Introduction

# Elucidating Human-Cycad Relationships in the Indigenous Ethnoecological and Agroecological Systems of the Americas and Beyond

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## Cycads: A Brief Introduction and History

Maize, beans, squash, and manioc initially come to mind as fundamental constituents of Mesoamerican and Caribbean foodways and agricultural systems—often viewed as the base on which regional cultures developed and flourished. Chilies, potatoes, and tomatoes emerge as other major American contributions to global foodways and agroecologies; however, cycads are essentially absent from this view. If recognized at all, these ancient plants might instead be regarded as ornamentals or associated with the intoxication of cattle and neurodegenerative diseases in humans (Cox and Sacks 2002; Patiño 1989; Thieret 1958; Whiting 1963, 1989). Yet, throughout Mesoamerica, the Caribbean, and the Americas more broadly, cycads figure prominently in regional culinary traditions, symbolism, and mythology from at least the Late Archaic period (ca. 3500–2000 BCE) to the present. These regional data parallel evidentiary patterns noted in other areas of the world, from Oceania to Asia to Africa, in which cycads held considerable alimentary and symbolic significance as a managed wild food since the Pleistocene–Holocene transition ca. 11 kya (see, e.g., Beck 1992; Bradley 2005; Hayward and Kuwahara 2012; Khuraijam and Singh 2012; Kira and Miyoshi 2000; Osborne et al. 1994, 2007; Patiño 1989; Smith 1951; Smith 1982; Thieret 1958; Tōyama and Ankei 2015, among numerous others). Their presence in

the early archaeological records of Mesoamerica and the Caribbean, their prominent place in regional mythologies and symbolism, and their continued use and cultural significance point to the conceptual saliency and alimentary role of cycads.

In *Under the Shade of Thipaak: The Ethnoecology of Cycads in Mesoamerica and the Caribbean,* we begin a conversation on human-cycad relationships in Mesoamerica and the circum-Caribbean world that extends our understanding of the role of cycads and biocultural heritage in this and other regions. The title of this book refers to the child fertility deity who brought maize to the Teenek, a Mayan language-speaking cultural group centered along the western coast of the Gulf of Mexico in what are now the Mexican states of San Luis Potosí, Veracruz, and Tamaulipas. Crucially, "Thipaak" is also used in a number of Teenek terms that refer to cycads (Alcorn 1984; Bonta et al. 2019; Bonta and Osborne 2007; Englehardt et al. 2020). Thus, Thipaak as both deity and concept encapsulates the multiple relationships between cycads and people, as well as illustrating conceptual convergence between cycads and maize in Teenek epistemology (Englehardt and Carrasco 2020)—a pattern noted in other regional Indigenous groups (Bonta et al. 2019; Englehardt et al. 2020).

This volume brings together contributions from specialists in a broad range of fields—from genomics to art history—to document and describe the multifaceted roles that cycads have played in Mesoamerican and Caribbean agroecologies, foodways, and symbolism. Through this, we hope to bring the American data on cycads, their cultural significance, and conservation status into conversation with global patterns of cycad use and ideation. Our collaboration developed from an initial focus on the compelling association between certain cycads and maize, initially described by Janice Alcorn (1984, Alcorn et al. 2006) and developed more fully in the work of Mark Bonta and colleagues (Bonta, 2007, 2009, this volume; see also Bonta and Osborne, 2007; Bonta et al. 2006, 2019; Vite-Reyes 2012; Vite-Reyes et al. 2010, among others). Our consideration of this intriguing connection resulted in a range of exciting research avenues, eventually evolving into the wider set of concerns examined in this volume, which include cycad biology and genomics, classification, conservation, and distribution in Mesoamerica, as well as the use of these plants in Indigenous agroecological systems, foodways, and their roles in mythology and art.

From this holistic perspective we see evidence for a millennial human-cycad relationship that dates to at least the Late Archaic period in Mesoamerica (ca. 3500–2000 BCE), and likely earlier. Genomic evidence suggesting that American cycads were in part dispersed by humans, in tandem with

their presence in the early archaeological record of the region, opens a vista onto a critical moment in Mesoamerican and wider Caribbean subsistence practices, at a time immediately prior to or concurrent with the domestication of maize and its rise to become the major staple crop of Mesoamerica. Considering cycads and similar managed wild plant resources encourages reflection on categories such as agriculture, horticulture, forest gardens, and managed resources, among others (see Ford 1985) that are fundamental to understanding pre-agricultural subsistence practices and attendant ideological systems. We find components of these Indigenous epistemologies in narratives of conflict, such as the opposition seen between cycads and the breadnut tree (*Brosimum alicastrum*) (Alcorn 1984; Alcorn et al. 2006; see also Lévi-Strauss 1969–1981).

