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TOWARDS A PHYLOGENETICALLY INFORMED TAXONOMY OF *CYRTANDRA* (GESNERIACEAE) IN THE SOLOMON ISLANDS

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ABSTRACT. The objective of this study was to build on a previously published molecular phylogenetic hypothesis for *Cyrtandra* to identify major clades of the genus in the Solomon Islands. Species of *Cyrtandra* in the Pacific are represented by locally uncommon, poorly known and rarely collected taxa, a large number of which are at particular risk of extinction due to high rates of deforestation. We propose that research in *Cyrtandra* has progressed to the point that regional taxonomic revisions can be conducted effectively following procedures developed for *Cyrtandra* in Malesia and Hawaii. We identify four distinct clades in the Solomon Islands, each characterized by suites of morphological characters that can be used to circumscribe taxa for revision. Both genetically sampled taxa for the phylogenetic analysis and unsampled taxa are evaluated based on morphological traits that differentiate these four clades. A hypothesis of relationship is proposed as a model for future taxonomic revision of the genus in this region that includes 24 species and two additional taxa possibly new to science. A diagnostic key to the clades currently recognized in the Solomons and an annotated checklist of recognized species are also included as a foundation for future work in the archipelago.

Key words: island biogeography, systematics, dispersal-mediated allopatry, floristics, southeast Asia

INTRODUCTION

The flowering plant family Gesneriaceae includes over 3000 species found throughout much of the world's tropics with centers of diversity in the tropical Americas, Africa, southeast Asia and the Pacific (Wiehler 1983, Burtt & Wiehler 1995, Weber 2004, Weber et al. 2013). Gesneriads have received great scientific attention in the last two decades resulting in substantial advances in our knowledge of this taxonomically challenging family (see Möller & Clark 2013; Weber et al. 2013). Of genera in the family, *Cyrtandra* J.R.Forst. & G.Forst. is perhaps the most challenging taxonomically, owing to a complex morphological diversification as well as the great geographic range and sheer number of reported species (Atkins et al. 2013).

Cyrtandra is the largest gesneriad genus (700 or more species; see Atkins et al. 2013) and has the greatest range for any genus in the family, extending from the Nicobar Islands in the Indian Ocean to the distant Hawaiian and Marquesan islands in the Pacific (Burtt 2001, Kiehn 2001, Atkins et al. 2013). The broad distribution and large number of species in *Cyrtandra* is in marked contrast to other gesneriads, including the genera *Aeschynanthus* Jack (~185 spp.), *Boea* Comm. ex. Lam. (~14 spp.), *Coronanthera* Vieill. ex C.B.Clarke (~11 spp.) and *Epithema* Blume

(~20 spp.), which reach their easternmost extent in the Solomon Islands (Skog & Boggan 2007).

Species of *Cyrtandra* are commonly found in wet upland tropical forests (Backer & Van den Brink 1965; Gillett 1967, 1973; Fosburg & Sachet 1981; Burtt 1990, 2001; Smith 1991; Cronk et al. 2005) but in some instances are also found growing at sea level (e.g., *C. samoensis* on the island of Niue; Gillett 1973). Morphologically, the genus is quite diverse, exhibiting a wide range of flower, fruit and habit types (Clarke 1883, Hillebrand 1888, Schlag-Edler & Kiehn 2001). *Cyrtandra* species are commonly understory shrubs or trees but can also be small terrestrial herbs, woody vines and sometimes epiphytic subshrubs (Burtt 2001). Flowers are commonly white but can be yellow, pink or red and are born in the axils of terminal stem leaves. Occasionally inflorescences are borne along the woody trunks or even on exposed roots (e.g., *C. kaulantha* H.St.John & Storrey from Oahu; Wagner et al. 1990, 1999). Fruits are hard, normally indehiscent capsules or, as is often the case in the Pacific and in a few species in Malesia, fleshy berries (Hilliard et al. 2003).

Tropical plant families like the Gesneriaceae are under threat of extinction from deforestation (Krupnick & Kress 2005), and warrant intensified in situ and ex situ study and conservation efforts (Pence 2002). This is particularly true for the genus *Cyrtandra*; despite the exceptional geographic range for the genus, frequently species are regionally restricted endemics rarely extending beyond archipelagos (Samuel et al. 1997). More often, species of *Cyrtandra* are restricted to single islands or even confined areas within islands (Atkins et al. 2001; Bramley et al. 2003, 2004a, 2004b; Bramley 2005; Cronk et al. 2005). As such, many species of *Cyrtandra* are threatened and can be summarily eliminated through destructive practices such as logging. Species of *Cyrtandra* are also quite susceptible to disturbance, and even areas where only selective logging has taken place, or livestock grazing has occurred, densities of the genus are greatly reduced or completely eliminated (authors this paper; pers. obs.).

Given the severity of loss in the genus, urgency exists to systematically sample, interpret relationships and apply accepted taxonomic concepts to both genetically sampled and unsampled taxa (see Emerson 2002, Hopper 2000). This methodology has been applied, in part, in Malesia to revise section *Dissimiles* C.B.Clarke (Bramley 2005) and as a basis for taxonomic revision in Hawaii (see Clark et al. 2009). Sixty morphologically unique species of *Cyrtandra* are now recognized in Hawaii based on a phylogenetically informed understanding of relationships in that archipelago (Wagner et al. in prep.). Applying these strategies in other areas where *Cyrtandra* is found will aid in both defining and revising taxonomy in this poorly circumscribed genus, and also in identifying monophyletic clades for future systematics work, field colleting prioritization and conservation assessment (Atkins et al. 2013).

Among areas warranting intensified study for *Cyrtandra*, the interface between continental Southeast Asia and the remote Pacific, an area ranging from the Solomon Islands to the west, and east into the Pacific as far as Samoa, has been implicated as a center of origin for the Pacific clade of *Cyrtandra* (Clark 2008; Clark et al. 2008, 2009). A general west to east trend is common among Pacific islands floras and areas like Fiji share as much as 90% of their plant genera with New Guinea and neighboring islands (Mueller-Dombois & Fosberg 1998). It is possible that other species have similar evolutionary histories tied to this region (Takhtajan 1969, 1986; Evenhuis & Bickel 2005; Balke et al. 2009; see also Cowie & Holland 2006 on dispersal). Results from biogeographic research (Clark et al. 2009) support the hypothesis that once the barrier to Pacific dispersal had been overcome (presumably a result of fleshy fruit dispersed by shore birds), *Cyrtandra* was well suited for island hopping (see Cronk et al. 2005), and continued to do so across the Pacific. As such, interpreting affinities for Pacific *Cyrtandra* all require a greater understanding of phylogenetic, taxonomic and biogeographic relationships in the genus in this region (Clark 2008).

The purpose of the current study is to present a new phylogeny for *Cyrtandra* inclusive of specimens collected on a 2009 expedition to the Solomon Islands. The first and only revision of the genus in this archipelago was conducted by Gillett (1975). Recent fieldwork in the Solomons by one of the authors (JRC) suggests that additional undescribed species of *Cyrtandra* exist there and current taxon delimitations are in need of amendment.

The archipelago represents a manageable system to both apply and refine techniques for addressing this genus taxonomically and can be used in the future to address similar issues in geographically more complex and less taxonomically treated regions including Borneo and New Guinea (see Atkins et al. 2013). The phylogeny presented in this study is meant to demonstrate the minimum number of estimated clades of *Cyrtandra* in the Solomon Islands, and to define these monophyletic clades using morphology as a basis for future taxonomic revision. A diagnostic key to these four clades is provided and an annotated checklist of recognized species is included with details on distribution and clade affinities, where appropriate.

TABLE 1. Taxon sampling list for 54 individuals sampled in the current study including four outgroup species (*Aeschynanthus* spp.). Specimens are organized alphabetically by species. ID numbers are J. R. Clark's DNA extraction numbers and are here used for reference. GenBank accession numbers are included for all taxa for each of the three genic regions analyzed in the current study. *C.* = *Cyrtandra*; *A.* = *Aeschynanthus*. ITS = internal transcribed spacer regions 1 and 2, including the 5.8S subunit; ETS = external transcribed spacer region; *psbA-trnH* = chloroplast sequence data.

