‘To call each thing by its right name'?

Exploring the potential of geometric morphometrics to interpret the diversity of archaeobotanical wheat grains

Tina Roushannafas

Merton College
School of Archaeology
University of Oxford

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Abstract

This research sets out to assess the potential of geometric morphometric (GMM) outline analysis to refine taxonomy and analyse diversity among charred wheat grains preserved in archaeological deposits. An equivalent methodology is applied across three archaeological case studies, allowing for specific research questions and the parameters and effectiveness of the GMM approach to be assessed. Analysis of experimentally charred modern wheat accessions demonstrates that a combination of two-dimensional views enables taxonomic separation based on grain shape. Morphological diversity of grains is further explored as relating to a range of factors, including varietal-level distinctions, domestication status, growing conditions and crop processing.

The first case study (Paper 1) concerns the taxonomic identification and domestication status of so-called 'new glume wheat' (NGW) at Neolithic Çatalhöyük (Central Anatolia), summarising existing evidence for a once-widely spread crop that has almost disappeared in the present day. Results indicate that NGW grains exhibit a strong morphological resemblance to Timopheev's wheat (*Triticum timopheevii*), while morphological analysis of both grain and chaff suggest that this crop underwent a gradual co-evolutionary process of domestication during the Neolithic occupation sequence. Development of the crop is interpreted in the context of diverse plant food strategies at the site which helped to offset the risk of individual resource failure.

The second case study (Paper 2) analyses 'free-threshing' wheat (FTW) grains from Neolithic Çatalhöyük and Kouphovouno (southern Greece), highlighting ambiguities in the early evidence for the two genetic groupings of 'naked' wheats. Results indicate that a tetraploid wheat resembling modern durum was cultivated at Kouphovouno, and support evidence of hexaploid wheat cultivation at Çatalhöyük. The findings build on theories of a more southerly route of tetraploid FTWs into Europe along the Mediterranean coast, with hexaploid FTW spreading through the Balkans and Carpathian basin into central Europe.

Interpretation of results considers the sustainability of the regimes associated with these crops in the long term.

The third case study (Paper 3) investigates the theorised introduction of tetraploid rivet wheat into Late Anglo-Saxon agriculture. Archaeological wheat grains are examined from twelve sites in central, eastern and south-west England, accessed through the 'FeedSax' (Feeding Anglo-Saxon England) project. Specimens closely resembling modern rivet wheat, and particularly traditional 'Blue Cone' rivet, are identified at multiple sites. The introduction of rivet is contextualised within a period of acceleration and innovation in arable production, including the strategic cultivation of a broader range of crops as corresponding to local conditions. The final study (Appendix 1) addresses related concerns, reporting on experiments comparing grain shape, size and yield of the same wheat variety grown under different agricultural regimes.

Across the case studies, insights into diverse and flexible practices of cultivation in the past are interpreted in the context of contemporary concerns regarding sustainability and the loss of genetic diversity in modern wheat farming. Overall, findings indicate much potential for further exploration of morphological diversity in archaeobotanical cereal remains using GMM, a rapidly evolving field for which new archaeological applications are continuously emerging.

Co-authorship statement

As an article-based (or 'integrated') thesis, the following is composed of three papers framed by a unifying introduction and conclusion. My academic supervisors, Profs. Amy Bogaard and Mike Charles, are listed as co-authors specifically for Papers 1 and 2 in reflection of their previous work on the material, but are acknowledged as having provided significant input through regular discussion meetings and providing feedback on work that I submitted to them for all three papers. Dr Mark McKerracher is listed as co-author for Paper 3 in recognition of previous analyses conducted on a proportion of the assemblages, assistance with accessing and selecting the archaeobotanical material and general guidance and commentary provided for the final paper. The generation of data and writing of the articles was, however, primarily my responsibility and completed by myself.

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Thanks, of course, to my family for their long-term support of my academic pursuits, and especially my mother — right back to reassuring me as I panicked before sitting my GCSEs, to cheerleading any subsequent minor achievement. Rachel Townsend is also thanked for being a wonderful human being and for checking in on me when I needed it.

Finally, I would like to dedicate this thesis to the memory of Dr Lisa Lodwick. While I don't feel it is my place to articulate the loss her death has been to the research community and to her friends and loved ones, I will say that I frequently have thought of her when working on my research. I hope, and feel, that continuing to ask myself 'what would Lisa think about this?' will help to make me a better researcher in the future.

0.0 Introduction

0.1 Overview

Wheat is a nutritional staple for a significant proportion of the global population and has held a key dietary role since the earliest stages of European, Western Asian and North African agriculture. The genus *Triticum* encompasses numerous species/sub-species (Table 1) and many hundreds of named varieties which represent over 20,000 years of experimentation, development and adaptation to a wide range of environmental conditions. Today, modern wheat production is dominated by a single sub-species of wheat — *Triticum aestivum* L. ssp. *aestivum* or 'bread wheat' — which accounts for over 90% of wheat cultivated globally (Giraldo *et al*. 2019). This dominance by just one sub-species has not only given rise to concerns over sustainability and loss of biodiversity in cereal agriculture (e.g. Camacho Villa *et al.* 2005; Mijatović *et al.* 2013; Pilling *et al*. 2020), but also belies the complex history of human interaction with the genus.

More fully understanding the trajectory and development of such an anthropogenically significant plant is an obvious goal for archaeobotanists, who study the role of plants in past human societies through their expression in the archaeological record. Indeed, current concerns over the loss of genetic diversity in modern wheat crops (Venske *et al*. 2019) can only be an incentive to better understand the varied forms and adaptations of wheat in the past. This aim is challenging due to the fact that the most archaeologically enduring form of wheat — its charred grain — presents distinct difficulties in terms of taxonomic classification on morphological grounds (Jones 1998). Refining taxonomic identifications of grains is therefore considered an initial priority, as it allows us to interpret archaeobotanical remains within a shared scientific framework.

With this acknowledged, identification in the sense of taxonomic classification is not necessarily the only goal worth pursuing. Beyond the desire 'to call each thing by its right name', there is value in describing variation not only between, but also *within* the classes we recognise. If we can approach variation in archaeobotanical remains not as an obstacle

to analysis, but as something worth exploring in its own right, we open up the potential to understanding the multitude of ways in which crops continuously adapt and are adapted to anthropogenic environments. Traditionally crops would have been grown not as the uniform blocks (or monocultures) we see in modern industrial farming, but as 'landraces' which were genetically diverse and co-evolved alongside humans in a way that reflects not just their environment, but also the habits, practices and requirements of the peoples that cultivated them. Studying crops with this perspective in mind, helps us to understand human-plant-environmental relationships in terms of situated processes as opposed to fixed categories (Bogaard *et al*. 2021) and to contextualise the limited diversity found in most modern agricultural systems.

The three papers presented here proceed on the hypothesis that geometric morphometric (GMM) analysis can offer specific advantages in classifying, analysing and describing variation in archaeobotanical charred wheat grains. The articles address research questions relating to the agricultural practices of specific archaeological case studies, while more broadly evaluating the effectiveness and potential of the GMM approach. Case studies examined include Neolithic Çatalhöyük (Central Anatolia) (Papers 1 & 2), Neolithic Kouphovouno (southern Greece) (Paper 2) and multiple sites included in the 'FeedSax' (Feeding Anglo-Saxon England) project dating to the early medieval period (Paper 3). Within these studies, the potential for GMM analysis of grain shape to assess ploidy-level, species and varietal-level distinctions, domestication status, crop processing and environmental influence on grain formation are all examined.

0.2 The Role of Wheat

The economic and cultural significance of wheat is not easily overstated. 'Wheat' refers not to a single cultivar, but rather a genus encompassing several related species arising from multiple domestication and hybridisation processes. Evidence of the pre-domestication cultivation of wheat stretches as far back as the early Epipaleolithic site of Ohalo II (Sea of Galilee, Israel), a lakeside camp submerged *c.* 23,000 years BP (Weide 2022). Here, waterlogged remains of wild emmer wheat grain and chaff were recovered, with artefactual

Section	Species	Ploidy Level	Genomic constitution	Subclassifications	Common name	Status	Type
Monococcon	*Triticum monococcum* L.	Diploid	AA	ssp. *monococcum*	Einkorn	Domesticated	Glume/Hulled
				ssp. *aegilopoides* (Link) Thell.	Wild einkorn	Wild	
	Triticum urartu Tum. ex Gand.			-	Red wild einkorn		
Dicoccoidea	*Triticum turgidum* L.	Tetraploid	BBAA	ssp. *turgidum*	Rivet/Cone/Pollard	Domesticated	Free-threshing
				ssp. *carthlicum* (Nevski) Löve & Löve	Persian/Dika wheat		
				ssp. *dicoccum** (Schrank) Thell.	Emmer		Glume/Hulled
				ssp. *durum* (Desf.) Husn.	Durum/macaroni		Free-threshing
				ssp. *paleocolchicum* (Menabde) Löve & Löve	-		Glume/Hulled
				ssp. *polonicum* (L.) Thell.	'Polish' wheat		Free-threshing
				ssp. *turanicum* (Jakubz.) Löve & Löve	Khorasan wheat		Free-threshing
				ssp. *dicoccoides* (Körn. ex Asch. & Graebn.)	Wild emmer	Wild	Glume/Hulled
	Triticum timopheevii (Zhuk.) Zhuk.		GGAA	ssp. *timopheevii*	Timopheev's wheat	Domesticated	Glume/Hulled
				ssp. *araraticum** (Jakubz.)	Wild Timopheev's	Wild	Glume/Hulled
Triticum	*Triticum aestivum* L.	Hexaploid	BBAADD	ssp. *aestivum*	Bread wheat	Domesticated	Free-threshing
				ssp. *compactum* (Host) MacKey	Club wheat		Free-threshing
				ssp. *macha* (Dekapr. & Menabde) MacKey	Makha wheat		Glume/Hulled
				ssp. *spelta* (L.) Thell.	Spelt wheat		Glume/Hulled
				ssp. *sphaerococcum* (Percival) MacKey	Indian dwarf wheat		Free-threshing
	Triticum zhukovskyi Menabde & Ericz.		GGAAAA	-	Zhukovsky's wheat		Glume/Hulled

Table 1 Taxonomic classification of wheats based on van Slageren 1994 *= modified after preferred/common usage, see note in Zohary *et al*. 2012, 29

and spatial evidence indicating that these grasses were processed using a grinding stone (Snir *et al.* 2015).

Domestication of wheat began in the early Holocene in the south-west Asian region known as the 'Fertile Crescent'. Defining precise boundaries of early cultivation and domestication is complex (see e.g. Asouti and Fuller 2012), but in approximate terms, the earliest domesticated wheat cultivars, einkorn and emmer, are recorded from around 10.7–10.2 ka Cal BP (Arranz-Otaegui *et al*. 2016). Wheat became a staple crop and was part of a 'founder crop package' which spread east and west across Eurasia, arriving in the Indus Valley and Turkmenistan by *c.* 6000 BCE and to the British Isles *c.* 4000 BCE, with dispersal also occurring southward into southern Arabia and northern Africa via Egypt, and further east into India and China along multiple routes (Fuller and Lucas 2014; Liu *et al.* 2017). By *c.* 1500 BCE the geographical range of wheat stretched from the Atlantic Ocean to the Pacific (Liu *et al.* 2016).

In modern times, the economic importance of wheat is clearly figured. For 2022 the forecast for global wheat production is set at 776.5 million tonnes, accounting for just under 30% of global cereal production, which includes rice and maize (FAO 2022). Wheat is a nutritional staple for around 40% of the world's population (Giraldo *et al.* 2019) and is gaining an increasingly important economic role in rapidly urbanising and industrialising countries around the world, including those of sub-Saharan Africa and eastern Asia (Shewry and Hey 2015). Wheat possesses many advantages as a crop; it can be high yielding in a wide range of soils, latitudes, moisture conditions and temperatures (Curtis 2002), is easily stored for later consumption and is of relatively high nutritive value, providing not only energy in the form of carbohydrates but also protein, dietary fibre, B vitamins and phytochemicals (Shewry and Hey 2015). Its gluten protein fraction confers viscoelastic properties which allow it to be processed into a variety of food products including bread, pasta, cakes and biscuits (Shewry 2009).

0.3 The Diversity of Wheat

As a result of thousands of years of intensive and extensive human utilisation and experimentation, wheat is found in a wide variety of forms and adaptations. There are three genetically distinct wheat groups based on ploidy level: diploid, tetraploid and hexaploid, and among these six species are recognised in the taxonomy used herein (van Slageren 1994; Table 1). Alternative taxonomies are proposed and used elsewhere (e.g. Goncharov 2011) but, in the absence of a definitive consensus, the aforementioned is used based on greater uptake in the archaeobotanical literature and the clarity with which genus relates to genetic groupings. Practically, wheat crops are often described at the sub-species level as defined by van Slageren, to which the common names can be seen to refer (Table 1). For ease of reference these are therefore often described herein as 'cultivars' or as '(sub-)species', to reflect the fact that in certain taxonomic systems, as well as common usage, they are often treated as distinct species.

Beyond the generally accepted taxonomic classifications, there exists a vast array of named varieties with different morphological and adaptive characteristics (see e.g. Percival 1921) and new varieties are continuously under development (Venske *et al.* 2019). As wheat spread across different geographic ranges, altitudes and climates it would have needed to adapt to a range of environments. However, cultural and culinary factors are also relevant. For example, selection for variants of *Triticum aestivum* with smaller, rounder grains in eastern Asia is likely to have been influenced by factors such as milling and cooking properties, nutritional content or flour colour, as well as environmental considerations (Liu *et al.* 2016).

In addition to the range of wheat varieties documented historically, there are instances of morphotypes recorded in archaeobotanical reports for which no apparent modern analogue is known. These archaeological wheat forms include the so called 'new type' glume wheat addressed in Paper 1, but also the short-grained, dense-eared naked wheats dubbed *Triticum parvicoccum* (Kislev 1979) and *Triticum vulgare antiquorum* (Heer 1865). While the validity of assigning new species names to these latter types has been questioned (Hillman

2001; Nesbitt 2001), the observation of distinct forms nevertheless has the potential to build towards an understanding of the diversity of wheat forms in prehistory. Characterisation and assessment of the distinctiveness of these archaeologically-defined cultivars is an area in which GMM may have much to contribute.

Despite the clear adaptive potential of the genus, modern production is focussed almost entirely on just one sub-species: modern hexaploid bread wheat (*Triticum aestivum* L. ssp. *aestivum*), which accounts for as much as 90–95% of global production (Giraldo *et al.* 2019). The wheat with the second-highest level of production is durum (*Triticum turgidum* L. ssp. *durum*), primarily used to make pasta. The evolutionary trajectory of bread wheat, as well as its relatively recent development and intensive selection through cultivation and modern breeding programs, have resulted in a restricted gene pool when compared to other crops (Venske *et al.* 2019). Indeed, there is evidence that emphasis by modern markets on uniformity in grain size and shape, as related to milling performance, has led to significant loss in phenotypic variation in grain form in the germplasm pool of modern wheat as compared to 'ancestral' forms (Gegas *et al.* 2010). More broadly, the loss of genetic diversity in modern crops has prompted increasing concern regarding the potential impact on the sustainability of current arable farming practice, particularly in the face of climate change (Mijatović *et al.* 2013; Pilling *et al.* 2020).

More genetically diverse populations, or landraces, of crops possess a range of specific traits relating to tolerance of pests, diseases and marginal environmental conditions which together contribute to the resilience and adaptability of that cultivar (Camacho Villa *et al.* 2005). The development of a wide range of wheat cultivars, therefore, influenced not only the development of a significant proportion of our human ancestry, but may also be key to our future survival. As such it is important that archaeobotany can contribute to as full a picture as possible of the trajectories of different cultivars and ways in which these were adapted to different environments. In this way, we may begin to assess what has been lost, and potentially inform, or motivate, the process by which biodiversity may be regained.

0.4 The Archaeobotanical Identification of Wheats

Charring reduces plant remains to inert carbon, allowing grains to survive for thousands of years while resisting biodegradation. This same process, however, distorts the dimensions of the grain and, at higher temperatures, can cause significant re-shaping as cavities form and the contents of the grain begin to exude (Charles *et al*. 2015). Indeed, charring experiments have shown that only grains charred within a quite narrow temperature range (~220–240°C) under low oxygen conditions are preserved well enough to be potentially identifiable to (sub-)species (*ibid.*). Charring also leads to loss of colour, hairs, surface texture and other features which may otherwise assist in taxonomic classification. Even when grains are well preserved, establishing reliable morphological characteristics in wheat grains by which to distinguish between taxa has been acknowledged as difficult (Hillman *et al*. 1996; Jones 1998).

Issues of grain morphology and charring distortion may be considered especially problematic because charred grains frequently form a high proportion of the archaeobotanical evidence. Survival of whole ears of wheat is rare outside the excellent preservation conditions of lakeshore settlements (Maier 1996). The most commonly recovered wheat remains are the more robust grains, rachis segments and glume bases, and, of these, grains are the most likely to survive charring (Boardman and Jones 1990). Most of the features used by botanists to distinguish between varieties, such as the presence of awns, overall shape of the inflorescence or characteristics of the leaves and straw (see e.g. Percival 1921), are unlikely to be preserved in most contexts, particularly when charred. Identification by means of genetic sequencing can also be problematic, as aDNA is significantly damaged by the charring process (Nistelberger *et al.* 2016). Furthermore, certain categories of wheats (i.e. naked wheats; see Papers 2 & 3) are usually processed in bulk away from domestic charring contexts, meaning that their chaff is even less likely to enter the archaeobotanical record (Jones 1987). As such, despite the acknowledged difficulties in interpreting their morphology, charred grains are not a resource archaeobotanists can afford to neglect.

In highlighting the difficulties of so-called ‘traditional’ identification of morphological features by eye, the intention is not to imply that this is not a valuable approach — indeed it has contributed to most of our archaeobotanical understanding so far. It is a rapid and efficient method suitable to analysing large datasets and cannot be replaced. There is, however, clearly scope to enhance the reliability and specificity of classifications of archaeobotanical wheat remains. The degree to which the eye can classify variation is limited, tending towards reduction of diversity in a population (Portillo *et al.* 2020), even if this can be offset to some extent by the use of descriptive categories (Jones 1998). GMM offers the potential both to enhance descriptions of form variation, as well as improve consistency of classifications, beyond what is possible by the human eye alone.

0.5 Geometric Morphometrics

Morphometrics is concerned with applying statistical analyses to variations in morphology, allowing one to analyse shapes in a comparable way to numeric data and to assign classifications probabilistically. The quantification of morphology has been a centuries-long concern of biologists, particularly as applied to taxonomy and the creation of models of evolutionary and developmental dynamics (Bardua *et al.* 2019). Traditional morphometrics involves the application of multivariate statistics to a predetermined set of variables, usually consisting of individually measured distances on an organism (Rohlf and Marcus 1993). The development of modern geometric morphometrics and a range of new techniques in the 1980–90s means we can now analyse shapes as a whole, capturing the overall geometry of organisms rather than reducing them to a pre-selected subset of measurements (Adams *et al.* 2004). The accessibility of these methods has been considerably improved through the development and publication of functions in R, the open software environment for statistical computing and graphics (Claude 2008). Two main branches of modern GMM hinge on the distinction between the study of landmark configurations and outline analysis.

A landmark-based approach requires strongly defined homologous points between individuals — for example the discrete juxtaposition of tissues that can be defined as a single point. While a cereal grain has points of maximum curvature or distinct tissue surface (e.g.

the distinction of the embryo from grain epidermis) its form is broadly ‘continuous’ and these types of shapes may be more suited to outline analysis (Bonhomme *et al.* 2014, 4–5). The form of outline analysis applied herein utilises ‘Fourier Series’, which describe shapes in terms of periodic functions. A Fourier transform decomposes outlines into a series of harmonic sums of trigonometric functions, weighted with harmonic coefficients (Bonhomme *et al.* 2014). The specific technique utilised is Elliptic Fourier Analysis (Giardina and Kuhl 1977; Kuhl and Giardina 1982), which has the advantage of not requiring equally spaced points and allowing for virtually any outline to be fitted (Bonhomme *et al.* 2014, 7).

Recent advances in imaging technology, such as micro-photogrammetry, computed tomography (CT) and structured light and laser surface scanning, mean that we are currently seeing an ‘explosion’ in the rapid generation of three-dimensional high-resolution reconstructions of specimens (Bardua *et al.* 2019). Only a few years ago the cost of this equipment, as well as the challenges of presenting results in a 2D format, were acknowledged as limiting factors (Zelditch *et al.* 2012). But this is rapidly changing, and 3D analysis has become widely applied by biologists and palaeontologists (Davies *et al.* 2017), with these developments now finding a home in archaeological research. As they become more accessible, 3D-scanning technologies are likely to become increasingly valuable, not only as a tool for analysis, but also as a means of creating records of specimens; this may be particularly useful for assemblages which for political or practical reasons cannot be relocated for further study. The increasing application of artificial intelligence in biology is also beginning to filter into bioarchaeological studies. Machine learning, and particularly deep learning using Convolutional Neural Networks, may be increasingly applied to GMM-related tasks such as automated landmark acquisition, normalisation of images prior to analysis and classification (Evin *et al*. 2022).

0.6 Geometric Morphometrics in Archaeology

In an archaeological context, GMM has been utilised for a range of specific applications, including analysis of both biological and artefactual remains. GMM-based artefact studies have often been focussed on lithics, and particularly projectile points (see reviews in

Okumura and Araujo 2020; Göldner *et al*. 2022), but also include analyses of pottery forms (Selden *et al*. 2014; Wilczek *et al*. 2014; Wang and Marwick 2020).

As a technique we might consider to have been 'borrowed' from the biological sciences (Okumura and Araujo 2020), applications of GMM to bioarchaeological studies have understandably been more diverse and widespread, including the analysis of human, faunal and floral remains. GMM analysis of human remains has been used to reconstruct evolutionary relationships in archaeological groups, for sex and age estimation and other contextually-specific applications, such as the study of artificial cranial deformation (Okumura and Araujo 2020). GMM techniques, and particularly landmark analysis, have found particularly fertile ground in zooarchaeological studies, often in combination with aDNA, isotopic and traditional morphometric studies. These have been conducted using both 2D and 3D data, depending on the faunal element being studied (Evin *et al*. 2022, 4). Applications predominantly feature the identification of domesticates, wild domestic progenitors and hybrids, as for example in studies of pigs (Cucchi *et al*. 2009; 2011; 2016; 2021; Bartosiewicz *et al.* 2013; Krause-Kyora *et al*. 2013; Ottoni *et al.* 2013; Owen *et al*. 2014; Evin *et al.* 2015; Balasse *et al*. 2016; Price and Evin 2019), dogs (Drake *et al*. 2015; 2017; Geiger *et al*. 2017; Fisher 2019) equids (Seetah *et al*. 2016; Cucchi *et al.* 2017; Hanot *et al.* 2017; Chuang and Bonhomme 2019; Clavel *et al*. 2021), camelids (Hernández *et al.* 2021), cats (Vigne *et al*. 2016), cattle (Cucchi *et al*. 2019) and sheep (Pöllath *et al*. 2019). In the case of ovicaprids (sheep and goats), GMM applications have also focussed on addressing the long-standing taxonomic ambiguity between the species (Haruda 2017; Jeanjean *et al*. 2022).

Within-species variation has also been the subject of GMM-based zooarchaeological studies, including the regional and temporal studies of phenotypic diversity in pigs (Duval *et al.* 2015; 2018; Bopp-Ito *et al*. 2018) and sheep (Colominas *et al.* 2019). A further example of the latter, examined morphological variance in sheep astragali between different Bronze Age populations in Central Asia, in order to make inferences about the mobility and connectivity of pastoralists (Haruda *et al*. 2019). Other studies have looked at the dispersal

of particular phenotypes into new regions, such as mice (Cucchi 2008; Valenzuela-Lamas *et al*. 2011) or, for example, the combined genetic and morphological evidence for specialised sled dogs which accompanied Inuit migrants into and across the North American Arctic (Ameen *et al*. 2019). In these intra-species studies we also see preliminary attempts to link form and function, as made explicit in the study of the Warmington Roman dog, which interpreted morphological characteristics in terms of breeding strategies (Schoenebeck *et al*. 2021). Similarly, analysis of fish bones from late pre-Hispanic New Mexico has been used to make inferences on both environmental conditions and fishing strategies as based on body size reconstructions (Dombrosky *et al*. 2022).

0.7 Geometric Morphometrics in Archaeobotany

As specifically regards archaeobotany, a number of previous studies applying geometric morphometric techniques have been made. Outside the realm of cereals, GMM analysis of seeds has been applied to grapes (e.g. Terral *et al.* 2010; Orrù *et al.* 2013, Pagnoux *et al.* 2015; Bacilieri *et al*. 2017; Bonhomme *et al.* 2020; 2021; Bouby *et al*. 2021; Margaritis *et al*. 2021), date palm (Terral *et al.* 2012; Gros-Balthazard *et al*. 2017; Sallon *et al*. 2020), opium poppy (Jesus *et al*. 2021), lemons (Grasso *et al*. 2018), cherry (Burger *et al*. 2011), melons (Sabato *et al*. 2019), pulses (Tarongi *et al*. 2021) and olives (Terral *et al.* 2004; 2021; Newton *et al.* 2006; 2014; Bourgeon *et al.* 2018; Margaritis *et al.* 2021). Most of these archaeobotanical studies have focussed on the identification of domestication traits in seeds and refining taxonomies, with a smaller proportion looking to explore the biogeography and biodiversity of cultivars more broadly. The majority have tended to utilise outline analysis through Elliptic Fourier transforms of 2D images (Evin *et al*. 2022), but a recent study has used 3D computed tomography to assess taxonomic distinctions and evidence of consumption in archaeological watermelon seeds (Wolcott *et al*. 2021). So-called 'traditional' morphometric methods based on individual measurements also continue to be applied to archaeobotanical seeds (e.g. Bouby *et al.* 2013) as well as phytoliths, pollen and starch grains (Portillo *et al.* 2020).

The body of published evidence for GMM analysis of archaeobotanical cereals is less extensive. Previous applications include the morphological distinction between charred browntop and foxtail millet (García-Granero *et al*. 2016) and the identification of two- and six-row barley in Roman material from southern France (Ros *et al*. 2014). Methodologically influential in the papers presented herein was a study comparing einkorn, emmer and barley using Elliptic Fourier transforms, which established the potential for species to be distinguished even when archaeologically-relevant levels of charring distortion were present (Bonhomme *et al.* 2017). Here, linear discriminant analyses of charred modern specimens produced an almost perfect reclassification rate by species (with only a single emmer grain classified as einkorn). The study went further in suggesting the potential for intra-species distinctions, i.e. between different accessions.

A subsequent paper by Wallace *et al*. (2018) expanded on these findings by focussing on barley landraces, using GMM to distinguish 'bere' barley from other British and Scandinavian landraces on the basis of grain form. Successful separation of landraces was also achieved when the same type was tested between different growing locations, with the implication that '…the primary determinant of grain morphology is genetic, and that effects on grain morphology due to environmental conditions do not mask this.'(*ibid.*, 1133). However, it was noted that the level of correct reclassification did differ slightly between different growing locations, suggesting environmental influence on grain morphology should not be ruled out entirely.

While these previous studies have paved the way to applying GMM techniques to archaeobotanical cereal grains, there remain challenges in terms of protocol standardisation, availability of data and the range of taxa represented (Portillo *et al*. 2020). Einkorn, emmer and barley as studied by Bonhomme *et al.* (2017) have notably distinct grain forms which can usually be identified by eye. The reliability of distinctions between, for example, different (sub-)species of free-threshing wheat remain more uncertain, and GMM gives us the potential to analyse the distinctions between these forms objectively. Once the (sub-)species-level variations between different wheats are better understood, we can begin

to delve into variability within cultivars and the impact of growing conditions on grain morphology with greater confidence. It is hoped that the present study can contribute to this growing field, by addressing methodological questions such as the number of views required to best distinguish between different wheat cultivars when analysing in two dimensions and how morphometric data might be more routinely captured as well as easily stored and shared. Furthermore, it is believed that this work represents the first GMM-based study of an extensive range of wheat (sub-)species and varieties, including comparison of wild and domesticated wheats, 'improved' or 'advanced' crops versus traditional landraces and of a single variety grown under different environmental conditions, as applied to specific archaeological research questions.

0.8 Approach

In this study, a broad range of wheats are approached as two categories: glume and free-threshing wheats. In glume (hulled) wheats the rachis is semi-brittle and when threshed the ear breaks into spikelets (i.e. grains enclosed by glumes, equivalent to the natural dispersule unit in wild wheats). The chaff adheres tightly to the grain and the tough glumes do not break during processing. These spikelets require further processing in the form of pounding to release the grain (Hillman 1984). In free-threshing wheats (FTWs) the rachis is thickened throughout, non-brittle and individual segments tend to remain attached to each other through the ear. The glumes are thinner and the grains are readily released during threshing. Glume wheats are the earliest cultivated type, with the free-threshing form representing a later agricultural development which would eventually become the dominant type of wheat cultivated on a global scale. Because the two groups have different processing requirements, they are usually grown as separate crops.

In order to assess the potential for outline analysis to distinguish between modern glume and FTW classes, Elliptic Fourier Analysis was performed on 2D views of grains across a range of wheat accessions sourced from gene banks. Analysis was then repeated on experimentally charred grains of these same accessions to assess whether charring distortion would hinder classification of archaeobotanical grains. Linear discriminant analysis

was performed on the transformed outlines of these grains to assess how accurately they could be classified on the basis of morphology. Different combinations of grain views were tested to see which were the most useful in terms of separating grains at the taxonomic level.

Once the potential for outline analysis to distinguish between modern wheat grain classes was established, findings were applied to archaeobotanical wheat remains across three different case studies. The first case study (Paper 1) concerns the taxonomic identification and domestication status of so-called 'new glume wheat' at Neolithic Çatalhöyük (Central Anatolia), summarising existing evidence for a once widespread crop that has almost completely disappeared in the present day. The published version of Paper 1 is included as an appendix at the end of the thesis document (Appendix 2).

The second case study (Paper 2) analyses FTW grains from Çatalhöyük and Kouphovouno (southern Greece). These sites were selected because they both had unusually substantial and well-preserved storage deposits of FTW grains dating to the Neolithic period. This paper considers the ambiguity regarding the early evidence of both tetraploid and hexaploid FTWs, both in terms of the initial development of the crop and the trajectory of its spread towards western Europe.

The third case study (Paper 3) sets out to assess whether or not morphological analysis of grain supports the theorised introduction of tetraploid rivet wheat in Late Anglo-Saxon agricultural systems, as well as more broadly to characterise morphological variation within FTW assemblages. The introduction of rivet has previously been proposed on the basis of relatively limited numbers of rachis segments which were identified as tetraploid FTW, but could not be further identified to cultivar. Archaeological grains are analysed from twelve sites in central, eastern and south-west England, which formed part of the 'FeedSax' (Feeding Anglo-Saxon England) project (Hamerow in press).

Appendix 1 describes the results of additional experiments undertaken to assess the degree to which environmental growing conditions could influence grain morphology relative to that

already observed in Papers 1–3 as corresponding to ploidy level, (sub-)species and variety. For this experiment, grains sampled from a single variety of bread wheat grown under different manuring and irrigation regimes as part of a controlled crop growing experiment on land near Aleppo, Syria in 2007–9 are analysed. These results are referenced in Paper 2, and have implications for the interpretation of morphological variation as relating to taxa, variety and geographic origin.

0.9 Aims of the Thesis

The aims of the thesis can be summarised as follows:

1) to establish whether Elliptic Fourier Analysis of grain outlines can allow us to distinguish charred wheat grains to ploidy, species, sub-species and varietal level and thereby establish the potential to refine taxonomic identifications of archaeobotanical wheat grains;
2) to identify methodological protocols, including the optimum combination of photographic views, when distinguishing grains at these taxonomic/varietal levels;
3) to establish whether the morphological variation associated with these taxonomic/varietal categories is more or less distinct than that caused by environmental growing conditions;
4) to apply these findings to archaeobotanical remains in order to answer specific archaeological research questions relating to morphological variation within assemblages and past crop developments, trajectories and usage; and
5) to consider the implications of these findings as regards the study of the co-evolution of crops and people, biodiversity in past and present agricultural systems and the potential for future research.

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1.0 Paper 1: Geometric Morphometrics Sheds New Light on the Identification and Domestication Status of 'New Glume Wheat' at Neolithic Çatalhöyük

Abstract

'New glume wheat' (NGW) is an archaeobotanical type increasingly recognised at Neolithic–Bronze Age sites across Europe and Western Asia. NGW has been recognised via aDNA and morphological analyses of chaff remains as a member of the *Triticum timopheevii* wheat group, recent cultivation of which is known only from western Georgia. This study combines geometric morphometric (GMM) analysis of NGW grains with updated results from a parallel study of chaff dehiscence, to assess the taxonomic classification and domestication status of NGW from the Neolithic East Mound at Çatalhöyük (central Anatolia).

Results confirm close comparability of NGW with modern wheats from the group *T. timopheevii*, in a form which has remained remarkably similar over thousands of years. Furthermore, the analysis suggests that NGW was undergoing selection for domestication traits in terms of shattering behaviour and grain form during the 1150-year East Mound sequence. These findings are interpreted in the context of substantial archaeobotanical evidence for a broad-spectrum plant strategy at Çatalhöyük which mitigated the risk of resource failure and supported experimentation in cropping. Possible cultural and practical incentives are considered for investment in the crop, made despite the availability of a fully-domesticated glume wheat (emmer) with similar growing and processing requirements. Alongside this, the study demonstrates the sensitivity of GMM to differences between and within wheat species, with methodological findings that can inform future studies.

Key words

Geometric morphometrics; Çatalhöyük; Domestication; Wheat; Neolithic; Anatolia

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Statements and Declarations

Declarations of interest: none

1.1 Introduction

1.1.1 'New glume wheat'

'New glume wheat' (NGW) was characterised by Jones *et al.* (2000) from a distinct group of archaeobotanical spikelet bases recovered from Neolithic and Bronze Age sites in northern Greece. Based on the chaff morphology and grain:chaff ratios of deposits it was concluded that these were remains of a tetraploid wheat. Of the modern specimens compared, Timopheev's wheat (*Triticum timopheevii* Zhuk.) most closely resembled the morphology of this newly-identified archaeobotanical group.

The *T. timopheevii* wheat group contains two tetraploid species: wild *T. araraticum* (syn. *T. timopheevii* Zhuk. ssp. *armeniacum* (Jakubz.) van Slageren) and domesticated *T. timopheevii* Zhuk. ssp. *timopheevii*. Cultivated Timopheev's wheat was first identified by Russian botanist P.M. Zhukovsky in Georgia in 1922 (Zhukovsky 1928) and is considered a narrowly endemic species, with cultivation documented in only a few villages of western Georgia (Badaeva *et al.* 2022). Grown as a 'maslin' crop known locally as 'Zanduri', *T. timopheevii* was mixed in varying proportions with einkorn wheat (Dekaprevelich and Menabde 1932). Wild *T. araraticum* was first collected by M.G. Tumanyan and A.G. Araratyan in 1925–28 in Armenia and has a broader distribution, with specimens recorded across Transcaucasia and in parts of Iran, Iraq, Syria and Turkey (Badaeva *et al.* 2022).

Despite recent cultivation of Timopheev's wheat not being known outside western Georgia, NGW has been recorded as a crop at a range of sites across Europe and Western Asia (Fig. 1; Table 1), dating from the Neolithic–Bronze Age and possibly into the Iron Age (Kenéz *et al.* 2014). In some cases, remains initially identified as 'atypical' emmer wheat were subsequently reassessed in the light of the newly characterised NGW class, such as the chaff recovered at Cafer Höyük, Turkey (Jones *et al.* 2000). Chiefly these identifications have been based on chaff remains, and while some morphological criteria of NGW grains have been published (Kohler-Schneider 2003), distinguishing the grains, particularly from those of emmer, has been noted as difficult (Valamoti 2017).

The relationship between the narrowly endemic modern Timopheev's wheat and the widespread archaeological NGW is uncertain. It is possible that the small population in Georgia is a relic of a formerly much wider cultivated crop. aDNA analysis of Neolithic NGW grains from Çatalhöyük and Miechowice 4, Poland (Czajkowska *et al.* 2020) has identified the presence of the G genome, indicating that NGW is a member of the Timopheevii section of wheats, distinct from other polyploid wheats which carry the B genome (Fig. 2). The Timopheevii section contains tetraploid wild and domesticated Timopheev's wheat and the hexaploid wheat *T. zhukovskyi* (Menabde & Ericzjan) (Badaeva *et al.* 2022). The presence of the G genome does not, therefore, in itself provide a precise identification.

The aDNA findings also do not preclude the possibility of a separate domestication event having led to a wheat form related, but not ancestor to, modern Timopheev's wheat. Indeed, wheats sharing a genomic constitution may differ significantly in form and function; for example, spelt and bread wheat are both 'BBAADD' hexaploid wheats, but have quite different processing requirements and culinary qualities. Furthermore, recent DNA analysis (Badaeva *et al.* 2022) has highlighted two distinct lineages of wild *Triticum araraticum*, with the authors positing potential hybridisation between Timopheev's wheats and wild emmer. These insights lend weight to the possibility of multiple evolutionary pathways within the *T. timopheevii* group.

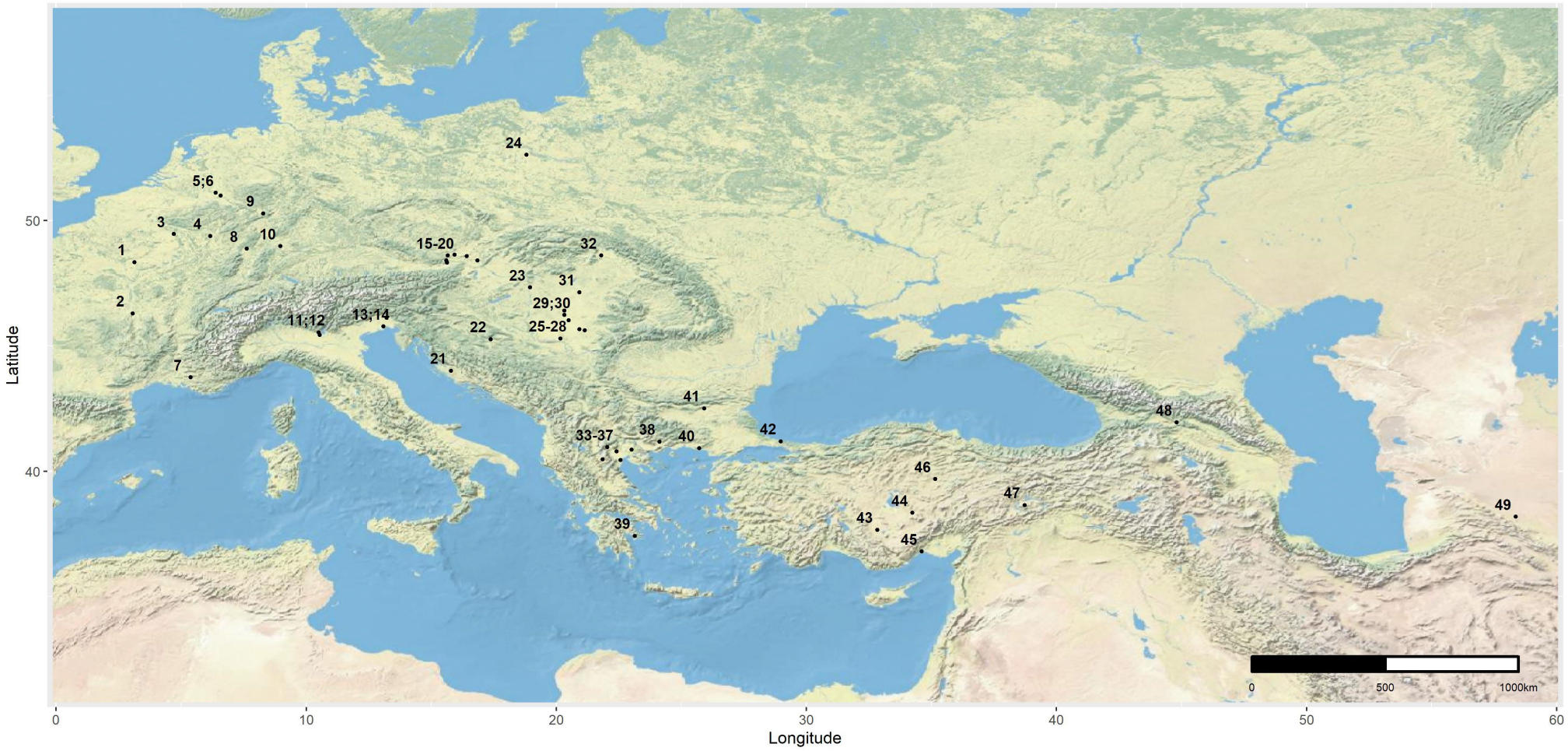

Fig. 1 Distribution map of NGW finds (see Table 1 for key)

Fig. 1 key	Site Name	Country	References
1	Upper Seine Valley (multiple sites)	France	Toulemonde *et al.* 2015
2	Petit Beaulieu	France	Toulemonde *et al.* 2015
3	Vouziers	France	Toulemonde *et al.* 2015
4	Hettange-Grande	France	Toulemonde *et al.* 2015
5	Wanlo	Germany	Knörzer 1980; cited Jones *et al.* 2000
6	Bedburg	Germany	Knörzer 1974; cited Jones *et al.* 2000
7	Pié Fouquet	France	Toulemonde *et al.* 2015
8	Gingsheim	France	Toulemonde *et al.* 2015
9	Bad Camberg-Würges	Germany	Kreuz *et al*. 2005
10	Vaihingen	Germany	Bogaard 2011
11	Lucone	Italy	Perego 2015
12	Lavagnone	Italy	Perego 2015
13	Piancada	Italy	Rottoli & Castiglioni 2009
14	Sammardenchia/Pavia di Udine	Italy	Rottoli & Castiglioni 2009
15	Kamegg	Austria	Link 2004; cited Kenéz *et al*. 2014
16(/17)	Krems/Hundssteig	Austria	Kohler-Schneider & Caneppele 2009
18	Sandberg	Austria	Caneppele *et al.* 2010
19	Michelstetten	Austria	Kohler-Schneider & Heiss 2010
20	Stillfried	Austria	Kohler-Schneider 2003
21	Velištak	Croatia	Reed and Podrug 2016
22	Slavča	Croatia	Reed 2017
23	Százhalombatta-Földvár	Hungary	Stika and Heiss 2012/2013
24	Kujawy District	Poland	Bieniek 2007; Bieniek 2002
25	Feudvar	Serbia	Borojevic 1991 cit. Kohler-Schneider 2003; Reed 2016
26	Dudeştii Vechi	Romania	Fischer and Rösch 2004
27	Uivar	Romania	Fischer and Rösch 2004
28	Parţa	Romania	Fischer and Rösch 2004
29	Hódmezővásárhely	Hungary	Kenéz *et al*. 2014
30	Klara Falva	Hungary	Kohler-Schneider 2003
31	Ecsegfalva	Hungary	Bogaard *et al.* 2007
32	Brehov-Pod	Slovakia	Hajnalova 2007
33	Apsalos	Greece	Valamoti 2017
34	Giannitsa	Greece	Valamoti and Kotsakis 2007
35	Kleitos-Kremasti	Greece	Valamoti 2017
36	Makriyialos	Greece	Jones *et al.* 2000
37	Assiros Toumba	Greece	Jones *et al.* 2000
38	Arkadikos	Greece	Jones *et al.* 2000
39	Franchthi Cave	Greece	Hansen 1991 cited Jones *et al.* 2000
40	Makri	Greece	Jones *et al.* 2000
41	Karanovo	Bulgaria	Kreuz *et al.* 2005
42	Yenikapı	Turkey	Ulaş and Fiorentino 2021
43	Boncuklu/Çatalhöyük	Turkey	Baird *et al*. 2018; Bogaard *et al.* 2013; 2017
44	Aşıklı Höyük	Turkey	Ergun *et al.* 2018
45	Mersin-Yumuktepe	Turkey	Ulaş and Fiorentino 2020
46	Çadır Höyük	Turkey	von Baeyer *et al*. 2021
47	Cafer Höyük	Turkey	de Moulins 1993 cited Jones *et al*. 2000
48	Atskouri	Georgia	Kenéz *et al*. 2014
49	Jeitun	Turkmenistan	Charles and Bogaard 2010

Table 1 Site names and references for NGW distribution map Fig. 1

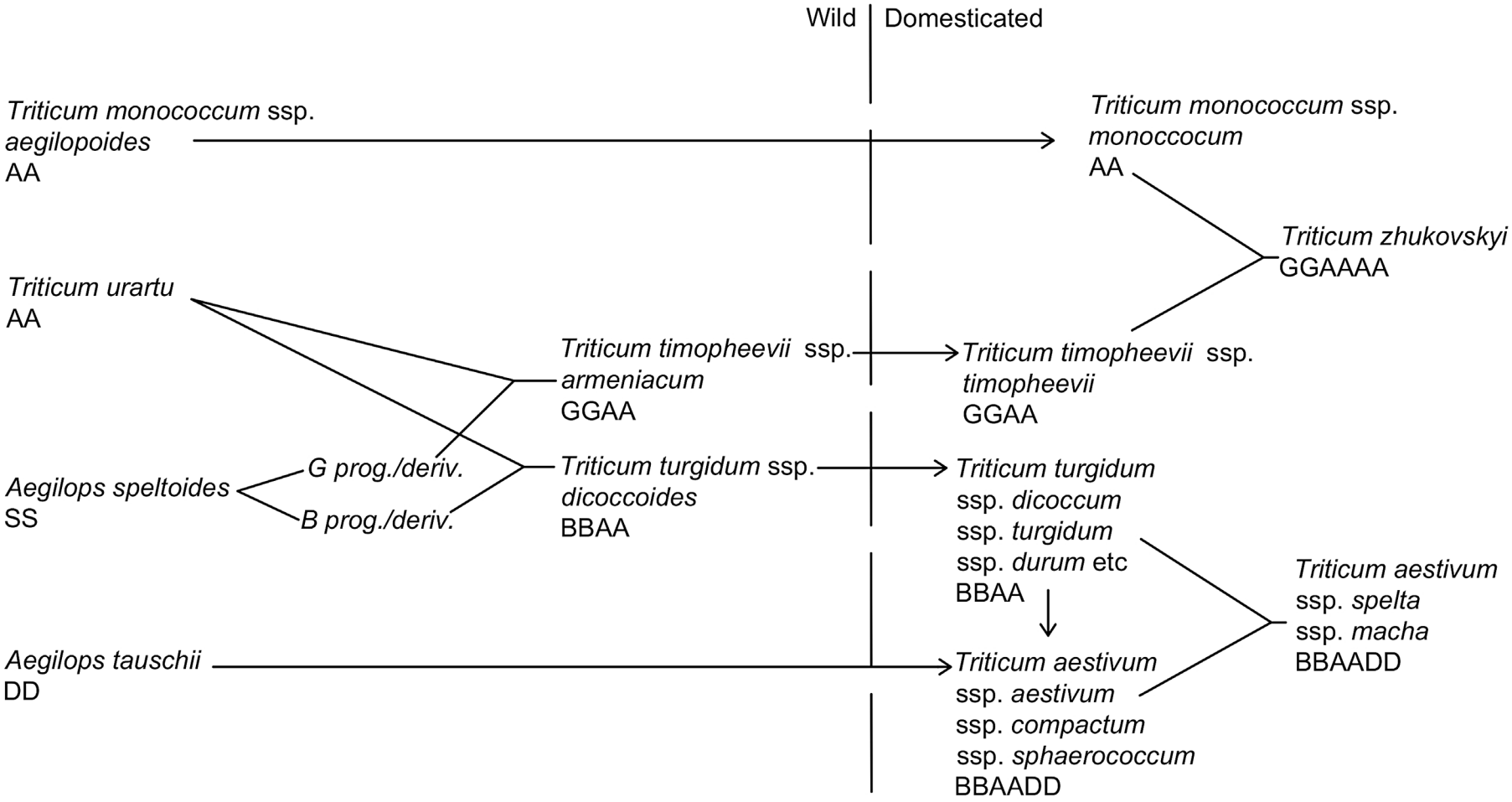

Fig. 2 Simplified genetic diagram showing relationships between wheat species after Li and Gill (2006). 'prog./deriv.'= progenitor/derivation. Genetic studies suggest chromosomes of the G and B genomes were donated by the S genome of *Aegilops speltoides* (or lineage close to it): see Kilian *et al*. 2007; Ruban & Badaeva 2018 and Miki *et al*. 2019

1.1.2 NGW at Çatalhöyük

A substantial body of Neolithic NGW remains have been recovered from Çatalhöyük, the archaeobotanical dataset of which is currently the largest available for an early farming community in western Asia (Bogaard *et al.* 2021b). The remains analysed in this study were recovered from the Neolithic East Mound dating 7100–5950 cal. BC. Within Turkey, the Çatalhöyük NGW remains are predated by NGW finds from the mid-9th millennium BC at Aşıklı Höyük (Ergun *et al.* 2018) and by two spikelet forks of the late 9th–early 8th millennium BC at Boncuklu Höyük (Baird *et al.* 2018). Spikelet bases at Cafer Höyük dating from the late 9th millennium BC and described as 'machaoid' emmer also appear to match the morphological characteristics of NGW, not yet characterised at the time of their identification (de Moulins 1993; Jones *et al.* 2000).

