Evolution of Dioecy in Schiedea (Caryophyllaceae: Alsinoideae) in the Hawaiian Islands: Biogeographical and Ecological Factors

Author(s): Stephen G. Weller, Ann K. Sakai, Warren L. Wagner and Derral R. Herbst

Source: *Systematic Botany*, Apr. – Jun., 1990, Vol. 15, No. 2 (Apr. – Jun., 1990), pp. 266–276

Published by: American Society of Plant Taxonomists

Stable URL: https://www.jstor.org/stable/2419182

Evolution of Dioecy in *Schiedea* (Caryophyllaceae: Alsinoideae) in the Hawaiian Islands: Biogeographical and Ecological Factors

STEPHEN G. WELLER and ANN K. SAKAI

Department of Ecology and Evolutionary Biology,
University of California, Irvine, California 92717

WARREN L. WAGNER

Department of Botany, National Museum of Natural History,
Smithsonian Institution, Washington, D.C. 20560

DERRAL R. HERBST

U.S. Fish and Wildlife Service, Environmental Services,
Pacific Islands Office, P.O. Box 50167, Honolulu, Hawaii 96850

ABSTRACT. Breeding systems in *Schiedea* and *Alsinidendron* (Caryophyllaceae: Alsinoideae) were characterized in order to determine whether the dioecy that occurs in *Schiedea* evolved in situ in the Hawaiian Islands. The occurrence of hermaphroditism in 14 of the 22 species of *Schiedea*, as well as outgroup comparison, indicate that dioecy is a derived breeding system. Species diversity and endemism are greatest on the older Hawaiian Islands, suggesting that these islands were colonized first. Diclinous breeding systems are more common on the older islands, probably because of the greater length of time available for the evolutionary transition from hermaphroditism to dicliny. Dicliny appears to reduce the probability of inter-island colonizations; among extant species those with hermaphroditic breeding systems are more likely to occur on more than a single island. Based on distributional patterns, it appears likely that dicliny has evolved at least three and possibly six times in *Schiedea*. Species occurring in dry areas are likely to have evolved from wet or diverse mesic forest ancestors. As species of *Schiedea* shifted to dry habitats, the evolution of dicliny appears to have been favored, perhaps by loss of pollinators and subsequent increased selfing rates. Under such conditions, the expression of inbreeding depression may have favored unisexual individuals and the evolution of dioecy.

The distribution of reproductive systems on islands vs. mainland areas has been used to support arguments about selective factors promoting the evolution of dioecy. Carlquist and others have noted that the frequency of dioecy appears to be high on isolated island archipelagoes (Baker 1955, 1967; Carlquist 1966, 1974; Gilmartin 1968; Lewis 1942). Self-compatible hermaphrodites, however, are generally more likely to colonize remote islands successfully than dioecious or self-incompatible species (Baker 1955, 1967), a relationship known as Baker's Law (Stebbins 1957) or Baker's Rule (Baker 1967). One argument explaining the apparent high frequency of dioecy on islands suggests that self-compatible hermaphrodites preferentially colonize remote islands, but strong selection for outcrossing may promote the evolution of dioecy once colonization has occurred, depending on the level of inbreeding depression resulting from self-fertilization. In this view, dioecy is more likely to evolve than self-incompatibility due to the simpler genetic basis for dioecy (Baker 1967; Gilmartin 1968). Self-incompatibility does appear to be rare on islands except for the Hawaiian silverswords and their relatives (Carlquist 1966; Carr et al. 1986).

Baker and Cox (1984) have suggested that the frequency of dioecy on remote islands is similar to the frequency of dioecy in continental subtropical and tropical forests that are most likely to have provided colonists for the islands. This pattern might result from similar colonizing potential of dioecious and hermaphroditic species. Alternatively, if dioecy is more common on remote islands, the higher frequency may result from a correlation between dioecy and fleshy bird-dispersed fruits (Bawa 1980, 1982; Givnish 1980), which are more likely to be carried to remote islands (Carlquist 1974). In

266

either case, the higher frequency of dioecy on tropical and subtropical islands could be explained without resorting to arguments for the autochthonous evolution of dioecy, and the role of selection for outcrossing in the evolution of dioecy on islands would be minimal. Despite the significance attached to the frequency of dioecy on remote islands, there have been few detailed studies that have attempted to determine whether dioecy has evolved in situ on islands, or resulted from colonization of dioecious ancestors.

In this study we have characterized the breeding systems of *Schiedea* (Cham. & Schldl.) and *Alsinidendron* H. Mann, a clearly monophyletic assemblage in the Caryophyllaceae endemic to the Hawaiian Islands. Our objective is to determine whether dioecy in *Schiedea* evolved in situ in the Hawaiian Islands. Because these islands vary in age and are progressively older to the northwest, they provide the opportunity to test hypotheses about the relationship of island age and the potential for evolution of dioecy, the effect of breeding system on the likelihood of inter-island colonizations, and the number of potential transitions from hermaphroditism to dioecy that may have occurred.

