in some populations glandular-puberulent, the hairs 0.05–0.25 mm long, margins conspicuously scarious, entire, glabrous, apex obtuse; nectary base 0.6–0.75 mm long, greenish yellow, the nectary shaft plump, 1.1–1.3 mm long, arched and usually making contact with the sepal surface and nectar pooling directly onto the sepal, apex unequally divided, the adaxial lobe longer than the abaxial one, each lobe notched; stamens 10 (–11), filaments subequal, 3.5–4.5 mm long, anthers 0.8–1.3 mm long, yellow; styles 3–6, green, short and non-functional, becoming shriveled. Hermaphroditic flowers occurring occasionally intermixed in staminate inflorescences, numbers varying with site and moisture, similar to staminate flowers except ovary and styles functioning. Pistillate flowers: Sepals 2.5–3 mm long, ovate, green or tinged purple toward the apex, opaque, reflexed and convex at the base, producing a small transverse bulge, deeply navicular, oriented at 100° to 130° angle to the pedicel, moderately puberulent or in some populations glandular-puberulent, the hairs 0.05–0.25 mm long, margins conspicuously scarious, entire, glabrous or with scattered hairs externally, apex obtuse;

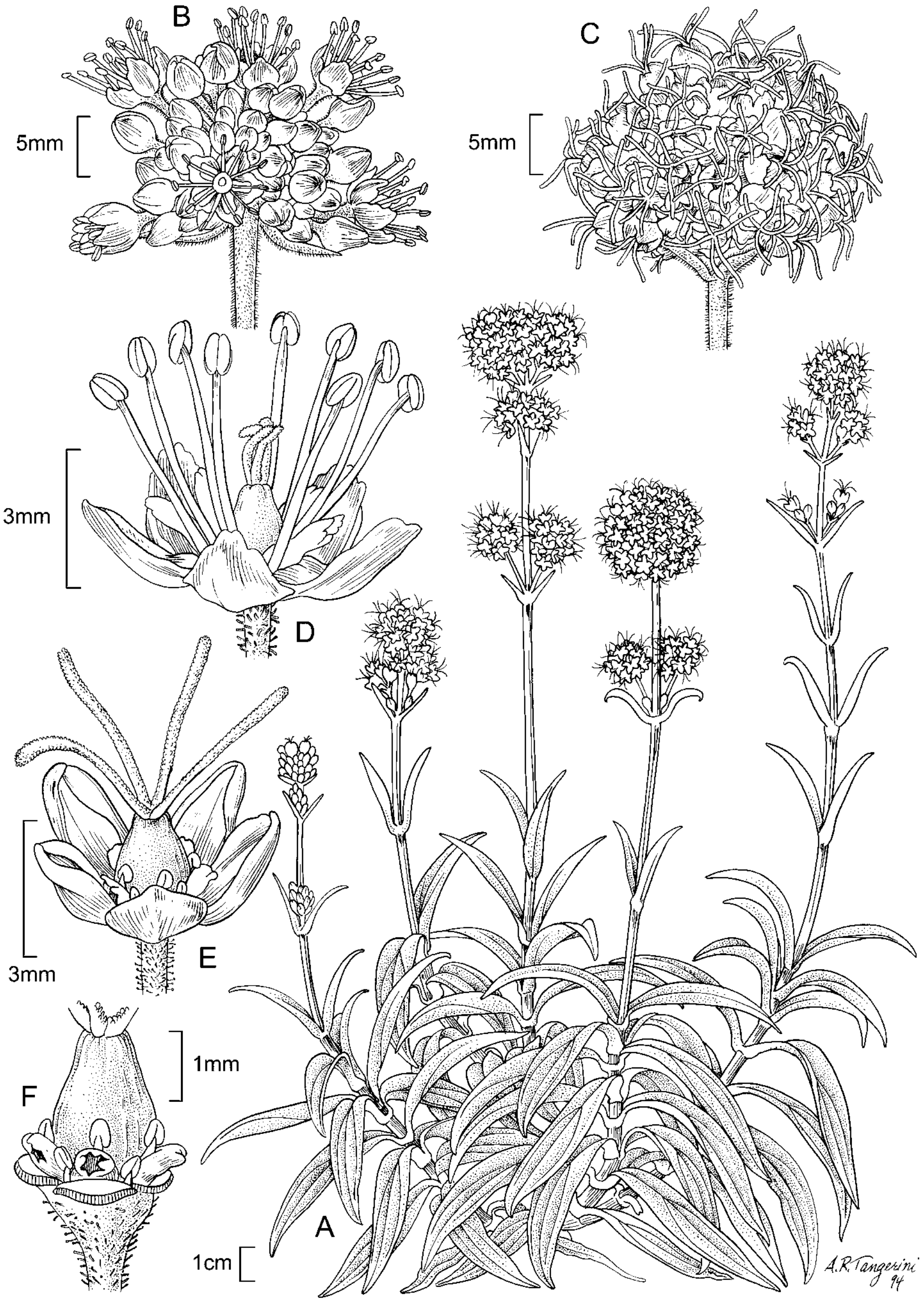

FIG. 52. *Schiedea globosa* (cult. from *Weller & Sakai 844*). A. Habit. B. Inflorescence, male. C. Inflorescence, female. D. Flower, male. E. Flower, female. F. Female flower, sepals removed to show vestigial stamens and nectary shafts.

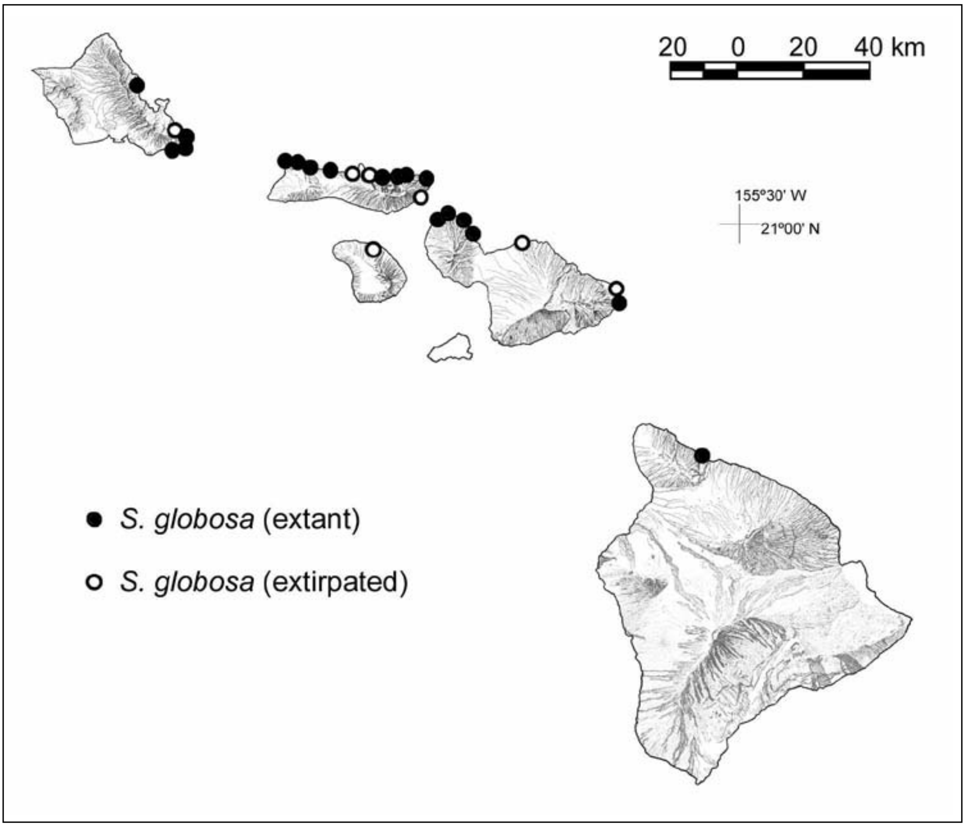

FIG. 53. Distribution of *Schiedea globosa*. (The Lana`i locality is based on the Rémy collection and thus approximate. The northwesternmost locality on Moloka`i at Ilio Point is based on field observations by William Garrett.)

nectary base vestigial, 0.2–0.5 mm long, sometimes divided into two unequal parts, producing little or no nectar, greenish yellow, the nectary shaft plump, 0.9–1.2 mm long, arched and usually making contact with the sepal surface and nectar, if produced, pooling directly onto the sepal, apex very unequally divided, the adaxial lobe longer than the abaxial one, each lobe deeply notched; stamens (9–) 10 (–11), vestigial, filaments unequal, but alternate whorl always shorter than the antisepalous whorl, 0.6–1.5 mm long, anthers 0.2–0.3 mm long, yellow, not producing pollen; styles 3–6. Capsules 2–4.5 mm long, narrowly ovoid. Seeds 0.7–0.8 mm long, relatively few, orbicular-reniform, compressed, the faces transversely rugose, the margins papillose. Chromosome number: 2n = 44–46 (*Weller & Sakai 844*). Figs. 2S, 4E, F, 52.

Distribution (Fig. 53). Eastern to southeastern O`ahu, northern coast of Moloka`i (one population on the south side of East Moloka`i: *Forbes 594.Mo*, Moanui), north coasts of East and West Maui, and coastal cliffs of Waipi`o Valley, Hawai`i, one collection from Lana`i; scattered to locally common on steep, north-facing rocky slopes or cliffs in coastal habitats; sea level to 460 m.

ADDITIONAL SPECIMENS EXAMINED. **Hawai`i.** Kohala Mts., Waipio Valley, seacliffs E of valley along coast ca. 300 m E of beach, [20°07′12.3″N, 155°35′4.2″W], *Perlman & Wood 15191* (PTBG, US). **Lana`i.** without locality, *Rémy 551bis* (P). **Maui.** EAST MAUI: Maliko near Pa`ia, [20°56′15.7″N, 156°20′29.3″W], *Degener 21952* (B, BISH, F, G, K, MO, NY, P, PH, UC); Hana, [20°45′26.1″N, 155°58′46.3″W], *Forbes 267.M* (BISH, MO, NY, UC, US); `Alau Island, [20°43′42.6″N, 155°58′38.8″W], *Hobdy 1302* (BISH).—WEST MAUI: Maui Zoological & Botanical Gardens, Lahaina side of valley, from Kahakuloa area, on 3 ridges, *Davis & Sylva 46* (BISH); Kahakuloa, [20°59′52.4″N, 156°32′35.5″W], *Degener 21964* (B, BISH, G, GB, MASS, MO, NY, P, S, UC, US); summit of Pu`ukoa`e, *Forbes & Stokes 314.M* (BH, BISH, NY); N coastline at Kukuipuka (N of Waihe`e), *Hobdy 2480* (BISH), *Hobdy 2481* (BISH); Honolua, scattered between Kamane and Punalau, *Oppenheimer H40017* (PTBG); Kahakuloa, on Pu`ukahulianapa, *Perlman & Wood 16202* (PTBG); Laho`ole, *St. John 26717* (BISH); Wailuku, Kahakuloa, right side mouth of Makamaka`ole Stream, 8 Jul 1979, *Sylva & Clarke s.n.* (HAW); rocky bluff overlooking Kahakuloa Bay, N and NW facing slope, *Weller & Sakai 852* (US). **Moloka`i.** Near Mo`omomi, [21°12′1.3″N, 157°9′37.2″W], Feb 1915, *Coore s.n.* (BISH); W side of Halawa Valley, [21°10′15.3″N, 156°44′20.6″W], *Degener 5938* (B, F, G, K, NY [2], UC); between Halawa Valley and Halawa Iki Gulch, *Degener 5939* (F, K, NY); cliffs just SW of Kalaupapa leper settlement, [21°10′53.9″N, 156°59′40.3″W], *Degener 5941* (F, NY); N of Ho`olehua, [21°11′20″N, 157°3′52″W], *Degener 5943* (F, GH, NY); Wailau Valley, *Degener & Nitta 5946* (F); in rupibus littoris Wailau, [21°10′5″N, 156°50′20″W], *Faurie 1086* (BISH, G, P); Settlement Trail, *Forbes 22.Mo* (BISH); near the coast between Wailau and Wai`ehu, *Forbes 529.Mo* (BISH, P, UC, US); Moanui, [21°6′14.7″N, 156°44′57.5″W], *Forbes 594.Mo* (A, BISH); seashore of Waikolu, s.d., *Hillebrand s.n.* (BISH-fragment from B); without locality, 1870, *Hillebrand s.n.* (BM, GH, K, MEL); Kaholaiki Bay, [21°9′53″N, 156°52′31″W], *Hobdy 2177* (BISH); Pala`au, Ho`olehua Homesteads abandoned dump on coastal Pali, *Lowrey 452* (BISH, UC); sea cliffs N of Ho`olehua near Manaeopapa, *Nagata 1856* (BISH), *Nagata 1857* (A); Ka`aloa, above Haupu Bay, *Perlman 6223* (PTBG); Waiehu, W of Wailau, coastal cliffs above Waiehu shelf, *Perlman & Wood 17531* (PTBG); Mokapu Islet, offshore islet off N coast, N side of islet, *Perlman et al. 16993* (PTBG); without locality, *Rémy 590?* (P); Waikolu, *Rock 6184* (BISH, F, GH [2], NY, P, US); Wailau Valley, *Rock 7007* (BISH); [locality uncertain] *Rock 14059* (B, BISH), *Rock 14067* (BISH); Pu`ukauwa, Waikolu, base of sea cliff, [21°10′9.2″N, 156°56′3.5″W], *St. John et. al. 23414* (BISH [2]); Anapuhi to Wainene, long coastal boulder-strewn beach, vertical cliff 10-30 m from water, [21°9′52.7″N, 156°54′40.3″W], *Wagner & Lorence 5741* (BISH); Huelo Islet, [21°10′15″N, 156°55′16.7″W], *Wood et. al. 3829* (PTBG, US); Wailau Valley, seacliffs of Wailau, *Wood 3818* (PTBG). **O`ahu.** E slope facing Hanauma Bay, in crevasses, *Bruegmann 106* (BISH, US); slopes of crater facing Hanauma Bay, SE O`ahu, *Carlquist 1688* (BISH, GH, RSA); Makapu`u, on cliffs makai of road, *Char 70* (HAW [2]); slopes of crater, 16 Nov 1924, *Christophersen s.n.* (BISH); above Hanauma Bay, [21°15′57.4″N, 157°39′37.2″W], *Cowan 946* (G, MIN, W); Makapu`u, highway turns from windward to leeward side, *Carlquist 2420* (BISH, RSA, UC); without locality, *Degener 5936* (coll. D. L. Topping) (F, NY); Waimanalo, *Degener 5961* (F, NY); on cliff SW of Waimanalo Landing, *Degener 17491* (GH, P); on cliff by roadside facing Waimanalo Bay, *Degener 21688* (coll. M. Kerr) (K); E of Waimanalo, on exposed ledge, [21°19′29.3″N, 157°41′10.9″W], *Degener & Degener 24085* (BM, GB, US); Makapu`u Head, [21°18′36.3″N, 157°39′1.4″W], *Degener & Park 5924* (B, F [2], G, GH [2], NY, P, UC); on side cone, [21°15′57.4″N, 157°39′37.2″W], *Fagerlind & Skottsberg 6849* (GB, S); Makapu`u, *Flynn 779* (PTBG); Hanauma Bay, *Forbes 2446.O* (BISH, F, K, NY, P, UC, US); 11 Jun 1909, *Forbes s.n.* (BISH, MO, NY); [21°15′57.4″N, 157°41′39″W], 25 Mar 1933, *Furmidge s.n.* (BISH); Wai`anae Range, Mt. Ka`ala, in center of open bog "meadow," just S of end of road, *Gillett 1612* (BISH) [probably mislabelled]; cliffs across from Makapu`u Beach Park, *Gustafson 2910* (RSA [2]); [21°15′57.4″N, 157°41′39″W], *Gustafson 2911* (RSA), Makapu`u Head, *Hatheway et. al. 149* (G, PH, US); arid cliffs above Makapu`u Beach, [21°18′35.4″N, 157°39′37.2″W], *Herbst 1370* (BH, GB, HAW); without locality, 1851–1871, *Hillebrand s.n.* (B, S, US); Koko Crater: in small valley bottom, *Hume 177* (BISH); Waimanalo, near road, 0.5 mi N of Hawaiian village, [21°19′29.3″N, 157°39′1.4″W], 8 May 1945, *Kerr s.n.* (BISH); Makapu`u Point, by road, 26 Jun 1945, *Kerr s.n.* (BISH); tuff cone S of Hanauma Bay, Maunaloa, *Lamoureux et. al. 565* (HAW); Makapu`u Point, cliff, 14 Dec 1957, *Kitamura s.n.* (HAW); Honolulu, *Meebold 20496* (M); Koko Head, *Meebold 28120* (M); Ko`olau Range: around Hanauma, *Nakamoto 68* (HAW); rim, 30 Mar 1930, *Neal s.n.* (BISH); rocks of Nu`uanu Pali, s.d., *Nuttall s.n.* (F); Ko`olau ridge top, above Sea Life Park, Waimanalo, *Obata & Funk 401* (BISH); without locality, *Ozaki 1446* (W-4172); Makapu`u Head, from head to next high peak W of slope, *Obata & Palmer 396* (BISH); Koko Head, Mar 1948, *Pearsall s.n.* (BISH); W side of Hanauma Bay near `Ihi`ihilauakea Crater, *Perlman & Bruegmann 9401* (BISH, PTBG); Makapu`u cliffs above road at Makapu`u Beach Park in gulch halfway down road toward beach, *Perlman et. al. 5451* (MO, PTBG); without locality, *Rémy 552 p.p.* (GH, P [2]); Waimanalo, *Rock 12924* (coll. McCaughey) (BISH, K); cliffs, 12 Jan 1957, *Rock s.n.* (BISH); Maunalua, *St. John 12981* (BISH); Kalama-Mau`uwaii summit, Maunalua, *St. John 20133* (A, BISH, G, UC), *St. John 20134* (BISH, GH); Makapu`u, on rocky vertical cliffs along road from lookout to beach, SE most O`ahu, *Stone 2738* (BISH [2], US); head of Kealakipapa [near Makapu`u Pt.], 4 Feb 1934, *Swezey s.n.* (BISH); rocky slopes above Makapu`u Beach, *Takeuchi Koolau 60a* (BISH), *Takeuchi Koolau 60b* (GB), *Takeuchi Koolau 60c* (F); NE slopes, *Takeuchi*

Koolau 72a (UC), *Takeuchi Koolau 72b* (BISH), *Takeuchi Koolau 73* (A); Crater, *Topping 3029* (F); cliffs above Makapu`u Beach, *Wagner et. al. 5312* (BISH); above Hanauma Bay, *Webster 1478* (US); Koko Head, *Wilbur 641* (BH); Haunauma [Hanauma] Bay, *Young 61* (HAW).

