

PROCEEDINGS OF CYCAD 2015

The 10th International Conference on Cycad Biology



Edited by

Cristina López-Gallego

Michael Calonje

M. Patrick Griffith

J. S. Khuraijam

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The Cycad Specialist Group (CSG) is a component of the IUCN Species Survival Commission (IUCN/SSC). It consists of a group of volunteer experts addressing conservation issues related to cycads, a highly threatened group of land plants. The CSG exists to bring together the world's cycad conservation expertise, and to disseminate this expertise to organizations and agencies which can use this guidance to advance cycad conservation.

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Front: *Zamia amplifolia*

Back: *Zamia roezlii*

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Website: <http://www.cycadgroup.org>

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Participants of Cycad 2015



IUCN/SSC Cycad Specialist Group Meeting

Photographs by James Clugston

Cycad 2015 - The 10th International Conference on Cycad Biology

The first International Conference on Cycad Biology was held in France in the year 1987. Twenty-eight years later, we had the 10th Cycad conference in Colombia. This is a testimony of the continuing work of the IUCN Cycad Specialist Group and the immense interest that these amazing plants generate among horticulturist, academics, conservationists, plant lovers in general and many other audiences. Recent cycad conferences are characterized by a strong academic component and an interesting combination with participants from many other areas. Cycad 2015 was no exception. The conference had 101 participants from 24 countries (ranging four continents), with institutional affiliations from universities, governmental and NGOs, herbaria, botanical gardens, plant collections, horticultural companies and others.

The 10th Cycad conference was held in the city of Medellin, from the 16th of the 21st of August of 2015. We started with an inaugural banquet in the Medellin Botanical Garden, including a brief visit to their cycad collection (the largest in the country). We had four days of academic activities, with 8 plenary talks, 55 talks and 10 posters. In between the academic activities, we had a couple of evening mixers and a nice field trip to the "Arvi" ecological park, where participants saw a little of the amazing biodiversity of the Andean cloud forest. We concluded the conference with another banquet at Medellin Botanical Garden, where we enjoyed to more Colombian music and dancing.

In addition to the impacts that Cycad 2015 could have had on the participants, this conference helped a great deal in rising visibility for cycad research and conservation in Colombia. We were proud to introduce the newly born at that time "Colombian Cycad Society" with a clear mandate to implement the "National Conservation Action Plan for Colombian Zamias". We produced a "Declaration" conveying the urgency for cycad conservation in the country that was highly publicized in local and national media. We should not underestimate the positive impacts that a group of cycad lovers from all over the world can have to promote awareness about the importance of plant conservation and biodiversity in general. By getting together to share our mutual interests for cycads we can do a lot. I hope we can have many more cycad conferences in the future, for our own sake and the sake of one of the most wonderful group of plants in the world.

Cristina López-Gallego

Universidad de Antioquia, Colombia & Colombian Cycad Society
Deputy-Chair, IUCN/SSC Cycad Specialist Group
Chair, CYCAD 2015

Preface

The 10th International Conference on Cycad Biology (Cycad 2015), taking place between August 16th and August 21st, 2020, was very well-attended and truly international in scope, with over 150 attendees hailing from 17 different countries. During this six-day meeting, four days were devoted to its academic schedule of presentations which included seven plenary talks, fifty-five oral presentations and a poster session with nine poster presentations. The subjects of the talks, separated into ten different sessions, spanned a range of varied topics including conservation, ethnobotany, ecology, genetics, systematics, and horticulture. The academic schedule was varied, informative, and well-received by the attendees, and it was an honor for me to participate in this endeavor as part of the Cycad 2015 Organizing committee. We are glad to present the proceedings of this remarkable conference in this special issue of CYCADS, the official newsletter of IUCN/SSC Cycad Specialist Group. We herewith present the proceedings of this remarkable conference in this special issue of CYCADS, the official newsletter of IUCN/SSC Cycad Specialist Group. We would like to thank J.S. Khuraijam for his efforts at putting this special issue of CYCADS together.

Michael Calonje
Academic Chair, Cycad 2015

Foreword

Making CYCAD 2015 Possible

The overwhelming success of CYCAD 2015 was the result of detailed planning, diligent organizing, boundless energy, and hard work from a huge number of people. Foremost among them is **Dr. Cristina López-Gallego** - as our hostess and Conference Chair, she made the entire event possible. Her leadership and vision deserves our praise! **Dr. Michael Calonje** also deserves our high accolades for organizing all academic aspects of the gathering, editing the abstracts, and keeping our conference theme on track. My own role as Treasurer placed me in the unique position to grasp how much support and enthusiasm our community has for excellent cycad research, and especially for developing new talent and broadening the geographic scope of our cycad community. Thus, on behalf of the entire organizing committee, please let me use this page to very gratefully acknowledge all of the funders and supporters that made CYCAD 2015 such a major success.

We are deeply grateful to the **Mohamed bin Zayed Species Conservation Fund**. This Fund provided a major grant to support a Cycad Red Listing Workshop which brought together experts from across the globe. This grant also allowed us to greatly expand and diversify our Cycad Specialist Group (*more on that below*) to include established specialists from Cuba, Kenya, Panama, the Philippines, and Vietnam, all critical range states where these living treasures are imperiled. It is no exaggeration to say that this key funding was responsible for the broad global reach and impact of the work we accomplished in Medellin.

Two major Cycad Societies: **The Cycad Society** and **The Cycad Society of South Africa** provided critical funds to support students and early career scientists to join the meeting and present their findings. The great importance of exactly this kind of support cannot be overstated - our cycad community depends on developing new talent and expertise to carry us forward into the future. Having these young experts join our gathering - to both learn and teach - ensures that our next generation will uphold our commitment to saving cycads from extinction. These funds brought energetic new talent from Australia, India, Mexico, and South Africa into our community, and we very grateful to both Societies for that vital support. If you are not yet a member of both societies, this is a great reason to join!

The **Instituto Humboldt Colombia**, **Parque Explora** and the **Martin-Rami Fund** provided essential funds and in-kind support to secure our meeting and event venues, transportation and logistics, and other incidentals. These funds were essential to host our meetings, opening and closing events, discussions, and meals. We are very thankful!

We remain deeply grateful to the IUCN SSC Cycad Specialist Group, for providing their decades-long leadership in cycad conservation, which provides the central and essential continuity to these worldwide gatherings. We placed conservation at the center of our themes, actions, and outcomes for this conference, and elevated the important scientific work that is central to keeping these cycads extant. The sponsorship and auspices of the CSG guided these efforts.

The unwavering commitment of the Organizing Committee's host institutions was also absolutely critical to this effort: **Universidad de Antioquia, Jardin Botanico Medellín, The New York Botanical Garden, and Montgomery Botanical Center** provided countless hours of staff time over years of planning and preparations, thereby demonstrating the importance of cycad conservation to these great institutions.

Finally, I wish to thank all of the fantastic people who attended! This conference was a resounding success because you contributed your time, your enthusiasm, and your great ideas. I smile every time I think about the great community we gathered together over that week in August 2015.

M. Patrick Griffith

Montgomery Botanical Center

Co-Chair IUCN SSC Cycad Specialist Group

Treasurer, CYCAD 2015



**DECLARACIÓN DE LOS PARTICIPANTES DE
"CYCAD 2015"
X CONFERENCIA INTERNACIONAL DE BIOLOGÍA
DE CYDADAS
16-21 de Agosto, Medellín (COLOMBIA)**

Las Cycadas son un linaje de plantas con semilla que existe en nuestro planeta desde hace más de 250 millones de años, con su esplendor en el Mesozoico al lado de los dinosaurios. En la actualidad tenemos relictos de estas enigmáticas plantas en los trópicos de todo el mundo. Desafortunadamente, la mayoría de estas especies están en riesgo de extinción, sobre todo por la destrucción y degradación de su hábitat, y en algunos casos por la sobre-explotación para su uso como ornamentales. En Colombia tenemos 21 especies de Cycadas, del grupo de las zamias, y somos el país del mundo con la mayor riqueza de zamias. La mayoría de las zamias que tenemos son exclusivas de nuestro país, y todas son vulnerables o están en riesgo de extinción por la deforestación principalmente.

Desde hace años en Colombia se vienen adelantando acciones de conservación para tratar de salvar a las zamias de la extinción. Estas acciones incluyen investigación de sus poblaciones remanentes, esfuerzos para proteger su hábitat natural y programas para rescatar y propagar plantas para ayudar a las poblaciones empobrecidas. Sin embargo, esta gestión por parte de algunos académicos de universidades, jardines botánicos y autoridades ambientales no ha sido suficiente para mejorar su situación. *Es fundamental que más actores de la sociedad se unan y apoyen nuestros esfuerzos de conservación para salvar nuestras zamias de la extinción.* ¡Estas acciones beneficiarían no sólo a nuestras zamias, sino a todos los organismos con quienes comparten nuestros bosques, y nos ayudarían a mejorar la situación de nuestra biodiversidad, de la cual todas las comunidades humanas dependemos!

*Para más información sobre nuestras zamias y cómo contribuir a su conservación,
por favor visita: <https://cycadascolombia.org/>*



**DECLARATION BY THE PARTICIPANTS OF
"CYCAD 2015"
THE 10th INTERNATIONAL CONFERENCE ON
CYCAD BIOLOGY
16th-21st of August, Medellín (COLOMBIA)**

Cycads are a lineage of seed plants that has been in our planet from more than 250 million years, with their splendor in the Mesozoic alongside the dinosaurs. Currently we have relicts of these enigmatic plants in all the tropics of the world. Unfortunately, most of these species are threatened with extinction, mostly because of habitat destruction and degradation, and in some cases by overexploitation for their use as ornamentals. In Colombia we have 21 species of Cycads, from the *Zamia* group, and we are the country with the highest richness of zamias in the world. Most of the *Zamia* species we have are unique to our country, and all of them are vulnerable or in high risk of extinction by deforestation mainly.

Since years ago, conservation actions have been carried out in Colombia to try to save the zamias from extinction. These actions include research in remnant populations, efforts to protect their natural habitat, and programs to rescue and propagate plants to help impoverished populations. Nevertheless, these activities by some academics from universities, botanical gardens and environmental authorities have not been enough to improve their situation. *It is imperative that more people from our society join us and support our conservation efforts to save our zamias from extinction.* These would benefit not only our zamias, but also all the organisms with whom they share our forests, and will help us improve the situation of our biodiversity, from which all human communities depend!

*For more information on our zamias and how to contribute to their conservation,
please visit: <https://cycadascolombia.org/>*

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CHAPTER 1

Cycads, Maize, and Garfish: Ethnoecological Systems in Formative Period Mesoamerican Art

Michael D. Carrasco

ABSTRACT

Interpretations of phytomorphic deities in Olmec iconography have often turned to maize (*Zea mays*), the staple crop of Mesoamerican peoples. Although maize clearly informs Maya art and is personified as in Maya Maize God, Middle Formative (900–300 BCE) Olmec imagery is often less specific and seemingly draws from a variety of sources to construct its deities visually. This fact complicates explanations that posit a direct correspondence between maize and specific Olmec deities. A review of the ethnographic, archaeological, and ethnobotanical sources demonstrate that cycads served as a significant food source, symbolized deities, and shared terminology with maize from the Archaic (3500–2000 BCE) to the present. Based on these data it is argued that maize, cycads, garfish, crocodilians, among other things converged conceptually in mythology and iconography to form composite beings such as the Olmec “Maize” God. By bringing these lines of information together this initial investigation suggests that cycads played a more prominent role in Formative period art and culture than has previously been suspected.

Keywords

Mesoamerica, Archaeology, Cycads, Botanical Iconography, Ethnobotany

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INTRODUCTION

Interpretations of phytomorphic deities in Olmec iconography look to maize (*Zea mays*) as a source for such imagery, particularly in relation to the entity known as God II (Joralemon, 1971) and later identified as the Olmec Maize God (Fig. 1, Taube 1996, 2004:27). While maize specific iconography clearly defines the Maize God in Classic Maya art, Middle Formative period (900-300 BCE) Olmec imagery draws from a diverse range of taxa and phenomena to construct deities visually. Thus, deities are amalgams and hybrids of various elements, a fact which complicates explanations that do not adequately consider the ecological, social, and symbolic processes that deities personify or that posit a simple one-to-one correspondence between maize and specific deities.

Multiple lines of evidence suggest that cycads may have been a source for Middle Formative Olmec imagery related to fertility and agroecosystems. Archaeological, ethnographic, linguistic, and art historical data indicate varying degrees of conceptual convergence between maize and cycads that was perhaps expressed in imagery. A similar process of convergence occurs later when maize and cacao (*Theobroma cacao* and possibly *bicolor*) merge in Classic Maya iconography, as seen in Figure 2 in which cacao pods hang from the body of a youth with features otherwise characteristic of the Maya Maize God (Martin, 2006:155). While hieroglyphs gloss this deity as *iximte'* (lit. maize tree), only the iconography suggests that cacao is involved. In Tzotzil *iximte'*, and its Yucatec cognate *iximche'*, refer to the breadnut tree *Brosimum alicastrum* Sw.; there is no attested use of the term to name *Zea mays* L. In this case terms that seem to have a clear meaning actually function within a more complex system of botanical and ecological reference that remains largely opaque. Drawing from the aforementioned sources, I take a multi-disciplinary approach to the study of cycads in Mesoamerica to propose a significant role for cycads in Formative period Mesoamerican ethnoecological systems.

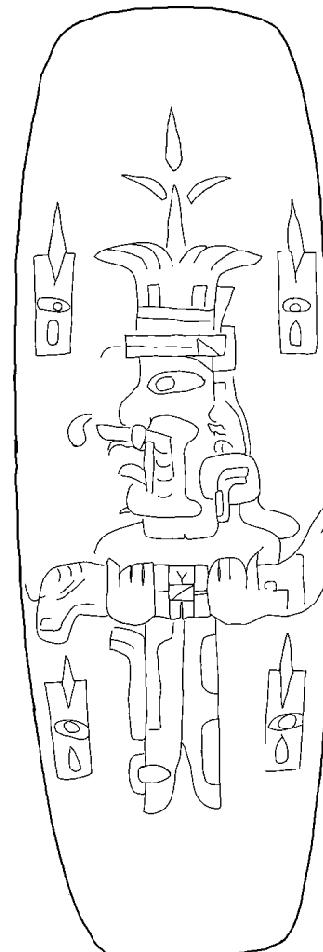


Figure 1. Olmec “Maize” God. Incised Olmec jadeite celt, Arroyo Pesquero, Veracruz. Drawing by author.

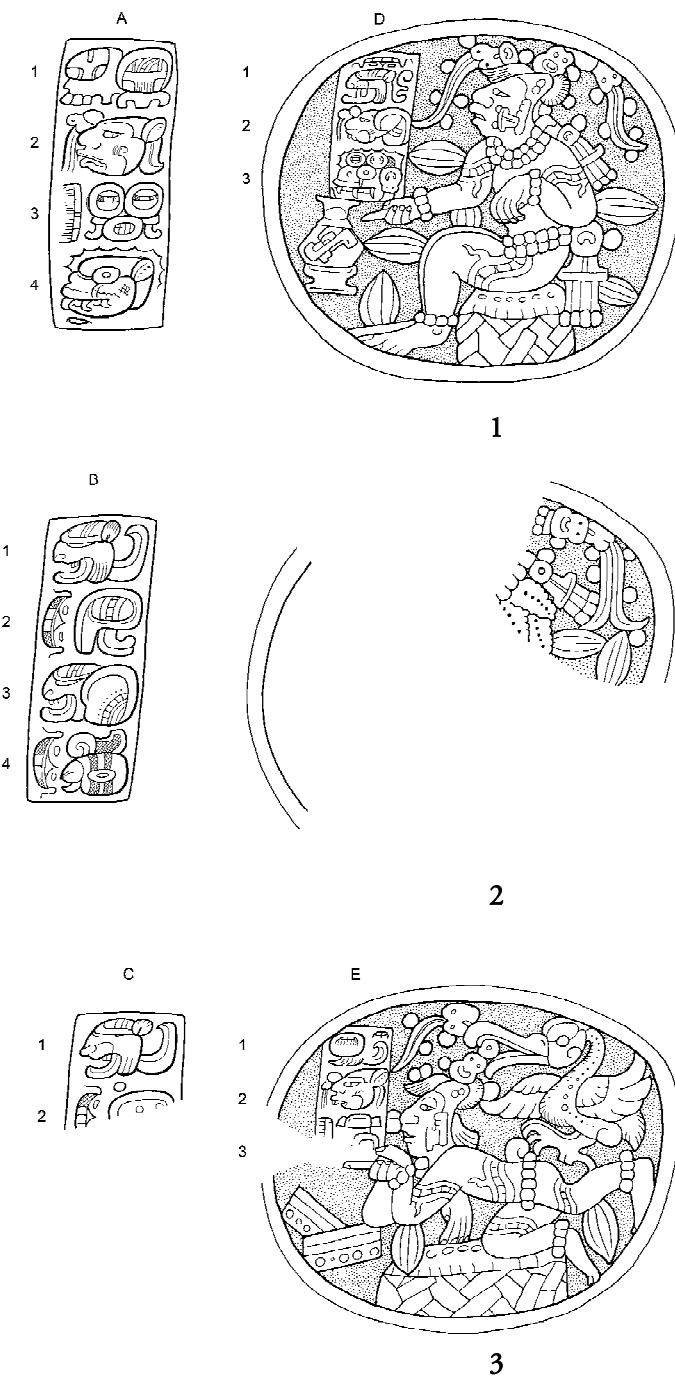


Figure 2. Hybrid maize-cacao deity named Iximte'. Uprovenanced stone bowl(K4331). Dumbarton Oaks collection, Washington DC. Drawing by Simon Martin (2006: fig. 8.1).

Archaeological Evidence

In the 1950s and 60s Richard MacNeish's excavations of dry cave sites in the Tehuacán Valley and Tamaulipas provided a detailed record of the dietary strategies of Archaic (3500–2000 BCE) and Early Formative (1800–600 BCE) period peoples in Mesoamerica. He uncovered a rich inventory of wild, managed, and cultivated foods, which by volume greatly surpassed the domesticated crops, such as corns, beans, and squash central to later Mesoamerican foodways. In particular the data demonstrated the alimentary importance of *Dioon edule* Lindl. and *D. angustifolium* Miq. as early as 6000 BP. For example, at a Tamaulipas cave site beginning as early as 4500 BP *D. angustifolium* seeds played a significant dietary role and were the “dominant plant remains” (Bonta, 2009, 2010; MacNeish, 1958:144). In these cave sites cultivated or wild foods represented 76 percent of the vegetal food by volume while domestic crops comprised only 9 percent in the La Perra horizon (2495 BCE ± 280, Libby, 1952). In terms of volume *D. angustifolium* was followed by *Pithecellobium confine* Standl., maguey (*Agave* sp.), and the palm *Sabal* sp.. Maize was also found, but it appears to have been chewed, popped, or possibly used for the stalk’s sugar content and fermented (Smalley and Blake 2003). At the earlier Tehuacán Valley sites cycad remains were scarcer; however, Smith (1967:235) notes that they were persistently used for thousands of years, but then concluded that cycads could not have played an important role because of their toxicity. He was apparently unaware of their widespread alimentary use. With seed cones on some species weighing over 40 pounds, dioons would have been a tremendous food source that required little to no labor to cultivate. Detoxification processing would be similar in effort to that used on manioc (*Manihot esculenta* Crantz, Pohl, 2001; Pohl et al. 1996), another important and already ancient starch resource (Isendahl, 2011).

The critical point is that by the Archaic Era (5500–4000 BP), at a time before or synchronous with the development of modern maize, cycads composed a major component of the Mesoamerican diet in certain regions and were consumed in quantities surpassing or similar to other plant resources, such as maguey and various palms. Linguistic and ethnohistoric records suggest that, like these other plants, various cycads species played significant symbolic and ritual roles (Pérez-Farrera and Vovides, 2006), were often associated with maize, and continue to be a part of Mesoamerican foodways among various groups including the Teeneek (Alcorn, 1984; Bonta, 2007, 2010), Nahua (Bonta et al. 2006; Vázquez Torres, 1990), and Xi’iuy (Tristán Martínez, 2012).

Ethnohistoric and Linguistic Evidence

Mesoamerican mythologies describe the origin of maize as co-occurring with the creation of the current fifth world age and the formation of people. In indigenous thought, maize becomes human flesh through its consumption, or in myth by a deity modeling it into human form—humans are beings of maize. These mythological and symbolic aspects of maize are well known, but maize and its ancestor, teosinte (*Zea mays* ssp. *parviglumis*

Iltis & Doebley, Classical Nahuatl *teōcentli*), figure in mythology and culture in other ways, especially in classificatory systems through which myth, history, agriculture, and ecology are interwoven. In Mesoamerican thought cosmic history unfolds through a series of cosmic ages each beginning through the destruction of the previous one and possessing its own presiding deity, people, food, etc. Central Mexican sources record the specific foods eaten by people in each of the five world ages (Table 1).

In this scenario wild and managed foods transition to the precursors of domesticates, and finally the sequence ends with maize (Berdan, 2014:223-224; Townsend 1992:120). It has generally been assumed that teosinte unambiguously names *Zea mays* ssp. *parviflora*; however, teosinte and its cognates also frequently refer to various cycad species (Bonta, 2003, 2010). This issue is too complex to explore fully here, but it suggests that the phytonyms in this myth might name regionally specific taxa that serve a similar conceptual and dietary role.

Table 1. Tenochtitlan sequence of the five ages (after Berdan, 2014: Table 7.3)

Name of Sun	Presiding deity	Human / Food	Fate of humanity	Type of destruction
Nauí Ocelotl (Four Jaguar)	Tezcatlipoca	Giants roots/wild foods	Eaten by jaguars	Jaguars
Hauí Ehecatl (Four Wind)	Quetzalcoatl	Humans pine nuts/acorns (<i>acocentli</i>)	Transformed into monkeys	Hurricanes
Nauí Quizhuitl (Four Rain)	Tláloc	Humans aquatic seed (<i>acecentli</i>)	Transformed into dogs, turkeys, butterflies	Fiery rain
Nauí Atl (Four Water)	Chalchiuhltlicue	Humans wild seeds (<i>teocentli</i>)	Transformed into fish	Great flood
Nauí Ollin (Four Movement)	Tonatiuh	Humans maize	To be devoured by tzitzimeme (celestial monsters)	Earthquakes

In any case, it is significant that the linguistic root *centli/cintli*, ‘dried ear of maize’ figures in all but one of the foods listed and shows that these past foods were likely retrospectively named after the more culturally salient maize or all tie into a classificatory scheme that eludes our current understanding. In addition to the examples of *B. alicastrum* and the maize-cycad relationship explored in this paper, maize terms also label the *pacaya* palm (Fig. 3) (*Chamaedorea tepejilote* Liebm.).

In some Mayan languages its immature male inflorescence is known as *ajan*, ‘young ear of maize.’ The pacaya’s inflorescence resembles the *jilote*, a word that forms part of the scientific name of the palm (*tepe* mountain *jilote* ‘maize en tierno’). In Spanish the pacaya is also called the Mother of Maize suggesting both an ancestral relationship with maize and the conception of this relationship in terms of kinship.

Nahuatl speakers in Veracruz apply the term ‘mountain maize’ (*tepētmaizte*, *tepēmaizte*) to *Ceratozamia morettii* (Vázquez Torres and Vovides, 1998).

Along similar lines Stross (2006:596) notes that maize terms were used as labels for other edible plants, such as *ixim ha'* (*Nelumbo lutea*), or trees of



Figure 3. Pacaya Palm (*Chamaedorea tepejilote*) immature male inflorescence. Photograph by author.

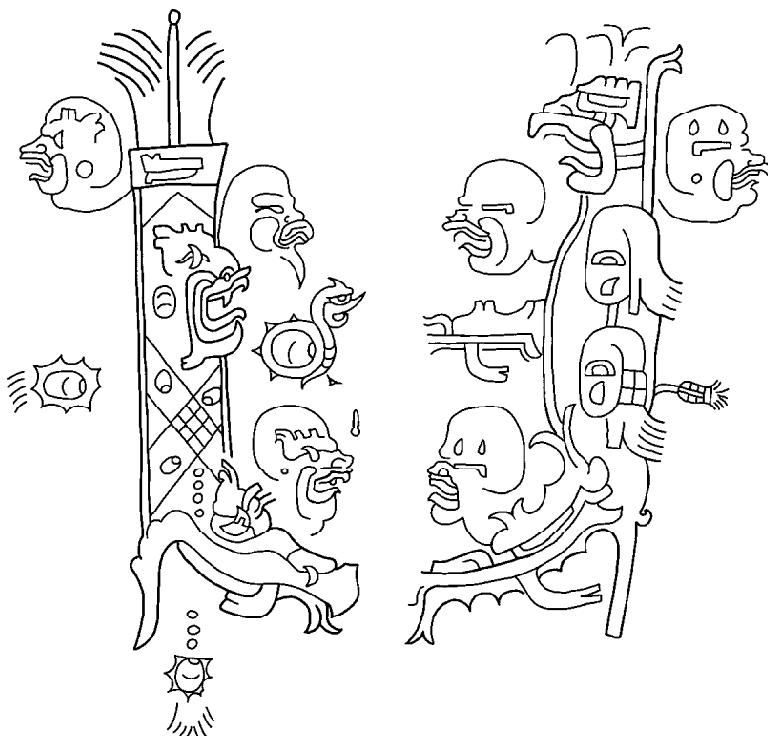


Figure 4. Figure 4. Detail of incised design of a garfish and crocodilian on “The Young Lord” sculpture. Unprovenanced Olmec jadeite sculpture. Drawing by author after Gillet Griffen in *The Olmec World: Ritual and Kingship* 1996:240.



Figure 5. Details of Izapa Stelas 25 (left) and 5 (right) showing crocodilian world tree. Drawing by author.



Figure. 6a-b. The cone-like element above the face on the sculpture resembles the strobili of a *Dioon* spp. a. Olmec “Maize” God. Stone monument. Harvard Peabody museum. Drawing by author after Taube 2004:fig. 13. b. *D. edule*. Botanical Garden, Palermo, 2006. Photograph by Tato Grasso.

cultural importance including particular names for the *Ceiba pentandra* (L.) Gaertn.. A similar mythological sequence is found among the Teeneek, a group of Mayan language speaking peoples who left the Mayan linguistic homeland in the highlands of Guatemala some four thousand years ago to settle in San Luis Potosí and northern Veracruz. The Teeneek's major cultural hero is the child deity Thipaak who brings maize to people and can induce plants to grow and transform into tobacco in some stories (Alcorn et al. 2006:603).

As the story of maize's introduction unfolds he defeats his raptorial, cannibalistic grandmother who is associated with the breadnut or *ojox* tree (*B. alicastrum*) (Alcorn, 2006). They believe that before Thipaak introduced maize, *ojox* was eaten. He is said to be the *ehatal*, 'soul', the *tz'itzin*, 'spirit', and *ichiich*, 'heart of maize' or 'embryo inside the seed' (Ochoa, 2010:542). He is not only the personification of the maize grain or plant, but also embodies fertility in his ability to control the growth of other plants, as well as having a close relationship to thunder in some traditions (Ariel de Vidas, 2004:360-363). His name is cognate to the Nahua earth related crocodilian deity Cipatli and the K'iche' god Zipacna, a telluric deity described in the *Popol Vuh* (Stross, 2006). Building on this string of associations Lorenzo Ochoa (2007:31, 2010) proposed that the term Thipaak is also linguistically related to the word 'zipac' for garfish (*Lepisosteus tristoechus*), thus also connecting this important food fish to maize. Thus, like the Nahua example, the Teeneek also preserve an alimentary history and encode ecological knowledge in mythology. Like teosinte, Thipaak, an ancestor of maize, also has significant associations with cycads. Alcorn (1984:826) records that certain zamia is known as the 'spirit of maize' and 'Maize Lord' and that the "ancestors ate it as maize."

The following Teeneek nomenclature for cycads reveals their conceptual convergence with maize either through the deity Thipaak or through the incorporation of a maize term such as *way'* or *eem*.

<i>Tsalam Thipaak</i>	Thipaak Shade
<i>Tsakam way'</i>	Small Maize Ear
<i>Tsakam Thipaak</i>	Little Thipaak
<i>Ahaatik a eem</i>	Maize Lord

These terms thus place cycads into the culinary evolution presented in the above narratives and suggest that they participate in the same symbolic web as maize, garfish, and the earth related Cipactli.

Iconography

Elements of this symbolic web may occur in Formative period iconography (Fig. 4). For instance, the connection between garfish and crocodilians exists on an Olmec

sculpture purportedly from the Pacific coast of Guatemala upon whose thighs these creatures are incised (Reilly, 1991). Kent Reilly suggests that the figure is a ruler represented as the *axis mundi*. The vertical position of the caiman on his thigh corresponds to other images of crocodilian trees as seen on such Late Formative period monuments as Izapa Stela 25 (Fig. 5) or the greenstone celt illustrated in Figure 1, whose legs are formed by the head of crocodilian. Izapa Stela 5 appears to show similar scenes in which the tree could be identified specifically as *B. alicastrum* (Fig. 5). The garfish's placement on the Young Lord indicates a conceptual equivalency with the crocodilian. Although the string of relationships is complex, the metonymic connection among garfish, crocodilians, Thipaak, maize, and cycads demonstrates that cycads also partake in this symbolic web, one that was likely formed in the Archaic and Early Formative periods.

Finally, the physical attributes and the growth habits of cycads mirror formal attributes of the Olmec Maize God. One of the most significant of the parallels is the similarity between the emergence of the strobili from what could be taken as the cycad's head and the sprout that emerges from God II's head (Fig. 6). If this is the case then it would align with the ethnographic and linguistic data presented above that demonstrate the conceptual convergence of maize and cycads in Mesoamerican ethnoecological systems. Therefore, the sprout-strobili could reference the emerging maize plant, mazorca, or cycad cone, among other possibilities. The image of this deity metonymically references all these instances thus making the attempt to isolate a "true" referent futile; indeed, it is the subject's ambiguity that gives these kinds of representations their symbolic richness.

CONCLUSION

In this paper, I have reviewed some of the most salient data supporting the significant symbolic role of cycads in Mesoamerica from the Archaic Era to the present so as to suggest that cycads might have contributed to Middle Formative period iconography. I have suggested that some images that have traditionally been seen as maize related might in fact be personified cycads or cycad-maize amalgams. This brief glimpse reveals the potential richness of the subject and pushes archaeologist and art historians to attend more fully to ecological contexts and to the wide range of plants that composed the Mesoamerican diet and were useful in the construction of their mythological systems.

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It was first through Mark Bonta's published works on cycads and later in conversations that I became aware of the relationship between cycads and maize. His work has brought to light the great time depth of cycad use in Mesoamerica, its association with maize, and its possible role in the domestication of maize. I owe a great debt to his generosity for sharing data and bringing me along into the fascinating world of cycad ethnobotany.

LITERATURE CITED

- Alcorn, J. B. 1984. *Huastec Mayan Ethnobotany*. University of Texas Press, Austin.
- Alcorn, J. B., B. Edmonson, and C. Hernández Vidales. 2006 Thipaak and the Origins of Maize in Northern Mesoamerica. In J. Staller, R. Tykot, and B. Benz [eds.] *Histories of Maize: Multidisciplinary Approaches to the Prehistory, Linguistics, Biogeography, Domestication, and Evolution of Maize*, pp.190–200. Academic Press, London.
- Ariel de Vidas, A. 2004. *Thunder doesn't Live here Anymore: The Culture of Marginality among the Teeneks of Tantoyuca*. Boulder: University Press of Colorado.
- Berdan, F. F. 2014. *Aztec Archaeology and Ethnohistory*. Cambridge University Press, Cambridge.
- Bonta, M. 2003. Teocinte, 'Ear of God'. *The Cycad Newsletter* 26(1): 7–12.
- Bonta, M. 2010. Human Geography and Ethnobotany of Cycads in Xi'ui, Teeneek, and Nahuatl communities of northeastern Mexico, Final Report. The Cycad Society.
- Bonta, M., and R. Osborne. 2007. *Cycads in the Vernacular A Compendium of Local Names*. Accessed January 23, 2018: <http://www.cycad.org/documents/Bonta-Osborne-Cycads-Vernacular.pdf>
- Bonta, M. O. Flores Pinot, D. Graham, J. Haynes, and G. Sandoval. 2006. Ethnobotany and Conservation of Tiusinte (*Dioon mejiae* Standl. & L.O. Williams, Zamiaceae) in Northeastern Honduras. *Journal of Ethnobiology* 26(2): 228–257.
- Brown, C. 2010. Development of Agriculture in Prehistoric Mesoamerica: The Linguistic Evidence. In J. E. Staller & M. D. Carrasco [eds.] *Pre-Columbian Foodways: Interdisciplinary approaches to Food, Culture, and Markets in ancient Mesoamerica*, pp. 71–107. Springer, New York.
- Haynes, J. L. and M. Bonta. 2007. An emended description of *Dioon mejiae* Standl. In A.P. Vovides, D.W. Stevenson & R. Osborne [eds.] Proceedings of the Seventh International Conference on Cycad Biology (Xalapa, Mexico, 2005). *Memoirs of the New York Botanical Garden* 97: 418–443.
- Isendahl, C. 2011. The Domestication and Early Spread of Manioc (Manihot Esculenta Crantz): A Brief Synthesis. *Latin American Antiquity*. 22(4): 452–468.
- Joralemon, P. D. 1971. A Study of Olmec Iconography, *Studies in Pre-Colombian Art and Archaeology*, No. 7. Dumbarton Oaks, Washington, DC.
- Libby, W. F. 1952. *Radiocarbon dating*. University of Chicago Press, Chicago.
- Martin, S. 2006. Cacao in Ancient Maya Religion: First Fruit from the Maize Tree and other Tales from the Underworld. In C.L. McNeil [ed.] *Chocolate in Mesoamerica: A Cultural History of Cacao* pp.154–183. University Press of Florida, Gainesville.
- Ochoa, L. 2010. Topophilia: A Tool for the Demarcation of Cultural Microregions: the Case of the Huaxteca. In J. E. Staller & M. D. Carrasco [eds.] *Pre-Columbian*

- foodways: Interdisciplinary approaches to food, culture, and markets in ancient Mesoamerica.* pp. 535–552. New York: Springer.
- Pérez-Farrera, M. A. and A. P. Vovides. 2006. The ceremonial use of the threatened “Espadaña” cycad (*Dioon merolae*, Zamiaceae) by a community of the Central Depression of Chiapas, Mexico. *Boletín de la Sociedad Botánica de México* 78: 107–113.
- Pohl, M. 2001. *Economic Foundations of Olmec Civilization in the Gulf Coast Lowlands of México.* Report to FAMSI. Accessed January 23, 2018: <http://www.famsi.org/reports/99069/99069Pohl01.pdf>
- Pohl, M. D., K. O. Pope, J. G. Jones, J. S. Jacob, D. R. Piperno, S. D. deFrance, D. L. Lentz, J. A. Gifford, M. E. Danforth, and J. K. Josserand. 1996. *Latin American Antiquity.* 7(4): 355–372.
- Townsend, R. 1992. *The Aztecs.* New York: Thames and Hudson.
- Smalley, J. and M. Blake. 2003. Sweet Beginnings: Stalk Sugar and the Domestication of Maize. *Current Anthropology* 44(5): 675–703.
- Smith, H. G. 1951. The ethnological and archeological significance of Zamia. *American Anthropologist* 53(2): 238–244.
- Smith, C. E. 1967. Plant remains. In R. S. MacNeish, J. Brunet, & J. E. Anderson [eds.] *The prehistory of the Tehuacan Valley: Environment and subsistence* (Chap. 12). Univ. of Texas Press, Austin.
- Stross, B. 2006. Maize in word and image in southeastern Mesoamerica. In J. Staller, R. Tykot, & B. Benz [eds.] *Histories of maize: Multidisciplinary approaches to the prehistory, linguistics, biogeography, domestication, and evolution of maize* (Chap. 42). Academic Press, London.
- Taube, K. 1996. The Olmec Maize God: The Face of Corn in Formative Mesoamerica, *Res* 29/30: 39–81
- Tristán, E. 2012. Aprovechamiento alimentario de *Dioon edule* Lindl. (Chamal) en comunidades de la región Xi’iuy del estado de San Luis Potosí. Undergraduate thesis, Universidad Autónoma de San Luis Potosí, Mexico.
- Vázquez Torres, M. 1990. Algunos datos etnobotánicos de las cicadas en Mexico. *Memoirs of the New York Botanical Garden* 57: 144–147.
- Vite Reyes, A. 2012. Etnobotánica de círcadas en comunidades nahuas y mestizas de Tlanchinol, Hidalgo. Master’s thesis, Universidad Autónoma del Estado de Hidalgo, Mexico.
- Whitaker, T. W., H. C. Cutler, and R. S. MacNeish. 1957. Cucurbit materials from three caves near Ocampo, Tamaulipas. *American Antiquity* 22(4): 352–358.

CHAPTER 2

New roads in, *Zamia* species out: The case for Isthmian Cycads

Alberto Sidney Taylor B.

ABSTRACT

New roads have been built with quite a frenzy across the Isthmus of Panama in the last 17 years (2000-2017). However, this improvement in government infrastructure has come with a negative cost to the protection of cycad (zamias) populations. Roads have been opened, paved or reconstructed from east, central and west Panama, and the populations of *Zamia* in those places have suffered destruction, illegal extraction or both. I give examples of the problem and the conclusion is to, once again, call the attention of the authorities, especially the Ministry of the Environment (previously known as the National Environmental Authority), to monitor all areas with cycads, because they are under great threat and, in many places, they are not seen anymore.

Keywords

Roads, zamias, extinction, protection, cycads.

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INTRODUCTION

Data have been collected during twenty-three years of fieldwork in the known *Zamia* (Cycadales: Zamiaceae) populations of the Isthmus of Panama, including islands (Taylor, 2007, 2009; Taylor et al., 2007, 2008a, 2008b; Taylor and Holzman, 2012). The data include annotations and figures of the status of roads and the associated cycad populations during those years. The result is the basis for this paper.

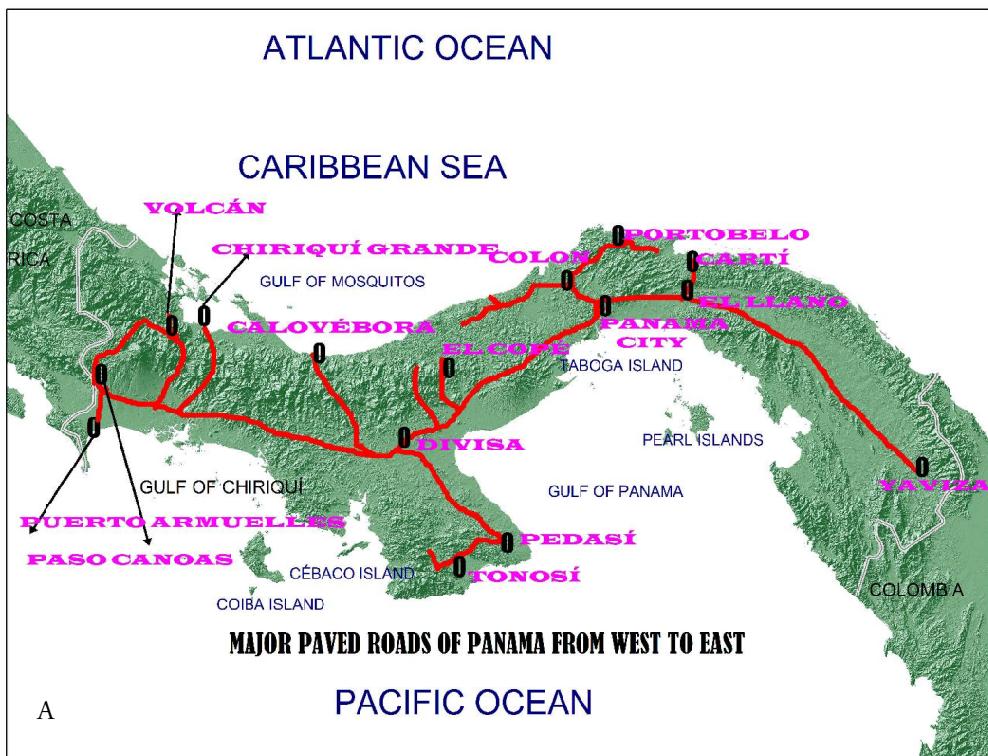
The objective of this presentation is to highlight the perils of cycad populations in view of new road building, a specific form of land clearing, in the Isthmus of Panama, without taking in account the direct or indirect damage to the few surviving plants in each population near the roadside built.

RESULTS AND DISCUSSION

There are now paved roads within a few meters of many cycad populations in Panama and the trend is to increase this situation in the near future. At present, new roads cover most of the provinces of the Republic of Panama, from Darién in the east to the Costa Rican border in the far west and northwest (Fig. 1A). Fig. 1B-C show the state of the road to the far east of the Isthmus (Darién) as it was in 2004 when plants could readily be found in populations of *Z. manicata* (Fig. 2C), *Z. obliqua* (Fig. 2D) and *Z. ipetensis* (Fig. 2E). In 2017, the plants can still be found in the population of *Z. manicata* in the Darién high peaks, because no road has been built to that site, however, the road to Darién where *Z. obliqua* and *Z. ipetensis* used to be found (Fig. 2A-2B) is well paved, and the species are not readily found as before. Figs. 3 and 4 are self explicative in the sense of showing the relationship between the building of roads or their absence and the presence of different cycad (*Zamia*) species populations. Fig. 5 shows clearly the state of unpaved and paved road in west central Panama. Before being paved (Fig. 5E-F) and after being paved (Fig. 5C-D). Most *Z. imperialis* and *Z. pseudoparasitica* were growing near the roadside (Fig. 6D) and, of course, they were removed when the new pavement was put in. There are still plants of *Z. lindleyi*, *Z. skinneri* and *Z. pseudoparasitica* to be found in southwest to northwest Chiriquí province (Figs. 7B, 7C and 7D), but not as frequent as before due to the very good paved road (Fig. 7A) that makes going to the populations of cycads along the highway very easy for poachers. The problem of cycad illegal extraction and destruction tied to road building and other activities that decimate important cycad populations is worldwide (Norstog and Nicholls, 1997; Jones, 2002; Whitelock, 2002; Donaldson, 2003; Walters and Osborne, 2004; Liddle, 2009; Taylor et al. 2012c).

CONCLUSION

Almost every *Zamia* species in the isthmus of panama in all of the seven provinces with the genus has been more or less negatively impacted by the building of new roads or the rehabilitation of old ones. In many cases, different populations of the same species



A

PACIFIC OCEAN



B



C

Figure 1. A. Map of roads to cycad (*Zamia*) populations in the Isthmus of Panama; B. Old mud-ridden road to Darién province in east Panama, C. Another view of the road with the author's previous vehicle in front and commercial trucks and buses in the background.

have been impacted by road construction. A species occurring exclusively on islands, *Z. nesophila*, is also in danger of extinction, because the new roads lead to ports where fast boats or other vessels can reach the island populations readily. The only remedy would be efficient monitoring by the Ministry of the Environment (formerly the National Environmental Authority), and giving lectures to students and interested listeners, utilizing



Figure 2. Contrast of new and old roads in east and northeast Panama and associated cycad populations.

the infrastructure of the cycad garden of the University of Panama to help the public understand the threats to our cycads.

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Figure 3. Paved highway from east Panama to the Atlantic coast and impact on cycad populations
 A-B. Entrance and long stretch of paved highway in central east Panama known as Llano Cartí,
 C. A plant of *Zamia cunaria* and D. of *Z. elegantissima*. These plants are now difficult to find,
 E. Border post of the Dule people, F. Caribbean coast.

Sciences and Technology, to Montgomery Botanical Center and its various directors for limited financial support, to Dr. Dennis W. Stevenson of the New York Botanical Garden for material and scientific support during many field trips and also to Russell Adams and Michael Calonje for their help during field trips, to the Ministry for the Environment (Previously named ANAM or the National Environmental Authority) for field trip



Figure 4. Paved highway in north Panama and *Zamia* populations in sites away from roads:
A. paved highway in north Panama, B. *Z. dressleri* *in-situ*, C. *Z. imperialis* *in-situ* in west central Panama, D. *Z. pseudoparsitica* in northwest Panama, E. *Z. obliqua* in northwest Panama, F. Ovulate cone of *Z. obliqua* in northwest Panama, G. *Z. imperialis* in northwest Panama.



Figure 5. Contrast between old and new roads in central Panama and associated cycad populations. A-B. Plants of *Z. imperialis* *in-situ* in central Panama away from paved roads, C-D. Different sections of paved road in west central Panama, home of populations of *Z. imperialis*, E-F. Old unpaved road in west central Panama, home of *Z. imperialis*, and *Z. pseudoparasitica*

permits. My gratitude goes for the help of previous students and colleagues, including our now retired secretary Ms. Josefina Vargas Yi de Figueroa, for her attentions and moral support. Last but not least I am very thankful for familiar support, especially from my wife, Isabel Herrera Antaneda de Taylor during this research.



Figure 6. Old unpaved road in west central Panama constricted with the same but paved: A-C. Different sectors of unpaved road with Dr. D. Stevenson trying to pry loose an off road vehicle in the mud in A and Dr. Taylor covering from the rain. D. Abundant plants of *Z. imperialis* along the old road, E-F. Same road but paved and cycads hard to see.



Figure 7. Paved road from southwest to northwest Panama known as the Chiriquí-Chiriquí Grande highway: A. Station along the highway, B. Robust plant of *Z. lindleyi*, C. A plant of *Z. pseudoparasitica* already disappeared, D. A plant of *Z. skinneri* in Rambala population.

LITERATURE CITED

- Donaldson, J. S. ed. 2003. Cycads, status survey and conservation action plan. IUCN/SSC Cycad Specialist Group, IUCN, Gland, Switzerland and Cambridge, UK.
- Jones, D. L. 2002. Cycads of the world: ancient plants in today's landscape. Second ed. Smithsonian Institution Press, Washington (DC). 456 p.
- Liddle, D. T. 2009. Management program for cycads in the Northern Territory of Australia. Darwin (Northern Terr.): Northern Territory Department of Natural Resources, Environment, the Arts and Sports. 37 p.

