THE EVOLUTION, DISSEMINATION &

CLASSIFICATION OF *COCOS NUCIFERA* L.

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INTRODUCTION

I know of no field of Tropical Agriculture that is so promising at the present moment as coco-nut planting, and I do not think in the whole world there is promise of so lucrative an investment of time and money as in this industry.

Sir W.H. Lever (later Lord Leverhulme), 1912

The danger of substitution of products or of the source of supply has very much darkened the future of the coconut economy of Asia.

United Nations, The Coconut Industry of Asia, 1969

The coconut palm, *Cocos nucifera* L., was first grown as a plantation crop in the 1840's (Child, 1974). The industrial process for making soap, patented in 1841, required a cheap source of oil. Coconut oil, from copra (the dried endosperm of the nut), provided it. Coconut cultivation needs a small labour force and provides year-round work. A change to coconut production suited many sugar plantations when the high and seasonal labour demands of that crop could no longer be met in the decade following the abolition of slavery. The development of dynamite from nitro-glycerine between 1846 and 1867 had the remarkable effect of turning a once discarded by-product of soap manufacture, glycerine, into the more profitable side of the business (Anonymous, 1912). Coconut oil also replaced animal fat in the manufacture of margarine (patented 1896). To the industrial and political empire builders coconut was a cheap source of raw material and of war material (Alcazar, 1941). The "coconut cult" and "coconut boom" were features of the stock market in the early years of the 20th century (Smith & Pape, 1912). Coconut plantations were established throughout the tropics, wherever conditions were suitable, and often where they were not. Even the possibility of growing coconuts in California was considered.

The importance of the coconut at the time of the First World War was clearly demonstrated when the German territories in Africa and the Pacific with their extensive plantations, were taken as reparation. As a result, Japan administered the Caroline, Marianna and Marshall islands. To these they added, in 1942, other important coconut growing countries. Indonesia and the Philippines together accounted for more than fifty percent of the world supply of copra; Indo-China, Malaya, Borneo, New Guinea, the Solomons and the Gilbert Islands for a further twenty-five percent (estimated from data in Patel, 1938). Deprived of access to so much coconut oil, European interest centred on the African oil palm, *Elaeis guineensis* Jacq., whilst in the USA other oil crops were developed. It is no coincidence that a germplasm bank for soybean, *Glycine max* (L.) Merr., was established by the USDA in the 1940's (Hymowitz, 1976). By the end of the Second World War, when nuclear weapons displaced high explosives, the strategic importance of the coconut had passed to other oil crops. For instance, the high palmitic acid content of palm oil and cotton seed oil was preferred for the new "conventional" weapon, napalm. Industrially, coconut oil soap, excellent for lathering in hard or saline water, and coconut fibre (coir), valued for resilient, water-resistant rope, were ousted by petroleum-based detergents and synthetic fibre.

The ascendancy of the coconut declined but such was the magnitude of the earlier plantings that it remained the predominant vegetable oil for export until 1962 (Purseglove, 1972). Since then the traditionally important copra-producing countries have been left with large investments of land tied up in over-aged and under-fertilized coconuts of doubtful provenance. Despite fluctuations in export production and price the coconut is still important in the countries where it grows because more than half of all coconuts are used domestically. The coconut palm thrives on coastal sands that do not suit oil palms and under rainfall that is too continuous for soybean. Much, or all, of the energy needed for processing could come from the production of shell charcoal, a valuable product by itself. The cost of fertilizer cannot be avoided but, by intercropping, under-planting or by grazing, economic production can be achieved by the small farmer or by the plantation. Naturally, farmers and governments wish to plant disease-resistant and high-yielding coconuts to replace old stands. Coconut breeders have devised ways to produce commercial quantities of hybrid seedlings despite the large size and low seed production of the individual palms and the long generation time (deNuce & Rognon, 1972; Harries, 1976). Yet one fundamental problem remains - how to identify coconut varieties.

Attempts to classify coconut varieties have not benefited from the pan-tropical distribution of this monospecific genus. Instead, there are conflicting theories on origins and domestication. For example, Fosberg (1962) considered that the coconut may have been domesticated from a wild species growing somewhere in the present optimum range of the modern coconut but with smaller, less satisfactory fruit. He thought that as it became domesticated it was spread through the agency of man, over an increasingly wide area. Eventually, it replaced its wild ancestor and the original habitat and centre of domestication became obscured. Whilst allowing that dissemination could take place by floating, it was his experience that when coconuts sprout where they have drifted ashore this has always been where there are planted coconuts nearby. Corner (1966) exclaimed, ". . . it has achieved a mechanism for long distance dispersal, yet it is nowhere wild!" These views were not accepted by Sauer (1971). He was anxious that the tremendous prehistoric range of the species should not be considered as testimony of long-range dispersal by ancient voyagers. he favoured the possibility that spontaneous coconut populations may be truly wild and capable of wide natural dispersal. he suggested that *Cocos nucifera* is best regarded as a semi-domesticated species, a complex of local populations with all degrees of dependence upon man, from nil to complete. This was succinctly expressed by Child (1974): "Inland every [coconut] tree owes its existence to man; on the coasts most of them do so." Now, by reassessing those elements that are not in dispute and by rearranging the disputed points into a logical sequence, it is possible to resolve the differences and establish a basis for coconut classification.

EVOLUTION BY NATURAL SELECTION

The history of this palm becomes one of the intriguing problems of botany. E.J.H. Corner, 1966

The fossils *Cocos zeylandica*, *C. sahnii*, *Palmoxylon sundaram* and *P. parthasarathyi*, which have been found as far apart as New Zealand and India (Sauer, 1967) and the suggestion that *Cocos* originated in South America (Purseglove, 1972) implicate such a wide area that, without extra evidence, further speculation on origin would be futile. However, speculation on the evolution of a large-fruited coconut from a small-fruited progenitor is rewarding. For instance, a primordial strand plant will be dispersed by floating if the fruit has a thick, fibrous mesocarp (husk). In this respect the coconut can be compared with the nipa palm, *Nypa fruticans* Wurmb., and contrasted with the coco de mer, *Lodoicea maldivica* (Gmel.) Pers. The small nipa fruit is dispersed by floating and the palm grows in river estuaries throughout south-east Asia. The very large*Lodoicea* has been washed up on the shores of the Maldive Islands but has never germinated there. The palm itself grows naturally only in the Seychelles Islands (Jeffrey, 1964). The large amount of solid endosperm (McCurrach, 1960) gives the *Lodoicea* fruit a density of 1.2 (Corner, 1962) and despite a husk about 25 mm thick, it sinks. Buoyancy in the coconut is not only the result of a thick husk but, because the endosperm is limited to a 12 mm layer lining the shell (endocarp), there is a large cavity. The liquid which partially fills this is absorbed as the fruit matures and it floats high in the water unless the husk becomes saturated (Edmonson, 1941; Rock, 1916).

Normally *Cocos*, *Lodoicea* and *Nypa* all have single seeded fruit, with a variable number on each bunch. The nipa fruit germinates on the palm and the seedling must tolerate brackish, estuarine water as it floats. The coconut seedling cannot survive long if it floats like this in sea water, despite the palm's tolerance of salinity. The distance a fruit can float and remain viable will therefore be limited by the time it takes to germinate. Dormancy is no advantage for the coconut, which is a perennial that flowers and sets fruit every month of the year in a constantly warm and humid climate. Successful inter-island or transoceanic dissemination will depend on a slow rate of germination. For coconut, germination may range from 30 to 220 days (Whitehead, 1965a). True germination, the development of the embryo through the "soft eye" of the nut beneath the husk cannot be observed. The point of the sprout emerging through the husk is counted as germination. A thick husk therefore contributes to slow germination as well as to floating ability.

Once germination begins, the amount of endosperm determines how long the seedling survives and how well it competes for establishment with the existing flora. When many fruit are produced and individual fruit size is limited, as with the nipa palm, less endosperm is available, the embryo is small and the resulting seedling grows best where there is little competition - the intermittently submerged banks of brackish tidal rivers (Corner, 1966). At the other extreme, a single *Lodoicea* fruit, which may weigh 20 kg (as much as a whole bunch of coconuts), is connected to the seedling for 3 to 4 years by a cotyledon stalk up to 4m long (Corner, 1966). The advantage afforded by this stalk probably allows successive generations to compete with other vegetation and even to establish up hillsides despite the tendency of the fruit to roll. By contrast, coconut endosperm is depleted in 12 to 15 months (Foale, 1968) and the shoot grows where the fruit falls, rolls or floats. This means that practically all inland sites are inaccessible to the naturally disseminated coconut.

Finally, in considering the evolution of the large-fruited coconut from a small-fruited progenitor, it is quite clear from the evolution of *Lodoicea* that fruit size can be attributed entirely to natural selection without human intervention. Earlier attempts to explain the range of coconut fruit size could not account for the absence of smaller fruited weedy species. These are found with other crops and would be expected if man had selected from a primitive *Cocos*. With natural selection operating for a much longer period than has been available to man, with successive generations of *Cocos* competing for a very limited habitat (the narrow strip of beach above the high-water mark) and with suitable inland habitats inaccessible, each early generation would in turn be obliterated by the more successful, larger fruited forms.

It is proposed here that a continuous cycle of natural selection (Fig. 1) could produce a coconut palm with the following characteristics: perennial growth (50-100 years), few fruit (50-100 per year), large fruit size (1-2 kg), thick husk (up to 70% fresh weight), much endosperm (200-300g), slow germination (more than 200 days). None of these parameters exceed the natural range found in the Palmae, as exemplified by *Nypa* and *Lodoicea*, yet taken together they represent a formidable dispersal mechanism. They also represent, very closely, the characteristics of varieties found as far apart as Palmyra Atoll in the Pacific and the Seychelles Islands in the Indian Ocean (Sauer, 1971).

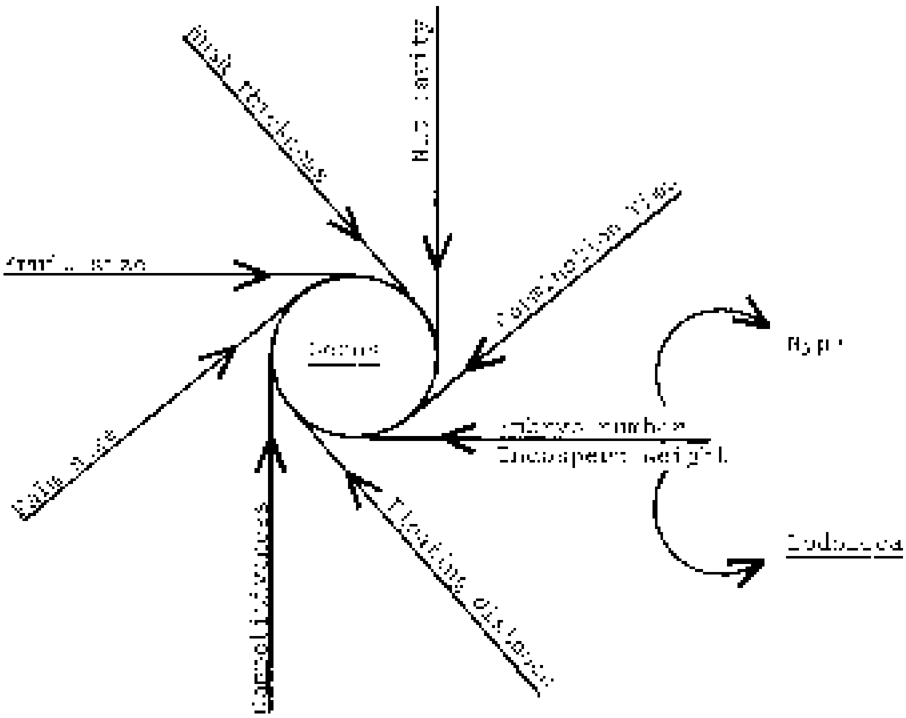

Fig. 1. Cycle of evolution of *Cocos nucifera* from a small-fruited progenitor.

Without knowing the origin of the primordial *Cocos* it is possible to conclude that if the coconut described above was present on these uninhabited islands when they were discovered by European explorers, it must also have occurred in the same form in south-east Asia. If the first cultivators in that region (where crops such as rice, taro, breadfruit, bananas and sugar were domesticated) applied even simple selection to this already acceptable plant then any changes under cultivation would be detrimental to natural dissemination by floating.

DISSEMINATION BY FLOATING

Some people believe that the germs of these trees were brought by the waves from unknown regions.

