Convergent evolution and parallelism in plant domestication revealed by an expanding archaeological record

Dorian Q Fuller1,a, Tim Denhamb, Manuel Arroyo-Kalinb, Leilani Lucasb, Chris J. Stevensc, Ling Qinb, Robin G. Allabyd, and Michael D. Puruggananea,ef

aInstitute of Archaeology, University College London, London WC1H 0PY, United Kingdom; bSchool of Archaeology and Anthropology, Australian National University, Canberra, ACT 0200, Australia; cSchool of Archaeology and Museology, Peking University, Beijing 100871, China; dSchool of Life Sciences, University of Warwick, Warwick CV3 9EF, United Kingdom; eDepartment of Biology, New York University, New York, NY 10003; and fCenter for Genomics and Systems Biology, New York University Abu Dhabi Institute, Abu Dhabi, United Arab Emirates

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Recent increases in archaeobotanical evidence offer insights into the processes of plant domestication and agricultural origins, which evolved in parallel in several world regions. Many different crop species underwent convergent evolution and acquired domestication syndrome traits. For a growing number of seed crop species, these traits can be quantified by proxy from archaeological evidence, providing measures of the rates of change during domestication. Among domestication traits, nonshattering cereal ears evolved more quickly in general than seed size. Nevertheless, most domestication traits show similarly slow rates of phenotypic change over several centuries to millennia, and these rates were similar across different regions of origin. Crops reproduced vegetatively, including tubers and many fruit trees, are less easily documented in terms of morphological domestication, but multiple lines of evidence outline some patterns in the development of vegicultural systems across the New World and Old World tropics. Pathways to plant domestication can also be compared in terms of the cultural and economic factors occurring at the start of the process. Whereas agricultural societies have tended to converge on higher population densities and sedentism, in some instances cultivation began among sedentary hunter-gatherers whereas more often it was initiated by mobile societies of hunter-gatherers or herder–gatherers.

Domestication offers an ideal laboratory for understanding evolution because it is a recent phenomenon in terms of geological time scales and because the selection pressures that affect harvestability by humans are often known (1). Domestication is a product of human behaviors that regulate or increase food supply, but may also inadvertently lock humans into an increased reliance on managed taxa (2). Archaeological research provides a fossil record of past organisms undergoing domestication, often accompanied by cultural artifacts associated with habitat management or niche construction (3, 4). The effects of agriculture in terms of intensifying land productivity to support larger populations has been fundamental to the development of civilizations and the ongoing impact on and management of ecosystems (5, 6).

Domestications have occurred separately on different continents and in different cultural traditions, and thus represent a set of parallel experiments from which to infer recurrent processes (Fig. 1). In some cases this represents parallelism of phylogenetically related organisms that have been subjected to similar selection pressures and developed identical or similar adaptations in different places. In others, we can consider domestication as convergent evolution, in as much as similar adaptations have evolved across crops in different plant families. These parallel adaptations have been defined as the “domestication syndrome” (7, 8). A distinction can be made between true convergence, in which analogous states have been reached from very different and unrelated starting points, versus parallelism, in which similar pathways of change follow on from similar starting points, for example, as with taxa that share the same underlying developmental ontogeny and orthologous genetic loci (9). Some domestication traits, such as seasonality controls, have evolved in parallel across many species on the basis of the same genetic and developmental mechanisms; other traits, such as loss of wild-type seed dispersal or changes to seed and fruit size, have been attained through homoplasy based on different genetic and developmental changes. Similarly, in terms of the trajectories of domestication and their cultural causes, we can consider whether these were truly parallel, as is the case for wheat, barley, and Chinese rice, or have converged on similarly domesticated forms through different pathways, as seen for domesticated pulses (Fabaceae) and probably African pearl millet (9, 10).

This paper develops the perspective of domestication as a laboratory to understand evolution in relation to different cultural contexts of domestication. It examines whether instances of early agriculture worldwide converged through very different processes and from different starting points, or were parallel in terms of working from the same behavioral and botanical materials. We offer an updated review on the archaeobotany of plant domestication, including key processes for both plant and cultural evolution. For the purposes of this paper we will use the term “cultivation” to refer to a group of behaviors aimed at modifying soil environments and the management of the plants that grow in them. “Domestication” will be restricted to phenotypic

Significance

Agriculture was a transformative development in the history of human societies and natural environments and drove the evolution of new domesticated species. Crop plants are the predominant domesticated species in most agricultural systems and are an essential component in all the food production systems that underpinned the development of urban societies. Archaeological plant remains provide a range of insights into the processes by which plants were domesticated in different parts of the world. The present paper provides a unique synthesis of evidence, including quantitative evidence on the trajectory and rate of domestication in seed crops and patterns in the development of tropical vegetatively propagated crops.
changes in cultivars that make them different from unmanaged wild populations. Such phenotypic changes necessarily increase gradually at a population level, and therefore form a process, or an episode (which may take centuries or millennia) (2, 11). While selection on crops continues to occur and is behind vari-etal improvement and crop diversification, we interpret the “domestication episode” as the period in which key domestication syndrome traits underwent directional change and approached fixation within cultivated populations; these traits are now normally shared among all populations of a specific crop. “Agriculture” represents systems of land use in which cultivation behaviors became dominant, with domesticated species often the major cultivated taxa, and which took place at a large enough scale to become the primary economic activity of past populations. In this sense domestication emerges following a period of predomestication cultivation (12), with agriculture an outcome of both cultivation and domestication.

