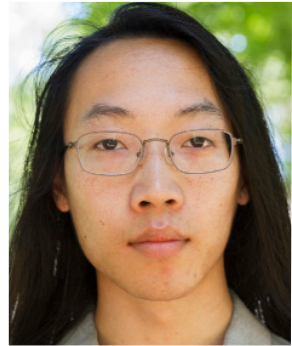


Tracing the origin of the coconut (*Cocos nucifera* L.)

CHRISTOPHER LEW



WRITER'S COMMENT: Dr. Gepts' "Evolution of Crop Plants" was one of the most interesting classes I had the pleasure to take as a Plant Sciences undergraduate. A holistic approach is taken to investigate domestication—not just of what and where, but by whom, how, when, and why the plants we chose are permanently interwoven into our lives. The scope of focus can be broad trends or narrowed to a single crop such as those covered in the "crop of the day" lectures; besides serving as a model for the term paper, the latter lecture type also offers the featured crop as a relished mid-morning snack. I chose coconut on a whim, figuring envisioning tropical beaches would feel more like a vacation than a literature review. While writing this paper was far from a vacation, I hope it captures your imagination and makes you more curious about the origin of crops important to you.

INSTRUCTOR'S COMMENT: Writing a term paper for PLB143 (Evolution of Crop Plants) is an essential didactic element for this course, which deals with the origins of agriculture and the domestication of crop plants. Christopher chose to write about the origin and evolution of the coconut, a tough nut to crack (if I may say so) because the species, growing preferentially near ocean shores, produces nuts that float on water and can, therefore, be carried by ocean currents. Furthermore, coconuts have multiple uses, so much so that humans have developed this symbiotic relationship with them during their migrations across the Earth. Thus, coconuts can be difficult to track back to their true origin. Nevertheless, Christopher has elegantly woven a discus-

sion based on multidisciplinary strands of (sometimes contradictory) evidence, including botanical, DNA, archaeobotanical, historical, and linguistic information, that has led him to conclude that coconut most likely originated in Southeast Asia. The outcome is a truly outstanding paper; I am glad that Prized Writing chose to recognize Christopher for his outstanding job.

—Paul Gepts, Plant Sciences Department

Abstract

The coconut palm (*Cocos nucifera*) and its fruit represent an important food and oil crop in tropical regions around the world; additionally, the entire plant provides myriad functions in the daily lives of peoples in the tropics, from potable water to sugar, charcoal, and bowls. This utility led to its establishment throughout the Old and New World tropics. Along with its pantropical distribution, the fruit's propensity to float on the ocean to new areas and the absence of clearly wild populations complicates locating the coconut palm's region of origin and domestication. This paper seeks to summarize and present the available research relevant to the origin of *C. nucifera* through the lens of Alphonse de Candolle, a Swiss botanist of the 19th century, who considered interdisciplinary evidence crucial to locating crop origins. Based on botanical, archaeological, historical, and linguistic evidence from around the world, Southeast Asia is the primary center of *C. nucifera* domestication, with ample evidence of the domestication syndrome from this region. This domestication event is the source of coconut populations now found in the Pacific Ocean and Madagascar. A secondary center of *C. nucifera* domestication likely exists based on genetic evidence, although the location of this event can only be hypothesized as somewhere in the eastern Indian or western Pacific Ocean, and is the source for coconut populations found throughout the Indian and Atlantic Oceans.

Future research characterizing ancient wild *C. nucifera* DNA would be an invaluable resource in locating existing wild genotypes. Furthermore, archaeological data from islands in the Indian Ocean and western Panama would help establish the timeline of *C. nucifera* dispersal if available, and could offer confirmation of the controversial hypothesis

that *C. nucifera* was introduced to the eastern Pacific in pre-Columbian times.

