

12

Phylogeny and Biogeography in *Schiedea* and *Alsinidendron* (Caryophyllaceae)

WARREN L. WAGNER,
STEPHEN G. WELLER, AND
ANN K. SAKAI

The current Hawaiian angiosperm flora arose from 270 to 282 successful colonization events (Wagner, 1991). In about 10% of these colonization events, spectacular radiations have followed, resulting in morphologically diverse species (Wagner, 1991). These species often occur in strikingly different habitats. Despite the past attention given to these radiations, there have been few attempts to study them from a phylogenetic perspective. A phylogenetic approach provides the opportunity to understand patterns of speciation (inter-island versus intra-island) and the association of habitat shifts with speciation and to examine the causes of breeding system evolution in islands. This chapter is about the fate of the monophyletic lineage comprising the endemic Caryophyllaceae subfamily Alsinoideae. The wide geographic and ecological distribution of this lineage in the Hawaiian Islands, coupled with the extensive range of breeding systems and habit, make it an excellent choice for study of adaptive radiation and biogeographic patterns.

Schiedea and *Alsinidendron* comprise the fifth or sixth largest endemic radiation of species in the Hawaiian angiosperm flora (Wagner et al., 1990; Wagner, 1991), depending on the number of colonizations of *Cyrtandra* (Gesneriaceae). Twenty-six species were recognized in the most recent taxonomic treatment (Wagner et al., 1990) with 22 in *Schiedea* and 4 in *Alsinidendron*. Subsequently, two new *Schiedea* species were discovered on Kaua'i (*S. attenuata* and an unnamed species discovered in mid-1993), and one gynodioecious species (*S. sarmentosa*) was resur-

TABLE 1. 2. 1. Breeding System, Habit, and Distribution for Species of *Alsindendron* and *Schiedea*

Species	Breeding system	Habit	Habitat	Distribution
<i>Alsindendron</i>				
<i>lychnoides</i> (Hillebr.) Sherff	Hermaphroditic, facultative autogamy	Vine	Wet forest	Kaua'i
<i>obovatum</i> Sherff	Hermaphroditic, facultative autogamy	Subshrub	Diverse mesic forest	O'ahu
<i>trinerve</i> H. Mann	Hermaphroditic, cleistogamous	Subshrub	Wet forest, diverse mesic forest	O'ahu
<i>viscosum</i> (H. Mann) Sherff	Hermaphroditic, facultative autogamy	Vine	Wet forest, diverse mesic forest	Kaua'i
<i>Schiedea</i>				
<i>adamantis</i> St. John	Gynodioecious	Shrub	Dry shrubland	O'ahu
<i>amplexicaulis</i> H. Mann	Hermaphroditic	Unknown	Unknown	Kaua'i (extinct)
<i>apokremmos</i> St. John	Gynodioecious	Shrub	Dry cliffs	Kaua'i
<i>attenuata</i> W. L. Wagner, Weller & Sakai	Hermaphroditic	Shrub	Diverse mesic forest pockets on cliffs	Kaua'i
<i>diffusa</i> A. Gray	Hermaphroditic	Vine	Wet forest	East Maui, Moloka'i, Hawai'i
<i>globosa</i> H. Mann	Subdioecious	Suffruticose herb	Dry coastal cliffs	O'ahu, Maui, Moloka'i
<i>haleakalensis</i> Degener & Sherff	Dioecious	Shrub	Dry subalpine cliffs	East Maui
<i>helleri</i> Sherff	Hermaphroditic	Vine	Wet forest cliffs	Kaua'i
<i>hookeri</i> A. Gray	Hermaphroditic	Subshrub	Diverse mesic forest	O'ahu
<i>implexa</i> (Hillebr.) Sherff	Hermaphroditic	Subshrub	Mesic forest?	Maui (extinct)

<i>kaalae</i> Wawra	Hermaphroditic	Perennial herb	Diverse mesic forest, wet forest	O'ahu
<i>kealiae</i> Caum & Hosaka	Subdioecious	Subshrub	Dry forest	O'ahu
<i>ligustrina</i> Cham. & Schlechtend.	Dioecious	Shrub	Dry shrubland, often cliffs	O'ahu
<i>lydgatei</i> Hillebr.	Hermaphroditic	Shrub	Dry shrubland	Moloka'i
<i>mannii</i> St. John	Subdioecious	Shrub	Dry ridges in diverse mesic forest	O'ahu
<i>membranacea</i> St. John	Hermaphroditic	Perennial herb	Diverse mesic forest	Kaua'i
<i>menziesii</i> Hook.	Hermaphroditic	Shrub	Shrubland	Lana'i and West Maui
<i>nuttallii</i> Hook. var. <i>nuttallii</i>	Hermaphroditic	Subshrub	Diverse mesic forest	O'ahu
<i>nuttallii</i> Hook. var. <i>pauciflora</i> Degener & Sherff	Hermaphroditic	Subshrub	Diverse mesic forest	Kaua'i
<i>pubescens</i> Hillebr.	Hermaphroditic	Vine	Diverse mesic forest	O'ahu, Moloka'i, Lana'i, and Maui
<i>salicaria</i> Hillebr.	Gynodioecious	Shrub	Dry shrubland	West Maui
<i>sarmentosa</i> Degener & Sherff	Gynodioecious	Shrub	Dry forest and shrubland	Moloka'i
<i>spergulina</i> A. Gray	Dioecious	Shrub	Cliffs in dry shrubland	Kaua'i
<i>stellarioides</i> H. Mann	Hermaphroditic	Subshrub	Diverse mesic forest	Kaua'i
<i>verticillata</i> F. Brown	Hermaphroditic	Perennial herb	Soil pockets and cracks on dry coastal cliffs	Nihoa
sp. nov. (<i>Pertlman</i> 13448)	Hermaphroditic	Subshrub	Mesic forest	Kaua'i

Note: Assessments based on herbarium, greenhouse, or field observations.

rected from the hermaphroditic *S. menziesii* (Wagner et al., 1994; W. L. Wagner et al., unpubl.).

These two genera are quite diverse in morphology, breeding system, and habitat (Table 12.1). The variation in habit within the two genera is among the most striking in the Caryophyllaceae (Figure 12.1). The species vary from large vines of wet forest to compact shrubs of dry areas, sprawling subshrubs, or even perennial herbs with swollen roots in which the aboveground stems are seasonal. Inflorescence structure encompasses tightly congested inflorescences up to 4 cm long with hundreds of flowers to relatively few-flowered inflorescences up to 1.5 m long with widely distant nodes.

These genera express a wide array of breeding systems (Weller et al., 1990), and detailed studies have focused especially on factors that promote the evolution of dioecy (Sakai et al., 1989; Weller and Sakai, 1990; Sakai and Weller, 1991). Ten species of *Schiedea* have dimorphic breeding systems, including dioecy (pistillate and staminate individuals present in populations), subdioecy (pistillate, staminate, and a few hermaphroditic individuals present in populations), and gynodioecy (pistillate and hermaphroditic individuals present in populations). All dimorphic species occur in dry habitats, whereas species with hermaphroditic breeding systems are largely restricted to more mesic or wet habitats (Weller et al., 1990). Most dimorphic species appear to be wind-pollinated; hermaphroditic species may be insect-pollinated or autogamous (Weller and Sakai, 1990). This information has been used to hypothesize that a scarcity of pollinators in dry, windy environments may have resulted in increased selfing rates, the expression of inbreeding depression, and the spread of male-sterile forms (Weller and Sakai, 1990). Coincident with the evolution of dioecy is the evolution of wind pollination, a second presumed response to loss of pollinators on the very windy cliffs and ridges occupied by most dimorphic species.

Schiedea and *Alsinidendron* have colonized nearly throughout the main islands of the Hawaiian archipelago. Most species are restricted to a single island, but 5 of the 29 species, all in *Schiedea*, occur on more than one island. Species of *Schiedea* are found on six of the eight main islands (Table 12.1). One other species is restricted to Nihoa, an older island northwest of Kaua'i that is the largest island of the leeward chain. In contrast, the four species of *Alsinidendron* are restricted to the two oldest main islands, Kaua'i and O'ahu.

Schiedea and *Alsinidendron* constitute a monophyletic radiation in the Hawaiian archipelago, based on the presence of highly specialized



FIGURE 12.1. Habits of the endemic Hawaiian Alsinoideae showing the great diversity in morphology in selected members of the four main clades. (A to C) *Schiedea membranacea* clade: (A) *S. membranacea*; (B) *Alsimidendron obovatum*; (C) *S. verticillata*. (D and E) *S. nuttallii* clade: (D) *S. diffusa*; (E) *S. nuttallii* var. *nuttallii*. (F) *S. adamantis*. (G) *S. globosa*.

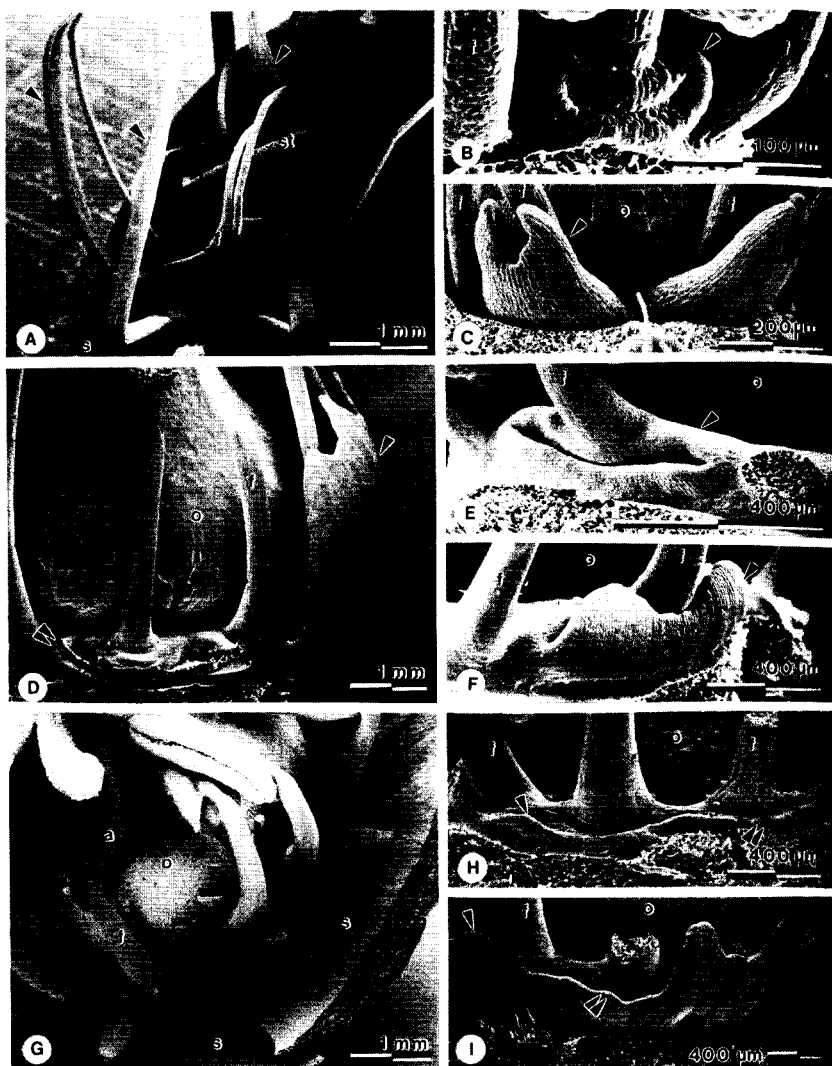


FIGURE 12.2. Stages of nectary development in representative species of *Schiedea* and *Alsinidendron*. Sepals removed in most cases. (A to C) *Schiedea hookeri*. (A) Mature nectaries (arrows) at anthesis. (B) Initiation of nectary at base of filament, inner whorl of stamens (arrow). (C) Early differentiation of nectary as both abaxial and adaxial bulges elongate to form the nectar shaft (arrow). (D to F) *Alsinidendron lychnoides*. (D) Nectary at anthesis consisting of an independent flap derived from the abaxial nectary bulge (single arrow) subtending the nectariferous furrow (flap removed, double arrow). (E) Initiation of nectary (arrow) as in *Schiedea* above. (F) Abaxial portion of nectary elongates to form the independent nectary flap (arrow). (G to I) *Alsinidendron obovatum*. (G) Nectaries forming a fused cuplike structure surrounding the filament bases. (H) Early stages of nectary initiation as elongated bulges (double arrow). After initiation of the nectaries proper, meristematic zones of neighbor-

floral nectaries and the absence of petals in all species. Nectar is collected and presented through a hypodermic-like shaft in *Schiedea* or at the base of a flap- or cup-like structure in *Alsinidendron*. In most members of the subfamily Alsinoideae, to which the endemic Hawaiian genera belong (Pax and Hoffmann, 1934; Weller et al., 1990), the nectary is represented by a mound of nectariferous tissue bisected by a lateral furrow located on the abaxial side of each antesealous stamen (Thomson, 1942).

