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Biogeography of the Coconut *Cocos nucifera* L.

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ABSTRACT

The conditions under which coconut (*Cocos nucifera* L.) evolved can be quite precisely specified. Those conditions still exist today and the coconut palm can be found growing in its original habitat where it will continue to thrive, with or without human intervention. The coconut can be considered as perhaps the most successful member of the world's oldest and most durable ecosystem. Yet the major component of that ecosystem, the coral reef, is constantly changing its form. As a result the precise location of a center of origin for the coconut will probably never be known.

The coconut, like the calabash and the bottle-gourd, is used as a convenient container wherever modern man has not yet brought the ubiquitous benefits of plastic. Unlike the calabash or the gourd, the coconut comes already filled with a drinkable liquid. This liquid is pure, it is palatable and it is portable. Unlike a plastic container the coconut fruit is non-returnable, absolutely disposable and totally recyclable. These qualities are found in the immature coconut and they are well known wherever the palm grows. But, for the last one hundred years, the fresh young coconut fruit has been taken for granted by agricultural scientists who have, instead, carefully studied the mature, hard-shelled, hairy, brown coconut of commerce. The water in this ripe nut is insipid and it is the high oil content of the dried endosperm, at around 70%, that interests the economic botanist. As far as the botany of the crop is concerned, the research worker has assumed the commercial plantation coconut to be representative of all coconuts. It has even been classified as *Cocos nucifera* var. *typica* (Narayana and John 1949, Liyanage 1948). This is misleading because the commercial coconut is not typical. It is nothing more than a random sample, taken into cultivation, of material that has achieved pan-tropical distribution for totally non-agricultural reasons (Harries 1978).

The concept that the coconut occurs as a wild species that survives without human intervention will only be accepted when two conditions are fulfilled. Firstly, applied scientists undertaking germplasm collections must not restrict themselves to the coconut palms that are conveniently lined up in plantation rows. Secondly, pure scientists collecting taxonomical specimens must no longer reject every *Cocos nucifera* as merely an escape from cultivation.

Center of Origin

The origin of the coconut has often been debated and there have been proposals for both New World and Old World origins for the genus *Cocos*. The taxonomic argument based on similarities between cocosoid palms native to Central and South America (Martius 1823–50) was taken to extreme lengths at a time when the commercial importance of coconut encouraged the idea of introducing it to southern California (Cook 1901, 1910). When the American palms were assigned to genera other than *Cocos* the coconut became monotypic with closest associations to *Jubaeopsis caffra* in southern Africa (Beccari 1916*a*, 1917).

Proponents for an Old World origin, have suggested Indian, Indo-Malesian and Melanesian centers for the specific type *Cocos nucifera*. An origin in the western Indian Ocean, although seemingly supported by the link with *Jubaeopsis caffra* and the presence of an Eocene fossil, *Cocos sahnii* in the Indian desert, has not been generally accepted (Chiovenda 1921). An Indo-Malesian origin was proposed in the region to the northwest of New Guinea, mainly for geological and biological reasons related to Wallace's line (Mayuranathan 1938). Prior to the time that this suggestion was made a fossilized coconut fruit had been found at Aitape on the north New Guinea coast in association with a human skull but the fact was not published until later (Hossfeld 1948). The material was estimated by radiocarbon dating to be 4,555 years old. Unfortunately, the whereabouts of the fossil coconut is not now known and it may well have been destroyed in the dating process. Very recently remains of coconuts, dated at about 3,500 before present, have been found associated with human settlements and Lapita pottery in the St. Matthias group of islands in Papua New Guinea (Kirch 1987, personal communication). A precise New Guinea origin cannot be based on such comparatively recent remains, but most modern text books generally favor somewhere in Melanesia (Child 1974, Fremond et al. 1966, Ohler 1984, Purseglove 1972, Williams 1975).