Peter Martyr d'Anghiera, circa 1552

Edmonson (1941) found that coconuts were capable of developing after having floated in the sea for periods of up to 110 days and gave an estimate of the distance that might be traversed in that time, if carried by a favourable current (of 1 knot or 0.5 m/s), as about 3,000 miles (or about 4,800 km). These results have been accepted uncritically by other authors whether supporting or refuting natural dissemination by floating (Sauer, 1971; Dennis & Gunn, 1971). Examination of Edmonson's data (table 1, p.296) shows that eight coconuts were floated for periods from 27 to 110 days. None were incapable of floating after the longest contact with the sea. All spent a further time in the nursery before germination. When the additional nursery time is taken into account, the mean time to germinate was 170 days with a range of 110 to 231 days. A ninth coconut that spent 91 days floating and 238 days in the nursery was probably set upside down after the sprout had already begun to develop within the husk.

Comparison with data from nearly 46,00 long-fruited, thick-husked seednuts (fruit) in Jamaica (Whitehead, 1965b: table 1, p.371), which had a mean germination time of 142 days and a range of 60 to 220 days, suggests that floating times in excess of 200 days are feasible. This estimate is comparable to that of 224 days for the bottle gourd, *Lagenaria siceraria* (Molina) Standl., another plant for which dissemination by ocean currents has been disputed (Whitaker & Carter, 1954). Bruman (1944), seeking the origins of coconuts found on the Pacific coast of America in the 16th century, suggested, on the basis of Edmonson's experiment, that coconuts would take about 7 months to float on the Pacific Equatorial Countercurrent from Palmyra Atoll. The re-evaluation of Edmonson's data implies that coconuts would be viable. However, a recent compilation (Kendall, 1970) suggests that the mean eastward speed of this current between Palmyra and Central America is about 0.25 m/s, equivalent to 400 days. The question of the origin of coconuts in America remains open, but natural dissemination over shorter distances elsewhere in the Pacific and Indian Oceans is a reasonable assumption. If present day currents do not favour dissemination to the eastern Pacific, nevertheless, the evolving *Cocos nucifera* might have reached the Marquesas, Tuamotu and Hawaiian archipelagos at a geological period when the oceans and continents had a different configuration. Only the Atlantic Ocean and Caribbean Sea are inaccessible to natural dissemination.

No matter how far the coconut might float and remain viable, dissemination is not successful unless the seedling grows where the fruit is washed up. This ability has been disputed on the grounds that human assistance is needed to overcome competition from other plants or predatory animals. such an extreme view is nowadays modified, but opinion remains divided upon the relative importance of natural and human-assisted dissemination. The general consensus favours the latter (see Child, 1974, for an informed review). However, it is suggested here that both have been equally important, but at different times. At first, the primordial *Cocos*, which might have originated on the continents which emerged or the land which submerged when Gondwanaland divided, became established on atolls or in regions where plant and animal competition had been destroyed by volcanic activity. This allowed the evolutionary cycle described above to take its course. The coast of America was just at, or beyond, the limits of natural dispersal. Africa was close to, or within, the limit but large stretches of coast were unfavourable, either because of animals or because it was too dry for all or part of the year. Australia was also too dry and, despite the proximity of coconut-growing islands to the north and north-east, the palm did not establish there. Asia alone provided a suitable climate. If the plant and animal competition was a constraint, then human cultivation became a mitigating factor. It is proposed that the coconut grows on mainland south-east Asia not because man took it there, but because he was there to receive it when it arrived. Perhaps he too was at an equally early evolutionary stage. The coconut not only became established, it was subjected to selection under cultivation. A different coconut variety emerged from this process, and it was this variety that became dependent on, and widely disseminated by, man.

SELECTION UNDER CULTIVATION

When the nut begins to grow, water begins to be produced within; and when the nut has arrived at perfection, it is full of water, so that there are some nuts which will contain four and five goblets of water, which water is a most excellent thing to drink . . .

Ludovici de Varthema, 1510

Fruit Number, Fruit Size and Fruit Composition

The success of natural dissemination must depend on a balance between fruit number and fruit size. Further selection for on would be antagonistic to the other. The facile explanation for the domestication of crop plants, that human selection increased the number or size of the edible parts, is inappropriate for an already large-fruited coconut. Moreover, for an emerging, yet primitive, society where the number of palms may exceed the human population, the number of fruit per palm would be relatively unimportant. For coconut, subjective estimates of small differences in fruit size or fruit number are unreliable, particularly when some palms are fertilized with human and animal waste. Coastal fishing communities that would be expected to be the first to come into contact with a naturally disseminated coconut would value it for one purpose in particular - as a source of liquid refreshment. The "water" in the immature fruit is not merely potable, it is very palatable and conveniently portable!

The selection value of increased fruit size or number is irrelevant. The important selection to be emphasised is for increased endosperm (the drinkable part of the immature fruit or the edible part of the mature one). Without reducing either the total number or the individual fruit weight it is possible for selection to change the proportions of the fruit components. The shell hardly changes for this is the foundation on which the increased endosperm is laid down. The shell is the most uniform of fruit components being approximately 12 to 16% of the fresh fruit, regardless of variety, growing conditions or fruit size. The shell is also the anchor for the husk, and it is the husk which is reduced from almost 70% to as little as 35% of the total fresh weight. Further reduction would eliminate the secondary function of the husk, which is to protect the nut inside when falling 30m or more to the ground. The amount of liquid endosperm is increased by 50%. Reduced ability to float is unimportant in cultivation.

Fruit Shape & Nut Shape

Although the weight of the fruit might be increased marginally by selection the shape of the fruit is radically altered. The coconut fruit with a high proportion of husk is long and angular. The husk is thickest at the ends and in ridges along the length corresponding to the fundamental tricarpellate ovary. These characters favour dissemination by floating. The long coconut floats high out of the water (Rock, 1916) and almost horizontally. When the embryo germinates the shoot is protected from the sea water by the thickest part of the husk. As the shoot grows and the endosperm is absorbed, the shift in centre of gravity is slight and the young sprout is at no risk of becoming submerged. The angular shape also prevents the fruit from rolling and shifting in the surf so that it remains on the beach to root and does not easily wash away again. Selection that reduces the amount of husk would lead to a shorter, less angular and, eventually, almost spherical fruit.

The change in shape of the fruit is reflected by a change in the shape of the nut inside. The long fruit has a long, spindle-shaped nut, pointed at the end opposite the embryo, and with a thick shell. The spherical fruit has a spherical or oblate nut and, because the proportion of shell does not change, the increased volume results in a thinner shell. A thin shell, more liable to crack, is a disadvantage to natural dissemination. In a primitive community a large nut with a flat base is useful as a bottle, a cup or a bowl. In the same way, the calabash, Crescentia cujete L., in America and the bottle gourd in dry areas of the tropics served primitive societies where coconuts did not grow. The antiquity of this use of the coconut can surely be equated with that of the gourd which has been found in archaeological sites in Peru (Whitaker & Carter, 1954). Of the three plants, coconut is the only one where the "bottle" comes already filled with a drinkable liquid, the monthly flowering pattern ensuring a year-round supply. Indeed, the coconut must come high on a list of plants first used by Palaeolithic man. If the immature fruit is banged on a rock the husk presents no problems to a good set of teeth, and no tools are needed to enjoy the liquid and partially developed endosperm, Unfortunately, no archaeological proof of this will be forthcoming because, on the seacoast of the humid tropics, the world's first non returnable container is eminently disposable and totally recyclable! The desirability of individual palms would become well known and they would be identified by name (as still occurs today). Visual selection for fruit shape is easy and would be applied automatically by adult or child, without conscious thought or effort, at every human and every coconut generation. Selection pressure under these circumstances would be high, despite cross-pollination. Any alternative explanation for coconut fruit variation would involve selection of the long-fruited type from a round or intermediate form. There are no compelling arguments for this.

Germination

A further unconscious selection readily made by primitive farmers is for speed of germination. Seedlings are taken from around the base of the palm, where they sprout after falling, or from nursery beds established for the purpose. In either case the slower germinating seedlings are over-shaded by early germinators, grow less well for that reason, and are not selected at planting time. Where there are differences in husk thickness, the sprout emerges from the thin husk. As the fruit gets less elongated and more spherical, they would come to rest after falling, or they would be set, on their base rather than their side. This is common practise (Child, 1974) because the position gives quicker germination. It also gives lower total germination, which is a disadvantage to natural dissemination and to commercial production but is immaterial to primitive cultivars who often allow a natural understory of seedlings to develop at higher plant densities than are desirable (Wickremasuriya, 1975).

Ultimately, selection could result in germination on the bunch, as with Nypa. This has been observed under conditions of high humidity (Whitehead, 1966) on the round fruited varieties. It has never been reported under any condition from long fruited varieties. The fruit of these fall from the palm when ripe. A spherical-fruited, thin husked variety and a dwarf variety included in the observations on the rate of germination mentioned above from Jamaica both began to germinate within 30 days. The former had a mean germination time of 66 days, the latter of 71 days. Both completed germination by 140 days and must be considered as varieties selected under cultivation. It need hardly be said that early germination is absolutely undesirable for dissemination by floating. Conversely, there is no reason to consider slow germination agriculturally desirable.

Windstorm Tolerance and Disease Resistance

Severe windstorms, which are common in many coconut-growing regions, have one result on natural evolution and a divergent result on selection under cultivation. For the naturally evolving *Cocos* high winds and rain assist dissemination of the fruit and, by destroying many or all of the bearing palms, allow the next generation to establish and outnumber the survivors. The shallow root system, capable of growing on thin soil over coral and able to exploit the fresh water lenses characteristically present on coastal sands, has little windstorm tolerance. Curvature of the trunk, notable in this form (Harries, 1971), occurs because the roots of the young palm do not provide sufficient anchorage for the large crown of leaves when a strong wind blows. This effect is often noticed on the seashore, where it may be accentuated by competition for light, or on hillsides where gravity weighs in. It is most remarkable when all the palms in a level field on good soil and at adequate spacing lean in the same direction.

Where coconuts are cultivated, windstorm is a disaster, destroying a source of food, drink, shelter and fuel on which primitive man comes to rely. Any palms that survive will, of necessity, be chosen to produce the next generation. In this way windstorm tolerance will increase. It results from a larger root system, recognised at ground level by a larger bole and increased trunk girth. Curvature still occurs, but less often and less markedly. When an old palm leans, the trunk remains straight. Differences in hurricane tolerance of the two types was observed in Jamaica after the 1944 hurricane, which destroyed over 12 million bearing palms, representing 41% of the total population of bearing palms in the island and reaching 72.5% in one instance (Taylor, 1946). At one site, where both forms grew under comparable conditions, 30,560 palms of the thick-husked form on 7722 acres (312.6 ha) lost 18,169 palms (59.5%) whilst 5,120 palms of the thin-husked form on 1272 acres (51.6 ha) lost only 281 palms (5.5%) (Cuthill, 1944).

If *Cocos nucifera* did evolve by floating from one island to another, then the isolation of each population and of each generation would reduce the chance of an infectious disease spreading (unless it was seed borne or wind borne, or until a vector could travel the same distances). If the naturally evolved variety was not exposed to disease, then natural selection for resistance would not occur. There are diseases associated with mycoplasma-like organisms (MLO), to which this coconut type is highly susceptible (Harries, 1974). In contrast, disease epidemics would progress unhindered once the coconut grew on a continental coast. Natural selection for resistance would occur and selection under cultivation would be superimposed. The spherical-fruited, thin-husked types do show resistance to lethal yellowing, an MLO-associated disease. For instance, in Jamaica, the same coconuts that survived the windstorm in 1944 also survived the disease twenty years later. They now dominate the area whereas the replants and windstorm survivors of the long, angular, thick-husked form have been completely destroyed. Varieties from south-east Asia show resistance to lethal yellowing when screened in Jamaica (Harries, 1974), yet MLO have not been reported from coconuts in the Far East. If such diseases once occurred there, then they probably still do so. However, then plant pathosystem could have achieved equilibrium (Robinson 1977). The disease might occur but it would not become epidemic unless the susceptible, thick-husked form should be reintroduced. Thus as a result of screening and extensive germplasm collection in Jamaica, there is now an additional factor which can be used to recognise distribution patterns when making variety classification.

