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ORIGINS OF DIOECY IN THE HAWAIIAN FLORA¹

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Abstract. Because of its presumed high levels of dioecy (separate male and female plants), study of the native Hawaiian angiosperm flora has been important in development of many hypotheses about conditions favoring the evolution of dioecy. The importance of ecological correlates with dioecy has proven difficult to assess, however, because of lack of data on the origins of dioecy in the Hawaiian Islands. Clearly, these correlations are of greater interest in taxa where dioecy evolved in the Hawaiian Islands (autochthonous evolution of dioecy) than in taxa that are the result of dioecious colonists with subsequent speciation in the Hawaiian Islands. Because the Hawaiian flora is small and extremely isolated, colonists can be identified and their breeding systems hypothesized, thus allowing inferences on the origins of dioecy. Using current taxonomic information, the incidence of dioecy in native Hawaiian angiosperm species is 14.7%, lower than previous estimates, but still the highest of any known flora worldwide. Ten percent of the colonists were sexually dimorphic (dioecious, gynodioecious, polygamodioecious, and subdioecious), and over half (55.2%) of current dimorphic species are in lineages arising from dimorphic colonists, showing that dimorphism is high in part because colonists were dimorphic. Autochthonous evolution of dimorphism occurred in at least 12 lineages (e.g., hermaphroditic colonists of *Bidens* (Asteraceae), the Hawaiian Alsinoideae (Caryophyllaceae), and *Hedyotis* (Rubiaceae) led to species-rich lineages that include many dimorphic species). One-third (31.8%) of current dimorphic species are in lineages arising from monomorphic colonists. Dioecy in the Hawaiian Islands is a result of both dimorphic colonists as well as evolution of dioecy in Hawaiian lineages from hermaphroditic colonists. The high incidence of dimorphism is not because dimorphic colonists evolved more species per colonist than monomorphic colonists. Detailed studies of individual lineages are critical to elucidate causal factors in the evolution of dioecy.

Key words: *autochthonous evolution; breeding systems; colonists; dimorphism; dioecy; endemism; evolution of plant breeding systems; gynodioecy; Hawaiian Islands; islands; long-distance dispersal of plants; sexual dimorphism of flowers.*

INTRODUCTION

The evolution of separate male and female plants in populations (dioecy) has occurred independently in many floras and in diverse taxa, and its repeated evolution has been of particular interest. The majority of flowering plant species are hermaphroditic, and worldwide only $\approx 4\%$ of flowering plant species are dioecious (Yampolsky and Yampolsky 1922). The incidence of dioecy varies considerably in different regional floras (summarized in Steiner 1988), including values as low

as 2.8% in California (Fox 1985) to 12–13% of species in New Zealand (Godley 1979; 18% of genera, Lloyd 1985; also see Webb and Kelley 1993). The Hawaiian flora is of particular interest for studies of dioecy. Gilmartin (1968, using Hillebrand's flora written in 1888) reported only 5% dioecy in the Hawaiian flora, but more recently Carlquist (1974), using data from a variety of sources including his own investigations, reported that 27.7% of the native Hawaiian angiosperm species and varieties were dioecious, a figure twice as high as that for the next highest flora of New Zealand.

Hypotheses on selective forces promoting the evolution of dioecy include those that suggest that dioecy has evolved as a mechanism to avoid inbreeding depression as well as those that suggest that resource allocation, sexual selection, and ecological factors are important (reviewed in Bawa 1980, Thomson and Bru-

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net 1990). Because of its high frequency of dioecy, the Hawaiian flora has been cited as critical evidence in support of some theories on factors promoting the evolution of dioecy (Baker 1967, Carlquist 1974, Bawa 1980, Thomson and Barrett 1981, Baker and Cox 1984). Carlquist (1966, 1974) suggested that the advantages of outcrossing with dioecy were sufficiently high in insular habitats that they outweighed the disadvantages of needing individuals of both sexes to establish populations after long distance dispersal. As a consequence, Carlquist suggested that the high incidence of dioecy in Hawaii was in part a result of dioecious colonists. In contrast, Baker (1967) contended that self-compatible hermaphrodites were much more likely to colonize after long-distance dispersal because a single propagule was sufficient to start a population (Baker's law). He suggested that the high incidence of dioecy in the Hawaiian Islands was the result of autochthonous (in situ) evolution of dioecy (Baker 1967), although in later work (Baker and Cox 1984) he suggested several mechanisms that allow establishment by dioecious colonists. Thomson and Barrett (1981) suggested that the high levels of autochthonous evolution of dioecy in the Hawaiian Islands support the importance of outcrossing as a factor. Bawa (1980) used the Hawaiian flora to support his hypothesis of a correlation of dioecy with pollination by small generalist insects and with fruit dispersal by birds.

Analysis of the Hawaiian flora can offer special insights into the evolution of dioecy because the great isolation of the archipelago (≈ 4000 km from the nearest large mass of North America) has limited the number of angiosperm colonists. Previous estimates suggest that only ≈ 272 – 282 long-distance colonists gave rise to the current native flowering plants (Fosberg 1948, Wagner et al. 1990, Wagner 1991). Phylogenetic considerations that have presented problems in analyses of other floras (Donoghue 1989) can be addressed by analysis of presumed colonists as well as extant species. With hypotheses about the colonists' breeding systems and lineages descended from these colonists, in lieu of more detailed phylogenies for most taxa, it is possible to distinguish current dioecious species that arose from dioecious colonists from those species where dioecy evolved autochthonously (in situ) within the Hawaiian Islands.

We analyzed current taxonomic information (Wagner et al. 1990; see also Sakai et al. 1995) on the breeding systems of known (extant and recently extinct) native species of the Hawaiian Islands as well as the breeding systems and lineages of colonists of the Hawaiian Islands with two objectives. The first objective was to report breeding system distributions of the Hawaiian flora, in light of recent systematic work, including better knowledge of breeding systems. The second objective was to distinguish whether the high incidence of dioecy in the Hawaiian flora results from (1) high rates of successful colonization by dioecious colonists (of

TABLE 1. Comparisons of breeding system distributions from Carlquist (1974) and Wagner et al. (1990). Letters represent the sex of the flowers (M = male, F = female, H = hermaphroditic) and parentheses indicate the types of flowers found on the same plant. Ellipses indicate categories that were not included in Carlquist's (1974) analysis; N/A = not applicable.

Breeding system	Species		Genera	
	1974	1990	1974	1990
Dioecy (M) (F)	27.7	14.7	15.3	11.4
Gynodioecy (F) (H)	2.6	3.8	2.7	1.3
Subdioecy (M) (F) (rare H)	...	0.6	...	0
Polygamodioecy (M, rare H)				
(F, rare H)	0.4	1.6	0.9	1.8
Hermaphroditism (H)	56.9	62.4	64.4	62.0
Monoecy (M, F)	5.0	7.6	7.2	10.9
Andromonoecy (M, H)	2.5	4.5	4.1	5.2
Gynomonoecy (F, H)	4.4	3.9	3.6	2.6
Polygamomonoecy (M, F, rare H)	0.5	0.1	1.8	0
Dimorphism	30.7	20.7	18.9	14.4
Monomorphism	69.3*	78.7	81.1	80.8
Unknown	...	0.5	...	0.4
Mixed genera (dimorphic and monomorphic spp.)	N/A	N/A	...	4.4
<i>N</i>	1490*	971	222	229

* Values were calculated using the sum of individual sexual conditions (Carlquist, 1974: Table 13.1) rather than his dimorphic total (based on $N = 1449$) or the data given ($N = 1430$). Note that Carlquist's (1974) totals include species plus varieties; our 1990 data include species but do not count infraspecific taxa.

endemic and indigenous species), (2) greater numbers of species in dioecious lineages than hermaphroditic lineages, or (3) evolution of dioecy in situ from hermaphroditic colonists. In the latter case, comparison of the ecological conditions associated with dioecious and hermaphroditic species may be especially relevant for ascertaining causal factors in the evolution of dioecy (see also Sakai et al. 1995).

