CYCAD CLASSIFICATION
CONCEPTS AND RECOMMENDATIONS

Cycad Classification
Concepts and Recommendations

Edited by

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and

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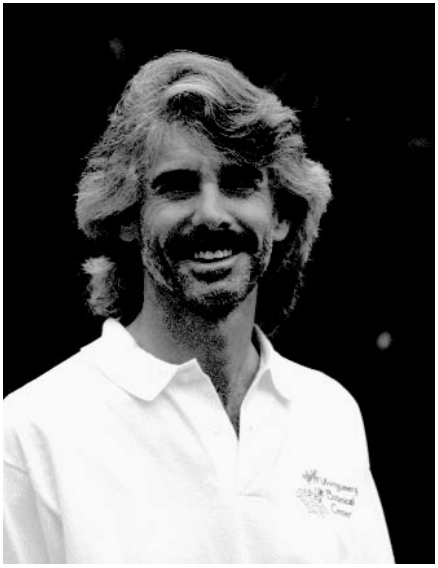
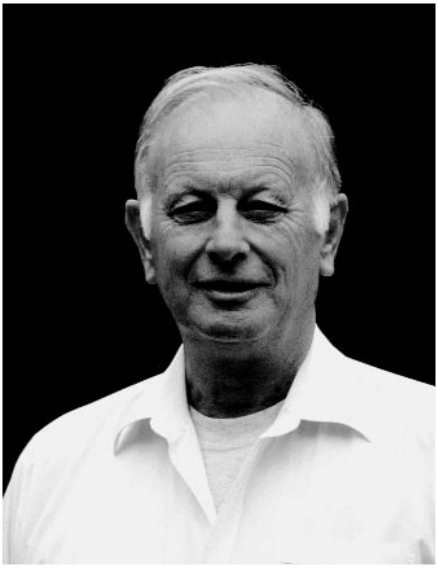
About the Editors

Terrence Walters is the executive director of Montgomery Botanical Center, a botanical garden in Miami, Florida, that concentrates on scientifically documented population-based collections of cycads and palms. Since 1990, he has conducted numerous field expeditions to parts of Asia, Africa and the Americas to investigate and document the cycad flora of the world. He is on the board of directors of the Cycad Society, a member of IUCN's Cycad Specialist Group and on the research faculty of Florida International University. (Photography by Mary Andrews.)



Roy Osborne has been studying and growing cycads in Africa and Australia for more than 20 years. He is a member of the IUCN's Cycad Specialist Group, and founder and first President of the Cycad Society of South Africa. Now living in Brisbane, Australia, he has published more than 100 scientific papers, books and book chapters and has participated in major international conferences on cycad biology. (Photography by Mary Andrews.)



Preface

On 7 April 2002, the Cycad Classification Concepts (CCC) Workshop was convened at Montgomery Botanical Center in Miami, Florida, USA. Seventeen of the world's leading authorities on cycad systematics were invited to participate in the workshop and to submit manuscripts for this volume. Fifteen of these systematists submitted manuscripts and 14 were able to attend the 3-day CCC Workshop.

The purpose of the CCC Workshop was to develop a suite of classification guidelines in support of the advancement of an internationally accepted and stable evolutionary classification system for taxa in the Cycadales. Increased research activity in the field of cycad systematics has led in some cases to increased confusion. As researchers across the globe pursue the many new lines of inquiry provided by technological advances of the past two decades (e.g. DNA sequencing, random amplified polymorphic DNA analysis, etc.), focus on consensus for how the approximately 300 species of cycads should be classified has become clouded. There is an urgent need for guidelines that all cycad systematists can follow in the designation of species, species boundaries and species groupings. The CCC Workshop provided the venue for the development of these guidelines.

Although workshops with a similar purpose have been held to examine critically the systematics of other plant groups, the CCC Workshop was uniquely designed using progressive business methodologies. Five arenas were identified as necessary for the planning and management of this event. The Personnel Arena dealt with the subject of who would be involved as CCC Participants, who would be on the CCC Support Team and who would be in leadership roles during the Workshop process. The Site Arena dealt with everything concerning the facilities required for the Workshop – such as rooms for the various events and work sessions, transportation, housing, furniture, catering and audio-visual equipment. The Operations Arena dealt with identifying and taking those actions required to produce the major product of the Workshop – this volume. The Planning Arena dealt with determining all of the tasks required, their flow, their content and their sequence – from the overall purpose and concept of the Workshop to the minute details associated with the organization and objectives of the Workshop sessions themselves. Finally, the Management Arena dealt with how all of the above would be led and managed.