- Norstog, K. J., and T. J. Nicholls. 1997. The biology of the cycads. Comstock Publishing Associates, Ithaca (NY) and London. 363 p.
- Taylor, A. S. 2007. Studies of reproductive biology, ecology, and conservation of cycads in Panama. *The Cycad Newsletter* 30(4): 11–13
- _____, Haynes, J., Holzman, G., and J. Mendieta. 2007. Variability of natural populations and conservation issues facing plicate-leaved *Zamia* species in central and western Panama. Proceedings of the 7th International Conference on Cycad Biology. *Memoirs of the New York Botanical Garden* 97: 556–77.
- _____, Haynes, J., and G. Holzman. 2008a. Taxonomical, nomenclatural and biogeographical revelations in the *Zamia skinneri* complex of Central America (Cycadales: Zamiaceae). *Botanical Journal of the Linnean Society* 158: 399–429.
- _____, Mendieta, J., Bernal, R., and G. Silvera. 2008b. Strange but true: A never-before-reported characteristic of *Zamia pseudoparasitica*. *The Cycad Newsletter* 31 (2/3): 8.
- _____, 2009. Continuing research on the biology and systematics of the *Zamia skinneri* complex of Central America (Cycadales: Zamiaceae). *The Cycad Newsletter* 32 (2/3) : 9–10
- _____, Haynes, J., and G. Holzman. 2012a. The *Zamia skinneri* (Cycadales: Zamiaceae) complex in Panama, In D. W. Stevenson, R. Osborne, and A. S. T. Blake [eds.], Proceedings of the 8th International Conference on Cycad Biology, Panamá, Panamá, January 2-8, 2008. *Memoirs of the New York Botanical Garden* 106: 518–530.
- _____, and G. Holzman. 2012. A new *Zamia* species from the Panama Canal Area. *Botanical Review* 78(4): 335–344.
- _____, Haynes, J. L., Stevenson, D. W., Mendieta, J., and G. Holzman. 2012b. Biogeographic Insights in Central American Cycad Biology. In L. Stevens [ed.] Global Advances in Biogeography. Intech, Rijeka (Croatia) p. 73–98.
- Walters, T., and R. Osborne. eds. 2004. Cycad classification: concepts and recommendations. Cabi Publishing, Wallingford, Oxfordshire OX108DE (UK). 86 p.
- Whitelock, L. M. 2002. The cycads. Timber Press, Portland (OR). 374 p.

CHAPTER 3

Chromosome architecture drives cycad evolution

Root Gorelick

ABSTRACT

I synthesize how chromosome architecture has driven evolution of cycads vis-à-vis effects on selection, drift, mutation, and reproductive isolation. I focus on two large-scale chromosomal alterations: whole genome duplication (polyploidy) and wholesale chromosomal fissioning (pseudopolyploidy), both of which double the number of chromosomes. Isochromosomes are formed by chromosomal fissioning followed immediately by chromosomal duplication, but there is no evidence of isochromosomes in cycads. Whole genome duplication causes instantaneous reproduction isolation plus increased genetic drift and mutation, none of which are usually adaptive. By contrast, chromosomal fissioning causes no genetic drift, no changes in mutation rate, and no reproductive isolation, but decreases linkage disequilibrium, which may have a selective advantage. Cycads show no signs of polyploidy, which explains their low levels of speciation/origination, as well as their ability to survive largely unchanged for millions of years. Cycads show no signs of chromosomal fissioning, except in the clade containing *Zamia* and *Microcycas*, in which some but not all chromosomes appear to have fissioned. The possible selective advantage of chromosomal fissioning may explain the morphological and ecological diversity in *Zamia*.

Keywords

Polyplloid, pseudopolyploid, reproductive isolation, chromosomal fission.

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INTRODUCTION

Cycads are strange, conservative beasts. Their morphology has not changed much in 250-300 million years (Delevoryas and Hope, 1976; Taylor et al., 2009). All 350 or so species of extant cycads (Osborne et al., 2012) have the same unusual set of morphological traits and closely resemble most extinct taxa (Norstog and Nicholls, 1997). They all have highly lignified compound leaves that arise in flushes that lack axillary buds at the adaxial base of the petiole. Cycads are dioecious, zoidogamous, with minuscule pollen droplets, and with large long-lived female and male gametophytes. It is impossible to confuse a cycad with any other plant, at least when reproductive structures are present (without reproductive structures, cycads superficially resemble some palms, the aptly named fern *Blechnum cycadifolium*, and many extinct Bennettitales). Why do cycads have so little morphological diversity and so little taxonomic diversity, especially for such a long-lived cosmopolitan group?

This is part of the difficult age-old questions of (1) why only some taxa are morphologically and ecologically diverse, (2) why only some taxa display evolutionary stasis over tens or hundreds of millions of years, and (3) why are some taxa more species-rich than others, with the caveat that species may be cryptic. It is relatively simple to falsify some hypotheses explaining relative diversity, such as debunking that animal-pollinated plants are diverse while wind-pollinated plants are depauperate, especially because cycads and most Gnetales are predominantly animal pollinated (Bino et al., 1984; Tang, 1987; Gorelick, 2001; Rydin and Bolinder, 2015). Here I proffer that relative lack of cycad diversity may be due to their chromosomal architecture. Extant cycads have very little diversity in their chromosome sizes and numbers, despite cycads having very large genomes compared with most other eukaryotes (Gregory, 2004), especially compared with other taxa that - like cycads - ostensibly lacking polyploidy. The most substantial changes in chromosomal architecture in cycads seem to be in fissioning of a subset of chromosomes in the clade containing *Zamia* and *Microcycas*. Probably not so coincidentally, *Zamia* also happens to be the modern cycad genus with the greatest morphological and ecological diversity.

Below, I first provide basic evolutionary theory on origin of species, then provide theory for how chromosomal duplication and fission can alter evolution in any population, including discussion of effects on reproductive evolution, selection, mutation, and drift. Only after that do I describe the patterns we see in cycad chromosomes and cycad evolution.

Selection, genetic drift, and reproductive isolation

Evolution of large eukaryotes with long generation times is typically dominated by genetic drift because of small effective population sizes. Modern humans are an exception because of our huge population size, frequent movement over long distances, and

promiscuity (although modern humans still are affected by historical genetic drift from a population bottleneck approximately 40,000 years ago (Marth et al., 2003)). It is no wonder that the definitive experimental evolution studies showing lots of selection come from the eubacterium *Escherichia coli*, which has huge effective population sizes, as well as a relatively low mutation rate (Bennett et al., 1990; Lynch, 2007). By contrast, evolution of modern cycads should be dominated by genetic drift and maybe a modicum of mutation, but not selection, simply because actual population sizes are so small, providing a minuscule upper bound on effective population sizes (Gorelick, 2009). Thus we should not expect that any new diversification (e.g. speciation) of cycads will be adaptive.

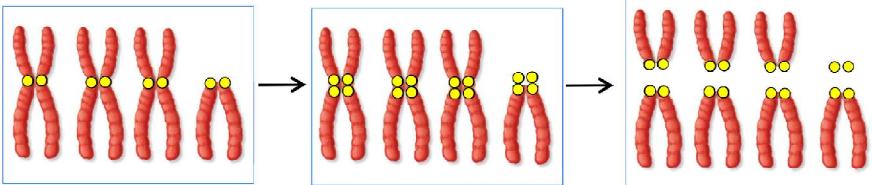
Lack of adaptation does not, however, mean lack of speciation. There is still vigorous debate about whether the major cause of speciation is selection versus reproductive isolation (Forsdyke, 2001). Charles Darwin (1859) suggested that selection helped induce reproductive isolation, whereas his disciple George Romanes (1897) suggested that reproductive isolation was much more important for speciation and that such speciation may have been non-adaptive. As Stephen Jay Gould (1980: 124) noted, "It is a stochastic event that establishes a species by the technical definition of reproductive isolation. To be sure, the latter success of this species in competition may depend on its subsequent acquisition of adaptations, but the origin itself may be non-adaptive". If this latter view is correct, then non-adaptive cycad radiations could have occurred. But how?

If reproductive isolation is discriminant, then maybe there is some selective advantage to the character upon which mates are discriminating. But if reproductive isolation is indiscriminate, then there is no selective advantage. Individuals simply have a randomly smaller population of potential mates. This will cause the relative effects of genetic drift to be larger, as well as cause non-genetic drift, such as the localization of relatively immobile populations to crossing geographic barriers, as seen with the remarkable radiation of land snails, each in their own valleys, in the Hawaiian Islands (Gulick, 1890), at least before many of these incipient snail species were extirpated by human influences (Chiba and Cowie, 2016). Polyploidy, aka whole genome duplication, is a form of indiscriminate reproductive isolation. Diploid and tetraploid individuals need not have any obvious phenotypic differences, save for the size of the genome per nucleus. Usually, there are subtle phenotypic differences caused by polyploidy, such as larger cell sizes, fewer cells per standard-sized individual, slower mitotic cell cycles, and maybe even altered photosynthetic rates or altered developmental rates (Fankhauser, 1945; Masterson, 1994; Vyas et al., 2007). But, other than the last two examples of altered photosynthetic or developmental rates, it is not obvious that polyploidy confers any selective advantage or disadvantage.

Polyplody, pseudopolyploidy, and their evolutionary effects

There are two ways to double the number of chromosomes: whole genome duplication (polyplody) and 'chopping' each chromosome in half at the centromere (pseudopolyploidy); see Figure 1 (Muller, 1925; Vandel, 1937; Stebbins, 1971; Kolnicki, 2000). Pseudo polyplody results in telocentric chromosomes, with a telomere at one end and a centromere at the other. If a chromosome is already telocentric, it will not be fissioned via pseudopolyploidy, thereby resulting in less than doubling the total number of chromosomes per nucleus. It is also possible for pseudopolyploidy to be immediately followed by whole genome duplication, forming isochromosomes (Perry et al., 2004). Isochromosomes are metacentric, with one arm being an inverted copy of the other.

Pseudopolyploidy via **duplication** of centromeres



Pseudopolyploidy via **fissioning** of centromeres

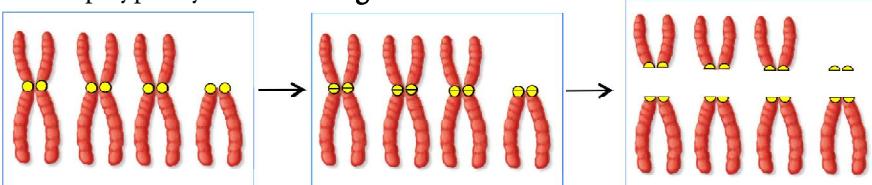


Figure 1. Depictions of pseudopolyploidy with metacentric and telocentric chromosomes.

Polyplody results in instantaneous reproductive isolation because the backcross of the nascent tetraploid with its diploid progenitor results in infertile triploid offspring (ignoring the triploid bridge hypothesis; Ramsey and Schemske, 1998). Polyplody causes speciation (Gorelick and Olson, 2011). Newly formed tetraploids are typically rare, meaning that the new tetraploid population will have small population size, sometimes as small as one self-fertile individual, and thus a tiny effective population size (Levin, 1975). Therefore, polyplody causes extensive genetic drift, with little opportunity for selection. "Additional genomic studies are needed...to determine when novel genes resulting from polyploidy have enabled *adaptive radiations*" (Soltis et al., 2009: 336; italics added). Furthermore, mutation rates increase with any genome duplication as a result of extra cytosine methylation on newly duplicated genomes - methylated cytosines mutate to thymine at much higher rates than do unmethylated cytosines (Jones et al.,

1992; Gorelick, 2003). Polyploidy thus causes non-adaptive radiations (Gorelick and Olson, 2013).

There is one way that whole genome duplication could confer selective advantage. If crosses between individuals of different varieties or races normally results in sexually sterile offspring, e.g. mules, then polyploidy via premeiotic doubling or gamete doubling (or unreduced gametes, if such entities truly exist) will restore meiosis in the offspring because there are now homologous chromosomes available for pairing during meiosis I. But these are not the typical physiological or morphological phenotypic changes usually envisioned when mentioning selective advantage.

Pseudopolyploidy does not cause reproductive isolation. In backcrosses, two fissioned telocentric chromosomes can synapse with the one chromosome that they evolved from (Kolnicki, 2000; Margulis and Sagan, 2002). Pseudopolyploidy therefore does not result in additional genetic drift. Pseudopolyploidy does not result in any genome duplication, except for maybe of centromeres (Fig. 1), hence does not result in higher mutation rates associated with additional cytosine methylation (Adams et al., 2003; Rapp and Wendel, 2005). Almost by definition, chromosomal fissioning results in reduced linkage disequilibrium, which may provide some selective advantage to pseudopolyploid individuals. Overall, pseudopolyploidy does not cause speciation or radiations, but may confer some selective advantage (Gorelick and Olson, 2013).

Isochromosomes have been much less studied than polyploids and pseudopolyploids, and usually only in B-chromosomes. Sometimes isochromosomes will synapse with homologues from which they apparently have been derived (Berend et al., 2001), much like with pseudopolyploidy. By contrast, sometimes the two arms of the isochromosomes will synapse with each other forming a hairpin at the centromere (Vega and Feldman, 1998), resulting in reproductive isolation of the nascent isochromosome-bearing lineage from its parental lineage, much like what occurs with back-crosses between diploid ancestors and their newly-formed tetraploid descendants. Therefore it is not obvious whether lineages with newly formed isochromosomes will be reproductively isolated and have minuscule effective population sizes.

Empirically, how can we distinguish polyploidy, from pseudopolyploidy, from their combination resulting in isochromosomes? Polyploidy will result in concomitant increases in chromosome number and C-value, i.e. weight of the entire nuclear genome. Pseudopolyploidy will result in a doubling of chromosome numbers without any change in C-value. If only a subset of chromosomes are fissioned, then we expect an increase in chromosome numbers that is less than doubling, but still without any change in C-value. Any such chromosomal fissioning will result in an increased proportion of telocentric chromosomes, with a corresponding diminution in the proportion of metacentric, submetacentric, subtelocentric, and acrocentric chromosomes. If pseudopolyploidy occurs in concert with whole genome duplication of the remaining telocentric chromosomes, resulting in isochromosomes, then there will be doubling of

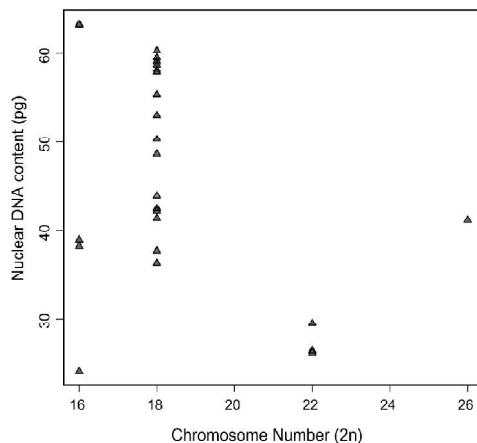


Figure 2. Theoretical effects of polyploidy, pseudopolyploidy, and isochromosome formation on the correlation between chromosome weight ($2C$) and chromosome number ($2n$) [Figure reproduced with permission of University of Chicago Press from Gorelick *et al.* (2014) *International Journal of Plant Sciences* 175(9): 986-997].

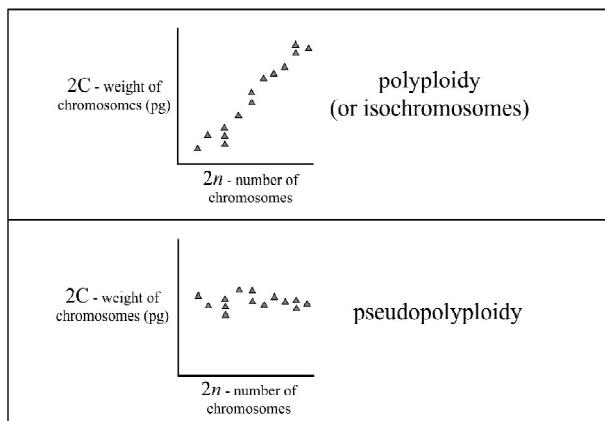


Figure 3. Chromosome weight ($2C$) versus chromosome number ($2n$) in Cycadales ($p = 0.06$, t -test = -1.975 , $R^2 = 0.17$). Without accounting for phylogeny, there is no correlation between cycad DNA content and chromosome number. Slope of the regression is statistically indistinguishable from zero.

both chromosome numbers and C-values, as with polyploidy, but all resulting chromosomes will be metacentric. Figures 2 and 3, respectively depict actual and theoretical relationship between chromosome numbers ($2n$) and chromosome weight ($2C$ -values) for polyploidy and pseudopolyploidy.

No polyploidy nor isochromosomes in cycads, but some chromosomal fissioning

There is less than a two-fold range in chromosome numbers in extant cycads, from a minimum of $2n=16$ in several *Zamia*, *Ceratozamia*, and *Stangeria* to a maximum of

$2n=28$ in some *Zamia* (Gorelick and Olson, 2011; Olson and Gorelick, 2011; Gorelick et al., 2014). This indicates lack of polyploidy and lack of isochromosomes formation in cycads. Lack of polyploidy in cycads is consistent with their relative lack of speciation. There are no reports of isochromosomes in cycads. Nor have we seen evidence of isochromosomes in our previous work on cycad karyotypes (Olson and Gorelick, 2011). Figure 2 shows no correlation between chromosome number and 2C-value, using data from 22 species in all 11 extant cycad genera, thereby indicating pseudopolyploidy (Gorelick et al., 2014). The negative slope in Figure 2 is not statistically significant. But in order to properly conduct this analysis, we cannot weight each data point equally, but must account for phylogeny. Using phylogenetic generalized least squares, i.e. PGLS (Grafen, 1989; Gorelick et al., 2014), on the same data points depicted in Figure 2 also demonstrated no statistically significant relationship between chromosome number and 2C-value (Gorelick et al., 2014). Thus, there seems to exist chromosomal fission amongst a subset of chromosomes in cycads.

Olson and Gorelick (2011) labeled a phylogenetic tree of the clade containing *Microcycas* and *Zamia*, including *Chigua*, with karyotype formulas. Karyotype formulas provide the number of metacentric/submetacentric chromosomes and the number of telocentric/submetacentric chromosomes per individual plant, noting that several species have individuals with multiple karyotype formulas. In general, the most highly derived species had the highest chromosome numbers, e.g. *Zamia roezlii*. Number of chromosomes across the *Zamia* + *Microcycas* clade is proportional to the ratio of telocentric-to-metacentric chromosomes. The few species with many different chromosome numbers, such as *Z. roezlii*, *Z. paucijuga*, and *Z. prasina*, also have many different karyotype formulas. These patterns are consistent with chromosomal fission of a subset of chromosomes.

Given only one species of *Microcycas*, which only has a single karyotype formula (5M:21T), it is impossible to directly infer chromosomal fission in this genus. Nonetheless, given the close relationship between *Microcycas* and *Zamia* and given that high chromosome numbers, $2n=26$, especially with mostly telocentric and subtelocentric chromosomes (Olson and Gorelick, 2011), it is reasonable to presume that *Microcycas* and/or its immediate ancestors may have experienced chromosomal fission.

Lack of pseudopolyploidy in most cycads is consistent with lack of adaptation. Thus we expect macroevolution of cycads to be conservative, with substantial stasis. However, chromosomal fission in the *Zamia* + *Microcycas* clade is the exception that proves the rule. Chromosomal fission should not result in new species, but could confer selective advantage due to reduced linkage disequilibrium. Consistent with such hypothesized adaptive non-radiation of the *Zamia* + *Microcycas* clade, we see more ecological and morphological diversity here than in any other cycad lineage. *Zamia* contains xerophytic, mesophytic, and hydrophytic species, including even mangrove species, e.g. *Z. roezlii*, which is a particularly unusual ecological niche. Leaf and plant sizes range from the diminutive *Z. pygmaea* to the mammoth *Z. imperialis*, not to mention

the arborescent *Microcycas calocoma*. This clade even contains the only obligate epiphytic cycad, *Z. pseudoparasitica*. I proffer that morphological and ecological diversity is largely a consequence of chromosomal fission in the *Zamia* + *Microcycas* clade.

Although undoubtedly overly simplistic, chromosome evolution seems to nicely explain large-scale patterns of cycad morphological and species diversity. But it raises another question: Why is chromosomal fission only common in the *Zamia* + *Microcycas* clade and not in other cycads? And why - unlike with angiosperms, monilophytes, and bryophytes - do cycads lack polyploidy?

ACKNOWLEDGEMENTS

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LITERATURE CITED

- Adams, K. L., Cronn, R., Percifield, R., and J. F. Wendel. 2003. Genes duplicated by polyploidy show unequal contributions to the transcriptome and organ-specific reciprocal silencing. *Proceedings of the National Academy of Sciences of the United States of America* 100(8): 4649–4654.
- Bennett, A. F., Dao, K.M., and R.E. Lenski. 1990. Rapid evolution in response to high-temperature selection. *Nature* 346(6279): 79–81.
- Berend, S. A., Hale, D. W., Engstrom, M. D., and I. F. Greenbaum. 2001. Cytogenetics of collared lemmings (*Dicrostonyx* × *groenlandicus*). II. Meiotic behavior of B chromosomes suggests a Y-chromosome origin of supernumerary chromosomes. *Cytogenetics and Cell Genetics* 95(1-2): 85–91.
- Bino, R. J., Devente, N., and A. D. J. Meeuse. 1984. Entomophily in the dioecious gymnosperm *Ephedra aphylla* Forsk. (=*E. alta* C.A. Mey) with some notes on *E. campylopoda* C.A. Mey. II. Pollination droplets, nectaries, and nectarial secretions in *Ephedra*. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series C* 87(1): 15–24.
- Chiba, S., and R. H. Cowie. 2016. Evolution and extinction of land snails on oceanic islands. *Annual Review of Ecology, Evolution, and Systematics* 47(1): 123–141.
- Darwin, C. R. 1859. On the origin of species by natural selection or the preservation of favoured races in the struggle for life. John Murray, London.
- Delevoryas, T., and R. C. Hope. 1976. More evidence for a slender growth habit in Mesozoic Cycadaphyta. *Review of Palaeobotany and Palynology* 21(1): 93–100.
- Fankhauser, G. 1945. The effects of changes in chromosome number on amphibian development. *Quarterly Review of Biology* 20(1): 20–78.
- Forsdyke, D. R. 2001. *The Origin of Species* revisited: a Victorian who anticipated modern developments in Darwin's theory. McGill-Queen's University Press, Kingston & Montréal.

- Gorelick, R. 2001. Did insect pollination cause increased seed plant diversity? *Biological Journal of the Linnean Society* 74(4): 407–427.
- Gorelick, R. 2003. Evolution of dioecy and sex chromosomes via methylation driving Muller's ratchet. *Biological Journal of the Linnean Society* 80(2): 353–368.
- Gorelick, R. 2009. Evolution of cacti is largely driven by genetic drift, not selection. *Bradleya* 27: 41–52.
- Gorelick, R., Fraser, D., Zonneveld, B. J. M., and D. P. Little. 2014. Cycad (Cycadales) chromosome numbers are not correlated with genome size. *International Journal of Plant Sciences* 175(9): 986–997.
- Gorelick, R., and K. Olson. 2011. Is lack of cycad (Cycadales) diversity a result of a lack of polyploidy? *Botanical Journal of the Linnean Society* 165(2): 156–167.
- Gorelick, R., and K. Olson. 2013. Polyploidy is genetic hence may cause non-adaptive radiations, whereas pseudopolyploidy is genomic hence may cause adaptive non-radiations. *Journal of Experimental Zoology (Part B. Molecular and Developmental Evolution)* 320B(5): 286–294.
- Gould, S. J. 1980. Is a new and general theory of evolution emerging? *Paleobiology* 6(1): 119–130.
- Grafen, A. 1989. The phylogenetic regression. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 326(1233): 119–157.
- Gregory, T. R. 2004. Macroevolution, hierarchy theory, and the C-value enigma. *Paleobiology* 30(2): 179–202.
- Gulick, J. T. 1890. Indiscriminate separation under the same environment, a cause of divergence. *Nature* 42: 369–370.
- Jones, P. A, Rideout, W. M, Shen, J. C, Spruck, C. H., and Y. C. Tsai. 1992. Methylation, mutation and cancer. *BioEssays* 14(1): 33–36.
- Kolnicki, R. L. 2000. Kinetochore reproduction in animal evolution: cell biological explanation of karyotypic fission theory. *Proceedings of the National Academy of Sciences of the United States of America* 97(17): 9493–9497.
- Levin, D. A. 1975. Minority cytotype exclusion in local plant populations. *Taxon* 24: 35–43.
- Lynch, M. 2007. The origins of genome architecture. Sinauer, Sunderland.
- Margulis, L., and D. Sagan. 2002. Acquiring genomes: a theory of the origin of species. Basic Books, New York.
- Marth, G., Schuler, G., Yeh, R., Davenport, R., Agarwala, R., Church, D., Wheelan, S., Baker, J., Ward, M., Kholodov, M., Phan, L., Czabarka, E., Murvai, J., Cutler, D., Wooding, S., Rogers, A., Chakravarti, A., Harpending, H.C., Kwok, P-Y., and S. T. Sherry. 2003. Sequence variations in the public human genome data reflect a bottlenecked population history. *Proceedings of the National Academy of Sciences of the United States of America* 100: 376–381.

- Masterson, J. 1994. Stomatal size in fossil plants: evidence for polyploidy in majority of angiosperms. *Science* 264: 421–424.
- Muller, H. J. 1925. Why polyploidy is rarer in animals than in plants. *American Naturalist* 59: 346–353.
- Norstog, K. J., and T. J. Nicholls. 1997. The biology of cycads. Cornell University Press, Ithaca.
- Olson, K., and R. Gorelick. 2011. Chromosomal fission accounts for small-scale radiations in *Zamia* (Zamiaceae; Cycadales). *Botanical Journal of the Linnean Society* 165(2): 168–185.
- Osborne, R., Calonje, M.A., Hill, K. D., Stanberg, L., and D. W. Stevenson. 2012. The world list of cycads. *Memoirs of the New York Botanical Garden* 106: 480–510.
- Perry, J., Slater, H. R., and K. H. A. Choo. 2004. Centric fission - simple and complex mechanisms. *Chromosome Research* 12(6): 627–640.
- Ramsey, J., and D. W. Schemske. 1998. Pathways, mechanisms, and rates of polyploid formation in flowering plants. *Annual Review of Ecology and Systematics* 29: 467–501.
- Rapp, R. A., and J. F. Wendel. 2005. Epigenetics and plant evolution. *New Phytologist* 168(1): 81–91.
- Romanes, G. J. 1897. Darwin and after Darwin - An exposition of the Darwinian theory and a discussion of post-Darwinian questions. Volume 3. Isolation and physiological selection. Longman, Green & Co., London.
- Rydin, C., and K. Bolinder. 2015. Moonlight pollination in the gymnosperm *Ephedra* (Gnetales). *Biology Letters* 11 (4): 20140993.<http://dx.doi.org/10.1098/rsbl.2014.0993>
- Soltis, D. E., Albert, V. A., Leebens-Mack, J., Bell, C. D., Paterson, A. H., Zheng, C. F., Sankoff, D., dePamphilis, C. W., Wall, P. K., and P. S. Soltis. 2009. Polyploidy and angiosperm diversification. *American Journal of Botany* 96(1): 336–348.
- Stebbins, G. L. 1971. Chromosomal evolution in higher plants. Edward Arnold, London.
- Tang, W. 1987. Insect pollination in the cycad *Zamia pumila* (Zamiaceae). *American Journal of Botany* 74(1): 90–99.
- Taylor, T. N., Taylor, E. L. and M. Krings. 2009. Paleobotany: the biology and evolution of fossil plants (2nd edition). Academic Press, Burlington, MA.
- Vandel, A. 1937. Chromosome number, polyploidy, and sex in the animal kingdom. *Proceedings of the Zoological Society of London, Series A: General and Experimental* 107(4, Special Issue): 519–541.
- Vega, J. M., and M. Feldman. 1998. Effect of the pairing gene *Ph1* and premeiotic colchicine treatment on intra- and interchromosome pairing of isochromosomes in common wheat. *Genetics* 150(3): 1199–1208.
- Vyas, P., Bisht, M. S., Miyazawa, S., Yano, S., Noguchi, K., Terashima, I., and S. Funayama-Noguchi. 2007. Effects of polyploidy on photosynthetic properties and anatomy in leaves of *Phlox drummondii*. *Functional Plant Biology* 34(8): 673–682.

CHAPTER 4

Cycad anatomy: Old techniques solving new problems

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ABSTRACT

In the age of genomics, many techniques of yesterday are being suspended in college curricula in favor of the modern molecular disciplines. This may leave an undesirable vacuum in the years to come as the older generation of morphologists and taxonomists retire from academia. This talk underscores the synergy that is obtained in the combination from the old and the modern in solving certain biological and taxonomic problems. This is a call not to abandon traditional techniques, since these contribute to an integrated approach to research and have much to offer. Fortunately, traditional techniques are not entirely abandoned in some institutions. We underline some examples where anatomical techniques solved problems in the genera *Ceratozamia*, *Dioon* and *Zamia*.

Keywords

Anatomy, cycad systematics, numerical analysis

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INTRODUCTION

In spite of the fact that the living cycads consist of 358 species worldwide (Calonje et al. 2020), there are remarkably few micromorphological and anatomical studies, in comparison to the work done on other gymnosperms. A lot of anatomical work has been done during the 19th and 20th centuries, but never systematically covering entire genera. A pioneer anatomical study for cycads was that done by Pant and Nautiyal (1963) they described cuticular and epidermal structures of 59 species. Greguss (1966) found similarity in the epidermis of *Dioon edule* Lindl. with the fossil *Elatocladus punctatus*, and later described the stem anatomy of 40 species and the epidermal and leaf structure of 83 species (Greguss, 1968). More recently, anatomical methods have been proven effective to solve issues related to cycad systematics and evolution. For example, Tang et al. (2004) described the leaflet anatomy of ten species from six genera, and found consistencies with the classification of Zamiaceae of Stevenson (1992), while the study of Barone-Lumaga et al. (2015) helped to understand the epidermal variation across 12 *Dioon* species. Here, we cite traditional morphology and micro-technique that we have used, and we mention a set of recommended modest laboratory equipment of easy access that is required in anatomical studies. Finally, we show case studies that helped us to solve problems in cycad systematics.

Setting up your anatomy laboratory

Essential items are a good photomicroscope and microtomes. It is advisable to acquire the best modular instruments your budget allows and that the model can be upgraded in the future.

Basic equipment for a plant anatomy laboratory:

- i) **Microscopes.** - For routine work, a stereoscopic dissecting microscope with incident and transmitted illumination for preview and selection of sections. A routine compound microscope for detailed observation and measurement; this ideally should be fitted with a mechanical stage and planachromatic objectives for measurement purposes. A stage micrometer for calibration of an eyepiece scale in a focusing eyepiece should be available for taking measurements "manually". Since most work is done under bright-field microscopy combined with staining, this should be sufficient. However, additional microscopic techniques that can be included are; phase contrast for visualizing live material and chromosome work; DIC (differential interference contrast) for applications as in phase contrast, with the advantage of "optical staining"; polarized light microscopy for detecting birefringence and crystals; epifluorescence for detecting auto-fluorescence, and combined with fluorochromes for a number applications such as pollen tube/stigma compatibility. A camera Lucida (a system of prisms and or mirrors) for making accurate scaled drawings is also desirable (an illustration is better than a thousand words for describing anatomical

structures). For high-resolution images, image analysis and photo stacking, a fully equipped high-resolution photomicroscope with motorized stage would be essential, it comes with specialized software as in the Zeiss Axio Imager™.

- ii) **Microtomes.** - For obtaining thin sections of biological material. There are basically three types; sliding microtome, for sectioning tough material such as wood, rotary microtome for sectioning bland material previously embedded in paraffin wax or resin (Fig. 1), and the freezing microtome or cryostat for sectioning frozen fresh material. Hand microtome also for taking hand sections, good preliminary sections can be obtained this way.
- iii) **Vacuum embedding oven.** - For infiltration and wax embedding of specimens. Application of vacuum enables the removal of air from the tissue to be infiltrated and embedded, a source of problems during sectioning. This equipment needs an external rotary vacuum pump.

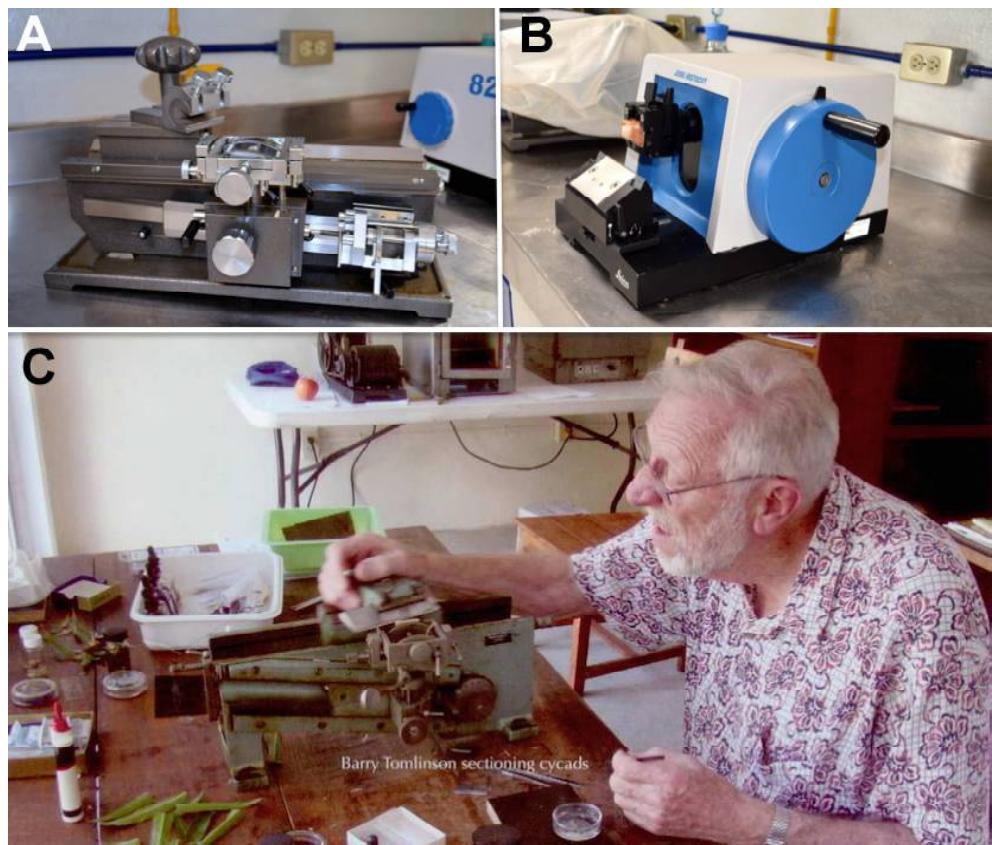


Figure 1. Anatomy laboratory: A. Sliding microtome, B. Rotary microtome, C. Barry Tomlinson taking cycad leaf sections with a sliding microtome at the Montgomery Botanical Center, Miami, from Griffith (2013) Montgomery Botanical News 21(1): 5.

- iv) **Drying oven.** - For general purpose drying of material and glassware.
- v) **Centrifuge.** - A bench centrifuge reaching ca 6,000 rpm with a swing rotor. For palynology and sucrose gradient separation of spores if mycorrhizal work is to be carried out.
- vi) **Slide warmer and flotation bath.** - For drying permanent preparations and flotation of wax embedded sections, respectively. The gentle heat removes wrinkles in the wax-embedded section by floating on the warm water surface making adhesion to the microscope slide even.
- vii) **Fume hood.** - Since organic solvents are commonly used in the anatomy laboratory, this should be equipped with a fume hood, since the fumes from these reagents may be toxic and/or carcinogenic.

Reagents. - Alcohol, usually ethyl alcohol or isopropyl alcohol, is used for dehydrating. Solvents such as chloroform, benzene and xylene are used as solvents for wax for infiltration and clearing of sections. A selection of aniline stains such as safranine, fast green, aniline blue, toluidine blue, haematoxylin, chlorazol black are fairly standard. Also, histochemical stains for specific reactions, i.e. Lugol solution for starch, Sudan for fatty acids and



Figure 2. The Mexican National Cycad Collection at the Francisco Javier Clavijero Botanic Garden, INECOL, Xalapa.

cutin, phloroglucinol HCl for lignin, ninhydrin for amino acids and protein, and periodic acid Schiff's reagent for carbohydrates (Locquin and Langeron, 1985).

Bibliography. - Good references for plant histological technique are: Johansen (1940), Sass (1958), Purvis et al. (1966), Berlyn and Miksche (1976). A good applied anatomy manual with basic techniques and for teaching is Cutler (1978). As more integrated approaches to systematics are appearing in the literature, some institutions encourage these studies. Figure 1 shows the eminent plant anatomist Barry Tomlinson taking cycad sections on a sliding microtome at the Montgomery Botanical Center.

Below, we present four case studies that combined traditional anatomical and micromorphological techniques, advanced microscopy, and molecular methods that helped us to solve vexing problems in species delimitation in the genera *Ceratozamia* Brongn., *Dioon* Lindl. and *Zamia* L..

Methods

Living field-collected specimens kept at the Francisco Javier Clavijero Botanic Garden at Xalapa, Mexico, have been analyzed. Most of specimens we analyzed have been under cultivation for over ten years under uniform environmental conditions, thus phenotypic plasticity may be disregarded (Fig. 2).

Particularities of each case study

For *Ceratozamia*, leaflet material was obtained from *Ceratozamia mexicana* Brongn., *C. brevifrons* Miq. and *C. tenuis* (Dyer) D.W.Stev. & Vovides. One to five samples per species were taken and vouchers were deposited at XAL. The median part of fresh leaflet tissue (ca. 1-2 cm length) was taken from the median part of mature leaves from each taxon for sectioning and epidermal studies, histological techniques for light microscopy.

For *Dioon*, the leaflet micromorphological variation of 14 species was studied; sampling and histological techniques were the same as for *Ceratozamia*. Additionally, epidermal peels were made for study under light microscopy (bright field, DIC and epifluorescence) and scanning electron microscope (SEM). Histological methods are fully described in Vovides et al. (2012, 2016, 2018).

For *Zamia*, the *Zamia katzeriana* species complex was revisited (Pérez-Farrera et al. 2016). Extensive field studies were made in populations of *Z. splendens* Schutzman, *Z. loddigesii* Miq., and a secondary succession zone consisting of a population of *Z. katzeriana* (Regel) E.Rettig. Cultivation, sampling and histological techniques were the same as in *Ceratozamia*.

Ovule development was investigated in both *C. mexicana* and *Zamia furfuracea* L.f. (Sánchez-Tinoco et al., 2018). Following the reproductive cycle of both species, ovules were collected and fixed in FAA and stored in GAA. The ovules were embedded in paraffin wax according to Sass (1958), then, serial transverse and longitudinal sections of

the gametophyte at the micropylar end were taken at 12 µm with a rotary microtome, double stained with safranine-O and fast green, and mounted in Canada balsam. Observations were made under bright field microscopy, and photomicrographs were taken with a Zeiss Fomi III fitted with a digital camera.

Measurements

Cross-sectional measurements were taken from 11 characters using a calibrated eyepiece micrometer; where cells were not isodiametric, the measurements were expressed as length and width, and 25 replicate measurements were taken for each character from each of the five leaflet samples as in Vovides et al. (2012, 2016, 2018) and Pérez-Farrera et al. (2014).

Results and discussion

Ceratozamia

In *Ceratozamia*, molecular, morphological and anatomical techniques have helped to clarify species in the *Ceratozamia mexicana*, and *C. norstogii* (González and Vovides, 2012; Vovides et al. 2012; Pérez-Farrera et al. 2014; Vovides et al. 2016) species complexes.

Two populations previously regarded as *C. mexicana*, though morphologically distinct, were also found to be anatomically different (Vovides et al., 2016). The El Mirador population (Veracruz, Mexico) morphologically identifies with a specimen at the French National Herbarium in Paris (P) collected by Ghiesbreght in Mexico, whereas the population at El Esquilón, near Xalapa, recognized by many authors as *C. mexicana*, is morphologically similar to Dyer's voucher at Kew labeled as *C. mexicana* var. *tenuis* (cultivated). The El Esquilón population has linear-lanceolate leaflets and lacks girder sclerenchyma associated with the vascular bundles, whereas *C. mexicana* from El Mirador is more robust and has oblong-lanceolate leaflets and presents girder sclerenchyma (Fig. 3).

Principal component and discriminant analyses showed significant differentiation ($P < 0.01$) and Mahalanobis squared distance between centroids ($P < 0.05$) (Fig. 4). Based on these results, the material corresponding to the El Esquilón population was recognized as distinct from *C. mexicana*, and the new nomenclatural combination *Ceratozamia tenuis* (Dyer) D.W. Stev. & Vovides was proposed for it (Vovides et al. 2016). In addition, the Ghiesbreght specimen in Paris and Dyer's specimen at Kew were designated as the lectotypes for the names *C. mexicana* and *C. mexicana* var. *tenuis*, respectively; and epitypes were designated for both lectotypes.

Ceratozamia brevifrons, previously considered either as synonymous to *C. mexicana* or a variety of it is morphologically distinct in presenting keeled leaves with shorter lanceolate leaflets. Anatomically, it is similar to *C. mexicana* in that both present girder sclerenchyma, but there are differences in leaflet margin sclerenchyma as well as other anatomical traits. A separation by discriminant functions with significant Mahalanobis

squared distance ($P < 0.001$) was also found. Since no type specimen was found for *C. brevifrons* which could be associated with Miquel's protologue description, a neotype was assigned: *S. Avendaño* 5699 (XAL) (Vovides et al., 2012; Fig. 5).

The *Ceratozamia norstogii* species complex was reassessed (Pérez-Farrera et al. 2014), with *C. alvarezii* Pérez-Farr, Vovides & Iglesias, *C. chimalapensis* Pérez-Farr. & Vovides, *C. mirandae* Vovides, Pérez-Farr. & Iglesias and *C. norstogii* D.W. Stev. considered as "good species". Significant difference in Mahalanobis squared distance for morphological and anatomical characters ($P < 0.001$) were obtained.

Dioon

Studies on leaflet and cuticle anatomy of the genus *Dioon* provided a set of epidermal traits that clarified species delimitation and relationships with their habitats. We were able to describe the leaflet anatomy, cuticles, and epidermal features for 14 *Dioon* species. The salient points were the identification of G-fibers and description of two types of Florin ring and epistomatal pore that identify species from the western Pacific seaboard of Mexico from those of the Gulf of Mexico and Caribbean seabards (Vovides and Galicia, 2016; Vovides et al. 2018) (Figure 6). The quantitative analysis was useful to reveal five geographically structured species groups. Character tracing on the phylogenetic tree of *Dioon* has amplified our current understanding of *Dioon* with respect to habitats. The presence/absence data suggest that the evolutionary acquisition-deletion of structural shapes is phylogenetically independent,

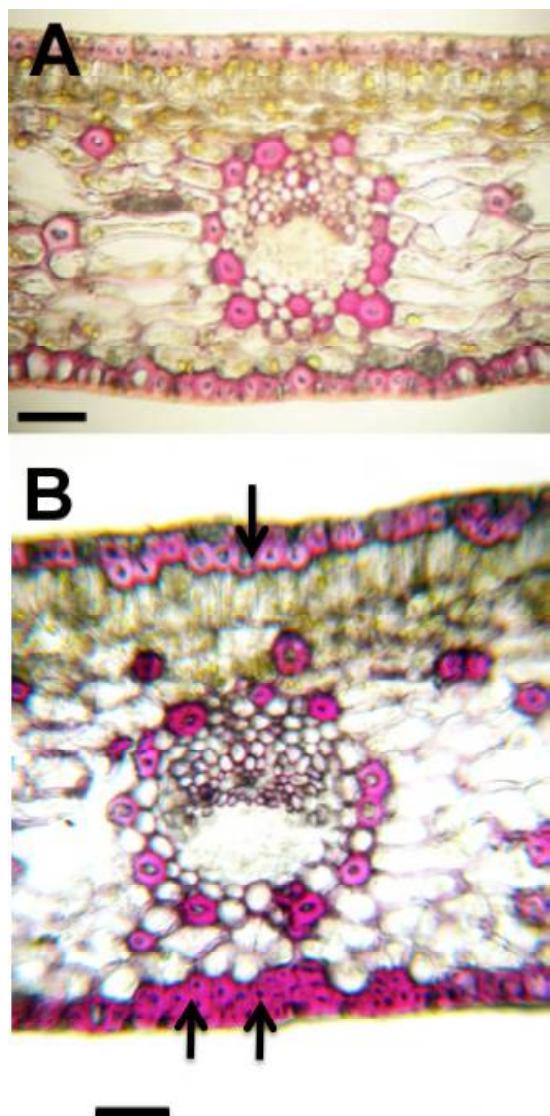


Figure 3. Transverse sections of *Ceratozamia* leaflets. A, *C. tenuis* lacking girder sclerenchyma; B, *C. mexicana* with girder sclerenchyma (arrows). Scale bars = 100µm. Modified from Vovides et al., (2016) Botanical Sciences 94(2): 419-429.