The monophyletic origin of the endemic Hawaiian Alsinoideae is also supported by ontogenetic studies. These studies indicate that the nectary differences between *Schiedea* and *Alsinidendron* represent changes in homologous structures (E. M. Harris and W. L. Wagner, unpubl.) (Figure 12.2). Moreover, the early stages of initiation and development of nectaries in the Hawaiian genera are homologous to comparable structures of outgroup taxa. The nectaries of *Schiedea* and *Alsinidendron* and the Californian *Minuartia douglasii* (Torr. & A. Gray) Mattf., however, display development beyond the ontogenetic endpoint of the other Alsinoideae, demonstrating a clear-cut case of hypermorphosis (a type of heterochrony; see Funk and Brooks, 1990). Nectary development in the Hawaiian lineage is even more protracted than in *M. douglasii*, yielding a distinctive synapomorphy of the strikingly large nectary appendages.

In this chapter, we use a phylogenetic analysis of the endemic Hawaiian Alsinoideae to examine the importance of island age, inter-versus intra-island colonizations, degree of specialization of successful colonists, habitat shifts, and breeding system modifications as components of speciation. Current distributions of the species are centered on the older islands. In the absence of fossil evidence or a "molecular clock," we ask whether the phylogenetic hypotheses can be used to differentiate lineages that originally colonized from a continental source directly onto one of the current main islands such as Kaua'i from those that first colonized, and perhaps even diversified, on older, now-eroded and largely submerged islands (i.e., the leeward chain). We are particularly interested in contrasting patterns found in more highly derived versus more

←
 ing nectaries extend and become fused for a more or less continuous nectary meristem (*single arrows*). (I) Growth of nectaries with abaxial flaps (*single arrows*) and internectary region (*double arrow*) elongating differentially, reflecting their respective sequence of initiation. Abbreviations are st, stigmatic surface of style; f, filament; o, ovary; a, anther; s, sepal.

plesiomorphic sublineages. If more highly derived species have become more specialized in morphology and habitat, plesiomorphic sublineages may be more successful at colonizing and diversifying on younger islands. We also examine whether colonization occurs from older to younger islands when habitats become available, as might be expected given the strongly linear pattern of geologic formation of the Hawaiian archipelago. The importance of habitat shifts as well as inter-island dispersal in promoting speciation is also examined. In the case of inter-island founder dispersal, the isolation may be great enough to allow speciation without an accompanying habitat shift. With intra-island dispersal, habitat shifts may be necessary to allow sufficient separation for speciation to occur, especially when dispersal occurs to other parts of the same volcano.

We begin by determining the phylogenetic relationships among the species based on morphological characters. The phylogenetic hypotheses are then used to examine the biogeographic patterns with respect to island age, direction of colonization, biogeographic patterns of specialization and diversification within the lineage, and patterns of habitat and breeding system diversification.

MATERIALS AND METHODS

Selection and Coding of Characters

Forty-two morphological characters were evaluated and studied using herbarium specimens for all taxa, and material of nearly all extant species was grown in the greenhouse (Appendix 12.1) (for detailed discussion of these, see Weller et al., in press b); (0) represents the state found in the generalized outgroup, and (1) or higher represents apomorphic states. Autapomorphic characters were excluded from the analysis. In all cases, outgroup comparison was used to determine the plesiomorphic (0) state. The character state matrix is presented in Appendix 12.2.

Two species of *Schiedea*, *S. amplexicaulis* and *S. implexa*, have not been collected in more than 80 years and appear to be extinct. *Schiedea amplexicaulis* was collected only twice in the early explorations of the archipelago. *Schiedea helleri* was known from only one collection made in 1895 until it was rediscovered in mid-1993. Both *Alsimidendron viscosum* and *S. stellarioides* were also rediscovered during the course of this study. Missing data for several characters of these species, especially of *S. amplexicaulis*, contributed to ambiguity in the phylogenetic hypotheses.

The breeding system of each species, the habitat, and the island distribution (characters 43, 44, and 45) were mapped onto trees but were never used in tree construction. Three additional characters thought to be related to the breeding system, inflorescence condensation (characters 19 and 20) and the ratio of stamen to sepal length (character 35), were eliminated from the analyses presented here because of the likelihood that these characters are homoplasious. The rationale for defining a character as associated with breeding system and the effect of inclusion of breeding system characters on tree topology are discussed in detail in a related paper in which all the characters and their polarizations are described (Weller et al., in press b).

Outgroup Selection

The Caryophyllaceae have the greatest number of species in temperate or boreal regions of the Northern Hemisphere, with only a few tropical representatives (Pax and Hoffmann, 1934; Mabberley, 1987). *Schiedea* and *Alsinidendron* are morphologically divergent within the family. Because of their extensive radiation and great isolation, identification of a continental sister group has proved difficult. McNeill (1962) described *Schiedea* and *Alsinidendron* as aberrant members of the "Arenaria complex" but also suggested that these genera might be better placed in subfamily Paronychiodeae. The presence of exstipulate leaves, capsules splitting into as many valves as styles, distinct sepals, and the absence of a strophiole on the seed clearly align *Schiedea* and *Alsinidendron* within the subfamily Alsinoideae. The hypermorphosis discussed above in the nectaries of *Alsinidendron*, *Schiedea*, and at least *Minuartia douglasii* and *M. howellii* (S. Wats.) Mattf. of California denote a synapomorphy. Therefore, the latter two taxa were used in this analysis as the most likely sister group to the endemic Hawaiian Alsinoideae. These *Minuartia* species show several specialized features within the genus, such as annual habit. Because of this, we also used a generalized outgroup in the parsimony analyses incorporating the most likely plesiomorphic condition for these characters.

Analysis of the Data Matrix

Phylogenetic Analysis Using Parsimony (PAUP version 3.1.1; Swofford, 1993) was used for analysis. Because of the large number of taxa involved, an heuristic search was performed using the branch swapping

option, MULPARS, and all three search options. The tree bisection-reconnection and subtree pruning-regrafting options yielded the shortest trees (132 steps), whereas the nearest neighbor interchanges gave consistently longer trees. Characters were unordered and unweighted.

Biogeography, habitat, and changes in breeding system were traced on the topologically different trees using PAUP version 3.1.1 (character state reconstruction) and MacClade 3.01 (Maddison and Maddison, 1992). Using PAUP, results from character reconstructions for biogeography, habitat shifts, and breeding system modifications were compared using both accelerated transformation (ACCTRAN) and delayed transformation (DELTRAN) optimization options. In character reconstructions, ACCTRAN minimizes and DELTRAN maximizes parallel evolution. PAUP makes no attempt to identify alternative delayed and accelerated transformation reconstructions, and one is selected arbitrarily (Swofford and Maddison, 1992).

RESULTS

Phylogenetic Reconstruction

Six equally parsimonious trees with 132 steps were produced using PAUP (Figure 12.3). The consistency index was 0.508, the homoplasy index was 0.515, the retention index was 0.710, and the rescaled consistency index was 0.360. Tests of confidence were conducted and are presented elsewhere (Weller et al., in press b). Tree topology differed only in the degree of resolution of *Schiedea hookeri*, *S. kealiae*, *S. menziesii*, and *S. sarmentosa* and in placement of the extinct *S. amplexicaulis*. *Schiedea kealiae* was either part of a trichotomy with *S. sarmentosa* and the *S. hookeri* and *S. menziesii* pair or the sister taxon to these species.

In all trees, five clades were present, as shown in the strict consensus tree (Figure 12.4). One clade consisted of the extinct hermaphroditic species, *Schiedea amplexicaulis*, which occurred in three different arrangements (see Figure 12.3), but was never included in the remaining clades. *Schiedea amplexicaulis* was placed either as the sister taxon to all other *Schiedea* and *Alsinidendron* species or as the sister taxon to all clades but the basal one or in an unresolved trichotomy (see Figure 12.3). Placement of this species in its own clade is problematic, largely because so much character information is missing. The only two collections are fragmentary, made during the early exploration of the Hawaiian Islands,

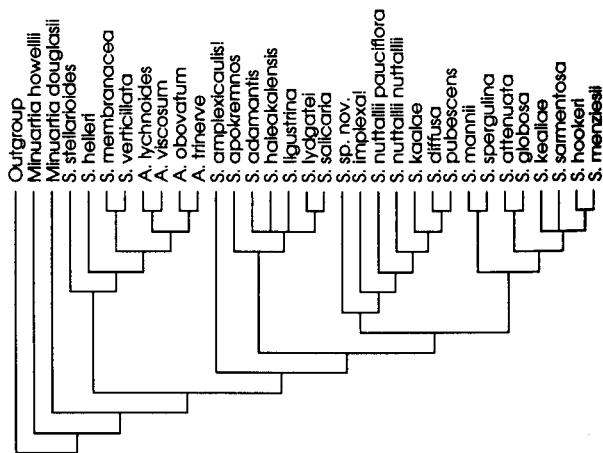
and do not provide the information available for the other species. Unless this species is rediscovered, it is unlikely that a satisfactory phylogenetic placement of it will be possible. Because of this, we will focus only on the four clearly defined clades.

A second, basal clade (the *Schiedea membranacea* clade) consisted of the four species of *Alsinidendron*, *S. verticillata* from Nihoa, and three morphologically divergent Kaua'i species of *Schiedea*. Species in this clade are characterized by broad, multinerved leaves with ciliate or toothed margins. Hermaphroditic breeding systems occur throughout the clade, although these range from cleistogamy (*A. trinerve*) to species that appear adapted to bird pollination but facultatively self-pollinate (*A. lychnoides*) and species that regularly outcross, probably via insects (*S. membranacea*).

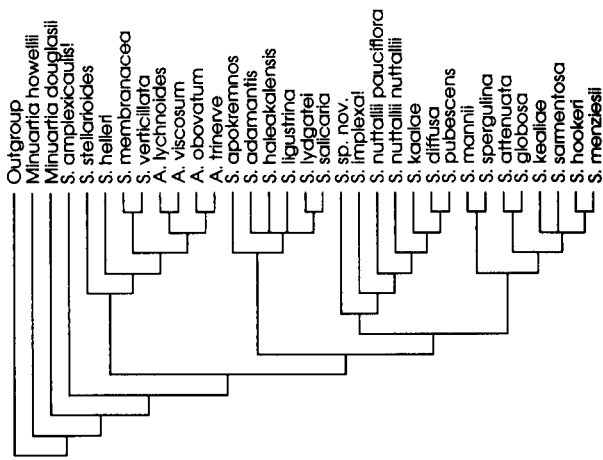
The basal *Schiedea membranacea* clade differs from the other three main clades in the greater degree of morphological diversity, the greater specialization among the constituent species, and the biogeography of these species. In addition to the considerable morphological differentiation between *Schiedea* and *Alsinidendron*, *Schiedea* species of this clade range from fleshy-rooted, herbaceous perennials with broad multinerved leaves (*S. verticillata* and *S. membranacea*) to large vines (*S. helleri*) and small upright subshrubs with single-nerved leaves (*S. stellarioides*). Overall, species in the *S. membranacea* clade are more specialized than those occurring in other clades, as demonstrated by the phylogram in Figure 12.5, in which branch lengths reflect the number of derived characters. This pattern is likely to result from extinctions in the *S. membranacea* lineage, which place more of the synapomorphies on single branches. Species of this clade are more divergent from the remaining three clades than these clades are from each other. The greater degree of differentiation is likely to result from the older age of the *S. membranacea* clade. Despite the morphological diversity, all species in this clade except *S. verticillata* occur in mesic or wet habitats.