The deep history of cycads in Mesoamerican foodways possibly explains their disproportionate role in regional mythologies and symbolic systems, the presence of shared ethnonyms with teosinte (*Zea mays parviglumis*) and maize, and the sustained use of cycads in the region, even when they are often considered now mainly as a "famine food"—a category to which many managed wild foods and resources have been relegated, often uncritically, in the academic literature. Nevertheless, human-cycad relationships appear to have shaped a rich symbolic world where plants parallel, manifest, and enact mythological structures—which themselves reflect Indigenous ecological perspectives. Unravelling these epistemologies offers another window on the significance of plants and their ecological contexts that is distinctly more complex than is typically recognized, and often posits somewhat uncomfortable challenges to traditional "Western" conceptions of human relationships with the natural world and its web of life, and the place of our own species in these wider ecologies.

At this point, it is perhaps necessary to clarify the status of cycads as "wild" plants. As many sources, and indeed, many chapters in the volume, attest, cycads can be discussed in reference and relation to a number of other plants that are not wild at all, such as maize, beans, and sweet potatoes. Further, it is possible that humans played a role in the genetic diversification and distribution of cycads across the landscape, perhaps by transporting seeds, transplanting live specimens, or even tending cycads in forest gardens or other horticultural, non-agricultural production systems (see Ford 1985). However, the crucial distinction is that cycads were never domesticated; at no point have these plants depended on humans—or artificial selection—for their biological reproduction. Moreover, as we have argued elsewhere (Bonta et al. 2019; Englehardt et al. 2020), the cultural links between cycads and other plants, particularly maize, are conceptual in nature—such as the

maize-cycad convergence in Teenek culture discussed above. We therefore do not suggest that such associations reflect actual genetic or biological relationships, although it is certainly possible that they were conceived of this way within Indigenous classificatory systems (see Carrasco 2020, and chapter 6, this volume). In this sense, and although humans may have moved cycads, or cultivated them at small scales, such "management" does not change the biological status of the plant as wild, despite the fact that cycads were, and continue to be, utilized as a foodstuff and in a variety of cultural practices throughout Mesoamerica and the Caribbean.

In addition to speaking to the cultural and botanical place of cycads within Mesoamerica and the circum-Caribbean world, this volume also models a way of approaching a botanical subject that may be used to examine other species and to explore questions of hybrid biocultural heritage more generally (Descola 2013). It demonstrates that the collaborative synergy arising from bringing disparate fields together offers a more revealing consideration of the significant role that a particular class of plants played in Indigenous American cultures—and also gives rise to subsequent research questions on an underexplored topic. Furthermore, the contributions collected here seek to diminish the notion that plants or animals stand in isometric relationship with specific deities, or held static roles in human cultural conceptions; rather, they emphasize the dynamic relationships that existed—and continue to operate—among subsistence practices, ecological epistemologies, and ideation. In short, the contributors show that to understand one element of a system requires a detailed knowledge of the complex holistic system of which it is but one part. Finally, to these cultural questions addressed by a number of contributors, we have invited other participants who describe the history of the study of American cycads, as well as their distribution, biology, genetics, and future conservation.

Because we recognize that some readers may not be conversant with cycad biology and their natural history, in the following section of the introduction we provide a brief overview of these issues, foreshadowing the first chapter by Calonje et al., which provides a more detailed exploration of these subjects. Likewise, stemming from our aim to bring the Mesoamerican evidence into conversation with worldwide discussions of cycads, we offer a cursory review of broader patterns of human-cycad relationships across the globe, before zeroing in on our specific regional focus on the Mesoamerican and circum-Caribbean worlds. Although this may at first appear counterintuitive for a volume whose avowed focus is the Americas, we feel that exploring relations between cycads and humans in other regions helps to provide both context and a point of reference for the considerations unpacked in the

individual chapters collected here. In this sense, we seek to first contextualize the Mesoamerican and Caribbean examples within broader global patterns that point to the vital place of these plants in human culture, as well as highlight the urgent need to better understand the role of such plants in both the past and present.