The native Caryophyllaceae in Hawai'i include the endemic genera *Schiedea* and *Alsinidendron* (subfam. Alsinoideae), and the indigenous *Silene* L. (subfam. Silenoideae), which represent at least three separate introductions, one for *Schiedea* and *Alsinidendron* and at least two for *Silene* (Wagner et al., in press). The Caryophyllaceae are a largely temperate and boreal family, with few tropical representatives (Pax and Hoffmann 1934). The probable ancestor and source of the endemic Hawaiian Alsinoideae are unknown, although Carlquist (pers. comm.) believes that a New World origin is most likely. *Schiedea* and *Alsinidendron* were described as aberrant members of the "*Arenaria* complex" by McNeill (1962). Without giving any arguments he stated that these genera may well be allied to members of subfam. Paronychioideae. Recent taxonomic study of *Schiedea* and *Alsinidendron* (Wagner et al., in press) shows that they are clearly members of the Alsinoideae as evidenced by their exstipulate leaves, capsules splitting into as many valves as styles, distinct sepals, and absence of a strophiole on the seed. More precisely, these features align *Schiedea* and *Alsinidendron* with the *Arenaria* L. segregate ge-

nus *Minuartia* L. In particular, the morphology of nectaries and seeds of *Schiedea* and *Alsinidendron* point toward a possible alliance with *Minuartia howellii* (S. Watson) Mattf. of western North America. This species differs, however, in its possession of petals and annual habit. All species of *Arenaria* and *Minuartia* have hermaphroditic breeding systems.

Evidence for the monophyletic origin of *Schiedea* and *Alsinidendron* includes their close morphological resemblance (Wagner et al., in press) and interfertility (Weller and Sakai, unpubl. data). Moreover, they share at least two synapomorphies: 1) specialized nectary sheaths (although highly modified in *Alsinidendron*), and 2) the occurrence of the woody habit. The 22 species of *Schiedea* are diverse in morphology, breeding systems, and habitat, ranging from hermaphroditic vines inhabiting wet forests to diclinous dry forest shrubs and suffruticose herbs occurring on coastal cliffs. The four species of *Alsinidendron* are strictly hermaphroditic shrubs or vines that occur in diverse mesic or wet forest. A full appreciation of the evolutionary relationships of *Schiedea* and *Alsinidendron* awaits more detailed systematic studies.

A thorough understanding of the distribution of breeding systems in *Schiedea* allows the following hypotheses to be tested: 1) inter-island colonizations are most common among hermaphroditic species, because of the greater likelihood of establishment of self-fertile individuals following dispersal, and 2) diclinous (gynodioecious, subdioecious, and dioecious) breeding systems are most common on the older islands, where there has been sufficient time for the evolutionary transition from hermaphroditism. The distributional pattern predicted by the second hypothesis will be most likely if dicliny results in the reduced likelihood of inter-island colonizations. If diclinous species of *Schiedea* prove to be poor colonists, our information can be used to ascertain the most likely number of independent origins of dicliny within *Schiedea*. This distributional pattern would provide indirect support for the importance of outcrossing in the evolution of dioecy on islands. The role of habitat preference was investigated because preliminary information indicated that shifts from wet or mesic forest to dry forest have accompanied the evolution of dicliny in *Schiedea*. Several aspects of

pollination biology, including nectar production and mode of pollen transfer, were investigated because shifts in habitat preference may have resulted in changes in pollination syndromes.

MATERIALS AND METHODS

Breeding systems were assessed in the field or greenhouse for at least one population for each of 17 of the 18 extant species of *Schiedea*, and all three extant species of *Alsinidendron*. In field surveys of six species of *Schiedea*, individuals were permanently tagged and sex was scored annually for up to three years. Repeated scoring on individuals was used to detect potential sex lability. In the remaining 14 species of *Schiedea* and *Alsinidendron*, untagged individuals were scored for sex on a single occasion in the field, or seeds or cuttings were collected and propagated in the greenhouse where sex was recorded. Plants grown in the greenhouse were also used to verify field assessments of sex expression, although sex lability was more pronounced for the subdioecious species in the greenhouse than in the field; in those cases sex ratios from field surveys are reported. Herbarium specimens at AC, BISH, F, MO, PTBG, and US were used for tentative identification of the breeding systems of extinct species and other species for which no field or greenhouse information was available. Herbarium specimens were also used to confirm field and greenhouse observations; herbarium records alone were not sufficient to assess aspects of breeding systems such as the occurrence of low frequencies of females in some populations.

Observations of pollinators were made in the field for several species. For *Schiedea adamantis* St. John visits to females and hermaphrodites were recorded during two minute intervals at different times during the day. Pollinators were captured following observation periods, and identified to species. Pollinator observations of *S. globosa* H. Mann, *S. kealiae* Caum & Hosaka, and *S. salicaria* Hillebrand were not systematic, but were made throughout several seasons while collecting flowers and seeds for other purposes. Presencce of floral odor and nectar production was noted under greenhouse conditions. Pollen dispersal resulting from air movement in the greenhouse was noted during the course of crossing programs.

Habitats of *Schiedea* species observed in the field were characterized using the community types recognized in the *Manual of flowering plants of Hawai'i* (Wagner et al., in press). Community types could not be determined for the extinct species due to lack of habitat information on many older herbarium records. Island age was taken from Macdonald et al. (1983). For each island or portion of an island, the oldest age estimate is used. Although Moloka'i, Maui, and Lāna'i are of different ages, they are considered a single island in discussions of colonization events because of their former connection during periods of lowered ocean levels in the Pleistocene (Macdonald et al. 1983).