Species	ID No.	Collector and no.; voucher	Origin	ITS	ETS	*psbA-trnH*
A. hartleyi P.Woods	C0217	Clark 826; PTBG	New Guinea	KF148661	KF148649	KF148673
A. longicaulis Wall. ex R.Brown	C0056	MSBG 1974-2207-W	Indonesia	EU919959	EU919898	EU920018
A. solomonensis P.Woods	C0203	Clark 767; PTBG	Solomon Islands, Isabel	KF148657	KF148645	KF148669
A. tricolor Hook.	C0055	MSBG 1974-1760-W	Indonesia	EU919958	EU919897	EU920017
C. anthropophagorum Seem. ex A.Gray	C0114	Clark 688; PTBG	Fiji, Viti Levu	EU919987	EU919926	EU920042
C. aurantiicarpa G.W.Gillett	C0076	Clark 655; PTBG	Samoa, Savai'i	EU919971	EU919910	EU920030
C. baileyi F.Muell. in Bailey, F.M.	DD6	Costion 1687; CNS	Australia, Queensland	KF148662	KF148650	KF148674
C. aff. *bidwillii* C.B.Clarke	C0130	Wood 11072; PTBG	Society Islands, Hua Hine	GQ475176	GQ475089	GQ475139
C. biserrata H.St.John	C0153	Wood 11386; PTBG	Hawai'i, Moloka'i	GQ475194	GQ475107	GQ475157
C. calpidicarpa (Rock) H.St.John & Storey	C0053	Clark 584; PTBG	Hawai'i, O'ahu	GQ475168	GQ475080	GQ475123
C. compressa C.B.Clarke	C0074	Clark 652; PTBG	Samoa, Savai'i	EU919970	EU919909	EU920029
C. confertiflora (Wawra) C.B.Clarke	C0159	Roalson 1584-01; WS	Hawai'i, Kaua'i	GQ475200	GQ475113	GQ475163
C. cordifolia Gaudich.	C0048	Clark 579; PTBG	Hawai'i, O'ahu	EU919955	EU919894	EU920014
C. erectiloba G.W.Gillett	C0179	Clark 745; E, K, PTBG, U.S.	Solomon Islands, Isabel	KF148652	KF148640	KF148664
C. falcifolia C.B.Clarke	C0141	Kiehn 940823-4/3; WU	Samoa, U'polu	GQ475184	GQ475097	GQ475147
C. feaniana F.Br.	C0059	Price 200; PTBG	Marquesas, Hiva Oa	EU919960	EU919899	EU920019
C. ferruginea Merr.	C0137	Cubey and Scott 226; E	Philippines, Luzon	GQ475181	GQ475094	GQ475144
C. filibracteata B.L.Burtt	C0205	Clark 770; E, K, PTBG, U.S.	Solomon Islands, Kolombangara	KF148658	KF148646	KF148670
C. fulvovillosa Rech.	C0183	Clark 786; E, K, PTBG, U.S.	Solomon Islands, Kolombangara	KF148654	KF148642	KF148666
C. grayana Hillebr.	C0103	Clark 666; PTBG	Hawai'i, Maui	EU919982	EU919921	EU920039
C. hawaiensis C.B.Clarke	C0155	Roalson 1569-04; WS	Hawai'i, O'ahu	GQ475196	GQ475109	GQ475159
C. kauaiensis Wawra	C0026	Clark 556A; PTBG	Hawai'i, Kaua'i	EU919940	EU919879	EU919999
C. kealiae Wawra ssp. *urceolata* W.L.Wagner & Lorence	C0054	Perlman 18805; PTBG	Hawai'i, Kaua'i	EU919957	EU919896	EU920016
C. kusaimontana Hosok.	C0033	Flynn 5995; PTBG	Micronesia, Kosrae	EU919945	EU919884	EU920004
C. laxiflora H.Mann	C0157	Roalson 1574-01; WS	Hawai'i, O'ahu	GQ475198	GQ475111	GQ475161
C. leucantha A.C.Sm.	C0116	Clark 693; PTBG	Fiji, Viti Levu	EU919988	EU919927	GQ475136
C. longifolia (Wawra) Hillebr. ex C.B.Clarke	C0023	Clark 551; PTBG	Hawai'i, Kaua'i	EU919939	EU919878	EU919998
C. macrotricha G.W.Gillett	C0180	Clark 747; PTBG	Solomon Islands, Isabel	KF148653	KF148641	KF148665
C. cf. *mesilauensis* B.L.Burtt	C0140	Cubey and Scott 229; E	Indonesia, Borneo	GQ475183	GQ475096	GQ475146
C. munroi C.N.Forbes	C0151	Oppenheimer H120638; BISH	Hawai'i, Lana'i	GQ475192	GQ475105	GQ475155
C. occulta A.C.Smith	C0117	Clark 694; PTBG	Fiji, Viti Levu	EU919989	EU919928	GQ475137
C. cf. *occulta* A.C.Smith	C0119	Clark 702; PTBG	Fiji, Viti Levu	EU919990	EU919929	GQ475138
C. pendula Blume	C0098	Wiriadinata, H. 12716; U.S.	Indonesia	EU919979	EU919918	EU920037
C. picta Blume	C0097	Wiriadinata, H. 12715; U.S.	Indonesia	EU919978	EU919917	EU920036
C. pogonantha A.Gray	C0081	Clark 660; PTBG	Samoa, U'polu	GQ475173	GQ475086	GQ475129
C. pulchella Rich ex A.Gray	C0029	Lorence 8525; PTBG	Samoa, Tau	EU919941	EU919880	EU920000
C. richii A.Gray	C0073	Clark 651; PTBG	Samoa, Savai'i	GQ475171	GQ475084	GQ475127
C. samoensis A.Gray	C0030	Lorence 8633; PTBG	Samoa, Ofu	EU919942	EU919881	EU920001

TABLE 1. Continued.

Species	ID No.	Collector and no.; voucher	Origin	ITS	ETS	*psbA-trnH*
C. samoensis A.Gray	C0031	RP 71221; PTBG	Tonga	EU919943	EU919882	GQ475122
C. samoensis A.Gray	C0142	Kiehn 940819-1/1; WU	Samoa, U'polu	GQ475185	GQ475098	GQ475148
C. samoensis A.Gray	C0144	Kiehn 940819-2/1; WU	Samoa, U'polu	GQ475187	GQ475100	GQ475150
C. serratifolia H.J.Atkins & Cronk	C0136	Cubey and Scott 225; E	Indonesia, Sulawesi	GQ475180	GQ475093	GQ475143
C. sp.	C0095	Wiriadinata, H. 12709; U.S.	Indonesia, Java	EU919976	EU919915	EU920034
C. sp. ''A''	C0173	Clark 724; PTBG	Solomon Islands, Isabel	KF148651	KF148639	KF148663
C. sp. ''B''	C0209	Clark 787; PTBG	Solomon Islands, Kolombangara	KF148659	KF148647	KF148671
C. sp. ''Java''	C0211	Clark 856 (= MSBG 2009-0654A); PTBG	Java	KF148660	KF148648	KF148672
C. subulibractea G.W.Gillett	C0184	Clark 788; E, K, PTBG, U.S.	Solomon Islands, Kolombangara	KF148655	KF148643	KF148667
C. subulibractea G.W.Gillett	C0191	Clark 805; K, PTBG	Solomon Islands, Vangunu	KF148656	KF148644	KF148668
C. tahuatensis Fosberg & Sachet	C0061	Perlman 18399; PTBG	Marquesas, Fatu Hiva	EU919962	EU919901	EU920021
C. thibaultii Fosberg & Sachet	C0062	Meyer 2541; PTBG	Marquesas, Ua Pou	EU919963	EU919902	EU920022
C. thibaultii Fosberg & Sachet	C0065	Wood 10428; PTBG	Marquesas, Ua Pou	EU919966	EU919905	EU920025
C. tintinnabula Rock	C0012	Perlman 17676; PTBG	Hawai'i, Hawai'i	EU919930	EU919869	GQ475114
C. urvillei C.B.Clarke	C0034	Lorence 7838; PTBG	Micronesia, Kosrae	EU919946	EU919885	EU920005
C. wainihaensis H.Lév.	C0021	Clark 549; PTBG	Hawai'i, Kaua'i	EU919937	EU919876	EU919996

MATERIALS AND METHODS

For the phylogenetic analysis, 50 ingroup taxa (*Cyrtandra*) and four outgroup taxa (*Aeschynanthus*) were sampled (Table 1). This study builds on two previously published studies, Clark et al. (2008, 2009), and incorporates 12 new samples including eight from the Solomon Islands representing at least five species, two of which are possibly new to science. Pacific taxa in the current study include representatives from all major supported clades reported by Clark et al. (2009). For a distribution map of the genus *Cyrtandra* see Figure 1 in Clark et al. (2008) and for current estimated numbers of species by region, see Atkins et al. (2013).

DNA isolation and purification from silica-dried leaf material, genic region amplification and sequencing were performed using protocols described by Clark et al. (2008). Cycle sequence products were purified using standard gel column purification methods and then analyzed on an automated DNA Sequencer at facilities at the University of Florida's Interdisciplinary Center for Biotech Research. Forward and reverse sequencing reactions were conducted for each taxon sampled. Sequence chromatograms were proofed, edited and contigs were assembled using Geneious 6.0.5 (Biomatters, Ltd., New Zealand). Edited contigs were then aligned using MUSCLE (v. 3.8.31; Edgar 2004) as implemented in SeaView (Gouy et al. 2010) with further editing by eye to correct minor alignment issues. The nuclear ribosomal internal transcribed spacer region, including ITS1, ITS2 and the 5.8S subunit, the 5′ end external transcribed spacer region (ETS) and the chloroplast *psbA-trnH* region, were amplified using protocols described in Clark et al. (2008).

Nucleotide substitution model parameters were estimated using DT-ModSel (Minin et al. 2003). Aligned sequences were analyzed using maximum likelihood (ML) and Bayesian inference (BI) methods. Maximum likelihood analyses were performed using PAUP* 4.0b10 (Swofford 2002) implementing heuristic searches with TBR branch swapping and initial starting trees generated using neighbor-joining reconstruction. Bootstrap support indices were estimated for each node using 100 heuristic bootstrap replicates executed over 100 random addition cycles with 10 trees saved per cycle (Hillis & Bull 1993). Bayesian analyses were performed using MrBayes v. 3.1 (Huelsenbeck & Ronquist 2001). Four chains were run for 30,000,000 generations each, sampled every 10,000 generations. Multiple independent BI analyses were run. The first 20% of trees were excluded from summary as burn-in. Posterior probabilities were compared between two identical runs to ensure convergence had been reached.

