

# The Cycad Newsletter

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# Coevolution of cycads and dinosaurs

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## INTRODUCTION

Cycads were a major component of forests during the Mesozoic Era, the shade of their fronds falling upon the scaly backs of multitudes of dinosaurs that roamed the land. Paleontologists have long postulated that cycad foliage provided an important food source for reptilian herbivores, but the extinction of dinosaurs and the contemporaneous precipitous decline in cycad populations at the close of the Cretaceous have generally been assumed to have resulted from different causes. Ecologic effects triggered by a cosmic impact are a widely-accepted explanation for dinosaur extinction; cycads are presumed to have suffered because of their inability to compete with fast-growing flowering plants that appeared during the mid-Cretaceous "angiosperm explosion." This paper explores a different hypothesis, i.e., that the evolutionary fates of cycads and dinosaurs were inextricably intertwined, and the Late Cretaceous extinction of these reptiles was the triggering event that caused cycads to diminish to their present status as "living fossils." The main tenet of this hypothesis is cycads depended on herbivorous dinosaurs to disperse their seeds, and the disappearance of these herbivores led to a precipitous decline in the geographic range and numerical abundance of cycads. Evidence comes from the toxicology of extant cycads, their seed dispersal strategies, anatomical characteristics of herbivorous dinosaurs, and the geographic distribution and taxonomic diversity of modern and fossil cycads.

## TOXICOLOGY OF EXTANT CYCADS

Illustrations in textbooks commonly depict herbivorous dinosaurs browsing on cycad fronds, but biochemical evidence from extant cycads suggests that these reconstructions are incorrect. Foliage of modern cycads is highly toxic to vertebrates because of the presence of two powerful neurotoxins and carcinogens, cycasin (methylazoxymethanol-beta-D-glucoside) and macrozamin (beta-N-methylamine-L-alanine). Acute symptoms triggered by cycad foliage ingestion include vomiting, diarrhea, and abdominal cramps, followed later by loss of coordination and paralysis of the limbs. Death may result from acute liver failure or starvation and dehydration stemming from paralysis (Whiting 1963, 1989

Adverse effects caused by cumulative low-dose exposures are less well understood. Cycad ingestion by humans has been proposed as a cause of amyotrophic lateral sclerosis/parkinsonian dementia complex (ALS/PDC), a fatal neurodegenerative disease prevalent in parts of Guam, New Guinea, and Japan (Spencer et al. 1991; Spencer and Kisby 1992; Sacks 1997; Cox and Sacks 2002; Brenner et al., 2003). Cycad toxins are mutagenic and they induce a variety of cancers, particularly of the liver and kidneys. Laboratory studies have implicated these compounds as a possible cause of diabetes. The only creatures known to consume cycad foliage with no discernible ill effects are a few types of insects, including Lepidoptera larvae that utilize cycasin absorbed during feeding as a defense against predators (Nash 1992).

The presence of cycasin and macrozamin in all genera of modern

cycads suggests that the biosynthesis of these compounds was a trait that evolved early in the history of the Cycadales. Brenner et al. (2002) suggested that macrozamin possibly serves a regulatory function during cycad growth, but a strong case can be made that the most important reason for the evolution of cycad toxins was their usefulness as a defense against foliage predation at a time when dinosaurs were the dominant herbivores. The protective role of these toxins is evidenced by the seed dispersal characteristics of modern cycads.

## CYCAD SEED DISPERSAL STRATEGIES

Seed dispersal is important to a species' survival for several reasons. Plants that are able to spread their seeds over a large area reap genetic benefits from the opportunities for cross-pollination among individuals that come from differing gene pools. Seed



Fig. 1. Cross-section of seed cone of *Zamia roezlii*. Adapted from André (1873) *L'illustration Horticole* 20, Planches 133-134, reproduced in Jones (1993), p.301.



Fig. 2. Cycads evolved three basic architectural strategies for making their seeds available to large browsing animals: individual seeds attached to long, flexible sporophylls (example: *Cycas media*), upright cones borne at the stem apex (example: *Encephalartos manikensis*), and cones suspended beneath the leaf crown on a short stalk (example: *Dioon spinulosum*) (Photos by Bart Schutzman).

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dispersal also provides a mechanism for geographic migration of plant populations in response to changing environmental conditions. Finally, most herbivorous insects and microbial plant pathogens are able to infest only a few closely related host species, and survival rates are much higher for seedlings that sprout far away from the parent plants because distance inhibits the spread of pests to the new generation (Janzen 1970).

