

Long-distance dispersal of the coconut palm by migration within the coral atoll ecosystem

Hugh C. Harries^{1,*} and Charles R. Clement²

¹Coconut Time Line, Weymouth, Dorset DT3 5NP, UK and ²Instituto Nacional de Pesquisas da Amazônia, Av. André Araújo, 2936, 69067–375 Manaus, AM, Brazil

* For correspondence. E-mail: hugh.harries@gmail.com

Received: 16 September 2013 Returned for revision: 16 October 2013 Accepted: 18 November 2013 Published electronically: 23 December 2013

• **Background** The location of the original home of the coconut palm, *Cocos nucifera*, and the extent of its natural dispersal are not known. Proponents of a South American origin must explain why it is not indigenous there and why it shows greatest diversity in southern Asia. Conversely, proponents of an Asian origin must explain why there are no Asian Coseae and why the closest botanical relative to *Cocos* is in South America. Both hypotheses share the common problems of how, when, where and in what directions long-distance dispersal occurred.

• **Hypothesis** These difficulties are resolved by accepting that *C. nucifera* originated and dispersed by populating emerging islands of the coral atoll ecosystem, where establishment conditions impose high selection pressures for survival. When lifted by wave action onto virtually sterile, soilless coralline rocks just above sea level and exposed to the full impact of the sun, seednuts must germinate, root and establish vigorous populations. The cavity within the nut augments the buoyancy provided by the thick husk, which in turn protects the embryo and, by delaying germination, simultaneously extends viability while floating and provides a moisture-retentive rooting medium for the young seedling. These adaptations allow coconuts to disperse widely through the coral atoll ecosystem.

• **Conclusions** The monthly production of fruit and the long floating duration ensure that viable seednuts are always available in the lagoon to replace those destroyed by hurricanes and tsunamis, or to populate newly emerged coral atolls elsewhere. Long-distance dispersal is secondary, because it was the spontaneous, independent migration of coral polyps on a prolonged geological time scale that generated new coral atolls in new areas where the coconuts would be amongst the earliest inhabitants. The coconut palm became an intermittent, itinerant, pioneer endemic there, and also on suitable beaches on volcanic or large islands and continental coastlines.

Key words: Coconut palm, *Cocos nucifera*, coral atoll ecosystem, coral island, floating duration, lagoon, long-distance dispersal, migration, slow germination.

INTRODUCTION

When coconut palms (*Cocos nucifera*) are the subject of a scientific report, the introductory paragraphs can mention only a few of the multiple uses that make this pan-tropical crop invaluable to thousands of smallholder farmers. A comment on the beauty and familiar appearance of coconut palms is hard to resist, and may be illustrated by a picture showing the graceful stems, supporting a crown of fronds, curving over a tropical lagoon, into which the ripe fruit can fall and float. The difficulty of dealing with a long-lived monocotyledon of unknown origin that cannot be vegetatively propagated may also be mentioned.

Coconut palms are commonly recognized as either tall or dwarf, but intermediate growth habits (natural or artificial hybrids) are frequently encountered. Depending upon circumstances, the fruits vary in size, shape and number, but the wide range of uses of practically every part of the coconut palm is common to all. The assumption that all present-day coconuts are cultivated, and that their wild progenitors have been displaced and can no longer be recognized, has prejudiced research into the origin and mode of dispersal of *C. nucifera*. Wild coconuts evolved naturally and dispersed by floating without any need for human assistance. Even though it was demonstrated that

coconut seednuts can still germinate after floating in sea water for up to 110 days (Edmondson, 1941), inter-continental, trans-oceanic movement is generally attributed to seafarers, both ancient and modern. Opinions differ as to the centre of origin, natural and human-mediated dispersal range, fruit size and proportions of buoyant fibrous mesocarp, seed cavity and endosperm composition.

Coconuts were once the exemplar of botany's 'first family' – Principles – but recently, as the economic value of copra (dried coconut kernel) declined in the 1960s, coconuts have come to be regarded as of unknown origin and not endemic anywhere. Those coconut palms in abandoned commercial plantations on Pacific islands have been condemned as an 'artificial forest' in contrast to 'native woodland vegetation', and were 'so widespread' that the coconut became accepted as 'typical of the vegetation' on south Pacific atolls, such as the Tuamotus, 'where in the 1830s it was rare or non-existent' (Stoddart, 1968). Yet, however rare, coconuts certainly existed in the Tuamotos as long ago as 1270–1360 years BP (Lepofsky *et al.*, 1992) and may have been present as wild coconuts before Polynesians introduced the domestic sort (Harries, 1978).

