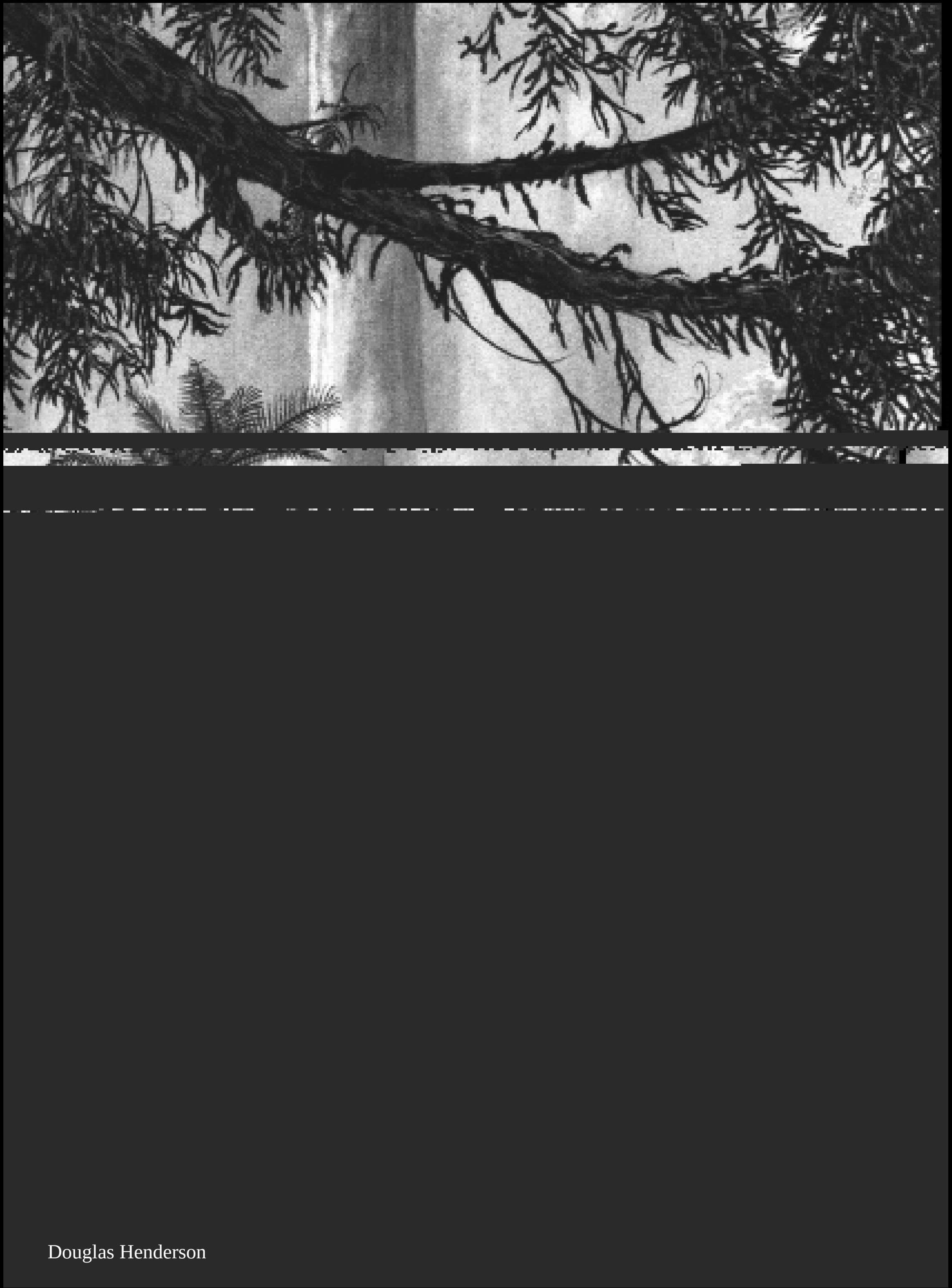

Douglas Henderson

A Brief Review of

The Fossil Cycads

by Robert Buckley

Illustations by:

Douglas Henderson,
John Sibbick
& Mark Hallett

Pseudoctenis-type Cycadales and a Cycadeoid,
Early Jurassic

Douglas Henderson

Ichthyostega, an early adventurer onto land in the first forests.
Devonian Period

Acknowledgements

*This publication has been prepared and donated to the **Palm and Cycad Society of Florida**, http://www.plantapalm.com as an overview of the fossil record of the Cycadales and is for informational purposes only.*

All photos, drawings and paintings are the property of and copyright by their respective photographers and artists. They are presented here to promote wider recognition of each artist's work. Talented technical artists too often go under appreciated, as they follow in the footsteps of Charles R. Knight and others who recreate the magic of lost worlds with their paintings. Cycads in art are also often relegated to the backgrounds, yet equal care is lavished on these reconstructions as is on the dinosaurian stars of the scene. This article brings some of these supporting players out of the shadows.

Books cited are available from http://www.amazon.com.
Visit the Palm and Cycad Society's web site and you will find a listing of books relating to palms and cycads, and a link to amazon.com.

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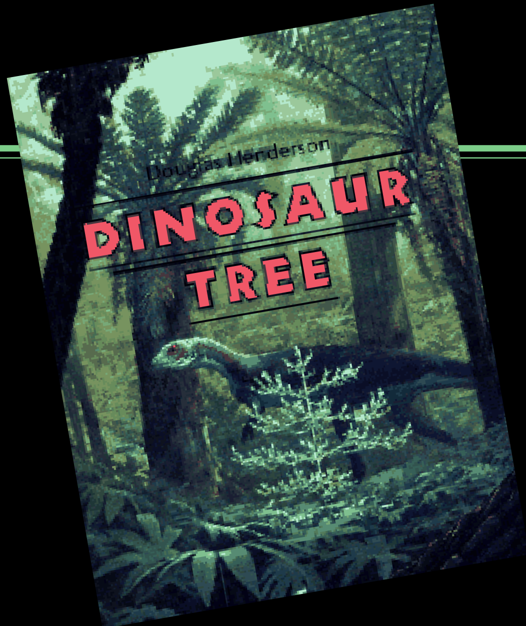
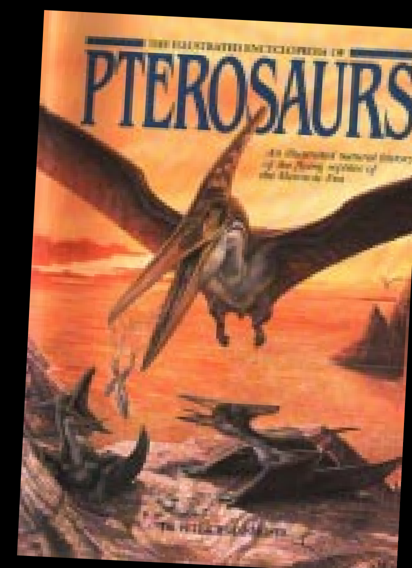
This is simply an overview since a systematic study of the fossil cycads has yet to be performed. Any errors or misconceptions in the information presented here are those of the author.

Robert Buckley
August, 1999.



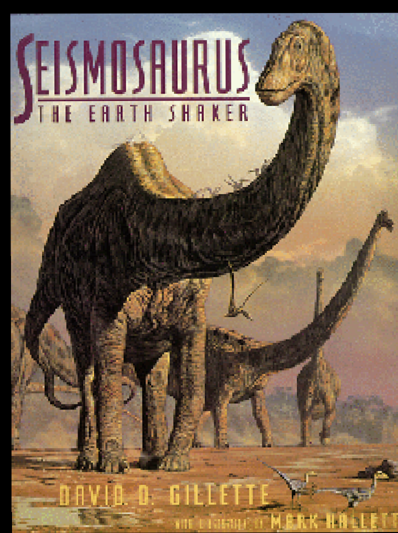
Douglas Henderson

His intense use of light and shadow, creative views, and brooding curtains of haze and mist allow Douglas Henderson's work to capture a real sense of environment. His art goes beyond scientific reconstruction to give the reader a real feel for the lost worlds being illustrated. One of the best overviews of his paintings, as well as the work of John Sibbick and Mark Hallett, appears in "Dinosaurs, a Global Perspective", by Sylvia and Stephen Czerkas. Although out of print, it is well worth obtaining a copy. A new work currently available tells the story of an early tree. It is for young readers, and highly recommended.



John Sibbick

John's work is both visually pleasing and scientifically exacting. In addition to the book named above, his work appears in "The Illustrated Encyclopedia of Dinosaurs," by Dr David Norman and "The Illustrated Encyclopedia of Pterosaurs," by Dr Peter Wellnhofer. Both are excellent from technical and graphic aspects and are published by Crescent Books, New York. John's illustrations can also be found in "Prehistoric Life," by Dr. David Norman.



