EVOLUTION OF *CYRTANDRA* (GESNERIACEAE) IN THE PACIFIC OCEAN: THE ORIGIN OF A SUPERTRAMP CLADE[1]

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Cyrtandra comprises at least 600 species distributed throughout Malesia, where it is known for many local endemics and in Polynesia and Micronesia, where it is present on most island groups, and is among the most successfully dispersing genera of the Pacific. To ascertain the origin of the oceanic Pacific island species of *Cyrtandra*, we sequenced the internal transcribed spacers of nuclear ribosomal DNA of samples from throughout its geographical range. Because all oceanic Pacific island species form a well-supported clade, these species apparently result from a single initial colonization into the Pacific, possibly by a species from the eastern rim of SE Asia via a NW-to-SE stepping stone migration. Hawaiian species form a monophyletic group, probably as a result of a single colonization. The Pacific island clade of *Cyrtandra* dispersed across huge distances, in contrast to the apparent localization of the SE Asian clades. Although highly vagile, the Pacific clade is restricted to oceanic islands. Individual species are often endemic to a single island, characteristic of the "supertramp" life form sensu Diamond (1974, *Science* 184: 803–806). The evolution of fleshy fruit within *Cyrtandra* provided an adaptation for colonization throughout the oceanic Pacific via bird dispersal from a single common ancestor.

Key words: biogeography; Gesneriaceae; Hawaiian Islands; internal transcribed spacer; long-distance dispersal; molecular phylogeny; nuclear ribosomal DNA; oceanic islands.

Pacific plant geography—The patterns of distribution, means of dispersal, and evolution of plant life on the islands of the Pacific Ocean have interested biologists for centuries. Close relationships with Asia and Australia have been proposed for some taxa (Knox et al., 1993; Wright et al., 2000; Jaramillo and Manos, 2001; Howarth et al., 2003), whereas other groups have been hypothesized to originate from the Americas (Baldwin et al., 1991; DeJoode and Wendel, 1992; Howarth et al., 1997; Alice and Campbell, 1999; Ganders et al., 2000; Lindqvist and Albert, 2002; Wagner et al., in press). An intriguing question has been the number of times various taxa expanded their ranges onto the oceanic Pacific islands via long-distance dispersal. Some groups obviously have a single origin because they are limited to a single endemic species. In contrast, other taxa seem to have experienced a much greater expansion into the Pacific, and (1) are widespread among many islands, such as *Pandanus tectorius* (Pandanaceae; Wagner et al., 1990), (2) have undergone diversification and evolution resulting in numerous island endemics, such as *Psychotria* (Rubiaceae; Nepokroeff et al., 2003), or (3) are a combination of a few widespread species and endemic island species, such as *Metrosideros* (Myrtaceae) or *Scaevola* (Goodeniaceae; Howarth et al., 2003). Among these latter examples, there is still uncertainty whether the invasion of the Pacific has been the result of one or multiple introductions. In the case of *Metrosideros*, the phylogenetic results imply an origin in New Zealand of the Pacific island clade, but whether one or several migrations occurred is still ambiguous (Wright et al., 2000, 2001). On the other hand, *Scaevola* certainly appears to have expanded its range into the Pacific several times (Howarth et al., 2003).

One region that has been of particular interest and received a great deal of attention is the Hawaiian Islands. These islands are some of the most remote land areas on the planet and have a diverse array of endemic species. Ever since Fosberg's estimate of 272 original colonists accounting for all of the native angiosperms, speculation on the number of times various taxa have colonized the Hawaiian Islands (Sakai et al., 1995; Wagner et al., 2001) has ranged from a single to many introductions. With an increasing number of phylogenetic analyses using morphological and especially molecular data, more robust hypotheses have resolved this question, often with unexpected results. Some taxa that now appear to be the result of a single introduction and subsequent adaptive radiation had been thought to represent multiple introductions and were often placed in different genera, for example the lobelioids (Givnish et al., 1996) and *Psychotria* (Nepokroeff et al., 2003). In other instances, phylogenetic analyses have supported previous hypotheses of multiple introductions, such as *Scaevola* (Howarth et al., 2003). In one case, *Rubus*, once thought to be the result of a single introduction, has been shown to result from two separate events (Howarth et al., 1997; Alice and Campbell, 1999).

Island biotas are often noted as being disharmonic. Some

groups (poor dispersers) are under-represented, while others (good dispersers) are over-represented (Carlquist, 1970; Gressitt, 1982). Carlquist (1970) distinguished a set of innovations promoting long-distance dispersal in plants. These traits variously characterize families, genera, or single species (tramp species). Diamond (1974) coined the term ''supertramp'' for species of high dispersability that are only found on small or isolated islands—evidence that, in these cases, high dispersability compensates for ecological specialization (as marked, for instance, by physiological characteristics) (McNab, 2002).

Certain lineages of plants (supertramp clades), although widely found on oceanic islands, are not present on continental regions. This is likely to be due to ecological factors rather than low dispersability. The New Zealand and Pacific island clade of *Metrosideros* (Wright et al., 2000; Wright et al., 2001) is one such supertramp clade. Notably, very few examples of back-colonization from oceanic islands to continents are known, even by groups of plants that are widely distributed around the Pacific Ocean. The phylogenetic investigation of taxa that are widely dispersed on oceanic islands (in relation to their continental relatives), is therefore of interest to shed light on the origin of these potential supertramp clades and to determine rates if any, of back-colonization and the frequency with which oceanic island colonization has occurred. For groups with large numbers of species distributed widely over the Pacific, there are two contrasting possibilities of origin. First, wide dispersal may result from frequent independent colonizations from the continental progenitor group. In this case, the adaptations for dispersal must reside widely within the ''springboard'' continental group (e.g., *Scaevola*: Howarth et al., 2003). Secondly, a single colonization may result in the wide distribution and evolutionary radiation from within a single oceanic clade. In this case, a key innovation is implicated that results in higher dispersability in a single supertramp lineage. The genus *Cyrtandra* (Gesneriaceae), which is common in the Pacific, provides an excellent case for investigation of patterns in Pacific-wide species. Phylogenetic methods have the potential to determine whether *Cyrtandra* is a springboard genus that has led to multiple colonizations of the Pacific, or whether a single supertramp clade has resulted in all the *Cyrtandra* species of Micronesia and Polynesia.

