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# CURRENT KNOWLEDGE AND FUTURE DIRECTIONS IN THE TAXONOMY OF *CYRTANDRA* (GESNERIACEAE), WITH A NEW ESTIMATE OF SPECIES NUMBER

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ABSTRACT. A summary of our current knowledge of the genus *Cyrtandra* is presented, including a new estimate of species numbers across its distribution. A substantial amount of taxonomic work will be necessary before a monograph of the genus can be considered. We propose a phylogenetically informed taxonomic strategy to tackle *Cyrtandra* and advocate for increased web-based access to specimens, collections data and taxonomic literature. Methodology described here is currently being used to address taxonomic revision in some regions where *Cyrtandra* is found. Remaining alpha taxonomic work will be addressed using this phylogenetically informed regional approach, with initial focus on Borneo, Sulawesi, New Guinea, and archipelagos in the Pacific. As a priority, a phylogeny of *Cyrtandra* is being developed through an international collaborative effort. To facilitate data sharing and communication in this collaboration, we advocate for increased digitization of herbarium collections and are exploring various cloud-based options for sharing and managing taxonomies and related data. With a robust phylogeny and increased access to data and collections, we aim to move closer to an infrageneric classification and to further the work that has already shown *Cyrtandra* to be a model genus for answering critical biological questions.

*Key words:* monograph, phylogeny, large genus, digitization, biogeography, evolution

## INTRODUCTION

Advances in systematics in the last 20 years have helped to revolutionize our understanding of angiosperm phylogeny (Stevens 2001). Ordinal and familial relationships in particular have been refined to encompass monophyletic groupings based largely on a new synthesis of molecular data (APG III 2009). Through the concerted efforts of numerous researchers, labs and working groups, well-resolved and thoroughly-sampled phylogenies at the family level are increasingly common in the literature (e.g., Acanthaceae, McDade et al. 2008; Arecaceae, Baker et al. 2009; Asteraceae, Funk et al. 2005; Bignoniaceae, Olmstead et al. 2009). These well-resolved phylogenetic hypotheses provide the basis for comparing, organizing, and understanding life on Earth (Heath et al. 2008) and also enable conservation biologists to identify evolutionary units requiring protection (Bordewich et al. 2008).

Although a comprehensive, family-level phylogeny for Gesneriaceae has yet to be produced (Weber & Skog 2007, Möller et al. 2009, Möller & Clark 2013), major clades are increasingly well known and remaining taxonomic challenges have been identified (Weber et al. 2013). Of these, the genus *Cyrtandra* J.R. & G.Forster poses the greatest taxonomic challenge in the family due to the high number of poorly known and undescribed species.

Research into large genera has the potential to provide answers to critical biological questions concerning ecology, conservation, evolution and biogeography (Frodin 2004). For example, it has been suggested that *Cyrtandra* in particular holds clues to the rapid expansion into and colonization of the Pacific high islands by vascular plants (Clark 2008, Clark et al. 2009). Despite the

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potential for great scientific insight, research on large genera is often insufficient because of the difficulty in completing the research in a reasonable period of time (Mabberley 1997). Developing concerted, multi-institutional, multi-national strategies to tackle these genera are required (Bramley 2003).

The genus *Cyrtandra*, exhibiting a broad geographic range but consisting of defined (and increasingly known) geographically-restricted monophyletic clades, is well-suited to a collaborative, geography-based methodology for classification, revision, and phylogenetic study. The purpose of this review is to briefly summarize the current state of knowledge in *Cyrtandra* and to outline a potential plan to systematically approach the challenges this genus presents. As part of this work, we here make a new estimate of species numbers in *Cyrtandra* as a baseline measure of diversity for future study in the genus.

## CURRENT STATE OF KNOWLEDGE

*Cyrtandra* is the largest genus in the Gesneriaceae, and previous species numbers have been estimated at around 600 or more species (Burtt 2001; but see new estimates below). Its distribution stretches east from the Nicobar Islands, across Malesia to the Philippines, Taiwan, southern Ryukyu Islands, northern Queensland and the Loyalty Islands, to the high islands of the Pacific including Hawaii and the Marquesas (Atkins et al. 2001, Bramley et al. 2004, Cronk et al. 2005, Clark et al. 2009; for a distribution map, see Clark et al. 2008). The richest centers of diversity for *Cytandra* include New Guinea and Borneo, the Philippines, and the Pacific islands (TABLE 1).