CULTIVATED. **Maui.** WEST MAUI: 0.7 mi W of Waihe`e along road to Kahakuloa, 16 Dec 1987, *Weller & Sakai s.n.* [cult. *Weller & Sakai 850*] (US), *Weller & Sakai 850* [cult. *Wagner & Shannon 6849*] (BISH, US); Kahakuloa Bay, [20°59′52.4″N, 156°32′35.5″W], *Weller & Sakai 852* (US); N of excavation pit near Honokohau Bay, 10 Mar 1994, *Weller & Sakai s.n.* [cult. *Weller & Sakai 905*] (BISH, US), *Weller & Sakai 905* [cult. *Wagner & Shannon 6852*] (BISH, US). **Moloka`i.** Mokio Point, 1994, *M. Bruegmann s.n.* [cult. *Weller & Sakai 909*] (US); N coast, cliffs near dump site near Hawaiian Home Lands, [21°11′20″N, 157°03′52″W], *Weller & Sakai 871*, *Weller & Sakai 871* [cult. *Wagner & Shannon 6850*] (US). **O`ahu.** Ko`olau Mountains, near the summit of Pu`ukanehoalani, grown from cuttings supplied by Joel Lau, *Weller & Sakai 964* (US); *Rock 34-57* [cult. 1 Sep 1958, *Souster s.n.a*] (K), *Rock 34-57* [cult. 1 Sep 1958, *Souster s.n.b*] (K); Ko`olau Range, slopes above Makapu`u Beach, 29 Dec 1984, *Weller & Sakai s.n.* [cult. *Weller & Sakai 844*] (BISH, GH, NY, PTBG, US), *Weller & Sakai 844* [cult. *Wagner & Shannon 6847*] (BISH, PTBG, US), *Weller & Sakai 844* [cult. *Wagner & Shannon 6848*] (BISH, PTBG, US); Koko Head, NE of Iheihelaualea overlooking Hanauma Bay, Mar 1994, *Weller & Sakai s.n.* [cult. *Weller & Sakai 906*] (BISH, US), *Weller & Sakai 906* [cult. *Wagner & Shannon 6843*] (BISH, US), *Weller & Sakai 906* [cult. *Wagner & Shannon 6844*] (BISH, PTBG, US); Hanauma Bay, [21°15′57.4″N, 157°41′39″W], *Weller & Sakai 845* (US); s.d. *Young s.n.* [cult. *Beckstrom-Sternberg 1071*] (RSA).

Schiedea globosa is one of the more distinctive species in the genus and is readily recognized by its long internodes just below the very condensed inflorescences, succulent-coriaceous stems and leaves, and subdioecious breeding system. The separation of *S. remyi* from *S. globosa* was based primarily on the occasional presence of parallel lateral nerves. This feature is highly variable, even within populations, and does not appear to support geographically nor ecologically defined infraspecific taxa. Plants from Kanehoalani on O`ahu have more diffuse inflorescences than individuals from other populations of this species.

Schiedea globosa is subdioecious, with the frequency of hermaphrodites varying among populations. Allozyme data (Weller et al. 1996) and studies of DNA diversity (Filatov & Burke 2004) indicate that populations on the Maui Nui complex are derived from those on O`ahu (Weller et al. 1996). Stems of plants from coastal cliffs (*Wagner & Lorence 5741*) were observed floating in the ocean and still capable of growing. *Schiedea globosa* is the most widespread species in the genus, possibly owing to the coastal habitat preference and the possibility of inter-island colonization via rafting (Wagner et al. 1995).

The specific epithet is based on the Latin adjective *globosus* ("spherical") and refers to the dense, head-like inflorescences in this species.

29. Schiedea spergulina A. Gray, U.S. Expl. Exped., Phan. 135. 1854.—TYPE: HAWAIIAN ISLANDS. KAUA`I: on mountains, [probably Oct 1840,] *U.S. Expl. Exped. s.n.* (holotype: US-10260!; isotypes: GH!, photo: F! P!).

Schiedea spergulina var. *leiopoda* Sherff, Amer. J. Bot. 31: 151. 1944.—TYPE: HAWAIIAN ISLANDS. Kaua`i: south-central Kaua`i, along the Hanapepe River, near the Falls, 24–26 Jun 1895, *A. A. Heller 2446 p.p.* (holotype: PH!, photo: F!; isotype: MIN! P-2sheets!).

Schiedea spergulina var. *major* Sherff, Amer. J. Bot. 31: 151. 1944.—TYPE: HAWAIIAN ISLANDS. Kaua`i: south-central Kaua`i, along the Hanapepe River, near the Falls, 24–26 Jun 1895, *A. A. Heller 2446 p.p.* (holotype: F-428945!, photo: F-2 sheets!; isotypes: A! AC! BM! CU! G! GH! NY! UC!).

Schiedea spergulina var. *degeneriana* Sherff, Amer. J. Bot. 43: 475. 1956.—TYPE: HAWAIIAN ISLANDS. Kaua`i: Waimea Canyon, near Powerhouse, on bare crevices of cliff above river, 20 Sep 1955, *O. Degener, I. Degener, H. W. Hansen 23965* (holotype: F-1458021!; isotypes: BISH! GH! K NY! US!).

Dioecious, weakly erect to sprawling shrubs; stems 3–6 dm long, few-stemmed from the base, forming tangled clumps, the primary stems branched, weakly ascending to sprawling, internodes 0.8–2.5 cm long, green, glabrous proximally, glabrous to puberulent on the distal stems and inflorescence. Leaves opposite, those of axillary stems often appearing fasciculate owing to condensed internodes, usually reflexed or recurved, becoming reflexed, 3–7 (–8.7) cm long, 0.08–0.12 (–0.22) cm wide, thin and membranous, linear or linear-subulate, inconspicuously falcate, weakly v-shaped in cross section, with only the midvein evident, the midvein slightly excentric, glabrous, but distal ones puberulent on the adaxial surface near and along the midvein, and on the margins at the base, the hairs 0.05–0.1 mm long, erect, white-opaque, margins slightly thickened, apex attenuate and often slightly curved, base slightly tapering, sessile. Inflorescence terminal, with 15–280 flowers, 6–10 cm long, laterally contracted, lateral branches short, the branches and pedicels ascending to somewhat spreading, glabrous or puberulent with hairs like those of the leaves, spreading to erect; bracts green, filiform to linear-subulate, those of central axis 4.5–6 mm long, those of branches and flowers 1.3–2 mm long. Staminate flowers: pedicels 5–8 mm long, slender, inconspicuously flattened, those of the central flower usually longer; sepals subequal, 2.5–2.65 mm long, narrowly ovate, yellowish green, yellow toward the base, opaque, reflexed and convex at the base, producing a small transverse bulge, the middle part concave, curved upward and broadly and shallowly navicular to nearly flat in the distal 1/3, sometimes irregularly inrolled toward the apex, oriented at 80° to 100° angle to the pedicel, moderately puberulent, the hairs 0.05–0.1 mm long, margins broadly and conspicuously scarious, sometimes ciliate in distal 1/2, apex obtuse; nectary base 0.55–0.7 mm long, spreading at 80° to 90° to the axis, pale yellow, the nectary shaft held well above the sepal surface, 1.6–1.9 mm long, apex notched, more deeply so on the abaxial side; stamens 10, the filaments dimorphic, the antisepalous whorl 2.8–3.9 mm long, the alternate whorl 2.3–3.5 mm long, anthers ca. 0.3 mm long, pale yellow; styles 2–3, weakly elongating but non-functional. Pistillate flowers: pedicels 3–5 mm long, slender, inconspicuously flattened, those of the central flower usually longer; sepals subequal, 2–2.25 mm long, narrowly ovate, yellowish green, yellow toward the base, opaque, reflexed and convex at the base, producing a small transverse bulge, the middle part concave, curved upward and broadly navicular to nearly flat in the distal 1/3, often irregularly inrolled toward the apex, oriented at 80° to 100° angle to the pedicel, moderately puberulent, the hairs 0.05–0.1 mm long, margins broadly and conspicuously scarious, sometimes ciliate in distal 1/2, apex obtuse; nectary base 0.5–0.75 mm long, spreading at 60° to the axis, pale yellow, the nectary shaft held well above the sepal surface, 0.8–1 mm long, apex notched and weakly lacerate, sometimes the shaft wider, flattened, and then stamens 11; stamens 10 (–11), vestigial, the filaments subequal, 0.55–0.7 mm long, anthers ca. 0.3 mm long, yellowish white, not producing pollen; styles 2–3. Capsules 2–3.5 mm long, narowly ovoid. Seeds 0.7–0.8 mm long, reniform, compressed, the surface transversely rugose. Chromosome number: 2n = 46–50 (*Weller & Sakai 863*). Figs. 2T, 54.

Distribution (Fig. 11). Western Kaua`i: Olokele, Waimea, and Wai`alae canyons, Kalalau, Hipalau, Hanapepe, ridge W of Wahiawa, and Lawai Valley; rare on cliffs and in diverse mesic forest; 60–800 m.

ADDITIONAL SPECIMENS EXAMINED. **Kaua`i.** Along trail between Alexander Dam and Wahiawa Bog, [21°57′47.9″N, 159°30′35.5″W], *Fagerlind & Skottsberg 6479* (GB, S); Waimea Canyon Drive, ca. 5.4 mi from Waimea, on ridge from that point leading into Waimea Canyon, *Flynn 998* (BISH, PTBG); Lawa`i Valley, Pacific Tropical Botanical Garden, on top of cliff above medicinal area, *Flynn 3117* (PTBG); Waimea Canyon, 5.4

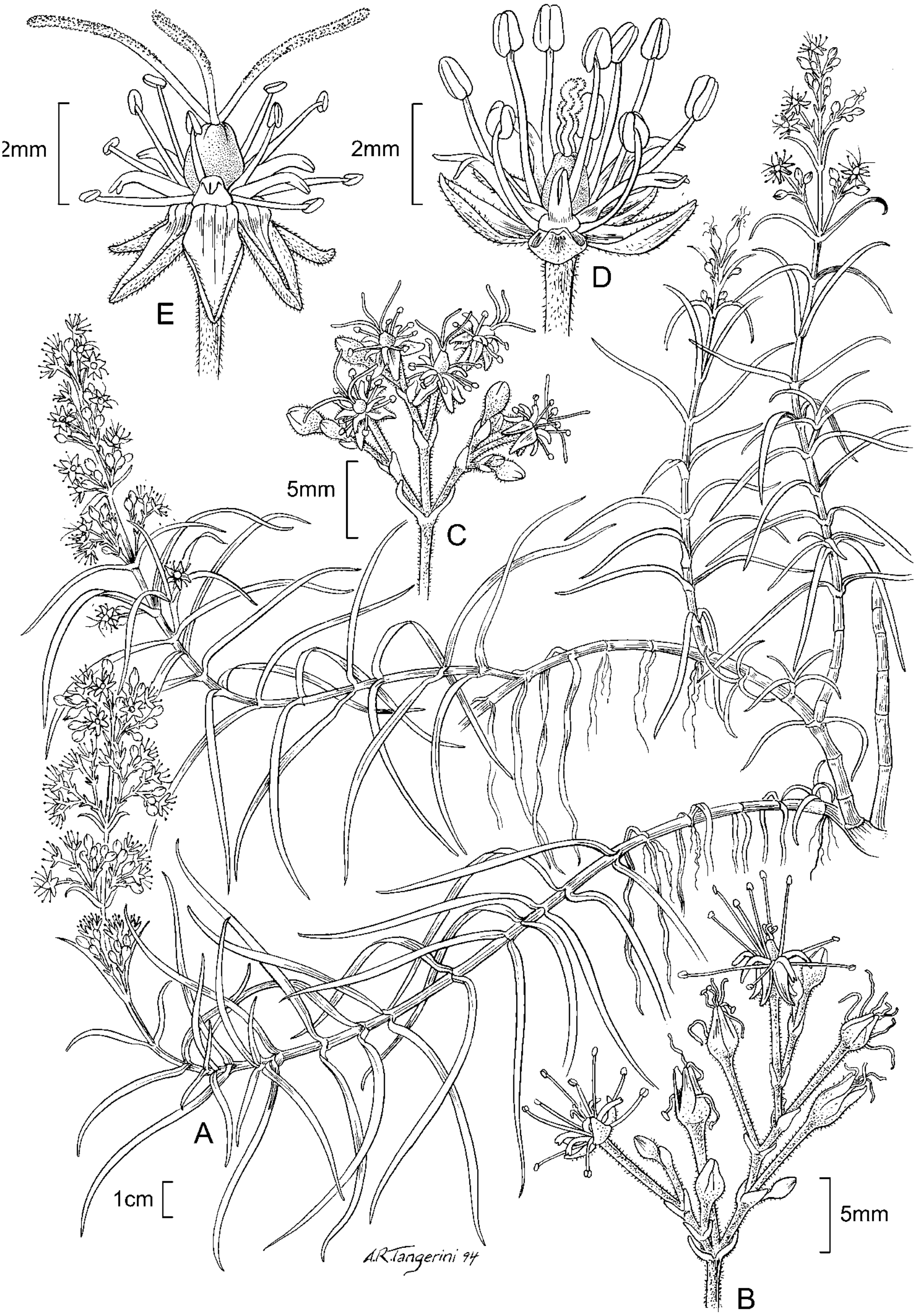

FIG. 54. *Schiedea spergulina* (cult. from *Weller & Sakai 863*). A. Habit. B. Portion of inflorescence, male. C. Portion of inflorescence, female. D. Flower, male. E. Flower, female.

mi up Waimea Canyon Drive, small ridge on W side of Canyon, [22°1′21.2″N, 159°40′30.4″W], *Flynn et. al. 1487* (PTBG); Koloa District, Lawa`i Valley, valley walls above the National Tropical Botanical Garden, *Flynn et. al. 3400* (PTBG); Waimea District, along Hwy 550 near mile 5.7, *Flynn et. al. 3420* (PTBG); E side Hanapepe on ridge, ridge W of Wahiawa, *Forbes 302.K* (BISH [2], MO); along Waimea River about 0.25 mi N of the base of Kukui Trail, [22°03′57.6″N, 159°38′40.9″W], *Herbst 2840* (BISH); Wahiawa Mts., s.d., *Lydgate s.n.* (BISH); without locality, *Rémy 550* (P); Waimea, outer section of Olokele on canyon wall, *Skottsberg 1030* (BISH, GB, S); ridge on W side of Waimea Canyon, 5.4 mi from Waimea on Hwy 550, *Weller & Sakai 863* (BISH, US); Hanalei District, Wai`alae Canyon, below falls along drainage, across poachers camp on stream walls, [22°03′16.2″N, 159°38′2.4″W], *Wood 6018* (NY, PTBG, US); Waimea canyon drainage, Koai`e canyon, above Lonomea camp, S side of stream, [22°05′29.1″N, 159°37′18.5″W], *Perlman & Lau 7033* (BISH, PTBG, US); Koloa District, NTBG cliff above medicinal area, open cliff, [21°54′0.5″N, 159°30′22.7″W], *Wood & Perlman 1079* (PTBG, US); Waimea District, Hipalau, [22°04′47.2″N, 159°38′24″W], *Wood & Perlman 2475* (BISH, PTBG, US); Waimea District, Waimea Canyon Road, 3 mile marker on canyon side of road, *Wood & Query 535* (PTBG, US); Hanalei District, Kalalau Rim, N of Kahuma Flat, [22°09′26.6″N, 159°38′38.8″W], *Wood & Query 1014* (PTBG, US); Hanalei District, Kalalau Rim, N below Pu`uokila, *Wood et al. 1094* (PTBG).

CULTIVATED. **Kaua`i.** Ridge on W side of Waimea Canyon, 5.4 mi from Waimea on Hwy 550, *Weller & Sakai 863* [cult. 1987, *Weller & Sakai s.n.*] (BISH, GH, NY, PTBG, US), 1987, *Weller & Sakai s.n.* [cult. *Wagner & Shannon 6798*] (BISH, US), 1987, *Weller & Sakai s.n.* [cult. *Wagner & Shannon 6820*] (US).

Schiedea spergulina is characterized by its recurved, very narrow leaves, which often appear to be fasciculate owing to the condensation of the internodes of short lateral branches.

Sherff (1945) recognized four varieties in *S. spergulina*, two of them based on different sheets of the same collection, and Wagner et al. (1990) recognized two varieties, based on presence or absence of pubescence and geographical separation. Here we do not subdivide the species; the only difference we have noted is the presence of hairs in the populations from Olokele and Waimea canyons, whereas populations from Hanapepe, Wahiawa, and Lawai are glabrous. A number of species of *Schiedea* exhibit variation in the presence or absence of hairs as well as their nature, gland-tipped or not. We are not giving formal recognition to these differences, because of the seemingly simple nature and lability of the traits.

The previously recognized varieties were federally listed as either threatened or endangered in 1994 (Mehrhoff et al. 1994). Wagner et al. (1999b) listed the species as threatened.

Sherff based two of his varieties on parts of *Heller 2446*, a collection that includes material gathered at one locality but different dates. Of the duplicates for var. *major* listed above Sherff did not cite the A, AC, and G sheets in the protologue, although he had annotated the A sheet; they are all placed here based on the description and diagnostic characters given by Sherff. Two additional sheets were distributed under *Heller 2446*, collected at the same locality but on 2–8 July 1895 (MO! US!) and annotated as “co-types” by Sherff; they were cited in the protologue as additional material. In addition, Sherff segregated two senescent specimens of the June gathering of *Heller 2446* as var. *leiopoda*.

The specific epithet refers to the resemblance of the fasciculate leaves to those of corn sperry, *Spergula arvensis* L.

30. Schiedea mannii St. John, Pacific Sci. 24: 252. 1970.—TYPE: HAWAIIAN ISLANDS. O`AHU: Wai`anae Mts., Makua-`Ohikilolo ridge, 2650 ft [808 m], 24 Feb 1952, *H. St. John 24793* (holotype: BISH-501322!; isotypes: GH! K, P!).

