The virtues of small grain size: potential pathways to a distinguishing feature of Asian wheats

Xinyi Liu^{a*}, Diane L. Lister^b, Zhijun Zhao^c, Richard A. Staff^d, Penelope J. Jones^b, Liping Zhou^e, Anil K. Pokharia^f, Cameron A. Petrie^b, Anubha Pathak^g, Hongliang Lu^h, Giedre Motuzaite Matuzeviciuteⁱ Jennifer Bates^b, Thomas K. Pilgram^a and Martin K. Jones^b

Liu XY, Lister DL, Zhao Z, Staff RA, Jones P, Zhou L, Pokharia AK, Petrie CA, Pathak A, Lu H, Motuzaite Matuzeviciute G, Bates J, Lu H, Pilgram TK and Jones MK (2016) The virtues of small grain size: potential pathways to a distinguishing feature of Asian wheats. *Quaternary International*, doi:10.1016/j.quaint.2016.02.059.

^a Department of Anthropology, Washington University in St. Louis, One Brookings Drive, St. Louis, MO 63130, USA

^b McDonald Institute for Archaeological Research, University of Cambridge, Downing Street, Cambridge, CB2 3ER, UK

^c Institute of Archaeology, Chinese Academy of Social Sciences, 27 Wangfujing Street, Beijing, 100710, China

^d Research Laboratory for Archaeology and the History of Art, University of Oxford, South Parks Road, Oxford, OX1 3QY, UK

^e Laboratory for Earth Surface Processes, Department of Geography, Peking University, 5 Yiheyuan Road, Beijing, 100871, China

^f Birbal Sahni Institute of Palaeobotany, 53 University Road, Lucknow 226007, U.P., India

^g Smt. C. H. M. College, Mumbai University, CST Road, Mumbai, Maharashtra 400098, India

^h Department of Archaeology, Sichuan University, 29 Wangjiang Road, Chengdu, 610064, China

ⁱDepartment of Archaeology, Vilnius University, Universiteto 7, Vilnius 01513, Lithuania

^{*}Corresponding author. E-mail address: liuxinyi@wustl.edu (X. Liu)

Abstract

Increase in grain/seed size recurrently features as a key element in the 'domestication syndrome' of plants (*cf.* Zohary and Hopf 2000; Fuller *et al.* 2014). In the context of its spread across Eurasia, however, the grain size of one of the world's major crop species underwent a substantial reduction. Between the fifth and second millennia BC, the grain length in a number of species of *Triticum*, collectively known as free-threshing wheat, decreased by around 30%. In order to understand and help account for this trend, we have obtained direct radiocarbon measurements from 51 charred wheat grains and measured the dimensions of several hundred grains from Asia to establish when and where that size diminution occurred.

Our results indicate that the pace of a eastward/southward spread was interrupted around 1800 BC on the borders of the distinct culinary zone recognized by Fuller and Rowlands (2011), but regained pace around 200-300 years later in central-east China with a diminished grain size. We interpret this as evidence of a period of active crop selection to suit culinary needs, and consider whether it constitutes a distinct episode in the general character of genetic intervention in domesticated species.

Key words

wheat, grain size, domestication, radiocarbon dating

1. Introduction

Recent developments in archaeobotanical research have shed fresh light on the processes of plant domestication and agricultural origins. Among domestication traits expressed in various crop species, two have received much scholarly attention, non-shattering cereal ears and seed/grain size (*cf.* Zohary *et al.* 2000; Fuller *et al.* 2014) . Non-shattering cereal ears have typically been studied in the context of a growing reliance on humans for seed dispersal. The increase in seed/grain size repeatedly observed in crop species is

presumed to increase production yield as well as aid seedling establishment in the context of deeper burial, and is the most widely documented change in archaeobotanical assemblages (*cf.* Purugganan and Fuller 2009; Harlan *et al.* 1973).

In this study, we consider the change in grain size of one of the world's major crops. As free threshing wheat spread eastward from a Southwest Asian region of origin, that change can be seen on several archaeological sites. However, in contrast to the classic domestication trajectory, the grains as they spread eastward became not larger, but smaller.

There has been an increase in scholarly interest in the nature and pathways of the eastward spread of wheat and barley (Jin, 2007; Li et al., 2007; Zhao, 2009; Flad et al., 2010; Frachetti et al., 2010; Zhao, 2011; Betts et al., 2013; Dodson et al., 2013; Barton and An, 2014; Liu et al., 2014; Spengler et al., 2014a). In light of these studies, and in order to understand the variation of wheat grain size in the context of food globalisation, we have directly radiocarbon dated 51 charred wheat grains and measured the dimensions of several hundred grains from China, India and Pakistan to establish when and where that size diminution occurred. By "direct radiocarbon dating" we mean that the wheat grains themselves have been analyzed rather than dating distinct organic items from the same contexts.

We will address two issues in this paper. Firstly, we will consider the pace of an eastward/southward spread. Secondly, we will attempt to understand the nature of the reduction in grain size, and consider whether it constitutes a distinct episode of human choice that drives changes in domesticated species.

2. Spread of wheat

It is now clear that by late prehistory a series of connections between human populations had been established across Eurasia. From the evidence of early horse management, metallurgy and a range of associated artifacts, we may trace the origins of these

connections in the latter part of the second millennium BC (Levine, 1999; Mei, 2003; Sherratt, 2005; Linduff and Mei, 2009; Rawson, 2013). Archaeobotanical evidence from cereal crops has the potential to push this date back yet further into at least the third millennium BC or even earlier, when exchanges between the various sectors of Eurasia have been documented. This process has been referred as 'food globalisation in prehistory' (*cf.* Jones *et al.* 2011; Liu and Jones 2014; Jones *et al.* in press) or the 'trans-Eurasian exchanges of crops' (Boivin et al., 2012). During the course of the third and second millennia BC, some of the crops that originated in the Fertile Crescent spread from southwest Asia to eastern China.

By *c*.1500 BC, the geographical range of one of the southwest Asian crops, free threshing wheat, extended from the Pacific to the Atlantic Ocean. In the context of early Chinese wheat, Zhao (2009) suggested three candidates for a trans-Asian route. One was a proto-Silk Route – essentially the topographically most convenient and economic land route between East and West. The second drew from discussions of shared traditions of pastoralism, horse management and metallurgical traditions and was characterized as the northern steppe route. The third related to the near-coastal position of some of the earliest wheat appearing in the east, raising the possibility of a sea route. These three potential routes presented a set of initial hypotheses that have stimulated useful discussion around the issue of the spread of wheat (Betts *et al.*, 2013; Dodson *et al.*, 2013; Barton and An, 2014; Spengler *et al.*, 2014a). Discussion has now moved beyond the scope of dates and routes, and has addressed such issues as social drivers, the pace of crop movement and dietary conservatism (Lightfoot et al., 2013; Liu and Jones, 2014; Liu et al., 2014; Jones et al., in press).

The pattern of the eastern movement of wheat from southwest Asia has also become clear. Early evidence for cultivation and domestication of various wheat species appears in southwest Asia from at least 8000 BC (*cf.* Weiss and Zohary 2011) . Wheat species (both free threshing and hulled) are documented in western Central Asia around 4000-3000 BC at Jeitun and Anau North (Miller, 2003; Harris, 2010) and in western South Asia by around 5000 BC in Mehgarh (Costantini, 1984; Meadow, 1996; Petrie, 2015).