Introduction

The coconut (*Cocos nucifera*) is a monotypic genus of palm tree cultivated primarily for its large edible nut. The coconut fruit is botanically classified as a monospermic drupe; a single embryo is embedded in a hollow sphere of white endosperm, surrounded by a hard endocarp (the shell), fibrous mesocarp, and thin outer exocarp variously colored green, yellow, or red (Frémond and de Nucé de Lamothe 1966). Immature nuts are filled with a liquid, coconut water, which gradually decreases as the fruit matures. The coconut palm is typically a single tall stem up to 30 meters tall, crowned with large, pinnate leaves arranged spirally around the trunk (Ohler 1984). The coconut palm has a fibrous root system typical of monocots, lacking a taproot. The inflorescence, consisting of individual male and female flowers, arises from the leaf axils of mature palms at any time of year. Coconut palms are long-lived perennials that may continue to bear fruit for many decades given good conditions (Thampan 1975).

The coconut palm is noteworthy for its utility. The endosperm of mature coconuts can be eaten fresh or dried into copra, which is boiled to extract coconut oil. Coconut water from immature fruit is gaining popularity as an electrolyte-rich beverage. Coir, the dried mesocarp, is a popular fiber and useful component in soil-less horticulture. Besides these commercial products, the entire palm has many local uses. The unopened inflorescence can be tapped for toddy, an alcoholic beverage, and boiled down to make jaggery, equivalent to brown sugar. Palm leaves can be used as thatching, brooms, or woven into baskets. The center core can be eaten as heart of palm, although this kills the palm due to its monopodial growth habit. Coconut trunks are useful as construction beams, and coconut shells can be made into charcoal (Thampan 1975). Even the roots have uses as a diuretic decoction or frayed into toothbrushes (Child 1974). Coconut meat is rich in lipids (primarily saturated fatty acids), potassium, and phosphorus, and coconut water is rich in potassium and sodium (Thampan 1975, USDA 2018).

The palm is grown in a belt between the Tropics of Cancer and Capricorn wherever conditions are hot, humid, and wet; the combination

of these traits restricts coconut cultivation to lowland areas, often by the coast (Ohler 1984, Nayer 2017). The palm shows many adaptations to a coastal lifestyle, including a tolerance for saltwater and the ability to disperse seeds over water by flotation. Most coconut production occurs in Southeast and South Asia, with approximately 80% of world production occurring in Indonesia, the Philippines, India, and Sri Lanka, who represent the top four coconut producers in 2017 by tonnage (FAO Stat 2017, Statista 2019). World demand for coconut continues to grow as coconut oil gains more popularity as a cooking oil and cosmetic component, and coconut water as a beverage, although production has stagnated over the last decade (Gro 2016).

Discussion and Results

A search of various research articles, books, and websites was conducted to compile the four types of evidence the 19th century Swiss botanist A. de Candolle considered useful in determining crop origins—botanical, archaeological, historical, and linguistic—to investigate the origin of *C. nucifera*. Additionally, traits consistent with the crop domestication syndrome are presented which demonstrate the effects of human selection on *C. nucifera*.

Botanical

A major issue in determining *C. nucifera* origin is a lack of conclusively wild populations (Frémond and de Nucé de Lamothe 1966). Molecular analysis of nuclear DNA, chloroplast DNA, and the WRKY and *prk* genes of the Coccoseae (coconut tribe) have consistently identified the closest living relatives to *C. nucifera* as several genera of South American palms (Gunn 2004, Nayer 2017). These phylogenies support older morphological evidence botanists such as Merrill and Cook used to deduce that *C. nucifera* evolved in the New World tropics (Menon and Pandalai 1958, Frémond and de Nucé de Lamothe 1966, Nayer 2017). However, Pliocene and Eocene fossils assigned to the genus *Cocos* were discovered in New Zealand and India respectively, which suggest the evolutionary history of *Cocos* was not limited to South America (Menon and Pandalai 1958, Maloney 1993). Still, the fossil record is too fragmentary to be useful in determining the evolutionary origin of *C. nucifera*.