Subdioecious shrubs; stems weakly erect 1.5–2.5 (–10) dm long, the primary stems branched, weakly erect to ascending, internodes 0.2–0.7 (–1.5) cm long, pale purple, becoming yellowish green sporadically tinged purple in the distal parts of the plant, glabrate proximally, minutely puberulent on the distal stems and inflorescence. Leaves opposite, recurved, 2.5–4 (–5) cm long, 0.15–0.4 (–0.5) cm wide, thick and membranous, linear or linear-elliptic or linear-oblanceolate, inconspicuously falcate, with only the midvein evident, the midvein slightly excentric, glabrous, margins inconspicuously thickened, apex acute, base attenuate, sessile. Inflorescence terminal, with 22–131 flowers, (2–) 4–9 cm long, laterally contracted, lateral branches short, the branches and pedicels ascending to spreading, puberulent with minute glandular hairs 0.02–0.04 mm long; bracts green becoming white toward the base, sometime tinged with purple, filiform to linear-subulate, those of central axis 1.5–10 mm long, those of branches and flowers 1–1.5 mm long. Staminate flowers: pedicels 4–9 mm long, slender, inconspicuously flattened, those of the central flower usually longest in each dichasium; sepals subequal, 2.2–2.8 mm long, narrowly ovate, yellowish green, often tinged purple toward the apex, opaque, reflexed and convex at the base, producing a conspicuous transverse bulge in the lower 1/3, the middle part concave, broadly and shallowly navicular to nearly flat in the distal 1/3, oriented at 60° to 80° angle to the pedicel, glabrous, margins broadly and conspicuously scarious in the upper half, apex rounded, and often weakly lacerate; nectary base 0.5–0.6 mm long, spreading at 70° to 80° to the axis, pale yellow, the nectary shaft held well above the sepal surface, 1.15–1.4 mm long, apex notched, much more deeply so on the abaxial side; stamens 10 (–11), the filaments subequal, 4.9–5 mm long, anthers 0.4–0.5 mm long, pale yellow; styles 3, weakly elongating but non-functional. Hermaphroditic flowers occurring occasionally intermixed in staminate inflorescences, numbers varying with site and moisture, similar to staminate flowers except ovary and styles functioning. Pistillate flowers: pedicels 2.5–8 mm long, slender, inconspicuously flattened, those of the central flower usually longer; sepals subequal, 2–2.25 mm long, narrowly ovate, yellowish green, yellow toward the base, opaque, reflexed and convex at the base, producing a small transverse bulge, the middle part concave, curved upward and broadly navicular to nearly flat in the distal 1/3, often irregularly inrolled toward the apex, oriented at 80° to 100° angle to the pedicel, moderately puberulent, the hairs 0.05–0.1 mm long, margins broadly and conspicuously scarious, sometimes ciliate in distal 1/2, apex obtuse; nectary base 0.5–0.75 mm long, spreading at 60° to the axis, pale yellow, the nectary shaft held well above the sepal surface, 0.8–1 mm long, apex notched and weakly lacerate, sometimes the shaft wider, flattened and stamens 11; stamens 10 (–11), vestigial, the filaments subequal, 2–3 mm long, anthers ca. 0.3 mm long, yellowish white, not producing pollen; styles 3. Capsules 2.5–3 mm long, narrowly ovoid. Seeds 0.6–0.8 mm long, reniform, compressed, the surface transversely rugose. Chromosome number: 2n = possibly 56 (*Weller & Sakai 793*). Figs. 2U, 55.

Distribution (Fig. 56). O`ahu, known only from a few areas in the northern Wai`anae Mountains, including Pu`uhapapa, Pu`ukawiwi, Makua Valley, Makua-Kea`au Ridge (`Ohikilolo), and Kamaile`unu Ridge; in scattered sites on open, sunny ridges in diverse mesic forest; 400–820 m.

ADDITIONAL SPECIMENS EXAMINED. **O`ahu.** Wai`anae District, along main ridge separating Makaha and Wai`anae Kai Valleys, *Gustafson 3317* (RSA); `Ohikilolo ridge, [21°30′46.8″N, 158°12′13.6″W], *Herbst et. al. 5699* (BH, M, UC); Wai`anae Kai Forest Reserve, Kamaile`unu Ridge near Pu`ukepau`ula, [21°28′52.5″N, 158°10′50.2″W], *Herbst et. al. 5764* (BISH, US); crest of Kamaile`una Ridge, just N of major peak N of Pu`ukawiwi, *Nagata & Spence 1104* (BISH); upper Makua Valley, on crest of spur into valley, 50 yds S of cabin at Peakock Flats, [21°31′55″N, 158°10′53.7″W], *Nagata et. al. 1151* (BISH); Makua-Kea`au Ridge (`Ohikilolo), [21°30′56.3″N, 158°12′48.6″W], *Obata 274* (BISH); on crest of Makaha-Wai`anae Kai ridge, towards Mt. Ka`ala from the two large pinnacled rocks, *Obata et. al. 341* (BISH); on ridge top near summit of Pu`uhapapa,

FIG. 55. *Schiedea mannii*. A. Habit. B. Portion of male inflorescence. C. Male flower in early anthesis. D. Hermaphroditic flower in late anthesis, female stage. E. Female flower. F. Nectary shafts (all other floral parts removed). (Based on: A–E, cult. from *Weller & Sakai 793*; F, *Wood et al. 2791* [PTBG].)

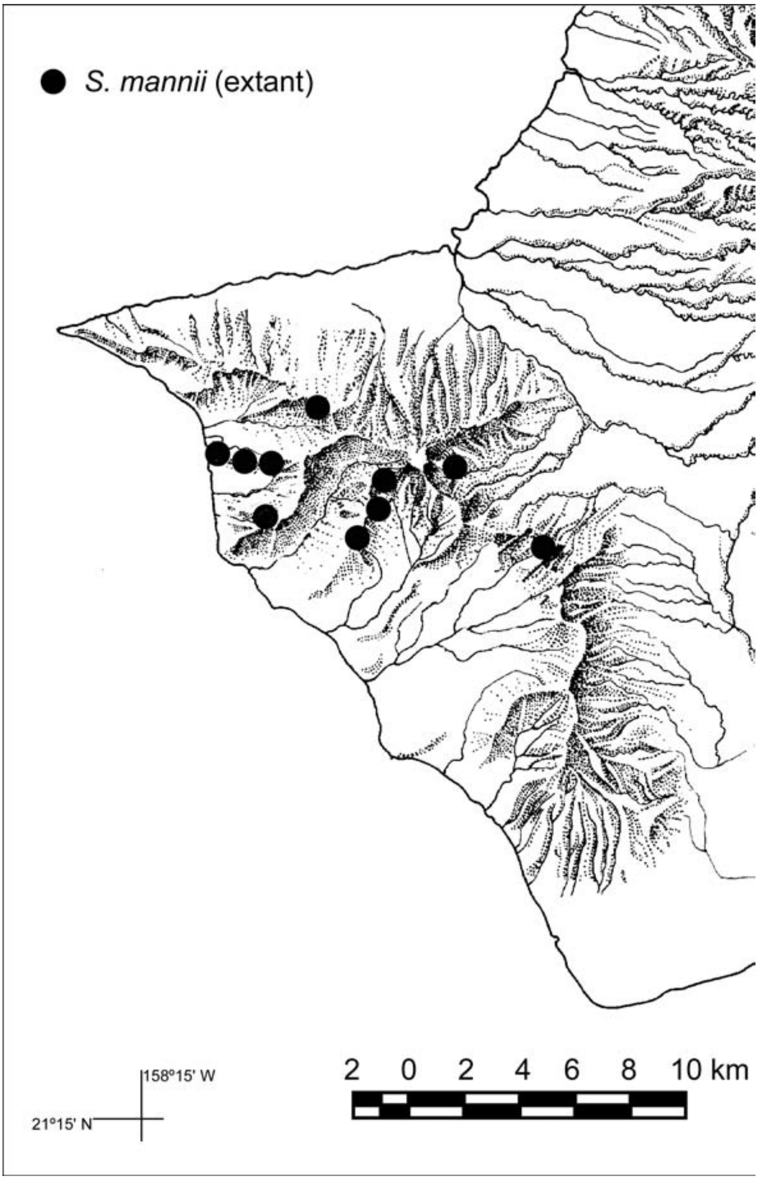

FIG. 56. Distribution of *Schiedea mannii*.

on ridge radiating towards Kolekole Pass, [21°28′6.6″N, 158°06′24.1″W], *Obata et. al. 369* (BISH); Wai`anae Kai, on ridge trail just below Pinnacle Rocks on Mt. Ka`ala side, [21°29′25.8″N, 158°09′49.6″W], *Perlman 5483* (BISH, PTBG); Wai`anae Valley, gulches below Pu`ukawiwi W of Wai`anae Kai, *Perlman & Obata 5502* (MO, PTBG); Wai`anae Range, S side of Kea`au Valley, *Perlman & Obata 5581* (PTBG); Wai`anae Kai, Kamaile`unu ridge near Pu`ukawiwi, near large pinnacle rocks, on Makaha valley side of ridge, *Perlman & Obata 5859* (BISH, PTBG, US [2]); Makua Valley, `Ohikilolo ridge, on central section past cone, *Perlman & Wood 13523* (PTBG); Ko`iahi gulch, in small subgulch off `Ohikilolo, on cliffs, *Perlman & Wood 13544* (PTBG, US); Kamaile`unu summit, slopes of Makaha valley, N facing cliffs, near ridge connecting with Pu`ukawiwi, *Perlman & Wood 17156* (PTBG, US); Kamaile`unu divide, ridgeline, [21°30′5.6″N, 158°09′54.1″W], *Takeuchi et. al.*

*Wai`anae 105* (UC); Kamaile`unu near Pinnacle Rock, *Takeuchi et. al. 2111* (BISH); Kamaile`unu Ridge, *Takeuchi et. al. 2113* (BISH); Wai`anae Kai, *Tate & Takeuchi 5* (BISH); ridge separating Wai`anae Kai and Makaha valleys, *Weller & Sakai 793* (US); Wai`anae District, `Ohikilolo area, Makua side, 10° N aspect, steep cliff, *Wood 2627* (PTBG); Makua Kea`au Forest Reserve, `Ohikilolo, cliffs with N aspect, *Wood et. al. 1828* (PTBG, US); Wai`anae District, Wai`anae Kai, E slopes of Mt. Ka`ala, [21°30′21.1″N, 158°07′45.3″W], *Wood et. al. 2791* (PTBG), *Wood et. al. 2794* (PTBG, US).

CULTIVATED. **O`ahu.** Wai`anae Range: ridge separating Wai`anae Kai and Makaha valleys, *Weller & Sakai 793* [cult. 1985, *Weller & Sakai s.n.*] (BISH, NY, PTBG, US), *Weller & Sakai s.n.* [cult. *Wagner & Shannon 6838*] (US).

Schiedea mannii is distinctive in its sparsely glandular-puberulent inflorescences and falcate, linear leaves (0.15–0.5 cm wide). It is known to hybridize with *S. ligustrina* (Weller et al. 2001), which it superficially resembles. The hybrids are known only from `Ohikilolo, where the *S. mannii* population seems to be fairly introgressed. Putative hybrids of *S. mannii* and *S. hookeri* have been found near Pu`ukawiwi (*Weller 901*, coll. by J. Obata), on a north-facing cliff on the eastern slopes of Mt. Ka`ala (*Wood et al. 2796*, PTBG), and grown from seed collected from *S. mannii* at Wai`anae Kai (Weller et al. 2001).

The specific epithet honors Horace Mann, Jr. (1844–1868), who collected in the Hawaiian Islands with William T. Brigham in 1864–1865. Mann initiated a flora of the Hawaiian Islands, and became an assistant to Asa Gray and instructor at Harvard College. Unfortunately, his promising career was cut short by tuberculosis. Mann published several papers on the Hawaiian flora, including accounts on a number of new species and the first detailed study of *Schiedea*.

31. Schiedea lydgatei Hillebrand, Fl. Hawaiian Isl. 34. 1888.—TYPE: HAWAIIAN ISLANDS. MOLOKA`I: Kalawao, near the sea (leper settlement), 1870, *W. Hillebrand s.n.* (holotype: B, destroyed, photo: BISH!; lectotype, here designated: BISH!; isotype: GH!, photo: F!).

Schiedea lydgatei var. *attenuata* Degener & Sherff in Sherff, Amer. J. Bot. 31: 153. 1944.—TYPE: HAWAIIAN ISLANDS. MOLOKA`I: up valley W of East `Ohi`a [Gulch], in dry region, 16 Jul 1928, *O. Degener 5937* (holotype: F-1137178!, photo: F!; isotypes: A! B! CU! G! GH! MO! NY-2 sheets! UC! US!).

Shrubs, 1–10 dm tall; stems erect to sprawling, with many short lateral branches, glabrous, internodes 0.5–7.5 cm long, green to greenish purple, older wood with tan bark. Leaves opposite; blades 2–5 cm long, 0.6–1.7 cm wide, thinly coriaceous, pale yellowish green, often slightly glaucous and reflective, elliptic to broadly elliptic, or elliptic-ovate or elliptic-lanceolate, with 3 principal veins, the outer pair often less conspicuous than the midvein, margins entire, slightly thickened and weakly revolute, apex acuminate, mucronate, base cuneate; petioles 0.4–0.6 cm long. Inflorescence terminal, with 7–109 flowers, 10–25 cm long, diffuse; bracts of central axis 2–6 mm long, those of branches and flowers 2–2.5 mm long, green to purple-tinged, subulate; pedicels (8–) 10–18 (–20) mm long, quadrangular and conspicuously flattened, the wider side usually grooved. Flowers hermaphroditic. Sepals 4–4.7 mm long, narrowly ovate, broadly and very shallowly navicular, oriented at 45° to 80° angle to the pedicel, green or tinged purple, the veins paler, opaque, reflexed and convex at the base, producing a small transverse bulge, glabrous, margins scarious, sometimes somewhat irregularly undulate, entire, glabrous, obtuse. Nectary base 0.5–0.6 mm long, spreading at 80° to the axis, pale yellow to dark yellow, the nectary shaft arched, held slightly above sepal surface, 2.6–3 mm long, apex with a deep wide unequal notch, more deeply slit on the abaxial side. Stamens 10, the filaments dimorphic, the antisepalous whorl 5.5–5.6 mm long, the alternate whorl 4.9–5.2 mm long, anthers 0.7–0.9 mm long, yellow. Styles 3 (–4), green. Capsules 4–5.5 mm long, ovoid. Seeds 0.8 mm long, orbicular, the faces rugose, the margins papillose. Chromosome number: 2n = possibly 50, 60 (*Weller & Sakai 870*). Plate 1A; Figs. 2V, 4G, H, 57.

Distribution (Fig. 58). Moloka`i, Pu`uo`oa, Makolelau, Kamalo, Kamiloloa, Makakupa`ia, and Poholua gulches; locally common in dry shrubland, especially before the fires of 1988 and 1991; 600–955 m.

ADDITIONAL SPECIMENS EXAMINED. **Moloka`i.** `Onini Gulch, [21°06′29.1″N, 156°56′58″W], *Bishop 1704* (HAW); one of the dry valleys between Kamalo and Kaunakakai (precise locality forgotten), *Degener 5949* (A [3], B, CU, G, GH, M, MIN, MO, PH, UC, US, W); Kamolo, *Faurie 1088* (A, BISH, G [2], P); Poholua, *Forbes 103.Mo* (BISH, MO, S); slopes below Pu`ukolekole, *Forbes 117.Mo* (BISH, BM, MO, UC); Moloka`i District, Kamiloloa Hts. trail, forest reserve boundary near gate along road, S of O`oa, *Gustafson & Wilson 3554* (PTBG); Kala`e, s.d., *Hillebrand s.n.* (BISH [fragment from B]); Kawela, forest reserve boundary [W of West Fork of Kawela Gulch], [21°06′22.2″N, 156°56′42″W], *Hobdy 540* (BISH [2]), *Hobdy 545* (BISH); Kamiloloa [near Pu`uo`oa], *Misaki 005* (BISH); Kamiloloa Road [near Pu`uo`oa], *Misaki 009* (BISH); Kamiloloa [near Pu`uo`oa], *Misaki 010* (BISH); Kamiloloa, W facing slopes, 13 Mar 1992, *Norman s.n.* (US); Makolelau, W facing slopes, 18 Mar 1992, *Norman s.n.* (US); forest reserve boundary at gate along road. S of O`oa, in Makakupa`ia, [21°06′35.2″N, 156°57′15″W], *Pekelo, Jr. 43?* (BISH); Makolelau Gulch, below Pu`u Kolekole, TNC survey, [21°5′15.8″N, 156°54′45″W], *Perlman 6677* (BISH [3], PTBG, US); Makakupa`ia ridge road, near Forest Reserve fence, *Perlman & Wood 12854* (PTBG); without locality, *Rémy 549* (P); below Kala`e, *Rock 7014* (BISH); Moloka`i District, Makolelau ahupua`a, Tr 7(21/22), trail on ridge S of Pu`ukolokole, [21°05′52.6″N, 156°54′13.4″W], *Stemmermann & Montgomery 3876* (BISH); Moloka`i District, Kawela ahupua`a, Tr 5(40/41), on ridge near road between West Fork of Kawela and `Onini Gulch, [21°06′33.4″N, 156°56′32.2″W], *Stemmermann & Montgomery 3904* (BISH); Moloka`i District, Land of Makakupa`ia, just inside forest reserve, [21°07′N, 156°55′W], *Wagner et. al. 6672* (US); Moloka`i District, Land of Makolelau, old jeep road (adjacent to E side of area) leading to Pu`ukolekole, [21°05′N, 156°55′W], *Wagner et. al. 6682* (US); Moloka`i District, Makolelau, first major gulch W of Makolelau, [21°06′N, 156°55′W], *Wagner et. al. 6741* (US); Makolelau Gulch, *Welton et. al. 835* (BISH); Makolelau, below and W of Pu`ukolekole, second drainage to E of nearby contour road, [21°05′41.6″N, 156°54′7″W], *Wood 6031* (PTBG), *6031a* (BISH, MO, NY, PTBG, US); Moloka`i District,Makakupa`ia Road turn-off up past Kaunakakai Boy Scout Camp, follow road 0.5 mi down, *Wood & Perlman 606* (BISH, PTBG, US [2]); below Pu`ukolekole, W of Makolelau, [21°05′31.1″N, 156°54′34.1″W], *Wood & Perlman 1993* (BISH, F, MO, NY, PTBG, US), *Wood & Perlman 2004* (PTBG, US); Moloka`i District, Makakupa`ia Road turn-off up past Kaunakakai Boy Scout Camp, follow road 0.5 mi down, *Wood & Perlman 606* (BISH, PTBG, US [2]).

CULTIVATED. **Moloka`i.** Kamiloloa tr, just above (N) of forest preserve gate, 3 Mar 1989, *Weller & Sakai s.n.* [cult. *Weller & Sakai 870*] (BISH, PTBG, US), *Weller & Sakai 870* [cult. *Wagner & Shannon 6857*] (BISH, PTBG, US); Moloka`i District, Land of Makolelau, old jeep road (adjacent to E side of area) leading to Pu`ukolekole, *Wagner et al. 6682* [cult. *Wagner & Shannon 6856*] (BISH, PTBG, US).

Schiedea lydgatei is morphologically very similar to *S. salicaria*, differing in its broader, 3-nerved leaves, less congested inflorescences, and hermaphroditic breeding system. Morphological features and molecular data from restriction site mapping indicated a sister relationship between *S. lydgatei* and *S. salicaria* (Soltis et al. 1997), although this relationship is not supported in more recent phylogenetic analyses (see section Phylogeny). *Schiedea lydgatei* is wind- and insect-pollinated (Norman 1994). Native moths in the family Pyralidae appear to be the major pollen vectors.

Schiedea lydgatei was federally listed as endangered in 1992 (Herbst et al. 1992b). Several fires that spread from Kaunakakai destroyed large stands of this species. Remaining plants are at risk from additional fires and the large feral goat population in this region of Moloka`i.