Hence, wild coconuts certainly evolved naturally and dispersed by floating without any need for assistance before

humans appeared, since the genus diverged from sister genera millions of years ago (Baker and Couvreur, 2013). Therefore, the characteristics that allow seednuts to float, remain viable for long periods and germinate in challenging circumstances are central to understanding coconut's evolution.

It is the purpose of this Viewpoint to propose that coconuts evolved and dispersed within the coral atoll ecosystem. In so doing, how the characteristics of wild coconuts may have arisen will become clear. This will also suggest answers to some of the long-standing questions about the origin and dispersal of the wild coconut, as topics for further research:

Is its origin in Asia or America?
 Is it indigenous anywhere?
 Did it disperse eastwards or westwards?
 Did it float and establish spontaneously?
 If so, how widely did it spread?
 When and where did all this happen?

ORIGIN AND DISPERSAL

Wherever it originated, and by whatever means it dispersed, the coconut palm gracefully curving over a lagoon (Fig. 1) is not picturesque romanticism but a true ecological effect. There is a positive benefit to the population of coconuts, on a small island, to have a growth habit that supports a much larger number of trees with a correspondingly larger vegetation canopy than would be possible if all the palms grew erect. As one of the first plants to reach a new island, the coconut is not in competition with taller vegetation, but only with another palm of the same population. Though naturally receiving high light intensity, both from overhead and from sun reflected from the sea, all younger palms would be forced to grow away from the shade of older palm canopies above them. Stem curvature is also encouraged by the shallow rooting habit resulting from the high water table and undercutting wave action. On a coral atoll, the survival of the coconut palm depends on its ability to tap the freshwater lens that is found above the saline groundwater



FIG. 1. Coconuts over a lagoon. Image: Vimla Patil (<http://www.vimlapatil.com/vimlablog/>).

(Harries, 1981, 1992). These and other factors indicate an island origin, but are not necessarily conclusive.

Origin: Asia or America?

There have been proposals of both Old World and New World origins for the genus *Cocos*. Botanists of the 17th century often regarded the species as Asiatic. The taxonomic argument for an American origin that Martius (1823–1850) advanced was based on similarities between cocosoid palms native to Central and South America. At much the same time, coconut was described as being in a foreign land and not applied to any useful purpose in Amazonia (Wallace, 1853). In his book *Origin of Cultivated Plants*, de Candolle said he had changed his mind when he could find only two reasons in favour of an American origin but ten in favour of Asia (de Candolle, 1855, pages 432–434, citing de Candolle, 1884, page 976). Despite these opinions, an American origin was preferred by Cook (1901) and his views were accepted by de Vries (1906), who tried to apply the new science of genetics to the problem. The subsequent speculation by Cook (1910) that the dry climates of interior localities in South America were the only conditions where this palm could be expected to maintain its existence in a wild state was not acceptable to Odoardo Beccari. He had reassigned all *Cocos* species, except *nucifera*, to other genera and suggested that the African species *Jubaeopsis caffra* had many more affinities with *C. nucifera* than any other palm (Beccari, 1917). Today, the nearest botanical relative is in South America (Meerow *et al.*, 2009), although whether it is *Syagrus* or *Attalea* is still somewhat ambiguous (A. W. Meerow, USDA-ARS-SHRS, National Germplasm Repository, USA, pers. comm.), which makes an American origin seem more likely and the lack of an endemic coconut more puzzling.

Chiovenda's contribution

Strong support for Beccari came from a fellow Italian, Emilio Chiovenda, of the Colonial Herbarium, Florence, and a global authority on the flora of East Africa. He wrote 'La culla del cocco' ('The cradle of the coconut'), a review amounting to 185 pages giving detailed conclusions about botanical, geological and ethnological arguments in the first part (Chiovenda, 1921) and historical arguments and a recapitulation in the second part (Chiovenda, 1923; see Supplementary Data for a synopsis of Chiovenda's arguments and conclusions).

Chiovenda's detailed contribution was favourably received by botanic garden directors in Britain (Hill, 1929, 1933) and Indonesia (van Leeuwen, 1933). Limited support came from the German Botanical Society, where Werth (1933) accepted an Asian origin but not spontaneous establishment. In the USA, the Director of the Arnold Arboretum recommended 'La culla del cocco' as an extensive and critical consideration of the problem of American versus Old World origin of the coconut (Merrill, 1938) and, when criticizing Heyerdahl's epic Kon Tiki expedition, subsequently reiterated that Beccari and Chiovenda had both ably refuted Cook's 1901 and 1910 theories on the coconut in America (Merrill, 1954). It is easy, with hindsight 90 years later, to find discrepancies in some of Chiovenda's statements, but it is fair to acknowledge that he was on the right track (Harries, 1999).

