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PHYLOGENETICS OF THE GENUS *SCAEVOLA* (GOODENIACEAE): IMPLICATION FOR DISPERSAL PATTERNS ACROSS THE PACIFIC BASIN AND COLONIZATION OF THE HAWAIIAN ISLANDS[1]

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Scaevola, the only genus of Goodeniaceae that has extensively radiated outside of Australia, has dispersed throughout the Pacific Basin, with a few species reaching the tropical coastal areas of the Atlantic and Indian Oceans. Five Australian and most of the non-Australian species are placed in *Scaevola* section *Scaevola* based on their fleshy fruits, indeterminate inflorescences, and more arborescent habits. Analyses of ITS sequence data demonstrate that *Scaevola* is a monophyletic group if *S. collaris* is excluded and *Diaspasis filifolia* is included. The genus is Australian in origin, but there have been at least six separate dispersal events from Australia. Four of these dispersals each resulted in single extra-Australian species. The remaining two were followed by radiations that gave rise to large groups, each including one of the widespread strand species, *S. taccada* and *S. plumieri*. Remarkably, three of the six dispersals established species on the remote Hawaiian Archipelago, representing at present the largest number of colonizations by any flowering plant genus to these islands.

Key words: Australia; dispersal; Goodeniaceae; Hawaiian Islands; ITS; Pacific biogeography; *Scaevola*.

The Goodeniaceae (Asterales), as currently circumscribed, (Carolin et al., 1992), contains approximately 400 species in 11 genera and constitutes a significant element of Australian and Pacific island floras. The family is contained within the Asterales as a possible sister group to the Asteraceae (Gustafsson et al., 1996) or more likely to Calyceraceae + Asteraceae. (Kårehed et al., 1999). While most genera of Goodeniaceae are almost entirely confined to Australia, one genus, *Scaevola*, has dispersed and radiated throughout much of the Pacific.

Of approximately 130 species of *Scaevola*, approximately 40 occur outside Australia. Two of these are widespread strand species with distributions throughout the Pacific and Indian Oceans (*S. taccada*) or in the tropical Americas and Africa (*S. plumieri*). The remaining species, in contrast, are narrower endemics often occurring well inland as forest trees or shrubs. Island species occur in the Pacific, northward to the Philippines and China, eastward as far as the Marquesas, and northeast to the Hawaiian Islands. Additionally, one species is known from Cuba and one from Socotra.

Most Australian *Scaevola* have dry fruits and sprawling, herbaceous to shrubby habits. In contrast, almost all of the extra-Australian species have fleshy fruits and are often tall shrubs or trees. These characteristics, coupled with axillary inflorescences, were used by Carolin (1990) to define *Scaevola* section *Scaevola*, which comprises all but two (*S. gracilis* and *S. oppositifolia*) of the extra-Australian species along with five species restricted to Australia. However, given the propensity of island colonists to show convergent evolution of such characteristics as fleshy fruits and arborescence (Carlquist, 1965, 1974, 1980) the monophyly of *Scaevola* sect. *Scaevola* should not be assumed without additional evidence.

Carolin et al. (1992) placed nearly all the rest of the genus (64 Australian species and *S. gracilis* from Tonga and New Zealand) in section *Xerocarpa*, defined by dry exocarps and determinate inflorescences. Two remaining species, *S. oppositifolia* and *S. enantophylla*, which have fleshy fruits, opposite leaves, a vining habit, and occur from northern Australia to the Philippines, have been segregated as a third section, *Scaevola* sect. *Enantiophyllum* (Carolin et al., 1992).

The most successful dispersers in the genus are *S. taccada* and *S. plumieri*, which together are pantropical in distribution, each occurring in both the northern and southern tropics, with overlapping distributions on the coasts of the Indian Ocean. Their wide distribution appears to be due in part to their ability

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to be transported both in avian guts and by oceanic floating (remaining viable after floating in seawater for several months; Guppy, 1917; Lesko and Walker, 1969). Given these efficient dispersal mechanisms, an obvious hypothesis to explain the numerous island endemic species would be that *S. taccada* and *S. plumieri* have been the prominent colonizers, giving rise to inland species on each of the high island groups where they have established. This hypothesis predicts that island endemics are closely related to populations of the widespread taxon that occurs on their island. Alternatively, if birds can disperse fleshy fruits long distances, islands could be colonized directly from other islands or Australia independent of oceanic dispersal of these widespread species.

The largest number of species in a single archipelago occurs in the Hawaiian Islands, which is home to *S. taccada* and nine endemic species, of which eight are diploid and one is tetraploid (Patterson, 1990). Using morphological data, Patterson (1995) concluded that the endemic diploid taxa form a monophyletic clade. The sister group to the Hawaiian diploids was *S. taccada* (Patterson, 1995), a taxon relationship favoring a scenario in which inland species are derived from widespread progenitors. *Scaevola glabra*, the single tetraploid species, is quite different from the Hawaiian diploids, being instead similar to the New Caledonian *S. coccinea*, with which it shares a similar tubular flower (Carlquist, 1969). *Scaevola glabra* is the only clear example of a stable tetraploid species known in the genus, although a few Australian species have varying chromosome numbers and many species have not been analyzed (Peacock, 1963; Carr, 1998). Patterson's (1995) analysis supported this conclusion, suggesting that, in this case, long-distance dispersal between islands has occurred. However, because Patterson (1995) included only a small number of taxa, none of them Australian, these suggestions are in need of confirmation.

In 1996, a new Hawaiian *Scaevola* species was described from the island of Maui (Wagner, 1996). This species, *Scaevola hobdyi*, still known only from a holotype with floral buds, is now presumed to be extinct. Based on its linear, spirally arranged leaves, which are very different from all other Hawaiian species, Wagner (1996) suggested that *S. hobdyi* represents an additional dispersal event to the Hawaiian Islands.

To examine the relationships and dispersal patterns of the extra-Australian *Scaevola* species, we sequenced the internal transcribed spacers and 5.8S gene (collectively, ITS) of nuclear ribosomal DNA for 51 *Scaevola* species and eight outgroup taxa. The outgroup includes species from *Goodenia*, *Diaspasis*, *Velleia*, and *Verreauxia* and were chosen based on their positions close to the *Scaevola* lineage in both *rbc*L and morphological studies (Gustafsson et al., 1996, 1997). The ITS region has the appropriate variation for intra-generic phylogenetic analyses, is flanked by highly conserved genic regions (18S and 26S), and encompasses the 5.8S gene, simplifying primer design and sequence alignment (Baldwin et al., 1995). These data were analyzed using phylogenetic methods to elucidate the dispersal patterns, biogeography, and evolutionary history of *Scaevola*.

MATERIALS AND METHODS

Plant material and extraction—Sampling of taxa was designed to attempt to include most of the *Scaevola* species that occur outside of Australia. Twenty-six species (listed in the Appendix [see Supplementary Data acccompanying the online version of this paper]) were sampled, including samples from all the geographical areas occupied by *Scaevola* except Hainan, which contains a single species, *S. hainanensis* Hance. Multiple specimens from different localities were used for widespread species. Additionally, 25 Australian species were sampled, selected to encompass each subsection and series recognized by Carolin et al. (1992). The DNA was extracted from fresh material, silica gel samples, or herbarium sheets. The fresh material (which included only the Hawaiian species) was extracted and purified with a modification of the cetyl trimethyl ammonium bromide (CTAB) isolation method (Doyle and Doyle, 1987). These samples were accessioned into the Hawaiian Plant DNA Library (HPDL; Morden et al., 1996). Silica gel and herbarium material were extracted with CTAB buffer, glass milk, and NaI solution (Bio 101, Qbiogene, Carlsbad, California, USA) as described in Struwe et al. (1998).