FIG. 57. *Schiedea lydgatei* (cult. from *Weller & Sakai 870*). A. Habit. B. Portion of inflorescence. C. Flower in early anthesis, male stage. D. Flower in later anthesis, female stage. E. Flower, one sepal removed to show nectary shafts.

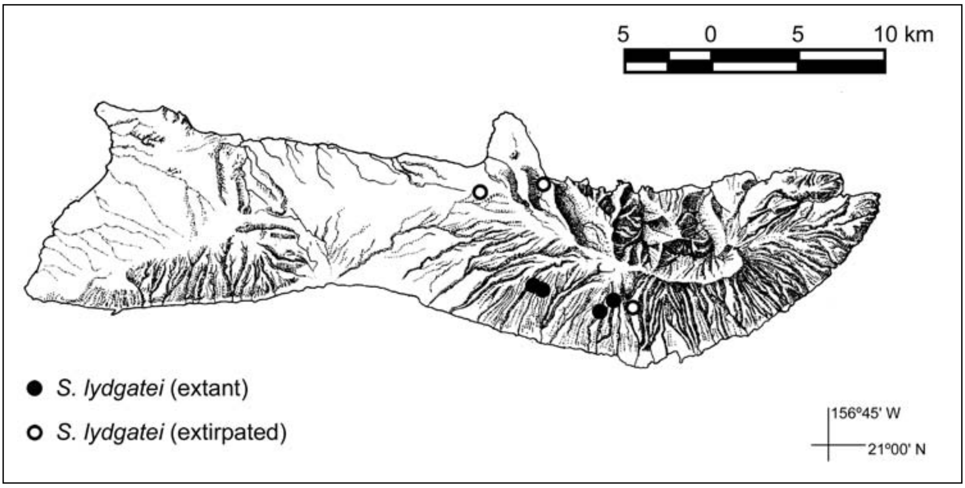

FIG. 58. Distribution of *Schiedea lydgatei*.

The specific epithet honors John M. Lydgate (1869–1920), who botanized on several of the Hawaiian Islands as a student with W. Hillebrand.

32. Schiedea salicaria Hillebrand, Fl. Hawaiian Isl. 33. 1888.—TYPE: HAWAIIAN ISLANDS. MAUI: West Maui, Ma`alaea, 1851–1872, *W. Hillebrand s.n.* (lectotype, here designated: BISH-501737!).

Gynodioecious shrubs, 3–8 (–18) dm tall; stems erect or strongly ascending, with few short lateral branches in the distal part of the stem, glabrous, internodes 0.5–5 cm long, green to greenish purple. Leaves opposite; blades 3–5 (–5.5) cm long, 0.6–1.5 cm wide, thinly coriaceous, pale yellowish green, often slightly glaucous and reflective, narrowly elliptic to elliptic, sometimes the lower ones elliptic-oblanceolate or oblanceolate, with 1 (–3) principal veins, the outer pair inconspicuous when present, margins entire, slightly thickened and weakly revolute, apex acute to acuminate, base attenuate to narrowly cuneate; petioles 0–0.3 cm long. Inflorescence terminal, with 13–117 flowers, (4–) 8–23 cm long, usually laterally contracted, weakly congested, the hermaphroditic inflorescences slightly less congested and broader than the pistillate inflorescences; bracts of central axis 2–8 mm long, those of branches and flowers 1.5–3 mm long, green to purple-tinged, linear to subulate. Flowers hermaphroditic or pistillate. Hermaphroditic flowers: pedicels 5–18 mm long, quadrangular and somewhat flattened; sepals 3.1–4.1 mm long, narrowly ovate, broadly and very shallowly navicular, oriented at 45° to 80° angle to the pedicel, green or tinged purple toward the apex, opaque, reflexed and convex at the base, producing a small transverse bulge, glabrous, margins scarious, sometimes somewhat irregularly undulate, entire, glabrous, apex sometimes inrolled, obtuse; nectary base 0.5–1 mm long, spreading at 80° to the axis, pale yellow to dark yellow, the nectary shaft held above sepal surface, (2–) 2.2–3.5 mm long, apex with a deep wide unequal notch; stamens 10 (–12), sometimes a few (especially of the antisepalous whorl) non-functional and short, the filaments dimorphic, the antisepalous whorl 4–5.8 mm long, the alternate whorl 3.5–5 mm long, anthers 0.6–0.9 mm long, yellow; styles (2–) 3 (–4), green. Pistillate flowers strongly to somewhat dimorphic in size, the first flower to 20% larger: pedicels of first flower of the dichasia 6–9 mm long, those of the subsequent ones 4–5 mm long, quadrangular and somewhat flattened; sepals 2.75–4.2 mm long, narrowly ovate, green or yellowish green, pale yellow at the base, opaque, reflexed and convex at the base, producing a small transverse bulge, broadly navicular to nearly flat, oriented at 60° to 90° angle to the pedicel, sometimes strongly upcurved near the middle, margins scarious and often irregularly undulate, glabrous, apex often inrolled, obtuse; nectary base, 0.5–0.75 mm long, spreading at 60° to the axis, yellow, the nectary shaft held above the sepal surface, 1.8–2.3 mm long, apex with deep unequal notch, the two teeth incurved; stamens 10 (–12), vestigial, filaments unequal, the antisepalous whorl 0.9–1.7 mm long, the alternate whorl (0.4–) 0.75–1 mm long, anthers 0.4–0.6 mm long, pale yellow, not producing pollen; styles (2–) 3 (–4), pale yellow. Capsules 4.5–5 mm long, ovoid. Seeds 0.7–0.9 mm long, orbicular-reniform, the surface papillose, papillae of the margins larger than those of the faces. Chromosome number: 2n = 55–60, probably 60 (*Weller & Sakai 842, 853*). Figs. 2W, 4I, J, 59.

Distribution (Fig. 47). West Maui, extant populations known only from south of Waikapu, Ka`onohua, and Ma`alaea; scattered on ridges and steep slopes usually beyond the reach of grazing animals in remnant dry shrubland; 180–670 m.

ADDITIONAL SPECIMENS EXAMINED. **Maui.** WEST MAUI: Ka`onohua Gulch, [20°49′18.7″N, 156°31′7.2″W], *Hobdy 2007* (BISH), *Hobdy 803* (BISH, PTBG); small gulch S of the gulch behind the Waikapu rock crusher, *Hobdy 1000* (BISH); on ridge above the rock crusher just S of Waikapu, [20°50′36.4″N, 156°31′21.6″W], *Hobdy 2118* (A, BISH, US); mountains behind Ma`alaea, across cow pasture from jct. of Kihei Rd and Wailuku–Ma`alaea hwy, [20°48′47.5″N, 156°31′21.4″W], *Perlman 5804* (BISH, MO, PTBG, RSA); West Maui Mts., Pu`uhona, *Weller & Sakai 842* (US); Wailuku District, Ka`onohua Gulch, *Wood & Perlman 328* (BISH, PTBG, US).

CULTIVATED. **Maui.** West Maui: Ka`onohua Gulch, 3 Mar 1987, *Weller & Sakai s.n.* [cult. *Weller & Sakai 853*] (US), *Weller & Sakai 853* [cult. *Wagner & Shannon 6799*] (BISH, PTBG, US), *Weller & Sakai 853* [cult. *Wagner & Shannon 6816*] (US); Palea`ahu Gulch, Mar 1994, *Weller & Sakai s.n.* [cult. *Weller & Sakai 911*] (US); Pu`uhona, *Weller & Sakai 842* [cult. 1985, *Weller & Sakai s.n.*] (BISH, GH, NY, PTBG, US), *Weller & Sakai 842* [cult. *Wagner & Shannon 6817*] (BISH, PTBG, US), *Weller & Sakai 842* [cult. *Wagner & Shannon 6818*] (US).

Schiedea salicaria is most closely related to *S. lydgatei* on Moloka`i (see notes under that species, no. 31). Narrow-leaved plants resembling *S. salicaria* occurring on `Ula`ula and Koai on the western side of West Maui appear to be the result of introgressive hybridization with *S. menziesii*. Plants in this area exhibit a wide range of variation, especially in leaves and inflorescences, from individuals nearly typical of *S. salicaria* to variants closely resembling *S. menziesii*. This hybrid population occurs from 760 to 915 m elevation, considerably higher than the populations of *S. salicaria* on the eastern side of West Maui. Other narrow-leaved collections from the Lahaina area mentioned by Hillebrand and shown in photos at BISH and F probably also represent hybrids involving *S. menziesii*. Sherff (1945) suggested that these plants perhaps represented a distinct variety (1945).

Schiedea salicaria must have been more widespread on West Maui in the past; hybrids between *S. salicaria* and *S. menziesii* are known from the western side of West Maui, but no plants resembling the populations of *S. salicaria* from eastern West Maui are presently known.

Schiedea salicaria is considered to be vulnerable to extinction by Wagner et al. (1999b), and is currently a candidate for listing as endangered (Williams 2002). Recent

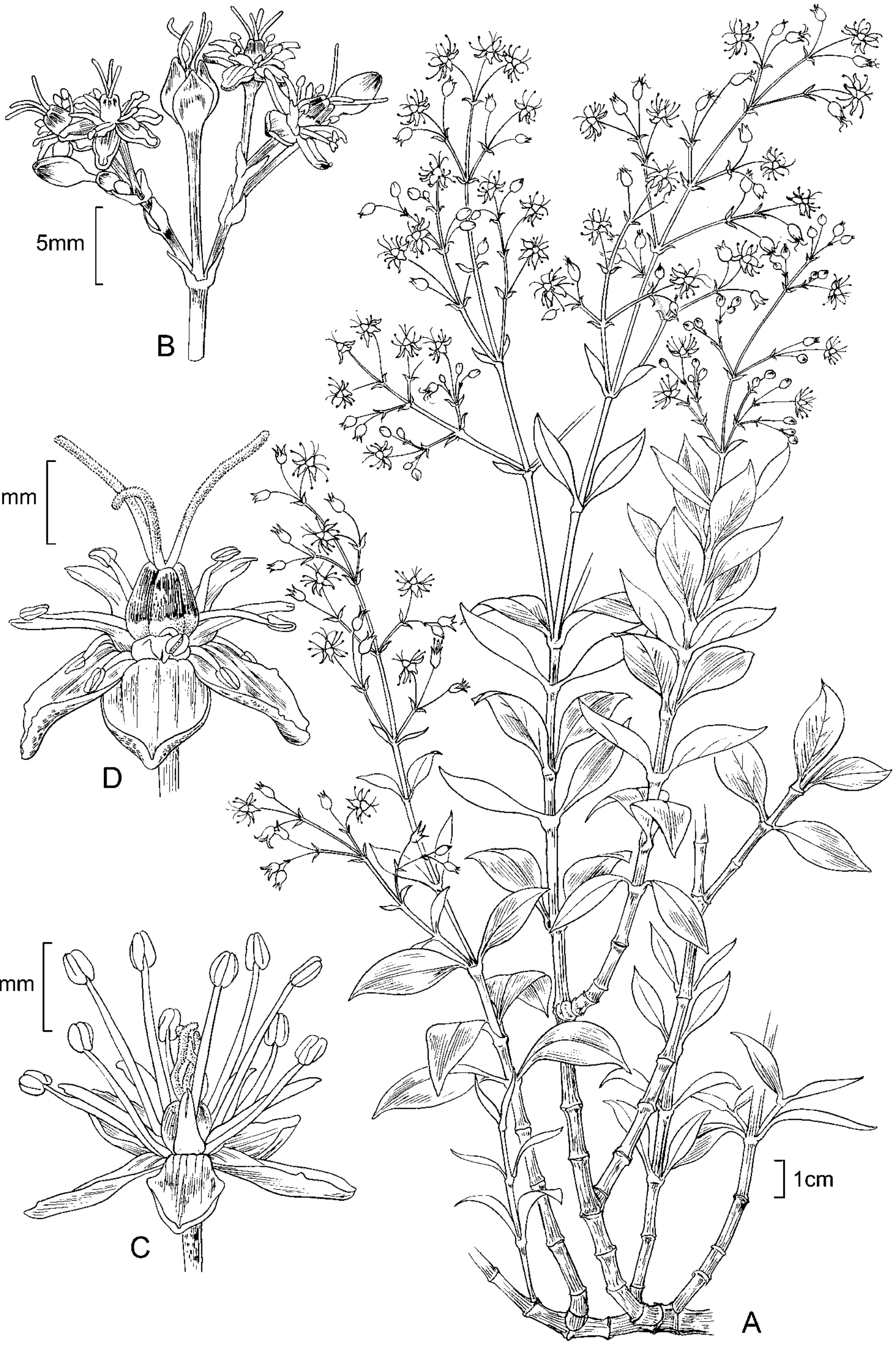

FIG. 59. *Schiedea salicaria* (cult. from *Weller & Sakai 842*). A. Habit. B. Portion of inflorescence of female plant. C. Flower, hermaphroditic, shown in male stage. D. Flower, female.

published references to *S. salicaria* (Sakai et al. 1989; Weller et al. 1990; Weller & Sakai 1990; Weller & Sakai 1991) refer to populations near Ma`alaea with variation similar to that found in the lectotype.

Hillebrand cited three elements in the protologue for *S. salicaria*: "Gulches back of Lahaina and Oloalu (a form with narrow linear leaves of thicker texture, with revolute margins the two lowest veins running parallel with the midrib and rather prominent), Ma`alaea." Two Hillebrand specimens from Lahaina are represented by photographs at BISH and F; the F photograph is of a fragment at BISH-46607! taken from the specimen then at B (now destroyed). The BISH photograph is apparently of one of the B syntypes, although there is no label information visible in the photograph. The sole extant collection (at BISH) is from Ma`alaea, which we here choose as the lectotype.

The specific epithet refers to a resemblance in general aspect to *Salix* L.

33. Schiedea ligustrina Chamisso & Schlechtendal, Linnea 1: 46. 1826.—TYPE: HAWAIIAN ISLANDS. O`AHU: "O-wahu" [27 Sep–14 Oct 1817], *L. C. A. von Chamisso s.n.* (holotype: LE; isotypes: B-destroyed, P!, fragment of B isotype: BISH!, photos of P isotype: B! F! GB!).

Schiedea ligustrina var. *nematopoda* Degener & Sherff in Sherff, Amer. J. Bot. 31: 151. 1944.—TYPE: HAWAIIAN ISLANDS. O`AHU: SW of Dillingham Ranch, Kawaihapai, on dry, grassy, rocky ridge, 12 Mar 1937, *O. Degener, D. Topping, F. C. Salucop 12106* (holotype: US-1731541!, photo: F!; isotypes: B! MASS! NY!).

Schiedea obatae St. John, Phytologia 64: 178. 1988.—TYPE: HAWAIIAN ISLANDS. O`AHU: Wai`anae Range, above firebreak trail heading S from Kolekole Pass, at the first prominent gulch at end of the *Melaleuca* grove under canopy of exotics and off trail, two plants, 549 m, 21 May 1978, *J. Obata, D. Palmer, E. Funk 368* (holotype: BISH-522856!; isotype: BISH!).

Dioecious shrubs, 3–6 dm tall; stems erect or strongly ascending, glabrous, internodes 0.5–2.5 cm long, green to greenish purple. Leaves opposite; blades (2–) 3–5 (–6) cm long, (0.2–) 0.5–1.5 cm wide, coriaceous, yellowish green, elliptic-oblanceolate, elliptic, or linear, with only the midvein evident, margins entire, somewhat thickened and weakly revolute, apex acute to mucronate, base attenuated to a winged petiole 0–0.6 cm long. Inflorescence terminal, with 15–138 flowers, 4–15 cm long, congested, especially laterally, the staminate inflorescences often less congested and broader than the pistillate inflorescences; bracts of central axis 2–15 mm long, those of branches and flowers 1–1.8 mm long, green to purple, linear to subulate; pedicels (1–) 3–7 (–10) mm long, quadrangular and somewhat flattened. Staminate flowers: Sepals 2.2–2.7 mm long, narrowly ovate, broadly and shallowly navicular, oriented at 100° to 130° angle to the pedicel, green or tinged purple toward the apex, opaque, reflexed and convex at the base, producing a small transverse bulge, glabrous, margins scarious, entire, glabrous, apex obtuse; nectary base 0.4–0.5 mm long, spreading at 60° to the axis, dark yellow, the shaft held well above sepal surface, plump, 1.2–1.3 mm long, apex with a deep wide unequal notch; stamens 10, sometimes 1–few weakly developed or with shorter filaments, the filaments slightly dimorphic, the antisepalous whorl 3.1–4 mm long, the alternate whorl 2.9–3.6 mm long, anthers 0.7–0.9 mm long, yellow; styles 3–4, green, short and non-functional, becoming shrivelled. Pistillate flowers: Sepals 2.1–2.3 mm long, narrowly ovate, green or tinged purple toward the apex, opaque, reflexed and convex at the base, producing a small transverse bulge, broadly and shallowly navicular, oriented at 100° to 130° angle to the pedicel, margins scarious, entire, glabrous, apex obtuse; nectary base 0.2–0.6 mm long, spreading at 60° to the axis, producing little nectar, dark yellow, the nectary shaft held well above the sepal surface, plump, 1.1–1.2 mm long, apex with a deep wide unequal notch, the two teeth incurved, sometimes also with a central tooth on the adaxial side; stamens 10, vestigial, filaments unequal, 0.7–0.9 mm long, anthers 0.3–0.4 mm long, yellow, not producing pollen; styles 3–4. Capsules 2–3.5 mm long, narrowly ovoid. Seeds relatively few, 0.6–0.8 mm long, reniform, compressed, the surface papillose, papillae of the margins larger than those of the faces. Chromosome number: 2n = possibly 56 (*Weller & Sakai 873*). Figs. 2X, 60.

Distribution (Fig. 61). O`ahu, Palehua to Pu`ukaua and Keawapilau Gulch, and Mokule`ia, Wai`anae Mountains; scattered in dry forest to diverse mesic forest, often on cliffs; (180–) 300–830 m.