In the previous studies (Clark et al. 2008, 2009), ML analyses were conducted on individual gene trees and then compared with one another to assess compatibility of genic regions for combined analysis. No well-supported branches (≥70% bootstrap support) among the various topologies were in conflict and thus the three genic regions were combined and analyzed. This precedent was followed for the current study.

Clade assignments were based on phylogenetic results from the above described analysis. Morphological assessments were made for Solomon Islands species in supported clades (with ≥70% ML bootstrap and/or ≥90% Bayesian posterior probability) by qualitatively comparing characters of species within and among monophyletic clades and then using these to define characters representative of each. Characters used include gross vegetative morphology, inflorescence location and type (e.g., cauliflorous vs. axillary, bracteate vs. nonbracteate). A diagnostic key was then constructed to morphologically define identified clades and also to serve as a tool to hypothesize relationships of taxa not genetically sampled in this study. In other words, the key provided is used to assign Solomon Islands species not sampled genetically to form a hypothesis of relationship for further study. Genetically unsampled species were assessed for inclusion in one of the defined clades using their descriptions in the literature (Gillett 1973, 1974, 1975) along with personal observations of type and other representative material including live specimens and photographs.

An annotated checklist of currently recognized species from the Solomon Islands was compiled from the literature (principally Gillett 1975, and literature cited therein). The Solomons are interpreted as a biogeographic continuum beginning in the eastern islands of the Bismarck Archipelago and extending into the southeastern islands of the Solomons including those geologically aligned with Vanuatu. This area corresponds with Mueller-Dombois and Fosberg's Western Melanesia Region (1998).

The Bismarck Archipelago is defined to include islands east of but not including New Guinea and ending north of Bougainville Island. The Solomon Islands include Bougainville (a UN-designated provisional independent state) and all those islands politically affiliated with the Solomons including the Santa Cruz group. While Vanuatu is not treated in this study, at least one species overlaps with the Solomons and is included for reference as the Banks Islands and southward.

Types and vouchers were examined, when possible, either physically or virtually via web-based image libraries maintained by relevant herbaria. For species observed in the wild by one of the authors (JRC) as well as additional herbarium specimens in various herbaria, comments on distribution and affinities are included where appropriate.

RESULTS

Phylogenetics

Aligned sequences were 788 bp for ITS, including the 5.8S subunit, 494 bp for ETS and 466 bp for *psbA-trnH* (excluding the 5′ end inversion, as described in Clark et al. 2009), for a total of 1748 bp of aligned sequence data. Nucleotide substitution parameters were estimated for the combined genic region matrix as the K80 plus gamma substitution model with a transition to transversion ratio of 1.429 and a gamma shape of 0.541. Combined ML analysis of ITS, ETS and *psbA-trnH* genic regions using this model resulted in one most likely tree (FIGURE 1).

Support values across the topology, as indicated with ML bootstrap values (BS) and Bayesian posterior probabilities (BI), illustrate a well-supported phylogenetic hypothesis. These results parallel relationships inferred in the previous studies (Clark et al. 2008, 2009). Southeast Asian taxa are situated in a grade of taxa leading to the Pacific clade (FIGURE 1). Four supported clades are recovered for sampled Solomon Islands specimens. These are distributed along the Southeast Asian grade (clade 1,100%BS, >99%PP; and clade 2,100%BS, >99%PP), sister to the monophyletic Pacific clade (clade 3,100% BS, >99% PP) and within the Pacific clade sister to the South Pacific clade (clade 4, 90% BS, >99% PP). While clades 1 and 2 could represent either one or two distinct clades for discussion based on their sister relationship, sufficient morphological differences exist between the two that we here recognize them as separate. See below for further rationale.

A long branch separating the monophyletic Pacific clade from the Southeast Asian grade was recovered in previous studies. In the current study, clade 3 containing two unidentified/undescribed species, are supported as sister to the Pacific clade (100% BS; >99% PP), effectively dividing this former long branch in half. Although this relationship is supported in both bootstrap and Bayesian support indices, the Pacific clade is only supported in the Bayesian analysis (FIGURE 1). The southeast Asian grade includes clades of Javan/Bornean, Javan, Australia/Solomon Islands, Solomon Islands, Philippines, and Javan/Sulawesian.

Fijian and Samoan geographic areas are polyphyletic within the Pacific clade (FIGURE 1). The Marquesas species are divided along two major supported clades but their relationship to one another remains unresolved leaving the possibility that Marquesan species of *Cyrtandra* might repre-

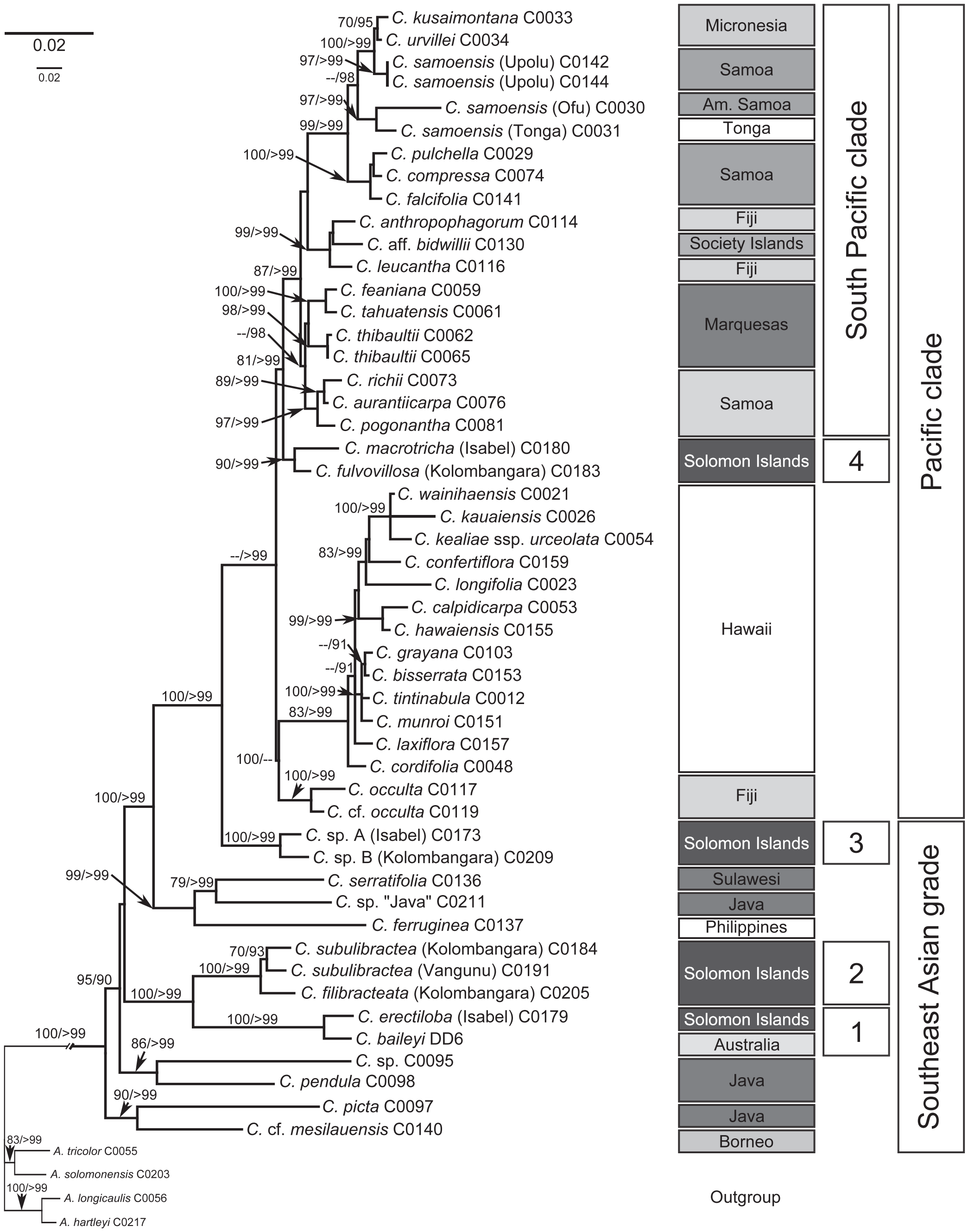

FIGURE 1. Maximum Likelihood phylogeny for the combined analysis of ITS, ETS and psbA-trnH genic regions. Support indices are shown on supported nodes in the format bootstrap/posterior probability. Line weights correspond with the branch length scale in the upper left; outgroup scaled for emphasis. Numbers 1–4 reference the clades discussed in the text. Additional clades and grades referenced in the text are indicated by name. Numbers following taxon names are those referenced in the text and in Table 1. *A.* = *Aeschynanthus*; *C.* = *Cyrtandra*.