Following the Russian botanist Nikolai Vavilov, the center of crop

diversity is likely a crop center of origin. Microsatellite analyses of coconut accessions from around the world suggest coconut was domesticated twice due to the presence of two distinct genetic lineages; one that encompasses the Atlantic and Indian Oceans, and the other that encompasses the Pacific. Within the Pacific group, genetic diversity is lowest in the Panama Tall variety, the oldest documented *C. nucifera* population in the New World (Gunn et al. 2011, Clement et al. 2013). This strongly supports the theory that *C. nucifera* originates from the western, not eastern, side of the Pacific. It is also unlikely that coconuts floated long-distance across the entire Pacific and Indian Ocean basins unaided, as experiments have suggested that coconuts only remain viable for approximately 110 days in saltwater (Maloney 1993). Drift simulations with the most favorable currents found that the fraction of fruit that would reach the Americas from western Pacific islands along the Equatorial Counter Current would land in the Galapagos, where *C. nucifera* was unknown at the time of European contact, and well after the maximum viability date (Clement et al. 2013). Furthermore, the Panama Tall is most closely allied to Philippine *niu vai* varieties, but ocean currents make this path highly unlikely (Baudouin and Lebrun 2009, Gunn et al. 2011). The reduced mesocarp of *niu vai* varieties lowers fruit buoyancy, making a natural trans-Pacific crossing even more unlikely (Harries 1978). High genetic diversity in the western Pacific lineage is supported by significant phenotypic variation in cultivated western Pacific coconuts, including at least two independently derived dwarf varieties from Malaysia and Fiji (Frémond and de Nuce de Lamothe 1966, Harries 1978, Gunn et al. 2011). Genetic variation is reduced in the Indo-Atlantic lineage, and is represented by a single phenotype, the Tall *niu kafa* variety (Gunn et al. 2011).

The distribution of pests and other organisms associated with *C. nucifera* may help pinpoint its geographic origin. 90% of insect pests specific to *C. nucifera* are found in Melanesia, while 20% are found in the Americas, and only 4% are found in Africa (Menon and Pandalai 1958, Child 1974). This excludes the western Indian Ocean as a probable center of origin, and the moderate presence of coconut insect pests in the Americas could be explained by endemic pests of New World Cocoseae palms. *Birgus latro*, commonly called the robber crab or coconut crab, has also been used as evidence for the origin of *C. nucifera* because of its close association with the palm. It is native to the Indian Ocean and

western Pacific. Older resources claim *B. latro* specializes in cutting and cracking coconuts as its only food source and demonstrated that *B. latro* lipid composition strongly resembles coconut oil (Menon and Pandalai 1958, Frémond and de Nuce de Lamothe 1966). However, recent research shows that *B. latro* is an opportunistic scavenger that, while able to open coconuts, has a very diverse diet (Drew et al. 2010). *B. latro* is even proposed to have prevented natural *C. nucifera* establishment on the Australian mainland (Maloney 1993). While the coevolution of *B. latro* and *C. nucifera* is not as strong as once suggested, the Old World range of *B. latro* provides further evidence against a New World *C. nucifera* origin.

Archaeological

Archaeological remains of *C. nucifera* are scarce but can suggest how the species spread over time with and without humans. In archaeological contexts, the *niu kafa* variety is sometimes noted as a wild *C. nucifera* variety because of its thick and angular mesocarp, theorized to aid seed dispersal and allow fruit anchorage against the tide in littoral zones (Summerhayes 2018). However, *niu kafa* is also an excellent source of coir useful in other cultural contexts—Polynesian cultures braid coir into sennit, cordage useful in house and boat construction, and traditional Arab dhows use coir cordage instead of nails (Harries 1978, Summerhayes 2018)—so the spread of *niu kafa* could still be facilitated by humans. The *niu vai* form has several domestication syndrome traits, so *niu vai* archaeological remains do represent human-mediated selection and spread, and are identifiable in archaeological remains because of their larger endocarp size and rounder shape (Summerhayes 2018).