Cycads are prolific seed producers, with individual cones containing 500 or more large seeds (Fig. 1). Each seed consists of a hard starchy kernel surrounded by a thick fleshy sarcotesta. The presence of a fleshy sarcotesta contrasts to the naked seeds produced by other gymnosperms, and the morphology of cycad seeds is functionally analogous to the fruit-borne seeds of angiosperms. Stevenson (1990) and Brenner et al. (2003) provide a detailed discussion of cycad anatomy and reproduction. The kernels of all extant cycads contain high levels of toxins, but in almost all species the sarcotesta is edible and possesses characteristics that attract animals. The sarcotesta is so rich in sugar that members of many indigenous cultures savor this tissue for its sweet flavor (Whiting 1963). Cycad sarcotesta are typically bright colored, often red, orange, or yellow, and they are densely clustered in large highly visible cones that are positioned within easy reach of browsers. These bright colors likely evolved to attract reptiles, which possess good color vision; except for primates, most mammals are color blind. Although birds see colors, their small body sizes make them ineffective dispersers of cycad seeds.

Although sarcotesta tissue is readily digested, the kernel is protected by a resistant outer coating (sclerotesta) that insures safe passage of the endosperm through the host's digestive tract. Horticulturists have learned that cycad germination rates are greatly improved when the sclerotesta is abraded with a knife or file (Smith 1978) and when the seeds are soaked in concentrated acid (Dehgan and Johnson 1983), mimicking passage of the seed through the digestive tract. Removal of the fleshy sarcotesta is an important preliminary step because this tissue contains chemicals that inhibit germination (Jones 2002).

### CYCAD/DINOSAUR COEVOLUTION

It is not a coincidence that the cycads acquired a combination of toxic foliage and large poisonous seeds that are enclosed within edible fleshy tissue. The simultaneous emergence of large populations of cycads and herbivorous dinosaurs during the Triassic suggests that these characteristics resulted from a process of coevolution, where chemical deterrents to foliage predation were combined with a sophisticated reproductive strategy that rewarded certain reptiles for dispersing cycad seeds. High concentrations of toxins in cycad kernels restrict seed ingestion to animals that are large enough to swallow them whole; seeds are unpalatable to small gnawing animals and to larger herbivores that masticate their food. Undigested seeds excreted in dung benefit both from their dispersal to new habitats and the excrement provides a supply of nutrients for juvenile plants. Dinosaurs benefited from this reproductive arrangement in two ways: cycad seed cones provided a nutritious treat, and the subsequent seed dispersal insured that future generations of cycads would continue to supply this food source.

Modern cycads have stiff, often spinose fronds that deter browsing, but seed cones are presented in a manner that allows herbivores to avoid the foliage. Cycad genera commonly bear upright cones positioned above the leaf crown (e.g., *Dioon*, *Encephalartos*, *Lepidozamia*, *Macrozamia*, *Stangeria*, and *Zamia*). In many species of *Cycas* the seeds are borne on flexible sporophylls that extend outside the protective fronds, and the large seed cones of *Dioon spinulosum* and *Dioon rzedowskii* dangle from a peduncle (Fig. 2). Although cycad seeds are positioned so that they can be easily reached by large browsing animals (Fig. 3), toxins within the kernels can be avoided only if the seeds are swallowed intact. This combination of properties probably evolved to attract consumption by prosauropods, sauropods and stegosaurs (Fig. 4), herbivores that used their teeth to rake in foliage, which was swallowed after

dominant Triassic herbivores, and the first group of dinosaurs to achieve great numerical abundance and widespread geographic distribution as evidenced by fossils from Europe, Asia, Africa, and North and South America (Galton 1985, VanHeerden 1997). The absence of wear facets suggest that prosauropods used their teeth for nipping off bits of vegetation. They relied on gastroliths to abrade unchewed ingested matter, a style of digestion that made prosauropods ideally suited for the dispersal of fertile cycad seeds.

Sauropods became dominant herbivores during the Jurassic Era. These reptiles had larger bodies than prosauropods, but both dinosaurs possessed similar dental and digestive characteristics. Stegosaurs, the other common Jurassic herbivore, likewise had teeth that were ill-suited for masticating foliage. Rather than being selective feeders, all of these herbivores consumed huge quantities of plant matter, relying on microbial fermentation to digest to digest cellulose (Weaver 1983; Farlow 1987).

Cycad seed cones were probably never a major food source for herbivorous dinosaurs, the sugar-rich sarcotesta having provided a tasty snack rather than the main course. Although some kernels may have been crushed during digestion by the abrasive action of gastroliths, the massive body sizes of these herbivorous dinosaurs kept toxin levels below the amount necessary to cause illness.