DNA sequencing and alignment—The ITS region, including ITS 1, 2, and 5.8S, was amplified using primers 90 (5′-TATGCTTAAAYTCAGCGGGT-3′) and 91 (5′-AACAAGGTTTCCGTAGGTGA-3′) modified from Baldwin (1992) or primers 4 (5′-TCCTCCGCTTATTGATATGC-3′) and LEU (or ITS-I) (5′-GTCCACTGAACCTTATCATTTAG-3′) (White et al., 1990; Urbatsch et al., 2000). These primer pairs were also used for sequencing along with two internal primers, 2 (GCTGCGTTCTTCATCGATGC) and 3b (GCATCGATGAAGAACGTAGC) (White et al., 1990; Baum et al., 1998). Amplifications utilized the following cycling program: 95°C, 50 s; 60°C, 50 s; 72°C, 1 min 50 s; repeat 30 cycles; hold 4°C. The reactions were performed using *Taq* DNA Polymerase (Boehringer Mannheim, Indianapolis, Indiana, USA or QIAGEN Valencia, California, USA) in 25 μL, with final concentrations of 2.5 mmol/L $MgCl_2$, 0.5 μmol/L of each primer, 0.8 mmol/L dNTPs, 0.004% BSA (New England Biolabs, Beverly, Massachusetts, USA), and 0.001 mmol/L TMACl (Sigma, St. Louis, Missouri, USA). The samples were cleaned with the Qiagen PCR cleanup kit (Qiagen). The PCR products were sequenced using BigDye or dRhod systems (PE Applied Biosystems, Foster City, California, USA) according to the manufacturer's instructions and viewed with an ABI 377 (Applied Biosystems). Sequences were initially aligned with Clustal W (Thompson et al., 1994) using a gap open penalty = 15 and gap extension penalty = 6.66. The alignment was modified by eye in Sequencher 3.0 (Gene Codes Corporation, Ann Arbor, Michigan, USA).

Phylogenetic analyses—In initial analyses all characters were coded as unordered with equal weight, and gaps were coded as missing. The matrix was analyzed using the maximum parsimony criterion (Fitch, 1971) with PAUP* 4.0b8 (Swofford, 2001). Heuristic searches were performed with 100 random taxon addition replicates using tree bisection-reconnection (TBR) branch-swapping, with steepest descent off. Internal branch support was estimated with a bootstrap analysis (Felsenstein, 1985) from 1000 pseudoreplicates subject to simple taxon addition heuristic searches as described but with MaxTrees set to 1000.

To evaluate the dependence of the phylogeny on the model of evolution assumed, we explored alternative weighting schemes: (1) transition : transversion (ti : tv) bias = 2:1 and 3:1, (2) gapmode = newstate, and (3) gaps scored as additional characters weighted 1, 2, or 3. Searches were conducted as in the flat-weighted analysis. These analyses are not reported unless they bear on the specific conclusions reached.

We tested a number of a priori hypotheses of monophyly (see Results) using the Wilcoxon signed ranks (WSR; Templeton, 1983) and Kishino-Hasegawa (KH; Kishino and Hasegawa, 1989) tests as implemented in PAUP*. The 864 most parsimonious trees were compared to the optimal trees found during constrained parsimony searches (using the same settings as for unconstrained searches). The Kishino-Hasegawa test was performed using a maximum likelihood optimality criterion with the HKY85 model of molecular evolution (Hasegawa et al., 1985) with empirical base frequencies both with and without allowance for heterogeneity of rates among sites using a discrete approximation to a gamma distribution.

RESULTS

The aligned matrix had a length of 805 characters with 329 variable and 236 parsimony-informative sites. The percentage

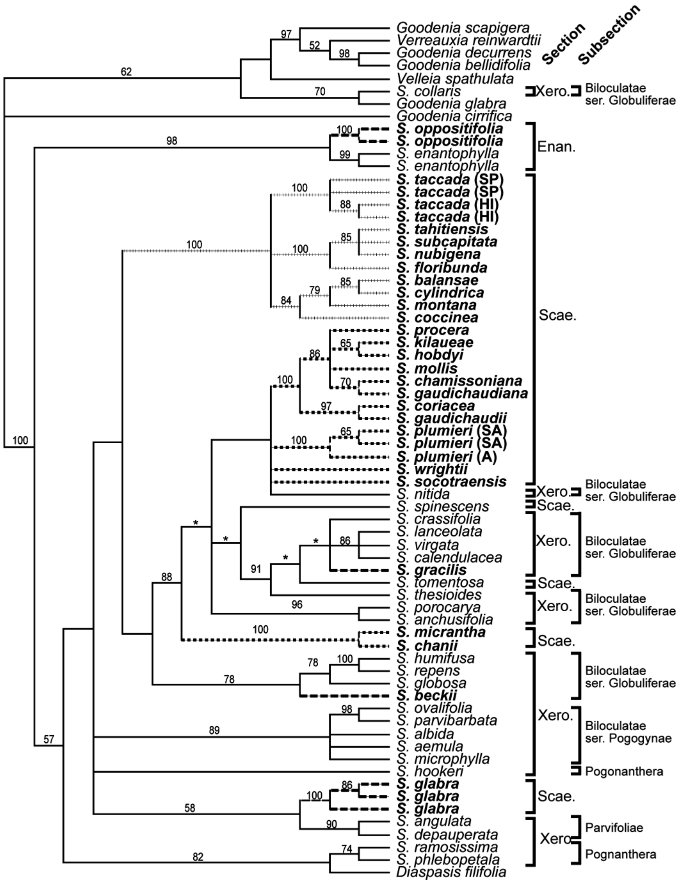

Fig. 1. Strict consensus of 864 most parsimonious trees. Bootstrap values are given above the branches. Asterisks indicate a lack of support for the clade under other weighting schemes. Section and subsection delineations based on Carolin et al. (1992) are indicated on the right (Enan. = *Scaevola* sect. *Enantiophyllum*; Xero. = *Scaevola* sect. *Xerocarpa*; Scae. = *Scaevola* sect. *Scaevola*;). Long dashes = single species dispersals, short dashes = Southern clade, medium dashes = Northern clade. SP = South Pacific, HI = Hawaiian Islands, SA = South America, A = Africa. Taxa in boldface type occur outside Australia.

