

Ancient crops provide first archaeological signature of the westward Austronesian expansion

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The Austronesian settlement of the remote island of Madagascar remains one of the great puzzles of Indo-Pacific prehistory. Although linguistic, ethnographic, and genetic evidence points clearly to a colonization of Madagascar by Austronesian language-speaking people from Island Southeast Asia, decades of archaeological research have failed to locate evidence for a Southeast Asian signature in the island's early material record. Here, we present new archaeobotanical data that show that Southeast Asian settlers brought Asian crops with them when they settled in Africa. These crops provide the first, to our knowledge, reliable archaeological window into the Southeast Asian colonization of Madagascar. They additionally suggest that initial Southeast Asian settlement in Africa was not limited to Madagascar, but also extended to the Comoros. Archaeobotanical data may support a model of indirect Austronesian colonization of Madagascar from the Comoros and/or elsewhere in eastern Africa.

archaeobotany | dispersal | Madagascar | language | rice

The island of Madagascar, situated in the southwestern corner of the Indian Ocean, is located some 500 km east of continental Africa and 6,000 km from Southeast Asia. The inhabitants of the island, nonetheless, speak a language, Malagasy, that is part of the Austronesian language family. Austronesian languages, which also include, for example, Hawaiian, Maori, Samoan, and Malay, are otherwise unique to Southeast Asia and the Pacific. Independent lines of molecular genetic and cultural evidence support the proposal that this linguistic anomaly reflects a colonization of Madagascar by Austronesian-speaking peoples (1–3). This migration, which is estimated on linguistic grounds to have taken place in the first millennium CE (approximately the seventh to eighth centuries according to ref. 4), has been described as “the single most astonishing fact of human geography for the entire world” (5).

The Austronesian colonization of Madagascar is also one of the major outstanding mysteries of human history. Not only is it not attested to in any written sources, it is also archaeologically elusive. Although archaeological research has identified human settlements in Madagascar that date to the first millennium CE, it has not been able to link these to Southeast Asia. Indeed, decades of survey and excavations across the island have so far failed to provide any substantive evidence for an early Austronesian signature (6, 7). Accordingly—and particularly in light of archaeological and paleoecological findings suggesting that Madagascar may have been occupied by hunter-gatherers, most likely from Africa, by the first or second millennium BCE (8, 9)—the timing and nature of the Austronesian settlement of the island and the relationship between Austronesian and African colonizations [both of which are suggested to have contributed to the genetic ancestry of contemporary Malagasy populations (2, 3)] remain unclear.

One line of evidence that has been largely overlooked in archaeological investigations of Madagascar and, indeed, eastern Africa more broadly is ancient plants. However, it is estimated that some 10% of Madagascar's flora was introduced from elsewhere (10), and plant introductions include a significant number of staple crops, spices, and arable weeds of Asian origin (11). Historically or currently important crops on Madagascar, like banana (*Musa* spp.), yam (*Dioscorea alata*), taro (*Colocasia esculenta*), and coconut (*Cocos nucifera*), are Southeast Asian cultivars (12, 13). Asian rice (*Oryza sativa*), which was domesticated separately in East and South Asia but is the basis of traditional agriculture across much of Madagascar today, was also widely grown in Southeast Asia by the first millennium CE (14–16). Other Asian crops, like mung bean (*Vigna radiata*) and Asian cotton (*Gossypium arboreum*), are also cultivated on Madagascar. The fact that early crop introductions to Madagascar may have arrived with Austronesian settlers seems particularly feasible given that Austronesian expansion into the Pacific was linked to the spread of a similar suite of cultivars (17).

Significance

The prehistoric settlement of Madagascar by people from distant Southeast Asia has long captured both scholarly and public imagination, but on the ground evidence for this colonization has eluded archaeologists for decades. Our study provides the first, to our knowledge, archaeological evidence for an early Southeast Asian presence in Madagascar and reveals that this settlement extended to the Comoros. Our findings point to a complex Malagasy settlement history and open new research avenues for linguists, geneticists, and archaeologists to further study the timing and process of this population movement. They also provide insight into early processes of Indian Ocean biological exchange and in particular, Madagascar's floral introductions, which account for one-tenth of its current vascular plant species diversity.

