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Revisiting the origin of the domestication of noni (*Morinda citrifolia* L.)

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Abstract

Based on the distribution, molecular similarity and use of *Morinda citrifolia* L., and occurrence of a wild *Morinda* species, Southeast Asia and Micronesia have been suggested to be the places where noni originated. The present article discusses the indices used by Vavilov and subsequent authorities on the origin of crop plants to argue that South Asia (Southeast India) has a greater probability of being the centre of domestication/origin for noni than Southeast Asia or Micronesia. The basic reasoning is that economically important plant cannot originate without richness in biodiversity and ingenuity of local people. India with rich floristic diversity, one of the centres of origin of crop plants with a natural distribution of *Morinda* species, including *M. citrifolia* L. and its immediate ancestors, has the oldest reference of occurrence, use and cultivation (Vedic literature); therefore, it appears to be the more probable centre of noni's origin. The ancient history of the expansion of Indian culture, religion and trade to Southeast Asian countries corroborate the possible role of Indians in the introduction of noni or knowledge regarding its value to Southeast Asia, from which it was carried to Micronesia and Polynesia, which provided a more favourable environmental niche for perpetuation and use.

Keywords: archaeological evidence; centre of origin; domestication; island biogeography; *Morinda citrifolia*

Introduction

There are diverse opinions about the origin of cultivated, large-fruited *Morinda citrifolia* L. (noni), but the most commonly held view is that it originated in Southeast Asia and dispersed by natural and human interventions to the rest of the tropics (Morton, 1992). Recently, Razafimandimbison *et al.* (2010), based on molecular marker phylogeny, proposed a Micronesian origin of *M. citrifolia*. The main reasons for these opinions are the naturally wide distribution of *M. citrifolia* L. (noni) in these regions along with related 30–35 wild *Morinda* species (Razafimandimbison *et al.*, 2009), being a major crop in many parts, and Southeast Asia, Micronesia and Polynesia have a rich healing heritage and knowledge about noni's medicinal uses, inherited over generations. However, these studies have ignored the documented natural occurrence and the knowledge of noni's medicinal value to ancient Indians (Aryans/Dravidians) long back, available in a number of ancient Sanskrit writings indicating that related wild *Morinda* species have been naturally distributed in more diverse ecologies in India, and that Southeast Asian countries, such as Singapore, Malaysia and Indonesia, that were considered to be the centre of origin were discovered by Indians during their voyage in the Asia-Pacific region, as reflected by their name and archaeological remains of these countries (Hindu and Buddhist).

The concept of centre of origin

The concept of centres of origin was first proposed by the Russian scientist Nikolai Vavilov (1887–1943). The 'centre

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of origin' of a crop plant is that geographical area where it is considered to have first appeared under cultivation and developed its distinctive properties. Many authorities believe centres of origin are also centres of diversity. Though centres of origin and diversity are highly correlated, they do occasionally diverge. This happens when high variation is recorded in cultivated or economically important plant species, but in the absence or presence of few wild relatives. The higher levels of variation occur due to environmental forces and human intervention conspiring to increase the plant's diversity away from its site of origin, such as groundnut, capsicum, potato, tomato, etc. Alternatively, a plant species can also have more than one centre of origin (domestication) or diversity, for example cotton with all the centres having wild relatives and other indicators for being the centre of origin. Such situation may arise either because of a polyphyletic origin (at more than one place) of cultivated species or because other centres may be a secondary or regional centre of origin or diversity.

The criteria for identifying centre of origin

The primary criterion in identifying a centre of origin is the presence of wild relatives of the concerned species. Vavilov observed that crop/species diversity tends to be concentrated around specific regions. He proposed that these concentrations of high variability indicated the regions where domestication of the economic species might have begun. However, this concept went against the prevailing view that cultivation of plants started randomly all over the world, and in certain cases, a particular species developed greater genetic diversity in regions away from their actual place of origin because of reasons such as ecological variability offered for adaptation, diverse use enforcing diverse selection pressures, geographical isolation of genotypes, etc.