MATERIALS AND METHODS

Information was taken from the *Manual of the Flowering Plants of Hawai'i* (Wagner et al. 1990; referred to hereafter as the *Manual*) with some updating (see Appendix; see also Sakai et al. 1995). Terminology of breeding systems follows that given in the *Manual*. Following Lloyd (1980), we also use the term sexually dimorphic to collectively refer to taxa with dioecious, subdioecious, polygamodioecious, or gynodioecious systems; monomorphic refers to taxa with hermaphroditic, monoecious, andromonoecious, gynomonoecious, or polygamomonoecious systems (see Table 1 for definitions). Breeding systems were generally taken as those listed in the *Manual*. If data on breeding systems in the *Manual* were ambiguous, specimens (BISH, US) were re-examined or authorities for those taxa were consulted when possible (*Schiedea*, A. Sakai and S. Weller; *Wikstroemia*, S. Mayer; *Bidens*, F. Ganders). Five species were omitted from analyses because their breeding systems were unknown; *Poa* also was ex-

cluded from the generic-level analysis because the breeding systems of the native species are not known. Most genera were easily classified with respect to breeding system because species within them all had the same breeding system or at least were all monomorphic or all dimorphic. Genera comprised of species with both dimorphic and monomorphic breeding systems were classified as mixed.

Native species included endemic species (found naturally only in the Hawaiian Islands), indigenous species (found naturally in the Hawaiian Islands as well as elsewhere), and also those species that were noted in the *Manual* as questionably naturalized (i.e., possibly native or questionably introduced by colonizing Polynesians). Each indigenous species was counted as one colonization, even for species such as *Scaevola sericea* that have colonized the islands on multiple occasions. Presumed original colonists were derived from consideration of two previous estimates of colonization events in the Hawaiian archipelago (Fosberg 1948, Carlquist 1974), and from phylogenetic relationships reported in the *Manual* by over 50 contributors, including more recent information communicated to us by them. Colonists for taxa without a specialist were inferred from morphological studies conducted (by W. L. Wagner and D. R. Herbst) in preparation of the *Manual* and from consultation of taxonomic works with more general discussions of relationships. Explicit phylogenetic discussion of Hawaiian angiosperm lineages has begun to emerge only recently (Baldwin et al. 1990; Wagner and Funk 1995; Weller et al. 1995; F. Ganders, unpublished manuscript).

In the absence of more specific information, we assigned the breeding system of the colonist based on genera or species related to the endemic Hawaiian taxa; in most cases, however, the closest sister taxon of the Hawaiian species is unknown. For nonendemic genera, we used the general conditions present in extra-Hawaiian species, unless more specific relationships within the genus could be determined. In more difficult cases, the breeding system of the colonist was assigned only a more general designation (e.g., monomorphic or dimorphic). Ten colonists had unknown breeding systems and were omitted from analyses of breeding systems, thus making our estimate of dimorphism in the colonists a conservative one.

Because the data set used in this paper is not available in any source in its entirety, a comprehensive list of the presumed colonists and their resulting Hawaiian lineages is listed in the Appendix. The Appendix also includes additional attributes for each presumed colonist that relate to ecological correlates of breeding systems in the Hawaiian flora (Sakai et al. 1995). Presumed colonists with breeding systems that were difficult to determine or where our determination differed from earlier works (e.g., Carlquist 1974, Bawa 1982; others in Appendix) are discussed in more detail in the notes to the Appendix.

RESULTS

Of the 971 native species, 14.7% are dioecious and 20.7% are dimorphic, proportions that are the highest of any flora studied, but far lower than Carlquist's earlier estimates that included infraspecific taxa (1974: Chapter 13; Table 1). Our results differ because we did not use infraspecific taxa (there was no variation in breeding system at that level), and because recent taxonomic changes (Wagner et al. 1990) reduced the total number of both hermaphroditic and dioecious taxa, but disproportionately affected dimorphic taxa, especially infraspecific taxa in Loganiaceae, Pittosporaceae, Rubiaceae, and Rutaceae. Changes also result in small part to more detailed studies of breeding systems. At the generic level, 11.4% are dioecious; 14.4% are dimorphic. Strictly dioecious genera have a mean of 3.04 species/genus ($N = 24$, $SD = 4.03$); strictly hermaphroditic genera have a mean of 3.65 species/genus ($N = 142$, $SD = 6.27$).

The 971 native Hawaiian species are the result of speciation from 291 presumed colonists, a number slightly higher than that of previous estimates (Fosberg 1948, Carlquist 1974, Wagner et al. 1990, Wagner 1991). Six colonists gave rise to more than one genus, and in 45 genera, the species are the result of more than one colonization. Two-thirds of the colonists (194/291) are represented by only a single species. Of the 119 indigenous colonists, all but 10 are represented by only one species. From those 10 colonists [*Lepidium* (Brassicaceae), *Gahnia* and *Mariscus* (Cyperaceae), *Eugenia* (Myrtaceae), *Boerhavia* and *Pisonia* (Nyctaginaceae), *Peperomia* (Piperaceae), *Portulaca* (Portulacaceae), and 2 colonists of *Korthalsella* (Viscaceae)], indigenous species are presumed to have given rise directly to endemic species and both indigenous and endemic species are extant.

At the other extreme, one colonist in the Campanulaceae has given rise to four genera (*Clermontia*, *Cyanea*, *Delissea*, and *Rollandia*) with a total of 91 species (>9% of the total flora) and the one colonist of *Stenogyne*, *Phyllostegia* and *Haplostachys* (Lamiaceae) has resulted in 53 species. Other species-rich lineages include those for *Melicope* (47 species, Rutaceae), the silversword complex (28 species of *Dubautia*, *Argyroxiphium*, and *Wilkesia*, Asteraceae), the Hawaiian Alsinoideae (*Schiedea* and *Alsinidendron*, 26 species, Caryophyllaceae), *Hedyotis* (20 species, Rubiaceae), *Myrsine* (20 species, Myrsinaceae), and one colonist of *Peperomia* (20 species, Piperaceae).

Dimorphic colonists resulting in only dimorphic Hawaiian species account for 10% (29/291) of the colonists, suggesting that dimorphism is high in part because colonists were dimorphic (Table 2). Over half (111/201) of current dimorphic species arose from dimorphic colonists. Monomorphic colonists resulting in only monomorphic species constitute 82% (238/291) of the colonists. Of the colonists leading to endemic

TABLE 2. Breeding systems (BS) of colonists and of the species that evolved from those colonists. M = monomorphic, D = dimorphic, U = unknown.

BS of Colonist	Number of colonists/species	BS of species in lineage (colonists/species)			
		Only monomorphic	Only dimorphic	Mixed M and D spp.	Unknown
Monomorphic	250/805	238/694M	7/31D	5/33D, 47M	...
Dimorphic	31/114	1/1M	29/66D	1/45D, 2M	...
Unknown	10/52	3/6M	2/15D	3/11D, 15M, 1U	2/4U
Total	291/971	242/701M	38/112D	9/89D, 64M, 1U	2/4U

species, 11% (19/173 colonists) were dimorphic and gave rise to only dimorphic species. Of the indigenous colonists, 8% (10/119 colonists) were dimorphic. Colonists that gave rise to endemic species were no more likely than indigenous colonists to be dimorphic ($N = 285$, $\bar{X} = 0.64$, $df = 1$, $P = 0.43$).

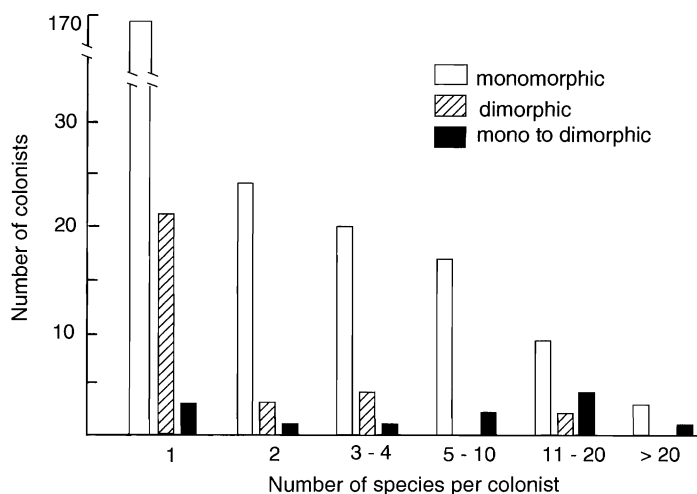
Although 10% of the colonists were dimorphic, 20.7% of current species are dimorphic, indicating that either dimorphic lineages have led to more species/colonist, or that dimorphism has arisen autochthonously (in situ). Our analysis suggests that the latter is true; approximately one-third (31.8%) of current dimorphic species arose from monomorphic colonists. At least 12 monomorphic colonists evolved dimorphism autochthonously [the Hawaiian Alsinoideae (*Schiedea*), *Bidens*, *Broussaisia*, *Cyrtandra*, *Hedyotis*, *Neraudia*, *Perrottetia*, 2 *Psychotria* (Rubiaceae) colonists, *Psydrax*, *Santalum*, and *Wikstroemia* (Table 3)]. In *Neraudia*, dioecy appears to have evolved from monoecy. In the two *Psychotria* colonists, separate sexes prob-

nously (in situ). Our analysis suggests that the latter is true; approximately one-third (31.8%) of current dimorphic species arose from monomorphic colonists. At least 12 monomorphic colonists evolved dimorphism autochthonously [the Hawaiian Alsinoideae (*Schiedea*), *Bidens*, *Broussaisia*, *Cyrtandra*, *Hedyotis*, *Neraudia*, *Perrottetia*, 2 *Psychotria* (Rubiaceae) colonists, *Psydrax*, *Santalum*, and *Wikstroemia* (Table 3)]. In *Neraudia*, dioecy appears to have evolved from monoecy. In the two *Psychotria* colonists, separate sexes prob-

TABLE 3. Colonists giving rise to dissimilar breeding systems in current taxa. Breeding systems (BS): am = andromonoecy, d = dioecy, gd = gynodioecy, gm = gynomonoecy, h = hermaphroditism, m = monoecy, p = polygamy, pd = polygamodioecy, pm = polygamomonoecy, sd = subdioecy, u = unknown.

