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A Phylogenetic Analysis of *Schiedea* and *Alsinidendron* (Caryophyllaceae: Alsinoideae): Implications for the Evolution of Breeding Systems

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ABSTRACT. Phylogenetic analysis of *Schiedea* and *Alsinidendron* (Caryophyllaceae), a monophyletic lineage endemic to the Hawaiian Islands, produced six equally most parsimonious trees with 132 steps using morphological characters. Four major clades were found in all trees. Breeding system characters were excluded from the analysis because of the likelihood that dimorphism (gynodioecy, subdioecy, dioecy) has evolved in parallel in *Schiedea,* although subsequent inclusion of these characters had little effect on topology. Dimorphism is found in the two clades occurring primarily in dry habitats. Mapping of breeding systems on the phylogeny suggests that dimorphism has probably evolved on two or more occasions, depending on the number of character states and whether the character is treated as ordered or unordered. One to several reversals from dimorphism to hermaphroditism have also occurred. Dimorphic species occur only in dry habitats, but mapping of habitat on the phylogeny suggests that hermaphroditic species originally may have invaded dry habitats without evolving a dimorphic breeding system. Ecological shifts to very wet habitats appear to have favored the evolution of autogamy, which has occurred independently in the two clades largely restricted to mesic or wet habitats. The striking variation in breeding systems found in *Schiedea* and *Alsinidendron* appears to result in large part from the invasion of diverse habitats in the Hawaiian Islands following colonization by the ancestor of this lineage.

Dioecy, the presence of separate pistillate (female) and staminate (male) plants in a population, occurs in about 4% of all flowering plants (Yampolsky and Yampolsky 1922). Numerous theoretical and empirical studies have addressed the question of why dioecy should evolve, given that female or male individuals suffer a 50% loss in reproductive potential relative to hermaphrodites. One set of arguments emphasizes the importance of inbreeding depression. In models developed by Lloyd (1975a) and Charlesworth and Charlesworth (1978), females may spread in populations if both inbreeding depression and selfing rates are high. Under these conditions, females spread because the progeny of females, which are always outcrossed, will have higher fitness than the progeny of hermaphrodites, which self to varying degrees. If females produce more seeds than hermaphrodites, which seems likely on the basis of resource reallocation, they may spread even when inbreeding depression and selfing rates of hermaphrodites are lower. Other models (Charnov 1982) emphasize the importance of shifts in resource allocation.

Empirical studies indicate the widespread occurrence of inbreeding depression (Schemske 1983; Schoen 1983; Sakai et al. 1989; Dudash 1990; Johnston 1992), and studies of selfing rates in several species with high inbreeding depression indicate that unisexual individuals should be favored by selection (Kohn 1988; Sakai and Weller, unpubl. data). Overall, little evidence has accumulated suggesting that either

TABLE 1. Breeding system, growth form, habitat, and distribution for species of *Alsinidendron* and *Schiedea*. Assessments based on herbarium, greenhouse, or field observations. From Weller et al. (1990), with modification.

Species	Breeding system	Habit	Habitat	Distribution
Alsinidendron H. Mann				
lychnoides (Hillebr.) Sherff	Hermaphroditic, facultative autogamy	Vine	Wet forest	Kauai
obovatum Sherff	Hermaphroditic, facultative autogamy	Subshrub	Diverse mesic forest	Oahu
trinerve H. Mann	Hermaphroditic, cleistogamous	Subshrub	Wet forest, diverse mesic forest	Oahu
viscosum (H. Mann) Sherff	Hermaphroditic, facultative autogamy	Vine	Wet forest, diverse mesic forest	Kauai
Schiedea Cham. & Schlechtend.				
adamantis St. John	Gynodioecious	Shrub	Dry shrubland	Oahu
amplexicaulis H. Mann	Hermaphroditic	?	?	Kauai (extinct)
apokremnos St. John	Gynodioecious	Shrub	Dry cliffs	Kauai
attenuata W. L. Wagner, Weller, & Sakai	Hermaphroditic	Shrub	Diverse mesic forest pockets on cliffs	Kauai
diffusa A. Gray	Hermaphroditic, facultative autogamy	Vine	Wet forest	East Maui, Molokai, Hawaii
globosa H. Mann	Subdioecious	Suffruticose herb	Dry coastal cliffs	Oahu, Maui, Molokai
haleakalensis Degener & Sherff	Dioecious	Shrub	Dry subalpine cliffs	East Maui
helleri Sherff	Hermaphroditic	Vine	Wet forest cliffs	Kauai
hookeri A. Gray	Hermaphroditic	Subshrub	Diverse mesic forest	Oahu
implexa (Hillebr.) Sherff	Hermaphroditic	Subshrub	Mesic forest?	Maui (extinct)
kaalae Wawra	Hermaphroditic	Perennial herb	Diverse mesic forest, wet forest	Oahu
kealiae Caum & Hosaka	Subdioecious	Subshrub	Dry forest	Oahu
ligustrina Cham. & Schlechtend.	Dioecious	Shrub	Dry shrubland, often cliffs	Oahu
lydgatei Hillebr.	Hermaphroditic	Shrub	Dry shrubland	Moloakai
mannii St. John	Subdioecious	Shrub	Dry ridges in diverse mesic forest	Oahu
membranacea St. John	Hermaphroditic	Perennial herb	Diverse mesic forest	Kauai
menziesii Hook.	Hermaphroditic	Shrub	Shrubland	Lanai and West Maui
nuttallii Hook. var. *nuttallii*	Hermaphroditic	Subshrub	Diverse mesic forest	Oahu

TABLE 1. Continued.

Species	Breeding system	Habit	Habitat	Distribution
nuttallii Hook. var. *pauciflora* Degener & Sherff	Hermaphroditic	Subshrub	Diverse mesic forest	Kauai
pubescens Hillebr.	Hermaphroditic	Vine	Diverse mesic forest	Oahu, Molokai, Lanai, and Maui
salicaria Hillebr.	Gynodioecious	Shrub	Dry shrubland	West Maui
sarmentosa Degener & Sherff	Gynodioecious	Shrub	Dry forest and shrubland	Molokai
spergulina A. Gray	Dioecious	Shrub	Cliffs in dry shrubland	Kauai
stellarioides H. Mann	Hermaphroditic	Subshrub	Diverse mesic forest	Kauai
verticillata F. Brown	Hermaphroditic	Perennial herb	Soil pockets and cracks on dry coastal cliffs	Nihoa
sp. nov. (*Perlman 13448*)	Hermaphroditic	Subshrub	Mesic forest	Kauai

inbreeding depression or accelerating fitness gains associated with shifts in resource allocation have played exclusive roles in the evolution of dioecy (Thomson and Brunet 1990).

Phylogenetic approaches may be critical for distinguishing among hypotheses for the evolution of dioecy (Felsenstein 1985; Hart 1985b; Donoghue 1989; Thomson and Brunet 1990; Lauder et al. 1993). If a character has evolved on several occasions, then correlations of the character with ecological traits may be used to infer causative factors for the evolution of the trait; without phylogenetic information such correlations may be misleading (Felsenstein 1985). Phylogenetic analyses may also indicate whether shifts in ecological factors preceded or were coincident with character evolution, and thus provide additional means for assessing whether such shifts were causative.

Dioecy, gynodioecy (the occurrence of females and hermaphrodites in populations), and subdioecy (the occurrence of females, males, and a few hermaphrodites in populations) are common in the Hawaiian species of *Schiedea* (Caryophyllaceae: Alsinoideae). Throughout this paper these breeding systems are collectively termed dimorphic. The diversity of breeding systems within *Schiedea*, habitat diversity of species, and their presumed monophyletic origin (see below) make this genus useful as a model system for the study of breeding systems using cladistic methods.

The endemic Hawaiian Caryophyllaceae subfam. Alsinoideae include 25 species of *Schiedea* and four species of *Alsinidendron* (Table 1; Wagner et al. 1990; Wagner et al. 1995). The number of species has increased by three since the treatment by Wagner et al. (1990) because of the discovery of two new species on Kauai (*Schiedea attenuata* and an unnamed species) and the resurrection of *S. sarmentosa*. *Schiedea* and *Alsinidendron* constitute a monophyletic group as evidenced by the synapomorphic nectary shafts [although these are highly modified in *Alsinidendron* (Weller et al. 1990; Harris and Wagner 1993; Wagner et al. 1995)] and probably apetaly. Ten species of *Schiedea* have dioecious, subdioecious, or gynodioecious breeding systems. These dimorphic species occur in dry habitats, while species with hermaphroditic breeding systems are largely restricted to mesic or wet forests (Weller et al. 1990). Most species with separate sexes appear to be wind pollinated; hermaphroditic species are apparently 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 presumed response to loss of pollinators on the very windy cliffs and ridges occupied by most dimorphic species.

A primary focus of our phylogenetic analysis was to assess the relationship of ecological shifts to breeding system evolution in the Hawaiian Alsinoideae. If species with dimorphic breeding systems form a clade within *Schiedea*, a single modification of breeding system, very possibly unrelated to ecological shifts, could explain the current distribution of breeding systems. In contrast, if dimorphism evolved repeatedly in association with ecological shifts, a causal role for these shifts might be inferred, especially if phylogenetic analysis indicates that habitat shifts preceded the evolution of dioecy (Donoghue 1989).

A second focus of our analysis was to explore the effect of inclusion of breeding system characters on the resulting phylogenies. The inclusion of characters that are to be mapped onto trees has been criticized as introducing circularity into phylogenetic analysis (Coddington 1988; Brooks and McLennan 1991). Swofford and Maddison (1992) suggested that if characters that are mapped onto phylogenetic trees contain useful phylogenetic information, they should be used in tree construction. Characters that are known to be homoplastic, and thus are likely to provide misleading phylogenetic information, should be excluded (Swofford and Maddison 1992). For example, Hart (1985a, b), in his study of the evolution of dioecy from gynodioecy in *Lepechinia* Willd. (Lamiaceae), excluded the presumably homoplastic breeding system character from his analysis. A difficulty with this approach is the degree of uncertainty over which characters are associated with breeding system (J. Doyle, pers. comm.). Information on the function of morphological features may be one useful approach for identifying sets of characters associated with the evolution of breeding systems (Lauder 1990). A second problem resulting from exclusion of characters may be the inability to resolve relationships because of the reduced number of characters (Swofford and Maddison 1992). Given the various approaches to this problem and the difficulty of unambiguously defining breeding system characters, we have investigated the effects on phylogenetic hypotheses of selective removal of characters likely to be directly or indirectly associated with breeding system.