RESULTS

Breeding Systems. Among the 18 extant species of *Schiedea*, eight species have gynodioecious (females and hermaphrodites occur in populations), subdioecious (males, females, and a few hermaphrodites occur in populations), or dioecious breeding systems (table 1). Full or nearly full dioecy is found in *S. spergulina* A. Gray, a species occurring on cliffs on Kaua'i (table 2). On O'ahu, *S. ligustrina* Cham. & Schldl. and *S. mannii* St. John are dioecious and subdioecious, respectively, based on herbarium, greenhouse, and field observations (tables 1, 2).

Subdioecious breeding systems are found in *Schiedea globosa*, which occurs on dry coastal cliffs of O'ahu, and the Moloka'i-Maui-Lāna'i complex, and *S. kealiae*, which is endemic to the northern portion of the Wai'anae Mts. of O'ahu (table 1). *Schiedea globosa* is the only diclinous species occurring on more than a single Hawaiian island (table 3).

Gynodioecious breeding systems are found in *Schiedea apokremnos* St. John, a species occurring on cliffs of the Napali coast of Kaua'i, *S. adamantis*, a species restricted to a single population occurring in dry shrubland on the rim of Diamond Head Crater on O'ahu, and *S. salicaria*, which occurs in dry shrubland on ridges of the West Maui Mts. (tables 1, 2). The breeding system of *S. apokremnos* was determined through observations of herbarium specimens and plants in the greenhouse; further field studies would be useful. For *S. salicaria* the frequency of females over two years in two populations ranged from 12–13%; in *S. adamantis*, the frequency of females was 41% (table 2). *Schiedea salicaria* was

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

Species	Breeding system	Habit	Habitat	Distribution
Alsinidendron H. Mann				
lychnoides (Hillebrand) Sherff	hermaphroditic	vine	wet forest	Kaua'i
obovatum Sherff	hermaphroditic	subshrub	diverse mesic forest	O'ahu
trinerve H. Mann	hermaphroditic	subshrub	wet forest, diverse mesic forest	O'ahu
viscosum (H. Mann) Sherff	hermaphroditic	vine	wet forest, diverse mesic forest	Kaua'i (extinct)
Schiedea (Cham. & Schldl.)				
adamantis St. John	gynodioecious	shrub	dry shrubland	O'ahu
amplexicaulis H. Mann	hermaphroditic	?	?	Kaua'i (extinct)
apokremnos St. John	gynodioecious	shrub	cliffs	Kaua'i
diffusa A. Gray	hermaphroditic	vine	wet forest	Maui, Moloka'i, Hawai'i
globosa H. Mann	subdioecious	suffruticose herb	dry coastal cliffs	O'ahu, Maui, Moloka'i
haleakalensis Degener & Sherff	hermaphroditic	shrub	dry subalpine cliffs	Maui
helleri Sherff	hermaphroditic	vine	?	Kaua'i (extinct)
hookeri A. Gray	hermaphroditic	subshrub	diverse mesic forest	O'ahu, possibly Maui
implexa (Hillebrand) Sherff	hermaphroditic	subshrub	?	Maui (extinct)
kaalae Wawra	hermaphroditic	perennial herb	diverse mesic forest, wet forest	O'ahu
kealiae Caum & Hosaka	subdioecious	subshrub	dry forest	O'ahu
ligustrina Cham. & Schldl.	dioecious	shrub	dry and diverse mesic forest	O'ahu
lydgatei Hillebrand	hermaphroditic	shrub	diverse mesic or dry forest	Moloka'i
mannii St. John	subdioecious	shrub	dry ridges in diverse mesic forest	O'ahu
membranacea St. John	hermaphroditic	perennial herb	diverse mesic forest	Kaua'i
menziesii Hook.	hermaphroditic	shrub	dry forest and shrubland	Moloka'i, Lāna'i, and Maui
nuttallii Hook.	hermaphroditic	subshrub	diverse mesic forest	Kaua'i and O'ahu
pubescens Hillebrand	hermaphroditic	vine	diverse mesic forest	O'ahu, Moloka'i, Lāna'i, and Maui
salicaria Hillebrand	gynodioecious	shrub	dry shrubland	Maui
spergulina A. Gray	dioecious	shrub	dry cliffs, diverse mesic forest	Kaua'i
stellarioides H. Mann	hermaphroditic	subshrub	?	Kaua'i (extinct)
verticillata F. Brown	hermaphroditic	perennial herb	soil pockets and cracks in coastal cliffs	Nihoa

TABLE 2. Sex ratios in *Schiedea* species, based on field observations in populations of permanently marked individuals (*), or surveys of individuals in unmarked populations. Voucher numbers refer to Weller and Sakai collections; specimens are deposited in BISH and US.

Species and locality	Year	Sample size	Sex ratios (%) in field		
			Female	Male	Hermaphrodite
S. adamantis (*) 847	1988	211	41	0	59
S. globosa (*) 844	1984	63	43	52	5
(Makapu'u, Oahu)	1986	223	44	46	10
	1987	73	55	45	0
S. globosa (*) 839	1984	20	55	45	0
(Kahakuloa, W. Maui)	1986	215	48	50	2
	1987	40	53	42	5
S. globosa (*) 850	1986	118	48	49	3
(Waihee, W. Maui)	1987	22	68	32	0
S. hookeri (*) 794	1988	22	0	0	100
S. kealiae (*) 791	1986	49	49	49	2
S. lydgatei 870	1988	0	23	0	100
S. mannii (*) 857	1986	22	50	36	14
S. membranacea 864	1986	22	0	0	100
S. menziesii 849	1986	6	0	0	100
S. salicaria (*) 842	1986	129	12	0	88
(W. Maui, Site 1)	1987	104	13	0	87
S. salicaria (*) 853	1986	104	13	0	87
(W. Maui, Site 2)	1987	52	13	0	87
S. spergulina 863	1986	12	58	42	0

thought originally to be hermaphroditic; herbarium collections did not include any of the small number of females found in natural populations.