ADDITIONAL SPECIMENS EXAMINED.**O`ahu.** Honolulu, 1852, *Andersson s.n.b* (S); without locality, s.d., *Beechey Voyage s.n.* (K-496-91/42); Pohakea Pass, [21°25′50.4″N, 158°05′27.7″W], 29 Apr 1967, *Bishop s.n.* (HAW); Wai`anae firebreak, *Campsall A-13* (HAW); below Pu`ukapu, [21°24′20.3″N, 158°5′48.5″W], *Christophersen et. al. 1534* (BISH); 2 ridges S of Pohakea Pass, [21°25′38.1″N, 158°05′26.7″W], *Christophersen et al. 1637* (BISH, US); gulch below Palikea, Honouliuli, *Cowan 622* (P, US); without locality, 26 Jun 1950, *Degener s.n.* (B); SE of Pu`ukamananui, [21°31′34.4″N, 158°05′32.1″W], *Degener & Carroll 20411* (B, BISH, NY); Palehua Ridge extending into Nanakuli Valley, [21°23′40.5″N, 158°06′30″W], *Degener & Greenwell 20389* (MIN, UC); N slope of Pu`uhapapa, [21°28′7.3″N, 158°06′19.3″W], *Degener & Hatheway 20993* (BM, PH); Schofield side of Pohakea Pass, *Degener & Murashige 19740* (B, BISH, BH, BM [2], G [2], GB, GH, K, M, MO, NY, P, PH); Wai`anae side of Pohakea Pass, *Degener & Murashige 19741* (BISH, NY, S); W side of Pohakea Pass, *Degener & Park 5917* (B, BM, CU, GH, M, MIN, MO, NY, P, PH, UC, US); summit at Palikea, [21°24′52″N, 158°06′1.5″W], *Degener & Park 5927* (F, GH, MASS, NY, US); third small valley NE of Palikea, *Degener et. al. 5915* (BISH, NY); middle Palawai Ridge, *Degener 10922 et al.* (B, BISH, CU, G, GH, MASS, MIN, MO, NY, P, US); E side of Palikea, *Degener et. al. 10923* (BISH); S of Kawaihapai, *Degener et. al. 11638* (F, GH, MASS, NY, S, US); Mokule`ia, gulch SW of Dillingham Ranch, *Degener et. al. 20617* (BISH, F, W); SW of Dillingham Ranch, Mokule`ia, *Degener et. al. 20619* (B, BM, G, PH, W); E of Maunakapu, *Degener et. al. 20853* (B [fragment], BISH, UC); Wai`anae, *Faurie 1087* (A, BM, G [2], P); Palehua, [21°23′49.7″N, 158°06′3.6″W], *Forbes 1677.O* (A, BH, BISH [2], M, MO, NY, P, UC [2], US); without locality, *Funk 134* (HAW); Mokule`ia, E side of Keawapilau Gulch, [21°32′52.9″N, 158°10′33.1″W], *Hatheway 230* (BISH, BM, F, G, PH, US); Kukui`ula, Mokule`ia, [21°33′24.6″N, 158°10′58.7″W], *Hatheway & Degener 133* (B, NY); Honouliuli Forest Reserve, 0.5 mi S of Maunakapu, *Hatheway et. al. 128* (BISH [2], US); Pohakea Pass, [21°25′50.4″N, 158°05′27.7″W], *Herbst 474* (BISH); Ka`ala, 1851–1871, *Hillebrand s.n.* (BISH); summit ridge 3/4 mi N of Pohakea Pass, [21°26′21.4″N, 158°05′57″W], *Kerr H.1130* (F); Pohakea Pass, [21°25′50.4″N, 158°5′27.7″W], *Lamoureux & Ozaki 609* (BISH, GH, HAW, K, UC); Wai`anae District, Wai`anae, section of Kahanahaiki, N-facing shoulder of ridgecrest, [21°32′3.2″N, 158°12′0.2″W], *Lau 1802.1* (BISH); Wai`anae Range: between Pu`umanawahua and Maunakapu, 5 May 1935, *Judd s.n.* (BISH); Makua, Piko Trail, 5 May 1946, *Kerr & King s.n.* (BISH); Ka`ala Mts., *Mann & Brigham 378* (K), *Mann & Brigham 578* (BISH [2], BM, CU, F [2], G, GH, MO, NY [2], UC, US), *Mann & Brigham 579* (G); Waimea firebreak trail, *Nakamoto 19* (HAW); without locality, 1792, *Menzies s.n.* (K, MO); ridge top 93 m N of Maunakapu, *Obata 412* (BISH); head of first ridge (small) S of `Ekahanui-Huliwai ridge (Kunia side), crest of `Ekahanui-Lualualei ridge, *Obata et. al. 442* (BISH, PTBG, US); N Palawai Gulch, middle branch, slightly N of Palikea, ridge top, N face only, [21°25′4.3″N, 158°05′35.8″W], *Obata & Palmer 425* (BISH); N Palawai-Napepeiauolelo Ridge, just N of Palikea, N face of ridge, [21°25′7.2″N, 158°05′24.6″W], *Obata & Palmer 426* (BISH, US); Palikea, 2 Feb 1954, *Pearsall s.n.* (G); Lualualei, slopes of Pu`ukaua, *Perlman 14061* (PTBG, US); (G); Nanakuli valley, DHHL survey by TNC, N side of valley, N-facing gulches, *Perlman & Lau 6173* (BISH, PTBG); Nanakuli valley, DHHL survey by TNC, cliffs on S side of valley, *Perlman & Lau 6200* (BISH, PTBG, US); on summit crest ridge between Pu`ukaua and Pu`ukanehoa, N side of Pu`ukaua near two pinnacle cones, *Perlman et. al. 5241* (BISH, PTBG); S side of Pohakea Pass, E side slopes, *Perlman et. al. 5271* (BISH, PTBG); Puali`i gulch, on N-facing slope, near ridge crest, TNC Honoliuli Preserve, *Perlman et al. 16498* (PTBG); Halona, Pohakea Pass, S side, 12 May 1933, *Russ s.n.* (BISH); Kupeha-Honouliuli, 5 Jun 1933, *Russ s.n.* (BISH [2]); Honouliuli, E of Palikea,

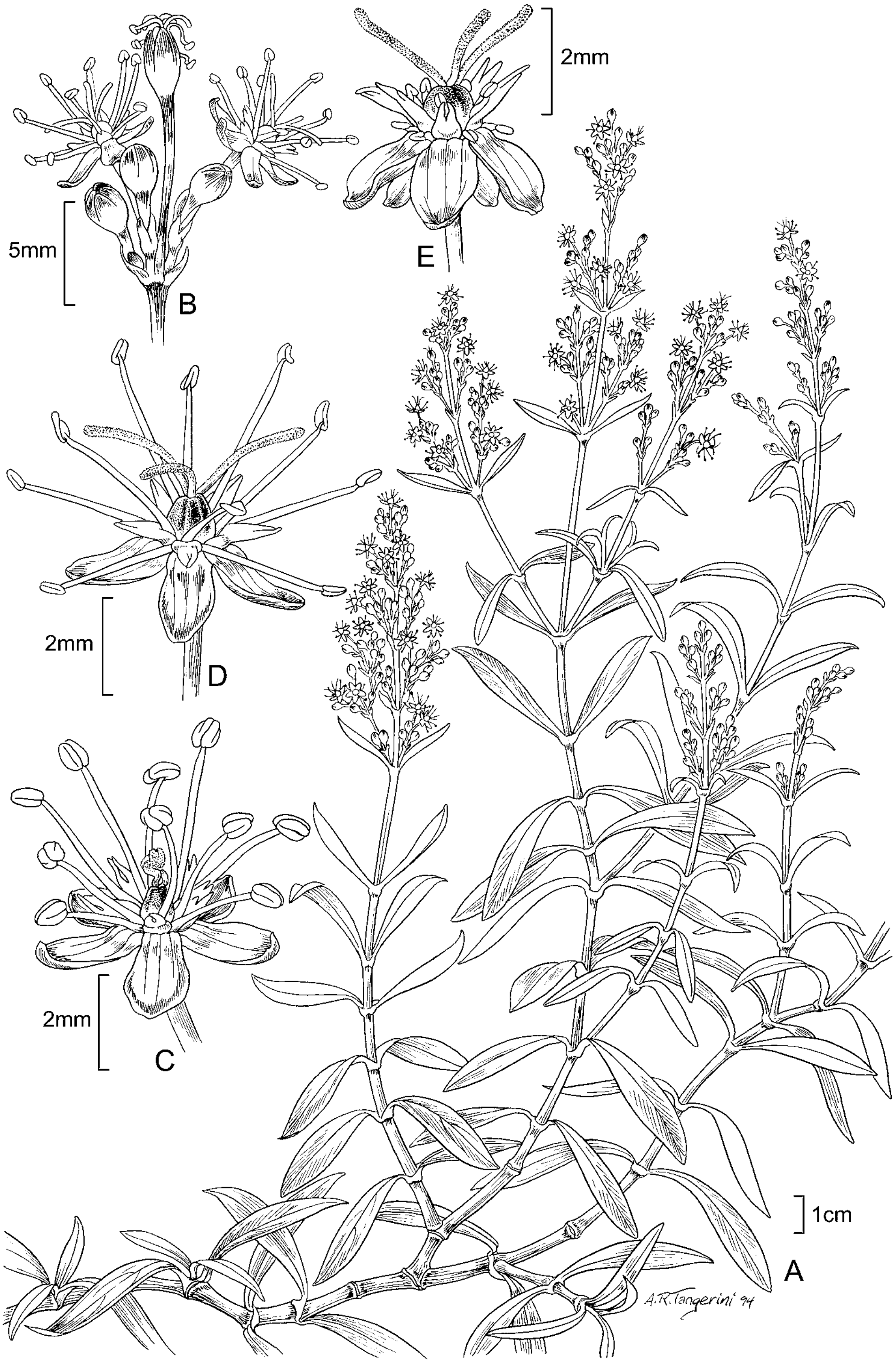

FIG. 60. *Schiedea ligustrina* (cult. from *Weller & Sakai 873*). A. Habit. B. Portion of male inflorescence. C. Flower in early anthesis, male. D. Male flower in late anthesis, with elongate, possibly receptive stigmas. E. Flower, female.

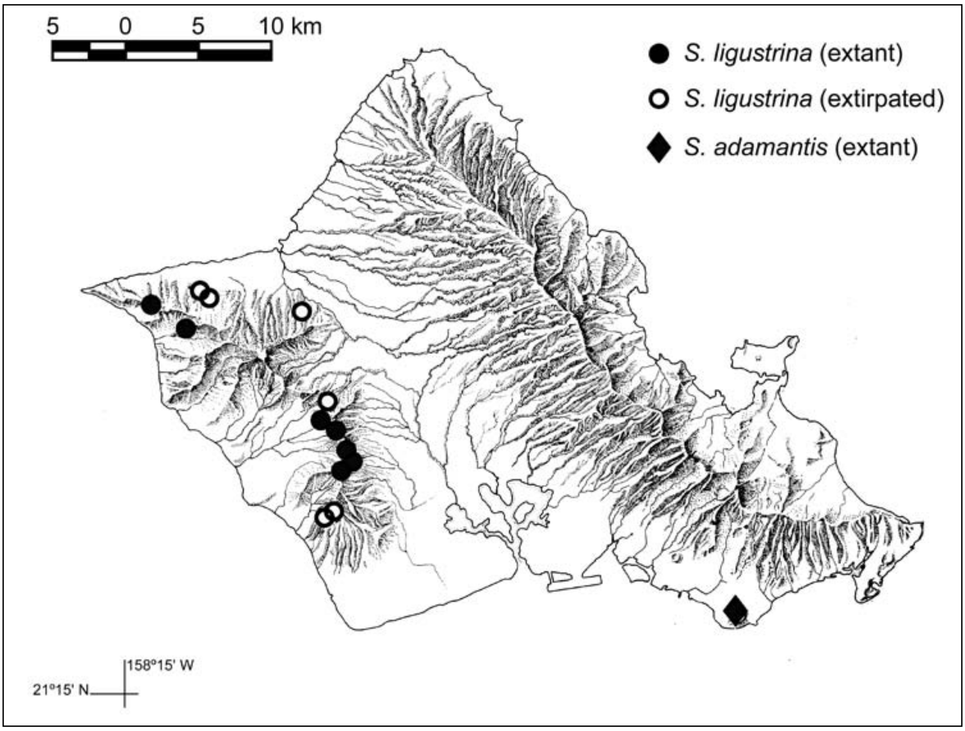

FIG. 61. Distribution of *S. ligustrina* and *S. adamantis*.

N fork of valley, *St. John 10381* (BISH); Pu`ukaua, Honouliuli, *St. John 20023* (A, BISH, G, UC); Palikea trail, *Stone 3474* (BISH [2]); Lualualei, ridge above, location code 4 AT 15, [21°27′14.4″N, 158°06′33.8″W], *Takeuchi 3275* (BISH); Lualualei, ridge spur, *Takeuchi 3280* (BISH); Lualualei, *Takeuchi 3287* (BISH), *Takeuchi 3288* (BISH), *Takeuchi 3289* (BISH); Lualualei, along trail in back of central valley, *Takeuchi 3416* (BISH); Lualualei Valley, subamphitheater by Palikea, [21°25′2.2″N, 158°06′15.7″W], *Takeuchi & Paquin 8512* (BISH [3]); Nihoa Gulch, [21°33′16.4″N, 158°13′21.5″W], *Takeuchi et. al. 3819* (BISH); without locality, s.d., *U.S. Expl. Exped. s.n.* (NY), 1838, *U.S. Expl. Exped. s.n.* (NY, US); Makaha side of dividing ridge, W of Wai`anae Kai N of Pu`ukawiwi, S. of pinnacle peaks, *Wood 7835* (PTBG); Pu`ukaua Region, Lualualei, steep ridge just S of Kaua, *Wood 10631* (PTBG); Wahiawa District, Kolekole Pass, ridge towards Pu`uhapapa, *Wood et al. 1885* (PTBG); Wai`anae District, Lualualei, below Pu`ukaua, *Wood et al. 3035* (PTBG).

CULTIVATED. **O`ahu.** Wai`anae Range: NE of Palikea Peak ca. 1 mi, ridge separating North Palawai and Napepeiauolelo Gulches, Jul 1985, *Obata & Perlman s.n.* [cult. *Weller & Sakai 846*] (US); ridge S of bunker 4AT15 at Lualualei Magazine, 27 Feb 1990, *Weller & Sakai s.n.* [cult. *Weller & Sakai 873*] (US); *Weller & Sakai 873* [cult. *Wagner & Shannon 6860*] (BISH, PTBG, US).

Schiedea ligustrina is a dioecious shrub with narrow linear to narrowly elliptic leaves usually 0.5–1.5 cm wide. It has the smallest flowers in sect. *Schiedea*.

Several other species of *Schiedea* grow in the Wai`anae Mountains, yet they occur only rarely with *S. ligustrina*. A population from `Ohikilolo has hybridized with the sympatric *S. mannii*. Sherff (1950) reported a hybrid between *S. ligustrina* and *S. hookeri*, but the specimen cited (*Degener 20619*) is not clearly a hybrid; it appears to represent merely a shade-grown individual of *S. ligustrina*. It was reported by Weller et al. (2001) as a possible hybrid.

Although *Schiedea ligustrina* is not currently under consideration for listing under the Endangered Species Act, Wagner et al. (1999b) consider it to vulnerable to extinction. The species now occupies only a fraction of its former range.

The specific epithet refers to a resemblance in aspect to the genus *Ligustrum* L.

34. Schiedea adamantis St. John, Pacific Sci. 24: 247. 1970.—TYPE: HAWAIIAN ISLANDS. O`AHU: NW rim of Diamond Head Crater, dry slope, 400 ft [125 m], 8 May 1955, *C. Lamoureux & E. T. Ozaki 567* (holotype: BISH-455976!).

Gynodioecious shrubs, 3–8 dm tall; stems erect or strongly ascending, glabrous, internodes 0.5–4.1 cm long, green to greenish purple. Leaves opposite; blades 1.5–3 (–6) cm long, 0.4–1.4 (–2.2) cm wide, weakly coriaceous, yellowish green, elliptic to elliptic-oblanceolate or oblanceolate, with only the midvein evident, margins entire, slightly thickened and weakly revolute, apex acute to acuminate, base cuneate; petioles 0.3–0.8 cm long. Inflorescence terminal, laterally contracted, somewhat congested; the hermaproditic inflorescences 3.1–12.3 cm long and with 22–170 flowers, less congested and broader than the pistillate inflorescences, these 2.3–11.4 cm long and with 30–140 flowers; bracts of central axis 2–15 mm long, those of branches and flowers 1–1.8 mm long, green to purple, linear to subulate. Flowers hermaphroditic or pistillate, (4-)5-merous. Hermaphroditic flowers: pedicels 4–12 mm long, quadrangular and somewhat flattened; sepals 3.4–4.5 mm long, narrowly ovate, broadly and shallowly navicular, oriented at 60° to 90° angle to the pedicel, green or tinged purple toward the apex, opaque, reflexed and convex at the base, producing a small transverse bulge, glabrous, margins scarious, sometimes somewhat irregularly undulate, entire, glabrous, apex obtuse; nectary base 0.5–0.85 mm long, spreading at 80° to the axis, dark yellow, the nectary shaft held above sepal surface, 2–2.5 mm long, apex with a deep wide unequal notch; stamens 10, the filaments slightly dimorphic, the antisepalous whorl 4.9–5.7 mm long, the alternate whorl 4.5–5.3 mm long, anthers 0.8–1.2 mm long, yellow; styles 3–4. Pistillate flowers: pedicels 2–7 mm long, quadrangular and somewhat flattened; sepals 2.6–3.2 mm long, narrowly ovate, green or yellowish green, pale yellow at the base, opaque, venation pale and translucent, reflexed and convex at the base, producing a small transverse bulge, broadly navicular, oriented at 60° to 100° angle to the pedicel, margins scarious and often irregularly undulate, entire or with 1–several lacerations, glabrous, apex often inrolled, obtuse; nectary base 0.5–0.65 mm long, spreading at 60° to the axis, dark yellow, the nectary shaft held well above the sepal surface, plump, 1–1.45 mm long, apex with a deep wide unequal notch, the two teeth incurved, adaxial side often slit to near the base; stamens 10, vestigial, filaments unequal, the antisepalous whorl 0.5–1.75 mm long, the alternate whorl 0.4–0.65 mm long, anthers 0.2–0.4 mm long, white, not producing pollen; styles 3–4 (–5). Capsules 3.5–5 mm long, narrowly ovoid. Seeds relatively few, 0.8–0.9 mm long, reniform, compressed, the surface papillose, papillae of the margins larger than those of the faces. Chromosome number: 2n = 52–56, 60 (*Weller & Sakai 847*). Plate 1D; Figs. 2Y, 4K, L, 62.

Distribution (Fig. 61). O`ahu, known only from steep, dry slopes in largely alien shrubland on the northwest rim of Diamond Head Crater, at ca. 125 m.

