Wheat evolution: integrating archaeological and biological evidence

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Abstract

Understanding of wheat evolution has benefited from improvements in identification techniques for archaeological wheat remains, and from the development of genetic characterisation of current-day wheats, most recently using DNA variability. Archaeological and botanical evidence agree well in locating the domestication of einkorn (*Triticum monococcum*) and emmer (*Triticum dicoccum*) in the fertile crescent of the Near East at about 7500 years BC (uncalibrated). DNA characterisation offers excellent potential for narrowing the area of origin, and tracing the spread of crops to Europe. The origin of spelt (*T. spelta*) is more complex. Biological and archaeological evidence agree that spelt first results from the hybridisation of a cultivated tetraploid wheat and *Aegilops tauschii* near the Caspian Sea or in Transcaucasia. However archaeobotanical evidence for spelt in this region or on its putative routes to Europe is still scanty and is based on doubtful identifications. The sudden appearance of spelt in Early Bronze Age central Europe may be the result of a local hybridisation of free-threshing hexaploid wheat (*T. aestivum*) and emmer wheat. The time and place of the origins of European spelt await resolution.

INTRODUCTION

The size of the literature on the history and evolution of the wheats reflects two factors: firstly, their central role in agricultural economies and human culture over the last ten millennia, and secondly, the rich and fascinating variety of forms of wheat and their complex genetic basis. John Percival made significant contributions in both areas – to the history of human use of wheat through his archaeobotanical analyses of ancient wheat remains from archaeological excavations (Carruthers, 1992), and to the history

of wheat evolution through his morphological and agronomic studies. My aim in this paper is to survey progress in the use of archaeological evidence to understand wheat evolution since Percival's *The Wheat Plant* (Percival, 1921), and in particular to investigate the degree of correlation between archaeological evidence, primarily in the form of plant remains, and biological evidence such as genetics and biogeography. Rather than attempt a comprehensive survey (cf. Harlan, 1981; Bell, 1987; for hulled wheats: Nesbitt & Samuel, 1996) I focus on two issues: the domestication of the earliest cultivated wheats, einkorn and emmer, and the origin of spelt and bread wheat.

Note on wheat nomenclature

The confused state of current-day wheat nomenclature reflects the diverse approaches of wheat scientists (Morrison, this volume). In this paper I have chosen to follow the traditional classification of Dorofeev & Migushova (1979), as conveniently summarised by Morrison (1994), as it is simple to use and is similar to the classification used by most agronomists and archaeobotanists (Table 1).[1]

Note on radiocarbon dating

Radiocarbon dating has been used since the 1950s to date archaeological material including, since the 1980s, single charred seeds (Legge, 1986). However, radiocarbon dating systematically underestimates the age of objects, by 1000 to 1500 years during the Neolithic of the Near East. Until recently, calibration has not been possible for radiocarbon dates prior to 6000 uncal BC. A recent calibration (Stuiver *et al.*, 1998) allows radiocarbon dates from before this period to be converted to calendar year dates, and these new dates are likely to be widely adopted by the archaeological community. However, as an interim measure in this paper, I have used uncalibrated dates (indicated as uncal BC) for these early periods (Table 2), and calibrated dates (cal BC) for discussion of later European prehistory.

TABLE 2. Dating of the main archaeological periods during which wheat domestication occurred in the Near East. Calibrated dates follow Stuiver *et al.* (1998). All dates are approximate and vary regionally.

	Uncalibrated yrs BC	Calibrated yrs BC
Epipalaeolithic		
Kebaran	18,000 – 10,800	21,700 – 13,400
Natufian	10,800 – 8,500	13,400 – 10,600
Neolithic		
Pre-Pottery Neolithic A	8,500 – 7,500	10,600 – 8,700
Pre-Pottery Neolithic B	7,500 – 5,500	8,700 – 6,300
Pottery Neolithic	5,500 – 4,200	6,300 – 5,200

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1   Current wheat taxonomies are conveniently summarised at the GrainTax website:
    http://wheat.pw.usda.gov/ggpages/GrainTax/

TABLE 1. The main wheat species arranged according to genome and domestication status. Nomenclature follows Dorofejev & Migushova (1979)

Domestication status	Hulled/ free-threshing	Diploid group *Geonome*: A	Tetraploid group A^{u}B	Transcaucasian tetraploid group A^{b}G	Hexaploid group A^{u}BD
Wild	Hulled, fully brittle rachis	*T. boeoticum* Boiss. (A^b) **Wild einkorn** *T. urartu* Tum. ex Gandil. (A^u)	*T. dicoccoides* (Körn. Ex Aschers. & Graebn.) Schweinf. **Wild emmer**	*T. araraticum* Jakubz.	None
Domesticated	Hulled, semi-tough rachis	*T. monococcum* L. (A^b) **Einkorn**	*T. dicoccum* Schrank ex Schübl. **Emmer** *T. ispahanicum* Heslot *T. paleocolchicum* Men.	*T. timopheevii* (Zhuk.) Zhuk.	*T. spelta* L. **Spelt** *T. macha* Dekapr. & Menabde *T. vavilovii* (Tum.) Jakubz.
Domesticated	Free-threshing, fully tough rachis	*T. sinskajae* Filat. & Kurk. (A^b) - rare mutant in Turkish einkorn fields	*T. durum* Desf. **Macaroni wheat** *T. turgidum* L. **Rivet wheat** *T. turanicum* Jakubz. **Khorasan wheat** *T. polonicum* L. **Polish wheat** *T. aethiopicum* Jakubz. *T. carthlicum* Nevski in Kom. **Persian wheat**		*T. aestivum* L. **Bread wheat** *T. compactum* Host **Compact wheat** *T. sphaerococcum* Percival

IDENTIFICATION OF ANCIENT WHEATS

Introduction

The basis of the identification of archaeological wheat remains is their comparison with living material of known identity. The major problem that faces archaeobotanists is incomplete preservation. Faced with a modern ear of wheat, the taxonomist can use a range of relatively well-documented morphological and genetical characters to determine identification to species. In contrast, archaeological material is usually the fragmented debris of crop-processing, preserved in very arid areas by desiccation or by special conditions such as thatch (Letts, 1999), but in most regions by charring.

Denied access to intact spikes, archaeobotanists have developed novel identification criteria based on careful examination of those parts of the ear that do survive, primarily the rachis segments and the grain. There is general agreement that reliable, repeatable identification criteria do exist for rachis remains, allowing hulled wheats to be separated from free-threshing ("naked") wheats, and determination of the ploidy level (Hillman et al., 1996, Hillman, this volume). In contrast, grain identification is far more problematic, in part because the effects of charring on the endosperm usually lead to swelling and changes in shape and size, and in part because grain shape is largely a function of glume shape and texture, which may be quite similar in wheats of different ploidy levels such as emmer and spelt, or macaroni and bread wheat (cf. Millet, 1986). Grain shape and size is also significantly affected by number of grains developing in the spikelet (Maier, 1996).