**Advances in the Archaeobotany of Plant Domestication**

Archaeobotany consists of the recovery and study of plant remains from archaeological sites. Although methods of recovery and analysis have improved, there has also been an increase in the number of sites and species studied and a broadening range of geographical regions subject to analysis (7, 9, 13–16). Along with botanical field studies of wild relatives of crops, this has led to recognition of a larger number of centers of agricultural origins, perhaps more than 20 (1, 8). For a number of crops, it is now becoming possible to compare domestication processes across species and geographical centers, thus allowing us to characterize similarities and differences. The present paper makes explicit comparisons of seed crop domestication and vegicultural domestication processes from several regions.

Cereal crops are at the core of many agricultural systems and the seeds are highly visible in the archaeological record, thus, lend themselves to quantitative studies on domestication. Methodological advances in identification criteria for crop subspecies and cereal varieties (e.g., refs. 16 and 17). Whereas the morphological distinction between wild and domesticated cereals has long been recognized (18), it is only in the last decade that substantial quantities of preserved remains have become available from Southwest Asia (7, 19, 20) and from Asian rice (21). In the New World, important pseudocereals, such as Chenopodium spp., have seen increased attention in terms of seed coat traits that relate to germination inhibition, an important target of selection during domestication (9, 15). In a wide range of taxa, metrical traits of seed size or phytolith size can be compared over time.

Where vegiculture was the focus of food production, poor preservation has made domestication traits harder to document. Advances have been made, however, in the study of phytoliths and starches, most notably of tuber crops, as well as evidence of landscape modification (22, 23). In the Neotropics, the field has been revolutionized by microfossil evidence of domesticated crops that precede, in some cases by many millennia, empirical evidence for established agricultural practices (22, 24). Additional inferences have relied on cross-examining geoarchaeological, genetic, and botanical evidence, suggesting, for example, the influence of cultivation practices on the development of varietal differences of manioc (Manihot esculenta) (25). In New Guinea, early human-managed habitats have been inferred. For instance, early agriculture based on the vegetative propagation of plants, including bananas, taro, and some yams, has been dated to 7000–6400 B.P. based on archaeological remains of former cultivation plots on old land surfaces, dramatic degradation of montane rainforest to grasslands, and microbotanical evidence for high frequencies of crop plants (26, 27). Plant micromeres have also recently allowed recognition of palm (sago) starch consumption in tropical South China (28) and Borneo (23).

Where evidence for the presence of morphological domesticates is available alongside regional environmental modification, it appears that agriculture succeeds the establishment of domesticated crops. In early Neolithic Europe, archaeobotanical evidence for the presence of domesticated cereals in archaeological sites precedes palynological indicators of forest reduction and increases in arable pollen indicators (29). Early European and Anatolian weed floras and N\(^{15}\) isotope data from cereal grains indicate that these first crops were manured, suggesting intensively managed, small-scale fields, or grain “gardens” (30). The earliest preserved field systems for rice cultivation in China, ca. 6000 B.P., indicate small individual fields less than 2 m in diameter which allowed the careful management of soil and water conditions (31). As in Europe, regional deforestation in China proceeds gradually after this period (32). In the millet-dominated area of northern China, forest reduction occurred from 5000 B.P., millennia after domesticated millet production was widespread (33), whereas deforestation of the South Indian hills is evident around 3500 B.P., centuries after the first village-farming cultures (34).

Similar delays in agricultural systems are evident in the New World. In the Eastern Woodlands of North America, morphological changes document the domestication of several seed crops by 4500–4000 B.P. (35, 36), although a shift toward these crops over wild nuts only happened after 2,000 y ago (37). In the Balsas region of Mexico, starch and phytoliths indicate the exclusive processing of domesticated maize, without comparable finds of wild teosinte, at 8700 B.P., whereas lake core data in the region indicate landscape modification for slash-and-burn agriculture starting from 7600 B.P. (38, 39). In the Nancoco Valley (northwestern Peru), starch from human teeth indicates the consumption of a range of crops, including introduced domesticates by 8000 B.P.; this is some 2,000 y before evidence for irrigation ditches indicate agricultural landscape modification in...
Comparing Timing and Tempo of Domestication in Seed Crops

The domestication syndrome is likely to differ for various crop plants, according primarily to how they are reproduced (by seed or by cuttings) and according to which plant organ is the target of selection. The best-defined and -studied domestication syndrome is for grain crops, including cereals, pulses, and oilseeds (7, 9). Foremost are the traits selected by harvesting and a crop’s growing reliance on humans for seed dispersal, including the loss of natural seed dispersal mechanisms. Second, there are traits related to the more friable soil conditions within tilled fields, leading to the deeper burial of seeds. The increase in seed size seen in most crops is hypothesized to aid seedling establishment, including from deeper burial (1, 7, 9), and is the most widely documented change in archaeobotanical evidence. Another key change is the loss of germination inhibition, in which germination occurs shortly after planting; this is regarded as the key domestication trait of pseudocereals like Chenopodium (7, 15, 35) and many pulses (9). For some taxa this is visible in preserved seed coat structure.