FIGURE 2. Example species photographed in the wild representing the four clades discussed in the text. Insets are flower details for each species. Numbers correspond with the clades referenced in the text. **1.** *Cyrtandra erectiloba*, Isabel Island; **2.** *C. filibracteata*, Kolombangara Island; **3.** *C.* sp. ''A,'' Isabel Island; **4.** *C. fulvovillosa*, Kolombangara Island. All photographs by J.R. Clark.

sent more than one introduction to that archipelago. These Marquesan clades are grouped in a Bayesian-supported clade with a supported clade of Samoan species of *Cyrtandra*. These latter species represent a unique clade in the Pacific characterized by distinctive orange fruit, a trait which is not represented in any species outside this clade in the entire genus (Clark in prep).

Diagnostic Key to Phylogenetic Clades

The four monophyletic Solomon Islands clades can be distinguished from one another based on a suite of vegetative and reproductive characters (FIGURE 2). It is important to note that this key is meant to be diagnostic for the purposes of on-going research on *Cyrtandra* in the Solomon Islands and is not comprehensive nor is it designed for species-level identification. A few described specimens do not readily key out well to any of the following four groups; details on these are discussed in the annotated checklist that follows. It is possible that these represent one or more additional evolutionary lines of *Cyrtandra* that occur in this biogeographically complex region.

1. Leaves anisophyllous or pseudo-alternate, having one leaf reduced to a bract-like scale, sometimes alternately anisophyllous/opposite (on the same plant), occasionally strictly opposite.

    2. Plants understory shrubs, weakly branched, generally less than 3 meters tall; inflorescences of one to few flowers, often axillary, corollas white to cream colored, never red. … Clade 1.
    Examples in the phylogeny:
    C. baileyi, *C. erectiloba*

    2. Plants large, woody shrubs or trees, often greater than 3 meters when mature; inflorescences of numerous flowers, variously cauliflorous or axillary on secondary leafy branches, corollas red, pink, occasionally striped or white (rarely greenish to yel-

TABLE 2. Species list for 26 taxa treated in the annotated checklist. Species are organized here according to phylogenetic lineages as described in the text. Order in the checklist is alphabetical; number of each species as treated in the text is listed here for convenience.

Species	Solomon Islands clade	Order in Checklist
Cyrtandra erectiloba G.W.Gillett	1	6
Cyrtandra wariana Schltr.	1	24
Cyrtandra filibracteata B.L.Burtt	2	7
Cyrtandra fuscovellea K.Schum.	2	10
Cyrtandra hentzelmaniana G.W.Gillett	2	11
Cyrtandra heteronema G.W.Gillett	2	13
Cyrtandra magentiflora G.W.Gillett	2	17
Cyrtandra purpurifolia G.W.Gillett	2	18
Cyrtandra subulibractea G.W.Gillett	2	20
Cyrtandra terraguilelmii K.Schum.	2	21
Cyrtandra cylindrocalyx G.W.Gillett	3	4
Cyrtandra laciniata G.W.Gillett	3	14
Cyrtandra sericifolia G.W.Gillett	3	19
Cyrtandra trichocalyx G.W.Gillett	3	22
Cyrtandra sp. ‘‘A’’	3	25
Cyrtandra sp. ‘‘B’’	3	26
Cyrtandra cominsii Hemsl.,	4	2
Cyrtandra floribunda K.Schum.	4	8
Cyrtandra fulvovillosa Rech.	4	9
Cyrtandra herbacea G.W.Gillett	4	12
Cyrtandra macrotricha G.W.Gillett	4	16
Cyrtandra atherocalyx G.W.Gillett	UNCLASSIFIED	1
Cyrtandra comocarpa G.W.Gillett	UNCLASSIFIED	3
Cyrtandra dinocalyx G.W.Gillett	UNCLASSIFIED	5
Cyrtandra lutescens G.W.Gillett	UNCLASSIFIED	15
Cyrtandra valviloba G.W.Gillett	UNCLASSIFIED	23

lowish). ……… Clade 2. Examples in the phylogeny: *C. filibracteata, C. subulibractea*

1. Leaves not anisophyllous or rarely so being only weakly and never pseudo-alternate, normally opposite or whorled.
   3. Inflorescences compact and congested, flowers one to many in dense, bracteate cymes in the axils of leaves; leaves opposite or often appearing whorled at or near the stem apex, at times restricted to the upper portion of fleshy (to woody) stems. …… Clade 3. Examples in the phylogeny: *C.* sp. ‘‘A,’’ *C.* sp. ‘‘B’’
   3. Inflorescences spreading and open, rarely if ever congested, flowers few to many, in spreading, open cymes, bracts if present, small and deciduous, born in leaf axils along younger portions of stem; leaves present along the entirety of stems, excluding older woody portions, often with consistently asymmetrical or unequal bases. …… Clade 4. Examples in the phylogeny: *C. fulvovillosa*, *C. macrotricha*

All species treated in this study are summarized in Table 2.

Annotated Checklist of *Cyrtandra* of the Solomon Islands and Surrounding Regions

What follows is an account of known taxonomy, disposition of type material, hypothesized relationships based on genetic and morphological data (‘Solomon Islands Clade’’), listing of additional specimens observed by one or more of the authors, and anecdotal accounts on the distribution and affinities of the 26 species in and/or near the Solomon Islands.

Cyrtandra J.R.Forst. & G.Forst., Char. Gen. Pl. 3, pl. 3. 1775. TYPE: *Cyrtandra biflora* J.R.Forst. & G.Forst.

1. Cyrtandra atherocalyx G.W.Gillett, Kew Bull. 30: 393. 1975. TYPE: Bismark Archipelago—New Ireland: Danfu River, 8 km upstream from Danfu Bridge, near Manga, 220 m, 2 February 1970, *Sands 771* (Holotype: K; Isotypes: E!, K, LAE, UC).

Soft-stemmed shrub to 3 m, sap oxidizing to orange (*Clark 729*), leaves opposite, often congested; inflorescences bracteate, axillary, congested, calyces greenish, pubescent, corollas greenish-cream to yellow, actinomorphic, fruits white, subglobose. Bismarck Archipelago (Malakata, New Ireland, New Britain), Solomon Islands (Choiseul, Wagina, Kolombangara, New Georgia, Isabel, Rendova, Guadalcanal, San Cristobal, Rennel). **Solomon Islands Clade UNCLASSIFIED**.

Cyrtandra atherocalyx is characterized by linear, acuminate inflorescence bracts (Gillett 1975) and is also unique in having nearly cylindrical corollas that tend to be yellowish. In preliminary phylogenetic analyses, a specimen tentatively identified to this species (*Clark 729*) was included (data not shown). This specimen was resolved sister to *Cyrtandra ferruginea* Merr. from the Philippines. If supported, this species represents a fifth clade in the archipelago. Due to an as yet unidentified error resulting in an inordinately long branch in the phylogeny, it was excluded from final analysis for this paper. Additional sequencing will be required to better ascertain affinities between this species and others in the region.

A peculiar feature of *Cyrtandra atherocalyx* is the sap oxidizes to an orange color upon exposure to air (J.R. Clark pers. obs.). This feature is apparently shared by *C. dinocalyx* G.W.Gillett from New Ireland (see that species, this paper) and suggests a possible relationship between the two species.

Other specimens examined: Solomon Islands—San Cristobal: Waiamura, 100 m, 11 August 1932, *Brass 2636* (BISH; note: Gillett (1975) has the specimen listed as ''8 November 1932'' but as this would post date the following specimen of a higher collection number, we speculate this is in error); Waiamura, 50 m, September 1932, *Brass 3147*(BISH). Isabel: Mt. Kubonitu, 11 May 2009, *Clark 729* (PTBG)

2. **Cyrtandra cominsii** Hemsl., in Kew Bull. Misc. Inf. 1895:137. 1895. TYPE: Vanuatu—Santa Maria Island (Banks Islands), *Comins 288* (Holotype: K!).

Shrub to 4 m, leaves opposite, bases unequal to acute; inflorescences axillary, bracteate open cymes, calyces greenish white with lobes divided nearly to base, corollas white to cream to pale yellow. Solomon Islands (Malaita, Rennell, Ulawa, San Cristobal), Vanuatu (Banks Islands). **Solomon Islands Clade 4**

Cyrtandra cominsii is widely dispersed and variable across its range. This species and other taxa in clade 4 are at least superficial similar to the *Cyrtandra samoensis* complex of species (see Clark et al. 2009) first hypothesized by Gillett (1974, 1975) to be closely related species. This complex includes a widespread assemblage of morphologically similar but likely distantly related species. Similarities in this group are here hypothesized to be a result of conserved plesiomorphic characters and not a close phylogenetic relationship. As such, assignment of genetically unsampled taxa to this clade is questionable at best until phylogenetics-based information becomes available.

In the original description, Hemsley (1895) indicates that plants can have pseudoalternate leaves. This has not been verified in any specimens we have observed and was not mentioned by Gillett (1973). This detail may have been a result of erroneous observation made by the Rev. R.B. Comins whom the species is named and from whom herbarium material and associated notes were received by Hemsley.

Gillett commented on the similarities and difficulties in distinguishing between *C. cominsii* and *C. fulvovillosa* Rech. (see the latter species, this paper), particularly in the southeastern Solomon Islands. Indeed, some specimens assigned by Gillett to this species (e.g., *Brass 2693*) might be more appropriately called *C. fulvovillosa* based on calyx shape and division of calyx lobes (2/3 the length rather than entirely divided as is typical for *C. cominsii*).