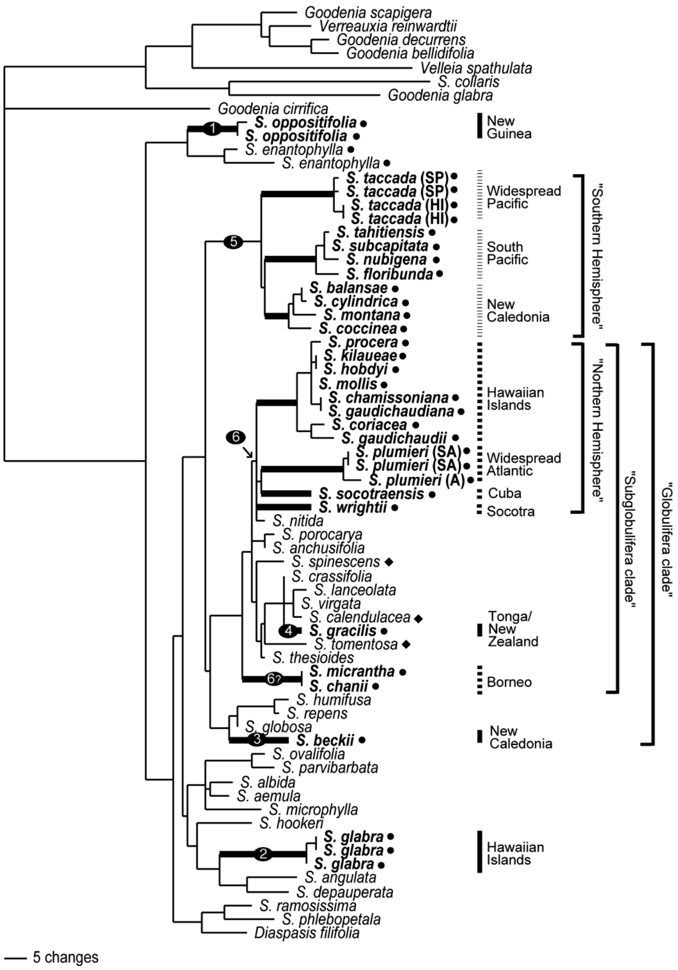

Fig. 2. Phylogram of one of the most parsimonious trees. Bold lines indicate hypothesized dispersal events from Australia with a question mark on the Bornean endemics. Each hypothesized dispersal is labeled 1–6. Solid lines = single species dispersals, short dashes = Southern clade, medium dashes = Northern clade. SP = South Pacific, HI = Hawaiian Islands, SA = South America, A = Africa. Taxa in boldface type occur outside Australia. Fleshy fruited taxa have a black dot at the end of their name, while partially fleshy fruits taxa have black diamonds.

of sequence divergence between taxa ranged from 0 to 8% within the ingroup taxa and from 0 to 18% including the outgroups. Fourteen parsimony-informative indel events were invoked to achieve this alignment. The complete matrix and individual sequences have been submitted to Genbank (accession numbers AY102728–AY102795).

Maximum parsimony analysis produced 864 trees of 767 steps, with a consistency index of 0.6310 and a retention index of 0.8180. Despite the limited sampling of taxa outside of *Scaevola*, these data indicate that *Goodenia* is not monophyletic and includes the genera *Verreauxia* and *Velleia* (Fig. 1). Additionally, the ITS data strongly support the removal of *Scaevola collaris* from the rest of the genus and the inclusion of the monotypic genus, *Diaspasis*, in *Scaevola*. The genus *Scaevola*, excluding *S. collaris* but including *Diaspasis*, was well supported with 100% bootstrap support (Fig. 1).

Within *Scaevola*, *S.* sect. *Enantiophyllum* is weakly supported as sister to the other *Scaevola* taxa (57% bootstrap). A second clade, including taxa from *S.* sect. *Xerocarpa* subsect. *Pogonanthera* and *Diaspasis filifolia* is weakly (<50% bootstrap) supported as sister to the remainder of *Scaevola*. The rest of the *Scaevola* species are divided into four major lineages, whose relationships to each other are unresolved. The first lineage includes all of the sampled species from *S.* sect. *Xerocarpa* subsect. *Parvifoliae* as well as *S. glabra* from the Hawaiian Islands (Fig. 2). The second lineage includes only *S. hookeri* (*S.* sect. *Xerocarpa* subsect. *Pogonanthera*). The third lineage includes all of the sampled taxa from *S.* sect. *Xerocarpa* subsect. *Biloculatae* ser. *Pogogynae*. Finally, the fourth clade includes all of the *S.* sect. *Scaevola* species except *S. glabra* and all the sampled species from *S.* sect. *Xerocarpa* subsect. *Biloculatae* ser. *Globuliferae*.

Within the fourth clade, the Southern Hemisphere lineage (or southern clade), which includes *S. taccada* and the South Pacific and New Caledonian taxa (excluding *S. gracilis* and *S. beckii*), is weakly supported as sister to the rest (Fig. 2). The remaining species (collectively the globulifera clade, Fig. 2) are broken into two clades, one containing multiple Australian species and *S. beckii*, and another that we refer to as the subglobulifera clade (Fig. 2), which includes most of the taxa from *S.* sect. *Xerocarpa* ser. *Globuliferae*, the Bornean taxa, and the

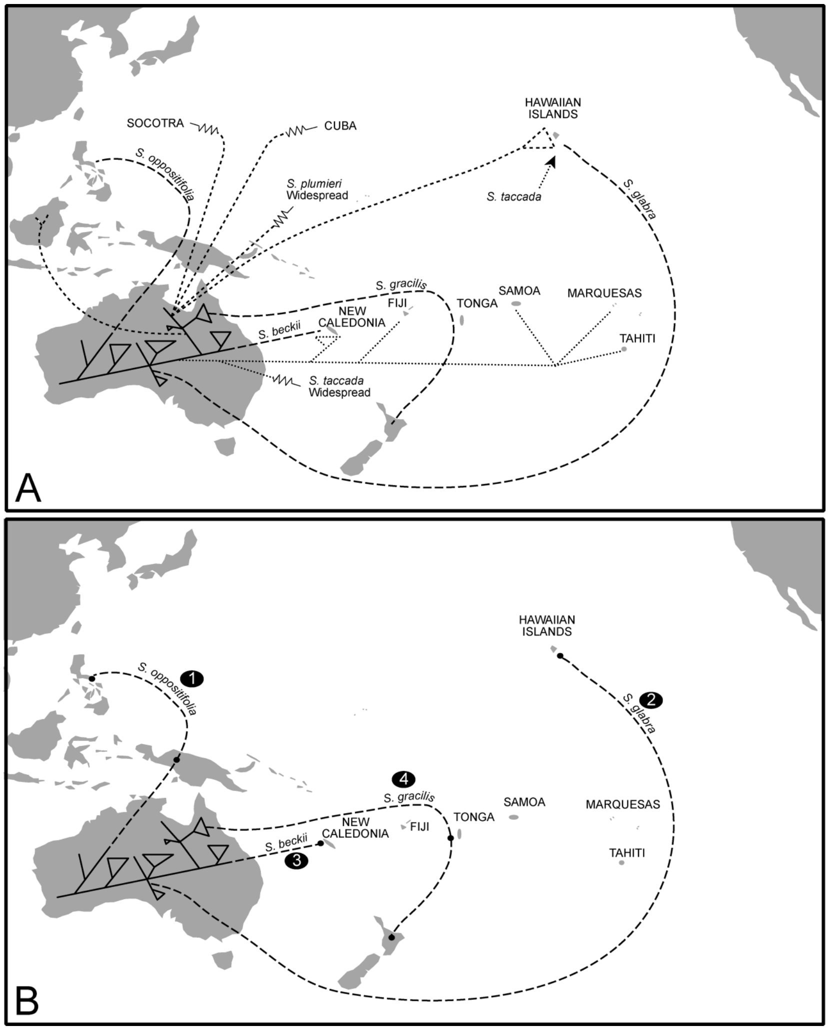

Fig. 3. Plausible dispersal scenario superimposed on a map of the Pacific Basin. (A) Overall pattern of dispersals from Australia. In order to simplify viewing of the biogeographic patterns each of the following is shown independently. (B) Four single species dispersals (Dispersals 1–4) with dots indicating localities of that species. (C) Southern Hemisphere radiation (Dispersal 5). (D) Northern Hemisphere radiation (Dispersal 6). Bolded coastlines in (C) and (D) indicate natural distribution of *S. taccada* and *S. plumieri*, respectively. Long dashes = four single species dispersals, short dashes = Southern clade, medium dashes = Northern clade.

Northern Hemisphere lineage (or northern clade, which includes *S. plumieri*, *S. socotraensis*, *S. wrightii*, and the Hawaiian endemic diploids).