*Cyrtandra* is variable in habit; they are mostly herbs and shrubs but can also be epiphytes or even trees (Burtt 2001). The fruit of *Cyrtandra* are either indehiscent, hard capsules or fleshy berries, the latter being predominant in the Pacific (Clark et al. 2013) whereas the former is characteristic of Malesian taxa (Atkins et al. 2001). Flowers in *Cyrtandra* range from white, to yellow, pink, red or even purple (FIGURE 1, this paper; for examples from the Solomon Islands, see Clark et al. 2013, FIGURE 2). They tend to be white in western Malesia and the Pacific but in New Guinea and surrounding regions flowers can be more brightly colored and are often tubular in shape, suggesting bird pollination. Examples of potentially bird-pollinated taxa include *C. roseiflora* H.J.Atkins and *C. fasciata* H.J.Atkins both from Sulawesi, a clade of species in the Solomon Islands including *C. filibracteata* B.L.Burtt (see Clark et al. 2013), and in section Glossophorae from New Guinea described by Schlechter (1923).

Despite the almost continuous distribution of the genus, species of *Cyrtandra* tend to be geographically restricted and throughout its range represented largely by localized endemics (e.g., Gillett 1973a, 1973b, 1975a, 1975b; Burtt 1978, 1982, 1990, 1992, 2001; Wagner et al. 1999; Atkins 2001, 2004; Bramley 2003, 2005; Clark et al. 2013). In instances where cyrtandras do appear to have wider ranges, taxonomic assignments tend to be questionable and remain the subject of continued study and debate (e.g., *C. samoensis* A.Gray and reportedly related species, Gillett 1973; Clark et al. 2009).

Molecular phylogenetic research has revealed a high degree of geographic structuring in *Cyrtandra* (Atkins et al. 2001; Bramley et al. 2004; Cronk et al. 2005; Atkins, Bramley and Pennington in prep.). Recently, Clark et al. (2009) utilized likelihood-based ancestral range reconstruction methods in reconstructing ancestral areas of *Cyrtandra* using the most complete phylogenetic sampling in the genus to date. Results from this study revealed a complex history of both within-area divergence events and dispersal-mediated allopatric divergence events leading to the great number of species found throughout the high islands of the Pacific. A general west to east migration of the genus from an origin in or around Southeast Asia, with subsequent range expansion into the Pacific, was also supported.

Despite this rapid radiation, identifiable and supported monophyletic clades are characteristic of the genus throughout much of its range (Bramley 2004, Clark et al. 2009, 2013). Island groups within Malesia and Melanesia consist of numerous separate clades, each representing unique introductions to these areas (Atkins et al. 2001, Bramley 2004, Clark et al. 2013). The majority of Pacific species appear to be rather closely related and the majority are monophyletic, biogeographically beginning in Fiji or neighboring archipelagos (Clark et al. 2008, 2009, and 2013). Within archipelagos, two or more clades are found in islands nearer to southeast Asia (e.g., Solomon Islands, Fiji, Samoa). Remote Pacific islands either share two or more clades with neighboring islands or are monophyletic in the most remote archipelagos (e.g., Hawaii and possibly the Marquesas). Many of these clades can be characterized by a suite of characters and are thus potentially diagnosable morphologically.

## A NEW ESTIMATE OF SPECIES NUMBERS

*Cyrtandra* has proven extremely challenging for taxonomists; most researchers focusing on the genus have commented on extreme difficulties in determining species boundaries (Clarke 1883, Hillebrand 1888, Rock 1917, Gillett 1973, Wagner

TABLE 1. A new estimate of species number in *Cyrtandra* by geographic area. Estimates are made based on historical literature, herbarium records and personal observations. Number ranges represent currently accepted published species (low) and estimated numbers of species (high). See text for more details. *New Guinea, Bismarck Archipelago, Solomon Islands, and Vanuatu share some species in common with one or more of each other. New Guinea is negligible as far as total estimated species and was not calibrated. For Bismarck Archipelago and Vanuatu, total species are shown in brackets and represent species in common with the Solomons; these are included in the total for the latter and, combined with numbers outside of brackets to calculate total species number used for total species summary. Similar overlaps exist in Malesia but again are negligible for total species number and are not accounted for.