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To directly explore early cultivated plants on Madagascar and their potential to inform on its colonization history, we collected new archaeobotanical data from the island as well as contemporaneous sites on the African mainland coast (Kenya and Tanzania) and nearshore islands (Pemba, Zanzibar, and Mafia) and the Comoros. These data were collected from 18 sites in total, dating between approximately 650 and 1200 calibrated years (cal) CE (Fig. 1 and Table S1). The archaeobotanical datasets derive primarily from recent excavations at 16 sites, during which systematic sampling for charred macrobotanical remains at high stratigraphic resolution was conducted (*Materials and Methods*). They are supplemented by existing records from one of the sites (Sima) as well as data from previous excavations at two other sites in the Comoros (18, 19). The combined dataset includes 2,443 identified crop remains recovered from >7,430 L sediment across the sites (Table 1 and Table S2) and is supported by 48 accelerator MS (AMS) radiocarbon dates, 43 of which were obtained directly on crop seeds (Fig. S1 and Table S3).

Results and Discussion

Contrasting Regional Archaeobotanical Patterns. Our analysis revealed the presence of crops of two main origins—African and Asian—on eastern African sites. African crops consisted of millets, pulses, and fruits domesticated on the continent: sorghum (*Sorghum bicolor*), pearl millet (*Pennisetum glaucum*), finger millet (*Eleusine coracana*), cowpea (*Vigna unguiculata*), and baobab (*Adansonia digitata*) (Fig. 2). Asian crops included Asian rice, mung bean, and cotton (Fig. 2). Data on coconut was only systematically collected for the sites of Tumbe and Kimimba on Pemba, and this species is, therefore, excluded from the site comparisons presented below (these results are shown in Table S2). Other Asian domesticates, like banana, yam, and taro, that generally do not produce seeds were not investigated as part of this study.

A clear pattern emerged in the dataset, differentiating sites dominated by African crops from sites dominated by Asian crops along a geographical cline (Fig. 1). On all 11 mainland and near-coastal eastern African sites that produced identifiable crop