From the earliest levels, a diverse range of cereal and pulse crops as well as wild food-plants are present at Çatalhöyük (Bogaard *et al.* 2017, 2021b). In early phases NGW is present but as a minor component only, with emmer (*Triticum turgidum* L. ssp. *dicoccum* (Schrank) Thell.) the dominant wheat crop. The earliest concentrated deposits of NGW were identified in neighbouring buildings of the mid-sequence phase 'North G', and it is not until the Late phase that we see concentrations in the South Area and the emergence of NGW as the most prevalent wheat crop (Bogaard *et al.* 2021b).

Emmer and NGW are both glume (or hulled) wheats. The ears of glume wheats are formed with a semi-brittle rachis, which when threshed break up into spikelets. These spikelets require further dehusking by pounding to release the grain from the tough glumes (Hillman 1984). In contrast, the rachis of 'free-threshing' wheats is thickened throughout, non-brittle and spikelets remain attached to the intact rachis. The glumes are thinner and the grains are easily released during threshing. Sample compositions indicate that, despite both being glume wheats with the same processing requirements, NGW and emmer were stored, and likely grown, separately, rather than as a mixed crop (Bogaard *et al.* 2017). Isotopic evidence (Vaiglova 2016; Stroud *et al.* 2021) and weed functional ecological analysis (Green *et al.*

2018) suggest that NGW was grown under similarly variable conditions to emmer. Therefore, rather than being environmentally-determined, adoption of NGW is interpreted as an example of household-level experimentation with an existing minor crop potentially relating to group-identity, culture and/or culinary preference (Bogaard *et al.* 2017, 2021b).

1.1.3 Archaeobotanical wheat grains and geometric morphometrics

In this study, modern and archaeological glume wheat grains are analysed and compared using geometric morphometrics (GMM). Archaeobotanical wheats grains can be challenging to identify with precision based on traditional morphological criteria (Jones 1998). Grains are usually preserved through charring but are distorted as a result, surviving in identifiable form only when charred within a narrow temperature range under low oxygen conditions (Charles *et al.* 2015). Charring aside, there is difficulty simply in establishing reliable characteristics by which to distinguish between taxa (Hillman *et al.* 1996). GMM offers new ways to approach these challenges of characterisation, with the potential to enhance descriptions of form variation and improve consistency of classifications.

Morphometrics is the application of statistical analyses to size and shape variables, enabling analysis of form in a comparable way to numeric data. In traditional morphometrics, multivariate statistics are applied to a predetermined set of variables, usually consisting of individually measured distances on an organism (Rohlf and Marcus 1993). The development of modern GMM and a suite of new techniques in the 1980s now allows us to analyse shapes as a whole (Adams *et al.* 2004). The accessibility of these methods has been vastly improved through the development and publication of functions in R (Claude 2008), the open software environment for statistical computing and graphics.

Within archaeobotany, GMM has been successfully applied to the study of grape seeds (Terral *et al.* 2010; Pagnoux *et al.* 2015), date palm stones (Terral *et al.* 2012) and olive stones (Terral *et al.* 2004; Newton *et al.* 2006, 2014). Previous studies of archaeobotanical cereals include that by Ros *et al.* (2014), in which GMM was used to identify two- and six-row barley from Roman contexts in southern France. Bonhomme *et al.* (2017) established the potential of GMM to distinguish between einkorn, emmer and barley grains before and

after charring, further suggesting the potential for intra-species distinction. Wallace *et al.* (2018) expanded on these findings, using GMM to distinguish 'bere' barley grains from other British and Scandinavian landraces. Building on these studies, the potential of GMM in relation to morphologically-similar classes of glume wheats of different domestication statuses is explored here for the first time. Methodological uncertainties are also addressed in seeking to quantify which photographic views best allow us to distinguish between wheat types.

1.2 Methodology

The GMM analysis comprised four stages and is followed by a summary and update of results from a parallel chaff dehiscence study (Charles *et al.* 2021).

1. Testing the potential for GMM to distinguish between grains of modern glume wheat species.
2. Comparing archaeobotanical glume wheat grains from Çatalhöyük with modern reference material.
3. Analysing chronological changes in the morphology of the Çatalhöyük glume wheat grains
4. Assessing the morphology of Çatalhöyük glume wheat grains as relating to processing stage

1.2.1 Approach

Because the form of a cereal grain is broadly 'continuous', the GMM methodology comprised a type of outline analysis, as opposed to a landmark-configuration approach dependent upon strongly-defined homologous points between individuals (Bonhomme *et al.* 2014). Here a set of points are still used to describe the shapes and 'landmarks' to align them, but the analysis assumes a closed outline in which the form is roughly circular or displays strong bilateral symmetry.

The outline analysis uses 'Fourier Series', which approach shapes as periodic functions, decomposing outlines into a series of harmonic sums of trigonometric functions weighted

with harmonic coefficients (Bonhomme *et al.* 2014). The specific technique utilised is Elliptic Fourier Analysis (Giardina and Kuhl 1977; Kuhl and Giardina 1982) which has the advantage of not requiring equally spaced points and allowing for virtually any outline to be fitted (Bonhomme *et al.* 2014). It is applied using the package 'Momocs' (1.2.9) in R (3.6.2), as developed by Vincent Bonhomme, based on functions published by Claude (2008).

To establish a basis of comparison for the archaeological wheat grains, the outlines of multiple accessions of modern wheat grains were captured. Modern grains were photographed before and after charring, with charring conditions designed to replicate well-preserved archaeological material. Photographs were digitised and aligned before extraction into Momocs. The same procedure (minus charring) was applied to the archaeobotanical grains.

1.2.2 Sampling and photography

Modern reference material was acquired primarily through gene banks with multiple ears used to assess variation within and between accessions. To account for in-ear variation, accessions for which whole ears could be obtained were prioritised, as were those from geographically proximate locations to Çatalhöyük. Grains were sampled from the base, middle and top of the ear with row number and spikelet position recorded. Where whole ears could not be obtained – e.g. as with wild forms which typically shatter before harvest – ear position was reconstructed by counting vascular bundles to procure an equivalent sample (after Whingwiri *et al.* 1981).

The final comparative dataset of modern material consisted of 438 grains (Table 2), with the primary dataset comprised of wild and domesticated emmer and Timopheev's wheat. Part-way through analysis it was observed that archaeological 'two-grained einkorn' (*Triticum monococcum* ssp. *monococcum* L.) was similar in appearance to modern *T. araraticum*. Therefore, reference specimens of two-grained einkorn were added to the dataset. As direct comparability of the (potentially environmentally-influenced) modern two-grained einkorn and the archaeologically-observed form remains uncertain (Kreuz and Boenke 2002), this category was represented by modern accessions (Table 2) supplemented by five well-

preserved, securely-identified grains from Neolithic Vaihingen, Germany (Bogaard 2011), numbering 38 grains in total. This category was added primarily to prevent misidentification between NGW and two-grain einkorn. However, as relatively limited quantities of material were available, a more systematic analysis of this wheat type would be desirable in the future.

Subspecies	Common name	Source	Accession	Origin	No. grains
monococcum	Einkorn (2-grain form)	Berzsenyi College	FOT145142	Romania	26
monococcum	Einkorn (2-grain form)	Mark Nesbitt (Kew)	RMN7537	Unknown	7
araraticum	Wild timopheev's	Gatersleben	TRI11509	Iran	27*(+27 in gl.)
araraticum	Wild timopheev's	John Innes	1150001	Azerbaijan	27*
araraticum	Wild timopheev's	John Innes	1150003	Unknown	27*
timopheevii	Domestic. timopheev's	John Innes	T1160001	Georgia	27*
timopheevii	Domestic. timopheev's	Gatersleben	TRI677	Soviet Union	27* (+27 in gl.)
timopheevii	Domestic. timopheev's	CGN Wageningen	CGN10497	Soviet Union	27*
dicoccoides	Wild emmer	Gatersleben	TRI11501	Turkey	27*
dicoccoides	Wild emmer	Gatersleben	TRI11502	Turkey	27*
dicoccoides	Wild emmer	Gatersleben	TRI16629	Israel	27*
dicoccum	Domestic. emmer	John Innes	1070018	Georgia	27*
dicoccum	Domestic. emmer	Gatersleben	TRI17251	Switzerland	27* (+27 in gl.)
dicoccum	Domestic. emmer	USDA	PI434999	Bosnia & Herzegov.	27*

Table 2 List of modern accessions used as comparative material for GMM analysis. 'In gl.' = in glume. * = used for Stage 1 analysis. In addition, five securely identified 2-grain einkorn grains from Vaihingen were included to a total comparative dataset of 443 grains.

Archaeological grains were selected based on preservation, with those exhibiting clear distortion or damage excluded. Observed signs of distortion resulting from high charring temperatures included protrusions resulting from endosperm exudation, severe blistering of pericarp and large cavities within the grain (Charles *et al.* 2015). Abraded grains for which there was little or no survival of the outer pericarp were also excluded.

Grains were photographed in dorsal, lateral and polar view (Fig. 3) using a Nikon SMZ25 stereo microscope with an apochromatic optical system and Pixelink M12BC-CYL microscopy camera.

1.2.3 Charring

Modern grains were charred to replicate well-preserved archaeological material after Charles *et al.* (2015). Grains were individually wrapped in foil and buried in beakers of sand to reduce oxygen availability. The beakers were then placed in a preheated oven at 230°C for 6 h. Temperature was monitored using thermacouples and a datalogger to ensure a consistent temperature was maintained throughout.

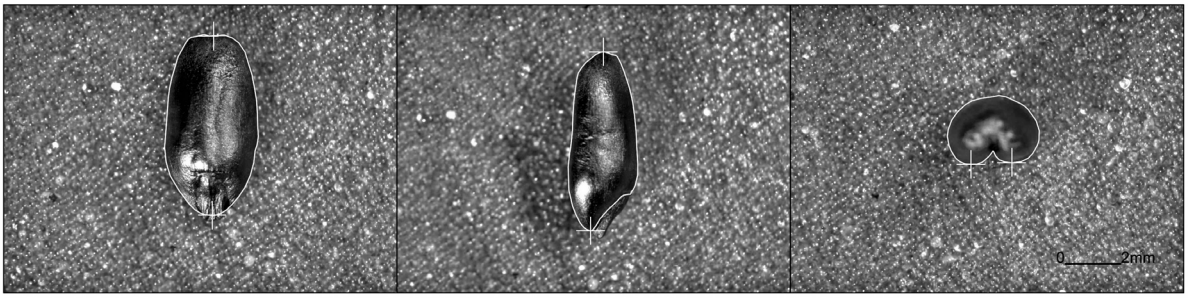

Fig. 3 Dorsal, lateral and polar views of a grain of domesticated Timopheev's wheat, traced and with alignment points added

1.2.4 Digitisation

Grain outlines were traced and aligned using AutoCAD, a design and drafting program. Embryos were excluded as these neither consistently remain attached, nor are likely to be equally developed across specimens (Fig. 3). After Bonhomme *et al.* (2017), polar views were flipped to face the same direction to account for the strong bilateral asymmetry often exhibited.

Coordinates of outlines were then extracted and saved as. txt files, which take up little file space, can be easily shared and avoid loss of resolution. The number of coordinate points per outline varied between 35 and 80. Comparison with outlines using a wider range (25–155 points) affected reclassification rates by <1%, suggesting the method is not sensitive to the precise number of points used. Repeatability was tested after Evin *et al.* (2020, 3–4), whereby five grains of the same species were each photographed and digitised five times in five separate sessions. When a principal components analysis (PCA) was performed on combined dorsal and lateral outlines (see Section 3, Stage 1, below) it produced clustering by specimen, although some variation was noted (Fig. 4). Measurement error was calculated after Claude (2008, 65), using Procrustes ANOVA of PCA scores, as 12.51% for the dorsal view and 9.55% for the lateral view. In both views, ANOVA produced significant scores ($p = 0.001$) when specimen was used as an independent variable, and non-significant scores (0.999–1.000) when session was used. This suggests the five sessions did not produce significantly different sets of grain shapes and that variation between session was less significant than variation between specimens.

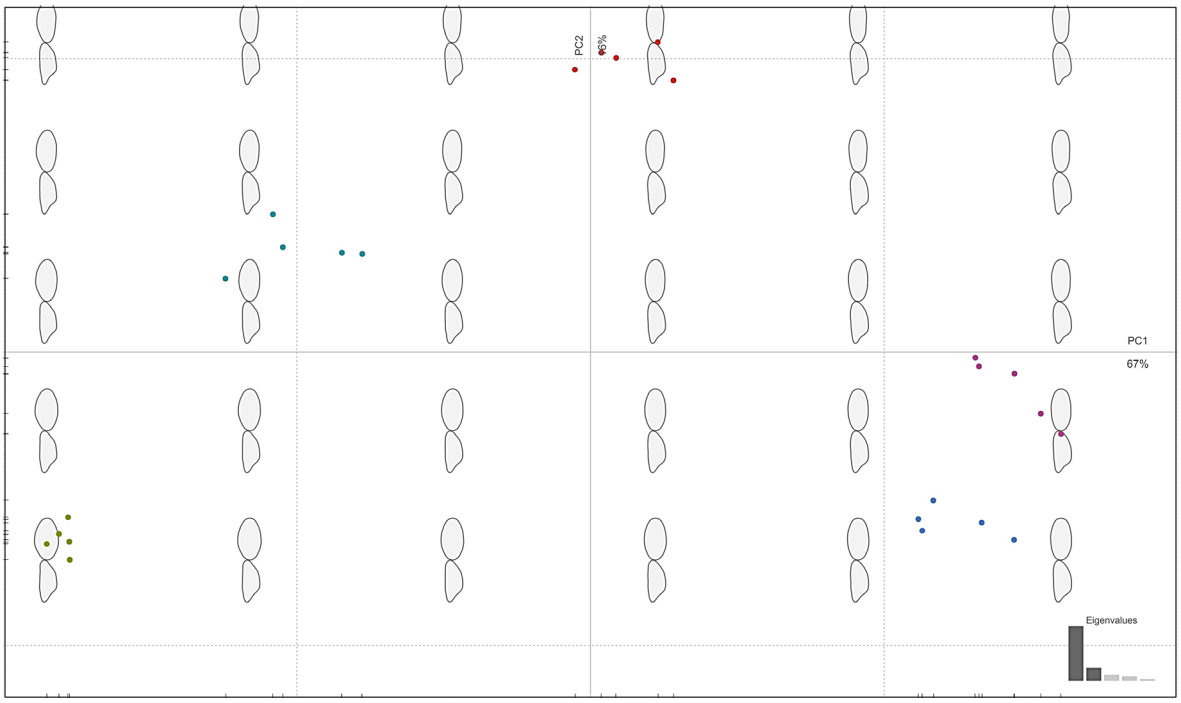

Fig. 4 PCA results of combined dorsal and lateral views when five grains from the same accession were each photographed and digitised five times (each colour = one specimen)

1.2.5 Analysis

Once imported into Momocs, outlines were scaled by centroid size to focus the analysis on shape differences. After Bonhomme *et al.* (2017), Elliptical Fourier Transforms were calculated for the outlines of each grain view individually, before being combined. Eight harmonics were retained for each view, gathering at least 99% of the total harmonic power. In Elliptic Fourier Analysis four coefficients per harmonic are obtained and multivariate analyses can then be performed on these Fourier coefficients (Bonhomme *et al.* 2014, 8).

Both principal components analysis (PCA) and linear discriminant analysis (LDA) were performed on the transforms, with the former allowing for visual exploration of the data including spotting alignment errors. LDA with leave-one-out cross-validation was used to test the extent to which grains which could be correctly reclassified by species, scoring each known species (‘actual’) against its designation using the model (‘classified’). When archaeobotanical material was introduced as an unknown category, the LDA classified it according to the known type it most closely resembled. When plotted, the LDA uses known class data (e.g. species) to visualise the maximum possible separation based on

morphology. When archaeobotanical material is introduced, the plot indicates where the material most closely aligns on the modern spectrum.

1.3 Results

The following results were generated using data available under supplementary material folders 'GrainCoordinates' (.txt grain outlines), 'GrainDataFrames' (associated.csv files) and 'ClassificationFiles' (summaries of classifications), together with the accompanying R script (also at: https://github.com/TinaRoushan/New-Glume-Wheat-Geometric-Morphometrics).

1.3.1 Stage 1: modern baseline study

Grains of wild and domesticated Timopheev's wheat (hereafter '*T. araraticum*' and '*T. timopheevii*') and domesticated emmer wheat ('*T. dicoccum*') were compared, to establish whether GMM could accurately reclassify them as the correct species and which photographic views were most useful in doing so. A total of 81 grains were used per species from nine accessions in total (Table 2).

Pre-charring, reclassification by species was almost perfect at 99.2% (Table 3). These rates decreased slightly after charring, with dorsal and lateral views in combination correctly reclassifying at 96.3% (Table 4), a slightly higher score than when all three views were used. Regardless of charring status, the polar proved the least useful single view, while the lateral view produced the highest scores when used alone (Tables 3 and 4). The polar view is seemingly not only the least diagnostic pre- charring, but also distorts more than other views during charring. It was therefore concluded that there was strong justification to exclude this view from further analyses.

Subsequently, the modern dataset was expanded using dorsal and lateral views of an equivalent sample of wild emmer grains (*Triticum turgidum* ssp. *dicoccoides* (Körn. ex Asch. & Graebn.) Thell.; Table 2). With this addition, separation between species after charring remained robust (Fig. 5), with reclassification rates reducing only slightly to 95.4%.

View	Uncharred reclassification rate (%)	Charred reclassification rate (%)
Dorsal	90.9	83.1
Lateral	97.5	94.2
Polar	72.4	60.5
Dorsal and lateral	**99.2**	**96.3**
Dorsal and polar	95.5	88.5
Lateral and polar	98.8	94.2
Dorsal, lateral and polar	**99.2**	95.1

Table 3 Results of LDA showing percentage of modern grains correctly classified by species before and after charring when different photographic views used. Highest scores before and after charring are in bold.

	Classified as		
Actual	*T. araraticum*	*T. dicoccum*	*T. timopheevii*
T. araraticum	78	0	3
T. dicoccum	0	79	2
T. timopheevii	1	3	77
Class correctness	96.3%	97.5%	95.1%
Leave-one-out cross validation	96.3% (234/243)		

Table 4 Results of LDA showing percentage of modern grains correctly classified by species after charring when dorsal and lateral views used in combination.

This stage of analysis was able to confirm the ability of the GMM model to distinguish between charred grains of wild/domesticated emmer and Timopheev's wheat to a high level of accuracy. The highest reclassification rates were achieved when the dorsal and lateral views were used in combination.

1.3.2 Stage 2: comparison with archaeobotanical material from Çatalhöyük

Dorsal and lateral views of well-preserved emmer and NGW grains from a range of East Mound contexts were subsequently compared with the modern wheat grains.

Initially, 86 archaeological grains were selected which had been confidently identified from securely identified storage deposits containing only either emmer or NGW, in association with chaff remains (Appendix A). These were added to the LDA as 'Arch_Emmer' and 'Arch_New', alongside the known modern types analysed above and the smaller sample of two-grain einkorn. It was observed that the archaeological grains plotted as two distinct groups: archaeological emmer ('Arch_Emmer') overlapping with modern emmer and NGW ('Arch_New') plotting between wild and domesticated Timopheev's wheat (Fig. 6). These

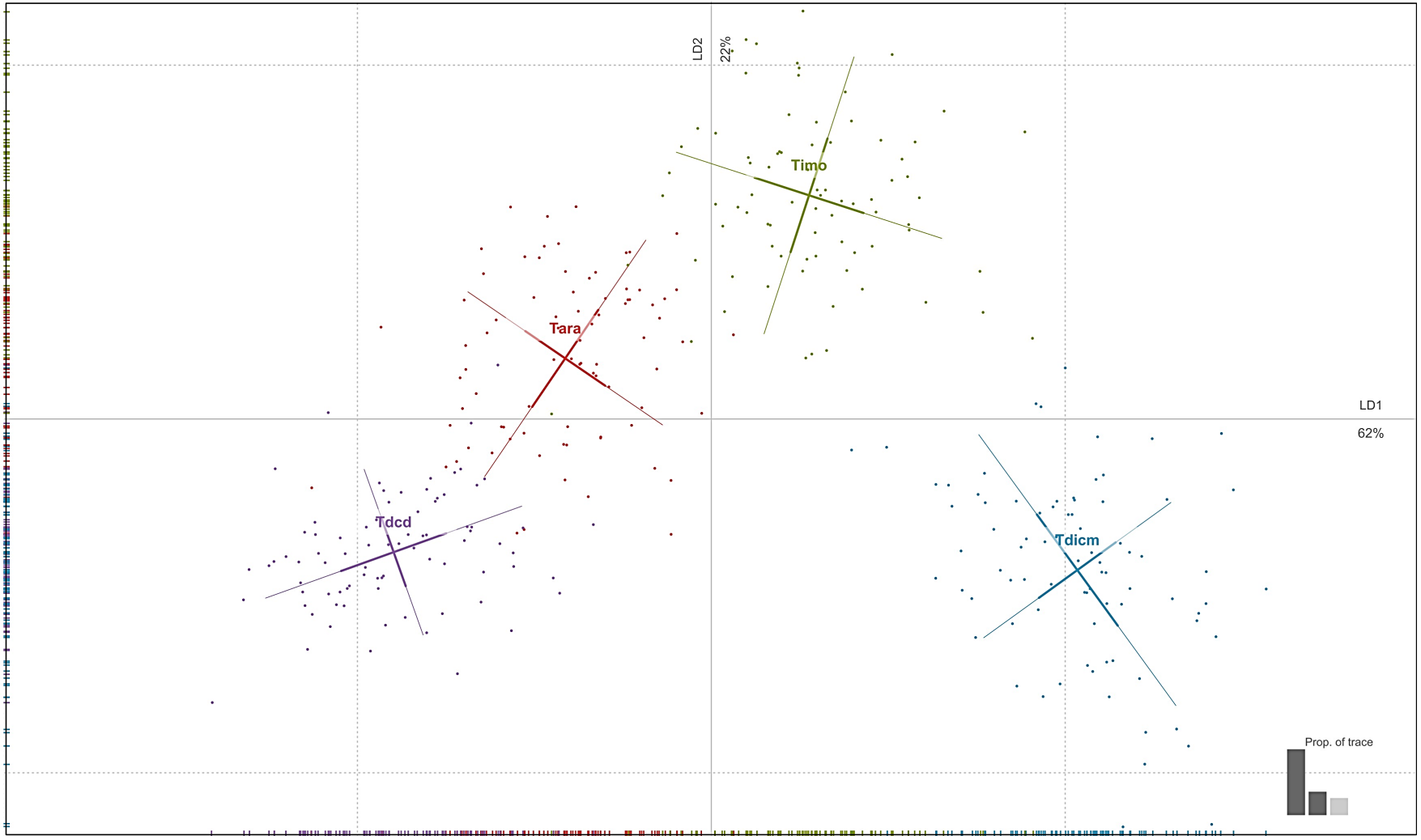

Fig. 5 LDA results showing separation of modern glume wheat species based on grain shape('Tdcd' = *T. dicoccoides*, 'Tara' = *T. araraticum*, 'Timo' = *T. timopheevii*, 'Tdicm' = *T. dicoccum*)

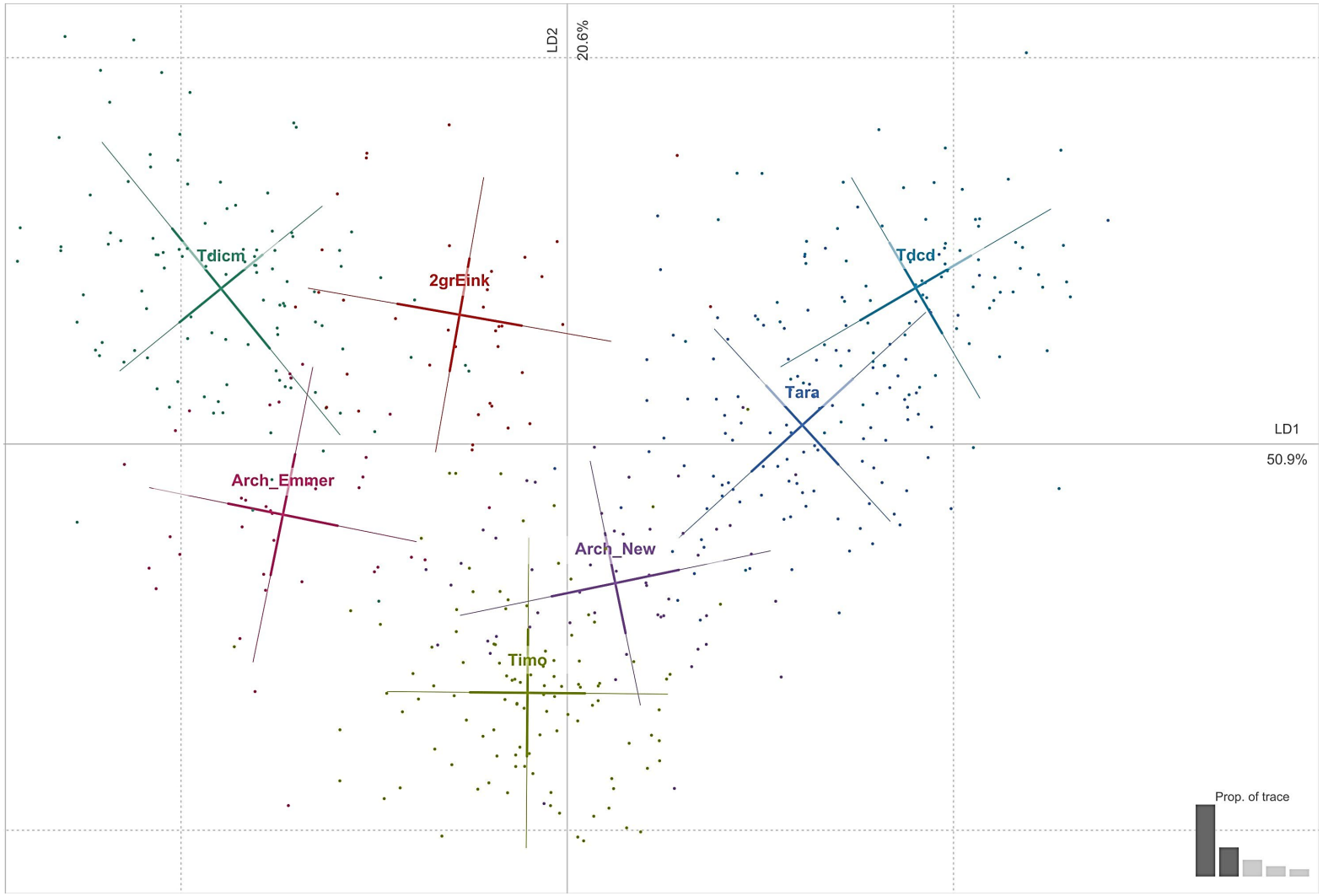

Fig. 6 LDA showing relationship of securely identified archaeological emmer ('Arch_Emmer') and NGW ('Arch_New') grains to comparative glume wheat dataset. NGW grains are positioned between wild ('Tara') and domesticated ('Timo') Timopheev's wheat. ('Tdicm' = *T. dicoccum*, '2grEink' = two-grained einkorn, 'Tdcd' = *T. dicoccoides*)

results support the morphological affinity between NGW and Timopheev's wheat as previously observed in chaff remains (Jones *et al.* 2000).

To expand the dataset, 156 less securely-identified glume wheat grains from deposits containing more than one type of wheat identification ('mixed' samples) were then added as 'unknowns' for reclassification. In order to make use of all morphological data, these 'unknown' grains were compared with both modern and archaeological grains. 'Unknown' grains classified as archaeological or modern emmer were assigned to the category 'Arch_Emmer' while those classified as either archaeological or modern timopheev's wheat were added to the category 'Arch_New'. Grains classified as '2-grained einkorn' were excluded in order to focus analysis on the two main glume wheats (see Appendix B for further details regarding reclassification of grains).

The aim of this approach was to not allow the original archaeobotanical identification of a grain to pre-determine the assigned category, but rather to rely on the GMM model. The result of the reclassification process was that 50/54 grains which could not previously be identified beyond 'glume wheat' were assigned as either archaeological emmer ('Arch_Emmer') or archaeological NGW ('Arch_New'). The majority (75/90) of grains previously identified as either emmer or NGW were confirmed as such by the LDA, with just 15 grains reassigned to a different cultivar. In addition, of twelve grains previously identified as 2-grain einkorn, nine were reclassified as NGW, and a single grain as emmer (Appendix B). The final dataset contained 443 grains of comparative material (Table 2) and 231 Çatalhöyük grains identified as emmer or NGW, combining both grains from securely identified deposits and those identified in comparison with these using GMM analysis, from a total of 60 contexts (Appendix A). This dataset was then used to conduct analyses by phase and relating to processing stage.

1.3.3 Stage 3: analysis by phase

Archaeological grains were subsequently coded by chronological phases as defined in Hodder (2021, 11): Early (7100–6700 cal. BC), Middle (6700–6500 cal. BC) and Late(-Final) (6500–5950 cal. BC). This time, the LDA showed that NGW grains from the Early phase

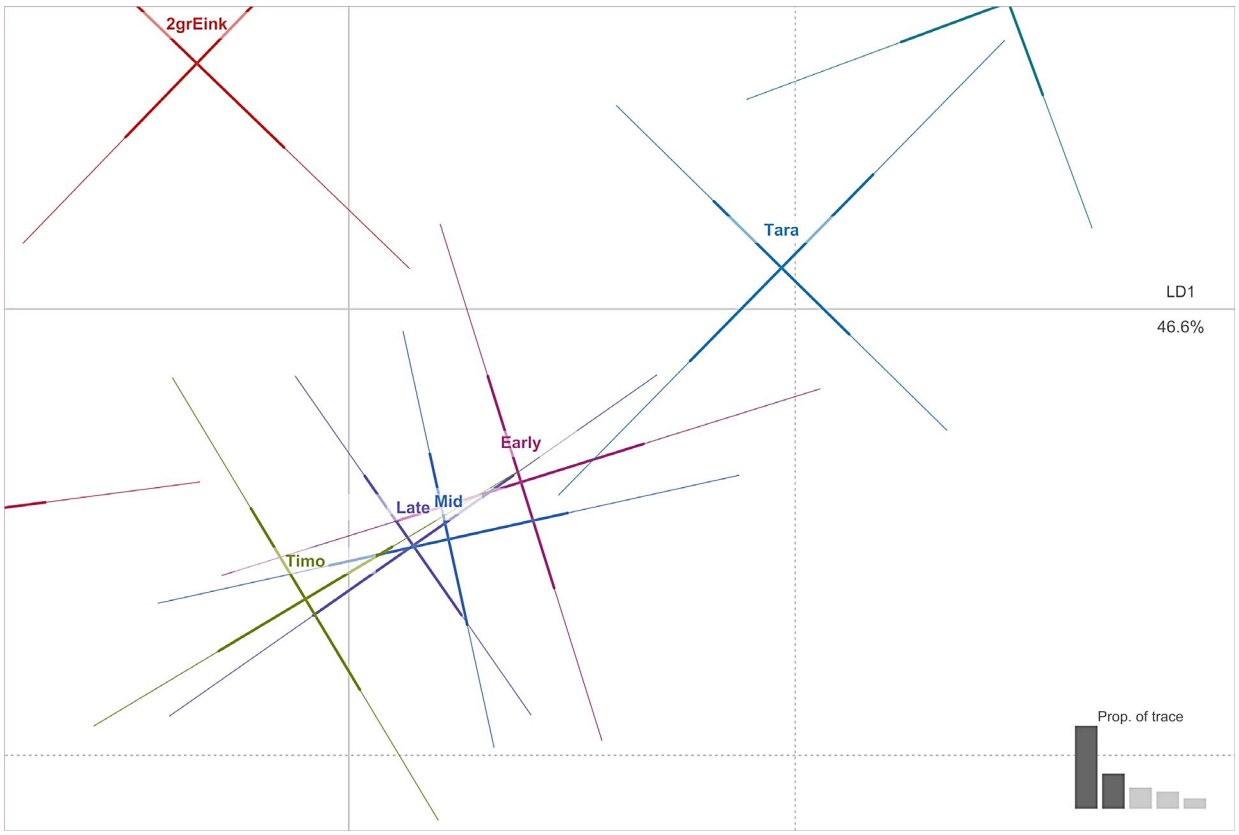

Fig. 7 LDA results when plotted with full dataset and NGW grains recoded as 'Early', 'Mid' and 'Late' phase (Timo = *T. timopheevii*, Tara = *T. araraticum*).

plotted more closely to wild Timopheev's wheat and over time plot increasingly closely to domesticated Timopheev's wheat, with the most significant shift apparent between Early and Middle phases (Fig. 7). When archaeological emmer grains were coded by phase no such pattern was apparent. NGW grains were then entered as 'unknowns' into an LDA using wild and domesticated Timopheev's wheat as classifiers. In the Early phase 57.1% of NGW grains classified as wild, decreasing to 20.4% by the Late phase (Table 5). A chi-squared test on the classifications produced p- values of <0.05 when comparing Early with Middle and Late phases, but produced a value of 0.3654 when Middle and Late phases were compared. This gives confidence in a significant shift between Early and Middle phases towards the domesticated form, if not between Middle and Late phases.

Comparing stacked outlines of NGW grains across phases revealed only subtle changes (Fig. 8). In the lateral view, dorsal curvature becomes slightly more pronounced, with the widest point of the grain shifting towards its apex. In the dorsal view, the widest point of the

Phase	Grains classified as *T. araraticum*	Percentage classified as *T. araraticum*
Early	16/28	57.1%
Middle	16/53	30.2%
Late	10/49	20.4%

P-value (all phases)	0.0037
P-value (early vs mid only)	0.0339
P-value (mid vs late only)	0.3654
P-value (early vs mid + late)	0.0032

Table 5 Results of LDA classification when NGW grains entered as unknowns against modern *T. araraticum* and *T. timopheevii* grains and p-values of chi-squared test performed on frequency tables

grain shifts slightly in the same direction, particularly in the Middle phase. Potentially these changes are concentrated towards the top of the grain because it is less tightly constrained by the glumes. These outlines provide useful identification criteria for NGW grains in line with those reported by Kohler-Schneider (2003), including a 'rather rounded apex' and dorsal edge running more parallel to the ventral than emmer when viewed laterally (Fig. 9).

Grain size was also measured, taking length and width in the dorsal view and depth in the lateral (after Charles *et al.* 2021). Between the Early and the Middle phase all three average NGW measurements increased, decreasing very slightly in the Late phase. For the emmer grains the largest measurements are from the Early phase with no clear differentiation between Middle and Late phases (Table 6).

	Average length (mm)	Average width (mm)	Average depth (mm)
Emmer			
Early	5.8834	2.9028	2.5585
Middle	5.4368	2.8435	2.4745
Late	5.7331	2.8368	2.4556
NGW			
Early	5.3095	2.1425	1.8984
Middle	5.6882	2.4428	2.0626
Late	5.6561	2.3823	2.0520

Table 6. Average dimensions of Çatalhöyük NGW and emmer grains summarised by phase. Depth = widest point of grain in lateral view

In summary, analysis of both shape and size suggest a shift in NGW grains between Early and Middle phases towards larger grains which more consistently resemble domesticated Timopheev's wheat in shape. This development in form persists into the Late phase, although a small size decrease is noted (<0.07 mm in any dimension). In contrast, emmer

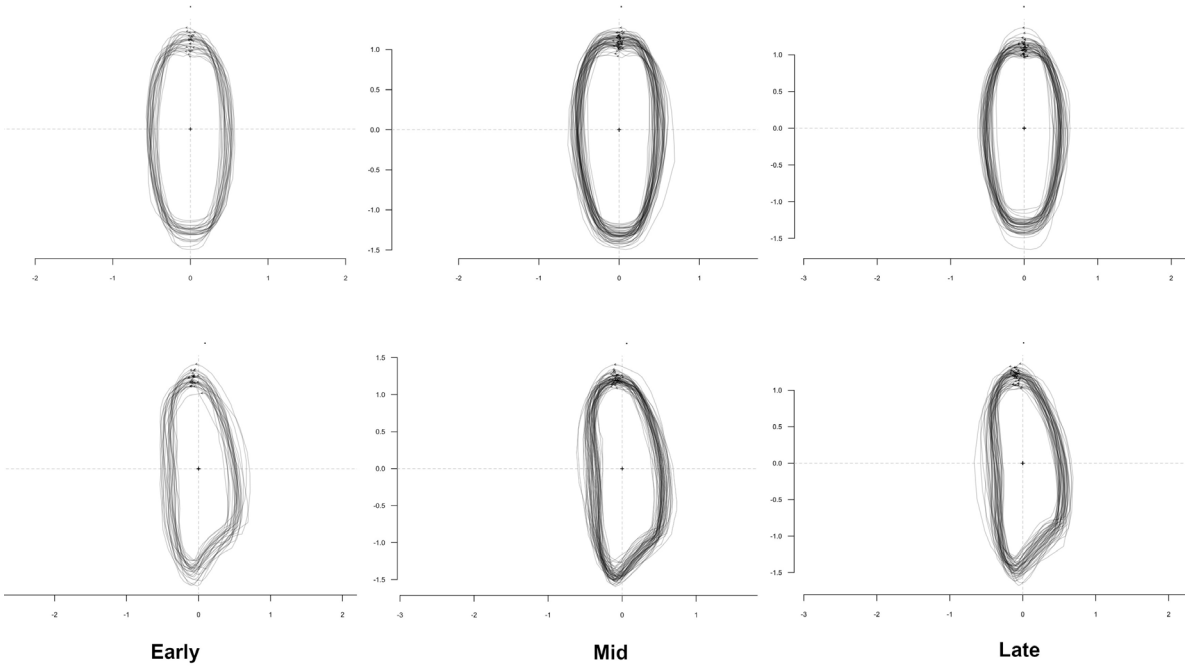

Fig. 8 Stacked outlines of Çatalhöyük NGW grains from Early, Mid and Late phase contexts

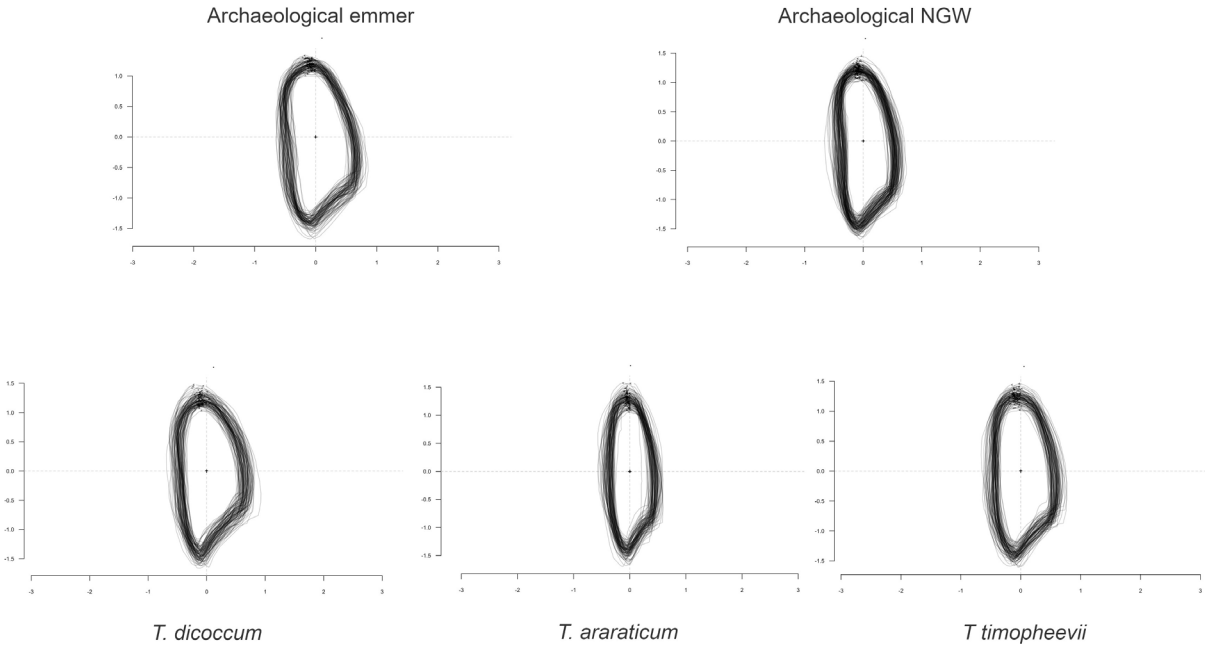

Fig. 9 Stacked outlines of Çatalhöyük emmer and NGW grains (all phases) alongside modern *T. dicoccum*, *T. araraticum* and *T. timopheevii* in lateral view

grains at no stage resemble wild emmer and are well-developed in size from the earliest phase.

1.3.4 Stage 4: analysis by processing stage

This stage sought to establish whether the archaeological grains were charred within their glumes (i.e. prior to dehusking) or as individual grains. Therefore, the data was recoded to reflect the subset of modern grains charred within their glumes (Table 2) and extracted before photographing.

In the LDA results, both NGW grains and emmer grains consistently plotted more closely to modern ‘in glume’ grains than those charred individually (Fig. 10), indicating that the archaeobotanical grains more closely resemble grains charred in their glumes. Results suggest a morphological distinction between grains charred, prior to, and after, dehusking, with glume-enclosed grains appearing slightly laterally compressed and ‘hunched’ in appearance (Fig. 11). Based on the analysis we can propose that the majority of grain at Çatalhöyük came to be charred whilst stored in its glume and prior to dehusking; this complements direct evidence of spikelet storage in the form of intact NGW spikelets recovered from Building 77 (Bogaard *et al.* 2013).

1.3.5 Assessing dehiscence from chaff morphology

A previous study of NGW chaff remains from Çatalhöyük supports the theory that the crop underwent domestication during the course of the settlement (Charles *et al.* 2021). Findings from this study are summarised and updated here, with further work undertaken to increase samples sizes — particularly of NGW from the early phase (which was increased from 28 to 90 chaff identifications), and of emmer across all phases. Overall an additional 127 emmer chaff identifications and 66 NGW chaff identifications were added to data from the previous study, with overall trends remaining consistent (Table 7).

The study analysed spikelet bases after Tanno and Willcox (2012), on the basis that domesticated wheats do not ‘shatter’ to distribute their seeds, i.e. the ear does not disarticulate into individual spikelets upon maturity but needs to be threshed after harvesting. The attachment point of each spikelet (or ‘abscission scar’) will therefore show signs of tearing, with part of the adjoining rachis segment more likely to remain attached. Wild forms detach naturally when ripe and the abscission scars are more likely to be smooth (Fig. 12; see also Charles *et al*. 2021). However, sometimes part of the rachis internode can remain attached to wild forms, and in emmer wheat these can be distinguished by profile (Weide 2015).