| Geographic region | Specific area | Estimated species numbers | Reference(s) |
|---|---|---|---|
| **SOUTHEAST ASIA - MALESIA** | | **467–610** | |
| | *Nicobar Islands* | *2* | Balakrishnan 1976, Balakrishnan and Burtt 1978 |
| | *Thailand* | *6* | Skog and Boggan 2007 |
| | *Peninsular Malaysia* | *9* | Bramley et al. 2004a and pers. obs. |
| | *Sumatra* | *40–44* | Bramley and Cronk 2003, Bramley et al. 2004b and pers. obs. |
| | *Java* | *19–32* | Skog and Boggan 2007 |
| | *Lesser Sunda Islands* | *3* | Bramley pers. obs. |
| | *Borneo* | *181–200* | Skog and Boggan 2007, O.M. Hilliard pers. comm. |
| | *Taiwan (Orchid Island)* | *1* | Merrill 1909, W.L. Wagner pers. comm. |
| | *Philippines* | *105–150* | Merrill 1923, Atkins and Cronk 2001, Skog and Boggan 2007 |
| | *Sulawesi* | *22–40* | Atkins 2004 and pers. obs. |
| | *Moluccas* | *3* | Skog and Boggan 2007 |
| | *New Guinea** | *107–120* | Schlechter 1923, Skog and Boggan 2007, B.L. Burtt and O.M. Hilliard pers. comm. |
| **BISMARCK ARCHIPELAGO and SOLOMON ISLANDS** | | **23–33** | |
| | *New Britain, New Ireland and related small islands** | *7(12)–12(18)* | Gillett 1975 |
| | *Solomon Islands, including Bougainville and Santa Cruz group** | *16–20* | Gillett 1975, J.R. Clark pers. obs. |
| **AUSTRALIA and PACIFIC ISLANDS** | | **162–175** | |
| | *Australia (North Queensland)* | *1* | Mueller 1890, M. Harrington pers. comm. |
| | *New Caledonia and Loyalty Islands* | *1* | Gillett 1973 |
| | *Vanuatu** | *9(10)–12(13)* | Gillett 1974, Pillion pers. comm. |
| | *Fed. States of Micronesia* | *2–3* | D. Lorence pers. comm. |
| | *Fiji* | *38–45* | Gillett 1966, Smith 1991, J.R. Clark pers. obs. |
| | *Samoa* | *20–22* | Gillett 1973, Clark in prep. |
| | *Tonga* | *1* | Gillett 1973 |
| | *Cook Islands* | *2* | Gillett 1973 |
| | *Society Islands* | *16* | Gillett 1973 |
| | *Marquesas* | *11* | Wagner et al. submitted |
| | *Austral Islands* | *1* | Gillett 1973 |
| | *Hawaii* | *60* | Wagner, Clark and Roalson. in prep. |
| **TOTAL ESTIMATED SPECIES** | | **652–818** | |

et al. 1990, Smith 1991, Burtt 2001, Clark et al., 2009). Recent radiation and rapid range expansion (see Clark et al. 2008, 2009), coupled with homoplastic character suites and in-situ hybridization (Burtt 2001), have contributed to these difficulties. A symptom of this challenging biology is that while current estimates of species numbers are about 600, over 1200 names have been published in the genus (IPNI 2012). While many of these have been reduced to synonomy, still many other taxa have not been described (O.M. Hilliard pers. comm; authors this paper pers. obs.).