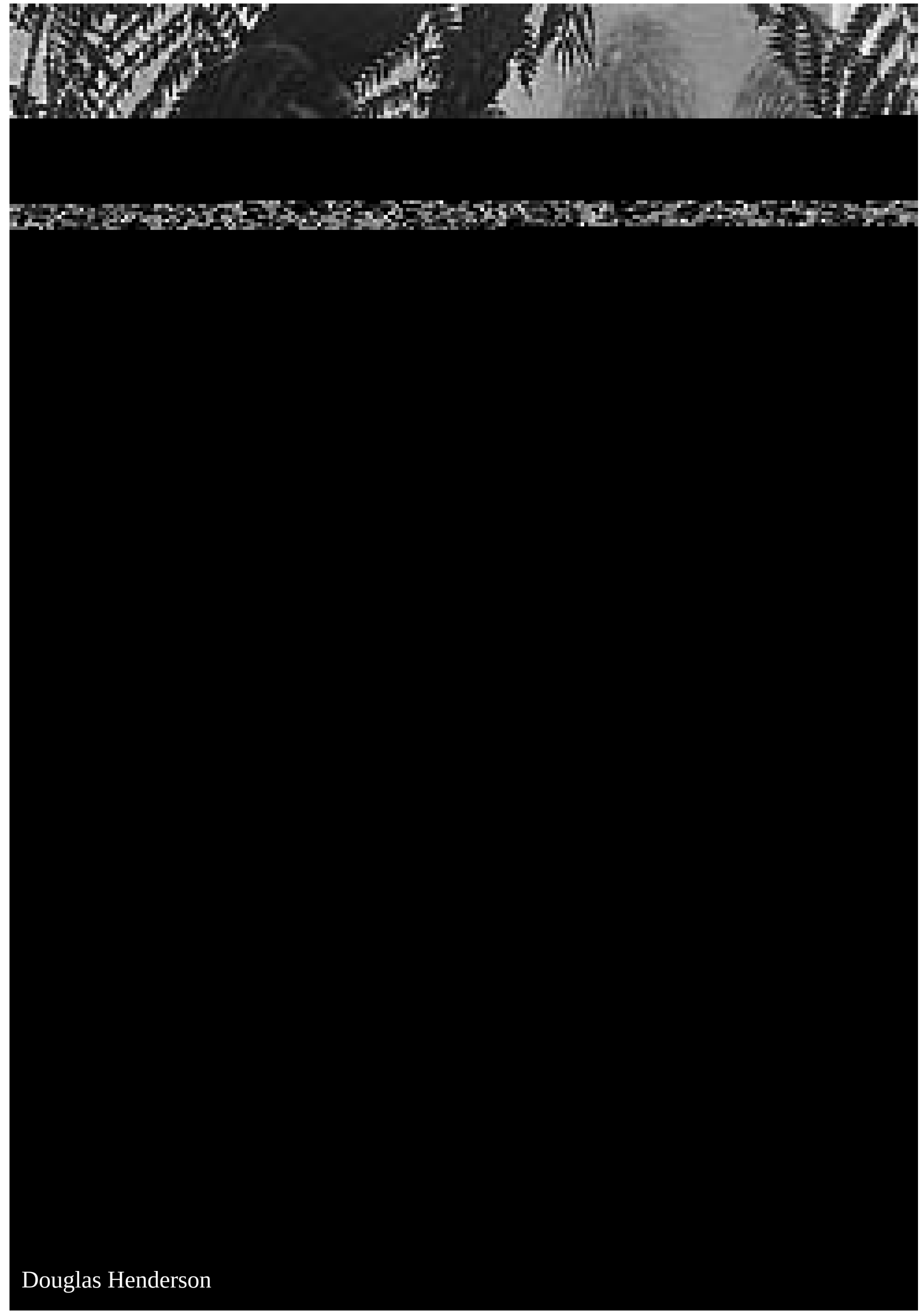
Mark Hallett

In addition to teaching classes in zoological illustration, Mark has painted magnificent murals for the Natural History Museum of Los Angeles, the Page Museum, the San Diego Natural History Museum, and the San Diego Zoo. His work appears frequently in books and magazines. One of his most memorable paintings is a huge mural of a Jurassic river that depicts the environment now preserved in stone at the Dinosaur National Monument. Two works currently in print for younger readers are "The Puzzle of the Dinosaur Bird", which is the story of Archaeopteryx, and "Seismosaurus, The Earth Shaker".

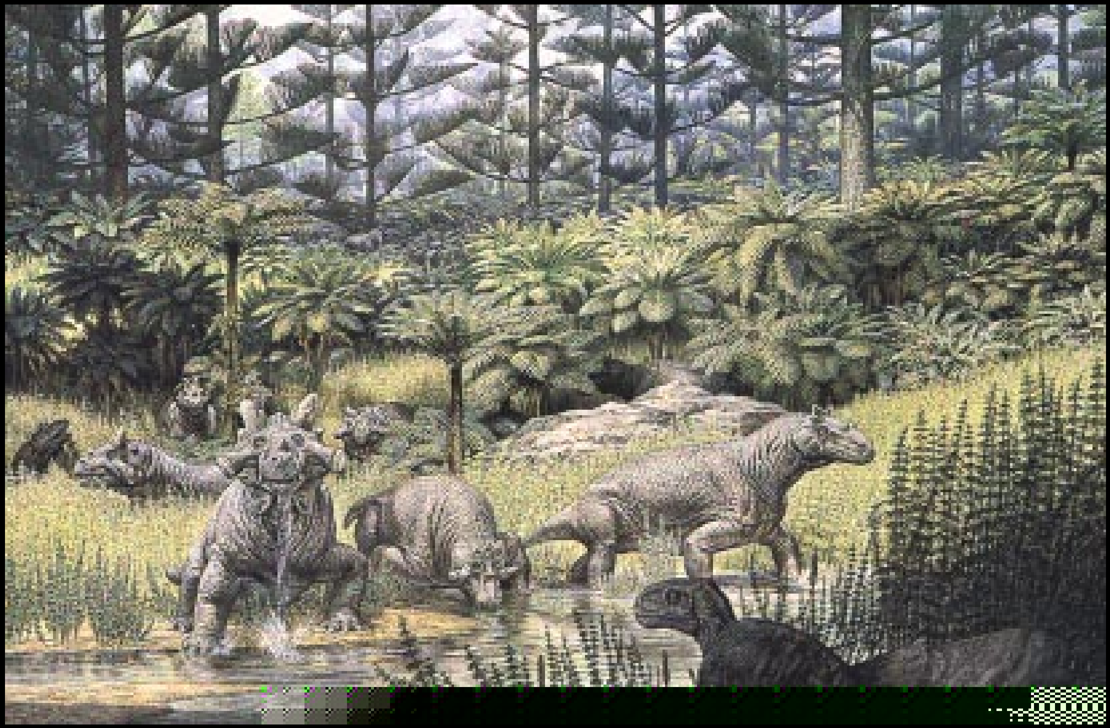
An Imperfect Window

Our view of the past is built from countless stony fragments and impressions left in sedimentary rocks by fortunate, yet improbable accidents of preservation of once living tissue. The history of the family of plants that we know as cycads is a long one, but they have left us only a few scattered clues to the richness of that reign. These fossils are named for leaves and leaf fragments, for cones, and for stems. Only rarely, as in fossil animals, does a generic name refer to the intact plant. This is because the vegetative fossils we find in ancient sediments are mostly the storm debris of prehistoric forests, a stump, or sodden log, or a pile of leafy debris gathered in an eddy and buried under silt and sand. If discovered, they become clues in the great puzzle of what the times that came before us were like.

When fossil cycads first began to be discovered in significant numbers decades ago, they attracted much interest. Researchers like Seward, Wieland, Williamson, and Chamberlain were foremost in the 30's and 40's. Wieland's "American Fossil Cycads," in two volumes, remains one of the landmark reference works in this area. Chamberlain, whose "The Living Cycads" is another classic, also wrote in depth on cycad evolution in his "Gymnosperms, Structure and Evolution." It is through the dogged physical labor of field paleontologists, the technician in the lab who frees the fossil for study, and the determination and insight of researchers who try to understand and describe these fragments out of time that we have any knowledge at all of vanished worlds. It has just been in the last century that an explosion of knowledge has occurred as the science of Paleontology has matured. Like a grimy window being wiped clean, our view of the past grows better and better with each passing day. This article is a brief review of the current knowledge of the fossil cycads. Photos and drawings of representative fossils are included. The clues remain scant. But with each new dig, the Cycadale fossil record is filled out with additional pieces of evidence.



Hylonomus, one of the earliest reptiles in a forest of lycopods, tree ferns and seed ferns. Carboniferous Period



Douglas Henderson

Ferns are homosporous, they produce one asexual spore. After it lands on a suitable moist medium, it produces both male and female gametes of similar genetic makeup. After they combine, the new fern that is produced from the prothallus is for the most part a clone of the parent plant. Sexual reproduction is a huge advantage because it allows considerable genetic variation in characteristics. In times of severe environmental change, this can mean the difference between survival and extinction. The Cycadofilicales (=Pteridospermales) were the first to transition from asexual reproduction to producing true seeds. The seeds of *Lyginopteris* were small and formed at the tips of short stalks at the ends of the leaves. *Neuropteris* was closer to the cycad pattern of reproduction. Its seeds were large and carried in a terminal crown of leaves. In appearance, this species resembled a tree fern and, judging from its numbers in fossil deposits, very successful in its time.

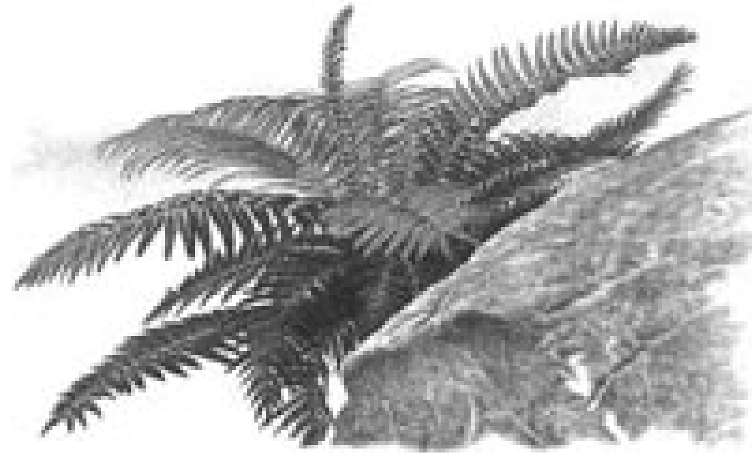
In the Beginning . . .

In the painting above a Carboniferous period meadow is dominated by a forest of araucarians and *Neuropteris*, a seed fern and a distant precursor to the modern cycad. Horsetails and other fern allies form the undergrowth. The large horned animals approaching the water hole are *Estemmosuchus*. Members of the therapsids, these herbivores were probably warm-blooded. Dinosaurs would not arise until after the therapsids had vanished in a series of worldwide extinctions, which brought forth a whole new set of plant and animal players of the Mesozoic Era.

The Carboniferous, known variously as the “Age of Ferns”, and the “Coal Age”, was a time of low lands and immense, swampy forests of simple vascular plants like horsetails and tree ferns. For plants, it was a time of experimentation in reproductive structures. Seed bearing plants had just appeared.

Ptilophyllum
A compund leaf fossil

Permian Cycadales



John Sibbick

Taeniopteris, (middle ground of painting below) and other early tree-fern like plants, possessed simple leaves, bore small seeds along their edges near the base. *Taeniopteris* is associated with fossil reproductive material (seed bearing leaves) given the name *Crossozamia*; these fossils resemble the modern day reproductive megasporophylls of the genus *Cycas*, although they are more highly divided. A reduction in leaf size and the number of seeds could conceivable replicate the loose, open cone of this modern cycad. From the many variations of seed leaves, simple and compound vegetative leaves it is apparent that even in the Permian period early cycads and cycad-like plants were a very diverse group. For example, in *Yuania chinensis*, from the Lower Permian of China the lower pinnae were reduced to thornlike structures similar to the prickles of the rachis of modern day *Cycas*.

The chart at right illustrates how compound leaves could be derived from a simple tree-fern-like leaf. *Stangeria*, *Bowenia*, and the multipinnate forms of *Cycas* have been added to show how cycads continue to adapt, developing more efficient leaf designs. Not shown are *Macrozamia stenomera*, *M. diplomera*, and others, and the newly discovered genus *Chigua* that also have developed multipinnate leaves. Such a leaf architecture increases the amount of photosynthetic surface of a leaf, while keeping wind loading to a minimum. Damage from insects would also be reduced. Since cycads produce new leaves no more than once or twice a year on average, they need to protect this major metabolic investment from damage.