It is generally believed that the centre of plant diversity is the centre of origin of crop/economically important plants. However, at the global level, if we consider the world flora, even a quick survey will show that there are many areas of rich plant diversity that has little to do with cultivated plant origins. For example, the 'fibs' plant formation on the very southernmost tip of South Africa is extremely diverse. In a very small area, one can find hundreds of species in very distinct genera and even plant families. These are very attractive and colourful, but were never brought into cultivation by the indigenous people, because of lack of ingenuity or lack of food value and interest in sustainable exploitation. Similar situation exists with southern Australian flora, and again, none of its species was brought into cultivation (Hawkes, 1998). Therefore, human ingenuity, interest, intervention and support were other factors influencing centre of origin (domestication), and these were mainly available in centres of human civilizations and had played a significant role in the domestication/origin of crop or economically important species and, therefore, needs due consideration.

The review of the literature on the centre of origin of crop plants corroborates that most areas of domestication are associated with those regions that have been the centres of ancient civilization, where people evolved agriculturally and socially together, through eco-friendly interaction with natural resources, particularly biodiversity and landscape, resulting in evolution from the stage of hunter-gatherers to agriculture via domiculture (planting economically important species together), cultivating domesticated plants and animals in concentration under diverse farming/production systems. For example, pigeonpea (*Cajanus cajan*), has a nearly equal number of wild relatives distributed in Australia (15, of which 13 are endemic) and India (16), but the domestication of the wild *Cajanus* species took place in India (van der Maesen, 1990), probably because of differences in the ingenuity of people.

This contention is corroborated by the fact that there is considerable wild plant diversity up to about 45–50°N latitude in Europe, Asia and North America, and southward to 35–40°S latitude in the southern continents, apart from desert and semi-desert areas. However, only in certain areas between 45°N and 30°S latitudes, potential crop plants were domesticated. Vavilov noted that the centres of origin of cultivated plants occurred mostly in mountainous regions between the tropic of Capricorn (23°28′), south of the equator, and about 45°N of the equator in the Old World. In the New World, crop domestication occurred approximately between the two tropics (Cancer and Capricorn). However, in all cases, agriculture originated and primitive crop diversity occurred either in high and complex mountainous regions or in river valleys along with diverse civilizations.

The review of the literature on the criteria, which have been used in deciding the centre of origin of economically important crop plants, indicates that the following indices have been given equal credit while inferring the origin/domestication of a species:

(1) Archaeological remains of specific crop species
(2) Richness in floristic and crop diversity (hot spot of diversity)
(3) Higher levels of endemism
(4) Prominent occurrence of the concerned family/genus and wild relatives
(5) Natural occurrence of concerned domesticated/economically important species

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(6) Occurrence of wild or weedy immediate ancestral relatives of the concerned species
(7) Level of interaction between human and nature
(8) Ecological and socio-political diversity
(9) Interest of Royals
(10) History of nomenclature/vernacular name used
(11) History of domestication of other crops
(12) History of ancient and diverse use of the concerned species

Solution to controversies

Whenever there are diverse opinions about the area of origin, the conclusions cannot be made only on one line of evidence, as it is difficult to look back in the time capsule based on one criterion, which may suit one economic species but not the other. Therefore, in such situation, all possible lines of evidence should be accounted for, and the credence to be given to the hypothesis supported by the majority. In the case of *M. citrifolia*, based on earlier studies on history, distribution and phylogeny, we should consider the above criteria one by one, and whichever hypothesis is supported by the greater number should be considered as the primary centre of origin.

Results and discussion

(1) *Archaeological remains of specific crop species*: Domestication of noni took place thousands of years ago, and being a non-food crop, archaeological evidence is difficult to provide and neither has been reported, and hence cannot be used in the present debate. Nevertheless, archaeological sites of Mahagarha and Koldihwa in Indo-Gangetic plains, identified with rice grains of the earliest rice cultivation in the world (Sharma, 1980), and recent archaeobotanical evidence of domestication in parts of South India (Fuller *et al.*, 2004) suggest India to be an important centre of crop origin/early domestication of valuable plant species. However, an archaeological relic of Ganesha from the 1st century CE, discovered in Indonesia from the Ujung Kulon National Park, West Java, reflects ancient connections and influence of Hinduism/India over Indonesia, spread through the distribution of knowledge and material.