Nonshattering is often taken as a sine qua non of domesticated seed crops, making these species dependent on humans for reproduction by planting (1, 18, 19). In cereals this difference can be documented by the preserved abscission scar on the base of spikelets or rachis segments. Domestication in terms of this trait took at least 2,000–2,500 y (Fig. 2). Grain size change is more gradual over the same period as the shift from shattering (wild-type) to nonshattering seed dispersal (Fig. 2). After the episode of domestication, grain size becomes variable, fluctuating both up and down, suggesting processes of varietal differentiation and local adaptation; however, by the time of diversification, directional selection of the domestication episode is complete. Nonshattering becomes fixed at ~100% in wheat and barley, whereas percentages as low as 70% are returned from archaeological rice populations, due to the persistence of weedy rices as a major contaminant of fields. Fig. 3 summarizes the variation in domestication rates and inferred coefficients of selection across 15 taxa and 18 traits (Tables S1–S4).

Evolutionary change in nonshattering is generally faster than grain size change, especially when measured in terms of haldanes (H). A haldane represents a change of one SD of a trait value per generation (11). For emmer wheat (Triticum dicoccum), the low estimate of H (Fig. 3) may be due to the relatively limited sample size available, as expanded datasets for Triticum monococcum and Hordeum vulgare have increased the estimates of rate somewhat over those made previously from a smaller dataset (11). Compared with reported phenotypic evolution rates in wild plant and animal studies that average around 0.03 H, our range of phenotypic evolution rates in domestication traits are generally similar. These rates of phenotypic change can be used to estimate the coefficient of selection, namely, the average increase per generation in gene(s) for a trait, which ranges from 0.0007 for nonshattering in T. dicoccum to ~0.1 in T. monococcum and H. vulgare.

Rates of phenotypic change for nonshattering were often one or two orders of magnitude greater than for grain size (Fig. 3), although this was still a protracted process. In the case of pearl millet (Pennisetum glaucum), domesticated in West Africa, chaff impressions in early Malian pottery indicate nonshattering types predominated by 4000 B.P., suggesting a preceding domestication episode of at least 1,000–2,000 y (10). In the case of maize (Zea mays), phytoliths indicative of nonshattering and absence of wild teosinte (Zea mays parviglumis) in the Rio Balsas region of Mexico at 8700 B.P. suggest that the domestication process and evolution of nonshattering occurred earlier (39). However, a sequence of evidence tracking the transition from nonshattering to shattering, or grain size changes, during this period is not yet available. For other cereals (various millets), archaeological evidence for nonshattering is similarly elusive. Remains of sorghum (Sorghum bicolor) from sites in the eastern Sahara indicate the consumption of wild (shattering) forms from 10000 to 5500 B.P. (42, 43), whereas the first domesticated forms are only documented following the crop’s introduction to India after 4000 B.P. (44). This suggests that domestication took place in Africa between 6000 and 4000 B.P., but hard evidence for the process is lacking. Widespread use of cultivars suggests they had evolved by 8000–7500 B.P. for north Chinese millets (45, 46) and before 4500 B.P. for some Indian millets (44).

A more widely documented domestication trait in seed crops is increased seed size (2, 47). Most seeds increase by 20–60% in one or two dimensions, mainly thickness or breadth (Figs. S1 and S4).
tication. In some starchy fruits, reduction of seeds correlates with initial domestication that took place by 11000 B.P.

...difference in grain thickness between modern wild and domesticated millet...reported thickness changes in some millets, including a 72% increase in peas. At the upper end are...2,000–6150 | (Echinochloa crus-galli (Echinochloa crus-galli) (Fig. 3). Showing a significant size increase in Ecuadorean assemblages (>40%) over the Early Holocene (53), but with a low H (1 × 10^{-3}). A more rapid increase (1 × 10^{-4} H) is associated with an initial domestication that took place by 11000 B.P.

Seed size increase may not always be an indicator of domestication. In some starchy fruits, reduction of seeds correlates with increase in starch content, as was clearly the case in the development of domesticated bananas (Musa cv.s) (54). In some cases, regional selection trajectories have been divergent. For example, breadfruit (Artocarpus altilis) has been selected for seedless cultivars with larger fruits (consumed for edible pulp), as well as seeded cultivars in which seeds are eaten. The degree of seediness decreases eastwards and away from the New Guinea region (55).

Comparing Timing of Domestication in Vegeticultural Crops

It has generally been thought that vegetative reproduction made the domestication of tuberous plants possible through piece-meal replication of the characteristics of parent clones followed by selection and multiplication of useful phenotypic variations arising in planted stock (e.g., larger and smooth-skinned tubers, or less toxic/bitter forms). Unlike domesticated seed crops, some vegetative crops are not dependent on human efforts to reproduce and spread (23). However, sexual reproduction cycles and cooptation of volunteer wild seedlings provide an important source of genetic diversity and local adaptations in at least some tubers (56). Indeed, it is clear that domesticated forms have been genetically altered from their wild progenitors on the basis of differing functional traits, such as those relating to toxicity, as well as on evidence for genetic bottlenecks between cultivars and wild relatives (57). Although increase in tuber size may be expected to correlate with an increase in the size of individual parenchyma cells, archaeologically recovered tuber fragments tend to preserve few morphological attributes more relevant to phenotypic change. However, some research suggests that micromotains such as starch grains have increased in size with tuber domestication (14, 58) and banana phytoliths have increased in size between diploid and triploid cultivars (59). Notwithstanding, compared with seed crops, it is harder to document archaeologically phenotypic changes in crops that are vegetatively propagated, such as tubers and some fruits, e.g., banana, grape, and olive (60, 61).