The data strongly reject the monophyly of the extra-Australian taxa (WSR test, $P = 0.0001$; KH test, $P = 0.0001$) suggesting, instead, at least six dispersal events from Australia into the Pacific basin. Four of these dispersal events each led to single species (Dispersals 1–4, Figs. 2 and 3): one, *S. oppositifolia* in *S.* sect. *Enantiophyllum*, involved its dispersal from Australia to the Philippines; another, in *S.* sect. *Xerocarpa* subsect. *Parvifoliae*, resulted in the tetraploid *S. glabra* in the Hawaiian Islands; and two events in *S.* sect. *Xerocarpa* subsect. *Biloculatae* ser. *Globuliferae*, one giving rise to *S. beckii* in New Caledonia and the other giving rise to *S. gracilis* in New Zealand and Tonga.

The phylogeny suggests two additional extra-Australian radiations that have each given rise to multiple island species. These clades each include one of the two widespread strand species, *S. taccada* and *S. plumieri* (Dispersals 5 and 6 respectively, Figs. 2 and 3C, D). The taxa related to *S. taccada* all occur in the southern hemisphere, while those related to *S. plumieri* all occur in the northern hemisphere. The southern clade includes all of the New Caledonian species (except *S. beckii*) and all of the southern Polynesian (Fiji, Samoa, Tahiti, and Marquesas) species (except *S. gracilis*). The northern clade is not as well resolved, but definitely includes the Hawaiian endemic species (excluding *S. glabra*), *S. socotraensis* (from Socotra), and *S. wrightii* (from Cuba). Worthy of note, the morphologically divergent Hawaiian *S. hobdyi* shows nearly no ITS sequence divergence from the six endemic Hawaiian diploids. The Bornean taxa, *S. chanii* and *S. micrantha*, do not appear sister to the other island taxa in the northern clade on the most-parsimonious tree. However, inclusion of the Bornean taxa within the northern lineage is not rejected by these data (WSR test, $P = 0.5637$; KH test, $P = 0.1344$ respectively [Table 1]). This clade was not recovered with maximum parsimony or maximum likelihood (analysis not shown); however, this area of the tree contains many long branches and few informative characters. Many of these clades were not

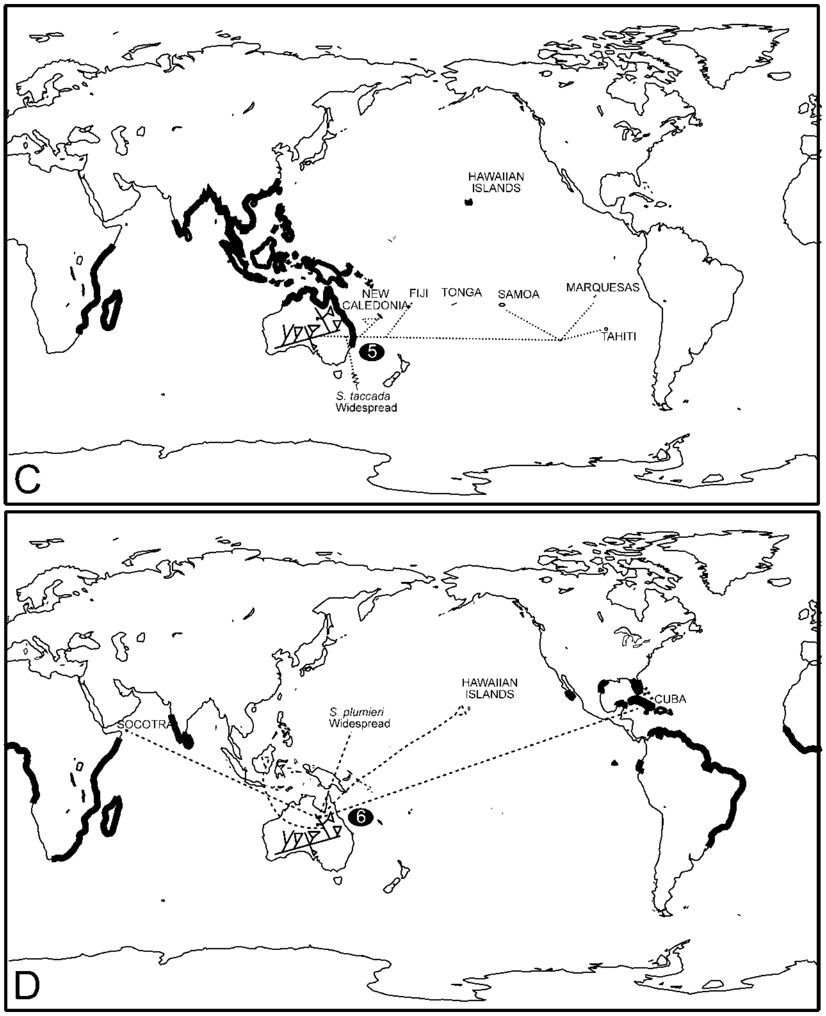

Fig. 3. Continued.

supported under different weighting schemes (asterisks, Fig. 1).

DISCUSSION

Classification and character evolution—*Monophyly of Scaevola*—The ITS data strongly support the monophyly of *Scaevola*, with the inclusion of *Diaspasis filifolia* and the exclusion of *S. collaris*. Although no unique synapomorphies define the genus, a suite of morphological characters delimits it. The most obvious character is the familiar, fan-shaped corolla of *Scaevola*, which occurs in nearly all species. In most Goodeniaceae, the two upper (adaxial) lobes are differentiated, forming a pronounced upper lip. Another putative synapomorphy of *Scaevola* is fruits that lack a clear demarcation between the hard endocarp and outer layers with unthickened cell walls (Carolin, 1966). Additionally, all *Scaevola* have 1–2 (–4) seeded, indehiscent fruit, although this character is also present in *Dampiera* and a few species of *Goodenia* sensu lato (including *Verreauxia*, Carolin et al., 1992). Finally, the presence of barbulae at the edge of petal wings and in the throat of the corolla is restricted to *Scaevola*, although not present in all species (Carolin et al., 1992).

Diaspasis correctly placed in the genus Scaevola—*Diaspasis filifolia* is a monotypic Australian genus that is very similar to *Scaevola* in fruit and seed morphology. The molecular data suggest that it is embedded within *Scaevola*, appar-

TABLE 1. Differing species of extra-Australian species of *Scaevola* were constrained with the northern island clade (excluding *S. nitida*) to form a monophyletic group. One of the most parsimonious "best" trees was then compared to one of the most parsimonious trees derived from each constrained search. The difference in number of steps between trees is shown below along with the calculated *P* value from the Wilcoxon signed ranks and Kashino-Hasegawa tests. Values were considered significant at $P < 0.05$ (indicated with an asterisk).

Monophyletic hypothesis	No. steps	Wilcoxon signed ranks test *P*	Kashino-Hasegawa *P*
S. chanii + *S. micrantha*	1	0.5637	0.1344
S. gracilis	7	0.0082*	0.0023*
S. beckii	11	0.0045*	0.0004*
S. gracilis + *S. chanii* + *S. micrantha*	7	0.0348*	0.0033*
S. gracilis + *S. beckii* + *S. chanii* + *S. micrantha*	16	0.0007*	0.0001*

ently as sister to representatives of *S*. sect. *Xerocarpa* subsect. *Pogonanthera* (Fig. 1). A similar close relationship was found with *rbc*L data (Gustafsson et al., 1996), and the overlapping similarities of the genera were discussed by Carolin (1978). These results suggest that the original classification of *D. filifolia* R. Br. as *Scaevola clandestina* F. Muell was correct (von Mueller, 1859).