The third clade (the *Schiedea adamantis* clade) is morphologically coherent. It consists of six species characterized by narrow coriaceous leaves broadest above the middle and, for all the species except *S. apokremnos*, papillate seeds and acute cell margins on the cells of the testa. All species are shrubs occurring in dry habitats, ranging from near sea level (*S. adamantis*) to dry subalpine cliffs (*S. haleakalensis*). Several species (*S. adamantis*, *S. haleakalensis*, *S. ligustrina*, and the branch with *S. lydgatei* and *S. salicaria*) are so similar that they form an unresolved polytomy in all trees (see Figure 12.3). They are distinguished primarily

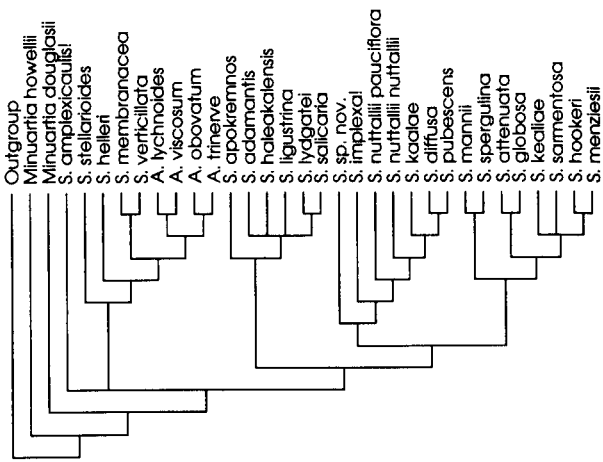
1



2



3



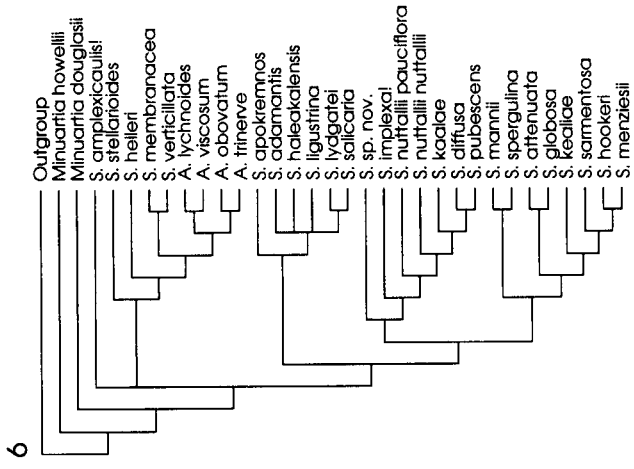
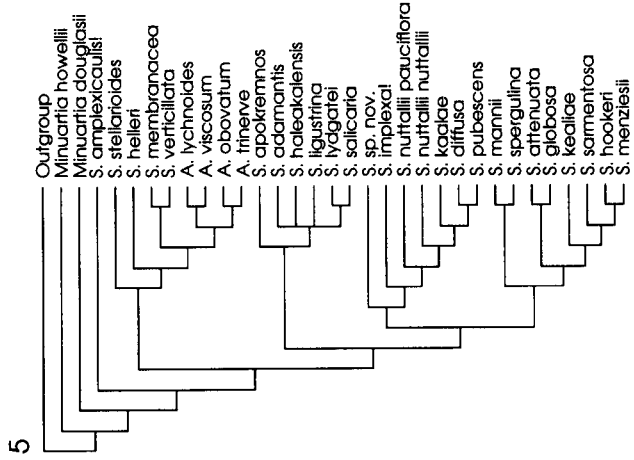
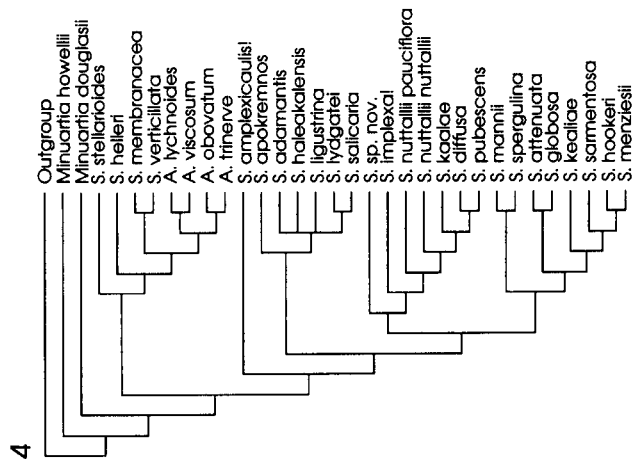


FIGURE 1 2 3. Six equally parsimonious trees obtained from the PAUP analysis. An *exclamation mark* indicates an extinct species. Tree 4 is the preferred tree.

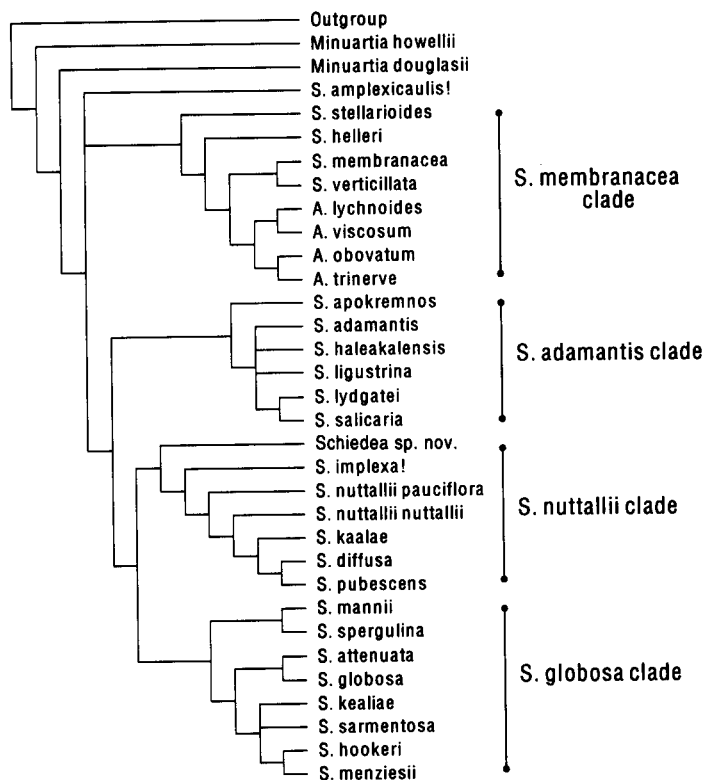


FIGURE 12.4. Strict consensus tree of six most-parsimonious trees for *Schiedea* and *Alsinidendron* shown in Figure 12.3. Tree length is 132 steps. The four main clades are named for characteristic species. An exclamation mark indicates an extinct species.

by differences in breeding systems and the degree of inflorescence condensation, characters that were not used in phylogenetic analysis. The divergent species in this clade, *S. apokremnos*, lacks the specialized seed traits characteristic of the other species in the clade. It possesses several unique features including glaucous leaves and occasionally globose inflorescences, and it apparently diverged early in the evolutionary history of the clade. All species in this clade except *S. lydgatei* have dimorphic breeding systems. Although species in this clade occur on five of the eight main islands, they are most diverse on O'ahu and the Maui Nui complex.

A fourth clade (the *Schiedea nuttallii* clade) has six species and is uniformly distinguished from the other clades by large, single-nerved

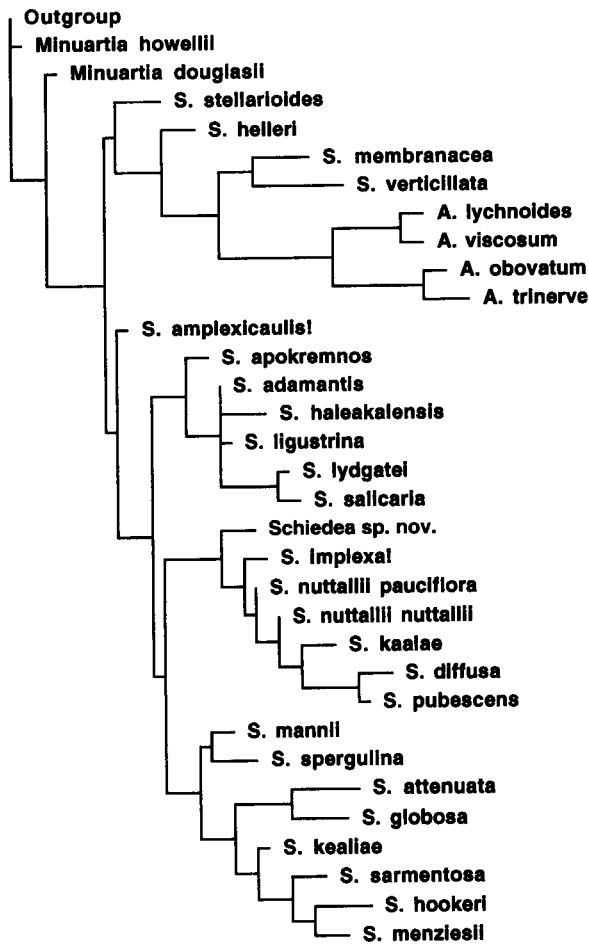


FIGURE 12.5. Phylogram of the preferred tree for *Schiedea* and *Alsinidendron* in which branch lengths reflect the number of derived characters, showing that the species in the *S. membranacea* clade are more specialized than those occurring in other clades. An exclamation mark indicates an extinct species.

leaves (except the undescribed species, which has three-nerved leaves) and distinctive attenuate to caudate, strongly reflexed sepals. *Schiedea implexa* and the undescribed species from Kaua'i lack the ciliate sepals typical of the remaining taxa, and for that reason, they occur in the basal positions in the clade. All species of this clade occur in mesic or wet habitats and possess hermaphroditic breeding systems. One species, *S. diffusa*, is apparently autogamous. Seeds of this species are retained in

the capsule and germinate in situ. The *S. nuttallii* clade is the most widely distributed of the five clades, occurring on six of the eight main islands.

A fifth clade (the *Schiedea globosa* clade) consists of eight species with narrow attenuate, asymmetric or falcate, and, in most cases, several-nerved leaves. Species in the *S. globosa* clade are shrubs and subshrubs occurring in mesic to dry environments, primarily on O'ahu, Maui, and Moloka'i. The degree of variability within this clade is similar to that found in the *S. adamantis* and *S. nuttallii* clades but far less than the variability in the *S. membranacea* clade (Figure 12.5). Breeding systems are diverse, with three hermaphroditic species (two of which occur in mesic environments) and five dimorphic species (all of which occur in dry habitats).

Three of the four main clades (all but the *Schiedea globosa* clade) are reasonably well supported, based on bootstrap and decay analysis (Weller et al., in press b). Molecular data (restriction analysis of chloroplast DNA and 18–26S rDNA) provide support for the same three clades (D. Soltis et al., unpubl.). The *S. globosa* clade, which is delimited by a single morphological synapomorphy, is not supported in the bootstrap analysis or from molecular data and may well represent a grade rather than a clade.

Biogeographic Patterns

Using PAUP with the ACCTRAN option, biogeographic analysis of all equally parsimonious trees indicates that all but one clade originated on Kaua'i (Figure 12.6). An O'ahu origin is suggested for the *Schiedea globosa* clade. The PAUP analysis indicates that most colonization events occurred from older to younger islands, and many were associated with speciation. There were 18 hypothesized colonizations from older to younger islands, 11 resulting in speciation and 7 occurring without speciation. Four back-colonizations from younger to older islands are hypothesized, three resulting in speciation and one that did not result in speciation. Thus, almost two-thirds (11 of 18) of the colonizations from older to younger islands resulted in speciation. The three back-colonizations resulting in speciation are *S. verticillata* on Nihoa from a Kaua'i ancestor and *S. attemuata* and *S. spergulina* on Kaua'i from different O'ahu ancestors. A back-colonization by *S. pubescens* is hypothesized, which did not result in speciation. Five of eight inter-island colonization events that occurred without speciation took place within the Maui Nui complex.