The first step was to bring in a management consultant, Don Decker, to support the Management Arena objectives and to oversee development of the other four arenas. The next steps were to articulate the purpose, or reason, for having the CCC Workshop, and to determine the products, or results, required to meet the purpose successfully. The overall process of actions that would be required to obtain the products was outlined and then the functioning capabilities, or resources, required for the process were identified. These processes and the development of the above five arenas provided the overall planning and execution structure for the CCC Workshop.

Bringing together a group of world-renowned cycad systematists representing several countries, cultures and languages for consensus building can be difficult. That this event was successful is a tribute to the considerable work that took place prior to, during and after the Workshop by the CCC Support Team and the CCC Participants.

The CCC Participants were 14 of the world's leading and most respected cycad systematists. Paolo Caputo from the Università degli Studi di Napoli Federico II in Italy represented one of the largest concentrations of cycad systematists at any one institution in the world. The Naples cycad group has worked extensively on New World taxa.

Participants representing Asia included Chia-Jui Chen from the Institute of Botany in Beijing, China, an expert on the cycads of China, and Anders Lindström, the cycad curator at Nong Nooch Tropical Gardens in Thailand. Lindström is one of the leading experts on the cycads of Thailand. *Cycas lindstromii* was named in his honour.

John Donaldson, from the National Botanical Institute, and Piet Vorster, from the University of Stellenbosch, were the workshop's representatives from South Africa. Donaldson is Chairman of the IUCN (World Conservation Union) Cycad Specialist Group. Vorster is currently the President of the Cycad Society of South Africa and is an authority on the African genus, *Encephalartos*.

Due to the large number of active cycad systematists in Australia, this country was well represented at the workshop. Attendees included Paul Forster of the Queensland Herbarium, Australia's expert on *Macrozamia*. Ken Hill, from the Royal Botanic Gardens in Sydney, is the world's expert on the taxonomically difficult genus *Cycas*. Roy Osborne, who currently resides in Queensland and formerly lived in South Africa, began the development many years ago of the world list of cycads. Hill and Osborne recently published the authoritative work *Cycads of Australia*.

Andrew Vovides directs the National Cycad Collection of Mexico, and has developed the concept of local conservation of native cycads by initiating projects in which local villagers create nurseries to grow native cycads from sustainable seed harvests. Americans Tim Gregory and Jeff Chemnick continue to undertake extensive systematic fieldwork in Mexico. Their commitment to walking up every canyon in search of each and every population of a species is to be admired.

Other participants from the United States included Bart Schutzman of the University of Florida, the editor of *The Cycad Society Newsletter* and expert on Meso-American *Zamia*. Dennis Stevenson of the New York Botanical Garden is the leading authority on Central and South American taxa and has published extensively on evolutionary concepts in the Cycadales. Loran Whitelock from California, after a decade of fieldwork, research and writing, has recently completed what will become the major reference work on the cycad flora of the world – *The Cycads*. *Ceratozamia whitelockiana* and *Encephalartos whitelockii* are named in recognition of Whitelock's extensive research on the world's cycad flora.

The first session of the CCC Workshop, held on 7 April, created the opportunity for each CCC Participant to give a 20-minute oral presentation of their professional views on cycad classification concepts, systematics and taxonomy. This 1-day work session was organized as a symposium (CCC Symposium) that included invited guests. The second work session, conducted on day 2, focused on elucidating the beliefs and philosophies that the participants held to be true concerning cycad systematics. Also on day 2, during work session three, Katherine Kron of Wake Forest University presented a discussion on a relatively new and somewhat controversial approach to plant nomenclature called 'phylocode'. On the third day of the Workshop, the fourth and fifth work sessions required that the CCC Participants come to alignment on a suite of classification concepts or guidelines that they, as a group, would support and encourage the use of presently and in the future.

In this volume, Chapter 1 presents why the CCC Workshop was convened and the beliefs, or working hypotheses and assumptions, that the CCC Participants hold to be true for cycad classification. This chapter resulted from work sessions two and three. The final chapter, Chapter 15, based on the products obtained from work sessions four and five, summarizes the classification guidelines that the CCC Participants have agreed to follow, support and encourage the use of to produce a universally accepted stable classification system for the Cycadales.

Prior to the Workshop, each CCC Participant submitted a manuscript to the editors. These manuscripts were detailed discussions of the oral presentations presented by the participants during the CCC Symposium (work session one). These manuscripts constitute Chapters 2–14 of this volume.