The corolla of *D. filifolia* differs from most *Scaevola* in having the lobes arranged almost radially or in a 2 + 3 arrangement (i.e., with two abaxial and three adaxial petals). However, this condition is approached in *S. striata*, which is also in subsect. *Pogonanthera* (Carolin et al., 1992). Characters that further support a close relationship of *D. filifolia* with *S. ramosissima* and *S. phlebopetala* include flowers in terminal racemes with leaf-like bracts, well-developed peduncle with obsolete pedicel, and a weak-stemmed (often decumbent, prostrate, or ascending) herbaceous habit.

Exclusion of Scaevola collaris from Scaevola—The molecular data suggest that *S. collaris* is more closely related to elements of the non-monophyletic *Goodenia* than to the remainder of *Scaevola*, despite having the fan-shaped corolla. The exclusion of *S. collaris* from *Scaevola* is also supported by seed testa anatomy, which is more similar to *Goodenia* species than to *Scaevola* species (M. H. G. Gustafsson, unpublished data). Additionally, the fruit of *S. collaris* is unique in *Scaevola* because of its beak and sponge-like (although hard), lacunate endocarp (Carolin et al., 1992). A more thorough sampling of *Goodenia* and related genera is necessary to clarify the placement of *S. collaris* within that genus.

Subgeneric classification—Carolin (1990) used morphological characters to separate the genus *Scaevola* into three sections—*Scaevola*, *Xerocarpa*, and *Enantiophyllum*. Species in *S*. sect. *Scaevola* are shrubs to small trees with fleshy exocarps. Although the section was also defined by axillary inflorescences (Carolin, 1990), this characterization is problematic because some species (e.g., *S. floribunda* from Fiji) assigned to the section have terminal inflorescences. *Scaevola* sect. *Xerocarpa* included all the remaining Australian species, which range from herbaceous to small shrubs, have terminal inflorescences, and generally have fruit with dry exocarps. *Scaevola gracilis* was also included in *S*. sect. *Xerocarpa* (despite having fleshy fruits) based on its terminal inflorescence. The third section, *Enantiophyllum*, has been circumscribed to include from one to 10 species (Leenhouts, 1957), but currently includes just two species (Carolin et al., 1992), *S. oppositifolia* and *S. enantophylla*. This section is characterized by fleshy mesocarps, axillary inflorescences, a vining habit, and opposite leaves. The latter two characteristics are unique in the family.

Scaevola sect. *Enantiophyllum* is represented in our study by both species. Based on ITS data, this section is monophyletic and sister to the remainder of the genus. Thus, our data support its recognition. In contrast, the molecular data do not support Carolin's sections *Scaevola* or *Xerocarpa*, which appear intermingled across the entire tree (Fig. 1).

Despite the non-monophyly of *S*. sect. *Xerocarpa*, the subsections and series recognized by Carolin et al. (1992) are broadly consistent with the molecular phylogenetic analysis. All species sampled from subsect. *Biloculatae* ser. *Globuliferae* (except for *S. collaris*; see earlier) fall in a clade, globulifera, that includes no other subsections or series of *S*. sect. *Xerocarpa* (but does include a number of species formerly assigned to *S*. sect. *Scaevola*). The five species sampled from the other series of subsect. *Biloculatae*, ser. *Pogogynae* form a well-supported clade. The two species from subsect. *Parvifoliae* form a clade, whereas the three species from subsect. *Pogonanthera* fall into two clades. Therefore, despite the limited sampling within the Australian clades, our data indicate that many of Carolin's smaller delineations within *S*. sect. *Xerocarpa* are monophyletic, despite the non-monophyly of the section itself.

Among the sampled species assigned to *S*. sect. *Scaevola*, three (*S. glabra*, *S. tomentosa*, and *S. spinescens*) appear to each be most closely related to separate species from *S*. sect. *Xerocarpa* rather than *S*. sect. *Scaevola*. The rest of *S*. sect. *Scaevola* is divided between two separate clades (northern and southern clades, Fig. 2) composed of multiple extra-Australian species (Fig. 1). The southern clade is sister to the entire globulifera clade, which includes the northern clade.

Some morphological characters are consistent with the northern and southern clades not being closely related. For instance, species in the southern clade have inflorescences in dense, many flowered, terminal racemes, whereas species in the northern clade have lax, axillary, cymose inflorescences with no more than eight flowers per cyme (one-flowered in *S. coriacea* and *S. gaudichaudii*). Additionally, the species in the southern clade have conspicuous barbulae in the throat of the corolla, a characteristic that is common in the family (Carolin et al., 1992), but completely absent in the Hawaiian endemic diploid lineage (although found in other members of the northern lineage).

Biogeography and dispersal—*Scaevola dispersal ability*—Our phylogenetic analyses suggest that *Scaevola*, despite being nested within a family otherwise confined to the Australian continent, has considerable dispersal ability. The phylogeny implies even more dispersal events than a pure count of species and geographic distributions would suggest. For example, it indicates that the most isolated island archipelago in the world, the Hawaiian Islands, was colonized three separate times.

While the traditional classification of *Scaevola* (Carolin, 1990) implies few origins of fleshy fruit, our molecular data suggest that fleshy fruits have evolved multiple times (Fig. 2). In fact, fruit fleshiness may have been a key innovation permitting transoceanic dispersal, given the fact that every species found outside of Australia has fleshy (drupaceous) fruits. Fleshy fruits likely facilitate dispersal by migrating sea birds, which can nest in montane habitats (Fosberg, 1947), and these birds occasionally add small fruits to their diets (Ziegler, 2002). In each case of extra-Australian dispersal (except in *S*. sect. *Enantiophyllum*), fleshy fruits appear to have evolved concomitantly (Fig. 2). Not all cases are as clear, however, because the Australian sister groups of *S. gracilis* (Dispersal 3) and of the northern clade (Dispersal 6) have partially fleshy fruits (Carolin et al., 1992; Sykes, 1998).

Single-species dispersal events—*Scaevola oppositifolia*, distributed in New Guinea, Indonesia, and the Philippines, is currently considered a separate species from *S. enantophylla* (Carolin et al., 1992), which occurs in northern Australia. *Scaevola oppositifolia* represents a case of dispersal northward from Australia, without subsequent speciation, although considerable morphological variability has resulted in descriptions of up to 10 separate species (Leenhouts, 1957).

Additionally, the ITS data suggest that the endemic Hawaiian tetraploid *Scaevola glabra* is sister to the two species in *S.* sect. *Xerocarpa* subsect. *Parvifoliae*, *S. angulata* and *S. depauperata* (Carolin et al., 1992). These two taxa are, like *S. glabra*, tall shrubs (≤1.5 m) and are often glabrous. The two Australian species differ from *S. glabra* in many morphological features, e.g., nontubular corollas and terminal inflorescences. Some similarity is seen, however, in the calyxes of the three species, which are basally fused with well-developed, free lobes. It is noteworthy that *S. angulata* has dispersed to islands off the coast of northern Australia, suggesting some significant dispersal ability.

Furthermore, the New Caledonian species *S. beckii* is not related to other New Caledonian species but rather to the Australian clade that includes *S. globosa*, *S. humifusa*, and *S. repens*. Phylogenetic reconstruction of the ITS data forcing *S. beckii* to associate with other island clades resulted in a significant increase in tree length (11 steps, Table 1). Additionally, the three Australian species are morphologically similar to each other and are united with *S. beckii* by having tiny flowers, bearded corollas, and one-seeded fruits. Thus, the evidence at hand supports *S. beckii* being a separate dispersal from Australia that has not resulted in subsequent speciation.