The genus Cyrtandra—*Cyrtandra* J. R. & G. Forst. (Gesneriaceae) is a genus of at least 600 species (the description of new species, especially in SE Asia and New Guinea, is still in progress). It is easily recognizable by a combination of ''cyrtandroid'' characters: its two-stamened flowers (anomalous five-stamened forms are very rare; Gillett, 1970), often somewhat fleshy leaves, and generally ellipsoidal indehiscent fruits. However, the genus is extremely variable in life history traits. It ranges from dwarf herbs through climbers, epiphytes, and even small trees. The flowers are usually white, but species with pink, red, yellow, and orange flowers are also known. It ranges from southern Thailand and the Nicobar Islands, through peninsular Malaysia, throughout Malaysia and Indonesia and the Philippines, to Papua New Guinea, the New Hebrides (Gillett, 1974), the Solomon Islands (Gillett, 1975), and Northern Queensland, Australia. Regions of particularly high diversity include Sumatra, Borneo, the Philippines (Merrill, 1922), Sulawesi, and (especially) New Guinea. Most of the species are regionally localized or even endemic to single mountains (Atkins and Cronk, 2001; Bramley and Cronk, 2003).

Cyrtandra is also extremely common on the oceanic islands of the Pacific with approximately 58 species in the Hawaiian Islands (Wagner, 1999), eight species in the Marquesas Islands, and 12 species in the Society Islands (Gillett, 1973). It also occurs in Micronesia, Fiji (Smith, 1953, 1991; Gillett, 1967), Samoa, Tonga, and throughout French Polynesia (Gillett, 1973). Most of the species occur on single islands only, often being extremely local endemics. For instance, the recently described Hawaiian endemic, *Cyrtandra paliku*, is known only from about 70 individuals on northern exposed rock faces on Mount Namahana (Wagner et al., 2001).

Ecologically, *Cyrtandra* is almost entirely restricted to rain forest regions, being absent from dry, seasonal areas. It is very sensitive to disturbance of the canopy and disappears quickly after logging; hence it is now almost entirely absent from regions of the SE Asian tropics where the forest experienced extensive human disturbance. This sensitivity, coupled with the large numbers of local endemics, suggests that *Cyrtandra* may have suffered a high rate of extinction in some areas. It is also vulnerable to extinction on oceanic islands, where it typically grows in submontane forests and thickets on steep slopes or gulches on the high islands. Thus the genus has potential as an indicator of historical and current disturbance of island forest systems (Kiehn, 2000). Relatively few hybrids have been reported, and it is only on Hawaii, where different species grow together that some species have been shown to hybridize (Wagner et al., 1990; Smith et al., 1996).

The last complete survey of the genus was carried out by Clarke (1883), who divided the species then known into several sections, although these sections have generally been regarded by subsequent taxonomists as highly tentative. Gillett (1973) did not consider any infrageneric classification (formal or informal) possible, based on the instability of character combinations. The most recent treatment of the genus for the Hawaiian islands (Wagner, 1999) divides the species among six sections. Considering the size and importance of the genus in SE Asia, little recent taxonomic work has been carried out on the Asian species. Most of the recent studies have been local studies describing new species (Burtt, 1970, 1978, 1990; Atkins and Cronk, 2001; Bramley and Cronk, 2003). However, recent molecular work suggests the existence of regional clades within SE Asia (Atkins et al., 2001). Despite considerable morphologic variability, certain geographical trends have been suggested. Foliar sclereids (Burtt and Bokhari, 1973) are very common in Bornean species, but are less common in species further east. Foliar sclereids are not found in Pacific Ocean species. As regards pollen morphology, Hawaiian and South Pacific species of *Cyrtandra* show a high degree of uniformity, whereas West Malaysian species proved rather heterogeneous (Luegmayr, 1993a, b; Kiehn, 2001; Schlag-Edler and Kiehn, 2001). Seed surface morphology studied by Beaufort-Murphy (1983) and Mühlbauer and Kiehn (1997) revealed two types (reticulate and striate) present across almost the whole distribution area of *Cyrtandra* except the Hawaiian Islands, where only the reticulate type occurs. Cytologically, the large majority of the counted *Cyrtandra* species revealed a diploid number of $2n = 34$, indicating a high degree of conservation of chromosome number in the genus (Möller and Kiehn, 2003). Differences may only be present at the chromosome structural level (Storey, 1966; Kokubugata and Madulid, 2000). Fruits of eastern species tend to be tough walled and green or brown at ripeness, whereas eastern species (and

particularly Pacific species) tend to have fleshy fruits, often ripening white.

Given such a large and widely distributed genus, it would not be surprising if the oceanic islands of the Pacific had been colonized several times independently from the species-rich source region in Asia. Nevertheless, compared to the genus as a whole, the Pacific island species are relatively uniform, but this may be due to the ecologically uniform conditions on oceanic islands. This paper addresses the question of the origin of the oceanic island species using phylogenetic methods, which with certain caveats (Emerson, 2002), are powerful tools for the study of oceanic island biogeography. Given the extremely wide dispersion of *Cyrtandra* among the oceanic islands of the Pacific, knowledge of the origin of these colonization events from the various continental progenitors might be expected to shed light on the interesting question of the evolution of dispersability.

MATERIALS AND METHODS

Sampling and plant material: outgroup and ingroup taxa—Twenty-three Pacific island species of *Cyrtandra*, including 14 species representing all six Hawaiian sections, along with 13 species from mainland Asia, Indonesia, Philippines, Australia, and Taiwan, representing all sections of Clarke (1883), and clades recovered from recent phylogenetic analyses (Atkins et al., 2001), were sampled for a total of 36 species (Appendix, see Supplemental Data accompanying online version of this article). A single species of *Aeschynanthus* was used as the outgroup for the analysis, following Atkins et al. (2001). *Aeschynanthus* is a genus unambiguously distinct from *Cyrtandra*, and available evidence (Mayer et al., 2003) suggests that *Aeschynanthus* is part of the sister clade to *Cyrtandra*.

Molecular methods—Fresh, frozen, or silica-gel-dried leaf material of one plant of each species was used for total DNA extraction using a modification of the CTAB procedure of Doyle and Doyle (1987) with no further purification or with Qiagen DNeasy extraction kits (Qiagen Ltd, Dorking, Surrey, UK) following the manufacturer's instructions. The complete ITS region was amplified with the polymerase chain reaction (PCR) using the primers and following the protocols of Möller and Cronk (1997) or those of Smith (2000). The PCR products were purified prior to sequencing using either the QIAquick PCR purification kit (Qiagen) or Wizard purification kits (Promega, Madison, Wisconsin, USA). Purified PCR products were sequenced using either a dye terminator cycle-sequencing ready-reaction kit on an ABI 377 Prism Automatic DNA sequencer (Perkin Elmer, Applied Biosystems, Foster City, California, USA) as described in Atkins et al. (2001), manually using silver sequencing (Promega) and the methods of Smith et al. (1997) or on a Li-Cor LongreadIR 4200 automated sequencer (Li-Cor, Lincoln, Nebraska, USA). For each taxon, forward and reverse sequencing reactions were performed for sequence confirmation. Both ITS regions were aligned using the CLUSTAL option in the multiple alignment program Sequence Navigator Version 1.0.1 software package (Perkin Elmer, Applied Biosystems), with minor manual adjustments. The GC content was determined by inspection. Sequence divergence among taxa was calculated using the distance matrix option in PAUP* 4.0b10 (Swofford, 2000), based on unambiguously alignable regions. All sequences have been submitted to Genbank (Appendix).