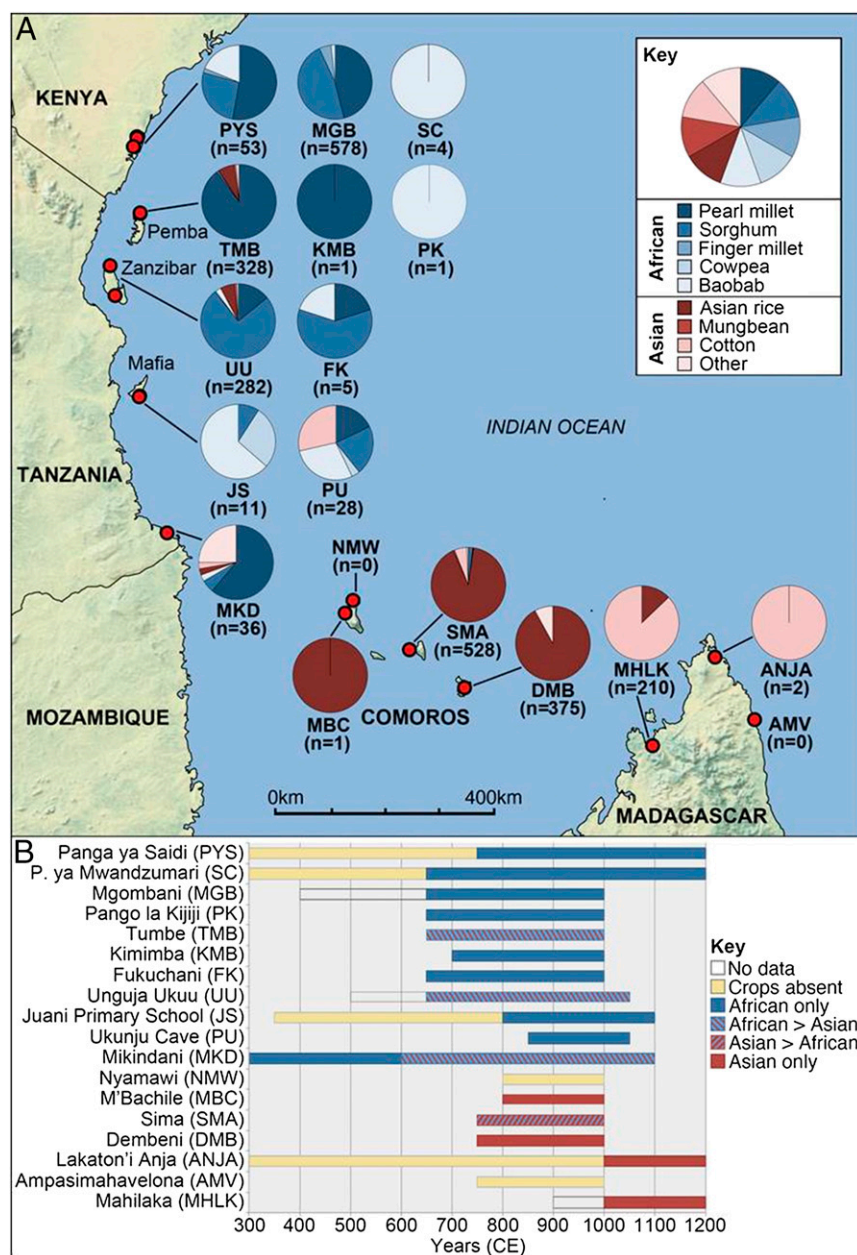


Fig. 1. (A) Map of eastern Africa, including the Comoros and Madagascar, showing the locations of sites included in this study. The relative proportions of African and Asian crops are shown for each site (percentages based on numbers of identified specimens per site) (Table 1). (B) Chronological summary of African vs. Asian crop patterns by site from north to south. (The data in A correspond to the time window shown in B. Fig. S1 shows OxCal plots of the calibrated AMS radiocarbon determinations on crop remains from these sites.)

Table 1. Summary of archaeobotanical crop data for each site (Table S2 shows the full analytical data)

| Site name | African crops | | | | | Asian crops | | | | Total |
|---------------------------------|---------------|---------|---------------|--------|--------|-------------|-----------|--------|-------------|-------|
| | Pearl millet | Sorghum | Finger millet | Cowpea | Baobab | Asian rice | Mung bean | Cotton | Other Asian | |
| Panga ya Saidi | 28 | 14 | 1 | 0 | 10 | 0 | 0 | 0 | 0 | 53 |
| Panga ya Mwandzumari | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 4 |
| Mgombani | 266 | 272 | 30 | 0 | 10 | 0 | 0 | 0 | 0 | 578 |
| Pango la Kijiji | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| Tumbe | 294 | 3 | 1 | 0 | 0 | 24 | 0 | 2 | 4 | 328 |
| Kimimba | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Unguja Ukuu | 40 | 212 | 0 | 1 | 7 | 17 | 3 | 0 | 2 | 282 |
| Fukuchani | 1 | 3 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 5 |
| Juani Primary School | 0 | 1 | 0 | 3 | 7 | 0 | 0 | 0 | 0 | 11 |
| Ukunju Cave | 5 | 6 | 0 | 1 | 8 | 0 | 0 | 8 | 0 | 28 |
| Mikindani | 22 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 9 | 36 |
| Coastal eastern Africa subtotal | 657 | 513 | 32 | 5 | 49 | 42 | 3 | 11 | 15 | 1,327 |
| Nyamawi | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| M'Bachile | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| Sima | 1 | 9 | 1 | 1 | 0 | 481 | 3 | 28 | 4 | 528 |
| Dembeni | 0 | 0 | 0 | 0 | 0 | 345 | 0 | 0 | 30 | 375 |
| Lakaton'i Anja | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 2 |
| Ampasimahavelona | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Mahilaka | 0 | 0 | 0 | 0 | 0 | 27 | 0 | 183 | 0 | 210 |
| Comoros and Madagascar subtotal | 1 | 9 | 1 | 1 | 0 | 854 | 3 | 213 | 34 | 1,116 |
| Total | 658 | 522 | 33 | 6 | 49 | 896 | 6 | 224 | 49 | 2,443 |