Nevertheless, precisely what Chiovenda said is less important than the fact his work was overlooked or misunderstood. For instance, Ridley (1930), writing about the dispersal of plants throughout the world, did not mention Chiovenda. Worse yet, Mayuranathan (1938) warned against basing conclusions about the original home of the coconut on the works of historians, and cited only Chiovenda's three recapitulation pages following the historical arguments of the second part. As a result, Menon and Pandalai (1958) took just one sentence to dismiss Chiovenda as a historian, which is probably the reason why others who have written on the subject of coconut origin and dispersal appear to have missed Chiovenda entirely. These include Fremont, Ziller and de Nuce de Lamothe (1966), Tammes and Whitehead (1969), Child (1974) and Mahabale (1976).

Dispersal

When Martius suggested that the coconut had been transported by currents from islands situated to the west of Central America to those of the Asiatic Archipelago, he had only seen coconuts in Amazonia and had not visited American west coast islands or Asia. Had he done so and seen the differences between the American coconut populations and the variability both within and among Asian populations, he might have specified that the coconut had floated comparatively short distances between conveniently placed Pacific islands rather than implying direct long-distance, trans-oceanic dispersal from America to Asia. Or he might have pre-empted Cook's ideas and said that coconuts had been carried in boats across the Pacific (see Dennis and Gunn, 1971, for a review). Although the origin of coconut must have occurred well before the genus *Homo* arose in Africa, some people thought that a wild coconut would be small and would require human intervention to account for anything more than local dispersal by floating.

It was the subsequent speculation by Cook (1910), that the dry climates of interior localities in South America were the only conditions where this palm could be expected to maintain its existence in a wild state, that stimulated Beccari (1917) to respond that *C. nucifera* was capable of maintaining its existence on sea coasts, that ocean currents were responsible for its wide distribution and that coral islands were the locality best adapted to the spontaneous reproduction of the coconut palm. Citing Darwin, he agreed that coral islands were mere water-washed reefs 'to which all the terrestrial products that existed on them must have been transported by the waves of the sea'. He maintained that the coconut palm had established itself, unaided by man, in the Palmyras, the Keelings and probably elsewhere. It was on islands of this kind, with their scanty soil, almost level with the water, that any coconut washed up on the beach and able to germinate without competition from pre-existing forest vegetation would grow and prosper, free from the many enemies that would hinder its independent development on the shores of a continent or on one of the great Asiatic islands (Beccari, 1917).

Discussing the origin of the coconut, Fosberg (1960) accepted that Beccari and Chiovenda had provided the preponderance of evidence for coconut as an Old World plant. In presenting his own theory, he said it may have been domesticated from a wild species growing somewhere in the present optimum range of the modern coconut, but with a smaller, less satisfactory fruit. Over time, better forms were selected and planted and the

original centre of domestication was lost. Since the coconut grew on lowland tropical continental coasts and high islands, there seemed no way to narrow the possibility down to a coral island, and, if coconuts sprout when cast up on the top of the beach, this happens where there were planted coconuts nearby.

Domestication in the Indo-Pacific area was also accepted by Pursglove (1968, 1972), who cited Beccari, noted that Chiovenda held the view that the coconut originated in lands, now submerged, somewhere in the north-western Indian Ocean, and added his own belief that it is not necessary to invoke the aid of man in the transfer of plants between the New and Old Worlds, and vice versa, before 1492. He accepted that coconut cannot tolerate shade from vegetation and realized that an ancestor that had a fibrous mesocarp and the ability to float, and had established itself on coral atolls or new volcanic islands, would be free from such competition. To arrive at its present state, it originated and was domesticated in Melanesia, but it could not evolve there *in vacuo*. He postulated that it was carried by ocean currents from South America to Polynesia, or by a southerly migration when Antarctica had a more favourable climate (an idea that has recently been revived by Pross *et al.*, 2012).

Although Fosberg and Pursglove considered that a wild coconut might have survived in a remote location, they took for granted that it would be inferior in size, less useful and not as widely dispersed as the cultivated coconuts that were selected for (unspecified) superior qualities and were planted to replace it, eventually becoming the pan-tropical crop that they were familiar with. Like almost all other people who have thought about the origin of the coconut, Fosberg and Pursglove were constrained by the idea that all the coconuts they found were cultivated varieties that had been planted. As Child (1974) phrased it, inland every coconut tree owes its existence to man and on the coasts most of them do so.