Using the DELTRAN option, the origin of the *Schiedea globosa* clade occurs on Kaua'i. If the origin of the *S. globosa* clade was on Kaua'i,

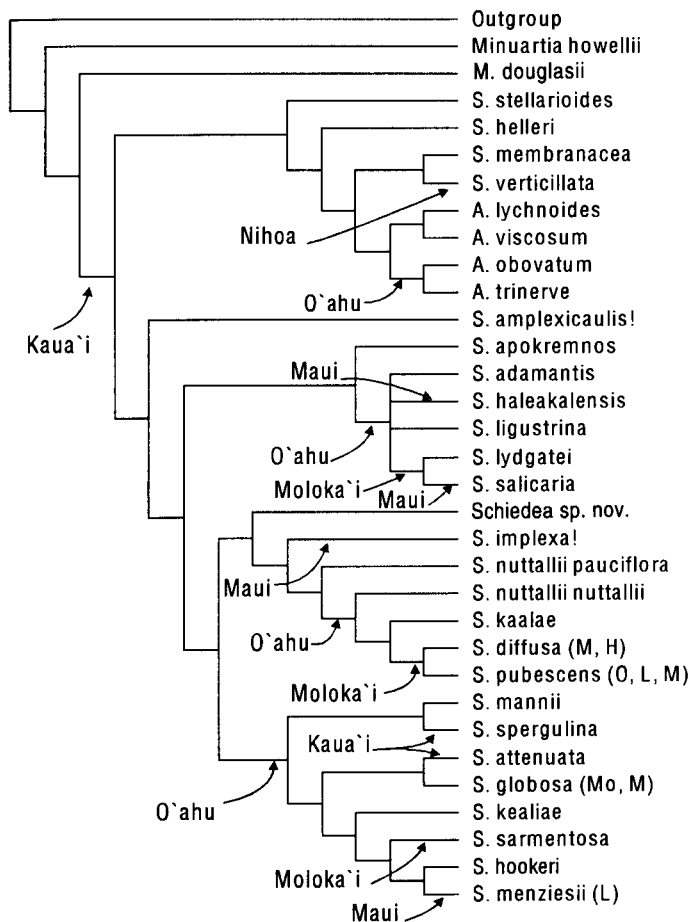


FIGURE 12.6. Biogeographic hypothesis for *Schiedea* and *Alsinidendron* mapped onto preferred tree using PAUP and the ACCTRAN option for character reconstruction. An exclamation mark indicates an extinct species. Colonizations resulting in speciation are shown on the tree; for those colonizations that did not result in speciation, the additional islands on which they occur are indicated next to the species as the first or first two letters of the island name. Both categories include colonizations from older to younger islands and back-colonizations. Eighteen hypothesized colonizations from older to younger islands occurred. Of these, 11 resulted in speciation; the remaining 7 colonizations occurred without speciation. Four back-colonizations are hypothesized; three of these resulted in speciation and one (for *S. pubescens*) did not. Using the DELTRAN option, however, three of the four back-colonizations (all but *S. verticillata*) are interpreted as colonizations from older to younger islands. Note that PAUP gives an arbitrary solution for the common ancestor of the *Schiedea lydgatei*-*S. salicaria* pair. Stepping-stone colonization from O'ahu (O) to Moloka'i (Mo) for the ancestor, followed by colonization to West Maui, may have occurred because of the Pleistocene connection of Maui (M) and Moloka'i. H, Hawai'i; L, Lana'i.

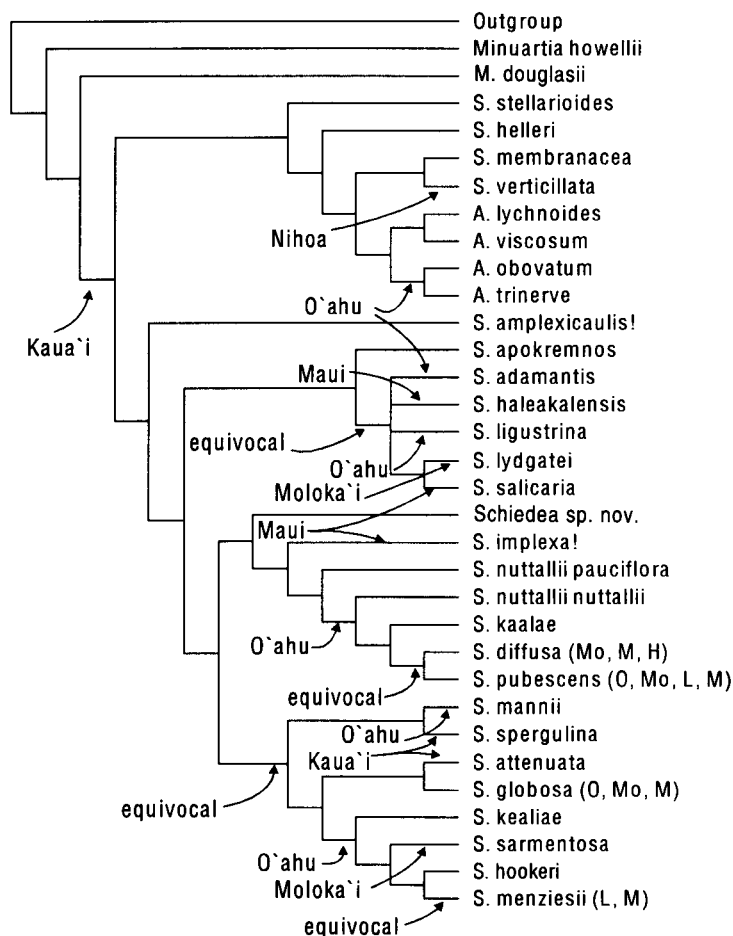


FIGURE 12.7. Biogeographic hypothesis for *Schiedea* and *Alsinidendron* mapped onto preferred tree using MacClade. Origin of the *S. globosa* clade is equivocal and may have occurred on Kaua'i or on O'ahu (O). If the origin of this clade was on Kaua'i, no back-colonizations are necessary to explain the distribution of *S. spergulina* and *S. attenuata*. Using MacClade, the origin of the *S. diffusa*–*S. pubescens* clade is also equivocal, and a hypothesized back-colonization for *S. pubescens* to O'ahu is no longer necessary. Species with multiple-island distributions (*S. diffusa*, *S. globosa*, *S. menziesii*, and *S. pubescens*) are interpreted as equivocal using MacClade. Their distributions are indicated as in Figure 12.6. M, Maui; Mo, Moloka'i; L, Lana'i; H, Hawai'i.

back-colonizations would not be necessary to explain the origin of *S. spergulina* and *S. attenuata* on Kaua'i, and colonization concomitant with speciation would be necessary to explain the origin on O'ahu of *S. globosa*, *S. mannii*, and the ancestor of *S. hookeri*, *S. kealiae*, *S. menziesii*, and *S. sarmentosa*. Another difference using DELTRAN is an O'ahu rather than a Moloka'i origin for *S. pubescens*, thus eliminating another hypothesized back-colonization. Using MacClade to trace characters (Figure 12.7), differences from the PAUP analysis include the equivocal origin of the *S. globosa* clade, which could have been on O'ahu or Kaua'i, and the equivocal origin of the polytomy including *S. adamantis*. The biogeography of four of the five species with multiple-island distributions is interpreted as equivocal by MacClade because terminal taxa are viewed as polymorphic.

Habitat Shifts

Using PAUP, a major habitat shift from a mesic ancestor to dry, often cliff habitats is suggested in the common ancestor of the *Schiedea adamantis*, *S. globosa*, and *S. nuttallii* clades (Figure 12.8). A reversal to mesic habitats occurred in the ancestor to the *S. nuttallii* clade, followed by progressive adaptation to wetter habitats within the clade. Adaptation to wet environments also appears to have occurred in *Alsinidendron* independently on both Kaua'i and O'ahu and in *S. helleri* on Kaua'i. Within the *S. globosa* clade, two additional reversals to mesic habitat have occurred in *S. attenuata* and *S. hookeri*. Adaptation to dry coastal cliffs has occurred independently in *S. verticillata* and *S. globosa*.

Using MacClade to trace habitat shifts, the status of the common ancestor in the archipelago is equivocal and could have been either mesic or dry (Figure 12.9). If the common ancestor occurred in a dry habitat, the only other difference from the PAUP analysis would be the extra shift to a mesic environment in the ancestor of the *Schiedea membranacea* clade. If the basal habitat condition was mesic, the analysis is either identical to the results obtained from PAUP or, alternatively, because of equivocal results, there could have been up to four independent shifts to dry habitats, once for the ancestor of the *S. adamantis* clade and three times within the *S. globosa* clade.

Breeding Systems

Character reconstruction of breeding systems using PAUP indicates that dimorphism has evolved in two of the four main clades (Figure 12.10A).

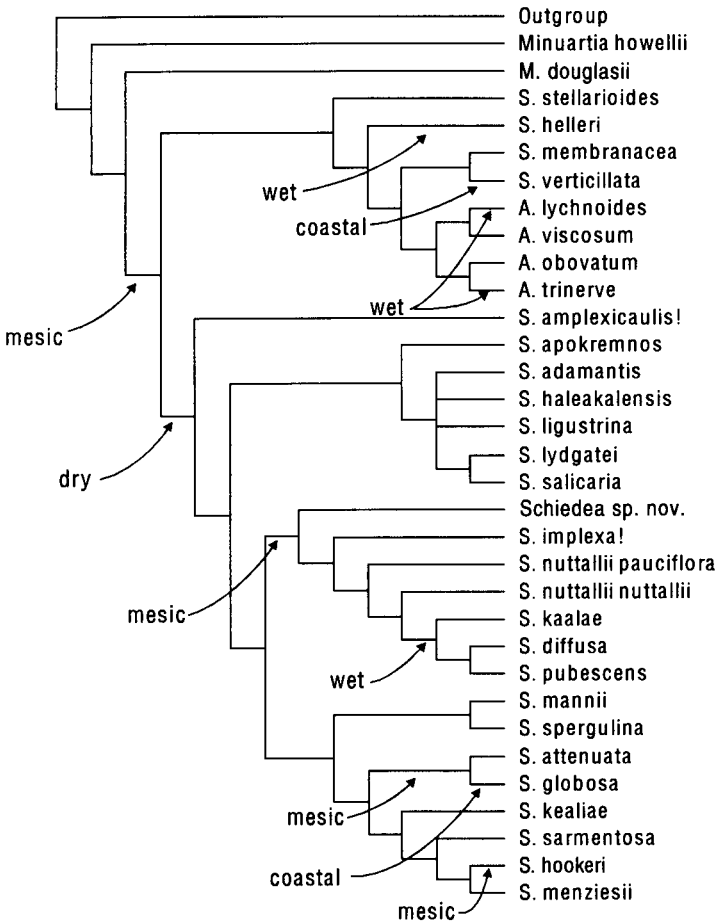


FIGURE 12.8. Hypothesis of habitat shifts in *Schiedea* and *Alsinidendron* mapped onto preferred tree using PAUP character reconstruction and the ACCTRAN option. An exclamation mark indicates an extinct species. A major shift from mesic to dry habitat is suggested in the common ancestor of the *S. adamantis*, *S. globosa*, and *S. nuttallii* clades, followed by a reversal to mesic habitats in the ancestor of the *S. nuttallii* clade. Coastal habitats are dry. Note that PAUP gives an arbitrary solution for the common ancestor of the *S. attenuata*-*S. globosa* pair.