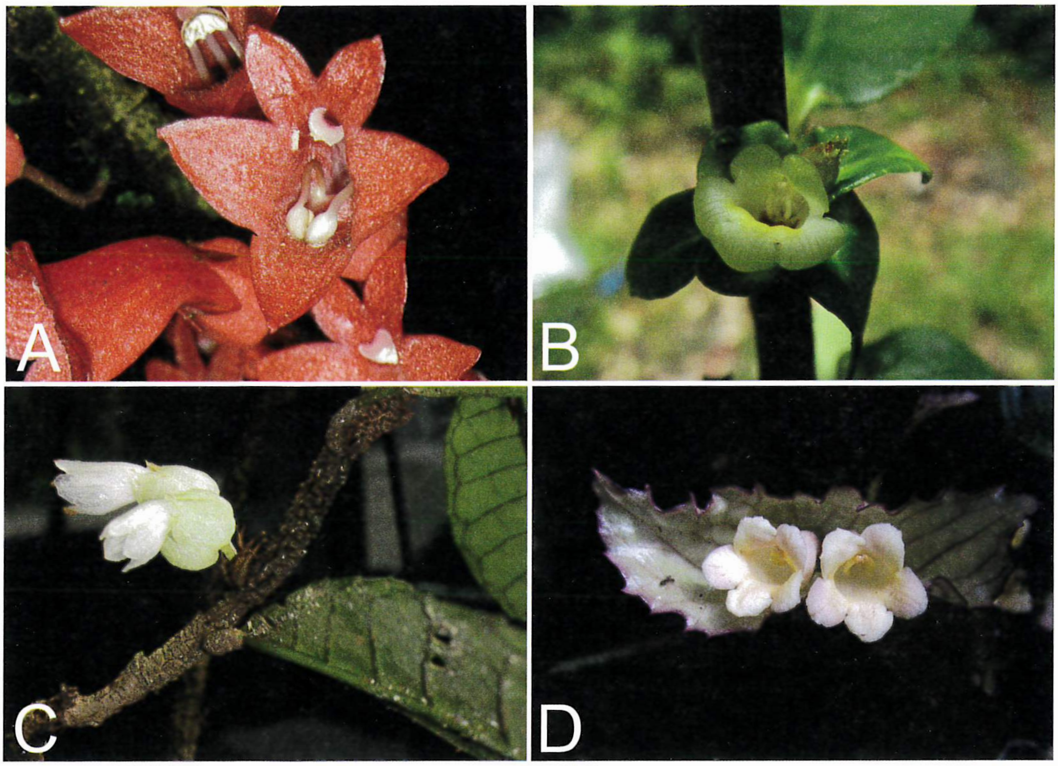

FIGURE 1. Variation in *Cyrtandra* corolla morphology. **A.** *Cyrtandra* sp., New Guinea. **B.** *C. fulvisericea* Bramley, Sabah. **C.** *C.* cf. *wariana* Schltr., New Guinea (photo T. Utteridge). **D.** *C.* sp., Sabah.

For this study, we undertook a cursory review of accepted species numbers in *Cyrtandra*, delineated by major political and/or geographic regions. Estimates were revised on this region by region basis using 1) published species accounts, 2) regional estimates for remaining species to be described, and 3) personal knowledge of the areas, where applicable. Results from this review are summarized in TABLE 1. We here estimate, conservatively, that 652–818 species of *Cyrtandra* exist. This estimate increases expected numbers of species by a maximum of over 30% but is still lower than some estimates of 1000 species (Q.C.B. Cronk pers. comm).

## PROPOSED STRATEGY

A strategy for addressing taxonomy in *Cyrtandra* is emerging from our increased phylogenetic knowledge in the genus as well as advances in technology. We propose that phylogenetically informed taxonomic revision on a region by region basis is a critical need. This, combined with an improved ability to share knowledge, particularly in the digitization of herbarium specimens and web or cloud-based resources to access up-to-date taxonomy as well as historical literature, will facilitate the completion of a genus-wide taxonomy for *Cyrtandra*.

### Phylogenetically Informed Taxonomic Revision

A survey of the taxonomic publications of large genera (Bramley 2003) illustrated that taxonomic work on those genera which are too big for a single researcher or a single publication are either divided by geography (by country, archipelago or island), are phylogenetically-based, or are addressed by a combination of both (e.g., a revision of a clade from a particular region). Based on our current phylogenetic knowledge in *Cyrtandra*, a phylogenetically informed regional approach is most appropriate, aspects of which have already proven effective (e.g., Bramley 2005) and has recently been refined to begin addressing poorly sampled clades in the genus (Clark et al. 2013).

The process involves knowledge of phylogeny acquired through as comprehensive sampling of individual species as possible. As constructed, the phylogeny becomes a tool to identify supported monophyletic clades that can be characterized morphologically by one or more salient characters. Taxa sampled genetically in the phylogeny are automatically assigned to these clades (see

Bramley et al. 2004a); unsampled taxa are tentatively included based on morphological similarities (Clark et al. 2013). Once assigned to a clade, species can then be assessed taxonomically and revisions of existing taxonomy can be streamlined by focusing on similar species identified through both morphological and molecular data.

This procedure is effective for not only described species in need of revision but also for newly discovered or undescribed taxa. When molecular data are available, the new taxon can be sequenced and included in the phylogeny and then compared to other related taxa as described above. If molecular data are currently unavailable, as is often the case with historical collections where DNA is not usable, the taxon can still be assigned to a particular clade and assessed morphologically then described based on similarities as well as differences with other putative close relatives. This method streamlines species characterization and description by limiting the total number of potential conspecifics and/or related species with which any new taxon should be compared.

