

The Domestication Process and Domestication Rate in Rice: Spikelet bases from the Lower Yangtze

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The process of rice domestication occurred in the Lower Yangtze region of Zhejiang, China between 6900 and 6600 years ago. Archaeobotanical evidence from the site of Tianluoshan shows that the proportion of nonshattering, domesticated, rice (*Oryza sativa*) spikelet bases increased over this period from 27% to 39%. Over the same period rice remains increased from 8% to 24% of all plant remains suggesting an increased consumption relative to wild gathered foods. In addition, an assemblage of annual grasses, sedges and other herbaceous plants indicates the presence of arable weeds typical of cultivated rice that also increased over this period.

The domestication of staple cereal crops represents the major economic and ecological transition that human societies made during the Holocene (1). A key change in domestication of cereals, resulting from cultivation, was the loss of natural seed dispersal resulting in domesticated cereals with dependence on humans (2, 3). Direct evidence for the evolution of this trait in wheat and barley in southwest Asia suggests that this process was slower than earlier hypothesized (3, 4, 5). Rice has been less well-documented, but, archaeological finds of rice grains and phytoliths indicate that it was an early crop in the Lower and Middle Yangtze region of China (6, 7).

Tianluoshan is a Neolithic site of the local Hemudu Neolithic culture in Zhejiang Province, China (Fig. 1). Tianluoshan is 2 to 3 meters above present day sea-level with a high below-ground water table that has preserved botanical remains in some contexts, along with charred remains throughout the site. Excavations between 2004 and 2007 revealed preserved wooden posts, boat paddles, wooden and bone tools, characteristic pottery and ground-stone axes, animals and fish remains as well as well-preserved plant remains (8). In total 23,615 plant remains were identified from 24 systematically sieved samples, in addition to more than 12,000 hand-picked remains. More than 50 species were identified; mainly acorns (including *Lithocarpus* and *Cyclobalanopsis* types), *Trapa* water chestnuts, *Euryale ferox* and rice. Probable storage pits retained acorns (*Quercus*

sensu lato and *Lithocarpus*), water chestnuts (*Trapa natans sensu lato*), foxnuts (*Euryale ferox*) and several other edible fruit remains and seeds. One area of excavation (K3) had preserved distinct lenses of rice husks, acorn shells, *Trapa* shells and persimmon seeds (*Diospyros* sp.).

Significant quantities of rice spikelet bases, as well as a range of small seeds of wild species, which may plausibly represent the arable weeds of rice cultivation, were recovered during the systematic sorting of sediment samples. Rice increased as a percentage of the total remains from sieved samples from 8% to 18% to 24% (Fig. 2). These phases were dated by direct AMS radiocarbon dates on nuts and rice grains (Fig. S1) indicating a sequence for the plant samples between ~6900 and 6600 years ago, and divided into three periods (K3-level 7, Layers 8-7, Layers 6-5). These data suggest that rice increased in dietary importance through time. The increase in the proportion of rice supports the hypothesis that people became increasingly reliant on rice cultivation, and gradually abandoned wild resources, such as acorns and *Trapa* water chestnuts.

Distinctions between wild and domestic rice are made through observations of the spikelet bases which show key morphological differences (9-12), although in archaeological specimens this distinction can be complicated if immature specimens were harvested. We classified spikelet bases on the basis of a comparative study of spikelet bases in 140 modern populations (see SOM text). In domesticated rice panicles are non-shattering, which allows most grains on the plant to reach maturity before being harvested. Spikelets are then separated through threshing which causes the uneven breakage at the spikelet base as well as the tearing of vascular strands resulting in a larger and more irregular pore (Fig. 3A). In addition, domesticated spikelet bases can be identified by their uneven profile, dimpled appearance and less symmetrical scars (10), whereas wild-type rice spikelets typically have a straight profile at their bases and shattering results in a smooth and round abscission scar and small distinct vascular pore (Fig. 3B). Rice harvested before maturity is expected to have protruding vascular bundles from the remnant of the attached rachilla (the fine stalk that attaches grains to the rice plant)(Fig. 3C), although this pattern is encountered in some modern domesticated varieties. To minimize the possibility of overestimating the proportion of domesticates, we classified seeds with rachilla remnants as immature.