(2) *Richness in floristic and crop diversity*: By virtue of physiognomy and climatic diversity, India harbours a rich flora; consequently, India (subcontinent) has been considered as one of the 12 mega-centres of biodiversity with three hot spots of biodiversity (Conservation International, 2005). However, while organizing the centre of origin according to the richness of cultivated floras, Vavilov (1934) put the Hindustani Centre second after the Chinese one. According to a recent generic assessment (Razafimandimbison *et al.*, 2009), the genus *Morinda* is represented by two species, *M. angustifolia* Roxb. and *M. persicaefolia* Buch.-Ham, in tropical Himalayas, as *M. villosa* Hook.f. found in the tropical Himalayas is now transferred to Gynochthodes, and by another two species, *M. reticulata* Gamble (syn. *M. coreia* Buch.-Ham) and *M. citrifolia* L. in South Eastern Ghats and Western Ghats, i.e. Andhra Pradesh, Tamil Nadu, Karnataka and Kerala (Gamble, 1921) and Andaman and Nicobar, as *M. pubescens* J.E. Smith (syn. *M. tinctoria* Roxb.) is considered an unplaced name in the Kew database (http://apps.kew.org/wcsp/qsearch.do), and *M. umbellata* L. distributed in the Andaman and Nicobar Islands is transferred to Gynochthodes. Therefore, Southeast Asia and Micronesia and Polynesia are comparatively less rich in floristic diversity and in crop species flora. In fact, these regions are dominated by the species that are an extension of Indo-Burma flora, as reflected by the commonality in the occurrence of a number of taxa both in the north-east region of India and Southeast Asia. It is even true for *Morinda*; for example, *M. angustifolia* occurs in continuum from the Himalayan region to Bangladesh, Burma, Thailand, Malaysia, Singapore, etc.

(3) *Higher levels of endemism*: Because of being bound by the Himalayas in the north and the peninsular region surrounded by the ocean, isolation of Indian flora has resulted in very high levels of endemism. Rubiaceae to which the genus *Morinda* belongs is one of the families represented by more than 500 species in India, of which 205 (41.0%) are endemic (Nayar, 1996).

(4) *Prominent occurrence of the concerned family/genus and wild relatives*: Like the family Rubiaceae, according to a revised phylogeny, the genus *Morinda* is represented by four species in India (Razafimandimbison *et al.*, 2010), distributed in ecologically diverse regions: *M. angustifolia* and *M. persicaefolia*, habitat to the tropical Himalayas, and *M. reticulata* (syn. *M. coreia*) and *M. citrifolia* and its two botanical varieties (*citrifolia* and *bracteata*) in the semi-arid Eastern Ghats of Andhra Pradesh and Tamil Nadu and the humid Andaman and Nicobar Islands and in the South Western Ghats of Kerala.

According to the latest assessment, the genus *Morinda* has 30–35 species with a pantropical distribution (Razafimandimbison *et al.*, 2009). A comparatively higher number of species in the tropical Pacific islands are probably the result of island biogeography, which has resulted in the differentiation of a number of morphologically distinct orthodox species in various islands. Genetically, they may be the same; however, further investigations using the principles of biological

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species and molecular markers are required to ascertain the actual number. Hence, in the prominence of occurrence of family, genus and related species, Southeast Asia, Micronesia and Polynesia and South Asia (India) appear to be similar. This is expected, based on the evolutionary geo-history of these regions, according to which India was basically part of the Southern Hemisphere that collided with the land mass of the Northern Hemisphere during the continental drift, resulting in present Indian land mass with floristic components of both the Northern and Southern Hemispheres. Thus, the common occurrence of the genus *Morinda* in South Asia (coasts of India's mainland and the Andaman and Nicobar Islands), Southeast Asia and the Pacific islands is a geo-historical fact, corroborated by the natural occurrence of *M. citrifolia* and wild *Morinda* species in the Asia-Pacific regions, touching the African continent (Razafimandimbison *et al.*, 2010).

(5) *Natural occurrence of concerned domesticated/economically important species*: The coastal areas of Tamil Nadu, Andhra Pradesh, Kerala, Karnataka and the Andaman and Nicobar Islands have naturally occurring cultivated noni, which is a small tree type with large to very large ovate to oval light green, green to dark green leaves, white flowers and large fruits with short to very short drooping peduncles. The distribution map presented by Razafimandimbison *et al.* (2010) includes these areas along with the Southeast Asia, Micronesia and Pacific regions. It is difficult to say whether they are spread through natural seed dispersal or escaped from local cultivations, or both.