In some cases, cultivation practices may induce phenotypic alteration without genotypic change. Larger tubers develop in years planted in loosed, plowed, or tilled soil as opposed to harder, unprepared soils (62, 63). Thus some tuber crops could be cultivated for long periods without undergoing morphological domestication. Recent work on SSR molecular markers of live germplasm of Ipomoea batatas (64) and Manihot esculenta (65) permit disentangling complex histories of domestication. The latter study provides support for the argument (25) that one of the two manioc macro varieties (sweet manioc, the lower starch yielder that is less resistant to pests and poor soils) was domesticated earlier than bitter manioc (which grows well on poor soils, is resistant to pests, and yields more starch). The selection most likely reflects an initial selection of plants in dump heaps with subsequent cultivation and range expansion. Subsequently in Amazonia, detoxification and cultivation techniques were innovated and led to the relaxation of selective pressures against cyanogenic glucosides to the point where a more toxic, but high starch-yielder evolved (66). Recent research has identified traits that facilitate vegetative propagation of cropped manioc, such as pronounced parenchymatous swellings at the nodes leading to brittle stems that can be readily broken for replanting, are absent in wild relatives (67).

Although it is not possible yet to provide quantitative data on domestication rates for vegetatively reproduced crops, we can provide comparisons of some general trajectories. In both New Guinea and Central/South America, evidence for consumption of starchy plants has been found back to the start of the Holocene or into the Pleistocene, whereas pollen evidence indicates human-disturbed forests, often including intentional burning (22, 24, 27, 68). This indicates human management of the landscape, within which some plants could be encouraged and planted. Artificial cultivation mounds in New Guinea (26, 27) suggest cultivation of tubers by the Mid-Holocene (7000–6400 B.P.), whereas microfossils beyond the range of the wild species, as well as dedicated lithic tools for cultivation and processing of roots, suggest tuber cultivation in Central and South America by 7000 B.P. (22, 24). In New Guinea, agricultural dependence and...
intensification of production can be suggested from 5000 to 3500 B.P., with ditched fields, wooden spades, and probable sedentism (68). A similar timing is suggested for the introduction of rice and possible spread of banana in Southeast Asia (28, 69). In northern South America, sedentism associated with tuber crops and other cultivars (squashes, fruit trees, and maize) dates to the Mid-Holocene in different regions (70). These data suggest a shift from initial management of forest gaps and edges, where gap-colonizing species were exploited for food, to the creation of patches of food plants through planting. Vicariance induced by deliberate diffusion beyond the range of the wild species before the adoption of dedicated agricultural practices, along with the formalization of systematic plots where selection pressures and genetic isolation from wild populations increased, both played a role in the trajectories of domestication of vegecultural crops.

Trajectories to Agriculture: Parallelism and Convergence in Cultural Evolution

The morphological changes of domestication are only one aspect of documenting the origins of agriculture. A domestication episode can be regarded as providing a species-specific time scale against which evidence for cultivation and management practices can be charted to reveal the interplay of human action and domestication. Although the evolution of domestication traits tends to increase the efficiency of harvests and yields, it also requires adjustments in human activities. Some of these may be characterized as labor traps, such as the additional requirement of threshing and winnowing as nonshattering rose to dominance, or the need to add nutrients to soils as erect crop growth habits packed more plants into the same units of soil, or the relocation of plots following nutrient depletion of soils (2). Thus, over the course of domestication there would have been fluctuations toward efficiency alternating with increased labor demands, but with an overall direction toward increasing yields and intensification of cultivation activities.

Taken at a comparative global level, the long-term impact of agricultural origins has been to support denser human populations through intensification of land use (5), including sedentism and fostering a greater reliance on a limited range of domesticated food stuffs. Although this represents convergence at a global level, the different domestication processes that can be documented across crops suggest that we should also look for multiple cultural patterns of agricultural origins, for example, in terms of the mobility of past societies and nature of crop reproduction.

Pristine domestications of crops have often occurred within mobile societies, which might include either hunter–gatherers or noncultivating pastoralists. In the case of vegecultural origins, both in New Guinea and Central/Amazon, sedentism dates back only 4,000–5,000 y, long after the earliest inferred cultivation in these regions. Similarly seed crop cultivation of maize in Mesoamerica precedes settled villages by ~5,000 y. In northern China, settled village farmers of millets date from at least 6500 B.P., whereas millet exploitation occurred by 9500 B.P., with clear cultivation by 8000 B.P. (45, 71). Both maize and Chinese millet cultivation correlate with periods of climatic amelioration in the Early Holocene (39, 46). In the case of the Old World, the creation of domesticated millet domestications, mobile gatherer–pastoralists with domesticated ungulates entered the Sahel of western Africa and then cultivated millet, whereas in peninsular India seasonally mobile herder–hunters precede sedentism or crops (44). In these cases of Mid-Holocene grain domestication, there was climatic aridification shortly before evidence for cultivation, including desertification processes of the Sahara or savannah expansion in South India (10, 44). In eastern North America, cultivation began seasonally mobile Late Archaic hunter–fisher–gatherers ca. 5000 B.P. (15, 35). Among the key factors suggested for domestication by mobile groups are risk avoidance and seasonal conflicts in resource availability, leading to cultivation to make such resources readily available when seasonally needed (44, 72) or to buffer risks in wild food availability (46, 73).