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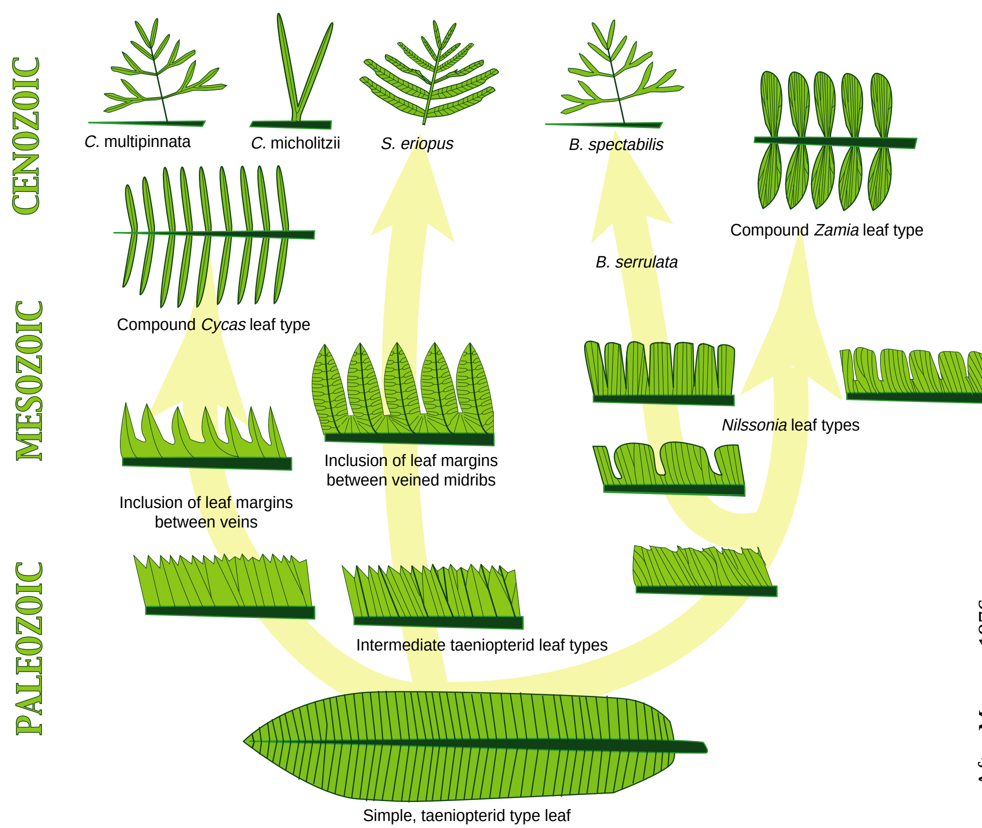
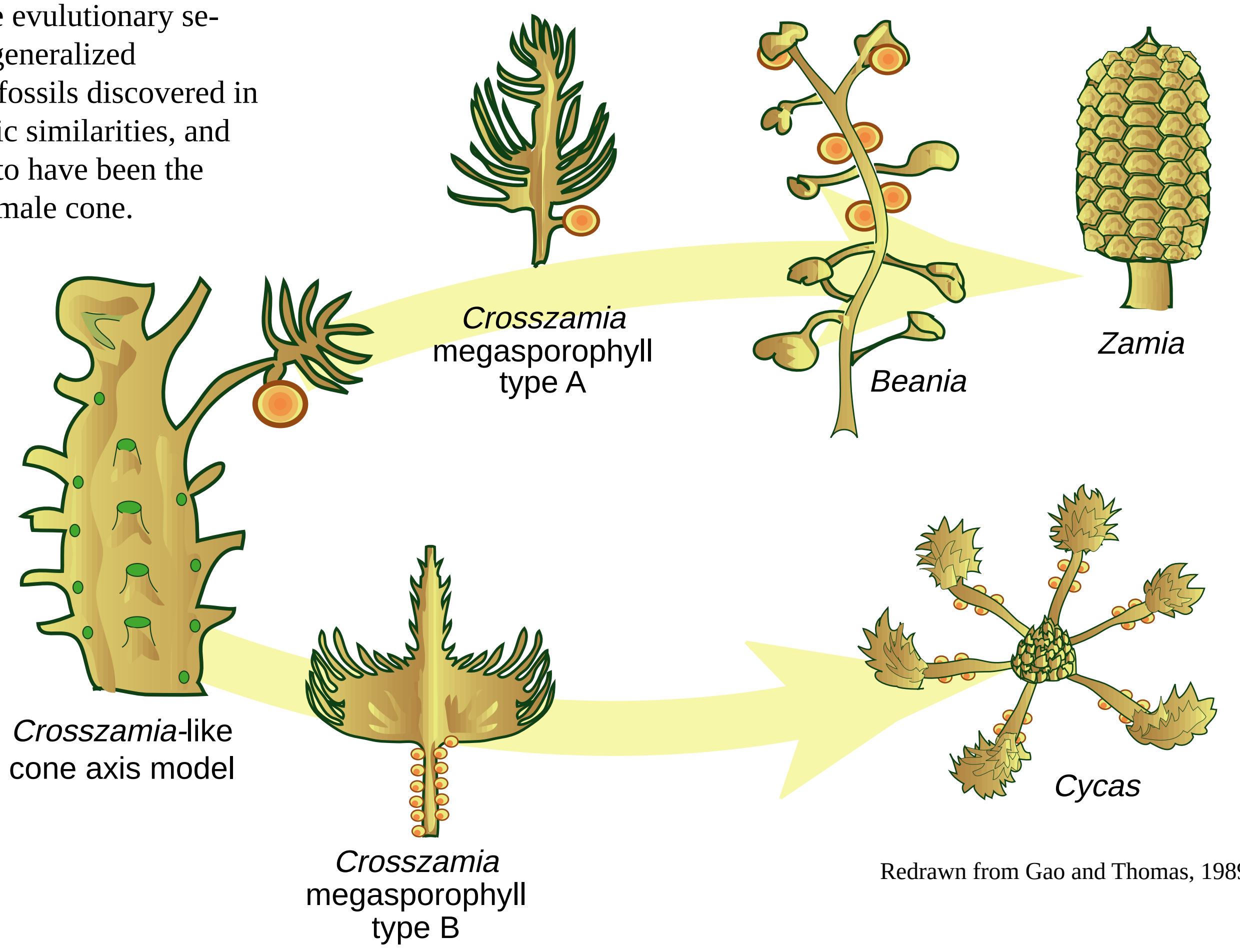


After Mamay, 1976

Several fossils from the Late Permian resemble male cycad-like cones, with twin spines on the cone scales like *Macrozamia*. Certainly, the male cone of Beania is very similar in appearance to modern cycad cones, even if the female cone is very open and elongated. If these fossil are truly of cycad cones, and not the fossilized impressions of club moss stems, they suggest that cycad structures were evolving at different rates. Although leaves initially remained primitive, reproductive structures were adopting more modern and efficient structural designs. The chart below shows a possible evulutionary sequence of cycad megasporophylls from a generalized *Crosszamia* cone axis design. *Crosszamia* fossils discovered in China, France and Sweden have many basic similarities, and yet are variable enough in construction as to have been the precursors to both the *Cycas* and *Zamia* female cone.

Modern cycads are very dependent on specific insects to pollinate their cones, and there's no reason to believe this wasn't also the case in the past. There may even have been co-evolution of these seed bearing structures and their pollinators. Cycad cones signal that they are ready to release pollen, or to be pollinated by broadcasting attractive odors and also distinctive heat signatures for those insects capable of sensing infrared radiation. Cone shapes were probably driven by how well they attracted and allowed access to specific pollenating insects. Afterwards, the cone had to become a protective shield for the developing seeds. Once mature, the cone had yet another function, to attract yet more co-agents, animals drawn by the fleshy seed coverings that would strip off this inhibiting coating and then transport the seeds away from the parent plant so that they might find a lucky spot to germinate. Over the millions of years that cycads have existed, these co-agents could have been insects, dinosaurs, pterosaurs, birds, various mammals, perhaps even fruit bats, who would find the open cone of *Cycas* an especially easy target.



Possible evolution of *Cycas* and *Zamia*-like female cones from variations of a *Crosszamia*-type cone axis. Type A and Type B refer to two different fossil variations. There was much variation in *Crosszamia* megasporophyll design.

Triassic Cycadales

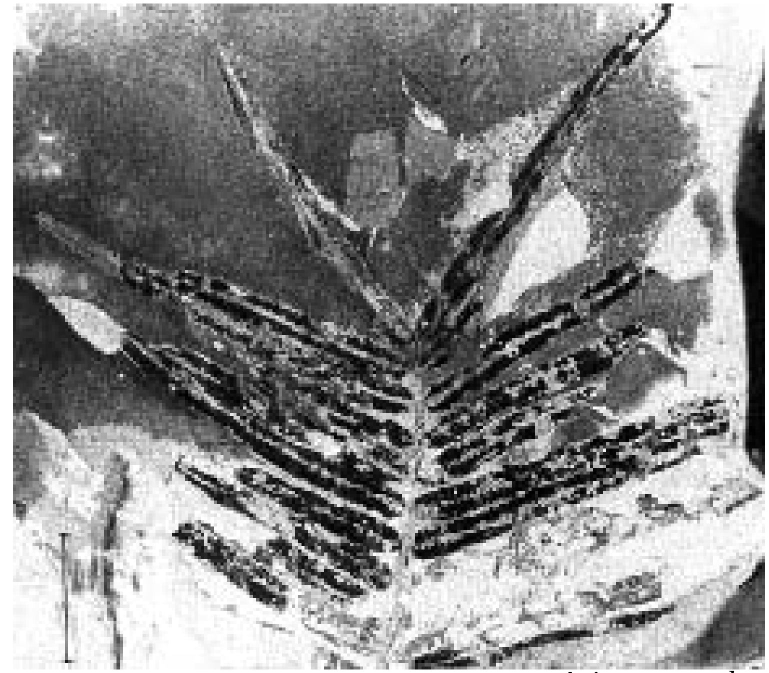
The Triassic period was a time of recovery, transition and diversification for much of the Earth's surviving life forms. A major global extinction caused in part by changing continental positions and redirected ocean currents has just occurred. The world was leaving an ice age, warming and plant life was having to adapt to a predominantly warm, dry climate. Many once dominant species faded to mere niche holders. Others found new opportunity. The cycads and their allies seized the day.

One of these new plants was *Aricycas paulae*, whose fossil leaves have been found in Arizona. Its leaves possessed a slender rachis and long narrow pinnae with a mid rib. The epidermal structure and stomata more resistant to water loss mark it as a Cycadale. There is a very strong resemblance to modern-day *Cycas*. Some reproductive structures have also been found similar to the Cycadale form, but it's not possible yet to attribute these fossils to *Aricycas*. Another possible precursor to Cycas was found in Triassic sediments in Antarctica. *Antarcticycas schopfii* consists of small fragments of stem, about 14 c, long. One stem is branched.

The Cycadales had competition, of course. Cycadeoids and the Williamsonia both found this new warm climate equally to their liking. Judging from fossils found so far, during the Mesozoic they may have actually been more populous than the Cycadales.

John Sibbick

A Cycadeoid being enjoyed by *Heterodontosaurus*, one of the dinosaurian locals of that time



Aricycas paulae
Arizona, Upper Triassic

In foreground, *Lyssoxylon grigsbyi*, an early Cycadale, New Mexico, Upper Triassic

Jurassic Cycadales

The gymnosperms dominated the Jurassic period. Ginkgoes, conifers, the true cycads, Williamsonias and the Cycadeoids filled a warm, humid world from nearly pole to pole. High sea levels meant many warm inland seas flooding the continents. Mountain ranges were relatively low and an immense double landmass straddling the equator (Gondwana in the south and Laurasia in the north) created a paradise for cycads-like vegetation. The fossil record of leaves, stems and cones indicates that it proliferated.