(6) *Occurrence of wild or weedy immediate ancestral relatives of the concerned species*: In addition to the naturally occurring cultivated, large-fruited type, the coastal areas of Tamil Nadu, Andhra Pradesh, Kerala and the Andaman and Nicobar Islands have another naturally occurring wild weedy shrub to a small tree type of *M. citrifolia*, with elliptic to lanceolate, thick, leathery, glossy leaves, white flowers and smaller fruits with long, erect peduncles, i.e. *M. citrifolia* var. *citrifolia*, which grows under diverse conditions in coastal areas, between rocks, marshy lands, field bunds, roadsides of urban areas, pits of old buildings, etc. Razafimandimbison *et al.* (2010) has restricted this variety only to Micronesia, and thus the present observation extends the distribution limits of this variety to India. Probably the similar natural principles of seed distribution are involved in the wide distribution of this variety. Additionally, the Andaman and Nicobar Islands have *M. citrifolia* var. *bracteata*, which is very similar to the small-fruited *M. citrifolia* var. *citrifolia*, except for the retention of floral bracts even at the fruit/syncarp stage. At the molecular level, *M. citrifolia* var. *potteri*, distributed in the Pacific region, has been found closest to the large- and small-fruited *M. citrifolia* var. *citrifolia* (Razafimandimbison *et al.*, 2010). Probably, single gene mutation or chimeras are responsible for its differentiation with leaf variegation. Nevertheless, these three varieties are closely related, based on cluster analysis on morphological traits (Waki *et al.*, 2008) and molecular marker analysis (Razafimandimbison *et al.*, 2010), establishing the monophyletic ancestry of *M. citrifolia*.

Two shrub or tree-type species, *M. angustifolia,* distributed in the eastern Himalayas of northeast India, Assam, Bihar and Andhra Pradesh, and *M. reticulata* (syn. *M. coreia*), distributed in the Eastern Ghats of Andhra Pradesh and Tamil Nadu and South Western Ghats, which are morphologically, taxonomically and molecularly part of the Asian clade of *Morinda*, are next close to *M. citrifolia*, after the Micronesian species *M. pedunculata*, *M. latibracteata* and the Australian species *M. bracteata* var. *celebica* (Razafimandimbison *et al.*, 2010), probably because the Micronesian species are genetically closer to geographically close accessions of the Pacific regions, from which most samples of the large- and small-fruited *M. citrifolia* var. *citrifolia* were sampled. These studies need to be extended, with the inclusion of a proportionate number of collections from all areas of geographical distribution, including India, to give a clear picture.

(7) *Level of interaction between human and nature*: The level of interaction of the human population with natural resources, particularly biodiversity, has been very high in the Indian subcontinent, resulting in the domestication of a large number of species. Vavilov (1935) recognized eight primary centres of origin, of which two are associated with India, namely 'the Indian Centre' (including the core of the subcontinent) – based originally on rice, millets and legumes, with a total of 117 (168) species – and 'the Indo-Malayan Centre' (including the northeast region of India and Southeast Asian countries such as Burma, Thailand, Malaysia, Indonesia, Philippines, etc.) – with root crops (*Dioscorea* spp., *Tacca*, etc.) and preponderant fruit crops, sugarcane, spices, etc., of about 55 species. Based on archaeological evidence and the scientifically authenticated Vedic literature, India has been recognized as one of the centres of ancient civilizations in continuity from the Saraswati Valley, Harappan (Indus Valley)/Indus Sarasvata civilization and the Ganga Valley (Vedic, Indo-Gangetic) civilization, and the more recently discovered Cambey region (Chengappa, 2002), and had played a major role in the domestication of plant species and evolution of agriculture (Lallanji and Srivastava, 2008). Therefore, it may be reasonable to conclude that noni was discovered and used by ancient Indians first while examining the nature, including plants, not only for food, but also for health and to treat diseases, long

before the recorded history of Southeast Asia and the surrounding Micronesian territories. In fact, archaeological and historical evidence from Indonesia, e.g. the discovery of the statue of the Hindu God Ganesha from the 1st century CE, 1500-year-old inscription in Sanskrit of King Purnavarman, and mention of 'Dvipantara' or 'Jawa Dwipa' by Indian scholars to be in Java and Sumatra in 200 BCE writings, suggests that the Indo-Malayan Centre/Region (Southeast Asia) was dominantly influenced by Indian culture and agriculture with extension of their knowledge and product to the region, a reason for Vavilov to combine this region with India (Indo).