After these initial dispersals, the subsequent, more extensive movement of different types of wheat appears to be restricted to free threshing forms. To the north of the Iranian Plateau, free threshing wheats have been documented in Turkmenistan sites such as Anau South and Gonur Depe around 2000 BC (Moore et al., 1994; Miller, 1999), and Ojakly/1211 around 1500 BC (Spengler *et al.*, 2014a). They appeared in Tajikistan between 3500 - 2000 BC at Sarazm (Spengler and Willcox, 2013), and in Afghanistan at Shortugai 2500-2000 BC (Willcox, 1991), and in Kyrgyzstan at Aigyrzhal-2 around 1800 BC (Motuzaite Matuzeviciute et al., 2015). Records from the south-eastern and eastern parts of the greater Iranian Plateau are even older. For example, free threshing wheat (often in association with hulled wheat) was recovered from Pakistani sites such as Sheri Khan Tarakai, Miri Qalat and Shahi Tump dating back to the fifth/fourth millennium BC (Tengberg, 1998; Desse et al., 2008; Petrie et al., 2010; Thomas and Cartwright, 2010). From there, it is plausible that these crops moved further east and south into the Indus region during the third millennium BC, and subsequently, into the Ganges and South India (Fuller and Madella, 2001; Fuller, 2006; Pokharia, 2011; Pokharia et al., 2011).

Recent research suggests that the 'Inner Asian Mountain Corridor' connecting the mountain territories of the Iranian Plateau and the Pamir Plateau played a key role in the dispersal of free threshing wheat to the east (and broomcorn millet to the west) during the third millennium BC (Frachetti, 2012). Work in eastern Central Asia reveals that both free threshing wheat and broomcorn millet were present from the same archaeological contexts in the middle third millennium BC (Frachetti *et al.*, 2010; Spengler *et al.*, 2014a; Spengler 2015). Currently, the earliest recorded wheat grain in Central Asia is from Tasbas, 4010 ± 30 (radiocarbon years) BP, which calibrates to 2617-2468 cal. BC at the 95.4% probability range (Doumani et al., 2015).

The 'Inner Asian Mountain Corridor' may be extended further eastwards to China along the foothills of the Tianshan Mountains and the Hexi Corridor (i.e. along the northern edge of the Tibetan Plateau), and finds of archaeobotanical wheat are distributed along these mountain ranges. Notwithstanding the debate around some allegedly older specimens (Li and Mo, 2004), recent studies have suggested that free threshing wheat

probably did not appear in northwest China until very late in the third or early in the second millennium BC (Flad *et al.*, 2010; Dodson *et al.*, 2013; Liu *et al.*, 2014). It is worth noting, however, that hexaploid free threshing wheat is also reported from the third millennium BC site of Longshan culture in eastern China (Zhao, 2009). At Zhaojiazhuang in Shandong, for example, a wheat grain has been directly dated to 3905±50 (radiocarbon years) BP, which calibrates to 2562-2209 cal. BC at 95.4% probability (Jin et al., 2008).

3. Variation in grain size

Turning from chronology to plant morphology, Fuller *et al.* (2014) have suggested that most seeds increased by 20-60% in one or two dimensions during the course of domestication. While there may be some variation in the precision and accuracy of the published measurements of early wheat, the following trends are regarded as secure. Emmer wheat, for example, increased in thickness from approximately 1.7mm to more than 2.5mm over a time period of between 9000 and 5000 BC. The breadth of einkorn wheat increased from about 1.2mm to 1.8mm between 10,000 and 6000 BC (Fuller *et al.* 2014, Fig. 2). It is worth noting though that einkorn and emmer measurements are not always reliable because of identification issues. Fuller *et al.* (2014) also noted that after the episode of initial increase, grain size became variable, fluctuating both up and down.

Grain shape and the compactness of the spike are important variables used in the taxonomy of hexaploid wheat (MacKey, 1966) Archaeobotanists have frequently observed a more compact form of wheat grain and chaff in regions east of the Fertile Crescent. For example, a compact form is recorded from Mehrgarh in Pakistan by at least the mid-fifth millennium BC (Costantini, 1984; Zohary and Hopf, 2000) and later in third/second millennium BC sites in the greater Indus and Ganges regions (Weber, 1991; Miller, 1999; Fuller et al., 2008; Pokharia, 2008, 2009; Pokharia et al., 2009; Pokharia, 2011; Pokharia et al., 2011). Compact wheat grains are documented in the third and second millennium BC sites in Central Asia (see Spengler, 2015 for review), such as Anau South, Gonur Depe, Ojakly and 1211 in Turkmenistan (Moore *et al.*, 1994; Miller,

1999; Spengler *et al.*, 2014a), and, notably, Begash and Tasbas in Kazakhstan (Frachetti et al., 2010; Spengler et al., 2014b). In East Asia, Crawford (1992) noted that early wheat grains in China, Japan and Korea are predominantly a hexaploid compact form. These short and rounded wheat grains have been placed in different taxa, including *T. aestivum* subsp. *sphaerococcum*, *T. sphaerococcum*, *T. aestivum* subsp. *compactum* and *T. compactum*. There are also two prehistoric wheats, namely *T. parvicoccum* and *T. antiquorum*, for which it was thought that no modern counterpart has survived. To clarify various issues, it is useful to consider the naming of small-grained wheats that have modern counterparts and the genetic basis of their small grain size.

3.1 Indian shot wheat

Indian shot wheat or dwarf wheat (*T. aestivum* subsp. *sphaerococcum*) is a hexaploid free-threshing wheat currently endemic to southern Pakistan and northwestern India. Today it is a relic crop in this region (Percival, 1921; Mori et al., 2013), yielding poorly in comparison with improved varieties of wheat. The name 'shot' wheat is a reflection of the small, round grains being similar in form to shot-gun pellets. A mutation in a single recessive gene, denoted as 's', is believed to affect many parts of the plant, and this wheat is characterised by having a short dense ear, a rigid short culm (stem), hemispherical glumes, and small, spherical grains (Salina et al., 2000). The precise mutation responsible for the sphaerococcoid features has not been identified, but is thought to be a tandem gene duplication near the centromere in chromosome 3D. The s mutation has been shown to affect a gene that determines the length of the grain, leading to a significant alteration in grain size and shape (Asakura et al., 2011). T. aestivum subsp. sphaerococcum is believed to have originated from a spontaneous mutation in T. aestivum from India or Pakistan (Asakura et al., 2011). A recent study by Kippes et al. (2015) has shown that a spring allele of the vernalization genes VRN4 originated from and is fixed in *T. aestivum* subsp. sphaerococcum in Southern Asia, and is responsible for the first spring wheats in this region. These authors propose that this allele was fixed in prehistory in South Asia (Kippes *et al.* 2015).

3.2 Club wheat

T. aestivum L. subsp. compactum (Host) Mackey, also known as club, dwarf, cluster or hedgehog wheat (Percival, 1921) is rarely cultivated these days, presumably because of its low yield relative to modern T. aestivum cultivars. The ears of this wheat are very short, dense and rigid, with closely packed spikelets. There appears to be a number of genetic loci affecting spike compactness: the compactum (C) locus on chromosome 2D, which in its dominant form results in a compact spike (Johnson et al., 2008); and another locus, distal to the C locus, on chromosome 5AL. The distinguishing feature of T. aestivum L. subsp. compactum is its compact spike. The plants themselves are not necessarily short in stature. The actual identity of the C locus and its mode of action are not yet fully understood. Both of these loci are completely separate from the locus of the gene responsible for the sphaerococcum phenotype.

T. antiquorum (Heer) Udachin and *T. parvicoccum* (Kislev) are both defined from archaeological macrofossils alone, and so no equivalent genetic information is available. Ostwald Heer originally delineated *T. antiquorum* as a variety of *T. compactum* (*Triticum compactum* Host var. *antiquorum* Heer). In both these taxa, macrofossil remains of caryopses, chaff and internode have been recovered. These latter remains retain some physical features for which the genetic control of grain size may be surmised, but this remains entirely speculative for these taxa.