Besides a single pollen grain from a deposit dated to 4000 BCE in Thailand, the majority of *C. nucifera* archaeological evidence is found in the Pacific islands, although no site shows continuous evidence from the Miocene to the present (Maloney 1993). The oldest potential human-associated *C. nucifera* evidence is an endocarp fragment dating to 20,000 BP in Buka, an island approximately 500 km to the east of New Guinea inhabited by humans for over 30,000 years (Summerhayes 2018). This Pleistocene finding predates the development of agriculture, providing evidence that *C. nucifera* is native to Melanesia. A single fossilized *C. nucifera* seedling covered by lava dating to the early Quaternary period on Pagan Island demonstrates *C. nucifera* range naturally extended from Melanesia into Micronesia (Maloney 1993). Other macro-botanical pieces

of *C. nucifera* shell have been found throughout Holocene New Guinea; although their variety cannot be determined, their association with obsidian suggests *C. nucifera* was part of a trade network between New Guinea and the Bismarck Islands (Summerhayes 2018). Large endocarp fragments found on the St. Matthias Islands in the Bismarck Archipelago, consistent with the *niu vai* variety, were dated to approximately 1000 BCE. This suggests that some level of artificial selection and cultivation was practiced by the Lapita culture in Melanesia, and the assemblage of other useful tree species at the site reflects development of arboriculture. Furthermore, scraping left on the inner endocarp suggests these coconuts were processed to make coconut cream or oil (Kirch 1989). *C. nucifera* archaeological evidence is absent from Southeast Asia before 4000 BCE (Summerhayes 2018).

C. nucifera could have dispersed into remote Oceania, areas east of the Solomon Islands, either naturally or mediated by the Lapita culture, who rapidly expanded eastward around 1000 BCE and reached Samoa within 200 years of the first expansion. After a significant pause, migrations brought people to the Marquesas (c. 1000 CE), Hawai'i (c. 1100 CE), Rapa Nui (c. 1250 CE), and New Zealand (c. 1300 CE). Palynology results demonstrate *C. nucifera* was already present in the Cook Islands (c. 6600 BCE), Society Islands (c. 600 CE), Guam (c. 2300 BCE), and potentially even Laysan (a northwestern Hawai'ian island), predating human habitation (Summerhayes 2018). This evidence extends the natural range of *C. nucifera* into Polynesia and contributes further evidence for its natural range in Micronesia.

The archaeological evidence for *C. nucifera* presence in the New World is practically nonexistent. No palynological studies have been conducted on the western South American coast, and confusion between *C. nucifera* and other Coccoseae pollen is possible without scanning electron microscopy (Maloney 1993). Baudouin and Lebrun (2009) use circumstantial evidence of ancient trans-Pacific voyages to suggest a pre-Columbian origin of the Panama Tall variety. However, they concede that neither evidence for the introduction of the chicken to Chile from Polynesia, nor any perceived cultural coincidences between Polynesia and Native Americans of the Pacific coast proves a pre-Columbian *C. nucifera* introduction. The lack of artifacts like coconut scrapers common to the western Pacific and remains of *C. nucifera* do not preclude the possibility of pre-Columbian *C. nucifera* introduction to the eastern Pacific, but is

highly unlikely when combined with historical and linguistic evidence.

Historical

Historical accounts of *C. nucifera* aid primarily in understanding its spread after domestication. The absence of *C. nucifera* in the Vedas suggests the coconut's absence in India, the possible center of domestication with a strong written tradition, until after the post-Vedic era, approximately 1000 BCE (Menon and Pandalai 1958, Maloney 1993, Nayer 2017).