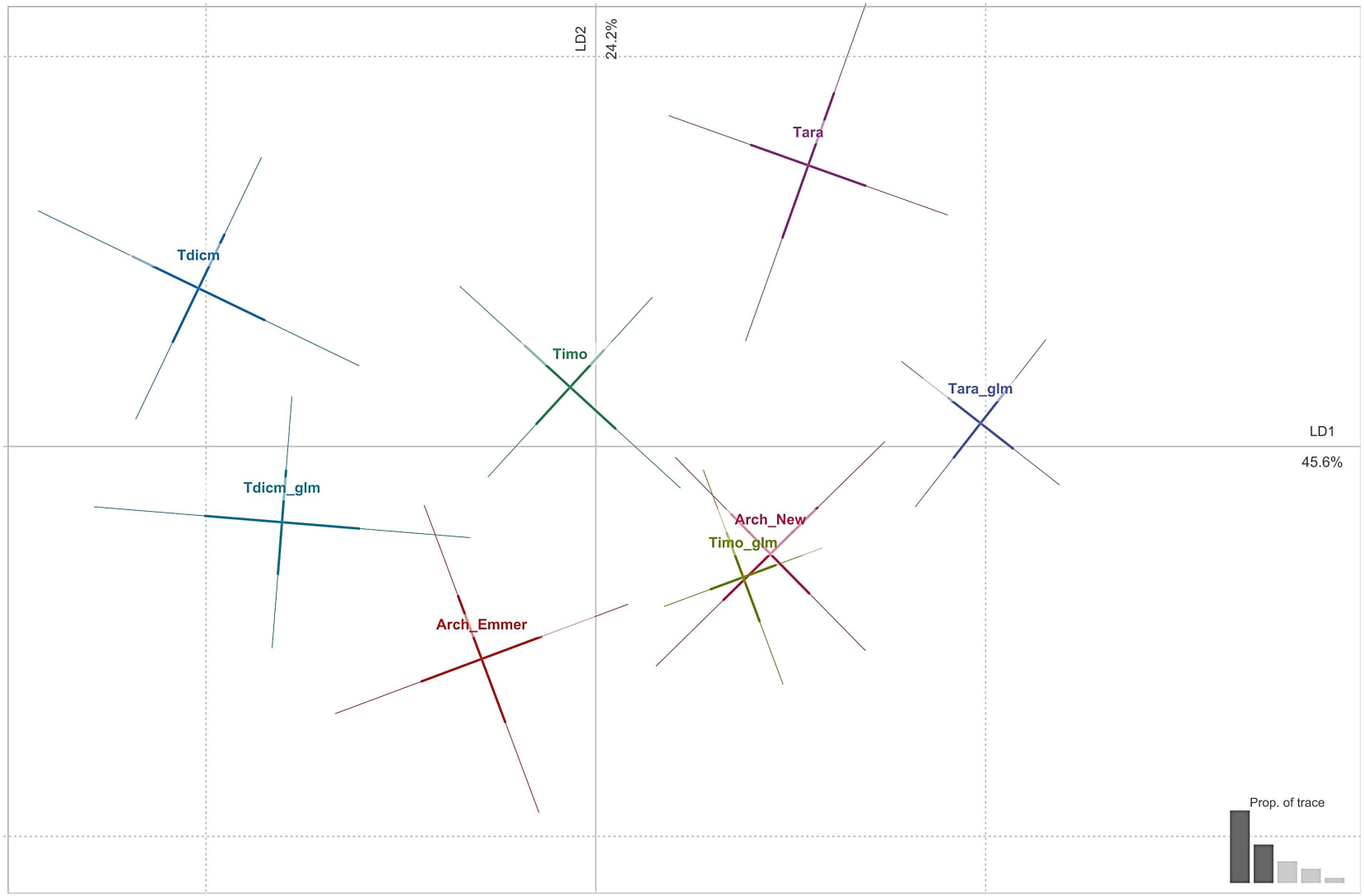

Fig. 10 LDA showing archaeological grains ('Arch_Emmer' and 'Arch_New') plotting more closely to modern grains which were charred in chaff ('_glm'). ('Tdicm' = *T. dicoccum*, 'Timo' = *T. timopheevii*, 'Tara' = *T. araraticum*)

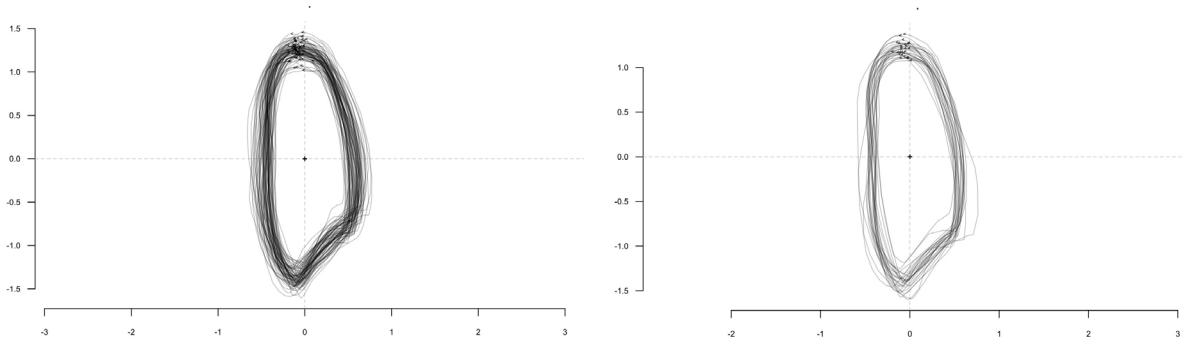

Fig. 11 Stacked outlines of *T. timopheevii* grains when charred as individual grains (left) and when charred within glume/chaff (right)

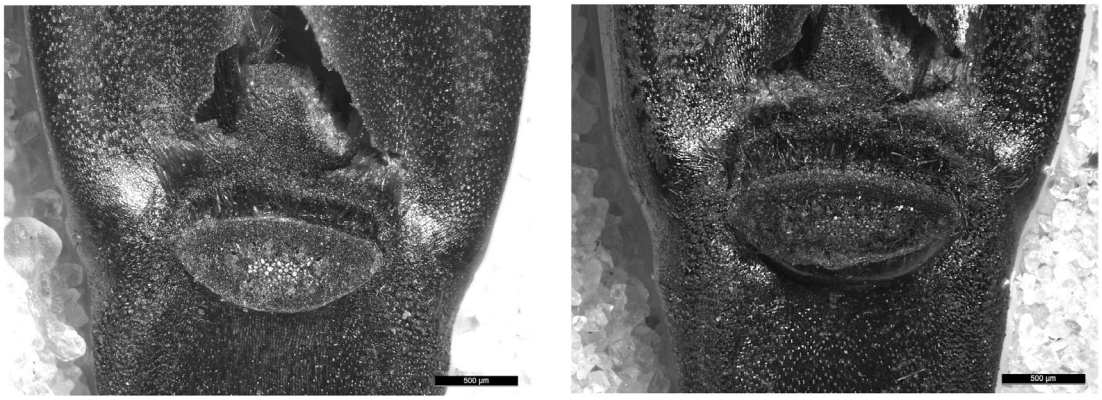

Fig. 12 Abscission scars of *T. araraticum*, showing the more common 'smooth' form (left) and the less common protruding form with tearing visible (right)

Analysis of modern Timopheev's wheat spikelets established that no distinction between wild and domesticated forms could be made based on individual scar profiles. However, there were clear differences in the proportions of scar types, with domesticated populations having a much higher proportion of 'rough' and 'protruding' (with partial rachis segment attached) scars while wild specimens had predominantly 'smooth' scars (Fig. 12). When NGW chaff from Çatalhöyük was examined it was observed that, where the rachis segment remained attached, it exhibited the same profile as in Timopheev's wheats: an abrupt or 'knee-shaped' transition to the upper rachis segment. Furthermore, a clear temporal trend from smoother to rougher scars was observed in the NGW remains, suggesting decreased shattering tendency over time (Fig. 13). Also observed in the original study, was an increase in 'terminal' spikelets (i.e. from the top of the ear) between the Early and Late phase, significant because these generally detach first in shattering forms. Emmer spikelet bases from Çatalhöyük neither exhibited a comparable trend as regards proportions of 'rough'

scars, nor were any spikelets identified which exhibited the 'wild-type' rachis attachment profile described in Weide (2015).

Overall the chaff evidence suggests selection for non-shattering forms in NGW over the course of the East Mound settlement sequence. In comparison, the morphology of emmer wheat as a non-shattering wheat was apparently established prior to the earliest settlement phase.

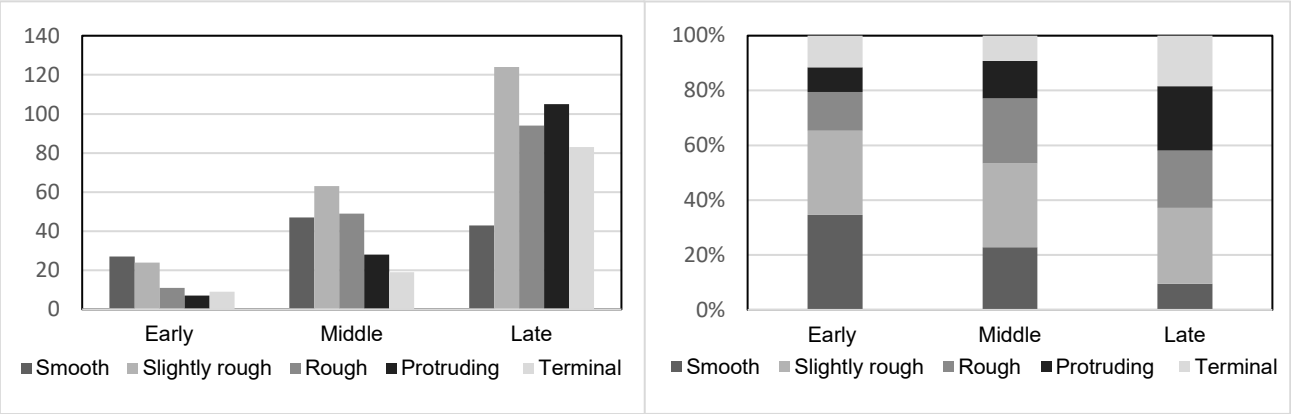

Fig. 13. Number and proportion of different categories of NGW abscission scar types at Çatalhöyük by phase

	Smooth	Slightly rough	Rough	Protruding	Terminal	Torn	Total
NGW							
Early	27	24	11	7	9	12	90
Middle	47	63	49	28	19	1	207
Late	43	124	94	105	83	166	615
Emmer							
Early	4	2	33	15	26	101	181
Middle	0	3	78	62	17	42	202
Late	0	3	25	16	14	41	99

Table 7 Summary of Çatalhöyük NGW and emmer abscission scar types

1.4 Discussion

1.4.1 Domestication processes

The GMM grain analysis and parallel chaff study support close comparability of NGW with modern Timopheev's wheats. Moreover, the findings demonstrate changes to grain size/shape and ear shattering behaviour during the East Mound sequence. These changes constitute a shift from remains more closely resembling wild Timopheev's wheat to those more closely resembling the domesticated crop. The developments emerged gradually over

a period of 1150 years, prompting consideration of the degree to which these traits were consciously selected by cultivators.

A co-evolutionary approach to domestication considers human-plant interactions as relationships with both intended and unintended consequences (Jones *et al.* 2021). Niche construction forms part of a broader process of co-evolution in which all organisms actively and continuously participate (Bogaard *et al.* 2021a). Human interaction with the environment creates specific conditions in which certain functional ecological traits may gain competitive advantage: for example, by modifying growing conditions or acting as dispersal agents. In turn, humans become increasingly dependent on those plants which thrive in anthropogenic environments (Rindos *et al.* 1980; Rindos 1984).

As regards ear shattering behaviour, selection for decreased dehiscence continued into the Late phase as the crop was increasingly relied upon as a staple across the settlement. Changes in dehiscence are usually explained in terms of harvesting methods (Charles *et al.* 2021). Chert and obsidian sickle-type blades are attested from Early phase levels at Çatalhöyük (Carter 2011) and use-wear analysis of blades indicates repeated cutting of cereals, albeit in a limited number of cases (Lemorini and D'Errico 2021). Sickle harvesting, or any harvesting method that recovers the entire ear (as opposed to hand-gathering mature spikelets), gives 'non-shattering' plants a competitive advantage, with seeds from non-shattering plants more likely to be harvested and sown the following year, whilst also enhancing reliability and yield of the crop for humans. However, sickle-harvesting is not the sole mechanism for increasing indehiscence, and annual harvesting and sowing cycles may also exert a gradual influence (or 'weak selection') even when ears are not cut (Maeda *et al*. 2016) which may over time increasingly encourage the use of sickles.

The gradual pace of change in grain form, and the fact that seed-size by itself is not a predictor of yield (Jones *et al.* 2021), mean we cannot explain this process purely in terms of human desire to increase harvests. Research has demonstrated that larger seeds of wild crop progenitors are more successful in rich, disturbed anthropogenic environments, germinating more quickly and producing larger seedlings/plants with more robust root

systems (Jones *et al.* 2021). Analysis of arable weed flora suggests that Çatalhöyük crops were grown in tilled and fertile soil (Green *et al.* 2018), i.e. conditions conducive to selection for larger seeds. As seed size increased, and the plants adapted to these types of conditions, they would become increasingly dependent on human amendment of the soil to thrive. It is therefore likely that both human intervention and environmental selection interacted to produce the developments in NGW at Çatalhöyük, and that the role of human intention was both 'complex and indirect' (Bogaard *et al.* 2021a, 10). It is possible that the small decrease in seed size we see in NGW, occurring between the Middle and Late Phases as selection for non-shattering forms continued, relates to changes in environmental conditions such as decreasing precipitation (Charles *et al*. 2021, 134) and/or cultivation practice e.g. the levels of tilling, watering and manuring (see also Section 4.2).

The observed changes do not represent an entire domestication sequence, as NGW remains from the earliest phase are not entirely 'wild'; rather, a greater proportion more closely resemble wild forms, and these early populations are perhaps best described as 'semi-shattering'. A possible alternate theory is that during periods of early adoption, seed stock of domesticated NGW was bolstered by wild stands (Willcox 2005). However, although wild Timopheev's wheat has been identified in Turkey, these observations are confined to the south-east of the country (Mitrofanova *et al.* 2016; Badaeva *et al.* 2022), outside Central Anatolia. While we cannot rule out *T. araraticum* having been present in the region during the Neolithic period, it seems more likely that a partially-domesticated form of the wheat was available from the earliest phases and continued to undergo adaptation during the course of the settlement.

1.4.2 Incentives for cultivation of NGW

The more widespread cultivation of NGW and its adoption in the South Area by the Late phase coincides with the development of desirable qualities in the crop relating to seed size and shattering. We may, however, question what motivated initial investment in this crop in the North Area — particularly when emmer wheat, a crop with similar processing and environmental requirements was readily available in domesticated form.

The inhabitants of Çatalhöyük had a broad subsistence base of cultivated and gathered food-plants, and experimentation with different resources was potentially a way of buffering risk against individual resource failures (Bogaard *et al.* 2017). It is therefore possible that cultivating multiple wheat crops was considered 'less risky' in the face of potential climate fluctuation or disease. While we cannot be certain of the specific traits of NGW or how they were perceived, modern Timopheev's wheat possesses significant resistance to fungal diseases including leaf and stem rust (Leonova *et al.* 2002). Both Turkey and Georgia fall within the region vulnerable to highly damaging wheat rust diseases (Food and Agriculture Organization of the United Nations 2014), so potentially this resistance was advantageous at Çatalhöyük and/or within the context of its cultivation in the recent past.

Other factors providing more personalised incentives might include the culinary qualities of specific plants and/or their ability to mark social differentiation between households. In Georgia, as part of the maslin 'Zanduri', fragile ears of Timopheev's wheat were harvested using a pair of wooden rods called 'shnakvi' (Mitrofanova *et al.* 2016). The grain was used to make 'Zanduri bread' which was associated with special occasions (Jorjadze *et al.* 2014) and for feeding fowl, while the straw was used for roofing (Mitrofanova *et al.* 2016). It is possible that while potentially adapted to multiple functions, NGW was also used in specific culinary preparations associated with particular households, other social groupings and/or occasions. Its cultivation may also have been associated with certain tools or practices which marked out its farmers as a distinct group.

1.5 Conclusion

GMM analysis of NGW grains from Çatalhöyük established a strong morphological similarity with modern Timopheev's wheat. These findings reinforce links previously made using chaff (Jones *et al.* 2000) and aDNA (Czajkowska *et al.* 2020) and we therefore propose that NGW be described in future as *Triticum timopheevii s.l. (sensu lato)* (after Badaeva *et al.* 2022), reserving *T. timopheevii s. str. (sensu stricto)* for the narrowly endemic modern form.

Results further demonstrate the potential of GMM to distinguish between charred grains of morphologically-similar wheat species and sub-species of differing domestication status; particularly when the dorsal and lateral views of the grain are used. The method even appears sufficiently sensitive to suggest whether grains were dehusked before storing. Applications of GMM to archaeobotanical studies of wheat therefore seem promising, including at sites where identification of *T. timopheevii s.l.* remains uncertain, or for further studies of the transition between wild and domesticated wheats. Research into refining identifications of free-threshing wheats forms and expanding modern comparative datasets is also currently underway.

At Çatalhöyük, comparison of NGW with modern Timopheev's wheats suggests that the crop underwent domestication processes during the Neolithic East Mound sequence. In the Early phase a higher proportion of NGW grains resemble wild Timopheev's wheat and become more similar to the domesticated form over time, accompanied by a size increase. Changes in grain form were most marked between the Early and Middle phases, coinciding with more widespread adoption of the crop in the North Area. Building on previous work (Charles *et al.* 2021) analysis of NGW chaff morphology also detected a reduction in shattering. This decrease in shattering continued into the Late Phase, by which time the NGW had apparently replaced emmer as the settlement's main wheat crop. In contrast to NGW, emmer wheat was found to be more fixed in form, being well-developed in both size and non-shattering properties from the earliest phase.

It is proposed that a partially-domesticated form of NGW was available from the earliest phases and continued to undergo adaptation over the course of the settlement. Sickle harvesting and cultivation in relatively fertile and disturbed soil facilitated a gradual co-evolutionary process whereby both human intervention and environmental conditions selected for mutually beneficent traits of reproduction and yield. The role of human intention in these changes is understood to be 'complex and indirect' (Bogaard *et al.* 2021a, 10) as opposed to a unidirectional process of selection. Possible incentives in the initial uptake of the crop may have included culinary qualities, cultural differentiation between households,

its resistance to fungal disease and/or its multi-functional properties. More broadly, investment in the crop may be understood within the context of a broad-spectrum plant strategy (Bogaard *et al.* 2017), in which risk of individual resource failure was offset by diverse strategies at the household level.

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Paper 1: Appendix A: List of archaeological samples used in study

Flot no.	Unit no.	Area	Context type	Description	Phase	Mixed	No. NT grains	No. emmer
78	1255	North G	Burnt primary fill	Occupation debris on floor	Mid	Y	0	5
173	1099	South ?L	Midden	Midden	Early	Y	0	1
282	1254	North G	Burnt primary fill	Lower layer of FI	Mid	N	0	1
295	1588	South ?L	Midden	Ashy layer	Early	Y	5	2
332	1291	North G	Burnt primary fill	Deposit on floor	Mid	Y	0	1
345	1612	South ?K	Midden	Midden with collapse	Early	Y	1	1
366	1513	South ?K	Midden	Midden	Early	Y	1	2
513	1664	South ?K	Midden	Dump	Early	Y	2	2
535	1442	North G	Burnt primary fill	Fill	Mid	Y	0	1
674	1845	South ?K	Midden	In bin	Early	Y	0	1
813	1889	South ?K	Building fill	Domestic dump	Early	Y	0	2
830	2032	South ?K	Midden	Bin infill	Early	Y	0	1
940	2306	South ?M	Internal fire installation	Oven rake out/scorching	Mid	Y	0	1
1010	2346	South ?L	Building fill	Occupation	Early	Y	1	0
1038	2364	South ?L	Midden	Conc. of material	Early	Y	1	1
1297	2845	South ?L	Midden	Midden	Early	Y	2	1
1804	3705	South ?L	Midden	Ash dump	Early	Y	2	1
2236	2024	South ?K	Penning	Barn floor?	Early	Y	1	1
2326	4125	South ?K	Floor	Ashy spread	Early	Y	0	1
2535	4256	South L	Building fill	Infill	Early	Y	0	1
2763	4793	South L	Building fill	Fill	Early	Y	0	1
2985	4917	South L	Pit fill	Bin fill	Early	Y	1	0
3099	4937	South L	Floor	Rake-out	Early	Y	0	1
3148	4866	South G	External fire spot	Burning event	Early	Y	0	1

Flot no.	Unit no.	Area	Context type	Description	Phase	Mixed	No. NT grains	No. emmer
3151	4866	South G	External fire spot	Burning event	Early	Y	3	2
3297	4879	South G	Midden	Dump	Early	Y	1	0
3324	5277	South G	External fire spot	Burning	Early	Y	1	0
3666	5302	South G	External activity	Spread	Early	Y	3	1
3742	5314	South G	External fire spot	Burning	Early	Y	1	0
4741	8253	North H	Midden	Midden	Late	Y	0	1
5030	8391	North G	Building fill	Bin	Mid	Y	1	0
6050	1911	North G	Burnt primary fill	Peas concentration	Mid	Y	0	1
7104	14305	South Q	Pit fill	Pit fill	Late	Y	3	0
7107	14132	North I	External fire spot	Burnt layer	Late	Y	8	2
7861	16268	South P	Internal fire installation	Make up	Late	Y	0	1
8326	17082	South P	External fire spot	Black burnt material within a fire spot	Late	Y	3	2
8328	17084	South P	External fire spot	Yellow burnt material within a fire spot	Late	Y	1	0
8413	16480	North G	Burnt primary fill	Spread of burnt grain	Mid	Y	4	0
9255	18949	South O	Burnt primary fill	Cluster of seeds	Mid	N	0	3
9798	20403	North G	Building fill	Burned area	Mid	Y	2	1
10830	20703	TPC.M	Burnt primary fill	Burnt construction layer	Late	Y	9	4
10922	30785	TPC.M	Burnt primary fill	Barley cluster	Late	N	5	0
10925	20703	TPC.M	Burnt primary fill	Burnt construction layer	Late	Y	9	1
11856	22713	TPC.M	Burnt primary fill	Rubble in-fill of bin	Late	Y	1	2
11995	22656	North G	Burnt primary fill	New type glume wheat spikelets	Mid	N	10	0
11996	22656	North G	Burnt primary fill	New type glume wheat spikelets	Mid	N	18	0
12015	22637	North G	Burnt primary fill	New type wheat	Mid	N	17	0
12089	31320	TPC.Q	Pit fill	Pit fill	Final	Y	2	3
12155	22834	GDN	Midden	Midden	Late	Y	1	2
12278	22850	GDN	Midden/pit fill	Midden/pit fill	Late	Y	3	2
12296	22823	GDN	Building fill	Fill	Late	Y	1	1

Flot no.	Unit no.	Area	Context type	Description	Phase	Mixed	No. NT grains	No. emmer
12317	22867	GDN	Midden/pit fill	Infill	Late	Y	1	2
12576	22334	South K	Building fill	Collapsed building material	Early	Y	1	1
12663	32405	South K	Floor	Dirty floor on SE part of building	Early	Y	1	0
12717	32046	North F	Floor	In-fill of a pit	Mid	Y	0	3
12755	32453	South. K	Floor	Dirty floor	Early	Y	0	1
12913	20747	TPC.M	Internal fire installation	Burned layer of fire installation on platform	Late	Y	0	1
12972	20789	TPC.M	Floor	Platform construction	Late	Y	2	0
13253	23203	South K,South ?I	Floor	Floor Layer with phyt., org. Mat. And pigment	Early	Y	1	0
13325	23214	South ?I	Midden/penning	Phytoliths surface	Early	Y	0	1
13850	32803	TPC.M	Burnt primary fill	Cluster	Late	N	0	1
13917	32837	TPC	Internal fire installation	Ovens base	Late	Y	1	0
18596	18596	South.O	Burnt primary fill	Charred seeds	Mid	N	0	31

Paper 1: Appendix B: Reclassification results when comparing Çatalhöyük grains from 'mixed' deposits with modern and securely identified archaeological grains

Photo ID	Grain no.	Sample no.	Phase	Originally ID'd	Mixed sample?	LDA Reclass	Assigned
9000	S1	1297	Early	New	Y	Arch_New	Arch_New
9003	S2	1297	Early	New	Y	Tara	Arch_New
9021	S1	10922	Late	Arch_New	N	N/A	Arch_New
9024	S2	10922	Late	Arch_New	N	N/A	Arch_New
9027	S3	10922	Late	Arch_New	N	N/A	Arch_New
9036	S3	10925	Late	New	Y	Arch_New	Arch_New
9048	S1	12015	Mid	Arch_New	N	N/A	Arch_New
9057	S1	3742	Early	cf New	Y	Arch_New	Arch_New
9072	S1	535	Mid	Emmer	Y	Arch_Emmer	Arch_Emmer
9078	S4	78	Mid	Emmer	Y	Arch_Emmer	Arch_Emmer
9114	S5	78	Mid	Emmer	Y	Timo	Arch_New
9117	S3	78	Mid	Emmer	Y	Timo	Arch_Emmer*
9120	S1	78	Mid	Emmer	Y	Timo	Arch_Emmer*
9123	S2	10830	Late	Emmer	Y	2gr eink	Left out
9135	S2	13917	Late	Not ID	Y	2gr eink	Left out
9138	S1	10830	Late	Emmer	Y	Timo	Arch_Emmer*
9141	S3	10830	Late	Emmer	Y	Timo	Arch_New
9144	S3	13917	Late	Not ID	Y	Arch_New	Arch_New
9150	S1	173	Early	Emmer	Y	Arch_Emmer	Arch_Emmer
9156	S1	1804	Early	Emmer/New	Y	Arch_New	Arch_New
9158	S4	11996	Mid	Arch_New	N	N/A	Arch_New
9160	S5	11996	Mid	Arch_New	N	N/A	Arch_New
9162	S6	11996	Mid	Arch_New	N	N/A	Arch_New
9166	S8	11996	Mid	Arch_New	N	N/A	Arch_New
9168	S9	11996	Mid	Arch_New	N	N/A	Arch_New
9174	S12	11996	Mid	Arch_New	N	N/A	Arch_New
9184	S4	10830	Late	Emmer	Y	Arch_Emmer	Arch_Emmer
9186	S4	10830	Late	New	Y	Arch_New	Arch_New
9188	S5	10830	Late	New	Y	Arch_New	Arch_New

Photo ID	Grain no.	Sample no.	Phase	Originally ID'd	Mixed sample?	LDA Reclass	Assigned
9190	S6	10830	Late	New	Y	Arch_New	Arch_New
9192	S7	10830	Late	New	Y	Arch_New	Arch_New
9194	S8	10830	Late	New	Y	Timo	Arch_New
9200	S11	10830	Late	New	Y	Arch_New	Arch_New
9210	S1	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9212	S2	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9214	S3	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9216	S4	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9220	S6	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9222	S7	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9224	S8	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9226	S9	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9228	S10	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9230	S11	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9232	S12	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9234	S13	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9236	S14	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9238	S15	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9240	S16	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9242	S17	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9244	S1	3297	Early	2gr einkorn	Y	Arch_New	Arch_New
9248	S1	3137	Early	2gr einkorn	Y	Tdcds	Left out
9254	S3	12913	Late	Emmer	Y	Arch_Emmer	Arch_Emmer
9256	S4	10925	Late	New	Y	Arch_New	Arch_New
9258	S5	10925	Late	New	Y	Arch_New	Arch_New
9260	S6	10925	Late	New	Y	Arch_New	Arch_New
9262	S7	10925	Late	New	Y	Timo	Arch_New
9264	S8	10925	Late	New	Y	Arch_New	Arch_New
9266	S9	10925	Late	New	Y	Timo	Arch_Emmer*
9268	S10	10925	Late	New	Y	Arch_New	Arch_New
9270	S11	10925	Late	New	Y	Arch_New	Arch_New
9274	S13	10925	Late	New	Y	Arch_New	Arch_New

Photo ID	Grain no.	Sample no.	Phase	Originally ID'd	Mixed sample?	LDA Reclass	Assigned
9288	S1	12972	Late	New	Y	Arch_New	Arch_New
9290	S2	12972	Late	New	Y	Arch_New	Arch_New
9292	S1	13850	Late	Arch_Emmer	N	N/A	Arch_Emmer
9294	S3	13917	Late	Not ID	Y	2gr eink	Left out
9296	S1	6050	Mid	Emmer	Y	Arch_Emmer	Arch_Emmer
9306	S2	1297	Early	Emmer	Y	Arch_Emmer	Arch_Emmer
9308	S1	12278	Late	New	Y	Timo	Arch_New
9310	S2	12278	Late	New	Y	Arch_New	Arch_New
9316	S5	8413	Mid	New	Y	Arch_New	Arch_New
9342	S18	8413	Mid	New	Y	Arch_New	Arch_New
9344	S19	8413	Mid	New	Y	Arch_New	Arch_New
9346	S20	8413	Mid	New	Y	Arch_New	Arch_New
9350	S4	12015	Mid	Arch_New	N	N/A	Arch_New
9352	S5	12015	Mid	Arch_New	N	N/A	Arch_New
9354	S6	12015	Mid	Arch_New	N	N/A	Arch_New
9356	S7	12015	Mid	Arch_New	N	N/A	Arch_New
9358	S8	12015	Mid	Arch_New	N	N/A	Arch_New
9360	S9	12015	Mid	Arch_New	N	N/A	Arch_New
9362	S10	12015	Mid	Arch_New	N	N/A	Arch_New
9364	S11	12015	Mid	Arch_New	N	N/A	Arch_New
9368	S13	12015	Mid	Arch_New	N	N/A	Arch_New
9370	S14	12015	Mid	Arch_New	N	N/A	Arch_New
9372	S15	12015	Mid	Arch_New	N	N/A	Arch_New
9374	S16	12015	Mid	Arch_New	N	N/A	Arch_New
9376	S17	12015	Mid	Arch_New	N	N/A	Arch_New
9378	S18	12015	Mid	Arch_New	N	N/A	Arch_New
9382	S20	12015	Mid	Arch_New	N	N/A	Arch_New
9384	S21	12015	Mid	Arch_New	N	N/A	Arch_New
9386	S4	10922	Late	Arch_New	N	N/A	Arch_New
9388	S5	10922	Late	Arch_New	N	N/A	Arch_New
9392	S2	940	Mid	Emmer	Y	Arch_Emmer	Arch_Emmer
9394	S15	11996	Mid	Arch_New	N	N/A	Arch_New

Photo ID	Grain no.	Sample no.	Phase	Originally ID'd	Mixed sample?	LDA Reclass	Assigned
9396	S16	11996	Mid	Arch_New	N	N/A	Arch_New
9398	S17	11996	Mid	Arch_New	N	N/A	Arch_New
9400	S18	11996	Mid	Arch_New	N	N/A	Arch_New
9402	S19	11996	Mid	Arch_New	N	N/A	Arch_New
9404	S20	11996	Mid	Arch_New	N	N/A	Arch_New
9406	S21	11996	Mid	Arch_New	N	N/A	Arch_New
9408	S22	11996	Mid	Arch_New	N	N/A	Arch_New
9412	S24	11996	Mid	Arch_New	N	N/A	Arch_New
9414	S25	11996	Mid	Arch_New	N	N/A	Arch_New
9416	S26	11996	Mid	Arch_New	N	N/A	Arch_New
9418	S27	11996	Mid	Arch_New	N	N/A	Arch_New
9428	S1	3151	Early	Emmer	Y	Arch_Emmer	Arch_Emmer
9430	S2	3151	Early	Emmer	Y	Arch_Emmer	Arch_Emmer
9432	S1	3151	Early	2gr einkorn	Y	Tara	Arch_New
9434	S1	3151	Early	indet	Y	Arch_New	Arch_New
9436	S1	12155	Late	Emmer/New	Y	Arch_Emmer	Arch_Emmer
9440	S3	12155	Late	Emmer/New	Y	Arch_New	Arch_New
9444	S6	12155	Late	Emmer/New	Y	Arch_Emmer	Arch_Emmer
9446	S1	1804	Early	2gr einkorn	Y	Tara	Arch_New
9448	S1	1804	Early	Emmer/Einkorn	Y	Arch_Emmer	Arch_Emmer
9454	S2	12717	Mid	Emmer	Y	Arch_Emmer	Arch_Emmer
9462	S4	12717	Mid	Emmer	Y	Arch_Emmer	Arch_Emmer
9464	S5	12717	Mid	Emmer	Y	Arch_Emmer	Arch_Emmer
9468	S2	7104	Late	Emmer	Y	Timo	Arch_New
9470	S1	7104	Late	Not ID	Y	Arch_New	Arch_New
9472	S1	7104	Late	New	Y	Arch_New	Arch_New
9476	S16	10830	Late	New	Y	Arch_New	Arch_New
9478	S17	10830	Late	New	Y	Arch_New	Arch_New
9506	S1	10830	Late	Not ID	Y	Arch_Emmer	Arch_Emmer
9508	S2	10830	Late	Not ID	Y	Tdicm	Arch_Emmer
9526	S1	295	Early	Not ID	Y	Arch_New	Arch_New
9532	S4	295	Early	Not ID	Y	Arch_Emmer	Arch_Emmer

Photo ID	Grain no.	Sample no.	Phase	Originally ID'd	Mixed sample?	LDA Reclass	Assigned
9534	S5	295	Early	Not ID	Y	Arch_New	Arch_New
9538	S7	295	Early	Not ID	Y	Tara	Arch_New
9540	S8	295	Early	Not ID	Y	Tara	Arch_New
9544	S10	295	Early	Not ID	Y	Arch_Emmer	Arch_Emmer
9546	S11	295	Early	Not ID	Y	Tdcd	Left out
9552	S14	295	Early	Not ID	Y	Arch_New	Arch_New
9554	S1	8328	Late	2 seeded GW	Y	Arch_New	Arch_New
9566	S1	7861	Late	Emmer	Y	Arch_Emmer	Arch_Emmer
9570	S3	7861	Late	Emmer	Y	2gr eink	Left out
9572	S4	7861	Late	Emmer	Y	2gr eink	Left out
9574	S1	9255	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9576	S2	9255	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9578	S1	9255	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9580	S1	12089	Late	Emmer	Y	Arch_Emmer	Arch_Emmer
9584	S2	12089	Late	Not ID	Y	Arch_New	Arch_New
9586	S2	12089	Late	Emmer	Y	Timo	Arch_New
9588	S3	12089	Late	Emmer	Y	Timo	Arch_Emmer*
9596	S6	12089	Late	Not ID	Y	Arch_emmer	Arch_Emmer
9602	S1	2985	Early	2gr einkorn	Y	Arch_New	Arch_New
9604	S1	345	Early	Emmer	Y	Arch_Emmer	Arch_Emmer
9606	S1	345	Early	2gr einkorn	Y	Tara	Arch_New
9608	S1	830	Early	Emmer	Y	Tdicm	Arch_Emmer
9610	S1	3099	Early	Emmer/new	Y	Arch_Emmer	Arch_Emmer
9612	S1	3546	Early	2gr einkorn	Y	Tdcd	Left out
9614	S1	13325	Early	Not ID	Y	Arch_Emmer	Arch_Emmer
9616	S1	13253	Early	2S GW	Y	Arch_New	Arch_New
9618	S1	2535	Early	Emmer	Y	Arch_Emmer	Arch_Emmer
9622	S1	513	Early	Not ID	Y	Arch_New	Arch_New
9624	S1	7107	Late	cf New	Y	Tara	Arch_New
9626	S1	7107	Late	Not ID	Y	Tara	Arch_New
9628	S2	7107	Late	Not ID	Y	Arch_New	Arch_New
9630	S3	7107	Late	Not ID	Y	Arch_Emmer	Arch_Emmer

Photo ID	Grain no.	Sample no.	Phase	Originally ID'd	Mixed sample?	LDA Reclass	Assigned
9632	S4	7107	Late	Not ID	Y	Arch_New	Arch_New
9634	S5	7107	Late	Not ID	Y	Arch_Emmer	Arch_Emmer
9636	S6	7107	Late	Not ID	Y	Arch_New	Arch_New
9638	S7	7107	Late	Not ID	Y	Arch_New	Arch_New
9640	S8	7107	Late	Not ID	Y	Arch_New	Arch_New
9642	S9	7107	Late	Not ID	Y	Arch_New	Arch_New
9650	S1	8326	Late	Emmer	Y	Arch_Emmer	Arch_Emmer
9654	S1	8326	Late	New	Y	Timo	Arch_New
9656	S2	8326	Late	New	Y	Tara	Arch_New
9660	S4	8326	Late	New	Y	Arch_New	Arch_New
9662	S1	8326	Late	Not ID	Y	Arch_Emmer	Arch_Emmer
9664	S1	12576	Early	Not ID	Y	Timo	Arch_New
9666	S2	12576	Early	Not ID	Y	Arch_Emmer	Arch_Emmer
9668	S1	12663	Early	Not ID	Y	Arch_Emmer	Arch_Emmer
9670	S1	11856	Late	Not ID	Y	Arch_New	Arch_New
9678	S5	11856	Late	Not ID	Y	Arch_Emmer	Arch_Emmer
9682	S1	11856	Late	cf emmer	Y	2gr eink	Left out
9684	S2	11856	Late	cf emmer	Y	Arch_Emmer	Arch_Emmer
9686	S1	12296	Late	New	Y	Arch_New	Arch_New
9686	S2	12296	Late	Emmer	Y	Arch_Emmer	Arch_Emmer
9690	S1	12755	Early	Not ID	Y	Arch_Emmer	Arch_Emmer
9692	S1	12317	Late	Emmer	Y	Arch_Emmer	Arch_Emmer
9694	S2	12317	Late	Emmer	Y	Arch_Emmer	Arch_Emmer
9698	S1	12317	Late	Not ID	Y	Arch_New	Arch_New
9702	S4	12317	Late	Emmer	Y	2gr eink	Left out
9704	S1	9798	Mid	Emmer	Y	Timo	Arch_New
9706	S2	9798	Mid	Not ID	Y	Tdicm	Arch_Emmer
9712	S2	9798	Mid	Emmer	Y	Arch_New	Arch_New
9714	S1	11995	Mid	New	N	N/A	Arch_New
9718	S3	11995	Mid	New	N	N/A	Arch_New
9720	S4	11995	Mid	New	N	N/A	Arch_New
9722	S5	11995	Mid	New	N	N/A	Arch_New

Photo ID	Grain no.	Sample no.	Phase	Originally ID'd	Mixed sample?	LDA Reclass	Assigned
9724	S6	11995	Mid	New	N	N/A	Arch_New
9730	S9	11995	Mid	New	N	N/A	Arch_New
9732	S10	11995	Mid	New	N	N/A	Arch_New
9738	S13	11995	Mid	New	N	N/A	Arch_New
9746	S17	11995	Mid	New	N	N/A	Arch_New
9748	S18	11995	Mid	New	N	N/A	Arch_New
9750	S1	366	Early	Emmer	Y	Arch_Emmer	Arch_Emmer
9752	S2	366	Early	Emmer/new	Y	Timo	Arch_New
9754	S1	366	Early	2gr einkorn	Y	Arch_Emmer	Arch_Emmer
9756	S1	128	Early	Emmer/einkorn	Y	2gr eink	Left out
9758	S1	332	Mid	Emmer	Y	Arch_Emmer	Arch_Emmer
9762	S1	282	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9766	S1	5030	Mid	Emmer	Y	Arch_New	Arch_New
9768	S1	4741	Late	Emmer	Y	Arch_Emmer	Arch_Emmer
9770	S1	813	Early	Emmer	Y	Arch_Emmer	Arch_Emmer
9772	S1	813	Early	Emmer/einkorn	Y	Tdicm	Arch_Emmer
9774	S18	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9776	S19	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9778	S20	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9780	S21	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9782	S22	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9784	S23	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9786	S24	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9788	S25	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9790	S26	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9792	S27	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9794	S28	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9796	S29	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9798	S30	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9800	S31	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9802	S32	18596	Mid	Arch_Emmer	N	N/A	Arch_Emmer
9804	S1	513	Early	Emmer	Y	Arch_New	Arch_New

Photo ID	Grain no.	Sample no.	Phase	Originally ID'd	Mixed sample?	LDA Reclass	Assigned
9806	S4	513	Early	Emmer	Y	Arch_Emmer	Arch_Emmer
9808	S2	513	Early	Emmer	Y	Arch_Emmer	Arch_Emmer
9810	S1	674	Early	Emmer	Y	Arch_Emmer	Arch_Emmer
9814	S1	2236	Early	NT	Y	Timo	Arch_New
9816	S1	2236	Early	Emmer	Y	Arch_Emmer	Arch_Emmer
9818	S1	2763	Early	Emmer	Y	Tdicm	Arch_Emmer
9822	S1	1038	Early	Emmer	Y	Arch_Emmer	Arch_Emmer
9824	S1	1038	Early	Not ID	Y	Arch_New	Arch_New
9836	S2	3666	Early	2gr einkorn	Y	Arch_New	Arch_New
9838	S1	3666	Early	Einkorn indet	Y	Tara	Arch_New
9840	S2	3666	Early	Einkorn indet	Y	Tara	Arch_New
9842	S1	3666	Early	emmer/einkorn	Y	Arch_Emmer	Arch_Emmer
9844	s1	3324	Early	cfEmmer	Y	Timo	Arch_New
9846	S1	1010	Early	2gr einkorn	Y	Arch_New	Arch_New
9848	S1	3148	Early	Emmer	Y	Arch_Emmer	Arch_Emmer
9850	S1	3151	Early	Emmer/einkorn	Y	Arch_New	Arch_New
9852	S1	2326	Early	Emmer	Y	Arch_Emmer	Arch_Emmer
9854	S6	78	Mid	Emmer	Y	Arch_Emmer	Arch_Emmer
9856	S1	12278	Late	Not ID	Y	Arch_Emmer	Arch_Emmer
9858	S2	12278	Late	Not ID	Y	Arch_Emmer	Arch_Emmer
9860	S3	12278	Late	Not ID	Y	Arch_Emmer	Arch_Emmer

'Tara'= *T. araraticum*, 'Timo'= *T. timopheevii,* 'Arch_New'= archaeological NGW, 'Arch_Emmer'= archaeological emmer. Securely identified grains from non-mixed deposits were not reclassified and are therefore listed as 'N/A'. Three grains classified as *T. dicoccoides* ('Tdcd') plotted as outliers and were therefore excluded, as were grains classified as two-grained einkorn ('2gr einkorn').

*Five grains initially classified as 'Timo' were subsequently reassigned as 'Arch_Emmer' due to plotting/scoring at the boundary between the two classes (with scores that corresponded more closely to the 'Arch_Emmer' than to the 'Arch_New' group).

2.0 Paper 2: Geometric Morphometric Analysis of Neolithic Wheat Grains: Insights into the Early Development of Free-Threshing Forms

Tina Roushannafas (0000-0001-6012-5401), Amy Bogaard, Michael Charles

School of Archaeology, University of Oxford, Oxford OX1 3TG, United Kingdom

Abstract

Current knowledge of the origin and trajectories of both tetraploid and hexaploid free-threshing wheats (FTWs) from western Asia into Europe remains imprecise. Archaeobotanical distinction of ploidy-level is often dependent on sparsely recovered rachis segments, while identification of specific cultivars using morphological characteristics of either grain *or* chaff is generally considered unreliable. This study offers an alternative approach by employing geometric morphometric (GMM) analysis of grain shape to assess taxonomic and varietal-level distinctions in archaeobotanical FTW remains.

Two substantial and well-preserved assemblages of Neolithic FTW grains from 7th millennium BC Çatalhöyük (Central Anatolia) and 6th millennium BC Kouphovouno (southern Greece) were analysed with the aim of shedding light on the naked wheats cultivated by these early agricultural communities. While chaff remains at Çatalhöyük indicate a hexaploid FTW crop, no such diagnostic remains were recovered from Kouphovouno. GMM analysis of the archaeobotanical grains corroborates early cultivation of hexaploid naked wheat at Çatalhöyük, whilst revealing that a tetraploid wheat, most closely resembling 'unimproved' durum wheat, was likely grown at Kouphovouno. The Kouphovouno findings are contextualised within existing theories of a Mediterranean route for tetraploid FTWs into south-west Europe. Assessment of the role of FTWs over time at both sites, suggests changes in the cultural value attributed to these crops and/or the sustainability of the agricultural regimes they were associated with.

Key words

Geometric Morphometrics; Wheat; Taxonomy; Neolithic; Anatolia; Greece

Acknowledgements

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Statements and Declarations

Declarations of interest: none

2.1 Introduction

2.1.1 Types of Free-Threshing Wheat and their Identification in the Archaeobotanical Record

The ears of free-threshing wheats (FTWs) have tough rachises and thin glumes, from which 'naked' grains are released upon threshing. In contrast, glume (hulled) wheats have tough glumes and, when threshed, break up into spikelets, which require further processing to release the grain (Hillman 1984, Fig. 1). FTWs are by far the most commercially significant group today, with 'bread wheat' (*Triticum aestivum* L. ssp. *aestivum*) accounting for as much as 90–95% of the global wheat market and durum (*Triticum turgidum* L. ssp. *turgidum*), primarily used for pasta, the second-highest produced (Giraldo *et al.* 2019).