The remaining 10 extant species of *Schiedea* are hermaphroditic (table 1). *Schiedea verticillata* F. Brown occurs in two small populations on Nihoa, a small island 250 km northwest of Kaua'i, and the oldest Hawaiian island supporting species of *Schiedea*. Based on herbarium records and a single cultivated plant this species is strictly hermaphroditic (table 1). On Kaua'i, a population of *S. membranacea* St. John growing in diverse mesic forest of Mahanaloa and Ku'ia Valleys was hermaphroditic based on field and greenhouse observations (tables 1, 2). *Schiedea nuttallii* Hook., which occurs in diverse mesic forest on Kaua'i and O'ahu is also hermaphroditic, based on herbarium records and greenhouse observations of individuals sampled from the north rim of Makua Valley on O'ahu (table 1).

Three populations of *S. hookeri* A. Gray on O'ahu were hermaphroditic, based on field observations of a population growing in the Wai'anae Kai Forest Reserve (table 2), and greenhouse observations of individuals from two other populations. This species is confined to diverse mesic forest habitat on O'ahu; the vegetation type for the single collection from Maui is unknown. In fact, the single collection from Maui is fragmentary, and may represent *S. menziesii* Hook. rather than *S. hookeri*. *Schiedea pubescens* Hillebrand is a vine found in diverse mesic forest on O'ahu and the Maui-Moloka'i-Lāna'i complex. Scattered individuals observed in the field on O'ahu were hermaphroditic, as were individuals from other areas that were grown in the greenhouse. *Schiedea kaalae* Wawra is a rare species occurring in diverse mesic forest on O'ahu. Individuals from two localities in the Wai'anae Mts. (O'ahu), and a locality in the Ko'olau Mts. (O'ahu) were hermaphroditic (table 1).

Most species of *Schiedea* occurring on the Maui-Moloka'i-Lāna'i complex have hermaphroditic breeding systems (table 3). *Schiedea diffusa* A. Gray is a large vine occurring in rain forest. Hermaphroditic individuals were observed in upper Kipahulu Valley and at the end of the Waikamoi Flume (East Maui); all progeny raised from seeds of these individuals were also

TABLE 3.   Geographical distribution of breeding systems of species of *Schiedea* and *Alsinidendron*. Islands are arranged from northwest to southeast, which is also the direction of decreasing island age; age in millions of years shown below each island or island complex. Species in **boldface** occur on more than a single island.

	Nihoa 7.5	Kaua'i 5.7	O'ahu 2.6–3.8	Maui, Moloka'i Lāna'i 0.86–1.84	Hawai'i 0.5
Diclinous species:			**S. globosa**	**S. globosa**	
		S. apokremnos	S. adamantis	S. salicaria	
		S. spergulina	S. kealiae		
			S. ligustrina		
			S. mannii		
Hermaphroditic species:		**S. nuttallii**	**S. nuttallii**		
			S. hookeri	**S. hookeri**	
			S. pubescens	**S. pubescens**	
				S. diffusa	**S. diffusa**
	S. verticillata	S. amplexicaulis	S. kaalae	S. haleakalensis	
		S. helleri		S. implexa	
		S. membranacea		S. lydgatei	
		S. stellarioides		S. menziesii	
		A. lychnoides	A. obovatum		
		A. viscosum	A. trinerve		

hermaphroditic. *Schiedea diffusa* is the only species in the genus found on the island of Hawai'i, where it is rare. The dry subalpine cliffs of the interior of Haleakala Crater (East Maui) harbor *S. haleakalensis* Degener & Sherff (table 1). This species is presumed to be hermaphroditic, based on study of only a few herbarium collections (table 1), but the possibility remains that this species is gynodioecious (A. Medeiros, pers. comm.). *Schiedea menziesii*, which occurs in the dry shrubland of West Maui, appears to be hermaphroditic (table 1) on the basis of field, greenhouse, and herbarium studies (table 2). *Schiedea lydgatei* Hillebrand, a species restricted to mesic and dry forests on Moloka'i, is hermaphroditic, based on a field survey (table 2), and observations of herbarium collections.

Presumably extinct species include *Schiedea amplexicaulis* H. Mann, *S. helleri* Sherff, *S. implexa* (Hillebrand) Sherff, and *S. stellarioides* H. Mann. On the basis of herbarium records, all four species appear to be hermaphroditic (table 1). No attempt was made to characterize the habitats of these species, because the herbarium records are old and locality information is incomplete.

All three extant species of *Alsinidendron* have hermaphroditic reproductive systems, based on observations of plants cultivated in the greenhouse. The presumably extinct *Alsinidendron viscosum* (H. Mann) Sherff is likely to be hermaphroditic, based on herbarium records (table 1). Species of *Alsinidendron* occur in wet or diverse mesic forest.