On the basis of the above criteria, 2,641 archaeological spikelet bases from Tianluoshan were divided into three categories: wild (Fig. 3E, H), domestic (Fig. 3D, G), and immature (Figure 3F, I); all three were found in all samples. When calculated by temporal period, the proportions change over time in favor of domesticated types which increase from 27.4% to 38.8% over ~300 years, while both wild and immature types decrease (see Fig. S2). To test for statistical significance, we treated each sampled context with 25 or more spikelet bases as an independent sample, allowing a mean and standard deviation to be calculated for the percentage of domesticated, wild and immature types (Fig. 4). These findings were supported by a comparison with a later domesticated population, a single sample (n=147) available from nearby Liangzhu (ca. 4200 BP), a quasi-urban centre of a culture known for stone plough tips and sickles (13). Our observed domesticated types may be an under-estimate, since some immature types may be domesticated (see SOM text). But this is likely to be slight since wild harvests should be biased towards immature types, as inferred from grain morphometrics (13, 14).

Through the three temporal phases at Tianluoshan there is a significant increase in average proportion of domesticated types ($p=0.0048$). This trend toward an increasing proportion of domesticated types through time implies that rice was under cultivation at this time and that domestication traits were under selection. However, as predicted from other lines of evidence from the region (13, 14) a substantial proportion of the rice crop may have been harvested while still immature to minimize wild-type grain loss due to shattering. We also observed many small and flattened rice grains, characteristic of highly immature spikelets, present amongst larger, mature grain types at Tianluoshan.

Additional support for rice cultivation at Tianluoshan is provided by the accompanying species, which include many likely arable weeds. Temporal increases in domesticated rice spikelet bases were accompanied by increases in both the overall proportion of rice and these weedy taxa (Fig. 2). These include well known wet-field rice weeds such as sedges, *Scirpus* spp., *Cyperus* spp., *Juncellus* spp., *Eleocharis* sp., rushes (*Juncus* spp.), and weedy annual grasses (*Echinochloa* sp., *Eragrostis* sp., *Isachne globosa*, *Festuca* sp., *Panicum* sp., *Setaria* sp.). Several dicotyledonous weeds were also found but with less frequency. All these species are present today as weeds in rice paddy fields (15-17).

Our data suggest that rice domestication culminated after the mid Seventh Millennium BP. This is consistent with the findings of a recent reanalysis of shifts in grain and phytolith size (3, 13, 14). The beginnings of the domestication process, however, remain unclear. Early rice cultivation in China was initially a supplementary resource alongside wild nuts (14). Cultivation had certainly begun by 8000-7700 BP as indicated by archaeobotanical evidence including domestic type spikelet bases found at Kuahuqiao (12). Pollen and micro-charcoal data suggest that cultivation at Kuahuqiao involved water management and clearance through burning (18).

Our data suggest that rice domestication was comparable in process to that of wheat and barley, in that the non-shattering phenotypes gradually became fixed in cultivated populations over at least two or three millennia (3, 4). Despite significantly higher cross-pollination rates in wild rice (19) compared with self-pollinating wheat and barley (20), pollination systems may not have had an appreciable impact on the rate of domestication. Instead the presence of sympatric populations of both wild and domesticated cereals may have dampened selection for domestication (21).

Genetic studies show a deep divergence between *indica* and *japonica* rice (22, 23), and it is possible that India paralleled the Chinese domestication (24). However, shared alleles (25 - 27) suggest that the domesticated Indian forms resulted from hybridization as domestic rice dispersed from China into South Asia. Additionally the spread of rice to Southeast Asia derived from rice domesticated in the Yangtze (1). These new data from Tianluoshan therefore would constrain the time frame for dispersal until some centuries after ca. 6600 BP.