The antiquity of the coconut in the Indo-Pacific region is borne out by the part it plays in the life of the people; as shown by the names it receives (Merrill 1946), the implements with which it is processed (Werth 1933) and the uses to which it is put (Chiovenda 1921). But these all represent factors of domestication and diversity rather than of origin. Similarly, the Miocene fossil, *Cocos zeylandica* in North

Island, New Zealand (Berry 1926, Couper 1952) could represent fruit which had floated from elsewhere and not necessarily have grown in situ. The best argument so far put forward in support of a Melanesian origin is that of Lepesme (1947), who drew attention to the high proportion of insects in the Melanesian region which have coconut as a primary host. He also supported the thesis that one animal, the coconut crab (*Birgos latro*), has a close biological association with the coconut. More recently it has been suggested that this land-living crab could not have achieved a widespread inter-island distribution with only a 30 day aquatic larval stage unless the post-larval glaucothoe stage was spent in the moist husk of a free floating coconut (Harries 1983). Evidence for wild type coconuts actually growing in the region has been found in Vanuatu where fossil shell and roots dated at 5,420 years before present apparently pre-date human settlement (Spriggs 1982). Taking all the foregoing factors into account, and using data from present day coconut populations in Vanuatu that have a large number of thick husked but comparatively small fruit it is possible to suggest an origin in the region of the Lord Howe Rise-Norfolk Island Ridge at a time when that fragment of Gondwanaland was submerging, some 15 million years ago (Harries 1978).

Dispersal

Natural dispersal by floating was readily accepted by earlier taxonomists but later workers assumed that coconuts were always closely associated with human activities and therefore were distributed by cultivation. Any references to wild coconuts, in the sense that they were indigenous and never cultivated, have been disregarded. For example, an excursion flora for Java (Koorders 1911) recorded that in 1889 such a form was easily recognized where it occurred on a remote coast by its very small fruit with extraordinarily thick and firm husk yet when a botanical reconnaissance was made of the area in 1957, coconuts were not even mentioned (Jacob 1958). Similarly, reports of coconut growing spontaneously at several points on the Queensland coast of Australia (Mueller 1867, Thozet 1869, Bentham 1863–1878) were ignored until recently when a self-sown coconut was found on a Great Barrier Reef island (Buckley and Harries 1984). Even in the Philippines, where coconuts have reached their most important commercial development and might be thought to have eliminated all progenitors, wild types can still be found (Gruezo and Harries 1984) close to the place where they were first described at the time of the 17th century European settlements (Alzina 1668).

Some of the antagonism against coconuts floating and establishing naturally arose from arguments about the Kon Tiki expedition (Dennis and Gunn 1971) because it was not even realized that the type of coconut in question was not the wild type. Only when it is understood that wild coconuts have particular characteristics and preferred localities is it possible to suggest what plant characteristics to look for and just where to look for them (Table 1).

In the absence of man and predatory animals such as pigs (the coconut crab might be considered a symbiont since its presence would aid natural selection for a thick husk and slow germination), coconut palms must have been restricted to the strip of beach just above the high water mark. Under exceptional circumstances Ernst (quoted by Beccari 1917) found strand plants, including coconuts, 300–500 meters inland after Krakatoa erupted in 1883 and fifty years later Hill and van Leeuwen (1933) reported forty-one germinating coconuts on the beach of the newly emerged Anak Krakatoa IV. Coral fringed islands, and particularly atolls, are preferred habitats and to get from one to the next the coconut must float. Thick-

Table 1. Characteristics of wild, domestic and cultivated coconuts.

	Tall Phenotypes		
	Wild	Domestic	Cultivated[1]
Predominant Form	Niu kafa Type	Niu vai Type	Introgressed
Where Found	Uninhabited islands isolated beaches	Certain isolated human settlements	Almost everywhere
Stem	Slender, curved, leaf scars are irregular	Robust, erect, base can be very large	Intermediate
Leaves	Long, may hang down when green	Not so long, rarely hang down	Intermediate
Flowering Pattern	Cross-pollination is not absolute	Cross-pollinated but selfed often	Intermediate
Fruit	Long, angular, thick husk	Spherical, thin husk	All combinations possible
Nut with Husk Removed	Ovoid or spindle shaped, thick shell, little water, thick endosperm, high oil content	Spherical to obovate, thinner shell, much water, thinner endosperm, lower oil content	All combinations possible
Germination	Slow	Fast	Intermediate
Growth rate	Slower	Quicker	Intermediate
Response to MLO Diseases	Susceptible	Tolerant	Intermediate
Response to Windstorm	Susceptible	Tolerant	Intermediate

[1] Wild and domestic types are also cultivated.

husked, long, angular fruit float better, the embryo is better protected (and so are any passengers, such as *Birgus latro*). Slow germination will allow longer distances to be traversed and germination data supports this. Even after 200 days from reaping, germination is not complete (Whitehead 1965).