Family	Colonist	Colonist BS	Species BS
A) Colonists resulting in both dimorphic and monomorphic systems			
Asteraceae	<i>Bidens</i>	h	9 gd, 10 h
Caryophyllaceae	<i>Schiedea/Alsinidendron</i>	h	18 h, 3 gd, 3 sd, 2 d
Gesneriaceae	<i>Cyrtandra</i> (one of four colonists)	h	12 h, 1 gd
Myrsinaceae	<i>Myrsine</i>	u	12 h, 1 gd, 1 sd, 5 d, 1 u
Rubiaceae	<i>Hedyotis</i>	h	14 gd, 6 h
Rutaceae	<i>Melicope</i>	d	1 h, 1 am, 7 pd, 38 d
Santalaceae	<i>Exocarpus</i>	u	2 h, 1 p
Santalaceae	<i>Santalum</i> (one of two colonists)	h	1 h, 1 d
Urticaceae	<i>Pipturus</i>	u	1 m, 2 gd, 1 d
B) Monomorphic or unknown breeding system of colonist resulting in dimorphic systems			
Amaranthaceae	<i>Charpentiera</i>	u	5 gd
Celastraceae	<i>Perrottetia</i>	h	1 pd
Hydrangeaceae	<i>Broussaisia</i>	h	1 d
Pittosporaceae	<i>Pittosporum</i>	u	9 d, 1 p
Rubiaceae	<i>Psychotria</i> (2 of 2 colonists)	h	8 d; 3 d
Rubiaceae	<i>Psydrax</i>	h	1 gd
Thymelaeaceae	<i>Wikstroemia</i>	h	10 d, 2 sd
Urticaceae	<i>Neraudia</i>	m	5 d
C) Monomorphic or unknown breeding system of colonist resulting in different monomorphic systems			
Asteraceae	<i>Dubautia/Argyroxiphium/Wilkesia</i>	h	5 gm, 23 h
Asteraceae	<i>Remya</i>	gm	3 m
Asteraceae	<i>Tetramolopium</i>	m	5 gm, 6 m
Gunneraceae	<i>Gunnera</i>	pm	1 pm, 1 h
Poaceae	<i>Isachne</i> (two of two colonists)	h	1 gm; 1 gm
Polygonaceae	<i>Rumex</i>	u	3 m
Rhamnaceae	<i>Gouania</i> (two of two colonists)	u	1 m, 1 am; 1 am
Sapindaceae	<i>Alectryon</i>	pm	1 am
D) Dimorphic breeding system of colonist resulting in different dimorphic systems			
Aquifoliaceae	<i>Ilex</i>	pd	1 d
Loganiaceae	<i>Labordia</i>	gd	15 d
Rubiaceae	<i>Bobea</i>	pd	3 pd, 1 d
E) Dimorphic breeding system of colonist resulting in monomorphic system			
Anacardiaceae	<i>Rhus</i>	pd	1 h

FIG. 1. Number of species per colonist. Monomorphic = monomorphic colonists giving rise to only monomorphic species. Dimorphic = dimorphic colonists giving rise to only dimorphic species. Mono to dimorphic = monomorphic colonists with autochthonous evolution of dimorphism. Seven colonists with unknown breeding systems (with 2, 3, 3, 4, 5, 10, and 20 species/colonist) are omitted from this histogram, as are two dimorphic colonists with evolution of monomorphism (with 1 and 47 species).



ably were derived from heterostyly. In the other nine colonists, separation of the sexes appears to have evolved from hermaphroditism or in lineages with hermaphroditism and gynodioecy. All 12 of these lineages (with the exception of *Psydrax*) contain only endemic species. In five other cases, dimorphism may have evolved from monomorphism, but we have conservatively listed the breeding system of the colonist as unknown (Table 3).

Other colonists had changes in breeding system within monomorphic or within dimorphic systems (Table 3). In two cases [*Rhus* (Anacardiaceae) and *Melicope* (Rutaceae)], evolution in the opposite direction apparently has occurred, and hermaphroditism has arisen from a presumably functionally dimorphic ancestor.

Lineage size was similar for dimorphic colonists that gave rise to only dimorphic species ($\bar{X} = 2.3$ dimorphic species/colonist) and monomorphic colonists that gave rise to only monomorphic species ($\bar{X} = 2.9$ monomorphic species/colonist; Fig. 1), but the 12 monomorphic colonists that gave rise to dimorphic species were significantly different in lineage size ($\bar{X} = 9.25$ species/colonist, Fig. 1; $N = 267$, $df = 2$, $\bar{X} = 11.0$, $P = 0.004$, Kruskal-Wallis test). A number of colonists with unknown breeding systems could affect this latter distribution if they were to be included. Because of this, we did not try to distinguish why the lineages that evolved dimorphism were apparently larger. Lineages that evolved dimorphism may be larger because factors associated with speciation may also favor the evolution of dimorphism in species-rich lineages. Alternatively, each species may have a similar probability of evolving dimorphism regardless of lineage size, and thus larger lineages will tend to have more autochthonous evolution of dimorphism, simply because they have more species.

DISCUSSION

Our work shows that the incidence of dioecy in the Hawaiian Islands is not as high as originally estimated,

but remains the highest of any flora where similar data are available. The percentage of dioecious species is slightly higher than that of New Zealand (12–13%), another insular flora with some tropical elements (Godley 1979, Webb and Kelly 1993). The high incidence of dioecy in the Hawaiian Islands is the result of a number of dimorphic colonists as well as autochthonous evolution of dimorphism within the archipelago. Of the 291 presumed colonists, 10% were dimorphic, considerably higher than the worldwide average for dioecy of $\approx 4\%$ (Yampolsky and Yampolsky 1922). Over half of the native Hawaiian flora has Malesian, Austral, or Pacific affinity (Fosberg 1948; W. L. Wagner, unpublished data), and this higher percentage of dioecy may reflect a higher incidence of dimorphism in the source floras, although these areas (especially Malesia) are not well studied. Other sources include pantropical elements as well as temperate areas (North America, Australia, New Zealand) and a few boreal elements (Wagner et al. 1990). Further studies of breeding systems (particularly in tropical source floras) are needed to determine if dioecious colonists are over-represented relative to the source flora, or conversely, if hermaphroditic taxa are disproportionately represented as colonists, as predicted by Baker's (1967) law. The number of dimorphic colonists to the Hawaiian Islands, however, suggests that dioecy has not been a severely limiting factor in dispersal and colonization of the Hawaiian Islands. Lloyd (1985) also found that most of the dimorphism in the New Zealand flora resulted from dimorphic colonists; only 5 of the 72 dimorphic genera were the result of autochthonous evolution of dimorphism.

The high incidence of dimorphism in the Hawaiian Islands has not resulted from different rates of speciation of dimorphic and monomorphic colonists as suggested by Bawa (1982), at least as measured by the current number of species per colonist. Two-thirds of the colonizations resulted in only one species, but in

a few notable cases (Asteraceae, Campanulaceae, Caryophyllaceae, Lamiaceae, Myrsinaceae, Rubiaceae, and Rutaceae), colonizations have led to a remarkable number and diversity of species, for both dimorphic and monomorphic colonists. Carlquist (1974: 526) reported that the average number of species per genus was twice as great in dioecious genera as the flora at large; in contrast, we found similar numbers of species per genus for monomorphic and dimorphic genera, with apparently more species per colonist in lineages where dimorphism has arisen in situ. This difference related in part to taxonomic differences in the data sets used. Further studies are needed to elucidate whether evolution of dimorphism has been associated with changes in addition to breeding system that resulted in greater speciation in these lineages than in lineages of colonists that did not evolve dimorphism.