remains, archaeobotanical assemblages contained a predominance of African crops: sorghum, pearl millet, finger millet, baobab, and/or cowpea (Table 1). These crops were most likely introduced to eastern Africa from their centers of origin in western and central Africa by migrating Iron Age groups or through contact between pastoralists and hunter-gatherers with these groups (20, 21). On these eastern African sites, Asian crops were absent or rare and mainly identified at major trading ports, such as Unguja Ukuu on Zanzibar and Tumbe on Pemba, where they were present in small quantities (approximately 8% of the total identified seeds). They occurred alongside rich evidence of Indian Ocean trade in the form of imported ceramics, glass, and metal artifacts (details in *SI Text*). Significant quantities (>10%) of Asian crops do not appear at any eastern African site until the 11th century CE (22).

This pattern contrasts sharply with the crop records found at contemporaneous sites on the Comoros Islands and Madagascar. Here, the earliest archaeobotanical assemblages date from the 8th to 10th centuries CE and are dominated by Asian crops (Table 1). Rice is by far the most abundant food crop present, found at levels of approximately 70–100% in nearly all tested assemblages that produced crop remains. Rice dominated food crop assemblages from the beginning of occupation on the Comoros in the 8th century and the earliest deposits tested at the site of Mahilaka on Madagascar, a trading port established on the northwest coast in approximately the 10th century. Morphometric study of the rice grains from the 8th to 10th century site of Sima in the Comoros, the only assemblage large enough to enable this analysis, indicates the presence of both *indica* and *japonica* varieties (Fig. S2). The Sima assemblage also included mung bean and cotton, both also likely from Asia (additional discussion is in *Materials and Methods*). Only small quantities of African sorghum, finger millet, and cowpea were present at Sima, and African crops were absent from Mahilaka.

The earlier Malagasy sites of Lakaton'i Anja, a second millennium BCE to 14th century CE hunter-gatherer-occupied rock shelter at the northern tip of the island, and Ampasimahavelona,

an 8th to 10th century CE village on the northeast coast, did not yield any ancient charred food crop remains, signaling that the earliest phase of agriculture in Madagascar may still be archaeologically invisible. Preservation of crops from all examined Madagascar sites was poor; one possibility is that early subsistence focused on vegetative crops, such as yams, taro, and banana (11), which are not represented in the types of macrobotanical records studied here but may be elucidated by future plant microfossil studies.

Archaeobotanical Signatures of Trade and Migration. The archaeobotanical patterns observed in mainland and near-coastal eastern Africa versus the Comoros and Madagascar show a stark contrast and suggest different histories of crop introduction to the two regions. In coastal and near-island eastern Africa, Asian crops seem to have arrived as part of commercial exchange activities, initially turning up in very small quantities and generally confined to major trading ports. There is minimal evidence for later time periods, but existing data (22, 23) suggest that Asian crops, like rice, only very gradually increased in quantity on sites in this region, reaching a peak in the 11th to 15th centuries at Chwaka on Pemba Island, where rice was, perhaps unusually, the dominant crop (22). The gradual introduction of rice to the immediate coastal eastern African region is notable and fits closely with patterns observed elsewhere for crops introduced through trade. Research across various Old World sites suggests that exotic crops introduced to a region as new plants usually featured as a minor component of subsistence systems for centuries and, in some cases, millennia after arrival before becoming a major resource (24, 25). This pattern is seen, for example, with the introduction of Asian crops at Roman Period port sites on the Red Sea (26, 27). The arrival at coastal sites in eastern Africa of rice and mung bean together with Near Eastern crops, like wheat and pea, can be understood as part of the broader acquisition of exotic goods that occurred with eastern Africa's entry into the Indian Ocean commercial sphere (28).