Minor Factors & Dwarf Habit

For simplicity, the development of an agriculturally desirable variety from an original, long-fruited coconut is described above as if it were a logical sequence. In reality, although the general direction of selection is clear, there would be every opportunity for variation because of the time span and great distances involved. In effect, however, the long-fruited variety would tend to have larger fruits with increasing distance from the centre of origin. Conversely, the spherical-fruited palms with the thinnest husk would be at the centre of cultivation. Moreover, until taken inland during the most recent periods of commercial development, coconuts would always have been cultivated on the seacoast or on river banks. Since both the original and the cultivated forms are so well adapted to coastal and to riverside habitats, further selection under those conditions would tend to be of a minor and possibly even a deleterious nature. Examples have been frequently described; inflorescences reduced to a single stalk with few or no branches and few male flowers (spicata); inflorescences with many branches, many male flowers, few female flowers (androgena); fused leaflets (plicata); viscous endosperm filling the nut cavity and preventing natural germination ('makapuno'); fragrant endosperm; edible mesocarp (when immature); pink mesocarp; various pericarp colours; striped pericarp.

One further set of characteristics, those associated with the dwarf form, calls for closer examination. The term dwarf implies that the first fruit are borne close to the ground. The palm is precocious. In 30 years a dwarf palm may reach a height of 15 m, but it is never as high as a tall of the same age. The leaf spread of the dwarf is less and, with the exception of one form known in Fiji and the other Pacific islands as 'Niu leka', the trunk is slender and the leaves have narrower leaflets. The early germination, the nut shape, the proportion of husk and, for some dwarf forms, the high resistance to lethal yellowing disease, all point to selection under cultivation. Unlike other selections, which although unplanned resulted in an improved agricultural variety, the dwarf is incapable of competing under primitive cultural conditions. However, the bright fruit colours and the conformity brought about by a high degree of self-pollination (once again excepting the 'Niu leka'), give particular selection advantages. Used as a decorative palm, purposefully planted around dwelling houses and temples, dwarf forms were not considered as a plantation crop until the 1920s (Jack and Sands, 1922). Commercial interest resulted in the distribution of dwarfs to all coconut-growing countries. There is, at present, a great demand for the introduction of certain varieties, both dwarf and tall, for use as F1 hybrid parents. The plant health and quarantine risks and the cost of coconut germplasm introductions might be significantly reduced if there were better knowledge of the extent to which varieties selected under cultivation have already been disseminated by man.

DISSEMINATION BY MAN

. . . and from these trees and their fruit are made the following things: sugar, honey, oil, wine, vinegar, charcoal and cordage . . ., and matting . . ., and it serves them for everything they need. Ant the aforesaid fruit, in addition to what is thus made of it, their chief food, particularly at sea.

Manuel, King of Portugal, 1501

Pacific and Indian Oceans

In the first extensive collection made from the Pacific islands, mature coconut fruit with 20 to 25 oz. of water (or about 600 to 700 g) and a very high kernel (endosperm) weight were reported from some of the more isolated islands, specifically Rennell, Rotuma and Wallis (Whitehead 1966). The Wallis Island type is known as 'Niu vai' and coconuts with this name occur in Samoa and Tonga. In Fiji large fruited palms are called 'Niu ni Toga' (i.e. coconut from Tonga). Whitehead suggested that Polynesian travellers would select and carry these coconuts as a source of water for the journey and establish them, either accidentally or deliberately, on arrival. In Micronesia, Sproat (1967) described the 'Thifow', which is the same type, and if varieties in other islands such as Bali (Liyanage, 1974) or the Andaman Islands (Narayana and John, 1949), in Rangoon it is 'kobbari' (Gangolly et al. 1957). Known in the southern province of Ceylon as 'kamandala', Liyanage (1958) equated it with the 'Lupisan' and 'San Ramon' in the Philippines (see Copeland, 1914) and with the 'Markham' in New Guinea (see Dwyer, 1938). Pieris (1960) mentions the 'Du'a Bi' in Vietnam and Rattanapruk (1970) gives fruit component data for the 'ka-loke' in Thailand. The absence of this type from the other Indian Ocean islands, such as the Laccadives, or from uninhabited Pacific islands such as Palmyra, makes the pattern of distribution clear. Carried for food and drink it was taken, not just to the isolated islands, but to any island en route. Once established, however, cross-pollination between the introduced round-fruited, early germinating coconut and the indigenous, long-fruited, slow germinating type gave a hybrid with intermediate characters. Introgression in subsequent generations and selection gave the apparently variable populations seen today.

The Polynesians, who made their first settlements in the islands around Samoa, could not prevent introgression of the coconut they introduced with the thick-husked coconut already growing there. When the data collected by Parham (1960) is re-examined in this light, it reveals that this is so. The average weight of 123,049 fruit from 11 sites in Western Samoa was 2.67 lb. (1.21 kg.) with 57.8% nut per fruit (42.2% husk per fruit)(from data summarised by Whitehead, 1966). Upon re-examination, the sites separate naturally into two groups. The mean proportion of husk is quite distinct between the two groups (47.7% and 35.5% respectively and the two groups do not overlap. The mean fruit weight of each group is close to the overall mean (1.16 kg. and 1.26 kg. respectively) and the groups overlap. Parham also includes analyses of three thick-husked 'Niu kafa' nuts in Tonga and Whitehead analysed one 'Niu vai' in Western Samoa. By comparing the husk proportions and fruit weight with those of two putative parental varieties, it can be seen (Fig. 2) how the Samoan coconuts could arise from introgression. Reselection of the agriculturally desirable form from the introgressed populations is far from complete for a number of reasons: in contrast to the ancient Asian civilisations, the arrival of the Polynesians in the Pacific is historically recent; the thick-husked form, that made coral atolls habitable in the years before the introduced coconut bore fruit, is many ways superior to these peculiar growing conditions; island isolation limits the number of fruit which might be carried, by man or the currents; and farming was, and often is less important than fishing.

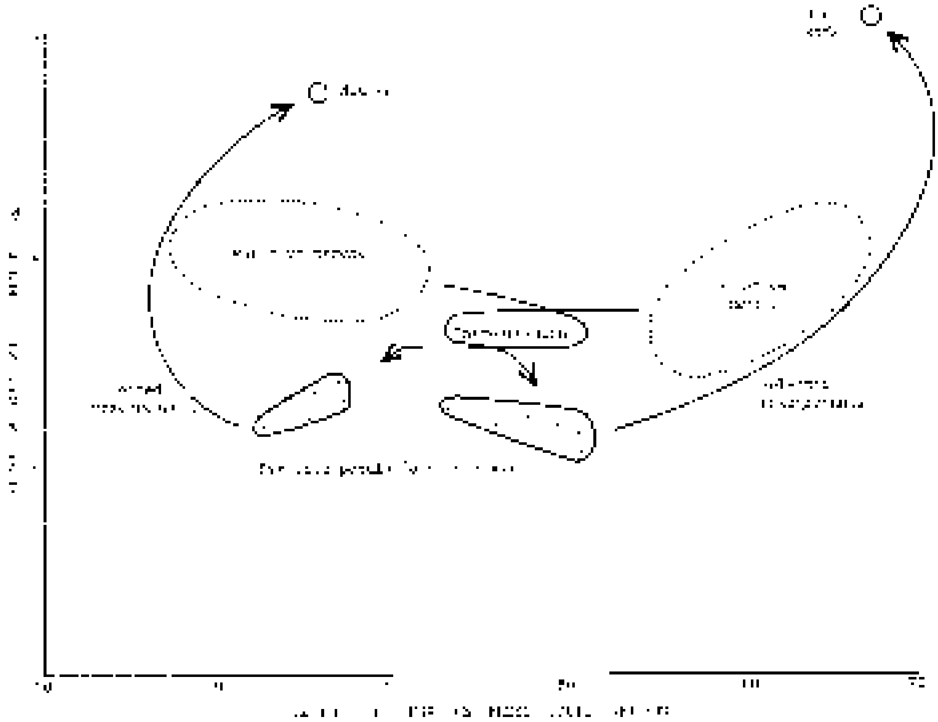

Fig. 3. Diagrammatic representation of the development of coconut populations and [illegible] by introgression, segregation and selection

Introgression between the two extreme types is not restricted to Western Samoa or even the Pacific; it has happened wherever the two extreme forms have come into contact. To mark this important concept (and to avoid repetitious description) the naturally evolved coconut will be referred to as the "Niu kafa type"; the coconut selected under cultivation as the "Niu vai type." These terms will be applied regardless of where the palms may grow and must not be taken to mean that there is any direct relationship with individual palms bearing those names in Polynesia. The decision to use Polynesian names rather than to adopt existing botanical formae or create new formae, can be readily justified. As Merrill (1946) shows, "niu, niue, nia, nyior, niog" as common words for coconut were part of a series found in all countries where it grew, extending from Madagascar to the Marquesas. Any other names were limited to geographic areas, until Linnaeus adopted *Cocos nucifera*. "Niu kafa" and "Niu vai" (and perhaps others such as 'Niu leka' and 'Nyior gading') deserve precedence established by use, if not by priority of publication.

The Western Hemisphere

Vasco da Gama's return from India and East Africa in 1499 marked the beginning of the final phase of the coconut palm's domination if the tropical coastline (Harries 1977a). Within fifty years, coconuts grew in the Cape Verde Islands and in Sao Tome and had been taken to Puerto Rica (and a few years later to Brazil). The long, angular, thick-husked, slow germinating varieties found around the Atlantic and Caribbean today (Harries 1971) are clearly the 'Niu kafa type'. The coast and islands of East Africa (including the Seychelles), where similar varieties are found, must have been beyond the range of distribution of the 'Niu vai type'. The Portuguese reached the Moluccas by 1512 but were ignorant of the agricultural advantages of the coconuts growing there. Coconuts were taken on board for refreshment during the voyage. Any remaining unconsumed would be sold as curiosities in Lisbon. Their value would be far less than that of the cargoes of spices and precious stones that were the prime purpose of the voyage.

The same reasons applied to the Spaniards. Returning home from the Philippines by way of America, they established a trans-Pacific route in 1565 that was not discontinued until 1815 (Merrill, 1954). In contrast, however, the 'Niu vai type' was carried simply because it grew in the Philippines. Nor would unconsumed fruit be taken to Europe since the mule trains crossing the Central American isthmus were loaded with much more valuable commodities. As for provisioning the Atlantic convoy, the coconuts established by the Spaniards ion the Caribbean islands, such as those on Puerto Rico in 1549, would serve that purpose. In the same way, the introduction of coconuts to Brazil served the Portuguese on their outward voyages; both great seafaring nations had known the nautical value of the coconut since 1502 (Harries, 1977b). Similarly ships sailing from America to the Philippines, and also the coastwise traffic to and from the Peruvian gold mines, would require fresh coconuts. These might originally come from palms already growing on the Pacific coast of America (Bruman, 1944; Patina, 1963). If these were the 'Niu kafa type' on the basis of the re-evaluation of Edmondson's floating experiment, then the superiority of the variety from the Philippines, in terms of water content, would become apparent. This would also be preferentially planted by the Filipinos, who established the coconut wine trade in Acapulco (Bruman, 1944, 1945, 1947). In Colima, the tall coconuts are known as the 'Filipino' and are thought to have come from Acapulco (Smith, 1970). The 'Niu vai type' is the main variety found in El Salvador (Dean and Velis, 1976) and on the Pacific coast of Costa Rica (Richardson et al, 1978), Panama (Romney, 1968) and Columbia (Harries, 1971). It occurs in Ecuador (Smith, 1974) and even in the northernmost part of Peru (Whitehead, 1968; Smit, 1970). The spread of the coconut on this coast has been so successful that America was once considered the centre of origin for *Cocos nucifera*. This is no longer accepted (for reviews, see Dennis and Gunn, 1971; Sauer, 1971; Purseglove, 1972; and Child, 1974).