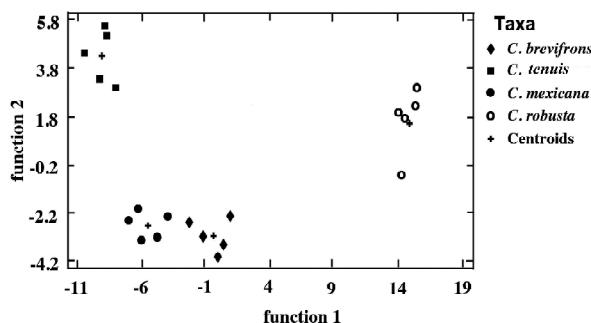


Figure 4. Scatter plot score derived from the functions produced by stepwise discriminant analysis of 11 anatomical characters occurring in *Ceratozamia tenuis*, *C. mexicana*, and *C. robusta* from San Fernando, Chiapas. Modified from Vovides *et al.*, (2016) Botanical Sciences 94(2): 419-429

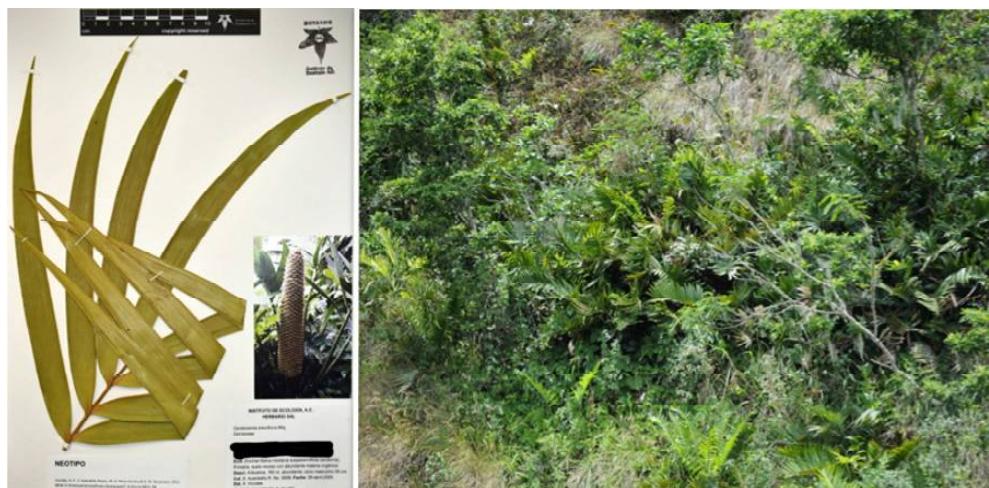


Figure 5. *Ceratozamia brevifrons* neotype and habitat.

indicating that climate influences the variation of cuticular and stomatal traits. Many epidermal traits, especially adaxial cuticle thickness and epistomatal pore width and depth, might be adaptations resulting from a long-term influence of climate, since they appear to correlate with climatic conditions in relation to their biogeography (Gutiérrez-Ortega *et al.* 2018).

Zamia katzeriana species complex

In *Zamia*, genetic, morphological and anatomical traits helped solve the relationship between *Zamia katzeriana* and *Z. splendens*, and a hybrid origin of *Z. katzeriana* has been proposed (Pérez-Farrera *et al.* 2016). *Zamia splendens* was placed under synonymy of *Z. katzeriana* by Nicolalde-Morejón *et al.* (2016) based on examination of the type of *Z. katzeriana* and morphometric studies of the known populations at the time.

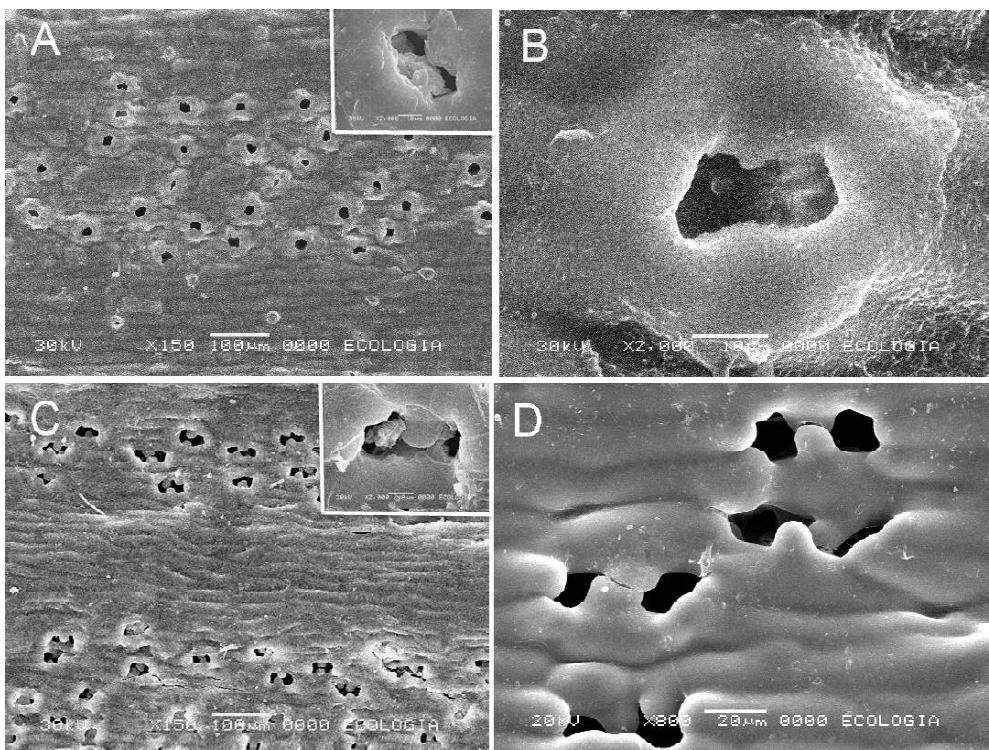


Figure 6. SEM of outer surface of abaxial cuticles of *Dioon*. A. *Dioon edule* type Florin rings, insert showing wax plug. B. Detail of *D. edule* ring with wax plug. C. *D. purpusii* type rings, insert shows aperture with wax plug. D. *D. purpusii* detail of pores showing protruding cuticular papillae partially occluding pores. Bar: 100 µm in A and C, 10 µm in B, 20 µm in D.

Morphometric analysis on morphology, anatomy and stomatal index, as well as preliminary genetic information, allowed us to recognize *Z. splendens* as a separate species and proposed *Z. katzeriana* as a hybrid between the putative parents *Z. splendens* and *Z. loddigesii*. Leaflet gross morphology, such as shape and width, places *Z. katzeriana* midway between *Z. splendens* and *Z. loddigesii*. Also, discriminant analysis and principal component analysis (PCA) shows 12 morphological variables placing *Z. katzeriana* midway between *Z. splendens* and *Z. loddigesii* ($P < 0.0002$). In *Z. splendens*, leaflet cross-sections show one layer of girder sclerenchyma below the vascular bundles, with little or no variation. In those of *Z. loddigesii*, there is a multiple layered girder sclerenchyma above and below the vascular bundle, with little or no variation. But in *Z. katzeriana* there is greater variation in the presence of girder sclerenchyma from as little as one to two layers below the vascular bundle in some individuals, and above and below the vascular bundle in others. PCA and discriminant analyses for 11 anatomical variables showed significant difference for Mahalanobis squared distance ($P < 0.001$) and for Wilk's lambda ($P < 0.001$). Also, ANOVA on stomatal index values was highly significant ($P < 0.001$)

placing *Z. katzeriana* as intermediate between *Z. splendens* and *Z. loddigesii* though *Z. splendens* and *Z. katzeriana* are closest probably due to introgression (Pérez-Farrera et al. 2016 in Fig. 7, Table 2.)

Ovule development

Building on the classic works of Chamberlain, Sánchez-Tinoco et al. (2018) described the female reproductive cycles in *Ceratozamia mexicana* and *Zamia furfuracea*. She described the structural components and the ergastic substances contained in the seed cover and the vegetative gametophyte (Sánchez-Tinoco et al., 2007). Revisiting the ontogeny of these structures, as well as the development of

Species	Mean Stomatal Index
<i>Zamia splendens</i>	6.72
<i>Zamia katzeriana</i>	6.90
<i>Zamia loddigesii</i>	9.35
ANOVA	P < 0.0001

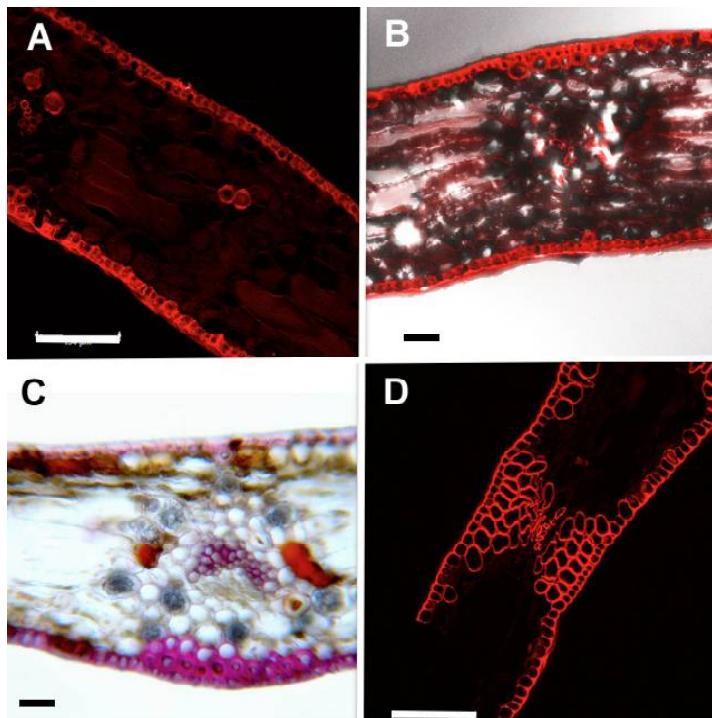


Figure 7. *Zamia katzeriana* complex (TS leaflets): A, B and D. Confocal microscopy images enhancing lignified tissues. A. *Z. splendens* with girder sclerenchyma absent, bar = 134 µm. B. Composite confocal and bright field image of *Z. katzeriana* showing one layer of girder sclerenchyma. C. Bright field image of *Z. katzeriana* showing two layers of girder sclerenchyma associated with the vascular bundle, stain safranine O and fast Green FCF, bar = 50 µm. D. *Z. loddigesii* showing ample girder sclerenchyma on both sides of vascular bundle, bar = 134 µm.

the ovule, has revealed some aspects of its anatomy such as size, number and position of the archegonial neck cells (Sánchez-Tinoco et al., 2018).

CONCLUSIONS

It can be seen that an integrated approach, including traditional techniques of anatomy and modern molecular techniques may clarify vexing problems in cycad systematics and evolution. This is a call to revisit older traditional techniques to cover the gaps left by researchers long gone and to integrate these findings with more modern approaches. It is sad to see the reduction or abandonment of alpha taxonomy, plant anatomy and morphology from college curricula to make space for the modern approaches. This will be regrettable in the near future when there will be a call back to these methods, but regrettably the older taxonomists and anatomists will be either retired or simply passed on.

LITERATURE CITED

- Barone-Lumaga, M., Coiro, M., Truernit, E., Erdei, B., and P. De Luca. 2015. Epidermal micromorphology in *Dioon*: did volcanism constrain *Dioon* evolution? *Botanical Journal of the Linnean Society* 179: 236–254.
- Berlyn, G. P., and J. P. Miksche. 1976. Botanical microtechnique and cytochemistry. The Iowa State University Press, Ames.
- Calonje, M., Stevenson, D. W., and R. Osborne. 2020. The World List of Cycads, online edition [Internet]. 2013-2020. [cited 2020 September 23]. Available from: <http://www.cycadlist.org>.
- Chamberlain, C. J. 1935. Gymnosperms. Structure and Evolution. University of Chicago Press, Chicago.
- Cutler, D. F. 1978. Applied plant anatomy. Longman, London.
- González, D., and A.P. Vovides. 2012. A modification to the SCAR (Sequence Characterized Amplified Region) method provides phylogenetic insights within *Ceratozamia* (Zamiaceae). *Revista Mexicana de Biodiversidad* 83: 929–938.
- Greguss, P. 1966. The relationships of cycadales on the basis of their xylotomy, branching and leaf epidermis. *Palaeobotanist* 14: 94–101.
- Greguss, P. 1968. Xylotomy of the Living Cycads. Akadémiai Kiadó, Budapest.
- Griffith, P. 2013. An anatomist's garden. *Montgomery Botanical News* 21(1): 5.
- Gutiérrez-Ortega, J. S., Yamamoto T., Vovides, A. P., Pérez-Farrera, M. A., Martínez J. F., Molina-Freaner, F., Watano Y., and T. Kajita. 2018. Aridification as a driver of biodiversity: A case study for the cycad genus *Dioon* (Zamiaceae). *Annals of Botany* 121: 47–60.
- Johansen, D. A. 1940. Plant microtechnique. McGraw-Hill, New York.
- Locquin, M., and M. Langeron. 1985. Manual de Microscopía. (Traducido del francés).

- Ed. Labor, Barcelona, España. 373 pp.
- McCune, B., and J. Mefford. 1997. Multivariate analysis of ecology data v3.17. JPM Software. Glenden Beach, Oregon.
- Nicolalde-Morejón, F., Vovides, A. P., Stevenson, D. W., and V. Sosa. 2008. The identity of *Zamia katzeriana* and *Z. verschaffeltii* (Zamiaceae). *Brittonia* 60: 38–48. <https://doi.org/10.1007/s12228-008-9000-9>
- Pant, D. D., and D. D. Nautiyal. 1963. Cuticle and epidermis of recent Cycadales leaves sporangia and seeds. *Senckenbergiana Biologica* 44: 257–347.
- Pérez-Farrera, M. A., Vovides, A. P., and S. Avendaño. 2014. Morphology and leaflet anatomy of the *Ceratozamia norstogii* (Zamiaceae: Cycadales) species complex in Mexico with comments on relationships and speciation. *International Journal of Plant Sciences* 175: 110–121.
- Pérez-Farrera, M. A., Vovides, A. P., Ruiz-Castillejos, C., Galicia, S., Cibrián-Jaramillo, A., and S. López. 2016. Anatomy and morphology suggest a hybrid origin of *Zamia katzeriana* (Zamiaceae). *Phytotaxa* 270: 161–181.
- Purvis, M. J., Collier, D. C., and D. Walls. 1966. Laboratory Techniques in Botany. Butterworths, London.
- Sánchez-Tinoco, M. Y., Vovides, A. P., and E. M. Engleman. 2018. Anatomical description of the cytoplasmic connections between the central cell and transfer cells in *Ceratozamia mexicana* Brongn., and *Zamia furfuracea* L.f. (Cycadales). *Memoirs of the New York Botanical Garden* 117: 33–42.
- Sánchez-Tinoco, M. Y., Engleman, E. M., and S. D. Koch. 2007. The vascularization of the seed of *Ceratozamia mexicana* (Zamiaceae). *Memoirs of the New York Botanical Garden* 97: 223–235.
- Sass, J. E. 1958. Botanical microtechnique. Ed. 3. Iowa State University Press, Ames.
- Stevenson, D. W. 1992. A formal classification of the extant cycads. *Brittonia* 44: 220–223.
- Tang, Y., Liu, N., Liao, J. P., Xie, Z.Y., Wu, Q.G., and J.R. Chen. 2004. Systematic implications of pinna venation and pinna anatomy in Zamiaceae. *Acta Phytotaxonomica Sinica* 42: 365–374.
- Vovides, A. P., Clugston, J. A. R., Gutiérrez-Ortega, J. S., Pérez-Farrera, M. A., Sánchez-Tinoco, M. Y., and S. Galicia. 2018. Epidermal morphology and leaflet anatomy of *Dioon* (Zamiaceae) with comments on climate and environment. *Flora* 239: 20–44.
- Vovides, A.P., and S. Galicia. 2016. G-fibers and florin ring-like structures in *Dioon* (Zamiaceae). *Botanical Sciences* 94: 263–268.
- Vovides, A. P., Stevenson, D. W., Pérez-Farrera, M. A., and S. López S, Avendaño. 2016. What is *Ceratozamia mexicana* (Zamiaceae)? *Botanical Sciences* 94(2): 419–429.
- Vovides, A. P., Avendaño, S., Pérez-Farrera, M. A., and D. W. Stevenson. 2012. What is *Ceratozamia brevifrons* (Zamiaceae)? *Brittonia* 64: 35–42.

CHAPTER 5

Eumaeus godartii butterfly: Pest friend or foe?

Alberto Sidney Taylor B.

ABSTRACT

Eumaeus godartii butterfly larvae and other growth stages similar to those of the coontie atala butterfly, have been observed to date in the Isthmus of Panama on 14 of the 17 described cycad species (*Zamia*: Zamiaceae), comprising all the known populations of Panamanian cycads. Small plants and young cones have been completely destroyed by the larvae, but larger plants and older cones have withstood the attacks. A recent study of the butterfly, from eggs to adults took 6 weeks. However, most of the time, the eggs are parasitized by an unknown predator. There is some evidence of very little or no harnessing of plant toxins by young larvae or some toxin tolerance by birds or insect predators. This could explain the low incidence of attacks of plants in the wild, most of which are sporadic. Larvae are easy to remove mechanically from plant parts. In some instances, the damage to mature cones simply free maturing seeds before natural cone disarticulation and these germinate prematurely, making possible an increase in population size.

Keywords

Coontie, *Eumaeus*, cycad, larvae, herbivory

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INTRODUCTION

Growth stages of the lycaenid butterfly *Eumaeus godartii*, the white-tipped cycadian (Warren et al. 2012) are frequently seen in most of the cycad (*Zamia*) populations of the Isthmus of Panama. These stages include eggs, different instar larvae, pupae and adult butterflies. In some cases all the stages are seen in the same cycad population albeit on different plants.

In view of the above, and having data on the spread and impact of a similar lycaenid butterfly, *Eumaeus atala* Poey, in the coontie cycad population in North America (*Zamia integrifolia* L.f.), its host cycad species (Smith et al. 1994; Minno and Emmel, 1993, Opler and Krizek, 1984), I decided to 1. Continue to research the extent of the presence and 2. The impact of *E. godartii* in all the known populations of Panamanian cycads (*Zamia*) from 1994 to the present. There is very scanty literature on the Panamanian species of *Eumaeus*, *E. godartii*, except for two relatively recent publications on the subject in two different *Zamia* populations of *Z. manicata* (Santos et al. 2016) and *Z. stevensonii* (Prado et al. 2014).

Methods

During the many survey trips to study the species of Panamanian cycads since 1994 to the present, data was taken of *E. godartii* presence, growth stages and different impacts in the cycad populations studied. This study also includes data from the impact of *E. godartii ex-situ* in the cycad garden of the University of Panama. Note: Because the presence of *E. godartii* is directly tied with its host species, exact geographical sites are not stated to protect the cycads from illegal extraction.

Results

Eumaeus godartii is well adapted to almost the whole range of the Isthmus of Panama, being found from Darien province in extreme east Panama to high peaks in extreme west Panama (Chiriquí and Bocas del Toro provinces) as stated in Fig.1(A-B) and Table 1. Fig. 1 is self explicative and Fig. 2A and 2B show large larvae of *E. godartii* consuming leaflets of *Z. elegantissima* and *Z. stevensonii* in central Panama. This behavior seems to be the same in all *Eumaeus* species in their host populations (Baggett, 1982; Culbert, 1994; Contreras-Medina et al. 2003; Landolt, 1984; Koi, 2013; Koi and Daniels, 2015; Minno et al., 2005; Opler and Krizek, 1984). Fig. 2C shows mature pupae of *E. godartii* hanging in a population of *Z. stevensonii* near Central Panama. As is the case with other *Eumaeus*, most of these form adult butterflies (Koi and Daniels, 2015). Fig. 2D shows freshly laid eggs of *E. godartii* on an ovulate cone of *Z. manicata*. Most of these eggs will not hatch, which is usual with the genus (Koi, 2013). Figs. 2E and 2F are of *E. godartii* (large larvae) and an adult butterfly respectively on leaves of *Z. nesophila* on an island in the Panamanian northeast Caribbean. Fig.2G is of an ovulate cone of *Z. cunaria* under attack by larvae of *E. godartii* on an island of north central Panama. Fig.2H shows the

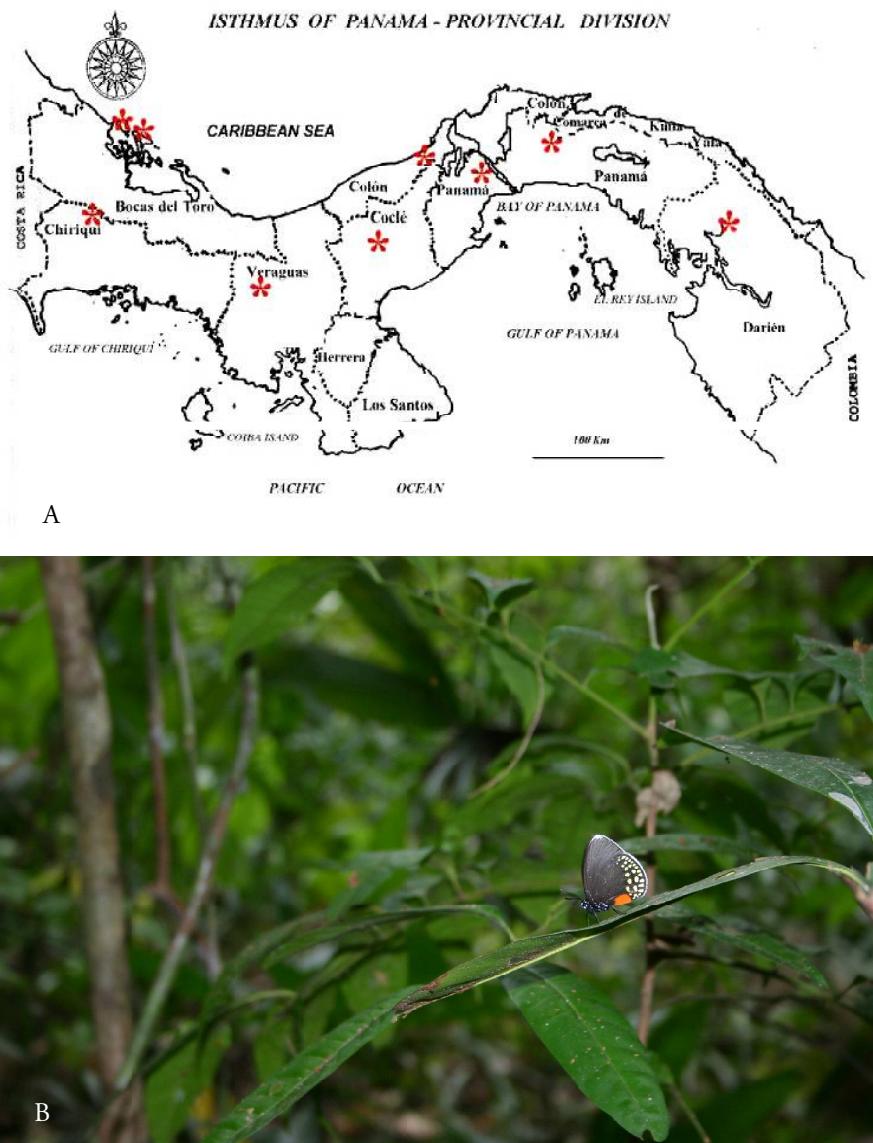


Figure 1. Presence and spread of *Eumaeus godartii* in the Isthmus of Panama: A. Sites of cycad (*Zamia*) populations with *Eumaeus godartii* in the Isthmus of Panama, B. *Eumaeus godartii* butterfly on leaf of *Zamia stevensonii* near the canal area of Central Panama.

complete destruction of an ovulate cone and a small plant of *Z. nana* by larvae of *E. godartii* in northwest Panama. Fig. 2I are eggs of *E. godartii* on an ovulate cone stalk of *Z. cunaria* near the Caribbean of north central Panama. Figs. 2J and 2K are of larvae and pupae respectively of *E. godartii* on leaflets of *Z. lindleyi* in west Panama.

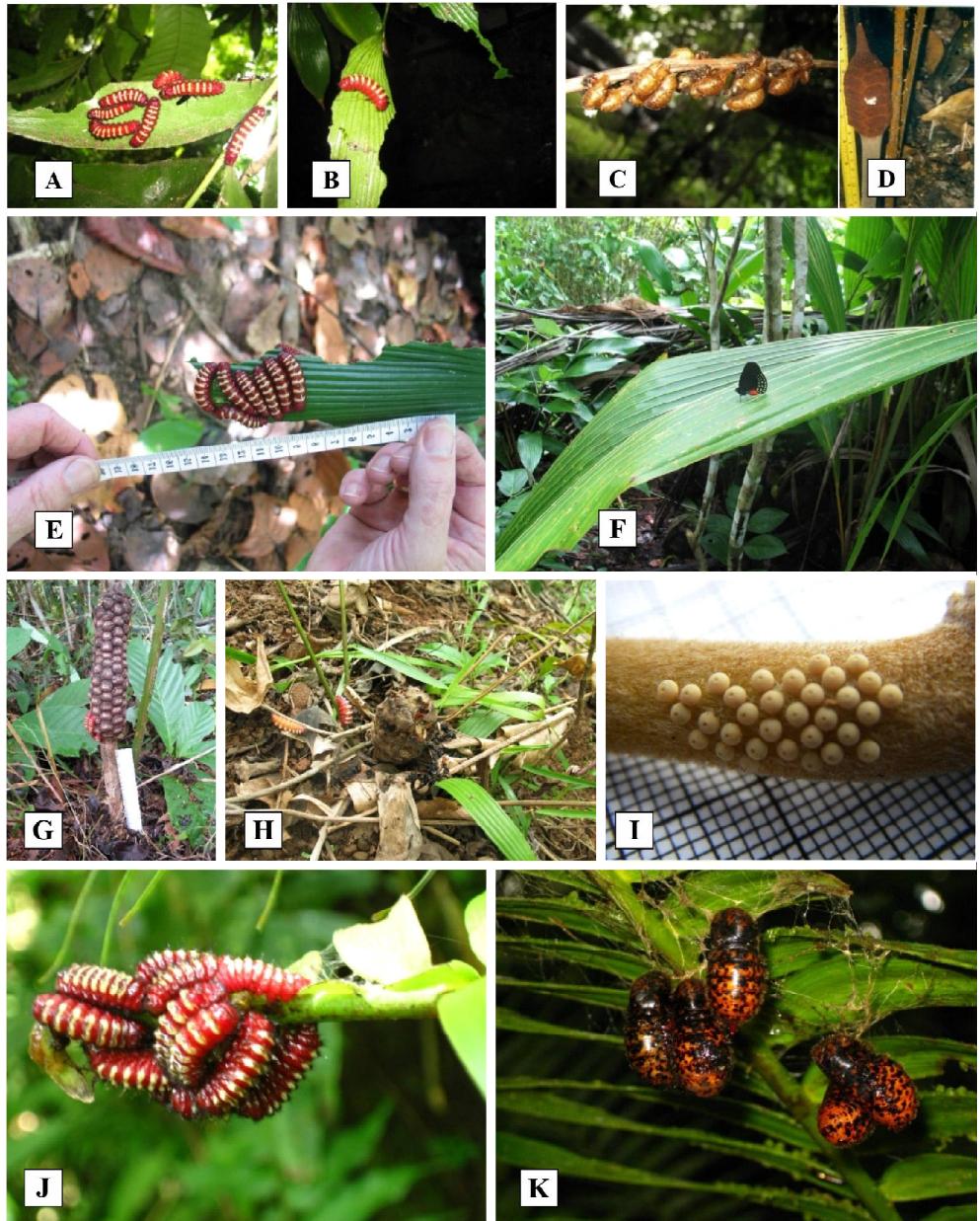


Figure 2. Presence of *Eumaeus godartii* in populations of cycad (*Zamia*) in the Isthmus of Panama. A. *Z. elegantissima*, north Panama, B. *Z. stevensonii* (Central Panama), C. Cycad Garden (Panama U), D. *Z. manicata* (east Panama), E-F. *Z. nesophila* (Island of northwest Panama), G. *Z. cunaria* (northeast Panama, near Caribbean coast), H. *Z. nana* (west central Panama), I. Cone stalk of *Z. cunaria* in north central Panama, J-K. *Z. lindleyi* (northwest Panama)

Observation of the initial development of *E. godartii ex-situ*

An *E. godartii* butterfly was observed flying to the base of a leaf of a *Z. nesophila* *ex-situ* in the cycad garden of the University of Panama and laying eggs (Fig.3A). For the following weeks, every day, the eggs were observed and photographed until the first eclosion of eggs was observed after 21 days (Figs 3B and 3C). No larvae was ever observed, probably due to some unknown predator and no other eggs hatched. This seems to be

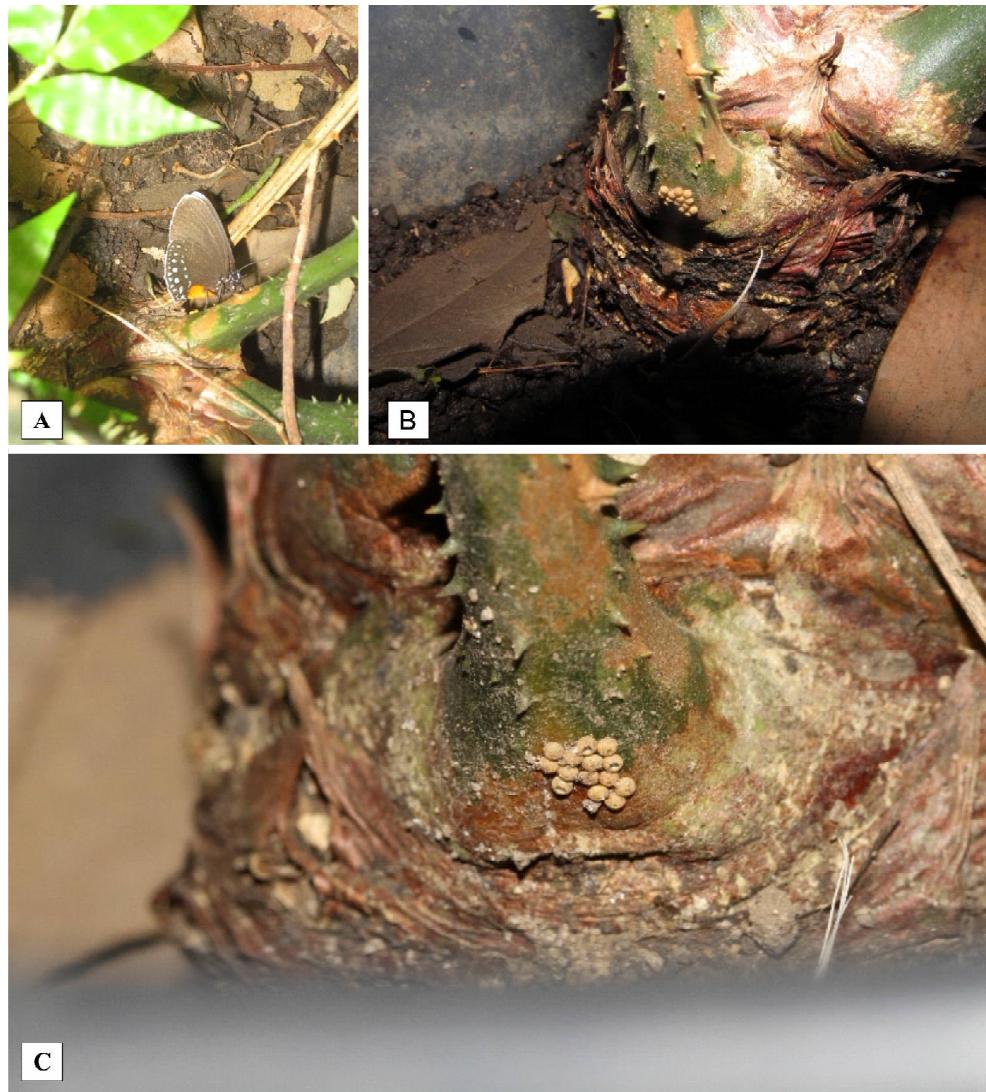


Figure 3. First developmental stages *ex-situ* of *E. godartii* on petiole of *Zamia nesophila*: A. Egg laying on the petiole, B. Set of fourteen eggs, C. First eclosion of eggs after 21 days of hatching. Three opened egg shells can be seen.

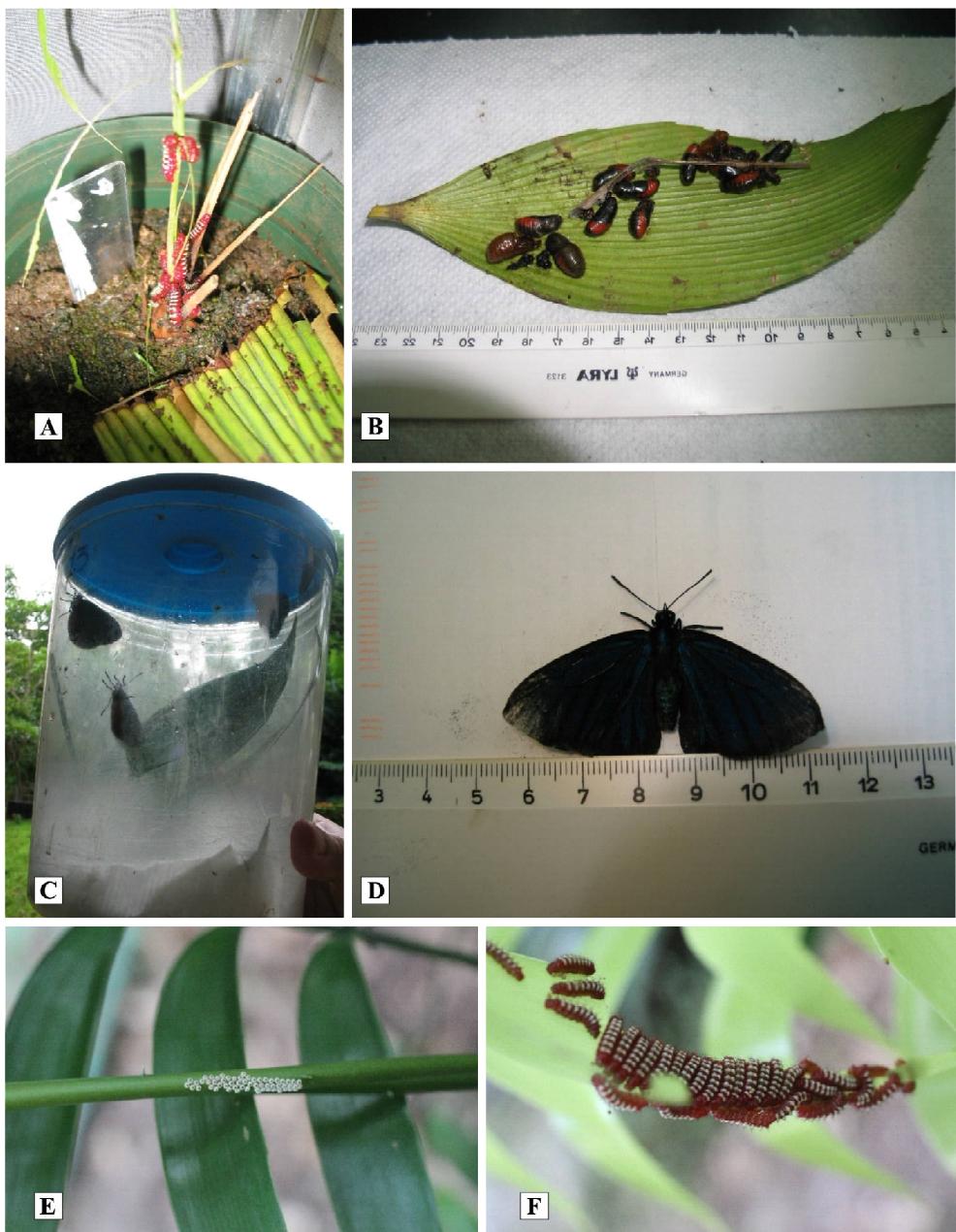


Figure 4. Developmental stages after egg laying of *Eumaeus godartii ex-situ* in a cycad garden. A. Juvenile larvae, B. Advanced pupae, C. Adult butterflies in experimental jar, D. Measurement of adult butterfly, E. Eclosed eggs, F. Large larvae.

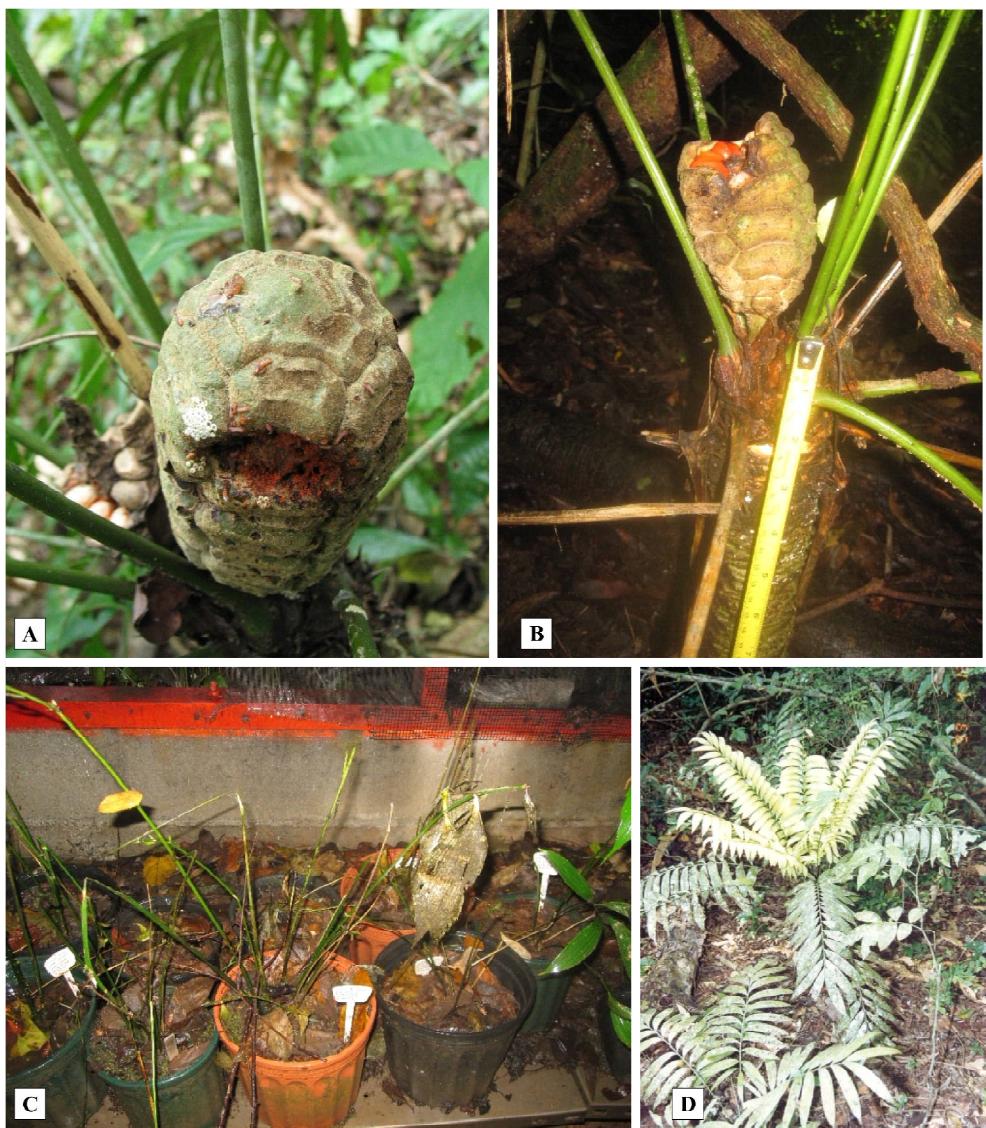


Figure 5. Variable response of cycads to *Eumaeus godartii* attacks: A. *Z. stevensonii* mature seed cone in natural population (one damaged and another with free seeds), B. *Z. stevensonii* slightly damaged mature cone in natural population, C. *Z. neurophyllidia* plantlet *ex-situ* completely damaged, D. *Z. stevensonii* in natural population completely recovered after attack.

another example of less than half of eggs of *E. godartii* and other *Eumaeus* being hatched after being laid (Koi, 2013; Santos, 2016).

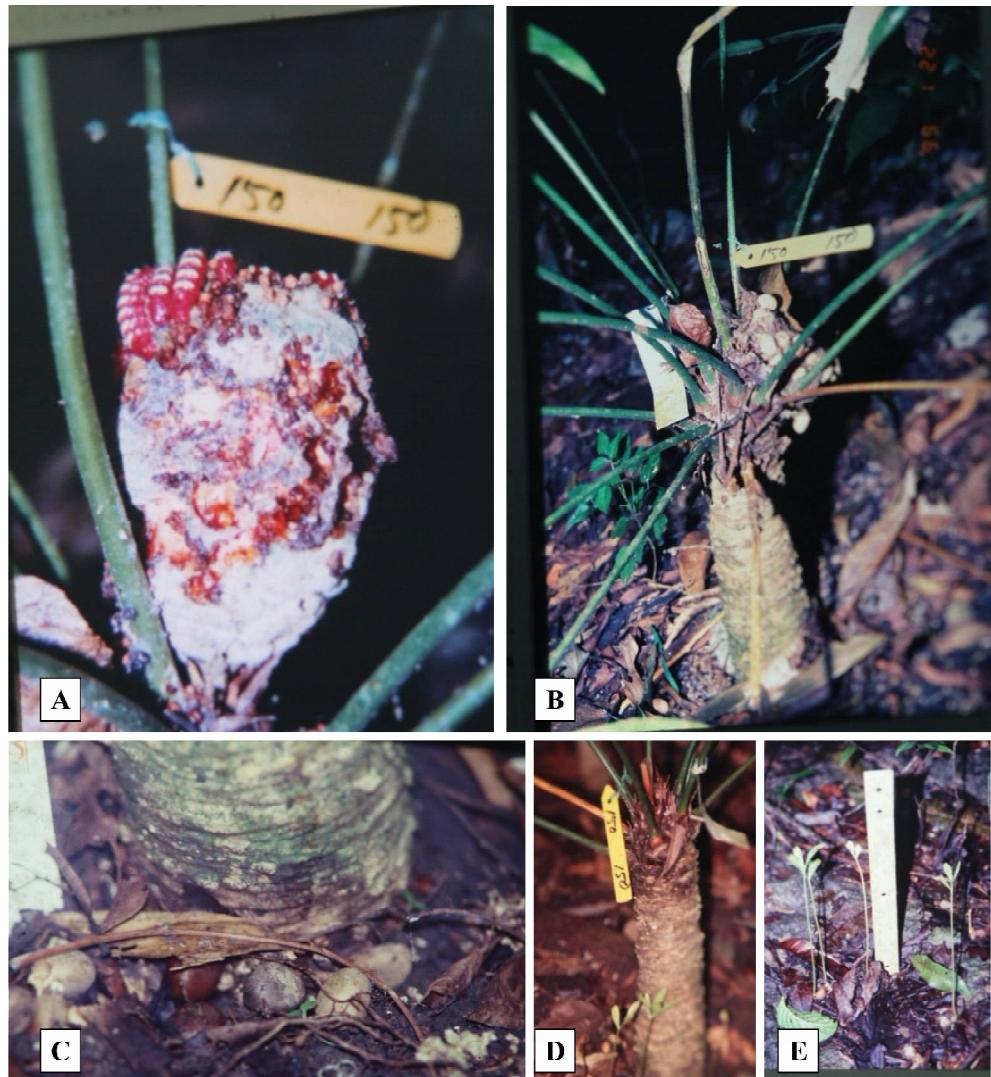


Figure 6. Result of *Zamia stevensonii* mature seed cone destruction by larvae of *Eumaeus godartii* butterfly in a natural population of the Cycad: A. Seed cone destruction, B. Healthy seeds freed from destroyed cone, C. Freed seeds at base of trunk, D. Germinating seeds at base of trunk, E. Small plants from freed seeds.

Observation of the development of *E. godartii* from Young Larvae to Adult.

Young larvae of *E. godartii* were seen on a small leaf of *Z. nesophila*, these seemingly having being hatched on previous days....the development from these small larvae to adult butterfly took 30 days (Fig.4 (A-D) which is within the time frame given for the genus in other research (Koi and Daniels, 2015). Fig.4 (E-F) shows almost 50% of larvae



Figure 7. Palatability of *Eumaeus godartii* young larvae: A. Recent larvae eclosion from eggs, B. Young larvae being attacked by the langurid *Nomutus* sp., C. Smashed larvae being consumed by green carrion flies.

grown from eclosion of eggs, probably because no predator was nearby at the time or because the larvae had sequestered enough toxins from the leaf to be immune to predatory attacks (Prado et al. 2014; Rivadeneyra-Dominguez and Rodriguez-Landa, 2014).

Table 1. Observed life cycle stages of *Eumaeus godartii* in Panama cycad populations.

Species	Life cycle: Observed (yes), Not Observed (no)
<i>Zamia cunaria</i>	yes
<i>Z. dressleri</i>	yes
<i>Z. elegantissima</i>	yes
<i>Z. fairchildiana</i>	no
<i>Z. hamannii</i>	no
<i>Z. imperialis</i>	no
<i>Z. ipetensis</i>	yes
<i>Z. manicata</i>	yes
<i>Z. nana</i>	yes
<i>Z. nesophila</i>	yes
<i>Z. neurophyllidia</i>	no
<i>Z. obliqua</i>	yes
<i>Z. pseudomonticola</i>	yes
<i>Z. pseudoparasitica</i>	no
<i>Z. skinneri</i>	no
<i>Z. stevensonii</i>	yes

Various responses of Cycads (*Zamia*) to *E. godartii* attack in a population within the Panama Canal Area

Figs. 5 and 6 show leaf and ovulate cones destruction by larvae of *E. godartii* in a natural population of *Z. stevensonii* and leaf destruction of plantlets of *Z. neurophyllidia* potted *ex-situ* (Fig. 5C). However, in every case, the plants withstood the attacks, either by growing new leaf flushes (Fig. 5D) or by having early seed germination, the seeds having been freed when the cone and sarcotesta of seeds were destroyed by *E. godartii* larvae (Fig. 6 D and E).

Predatory activity against *E. godartii* larvae

Fig.7A shows small newly hatched *E. godartii* on a dry leaflet of *Z. stevensonii* in the natural population of the cycad around the Panama Canal Area. As expected, few larvae are hatched but even when mature, can be preyed on by other insects such as *Nomutus* sp. (Fig.7B) on *Z. elegantissima* leaflet in north Panama and smashed larvae are seen being avidly consumed by green carrion flies in an *ex-situ* plant of *Z. stevensonii* in the cycad garden at the University of Panama. Obviously, the very small larvae do not have so much toxic principles, such as cycasin and or methylazoxymethanol (Rivadeneyra-Dominguez and Rodríguez-Landa 2014). This reaction of cycad by early seed germination after being attacked by larvae of *E. godartii* in natural populations, is also seen in *Z. nana* and *Z. manicata*. Although there is an ample literature on toxins in cycads (Nash et al. 1992; Norstog and Nichols, 1997; Rothschild et al. 1986; Vega and Bell, 1967; Yagi 2004) almost nothing has been done in searching for the toxins in the leaves and seeds of all the 17 species that have been described for the Isthmus of Panama. This is a necessary homework for us to truly grasp the extent of herbivory of *E. godartii* and its meaning in all the population of Panamanian cycads.