In Chapter 2, John Donaldson discusses the practical need for a durable classification system in the Cycadales when dealing with cycad conservation issues and planning. In Chapters 3 and 4, Ken Hill and Anders Lindström critically examine the usefulness of various characters for defining species and species concepts within *Cycas*. Three of the CCC Participants, Chia-Jui Chen, Ken Hill and Dennis Stevenson, report on a study of a recently described genus in the Cycadaceae in Chapter 5. They present a methodology for how cycad systematists should critically evaluate proposed new taxa. Cycad experts Piet Vorster, Paul Forster and Loran Whitelock present their individual thoughts on infrageneric classification concepts for African *Encephalartos* taxa, Australian *Macrozamia* taxa and New World *Ceratozamia* taxa in Chapters 6, 7 and 8, respectively. Chapters 9 and 10 were submitted by the participants from Mexico, Andrew Vovides and Miguel A. Pérez-Farrera. Unfortunately, Miguel was not able to attend the Workshop. These two researchers evaluate the usefulness of characters for defining species and species complexes within *Ceratozamia*. Tim Gregory and Jeff Chemnick develop in Chapter 11 an exciting hypothesis that extant species of *Dioon* are the result of rapid evolution in a dynamic group of plants. Two of the participants, Paolo Caputo and Dennis Stevenson, along with their colleagues, report on a molecular study in Chapter 12 that examines the usefulness of molecular and morphological data sets when trying to develop a phylogenetic tree for species of *Zamia*. Results from Bart Schutzman's extensive and detailed morphological studies on Meso-American species of *Zamia* are given in Chapter 13. Dennis Stevenson, in Chapter 14, presents a monograph on the Zamiaceae from Bolivia, Ecuador and Peru. His chapter illustrates many of the guidelines the participants discussed during the last day of the workshop concerning content, style and format for the type of publication resulting from floristic cycad research.

Two appendices are included in this volume. Firstly, the ongoing discovery of new species and the continuous refinements to the taxonomy of the already-known taxa mean that the list of 'officially recognized' taxa needs to be timeously revised. Appendix 1 gives details of the 'World List of Cycads' at the time the manuscript for this volume was submitted to the publisher and is based on 'The Cycad Pages' website (http://plantnet.rbgsyd.nsw.gov.au/PlantNet/cycad). Secondly, the interdisciplinary nature of work on cycad systematics has led to a large and complex vocabulary of terms, the precise meanings of which are sometimes obscure and occasionally misused. Appendix 2 provides a glossary of these terms, drawn up after extensive consultations with specialists, and amplified where possible with cycad-specific examples.

For consistency with author citations for taxa, we have followed the International Plant Names Index (IPNI Website: http://www.ipni.org/index.html) for the chapters and appendices. In Chapters 1–15, authors' names are unabbreviated. They are cited when the taxon first appears within a chapter and are also cited when appropriate in figure captions and tables. For Appendix 1, authors' names are abbreviated.

Taxa known to be distinct by the authors of each chapter, but as yet not 'officially' published, are indicated by double quotes in Chapters 1–15.

The work presented in this volume is not only a report on the current state of affairs in cycad classification, but also highlights areas of difficulty and leads to guidelines for meaningful future advances. We hope it will become a widely used reference for the benefit of all cycad researchers, enthusiasts, conservation-related public and private agencies and students of plant systematics.

Terrence Walters and Roy Osborne

Acknowledgements

The directors, members, staff and volunteers of Montgomery Botanical Center (MBC) deserve thanks and gratitude for their commitment to planning, hosting and sponsoring the Cycad Classification Concepts (CCC) Workshop. The Workshop was the first of its kind held at MBC, and therefore demanded an extremely fast learning curve by the MBC Team. We hope they will consider organizing and hosting CCC Workshop II in the future.

The Workshop was 11 months in the planning stage. Numerous meetings were held during this period to define clearly the purpose, expected products and agenda for the Workshop. Tim Gregory and William Tang provided much needed guidance during the early planning stages. Don and Sonja Decker are thanked for hosting a pre-Workshop planning session at their home in December 2001. At this 1-day session, Don Decker, Tim Gregory, Deena Walters and Terrence Walters clearly identified the purpose and the products expected from the Workshop, as well as plotting the 3-day agenda. Jeff Chemnick, Tim Gregory and Loran Whitelock provided encouragement and support throughout the entire planning period for the Workshop. Their input was much appreciated.

The CCC Participants' commitment to the success of the Workshop was greatly valued, given their own responsibilities and time constraints. They were truly an amazing group of individuals with whom to collaborate.