Other specimens examined: Bismarck Archipelago—New Britain: Gasmata, 6 miles east of Fullerborn Harbour, 300 m, 8 May 1973, *Womersley 55342* (US; K). Solomon Islands—San Cristobal: Anganawai, 11 October 1968, *Runikera 10881* (K); Balego, Nagonago, 100 m, 19 August 1932, *Brass 2693* (A, BISH!). Malaita: near the Mannu Anchorage, edge of beach rain-forest, in coral sand, 25 August 1945, *White 98* (K). Rennell: West Lavangu Village, 21 May 1969, *Gafui 14973* (K). Ulawa: lowland rainforest, 4 October 1932, *Brass* 2944 (A, BISH, BM). Vanikoro (Santa Cruz Group): upper Lawrence River Valley, 28 April 1955, *Hadley 75* (BISH).

3. **Cyrtandra comocarpa** G.W.Gillett, Kew Bull. 30: 387. 1975. TYPE: Bismarck Archipelago—New Britain: Bialla, 4–8 km inland, on vertical face of gorge running through upland rain forest, 120 m, 3 July 1973, *Gillett 2555* (Holotype: K; Isotypes: A, E!, LAE, UC).

Shrub to 2 m, leaves opposite to anisophyllous; cauliflorous, bracteate inflorescences, calyces white, corollas green, fruits white. Known only from the type locality. **Solomon Islands Clade UNCLASSIFIED**

Material was not available at the time of this study.

4. **Cyrtandra cylindrocalyx** G.W.Gillett, Kew Bull. 30: 394. 1975. TYPE: Solomon Islands—Bougainville Island: along trail between Arawa and Panguna, near the summit ridge of the Crown Prince Range, 200–300 m, 20 July

1973, *Gillett 2571* (Holotype: K; Isotypes: E!, LAE, UC).

Virgate, pubescent shrub 1–2 m high; inflorescences axillary, conspicuous bracts, calyces light green, corollas greenish white, fruit white, fleshy. Known only from the type locality. **Solomon Islands Clade 3**

This species demonstrates morphological similarities with *Cyrtandra hawaiensis* C.B.Clarke and other superficially similar species in having bracteate inflorescences and leaf arrangement and shape. However, a close relationship between these species is not supported (FIGURE 1).

5. **Cyrtandra dinocalyx** G.W.Gillett, Kew Bull. 30: 375. 1975. TYPE: Bismarck Archipelago—New Ireland: 8 km west and upstream of Danfu River Bridge, near Manga, 900 m, 14 February 1970, *Sands 863* (Holotype: K; Isotypes: A, CANB, E!, L, LAE, UC).

Small tree to 4 m high, sap oxidizing to orange, leaves opposite; inflorescences axillary, bracts present, often bilobed, calyces leathery, greenish-cream to flushed pink, corollas funnelform, pale lime-green, fruit ovoid, color not specified. Restricted to New Ireland. **Solomon Islands Clade UNCLASSIFIED**

Placement of this species is currently not possible; *Cyrtandra dinocalyx* might represent an additional clade, possibly inclusive of *C. atherocalyx*. Gillett (1975) commented on similarities between *C. dinocalyx* and several others west of the Solomons in New Guinea. The relatively large, coriaceous calyces are also superficially similar to cyrtandras known from the Marquesas (Wagner et al. submitted). Other features such as general habit, leaf shape, and indumentum are suggestive of characteristics representative of clade 3, this paper.

6. **Cyrtandra erectiloba** G.W.Gillett, Kew Bull. 30: 407. 1975. TYPE: Solomon Islands—Bougainville Island: near summit of Arawa-Panguna highway, 975 m, 19 July 1973, *Gillett 2569* (Holotype: K; Isotypes: A, BRI, E!, L, LAE, UC). FIGURE 2.1.

Erect, branching shrub to 3 m, strongly anisophyllous/pseudo-alternate leaves; calyces corolloid, white, corolla white, stigmas bilobed. Bismarck Archipelago (New Ireland), Solomon Islands (Bougainville, Kolambangara, Isabel, Vangunu, San Cristobal). **Solomon Islands Clade 1**

This species is representative of a widely dispersed group of species common throughout New Guinea, Bismarck Archipelago and Solomon Islands first recognized by Gillett (1975). Representatives are also present in north Queensland, Australia (*C. baileyi*; DD6 sampled in the phylogeny) and Vanuatu (*C. efaitensis* Guill.; *sensu* Gillett 1975). *Cyrtandra wariana* Schltr. is scarcely distinguishable from *C. erectiloba* and is principally differentiated in having a discoid rather than bilobed stigma. Ranges for the two species overlap in the Bismarck Archipelago.

Other specimens examined: Bismarck Archipelago—New Ireland: Namatanai Sub-district, Hans Meyer Range, Danfu river Valley, 2 February 1970, *Sands 782* (BISH). Solomon Islands—Isabel: along trial to island summit, 1200 m, 13 May 2009, *Clark 745* (E, K, PTBG, U.S.; = C0179 in phylogeny). Kolombangara: Forest Management Area L5, interior to KFPL Field Station along stream camp, 1000 m, 2 June 2009, *Clark 789* (E, K, PTBG, U.S.). Vangunu: inland from Western coast logging camp, 600 m, 10 June 2009, *Clark 801* (E, K, PTBG, U.S.).

Two additional specimens examined from the southeastern Solomons are tentatively assigned to this species: Solomon Islands—San Cristobal: S of Rarasi Village, 365–457 m, 10 March 1966, *Kondo Loc. 50 s.n.* (BISH); Ngonangonamela, above Archane, 1 May 1972, *Powell BSIP 19447* (CSIRO, BISH).

Both of these specimens from San Cristobal are distinctive in having opposite leaves and not pseudoalternate as is the case in *C. erectiloba*. The *Kondo Loc. 50 s.n.* specimen looks overall similar to *C. erectiloba*, although the flowers are rather different; neither the calyx nor the corolla are urceolate and appear more elongate-bilabiate; they are also larger (~2 cm) than is typical for the species (<2 cm).

The latter specimen, *Powell BSIP 19447*, is even more distinctive. The leaves are anisophyllous but the smaller leaf of each pair is still substantial in size and not at all trending towards ‘‘bract-like.’’ The flowers are also larger than typical for *C. erectiloba*, and are bilabiate, similar in many respects to *Cyrtandra efatensis* From Vanuatu. Gillett (1974, 1975) hypothesized *C. erectiloba, C. efatensis,* and *C. wariana* and other similar species represent a complex throughout the region. Of these three species, specimens observed to date are strictly pseudoalternate. The San Cristobal specimens might thus represent yet another unique member of this complex worthy of species-level rank.

7. **Cyrtandra filibracteata** B.L.Burtt, Kew Bull. Misc. Inf. 1936: 463. 1936. TYPE: Solomon Islands—Bougainville Island: Siwai, July 1930, *Waterhouse 132* (Holotype: K; Isotypes: A, BISH!). FIGURE 2.2.

Tree or shrub to 6 m, opposite to anisophyllous leaves; cauliflorous, bracts villiform, calyces corolloid, green, white or pink, corollas pink to red or striped red and white/pinkish. Solomon Islands (Bougainville, Shortland Island, Mono Island, Treasury Island, Choiseul, Baga Island, Kolombangara, New Georgia, Isabel, Guadalcanal). **Solomon Islands Clade 2**

Widespread and conspicuous throughout its range, this species is closely allied with *Cyrtandra subulibractea* and other red-flowered species found distributed broadly in the Bismarck Archipelago and the Solomons. This species in particular shows characters suggestive of bird pollination including showy, red, tubular corollas, and cauliflorous inflorescences. Honeyeaters in the genus *Myzomela* (Meliphagidae) are suspected pollinators (C. Filardi pers. comm.).

Other specimens examined: Solomon Islands—Bougainville: Korowai Hills, west of Toiumonapu Plantation, 60 m, *Van Royen N.G.F. 16375* (BISH). Kolombangara: NE Coast, Shoulder Hill Area, 250–400 m, *Regalado & Sirikolo 777* (BISH); KFPL Forest Management Area R2, 260 m, 26 May 2009, *Clark 770* (E, K, PTBG, U.S.; = C0205 in phylogeny); KFPL Forest Management Area L5 along trail to crater, 1000 m, 31 May 2009, *Clark 782* (E, K, PTBG, U.S.). Vangunu: upland from logging camp, 900 m, 13 June 2009, *Clark 806* (E, K, PTBG, U.S.).

8. Cyrtandra floribunda K.Schum., Fl. Schutzgeb. Südsee: 377. 1905. Type: Papua New Guinea—New Guinea: Bismarck Mtns., 1200 m, January 1902, *Schlechter 14070* [Holotype destroyed (?); Isotype WRSL!].

Cyrtandra rhynchotechoides Hatusima, Bot. Mag. Tokyo 57: 121 (1943).

Shrub to 1 m, leaves opposite, bases strongly unequal, inflorescences axillary, branched cyme of many flowers (as many as 50), calyces corolloid, funnelform, corollas white to greenish white, funnelform. Bismarck Archipelago (New Guinea, New Britain). **Solomon Islands Clade 4**

This species is conspicuous in its copious number of flowers per inflorescence. *Cyrtandra floribunda* overlaps in range with *C. fulvovillosa* Rech. in the Bismarck Archipelago. If phylogenetic analysis supports inclusion in Clade 4 as here hypothesized (which is nested within the Pacific clade), *C. floribunda* would represent a verified ‘‘back’’ dispersal to New Guinea from the Pacific islands.