A final goal of the study was to investigate how differences in coding and ordering of characters mapped onto trees may affect interpretation of evolution of traits. Swofford and Maddison (1992) have emphasized the difficulties entailed in the process of character-mapping that result from uncertainty about the true phylogeny, and the sensitivity of results to underlying assumptions about characters. These uncertainties were investigated for the evolution of breeding systems in *Schiedea* by assessing the influence of differences in coding and assumptions about ordering of character states on hypotheses for the evolution of dimorphism.

Materials and Methods

Monophyly in the endemic Hawaiian Alsinoideae. Floral nectaries in *Schiedea* and *Alsinidendron* are very distinctive within the subfamily and serve as the key feature delineating the Hawaiian Alsinoideae as a monophyletic group. In *Schiedea* each nectary is terminated by a tubular structure that extrudes drops of nectar at the tip. In *Alsinidendron*, nectary appendages are flap-like structures that are either separate, connate at the base, or connate into a cup. Despite the use of differences in nectaries for separation of the genera (Wagner et al. 1990), developmental studies clearly indicate that the structures are homologous in *Schiedea* and *Alsinidendron* (Harris and Wagner 1993, unpubl. data; Wagner et al. 1995).

Outgroup Selection. The Caryophyllaceae are largely temperate or boreal, with only a few tropical representatives (Pax and Hoffman 1934). *Schiedea* and *Alsinidendron* are morphologically divergent from mainland representatives of the family, probably due to their adaptive radiation in the Hawaiian Islands and their occurrence in a subtropical environment. Biogeographic analyses of the endemic Hawaiian Alsinoideae employing phylogenetic information (Wagner et al. 1995) indicate that this lineage may have undergone substantial diversification on islands at least as old as Necker and Nihoa (ages

>7.5 millions of years ago), islands to the northwest of Kauai that are now largely eroded and subsided into the ocean. Early diversification of the Hawaiian Alsinoideae may have contributed to divergence from continental relatives, and complicates identification of a mainland sister group.

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. Despite McNeill's comments, the presence of exstipulate leaves, capsules splitting into as many valves as styles, and distinct sepals clearly align *Schiedea* and *Alsinidendron* with the exstipulate Alsinoideae. There is little additional information currently available for the infrageneric relationships within the Alsinoideae, which led us to employ a hypothetical subfam. Alsinoideae ancestor in all of our analyses.

Because of similarities in nectary structure and type of capsule dehiscence, we also included two species of *Minuartia* L. (Alsinoideae) in the analyses as additional outgroups. The related western North American species *Minuartia howellii* (S. Wats.) Mattf. and *M. douglasii* (Torr. & A. Gray) Mattf. have small nectary extensions similar in form to those in the Hawaiian genera (Harris and Wagner 1993; Wagner et al. 1995). Current ontogenetic studies, although not yet comprehensive for all genera of the subfamily, show that the early stages of initiation and development of nectaries in the Hawaiian genera are homologous to comparable structures of many taxa of subfam. Alsinoideae. The nectaries of *Schiedea* and *Alsinidendron* and *Minuartia douglasii*, however, display development beyond the ontogenetic endpoint of the other Alsinoideae. The strikingly large nectary appendages in *Schiedea* and *Alsinidendron* are even larger than in *Minuartia douglasii*, yielding a distinctive synapomorphy for the Hawaiian lineage. *Minuartia* is specialized in several respects, including its annual habit and small, linear leaves, both presumed adaptations to the arid environments. For most traits, the codings for the generalized outgroup and the *Minuartia* species were identical.

Character Selection and Coding. Characters were selected and studied using herbarium specimens of all taxa and flowering material of all but four species grown in the greenhouse. *Schiedea amplexicaulis* and *S. implexa*, the former represented by only two herbarium collections, are apparently extinct. Missing data for *S. amplexicaulis* contributed to ambiguity in resolving the phylogenetic position of this species.

Vegetative and floral characters were classified as either associated with breeding system evolution, or independent of breeding system. Functional analyses and field observations were used to identify characters that appeared to be correlated with the evolution of dioecy. For example, inflorescence condensation (characters 19 and 20; Appendix 1) is strongly correlated with expression of dioecy, apparently because of a functional relationship to wind pollination (Weller and Sakai 1990). These characters and the breeding system character (character 43) were excluded in varying combinations from those analyses where the outcome was putatively independent of breeding system features. The rationale for defining a character as indirectly associated with breeding system is given in the character list (Appendix 1).

Forty-three characters were used in phylogenetic reconstruction (Appendix 1); (0) represents the plesiomorphic state, and (1) or higher represents apomorphic states (Appendix 2). No autapomorphic characters were included in the data matrix. With the exception of the breeding systems character, multi-state characters were unordered because of uncertainties in determining likely transition series among these character states. In some analyses the breeding system character (43) was ordered to determine the effect of character ordering on tree topology and optimization of breeding system. This character was also coded as a binary character (hermaphroditic vs. dimorphic) to determine the effect of this coding on interpretation of breeding system evolution.

Analysis. Phylogenetic Analysis Using Parsimony (PAUP) was used for tree construction (Swofford 1993). In view of the large number of taxa involved, a heuristic search was performed using all branch swapping options. The tree-bisection reconnection (TBR) algorithm yielded trees identical to those produced by the subtree-pruning regrafting option (SPR), and was used in subsequent analyses. The generalized outgroup was used as the outgroup for all runs, and characters were unweighted. The random addition sequence option (10 replications) was used to increase the likelihood of obtaining all equally most parsimonious trees (Maddison 1991). Accelerated transformation

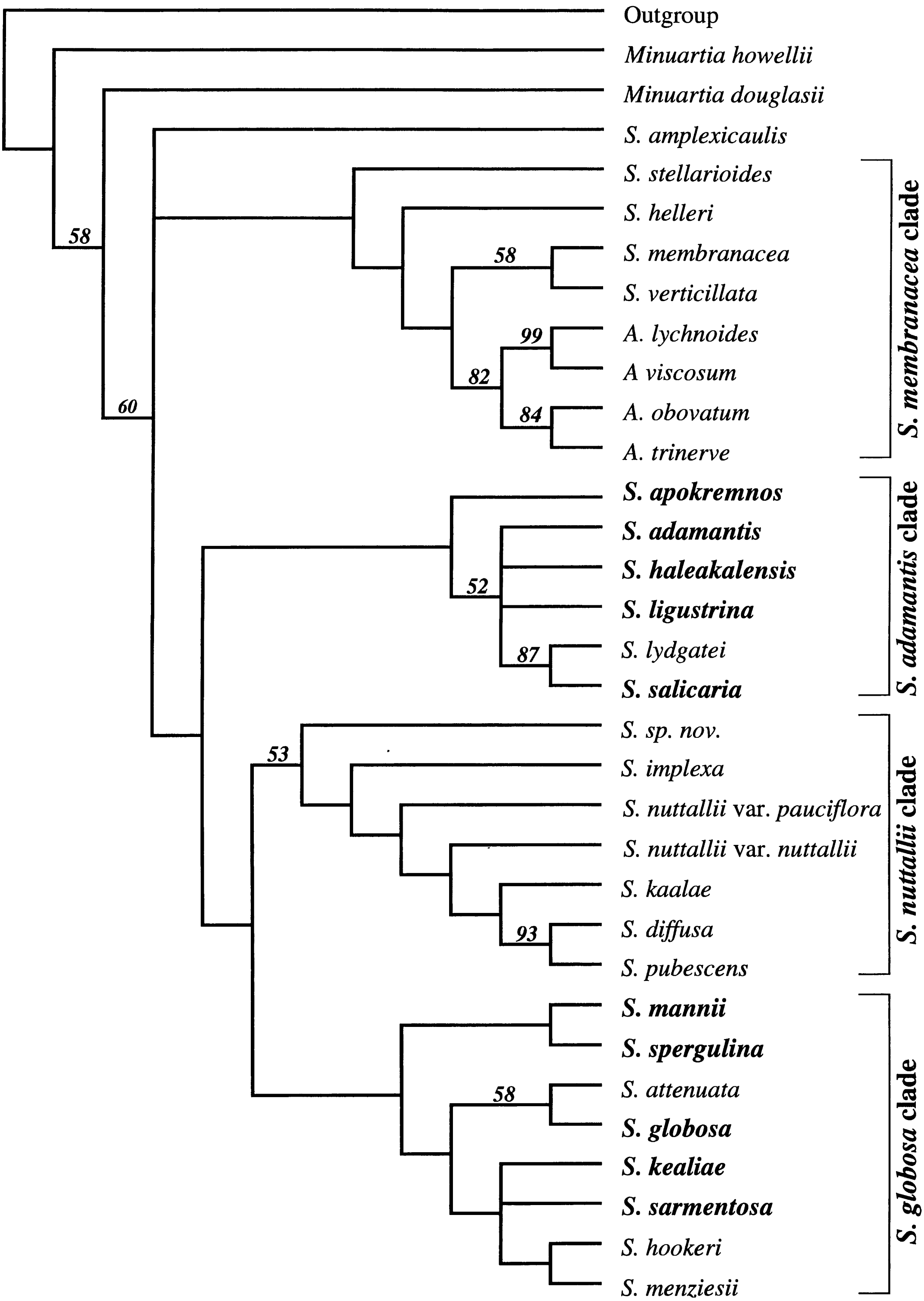

FIG. 1. Strict consensus of six equally most parsimonious trees showing presence of four major clades, named for convenience. Also shown are results of bootstrap analysis of morphological data, based on 1,000

(ACCTRAN) and delayed transformation (DELTRAN) were used to investigate character reconstruction. In cases where transitions between character states could occur at several places on a tree, use of the ACCTRAN option results in the earliest possible occurrence of the transition. Reversals then account for cases of homoplasy. Use of DELTRAN delays transitions on trees, and cases of homoplasy are interpreted as parallel evolution. Consistency indices were calculated to assess the extent of homoplasy. Confidence in phylogenetic results was assessed using the bootstrapping procedure in PAUP with 1,000 replications. Decay indices (Bremer 1988; Donoghue et al. 1992) were also calculated to further examine the robustness of the major clades.

RESULTS

In most analyses four major clades were found within the Hawaiian Alsinoideae. The exclusion or inclusion of breeding system characters had little effect on this result. Major clades are described in the following section.