Although over half of the dimorphism in current species is the result of dimorphic colonists, selective pressures have presumably been sufficient to promote a diversity of pathways to dimorphism in the Hawaiian flora, and about one-third of the dimorphic species occur in lineages from a monomorphic colonist. Dioecious and dimorphic breeding systems apparently have been derived from heterostyly, from monoecy, or most commonly directly from hermaphroditism or from hermaphroditism via gynodioecy. In two cases, hermaphroditism apparently arose from a functionally dimorphic ancestor. Further study of the presumed colonist, phylogeny, and breeding system of these taxa (*Rhus*, *Melicope*) is needed. In general, the assumption has been that evolution of breeding systems away from dioecy is extremely difficult, and very few cases of this have been documented [e.g., androdioecy from dioecy in *Datisca* (Datisceae), Rieseberg et al. 1992]. Hermaphroditic plants in some Hawaiian populations of *Wikstroemia* (Thymeliaceae) may be secondarily derived as hybrids from individuals with different modes of control of dioecy or from the breakdown of dioecy (Mayer and Charlesworth 1992). Within the Hawaiian Alsinoideae, some species may have secondarily evolved hermaphroditism from gynodioecious ancestors (Wagner et al. 1995, Weller et al. 1995). Strong self-incompatibility in the Hawaiian flora is known only in one lineage of the Hawaiian Madiinae (Compositae; Carr et al. 1986). In general, the evolution of dioecy and the apparent lack of self-incompatibility in the endemic flora support the notion that dioecy may be easier to evolve than self-incompatibility (Thomson and Barrett 1981, Charlesworth 1985), although few Hawaiian taxa have been investigated for the occurrence of self-incompatibility.

The limited number of lineages comprising the Hawaiian angiosperm flora also creates a unique opportunity for detailed studies within lineages of the number of independent origins of dioecy and associated traits (e.g., Sakai et al. 1995, Wagner et al. 1995, Weller et al. 1995). Better knowledge of phylogenetic patterns

and further ecological studies, particularly within those groups evolving dioecy autochthonously, are needed to determine causality.

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APPENDIX

Presumed colonists of the native Hawaiian flora. Colonist = genera resulting from one colonist. If more than one genus resulted, genera are separated by a slash (/). If a genus resulted from more than one colonist, each colonist is listed separately and the generic name is followed by a number to identify each successful colonization; no. spp. = number of species derived from that colonist; indig. = endemic, indigenous, questionably naturalized, questionably Polynesian; colonist lineage BS = breeding system of that colonist's lineage: di = both colonist and current species dimorphic, mo = both colonist and current species monomorphic, sdm = colonist dimorphic with some current species monomorphic, smd = colonist monomorphic with some dimorphic current species, u = breeding system of colonist unknown; colonist BS = presumed breeding system of colonist; species breeding system = breeding system of current species with number of species indicated if variable within lineage, where breeding systems are am = andromonoecy, d = dioecy, gd = gynodioecy, gm = gynomonoecy, h = hermaphroditism, m = monoecy, pm = polygamomonoecy, pd = polygamodioecy, sd = subdioecy, u = unknown; presumed pollinator = presumed pollinator of colonist; presumed original long distance dispersal mode: internal bird dispersal (bi); external bird dispersal includes bm = bird (mud), bb = bird (barbs), bv = bird (viscid); abiotic dispersal includes dr (oceanic drift-rare), df (oceanic drift-frequent) and by air (a); fleshy fruit = fruits fleshy (f) or dry (d).

Family	Colonist	No. spp.	Indig.	Colonist lineage BS	Colonist BS	Species breeding system	Presumed pollinator	Presumed dispersal	Fleshy fruit
Agavaceae	<i>Pleomele</i>	6	end	mo	h	h	insect	bi	f
Aizoaceae	<i>Sesuvium</i>	1	ind	mo	h	h	insect	df	d
Amaranthaceae	<i>Achyranthes</i>	3	end	mo	h	h	wind	bb	d
Amaranthaceae	<i>Amaranthus</i>	1	end	mo	m	m	wind	bi/bm	d
Amaranthaceae	* <i>Charpentiera</i>	5	end	u	u	gd	wind	bi/bm	d
Amaranthaceae	<i>Nototrichium</i>	2	end	mo	h	h	wind	bb	d
Anacardiaceae	* <i>Rhus</i>	1	end	sdm	pd	h	insect	bi	f
Apiaceae	<i>Daucus</i>	1	nat?	mo	h	h	insect	bb	d
Apiaceae	<i>Hydrocotyle</i>	1	nat?	mo	h	h	insect	bi	d
Apiaceae	<i>Peucedanum</i>	1	end	mo	am	am	insect	dr	d
Apiaceae	<i>Sanicula</i>	4	end	mo	am	am	insect	bb	d
Apiaceae	<i>Spermolepis</i>	1	end	mo	h	h	insect	bb	d
Apocynaceae	<i>Alyxia</i>	1	end	mo	h	h	insect	bi	f
Apocynaceae	<i>Ochrosia</i>	4	end	mo	h	h	insect	dr	f
Apocynaceae	<i>Pteralyxia</i>	2	end	mo	h	h	insect	dr	f
Apocynaceae	<i>Rauvolfia</i>	1	end	mo	h	h	insect	bi	f
Aquifoliaceae	* <i>Ilex</i>	1	ind	di	pd	d	insect	bi	f
Araliaceae	<i>Cheirodendron</i>	5	end	mo	am	am	insect	bi	f
Araliaceae	<i>Reynoldsia</i>	1	end	mo	h	h	insect	bi	f
Araliaceae	<i>Tetraplasandra/Munro</i>	7	end	mo	h	h	insect	bi	f
Arecaceae	<i>Pritchardia</i>	19	end	mo	h	h	insect	bi/dr	f
Asteraceae	<i>Adenostemma</i>	1	ind	mo	h	h	insect	bv	d
Asteraceae	<i>Artemisia</i>	3	end	mo	gm	gm	wind	bv	d
Asteraceae	<i>Bidens</i>	19	end	smd	h	9 gd, 10 h	insect	bb	d
Asteraceae	<i>Dubaut/Argyro/Wilks</i>	28	end	mo	h	5 gm, 23 h	insect	bv/bb	d
Asteraceae	<i>Gnaphalium</i>	1	end	mo	gm	gm	insect	bb	d
Asteraceae	<i>Hesperomannia</i>	3	end	mo	h	h	bird	bb	d
Asteraceae	<i>Lagenifera</i>	3	end	mo	gm	gm	insect	bv	d
Asteraceae	* <i>Lipochaeta1</i>	13	end	mo	gm	gm	insect	bb	d
Asteraceae	* <i>Lipochaeta2</i>	6	end	mo	gm	gm	insect	bb	d
Asteraceae	<i>Remya</i>	3	end	mo	gm	m	insect	bb	d
Asteraceae	<i>Tetramolopium</i>	11	end	mo	m	5 gm, 6 m	insect	bb	d
Begoniaceae	<i>Hillebrandia</i>	1	end	mo	m	m	insect	bm	d
Boraginaceae	<i>Heliotropium1</i>	1	ind	mo	h	h	insect	df	d
Boraginaceae	<i>Heliotropium2</i>	1	ind	mo	h	h	insect	df	d
Brassicaceae	<i>Lepidium</i>	3	both	mo	h	h	insect	bv	d
Brassicaceae	<i>Rorippa (Nasturtium)</i>	1	ind	mo	h	h	insect	bv/bi	d
Campanulaceae	<i>Brighamia</i>	2	end	mo	h	h	bird	bi	d
Campanulaceae	<i>Clerm/Cyan/Dell/Rolla</i>	91	end	mo	h	h	bird	bi/bv	f
Campanulaceae	<i>Lobelia1/Trematolobe</i>	8	end	mo	h	h	bird	bm	d
Campanulaceae	<i>Lobelia2</i>	9	end	mo	h	h	bird	bm	d
Capparaceae	<i>Capparis</i>	1	end	mo	h	h	insect	dr	f
Capparaceae	<i>Cleome</i>	1	ind?	mo	h	h	insect	bm/bi	d
Caryophyllaceae	<i>Alsiniidend/Schiedea</i>	26	end	smd	h	18 h, 2 d, 3 gd, 3 sd	insect	bm	d
Caryophyllaceae	<i>Silene1</i>	2	end	mo	h	h	insect	bi/bm	d
Caryophyllaceae	<i>Silene2</i>	5	end	mo	h	h	insect	bi/bm	d
Celastraceae	* <i>Perrottetia</i>	1	end	smd	h	pd	insect	bi	f
Chenopodiaceae	<i>Chenopodium</i>	1	end	mo	h	h	wind	bm	d
Convolvulaceae	<i>Bonamia</i>	1	end	mo	h	h	insect	bv/dr	d
Convolvulaceae	<i>Cressa</i>	1	ind	mo	h	h	insect	df	d
Convolvulaceae	<i>Ipomoea1</i>	1	ind	mo	h	h	insect	df	d
Convolvulaceae	<i>Ipomoea2</i>	1	ind	mo	h	h	insect	df	d

APPENDIX. Continued.