In contrast to Fosberg and Pursglove, a review of coconut evolution, dissemination and classification showed how natural selection for dissemination by floating over a long period before human involvement could produce a wild coconut palm with the following characteristics (Harries, 1978): perennial growth (50–100 years), few fruits (50–100 per year), large fruit size (1–2 kg), thick husk (up to 70 % of fresh weight), abundant endosperm (200–300 g) with a high oil content (70 %), and slow germination (> 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 coconuts found as far apart as Palmyra Atoll in the Pacific Ocean and the Seychelles Islands in the Indian Ocean (Harries, 1978). It was also realized that the spontaneous presence of naturally dispersed, thick-husked coconuts would make coral atolls habitable before seednuts planted by settlers could bear fruit, but the important and significant relationship between slow germination and the atoll ecosystem was not appreciated at that time.

Long-distance dispersal

A subsequent study of coconut biogeography (Harries, 1992) examined differences between wild, domestic, introgressed and cultivated coconuts, whilst a chapter on the coconut as a tree crop

contrasted its prehistoric, ancient, nautical, mercantile and agricultural ecosystems, and predicted it might have a future ecosystem as a renewable energy resource (Harries, 2001). However, it was only when investigation showed that coconuts on the Pacific coast of America were unlikely to be either indigenous or the result of pre-Columbian voyaging (Clement *et al.*, 2013) that long-distance dissemination by floating was questioned and the full importance of the coral atoll ecosystem was realized.

The coral atoll has been called the earth's oldest ecosystem (Alkire, 1978) because of its stability. This ecosystem occurs worldwide between the Tropics of Cancer and Capricorn where waters are shallow and clear enough for sufficient light to reach the bottom. Hence, there are numerous coral atolls. Despite sea level changes during the ice ages, sea and air temperatures in the tropics remained high enough for both corals and coconuts to grow. When Fosberg (1960) said 'if coconuts sprouted when cast up on the top of the beach, this happens where there were planted coconuts nearby', he implied cultivated coconuts. If he had said 'growing nearby', this could mean any coconuts, anywhere. Had he said 'floating nearby', then wild coconuts in the lagoon of the atoll would be indicated. The seednuts that floated longest would be those most likely to survive to regenerate the atoll with a new generation. So it is duration rather than distance that is important. Edmondson's (1941) coconuts were still able to germinate after floating for 110 days, but an estimate of 3000 miles is not helpful because it may be in the wrong direction away from land or towards cooler regions, or in ever-decreasing circles until the seednut sinks. When Werth (1933) said that for more than 30 years he opposed the idea that the fibrous exocarp was a 'flotation organ' and denied that the coconut palm growing wild on tropical coasts was self-sown after dispersal by ocean currents, he was correctly estimating the probability that only a few seednuts would reach favourable new locations by freely floating over long distances; but he was wrong to overlook the continual presence of large numbers of coconuts floating in the lagoon. It was the slow but perpetual movement of the coral atoll ecosystem in warmer regions that ensured the survival of coconut and its inter-continental and trans-oceanic dispersal.

The trade in copra to Europe or North America did not begin until after 1840 (Child, 1974), which is why coconuts might have been rare in the Tuamotus, making it 'possible to treat these systems as relatively unaltered by man... when Darwin crossed the Pacific in the Beagle in 1835' (Stoddart, 1968). Coincidentally, when Darwin reached the Cocos-Keeling atoll in 1836, he took the opportunity to collect data that he subsequently used to develop his theory of atoll formation. He also took an interest in eating the robber (or coconut) crab, *Birgus latro* (Lewis, 2013). Both Beccari and Darwin would have been aware of this crab's mythical reputation for climbing palms to cut coconuts before returning to ground level to peel, crack and eat the contents. Darwin doubted the crab's ability to climb the palm stem, while Beccari thought the thick husk had developed as a defence against the crab. A more rational association (cited by Lewis, 2013, page 41) suggests that the long-distance oceanic dispersal of an otherwise land-living crab occurs when its post-larval stage chooses to live in cracks and crevices of the coconut husk (where other marine organisms would be its prey), while the seednut is floating in the warm tropical waters that are absolutely essential for coral atoll

development. A similar method of dispersal has also been suggested for the larvae of coral polyps and other organisms that raft on pieces of floating pumice (Jokiel and Cox, 2003). In more general terms, atolls stop growing and contract in cooler waters but they grow and expand in warmer waters. Thus, the atoll ecosystem effectively migrates by building new atolls to which obligate coral-dwelling species disperse as their hosts move (Yamano *et al.*, 2012).