There is some skepticism over whether the actual species of free-threshing wheat can be identified on the basis of the charred grain evidence alone (Nesbitt, 2001). Hillman (2001), for example, warns against creating new species names from such evidence, and suggested that *T. parvicoccum* is most likely a short-grained form of a dense eared *T. turgidum* subsp. *durum*. Free threshing wheat remains from South Asia are often identified as *T. aestivum* subsp. *sphaerococcum* because of their short, compact grains. However, most charred naked wheats from the Near East, Europe and China also have small compact grains of less than 5 mm length, regardless of their species or ploidy (*cf.* Nesbitt 2001) and there has been a great deal of inconsistency in the naming of

archaeobotanical wheats. In light of these concerns, we present in this paper the grain sizes of free-threshing wheat without assigning them to species. This work aims to understand a reduction in size for all free-threshing species in the context of the eastward and southward dispersals of free threshing wheat. The statistical analyses are based on groups of free-threshing wheat from different geographical regions, regardless of their initial archaeobotanical identification.

4. Materials and methods

Fifty-one carbonized grains of wheat from China (n=40), India (n=8), Kyrgyzstan (n=2) and Pakistan (n=1) were selected for radiocarbon (¹⁴C) analyses at several laboratories, including Oxford Radiocarbon Accelerator Unit (ORAU), the Laboratory of Earth Surface Processes and Institute for Heavy Ion Physics, Peking University, Centre for Climate, the Environment, and Chronology, Queen's University Belfast, and Beta-Analytic. The sample preparation methods undertaken at these laboratories were similar, with a standard acid-base-acid (ABA) chemical pre-treatment method followed by combustion and graphitization prior to accelerator mass spectrometry (AMS) dating (Brock et al., 2010). These new radiocarbon determinations were subsequently collated with previously published data and analysed using the Bayesian statistical software OxCal ver. 4.2 (Bronk Ramsey, 2009), applying the IntCal13 calibration curve (Reimer *et al.*, 2013). A summary of these data is presented in Table 1.

In addition, charred grains from 21 archaeological sites from the third, second and first millennia BC from China, India, Pakistan and Kazakhstan were morphometrically measured in two or three dimensions. These measurements are combined with previously published measurements of hexaploid wheat from southwest Asia and west Asia. Archaeobotanical analyses and measurements were undertaken in the George Pitt-Rivers Laboratory, University of Cambridge, the Archaeobotanical Laboratory at the Institute of Archaeology, Beijing, and the Archaeobotany Laboratory at Birbal Sahni Institute of Palaeobotany, Lucknow. A summary of these data is presented in Tables 2 and 3. There are several factors apart from initial grain dimensions that influence the observed

dimension, including crop-processing activities (e.g. sieving) and mode of preservation. While the former is less easy to control, and for this exercise is essentially a source of 'noise', the latter is mitigated by restricted attention to a singular category of preservation (carbonization) such that grain dimensions will tend to be affected in a similar way.

5. Results

5.1 Direct radiocarbon dates

All 51 radiocarbon samples provided good pre-treatment and combustion yields. Table 1 shows the radiocarbon determinations obtained in this study, along with previously published data. Herein, all calibrated radiocarbon data are presented at the 95.4% probability range (which approximates the 2σ range of normally distributed data). The oldest directly measured age in Central Asia is from Tasbas, Kazakhstan (dating to between 2617 and 2468 cal. BC), which is several hundred years older than that from Begash. In the northwestern Chinese provinces, the oldest age is from Xintala in Xinjiang (between 1972 and 1694 cal. BC), Jinchankou in Qinghai (between 1878 and 1664 cal. BC), and Huoshiliang in Gansu (between 2135 and 1896 cal. BC). Karuo (between 1665 and 1518 cal. BC) provides the oldest age for wheat in Tibet. In central China, there are no data at present from earlier than 1650 cal. BC. The oldest ages occur in Nansha (between 1643 and 1504 cal. BC) and Wangchenggang (between 1608 and 1412 cal. BC) in Henan. As indicated above, the oldest age for wheat in eastern China occurs in Zhaojiazhuang, and falls in the third millennium BC. Apart from this one very early date, wheat is not recorded in Shandong until the latter half of the second millennium BC in Daxinzhuang (between 1442 and 1290 cal. BC). The remaining dates in eastern China all fall in the first millennium BC.

Turning to the south of the Himalayan Mountains, the earliest date for free threshing wheat is currently from Tigrana (between 2847 and 2477 cal BC), followed by Ojiyana (between 2456 and 2151 cal BC). Although there is an abundance of radiocarbon dates from Harappa (e.g. Meadow 1996; Weber 2003; Meadow and Kenoyer 2005), as yet,

the oldest directly dated wheat grain from the site is dated to between 1901 and 1743 cal. BC; and was recovered from the later phases of occupation at the site. The earliest age for free threshing wheat from south India is from Sannarachamma, dating between 2016 and 1756 cal. BC (Fuller *et al.*, 2008). There are no direct radiocarbon measurements of wheat grains from the Ganges region at present.

In order to provide more refined estimates of the 'first appearance dates' of wheat within each region, we undertook Bayesian statistical modelling of the collated dataset. All radiocarbon determinations were inserted into a series of sixteen independent 'Phases', representing the sixteen geographical regions identified in Table 1. These sixteen *Phases* were unrelated to each other; i.e. there were no assumptions, a priori, as to the relative ordering of the respective *Phases*. A combination of 'Boundaries' and 'Tau Boundaries' were applied at the 'Start' and 'End' of each of the sixteen model *Phases*, respectively (see Supporting Document, Fig. S1.). This combination of *Boundaries* and Tau Boundaries provides an exponentially decreasing Phase prior, allowing for the bias towards older samples within each *Phase* that results from our research focus on providing the earliest dating wheat grains from each site. The Start *Boundaries* of each *Phase* thus provide the model estimated 'first appearance' date from each of the sixteen regions, and slightly pre-date the earliest individual radiocarbon dated sample from each region. A second, parallel series of six *Phases* representing broader geographical scale regions from which the sixteen more localized geographical regions were located (namely: East Central Asia, northwest (NW) China, southwest (SW) China, central-east (CE) China, Indus/northwest (NW) India and South India) was run within the same OxCal model. By grouping more radiocarbon dated samples within these broader regional *Phases*, the model could produce more precise Start *Boundaries* – i.e. more precise 'first appearance dates' – which allow for more rigorous archaeological interpretation. Finally, an 'Order' function was applied to each of the sixteen Start Boundaries to ascertain a matrix of the most likely relative ordering of the first appearance of wheat from each (smaller scale) region (see Fig. 2). These results confirm a west to east chronological sequence in China and a north to south sequence in South Asia, as indicated by the dates and associated locations shown in Fig. 1.

5.2 Grain measurements

Grain measurements are summarized in Tables 2 and 3. Fig. 3 shows (a) the scattered and (b) the average values of charred grain length and breadth from six regions (desiccated samples excluded): West Asia, Kazakhstan, and NW and CE China, Indus/NW India and Ganges. Fig. 4 (a and b) shows a similar dataset within China. Visual inspection indicates that free threshing wheat grains from CE China are shorter and narrower than those from NW China, West Asia and South Asia. While noting that the number of Kazakh grains measured is small (n=2), they too show a pattern similar to that from CE China. Similar observations have been made by Motuzaite Matuzeviciute *et al.* (2015) from a second millennium BC site in Kyrgyzstan. Within China, grains appeared to have become shorter and narrower while moving from NW China to CE China.

In order to clearly show grain size/shape differences, various forms of statistical analyses have been applied. Desiccated samples from Xinjiang are excluded because of their distinct preservation state; and the Kazakh samples are also excluded because of the small population size (n=2). Analysis of variance (ANOVA) shows that the differences among the four groups were statistically significant for both length and breadth (p<0.001). Therefore, the differences between individual pairs of regions were tested as a follow-up analysis. A statistical test using Tukey's Honest Significant Difference (HSD) shows that the grain lengths were identical for South and West Asia, and that NW China and CE China differed from them, and from each other, at a statistically significant level (see Fig. 5-a). For the measurement of breadth, however, CE China wheat grains were different from all other groups, which otherwise display no significant differences from each other (see Fig. 5-b).