The CCC Support Team oversaw the planning and logistics of the Workshop beginning in April, 2001. Jean Stark of Stark Connections took care of all the details associated with the participants' travel and housing needs before, during and after the Workshop. Don Decker of Decker & Associates was the management consultant and leader for the Workshop. Katherine Kron of Wake Forest University was kind enough to lecture and field numerous questions on 'phylocode' during one of the work sessions. Evelyn Young planned and coordinated all of the on-site meals and events at MBC during the 3 days. Larry Noblick coordinated the audio-visual equipment and supplies required for the Workshop. Lee Anderson oversaw facility preparations for all of the events each day during the Workshop. Deena Walters and Mary Andrews documented the Workshop photographically. Mayna Hutchinson created magnificent cycad arrangements for all of the facilities used at MBC during the Workshop. Barbara Judd, Sue Katz and Eric Shroyer were scribes for the break-out groups. All of the above individuals, as well as their own support teams, ensured that every aspect of the Workshop ran smoothly and according to the agenda.

The CCC Workshop was supported through grants from the Bressler Foundation, Ajax Foundation and General Mills Foundation. Libby and By Besse, Judith and Richard Bressler, Tim Gregory, Eileen and Loyd Kelly and Linda and Mark Smith were significant contributors to the Workshop. The commitment of these foundations and individuals to the Workshop was very much appreciated. The officers, directors and members of the Central Florida Palm & Cycad Society are acknowledged for providing support towards the publication of this volume.

A number of individuals were involved in the preparation and publication of this volume. The Montgomery Botanical Center directors, members and staff gave the editors the time and resources to prepare the manuscript. The first editor gratefully acknowledges Deena Walters for graphic design and illustration production assistance and, most of all, for her support during the preparation of the manuscript. The second editor similarly acknowledges the support of the Osborne family and friends.

Finally, we wish to express our thanks to Tim Hardwick and the many individuals at CAB International who have so professionally managed the publication aspects of this volume.

Cycad Classification Concepts Workshop support team seated from left to right: Terrence Walters; Jean Stark; Don Decker and Katherine Kron. (Reprinted by permission of Montgomery Botanical Center, Miami, Florida, USA.)

Cycad Classification Concepts Workshop participants seated from left to right: Andrew P. Vovides; Ken D. Hill; Chia-Jui Chen; Roy Osborne; Paolo Caputo; John Donaldson; Loran Whitelock; Paul I. Forster; Dennis Wm. Stevenson; Jeffrey Chemnick and Piet Vorster. On the floor in front: Anders Lindström; Bart Schutzman and Timothy J. Gregory. (Reprinted by permission of Montgomery Botanical Center, Miami, Florida, USA.)

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'We Hold these Truths …'

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Abstract

In order to develop classification guidelines for the Cycadales, a workshop was held in April 2002, at Montgomery Botanical Center in Miami, Florida, USA. Fourteen internationally-renowned cycad systematists spent 3 days identifying and developing guidelines that would provide a stable, practical and informative classification scheme for cycads. The participants agreed that convening such a workshop was vital, timely and necessary to produce a universally accepted evolutionary classification for the Cycadales in the near future. Before developing the guidelines, the participants first needed to identify the assumptions, or beliefs, that they hold to be true about cycad classification. These beliefs are presented under three categories: (i) beliefs about biological relationships; (ii) beliefs about what systematists can and should do in order to understand biological relationships; and (iii) beliefs about what cycad systematists can and should do in order to understand relationships in the Cycadales.

Cycad Classification Concepts Workshop

The field of cycad systematics, which focuses on all members of the plant order Cycadales, has seen a flurry of activity during the past 20 years. New species are being discovered and described on an annual basis. Existing species circumscriptions are being critically tested for their scientific soundness. Familial and generic circumscriptions and relationships are being re-evaluated by a number of laboratories worldwide. Certain key developments in recent years (e.g. advances in systematic technologies and tools; ease of international travel, including access to countries previously unavailable to systematists; horticultural demand for rare

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cycads; recognition of the rare and endangered status of cycads; and an urgency for cycad conservation in many countries) have collectively stimulated cycad systematists to try to better understand and manage the taxonomy of the world's cycad flora.

Today, field and laboratory equipment can quickly generate massive amounts of systematic data, which often far surpass the immediate needs of systematists. This is particularly true for molecular data, which are being analysed in a multitude of ways with a plethora of user-friendly software programs. Consequently, systematists sometimes find it difficult to decide which analyses are appropriate for their work and how to interpret the hundreds of statistical summaries produced from these computer programs. Also, with these wonderful new opportunities and ever-increasing knowledge of cycads, it is easy to lose sight of the ultimate mission, which is to provide a universally accepted, consistent and informative evolutionary classification scheme.

Although scientists do not believe that any truth can be exactly known, it is the purpose of science to approach truths as closely as possible. Scientists are forced to perform this work in an unsteady grounding of assumptions. These assumptions are not self-evident, but arise from the observations and experimentations of previous researchers. So, for any particular scientific field, there is a collection of assumptions, or beliefs, based on previous work that forms the framework for further discovery. As the scientific method proceeds, these assumptions are subject to change, usually in the form of minor modifications but sometimes in the form of radical reassessment. But, whatever insights future inquiry may bring, current hypotheses and guidelines for future research must be rooted in presently held assumptions.