In contrast, the overwhelming dominance of Asian crops in the earliest records of the Comoros and Madagascar is consistent

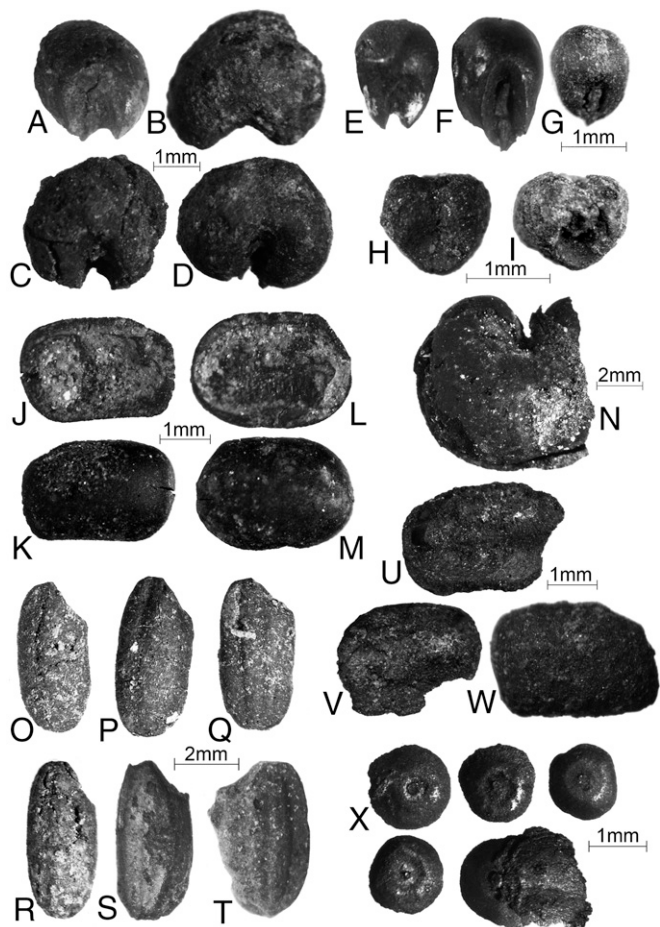


Fig. 2. Examples of crop remains recovered from the sites. (A–D) *S. bicolor*. (E–G) *P. glaucum*. (H and I) *E. coracana*. (J–M) *V. cf unguiculata* [(J and L) interior; (K and M) exterior]. (N) *A. digitata*. (O–T) *O. sativa*. (U–W) *V. radiata*. (X) *Gossypium* sp. (funicular seed caps). (A, E, F, and T) Unguja Ukuu. (B–D, H, O–R, and U–W) Sima. (G and I) Mgombani. (J–N) Juani Primary School. (S and X) Mahilaka.

with patterns observed when crops move through human colonization. Such a pattern is observed in Japan, where the immigration of new groups from the mainland after approximately 2,800 y B.P. is associated with the arrival of wet rice cultivation (29). It is also observed, for example, in Neolithic Europe, where the first crops are entirely Near Eastern, reflecting the arrival of migrants from this region (30). The presence of Asian crops apparently brought by migrating people on the Comoros and Madagascar is important given that Madagascar is known to have been colonized by settlers from Asia. The findings, nonetheless, require careful consideration given that there are diverse potential sources for the crops and that the present day inhabitants of the Comoros speak Bantu rather than Austronesian languages (31).