The evolutionary fate of cycads took a down-turn in the Late Cretaceous, when hadrosaurs and other ornithomorphs emerged as the dominant herbivores. These dinosaurs possessed banks of compound shearing teeth that allowed them to chew tough food with great efficiency. Cycad seeds would have been inedible for these dinosaurs because potent toxins would have been released during mastication. Increased efficiency in consumption of non-cycadaceous foliage provided a nutritional benefit that

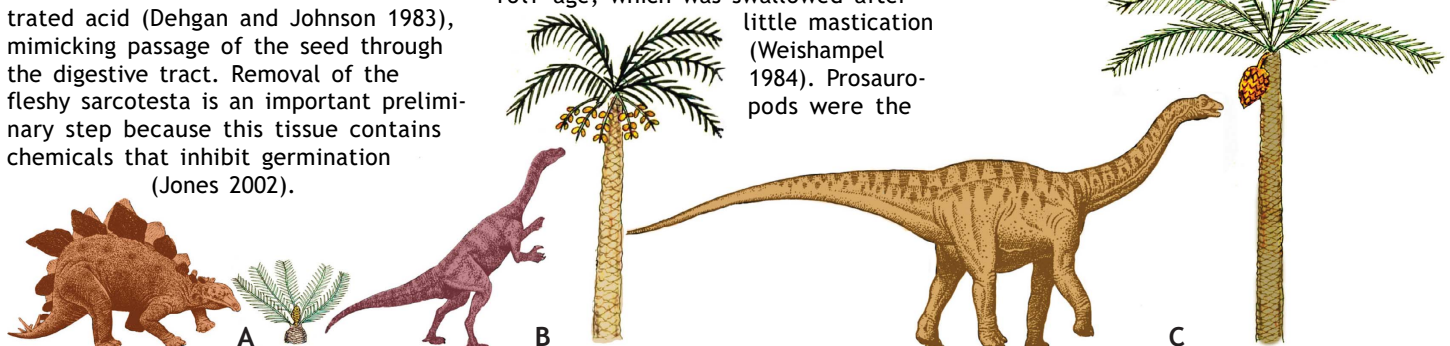


Fig. 3. The heights and positions of cycad seeds appear to have evolved to make them easily accessible to herbivorous dinosaurs. A) stegosaur shown with *Encephalartos lebomboensis*; B) prosauropod shown with *Cycas armstrongii*; C) sauropod shown with *Dioon spinulosum*. Dinosaur sketches adapted from reconstructions by Farlow and Brett-Surman (1997).



offset the inability of these dinosaurs to consume cycad seed cones. In addition, the rise of angiosperms offered a rich new food source during the Late Cretaceous. As a result of changing dinosaur dentition, cycad populations markedly declined, but the plants did not become extinct because a few species of dinosaurs continued to disperse cycad seeds, albeit less effectively than the sauropod herds of earlier times. The sauropod *Alamosaurus* survived in North America until the close of the Mesozoic, and diverse assortment of Upper Cretaceous dinosaurs included ankylosaurs and a few other herbivores that lacked efficient chewing ability.

The world-wide demise of dinosaurs at the end of the Cretaceous Era must have dealt a severe blow to cycads, who suddenly found themselves lacking any effective mechanism for seed dispersal. As a modern analog, May (1977) and Temple (1977) attributed extinction of the dodo (*Raphus cuculatus*) as a cause of the near-extinction of *Calvaria major*, once an abundant tree in the forests of Mauritius. *Calvaria* seeds are enclosed within a thick endocarp durable enough to withstand being crushed during their passage through the dodo's powerful gizzard, and these seeds germinate only after this coating has been partially abraded. Following the death of the last remaining dodo by hunters in 1681, *Calveria* populations declined precipitously. Quammen (1996) discussed a variety of factors that may have contributed to this decline, but the disappearance of the island's only large herbivore likely played a major role. Other analogies can be found in Janzen and Martin (1982), who described the decline certain Central American plant species that had evolved fruits to attract gomphotheres, ground sloth, glyptodonts, and other large herbivores that became extinct during the Pleistocene. Subsequent investigators reported similar "neotropical anachronisms" from other continents (Barlow 2000).