(8) *Ecological and socio-political diversity*: India offers great diversity both in terms of ecological and socio-political context. Because of being a large landmass with all possible ecological variations from the tropical rainforest of Western Ghats, to the temperate high-altitude regions of the Himalayas, to the Thar Desert of north-western plains, India offers most diverse ecologies for the adaptation of plants. The Gangetic plains, blessed with fertile soil and hospitable climate, have attracted settlers. Because of these attributes, fundamental to agricultural productivity, the Gangetic plains have evolved as a primary centre of plant and animal domestication and agriculture (Tripathi, 2008). Subsequent activities have led the region to evolve into a seat of one of the oldest civilizations in continuity, including the Vedic civilization (Indo-Gangetic civilization; Indo-Aryan civilization) in northern India, credited to the people referred to as the Aryans (1700–1300 BCE). The myth that the Aryans came from Central Asia is being elucidated by recent scientific and archaeological evidence, and the Vedic literature, concluding that the Aryans were the local people and did not come from anywhere (Swami, 2008). Similarly, in the recent past, evidence has been growing for early plant domestication in South India, such as minor millets, *Vigna* spp., fruits, etc. (Fuller *et al.*, 2004), which were indigenous to the Indian peninsula. However, most information about these developments across the Indian continent was documented in the ancient Sanskrit language, the language of the Aryans, the rulers. Therefore, it may be logical to conclude that *M. citrifolia* being a small tree, native to the South Eastern Ghats and Western Ghats of peninsular India, might have been domesticated in South India, and the information on its potential value was documented in Sanskrit, the language of the ruling Aryans, mother of all the Indian languages, and used all over the country in ancient times. Such probability is corroborated by the discovery of the seeds of jackfruit (*Artocarpus integrifolia* L.) from Chalcolithic sites at Narhan in the middle Gangetic plains (Saraswat *et al.*, 1994), along with the seeds of *Vigna* spp., which are wild to Western Ghats, from where they would have probably been taken to North India for cultivation. A probability supported by the fact that the Sena kings who ruled over Bengal (Vanga) during the 11th to 13th century CE, in the north, originally came from Karnataka, South India (Sengupta, 2008).

The socio-political and trade expediency of Indian kingdoms led to the expansion of Indian culture (knowledge) during the period of Emperor Ashok to Southeast Asia *c.* 260 BC, which is evident from the main religion Buddhism being prevalent in the Southeast Asian countries, starting from Burma, Thailand, Malaysia, Indonesia, in south, to China, Vietnam, Mongolia, Japan, etc., in north, and later during the period between 1010 and 1200, by the Chola dynasty, extending their influence up to Malay and the far east, which is evident from the influence of Hinduism in Southeast Asian countries, such as Cambodia (the Temple of Angkor Wat by King Suryavarman II between AD 1131 and 1150) and Indonesia (Prince Aji Saka introduced the writing system to Java based on the scripts of southern India; Hindu kings ruled the area around Kutai on Kalimantan); further to this is the fact that the name Singapore is derived from the Sanskrit word Simha Pura and the name Indonesia from Hind-Asia, translated into Indonesia (Indo-Asia) during the colonial times. Southeast Asia was frequented by traders from eastern India, particularly Magadha (Ashok), as well as from the kingdoms of South India. The trading expeditions during these periods extended up to China via Sumatra, leading to the probable introduction of important crops and medicinal plants, including *M. citrifolia* (Fig. 1). Similar accounts are not available from Southeast Asia or Polynesia, as observed by Razafimandimbison *et al.* (2010): 'whether or not this form of *M. citrifolia* var. *citrifolia* was already present before the arrival of Micronesian and Polynesian ancestors, question on which historical records is silent'.

(9) *Interest of Royals*: The royalties played a major role in the domestication and improvement of plant species (Janick, 2007). There is documented information that ancient Indians, called the Aryans, ruled India in *c.* 1700–1300 BCE (*c.* 3500 years ago, or even earlier). Their physicians developed the medicine system 'Ayurveda' (1500 BCE), from 'Atharvaveda' (one of the four most ancient books of Vedic knowledge, wisdom and culture; Bloomfield, 1899; Chopra, 2003). 'Ayurveda' has reference of *M. citrifolia*, being held in very high esteem because of its properties to protect the skin. Compared with this, the documented information on the use of noni by the Polynesians for food and medicinal purposes is 2000 years old (Whistler, 1985).