Phylogenetic analysis—The data were analyzed using PAUP* 4.0b10 (Swofford, 2000). Maximum parsimony (MP) analyses were conducted for each data set using 1000 random stepwise addition replicates with tree-bisection-reconnection (TBR) branch swapping algorithm and MulTrees on, saving all shortest trees. The shortest trees from all searches were used to generate a strict consensus. Bootstrap support (BS) for nodes (Felsenstein, 1985) was estimated with 100 heuristic simple taxon addition searches using TBR and Multrees on. Decay indices (DI; Bremer, 1988) for individual clades were obtained by comparing the strict consensus of all equal-length trees up to six

TABLE 1. Summary of ITS sequence variability for all taxa and for Pacific and non-Pacific species. Non-Pacific species include information for the outgroup.

	Pacific species	Non-Pacific species	Total
Length range	427–464	438–506	427–506
Sequence divergence (%)	0.22–9.62	6.87–27.4	0.22–27.4
Number of indels	19	27	75
Indel size	1–15	1–9	1–15
GC content (%)	55.7	57.2	56.3
Phylogenetically informative sites (%)	9.0	17.9	28.7

steps longer than the shortest tree, using simple addition sequence and TBR in PAUP*. Clades that persisted in the strict consensus for six steps longer than the most parsimonious trees were examined using the constraint option of PAUP*. Descriptive statistics reflecting the amount of phylogenetic signal in the parsimony analyses were given by the consistency index (CI; Kluge and Farris, 1969), retention index (RI; Farris, 1989), and the resulting rescaled consistency index (RC). Only combined ITS-1 and ITS-2 sequence data (boundaries determined by alignment with known sequences) were subjected to phylogenetic analyses. Indels were scored as a separate presence/absence character and added to the sequence data matrix. To investigate the effect of these additional data, separate analyses with and without a gap matrix were undertaken.

Bayesian analyses were conducted using MRBAYES version 3.0B4 (Huelsenbeck and Ronquist, 2001). Initial analyses used 100 000 generations, four chains, and temperature of 0.2 to determine the burn-in period. These results indicated that a burn-in of 25 000 generations was more than sufficient to reach a plateau, and subsequent analyses used two million generations and the general time reversible (GTR) model with a gamma distribution and invariant characters as suggested by the Aikake information criterion (AIC) of MODELTEST (Posada and Crandall, 1998).

RESULTS

Sequence analysis—Sequences for combined ITS-1 and ITS-2 (excluding the 5.8S gene) ranged from 427 to 506 bp with a mean of 465 bp. In general, sequences for the non-Pacific species were longer than those of the Pacific species, ranging from 438 to 506 and 427 to 464, respectively. Pairwise sequence variability ranged from 0.22 to 27.4%, and again, the greater variability was among the non-Pacific species, 6.87–27.4% compared with 0.22–9.62%. Aligned sequences had a length of 564 bp that included a total of 75 indels (based on opening a gap in the sequence, regardless of length), ranging from one to 15 bp. Of these indels, 31 were a single bp and 16 were autapomorphic (often for the outgroup *Aeschynanthus*). A summary of sequence variability for both the Pacific and non-Pacific clades is presented in Table 1.

Phylogenetic analysis—Maximum parsimony analysis of the aligned matrix of 37 taxa resulted in 5905 most parsimonious trees of length 693 with indels excluded from the analysis (CI = 0.56, RI = 0.71). A strict consensus tree based on the results of analyses that included the gap matrix did not differ from the strict consensus that excluded indels, therefore only the data that excluded indels will be presented herein. In addition, a Bayesian analysis was performed using a GTR model with gamma distribution and invariant characters as the best fit determined using the AIC of MODELTEST (Posada and Crandall, 1998). The MP strict consensus and the Bayesian analysis resulted in identical topologies, although the Bayesian consensus was better resolved. The MP strict con-
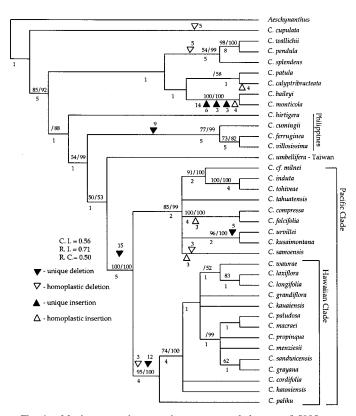
Fig. 1. Maximum parsimony strict consensus cladogram of 5905 trees. Numbers above branches are bootstrap values before the slash (only values greater than 50% are shown), Bayesian inference values after the slash. Decay indices are below branches. Triangles represent insertions relative to other taxa, and inverted triangles represent deletions. Only indels of 3 bp or greater that could be plotted onto the strict consensus tree are shown. The size of the indels is indicated with each triangle. Solid triangles are unique, open ones indicate homoplasy elsewhere in the tree. The consistency index is 0.56, retention index 0.71, and rescaled consistency index 0.50.
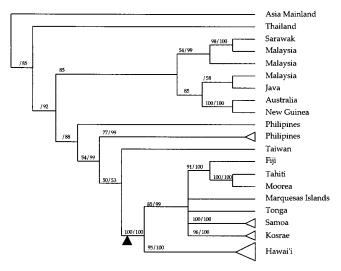

Fig. 2. Area cladogram showing the geographic structuring of the analysis. Numbers above branches are bootstrap values before the slash (only values greater than 50% are shown), Bayesian inference values after the slash. The solid triangle marks a 15-bp deletion. The size of the triangles used as terminals is relative to the number of species sampled from that geographic region.

sensus is shown in Fig. 1, with bootstrap values greater than 50% and Bayesian inference (BI) values shown. *Cyrtandra cupulata*, a species from peninsular Malaysia, is sister to the rest of the sample (BS = 85, BI = 92). Next, the phylogeny divides into two groups, although with weak (<50%) bootstrap support. One includes all the Pacific species, the Philippine species, and a species from the Bataan Islands (Taiwan). The other clade includes species from Malaysia, Indonesia, Borneo, Australia, and New Guinea. Within the former clade, two large subgroups have high support. These are the "Pacific clade" (BS = 100, BI = 100), sister to *C. umbellifera* of the Bataan Islands (Taiwan), and the "Hawaiian clade" (BS = 95, BI = 100). A 15-bp deletion supports the monophyly of the Pacific species, and a 12-bp deletion supports the monophyly of the Hawaiian clade. The species from northern Queensland (*C. baileyii*) groups closely with *C. monticola* (BS = 100, BI = 100), which is from adjacent parts of Papua New Guinea, implying that the only species in Australia is the result of colonization from the hugely species-rich New Guinea *Cyrtandra* flora.