Parsimony Analyses Excluding Breeding System Characters. Using only those characters presumed to be independent of the evolution of dioecy, six equally most parsimonious trees with 132 steps were obtained using PAUP. No additional trees were discovered using 10 random-addition-sequence replicates. The consistency index (CI), homoplasy index (HI), retention index (RI), and rescaled consistency index (RC) were 0.508, 0.515, 0.710, and 0.360, respectively. The strict consensus (Fig. 1) shows five distinct clades, one consisting of a single species, the extinct *Schiedea amplexicaulis*. The six trees differ in the position of *S. amplexicaulis*, and the degree of resolution within the *S. globosa* clade. *Schiedea amplexicaulis* is placed either 1) in an unresolved trichotomy with the *S. membranacea* clade and the three remaining clades, 2) as the sister taxon to all other *Schiedea* and *Alsinidendron* species, or 3) as the sister taxon to all but the *S. membranacea* clade. In the *S. globosa* clade, *S. hookeri*, *S. kealiae*, *S. menziesii*, and *S. sarmentosa* are found in two arrangements. One of the six trees was arbitrarily selected to map characters (Figs. 2a and 2b).

SCHIEDEA MEMBRANACEA CLADE. With the exception of *S. stellarioides*, which has narrow, single-nerved leaves, the *S. membranacea* clade is characterized by the occurrence of broad, multinerved leaves and leaf margins that are ciliate or toothed (Fig. 2b). *Schiedea helleri*, rediscovered on Kauai in mid-1993, is a large vine with coriaceous, cordate leaves. *Schiedea verticillata* and *S. membranacea* have deciduous stems and thick, fleshy roots; the latter are very likely to be a specialized trait based on outgroup comparison.

Synapomorphies delimiting the four *Alsinidendron* species include the campanulate calyx, petaloid sepal texture, flap-like nectary extensions, black nectar, and gray pollen (Fig. 2b). The Kauai species are vines with membranous sepals that become papery in fruit. The Oahu species of *Alsinidendron* have fleshy sepals that become juicy and contain a dark purple pigment when the seeds are ripe. The stems are thick and fleshy, eventually becoming woody. The woody habit has evolved on several occasions in *Schiedea* as well, in species with fleshy stems, and those with slender, non-fleshy stems (see below).

The *S. membranacea* clade is not supported in the bootstrap analysis (Fig. 1). Relaxing parsimony by three steps results in decay of the clade containing all species nested within *S. stellarioides* except *Alsinidendron* (Fig. 2b). Two species, *S. membranacea* and *S. verticillata*, are supported as sister taxa in the bootstrap analysis in 58% of the replications, although the clade decays in a single step (Figs. 1 and 2b). The clade comprising the four species of *Alsinidendron*, which is defined by a number of synapomorphies (Fig. 2b), is strongly supported in the bootstrap analysis (82%) as well as decay analysis (parsimony must be relaxed by four steps before the clade disintegrates). The *A. lychnoides*-*A. viscosum* species pair on Kauai and the *A. obovatum*-*A. trinerve* species pair on Oahu are also well-supported in bootstrap and decay analyses (Figs. 1 and 2b).

SCHIEDEA ADAMANTIS CLADE. This clade, characterized by leaves that are broadest above the mid-point and, for all species but *S. apokremnos*,

←

replicates. One thousand trees were saved for each replication. Boldface indicates species with dimorphic breeding systems.

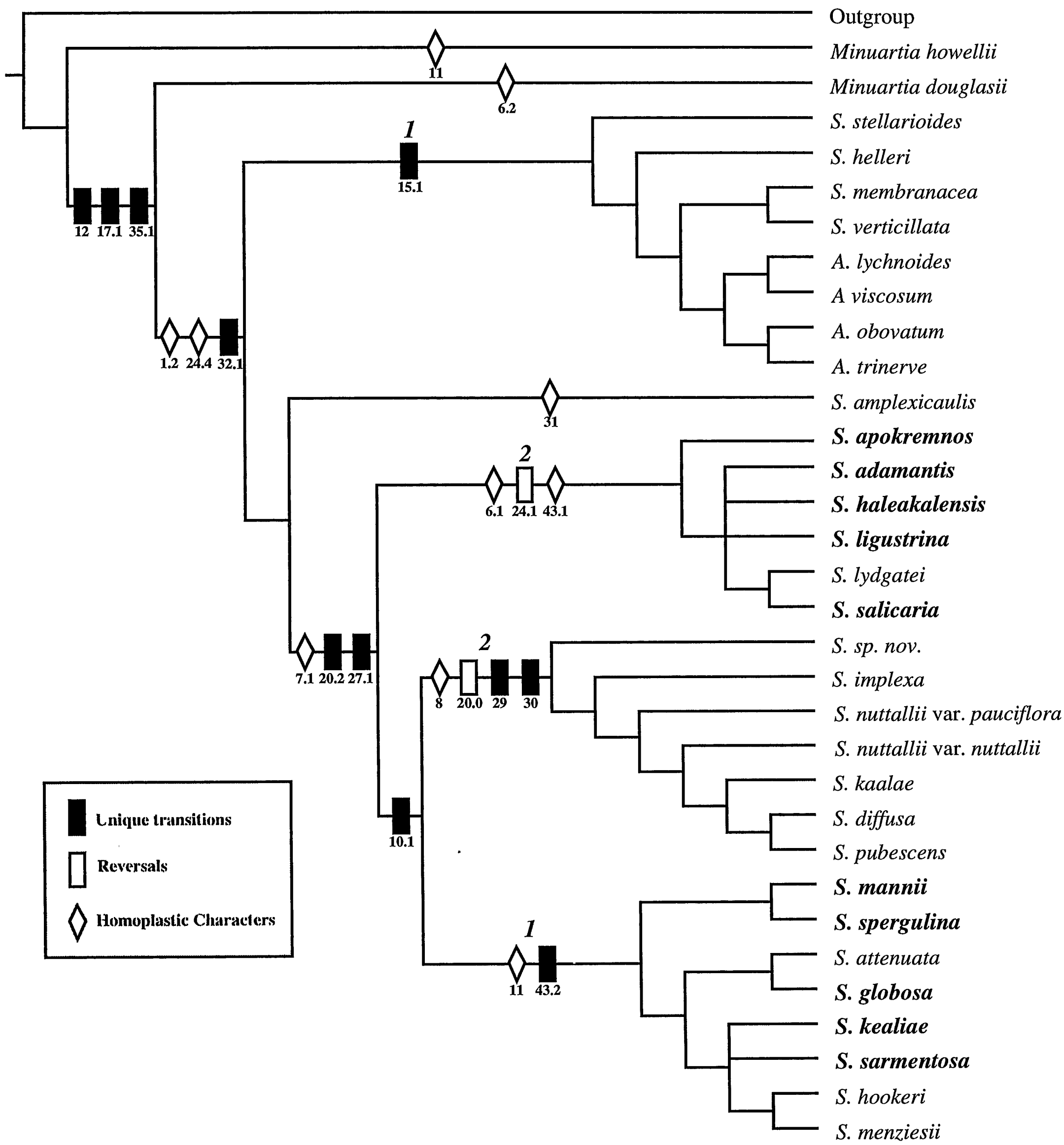

FIG. 2a–2b. Synapomorphies mapped on the preferred tree. Numbers refer to characters listed in Appendix 1. Unique transitions indicated by solid bars, homoplastic transitions indicated by open diamonds, and reversals indicated by open bars. Boldface indicates species with dimorphic breeding systems. a. Synapomorphies delimiting basal portion of tree. b. Synapomorphies delimiting the four major clades. Number of steps required for decay of major clades shown above branches.

by papillate seeds and acute margins on the epidermal cells of the seeds (Fig. 2b), is supported at the 52% level in the bootstrap analysis when *S. apokremnos* is excluded (Fig. 1). Relaxing parsimony by two steps results in decay of this clade (Fig. 2b). Without the use of breeding system characters, *S. adamantis, S. haleakalensis, S. ligustrina,* and the *S. lydgatei-S. salicaria* species pair form an unresolved polytomy in all of the equally most parsimonious trees and the strict consensus tree (Figs. 1, 2b). The polytomy decays in two steps. The *S. lydgatei -S. salicaria* sister

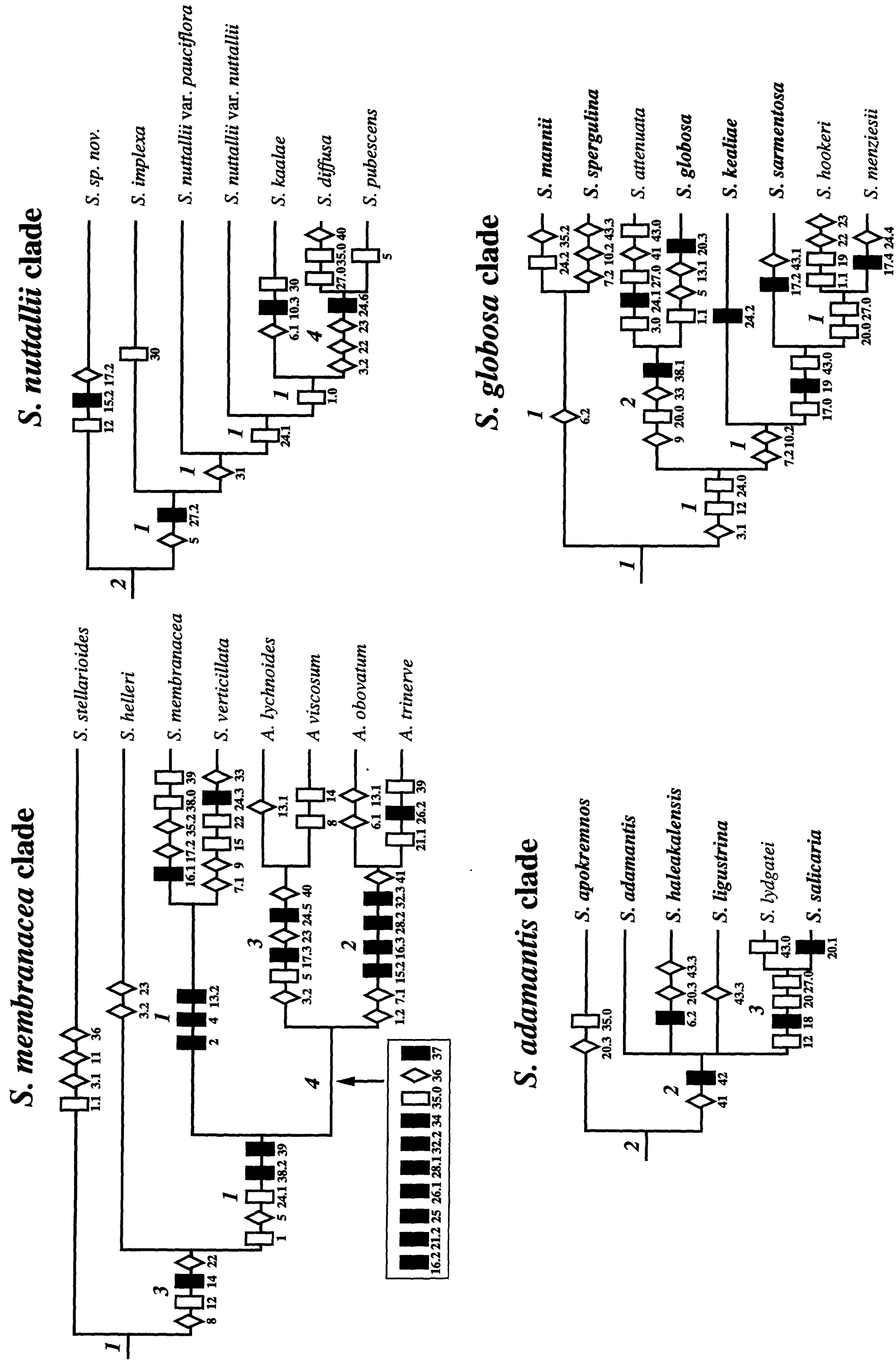

FIG. 2. Continued.