(10) *History of nomenclature/vernacular name used*: The oldest references to noni are found only in the ancient Indian language Sanskrit, dating back to tens of centuries, with the name of 'Och' plant or 'Ashyuka',

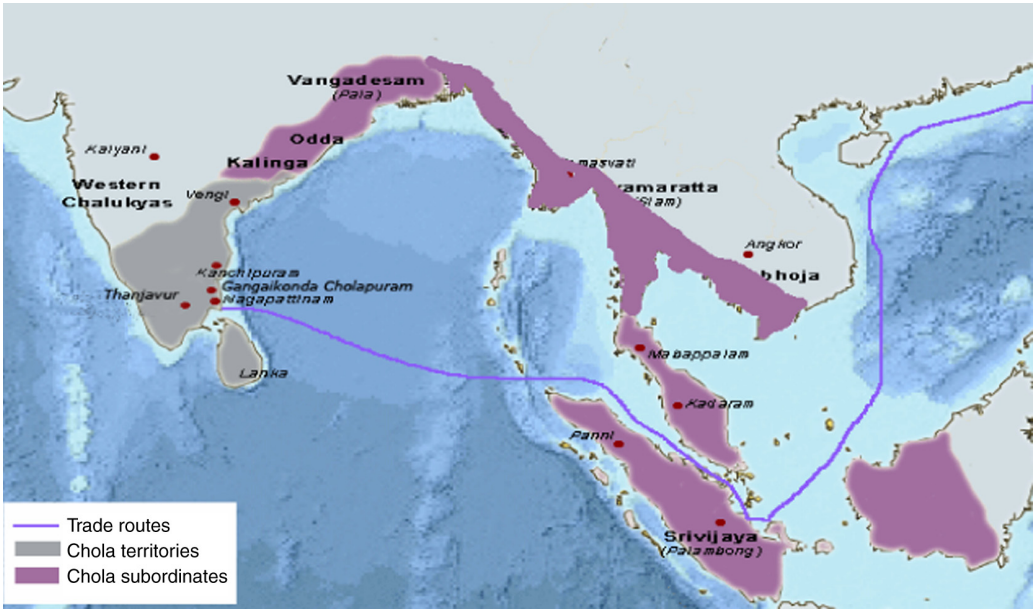

Fig. 1. Chola Dynasty territories and their trade route *c.* 1050. A colour version of this figure can be found online at journals.cambridge.org/pgr.

which means 'longevity' (Gerson, 1997). It was noted to be a balancing agent, stabilizing the body in perfect health (Anonymous (2009a), toptropicals.com/html/toptropicals/plant_wk/noni.htm; Anonymous (2009b), www.immuno-research.com/enoni.htm). In the literature search of Gerson (1997), more than 100 Indian Sanskrit writings pertaining to noni have been recorded. This reflects that noni was discovered and used by Sanskrit-speaking people, long before the recorded history in Southeast Asia. Noni has names in other South Indian ancient languages from the Eastern Ghats, i.e. Andhra Pradesh and Tamil Nadu. In Tamil, it is called 'Munja pavattay', and in Telugu 'Maddi chettu, Molagha'. The same cannot be said either for Southeast Asian, Micronesian or Polynesian countries, using the noni for food and medicinal purposes since 2000 years (Whistler, 1985). Furthermore, in the international languages, in English, noni is called Indian mulberry and in Spanish, Mora de la India, reflecting the recent global discovery of noni, probably during the quest of the West on a route to the spice-rich East. These facts reveal that Indian knowledge about the potential value of *M. citrifolia* is older than Southeast Asia, from where the ancestors of Micronesia and Polynesia arrived (Razafimandimbison *et al.*, 2010).

(11) *History of domestication of other crops*: India is associated with two primary centres of origin, i.e. Hindustani and Indo-Burma, and has domesticated about 168 plant species (Vavilov, 1935) for food. Additionally, according to the early Vedic literature, a medicinal system called 'Ayurveda', meaning 'the science of life' in Sanskrit, was developed by ancient Indian settlers (the Aryans in 1500 BCE), using plants for natural treatments. This indicates that these initial settlers, while bio-prospecting plants for food, were also looking for plants for health, generating knowledge about the medicinal properties of plants. 'Ayurveda' describes the regular use of about 1500 plant species, including *M. citrifolia* (Anonymous (2007), www.all4naturalhealth.com/ayurvedic-medicinal-plants.html).