Further analyses indicate the grains from Indus/NW India and Ganges differ from each other in both dimensions, with the grains from the Ganges being shorter and wider (See Supporting Document; Fig. S2); the difference in width is statistically significant (t-test, p=0.005), while the difference in length is not (t-test, p=0.103). Our lack of sufficient

measurement data does not permit us to test the statistical difference between south India and north India. Further studies to consider the difference between those regions are required.

6. Discussion

6.1 Pace of a southward/eastward spread

In the context of food globalisation in prehistory, various authors have drawn attention to the nature and context of the Trans-Eurasian exchange of cereal crops (*cf.* Jones *et al.* 2010). Previous publications provide us with plausible views on the potential pathways of wheat translocation through Central Asia, and its introduction to China and India (see Section 2).

Barton and An (2014) have emphasised the role of archaeological visibility, and suggest that wheat may have arrived in different parts of China through different channels and at different times. We concur with their argument, as these current dates probably reflect the establishment of the wheat cultivation, on some reasonable scale, leading to archaeological visibility. Our evidence adds two things, however. Firstly, the spread of wheat across East and South Asia was a more gradual and intermittent process than has previously been inferred (*cf.* Zhao 2009; Barton and An 2014). The dates for the first appearance of wheat ranged between 2650 and 800 cal. BC, from Tasbas to Jiaochangpu in the north (Zhaojiazhuang notwithstanding), and between 2850 and 1700 cal. BC from Tigrana to Sannarachamma in the south (see Fig. 1). In the case of China, there is evidence that this process of spread was protracted over almost two millennia.

Secondly, we could distinguish separate sequences along the north and south of the Tibetan Plateau (see Fig. 1 and 2). In the north, the sequence runs from the eastern range of the Inner Asian Mountain Corridor through the Tianshan Mountains and the Hexi Corridor. It then extends to the middle and lower reaches of the Yellow River. In the south, though on the basis of less data, the sequence runs from northwest India through to

south India and the Ganges region. The source of wheat in Tibet could be from either the northern or the southern corridor. Here, two points are worth noting. In the north, although the directly dated wheat grains from the lower Yellow River post-date 1500 cal. BC, there have been reports of earlier wheat grains. As discussed above, a grain from one of the Longshan culture sites, Zhaojiazhuang, is dated to the mid-third millennium BC. Although there are fewer data points in the south, the limited evidence we have reveals a sequence running from the southern Iranian Plateau, to the greater Indus region and northwest India, and subsequently to the Ganges region in the east, and to south India. Although the directly dated wheat grains from Harappa itself (in modern Pakistan) postdate those from northwest India, free-threshing wheat is ubiquitous throughout earlier phases of occupation there (Weber 1999, 2003), as well as at other early-mid third millennium sites in the area (see Fuller and Madella, 2001; Fuller, 2006; Thomas and Cartwright, 2010). It is likely that free threshing wheat spread into northwest India via the Indus valley and Punjab. While further dating will be undertaken to confirm these hypotheses, these data support the argument that the current dates probably reflect the establishment of some large-scale cultivation of wheat, rather than the initial introduction ('first appearance' dates) of wheat into China and India.

Changes in the pace of the spread of free threshing wheat is worthy of note. In the north, the adoption of wheat was initially rapid. The earliest dates from the western Chinese provinces of Xinjiang, Qinghai and Gansu, for example, fall within a few centuries, from about 2100 to 1800 cal. BC. This rapid pace is then interrupted in eastern Gansu and eastern Qinghai. The pace then recovered in the central plains (*zhong yuan*) after 1650 cal. BC. Although the current data do not allow us to comment on the pattern in South Asia with similar clarity, there might be a parallel pattern of interruption moving from the Indus plains and northwest India to south India.

This pause may be understood in both its environmental and cultural contexts. In terms of the environment, the Asian summer monsoons bring water from the Pacific and Indian Ocean into much of southeastern China and the subcontinent, and have a powerful ameliorative effect on the intrinsic aridity of the continental interior. Northwest China lies

beyond the monsoon, while central-east China lies within it. Similarly, the Indus region is situated at or just beyond the monsoonal zone, while northwest and south India both lie well within it. This effect would have an impact on crop choice in these regions. In the case of China, despite the debates about the variations of the East Asian monsoon in the Holocene, the monsoon probably found its limit during the third and second millennia BC in eastern Gansu and Qinghai (An et al., 2005; Chen et al., 2008).

Turning to the cultural context, archaeologists have noticed that the monsoonal divide also forms cultural boundaries between eastern and western sectors of China in the past. In the context of the trans-Eurasian exchange of material goods, Rawson (2013) has highlighted differences in prehistoric material culture traditions between areas within the monsoon and areas immediately outside it. There tended to be a fast adoption and adaptation of western technologies, luxury goods and weapons in regions beyond the monsoon, and with some interruption of that pace, moving into the central plains. A pattern apparent in the material culture record thus resonates with the early evidence for wheat discussed here. In contrast, the Indus Civilisation spans both winter and summer rainfall zones, and while there are clear material culture differences between neighbouring regions that lie within one or other rainfall zone, the Indus is notable for the exploitation of a number of similar elements of material culture in both zones (Petrie *et al.* in press).

6.2 Grains become smaller as they move east

Turning from radiocarbon dates to seed/grain size, a general trend is that the length and breadth of grain measurements both decrease from west to east, most particularly the length. The smallest wheat grains are those encountered in central-eastern China. They show statistically significant differences in both length and breadth from grains in northwest China, West Asia and South Asia. Although grains from northwest China are smaller, on average, than those from West Asia and South Asia, these differences are not statistically significant. Within China, there is a clear pattern of decreasing grain length and breadth from northwest to southeast (the geographical trend in grain size reduction is

shown in Fig. 4). Within India, to a less statistically significant degree, there is a pattern of decreasing grain length and increasing grain breadth from the Indus/NW India to the Ganges region.

These findings must be viewed in the context of the effect that charring has on size and shape. A study by Braadbaart (2008) on artificial charring of *T. aestivum* grains at different temperatures and for different time periods shows some increase in breadth and decrease in length. Through experimental charring of grain, a subsequent study demonstrated that distortion is less likely to occur at temperatures below 250 °C and proposed that this undistorted type is the state of grain found at well-preserved archaeological sites (Styring et al., 2013). A further study will clarify the archaeobotanical identification of different *Triticum* species and sub-species (Lister et al., in prep.). In this paper we consider the small wheats in the context of culinary choices.

6.3 Getting smaller in the context of culinary choices

While a range of factors, taphonomic as well as biological, can lead to a prevalence of small grains in the archaeobotanical record, the consistency of size across a range of Asian archaeological contexts suggests an underlying shift through the selection of smaller grained plants. Various hypotheses have been put forward to account for the selection of compact forms, particularly *T. aestivum* subsp. *sphaerococcum* (*cf.* Crawford 1992). For example, a short rigid culm may confer greater stability against lodging in monsoonal climates. A similar observation was made in relating the small grains in Kyrgyzstan to the adaptation to the altitude and strong valley winds in the region (Motuzaite Matuzeviciute et al., 2015). Compact forms also show resistance to drought and, specifically, *T. aestivum* subsp. *sphaerococcum* shows resistance to the yellow rust caused by the pathogen *Puccinia striiformis* (Chen et al., 2012). Rounder grains are easier to mill, and the shallow crease of the grain produces a whiter flour which may be more desirable culturally, as this flour is said to make higher quality bread than regular wheat. The grains also have a higher protein content than *T. aestivum* (Josekutty, 2008). During the 'green revolution' of the 1960s, other dwarfing genes were bred into modern wheat,

producing wheat varieties suitable for the climate of South Asia without compromising yield (Mori *et al.*, 2013). Spengler (2015) has suggested parallel evolutionary pathways for highly compact wheat forms in Central Asia and East Asia.