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Figure Captions

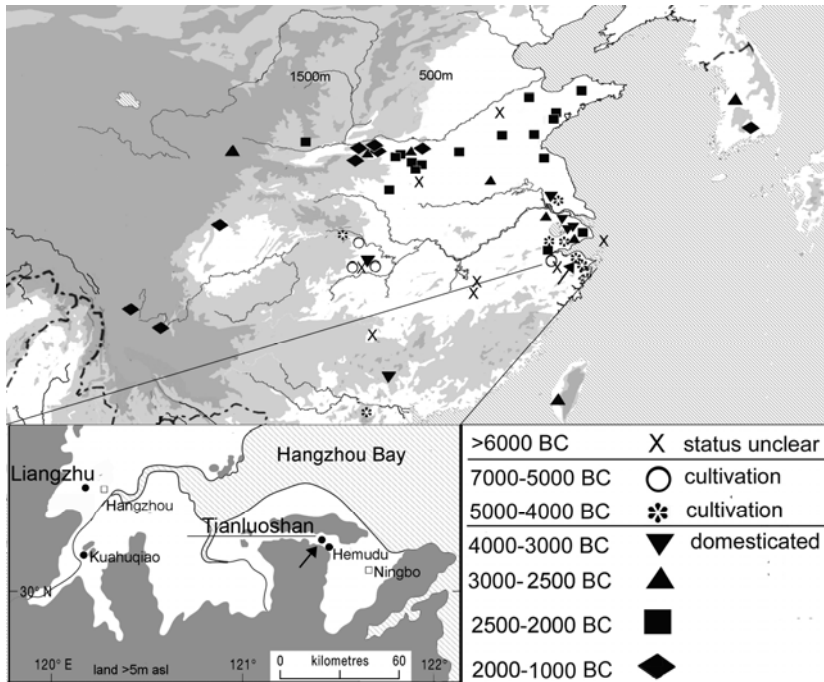


Fig. 1. Map of representative early rice finds in China, with arrow indicating Tianluoshan, with an inset of local region of Tianluoshan and Liangzhu.

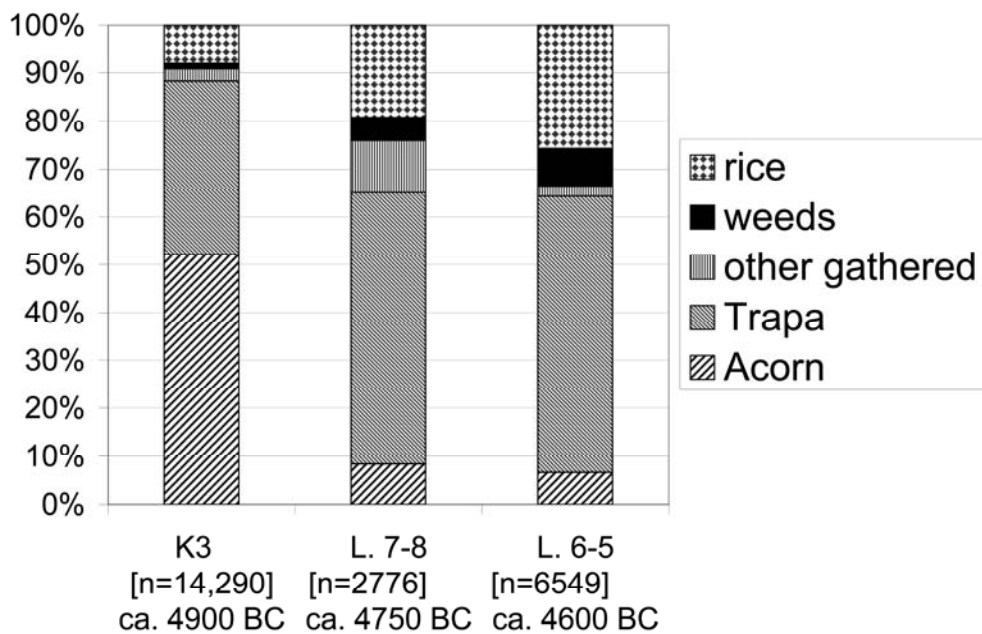


Fig. 2. Proportion of plant remains from sieved samples from the three periods, indicating percentages of rice, probable weeds of rice, acorns, *Trapa* water chestnuts and other gathered fruits/nuts .