Agriculture, Commerce and Industry

Less than 150 years after coconuts had been introduced to Puerto Rico, they were considered to be ubiquitous in the dry (sic) and sandy parts of Caribbean islands such as Jamaica (Sloane, 1696). Coconuts introduced to Dutch Guiana (Suriname) in 1685 (Child, 1974) could, therefore, have come from the Caribbean, from Dutch trading posts in West Africa or from Dutch possessions in the East Indies. At that time the long distance transfer of seed (or seedlings when the sailing ship had completed the journey) would be unlikely to involve large numbers. The result of such introduction will be identifiable today only if the original plants multiplied without cross-pollinating with pre-existing coconuts or if they were sufficiently different to be remarkable. An example is Bligh's second and successful voyage from Tahiti to the West Indies (1791-1793) when he carried many exotic plants. The most notable of these was the breadfruit, Artocarpus altilis (Park.) Fosberg, and the original plants, as mature trees, were photographed in Jamaica 180 years later (Powell, 1973). Of the coconut seed carried on the voyage, twelve germinated: four seedlings were left at St. Vincent and four at Jamaica. None of these, nor any progeny are now known. Unlike breadfruit plants, coconut seedlings were not a novelty. Even if their origins were exotic, the palm could not have been sufficiently different in habit, fruit shape, size or colour to be memorable. This evidence, albeit negative, that extreme geographical isolation has not led to extreme varietal differences is supported by fruit component analysis of modern introductions. (Whitehead, 1966) and susceptibility to lethal yellowing disease (Harries, 1974). Further indirect evidence is found when coir production is considered. Coir, the lignified fibre from the mesocarp, is highly elastic (Patel, 1938). It is used to make a water resistant, resilient rope and was unsurpassed for purposes such as towing or for mooring "springs," until the advent of nylon. In the Polynesian Islands sennit, a braided cord, is made from coir. Moreover at the other end of the natural range of the coconut dispersal the Arab dhows can still be found, as recorded by Marco Polo and Vasco da Gama, held together with coir instead of nails (Kaplan, 1974). The importance of coir to two widely separated seafaring peoples is directly related to the original range of distribution of the 'Niu kafa type' as influenced by the subsequent introduction of the 'Niu vai type'. Further evidence of this is seen from the fact that when the Dutch East Indies Company began the commercialisation of coir, it did not do so at its headquarters in Java but in India, and in Ceylon. Rope was exported to Batavia (Djakarta) (Child, 1974) despite the fact that coconuts were abundant there. Neither Indonesia nor the Philippines, which both became and remained major exporters of coconut products, have matched India or Ceylon for quality or quantity of coir (Child, 1974). The `Niu kafa type' producing the longest fibres, was the variety of choice whether for the native artisan or for foreign commerce. Across the Pacific, the predominance of the 'Niu kafa type' increases with increasing distance from Asia and from Polynesian settlements. Less than 1% 'Niu kafa' are estimated in Samoa (Whitehead, 1966) and 6% in Tonga (Parham, 1960). Both extreme types are considered unusual in Tahiti (Millaud, 1959); the 'Niu kafa' because it is not so obviously different from the indigenous coconut population; the 'Niu vai' because that germplasm is greatly diluted.

With coconut present on all tropical coasts, dissemination by floating and by human agency continued, but it became relatively unimportant. Where the 'Niu kafa type' had been introduced into the Western Hemisphere, there was little or no selection under cultivation because the coconut lacked the cultural importance that it enjoyed in Asia and Oceania. As late as the middle of the 19th century, Wallace (1853) could report that coconuts planted in the Portuguese towns and villages of the Amazon region were not applied to any useful purpose, the fruit only being consumed as an occasional luxury. The lack of purpose may have been worthy of remark at that time because elsewhere Europeans were taking an active interest in coconut plantations (for the reasons given in the introduction).

After the establishment of the East India Company's trading base in Singapore in 1819, coconut planting began on the south-east coast of Malaya but did not extend much until after 1837. In Ceylon commercial plantations were first laid down during the 1840's. The Dutch produced regular reports on coconut cultivation in Indonesia between 1850 and 1881. In Western Samoa commercial planting by German companies took place mainly between 1865 and 1881. The largest company-owned plantations in the worlds were developed by the Portuguese in Mozambique, beginning in 1892. Exports of copra from the Philippines to America began to assume importance after 1898 as a result of the Spanish-American War. In French Polynesia, palms planted between 1898 and 1918 accounted for more than a quarter of those growing 40 or 50 years later (for references see Child. 1974).

The steamships (also a development of the 19th century) that carried copra and indentured labourers between plantations in different areas could also carry seed or plants in sufficient quantities to affect the indigenous coconut populations. Dwyer (1939) gives some details of German activities between New Guinea and Samoa (in both directions), and Whitehead (1966) remarks on the greater uniformity of the German plantations on Tahiti (sic) and Samoa. More information could probably be obtained from the various company reports of the period. The King coconut was certainly introduced to Jamaica in 1869 from Ceylon (via Kew Gardens). It cannot now be traced, nor can the coconuts introduced after the 1904 hurricane from the San Blas islands (on the Caribbean coast of Panama). A variety which came to be known, incorrectly, as 'San Blas' was brought to Jamaica from Choco on the Pacific coast of Panama after the canal was opened in 1915 (Harries, 1971). It is the original plating of this variety which showed both windstorm tolerance and disease resistance (pages 275-276). In the Seychelles, palms raised from seed introduced from Ceylon in 1905-1910 apparently proved unpopular (Durocher-Yvon, 1953). This period also saw the first attempts to collect varieties, at Tamatave, Madagascar (Prudhomme, 1906) and Buitenzorg, Java (Hunger, 1920), although no results were forthcoming. Coconut research started in India in 1916, and a variety collection was started there in 1921. Foreign varieties were introduced to the British West Indies in 1921 and 1923. The first controlled hybridisation was made in Fiji in 1926 (Marechal, 1928). In Ceylon, the Coconut Research Scheme was established in 1929. The depressed copra market of the 1930's impeded research, and when a variety survey was begun in 1939, it had to be terminated after a few months (W.V.D. Pieris, personal communication). The Second World War also cancelled plans for coconut breeding in New Guinea (Dwyer, 1938) and prevented any further experiments on coconut dissemination by floating in Pearl Harbour (Edmondson, 1941; see also Bruman, 1944, footnote 73). Each of these activities would have contributed to a better understanding of coconut varieties.

CLASSIFICATION

On the palms called Cocos and their great usefulness.

Francisco Ignacio Alzina S.J. 1668

Present Classification Systems

Vernacular names known in the 17th century still survive, and classifications have been attempted ever since. However, the first systematic classification of varieties and forms by Narayana and John was not made until 1949. They identified two groups, Tall and Dwarf. The Tall group was composed of three botanical varieties: *typica*, with nine forms, and *spicata* and *androgena*. The Dwarf group had two varieties: *nana*, with two forms, and *javanica*. The major Tall variety, was considered to be the common variety extensively grown on a plantation scale in India and elsewhere. It forms were distinguished mainly on fruit size (as volume): *pusilla* (about 1,000 cc), *gigantea* (7,000 cc), *ramona* and *kappadam* (about 6,000 cc, the first producing 100 nuts per year, the second about 35) and (at about 4,000 cc) *siamea*, *nova-guineana*, *malayensis*, *cochin-chinensis* and *laccadive*. The dwarf varieties were classified either a delicate, bearing in three years, *nana*, or as vigorous, bearing in four years, *javanica*. Colour variants were ignored, but geographical sources were distinguished - *nana* forma *maldiviana* and *javanica*. The seven geographically named forms and *ramona* (the 'San Ramon' of the Philippines) accounted for most of the accessions obtained in 1921 and 1924 that were intended to be representative of the chief coconut-growing countries. however, varieties from the Pacific islands, Africa or America were not included; nor was the classification considered to be complete or comprehensive. The imported varieties were planted at the Coconut Research Station, Pilicode. Many were highly susceptible to attacks of pests and diseases and did not come up to expectations. The data presented by Narayana and John in the table of quantitative characters (p.366) gave the age of the introduced palms as 15 to 16 years, indicating that they were recorded between 1936 and 1940. The evaluation at that date and presentation of the results in 1949 suggests another delay attributable to the Second World War.

A survey of literature about coconut varieties by Gangolly, Satyabalan and Pandalai (1957) became the basis for a chapter in the monograph of Menon and Pandalai (1958). The tall and Dwarf groups of Narayana and John were retained. Their systematic classification key was included, yet none of the 97 named forms were assigned to any of the five varieties. In contrast, Liyanage (1958) discounted geographical variants, since he was concerned only with Ceylon, and reduced the coconut varieties to three - *typica*, *nana* and *aurantiaca*. *Androgena* and *spicata* were considered doubtful and were omitted. *Javanica* was also omitted but the description of *nana* was broadened sufficiently to include it. The new variety, *aurantiaca*, was considered to be semi-tall and therefore distinct from either the tall or the dwarf groups. The terms semi-tall and medium-dwarf had already been used by Narayana and John and the others when referring to the Malayan form of *javanica*, the 'Nyior Gading'. Liyanage gave quantitative data for some fruit components and economic characters, but the key for the identification of varieties in Ceylon was based on subjective estimates of fruit size and appearance. The forms correspond with some of those in the Indian system, but had different names. Both classifications agree that the tall varieties are predominantly cross-pollinated and out-breeding and the dwarf varieties highly self-pollinated and inbreeding. Pollination characteristics were made the basis for a third classification system by Fremond, Ziller and de Nuce de Lamothe (1966), who contrasted the flowering pattern of dwarf (autogamous or self-pollinating) and tall (allogamous or cross-pollinating). However, the dwarf is easily cross-pollinated, especially when surrounded by tall palms (as often happens) and tall palms are known to be capable of self-pollination (Whitehead, 1965b; Rognon, 1975). If the flowering pattern of coconut is considered as a function of evolution, then the ability, however slight, of the tall to self-pollinate ensures the arrival of a single fruit at a new location will not prevent the next generation from being produced and disseminated, even if no more arrive. Thereafter, cross-pollination between the heterozygous progenies would reduce the risk of inbreeding depression. The ability to self-pollinate also undermines the suggestion that dwarfs arose as a result of inbreeding among tall palms rather than by discontinuous mutation. (Swaminathan and Nambiar, 1961), a proposal which has not been supported by subsequent cytological studies (Raveendranath and Ninan, 1973). Self-pollination is a function of selection under cultivation. The less vigorous dwarf survives because its colour markers can be recognised. Whatever the origin of the dwarf form, it is clear that it was selected for its precocity, easy reaping and different fruit colours.

It is generally considered that local forms from different countries have to be tested under controlled conditions before they can be classified. This has proven difficult to put into practise, most variety collections being too small and unrepresentative of the populations sampled. To allow different accessions to be referred to without pre-judgement, current terminology corresponds tall with '*typica* allogamous' and dwarf with '*nana* autogamous' prefixed by the country of origin, e.g. Rennell Tall, Malayan Dwarf, etc. Each method had its proponents, none has received general acceptance. In effect, a catalogue of local names, a Latin index, a Greek lexicon or a geographical gazetteer can only emphasise differences between varieties rather than relationships.

Classification criteria

One criterion for classification that is common to each of the systems described above is the weight of the endosperm (fresh or as copra). This is understandable; crop specialists recognise the industrial importance of coconut and see increased oil production from copra as their main objective. Animal feed, shell charcoal and coir are by-products; desiccated coconut, coconut cream and toddy detract from copra production; drinking immature fruit is a domestic use. With this approach, plantation coconuts are therefore considered the norm, anything else is relegated to a minor position. Non-botanists who deal with the subject are necessarily constrained to think along the same lines because the basic information about coconuts comes from crop specialists. The realisation that oil production is not the most important botanical factor (and is now no longer the only economic factor) allows a reconsideration of the first principals. It then follows logically that one sort of coconut evolved naturally and that another arose under cultivation. Which form night be considered 'typica' may be debated; certainly the populations that have arisen by hybridisation, introgression and selection cannot be considered typical, except for the one particular locality. It is recommended that this terminology be allowed to drop. This is not to say that the new classification will entirely replace the old. It replaces the rationale only. Differences have been repeatedly recognised, e.g. tall and dwarf, early and late bearing, cross- and self-pollinating, large and small fruit, and so on. These are real differences and must be included in the new classification.

For the purpose of demonstrating the new classification, it is necessary to use data that are commonly available yet more diagnostic than the number of fruit required to make one ton of copra (which is otherwise the most accessible statistic). It is also useful to choose parameters that can be assessed simply and accurately and which do not require repeated or continuous observation (as does the rate of germination, the flowering cycle, or the annual nut production, for example), or subjective estimates (such as fruit shape or colour). Measurements made in terms of absolute values (palm height, leaf length, fruit weight) can again be used only if allowance can be made for the age of the palms, and the seasonal, climatic and geographical conditions to which they are exposed. This is possible only under optimum conditions, such as at a research station (and not always then).