ADDITIONAL SPECIMENS EXAMINED. **O`ahu.** [all from Diamond Head, 21°16′03″N, 157°48′15″W]: Mauka or N side of outer rim of crater, *Flynn 780* (PTBG); NW rim of crater, *Gustafson 2907* (RSA), N rim above W tunnel, *Herbst et. al. 5612* (BISH, US [2]); NW rim of crater, *Lamoureux 1937, 1938, 1939, 1940,*

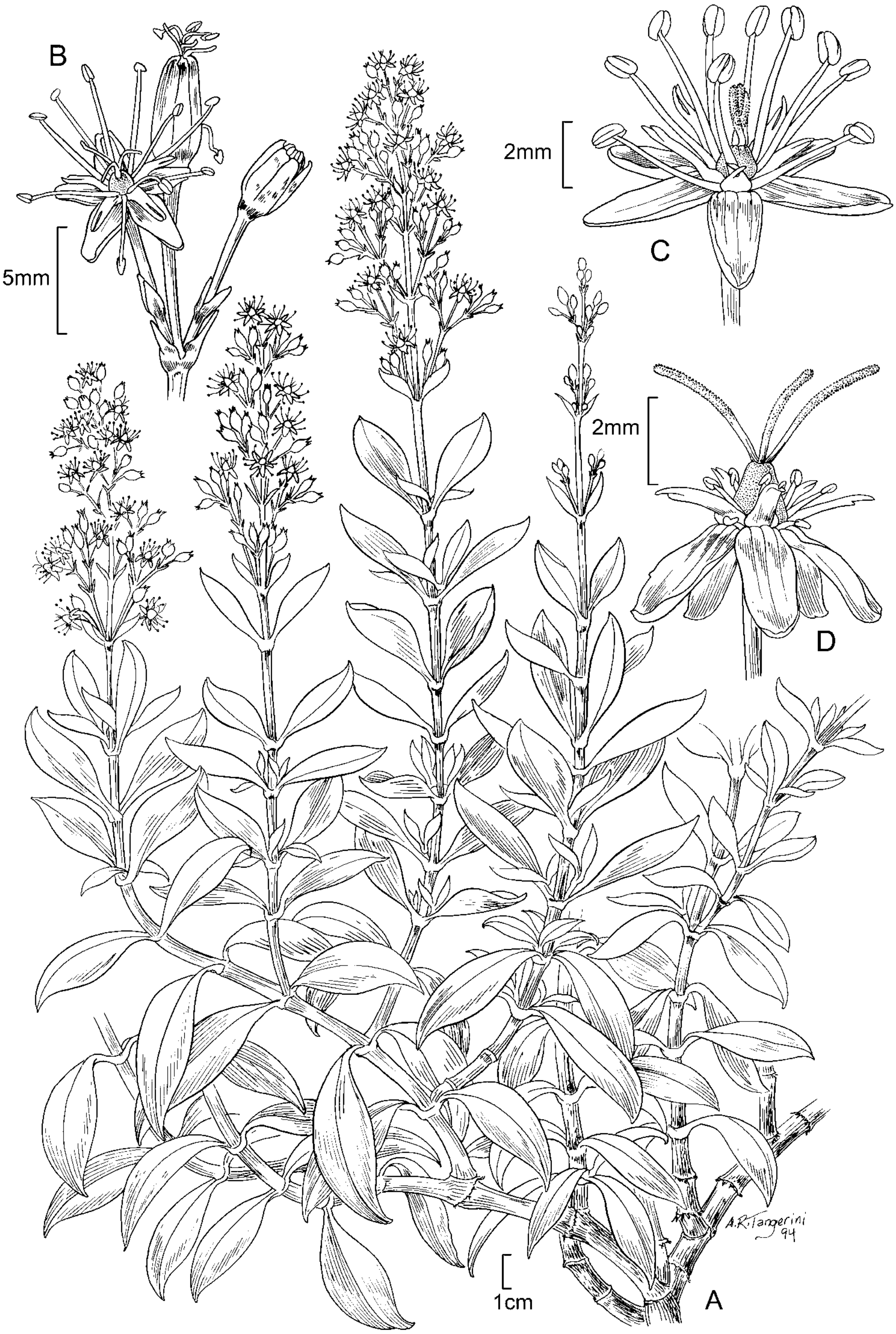

FIG. 62. *Schiedea adamantis* (cult. from *Weller & Sakai 847*). A. Habit. B. Portion of hermaphroditic inflorescence. C. Flower in early anthesis, hermaphroditic. D. Flower, female.

1941, *1942* (HAW); rim above W tunnel and ca. 3 m off crater rim on outside slope, *Obata & Palmer 409* (BISH); Diamond Head, 1956, *Ozaki & Lamouroux s.n.* (BM, G); outer side of N rim 15 ft below rim, *Ozaki et. al. 1448* (BISH); N rim above tunnel, Waikiki Side Tunnel, *Perlman et. al. 5450* (PTBG); Diamond Head, *Takeuchi 1919* (BISH), *1920* (BISH), *3817* (BISH, F); antenna road, just W of North tunnel, opposite Manalani Hts. on outer side of rim, *Weller & Sakai 847* (US).

CULTIVATED. **O`ahu.** Diamond Head: antenna road, just W of North tunnel, opposite Manalani Hts. on outer side of rim, *Weller & Sakai 847* [cult. 1984, *Weller & Sakai s.n.*] (BISH, GH, K, NY, PTBG, US), 1984, *Weller & Sakai s.n.* [cult. *Wagner & Shannon 6845*] (BISH, PTBG, US); 1984, *Weller & Sakai s.n.* [cult. *Wagner & Shannon 6846*] (BISH, PTBG, US).

Schiedea adamantis is similar to *S. ligustrina* (no. 33) and may have shared a common ancestor with it. It differs from *S. ligustrina* in its larger flowers, much wider leaves, and gynodioecious breeding system, and from *S. salicaria* in the somewhat narrower inflorescence and yellow-green leaves.

Despite the formerly larger population size and gynodioecious breeding system, *S. adamantis* has very low variability at isozyme loci, possibly as a result of founder effect during establishment (Weller et al. 1996). This species may never have occurred in more than a few populations.

Schiedea adamantis was the first species of *Schiedea* to be federally listed (as endangered) under the Endangered Species Act (Herbst 1984). Despite restoration efforts, the species is on the verge of extinction, and only three individuals remain in the natural population (compared to over 250 flowering individuals in 1992). Drought is the most likely proximate cause of the recent decline, although invasion by koa haole (*Leucaena leucocephala*) and other alien species may have resulted in the restriction of *S. adamantis* to marginal parts of the habitat where drought would have the greatest impact.

St. John did not indicate in the protologue where the type is deposited; however, the specimen at BISH is annotated as “holotype” in his hand. Specimens formerly presumed to be isotypes (GH! HAW! UC!) bear the collection date 5 Apr 1955 instead of 8 May 1955, as on the holotype label.

The specific epithet refers to the geographical range of the species, which is restricted to Diamond Head and is derived from the Greek noun *adamas* (“diamond”).

PRESUMED HYBRIDS OF SCHIEDEA

Below we list wild-collected presumed hybrids; the direction of the cross is unknown. The species involved are listed alphabetically.

S. menziesii × *S. salicaria*

SPECIMENS EXAMINED. **Maui.** WEST MAUI: Lahaina District, Lihau, on SE rim of Launiupoko Valley [20°51′00″N, 156°36′47″W], *Oppenheimer et al. H30405* (PTBG); Hale Pohaku, `Ula`ula, NW-facing cliff above Olowalu valley, [20°50′1.8″N, 156°35′21.6″W], *Perlman & Wood 14671* (BISH, PTBG, UC, US); near `Ula`ula, *Perlman & Wood 12836* (PTBG); *Perlman & Wood 12523* (PTBG, US); Lahaina District, `Ula`ula and along ridge to Ko`ai, [20°50′1.8″N, 156°35′21.6″W], *Wood & Perlman 4029* (US); *Wood & Perlman 4031* (US); *Wood & Perlman 4044* (US); [20°49′40.9″N, 156°35′20.7″W], *Wood & Perlman 4054* (US); *Wood & Perlman 4055* (US); *Wood & Perlman 4050* (US); just NE of `Ula`ula, [20°50′1.8″N, 156°35′21.6″W], *Wood & Perlman 4030* (US); W side of Ko`ai, [20°49′40.9″N, 156°35′20.7″W], *Wood & Perlman 4052* (US); *Wood & Perlman 4053* (US); *Wood & Perlman 4056* (US); Lihau Natural Area Reserve, on E side, *Perlman & Wood 15722* (PTBG, US); without locality, *Rémy 548* (P).

CULTIVATED. **Maui.** WEST MAUI: Hale Pohaku, `Ula`ula, NW-facing cliff above Olowalu valley, *Perlman & Wood 14671* [cult. *Wagner & Shannon 6827*] (BISH, PTBG, US); Hale Pohaku, slopes of `Ula`ula, between `Ula`ula and Ko`ai, *Perlman & Wood 14672* [cult. *Wagner & Shannon 6790*] (BISH, PTBG, US), *Perlman & Wood 14672* [cult. *Wagner & Shannon 6821*] (BISH, PTBG, US); Lahaina District, `Ula`ula and along ridge to

Ko`ai, W side of Ko`ai, *Wood & Perlman 4052* [cult. *Wagner & Shannon 6789*] (BISH, F, GH, K, NY, PTBG, US); *Wood & Perlman 4053* [cult. *Wagner & Shannon 6791*] (BISH, PTBG, US); next ridge S of Lihau, between Pu`uko`ai and Pu`u`ula`ula, *Weller & Sakai 902* [cult. *Wagner & Shannon 6788*] (BISH, PTBG, US), *Weller & Sakai 902* [cult. *Wagner & Shannon 6822*] (B, BISH, BM, CHR, E, F, GH, HAW, K, LE, MASS, MEL, MO, NSW, NY, P, PTBG, RSA, S, UC, US).

S. hookeri × *S. mannii*

SPECIMENS EXAMINED. **O`ahu.** Wai`anae Range, Wai`anae District, `Ohikilolo, *Nagata & Hall 3174* (BISH); Wai`anae Kai, E slopes of Mt. Ka`ala, N facing cliffs, *Wood et. al. 2796* (PTBG, US).

CULTIVATED. **O`ahu.** Wai`anae Range: high above entrance to first deep gulch that heads toward Pu`ukawiwi, putative hybrid, *Weller & Sakai 901* [cult. *Wagner & Shannon 6813*] (BISH, PTBG, US).

S. hookeri × *S. pentandra*

SPECIMENS EXAMINED. **O`ahu.** Wai`anae Range, Wai`anae District, Pu`ukaua, *Wood et. al. 3073* (PTBG).

S. lydgatei × *S. sarmentosa*

SPECIMENS EXAMINED. **Moloka`i.** Makolelau Ahu`pua`a, [21°5′11.9″N, 156°54′50.2″W], *Weller & Sakai 944* (US); *Weller & Sakai 945* (US); *Weller & Sakai 946* (US); *Weller & Sakai 947* (US); *Weller & Sakai 948* (US); Moloka`i District, Makolelau ahupua`a, Tr 7(26); along ridge S of Pu`ukolekole, first large gulch W of trail., *Stemmermann & Montgomery 3884* (BISH); Makolelau, first major gulch W of Makolelau, [21°6′N, 156°55′W], *Wagner et. al. 6738* (US [3]), *Wagner et. al. 6739* (US).

S. ligustrina × *S. mannii*

SPECIMENS EXAMINED. **O`ahu.** Wai`anae Range: `Ohikilolo ridge, *Bishop 1201* (HAW), *Bishop 1203* (HAW); Makua Valley, on `Ohikilolo ridge trail, *Perlman & Obata 5654* (PTBG); on climb to marker flag on `Ohikilolo ridge, *Perlman & Obata 5651* (BISH, PTBG); Makua-Kea`au ridge, a little inland of the low point of saddle, *Lau 2764* (BISH).

EXPERIMENTAL HYBRIDS OF SCHIEDEA

The hybrids listed below were produced and grown in the greenhouse at the University of California at Irvine by S. G. Weller and A. K. Sakai. The female parent is listed first in the cross; the voucher for the parent given in square brackets.

S. adamantis [from O`ahu, Diamond Head, *Weller & Sakai 847*]
- × *S. apokremnos* [from Kaua`i, Na Pali cliff, *Weller & Sakai 865*], cult. 1993, *Weller & Sakai s.n.* (BISH, US).
- × *S. globosa* [from O`ahu, Makapu`u Beach, *Weller & Sakai 844*], cult. 1993, *Weller & Sakai s.n.* (BISH, F, GH, K, NY, PTBG, US).
- × *S. hookeri* [from O`ahu, Wai`anae Mts., *Weller & Sakai 794*], cult. 1993, *Weller & Sakai s.n.* (BISH, GH, K, NY, PTBG, US).
- × *S. kaalae* [from O`ahu, Wai`anae Mts., *Takeuchi 3587*], cult. 1993, *Weller & Sakai s.n.* (BISH, PTBG, US).
- × *S. kealiae* [from O`ahu, Kealia Trail, *Weller & Sakai 791*], cult. 1993, *Weller & Sakai s.n.* (BISH, BM, E, F, GH, K, MO, NSW, NY, P, PTBG, UC, US).
- × *S. ligustrina* [from O`ahu, Wai`anae Mts., *Weller & Sakai 846*], cult. 1993, *Weller & Sakai s.n.* (BISH, F, GH, K, NY, PTBG, US).
- × *S. mannii* [from O`ahu, Wai`anae Mts., *Weller & Sakai 793*], cult. 1993, *Weller & Sakai s.n.* (BISH, GH, NY, PTBG, US).
- × *S. salicaria* [from Maui, West Maui, West Maui Mts., *Weller & Sakai 842*], cult. 1993, *Weller & Sakai s.n.* (BISH, F, GH, K, MO, NY, PTBG, US).

S. apokremnos [from Kaua`i, Na Pali cliff, *Weller & Sakai 865*]
  × *S. membranacea* [from Kaua`i, Mahanaloa and Ku`ia Gulches, *Weller & Sakai 864*], cult. 1993, *Weller & Sakai s.n.* (BISH, NY, PTBG, US).

S. diffusa subsp. *diffusa* [from Maui, East Maui, *Weller & Sakai 848*]
  × *S. adamantis* [from O`ahu, Diamond Head, Weller & Sakai 847], cult. 1993, *Weller & Sakai s.n.* (US).
  × *S. globosa* [from O`ahu, Makapu`u Beach, *Weller & Sakai 844*], cult. 1993, *Weller & Sakai s.n.* (BISH, GH, NY, PTBG, US).
  × *S. salicaria* [from Maui, West Maui, West Maui Mts., *Weller & Sakai 842*], cult. 1993, *Weller & Sakai s.n.* (US).

S. globosa [from O`ahu, Makapu`u Beach, *Weller & Sakai 844*]
  × *S. adamantis* [from O`ahu, Diamond Head, *Weller & Sakai 847*], cult. 1993, *Weller & Sakai s.n.* (BISH, NY, PTBG, US).
  × *S. apokremnos* [from Kaua`i, Na Pali cliff, *Weller & Sakai 865*], cult. 1993, *Weller & Sakai s.n.* (BISH, PTBG, US).
  × *S. hookeri* [from O`ahu, Wai`anae Mts., *Weller & Sakai 794*], cult. 1993, *Weller & Sakai s.n.* (BISH, PTBG, US).
  × *S. kaalae* [from O`ahu, Wai`anae Mts., *Takeuchi 3587*], cult. 1993, *Weller & Sakai s.n.* (US).
  × *S. kaalae* [from O`ahu, Ko`olau Mts., *Weller & Sakai 881*], cult. 1993, *Weller & Sakai s.n.* (BISH, BM, E, F, GH, K, MO, NY, PTBG, UC, US).
  × *S. kealiae* [from O`ahu, Kealia Trail, *Weller & Sakai 791*], cult. 1993, *Weller & Sakai s.n.* (BISH, NY, PTBG, US).
  × *S. ligustrina* [from O`ahu, Wai`anae Mts., *Weller & Sakai 846*], cult. 1993, *Weller & Sakai s.n.* (BISH, GH, K, NY, PTBG, US).
  × *S. ligustrina* [from O`ahu, Wai`anae Mts., *Weller & Sakai 873*], cult. 1993, *Weller & Sakai s.n.* (BISH, US).
  × *S. lychnoides* [from Kaua`i, Alaka`i, Nagata s.n.], cult. 1993, *Weller & Sakai s.n.* (BISH, BM, E, F, GH, K, MO, NSW, NY, PTBG, UC, US).
  × *S. lychnoides* [from Kaua`i, Napali-Kona Forest Reserve, *Weller & Sakai 867*], cult. 1993, *Weller & Sakai s.n.* (BISH, F, GH, K, MO, NY, PTBG, UC, US).
  × *S. membranacea* [from Kaua`i, Mahanaloa and Ku`ia Gulches, *Weller & Sakai 864*], cult. 1993, *Weller & Sakai s.n.* (BISH, GH, NY, PTBG, US).
  × *S. menziesii* [from Maui, West Maui, Lihau Ridge, *Weller & Sakai 849*], cult. 1993, *Weller & Sakai s.n.* (BISH, F, GH, K, MO, NY, PTBG, US).
  × *S. nuttallii* [from O`ahu, Wai`anae Mts., *Weller & Sakai 861*], cult. 1993, *Weller & Sakai s.n.* (BISH, BM, E, F, GH, K, MO, NSW, NY, P, PTBG, UC, US).
  × *S. pentandra* [from O`ahu, Wai`anae Mts., *Weller & Sakai 860*], cult. 1993, *Weller & Sakai s.n.* (BISH, US).
  × *S. salicaria* [from Maui, West Maui Mts., Pu`uhona, *Weller & Sakai 842*], cult. 1993, *Weller & Sakai s.n.* (BISH, NY, PTBG, US).
  × *S. spergulina* [from Kaua`i, Waimea Canyon, *Weller & Sakai 863*], cult. 1993, *Weller & Sakai s.n.* (BISH, US).
  × *S. trinervis* [from O`ahu, Wai`anae Mts., *Perlman 5448*], cult. 1993, *Weller & Sakai s.n.* (BISH, US).

× *S. verticillata* [from Nihoa, Devil's Slide and Dog's Head, *Weller & Sakai 880*], cult. 1993, *Weller & Sakai s.n.* (BISH, PTBG, US).

S. hookeri [from O`ahu, Wai`anae Mts., *Weller & Sakai 866*]
× *S. menziesii* [from Maui, West Maui, Lihau ridge, *Weller & Sakai 849*], cult. 1993, *Weller & Sakai s.n.* (BISH, PTBG, US).

S. kaalae [from O`ahu, Ko`olau Mts., *Weller & Sakai 881*]
× *S. membranacea* [from Kaua`i, Mahanaloa and Ku`ia Gulches, *Weller & Sakai 864*], cult. 1993, *Weller & Sakai s.n.* (BISH, PTBG, US).