Family	Colonist	No. spp.	Indig.	Colo-nist line-age BS	Colo-nist BS	Species breeding system	Presumed pollinator	Pre-sumed dis-persal	Fle-shy fruit
Convolvulaceae	<i>Ipomoea3</i>	1	ind	mo	h	h	insect	df	d
Convolvulaceae	<i>Ipomoea4</i>	1	ind?	mo	h	h	insect	df	d
Convolvulaceae	<i>Ipomoea5</i>	1	nat?	mo	h	h	insect	df	d
Convolvulaceae	<i>Ipomoea6</i>	1	end	mo	h	h	insect	df	d
Convolvulaceae	<i>Jacquemontia</i>	1	ind	mo	h	h	insect	dr	d
Convolvulaceae	<i>Merremia</i>	1	nat?	mo	h	h	insect	dr	d
Cucurbitaceae	<i>Sicyos</i>	14	end	mo	m	m	insect	bb	d
Cuscutaceae	<i>Cuscuta</i>	1	end	mo	h	h	insect	bi	d
Cyperaceae	<i>Bolboschoenus</i>	1	ind	mo	h	h	wind	bm	d
Cyperaceae	<i>Carex1</i>	1	ind	mo	m	m	wind	bm/bi	d
Cyperaceae	<i>Carex2</i>	1	ind	mo	m	m	wind	bm/bi	d
Cyperaceae	<i>Carex3</i>	1	ind	mo	m	m	wind	bm/bi	d
Cyperaceae	<i>Carex4</i>	1	ind?	mo	m	m	wind	bm/bi	d
Cyperaceae	<i>Carex5</i>	1	end	mo	m	m	wind	bm/bi	d
Cyperaceae	<i>Carex6</i>	1	end	mo	m	m	wind	bm/bi	d
Cyperaceae	<i>Carex7</i>	2	end	mo	m	m	wind	bm/bi	d
Cyperaceae	<i>Cladium</i>	1	ind	mo	am	am	wind	bi	f
Cyperaceae	<i>Cyperus1</i>	1	end	mo	h	h	wind	bi/bm	d
Cyperaceae	<i>Cyperus2</i>	1	ind	mo	h	h	wind	bi/bm	d
Cyperaceae	<i>Eleocharis1</i>	1	ind	mo	h	h	wind	bm	d
Cyperaceae	<i>Eleocharis2</i>	1	ind?	mo	h	h	wind	bm	d
Cyperaceae	<i>Fimbristylis1</i>	1	end	mo	h	h	wind	bm/bi	d
Cyperaceae	<i>Fimbristylis2</i>	1	ind	mo	h	h	wind	bm/bi	d
Cyperaceae	<i>Fimbristylis3</i>	1	ind	mo	h	h	wind	bm/bi	d
Cyperaceae	<i>Gahnia1</i>	1	ind	mo	am	am	wind	bi/bm	d
Cyperaceae	<i>Gahnia2</i>	2	both	mo	am	am	wind	bi/bm	d
Cyperaceae	<i>Gahnia3</i>	1	end	mo	am	am	wind	bi/bm	d
Cyperaceae	<i>Machaerina1</i>	1	ind	mo	am	am	wind	bi	d
Cyperaceae	<i>Machaerina2</i>	1	ind	mo	am	am	wind	bi	d
Cyperaceae	<i>Mariscus1</i>	4	end	mo	h	h	wind	bi/bm	d
Cyperaceae	<i>Mariscus2</i>	2	both	mo	h	h	wind	bi	d
Cyperaceae	<i>Mariscus3</i>	3	end	mo	h	h	wind	bi/bm	d
Cyperaceae	<i>Mariscus4</i>	1	ind	mo	h	h	wind	bi	d
Cyperaceae	<i>Morelotia</i>	1	end	mo	h	h	wind	bi/bm	d
Cyperaceae	<i>Oreobolus</i>	1	end	mo	h	h	wind	bb	d
Cyperaceae	<i>Pycreus</i>	1	ind	mo	h	h	wind	bi	d
Cyperaceae	<i>Rhynchospora1</i>	1	ind	mo	am	am	wind	bi/bb	d
Cyperaceae	<i>Rhynchospora2</i>	1	ind	mo	am	am	wind	bi/bb	d
Cyperaceae	<i>Rhynchospora3</i>	1	ind	mo	am	am	wind	bi/bb	d
Cyperaceae	<i>Schoenoplectus1</i>	1	ind	mo	h	h	wind	bm/bi	d
Cyperaceae	<i>Schoenoplectus2</i>	1	ind	mo	h	h	wind	bm/bi	d
Cyperaceae	<i>Scleria</i>	1	ind	mo	m	m	wind	bm	d
Cyperaceae	<i>Torulinium</i>	1	ind	mo	h	h	wind	bm/bi	d
Cyperaceae	<i>Uncinia1</i>	1	ind	mo	m	m	wind	bb	d
Cyperaceae	<i>Uncinia2</i>	1	ind	mo	m	m	wind	bb	d
Droseraceae	<i>Drosera</i>	1	ind	mo	h	h	insect	bm	d
Ebenaceae	<i>Diospyros</i>	2	end	di	d	d	insect	bi	d
Elaeocarpaceae	<i>Elaeocarpus</i>	1	end	mo	h	h	insect	bi	f
Epacridaceae	<i>Styphelia</i>	1	ind	di	pd	pd	insect	bi	f
Ericaceae	<i>Vaccinium</i>	3	end	mo	h	h	insect/self	bi	f
Euphorbiaceae	<i>Antidesma</i>	2	end	di	d	d	insect	bi	f
Euphorbiaceae	<i>Chamaesyce</i>	15	end	mo	m	m	insect	bi	d
Euphorbiaceae	<i>Claoxylon</i>	1	end	mo	m	m	wind	bi	d
Euphorbiaceae	<i>Euphorbia</i>	1	end	di	d	d	insect	bi	d
Euphorbiaceae	<i>Flueggea</i>	1	end	di	d	d	insect	bi	f
Euphorbiaceae	<i>Phyllanthus</i>	1	end	mo	m	m	insect	bi	d
Fabaceae	<i>Acacia</i>	1	end	mo	am	am	insect	dr	d
Fabaceae	<i>Caesalpinia1</i>	1	end	mo	h	h	bird	df	d
Fabaceae	<i>Caesalpinia2</i>	1	ind	mo	m	m	insect	df	d
Fabaceae	<i>Caesalpinia3</i>	1	nat?	mo	m	m	insect	df	d
Fabaceae	<i>Canavalia</i>	6	end	mo	h	h	insect	df/dr	d
Fabaceae	<i>Dioclea</i>	1	nat?	mo	h	h	insect	dr	d
Fabaceae	<i>Entada</i>	1	ind?	mo	am	am	insect	df	d
Fabaceae	<i>Erythrina</i>	1	end	mo	h	h	bird	dr/bi	d
Fabaceae	<i>Mucuna1</i>	1	ind	mo	h	h	insect	df	d
Fabaceae	<i>Mucuna2</i>	1	ind	mo	h	h	insect	df	d

APPENDIX. Continued.