Three fossil leaf types attributed to the Cycadales are *Nilssonia, Ctenis,* and *Pseudoctenis*. The nilssonians were an undecided lot, some had simple entire leaves, while others adopted the compound leaf first adopted by the majority of ferns back in the Carboniferous. In the end, a compound leaf design won out.

The compound nilssonnian leaf pattern had short, blunt, and wide leaflets similar to *Pentoxylon*, shown lower right of page 12. (Some authorities feel that simple leaves are better grouped with *Taeniopteris*, a seed fern, and that compound leaves are actually *Pseudoctenis*.) The leaflets of *Nilsonnia* attached to the upper surface of the rachis (as in the modern *Lepidozamia* and *Dioon*) and the veins are parallel, as in *Macrozamia* and *Encephalartos*. Fossilized stems suggest that the leaves of *Nilssonia* did not leave leaf bases behind when they dropped away, instead they abscised cleanly. Some researchers feel that *Nilsonnia* is different enough from the Cycadale norm to deserve family rank of its own alongside the Cycadaceae, Stangeriaceae, and the Zamiaceae.

The leaves of *Ctenis* were also similar to modern cycads. The broad rachis had compound leaflets attached along it. Some fossils have been found of leaves measuring six feet in length. The parallel venation in *Ctenis* had occasional cross connections. *Ctenis* was distributed all across the Jurassic landmass and so far fossils have been assigned to approximately 50 species.

Pseudoctenis lanei-type Cycadale with a striking similarity to the modern *Encephalartos*, Middle Jurassic. John Sibbick

Pseudoctenis also had a worldwide distribution during the Jurassic and differed from *Ctenis* in one detail . . . the parallel venation of its leaflets had far fewer cross connections. Harris (1964) has observed that if leaves of the more generalized modern genera of *Dioon*, *Macrozamia*, *Lepidozamia*, and *Encephalartos* were to be discovered as fossils, they would be classified within the *Pseudoctenis* model.

Yorkshire, England is a fertile area for cycad fossils from the Jurassic. In addition to foliage leaves, many fossils of vegetative structures have been found, enough to hint at the route to both

The ancient heritage of the cycadales means they have been witness to many exotic encounters. Here a flock of pterosaurs (*Rhamphorhynchus*) are startled into flight by a ceratosaur's attack on a lone *Brachiosaurus*. The *Encephalartos*-like cycads shown in the foreground probably did not survive the battle unscathed.

Reconstruction of a generalized *Encephalartos*-like Cycadale. Fossil material suggests that by the beginning of the Jurassic the structural evolution of the Cycadales had settled on the pattern seen today in Cycas and perhaps other modern genera of cycads.

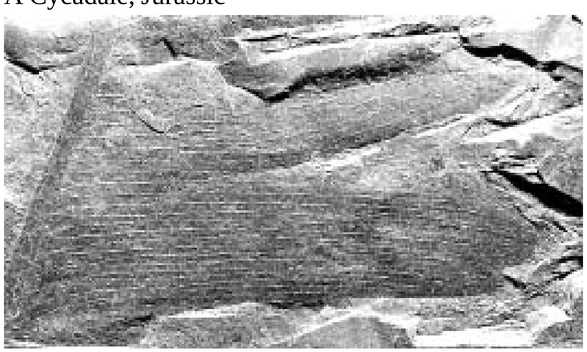
The scene at left, by John Sibbick, is set in North America during the Jurassic period.

Pseudoctenis spatula
world-wide, Jurassic

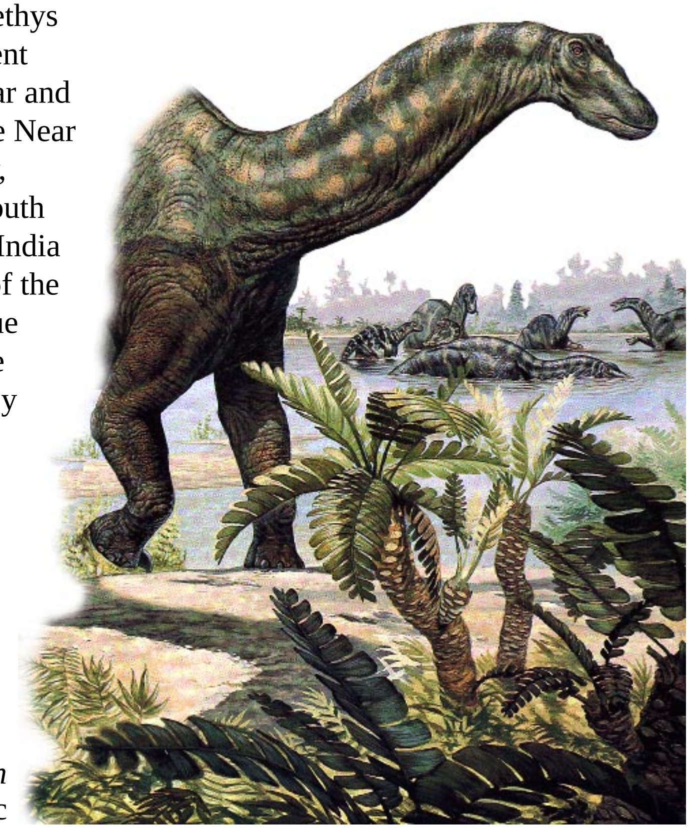
the loose megasporophyll design of *Cycas* and the tight closed cone design of the Zamiaceae. The cones of some of these cycads hung down from the leaf apex like pendulous fruit. While another of that same time (*Pseudoctenis lanei*) was quite similar in form to the modern Encephalartos, having a massive and compact male cone (named *Androstrobus manis*) and regularly pinnate leaves with parallel venation in the leaflets, enough that if further discoveries bear out these similarities the cycad may be classified within this genus. This would provide evidence for at least one of the early home ranges of *Encephalartos*, and indicate the antiquity of its origins. Another fossil cone, *Androstrobus zamioides*, from the Middle Jurassic sediments of North Yorkshire may be a *Stangeria* relative. Another *Stangeria*-like fossil from Argentina suggests that this monotypic and isolated Africa cycad originated in South America and was once global in range. The leaves of the newly discovered genus *Chigua* from Columbia are strikingly similar to the forked venation, serrated leaf edges, and strong midrib of *Stangeria*. Could this rare and relict genus be a surviving fragment of *Stangeria* in the New World?

Ctenis biloba
A Cycadale, Jurassic

As the Jurassic period came to a close, the continents continued shifting. The Tethys seaway opened a corridor from the present Caribbean through the Straits of Gibraltar and continuing south between Arabia and the Near East to the South Polar sea. Additionally, Africa had begun to break away from South America in the west and Antarctica and India in the east. The worldwide distribution of the Cycadales was now sundered. The unique characteristics of the major genera of the modern cycads would now appear as they began to specialize within much smaller ranges.



Closeup of leaflets showing the broad connection to the rachis. Note how the veins divide as they leave the rachis.



Pentoxylon
A *Nilsonnia*-type Cycadale, Jurassic

Cretaceous Cycadales

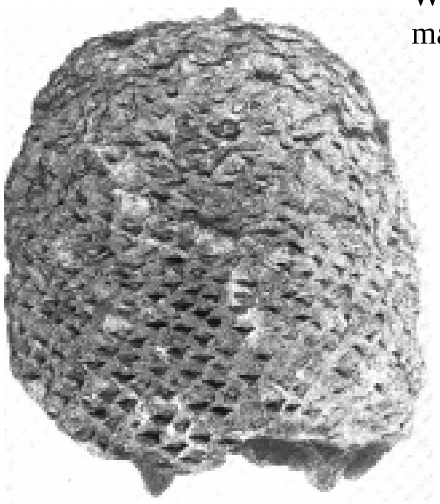
By the Cretaceous the true cycads were apparently quite large. One fossil from Japan, a large stem over 4 feet in diameter named Sanchucycas gigantea shows structural characteristics similar to both Cycas and Encephalartos.

Another fossil from Japan is a unique form of cycad unknown today. It's compound leaves had regular rows of pinnae that grew from a series of short shoots extending radially from a slender stem. Nilssoniocladus nipponense had leaves similar to the Nilssonia pattern. No reproductive material was associated with the fossil.

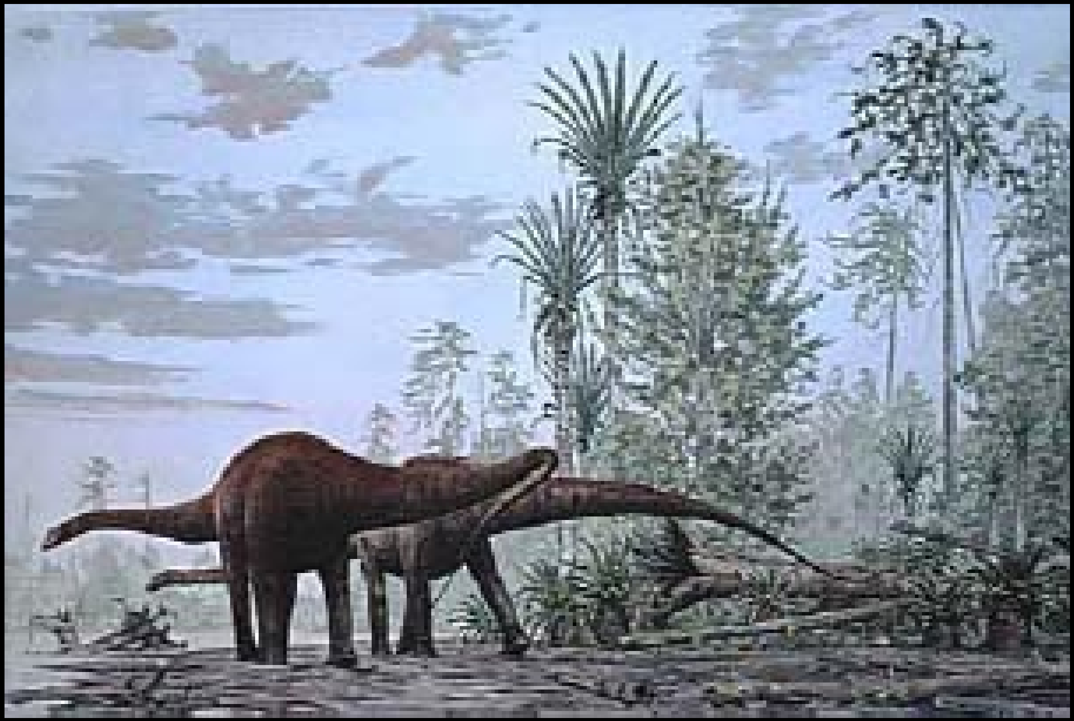
The Williamsonia were still present in Mexico, England and India during the Cretaceous period. This slender cycadophyte apparently depended heavily on large herbivores consuming the ripening cones and distributing the undigested seeds in its dung. This would be an obvious disadvantage should the large herbivore disappear suddenly. The cycadeoids also remained numerous, and many fossils have been discovered in the Black Hills of South Dakota, and in Wyoming. Their low growing, stocky trunks with a prominent armor of leaf bases were often mistakenly taken for cycads. The female reproductive structures resembled flowers, but were really loose cones. Beetles apparently served as both pollinators and seed predators.