C. nucifera was first introduced to Europeans through Arab traders, who documented coconut export from the Maldives, Lakshadweep, and islands off the east African coast in the Medieval period. Marco Polo noted *C. nucifera* grew in Sumatra and the Andaman and Nicobar Islands in the eastern Indian Ocean circa 1280 CE (Maloney 1993). This demonstrates *C. nucifera* was found throughout the Indian Ocean in the Middle Ages. European explorers were familiar enough with the coconut that Christopher Columbus misidentified a *Roystonea* palm as coconut during his first voyage while on the north coast of Cuba (Clement et al. 2013). During the Age of Exploration, coconuts were common provisions on Spanish and Portuguese ships, which led to their introduction to Puerto Rico and Brazil in the mid-16th century CE. These plants were derived from *C. nucifera* planted in the Cape Verde Islands by Vasco da Gama, originally from African stock (Menon and Pandalai 1958, Child 1974, Clement et al. 2013). The establishment of the Manila-Acapulco commercial route in 1571 facilitated the spread of *C. nucifera* from the Philippines to the Pacific coast of Mexico (Clement et al. 2013).

The most confounding piece of historical evidence in the spread of *C. nucifera* is the possible pre-Columbian origin of the Panama Tall variety. While accounts of *C. nucifera* on the Atlantic coast of the New World were misidentifications, Oviedo reported the presence of a plant identical to Indian *C. nucifera* on the Pacific coast of Panama. While 30 years after Columbus' first voyage, the date is close enough to Balboa's discovery of the Pacific Ocean across the Isthmus of Panama that European explorers presumed *C. nucifera* was native to Panama. However, Oviedo was not a botanist and the Treaty of Tordesillas prevented Spaniards from seeing live, fruiting *C. nucifera* in Asia. Scrutiny of his description leaves doubt about whether *C. nucifera* was present before European conquest or if he simply misidentified the native Cocoseae palm *Attalea butyracea*. The similarity of the Panama Tall to Philippine varieties could also be attributed to

later, very limited introduction by the Manila-Acapulco trade route via Mexico (Clement et al. 2013). Palm agriculture was known to the people throughout the New World, and coconut's absence from well-established Mesoamerican trade routes that involved agricultural products like cacao is further evidence against pre-Columbian *C. nucifera* presence in the New World (Clement et al. 2013, Nayer 2017).

Linguistic

The origin of the term *coco* (sometimes *coker* or spelled *cocoa*, though not to be confused with the cacao plant *Theobroma cacao*) is generally accepted to come from the Spanish or Portuguese word *coco*—a grinning face, applied by sailors to the husked nut because the three endocarp indentations resemble a face—and dates to the late-15th to early-16th century CE (Child 1974, Harper 2019). Other etymologies speculate that *coco* came from dialectical Arabic *goz-goz*, from *djaz* in *al-djaz al-Hindi* (the Indian nut) through Portuguese, although this etymology is poorly documented. Linnaeus Latinized *coco* into *Coccus*, though later adopted *Cocos* as the genus name (Child 1974). Previously, the fruit was known in Europe as *nux Indica*, and unknown in Europe before the Medieval period (Menon and Pandalai 1958, Child 1974).

While Arabic and Medieval European languages suggest *C. nucifera* is indigenous to India, it is absent from the oldest texts there. Despite toponyms like *Kerala* (the place of coconuts), the absence of coconuts in the Vedas, as mentioned earlier, suggests *C. nucifera* was a post-Vedic introduction to South Asia. This is supported by few names for coconut in Sanskrit, which suggest *C. nucifera* was introduced to the subcontinent. While the Tamil word for coconut *tennai* is purportedly related to the root *ten* (south), suggesting an introduction from Sri Lanka, legendary accounts suggest that *C. nucifera* was likewise introduced into Sri Lanka from elsewhere (Menon and Pandalai 1958, Child 1974, Nayer 2017).

Linguistic evidence does not strongly support a New World origin of *C. nucifera*. Reconstruction of two protolanguage families once indigenous to western Panama show that 11 of 12 names for *C. nucifera* are derived from the European term *coco*, strongly suggesting its introduction to the region by Europeans. The single term *siahuá* in the Boruca language is plausibly linked to another Cocoseae palm indigenous to the Neotropics, *Acrocomia aculeata*, which was probably reapplied to coconut (Clement et al. 2013). Similarly, *siahuá* appears to

have no relation to the Austronesian *niur*, which would be expected if *C. nucifera* was a pre-Columbian introduction to the New World.