THE ATOLL ECOSYSTEM HYPOTHESIS

The atoll ecosystem hypothesis applies to the origin and dispersal of *C. nucifera* before any human intervention and proposes that:

- (1) Coconuts originated and dispersed by populating emerging islands of the coral atoll ecosystem.
- (2) The fruit that developed a thick husk protected the embryo while floating, extended the duration of floating and delayed germination, while simultaneously providing a moisture-retentive rooting medium for the young seedling.
- (3) The establishment conditions on coral islands impose high selection pressures for survival because seednuts had to germinate, root and establish when lifted by wave action onto virtually sterile, soil-less rocks just above sea level.
- (4) Palms were not competing with more vigorous vegetation, were free from pests and diseases, and benefited from the full sunlight.
- (5) All the coconut palms on all the islands within the atoll ecosystem become members of one open-pollinated population.
- (6) Palms were not significantly isolated or subject to founder effect, genetic drift etc., because the seednuts float freely and frequently between adjacent atolls, occasionally to more distant atolls and beaches beyond.
- (7) Hurricanes and tsunamis were not disastrous, but served the purpose of providing both the space for and the source of the next generation.
- (8) The long floating time ensured viable seednuts were available in the lagoon to replace those destroyed by inclement weather or to populate newly emerged coral islands nearby.
- (9) Long-distance floating was of secondary importance, but allowed dispersal to more distant locations.
- (10) The coconut palm also became an intermittent, itinerant, pioneer endemic on suitable beaches on volcanic or large islands and continental coastlines.

The lagoon is important to the coral atoll hypothesis. Normally, nuts fall into the lagoon every month of every year for as long as the palm lives. Even when those palms are destroyed by a typhoon or a tsunami, many seednuts will remain in the lagoon and they have a greater chance of populating the same or nearby coral atolls than seednuts in the ocean have of finding any suitable beach.

Preferential out-crossing is another important part of the wild syndrome because it is the only way to avoid inbreeding and divergence of small populations on coral atolls in the direction of speciation, and to maintain the adaptations necessary for dispersal, germination and establishment in the demanding conditions of the coral atoll ecosystem. Combined with the constant supply

of seednuts in lagoons that disperse among atolls in the ecosystem, genetic diversity is maintained.

Testing the hypothesis

Any hypothesis has to be tested and testing the atoll ecosystem hypothesis will require inputs from specialists in taxonomy, phylogenetics, genomics, palaeobiogeography, palaeoclimatology, etc., if others are to be encouraged to reconsider coconut in a fresh light.

A world map of present-day coral atolls and reefs shows long distances between their locations and does not help to explain how coconut-like fossils on the Caribbean coast of Colombia (Gomez-Navarro *et al.*, 2009) and those on the Indian subcontinent (Shukla *et al.*, 2012) can both be ancestral to coconut. A map for the period when those fossils were laid down (an option not available to Beccari, Chioyenda, Fosberg or Purseglove) is more helpful. The position of land masses during the Eocene (Fig. 2) shows a deep Andean split where Colombia and Africa is not very wide (Blakey, 2008). Although long-distance dispersal is less important than short-distance dispersal for coconut, there may have been occasions when floating seednuts made a jump possible across water too deep for coral atolls to form. Such events will not be easy to recognize today, but can be modelled. There is also a convenient corridor between North Africa and Europe going through to southern Asia and the independent Indian plate. The currents would be altogether different from today and, assuming tropical temperatures, there could be atoll-forming corals practically lining the route. Such a route, if eventually validated, would accommodate the recent phylogenetic evidence that indicates the coconut is most closely related to American genera (Meerow *et al.*, 2009) by associating the fossil fruits attributed to *Cocos* recovered in Colombia (Gomez-Navarro *et al.*, 2009) with those in India

(Shukla *et al.*, 2012). Modern phylogenetic and biogeographical analyses are suggestive of such a connection (Baker and Couvreur, 2009, 2013), but still need further work.