Similarly, *Scaevola gracilis*, occurring in New Zealand, the Kermadec Islands, and Tonga, is nested within an Australian lineage in our analysis (Fig. 2). Although, it falls in the general vicinity of the northern island clade, forcing it into that clade resulted in significantly longer trees (seven steps, Table 1).

The exact affinities of *S. gracilis* are unclear based on ITS data (Fig. 1). *Scaevola gracilis* is a broader endemic, being unusual among island species in its presence on multiple islands. This distribution may reflect the fact that this species has fruit that, unlike other montane species (Guppy, 1906), have retained the ability to float in seawater for up to 10 d (Sykes, 1998). Additionally, birds have been witnessed eating its fruits (Oliver, 1910) and may contribute to inter-island dispersal. Carolin's (1990) morphological analysis resolved *S. gracilis* and *S. calendulacea* as sister species. Other authors have also noted significant similarities between these two species as well as the other members of this clade (*S. crassifolia*, *S. lanceolata*, and *S. virgata*) in habit, type of indumentum, and presence of terminal spikes of sessile flowers (Carolin et al., 1992; Sykes, 1998). Interestingly, *Scaevola calendulacea* has white, partially fleshy fruits and occurs on the southeastern coast of Australia (Sykes, 1998). The relationships among these taxa require further investigation.

Southern clade—The southern clade comprises three well-supported lineages: (1) the widespread, strand species *S. taccada*, (2) the New Caledonian species (excluding *S. beckii*), and (3) the South Pacific taxa (excluding *S. gracilis*). The relationship among these three clades is unresolved.

Scaevola taccada occurs on tropical Pacific and Indian Ocean coasts including most islands that house endemic montane *Scaevola* species (Fig. 3C). The fruit morphology of *S. taccada* is distinct from the island endemics in its white fleshy exocarp and an additional corky layer underneath, which aids in oceanic flotation. The potential for *S. taccada* to disperse between islands appears greater than that for the montane endemics (Guppy, 1917; Lesko and Walker, 1969), supporting the possibility that on each island strand *S. taccada* have spawned montane endemic radiations. However, this hypothesis is contradicted by the fact that all accessions of *S. taccada*, from diverse geographic locations, form a well-supported monophyletic clade (Fig. 1).

An alternative scenario to explain the distribution of island endemics is via stepping-stone dispersal eastward from New Caledonia across the South Pacific into Fiji, Tahiti, Samoa, and the Marquesas Islands (Fig. 3C). This scenario is compatible with an apparent trend in inflorescence evolution. Island endemics in the southern clade have characteristically dense thyrsoid inflorescences. This feature becomes successively more pronounced from west to east, with the inflorescence in the Marquesan Island species superficially resembling a capitulum.

Northern clade—The northern clade contains four island lineages: (1) the widespread *Scaevola plumieri*, (2) the endemic Hawaiian diploids, (3) *S. socotraensis* (Socotra), and (4) *S. wrightii* (Cuba). Also included in the clade is *S. nitida* (Australia). Monophyly of this clade is not well supported based on ITS data nor is the relationship among the five component lineages resolved. Additionally, due to a lack of variation, the ITS data does not rule out the possibility that the Bornean taxa, *S. chanii* and *S. micrantha*, may be part of the same dispersal from Australia.

Scaevola plumieri is a widespread strand species that occurs on coasts of the tropical Americas and Africa, Madagascar, Ceylon, southern India, the Mascarenes, and the Galapagos Islands (van Balgooy, 1975, Fig. 3D). This species occurs in coastal habitats and has seeds that can float and remain viable for 4–5 mo (Guppy, 1917; Carlquist, 1974), although it lacks the corky layer of *S. taccada*. The finding that *S. socotraensis* and *S. wrightii* are closely related to *S. plumieri* is not surprising, given the biogeography of these species and their morphological similarity (M. H. G. Gustafsson, personal observation). Biogeographically, the relationship of the Hawaiian endemic diploids to these lineages is more anomalous because *S. plumieri* does not occur in the Hawaiian Islands, although the coastal species *S. coriacea* (from the Hawaiian Islands) shares more morphological similarity with *S. plumieri* than with *S. taccada* (observed by Carlquist, 1969). Additionally, St. John (1962) described *S. coriacea* as being the most similar to *S. socotraensis*.

Due to a lack of parsimony informative variation, the northern clade is a polytomy in the strict consensus tree. A single point mutation supports a clade of *S. plumieri* and *S. socotraensis*, and a different point mutation supports a clade of *S. plumieri* and the Hawaiian diploid clade. No base changes support the clade of *S. plumieri* and *S. wrightii* with the exclusion of the other two taxon groups. As with *S. taccada*, the monophyly of *S. plumieri* accessions (from Baja California to Senegal) argues against *S. plumieri* itself being the progenitor of multiple insular endemics.

The placement of *S. nitida* within this clade is not well supported by molecular data nor are there morphological characters that support this result. Therefore, *S. nitida* may be misplaced by these data (due to insufficient taxon sampling of Australian species), and a single, widely dispersed fleshy-fruited ancestor may have given rise to the northern clade (and perhaps also the Bornean species).

Colonization of the Hawaiian Islands—Fosberg (1947) hypothesized a single origin for all Hawaiian *Scaevola* species. The morphological analysis by Patterson (1995) with limited taxon sampling, on the other hand, supported at least two dispersal events with *S. glabra* clearly separate from the rest. Patterson (1995) argued for a third introduction; however, this was not strongly supported by his data, which resolved *S. taccada* as sister to the endemic Hawaiian diploid taxa. Most workers (Carlquist, 1967; Patterson, 1990, 1995; Sakai et al., 1995) have proposed three separate introductions, which concurs with our molecular phylogeny. Wagner (1996) suggested that *S. hobdyi* represented a fourth, separate introduction. In fact, because the single known specimen of *S. hobdyi* has anomalous vegetative features (narrowly linear, whorled leaves) and only a single floral bud, its relationships to *Scaevola* were initially overlooked. However, the ITS sequence from DNA extracted from the type specimen of *S. hobdyi* is identical to *S. kilaueae*, thus firmly placing it within the Hawaiian diploid clade and rejecting the four introductions hypothesis.

Hawaiian *Scaevola* represents immigrations from Australia (*S. glabra*), Polynesia (*S. taccada*), and possibly the Americas (the diploid endemic clade from Pacific coast *S. plumieri*). Molecular phylogenetic studies of other Hawaiian plant groups have found evidence of affinities with various geographic areas: Africa/Madagascar (*Kokia* [Seelanan et al., 1997], *Hesperomannia* [Kim et al., 1998]), the Americas (mints [Lindqvist and Albert, 2002], silversword alliance [Baldwin et al., 1991], *Geranium* [Pax et al., 1997], *Gossypium* [Dejoode and Wendel, 1992], *Bidens* [Ganders et al., 2000], *Rubus* [Howarth et al., 1997]), the Arctic (*Viola* [Ballard and Sytsma, 2000]), Polynesia (*Bidens* [Ganders et al., 2000], *Metrosideros* [Wright et al., 2000], *Pittosporum* [Gemmill et al., 2001], *Tetraplasandra* [Costello and Motley, 2001], *Tetramolopium* [Lowrey, 1995]), and Asia (Lobelioideae [Knox et al., 1993]). It is perhaps not surprising, therefore, that *Scaevola* lineages appear to have dispersed into the Hawaiian Islands from three divergent localities.