Relationships of Pacific Cyrtandra—The Pacific clade is divided into two distinct clades, each receiving high support. The first clade, with BS of 95 and BI of 100 (Fig. 1) is comprised of the Hawaiian endemic species. This clade is clearly

monophyletic based on the data presented here. Further support comes from a 12-bp indel unique to the Hawaiian species. Current sampling places *C. paliku* as the sister to all remaining species, with moderate to strong support from these data (BS = 74, BI = 100). *Cyrtandra paliku* is a recently described species from Kaua'i, and although it is tempting to speculate on a Kaua'i origin for the Hawaiian clade, this can only be speculative based on the current sampling (14 of 58 species). Three other species—*C. longifolia*, *C. kauaiensis*, and *C. wawrae*—are also endemic to Kaua'i, but do not show a closer relationship to *C. paliku* than to other species, nor do they form a monophyletic group. Beyond the placement of *C. paliku*, no relationship within the Hawaiian clade receives strong support from BS, although one clade of species is supported with BI of 99 (*C. propinqua*, *C. menziesii*, *C. paludosa*, *C. macraei*, *C. sandwicensis*, and *C. grayana*).

The second clade with BS of 85 and BI of 99 (Figs. 1, 2) comprises the non-Hawaiian Pacific species. As with the Hawaiian clade, different island groups of species receive moderate to strong support, but relationships among these clades are less strongly supported. The MP analysis does not resolve relationships among the different island clades, although a BS consensus tree weakly (BS = 38, data not shown) places *C. samoensis* from Tonga as sister to the remaining sampled species. In contrast, the Bayesian analysis tree (data not shown) places *C. tahuatensis* from the Marquesas Islands as sister to the remaining species, although again with much less support than is seen in other parts of the tree (BI = 68), and places *C. samoensis* from Tonga as sister to the Samoan species (BI = 84). Two clades for the Tongan/Samoan species, one comprising *C. samoensis* and the other the "inland species," were revealed by AFLP analysis (M. Kiehn, unpublished results).

DISCUSSION

Phylogenetic relationships between Pacific and continental Cyrtandra—The area cladogram (Fig. 2) shows that the samples of *Cyrtandra* analyzed here (36 of ~600 species) fall into

a series of geographically structured clades, as also noted by Atkins et al. (2001). All current evidence indicates that *Cyrtandra* as a whole is monophyletic. Although it is possible that other genera will be found to be phylogenetically nested within *Cyrtandra*, no morphological evidence supports this, and generic-level sequencing work in the Cyrtandroideae has not revealed any likely candidates. The geographical structuring of clades within an apparently monophyletic *Cyrtandra*, therefore, represents an interaction between the evolution of the genus and geotectonic, climatological, and dispersal events.

The Pacific species (Polynesian and Micronesian) form a highly supported monophyletic group (BS = 100, BI = 100). Because most of the islands are oceanic in origin, tectonically driven vicariance or land connection events can be ruled out, and a single dispersal into the Pacific followed by numerous subsequent interisland dispersals is the most likely explanation. Although the Pacific *Cyrtandra* species have been considered highly variable (and have been placed in several sections), they are remarkably uniform relative to the diversity across all species. The overwhelming majority are medium-sized shrubs with white, somewhat campanulate flowers and fleshy leaves. The pollen of these species is uniform (Luegmayr, 1993a, b; Schlag-Edler and Kiehn, 2001), and foliar sclereids are absent (Burtt and Bokhari, 1973). Even in the Hawaiian Islands where the morphological variation is greatest, Carlquist (1970, p. 155.) was of the opinion that "[v]ery likely, the Hawaiian species represent a single stock." The Pacific clade in this analysis is sister to the Taiwanese species *C. umbellifera*, and together with this species they are sister to a group of primarily eastern SE Asian species that share the shrubby habit, fleshy leaves, and white, somewhat campanulate corollas. The apparent relationship with *C. umbellifera* is interesting because this species is restricted to the Bataan Islands (between Taiwan and the Philippines) and so is an insular species itself. It therefore appears that the major barrier to dispersal has been leaving the SE Asian rainforests; once the Pacific Ocean was colonized, frequent long-distance dispersal between islands across the Pacific subsequently occurred.

Radiation within the Pacific clade and the origin of the Hawaiian species—Within the Pacific *Cyrtandra* clade are two relatively well-supported clades (Figs. 1, 2). One of these represents the Hawaiian clade, the second all other Pacific island species (Fig. 2). The sister group relationship between the Hawaiian clade and all other Pacific islands implies an early dispersal into the Hawaiian Islands. The pattern is suggestive of a stepping stone model with the Hawaiian Islands being the first stop into the Pacific. However, from these data it is clear that the origin of the non-Hawaiian Pacific species is not from within the extant Hawaiian species of *Cyrtandra*. The Hawaiian clade is well-supported as sister to the non-Hawaiian clade, rather than being a paraphyletic assemblage that includes a monophyletic non-Hawaiian group, as would be expected if the Hawaiian Islands were serving as a stepping stone as seen with *Metrosideros* (Wright et al., 2000). One alternative explanation may be sampling. The Hawaiian Islands are home to 58 endemic species of *Cyrtandra* (Wagner, 1999), and with only 14 species sampled here, it is possible that greater sampling may reveal the non-Hawaiian clade to be imbedded within the group of Hawaiian species. However, ITS sequences from 32 additional species of Hawaiian *Cyrtandra* align more completely with the Hawaiian species sampled here and share

a 12-bp deletion unique to the Hawaiian *Cyrtandra* species sampled here (J. Smith, unpublished results). A better explanation for the sister group relationship among the Pacific species may be a missing ancestor that either has not been sampled (e.g., many Fijian species have not been sampled) or is extinct. The current high islands of the Hawaiian chain are of recent origin; however, the Hawaiian hot spot is known to have existed in the same general region for 84 million years (Clague, 1997), and it is possible that one of these earlier islands served as the first stepping stone for *Cyrtandra* into the Pacific. This missing ancestor may have given rise to two separate radiations, one in the Hawaiian Islands, the other in the remaining Pacific islands.