The major objectives of this volume are to enumerate the currently held assumptions, or beliefs, in the field of cycad systematics, and to present guidelines for future systematic work within the Cycadales. These concepts were fleshed out during a Cycad Classification Concepts (CCC) Workshop held in April 2002, at Montgomery Botanical Center in Miami, Florida. The CCC Workshop provided a forum for cycad systematists to 'regroup' and clarify as a team what they believe to be true (the best working assumptions) and important in the realm of cycad systematics. The participants then went a step further, agreeing on a suite of guidelines that they would follow in support of actualizing the team's beliefs when engaging in future research (see Osborne and Walters, Chapter 15 this volume). The participants agreed not only to follow these guidelines in their own systematic studies, but also to encourage the global use of these guidelines by all cycad systematists and students.

This chapter attempts to record the beliefs raised by the participants during the CCC Workshop, whereas the final chapter enumerates the proposed guidelines for developing a useful, evolutionary-based classification system for cycads. Before presenting the beliefs, it is necessary to provide some background on cycads and systematics and to explain some terms that the reader will encounter either in the list of beliefs or in other chapters of this volume.

What is a Cycad?

Cycads are an ancient group of seed plants that evolved in the Carboniferous or early Permian, some 280 million years ago (Norstog and Nicholls, 1997). They reached their zenith of abundance and diversity in the Mesozoic era. Cycads are one of four groups (cycads, ginkgos, conifers and gnetophytes) that are collectively and commonly referred to as gymnosperms.

The Cycadales (the order containing all cycad families) is considered to be monophyletic. A monophyletic group is composed of an ancestor and all of its descendants based on a suite of shared derived characters, called synapomorphies. Some synapomorphies within the Cycadales include girdling leaf traces, a specialized pattern of vascular bundles in the petiole, distinctive meristems, buffer cells surrounding the archegonium, and the presence of mucilage canals, methylazoxymethanol glycosides and the non-protein amino acid BMAA (β-n-methylamino-L-alanine). Coralloid roots (specialized roots that host cyanobacteria) are found in all cycad taxa. Cycads also bear cataphylls, which are scale-like leaves that serve to protect the apical meristem.

Cycad reproductive structures typically occur in cones, with each strobilus consisting of an axis and a series of spirally arranged megasporophylls ('leaves' bearing ovules) or microsporophylls ('leaves' bearing pollen sacs). All cycads are dioecious, with male and female reproductive structures on separate plants. Insects appear to be the primary vectors for pollination, although wind may be a factor for some genera (see discussion by Grobbelaar, 2002). Although not fully substantiated yet, evidence is accumulating to suggest coevolutionary processes between cycads and their pollinators. Once these processes are uncovered, resulting data will probably have a significant impact on how cycad taxa are classified.

All genera except *Cycas* Linnaeus form a determinate female cone. In *Cycas*, the female 'cones' are indeterminate. Ovules are borne on loosely arranged whorls of megasporophylls (for an interpretive discussion on female 'cones' in *Cycas*, see Norstog and Nicholls, 1997). Cycad seeds usually have a brightly coloured, fleshy outer layer called the sarcotesta that encourages dispersal by animals. Birds, rodents and probably many other animals disperse cycad seeds by digesting the sarcotesta and dropping the stony layer and its contents away from the mother plant (Hill and Osborne, 2001). Seeds of some species of *Cycas* have a thick layer of spongy tissue, instead of the usual fleshy layer. This spongy layer allows these seeds to remain buoyant and viable for long periods of time in salt water. This may explain the wide distribution of this genus compared with the narrower ranges of other cycad genera.

With the exception of *Cycas*, all cycad genera are restricted to single landmasses (Jones, 2002). *Encephalartos* Lehmann and *Stangeria* T. Moore occur only on the continent of Africa. *Bowenia* Hooker ex Hooker *filius*, *Lepidozamia* Regel and *Macrozamia* Miquel are endemic to Australia. *Microcycas* (Miquel) A. de Candolle is restricted to the island of Cuba. *Ceratozamia* Brongniart, *Chigua* D.W. Stevenson, *Dioon* Lindley and *Zamia* Linnaeus are endemic New World genera. *Cycas* is found in subtropical and tropical countries of the Old World that have Pacific or Indian Ocean coastlines and in neighbouring countries.