Durum and bread wheat represent two 'ploidy' groups: respectively, the tetraploid *turgidum* group and the hexaploid *aestivum* group. Tetraploid wheats have four sets of chromosomes (BBAA) while hexaploid wheats have six (BBAADD). The latter evolved from tetraploid wheats via polyploidisation, the result of inter-specific hybridisation with the wild grass *Aegilops* (Fig. 2). Polyploidy is linked to greater adaptive potential, as genomes previously adapted to different environments converge within a single organism, and this has doubtless

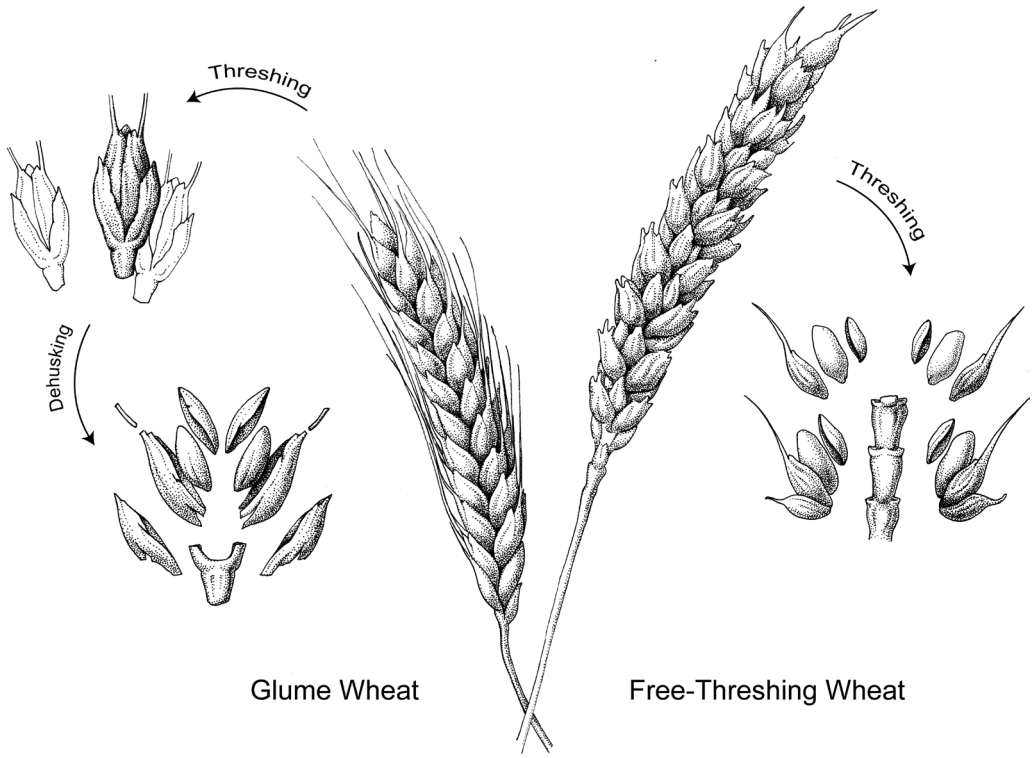

Fig. 1 Schematic representation of crop processing sequences for glume and free-threshing wheats, adapted from illustration by Kathryn Killackey ©

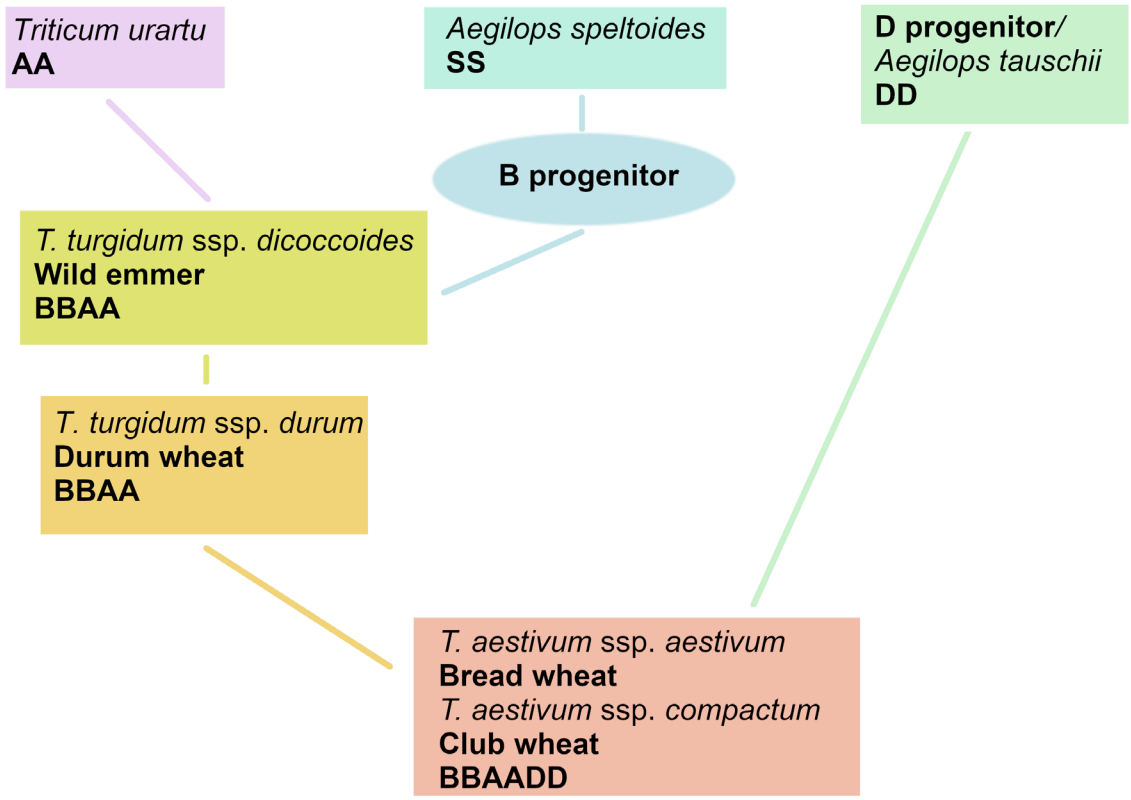

Fig. 2 Schematic diagram of the evolution of durum, bread and club wheats (adapted after Pont *et al.* 2019)

played a role in the near-global predominance of hexaploid bread wheat today (Dubcovsky and Dvorak 2007).

Within these ploidy groups are a range of accepted sub-species of FTW with distinct distributions, culinary properties and growing requirements (Table 1). Herein we use the widely-adopted taxonomy of van Slageren (1994), but alternative taxonomies consider these wheat types sufficiently distinct to categorise them as different species (Goncharov 2011). Beyond the accepted (sub-)species, a much wider array of named varieties with different morphological and adaptive characteristics are documented in recent history.

To date, the most extensive survey of wheat varieties is found in John Percival's 1921 'The Wheat Plant', which includes information on the morphology, traits and social roles of ~2000 wheat lines collected from all over the world. On publication, this work was described by the famous agricultural botanist N.I Vavilov as 'the greatest event in all applied botany — a great achievement— the best book on wheat from the existence (sic) of this world' (Bunting 2001, 20). Such surveys are a highly useful starting point for understanding wheat diversity and will be referenced frequently herein (e.g. Table 1). However, it is important to note that, as this is a crop which has been continuously adapting to anthropogenic environments for thousands of years, we must be cautious in retrospectively applying 20th century understandings of varietal tolerances and preferences to ancient cultivars.

Despite the well-documented diversity of wheat, charred remains in archaeobotanical contexts are often identified with limited precision as 'free-threshing', 'turgidum-aestivum' or 'aestivo-compactum' types. It is possible to distinguish between tetraploid and hexaploid FTW remains based on diagnostic criteria of the rachis segments (Hillman *et al.* 1996; Hillman 2001). However, due to greater susceptibility of these remains to destruction during charring (Boardman and Jones 1990) and an apparent tendency for FTWs to be processed in bulk, immediately following the harvest and away from domestic charring contexts (Jones 1987), these diagnostic elements are often not preserved in the archaeobotanical record, or present only in small quantities.

Common name	Latin name	Main locality (recent history)	Main uses	Environmental preference	Resistant to:	Add. notes
Bread wheat	*aestivum* L. ssp. *aestivum*	Widespread	Bread, baking	Variably adapted (Percival 1921)	Variably adapted (Percival 1921)	-
Club wheat	*aestivum* L. ssp. *compactum* (Host) MK	Central Asia, N. American Pacific Coast (Percival 1921)	Cakes, biscuits (Bettge 2009)	Mild wet winter, hot dry summer (Zwer *et al*. 1995). Tolerant of poorer soils (Percival 1921).	Frost, drought, fungi (Percival 1921)	-
Rivet wheat	*turgidum* L. ssp. *turgidum*	Mediterranean (Percival 1921)	Biscuits, flour additive (Percival 1921), thatch (Letts 1999)	Frost-free, well-drained, warm soils (Percival 1921)	Rust fungi, birds (Percival 1921)	-
Durum wheat	*turgidum* ssp. *durum* (Desf.) Husn.	Mediterranean (Percival 1921)	Pasta, couscous, bread (Giraldo *et al*. 2019)	Dry, hot, frost-free. Deep, fertile soil (Percival 1921)	Drought, rust, smut fungi (Percival 1921)	-
'Persian'/Dika wheat	*turgidum* ssp. *carthlicum* (Nevski) Löve & Löve	Transcaucasus (Matsuoka 2011)	Bread (Pruidze *et al*. 2016)	Tolerant of low temps (Zhuang *et al*. 2011) and highland conditions (Pruidze *et al*. 2016)	Mildew, rust (Kuckuck 1979), drought, frost (Haque *et al*. 2011)	Hybrid of emmer & *T. aestivum* (Kuckuck 1979)
'Polish' wheat	*turgidum* ssp. *polonicum* (L.) Thell.	Mediterranean (Percival 1921)	Cooked as cereal, noodles, flat bread (Rogosa 2016)	Hot climate, high soil fertility (Percival 1921)	-	No evidence before 17th century AD (Percival 1921)
Indian dwarf wheat	*aestivum* L. ssp. *sphaerococcum* (Percival) MK	Pakistan/India (Szczepanek *et al*. 2020)	(Unleavened) bread (Mori *et al*. 2013)	Hot, dry (Kushnareva 1997, 182)	Drought, yellow rust (Percival 1921)	Endemic to NW India (Kushnareva 1997, 182)
Khorasan wheat	*turgidum* ssp. *turanicum* Jakubz. Löve & Löve	West and Central Asia, N. Africa (Grausgruber *et al*. 2005)	Pastries, 'health food' (Michalcová *et al.* 2014)	Relatively poor cold & drought tolerance (Grausgruber *et al*. 2005)	Competition from weeds (Grausgruber *et al*. 2005)	Hybrid of Polish wheat & emmer (Michalcová *et al.* 2014)

Table 1 Accepted sub-species of FTWs classified after van Slageren (1994). Bold = wheat types included in main study

The charred grain of FTW is more commonly recovered than the chaff, but has proven problematic to identify to ploidy level reliably. While possible distinguishing criteria have been noted — e.g. the depth of the ventral furrow relative to the height of the grain — the same sources acknowledge a lack of consistency in these characteristics (e.g. Moffett 1987; Hillman *et al.* 1996). Analysis of aDNA extracted from grains presents an alternative approach (e.g. Schlumbaum *et al.* 1998; Fernàndez *et al.* 2013; Bilgic *et al*. 2016) but issues of preservation and contamination (as well as cost) inhibit widespread application. As regards distinguishing wheat remains *within* ploidy levels, i.e. to (sub-)species level, there is even less established basis of separation using either grain or rachis segments (Hillman *et al*. 1996, 204; Jones 1998).

As such, there are significant limitations to traditional morphological approaches when identifying archaeobotanical FTW remains. Geometric morphometric (GMM) analysis of grain form is therefore offered here as an alternative approach. The application of GMM to archaeobotanical research has flourished in recent years and there is much scope for further development and application in the field (Portillo *et al*. 2020; Evin *et al*. 2022), to which this study seeks to contribute.

2.1.2 Early archaeobotanical evidence for FTWs, potential origins and trajectories

The earliest cultivated wheats were the glume wheats einkorn and emmer, domesticated forms of which emerged in the 'Fertile Crescent' of south-west Asia from the Early Pre-Pottery Neolithic B, around 8,700–8,200 cal BC. (Arranz-Otaegui *et al*. 2016). Genetic sequencing suggests that the earliest FTWs were tetraploids which evolved from emmer wheat, with hexaploid wheats subsequently originating from hybridisation between a tetraploid FTW and the wild grass *Aegilops tauschii* Coss. or a lineage close to it (Dvorak *et al.* 2012; Pont *et al*. 2019; Fig. 2). It has been proposed that this tetraploid FTW was durum (Pont *et al*. 2019), although parentage by a now-extinct ancestral form is also posited (Levy and Feldman 2022). It has also been proposed that the offspring of this hybridisation would have initially been hulled (Dvorak *et al*. 2012), but this form has yet to be identified

archaeobotanically. The earliest recorded FTW remains have little chronological separation from the earliest domesticated glume wheats, with free-threshing examples of unknown ploidy-level from the second half of the 9th millennium BCE at Aşıklı Höyük, Turkey (Ergun *et al.* 2018) and late 9th–early 8th millennium BCE Tell Aswad, Syria (van Zeist and Bakker-Heeres 1982; Zohary *et al*. 2012, 45).

It has been proposed that, based on the primary distribution of *Aegilops tauschii* (syn. *A. squarrosa*) (Zohary 1969; van Zeist 1976) and links with specific gene pools (Dvorak *et al*. 1998), hexaploid wheat could only have developed after tetraploid FTW spread to Transcaucasia and Caspian Iran in the 6th millennium BCE. However, hexaploid FTW is reported as early as the late 9th–mid 8th millennium cal BC at Cafer Höyük, south-east Turkey (de Moulins 1993; 1997; radiocarbon dates corrected after ex oriente e.V.) and from the late 8th–early 7th millennium cal BC at Çatalhöyük, south-central Turkey (Bogaard *et al*. 2013; 2017; 2021). Tetraploid and hexaploid FTW remains are also recorded for the 8th millennium cal BC at Abu Hureyra, Syria (de Moulins 1997; ex oriente e.V.), the first half of the 7th millennium cal BC at El-Kowm, Syria (de Moulins 1997; Borrell *et al*. 2011) and for the mid–late 8th millennium cal BC at Can Hasan III, near Çatalhöyük (Hillman 1972; Hillman 1978; Fairbairn *et al.* 2020). Notably, at Can Hasan III tetraploid rachis is only found in the latest two phases of occupation, while hexaploid rachis is present throughout the sequence (Hillman 1978, 168). In line with these findings, Giles and Brown (2006) propose an origin of hexaploid FTW in south-east Turkey or northern Syria, arguing that the genetic evidence theoretically supports a scenario where 'peripheral' communities of *Aegilops tauschii* first came into contact with tetraploid FTW in these regions, with a second hexaploidisation possibly occurring in Iran.

Cultivation of FTW spread east and west, reaching China by the 3rd millennium BCE (Liu *et al*. 2016) and Britain by the early 4th millennium BCE (Jones & Rowley-Conwy 2007; Carruthers 2019). A cache of grains found in an aceramic Neolithic level at Knossos, Crete indicates that FTW reached the Mediterranean region by the earlier 7th millennium BCE (Sarpaki 2013; Douka *et al*. 2017). However, while identified as bread wheat in Hans

Helbaek's original report (1968, cited in Sarpaki 2013), the ploidy level of these remains has not been conclusively demonstrated (Sarpaki 2013). Elsewhere in the region, tetraploid rachis remains are recorded for the later 6th millennium BCE Cardial lakeshore settlements of La Marmotta, central Italy and La Draga, Catalonia (Jacomet 2007, 246; Rottoli and Pessina 2007; Antolín 2016). Interpretation of the written evidence, based on both terminology and described traits, suggests that by Classical Antiquity, tetraploid durum, and to a lesser extent rivet, were the predominant wheat crops grown in the Mediterranean (Jasny 1944); although it is again noted that we cannot be sure to which degree crops described in antiquity equate with cultivars as we know them today.

Historically, it was believed that the FTW of Neolithic Europe was a compact form of hexaploid wheat equated with modern-day club wheat (Percival 1921). However, studies of exceptionally preserved whole ears by Ursula Maier (1996), demonstrated cultivation of tetraploid FTWs at the early fourth millennium BCE lakeshore settlement of Hornstaad-Hörnle, south-west Germany. The author therefore proposed a Mediterranean route of tetraploid FTWs to south-west Europe, reaching the northern foothills of the Alps ~4000BCE. This theory was developed by Kirleis and Fischer (2014), who defined two agricultural traditions using archaeobotanical data from Central and Northern Europe. The first tradition relates to predominantly hexaploid FTW cultivation by the late Linearbandkeramik culture, associated with Neolithisation from the east through the Balkans and Carpathian Basin. The second, predominantly tetraploid, tradition was associated with early Neolithic groups in the northern Alpine foreland, arriving via the Mediterranean and southern France. This tradition subsequently diffused north via contacts between the Michelsberg and Funnel Beaker Cultures of northern Germany and southern Scandinavia.

A review of identified rachis segments would appear to support the theory of more northerly hexaploid and more southerly tetraploid route into western Europe (Fig. 3). Data for this survey was gathered using the '*Cultural Evolution of Neolithic Europe (EUROEVOL)*' dataset (Manning *et al.* 2015), an archaeobotanical survey of the central-western Balkans and Hungarian Plain (de Vareilles *et al*. 2022) and other published (predominantly English-

language) material. The survey was designed as a preliminary overview to provide context for the present study, and it is anticipated that further data collection would provide a more comprehensive picture, particularly in currently under-represented regions.

Overall, while understanding of the origins and trajectories of FTWs across western Asia and Europe is improving, much remains unclear. It is notable that, despite our expectation of tetraploid FTWs evolutionarily predating hexaploid FTWs, there is a lack of securely identified archaeobotanical evidence to confirm this. The morphological ambiguity reported for certain early FTW rachis finds, as at Aşıklı Höyük (Ergun pers. comm.) and Bulgaria (Marinova 2007, 102), may relate to transitional stages in the evolutionary development of FTW that we are yet to define. While our knowledge may be improved by the recovery of further archaeobotanical data (or reviewing existing material), GMM may also help to refine this picture.

2.1.3 The Archaeobotanical Material

To assess the potential of GMM in relation to early FTW cultivation, material was selected from two sites with unusually substantial and well-preserved assemblages of Neolithic FTW grains: Çatalhöyük in Central Anatolia and Kouphovouno in southern Greece (Fig. 3). Çatalhöyük represents a notably early assemblage of FTW in the region it potentially first evolved, while Kouphovouno is situated along the key Mediterranean route through which the spread of tetraploid FTW is hypothesised (Maier 1996; Kirleis and Fischer 2014; Fig. 3).

2.1.4 Çatalhöyük

Çatalhöyük is the source of one of the largest and most well-studied archaeobotanical assemblages relating to an early farming community in western Asia. The tell site is one of a number of densely occupied ‘megasites’ that emerged in the Near East during the latter half of the Neolithic (Der and Issavi 2017). Inhabitants used a broad spectrum of crops and other food plants throughout the occupation sequence (Bogaard *et al.* 2017; 2021).

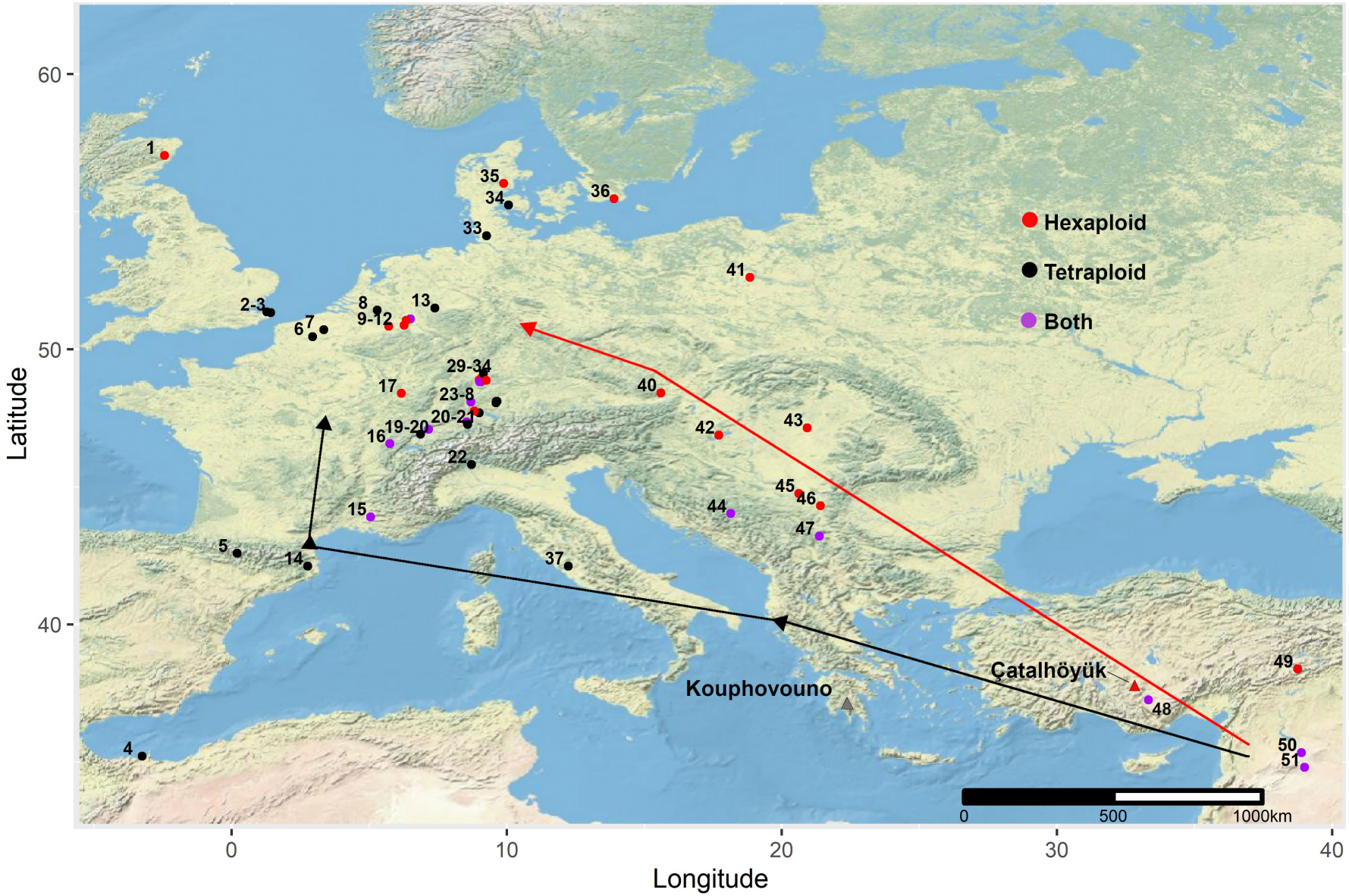

Fig. 3 Distribution map of identified FTW rachis segments from Neolithic sites in Europe and western Asia. Arrows = potential trajectories of hexaploid and tetraploid FTW. Triangles= sites included in present GMM study. See Appendix A for site names and references.

The grains examined from Çatalhöyük derive from the Neolithic East Mound (7100–5950 cal BC), mostly from the Middle phase (6700–6500 cal BC) and the majority preserved by *in-situ* charring (see Appendix B). While initial studies suggested the potential presence of tetraploid FTW (Fairbairn *et al*. 2002) subsequent work identified the rachis as hexaploid (Bogaard *et al*. 2013; 2017; Fig. 4). This identification was supported by aDNA analysis of the grains which demonstrated a sequence similar to modern hexaploid wheats (Bilgic *et al*. 2016). While the proportion of FTW in relation to other cereals does not follow a clear temporal trajectory at Çatalhöyük, there is a shift towards free-threshing forms (especially naked barley) as a whole, perhaps indicating increasing preference for less labour-intensive crops over time (Bogaard *et al*. 2017; 2021). However, in the Late-Final East Mound and Chalcolithic West Mound phases we see a more even balance between glume wheats and free-threshing cereals (Bogaard *et al.* 2021).

Palaeoenvironmental studies suggest a landscape in which small low-energy channels across the alluvial plain created a mosaic of both dry and wetland environments within the site catchment (Ayala *et al*. 2021; Hodder 2021; Veropoulidou 2021). Isotopic analysis indicates that wheat was generally grown under better-watered conditions than barley (Wallace *et al*. 2015) but that growing conditions were highly variable even within the storage deposits of individual burned buildings (Vaiglova 2016; Stroud *et al*. 2021). Analysis of arable weed flora supports this ‘mosaic’ of growing environments, but also identified a single FTW deposit associated with flora indicative of particularly high-input management, comparable to modern plots which are regularly irrigated, tilled, weeded and manured (Green *et al*. 2018).

Overall, FTW was a staple crop of the Neolithic East Mound settlement, the importance of which may have increased over time as free-threshing cereals were increasingly favoured. While grown under a range of conditions, it seems likely that FTW would have been planted in better-watered areas of the landscape, at least in comparison to barley and, at least in some circumstances, was considered worth the investment of high-input management.

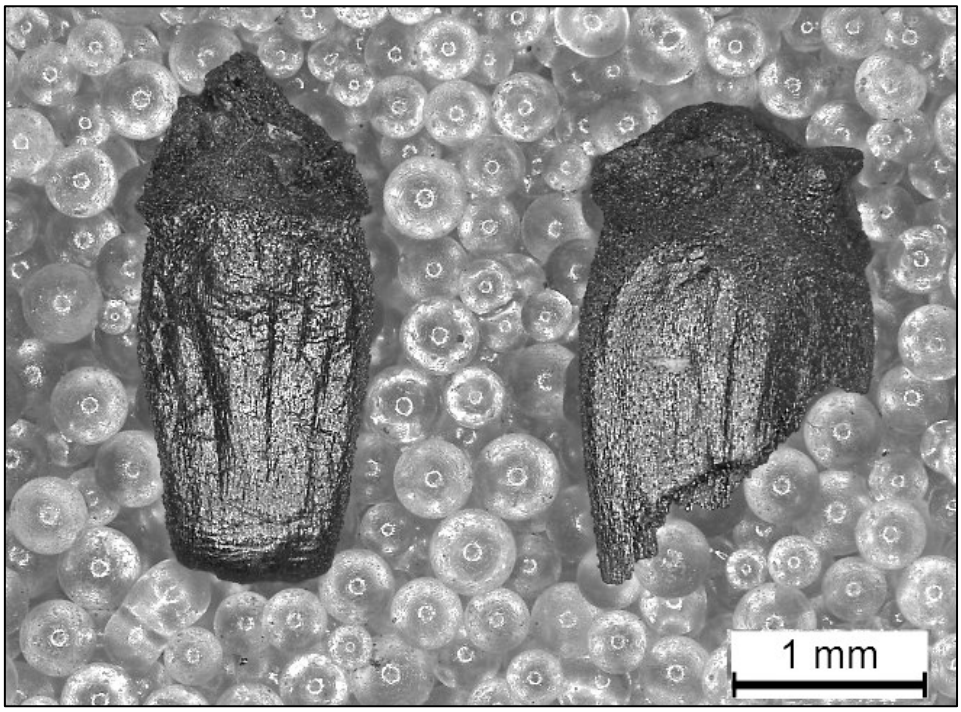

Fig. 4 Hexaploid FTW rachis from Çatalhöyük

2.1.5 Kouphovouno

Kouphovouno is a tell site located in the southern Peloponnese, on the outskirts of modern Sparta. While occupied intermittently for much of the prehistoric period, the analysed remains date to the Middle and Late Neolithic (~5800–5000 BCE) settlement, an area extending over approximately 4–5 ha (Cavanagh *et al*. 2017). Archaeobotanically, southern Greece is relatively poorly represented in this period (Livarda 2014), and the site therefore presents a valuable opportunity to characterise plant husbandry in the region.

While hulled barley was the most ubiquitous crop at the site, FTW is well represented. The majority of FTW remains were derived from ten grain-rich units interpreted as *in situ* charring of grain stores in domestic contexts (Diffey & Bogaard in prep.; Appendix B). The largest proportion were associated with ‘Structure CIV’, a burnt building dating to the Middle Neolithic period. The assemblage is generally chaff-poor and no rachis internodes were identified which would allow for identification of the FTW as either hexaploid or tetraploid. Previous archaeobotanical findings suggest a geographical divide in wheat preference during the Neolithic in Greece, with einkorn more common in the north and emmer and FTW more common in the south (Livarda 2014). However, at Kouphovouno, einkorn appears to replace FTW as the major wheat type during the Late Neolithic (Diffey and Bogaard in prep.).

Analysis of crop-associated weed seeds indicates that arable plots were long established, autumn-sown and tended towards high soil fertility, suggesting a high-input regime (*ibid*.). Isotopic analysis indicates that FTW was preferentially managed through manuring, mulching and/or tilling in comparison to hulled barley and einkorn, with pulse crops also grown under high-input regimes (Vaiglova *et al*. 2014; 2020). Comparison with faunal isotopic values suggests that FTW was reserved exclusively for human consumption (Vaiglova *et al*. 2014). These findings present a system in which crops for human consumption, including FTW and pulses, were intensively managed under rotation in plots proximal to habitation, while potential fodder crops such as barley were grown more extensively on the periphery of the settlement (Vaiglova *et al*. 2014). As settlement size decreased into the Late Neolithic (Renard & Cavanagh 2017), emphasis apparently shifted towards the less intensively-managed einkorn (Diffey & Bogaard in prep.). This shift appears to have taken place in the context of reduced cooperation between households; as suggested by an apparent reduction in communal activity areas (*ibid*.) and a change in ceramic styles. The latter can be seen in the move from larger to smaller vessels for the consumption of food and drink, as well as an increase in storage vessels; perhaps representing a change in emphasis from communal consumption to individual household identities (Mee *et al*. 2014; Renard & Cavanagh 2017).

2.2 Methodology

2.2.1 Approach

In order to gain insight into the types of FTWs cultivated by early farming communities at Çatalhöyük and Kouphovouno, Elliptic Fourier analysis was conducted on modern and archaeological grain specimens. The first stage of analysis sought to establish the degree to which different classes of modern wheat could be distinguished based on grain shape, while the second stage compared archaeological specimens with the modern material.

2.2.2 Sampling and Photography

Modern reference material was sourced through gene banks (Table 2). Modern bread, club, durum and rivet wheat were selected for the main study as crops known in Europe and western Asia with potentially prehistoric provenance.

A more limited examination was also made of 'Persian' wheat (ssp. *carthlicum*; Table 1; 2). This wheat is believed to derive from hybridisation between a form of *T. aestivum* ('ssp. *carthlicoides*') with domesticated emmer (Kuckuck 1979; Haque *et al*. 2011; Oliveira *et al*. 2020). 'Persian' wheat is distinct in being genetically tetraploid, but shares features of rachis morphology with hexaploid wheats (Hillman 2001). When a single accession of *carthlicum* was compared with modern and archaeological material, the charred grains were noted to be longer and narrower than any of the study material, and of quite distinct proportions overall. Therefore while initial examination would not suggest *carthlicum* to be a morphological match for the material studied herein, it would merit further study given its ambiguous history and morphology.

Selection of material prioritised availability of whole ears as well as geographical proximity of origin to the study sites where possible (rivet here being the exception). This resulted in a combination of accessions classified as 'landraces' and a smaller number of modern-bred 'advanced/improved' cultivars. Grains were sampled equally from the base, middle and top of each ear to account for intra-ear variation (9 grains per ear), with three ears sampled per accession. Archaeological material was assessed for inclusion on the basis of preservation and grains exhibiting significant distortion or damage excluded. Examples of severe charring distortion include the exudation of endosperm to form protrusions and cavities within the grain (Charles *et al*. 2015). Grains damaged mechanically or with minimal survival of the outer pericarp were also excluded.

Grains were photographed using a Nikon SMZ25 stereo microscope with apochromatic optical system and Pixelink M12BC-CYL microscopy camera. Initially grains were photographed in dorsal, lateral and polar views (Fig. 5). However, once established that the polar view was of limited value (Paper 1; Paper 3), dorsal and lateral views only were taken.

Sub-species	Accession code	Variety (if named)	Gene bank	Improvement status	Country of origin	No. of grains
aestivum	**ICA09-11W**	**Sham4**	**ICARDA**	**Advanced/improved**	**Syria**	**27**
aestivum	**TRI29935**	**var. *ferrugineum***	**Gatersleben**	**Landrace/traditional**	**Georgia**	**27**
aestivum	**USDA625842**		**USDA**	**Landrace/traditional**	**Iran**	**27**
compactum	**T1200010**		**John Innes**	**Landrace/traditional**	**Georgia**	**27**
compactum	**T1200011**		**John Innes**	**Landrace/traditional**	**Turkestan**	**27**
compactum	**T1200012**		**John Innes**	**Landrace/traditional**	**Cyprus**	**27**
durum	**USDA362637**		**USDA**	**Landrace/traditional**	**N.Macedonia**	**27**
durum	**CGN6554**	**Kyperounda**	**CGN Wageningen**	**Landrace/traditional**	**Cyprus**	**27**
durum	**TRI 8005**	**Kjachraba 10**	**Gatersleben**	**Advanced/improved**	**USSR**	**27**
turgidum	**W1022**	**Percival's Blue Cone**	**John Innes**	**Landrace/traditional**	**England**	**27**
turgidum	**W0508**	**Rampton Rivet**	**John Innes**	**Advanced/improved**	**England**	**27**
turgidum	**USDA190157**	**Roter Tiroler**	**USDA**	**Landrace/traditional**	**Germany**	**27**
aestivum	W6537	Squarehead's Master	John Innes	Advanced/improved	England	27
aestivum	USDA350071		USDA	Landrace/traditional	Serbia	27
durum	W8612	Ambral	John Innes	Advanced/improved	France	27
durum	TRI12894	Kunduru 1149	Gatersleben	Advanced/improved	Turkey	27
carthlicum	470729		ICARDA	Uncertain	Turkey	9

Table 2 Modern accessions of FTWs used in study. Accessions in bold were used in Stage 1 of Analysis

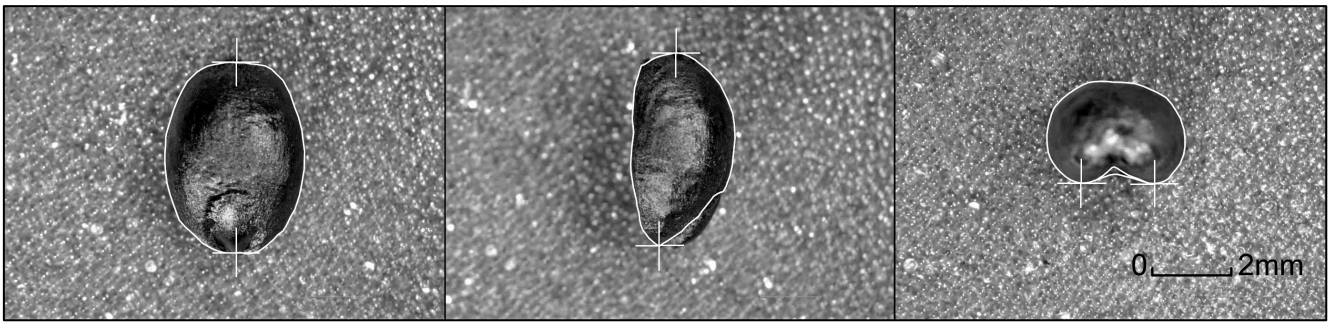

Fig. 5 Dorsal, lateral and polar views of a FTW grain with alignment points added

2.2.3 Charring

Charring of modern reference material was undertaken to replicate well-preserved archaeological material using parameters established in Charles *et al.* (2015). Grains were wrapped in foil and placed in beakers of sand to reduce oxygen availability and then charred in a preheated oven at 230°C for six hours. The temperature in both the oven and beakers was monitored using a data logger.

2.2.4 Digitisation

Grain outlines were traced using a computer-aided design (CAD) program, with each grain view represented by 40–80 individually placed points. While, ideally, the number of points would be higher and less variable, previous experimentation with a wider range of points found there to be a minimal effect on reclassification (Paper 1). Elliptic Fourier Analysis is also advantageous in not requiring points to be evenly spaced (Bonhomme *et al*. 2014). Alignment points were added to minimise differences in orientation between the grains (Fig. 5) and the coordinates of each outline were then extracted.

2.2.5 Analysis

Elliptic Fourier analysis (Giardina and Kuhl 1977; Kuhl and Giardina 1982) of grains was employed, a type of outline analysis appropriate to ‘continuous’ forms (Bonhomme *et al*. 2014). In this approach, outlines are decomposed into ‘Fourier Series’ or harmonic sums of trigonometric functions weighted with harmonic coefficients (Bonhomme *et al.* 2014). Analysis was conducted in an R (3.6.2) environment using the packages ‘geomorph’ (3.2.1) and ‘Momocs’ (1.2.9), the latter developed by Vincent Bonhomme based on functions

published by Claude (2008). Grains were imported into Momocs as coordinates and then scaled by centroid size in order to emphasise shape over dimension. Fourier Transforms were calculated for the outlines of each grain individually and then combined (Bonhomme *et al*. 2017). Eight harmonics were retained for each view, gathering at least 99% of the total harmonic power.

Results were primarily obtained by means of linear discriminant analysis (LDA) with leave-one-out cross-validation. This was used to test the degree to which grains could be correctly reclassified to type based on grain shape, scoring each known specimen ('actual') against the group it most closely resembled according to the model ('classified'). LDA was also used to reclassify unknown, i.e. archaeobotanical, material into the group with the closest morphological affinity. When plotted, the LDA visually represents the relationships between different morphological types, with similar groups plotting more closely together, and anomalous forms occupying more peripheral positions, which are nevertheless informed by group membership.

2.2.6 Repeatability and Measurement Error

Repeatability was assessed after Evin *et al*. (2020) whereby five specimens from the same ear of ssp. *aestivum* were each photographed in both views and digitised in five separate sessions. Procrustes ANOVA (analysis of variance) on the PCA (principal components analysis) scores for these outlines produced a non-significant value (≥0.05) when session was used as the dependent variable, and a significant value when specimen ID was used as the dependent variable. This suggested that when the same grain was photographed, digitised and aligned multiple times, different sessions did not produce significantly different outlines, and that any session variation was less significant than the variation between specimens.

Measurement error was calculated using the results of the ANOVA after the equation defined in Claude (2008, 65–66) as 'the ratio of the within-measurement component of variance on the sum of the within- and among-measurement component':

$$\%ME = \frac{\mathrm{s}^2\mathrm{within}}{(\mathrm{s}^2\,\mathrm{within} + \mathrm{s}^2\mathrm{among})}\ x\ 100$$

Using this equation, the measurement error for the dorsal view was calculated at 4.38% and for the lateral view at 5.94%.

2.3 Results

2.3.1 Stage 1: Modern Baseline Study

The first stage of analysis sought to establish whether different (sub-)species of FTW could be reliably separated by grain morphology. Charred modern specimens of bread wheat (hereafter '*aestivum'*), club wheat ('*compactum'*), durum wheat (*'durum'*), rivet wheat ('*turgidum'*) (Table 2) were analysed.

An LDA of all 324 modern grains correctly reclassified 89.8% of grains to ploidy level, and 86.1% to (sub-)species, when using the dorsal and lateral views (Table 3; 4). When plotted, the greatest overlap is observed between bread and club wheat when using the first two linear discriminants, however these can be seen to separate along the third discriminant axis (Fig. 6). When accession was used as a discriminating factor, the reclassification rate was only slightly lower at 82.1% (Table 3), suggesting the model is sensitive to varietal differences. When all 'improved/advanced' cultivars were removed from the model dataset, correct reclassification by taxon remained similar at 85.6% (Table 3). The results suggest

Discriminant variable	**Reclassification rate**	**Reclassification rate %**
(Sub-)species	279/324	86.1%
(Sub-)species (no advanced varieties)	208/243	85.6%
Ploidy level	291/324	89.8%
Accession	266/324	82.1%

Table 3 Results of LDA classifying modern material according to different variables

that at the group, if not individual, level, there are predictable morphological differences between grains of different classes and that these distinctions are preserved despite charring distortion.

	Classified as			
Actual	*aestivum*	*compactum*	*durum*	*turgidum*
aestivum	72	5	2	2
compactum	7	67	2	5
durum	9	1	68	3
turgidum	5	3	1	72
Class correctness	88.9%	82.7%	84.0%	88.9%
Overall		**86.1%- 279/324**		

Table 4 Results of LDA on combined dorsal and lateral views of modern reference grains as classified by (sub-)species

2.3.2 Stage 2a: Comparison with Archaeobotanical Material

The next stage of analysis compared archaeobotanical grains from Kouphovouno and Çatalhöyük with the modern reference material. Eighty well-preserved grains from each site were selected from a range of deposits (see Appendix B). Archaeological grains were compared with both the full dataset and 'unimproved' subset, with the strongest association observed with the grains from the latter group. When plotted against the unimproved varieties we see significant overlap between the Çatalhöyük grains and both the *compactum* and *aestivum* grains (Fig. 7) and the Kouphovouno material with the *durum* group (Fig. 8).

When the archaeological grains were entered as unknowns for reclassification against unimproved varieties, 82.6% of Çatalhöyük grains classified as either *aestivum* or *compactum*, and 15.0% as *durum* (Table 5). From this we may infer that the predominant FTW cultivated was a form most closely resembling modern hexaploid wheats. Since, based on the Stage 1 results, we would expect at least 14% of grains to be classified incorrectly, we cannot say whether grains classified as *durum* represent a minority crop or merely atypical grains.