Fruit component analysis is the method of choice. It looks at that part of the palm that not only is of the most interest but also is the most uniform despite the growing conditions to which the palm is exposed, because it is the physiological sink. Moreover, by considering the relationship between components rather than the absolute values, the effects of large or small fruit size or large or small fruit number are diminished. Fruit component analysis was carried out on a large sample of San Ramon coconuts more than sixty years ago (Copeland, 1914), on individual fruits from nineteen selections in Ceylon over fifty years ago (Stockdale, 1924), on an imported and local variety in Malaya forty-five years ago (Smith, 1932), and at one site in New Guinea nearly forty years ago (Dwyer, 1938). Narayana and John (1949), Liyanage (1959) and Parham (1960) sustained this decennial publication frequency. Many analyses are incomplete and all share one major drawback: the fruit maturity ranged from those which were fresh-picked to others that had been stored for some weeks (as is common practise in copra manufacture). Since the period of maturation is really partial drying, the weight of the husk can be greatly reduced. Ideally, dry weights would be used, as Foale (1964) did on Rennell Island, or possibly volumes, at least for measuring fruit size and nut size (Narayana and John, 1949). However, these approaches call for laboratory equipment. Similarly, Stockdale's (1924) exhaustive measurements of husk thickness and nut diameters are not correlated with other measurements because of the irregular shape of the coconut fruit.

Fortunately, unlike most almost all of the previous attempts, Whitehead's first tests of fruit component analysis in 1963 were made on the two extreme types that occur in Jamaica (Whitehead, 1966). He was able to standardise the procedure into one that can be carried out in the fields on coconuts at a definable stage of maturity, with nothing more than a machete, a spring balance, a few plastic bags, paper and pencil and an intelligent approach to random sampling. This method has been used extensively since, with little need for modification. It is a method which can be applied to ten-nut samples, as Whitehead did in the Pacific and Asia (1966; 1968), or to ten thousand-nut samples, such as those of Parham in Western Samoa (1960). Fruit component analysis allows the principal underlying the system of classification to be tested on any material anywhere at any time. It is important to take into account information on coconut introduction that may be known locally but not yet incorporated into texts such as this. Breeders and conservationists collecting seed in the field can evaluate and differentiate accessions as they go along. A pro-forma, outlining data collection procedures for fruit component analysis is given in Appendix A.

Geographical Distribution

Fruit component analysis was made the main criterion for the assessment of coconut populations in the Pacific and Asia (Whitehead, 1966;1968) and the results were compared with those obtained from two contrasting varieties that grew in Jamaica. The general conclusions were that the Asian coconuts fell naturally into two broad groups resembling the two varieties in Jamaica whereas, with the exception of some in Tahiti and Samoa, the Pacific island coconuts resembled only one of the two varieties. Subsequently, others have made analyses, from the Philippines, Indonesia and countries in America and Africa which were not included in the original two surveys. Allowing latitude for unavoidable differences which must arise as a result of random sampling and from subjective estimates of fruit maturity, it is possible to summarise fruit component analysis world-wide. The results are not quite as clear-cut as Whitehead's summaries suggest because many of the populations examined are intermediate between the two extreme forms that occur in Jamaica. But the identification of these two varieties is the basis for a system of classification which justifies the main points of coconut evolution that have been described at length above. This can best be illustrated in terms of the distribution of coconut varieties. For this purpose it is sufficient to contrast the proportion of husk in the fruit (data obtained by two simple weighings and yet directly related to the fundamental difference between a naturally evolved variety and a variety selected under cultivation). Appendix B gives 231 husk percentage/fruit weight values from 23 independent reports of populations and named forms in 24 countries. Figures 3 to 8 treat each of the following regions: America and West Africa; the Seychelles islands, India and Sri Lanka; Malaya and Thailand; Indonesia, Sarawak and the Philippines; Papua New Guinea; the Pacific islands. These regions are selected for availability of information, convenience and clarity. They also represent real differences, but this must not be taken to mean that all countries in one region necessarily have the same varieties or that countries in different regions necessarily have different varieties. This will become clear as each figure is examined. Dwarf varieties are considered separately (Fig. 9), and a generalised map (Fig. 10) summarises coconut dissemination. This map incorporates disease resistance as a factor in determining the pattern of variety distribution.

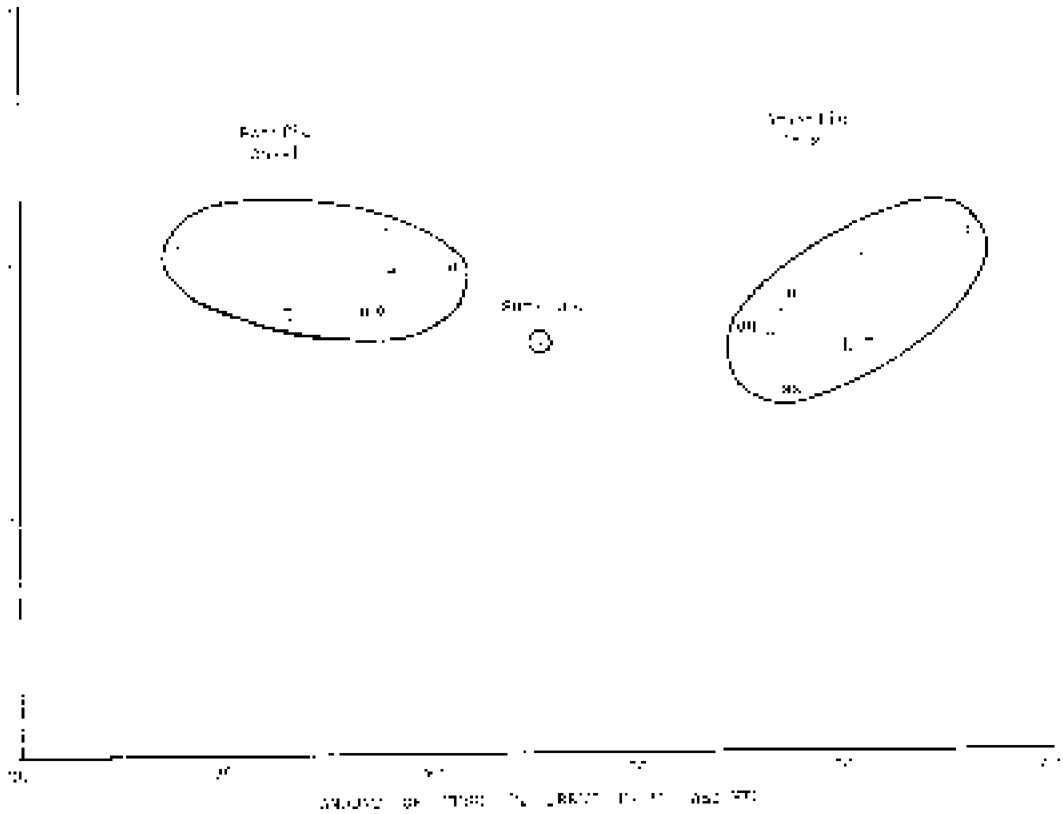

Fig. 3. Jamaica and West Africa.

In Fig. 3 the two groups identified in Jamaica by Whitehead are representative of the regional populations. These groupings are so distinct that they have been used to represent the two putative parental types for the Samoan coconut populations examined in Fig. 2 (and they are also indicated in figs. 4 to 9). Those in the 'Niu kafa group' are found on the Atlantic coasts of Africa and America and on the islands of the Caribbean. The members of the 'Niu vai group' occur on the Pacific coasts of America only and not in Africa at all. The geographical isolation of the two types in the region and the lack of more than casual cultivation of the coconut from the mid-19th century has kept them free from introgression and selection. Exceptions can be accounted for. The intermediate figure from Suriname is matched by some of the Indonesian general population (Fig. 6), and this lends support to the possibility of an introduction from Indonesia in 1685 (see page 281). In fact the ten fruit sampled (Bor, 1970) fall into two groups of five on the basis of husk proportion. This strongly indicates that the two extreme types were once present. In Jamaica both extreme types are found because seed was introduced from the Pacific coast of Panama as already described (page 283). The presence of the Caribbean type on the western shore of Lake Nicaragua (Romney, 1970) and of the Pacific type at the mouth of the San Juan river on the Caribbean coast of Costa Rica (Richardson, Harries and Balsevicius, 1978) can be attributed to the importance of the river and the lake as a route for the Vanderbilt Accessory Transit Company during the California gold rush of the 1850's. No conflicting data have been obtained from West Africa, although it is reasonable to presume that attempts to develop a coconut industry there in competition with the indigenous African oil palm probably involved introduction of material from elsewhere. Excepting scientific introductions in the last twenty years, only one introduction is known, that of Ceylon coconuts introduced to Ghana in 1910 (Johnson and Harries, 1976).

No data are available from East Africa, but the similarity of the Seychelles, Indian and Sri Lanka coconut populations (Fig 4) it is clear that, as for West Africa, the 'Niu kafa type' is predominant. This accords with movements of coconut presumed to have been made after 1499 by the Portuguese (Harries, 1977a). The 'Niu vai type' has had limited introgressive effect, as can be seen from one Indian and one Sri Lanka population sampled by Whitehead (1968) and by the data for 'kappadan' and the gigantea in India (Narayana & John, 1949). From the descriptions of Gangolly et al (1957) and Liyanage (1958), it can be anticipated that discrete populations showing effects of introgression and selection will be found when more detailed fruit analyses are made. The coconuts from the Laccadive islands favoured by Ninan (1976) represent the less introgressed and therefore most distinct 'Niu kafa type', as do the coconuts from the Seychelles and the isolated island group in the western Indian Ocean.

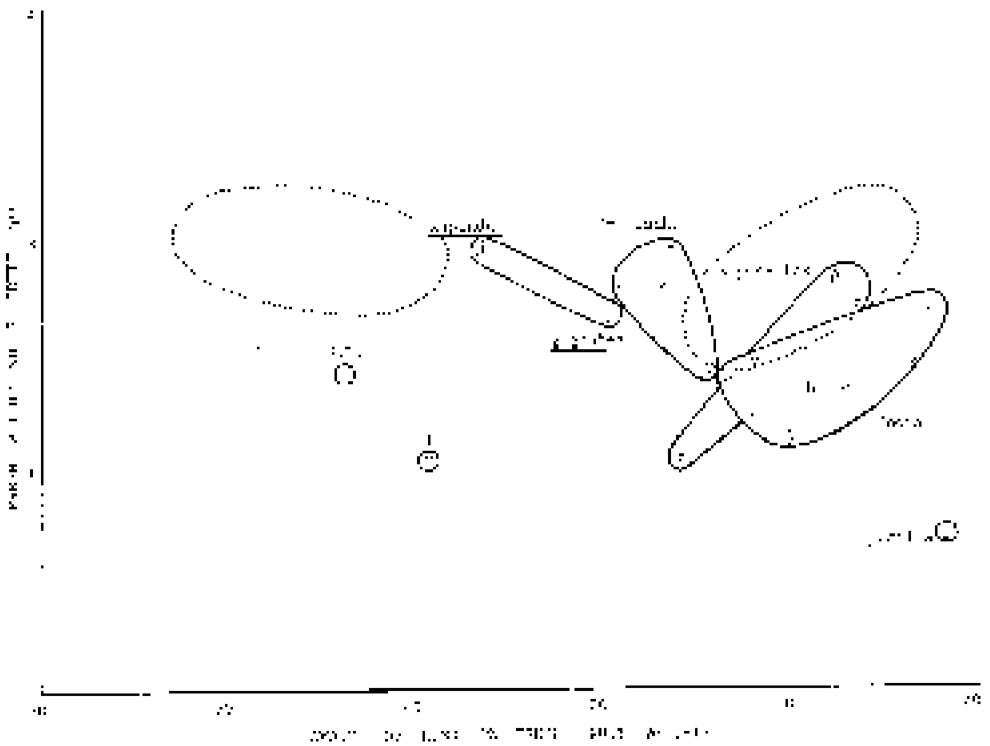

Fig. 4. India, Seychelles and Sri Lanka

The isolation of the 'Niu kafa type', as indicated in figs. 3 and 4, explains three apparently unrelated events: the confused identity of the 'San Blas' coconuts in Jamaica; the unpopularity of Ceylon coconuts in the Seychelles; and the present day introduction of F1 hybrids from West Africa to the Far East. The 'Niu kafa type' has well developed endosperm, thick, dense and characterised by high oil content. These characters are consistent with natural selection and competitive success during the evolutionary period. To the farmers in Jamaica and on the Seychelles the thick meat makes better copra which is easy to remove from the half shell [a fact noted by Dwyer (1938) for coconuts from some areas of the Solomon Islands]. Thus any 'Niu kafa type' introduced from Ceylon to the Seychelles would not be recognised after a few years. This happened with the San Blas island coconuts in Jamaica. The name 'San Blas' became misapplied to the Pacific coast coconuts because these were very different to the common coconut in Jamaica. Similarly, in the Seychelles the 'Niu vai type' from Ceylon would become identified as the Ceylon coconut [pictured on page 439 of the paper by Durocher- Yvon (1953)]. In those parts of the Far East where the 'Niu kafa type' no longer predominates (see figs. 5 to 8) the quantity of copra or oil per nut from the 'Niu vai type' were held to be most important. However the need to increase copra or oil production per hectare makes the endosperm characteristics of the 'Niu kafa type' desirable. Use as an F1 hybrid parent in West Africa has allowed 'Niu kafa type' germplasm to be reintroduced to the Far East. As pointed out above, this movement carries with it the danger of upsetting the plant pathosystem equilibrium of MLO associated diseases.