### CYCAD SURVIVAL IN A DINOSAUR-FREE WORLD

Warm, humid early Tertiary forests provided suitable growing conditions for cycads, but most of these populations fell victim to global climatic cooling that began in the late Eocene. Episodes of unfavorable climatic change caused cycad populations to shrink, and in the absence of large herbivores to disperse seeds, these species were not able migrate or to re-colonize their original their range when favorable conditions returned. Evidence of this process comes both from fossil occurrences and from extant cycad populations. The fossil record of Mesozoic cycads shows

that species such as *Nilsonnia*, *Ctenis*, and *Pseudoctenis* had wide geographic distribution. In contrast, the only Cenozoic genus having transcontinental distribution is *Zamia*, found as fossils in scattered formations from Wyoming to Chile. Cycads grew in much of Europe as late as the Miocene Epoch, but none are native to the region today. In North America, early Tertiary cycad populations extended as far north as Alaska, and from the California coast east to Missouri and Tennessee. Fifty million years later, only five cycad genera remain native to the New World, restricted to local regions of Florida and Georgia, the Caribbean Islands, Mexico, Central America, and northern South America (Jones 2002, Whitelock 2002).

Though never a dominant constituent of Cenozoic forests, cycads are well represented in Early Tertiary paleofloras in North America. Hopkins et al. (1998) reported the presence of cycad leaf fossils from twelve localities in Paleocene formations of Colorado and Wyoming. Other cycads have been discovered in Eocene rocks of the Pacific Northwest (Manchester 1981, Hopkins and Johnson 1997). These early Tertiary cycad fossils have two important characteristics: (1) foliar and cuticular characteristics indicate that they cannot be assigned to extant genera, and (2) each leaf form typically occurs only within a single geologic formation, often restricted to a single locality. These features represent island-like biogeographic patterns (MacArthur and Wilson 1967; Quammen 1996) where isolated populations gave rise to great taxonomic diversity, with each taxon having very restricted range. Lacking large animals to disperse their seeds, cycad populations became genetically isolated much like populations of plants and animals that become separated by vast stretches of ocean.

Similar evidence can be found in the distribution of extant cycad species, which typically inhabit small areas where they occupy specialized ecological niches. As an example, the Mexican genus *Dioon* is comprised of eleven species and subspecies, each limited to a small geographic range, with habitats that range from near sea level to above 2500 m (Fig. 5). The environmental tolerances of these individual populations are quite varied. *D. spinulosum* and *D. rzedowskii* both grow in moist habitats that have minimal temperature variation, while other species of *Dioon* are restricted to arid regions that are subject to large temperature fluctuations (Jones 2002) These plants all appear to have diversified from a common late Cenozoic ancestor (Sabato and DeLuca 1985). Other extant cycads show similar

trends. Most species of *Zamia* are understory plants distributed sporadically from Florida to Bolivia, but *Z. pseudoparasitica* is a rain forest epiphyte found only in one small area of Columbia. Another highly specialized cycad, *Z. roezlii*, grows in brackish intertidal mud at a single area on the nearby coast (Sabato 1990).

These occurrences reveal that extant cycads continue to respond to the pressures of natural selection, but they have achieved only very limited progress toward overcoming the problem of seed dispersal. In the mountains of Mexico some *Dioon* populations take advantage of gravity when their smooth ovoid seeds roll downhill to colonize new sites. Seeds of three species of *Cycas* have a layer of spongy tissue that provides buoyancy that permits them to be transported great distances by ocean currents (Dehgan and Yuen 1983). Seed flotation has allowed *C. circinalis* and *C. rumphii* to spread from the coasts of India and Southeast Asia to Madagascar, Comoros, and Seychelles Islands. In contrast, *Macrozamia communis* forms dense coastal thickets in eastern Australia and *Stangeria eriopus* populations are distributed along the coast of South Africa, but lack of seed buoyancy prevents these cycads from reaching other regions (Jones 2002).

Most modern cycads rely on birds and animals to disperse their seeds, even though this process is usually not very effective. Crows, emus, hornbills,