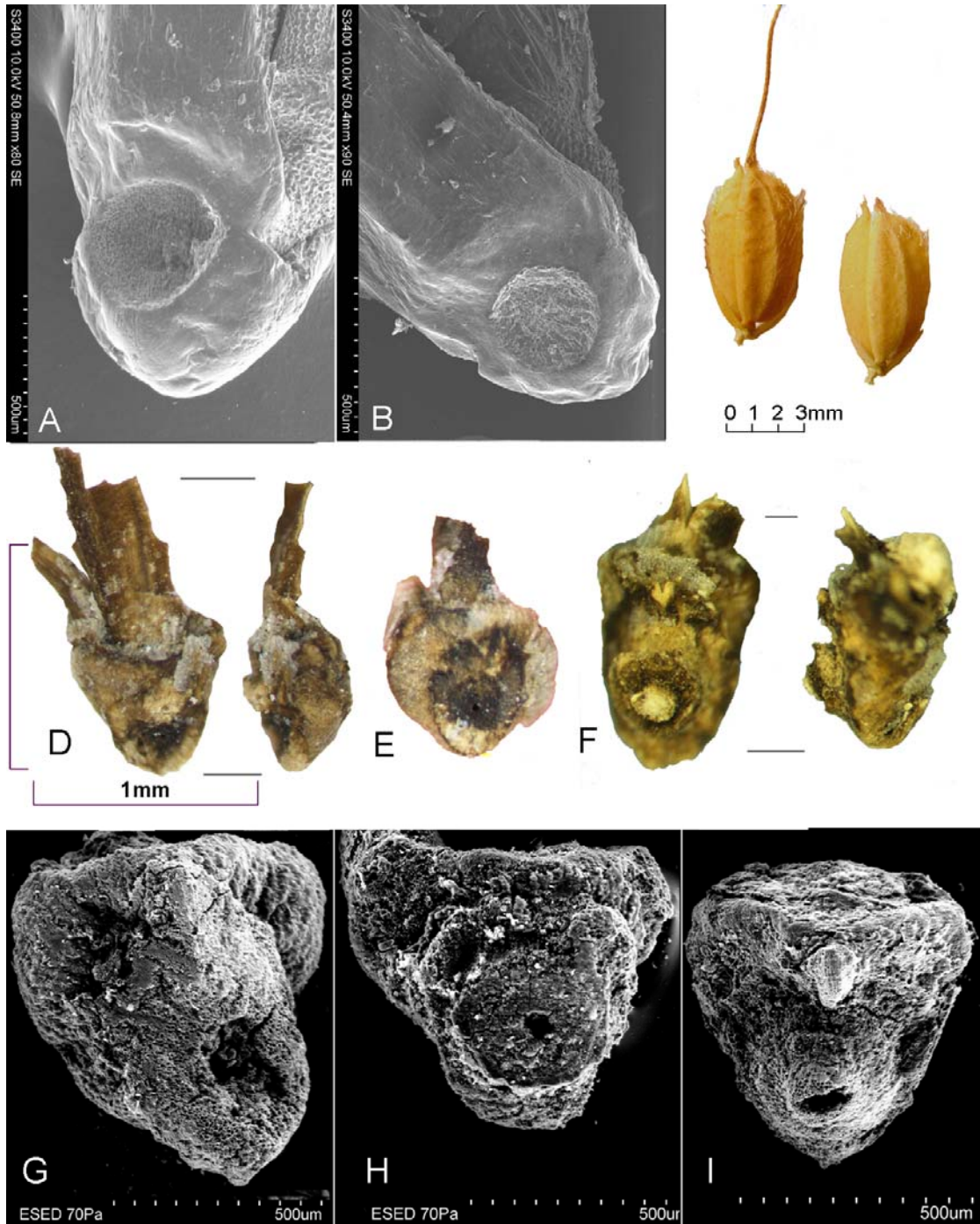


Fig. 3. Examples of modern and archaeological rice spikelet base abscission scars. A. Modern *Oryza sativa* subsp. *japonica*. B. Modern *Oryza rufipogon*. C. Immature harvested *Oryza sativa*. D. Domesticated type spikelet base (front and profile), waterlogged, from Tianluoshan K3 (7). E. Wild type, waterlogged, from Tianluoshan K3(7). F. Immature type (front and profile) from Tianluoshan K3 (7). G. SEM of domesticated type, charred, from Tianluoshan H28. H. SEM of wild type, charred, from Tianluoshan H28. I. SEM of immature type, charred, from Tianluoshan H28.