Other specimens examined: Papua New Guinea—New Guinea: MI. road to Mt. Suckling, 488 m, *Katik LAE 56326* (BISH). New Britain: East New Britain, Gasmata Sub-district, 6 miles east of Fullerborn Harbour, 300 m, *Womersley et al. LAE 55342* (BISH).

9. Cyrtandra fulvovillosa Rech., Repert. Spec. Nov. Regni Veg. 11: 185. 1912. Type: Papua New Guinea—New Britain: in rain forest near Toma, October 1905, *Rechinger 4993* [Holotype W] Figure 2.4.

Cyrtandra malaccocaulos Schlechter, Bot. Jahrb. Syst. 58: 313 (1923).

Herb to shrub, up to 3 m, leaves opposite, bases unequal; inflorescences axillary, simple to several-branching cymes, flowers 2–15 or more, calyces deciduous, greenish-white, corollas white, funnelform, fruit white. Papua New Guinea (New Guinea), Bismarck Archipelago (New Britain) Solomon Islands (Treasury Island, Vella Lavella, Ganongga, Gizo, Kolombangara, Vangunu, Tetepare, Guadalcanal). **Solomon Islands Clade 4**

A relatively common but variable species in the Solomon Islands. *Cyrtandra fulvovillosa* overlaps extensively with *C. cominsii* in habit and morphology as well as range in the southeastern Solomon Islands.

Other specimens examined: Papua New Guinea—New Guinea: Kani Mts., 700 m, 23 June 1908, *Schlechter 17849* (WRSL, isotype of *C. malaccocaulos*). Solomon Islands—Kolombangara: Forestry Division L5, interior of crater north of field station, 600 m, 31 May 2009, *Clark 786* (E, K, PTBG, SEL, U.S.; = C0183 in phylogeny). Gizo: 1 mile north of Gizo Town, *Kondo 507*(BISH). Vangunu: inland from western coast logging camp, 1000 m, 13 June 2009, *Clark 808* (PTBG).

10. Cyrtandra fuscovellea K. Schum., Fl. Schutzgeb. Südsee: 379. 1905. Type: Papua New Guinea—New Guinea: Torricelli Mtns., 600 m, April 1902, *Schlechter 14552* [Holotype destroyed (?), Isotype: WRSL!].

Shrub to 1 m, leaves anisophyllous or pseudo-alternate, inflorescences axillary, calyces green, corollas red; fruit white. Papua New Guinea (New Guinea), Bismarck Archipelago (New Britain). **Solomon Islands Clade 2**

From observations of the type, this species shares many traits with others in our clade 2 including the red corollas. The low-growing habit is similar to species in clade 1 but might represent a convergence in form rather than a shared, derived trait. Its affinities and distribution in New Guinea and the Bismarck Archipelago suggest more than a superficial relationship among the red-flowered cyrtandras.

11. Cyrtandra hentzelmaniana G.W.Gillett, Kew Bull. 30: 403. 1975. Type: Solomon Islands—Bougainville: Panguna - Arawa Trail, 1 km above Panguna, Crown Prince Range, 920 m, 20 July 1973, *Gillett 2570* (K holotype, A, BRI, E!, LAE, UC isotypes).

Shrub or tree to 7 m, leaves pseudoalternate, inflorescences axillary on woody branches, calyces corolloid, red, pink or white; corollas red, pink or white, fleshy; fruit white. Solomon Islands (Bougainville, Baga Island, Kolombangara, Guadalcanal). **Solomon Islands Clade 2**

As described by Gillett (1975), this broadly circumscribed species appears to share many characters with an assortment of species throughout the Solomons, most similar to *Cyrtandra heteronema* G.W.Gillett, described below, *C. filibracteata* and *C. subulibractea* G.W.Gillett. However, the isotype (E) observed differs dramatically in having markedly hirsute corollas, similar to many species of *Cyrtandra* found throughout Malesia. Many species complexes are known to exist in the genus and rather unsatisfactory taxonomies have been proposed to account for these relationships (Burtt 2001). Depending on geographic structure in *C. heintzelmaniana*, recognition of regional subspecies or varieties might be warranted although such structure might not be expected.

Other specimens examined: Solomon Islands—Bougainville: Koniguru, Buin, 900 m, 17 August 1930, *Kajewski 2103* (BISH).

12. Cyrtandra herbacea G.W.Gillett, Kew Bull. 30: 382. 1975. TYPE: Solomon Islands—Bougainville: 6 mi (10 km) north of Buin, 145 m, 4 September 1964, *Craven & Schodde 402* (Holotype: K; Isotype: LAE!).

Weak-stemmed herb to 0.5 m, leaves characteristically pubescent; inflorescences pubescent, 6–40 flowers; calyces green; corollas white, funnelform; fruit pale green. Solomon Islands (Bougainville). **Solomon Islands Clade 4**

This species is perhaps the most vegetatively specialized of the Solomon cyrtandras, exhibiting a consistently herbaceous habit. Gillett based his recognition of this species on this unique habit and also on the smallish flowers that differentiate it, although tenuously, from *Cyrtandra floribunda*.

13. Cyrtandra heteronema G.W.Gillett, Kew Bull. 30: 402. 1975. TYPE: Solomon Islands—Bougainville: Panguna-Arawa trail, north of summit, ridge, Crown Prince Range, near Kupei, 1000 m, 20 July 1973, *Gillett 2578* (Holotype: K; Isotypes: BRI, E!, LAE, UC).

Shrub to 2 m, leaves opposite or pseudoalternate, inflorescences axillary, calyces and corollas both red; anthers conspicuously excerted; fruit white. Solomon Islands (Bougainville). **Solomon Islands Clade 2**

Gillett (1975) chose to recognize this species as separate from *Cyrtandra heintzelmaniana* based principally on stamen filament length and presence or absence of an indumentum on the inner corolla tube (present on *C. heteronema*). However, as mentioned under *C. heintzelmaniana*, a wide range of variability exists. For example, *Kajewski 1733* is most similar to *C. heteronema*, but lacks significant pubescence on the inner calyx lobes. Either inclusion of this species in the former is warranted or, as suggested, further subdivision of *C. heintzelmaniana* may be warranted to standardize species concepts here.

Other specimens examined: Solomon Islands—Bougainville: Kupei Gold Field, 1000 m, 17 April 1930, *Kajewski 1733* (BISH).

14. Cyrtandra laciniata G.W.Gillett, Kew Bull. 30: 388. 1975. TYPE: Bismarck Archipelago—New Britain: gorge below Yau Yau Village, Nakanai Range, 750 m, 5 July 1973, *Gillett 2559* (Holotype: K; Isotypes A, BRI, E!, LAE, UC).

Shrub to 3.5 m, leaves opposite, fleshy, inflorescences congested, bracteate, flowers often concealed in decaying plant matter; plants highly variable as circumscribed. Bismarck Archipelago (New Ireland, New Britain), Solomon Islands (Kolombangara, Isabel, Guadalcanal). **Solomon Islands Clade 3**

Two species sampled in this study, labeled *Cyrtandra* sp. ''A'' and *C.* sp. ''B,'' share many characteristics with the description for *C. laciniata* including common ranges. However, these differ in significant ways as detailed under their respective descriptions. It is possible that Gillett has defined a continuum of species ranging from New Guinea to the Southern Solomon Islands. Additional taxonomic work will be required to resolve these relationships.

15. Cyrtandra lutescens G.W.Gillett, Kew Bull. 30: 386. 1975. TYPE: Bismarck Archipelago—New Britain: Mt. Bango, 275 m, 19 May 1968, *Henty & Lelean 29451* (Holotype: E!; Isotype: LAE).

Shrub to 3 m, leaves opposite, bases unequal; inflorescences axillary on older woody stems, on stout peduncles, calyces deciduous, corollas white to green, bilabiate. Bismarck Archipelago (New Britain). **Solomon Islands Clade UNCLASSIFIED**

While many characters including vegetative traits such as leaf shape and overall habit align this species with Clade 4, its exclusive range in New Britain, coupled with the stoutly peduncled, bracteate inflorescences, suggest affinities to Clade 3.

16. Cyrtandra macrotricha G.W.Gillett, Kew Bull. 30: 383. 1975. TYPE: Solomon Islands—Guadalcanal: Vulolo, Tutuve Mt., 1000 m, 17 April 1931, *Kajewski 2531* (Holotype: A; Isotypes: BM, G, P).

Herb to tree, smallish in stature, although up to 6 m according to Gillett (1975, and specimens referenced therein), leaves opposite, bases unequal to cordate; inflorescences axillary, branching cymes of 25–30 flowers, calyces deciduous, corollas funnelform, white to greenish white; fruit a white berry. Solomon Islands (Guadalcanal, Isabel, San Cristobal). **Solomon Islands Clade 4**

As one of the sampled specimens in our phylogenetic analysis, this species is verified as part of Clade 4. As such, a clade of no fewer than two distinct Solomon Islands species is supported as nested within the monophyletic Pacific clade (BS 90%; PP $>$ 99%).

Other specimens examined: Solomon Islands—Isabel: inland from coast on trail to Mt. Kubonito, near permanent camp near stream, 650 m, 14 May 2009, *Clark 747* (PTBG). San Cristobal: Hinuahaoro, 900 m, *Brass 3033* (BISH).