Island Age and the Distribution of Schiedea and Alsinidendron. The highest diversity and greatest degree of single-island endemism of *Schiedea* and *Alsinidendron* occur on the older major Hawaiian Islands (table 3). Eight of the nine species occurring on Kaua'i (5.7 million years in age) are endemic only to that island. Seven of the 11 species occurring on O'ahu are endemic. All O'ahu species except *S. adamantis*, *S. globosa*, and *S. kaalae* are restricted to the Wai'anae Mts., which are about 3.8 million years in age in contrast to the Ko'olau Mts., which are only 2.6 million years in age. In general, plants of the Wai'anae Mts. show much greater affinity to the flora of Kaua'i than the rest of O'ahu. The joint occurrence of *Schiedea* and *Alsinidendron* is restricted to the two oldest islands, another indication that the greatest diversity of the endemic Alsinoideae is found on the older islands. Five of the nine species of *Schiedea* occurring on the Moloka'i-Maui-Lāna'i complex are endemic. The single species (*Schiedea diffusa*) occurring on Hawai'i is also found on Maui and Moloka'i.

Considering the overall distribution of reproductive systems, seven of the eight species with diclinous reproductive systems are found on the older islands of Kaua'i and O'ahu (table

TABLE 4. The relationship of habitat and reproductive systems in extant species of *Schiedea* and *Alsinidendron*.

Breeding system	Habitat	
	Diverse mesic forest, wet forest	Coastal and interior cliffs, dry shrubland
Hermaphroditic	9	4
Gynodioecious, subdioecious, or dioecious	0	8
$\chi^2 = 9.68$ $P < 0.005$		

3). Only one (*S. salicaria*) of the two diclinous species found on the Maui-Moloka'i-Lāna'i complex is endemic to this group of islands. Species occurring on two or more islands usually have hermaphroditic reproductive systems (table 3). *Schiedea nuttallii*, *S. hookeri*, *S. pubescens*, and *S. diffusa*, which all occur on more than a single major island, are hermaphroditic species found in wet forest or diverse mesic forest. Among the five species occurring on two or more islands, the only one with a diclinous breeding system is *S. globosa*, which occurs on coastal cliffs. For the genus as a whole, 36% have diclinous breeding systems. No statistical analysis of the association between breeding system and single-island endemism was attempted because of small sample size.

The eight extant species of *Schiedea* with diclinous reproductive systems are restricted to coastal and interior cliffs and dry shrubland (table 4). Six of the 10 extant hermaphroditic species of *Schiedea* are found in diverse mesic forest or wet forest; three of the remaining four hermaphroditic species occur in dry habitats (*S. lydgatei* may occur in mesic as well as dry forest). The three extant species of *Alsinidendron* are found in wet or diverse mesic forest. A contingency analysis using hermaphroditic vs. diclinous reproductive systems of both *Schiedea* and *Alsinidendron* and wet vs. dry habitats as the classifications (and classifying *S. lydgatei* as a dry forest inhabitant) was significant ($P < 0.05$; one cell of the contingency table had an expected value slightly less than four, table 4). Three of the four hermaphroditic species occurring in dry areas are found on Moloka'i and Maui, the youngest of the Hawaiian Islands where *Schiedea* species occur in appreciable numbers.

Pollination Biology. No native insects were observed on any *Schiedea* species. The most common visitor to *S. adamantis*, *S. globosa*, *S. kealiae*, and *S. salicaria* was *Simosyrphus grandicornis* (Macquart), an introduced syrphid fly. Occasional visits by *Allograpta exotica* (Wiedemann), another introduced syrphid species, were also noted. During timed, two minute intervals flies were more likely to approach rather than land on hermaphroditic flowers of *S. adamantis* (table 5A). No differences in the number of approaches or landings were noted during visits to female flowers (table 5A). Flies were equally likely to land on females and hermaphrodites (for two minute intervals, $\bar{x} = 0.56$, s.d. = 1.0, $N = 9$ for hermaphrodites; $\bar{x} = 0.67$, s.d. = 1.0, $N = 9$ for females; $t = 0.23$, d.f. = 16). When flies landed on flowers, the lengths of foraging bouts were not significantly different for females vs. hermaphrodites ($t = 0.10$, d.f. = 14, for hermaphrodites, $\bar{x} = 5.3$, s.d. = 3.5, $N = 10$; for females, $\bar{x} = 5.5$, s.d. = 4.9, $N = 6$). Flies were much more likely to land on than simply approach flowers of *Lipochaeta lobata* (Gaudich.) DC. var. *lobata* (Asteraceae, table 5A), a native species growing intermingled with *S. adamantis*. Foraging bouts on *L. lobata* were significantly longer than those on *S. adamantis* ($\chi^2 = 7.3$, d.f. = 2, $P < 0.05$; table 5B). Flies did not appear to be foraging for nectar on either species but may have been feeding on pollen.

Species of *Schiedea* produce small or unmeasurable quantities of nectar (table 5C). Two of the three extant species of *Alsinidendron* produce substantial quantities of nectar in the greenhouse (table 5C). The nectar produced by *A. lychnoides* (Hillebrand) Sherff from Kaua'i and *A. obovatum* Sherff from O'ahu is strongly hexose-dominant (I. Baker, pers. comm.). Sugar concentrations were 6.9–8.3% for *A. obovatum* and 12.7–13.6% for *A. lychnoides* (I. Baker, pers. comm.). Nectar constituents have not been analyzed for *A. trinerve* H. Mann. Flowers of the latter species remain nearly closed. All three species produced seed autogamously in the greenhouse, although not all flowers matured capsules. In contrast, autogamous seed production by hermaphroditic individuals of *Schiedea* is uncommon (Weller and Sakai, unpubl. data). *Schiedea adamantis*, *S. globosa*, and *S. kealiae* produce pollen that is easily dislodged from the anthers under greenhouse conditions.