The greatest range of names for coconut varieties is found in Southeast Asia (Child 1974). Polynesian terms such as *niu kafa*, *niu vai*, and *niu leka* are adopted by the scientific community to describe major coconut varieties, and the shared Austronesian root *niur* is linked to coconut introduction by Austronesian voyagers through Polynesia and to Madagascar (Harries 1978, Baudouin and Lebrun 2009, Gunn et al. 2011). Because Taiwan, the proposed homeland of the Austronesian languages, lacks reconstructions for shared Malayo-Polynesian coconut terminology, an Austronesian coconut culture likely developed only after Austronesian peoples reached the Philippines. The existence of common, shared terminology for very specific parts and uses of the palm, such as words for a strainer made from the leaf sheaths, emphasizes the importance of *C. nucifera* in Austronesian cultures (Summerhayes 2018).

The Domestication Syndrome

Various traits consistent with the domestication syndrome are present in some varieties of *C. nucifera*. Between *niu kafa* and *niu vai*, the former is interpreted as closer to a theoretical wild *C. nucifera*. By contrast, *niu vai* fruits are larger and rounder, demonstrating human selection for more endosperm and water volume paired with reduction of the fibrous mesocarp, and only occurs in the Pacific *C. nucifera* population. *Niu vai* type fruit have lower fitness than *niu kafa* under natural dispersal conditions; its thinner mesocarp provides less cushioning to the seed after it detaches from the palm and poorer buoyancy, while its round shape provides less anchorage in a littoral environment than the oblong and angular *niu kafa* (Harries 1978). Even more drastic selection has led to at least one *C. nucifera* variety with a chewable, sweet mesocarp comparable to sugarcane, as well as a variety that produces a high proportion of sterile *makapuno* nuts filled with a jelly-like substance. Breeding trials demonstrate that the latter trait is controlled by a single gene inherited recessively (Ohler 1984).

Selection for early germination represents another domestication trait in *C. nucifera*. *Niu vai* varieties have mean germination times around 60-70 days, and under certain conditions will germinate while still attached to the tree (Thampan 1975, Harries 1978). Early, uniform germination is a competitive disadvantage for a hydrochoric species

like *C. nucifera*, in which wild types should favor a slower, staggered germination model to prevent germination while still floating.

Changes in plant architecture and development also demonstrate selection in *C. nucifera* under cultivation. The deep roots of some varieties are hypothesized to resist toppling by high wind, which diverges from the shallow roots a littoral variety typically favors for freshwater access (Harries 1978). Additionally, precocious dwarf forms from Malaysia (occasionally called *nyior gading* or *kelapa gading*) have thinner trunks and short internodes with smaller and fewer leaves. The dwarf form demonstrates the most selection for a wide array of domestication traits—not only is the plant smaller, it germinates and bears fruit earlier, and has a thinner mesocarp often with a colorful exocarp (Ohler 1984). Unlike all other forms of *C. nucifera*, the dwarf variety also demonstrates a high degree of self-pollination facilitated by temporal overlap the male and female phase on a single inflorescence. All other *C. nucifera* varieties are protandrous, and genetic studies support a high level of allogamy (Menon and Pandalai 1958, Frémond and de Nucé de Lamothe 1966, Gunn et al. 2011). *Niu leka*, another dwarf variety independently developed in Fiji, differs from the more widely grown *nyior gading* by its thicker trunk and inability to self-pollinate (Frémond and de Nucé de Lamothe 1966, Ohler 1984).