Although cycad taxa are widely distributed in subtropical and tropical regions worldwide, extant populations are often widely disjunct. A cycad population is frequently found as an isolated pocket of individuals quite far removed from other such pockets. A major dilemma that faces today's cycad systematists is understanding the evolutionary histories and futures of these populations. Part of the problem is determining whether these populations have been artificially separated because of human fracturing of the habitat, or are naturally occurring entities that are either gradually going extinct, are restricted to a very specialized niche, or are continuing to evolve as separate entities.

Cycad Taxonomy and Systematics

Taxonomy is the process of circumscribing and assigning scientific names to the diversity of taxa, and then ordering this diversity into an appropriate classification system. In the realm of biology, a 'taxon' (plural 'taxa') is a group of individuals given a proper name or a group that could be given a proper name. For example, the taxon *Dioon* includes all named and as yet unnamed groups of individuals within this genus. An important aim of the cycad systematist is to describe and name only 'natural taxa' and to place these in a classification system that represents the order of nature. A natural taxon is a taxon that exists in nature independent of human ability to perceive it. It can be discovered, but not invented (Wiley, 1981). The same assumption can be applied to the order of nature, i.e. that it can be discovered for what and how it is. The basic assumption for biological order is that it is based on reproductive ties (genealogy) as they are affected by the process(es) of evolution.

Classification is the process of organizing knowledge so that it facilitates communication and comprehension. The objectives of classification are: (i) to define and distinguish among 'kinds'; and (ii) to position these kinds in a system that reflects their natural relationships and imparts information about these kinds. A classification system is a human construct that attempts to make natural order comprehensible to the human mind.

The classification of biological organisms has its own language and rules of language use. For assigning a taxonomic name and having the name recognized by the botanical community, cycad systematists must follow recommendations outlined in the most recent edition of the International Code of Botanical Nomenclature (ICBN; Greuter *et al.*, 2000). These recommendations are built on a hierarchical system of classification wherein each level of the hierarchy is referred to as a distinct rank. Typical ranks of use in the field of cycad systematics start with the all-inclusive 'order' (Cycadales) and move down to increasingly less inclusive ranks such as family (e.g. Zamiaceae), genus (e.g. *Macrozamia*), section (e.g. *Parazamia*) and species (e.g. *Macrozamia lucida*). The basic rank of species holds a special place in terms of the usefulness and importance of biological entities to humanity; therefore, most cycad systematists undertake studies at the species level.

Cycad systematics is the study of the cycad diversity that exists on earth today and the evolutionary history of this diversity. One of the main objectives is to convey knowledge about the genealogical relationships among cycad taxa in a hierarchical system of classification. The field of cycad systematics often requires that systematists have knowledge from many other scientific disciplines, such as taxonomy, morphology, ecology, molecular biology, pollination biology, anatomy, embryology, genetics, physiology, phytochemistry and palaeontology, so we are better able to uncover the true genealogical relationships among taxa.

The number of described cycad species has almost doubled since 1985. Today, over 300 species are known (see Hill *et al.*, Appendix 1 this volume) and many researchers believe the number may reach as many as 400 species when all potential cycad habitats have been investigated and taxonomic studies have been completed. Exactly what constitutes a cycad species remains unclear. Defining what makes a species is not a problem limited to cycad taxonomists, but is a basic source of consternation throughout the biological world. Generally, delimitation of a population or suite of populations as a new species is based on the training, background, knowledge and the basic scientific philosophy of the describer. No unified concept is in place to guide cycad systematists in defining and circumscribing new species.

A variety of species concepts are used throughout the biological world. One of these, the biological species concept, does not work particularly well with cycads. The major premise of the biological species concept is that individuals within a species, when tested, are interfertile, while interspecific individuals are not. However, clearly defined and widely accepted species within a number of cycad genera can produce viable offspring with one or more other species in the same genus (Norstog and Nicholls, 1997). Consequently, cycad systematists generally agree that interspecific fertility, when tested, is just another character for systematic studies, and that the character of interspecific sterility should not be unduly weighted in the determination of cycad species. Moreover, the determination of the production of fertile offspring from putative hybrids is not practical for those species, like cycads, with long life cycles.

Another out-of-favour species concept for cycad taxonomists is the phenetic species concept. This concept defines a species based on the overall similarity of its individuals combined with a significant gap in variation when these individuals are compared with individuals of another species. In practice, this qualitative approach does not always define natural taxa (Judd *et al.*, 1999).

The CCC Workshop participants agreed that the most common (unstated, but *de facto*) species concept in use by cycad systematists is what they termed a 'morphogeographic' species concept. This concept recognizes the importance of both morphological characters and geographical isolation in circumscribing a species. The large geographical disjunctions among cycad populations have greatly influenced the cycad systematist's species concept. These disjunct populations are viewed as maintaining separate identities and having their own evolutionary tendencies and fates. In this respect, the cycad systematist's view is a form of the evolutionary species concept.