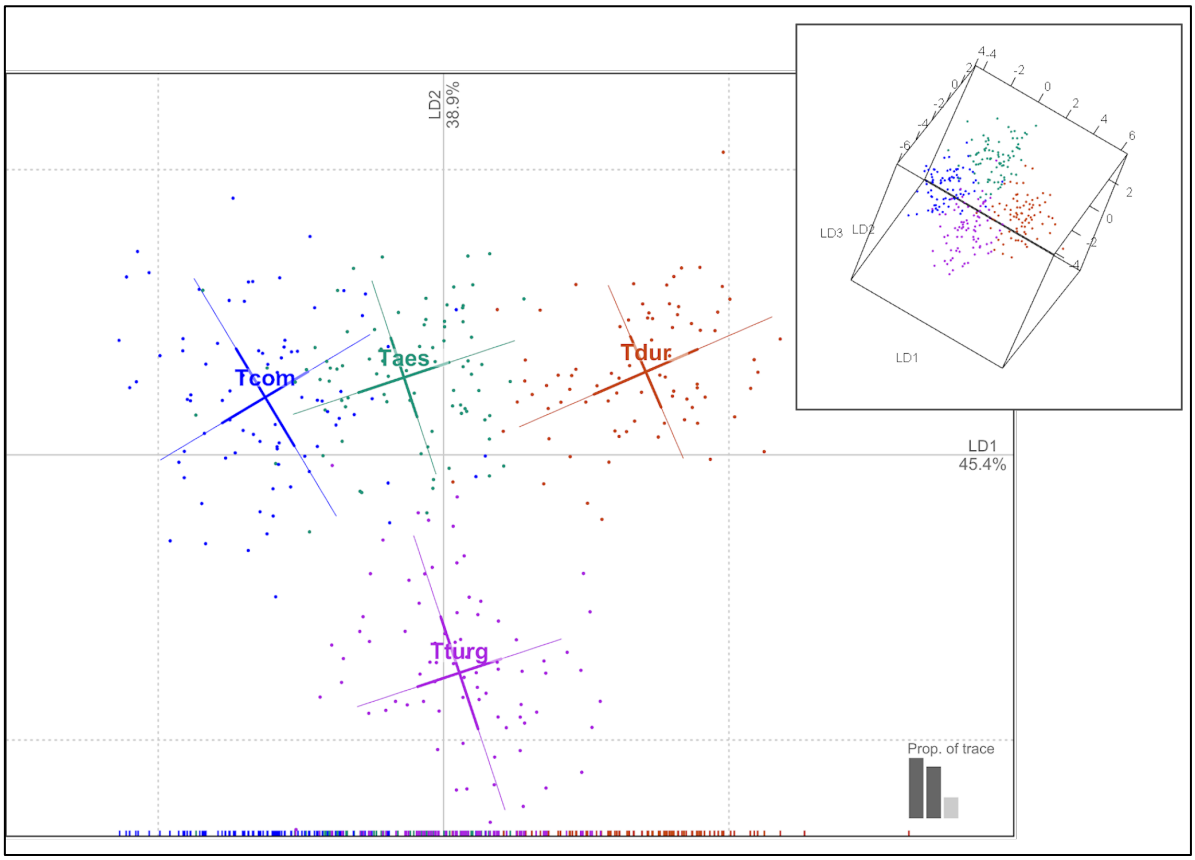

Fig. 6 LDA comparing charred modern FTW (sub-)species based on grain shape. 'Tcom'= *compactum*, 'Taes'= *aestivum*, 'Tdur'= *durum*, 'Tturg'= *turgidum*. Insert shows separation along third axis when viewed as a 3D plot

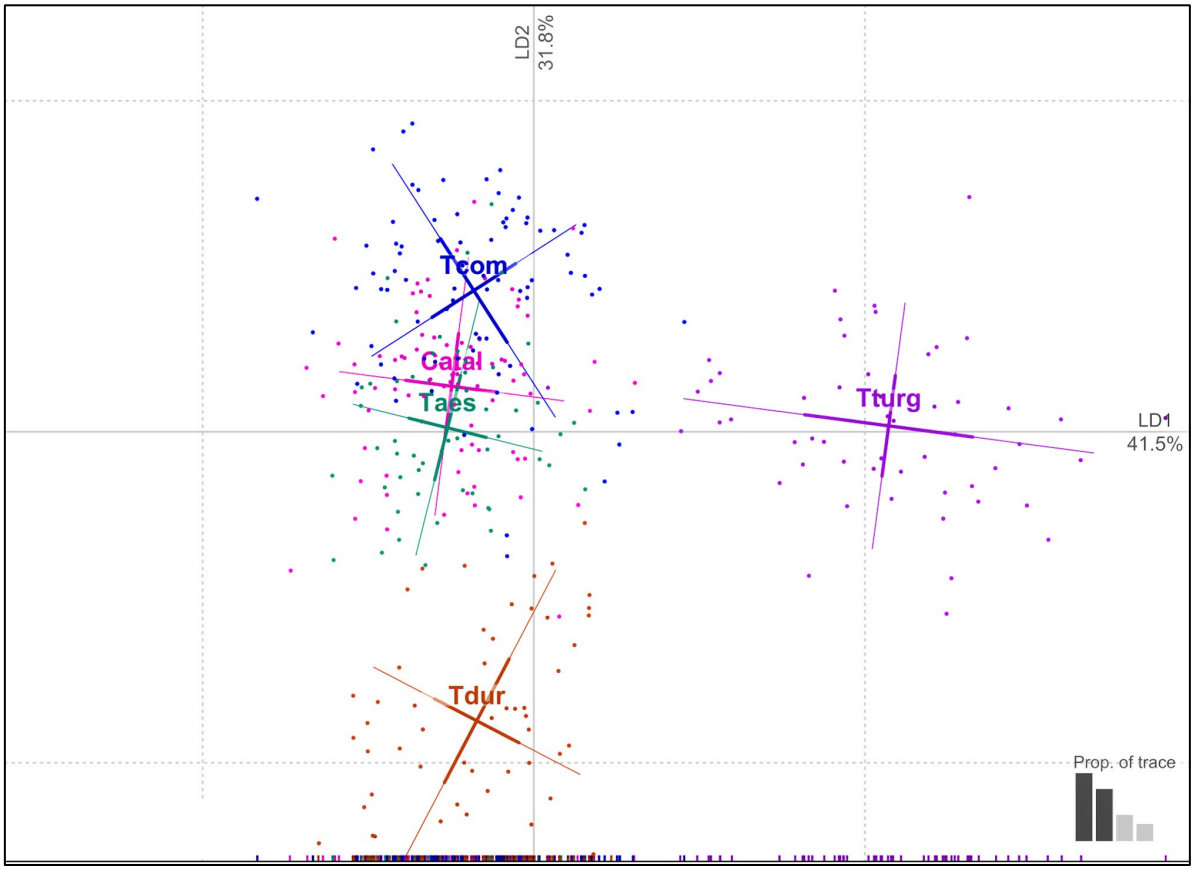

Fig. 7 LDA comparing Çatalhöyük ('Catal') material with modern 'landrace/traditional' varieties. 'Taes'= *aestivum*, 'Tcom'= *compactum*, 'Tdur'= *durum*, 'Tturg'= *turgidum*

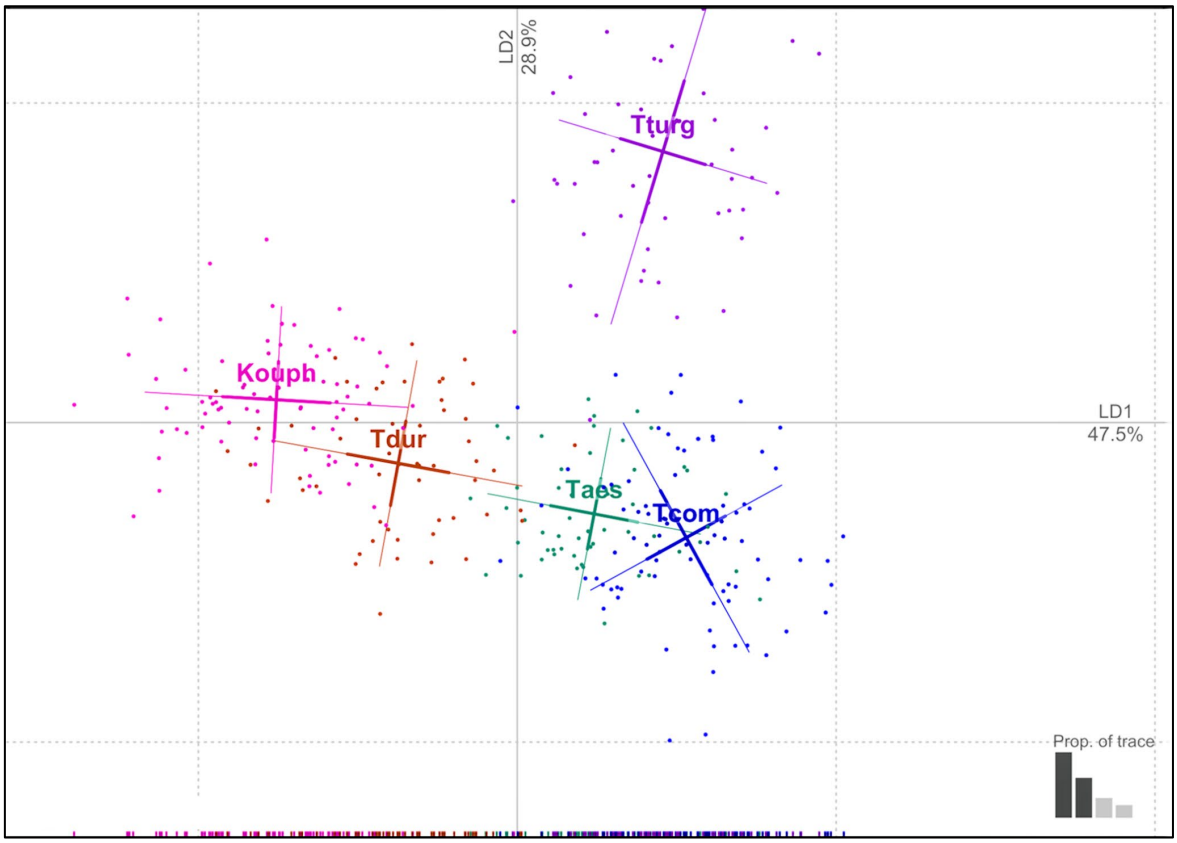

Fig. 8. LDA comparing Kouphovouno ('Kouph') material with modern 'landrace/traditional' varieties. 'Taes'= *aestivum*, 'Tcom'= *compactum*, 'Tdur'= *durum*, 'Tturg'= *turgidum*

The same analysis on the Kouphovouno material classified 81.3% as *durum* and 17.5% as either *aestivum* or *compactum* (Table 5). We may infer therefore that the main FTW crop resembled a tetraploid wheat most similar to *durum*, although we cannot rule out a hexaploid wheat having been present. Pairwise comparisons of mean shapes (Fig. 9) reinforced results of the LDA, with the Çatalhöyük material bearing the strongest resemblance to hexaploid wheat (particularly *aestivum*) and the Kouphovouno grains to *durum*. Procrustes ANOVA of PCA scores found significant differences (p= 0.001) in form between the Çatalhöyük and Kouphovouno assemblages in both dorsal and lateral views.

	Classified as							
Site	*T. aestivum*		*T. compactum*		*T. durum*		*T. turgidum*	
Çatalhöyük	37	46.3%	29	36.3%	12	15.0%	2	2.5%
Kouphovouno	8	10.0%	6	7.50%	65	81.3%	1	1.3%

Table 5 Results of LDA when archaeological grain outlines entered as unknowns and compared with modern reference grains (non-improved varieties)

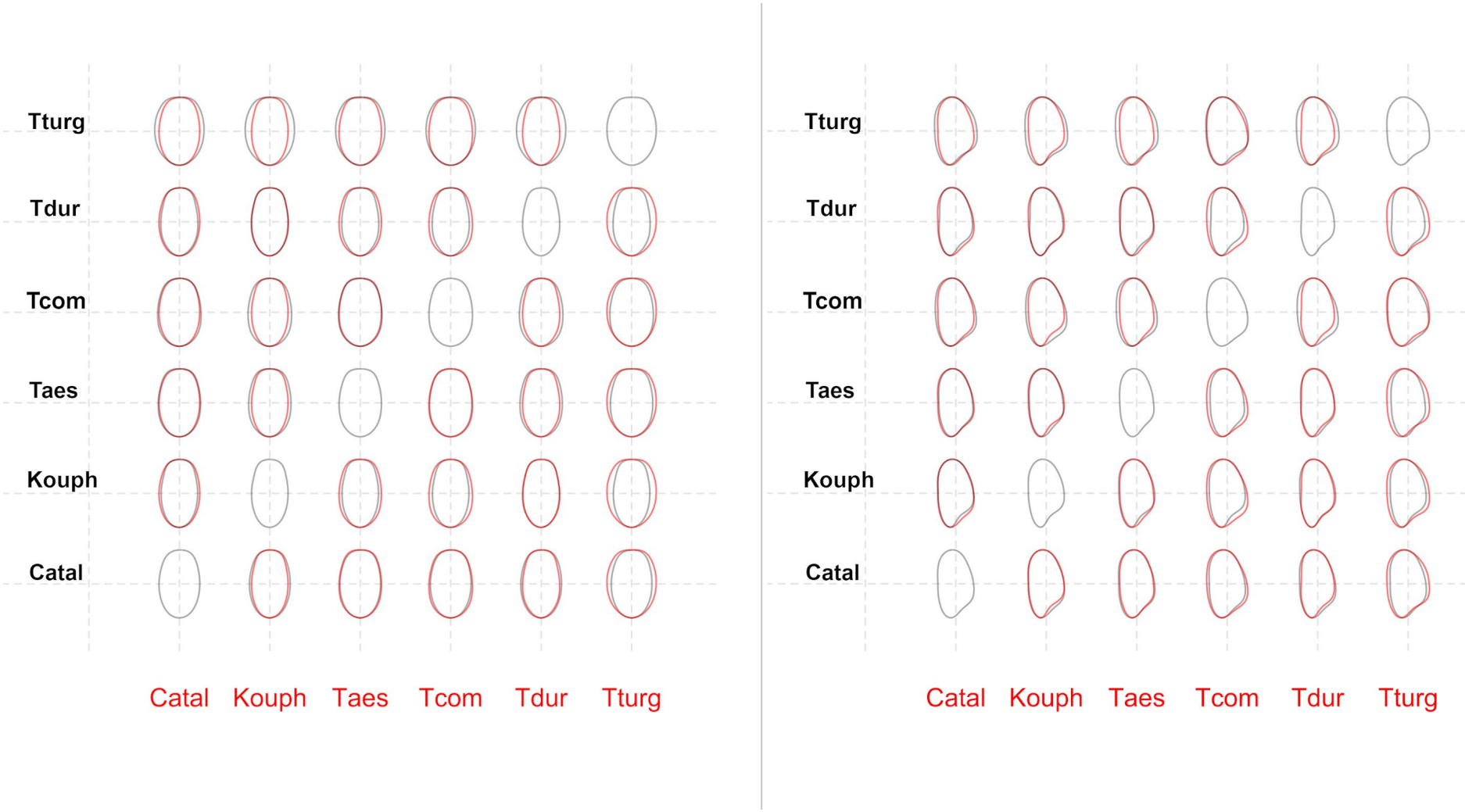

Fig. 9 Pairwise comparisons of mean shapes of grains including archaeological material (dorsal and lateral views). 'Catal'= Çatalhöyük, 'Kouph'= Kouphovouno, 'Taes'= *aestivum*, 'Tcom'= *compactum*, 'Tdur'= *durum*, Tturg= *turgidum*

2.3.3 Stage 2b: Varietal-level Comparisons with Archaeological Material

Having established a potentially closer association between archaeological material and traditional varieties of modern wheat, the next stage was to look more closely at variation *within* ploidy and (sub-)species in comparison to the archaeological material.

The Çatalhöyük material was compared with five *aestivum* and three *compactum* accessions from Europe and western Asia (Table 2). An LDA of these eight modern accessions correctly classified 95.8% of grains to (sub-)species. However, when the archaeological grains were classified against these modern accessions they showed no clear association with either (sub-)species or accession (Table 6). It is notable that accessions with collection sites furthest away in terms of latitude (England and Serbia) appear to be the least similar to the Çatalhöyük material, with higher proportions of grains classifying as traditional varieties from central and western Asia. Similarly, when the Kouphovouno grains were compared with modern durum accessions, the highest proportions of grains were classified as 'traditional' accessions from North Macedonia, and to a lesser extent Cyprus, while the grains least resembled 'improved' varieties from Turkey and France (Table 7).

These results begin to suggest a relationship between geographical origin, improvement status and grain shape, although further work would be needed to elaborate this. As such, we should be mindful of the fact that, due to restricted availability of whole ears, the rivet accessions compared with the Kouphovouno material were derived from a different geographic region (Table 2), and this may have contributed to the level of morphological dissimilarity with the archaeological material.

While we cannot draw firm conclusions purely on the range of accessions represented herein, it is possible that regional variations in grain shape have persisted from the earliest stages of farming to the present day. Even if this suggestion remains tentative, results point towards the importance of comparing archaeological grains with modern reference material from geographically proximate locations, and these ideally being traditional landraces. The suggestion of geographically-based variation naturally gives rise to the question of how growing environment influences grain form. GMM analysis of grains grown under different

Accession code	TRI29935		USDA625842		ICA09-11W		USDA350071		W6537		T1200011		T1200010		T1200012	
Taxon	*aestivum*		*aestivum*		*aestivum*		*aestivum*		*aestivum*		*compactum*		*compactum*		*compactum*	
Origin	Georgia		Iran		Syria		Serbia		England		Turkestan		Georgia		Cyprus	
Status	Landrace/trad.		Landrace/trad.		Adv./improved		Landrace/trad.		Adv./improved		Landrace/trad.		Landrace/trad.		Landrace/trad.	
Grains classified	21	26.3%	14	17.5%	9	11.3%	1	1.3%	1	1.3%	14	17.5%	12	15.0%	8	10.0%

Table 6 LDA reclassification results for Çatalhöyük grains when compared with different modern hexaploid wheat accessions

Accession code	USDA362637		CGN6554		W8612		TRI12894		TRI 8005	
Taxon	*durum*		*durum*		*durum*		*durum*		*durum*	
Origin	N. Macedonia		Cyprus		France		Turkey		USSR	
Status	Landrace/traditional		Landrace/traditional		Advanced/improved		Advanced/improved		Advanced/improved	
Grains classified	43	53.8%	18	22.5%	8	10.0%	8	10.0%	3	3.8%

Table 7 LDA reclassification results for Kouphovouno grains when compared with different modern durum accessions

agricultural regimes has been undertaken to address this. Initial results from the study of a single accession of bread wheat ('Sham4'; Table 2) grown in crop trials at Tal Jebeen near Aleppo, Syria (Fraser *et al.* 2011; Wallace *et al*. 2013), suggest that variations in size and shape corresponding to different manuring and irrigation regimes are similar in scale to natural variations occurring along the ear and within individual spikelets (Appendix 1). Within-ear variation does, however, seem to be influenced by growing condition, in that, under more water- (and perhaps also nutrient-) stressed conditions, ears produce fewer grains overall and per spikelet. Further research may be able to untangle these interrelated factors, but results so far do not indicate that these morphological differences are more distinctive than those seen at the (sub-)species or varietal level.

2.4 Discussion

2.4.1 Potential for identification of ploidy and (sub-)species using GMM

The first stage of analysis assessed whether outline analysis could be used to distinguish charred FTW grains to ploidy or (sub-)species level. The modern baseline study (Tables 3 and 4) correctly assigned 89.8% of charred modern grains to ploidy level and 85.6–86.1% to (sub-)species, a slightly lower rate than the 96.3% obtained in a parallel study of glume wheat grains (Paper 1). However, in practice, our ability to distinguish between the two hexaploid FTW forms (bread and club wheat) proved more complex, particularly when comparing them to archaeological material. The relatively high reclassification rates obtained for the modern reference material when accession was used as a discriminating factor (82.1%, Table 3) does suggest that the model is sensitive to varietal-level differences. It is therefore possible that adding more (landrace) accessions to the modern reference dataset could provide the model with enough information to establish a more consistent morphological separation of the bread and club wheats. This is also suggested by the fact that the eight hexaploid accessions analysed in Stage 2b could be correctly reclassified to (sub-)species at 95.8%.

It was also observed that, at the individual level, a grain may stray quite far from the 'normal' shape range for its type, and such analysis should therefore be interpreted in terms of the overall assemblage. A small number of grains classifying or plotting against a particular (sub-)species does not constitute unambiguous evidence that this taxon was cultivated. The proposed reclassification rates are also based on the presumption that the grain being classified belongs to one of the represented taxonomic categories, and that the comparative material covers the morphological range of those (sub-)species reasonably well, of which we cannot be certain. Such limitations are not unique to the GMM approach. Comparative models can only be improved by increasing the range and relevance of the comparative material used. However, while increasing the size of a physical reference collection may improve the accuracy of identifications, cross-referencing additional specimens can add significantly to the workload of a researcher. The advantage of a GMM approach is that specimens can be compared simultaneously and a dataset can be built up cumulatively, without overwhelming the capacity of the researcher.

2.4.2 Archaeological Results

The identification of two morphologically distinct groups of FTW at the two archaeological sites examined may be considered relevant to our understanding of the early origins and trajectories of FTW. At Çatalhöyük, chaff evidence identified the presence of hexaploid FTW (Bogaard 2016). Results here would seem to confirm that a hexaploid form was the dominant FTW crop (although we cannot rule out the minor presence of a tetraploid wheat). Analysis established a strong morphological similarity of the archaeobotanical material to modern-day examples from the *aestivo-compactum* group, particularly 'traditional' varieties from central and western Asia. Despite initial analysis suggesting that modern bread and club wheat can be separated by grain shape, the Çatalhöyük grains could not be clearly identified as either *aestivum* or *compactum*, although a higher proportion classified as the former. This result could be interpreted in a number of ways:

1) There is a diversity of forms/cultivars among the Çatalhöyük FTW grains

2) The Çatalhöyük grains are of a type with morphology that is distinct from/intermediate between modern bread and club wheat.

3) The method is not sufficiently sensitive to distinguish between bread and club wheat when comparing with archaeological material.

4) The model requires more data to distinguish between bread and club wheat when making comparisons with archaeological material.

With a sequence beginning in the late 8th millennium BCE, Çatalhöyük is one of several sites with attestations of hexaploid FTW during a period in which evidence for the earliest cultivation of the tetraploid form remains elusive. These findings highlight the apparently rapid evolution and adoption of the hexaploid form and the need for further investigation into the mechanisms of this process.

At Kouphovouno no chaff was present by which the FTW remains could be identified to ploidy level. Results show that the 6th millennium BCE Kouphovouno grains most closely resemble tetraploid durum wheat, particularly 'traditional' varieties originating from North Macedonia and Cyprus (Table 7); although, as noted, its dissimilarity from the other tetraploid form it was compared with — rivet — may be influenced by the geographic origin of available accessions. The Kouphovouno results contribute to the theory of early FTW cultivation in the Mediterranean which focussed on tetraploid forms. This was most likely a durum-like wheat, suited to warm and relatively dry conditions, and which was, seemingly by the period of Classical Antiquity, 'the greatly predominant naked wheat' of the region (Jasny 1944, 27). This tradition survived into the present day, and the region has remained a centre of diversity for durum wheats (Soriano *et al*. 2018). The same tradition diffused through southern France to arrive in the Alpine foreland lakeshore settlements by ~4000 BCE (Maier 1996), while hexaploid wheats spread from western Asia through the Balkans and Carpathian basin (Kirleis and Fischer 2014).

Research suggests that durum prefers a deep rich soil (Percival 1921; Hirzel and Matus 2013) and isotopic evidence indicates that at Kouphovouno FTW was preferentially manured

in comparison to barley and einkorn (Vaiglova *et al*. 2014; 2020). While we cannot be certain of the ecological requirements of past crops, it is possible that this distinction in practice reflects farmers' understanding of the crops' relative growing preferences and/or their prioritisation of FTW as a crop designed exclusively for human consumption (Vaiglova *et al*. 2014). Preferential manuring of tetraploid FTW over barley has also been observed at the Neolithic Alpine foreland settlement of Sipplingen (Styring *et al*. 2016). Conversely, at Neolithic Halai (Central Greece), isotopic results for multiple crops, including FTW, indicate cultivation under a range of conditions, interpreted as an overall risk management strategy in the context of relatively drier conditions than those at Kouphovouno (Vaiglova *et al*. 2021). It is likely that the intensive management of FTW at Kouphovouno related to a combination of factors, including the cultural value ascribed to the crop, the environmental context, the crop's ecological requirements and available resources.

Hexaploid FTW at Çatalhöyük was apparently grown under more variable conditions, also likely reflecting risk-management in a semi-arid landscape (Bogaard *et al.* 2017), and potentially the result of households cultivating plots of different size and proximity to the main settlement in a 'radial 'wedge' model' (Bogaard *et al*. 2021), with smaller, more intensely cultivated plots situated more closely to the settlement. It is possible that from an early stage hexaploid FTW possessed greater adaptive potential than tetraploid wheat in accordance with its higher ploidy status (Dubcovsky and Dvorak 2007), allowing it to be grown under a wider range of conditions. In particular storage contexts, FTW was clearly grown under high-input regimes (Green *et al*. 2018) and under generally better-watered conditions than barley (Wallace *et al*. 2015), suggesting that, at least in some cases, the crop was considered worth the relatively high labour investment.

At both sites we see a shift in the final phases towards increased cultivation of hulled cereals. At Çatalhöyük the Final Neolithic and Chalcolithic West Mound phases see increasing proportions of hulled barley and glume wheats, and at Kouphovouno einkorn became the main wheat crop in the Late Neolithic as the settlement contracted. A similar pattern is observed in the final (Horgen, *c.* 3300–2800 cal BC) cultural phase at Neolithic Hornstaad-

Hörnle (SW Germany), where $\delta^{15}N$ values and relative abundance of FTW tetraploid wheat in comparison to emmer decrease (Styring *et al*. 2016). This trend suggests a change in the cultural value of FTWs and/or in the ability to meet their growing requirements. It is possible that the high-input regime associated with FTW, at least at Kouphovouno, became difficult to sustain. A shift towards glume wheats/hulled barley may also relate to the fact that their 'hulledness' provides better resistance to pest or fungal attack, both in the field and in storage, as compared to FTWs (Nesbitt and Samuel 1996). The progression of bread and durum wheat towards the pre-eminence over other (hulled) wheat forms we see today was not, apparently, a linear process.

2.5 Conclusion

The study established that outline analysis can distinguish between charred FTW grains of different ploidy and (sub-)species using the dorsal and lateral views. Separation of durum, rivet, club and bread wheat grains was successful to a reclassification level of 85.6–86.1%. However, in practice it proved more difficult to distinguish within the hexaploid group when comparing modern and archaeological material. Whether this is because the archaeological material is morphologically diverse/distinct or simply due to limitations of the methodology is unclear. Classification according to accession was relatively high at 82.1%, suggesting sensitivity of the model to intra-species variation. It is therefore possible that morphological variation within the hexaploid group could be clarified by expanding modern reference datasets. Overall, results suggest that there is significant potential for GMM analysis to refine taxonomic classifications of archaeobotanical grains at the group (if not individual) level.

Analysis of charred archaeobotanical material from Kouphovouno and Çatalhöyük revealed two distinct morphological types relating to tetraploid and hexaploid FTW forms respectively, although the minority presence of other types could not be ruled out. At Çatalhöyük, remains from the 7th millennium BCE most closely resembled modern grains from the hexaploid *aestivum-compactum* group. These findings reinforce previous chaff and aDNA analysis, providing multi-stranded evidence for early cultivation of hexaploid FTW. Reinforcement of the hexaploid identification highlights the dearth of early evidence for the tetraploid form

which should logically have preceded it, and the need to elucidate the apparently relatively short timeline in which hexaploid wheat evolved.

At Kouphovouno, where diagnostic chaff remains were absent, results suggest cultivation of a tetraploid wheat closely resembling durum wheat. While the importance of durum in the Mediterranean region is evident today, archaeobotanical evidence of the earliest cultivation of tetraploid FTW remains fairly limited. The Kouphovouno material therefore represents a significant addition to evidence for a Neolithic tradition of predominantly tetraploid FTW cultivation which spread west along the Mediterranean coast. Previous research indicates FTW at Kouphovouno was grown under a high-input regime, potentially reflecting the culinary significance of the crop and/or knowledge of its particular environmental preferences. Growing conditions for FTWs at Çatalhöyük were more variable, but intensive management is evident in certain contexts. At both sites, a revival in cultivation of hulled wheat forms is evidenced in later phases, suggesting a shift in the balance between the cultural value of FTW and the desire or ability to meet its growing and storage requirements. The current widespread preference for FTWs was not, therefore, a foregone conclusion; we do not see early farming societies progressing linearly towards the crops we now consider to be ‘optimal’, but rather making contextually-situated decisions.

At both sites, comparisons between modern and archaeological FTW grains suggested that archaeological material was more similar to ‘traditional’ varieties from regions closest to the site of study. Findings suggest the importance of careful selection of comparative material for morphological studies of archaeobotanical material, with geographic region and improvement status potentially highly significant. The role played by the growing environment is less clear, with preliminary results suggesting a possible link between growth stress, grain production and grain morphology, which influences form less distinctly than taxon or variety.

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Paper 2: Appendix A. Key and references for Fig. 3 distribution map

ID	Site	Country	Rachis	Reference
1	Balbridie	UK	Hexaploid	Manning *et al*. 2015
2	Thanet Earth, Kent	UK	Tetraploid	Carruthers 2019
3	Ramsgate Kent	UK	Tetraploid	Carruthers 2019
4	Ifri Oudadane	Morocco	Tetraploid	Morales *et al.* 2013
5	Coro Trasito	Spain	Tetraploid	Antolín *et al.* 2018 (supplementary data)
6	Courrières, Pas-de-Calais	France	Tetraploid	Bostyn *et al*. 2012
7	Spiere, W-Vlaanderen	Belgium	Tetraploid	Vanmontfort *et al.* 2004
8	Arbon-Bleiche 3	Switzerland	Tetraploid	Manning *et al*. 2015
9	Maastricht-Randwijck	Belgium	Hexaploid	Maier 1996; cit. Bakels 1993
10	Laurenzberg 7	Germany	Hexaploid	Manning *et al*. 2015
11	Karlsfält	Sweden	Hexaploid	Manning *et al*. 2015
12	Jüchen, Rhein-Kreis Neuss	Germany	Both	Arora and Zerl 2003
13	Oespeler Bach, Dortmund	Germany	Tetraploid	Kirleis & Fischer 2014 cit. Becker & Pasternak 2003
14	La Draga, Lake Banyoles, Catalonia	Spain	Tetraploid	Antolín 2016
15	Les Bagnoles (L'Isle-sur-la-Sorgue)	France	Both	Jesus *et al*. 2021
16	Clairvaux-les-Lacs Station	France	Both	Manning *et al*. 2015; Neveu & Zech-Matterne 2015
17	Marainville-sur-Madon	France	Hexaploid	Manning *et al*. 2015
18	Lake Neuchâtel (various sites)	Switzerland	Tetraploid	Akeret & Geith-Chauvière 2003; 2011a;b
19	Twann	Switzerland	Both	Manning *et al*. 2015

ID	Site	Country	Rachis	Reference
20	Oberrieden ZH-Riet	Switzerland	Tetraploid	Manning *et al*. 2015
21	Lake Zürich (various sites)	Switzerland	Both	Schlumbaum *et al*. 1998; Kirleis & Fischer 2014 cit. Jacomet *et al.* 1989
22	Isolino Virginia	Italy	Tetraploid	Antolín *et al.* 2022 (supplementary data)
23	Aldingen	Germany	Both	Piening 1986; 1992; 2005
24	Singen-Offwiese	Germany	Hexaploid	Jacomet 2007, 236 cit. Dieckmann *et al.* 1998
25	Hornstaad, Hörnle I/Sipplingen	Germany	Tetraploid	Maier 1996; Manning *et al*. 2015
26	Alleshausen, Grundwiesen	Germany	Tetraploid	Manning *et al*. 2015
27	Seekirch, Achwiesen	Germany	Tetraploid	Manning *et al*. 2015
28	Bad Buchau, Torwiesen	Germany	Tetraploid	Manning *et al*. 2015
29	Heilbronn-Klingenberg	Germany	Tetraploid	Stika 1996
30	Großsachsenheim	Germany	Hexaploid	Manning *et al*. 2015
31	Eberdingen-Hochdorf	Germany	Hexaploid	Manning *et al*. 2015
32	Leonberg-Höfingen	Germany	Both	Maier 2004
33	Ditzingen	Germany	Hexaploid	Piening 1998
34	Remseck-Aldingen	Germany	Hexaploid	Manning *et al*. 2015
35	Dieksknöll, Schleswig-Holstein	Germany	Tetraploid	Kirleis & Fischer 2014
36	Frydenlund, Fyn	Denmark	Tetraploid	Kirleis & Fischer 2014
37	Vrold	Denmark	Hexaploid	Manning *et al*. 2015
38	Kückhoven	Germany	Hexaploid	Knörzer 1998
39	La Marmotta (Lago di Bracciano)	Italy	Tetraploid	Jacomet 2007; Rottoli and Pessina 2007
40	Hundssteig/Kleiner Anzingerberg	Austria	Hexaploid	Kohler-Schneider & Cannepele 2009

ID	Site	Country	Rachis	Reference
41	Kujawy region	Poland	Hexaploid	Bieniek 2002
42	Zánka-Vasúti bevágás	Hungary	Hexaploid	de Vareilles *et al.* 2022
43	Ecsegfalva	Hungary	Hexaploid	de Vareilles *et al.* 2022
44	Okolište	Bosnia & Herz.	Both	de Vareilles *et al.* 2022
45	Vinča-Belo Brdo	Serbia	Hexaploid	de Vareilles *et al.* 2022
46	Belovode	Serbia	Hexaploid	de Vareilles *et al.* 2022
47	Pločnik	Serbia	Both	de Vareilles *et al.* 2022
48	Can Hasan	Turkey	Both	Hillman 1972; 1978
49	Cafer Höyük	Turkey	Hexaploid	de Moulins 1993; 1997
50	El Kowm	Syria	Both	de Moulins 1997
51	Abu Hureyra	Syria	Both	de Moulins 1997

Paper 2: Appendix B. Contextual information for archaeological samples

Site	Area/Trench	Context	Context type	Site phase	Sample no.	No. grains	% Bread	%Club	%Durum	%Rivet
Kouphovouno	B	B1085	*In situ* burning of cereal grain stores	Late	1242	32	15.6%	6.3%	78.1%	0.0%
Kouphovouno	C	C0918	*In situ* burning of cereal grain stores	Middle	1240	13	7.7%	15.4%	76.9%	0.0%
Kouphovouno	C	C0905	*In situ* burning of cereal grain stores	Middle	1223	5	0.0%	0.0%	100.0%	0.0%
Kouphovouno	C	C0804	*In situ* burning of cereal grain stores	Middle	1010	9	10.0%	0.0%	90.0%	0.0%
Kouphovouno	C	C0911	*In situ* burning of cereal grain stores	Middle	1190	21	4.8%	9.5%	81.0%	4.8%
Çatalhöyük	South O	18596	Burnt primary fill - Charred seeds	Middle	Archive sample	21	47.6%	47.6%	4.8%	0.0%
Çatalhöyük	TPC.M	20747	Burned layer of fire installation on platform	Late	12913	2	100.0%	0.0%	0.0%	0.0%
Çatalhöyük	North G	11908	Burnt primary fill - Bin fill	Middle	6059	24	45.8%	37.5%	12.5%	4.20%
Çatalhöyük	South O	18598	Burnt primary fill - Charred seeds	Middle	Archive sample	4	50.0%	50.0%	0.0%	0.0%
Çatalhöyük	South G	4879	Midden	Early	3297	2	0.0%	100.0%	0.0%	0.0%
Çatalhöyük	South	23956	Midden	Late	13827	2	50.0%	50.0%	0.0%	0.0%
Çatalhöyük	South O	18595	Burnt primary fill - Floor collapse	Middle	9134	9	44.4%	22.2%	33.3%	0.0%
Çatalhöyük	South O	18597	Burnt primary fill - Building collapse	Middle	9144	1	0.0%	0.0%	100.0%	0.0%
Çatalhöyük	North G	10305	Burnt primary fill - Charred seeds	Middle	6023	6	50.0%	33.3%	0.0%	16.7%
Çatalhöyük	North G	11906	Burnt primary fill - Bin fill	Middle	6044	4	75.0%	0.0%	25.0%	0.0%
Çatalhöyük	North G	11908	Burnt primary fill - Bin fill	Middle	6049	5	20.0%	20.0%	60.0%	0.0%

3.0 Paper 3: Diversity of Free-threshing Wheat Cultivars in Early Medieval England Supported by Geometric Morphometric Analysis of Grains

Tina Roushannafas, Mark McKerracher

School of Archaeology, University of Oxford, Oxford OX1 3TG, United Kingdom

Abstract

Archaeobotanical observations of atypical grains and relatively small numbers of diagnostic rachis fragments have led to suggestions of the introduction of a new type of wheat into Late Anglo-Saxon agriculture (*c.* AD 850–1066). This crop was a tetraploid free-threshing wheat (FTW), a form potentially not known in Britain since the Neolithic. Based on environmental requirements, this wheat is considered to have most likely been rivet, a tall cultivar typically associated with thatching, presumably grown alongside widely cultivated free-threshing hexaploid bread wheat. However, cultivation of this crop has not been conclusively demonstrated because traditional morphological approaches do not allow us to identify specific FTW cultivars.

Results here indicate that geometric morphometric analysis of grain outlines can distinguish FTWs at different taxonomic levels. These distinctions are preserved when modern grains are charred to replicate well-preserved archaeobotanical material. Modern wheat specimens were compared with >450 charred grains from contexts spanning the 7th–14th centuries at twelve sites, accessed through the 'Feeding Anglo-Saxon England' (FeedSax) project. Results suggest the presence of rivet wheat at several sites, both before and after the Norman Conquest (AD 1066), with intra-species comparisons indicating greater morphological similarity to 'traditional' varieties than to modern 'improved' forms. Morphological variation is described as relating to diversity both between and among cultivars and is interpreted within the context of rapid acceleration and innovation in arable production in the later Anglo-Saxon period.

Keywords

Geometric Morphometrics; Wheat; Taxonomy; Agriculture; Anglo-Saxon; Biodiversity

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3.1 Introduction

3.1.1 Archaeobotanical Identification of Free-Threshing Wheats

The beginning of the Anglo-Saxon period in fifth-century England saw a shift from cultivation of glume wheats, and particularly spelt as favoured in Romano-British agriculture (van der Veen 2016), to predominantly free-threshing forms (Moffett 2011). Free-threshing wheats (FTWs) have non-toughened glumes which release the grains upon threshing (Fig. 1), rather than breaking up into spikelets which require further dehusking, as for 'glume' wheats (Hillman 1984). While a radiocarbon review of material from central and southern England has suggested that many finds of prehistoric FTW in Britain may be intrusive from later deposits (Pelling *et al*. 2015), it would appear that FTW was present in the British Isles from the Neolithic period (Carruthers 2019). It is therefore likely that the shift towards free-threshing forms in the Anglo-Saxon period related to cultural preference rather than the inevitable outcome of a revolution in agricultural technique (Moffett 2011).

FTWs are categorised at increasing levels of specificity according to ploidy, species, sub-species and variety. Most broadly, they are represented by tetraploid (*Triticum turgidum* L.) and hexaploid forms (*Triticum aestivum* L.) (Fig. 2). Tetraploid wheats have four sets of

chromosomes (BBAA) while hexaploid have six (BBAADD), the latter having evolved from the former as a result of inter-specific hybridisation (Pont *et al*. 2019). Cultivars are defined here at the sub-species level after van Slageren (1994), but are treated by some taxonomists as distinct species (Goncharov 2011).

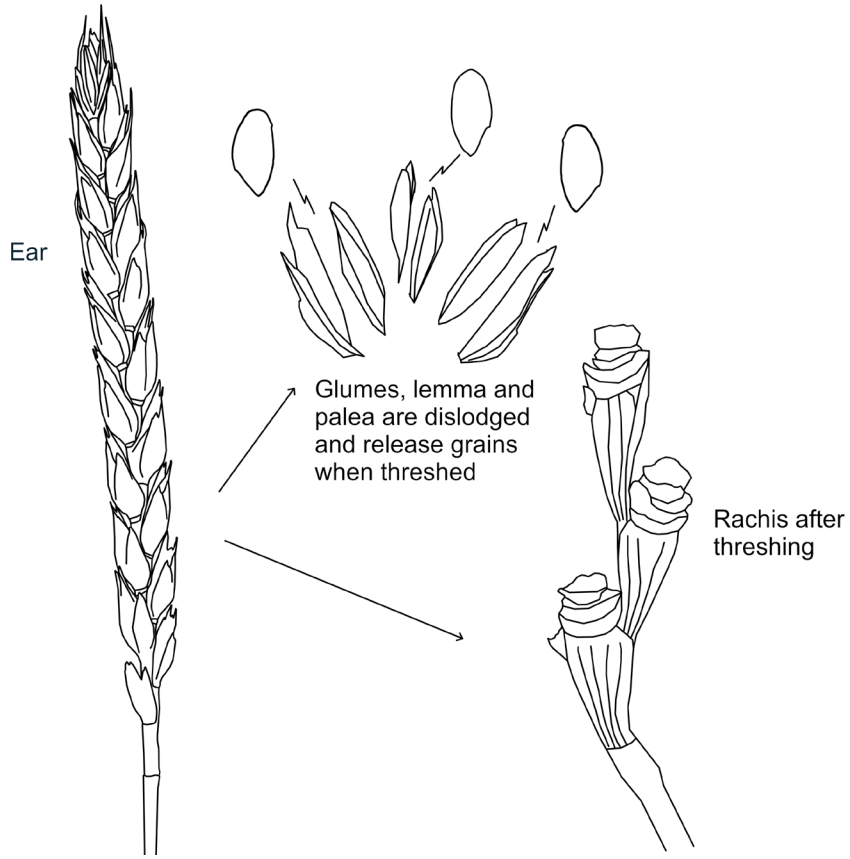

Fig. 1 Schematic diagram showing how FTWs are processed

Hexaploid (BBAADD) ***Triticum aestivum* group**	**Tetraploid (BBAA)** ***Triticum turgidum* group**
Bread wheat (subsp. *aestivum)*	**Durum wheat (subsp. *durum*)**
Club wheat (subsp. *compactum*)	**Rivet wheat (subsp. *turgidum)***
Indian dwarf wheat (subsp. *sphaerococcum*)	‘Persian’ Wheat (subsp. *carthlicum*)
	‘Polish’ Wheat (post-17th century) (subsp. *polonicum*)
	Khorasan wheat (subsp. *turanicum*) (hybrid of Polish wheat)

Fig. 2 Summary of ploidy groups for FTWs. Bold= included in study

A single sub-species of hexaploid FTW, *T. aestivum* L. ssp. *aestivum*, or 'bread wheat', accounts for ~90–95% of modern wheat production globally (Giraldo *et al*. 2019). This overwhelming dominance by one sub-species belies not only the adaptive diversity within the genus (Dubcovsky and Dvorak 2007) but also the complex history of coevolution between humans and one of our most significant food-sources. The progressive replacement of diverse landraces with increasingly genetically uniform modern varieties has prompted sustainability concerns in the face of factors such as climate change and disease (Camacho Villa *et al.* 2005; Mijatović *et al.* 2013; Venske *et al*. 2019; Pilling *et al*. 2020). Improving our understanding of diversity and environmental adaptation in archaeobotanical wheat assemblages may help to contextualise this debate by providing a counterpoint to modern monoculture cropping.

When identifying archaeobotanical FTW remains, it is possible to determine ploidy level using diagnostic criteria of rachis segments (Hillman *et al.* 1996; Hillman 2001). Unfortunately, rachis remains are relatively rare in Anglo-Saxon archaeobotanical assemblages, which are principally preserved through charring (Moffett 1991; McKerracher 2018, 97). This scarcity is potentially due to chaff being less likely to survive charring (Boardman and Jones 1990), but also because rachis is separated from the crop after bulk threshing, usually away from domestic charring contexts (Jones 1987). Grains are more frequently recovered, but are distorted by charring and notoriously difficult to identify beyond the genus-level by traditional morphological approaches even when well-preserved (Moffett 1991; Jones 1998). Furthermore, neither grain nor chaff can reliably identify FTW remains to the (sub-)species, i.e. crop-specific, level (Hillman *et al*. 1996).

Therefore, in most cases, we can say only that a free-threshing form of wheat was cultivated at a site during the Anglo-Saxon period, without greater specificity. Nevertheless, archaeobotanical reports for the period frequently gloss remains as ssp. *aestivum*, *T. aestivum 'sensu lato'* or '*T. aestivo-compactum'* (McKerracher 2018, 96). These definitions can be misleading when not supported by rachis identifications, and assume a hexaploid form corresponding to either bread or club wheat (*T. aestivum* L. ssp. *compactum* (Host)

MK). Club wheat is similar to bread wheat but is associated with greater drought tolerance and has a more compact ear; in recent history it was cultivated mainly within central Asia and the Pacific coast of North America (Percival 1921). Where the distinction can be made, hexaploid wheats appear to have been the prevalent form in medieval England (Robinson 2018). However, refinements in morphological analyses mean that identification as *T. aestivum* can no longer be the default assumption, as further demonstrated below.

3.1.2 Archaeobotanical Evidence for Tetraploid Wheats in Britain

Cultivation of tetraploid FTWs is mostly associated with the Mediterranean region. Interpretation of written evidence suggests that the tetraploid wheats rivet (*Triticum turgidum* L. ssp. *turgidum*) and durum (*Triticum turgidum* L. ssp. *durum* (Desf.) Husn.) were cultivated in Classical Antiquity, the latter apparently the 'greatly predominant naked wheat' (Jasny 1944, 27). In recent history, cultivation of these wheats has continued to be associated with the region (Percival 1921; Soriano *et al*. 2018), with durum wheat having particular economic significance in the production of pasta (Giraldo *et al*. 2019).

Although associated with warmer climes, recent work has identified cultivation of tetraploid FTWs in Britain as far back as the Neolithic. Diagnostic rachis segments and associated 'compact-type' grains were characterised at Thanet dating to the early 4th millennium BC, and also reported for Ellington Road, Ramsgate, both in Kent (Carruthers 2019). Such reports follow the identification of whole ears recovered from waterlogged Neolithic pile-dwellings in the Alpine foreland as tetraploid, which challenged existing assumptions that the FTW cultivars of early European agriculture were exclusively hexaploid (Maier 1996). Based on these and subsequent findings, it has been proposed that tetraploid FTWs arrived in south-west Europe from the Mediterranean via southern France, spreading north via contacts with the Michelsberg group of west-central Europe before reaching Britain (Kirleis and Fischer 2014).

Bread wheat was long regarded as the only wheat grown in Britain during the medieval period (Robinson 2018). However, following the development of diagnostic criteria for rachis segments, tetraploid wheats have been identified at numerous sites post-dating the Norman

Conquest (Moffett 1991; 2018), mainly south of a line drawn from Chester to Ipswich (Moffett 2006). They are less commonly identified than hexaploid FTWs and usually identified alongside them, and it is not clear whether the two wheats were grown or merely processed together (*ibid.*, 49). A relatively small number of identifications have been made for the Late Anglo-Saxon period, notably at Higham Ferrers (Northamptonshire), radiocarbon dated to cal. AD 770–1000 (1150 ± 45 BP) (Moffett 2007, 169). On this basis, Moffett (2011) proposes a probable Late Anglo-Saxon introduction of a tetraploid FTW, most likely rivet, on the grounds that it is more tolerant of cold and damp conditions than durum. However, given the proven ability of wheat to adapt to more northerly climes in the past, there is no absolute reason to rule out historical durum cultivation in Britain (Letts 1999, 35). Late Anglo-Saxon rivet cultivation is also proposed at West Cotton (Northants), believed to have been 'introduced as part of an agricultural package associated with the laying out of open fields' (Campbell and Robinson 2010, 430).

That a wheat we would taxonomically identify as rivet today was cultivated in the later medieval period was demonstrated by John Letts' analysis of smoke blackened thatch from 14th- and 15th-century buildings in southern England (Letts 1999). The base coat of the thatch, contemporary with the buildings' construction, survived by being gently charred by the passage of smoke from the open fireplace below. Due to these excellent preservation conditions, whole wheat ears had been preserved which made it possible to identify the use of rivet in the thatching. Rivet's presence in the majority of buildings studied 'came as a revelation considering its rarity in archaeobotanical assemblages and its virtual disappearance from British wheat fields in the late 19th century' (*ibid*., 38).

3.1.3 Rivet Wheat: History and Usage

References to 'rivet' are found in medieval agricultural treatises, as well as 'pollard' and 'cone wheat', all names for ssp. *turgidum* still used today (Moffett 1991). The varying terms used by medieval writers mean that we cannot always confidently identify descriptions with particular cultivars. For example, Thomas Tusser's 'Five Hundred Points of Good Husbandry' (1599) references both 'red riuet' suitable for light soils and 'white pollard or red'

suitable for heavy soils, while Henry Best's 1642 'Farming Book' seemingly refers to rivet as 'longe reade' (Best and Woodward 1984). Where a detailed description is provided, identification is less ambiguous: the preferences and habits of 'long cone wheat' given by Plot (1705) are remarkably similar to the description given for rivet wheat in Percival (1921) (Moffett 1991). Therefore, while there is some ambiguity, we can be reasonably confident that rivet was considered a distinct crop by later/post-medieval agricultural writers.

Rivet straw is tall and strong (Percival 1921), making the crop an ideal source of thatching material and allowing it to compete effectively with weeds for sunlight. Rivet flour has been considered as most suited to biscuit-making (Percival 1921) and less to bread production due to relatively weak gluten and a 'mealy' texture (Moffett 1991). Rivet can, however, be mixed with other wheats in bread flour (Gill *et al.* 1980) and this was apparently found by 17th-century bakers to give quite satisfactory results (Best and Woodward 1984, 166). Recent analyses of landraces have demonstrated considerable variability in kernel hardness and gluten protein composition amongst rivets, suggesting a range of potential culinary applications (Chable 2018).

Rivet wheats have strong resistance to rust fungi and stiff awns which limit damage by birds (Percival 1921). Tetraploid FTWs are also generally more drought-tolerant than their hexaploid counterparts but are vulnerable to frost and waterlogged conditions (Percival 1921). It would therefore seem unlikely that rivet would perform well in the north of England or on waterlogged soils. The co-occurrence of tetraploid FTW remains at West Cotton with *Tripleurospermum inodorum*, a weed associated with well-drained soils (Campbell and Robinson 2010, 497), may indicate consideration of these requirements. Rivet generally requires a long growing season to produce a good crop, being sown in the autumn and harvested in September, while other cereals can be harvested in July–August (Letts 1999, 24). That the crop cannot be adapted to a shorter season under a British climate has, however, been challenged in recent trials, which demonstrated that a modern spring variety of ssp. *turgidum* could be successfully grown alongside bread wheat (Robinson 2018).