Based on the available evidence, *C. nucifera* likely originates in Southeast Asia. The western Pacific is where maximum genetic and phenotypic diversity is observed in *C. nucifera*, and where the most insect pests of *C. nucifera* are native. Its pre-human presence in Melanesia, Micronesia, and Polynesia is established in the archaeological record, and demonstrates that *C. nucifera* readily colonized distant habitats by flotation as far as the Society Islands and possibly Laysan. Later archaeological evidence establishes coconuts consistent with the human-selected *niu vai* variety present in the Bismarck Archipelago around 3000 BP. While the region lacks a written history, the importance of the coconut in rituals and oral history in the western Pacific also suggests a longstanding historical connection to the region (Nayer 2017). The linguistic evidence suggests that as Austronesian peoples expanded from the Philippines, they spread a culture intimately familiar with the coconut and highly knowledgeable of its utility. Finally, the most domesticated forms of *C. nucifera*, the *niu vai*, dwarf, and *niu leka*, all originate in the western Pacific.

It is probable *C. nucifera* has no recent origin in South America.

The Panama Tall variety has the lowest level of diversity of all coconut populations, suggesting the population underwent a strong bottleneck from a founder Philippine population, inconsistent with the eastern Pacific as a potential center of origin. Viable coconuts cannot float from the Philippines to western Panama, and the Philippines lack a strong long-distance sailing tradition (Clement et al. 2013). No direct archaeological evidence of coconut is present in western Panama to suggest its presence as a pre-Columbian introduction. Furthermore, the historical reports of *C. nucifera* growing on the west coast of Panama around the time of European arrival could easily be misidentifications of various New World Cocoseae palms, and linguistic evidence supports a European introduction of coconut to the region rather than an Austronesian introduction.

The existence of a genetically distinct population of *C. nucifera* in the Indo-Atlantic suggests a possible secondary domestication of coconut, as this population is more uniform genetically and phenotypically than *C. nucifera* of the western Pacific. Historical and linguistic evidence demonstrates the spread of *C. nucifera* into the Atlantic was through European introduction. Its spread in the Indian Ocean requires further archaeological research to clarify if *C. nucifera* spread was associated with human settlement, although linguistic and genetic evidence support an Austronesian introduction of *C. nucifera* to Madagascar. The very low number of insect pests in Africa suggest *C. nucifera* was a human introduction to the east African coast, probably through Arab traders historically linked to islands in the western Indian Ocean. Circumstantial historical and some linguistic evidence suggests this secondary center was neither in India nor Sri Lanka, as *C. nucifera* is considered a historically introduced species in both regions.

Recommended Future Lines of Research

The difficulty in locating a truly wild *C. nucifera* remains an issue for locating the region of coconut domestication, as the modern *niu kafa* variety is often used as a proxy for ancestral undomesticated *C. nucifera*. However, *niu kafa* traits could represent human selection for enhanced coir production. Ancient DNA from archaeological coconut remains, dispersed well before human habitation in the western Pacific, could be compared against modern cultivated and feral *C. nucifera* populations to

locate populations matching ancient wild *C. nucifera*. There are several inherent difficulties to this approach—ancient DNA has a low level of preservation in the tropics, ancient wild coconut samples could still represent escapes from cultivation, and potential ancient lowland sites in Southeast Asia are underwater. Additionally, samples from modern populations must be analyzed carefully and with a representative sample size, otherwise the relationships between different cultivars may be misleading (Mauro-Herrera et al. 2009). Improved phylogenies of the Cocoseae tribe may be constructed by including more species from each genus and more accessions of each species to reflect the extent of diversity and better infer the coconut's evolutionary history. Archaeological data could clarify the spread of *C. nucifera* in the Indian Ocean, and genetic characterization of more accessions from South and Southeast Asia could locate a possible area for the secondary domestication which led to the modern Indo-Atlantic population. Likewise, direct archaeological evidence of coconut in western Panama is required to support a pre-Columbian trans-Pacific dispersal of *C. nucifera* to the Americas. The genetic evidence alone does not suggest a date of arrival of the Panama Tall variety, and doubt remains whether palms on the western Panamanian coast were correctly identified in initial accounts.

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