Using both ACCTRAN and DELTRAN, gynodioecy is basal in the *Schiedea adamantis* clade, for which the topology is invariant in all six equally parsimonious trees. Using the ACCTRAN option, the number of times dimorphism has evolved in the *S. globosa* clade varies depending on which of two phylogenetic hypotheses most closely represents the course

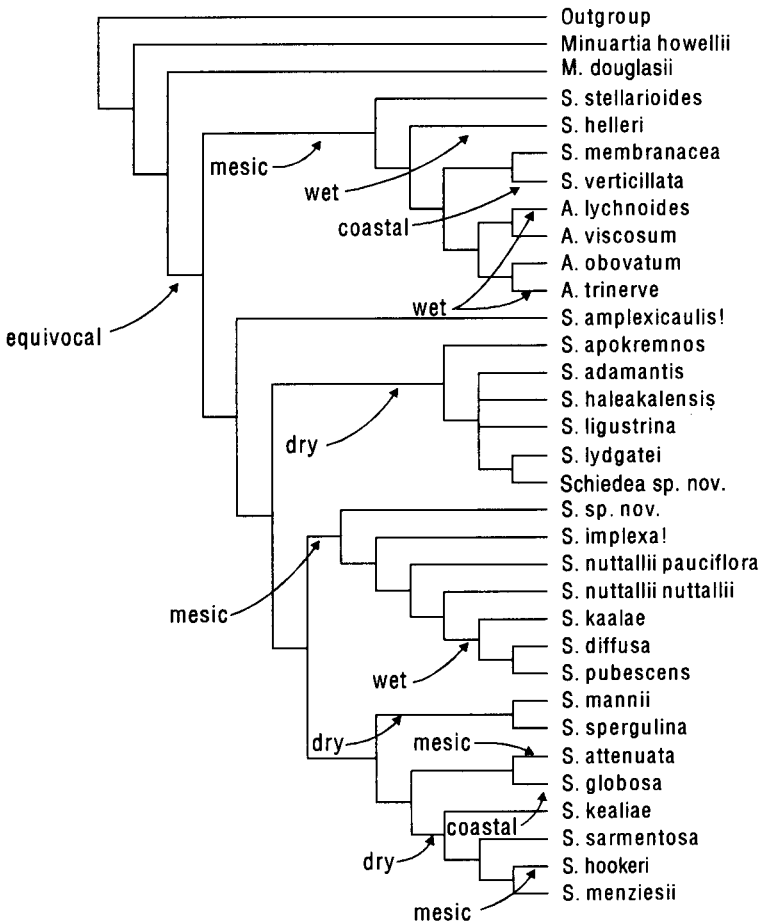


FIGURE 12.9. Hypothesis of habitat shifts in *Schiedea* and *Alsimidendron* mapped onto preferred tree using MacClade. The status of the common ancestor in the archipelago is equivocal and could have been in either a dry or a mesic habitat. Coastal habitats are dry.

of evolution in the clade comprising *S. hookeri*, *S. menziesii*, and *S. sarmentosa*. In one hypothesis (Figure 12.10A), a subdioecious ancestor gave rise to a hermaphroditic ancestor, followed by the evolution of gynodioecy in *S. sarmentosa*. In the other hypothesis (Figure 12.10B), a subdioecious ancestor gave rise to subdioecious, gynodioecious, and hermaphroditic derivatives. Using the DELTRAN option, however, there are five independent gains of dimorphism in the *S. globosa* clade in either topology. The results using MacClade were similar (Figure 12.10C),

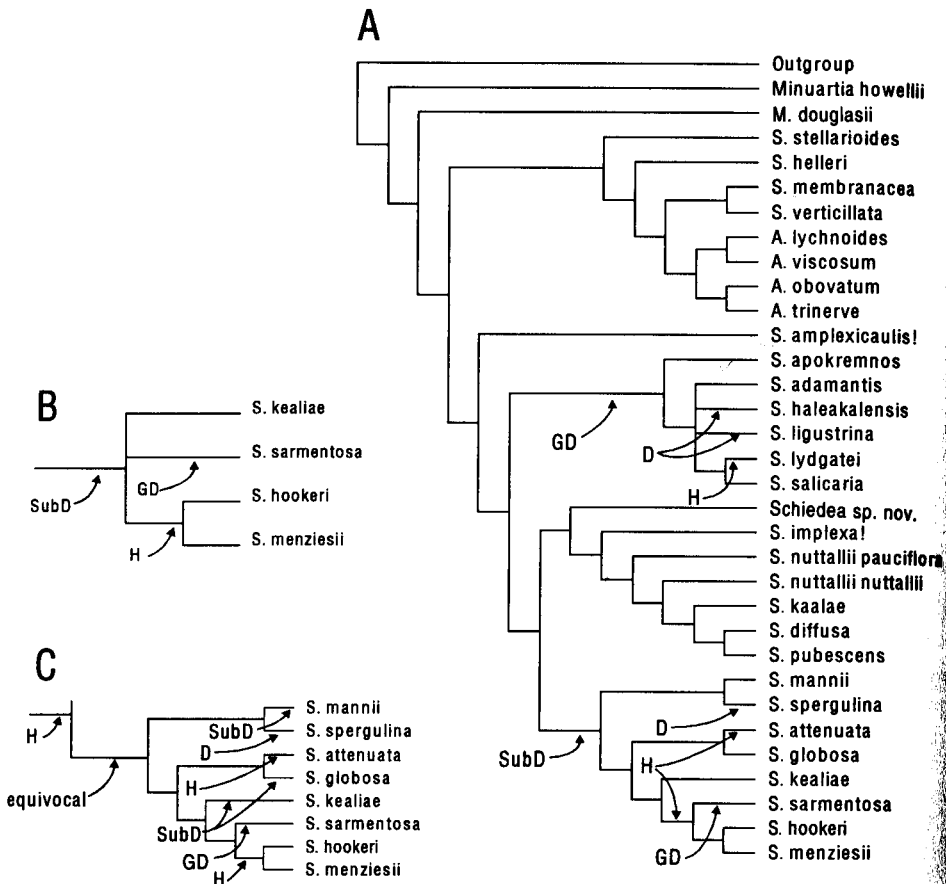


FIGURE 12.10. (A) Hypothesis of breeding system modifications in *Schiedea* and *Alsinidendron* mapped onto preferred tree using PAUP character reconstruction and the ACCTRAN option. An exclamation mark indicates an extinct species. Breeding system abbreviations are D, dioecious; GD, gynodioecious; H, hermaphroditic; SubD, subdioecious. Evolution of dimorphism is hypothesized to have occurred on three occasions; once in the *S. adamantis* clade and twice in the *S. globosa* clade. Note that reversals to hermaphroditism are hypothesized for both clades. (B) Alternative hypothesis of breeding system modifications in the *S. globosa* clade based on the other equally parsimonious topology. Evolution of both hermaphroditism and gynodioecy from a subdioecious ancestor is required. (C) Hypothesis of breeding system modifications in the *S. globosa* clade mapped onto preferred tree using MacClade. All branches leading to lineages within the *S. globosa* clade are equivocal, except for the common ancestor of *S. hookeri* and *S. menziesii*, which is hermaphroditic.

except that all interior nodes within the *S. globosa* clade were equivocal (either dimorphic or hermaphroditic), and the common ancestor of *S. hookeri* and *S. menziesii* was hermaphroditic.

DISCUSSION

Biogeographic Patterns

The known ages of the Hawaiian Islands coupled with our hypothesized phylogeny of the endemic Alsinoideae allow us to infer several biogeographic patterns. The phylogenetic hypotheses also clearly show how missing taxa, either because they are undiscovered or extinct, may obscure patterns of origin and colonization. The pattern exhibited within the basal *Schiedea membranacea* clade suggests that the original colonization to the archipelago for the endemic Hawaiian Alsinoideae occurred on islands that are now severely eroded and subsided. The *S. adamantis* and *S. nuttallii* clades originated on the oldest of the current main Hawaiian Islands (Kaua'i), and the *S. globosa* clade shows evidence of a more recent origin on O'ahu, although this result is equivocal using MacClade. Our phylogenetic analysis suggests that colonization then occurred from older to younger islands, with major diversification occurring on islands as they began their post-eruptive erosional stage. Inter-island colonizations (including back-colonizations) were often accompanied by speciation; two-thirds (14 of 22) of these colonizations have resulted in speciation.

Origin of the three terminal clades (the *Schiedea adamantis*, *S. nuttallii*, and *S. globosa* clades) on Kaua'i is suggested because of the basal species that occur on Kaua'i (see Figures 12.6 and 12.7). The origin of each clade appears to have been followed by parallel inter-island colonization to younger islands.

The analysis shows a different pattern within the *Schiedea membranacea* clade because its member species are largely restricted to Kaua'i (see Figures 12.6 and 12.7). A possible explanation is that extinction in this basal clade has obscured the process of colonization and diversification in this lineage. The *S. membranacea* lineage may have originated and diversified on an island older than Kaua'i and subsequently experienced significant extinction of all but a few species. An alternative hypothesis is that the pattern of diversification and colonization was different in the past, although there is little reason to believe that this would have occurred.

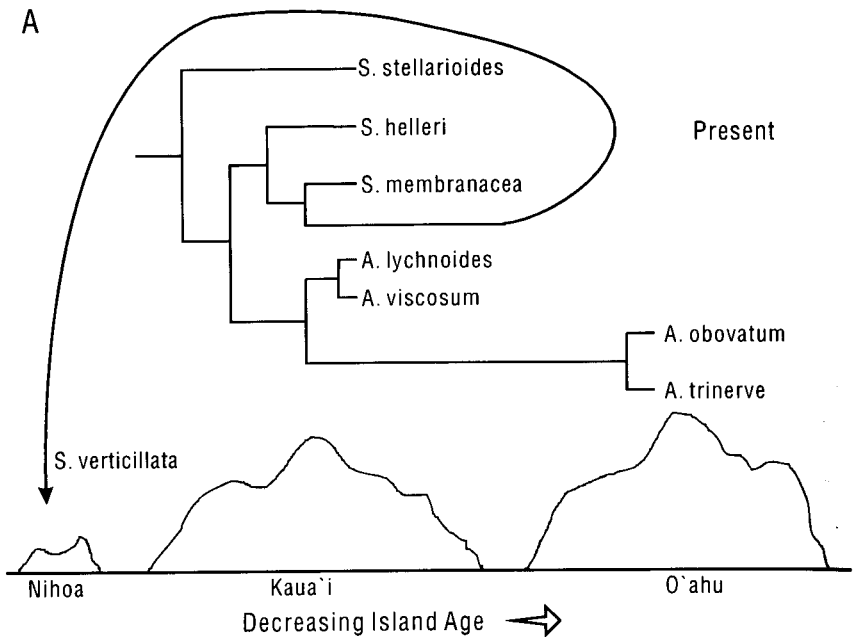


FIGURE 12.11. Comparison of two alternative interpretations of the biogeography of the *Schiedea membranacea* clade, which includes diverse species of *Schiedea* and the four species of *Alsinidendron*. (A) The biogeographic hypothesis directly indicated by our analyses for the *S. membranacea* clade. A back-colonization to Nihoa is indicated for *S. verticillata*. (B) Hypothetical pattern in which the pattern of diversification is modeled after a pattern similar to those currently observed for the clades on the current younger islands. Dashed lines indicate extinct lineages. (Continued on next page)

If Kaua'i was colonized by several elements of a diversified *Schiedea membranacea* clade, subsequent extinction has allowed disparate surviving species to be grouped together as a monophyletic clade of approximately the same size as the remaining three lineages in which there has been less extinction. To illustrate this, we contrasted the biogeographic hypothesis directly indicated by our analyses for the *S. membranacea* clade (Figure 12.11A) with a hypothetical pattern (Figure 12.11B) in which the pattern of diversification on older islands was similar to that currently observed for the clades on the current younger islands. The direct hypothesis indicates an origin on Kaua'i with a back-colonization to Nihoa for *S. verticillata* (Figure 12.11A), whereas in our hypothetical phylogeny, the clade originated on Necker Island, with subsequent further diversification on Nihoa and Necker (Figure 12.11B). The hypothet-

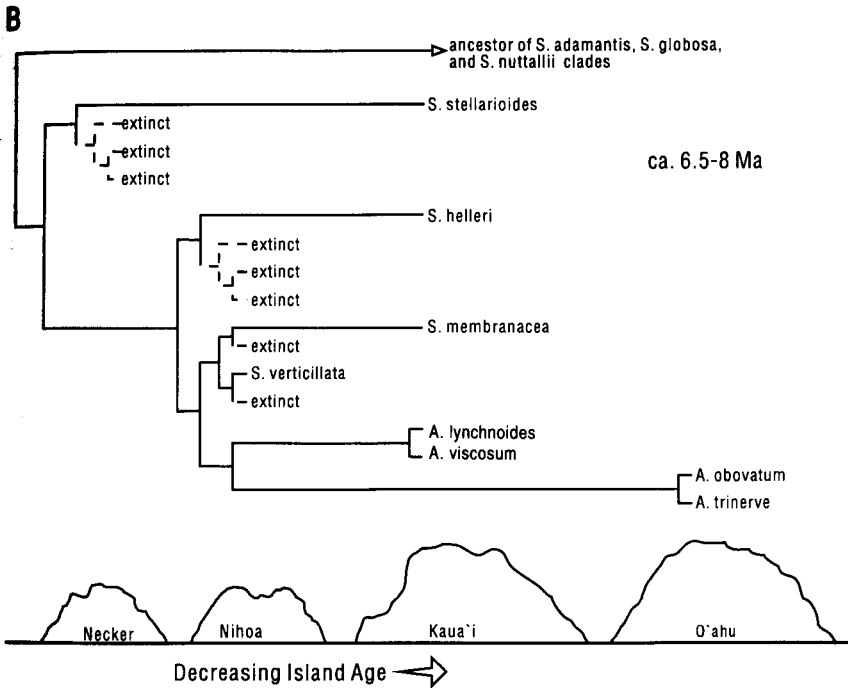


FIGURE 12.11. (Continued)

ical diversification of the *S. membranacea* lineage could have occurred between 6.5 and 8 million years ago (Ma), when these islands were considerably larger (see Carson and Clague, this volume, Chapter 2) and in the positions occupied by the current younger main Hawaiian Islands of Maui and Hawai'i. 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 *S. membranacea* clade that were able to colonize the young island of Kaua'i, and *S. verticillata* on Nihoa. If this scenario is true, the *S. membranacea* clade, after extinction of most of its members, would represent the remnants of an older radiation of which only two species (*Alsinidendron obovatum* and *A. trinerve*) have colonized beyond Kaua'i.