Family	Colonist	No. spp.	Indig.	Colo- nist line- age BS	Colo- nist BS	Species breeding system	Presumed pollinator	Pre- sumed dis- persal	Fle- shy fruit
Fabaceae	<i>Senna</i>	1	ind	mo	h	h	insect	bi	d
Fabaceae	<i>Sesbania</i>	1	end	mo	h	h	insect	dr	d
Fabaceae	<i>Sophora</i>	1	end	mo	h	h	insect	dr	d
Fabaceae	<i>Strongylodon</i>	1	end	mo	h	h	bird	df	d
Fabaceae	<i>Vicia</i>	1	end	mo	h	h	insect	bi	d
Fabaceae	<i>Vigna1</i>	1	end	mo	h	h	insect	df	d
Fabaceae	<i>Vigna2</i>	1	ind	mo	h	h	insect	df	d
Fabaceae	<i>Vigna3</i>	1	ind	mo	h	h	insect	df	d
Flacourtiaceae	<i>Xylosma</i>	2	end	di	d	d	insect	bi	f
Gentianaceae	<i>Centaurium</i>	1	end	mo	h	h	insect	bm/bi	d
Geraniaceae	<i>Geranium</i>	6	end	mo	h	h	insect	bb	d
Gesneriaceae	<i>Cyrtandra1</i>	13	end	smd	h	12 h, 1 gd	insect	bm	f
Gesneriaceae	<i>Cyrtandra2</i>	13	end	mo	h	h	insect	bm	f
Gesneriaceae	<i>Cyrtandra3</i>	14	end	mo	h	h	insect	bm	f
Gesneriaceae	<i>Cyrtandra4</i>	13	end	mo	h	h	insect	bm	f
Goodeniaceae	<i>Scaevola1</i>	1	ind	mo	h	h	insect/self	df	f
Goodeniaceae	<i>Scaevola2</i>	1	end	mo	h	h	bird	bi/dr	f
Goodeniaceae	<i>Scaevola3</i>	7	end	mo	h	h	insect/self	bi	f
Gunneraceae	* <i>Gunnera</i>	2	end	mo	pm	1 h, 1 pm	insect	bi	f
Hydrangeaceae	* <i>Broussaisia</i>	1	end	smd	h	d	insect/bird	bi	f
Hydrocharitaceae	<i>Halophila</i>	1	end	di	d	d	water	df	f
Hydrophyllaceae	<i>Nama</i>	1	end	mo	h	h	insect	bb	d
Iridaceae	<i>Sisyrinchium</i>	1	end	mo	h	h	insect	bm	d
Joinvilleaceae	<i>Joinvillea</i>	1	ind	mo	h	h	wind	bi	f
Juncaceae	<i>Luzula</i>	1	end	mo	h	h	wind	bm	d
Lamiaceae	<i>Lepechinia</i>	1	ind?	mo	h	h	insect	bv	d
Lamiaceae	<i>Pelctranthus</i>	1	ind	mo	h	h	insect	bb	d
Lamiaceae	<i>Stenog/Phyllol/Haplos</i>	53	end	mo	h	h	insect	bi	f
Lauraceae	<i>Cassytha</i>	1	ind	mo	h	h	insect	df	f
Lauraceae	<i>Cryptocarya</i>	1	end	mo	h	h	insect	bi	f
Lemnaceae	<i>Lemna</i>	1	nat?	mo	m	m	wind	bm	d
Lemnaceae	<i>Spirodela</i>	1	nat?	mo	m	m	wind	bm	d
Liliaceae	<i>Astelia</i>	3	end	di	d	d	insect	bi/bv	f
Liliaceae	<i>Dianella</i>	1	ind	mo	h	h	insect	bi	f
Loganiaceae	* <i>Labordia</i>	15	end	di	gd	d	insect	bi	d
Lythraceae	<i>Lythrum</i>	1	ind?	mo	h	h	insect	bi	d
Malvaceae	<i>Abutilon1</i>	1	ind?	mo	h	h	insect	df	d
Malvaceae	<i>Abutilon2</i>	2	end	mo	h	h	insect	df	d
Malvaceae	<i>Abutilon3</i>	1	end	mo	h	h	insect	df	d
Malvaceae	<i>Gossypium</i>	1	end	mo	h	h	insect	dr	d
Malvaceae	<i>Hibiscadelphus</i>	6	end	mo	h	h	insect	dr	d
Malvaceae	<i>Hibiscus1</i>	1	ind	mo	h	h	insect	dr	d
Malvaceae	<i>Hibiscus2</i>	1	ind?	mo	h	h	insect	dr	d
Malvaceae	<i>Hibiscus3</i>	1	end	mo	h	h	insect	dr	d
Malvaceae	<i>Hibiscus4</i>	2	end	mo	h	h	insect	dr	d
Malvaceae	<i>Hibiscus5</i>	2	end	mo	h	h	insect	dr	d
Malvaceae	<i>Kokia</i>	4	end	mo	h	h	insect	dr	d
Malvaceae	<i>Sida</i>	1	ind	mo	h	h	insect	df	d
Malvaceae	<i>Thespesia</i>	1	ind?	mo	h	h	insect	df	d
Menispermaceae	<i>Cocculus</i>	1	ind	di	d	d	insect	bi	f
Moraceae	<i>Streblus</i>	1	ind	di	d	d	wind	bi	f
Myoporaceae	<i>Myoporum</i>	1	ind	mo	h	h	insect	bi	f
Myrsinaceae	<i>Embelia</i>	1	end	di	d	d	insect	bi	f
Myrsinaceae	* <i>Myrsine</i>	20	end	u	u	12 h, 1 gd, 5 d, 1 sd, 1u	insect	bi	f
Myrtaceae	<i>Eugenia</i>	2	both	mo	h	h	insect	bi	f
Myrtaceae	<i>Metrosideros</i>	5	end	mo	h	h	bird	a	d
Myrtaceae	<i>Syzygium</i>	1	end	mo	h	h	insect	bi	f
Nyctaginaceae	<i>Boerhavia1</i>	1	ind	mo	h	h	insect/self	bv	d
Nyctaginaceae	<i>Boerhavia2</i>	2	both	mo	h	h	insect/self	bv	d
Nyctaginaceae	* <i>Pisonia1</i>	3	both	di	d	d	insect	bv	d
Nyctaginaceae	* <i>Pisonia2</i>	1	ind	di	d or m	m or d	insect	bv	d
Nyctaginaceae	* <i>Pisonia3</i>	1	ind	mo	h	h	insect	bv	d
Oleaceae	<i>Nestegis</i>	1	end	mo	h	h	insect	bi	f
Onagraceae	<i>Ludwigia</i>	1	pol?	mo	h	h	insect	bm	d
Orchidaceae	<i>Anoectochilus</i>	1	end	mo	h	h	insect	a	d

APPENDIX. Continued.