In 2011, Fuller and Rowlands discussed difference between eastern and western traditions of food preparation and ingestion that may be deeply rooted in prehistory. Ethnographic and archaeological evidence would indicate a contrast between two traditions: a wholegrain steaming and boiling tradition in East and South Asia, and a grinding and bread-baking tradition in West and Central Asia and north India. Fuller and Rowlands (2011) point out that the boundaries between these culinary traditions correlate with the limits of the East Asian and Indian summer monsoon. The eastward spread of free threshing wheat into China thus crossed not only an environmental divide, but also a culinary one. Its southward spread into southern India and eastward into the Ganges also involved culinary transitions, as it moved into areas previously dominated by alternative boiling (Ganges) and pulse and millet-based (South India) traditions (Fuller and Rowlands 2011).

The actual manner of selection merits further enquiry. In the case of China, given the pace of the eastward spread, we propose that the grain size of free threshing wheat was selected consciously. It would be interesting to explore and model how quickly such intense selection upon these cereal ear characteristics would impact upon average grain size. There is also the issue of how other factors, such as sowing practice, may connect with selection for this trait.

In conclusion, although regional variations in timing, pace and selection pressure lease much to explore, we suggest that differences in long standing culinary tradition offer the parsimonious explanation of the widespread substantial diminution in grain size of one the world's most important cereal crops.

Acknowledgements

The authors are grateful to Hongen Jiang, Guiyun Jin, Xuexiang Chen, and Jixiang Song from China; Shalini Sharma, Mukund Kajale, R.N. Singh, DWR Karnal, IARI Wellington from India; George Willcox from France; and Steven Weber and the directors of the Harappa Archaeological Research Project from the United States for assistance in accessing samples. We are also grateful to Naomi Miller from the University of Pennsylvania, Michael Frachetti and Robert Spengler from Washington University in St. Louis, Dorian Fuller from University College London, Jessica Rawson from the University of Oxford, Guanghui Dong from Lanzhou University and the Food Globalisation in Prehistory Project (FOGLIP) team from the University of Cambridge for useful discussions. We also thank the laboratory staff at Oxford Radiocarbon Accelerator Unit, University of Oxford, and at the Laboratory of Earth Surface Processes and Institute of Heavy Ion Physics, Peking University. Financial support was provided by the European Research Council, under grant 249642 (FOGLIP), UKIERI – UK & India Collaborative Educational Research Initiative, and the International Center for Advanced Renewable Energy and Sustainability, Washington University in St. Louis.

References

An, C.-B., Feng, Z.-D., Barton, L., 2005. Dry or humid? Mid-Holocene humidity changes in arid and semi arid China. Quaternary Science Reviews 25, 351-361.

Asakura, N., Mori, N., Nakamura, C., Ohtsuka, I., 2011. Comparative nucleotide sequence analysis of the D genome-specific sequence-tagged-site locus A1 in *Triticum aesticum* and its implication for the origin of subspecies *sphaerococcum*. Breeding Science 61, 212-216.

Barton, L., An, C.-B., 2014. An evaluation of competing hypotheses for the early adoption of wheat in East Asia. World Archaeology 46, 775-798.

Betts, A., Jia, P.W., Dodson, J., 2013. The origins of wheat in China and potential pathways for its introduction: A review. Quaternary International 30, 1-11.

Boivin, N., Fuller, D., Crowther, A., 2012. Old World globalization and the Columbian exchange: comparison and contrast. World Archaeology 44, 452-469.

Braadbaart, F., 2008. Carbonisation and morphological changes in modern dehusked and husked *Triticum dicoccum* and *Triticum aestivum* grains. Vegetation History and Archaeobotany 17, 155-166.

Brock, F., Higham, T., Ditchfield, P., Ramsey, C.B., 2010. Current pre-treatment methods for AMS radiocarbon dating at the Oxford Radiocarbon Accelerator Unit (ORAU). Radiocarbon 52, 103-112.

Bronk Ramsey, C., 2009. Bayesian analysis of radiocarbon dates. Radiocarbon 51, 337-360.

Chen, F.H., Holmes, J.A., Wunnemann, B., Yu, Z.C., 2008. Holocene climate variability in arid Asia: Nature and mechanisms. Quaternary International 194, 1-5.

Chen, S.-S., Chen, G.-Y., Chen, H., Wei, Y.-M., Li, W., Liu, Y.-X., Liu, D.-C., Lan, X.-J., Zheng, Y.-L., 2012. Mapping stripe rust resistance gene YrSph derived from *Triticum sphaerococcum* Perc. with SSR, SRAP, and TRAP markers. Euphytica 185, 19-26.

Costantini, L., 1984. The beginning of agriculture in the Kachi Plain: the evidence of Mehrgarh, in: Allchin, B. (Ed.), South Asian Archaeology. Cambridge University Press, Cambridge, pp. 29-33.

Crawford, G.W., 1992. Prehistoric plant domestication in East Asia, in: Cowan, C.W., Watson, W.J. (Eds.), The Origins of Agriculture: an International Perspective.

Smithsonian Institution Press, Washington, pp. 7-38.

Desse, J., Desse-Berset, D., Henry, A., Tengberg, M., Besenval, R., 2008. Faune et flore des niveaux profonds de Shahi-Tump (Balochistan, Pakistan): Premiers résultats. Paléorient 34, 159-171.

Dodson, J.R., Li, X., Zhou, X., Zhao, K., Sun, N., Atahan, P., 2013. Origin and spread of wheat in China. Quaternary Science Reviews 72, 108-111.

Doumani, P.N., Frachetti, M.D., Beardmore, R., Schmaus, T., Spengler, R.N.,

Mar'yashev, A.N., 2015. Burial ritual, agriculture, and craft production among Bronze Age pastoralists at Tasbas (Kazakhstan). Archaeological Research in Asia 1-2, 17-32.

Flad, R., Li, S., Wu, X., Zhao, Z., 2010. Early wheat in China: results from new studies at Donhuishan in the Hexi Corridor. The Holocene 17, 555-560.

Frachetti, M.D., 2012. Multiregional emergence of mobile pastoralism and nonuniform institutional complexity across Eurasia. Current Anthropology 53, 2-38.

Frachetti, M.D., Spengler, R.N., Fritz, G.J., Mar'yashev, A.N., 2010. Earliest direct evidence for broomcorn millet and wheat in the central Eurasia steppe region. Antiquity 84, 993-1010.

Fuller, D., Boivin, N., Korisettar, R., 2008. Dating the Neolithic of South India: new radiometric evidence for key economic, social and ritual transformations. Antiquity 81, 755-778.

Fuller, D., Rowlands, M., 2011. Ingestion and Food Technologies: Maintaining Differences over the Long-term in West, South and East Asia, in: Wilkinson, T.C., Sherratt, S., Bennet, J. (Eds.), Interveaving Worlds: systemic interactions in Eurasia, 7th to 1st millennia BC. Oxbow Books, Oxford.

Fuller, D.Q., 2006. Agircultural origins and frontiers in South Asia: A working synthesis. Journal of World Prehistory 20, 1-86.

Fuller, D.Q., Denham, T., Arroyo-Kalin, M., Lucas, L., Stevens, C.J., Qin, L., Allaby, R.G., Purugganan, M.D., 2014. Convergent evolution and parallelism in plant domestication revealed by an expanding archaeological record. PNAS 111.