group is strongly supported by bootstrap (87% of replicates, Fig. 1) and decay analysis (three extra steps required for decay of clade, Fig. 2b).

SCHIEDEA NUTTALLII CLADE. The *S. nuttallii* clade, delimited by the presence of fleshy stems (with one reversal in *S. pubescens*), large leaves possessing a single vein (with the exception of the new species), and attenuate to caudate, strongly reflexed sepals (Fig. 2b), is supported at the 53% level by the bootstrap analysis (Fig. 1). Relaxation of parsimony by two steps results in decay of this clade. The *S. diffusa*-*S. pubescens* sister group is very strongly supported by the bootstrap (clade present in 93% of the runs) and decay analyses (four steps required for decay). *Schiedea diffusa* and *S. pubescens* are vines possessing pendent flowers and inflorescences as well as nonglandular, purple pubescence on the inflorescences. *Schiedea implexa*, an extinct species formerly occurring on Maui, lacks the ciliate sepals typical of the remaining members of the clade, and for this reason occurs next to the new species in the basal position.

SCHIEDEA GLOBOSA CLADE. The *S. globosa* clade is delimited by a single synapomorphy, the presence of long, attenuate leaf tips (Fig. 2b). The clade is not supported by bootstrap or decay analyses, although one well-defined group within this clade consists of *S. globosa* and *S. attenuata*, marked by the presence of succulent leaves, a reversal from one to several leaf veins, recurved nectaries, and four to six stigmas instead of the typical three (Fig. 2b). This grouping is found in 58% of the bootstrap replicates (Fig. 1), and decays when parsimony is relaxed by two steps (Fig. 2b). *Schiedea spergulina* and *S. mannii* are similar in possessing linear, single-nerved leaves. The softly membranous, strongly falcate leaves, and nonglandular inflorescence pubescence of *S. spergulina* distinguish it from *S. mannii*, which has straighter, coriaceous leaves, and short, glandular hairs in the inflorescence. *Schiedea kealiae*, *S. sarmentosa*, *S. menziesii*, and *S. hookeri* are delimited as a group by multi-nerved, softly membranous leaves with falcate leaf tips.

The *S. globosa* and *S. nuttallii* clades are linked together in all trees by the presence of slightly asymmetric leaves (Fig. 2a). The *S. globosa* -*S. nuttallii* clade is inferred to share common ancestry with the *S. adamantis* clade by the synapomorphy woody tissue (Fig. 2a), and all clades of the Hawaiian Alsinoideae share the presence of the specialized nectary shafts and nonglandular hairs in the inflorescence, although the latter character reverses frequently.

Character mapping using ACCTRAN and DELTRAN. When hermaphroditic, gynodioecious, subdioecious, and dioecious breeding systems were coded as different, unordered character states, and the ACCTRAN option (accelerated transformation) was used for optimization, dimorphism was found to evolve once at the base of the *S. adamantis* clade and once at the base of the *S. globosa* clade in each of the six equally most parsimonious trees (Table 2). Gynodioecy is basal in the *S. adamantis* clade, and full dioecy evolves in *S. haleakalensis* and *S. ligustrina*. Hermaphroditism in *S. lydgatei* appears to have resulted from a reversal to hermaphroditism from a gynodioecious ancestor (Figs. 3a, b).

Variation in the topology in part of the *S. globosa* clade results in different hypotheses for the evolution of dimorphism. In one arrangement of taxa a reversal to hermaphroditism occurs in the ancestor of *S. hookeri*, *S. menziesii*, and *S. sarmentosa*, followed by the evolution of gynodioecy in *S. sarmentosa* (Fig. 3a). In the second arrangement, *S. kealiae*, *S. sarmentosa*, and the *S. hookeri* -*S. menziesii* species pair form a polytomy and may have had a subdioecious ancestor. Independent reversals are required from subdioecy to gynodioecy in *S. sarmentosa* and subdioecy to hermaphroditism in the ancestor of *S. hookeri* and *S. menziesii* (Fig. 3b). In both arrangements additional reversals to hermaphroditism occur in *S. lydgatei* and *S. attenuata*.

As expected, use of the DELTRAN option results in additional independent transitions to dimorphism, and minimizes reversals to hermaphroditism. Differences resulting from use of the DELTRAN rather than ACCTRAN option occur in the *S. globosa* clade, where dimorphism

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FIG. 3a–3b. Optimization using ACCTRAN of unordered breeding system character on portions of two equally most parsimonious trees. Variation in topology affects hypotheses for breeding system evolution. Breeding system character coded as hermaphroditic, gynodioecious, subdioecious, or dioecious. Symbols as in Figs. 1 and 2.

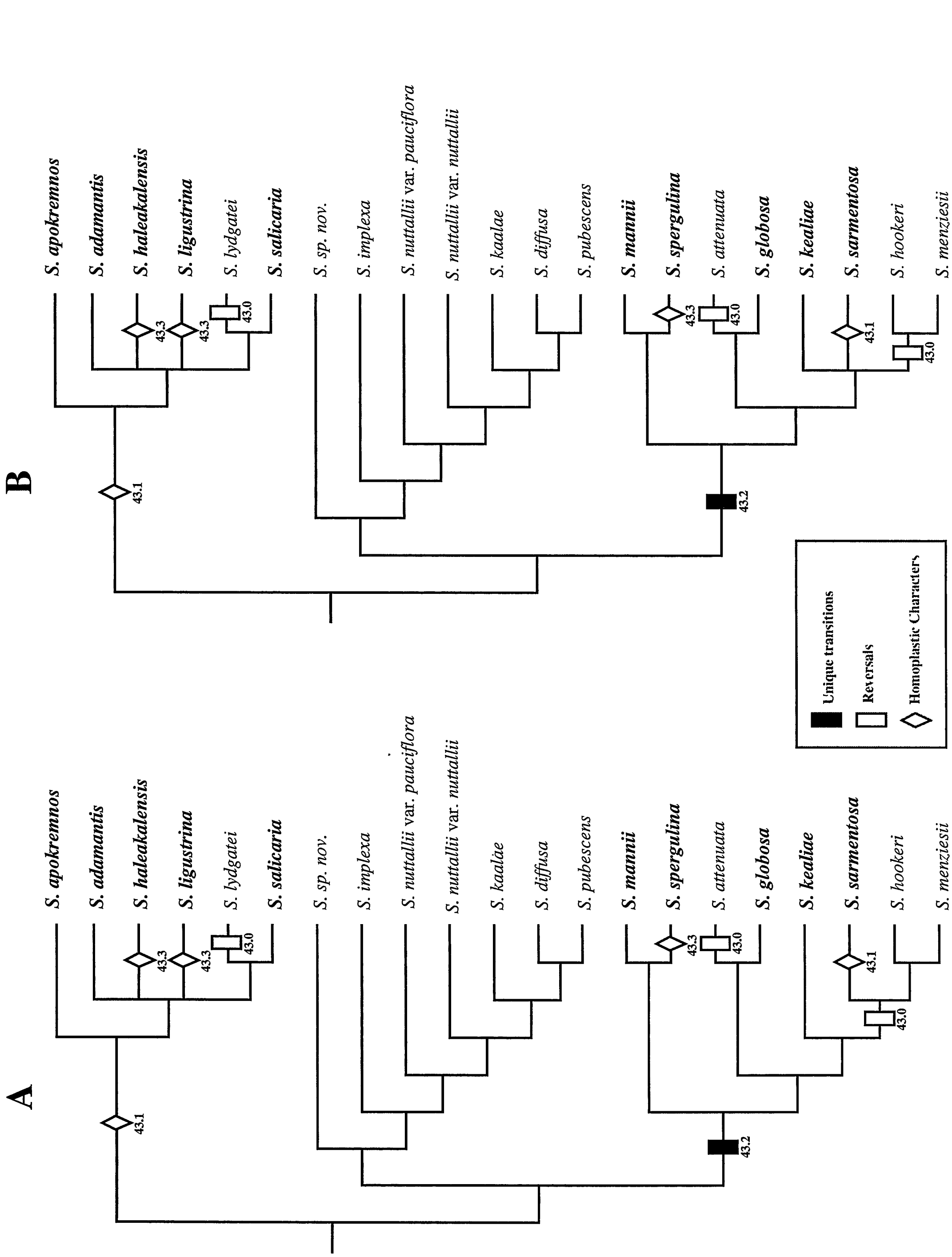
A
B
S. apokremnos
S. adamantis
S. haleakalensis
S. ligustrina
S. lydgatei
S. salicaria
S. sp. nov.
S. implexa
S. nuttallii var. pauciflora
S. nuttallii var. nuttallii
S. kaalae
S. diffusa
S. pubescens
S. mannii
S. spergulina
S. attenuata
S. globosa
S. kealiae
S. sarmentosa
S. hookeri
S. menziesii
43.0
43.1
43.2
43.3
Unique transitions
Reversals
Homoplastic Characters

TABLE 2. Summary of results for optimization of breeding system character (43) on various trees. Number of times dimorphism has evolved is shown for each combination of character coding, selection, and ordering. Number of equally most parsimonious trees shown in parentheses. Breeding system characters (19, 20, 35, and 43) were excluded in various combinations.