On the mainland south-east Asia, represented by Thailand and peninsular Malaya (Fig. 5) the 'Niu kafa form' appears to be uncommon. This is in accord with the theory that it was on this continental coast (perhaps extending north to the Si Kiang river delta) that selection under cultivation took place in prehistoric timed. Again it may be anticipated that a closer examination will reveal introgression. For example, Rattanapruk (1970) states that the 'Park-choke', found growing along the coast of the Indian Ocean, resembles coconuts from Ceylon. This might explain the apparent discrepancy of the siamea figure. Narayana and John could have obtained seed from that coast; a strong possibility since the distance by sea is only half that to the Gulf of Siam. The geographical isolation presented by an isthmus, clearly demonstrated in Central America, must also occur on the Kra isthmus in south-east Asia. The longer span of time and the greater involvement in coconut cultivation had allowed for a greater degree of introgression.

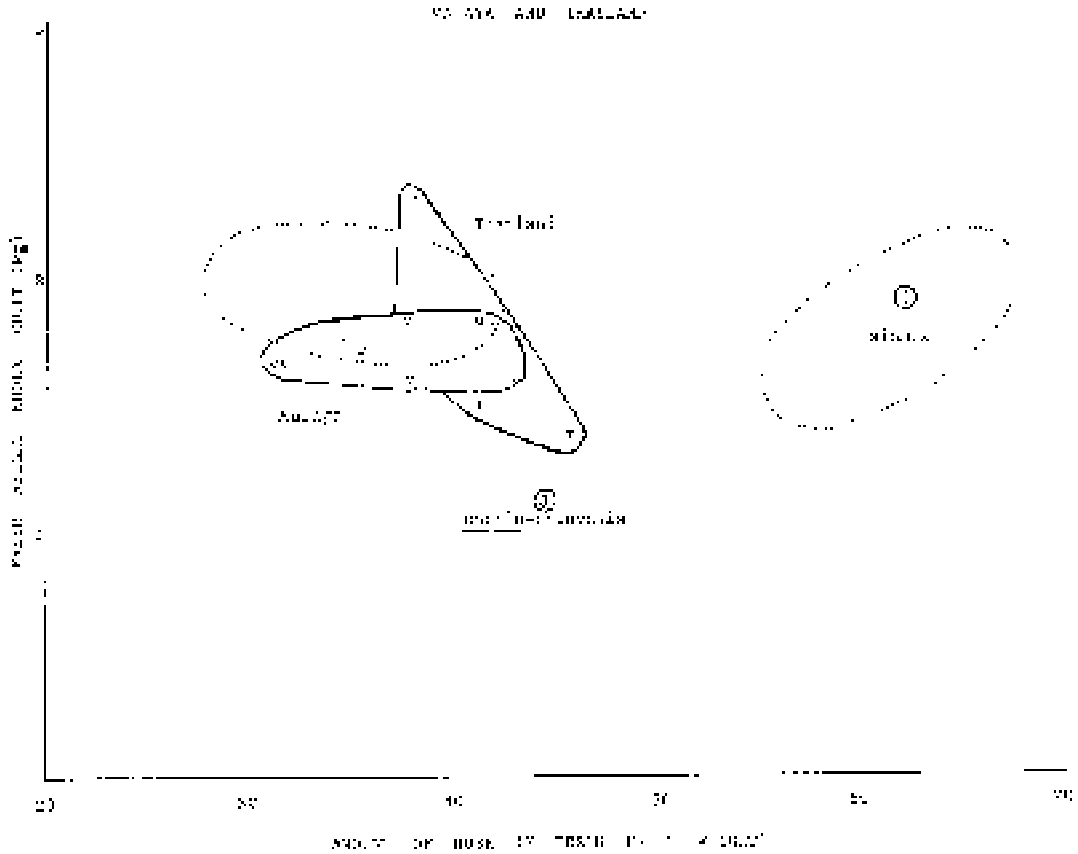

Fig. 5. Malaya and Thailand

Although separated for clarity, the islands of Indonesia, the Philippines and Papua New Guinea (Figs. 6 & 7) have much in common. Hunger (1920), Copeland (1914) and Charles (1961), all express similar opinions about the great range of variability to be found in the respective countries. On the basis of the theory expounded here, the two extreme forms would have introgressed first in these regions but, unlike the continental coast where the 'Niu kafa type' could be exposed to continual elimination by human selection (or disease incidence), the islands (over 7,000 in the Philippines) would become havens for every type. The short inter-island distances would allow the 'Niu vai type' or the intermediate forms to be disseminated by floating, as was shown to be the case when coconuts were found sprouting within 18 months of the emergence of a volcanic island Anak Krakatoa IV from the sea (Hill & van Leeuwen, 1933). In some sampled populations the apparent intermediate husk thickness may be due to the averaging of unlike types, as suggested for the Surinam coconuts (Fig. 3). In the data for Indonesia collected by Liyanage (1974) different fruit and nut shapes are indicated, and it is clear that some angular and some spherical types occur. No doubt differences will be found. With the data presently to hand, the coconut population on Bali is notable and would seem to have influenced nearby islands such as Java or Sulawesi. This may be due to Dutch trading activities, but the earlier religious isolation of Bali may account for the original isolation of this form here. Similarly, the 'Niu vai type' of San Ramon in the Philippines was probably encouraged by the early Spanish interest and carried to the west coast of America after 1565 as a source of refreshment on the trans-Pacific galleons.

The Sarawak coconuts (Fig. 6) appear to be quite distinct from those of Indonesia and the Philippines. However, one Sarawak sample (from Sungei Pinang) and one Indonesian sample (from Padang Tikar in Kalimantan) are almost identical (fruit weight 1800 : 1786 g, husk 45.0 : 44.9%). The two sites are only a few hundred kilometres apart on the west coast of Borneo - a very small distance when the entire region is considered. These coconuts are similar to the rest of the Indonesian and Philippine samples. The other Sarawak samples, therefore, require explanation. Wong Ting Hung, of the Sarawak Department of Agriculture, states (personal communication) that coconut improvement probably took place from neighbouring territories, especially peninsular Malaya, during the colonial period but that no record was kept. By comparing figs. 6 and 4 it can be seen that there is a close coincidence between the Sarawak and the Sri Lanka samples. It has already been shown that coconuts from Sri

Lanka were taken to Jamaica (1869), Seychelles (1905-1910) and Ghana (1910), and it is suggested here that an introduction was also made to Sarawak. Such an introduction would probably have arrived at, and been planted near, the main seaport. All of the Sarawak data were collected a few miles from Kuching. Fruit component analysis elsewhere in Sarawak may confirm that the Kuching samples are atypical. In that case further investigations would be appropriate. There may be no government records in Kuching, but Colombo and London, particularly Kew, might have kept the records at a time when Sarawak had just been made a colony (in 1842, during a decade that has been shown to be critical to the dissemination of coconut). If the services of the botanic garden were not used, for what could have been a direct commercial transaction, then there might be private company records somewhere. If the final result of this 'non-agricultural research' should confirm an introduction from Sri Lanka, it would be a practical, if unanticipated, demonstration of the value of fruit component analysis and of the distinctness of the two types of coconut.

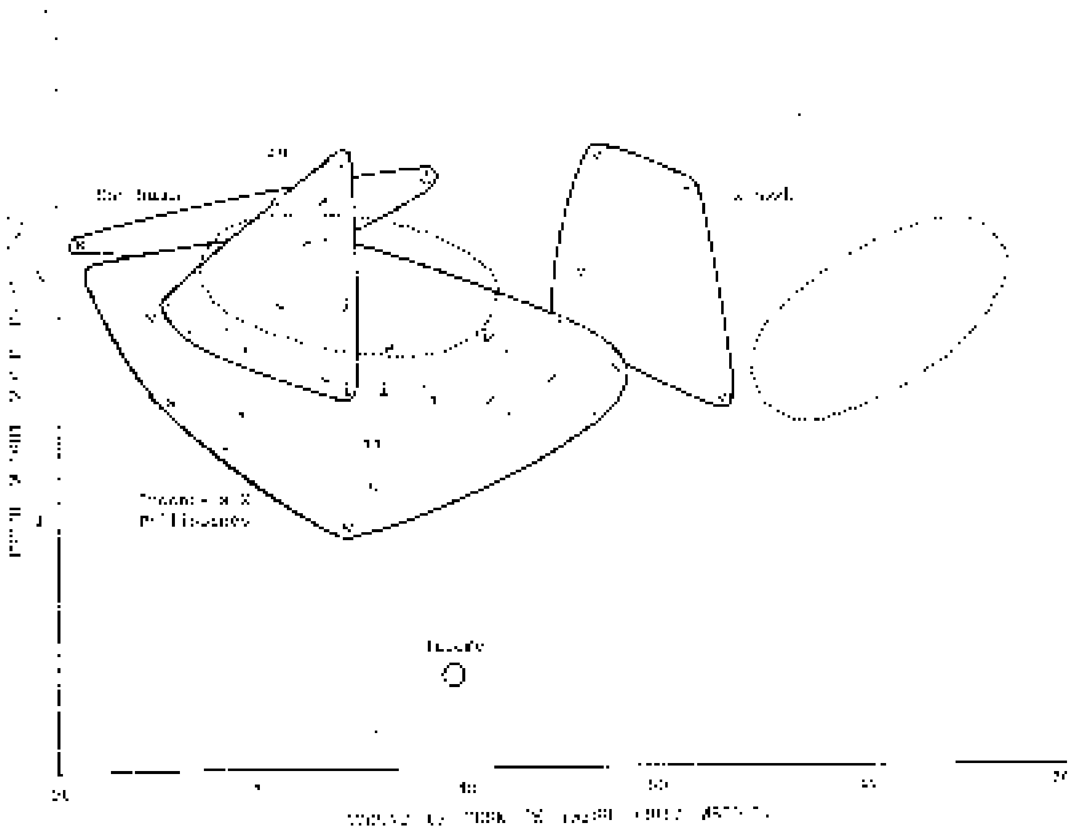

Fig. 6. Indonesia, Sarawak and the Philippines

From the data collected by Whitehead (1966), the coconut populations of Papua New Guinea appear very uniform (Fig. 7) yet completely different from the nova guineana of Narayana and John (1949). This may be accounted for by the fact that comparatively large areas of New Guinea plantations, at such places as Madang and Aitape on the mainland, Bouganville, New Britain and possibly Kar Kar Island were derived from selected and marked palms on one of the Witu (Vitu) islands (Dwyer, 1938). In 1937 Dwyer found that even the original old palms from this source were healthy and bearing heavily. He described the nuts as usually round, of medium size, very meaty and heavy in proportion to the size and with a husk that a was not unduly thick. However, on a different group of islands he found a thick-husked coconut that had an elliptical or ovate nut. Palms with the distinct fruit characteristics grew under comparable conditions on Matty island and his descriptions, together with photographs of the whole, husked and split fruit, leave no doubt that both the 'Niu vai type' and the 'Niu kafa type' occur in Papua New Guinea. Whitehead sampled one form, whereas Narayana and John sampled the other.