By the end of the CCC Workshop, participants were still not able to agree on exactly what constitutes a cycad species. This was not surprising, since cycad lineages have a variety of unique and long histories. Species differ to varying degrees and, therefore, a single species concept does not work for all cycads. Today, data from a wide variety of sources, including molecular analyses, ecology, geography, pollination biology and life history strategies, are providing independent measures of the evolutionary reality of existing and proposed species in the Cycadales.

In contrast with species, circumscriptions of cycad genera are clearly defined and stable, with the possible exception of *Chigua*, which may be congeneric within *Zamia* (Whitelock, 2002; and see Caputo *et al.*, Chapter 12 this volume). Cycad genera can usually be identified using gross vegetative features and can always be identified with gross features of the female reproductive structures.

Family circumscriptions within the Cycadales are still somewhat unclear, being confounded by the age of the group and the inability of cycad systematists to decide on the amount of character differentiation required for family recognition within the order. Three to four families are typically recognized, with the only uncertainties revolving around the placement of two genera, *Stangeria* and *Bowenia*. Given recent advances in molecular systematics and the number of laboratories actively studying generic and familial relationships, it is predicted that a stable familial classification will be available in the very near future.

Historically, the characters chosen, the importance of specific characters for differentiating genera and species, and the analyses used for describing new cycad species have been left to the discretion of each investigator. Vegetative characters, especially those associated with the leaf, along with characters related to various aspects of the female reproductive structure, are commonly used for distinguishing taxa. Male cone characters are usually not used for differentiating taxa. Cycad systematists are well aware of the plasticity of various morphological features among plants within a taxon, especially when plants are brought under cultivation. However, the degree of plasticity and the taxonomic importance of this plasticity continue to remain unclear.

Another ongoing problem for cycad systematists is the lack of a consistent terminology for describing morphological features that are unique within the Cycadales. This lack of standardized morphological terminology creates problems when trying to compare characters in one taxonomic description with those in another description, or when trying to identify an individual plant based on specific characters. For this reason, a glossary of terms commonly encountered in cycad systematics is included in this volume (see Osborne and Walters, Appendix 2 this volume).

Cycad Phylogenetics – Uncovering Genealogical Relationships

Although never really attainable, systematists work toward producing a natural classification system that arranges taxa in a way that reflects the natural evolutionary order of the taxa. Since the first basic assumption is that the natural order is created by the process(es) of evolution, systematists typically strive to produce an evolutionary classification scheme. More specifically, phylogeneticists aim to recover the broad genealogical lineages within a group of taxa and to produce a classification system that reflects these genealogical or phylogenetic relationships.

The starting point in phylogenetic analysis is usually the divergence of a previously occurring lineage into two or more progeny lineages. The next step is to reconstruct the separation of these lineages by identifying changes, or modifications, in characters. A character is a feature having one or more states that can be described, figured, measured, weighed, counted, scored or otherwise communicated from one systematist to another. Certain characters are biologically connected to the concept of genealogy and these characters can provide cycad systematists with justification for group membership in a phylogenetic tree. These types of characters are called apomorphies. An apomorphic character (sometimes referred to as a specialized character or a derived character) has evolved directly from its pre-existing homologue (Wiley, 1981).

The task of phylogeneticists is to attempt to discover those characters that reflect the phylogeny of natural taxa. Because species are considered to be naturally occurring entities, by inference, phylogenetic characters are inherent to species. A phylogenetic character is one in which its occurrence in two or more taxa is believed to be the product of descent from a shared ancestor. A phylogenetic character shared by two organisms implies a phylogenetic relationship. Of particular importance is the synapomorphy, which is a genealogically shared, derived character state that arose in an ancestor of a lineage and is present in all of that lineage's descendants (Hennig, 1966). Synapomorphies are the strongest evidence for shared ancestry. They are distinguished from symplesiomorphies, which are earlier character states that are shared by members of a lineage and by a more ancient ancestor to the lineage. In practice, symplesiomorphic *versus* synapomorphic character states for a lineage are determined by comparison with an outgroup (i.e. a related taxon that is not part of the monophyletic lineage being examined). The outgroup of choice is the 'sister group' to the lineage, which is genealogically the closest non-ancestral relative of the lineage. In other words, two or more taxa are sister groups if they share an ancestor not shared by any other taxon.

Phylogenetic studies depict results by a graphical representation of the genealogy of one or more descendants from a common ancestor. Phylogenetic trees are branching diagrams that portray the hypothesized genealogical relationships and sequence of historical events linking taxa. A clade within a phylogenetic tree incorporates the common ancestor of a group and all of its descendants.