17. Cyrtandra magentiflora G.W.Gillett, Kew Bull., 30: 384. 1975. TYPE: Solomon Islands—Bougainville: near Koniguru No. 1, ca. 11 miles (18 km) north of Buin, 270 m, 20 July 1964, *Craven & Schodde 50* (Holotype: CANB; Isotypes: E!, LAE).

Tree to 9 m, leaves anisophyllous; inflorescences cauliflorous, bracts linear, calyces concealed, corollas crimson-purple, bilabiate, fruits not known. Solomon Islands (Bougainville). **Solomon Islands Clade 2**

This species is most likely allied with *Cyrtandra filibracteata*. Greater scrutiny of the type is required to ascertain what characters can be used to warrant continued recognition of this species. Known only from the type specimens.

18. Cyrtandra purpurifolia G.W.Gillett, Kew Bull. 30: 400. 1975. TYPE: Solomon Islands—Bougainville: Arawa trail, below Kupei, north side of Crown Prince Range, 20 July 1973, *Gillett 2579* (Holotype: K; Isotypes: A, BRI, E!, L, LAE, UC).

Shrub or branching tree to 2 m (6 m), leaves pseudoalternate, distinctively purple underneath; inflorescences axillary, bracteate with linear bracts, flowers few, calyces small and deciduous, corollas pink, fruit white. Solomon Islands (Bougainville, Guadalcanal). **Solomon Islands Clade 2**

In many respects, this species is allied with both clades 1 and 2. However, the colored corollas are suggestive of the latter. The species is not always distinguishable from *Cyrtandra subulibractea* specimens aside from the distinctive purple undersides of the leaves.

Other specimens examined: Solomon Islands. Bougainville: Kupei goldmine, 900 m, 5 April 1930, *Kajewski 1621* (BISH). Guadalcanal: Tutive Mt., 1200 m, 13 May 1931, *Kajewski 2659* (BISH).

19. Cyrtandra sericifolia G.W.Gillett, Kew Bull. 30: 392. 1975. TYPE: Solomon Islands—Bougainville: Summit ridge of Crown Prince Range, between Arawa and Panguna above Kupei, 1270 m, 20 July 1973, *Gillett 2575* (Holotype K; Isotypes: E!, LAE, UC).

Shrub to 3 m, leaves opposite, glabrous at maturity; inflorescences axillary, congested, up to 20 flowers, calyces and corollas tubular, the latter cream white, fruit white. Solomon Islands (Bougainville). **Solomon Islands Clade 3**

Based on specimens observed and Gillett's description, this species is aligned most likely with clade 3. Apparently a widespread group in the Solomons, species in this clade are superficially similar to *Cyrtandra hawaiensis* C.B.Clarke from Hawaii (Wagner et al. 1990) and several species from Fiji (Smith, 1991, Clark et al., 2009). All possess common features such as large leaf blades often restricted to the stem apex and conspicuously bracteate inflorescences. Phylogenetic data, however, suggest these species are not closely related (FIGURE 1).

Other specimens examined: Solomon Islands—Bougainville: Koniguru, Buin, 950 m, 12 August 1930, *Kajewski 2079* (BISH).

20. Cyrtandra subulibractea G.W.Gillett, Kew Bull. 30: 409. 1975. TYPE: Solomon Islands—Bougainville: Crown Prince Range, Panguna, Arawa trail, 1040 m, 20 July 1973, *Gillett 2572* (Holotype: K; Isotypes: A, BRI, E!, LAE, UC).

Shrub or tree to 5 m, gynodioecious, anisophyllous, inflorescences axillary, 1–few flowers each, calyces petaloid, green to red, corollas pale yellow, white to pink, fruit white. Solomon Islands (Bougainville, Kolombangara, Vangunu, Isabel, Guadalcanal, Malaita, Rennell). **Solomon Islands Clade 2**

Plants identifiable to this species were often seen growing sympatrically with *Cyrtandra filibracteata* on Kolombangara and Vangunu islands (J.R. Clark pers. obs.) and, as noted earlier by Gillett (1975), discerning between the two is problematic. Never-the-less, the distinctiveness of the two, when taken in context of ''typical'' for each species, combined with more rigorous multi-island sampling and phylogenetic analysis (J.R. Clark current research; data not shown), support the recognition of the two species as distinct. The occurrence of gynodioecy, while uncommon in

Cyrtandra, is not unheard of; *Cyrtandra longifolia* (Wawra) Hillebrand ex C.B.Clarke has been documented as such on Kauai, Hawaii (Wagner et al. in prep.).

Several specimens observed including *Kajewski 1742* and *Kajewski 2711* were identified as having white corollas. The variability in corolla color is noteworthy in this species although geographical structuring in this variation is not currently known. This, coupled with variability in vegetative characters warrants further scrutiny, particularly in how they overlap with taxa considered part of clade 1 which are exclusively white-flowered.

Other specimens examined: Solomon Islands—Bougainville: Kupei Gold Field, 1000 m, 18 April 1930, *Kajewski 1742* (BISH); Kugumaru, Buin, 150 m, 7 June 1930, *Kajewski 1854* (BISH). Kolombangara: KFPL Forestry Area L5, interior of crater from Field Station, 1000 m, 31 May 2009, *Clark 788* (E, K, PTBG, U.S.; = C0184 in phylogeny). Vangunu: near Mbope, 500 m, 12 June 2009, *Clark 805* (K, PTBG; = C0191 in phylogeny). Isabel: Tiratona (*sic.*), 170 m, 29 December 1932, *Brass 3398* (BISH). Guadalcanal: Sorvorhio Basin, 185 m, 23 January 1932, *Kajewski 2711* (BISH).

21. **Cyrtandra terraeguilelmi** K.Schum., Bot. Jahrb. Syst. 9: 217. 1888. TYPE: Bismarck Archipelago—New Guinea: Sattleberg, near Finschhafen, July 1886, *Hollrung 203* [Holotype destroyed (?); Isotype: WRSL!].

Shrub to 2.5 m, pseudoalternate leaves; inflorescences axillary, bracteate, calyces fleshy, campanulate, pink or red, corolla red, fleshy, densely pubescent, fruit white. Papua New Guinea (New Guinea), Bismarck Archipelago (New Britain). **Solomon Islands Clade 2**

This species, restricted to New Guinea and New Britain, shares many features in common with the Solomon Islands species *Cyrtandra filibracteata* and *C. subulibractea*, both of which were sampled in this molecular analysis. Taxonomic revision in this clade will require a thorough sampling of New Guinea species; Bismarck Archipelago and Solomon Islands members of this group are possibly not restricted to these archipelagos and conceivably extend into New Guinea. Note: this species was listed as ''*Cyrtandra terra-guilelmii*'' in Gillett's 1974 treatment.

Other specimens examined: Bismarck Archipelago—New Britain: West Nakanai, Lairu Cr., near Gule, Cape Hoskins, 23 August 1954, *Floyd 6596* (BISH).

22. **Cyrtandra trichocalyx** G.W.Gillett, Kew Bull., 30: 396. 1975. TYPE: Bismarck Archipelago—Bougainville: Isina Village, 425 m, 1 February 1967, *Lavarack & Ridsdale 31280-A* (Holotype: E!; Isotype: LAE).

Herbaceous shrub to 3 m, leaves opposite, bases rounded to acute, inflorescences axillary, congested, calyces greenish, corollas white, fruit greenish white to yellowish. Bismarck Archipelago (New Britain) and Solomon Islands (Bougainville). **Solomon Islands Clade 3**

The distinctive congested, bracteate inflorescences align this species with clade 3.

23. **Cyrtandra valviloba** G.W.Gillett, Kew Bull. 30: 384. 1975. TYPE: Bismarck Archipelago—New Britain: NNE. slope Mt. Ulawon, 400 m, 20 February 1971, *Lelean & Stevens 51236* (Holotype: K; Isotype: LAE).

Branching shrub to 3 m, woody, leaves opposite, cauliflorous, bracteate, bracts large, nearly as wide as long, calyces cylindrical, corollas pale green, nearly actinomorphic, fruit white, ovoid. Bismarck Archipelago (New Britain, New Ireland). **Solomon Islands UNCLASSIFIED**

Material was not available for study of this species.

24. **Cyrtandra wariana** Schltr., Bot. Jahrb. Syst. 58: 360. 1923. TYPE: Papua New Guinea—New Guinea: near Udu, on the Waria River (near Morobe), 300 m, 12 March 1908, *Schlechter 17448* [Holotype destroyed (?); Isotypes: P, WRSL!].

Branching shrub to 3 m, woody, leaves pseudoalternate, rarely anisophyllous; inflorescences axillary, bracteate, bracts small and inconspicuous, calyces urceolate and inflated, corolloid, corollas white to pale green, stigma discoid, fruit white. Papua New Guinea (New Guinea), Bismarck Archipelago (New Britain, New Ireland). **Solomon Islands Clade 1**

Cyrtandra wariana shares many features in common with *C. erectiloba*, as mentioned previously. Their ranges overlap in the Bismark Archipelago and intact flowers are required to discern between the two. The feature of discoid stigma in this species vs. bilobed in *C. erectiloba* warrants additional study.

Additional taxa sampled and identified here, but not currently described:

25. **Cyrtandra sp. ''A''** FIGURE 2.3.