Seed Dispersal. All species of *Schiedea* produce capsules that open along as many valves

TABLE 5.   Insect visitors and nectar production in *Schiedea* and *Alsinidendron*.

A. Visits and approaches of introduced Syrphidae to flowers of *Schiedea adamantis* and *Lipochaeta lobata*. Significance of differences in visits and approaches examined using the sign test.

Species and sex	No. of approaches Mean (s.d., N)	No. of landings Mean (s.d., N)	Prob.
S. adamantis hermaphrodites	2.33 (2.87, 9)	0.56 (1.01, 9)	<0.05
S. adamantis females	1.56 (2.01, 9)	0.67 (1.00, 9)	ns
L. lobata	0.60 (0.70, 10)	12.8 (10.0, 10)	<0.01

B. Length of foraging bouts on *S. adamantis* and *L. lobata*. Chi square analysis used to test for significance of difference in lengths of foraging bouts.

Species	Length of bout in seconds Mean (s.d., N)	Prob.
S. adamantis	5.4 (3.9, 16)	$P < 0.05$
L. lobata	15.2 (22.2, 36)	

C. Nectar production in *Alsinidendron* and *Schiedea*.

Species	Nectar production in μl Mean (s.d., N)
A. lychnoides	21.4 (8.4, 5)
A. obovatum	34.3 (22.9, 4)
A. trinerve	5.9 (1.1, 5)
S. adamantis	0.4 (0.4, 5)
S. globosa	not measurable
S. salicaria	1.0 (0.6, 6)
S. verticillata	4.7 (3.0, 7)

as styles when ripe. Seeds fall out of capsules or are shaken out in the wind, and seeds probably have limited dispersal. Dispersal mechanisms in *Alsinidendron* are more variable. The calyces of *A. lychnoides* and *A. viscosum* are papery and somewhat inflated at maturity. The calyces of *A. obovatum* and *A. trinerve* become thickened, fleshy, and purple in color at maturity. The agents of inter-island colonization are unknown, but the fleshy calyces of *A. obovatum* and *A. trinerve* may result in bird dispersal of seeds.

DISCUSSION

The occurrence of hermaphroditism in 14 of the 22 species of *Schiedea* and all four species of *Alsinidendron*, as well as outgroup comparison to *Arenaria* and *Minuartia*, suggest that dioecy is a derived breeding system in the Hawaiian Islands. If *Schiedea* and *Alsinidendron* originated from a common ancestor, as seems likely, the argument for the ancestral condition of hermaphroditism would be strengthened. The greater number of species on the older Hawaiian Islands (table 3), and the occurrence of hermaphroditic *S. verticillata* on the eroded, 7.5 mil-

lion-year-old island of Nihoa, indicates that the ancestor of *Schiedea* and *Alsinidendron* may have colonized the Hawaiian Islands well before the appearance of the current major islands. *Schiedea verticillata* is morphologically divergent from other species of *Schiedea* (Wagner et al., in press), and may represent the sole extant descendant of other, extinct lineages of *Schiedea* that inhabited islands in the Hawaiian chain that have for the most part eroded and disappeared.

The proportion of endemism is greatest on the older islands, dropping monotonically from the northwest to the southeast (table 3), where there may have been insufficient time following colonization of the younger islands for the evolution of more than a few endemic species. The youngest island of Hawai'i has no endemic species. The greater degree of endemism on the older islands is a further indication that the older islands were colonized first, and inter-island colonizations have proceeded from the older to the newer islands. Moreover, increasing morphological diversity is directly correlated with island age, and species with the fewest apomorphies such as *S. stellarioides* occur on Kaua'i (Wagner, unpubl. data). Habitat diversity as well as greater island age may in part

explain the greater diversity in the Alsinoideae on the older Hawaiian islands relative to the youngest island of Hawai'i. It would be more difficult, however, to explain the greater endemism on Kaua'i and O'ahu relative to Maui on this basis, because habitats appropriate for *Schiedea* are present on all three islands (Macdonald et al. 1983).

Island age and endemism are positively associated in the Hawaiian silverswords and their relatives (Carr 1985) as well as *Drosophila* (Carson et al. 1970). Among the silverswords and their allies, 85% of the species occurring on Kaua'i are endemic to that island; this proportion drops to 43% on the island of Hawai'i. Species diversity in the Hawaiian Madiinae is greatest on Kaua'i and Maui, and lowest on O'ahu. Overall, 82% of the species of silverswords and their relatives are single island endemics (considering Maui, Moloka'i, and Lāna'i as a single island complex, as we have for our calculations), a value very similar to the 81% figure for *Schiedea* and *Alsinidendron*. In contrast to the Madiinae and the endemic Alsinoideae, the baccate Hawaiian Lobelioids show the greatest diversity on the youngest islands, and may represent relatively recent additions to the Hawaiian flora (Lammers 1988). A similar situation is found in the Hawaiian species of *Geranium* L., where the center of diversity and presumably the site of the original colonization is Maui (Carlquist and Bissing 1976). In a highly dispersable group such as *Peperomia* Ruíz-Lopez & Pavón, however, single island endemism is only 65% (Wagner, unpubl. data), and interpreting patterns of colonization is more difficult.