The phylogenetically informed taxonomic approach described here is self-improving over time. As more and more species are sampled, phylogenetically analyzed, and taxonomically treated, the more robust the system becomes. Areas that are clearly defined phylogenetically can be addressed taxonomically first. Lesser resolved areas will be highlighted by the system and can help to prioritize areas where additional fieldwork and alpha taxonomic work are most needed.

Larger islands in particular will benefit from this methodology. These areas, with high species richness, could be further divided or worked on by a team of taxonomists, first in gross acquisition of specimens for description and phylogenetic analysis. A regional framework will quickly evolve from these efforts and can be effectively ''plugged in'' to the overall phylogeny in the genus. Areas including New Guinea and Sulawesi for example, two of the areas about which we have the least information but which appear to have high species diversity, can be systematically approached in this way. Borneo, where a rather piecemeal publication of species descriptions has occurred to date, could be tackled first by organizing species by major clades identified in preliminary phylogenies and then refined as data and collections increase.

## Sectional Classification

The system described here will ultimately lead to a more satisfactory sectional classification in *Cyrtandra*. As with species-level taxonomy, sectional classification has been variable and not widely used or accepted (Gillett 1973, Wagner et al. 1999, Burtt 2001, Schlag-Edler 2001, Cronk et al. 2005). Many of these efforts were regional (e.g., Hawai'i, Hillebrand 1888; New Guinea, Schlechter 1923; Borneo (Kalimantan), Kraenzlin 1927; Hawai'i, St. John 1966, 1987, Wagner et al. 1990; west Malaysia, Burtt 1990), but failed to encompass the breadth of diversity in the proposed section or created groups that were largely artificial. Currently, over 40 sections are recognized (Burtt 2001) but no satisfactory genus-wide sectional classification exists, owing to the previous lack of phylogenetic knowledge.

Our phylogenetically informed taxonomic approach focusing on monophyletic, regional clades, lends itself well to developing a sectional classification in *Cyrtandra* (authors this paper, current research). This follows existing efforts in other large flowering plant genera (e.g., Forrest et al. 2005, Monro 2006). Monophyly has increasingly been used to justify or even define supraspecific taxonomy (Batista et al. 2013). If carried out in conjunction with the fundamental taxonomic work as described here, the process will provide a framework for taxonomy within and among discrete geographical regions and help us to decide whether and when to recognize sections at any particularly phylogenetic or regional level.

## Data Sharing

With the great number of described species in *Cyrtandra*, access to the multitude of type material and specimens is exceedingly challenging. Previous methods of specimen sharing required physically mailing specimens to researchers around the world. Inherent risks in loaning specimens include damage or loss during shipment and/or while specimens are being used for study. Additional drawbacks to specimen loans include further limiting access to specimens; while on loan, specimens are essentially the exclusive object of study by the loan recipient. For large genera like *Cyrtandra*, these drawbacks are amplified and have historically limited multi-institutional collaborations.

Digitization of herbarium sheets, and providing open access to these images via the World Wide Web, increases the efficiency of specimens sharing and has proven effective in *Cyrtandra*. A recent study of the genus in the Solomon Islands (Clark et al. 2013) was dramatically expedited by on-line access to digitized herbarium collections at BISH, E, K and U.S. Increased funding should be allocated to digitization projects around the world. In particular, assistance should be given to smaller herbaria by supplying resources and technology to digitize these less frequently accessed but equally valuable collections.

In addition to advancing herbarium specimen digitization, an up-to-date taxonomic resource is needed that includes current hypotheses, and information on identified clades and taxonomic assemblages. This ''clearing house'' of taxonomic data will aid researchers in prioritizing areas in need of review and in identifying gaps in taxonomic knowledge. By effectively and efficientl sharing data and knowledge, research efforts can be distributed among active researchers of *Cyrtandra*.