Identifying domestication

Domestication is the process by which humans take reproductive control of plants or animals, modifying them for their own purposes. Selection pressures applied – consciously or unconsciously – in cultivation and harvesting have resulted in significant adaptations of crops to human needs. In wheat, these include the tough rachis (ensuring that grain is not lost during harvest), larger grains (ensuring better germination), higher ratio of starch to bran, and a range of physiological changes linked to higher yields (Evans, 1993). Of these characteristics, the first two are most easily detected in archaeological material. In wheat, unlike in barley, there are significant changes in size and shape of grain at domestication, although their detection is complicated by effects of charring. Identification of grains of wild einkorn is complicated by their close resemblance to wild rye grains and, without chaff, identification to genus is difficult. Identification of chaff is similarly complicated by the presence in the fertile crescent of morphologically similar, but reproductively isolated, species that are sibling to the wild wheats (Johnson & Dhaliwal, 1976). The morphological characters that separate T. urartu from T. boeoticum and T. araraticum from T. dicoccoides do not allow separation of archaeobotanical material.

The spike of wild cereals breaks up at maturity, allowing the grain-containing spikelets to be distributed. In domesticated wheat the rachis is tough, and disarticulation of the spike is done by humans after harvest. The spikelets of wild wheat break apart at the base of each rachis segment, leaving a neat, smooth abscission scar, in contrast to the ragged, torn scar of broken domesticated spikes (Hillman & Davies, 1990; Willcox, 1992). However, small numbers of torn rachis scars may result from

threshing of the lower spikelets which usually remain attached to the culm, even in mature ears (Hillman & Davies, 1992; Kislev, 1992). At established agricultural sites we do indeed find that most of the spikelets have torn scars, but the interpretation of very small numbers of torn scars at hunter-gatherer sites is problematic (Kislev, 1997).

There are also problems in dating early material. For example, the charred plant remains from the Pre-Pottery Neolithic A levels at Jericho consist of a few fragments of grain of uncertain status. The best evidence for domestication is a single clay imprint of two spikelets of an intact (and, therefore, domesticated) einkorn spike from level X, dating to the very latest part of the PPNA (c. 7600–7400 uncal BC). However, this is one of just three einkorn imprints still dated to the PPNA; a further 19 were redated from PPNA to Pottery Neolithic (Hopf, 1983: 609–10). In view of uncertainties about PPNA stratigraphy at the site, the remaining PPNA imprints are not secure evidence for domestication. The only other PPNA find of einkorn in the southern Levant is at Iraq ed-Dubb, where spikelet forks of domesticated einkorn or emmer were recovered from both Natufian and PPNA levels, and may be intrusive from later occupation of the Iron Age (Colledge, 1994). Without accelerator dating of individual spikelet forks, the significance of this material remains uncertain. The presence of domesticated emmer at PPNA Aswad (Phase Ia) is based on *Triticum* spikelet forks of unknown status and the presence of a small number of *T. dicoccum* grains that have not been directly dated (van Zeist & Bakker-Heeres, 1982: 184–5). Overall, evidence for domestication in the Pre-Pottery Neolithic A (PPNA, 8300–7600 uncal BC) is either lacking, as in the very abundant and well-preserved plant remains from Netiv Hagdud (Kislev, 1997), or based on small quantities of ambiguous material.

Free-threshing wheats

Both the wild wheats and their domesticated derivatives are hulled. The glumes are thickened and tough, while the mature rachis is brittle in wild wheats, and semi-tough in domesticates. In either case, on threshing the spike will break up into spikelets in which the grain is surrounded by the tough glumes (Nesbitt & Samuel, 1996). In the free-threshing ("naked") wheats the glumes are thin and easily broken off, while the rachis is fully tough. Threshing will separate the chaff from the grain. Both the grain and chaff of free-threshing wheats are very distinctive, the rachis segments lacking the prominent glume bases typical of hulled wheats, and the grains lacking the longitudinal creases impressed by tough glumes. However, further identification of free-threshing wheats has proved controversial since the earliest days of archaeobotany.

In 1853 falling lake levels in Switzerland led to the discovery of numerous lakeside dwellings. Abundant, well-preserved plant remains, including intact charred ears of wheat, were collected during excavations and were studied by the palaeobotanist Oswald Heer (Heer, 1865). He identified the hulled wheats einkorn, emmer and spelt, and three free-threshing wheats, dominated by hexa- ploid *Triticum vulgare antiquorum*. Subsequent archaeobotanists followed Heer's lead for the next century in ascribing remains of free-threshing wheats in Europe and elsewhere to hexaploid "bread wheat" (*T. aestivum* or *T. compactum*), on the basis of their short, wide grains and short rachis segments.

The 1970s saw a resurgence in excavations of Swiss lake villages, in connection with a major road-building programme. Archaeobotanists applied the new, rigorous rachis

criteria for free-threshing wheats (Hillman, this volume) to newly-excavated Swiss
material dating from the Late Neolithic (Jungneolithikum, 4300–3500 cal BC)
onwards and found that most rachis remains of free-threshing wheat were
unmistakably tetraploid (Jacomet, Brombacher & Dick, 1989: 319–329; Jacomet &
Schlichtherle, 1984). Further work on naked wheats from German Neolithic sites on
Lake Constance has confirmed these results (Maier, 1996). Outside central Europe,
relatively little systematic application of these identification criteria has been made, but
archaeological records of tetraploid free-threshing wheats are known from medieval
Britain and from the Neolithic period onwards in the Near East (Maier, 1996; Moffett,
1991). Clearly, the previous practice of blanket determination of free-threshing wheats
as bread wheat was wrong; it appears to have been based on the belief that the short,
compact grains typical of ancient charred free-threshing wheat could come only from
bread wheat. However there is general agreement amongst archaeobotanists (Hillman
et al., 1996 for 1995; Jacomet *et al.*, 1989; Jones, 1998; Moffett, 1991) that grains of
free-threshing wheat cannot be separated by morphology save in exceptional
circumstances. Identifications that are not supported by explicit rachis criteria – that is,
most identifications prior to the 1980s – can be accepted only as free- threshing wheat
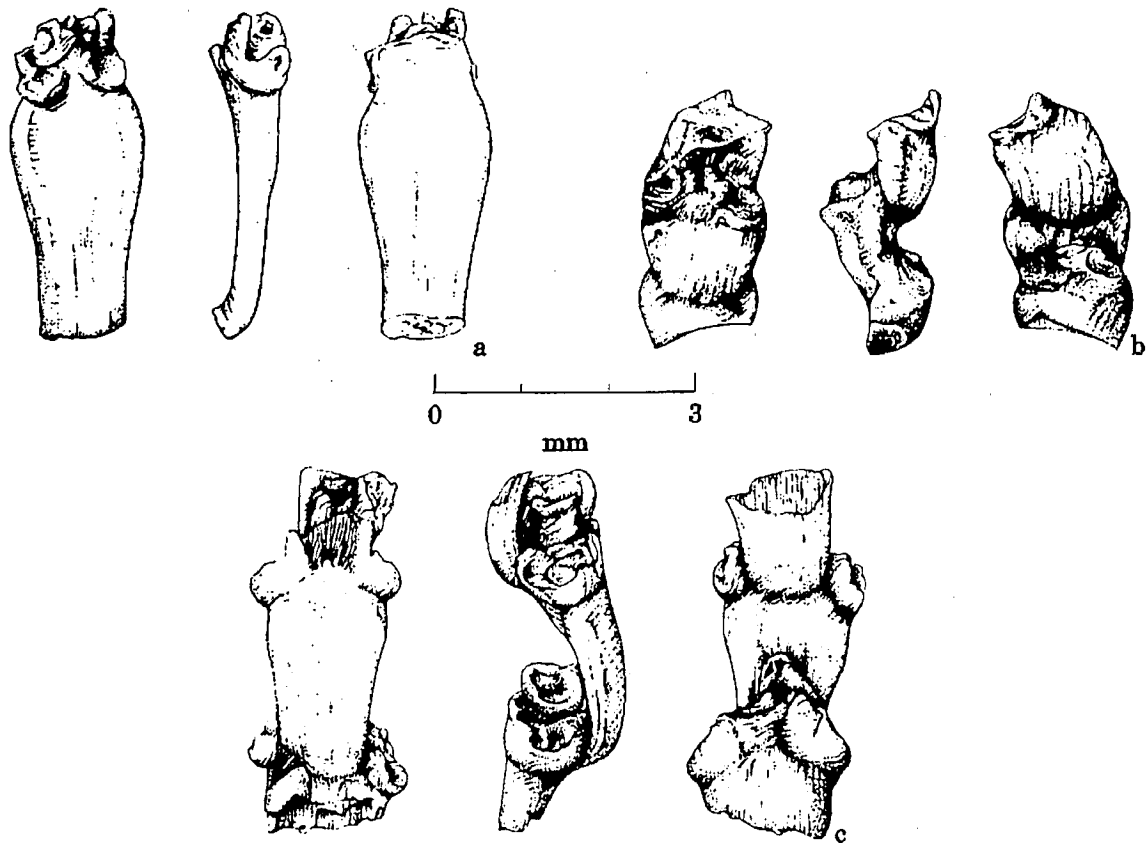of unknown ploidy level.