Rice and mung bean are the two main Asian food crops identified in archaeological assemblages from the Comoros and Madagascar. Fig. 3 presents a summary of Indian Ocean sites at which these two crops have been identified. Given the paucity of data for the period of 650–1200 CE, sites from an earlier period, 500 BCE to 650 CE, are also included for comparison. The fact that the combination of rice and mung bean is rare in the Near East and Arabia is notable. Indeed, it is only recorded at two Roman-period sites on the Egyptian side of the Red Sea, where it was associated with the presence of Indian traders engaged in the pepper trade (26, 27). At these sites, the crops are found in small quantities within overall assemblages dominated by Mediterranean crops. Mung bean seems to be absent from Medieval cookbooks of the Islamic world, and these sources

also indicate that rice played a minor role in the cuisine of the Arab world (32). Although rice was adopted into cultivation in parts of Iran and Mesopotamia more than 2,000 y ago, it was not a staple in the Middle East in the Medieval Period (33).

Both rice and mung bean are, in contrast, common crops in archaeobotanical assemblages of the Indian subcontinent and Sri Lanka from at least 500 BCE onward (Fig. 3). Mung bean and *indica* rice are both South Asian domesticates, with domestication processes likely well underway before 1000 BCE (34, 35). Although it is, thus, possible that rice and mung bean were brought to the Comoros and Madagascar by Indian settlers, there is no other historical, linguistic, or archaeological evidence as yet to support such a colonization. The archaeobotanical absence of other South Asian crops, such as horse gram (*Macrotyloma uniflorum*) and urd (*Vigna mungo*), in the Comorian and Malagasy assemblages also suggests an introduction from outside South Asia.

Evidence of domesticated rice is common on sites in mainland Southeast Asia by the Late Prehistoric Period (approximately 300 BCE to 100 CE), reflecting the arrival of the *japonica* subspecies of the crop to northeast Thailand by at least 1000 BCE (15, 16, 36). Mung bean is much less prevalent archaeologically than rice in this region, although it has been recovered from some sites in southern Thailand also dating to the last two millennia (14, 37). The combination of rice and mung bean is also found at one site in Island Southeast Asia: at Pacung, in Bali, which dates to approximately the second century BCE to the second century CE (14, 34). The implications of even a minimal presence of rice and mung bean in southern Thailand and Island Southeast Asia are significant, however, given that these are the only southern Southeast Asian sites of the relevant time frame at which archaeobotanical studies have been conducted. Historical and archaeological data also suggest the likelihood of strong South Asian culinary influence on the southern Thailand–Island Southeast Asian cultural sphere because of the presence of commercial and cultural ties across the Bay of Bengal (38). Island Southeast Asia is, therefore, a feasible source for early Asian crops in the Comoros and Madagascar.

Other types of data offer additional support for this suggestion. As noted, morphometric study of the rice grains from Sima suggests the presence of both *indica* and *japonica* rice (Fig. S2). Morphometric and ancient DNA analyses of early rice assemblages from South Asia similarly show the presence of a mixed *indica*–*japonica* signal (Fig. S2) (16). Such data support the notion that most early *indica* cultivation was mixed, involving both *indica* and *japonica* varieties. Although archaeological rice in Island Southeast Asia has not yet been measured, a morphometric study of grains from Iron Age mainland Southeast Asian sites dating

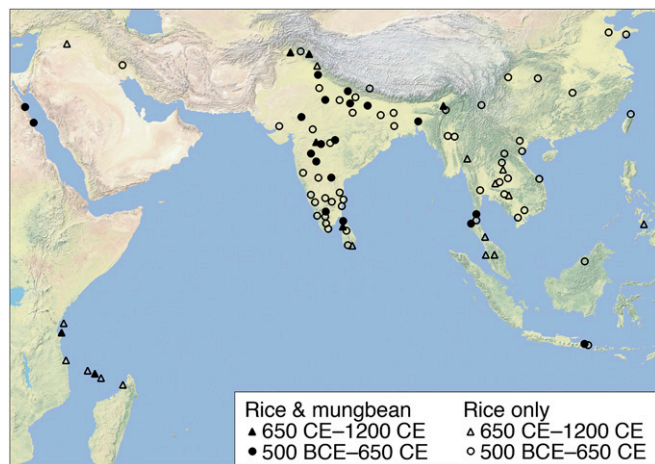


Fig. 3. Distribution of archaeobotanical assemblages from the Indian Ocean region (approximately 500 BCE to 1200 CE, including sites from this study) with both mung bean and domesticated Asian rice contrasted with sites that have evidence for rice alone. Fig. S3 shows site names.