Family	Colonist	No. spp.	Indig.	Colo- nist line- age BS	Colo- nist BS	Species breeding system	Presumed pollinator	Pre- sumed dis- persal	Fle- shy fruit
Orchidaceae	<i>Liparis</i>	1	end	mo	h	h	insect	a	d
Orchidaceae	<i>Platanthera</i>	1	end	mo	h	h	insect	a	d
Oxalidaceae	<i>Oxalis</i>	1	pol?	mo	h	h	insect/self	bm	d
Pandanaceae	<i>Freycinetia</i>	1	ind	di	d	d	bird	bi	f
Pandanaceae	<i>Pandanus</i>	1	ind?	di	d	d	wind/insect	df	d
Papaveraceae	<i>Argemone</i>	1	end	mo	h	h	insect	bi	d
Phytolaccaceae	<i>Phytolacca</i>	1	end	mo	h	h	insect	bi	f
Piperaceae	<i>Peperomia1</i>	1	end	mo	h	h	insect/wind	bv	f
Piperaceae	<i>Peperomia2</i>	20	both	mo	h	h	insect/wind	bv	f
Piperaceae	<i>Peperomia3</i>	3	end	mo	h	h	insect/wind	bv	f
Piperaceae	<i>Peperomia4</i>	1	end	mo	h	h	insect/wind	bv	f
Pittosporaceae	<i>Pittosporum</i>	10	end	u	u	9 d, 1 p	insect	bv	d
Plantaginaceae	<i>Plantago1</i>	2	end	mo	h	h	wind	bv	d
Plantaginaceae	<i>Plantago2</i>	1	end	mo	h	h	wind	bv	d
Plumbaginaceae	<i>Plumbago</i>	1	ind	mo	h	h	insect	bv	d
Poaceae	<i>Agrostis1</i>	1	end	mo	h	h	wind	bb	d
Poaceae	<i>Agrostis2</i>	1	ind	mo	h	h	wind	bb	d
Poaceae	<i>Calamagrostis1</i>	1	end	mo	h	h	wind	bb	d
Poaceae	<i>Calamagrostis2</i>	1	end	mo	h	h	wind	bb	d
Poaceae	<i>Cenchrus</i>	1	end	mo	h	h	wind	bb	d
Poaceae	<i>Chrysopogon</i>	1	ind?	mo	h	h	wind	bb	d
Poaceae	<i>Deschampsia</i>	1	end	mo	h	h	wind	bb	d
Poaceae	<i>Dichantherium</i>	4	end	mo	am	am	wind	bm	d
Poaceae	<i>Digitaria</i>	1	ind?	mo	h	h	wind	bb	d
Poaceae	<i>Dissochondrus</i>	1	end	mo	h	h	wind	bb	d
Poaceae	<i>Eragrostis1</i>	9	end	mo	h	h	wind	bi	d
Poaceae	<i>Eragrostis2</i>	1	ind	mo	h	h	wind	bi/bb	d
Poaceae	<i>Festuca</i>	1	end?	mo	h	h	wind	bb	d
Poaceae	<i>Garnotia</i>	1	nat?	mo	h	h	wind	bb	d
Poaceae	<i>Heteropogon</i>	1	ind?	mo	am	am	wind	bb	d
Poaceae	* <i>Isachne1</i>	1	end	mo	h	gm	wind	bb	d
Poaceae	* <i>Isachne2</i>	1	end	mo	h	gm	wind	bb	d
Poaceae	<i>Ischaemum</i>	1	ind	mo	am	am	wind	bb	d
Poaceae	<i>Lepturus</i>	1	ind	mo	h	h	wind	df	d
Poaceae	* <i>Panicum1</i>	1	end	mo	am	am	wind	bi/bb	d
Poaceae	* <i>Panicum2</i>	10	end	mo	am	am	wind	bi/bb	d
Poaceae	<i>Paspalum</i>	1	ind?	mo	h	h	wind	bb	d
Poaceae	<i>Poa</i>	3	end	u	u	u	wind	bb	d
Poaceae	<i>Sporobolus</i>	1	ind	mo	h	h	wind	bv	d
Poaceae	<i>Trisetum</i>	2	end	mo	h	h	wind	bb	d
Polygonaceae	<i>Polygonum</i>	1	nat?	mo	h	h	insect	bi	d
Polygonaceae	<i>Rumex</i>	3	end	u	u	m	insect	dr/bi	d
Portulacaceae	<i>Portulaca1</i>	2	both	mo	h	h	insect/self	df	d
Portulacaceae	<i>Portulaca2</i>	2	end	mo	h	h	insect/self	df	d
Potamogetonaceae	<i>Potamogeton1</i>	1	ind?	mo	h	h	wind	bi	d
Potamogetonaceae	<i>Potamogeton2</i>	1	ind?	mo	h	h	wind	bi	d
Primulaceae	<i>Lysimachia1</i>	1	ind	mo	h	h	insect	df	d
Primulaceae	<i>Lysimachia2</i>	10	end	mo	h	h	insect	bm	d
Ranunculaceae	<i>Ranunculus</i>	2	end	mo	h	h	insect	bm	d
Rhamnaceae	<i>Alphitonia</i>	1	end	mo	h	h	insect	bi	f
Rhamnaceae	<i>Colubrina1</i>	1	ind	mo	am	am	insect	df	d
Rhamnaceae	<i>Colubrina2</i>	1	end	mo	h	h	insect	df	d
Rhamnaceae	<i>Gouania1</i>	1	end	u	u	am	insect	dr	d
Rhamnaceae	<i>Gouania2</i>	2	end	u	u	1 m, 1 am	insect	dr	d
Rosaceae	<i>Acaena</i>	1	end	mo	h	h	insect	bb	f
Rosaceae	* <i>Fragaria</i>	1	ind	di	pd	pd	insect	bi	f
Rosaceae	* <i>Osteomeles</i>	1	ind	mo	h	h	insect	bi	f
Rosaceae	<i>Rubus</i>	2	end	mo	h	h	insect	bi	f
Rubiaceae	* <i>Bobea</i>	4	end	di	pd	3 pd, 1 d	insect	bi	f
Rubiaceae	* <i>Coprosma1</i>	1	end	di	d	d	wind	bi	f
Rubiaceae	* <i>Coprosma2</i>	12	end	di	d	d	wind	bi	f
Rubiaceae	<i>Gardenia1</i>	1	end	mo	h	h	insect	bi	f
Rubiaceae	<i>Gardenia2</i>	2	end	mo	h	h	insect	bi	f
Rubiaceae	<i>Hedyotis</i>	20	end	smd	h	14 gd, 6 h	insect	bi/bm	d
Rubiaceae	<i>Morinda</i>	1	end	mo	h	h	insect	dr	f
Rubiaceae	<i>Nertera</i>	1	ind	mo	h	h	water/insect	bi	f
Rubiaceae	<i>Psychotria1</i>	8	end	smd	h	d	insect	bi	f

APPENDIX. Continued.

Family	Colonist	No. spp.	Indig.	Colo- nist line- age BS	Colo- nist BS	Species breeding system	Presumed pollinator	Pre- sumed dis- persal	Fle- shy fruit
Rubiaceae	<i>Psychotria</i> 2	3	end	smd	h	d	insect	bi	f
Rubiaceae	* <i>Psydrax</i>	1	ind	smd	h	gd	insect	bi	f
Ruppiaceae	<i>Ruppia</i>	1	ind	mo	h	h	wind	bm	f
Rutaceae	<i>Melicope</i>	47	end	sdm	dfunc	38 d, 7 pd, 1 h, 1 am	insect	bi	d
Rutaceae	<i>Platydesma</i>	4	end	mo	h	h	insect	bi	f
Rutaceae	<i>Zanthoxylum</i> 1	1	end	di	d	d	insect	bi	d
Rutaceae	<i>Zanthoxylum</i> 2	3	end	di	d	d	insect	bi	d
Santalaceae	<i>Exocarpos</i>	3	end	u	u	2 h, 1 p	insect	bi	f
Santalaceae	* <i>Santalum</i> 1	2	end	smd	h	1 h, 1 dfunc.	insect	bi	f
Santalaceae	* <i>Santalum</i> 2	2	end	mo	h	h	insect	bi	f
Sapindaceae	<i>Alectryon</i>	1	end	mo	pm	am	insect	bi	f
Sapindaceae	<i>Cardiospermum</i>	1	nat?	mo	m	m	insect	dr	f
Sapindaceae	* <i>Dodonaea</i>	1	ind	di	d	d	wind	df/dr	d
Sapindaceae	<i>Sapindus</i> 1	1	end	mo	m	m	insect	bi	f
Sapindaceae	<i>Sapindus</i> 2	1	ind	mo	m	m	insect	bi	f
Sapotaceae	* <i>Nesoluma</i>	1	ind	di	pd	pd	insect	dr	f
Sapotaceae	<i>Pouteria</i>	1	end	mo	h	h	insect	bi	f
Scrophulariaceae	<i>Bacopa</i>	1	ind	mo	h	h	insect	bm	d
Smilacaceae	<i>Smilax</i>	1	end	di	d	d	insect	bi	f
Solanaceae	<i>Lycium</i>	1	ind	mo	h	h	insect	dr	f
Solanaceae	<i>Nothoecstrum</i>	4	end	mo	h	h	insect	bi	f
Solanaceae	<i>Solanum</i> 1	3	end	mo	h	h	insect	bi	f
Solanaceae	<i>Solanum</i> 2	1	ind?	mo	h	h	insect	bi	f
Sterculiaceae	<i>Waltheria</i>	1	ind?	mo	h	h	insect	dr	d
Theaceae	<i>Eurya</i>	1	end	di	d	d	insect	bi	f
Thymelaeaceae	<i>Wikstroemia</i>	12	end	smd	h	10 d, 2 sd	insect	bi	f
Urticaceae	<i>Boehmeria</i>	1	end	mo	m	m	wind	bm	d
Urticaceae	<i>Hesperocnide</i>	1	end	mo	m	m	wind	bb	d
Urticaceae	<i>Neraudia</i>	5	end	smd	m	d	wind/insect	bi	d
Urticaceae	<i>Pilea</i>	1	ind	mo	m	m	wind	bm	d
Urticaceae	<i>Pipturus</i>	4	end	u	u	1 d, 2 gd, 1 m	insect	bv	d
Urticaceae	* <i>Touchardia</i>	1	end	di	d	d	wind	bi	f
Urticaceae	* <i>Uvera</i> 1	1	end	di	d	d	wind	bi	f
Urticaceae	* <i>Uvera</i> 2	1	end	di	d	d	wind	bi	f
Verbenaceae	<i>Vitex</i>	1	ind	mo	h	h	insect	dr	f
Violaceae	<i>Isodendron</i>	4	end	mo	h	h	insect	bi/bm	d
Violaceae	<i>Viola</i>	7	end	mo	h	h	insect	bi/bm	d
Viscaceae	<i>Korthalsella</i> 1	2	both	mo	m	m	insect	bv/bi	f
Viscaceae	<i>Korthalsella</i> 2	2	both	mo	m	m	insect	bv/bi	f
Viscaceae	<i>Korthalsella</i> 3	2	end	mo	m	m	insect	bv/bi	f
Zygophyllaceae	<i>Tribulus</i>	1	ind	mo	h	h	insect	bb	d

* Denotes additional information below (arranged alphabetically) on colonist.