The ITS data presented here also imply that *Cyrtandra* colonized the Hawaiian Islands once (Figs. 1, 2). This is contrary to previous hypotheses based on morphological diversity (St. John, 1966; Gillett, 1973; Wagner, 1990), but in accordance with earlier molecular studies (Samuel et al., 1997; Kiehn, 2001) and with the proposal of a single (or two) origin(s) for the Hawaiian *Cyrtandra* by Carlquist (1970). The 58 Hawaiian species of *Cyrtandra* are morphologically disparate and have been classified into six distinct sections, each thought to represent a separate introduction (except section *Apertae*), with possibly one additional introduction within section *Crotonocalyces* for *C. kealiae*. The separate colonizations have been proposed because of the shared morphological characters within each of these groups of species and morphological similarities to non-Hawaiian species. Despite the high degree of morphological diversity among the Hawaiian species and shared morphological characteristics with some non-Hawaiian, especially Fijian, species, the ITS data presented here imply a single colonization of the Hawaiian Islands (Figs. 1–3). Again, a limitation may be in our sampling, both from within the Hawaiian species and from the non-Hawaiian clades. However, we have sampled from many of the other Pacific islands that have been presumed to be the ancestral home of the Hawaiian species (Samoa, Fiji, Marquesas, New Guinea), and we have sampled from each of the sections (Appendix) of the Hawaiian species. (ITS sequence variability in *C. kealiae* also implies it is monophyletic with the Hawaiian species sampled here and is not more closely related to any of the non-Hawaiian species [J. Smith, unpublished results].) Although a slight chance remains that some of the Hawaiian species may be from an independent colonization event, the evidence currently available strongly suggests a single event. Single colonization events for Hawaiian island plants have become the most common scenario since they were analyzed phylogenetically and is now the current hypothesis for *Psychotria* (Nepokroeff et al., 2003), the lobelioids (Givnish et al. 1996), and some members of Araliaceae (Costello and Motley, 2001).

Biogeography of Cyrtandra in the Pacific: the supertramp clade—The monophyly of the Pacific oceanic species raises two questions: Why did *Cyrtandra* colonize the Pacific only once? How was *Cyrtandra* subsequently able to disperse to all the larger Micronesian and Polynesian islands? It is possible that the successful colonization of the Pacific required pre-adaptations for long-distance dispersal, both in dispersal mechanism itself and in the ecological potential for establishment on oceanic islands, which are not widely present in the species of the SE Asian rainforests. One possible factor is fruit type: the Pacific species have rather fleshy fruits (usually ripening to white, but also to orange or green), whereas many (but not
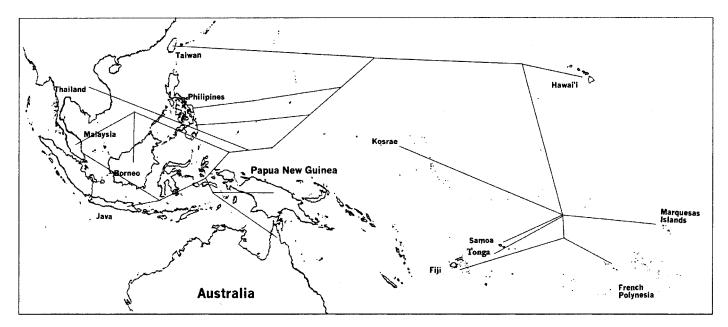
Fig. 3. The topology of the cladogram superimposed onto a map of the Pacific showing the relationships of the species from the various areas.

all) of the western species, for instance from Borneo and Sumatra, have hard fruits that ripen to green or brown. Columbiform birds, highly dispersant frugivores, are characteristic features of the Pacific islands (and were more so before anthropically caused extinctions; Steadman, 1997). However, although columbiforms would be good candidates for interisland dispersal of the fleshy fruits, no observations have yet been made of fruit dispersal in *Cyrtandra*. Palatability tests of *Cyrtandra* fruits by various vertebrate candidates would be interesting in this regard. The seeds of *Cyrtandra* are numerous, minute, and covered by sticky fruit flesh, making external (as well as internal) transport by birds a further possibility, as pointed out by Carlquist (1970). Short-distance transport of seeds could also be through water because some of the fleshy fruits (e.g., Hawaiian *C. paludosa*) open with slits and release the seeds as dispersal units (Kiehn, 2001). Sakai et al. (1995) and Price and Wagner (2004) have hypothesized external bird dispersal of the minute seeds by shore birds, such as the Pacific Golden Plover.

The other important possible pre-adaptation is the ecological potential for colonization. One aspect of this is the potential for pollination by pollen vectors present on oceanic islands. Yet again, however, there are no data on pollination in *Cyrtandra*. However, floral shape and color differs greatly among SE Asian species, suggesting possible adaptation to specialist pollinators. The rather open, white flowers of the Pacific species suggest possible pollination by generalist insects, which may be an advantage for colonists. Autogamy is another potential mechanism to promote vagility, but the showy flowers, the tendency to gynodioecy in *C. longifolia* (Carlquist, 1970; Wagner et al., 1990; Kiehn, personal observation) and interspecific hybrids (Wagner et al., 1990; Smith et al., 1996; Kiehn et al., 2001) suggest out-crossing. However, studies should be conducted to determine if autogamy occurs in both island and nonoceanic species. Habitat versatility has been suggested as another important factor in vagility (Wilson, 1959; Williams, 1969; Carlquist, 1970), based on animal studies, which indicate that habitat generalists, particularly those capable of sur-

viving in dry sites, are responsible for colonization, followed by evolutionary specialization into wet sites. However, there is no evidence of this in Pacific *Cyrtandra*, a genus of ecological specialists of wet shady sites, typically in wet montane gullies.

In gaining the extraordinary dispersability that has made it ubiquitous in the Pacific, the Pacific *Cyrtandra* clade has apparently become a supertramp clade (following the terminology of Diamond, 1974). Tramp species have high dispersability, whereas supertramp species are adapted to conditions on small and remote islands, which they can reach because of their extremely high vagility. Evidence for the supertramp hypothesis in birds comes from disharmonic patterns of distribution of bird species on islands (Diamond, 1974, 1975, 1982). Pacific *Cyrtandra* species are all island endemics because they have evolved into endemic species wherever interisland colonization events have occurred. It is therefore necessary to think in terms of a supertramp clade with high interisland dispersability, but where there is no evidence of backcolonization to the rainforest habitats of SE Asia. The single colonization of the Pacific followed by wide dispersion within Micronesia and Polynesia suggests that the Pacific *Cyrtandra* clade, by gaining adaptations for dispersal as well as specialist adaptations to island ecology, has become a supertramp clade with only limited evolutionary potential to recolonize the tropical rainforest from whence it came. To test the supertramp hypothesis, and hence absence of back-colonization of rainforest (which the dispersability of Pacific *Cyrtandra* would certainly make possible), extensive further sampling of *Cyrtandra* species along the eastern margin of the SE Asian plate, particularly the Philippines, New Guinea, New Hebrides, and the Bismark Archipelago would be necessary. This further sampling would also help to refine the origins of the Pacific clade.