Fuller, D.Q., Madella, M., 2001. Issues in Harappan archaeobotany: Retrospect and prospect, in: Settar, S., Korisettar, R. (Eds.), Indian Archaeology in Retrospect, Volume II - Protohistory Publications of the Indian Council for Historical Research. Manohar, New Dehli, pp. 317-390.

Harlan, J.R., De Wet, J.W.J., Price, E.G., 1973. Comparative evolution of cereals. Evolutionary Anthropology 27, 311-325.

Harris, D., 2010. Origins of Agriculture in Western Central Asia. University of Pennsylvania Museum, Philadelphia.

Jacomet, S., Borombacher, C., Dick, M., 1989. Archäobotanik am Zürichsee. Orell Füssli, Zürich.

Jin, G., 2007. Zhongguo zaoqi xiaomai de kaogu faxian yu yanjiu (Studies on early wheat in China). Nongye Kaogu (Agricultural Archaeology) 92, 11-20.

Jin, G., Yan, D., Liu, C., 2008. Wheat grains are recovered from a Longshan cultural site, Zhaojiazhuang, in Jiaozhou, Shandong Province, Cultural Relics in China.

Johnson, E.B., Nalam, V.J., Zemetra, R.S., Riera-Lizarazu, O., 2008. Mapping the *compactum* locus in wheat (*Triticum aestivum* L.) and its relationship to other spike morphology genes of the Triticeae. Euphytica 163, 193-201.

Jones, M.K., Harriet, H., Kneale, C.J., Lightfoot, E., Lister, D., Liu, X.-Y., Motuzaite Matuzeviciute, G., in press. Food Globalisation in PrehistoryL the agrarian foundation of an interconnected continent. Journal of the British Academy.

Jones, M.K., Hunt, H.V., Lightfoot, E., Lister, D., Liu, X., Motuzaite-Matuziviciute, G., 2011. Food globalization in prehistory. World Archaeology 43, 665-675.

Josekutty, P.C., 2008. Defining the genetic and physiological basis of *Triticum sphaerococcum* Perc. . University of Canterbury, New Zealand.

Kippes, N., Debernardi, J.M., Vasquez-Gross, H.A., Akpinar, B.A., Budak, H., Kato, K., Chao, S., Akhunov, E., Dubcovsky, J., 2015. Identification of the VERNALIZATION 4 gene reveals the origin of spring growth habit in ancient wheats from South Asia Proceedings of National Academy of Science of the United States of America 112, E5401-E5410.

Kislev, M.E., 1979. Triticum parvicoccum sp. nov., the oldest naked wheat Israel Journal of Botany 28, 95-107.

Kislev, M.E., Mahler-Slasky, Y., 2009. Food remains, in: Gadot, Y., Yadin, E. (Eds.), Aphek-Antipatris II: The remains of the acropolis. Tel Aviv University, Tel Aviv, p. 158. Kislev, M.E., Simchoni, O., Melamed, Y., Maroz, L., 2009. Food and Industrial Crops, in: Panitz-Cohen, N., Mazar, A. (Eds.), Excavations at Tel Beth-Shean 1989-1996 (Volume III). The Israel Exploration Society / The Institute of Archaeology, The Hebrew University of Jerusalem Jerusalem, p. 767.

Levine, M., 1999. Late Prehistoric Exploitation of the Eurasian Steppe. McDonald Institute for Archaeological Research, Cambridge.

Li, S., Mo, D., 2004. Donghuishan yizhi tanhua xiaomai niandai kao [Discussion on the chronology of the charred wheat from Donghuishan]. Kaogu yu Wenwu [Archaeology and Cultural Relics] 146, 51-60.

Li, X., Dodson, J., Zhou, X., Zhang, H., Masutomoto, R., 2007. Early cultivated wheat and broadening of agriculture in Neolithic China. The Holocene 15, 555-560.

Lightfoot, E., Liu, X., Jones, M.K., 2013. Why move starchy cereals? a review of the isotopic evidence for prehistoric millet consumption across Eurasia. World Archaeology 45, 574-623.

Linduff, K.M., Mei, J., 2009. Metallurgy in ancient Eastern Asia: Retrospect and prospects. Journal of World Prehistory 22, 265-281.

Lister, L.D., Liu, X.-Y., Pathak, A., Bate, J., Pilgram, T., Jones, M.K., in prep. Sphaerococcoid wheats in India and Central Asia - are they related? Veget Hist Archaeobot.

Liu, X., Jones, M.K., 2014. Food globalisation in prehistory: top down or bottom up? Antiquity 88, 956-963.

Liu, X., Lightfoot, E., O'Connell, T.C., Wang, H., Li, S., Zhou, L., Hu, Y., Motuzaite-Matuzeviciute, G., Jones, M.K., 2014. From necessity to choice: dietary revolutions in west China in the second millennium BC. World Archaeology 46, 661-680.

Lu, H.-L., in press. Colonization of the Tibetan Plateau, Permanent Settlement, and the Spread of Wheat: Reflection on Current Debates on the Prehistoric Archaeology of the Tibetan Plateau. Archaeological Research In Asia, doi:10.1016/j.ara.2016.1002.1010. MacKey, J., 1966. Species relationship in *Triticum*., in: MacKey, J. (Ed.), Proc Int Wheat Genet Symp. Hereditas(Suppl).

Maier, U., 1996. Morphological studies of free-threshing wheat ears from a Neolithic site in southwest Germany, and the history of the naked wheats. Vegetation History and Archaeobotany 5, 39-55.

Meadow, R.H., 1996. The origins and spread of agriculture and pastoralism in north western South Asia, in: Harris, D. (Ed.), The Origins and Spread of Agriculture and Pastoralism in Eurasi. UCL Press, London, pp. 390-412.

Measow, R., Kenoyer, M.J., 2005. Excavations at Harappa 2000-2001: New insights on chronology and city organization, in: Jarriage, C.N., Lefèvre, V. (Eds.), South Asian Archaeology 2001. Editions Recherche sur les Civilisations, Paris, pp. 207-225.

Mei, J., 2003. Qijia and Seima-Turbino: the question of early contacts between Northwest China and Eurasian Setppe, The Museum of Far Eastern Antiquities - Bulletin No. 75. The Museum of Far Eastern Antiquities, Stockholm, pp. 31-55.

Miller, N.F., 1999. Agricultural development in western central Asia in the Chalcolithic and Bronze Age. Vegetation History and Archaeobotany 8, 13-19.

Miller, N.F., 2003. The use of plants at Anau North, in: Hiebert, F.T., Kurdansakhatov, K. (Eds.), A Central Asian village at the dawn of civilization: Excavations at Anau, Turkmenistan. University of Pennsylvania Museum, Philadelphia.

Moore, K., Miller, N.F., Heibert, F.T., Meadow, R.H., 1994. Agriculture and herding in early oasis settlements of the Oxus civilization. Antiquity 68, 418-427.

Mori, N., Ohta, S., Chiba, H., Takagi, T., Niini, Y., Shinde, V., Kajale, M.D., Osada, T., 2013. Rediscovery of Indian dwarf wheat (*Triticum aestivum* L. ssp. *sphaerococcum* (Perc.) MK.) an ancient crop of the Indian subcontinent. Genetic Resources and Crop Evolution 60, 1771-1775.

Motuzaite Matuzeviciute, G.M., Preece, R.C., Wang, S., Colominas, L., Ohnuma, K., Kume, S., Abdykanova, A., Jones, M.J., 2015. Ecology and subsistence at the Mesolithic and Bronze Age site of Aigyrzhal-2, Naryn valley, Kyrgystan. Quaternary International, Available online 18 August 2015 - doi:2010.1016/j.quaint.2015.2006.2065.

Nesbitt, M., 2001. Wheat evolution: integrating archaeological and biological evidence, in: Caligari, P.D.S., Brandham, P.E. (Eds.), Wheat taxonomy: the legacy of John Percival (Linnean Special Issue 3). Linnean Society, London, pp. 37-59.