Fossil leaves from the Lower Cretaceous of Argentina described as Mesodoscolea have been assigned to the Stangeriaceae (Archangelski & Petriella, 1971). The only surviving member of this genera, Stangeria, is endemic to the coastal region of South Africa. Mesodoscolea suggests that the Stangeriaceae were a much more important family 200 million years ago, with an extensive range in Gondwana. With so many gaps in the fossil record it is possible that major families of the Cycadales that were once quite common remain completely unknown. The curious genus Pterosoma known only from Lower Eocene fossils found near Victoria, Australia, is another example. It possessed forked veins in it's leaves, like the Stangericeae and must have been widespread in southern Australia during the Cretaceous.

Williamsonia sp., a Bennettitalian Cycadophyte with a compound leaf pattern (see above) and arborescent trunk.
Jurassic thru Cretaceous



Cycadeoidea marylandica, fossilized stem of a cycadeoid, Maryland, Jurassic thru Cretaceous



Left: in this reconstruction of a lowland Jurassic forest by Douglas Henderson a pair of diplodoci make their way across a floodplain dotted with cycadeoid-type plants. By the end of the Jurassic the predominantly lowland character of the continents had begun to change. The climate became less humid, vegetation thinned and in many areas like Asia and North America adapted to more arid conditions. Flowering trees and bushy angiosperms appeared. Beeches, oaks, magnolias, and hickory now shared the landscape with cycads, conifers and ferns.

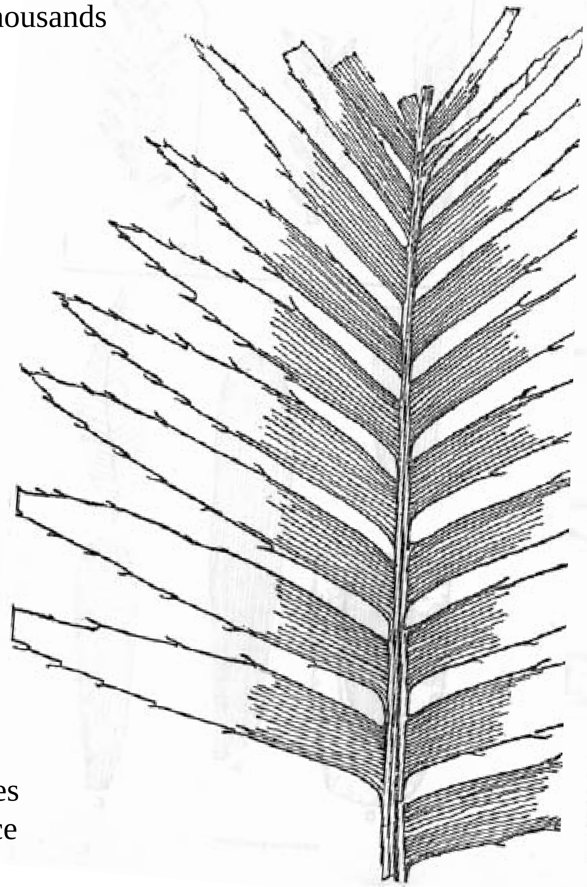
Below: an upland Cretaceous forest where dawn redwoods and early angiosperms dominate while Cycadales and Cycadeoides make up the understory vegetation. The appearance of woody, tough-leafed vegetation also produced a shift in herbivores. The long necked pegtoothed sauropods were replaced by hadrosaurs, iguanodons, and ceratopsians with massive batteries of teeth capable of rending anything frompine needles to thorny cycad leaves.

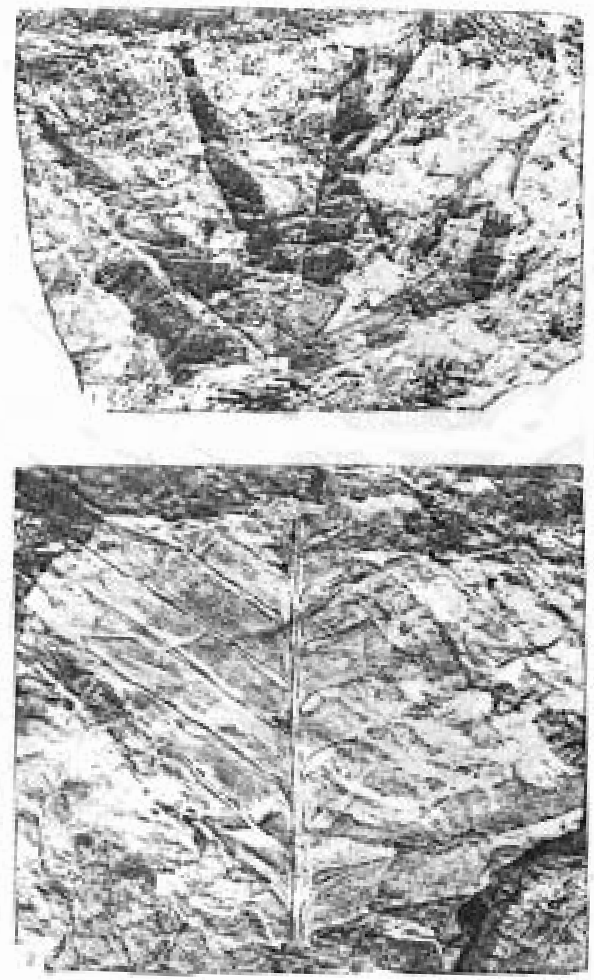
The Upper or Late Cretaceous was a time of growing environmental stress. Gondwana and Laurasia were now in the process of breaking apart. India had become a wild runaway (geologically speaking) shooting across the Indian Ocean toward Asia, and a vast outpouring of magma was forming the Deccan Traps (steps). Sea levels were dropping, the deep ocean was turning cold, and the world climate was now more seasonal as mountain ranges thrust up in the Americas, Europe, and Asia. The three cycad-like families, the Williamsonia, Cycadeoidea, and the Cycadales, were in a contest for survival and the future would go to the most adaptable. But what no one figured on was a wild card player arriving out of the asteroid belt.

Cenozoic Cycadales

The early Cenozoic was a world in disarray. The lengthy volcanic outpourings that mantled 350.000 square miles in India over millions of years must have had a powerful influence on the world's climate, causing abnormally cold winters and summer temperatures far below normal. This was a climate already in flux due to mountain building and the retreat of inland seas. Then, in a final insulting hammerstroke came the devastating asteroid impact on the Yucatan peninsula. Life in southern North America was decimated in a blast wave and fan of white hot ejecta that extended far out into the Atlantic. The mushroom cloud that towered into that Late Cretaceous sky must have dwarfed modern nuclear tests. Fire storms may have incinerated forests in Central and North America for thousands of miles around the strike zone and the European coast would have shuddered under the impact of massive tidal waves surging across the Atlantic ocean.

Cycadales were impacted negatively along with other life of the time. Of the Bennettales, the tall arborescent Williamsonias and the more compact Cycadeiodeae both vanished, probably due to the loss of their dinosaurian grazers and insect pollinators, for the climate of the Eocene period eventually became warm and moist. And this was yet another defining moment for the modern Cycadales. Shaped by millions of years of structural refinement, they reestablished their ranges in an empty world as denuded stumps and buried root masses regenerated and here and there isolated, long dormant seeds sprouted as temperatures began to moderate and the sun began to shine once more through a thinning mantle of clouds.

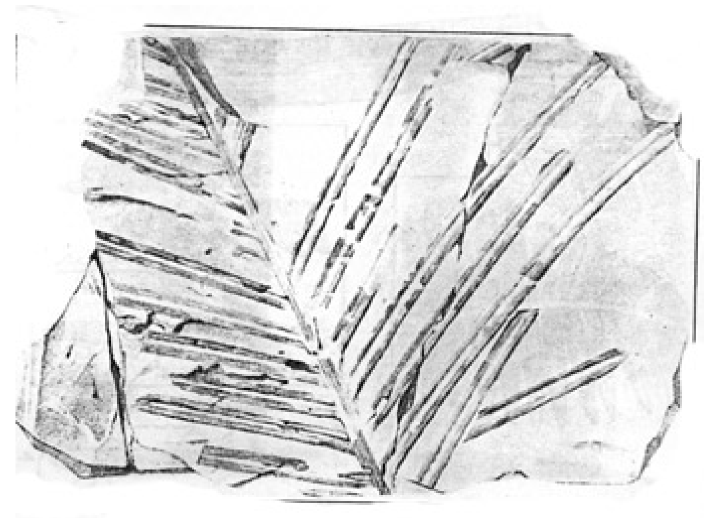




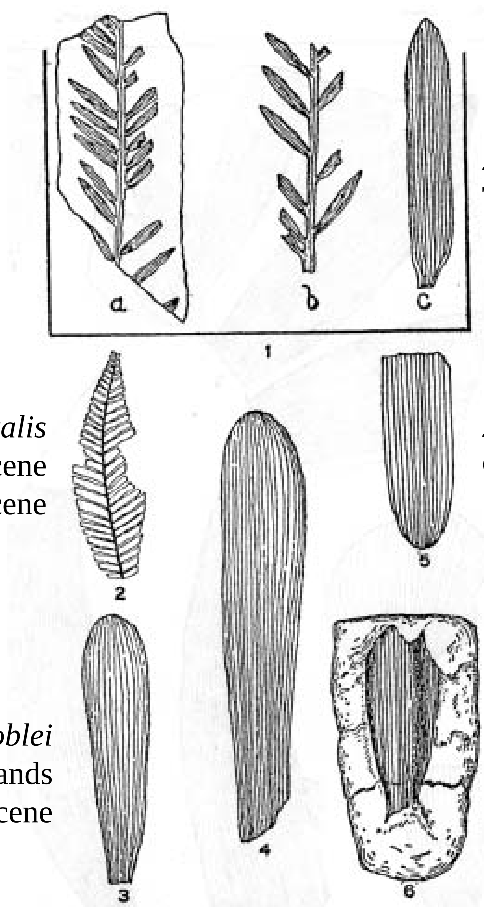
In the early Cenozoic the Cycadales grew in higher latitudes. The Eocene Period was warmer than today. *Cycas* was represented in Europe and Asia through fossils found in Bulgaria, Britain, and in Japan.

Dioon prespinulosum,
Tip & median portion with drawing of *Dioon spinulosum* for reference
Kupreanof Island, Alaska, Eocene

Fossils of *Lepidozamia hopites* in southern Australia reveal a cycad very similar to the modern *L. hopei*. There are also Australian fossils attributed to *Bowenia* (*B. papillosa* and *B. eocenica*) from the Eocene. *Bowenia* is considered one of the more advanced of the Cycadales, yet here it was in recognizable form sixty million years ago. Fossils attributed to *Ceratozamia* and *Dioon* have been discovered in Alaska, and there is even an incidence of *Ceratozamia* in Switzerland, suggesting that this genus was once present worldwide. A fossil of *Encephalartos* was discovered in Greece, placing this Africa genera far to the north of its present day range. *Encephalartos*-like fossils (*E. cretaceus*) have also been found in South Dakota and Kansas, and fossilized stems with a polyxylic structure similar to *Encephalartos* or *Cycas* have been discovered in Lower Teritary and Paleocene sediments of Argentina. If *Encephalartos* was also present in North and South America at one time, it's ranges must have been such that it could not survive the Pleistocene glaciations, while the more equatorial range of it's close relative *Dioon*



Cycas Fujiiana,
Japan, Eocene (Paleocene?)