However, a successful species such as the coconut keeps its options open and the germination rate is much quicker when the same type is generously supplied with fresh water. It is possible to show from the results of two experiments where coconuts were floated in the open sea, that such immersion can delay germination (Edmondson 1941). It has been argued that dormancy is induced and that germination is controlled, to a large extent by the osmotic potentials in the husk (Harries 1981*a*). For the wild coconut under atoll conditions the fruit that falls to the ground germinates slowly depending on how much rainfall there is and on the amount of shade. In this situation a seedling can be present to replace any mother palm that is destroyed by lightning, old age or pests, any time for the best part of a year after the fruit matures. The fruit that falls into the relatively calm waters of the lagoon does not get saturated with salt water. Instead, the embryo is in an aerated, humid and non-saline environment produced by continual absorption, diffusion and evaporation of water through the husk under the hot tropical sun. It germinates quickly, as Edmondson's floating experiment on a sea water reservoir demonstrated. The end result is, that by the time the seednut washes ashore at another part of the same atoll, where adult palms, seedlings and seed might have been destroyed and washed away by a windstorm or tsunami, it can already be growing and can thus maintain a population of coconuts with a common genotype against competition from other plant species.

On a coral island, the only other place that a coconut can fall is into the open sea where, due to normal wave action, it will absorb considerable amounts of sea water into the husk, thereby inducing dormancy (Harries 1981*a*). If currents and winds are favorable this fruit might drift, along with any passenger crabs it may carry, to another coastline, perhaps one where coconuts (and the crab) do not already occur. Just how far this might be is a matter of opinion and computer simulation studies on long distance dispersal (Ward and Allen 1980) and plans for a free-floating experiment between mid-Pacific atolls and the coast of Central America must use the proper, wild type, coconut and take into account the possibility of sea-water induced dormancy.

It may never be known whether the coconut originated in the Indian Ocean or the Pacific Ocean or somewhere in between but wherever it started from, given enough time the truly wild coconut could, and probably did, spread from island to island as far as the Seychelles Islands to the west (Sauer 1967) and the Line Islands to the east (Beccari 1916*b*). It is also probable that the coasts of Africa, Asia, Australia and America did receive, and still do receive, coconuts that have floated from oceanic islands. These islands, which on a geographical time scale are constantly changing their size and position, have acted, and still act, as a natural conservatory for coconut genetic resources, at least for the wild type.

Domestication

Once the coconut came into contact with man there would be selection pressure for other characteristics that were unimportant to the wild type, or indeed downright disadvantageous to it. These characteristics represent the results of domestication, not agricultural cultivation which did not happen till very much later. Unconscious selection pressure for many generations (both human and coconut) improved one characteristic, the water content, and other changes depended on this. The first human contact with a coconut must have been on the sea-shore and it is possible to argue that the sea-shore is an optimal habitat for both man and the coconut. The coconut is a source of drinking water, and one that can be obtained without digging and without tools. The immature fruit is simply banged on a rock to split it. Originally, man may just have been another predator, picking up and eating coconuts that floated ashore, even as Australian aboriginal children do today (Hynes and Chase 1982). Mature palms might be considered tabu and would certainly not willingly or easily have been cut down until good steel axes became available. If the Vanuatu fossil shows that coconuts grew there for at least 2,000 years before the present Melanesian people reached these islands then, in the same way, it may have been the presence of the coconut palm, purely and simply as a source of water, that assisted the aboriginal migrations from Asia to Australasia at an earlier time. An even more radical idea is that man and the coconut may have been interdependent, in much the same way that the robber crab and the coconut may have been, and at a very early, possibly aquatic stage in human evolution (Harries 1979).