Although sedentism based on agricultural economies was to become universal, only in a few instances is there possible evidence for sedentary foragers involved in the initial cultivation of crops. In China’s Yangtze Valley, substantial settlements at ~8000 B.P. indicate sedentism before morphological domestication of rice and alongside early cultivation (31, 32). In Southwest Asia, the Late Pleistocene Natufian culture is often regarded as sedentary or nearly so, by 13,500 y ago, and a precursor of the cultivating villages during the Pre-Pottery Neolithic from ca. 11500 B.P. (74). Although the extent of year-round sedentism at villages focused on farming can be queried (74), it is nevertheless the case that architecturally permanent sites became increasingly important for cultivation, storage, and consumption of early crops like wheats and barley. Early cultivation by the Jomon of Japan was in the context of sedentism (48). The adoption of crops in the Nanchoc Valley of northwestern Peru after 9000 B.P. is associated with sedentism (76). In these cases, pressure on resources and the need to support growing, and sedentary, populations are often considered part of the explanation of the origins of cultivation (77).

Conclusion

Agriculture is increasingly recognized as the coalescence of human activities and genetically transformed species that extends the widespread proclivity of Homo sapiens for niche construction (4–6) into a more intensive coevolutionary relationship that enhances the fitness, population size, and density of both humans and their crop plants. The pathways to agriculture were prolong episodes of coevolution, genetic adaptations on the part of the plants, and cultural shifts and innovations on the part of people. These processes demand long-term and interregional comparative study. For seed crops, domestication trajectories are increasingly documented by quantitative patterns in archaeological plant assemblages, whereas for vegeculture only some general outlines have begun to emerge. The development of cultivation among mobile forager societies focusing on tubers as well as seeds indicates some parallelism across the seed crop and vegetative crop divide, whereas sedentary collectors turned cultivators was a less common development. In terms of cultural history, the domestication of wild plant species has been a process of convergence from different regional, environmental, and economic starting points.

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Supporting Information

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SI Text

Methods. Documenting the evolution of domestication traits requires data that can be related to past populations and changes over time. In archaeobotany this has focused predominantly on metrical traits, such as seed size, and percentage presence of qualitative traits, such as shattering or nonshattering spikelet bases in cereals. By aggregating such data by assemblage (an archaeological approximation of a population) and plotting these against an estimate of time (provided by archaeological chronology and aggregated radiocarbon dates), it is possible to document degrees of change and the timelines of change for a specific trait in a crop.

Modeling Chronologies. The date of assemblages was converted to a point estimate of age based on the median of calibrated radiocarbon dates, as described in Fuller et al. (1). By this method all available dates for a site or phase were summed with OxCal 3.10 (2), using the IntCal09 calibration curve (3). If a very strong modal peak was evident in the resulting calibration image this age was taken visually; otherwise, the median of the 1-sigma probability distribution was used. For most Southwest Asian sites, calibration information can be found in the supplementary material of Asouti and Fuller (4). Additional dates used were recalibrated for the present study. If radiocarbon dates were not available then the age was either interpolated between later and earlier dates in the same sequence, or the median of the estimated date range provided in the publications was used.

Domestication episodes were determined from empirical data, with assemblage averages plotted against time (Fig. 2 and Figs. S1–S3). A domestication episode was taken as a near-linear change in a morphological trait against time, whether a percentage trait, such as percentage nonshattering, or a metrical trait. After the episode, the change in trait leveled off and in some cases fluctuated slightly and unpredictably, and was especially evident in grain size traits (Fig. 2 and Figs. S1 and S2). In the case of nonshattering in Near Eastern cereals, this appears to level off near fixation (~100%), whereas in rice this leveled off at 70–85%. This is indicated by comparable levels in later Neolithic assemblages both within and beyond the likely region of wild populations and the indigenous domestication process (Fig. 2 and Table S1). In the case of grain size, it appears that the most marked change, and one that is directional occurred early, and in the case of rice, barley, einkorn, and emmer, clearly is mostly coincident with the period of increasing frequencies of nonshattering. There have been cases of size change subsequent to this but usually within some regional populations of a crop only, and these are regarded as evolution of postdomestication improvement traits, as defined by Purugganan and Fuller (5). There is currently no grain metrical evidence for maize of comparable age to the earliest phytolith evidence.

Rates of change were calculated by two methods.

Calculation of Percent Change. First a simple percent change was determined between the latest (or largest average trait value) and the earliest in the domestication episode. This was then divided by the number of years covered by the domestication episode. This rate is similar to that of the darwin unit in which the log of the difference in averages is divided by 1 My (6, 7).

Calculation of Haldanes. To better take into account variation at the population level, we calculated haldanes (H), borrowed from evolutionary biology (6, 7). This provides a unit by which change in metrical traits, like grain size, can be compared with change in percentage occurrence traits, like nonshattering. Previous estimates assumed a fixed domestication episode period of 4,000 y, or 2,000 y for some legume species (1, 6). The present study not only includes datasets that relate to the domestication process but also archaeobotanical evidence from periods that date long after the evidence for the beginnings of domestication. By including later periods we are able to see long periods in which traits did not change in a consistent or directional manner. By comparing plots of such data, it is possible to infer periods in which change was most rapid and directional, i.e., episodes of domestication. During these periods, directional change approximates a linear regression of a trait’s value (percentage or measurement) against time. Therefore, instead of assuming an arbitrary time period for domestication, the episode of domestication has been taken visually from a plot of the data, and then the domestication rate estimated for this period by the best-fitting linear regression of x/s (where x is the trait frequency and s is the pooled standard deviation) against time since the start of the domestication episode. Haldanes are taken as the slope of this regression, whereas the $r^2$ value (coefficient of determination) provides a goodness of fit measure.

Where SDs were not available from original sources, they have been estimated on the basis of the maximum and minimum, and sample sizes on the basis of Pearson and Hartley’s table 27 in ref. 8.