Diclinous breeding systems are more common on the older Hawaiian Islands, reaching their greatest frequency (⅚, including only *Schiedea*) on O'ahu (table 3). Fully developed dioecy is restricted to *S. spergulina* on Kaua'i and *S. ligustrina* on O'ahu. Subdioecy is found in three additional species occurring on O'ahu and Maui. The remaining diclinous species on O'ahu is gynodioecious *S. adamantis*. The only endemic species on Maui showing dicliny is gynodioecious *S. salicaria*. The greater number of diclinous species on the older islands of Kaua'i and O'ahu, as well as the fuller expression of dioecy on those islands, is consistent with the more advanced evolutionary development of dioecy on these islands. On the younger islands, ap-

parently there has not been enough time for the evolution of full dioecy, as there are no endemic dioecious species on the Maui-Moloka'i-Lāna'i complex or the island of Hawai'i (table 3).

If diclinous and hermaphroditic species had similar colonizing potential, we would expect similar proportions of diclinous and hermaphroditic species on each of the islands colonized by *Schiedea*. Instead, it appears that hermaphroditism and self-compatibility favor inter-island colonizations of *Schiedea*, because hermaphroditic species of *Schiedea* are more likely than diclinous species to occur on more than a single island (table 3). The difference in colonizing ability cannot be explained on the basis of different dispersal mechanisms, because all species of *Schiedea* have dehiscent fruits and gravity or wind dispersed seeds.

Diclinous species also may be rarer on younger islands if the recent evolution of dicliny on the older islands has limited possibilities for dispersal of diclinous species to younger islands. The occurrence of gynodioecious species in geologically recent areas (*S. adamantis* on Diamond Head Crater and *S. salicaria* in the West Maui Mts.), however, indicates that dicliny may have evolved early in the history of the older islands, and diclinous species could have served as sources for colonization of the younger islands.

The high degree of single-island endemism found among the diclinous species suggests that these breeding systems may have evolved autochthonously on each of the islands. The sole exception to this pattern is *S. globosa*, a coastal species often occurring within meters of the ocean. Proximity to the water may provide greater opportunities for inter-island dispersal of *S. globosa* than for other species of *Schiedea* occurring in the interiors of islands. The most likely dispersal agents for this species are shore birds which frequent the islands. The occurrence of seemingly divergent dispersal systems in *Schiedea* and *Alsinidendron* appears to have had little effect on the potential for inter-island dispersal, despite the possibility that *Alsinidendron* species with fleshy calyces are adapted for bird dispersal.

The distribution of dicliny in *Schiedea* provides evidence for the independent evolution of dioecy on at least three separate occasions, once each on Kaua'i, O'ahu, and Maui. This is

a minimal estimate; given the dissimilarity between the two diclinous Kaua'i species, and among three of the five O'ahu species (Wagner et al., in press), it seems likely that dicliny has evolved a total of six times within the genus, including gynodioecious *S. salicaria* on Maui. The appearance of the initial stage of dioecy in *S. adamantis* and *S. salicaria*, which occur on different islands, is further evidence for the independent evolution of dioecy in *Schiedea*.

Further resolution of the number of independent times dicliny has evolved in *Schiedea* is contingent on understanding the phylogeny of the genus. A number of diclinous species appear to be closely related. *Schiedea ligustrina*, *S. mannii*, and *S. adamantis*, all on O'ahu, seem to share a common ancestor, based primarily on condensed inflorescences and vegetative features. These species, in turn, are similar to and perhaps directly related to *S. apokremnos* and *S. salicaria*. If this hypothesis is correct, dicliny may has evolved as few as once or twice in this alliance, and the total number of transitions from hermaphroditism to dicliny would drop to four for the genus as a whole. Because of the possibility that the evolution of dicliny and of morphological characters used to separate species have occurred in parallel in response to shifts to arid environments, independent estimates of species relationships are essential for determining the number of times dicliny has evolved in *Schiedea*.

The restriction of diclinous species to dry habitats indicates that ecological factors may be instrumental in the evolution of dioecy (table 4). Although not all species occurring in dry areas have diclinous breeding systems, three of the four exceptions to the generalization are found on Moloka'i and Maui, the youngest of the Hawaiian Islands where *Schiedea* species occur in appreciable numbers. The only endemic diclinous species occurring on Moloka'i or Maui is *S. salicaria*, which shows the lowest frequency of unisexual individuals of any diclinous species of *Schiedea*. Although dry habitats appear to favor the evolution of dioecy, there may not have been sufficient time for the development of dicliny on these relatively young islands. Scarcity of dry cliffs and similar habitats suitable for *Schiedea* is unlikely to have limited the evolution of dicliny on any of the islands with the possible exception of the island of Hawai'i.

Species occurring in dry areas are likely to have evolved from wet forest or diverse mesic forest ancestors. This assumption is based on the predominance in dry areas of species of *Schiedea* with the most extensively developed woody tissue (table 1), a character state which is undoubtedly secondarily derived in the Caryophyllaceae. As species of *Schiedea* shifted to dry habitats, the evolution of dioecy appears to have been favored, perhaps by loss of pollinators. At present, little is known about the pollination biology of *Alsinidendron* or *Schiedea*. The abundant production of hexose-dominant nectar by some species of *Alsinidendron* is circumstantial evidence for animal pollination, although there have been no attempts to observe pollinators in natural habitats. Several species of *Schiedea* produce nectar, and in some cases, a strong, unpleasant odor, but no native pollinators have been observed visiting any *Schiedea* (table 5).