Sparsely branching shrub or small tree to 3 m, often monopodial with leaves restricted to the upper half or near the apex, leaves opposite, often congested near the apex and appearing whorled, petioles up to 70 cm, distinctively white to whitish-green, blades elliptic to acuminate, to 50 cm long, inflorescences axillary in bracteate, congested cymes with stout pedicels, corollas five-lobed, campanulate, fruit a white ellipsoid berry. **Solomon Islands Clade 3**

This undescribed species appears to be related to *Cyrtandra laciniata* but differs in its distinctive leaves and petioles and characteristic monopodial habit. It is relatively common throughout its range and is therefore somewhat surprising that no historical collections examined to date are of this species. More field and herbarium studies are warranted prior to formal description of this species.

Specimens examined: Solomon Islands—Kolombangara: KFPL Management Area R2, 260 m, 26 May 2009, *Clark 772* (K, PTBG); KFPL Forest Management Area L5, near camp along stream, 2 June 2009, *Clark 790* (PTBG). Isabel: on trail to Mt. Kubonitu, 800 m, *Clark 722* (PTBG); Mt. Kubonitu, 800 m, 14 May 2009, *Clark 724* (PTBG = C0173 in phylogeny).

26. Cyrtandra sp. ''B'' (not shown)

Sparsely branching shrub, leaves opposite, hirsute, inflorescences in congested bracteate clusters in the leaf axils, bracts distinctively linear, long acuminate, flowers white, campanulate, fruit a white berry. **Solomon Islands Clade 3**

Cyrtandra sp. ''B'' appears to be of an undescribed taxon similar to but differing from *C. laciniata* and *C.* sp. ''A'' in its uniformly linear, acuminate bracts. While no material examined to date appears to be conspecific with this species, a more exhaustive examination of herbarium material is warranted. The specimen is here referenced for purposes of documenting the voucher for this study and as a foundation for future work.

Specimens examined: Solomon Islands—Kolombangara: interior of crater north of Forest Management Area L5, 31 May 2009, *Clark 787* (PTBG = C0209 in phylogeny).

DISCUSSION

With the addition of new samples from the Solomon Islands, a greater resolution and knowledge of distribution patterns has been gained. It was first hypothesized by Clark et al. (2009) that the Solomon Islands might harbor cyrtandras that are intermediate between Malesian and Pacific clades. Our results support this hypothesis with clade 3 being resolved conclusively as sister to the Pacific clade and thus separating the former long branch between these as was resolved in all previous studies (Cronk et al. 2005; Clark et al. 2008, 2009). The discovery of clade 4 being firmly nested within the Pacific clade suggests a potential ''back'' dispersal ability in some groups where clades from decidedly Pacific cyrtandras can and do colonize and become established in older, more established ecosystems. It is not conclusively known if these clades will also be found in more central continental origin areas like Borneo and New Guinea, although species hypothesized to be conspecific are known from there (Gillett 1975). Further sampling and study in these areas is greatly needed to better understand the biogeographic history of this genus.

The phylogenetic placement of four distinct clades of *Cyrtandra* in the Solomon Islands is not all that unexpected in the archipelago. Gillett (1975) suggested as many as eight independent introductions of *Cyrtandra* are found there. The islands' proximity to more mainland centers of diversity for the genus, in particular New Guinea, intuitively increases the probability of multiple dispersal events (Carlquist 1981). As such, distinct evolutionary lines are expected to occur here, similar to other areas in the western range for the genus (Atkins et al. 2001) and in contrast with remote island areas such as Hawaii and possibly the Marquesas (Wagner et al. 1990; Wagner et al. submitted). Of the 26 taxa considered in this study, two were assigned to clade 1, eight to clade 2, six to clade 3, five to clade 4, and five remained unclassified (Table 2).

Clade 1 and clade 2 in this study, while forming a single well supported clade, are here treated as two recognizable groups. Although species in both clades are similar in many ways including a trend towards anisophylly, separation along flower color and hypothesized pollination syndrome is warranted. Clade 1 appears to be a small sampling of a much wider dispersed group of cyrtandras found throughout the western range for the genus including Borneo, New Guinea, the Philippines, and the Solomon Islands (Gillett 1975, Burtt 2001, J.R. Clark pers. obs.). Representatives of this clade also appear to have potential to disperse to other more remote regions including *C. baileyi* (sampled in this study) from North Queensland, Australia and *C. efatensis* from Vanuatu. The unique morphology of specimens from San Cristobal Island also suggests a propensity for regional variation in this complex despite its overall extensive range.

The red-flowered clade 2 is separated from clade 1 and all other clades known to occur in the Solomons and the Pacific by the red flowers and apparent bird pollination (Cronk et al. 2005). This evolutionary transition to ornithophily is not common in *Cyrtandra* to begin with; while red-pigmented flowers do occur in some species, the vast majority are either white, cream or pale yellow (Burtt 2001). A parsimonious hypothesis assumes a limited shift to this syndrome over time (Barret 1998, Grant 1998) and further supports the monophyly of this clade. Clade 1 is either the sister clade of the ornithophilous clade 2, or, perhaps more likely given the current limited sampling, either could be a nested subclade within a broadly dispersed larger clade. Regardless, additional sampling and character state reconstruction analyses are warranted to better understand the evolution of these two related groups of *Cyrtandra* and this apparent shift to bird pollination.

Clade 3, here represented by two as yet unidentified/undescribed species, is phylogenetically situated as sister to the entire Pacific clade of *Cyrtandra* (FIGURE 1). In previous studies, a long branch connected the southeast Asian grade of species with the monophyletic Pacific clade (Clark et al. 2008, 2009). Discovery of a clade that effectively splits this branch in half further refines our biogeographic knowledge of the eastward expansion of *Cyrtandra* into the Pacific.

Cyrtandra laciniata and other species from the Bismarck and Solomon Islands archipelagos are here hypothesized to belong in clade 3; all of these share among other characters, congested, bracteate axillary inflorescences. While these species are morphologically similar to other Pacific cyrtandras including *C. occulta* from Fiji and *C. hawaiensis* from Hawaii, phylogenetic data suggest no close relationship. However, in the latter two mentioned species, Wagner et al. (1990, 1999) hypothesized a relationship between these based on said morphological characteristics. This hypothesis is supported in our study. In the analysis, *C. occulta* and a related Fijian species form a clade that is resolved sister to the Hawaiian clade (FIGURE 1). It remains unclear as to what significance these shared, apparently pleisiomorphic, traits, outside of the fleshy berries common to most all Pacific cyrtandras, have, if anything, in regard to the expansion of the genus throughout the Pacific.

Much like clade 3, clade 4 includes species that share superficial similarities with taxa that are not all that closely related to one another. *Cyrtandra fulvovillosa* and *C. macrotricha* (clade 4, sampled here) have been hypothesized to be part of the *Cyrtandra samoensis* complex of species (*sensu* Clark et al. 2009; see Gillett 1973, 1974). However, clade 4 is actually resolved as sister to the South Pacific clade, in which *C. samoensis* A.Gray is firmly nested among other morphologically dissimilar species of *Cyrtandra*.

CONCLUSIONS AND FUTURE DIRECTIONS

Understanding the evolutionary and taxonomic relationships in *Cyrtandra* are complicated by a broad geographic range, large number of species, and a recent radiation of these species in the Pacific and possibly elsewhere, potentially confounded by hybridization (Atkins et al. 2001, Cronk et al. 2005, Clark et al. 2009). In addition, fresh or silica gel-dried plant material is usually required for successful DNA extraction and analysis thus requiring extensive fieldwork to complete molecular studies (Clark et al. 2008). Despite a concerted recent effort to sample *Cyrtandra* across its range (principally by authors in this paper), sampling is far from comprehensive and many clades are only partially or not at all sampled. Even when sampling is near complete, species-level relationships cannot be resolved using commonly used markers (Atkins et al. 2001; Bramley et al. 2004a, 2004b; Clark et al. 2008, 2009). A recent study suggests using next-generation sequencing and a large number of genic regions is also unsuccessful in finding molecular solutions to resolving these relationships (Pillon et al. 2013). To advance our understanding in *Cyrtandra* it becomes currently necessary to use a combination of molecular and morphological approaches as applied in this study.

In the Solomons, we have chosen to use this phylogenetically-informed assessment for defining clades and subsequent morphological categorization of genetically sampled and unsampled species. This approach is warranted in that it has been successfully applied in well-sampled areas such as Hawaii to arrive at a more satisfactory taxonomy than using morphology or genetics alone (Wagner et al. in prep). The challenge remains to accurately interpret synapomorphic characters verses pleisiomorphic ones. It has been shown that some clades, including the *Cyrtandra samoensis* complex (*sensu* Clark et al. 2009), include a disparate group of species that are only superficially similar. Clades 3 and 4 in the current study both exemplify this phenomenon. Geographical proximity of similar species must also be considered; based on our current understanding of species in the Pacific, those taxa that share many morphological similarities and occur within common or neighboring areas are more consistently resolved as closely related. These caveats have been used to interpret relationships in the Solomons based on our current knowledge. As such, these hypotheses form the basis for ongoing research in the Pacific and serve as a proof of concept for methodology described here. Future advances in knowledge will require ongoing field sampling and study combined with molecular and morphological analysis to both establish and refine taxonomy (see Atkins et al. 2013).

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