	Character combinations used in analysis	Unordered		Ordered	
		ACCTRAN	DELTRAN	ACCTRAN	DELTRAN
Coding for character 43: 0 = hermaphroditic 1 = gynodioecious 2 = subdioecious 3 = dioecious	No breeding system characters	2 (6)	6 (6)	1 (6)	2 (6)
	Character 43 included	2 (9)	6 (9)	1–3 (91)	1–4 (91)
	All characters analyzed (including 19, 20, 35, and 43)	2–3 (48)	4–6 (48)	2–3 (45)	4 (45)
Coding for character 43: 0 = hermaphroditic 1 = gynodioecy 2 = subdioecy and dioecy	No breeding system characters used in analysis	2 (6)	5 (6)	1 (6)	2 (6)
	Character 43 included	2 (9)	5 (9)	1–3 (91)	1–4 (91)
	All characters included	2–3 (48)	4–5 (48)	2–3 (45)	3 (45)
Coding for character 43: 0 = hermaphroditic 1 = gynodioecious, subdioecious, or dioecious	No breeding system characters	1 (6)	2 (6)	1 (6)	2 (6)
	Character 43 included	1 (18)	1–4 (18)	1 (18)	1–4 (18)
	All characters included	1–3 (412)	1–3 (412)	1–3 (412)	1–3 (412)

evolves independently from a hermaphroditic ancestor in each instance where it occurs, regardless of topology, and no reversions to hermaphroditism are necessary (Fig. 4). Use of the DELTRAN option had no effect on optimization in the *S. adamantis* clade, with dimorphism evolving once.

When the breeding system character (43) is ordered and the ACCTRAN option is used, dimorphism is hypothesized to evolve at the base of the *S. adamantis*, *S. nuttallii*, and *S. globosa* clades (Table 2; Fig. 5). Reversals to hermaphroditism occur at the base of the *S. nuttallii* clade, in *S. lydgatei* and *S. attenuata*, and at the base of the clade comprising *S. sarmentosa*, *S. hookeri*, and *S. menziesii*. When the DELTRAN option was used, two independent shifts to dimorphism are hypothesized for the *S. adamantis* and *S. globosa* clades (Table 2).

The Effect on Parsimony Analyses of Inclusion of Breeding System Characters. Inclusion of breeding system in the parsimony analysis resulted in nine equally most parsimonious trees (length = 140) and the same four major clades that were produced when no breeding system characters were used. Dimorphism is hypothesized to evolve on two occasions for all nine equally most parsimonious trees (Table 2). Reversals to hermaphroditism occur in the *S. adamantis* and *S. globosa* clades. Use of the DELTRAN option resulted in five independent transitions to dimorphism and no reversals to hermaphroditism in the *S. globosa* clade. As before, optimization results for the *S. adamantis* clade remain unchanged using the ACCTRAN or DELTRAN options. When most or all of the reproductive characters were included in the analysis 48 equally most parsimonious trees were produced. Although use of characters related to breeding system in tree construction resulted in changes in topology and increased the number of equally most parsimonious trees substantially, it has no major effect on estimates of the number of transitions to dimorphism (Table 2).

When the breeding system character was ordered and used for tree construction, the same four basic clades (excluding *S. stellarioides*) were again obtained. The number of equally most parsimonious trees was 91 and the tree length was 143. Inclusion of some or all of the remaining reproductive characters resulted in 45 equally most parsimonious trees in each case. In general, ordering the reproductive character resulted in fewer transitions to dimorphism (Table 2). Use of all characters, especially those related to inflorescence structure, often resulted in basal positioning of hermaphroditic species in the *S. globosa* clade, and the hypothesis that dimorphism evolved independently in the *S. globosa* and *S. adamantis* clades. As expected, use

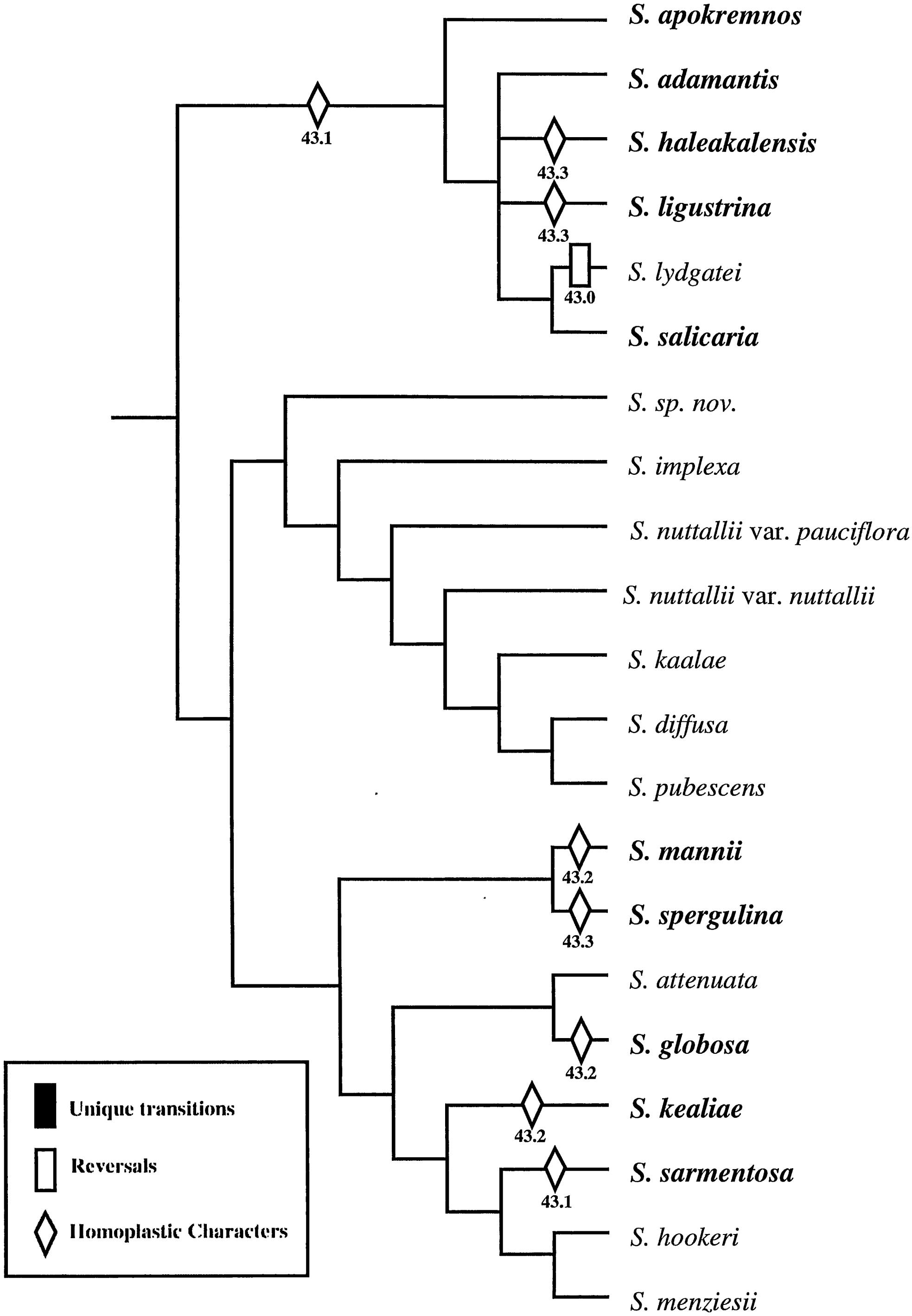

FIG. 4. Optimization of using DELTRAN of breeding system character on portion of one of six equally most parsimonious trees (variation in topology had no effect on hypotheses for breeding system evolution). Breeding system character coded as hermaphroditic, gynodioecious, subdioecious, or dioecious. Symbols as in Figs. 1 and 2.