CONCLUSION

The presence of growth stages of the white-tipped cycadian, *Eumaeus godartii* has been observed in populations of 14 of the 17 described species of *Zamia* in Panama.

Although not as yet sighted, it probably is found in every population of isthmian cycads (*Zamia*) from the Colombian border to the east to that of Costa Rica to the west. Exceptions being the central provinces of Herrera and Los Santos in south central Panama, due, in large measure, to environmental erosion for agriculture and pasture for animal husbandry. Sturdy plants of more than a foot in length can withstand attack of *E. godartii* larvae by new leaf flushes and/or early germination of freed seeds from mature ovulate cones destroyed by the larvae. Future work on extraction and analysis of toxins in all isthmian zamias is warranted and, because the attacks of the larvae are quite sporadic with no long term damage to the cycad population, at the moment there is no need to protect the population from this herbivore. We conclude that when *E. godartii* is very abundant in a population of cycads, the larvae destroy leaflets, small plants and immature cones and may be considered a veritable foe. Conversely, when the attacks end in new leaf flushes and early seed germination, *E. godartii* can be considered a friend.

ACKNOWLEDGEMENTS

I acknowledge the support by the administration of the University of Panama (President, Vice-President for Research and Graduate Studies, and various deans of the Faculty of Natural and Exact Sciences and Technology) of the author as Research Emeritus Professor and also for infrastructure when and where possible (partial support for a cycad garden and survey trips to many cycad populations with presence of *E. godartii*). I am also grateful for the support of the Ministry of the Environment (Ministerio de Ambiente, in the original Spanish) for official permits to survey cycad populations, even within many of the so-called “original people homelands” and national parks. My thanks to Professor Alonso Santos Murgas of the Invertebrate Zoology Laboratory of the University of Panama for his great help with the cycad *Z. manicata* and its herbivore partner *E. godartii* in the Darién Province of the Isthmus. Thanks are also due to Professor Roberto Cambra, also of the invertebrate office of the University of Panama for help in the identification of *Nomotus*, a predator of *E. godartii*. The following are also acknowledged for the many cooperative attention given me during the long research time undertaken: Dr. Dora Quirós of the zoology department of the University of Panama, ex student José Jiménez, who accompanied the author on many of his trips to study *E. godartii* in natural cycad populations, to Professor Jorge Mendieta Bonilla who has taken over the care of the cycad garden where many of the impacts of *E. godartii* was observed while attacking cycad species *ex-situ*. My thanks also goes to Professor Emeritus Diomedes Quintero for helping with the correct spelling of the original name of *E. godartii*, and to former students Eduardo Sánchez, who took a long research trip in northern Panama, obtaining data of coning and *E. godartii* attacks in a *Z. elegantissima* population and to Cycad biologist Michael Calonje of Montgomery Botanical Center his outstanding help and many of his observations during research trips together in northern Panama. Lastly, but not least, I am forever indebted to the staunch support of my wife, Isabel Débora Herrera Antaneda, during all my research wanderings, this one included.

LITERATURE CITED

- Baggett, H. D. 1982. Florida atala. In R. Franz [ed.]. Rare and endangered Biota of Florida, Vol. Invertebrates, 75–77. University Presses of Florida, Gainsville (FL).
- Contreras-Medina, R., Ruiz-Jiménez, C. A., and I. Luna Vega. 2003. Caterpillars of *Eumaeus childrenae* (Lepidoptera: Lycaenidae) feeding on two species of cycads (zamiaceae) in the Huasteca region, Mexico. *Revista de Biología Tropical* 51(1): 201–204.
- Culbert, D. F. 1994. An IPM approach for the control of atala (*Eumaeus atala*) on Florida coonties (*Zamia floridana*). *Proceedings of the Florida State Horticultural Society* 107: 427–430.
- Koi, S. E. 2013. Ecology and conservation of *Eumaeus atala* Poey 1832 (Lepidoptera: Lycaenidae). Master's thesis. University of Florida. 295 p.
- Koi, S., and J. Daniels. 2015. New and revised life history of the Florida hairstreak *Eumaeus atala* (Lepidoptera: Lycaenidae) with notes on its current conservation status. *Florida Entomologist* 98(4): 1134–1147.
- Landolt PJ. 1984. The Florida atala butterfly, *Eumaeus atala floridana* Rueber (Lepidoptera: Lycaenidae), in Dade County, Florida. *Florida Entomologist* 67: 570–571
- Minno, M. C., and T. C. Emmel. 1993. Butterflies of the Florida Keys. Scientific Publishers, Gainesville, Florida
- Minno, M. C., Butler, J. F., and D. W. Hall. 2005. Florida butterfly caterpillars and their host plants. University Press of Florida. Gainesville, Florida. 360 pp.
- Nash, R. J., Bell, E. A., and P. R. Ackery. 1992. The protective role of cycasin in cycad-feeding lepidoptera. *Phytochemistry* 31: 1955–1957
- Norstog, K. J., and T. J. Nicholls. 1997. The biology of the cycads. Cornell University Press, Ithaca and London. 363 p.
- Opler, P. A., and G. O. Krizek. 1984. Butterflies East of the Great Plains: An Illustrated Natural History. The Johns Hopkins University Press. Baltimore, MD. 294 p.
- Prado, A., Sierra, A. Windsor, D., and J. C. Bede. 2014. Leaf traits and herbivory levels in a tropical gymnosperm, *Zamia stevensonii* (Zamiaceae). *American Journal of Botany* 101(3): 437–47.
- Rivadeneyra-Domínguez, E., and J. F. Rodríguez-Landa. 2014. Las cícadas y su relación con algunas enfermedades neurodegenerativas. *Neurología* 29: 517–522.
- Rothschild, M., Nash, R. J., and E. A. Bell. 1986. Cycasin in the endangered butterfly *Eumaeus atala*. *Phytochemistry* 25: 1853
- Santos, A., and J. C. Ábrego. 2016. Historia natural de *Eumaeus godartii* (Lycaenidae: Lepidoptera) y herbivoría en *Zamia manicata*. *Revista Colón, Ciencias, Tecnología y Negocios* 3(1): 36–48.

- Smith, D. S., Miller, L. D., and J. Y. Miller. 1994. Butterflies of the West Indies and South Florida. University of Oxford Press. 346 pp.
- Vega, A., and E. A. Bell. 1967. α -Amino-methylaminopropionic acid, a new amino acid from seeds of *Cycas circinalis*. *Phytochemistry* 6: 759–762.
- Warren, A. D., Davis, K. J., Grishin, N. V., Pelham, J. P., and E. M. Strangeland. 2012. Interactive Listing of American Butterflies <http://www.butterfliesofamerica.com/>
- Yagi, F. 2004. Azoxyglycoside content and α -glycosidase activities in leaves of various cycads. *Phytochemistry* 65: 3243–3247.

CHAPTER 6

Taxonomic status of the *Cycas pectinata* complex

Jibankumar Singh Khuraijam & Rita Singh

ABSTRACT

The *Cycas pectinata* is a taxonomically complex, confused entity distributed naturally in Northeast India, Bhutan, Bangladesh, Nepal, Southwest China, Myanmar, Thailand and Vietnam. A detailed morphometric analysis of taxonomically distinct vegetative and reproductive structures of *Cycas* populations in India revealed differences among populations supporting their separation into two species: *Cycas pectinata* is confined to the western part of the Indo Burma Range (IBR), and to the east of the IBR, a Southeast Asian taxon which is described and illustrated here as a new species, *Cycas divyadarshani*. The new species is distinguished from *Cycas pectinata* by its long narrow microsporophylls and lack of a thickened protrusion on the adaxial surface which is prominent in *C. pectinata*. Anatomical characters and pollen structure of both the species also differ. The separation of these taxa is also supported by their association with different putative beetle pollinators.

Keywords

Cycas pectinata, *Cycas divyadarshani*, morphology, India, Southeast Asia.

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INTRODUCTION

Cycas pectinata Buch.-Ham. was described from Assam in north-eastern India and has been reported from adjoining countries, Nepal, Bangladesh, China, Myanmar, Thailand and Vietnam making it the second most widely distributed *Cycas* L. species, the first being an insular species *C. rumphii* Miq. Such vast distribution may have resulted from the expansion of distribution or migration of the genus *Cycas* during Pleistocene (Mankga et al., 2020). The genus *Cycas*, with 117 species (Calonje et al., 2020), is the most rapidly diversified clade in the cycad group (Yessoufou et al., 2017; Mankga et al., 2020). Tang (2004) suggested continental drift triggered cycad migration, theorizing that ancestral *Cycas* may have originated in southern Pangea and rode to Asia on one of the many travelling continental arks. Fossil evidence points to Asia as the origin of the genus (Hill, 1995; Xiao and Möller, 2015). The presence of *C. pectinata* in India and adjoining countries like Nepal, Bhutan and Bangladesh suggest that the localities where they occur may be the last limit of the distribution of the species with deeply pectinate megasporophylls. Yang and Merrow (1996) also pointed out that *C. pectinata* complex is comprised of *C. pectinata*, *C. siamensis* Miq. and five to seven undescribed taxa in southern Asia. Recently, Nagalingum et al. (2011) distinguished two undescribed species of *C. pectinata* complex as *C. pectinata* A and *C. pectinata* B based on their positions in the phylogeny. However, Nagalingum et al. (2011) did not include Indian plants in the study. This clearly indicates that there are still many more undescribed species within the *C. pectinata* complex.

As *Cycas* species generally dwell in warm, high rainfall, hilly regions, most of the cycad localities of South Asian and Southeast Asian countries are confined to the warm tropical forest and are endemic to areas of occurrence restricted to a few localities. The isolated and scattered, allochthonous populations adapting to different landscapes and climatic conditions might have led to parallel speciation. In the last few decades, many new species have been described from this region. Recently, Mankga et al. (2020) also suggested that *Cycas* from Indochina may have diversified and occupied its current ranges through vicariance and dispersal events.

Taxonomic history

Cycas pectinata was described by a Scottish naturalist, Francis Buchanan-Hamilton (1762–1829) from Kamrup (at that time part of Myanmar but currently within the state of Assam in India). As Buchanan-Hamilton did not cite any specimens in the protologue, De Laubenfels & Adema (1998) designated a specimen collected by Hooker in 1855 as lectotype of *C. pectinata*, a designation to be corrected to neotype as the specimen was not from the original material. Even this neotypification was invalid. In the absence of type and to maintain nomenclature stability, Khuraijam et al. (2018) proposed to conserve the name *C. pectinata* with a new type consisting of specimen collected from Kamrup (Assam), the single locality mentioned by Buchanan-Hamilton in the protologue.

The taxon here treated as *C. pectinata*, was also described by many authors based on material from the same region (Kamrup) as *C. pectinata* Griff, *Cycas jenkinsiana* Griff and *C. circinalis* var. *pectinata* (Griff.) Schuster. Griffith (1854) gave the same specific name, *C. pectinata* and *C. jenkinsiana* to plants growing in the same region but did not mention Hamilton's earlier use of the specific epithet, *C. pectinata*. Pant (2002) opined that the *C. pectinata* Buch.-Ham. has priority and *C. pectinata* Griff. is a synonym based on erroneous attribution of the specific epithet to Griffith by Kurz (1877), Thiselton-Dyer (1890) and many subsequent authors (Pant, 2002; Pant *et al.*, 1994). Pant *et al.* (1994) also pointed out that *C. pectinata* Buch.-Ham. is a distinct species and not a form of *C. circinalis* L. as claimed by Schuster (1932) or a variety of *C. siamensis* Miq. as suggested by Thiselton-Dyer (1890).

Cycas pectinata complex in India

Pant (2002) in his monumental monograph on *Cycas* considered *C. pectinata* as the least studied species among the Indian cycads. A perusal of literature revealed several reports on the occurrence of *C. pectinata* in Assam (Kanjilal and Bor, 1940; Kanjilal *et al.*, 1940; Sahni, 1990; Kar and Borthakur, 2008), Manipur (Deb, 1958; Sahni, 1990), Meghalaya (Sahni, 1990; Roy and Joshi, 2002), Mizoram, Sikkim (Hooker, 1854; Srivastava, 1993; Hajra and Verma, 1996) and Tripura (Deb, 1983). However, none of these authors have done critical taxonomic studies on the species. Interestingly, Yang and Merrow (1995) used a plant sample of *C. pectinata* from Assam, India provided by Prof. D.D. Pant of University of Allahabad (pers. comm.) in their study to suggest that *C. pectinata* found in Southeast Asia is a complex species. Our study spanning more than ten years of extensive field surveys, herbarium consultation and taxonomic studies, has led us to decipher and understand the *C. pectinata* complex in India. Field expeditions to neighbouring countries Bhutan, Myanmar, Thailand and consultation of virtual specimens and literatures pertaining to *C. pectinata* complex in Thailand, Vietnam, Nepal, Bangladesh and China have resulted in the description of a new species, *Cycas divyadarshnii* from the north eastern state of Manipur, India.

Materials and methods

The present work provides a detailed study on morphology and present distribution of the *C. pectinata* complex in the Southern and Southeast Asia with special emphasis in north-eastern part of India. For taxonomic and phylogenetic interpretation, the first-hand observations and measurements were carried out (irrespective of the prior information available) on *Cycas* growing naturally in Northeast India. Morphological parameters laid down by Lindström (2004) for determining species boundaries in *Cycas* were used in the study. Morpho-anatomical and pollen morphological studies were done on materials collected from the several populations to assess the similarities and differences between and among the populations in order to assign weight to these characters to critically resolve the taxonomy of the species.

Taxonomy

Cycas pectinata Buch.-Ham. In Mem. Wern. Nat. Hist. Soc. 5: 322. 1826.

Type: India, Assam, Kamrup, 2008, Rita Singh & Khuraijam 36106 (♀)(LWG No. 102998!) [typ. cons. prop. 2653, Taxon 67(6): 1213, 2018]

Cycas circinalis L. subsp. *vera* var. *pectinata* (Griff.) Schuster. Pflanzenr. 99: 68. 1932.

Cycas pectinata Griff. Not. Pl. Asiat. 4: 10. 1854.

Type: Icones Plantarum Asiatarum 4: Plate 360, fig. 3. (1854)

Cycas jenkinsiana Griff. Not. Pl. Asiat. 4: 9-10, pl. 360, figs. 1-2, pl. 362, fig. 1. 1854.

Lectotype (designated by Lindström & Hill): India, Assam., Jenkins s.n. (K000961259!); isolect. L 0050752!

Description

Stems arborescent, tall, up to 16 m in height, branched or unbranched. Leaves dark green, 90–264 cm long, 100–230 pairs of pinnae, 6–10 mm apart, glabrous. Petiole 18–58 cm long with 11–30 spines on either side. Median pinnae 130–220 mm long, 6–12 mm wide, tapering into a minute apical spine. Pinnae base decurrent, attached to the rachis at 40°–55° on adaxial side, margins beak shaped in cross section. Emergent pinnae covered with yellow trichomes which are shed subsequently with their maturation. Male cones cylindric-ovoid having spirally arranged broad microsporophylls with upturned green apical spines covered with brownish ramenta, cone yellowish green till the dehiscence subsequently turns brownish yellow at maturity, 24–62 cm long, 12–24 cm in diameter. Microsporophyll deltoid 45–60 mm long, 20–32 mm wide at expanded distal portion; fertile zone 33–55 mm long, 18–28 mm wide; sterile apex portion deltoid, with upcurved apical spine attenuate, 20–35 mm long, green in young cones, sterile apex raised towards median adaxial side up to ¼ of the fertile zone. Megasporophylls tightly arranged in a compact and vertically compressed (laterally flattened) cone, innermost megasporophylls are mostly sterile. Megasporophylls 110–250 mm long, densely yellowish-brown silky throughout, lamina 70–150 mm wide, deeply pectinate, 14–30 lateral spines on either side, strong subulate apical spine, 22–70 mm long. Ovules 1–5, glabrous, laterally attached. Seed ovoid or obovoid, 3.4–5.2 × 3.2–4.7 cm, sarcotesta yellowish when young turns dark yellow-orange to orange red at maturity, sarcotesta 3–4 mm thick, fibrous layer present, sclerotesta stony, endotesta scaly and papery, spongy layer absent. Mature seeds platyspermic, tapering towards chalazal end, cryptocotylar.

Distribution:— India (Assam, Meghalaya, northern West Bengal, Sikkim, Bihar), Nepal, Bhutan, Bangladesh

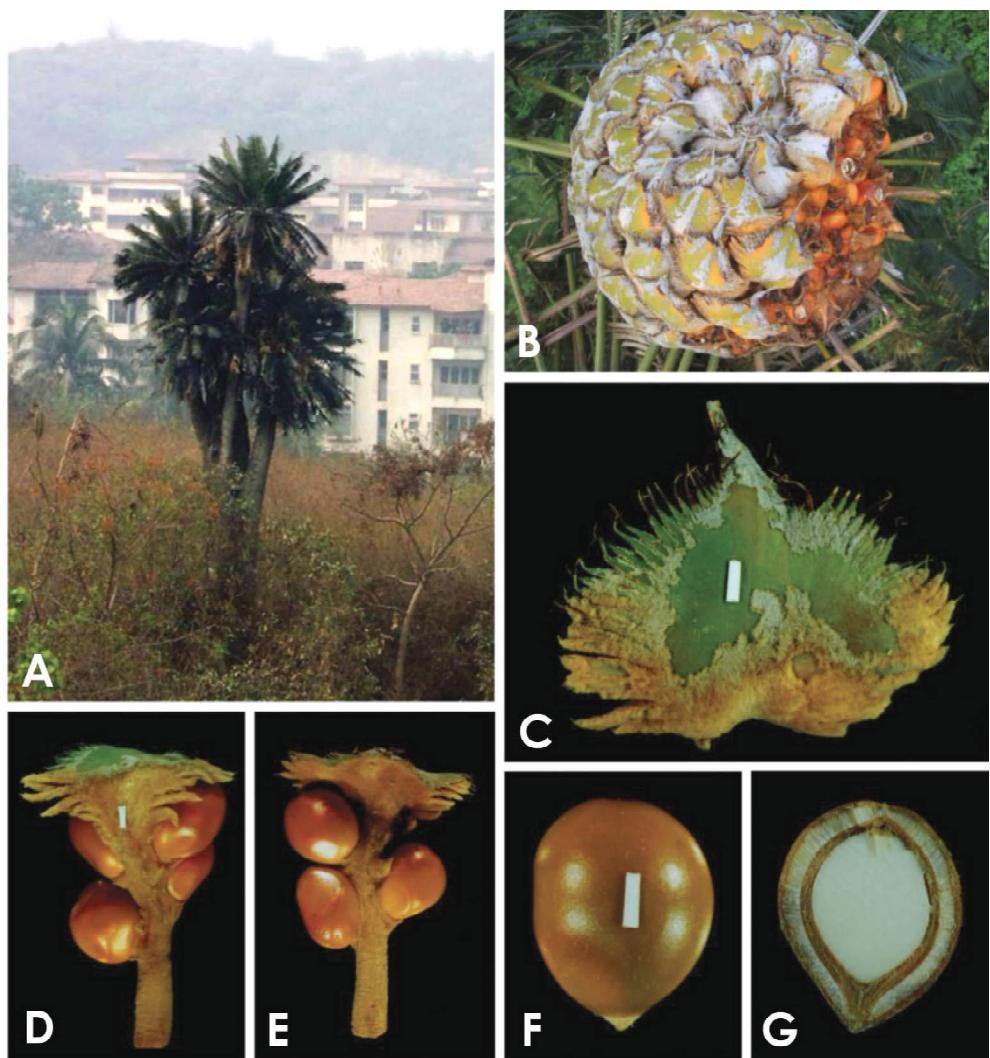


Figure 1. *Cycas pectinata* Buch.-Ham. A. Tall, robust trunk, B. Compact female cone, C. Top view of Hooded pectinate lamina of sterile apex of megasporophyll, D. Back and E. Front view of megasporophyll with mature orange coloured ovules. F. Fertilized ovule. G. Median longitudinal section of a fertilized ovule.

Habitat: — The species grow in warm deciduous forest at an elevation of 52-250 msl. In Bhutan, it grows on hill slopes along with pines sometime reaching up to maximum elevation of 1300 msl. In Nepal, it grows in Sal (*Shorea robusta*) forest at altitude 300-730 msl.

Conservation status:— Vulnerable

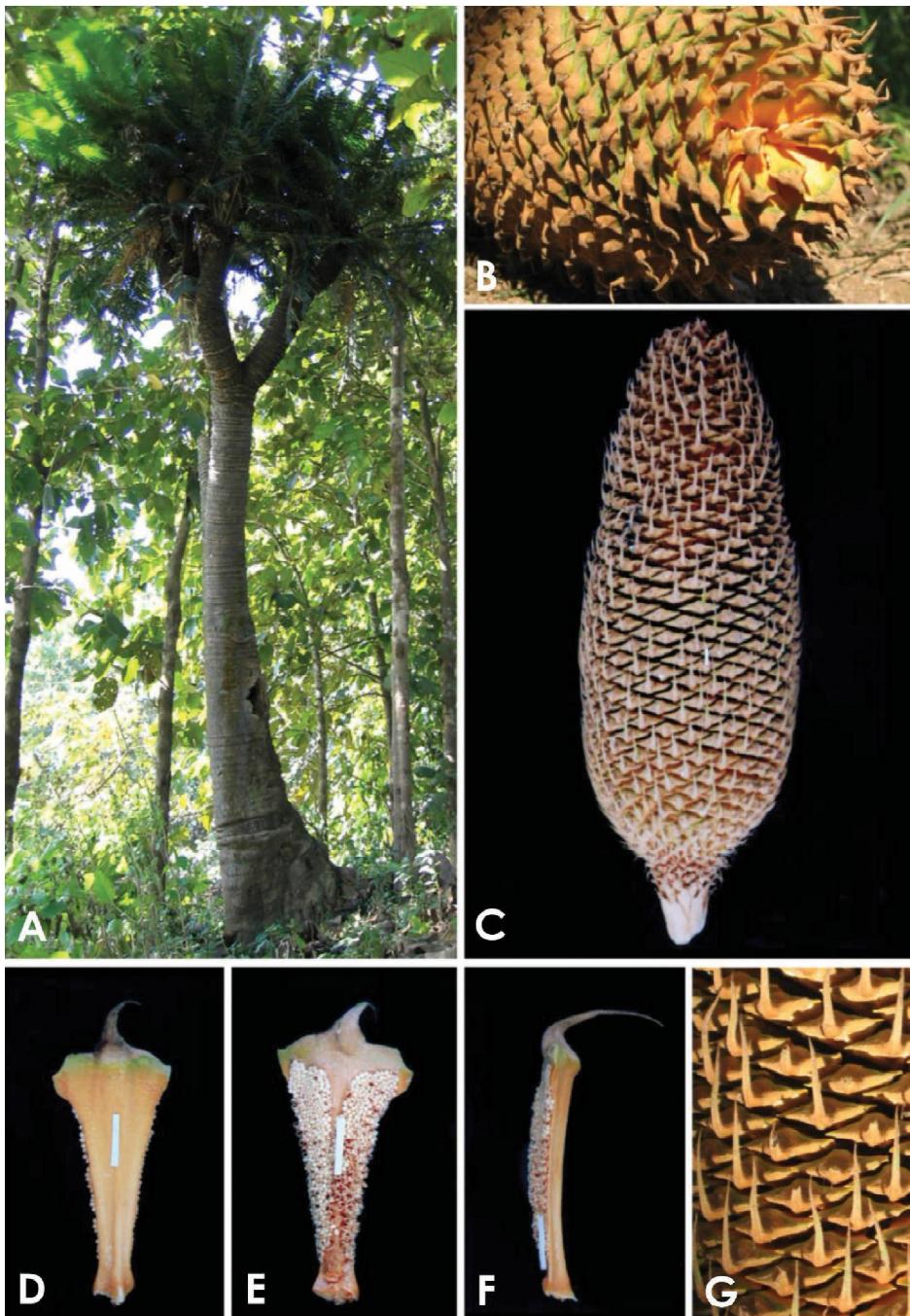


Figure 2. *Cycas pectinata* Buch.-Ham. A. Tall male plant on the bank of Brahmaputra River, B-C. Male cone, D-F. Microsporophylls, adaxial surface, abaxial surface and lateral view, G. A portion of male showing the long apical spine.

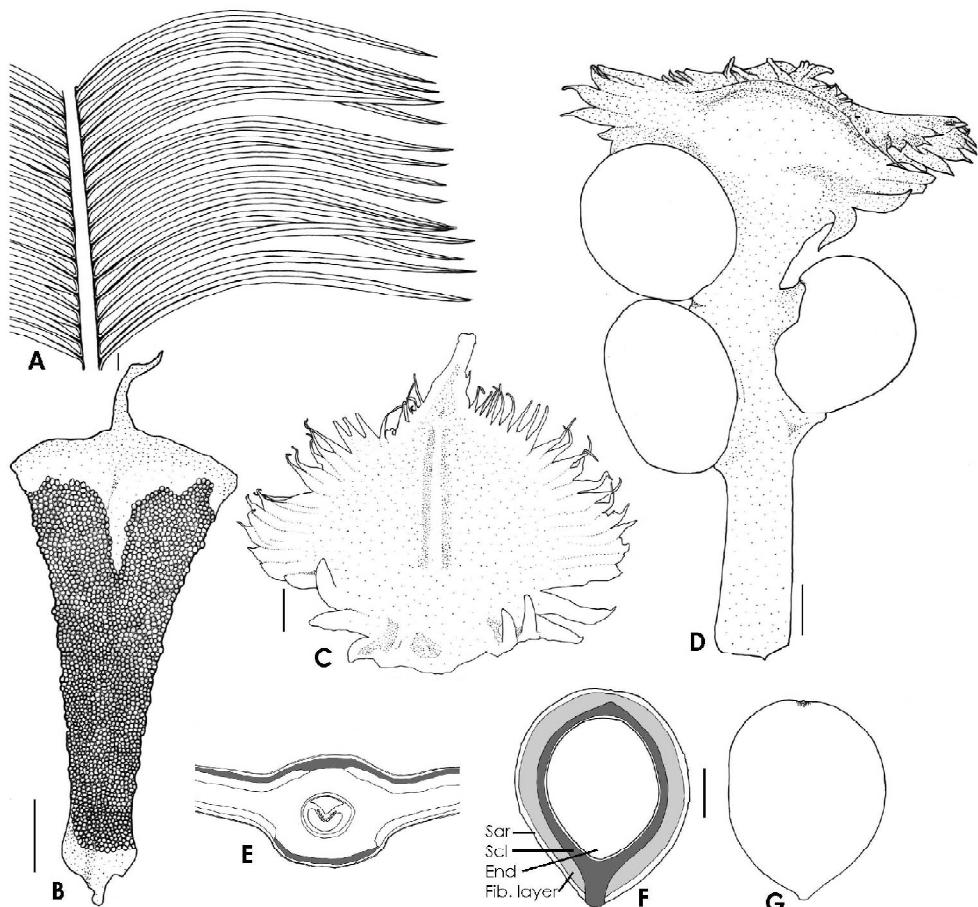


Figure 3. *Cycas pectinata* Buch.-Ham. A. A portion of leaf showing falcate leaflets, B. Microsporophylls; abaxial view with microsporangia, C. Lamina of megasporophylls showing pectinate lateral spines, D. Megasporophyll with ovoid shape ovules attached laterally, E. Section of median portion showing internal structure, F. Cross section of ovules showing prominent fibrous layer (Sar: Sarcotesta, Scl: Sclerotesta, End.: Endotesta, Fl.: Fibrous layer), G. Ovule. Scale bar: 1 cm.

Vernacular names:—*Nagphal*, *Nagchampa*, *Ak Phal* (Assam), *dieng-sia-goda* (Khasi, Meghalaya); *Khu-tha* (Tharu, Bihar); *Thakal* (Sikkim); *Jaggar* (Nepal), *Bango-shing* (Bhutan)

Specimens examined:—INDIA. Assam: Singh, Radha & Khuraijam 36101 to 36105, March 2007; Singh & Khuraijam 36106 to 36114, June. 2007; Khuraijam 36115 to 36131, Nov. 2007; Khuraijam 36132-36145, March 2009, Khuraijam 36146 to 36154, Sept. 2009; Meghalaya: Hooker & Thomson. s.n. (K001328056); Sikkim: Khuraijam 35901 to 33912, Sept, 2009; Hooker s.n. (K001328059); West Bengal: Khuraijam 3541-3548, 2009; Bihar: Haines 3983 (K001273051, K001273052) Nov. 1916; BANGLADESH.

Chittagong: Hooker & Thompson 595 (K001273047); BHUTAN. Mongar: Balakrishnan 44604 Nov. 1965; Trashigang: Grierson & Long 2357 (K001328057, K001328058) June 1979.

Cycas divyadarshani Khurajam & Rita Singh. sp.nov., figs.4,5

Holotype: India, Manipur, Sadar Hills, Khurajam 38522 (♂) November 2007, Indraprastha University Herbarium (IPUH)

Description

Stems arborescent, cylindric, up to 10 m in height, branched or unbranched. Leaves dark green or bright green, 100–220 cm long, 100–230 pairs of pinnae, 6–10 mm apart, glabrous. Petiole 17–36 cm long with 12–22 spines on either side. Median pinnae straight to falcate, 160–230 mm long, 6–9 mm wide, tapering into a minute apical spine. Pinnae

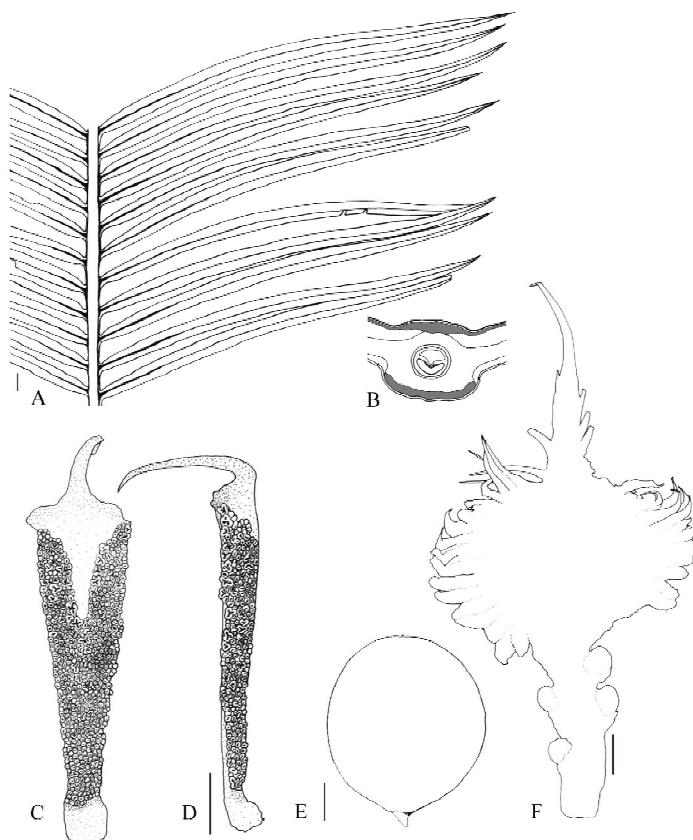


Figure 4. *Cycas divyadarshani* Khurajam & Rita Singh sp.nov. A. A portion of leaf, B. Cross section of a pinna (midrib region), C-D. Microsporophylls, E. Seed, F. Megasporophyll having long appendiculate apical spine and deeply pectinate lamina. Scale bar: 1 cm.

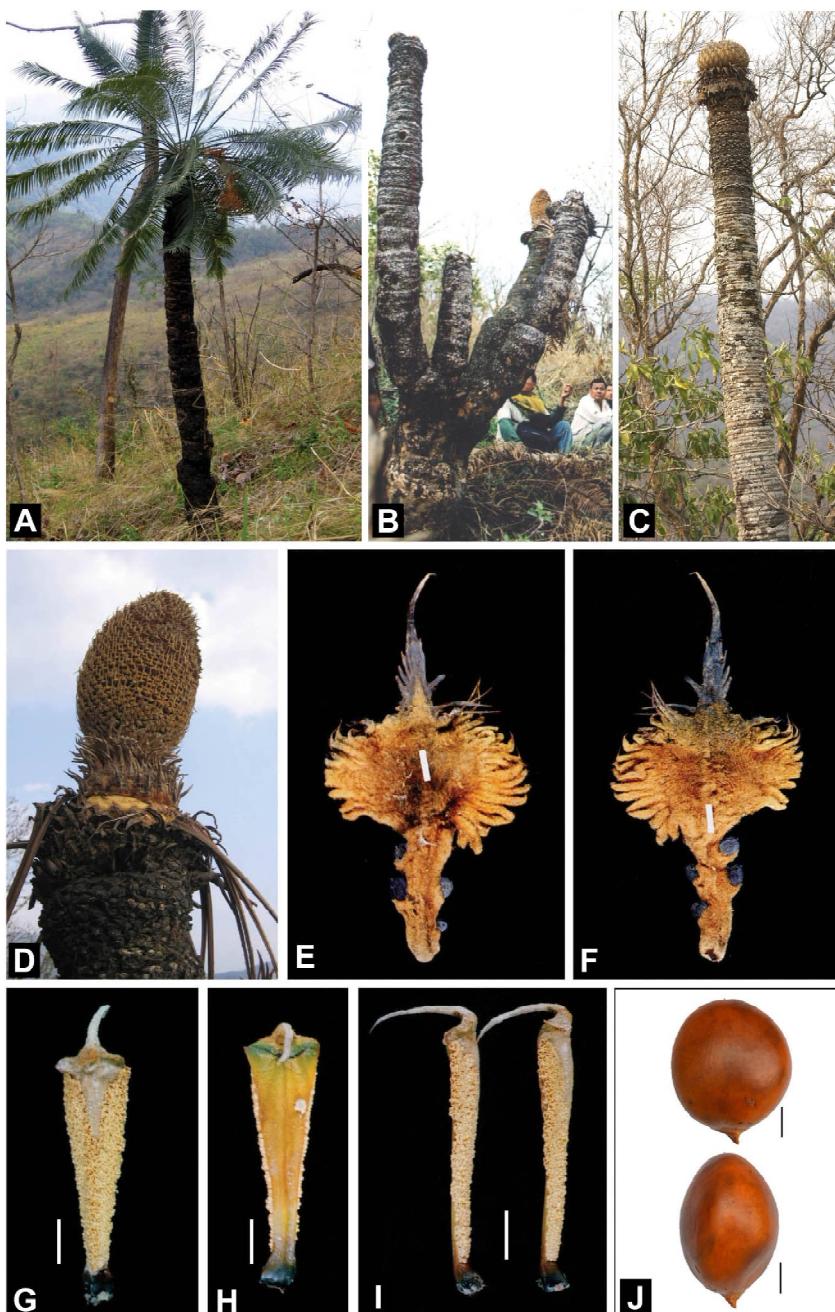


Figure 5. *Cycas divyadarshani* Khuraijam & Rita Singh sp. nov. A. A slender tree, B. A branched male plant with male cone, C. An unbranched female plant, D. A mature male cone, E-F. Megasporophyll with long apical spine and deeply pectinate woolly lamina and stalk with aborted ovules, G-I. Microplosorophylls with inflexed apical spine, J. Mature seeds. Scale bar: 1 cm.

longitudinally inserted at 50–60° to rachis, base decurrent, margin recurved or revolute in cross section. Cataphylls narrowly triangular, 3–5 × 1.2–2 cm, brown tomentose, apex soft. Male cones cylindric-ovoid, fusiform, yellow or green (young) in colour, 26–50 cm long, 15–19 cm in diameter. Microsporophyll deltoid not dorsiventrally thickened, 50–62 mm long, 17–24 mm wide at expanded distal portion; fertile zone 48–55 mm long, 15–21 mm wide; with inflexed apical spine, 20–42 mm long. sterile apex flat towards median adaxial side up to ¼ of the fertile zone. Megasporophylls compactly arranged, densely tomentose, 14–20 cm long, stalk 4–7 cm; sterile blade deltoid-ovate or suborbicular, 5–9 × 8–10 cm, margin deeply pectinate, with 23–34 lateral lobes, apical spine 3–6 cm long. Seeds 2–6, yellow when young and orange to dark brown on maturity, often obovoid, compressed, 3.6–4.6 × 3.9–4.5 cm; sclerotesta smooth, sarcotesta with thick fibrous layer, spongy layer absent. Seeds platyspermic tapering towards chalazal end, cryptocotylar.

Distribution:— India (Manipur), Myanmar, China, Thailand, Vietnam

Habitat:— In Manipur, the species grows in dry open deciduous forest at elevations ranging from 770 to 1400 msl.

Etymology:— The specific epithet is in honour of Prof. Divya Darshan Pant (1919–2001), the renowned cycadologist and paleobotanist.

Conservation status:— Vulnerable

Distinguishing characters:— large cylindrical ovoid male cone with long narrow microsporophylls with long apical spines, deeply pectinate wooly megasporophylls with appendiculate apical spine.

Vernacular name:— *Yendang* (Manipuri), *Mondang* (Burmese)

Discussion

Cycas pectinata Buch.-Ham has been considered widespread in distribution and has been frequently misidentified. It belongs to the Section Indosinenses which is characterised by deeply pectinate megasporophylls. Members of this section resemble each other and are difficult to identify in vegetative stage. The smooth trunk of mature *C. pectinata* can be confused with those of *C. clivicola* K.D. Hill. Even though, *C. pectinata* shared many similarities with other species in the section, the species has unique features that have been neglected by previous workers. Most of the available literature on the taxonomy of the species are from China, Thailand and Vietnam (Hill and Yang, 1999; Hill, 2004, 2008; Osborne *et al.*, 2007; Wang, 1996). However, the morphological information available in these references are uniform and almost similar. Literature on Indian plants is more limited and only scattered information is available in floristic survey reports and books. While revising the *Cycas* of India, Lindström and Hill (2007) also gave details about *C. pectinata* however, measurements of many of the morphological characters

given in the description are coincidentally similar or same to those described from the plants of China, Thailand and Vietnam.

C. pectinata is geographically separated from Southeast Asian *C. divyadarshani* by Barak Valley and Brahmaputra Valley. The ecological trap of *C. pectinata* between the Himalaya and Indo Burman Range can also be correlated with the beetle discovered from the *C. pectinata* of Kamrup, *Cycadophila (Strobilophila) assamensis* Skelley, Xu & Tang which is specific to *C. pectinata* of Assam (Skelley et al. 2017). Similarly, *Cycadophila (Cycadophila) yunnanensis* (Grouvelle) which is found in Southeast Asian *Cycas* was also reported from the plants of Manipur, which indicates the affinity of *C. divyadarshani* with Southeast Asian species. The long and narrow microsporophylls of *C. divyadarshani* is a distinctive character that separates the species from other members of *Cycas pectinata* complex (Figs. 6). Microsporophylls of *C. pectinata* have a thickened protrusion on the adaxial surface which is lacking in *C. divyadarshani* (Fig. 7). Osborne et al. (2007) pointed out that Vietnamese *C. pectinata* (here *C. divyadarshani*) is distinguishable from its allies in *C. pectinata* group in having very large, ovoid male cones with long narrow microsporophylls with long apical spines.

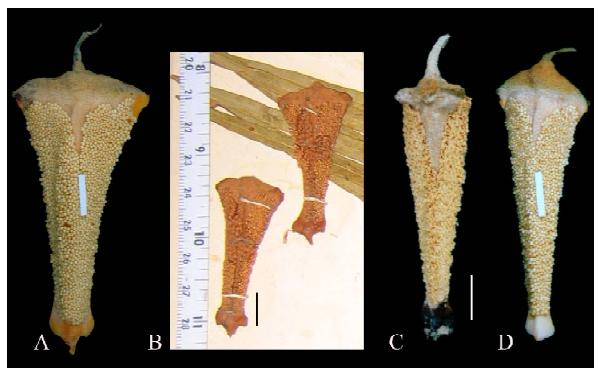


Figure 6. Microsporophylls of *Cycas pectinata* (A, B) and *C. divyadarshani* (C,D), B. A portion of Kanjilal 5146, ASSAM. Reproduced with permission from the Director of the Botanical Survey of India.

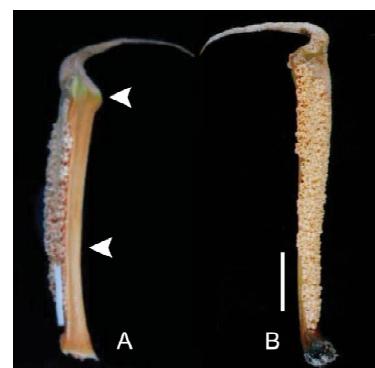


Figure 7. Lateral view of microsporophylls of *Cycas pectinata* (A) and *C. divyadarshani* (B)

Anatomical characters of leaflets/pinnae of both the species are of taxonomic significance. Like all members of *C. pectinata* group, mucilage canals below or adjacent to the vascular bundle are conspicuously absent in both the species. Idioblasts are uniformly distributed in the midrib region in *C. pectinata* however, in *C. divyadarshani* they are less and irregularly scattered. Lamina straight in *C. pectinata* and slightly revolute in *C. divyadarshani* with beak shaped margin in cross section (Fig. 8).

In epidermal peel of pinnae of these two species, the epidermal cells on the adaxial surface are arranged in irregular profiles which are longer than broad, usually each profile has larger cells in the middle and smaller ones either at both the ends or at one end. In

C. pectinata, the pits are more or less circular or oval. *C. divyadarshani* has circular pits and are scattered and almost crowded on the surface of the epidermal wall and also arranged near the anticlinal walls. On abaxial side of the pinnae, epidermal cells at the laminar region are more sinuous compared to the adaxial epidermis. Both the adaxial and abaxial epidermis has one-two celled hair bases. Pinnae in both species are hypostomatic. Guard cells are either one- or two-celled sunken in *C. pectinata* but is one-celled deep in *C. divyadarshani* with characteristic polar and lateral lamellae.

Table 1. Micromorphological details of pinnae of *Cycas pectinata* and *Cycas divyadarshani*.

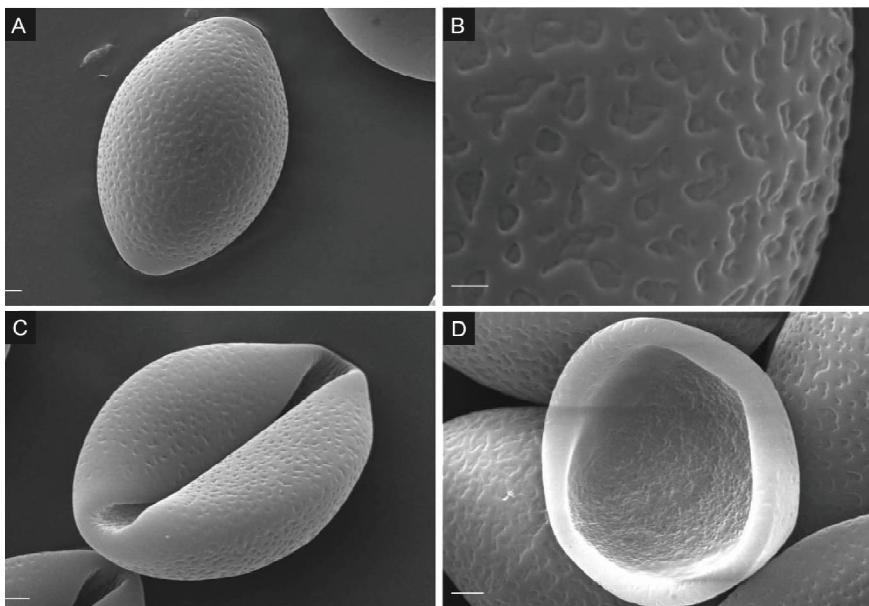
Characters	<i>Cycas pectinata</i>	<i>Cycas divyadarshani</i>
Palisade cells size in μm (adaxial surface)	$78-100 \times 13-17$	$130-164 \times 13-21$
Shape of vascular bundle	Elliptic to spherical	Elliptic
Stomatal index	6.7-7.4	8
Guard cells size (μm)	48.5×24	49×21.5



Figure 8. T.S. of a median pinna ($\times 50$). A. *Cycas pectinata* Buch.-Ham. B. *Cycas divyadarshani* Khuraijam & Rita Singh sp.nov.

Pollen grains of the species of *Cycas* are boat shaped, monocolpate, bilaterally symmetrical, anisopolar having a distal colpus and range from widely elliptical or subcircular or subprolate (Agashe, 2006). The ornamentation ranges from fossulate to foveolate. Exine ornamentation is more prominent towards the proximal surface and is less ornamented towards the brim between the two surfaces. The distal side is totally devoid of exine. Taxonomically, the pollen morphology can be used to identify geographical groups of *Cycas* and infrageneric taxonomic relationships. Pollens of *C. pectinata* and *C. divyadarshani* are ellipsoidal (boat shaped), monosulcate and bilaterally symmetrical. Pollens of *C. pectinata* are usually broadly elliptic ($24.8 \times 21 \mu\text{m}$) while those of *C. divyadarshani* are elliptic ($25.2 \times 20.2 \mu\text{m}$). Proximal surface convex and exine foveolate. Exine of distal surface of oblate pollen grain has fossulate surface. Enlarged view of proximal surface revealed coarsely faveolate exine with bigger cavity in *C. pectinata* compared to *C. divyadarshani*.