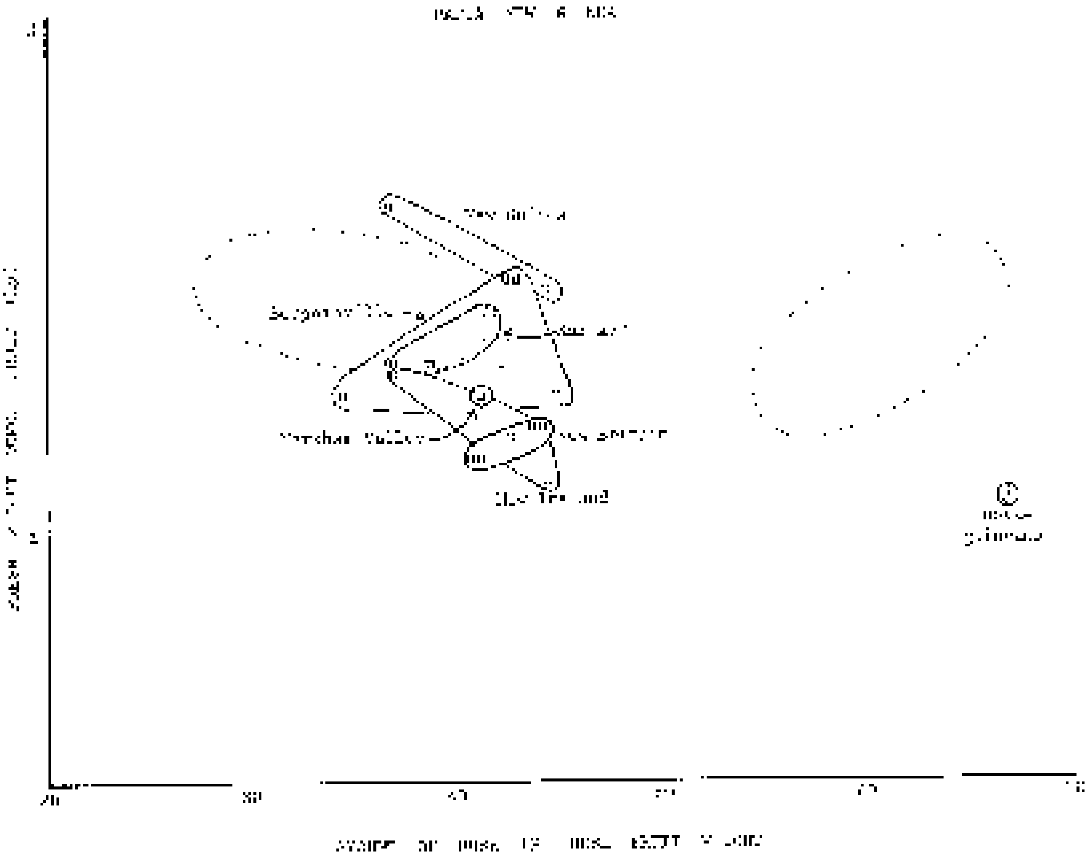

Fig. 7. Papua New Guinea.

On the Pacific islands, the influence of the 'Niu kafa type' once more becomes obvious (Fig. 8) for reasons already discussed. Each group of islands appear to have one or two intermediate forms and one or both of the extreme types. In the isolated, Polynesian settled islands the 'Niu vai type' predominates. Isolated islands without settlements might be expected to have a uniform 'Niu kafa' population. However, there might be no evidence of temporary settlements on small atolls, and it has been recorded that some Polynesians destroyed coconut palms to discourage others from visiting islands where there was good fishing (Sharp, 1957). Captain Cook planted coconuts on Christmas Island in 1770, and 103 years later the first plantation was established (Jenkin and Foale, 1968). A very characteristic long-fruited form is found on Christmas Island (Friend, 1975). However, seed introduced to the Solomon Islands has resulted in a variable population. Fruit component analysis is similar to those of the Fiji, Tahiti, Rangiroa and Tonga types, but most of the individual data are well into the putative 'Niu kafa group' (Friend, unpublished data). The New Hebrides coconuts are notable for small fruit, with predominantly 'Niu kafa type' characteristics. If all the Pacific island coconuts are now re-examined, with the differences between the two types in mind, it should be possible to estimate the degree of introgression for each coconut population. This must be done with due regard for Polynesian, European, American and Japanese activities.

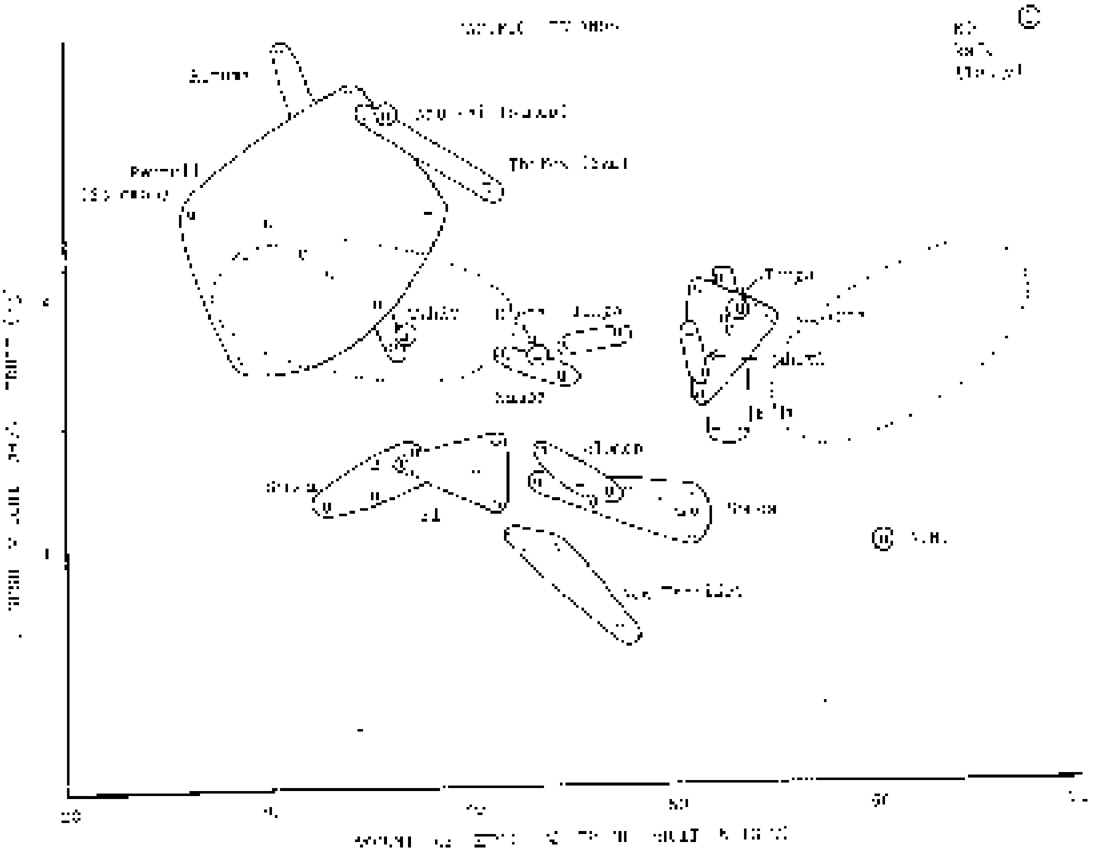

Fig. 8. Pacific Islands.

Dwarf Varieties

Dwarf varieties have been selected and maintained in cultivation and disseminated by man. Despite a high degree of self-pollination, they cross-pollinate quite freely with one another and with tall varieties. There have been many opportunities for this to happen where a few dwarfs have been surrounded by many tall palms. Reselection of the dwarf forms following such hybridisation is possible because the bright fruit colour can be identified in the colour of the leaf petiole of the seedling. The red, yellow and green fruited dwarfs that occur in many Asian countries are not necessarily synonymous although they may well have had similar, or even identical, origins. Hybridisation allows introgression of some of the characters from the predominant tall type, and in time the dwarfs will come to reflect the differences found in the tall populations. This is clear from the range of husk thickness shown in Fig. 9 However, three basic dwarf types can be recognised. Two correspond to the nana and javanica varieties of Narayana and John (1949); the third, the 'Niu leka' from the Pacific was apparently not known to them although it had been used by Marechal as early as 1926.

In Fig. 9 the group of small-fruited dwarf types, corresponding to the nana classification, consist of the 'coconino' and 'mangipod' in the Philippines, the red and green colour forms of the 'Chowgat Dwarf' in India, the red-fruited dwarf in New Ireland (Papua New Guinea), and the red-fruited 'Haari papua' in Rangiroa (French Polynesia). Others of the same type, for which fruit component analysis data are not yet available will probably include the dwarf of the Maldive Islands (maldiviana), the 'klapah puyoh' in Malaysia, the 'Manila' in Colombia and Ecuador, and the red 'Cameroon Dwarf' in West Africa. The New Ireland and Rangiroa dwarfs were considered morphologically similar by Whitehead (1966), who also found them in other parts of the Territory of Papua and New Guinea and French Polynesia as well as in the New Hebrides. The original palm in Rangiroa was supposed to have been introduced in the 1930s (Whitehead, 1966), and although the source is not stated, it is surely implied in the name 'Haari papua'. Likewise, in Western Samoa a small-fruited red dwarf regarded as of New Guinea origin is known as 'Niu niukini' (B.J. Leach, unpublished observation). The presence of the red-fruited dwarf in parts of New Guinea and in Papua was noted by Dwyer (1938), who considered that they might have been brought there by natives from the Dutch-controlled western region of New Guinea (i.e. West Irian). Recently, de Nuce and Rognon (1977), describing four geographically differentiated dwarf coconut varieties in

West Africa, suggested that the small-fruited red dwarf in Cameroon might have come from former German possessions in the Pacific. Support for this proposal is apparent not only from colonial history but also from the fact that the 'Cameroon Dwarf' is susceptible to Kribi disease (Dollet et al., 1977) whilst the `Rangiroa Dwarf' is susceptible to lethal yellowing disease (Harries, 1974). Both diseases have an MLO etiology. Further work on this aspect of variety identification is needed because the resistance of other dwarf types to MLO diseases has become an important commercial consideration. Moreover, although hybrids between small-fruited dwarf and larger fruited tall varieties tend to be small-fruited, subsequent progenies may have been selected to recombine characteristics from each parent. The colour, fruit shape and inflorescence stalk of the 'King' coconut in Sri Lanka are like those of the red dwarf, whereas the fruit size, bole, trunk girth and absence of precocity are not. Many of the named Philippines types may have originated from dwarf x tall hybrids.

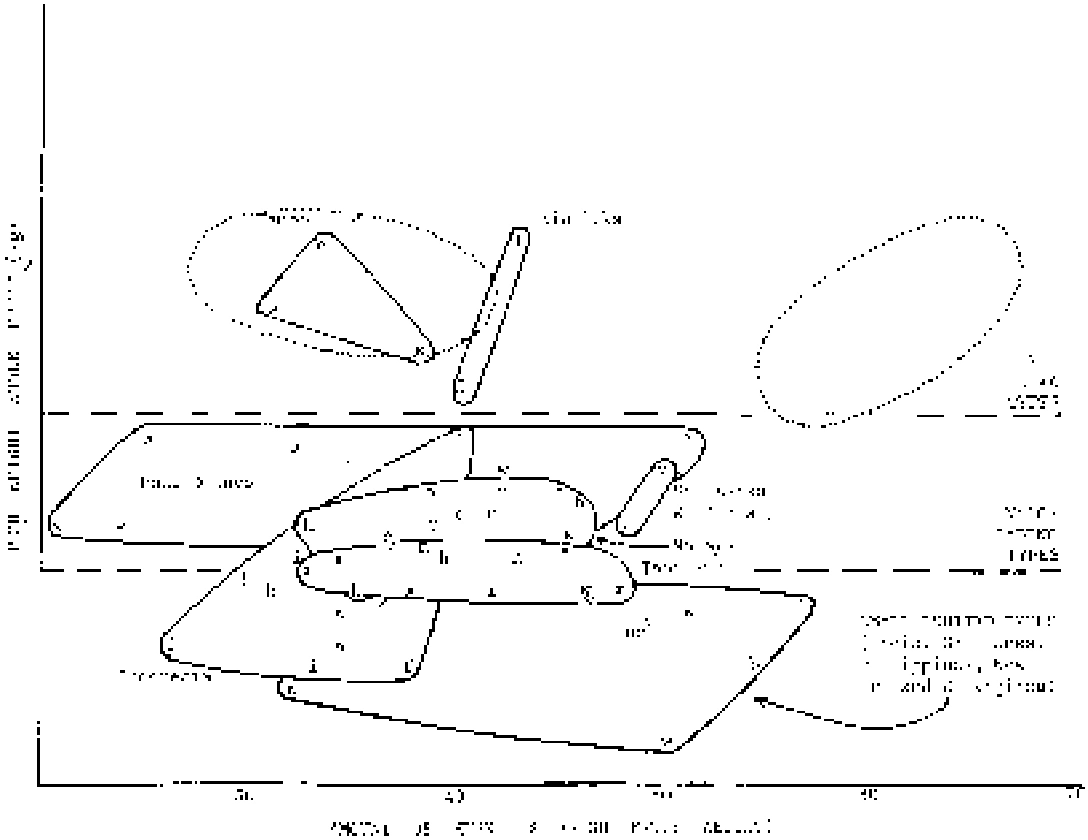

Fig. 0. Dwarf varieties.