One concern with the use of haldanes for percentage data are that percentage traits, such as nonshattering, represent frequency-dependent selection, which is expected to be sigmoidal. Values of ~0% or ~100% should artifically exaggerate the predicted rate, as the sigmoidal curve will by asymptotic near these values. Thus, we have removed such values from the calculations of rate of change.

Rates of Domestication. Table S1 summarizes the results of the domestication rate calculations, which form the basis of Fig. 3. Subsequent sections and figures summarize the datasets for each species and trait, and list sources of data additional to those summarized in Purugganan and Fuller (6). Nonshattering data are presented first, followed by cereal grain size, pulse seed size, and other traits.

The robustness of these calculations was explored by removing individual sites and assemblages from the calculations and by combining and dividing the overall dataset for some species. In most cases this made little difference to the calculated rate or the regression $r^2$ value. For those species in which the domestication episode is less clear, e.g., phytoliths from Cucurbita, grain size in Oryza sativa subsp. indica, some alternative estimates are included in Fig. 3 and Table S1, indicating longer or shorter episodes. Most grain size changes were represented by a single metric (either width or breadth) for each species, as calculated haldane rates were found to be similar (6, 9). In some cases, such as Helianthus annus, where rates were rather more divergent between seed length and breadth changes, both were included in the table.

The one case in which rates varied considerably on the basis of which sites were included was nonshattering in Hordeum vulgare (barley), currently the most extensively documented case of nonshattering evolution in cereals. The dataset is potentially large enough to separate a southern Levantine barley domestication episode from a northern Levant and northern Fertile Crescent episode, which are separated in Table S1, as well as combined dataset (included in Figs. 2 and 3. The highest rates
are for nonshattering in einkorn wheat and barley. We explored the effects of removing or including individual data points on rates. For example, inclusion of the very large sample from Netiv Hagdud (n = 3,277), for which there is no reported uncertainty (10), leads to an inflated rate for barley nonshattering. The inclusion of this site greatly increases haldane estimates, from 0.1 to 0.44. The lower rate excluding this dataset comes closer to the upper estimates of other taxa. Inclusion of this site puts excessive weight on a value of ~0.1.

Selection coefficients (s) are estimated following the method of Kinnison and Hendry (11). The selection coefficient for a trait, s, is given as haldane rate/h², where h² is the trait heritability. Trait heritability was taken from a few published estimates that are available. For nonshattering, trait heritability was estimated at h² = 0.4 in a cross between wild Oryza rufipogon and cultivated O. sativa (12), although Peleg et al. (13) estimated h² = 0.66 in emmer wheat. We have therefore taken 0.6 as the h² estimate for all cereal nonshattering traits in Table S1 and Fig. 3C. The heritabilities of grain size have been measured for barley (h² > 0.88) (14). Seed mass in Helianthus, Pisum, and Triticum, which should be correlated to seed size, has h² estimates ranging from 0.75 to 0.99 (15), so we have retained h² = 0.9 (12) for grains or seed size in general (Table S1 and Fig. 3C). Heritability of rice bulbiform phytolith form was estimated as h² = 0.55 (16), and we have used the same estimate for Cucurbita scoloped phytoliths. Future research should aim to achieve better estimates of heritability and its variation across species and phenotypic characters. Nevertheless, our estimated selection coefficients fit well within the range of those reported across evolutionary studies (17), and generally they are slightly higher than the previous estimates of Purugganan and Fuller (6).

**Nonshattering (Fig. 2, Upper and Table S2)**

**Barley (H. vulgare) Nonshattering.** The barley rachis dataset has been expanded from that presented earlier (1, 6) with additional data (18–20). It can be viewed as suggesting a separate trajectory to nonshattering in the southern Levant and in the northern Fertile Crescent, with the latter starting earlier and taking longer and the former starting just before 9000 B.C. For the purpose of estimating rates, these data have been combined into a single estimate of haldanes, with the exception of sites with 100% nonshattering, one case of an early pure domesticated assemblage which had a small samples size, and sites with ~0% nonshattering, including Tell Mureybit and Netiv Hagdud. The data that contributed to the H = haldane rate calculation are indicated with an asterisk in Table S2.

**Einkorn (Triticum monococcum) Nonshattering.** The einkorn rachis dataset has been expanded from that presented earlier (1, 6) with additional data from Tanno and Willcox (18). Excluded from the haldane calculation are data from Dederiyeh (ca. 11000 B.C.), Jerf el Ahmar and Dja’de (both 0% nonshattering), El Kown (100% nonshattering), and Kosuk Shamali (ca. 5500 B.C.). The data that contributed to the H = haldane rate calculation are indicated with an asterisk in Table S2.

**Emmer (Triticum dicoccum) Nonshattering.** Emmer data on nonshattering has been taken from Tanno and Willcox (18) and remains a fairly limited dataset. Earlier, entirely wild assemblages come from Netiv Hagdud and el-Hemneh (10, 14). The dataset for haldane estimation is given in Table S2.

**Rice (O. sativa subsp. japonica) Nonshattering.** Rice nonshattering rachis data includes three phases of Tianluoshan (21) (Table S2), a preliminary dataset from Caoxieshan (Table S2), and a combined dataset from Maoshan (Liangzhu period) (22) and Liangzhu (21). The earliest data point is from Kuahuqiao in which only wild and nonwild were originally distinguished (23), among which immature were not separated from domesticated types following criteria in ref. 21. The component includes estimated percentages for Kuahuqiao, a combined Maoshan dataset (of all site subphases), and preliminary Caoxieshan data. Gray dots (Fig. 2), not included in rate estimate, are from northern Chinese sites with data, which represent a secondary dispersal of domesticated rice (24, 25). Error bars represent SD calculated directly from multiple samples from each site (Fig. 2). The data that contributed to the H = haldane rate calculation are indicated with an asterisk in Table S2.