Figure 1. Charred free-threshing rachis segments from archaeological sites. a. Hexaploid (bread wheat, *Triticum aestivum*), Dilkaya Höyük, eastern Turkey; b. Hexaploid (compact type), Qaryat Medad, Syria; c. Tetraploid (macaroni wheat, *T. durum/turgidum*), Qaryat Medad, Syria. From Nesbitt & Goddard (1997).

A further controversial topic is the identification of ancient free-threshing wheat remains to specific taxa within their ploidy group, on the same lines as Heer's archaeological variant of bread wheat, *"Triticum vulgare antiquorum"*. For example, free-threshing wheat remains from the Indian sub-continent are often identified as *T. sphaerococcum* on the basis of their short, compact grains. In fact, most charred grains of naked wheat reported from Europe and the Near East have short grains (less than 5 mm long), regardless of whether they originate from tetraploid or hexaploid wheats. Identification as *T. sphaerococcum* would first require a much better understanding of the morphological traits of current-day populations, and second, demonstration that traits found in ancient material are sufficiently distinct to rule out other tetraploid and hexaploid wheats (Fuller, in press; Hillman *et al.*, 1996; Miller, 1992). Identification of compact-eared forms of wheat is complicated by the effects of charring, which can reduce grain length by 10% on average and rachis length by up to 25% (Hopf, 1955; Villaret-von Rochow, 1967). Some rachis segments are so short (Fig. 1) that they may genuinely represent a compact type. The very limited number of finds of free-threshing wheat that have been fully characterised by reliable rachis criteria, and our poor understanding of the effects of charring, makes premature attempts at definition of new species such as Kislev's ancient tetraploid free-threshing wheat, *T. parvicoccum* (Kislev, 1979/80).

DOMESTICATION OF EINKORN AND EMMER WHEAT

A brief history of research

The origins of agriculture have been a major focus of archaeological enquiry in the Near East for the last 50 years. The enhanced productivity of agriculture, compared to hunter-gatherer subsistence, underlies the rise of urban and literate civilisations in the ancient Near East, and their spread to Europe and, eventually, much of the globe (Diamond, 1997; Harris, 1996). By the Pre-Pottery Neolithic B period (PPNB, 7600–6000 uncal BC) a well-documented set of Neolithic "founder crops" is present at farming villages throughout the fertile crescent (Harris, 1998; Zohary & Hopf, 1993). These crops include two-row hulled barley, lentils, horsebean, chickpea, pea, and einkorn and emmer wheat (Zohary, 1996; Zohary & Hopf, 1993).

The combination of archaeobotany and botany has been successful in answering the broad "when" and "where" that led to plant domestication in the fertile crescent. Evidence from current-day distribution of wild cereals pointed to the fertile crescent, the "hilly flanks" surrounding the deserts and steppe of Syria, Iraq and Iran (Fig. 2), as the area in which domestication would have first occurred. Archaeological fieldwork has since confirmed that the earliest farming villages are indeed within or on the fringes of the fertile crescent, and date from about 7500 uncal BC (Table 3).

Archaeological evidence

If we are to explain the "why" of agricultural origins, we need a far more detailed understanding of the processes involved in the shift from foraging to farming. It is reasonably certain that most Epipalaeolithic people were hunter-gatherers, and that at least by the middle PPNB (7500–5500 uncal BC) most villagers in the Near East were farmers. The key question is what was happening in the PPNA (8300–7500 uncal BC), the earliest Neolithic period. As discussed above with reference to identification of

TABLE 3. Selected occurrences of wheat at Epipalaeolithic and Pre-Pottery Neolithic Near Eastern archaeological sites. Solid shading indicates identification on basis of chaff; grey shading is on basis of grain; ? indicates uncertain identification. EIN = einkorn, EM = emmer, NAK = free-threshing wheat, 4 or 6 refers to ploidy level based on reliable rachis criteria. Identifications of wild einkorn based on grain alone cannot usually be separated from *Triticum urartu* or wild rye (Secale). Identifications of wild emmer may refer to *T. dicoccoides* or *T. araraticum*. Bibliography for site reports is in Nesbitt & Samuel (1996).