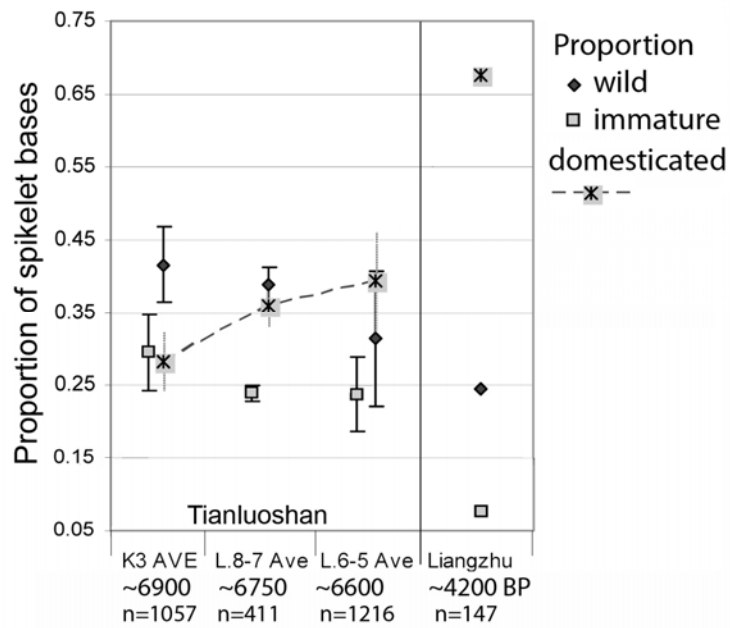


Fig. 4. Proportions of wild, immature and domesticated rice spikelet bases from three sequential periods at Tianluoshan, with later Liangzhu for comparison. Means and standard deviations are shown for the Tianluoshan periods, on the basis of all samples of 25 or more spikelet bases.

Supplementary Information for The Domestication Process and Domestication Rate in Rice: Spikelet bases from the Lower Yangzte

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Materials and Methods

Chronometric Data

Radiocarbon dates were performed with accelerator mass spectrometry using a National Electrostatics (NEC) 0.5 MV 1.5SDH-1 accelerator mass spectrometry (AMS) system with 40-sample MC-SNICS ion source at Peking University(Beijing), as described in (S1). Approximate ages (Fig. S1) were calculated using the computer program OxCal 3.10 (S2), on the basis of near modal values of tree-ring calibrated ages with a Bayesian statistical model of the most probable ages as calculated on the basis of stratigraphic ordering

Sampling

We collected over 200 sediment samples including 2L of bulk sediment from the lenses of waterlogged plant remains in trench K3 (2006) and from all excavation units and contexts in the 2006-07 excavations.. Our analysis was performed on a subset of 24 samples drawn from across the main strata of excavation, including pit fills and occupation layers and the K3 midden contexts. Samples were wet-sieved through mesh sizes of 2mm, 0.9mm, 0.45mm and 0.28 mm. Fractions larger than 2mm were hand sorted in their entirety, while smaller fractions, 0.9, 0.45 and 0.28 mm, were sub-sampled in recorded volumes and sorted under a 10x - 40x. binocular stereomicroscope, model XTB-01, manufactured by Guilin Guiguang Instrument company (Guangxi Province, China), Selected specimens were examined further and photographed with a Nikon SMZ1000 microscope with a Nikon DS-5M-L1 digital camera. Further selected specimens were imaged with a Hitachi 3400 Variable Pressure Scanning Electron Microscope. Identified seeds, fruit and rice chaff were counted and standardized across samples on the basis of the measured volume of sediment sieved and sorted. Because K3 is the only intact midden context that was excavated, the total quantities of remains from this context are not entirely comparable to those from pit fills and other layers of the main