The lack of any observations of native pollinators on *Schiedea* may result from the severe disruption of the native insect fauna, including the extinction of over half of the native Diptera (W. Gagné, pers. comm.). A second possibility is the occurrence of wind pollination among several species occurring in dry, often very windy habitats. In the greenhouse, these species produce abundant, easily dislodged pollen. Inflorescences are compact, and carried above the foliage, suggesting wind pollination (Niklas 1985). In contrast, the species occurring in wet habitats have large, open inflorescences, which are pendant in the species that produce vines. These areas are not typically windy and there is little reason to suspect wind pollination.

A shift to wind pollination as species of *Schiedea* invaded dry areas may have resulted from absence or reduction in the number of insect pollinators in windy open environments. Increased rates of selfing may be one consequence of either loss of pollinators or the evolution of wind pollination. Depending on the degree of inbreeding depression present in these populations, unisexual individuals would be favored by the joint occurrence of high selfing rates and high inbreeding depression (Charlesworth and Charlesworth 1978). Substantial levels of inbreeding depression have been documented in gynodioecious *S. salicaria* and subdioecious *S. globosa* (Sakai et al. 1989); if enforced selfing occurs in drier habitats the predominance of

dicliny in these areas may be explained, assuming that ancestors of extant, diclinous species experienced similar levels of inbreeding depression.

LITERATURE CITED

BAKER, H. G. 1955. Self-compatibility and establishment after "long-distance" dispersal. Evolution 9:347–349.

————. 1967. Support for Baker's Law—As a rule. Evolution 21:853–856.

———— and P. A. COX. 1984. Further thoughts on dioecism and islands. Ann. Missouri Bot. Gard. 71:244–253.

BAWA, K. S. 1980. Evolution of dioecy in flowering plants. Annual Rev. Ecol. Syst. 11:15–39.

————. 1982. Outcrossing and the incidence of dioecism in island floras. Amer. Naturalist 119:866–871.

CARLQUIST, S. 1966. The biota of long-distance dispersal. IV. Genetic systems in the floras of oceanic islands. Evolution 20:433–455.

————. 1974. *Island biology*. New York: Columbia Univ. Press.

———— and D. R. BISSING. 1976. Leaf anatomy of Hawaiian geraniums in relation to ecology and taxonomy. Biotropica 8:248–249.

CARR, G. D. 1985. Monograph of the Hawaiian Madiinae (Asteraceae): *Argyroxiphium, Dubautia*, and *Wilkesia*. Allertonia 4:1–123.

————, E. A. POWELL, and D. W. KYHOS. 1986. Self-incompatibility in the Hawaiian Madiinae (Compositae): An exception to Baker's rule. Evolution 40:430–434.

CARSON, H. L., D. E. HARDY, H. T. SPIETH, and W. S. STONE. 1970. The evolutionary biology of the Hawaiian Drosophilidae. Pp. 437–543 in *Essays in evolution and genetics in honor of Theodosius Dobzhansky*, eds. M. K. Hecht and W. C. Steere. New York: Appleton-Century-Crofts.

CHARLESWORTH, B. and D. CHARLESWORTH. 1978. A model for the evolution of dioecy and gynodioecy. Amer. Naturalist 112:975–997.

GILMARTIN, A. J. 1968. Baker's law and dioecism in the Hawaiian flora: An apparent contradiction. Pacific Sci. 22:285–292.

GIVNISH, T. J. 1980. Ecological constraints on the evolution of breeding systems in seed plants: Dioecy and dispersal in gymnosperms. Evolution 34:959–972.

LAMMERS, T. G. 1988. Evolution of the endemic Hawaiian genus *Clermontia* Gaudich. (Campanulaceae: Lobelioideae). P. 188 in Botanical Society of America (Abstracts—1988).

LEWIS, D. 1942. The evolution of sex in flowering plants. Biol. Rev. Cambridge Philos. Soc. 17:46–67.

MACDONALD, G. A., A. T. ABBOTT, and F. L. PETERSON. 1983. *Volcanoes in the sea*, 2nd ed. Honolulu: Univ. Hawaii Press.

MCNEILL, J. 1962. Taxonomic studies in the Alsinoideae: I. Generic and infra-generic groups. Notes Roy. Bot. Gard. Edinburgh 24:79–155.

NIKLAS, K. J. 1985. The aerodynamics of wind pollination. Bot. Rev. 51:328–386.

PAX, F. and K. HOFFMANN. 1934. Caryophyllaceae. Pp. 275–364 in *Die Natürlichen Pflanzenfamilien* 2nd ed., Bd. 16c, eds. A. Engler and K. Prantl. Leipzig: Wilhelm Engelmann.

SAKAI, A. K., K. KAROLY, and S. G. WELLER. 1989. Inbreeding depression in *Schiedea globosa* and *S. salicaria* (Caryophyllaceae), subdioecious and gynodioecious Hawaiian species. Amer. J. Bot. 76: 437–444.

STEBBINS, G. L. 1957. Self fertilization and population variability in the higher plants. Amer. Naturalist 91:337–354.

WAGNER, W. L., D. R. HERBST, and S. H. SOHMER. In press. *Manual of the flowering plants of Hawai'i*. Honolulu: Univ. Hawaii Press and Bishop Museum (Special publication 83).