Site (phase)	Country	Period	Date (uncal BC)	Economy	WILD EIN	WILD EM	WILD RYE	DOMESTIC EIN	DOMESTIC EM	DOMESTIC NAK
Ohalo II	Israel	Epipalaeolithic (Kebaran)	17000	Foraging						
Abu Hureyra (I)	Syria	Epipalaeolithic (Natufian)	9500-8000	Foraging	▒		▒			
Mureybit (I-III)	Syria	Epipalaeolithic & PPNA	8500-7600	Foraging	▒					
Qermez Dere	Iraq	PPNA	8200-7700	Foraging					?	
Netiv Hagdud	Israel	PPNA	8000-7400	Foraging	■					
M'lefaat	Iraq	PPNA	7900-7700	Foraging						
Jerf al Ahmar	Syria	PPNA	7800-7700	Foraging						
Dja'de	Syria	PPNB	7600-7000	Foraging	?			▒		
Abu Hureyra (2A)	Syria	PPNB	7500-6000	Foraging	▒			▒	■	■
Beidha	Jordan	PPNB	7200-6600	Farming					■	■
Cafer Höyük (XIII-IX)	Turkey	PPNB	7200-?7000	Farming	■	■	?	■	■	
Jericho	Palestine	PPNB	7200-6800	Farming					■	
Nahal Hemar (3-4)	Israel	PPNB	7100-6000	Farming						■
Nevalı Çon	Turkey	PPNB	7200	Farming						
Çayönü (g - c)	Turkey	PPNB	7000-6700?	Farming		?		■	▒	
Tell Aswad (II)	Syria	PPNB	6900-6500	Farming		?			■	
Aşıklı Höyük	Turkey	PPNB	6900-6500	Farming				■	▒	
Wadi el-Jilat 7	Jordan	PPNB	6800-6400	Farming		?			▒	
Ghoraife	Syria	PPNB	6800-6200	Farming	▒			▒	▒	
Halula	Syria	PPNB	6700-6600	Farming	▒	■		▒	▒	
Can Hasan III	Turkey	PPNB	6600-5800	Farming				▒	■	▒ 4 6
Cafer Höyük (III-IV)	Turkey	PPNB	?6500-6200	Farming			?	▒	▒	6
Abdul Hosein	Iran	PPNB	6500	Farming	▒			▒	■	
Ras Shamra (Vc)	Syria	PPNB	6500-6000	Farming					■	■
Jarmo	Iran	PPN	6400?	Farming	▒	■		▒	■	
Ali Kosh (BM)	Iran	PPN	?6400-6000	Farming	▒			▒	▒	
Tell Bouqras	Syria	PPN	6350-5850	Farming						
Tell Ramad (I)	Syria	PPNB (late)	6200-6100	Farming	▒			▒	▒	
Wadi Fidan A	Jordan	PPNB (late)	6000	Farming	▒			▒	▒	
Wadi el-Jilat 13	Jordan	Late Neolithic	5900-5800	Farming	▒			▒	▒	■
El Kowm II - Caracol	Syria	PPNB	5800-5700	Farming						4 6

This table replaces that published on pages 44-45. Unfortunately a number of errors were introduced into this table (and elsewhere in this paper) during editing. Proofs were not made available to the authors.

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domestication, the farming status of PPNA sites is much less certain than appeared a decade ago. Instead, efforts are concentrating on detecting changes in harvested species that might indicate cultivation of wild plants – an essential prelude to their domestication (Colledge, 1994, 1999). Experimental cultivation (Willcox, 1992) and modelling of wheat domestication (Hillman & Davies, 1990) suggest both that cultivation of wild cereals could occur indefinitely under harvesting conditions that do not apply selective pressure for domestication characters, but could occur very rapidly once the right set of circumstances – such as sickle harvest – came into place. It is therefore unlikely that we can track the process of domestication at any one archaeological site.

At the same time, more detailed questions are being asked from the biological record. The small number of excavated sites from this early period, and continuing uncertainties about their dating, mean that we cannot currently locate domestication of wild cereals to any given part of the fertile crescent. If biological evidence showed that domestications of the Neolithic crops were single events occurring in one area, this would require significantly different explanations to a shift to farming occurring over a large part of the fertile crescent.

Botany of the wild ancestors

How reliable is the 1960s consensus on the distribution of the wild ancestors as an indication of their distribution 10,000 years ago? There is good reason to believe that current distribution both under and over-estimates the early Holocene distribution. The distribution shown in Figure 2 is of wild einkorn and wild emmer growing today in primary habitats; that is, those relatively undisturbed by humans. Wild einkorn is abundant in secondary, anthropogenic habitats such as roadsides and field edges over a far wider area, stretching from Yugoslavia to Transcaucasia (Harlan & Zohary, 1966; Zohary & Hopf, 1993). Its sibling species *T. urartu*, and both wild emmers are largely restricted to primary habitats. Given that the habitats of wild einkorn outside the fertile crescent are linked so closely to human activity, it seems reasonable to assume this distribution is the result of wild einkorn spreading as a weed alongside the spread of agriculture. Although the presence of wild einkorn (and wild barley) in the Aegean and the Balkans has led some scholars to suggest that einkorn could have been domesticated independently of its fertile crescent domestication (Dennell, 1985), archaeobotanical evidence demonstrates very clearly that agriculture and the Neolithic founder crops arrived in southeast Europe from the fertile crescent (Hansen, 1992; Nesbitt & Samuel, 1996). Support for this comes from recent DNA finger-printing and morphological analysis of wild einkorn forms from Greece. These proved to be only partly brittle-rachised, to share other morphological characters with domesticated einkorn, and to be genetically so closely related that they are best interpreted as a feral derivative of domesticated einkorn rather than its ancestor (Heun *et al.*, 1997).

Changing distribution of the wild wheats

There is also evidence that modern distribution underestimates early Holocene distribution. In part this is because of inadequate records of distribution. My map of wild einkorn distribution takes into account primary – though relatively sparse – stands in northwest Syria and western Jordan found in recent intensive exploration by ICARDA scientists (Valkoun, Waines & Konopka, 1999; Valkoun, this volume). The
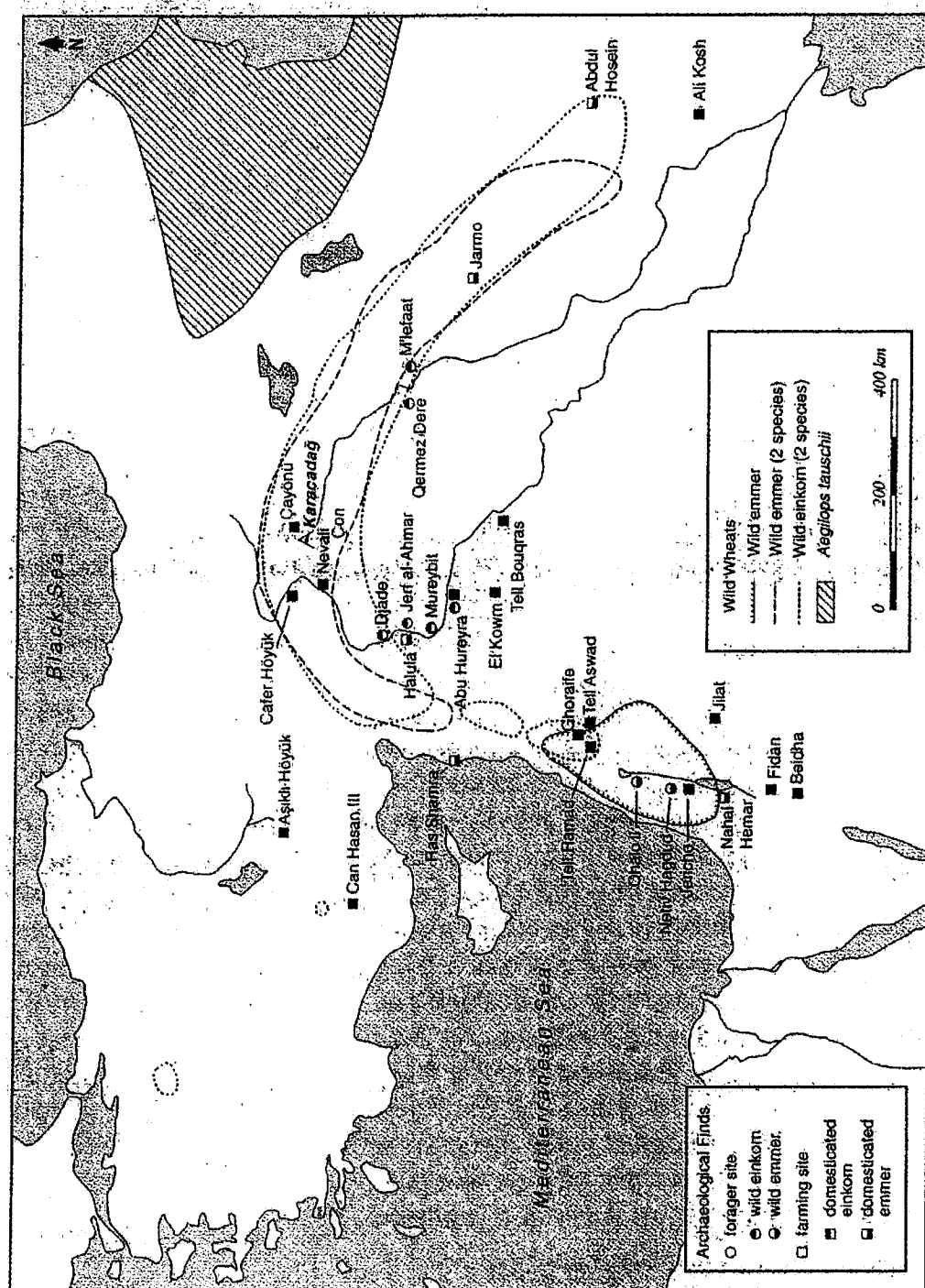
Figure 2. Distribution of early village sites in relation to wild ancestors of wheat. Southern zone of emmer is pure *T. dicoccoides*; northern zone also encompasses *T. araraticum*. Transcaucasian wild wheats are not shown. Wild einkorn distribution includes both *T. boeoticum* and *T. urartu*. The small einkorn zones in western Turkey represent primary stands in central Anatolia, where Gordon Hillman (in the 1970s) and I (in 1998) observed primary stands of wild einkorn on Karadaǧ mountain north of Can Hasan, and in northwest Turkey, where Zohary (pers. comm.) describes primary stands of wild einkorn west of Kutahya. Archaeological finds of wild einkorn may include wild rye.