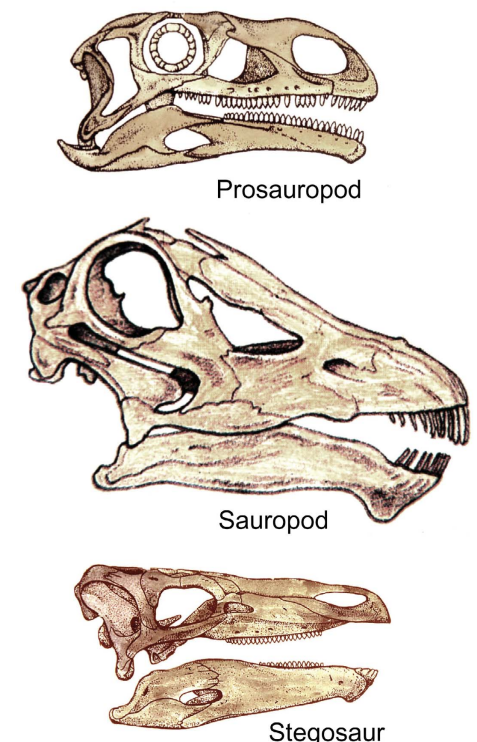


Fig. 4. Skulls of herbivorous dinosaurs that possessed teeth suited for stripping vegetation that was swallowed with minimal mastication.

and cassowaries are large enough to swallow whole cycad seeds but other birds typically carry a single seed to a nearby perch where they use their beaks to strip away the edible sarcotesta. Eckenwalder (1980) observed Northern Mockingbirds (*Mimus polyglottos*) enthusiastically feeding on seeds of *Zamia* and *Encephalartos* at a Florida botanical garden, but the kernels were dropped a short distance away. In natural habitats, only 3% of *Z. pumila* seedlings were located more than 4 m from the nearest mature female plant. In many regions of the world, rodents and small birds peel away the sarcotesta of cycad seeds, abandoning the kernels at the base of the host plant. Baboons and monkeys carry away intact cones, eating the fleshy pulp and spitting out the poisonous kernels. In Afrikaans, the common name for *Stangeria eriopus* is *bobbejaankes* ("baboon food"), because of the primate's fondness for the cones (Whitelock 2002). African elephants have been observed eating whole cones of *Encephalartos poggei*, excreting the seeds a day or two later (Jones 2002). In Mexico, seeds of *Dioon* are swallowed by deer, bears, and peccaries. However, no modern mammal can match the ability of a browsing dinosaur that could consume thousands of cycad seeds in a single afternoon, and seed size and toxicity are phylogenetic constraints that restrict cycads to their present status as botanical relicts.

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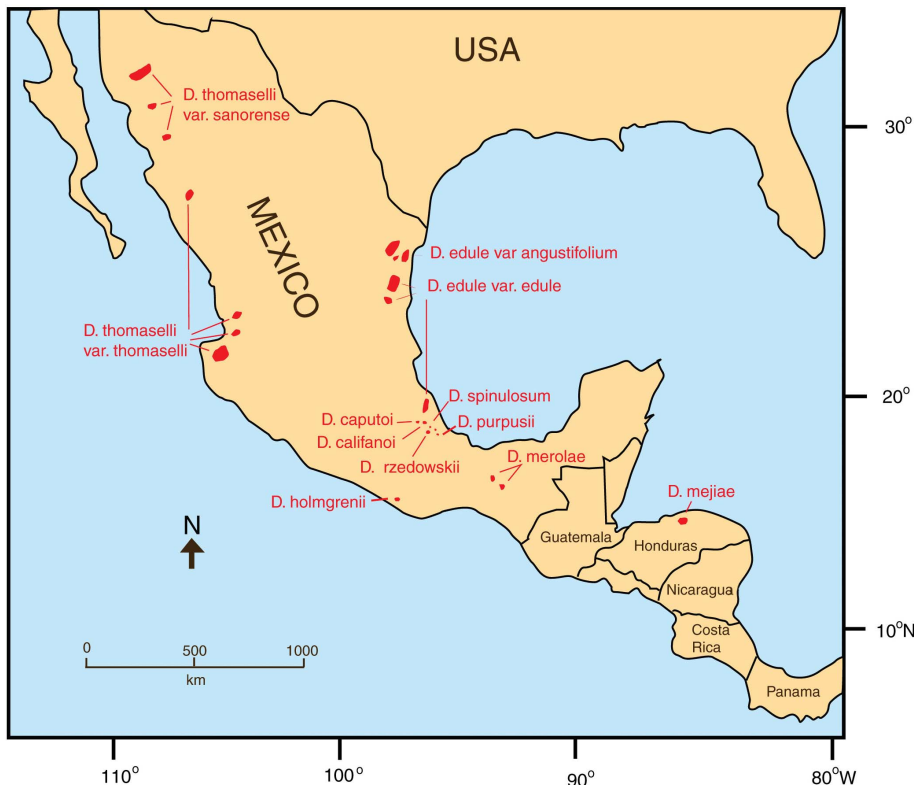


Fig. 5. Geographic ranges of extant species of *Dioon*. Map based on data from Jones (1993) and Whitelock (2002).