Cycas pectinata



Cycas divyadarshani

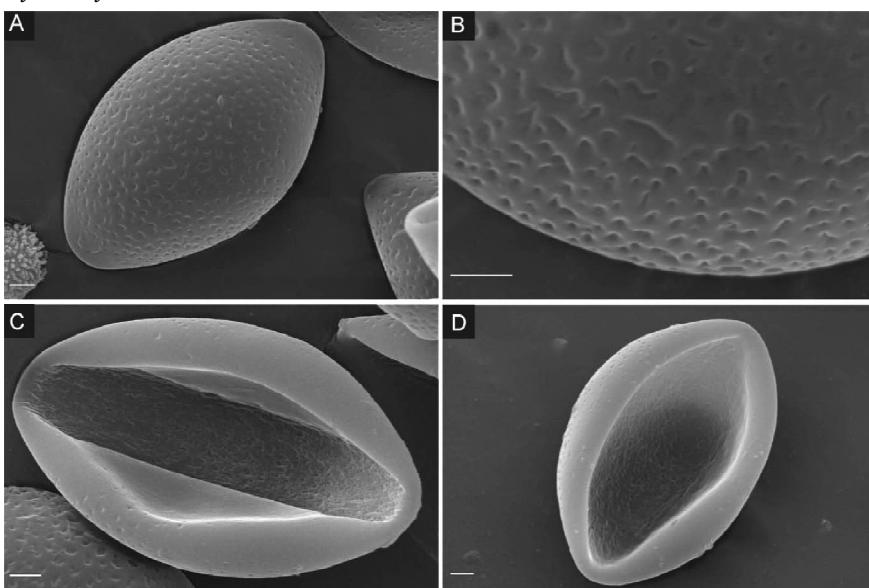


Figure 9. SEM micrograph of pollen grain (*Cycas pectinata* Buch.-Ham. and *Cycas divyadarshani* Khuraijam & Rita Singh *sp.nov*). A. Proximal view (scale = 2 μ m), B. Enlarged portion of proximal surface showing foveolate to irregular reticulate exine sculpturing (scale = 2 μ m), C. Distal view showing colpus (scale = 1 μ m), D. Enlarged portion of distal surface showing colpus (scale = 2 μ m).

***Cycas pectinata* complex migration route**

Diversification of *Cycas* in Southeast Asia and Northeast India may have resulted from the ecological traps and geographical barriers. The Northeast India lies at the easternmost part of India stretching from the Eastern Himalayas to the sub-Himalayan region bordering Bangladesh towards its southwest and Myanmar in the southeast. The region was created 40 million years ago when the Indian subcontinent collide with the Asian landmass to form the earth's youngest mountain range (Favre et al., 2015). Tectonically the Himalayan extension of Northeast India comprises of two main regions a) the Himalayan mountain ranges in the north and a) the Indo Burman Range in the east (Westerweel et al., 2019). The states of Sikkim and Arunachal Pradesh along with the neighbouring country Bhutan form the Eastern Himalayas mountain belt. Foredeep Folded Belt in the Indo Burman Range (IBR) comprises the low-lying hills of Nagaland, Manipur, Mizoram and Tripura. The physiography of the Northeast comprises of four main regions: a) the Himalayan mountain belt in the North, b) the Indo Burman Range in the east, c) Shillong Massif Plateau in the south and c) the Brahmaputra Valley forming the extensive Assam plains between East Himalayas and Shillong Plateau and Indo Burman Range. The periodic orogenic events in the region led to physiographic and environmental changes and served as key drivers of the newly evolving ecosystems resulting in geographical isolation of taxa, vicariance, and evolutionary divergence of life forms (Pandit, 2017; Manish and Pandit, 2018). As the region lies at the confluence of Indo Malayan, Indo Chinese, and Indian biogeographical realms, the region experiences a predominantly humid sub-tropical climate with hot, humid summers, severe monsoons and mild winters. Owing to unique land formations and climatic condition, the region is very rich in biodiversity and harbours a great number of endemic species both flora and fauna (Tiwari et al., 2017). The region is centre of diversity of many species. Northeast India has the highest diversity of *Citrus*, *Musa* and has been regarded as centre of diversity of these genera (Gogoi and Häkkinen, 2013; Govind and Yadav, 1999). The region comes under major migration route of mammals like Rhinoceros, Cats, Cervids which had vast distribution in the past and now confined to few areas and become endemic and even some have become extinct (Tougard, 2001). Interestingly, distribution of *Cycas* in Southeast Asia and Himalayan region have apparently similar migration route. It seems the species in Section Indosinenses diversified in Yunnan Province in China and Shan Province of Myanmar, and followed multiple routes to enter a) Himalayan and sub-himalayan region after crossing Indo Burman Range, b) towards southern Myanmar and Thailand, and c) Vietnam (Fig. 10). Presence of plants allied to *C. divyadarshani*, *C. siamensis* and *C. clivicola* in Myanmar clearly indicate the potential migration route of the Indosinenses through Myanmar into Indian subcontinent and Thailand. Xiao and Möller (2015) and Mankga et al. (2020) proposed potential colonization routes of the genus *Cycas* from China and Indochina region to Malay archipelagos and then diversification to Africa and Australia. However, both the studies omitted colonization route to Myanmar and Indian sub-continent.

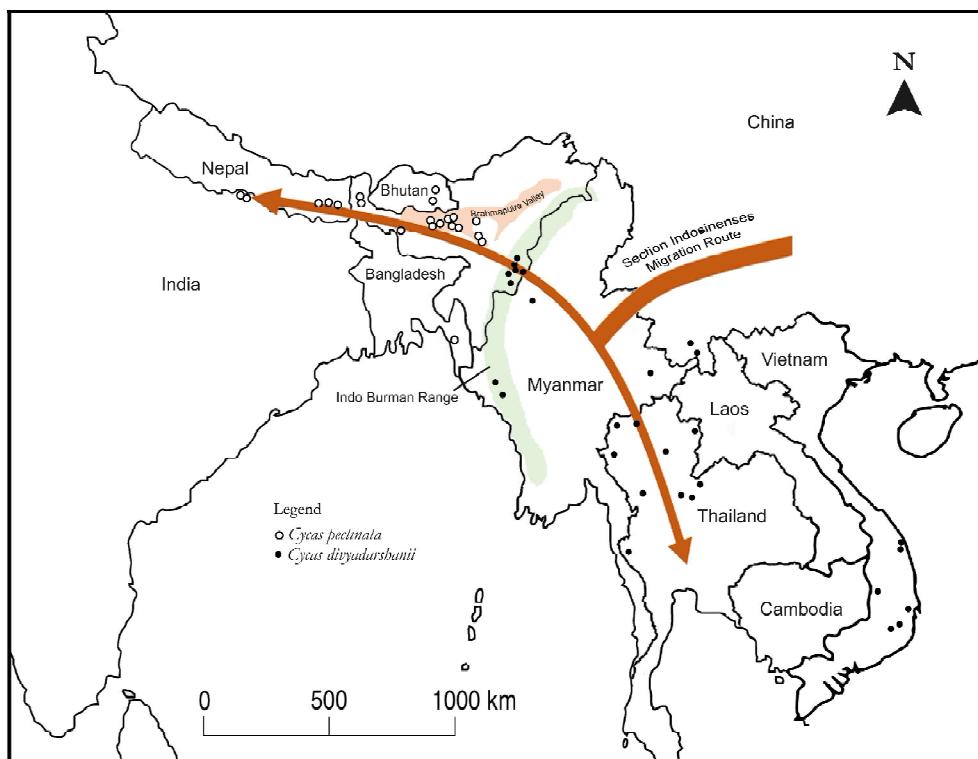


Figure 10. Distribution of *Cycas pectinata* Buch.-Ham. and *Cycas divyadarshani* Khuraijam & Rita Singh sp.nov, with probable migration route of members of Section Indosinenses in South Asia and Southeast Asia.

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LITERATURE CITED

- Agashe, S.N. 2006. Palynology and its applications. Oxford and IBH Publishing Co. Pvt. Ltd., New Delhi.
- Buchanan-Hamilton, F. 1826. Commentary on *Cycas pectinata*. *Memoirs of the Wernerian Natural History Society* 5(2): 322–323.

- Calonje, M., Stevenson, D. W., and R. Osborne. 2020. The World List of Cycads, online edition [Internet]. 2013-2020. [cited 2020 Oct 08]. Available from: <http://www.cycadlist.org>.
- de Laubenfels, D. J., and Adema, F. A. 1998. Taxonomic revision of the genera *Cycas* and *Epicycas* gen. nov. (Cycadaceae). *Blumea* 43: 351–400.
- Deb, D. B. 1958. Endemism and outside influence on the flora of Manipur. *Journal of Bombay Natural History Society* 55: 313–317.
- Deb, D. B. 1983. *Flora of Tripura State*. Vol. 2. Today and Tomorrow Printer and Publisher, New Delhi.
- Favre, A., Päckert, M., Pauls, S. U., Jähnig, S. C., Uhl, D., Michalak, I., and A. N. Muellner-Riehl. 2015. The role of the uplift of the Qinghai-Tibetan Plateau for the evolution of Tibetan biotas. *Biological reviews of the Cambridge Philosophical Society* 90(1): 236–253. doi: 10.1111/brv.12107
- Gogoi, R. and M. Häkkinen. 2013. *Musa puspanjaliae* (Musaceae) sp. nov. from Arunachal Pradesh, India. *Nordic Journal of Botany* 31: 473–477.
- Govind, S., and D. S. Yadav. 1999. Genetic resources of Citrus in North Eastern Hill region of India. In S. Singh, and S. P. Ghosh [eds.] Hi-Tech Citrus Management, 38–46. ISC, ICAR, NRCC, Nagpur.
- Griffith, W. 1854. Notulae ad Plantas Asiaticas, Vol. 4. Bishops College Press, Calcutta.
- Haines, H.H. 1924. The Botany of Bihar and Orissa. Part V-VI. Adlard, London.
- Hajra, P. K., and D. M. Verma. 1996. Flora of Sikkim. Botanical Survey of India, Calcutta.
- Hill, K. D. 1995. Infrageneric relationships, phylogeny and biogeography of the genus *Cycas* (Cycadaceae). In P. Vorster & Pesnm [ed.], CYCAD 93, The 3rd International Conference on Cycad Biology, Proceedings, 139–162. Cycad Society of South Africa, Stellenbosch.
- Hill, K. D. 2004. The genus *Cycas* (Cycadaceae) in Vietnam. *The Botanical Review* 70 (2): 134–193.
- Hill, K. D. 2008. The genus *Cycas* (Cycadaceae) in China. *Telopea* 12 (1): 71–118.
- Hill, K. D., and Yang, S. L. 1999. The genus *Cycas* (Cycadaceae) in Thailand. *Brittonia* 51: 48–73.
- Hooker, J. D. 1854. Himalayan Journals. vol. 2. John Murray, London.
- Kanjilal, U. N., and N. L. Bor. 1940. Flora of Assam. Vol. 4. Botany Survey of India, Calcutta.
- Kanjilal, U. N., Kanjilal, P. C., De, R. N., and A. Das. 1940. Flora of Assam. Government of Assam.
- Khuraijam, J. S., Singh, R., Calonje, M., and J. Mazumdar. 2018. (2653) Proposal to conserve the name *Cycas pectinata* (Cycadaceae) with a conserved type. *Taxon* 67(6): 1213. doi: 10.12705/676.22

- Kurz, S. 1877. Forest Flora of British Burma, 2. Office of the Superintendent of Government Printing, Calcutta.
- Lindström, A. 2004. Morphological characters useful in determining species boundaries in *Cycas* (Cycadaceae). In T. Walters and R. Osborne [eds.] Cycad Classification. Concepts and Recommendations, 23–44. CAB International Publishing, Wallingford, Oxfordshire, UK.
- Lindström, A. J., and K. D. Hill, K. D. 2007. The genus *Cycas* (Cycadaceae) in India. *Telopea* 11(4): 463–488.
- Manish, K., and M. K. Pandit. 2018. Geophysical upheavals and evolutionary diversification of plant species in the Himalaya. *PeerJ*, 6, e5919. <https://doi.org/10.7717/peerj.5919>
- Mankga, L. T., Yessoufou, K., Mugwena, T., and M. Chitakira. 2020. The cycad genus *Cycas* may have diversified from Indochina and occupied its current ranges through vicariance and dispersal events. *Frontiers in Ecology and Evolution* 8:44. doi: 10.3389/fevo.2020.00044
- Nagalingum, N. S., Marshall, C. R., Quental, T. B., Rai, H. S., Little, D. P., and S. Mathews, S. 2011. Recent synchronous radiation of a living fossil. *Science* 334: 796–799. doi: 10.1126/science.1209926
- Osborne, R., Hill, K. D., Nguyen, H. T., and L. Phan Ke, L. 2007. Cycads of Vietnam. Roy Osborne, Brisbane and Wynand van Eeden, Cape Town.
- Pandit, M. K. 2017. Life in the Himalaya: an ecosystem at risk. Harvard University Press; Cambridge.
- Pant, D. D. 2002. An Introduction to Gymnosperms, *Cycas* and Cycadales. Birbal Sahni Institute of Palaeobotany, Lucknow.
- Pant, D. D., Singh, R. and D. V. Chauhan. 1994. On *Cycas pectinata* Hamilton from North-East India. *Encephalartos* 38: 17–30.
- Sahni, K. C. 1990. Gymnosperms of India and adjacent countries. Bishen Singh Mahendra Pal Singh, Dehradun.
- Schuster, J. 1932. Cycadaceae. In A. Engler [ed.] *Das Pflanzenreich* 99 (IV): 86–103.
- Singh, K. P., and V. Mudgal. 1997. Gymnosperms. In V. Mudgal and R.K. Hajra [eds.], Floristic diversity and conservation strategies in India. vol 1: Cryptogams and Gymnosperms. Botanical Survey of India, Calcutta
- Skelley, P., Xu, G., Tang, W., Lindström, A. J., Marler, T., Khuraijam, J. S., Singh, R., Radha, P., and S. Rich. 2017. Review of *Cycadophila* Xu, Tang & Skelley (Coleoptera: Erotylidae: Pharaxonothinae) inhabiting *Cycas* (Cycadaceae) in Asia, with descriptions of a new subgenus and thirteen new species. *Zootaxa* 4267(1): 1–63.
- Srivastava, R. C. 1993. Gymnosperms of Sikkim, India. *Asia Life Sciences* 2(1): 71–87.

- Tang, W. 2004. Continental drift and the evolution of Asian *Cycas*. *Encephalartos* 80:23–28.
- Thiselton-Dyer, W. T. 1888. Cycadaceae. In W. J. Hooker [ed.] Flora of British India, vol. 5. 655–658. Reeve, London.
- Tiwari, A., Upadhyay, Y., and S. K. Rana. 2019. Plant endemism in the Nepal Himalayas and phytogeographical implications. *Plant Diversity* 41(3): 174–182.
- Tougard, C. 2001. Biogeography and migration routes of large mammal faunas in South East Asia during the Late Middle Pleistocene: focus on the fossil and extant faunas from Thailand. *Palaeogeography, Palaeoclimatology, Palaeoecology* 168: 337–358. doi: 10.1016/S0031-0182(00)00243-1
- Wang, D. Y. 1996. Taxonomy of *Cycas* in China. In F. X. Wang and H. B. Liang [eds.] *Cycads in China*, 33–142. Guangdong Science and Technology Press, Guangdong.
- Wang, D. Y. 1996. Taxonomy of *Cycas* in China. In F. X. Wang, and H. B. Liang [eds.], *Cycads in China*, 33–142. Guangdong Science and Technology Press, Guangdong.
- Westerweel, J., Roperch, P., Licht, A., Dupont-Nivet, G., Win, Z., Poblete, F., Ruffet, G., Swe, h.h., Thi, M.K., and Day Wa Aung. 2019. Burma Terrane part of the Trans-Tethyan arc during collision with India according to palaeomagnetic data. *Nature Geoscience* 12: 863–868. doi: 10.1038/s41561-019-0443-2
- Xiao, L. Q., and M. Möller. 2015. Nuclear ribosomal ITS functional paralogs resolve the phylogenetic relationships of a late-Miocene radiation cycad *Cycas* (Cycadaceae). *PLoS One* 10: e0117971. doi: 10.1371/journal.pone.0117971
- Yang, S. L., and A. W. Meerow. 1996. The *Cycas pectinata* (Cycadaceae) complex: genetic structure and gene flow. *International Journal of Plant Sciences* 157: 468–483. doi: 10.1086/297364
- Yessoufou, K., Daru, B. H., Tafirei, R., Elansary, H. O., and I. Rampedi. 2017. Integrating biogeography, threat and evolutionary data to explore extinction crisis in the taxonomic group of cycads. *Ecology and Evolution* 7: 2735–2746. doi: 10.1002/ece3.2660

The World List of Cycads

Michael Calonje, Dennis Wm. Stevenson & Roy Osborne

ABSTRACT

The authors present an update of the World List of Cycads. This is a list of the validly published names of all extant cycads accompanied by details of their publication, geographic distribution, nomenclatural types and conservation status. For each genus, a list of synonyms is presented as well as *nomina dubia* and illegitimate names. The number of species on the current list is as follows: *Bowenia* (2), *Ceratozamia* (32), *Cycas* (118), *Dioon* (16), *Encephalartos* (65), *Lepidozamia* (2), *Macrozamia* (41), *Microcycas* (1), *Stangeria* (1) and *Zamia* (81), giving a total of 359 species.

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Available online at <http://www.cycadgroup.org/>

INTRODUCTION

The first World List of Cycads was published in *Encephalartos* (Journal of the Cycad Society of South Africa) (Osborne & Hendricks, 1985), with minor amendments in a supplementary list in a subsequent issue of the same journal (Osborne & Hendricks, 1986). A number of successive updates followed as changes in taxonomy and outlook made the previous lists obsolete. These have been presented at the various International Conferences on Cycad Biology (Stevenson et al., 1990, 1995, 2018; Stevenson & Osborne, 1993a; Osborne et al., 1999, 2012; Hill et al., 2004a, 2004c, 2007) and elsewhere (Stevenson & Osborne, 1993b; Hill et al., 2004b; Osborne et al., 2013). An online version of The World List of Cycads is available at the time of this printing at <http://www.cycadlist.org>.

The list that follows provides the valid names (column 1) of all known extant cycads at the time of final editing of this text. Compilation is alphabetical by genus/species, and authors' names are abbreviated in accordance with Brummitt & Powell (1992) and the International Plant Names Index (2012). Species names representing the types for the genus are indicated with an asterisk. Column 2 gives details of the countries of appearance (states, provinces, departments or districts in parenthesis), and "?" indicates probable occurrence but not validated by any voucher. Dates (column 3) refer to the year of publication of the name. Publication titles in the citations (column 4) are abbreviated in accordance with *BPH-2: Periodicals with Botanical Content* (Bridson et al., 2004) and *Taxonomic Literature*, second edition (Stafleu & Cowan, 1976-1988, with supplements 1-6 by Stafleu & Mennega, 1992-2000), except in cases where *Taxonomic Literature* provides the same abbreviations for different works. In such cases, publications are abbreviated as listed in the International Plant Names Index (2012). Column 5 gives details of the nature of the specimens or illustrations serving as the type for each name and the herbarium repository or publication hosting these types.

The following abbreviations are used: H = holotype, IT = isotype, LT = lectotype, NT = neotype; SYN = syntype, BAS = see basionym and AUT = autonym. Abbreviations for herbaria follow those of *Index Herbariorum* (Holmgren et al., 1990; Theirs, 2009). The final column (column 6) gives the threatened status as listed in the current IUCN Red List of Threatened Species (IUCN, 2017). Where the taxon is not present in that list, the proposed status given by the species authors or other authoritative sources is indicated in square brackets. We use the following Red List abbreviations: EW = extinct in the wild, CR = critically endangered, EN = endangered, VU = vulnerable, NT = near threatened, LC = least concern, DD = data deficient, NE = not evaluated. After each genus we give a partial list of synonyms, *nomina dubia* and illegitimate names.

Changes made since the previous version of this list (Stevenson et al., 2018) include the addition of several new names and type information. Further locality details have been added to the areas of occurrence, and the levels of threat have been updated following version 2017.3 of the IUCN Red List.

The World List of Cycads

Name	Distribution / synonymy	Date	Citation	Type	IUCN
BOWENIA Hook. ex Hook.f. (2 species: Australia)		1912	<i>Bot. Mag.</i> 89: t. 5398		
<i>B. serrulata</i> (W.Bull) Chamb.	Australia (Qld)	1912	<i>Bot. Gaz.</i> 54: 419	BAS: <i>B. spectabilis</i> LC <i>var. serrulata</i>	
* <i>B. spectabilis</i> Hook. ex Hook.f.	Australia (Qld)	1863	<i>Bot. Mag.</i> 89: t. 5398	LT—t. 5398	LC
Synonyms and other names:					
<i>B. spectabilis</i> var. <i>serrata</i> F.M.Bailey	= <i>B. serrulata</i>	1883	<i>Syn. Queensl. Fl.</i> : 501	IT—K	
<i>B. spectabilis</i> var. <i>serrulata</i> W.Bull	= <i>B. serrulata</i>	1878	<i>Retail List [Bull]</i> No. 143: 4, t. 5	LT—t. 5	
<i>B. spectabilis</i> var. <i>spectabilis</i>	= <i>B. spectabilis</i>	1878	<i>Retail List [Bull]</i> No. 143: 4, t. 5	AUT	
CERATOZAMIA Bongn. (32 species: Belize, Guatemala, Honduras, Mexico)					
<i>C. alvarezii</i> Pérez-Farr., Vovides & Iglesias	Mexico (Chiapas)	1999	<i>Novon</i> 9(3): 410–413, fig. 1	H—CHIP	EN
<i>C. beccerae</i> Pérez-Farr., Vovides & Schutzman	Mexico (Chiapas, Tabasco)	2004	<i>Bot. J. Linn. Soc.</i> 146(1): 123–128, figs. 1–7	H—XAL	EN
<i>C. brevifrons</i> Miq.	Mexico (Veracruz)	1847	<i>Tijdschr. Wis- Natuurk. Wetensch. Eerste Kl. Kon.</i> Ned. Inst. Wetensch. 1(1): 41–42	N—XAL	[VU]
<i>C. chamberlainii</i> Mart.-Domínguez, Nic.-Mor. & D.W.Stev.	Mexico (Hidalgo, Querétaro, San Luis Potosí)	2017	<i>Phytotaxa</i> 317(1): 17–28	H—CIB	[NE]
<i>C. chimalapensis</i> Pérez-Farr. & Vovides	Mexico (Oaxaca)	2008	<i>Bot. J. Linn. Soc.</i> 157(2): 169–175, figs. 1–4	H—HEM	[CR]
<i>C. decumbens</i> Vovides, Avendaño, Pérez-Farr. & Gonz.-Astorga	Mexico (Veracruz)	2008	<i>Novon</i> 18(1): 109–114, fig. 1	H—XAL	[CR]
<i>C. delucana</i> Vázq.Torres, A.Moretti & Carvajal-Hern.	Mexico (Puebla, Veracruz)	2013	<i>Delpinoa</i> 50–51: 129–133, figs. 1–5 (2008–2009, issued 2013)	H—CIB	[NE]
<i>C. euryphyllidia</i> Vázq.Torres, Sabato & D.W.Stev.	Mexico (Oaxaca, Veracruz)	1986	<i>Brittonia</i> 38(1): 17–26, figs. 1–5	H—NY	CR
<i>C. fuscoviridis</i> W.Bull	Mexico (Hidalgo)	1879	<i>Retail List [Bull]</i> No. 154: 4	NT—K	CR
<i>C. hildae</i> G.P.Landry & M.C.Wilson	Mexico (Querétaro, San Luis Potosí)	1979	<i>Brittonia</i> 31(3): 422–424, fig. 1	H—GH	EN
<i>C. hondurensis</i> J.L.Haynes, Whitelock, Schutzman & R.S.Adams	Honduras (Atlántida)	2008	<i>Cycad Newslett.</i> 31 (2–3): 16–21, figs. 1–2	H—EAP	[CR]
<i>C. huastecorum</i> Avendaño, Vovides & Cast.-Campos	Mexico (Veracruz)	2003	<i>Bot. J. Linn. Soc.</i> 141(3): 395–398, figs. 1–2	H—XAL	CR
<i>C. kuesteriana</i> Regel	Mexico (Tamaulipas)	1857	<i>Bull. Soc. Imp. Naturalistes Moscou</i> 30: 187–188, H—LE t. 3, fig. 6; t. 4, fig. 22		CR
<i>C. latifolia</i> Miq.	Mexico (San Luis Potosí)	1847	<i>Tijdschr. Wis- Natuurk. Wetensch. Eerste Kl. Kon.</i> Ned. Inst. Wetensch. 1(4): 206	N—NY	VU

Name	Distribution / synonymy	Date	Citation	Type	IUCN
<i>C. leptoceras</i> Mart.-Domínguez, Nic.-Mor., D.W.Stev. & Lorea-Hern.	Mexico (Guerrero)	2020	<i>Phytotaxa</i> 156:1-25	H—CIB	[NE]
<i>C. matudae</i> Lundell	Guatemala (Huehuetenango), 1939 Mexico (Chiapas)	1939	<i>Lloydia</i> 2(2): 75–76	H—MICH	EN
* <i>C. mexicana</i> Brongn.	Mexico (Veracruz)	1846	<i>Ann. Sci. Nat., Bot. ser. 3, ser. 3, 5:</i> 7–8, t. 1	H—P	VU
<i>C. miqueliania</i> H.Wendl.	Mexico (Chiapas, Tabasco, Veracruz)	1854	<i>Index Palm.</i> : 68	N—NY	CR
<i>C. mirandae</i> Vovides, Pérez-Farr. & Iglesias	Mexico (Chiapas)	2001	<i>Bot. J. Linn. Soc.</i> 137(1): 81–85, fig. 1–2	H—CHIP	EN
<i>C. mixeorum</i> Chemnick, T.J.Greg. & Salas-Mor.	Mexico (Oaxaca)	1998	<i>Phytologia</i> 83(1): 47–52 (1997 publ. 1998)	LT—XAL	EN
<i>C. morettii</i> Vázq.Torres & Vovides	Mexico (Veracruz)	1998	<i>Novon</i> 8(1): 87–90, fig. 1	H—CIB	EN
<i>C. norstogii</i> D.W.Stev.	Mexico (Chiapas, Oaxaca)	1982	<i>Brittonia</i> 34(2): 181–184, figs. 1–2	H—NY	EN
<i>C. robusta</i> Miq.	Belize (Cayo, Stann Creek, Toledo), Guatemala (Alta Verapaz, Petén, Quiché, Huehuetenango, Izabal), Mexico (Chiapas, Oaxaca, Veracruz)	1847	<i>Tijdschr. Wis- Natuurk. Wetensch. Eerste Kl. Kon. Ned. Inst. Wetensch.</i> 1(1): 42–43	N—NY	EN
<i>C. sabatieri</i> Vovides, Vázq.Torres, Schutzman & Iglesias	Mexico (Hidalgo, Querétaro)	1993	<i>Novon</i> 3(4): 502–504, fig. 1	H—XAL	EN
<i>C. santillanii</i> Pérez-Farr. & Vovides	Mexico (Chiapas)	2009	<i>Syst. Biodivers.</i> 7(4): 433–443, figs. 3, 7	H—HEM	[CR]
<i>C. subroseophylla</i> Mart.-Domínguez & Nic.-Mor.	Mexico (Veracruz)	2016	<i>Phytotaxa</i> 268(1): 25–45	H—CIB	[NE]
<i>C. tenuis</i> (Dyer) D.W.Stev. & Vovides	Mexico (Veracruz)	2016	<i>Bot. Sci.</i> 94(2): 419–429	BAS: <i>C. mexicana</i> var. <i>tenuis</i>	[NE]
<i>C. totonacorum</i> Mart.-Domínguez & Nic.-Mor.	Mexico (Hidalgo, Puebla, Veracruz)	2017	<i>Brittonia</i> 69(4): 518. [epublished 31 May 2017]	H—CIB	[NE]
<i>C. vovidesii</i> Pérez-Farr. & Iglesias	Mexico (Chiapas)	2007	<i>Bot. J. Linn. Soc.</i> 153(4): 393–400, figs. 1–6	H—HEM	VU
<i>C. whitelockiana</i> Chemnick & T.J.Greg.	Mexico (Oaxaca)	1996	<i>Phytologia</i> 79(1): 51–57 (1995 publ. 1996)	H—HNT	EN
<i>C. zaragozae</i> Medellín	Mexico (San Luis Potosí)	1963	<i>Brittonia</i> 15(2): 175–176, figs. 1–4	H—SLPM	CR
<i>C. zoquorum</i> Pérez-Farr., Vovides & Iglesias	Mexico (Chiapas)	2001	<i>Bot. J. Linn. Soc.</i> 137(1): 77–80, fig. 1	H—CHIP	CR
Synonyms and other names:					
<i>C. boliviiana</i> Brongn.	= <i>Zamia boliviiana</i>	1846	<i>Ann. Sci. Nat., Bot. ser. 3 5:</i> 7–9, pl. 1	LT—P	

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<i>C. intermedia</i> Miq.	= <i>C. mexicana</i>	1847	<i>Tijdschr. Wis- Natuurk. Wetensch. Eerste Kl. Kon. Ned. Inst. Wetensch.</i> 1(1): 40–41	?	
<i>C. katzeriana</i> Regel	= <i>Z. katzeriana</i>	1876	<i>Trudy Imp. S.-Peterburgsk. Bot. Sada</i> 4(4): 298	LT—LE	
<i>C. longifolia</i> Miq.	= <i>C. mexicana</i>	1847	<i>Tijdschr. Wis- Natuurk. Wetensch. Eerste Kl. Kon. Ned. Inst. Wetensch.</i> 1(1): 40	?	
<i>C. mexicana</i> var. <i>longifolia</i> f. <i>fuscoviridis</i> (W.Bull) J.Schust.	= <i>C. fuscoviridis</i>	1932	<i>in Engler, Pflanzenr.</i> 99: 132	BAS: <i>C. fuscoviridis</i>	
<i>C. mexicana</i> var. <i>mexicana</i>	= <i>C. mexicana</i>	1884	<i>Biol. Cent.-Amer., Bot.</i> 3: 193	AUT	
<i>C. mexicana</i> var. <i>robusta</i> (Miq.) Dyer	= <i>C. robusta</i>	1884	<i>Biol. Cent.-Amer., Bot.</i> 3: 193	BAS: <i>C. robusta</i>	
<i>C. mexicana</i> var. <i>tenuis</i> Dyer	= <i>C. tenuis</i>	1884	<i>Biol. Cent.-Amer., Bot.</i> 3: 193	H—K	
<i>C. microstrobila</i> Vovides & J.D.Rees	= <i>C. latifolia</i>	1983	<i>Madroño</i> 30(1): 39–42	H—XAL	
<i>CYCAS</i> L. (118 species: Africa, Asia, Australia, Indian & SW Pacific countries)		1763	<i>Sp. Pl.</i> 2: 1188		
<i>C. aculeata</i> K.D.Hill & T.H.Nguyễn	Vietnam (Da Nang)	2004	<i>Bot. Rev. (Lancaster)</i> 70(2): 149–150	H—HN	VU
<i>C. aerigna</i> K.D.Hill & A.Lindstr.	Philippines (Palawan - cult.)	2008	<i>Telopea</i> 12(1): 130–132, fig. 3	H—LBC	[DD]
<i>C. angulata</i> R.Br.	Australia (NT, Qld)	1810	<i>Prodr. Fl. Nov. Holland.</i> 1: 348	H—BM	LC
<i>C. annaikalensis</i> Rita Singh & P.Radha	India (Kerala)	2006	<i>Brittonia</i> 58(2): 119–123, figs. 1–2	H—IUPH	CR
<i>C. apoa</i> K.D.Hill	Indonesia (Maluku Utara, Nusa Tenggara Timur, Papua, Papua Barat), Papua New Guinea (West Sepik, Morobe)	1994	<i>Austral. Syst. Bot.</i> 7(6): 553–554, fig. 9	H—CANB	NT
<i>C. arenicola</i> K.D.Hill	Australia (NT)	1993	<i>Telopea</i> 5(2): 419–422	H—NSW	NT
<i>C. armstrongii</i> Miq.	Australia (NT)	1868	<i>Arch. Néerl. Sci. Exact. Nat.</i> 3: 235–236	H—U	VU
<i>C. arnhemica</i> K.D.Hill	Australia (NT)	1994	<i>Telopea</i> 5(4): 693–696, fig. 1	H—NSW	LC
<i>C. badensis</i> K.D.Hill	Australia (Qld)	1996	<i>Telopea</i> 7(1): 20–21, fig. 9	H—BRI	NT
<i>C. baiseensis</i> Y.Y.Huang, Y.C.Zhong & Z.F.Lu	China (Guangxi)	2018	<i>Mem. New York Bot. Gard.</i> 117: 504–518.	H—SZECH	[NE]
<i>C. balansae</i> Warb.	China (Guangxi), Vietnam (Lang Son, Quang Ninh, Thai Nguyen, Vinh Phuc)	1900	<i>Monsunia</i> 1: 179	LT—P	NT
<i>C. basaltica</i> C.A.Gardner	Australia (WA)	1923	<i>For. Dep. Bull., W. Austral.</i> 32: 31	H—PERTH	LC
<i>C. beddomei</i> Dyer	India (Andhra Pradesh)	1883	<i>Trans. Linn. Soc. London, Bot.</i> 2(5): 85–86, pl. 17	LT—K	EN

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<i>C. bifida</i> (Dyer) K.D.Hill	China (Guangxi, ?Hainan), Vietnam (Cao Bang, Lang Son, Tuyen Quang)	2004	<i>Bot. Rev. (Lancaster)</i> 70(2): 161–163	BAS: <i>C. rumphii</i> var. <i>bifida</i>	VU
<i>C. bougainvilleana</i> K.D.Hill	Papua New Guinea (Bougainville, New Britain), Solomon Islands	1994	<i>Austral. Syst. Bot.</i> 7(6): 557–560, fig. 11	H—NSW	NT
<i>C. brachycantha</i> K.D.Hill, T.H.Nguyễn & P.K.Lôc	Vietnam (Bac Kan)	2004	<i>Bot. Rev. (Lancaster)</i> 70(2): 155–157, fig. 6	H—HN	NT
<i>C. brunnea</i> K.D.Hill	Australia (Qld)	1992	<i>Telopea</i> 5(1): 200–201, fig. 15	H—DNA	NT
<i>C. cairnsiana</i> F.Muell.	Australia (Qld)	1876	<i>Fragm. (Mueller)</i> 10(83): 63, 121	H—MEL	VU
<i>C. calcicola</i> Maconochie	Australia (NT)	1978	<i>J. Adelaide Bot. Gard.</i> 1(3): 175, fig. 1	H—DNA	LC
<i>C. campestris</i> K.D.Hill	Papua New Guinea (Central, Gulf)	1994	<i>Austral. Syst. Bot.</i> 7(6): 538–540	H—NSW	NT
<i>C. canalis</i> K.D.Hill	Australia (NT)	1994	<i>Telopea</i> 5(4): 698–700, fig. 4a-d	H—NSW	LC
<i>C. candida</i> K.D.Hill	Australia (Qld)	2004	<i>Telopea</i> 10(2): 607–611, figs. 1–2	H—NSW	EN
<i>C. cantafolia</i> Jutta, K.L.Chew & Saw	Malaysia (Johor)	2010	<i>Blumea</i> 55(3): 249–252, figs. 1–2	H—KEP	[CR]
<i>C. chamaoensis</i> K.D.Hill	Thailand (Chantaburi)	1999	<i>Brittonia</i> 51(1): 58, fig. 6	H—NSW	CR
<i>C. changjiangensis</i> N.Liu	China (Hainan)	1998	<i>Acta Phytotax. Sin.</i> 36(6): 552–554, fig. 1	H—IBSC	EN
<i>C. chevalieri</i> Leandri	Vietnam (Ha Tinh, Nghe An, Quang Binh, Quang Tri)	1931	<i>Fl. Indo-Chine</i> 5(10): 1092	LT—P	NT
<i>C. chenii</i> X.Gong & Wei Zhou	China (Yunnan)	2015	<i>J. Syst. Evol.</i> 53(6): 497. [epublished 15 Apr 2015]	H—KUN	[EN]
* <i>C. circinalis</i> L.	India (Andhra Pradesh, Karnataka, Kerala, Maharashtra, Tamil Nadu)	1753	<i>Sp. Pl.</i> 2: 1188	LT—t. 19, in Rheede, Hort. Malab, 3 (1682)	EN
<i>C. clivicola</i> K.D.Hill	Cambodia, Malaysia (Kedah, Perak, Selangor), Thailand (Chumphon, Krabi, Narathiwat, Phang Nga, Phuket, Prachin Buri, Rayong, Ranong, Trang), Vietnam (An Giang, Kien Giang)	1999	<i>Brittonia</i> 51(1): 62–63, fig. 8a-d, g-h	H—NSW	LC

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<i>C. collina</i> K.D.Hill, T.H.Nguyên & P.K.Lôc	Vietnam (Son La)	2004	<i>Bot. Rev. (Lancaster)</i> 70(2): 142– 144, fig. 2	H—HN	VU
<i>C. condaoensis</i> K.D.Hill & S.L.Yang	Vietnam (Ba Ria-Vung Tau)	2004	<i>Bot. Rev. (Lancaster)</i> 70(2): 178– 179, fig. 14	H—K	VU
<i>C. conferta</i> Chirgwin	Australia (NT)	1993	<i>J. Adelaide Bot. Gard.</i> 15(2): 147	H—DNA	NT
<i>C. couttsiana</i> K.D.Hill	Australia (Qld)	1992	<i>Telopea</i> 5(1): 197–198, fig. 13	H—NSW	NT
<i>C. cupida</i> P.I.Forst.	Australia (Qld)	2001	<i>Austrobaileya</i> 6(1): 153, figs. 1–5	H—BRI	VU
<i>C. curranii</i> (J.Schust.) K.D.Hill	Philippines (Oriental Mindoro, Palawan)	1995	<i>Proc. Third Int. Conf. Cycad Biol.</i> : BAS: <i>C. circinalis</i> 150 subsp. <i>riuminiana</i> var. <i>curranii</i>	CR	
<i>C. debaoensis</i> Y.C. Zhong & C.J.Chen	China (Guangxi)	1997	<i>Acta Phytotax. Sin.</i> 35(6): 571	H—PE	CR
<i>C. desolata</i> P.I.Forst.	Australia (Qld)	1995	<i>Austrobaileya</i> 4(3): 345–352, figs. 1–5	H—BRI	VU
<i>C. diannanensis</i> Z.T.Guan & G.D.Tao	China (Yunnan), ?N Vietnam	1995	<i>Sichuan Forest. Surv. Design</i> 1995(4): 1	?H—IBSC	VU
<i>C. distans</i> P.I.Forst. & B.Gray	Australia (Qld)	2017	<i>Austrobaileya</i> 10(1): 74–84	H—BRI	[EN]
<i>C. divyadarshani</i> Khurajam & Rita Singh	India (Manipur), Myanmar, Thailand (Chiang Mai, Mae Hong Son, Kanchanaburi, Phetchabun, Phrae, Sukhothai), China (Yunnan), Vietnam (Binh Dinh, Gia Lai, Kon Tum, Lam Dong, Ninh Thuan, Phu Yen, Quang Nam, Quang Ngai) China (Guangxi, Yunnan), Laos (Luang Prabang), Vietnam (Bac Kan, Cao Bang, Ha Giang, Hoa Binh, Lai Chau, Lao Cai, Ninh Binh, Son La, Thai Nguyen, Thanh Hoa, Tuyen Quang)	2020	<i>Cycads</i> 5(1): 66–68, figs. 4,5	H—IPUH	VU
<i>C. dolichophylla</i> K.D.Hill, T.H.Nguyên & P.K.Lôc	Indonesia (Bali, Banten, Bengkulu, Jawa Barat, Jawa Tengah, Jawa Timur, Kepulauan Riau, Lampung, Sumatra Utara), Malaysia (Johore, Kedah, Malacca, Negri Sembilan, Pahang, Perak, Sabah, Sarawak, Terengganu), Myanmar, Philippines (Basilan, Cebu, Masbate, Davao del Sur, Davao Oriental, Oriental Mindoro, Negros Oriental, Palawan, Panay, Quezon, Sulu), Singapore (Changi), Thailand (Chumphon, Narathiwat, Phang Nga, Phuket, Satun, Trang, Trat), Vietnam (Kien Giang)	2004	<i>Blumea</i> 70(2): 157–160, fig. 7	H—HN	NT
<i>C. edentata</i> de Laub.		1998	<i>Blumea</i> 43(2): 372	H—L	NT

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<i>C. elephantipes</i> A.Lindstr. & K.D.Hill	Thailand (Chaiyaphum)	2003	<i>Brittonia</i> 54(4): 301, fig. 3 (2002 publ. 2003)	H—BKF	EN
<i>C. elongata</i> (Leandri) D.Yue Wang	Vietnam (Binh Dinh, Khanh Hoa, Ninh Thuan, Phu Yen, Quang Ngai)	1996	<i>Cycads China</i> : 51	BAS: <i>C. pectinata</i> var. <i>elongata</i>	EN
<i>C. fairylakea</i> D.Yue Wang	China (Guangdong)	1996	<i>Cycads China</i> : 54	H—SZG	[EN]
<i>C. falcata</i> K.D.Hill	Indonesia (Sulawesi Selatan, Sulawesi Tenggara)	1999	<i>Kew Bull.</i> 54(1): 209	H—K	VU
<i>C. ferruginea</i> F.N.Wei	China (Guangxi), Vietnam (Lang Son, Thai Nguyen)	1994	<i>Guiboria</i> 14(4): 300, fig. 1	H—IBK	NT
<i>C. fugax</i> K.D.Hill, T.H.Nguyễn & P.K.Lộc	Vietnam (Phu Tho)	2004	<i>Bot. Rev. (Lancaster)</i> 70(2): 145–146, figs. 2–3	H—HN	CR
<i>C. furfuracea</i> W.Fitzg.	Australia (WA)	1918	<i>J. Proc. Roy. Soc. Western Australia</i> 3: 108	LT—NSW	LC
<i>C. glauca</i> Hort. ex Miq.	Timor-Leste, Indonesia (Nusa Tenggara Timur)	1840	<i>Comm. Phytogr.</i> : 127	LT—U	DD
<i>C. guizhouensis</i> K.M.Lan & R.F.Zou	China (Guangxi, Guizhou, Yunnan)	1983	<i>Acta Phytotax. Sin.</i> 21(2): 209–210	H—PE	VU
<i>C. hainanensis</i> C.J.Chen	China (Hainan)	1975	<i>Acta Phytotax. Sin.</i> 13(4): 82, t. 2, figs. 5–6	H—IBSC	EN
<i>C. hoabinhensis</i> P.K.Lộc & T.H.Nguyễn	Vietnam (Ha Nam, Ha Tay, Hoa Binh, Ninh Binh)	2004	<i>Bot. Rev. (Lancaster)</i> 70(2): 153–155, fig. 5	H—HNU	EN
<i>C. hongheensis</i> S.Y.Yang & S.L.Yang ex D.Yue Wang	China (Yunnan)	1996	<i>Cycads China</i> : 62	H—Panzhihua Inst. Hort.	CR
<i>C. indica</i> A.Lindstr. & K.D.Hill	India (Karnataka)	2007	<i>Telopea</i> 11(4): 481–483, fig. 3	H—E	[DD]
<i>C. inermis</i> Lour.	Laos (Khammouan), Vietnam (Da Nang, Dong Nai, Khanh Hoa, Quang Nam)	1793	<i>Fl. Cochinch.</i> 2: 632	H—BM	VU
<i>C. javana</i> (Miq.) de Laub.	Indonesia (Jawa Barat, Jawa Tengah, Jawa Timur)	1996	<i>Cycads China</i> : 65	BAS: <i>C. circinalis</i> var. <i>javana</i>	EN
<i>C. lacrimans</i> A.Lindstr. & K.D.Hill	Philippines (Davao Oriental)	2008	<i>Telopea</i> 12(1): 136–138, fig. 5	H—NY	[EN]
<i>C. lane-poolei</i> C.A.Gardner	Australia (WA)	1923	<i>For. Dep. Bull., W. Austral.</i> 32: 30–32, fig. e	H—PERTH	LC
<i>C. laotica</i> Aver., T.H.Nguyễn & S.K.Nguyễn	Laos (Khammouan)	2014	<i>Nordic J. Bot.</i> [epublished 10 Sep 2014, DOI: 10.1111/njb.00498]	H—NUOL	[VU or EN]

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<i>C. lindstromii</i> S.L.Yang, K.D.Hill & T.H.Nguyễn	Vietnam (Ba Ria-Vung Tau, Binh Thuan, Khanh Hoa, Ninh Thuan)	1997	<i>Novon</i> 7(2): 213–215, fig. 1	H—FTG	EN
<i>C. maconochie</i> Chirgwin & K.D.Hill	Australia (NT)	1996	<i>Telopea</i> 7(1): 48–49, fig. 22	H—NSW	LC
subsp. <i>lanata</i> K.D.Hill	Australia (NT)	1996	<i>Telopea</i> 7(1): 49–51	H—DNA	NT
subsp. <i>maconochie</i>	Australia (NT)	1996	<i>Telopea</i> 7(1): 48	AUT	LC
subsp. <i>viridis</i> K.D.Hill	Australia (NT)	1996	<i>Telopea</i> 7(1): 51–52, fig. 23	H—NSW	LC
<i>C. macrocarpa</i> Griff.	Laos (Vientiane), Malaysia (Kelantan, Pahang, Terengganu), Thailand (Chanthaburi, Chumphon, Narathiwat, Ranong)	1854	<i>Not. Pl. Asiat.</i> 4: 11–14, pl. 362, fig. 2	H—K	VU
<i>C. media</i> R.Br.	Australia (Qld)	1810	<i>Prodr. Fl. Nov. Holland.</i> 1: 348	H—BM	LC
subsp. <i>ensata</i> K.D.Hill	Australia (Qld)	1996	<i>Telopea</i> 7(1): 14–15, fig. 6	H—NSW	LC
subsp. <i>banksii</i> K.D.Hill	Australia (Qld)	1996	<i>Telopea</i> 7(1): 15–16	H—NSW	LC
subsp. <i>media</i>	Australia (Qld)	1996	<i>Telopea</i> 7(1): 12–14, fig. 5	AUT	LC
<i>C. megacarpa</i> K.D.Hill	Australia (Qld)	1992	<i>Telopea</i> 5(1): 188–189, fig. 5	H—NSW	VU
<i>C. micholitzii</i> Dyer	Laos (Champasak, Saravan), Vietnam (Dac Lak, Gia Lai, Kon Tum)	1905	<i>Gard. Chron., ser. 3</i> 38: 142–144, figs. 48–49	H—K	VU
<i>C. micronesica</i> K.D.Hill	Guam, Micronesia (Yap), Northern Mariana Islands (Rota), Palau	1994	<i>Austral. Syst. Bot.</i> 7(6): 554–556, fig. 10	H—NSW	EN
<i>C. montana</i> A.Lindstr. & K.D.Hill	Indonesia (Nusa Tenggara Timur)	2009	<i>Telopea</i> 12(3): 396–397, fig. 3	H—BO	[NT]
<i>C. multifrondis</i> D.Yue Wang	China (Yunnan)	1996	<i>Cycads China:</i> 80	H—SYS	[EN]
<i>C. multipinnata</i> C.J.Chen & S.Y.Yang	China (Yunnan), Vietnam (Yen Bai)	1994	<i>Acta Phytotax. Sin.</i> 32(3): 239, 480–481	H—PE	EN
<i>C. natherstii</i> J.Schust.	India (Tamil Nadu), N Sri Lanka	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 76, fig. 10e	LT—G	VU
<i>C. nayagarhensis</i> Rita Singh, P.Radha & Khuraijam	India (Odisha)	2015	<i>Asian J. Conserv. Biol.</i> 4(1): 3–14, figs. 1–3	H—CAL	[CR]
<i>C. nitida</i> K.D.Hill & A.Lindstr.	Philippines (Albay, Cagayan, Quezon, Northern Samar)	2008	<i>Telopea</i> 12(1): 142–143, fig. 6	H—NSW	[NT]