relatively recent documentation of these stands is a reminder of just how incomplete our understanding is of the distribution and, especially, the ecology of wild wheats. Little is known of the climatic parameters that define distribution. Further evidence for changing distribution comes from archaeological finds of wild einkorn at pre-agrarian sites south of its current distribution, at Abu Hureyra, Mureybit and Jerf al-Ahmar (Table 3). These finds alone are not conclusive, as foodstuffs such as wild einkorn could have been imported from the north. However, the overall spectrum of plant species represented by the seeds and charcoal has led both Hillman (1996) and Willcox (1996) to argue convincingly that terebinth woodland and wild einkorn and rye extended as far south as Abu Hureyra and Jerf al-Ahmar in the past. Its current-day boundaries must be due in part to the impact of cultivation and grazing – particularly at these arid margins of growth – and in part to climatic change.

The overall picture is clear from pollen analysis of lake cores: at about 11,000 uncal BC wild cereals spread from their Ice Age refugia in the Levant (and perhaps elsewhere) into the fertile crescent. The presence of wild rye at the Euphrates sites suggests that the climate may even have been moister than today. The Younger Dryas climatic episode, in which temperatures and precipitation fell – to an unknown extent in southwest Asia – occurred between about 9000 and 8000 uncal BC (Helmer et al., 1998; Hillman, 1996). The impact of the Younger Dryas on distribution of wild cereals is controversial, beyond the likely retreat of wild einkorn from the north Syrian steppe (Moore & Hillman, 1992). Although Jones, Allaby & Brown (1998) and Hole (1998) have suggested that wild einkorn distribution could have changed in a highly unpredictable manner, there is archaeobotanical evidence that wheat distribution may have been relatively stable. First, there is an excellent match in the broad picture of archaeobotanical finds of wild wheat prior to the beginning of farming and current-day distribution, at least in the Levant and northern fertile crescent. At the two sites in the southern Levant wild emmer zone – Ohalo II and Netiv Hagdud, wild emmer is the only wheat. At the six forager sites in the wild einkorn zone of the northern fertile crescent, only wild einkorn or wild rye is present (Table 3, Fig. 2). While the sample of suitable hunter- gather sites is small, these results suggest that – as today – wild einkorn did not extend to the southern Levant, while wild emmer did not extend as far south as wild einkorn in the northern fertile crescent (Nesbitt & Samuel, 1998).

Where were einkorn and emmer domesticated?