Despite the fact that multiple introductions into the Hawaiian Islands have been hypothesized for other plant groups (e.g., Fosberg, 1947; Sakai et al., 1995), this case is the first in which three separate introductions in a single angiosperm genus have been supported with molecular data. Application of molecular data, while supporting some hypotheses, has refuted many others. The most notable cases where multiple introductions were hypothesized were the three genera comprising the Hawaiian silversword alliance (*Argyroxiphium*, *Dubautia*, and *Wilkesia*) and the six genera of the Hawaiian lobeliods (*Brighamia*, *Cyanea*, *Clermontia*, *Delissia*, *Lobelia*, and *Trematolobelia*) that are each now thought to be the result of single introduction events (Baldwin et al., 1991; Givnish et al., 1996). Furthermore, the three genera of Araliaceae, *Tetraplasandra*, *Munroidendron*, and *Reynoldsia*, are now presumed to be the result of one introduction event (Costello and Motley, 2001), while alternatively, the two morphologically similar species of Hawaiian *Rubus* are now considered the result of two introductions, rather than one (Howarth et al., 1997).

It is also interesting that neither of the Hawaiian endemic *Scaevola* lineages (*S. glabra* and the Hawaiian diploids) share affinities with any South Pacific or Polynesian species. In other Hawaiian genera with relatives in Polynesia (*Metrosideros* [Wright et al., 2000], *Pittosporum* [Gemmill et al., 2001], *Tetraplasandra* [Costello and Motley, 2001], *Tetramolopium* [Lowrey, 1995], and *Bidens* [Ganders et al., 2000]), the Hawaiian groups appear to be closely related to their Polynesian cousins. Based on the present *Scaevola* distribution, it is startling that Hawaiian endemic *Scaevola* species are related to species in northern Australia and an American/African strand species, and not to the Polynesian species.

The Hawaiian Islands appear to have been colonized by both the southern clade (*S. taccada*) and the northern clade (the eight endemic diploids). Additionally, it appears that *S. glabra* originated from a third long-distance dispersal event. Therefore, despite their extreme isolation, the Hawaiian Islands have been colonized by three distinct lineages. Given that areas closer to Australia contain fewer lineages, the multiple colonizations of the Hawaiian Islands is surprising. One possible explanation is that, in *Scaevola*, niche availability is a greater barrier to ecological establishment than fruit dispersal. If so, it should not be surprising that more colonization could occur on the isolated but ecologically open Hawaiian Islands than in more proximate but more heavily occupied land masses. This hypothesis is supported by the fact that no new species of *Scaevola* have established themselves on continental areas outside Australia, despite the colonization by *S. taccada* and *S. plumieri*.

LITERATURE CITED

BALDWIN, B. G. 1992. Phylogenetic utility of the internal transcribed spacers of nuclear ribosomal DNA in plants: an example from the compositae. *Molecular Phylogenetics and Evolution* 1: 3–16.

BALDWIN, B. G., D. W. KYHOS, J. DVORAK, AND G. D. CARR. 1991. Chloroplast DNA evidence for a North American origin of the Hawaiian silversword alliance (Asteraceae). *Proceedings of the National Academy of Sciences, USA* 88: 1840–1843.

BALDWIN, B. G., M. J. SANDERSON, J. M. PORTER, M. F. WOJCIECHOWSKI, C. S. CAMPBELL, AND M. J. DONOGHUE. 1995. The ITS region of nuclear ribosomal DNA: a valuable source of evidence on angiosperm phylogeny. *Annals of the Missouri Botanical Garden* 82: 247–277.

BALLARD, J. H. E., AND K. J. SYTSMA. 2000. Evolution and biogeography of the woody Hawaiian violets (*Viola*, Violaceae): arctic origins, herbaceous ancestry and bird dispersal. *Evolution* 54: 1521–1532.

BAUM, D. A., R. L. SMALL, AND J. F. WENDEL. 1998. Biogeography and floral evolution of Baobabs (*Adansonia*, Bombacaceae) as inferred from multiple data sets. *Systematic Biology* 47: 181–207.

CARLQUIST, S. 1965. Island life: a natural history of the islands of the world. The Natural History Press, Garden City, New York, USA.

CARLQUIST, S. 1967. The biota of long distance dispersal. V. Plant dispersal to Pacific Islands. *Bulletin of the Torrey Botanical Club* 94: 129–162.

CARLQUIST, S. 1969. Wood anatomy of Goodeniaceae and the problem of insular woodiness. *Annals of the Missouri Botanical Garden* 56: 358–390.

CARLQUIST, S. 1974. Island biology. Columbia University Press, New York, New York, USA.

CARLQUIST, S. 1980. Hawaii, a natural history. Pacific Tropical Botanical Garden, Lawai, Hawai‘i, USA.

CAROLIN, R. C. 1966. Seeds and fruit of the Goodeniaceae. *Proceedings of the Linnean Society of New South Wales* 91: 58–83.

CAROLIN, R. C. 1978. The systematic relationships of *Brunonia*. *Brunonia* 1: 9–29.

CAROLIN, R. C. 1990. Nomenclatural notes, new taxa and the systematic arrangement in the genus *Scaevola* (Goodeniaceae) including synonyms. *Telopea* 3: 477–516.

CAROLIN, R. C., D. A. MORRISON, AND T. RAJPUT. 1992. Flora of Australia volume 35, Brunoniaceae, Goodeniaceae. Australian Government Publishing Service, Canberra, Australian Capital Territory Australia.

CARR, G. D. 1998. Chromosome evolution and speciation in Hawaiian flowering plants. *In* T. F. Stuessy and M. Ono [eds.], Evolution and speciation of island plants, 5–47. Cambridge University Press, Cambridge, UK.

COSTELLO, A., AND T. J. MOTLEY. 2001. Molecular systematics of *Tetraplasandra*, *Munroidendron* and *Reynoldsia sandwicensis* (Araliaceae) and the evolution of superior ovaries in *Tetraplasandra*. *Edinburgh Journal of Botany* 58: 229–242.

DEJOODE, D. R., AND J. F. WENDEL. 1992. Genetic diversity and origin of the Hawaiian Islands cotton, *Gossypium tomentosum*. *American Journal of Botany* 79: 1311–1319.

DOYLE, J. J., AND J. L. DOYLE. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf material. *Phytochemical Bulletin* 19: 11–15.

FELSENSTEIN, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791.

FITCH, W. M. 1971. Toward defining course of evolution: minimum change for a specific tree topology. *Systematic Zoology* 20: 406–416.

FOSBERG, F. R. 1947. Derivation of the flora of the Hawaiian Islands. *In* E. C. Zimmerman [ed.], Insects of Hawaii, vol. 1, 107–119. University of Hawai'i Press, Honolulu, Hawai'i, USA.

GANDERS, F. R., M. BERBEE, AND M. PIRSEYEDI. 2000. ITS base sequence phylogeny in *Bidens* (Asteraceae): evidence for the continental relatives of Hawaiian and Marquesan *Bidens*. *Systematic Botany* 25: 122–133.

GEMMILL, C. E. C., G. J. ALLAN, W. L. WAGNER, AND E. A. ZIMMER. 2001. Evolution of insular Pacific *Pittosporum* (Pittosporaceae): origin of the Hawaiian radiation. *Molecular Phylogenetics and Evolution* 22: 31–42.

GIVNISH, T. J., E. KNOX, T. B. PATTERSON, J. R. HAPEMAN, J. D. PALMER, AND K. J. SYTSMA. 1996. The Hawaiian lobelioides are monophyletic and underwent a rapid initial radiation roughly 15 million years ago. *American Journal of Botany* 83: 159 (Abstract).