**Grain Size (Fig. 2, Lower and Table S3)**

**Barley Grain Size.** Barley grain metrics were gathered from Southwest Asia and southeastern Europe through the Neolithic and later. Data from Purugganan and Fuller (6) has been augmented (26–29). Both breadth and thickness of grains change in a comparable pattern, so only thickness has been taken as representative of grain size change. The domestication episode compared with postdomestication size is illustrated in Fig. 2.

**Einkorn Grain Size.** For einkorn grain size we compiled data from Southwest Asia and southeastern Europe from the Pre-Pottery Neolithic period up to the Iron Age. From these data the period of directional grain size increase can be seen as restricted to the Pre-Pottery Neolithic period, as illustrated in Fig. 2. Data in Purugganan and Fuller (6) has been augmented (26, 27, 30–34).

**Emmer Grain Size.** For emmer grain size we compiled data from Southwest Asia and southeastern Europe from the Pre-Pottery Neolithic period up to the Iron Age. From these data the period of directional grain size increase can be seen as restricted to the Pre-Pottery Neolithic period, as illustrated in Fig. 2. Data in Purugganan and Fuller (6) has been augmented (26, 27, 33–38).

**O. sativa subsp. japonica Grain Size.** Subspecies japonica grain size data are taken from the Lower Yangtze region. It has been augmented from Fuller et al. (24) with new sites by Gao (22). Primary sources cited in Fuller et al. (24) are not repeated here. These data and the inferred domestication episode are illustrated in Fig. 2.

**O. sativa subsp. indica Grain Size.** Indian rice grain size data are from Fuller et al. (24) with additional data from Senuwar (39). In the case of Senuwar, sizes have been estimated from grain populations from scaled photographs. These are presumed to represent early subspecies indica rice, or in the case of the earliest sites, proto-indica before nuclear genome gene flow from introduced domesticated indica (24). A short and long episode of grain size increase has been considered from comparison (Fig. S1).

**Pennisetum glaucum Grain Size.** For pearl millet we have used the same data as ref. 6.

**Vigna radiata Seed Size.** For mungbean we have used the same data as in refs. 6 and 40 for southern India only, but we visually determined a domestication episode for the rate calculation (indicated with an asterisk in Table S3). The domestication episode is inferred for the period of ~1650 to 1100 B.C.

**Lens culinaris Seed Size.** Lentil seed size data were compiled from the Pre-Pottery Neolithic up to the Bronze Age of Southwest Asia, Cyprus, and southeastern Europe. Data from ref. 6 have been augmented (26, 30, 31, 33, 41–55). An episode of increase in seed size is evident through most of the Pre-Pottery Neolithic of Southwest Asia (Fig. S1).
Glycine max Seed Size. Soybean data are taken from Lee et al. (56), and only considered from northern or central China. An episode of seed size increase can be traced from the Late Yangshao through the Bronze Age (Fig. S1).

Pisum sativum Seed Size. Pea size data are compiled from Southwest Asia and southeastern Europe from the Pre-Pottery Neolithic. Data from ref. 6 have been augmented (26, 30, 31, 33, 41–55). There are difficulties in interpreting current pea size data, as size appears to decline in the Mid-Holocene in Europe to sizes below even what is expected of wild populations. The possible presence of wild populations or temperate adaptations involving small seed size must be considered. Nevertheless, focusing on early Southwest Asian finds, there does appear to be a trend for seed size increase. The short domestication episode (Fig. S1, square), takes data only from Mureybet, Çayönü, Aswad, and Jericho, whereas a longer episode has also been calculated (Fig. S1, squares and red circles). A few data points have been excluded from the calculations as outliers or because they lacked information on variation around the mean.

Cicer arietinum Seed Size. Chickpea data are rather scarce, but such as are available from Southwest Asia and southeastern Europe have been collated from various sources (37, 47, 54–64). Thickness appears the most diagnostic measurement for domestication. Specimens recovered from Tell Ghoraifé are notably small and have been excluded from the calculation of domestication rate (Fig. S1).

Iva annua Achene Size. I. annua measurements have been collected from a number of sites (65–71). Achenes measurements are reported as corrected to account for change due to carbonization, and this correction factor has been retained. When the domestication process began is unclear, but we have used the Koster Late Middle Archaic assemblage (stratigraphic levels 7-6) as representative of wild size range before evolution of larger-seeded forms (Fig. S2).

H. annus Achene Size. For sunflowers we have attempted to use only raw, uncorrected measurements (65, 66, 72–75). Although the data include some achenes and some inner kernals (without correction between them), there has been little effect on the overall shape of the data over time. Both length and width have been considered as these provide somewhat different rate estimates for the same episode between ca. 3000 and 1000 B.C. (Fig. S2).

Cucumis melo Seed Size. This dataset is that of Purugganan and Fuller (6). The rate of change in seed width and seed length was comparable. In this study, shorter domestication episode is inferred to take place from the later Liangzhu period between 2500 and 1900 B.C. The haldane calculation based on seed length includes sites indicated with an asterisk in Table S3.