S. kealiae [from O`ahu, Kealia Trail, *Weller & Sakai 791*]
× *S. adamantis* [from O`ahu, Diamond Head, *Weller & Sakai 847*], cult. 1993, *Weller & Sakai s.n.* (BISH, NY, PTBG, US).
× *S. apokremnos* [from Kaua`i, Na Pali cliff, *Weller & Sakai 865*], cult. 1993, *Weller & Sakai s.n.* (US).
× *S. globosa* [from O`ahu, Makapu`u Beach, *Weller & Sakai 844*], cult. 1993, *Weller & Sakai s.n.* (BISH, US).
× *S. globosa* [from Maui, West Maui, Kahakuloa Bay, *Weller & Sakai 852*], cult. 1993, *Weller & Sakai s.n.* (BISH, US).
× *S. hookeri* [from O`ahu, Wai`anae Mts., *Weller & Sakai 794*], cult. 1993, *Weller & Sakai s.n.* (US).
× *S. kaalae* [from O`ahu, Ko`olau Mts., *Weller & Sakai 881*], cult. 1993, *Weller & Sakai s.n.* (BISH, NY, PTBG, US).
× *S. ligustrina* [from O`ahu, Wai`anae Mts., *Weller & Sakai 846*], cult. 1993, *Weller & Sakai s.n.* (BISH, GH, NY, PTBG, US).
× *S. mannii* [from O`ahu, Wai`anae Mts., *Weller & Sakai 793*], cult. 1993, *Weller & Sakai s.n.* (BISH, F, GH, K, NY, PTBG, US).
× *S. menziesii* [from Maui, West Maui, Lihau ridge, *Weller & Sakai 849*], cult. 1993, *Weller & Sakai s.n.* (BISH, F, GH, K, MO, NY, PTBG, US).
× *S. nuttallii* [from O`ahu, Wai`anae Mts., *Weller & Sakai 861*], cult. 1993, *Weller & Sakai s.n.* (BISH, F, GH, K, NY, PTBG, US).
× *S. salicaria* [from Maui, West Maui, West Maui Mts., *Weller & Sakai 842*], cult. 1993, *Weller & Sakai s.n.* (BISH, GH, NY, PTBG, US).
× *S. spergulina* [from Kaua`i, Waimea Canyon, *Weller & Sakai 863*], cult. 1993, *Weller & Sakai s.n.* (BISH, US).
× *S. verticillata* [from Nihoa, Devil's Slide and Dog's Head, *Weller & Sakai 880*], cult. 1993, *Weller & Sakai s.n.* (BISH, NY, PTBG, US).

S. ligustrina [from O`ahu, Wai`anae Mts., *Weller & Sakai 873*]
× *S. hookeri* [from O`ahu, Wai`anae Mts., *Weller & Sakai 866*], cult. 1993, *Weller & Sakai s.n.* (BISH, US);
× *S. verticillata* [from Nihoa, Devil's Slide and Dog's Head, *Weller & Sakai 880*], cult. 1993, *Weller & Sakai s.n.* (BISH, US).

S. lychnoides [from Kaua`i, Napali-Kona Forest Reserve, *Weller & Sakai 867*]
× *S. globosa* [from O`ahu, Makapu`u Beach, *Weller & Sakai 844*], cult. 1993, *Weller & Sakai s.n.* (BISH, GH, K, NY, PTBG, US).

S. membranacea [from Kaua`i, Mahanaloa and Ku`ia Gulches, *Weller & Sakai 864*]
× *S. verticillata* [from Nihoa, Devil's Slide and Dog's Head, *Weller & Sakai 880*], cult. 1993, *Weller & Sakai s.n.* (US).

S. nuttallii [from O`ahu, Wai`anae Mts., *Weller & Sakai 861*]
× *S. menziesii* [from Maui, West Maui, Lihau ridge, *Weller & Sakai 849*], cult. 1993, *Weller & Sakai s.n.* (BISH, F, GH, K, MO, NY, PTBG, US).

S. spergulina [from Kaua`i, Waimea Canyon, *Weller & Sakai 863*]
× *S. adamantis* [from O`ahu, Diamond Head, *Weller & Sakai 847*], cult. 1993, *Weller & Sakai s.n.* (BISH, PTBG, US);
× *S. nuttallii* [from O`ahu, Wai`anae Mts., *Weller & Sakai 861*], cult. 1993, *Weller & Sakai s.n.* (BISH, US).

S. verticillata [from Nihoa, Devil's Slide and Dog's Head, *Weller & Sakai 880*]
× *S. kaalae* [from O`ahu, Ko`olau Mts., *Weller & Sakai 881*], cult. 1993, *Weller & Sakai s.n.* (BISH, NY, PTBG, US).
× *S. globosa* [from O`ahu, Makapu`u Beach, *Weller & Sakai 844*], cult. 1993, *Weller & Sakai s.n.* (BISH, F, GH, K, MO, NY, PTBG, US).
× *S. salicaria* [from Maui, West Maui, West Maui Mts., *Weller & Sakai 842*], cult. 1993, *Weller & Sakai s.n.* (BISH, PTBG, US).

S. globosa × *S. verticillata* [specimens from cultivated plants]
S. globosa [female, *Herbst 1370*] × *S. verticillata* [*Herbst 1401*] [cult. *Herbst 1907*] (BISH).

EXCLUDED NAMES

Alsinodendron H. Mann ex Bentham & J. D. Hooker, Gen. pl. 1: 978. 1867, orthographic variant.

Eucladus Nuttall ex A. Gray, U.S. Expl. Exped., Phan. 132. 1854, pro syn.

Eucladus suffruticosus Nuttall ex Hooker, Hooker's Icon. Pl. 7: t. 649. 1844, pro syn.

Schiedea gregoriana Degener, Fl. Hawaiiensis, fam. 344. *Schiedea gregoriana*. 1936.—The name is not validly published, because Degener did not include a Latin description or diagnosis.

Schiedea pubescens var. *purpurascens* Sherff, Amer. J. Bot. 30: 607. 1943.—The name is not validly published, because Sherff did not include a Latin description or diagnosis.

Schiedea pubescens var. *hillebrandii* Sherff, Amer. J. Bot. 30: 607. 1943.—The name is not validly published, because Sherff did not include a Latin description or diagnosis.

Schiedea stellarioides var. *brevifolia* Sherff, Amer. J. Bot. 30: 606. 1943.—The name is not validly published, because Sherff did not include a Latin description or diagnosis.

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APPENDIX 1

COLLECTION DATA AND GENBANK ACCESSION NUMBERS FOR SCHIEDEA ITS AND ETS SEQUENCES

TAXON	ACCESSION	GENBANK ACCESSION NUMBER ITS	GENBANK ACCESSION NUMBER ETS	REPOSITORIES
Geocarpon minimum	Seeds from Missouri Botanical Garden, Plant Conservation Center, Provenance #991620 /991621	AY517648 —	— —	—
Honckenya peploides (Oregon population)	*Wagner 6915*	AY517653	—	US
H. peploides (Baffin Island population)	*Gillespie et al. 6784*	AY517654	AY517687	US
Minuartia rossii	*Gillespie et al. 6726*	AY517649	—	US
M. moehringioides	*S. Gonzalez-Elizondo s.n.*	AY517650	—	US
Scleranthus biflorus	*Smisson WELTU 19660*	AY517651	—	WELTU
Wilhemsia physodes	*Parker 8422*	AY517652	—	US
Schiedea adamantis	*Weller & Sakai 847*	AY517659	AY517692	BISH, GH, K, NY, PTBG, US
S. apokremnos	*Weller & Sakai 865*	AY517665	AY517697	BISH, US
S. attenuata	*Wood 1394*	AY517666	AY517698	US, PTBG
S. diffusa	*Weller & Sakai 910*	AY517682	AY517714	BISH, US
S. globosa	*Weller & Sakai 844*	AY517663	AY517695	BISH, GH, NY, PTBG, US
S. haleakalensis	*Weller & Sakai 851*	AY517667	AY517699	BISH, NY, PTBG, US
S. hawaiiensis	*Weller & Sakai 932*	AY517685	AY517717	BISH, F, GH, K, MO, NY, PTBG, US
S. helleri	*Wagner & Shannon 6809*	AY517668	AY517700	BISH, PTBG,US
S. hookeri	*Weller & Sakai 862*	AY517669	AY517701	US
S. jacobii	*Perlman et al. 14807*	AY517684	AY517716	BISH, CANB, CHR,K, MO, NY, PTBG, US
S. kaalae	*Takeuchi 3587*	AY517678	AY517710	US
S. kauaiensis	*Perlman & Obata 12074*	AY517660	AY517693	US
S. kealiae	*Weller & Sakai 791*	AY517680	AY517712	BISH, F, GH, K, NY, PTBG, US

TAXON	ACCESSION	GENBANK ACCESSION NUMBER ITS	GENBANK ACCESSION NUMBER ETS	REPOSITORIES
S. laui	*Weller & Sakai 952*	AY517686	—	US
S. ligustrina	*Weller & Sakai 846*	AY517670	AY517702	US
S. lychnoides	*Weller & Sakai 867*	AY517656	AY517689	US
S. lydgatei	*Weller & Sakai 870*	AY517671	AY517703	BISH, PTBG, US
S. mannii[1]	*Weller & Sakai 901*	AY517672	AY517704	BISH, PTBG, US
S. membranacea	*Weller & Sakai 864*	AY517662	AY517694	BISH, US
S. menziesii	*Weller & Sakai 849*	AY517673	AY517705	BISH, NY, PTBG, US
S. nuttallii	*Wagner & Shannon 6795*	AY517661	—	BISH, GH, NY, PTBG, US
S. obovata	*Weller & Sakai 868*	AY517657	AY517690	US
S. pentandra	*Weller & Sakai 860*	AY517683	AY517715	No voucher
S. perlmanii	*Wagner & Shannon 6795*	AY517681	AY517713	BISH, GH, NY, PTBG, US
S. pubescens	*Perlman 14682*	AY517674	AY517706	BISH, US
S. salicaria	*Weller & Sakai 853*	AY517664	AY517696	US
S. sarmentosa	*Weller & Sakai 896*	AY517675	AY517707	—
S. spergulina	*Weller & Sakai 863*	AY517679	AY517711	BISH, GH, NY, PTBG, US
S. stellarioides	*Wagner & Shannon 6854*	AY517676	AY517708	BISH, PTBG, US
S. trinervis	*Perlman 5448*	AY517658	AY517691	US
S. verticillata	*Wagner & Shannon 6819*	AY517677	AY517709	BISH, PTBG, US
S. viscosa	*Wagner & Shannon 6810*	AY517655	AY517688	BISH, PTBG, US

[1] This collection was used in the study before it was thought to represent a putative hybrid of *S. hookeri* × *S. mannii*. Another collection of *S. mannii* (*Weller & Sakai 793*) was recently sequenced (Nepokroeff et al., unpubl.) and proved to have sequences identical to those of the putative hybrid (*Weller & Sakai* 901).

APPENDIX 2

MORPHOLOGICAL CHARACTER LIST FOR SCHIEDEA

The plesiomorphic state (0) is determined by the condition in the two genera determined to be the closest extant taxa to *Schiedea*, *Wilhelmsia* and *Honckenya,* or to a generalized outgroup. Multistate characters are unordered because of uncertainties about transitions between the character states. This character set is modified and extended from that used in earlier morphological phylogenetic analyses of these genera (Wagner et al. 1995; Weller et al. 1995). Characters that were mapped onto the phylogeny were not used in tree construction. Several other characters potentially related to breeding system evolution were excluded.

1. *Presence of woody tissue*. 0 = Herbaceous. 1 = Suffrutescent. 2 = Woody.—Woody tissue in Caryophyllaceae is secondarily derived (Carlquist 1996), and the shrubby members of this lineage are the most woody members of the family. We have not ordered this character state because of uncertainties of the relationship of the herbaceous and suffrutescent traits.
2. *Stems persistent or deciduous*. 0 = Persistent stems. 1 = Deciduous stems.—Most species have persistent above-ground stems, but two species of *Schiedea* die back to the ground during the dry season. Deciduous stems are coded as derived, which they appear to be in *Schiedea*; this matter is difficult to resolve through outgroup comparison, since outgroups grow in very different temperate environments.
3. *Habit, stem orientation*. 0 = Stems upright. 1 = Stems sprawling. 2 = Vine.—*Schiedea* species are upright, sprawling, or vines. The distinction between sprawling species and vines is somewhat arbitrary, but is based on the lengths of stems and their tendency to clamber through vegetation.
4. *Habit, stem number*. 0 = Plants single or few-stemmed from the base, usually not forming clumps, stems slender to stout. 1 = Plants multi-stemmed from the base, forming clumps, stems slender.
5. *Roots*. 0 = Fibrous roots. 1 = Swollen, fleshy roots.
6. *Stem succulence*. 0 = Slender, non-fleshy stems. 1 = Thick, somewhat fleshy stems.—Woody as well as herbaceous species may possess fleshy, somewhat succulent stems.
7. *Leaf shape*. 0 = Leaves broadest at or below the middle, usually elliptic to lanceolate or ovate. 1 = Leaves broadest above the middle, usually elliptic-oblanceolate to oblanceolate. 2 = Leaves linear or oblong.
8. *Leaf texture*. 0 = Leaves membranous. 1 = Leaves coriaceous. 2 = Leaves softly membranous.
9. *Leaf size*. 0 = Leaves of intermediate area. 1 = Leaf area large.—Very large leaves atypical of mainland Caryophyllaceae are characteristic of several species of *Schiedea*.
10. *Leaf succulence*. 0 = Leaves lacking succulence. 1 = Leaves succulent.—Leaf succulence is not necessarily correlated with fleshy stems.
11. *Leaf symmetry*. 0 = Leaves symmetric. 1 = Leaves slightly asymmetric. 2 = Leaves falcate. 3 = Midvein of leaf off-center.
12. *Leaf apex*. 0 = Acute or acuminate. 1 = Long-attenuate.
13. *Reduction in leaf venation*. 0 = Leaves 3- or more nerved. 1 = Leaves 1-nerved.—Some species of *Schiedea* have a single prominent nerve, a feature found in broad-leaved as well as linear-leaved species. By comparison with most continental Caryophyllaceae this trait is considered derived; the groups that appear to be most closely related to *Schiedea* have narrow leaves with a single nerve.
14. *Increase in leaf venation*. 0 = 1- or 3-nerved; 1 = 5-nerved; 2 = 7-nerved.—Several of the large-leaved species of *Schiedea* have very large leaves with 5 or 7 prominent nerves, as opposed to the majority of species, which have 3 or fewer nerves.
15. *Morphology of outer pair of leaf veins*. 0 = Outer primary veins forming smooth arcs. 1 = Outer pair of veins widely looping along the length of the leaf.
16. *Pubescence on leaf margin*. 0 = No pubescence. 1 = Thin, usually antrorse hairs present. 2 = Hooked hairs present.
17. *Leaf margin pubescence*. 0 = Margins entire. 1 = Leaf margins with minute, irregular teeth. 2 = Margin serrulate in distal part to serrate throughout.
18. *Leaf pubescence*. 0 = Translucent glandular hairs, ca. 0.2–0.3 mm long. 1 = Glabrous. 2 = Translucent non-glandular hairs, ca. 0.1–0.2 mm long. 3 = Purple-pigmented hairs, ca. 0.3–0.6 mm long. 4 = Translucent non-glandular hairs, ca. 0.2–0.3 mm long, restricted to the adaxial midrib and leaf base margin.
19. *Leaf surface*. 0 = Leaves not glaucous. 1 = Leaves slightly glaucous, dark green. 2 = Leaves slightly glaucous, pale and reflective.

20. *Inflorescence presentation*. 0 = Inflorescence terminal. 1 = Inflorescence pseudolateral.—In sections *Alsinidendron* and *Nothoschiedea* the lateral branch of the next node below the inflorescence elongates coincident with flowering and assumes subsequent vegetative growth.
21. *Inflorescence main axis suppression*. 0 = Not suppressed; main axis of multiple internodes.—This state occurs in most species of *Schiedea*, although the inflorescence can be variously condensed (Character 22). 1 = Suppressed; the main axis consisting of 1 (2) internodes.
22. *Lateral inflorescence condensation* (breeding system). 0 = Inflorescence open, diffuse. 1 = Lateral inflorescence branches shortened, main axis of inflorescence elongate.—This and the following character are very likely related to breeding system. Suppression of the lateral or main axis in *Schiedea* is related to the mechanics of wind-pollination. Niklas (1985) has shown that compact inflorescences are likely to disperse and capture pollen carried by wind. In *Schiedea*, the degree of inflorescence condensation is correlated with the frequency of females in populations (Weller et al. 1998).
23. *Inflorescence main axis condensation* (breeding system). 0 = Inflorescence diffuse, panicle-like. 1 = Main axis of inflorescence somewhat vertically condensed. 2 = Main axis of inflorescence highly vertically condensed. 3 = Inflorescence globose due to main axis strongly condensed.
24. *Flower orientation*. 0 = Spreading, ascending, or upright. 1 = Pendent.—Variation in this character is related to habitat; pendent flowers are typical of species occurring in mesic to wet forest. This floral orientation may help in preventing wetting of pollen.
25. *Pedicel orientation*. 0 = Spreading. 1 = Strongly ascending to appressed to internode.
26. *Inflorescence presentation*. 0 = Inflorescence upright. 1 = Inflorescence pendent.—Species occurring in mesic or wet habitats produce pendent infloresences, possibly a feature that may help in keeping pollen dry, as in the case of flower orientation.
27. *Inflorescence internode pubescence*. 0 = Glandular pubescent, hairs intermediate in length, ca. 0.2–0.3 mm long. 1 = Glabrous. 2 = Short glandular pubescence, hairs <0.5 mm long. 3 = Long glandular pubescence, hairs ca. 0.9–1.2 mm long. 4 = Nonglandular pubescence, hairs 0.15–0.5 mm long. 5 = Glandular, purple pubescence, hairs 0.3–0.6 mm long. 6 = Nonglandular, purple pubescence, hairs 0.15–0.3 mm long.—Inflorescence pubescence appears to vary independently of pubescence on vegetative portions of plants; for example, several species with glabrous stems and leaves have dense glandular pubescence in the inflorescence.
28. *Sepal width*. 0 = Sepals < 3 mm in width. 1 = Sepals > 4 mm in width.
29. *Calyx form*. 0 = Calyx rotate to reflexed. 1 = Calyx campanulate, open. 2 = Calyx tightly closed or very slightly open at anthesis.
30. *Sepal orientation*. 0 = Spreading to somewhat reflexed. 1 = Ascending. 2 = Strongly reflexed. 3. Strongly reflexed in distal half, then curved outward at 90%.
31. *Sepal texture*. 0 = Membranous and green. 1 = Membranous, white, remaining papery as fruit matures. 2 = Fleshy, white or green, becoming dark purple and very juicy as seeds mature.
32. *Sepal apex*. 0 = Obtuse to acute. 1 = Attenuate. 2 = Long-attenuate.
33. *Sepal shape*. 0 = Lanceolate. 1 = Narrowly ovate. 2 = Ovate. 3 = Broadly ovate. 4 = Rhombic to oblanceolate, obovate or elliptic.—Sepal shape is variable in *Schiedea;* therefore, we treat this as an unordered character.
34. *Sepal pubescence*. 0 = Glabrous. 1 = Pubescent abaxially (sometimes sparsely so) and ciliate. 2 = Pubescent abaxially, but not ciliate on margin. 3 = Ciliate on margin only.
35. *Sepal configuration*. 0 = Flat to shallowly concave. 1 = Shallowly navicular, at least in distal half. 2 = Deeply navicular, at least in distal half.
36. *Sepal apex inrolled*. 0 = No. 1 = Yes.
37. *Nectary type*. 0 = Small mound. 1 = Nectary a well-developed syringe-like shaft. 2 = Nectary with well-developed flaps, extending beyond the bulbous nectariferous portion, the flaps not connate at base. 3 = Similar to 2, but flaps connate at base or into a cup around ovary.
38. *Nectary shaft curvature* (*Schiedea* only): 0 = Straight, nectar collecting in drops at apex of shaft. 1 = Recurved and arching from surface of sepal, except for contact at apex, nectar deposited on the concave surface of the sepal.—One species, *S. stellarioides*, has nectary shafts that are appressed against the sepals until late in anthesis, when the shaft curls forward. This feature is coded as straight (0) because of the shaft's initial position.
39. *Nectary base color*. 0 = Bright green. 1 = Greenish yellow. 2 = Pale yellow. 3 = Dull yellow. 4 = Dark yellow. 5 = Dark yellowish orange.
40. *Nectar color*. 0 = Clear. 1 = Nectar appears black when large amounts accumulate.