Percival, J., 1921. The Wheat Plant. Duckworth, London.

subsistence economy. Current Science 94, 612-622.

Petrie, C.A., 2015. Mehgarh, Pakistan, in: Barker, G., Goucher, C. (Eds.), The Cambridge World History Volume II - A World with Agriculture, 12000 BCE-500 CE. Cambridge University Press, Cambridge, pp. 289-309.

Petrie, C.A., Thomas, K.D., Morris, J., 2010. Chronology of Sheri Khan Tarakai, in: Petrie, C.A. (Ed.), Sheri Khan Tarakai and early village life in the borderlands of northwest Pakistan. Oxbow, Oxford and Oakville, pp. 343-352.

Pokharia, A.K., 2008. Record of macrobotanical remains from the Aravalli Hill, Ojiyana, Rajasthan: Evidence for agriculture-based subsistence economy. Current Science 94. Pokharia, A.K., 2009. Aravalli Hill, Ojiyana, Rajasthan: Evidence for agriculture-based

Pokharia, A.K., 2011. Palaeoethnobotany at Lahuradewa: a contribution to the 2nd millennium BC agriculture of the Ganga Plain, India. Current Science 101, 1569-1578.

Pokharia, A.K., Kharakwal, J.S., Rawat, Y.S., Osada, T., Nautiyal, C.M., Srivastava, A., 2011. Archaeobotany and archaeology at Kanmer, a Harappan site in Kachchh, Gujarat: Evidence for adaptation in response to climatic variability. Current Science 100, 1833-1846.

Pokharia, A.K., Pal, J.N., Srivastava, A., 2009. Plant macro-remains from Neolithic Jhusi in Ganga Plain: Evidence for grain-based agriculture. Current Science 97, 564-572.

Purugganan, M.D., Fuller, D.Q., 2009. The nature of selection during plant domestication. Nature 457, 843-848.

Rawson, J., 2013. Ordering the exotic: Ritual practices in the late Western and early Eastern Zhou. Artibus Asiae 73, 5-24.

Rivera, D., Matilla, G., Obon, C., Alcaraz, F., 2011. Plants and Humans in the Near East and the Caucasus. Ediciones de la Unverisdad de Murcia, Murcia.

Salina, E., Börner, A., Leonova, I., Korzun, V., Laikova, L., Maystrenko, O., Röder, M.S., 2000. Microsatellite mapping of the induced sphaerococcoid mutation genes in Tiricum aestivum. Theoretical and Applied Genetics 100, 686-689.

Sherratt, A., 2005. The Trans-Eurasian exchange: the prehistory of Chinese relations with the West, in: Mair, V. (Ed.), Contact and Exchange in the Ancient World. Hawaii University Press, Honolulu, pp. 30-61.

Spengler, R., Frachetti, M., Doumani, P., Rouse, L., Cerasetti, B., Bullion, E., Mar'yashev, A., 2014a. Early agriculture and crop transmission among Bronze Age mobile pastoralists of Central Eurasia. Proceedings of the Royal Society B: Biological Sciences 281, 1-7.

Spengler, R.N., 2015. Agriculture in the Central Asian Bronze Age. Journal of World Prehistory 28, 215-253.

Spengler, R.N., Frachetti, M.D., Domani, P.N., 2014b. Late Bronze Age agriculture at Rasbas in the Dzhungar Mountains of eastern Kazakhstan. Quaternary International 348, 147-157.

Spengler, R.N., Willcox, G., 2013. Archaeobotanical results from Sarazm, Tajikistan, an Early Bronze Age Settlement on the edge: Agriculture and exchange. Journal of Environmental Archaeology 18, 211-221.

Styring, A.K., Manning, H., Fraser, R.A., Wallace, M., Jones, G., Charles, M., Heaton, T.H.E., Bogaard, A., Evershed, R.P., 2013. The effect of charring and burial on the biochemical composition of cereal grains: investigating the integrity of archaeological plant material. Journal of Archaeological Science 40, 4767-4779.

Tengberg, M., 1998. Crop husbandry at Miri Qalat, Makran, SW Pakistan (4000-2000 BC). Vegetation History and Archaeobotany 8, 3-12.

Thomas, K.D., Cartwright, C., 2010. The biological remains from Sheri Khan Tarakai, in: Petrie, C.A. (Ed.), Sheri Khan Tarakai and early village life in the borderlands of northwest Pakistan. Oxbow, Oxford and Oakville, pp. 305-342.

Weber, S.A., 1991. Plants and Harappan subsistence: An example of stability and change from Rojdi Boulder: . Westview, Boulder.

Weber, S.A., 1999. Seeds of urbanism: palaeoethnobotany and the Indus Civilization. Antiquity 73, 813-826.

Weber, S.A., 2003. Archaeobotany at Harappa: Indications for Change, in: Weber, S., Belcher, B. (Eds.), Indus Ethnobiology: New Perspectives from the Field. Lexington Books, pp. 175-198.

Weiss, E., Zohary, D., 2011. The Neollithic Southwest Asian Founder Crops: Their biology and archaeobotany. Current Anthropology 52, S237-S254.

Willcox, G., 1991. Carbonised plant remains from Shortughai, Gafhanistan, in: Renfrew, J.M. (Ed.), New Light on Early Farming - Recent Developments in Palaeoethnobotany. Edinburgh University Press, Edinburgh, pp. 139-152.

Yang, R., Yang, Y., Li, W., Abuduresule, Y., Hu, X., Wang, C., Jiang, H., 2014. Investigation of cereal remains at the Xiaohe Cemetery in Xinjiang, China. Journal of Archaeological Science 49, 42-47.

Zhang, G., Wang, S., Ferguson, D.K., Yang, Y., Liu, X., Jiang, H., 2015. Ancient plant use and palaeoenvironmental analysis at the Gumugou Cemetery, Xinjiang, China: implication from desiccated plant remains. Archaeological and Anthropological Sciences, published online: DOI 10.1007/s12520-12015-10246-12523.

Zhao, Z., 2009. Eastward spread of wheat into China - new data and new issues, in: Liu, Q., Bai, Y. (Eds.), Chinese Archaeology - Volume Nine. China Social Press, Beijing, pp. 1-9.

Zhao, Z., 2011. New archaeobotanic data for the study of the origins of agriculture in China. Current Anthropology 52, S295-S304.

Zohary, D., Hopf, M., 2000. Domestication of Plants in the Old World. Clarendon Press, Oxford.

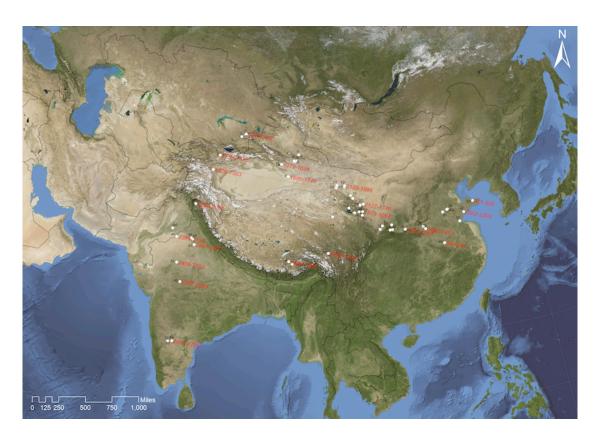


Figure 1. Key sites mentioned in the text. The oldest individually dated grains of free-threshing wheat from each region are indicated. 1. Begash, 2. Tasbas 1, 3. Aigyrzhal-2, 4. Gumugou, 5. Shengjindian, 6. Yanghai, 7. Astana, 8. Sidaogou, 9. Xicaozi, 10. Wupaer, 11. Xintala, 12. Karou, 13. Bangga, 14. Changgougou, 15. Xishanping, 16. Heishuiguo, 17. Donghuishan, 18. Ganggangwa, 19. Huoshiliang, 20. Mozuizi, 21. Shaguoliang, 22. Huangniangniangtai, 23. Dadiwan, 24. Huoshaogou, 25. Qiaocun, 26. Fengtai, 27. Jinchankou, 28. Aiqingya, 29. Xiariyamakebu, 30. Shuangerdongping, 31. Longshan, 32. Zhouyuan, 33. Shangguancun, 34. Nansha, 35. Wangchenggang, 36. Yanshishangcheng, 37. Zhaogezhuang, 38. Dongpan, 39. Daxinzhuang, 40. Liujiazhuang, 41. Jiaochangpu, 42. Zhaojiazhuang, 43. Yantai, 44. Harappa, 45. Khirsara, 46. 4-MSR/Binjore, 47. Tigrana, 48. Kunal, 49. Banawali, 50. Kanispur, 51. Ojiyana, 51. Pikliha, 53. Sannarachamma, 54. Hiregudda.