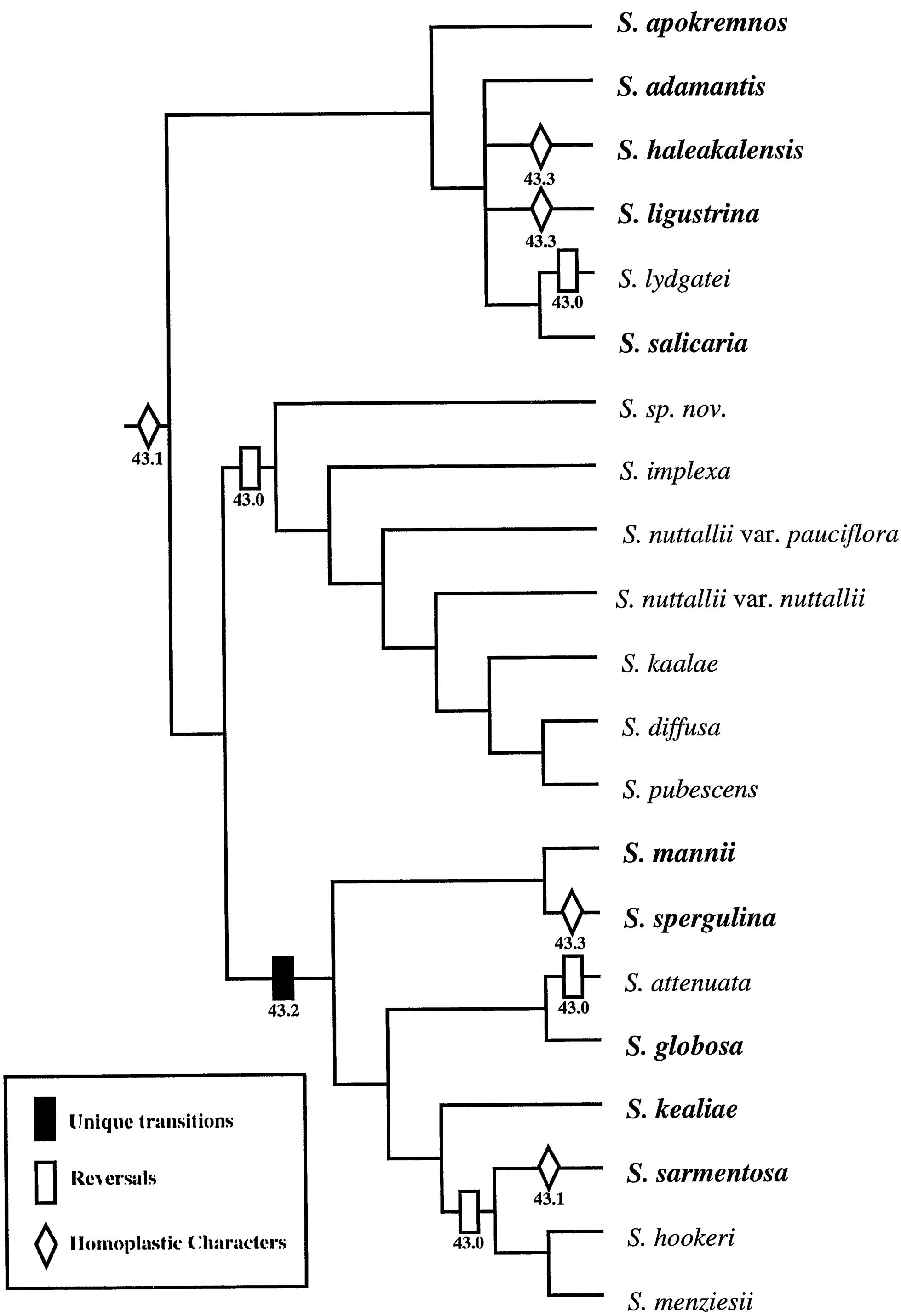

FIG. 5. Single transition to dimorphism resulting from coding breeding system as hermaphroditic, gynodioecious, subdioecious, and dioecious, use of ACCTRAN optimization, and ordering the breeding system character. Symbols as in Figs. 1 and 2.

of DELTRAN optimization resulted in additional hypothesized transitions to dimorphism (Table 2).

Effect of Variation in the Number of Character States Used to Represent Breeding System Diversity. The number of character states used to represent breeding systems had major effects on hypotheses for the evolution of dimorphism in some cases. In one modification of coding for the breeding system character, subdioecious and dioecious breeding systems were combined as a single character state (43, 2) because of the functional and morphological similarity of these breeding systems; hermaphroditism (43, 0) and gynodioecy (43, 1) represented alternative character states. This modification of coding had little effect on estimates of the number of transitions to dimorphism (Table 2). Because the critical step in the evolution of dioecy may be the initial appearance of females in populations, gynodieocy, subdioecy, and dioecy were combined as a single character state in a second modification of coding. The effect of this binary coding of the breeding system (hermaphroditic species = 0; dimorphic species = 1) was substantial (Table 2). Use of this coding scheme strongly favored a single transition to dimorphism in all cases using ACCTRAN optimization, and in most cases using DELTRAN (Table 2). With binary coding, ordering of the reproductive character had little effect on estimates of the number of transitions to dimorphism (Table 2).

Evolution of Habitat Preference in Dimorphic Species. When changes in breeding systems and habitat are compared, there is little evidence suggesting that shifts to dry habitats precede the evolution of dimorphism in *Schiedea.* The question cannot be resolved in the *S. adamantis* clade, where the evolution of dimorphism and shift to dry habitats are coincident. The reversal to hermaphroditism in *S. lydgatei* takes place without a reversal to a mesic habitat (Table 1; Fig. 4). The relationship of habitat shifts and evolution of dimorphism is harder to assess for the *S. globosa* clade, where transitions are equivocal for both traits.

In all trees, regardless of which characters were used to produce the trees, a switch to dry coastal habitats occurs for hermaphroditic *S. verticillata* (Table 1), indicating that colonization of dry habitats may occur without modification of the reproductive system. The ancestor of *S. verticillata* was probably hermaphroditic; in contrast, hermaphroditic *S. lydgatei* was apparently derived from a dimorphic ancestor.

Evolution of Autogamy. Facultative or obligate autogamy occurs in all four species of *Alsinidendron* and *S. diffusa,* based on observations of fruit and seed production in the absence of pollinators. Phylogenetic analysis indicates clearly that selfing species occur in clades that have become specialized for wet habitats (Wagner et al. 1995). The shift has occurred independently in the *S. membranacea* and *S. nuttallii* clades.

Discussion

Selection of Characters for Phylogenetic Analysis. Armbruster (1992), Brooks and McLennan (1991), and Coddington (1988) have argued that characters mapped onto cladograms should not be used in constructing the cladogram. Hart (1985a, b), in a study of the phylogeny and evolution of dioecy in *Lepechinia,* compared cladograms with and without the breeding system character and found substantial differences in the number of times dioecy was hypothesized to have evolved. Eckenwalder and Barrett (1986) used cladistic analysis for the study of breeding system evolution in the Pontederiaceae. They eliminated breeding system (in this case the occurrence of tristyly) from their analysis but retained other traits such as flower size that are likely to be correlated with breeding system evolution (Eckenwalder and Barrett 1986). Possibly as a result of traits correlated with breeding system, homostyly was found to have evolved independently of tristyly for some trees, while in other trees of the same length homostyly was found to have evolved from tristyly.

The degree of influence reproductive characters have on the phylogeny will clearly depend on their relative number in the analysis, as well as the utility of non-reproductive characters in the phylogenetic analysis. If characters are deleted from an analysis, there should be a strong rationale for suspecting they are misleading for phylogenetic analysis because of correlation with breeding system evolution. Hart (1985b), for example, excluded the breeding system character to determine the outcome on phylogenetic analysis, but retained other characters (such as flower size) that appeared to be strongly correlated with evolution of dioecy. Removal of increasing fractions of the total number of characters would at some point result in failure of the analysis to yield any phylogenetic resolution.

In *Schiedea* and *Alsinidendron* characters thought to be closely associated with breeding system evolution are those related to a presumed shift from insect pollination in hermaphroditic species to wind pollination in dimorphic species. In wind pollinated species, condensed inflorescences, often produced on leafless stems held above the foliage, have been shown to disperse and receive pollen with greater efficiency than species with more diffuse inflorescences (Niklas 1985). One of the most conspicuous differences among *Schiedea* species is the degree of condensation of the inflorescence, a feature positively correlated with the frequency of females in populations (Weller and Sakai, unpubl. data). Observations of pollen dispersal in a wind tunnel indicate that those *Schiedea* species with compact inflorescences disperse significantly more pollen than species with diffuse inflorescences (Weller, Sakai, and McGrath, unpubl. data). *Schiedea* species with condensed inflorescences also have low nectar production, high pollen-ovule ratios, and small pollen diameter, additional features thought to be characteristic of wind-pollinated species (Cruden 1977; Niklas 1985; Richards 1986). The ratio of stamen length to sepal length is also apparently related to breeding system, because dimorphic species produce relatively longer filaments, presumably to aid in dispersal of pollen by wind. These results indicate that breeding system is strongly correlated with pollination syndrome in *Schiedea*.

Addition or deletion of characters judged to be related to dimorphism modified the number of equally most parsimonious trees, but had little effect on the topological relationships of *Schiedea* and *Alsinidendron* species, suggesting a strong phylogenetic signal for the remaining vegetative and reproductive characters. Phylogenetically useful vegetative traits included leaf size, the number of nerves in the leaves, stem succulence, and the presence of cilia or minute teeth on the leaf margins. Seed characters, important synapomorphies for most species in the *S. adamantis* clade, included the presence of papillae on the margins of the seeds and the shape of the seed testa cells. Phylogenetically useful floral traits included features such as anther, pollen, and nectar color, nectary morphology and orientation, presence of cilia on sepal margins, degree of reflection of sepals, and style number. These floral traits appeared to have little correlation with the evolution of dimorphism. For example, anther, nectar, and pollen color separated the *Alsinidendron* lineage from *Schiedea*, and therefore had little or no potential for affecting the relationships of hermaphroditic and dimorphic species within *Schiedea*.

Some vegetative traits appear to be indirectly correlated with breeding system evolution. For example, most dimorphic species have small, often narrow leaves and woody stems, but these traits appear dependent on habitat rather than breeding system, as nearly all *Schiedea* taxa occupying dry habitats have small, often linear leaves and woody tissue, regardless of breeding system. Despite the overriding effect of habitat, two clades with narrow leaves were recognized, primarily because even among species in the *S. globosa* clade with narrow leaves, leaf venation is characteristically multinerved compared to the one-nerved leaves of the *S. adamantis* clade. Physiological studies might reveal different syndromes of adaptation to dry habitats in these clades.

Effect of Character Selection and Coding on Interpretation of the Evolution of Dimorphism. Dimorphism is hypothesized to evolve from one to six times in *Schiedea*, depending on the characters used to construct trees and whether accelerated or delayed transformations were used for optimization (Table 2). Estimation of the number of independent transitions to dimorphism also depended on whether the various stages in the evolution of dioecy were ordered and the number of states used for the breeding system character (Table 2).

Exclusion of breeding system characters had relatively little effect on interpretation of evolution of dimorphism in the Hawaiian Alsinoideae (Table 2), presumably because of their modest impact on the phylogenetic analysis. More significant effects on the interpretation of the evolution of dimorphism resulted from use of ACCTRAN versus DELTRAN in PAUP. Use of accelerated transformation is probably most appropriate because this approach minimizes parallel evolution of dimorphism (Swofford and Maddison 1992), predicted at the outset of the study. Even with bias against parallel evolution of dimorphism, at least two transitions to dimorphism were found in cases where multistate coding was used and the breeding system character was unordered. Dimorphism always evolved at the base of the *S. adamantis* clade because nearly all species in this clade are dimorphic. Using accelerated transformation, dimorphism evolved one or several times in the *S. globosa* clade, depending on the combination of breeding system characters (19, 20, 35, and 43) included in the analysis. As more breeding system characters were used, trees were produced where dimorphism evolved independently in *S. globosa* as well as elsewhere in the clade. The exact number of evolutionary transitions was equivocal in the *S. globosa* clade because several species are hermaphroditic.

Differences in the number of states used to represent breeding systems had the greatest impact on interpretation of breeding system evolution in *Schiedea*. When two character states were used to represent breeding system diversity, a single transition to dimorphism was favored in most cases (Table 2). With this coding scheme, additional transitions to dimorphism were favored only when breeding system characters were eliminated and DELTRAN optimization was used. Use of two character states favored a single transition to dimorphism because changes in ancestral nodes were more parsimonious.