between approximately 200 BCE and 400 CE shows that assemblages there are dominated by a *japonica* signal (Fig. S2) (16). This pattern is in agreement with archaeobotanical models suggesting a late spread of *indica* rice to Southeast Asia, probably at least 1,000 y after the introduction of *japonica* rice (16, 36). This *indica* rice, which likely involved the same mix of *japonica* and *indica* seen in South Asia, probably then spread to Madagascar. Linguistic terminology, like the Dayak–Malagasy term *bari/vary*, a loan from Dravidian, is also suggested to trace the movement of *indica* rice from southern India to Borneo and then Madagascar in prehistory (39).

Morphometric analysis of rice from Chwaka on the island of Pemba has suggested the possible presence, meanwhile, of the *japonica* subvariety of rice (22). It is possible that rice reached eastern Africa by multiple routes at different times, with the Chwaka rice reflecting a separate rice introduction through Indian Ocean trade in the 11th to 15th centuries. Interestingly, molecular phylogenetic studies also indicate that rice as well as mung bean reached Africa as part of at least two separate dispersals, with one route in each case being linked to a potential direct Southeast Asian translocation to the Comoros or Madagascar (40, 41). Thus, despite a paucity of archaeobotanical data from the key potential source region, an Island Southeast Asian source for the early Asian crops of the Comoros and Madagascar seems to offer the best fit for the patterns observed in the available records.

Were the Comoros Part of the Westward Austronesian Expansion?

Although the presence of Asian crops that likely originate from Southeast Asia on early sites in Madagascar corresponds well with linguistic, genetic, and ethnographic evidence for a prehistoric migration of people from this region, the finding that these crops also dominate early assemblages on the Comoros is rather unexpected. In particular, the presence of Asian crops at sites in the Comoros earlier than at sites on Madagascar (Fig. 1B) is of significant interest, and although sampling and preservation biases cannot be discounted, may reflect Austronesian colonization of the Comoros before Madagascar. As noted, however, Comorians today speak Bantu languages, and in addition, preliminary molecular genetic studies suggest that they possess only a small proportion of Southeast Asian ancestry (31, 42). Nonetheless, the population of the Comoros is small and has been historically subject to significant population bottlenecks and Bantu input as a result of slave raiding and trading over many centuries (43, 44). Thus, it is possible that the Comoros were settled at an early date by a Southeast Asian population that was later genetically and linguistically swamped.

Direct colonization from Southeast Asia is common to many models of Madagascar's Austronesian settlement, particularly those put forward by archaeologists and geneticists (3, 45). However, linguistics have offered another perspective, with some linguists taking the view that the remarkable unity of Bantu loanwords and grammatical features throughout Malagasy dialects can only be explained through initial Austronesian settlement on the African mainland and/or the Comoros (4, 46, 47). Early Southeast Asian presence or influence on the Comoros has also been suggested on the basis of the apparent presence of several 10th or 11th century "Austronesian-type" furnaces on Mayotte (6) as well as findings of shell-impressed pottery at early sites on the islands (45) (SI Text). These suggested Austronesian linkages, however, have been both limited and contentious. This study suggests that they deserve reinvestigation together with the argument that the Comoros may have served as a key base for Southeast Asian commercial activity in the western Indian Ocean, including an alternative slave-trading corridor (6). Independent linguistic, genetic, and archaeological studies are required to examine the role of the Comoros in early Indian Ocean population movements and commercial trade (cf. refs. 19, 42, and 48).

Whatever the place of the Comoros in the story of the westward Austronesian expansion, the discovery that eastern African archaeobotanical data provide a strong signature of this population migration offers a novel strategy with which to explore the timing and process of Southeast Asian migration, colonization, and assimilation with African populations. Our findings open

the way to new avenues of research for linguists, geneticists, and archaeologists and provide crucial insight into early processes of biological exchange across the Indian Ocean.