LITERATURE CITED

ALICE, L. A., AND C. S. CAMPBELL. 1999. Phylogeny of *Rubus* (Rosaceae) based on nuclear ribosomal DNA internal transcribed spacer region sequences. *American Journal of Botany* 86: 81–97.

ATKINS, H., AND Q. C. B. CRONK. 2001. The genus *Cyrtandra* (Gesneriaceae) in Palawan, Philippines. *Edinburgh Journal of Botany* 58(3): 443–458.

ATKINS, H. J., J. PRESTON, AND Q. C. B. CRONK. 2001. A molecular test of Huxley's line: *Cyrtandra* (Gesneriaceae) in Borneo and the Philippines. *Biological Journal of the Linnean Society* 72: 143–159.

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.

BEAUFORT-MURPHY, H. T. 1983. The seed surface morphology of the Gesneriaceae utilizing the scanning electron microscope and a new system for diagnosing seed morphology. *Selbyana* 6: 220–422.

BRAMLEY, G. L. C., AND Q. C. B. CRONK. 2003. The *Cyrtandra* (Gesneriaceae) species of Mount Kerinci, Sumatra. *Harvard Papers in Botany* 7: 407–421.

BREMER, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* 42: 795–803.

BURTT, B. L. 1970. Studies in the Gesneriaceae of the Old World. XXXIII. Some species of *Cyrtandra*, chiefly Bornean. *Notes from the Royal Botanic Garden Edinburgh* 30: 23–42.

BURTT, B. L. 1978. Studies in the Gesneriaceae of the Old World. XLIV. New and little-known species of *Cyrtandra*, chiefly from Sarawak. *Notes from the Royal Botanic Garden Edinburgh* 36: 157–179.

BURTT, B. L. 1990. Gesneriaceae of the Old World, I. New and little-known species of *Cyrtandra* from Malesia. *Edinburgh Journal of Botany* 47: 201–233.

BURTT, B. L., AND M. H. BOKHARI. 1973. Studies in the Gesneriaceae of the Old World. XXXVI. Foliar sclereids in New Guinea and Pacific *Cyrtandra*. *Notes from the Royal Botanic Garden Edinburgh* 32: 397–402.

CARLQUIST, S. 1970. Island biology. Columbia University Press, New York, New York, USA.

CLAGUE, D. A. 1997. The growth and subsidence of the Hawaiian-Emperor volcanic chain. *In* A. Keast and S. E. Miller [eds.], The origin and evolution of Pacific Island biotas, New Guinea to Eastern Polynesia: patterns and processes, 35–50. SPB Academic Publishing, Amsterdam, Netherlands.

CLARKE, C. B. 1883. Cyrtandreae. *In* A. de Candolle and C. de Candolle [eds.], Monographia phanerogamarum, vol. 5, 1–303, 32 plates. G. Masson, Paris, France.

COSTELLO, A., AND T. J. MOTLEY. 2001. Molecular systematics of *Tetraplesandra*, *Munroidendron*, and *Reynoldsia sandwicensis* (Araliaceae) and the evolution of superior ovaries in *Tetraplesandra*. *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.

DIAMOND, J. M. 1974. Colonization of exploded volcanic islands by birds: the supertramp strategy. *Science* 184: 803–806.

DIAMOND, J. M. 1975. Assembly of species communities. *In* M. L. Cody and J. M. Diamond [eds.], Ecology and evolution of communities, 342–444. Harvard University Press, Cambridge, Massachusetts, USA.

DIAMOND, J. M. 1982. The biogeography of the Pacific Basin. *Nature* 298: 604–5.

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

EMERSON, B. C. 2002. Evolution on oceanic islands: molecular phylogenetic approaches to understanding pattern and process. *Molecular Ecology* 11: 951–966.

FARRIS, J. S. 1989. The retention index and homoplasy excess. *Systematic Zoology* 38: 406–407.

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

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.

GILLETT, G. W. 1967. The genus *Cyrtandra* in Fiji. *Contributions of the U.S. National Herbarium* 37: 107–159.

GILLETT, G. W. 1970. The taxonomic status of *Protocyrtandra* (Gesneriaceae). *Journal of the Arnold Arboretum* 51: 241–246.

GILLETT, G. W. 1973. The genus *Cyrtandra* (Gesneriaceae) in the South Pacific. *University of California Publications in Botany* 66: 1–59.

GILLETT, G. W. 1974. New records for *Cyrtandra* (Gesneriaceae) in the New Hebrides. *Kew Bulletin* 29: 699–709.

GILLETT, G. W. 1975. *Cyrtandra* (Gesneriaceae) in the Bismarck Archipelago and Solomon Islands. *Kew Bulletin* 30: 371–412.

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

GRESSITT, J. L. 1982. Pacific-Asian biogeography with examples from the Coleoptera. *Entomologia Generalis* 8: 1–11.

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

HOWARTH, D. G., M. H. G. GUSTAFSSON, D. A. BAUM, AND T. J. MOTLEY. 2003. Phylogenetics of the genus *Scaevola* (Goodeniaceae): implication for dispersal patterns across the Pacific Basin and colonization of the Hawaiian Islands. *American Journal of Botany* 90: 915–923.

HUELSENBECK, J. P., AND F. RONQUIST. 2001. MRBAYES: Bayesian inference of phylogeny. *Bioinformatics* 17: 754–755.

JARAMILLO, M. A., AND P. S. MANOS. 2001. Phylogeny and patterns of floral diversity in the genus *Piper* (Piperaceae). *American Journal of Botany* 89: 1709–1724.

KIEHN, M. 2000. The genus *Cyrtandra* (Gesneriaceae): its indicative potential for assessing historical and actual disturbance of island forest systems. *In* Program Committee and Secretariat of IAVS 2000 [eds.], 43rd Symposium of the International Association for Vegetation Science, 79 (Abstract). Institute of Environmental Science and Technology, Yokohama National University, Yokohama, Japan.