Bobea (Rubiaceae). According to Darwin and Chaw (in Wagner et al. 1990), the genus *Timonius* is clearly the closest relative of the Hawaiian endemic genus *Bobea*. Smith and Darwin (in Smith 1988) indicate that most species of *Timonius* are dioecious or perhaps rarely polygamodioecious, as are three of the four Hawaiian species of *Bobea*. We have therefore assumed that the ancestor of *Bobea* had a polygamodioecious rather than dioecious breeding system.

Broussaisia (Hydrangeaceae). Fosberg (1939) has indicated that the endemic Hawaiian genus *Broussaisia* is related to the Old World genus *Dichroa*; if so, then the ancestor of *Broussaisia* had perfect flowers.

Charpentiera (Amaranthaceae). This genus sometimes expresses a functionally dioecious condition because either perfect flowers quickly abscise or morphologically perfect flowers are functionally staminate by lack of maturation of the pistil. Carlquist (1974: 522) provides an illustration. Moreover, *Charpentiera* is apparently most closely allied to *Chamissoa* (Sohmer 1972, Eliasson 1988) in which one species has perfect flowers while the other species is gynodioecious.

Coprosma (Rubiaceae). The ancestry of *Coprosma ernodeoides* is somewhat doubtful, but Oliver (1935) suggests that its closest relative is *C. pumila*, another dioecious species. Thus both of the colonizations of Hawaii by *Coprosma* appear to have been by dioecious colonists.

Dodonaea (Sapindaceae). *Dodonaea* has a variable breeding system and sex expression may vary among plants as well as through time on the same plant.

Fragaria (Rosaceae). Populations of *Fragaria chiloensis* have a variable breeding system (Staudt 1967, Hancock and Bringhurst 1979, 1980), including dioecy, polygamodioecy, and occasionally hermaphroditism. Similar variation occurs in much of the genus. In the absence of information on the relationships and breeding system of the Hawaiian populations, we assumed a polygamodioecious colonist to the Hawaiian Islands and further that no change occurred in the evolution of the endemic Hawaiian subspecies. Baker and Cox (1984) indicated a hermaphroditic breeding system for the Hawaiian subspecies

APPENDIX. Continued.

based on an incorrect reading of Staudt (1962), which indicated that several populations from South America were hermaphroditic. Subsequent studies cited above suggest that the breeding system in South America is also variable.

Gunnera (Gunneraceae). *Gunnera* species exhibit a wide variety of breeding systems including dioecy, monoecy, polygamodioecy, polygamomonoeicy, and rarely hermaphroditism. In the absence of good information on the relationships and breeding system of the Hawaiian species, we have assumed a polygamomonoeicy colonist, a condition found in the South American species apparently related to the Hawaiian species (cf. Molina 1978).

Ilex (Aquifoliaceae). *Ilex anomala* was treated as including *I. marquesensis* and *I. tahitensis* by Wagner et al. (1990) because the populations from these three archipelagos have completely overlapping morphological patterns of variation and differ only apparently in being polygamodioecious (cf. Brown 1935, Carlquist 1974).

Isachne (Poaceae). Following the relationships suggested by Hillebrand (1888) of Hawaiian *Isachne* and following the sex of flowers suggested by Backer and Bakhuizen van den Brink (1968), the ancestor of *I. pallens* (*I. albens* sensu Hillebrand [(1888)]) could have been hermaphroditic, and the ancestor of *I. distichophylla* (*I. pangerangensis* [*I. firmula* sensu Hillebrand]) could have been hermaphroditic (sometimes also andromonoecious).

Labordia (Loganiaceae). Apparently the Polynesian species of *Geniostema* are ancestral to the endemic Hawaiian genus *Labordia* (Conn 1980, Smith 1988, Wagner et al. 1990). Unfortunately, the monographer of the genus (Conn 1980) does not discuss breeding systems at all. However, Smith (1988) indicates that many of the species of *Geniostema* are at least "incipiently gynodioecious," and thus we have assumed such an ancestor of the Hawaiian *Labordia*.

Lipochaeta (Asteraceae). *Lipochaeta ovata* was described by Gardner (1979) from a single collection (*Anderson s.n.* GB, OS). Several species have been included in the Hawaiian flora based on single collections by Anderson. Subsequent study has indicated that all of these species are common in southeastern Polynesia, where Anderson also collected. W. L. Wagner (*unpublished data*) has concluded that all of these collections were probably collected in Polynesia, and mislabelled as being from the Hawaiian Islands. Thus, *Lipochaeta ovata* is probably not part of the Hawaiian flora. Closer examination of this specimen has shown that it is the common Pacific species *Wollastonia biflora*, the probable progenitor to most of the Hawaiian species of *Lipochaeta*.

Myrsine (Myrsinaceae). Carlquist treated *Myrsine knudsenii* and *M. lanaiensis* as dioecious because some individuals had anthers that contained no pollen and because in individuals with functional anthers, the ovaries were apparently smaller. Examination of large numbers of herbarium material of these species suggested that the flowers were hermaphroditic (Wagner et al. 1990). Re-examination of Carlquist's vouchers should be made to verify his species determinations given the revised taxonomy presented in the *Manual*. It is more likely that these species have variable breeding systems since this is apparently common in the family (J. J. Pipoly III, *personal communication*). Detailed experimental studies of all of the species in this genus are needed to confirm the designations of breeding systems given here and in the *Manual*.

Nesoluma (Sapotaceae). Carlquist (1974) concluded that *Nesoluma* was gynodioecious based on Lam's (1938) data; however, Pennington (in Wagner et al. 1990) indicates that it is probably dioecious, yet the description suggests that there may be some perfect flowers.

Osteomeles (Rosaceae). The *Manual* (Wagner et al. 1990) indicates that plants of *Osteomeles* are sometimes andromonoecious, but are usually hermaphroditic. Thus, we treat *O. anthyllidifolia* as hermaphroditic as did Carlquist (1974) and Bawa (1982).

Panicum (Poaceae). Both Fosberg (1948) and subsequent authors (e.g., Carlquist 1974) treated Hawaiian *Panicum* (excluding species of *Dichantherium*) as arising from two independent colonizations. Davidse (in Wagner et al. 1990) does not indicate specifically that the Hawaiian species arose from two colonizations, but points out that the newest described species, *P. lineale*, which was not known to Fosberg or Carlquist, is highly distinctive morphologically from the remaining species. Thus we presume an independent colonization leading to this species. The remaining species share a unique character according to Davidse and thus these other species probably arose from one additional colonization, rather than the previously hypothesized two colonizations.

Perrottetia (Celastraceae). Most species of *Perrottetia* usually have perfect flowers, and are only rarely unisexual, as in the Hawaiian species. Therefore, the ancestor of the Hawaiian species was almost certain to have been hermaphroditic.

Pisonia (Nyctaginaceae). *Pisonia grandis* most likely has a variable breeding system and the colonizing individual(s) could have been either dioecious or monoecious.

Psydrax (*Canthium*; Rubiaceae). Although Skottsberg's data (1945) show the occurrence of pistillate flowers, his data are based on a sample of only one Hawaiian population, and no extra-Hawaiian populations were examined. We have followed Carlquist (1974) and Bawa (1982) and assumed that the ancestor was hermaphroditic.

Rhus (Anacardiaceae). These flowers appear morphologically perfect in the Hawaiian species although there is no indication of full hermaphroditism elsewhere in the genus. Hillebrand (1888) indicates an apparent dioecious condition, while Carlquist (1974) treats the species as polygamomonoeicy. The related *R. chinensis* has at least some unisexual flowers according to a recent treatment of Ding Hou (1978), and it is probably polygamomonoeicy.

Santalum (Santalaceae). Carlquist (1974) gives results of morphological sections showing functional dioecy in *Santalum haleakalae*. He generalizes this condition to all Hawaiian species; we have treated only this one species as functionally dioecious.

Touchardia (Urticaceae). See note for *Urera*.

Urera (Urticaceae). Carlquist (1974) indicated that the breeding systems of the ancestors for the two Hawaiian *Urera* species as well as for the endemic monotypic genus *Touchardia* were nondioecious. The ancestor of *Urera kaalae* almost certainly had the same breeding system (dioecious, occasionally monoecious) as the present *Urera kaalae* and the closely related New World species, *U. caracasana*. The relationship of *Touchardia* to other urticaceous genera was considered by Hutchinson (1967) to be with the tribe Boehmerieae. Study of *Touchardia* for the *Manual* suggested that it may have shared a common ancestor with *U. glabra*. If so, then the ancestor was most likely dioecious, and this is not a case of autochthonous evolution of dioecy in the Hawaiian Islands.