Materials and Methods

Sites. Archaeobotanical data were collected from 18 sites in Madagascar ($n = 3$), the Comoros ($n = 4$), and coastal eastern Africa and offshore islands ($n = 11$) (Table S1). The majority of these sites were excavated in 2010–2013 by the Sealinks Project. Sites with known good stratigraphic integrity, high potential for the preservation of charred plant remains, and occupation dating to the mid-first to early second millennium CE were targeted. Trenches were between 2 and 9 m² in size and excavated according to natural stratigraphic units combined with smaller arbitrary levels for thicker contexts. Archaeobotanical remains were retrieved from composite sediment samples collected from each major context/cultural layer, except at Sima and Nyamawi, where exposed sections were cleaned and sampled without areal excavation. Sample volumes varied between 1 and 700 L per context (average of 35 L). The sediments were processed by bucket flotation using 0.3- to 0.5-mm sieves to collect the charred plant remains.

Archaeobotany. Flotation samples were sieved into size fractions, and at minimum, the ≥ 1 -mm fractions were scanned for charred remains (seeds, chaff, etc.) using a stereomicroscope (10–40 \times). Taxonomic identifications of crop remains were made using published criteria (20, 27, 35, 49) and botanical reference collections at University College London (A.C., L.L., and D.Q.F.), Washington University in St. Louis (S.W.), and the University of Virginia (M.P.). The numbers of specimens per remain type were counted for each taxon per sample. To generate the graphs shown in Fig. 1, counts for a taxon were combined for specimens identified to different levels of confidence (e.g., *S. bicolor*, cf *Sorghum*, and *S. cf bicolor*). A count of one was used where presence only was recorded in a sample (shown in parentheses in Table S2). Rice morphometric analyses followed the methods in the work in ref. 16.

Although native African cotton (*Gossypium herbaceum*) and Asian tree cotton (*G. arboreum*) cannot be differentiated archaeologically on the basis of seed morphology, the majority of specimens recovered from our assemblages are most likely the Asian species. At this period, cotton is found in Nubia, Axum, the Middle East, India, and Southeast Asia (49, 50) but is absent from mainland eastern African Iron Age crop assemblages (20) aside from the evidence reported here. Taking into account the traditional cultivation of Asian but not African cotton throughout southeastern Africa and Madagascar (51), we infer that the cotton in this region arrived from tropical Asia.

The other Asian category in Fig. 1A includes Asian millets (*Setaria* spp.), sesame (*Sesamum* sp.), wheat (*Triticum* sp.), pea (*Pisum sativum*), and citrus (cf *Citrus* sp./Rutaceae). Coconut was excluded from this analysis, because it was only recorded systematically for assemblages from Tumbé and Kimimba, although two large fragments each were also recovered at Sima and Dembeni (19). Counts of coconut shell fragments are also likely to significantly skew the results, because a single endocarp can produce disproportionately large numbers of shell fragments relative to cereals. The data relating to coconut finds are provided in Table S2 for reference.

Radiocarbon-dated charcoal fragments were identified with reference to wood anatomy atlases of flora from Africa and adjacent regions (52–54).

Radiocarbon Dating. Forty-eight AMS radiocarbon dates were obtained from the Oxford Radiocarbon Accelerator Unit, the University of Waikato Radiocarbon Facility, and Beta Analytic (Table S3). For dates on charcoal, single fragments identified to the Rhizophoraceae (mangrove) family were selected, because species within this group generally do not form large girth trees and are, therefore, unlikely to have a large built-in age error. Radiocarbon dates were calibrated using OxCal, version 4.2.4 (55) (95.4% probability) employing a mixed curve that combines the SHCal13 (56) and IntCal13 (57) curves at ratios of either 70:30 (Kenya and Tanzania's immediate offshore islands) or 80:20 (Comoros and Madagascar) to account for the differential effects of the intertropical convergence zone. Where appropriate, dates from each site were modeled using Bayesian analysis (Fig. S1), incorporating prior information regarding the stratigraphic relationships between samples.

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