Robinson (2018) highlights that much of our understanding of rivet's potential is based on accounts such as Percival (1921), written when cultivation of rivet in Britain was limited. From the late 18th century the thatching industry declined, while at the same time farmers demanded higher-yielding wheats that were better adapted to mechanical harvesting. Breeders began to develop stronger, shorter-stemmed varieties which were more uniform in height and ripening habit (Letts 1999, 7). In this context, cultivation of rivet declined and in the early 1920s Percival noted that only one or two forms were grown in England, in relatively small areas and chiefly in the southern counties (Percival 1921). Cultivation of rivet revived slightly in the 1930s with the development of the 'rather hardier' variety 'Rampton Rivet', favoured on heavy soils in southern England up until the 1950s (Gill *et al.* 1980, 62). It seems likely that, prior to the decline in rivet cultivation, a wider range of cultivars with different adaptations existed, borne out of centuries of cultivation. Genetic 'bottlenecking' caused by modern farming techniques and narrow breeding requirements means that we cannot make assumptions on the tolerance and capabilities of ancient crops represented now only by a small number of surviving cultivars (Robinson 2018).

3.2 Methodology

3.2.1 Approach

In order to gain further insight into the FTW crops of early medieval agriculture, geometric morphometric (GMM) analysis of modern and archaeological grains was employed. Analysis sought to establish whether grain shape could distinguish FTWs to (sub-)species, and whether this could be applied to charred archaeobotanical material. Bread, club, durum and rivet wheat were selected as the most relevant (sub-)species for the period and region (Fig. 2) and the types most commonly identified with archaeobotanical remains.

Morphometric approaches analyse shapes as numeric data, allowing for morphological variation to be explored using multivariate statistics. GMM differs from traditional morphometric approaches in that, rather than relying on individual measurements taken from a specimen, more of the complexity of the overall geometry is captured (Adams *et al.*

2004). The technique utilised was Elliptic Fourier Analysis (Giardina and Kuhl 1977; Kuhl and Giardina 1982), a form of outline analysis suited to the broadly 'continuous' form of a wheat grain. This method does not require points to be equally-spaced and allows for virtually any outline to be fitted (Bonhomme *et al*. 2014). Previous studies suggest that Elliptic Fourier Analysis can be an effective tool for the taxonomic identification of wheat grains (Bonhomme *et al.* 2017; Paper 1). Moreover, while environmental conditions are anticipated to influence form, morphological variation relating to cultivation conditions appears less distinct than that between cultivars (Appendix 1).

3.2.2 Sampling, Charring and Photography

Modern material was primarily obtained through gene-banks, with a single accession collected from organically-farmed land at the Highgrove estate, Gloucestershire (Table 1). Selection of material prioritised availability of whole ears to account for within-ear variation and, as such, the dataset included both 'advanced/improved' cultivars associated with modern crop breeding programs and 'traditional' varieties. Each accession was represented by three ears, with nine grains sampled equally from across the base, middle and top of each ear.

Modern grains were photographed before and after charring in dorsal, lateral and polar view using a Nikon SMZ25 stereo microscope and Pixelink M12BC-CYL microscopy camera (Fig. 3). Grains were charred under conditions designed to replicate well-preserved archaeological material, with parameters guided by experiments in Charles *et al*. (2015). Grains were packaged in foil and buried in sand to reduce oxygen availability, before being placed in a 230°C preheated oven for six hours. The sand and oven temperature were monitored using thermacouples and a datalogger.

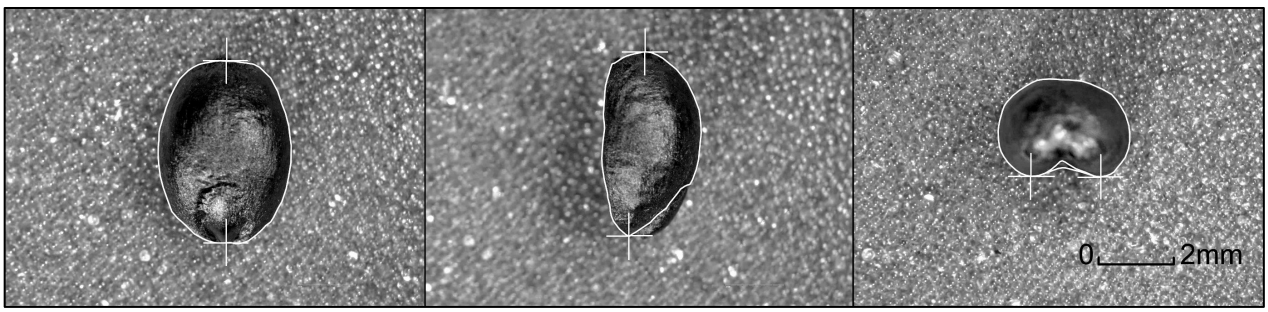

Fig. 3 Dorsal, lateral and polar view of a FTW grain with alignment points added

Taxon	Common name	Accession code	Variety (if named)	Source	Improvement status	Country of origin	No. of grains
T. aestivum* ssp. *aestivum	Bread wheat	High09	Maris Widgeon	Highgrove	Advanced/improved	England	27
T. aestivum* ssp. *aestivum	Bread wheat	W6537	Squarehead's Master	John Innes	Advanced/improved	England	27
T. aestivum* ssp. *aestivum	Bread wheat	USDA350071		USDA	Landrace/traditional	Serbia	27
T. aestivum* ssp. *compactum	Club wheat	T1200010		John Innes	Landrace/traditional	Georgia	27
T. aestivum* ssp. *compactum	Club wheat	T1200011		John Innes	Landrace/traditional	USSR	27
T. aestivum* ssp. *compactum	Club wheat	T1200012		John Innes	Landrace/traditional	Cyprus	27
T. turgidum* ssp. *durum	Durum wheat	TRI 8005	Kjachraba 10	Gatersleben	Advanced/improved	USSR	27
T. turgidum* ssp. *durum	Durum wheat	PI362637		USDA	Landrace/traditional	N.Macedonia	27
T. turgidum* ssp. *durum	Durum wheat	CGN6554	Kyperounda	CGN Wageningen	Landrace/traditional	Cyprus	27
T. turgidum* ssp. *durum	Durum wheat	W8612	Ambral*	John Innes	Advanced/improved	France	27
T. turdigum* ssp. *turgidum	Rivet wheat	W1022	Percival's Blue Cone	John Innes	Landrace/traditional	England	27
T. turdigum* ssp. *turgidum	Rivet wheat	W0508	Rampton Rivet	John Innes	Advanced/improved	England	27
T. turdigum* ssp. *turgidum	Rivet wheat	USDA190157	Roter Tiroler	USDA	Landrace/traditional	Germany	27

Table 1 Modern material used in GMM study. *Replaced in final dataset with 'Kyperounda'

Site	Site type	County	Date range of samples	Grains analysed	Specialist reference
Botolph Bridge	Manor/rural settlement	Peterborough	880–1400	34	Clapham (2015)
Coton Park	Rural settlement	Warwickshire	1030–1260	30	Maull (2001); McKerracher *et al*. forthcoming
Eckweek	Manor/rural settlement	Avon	1000–1220	26	Carruthers (1995; 2020)
Houghton	Rural settlement	Cambridgeshire	780–1030	58	McKerracher *et al*. forthcoming
Lyminge	Royal monastery/archiepiscopal estate	Kent	780–1220	31	Campbell 2012; Ballantyne 2014; McKerracher (2013; 2014; 2017); McKerracher *et al.* forthcoming
Mildenhall	Rural settlement	Suffolk	780–1030	28	Cobain (2019)
North Raunds/West Cotton	Manor/rural settlement	Northamptonshire	880–1400	20	Campbell and Robinson (2009; 2010)
Pudding Lane	Manor/rural settlement	Hertfordshire	950–1100	46	Hunter Dowse (2018)
Sedgeford	Settlement/malting complex	Norfolk	600–800	40	Caroe (in press; in prep.); McKerracher in prep.
Stafford	Burh/early town	Staffordshire	875–1220	86	Moffett 1987; Druce 2014; Hamerow *et al*. 2020
Walsingham Way/West Fen Rd, Ely	Rural settlement/ecclesiastical centre	Cambridgeshire	725–1400	27	Ballantyne 2005; de Vareilles (2011)
Wolverton Mill	Rural settlement	Buckinghamshire	450–1400	37	Carruthers (2011)
Total				**463**	

Table 2 Summary of sites and specimens studied. Sample dates summarised using the FeedSax database (McKerracher *et al.* forthcoming)

Archaeological grains were derived from 12 sites in central, eastern and south-west England, as studied by the Feeding Anglo-Saxon England (FeedSax) project at the University of Oxford (Hamerow in press), the majority characterised as rural settlements (Table 2; Fig. 4). There is some bias towards the east of England, this being a function of both the availability of material and often poor preservation of grains, which excluded several sites with insufficient sample sizes. Archaeological grains were photographed as above for modern grains and selected on the basis of preservation, excluding incomplete specimens and grains with significant distortion, formation of large cavities and/or exudation of grain contents resulting from high charring temperatures (Charles *et al*. 2015).

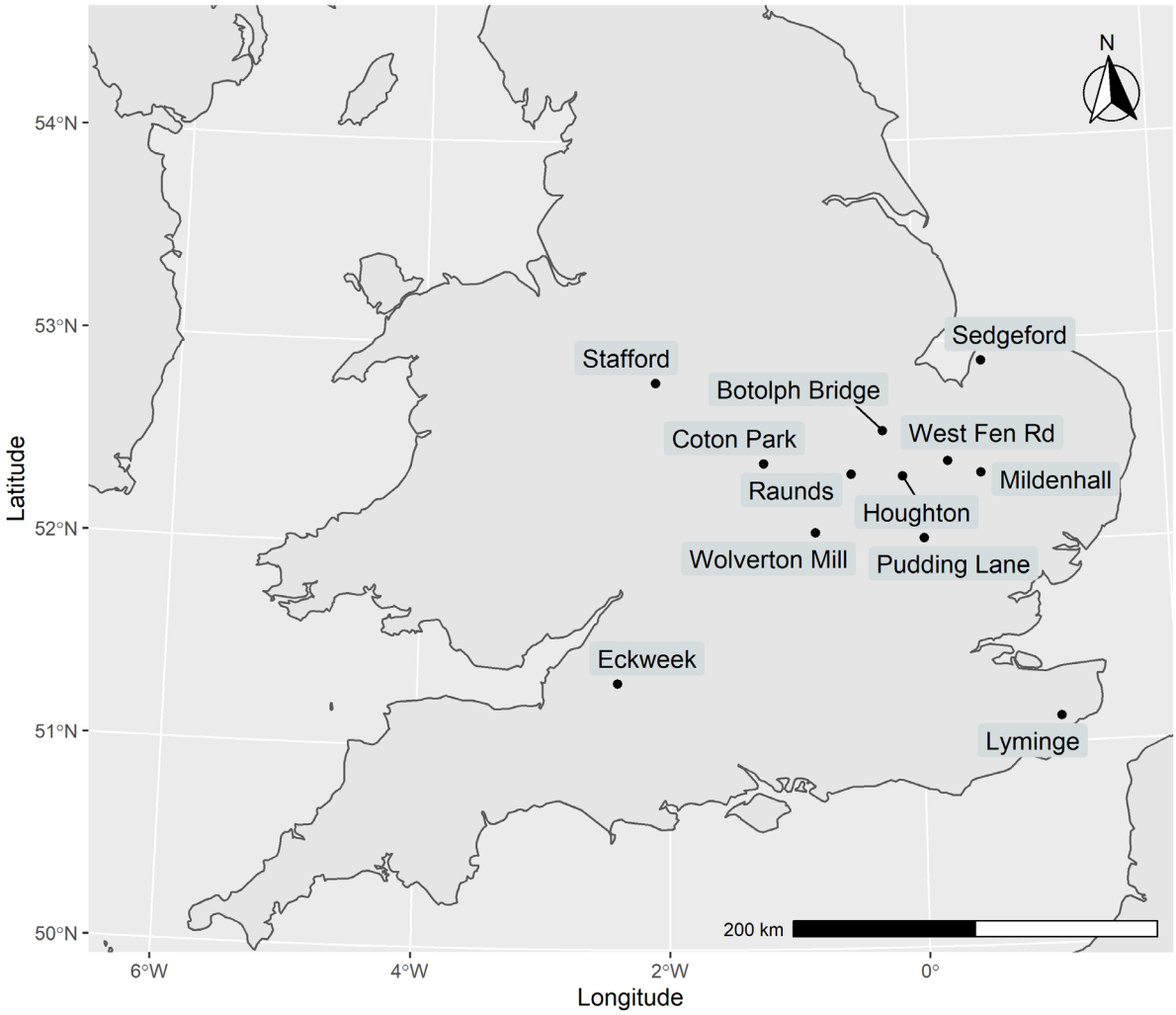

Fig. 4 Map of study sites

As a result of often poor preservation, sample sizes are in some cases smaller than would be desirable and for some sites multiple excavations in the same locale have been grouped (Table 2). Contexts have a wide potential date range (450–1400), but are predominantly of

8th–13th-century date, with the exception of Sedgeford, which dates to the 7th–9th century AD (Table 2; see also Appendix A). Phasing and site/context information were obtained from the FeedSax 'Haystack' database (McKerracher *et al*. forthcoming) in conjunction with the references listed in Table 2.

3.2.3 Digitisation

The outline of each photographed grain was digitally traced in AutoCAD (a design and drafting program). Embryos were excluded as these are frequently damaged and may not be equally developed across specimens. Each outline was ultimately represented by 40–80 coordinate points. This level of variation does not appear to affect the results of classification to a significant degree (Paper 1). Alignment points were added to each outline to minimise differences in orientation (Fig. 3). Once aligned, the coordinates for each grain were extracted and saved as .txt files.

3.2.4 Analysis

Once digitised, Elliptic Fourier Analysis of the grains was performed in R (3.6.2) using the GMM packages 'geomorph' (3.2.1) and 'Momocs' (1.2.9), the latter developed by Vincent Bonhomme based on functions published by Claude (2008). Grain coordinates were scaled by centroid size and Fourier Transforms were calculated for each view before being combined (after Bonhomme *et al*. 2017). Eight harmonics were retained for each view, gathering at least 99% of the total harmonic power. Linear discriminant analysis (LDA) with leave-one-out cross-validation was used to assess how accurately grains could be classified according to their shape, scoring each known specimen ('actual') against the group it most closely resembled ('classified').

Repeatability and measurement error were tested after the protocol described in Claude (2008) and Evin *et al*. (2020). Five specimens from the same ear of ssp. *aestivum* were photographed and digitised in five separate sessions. Procrustes ANOVA (analysis of variance) on PCA (principal components analysis) scores of the coefficients produced a non-significant value (≥0.05) with session as the dependent variable, and a significant value when individual ID was used as the dependent variable. This was true of both dorsal and

lateral views, and suggests that different sessions did not produce significantly different outlines, and that variation between sessions was less significant than between specimens. Measurement error was calculated using ANOVA results after the equation defined in Claude (2008, 65–6) at 4.38% for the dorsal view and 5.94% for the lateral view.

3.3 Results

3.3.1 Modern Baseline Study

The modern baseline study replicates elements of Paper 2, Section 2.3.1, but also includes comparative assessment of uncharred grains, all three photographic views and a different combination of accessions. Uncharred grains of durum, rivet and bread wheat were compared to assess the viability of Fourier Analysis to detect morphological differences at the (sub-)species level, and which views were most effective in doing so. Each sub-species was represented by three accessions and a total of 81 grains (Table 1). Linear discriminant analysis (LDA) indicated that up to 95.1% of uncharred grains could be correctly assigned to (sub-)species depending on the combination of views used (Table 3). The polar view was found to be the least useful single view and the lateral the most useful (Table 3).

	Pre-Charring	Post-Charring	Post-charring +compactum	Final dataset
View				
Dorsal	86.4% - 210/243	77.4% - 188/243	67.6% - 219/324	66.0% - 214/324
Lateral	88.9% - 216/243	89.3% - 217/243	84.6% - 274/324	84.6% - 274/324
Polar	67.5% - 164/243	55.6% - 135/243	n/a	n/a
Dorsal + lateral	94.7% - 230/243	89.3% - 217/243	86.7% - 281/324	88.3% - 286/324
Dorsal, lateral + polar	95.1% - 231/243	89.3% - 217/243	n/a	n/a

Table 3 Summary of LDA results comparing charred modern bread, durum, rivet (and subsequently club) wheat grains. Values indicate percentage/number of grains correctly classified to taxon

When the same dataset was charred to replicate archaeological material, the reclassification rate decreased slightly to 89.3%. This score was obtained whether the lateral view, dorsal and lateral view, or all three views combined were used (Table 3). The least useful view was again the polar view, and it was therefore excluded from further data-collection. Subsequently dorsal and lateral views of club wheat grains were added, and using these two views the reclassification rate was 86.7%. This increased to 88.3% in the final dataset,

which replaced one durum accession in order to improve representation of traditional varieties (Tables 1; 4). When plotted, significant overlap was observed between bread (ssp. *aestivum*) and club (ssp. *compactum*) wheat along the first two linear discriminants; however, along the third axis we see relatively clear separation between the groups (Fig. 5). When 'accession' was used as the discriminating factor, reclassification scored only slightly lower at 84.6%.

		Classified as		
Actual	*aestivum*	*compactum*	*durum*	*turgidum*
ssp. *aestivum*	75	2	2	2
ssp. *compactum*	6	65	3	7
ssp. *durum*	0	1	75	5
ssp. *turgidum*	5	3	2	71
Class correctness	92.6%	80.2%	92.6%	87.7%
Leave-one-out cross validation		88.3% - 286/324		

Table 4 Results of LDA comparing charred modern bread, club, durum and rivet wheat grains (final dataset), when dorsal and lateral views combined'

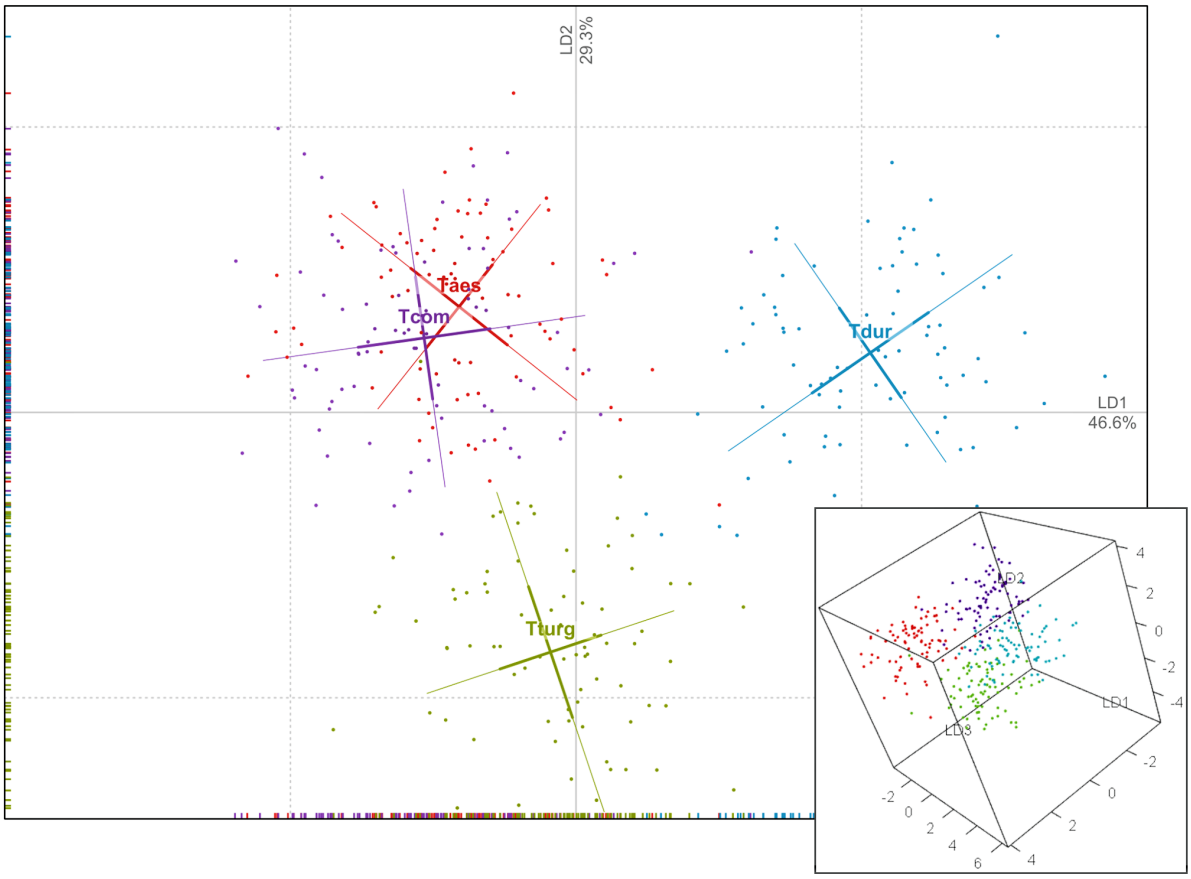

Fig. 5 LDA of different (sub-)species of modern FTW grains (charred). 'Taes'= ssp. *aestivum*, 'Tcom'= ssp. *compactum*, 'Tturg'= ssp. *turgidum*, 'Tdur'= ssp. *durum*. Insert: 3D plot showing separation along LD3

Overall the baseline study demonstrated that the most taxonomically distinctive views are the dorsal and lateral, of which the latter is apparently the most useful. These findings closely mirror those from a previous study of glume wheat grains (Paper 1). Separation decreases slightly after charring, but remains >86%, varying slightly according to which accessions are included. A margin of error for classification of 10–15% was therefore anticipated when comparing with archaeological material.

3.3.2 Comparison with Archaeological Material

Subsequently, an LDA with archaeological grains entered as unknown categories was performed. The LDA compared 463 archaeological grains with 324 modern specimens of bread (hereafter '*aestivum*'), club ('*compactum*'), durum ('*durum*') and rivet ('*turgidum*') wheat, and assigned each archaeological grain to a category based on the modern type it most resembled. A total of 88 archaeological grains (19.0%) were classified as *turgidum*, ranging from 0–69.0% of the grains analysed per site (Table 5). Of these grains, 54/88 are associated with mid-9th to mid-11th-century contexts, of which 40 are derived from one site (Houghton). A further 23 of these grains are assigned to a broader 11th–12th-century period which may pre- or post-date the Norman Conquest (Table 6).

Grains classified as either hexaploid *aestivum* or *compactum* ranged from 26.5–100% of the grains per site, with 41.7% of grains classified as *aestivum* and 32.2% as *compactum* overall (Table 5). A smaller proportion of grains (7.1%) were classified as *durum*; this being within the margin of error for classification and not necessarily indicative of the presence of this crop. At two sites the proportions were somewhat higher (15–25%; Table 5) and these are considered separately below, alongside evidence of germination/malting of grains.

3.3.3 Sites with No Grains Classified as Rivet Wheat

At the easternmost sites of Lyminge (Kent), Mildenhall (Suffolk) and Sedgeford (Norfolk), none of the grains analysed were classified as rivet, and the vast majority of grains were identified as hexaploid *aestivum*/*compactum* wheat types (Table 5). These findings are in agreement with chaff identifications at Sedgeford (H. Caroe, pers. comm), while at Lyminge

the vast majority of chaff is similarly identified as hexaploid (McKerracher 2014, 527), with only 2(/3) tetraploid identifications for the Mid Saxon period (Campbell 2012) and two tetraploid segments dated to the 11th–12th century (Ballantyne 2014; McKerracher *et al*. forthcoming). However, numerous tetraploid rachis segments were recorded at Mildenhall (Cobain 2019), from samples which did not produce grains classified here as durum or rivet-type.

At both Lyminge and Mildenhall, the discriminant plot indicates a much closer association of the archaeological material to the modern hexaploid wheats than to the tetraploid forms (Fig 6). As at other sites, a significant proportion of grains were classified as *compactum* as well as *aestivum*-type, potentially suggesting that a diversity of hexaploid grain forms are represented. The earlier site of Sedgeford is discussed further below, due to its unusually high proportion of '*durum*-type' grains.

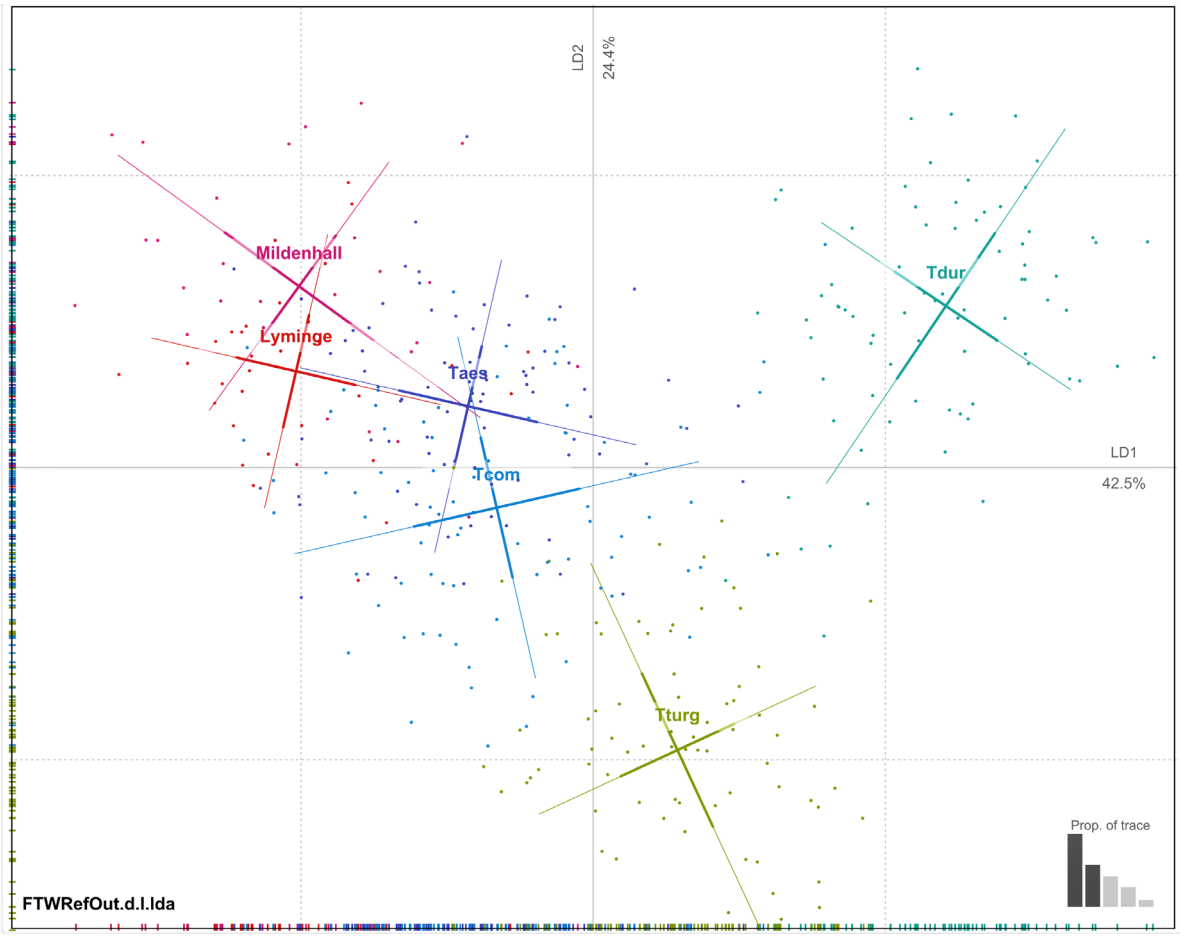

Fig. 6 LDA of sites where no grains were classified as rivet wheat (Mildenhall and Lyminge). 'Taes'= ssp. *aestivum*, 'Tcom'= ssp. *compactum*, 'Tturg'= ssp. *turgidum*, 'Tdur'= ssp. *durum*

Site	County	Grains analysed	Classified *turgidum*		Classified *aestivum*		Classified *compactum*		Classified *durum*	
Botolph Bridge	Peterborough	34	7	20.60%	10	29.40%	17	50.00%	0	0.00%
Coton Park	Warwickshire	30	1	3.30%	14	46.70%	15	50.00%	0	0.00%
Eckweek	Avon	26	9	34.60%	5	19.20%	9	34.60%	3	11.50%
Houghton	Cambridgeshire	58	40	69.00%	7	12.70%	8	13.80%	3	5.20%
Lyminge	Kent	31	0	0.00%	21	67.70%	10	32.30%	0	0.00%
Mildenhall	Suffolk	28	0	0.00%	13	46.40%	14	50.00%	1	3.60%
North Raunds/West Cotton	Northamptonshire	20	8	40.00%	7	35.00%	4	20.00%	1	5.00%
Pudding Lane	Hertfordshire	46	3	6.50%	26	56.50%	10	21.70%	7	15.20%
Sedgeford	Norfolk	40	0	0.00%	19	47.50%	11	27.50%	10	25.00%
Stafford	Staffordshire	86	14	16.30%	35	40.70%	31	36.00%	6	7.00%
Walsingham Way/West Fen Rd, Ely	Cambridgeshire	27	1	3.70%	15	55.60%	11	40.70%	0	0.00%
Wolverton Mill	Buckinghamshire	37	5	13.50%	21	56.80%	9	24.30%	2	5.40%
Total		**463**	**88**	**19.0%**	**193**	**41.7%**	**149**	**32.2%**	**33**	**7.1%**

Table 5 Results of LDA comparing archaeological grains with modern reference grains, summarised by site

3.3.4 Sites with Significant Proportions of Grains Classified as Rivet Wheat

A significant proportion of *turgidum*-type grains were identified at Houghton (Cambs), Stafford, Botolph Bridge (Peterborough), Eckweek (Avon) and North Raunds/West Cotton (Northants). A 'significant proportion' is defined here as >15% of grains, given that a margin of error of ~10–15% was anticipated based on the modern grain study. Stafford is borderline at 16.3%, with the other sites ranging from 20.6–69.0% (Table 5). Tetraploid rachis has been identified at all of these sites with the notable exception of Houghton (Table 6). Full data for the latter excavation are not yet published; however, within the six additional samples analysed for the FeedSax project, only hexaploid rachis remains were identified (McKerracher *et al*. forthcoming).

A particularly high proportion of grains (40/58) were classified as *turgidum* at Houghton (Table 6) from two samples dated to the late 10th–early 11th century (see Appendix A). Two distinct groupings can be seen in the archaeological grains when plotted, as corresponding to hexaploid ('Arch_Taes_com') and *turgidum* ('Arch_Tturg') forms, with just three grains classified as *durum* ('Arch_Tdur') at the border between *durum* and *turgidum* forms (Fig. 7).

3.3.5 Sites with Significant Proportions of Grains Classified as Durum Wheat

'Significant' proportions of grains (15.2–25.0%) were classified by the model as *durum* at Pudding Lane (Herts) and Sedgeford (Norfolk), prompting the question of whether durum wheat should be considered as a possible cultivar. At Pudding Lane the number of grains assigned as *durum* was quite small (Table 5) and when plotted did not exhibit a close association with modern durum wheat grains (Fig. 8), overall providing less than convincing evidence of cultivation

At Sedgeford, 25% of grains were classified as *durum*, but here again a close association with modern durum was not observed when plotted. The Sedgeford material was recovered from kiln structures containing a high percentage of grains exhibiting signs of germination, interpreted as evidence of malting (Caroe in press; in prep). Identification criteria for germination were created by experimentally 'steeping' bread wheat grains, which were then

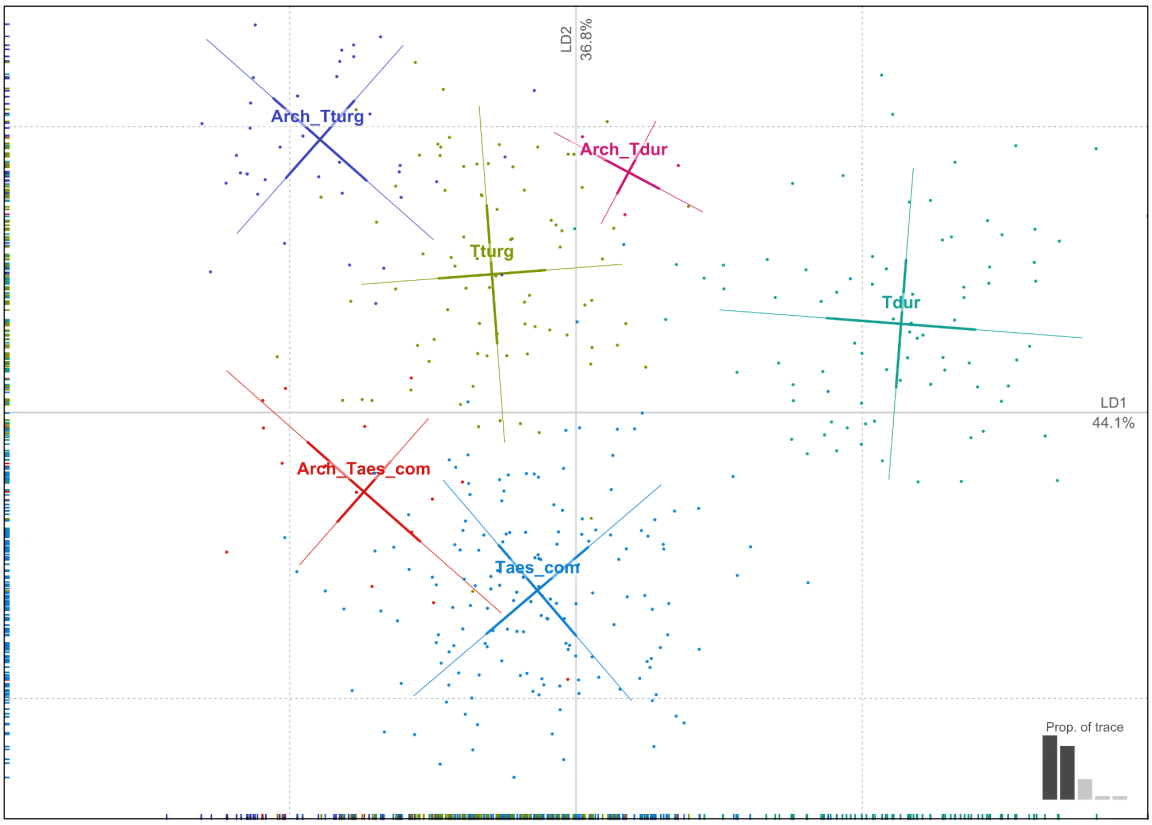

Fig. 7 LDA of FTW grains from Houghton compared with modern reference dataset. 'Taes_com' = ssp. *aestivum*/*compactum*, 'Tturg'= ssp. *turgidum*, 'Tdur'= ssp. *durum*, 'Arch_' =archaeological grains classified by the model

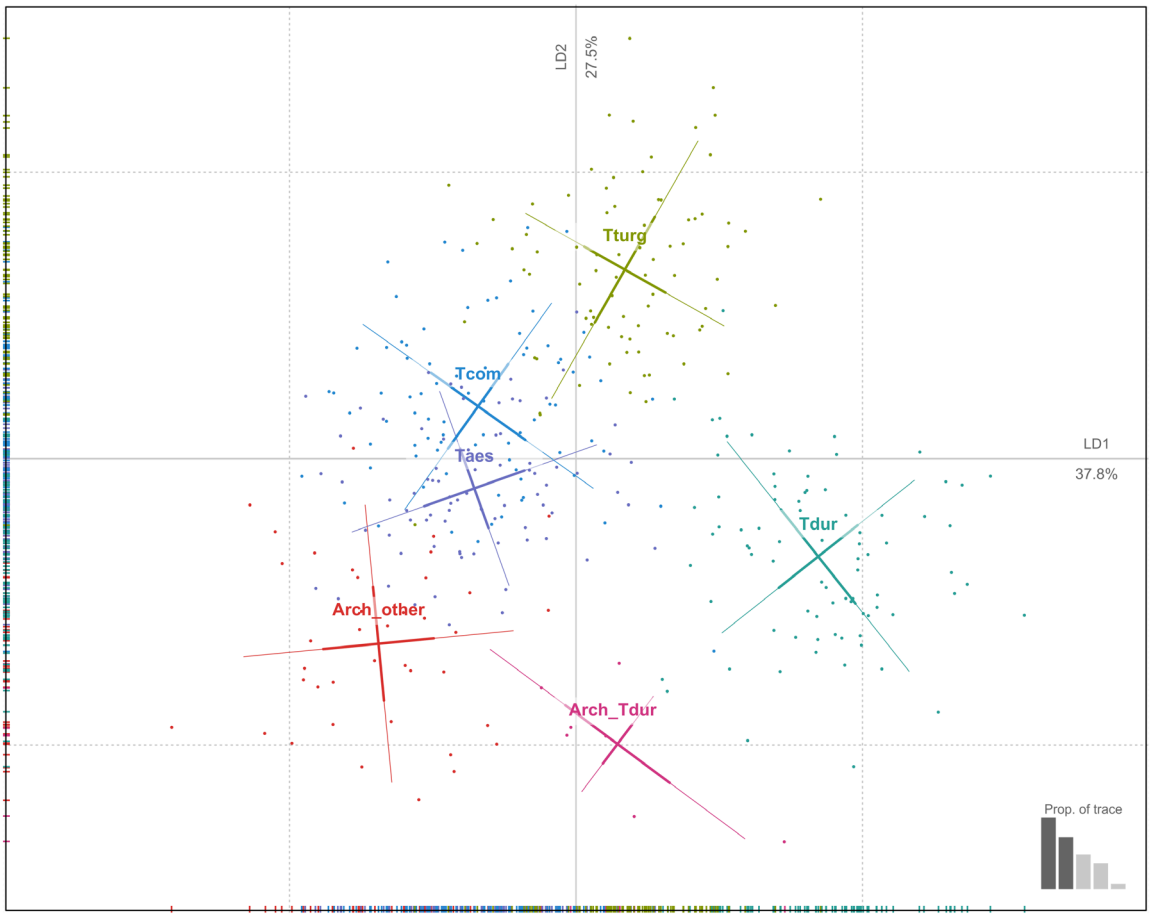

Fig. 8 LDA of FTW grains from Pudding Lane compared with modern reference dataset. 'Arch_Tdur'= archaeological grains classified by the model as *durum*, 'Arch_other'= all other archaeological grains from site 'Taes' = ssp. *aestivum*, 'Tcom'= ssp. *compactum*, 'Tturg'= ssp. *turgidum*, 'Tdur'= ssp. *durum*

	Classified *turgidum*	Of which pre-date the mid 9th century	Of which date to the mid 9th–mid 11th century	Of which may either pre- or post-date Conquest	Tetraploid Rachis present?	Pre-Conquest tetraploid rachis present?
Botolph Bridge	7/34	0	1	3	Y	Y
Coton Park	1/30	0	0	1	N	N
Eckweek	9/26	0	2	6	Y	Y
Houghton	40/58	0	40	0	?	?
Lyminge	0/31	0	0	0	Y	Y
Mildenhall	0/28	0	0	0	Y	Y
North Raunds/West Cotton	8/20	0	0	3	Y	Y
Pudding Lane	3/46	0	2	1	Y	Y
Sedgeford	0/40	0	0	0	N	N
Stafford	14/86	0	9	4	Y	N
Walsingham Way/West Fen Rd	1/27	0	0	1	Y	Y
Wolverton Mill	5/37	1	0	4	N	N
Total	88/463	1	54	23		

Table 6 Grains classified as *turgidum* (rivet) by LDA alongside presence/absence data of tetraploid rachis, summarised by site

dried and charred (Caroe in prep.). Twenty-four of these germinated grains were added to the modern reference dataset for comparison with the Sedgeford material. The resulting LDA classified 60% of the Sedgeford grains as 'germinated', showing a close association between the Sedgeford and modern 'steeped' grains when plotted (Fig. 9). While further investigation is needed, the results suggest that the morphology of the Sedgeford grains was affected by the malting process, and that this is detectable through GMM analysis. While 7/40 grains still classified as *durum* in the repeated analysis, and the crop cannot be ruled out, it is worth underlining that only hexaploid-type rachis remains have been observed at the site (H. Caroe pers. comm).

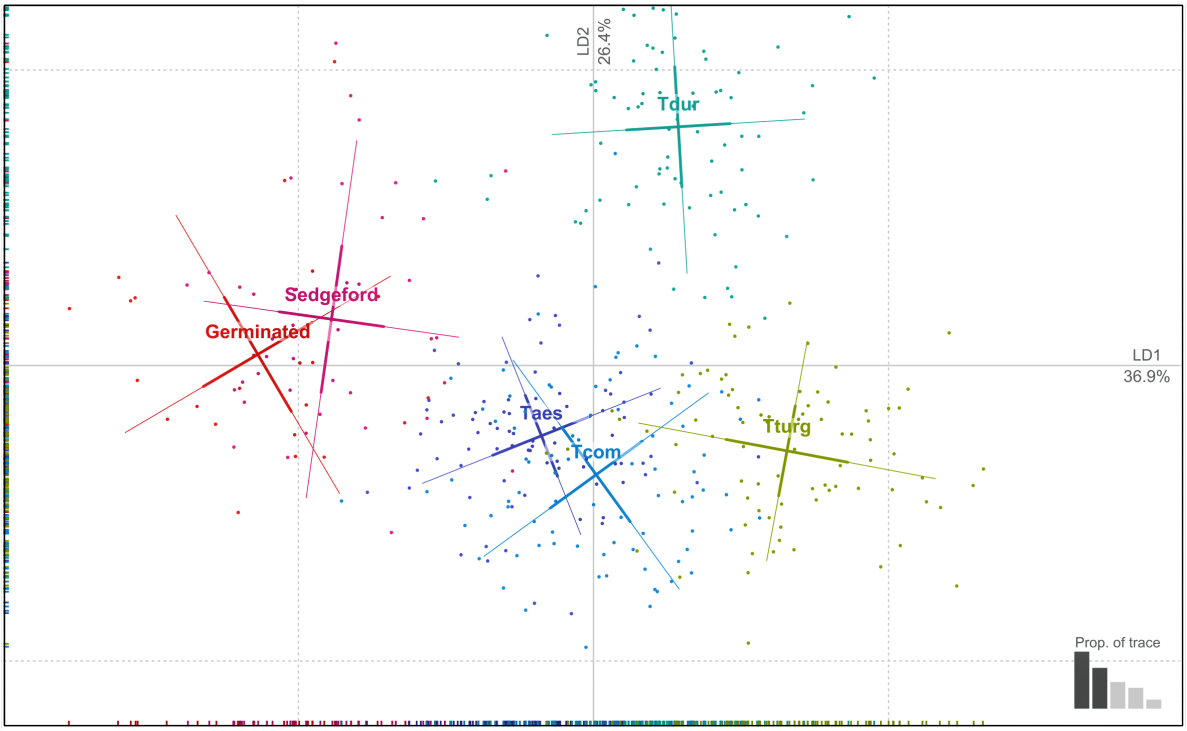

Fig. 9 LDA of FTW grains from Sedgeford compared with reference dataset and germinated grains. 'Taes' = ssp. *aestivum*, 'Tcom'= ssp. *compactum*, 'Tturg'= ssp. *turgidum*, 'Tdur'= ssp. *durum*, 'Germinated'= experimentally germinated ssp. *aestivum* grains

3.3.6 Overall Morphology

Comparison of average outlines for modern and archaeological grain classes demonstrates distinct morphological features according to (sub-)species (Fig. 10; Table 7). Some differences can be observed between the modern and archaeological classes, and this may to some extent be attributable to variable preservation conditions, especially charring temperature. It is possible that this has contributed to a less clear distinction between the

archaeological bread and club wheat-types than their modern counterparts e.g. as regards roundness of profile and indentation at the apex.

Turgidum- (or rivet-) type grains distinctly widen towards the apex in both the dorsal and lateral view, with pronounced dorsal curvature and strongly tapering embryo in the lateral view. When compared, there are observable morphological differences between the modern rivet varieties (Fig. 11). The grains of the 'improved' variety 'Rampton Rivet' are longer and narrower and least resemble the archaeological grains, while the traditional English variety 'Percival's Blue Cone', which widens towards a slightly blunted apex, is the most similar. Gene bank records for the latter accession give multiple regional synonyms including 'Blue Poll', 'Grey Poll', 'Ducksbill', 'Dugdale' and 'Dunover', noting this variety to have been 'widely cultivated in the 17th century' (https://www.seedstor.ac.uk/). These observations suggest that differences between modern and archaeological grains may relate not only to preservation, but also to modern crop developments and intra-species variation.

3.4 Discussion

3.4.1 Evidence for the cultivation of different forms of FTW

The results are in line with the understanding that hexaploid FTW was the prevalent wheat crop in the early medieval period. Within this group, a diversity in forms was observed corresponding with both modern bread and compact-eared club wheats. Once dubbed by Percival as 'the most ancient of wheats', there is currently limited knowledge of the historical cultivation of club wheats, and little surviving tradition in recent history outside the Pacific North-West and central Asia (Percival 1921). These findings raise the question of whether identification as bread wheat can be assumed, and highlight the need for further research.