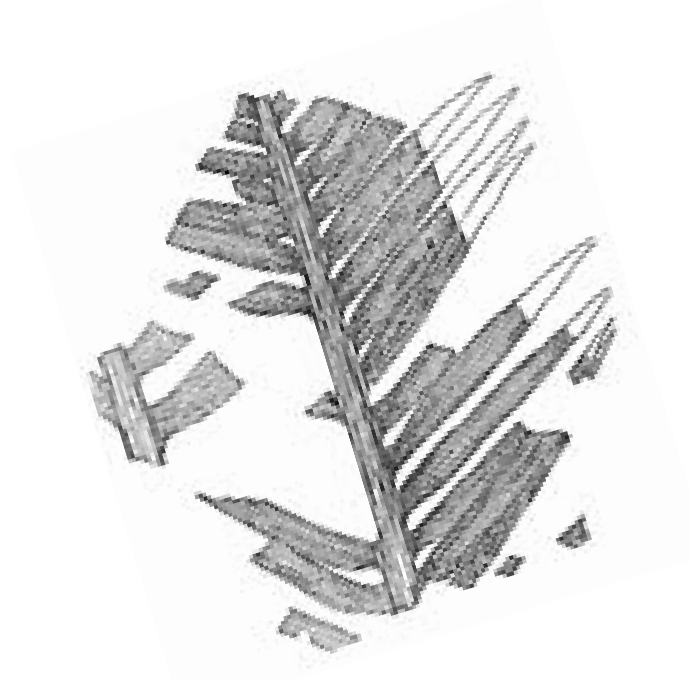
Zamia mississippiensis
Tennessee, Lower Eocene

Zamia australis
Argentina, Oligocene
or Lower Miocene

Zamia sp.
Columbia, Oligocene (?)

Zamia noblei
Porto Rico & Virgin islands
Upper Eocene or Oligocene

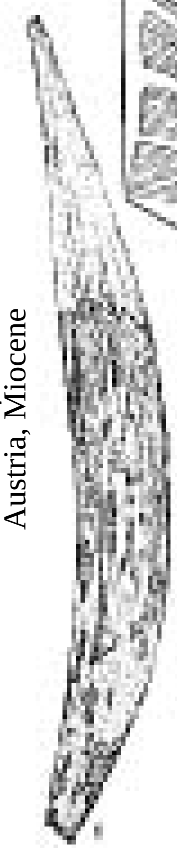
Zamia? wilcoxensis
Louisiana, Lower Eocene



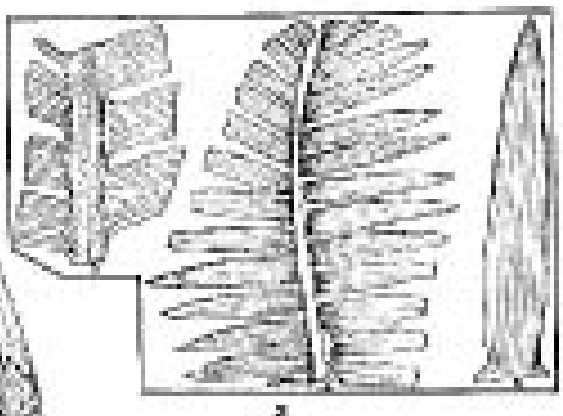
Encephlartos gorceixianus,
Greece, Miocene

permitted this genus to maintain it's New World hold. *Zamia* is also represented in the fossil record of the South America. Paleocene fossils attributed to the Zamiaceae consist of an ancient forest deposit in Patagonia (Argentina) at the southern tip of South America and other *Zamia* fossils have been discovered in Chile and Argentina, far to the south of present day ranges. Apparently a rich Cycadale flora was present in Argentina before the advent of the Pleistocene glaciers.

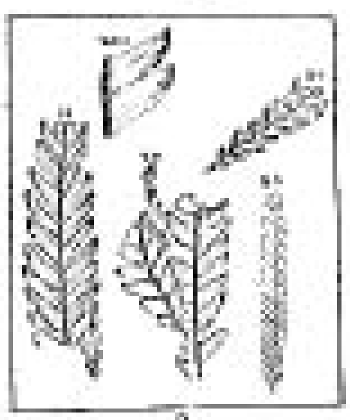
Eocene fossils suggestive of *Zamia intregrifolia*, *Z. pumila* and *Z. augustifolia* have also been found in Louisiana, Tennessee and Mississippi, extending the ancient range of *Zamia* northwards.



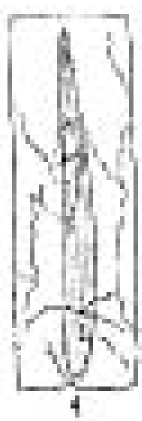
Ceratozamia hofmanni, Austria, Miocene



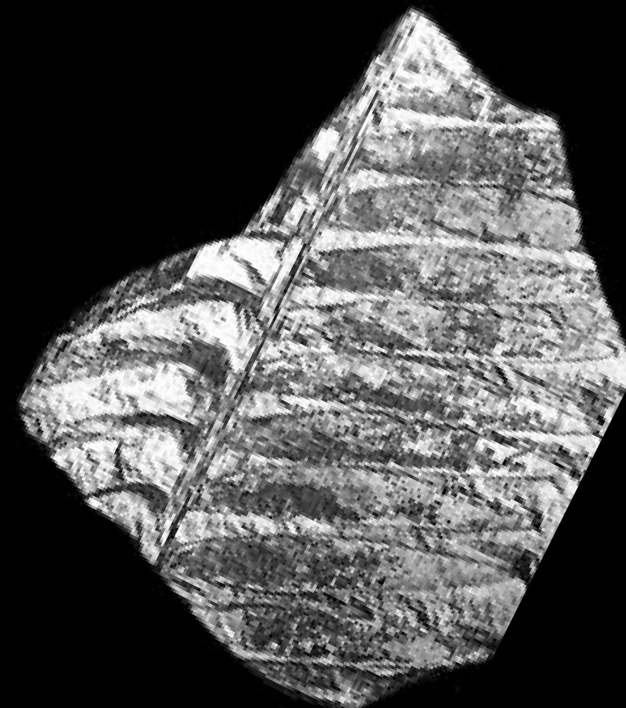
Zamites epibius, France, Miocene



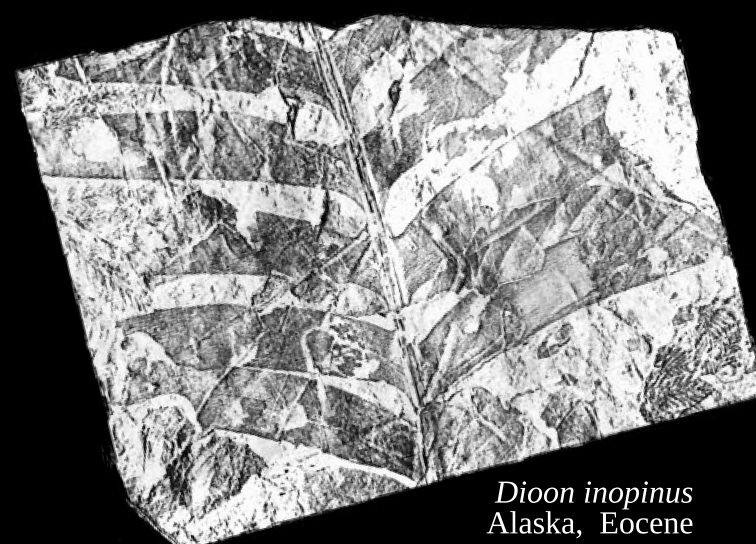
Anomozamites muelleri, New South Wales, Australia, Lower (?) Eocene



Zamia tennesseana, Tennessee, Lower Eocene

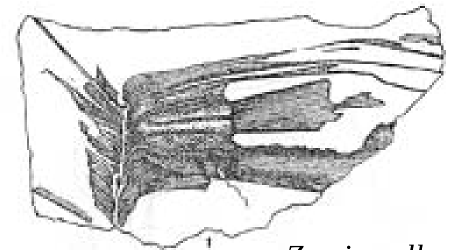


Ceratozamia wrightii, Kupreanof Island, Alaska, Eocene

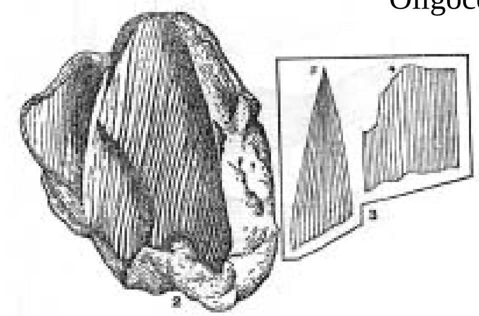


Dioon inopinus Alaska, Eocene

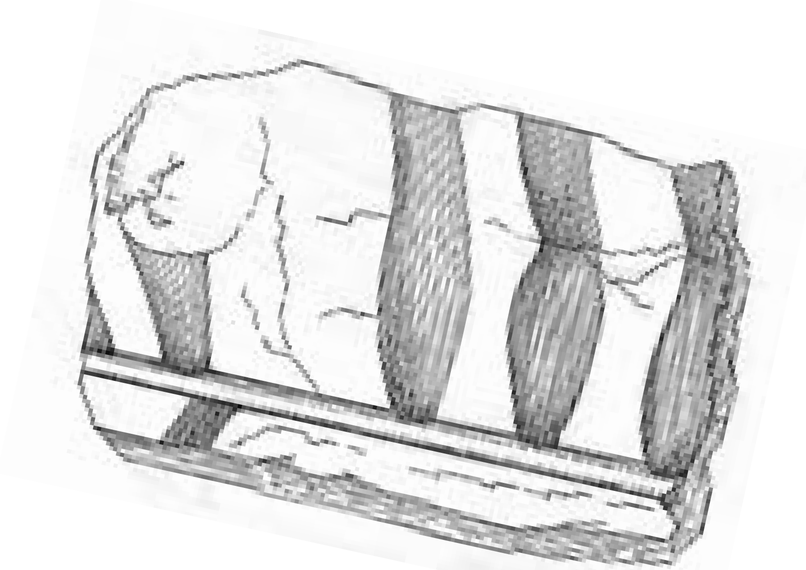
An interesting genus *Pterosoma* is known from the Eocene of sediments near Victoria, Australia. These fossilized leaf fragments are assigned to two species, *P. ananstomosans* and *P. zamiodes*. The veins of the pinnae are forked (as in *Stangeria* and *Chigua*) and in *P. anastomosans,* form a conspicuous network. Fossils of *Pterosoma* have also been found in Tasmanian sediments of the same age. Apparently this genus of cycad was unable to retreat north and became extinct during or before the Pleistocene glaciations. *Pterosoma* does not seem to have been related to *Macrozamia* or *Lepidozamia* and is apparently an extinct line of the Cycadales.