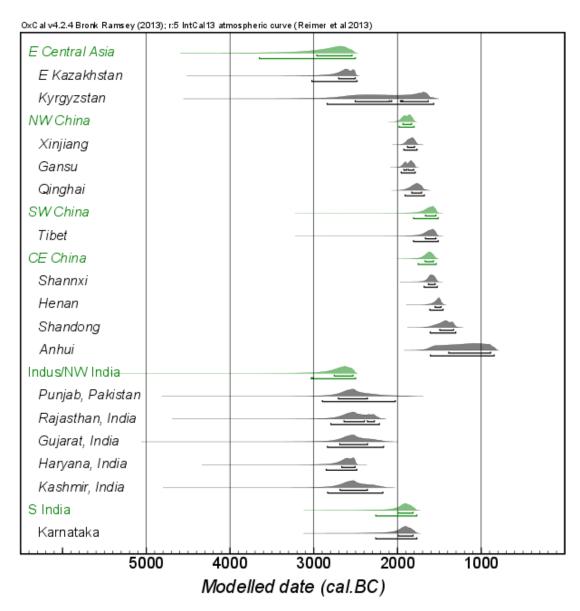


Figure 2. The implied 'first appearance dates' (i.e. 'Start' *Boundaries*) of the sixteen regions (grouped in six broader regional groups) derived from the Bayesian statistical model. The horizontal bars below each of the probability density functions reflect the 68.2% and 95.4% highest probability density ranges, respectively. These results show a west-east chronological sequence in Central and East Asia, and a north-south sequence in South Asia.

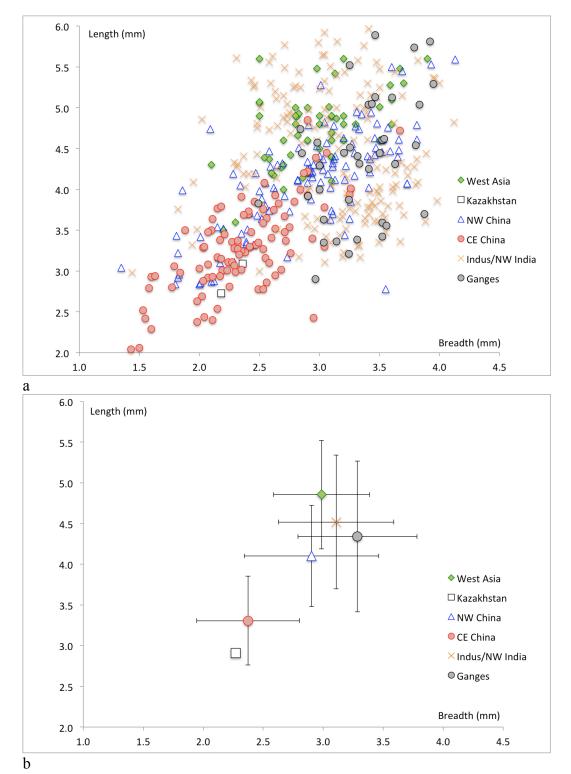


Figure 3. (a) Scatterplot and (b) the average values of charred grain length and breadth from six regions (desiccated samples not included). The length and breadth of wheat grains from China are smaller than those of other regions. The size of grains from central-east China is particularly diminished. Due to the small sample size (n=2), similar observations cannot be drawn from Kazakhstan.

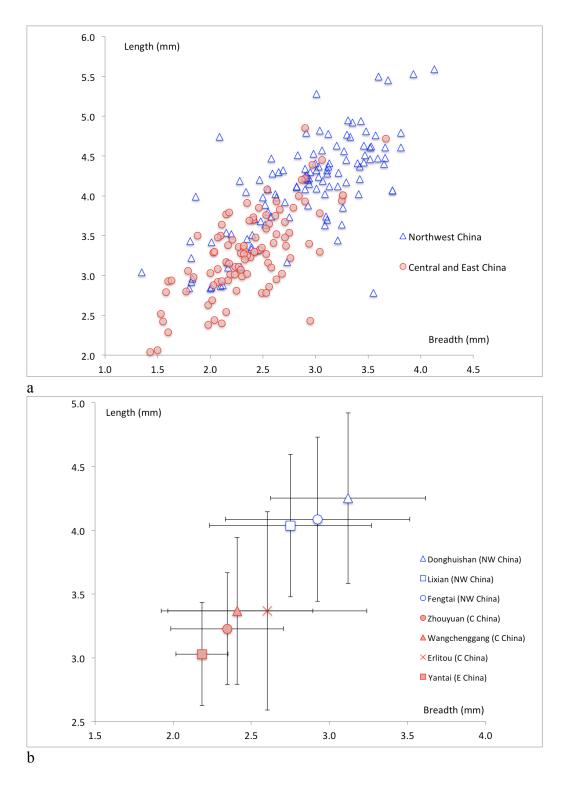


Figure 4. (a) Scatterplot and (b) average values of charred grain length and breadth from China (desiccated samples not included). The grain length and breadth decreased as free threshing wheat moved from northwest China to central-east China.

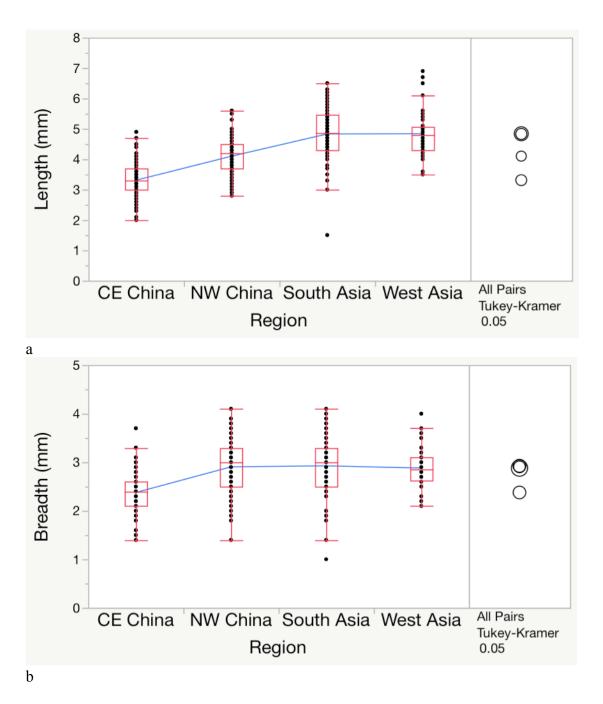


Figure 5. Boxplot of grain length vs breadth from four different regions. The horizontal line connects the means. Grains from South Asia and West Asia are identical in length, while grains from CE China and NW China differ from them and from each other. Chinese grains are smaller, particularly those from CE China (a). For the measurement of breadth, however, NW China is identical to South Asia and West Asia, while CE China is smaller than the others. (b).