Recently, medium to large scale research collaborations have sought to develop their own web sites to focus and coordinate research efforts. Examples of these include those already successfully being used for the family Sapotaceae (http://elmer.rbge.org.uk/sapotaceae/), the large genus *Begonia* L. (http://elmer.rbge.org.uk/begonia/), and others. A relatively new system for managing taxonomic data and supporting a research network is the cloud-based ''Scratchpads'' (Smith et al., 2012; http://scratchpads.eu; see www.e-monocot.org for an example). Scratchpads enables researchers to create their own tailor-made, online virtual research environment while reducing the time and expertise needed to create stand-alone websites. Key features of Scratchpads include the ability to create species pages (with descriptions, images, distribution maps and specimen data), capacity to upload and share various text and data files (bibliographies, character matrices, classifications, etc.) as well as other media (images, video). Scratchpads supports and enables blogs, online forums, and digital newsletters. The system also provides a platform for peer-editing and commenting, facilitating communication between team members as well as the wider scientific community.

Other options for cloud-based data sharing include the My-Plant initiative (www.myplant.org) that has proven useful in facilitating communication among the world's botanical researchers. My-Plant.org is a freely available, phylogenetically structured social networking website for plant scientists, educators, and other interested parties. Users can easily view current information, collaborate, as well as contribute to the available information, including image galleries, forum discussions, and gain access to external sources of data.

Still other options include using more general cloud-based networking options such as Google Drive (www.google.com/drive/). Google Drive can be used to maintain and share spreadsheets, lists, documents, and taxonomies among collaborators. These could then be shared selectively among other researchers or the public as determined appropriate and as needed.

In practice, facilitating the broad-scale collaboration required to complete a genus-wide phylogeny and taxonomy of *Cyrtandra* will undoubtedly use a variety of methods and technologies. While cloud-based information sharing will be critical to advancing the goals set forth in this paper, in depth communication and face to face interactions will also be instrumental. Joint field expeditions and on-going meetings combined with reciprocal herbarium visits will strengthen partnerships and maintain international ties required to further our understanding of *Cyrtandra*.

## FUTURE DIRECTIONS

Detailed phylogenetic information supported by a robust taxonomy can be useful in answering questions on many different levels from community analysis to large scale biogeography. Large genera such as *Cyrtandra* are particularly useful in examining various biological trends because of their often broad geographic ranges and large number of species adapted to a variety of habitats (Clark 2008). For example, a study of Bramley et al. (2004), investigated ecological character evolution and phylogenetic community structure in *Cyrtandra*. Broader-scale studies in the genus could be conducted following studies and suggestions by Webb *et al.* (2008) including investigations into whether there has been evolution of particular traits that enable species to occupy particular niches and whether these traits can be associated with particular groups of species.

A well-resolved understanding of *Cyrtandra* lends itself to answering a broad range of questions including clade diversification rates and factors affecting changes in diversification rates through time (Moore & Donoghue 2007, Alfaro et al. 2009). Novel evolutionary change, resulting in increased diversity, has been implicated in the formation of species-rich clades (Sanderson & Donoghue 1994) and this phenomenon could be better understood by studying *Cyrtandra*. Such changes, morphological, physiological, and/or reproductive, can cause diversification within a clade (phylogenesis, Goudet 1999) through speciation and/or reduced extinction rates (Stebbins 1981). A well classified and comprehensive taxonomic treatment in *Cyrtandra* would facilitate such studies and provide a model on a scale heretofore unavailable.

Increasing our overall understanding of *Cyrtandra* will also benefit ongoing and future conservation efforts with the genus. Conservation assessment could be informed by well-documented and known species distributions, facilitated by in depth field survey required to fulfill the goals proposed in this review. For example, in areas where *Cyrtandra* is relatively well-known such as Hawaii, it has been possible to accurately assess levels of species threats (9 of 60 Hawaiian

*Cyrtandra* species are federally listed as threatened or endangered under the U.S. Endangered Species Act; USFWS 2012). It is thought that many other *Cyrtandra* species are similarly at risk and can be assessed using comparable strategies as taxonomic and phylogenetic knowledge increase.

A greater knowledge in *Cyrtandra* might also facilitate ecosystem-level conservation initiatives. Because of their apparent preference for humid, intact forest environments, *Cyrtandra* species can be thought of as indicators of undisturbed forest. Understanding the functional traits associated with requirements for this environment, as well as sensitivity to disturbance, may be important in attempts at restoration ecology; it is now recognized that classifying species on functional grounds is a way forward in predicting responses of plant species facing environmental variation or change (Cornelissen et al. 2003). While the concept of indicators of environmental change is not new, *Cyrtandra* can be seen as an indicator to help determine habitat quality wherever it is found. Knowledge of its distribution and ecology could thus be used to assess the relative level of ecosystem integrity within a region and help guide conservation practitioners towards areas requiring additional study and/or protection.

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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