CONCLUSIONS

The importance of the coral atoll as a home for the coconut, originally understood by Beccari and supported by Chioyenda, did not register with Fosberg or Purseglove, who assumed that wild coconuts would be small, limited in dispersal and everywhere replaced by selected cultivars. Even when presenting reasons for a larger, more widespread and immediately useful wild type, Harries (1978, 1991, 1995, 2012) did not realize the full consequences – until now! Ignorance of Chioyenda's work probably delayed the appearance of the atoll hypothesis for 30–90 years.

The coral atoll ecosystem for coconut evolution and dispersal is defined here for the first time. It provides a logical, and ecological, framework for natural selection to adapt a coconut ancestor to take advantage of the 'clean slate' of a newly emerged coral atoll, with specific modifications in fruit characteristics and subsequent germination that enable growth despite the severe constraints from exposure to the elements (sun, sea, wind, etc.). The coral atoll ecosystem contains large numbers of coral atolls that extend over large areas. With any one atoll seldom far from another, dispersal is a not question of chance and low-probability arrival by randomly targeted, long-distance island hopping, but of frequent, high-probability, short- to middle-distance drifting to relatively close neighbours. Moreover, the seednuts that fall into the lagoon every month provide a continuous supply of planting material to ensure the coconut population survives natural hazards such as typhoons and tsunamis. The few long-distance arrivals help to ensure that genetic drift from founder events does not cause the population to diverge towards speciation. The original natural distribution of wild coconut between the Seychelles in the west to Palmyra in the east (Sauer,

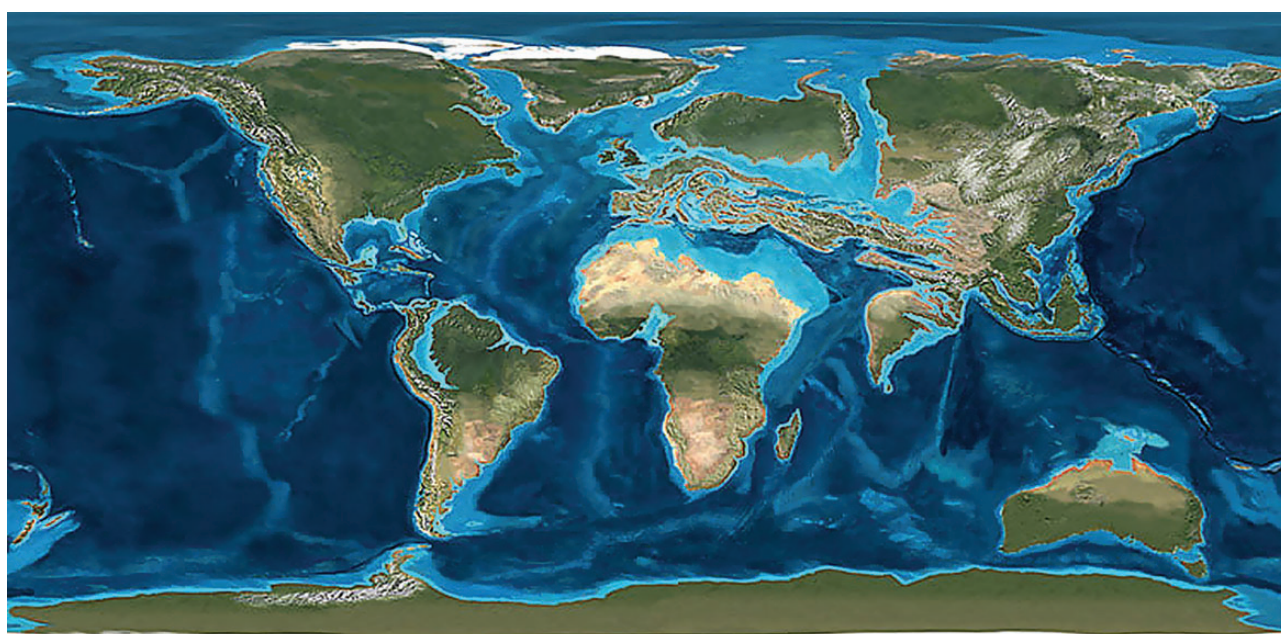


FIG. 2. Paleogeography in the Eocene, ~50 million years ago. Image: Ron Blakey (Colorado Plateau Geosystems, Inc.; <http://cpgeosystems.com/paleomaps.html>).

1971, cited by Harries, 1978) has yet to be confirmed because of the activities of Polynesians 4000 years ago and commercial plantation companies 100 years ago in moving planting material over considerable distances.