Overall, both archaeological and botanical evidence suggests that current- day distribution of wild wheats is a reasonable guide to their distribution 10,000 years ago, with the proviso that the distribution of wild einkorn has shrunk. The next question is whether we can further localise wheat domestication within this area. T. boeoticum and T. dicoccoides are morphologically and genetically very close to their domesticated derivatives, and were identified as wild ancestors by some botanists relatively early – the 1880s for wild einkorn and the 1890s for wild emmer [see Feldman (1977) for the full story of the discovery of the wild ancestors]. However, populations of both wild species show not enough morphological variation to point to populations from any one area as more likely candidates as the wild ancestors. It has been suggested that as most domesticated einkorn has one-grained spikelets, it is more likely to derive from wild einkorns at the westerly end of its distribution (subspecies. aegilopoides), as these have
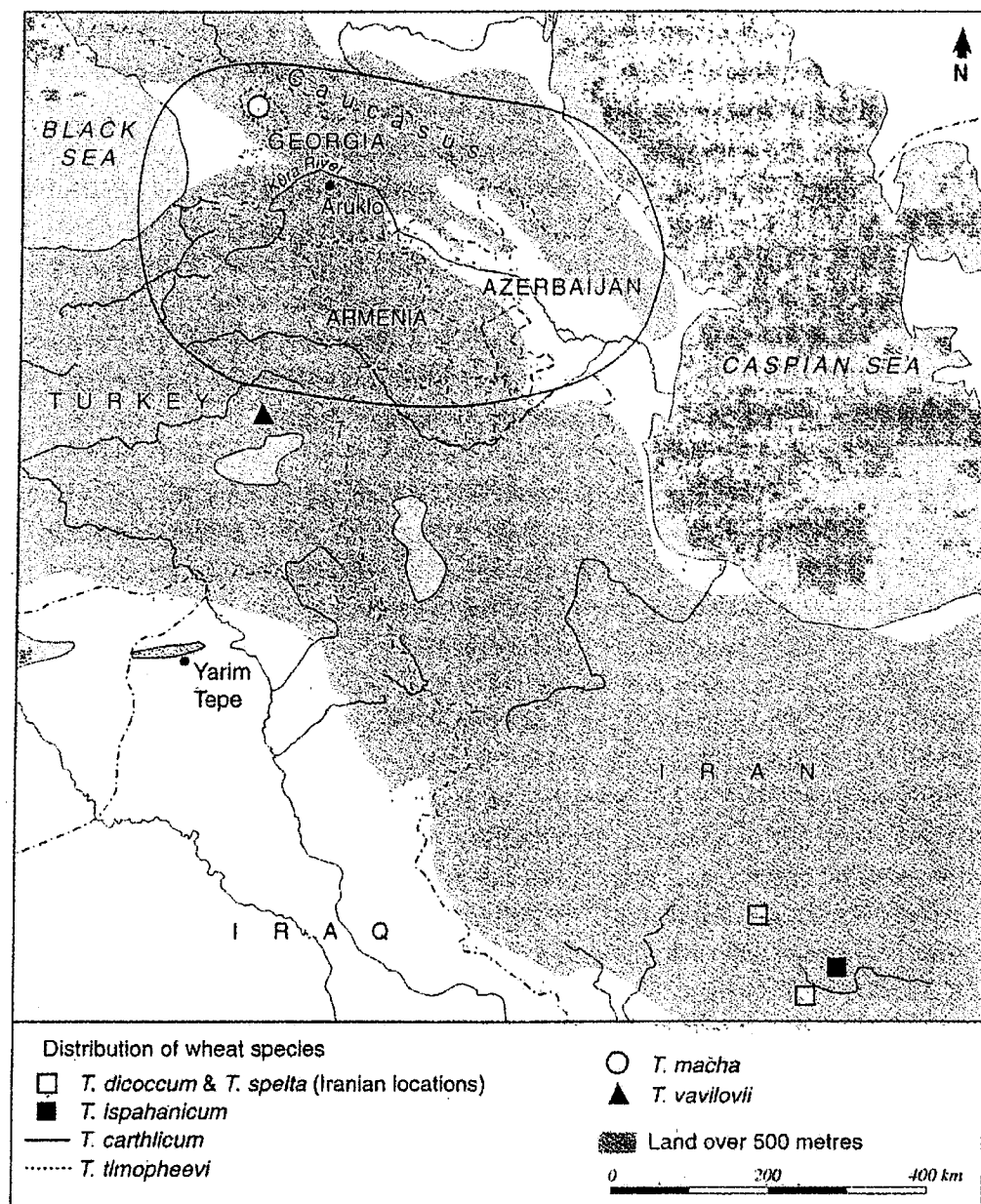
Figure 3. Distribution of endemic wheat species in Transcaucasia and Iran.

exclusively one-grained spikelets (van Zeist & Bakker-Heeres, 1982: 190–191; van Zeist & de Roller, 1991/1992). However, the spikes of wild einkorn from the eastern part (ssp. *thaoudar*) contain a mixture of one and two-grained spikelets. One-grained domesticated einkorn is always substantially larger than the grain of the two-grained form, so under strong selection pressure (e.g. for larger spikelets for sowing) it is likely that the one-grained form would have evolved very quickly from two-grained wild einkorn.

There is some evidence of morphological diversity in emmer. An exception- ally large-grained form of wild emmer, that closely resembles domesticated wheats in many other respects, grows in the upper Jordan valley (Poyarkova & Gerechter-Amitai, 1991). However, Blumler (1999) has argued convincingly that this similarity has resulted from introgression of *T. durum* into wild emmer in this region, and therefore

does not point to these populations as more probable wild ancestors. Differences have been noted between ancient European and Near Eastern domesticated emmers, for example in heavier glume venation on the latter (Hillman *et al.*, 1996; de Moulins, 1997: 36–37). Once the geo- graphical patterning of these differences is better known, they may throw light on patterns of spread of emmer wheat.

Genetics has proved more informative than morphology. Two lines of evidence have been explored. First is the non-domestication in the fertile crescent proper of the two sibling species, *T. urartu* and *T. araraticum*, even though these grow mixed with wild einkorn and emmer throughout most of their range. Although *T. araraticum* was to be domesticated as *T. timopheevi*, its narrow distribution restricted to western Georgia (Fig. 3), suggests it was domesticated later, outside the fertile crescent. Although it is only circumstantial evidence, the fact that only two* of the four species were domesticated suggests that one or few domestication events occurred (Zohary, 1996; Zohary, 1999). However this, like all arguments based on study of the current-day domesticates, cannot take account of the possible disappearance of other domesticated populations. It is possible that multiple domestications occurred, but that other domesticated populations have since been displaced by one dominant package of crops and are extinct. In the case of wild einkorn, however, more detailed genetic evidence does point to a single domestication. DNA finger-printing points conclusively to populations of wild einkorn on Karacadağ in southeast Turkey (Fig. 2, not to be confused with Karadağ in central Turkey) as by far the closest wild relative of einkorn, and thus its wild ancestor (Heun *et al.*, 1997, see also Nesbitt, 1998). In general, genetic evidence points to single or few domestication events for the Neolithic founder crops (Zohary, 1999). Assessment of evidence from DNA variation in domesticated emmer for two waves of emmer spreading into Europe – perhaps resulting from separate domestications – awaits characterisation of the wild ancestors (Allaby, Banerjee & Brown, 1999; Brown, 1999).

ORIGIN OF SPELT WHEAT AND BREAD WHEAT

Early research

Pioneering cytogenetical work in the years immediately before and after publication of Percival's monograph was to demonstrate that wheat was a polyploid series of, respectively, diploid, tetraploid and hexaploid wheats (Table 1). Percival's hypothesis that the spelt group was the result of hybridisation between the tetraploid group and one or more diploid *Aegilops* species was confirmed in the 1940s by experimental hybridisation of *T. dicoccum* and *Aegilops tauschii* (= *Ae. squarrosa*), resulting in a hybrid wheat with strong morphological similarities to *T. spelta* and which crossed easily with *T. spelta* and *T. aestivum* (Kihara, 1944; McFadden & Sears, 1946)[1]. Subsequent experiments have shown that all crosses of tetraploid wheats, whether or not free-threshing, with *Ae. tauschii* result in hulled spelt wheat (Kerber & Rowland, 1974).

Once the hybrid origin of the hexaploid wheats had been established by the 1920s, it was clear that hulled *T. spelta* was the more primitive form and that *T. aestivum* was

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1   Although the tetraploid parent was reported as *T. dicoccoides*, it has subsequently been re-identified as *T. dicoccum* (Sears, 1976).

derived from it. However, archaeobotanical evidence indicated that spelt wheat appeared in a geographically circumscribed region of central Europe well after the arrival of the original Neolithic founder crops, which included abundant hexaploid naked wheats (now recognised as including tetraploids – see above). Therefore, European spelt wheat could be understood best as originating from bread wheat, either by a simple mutation, or by introgression (hybridisation followed by back-crossing with *T. aestivum*) of *T. aestivum* and *T. dicoccum*. Experiments in artificial hybridisation of these two species produced progeny very similar in morphology to spelt wheat (Mac Key, 1966).