Cucurbita pepo Seed Size. The data for C. pepo seed size change is that from Guila Naquitz in Mesoamerica (76). This is an extremely small sample but may, nevertheless, be used to suggest a rate until better data become available. Whereas the Guila Naquitz B and C seed assemblages can be dated on the basis of a number of accelerator mass spectrometry (AMS)—radiocarbon dates, the date of Guila Naquitz D is estimated. These data are tabulated in Table S3.

Chenopodium berlanderi Seed Size and Testa Thickness. In the case of testa thickness in North American C. berlanderi, we have taken into account whether or not populations of later periods represent the crop or an inferred weed, as Gremillion has demonstrated that weedy Chenopodium with thick seed coats co-occurs in thin-testa crops (77). Several sources provided data (67, 74, 77–80). Although it appears that a least some domesticated-type, thin-testa specimens date to the early second millennium B.C., with direct AMS–radiocarbon dates (69, 74), we lack large measured assemblages of this period or of earlier wild assemblages. Therefore the episode considered here relies on larger and some later assemblages (Fig. S2). Although this provides a satisfactory estimate, the rate of change in this trait may be the result of an earlier process involved in the domestication.

Seed diameter has also been considered for C. berlanderi (74, 77–80). We have removed inferred weedy populations from consideration as these have smaller, wild-type seeds (76). Seed diameter data are in Table S3 and plotted illustrating the domestication episode in Fig. S2.

Phytolith Size Change

O. sativa subsp. japonica Bulliform Phytolith Size. Bulliform phytoliths from rice leaves appear to increase in size (Fig. S1) over the same period as grain size increases and nonshattering becomes dominant in the rice assemblages of the Lower Yangtze region (81). Although it is not yet clear whether or not this represents a morphological and genetic adaptation related to rice domestication, the timing makes it worth considering. There is evidence for a significant genetic component to bulliform morphology (16). The data of bulliform size is taken from Zheng et al. (82, 83). These data are included at the base of Table S3.

Cucurbita ecuadorensis Rind Phytolith Size. Early Cucurbita phytoliths from the Las Vegas culture of Ecuador provide evidence for early domesticated squashes (84, 85). Large phytoliths correlated in modern samples with larger seeds and fruits. This phytoliths are consistent in form with C. ecuadorensis, which is considered native to this part of South America; although, it is also possible, especially for later periods that samples also include the introduced Cucurbita moschata. The earliest large phytoliths considered domesticated, at ~80 μm, occur at site M5 A4-67 at an undated level that occurs immediately above a level dated ca. 10800 B.C. (which is the median of a wide probability distribution). The earlier level dated ca. 10800 B.C. has smaller phytoliths that would match wild size, and thus the beginnings of cultivation and the domestication process can only be inferred to sometime after this date, ca. 10800 B.C. In addition, larger phytoliths at ~90 μm occur by 7000 B.C. which could represent continued evolution of larger fruits as well as the introduction of some larger-fruited C. moschata. At Las Vegas site OGSE-80, a significant increase in the size of phytoliths from the fruit rinds of Cucurbita (probably C. ecuadorensis, which is native to the region) takes place (table 7 in ref. 84). In summary, these data have been interpreted as indicating some domestication perhaps by ca. 10000 B.C. and certainly by ca. 8000 B.C. (86), with the start of cultivation still undated. Although size trends may be complicated by the addition of a second Cucurbita species in later periods, the clear directionality of size change is suggestive of an evolutionary process for which a rate can be estimated.

As there is a wide range of variation, the SDS are larger and this tends to lead to depressed haldane rates, even if the rate of change in terms of percentage of the mean overlaps with that found in other taxa and traits. Both thickness and length of phytoliths show similar temporal trends of increase. Although dates are largely estimations, a short episode has been calculated for the earliest levels of M5 A4-67 (Fig. S3). A longer episode from that site takes the trend up in time to when size increase stops, at ~7200 B.C. (Fig. S3). Similarly, a rate can be calculated from site 80 data (Fig. S3). Data are listed in Table S4.


Fig. S1. Plots of archaeological seed size against time for Old World crops, including soybean (G. max), lentil (L. culinaris), chickpea (C. arietinum), pea (P. sativum), and rice (O. sativa) from northern India, as well as rice bulliform phytoliths from the Lower Yangtze. Each archaeological population is plotted as an average and SD against the estimated median age for the site or site phase. These charts differentiate the inferred domestication episodes used for calculating rates of evolution (results in Table S1 and Fig. 3). Data used can be found in Table S3.
Fig. S2. Plots of archaeological seed size against time for New World crops, including sumpweed (*I. annua*), Mesoamerican squash (*C. pepo*), sunflower (*H. annus*) length and breadth, pitseed goosefoot (*C. berlanderi*), as well as pitseed goosefoot testa thickness. Each archaeological population is plotted as an average and standard deviation against estimated median age for the site or site-phase. These charts differentiate the inferred domestication episodes used for calculating rates of evolution (results in Table S1 and Fig. 3). Data used can be found in Table S3.
Fig. S3. Plots of archaeological *Cucurbita* phytolith size from sites Las Vegas OGSSE-80 and M5 A4-67 in Ecuador (Upper Left and Upper Right). Samples means and SDs are plots against a median estimate of age for the stratigraphic sample. For site M5 A4-67, short and long episodes of morphological change are indicated (Lower Left and Lower Right). In the lower row calculated haldane rates are graphed for the short and long episodes based on the data from site M5 A4-67. Data used can be found in Table S4.

Other Supporting Information Files

Table S1 (DOCX)
Table S2 (DOCX)
Table S3 (DOCX)
Table S4 (DOCX)