Origins & Dispersals

The Cycadales have been present on the Earth long enough to have experienced (and survived) two major worldwide extinction events at the beginning and end of the Mesozoic Era, one major glaciation in the Permian period and four in the Pleistocene. They have also rafted about the world on continental fragments driven by relentless tectonic forces. When the continents were fused and the world's climate was mild, the Cycadales flourished nearly worldwide from Greenland to Antarctica (Note: the continents were not at their present latitudes in that time). When the ice ages made much of the higher lattitudes frozen waste-lands, populations unable to retreat south (or North, in the case of *Pterosoma* in Australia and Tasmania) because of rift valleys, oceans and mountain barriers like the Alps, Andes, Dolomites and Pyrenees, perished in the cold. In Asia, ancient cycad habitats were lifted to inhospitable heights by the birth of the Himalayas. In South America, the uplift of the Andes and glaciers advancing from the south caused cycads to retreat north to refugias in the tropics. There were also barriers in the good times. It is curious that although South America and Africa were joined during the Jurassic, *Encephalartos* is not present today in Brazil (although fossil material hints at the presense of a close relative in North America and Argenina during the Tertiary Period) and *Zamia* shows up nowhere in Africa. Was this range was inhabited by an early precursor of both genera and their divergence only occurred at the close of the Jurassic period as that common range was broken apart? Or perhaps *Encephalartos* reached North and South America by different routes, and was unable to penetrate Central and northern South America due to geologic barriers. Fossil material dating from the Jurassic found in Yorkshire in Great Britain and attributed tentatively to *Encephalartos* suggests this may have been the doorway to North America for this genera. During a 150 million year isolation, perhaps the surviving antecedents of *Encephalartos* in the Americas were gradually transformed into *Dioon*, what we know today as a close relative of *Encephalartos*.

Late Jurassic World

Mid-Cretaceous World

Africa and Australia are stable continental masses, they have changed little over the ages, while North and South America have experienced episodes of mountain building in what were ancient sea beds and have been joined and separated a number of times as the land bridge through Central America and chains of volcanic islands either moved or were immersed. An understanding of *Zamia* and its roots in the Americas has long been in a state of confusion. Is the current domain of *Zamia* a fading relic of a global range, or was *Zamia* always a local and specialized American phenomenon? Did preColumbian Indians confuse the issue even more by establishing populations on remote islands to serve as a food source? The origins of *Microcycas* are equally shrouded in mystery. This monotypic genus possesses many ancient traits linking it to *Ceratozamia* and *Zamia*, but is not present in the fossil record. Was it's ancestral homeland always restricted to Cuba? That seems unlikely. The Cretaceous asteroid impact in the Yucatan threw a vast fan of deep ocean sediments and fiery debris over western Cuba at the close of the Cretaceous. Deep sea cores in the Atlantic and Caribbean reveal sorted materials, layers of mud, then sand, gravel, and finally huge fragments of stone carried by great waves that were more mud and gravel than water. All life on Cuba, Hispaniola, the perhaps the Antilles must have been scoured away in this calamitous event. It's hard to conceive of even seeds or uprooted trunks surviving a catastrophe of such a scale.

The devastation in Central America might have been minimized if the impactor had descended at a low angle so that much of the ejecta was directed toward the north and east. Perhaps *Microcycas* is a rare, uniquely specialized survivor of the precursor of *Zamia*. During the Pleistocene glaciations, when sea levels were much lower and Cuba and Florida and Central America were all part of one land mass, scattered *Microcycas* populations might have become established all through the area. When sea levels rose, climates changed, and the main land populations died out, *Microcycas* was restricted as an island relic. The puzzle remains, what might have been fatal to *Microcycas* in Mexico or Central America, where the climate has always been very similar to Cuba's? A disease that might have wiped out a specific pollinator?

The Yucatan impact. *Douglas Henderson*

Formation of the Deccan Traps. *Douglas Henderson*

The fossil record of the cycads of the Indian subcontinent is a classic example of the effects of plate tectonics. India was joined with Northeast Africa and Madagascar up until the early Jurassic period. Toward the end of the Jurassic it pivoted away from Africa to remain joined briefly (geologically speaking) to Northwest Australia before heading out to sea. For the remainder of the Mesozoic and the early Cenozoic, India rafted across the Indian ocean toward Asia. During this time its array of plants and animals were completely isolated. Only after India began to merge with Asia in the early Oligocene, pushing up immense mountain ranges, did its once isolated life-forms begin to intermingle with the plant and animal life of Laurasia. This must have been an exciting and dangerous time of heightened interspecies competition and adjustment to new diseases.

The Indian fossil record from the Permian through the Upper Cretaceous period suggests a diverse mixture of Bennettitales, and simple leaved seed-ferns: *Taeniopterids, Glandulatanids, Glossopterids*, and several "possible" cycadales. One, *Cycadinorachis omegoides* from the Jurassic shares some similarities with the modern *Dioon spinulosum* in the attachment of its pinnae. However, it's a somewhat tenuous similarity and some researchers believe *Cycadinorachis omegoides* actually belongs to the Bennettiales. Of the fossil leaves with similarities to cycads, one is *Nipaniophyllum raoi*. And another is *Cycadites jabalpurensis* from the Cretaceous, whose slender, pinnate leaves appear to possess a *Cycas*-like midrib. A single fossil seed from the Upper Cretaceous or Lower Eocene might also be attributed cautiously to the Cycadales. The Asian *Cycas* might well have been present in India. By this time India was in Asian waters and some modern *Cycas* seeds have adapted themselves to dispersal by ocean currents - they float. Overall, there is a dearth of material that can definitely be attributed to the Cycadales. Were true cycads rare on the Indian subcontinent, or perhaps never present at all? Did they inhabit areas where leaves and stems had no chance of being fossilized? Does this indicate that the four species of *Cycas* now in India are all recent immigrants by land and sea? If so, it speaks highly of the migratory capabilities of this genus. Certainly the oriental cycads, all members of *Cycas*, have a very long history. *Cycas thouarsii*, apparently the most ancient of the many species judging from chromosome pattern studies, is present in both India, Madagascar, and Africa. It is still debatable, though, whether it is a native or was introduced. Perhaps seeds were carried there, and to the Mascarene Islands, and around Asia by tropical storms. Or it might have been brought west out of Asia in "recent" by Arab traders. Mankind has had a long fascination with cycads as a thing of beauty and as a source of food (however deadly).