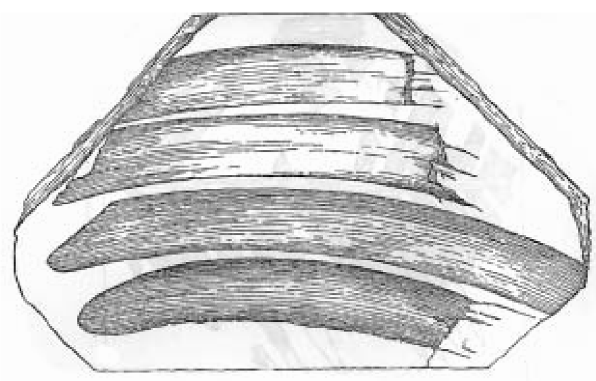
Zamia collazensis
Porto Rico & Virgin Islands, Upper Eocene or Oligocene



Zamia tertiara
Chile, Lower (?) Miocene

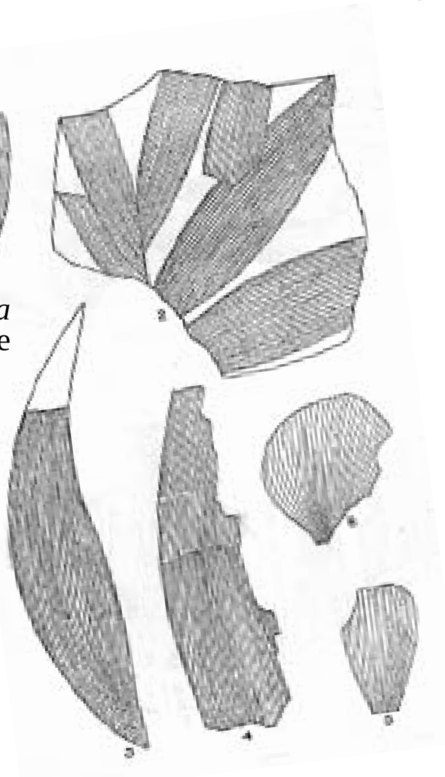


Ceratozamia vicetinus,
Switzerland, Oligocene



Ceratozamia vicetinus,
Switzerland, Oligocene
(pinnae detail)

Zamia tertiaria
Chile, Lower (?) Miocene



Zamia collazoiensis
Porto Rico,
Upper Eocene
or Oligocene

Like the genus *Pterosoma*, there were undoubtedly unknown species of cycad that lived and then vanished utterly as their specific environments vanished. The limited fossils we have discovered so far only give us a tantalizing glimpse of the true nature of cycads as they existed in the past.

Cycads are sometimes referred to as "living fossils", yet they have shown great adaptability over hundreds of millions of years, persisting strongly into the present. They have managed to outlive the dominant land animals of the Paleozoic (Therapsids) and the Mesozoic (Dinosauria) and now find themselves in the Angiosperm dominated Cenozoic, the domain of the Mammalia. Will some hardy future species of cycad outlive us as well?

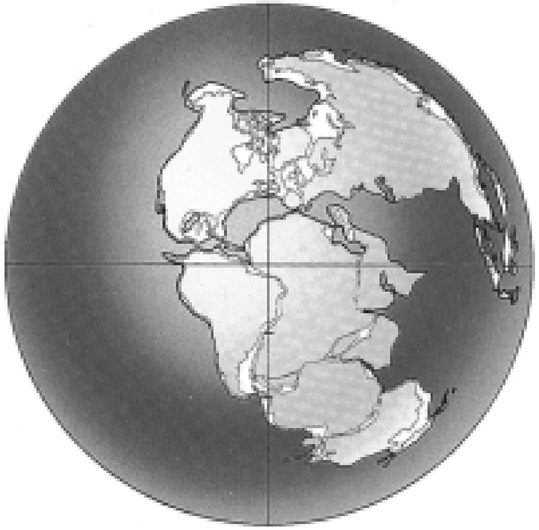
It is entirely possible that the true cycads were never present in vast numbers even at their climax. Many of today's cycadales, like conifers, have adapted to exploit inhospitable nutrient poor sandy and rocky soils, often in desert areas. (Plants living in these conditions rarely fossil-ize.) While others, like *Zamia roezlii* and *Z. chigua* live in near mangrove conditions. Com-mon or not, cycads have shown themselves to be a stubborn, hardy family, difficult to kill and easy to admire.

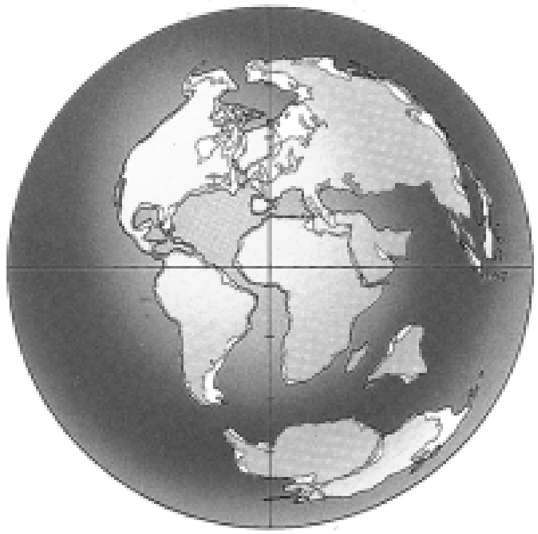
Douglas Henderson

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



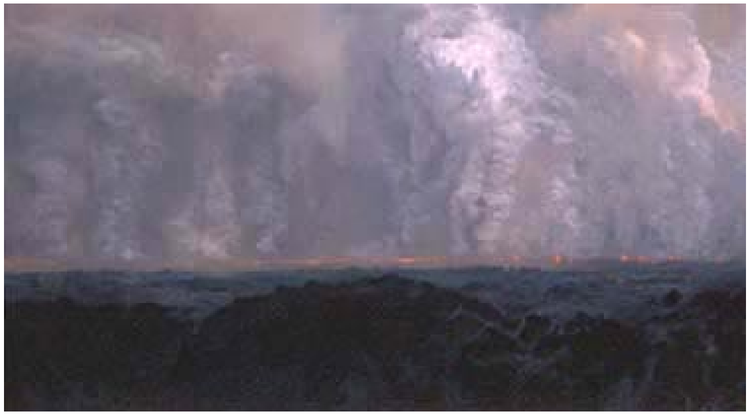


Mid-Cretaceous World

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 Yucatan impact. *Douglas Henderson*

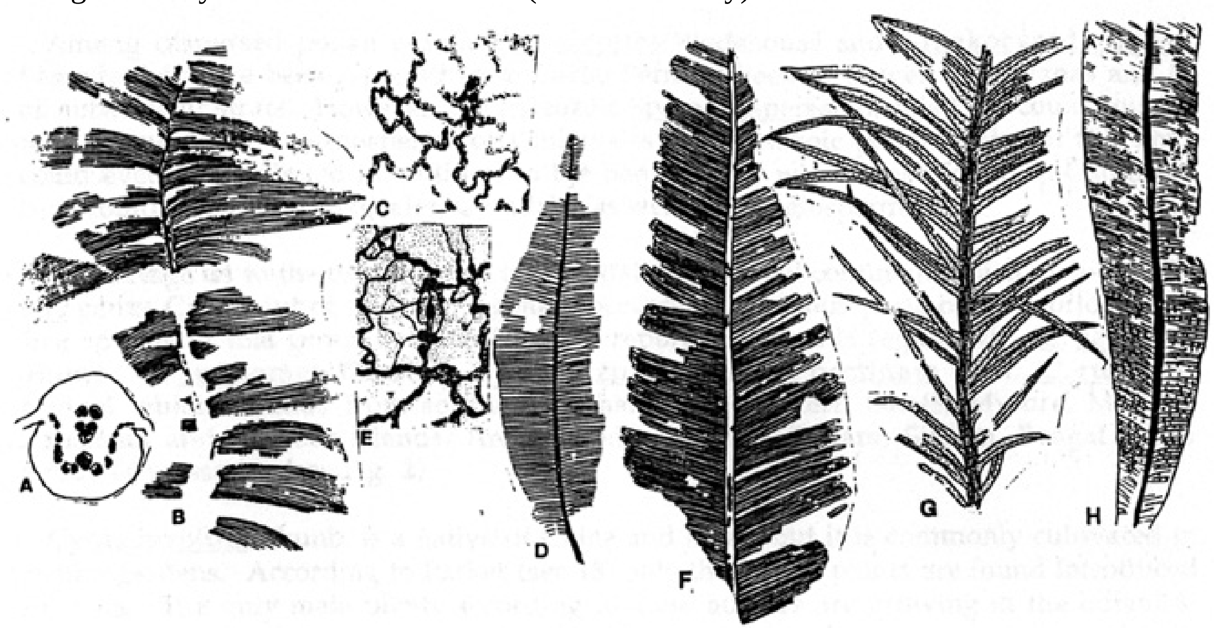
The devastation in Central America might have been minimized if the impactor had descended at a low angle so that much of the ejecta was directed toward the north and east. Perhaps *Microcycas* is a rare, uniquely specialized survivor of the precursor of *Zamia*. During the Pleistocene glaciations, when 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?