Previous analysis has suggested that expanding modern reference datasets could elucidate the morphological distinction between bread and club wheats (Paper 2). This could allow us to clarify whether these findings truly indicate variation in hexaploid forms among archaeological wheats, or reflect limitations of the current model. It is noted that, due to limited availability of whole ears of club wheat, the accessions of *compactum* used in this

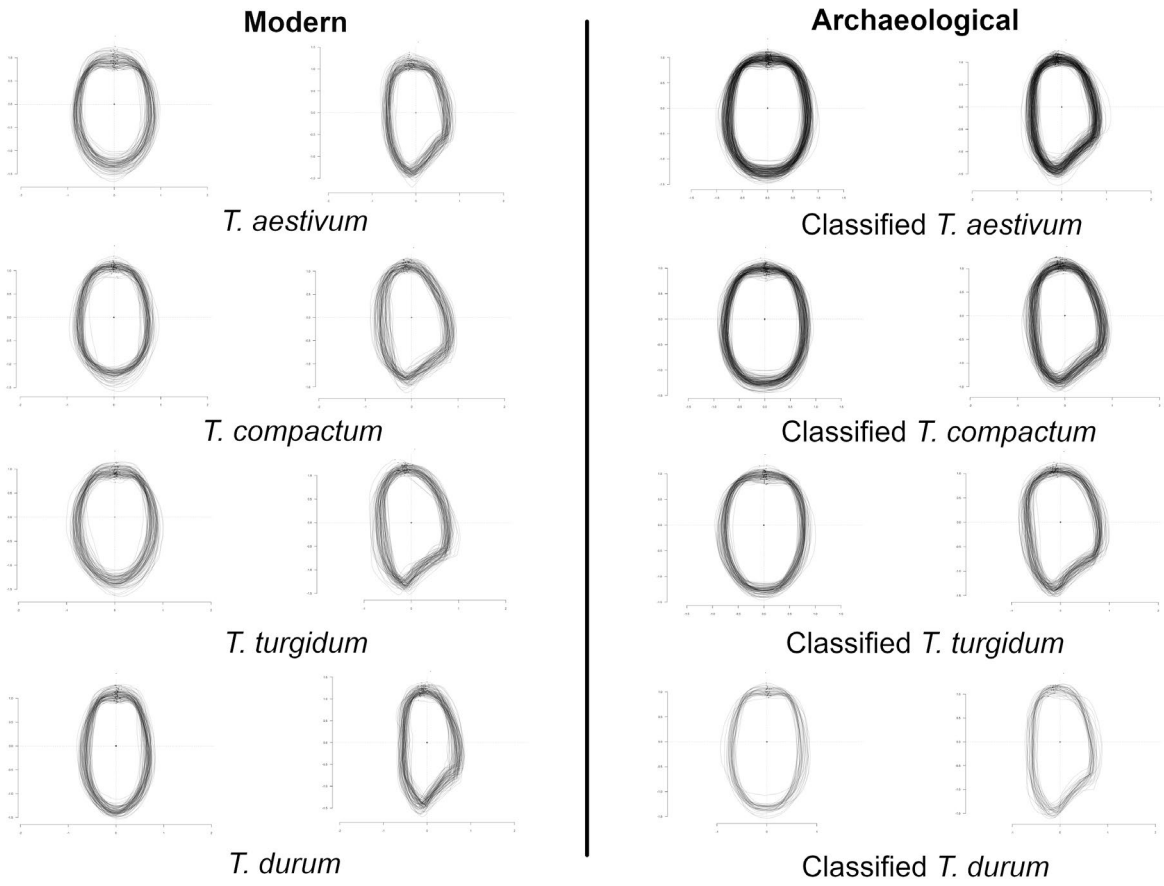

Fig. 10 Average outlines of different modern FTW (sub-)species compared with archaeological grains as classified by LDA

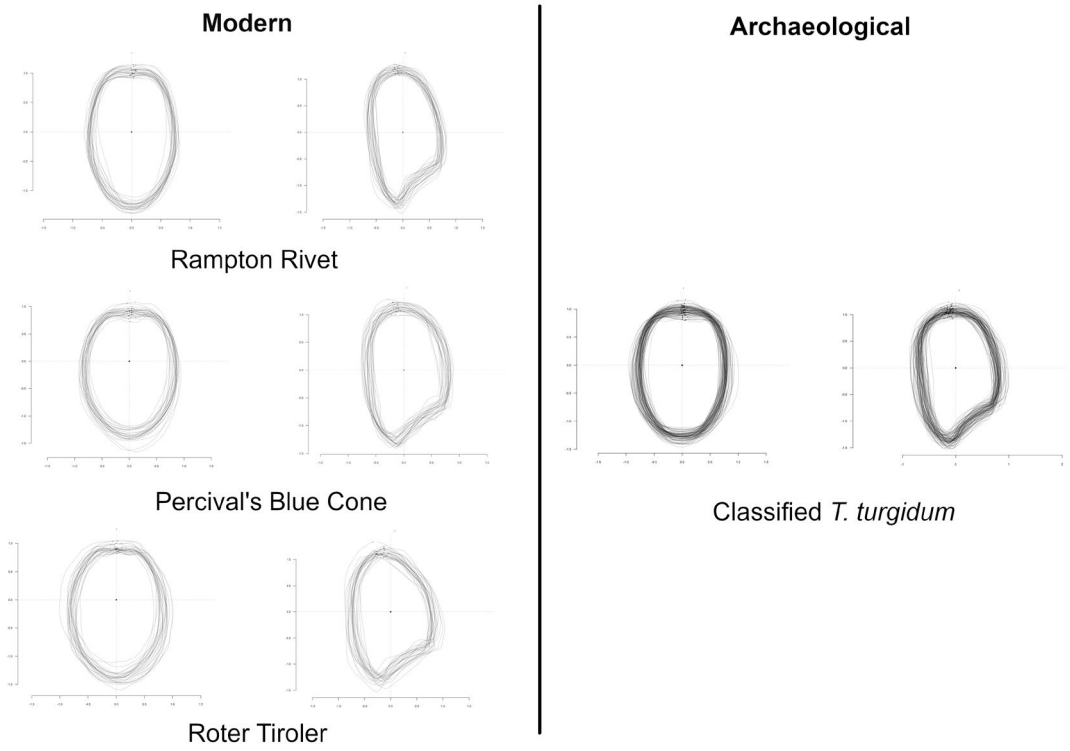

Fig. 11 Average outlines of different modern rivet accessions compared with archaeological grains classified as *turgidum* (rivet) by the model

Criteria	***aestivum***	***compactum***	***turgidum***	***durum***
Shape in dorsal and lateral view	Widest towards centre of grain	Widest just below centre of grain	Widening towards apex of grain	Widening towards centre of grain
Embryo shape and position	Tapering, extending relatively high into the grain	Less tapered, extending relatively lower into the grain	Strongly tapered	Strongly tapered, extending relatively lower into the grain
Ventral face	Gradual curvature, widening towards centre	Pronounced curvature, widening towards centre	Moderate curvature, widening towards apex	Slight curvature, widening below centre
Dorsal face	Gradual curvature, widening towards centre	Pronounced curvature, widening towards embryo	Pronounced curvature widening towards apex (‘humped’)	Gradual curvature, widening towards centre
Apex	Relatively blunt, indented (less clear in archaeological specimens)	Rounded, slightly narrowing in lateral view	Relatively blunt/flattened and wide in lateral view	Rounded, narrowing in lateral view
Proportions in lateral view	Relatively narrow in relation to length	Relatively wide in relation to length	Widest in relation to length	Clearly narrow in relation to length

Table 7 Identification criteria for bread, club, rivet and durum wheat grains

study lack examples deriving from Britain or (North-)Western Europe more generally (Table 1). Given the apparent significance of geographic origin in varietal comparisons of wheat grain form (Paper 2), comparable future studies would benefit from comparison with club wheat grains from more proximate geographic regions, if such examples can be sourced.

Analysis identified a significant minority of grains with characteristics analogous to modern rivet wheat at multiple sites. Soil mapping (LandIS), indicates that sites with significant proportions of *turgidum*- (or rivet-) type grains (Houghton, Eckweek, Raunds/West Cotton and Botolph Bridge) are situated on, or border, areas of free-draining soils potentially suited to rivet cultivation. Stafford, situated on floodplain soils, had a borderline proportion of *turgidum*-type grains, and as an urban settlement would likely have received grain stores from the surrounding countryside. Comparison of rivet wheat accessions further demonstrated greater morphological similarity between archaeological grains and the traditional 'Blue Cone' variety than with 'Rampton Rivet', an 'improved' form developed in the 1930s. This indicates the importance of carefully selecting accessions for comparison with archaeological material in terms of improvement status.

A number of grains identified as *turgidum*-type are associated with the pre-Conquest period, or derive from phases spanning the transition, adding to the growing evidence of a Late Anglo-Saxon introduction. The strongest evidence comes from the rural settlement of Houghton (Cambridgeshire), where late 10th- to early 11th-century samples noted to contain unusual 'rye-form' wheat grains (in reference to the rather blunt apex and strongly tapering embryo) were targeted. Similarly, at Stafford grains were described as 'bullet-shaped' and at Eckweek as 'hump-backed' (Moffett 1987; Carruthers 1995), and it would seem that rivet-like grains have frequently been noted by archaeobotanists, but have been difficult to classify systematically. Prioritisation of these samples is likely responsible for the high proportion of rivet-type grains observed at Houghton (69.0%), but the quantities nevertheless suggest the cultivation of a distinct crop.

Broader archaeobotanical analysis at Houghton may further support the cultivation of two wheat types. Isotopic evidence of a bimodal distribution in the $\delta^{15}N$ values of wheat grains

could be interpreted as indicating differential treatment of two cultivars (Hamerow *et al*. in prep.). This may also be suggested by correspondence analysis of sample compositional data, which suggested two potentially distinct wheat taxa, one associated with weeds of spring-sown fields and the other with autumn-sown weeds (*ibid.*). Given that rivet usually requires a long growing season, this would likely (although not necessarily) have been autumn-sown, while another wheat could have been sown in the spring. Cultivating two wheats with different-length growing seasons may have helped spread the workload of the harvest over a longer period within the context of a three-course rotation system (*ibid.*). Other motivations for cultivating rivet could include the production of long-straw for thatching, insurance against other crop failures and less tangible incentives such as regional connections, traditions or practices.

Recent research has highlighted long-lasting changes in agricultural practices beginning in the so-called 'long eighth century' (*c.* 680–830) (McKerracher 2018). These changes resulted in greater arable surpluses being produced, processed and stored. The mechanisms behind the intensification of cereal farming in early medieval England, and the rapid demographic and economic growth of the 8th–13th centuries, have been the focus of the FeedSax project (Hamerow in press). In this period we see a 'cellularization of the landscape' with settlement and agricultural activity fundamentally restructured around the spiritual authority of the parish church and its landowner patrons, including, in some regions, the communal farming of open fields (Ten Harkel *et al*. 2017).

The introduction of rivet wheat potentially falls within this substantial shift in practice, together with innovations such as systematic rotation and the introduction of the mouldboard plough. Strategic adaptation of a diversified range of cereal crops to local conditions appears to have been an important factor in increasing arable output in this period, with regional patterns in the composition of cereal assemblages broadly correlating with soil type (McKerracher 2016). Increasingly warm conditions towards the end of the 1st millennium AD, characterised as the 'Medieval Climate Anomaly', may also have benefitted rivet cultivation

by lengthening the growing season; although the precise timing and nature of this event are debated (Mann *et al*. 2009; Graham *et al*. 2011).

3.4.2 Assessment of the Methodology

The sites analysed happen to fall south of the line from Chester to Ipswich (Fig. 4), in the area defined by Moffett (2006) as being associated with tetraploid FTW finds. Because of the relatively limited availability of grains sufficiently well-preserved for GMM analysis, the sample of 463 grains is spread quite thinly by site and time period (Table 2; see also Appendix A). In some cases, we have arguably traded a relatively small number of rachis identifications for a similar number of grain identifications. At sites such as Mildenhall the results here are potentially less representative than the initial archaeobotanical analysis, as tetraploid wheats were identified among the rachis segments but not detected in the grains, most likely due to small sample size. That is to say, this type of GMM approach is not intended as a replacement for rapid analysis of large datasets by a skilled archaeobotanist.

However, GMM can target specific questions beyond what is possible by eye alone, including going beyond ploidy-level distinctions of rachis criteria. In this study, GMM strengthens evidence for the link between early medieval tetraploid wheat cultivation and rivet wheat and demonstrates predictable morphological differences between FTW cultivars under archaeological conditions. (Sub-)species-level differences between charred grains were correctly classified at above >86%, a little lower than the ~95% accuracy rate previously observed for charred glume wheat grains (Paper 1). Classification by accession (within (sub-)species) was also relatively high at 84.6%, suggesting sensitivity of the method to diversity at the varietal level. GMM further allows us to easily isolate identification criteria of morphological types by looking at numerous grains simultaneously (Table 7). These criteria can guide subsequent analysis and support previously-made archaeobotanical observations.

As a pilot study in the application of GMM to medieval wheat grains, the scope here is broad but the results demonstrate potential for targeted analysis of larger, well-preserved grain assemblages and/or for periods or areas of particular interest. For example, GMM could

offer additional insight into the Neolithic period, for which evidence of the cultivation of tetraploid wheats in Britain is just emerging (Carruthers 2019) and corresponding chaff remains are particularly rare. Questions remain as to the route or mechanism by which this crop-form was introduced in both the Neolithic and early medieval periods, and, if addressed, may shed light on past migrations, trade or other contacts between groups. Expansion of comparative databases of modern material with an emphasis on traditional varieties is likely to enhance the method, with the potential to analyse particularly well-preserved remains, such as grains from smoke-blackened thatch (Letts 1999), at the varietal level. While only preliminary, evidence from Sedgeford further suggests that there is potential for GMM to shed light on morphological changes arising from the germination of grains, as relating to storage conditions or malting.

Additionally, it is noted that many of the images used in this study were taken by the FeedSax team prior to grains being used for isotopic analysis. Successful utilisation of these images has highlighted the value of creating a high-quality photographic record when destructive analytical methods are used. These photographs have now been hosted in an open-access online archive in partnership with the Sustainable Digital Scholarship group (https://portal.sds.ox.ac.uk/feedsax), enhancing the potential for future analysis of the material.

3.5 Conclusion

GMM analysis was able to effectively distinguish between different (sub-)species of hexaploid and tetraploid FTW using grain outlines. It was possible to classify grains to a >86% level of accuracy after charring, by using the dorsal and lateral views. By comparing multiple grains simultaneously, it was possible to identify distinct characteristics between crop types which correspond with previous archaeobotanical descriptions of atypical grains. Distinction within the hexaploid group (bread/club wheat) was less clear when applied archaeologically, and is an area in which further research is likely to be worthwhile. Relatively high reclassification rates when comparing grains at the accession-level suggest

there is further potential for the method to analyse diversity in wheat forms at the varietal level, particularly if modern reference datasets are expanded.

Results demonstrated a close morphological relationship between grains from pre- and post-Conquest contexts and modern rivet at multiple sites; with the traditional variety 'Blue Cone' proving particularly similar to the archaeological '*turgidum*-type' grains. Findings strengthen the case for the introduction of rivet wheat in the Late Anglo-Saxon period, and highlight the importance of improvement status when selecting modern reference material. The strongest evidence for pre-Conquest cultivation of rivet came from Houghton (Cambs), where isotopic and weed ecology data support two distinct wheat crops being grown under different conditions/regimes. The introduction of rivet is in line with trends beginning in the 'long eighth century' of increased arable outputs and strategic cultivation of a broader range of crops adapted to local conditions.

While archaeological grains classified as *turgidum* (rivet) formed a significant minority of the dataset, the majority were classified as hexaploid *aestivum*/*compactum* (bread/club) wheats, in line with current understanding of medieval wheat agriculture. Results suggest variable morphology within the hexaploid group potentially relating to diversity in cultivars, while at Sedgeford atypical morphology may be attributable to malting of grains for brewing. As a pilot study in the application of GMM to medieval wheat grains, the scope of analysis was quite broad and, at some sites, was limited by numbers of well-preserved grains. With this acknowledged, the results are considered promising in terms of GMM's capability to refine identifications and open up our understanding of wheat diversity in past agricultural systems.

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Paper 3: Appendix A. Sample data for archaeological specimens

ID	Site	Sample	Context	Classified	Feature	FeedSax database phase
13009	Stafford St Mary's Grove	1929	1929	Tturg	Pit	FeedSax 3.3 (early C13) (1200 to 1220)
13015	Stafford St Mary's Grove	66/079	2102	Tturg	Quarry	FeedSax 3.1 (mid C11 - mid C12) (1060 to 1160)
13018	Stafford St Mary's Grove	66/079	2102	Tcom	Quarry	FeedSax 3.1 (mid C11 - mid C12) (1060 to 1160)
13021	Stafford St Mary's Grove	66/079	2102	Taes	Quarry	FeedSax 3.1 (mid C11 - mid C12) (1060 to 1160)
13024	Stafford St Mary's Grove	2134	2134	Tcom	Pit	FeedSax 2.2 (mid - late C10) (950 to 980)
13033	Stafford Bath St	1069B	1069B	Taes	Pit	1030-1160 (1030 to 1160)
13036	Stafford Bath St	1069B	1069B	Taes	Pit	1030-1160 (1030 to 1160)
13039	Stafford Bath St	1069B	1069B	Tcom	Pit	1030-1160 (1030 to 1160)
13045	Stafford Tipping Street	203	3201	Taes	Kiln	FeedSax 2.1 (mid C10) (925 to 950)
13048	Stafford Tipping Street	203	3201	Tcom	Kiln	FeedSax 2.1 (mid C10) (925 to 950)
13051	Stafford Tipping Street	203	3201	Tcom	Kiln	FeedSax 2.1 (mid C10) (925 to 950)
13054	Stafford Tipping Street	406	4319	Taes	Pit	FeedSax 2.1 (mid C10) (925 to 950)
13057	Stafford Tipping Street	406	4319	Tcom	Pit	FeedSax 2.1 (mid C10) (925 to 950)
13060	Stafford Tipping Street	406	4319	Taes	Pit	FeedSax 2.1 (mid C10) (925 to 950)
13063	Stafford Tipping Street	11	381	Taes	Pit	FeedSax 1.1 (late C9 - early C10) (875 to 920)
13066	Stafford Tipping Street	11	381	Taes	Pit	FeedSax 1.1 (late C9 - early C10) (875 to 920)
13069	Stafford Tipping Street	11	381	Taes	Pit	FeedSax 1.1 (late C9 - early C10) (875 to 920)
13072	Lyminge	44	LYM14 - 9395	Taes	Pit	11th-12th century (1030 to 1160)
13075	Lyminge	44	LYM14 - 9395	Taes	Pit	11th-12th century (1030 to 1160)
13078	Lyminge	44	LYM14 - 9395	Taes	Pit	11th-12th century (1030 to 1160)
13081	Lyminge	30	LYM14 - 9373	Taes	Pit	11th-12th century (1030 to 1160)
13084	Lyminge	30	LYM14 - 9373	Taes	Pit	11th-12th century (1030 to 1160)
13087	Lyminge	30	LYM14 - 9373	Tcom	Pit	11th-12th century (1030 to 1160)
13090	Lyminge	31	LYM14 - 9374	Taes	Pit	11th-12th century (1030 to 1160)
13093	Lyminge	31	LYM14 - 9374	Tcom	Pit	11th-12th century (1030 to 1160)
13096	Lyminge	31	LYM14 - 9374	Taes	Pit	11th-12th century (1030 to 1160)
13099	Lyminge	42	LYM14 - 9397	Tcom	Pit	Early 12th - early 13th (1120 to 1220)
13102	Lyminge	42	LYM14 - 9397	Taes	Pit	Early 12th - early 13th (1120 to 1220)
13108	Lyminge	5	LYM08 - 164	Taes	Pit	8th-9th century (780 to 880)
13111	Lyminge	5	LYM08 - 164	Taes	Pit	8th-9th century (780 to 880)

ID	Site	Sample	Context	Classified	Feature	FeedSax database phase
13117	Lyminge	24	LYM08 - 270	Taes	Pit	8th-9th century (780 to 880)
13120	Lyminge	24	LYM08 - 270	Tcom	Pit	8th-9th century (780 to 880)
13123	Lyminge	24	LYM08 - 270	Tcom	Pit	8th-9th century (780 to 880)
13126	Lyminge	30	LYM08 - 223	Tcom	Pit	8th-9th century (780 to 880)
13129	Lyminge	30	LYM08 - 223	Tcom	Pit	8th-9th century (780 to 880)
13132	Lyminge	30	LYM08 - 223	Tcom	Pit	8th-9th century (780 to 880)
13135	Lyminge	37	LYM12 - 3525	Taes	Pit	9th-10th century (880 to 980)
13138	Lyminge	38	LYM12 - 3535	Taes	Pit	9th-10th century (880 to 980)
13141	Lyminge	38	LYM12 - 3535	Taes	Pit	9th-10th century (880 to 980)
13144	Lyminge	38	LYM12 - 3535	Tcom	Pit	9th-10th century (880 to 980)
13147	Lyminge	42	LYM12 - 3641	Taes	Pit	9th-10th century (880 to 980)
13153	Lyminge	42	LYM12 - 3641	Taes	Pit	9th-10th century (880 to 980)
13156	Lyminge	20	LYM13 - 6594	Tcom	Ditch	11th-12th century (1030 to 1160)
13159	Lyminge	20	LYM13 - 6594	Taes	Ditch	11th-12th century (1030 to 1160)
13162	Lyminge	20	LYM13 - 6594	Taes	Ditch	11th-12th century (1030 to 1160)
13165	Lyminge	24	LYM13 - 6745	Taes	Ditch	11th-12th century (1030 to 1160)
13174	Lyminge	27	LYM13 - 6764	Taes	Ditch	11th-12th century (1030 to 1160)
13177	Lyminge	27	LYM13 - 6764	Taes	Ditch	11th-12th century (1030 to 1160)
13189	Botolph Bridge	156	4	Taes	Pit	FeedSax E5 (Period 2.2) (1160 to 1220)
13195	Botolph Bridge	79	Ditch 1	Tcom	Ditch	FeedSax D1-D3 (880 to 980)
13210	Raunds Burystead	596	BSP1	Tcom	"Pit (water hole)"	Late 9th to late 10th c. (880 to 980)
13213	Raunds Burystead	28	28	Taes	Quarry pit	FeedSax 4 (prev 12th century 1101-1200) (1030 to 1160)
13216	Raunds Burystead	28	28	Tturg	Quarry pit	FeedSax 4 (prev 12th century 1101-1200) (1030 to 1160)
13219	Raunds Burystead	28	28	Tcom	Quarry pit	FeedSax 4 (prev 12th century 1101-1200) (1030 to 1160)
13222	Raunds Furnells	2	2	Tturg	Layer	FeedSax 7 (Later medieval 1200-1400) (1220 to 1400)
13225	Raunds Furnells	2	2	Tturg	Layer	FeedSax 7 (Later medieval 1200-1400) (1220 to 1400)
13228	Raunds Furnells	2	2	Tturg	Layer	FeedSax 7 (Later medieval 1200-1400) (1220 to 1400)
13231	West Cotton	621	4039	Tturg	Oven	FeedSax 5 (prev Manor final phase 1200-1250) (1160 to
13234	West Cotton	621	4039	Taes	Oven	FeedSax 5 (prev Manor final phase 1200-1250) (1160 to
13237	West Cotton	621	4039	Tdur	Oven	FeedSax 5 (prev Manor final phase 1200-1250) (1160 to
13240	West Cotton	804	804	Tturg	Leat	FeedSax 4 (prev Final watermill 1100-1150) (1030 to 1160)
13243	West Cotton	1058	1058	Taes	Undefined	FeedSax 4 (prev Final watermill 1100-1150) (1030 to 1160)
13249	Houghton	7094	72320	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
13252	Houghton	7094	72320	Taes	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)

ID	Site	Sample	Context	Classified	Feature	FeedSax database phase
13255	Houghton	7094	72320	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
13258	Houghton	7225	72352	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
13261	Houghton	7225	72352	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
13264	Houghton	7225	72352	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
13267	Houghton	73098	763148	Taes	Pit	Mid Saxon (8th-9th c.) (780 to 880)
13270	Houghton	73098	763148	Tcom	Pit	Mid Saxon (8th-9th c.) (780 to 880)
13273	Houghton	73098	763148	Tcom	Pit	Mid Saxon (8th-9th c.) (780 to 880)
13354	Coton Park	1	489	Tcom	Undefined	FeedSax E1-E4 (1030 to 1160)
13357	Coton Park	1	489	Taes	Undefined	FeedSax E1-E4 (1030 to 1160)
13360	Coton Park	5	782	Taes	Undefined	FeedSax E1-E4 (1030 to 1160)
13363	Coton Park	35	1625	Tcom	Undefined	FeedSax E5-F1 (1160 to 1260)
13366	Coton Park	35	1625	Taes	Undefined	FeedSax E5-F1 (1160 to 1260)
13369	Coton Park	36	1703	Taes	Undefined	FeedSax E1-E4 (1030 to 1160)
13372	Coton Park	36	1703	Tcom	Undefined	FeedSax E1-E4 (1030 to 1160)
13375	Coton Park	40	2257	Tcom	Undefined	FeedSax E1-E4 (1030 to 1160)
13381	Coton Park	41	2329	Tcom	Undefined	FeedSax E1-E4 (1030 to 1160)
13387	Coton Park	50	4096	Tcom	Undefined	FeedSax E1-E4 (1030 to 1160)
13390	Coton Park	50	4096	Tcom	Undefined	FeedSax E1-E4 (1030 to 1160)
13393	Mildenhall	2013	2084	Tcom	Pit	FeedSax C3-C4 (780 to 880)
13402	Mildenhall	2013	2084	Tdur	Pit	FeedSax C3-C4 (780 to 880)
13405	Mildenhall	2013	2084	Tcom	Pit	FeedSax C3-C4 (780 to 880)
13408	Mildenhall	3044	3943	Tcom	Ditch	FeedSax D1-D3 (880 to 980)
13411	Mildenhall	3044	3943	Taes	Ditch	FeedSax D1-D3 (880 to 980)
13414	Mildenhall	3044	3943	Tcom	Ditch	FeedSax D1-D3 (880 to 980)
13417	Mildenhall	2005	2027	Tcom	Pit	FeedSax C3-C4 (780 to 880)
13420	Mildenhall	2005	2027	Tcom	Pit	FeedSax C3-C4 (780 to 880)
13423	Mildenhall	2009	2064	Taes	Pit	FeedSax D1-D3 (880 to 980)
13426	Mildenhall	2009	2064	Taes	Pit	FeedSax D1-D3 (880 to 980)
13429	Mildenhall	2009	2064	Taes	Pit	FeedSax D1-D3 (880 to 980)
13432	Mildenhall	2016	2091	Taes	Pit	FeedSax C3-C4 (780 to 880)
13435	Mildenhall	2016	2091	Tcom	Pit	FeedSax C3-C4 (780 to 880)
13438	Mildenhall	2016	2091	Taes	Pit	FeedSax C3-C4 (780 to 880)
13441	Mildenhall	2011	2071	Taes	Pit	FeedSax C3-C4 (780 to 880)
13444	Mildenhall	2011	2071	Tcom	Pit	FeedSax C3-C4 (780 to 880)

ID	Site	Sample	Context	Classified	Feature	FeedSax database phase
13447	Mildenhall	2011	2071	Taes	Pit	FeedSax C3-C4 (780 to 880)
13450	Mildenhall	2008	2034	Tcom	Pit	FeedSax C3-C4 (780 to 880)
13453	Mildenhall	2008	2034	Taes	Pit	FeedSax C3-C4 (780 to 880)
13456	Mildenhall	2025	2055	Taes	Peat layer	FeedSax D3-D4 (950 to 1030)
13459	Mildenhall	2025	2055	Taes	Peat layer	FeedSax D3-D4 (950 to 1030)
13462	Mildenhall	2025	2055	Taes	Peat layer	FeedSax D3-D4 (950 to 1030)
13465	Mildenhall	2026	2050	Tcom	Peat layer	FeedSax D1-D2 (880 to 950)
13468	Mildenhall	2026	2050	Tcom	Peat layer	FeedSax D1-D2 (880 to 950)
13471	Mildenhall	2026	2050	Taes	Peat layer	FeedSax D1-D2 (880 to 950)
13474	Mildenhall	2045	2115	Tcom	Peat layer	FeedSax C3-C4 (780 to 880)
13477	Mildenhall	2045	2115	Tcom	Peat layer	FeedSax C3-C4 (780 to 880)
13480	Mildenhall	2017	2092	Tcom	Pit	FeedSax C3-C4 (780 to 880)
13483	Botolph Bridge	156	Pit 4	Tcom	Pit	FeedSax E5 (Period 2.2) (1160 to 1220)
13485	Botolph Bridge	193	Ditch 3	Tturg	Ditch	FeedSax E1-E4 (1030 to 1160)
13487	Botolph Bridge	193	Ditch 3	Tturg	Ditch	FeedSax E1-E4 (1030 to 1160)
13489	Botolph Bridge	194	Ditch 3	Taes	Ditch	FeedSax E1-E4 (1030 to 1160)
13491	Botolph Bridge	194	Ditch 3	Tcom	Ditch	FeedSax E1-E4 (1030 to 1160)
13493	Botolph Bridge	96	Ditch 8	Taes	Ditch	FeedSax E3-E4 (1080 to 1160)
13495	Botolph Bridge	97	Ditch 8	Tcom	Ditch	FeedSax E3-E4 (1080 to 1160)
13497	Botolph Bridge	18	Ditch 26	Tturg	Ditch	FeedSax F2-G2 (Period 3.2) (1270 to 1400)
13499	Botolph Bridge	18	Ditch 26	Taes	Ditch	FeedSax F2-G2 (Period 3.2) (1270 to 1400)
13501	Botolph Bridge	18	Ditch 26	Taes	Ditch	FeedSax F2-G2 (Period 3.2) (1270 to 1400)
13503	Botolph Bridge	74	Ditch 27	Tcom	Ditch	FeedSax E5 (Period 2.2) (1160 to 1220)
13505	Botolph Bridge	74	Ditch 27	Tturg	Ditch	FeedSax E5 (Period 2.2) (1160 to 1220)
13507	Botolph Bridge	78	Ditch 27	Taes	Ditch	FeedSax E5 (Period 2.2) (1160 to 1220)
13509	Botolph Bridge	59	Ditch 48	Tcom	Ditch	FeedSax E5 (Period 2.2) (1160 to 1220)
13511	Botolph Bridge	23	Ditch 68	Tturg	Ditch	FeedSax E (1030 to 1220)
13513	Botolph Bridge	23	Ditch 68	Tcom	Ditch	FeedSax E (1030 to 1220)
13515	Botolph Bridge	23	Ditch 68	Tcom	Ditch	FeedSax E (1030 to 1220)
13517	Botolph Bridge	229	Pit 27	Tcom	Pit	FeedSax F1 (Period 3.1) (1200 to 1250)
13519	Botolph Bridge	49	Ditch 29	Tcom	Ditch	FeedSax E1-E4 (1030 to 1160)
13521	Botolph Bridge	49	Ditch 29	Tcom	Ditch	FeedSax E1-E4 (1030 to 1160)
13523	Botolph Bridge	49	Ditch 29	Taes	Ditch	FeedSax E1-E4 (1030 to 1160)
13525	Coton Park	41	2329	Tcom	Undefined	FeedSax E1-E4 (1030 to 1160)

ID	Site	Sample	Context	Classified	Feature	FeedSax database phase
13527	Botolph Bridge	59	Ditch 48	Taes	Ditch	FeedSax E5 (Period 2.2) (1160 to 1220)
13529	Botolph Bridge	79	Ditch 1	Tturg	Ditch	FeedSax D1-D3 (880 to 980)
13531	Botolph Bridge	79	Ditch 1	Tcom	Ditch	FeedSax D1-D3 (880 to 980)
13535	Botolph Bridge	78	Ditch 27	Tturg	Ditch	FeedSax E5 (Period 2.2) (1160 to 1220)
14000	Botolph Bridge	97	Ditch 8	Tcom	Ditch	FeedSax E3-E4 (1080 to 1160)
14002	Botolph Bridge	97	Ditch 8	Tcom	Ditch	FeedSax E3-E4 (1080 to 1160)
14004	Botolph Bridge	97	Ditch 8	Tcom	Ditch	FeedSax E3-E4 (1080 to 1160)
14006	Botolph Bridge	18	Ditch 26	Taes	Ditch	FeedSax F2-G2 (Period 3.2) (1270 to 1400)
14008	Botolph Bridge	36	Pit 42	Taes	Pit	FeedSax F1 (Period 3.1) (1200 to 1250)
14010	Botolph Bridge	145	Ditch 42	Tcom	Ditch	FeedSax D4-E1 (980 to 1060)
14012	Botolph Bridge	145	Ditch 42	Tcom	Ditch	FeedSax D4-E1 (980 to 1060)
14014	Houghton	7094	72320	Tcom	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14016	Houghton	7094	72320	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14018	Houghton	7094	72320	Tdur	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14020	Houghton	7094	72320	Tcom	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14022	Houghton	7094	72320	Tcom	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14024	Houghton	7094	72320	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14026	Houghton	7094	72320	Tdur	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14028	Houghton	7094	72320	Tcom	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14030	Houghton	7094	72320	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14032	Houghton	7094	72320	Tcom	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14034	Houghton	7094	72320	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14036	Houghton	7094	72320	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14038	Houghton	7094	72320	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14040	Houghton	7094	72320	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14042	Houghton	7094	72320	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14044	Houghton	7094	72320	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14046	Houghton	7094	72320	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14048	Houghton	7094	72320	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14050	Houghton	7094	72320	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14052	Houghton	7094	72320	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14054	Houghton	7094	72320	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14056	Houghton	7094	72320	Taes	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14058	Houghton	7094	72320	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)

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14060	Houghton	7094	72320	Taes	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14062	Houghton	7094	72320	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14066	Houghton	7225	72352	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14068	Houghton	7225	72352	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14070	Houghton	7225	72352	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14072	Houghton	7225	72352	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14074	Houghton	7225	72352	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14076	Houghton	7225	72352	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14078	Houghton	7225	72352	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14080	Houghton	7225	72352	Taes	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14082	Houghton	7225	72352	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14084	Houghton	7225	72352	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14086	Houghton	7225	72352	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14088	Houghton	7225	72352	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14090	Houghton	7225	72352	Taes	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14092	Houghton	7225	72352	Tcom	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14094	Houghton	7225	72352	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14098	Houghton	7225	72352	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14100	Houghton	7225	72352	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14102	Houghton	7225	72352	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14104	Houghton	7225	72352	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14106	Houghton	7225	72352	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14108	Houghton	7225	72352	Tdur	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14110	Houghton	7225	72352	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14112	Houghton	7225	72352	Taes	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14114	Houghton	7225	72352	Tturg	Posthole	Late Saxon (10th-early 11th c.) (980 to 1030)
14120	West Cotton	45	114	Taes	Ditch	FeedSax 4 (prev Medieval 1100-1250) (1030 to 1150)
14122	West Cotton	45	114	Taes	Ditch	FeedSax 4 (prev Medieval 1100-1250) (1030 to 1150)
14124	West Cotton	615	4039	Taes	Oven	FeedSax 5 (prev Manor final phase 1200-1250) (1160 to
14126	West Cotton	58	50,58	Tcom	Layer	FeedSax 4 (prev Medieval 1100-1250) (1030 to 1150)
14128	Raunds Furnells	2	2	Tturg	Layer	FeedSax 7 (Later medieval 1200-1400) (1220 to 1400)
14130	Raunds Furnells	2	2	Tcom	Layer	FeedSax 7 (Later medieval 1200-1400) (1220 to 1400)
14132	Raunds Furnells	2	2	Tturg	Layer	FeedSax 7 (Later medieval 1200-1400) (1220 to 1400)
14134	Eckweek	2539	359	Tturg	Pit	3 (late 11th century) (1030 to 1160)

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14136	Eckweek	2539	359	Tcom	Pit	3 (late 11th century) (1030 to 1160)
14138	Eckweek	2539	359	Tcom	Pit	3 (late 11th century) (1030 to 1160)
14140	Eckweek	2539	359	Tcom	Pit	3 (late 11th century) (1030 to 1160)
14142	Eckweek	2539	359	Tturg	Pit	3 (late 11th century) (1030 to 1160)
14144	Eckweek	2539	359	Taes	Pit	3 (late 11th century) (1030 to 1160)
14148	Eckweek	2539	359	Tcom	Pit	3 (late 11th century) (1030 to 1160)
14150	Eckweek	2539	359	Tdur	Pit	3 (late 11th century) (1030 to 1160)
14152	Eckweek	2539	359	Tcom	Pit	3 (late 11th century) (1030 to 1160)
14154	Eckweek	2539	359	Tcom	Pit	3 (late 11th century) (1030 to 1160)
14156	Eckweek	2539	359	Tturg	Pit	3 (late 11th century) (1030 to 1160)
14158	Eckweek	2539	359	Tdur	Pit	3 (late 11th century) (1030 to 1160)
14160	Eckweek	2539	359	Tturg	Pit	3 (late 11th century) (1030 to 1160)
14162	Eckweek	2539	359	Taes	Pit	3 (late 11th century) (1030 to 1160)
14164	Eckweek	2539	359	Tturg	Pit	3 (late 11th century) (1030 to 1160)
14166	Eckweek	2539	359	Tcom	Pit	3 (late 11th century) (1030 to 1160)
14168	Eckweek	2539	359	Tturg	Pit	3 (late 11th century) (1030 to 1160)
14170	Eckweek	2539	359	Taes	Pit	3 (late 11th century) (1030 to 1160)
14172	Eckweek	2539	359	Taes	Pit	3 (late 11th century) (1030 to 1160)
14176	Eckweek	2556	3062	Tturg	Undefined	2 (early 11th century) (1000 to 1030)
14178	Eckweek	2511	170	Tcom	Undefined	4 (12th-13th century) (1160 to 1220)
14180	Eckweek	2511	170	Taes	Undefined	4 (12th-13th century) (1160 to 1220)
14182	Eckweek	2511	170	Tdur	Undefined	4 (12th-13th century) (1160 to 1220)
14184	Eckweek	2511	170	Tturg	Undefined	4 (12th-13th century) (1160 to 1220)
14186	Eckweek	2552	207	Tturg	Undefined	2 (early 11th century) (1000 to 1030)
14188	Eckweek	2548	291	Tcom	Undefined	3 (late 11th century) (1030 to 1160)
14264	Stafford Bath St	1069B	1069B	Taes	Pit	1030-1160 (1030 to 1160)
14266	Stafford Bath St	1069B	1069B	Taes	Pit	1030-1160 (1030 to 1160)
14268	Stafford Tipping Street	11	381	Taes	Pit	FeedSax 1.1 (late C9 - early C10) (875 to 920)
14270	Stafford Tipping Street	11	381	Tcom	Pit	FeedSax 1.1 (late C9 - early C10) (875 to 920)
14272	Stafford Tipping Street	11	381	Taes	Pit	FeedSax 1.1 (late C9 - early C10) (875 to 920)
14274	Stafford Tipping Street	11	381	Tturg	Pit	FeedSax 1.1 (late C9 - early C10) (875 to 920)
14276	Stafford Tipping Street	11	381	Taes	Pit	FeedSax 1.1 (late C9 - early C10) (875 to 920)
14282	Stafford Tipping Street	406	4319	Taes	Pit	FeedSax 2.1 (mid C10) (925 to 950)
14284	Stafford Tipping Street	406	4319	Taes	Pit	FeedSax 2.1 (mid C10) (925 to 950)

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14286	Stafford Tipping Street	406	4319	Tcom	Pit	FeedSax 2.1 (mid C10) (925 to 950)
14288	Stafford Tipping Street	406	4319	Tcom	Pit	FeedSax 2.1 (mid C10) (925 to 950)
14292	Stafford Tipping Street	406	4319	Tturg	Pit	FeedSax 2.1 (mid C10) (925 to 950)
14294	Stafford Tipping Street	406	4319	Tturg	Pit	FeedSax 2.1 (mid C10) (925 to 950)
14300	Stafford Tipping Street	406	4319	Tturg	Pit	FeedSax 2.1 (mid C10) (925 to 950)
14304	Stafford Tipping Street	406	4319	Taes	Pit	FeedSax 2.1 (mid C10) (925 to 950)
14310	Stafford Tipping Street	205	3203	Tdur	Stoke pit	FeedSax 1.1 (late C9 - early C10) (875 to 920)
14312	Stafford Tipping Street	205	3203	Taes	Stoke pit	FeedSax 1.1 (late C9 - early C10) (875 to 920)
14314	Stafford Tipping Street	205	3203	Tdur	Stoke pit	FeedSax 1.1 (late C9 - early C10) (875 to 920)
14320	Stafford Tipping Street	205	3203	Tturg	Stoke pit	FeedSax 1.1 (late C9 - early C10) (875 to 920)
14322	Stafford Tipping Street	205	3203	Tcom	Stoke pit	FeedSax 1.1 (late C9 - early C10) (875 to 920)
14326	Stafford Tipping Street	205	3203	Taes	Stoke pit	FeedSax 1.1 (late C9 - early C10) (875 to 920)
14330	Stafford Tipping Street	205	3203	Tcom	Stoke pit	FeedSax 1.1 (late C9 - early C10) (875 to 920)
14334	Stafford Tipping Street	205	3203	Taes	Stoke pit	FeedSax 1.1 (late C9 - early C10) (875 to 920)
14336	Stafford Tipping Street	205	3203	Tcom	Stoke pit	FeedSax 1.1 (late C9 - early C10) (875 to 920)
14338	Stafford Tipping Street	203	3201	Taes	Kiln	FeedSax 2.1 (mid C10) (925 to 950)
14340	Stafford Tipping Street	203	3201	Taes	Kiln	FeedSax 2.1 (mid C10) (925 to 950)
14342	Stafford Tipping Street	203	3201	Taes	Kiln	FeedSax 2.1 (mid C10) (925 to 950)
14344	Stafford Tipping Street	203	3201	Tcom	Kiln	FeedSax 2.1 (mid C10) (925 to 950)
14346	Stafford Tipping Street	204	3205	Taes	Demolition layer of kiln 3408	FeedSax 1.1 (late C9 - early C10) (875 to 920)
14348	Stafford Tipping Street	204	3205	Tcom	Demolition layer of kiln 3408	FeedSax 1.1 (late C9 - early C10) (875 to 920)
14350	Stafford Tipping Street	204	3205	Tturg	Demolition layer of kiln 3408	FeedSax 1.1 (late C9 - early C10) (875 to 920)
14352	Stafford Tipping Street	204	3205	Tturg	Demolition layer of kiln 3408	FeedSax 1.1 (late C9 - early C10) (875 to 920)
14354	Stafford Tipping Street	204	3205	Taes	Demolition layer of kiln 3408	FeedSax 1.1 (late C9 - early C10) (875 to 920)
14356	Stafford Tipping Street	204	3205	Tcom	Demolition layer of kiln 3408	FeedSax 1.1 (late C9 - early C10) (875 to 920)
14358	Stafford Tipping Street	204	3205	Tcom	Demolition layer of kiln 3408	FeedSax 1.1 (late C9 - early C10) (875 to 920)
14360	Stafford Tipping Street	204	3205	Taes	Demolition layer of kiln 3408	FeedSax 1.1 (late C9 - early C10) (875 to 920)
14362	Stafford Tipping Street	405	4306	Tturg	Kiln	FeedSax 2.1 (mid C10) (925 to 950)
14364	Stafford Tipping Street	405	4306	Taes	Kiln	FeedSax 2.1 (mid C10) (925 to 950)
14366	Stafford St Mary's Grove	2134	2134	Taes	Pit	FeedSax 2.2 (mid - late C10) (950 to 980)
14368	Stafford St Mary's Grove	2134	2134	Tturg	Pit	FeedSax 2.2 (mid - late C10) (950 to 980)
14370	Stafford St Mary's Grove	2134	2134	Tcom	Pit	FeedSax 2.2 (mid - late C10) (950 to 980)
14372	Stafford St Mary's Grove	2134	2134	Tdur	Pit	FeedSax 2.2 (mid - late C10) (950 to 980)
14374	Stafford St Mary's Grove	66/077	2102	Tturg	Quarry	FeedSax 3.1 (mid C11 - mid C12) (1060 to 1160)

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14376	Stafford St Mary's Grove	66/077	2102	Taes	Quarry	FeedSax 3.1 (mid C11 - mid C12) (1060 to 1160)
14378	Stafford St Mary's Grove	66/077	2102	Tcom	Quarry	FeedSax 3.1 (mid C11 - mid C12) (1060 to 1160)
14382	Stafford St Mary's Grove	1988	1988	Tdur	Sunken-featured building	FeedSax 3.1 (mid C11 - mid C12) (1060 to 1160)
14384	Stafford St Mary's Grove	1988	1988	Tcom	Sunken-featured building	FeedSax 3.1 (mid C11 - mid C12) (1060 to 1160)
14386	Stafford St Mary's Grove	1988	1988	Tcom	Sunken-featured building	FeedSax 3.1 (mid C11 - mid C12) (1060 to 1160)
14390	Stafford St Mary's Grove	1988	1988	Tcom	Sunken-featured building	FeedSax 3.1 (mid C11 - mid C12) (1060 to 1160)
14392	Stafford St Mary's Grove	2178	2178	Tdur	Pit	FeedSax 3.2 (early C12 - mid C12) (1120 to 1150)
14394	Stafford St Mary's Grove	2178	2178	Tcom	Pit	FeedSax 3.2 (early C12 - mid C12) (1120 to 1150)
14396	Stafford St Mary's Grove	2178	2178	Tcom	Pit	FeedSax 3.2 (early C12 - mid C12) (1120 to 1150)
14398	Stafford St Mary's Grove	69/078	2102	Tcom	Quarry	FeedSax 3.1 (mid C11 - mid C12) (1060 to 1160)
14400	Stafford St Mary's Grove	2223	2223	Taes	Oven	FeedSax 2.3 (late C10 - mid C11) (980 to 1060)
14402	Stafford St Mary's Grove	66/079	2102	Tcom	Quarry	FeedSax 3.1 (mid C11 - mid C12) (1060 to 1160)
14404	Stafford St Mary's Grove	66/079	2102	Tcom	Quarry	FeedSax 3.1 (mid C11 - mid C12) (1060 to 1160)
14406	Stafford St Mary's Grove	66/079	2102	Tturg	Quarry	FeedSax 3.1 (mid C11 - mid C12) (1060 to 1160)
14408	Stafford St Mary's Grove	66/079	2102	Tturg	Quarry	FeedSax 3.1 (mid C11 - mid C12) (1060 to 1160)
14410	Stafford St Mary's Grove	66/079	2102	Taes	Quarry	FeedSax 3.1 (mid C11 - mid C12) (1060 to 1160)
14412	Stafford St Mary's Grove	1682	1682	Tcom	Oven	FeedSax 2.2 (mid - late C10) (950 to 980)
14414	Stafford St Mary's Grove	1682	1682	Taes	Oven	FeedSax 2.2 (mid - late C10) (950 to 980)
14416	Stafford St Mary's Grove	1682	1682	Taes	Oven	FeedSax 2.2 (mid - late C10) (950 to 980)
14418	Stafford St Mary's Grove	1682	1682	Tcom	Oven	FeedSax 2.2 (mid - late C10) (950 to 980)
14420	Stafford St Mary's Grove	1682	1682	Tcom	Oven	FeedSax 2.2 (mid - late C10) (950 to 980)
14422	Stafford St Mary's Grove	1682	1682	Taes	Oven	FeedSax 2.2 (mid - late C10) (950 to 980)
14424	Stafford St Mary's Grove	1682	1682	Taes	Oven	FeedSax 2.2 (mid - late C10) (950 to 980)
14426	Stafford St Mary's Grove	1682	1682	Tcom	Oven	FeedSax 2.2 (mid - late C10) (950 to 980)
14428	Stafford St Mary's Grove	1682	1682	Tdur	Oven	FeedSax 2.2 (mid - late C10) (950 to 980)
14430	Stafford St Mary's Grove	1682	1682	Tcom	Oven	FeedSax 2.2 (mid - late C10) (950 to 980)
14456	Wolverton Mill	91	14	Taes	Posthole	Late Saxon/Saxo-Norman (900 to 1100)
14458	Wolverton Mill	91	14	Tcom	Posthole	Late Saxon/Saxo-Norman (900 to 1100)
14460	Wolverton Mill	91	14	Tturg	Posthole	Late Saxon/Saxo-Norman (900 to 1100)
14462	Wolverton Mill	101	855	Tdur	Cess pit	Late Saxon/Saxo-Norman (900 to 1100)
14464	Wolverton Mill	77	215	Taes	Posthole	Late Saxon/Saxo-Norman (900 to 1100)
14466	Wolverton Mill	52	651	Taes	Ditch	Late Saxon/Saxo-Norman (900 to 1100)
14470	Wolverton Mill	88	487	Taes	Posthole	Late Saxon/Saxo-Norman (900 to 1100)
14472	Wolverton Mill	88	487	Taes	Posthole	Late Saxon/Saxo-Norman (900 to 1100)