The cladistic analysis suggests that the genus *Schiedea* is paraphyletic through exclusion of the four species of *Alsinidendron*. In our analysis, nine synapomorphies delimit *Alsinidendron*, and there is no doubt that these species form a highly distinctive monophyletic group within this Hawaiian radiation. Evidence for the paraphyletic nature of

Schiedea comes from Kaua'i alone, where the clade with *Alsinidendron* forms a sister-taxon relationship to several Kaua'i species of *Schiedea*. If these basal Kaua'i and the Nihoa species in the *S. membranacea* clade (*S. helleri*, *S. membranacea*, *S. stellarioides*, and *S. verticillata*) (see Figures 12.6 and 12.7) were to go extinct, as they will (unless they colonize a younger island) when Nihoa and Kaua'i erode and subside into the ocean, then the remaining species of *Alsinidendron* on O'ahu would have a sister-taxon relationship to *Schiedea*. At this point, there would be no argument that *Alsinidendron* would be recognized at the generic level. Hawaiian taxa for which there is no current evidence for parphyly would undoubtedly have been classified as paraphyletic if phylogenetic analysis could have included extinct species on islands that are now nearly submerged. The distribution of taxa on islands arranged in a linear chronology of increasing age makes it easy to visualize the process of the conversion of Hawaiian taxa from paraphyletic to nonparaphyletic status, although clearly the process is not unique to this type of archipelago. We favor retention of generic rank for *Alsinidendron* because submerging the genus into *Schiedea* ignores the processes of evolutionary diversification and extinction evident in the Hawaiian Islands, especially on those islands that formerly occurred to the northwest of Kaua'i, which are now eroded and nearly submerged.

Terminal, more highly derived species may be less likely to initiate new radiations. For example, *Alsinidendron obovatum* and *A. trinerve* on O'ahu are autogamous species (Weller et al., in press a) that may lack the genetic variability necessary to exploit new habitats or undergo significant morphological modifications (cf. Soulé, 1980). In contrast, the remaining clades have radiated on the younger islands from a more plesiomorphic ancestor (see Figure 12.5). Because radiations on the younger islands have presumably involved less extinction than those on older islands, these clades are also more morphologically cohesive.

A summary of the biogeography of the endemic Alsinoideae indicates that colonization appears to occur from older to younger islands, as shown in Figures 12.12 and 12.13. Twenty-two inter-island colonizations are shown. The phylogenetic analysis did not fully resolve biogeographic patterns of colonization. Therefore, we have assumed a Kaua'i origin for the *Schiedea globosa* clade because this reduces back-colonizations, and in virtually all unambiguous cases in the analysis, colonization has been from older to younger islands. An O'ahu origin is assumed for the ancestor of the polytomy in the *S. adamantis* clade as in the PAUP analysis. We have also assumed a Moloka'i origin for the common ancestor of

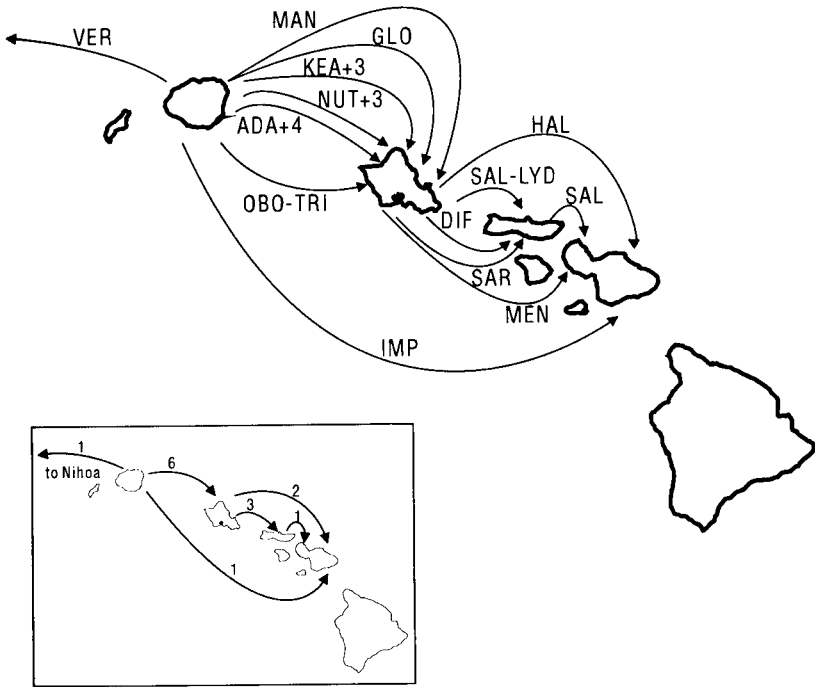


FIGURE 12.12. Summary of colonization events associated with speciation for current taxa and ancestors hypothesized for *Schiedea* and *Alsinidendron*. The first three letters of the specific epithets are used to indicate the species, except KEA+3, ancestor of *S. hookeri*, *S. kealiae*, *S. menziesii*, and *S. sarmentosa*; NUT+3, ancestor of *S. diffusa*, *S. kaalae*, *S. nuttallii* var. *nuttallii*, and *S. pubescens*; and ADA+4, ancestor of *S. adamantis*, *S. haleakalensis*, *S. ligustrina*, *S. lydgatei*, and *S. salicaria*. Ancestors of species pairs are indicated by a hyphenated acronym. Inter-island colonizations involving speciation are those indicated by the biogeographic analysis (using Figure 12.7 and assuming a Kauai origin for the *S. globosa* clade and an Oahu origin for the ancestor of the polytomy in the *S. adamantis* clade). We have made three other assumptions in constructing the diagram: (1) a Moloka'i origin for the common ancestor of the *S. lydgatei*-*S. salicaria* pair, as discussed for Figure 12.6; (2) an Oahu origin for *S. pubescens* and a Moloka'i origin for *S. diffusa*; and (3) and a West Maui origin for *S. menziesii*. The inset provides a summary of inter-island colonizations associated with speciation.

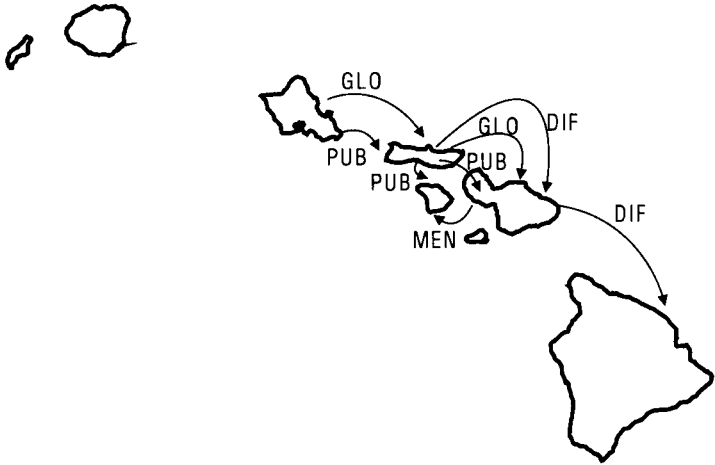


FIGURE 12.13. Possible sequence of inter-island colonizations for *Schiedea* and *Alsimidendron* without speciation implied by the biogeographic analysis. When more than one interpretation is possible, we have shown colonization to occur over the shortest distance. The pattern of colonization we prefer among several alternatives for *S. globosa* is a stepping-stone hypothesis. The first three letters of the specific epithets are used to indicate the species.

S. lydgatei and *S. salicaria* because this assumption involves a shorter colonization distance and follows the past land connection between O'ahu, Moloka'i, and Maui (see Carson and Clague, this volume, Chapter 2). The origins of species with multiple-island distributions are not resolved by our analysis, and we have made arbitrary assumptions for these. They include an O'ahu origin for *S. pubescens*, a Moloka'i origin for *S. diffusa*, and a West Maui origin for *S. menziesii*.

Patterns of origin and colonization must be interpreted in the light of the potentially strong influence of unknown extinct and undiscovered extant taxa. The back-colonization to Nihoa by *Schiedea verticillata* may represent an artifact resulting from significant extinction of a clade that occurred on older islands (cf. Figure 12.11B). This species is characterized by many specialized features and seems unlikely to have the Kaua'i ancestor implied in the analysis. The back-colonizations indicated by PAUP in the *S. globosa* clade also could be artifacts if there are extinct or undiscovered basal taxa in the *S. globosa* clade occurring on Kaua'i. This point is illustrated by the recent discovery of a new, undescribed basal species in the *S. nuttallii* clade that, when included in the analysis

indicates clearly that this clade originated on Kaua'i. Until the discovery of this species, our analyses suggested that the *S. nuttallii* clade had originated on O'ahu, with the occurrence of *S. nuttallii* var. *pauciflora* on Kaua'i explained by a back-colonization.

Using MacClade's character reconstructions, the origin of the *Schiedea globosa* clade is uncertain, and thus it becomes unclear whether *S. spergulina* and *S. attenuata* represent back-colonizations. As discussed above, we tend to favor the interpretation of a Kaua'i or older island origin for all the clades.

Most inter-island colonizations also resulted in speciation (Figure 12.12); only eight inter-island colonizations did not involve speciation (Figure 12.13). Of the latter, five colonizations occurred within the Maui Nui complex. Colonization within the Maui Nui complex was presumably easier because these islands formed a single island during the Pleistocene. *Schiedea globosa* apparently colonized from Moloka'i to Maui or vice versa rather than with a second colonization from O'ahu. Colonization between Moloka'i and Maui seems more likely because these islands are closer to each other than to O'ahu and because allozyme data for *S. globosa* (Weller et al., in press a) show a closer relationship between the Maui and Moloka'i populations than either shows to the O'ahu populations.

Habitat Shifts

Character reconstruction using PAUP suggests that when the ancestor of *Schiedea* and *Alsimidendron* colonized the Hawaiian Islands it occurred in mesic habitats (see Figure 12.8). The members of the basal *S. membranacea* clade are still largely restricted to these habitats. A major shift from mesic to dry habitats occurred in the ancestor of the three terminal clades, followed by a reversal to mesic habitats at the base of the *S. nuttallii* clade. Species in this clade have apparently adapted to progressively wetter habitats, culminating in *S. diffusa*, where seeds germinate in situ on the plant, an adaptation to extremely wet habitats. In addition to the invasion of dry habitats that occurred in the ancestor of the three terminal clades, a second switch to dry habitats has occurred for *S. verticillata*. Because this species may be the sole extant remnant of a much larger clade within the *S. membranacea* complex, there may have been a larger radiation of species into dry habitats in the basal lineage than suggested by the current distribution of species. Shifts from mesic to dry habitats may have occurred repeatedly throughout the evolutionary history of the endemic Hawaiian Alsinoideae.