Cycad systematists use phylogenetic trees to try to produce a phylogenetic classification that reflects the best estimate of the evolutionary history of cycads. Construction of a classification based on a phylogenetic tree essentially involves two steps: (i) the delimitation and naming of groups that are monophyletic in the tree; and (ii) the ranking of these monophyletic groups and placement of them into a hierarchical classification system (Wiley, 1981). Phylogenetic studies do not always lead to a new classification. These studies can provide support to an existing classification. Also, naming every monophyletic group would become cumbersome and in some cases not provide any additional information to the end-user.

Cycad systematists continue to put forth hypotheses about the genealogical relationships among taxa in the Cycadales. These hypotheses are tested with evidence derived from a wide variety of sources. Hypotheses and test results are published, usually peer-reviewed, and evaluated, and some phylogenetic trees are provisionally chosen over others. In other words, the evolutionary tree for the Cycadales continues to be tested as additional and new types of data become available.

An important conclusion made by the CCC Workshop participants was that the knowledge of genealogical relationships among taxa should be placed in an unambiguous and stable natural classification system that is useful for a multitude of end-users and purposes. It is believed that such a system can orient human understanding of life and the world around us.

CCC Workshop Beliefs

The CCC Workshop participants enumerated their beliefs concerning cycad classification during the second day of the Workshop. Clarity and consensus with regard to these beliefs were needed so that the participants could go on to produce a final set of guidelines for future research aimed at establishing a suitable classification scheme for cycads (see Osborne and Walters, Chapter 15 this volume).

For purposes associated with the production of this chapter, the suite of beliefs generated during the work sessions at the CCC Workshop has been reworded and organized to provide consistency in wording, style and format. The authors have organized the beliefs under the following three categories: (i) beliefs about biological relationships; (ii) beliefs about what systematists can and should do in order to understand biological relationships; and (iii) beliefs about what cycad systematists can and should do in order to understand relationships in the Cycadales.

Beliefs about biological relationships

- We believe there is value in the biological world.
- We believe there is a natural order to the biological world.

- We believe that the natural order is based on genealogical relationships.
- We believe that the pattern of genealogical relationships naturally produces a hierarchical structure of lineages.
- We believe that each species (as a natural group) is a monophyletic lineage that evolves independently of other such lineages.

Beliefs about what plant systematists can and should do in order to understand biological relationships

- We believe we can construct hypotheses that are testable, and that the process of testing and refining hypotheses leads to a better understanding of the natural world.
- We believe that genealogical relationships can be recovered through hypothesis testing.
- We believe that as technology, resources and data increase and change, we will be better able to construct a classification scheme that approximates true genealogical relationships.
- We believe that we should construct hierarchical classification schemes that best reflect actual genealogical relationships. Such schemes have greater predictive power, have greater heuristic value, and improve our ability to understand and communicate about the biological world as it existed, as it exists, and as it may exist in the future.
- We believe that the process of refining classification schemes brings us closer to approximating true genealogical relationships and therefore converges towards stability of the classification.
- We believe that the most important evolutionary entity to define and circumscribe is the species.
- We believe that species are not evolutionarily static (i.e. they change through time).
- We believe that species can be difficult to recognize, and, therefore, the definitions and circumscriptions that we apply to particular species are hypotheses to be tested.
- We believe that the exploration of species and species concepts will provide the common language for understanding speciation, species interactions and plant systematics.
- We recognize the existence of the International Code of Botanical Nomenclature (ICBN) and support the beliefs, philosophies, and principles of the Code to provide one correct name for each taxonomic group within a stable classification system.
- We believe that systematists should share information through the publication of data and analyses.

Beliefs about what cycad systematists can and should do in order to understand relationships in the Cycadales

- We believe that the Cycadales forms a distinct monophyletic lineage, and genealogical relationships within this lineage can be inferred through the collection and analysis of data.
- We believe that higher ranks in the Cycadales (e.g. genera and above) are easily recognizable and definable.
- We believe that the greatest challenge in cycad systematics is recognizing appropriate units to call species.
- We believe that there are differing opinions concerning cycad species definitions and circumscriptions.
- Given the uncertainty of species definitions and the lack of infraspecific data on cycads, we believe that it is not yet appropriate to try to define and identify relationships of taxa below the species level.
- We believe that to better understand cycad species, we must concentrate our resources on variation and relationships at the population level.
- We believe that there is a wealth of available data on cycads that still must be captured and analysed.
- We believe that a classification system should be valuable for a variety of known and unknown end-users and purposes.
- We believe that the extinction of cycad species is accelerating and that access to native populations is decreasing rapidly. Actions must be undertaken immediately to describe, classify, conserve and preserve species for continuing scientific studies.
- We believe that the process of understanding cycad systematics should be a collaborative endeavour.

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