KIEHN, M. 2001. South Pacific and Hawaiian *Cyrtandra*: molecular and micromorphological studies. *Malayan Nature Journal* 55: 21–27.

KIEHN, M., M. PFOSSER, AND C. G. JANG. 2001. Implications of infra- and interspecific AFLP variation in Hawaiian *Cyrtandra*. *In* M. Koch and K.-G. Bernhardt [eds.], Evolution and plasticity in plant populations, 15. Institute of Botany, University of Agricultural Sciences, Vienna, Austria.

KLUGE, A. G., AND J. S. FARRIS. 1969. Quantitative phyletics and the evolution of anurans. *Systematic Zoology* 18: 1–32.

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.

KOKUBUGATA, G., AND D. A. MADULID. 2000. Comparative study of chromosome number and karyotype of *Cyrtandra cumingii* var. *yaeyamana* (Gesneriaceae) from Batan Island, the Philippines, and Iriomote Island, Japan. *Japanese Biological Magazine, Okinawa* 38: 27–31.

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.

LUEGMAYR, E. 1993a. Pollen characters of Old World Gesneriaceae (Cyrtandroideae) with special reference to SE Asian taxa. *Grana* 32: 221–232.

LUEGMAYR, E. 1993b. Pollen of Hawaiian *Cyrtandra* (Gesneriaceae) including notes on Southeast Asian taxa. *Blumea* 38: 25–38.

MAYER, V., M. MÖLLER, M. PERRET, AND A. WEBER. 2003. Phylogenetic position and generic differentiation of Epithemateae (Gesneriaceae) inferred from plastid DNA sequence data. *American Journal of Botany* 90: 321–329.

MCNAB, B. K. 2002. Minimizing energy expenditure facilitates vertebrate persistence on oceanic islands. *Ecology Letters* 5: 693.

MERRILL, E. D. 1922. Gesneriaceae. New or noteworthy Philippines plants. XVII. *Philippine Journal of Science* 20: 439–448.

MÖLLER, M., AND Q. C. B. CRONK. 1997. Origin and relationships of *Saintpaulia* (Gesneriaceae) based on ribosomal DNA internal transcribed spacer (ITS) sequences. *American Journal of Botany* 84: 956–965.

MÖLLER, M., AND M. KIEHN. 2003. Synopsis of cytological studies in Gesneriaceae. *Edinburgh Journal of Botany* 60: 425–447.

MÜHLBAUER, I., AND M. KIEHN. 1997. Seed morphology of *Cyrtandra* (Gesneriaceae). *Scripta Botanica Belgica* 15: 117.

NEPOKROEFF, M., K. J. SYTSMA, W. L. WAGNER, AND E. A. ZIMMER. 2003. Reconstructing ancestral patterns of colonization and dispersal in the Hawaiian understory tree genus *Psychotria* (Rubiaceae): a comparison of parsimony and likelihood approaches. *Systematic Biology* 52: 820–838.

POSADA, D., AND K. A. CRANDALL. 1998. MODELTEST: testing the model of DNA substitution. *Bioinformatics* 14: 817–818.

PRICE, J. P., AND W. L. WAGNER. 2004. Speciation in Hawaiian angiosperm lineages: cause, consequence, and mode. *Evolution* 58: 2185–2200.

SAKAI, A. K., W. L. WAGNER, D. M. FERGUSON, AND D. R. HERBST. 1995.

Biogeographical and ecological correlates of dioecy in the Hawaiian flora. *Ecology* 76: 2530–2543.

SAMUEL, R., W. PINSKER, AND M. KIEHN. 1997. Phylogeny of some species of *Cyrtandra* (Gesneriaceae) inferred from the *atp*B/*rbc*L cpDNA intergene region. *Botanica Acta* 110: 503–510.

SCHLAG-EDLER, B., AND M. KIEHN. 2001. Palynology of South Pacific *Cyrtandra* (Gesneriaceae) with notes on some Hawaiian taxa. *Grana* 40: 192–196.

SMITH, A. C. 1953. Studies of Pacific island plants. XIV. Notes on the Fijian species of *Cyrtandra*. *Journal of the Arnold Arboretum* 34: 37–50.

SMITH, A. C. 1991. Gesneriaceae. *In* A. C. Smith [ed.], Flora vitiensis nova, a new flora of Fiji (spermatophytes only), vol. 5, 88–115. National Tropical Botanical Garden, Lawai, Hawaii, USA.

SMITH, J. F. 2000. Phylogenetic resolution within the tribe Episcieae (Gesneriaceae): congruence of ITS and *ndh*F sequences from parsimony and maximum-likelihood analyses. *American Journal of Botany* 87: 883–897.

SMITH, J. F., C. C. BURKE, AND W. L. WAGNER. 1996. Interspecific hybridization in natural populations of *Cyrtandra* (Gesneriaceae) on the Hawaiian Islands: evidence from RAPD markers. *Plant Systematics and Evolution* 200: 61–77.

SMITH, J. F., J. C. WOLFRAM, K. D. BROWN, C. L. CARROLL, AND D. S. DENTON. 1997. Tribal relationships in the Gesneriaceae: evidence from DNA sequences of the chloroplast gene *ndh*F. *Annals of the Missouri Botanical Garden* 84: 50–66.

ST. JOHN, H. [ED.]. 1966. Monograph of *Cyrtandra* (Gesneriaceae) on Oahu, Hawaiian Islands. *Bernice P. Bishop Museum Bulletin* 229: 1–465.

STEADMAN, D. W. 1997. The historic biogeography and community ecology of Polynesian pigeons and doves. *Journal of Biogeography* 24: 737–753.

STOREY, W. B. 1966. Chromosome numbers in *Cyrtandra*. *In* H. St. John [ed.], Monograph of *Cyrtandra* (Gesneriaceae) on Oahu, Hawaiian Islands. *Bernice P. Bishop Museum Bulletin* 229: 31–33.

SWOFFORD, D. L. 2000. PAUP*: phylogenetic analysis using parsimony (* and other methods), version 4. Sinauer Associates, Sunderland, Massachusetts, USA.

WAGNER, W. L. 1990. *Cyrtandra*. *In* W. L. Wagner, D. R. Herbst, and S. H. Sohmer [eds.], Manual of the flowering plants of Hawai'i, 735–781. University of Hawaii Press, Honolulu, Hawaii, USA.

WAGNER, W. L. 1999. *Cyrtandra*. *In* W. L. Wagner, D. R. Herbst, and S. H. Sohmer [eds.], Manual of the flowering plants of Hawai'i, rev. ed., 735–781. University of Hawaii Press, Honolulu, Hawaii, USA.