## What are Cycads?

Cycads are seed-bearing plants that belong to the ancient order of Cycadales, of a lineage that originated ca. 300 million years ago. They are related to other gymnosperms including conifers, araucaria, and ginkgo. Like other gymnosperms, they do not produce flowers, but instead reproduce via cones or strobili (Figure 0.1) on male or female plants, and thus are dioecious. Each plant produces a morphologically distinct strobilus; male plants produce pollen cones (microstrobili), while female plants produce ovuliferous or seed cones (megastrobili) (Norstog and Nicholls 1997; Whitelock 2002; see also Calonje et al., this volume). Pollination depends mostly on specialized pollinators, usually a species of beetle (Terry, Tang, Taylor, et al. 2012) or other insects (Tang et al. 2018; Terry, Tang, and Marler 2012). Both sexes have woody, pachycaul or thick cylindrical trunks with a large rosette crown

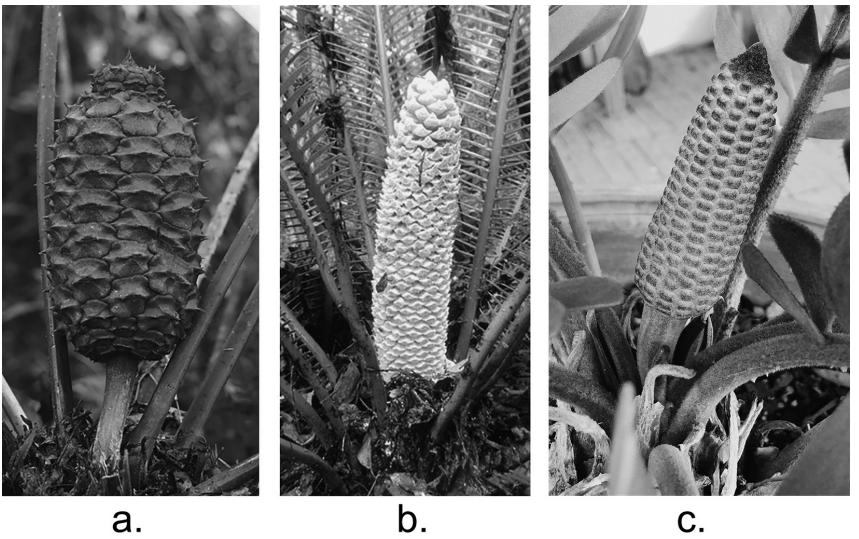


Figure 0.1. Strobili of three Mexican cycad species: *a,* female *Ceratozamia fuscoviridis*; *b,* male *Dioon edule*; *c,* female *Zamia furfuracea* (*a,* courtesy Michael Calonje; *b,* photograph by Chip Jones, used under CC BY-NC-SA 4.0 license; *c,* photograph by Angélica Cibrián-Jaramillo).


Figure 0.2. Pachycaul stem, rosette crown, and pinnate leaves of cycads: *a, Dioon edule* (photograph by Andrew P. Vovides); *b, Ceratozamia fuscoviridis* (photograph by Michael Calonje).

of stiff evergreen pinnate leaves (Figure 0.2), giving them a hard and leathery texture. In this way, cycads superficially resemble—and are often mistaken for—palms or even ferns, given their circinate leaves, but they are not closely related to either of these groups.

The more than 350 extant species of cycads are classified into three families (Cycadaceae, Stangeriaceae, and Zamiaceae) and ten genera (Calonje et al. 2022; Christenhusz, Reveal, et al. 2011; Stevenson 1992). Species vary greatly in size, from diminutive ones with subterranean stems to arborescent examples reaching more than 10 meters in height. Like trees, they are slow-growing, long-lived plants (Octavio-Aguilar 2008), with some specimens known to be several thousand years old. Cycads are resilient plants and thrive in a variety of ecosystems throughout the tropical and subtropical regions of the world (see Figure 0.3; Norstog and Nicholls 1997), oftentimes in locations with extreme environmental conditions.

Cycad root adaptations allow them to exploit what are for other plants inhospitable or nutrient-poor ecological niches. Their complex roots possess two main structures: a contractile taproot that anchors the plant to the soil and stores starches, in some cases actively pulling the plant into the earth, and coralloid roots (Figure 0.4) that are lateral roots with specialized palisade cells that host facultative symbioses with cyanobacteria and other bacterial groups (Gutiérrez-García et al. 2019). These cyanobacteria and other bacterial groups, such as Rhizobiales and Actinobacteria, together help the plant fix nitrogen, transport other nutrients, and produce the neurotoxin