settlement area. Thus the low count of rice and rice weeds in the first period may be partly due to formation processes, which may have biased the preserved lenses of midden towards by-products of acorns and *Trapa* processing. We interpret the K3 lenses as the results of periodic/seasonal bulk-processing events, whereas the dispersed remains in Layers 8 through 5 were mainly the by-products of routine, small-scale domestic processing events. Nuts could have been leached of tannins in bulk in the shell, as suggested by acorn pits, and then deshelled in bulk. Rice is more likely to have been dehusked in domestic contexts on a routine basis as needed. Nevertheless the ubiquitous presence of rice and weeds throughout the midden (even if in lower density), and the recurrence of small acorn nut shell fragments, and *Trapa* fragments in later layers indicates that the absence of later midden deposits does not bias entirely against the presence of these or other wild taxa. In particular, in Layers 8-7 acorns and *Euryale* are more frequent than in Layers 6-5, although the context types are the same. That relative frequency data is indicative of long-term trends in the use of taxa is also indicated by calculations of ubiquity (the percentage of samples in which a species is present), a measure less prone to quantitative biases between taxa. Based on sieved samples acorns are nearly ubiquitous in U3 and Layers 8-7 (100% of samples), but decline to 50% of samples in Layers 6-5. Wild *Euryale* shows a similar trend, dropping from 100% to 63% to 57%. By contrast *Trapa* and rice show consistently high levels, including 100% of samples from Layers 6-5.

Rice Spikelet Base Morphology

Rice spikelet bases were separated into four categories: (1) wild, (2) immature/domesticated, (3) domesticated, and (4) indeterminate/poorly preserved. These categories were designated by study of a reference collection which included spikelet bases from 53 populations of domesticated rice accessions, representing East, Southeast and South Asia as well as 87 populations of wild species (currently in the UCL reference collection- <http://www.ucl.ac.uk/archaeology/facilities/laboratories/science.htm>). This collection was augmented by experimentally harvested immature rice near Kyoto, Japan and provides ethnographic observations of rice harvesting in rural Henan Province, China.

The condition of a protruding rachilla is typical of immature harvested spikelets observed in experimental and ethnographic studies. This morphological characteristic rarely occurs in mature grains of domesticated rice. Nevertheless, this morphotype is present in 18 (33%) of the domesticated populations, and in those populations normally accounts for 1-5% of individuals spikelets. The presence of this immature type rarely occurs in frequencies greater than 30%, noted in just two populations including a modern population from Zhejiang. Protruding rachillae appear to be more frequent in modern cultivars in regions where machine harvesting is normally practiced, such as Zhejiang and Japan. Because this category may include domesticated or wild forms harvested when immature, we have recorded it separately from the next category.

Domestication scars are typically vertically asymmetric rather than round, deeply recessed rather than flat, and often have wide and irregular or elongate holes where the vasculature has torn; concurring with previous studies (S5, S6). These features are absent in reference collection specimens from wild populations, suggesting such types are extremely rare in the wild. Domesticated-type attachments are typical of later

archaeological rice spikelet bases from the Late Neolithic of China (Longshan, 4500-1900 BP) (S7) and Early Historic Southern India (S8), as well as west African domesticated rice (S9) or Yayoi Japan (S10). Our three category classification (plus indeterminate) differs from that of one previous study (S11), which lumped immature types into the domesticated category, and thus may result in an over estimate of the proportion of domesticated rice.

Theoretically we expect harvests of domesticated rice to include proportions of wild-type spikelet bases due to the presence of weedy rice (*Oryza spontanea*) in ancient fields. Regular introgression between these and planted crops would have maintained a small proportion of morphologically wild rice in harvested crops. Although accurate experimental data on this is needed, our comparison with later archaeological cultures, such as Liangzhu, suggest that wild morphotypes should not exceed 25% of populations dominated by domesticated cultivars. This represents a likely upper limit of the wild proportion once the domestication process was completed.

Quantification of spikelet bases

From a total of 2727 spikelet bases, 2641 were classified as immature, domesticated or wild. After removing samples with fewer than 25 spikelet bases, an analysis of variance within each of the phases was performed by treating each set of remains as a replicate sample of the period. The analyzed sample sizes were as follows: Period 1 (K3), 6 samples (n=1057, including 14 indeterminate); Period 2 (Layer 8-7), 5 samples (n=411, including 14 indeterminate); Period 3 (Layers 6-5), 6 samples (n= 1216, including 58 indeterminate). For each of these periods a mean and standard deviation was calculated for the percentage of wild, domesticated and immature grains, as shown in Fig. 4. The percentages for each of the three categories, classed by period, were then subjected to a one-way ANOVA test to assess if there were significant changes in composition over time. The increase in the mean percentage of domestic types was significant at the $p=0.005$ level. The change in the mean percentage of wild types, was also significant ($p=0.0392$). The change in immature percentage was not significant ($p=0.067$). The differences in mean percentages of domesticated type was 11%, which over 300 years represents a change of 0.037% per year. Calculating the total change in proportions per period (Fig. S2) results in a similar estimated change of 0.038% per year.