41. *Ratio, staminal filament length to sepal length* (breeding system). 0 = <1.0. 1 = 1.0 - 1.9. 2 = >2.0.—This feature may be related to wind pollination (and sexual dimorphism), because many studies have shown that exserted stamens are characteristic of wind pollination. Autogamous species of *Schiedea* have stamens that are shorter than the sepals or enclosed within them.
42. *Length of antisepalous and alternate staminal filaments* (excluded). 0 = Equal or subequal. 1 = Dimorphic.
43. *Antisepalous staminal filament orientation.* 0 = Spreading. 1 = Erect.—The derived state of this character occurs only in two species, *S. pentandra* and *S. pubescens*.
44. *Anther color*. 0 = Yellow. 1 = Reddish purple.
45. *Pollen color*. 0 = Yellow. 1 = Gray.
46. *Style number*. 0 = Usually 3, occasionally 4, rarely 5. 1 = 4–6, rarely 3 or 7. 2 = 5–11, rarely 4.—Although overlapping, these character states specify modal differences that characterize species. Variation in style number may occur among flowers on a plant, but the range within a species falls unambiguously into one of the three categories. Common style numbers may be placed in non-overlapping categories.
47. *Style receptive surface extent* (excluded). 0 = Apex to about 2 to 2/3. 1 = Entire length. 2 = Apex to 1/10, style clavate.
48. *Ovule number*. 0 = < 100. 1 = > 100.
49. *Seed retention* (excluded). 0 = Seeds dispersed through valves. 1 = Seeds retained within capsule, which gradually rots to release seeds, or (in *S. jacobii*) remaining coherent as a unit and persistent on the placenta after dehiscence of capsule, seeds eventually dispersing (or perhaps germinating *in situ* in the wild), or in *S. diffusa* seeds also may germinate before dispersal occurs.—Species with non-dispersing fruits occur in wet forests.
50. *Seed margin*. 0 = Cells along the seed margin not elongated. 1 = Cells along seed margin moderately to strongly elongated into papillae.
51. *Shape of cell margins on seed surface*. 0 = Cell lobes appear rounded because of the convex nature of the cell. 1 = Cells appear acute because cell surfaces are flat and cell margins are readily visible.
52. *Breeding system* (excluded). 0 = Hermaphroditic. 1 = Gynodioecious. 2 = Subdioecious. 3 = Dioecious.—This character is used to differentiate all species with hermaphroditic breeding systems (which may vary from outcrossing to cleistogamous) from species with dimorphic breeding systems.
53. *Habitat* (excluded). 0 = Arctic. 1 = Mesic forest, shrubland or cliffs. 2 = Dry forest, shrubland or cliffs. 3 = Coastal. 4 = Wet forest.
54. *Biogeography* (excluded). 0 = Extra-Hawaiian. 1 = Kaua`i. 2 = O`ahu. 3 = Moloka`i. 4 = West Maui. 5 = East Maui. 6 = Lana`i. 7 = Hawai`i. 8 = Nihoa.
55. *Habit, duration*. 0 = Perennial. 1 = Annual.
56. *Habit, internode rooting*. 0 = No. 1 = Yes.
57. *Flower parts position relative to ovary*. 0 = Hypogynous. 1 = Subperigynous.
58. *Nectary, lobing*. 0 = Entire. 1 = Bilobed.
59. *Nectary, reduction*. 0 = No. 1 = Yes.
60. *Ovary, carpels*. 0 = 1-celled. 1 = 3-celled.
61. *Petals present.* 0 = Yes. 1 = No.

APPENDIX 3

MATRIX OF MORPHOPLOGICAL CHARACTERS

Polymorphic characters are indicated in the following matrix by a letter. The characters for each letter are: A = 0,1; B = 3,5,7; C = 2,3,4,5,7; D = 1,4; E = 4,6; and F = 3,4,5,6. A question mark indicates the state is unknown for that taxon.

CHARACTER		1		2		3		4		5		6	
	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	1
Honckenya	00000	11001	00000	01100	00000	01000	00100	00010	01000	0?00?	?1000	11100	0
Wilhelmsia	01100	00000	00100	11000	00000	00000	00010	00010	00010	0000?	?0000	10011	0
S. adamantis	20000	01100	00100	00100	00200	01001	00101	11010	10000	01001	11220	00000	1
S. amplexicaulis	?0???	00000	00100	10A00	000?0	?4002	01011	010?0	11000	0?000	00?10	00000	1
S. apokremnos	20100	01101	00100	00110	00300	01001	00301	01010	00000	01000	01210	00000	1
S. attenuata	20110	00101	11000	00100	00000	01000	00001	11110	11000	10001	00110	00000	1
S. diffusa	00200	10110	10100	00100	00010	16002	01211	01040	01000	01010	004B0	00000	1
S. globosa	10110	10101	11010	00100	00300	00001	00221	01110	10000	11000	023C0	00000	1
S. haleakalensis	20000	02100	20100	00100	00300	0D001	00221	01020	11000	01001	13250	00000	1
S. hawaiiensis	01200	00110	10100	00100	00010	14000	01011	01040	11000	00000	00270	00000	1
S. helleri	20200	00110	10001	11100	00010	14003	01212	11010	11000	02000	00410	00000	1
S. hookeri	10110	00200	21000	00000	00010	10002	01011	01010	11000	00000	00120	00000	1
S. implexa	20000	10110	10100	00100	00000	0?002	01011	010?0	11000	0?000	00150	00000	1
S. jacobi	00000	10110	10100	00100	00000	01001	01031	01040	00000	11010	00450	00000	1
S. kaalae	00000	11110	30100	00100	00001	01002	01031	01040	11000	00000	00420	00000	1
S. kauaiensis	20000	10110	10100	00100	00000	04002	02010	01040	11000	00000	00110	00000	1
S. kealiae	20110	00200	21000	00100	00200	02001	00121	11010	11000	0?000	02220	00000	1
S. laui	10000	10110	10100	00100	00001	01001	01031	010?0	01000	01000	00430	00000	1
S. ligustrina	20000	01100	00100	00100	00200	01001	00101	01020	10000	01001	13220	00000	1
S. lychnoides	00200	00010	00011	11301	10010	15111	10410	02001	00011	21110	00410	00000	1
S. lydgatei	20000	01100	00000	00120	00000	01000	00101	01020	11000	01001	10230	00000	1

(Continued)

APPENDIX 3 cont.

CHARACTER		1		2		3		4		5		6	
	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	1
S. mannii	20000	02100	11100	00100	00200	02001	00101	01020	20000	0?000	02220	00000	1
S. membranacea	01001	10010	00021	11200	00010	01003	01202	11010	21000	00000	00110	00000	1
S. menziesii	20110	00200	21000	00400	01000	04002	00011	01030	10000	00000	002E0	00000	1
S. nuttallii	20000	10110	10100	00100	00001	01002	01031	01040	11000	00000	00120	00000	1
S. obovata	20000	11110	00011	22101	10010	01111	20400	03001	00011	21101	00120	00000	1
S. pentandra	00200	00110	11100	10100	00010	16002	02012	11050	11100	02000	00120	10000	1
S. perlmanii	00200	00110	10100	00100	00010	11002	01211	01040	11000	02000	00110	00000	1
S. pubescens	00200	00110	10100	00100	00010	16002	02012	11050	11100	02000	004F0	10000	1
S. salicaria	20000	01100	00000	00120	00100	01000	00101	11020	11000	01001	11240	00000	1
S. sarmentosa	20110	00200	21000	00200	00200	00001	00111	11030	10000	00000	01230	00000	1
S. spergulina	20000	02200	21100	00100	00200	04001	00131	11020	11000	01000	03210	00000	1
S. stellarioides	10100	00000	01100	10100	00000	04003	01012	11040	11010	00000	00110	00000	1
S. trinervis	20000	10110	00001	22101	10010	01121	20400	03001	00011	21001	00420	00000	1
S. verticillata	01001	10111	00021	00100	00000	03000	01020	01110	10000	20100	00380	00000	1
S. viscosa	00200	00000	00000	11301	10010	15111	10410	02001	00011	21110	00110	00000	1

APPENDIX 4

CHROMOSOME COUNTS OF SCHIEDEA

One count was made for each collection, although sometimes from multiple buds or root tips of one individual.

S. adamantis: 2n = 52–56, 60; *Weller & Sakai 847.*
S. apokremnos: 2n = possibly 48; *Weller & Sakai 865.*
S. diffusa subsp. *diffusa*: 2n = 54; *Weller & Sakai 848.*
S. globosa: 2n = 44–46; *Weller & Sakai 844.*
S. hookeri: 2n = 60; *Weller & Sakai 871.*
S. kaalae: 2n = 60; *Takeuchi 3587.*
S. kealiae: 2n = 58, possibly 60; *Weller & Sakai 791.*
S. ligustrina: 2n = 56; *Weller & Sakai 873.*
S. lychnoides: 2n = 58, possibly 60; *Weller & Sakai 867.*
S. lydgatei: 2n = 50, 60; *Weller & Sakai 870.*
S. mannii: 2n = 56; *Weller & Sakai 793.*
S. menziesii: 2n = 50–52; *Weller & Sakai 849.*
S. nuttallii: 2n = 56; *Weller & Sakai 861.*
S. obovata: 2n = 48–50; *Weller & Sakai 868.*
S. salicaria: 2n = 55–60, 60; *Weller & Sakai 842, 853.*
S. sarmentosa: 2n = 55–60; *Wagner et al. 6675, 6681.*
S. spergulina: 2n = 46–50; *Weller & Sakai 863.*
S. stellarioides: 2n = 56–60; *Perlman 11903.*
S. trinervis: 2n = 50–54, 60; *Perlman 5448.*
S. verticillata: 2n = 60; *Conant 115.*
S. viscosa: 2n = 52–56; *Perlman 11904.*

NUMERICAL LIST OF TAXA

1. S. helleri
2. S. membranacea
3. S. attenuata
4. S. verticillata
5. S. lychnoides
6. S. viscosa
7. S. obovata
8. S. trinervis
9. S. apokremnos
10. S. stellarioides
11. S. amplexicaulis
12. S. perlmanii
13. S. kauaiensis
14. S. nuttallii
15. S. laui
16. S. kaalae
17. S. implexa
18. S. jacobii
19. S. hawaiiensis
20. S. pentandra
21. S. pubescens
22a. S. diffusa subsp. diffusa
22b. S. diffusa subsp. macraei
23. S. kealiae
24. S. hookeri
25. S. menziesii
26. S. sarmentosa
27. S. haleakalensis
28. S. globosa
29. S. spergulina
30. S. mannii
31. S. lydgatei
32. S. salicaria
33. S. ligustrina
34. S. adamantis

INDEX TO NUMBERED COLLECTIONS EXAMINED

The numbers in parentheses refer to the corresponding species in the text and in the Numerical List of Species presented above. (× indicates a presumed or greenhouse-produced hybrid.)

16068 (22a); 16496 (20); 16498 (33); 16993 (28); 17630 (1); 17808 (22b).

Plews, J. H. 138 (2).

Rémy, J. 546 (22b); 547 (14); 548 (32×25); 548bis (11); 549 (31); 550 (29); 551 (28); 551bis (28); 552 (28); 590? (28); 591 (26).

Rock, J. F. 27(5934) (10); 27(5935) (10); 27(5468) (10); 27(5471) (10); 27(5473) (10); 2638 (5); 4876 (5); 4877 (5); 5459 (5); 5460 (5); 5461 (5); 5464 (10); 5474 (10); 5475 (10); 5907 (5); 6184 (28); 7007 (28); 7008 (28); 7014 (31); 8360 (22b); 8544 (22a); 8643 (17); 12924 (28); 12932 (22a); 14059 (28); 14067 (28); 17004 (14); 17095 (10); 17105 (5).

Sakai, W. S. 134A (20).

Seemann, B. C. 2271 (14).

Selling, O. 3590 (8); 3608 (14); 3844 (23).

Shigematsu, K., et al. 76.38 (23).

Skottsberg, C. 251 (14); 335 (7); 855 (22a); 1030 (29).

St. John, H. 9888 (7); 10060 (8); 10381 (33); 10645 (8); 11096 (14); 12981 (28); 14082 (14); 14083 (7); 17553 (8); 19970 (8); 20023 (33); 20028 (23); 20133 (28); 20134 (28); 21536 (14); 24793 (30); 25224 (22a); 26688 (9); 26717 (28).

St. John, H., & R. J. Catto 17960 (22a).

St. John, H., et al. 12393 (22a); 12615 (22a); 23414 (28).

Stemmermann, L. 1004 (27).

Stemmermann, R. L., & S. Montgomery 3876 (31); 3884 (31×26); 3904 (31).

Stone, B. C. 2738 (28); 3474 (33).

Suehiro, A. 87 (8).

Swezey, O. 12770 (14).

Takeuchi, W. Waianae 57 (23); Koolau 60a (28); Koolau 60b (28); Koolau 60c (28); Waianae 68a (23); Waianae 68b (23); Koolau 72a (28); Koolau 72b (28); Koolau 73 (28); 1919 (34); 1920 (34); 3275 (33); 3280 (33); 3287 (33); 3288 (33); 3289 (33); 3416 (33); 3417 (16); 3587 (16); 3817 (34).

Takeuchi, W., & D. Paquin 3438 (16); 3442 (16); 3858 (23); 8512 (33).

Takeuchi, W., & B. Tate 3574 (16); 3575 (16).

Takeuchi, W., et al. Waianae 105 (30); Waianae 106 (24); 2111 (30); 2112 (24); 2113 (30); 3819 (33).

Tate, B., & W. Takeuchi 5 (30).

Thorne, R. F. 33338 (20).

Topping, D. L. 3029 (28).

Wagner, W. L., & D. H. Lorence 5741 (28).

Wagner, W. L., & R. K. Shannon 6787 (25); 6788 (25×32); 6789 (25×32); 6790 (32); 6791 (25×32); 6792 (14); 6793 (14); 6794 (2); 6795 (12); 6796 (22b); 6797 (22a); 6798 (29); 6799 (32); 6800 (10); 6801 (16); 6802 (20); 6803 (7); 6804 (16); 6805 (13); 6806 (14); 6807 (8); 6808 (7); 6809 (1); 6810 (6); 6811 (6); 6812 (10); 6813 (24×30); 6814 (6); 6815 (7); 6816 (32); 6817 (32); 6818 (32); 6819 (4); 6820 (29); 6821 (32); 6822 (25×32); 6823 (25); 6827 (25×32); 6838 (30); 6839 (24); 6840 (24); 6841 (24); 6842 (24); 6843 (28); 6844 (28); 6845 (34); 6846 (34); 6847 (28); 6848 (28); 6849 (28); 6850 (28); 6851 (24); 6852 (28); 6853 (8); 6854 (10); 6855 (10); 6856 (31); 6857 (31); 6858 (23); 6859 (23); 6860 (33).

Wagner, W. L., et al. 4802 (22a); 5312 (28); 5325 (23); 5926 (22a); 6031 (5); 6672 (31); 6675 (26); 6681 (26); 6682 (31); 6738 (31×26); 6739 (31×26); 6740 (26); 6741 (31).

Warshauer, F. R. 2864 (22a); 1056 (16); 1184 (12).

Warshauer, F. R., & P. H. McEldowney 3020 (22a).

Warshauer, F. R., et al. 2546 (22a).

Wawra, H. 1825 (22a); 2220 (16); 2280 (14).

Webster, G. L. 1442 (20); 1470 (20); 1478 (28); 1632 (20); 1644 (14).

Weller, S. G., & A. K. Sakai 791 (23); 793 (30); 794 (24); 796 (20); 842 (32); 844 (28); 845 (28); 846 (33); 847 (34); 848 (22a); 849 (25); 850 (28); 851 (27); 852 (28); 853 (32); 861 (14); 862 (24); 863 (29); 864 (2); 865 (9); 866 (24); 867 (5); 868 (7); 870 (31); 873 (33); 879 (24); 881 (16); 889 (9); 892 (16); 898 (22a); 899 (24); 903 (14); 905 (28); 906 (28); 909 (28); 910 (22a); 911 (32); 932 (19); 944 (31×26); 945 (31×26); 946 (31×26); 947 (31×26); 948 (31×26); 964 (28).

Welton, P. 768 (14).

Welton, P., & R. Fenstermacher 319 (24).

Welton, P., & B. Haus 632 (14); 1118 (25); 1569 (21).

Welton, P., & K. Marr 705 (24).

Welton, P., et al. 164 (24); 835 (31).

Wilbur, R. L. 625 (20); 641 (28); 767 (20); 783 (14).

Wood, K. R. 1033a (2); 1394 (3); 1423 (3); 2627 (30); 2911 (8); 3438 (24); 3818 (28); 3861 (5); 5970 (21); 6015 (10); 6018 (29); 6031 (31); 6031a (31); 6038 (26); 7831 (24); 7835 (33); 8639 (6); 10631 (33); 10640 (24).

Wood, K R., & J. J. Fay 7869 (9); 7870 (9).

Wood, K. R., & J. Lau 2893 (26); 5900 (8); 10585 (24); 10586 (20); 10633 (24); 10634 (24).

Wood, K. R., & T. Menard 10573 (1).

Wood, K. R., & S. Perlman 328 (32); 330 (25); 606 (31); 1073 (2); 1079 (29); 1615 (32×25); 1993 (31); 1994 (26); 2003 (26); 2004 (31); 2376 (2); 2475 (29); 2527 (2); 2543 (1); 2846 (10); 2847 (10); 3382 (3); 3983 (10); 3984 (10); 3985 (10); 3986 (10); 3987 (10); 3989 (10); 3990 (10); 3991 (10); 3992 (10); 3998 (6); 3999 (6); 4000 (6); 4001 (6); 4002 (6); 4003 (6); 4004 (6); 4005 (6); 4006 (6); 4007 (6); 4009 (10); 4029 (32×25); 4030 (32×25); 4031 (32×25); 4044 (32×25); 4050 (32×25); 4052 (32×25); 4053 (32×25); 4054 (32×25); 4055 (32×25); 4056 (32×25); 4087 (21); 5109 (23); 5306 (9); 8611A-C (6); 8620 (10).

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