Coding the breeding system character as ordered also increased the likelihood of trees indicating a single shift to dimorphism. Ordering the breeding system character state resulted in optimization of earlier nodes in trees as gynodioecious and increased the probability that a single change to dimorphism was most parsimonious, as in the case of binary coding. When characters related to breeding system were included in the analysis, hermaphroditic species with diffuse inflorescences occurred in basal positions in clades, and several transitions to dimorphism were hypothesized, despite ordering of the character.

Although binary coding and ordered transitions favor a single transition to dimorphism, and thus may represent a conservative approach to understanding the evolution of breeding systems in the Hawaiian Alsinoideae, these methods are likely to underestimate the number of transitions to dimorphic breeding systems. Binary coding combines breeding systems as diverse as gynodioecy, where females may be rare and hermaphrodites indistinguishable from those of strictly hermaphroditic species, and full dioecy, where females constitute about half the population, and males bear very little resemblance to hermaphrodites. Thus binary coding may unduly force ancestral nodes to become dimorphic. Similarly, when the character is coded as multistate, ordering the breeding system character forces ancestral nodes to become dimorphic. Although gynodioecy and subdioecy are thought to be intermediate stages in the evolution of dioecy (Charlesworth and Charlesworth 1978), if breeding system modifications occur on a shorter time scale than speciation events, ordering the trait will bias against independent acquisition of gynodioecy. In view of these considerations, at least two transitions to dimorphism are likely to have occurred in *Schiedea*. This analysis does not rule out the possibility that more transitions to dimorphism have occurred independently, in a non-parsimonious manner, along terminal branches of the cladogram (Felsenstein 1985).

Dimorphism and Habitat Shifts. At a minimum, *Schiedea* has invaded dry environments on two occasions (Wagner et al. 1995). One invasion occurred in the *S. membranacea* clade when the ancestor of *S. verticillata* colonized dry coastal environments (Table 1). All species in the *S. membranacea* clade have hermaphroditic breeding systems, indicating that transitions to dry habitats do not necessarily entail a shift to dimorphism. Interpretation of habitat shifts is more difficult for the *S. adamantis* and *S. globosa* clades, where one or several shifts may have occurred (Wagner et al. 1995). Because dimorphic species do not occur in mesic or wet habitats, but hermaphroditic species occur in dry habitats, occurrence in dry habitats is necessary but not sufficient for the evolution of dimorphism.

The association of arid habitat with evolution of dimorphism may be a general phenomenon. In a phylogenetic study of *Lepechinia*, Hart (1985a, b) found that dioecious species occurred in more xeric habitats, and he concluded that dioecy had evolved on two occasions from gynodioecy. When breeding system and several characters related to breeding system were removed from the cladistic analysis, dioecy evolved on four occasions (Hart 1985b). In the

Australian geophyte *Wurmbea dioica* (R. Br.) F. Muell., for which no phylogenetic information is available, dioecious populations were found at the dry end of an environmental gradient, while hermaphroditic populations were found in more mesic environments (Barrett 1992). Similar relationships between aridity and dimorphism have been observed for Hawaiian *Bidens* L. (Ganders, pers. comm.; Sakai et al. in press), as well as other species (Freeman et al. 1980).

Reversals to Hermaphroditism. Apparent reversals to hermaphroditism have occurred in *S. lydgatei* in the *S. adamantis* clade and possibly in *S. attenuata, S. hookeri,* and *S. menziesii* in the *S. globosa* clade. Reversals to hermaphroditism do not seem to be obligately dependent on a shift from dry habitats, because *S. lydgatei* and *S. menziesii* occur in dry shrublands rather than mesic or wet forest. On theoretical grounds, there is little reason to doubt that reversals could occur, especially during the early stages of the evolution of dioecy when females are predicted to be rare, and the conditions favoring the spread of females are stringent (Charlesworth and Charlesworth 1978; Ganders, pers. comm.). The low frequency of females in *S. salicaria* suggests the possibility that similarly low female frequency in the ancestor of *S. salicaria* and *S. lydgatei* facilitated the reversal to hermaphroditism in *S. lydgatei.* In the *S. globosa* clade there is less evidence that ancestors of the hermaphroditic species had a low frequency of females. *Schiedea sarmentosa,* the sister taxon to the hermaphroditic species in several equally most parsimonious trees, has a frequency of females in the population of about 31%, considerably greater than the 12% value for *S. salicaria.* Presumably the frequency of females may have been lower when *S. hookeri* and *S. menziesii* diverged and the potential reversal to hermaphroditism occurred.

Is there other evidence supporting a reversal to hermaphroditism? Strong inbreeding depression in *S. salicaria* (Sakai et al. 1989) and moderately high selfing rates (Sakai and Weller, unpubl. data) indicate that selection is favoring the spread of females in populations of this species. Thus, even at this early stage in the evolution of gynodioecy, there is little indication that reversal to hermaphroditism would be likely. In *S. lydgatei,* high inbreeding depression and low selfing rates indicate that hermaphroditism is stable (Norman et al., in press), but this pattern would be expected whether hermaphroditism were the ancestral state or derived through a reversal from dimorphism. *Schiedea lydgatei* is typical of hermaphroditic species in possessing diffuse inflorescences and large nectaries, traits that would not be expected if the putative dimorphic ancestor of *S. lydgatei* had possessed a high frequency of females. If the common ancestor of *S. lydgatei* and *S. salicaria* were gynodioecious, however, and the frequency of females low, few modifications of the nectaries or inflorescence structure would be expected, and the reversal to hermaphroditism could occur without entailing reversals in any of the traits associated with dioecy.

Schiedea menziesii is unusual among hermaphroditic species in possessing a cylindrically compact inflorescence, a feature typically associated with wind pollination in general (Niklas 1985), and dimorphism in *Schiedea* (Weller et al., unpubl. data). If hermaphroditism evolved via a reversal from dimorphism, the presence of compact inflorescences may result from its dimorphic ancestry. In contrast, the large flowers, large nectaries, and low pollen-ovule ratios of *S. menziesii* are not likely to be characters retained from a dimorphic, wind pollinated ancestor. Further studies of *S. menziesii,* and other hermaphroditic species closely related to dimorphic species, might suggest whether wind pollination is strictly associated with the appearance of females in populations or is primarily related to shifts to dry habitats.

Although reversals to hermaphroditism may be common (Lloyd 1975b), there are few documented cases. In *Cotula* L., monoecy appears to have evolved from dioecy through selection for hermaphroditism in populations consisting solely of males (Lloyd 1975b). This is possible because of the tendency of males to produce a few female flowers. Lloyd's observations were based on comparative, though not phylogenetic information.

Breeding System Evolution. Phylogenetic information suggests only that species of *Schiedea* can invade dry habitats without the evolution of dimorphism, but the strong correlation between dry habitats and dimorphism, and the likelihood that these shifts have occurred more than once, indicate that dimorphism usually evolves in response to dry habitats. On the basis of the correlation between dimorphism and dry habitats, we have suggested that as *Schiedea* species colonized dry habitats, reduction or absence in pollinator service may have led to temporary increases in selfing rates and consequently the expression of inbreeding depression (Weller and Sakai 1990). Under these conditions, mutations leading to male sterility should spread in populations, as the progeny of females are strictly outcrossed, while the progeny of hermaphrodites may show varying degrees of selfing. Loss of pollinators or shifts to pollinators less efficient at cross pollination have been used to explain the evolution of dimorphism in *Nemophila menziesii* Hook. & Arn. (Ganders 1978) and *Hebe* Comm. ex Juss. (Delph 1990).

A second trend involving breeding systems is the evolution of self-fertilization. Facultative or obligate autogamy occurs among all *Alsinidendron* species in the *S. membranacea* clade and in *S. diffusa* in the *S. nuttallii* clade. These parallel trends toward adaptation to very wet habitats suggest a second causal connection between habitat shifts and breeding system evolution. Flowers of species inhabiting wet forests are pendent, with sepals that may protect pollen from damaging effects of wetting. Such an arrangement may also favor self-fertilization, because the anthers are located within the sepals and close to the stigmatic surfaces. Autogamy may also be an adaptation to low population density, because wet forest species are usually found as isolated individuals or in very small populations.

Selfing within *Schiedea* and *Alsinidendron* results in distinctive patterns of genetic variation that aid in the detection of phylogenetic relationships. Phylogenetic analysis of allozyme variation using FREQPARS (Swofford and Berlocher 1987) was successful in identifying the *Alsinidendron* and *S. nuttallii* clades (Weller et al. 1995). Both clades consist of selfing species and species occurring in small populations, factors that presumably have led to fixation of alleles in the ancestors of these lineages and the retention of these alleles during cladogenesis (Weller et al. 1995).

Radiation into ecologically extreme habitats appears to have led to the extraordinary diversity of breeding systems in the endemic Hawaiian Alsinoideae. Dimorphic breeding systems are favored in dry habitats, while shifts to very wet habitats promote the evolution of autogamy. Inclusion of reproductive characters had relatively little effect on these results, probably because vegetative traits are responsible for separating major clades of the Hawaiian Alsinoideae. In other groups the results of character mapping could depend very strongly on the choice of characters used in phylogenetic analysis. For the Hawaiian Alsinoideae, estimates of the number of independent transitions to dimorphism were very strongly dependent on the method of character coding and whether breeding system transitions were viewed as ordered. These latter results suggest that the process of character mapping is liable to yield very different results depending on views of how dimorphism evolves, and the time frame for evolution of dioecy relative to diversification in lineages. Interpretation of patterns of breeding system evolution will depend greatly on the topology of the phylogenetic trees, and in some cases resolution of breeding system questions will be limited, even when phylogenetic hypotheses are very robust.

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APPENDIX 1. Character list for *Schiedea* and *Alsinidendron*. The plesiomorphic state (0) is determined by the condition in the generalized outgroup. Multistate characters are unordered because of uncertainties about transitions between the character states.

1. *Presence of woody tissue.* 0 = Herbaceous. 1 = Suffrutescent. 2 = Woody. Woody tissue in Caryophyllaceae is secondarily derived (Carlquist, pers. comm.), but we have not ordered this character state because of uncertainties of the relationship of the herbaceous and suffrutescent character states.
2. *Stems persistent or deciduous.* 0 = Persistent stems. 1 = Deciduous stems. Most taxa 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*, but this matter is difficult to resolve through outgroup comparison to the *Minuartia* outgroups, because these species are herbaceous annuals.
3. *Habit.* 0 = Stems upright. 1 = Stems sprawling. 2 = Vine. *Schiedea* and *Alsinidendron* 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 foliage.

APPENDIX 1. Continued.