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<i>C. nongnoochiae</i> K.D.Hill	Laos, (Vientiane), Thailand (Nakhon Sawan)	1999	<i>Brittonia</i> 51(1): 60–62, fig. 7	H—NSW	VU
<i>C. ophiolitica</i> K.D.Hill	Australia (Qld)	1992	<i>Telopea</i> 5(1): 190–191, fig. 7	H—NSW	VU
<i>C. orientis</i> K.D.Hill	Australia (NT)	1994	<i>Telopea</i> 5(4): 696–697, fig. 3	H—NSW	LC
<i>C. orixensis</i> (Haines) Rita Singh, P. Radha & Khuraijam	India (Odisha)	2015	<i>Asian J. Conserv. Biol.</i> 4(1): 3–14, figs. 4–6	BAS: <i>C. circinalis</i> var. <i>orixensis</i>	[EN]
<i>C. pachypoda</i> K. D. Hill	Vietnam (Binh Thuan, Ninh Thuan)	2004	<i>Bot. Rev. (Lancaster)</i> 70(2): 176–178, fig. 13	H—HN	CR
<i>C. panzhibhuaensis</i> L.Zhou & S.Y.Yang	China (Sichuan, Yunnan)	1981	<i>Acta Phytotax. Sin.</i> 19(3): 335, t. 10, figs. 1–6; t. 11, figs. 1–10	H—PE	VU
<i>C. papuana</i> F.Muell.	Australia (Queensland [Prince of Wales Island]), Indonesia (Papua), Papua New Guinea (Western)	1876	<i>Descr. Notes Papuan Pl.</i> 4: 71–72	LT—MEL	NT
<i>C. pectinata</i> Buch.-Ham.	India (Assam, Bihar, Meghalaya, Sikkim, northern West Bengal) Bangladesh, Bhutan, Nepal	1826	<i>Mem. Wern. Nat. Hist. Soc.</i> 5(2): 322–323, figs. 3,5	LT—K	VU
<i>C. petraea</i> A.Lindstr. & K.D.Hill	Laos (Vientiane), Thailand (Loei)	2003	<i>Brittonia</i> 54(4): 299, fig. 1 (2002 publ. 2003)	H—BKF	NT
<i>C. platyphylla</i> K.D.Hill	Australia (Qld)	1992	<i>Telopea</i> 5(1): 193–194, fig. 9	H—NSW	EN
<i>C. pranburiensis</i> S.L.Yang, W.Tang, K.D.Hill & Vatch.	Thailand (Prachuap Khiri Khan)	1999	<i>Brittonia</i> 51(1): 44–47, fig. 1	H—K	VU
<i>C. pruinosa</i> Maconochie	Australia (NT, WA)	1978	<i>J. Adelaide Bot. Gard.</i> 1(3): 177–178, fig. 2	H—DNA	LC
<i>C. revoluta</i> Thunb.	China (Fujian), Japan (Ryukyu Islands)	1782	<i>Verh. Holl. Maatsch. Wetensch. Haarlem</i> 20(2): 424, 426–427	LT—UPS	LC

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<i>C. ruminiana</i> Porte ex Regel	Philippines (Bataan, Batanes, Batangas, Cagayan, Cavite, Isabela, Laguna, Pampanga)	1863	<i>Gartenflora</i> 12: 16–17	H—LE	EN
<i>C. rumphii</i> Miq.	Australia (Ashmore Reef, Christmas Island), Indonesia (Jawa Timur, Kalimantan Barat, Maluku, Papua, Papua Barat, Sulawesi Utara, Sulawesi Tengah, Sulawesi Selatan), Papua New Guinea (West Sepik).	1839	<i>Bull. Sci. Phys. Nat. Néerl.</i> 2:45	LT—t. 23, <i>Rumphius Herb.</i> <i>Amb.</i> 1741	NT
<i>C. sainathii</i> R.C.Srivast.	India (Andaman and Nicobar Islands Territory)	2014	<i>Indian J. Pl. Sci. [Jaipur]</i> 3(1): 109–110, pl. 1	H—CAL	[CR]
<i>C. sancti-lasallei</i> Agoo & Madulid	Philippines (Misamis Oriental)	2012	<i>Blumea</i> 57(2): 131	H—PNH	[CR]
<i>C. saxatilis</i> K.D.Hill & A.Lindstr.	Philippines (Palawan)	2008	<i>Telopea</i> 12(1): 128–129, fig. 2	H—L	VU
<i>C. schumanniana</i> Lauterb.	Papua New Guinea (Eastern Highlands, Madang, Morobe)	1900	<i>Fl. Schutzgeb. Südsee:</i> 154–155	LT—WRSL	NT
<i>C. scratchleyana</i> F.Muell.	Australia (Murray Island), Indonesia (Maluku, Maluku Utara, Papua, Papua Barat), Papua New Guinea (Central, Gulf, Milne Bay, Western)	1885	<i>Vict. Naturalist</i> 2(2): 18–19	H—MEL	NT
<i>C. seemannii</i> A.Braun	Fiji, New Caledonia, Tonga, Vanuatu	1876	<i>Sitzungsber. Ges. Naturf. Freunde Berlin:</i> 114–115	LT—K	VU
<i>C. segmentifida</i> D.Yue Wang & C.Y. Deng	China (Guangxi, Guizhou, Yunnan), ?N Vietnam	1995	<i>Encephalartos</i> 43: 11–14	H—SZG	VU

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<i>C. seshachalamensis</i> P.V.C.Rao, N.V.S.Prasad, P.M.Babu, K.Prasad & Prasanna	India (Andhra Pradesh)	2016	<i>Asian J. Conservation Biol.</i> 5(1): 55-58, figs. 1-2	H—CAL	[CR]
<i>C. semota</i> K.D.Hill	Australia (Qld)	1996	<i>Telopea</i> 7(1): 23–26, fig. 11	H—NSW	VU
<i>C. sexseminifera</i> F.N.Wei	China (Guangxi), Vietnam (Cao Bang, Ninh Binh, Thanh Hoa)	1996	<i>Guishaia</i> 16(1): 1	H—IBK	NT
<i>C. siamensis</i> Miq.	Cambodia, Laos (Champsak, Saravan), Myanmar, Thailand (Chachoengsao, Chaiyaphum, Chon Buri, Kanchanaburi, Lampang, Nakhon Ratchasima, Phetchabun, Ratchaburi, Sakon Nakhon, Tak, Uthai Thani, Uttaridit), Vietnam (Dac Lak, Gia Lai, Kon Tum, Nghe An, Thanh Hoa)	1863	<i>Bot. Zeitung (Berlin)</i> 21: 334	H—U	VU
<i>C. silvestris</i> K.D.Hill	Australia (Qld)	1992	<i>Telopea</i> 5(1): 181–182, fig. 1	H—NSW	VU
<i>C. simplicipinna</i> (Smitinand) K.D.Hill	China (Yunnan), Laos (Saravan), ?Myanmar, Thailand (Chiang Mai, Loei, Mae Hong Song, Phrae), Vietnam (Quang Tri)	1995	<i>Proc. Third Int. Conf. Cycad Biol.</i> : 150	BAS: <i>C. micholitzii</i> var. <i>simplicipinna</i>	NT
<i>C. sphaerica</i> Roxb.	India (Andhra Pradesh, Karnataka, Tamil Nadu)	1832	<i>Fl. Ind. (Roxburgh)</i> 3: 747	LT—BM	DD
<i>C. sundaica</i> Miq. ex A.Lindstr. & K.D.Hill	Indonesia (Nusa Tenggara Barat, Nusa Tenggara Timur)	2009	<i>Telopea</i> 12(3): 408–410, fig. 6	H—BO	[LC]
<i>C. szechuanensis</i> W.C.Cheng & L.K.Fu	China (Fujian)	1975	<i>Acta Phytotax. Sin.</i> 13(4): 81, t. 1, figs. 7–8	H—PE	CR
<i>C. taitungensis</i> C.F.Shen, K.D.Hill, C.H.Tsou & C.J.Chen	China (Taiwan)	1994	<i>Bot. Bull. Acad. Sin.</i> 35(2): 135–138	H—HAST	EN

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<i>C. taiwaniana</i> Carruth.	China (Fujian, Guangdong)	1893	<i>J. Bot.</i> 31: 1–3, pl. 331	H—BM	EN
<i>C. tanqingii</i> D.Yue Wang	China (Yunnan), ?Vietnam (Lai Chau)	1996	<i>Cycads China:</i> 134, fig. 4	H—SZG	NT
<i>C. tansachana</i> K.D.Hill & S.L.Yang	Thailand (Saraburi)	1999	<i>Brittonia</i> 51(1): 65–66	H—NSW	CR
<i>C. terriana</i> P.I.Forst.	Australia (Qld)	2011	<i>Austrobaileya</i> 8(3): 356–363, t.1, figs. 1–4	H—BRI	[VU]
<i>C. thouarsii</i> R.Br. ex Gaudich.	Comoros, Kenya, Madagascar, Mozambique, Seychelles, Tanzania	1826	<i>Voy. Uranie, Bot.:</i> 434	?H—P	LC
<i>C. tropophylla</i> K.D.Hill & P.K.Lôc	Vietnam (Hai Phong, Quang Ninh)	2004	<i>Bot. Rev. (Lancaster)</i> 70(2): 168–170, fig. 10	H—HN	NT
<i>C. tuckeri</i> K.D.Hill	Australia (Qld)	1996	<i>Telopea</i> 7(1): 20–23, fig. 10	H—NSW	VU
<i>C. vespertilio</i> A.Lindstr. & K.D.Hill	Philippines (Camarines Sur, Cebu, Iloilo, Southern Leyte, Marinduque, Oriental Mindoro, Negros Oriental, Samar)	2008	<i>Telopea</i> 12(1): 134–136, fig. 4	H—LBC	[NT]
<i>C. wadei</i> Merr.	Philippines (Palawan)	1936	<i>Philipp. J. Sci.</i> 60(3): 234–236, pls 1–4	LT—NY	CR
<i>C. xipholepis</i> K.D.Hill	Australia (Qld)	1996	<i>Telopea</i> 7(1): 32–33, fig. 15	H—NSW	LC
<i>C. yorkiana</i> K.D.Hill	Australia (Qld)	1996	<i>Telopea</i> 7(1): 18–19, fig. 8	H—NSW	NT
<i>C. zambalensis</i> Madulid & Agoo	Philippines (Zambales)	2005	<i>Blumea</i> 50(3): 519–522, fig. 1.	H—PNH	CR
<i>C. zeylanica</i> (J.Schust.) A.Lindstr. & K.D.Hill	India (Andaman and Nicobar Islands), S Sri Lanka	2002	<i>Novon</i> 12(2): 238	BAS: <i>C. rumphii</i> subsp. <i>zeylanica</i>	VU
Synonyms and other names:					
<i>C. acuminatissima</i> Hung T.Chang, Y.C.Zhong & Z.F.Lu	= <i>C. sexseminifera</i>	1998	<i>Acta Sci. Nat. Univ. Sunyatseni</i> 37(4): 6	H—SYS	
<i>C. andamanica</i> K.Prasad, M.V.Ramana, Sanjappa & B.R.P.Rao	= <i>C. sainathii</i>	2015	<i>Int. J. Innov. Sci. Res.</i> 4 (1): 473–476	H—CAL	
<i>C. arnhemica</i> subsp. <i>arnhemica</i>	= <i>C. arnhemica</i>	1996	<i>Telopea</i> 7(1): 43–44	AUT	
<i>C. arnhemica</i> subsp. <i>muninga</i> Chirgwin & K.D.Hill	= <i>C. arnhemica</i>	1996	<i>Telopea</i> 7(1): 44–46, fig. 20	H—NSW	
<i>C. arnhemica</i> subsp. <i>natja</i> K.D.Hill	= <i>C. arnhemica</i>	1996	<i>Telopea</i> 7(1): 46–47, fig. 21	H—DNA	
<i>C. baguanheensis</i> L.K.Fu & S.Z.Cheng	= <i>C. panzhibhuaensis</i>	1981	<i>Acta Phytotax. Sin.</i> 19(3): 337	H—PE	
<i>C. bellefontii</i> L.Linden & Rodigas	<i>nomen dubium</i>	1886	<i>Ill. Hort.</i> 33: 27, pl. 586	?LT—pl. 586	

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<i>C. brevipinnata</i> Hung T.Chang, Y.Y. Huang & Y.C.Zhong	= <i>C. sexseminifera</i>	1998	<i>Acta Sci. Nat. Univ. Sunyatseni</i> 37(4): 8	H—SYS	
<i>C. caffra</i> Thunb.	= <i>Encephalartos caffer</i>	1775	<i>Nova Acta Regiae Soc. Sci. Upsal.</i> 2: 283–288, ? t. 5		
<i>C. canalis</i> subsp. <i>canalis</i>	= <i>C. canalis</i>	1994	<i>Telopea</i> 5(4): 699	AUT	
<i>C. canalis</i> subsp. <i>carinata</i> K.D.Hill	= <i>C. canalis</i>	1994	<i>Telopea</i> 5(4): 699–700, fig. 4e-g	H—NSW	
<i>C. celebica</i> Miq.	= <i>C. rumphii</i>	1839	<i>Bull. Sci. Phys. Nat. Néerl.</i> 1839: 45	LT—tt. 20-21 <i>Rumphius</i> Herb. <i>Amb.</i> 1741	
<i>C. chamberlainii</i> W.H.Br. & Kienholz	= <i>C. ruminiana</i>	1925	<i>Philipp. J. Sci.</i> 26: 47–48, pls 1–2, fig. 1	H—NY	
<i>C. circinalis</i> f. <i>circinalis</i>	= <i>C. circinalis</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 66	AUT	
<i>C. circinalis</i> f. <i>glauca</i> (Miq.) J.Schust.	= <i>C. glauca</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 66	BAS: <i>C. glauca</i>	
<i>C. circinalis</i> f. <i>gothanii</i> J.Schust.	<i>nomen dubium</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 66	?	
<i>C. circinalis</i> f. <i>undulata</i> (Desf. ex Gaudich.) J.Schust.	= <i>C. circinalis</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 66	BAS: <i>C. undulata</i>	
<i>C. circinalis</i> subsp. <i>circinalis</i>	= <i>C. circinalis</i>	1840	<i>Comm. Phytogr.</i> : 119	AUT	
<i>C. circinalis</i> subsp. <i>madagascariensis</i> (Miq.) J.Schust.	= <i>C. thouarsii</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 73	BAS: <i>C. madagascariensis</i>	
<i>C. circinalis</i> subsp. <i>madagascariensis</i> f. <i>trigonocarpoides</i> J.Schust.	= <i>C. thouarsii</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 74	?	
<i>C. circinalis</i> subsp. <i>papuana</i> (F.Muell.) J.Schust.	= <i>C. papuana</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 70	BAS: <i>C. papuana</i>	
<i>C. circinalis</i> subsp. <i>papuana</i> var. <i>papuana</i>	= <i>C. papuana</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 70	AUT	
<i>C. circinalis</i> subsp. <i>papuana</i> var. <i>scratchleyana</i> (F.Muell.) J.Schust.	= <i>C. scratchleyana</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 70	BAS: <i>C. scratchleyana</i>	
<i>C. circinalis</i> subsp. <i>riuminiana</i> (Porte ex Regel) J.Schust.	= <i>C. ruminiana</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 68	BAS: <i>C. riuminiana</i>	
<i>C. circinalis</i> subsp. <i>riuminiana</i> var. <i>curranii</i> f. <i>chamberlainii</i> (W.H.Br. & Kienholz) J.Schust.	= <i>C. ruminiana</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 69	BAS: <i>C. chamberlainii</i>	
<i>C. circinalis</i> subsp. <i>riuminiana</i> var. <i>curranii</i> f. <i>graminea</i> J.Schust.	= <i>C. wadei</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 69	LT—NY	
<i>C. circinalis</i> subsp. <i>riuminiana</i> var. <i>curranii</i> f. <i>maritima</i> J.Schust.	= <i>C. edentata</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 69	IT—K, P	

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<i>C. circinalis</i> subsp. <i>riuminiana</i> var. <i>curranii</i> J.Schust.	= <i>C. curranii</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 69	LT—K	
<i>C. circinalis</i> subsp. <i>seemannii</i> (A.Braun) J.Schust.	= <i>C. seemannii</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 71, 73	BAS: <i>C. seemannii</i>	
<i>C. circinalis</i> subsp. <i>thouarsii</i> (R.Br. ex Gaudich.) Engl.	= <i>C. thouarsii</i>	1908	<i>Veg. Erde [Engler]</i> 9(2): 82	BAS: <i>C. thouarsii</i>	
<i>C. circinalis</i> subsp. <i>vera</i> J.Schust.	= <i>C. circinalis</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 66-67	?	
<i>C. circinalis</i> subsp. <i>vera</i> var. <i>beddomei</i> (Dyer) J.Schust.	= <i>C. beddomei</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 67	BAS: <i>C. beddomei</i>	
<i>C. circinalis</i> subsp. <i>vera</i> var. <i>pectinata</i> (Griff.) J.Schust.	= <i>C. pectinata</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 68	BAS: <i>C. pectinata</i>	
<i>C. circinalis</i> subsp. <i>vera</i> var. <i>vera</i>	= <i>C. circinalis</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 67	AUT	
<i>C. circinalis</i> var. <i>angustifolia</i> Miq.	= <i>C. circinalis</i>	1840	<i>Comm. Phytogr.</i> : 119	LT—U	
<i>C. circinalis</i> var. <i>circinalis</i>	= <i>C. circinalis</i>	1840	<i>Comm. Phytogr.</i> : 119	AUT	
<i>C. circinalis</i> var. <i>javana</i> Miq.	= <i>C. javana</i>	1842	<i>Monogr. Cycad.</i> : 28. t. 1, figs. t, u, t II, fig. eI	H—L	
<i>C. circinalis</i> var. <i>orixensis</i> Haines	= <i>C. orixensis</i>	1924	<i>Bot. Bihar Orissa</i> 6: 1228	SYN—K	
<i>C. clivicola</i> subsp. <i>clivicola</i>	= <i>C. clivicola</i>	1999	<i>Brittonia</i> 51(1): 64, fig. 8e,f,i	AUT	
<i>C. clivicola</i> subsp. <i>lutea</i> K.D.Hill	= <i>C. clivicola</i>	1999	<i>Brittonia</i> 51(1): 64, fig. 8e,f,i	H—NSW	
<i>C. comorensis</i> Brault	= <i>C. thouarsii</i>	1888	<i>Cat. Gén.</i> 195: 5	H—P	
<i>C. crassipes</i> Hung T.Chang, Y.C.Zhong & Z.F.Lu	= <i>C. sexseminifera</i>	1999	<i>Acta Sci. Nat. Univ. Sunyatseni</i> 38(3): 121– 122	H—SYS	
<i>C. darshii</i> R.C.Srivast. & Jana	nomen dubium	2014	<i>Indian J. Pl. Sci. [Jaipur]</i> 3(2): 151-153, t. II	H—CAL	
<i>C. dharmrajii</i> L.J.Singh	= <i>C. sainathii</i>	2017	<i>Nordic J. Bot.</i> 35(1): 69–76.	H—CAL	
<i>C. dilatata</i> Griff.	nomen dubium	1854	<i>Not. Pl. Asiat.</i> 4 (1): 15	?	
<i>C. gracilis</i> Miq.	= <i>C. media</i> subsp. <i>media</i>	1863	<i>Verslagen Meded. Afd. Natuurk. Kon. Akad. Wetensch.</i> 15: 366–367	H—U	
<i>C. gracilis</i> var. <i>glauca</i> Regel	= <i>C. media</i> subsp. <i>media</i>	1876	<i>Trudy Imp. S.-Peterburgsk. Bot. Sada</i> 4(4): 282	H—LE	
<i>C. gracilis</i> var. <i>gracilis</i>	= <i>C. media</i> subsp. <i>media</i>	1876	<i>Trudy Imp. S.-Peterburgsk. Bot. Sada</i> 4(4): 282	AUT	
<i>C. gracilis</i> var. <i>viridis</i> Regel	= <i>C. media</i> subsp. <i>media</i>	1876	<i>Trudy Imp. S.-Peterburgsk. Bot. Sada</i> 4(4): 282	LT—LE	

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<i>C. gracilis</i> Y.Y.Huang, Y.C.Zhong & Z.F.Lu	= <i>nom. illeg.</i>	2008	<i>J. Pl. Genet. Resources</i> 9(4): 525–527	H—SYS	
<i>C. hainanensis</i> subsp. <i>changjiangensis</i> (N.Liu)	= <i>C. changjiangensis</i>	2004	<i>Proc. Sixth Int. Conf. Cycad Biol.</i> : 3	BAS: <i>C. changjiangensis</i>	
<i>N.Liu</i>					
<i>C. hainanensis</i> subsp. <i>hainanensis</i>	= <i>C. hainanensis</i>	2004	<i>Proc. Sixth Int. Conf. Cycad Biol.</i> : 3	AUT	
<i>C. hypoleuca</i> C.Presl.	= <i>nomen dubium</i>	1849	<i>Epimel. Bot.</i> : 238	?	
<i>C. immersa</i> Craib	= <i>C. siamensis</i>	1912	<i>Bull. Misc. Inform. Kew</i> 1912(10): 434–435	H—K	
<i>C. jenkinsiana</i> Griff.	= <i>C. pectinata</i>	1854	<i>Not. Pl. Asiat.</i> 4: 9–10, pl. 360, figs. 1–2, pl. 362, fig. 1	H—K	
<i>C. kennedyana</i> F.Muell.	= <i>C. media</i> subsp. <i>media</i>	1882	<i>Australas. Chem. Druggist.</i> 16	H—MEL	
<i>C. lingshuiensis</i> G.A.Fu	= <i>C. hainanensis</i>	2004	<i>Bull. Bot. Res., Harbin</i> 24(4): 387–388	H—HFB	
<i>C. litoralis</i> K.D.Hill	= <i>C. edentata</i>	1999	<i>Brittonia</i> 51(1): 70–72, fig. 11	H—NSW	
<i>C. longiconifera</i> Hung T.Chang, Y.C. Zhong & Y.Y. Huang	= <i>C. segmentifida</i>	1998	<i>Acta Sci. Nat. Univ. Sunyatseni</i> 37(4): 6	H—SYS	
<i>C. longipetiolula</i> D.Yue Wang	= <i>C. bifida</i> x <i>C. multipinnata</i>	1996	<i>Cycads China</i> : 68	H—SZG	
<i>C. longisporophylla</i> F.N.Wei	= <i>C. sexseminifera</i>	1997	<i>Guizhaia</i> 17(3): 209	H—IBK	
<i>C. longlinensis</i> Hung T.Chang & Y.C.Zhong	= <i>C. segmentifida</i>	1997	<i>Acta Sci. Nat. Univ. Sunyatseni</i> 36(3): 68	H—SYS	
<i>C. madagascariensis</i> Miq.	= <i>C. thouarsii</i>	1840	<i>Comm. Phytogr.</i> : 127	LT—t. 2a-e <i>Petit-Thouars, Hist. Veg.</i> , 1804	
<i>C. micholitzii</i> var. <i>micholitzii</i>	= <i>C. micholitzii</i>	1971	<i>Nat. Hist. Bull. Siam Soc.</i> 24: 164	AUT	
<i>C. micholitzii</i> var. <i>simplicipinna</i> Smitinand	= <i>C. simplicipinna</i>	1971	<i>Nat. Hist. Bull. Siam Soc.</i> 24: 164, figs. 2–3, 4f	LT—BKF	
<i>C. miquelii</i> Warb.	= <i>C. revoluta</i>	1900	<i>Monsunia</i> 1: 179, 181	LT—U	
<i>C. multifida</i> Hung T.Chang & Y.C.Zhong	= <i>C. segmentifida</i>	1997	<i>Acta Sci. Nat. Univ. Sunyatseni</i> 36(3): 70	LT—U	
<i>C. multiovula</i> D.Yue Wang	= <i>C. guizhouensis</i>	1996	<i>Cycads China</i> : 83	H—SZG	
<i>C. normanbyana</i> F.Muell.	= <i>C. media</i> subsp. <i>media</i>	1874	<i>Fragm. (Mueller)</i> 8(66): 169–171, Icon. 65–66	H—SZG	
<i>C. palmatifida</i> Hung T.Chang, Y.Y.Huang & Y.C.Zhong	= <i>C. balansae</i>	1998	<i>Acta Sci. Nat. Univ. Sunyatseni</i> 37(4): 7	H—MEL	
<i>C. parvula</i> S.L.Yang ex D.Yue Wang	= <i>C. diannanensis</i>	1996	<i>Cycads China</i> : 93	H—SYS	
<i>C. pectinata</i> var. <i>elongata</i> Leandri	= <i>C. elongata</i>	1931	<i>Fl. Indo-Chine</i> 5(10): 1091	LT—P	
<i>C. pectinata</i> var. <i>manhaoensis</i> C.J.Chen & P.Yun	= <i>C. diannanensis</i>	1995	<i>Acta Bot. Yunnan.</i> 17(4): 400	LT—P	
<i>C. pectinata</i> var. <i>pectinata</i>	= <i>C. pectinata</i>	1931	<i>Fl. Indo-Chine</i> 5(10): 1091	AUT	

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<i>C. pschannae</i> R.C. Srivast. & L.J.Singh	= <i>C. sainathii</i>	2015	<i>Int. J. Curr. Res. Biosci. Plant Biol.</i> 2 (8): 35-37	H—CAL	
<i>C. pygmaea</i> Blume	<i>nomen dubium</i>	1848	<i>Rumphia</i> 4:16	H—YUN	
<i>C. revoluta</i> var. <i>brevifrons</i> Miq.	= <i>C. revoluta</i>	1847	<i>Tijdschr. Wis- Natuurk. Wetensch. Eerste Kl. Kon. Ned. Inst. Wetensch.</i> 1(1): 207	apparently not preserved	
<i>C. revoluta</i> var. <i>planifolia</i> Miq.	= <i>C. revoluta</i>	1842	<i>Monogr. Cycad.</i> : 25-26	H—U	
<i>C. revoluta</i> var. <i>prolifera</i> Siebold & Zucc.	= <i>C. revoluta</i>	1846	<i>Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss.</i> 14(3): 236	apparently not preserved	
<i>C. revoluta</i> var. <i>revoluta</i>	= <i>C. revoluta</i>	1842	<i>Monogr. Cycad.</i> : 25	AUT	
<i>C. revoluta</i> var. <i>robusta</i> Messeri	= <i>C. revoluta</i>	1927	<i>Nuovo Giorn. Bot. Ital., n.s.</i> , 34: 324, 327	apparently not preserved	
<i>C. revoluta</i> var. <i>taiwaniana</i> (Carruth.) J.Schust.	= <i>C. taiwaniana</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 84	BAS: <i>C. taiwaniana</i>	
<i>C. rumphii</i> f. <i>rumphii</i>	= <i>C. rumphii</i>	1938	<i>J. Jap. Bot.</i> 14(9): 587	AUT	
<i>C. rumphii</i> f. <i>undulata</i> (Desf. ex Gaudich.) Kaneh.	= <i>C. circinalis</i>	1938	<i>J. Jap. Bot.</i> 14(9): 587	BAS: <i>C. undulata</i>	
<i>C. rumphii</i> subsp. <i>normanbyana</i> (F.Muell.) J.Schust.	= <i>C. media</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 75	BAS: <i>C. normanbyana</i>	
<i>C. rumphii</i> subsp. <i>rumphii</i>	= <i>C. rumphii</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 75	AUT	
<i>C. rumphii</i> subsp. <i>zeylanica</i> J.Schust.	= <i>C. zeylanica</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 75, figs. 10c-d, 11m	LT—G	
<i>C. rumphii</i> var. <i>bifida</i> Dyer	= <i>C. bifida</i>	1902	<i>J. Linn. Soc., Bot.</i> 26: 560	H—K	
<i>C. rumphii</i> var. <i>rumphii</i>	= <i>C. rumphii</i>	1840	<i>Comm. Phytogr.</i> : 125	AUT	
<i>C. rumphii</i> var. <i>seemannii</i> (A.Braun) Parham	= <i>C. seemannii</i>	1948	<i>Agric. J. (Suva)</i> 19: 94, f. 7	BAS: <i>C. seemannii</i>	
<i>C. rumphii</i> var. <i>timorensis</i> Miq.	= <i>C. glauca</i>	1840	<i>Comm. Phytogr.</i> : 125-126	H—L	
<i>C. septemperma</i> Hung T.Chang, Y.Y.Huang & H.X.Zheng	= <i>C. sexseminifera</i>	1998	<i>Acta Sci. Nat. Univ. Sunyatseni</i> 37(4): 8	H—SYS	
<i>C. shanyaensis</i> G.A.Fu	= <i>C. hainanensis</i>	2006	<i>Bull. Bot. Res., Harbin</i> 26(1): 2-3, fig. 1	H—HFB	
<i>C. shiwindashanica</i> Hung T.Chang & Y.C.Zhong	= <i>C. balansae</i>	1995	<i>Chin. Bull. Bot.</i> 12:12	H—GXF	
<i>C. siamensis</i> subsp. <i>balansae</i> (Warb.) J.Schust.	= <i>C. balansae</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 81	BAS: <i>C. balansae</i>	
<i>C. siamensis</i> subsp. <i>siamensis</i>	= <i>C. siamensis</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 81	AUT	
<i>C. spiniformis</i> J.Y.Liang	= <i>C. sexseminifera</i>	1997	<i>Guizhou</i> 17(3): 211	H—IBK	
<i>C. swamyi</i> Rita Singh & P.Radha	= <i>C. indica</i>	2008	<i>Bot. J. Linn. Soc.</i> 158(3): 430-435	H—CAL	

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<i>C. szechuanensis</i> subsp. <i>fairylakea</i> (D.Yue Wang N.Liu	= <i>C. fairylakea</i>	2004	<i>Proc. Sixth Int. Conf. Cycad Biol.</i> : 2	BAS: <i>C. fairylakea</i>	
<i>C. szechuanensis</i> subsp. <i>szechuanensis</i>	= <i>C. szechuanensis</i>	2004	<i>Proc. Sixth Int. Conf. Cycad Biol.</i> : 1-4	AUT	
<i>C. tonkinensis</i> (L.Linden & Rodigas) Rodigas	<i>nomen dubium</i>	1886	<i>Ill. Hort.</i> 33: 27	BAS: <i>Zamia tonkinensis</i>	
<i>C. truncata</i> de Laub.	= <i>C. ruminiana</i>	2007	<i>Encephalartos</i> 92: 17	H-US	
<i>C. undulata</i> Desf. ex Gaudich.	= <i>C. circinalis</i>	1829	<i>Voy. Uranie, Bot.</i> : 434	H-P	
<i>C. wallichii</i> Miq.	= <i>C. circinalis</i>	1842	<i>Monogr. Cycad.</i> : 32	H-U	
<i>C. xilingensis</i> Hung T.Chang & Y.C.Zhong	= <i>C. segmentifida</i>	1997	<i>Acta Sci. Nat. Univ. Sunyatseni</i> 36(3): 69	H-SYS	
<i>DYEROCYCAS</i> Nakai	= <i>CYCAS</i>	1943	<i>Ord. Fam. Prof. Nakai</i> : 208		
<i>D. micholitzii</i> (Dyer) Nakai	= <i>C. micholitzii</i>	1943	<i>Ord. Fam. Prof. Nakai</i> : 208	BAS: <i>C. micholitzii</i>	
<i>EPICYCAS</i> de Laub.	= <i>CYCAS</i>	1998	<i>Blumea</i> 43(2): 388		
<i>E. elongata</i> (Leandri) S.L.Yang ex de Laub.	= <i>C. elongata</i>	1998	<i>Blumea</i> 43(2): 393	BAS: <i>C. pectinata</i> var. <i>elongata</i>	
<i>E. lindstromii</i> (S.L.Yang, K.D.Hill & T.H.Nguyêñ) de Laub.	= <i>C. lindstromii</i>	1998	<i>Blumea</i> 43(2): 395	BAS: <i>C. lindstromii</i>	
<i>E. micholitzii</i> (Dyer) de Laub.	= <i>C. micholitzii</i>	1998	<i>Blumea</i> 43(2): 389	BAS: <i>C. micholitzii</i>	
<i>E. miquelii</i> (Warb.) de Laub.	= <i>C. revoluta</i>	1998	<i>Blumea</i> 43(2): 393	BAS: <i>C. miquelii</i>	
<i>E. multipinnata</i> (C.J.Chen & S.Y.Yang) de Laub.	= <i>C. multipinnata</i>	1998	<i>Blumea</i> 43(2): 391	BAS: <i>C. multipinnata</i>	
<i>E. siamensis</i> (Miq.) de Laub.	= <i>C. siamensis</i>	1998	<i>Blumea</i> 43(2): 393	BAS: <i>C. siamensis</i>	
<i>E. tonkinensis</i> (L.Linden & Rodigas) de Laub.	<i>nomen dubium</i>	1998	<i>Blumea</i> 43(2): 391	BAS: <i>Z. tonkinensis</i>	
<i>DIOON</i> Lindl. (16 species: Honduras, Mexico)		1843	<i>Edwards's Bot. Reg.</i> 29: misc. 59-60		
<i>D. angustifolium</i> Miq.	Mexico (Nuevo León, Tamaulipas)	1847	<i>Tijdschr. Wis- Natuurk. Wetensch. Eerste Kl. Kon. Ned. Inst. Wetensch.</i> 1(1): 37-38	LT-K	VU
<i>D. argenteum</i> T.J.Greg., Chemnick, Salas-Mor. & Vovides	Mexico (Oaxaca)	2003	<i>Bot. J. Linn. Soc.</i> 141(4): 471-476, figs. 1-8	H-XAL	VU
<i>D. califanoi</i> De Luca & Sabato	Mexico (Oaxaca, Puebla)	1979	<i>Brittonia</i> 31(1): 170-172, figs. 2-3	H-NAP	EN
<i>D. caputoi</i> De Luca, Sabato & Vázq.Torres	Mexico (Oaxaca, Puebla)	1980	<i>Brittonia</i> 32(1): 44-46, figs. 3-4	H-XALU	EN
* <i>D. edule</i> Lindl.	Mexico (Hidalgo, Querétaro, San Luis Potosí, Tamaulipas, Veracruz)	1843	<i>Edwards's Bot. Reg.</i> 29: misc. 59-60	H-CGE	NT

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<i>D. holmgrenii</i> De Luca, Sabato & Vázq.Torres	Mexico (Oaxaca)	1981	<i>Brittonia</i> 33(4): 552–554, figs. 1–2	H—XALU	EN
<i>D. mejiae</i> Standl. & L.O.Williams	Honduras (Colón, Olancho, Yoro)	1951	<i>Ceiba</i> 1(1): 36–38	H—US	LC
<i>D. merolae</i> De Luca, Sabato & Vázq.Torres	Mexico (Chiapas, Oaxaca)	1981	<i>Brittonia</i> 33(2): 180–184, figs. 2–3	H—NAP	VU
<i>D. planifolium</i> Salas-Mor., Chemnick & T.J.Greg.	Mexico (Oaxaca)	2016	<i>Cact. Succ. J. (Los Angeles)</i> 88(1): 35–42	H—MEXU	VU
<i>D. purpusii</i> Rose	Mexico (Oaxaca)	1909	<i>Contr. U.S. Natl. Herb.</i> 12(7): 260–261	H—US	VU
<i>D. rzedowskii</i> De Luca, A.Moretti, Sabato & Vázq.Torres	Mexico (Oaxaca)	1980	<i>Brittonia</i> 32(2): 225–229	H—XALU	EN
<i>D. sonorense</i> (De Luca, Sabato & Vázq.Torres) Chemnick, T.J.Greg. & Salas-Mor.	Mexico (Sinaloa, Sonora)	1998	<i>Phytologia</i> 83(1): 1–6 (1997 publ. 1998)	BAS: <i>D. tomasellii</i> var. <i>sonorense</i>	EN
<i>D. spinulosum</i> Dyer ex Eichler	Mexico (Oaxaca, Veracruz)	1883	<i>Gart.-Zeitung (Berlin)</i> 2: 411–413, 438–439, fig. 80	H—K	EN
<i>D. stevensonii</i> Nic.-Mor. & Vovides	Mexico (Guerrero, Michoacán)	2009	<i>Syst. Biodivers.</i> 7(1): 73–79, figs. 1–2	H—XAL	[CR]
<i>D. tomasellii</i> De Luca, Sabato & Vázq.Torres	Mexico (Durango, Jalisco, Nayarit, Sinaloa)	1984	<i>Brittonia</i> 36(3): 225–227, figs. 2–5	H—NAP	VU
<i>D. vovidesii</i> Gut.Ortega & Pérez-Farr.	Mexico (Sonora)	2018	<i>Phytotaxa</i> 369 (2): 109.	H—HEM	[EN]
Synonyms and other names:					
<i>D. aculeatum</i> Lem.	= <i>D. angustifolium</i>	1846	<i>Cat. (Vanhoutt.)</i> 27: 45	?	
<i>D. edule</i> f. <i>angustifolium</i> (Miq.) Miq.	= <i>D. angustifolium</i>	1861	<i>Prodr. Syst. Cycad.</i> : 10, 22	BAS: <i>D. angustifolium</i>	
<i>D. edule</i> f. <i>edule</i>	= <i>D. edule</i>	1861	<i>Prodr. Syst. Cycad.</i> : 10	AUT	
<i>D. edule</i> f. <i>imbricatum</i> (Miq.) Miq.	= <i>D. edule</i>	1861	<i>Prodr. Syst. Cycad.</i> : 10, 22	BAS: <i>D. imbricatum</i>	
<i>D. edule</i> f. <i>lanuginosum</i> (Wittm.) J.Schust.	= <i>D. edule</i>	1932	in <i>Engler, Pflanzenr.</i> 99: 127	BAS: <i>D. edule</i> var. <i>lanuginosum</i>	
<i>D. edule</i> subsp. <i>angustifolium</i> (Miq.) A.E.Murray	= <i>D. angustifolium</i>	1983	<i>Kalmia</i> 13: 5	BAS: <i>D. angustifolium</i>	
<i>D. edule</i> var. <i>angustifolium</i> (Miq.) Miq.	= <i>D. angustifolium</i>	1868	<i>Arch. Néerl. Sci. Exact. Nat.</i> 3: 427	BAS: <i>D. angustifolium</i>	
<i>D. edule</i> var. <i>edule</i>	= <i>D. edule</i>	1868	<i>Arch. Neerl. Sci. Exact. Nat.</i> 3: 427	AUT	
<i>D. edule</i> var. <i>imbricatum</i> (Miq.) Miq.	= <i>D. edule</i>	1868	<i>Arch. Neerl. Sci. Exact. Nat.</i> 3: 427	BAS: <i>D. imbricatum</i>	
<i>D. edule</i> var. <i>lanuginosum</i> Wittm.	= <i>D. edule</i>	1899	<i>Gartenflora</i> 48: 153	LT—K	

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<i>D. edule</i> var. <i>latipinnium</i> Dyer	= <i>D. mejiae</i>	1884	<i>Biol. Cent.-Amer., Bot.</i> 3: 191, t. 81, figs. 1–3	H—K	
<i>D. edule</i> var. <i>sonorense</i> (De Luca, Sabato & Vázq.Torres) McVaugh & Pérez de la Rosa	= <i>D. sonorense</i>	1992	<i>Fl. Novo-Galicianana</i> 17: 112	BAS: <i>D. tomasellii</i> var. <i>sonorense</i>	
<i>D. imbricatum</i> Miq.	= <i>D. edule</i>	1847	<i>Tijdschr. Wis- Natuurk. Wetensch. Eerste Kl. Kon. Ned. Inst. Wetensch.</i> 1(1): 36	LT—t. 4d-e in <i>Verh. Eerste Kl. Kon. Ned. Inst. Wetensch.</i> 3, 1851	
<i>D. pectinatum</i> Mast.	<i>nomen dubium</i>	1893	<i>Gard. Chron.</i> 73(338): 718	LT: Icone, in <i>Gard. Chron.</i> 73(338): 718, t.	
<i>D. strobilaceum</i> Lem.	= <i>D. edule</i>	1863	<i>Ill. Hort.</i> 10(Misc.): 4	?	
<i>D. tomasellii</i> var. <i>sonorense</i> De Luca, Sabato & Vázq.Torres	= <i>D. sonorense</i>	1984	<i>Brittonia</i> 36(3): 226–227, figs. 2B, 3C, 5	H—NAP	
<i>D. tomasellii</i> var. <i>tomasellii</i>	= <i>D. tomasellii</i>	1984	<i>Brittonia</i> 36(3): 226	AUT	
<i>PLATYZAMIA</i> Zucc.	= <i>DIOON</i>	1845	<i>Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss.</i> 4(2): 23, t. 4		
<i>Platyzamia rigida</i> Zucc.	= <i>D. edule</i>	1845	<i>Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss.</i> 4(2): 23, t. 4	H—M	
ENCEPHALARTOS Lehm. (65 species: Africa)		1834	<i>Nov. Stirp. Pug.</i> 6: 3–8, tt. 1–5		
<i>E. aemulans</i> Vorster	South Africa (KwaZulu-Natal)	1990	<i>S. African J. Bot.</i> 56(2): 239–243	H—PRE	CR
<i>E. altensteinii</i> Lehm.	South Africa (E Cape)	1834	<i>Nov. Stirp. Pug.</i> 6: 11, t. 4–5	?LT—tt. 4–5	VU
<i>E. aplanatus</i> Vorster	Swaziland	1996	<i>S. African J. Bot.</i> 62: 57–60	H—PRE	VU
<i>E. arenarius</i> R.A.Dyer	South Africa (E Cape)	1956	<i>J. S. African Bot.</i> 22(1): 1–4	H—PRE	EN
<i>E. barteri</i> Carruth. ex Miq.	Benin (Bergu), Ghana, Nigeria (Plateau), ?Togo	1868	<i>Arch. Néerl. Sci. Exact. Nat.</i> 3: 243	IT—K	VU
subsp. <i>allocbrous</i> L.E.Newton	Nigeria (Plateau)	1978	<i>J. Linn. Soc., Bot.</i> 77(2): 125–129	H—K	EN
subsp. <i>barteri</i>	Benin (Bergu), Ghana, Nigeria, ?Togo	1978	<i>J. Linn. Soc., Bot.</i> 77(2): 125–129	AUT	VU
<i>E. brevifoliolatus</i> Vorster	South Africa (Limpopo)	1996	<i>S. African J. Bot.</i> 62(1): 61–64	H—PRE	EW
<i>E. bubalinus</i> Melville	Kenya, Tanzania (Arusha)	1957	<i>Kew Bull.</i> 1957: 252	H—K	NT
* <i>E. caffer</i> (Thunb.) Lehm.	South Africa (E Cape)	1834	<i>Nov. Stirp. Pug.</i> 6:14	BAS: <i>Cycas caffra</i>	NT
<i>E. cerinus</i> Lavranos & D.L.Goode	South Africa (KwaZulu-Natal)	1989	<i>Durban Mus. Novit.</i> 14: 153–156	H—NH	CR

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<i>E. chimanmaniensis</i> R.A.Dyer & I.Verdi.	Mozambique (Manica), Zimbabwe (Manicaland)	1969	<i>Kirkia</i> 7: 147–158	H—PRE	EN
<i>E. concinnus</i> R.A.Dyer & I.Verdi.	Zimbabwe (Matabeleland South, Midlands and Masvingo)	1969	<i>Kirkia</i> 7: 147–158	H—PRE	EN
<i>E. cupidus</i> R.A.Dyer	South Africa (Mpumalanga)	1971	<i>Bothalia</i> 10(2): 379–383	H—PRE	CR
<i>E. cycadifolius</i> (Jacq.) Lehm.	South Africa (E Cape)	1834	<i>Nov. Stirp. Pug.</i> 6:13	BAS: <i>Zamia cycadifolia</i>	LC
<i>E. delucanus</i> Malaisse, Sclavo & Crosiers	Tanzania (Mpanda)	1992	<i>Ann. Gembloux</i> 98(2): 153–155, fig. 1	H—BR	EN
<i>E. dolomiticus</i> Lavranos & D.L.Goode	South Africa (Limpopo)	1988	<i>Bull. Jard. Bot. Natl. Belg.</i> 58(1–2): 219–224	H—NH	CR
<i>E. dyerianus</i> Lavranos & D.L.Goode	South Africa (Limpopo)	1988	<i>Bull. Jard. Bot. Natl. Belg.</i> 58(1–2): 219–224	H—PRE	CR
<i>E. equatorialis</i> P.J.H.Hurter	Uganda (Eastern)	1995	<i>S. African J. Bot.</i> 61(4): 226–229	H—PRE	CR
<i>E. eugene-maraisii</i> I.Verdi.	South Africa (Limpopo)	1945	<i>J. S. African Bot.</i> 11(1): 1–3	H—PRE	EN
<i>E. ferox</i> G.Bertol	Mozambique (Gaza, Inhambane, Maputo, Sofala), South Africa (KwaZulu-Natal)	1851	<i>Mem. Reale Accad. Sci. Ist. Bologna</i> 3: 264–265	?	NT
subsp. <i>ferox</i>	Mozambique (Gaza, Inhambane, Maputo, Sofala), South Africa (KwaZulu-Natal)	2015	<i>Phytotaxa</i> 204(2): 99–115	AUT	NT
subsp. <i>emersus</i> P.Rousseau, Vorster & A.E.van Wyk	Mozambique (Inhambane)	2015	<i>Phytotaxa</i> 204(2): 99–115	H—PRE	[CR]
<i>E. friderici-guilielmi</i> Lehm.	South Africa (E Cape, Kwa Zulu-Natal)	1834	<i>Nov. Stirp. Pug.</i> 6: 8, tt. 1–3	?LT—tt. 1–3	NT
<i>E. ghellinckii</i> Lem.	South Africa (E Cape, KwaZulu-Natal)	1867	<i>Ill. Hort.</i> 14, misc.: 80–81, pl. 567	?LT—pl. 567	VU
<i>E. gratus</i> Prain	Malawi (Mulanje), Mozambique (Zambézia)	1916	<i>Bull. Misc. Inform. Kew</i> 1916: 181	LT—K	VU
<i>E. heenanii</i> R.A.Dyer	South Africa (Mpumalanga), Swaziland	1972	<i>Bothalia</i> 10(4): 539–546	H—PRE	CR
<i>E. hildebrandtii</i> A.Braun & C.D.Bouché	Kenya (Coast), Tanzania (Lushoto, Tanga, Zanzibar Island)	1874	<i>Index Palm.</i> 1874: 18	H—B	NT