We also estimated the likely upper limit of domesticated types in a given assemblage to account for the fact that there may be some domesticated rice amongst the protruding immature/domestic types. We expect wild harvests to be biased towards immature types, as discussed in (13, 14). In wild rice, spikelets are shed by abscission as they come into maturity during a period of several days (~2 weeks), and these mature wild spikelets would fall into the mud and be difficult to gather. Therefore, in order to obtain grains, collectors of wild rice need to harvest while many spikelets are still immature. Stands of plants may have continued to be targeted somewhat immature even when they were composed of a mixture of morphologically wild and domesticated individuals. Counts of domesticated types represent only a minimal estimate of true proportion of domesticates. By excluding immature types and calculating the proportion of definitely (mature) wild and domesticated spikelet bases, we obtain a ratio that implies that immature types are split between wild and domesticated genotypes proportionate to the mature types. Since wild harvests should be biased towards wild immature types this

percentage should be regarded as an overestimate, or an upper limit of domesticates. On the basis of the total dataset from Tianluoshan, this domesticated upper limit would be 38% for Period 1 (K3), 47% for Period 2 (L.8-7) and 51% for Period 3 (L.6-5). The true proportion of domesticated rice presumably falls between this upper limit and the observed percentage of mature domesticated spikelet bases illustrated in Figures 4 and S2.

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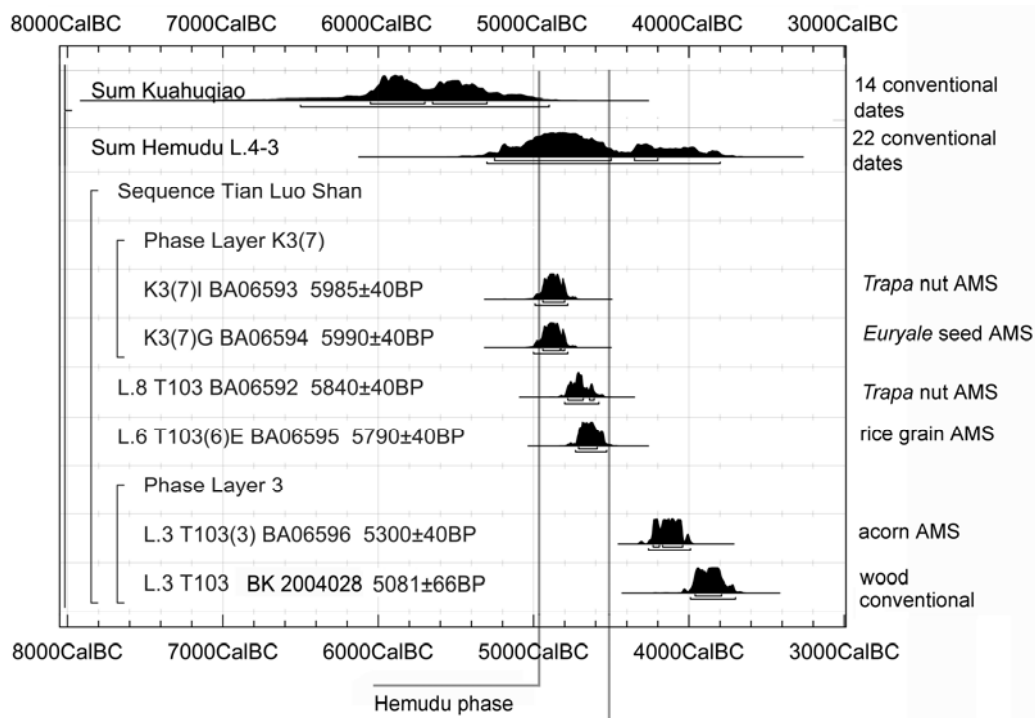


Fig. S1. Sequence of AMS radiocarbon dates for periodization of Tianluoshan archaeobotanical information, showing the probability distribution of calibrated age for each date. All dates on individual specimen of species are indicated at right. At the top of the chart the sums of radiocarbon dates from the sites of Kuahuqiao and Hemudu are indicated for comparison (S3, S4).