Using MacClade, the number and timing of habitat shifts are less resolved (see Figure 12.9). In one alternative, the ancestor of the entire Hawaiian lineage colonized a dry habitat, followed by two independent shifts to mesic habitats in the *Schiedea nuttallii* and *S. membranacea* clades. In the other alternative, the original ancestor colonized a mesic habitat, with four separate ecological shifts to dry habitats. *Minuartia douglasii* and *M. howellii*, outgroup species for the endemic Hawaiian Alsinoideae, occur in dry habitats, providing some support for the former hypothesis. This outgroup comparison is not particularly helpful, however, because the extra-Hawaiian habitats of these two annual *Minuartia* species, although dry, are not comparable in other respects to the habitats in the Hawaiian Islands.

Evolution of Breeding Systems

Character reconstructions using PAUP with the ACCTRAN and DELTRAN options indicate that dimorphism has evolved independently in the *Schiedea adamantis* and *S. globosa* lineages (see Figure 12.10A). Gynodioecy is basal in the *S. adamantis* clade, with subsequent evolution of dioecy in *S. haleakalensis* and *S. ligustrina*. Hermaphroditism in *S. lydgatei* apparently represents a reversal from dimorphism, as this species is well nested within a clade containing only dimorphic species. *Schiedea salicaria*, the sister taxon of *S. lydgatei*, has a gynodioecious breeding system with only 12% females in the populations investigated (Weller et al., 1990; A. K. Sakai and S. G. Weller, unpubl.), suggesting that a reversal to hermaphroditism from gynodioecy in the common ancestor would be relatively easy (F. R. Ganders, unpubl.).

Subdioecy is basal in the *Schiedea globosa* lineage using character reconstruction with ACCTRAN. Two alternative phylogenies in this lineage yield different suggestions for the evolution of dimorphism, and both involve the reversion to hermaphroditism from subdioecy. In one tree (see Figure 12.10A), hermaphroditism evolves from subdioecy, and gynodioecy subsequently evolves in *S. sarmentosa*. The extra instance of the evolution of dimorphism in this tree seems reasonable, as this breeding system is often predicted to be the first stage in the evolution of full dioecy (Lloyd, 1975; Charlesworth and Charlesworth, 1978). In the alternative tree (see Figure 12.10B), gynodioecy and hermaphroditism evolve from a subdioecious ancestor.

Use of DELTRAN for character reconstruction results in five independent transitions to dimorphism in terminal taxa of the *Schiedea globosa*

clade, in contrast to the reversal from dimorphism to hermaphroditism resulting with ACCTRAN. That such reversals can occur is suggested unequivocally for the *S. adamantis* clade, although the reversal in the *S. adamantis* clade involves a change from gynodioecy to hermaphroditism rather than a change from subdioecy to hermaphroditism. If such reversals are unlikely, character reconstructions using ACCTRAN may provide a less realistic view of breeding system evolution in the *S. globosa* clade than reconstructions using DELTRAN. Because character reconstructions using MacClade were equivocal for the *S. globosa* clade, dimorphism may have independently evolved only once or as many as five times (see Figure 12.10C) in the *S. globosa* clade.

Earlier work (Weller et al., 1990) suggested that hermaphroditic species were more likely to undergo inter-island colonization than dimorphic species, a suggestion consistent with Baker's (1967) law applied within the Hawaiian Islands. The subsequent discovery of two additional single-island endemic hermaphroditic species (*Schiedea attenuata* and *Schiedea* sp. nov.) now indicates that breeding systems in the endemic Hawaiian Alsinoideae have little effect on the likelihood of inter-island colonization. Moreover, it originally appeared that dimorphic species were more likely to be found on the older islands of Kaua'i and O'ahu (Weller et al., 1990). With the discovery of gynodioecy in the recently resurrected *S. sarmentosa* on Moloka'i and dioecy in *S. haleakalensis* on East Maui, it is now clear that dimorphism is as likely to occur on the younger as the older Hawaiian Islands.

Patterns of Speciation

In addition to the original transoceanic colonization of the Hawaiian Islands, the phylogenetic analysis implies that at least 56 speciation events have occurred in the radiation of the endemic Hawaiian Alsinoideae. This number includes interior and terminal nodes of a phylogeny constructed from extant taxa and assumes that the ancestral species go extinct at each branching point. Of these, 14 (25%) appear to have been inter-island colonizations and 42 appear to have occurred within islands. Using only the extant taxa, 9 (30%) of 30 taxa evolved concomitant with inter-island colonization (cf. Figures 12.12 and 12.13), suggesting that patterns of speciation during colonization at interior nodes of the cladogram are consistent with those occurring at the endpoints. Thus, biogeographic analysis indicates that most speciation in the endemic Hawaiian Alsinoideae has been intra-island. Unfortunately, it is impossible to deter-

mine if speciation is disproportionately associated with intra-island rather than inter-island colonization events. Although we can identify the number of successful inter-island colonization events with and without speciation and we can identify the successful intra-island colonizations with speciation, it is extremely difficult to know the number of independent colonizations within an island that did not result in speciation but simply led to new populations of the same species.

Inter-island speciation may be overestimated because of past land connections between most of the current islands (see Carson and Clague, this volume, Chapter 2). For example, two very similar sister taxa, *Schiedea lydgatei* and *S. salicaria*, occur on eastern Moloka'i and West Maui, islands that were connected in the past. Speciation could have occurred as a consequence of the recent isolation and separation of the volcanoes as separate islands formed with increasing post-Pleistocene sea levels.

Other evidence for this phenomenon is found for species with multiple-island distributions. Three of the five species occurring on more than one island have distributions within the Maui Nui complex (*Schiedea diffusa*, *S. menziesii*, and *S. pubescens*). All these may have spread throughout Maui Nui when it was a single island. In contrast, the distribution of *S. globosa* on dry coastal cliffs of O'ahu, Moloka'i, and Maui may be the result of inter-island rafting, as fragments of this species have been observed floating below sea cliffs (W. L. Wagner, unpubl.).

If the hypothesized collapse of the *Schiedea membranacea* clade actually occurred, this would result in a failure to detect colonization from older, now-eroded and nearly submerged islands. Consequently, the number of intra-island speciation events would be overestimated. As discussed earlier, some species of the *S. membranacea* lineage are likely to represent the remnants of clades in which most species are extinct, and speciation events may well have been inter-island but undetected. The morphological similarity of *Alsimidendron lychnoides* and *A. viscosum*, however, suggests that these species probably share a recent origin on Kaua'i. They occur in different habitats, indicating that ecological differentiation has played a significant role in speciation. Similarly, *A. obovatum* and *A. trinerve* appear closely related but occur in different habitats in the Wai'anae Mountains on O'ahu.

Within the *Schiedea adamantis* clade, the origins of *S. adamantis* and *S. ligustrina* represent intra-island speciation events that occurred in similar habitats but involved colonization of different volcanoes. *Schiedea ligustrina* is scattered throughout the Wai'anae Mountains of

western O'ahu, whereas *S. adamantis* is now restricted to a single population consisting of several hundred individuals on Diamond Head Crater of southeastern O'ahu. *Schiedea adamantis* may have been more widespread in the leeward Ko'olau Mountains before the expansion of Honolulu, although the very restricted allozyme variation found in this population suggests that the species may have originated through a recent founder event and never occurred in more than a single population (Weller et al., in press a). In either case, there is no indication that *S. adamantis* ever occurred in or near the Wai'anae Mountains. The remaining intra-island speciation event in the *S. adamantis* clade involves *S. apokremnos*, which our phylogeny suggests evolved from an ancestor occurring in dry habitats on Kaua'i.

Considering intra-island speciation events in the *Schiedea globosa* clade, *S. hookeri* and *S. kealiae* originated in the Wai'anae Mountains but now occupy different habitats (see Table 12.1) and occur in slightly different geographic regions of the Wai'anae Mountains. On O'ahu, *S. globosa* occurs at the southeastern tip of the island, well removed from the center of diversity of the clade in the Wai'anae Mountains, and is restricted to dry coastal cliffs. Thus, if the clade originated on O'ahu, *S. globosa* had an intra-island allopatric origin as well as a concomitant shift in habitat. If the clade arose on Kaua'i, then *S. globosa* had an inter-island origin. *Schiedea mannii* represents an intra-island speciation event (unless the clade originated on Kaua'i), but as in the case of *S. apokremnos*, *S. mannii* is hypothesized to have evolved from an ancestor occurring in dry habitats.

Within the *Schiedea nuttallii* clade, several intra-island speciation events occurred on Kaua'i and in the Wai'anae Mountains. *Schiedea nuttallii* var. *pauciflora* and the new species represent intra-island speciation events on Kaua'i. No habitat shifts are indicated. Present distributions suggest allopatric origins for both species, although habitat and distributional data are fragmentary. On O'ahu, *S. kaalae* overlaps in geographic distribution with *S. nuttallii* var. *nuttallii* but occurs in wetter habitats. A third species, *S. pubescens*, occurs in wet habitats but at generally higher elevations. *Schiedea diffusa*, which probably originated on Moloka'i, presumably represents colonization associated with speciation and prefers far wetter habitats than any other species in the *S. nuttallii* clade.

Intra- and inter-island speciation events for the 30 extant taxa of the endemic Alsinoideae are summarized in Figure 12.14. This figure represents a subset of the inter-island colonizations present in Figure 12.12. More than two-thirds of these represent intra-island speciation events, suggesting that inter-island colonization is not necessary for speciation in

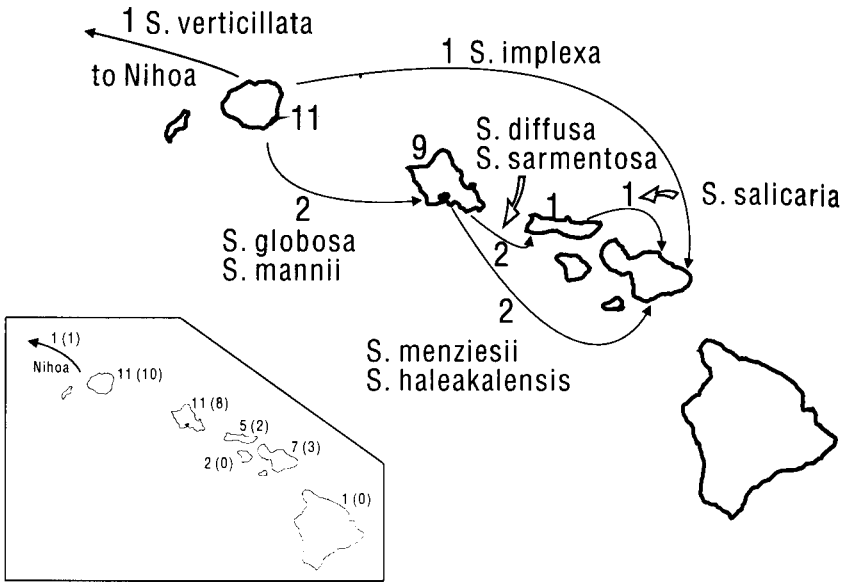


FIGURE 12.14. Summary of inter-island and intra-island speciation events, based on Figures 12.12 and 12.13 (excluding interior node ancestor colonizations; see Figures 12.6 and 12.7). The numbers adjacent to Kaua'i, O'ahu, and Moloka'i indicate the numbers of intra-island speciation events on those islands. The *inset* shows the total number of species occurring on each island, and the number of endemic taxa is given in parentheses.

this group. Many of these intra-island speciation events, however, are associated with ecological shifts. In contrast, only three of the eight cases of inter-island colonization associated with speciation seem to be associated with habitat shifts. *Schiedea haleakalensis*, found in dry subalpine habitat, represents the most striking case of a habitat shift associated with colonization. *Schiedea verticillata* and *S. attenuata* may be cases of habitat shifts associated with colonization, but their apparent sister-taxa relationships may be artifacts (see discussion above). The remaining five cases of inter-island speciation with colonization events probably occurred without habitat shifts, although in the MacClade analysis, two of the five cases are equivocal.

SUMMARY

Diversification in the monophyletic lineage that comprises the endemic Alsinoideae, perhaps from a North American ancestor related to

Minuartia, has resulted in remarkable shifts in morphology, habitat, and breeding system. This diversification has involved the evolution of four main clades, with *Alsinidendron* nested within the basal clade. These changes have occurred primarily as colonization has proceeded from older to younger islands. Phylogenetic evidence suggests that the endemic Alsinoideae originally diversified on islands that have now largely eroded and subsided beneath the ocean. Extinction of species in basal lineages results in compression of older lineages into a single diverse basal clade containing species that have accumulated many specialized characters. In the endemic Alsinoideae, diversification apparently has occurred during the first 1 to 2 million years after an island emerges from the ocean. As these islands age, the occasional colonization to a newly formed island by unspecialized species results in the diversification of new lineages. Despite the significance of colonization, more than two-thirds of the speciation events have taken place without inter-island colonization. These intra-island speciation events usually are associated with geographic or ecological shifts. When speciation has been associated with inter-island colonization, there is less evidence for significant changes in habitat.