GUPPY, H. B. 1906. Observations of a naturalist in the Pacific between 1896 and 1899, Plant dispersal. Macmillan, London, UK.

GUPPY, H. B. 1917. Plants, seeds and currents in the West Indies and Azores. Williams and Norgate, London, UK.

GUSTAFSSON, M. H. G., A. BACKLUND, AND B. BREMER. 1996. Phylogeny of the Asterales *sensu lato* based on *rbc*L sequences with particular reference to the Goodeniaceae. *Plant Systematics and Evolution* 199: 217–242.

GUSTAFSSON, M. H. G., E. GRAFSTROM, AND S. NILSSON. 1997. Pollen morphology of the Goodeniaceae and comparisons with related families. *Grana* 36: 185–207.

HASEGAWA, M., H. KISHINO, AND T. YANO. 1985. Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. *Journal of Molecular Evolution* 22: 160–174.

HOWARTH, D. G., D. E. GARDNER, AND C. W. MORDEN. 1997. Phylogeny of *Rubus* subgenus *Idaeobatus* (Rosaceae) and its implication toward colonization of the Hawaiian Islands. *Systematic Botany* 22: 433–441.

KÅREHED, J., J. LUNDBERG, B. BREMER, AND K. BREMER. 1999. Evolution of the Australasian families Alseuosmiaceae, Argophyllaceae and Phellinaceae. *Systematic Botany* 24: 660–682.

KIM, H.-G., S. C. KEELEY, P. S. VROOM, AND R. K. JANSEN. 1998. Molecular evidence for an African origin of the Hawaiian endemic *Hesperomannia* (Asteraceae). *Proceedings of the National Academy of Sciences, USA* 95: 15 440–15 445.

KISHINO, H., AND M. HASEGAWA. 1989. Evaluation of the maximum likelihood estimate of the evolutionary tree topologies from DNA sequence data, and the branching order in Hominoidea. *Journal of Molecular Evolution* 29: 170–179.

KNOX, E. B., S. R. DOWNIE, AND J. D. PALMER. 1993. Chloroplast genome rearrangements and the evolution of giant lobelias from herbaceous ancestors. *Molecular Biology and Evolution* 10: 414–430.

LEENHOUTS, P. W. 1957. Goodeniaceae. *Flora Malesiana ser. 1* 5: 335–344.

LESKO, G. L., AND R. B. WALKER. 1969. Effect of seawater on seed germination of two Pacific atoll beach species. *Ecology* 50: 730–734.

LINDQVIST, C., AND V. A. ALBERT. 2002. Origin of the Hawaiian endemic mints within North American *Stachys* (Lamiaceae). *American Journal of Botany* 89: 1709–1724.

LOWREY, T. K. 1995. Phylogeny, adaptive radiation, and biogeography of Hawaiian *Tetramolopium* (Asteraceae, Astereae). *In* W. L. Wagner and V. A. Funk [eds.], Hawaiian biogeography, evolution on a hot spot archipelago, 195–220. Smithsonian Institution Press, Washington, D.C. USA.

MORDEN, C. W., V. CARAWAY, AND T. J. MOTLEY. 1996. Development of a DNA library for native Hawaiian plants. *Pacific Science* 50: 324–335.

OLIVER, W. R. B. 1910. The vegetation of the Kermadec Islands. *Transactions and Proceedings of the New Zealand Institute* 42: 118–175.

PATTERSON, R. 1990. Goodeniaceae. *In* W. L. Wagner, D. R. Herbst, and S. H. Sohmer [eds.], Manual of the flowering plants of Hawai'i. University of Hawai'i Press and Bernice P. Bishop Museum Press, Honolulu, Hawai'i, USA.

PATTERSON, R. 1995. Phylogenetic analysis of Hawaiian and other Pacific species of Scaevola (Goodeniaceae). *In* W. L. Wagner and V. A. Funk [eds.], Hawaiian biogeography: evolution on a hot spot archipelago, 363–378. Smithsonian Institution Press, Washington, D.C., USA.

PAX, D. L., R. A. PRICE, AND H. J. MICHAELS. 1997. Phylogenetic position of the Hawaiian geraniums based on *rbc*L sequences. *American Journal of Botany* 84: 72–78.

PEACOCK, W. J. 1963. Chromosome numbers and cytoevolution in the Goodeniaceae. *Proceedings of the Linnean Society of New South Wales* 88: 8–27.

SAKAI, A. K., W. L. WAGNER, D. M. FERGUSON, AND D. R. HERBST. 1995. Origins of dioecy in the Hawaiian flora. *Ecology* 76: 2517–2529.

SEELANAN, T., A. SCHNABEL, AND J. F. WENDEL. 1997. Congruence and consensus in the cotton tribe (Malvaceae). *Systematic Botany* 22: 259–290.

ST. JOHN, H. 1962. A new *Scaevola* (Goodeniaceae) from Socotra Island. *Webbia* 17: 45–48.

STRUWE, L., M. THIV, J. W. KADEREIT, A. S. R. PEPPER, T. J. MOTLEY, P. WHITE, J. H. E. ROVA, K. POTGIETER, AND V. A. ALBERT. 1998. *Saccifolium* (Saccifoliaceae), an endemic of Sierra de la Neblina on the Brazilian-Venezuelan border, is related to a temperate alpine lineage of Gentianaceae. *Harvard Papers in Botany* 3: 199–214.

SWOFFORD, D. L. 2001. PAUP*: phylogenetic analysis using parsimony (*and other methods). Sinauer, Sunderland, Massachusetts, USA.

SYKES, W. R. 1998. *Scaevola gracilis* (Goodeniaceae) in the Kermadec Islands and Tonga. *New Zealand Journal of Botany* 36: 671–674.

TEMPLETON, A. R. 1983. Phylogenetic inference from restriction endonuclease cleavage site maps with particular reference to the evolution of humans and the apes. *Evolution* 37: 221–244.

THOMPSON, J. D., D. G. HIGGINS, AND T. J. GIBSON. 1994. Clustal W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research* 22: 4673–4680.

URBATSCH, L. E., B. G. BALDWIN, AND M. J. DONOGHUE. 2000. Phylogeny of the coneflowers and relatives (Heliantheae: Asteraceae) based on nuclear rDNA internal transcribed spacer (ITS) sequences and chloroplast DNA restriction site data. *Systematic Botany* 25: 539–565.

VAN BALGOOY, M. M. J. 1975. Pacific plant areas 3, Rijksherbarium, Leiden, Netherlands.

VON MUELLER, F. 1859. Goodeniaceae volume 9. *Fragmenta Phytographiae Australiae* 1: 203–207.

WAGNER, W. L. 1996. *Scaevola hobdyi* (Goodeniaceae), an enigmatic new species from West Maui, Hawaiian Islands. *Novon* 6: 225–227.

WHITE, T. J., T. BIRNS, S. LEE, AND J. TAYLOR. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. *In* M. Innis, D. Gelfand, J. Sninsky, and T. White [eds.], PCR protocols: a guide to methods and applications, 315–322. Academic Press, San Diego, California, USA.

WRIGHT, S. D., C. G. YONG, J. W. DAWSON, D. J. WHITTAKER, AND R. C. GARDNER. 2000. Riding the ice age El Nino? Pacific biogeography and evolution of *Metrosideros* subg. *Metrosideros* (Myrtaceae) inferred from nuclear ribosomal DNA. *Proceedings of the National Academy of Sciences, USA* 97: 4118–4123.

ZIEGLER, A. C. 2002. Hawaiian natural history, ecology, and evolution. University of Hawai'i Press, Honolulu, Hawai'i, USA.