

Evolution of the genus *Cycas*

Contributed by David J. de Laubenfels
Wednesday, 10 October 2007

The genus *Cycas* appears to be the most primitive of its order. These plants were originally relatively small tropical forest plants growing from a subterranean bulb that eventually developed an aerial stem that sometimes might develop branches. The large compound (many vascular traces) pinnate leaves to several meters long had linear simple to dichotomous pinnae. Reproduction was achieved on specialized leaves (sporophylls), the lower part fertile and the apical part with reduced pinnae. Normally a fertile shoot with many sporophylls would be determinate and therefore essentially lateral.

In all living cycads the pollen producing structure is compacted and reduced into a tight lateral cone to more than half a meter long with the apical sterile part of the microsporophylls a blunt or pyramidal shield 2 cm wide protecting the fertile zone until time for pollination. In *Cycas* the pinnae of the microsporophyll survive in a few species as a few serrations or small prickles. The seed producing structure in *Cycas* began as a globular aggregation up to half a meter in diameter of megasporophylls, the apical sterile part of which bore reduced but distinct pinnae of several centimeters and the center expanded into a protective shield something like the microsporophyll. Unlike all other cycads and not necessarily primitive, the aggregation is not determinate, spreading apart as the stem resumes growth. The seed coat shed readily releasing a smooth ovoid seed several centimeters long. The pollen cone had a cylindrical shape. The apex of the sporophylls bore a projecting spine or acumen, which in the microsporophyll was bent sharply upward. The acute tipped leaf pinnae were flat with the midvein prominent on both sides and the margins just slightly bent.

The homeland of the genus *Cycas* appears to have been the southeastern part of Asia, apart from the other families and genera of cycads which clustered in the three other tropical zones of the world. In Asia the genus *Cycas* divided from north to south into three parts (sections). The northernmost, which survives in rather isolated remnants, surrendered its subterranean base. The leaves are relatively small with short petioles and the pinnae narrow with the midrib not showing above. The apex of the microsporophyll is almost blunt and the acumen weak. It includes the widely cultivated *C. revoluta*.

The middle section survives today near the border of China and Viet Nam. These plants very much preserve their subterranean stems and achieve only weak aerial stems if at all. The leaves are large with long petioles. The apex of the microsporophyll is blunt and only in some cases is there a prickle or acumen. The seed has a verrucose surface. In the more extreme cases there is no distinct acumen on the megasporophyll and the pinnae are broad and undulate with the midvein not raised below. Some have dichotomizing pinnae. Only recently have the members of this section become fully described.

The southern section in Asia started out with a large bulbous base which progressively was reduced to a broad expanded base and even to a simple aerial stem. The pollen cones expanded to an ovoid form and the apex of the microsporophyll is not blunt. The seed coat developed a fibrous layer meaning that it remained tightly around the seed. Included is the widely distributed *C. pectinata*.

The further development of the genus came with a spread to the Australian region which had been remote but was drifting towards Asia. Remnants of a transitional form of the genus can still be found isolated in the northwestern part of Australia. The segments or pinnae on the megasporophylls became shortened to no more than blunt pegs. For some reason, the surviving species of this transitional group have spindle-shaped pollen cones reminiscent of the more northerly sections in Asia while all the remaining southern species have ovoid-shaped pollen cones corresponding to the more southern Asian ancestors. The apex of the microsporophylls developed a robust acumen that begins erect and then hooks sharply upward claw-like. In only some species is the midvein of the pinnae prominent above as well as below. The stems are not subterranean but often have an enlarged base. The descendants of the transitional species divided geographically three ways, all with the segments on the apex of the megasporophyll reduced to sharp narrow teeth or prickles which, unlike the larger ancestral segments that are largest basally, these are largest apically.

The section of the genus in Australia, along with the transitional remnants, has completely lost the fibrous layer in the seed coat while retaining the same claw-like apex to the microsporophyll. Compared to the genus as a whole, the leaves tend to be somewhat moderate in size, which suggests a response to more rigorous environmental conditions. The well-known *C. media* comes from Australia.

Another branch of southern *Cycas* species spread to the rainforest zone of Malesia and eventually to some Pacific islands. Like the conifers, the Asian species seem to have retreated while the southern species expanded westward across Wallace's Line. This section began with a fibrous layer in the seed coat but then produced a series of coastal species that have a spongy layer inside the seed (buoyancy) and at the same time have lost the fibrous layer. All these species share a blunt truncated apex to the microsporophyll which is bent sharply upward along with a narrow

apical spine. These are mostly robust plants with large, several meters long, leaves. Like most of the Australian species, the midrib is weakly expressed if at all on the upper side of the pinnae. *C. celebica* from Guam may be the best known species in this section.

Finally, representatives of the genus *Cycas* made their way to India, probably while it was still an equatorial island. There are one or two species in that part of the world with buoyant seeds suggesting that they at least were the pioneers. One of these has further found its way to Madagascar and nearby areas. These Indian representatives have erect acuminate to almost lanceolate apices to their microsporophylls, which curve more or less gradually upward. As in the previous section, the seeds without a spongy layer retain a fibrous layer in the seed coat. Included is the type of the genus, *C. circinalis*.