The larger-fruited, more vigorous dwarf, represented by the javanica classification, has now become well known in most coconut growing countries of the world as the 'Malayan Dwarf', as a result of the popularisation in the 1920s (Jack & Sands, 1922) and, more recently, of high disease resistance to lethal yellowing disease (Harries, 1974). Originally known in Malaya as 'Nyior gading', it was considered to have come from Java in about 1890 (hence the term javanica). Its origin cannot be traced, although it would appear to be included among the earliest European descriptions. The predominant colour form at the time of its popularisation was yellow. Red and green forms are now common. It is possible to confuse the green 'Malayan Dwarf' with the green 'coconino' since the difference in fruit size, particularly under poor growing conditions, may be slight. In Malaya introgression with the tall variety not only gives occasional yellow fruited tall palms but also makes the green dwarf more variable than the yellow or red in plant habit. In Jamaica where the dwarf was introduced recently and from a very limited source, the green dwarf is remarkably uniform. Resistance to lethal yellowing disease of all three colour forms is much higher than for any tall variety, perhaps because factors for resistance are retained in an homozygous condition by self-pollination. Hybrids with tall palms are at present becoming commercially popular, for precocity, high yield and for resistance to lethal yellowing disease. The terms medium-dwarf and semi-tall, applied to this dwarf, are misleading and might better be applied to known hybrids or to suspected progenies. Once more the various named forms in the Philippines should be considered and perhaps the 'Gangobondam' in

India.

The third dwarf type is quite different to the other two. Except for the very short internodes, which reduce trunk height and produce a dense leaf canopy, all other characteristics resemble those of tall varieties. The well developed bole, the trunk girth, the predominantly cross-pollinating flowering pattern, the lack of bright red or yellow fruit colours, the large fruit size and an exclusive distribution (until very recently) within certain Pacific islands all point to a completely distinct selection process. It was reported from Samoa more than 100 years ago under the same name 'Niu leka' (Powell, 1868), and is found under the same name in Tonga and Fiji. The same type in the Cook Islands was taken to Tahiti where it is known as 'Haari haeha'. It is called the Fiji dwarf, perhaps because its commercial possibilities were first investigated there. The extreme expression of the dwarf form is so dense as to be unfruitful, and the segregation for palm height, because of cross pollination with tall palms and between heterozygous forms, has prevented successful commercialisation. It was used to make the first controlled pollination with the 'Malayan Dwarf' in 1926 (Marechal, 1928). Although this work was not followed up, late generation progenies in Jamaica, known as 'Fiji-Malayan' have possibilities for breeding because they are red or yellow fruited and resistant to lethal yellowing. A dwarf variety known as 'Tambolilid' that occurs in the Philippines has a similar habit to the 'Niu leka' (Smith, 1971). Fruit component analysis shows great similarities. The fact that the "original palm" on San Miguel Island was about 30 years old in 1959 (Pancho, 1959) points to an introduction made at a time that coconut breeding research was being initiated in many countries. A coincidence not previously commented upon is the fact that cadang-cadang disease was first positively identified from the same island and at the same periods of time (Ocfemia, 1937). This is not a suggestion that cadang-cadang was introduced from a Pacific island; it has been found only on coconuts from the Philippines. A variety collection could have included coconuts from other countries or other palm species which are affected by cadang cadang, such as oil palm, might have been the source.

Fruit size and Fruit number

Although the importance of fruit selection for fruit size and fruit number has been discounted, it cannot be denied that such selection could occur. Thus the large-fruited gigantea of Narayana and John apparently sets few fruit, as would be expected since selection for one characteristic must be at the expense of the other. Similarly, varieties with many small fruit, such as pusilla in India (Fig. 4), 'Laccadive micro', in Sri Lanka, 'tacome' in Indonesia (Fig. 6), and some of the Philippine named types, might represent selection for fruit number. It is also possible that selection from dwarf x tall hybrid progenies (and from the reciprocal tall x dwarf) could produce small-fruited tall varieties. In that case these forms would tend to be subordinate to the local tall variety yet have similar proportions of husk and other fruit components. This would appear to be the case with types named here. Unfortunately, the extent of these minor types, and thorough fruit analyses for most of them, remain to be evaluated. In contrast, Whitehead (1966) has shown that the predominant variety in the New Hebrides is small-fruited (as can be seen in Fig. 8), and he considers the characteristic to be evident in the Fiji and Solomon populations. Since the dwarf in that part of the world is the large-fruited 'Niu leka', it would appear that introgression between tall and dwarf is not the answer. Nor would selection under cultivation favour the wide dispersal of a small-fruited type. The high proportion of husk and almost total susceptibility to lethal yellowing disease in Jamaica allows an alternative explanation. Under the proposed cycle of natural selection (Fig. 1) the fruit size increases with increasing distance from the centre of origin. The New Hebrides Islands might lie closest to that centre.

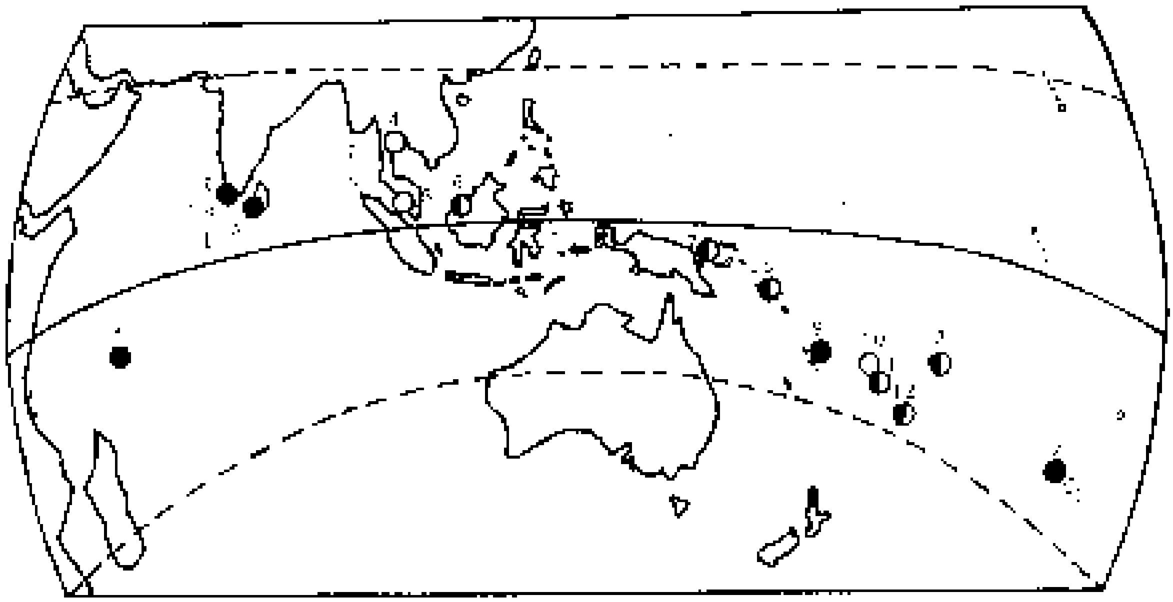

Fig. 10. Coconut fruit component analysis and disease reaction indicate the range of natural dissemination and the extent of selection and dissemination by man. 1. Seychelles. 2. India. 3. Sri Lanka. 4. Thailand. 5. Malaysia. 6. Sarawak. 7. New Guinea. 8. Solomon Islands. 9. New Hebrides. 10. Rotuma. 11. Fiji. 12. Tonga. 13. Samoa. 14. Tahiti & Rarotonga.

● Niu kafa types predominate; susceptible to lethal yellowing disease in Jamaica.
◐ Introgressed types predominate; some resistance to lethal yellowing.
○ Niu vai types predominate; better resistance to lethal yellowing.

DISCUSSION

Whence came this most widely cultivated and now pan-tropical palm . . .?

E.J.H. Corner, 1966

This has been a topic of controversy, often heated, for over a century.

J.W. Purseglove, 1972

In the introduction to his compendious volume, Simmonds (1976) wrote that he thought that knowledge of crop plant evolution was often insecure and that, even now, the right questions have not been asked. This would certainly seem to be so with coconuts, which has received more than its share of ill-advised answers. Are the dry climates of interior localities really "the only conditions where this palm could be expected to maintain its existence in a wild state"? Has the thick husk of the Palmyra coconut really developed by "hypertrophy of the tissues of the pericarp" stimulated by the efforts of the robber crab, Birgus latro L., to reach the seed in the young fruit? Would the "most likely route" for coconuts to reach West Africa really have been overland? It would be invidious to name the reputable botanists who made these suggestions. Their other, considerable, contributions to coconut research cannot be denigrated. These answers tried to justify preconceptions: that a coconut variety could be found that would grow in California and Arizona; that the Palmyra coconut had an abnormally thick husk; that coconut fruit could not float to West Africa. To follow Simmond's advice, the questions asked must be more fundamental. For instance:

(1) What coconut might evolve naturally?

(2) Where might natural dissemination take it?

(3) How might a coconut selected under cultivation be different?

(4) Who might disseminate this?

(5) Why do two completely different varieties predominate in the Western Hemisphere yet occur as only a subordinate type in Asia and Oceania?

(6) When might all this have taken place?

The answers to this catechism form the basis for this paper. The key question is the fifth, because it is only when the two distinct and geographically isolated varieties are contrasted that the other questions become obvious. In the major coconut-growing areas of the world, the long history of coconut cultivation and the recent history of copra production on a plantation scale served to conceal the differences between natural evolution and selection under cultivation. The seventh question, asked in the quotation which opens this section, concerns the origin of *Cocos*. No firm answer can be given, but if the smaller-fruited coconuts identified in the New Hebrides Islands are taken into consideration, together with the fossil in New Zealand, it may be suggested that the centre of origin was in the region of the submerged continental fragment of the Lord Howe Rise-Norfolk Ridge complex. This was isolated from Australia about 80 m years ago and apparently submerged below sea level about 15 m years ago. (Scrutton, 1976; and personal communication).

Interesting though it may be, the question of where coconuts came from must not distract attention from the question of where it is going. Evolution has not stopped. Any review of agricultural, commercial and industrial uses suggests that coconut will continue to be important both to the domestic agriculture and to the export industries of countries in the humid tropics. Coconut breeders and other crop specialists therefore need to know more about coconut varieties. However, the evaluation here is not intended to be a classification in detail. Now, breeders or botanists in each coconut-growing country should investigate the endemic coconut populations, and variety trials where these are available and suitable. Using the simple pro-forma in the Appendix as a guide only, each of the suggestions made in the paper must be tested, and confirmed or corrected. When sufficient data of comparable quality have been accumulated, then, and only then, can the detailed classification of varieties be considered. As much additional descriptive data as possible, botanical, ecological and even historical, must be included. This will have to be a co-operative effort and might be suitably co-ordinated by the FAO ad hoc Coconut Breeders' Consultative Committee acting with the International Board for Plant Genetic Resources and other interested bodies.

SUMMARY

In conclusion, it is the most perfect tree that is found, to our knowledge.

The Account of Priest Joseph, circa 1505.

The evolution, dissemination and classification of the coconut can be considered as a logical sequence. First came the natural evolution and dissemination by floating of a variety with large, long, angular, thick-husked and slow-germinating fruit. It had a theoretical range anywhere between the east coast of Africa and the west coast of America, wherever currents were favourable. From this type, selection under cultivation produced a spherical-fruited variety, not necessarily larger but with increased endosperm, reduced husk thickness, earlier germination and disease resistance. Man came to rely on this coconut for food, drink, shelter and fuel, the basic necessities of life. Although not suited for dissemination by floating, it was taken long distances by boat, reaching initially as far west as southern India and Sri Lanka and as far east as the Samoan Islands. Subsequently, hybridisation and introgression of the two contrasting forms gave the wide range of varieties and pan-tropical distribution seen today. A classification system in which the varieties are identified by the degree of introgression (based in the first place on fruit component analysis) is described. This in turn allows a suggestion to be made concerning the location of the much-debated centre of origin for *Cocos nucifera*. It is intended that this review will not just provoke discussion but that it will provide a basis for a more detailed study of coconut varieties.

Figures 1-10 and Appendices A & B to follow

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