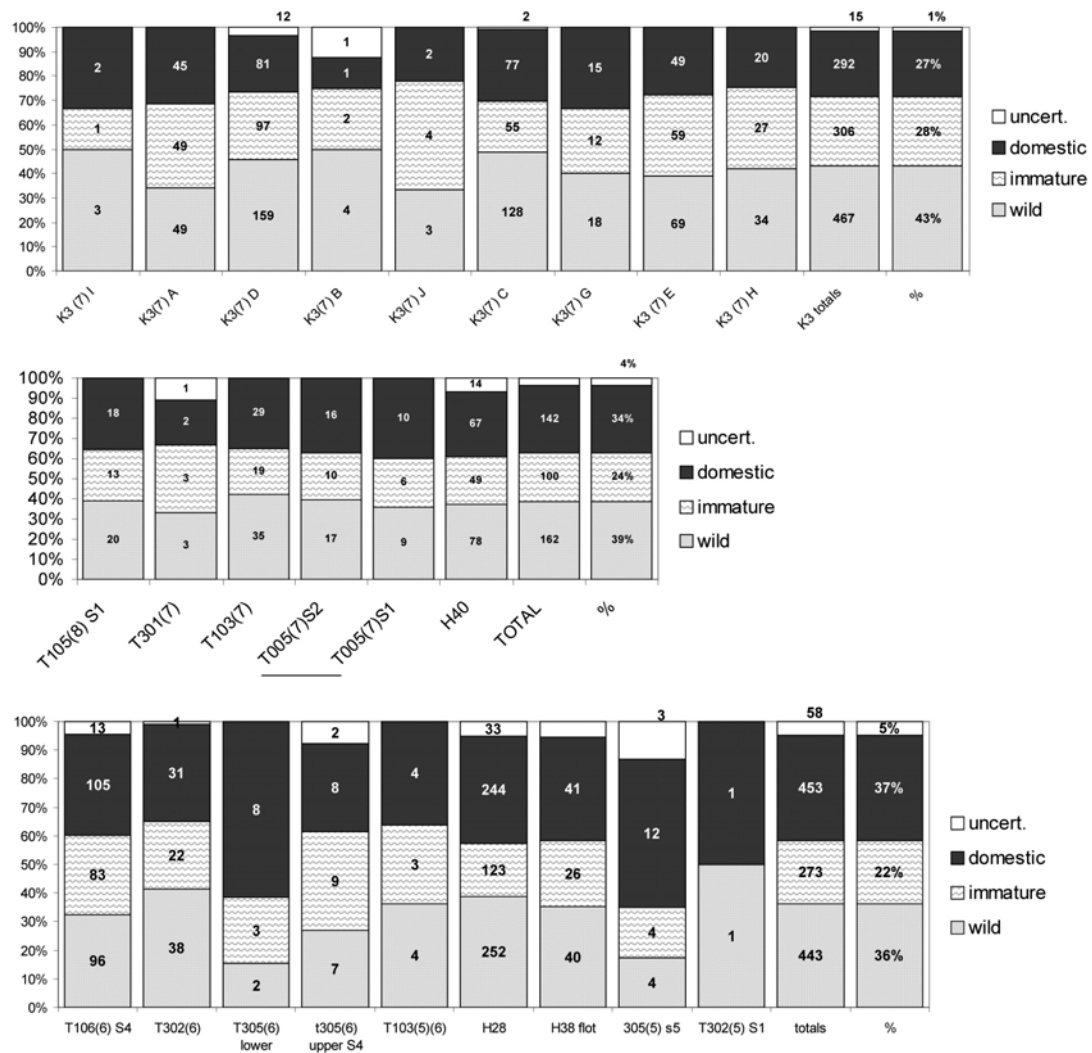


Fig. S2. Proportions of rice spikelet base types in individual samples. Numbers indicate actual counts. In this figure early K3(7) samples, top, are compared to Layers 8-7 of the main excavation area (middle) and Layers 6-5 from the main excavation area (bottom)

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