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

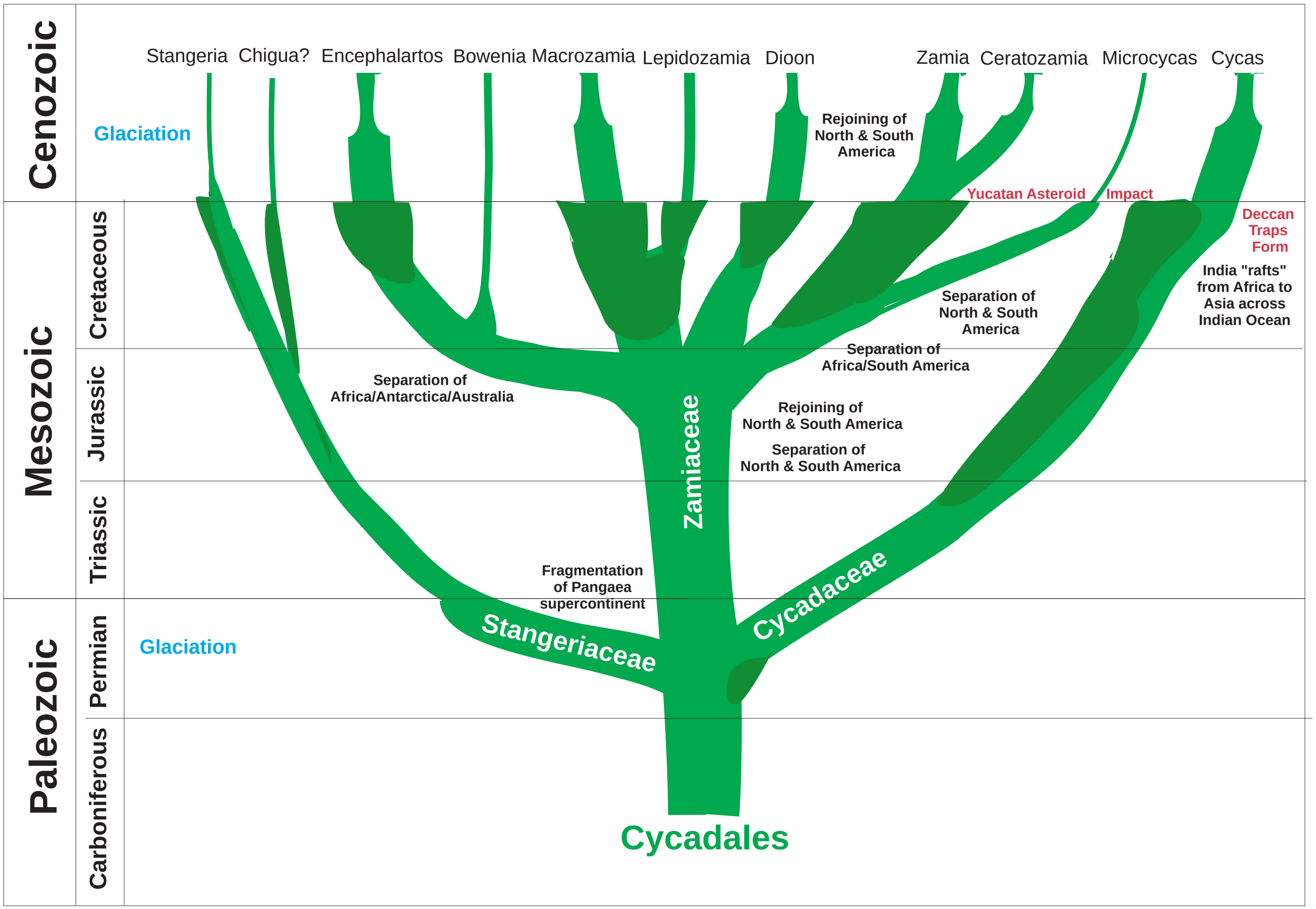
E. Stoma from cuticle of *R. fibrosa*

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.



The New Mellenium & the Cycadales

As we have seen, the fossil record provides only a sketchy image of past populations, much distorted by accidents of preservation. Still, it seems to indicate that the cycads came out of the Mesozoic as a diverse family and reestablished themselves quickly in the Cenozoic, many of them surviving vigorously into the present.

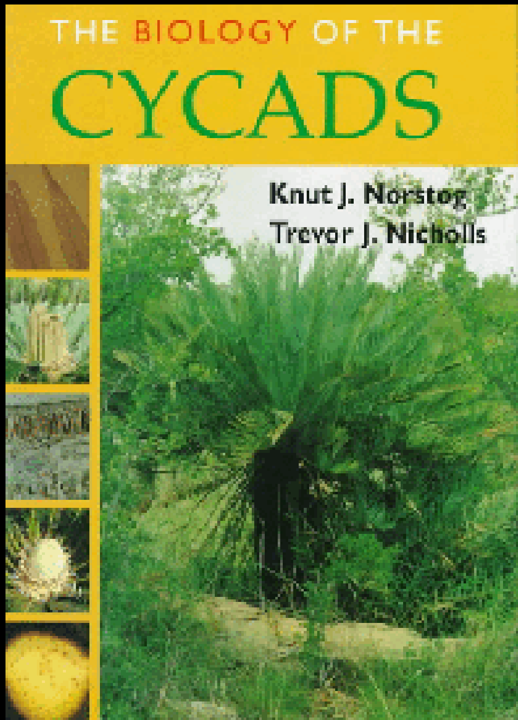
Although referred to as "living fossils", this is both unfair and inaccurate because it implies that cycads are like horseshoe crabs, or the Coelacanth, unchanged and unchanging. Yet the Cycadales have shown themselves to be a durable and vital family, with many advanced adaptations, such as contractile roots, underground stems, seed and pollen cones that attract pollinators by producing heat and odor, and multibranched leaves with compound leaflets. Primitive in some characteristics, they are also as modern as Angiosperms in others. They deserve our respect, admiration, and our protection.

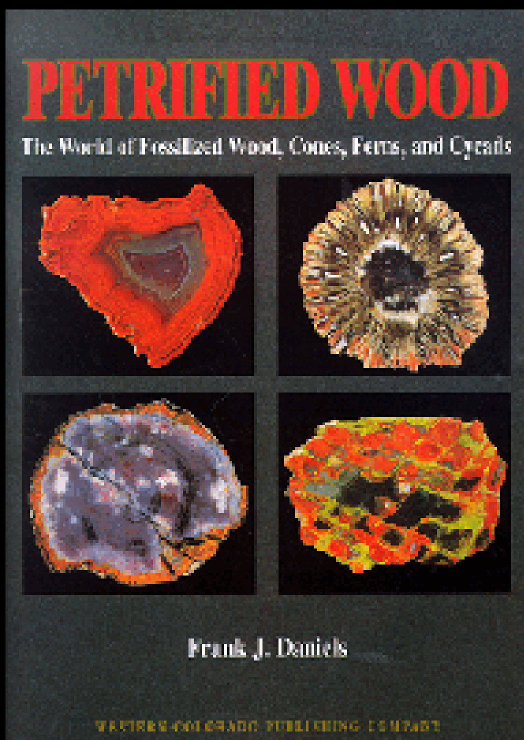
While some species of the Cycadales are on the verge of extinction, many genera as a whole, like *Cycas*, *Encephalartos*, and *Macrozamia* continue vigorously. The chief threat to their continued survival has appeared so recently that they have not had time to adapt to it. Sadly, that threat is ourselves. Whether the Cycadales continue depends not on world climate, on tectonic forces, or other accidents of nature (cycads have shown themselves perfectly capable of dealing with such mundane disasters). Put simply, if today's cycads are to survive, we must master ourselves. We have the intellect, and we can acquire the knowledge necessary. All that is wanting is the will.

On the positive side, cycads are much admired and desired. Since ancient times humans have been actively moving "wild" cycads about on this planet, making a mess of their natural ranges while using them as risky food sources and even expensive status symbols. Fortunately, many are now beginning to realize that these magnificent and expensive acquisitions must reproduce if they are to survive, and that there may even be economic rewards in producing seeds and seedlings. So we and the cycads are in a period of difficult transition as we learn each other's needs. The cycad's ancient living spaces are being lost at a terrible rate at the same time that they are being transformed into a domestic horticultural plants, like the rose, and cacti, and orchids. The ancient, solitary cycad growing alone in majestic solitude on its granite outcropping may well be doomed. And to lose this will be a terrible thing; we should fight hard to against it because we'll all lose something very precious when that happens. But cycads will go on. Someday, on the sunny balcony of some distant space habitat on the moon, or in orbit, a colonist will proudly show off his latest potted miniatures to visitors - a male and female *Encephalartos woodii*. Far fetched? Perhaps. But while it's true that today's cycads face powerful enemies, they also have some very creative and ingenious friends!

Photo: Tom Bihr

A male Cycas revoluta apparently thriving magnificiently under "domestication." *Photo: Tom Bihr*





References & Additional Reading

"The Biology of the Cycads," Kurt J. Norstag & Trevor J. Nicholls. Cornell University Press, 1997.

Contains an in-depth section on prehistory of the cycads, in addition to being an excellent and up-to-date reference on the living cycads. A "must-have" book for anyone interested in cycads.

"Dinosaurs, A Global View," Sylvia & Stephen Czerkas. Mallard Press, New York, 1991.

This is a comprehensive and thought provoking work with excellent illustrations.

"Gymnosperms, Structure and Evolution," Charles J. Chamberlain, Univ. of Chicago Press, 1935

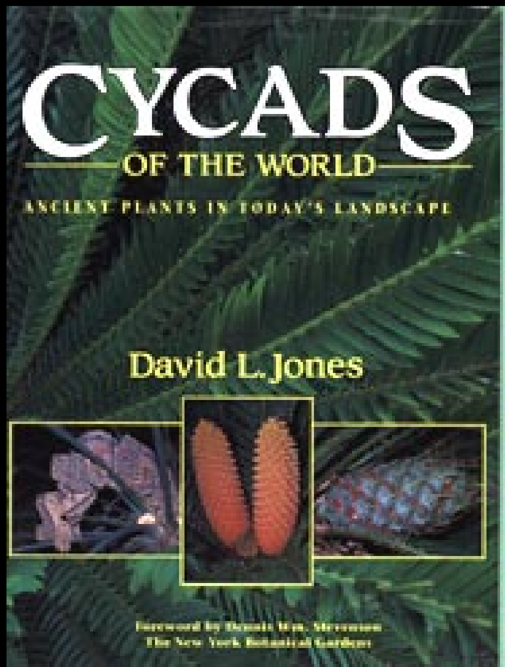
A classic work on the evolution of the Cycadales.

"Indian Cycads," Rita Singh & Willie Tang, Editors, Special Issue of the Cycad Newsletter, Vol. XVI No. 2, 1993

"Descriptions of New Species of Tertiary Cycads, with a Review of those previously recorded," Authur Hollick, Bulletin of the Torry Club, Vol. 59, No. 4, 1932.

"Petrified Wood," Frank J. Daniels, Western Colorado Publishing Company, 1998

A modern work on an ancient subject.



References & Additional Reading continued

"Cycads of the World," David L. Jones,
Smithsonian Institution Press, Washington. D.C., 1993.

An important book on cycads recently reprinted. Contains an overview of fossil cycads, and is another excellent reference on the living cycads.

"The Biology, Structure, and Systematics of the Cycadales,"
Dennis Wm. Stevenson, Editor.
Memoirs of the New York Botanical Garden Vol. 57., 1990
The New York Botanical Garden, Bronx, New York 10458, U.S.A.

"Morphology and Systematics of the Cycadales," Dennis Wm. Stevenson, pp. 8-55.

Contains important references on the structure and evolution of the Cycadales.

"Chigua, A New Genus in the Zamiaceae with Comments on its Biogeographic Significance," Dennis Wm. Stevenson, pp. 169-172.

Describes *Chigua* as a new genus.

"The Fossil History and Phylogeny of the Cycadales," D. D. Pant,
Geophytology 1987:17(2):125-162

A modern synopsis of the status of fossil cycads.

"Origin, Evolution, and Growth Patterns of Cycads," T. Delevoryas,
Proceedings of CYCAD 90, the Second International Conference on Cycad Biology, Palm & Cycad Societies of Australia Ltd.,1993, pp. 236-245

A discussion of fossil cycad leaves.

References & Additional Reading continued

"The Biology, Structure, and Systematics of the Cycadales,"
Dennis Wm. Stevenson, Editor. Memoirs of the New York Botanical Garden Vol. 57., 1990. The New York Botanical Garden, Bronx, New York 10458, U.S.A.

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"Chigua, A New Genus in the Zamiaceae with Comments on its Biogeographic Significance," Dennis Wm. Stevenson, pp. 169-172.
Describes Chigua as a new genus.

"West Indian and South American Cycads," S. Sabato, pp. 173-185.
Includes a discussion of the origins of New World cycads.

"Global Environment and Diversification of Plants through Geologic Time: Proceedings of the International Conference, Allahabad, India,"
Pant, D.D., editor, Vedams Books International, New Delhi, India,

A very diverse series of modern papers dealing with fossil plants.