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<i>E. hirsutus</i> P.J.H.Hurter	South Africa (Limpopo)	1996	<i>S. African J. Bot.</i> 62(1): 46–48, fig. 1	H—PRE	CR
<i>E. horridus</i> (Jacq.) Lehm.	South Africa (E Cape)	1834	<i>Nov. Stirp. Pug.</i> 6:14	BAS: <i>Z. horrida</i>	EN
<i>E. humilis</i> I.Verd.	South Africa (Mpumalanga)	1951	<i>Bothalia</i> 6(1): 220, 241, pl. 3	H—PRE	VU
<i>E. inopinus</i> R.A.Dyer	South Africa (Limpopo)	1964	<i>Bothalia</i> 8(2): 169–170	H—PRE	CR
<i>E. ituriensis</i> Bamps & Lisowski	Democratic Republic of Congo (Oriental)	1990	<i>Mem. New York Bot. Gard.</i> 57: 152–155	H—BR	NT
<i>E. kisambo</i> Faden & Beentje	Kenya (Taita-Taveta), Tanzania (Kilimanjaro, ?Morogoro)	1989	<i>Utafuti</i> 2(1): 7–10	H—K	EN
<i>E. laevifolius</i> Stapf & Burtt Davy	South Africa (E Cape, KwaZulu-Natal, Limpopo, Mpumalanga), Swaziland	1926	<i>Man. Pl. Transvaal</i> 1: 40, 99	H—K	CR
<i>E. lanatus</i> Stapf & Burtt Davy	South Africa (Mpumalanga)	1926	<i>Man. Pl. Transvaal</i> 1: 40, 90, fig. 4d	H—K	NT
<i>E. latifrons</i> Lehm.	South Africa (E Cape)	1838	<i>Tijdschr. Natuurl. Gesch. Physiol.</i> 4(4): 424, t.9	?LT—t. 9	CR
<i>E. laurentianus</i> De Wild.	Angola, Democratic Republic of Congo	1903	<i>Ann. Mus. Congo Belge, Bot. sér. 5, 1(1): 10, t. 25</i>	H—BR	NT
<i>E. lebomboensis</i> I.Verd.	Mozambique, South Africa (KwaZulu-Natal), Swaziland	1949	<i>Fl. Pl. Africa</i> 27: pls. 1078–1079	H—PRE	EN
<i>E. lehmannii</i> Lehm.	South Africa (E Cape)	1834	<i>Nov. Stirp. Pug.</i> 6:14	?	NT
<i>E. longifolius</i> (Jacq.) Lehm.	South Africa (E Cape)	1834	<i>Nov. Stirp. Pug.</i> 6:14	BAS: <i>Z. longifolia</i>	NT
<i>E. mackenziei</i> L.E.Newton	South Sudan (Eastern Equatoria)	2002	<i>Bot. J. Linn. Soc.</i> 140(2): 187–192, figs. 1–6	H—EA	NT
<i>E. macrostrobilus</i> S.Jones & Wynants	Uganda (Northern)	1997	<i>Encephalartos</i> 50: 13–17, figs. 1–2	H—BR	EN
<i>E. manikensis</i> (Gilliland) Gilliland	Mozambique (Manica), Zimbabwe	1939	<i>Proc. Rhodesia Sci. Assoc.</i> 37: 133–134	BAS: <i>E. gratus</i> var. <i>manikensis</i>	VU
<i>E. marunguensis</i> Devred	Democratic Republic of Congo (Katanga)	1958	<i>Bull. Soc. Roy. Bot. Belgique</i> 91: 104–110	H—BR	VU
<i>E. middelburgensis</i> Vorster, Robbertse & S.van der Westh.	South Africa (Mpumalanga)	1989	<i>S. African J. Bot.</i> 55(1): 122–126	H—PRE	CR
<i>E. msinganus</i> Vorster	South Africa (KwaZulu-Natal)	1996	<i>S. African J. Bot.</i> 62(2): 67–70	H—PRE	CR

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<i>E. munchii</i> R.A.Dyer & I.Verdi	Mozambique (Manica)	1969	<i>Kirkia</i> 7: 147–158	H—PRE	CR
<i>E. natalensis</i> R.A.Dyer & I.Verdi	South Africa (KwaZulu-Natal)	1951	<i>Bothalia</i> 6(1): 205–211, pls 1–3	H—PRE	NT
<i>E. ngoyanus</i> I.Verdi	South Africa (KwaZulu-Natal), Swaziland	1949	<i>Fl. Pl. Africa</i> 27: pls 1053–1054	?H—PRE	VU
<i>E. nubimontanus</i> P.J.H.Hurter	South Africa (Limpopo)	1995	<i>Phytologia</i> 78(6): 409–410, fig. 1	H—PRE	EW
<i>E. paucidentatus</i> Stapf & Burtt Davy	South Africa (Mpumalanga), Swaziland	1926	<i>Man. Pl. Transvaal</i> 1: 40, 99, fig. 4a	H—PRE	VU
<i>E. poggei</i> Asch.	Democratic Republic of Congo (Kasai-Occidental, Katanga)	1878	<i>Verb. Bot. Vereins Prov. Brandenburg</i> 20: 35–36	?	LC
<i>E. princeps</i> R.A.Dyer	South Africa (E Cape)	1965	<i>J. S. African Bot.</i> 31(2): 111–112, pl. 19	H—PRE	VU
<i>E. pterogonus</i> R.A.Dyer & I.Verdi	Mozambique (Manica)	1969	<i>Kirkia</i> 7: 147–158	H—PRE	CR
<i>E. relictus</i> P.J.H.Hurter	Swaziland	2001	<i>Bothalia</i> 31(2): 197–199	H—PRE	EW
<i>E. schaifesii</i> Malaisse, Sclavo & Crosiers	Democratic Republic of Congo (Katanga)	1993	<i>Bull. Jard. Bot. Natl. Belg.</i> 62: 215–219	H—BR	VU
<i>E. schmitzii</i> Malaisse	Democratic Republic of Congo (Haut-Katanga), Zambia (Muchinga)	1969	<i>Bull. Jard. Bot. Natl. Belg.</i> 39(4): 401–406	H—BR	VU
<i>E. sclavoi</i> A.Moretti, D.W.Stev. & De Luca	Tanzania (Tanga)	1990	<i>Mem. New York Bot. Gard.</i> 57: 156–161	H—K	CR
<i>E. senticosus</i> Vorster	South Africa (KwaZulu-Natal), Swaziland	1996	<i>S. African J. Bot.</i> 62(2): 76–79	H—PRE	VU
<i>E. septentrionalis</i> Schweinf.	South Sudan (Western Equatoria), Uganda	1871	<i>Bot. Zeitung (Berlin)</i> 29(20): 334	SYN—K	NT
<i>E. tegulaneus</i> Melville	Kenya (Eastern, Rift Valley)	1957	<i>Kew Bull.</i> 1957: 249	H—K	LC
subsp. <i>pouysii</i> Miringu & Beentje	Kenya (Eastern)	1999	<i>J. E. Afr. Nat. Hist.</i> 88: 35	H—EA	CR
subsp. <i>tegulaneus</i>	Kenya (Rift Valley)	1999	<i>J. E. Afr. Nat. Hist.</i> 88: 35	AUT	LC
<i>E. transvenosus</i> Stapf & Burtt Davy	South Africa (Limpopo)	1926	<i>Man. Pl. Transvaal</i> 1: 40, 99, fig. 4b	H—PRE	LC
<i>E. trispinosus</i> (Hook.) R.A.Dyer	South Africa (E Cape)	1965	<i>J. S. African Bot.</i> 31(2): 112–116, pl. 20	BAS: <i>E. horridus</i> var. <i>trispinosus</i>	VU
<i>E. turneri</i> Lavranos & D.L.Goode	Mozambique (Nampula)	1985	<i>Garcia de Orta, Ser. Bot.</i> 7(1–2): 11–14	H—LISC	LC
<i>E. umbeluziensis</i> R.A.Dyer	Mozambique, Swaziland	1951	<i>Fl. Pl. Africa</i> 28: pl. 1100	H—PRE	EN

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<i>E. villosus</i> Lem.	South Africa (E Cape, KwaZulu-Natal), Swaziland	1867	<i>Ill. Hort.</i> 14, misc.: 79–80; 15: pl. 557	?	LC
<i>E. whitelockii</i> P.J.H.Hurter	Uganda (Western)	1995	<i>Phytologia</i> 78(6): 410–411, fig. 3	H—PRE	CR
<i>E. woodii</i> Sander	South Africa (KwaZulu-Natal)	1908	<i>Gard. Chron., ser. 3</i> 43: 257	?	EW
Synonyms and other names:					
<i>E. acanthus</i> Mast.	= <i>E. friderici-guilielmi</i>	1878	<i>Gard. Chron., n.s.</i> 10(261): 810	?	
<i>E. altensteinii</i> var. <i>altensteinii</i>	= <i>E. altensteinii</i>	1842	<i>Monogr. Cycad.</i> : 52	AUT	
<i>E. altensteinii</i> var. <i>angustifolius</i> Miq.	= <i>E. altensteinii</i>	1842	<i>Monogr. Cycad.</i> : 52	?	
<i>E. altensteinii</i> var. <i>bispinnus</i> J.M.Wood	= <i>E. woodii</i>	1907	<i>Ann. Rep. Bot. Gard. Natal.</i> : 8-9	?	
<i>E. altensteinii</i> var. <i>distans</i> Regel	= <i>E. altensteinii</i>	1874	<i>Trudy Imp. S.-Peterburgsk. Bot. Sada</i> 3(1): 114	?	
<i>E. altensteinii</i> var. <i>eriocephalus</i> de Vriese	= <i>E. horridus</i>	1846	<i>Nederl. Kruidk Arch.</i> 1:171-175	?	
<i>E. altensteinii</i> var. <i>grandis</i> Regel	= <i>E. altensteinii</i>	1875	<i>Gartenflora</i> 24: 40	?	
<i>E. altensteinii</i> var. <i>macrophyllus</i> Regel	= <i>E. altensteinii</i>	1875	<i>Gartenflora</i> 24: 41	?	
<i>E. altensteinii</i> var. <i>parvifolius</i> Regel	= <i>E. altensteinii</i>	1874	<i>Trudy Imp. S.-Peterburgsk. Bot. Sada</i> 3(1): 114	?	
<i>E. altensteinii</i> var. <i>paucidentatus</i> Regel	= <i>E. paucidentatus</i>	1874	<i>Trudy Imp. S.-Peterburgsk. Bot. Sada</i> 3(1): 114	?	
<i>E. altensteinii</i> var. <i>semidentatus</i> Miq.	= <i>E. altensteinii</i>	1842	<i>Monogr. Cycad.</i> : 52	?	
<i>E. altensteinii</i> var. <i>spinosior</i> Regel	= <i>E. altensteinii</i>	1875	<i>Gartenflora</i> 24: 40	?	
<i>E. brachyphyllus</i> Lehm. & de Vriese	= <i>E. caffer</i>	1838	<i>Tijdschr. Natuurl. Gesch. Physiol.</i> 4(4): 414, tt. 6–7	?LT—tt. 6-7	
<i>E. caffer</i> var. <i>brachyphyllus</i> (Lehm. & de Vriese) A.DC.	= <i>E. caffer</i>	1868	<i>Prodr. [A. P. de Candolle]</i> 16(2): 532	BAS: <i>E. brachyphyllus</i>	
<i>E. caffer</i> var. <i>caffer</i>	= <i>E. caffer</i>	1868	<i>Prodr. [A. P. de Candolle]</i> 16(2): 532	AUT	
<i>E. caffer</i> var. <i>integrifolius</i> Regel	= <i>E. caffer</i>	1874	<i>Trudy Imp. S.-Peterburgsk. Bot. Sada</i> 3(1): 113	?	
<i>E. caffer</i> var. <i>unidentatus</i> Regel	= <i>E. caffer</i>	1874	<i>Trudy Imp. S.-Peterburgsk. Bot. Sada</i> 3(1): 113	?	

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<i>E. cycadifolius</i> var. <i>cycadifolius</i>	= <i>E. cycadifolius</i>	1874	<i>Trudy Imp. S.-Peterburgsk. Bot. Sada</i> 3(1): 111	AUT	
<i>E. cycadifolius</i> var. <i>friderici-guilielmi</i> (Lehm.) Regel	= <i>E. friderici-guilielmi</i>	1874	<i>Trudy Imp. S.-Peterburgsk. Bot. Sada</i> 3(1): 111	BAS: <i>E. friderici-guilielmi</i>	
<i>E. cycadifolius</i> var. <i>glaber</i> Regel	= <i>E. cycadifolius</i>	1874	<i>Trudy Imp. S.-Peterburgsk. Bot. Sada</i> 3(1): 111	?	
<i>E. denisonii</i> (C.Moore & F.Muell.) F.Muell.	= <i>Lepidozamia peroffskyana</i>	1859	<i>Quart. J. Trans. Pharm. Soc. Victoria</i> 2: 90	BAS: <i>Macrozamia denisonii</i>	
<i>E. dyeri</i> F.Muell.	= <i>Macrozamia dyeri</i>	1885	<i>Australas. Chem. Druggist</i> 4: 84	H—MEL	
<i>E. elongatus</i> Lehm.	= <i>E. lehmannii</i>	1838	<i>Tijdschr. Natuurl. Gesch. Physiol.</i> 4(4): 419	?	
<i>E. eugene-maraisii</i> subsp. <i>eugene-maraisii</i>	= <i>E. eugene-maraisii</i>	1988	<i>Bull. Jard. Bot. Natl. Belg.</i> 58(1–2): 219–224	AUT	
<i>E. Eugenemaraisii</i> subsp. <i>middelburgensis</i> Lavranos & D.L.Goode	= <i>E. middelburgensis</i>	1988	<i>Bull. Jard. Bot. Natl. Belg.</i> 58(1–2): 219–224	H—PRE	
<i>E. eximius</i> I.Verdi	= <i>E. cycadifolius</i>	1954	<i>Bothalia</i> 6(2): 426	H—PRE	
<i>E. flavistrobilus</i> I.Turner & Scelavo	= ? <i>E. schaifesii</i>	2006	<i>Biotechnol. Agron. Soc. Environm.</i> 10(3): 181–183, figs. 1–4	H—BR	
<i>E. fraseri</i> (Miq.) Miq.	= <i>Macrozamia fraseri</i>	1863	<i>Verslagen Meded. Afd. Natuurk. Kon. Akad. Wetensch.</i> 15: 368	BAS: <i>M. fraseri</i>	
<i>E. gracilis</i> Mast.	= <i>E. ghellinckii</i>	1868	<i>Gard. Chron.</i> 25(14): 349	?	
<i>E. graniticola</i> Vorster, Robbertse & S.van der Westh.	= <i>E. dyerianus</i>	1988	<i>S. African J. Bot.</i> 54(4): 363–366, figs. 1–2	H—PRE	
<i>E. gratus</i> var. <i>gratus</i>	= <i>E. gratus</i>	1938	<i>J. S. African Bot.</i> 4: 153	AUT	
<i>E. gratus</i> var. <i>manikensis</i> Gilliland	= <i>E. manikensis</i>	1938	<i>J. S. African Bot.</i> 4: 153	H—BM	
<i>E. hildebrandtii</i> var. <i>dentatus</i> Melville	= ? <i>E. hildebrandtii</i>	1957	<i>Kew Bull.</i> 1957: 248	H—K	
<i>E. hildebrandtii</i> var. <i>hildebrandtii</i>	= <i>E. hildebrandtii</i>	1957	<i>Kew Bull.</i> 1957: 248	AUT	
<i>E. horridus</i> var. <i>hallianus</i> (de Vriese) Miq.	= <i>E. horridus</i>	1842	<i>Monogr. Cycad.</i> : 58–59	BAS: <i>E. hallianus</i>	
<i>E. horridus</i> var. <i>horridus</i>	= <i>E. horridus</i>	1842	<i>Monogr. Cycad.</i> : 58	AUT	
<i>E. horridus</i> var. <i>lanuginosus</i> (Jacq.) Miq.	= <i>E. longifolius</i>	1838	<i>Ann. Sci. Nat., Bot. ser. 2</i> , 10: 367	BAS: <i>Zamia lanuginosa</i>	
<i>E. horridus</i> var. <i>latifrons</i> (Lehm.) J.Schust.	nom. illeg.; = <i>E. latifrons</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 117	BAS: <i>E. latifrons</i>	
<i>E. horridus</i> var. <i>latifrons</i> (Lehm.) Miq.	= <i>E. latifrons</i>	1842	<i>Monogr. Cycad.</i> : 59	BAS: <i>E. latifrons</i>	
<i>E. horridus</i> var. <i>nanus</i> (Lehm.) J.Schust.	= <i>E. horridus</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 117	BAS: <i>E. nanus</i>	
<i>E. horridus</i> var. <i>trispinosus</i> Hook.	= <i>E. trispinosus</i>	1863	<i>Bot. Mag.</i> 89: t. 5371	?LT—t. 5371	

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<i>E. horridus</i> var. <i>van-hallii</i> (de Vriese) J.Schust.	<i>nom. illeg.; = E. horridus</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 117	BAS: <i>E. van-hallii</i>	
<i>E. imbricans</i> Vorster	= <i>E. equatorialis</i>	1995	<i>Novon</i> 5(4): 388, figs. 2–5	H—K	
<i>E. kanga</i> Pócs & Q.Luke	= ? <i>E. kisambo</i>	2007	<i>J. E. Afr. Nat. Hist.</i> 96(2): 193–201	H—NHT	
<i>E. kosiensis</i> Hutch.	= <i>E. ferox</i>	1932	<i>Bull. Misc. Inform. Kew</i> 1932: 512	?	
<i>E. lanuginosus</i> (Jacq.) Lehm.	= <i>E. longifolius</i>	1834	<i>Nov. Stirp. Pug.</i> 6:14	BAS: <i>Z. lanuginosa</i>	
<i>E. lanuginosus</i> var. <i>lanuginosus</i>	= <i>E. longifolius</i>	1842	<i>Monogr. Cycad.</i> : 57	AUT	
<i>E. lanuginosus</i> var. <i>tridens</i> Miq.	= <i>Macrozamia</i> sp.	1842	<i>Monogr. Cycad.</i> : 57	?	
<i>E. lebmannii</i> f. <i>dentatus</i> Regel ex J.Schust.	= <i>E. lebmannii</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 115	?	
<i>E. lebmannii</i> f. <i>lebmannii</i>	= <i>E. lebmannii</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 115	AUT	
<i>E. lebmannii</i> f. <i>spinulosus</i> (Lehm.) J.Schust.	= <i>E. lebmannii</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 115	BAS: <i>E. spinulosus</i>	
<i>E. lebmannii</i> var. <i>lebmannii</i>	= <i>E. lebmannii</i>	1868	<i>Prodr. [A. P. de Candolle]</i> 16(2): 531	AUT	
<i>E. lebmannii</i> var. <i>spinulosus</i> (Lehm.) Regel	= <i>E. lebmannii</i>	1868	<i>Prodr. [A. P. de Candolle]</i> 16(2): 531	BAS: <i>E. spinulosus</i>	
<i>E. lemarielianus</i> De Wild. & T.Durand	= <i>E. poggei</i>	1900	<i>Bull. Soc. Roy. Bot. Belgique</i> 39: 80	H—BR	
<i>E. longifolius</i> var. <i>angustifolius</i> Miq.	= <i>E. longifolius</i>	1842	<i>Monogr. Cycad.</i> : 56	?	
<i>E. longifolius</i> var. <i>hookeri</i> Miq.	= <i>E. altensteinii</i>	1868	<i>Prodr. [A. P. de Candolle]</i> 16(2): 531–532	?	
<i>E. longifolius</i> var. <i>latifolius</i> Regel	= <i>E. longifolius</i>	1874	<i>Trudy Imp. S.-Peterburgsk. Bot. Sada</i> 3(1): 113	?	
<i>E. longifolius</i> var. <i>longifolius</i>	= <i>E. longifolius</i>	1842	<i>Monogr. Cycad.</i> : 55	AUT	
<i>E. longifolius</i> var. <i>revolutus</i> Miq.	= <i>E. longifolius</i>	1842	<i>Monogr. Cycad.</i> : 55–56	?	
<i>E. macdonnellii</i> F.Muell. ex Miq.	= <i>Macrozamia macdonnellii</i>	1863	<i>Verslagen Meded. Afd. Natuurk. Kon. Akad. Wetensch.</i> 15: 370	H—MEL	
<i>E. mackenii</i> W.Bull	<i>nomen dubium</i>	1870	<i>Retail List [Bull]</i> No. 54: 116	?	
<i>E. majesticus</i> W.Bull	<i>nomen dubium</i>	1873	<i>Retail List [Bull]</i> No. 83: 187	?	
<i>E. marumii</i> de Vriese	<i>E. altensteinii</i>	1838	<i>Tijdschr. Natuurl. Gesch. Physiol.</i> 5: 187–189	?	
<i>E. mauritianus</i> Miq.	<i>E. longifolius</i>	1842	<i>Monogr. Cycad.</i> : 48	H—U	
<i>E. miquelianii</i> F.Muell.	= <i>Macrozamia miquelianii</i>	1862	<i>Fragm. (Mueller)</i> 3(18): 38	LT—MEL	
<i>E. moorei</i> (F.Muell.) F.Muell.	= <i>Macrozamia moorei</i>	1881	<i>Fragm. (Mueller)</i> 11: 125	BAS: <i>M. moorei</i>	
<i>E. nanus</i> Lehm.	= <i>E. horridus</i>	1838	<i>Tijdschr. Natuurl. Gesch. Physiol.</i> 4(4): 421, t. 8c	?LT—t. 8C	
<i>E. oldfieldii</i> Miq.	= <i>Macrozamia riedlei</i>	1863	<i>Verslagen Meded. Afd. Natuurk. Kon. Akad. Wetensch.</i> 15: 370	H—MEL	
<i>E. pauli-guilielmi</i> (W.Hill & F.Muell.) F.Muell.	= <i>Macrozamia pauli-guilielmi</i>	1859	<i>Quart. J. Trans. Pharm. Soc. Victoria</i> 2: 90	BAS: <i>M. pauli-guilielmi</i>	

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<i>E. preissii</i> (Lehm.) F.Muell.	= <i>Macrozamia riedlei</i>	1858	<i>Quart. J. Trans. Pharm. Soc. Victoria</i> 2: 90	BAS: <i>M. preissii</i>	
<i>E. pungens</i> (L.f.) Lehm.	<i>nomen dubium</i>	1834	<i>Nov. Stirp. Pug.</i> 6:13	BAS: <i>Z. pungens</i>	
<i>E. regalis</i> W.Bull	= <i>E. altensteinii</i>	1889	<i>Retail List [Bull]</i> : 4, t. 8	?	
<i>E. sclavoi</i> De Luca, D.W.Stev. & A.Moretti	<i>nom. illeg.</i>	1991	<i>Delpinoa</i> 29–30: 3–5 (1989 issued 1991 Oct. H—K 24)	H—K	
<i>E. spinulosus</i> Lehm.	= <i>E. lehmannii</i>	1838	<i>Tijdschr. Natuurl. Gesch. Physiol.</i> 4(4): 419, t. ?LT—t. 8C 8c	?LT—t. 8C	
<i>E. spiralis</i> (Salisb.) Lehm.	= <i>Macrozamia spiralis</i>	1834	<i>Nov. Stirp. Pug.</i> 6:13	BAS: <i>Z. spiralis</i>	
<i>E. spiralis</i> var. <i>diplomera</i> F.Muell.	= <i>Macrozamia diplomera</i>	1866	<i>Fragm. (Mueller)</i> 5: 172	LT—MEL	
<i>E. spiralis</i> var. <i>major</i> Miq.	= <i>Macrozamia miquelii</i>	1863	<i>Verslagen Meded. Afd. Natuurk. Kon. Akad. Wetensch.</i> 15: 368	?	
<i>E. spiralis</i> var. <i>spiralis</i>	= <i>Macrozamia spiralis</i>	1863	<i>Verslagen Meded. Afd. Natuurk. Kon. Akad. Wetensch.</i> 15: 368	AUT	
<i>E. striatus</i> Stapf & Burtt Davy	= <i>E. villosus</i>	1926	<i>Man. Pl. Transvaal</i> 1: 40 & 99	H—PRE	
<i>E. successibus</i> Vorster	= <i>E. whitelockii</i>	1995	<i>S. African J. Bot.</i> 61(6): 347	H—K	
<i>E. tridentatus</i> (Willd.) Lehm.	= <i>Macrozamia</i> sp.	1834	<i>Nov. Stirp. Pug.</i> 6:13	BAS: <i>Z. tridentata</i>	
<i>E. van-hallii</i> de Vriese	= <i>E. horridus</i>	1838	<i>Tijdschr. Natuurl. Gesch. Physiol.</i> 4(4): 422	?	
<i>E. venetus</i> Vorster	= <i>E. nubimontanus</i>	1996	<i>S. African J. Bot.</i> 62(2): 71	H—PRE	
<i>E. verrucosus</i> Vorster, Robbertse & S.van der Westh.	= <i>E. dolomiticus</i>	1988	<i>S. African J. Bot.</i> 54(5): 487–490, figs. 1–3	H—PRE	
<i>E. verschaffeltii</i> Regel	= <i>E. caffer</i>	1874	<i>Trudy Imp. S.-Peterburgsk. Bot. Sada</i> 3(1): 111	?	
<i>E. villosus</i> f. <i>hildebrandtii</i> (A.Braun & C.D.Bouché) Henn.	= <i>E. hildebrandtii</i>	1890	<i>Gartenflora</i> 39: 238	BAS: <i>E. hildebrandtii</i>	
<i>E. villosus</i> f. <i>intermedius</i> Henn.	= <i>E. villosus</i>	1890	<i>Gartenflora</i> 39: 238	?	
<i>E. villosus</i> f. <i>villosus</i>	= <i>E. villosus</i>	1890	<i>Gartenflora</i> 39: 238	AUT	
<i>E. villosus</i> var. <i>amplicatus</i> W.Bull	<i>nomen dubium</i>	1873	<i>Retail List [Bull]</i> No. 83: 187	?	
<i>E. villosus</i> var. <i>villosus</i>	= <i>E. villosus</i>	1873	<i>Retail List [Bull]</i> No. 83: 187	?	
<i>E. voiensis</i> A.Moretti, D.W.Stev. & Sclavo	= <i>E. kisambo</i>	1989	<i>Ann. Missouri Bot. Gard.</i> 76(3): 935	H—K	
<i>E. vroomii</i> Mast.	<i>nomen dubium</i>	1868	<i>Gard. Chron.</i> 25(14): 349	?	
LEPIDOZAMIA Regel (2 species: Australia)		1857	<i>Bull. Soc. Imp. Naturalistes Moscou</i> 30: 182		
<i>L. hopei</i> Regel	Australia (Qld)	1876	<i>Gartenflora</i> 25: 6	?	LC

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* <i>L. peroffskyana</i> Regel	Australia (NSW, Qld)	1857	<i>Bull. Soc. Imp. Naturalistes Moscou</i> 30: 184–185, fig. 21	H—LE	LC
Synonyms and other names:					
<i>CATAKIDOZAMIA</i> W. Hill	= <i>LEPIDOZAMIA</i>	1865	<i>Gard. Chron.</i> 22(47): 1107		
<i>C. hopei</i> W. Hill	= <i>L. hopei</i>	1865	<i>Gard. Chron.</i> 22(47): 1107	?	
<i>MACROZAMIA</i> Miq. (41 species: Australia)		1842	<i>Monogr. Cycad.</i> : 35		
<i>M. cardiaca</i> P.I.Forst. & D.L.Jones	Australia (Qld)	1998	<i>Fl. Australia</i> 48: 717	H—BRI	VU
<i>M. communis</i> L.A.S.Johnson	Australia (NSW)	1959	<i>Proc. Linn. Soc. New South Wales</i> , ser. 2, 84(1): 98	H—NSW	LC
<i>M. concinna</i> D.L.Jones	Australia (NSW)	1998	<i>Fl. Australia</i> 48: 718	H—BRI	LC
<i>M. conferta</i> D.L.Jones & P.I.Forst.	Australia (Qld)	1994	<i>Austrobaileya</i> 4(2): 271–273, fig. 1	H—BRI	VU
<i>M. cranei</i> D.L.Jones & P.I.Forst.	Australia (Qld)	1994	<i>Austrobaileya</i> 4(2): 273–275, fig. 2	H—BRI	EN
<i>M. crassifolia</i> P.I.Forst. & D.L.Jones	Australia (Qld)	1994	<i>Austrobaileya</i> 4(2): 275–276, fig. 3	H—BRI	VU
<i>M. diplomera</i> (F.Muell.) L.A.S.Johnson	Australia (NSW)	1959	<i>Proc. Linn. Soc. New South Wales</i> , ser. 2, 84(1): 98	BAS: <i>E. spiralis</i> var. <i>diplomera</i>	LC
<i>M. douglasii</i> W.Hill ex F.M.Bailey	Australia (Qld)	1883	<i>Syn. Queensl. Fl.</i> : 500	?H—MEL	LC
<i>M. dyeri</i> (F.Muell.) C.A.Gardner	Australia (WA)	1930	<i>Enum. Pl. Austral. Occ.</i> : 3	BAS: <i>E. dyeri</i>	LC
<i>M. elegans</i> K.D.Hill & D.L.Jones	Australia (NSW)	1998	<i>Fl. Australia</i> 48: 718	H—NSW	EN
<i>M. fawcettii</i> C.Moore	Australia (NSW)	1884	<i>J. Proc. Roy. Soc. New S. Wales</i> 17: 120	H—NSW	NT
<i>M. fearnsidei</i> D.L.Jones	Australia (Qld)	1991	<i>Austrobaileya</i> 3(3): 481	H—CANB	LC
<i>M. flexuosa</i> C.Moore	Australia (NSW)	1884	<i>J. Proc. Roy. Soc. New S. Wales</i> 17: 121	H—NSW	EN
<i>M. fraseri</i> Miq.	Australia (WA)	1842	<i>Monogr. Cycad.</i> : 37	?H—MEL	LC
<i>M. glaucophylla</i> D.L.Jones	Australia (NSW)	1998	<i>Fl. Australia</i> 48: 718–719	H—CANB	LC
<i>M. heteromera</i> C.Moore	Australia (NSW)	1884	<i>J. Proc. Roy. Soc. New S. Wales</i> 17: 122	LT—NSW	LC
<i>M. humilis</i> D.L.Jones	Australia (NSW)	1998	<i>Fl. Australia</i> 48: 719	H—CANB	VU
<i>M. johnsonii</i> D.L.Jones & K.D.Hill	Australia (NSW)	1992	<i>Telopea</i> 5(1): 31	H—CANB	LC
<i>M. lomandroidea</i> D.L.Jones	Australia (Qld)	1991	<i>Austrobaileya</i> 3(3): 483	H—CANB	EN
<i>M. longispina</i> P.I.Forst. & D.L.Jones	Australia (Qld)	1998	<i>Fl. Australia</i> 48: 717	H—BRI	NT
<i>M. lucida</i> L.A.S.Johnson	Australia (NSW, Qld)	1959	<i>Proc. Linn. Soc. New South Wales</i> , ser. 2, 84(1): 102	H—NSW	LC
<i>M. macdonnellii</i> (F.Muell. ex Miq.) A.DC.	Australia (NT)	1868	<i>Prodr. [A. P. de Candolle]</i> 16(2): 537	BAS: <i>E. macdonnellii</i>	LC
<i>M. machinii</i> P.I.Forst. & D.L.Jones	Australia (Qld)	1994	<i>Austrobaileya</i> 4(2): 276	H—BRI	VU
<i>M. macleayi</i> Miq.	Australia (Qld)	1868	<i>Arch. Néerl. Sci. Exact. Nat.</i> 3: 250	?H—U	LC

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<i>M. miquelii</i> (F.Muell.) A.DC.	Australia (Qld)	1868	<i>Prodr. [A. P. de Candolle]</i> 16(2): 535	BAS: <i>E. miquelii</i>	LC
<i>M. montana</i> K.D.Hill	Australia (NSW)	1998	<i>Fl. Australia</i> 48: 717	H—NSW	LC
<i>M. moorei</i> F.Muell.	Australia (Qld)	1881	<i>Australas. Chem. Druggist</i> 4: 84	?H—MEL	NT
<i>M. mountperriensis</i> F.M.Bailey	Australia (Qld)	1886	<i>Syn. Queensl. Fl. Suppl.</i> 1: 50	N—CANB	LC
<i>M. occidua</i> D.L.Jones & P.I.Forst.	Australia (Qld)	1994	<i>Austrobaileya</i> 4(2): 278, fig. 5	H—BRI	VU
<i>M. parcifolia</i> P.I.Forst. & D.L.Jones	Australia (Qld)	1994	<i>Austrobaileya</i> 4(2): 279–281, fig. 6	H—BRI	VU
<i>M. pauli-guilielmi</i> W.Hill & F.Muell.	Australia (Qld)	1859	<i>Fragm. (Mueller)</i> 1(4): 86	H—MEL	EN
<i>M. platyrhachis</i> F.M.Bailey	Australia (Qld)	1898	<i>Queensland Agric. J.</i> 3: 356	H—BRI	VU
<i>M. plurinervia</i> (L.A.S.Johnson) D.L.Jones	Australia (NSW, Qld)	1991	<i>Austrobaileya</i> 3(3): 484	BAS: <i>M. pauli-guilielmi</i> subsp. <i>plurinervia</i>	EN
<i>M. polymorpha</i> D.L.Jones	Australia (NSW)	1998	<i>Fl. Australia</i> 48: 718	H—CANB	LC
<i>M. reducta</i> K.D.Hill & D.L.Jones	Australia (NSW)	1998	<i>Fl. Australia</i> 48: 718	H—NSW	LC
* <i>M. riedlei</i> (Gaudich.) C.A.Gardner	Australia (WA)	1930	<i>Enum. Pl. Austral. Occ.</i> : 3	H—P	LC
<i>M. secunda</i> C.Moore	Australia (NSW)	1884	<i>J. Proc. Roy. Soc. New S. Wales</i> 17: 122	LT—MEL	VU
<i>M. serpentina</i> D.L.Jones & P.I.Forst.	Australia (Qld)	2001	<i>Austrobaileya</i> 6(1): 90–92, figs. 20–21	H—BRI	NT
<i>M. spiralis</i> (Salisb.) Miq.	Australia (NSW)	1842	<i>Monogr. Cycad.</i> : 36	BAS: <i>Z. spiralis</i>	EN
<i>M. stenomera</i> L.A.S.Johnson	Australia (NSW)	1959	<i>Proc. Linn. Soc. New South Wales</i> , ser. 2, 84(1): 106	H—NSW	NT
<i>M. viridis</i> D.L.Jones & P.I.Forst.	Australia (Qld)	1994	<i>Austrobaileya</i> 4(2): 281–283, fig. 7	H—BRI	EN
Synonyms and other names:					
<i>M. corallipes</i> Hook.f.	= <i>M. spiralis</i>	1872	<i>Bot. Mag.</i> 98: t. 5943	LT—t. 5943	
<i>M. corallipes</i> var. <i>gyrata</i> W.Bull	<i>nomen dubium</i>	1873	<i>Retail List [Bull]</i> No. 83: 8	?	
<i>M. cylindrica</i> C.Moore	<i>nom. illeg.</i> ; = <i>M. miquelii</i>	1884	<i>J. Proc. Roy. Soc. New S. Wales</i> 17: 119	H—NSW	
<i>M. cylindrica</i> W.Bull	= <i>nomen dubium</i>	1874	<i>Gard. Chron., n.s.</i> 1(17): 532	?	
<i>M. denisonii</i> C.Moore & F.Muell.	= <i>Lepidozamia peroffskyana</i>	1858	<i>Fragm. (Mueller)</i> 1(2): 41	LT—MEL	
<i>M. eburnea</i> W.Bull	<i>nomen dubium</i>	1873	<i>Gard. Chron.</i> 30(11): 358	?	
<i>M. elegantissima</i> W.Bull	<i>nomen dubium</i>	1873	<i>Gard. Chron.</i> 30(11): 358	?	
<i>M. hopei</i> W.Hill	= <i>L. hopei</i>	1886	<i>Syn. Queensl. Fl. Suppl.</i> 1: 52	?	
<i>M. mackenziei</i> Mast.	= <i>M. miquelii</i>	1877	<i>Gard. Chron., n.s.</i> 7(178): 665	H—BRI	
<i>M. mackenziei</i> W.Bull	= <i>M. miquelii</i>	1877	<i>Retail List [Bull]</i> No. 129: 7	?	
<i>M. oldfieldii</i> (Miq.) A.DC.	= <i>M. riedlei</i>	1868	<i>Prodr. [A. P. de Candolle]</i> 16(2): 535	BAS: <i>Encephalartos oldfieldii</i>	

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<i>M. pauliguielmi</i> subsp. <i>flexuosa</i> (C.Moore) L.A.S.Johnson	= <i>M. flexuosa</i>	1959	<i>Proc. Linn. Soc. New South Wales</i> , ser. 2, 84(1): 109	BAS: <i>M. flexuosa</i>	
<i>M. pauli-guilielmi</i> subsp. <i>pauli-guilielmi</i>	<i>M. pauli-guilielmi</i>	1959	<i>Proc. Linn. Soc. New South Wales</i> , ser. 2, 84(1): 108	AUT	
<i>M. pauliguielmi</i> subsp. <i>plurinervia</i> L.A.S.Johnson	= <i>M. plurinervia</i>	1959	<i>Proc. Linn. Soc. New South Wales</i> , ser. 2, 84(1): 108	H—NSW	
<i>M. peroffskyana</i> (Regel) Miq.	= <i>L. peroffskyana</i>	1868	<i>Arch. Néerl. Sci. Exact. Nat.</i> 3: 252	BAS: <i>Lepidozamia peroffskyana</i>	
<i>M. plumosa</i> W.Bull	<i>nomen dubium</i>	1874	<i>Gard. Chron., n.s.</i> 1(17): 532	?	
<i>M. preissii</i> Lehm.	= <i>M. riedlei</i>	1844	<i>Nov. Stirp. Pug.</i> 8: 31	?	
<i>M. spiralis</i> var. <i>eburnea</i> W.Bull	<i>nomen dubium</i>	1873	<i>Retail List [Bull]</i> No. 83: 8	?	
<i>M. spiralis</i> var. <i>princeps</i> W.Bull	<i>nomen dubium</i>	1873	<i>Retail List [Bull]</i> No. 83: 187	?	
<i>M. tridentata</i> (Willd.) Regel	<i>nomen dubium</i> ; = <i>Macrozamia</i> sp.	1876	<i>Gartenflora</i> 25: 229	BAS: <i>Z. tridentata</i>	
<i>MICROCYCAS</i> (Miq.) A.DC. (1 species: Cuba)		1868	<i>Prodr. [A. P. de Candolle]</i> 16(2): 538		
* <i>M. calocoma</i> (Miq.) A.DC.	Cuba (Pinar del Río)	1868	<i>Prodr. [A. P. de Candolle]</i> 16(2): 538	BAS: <i>Z. calocoma</i>	CR
<i>STANGERIA</i> T.Moore (1 species: South Africa)		1853	<i>Hooker's J. Bot. Kew Gard. Misc.</i> 5: 228		
* <i>S. eriopus</i> (Kunze) Baill.	South Africa (E Cape, KwaZulu-Natal)	1894	<i>Hist. Pl. (Baillon)</i> 12: 68, in adnot.	BAS: <i>Lomaria eriopus</i>	VU
Synonyms and other names:					
<i>Lomaria eriopus</i> Kunze	= <i>S. eriopus</i>	1839	<i>Linnaea</i> 13: 152	?	
<i>S. katzneri</i> Regel	= <i>S. eriopus</i>	1874	<i>Gartenflora</i> 23: 163, t. 798	H—LE	
<i>S. paradoxa</i> T.Moore	= <i>S. eriopus</i>	1853	<i>Hooker's J. Bot. Kew Gard. Misc.</i> 5: 228	?	
<i>S. schizodon</i> W.Bull	= <i>S. eriopus</i>	1872	<i>Cat. (Bull)</i> 72: 8	?	
<i>ZAMIA</i> L. (81 species: South, Central & North America)		1763	<i>Sp. Pl., ed. 2.</i> 2: 1659		
<i>Z. acuminata</i> Oerst. ex Dyer	Costa Rica (San José)	1884	<i>Biol. Cent.-Amer., Bot.</i> 3: 194	H—C	VU
<i>Z. amazonum</i> D.W.Stev.	Brazil (Amazonas), Colombia, (Amazonas, Vaupés), Ecuador (Morona-Santiago, Napo, Sucumbíos), Peru (Loreto), S Venezuela	2001	<i>Fl. Colombia (1983+)</i> 21: 33, fig. 3	H—INPA	NT

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<i>Z. amplifolia</i> W.Bull ex Mast.	Colombia (Valle del Cauca)	1878	<i>Gard. Chron., n.s.</i> 10(261): 810	LT—K	CR
<i>Z. angustifolia</i> Jacq.	Bahamas (Eleuthera), Cuba (Guantánamo, Oriente, Santiago de Cuba)	1789	<i>Collectanea [Jacquin]</i> 3: 263 <i>Pl. Rar. [Jacquin]</i> 3, 1792	LT—pl. 636 in <i>Icon.</i> VU	
<i>Z. boliviiana</i> (Brongn.) A.DC.	Bolivia (El Beni, Cochabamba, Santa Cruz), Brazil (Mato Grosso)	1868	<i>Prodr. [A. P. de Candolle]</i> 16(2): 540	BAS: <i>Ceratozamia</i> <i>boliviiana</i>	NT
<i>Z. brasiliensis</i> Calonje & Segalla	Brazil (Matto Grosso, Rondônia)	2019	<i>Phytotaxa</i> 404 (1): 1-11. 2019	HT—UFMT	[EN]
<i>Z. chigua</i> Seem.	Colombia (Chocó, Valle del Cauca)	1854	<i>Bot. Voy. Herald</i> 6: 201–203, t. 43	LT—t. 43	NT
<i>Z. cremnophila</i> Vovides, Schutzman & Dehgan	Mexico (Chiapas, Tabasco)	1988	<i>Bot. Gaz.</i> 149(3): 351	H—MEXU	EN
<i>Z. cunaria</i> Dressler & D.W.Stev.	Panama (Colón, Panamá, Kuna de Wargandi, Kuna Yala)	1993	<i>Brittonia</i> 45(1): 5–6, fig. 2	H—NY	VU
<i>Z. decumbens</i> Calonje, Meerman, M.P.Griff. & Hoese	Belize (Cayo, Stann Creek, Toledo)	2009	<i>J. Bot. Res. Inst. Texas</i> 3(1): 31–41, figs. 1–3	H—BRH	[CR]
<i>Z. disodon</i> D.W.Stev. & Sabato	Colombia (Antioquia)	2001	<i>Fl. Colombia (1983+)</i> 21: 38–40, fig. 4	H—COL	CR
<i>Z. dressleri</i> D.W.Stev.	Panama (Colón, Kuna Yala)	1993	<i>Brittonia</i> 45(1): 6, fig. 3	H—NY	EN
<i>Z. elegantissima</i> Schutzman, Vovides & R.S.Adams	Panama (Colón, Kuna Yala)	2003	<i>Phytologia</i> 85(6): 389 (1998 publ. 21 Aug. 2003)	H—MO	EN
<i>Z. encephalartoides</i> D.W.Stev.	Colombia (Santander)	2001	<i>Fl. Colombia (1983+)</i> 21: 40–42, fig. 5	H—COL	VU, [EN]
<i>Z. erosa</i> O.F.Cook & G.N.Collins	Cuba, Jamaica, Puerto Rico	1903	<i>Contr. U.S. Natl. Herb.</i> 8(2): 267	NT—NA	VU
<i>Z. fairchildiana</i> L.D.Gómez	Costa Rica (Puntarenas, San José), Panama (Chiriquí)	1982	<i>Phytologia</i> 50(6): 401–404	LT—USJ	NT
<i>Z. fischeri</i> Miq.	Mexico (Hidalgo, Querétaro, San Luis Potosí, Tamaulipas)	1845	<i>Hort. Vanhoult.</i> 1(1): 20	NT—U	EN
<i>Z. furfuracea</i> L.f.	Mexico (Veracruz)	1789	<i>Hort. Kew. (W. Aiton)</i> 3: 477 <i>Herm. Parad. Bat.,</i> 1698	LT—pl. 210 in <i>Herm. Parad. Bat.,</i> 1698	EN