(12) *History of ancient and diverse use of the concerned species*: Most of the facts discussed above reflect that the potential medicinal value of noni was known to Indians 3500 years ago (*c.* 1700–1300 BCE), long before the Southeast Asians, Micronesians and Polynesians. However, in these regions, noni has been used more traditionally (Davis, 2007). It has been used as food (during famine), consumed raw or in the form of fruit juice; its leaves, flowers, bark and roots have also been used (red and yellow dye) (Dixon *et al.*, 1999). In Australia, indigenous people usually eat its fruit raw with salt, whereas in Southeast Asian cultures, it is often cooked in curries. In this regard, India lags behind; probably the richness of floral diversity and domestication of a large number of plants for various purposes facilitated the availability of alternative sources of food and medicine, limiting the use of noni, to a narrow ecological niche of coastal regions, a factor considered to have contributed to non-domestication plant species in the biodiversity-rich region. Nevertheless, there are reports that in Tamil Nadu, noni was cultivated near temples, like Basil ('tulsi'). Such social domestication cannot be associated with Southeast Asian countries.

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Conclusion

Thus, based on the comparative richness of the Indian subcontinent in floristic and crop diversity, higher levels of plant species endemism, prominent occurrence of the family Rubiaceae and the genus *Morinda*, the natural occurrence of large-fruited, cultivated noni, its wild or weedy immediate ancestors, *M. citrifolia* var. *citrifolia* and *M. citrifolia* var. *bracteata*, several wild *Morinda* species, including morphologically and molecularly close, *M. angustifolia* and *M. reticulata* (syn. *M. coreia*) belonging to the Asian clade, home to ecological diversity and that India being one of the primary centres of crop origin (domestication) and diversity with the documented socio-political history of rulers supporting bioprospecting, domestication of plants both for food and medicine from ancient times (1500 BCE; developing 'Ayurveda'), and later dispersal (useful plants and products) during the voyage to Southeast Asia and China under the barter trade (still practised with Myanmar), Southeast India appears to be a more probable centre of domestication/origin of noni than Southeast Asia and Micronesia. Furthermore, the oldest reference of noni in the ancient Aryan literature in Sanskrit, describing its medicinal properties, corroborates that it was known to the Indians long before (3500 years) than the Southeast Asians, Micronesians and Polynesians. Morton (1992) also mentioned southern Asia, and Australia as its native land. The occurrence of a greater number of wild *Morinda* species endemic to various island nations of Southeast Asia, Micronesia and Polynesia can be explained, as a result of island biogeography, isolating populations. However, a comparatively wide distribution of the wild and weedy form of large-fruited *M. citrifolia* and its two varieties, small-fruited variety, *citrifolia* and *bracteata*, across the tropics is due to efficient natural seed dispersal through buoyancy (noni seeds have large air sacs and pits in the cells of the seed's testa, giving them buoyancy), and intentional introduction by migrating humans, who colonized the Indo-Pacific islands (Whistler, 1992). It was further aided by self-pollinating and round-the-year flowering and fruiting capacities. Dispersal might have also been aided by fruit-eating birds and animals.

On the basis of these inferences, it is proposed that *M. citrifolia* was first domesticated in India in the Eastern or South Western Ghats of peninsular India, documenting the information on its medicinal properties in ancient 'Ayurveda' and other Sanskrit writings. At the time of cultural expansion during the period of the Ashoka and/or Chola dynasty or trade voyages from Orissa, Andhra Pradesh or Tamil Nadu, it was carried to Southeast Asian countries (Malaysia, Indonesia), from where the Southeast Asian ancestors of Micronesia and Polynesia brought it to various island nations (Fig. 2). The seafaring Micronesians might have contributed to the further spread of *M. citrifolia*, through their ocean-going canoes.

The geological relationship between the Indian subcontinent, Southeast Asia and Micronesia, being part of the same land mass before the continental drift forming the present India, might also suggest the ancient natural

Fig. 2. Proposed route regarding the origin and distribution of noni, *Morinda citrifolia*. A colour version of this figure can be found online at journals.cambridge.org/pgr.

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distribution of *M. citrifolia* across these regions and, simultaneously or at different times, polyphyletic domestication. Therefore, Southeast Asia and Micronesia might be the other centre of origin or a secondary centre of origin for noni, as a result of polyphyletic domestication. Nevertheless, detailed phylogenetic investigations are required, including a proportionate number of accessions from all bio-geographical regions of noni and *Morinda* species, using highly polymorphic molecular markers covering the whole genome, and cluster analysis that will trace the factual phylogenetic relationships among accessions of noni, and between noni and wild *Morinda* species, identifying the actual bio-geographical region(s) for noni's origin.

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