The hypothesis allows fresh thinking about some of the long-standing questions, such as an origin in America or Asia, or dispersal east or west, or when and where these events happened. This will encourage work in phylogenetics, paleobiogeography and related disciplines. The hypothesis supports the idea that the coconut palm originated, evolved and dispersed by floating in the coral atoll ecosystem, but as this ecosystem is widespread and constantly changing its form, a geographical location for a centre of origin for the coconut will probably never be found – but it can no longer be described as ‘unknown’.

SUPPLEMENTARY DATA

Supplementary Data are available online at www.aob.oxfordjournals.org and consist of an extract from Harries (1999), plus a (translated) contents list for Chioyenda (1921, 1923).

ACKNOWLEDGEMENTS

We are grateful to Vimla Patil and Ron Blakey for supplying the images for Figs 1 and 2, respectively. And thanks, in advance, to the person who makes a good English language version of Chioyenda's original document.

LITERATURE CITED

- Alkire WH. 1978. *Coral Islanders*. Arlington Heights, IL: AHM Publishing.
- Baker WJ, Couvreur TLP. 2009. Biogeography and distribution patterns of Southeast Asian palms. In: Gower D, Johnson K, Richardson J. eds. *Biotic evolution and environmental change in Southeast Asia*. Cambridge: Cambridge University Press, 164–190.
- Baker WJ, Couvreur TLP. 2013. Global biogeography and diversification of palms sheds light on the evolution of tropical lineages. I. Historical biogeography. *Journal of Biogeography* 40: 274–285.
- Beccari O. 1917. The origin and dispersal of *Cocos nucifera*. *Philippines Journal of Science, C. Botany* 12: 27–43.
- Blakey RC. 2008. Gondwana paleogeography from assembly to breakup—a 500 m.y. odyssey. In: Fielding CR, Frank TD, Isbell JL. eds. *Resolving the Late Paleozoic ice age in time and space*. *Geological Society of America Special Papers* 441: 1–28.
- de Candolle A. 1855. *Géographie botanique raisonnée*. Paris: V. Masson, 976–979. <https://archive.org/stream/gographiebotan02candouft#page/n8/mode/1up>.
- de Candolle A. 1884. *Origin of cultivated plants*. New York: D. Appleton, 429–435. <http://www.biodiversitylibrary.org/item/48617#page/9/mode/1up>.
- Child R. 1974. *Coconuts*, 2nd edn. London: Longman.
- Chioyenda E. 1921. La culla del cocco. *Webbia* 5: 199–294.
- Chioyenda E. 1923. La culla del cocco. *Webbia* 5: 359–449.
- Clement CR, Zizumbo-Villarreal D, Brown CH, Ward RG, Alves-Pereira A, Harries HC. 2013. Coconuts in the Americas. *Botanical Review* 79: 342–370.
- Cook OF. 1901. The origin and distribution of the cocoa palm. *Contributions from the United States National Herbarium* 7: 257–298.
- Cook OF. 1910. History of the coconut palm in America. *Contributions from the United States National Herbarium* 14: 271–342.
- Dennis JV, Gunn CR. 1971. Case against trans-Pacific dispersal of the coconut by ocean currents. *Economic Botany* 25: 407–413.
- Edmondson CH. 1941. Viability of coconut after floating in sea. *Occasional Papers of the Bernice Pauahi Bishop Museum of Polynesian Ethnology and Natural History, Hawaii* 16: 293–304.
- Fosberg FR. 1960. A theory on the origin of the coconut. In: Arthur AJ. ed. *Symposium on the impact of man on humid tropics vegetation, Goroka, Territory of Papua and New Guinea, September, 1960*. Canberra: Commonwealth Government Printers, 73–75.
- Fremont Y, Ziller R, Nuce de Lamothe M. 1966. *Le Cocotier*. Paris: Maisonneuve & Larose.
- Gomez-Navarro C, Jaramillo C, Herrera F, Wing SL, Callejas R. 2009. Palms (Arecaceae) from a Paleocene rainforest of northern Colombia. *American Journal of Botany* 96: 1300–1312.
- Harries HC. 1978. The evolution, dissemination and classification of *Cocos nucifera*. *Botanical Review* 44: 265–320.
- Harries HC. 1981. Germination and taxonomy of the coconut palm. *Annals of Botany* 48: 873–883.