4. *Roots.* 0 = Fibrous roots. 1 = Swollen, fleshy roots.
5. *Stem succulence.* 0 = Slender, non-fleshy stems. 1 = Thick, somewhat fleshy stems. Woody as well as herbaceous species may possess fleshy, somewhat succulent stems.
6. *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.
7. *Leaf texture.* 0 = Leaves membranous. 1 = Leaves coriaceous. 2 = Leaves softly membranous.
8. *Leaf size.* 0 = Leaves of intermediate area. 1 = Leaf area large. Very large leaves atypical of continental Caryophyllaceae are characteristic of several Hawaiian Alsinoideae.
9. *Leaf succulence.* 0 = Leaves lacking succulence. 1 = Leaves succulent. Leaf succulence is not necessarily correlated with fleshy stems.
10. *Leaf symmetry.* 0 = Leaves symmetric. 1 = Leaves slightly asymmetric. 2 = Leaves falcate. 3 = Midvein of leaf off-center.
11. *Leaf apex.* 0 = Acute or acuminate. 1 = Long-attenuate.
12. *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 taxa. By comparison with most continental Caryophyllaceae this trait is considered derived, although *Minuartia* species most closely related to Hawaiian Alsinoideae have linear leaves with a single nerve.
13. *Increase in leaf venation.* 0 = 1- or 3-nerved; 1 = 5-nerved; 2 = 7-nerved. Several of the large-leaved *Schiedea* and *Alsinidendron* species have very large leaves with 5 or 7 major nerves, as opposed to the majority of species having 3 or fewer nerves.
14. *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.
15. *Pubescence on leaf margin.* 0 = No pubescence. 1 = Thin hairs present. 2 = Hooked hairs present.
16. *Leaf margin.* 0 = Margins entire. 1 = Leaf margins with minute, irregular teeth. 2 = Margins with minute serrations, especially in distal part. 3 = Margin serrate.
17. *Pubescence of leaf surface.* 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.

APPENDIX 1. Continued.

0.2–0.3 mm long, restricted to adaxial midrib and leaf base margin.

18. *Appearance of leaf surface.* 0 = Leaves not glaucous. 1 = Leaves slightly glaucous.
19. *Lateral inflorescence condensation* (breeding system). 0 = Inflorescences open, paniculate cymes. 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 more likely to disperse and capture pollen carried by wind than open, diffuse inflorescences. In *Schiedea,* the degree of inflorescence condensation is correlated with the frequency of females in populations (Weller and Sakai, unpubl. data).
20. *Inflorescence main axis condensation* (breeding system). 0 = Inflorescences open, paniculate cymes. 1 = Main axis of inflorescence somewhat vertically condensed. 2 = Main axis of inflorescence highly vertically condensed. 3 = Inflorescences globose due to nearly complete suppression of main axis. See comments for character 19.
21. *Suppression of inflorescence branches.* 0 = Main axis present. 1 = Main axis greatly suppressed, lateral branches expressed. 2 = Main axis moderately suppressed, lateral branches weakly expressed.
22. *Flower orientation.* 0 = Spreading, ascending, or upright. 1 = Pendent. Variation in this character is related to habitat, with pendent flowers typical of species occurring in mesic to wet forest. This floral orientation may help in preventing wetting of pollen.
23. *Inflorescence presentation.* 0 = Inflorescence upright. 1 = Inflorescences pendent. Species occurring in mesic or wet habitats produce pendent inflorescences, possibly a feature that may help in keeping pollen dry, as in the case of pedicel orientation.
24. *Inflorescence 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, the hairs ca. 0.15–0.3 mm long. 5 = Glandular, purple pubescence, the hairs ca. 0.3–0.6 mm long. 6 = Nonglandular, purple pubescence, the hairs 0.15–0.3 mm long. Inflorescence pubescence appears to vary independently of pubescence on vegetative portions of plants; thus, several species that have glabrous stems and leaves are densely glandular pubescent in the inflorescences.
25. *Sepal width.* 0 = Sepals <3 mm in width. 1 = Sepals >4 mm in width. This character is a measure of floral size differentiating larger-flowered *Alsinidendron* species from *Schiedea.*
26. *Calyx Form.* 0 = Calyx rotate to reflexed. 1 = Calyx campanulate, open. 2 = Calyx tightly closed or very slightly open at anthesis. This character differentiates *Schiedea,* with rotate to reflexed sepals, from *Alsinidendron,* which has campanulate calyces that are either open, or in the case of cleistogamous *A. trinerve,* usually remain tightly closed throughout the duration of anthesis.
27. *Sepal orientation.* 0 = spreading to somewhat reflexed. 1 = Ascending. 2 = Strongly reflexed.
28. *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. All *Schiedea* species have membranous, green or green tinged with purple sepals. In contrast, *Alsinidendron* species have petaloid, membranous or fleshy sepals.
29. *Sepal apex.* 0 = Obtuse to acute. 1 = Sepals attenuate to caudate.
30. *Sepal symmetry.* 0 = Symmetrical. 1 = Irregular.
31. *Sepal margin pubescence.* 0 = Glabrous, or with some hairs on proximal one half of sepal. 1 = Ciliate throughout.
32. *Nectary type.* 0 = Small mound. 1 = Nectary a well-developed hypodermic 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. Nectary type differentiates *Schiedea,* which has syringe-shaped nectary shafts, from *Alsinidendron,* which has flap-shaped nectary appendages that may be connate to varying degrees.
33. *Nectary shaft curvature* (*Schiedea* only): 0 = Straight, nectar collecting in drops at tip of shaft. 1 = Recurved and arching from surface of sepal, except for contact at tip, nectar deposited directly on the concave surface of the sepal.
34. *Nectar color.* 0 = Clear. 1 = Nectar appears black when large amounts accumulate. *Alsinidendron* species produce black nectar; all *Schiedea* species produce clear nectar.
35. *Ratio, staminal filament length to sepal length* (breeding system). 0 = ≤1. 1 = 1–1.9. 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. Selfing species of *Schiedea* and *Alsinidendron* have stamens that are shorter than the sepals or enclosed within them.
36. *Anther color.* 0 = Yellow. 1 = Reddish purple.
37. *Pollen color.* 0 = Yellow. 1 = Gray.
38. *Style number.* 0 = Usually 3, occasionally 4, rarely 5. 1 = 4–6, rarely 3 or 7. 2 = 5–11, rarely 4. Al-

APPENDIX 1. Continued.

though 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 nonoverlapping categories.

39. *Ovule number.* 0 = <100. 1 = >100. The number of ovules is generally well below 50 for *Schiedea* species, and greater than 100 for *Alsinidendron* and *S. verticillata*.
40. *Seed retention.* 0 = Seeds dispersed through open valves. 1 = Seeds retained within capsule, which gradually rots to release seeds, or in *S. diffusa*, seeds may germinate before dispersal occurs. Species with non-dispersing fruits occur in wet forests.

APPENDIX 1. Continued.

41. *Seed margin.* 0 = Cells along the seed margin not elongated. 1 = Cells along seed margin moderately to strongly elongated into papillae.
42. *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.
43. *Breeding system.* 0 = Hermaphroditic. 1 = Gynodioecious. 2 = Subdioecious. 3 = Dioecious. This character is used to differentiate all hermaphroditic breeding systems (which may vary from outcrossing to cleistogamous) from species with dimorphic breeding systems. Additional codings of this character were used in some computer runs.

APPENDIX 2. Data matrix of characters used for phylogenetic analysis of *Schiedea* and *Alsinidendron*. For polymorphic characters, a = 0 or 1 and b = 1 or 4. Missing data indicated by ?.

	Character state								
	12345	67891	11111	11112	22222	22223	33333	33334	444
Taxon		0	12345	67890	12345	67890	12345	67890	123
Outgroup	00000	00000	00000	00000	00000	00000	00000	00000	000
M. douglasii	00000	20000	01000	01000	00000	00000	00001	00000	000
M. howellii	00000	00000	10000	00000	00000	00000	00000	00000	000
A. lychnoides	00200	00100	00111	23000	21151	10100	02010	11211	000
A. obovatum	20001	11100	00112	31000	21011	10200	03010	11210	100
A. trinerve	20001	01100	00012	31000	11011	20200	03010	11200	100
A. viscosum	00200	00000	00001	23000	21151	10100	02010	11211	000
S. adamantis	20000	11000	01000	01002	00010	01000	01001	00000	111
S. amplexicaulis	?0??0	00000	01000	0a000	0??40	00000	11001	00000	000
S. apokremnos	20000	11000	01000	01003	00010	01000	01000	00000	001
S. attenuata	20000	01011	10000	01000	00010	00000	01101	00100	100
S. diffusa	00201	01101	01000	01000	01160	00011	11000	00001	000
S. globosa	10101	01011	10100	01003	00000	01000	01101	00100	002
S. haleakalensis	20000	21000	01000	01003	000b0	01000	01001	00000	113
S. helleri	20200	00100	00011	01000	0??40	00000	0100?	00000	000
S. hookeri	10100	02002	10000	00000	01100	00000	01001	00000	000
S. implexa	20001	01101	01000	01000	000b0	02010	01001	00000	000
S. kaalae	00001	11103	01000	01000	00010	02010	11001	00000	000
S. kealiae	20100	02002	10000	01002	00020	01000	01001	00000	002
S. ligustrina	20000	11000	01000	01002	00010	01000	01001	00000	113
S. lydgatei	20000	11000	00000	01100	00010	00000	01001	00000	110
S. mannii	20000	21001	11000	01002	00020	01000	01002	00000	002
S. membranacea	01011	00100	00211	12000	01010	00000	01002	00000	000
S. menziesii	20100	02002	10000	04010	00040	00000	01001	00000	000
S. nuttallii var. *nuttallii*	20001	01101	01000	01000	00010	02011	11001	00000	000
S. nuttallii var. *pauciflora*	20001	01101	01000	01000	00040	02011	11001	00000	000
S. pubescens	00200	01101	01000	01000	01160	02011	11001	00000	000
S. salicaria	20000	11000	00000	01101	00010	00000	01001	00000	111
S. sarmentosa	20100	02002	10000	02012	00000	01000	01001	00000	001
S. spergulina	20000	22002	11000	01002	00040	01000	01001	00000	003
S. stellarioides	10100	00000	11001	01000	00040	00000	01001	10000	000
S. verticillata	01011	01110	00210	01000	00030	00000	00110	00021	000
S. sp. nov.	20000	01101	00002	02000	00040	01011	01001	00000	??0