The contrasts between the characteristics of the wild and domestic coconuts (Table 1) reflects the contrasts between the environments in which the first evolved and the second was domesticated. For the wild type the curved stem allows palms to lean out over the water, gaining space and light, effectively increasing the leaf and fruiting functions despite the limited rooting area on a narrow beach. In contrast the domestic type develops a sturdy bole and erect stem to withstand hurricanes and compete with other tree crops. The wild type is susceptible to certain (MLO) diseases because it was isolated from infection whereas the domestic type show tolerance brought about by repeated exposure to infection (Harries 1978).

At some stage the domestic type would have been taken a little way inland around coastal and river settlements on the continental mainland and the larger islands of southeast Asia. The two types would remain geographically isolated from one another and the domesticated coconut would be preferentially planted in new settlements, for instance, those made by Polynesians on isolated Pacific Islands. At about the same time it was probably carried to India (Mayuranathan 1938). In Africa, coconut dissemination did not follow the route that bananas took—overland from east to west across the continent—but they were carried by sea to a specific region and within a specific 50 year period. The Portuguese took the predominately wild type from the western Indian Ocean into the Atlantic Ocean, around the Cape of Good Hope to the Cape Verde region between 1499 and 1549 and from there it went to the Caribbean and to Brazil (Harries 1977). Nor were coconuts carried across the Central American isthmus by the Spaniards as is often supposed. The Spaniards took the predominately domestic type from the Philippines after 1650 and disseminated them along the coast of Central and South America. The type of coconut found on the Caribbean coast of America is totally and unmistakably different from the one on the Pacific coast. It was realization of this fact that gave the original clue to the recognition of wild and domestic types. Not until there was extensive river travel during the Californian gold rush, around 1850, and again after 1915 when the Panama Canal was opened, did the two types come into contact there (Richardson et al. 1978).

Elsewhere the two contrasting types the wild and the domesticated have undergone introgressive hybridization whenever they have been brought into proximity because there seems to be no barriers to cross-fertilization.[2] The introgressed populations which developed show characteristics of both types or some intermediate condition. They are so common and yet so variable—both within populations and between populations—that calling any of them *typica* is meaningless. Yet, once industrial demand for vegetable oil production accelerated in the 19th and 20th centuries, all the forms—the introgressed, the domestic and even the wild—have been taken into cultivation.

A convenient way to distinguish wild, domesticated and introgressed populations is by fruit component analysis. The wild, or Niu kafa type, is found to have a higher proportion of husk and a slightly lower fruit weight than the domestic or Niu vai type. The proportions of water, shell and endosperm also differ in characteristic ways. The great advantage of fruit component analysis is that it avoids the subjective descriptions upon which previous classifications were based. It has already been used to generate data from many 10-nut samples taken in the field during germplasm collecting expeditions, from larger samples on agricultural research stations and even from 10 thousand-nut samples on commercial estates (Harries 1981*b*). However, many more data need to be accumulated and correlated with other studies, such as germination rates and so on, before coconut varieties can be considered to be well and truly documented.

Finally, even the shapes of the nuts are diagnostic and make it easy to distinguish the wild and domestic types. This observation has been applied to interpretation of archeological coconut remains from Brunei in Borneo (Harries 1981*c*).

Conclusion

Wild, domestic and cultivated coconuts are quite distinct in all biogeographical features except one—they can interpollinate—and the resulting introgressed populations have made classification difficult in the past. The conditions under which

[2] Dwarf coconut types (with the exception of the Niu leka, or Fiji Dwarf type), are fundamentally domestics since they cannot survive without human involvement. They show predominately domestic characteristics and, in particular, very bright fruit colors.

coconut evolved can be quite precisely specified as can the purpose for which it was first domesticated. The isolated conditions still exist today and the coconut palm can be found growing in its original habitat where it will continue to thrive, with or without human intervention. But the importance of the domestic form was displaced by the production of copra and this, in its turn, has been superseded by other sources of vegetable oil. The coconut can be considered as perhaps the most successful member of the world's oldest and most durable ecosystem. It is also the most widespread and well known tropical tree crop. The coral reef ecosystem is constantly changing its form and as a result the precise location of a center of origin for the coconut will probably never be known. The agro-industrial specifications for the cultivated form of the coconut are not inflexible and the type that has the highest oil content, which does not deteriorate by early germination and which has many small fruit suitable for mechanical processing—the wild type—may yet again come into its own as a renewable energy resource wherever and whenever nuclear or fossil fuels are not available.

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