The origins of spelt wheat in Europe

Once accurate wheat identification criteria were developed in the 1980s, it became clear that naked wheat – some of it certainly hexaploid – is present in the earliest Neolithic (Bandkeramik) of central Europe (5400–4900 cal BC), although it is far less common than emmer. Although most free-threshing wheats in the Swiss lake settlements discussed above have been re-identified as tetraploid, hexaploid free-threshing wheats are abundant at Middle Neolithic sites (Rössen culture, 4700–4300 cal BC) outside the Swiss lake area (Maier, 1996: 50). Even in the lake settlements, ancient DNA gives evidence for the presence of hexaploid free-threshing wheat (Schlumbaum, Jacomet & Neuhaus, 1998).

Spelt appears in the Swiss lake district in the Early Bronze Age (2200–1500 cal BC) and during the same period elsewhere in Europe, at sites ranging from Germany to Greece. Re-examination of some finds has shown Early Bronze Age finds to be reliable but claimed Late Neolithic identifications to be unreliable (S. Jacomet, personal communication). Spelt is absent from the now very extensive range of Near Eastern archaeobotanical assemblages (Miller, 1991). Isolated occurrences are due to mis-identification of *Aegilops* chaff, abundant and morphologically somewhat similar, as at Yarym Tepe in northern Iraq (Bakhteyev & Yanushevich, 1980, illustrated in Bakhteev, Lisitsina & Yanushevich, 1992: 150) or to isolated finds as at Erbaba in Turkey (van Zeist, 1983) which perhaps represent mutant forms of *T. aestivum*.

Archaeobotanical evidence for the presence of hexaploid free-threshing wheat and emmer in Neolithic Europe shows that spelt *could* therefore have originated from a hybridisation event of a free-threshing hexaploid and a hulled tetraploid wheat in this region. However, this has been overshadowed by new archaeobotanical evidence for spelt in Transcaucasia and north of the Black Sea, suggesting an alternative route of travel to Europe that avoids the Near East, explaining why there are no Near Eastern finds of spelt. This archaeobotanical evidence forms the basis of the most widespread current interpretation (e.g. Andrews, 1964; van Zeist, 1976: 37; Zohary & Hopf, 1993: 52–53), that spelt originated once, in Transcaucasia or northwest Iran, and travelled westwards to Europe, arriving in Europe as a second-wave crop several millennia after the arrival of agriculture.

The origins of spelt and bread wheat in the Near East

The origin of bread wheat in the Near East remains as problematic as the origins of spelt in Europe. The hybridisation between a tetraploid wheat and *Aegilops tauschii* could take place only once agriculture with tetraploid wheats reached the distribution zone of *Aegilops tauschii*. This extends from northern China westwards to west and

southwest of the Caspian Sea, well northeast of the fertile crescent (Fig. 2). As agriculture did not reach the Caspian Sea until after 6000 uncal BC, the hybridisation could not have occurred until then (van Zeist, 1976). However, reliable rachis criteria (discussed above) have been used to identify hexaploid free-threshing wheats in 30 different samples from all the excavated phases at Can Hasan III, dating from 6400–5700 uncal BC (Hillman, 1978: 168), and at Cafer Höyük, in levels III and IV dating to about 7000–6200 uncal BC (de Moulins, 1993). There is thus a conflict between the archaeobotanical evidence for seventh millennium uncal BC domestication of hexaploid bread wheat, and archaeological and biological evidence that the hybridisation of its ancestor, *T. spelta*, could not have occurred until after 6000 uncal BC.

Archaeological work since the 1960s has confirmed van Zeist's dating of the earliest agricultural sites around the Caspian. Sites further to the south, in the Zagros mountains, such as Jarmo, Ali Kosh and Abdul Hosein have good evidence of farming (including emmer) by 6500–6400 uncal BC (Table 3). In contrast, intensive surface survey around Haji Firuz Tepe and Yanik Tepe, both in Iranian Azerbaijan southwest of the Caspian Sea, failed to uncover any evidence of occupation earlier than 5500 uncal BC (Hole, 1987: 44–45). The Zagros mountains appear to have acted as a barrier to the rapid spread of agriculture in this direction. Is it possible that the distribution of *Aegilops tauschii* in fact extended further west, allowing the hybridisation to occur much earlier?

Distribution of *Aegilops tauschii*

Today *Aegilops tauschii* grows abundantly in northern Iraq, eastern Turkey, Armenia and Azerbaijan, as well as in the southern fringes of the Caspian and to the east (van Slageren, 1994: 330;Zohary & Hopf 1993: 51). However many of the western occurrences are in secondary habitats (Zohary, Harlan & Vardi, 1969). In Figure 2 I have extended the possible primary distribution to include more of the relatively frequent records from Armenia and Azerbaijan. *Ae. tauschii* is divided into two subspecies, *tauschii* and *strangulata*. Evidence from isozymes (Jaaska, 1980; Nishikawa, 1983) points to *strangulata* as the most likely contributor of the D-genome. This is distributed in two separate regions, in Transcaucasia and southeast of the Caspian. More detailed studies using variation in DNA have shown that some accessions identified as *tauschii* on morphological grounds in fact share the genepool of *strangulata*, and that this genepool is more geographically widespread than first thought, stretching to north-central Iran and southwest Caspian (Dvořák *et al.*, 1998). *T. aestivum* is most closely related to *strangulata* accessions from southwest Caspian and Transcaucasia (in particular Armenia). *Ae. tauschii* accessions from southeast Turkey and western Iran are subspecies *tauschii* and are therefore not closely related to bread wheat. It appears that the hybridisation event(s) must indeed have occurred in the Caspian or Transcaucasian regions.

Recent cultivation of spelt in Transcaucasia

If Transcaucasia did play any role in the origin of spelt or its spread to Europe, given the remarkable diversity of wheats in the region today, it seems likely that spelt could still be present. In the recent past spelt has been recorded in southeast Transcaucasia in Azerbaijan, cultivated with *T. aestivum* (Dorofejev, 1971), and in southeast Iran (Fig. 3) (Kuckuck, 1959; Kuckuck & Schiemann, 1957). Dorofejev suggests that both the Azerbaijan spelt and Kuckuck's Iranian spelt might be of secondary origin, while a rare

form of spelt with denser ears known as *T. macha* Dek. et Men. might be a remnant of the primary domestication of spelt. However, *T. macha* has a remarkably limited distribution, grown only on about 50 hectares of land in western Georgia (Fig. 3), mixed with a form of *T. dicoccum* known as *T. paleocolchicum* (Dekaprelevich & Menabde, 1932). Given that *T. macha* has a very limited distribution, is somewhat weedy with very brittle ears, and has a rachis disarticulation (wedge-type) different from that of spelt, it most probably has a late, secondary origin, perhaps by crossing of *T. dicoccum* and *T. aestivum*. Jakubziner suggests *T. macha* is derived from *T. paleocolchicum* (a form of *T. dicoccum*) which it closely resembles, presumably by introgression to *T. aestivum*. Investigations of alcohol dehydrogenase isoenzymes showed that *T. macha* does not share the same type of isoenzyme with *T. paleocolchicum*, but rather with other Transcaucasian emmer and spelt (Jaaska, 1978: 214). However, recent RFLP DNA analyses suggest that both *T. macha* and *T. paleocolchicum* derive from a cross between hexaploid wheat and wild emmer, confirming that *T. macha* is not an ancestral form of hexaploid wheat (Dvořák & Luo, this volume). All the hexaploid wheats, including *T. macha*, share a common D-genome genepool, and there is thus no evidence for separate hybridisation with *Ae. tauschii* leading to *T. macha* (Dvořák *et al.*, 1998).