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<i>Z. gentryi</i> Dodson	Ecuador (Carchi, Esmeraldas)	1998	<i>Novon</i> 8(1): 12–14, fig. 1a-f	H—QCNE	CR
<i>Z. gomeziana</i> R.H.Acuña	Costa Rica (Limón)	2010	<i>Brenesia</i> 73–74: 29–33, fig. 1	H—CR	[VU]
<i>Z. grjalvensis</i> Pérez-Farr., Vovides & Mart.-Camilo	Mexico (Chiapas)	2012	<i>Nordic J. Bot.</i> 30(5): 565–570	H—HEM	[CR]
<i>Z. hamannii</i> A.S.Taylor, J.L.Haynes & Holzman	Panama (Bocas del Toro)	2008	<i>Bot. J. Linn. Soc.</i> 158(3): 399–429, figs. 6, 7a, 8a	H—PMA	[CR]
<i>Z. herrerae</i> S.Calderón & Standl.	El Salvador (Sonsonate), Guatemala (Quetzaltenango Retalhuleu, Santa Rosa, Suchitepéquez), Mexico (Chiapas)	1924	<i>J. Wash. Acad. Sci.</i> 14(4): 93–94, fig. 1	H—US	VU
<i>Z. huilensis</i> Calonje, H.E.Esquível & D.W.Stev.	Colombia (Huila)	2012	<i>Caldasia</i> 34(2): 283–290	H—TOLI	[CR]
<i>Z. hymenophyllidia</i> D.W.Stev.	Colombia (Amazonas), Peru (Loreto)	2001	<i>Fl. Colombia</i> (1983+) 21: 43–44, fig. 6	H—COAH	CR
<i>Z. imperialis</i> A.S.Taylor, J.L.Haynes & Holzman	Panama (Coclé, Panamá, Veraguas)	2008	<i>Bot. J. Linn. Soc.</i> 158(3): 399–429, figs. 7c, 8c, 11	H—PMA	[CR]
<i>Z. incognita</i> A.Lindstr. & Idárraga	Colombia (Antioquia, Boyacá, Caldas, Santander)	2009	<i>Phytotaxa</i> 2: 29–34, figs. 1–3	H—HUA	[VU]
<i>Z. inermis</i> Vovides, J.D.Rees & Vázq.Torres	Mexico (Veracruz)	1983	<i>Fl. Veracruz</i> 26: 22–24, fig. 3	H—XAL	CR
<i>Z. integrifolia</i> L.f.	Bahamas, Cayman Islands, Cuba, United States (Florida, Georgia)	1789	<i>Hort. Kew. (W. Aiton)</i> 3: 478	H—BM	NT
var. <i>broomei</i> D.B.Ward	United States (Florida)	2016	<i>Phytologia</i> 98(3): 175	FLAS	[NE]
var. <i>floridana</i> (A.DC.) D.B.Ward	United States (Florida)	2016	<i>Phytologia</i> 98(3): 175	BAS: <i>Z. floridana</i>	[NE]
var. <i>integrifolia</i>	United States (Florida)	2016	<i>Phytologia</i> 98(3): 174	AUT	[NE]
var. <i>silvicola</i> (Small) D.B.Ward	United States (Florida)	2016	<i>Phytologia</i> 98(3): 176	BAS: <i>Z. silvicola</i>	[NE]
var. <i>umbrosa</i> (Small) D.B.Ward	United States (Florida)	2016	<i>Phytologia</i> 98(3): 174	BAS: <i>Z. umbrosa</i>	[NE]
<i>Z. ipetensis</i> D.W.Stev.	Panama (Panamá, Kuna Yala)	1993	<i>Brittonia</i> 45(1): 7–9, fig. 4	H—NY	EN
<i>Z. katzeriana</i> (Regel) E.Rettig	Mexico (Chiapas, Tabasco, Veracruz)	1896	<i>Gartenflora</i> 45: 148–149, fig. 31	BAS: <i>Ceratozamia katzeriana</i>	EN

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<i>Z. lacandona</i> Schutzman & Vovides	Mexico (Chiapas)	1998	<i>Novon</i> 8(4): 441–446, figs. 1–3	H—FLAS	EN
<i>Z. lecointei</i> Ducke	Brazil (Pará), Colombia (Amazonas), Venezuela (Amazonas)	1915	<i>Arch. Jard. Bot. Rio de Janeiro</i> 1: 9–10, pls 1–2	H—MG	NT
<i>Z. lindenii</i> Regel ex André	Ecuador (Azuay, Bolívar, Chimborazo, El Oro, Esmeraldas, Guayas, Los Ríos, Manabí, Pichincha), Perú (Tumbes)	1875	<i>Ill. Hort.</i> 22: 23, pl. 195	LT—K	[DD]
<i>Z. lindensis</i> D.W.Stev., D.Cárdenas & N.Castaño	Colombia (Guaviare)	2018	<i>Brittonia</i> 70(3): 364 [epublished 19 Jun 2018]	H—COAH	[EN]
<i>Z. lindleyi</i> Warsz.	Panama (Bocas del Toro, Chiriquí)	1851	<i>Allg. Gartenzeitung</i> 19: 145–146, fig. s.n.	LT—iconic s.n.	[DD]
<i>Z. loddigesii</i> Miq.	Mexico (Chiapas, Hidalgo, Oaxaca, Tabasco, Tamaulipas, Veracruz)	1843	<i>Tijdschr. Natuurl. Gesch. Physiol.</i> 10: 72–73	LT—U	NT
<i>Z. lucayana</i> Britton	Bahamas (Abaco, Long Island)	1907	<i>Bull. New York Bot. Gard.</i> 5(18): 311	H—NY	EN, [CR]
<i>Z. macrochiera</i> D.W.Stev.	Colombia (Amazonas), Peru (Loreto)	2004	<i>Cycad Classific. Concepts & Recommend.</i> : 185–186, fig. 14.7	H—NY	CR
<i>Z. manicata</i> Linden ex Regel	Colombia (Antioquia, Chocó), Panama (Darién)	1876	<i>Trudy Imp. S.-Peterburgsk. Bot. Sada</i> 4(4): 310, t. 926, fig. e	LT—t. 926, fig. e in Gartenflora 27, 1878	NT
<i>Z. meermanii</i> Calonje	Belize (Belice, Cayo, Toledo)	2009	<i>J. Bot. Res. Inst. Texas</i> 3(1): 23–29, figs. 1–2	H—BRH	[EN]
<i>Z. melanorrhachis</i> D.W.Stev.	Colombia (Antioquia, Bolívar, Córdoba, Santander)	2001	<i>Fl. Colombia (1983+)</i> 21: 55, fig. 11	H—COL	EN
<i>Z. montana</i> A.Braun	Colombia (Antioquia, Risaralda)	1875	<i>Monatsber. Königl. Preuss. Akad. Wiss. Berlin</i> : 376–377	N—NY	CR
<i>Z. monticola</i> Chamb.	Guatemala (Alta Verapaz)	1926	<i>Bot. Gaz.</i> 81: 219, 223, figs. 1–3	H—MO	CR
<i>Z. muricata</i> Willd.	Colombia (La Guajira, Meta), Venezuela (Aragua, Carabobo, Falcón, Lara, Yaracuy)	1806	<i>Sp. Pl. ed. 2. 4:</i> 847–848	H—B-W	NT

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<i>Z. nana</i> A.Lindstr., Calonje, D.W.Stev. & A.S.Taylor	Panama (Coclé)	2013	<i>Phytotaxa</i> 98(2): 27–42, figs. 6–7	H—PMA	[EN]
<i>Z. nesophila</i> A.S.Taylor, J.L.Haynes & Holzman	Panama (Bocas del Toro)	2008	<i>Bot. J. Linn. Soc.</i> 158(3): 399–429, figs. 7b, 8b, 10	H—PMA	[CR]
<i>Z. neurophyllidia</i> D.W.Stev.	Costa Rica, Nicaragua (Río San Juan, Atlántico Sur), Panama (Bocas del Toro)	1993	<i>Brittonia</i> 45(1): 10, fig. 5	H—PMA	VU
<i>Z. obliqua</i> A.Braun	Colombia (Antioquia, Chocó, Valle del Cauca), Costa Rica (Puntarenas), Panama (Colón, Darién, Panamá)	1875	<i>Monatsber. Königl. Preuss. Akad. Wiss. Berlin:</i> 376	N—BM	NT
<i>Z. oligodonta</i> E.Calderón & D.W.Stev.	Colombia (Risaralda)	2003	<i>Revista Acad. Colomb. Ci. Exact.</i> 27(105): 486–490	H—FMB	DD, [EN]
<i>Z. onan-reyesii</i> C.Nelson & Sandoval	Honduras (Cortés)	2008	<i>Ceiba</i> 49(1): 135–136, figs. 1–6	H—TEFH	[CR]
<i>Z. oreillyi</i> C.Nelson	Honduras (Atlántida)	2006	<i>Ceiba</i> 46(1): 42, figs. 11–13	H—TEFH	VU
<i>Z. paucijuga</i> Wieland	Mexico (Colima, Guerrero, Jalisco, Michoacán, Nayarit, Oaxaca)	1916	<i>Amer. Foss. Cycads</i> 2: 212, fig. 86	LT—fig. 86	NT
<i>Z. paucifoliolata</i> Calonje	Colombia (Valle del Cauca)	2018	<i>Phytotaxa</i> 385(2): 85–93 [epublished 27 Dec 2018]	H—HUA	[EN]
<i>Z. poeppigiana</i> Mart. & Eichler	Brazil (Acre), Peru (Amazonas, Huánuco, Loreto, Pasco, San Martín, Ucayali)	1863	<i>Fl. Bras. (Martius)</i> 4(1): 414–416, t. 109	LT—F	NT
<i>Z. portoricensis</i> Urb.	W Puerto Rico	1899	<i>Symb. Antill.</i> 1(2): 291	IT—NY	EN
<i>Z. prasina</i> W.Bull	Belize (Belize, Cayo, Orange Walk, Stann Creek, Toledo), Guatemala (Petén), Mexico (Campeche, Chiapas, Tabasco, Quintana Roo, Yucatán)	1881	<i>Retail List [Bull]:</i> 20	LT—K	[NT]

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<i>Z. pseudomonticola</i> L.D.Gómez ex D.W.Stev. & Sabato	Costa Rica (Puntarenas), Panama (Chiriquí)	1986	<i>Taxon</i> 35(1): 141	H—CR	NT
<i>Z. pseudoparasitica</i> J.Yates	Panama (Bocas del Toro, Coclé, Colón, Veraguas)	1854	<i>Bot. Voy. Herald</i> 6: 201–203, 253	H—BM	NT
* <i>Z. pumila</i> L.	Cuba, Dominican Republic, Puerto Rico	1763	<i>Sp. Pl., ed. 2.</i> 2: 1659	LT—t. 58 in <i>Horti Med. Amstelod</i> 1, 1697	NT
<i>Z. purpurea</i> Vovides, J.D.Rees & Vázq.Torres	Mexico (Oaxaca, Veracruz)	1983	<i>Fl. Veracruz</i> 26: 28–31, fig. 5	H—XAL	CR
<i>Z. pygmaea</i> Sims	Cuba (W Cuba, Isla de la Juventud)	1815	<i>Bot. Mag.</i> 42: t.1741	H—BM	CR
<i>Z. pyrophylla</i> Calonje, D.W.Stev. & A.Lindstr.	Colombia (Chocó)	2010	<i>Brittonia</i> 62(1): 80–85, figs. 1–2	H—CHOCO	[CR]
<i>Z. restrepoi</i> (D.W.Stev.) A.Lindstr.	Colombia (Córdoba)	2009	<i>Taxon</i> 58(1): 268	BAS: <i>Chigua restrepoi</i>	CR
<i>Z. roezlii</i> Linden	Colombia (Chocó, Nariño, Valle del Cauca), Ecuador (Esmeraldas, Imbabura)	1873	<i>Cat. General</i> 90: 10	H—K	NT
<i>Z. sandovalii</i> C.Nelson	Honduras (Atlántida)	2006	<i>Ceiba</i> 46(1): 41–42, figs. 1–10	H—TEFH	NT
<i>Z. skinneri</i> Warsz.	Panama (Bocas del Toro)	1851	<i>Allg. Gartenzeitung</i> 19: 146, fig. s.n.	LT—fig. s.n.	EN
<i>Z. soconuscensis</i> Schutzman, Vovides & Dehgan	Mexico (Chiapas)	1988	<i>Bot. Gaz.</i> 149(3): 347–351, figs. 1–3	H—F	VU
<i>Z. sparcea</i> A.DC.	Mexico (Oaxaca)	1868	<i>Prodr. [A. P. de Candolle]</i> 16(2): 539	H—G-DC	CR
<i>Z. splendens</i> Schutzman	Mexico (Chiapas, Tabasco, Veracruz)	1984	<i>Phytologia</i> 55(5): 299–303	H—FTG	EN
<i>Z. standleyi</i> Schutzman	Guatemala (Izabal), Honduras (Atlántida, Colón, Cortés, Olancho, Yoro)	1989	<i>Syst. Bot.</i> 14(2): 214–219, figs. 1–2	H—FLAS	VU
<i>Z. stenophyllidia</i> Nic.-Mor., Mart.-Domínguez & D.W.Stev.	Mexico (Oaxaca)	2019	<i>Nordic J. Bot.</i> 37(9)-e02430: 1–11, figs. 3, 4	HT—IBUG	[NE]
<i>Z. stevensonii</i> A.S.Taylor & Holzman	Panama (Panamá)	2012	<i>Bot. Rev. (Lancaster)</i> 78(4): 335–344, figs. 1–4	H—PMA	[CR]
<i>Z. stricta</i> Miq.	Cuba (Oriente)	1851	<i>Nieuwe Verh. Eerste Kl. Kon. Ned. Inst. Wetensch. Amsterdam</i> 3(4): 183	H—U	VU
<i>Z. tolimensis</i> Calonje, H.E.Esquível & D.W.Stev.	Colombia (Tolima)	2011	<i>Brittonia</i> 63(4): 442–451 , figs. 1–2	H—TOLI	[CR]

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<i>Z. tuerckheimii</i> Donn.Sm.	Guatemala (Alta Verapaz)	1903	<i>Bot. Gaz.</i> 35(1): 8, pl. 1	H—US	NT
<i>Z. ulei</i> Dammer	Bolivia (Pando), Brazil (Acre, Amazonas, Rondônia), Colombia (Amazonas, Caquetá, Guainía, Putumayo, Vaupés), Ecuador (Napo, Pastaza, Sucumbíos), Peru (Loreto, Madre de Dios, Ucayali)	1907	<i>Verh. Bot. Vereins Prov. Brandenburg</i> 48: 117–118	LT—HBG	NT
<i>Z. urep</i> B.Walln.	Peru (Huánuco)	1996	<i>Linzer Biol. Beitr.</i> 28(2): 1056	H—W	CR
<i>Z. variegata</i> Warsz.	Belize (Toledo), Guatemala (Alta Verapaz, Izabal), Mexico (Chiapas)	1845	<i>Allg. Gartenzeitung</i> 13: 252–253	N—NY	EN
<i>Z. vazquezii</i> D.W.Stev., Sabato & De Luca	Mexico (Veracruz)	1998	<i>Delpinoa</i> 37–38: 9–17 , figs. 1–4 (1995–96 issued 1998)	H—NY	CR
<i>Z. wallisii</i> A.Braun	Colombia (Antioquia)	1875	<i>Monatsber. Königl. Preuss. Akad. Wiss. Berlin:</i> 376	LT—S	CR
Synonyms and other names:					
<i>AULACOPHYLLUM</i> Regel	= <i>ZAMIA</i>	1876	<i>Gartenflora</i> 25: 141		
<i>A. lindenii</i> (Regel ex André) Regel	= <i>Z. lindenii</i>	1876	<i>Gartenflora</i> 25: 141	BAS: <i>Z. lindenii</i>	
<i>A. montanum</i> (A.Braun) Regel	= <i>Z. montana</i>	1876	<i>Gartenflora</i> 25: 141	BAS: <i>Z. montana</i>	
<i>A. ortgiesii</i> Regel	= <i>Z. chigua</i>	1876	<i>Gartenflora</i> 25: 141	H—LE	
<i>A. roezlii</i> (Linden) Regel	= <i>Z. roezlii</i>	1876	<i>Gartenflora</i> 25: 141	BAS: <i>Z. roezlii</i>	
* <i>A. skinneri</i> (Warsz.) Regel	= <i>Z. skinneri</i>	1876	<i>Gartenflora</i> 25: 143	BAS: <i>Z. skinneri</i>	
<i>A. wallisii</i> (A.Braun) Regel	= <i>Z. wallisii</i>	1876	<i>Gartenflora</i> 25: 143 <i>Mem. New York Bot. Gard.</i> 57: 169–172	BAS: <i>Z. wallisii</i>	
<i>CHIGUA</i> D.W.Stev.	= <i>ZAMIA</i>	1876	<i>Mem. New York Bot. Gard.</i> 57: 169–172		
<i>C. bernalii</i> D.W.Stev.	= <i>Z. restrepoi</i>	1990	<i>Mem. New York Bot. Gard.</i> 57: 169–172, fig. 1i	H—COL	
* <i>C. restrepoi</i> D.W.Stev.	= <i>Z. restrepoi</i>	1990	<i>Mem. New York Bot. Gard.</i> 57: 169–172, figs. 1a-h	H—COL	
<i>PALMIFOLIUM</i> Kuntze	= <i>ZAMIA</i>	1891	<i>Revis. Gen. Pl.</i> 2: 803		
<i>P. angustifolium</i> (Jacq.) Kuntze	= <i>Z. angustifolia</i>	1891	<i>Revis. Gen. Pl.</i> 2: 803	BAS: <i>Z. angustifolia</i>	
<i>P. angustissimum</i> (Miq.) Kuntze	= <i>Z. angustifolia</i>	1891	<i>Revis. Gen. Pl.</i> 2: 803	BAS: <i>Z. angustissima</i>	

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<i>P. bolivianum</i> (Brongn.) Kuntze	= <i>Z. boliviiana</i>	1891	<i>Revis. Gen. Pl.</i> 2: 803	BAS: <i>Z. boliviiana</i>	
<i>P. chigua</i> (Seem.) Kuntze	= <i>Z. chigua</i>	1891	<i>Revis. Gen. Pl.</i> 2: 803	BAS: <i>Z. chigua</i>	
<i>P. debile</i> (Aiton) Kuntze	= <i>Z. pumila</i>	1891	<i>Revis. Gen. Pl.</i> 2: 803	BAS: <i>Z. debilis</i>	
<i>P. fischeri</i> (Miq.) Kuntze	= <i>Z. fischeri</i>	1891	<i>Revis. Gen. Pl.</i> 2: 803	BAS: <i>Z. fischeri</i>	
<i>P. floridanum</i> (A.DC.) Kuntze	= <i>Z. integrifolia</i>	1891	<i>Revis. Gen. Pl.</i> 2: 803	BAS: <i>Z. floridana</i>	
<i>P. furfuraceum</i> (L.f.) Kuntze	= <i>Z. furfuracea</i>	1891	<i>Revis. Gen. Pl.</i> 2: 803	BAS: <i>Z. furfuracea</i>	
<i>P. galeottii</i> (de Vries) Kuntze	= <i>Z. loddigesii</i>	1891	<i>Revis. Gen. Pl.</i> 2: 803	BAS: <i>Z. galeottii</i>	
<i>P. integrifolium</i> (L.f.) Kuntze	= <i>Z. integrifolia</i>	1891	<i>Revis. Gen. Pl.</i> 2: 803	BAS: <i>Z. integrifolia</i>	
<i>P. kickxii</i> (Miq.) Kuntze	= <i>Z. pygmaea</i>	1891	<i>Revis. Gen. Pl.</i> 2: 803	BAS: <i>Z. kickxii</i>	
<i>P. latifolium</i> (Lodd. ex Miq.) Kuntze	= <i>Z. furfuracea</i>	1891	<i>Revis. Gen. Pl.</i> 2: 803	BAS: <i>Z. latifolia</i>	
<i>P. loddigesii</i> (Miq.) Kuntze	= <i>Z. loddigesii</i>	1891	<i>Revis. Gen. Pl.</i> 2: 803	BAS: <i>Z. loddigesii</i>	
<i>P. medium</i> (Jacq.) Kuntze	= <i>Z. integrifolia</i>	1891	<i>Revis. Gen. Pl.</i> 2: 803	BAS: <i>Z. media</i>	
<i>P. mexicanum</i> (Miq.) Kuntze	= <i>Z. loddigesii</i>	1891	<i>Revis. Gen. Pl.</i> 2: 803	BAS: <i>Z. mexicana</i>	
<i>P. multifoliolatum</i> (A.DC.) Kuntze	= <i>Z. angustifolia</i>	1891	<i>Revis. Gen. Pl.</i> 2: 803	BAS: <i>Z.</i> <i>multifoliolata</i>	
<i>P. muricatum</i> (Willd.) Kuntze	= <i>Z. muricata</i>	1891	<i>Revis. Gen. Pl.</i> 2: 803	BAS: <i>Z. muricata</i>	
<i>P. ottonis</i> (Miq.) Kuntze	= <i>Z. pygmaea</i>	1891	<i>Revis. Gen. Pl.</i> 2: 803	BAS: <i>Z. ottonis</i>	
<i>P. poeppigianum</i> (Mart. & Eichler) Kuntze	= <i>Z. poeppigiana</i>	1891	<i>Revis. Gen. Pl.</i> 2: 803	BAS: <i>Z. poeppigiana</i>	
<i>P. pseudoparasiticum</i> (J.Yates) Kuntze	= <i>Z. pseudoparasitica</i>	1891	<i>Revis. Gen. Pl.</i> 2: 803	BAS: <i>Z.</i> <i>pseudoparasitica</i>	
<i>P. pumilum</i> (L.) Kuntze	= <i>Z. pumila</i>	1891	<i>Revis. Gen. Pl.</i> 2: 803	BAS: <i>Z. pumila</i>	
<i>P. pygmaeum</i> (Sims) Kuntze	= <i>Z. pygmaea</i>	1891	<i>Revis. Gen. Pl.</i> 2: 803	BAS: <i>Z. pygmaea</i>	
<i>P. skinneri</i> (Warsz.) Kuntze	= <i>Z. skinneri</i>	1891	<i>Revis. Gen. Pl.</i> 2: 803	BAS: <i>Z. skinneri</i>	
<i>P. sparteum</i> (A.DC.) Kuntze	= <i>Z. spartea</i>	1891	<i>Revis. Gen. Pl.</i> 2: 803	BAS: <i>Z. spartea</i>	
<i>P. strictum</i> (Miq.) Kuntze	= <i>Z. stricta</i>	1891	<i>Revis. Gen. Pl.</i> 2: 803	BAS: <i>Z. stricta</i>	
<i>P. tenue</i> (Willd.) Kuntze	= <i>Z. integrifolia</i>	1891	<i>Revis. Gen. Pl.</i> 2: 803	BAS: <i>Z. tenuis</i>	
<i>P. Yatesii</i> (Miq.) Kuntze	= <i>Z. angustifolia</i>	1891	<i>Revis. Gen. Pl.</i> 2: 803	BAS: <i>Z. Yatesii</i>	
<i>Z. allison-armourii</i> Millsp.	= <i>Z. pumila</i>	1900	<i>Publ. Field Columb. Mus., Bot. Ser.</i> 2:23	H—F	
<i>Z. amblyphyllidia</i> D.W.Stev.	= <i>Z. erosa</i>	1987	<i>Fairchild Trop. Gard. Bull.</i> 42(3): 26	H—NY	
<i>Z. angustifolia</i> var. <i>angustifolia</i>	= <i>Z. angustifolia</i>	1878	<i>Gartenflora</i> 27: 13	AUT	
<i>Z. angustifolia</i> var. <i>angustissima</i> (Miq.) Regel	= <i>Z. angustifolia</i>	1878	<i>Gartenflora</i> 27: 13	BAS: <i>Z. angustissima</i>	
<i>Z. angustifolia</i> var. <i>floridana</i> (A.DC.) Regel	= <i>Z. integrifolia</i>	1878	<i>Gartenflora</i> 27: 13	BAS: <i>Z. floridana</i>	
<i>Z. angustifolia</i> var. <i>stricta</i> (Miq.) Regel	= <i>Z. stricta</i>	1878	<i>Gartenflora</i> 27: 13	BAS: <i>Z. stricta</i>	

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<i>Z. angustifolia</i> var. <i>yatesii</i> (Miq.) Regel	= <i>Z. angustifolia</i>	1878	<i>Gartenflora</i> 27: 13	BAS: <i>Z. yatesii</i>	
<i>Z. angustissima</i> Miq.	= <i>Z. angustifolia</i>	1851	<i>Nieuwe Verb. Eerste Kl. Kon. Ned. Inst. Wetensch. Amsterdam</i> 3(4): 184	H—U	
<i>Z. baraguiniana</i> Hort. ex Regel	<i>nom. illeg.</i>	1876	<i>Trudy Imp. S.-Peterburgsk. Bot. Sada</i> 4(4): 308	?	
<i>Z. baraguiniana</i> Mast.	= <i>Z. poeppigiana</i>	1868	<i>Gard. Chron.</i> 25(14): 349	N—LE	
<i>Z. bronniartii</i> Wedd.	= <i>Z. boliviiana</i>	1849	<i>Ann. Sci. Nat., Bot. ser. 3,</i> 13: 249, pl. 3	H—P	
<i>Z. bussellii</i> Schutzman, R.S.Adams, J.L.Haynes & Whitelock	= <i>Z. onan-reyesii</i>	2008	<i>Cycad Newslett.</i> 31(2/3): 22–26, figs 1–16, 18–19	H—FLAS	
<i>Z. caffra</i> (Thunb.) Thunb.	= <i>Encephalartos caffer</i>	1800	<i>Prodr. Pl. Cap.</i> 2: 92	BAS: <i>Cycas caffra</i>	
<i>Z. calocoma</i> Miq.	= <i>Microcycas calocoma</i>	1852	<i>Fl. Serres Jard. Eur.</i> 7(6): 141	N—G-DC	
<i>Z. chamberlainii</i> J.Schust.	= <i>Z. pygmaea</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 153	?	
<i>Z. cupatiensis</i> Ducke	= <i>Z. ulei</i>	1922	<i>Arch. Jard. Bot. Rio de Janeiro</i> 3: 20, pl. 1	LT—pl. 1	
<i>Z. cycadifolia</i> Dyer	= <i>Z. loddigesii</i>	1884	<i>Biol. Cent.-Amer., Bot.</i> 3: 195	H—C	
<i>Z. cycadifolia</i> Jacq.	= <i>E. cycadifolius</i>	1801	<i>Fragm. Bot.</i> : 27, tt. 25–26	?LT—tt. 25-26	
<i>Z. cycadifolia</i> S.Brunner	<i>nom. illeg.</i>	1825	<i>Flora</i> 8: 733	?	
<i>Z. cycadis</i> L.f.	= <i>E. caffer</i>	1782	<i>Suppl. Pl. Suppl. Pl.</i> : 443	?	
<i>Z. debilis</i> L.f.	= <i>Z. pumila</i>	1789	<i>Hort. Kew. (W. Aiton)</i> 3: 478	LT—t. 58 in <i>Horti Med. Amstelod</i> 1, 1697	
<i>Z. dentata</i> Voigt	= <i>Z. integrifolia</i>	1828	<i>Syll. Pl. Nov.</i> 2:53	?	
<i>Z. floridana</i> A.DC.	= <i>Z. integrifolia</i>	1868	<i>Prodr. [A. P. de Candolle]</i> 16(2): 544	LT—G-DC	
<i>Z. floridana</i> f. <i>floridana</i>	= <i>Z. integrifolia</i> var. <i>floridana</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 152	AUT	
<i>Z. floridana</i> f. <i>silvicola</i> (Small) J.Schust.	= <i>Z. integrifolia</i> var. <i>silvicola</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 152	BAS: <i>Z. silvicola</i>	
<i>Z. floridana</i> var. <i>floridana</i>	= <i>Z. integrifolia</i> var. <i>floridana</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 152	AUT	
<i>Z. floridana</i> var. <i>purshiana</i> J.Schust.	<i>nomen dubium</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 152	?	
<i>Z. floridana</i> var. <i>purshiana</i> f. <i>silvicola</i> (Small) J.Schust.	= <i>Z. integrifolia</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 152	BAS: <i>Z. silvicola</i>	
<i>Z. floridana</i> var. <i>umbrosa</i> (Small) D.B.Ward	= <i>Z. integrifolia</i> var. <i>umbrosa</i>	2001	<i>Novon</i> 11(3): 363	BAS: <i>Z. umbrosa</i>	
<i>Z. furfuracea</i> var. <i>furfuracea</i>	= <i>Z. furfuracea</i>	1868	<i>Prodr. [A. P. de Candolle]</i> 16(2): 541	AUT	
<i>Z. furfuracea</i> var. <i>trewii</i> A.DC.	= <i>Z. furfuracea</i>	1868	<i>Prodr. [A. P. de Candolle]</i> 16(2): 541	LT—t. 26 in <i>C.J. Trew, Pl. Select. t. 26 (G)</i>	

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<i>Z. galeottii</i> de Vriese	= <i>Z. loddigesii</i>	1845	<i>Tijdschr. Natuurl. Gesch. Physiol.</i> 12:24	N—NY	
<i>Z. guggenheimiana</i> Carabia	= <i>Z. angustifolia</i>	1941	<i>Caribbean Forest.</i> 2: 89	H—NY	
<i>Z. gutierrezii</i> Sauvalle	= <i>Z. muricata</i>	1868	<i>Anales Acad. Ci. Med. Habana</i> 5: 54–55	H—HAC	
<i>Z. horrida</i> Jacq.	= <i>E. horridus</i>	1801	<i>Fragsm. Bot.</i> : 27, t. 28	?LT—tt. 28	
<i>Z. humiliis</i> Salisb.	= <i>Z. pumila</i>	1796	<i>Prodr. Stirp. Chap. Allerton</i> : 400	?	
<i>Z. jirijirimensis</i> R.E.Schult.	= <i>Z. lecointei</i>	1953	<i>Mutisia</i> 15: 2, fig. p. 5 s.n.	H—GH	
<i>Z. kickxii</i> Miq.	= <i>Z. pygmaea</i>	1842	<i>Monogr. Cycad.</i> 71, t. 8	H—U	
<i>Z. laeta</i> Salisb.	= <i>Z. pumila</i>	1796	<i>Prodr. Stirp. Chap. Allerton</i> : 400	?	
<i>Z. lanuginosa</i> Jacq.	= <i>E. longifolius</i>	1801	<i>Fragsm. Bot.</i> : 28, tt. 30–31	?LT—tt. 30-31	
<i>Z. latifolia</i> Lodd. ex Miq.	= <i>Z. furfuracea</i>	1849	<i>Tijdschr. Wis-Natuurk. Wetensch. Eerste Kl. Kon. Ned. Inst. Wetensch.</i> 2(4): 298	LT—t. 7, fig. a in <i>Linnaea</i> 19, 1847	
<i>Z. latifoliolata</i> Prenlel.	= <i>Z. pumila</i>	1872	<i>Bull. Soc. Vaud. Sci. Nat.</i> 11: 278	H—LAU	
<i>Z. lawsoniana</i> Dyer	= <i>Z. loddigesii</i>	1884	<i>Biol. Cent.-Amer., Bot.</i> 3: 195	H—OXF	
<i>Z. leiboldii</i> Miq.	= <i>Z. loddigesii</i>	1847	<i>Linnaea</i> 19: 425	H—U	
<i>Z. leiboldii</i> var. <i>angustifolia</i>	= <i>Z. loddigesii</i>	1876	<i>Trudy Imp. S.-Peterburgsk. Bot. Sada</i> 4(4): 307	N—NY	
<i>Z. leiboldii</i> var. <i>latifolia</i> Regel	= <i>Z. loddigesii</i>	1876	<i>Trudy Imp. S.-Peterburgsk. Bot. Sada</i> 4(4): 307	H—LE	
<i>Z. leiboldii</i> var. <i>leiboldii</i>	= <i>Z. loddigesii</i>	1876	<i>Trudy Imp. S.-Peterburgsk. Bot. Sada</i> 4(4): 307	AUT	
<i>Z. loddigesii</i> var. <i>angustifolia</i> Regel	= <i>Z. loddigesii</i>	1857	<i>Bull. Soc. Imp. Naturalistes Moscou</i> 30: 190	H—LE	
<i>Z. loddigesii</i> var. <i>loddigesii</i>	= <i>Z. loddigesii</i>	1857	<i>Bull. Soc. Imp. Naturalistes Moscou</i> 30: 190	AUT	
<i>Z. loddigesii</i> var. <i>longifolia</i> J.Schust.	= <i>Z. loddigesii</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 147	LT—LE	
<i>Z. loddigesii</i> var. <i>obtusifolia</i> Regel	= <i>Z. loddigesii</i>	1857	<i>Bull. Soc. Imp. Naturalistes Moscou</i> 30: 190	LT—t. 186, figs 27–28 in <i>Gartenflora</i> 6, 1857	
<i>Z. longifolia</i> Jacq.	= <i>E. longifolius</i>	1801	<i>Fragsm. Bot.</i> : 28, t. 29	LT—t. 29	
<i>Z. madida</i> R.E. Schult.	= <i>Z. manicata</i>	1958	<i>Bot. Mus. Leafl.</i> 18: 114, pl. 18	H—GH	
<i>Z. maelenii</i> Miq.	= <i>Dioon edule</i>	1844	<i>Linnaea</i> 18(1): 97–98	H—U	
<i>Z. media</i> Jacq.	= <i>Z. integrifolia</i>	1798	<i>Pl. Rar. Hort. Schoenbr.</i> 3: 77, tt. 397, 398	t. 398	
<i>Z. media</i> var. <i>commeliniana</i> J.Schust.	= <i>Z. pumila</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 155–157	?	
<i>Z. media</i> var. <i>commeliniana</i> f. <i>silicea</i> (Britton) J.Schust.	= <i>Z. pygmaea</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 157	BAS: <i>Z. silicea</i>	

Name	Distribution / synonymy	Date	Citation	Type	IUCN
<i>Z. media</i> var. <i>gutierrezii</i> (Sauvalle) J.Schust.	= <i>Z. muricata</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 154-155	BAS: <i>Z. gutierrezii</i>	
<i>Z. media</i> var. <i>gutierrezii</i> f. <i>calcicola</i> J.Schust.	<i>nomen dubium</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 155	?	
<i>Z. media</i> var. <i>jacquiniana</i> J.Schust.	= <i>Z. integrifolia</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 157-158	?	
<i>Z. media</i> var. <i>jacquiniana</i> f. <i>brevipinnata</i> J.Schust.	<i>nomen dubium</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 158	?	
<i>Z. media</i> var. <i>portoricensis</i> (Urb.) J.Schust.	= <i>Z. portoricensis</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 158	BAS: <i>Z. portoricensis</i>	
<i>Z. media</i> var. <i>tenuis</i> (Willd.) J.Schust.	= <i>Z. integrifolia</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 158	BAS: <i>Z. tenuis</i>	
<i>Z. mexicana</i> Miq.	= <i>Z. loddigesii</i>	1861	<i>Prodr. Syst. Cycad.</i> : 13-14, 25-26	H—U	
<i>Z. miquelianii</i> W.Bull	<i>nomen dubium</i>	1876	<i>Retail List [Bull]</i> No. 121: 149	?	
<i>Z. multifoliolata</i> A.DC.	= <i>Z. angustifolia</i>	1868	<i>Prodr. [A. P. de Candolle]</i> 16(2): 545	H—G-DC	
<i>Z. muricata</i> var. <i>angustifolia</i> Miq.	= <i>Z. muricata</i>	1842	<i>Monogr. Cycad.</i> : 66	H—U	
<i>Z. muricata</i> var. <i>muricata</i>	= <i>Z. muricata</i>	1842	<i>Monogr. Cycad.</i> : 66	AUT	
<i>Z. muricata</i> var. <i>obtusifolia</i> Miq.	= <i>Z. furfuracea</i>	1843	<i>Tijdschr. Natuurl. Gesch. Physiol.</i> 10: 71-72	LT—t. 7, fig. a in <i>Linnaea</i> 19, 1847	
<i>Z. noeffiana</i> Linden ex Wittm.	<i>nomen dubium</i>	1897	<i>Gartenflora</i> 46: 358	?	
<i>Z. obidensis</i> Ducke	= <i>Z. lecointei</i>	1922	<i>Arch. Jard. Bot. Rio de Janeiro</i> 3:19	H—MG	
<i>Z. obliqua</i> Regel ex Ducos	<i>nom. illeg.</i>	1877	<i>Ill. Hort.</i> 24: 140, pl. 289	pl. 289	
<i>Z. ottonis</i> Miq.	= <i>Z. pygmaea</i>	1844	<i>Linnaea</i> 17: 740	H—U	
<i>Z. pallida</i> Salisb.	<i>nom. illeg.</i>	1796	<i>Prod. Stirp. Chap. Allerton</i> : 401	?	
<i>Z. picta</i> Dyer	= <i>Z. variegata</i>	1884	<i>Biol. Cent.-Amer., Bot.</i> 3: 194	H—U	
<i>Z. polymorpha</i> D.W.Stev., A. Moretti & Vázq.Torres	= <i>Z. prasina</i>	1998	<i>Delpinoa</i> 37-38: 3-8, fig. 1 (1995-96 issued 1998)	H—NY	
<i>Z. potemkinii</i> Hort. ex Miq.	<i>nomen dubium</i>	1869	<i>Verb. Kon. Ned. Akad. Wetensch., Afd. Natuurk.</i> 2(4): 30	?	
<i>Z. princeps</i> Rob.	= <i>Z. chigua</i>	1876	<i>The Garden</i> 9: 559	?	
<i>Z. pumila</i> subsp. <i>pumila</i>	= <i>Z. pumila</i>	1981	<i>J. Arnold Arbor.</i> 61: 719	AUT	
<i>Z. pumila</i> subsp. <i>pygmaea</i> (Sims) Eckenw.	= <i>Z. pygmaea</i>	1981	<i>J. Arnold Arbor.</i> 61: 719	BAS: <i>Z. pygmaea</i>	
<i>Z. pungens</i> L.f.	<i>nomen dubium</i>	1789	<i>Hort. Kew. (W. Aiton)</i> 3: 478	?	
<i>Z. pygmaea</i> var. <i>kickxii</i> (Miq.) J.Schust.	= <i>Z. pygmaea</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 152-153	BAS: <i>Z. kickxii</i>	
<i>Z. pygmaea</i> var. <i>ottonis</i> (Miq.) J.Schust.	= <i>Z. pygmaea</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV. 1): 153	BAS: <i>Z. ottonis</i>	
<i>Z. pygmaea</i> var. <i>wrightii</i> A.DC.	= <i>Z. pygmaea</i>	1868	<i>Prodr. [A. P. de Candolle]</i> 16(2): 543-544	?	
<i>Z. silicea</i> Britton	= <i>Z. pygmaea</i>	1916	<i>Bull. Torrey Bot. Club</i> 43: 462	H—NY	

Name	Distribution / synonymy	Date	Citation	Type	IUCN
<i>Z. silvicola</i> Small	= <i>Z. integrifolia</i> var. <i>silvicola</i>	1926	<i>J. New York Bot. Gard.</i> 27(318): 128, figs. 1,2	H—NY	
<i>Z. spiralis</i> Salisb.	= <i>Macrozamia spiralis</i>	1796	<i>Prodr. Stirp. Chap. Allerton:</i> 401	?	
<i>Z. sylvatica</i> Chamb.	= <i>Z. loddigesii</i>	1926	<i>Bot. Gaz.</i> 81: 223, 225, fig. 4	LT—NY	
<i>Z. tenuifolia</i> W.Bull	<i>nomen dubium</i>	1872	<i>Retail List [Bull]</i> No. 72: 8	?	
<i>Z. tenuis</i> Willd.	= <i>Z. integrifolia</i>	1806	<i>Sp. Pl., ed. 2.</i> 4(2): 846	H—B-W	
<i>Z. tonkinensis</i> L.Linden & Rodigas	= <i>Cycas tonkinensis</i>	1885	<i>Ill. Hort.</i> 32: 27, pl. 547	H—t.547	
<i>Z. tridentata</i> Willd.	<i>nomen dubium</i> = <i>Macrozamia</i> sp.	1806	<i>Sp. Pl., ed. 2.</i> 4(2): 845–845	?	
<i>Z. ulei</i> subsp. <i>lecointei</i> (Ducke) Ducke	= <i>Z. lecointei</i>	1935	<i>Arq. Inst. Biol. Veg.</i> 2(1): 27	BAS: <i>Z. lecointei</i>	
<i>Z. ulei</i> subsp. <i>ulei</i>	= <i>Z. ulei</i>	1935	<i>Arq. Inst. Biol. Veg.</i> 2(1): 27	AUT	
<i>Z. umbrosa</i> Small	= <i>Z. integrifolia</i> var. <i>umbrosa</i>	1921	<i>J. New York Bot. Gard.</i> 22: 136, in adnot.	LT—NY	
<i>Z. vernicosa</i> Mast.	= <i>E. altensteinii</i>	1868	<i>Gard. Chron.</i> 25(14): 349	?	
<i>Z. verschaffeltii</i> Miq.	<i>nomen dubium</i>	1869	<i>Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk.</i> 2(4): 31–32	H—U	
<i>Z. wallisii</i> H.J.Veitch	<i>nom. illeg.</i>	1875	<i>Gard. Chron. n.s., 3:</i> 795	?	
<i>Z. wielandii</i> J.Schust.	= <i>Z. poeppigiana</i>	1932	<i>Pflanzenr. (Engler)</i> 99 (IV, 1): 149	?	
<i>Z. Yatesii</i> Miq.	= <i>Z. angustifolia</i>	1851	<i>Nieuwe Verh. Eerste Kl. Kon. Ned. Inst. Wetensch. Amsterdam</i> 3(4): 182	H—U	

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LITERATURE CITED

- Bridson, G., Scarlett, D. R., Townsend, T., Polen, E. A., and E. R. Smith. 2004. BPH-2: Periodicals with Botanical Content: Constituting a Second Edition of *Botanico-Periodicum-Huntianum*. Hunt Institute for Botanical Documentation, Carnegie Mellon University, Pittsburgh, PA.
- Brummitt, R. K., and C. E. Powell (eds.). 1992. Authors of Plant Names. Royal Botanic Gardens, Kew, UK.
- Hill, K. D., D. W. Stevenson, and R. Osborne. 2004a. The world list of cycads. *Proceedings of the Fifth International Conference on Cycad Biology. Botanical Review* 70: 274–298.
- _____, _____, and _____. 2004b. The world list of cycads. Pp. 219-235 (Appendix 1). In T. Walters & R. Osborne (eds.), *Cycad Classification: Concepts and Recommendations*. CABI Publishing, Wallingford, UK.
- _____, _____, and _____. 2004c. The world list of cycads. Pp. 195-212. In A.J. Lindström (ed.), *Proceedings of the Sixth International Conference on Cycad Biology*. Nong Nooch Tropical Botanical Garden, Thailand.
- _____, _____, and _____. 2007. The world list of cycads. Proceedings of the Seventh International Conference on Cycad Biology (Xapala, Mexico, 2005). *Memoirs of the New York Botanical Garden* 97: 454–483.
- Holmgren, P. K., N. H. Holmgren, and L. C. Barnett. 1990. Index Herbariorum. Part I: The Herbaria of the World, 8th ed. Regnum Vegetabile 120. New York Botanical Garden, Bronx, NY.
- International Plant Names Index. 2012. Published on the Internet www.ipni.org [accessed 8 March 2012].
- IUCN. 2017. IUCN Red List of Threatened Species, version 2017.3. www.iucnredlist.org [downloaded 6 June 2018].
- Osborne, R., and J. Hendricks. 1985. A world list of cycads. *Encephalartos* 3: 13–17.
- _____, and _____. 1986. A world list of cycads-supplement. *Encephalartos* 5: 27.
- _____, Stevenson, D. W., and K. D. Hill. 1999. The world list of cycads. Pp. 224–239. In C. J. Chen (ed.), *Proceedings of the Fourth International Conference on Cycad Biology*. International Academic Publishers, Beijing, China.
- _____, Calonje, M., Hill, K. D., Stanberg, L., and D. W. Stevenson. 2012. The World List of Cycads. Pp. 480-506 in D. W. Stevenson, R. Osborne, & A. S. Taylor (eds.), *Proceedings of Cycad 2008: The 8th International Conference on Cycad Biology*. Mem. New York Bot. Gard. 106: 480–508.

- _____, ____, ____, ____, and _____. 2013. CITES and Cycads: Checklist 2013. Pp. 63–114 in Rutherford, C., J. Donaldson, A. Hudson, H. N. McGough, M. Sajeva, U. Schippmann & M. Tse-Laurence. *CITES and Cycads: A User's Guide*. Kew Publishing, Royal Botanic Gardens, Kew, UK.
- Stafleu, F. A., and R. S. Cowan. 1976–1988. *Taxonomic Literature: A Selective Guide to Botanical Publications and Collections with Dates, Commentaries and Types*, 2nd ed. Utrecht, Bohn, Scheltema, and Holkema.
- _____, and E. A. Mennega. 1992–2000. *Taxonomic Literature. Supplements to Ed. 2*. Koeltz Scientific Books, Konigstein, Germany. 6 vols.
- Stevenson, D. W., and R. Osborne. 1993a. The world list of cycads. Pp. 354–364 in D. W. Stevenson & K. J. Norstog (eds.), *Proceedings of the Second International Conference on Cycad Biology*. Palm & Cycad Societies of Australia Ltd., Milton, Queensland, Australia.
- _____, and _____. 1993b. The world list of cycads. *Encephalartos* 33: 19–25.
- _____, ____, and J. Hendricks. 1990. A world list of cycads. *Memoirs of the New York Botanical Garden* 57: 200–206.
- _____, ____, and K. D. Hill. 1995. The world list of cycads. Pp. 55–56. In P. Vorster (ed.), *Proceedings of the Third International Conference on Cycad Biology*. Cycad Society of South Africa, Stellenbosch, South Africa.
- _____, Stanberg, L., and M. A. Calonje. 2018. The world list of cycads. *Memoirs of the New York Botanical Garden*. 117: 540–576.
- Thiers, B. 2009. Index Herbariorum: A global directory of public herbaria and associated staff. The New York Botanical Garden Virtual Herbarium. <http://sweetgum.nybg.org/ih/> [downloaded on 30 August 2014].

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