WAGNER, W. L., S. G. WELLER, AND A. K. SAKAI. 2004. Monograph of *Schiedea* (Caryophyllaceae subfam. Alsinoideae). *Systematic Botany Monographs* 72: 1–169.

WAGNER, W. L., K. R. WOOD, AND D. H. LORENCE. 2001. A new species of *Cyrtandra* (Gesneriaceae) from Kaua'i, Hawaiian Islands. *Novon* 11: 146–152.

WILLIAMS, E. 1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. *Quarterly Review of Biology* 44: 345–389.

WILSON, E. O. 1959. Adaptive shift and dispersal in a tropical ant fauna. *Evolution* 13: 122–144.

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.

WRIGHT, S. D., C. G. YONG, J. W. DAWSON, D. J. WHITTAKER, AND R. C. GARDNER. 2001. Stepping stones to Hawaii: a trans-equatorial dispersal pathway for *Metrosideros* (Myrtaceae) inferred from nrDNA (ITS plus ETS). *Journal of Biogeography* 28: 769–774.

CRONK, QUENTIN C. B., MICHAEL KIEHN, WARREN L. WAGNER, AND JAMES F. SMITH. 2005. Evolution of *Cyrtandra* (Gesneriaceae) in the Pacific Ocean: the origin of a supertramp clade. *American Journal of Botany* 92(6): 1017–1024.

APPENDIX. Species used in the phylogenetic analysis, voucher information, and GenBank numbers for ITS.

Species	Distribution	Section	Voucher	GenBank number
Aeschynanthus tricolor	Malaysia: Sabah, Sarawak (Sabah)	*Aeschynanthus*	19812968 (E)	AF349170/AF349251
Cyrtandra baileyi F. Muell.	Australia (North Queensland)		Cronk T118 (E)	AF349151/AF349232
C. calyptribracteata Bakh. f.	Java		Van Balgooy 6193 (WU)	AY818830/AY818865
C. compressa C.B. Clarke	Samoa		Kiehn et al. 940823-2/1 (WU)	AY818840/ AY818875
C. cordifolia Gaud.	Hawai'i, Oahu, Manoa	*Crotonocalyces*	Smith 2848 (BISH)	AY818854/ AY818889
C. cumingii C.B. Clarke	Philippines		Mendum 29034 (E)	AY818833/ AY818868
C. cupulata Ridley	Malaysia		Weber s.n. (WU)	AY818826/ AY818861
C. falcifolia C.B. Clarke	Samoa		Kiehn et al. 940823-3/1 (WU)	AY818841/ AY818876
C. ferruginea Merrill	Philippines		Mendum 29182 (E)	AY818834/ AY818869
C. grandiflora Gaud.	Hawai'i, Oahu, Manoa	*Verticillatae*	Smith 2891 (BISH)	AY818844/ AY818879
C. grayana Hillebr.	Hawai'i	*Macrosepalae*	Wagner 6472 (US)	AY818851/ AY818886
C. hawaiiensis C.B. Clarke	Hawai'i, Oahu, Waiahole	*Verticillatae*	Smith 2853 (BISH)	AY818855/ AY818890
C. hirtigera H.J. Atkins and Cronk	Philippines		Cronk et al. 25433 (E)	AY818832/ AY818867
C. induta A. Gray	Tahiti		Cronk T97 (E)	AY818858/ AY818893
C. kauaiensis Wawra	Hawai'i, Kaua'i	*Macrosepalae*	Kiehn 920825-3/4 (WU)	AY818847/ AY818882
C. kusaimontana Hosokawa	Kosrae		T. Flynn et al. 5995 (PTBG)	AY818857/ AY818892
C. laxiflora H. Mann	Hawai'i, Oahu, Waiahole	*Apertae*	Smith 2858 (BISH)	AY818845/ AY818880
C. longifolia (Wawra) Hillebr. ex C.B. Clarke	Hawai'i, Kaua'i	*Cylindrocalyces*	Kiehn 920825-2/1 (WU)	AY818846/ AY818881
C. macraei A. Gray	Hawai'i, Oahu, Wailupe	*Chaetocalyces*	Smith 2902 (BISH)	AY818853/ AY818888
C. menziesii Hook. & Arnott	Hawai'i	*Chaetocalyces*	Wagner 6757 (US)	AY818852/ AY818887
C. cf. *milnei* Seemann ex A. Gray	Fiji		Vodonaivalu et al. 940807-1/1 (WU)	AY818837/ AY818872
C. monticola Gillespie	New Guinea		Takeuchi 6002 (E)	AY818860/ AY818895

C. paliku W.L. Wagner, K.R. Wood & D.H. Lorence	Hawai'i, Kaua'i, Mt. Namahana		Wood 7307 (PTBG)	AY818842/ AY818877
C. paludosa Gaud.	Hawai'i, Oahu, Palolo	*Cylindrocalyces*	Smith 2884 (BISH)	AY818848/ AY818883
C. patula Ridley	Malaysia		Weber s.n. (WU)	AY818829/ AY818864
C. pendula Blume	Malaysia		Weber & Antonysamy 860730-1/2 (WU)	AY818828/ AY818863
C. propinqua C. Forbes	Hawai'i, Oahu, Waiahole	*Crotonocalyces*	Smith 2870 (BISH)	AY818849/ AY818884
C. samoensis A. Gray	Tonga		Wood 6873 (PTBG)	AY818839/ AY818874
C. sandwicensis (H. Lév.) St. John & Storey	Hawai'i, Oahu, Manoa	*Apertae*	Smith 2850 (BISH)	AY818850/ AY818885
C. splendens C.B. Clarke	Sarawak		cult. in Univ. of Vienna Botanical Garden GS-89-04 (WU)	AY818827/ AY818862
C. tahuatensis F.R. Fosberg & M.-H. Sachet	Marquesas		Wood 6563 (PTBG)	AY818838/ AY818873
C. tohiveaensis G.W. Gillett	Moorea		Cronk T28 (E)	AY818859/ AY818894
C. umbellifera Merrill	Taiwan		Wagner 6701 (US)	AY818836/ AY818871
C. urvillei C.B. Clarke	Kosrae		D. Lorence et al. 7838 (PTBG)	AY818856/ AY818891
C. villosissima Merrill	Philippines		Mendum 29053 (E)	AY818835/ AY818870
C. wallichii (C.B. Clarke) Burtt	Malaysia		Weber s.n. (WU)	AY818831/ AY818866
C. wawrae C.B. Clarke	Hawai'i, Kaua'i	*Crotonocalyces*	Kiehn 920901-1/1	AY818843/ AY818878