A. *Cycadinorachis omegoides,* (cross-section of rachis) India, Jurassic

B. *Pternulssonia gopalii,* India, Permian

C. Stoma from cuticle of *P. gopalii*

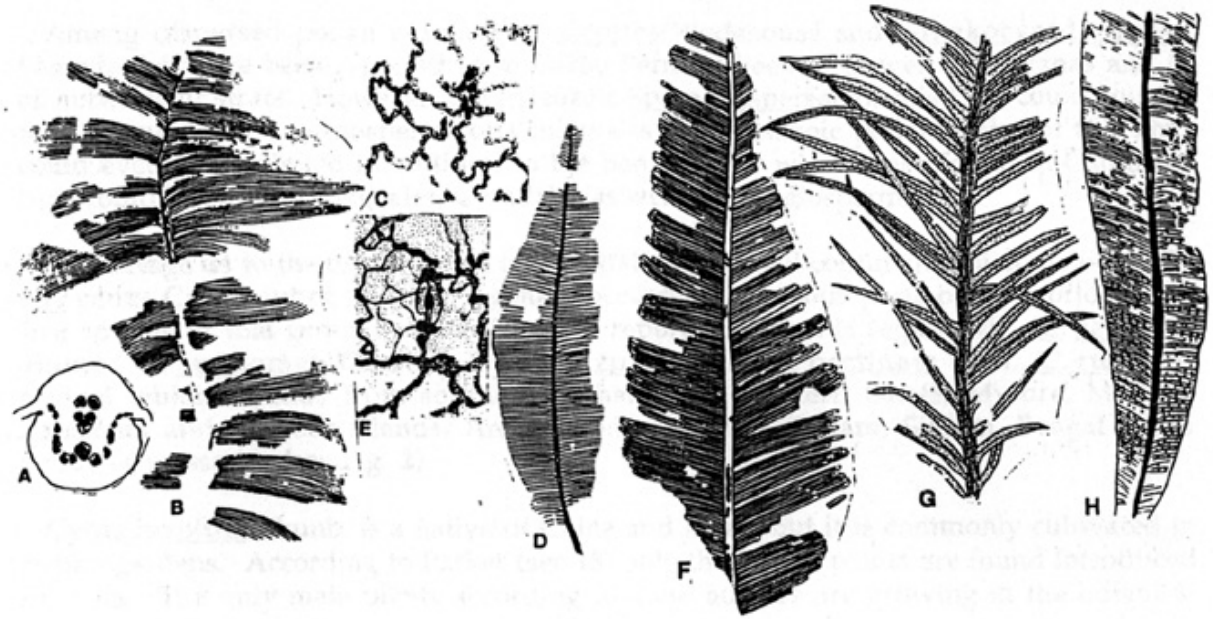
D. *Rhabdotaenia fibrosa,* India, Permian

E. Stoma from cuticle of *R. fibrosa*

F. *Cycadites rajmahalensis,* India, Jurassic

G. *Cycadites jabalpurensis,* India, Jurassic

H. *Glandulataenia glandulata,* India, Triassic



The tentative Cycadale family tree below is based plate tectonics data and leaf and cone structure. It illustrates a hypothetical evolutionary tree for the Cycadales and three families: the Stangeriaceae, Cycadaceae, and the Zamiaceae (after Johnson, 1959). For the purposes of discussion, the genus *Chigua* is provisionally reassigned as an ancient Gondwanan relative of the *Stangeriaceae* instead of the New World genus *Zamia*, as currently accepted, based on similarities in leaf venation to *Stangeria* (no modern cycad other than *Stangeria* possesses a midrib and forked venation like that of *Chigua*) and the presense of stomata on both surfaces of the leaves (a trait shared only by *Stangeria*, *Bowenia* and some species of *Macrozamia*, but not *Zamia*). An interesting, little-known mystery located in a dangerous part of the world, *Chigua* also possesses prickles on its leaf petioles and has cataphylls, traits *Stangeria* lacks (lost perhaps due to *Stangeria*'s underground habit). *Chigua* also more closely follows the mucilage chemistry of *Zamia*, which differs from *Stangeria* and the other Old World cycads, although this might be due to having existed in the same environment with *Zamia* for over one hundred million years. Considering this mixed bag of similarities and differences, if these two genera are indeed related, albeit it distantly, *Stangeria* appears to be by far the more ancient of the two. Although also sometimes grouped with the Stangeriaceae, here the genus *Bowenia* has been assigned as a Cretaceous offshoot of *Encephalartos* due to cone structure and leaf similarities with the Zamiaceae. The chief triggering agent for the formation of our modern genera appears to have been the fragmentation of the world-wide range of the Cycadales due to shifts in plate tectonics, fluctuating sea levels, and climate.