Main trends in the endemic Alsinoideae include the invasion of dry habitats and shifts on several occasions from hermaphroditic to dimorphic breeding systems. Phylogenetic information, however, provides clear evidence that in at least one case (*Schiedea lydgatei*) a reversal from dimorphism to hermaphroditism has occurred. A second reversal is indicated, but results are less conclusive. This study provides insights into the overall patterns of morphological diversity in *Schiedea* and *Alsinidendron* and aids in the interpretation of evolutionary events associated with breeding system modification.

ACKNOWLEDGMENTS

We thank the Scholarly Studies Program of the Smithsonian Institution, the National Geographic Society, and the National Science Foundation (BSR 88-17616, BSR 89-18366, DEB 92-07724) for support of this research. We appreciate support from the National Tropical Botanical Garden, Lawa'i; in particular, the Hawaii Plant Conservation Center provided seeds of *Alsinidendron lychnoides*, *A. obovatum*, *A. viscosum*, *Schiedea apokremnos*, *S. attenuata*, *S. helleri*, *S. membranacea*, *S. pubescens*, *S. spergulina*, and *S. stellarioides*. The resources of the Bishop Museum have been invaluable. We appreciate the assistance in

collection of morphological data from Mike Sisson. We thank Elizabeth Harris, Robynn Shannon, and Alice Tangerini for adding clarity and dimension to this chapter through preparation of the scanning electron microscopy study presented in Figure 12.2, Figures 12.3 to 12.14, and the habit drawings in Figure 12.1, respectively. We thank V. A. Funk for discussion of ideas and Tim Lowrey and Richard Rabeler for comments on the manuscript. Without the help of Joan Aidem, Melany Chapin, Tom Egeland, Bruce Eilerts, Tim Flynn, Norm Glenn, Bill Haus, Robert Hobby, Guy Hughes, Joel Lau, David Lorence, John Obata, Art Medeiros, Steve Perlman, Lyman Perry, Diane Ragone, Wayne Takeuchi, Patti Welton, and Ken Wood, this research would not have been possible.

APPENDIX 12.1. Character List for *Schiedea* and *Alsinidendron*

1. Presence of woody tissue: 0 = herbaceous; 1 = suffrutescent sprawler; 2 = woody.
2. Stems persistent or deciduous: 0 = stems persistent; 1 = stems deciduous above ground.
3. Habit: 0 = stems upright; 1 = stems sprawling; 2 = vine.
4. Roots: 0 = fibrous roots; 1 = swollen, fleshy root.
5. Stem succulence: 0 = stems slender; 1 = stems thick and somewhat fleshy.
6. Leaf shape: 0 = leaves broadest at or below middle; 1 = leaves broadest above middle; 2 = leaves linear or oblong.
7. Leaf texture: 0 = leaves membranous; 1 = leaves coriaceous; 2 = leaves softly membranous.
8. Leaf size: 0 = leaf of intermediate area; 1 = leaf area large.
9. Leaf succulence: 0 = leaves not succulent; 1 = leaves succulent.
10. Leaf symmetry: 0 = leaves symmetric; 1 = leaves slightly asymmetric; 2 = leaves falcate; 3 = midvein of leaf conspicuously off-center.
11. Leaf apex: 0 = acute or acuminate; 1 = long-attenuate.
12. Reduction in leaf venation: 0 = leaves 3-nerved or more; 1 = 1-nerved.
13. Increase in leaf venation: 0 = 1- or 3-nerved; 1 = 5-nerved; 2 = 7-nerved or more.
14. Outer leaf veins arc: 0 = outer primary veins forming a broadly rounded arch; 1 = outer primary veins widely looping along margin.
15. Pubescence of leaf margin: 0 = no pubescence; 1 = thin hairs; 2 = hooked hairs.
16. Leaf margin: 0 = margin entire; 1 = minute irregular teeth; 2 = minute serrations, especially distal part; 3 = serrate.
17. Leaf pubescence: 0 = hairs glandular, clear; 1 = glabrous; 2 = nonglandular hairs, clear; 3 = hairs with purple pigment; 4 = hairs on adaxial midrib and leaf base margin.

18. Leaf surface: 0 = not glaucous; 1 = leaves slightly glaucous.
19. Lateral inflorescence condensation (breeding system): 0 = inflorescence open, paniculate cymes; 1 = lateral inflorescence branches shortened, main axis elongate.
20. Inflorescence main axis condensation (breeding system): 0 = inflorescence open, paniculate cymes; 1 = main axis somewhat vertically condensed; 2 = main axis highly vertically condensed; 3 = inflorescence globose, due to nearly complete suppression of main axis.
21. Suppression of inflorescence main axis: 0 = main axis present and developed; 1 = main axis suppressed, represented by a single terminal flower; 2 = main axis suppressed, laterals moderately suppressed.
22. Pedicel presentation: 0 = strongly ascending, flowers upright; 1 = recurved, flowers pendent.
23. Inflorescence presentation: 0 = inflorescences upright; 1 = inflorescences pendent.
24. Inflorescence pubescence: 0 = glandular pubescence, hairs of medium length; 1 = glabrous; 2 = short glandular pubescence; 3 = long glandular pubescence; 4 = nonglandular pubescence; 5 = glandular purple pubescence; 6 = nonglandular purple pubescence.
25. Sepal width: 0 = <3 mm; 1 = >5 mm.
26. Calyx configuration: 0 = erect or reflexed; 1 = calyx campanulate; 2 = calyx closed or nearly so at anthesis.
27. Sepal orientation: 0 = spreading to slightly reflexed; 1 = ascending; 2 = strongly reflexed.
28. Sepal texture: 0 = membranous, green; 1 = membranous, white, remaining papery as fruit matures; 2 = fleshy, white or green, becoming dark purple and juicy as fruit matures.
29. Sepal apex: 0 = obtuse to acute; 1 = attenuate to caudate.
30. Sepal symmetry: 0 = symmetric; 1 = irregular.
31. Sepal margin pubescence: 0 = glabrous; 1 = ciliate.
32. Nectary type: 0 = small mound; 1 = nectary with well-developed hypodermic syringelike shaft, extending beyond the \pm bulbous basal nectariferous portion; 2 = nectary with well-developed flap, 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.
33. Nectary curvature (*Schideea* only): 0 = straight, nectar deposited in a drop at apex; 1 = recurved, nectar deposited on concave surface of sepal.
34. Nectar color: 0 = clear; 1 = black, when large amount accumulates.
35. Ratio, staminal filament/sepal length (breeding system): 0 = <1; 1 = 1–1.9; 2 = ≥ 2.0 .
36. Anther color: 0 = yellow; 1 = coral.
37. Pollen color: 0 = yellow; 1 = gray.
38. Style number: 0 = 3–4; 1 = 4–6; 2 = 5–11.

39. Ovule number: 0 = <100; 1 = >100.
40. Seed retention: 0 = seeds dispersed through open valves; 1 = seeds retained in capsule, gradual rotting releases seeds.
41. Seed margin: 0 = cells along seed margin not elongate; 1 = cells along margin moderately to strongly elongated into papillae.
42. Cell margin shape on seed surface: 0 = cell lobes appear rounded to convex because cells convex; 1 = cell lobes appear acute because cells flat.
43. Breeding system (excluded): 0 = hermaphroditic; 1 = gynodioecious; 2 = subdioecious; 3 = dioecious.
44. Habitat (excluded): 0 = California chaparral and woodland; 1 = mesic forest; 2 = dry slopes and cliffs; 3 = coastal; 4 = wet forest.
45. Island distribution (excluded): 0 = California; 1 = Kaua'i; 2 = O'ahu; 3 = Moloka'i; 4 = West Maui; 5 = East Maui; 6 = Lana'i; 7 = Hawai'i; 8 = Nihoa.

APPENDIX 12.2. Data Matrix of Morphological Character States of *Schiedea* and *Alsinidendron*

The characters and character states are defined in Appendix 12.1 Missing data are indicated by question marks. Other symbols for polymorphic characters or multiple-island distributions are a = 0, 1; b = 1, 2; c = 1, 4; d = 2, 3, 4, 5; e = 3, 5, 7; f = 4, 6; g = 2, 3, 4, 5, 6. Information on characters 43 to 45 is also given in Table 12.1.

Taxon	Character															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Minuartia douglasii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Minuartia howellii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Alsinidendron lychnoides</i>	0	0	2	0	0	0	1	1	2	3	0	0	2	1	1	0
<i>Alsinidendron obovatum</i>	2	0	0	1	1	1	0	0	0	0	1	1	0	2	0	1
<i>Alsinidendron trinerve</i>	2	0	0	1	1	1	0	0	0	0	1	1	0	2	0	1
<i>Alsinidendron viscosum</i>	2	0	0	1	1	1	0	0	0	0	1	1	0	2	0	1
<i>Schiedea adamantis</i>	2	0	0	1	1	1	0	0	0	0	1	1	0	2	0	1
<i>Schiedea amplexicaulis</i>	?	?	?	0	0	0	0	0	0	0	?	?	4	0	0	0
<i>Schiedea apokremnos</i>	2	0	0	1	1	1	0	0	0	0	1	1	0	2	0	1
<i>Schiedea attenuata</i>	2	0	0	1	1	1	0	0	0	0	1	1	0	2	0	1
<i>Schiedea diffusa</i>	0	0	2	1	0	1	0	0	0	0	1	1	1	0	0	0
<i>Schiedea globosa</i>	1	0	1	0	1	1	0	0	0	0	1	1	0	1	0	0
<i>Schiedea haleakalensis</i>	2	0	0	1	1	1	0	0	0	0	1	1	0	2	0	1
<i>Schiedea helleri</i>	2	0	0	1	1	1	0	0	0	0	1	1	0	2	0	1
<i>Schiedea hookeri</i>	1	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0
<i>Schiedea implexa</i>	2	0	0	1	1	1	0	0	0	0	1	1	0	2	0	1
<i>Schiedea kaalae</i>	0	0	0	1	1	1	0	0	0	0	1	1	0	2	0	1
<i>Schiedea kealiae</i>	2	0	0	1	1	1	0	0	0	0	1	1	0	2	0	1
<i>Schiedea liqustrina</i>	2	0	0	1	1	1	0	0	0	0	1	1	0	2	0	1
<i>Schiedea lydgatei</i>	2	0	0	1	1	1	0	0	0	0	1	1	0	2	0	1
<i>Schiedea mannii</i>	2	0	0	1	1	1	0	0	0	0	1	1	0	2	0	1
<i>Schiedea membranacea</i>	0	1	0	1	0	1	0	0	0	0	1	1	0	0	0	0
<i>Schiedea menziesii</i>	2	0	0	1	1	1	0	0	0	0	1	1	0	2	0	1
<i>Schiedea nuttallii nuttallii</i>	2	0	0	1	1	1	0	0	0	0	1	1	0	2	0	1
<i>Schiedea nuttallii pauciflora</i>	2	0	0	1	1	1	0	0	0	0	1	1	0	2	0	1
<i>Schiedea pubescens</i>	0	2	0	0	1	0	0	0	0	0	1	1	0	0	0	0
<i>Schiedea salicaria</i>	2	0	0	1	1	1	0	0	0	0	1	1	0	2	0	1
<i>Schiedea sarmentosae</i>	2	0	0	1	1	1	0	0	0	0	1	1	0	2	0	1
<i>Schiedea spergulina</i>	2	0	0	1	1	1	0	0	0	0	1	1	0	2	0	1
<i>Schiedea stellarioides</i>	1	0	1	0	1	0	0	0	0	0	4	0	0	0	0	0
<i>Schiedea verticillata</i>	0	1	0	1	0	1	0	0	0	0	3	0	0	0	0	0
<i>Schiedea</i> sp. nov. (Kaua'i)	2	0	0	1	1	1	0	0	0	0	1	1	0	2	0	1