- Harries HC. 1991. Wild, domestic and cultivated coconuts. In: Green AH. ed. *Coconut production: present status and priorities for research*. *World Bank Technical Paper no. 136*. Washington: World Bank, 137–146.
- Harries HC. 1992. Biogeography of the coconut *Cocos nucifera* L. *Principes* 36: 155–162.
- Harries HC. 1995. Coconut. In: Smartt J, Simmonds NW. eds. *Evolution of crop plants*, 2nd edn. London: Longman, 389–394.
- Harries HC. 1999. The cradle of the coconut: a contribution to the search for the country of origin of the coconut palm. *Cocoinfo International* 6: 14–17.
- Harries HC. 2001. The coconut palm (*Cocos nucifera*). In: Last FT. ed. *Tree crop ecosystems*. Elsevier: Amsterdam, 321–338.
- Harries HC. 2012. Germination rate is the significant characteristic determining coconut palm diversity. *AoB PLANTS* doi: 10.1093/aobpla/pls045.
- Hill AW. 1929. The original home and mode of dispersal of the coconut. *Nature* 124: 133–134, 151–153.
- Hill AW. 1933. Germinating coconuts on a new volcanic island, Krakatoa. *Nature* 132: 674.
- Jokiel PL, Cox EF. 2003. Drift pumice at Christmas Island and Hawaii: evidence of oceanic dispersal patterns. *Marine Geology* 202: 121–133.
- van Leeuwen WD. 1933. Germinating coconuts on a new volcanic island, Krakatoa. *Nature* 132: 674–675.
- Lepofsky D, Harries HC, Kellum M. 1992. Early coconuts on Mo'orea Island, French Polynesia. *Journal of the Polynesian Society* 101: 299–308.
- Lewis JB. 2013. *Darwin's coral atoll*. Victoria, BC: Friesen Press.
- Mahabale TS. 1976. The origin of the coconut. *Palaeobotanist* 25: 28–248.
- Martius CFP. 1823–1850. *Historia naturalis palmarum*. Leipzig: T. O. Weigel.
- Mayuranathan PV. 1938. The original home of the coconut. *Journal of the Bombay Natural History Society* 40: 174–182.
- Meerow AW, Noblick L, Borrone JW. 2009. Phylogenetic analysis of seven WRKY genes across the palm subtribe Attaleinae (Arecaceae) identifies *Syagrus* as sister group of the coconut. *PLoS ONE* 4: e7353. doi:10.1371/journal.pone.0007353
- Menon KPV, Pandalai KM. 1958. *The coconut palm: a monograph*. Ernakulum: Indian Coconut Committee.
- Merrill EHD. 1938. On the significance of certain oriental plant names in relation to introduced species. *Proceedings of the American Philosophical Society* 78: 111–146.
- Merrill EHD. 1954. The botany of Cook's voyages. *Chronica Botanica* 14: 161–384.
- Pross J, Contreras L, Bijl PK, et al. 2012. Persistent near-tropical warmth on the Antarctic continent during the early Eocene epoch. *Nature* 488: 73–77.
- Purseglove JW. 1968. Origin and distribution of the coconut. *Tropical Science* 10: 191–199.
- Purseglove JW. 1972. *Tropical crops: monocotyledons*. London: Longman.
- Ridley JN. 1930. *The dispersal of plants throughout the world*. Kent: Reeve.
- Sauer JD. 1971. A re-evaluation of the coconut as an indicator of human dispersal. In: Riley CL, et al. eds. *Man across the sea*. Austin: Texas University Press, 309–319.
- Shukla A, Mehrotra RC, Guleria JS. 2012. *Cocos sahnii* Kaul: a *Cocos nucifera* L.-like fruit from the Early Eocene rainforest of Rajasthan, western India. *Journal of Biosciences* 37: 769–776.
- Stoddart DR. 1968. Catastrophic human interference with coral atoll ecosystems. *Geography* 53: 25–40.
- Tammes PML, Whitehead RA. 1969. Coconut (*Cocos nucifera* L.). In: Ferwerda FP, Wit F. eds. *Outlines of perennial crop breeding in the tropics. Misc. papers 4*. Wageningen: Landbouwhogeschool, 175–188.
- de Vries H. 1906. *Species and varieties. Their origin by mutation*, 2nd edn. London: Kegan Paul, Trench, Trübner.
- Wallace AR. 1853. *Palm trees of the Amazon and their uses*. London: J. Van Voorst.
- Werth E. 1933. Verbreitung, Urheimat und Kultur der Kokospalme. *Berichte der Deutschen Botanischen Gesellschaft* 51: 301–314.
- Yamano H, Sugihara K, Goto K. 2012. Ranges of obligate coral-dwelling crabs extend northward as their hosts move north. *Coral Reefs* 31: 663.