Archaeological evidence for spelt in Transcaucasia

Given the problems in chronology with a Caspian origin of spelt, how does the alternative location, Transcaucasia, compare? A shadowy Aceramic Neolithic period, of unknown agricultural status, is followed by a widespread Neolithic, characterised by round-housed farming villages, in Georgia, Armenia and Azerbaijan. This is contemporary with sites such as Haji Firuz further to the south, beginning at about 5500 uncal BC (Chataigner, 1995: 37; Mellaart, 1975: 201–202). A Transcaucasian origin of spelt therefore does not resolve the dating problem.

Is spelt present at these Neolithic settlements? *T. spelta* is recorded from Arukhlo 1 in Georgia (5500 uncal BC and later) and the published drawings, although unclear, do seem to show a spikelet with barrel-type articulation and elliptical transverse section (Janushevich, 1984: 271). However, spelt is apparently absent from those Armenian and Azerbaijan sites for which we have published plant remains (Chataigner, 1995: 202). Without further documentation of the Arukhlo find, the sporadic nature and uncertain identification of spelt finds in Transcaucasia is insufficient evidence for their presence in prehistory. Then, as today, most wheat was free-threshing. Although a wide variety of identifications are made (e.g. *T. turgidum*, *T. durum*, *T. compactum*, *T. carthlicum*, *T. aestivum* and *T. compactum*) these are not documented by detailed morphological criteria (Lisitsina & Prishchepenko, 1977). In practice, the ploidy level of free-threshing archaeological material is unknown. Plant remains from a number of Georgian sites examined and comprehensively published by Schultze-Motel (1988a, b) are comparable to those found at Near Eastern sites, containing abundant free-threshing wheat and none of the unusual species recorded by other archaeobotanists. The wide range of wheat species identified in ancient material undoubtedly reflects knowledge of the current-day diversity of wheats in the region, and the desire to claim its pivotal role in wheat evolution (cf. Lisitsina,1978; Menabde, 1970).

Evidence of spelt on the northerly route around the Black Sea is also uncertain. Janushevitch has published a series of well-illustrated archaeobotanical reports on

material from Moldavia, Ukraine and the Crimea, through which spelt must have passed. All the spelt spikelets illustrated are narrow and rounded, with a thickened base (Janushevich, 1984: 268, 270; Janushevitch, 1986: 8). They strikingly resemble the spikelets of *Aegilops cylindrica*, a weedy species that is abundant in the Balkans and north of the Black Sea and Transcaucasia. In Transcaucasia *Ae. tauschii* is also a candidate species.

Summary

Neither biological nor archaeobotanical evidence allow any definite statement on where and when current day populations of spelt had their origin. The experimental evidence of genetics demonstrates that a hybridisation of spelt must have occurred before the evolution of hexaploid free-threshing wheat. Evidence from DNA (Dvorák *et al.*, 1998, 1999) and from isozymes (Jaaska, 1980) points to a monophyletic origin of hexaploid wheat. Suggestions that *T. aestivum* originated independently in China (Yen, Luo & Yang, 1988) are not supported by DNA analyses. These show that Chinese *T. aestivum* shares the same rDNA genotype as *Ae. tauschii strangulata* in the Caspian and Transcaucasian regions, rather than the genotype present in *Ae. tauschii* in China (Lagudah, Appels & McNeil, 1991: 393). Isozyme evidence (Jaaska, 1978) however does show relatively consistent differences in alcohol dehydrogenase isoenzymes between Asian and European forms of spelt, suggesting that the European forms did not originate simply by migration from Asia. This is supported by RFLP DNA analyses that find European spelts to be most closely related to European bread wheats (in particular, Alpine club wheats) and only distantly related to Asian spelt (Dvorák *et al.*, 1999; Dvorák & Luo, this volume). This is consistent with origin of spelt in Europe by introgression of emmer into free-threshing hexaploid wheats.

The lack of archaeological evidence for spelt in the Near East or Transcaucasus suggests that spelt was a brief transitory form prior to the emergence of bread wheat. If, for example, the hybridisation was of *T. durum* and *Ae. tauschii*, rather than *T. dicoccum*, the result would have been a hulled wheat in a free-threshing field. Because the crop-processing requirements of hulled wheats are different to those of free-threshing wheats, there would be a strong selection pressure for free-threshing characters, combined with a strong selection pressure in the upland areas for the more cold-resistant properties given by the D-genome to hexaploid wheats. This scenario would suggest that, as with domestication of wild wheats, the process may be so quick that the transitional stage (i.e. spelt) would not be visible in the archaeological record. Evidence from genetics is equivocal on the identity of the tetraploid ancestor. Reconstitution of the tetraploid component of bread wheat, by removal of the D genome, resulted in a free-threshing wheat (Kerber, 1964). Evidence of genes for waxiness points to emmer (Tsunewaki, 1966). Further genetical investigation of the nature of the tetraploid ancestor of hexaploid wheats would be valuable. In the meantime, neither archaeological nor genetical evidence resolve the problem of the origin of European spelt.

CONCLUSIONS

My two case-studies offer different perspectives on progress since Percival's time. Our understanding of einkorn and emmer domestication has benefited enormously from

the far greater range of excavations in the Near East and improvements in dating and recovery of archaeological plant remains. While the differentiation between hunter-gatherer and early farming settlements is recognised as problematic, this has driven archaeobotanists to record plant remains more carefully – particularly for characters relating to rachis fragility – and to explore new techniques of detecting pre-domestication cultivation, especially during the PPNA period. Botanical evidence has benefited from the great increase in collection of wild and cultivated plants, particularly by Russian botanists in the 1920s, and Japanese and American botanists in the 1960s and 70s. Genetic characterisation of the wild wheats has been successful in showing their relationships to the domesticated wheats, and in the case of einkorn, in narrowing down the likely area of domestication. However, the ecology of the wild wheats is still insufficiently studied, and as a result key questions about its past distribution are difficult to answer. Overall, biological and archaeological evidence have meshed well in understanding the domestication of einkorn and emmer.

In the case of spelt wheat and bread wheat, re-examination of archaeo- botanical evidence suggests that the origins of spelt are as unresolved now as in the 1920s. Botanical and archaeological evidence make it absolutely clear that the initial hybridisation of spelt must have occurred in the Caspian or Transcaucasian region by 6500 uncal BC, but evidence of spelt itself remains highly elusive. Botanical evidence has in part confused issues by drawing attention to sporadic current-day occurrences of *T. spelta* and *T. macha* in Transcaucasia and Iran which might, like the European spelt, result from hybridisation of emmer and bread wheat. Older identifications of spelt need checking urgently. Improved characterisation of the D genome and the application of DNA analyses now suggest that older views (of Percival's day) are perhaps correct, that European spelt originated independently in Europe from hybridisation of tetraploid wheat and *T. aestivum*. Integration of biological and archaeobotanical work will continue to be essential in solving this problem.

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