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14474	Wolverton Mill	88	487	Taes	Posthole	Late Saxon/Saxo-Norman (900 to 1100)
14476	Wolverton Mill	88	487	Tcom	Posthole	Late Saxon/Saxo-Norman (900 to 1100)
14478	Wolverton Mill	94	136	Taes	Posthole	Late Saxon/Saxo-Norman (900 to 1100)
14480	Wolverton Mill	94	136	Tdur	Posthole	Late Saxon/Saxo-Norman (900 to 1100)
14482	Wolverton Mill	10	374	Tturg	Pit	Late Saxon/Saxo-Norman (900 to 1100)
14484	Wolverton Mill	78	225	Taes	Posthole	Late Saxon/Saxo-Norman (900 to 1100)
14486	Wolverton Mill	100	458	Taes	Gully	Late Saxon/Saxo-Norman (900 to 1100)
14488	Wolverton Mill	78	225	Taes	Posthole	Late Saxon/Saxo-Norman (900 to 1100)
14490	Wolverton Mill	78	225	Taes	Posthole	Late Saxon/Saxo-Norman (900 to 1100)
14492	Wolverton Mill	54	709	Taes	Pit	FS Early/mid-11th to mid-12th (1030 to 1160)
14494	Wolverton Mill	79	786	Tcom	Gully	FS Late 8th to late 9th (770 to 880)
14496	Wolverton Mill	93	157	Tcom	Posthole	FS Early/mid-11th to mid-12th (1030 to 1160)
14498	Wolverton Mill	93	157	Taes	Posthole	FS Early/mid-11th to mid-12th (1030 to 1160)
14500	Wolverton Mill	93	157	Taes	Posthole	FS Early/mid-11th to mid-12th (1030 to 1160)
14502	Wolverton Mill	93	157	Tturg	Posthole	FS Early/mid-11th to mid-12th (1030 to 1160)
14504	Wolverton Mill	75	211	Tcom	Posthole	FS Late 6th - mid 7th (600 to 653)
14506	Wolverton Mill	75	211	Taes	Posthole	FS Late 6th - mid 7th (600 to 653)
14508	Wolverton Mill	75	211	Tcom	Posthole	FS Late 6th - mid 7th (600 to 653)
14512	Wolverton Mill	107	462	Taes	Pit	Medieval (1100 to 1400)
14514	Wolverton Mill	22	509	Tcom	Pit	Early/Middle Saxon (450 to 750)
14516	West Fen Road	35	2220	Tcom	Pit	FS late 8th-late 9th (780 to 880)
14518	West Fen Road	142	5973	Taes	Ditch	FeedSax 3 (late C10 - early C11) (980 to 1030)
14520	West Fen Road	60	2191	Tcom	Pit	FeedSax 5 (mid C12 - early C13) (1160 to 1220
14522	West Fen Road	103	3324	Tcom	Cess pit	FeedSax 6 (early C13 - late C13) (1225 to 1300)
14524	West Fen Road	51	2207	Taes	Pit	FeedSax 5 (mid C12 - early C13) (1160 to 1220)
14526	West Fen Road	80	2802	Taes	Posthole	FeedSax 3 (late C10 - early C11) (980 to 1030)
14528	West Fen Road	23	2113	Taes	Ditch	FeedSax 3 (late C10 - early C11) (980 to 1030)
14530	West Fen Road	97	3314	Tcom	Pit	FeedSax 5 (mid C12 - early C13) (1160 to 1220)
14532	Pudding Ln	25	229	Taes	Oven	Phase 3: Late Saxon (1030 to 1050)
14534	Pudding Ln	25	229	Taes	Oven	Phase 3: Late Saxon (1030 to 1050)
14536	Pudding Ln	25	229	Taes	Oven	Phase 3: Late Saxon (1030 to 1050)
14538	Pudding Ln	25	229	Taes	Oven	Phase 3: Late Saxon (1030 to 1050)
14540	Pudding Ln	25	229	Taes	Oven	Phase 3: Late Saxon (1030 to 1050)
14542	Pudding Ln	25	229	Tdur	Oven	Phase 3: Late Saxon (1030 to 1050)

ID	Site	Sample	Context	Classified	Feature	FeedSax database phase
14544	Pudding Ln	25	229	Taes	Oven	Phase 3: Late Saxon (1030 to 1050)
14546	Pudding Ln	25	229	Tdur	Oven	Phase 3: Late Saxon (1030 to 1050)
14548	Pudding Ln	25	229	Tdur	Oven	Phase 3: Late Saxon (1030 to 1050)
14550	Pudding Ln	20	227	Taes	Oven	Phase 3: Late Saxon (1030 to 1050)
14552	Pudding Ln	20	227	Tturg	Oven	Phase 3: Late Saxon (1030 to 1050)
14554	West Fen Road	16	1834	Tcom	Pit	FS late 8th-late 9th (780 to 880)
14556	West Fen Road	16	1834	Taes	Pit	FS late 8th-late 9th (780 to 880)
14558	West Fen Road	165	7162	Taes	Pit	FeedSax 4 (early C11 - mid C12) (1030 to 1160)
14560	West Fen Road	165	7162	Tturg	Pit	FeedSax 4 (early C11 - mid C12) (1030 to 1160)
14562	West Fen Road	165	7162	Tcom	Pit	FeedSax 4 (early C11 - mid C12) (1030 to 1160)
14564	West Fen Road	151	6017	Taes	Ditch	FeedSax 3 (late C10 - early C11) (980 to 1030)
14566	West Fen Road	151	6017	Taes	Ditch	FeedSax 3 (late C10 - early C11) (980 to 1030)
14570	West Fen Road	147	6202	Taes	Pit	FeedSax 3 (late C10 - early C11) (980 to 1030)
14572	West Fen Road	147	6202	Tcom	Pit	FeedSax 3 (late C10 - early C11) (980 to 1030)
14574	West Fen Road	56	2461	Taes	Posthole	FeedSax 6 (early C13 - late C13) (1225 to 1300)
14576	West Fen Road	148	6238	Taes	Pit	FeedSax 4 (early C11 - mid C12) (1030 to 1160)
14578	West Fen Road	148	6238	Taes	Pit	FeedSax 4 (early C11 - mid C12) (1030 to 1160)
14580	West Fen Road	148	6238	Taes	Pit	FeedSax 4 (early C11 - mid C12) (1030 to 1160)
14582	West Cotton	804	804	Taes	Leat	FeedSax 4 (prev Final watermill 1100-1150) (1030-1160)
14584	Pudding Ln	19	214	Tcom	Oven	Phase 4: Early Medieval (1060 to 1100)
14586	Pudding Ln	19	214	Tcom	Oven	Phase 4: Early Medieval (1060 to 1100)
14588	Pudding Ln	19	214	Taes	Oven	Phase 4: Early Medieval (1060 to 1100)
14590	Pudding Ln	19	214	Tcom	Oven	Phase 4: Early Medieval (1060 to 1100)
14592	Pudding Ln	20	227	Tcom	Oven	Phase 3: Late Saxon (1030 to 1050)
14598	Pudding Ln	21	220	Taes	Oven	Phase 3: Late Saxon (1030 to 1050)
14600	Pudding Ln	21	220	Taes	Oven	Phase 3: Late Saxon (1030 to 1050)
14604	Pudding Ln	15	207	Taes	Oven	Phase 4: Early Medieval (1060 to 1100)
14606	Pudding Ln	15	207	Taes	Oven	Phase 4: Early Medieval (1060 to 1100)
14608	Pudding Ln	15	207	Taes	Oven	Phase 4: Early Medieval (1060 to 1100)
14610	Pudding Ln	15	207	Tcom	Oven	Phase 4: Early Medieval (1060 to 1100)
14612	Pudding Ln	15	207	Taes	Oven	Phase 4: Early Medieval (1060 to 1100)
14614	Pudding Ln	5	152	Tcom	Ditch	Phase 2: Late Saxon (950 to 1000)
14616	Pudding Ln	25	229	Taes	Oven	Phase 3: Late Saxon (1030 to 1050)
14618	Pudding Ln	25	229	Taes	Oven	Phase 3: Late Saxon (1030 to 1050)

ID	Site	Sample	Context	Classified	Feature	FeedSax database phase
14620	Pudding Ln	25	229	Tcom	Oven	Phase 3: Late Saxon (1030 to 1050)
14622	Pudding Ln	25	229	Taes	Oven	Phase 3: Late Saxon (1030 to 1050)
14624	Pudding Ln	25	229	Tcom	Oven	Phase 3: Late Saxon (1030 to 1050)
14626	Pudding Ln	25	229	Tdur	Oven	Phase 3: Late Saxon (1030 to 1050)
14628	Pudding Ln	25	229	Tdur	Oven	Phase 3: Late Saxon (1030 to 1050)
14630	Pudding Ln	25	229	Tcom	Oven	Phase 3: Late Saxon (1030 to 1050)
14632	Pudding Ln	25	229	Taes	Oven	Phase 3: Late Saxon (1030 to 1050)
14634	Pudding Ln	25	229	Taes	Oven	Phase 3: Late Saxon (1030 to 1050)
14636	Pudding Ln	25	229	Taes	Oven	Phase 3: Late Saxon (1030 to 1050)
14638	Pudding Ln	25	229	Tdur	Oven	Phase 3: Late Saxon (1030 to 1050)
14640	Pudding Ln	25	229	Taes	Oven	Phase 3: Late Saxon (1030 to 1050)
14642	Pudding Ln	25	229	Taes	Oven	Phase 3: Late Saxon (1030 to 1050)
14644	Pudding Ln	25	229	Taes	Oven	Phase 3: Late Saxon (1030 to 1050)
14646	Pudding Ln	25	229	Tdur	Oven	Phase 3: Late Saxon (1030 to 1050)
14648	Wolverton Mill	58	658	Tturg	Cess pit	FS Early/mid-11th to mid-12th (1030 to 1160)
14650	Wolverton Mill	75	211	Tturg	Posthole	FS Late 6th - mid 7th (600 to 653)
14652	Wolverton Mill	93	157	Taes	Posthole	FS Early/mid-11th to mid-12th (1030 to 1160)
14654	Wolverton Mill	93	157	Taes	Posthole	FS Early/mid-11th to mid-12th (1030 to 1160)
14656	Wolverton Mill	114	1004	Taes	Ditch	Late Saxon/Saxo-Norman (900 to 1100)
14658	Wolverton Mill	98	808	Taes	Pit	FS Early/mid-11th to mid-12th (1030 to 1160)
14660	Wolverton Mill	113	946	Tcom	Pit	FS Early/mid-11th to mid-12th (1030 to 1160)
14662	Wolverton Mill	58	658	Tcom	Cess pit	FS Early/mid-11th to mid-12th (1030 to 1160)
14664	Walsingham	45	844	Tcom	Pit	FeedSax 5 (mid C12 - early C13) (1160 to 1220)
14670	Walsingham	2	89	Taes	Linear	FeedSax 1 (early C8 - mid C9) (725 to 850)
14672	Walsingham	68	1880	Tcom	Linear	FeedSax 2 (late C9 - late C10) (875 to 975)
14674	Pudding Ln	25	229	Tturg	Oven	Phase 3: Late Saxon (1030 to 1050)
14676	Pudding Ln	20	227	Taes	Oven	Phase 3: Late Saxon (1030 to 1050)
14678	Pudding Ln	19	214	Taes	Oven	Phase 4: Early Medieval (1060 to 1100)
14680	Pudding Ln	15	207	Tcom	Oven	Phase 4: Early Medieval (1060 to 1100)
14682	Pudding Ln	15	207	Taes	Oven	Phase 4: Early Medieval (1060 to 1100)
14684	Wolverton Mill	79	786	Taes	Gully	FS Late 8th to late 9th (770 to 880)
14686	Walsingham	34	640	Taes	Linear	FeedSax 2 (late C9 - late C10) (875 to 975)
14688	Walsingham	37	751	Tcom	Beam slot	FeedSax 4-7 (C12-C14) (1120 to 1400)
14690	Walsingham	37	751	Tcom	Beam slot	FeedSax 4-7 (C12-C14) (1120 to 1400)

ID	Site	Sample	Context	Classified	Feature	FeedSax database phase
14692	Coton Park	41	2329	Tcom	Undefined	FeedSax E1-E4 (1030 to 1160)
14694	Coton Park	41	2329	Tcom	Undefined	FeedSax E1-E4 (1030 to 1160)
14696	Coton Park	41	2329	Taes	Undefined	FeedSax E1-E4 (1030 to 1160)
14698	Coton Park	41	2329	Taes	Undefined	FeedSax E1-E4 (1030 to 1160)
14700	Coton Park	41	2329	Taes	Undefined	FeedSax E1-E4 (1030 to 1160)
14702	Coton Park	40	2257	Taes	Undefined	FeedSax E1-E4 (1030 to 1160)
14704	Coton Park	40	2257	Taes	Undefined	FeedSax E1-E4 (1030 to 1160)
14706	Coton Park	40	2257	Tcom	Undefined	FeedSax E1-E4 (1030 to 1160)
14708	Coton Park	40	2257	Tturg	Undefined	FeedSax E1-E4 (1030 to 1160)
14710	Coton Park	40	2257	Tcom	Undefined	FeedSax E1-E4 (1030 to 1160)
14712	Coton Park	40	2257	Tcom	Undefined	FeedSax E1-E4 (1030 to 1160)
14726	Coton Park	5	782	Tcom	Undefined	FeedSax E1-E4 (1030 to 1160)
14728	Coton Park	50	4096	Taes	Undefined	FeedSax E1-E4 (1030 to 1160)
14730	Coton Park	1	489	Tcom	Undefined	FeedSax E1-E4 (1030 to 1160)
14732	Coton Park	35	1625	Taes	Undefined	FeedSax E5-F1 (1160 to 1260)
14734	Coton Park	35	1625	Taes	Undefined	FeedSax E5-F1 (1160 to 1260)
14736	Coton Park	35	1625	Taes	Undefined	FeedSax E5-F1 (1160 to 1260)
14738	Coton Park	35	1625	Taes	Undefined	FeedSax E5-F1 (1160 to 1260)
14748	Pudding Ln	19	214	Tturg	Oven	Phase 4: Early Medieval (1060 to 1100)
14752	Sedgeford		17023	Taes	Oven fill of kiln 1	Mid Saxon 600-800
14760	Sedgeford		17013	Tcom	Collapsed roof of kiln 1	Mid Saxon 600-800
14768	Sedgeford		17013	Tcom	Collapsed roof of kiln 1	Mid Saxon 600-800
14770	Sedgeford		17026	Taes	Bottom fill of kiln 1	Mid Saxon 600-800
14772	Sedgeford		17026	Tdur	Bottom fill of kiln 1	Mid Saxon 600-800
14776	Sedgeford		17026	Taes	Bottom fill of kiln 1	Mid Saxon 600-800
14780	Sedgeford		17026	Taes	Bottom fill of kiln 1	Mid Saxon 600-800
14784	Sedgeford		17026	Tdur	Bottom fill of kiln 1	Mid Saxon 600-800
14786	Sedgeford		17026	Taes	Bottom fill of kiln 1	Mid Saxon 600-800
14796	Sedgeford		17026	Tcom	Bottom fill of kiln 1	Mid Saxon 600-800
14798	Sedgeford		17026	Tcom	Bottom fill of kiln 1	Mid Saxon 600-800
14804	Sedgeford		17026	Tcom	Bottom fill of kiln 1	Mid Saxon 600-800
14806	Sedgeford		17026	Taes	Bottom fill of kiln 1	Mid Saxon 600-800
14808	Sedgeford		17026	Taes	Bottom fill of kiln 1	Mid Saxon 600-800
14810	Sedgeford		17026	Taes	Bottom fill of kiln 1	Mid Saxon 600-800

ID	Site	Sample	Context	Classified	Feature	FeedSax database phase
14812	Sedgeford		17026	Tdur	Bottom fill of kiln 1	Mid Saxon 600-800
14814	Sedgeford		17026	Tdur	Bottom fill of kiln 1	Mid Saxon 600-800
14820	Sedgeford		17026	Taes	Bottom fill of kiln 1	Mid Saxon 600-800
14828	Sedgeford		17023	Taes	Oven fill of kiln 1	Mid Saxon 600-800
14830	Sedgeford		17023	Tcom	Oven fill of kiln 1	Mid Saxon 600-800
14832	Sedgeford		17023	Taes	Oven fill of kiln 1	Mid Saxon 600-800
14834	Sedgeford		17023	Tdur	Oven fill of kiln 1	Mid Saxon 600-800
14836	Sedgeford		17023	Taes	Oven fill of kiln 1	Mid Saxon 600-800
14838	Sedgeford		17023	Tdur	Oven fill of kiln 1	Mid Saxon 600-800
14840	Sedgeford		17023	Taes	Oven fill of kiln 1	Mid Saxon 600-800
14842	Sedgeford		17023	Tcom	Oven fill of kiln 1	Mid Saxon 600-800
14846	Sedgeford		17023	Taes	Oven fill of kiln 1	Mid Saxon 600-800
14850	Sedgeford		17023	Tcom	Oven fill of kiln 1	Mid Saxon 600-800
14854	Sedgeford		17023	Tcom	Oven fill of kiln 1	Mid Saxon 600-800
14858	Sedgeford		17013	Tdur	Collapsed roof of kiln 1	Mid Saxon 600-800
14860	Sedgeford		17013	Tdur	Collapsed roof of kiln 1	Mid Saxon 600-800
14862	Sedgeford		17013	Taes	Collapsed roof of kiln 1	Mid Saxon 600-800
14866	Sedgeford		17013	Tdur	Collapsed roof of kiln 1	Mid Saxon 600-800
14868	Sedgeford		17013	Tdur	Collapsed roof of kiln 1	Mid Saxon 600-800
14870	Sedgeford		17013	Taes	Collapsed roof of kiln 1	Mid Saxon 600-800
14872	Sedgeford		17013	Taes	Collapsed roof of kiln 1	Mid Saxon 600-800
14874	Sedgeford		17013	Taes	Collapsed roof of kiln 1	Mid Saxon 600-800
14876	Sedgeford		17013	Tcom	Collapsed roof of kiln 1	Mid Saxon 600-800
14878	Sedgeford		17013	Taes	Collapsed roof of kiln 1	Mid Saxon 600-800
14880	Sedgeford		17013	Tcom	Collapsed roof of kiln 1	Mid Saxon 600-800

'Taes'= ssp *aestivum,* 'Tcom'= ssp. *compactum*, 'Tturg'= ssp. *turgidum*, 'Tdur'= ssp. *durum*

4.0 Appendix 1: Study of grain size, shape and yield under different growing conditions as compared to natural within-ear variation in *Triticum aestivum* ssp. *aestivum*

4.1 Introduction

In order to assess the influence of growing conditions on grain size, shape and yield, ears of a single accession of *Triticum aestivum* ssp. *aestivum* (variety: 'Sham4') grown under different manuring and watering regimes were analysed. Ears were grown under controlled conditions at Tal Jebeen near Aleppo, Syria over two seasons in 2007/8 and 2008/9, and have previously been analysed for isotopic variation (Fraser *et al.* 2011; Wallace *et al.* 2013). In the second harvest year (2009), rainfall was more evenly distributed throughout the season, and $\delta^{13}C$ values for the grains suggest water availability did not differ significantly between regimes in this year; being collectively comparable to the fully irrigated plots harvested in 2008 (Wallace *et al.* 2013). It was therefore anticipated that any variation observed from the 2009 crop would be less closely tied to irrigation regime than in 2008.

Grains were equally sampled across the base, middle and top of the ears, with each ear represented by nine grains, and each growing regime by three ears. Each regime was therefore represented by 27 grains per year (with the exception of Plot W17 in 2008 due to insufficient grain production) to a total of 209 specimens (Table 1).

Code	Year	Regime	Grains sampled
W11_08	2008	Full manure, full irrigation	27
W11	2009	Full manure, full irrigation	27
W13_08	2008	No manure, full irrigation	27
W13	2009	No manure, full irrigation	27
W16_08	2008	Medium manure, no irrigation	27
W16	2009	Medium manure, no irrigation	27
W17_08	2008	No manure, no irrigation	20
W17	2009	No manure, no irrigation	27

Table 1 Summary of grains analysed from different growing regimes in both years

4.2 Grain Size

Average grain size under different growing regimes was analysed separately for the two growing years. Length and width of grains was recorded in the dorsal view, while depth was recorded from the widest point in the lateral view (see also Charles *et al*. 2021).

In the potentially more water-stressed year (2008), we see a positive correlation between grain size and irrigation, with manuring apparently having an ameliorating effect in also producing larger grains under no irrigation regimes when compared to no manuring (Fig. 1). In the relatively well-watered year (2009) we see less of a clear trend (Fig. 2), although full manuring and irrigation (W11) grains are slightly larger than no-input (W17) grains. In both years, variation between regimes was <0.53mm in any one dimension.

Grain size was also compared within ears across the growing years (Table 2). On average, grains from the middle of the ear were found to be larger than from the base or top of the ear, with a slightly smaller level of variation than was observed between growing regimes (<0.31mm). Grains were also analysed on the basis of spikelet position, comparing grains from single-grain spikelets ('solo'), with grains enclosed by two or more outer grains ('internal') and grains from multi-grain spikelets occupying the outer florets ('external') (Fig. 3). Of these the 'external' grains were the largest, by a narrow margin, with the 'internal' category apparently narrower but longer than the 'solo' grains. It was noted during sampling that one-grain spikelets are more common at the base and top of the ear. Therefore, ear position and spikelet position are related categories: grains may be smaller at the base and top of the ear, but they may also be 'plumper' than 'internal' grains from the middle of the ear. Overall, we see that agricultural regime may influence grain size, particularly in conditions of relatively low rainfall, but that the level of variation in size is not much greater than that found within a single ear.

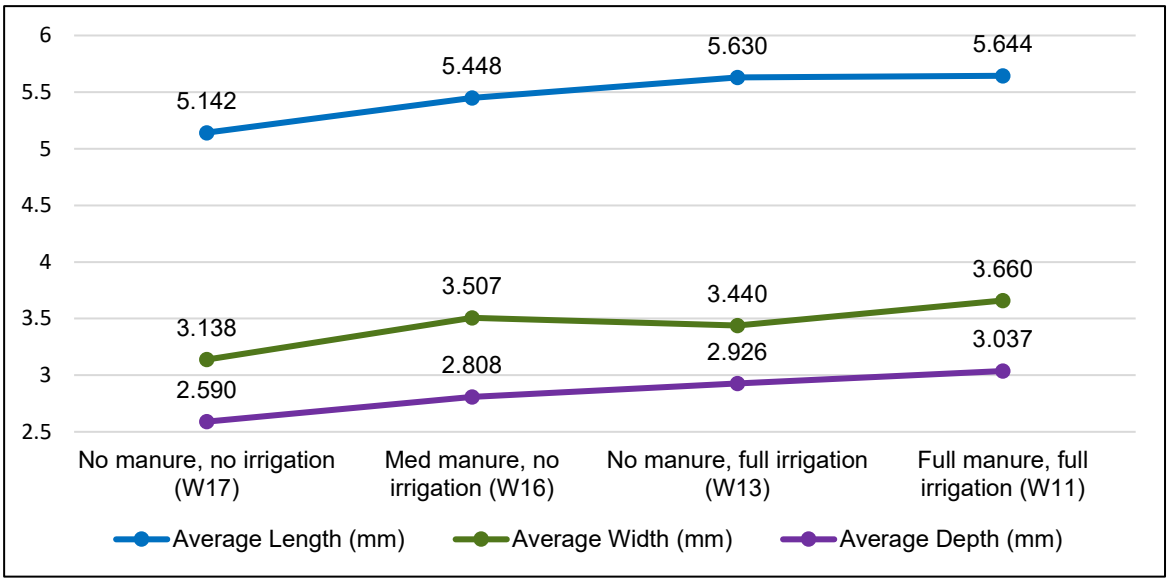

Fig. 1 Comparison of average grain length, width and depth for bread wheat grown under different growing regimes in 2008 (more water-stressed year)

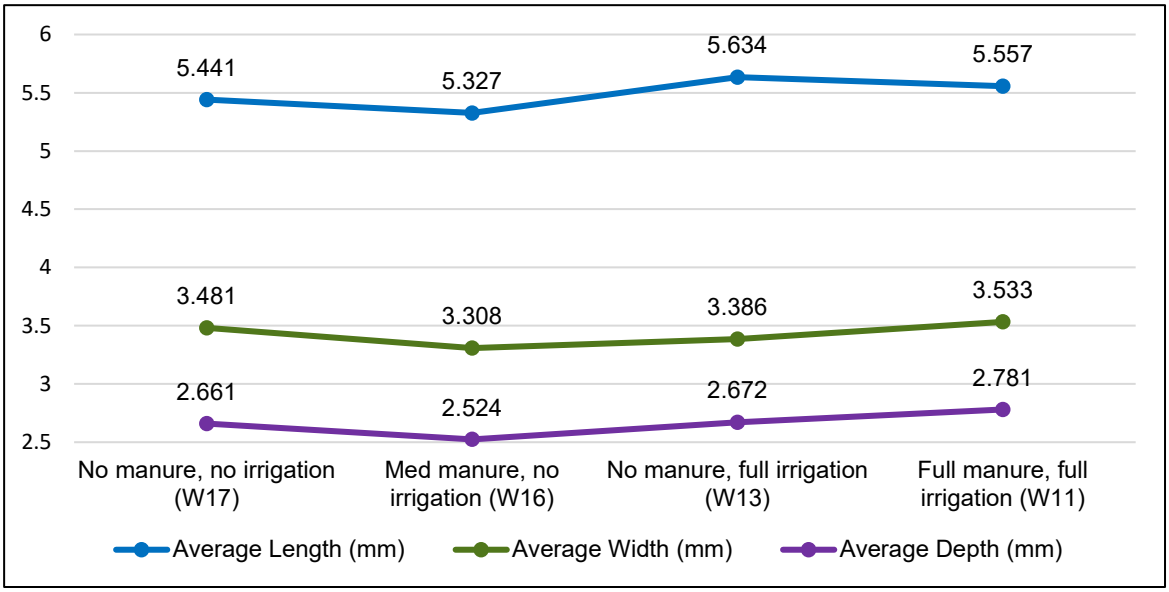

Fig. 2 Comparison of average grain length, width and depth for bread wheat grown under different growing regimes in 2009 (less water-stressed year)

	Average length (mm)	Average width (mm)	Average depth (mm)
Ear position			
Top grains	5.480	3.373	2.674
Middle grains	5.647	3.573	2.841
Bottom grains	5.340	3.377	2.750
Spikelet position			
Internal grains	5.473	3.286	2.555
External grains	5.546	3.500	2.794
Solo grains	5.290	3.307	2.714

Table 2 Average dimensions of grains from different points of the ear and spikelet

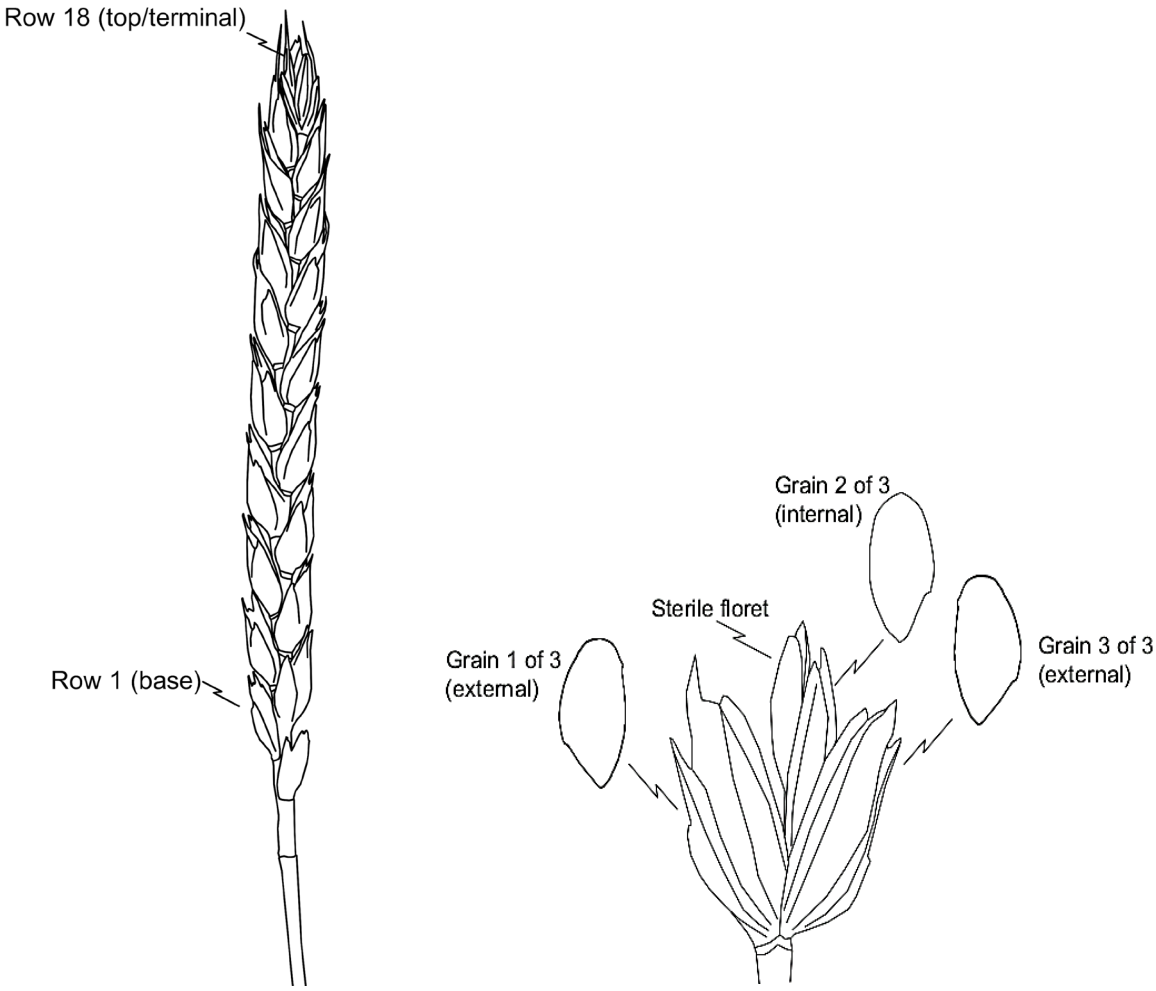

Fig. 3 Ear and spikelet of ssp. *aestivum* showing relative positions of grains as coded in the study (Row 1 = first fertile spikelet)

4.3 Grain Shape

Elliptic Fourier Analysis was performed on grains from the different agricultural regimes to establish whether grain shape was a reliable indicator of growing conditions. Grains were analysed in combined dorsal and lateral views as demonstrated to be the most useful in terms of separating (sub-)species (see Papers 1–3).

A linear discriminant analysis (LDA) of grains with growing regime as the discriminant factor produced low (<50%) rates of correct reclassification (Table 3). Even when full manuring and irrigation (W11) was compared only with the no-input regime (W17) reclassification remained poor (<60%, Table 3) — this being despite the model only having two categories to choose between. When compared to the approximately 85–96% correct reclassification to (sub-)species using the same methodology (Papers 1–3), it appears that shape is a less clear signifier of growing condition than it is of taxa.

Variables	Reclassification score	Reclassification score %
All four growing regimes (2008)	36/101	35.6%
All four growing regimes (2009)	45/108	41.7%
Full manuring/irrig. vs no manuring/irrig. (both years)	58/101	57.4%
Ear position (base vs middle vs top)	110/209	52.6%
Ear position (middle vs base/top)	140/209	67.0%
Spikelet position (solo vs internal vs external)	155/209	74.2%
Spikelet position (internal vs external/solo)	194/209	92.8%

Table 3 Results of LDA comparing grains from different growing regimes when dorsal and lateral views were combined

Grain shape was also analysed for within-ear variation across ear position and spikelet position categories, combining data from both years. For ear position (base, middle or top), 52.6% were correctly reclassified and for spikelet position (‘solo’, ‘internal’ or ‘external’) the reclassification rate was 74.2%, increasing to 92.8% when ‘internal’ grains were compared with ‘solo’ and ‘external’ in combination (Table 3). Because the sampling strategy prioritised sampling grains equally along the ear, and because ‘internal’ grains are, by definition, less

common than the surrounding ‘external’ ones, internal grains were underrepresented in this study, comprising only 20/209 grains. If the dataset were expanded to include more ‘internal’ grains, and categories were more evenly distributed, it is possible that we would see higher reclassification rates.

A comparison of mean shapes (Fig. 4) demonstrated that ‘internal’ grains were more slender, particularly in the lateral view (as also suggested by the dimensions in Table 2, above) and apparently compressed dorsally by the surrounding ‘external’ grains (see also Fig. 3). Comparison with the mean shapes of the different growing regimes from 2008 (the drier year) (Fig. 5), suggests that while grains from the no-input regime are also slightly narrower in the lateral view, this difference is less pronounced than when comparing grains based on spikelet position.

4.4 Grain Production/Yield

Grain production (i.e. yield) across growing regimes was assessed for both years on the basis of data gathered during sampling on the maximum number of spikelet rows per ear (corresponding to ear length) and the maximum number of grains sampled per spikelet. Also given are the average number of grains per spikelet and the maximum number of grains per ear (Table 4).

In the year with lower water availability (2008), the highest-input regime (W11) produced the ears with the most rows, the largest number of grains per ear and a higher average number of grains per spikelet. The opposite is true of the no-input regime (W17), which produced markedly smaller ears with a very low number of grains (<6 per ear). In the less water-stressed year (2009), there appears to be less variation in grain production between regimes; however, there is still a positive correlation between higher inputs and row number, and the average number of grains per spikelet is also lowest under the no-input regime.

Overall, it appears that there is a significant correlation between growing regime and grain production, which is particularly marked under conditions of lower water availability. The

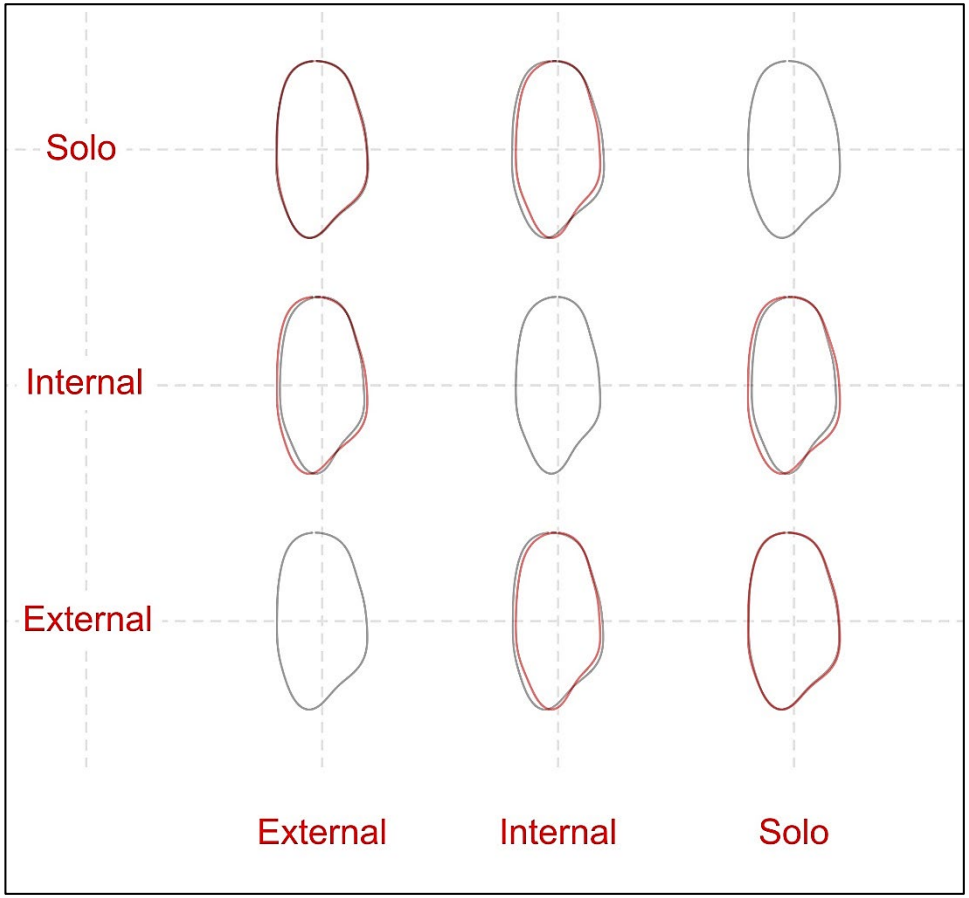

Fig. 4 Pairwise comparisons of mean shapes of grains occupying different positions within a spikelet (lateral view) (both years)



Fig. 5 Pairwise comparisons of mean shapes of grains grown under different agricultural regimes in 2008 (lower water availability year) (lateral view)

Regime	No. rows per ear	Max. no of grains per ear	Max. grains per spikelet	Average grains per spk
2008				
Full manure, full irrigation	14	33	3	2.10
No manure, full irrigation	12	18	3	1.73
Med. manure, no irrigation	10	21	3	2.07
No manure, no irrigation	4	5	2	1.05
2009				
Full manure, full irrigation	15	39	4	2.46
No manure, full irrigation	14	37	3	2.53
Med. manure, no irrigation	14	43	4	2.80
No manure, no irrigation	13	21	3	1.73

Table 4 Observations on traits relating to grain production/yield across different growing regimes and years

grain production or yield varies according to both the height of the ear (or number of spikelet rows) as well as the number of grains produced per spikelet.

4.5 Conclusion

The results suggest that while there is a relationship between growing regime and grain size, and potentially also shape, these differences are similar in degree to natural in-ear variation. Size variation between lower and higher input regimes is not much greater than that found between different points of the ear, and GMM analysis was not able to assign grains more reliably to different growing regimes than it was able to distinguish between ear or spikelet position. Indeed, shape differences as based on grain position within a spikelet appeared to be more distinct than those between growing regimes. We therefore encounter the potential for equifinality, in that a sample of atypically small and/or narrow grains could be the result of poor growing conditions, but could also represent the separation of smaller ‘tail’ grain from within a ‘healthy’ ear e.g. by sieving. In this case isotopic measurements of grains would

provide a useful additional environmental proxy, which when combined with size and shape data, could be used to test the hypothesis that the growing environment was responsible.

The study did identify a strong association between grain yield and growing conditions, and particularly with water availability. This is in line with research indicating that annual grain crops show greater plasticity in seed production in comparison to relatively narrow variability in seed size relative to their wild counterparts (Sadras 2007). Increased grain production under better-watered conditions is linked not just to the size of the ear (as expressed by the number of spikelet rows) but also to the number of grains per spikelet. Initial GMM analysis suggests that 'internal' grains enclosed by at least two other grains can be distinguished by shape. While the sample of 'internal' grains was too small to draw firm conclusions from this study, it may be possible to draw inferences on grain production/yield by using GMM to quantify 'internal' grains in future studies (with each 'internal' grain indicating a spikelet with three or more grains). In contrast to what is perhaps the intuitive expectation, high proportions of 'slim' internal-type grains could indicate the production of more grains per spikelet and therefore of favourable growing conditions. In wheat crops which typically produce two or fewer grains per spikelet (e.g. einkorn, emmer), we are unlikely to see the same degree of within-ear morphological variation as we do for bread wheat, and analysis of these grains may help to further elucidate the relationship between growing conditions and grain morphology.

Comparison with previous GMM studies analysing different (sub-)species and varieties of both glume and free-threshing wheats (Papers 1–3), indicates that shape is a less straightforward indicator of growing conditions than it is of taxa. While this study suggests that, under poorly-watered conditions, grains will be smaller and possibly slimmer (with manuring potentially offsetting this to some degree), these small variations proved complex to disentangle from natural within-ear diversity in size and shape. A clearer understanding of the role of spikelet position, as well as analysis of 1- and 2-grained wheat crops in which in-ear variation is less pronounced, are likely to help elucidate these difficulties. Furthermore, while the use of 2D images appears to be sufficient to distinguish between (sub-)species

and, potentially, varietal-level differences, more advanced forms of image-capture including 3D imagery may be required to detect the more subtle differences between wheat grains cultivated under different agricultural regimes.

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5.0 Conclusions

5.1 Methodological Findings

Across the three case studies (Papers 1–3) and additional experiments (Appendix 1), a total of 1093 modern and 865 archaeological wheat grains were taken to full analysis. The coordinates describing the outlines of these grains, as well as the corresponding data frames and R scripts are available for further research in an open-access repository at the author's Github account (https://github.com/TinaRoushan). Generating outlines as sets of coordinates proved advantageous in allowing for large amounts of data to be stored and shared in .txt format, which requires relatively little file space and is easy to transfer. Tracing grains in a CAD (computer-aided design) program to generate coordinates also has advantages in allowing for a relatively simple process of normalisation for rotation and for the operator to exercise reasonable judgement in excluding, for example, differentially developed grain embryos, small areas of mechanical damage or adhering sediment. However, these same advantages do incur an acknowledged level of subjectivity. Difficulties of reproducibility in such instances have previously been addressed in the documentation for the Momocs program, particularly as regards prior alignment of shapes which are roughly circular or exhibit strong bilateral symmetry (see https://cran.r-project.org/web/packages/Momocs/Momocs.pdf, subheading 'Efourier'). This method is also moderately time-consuming, and in future, exploration of developments in automated outline extraction methods and Procrustes alignment of outlines would be considered.

However, with these potential issues acknowledged, when measurement error was calculated after the formula described in Claude (2008, 65), the percentage error ranged between 4.38–12.51%, which may be considered to be within an acceptable margin when compared with other recent studies (Jesus *et al*. 2022). Measurement error was calculated based on data captured by photographing and digitising five specimens from the same ear five times each, over five separate sessions, after Evin *et al*. (2020). This process was performed on examples of both glume and free-threshing wheats. In both cases, ANOVA

indicated that there were significant differences between the PCA scores of different specimens, with non-significant differences when the same grain was digitised across multiple sessions. This suggests that repeated outline capture of the same grain did not produce significantly different outlines, and that any variation detected was less significant than that between specimens. As such, while a degree of subjectivity is acknowledged in the methodology, it is hoped that this is presented transparently and the potential for error sufficiently quantified.

When the diagnostic potential of different grain views was compared using a range of modern glume and free-threshing wheat specimens, results indicated clear advantages of certain photographic views over others. Dorsal, lateral and polar views, as utilised in a previous GMM study of wheat grains (Bonhomme *et al.* 2017), were analysed both separately and in combination to assess which allowed for the highest proportion of grains to be assigned to the correct taxa. When the linear discriminant reclassification scores for different views were compared, the lateral view consistently produced the highest scores, while the polar view was seen to be the least effective. Across both the glume and FTW groups, analysis using both the dorsal and lateral views in combination was found to be the most successful way of distinguishing wheat types, with reclassification scores suggesting that the lateral view by itself was only marginally less diagnostic. This is significant in terms of future research, as the polar view, in particular, is relatively time-consuming to photograph accurately and the data-capture of one or two views presents a significantly reduced workload from that required for using all three views in combination.

Having compared the diagnostic potential of different grain views, the research demonstrated that a relatively simple 2D approach can be a useful tool for refining identifications at the (sub-)species and varietal levels, and for further exploring variations within and between these categories. At the (sub-)species level, reclassification rates of charred grains ranged between 85.6–96.3%, depending on the combination of taxa and accessions used. Glume wheats were at the higher end of this reclassification scale (Paper 1), while the potentially less distinct FTWs were at the lower end (Papers 2 and 3). When

classifying by accession (i.e. to variety), twelve glume wheat accessions could be correctly classified at 74.7% and twelve FTW accessions at 82.1–84.6% (Papers 2 and 3), suggesting sensitivity of the model to variation within (sub-)species. It seems likely that expanding the modern reference dataset would improve the accuracy of the model, particularly as regards clarifying the morphological variation between different classes of hexaploid wheat when applied to archaeological remains.

The implication of these results, while promising, is that grains need to be described at the group, rather than individual, level when using this type of methodology, particularly as it was noted that a single specimen may stray quite considerably outside the typical shape range for its class, or plot at the boundary between two classes. As such, the method is suited to larger assemblages with a high proportion of well-preserved grains, and, as acknowledged in Paper 3, this can be challenging in certain archaeological contexts. Furthermore, it was noted in Paper 2 that predicted reclassification scores necessarily assume that the specimen selected for classification is represented within the modern reference dataset, and that the comparative material covers the morphological range of that taxon reasonably well. This is a problem common to all types of reference collection, but the advantage of reference datasets used in GMM is that they can be expanded cumulatively without significantly impacting the speed of analysis. Furthermore, it is possible to detect when archaeological grains occupy an anomalous position and do not fit well into any category — as observed for the seemingly germinated grains from early medieval Sedgeford in Paper 3.

Finally, it is noted that even when GMM is not used to classify digitised grains, it is a highly useful visual tool for the identification of archaeobotanical wheat remains; as seen in the generation of stacked outlines and mean shapes in Papers 1–3. Visualising numerous grains simultaneously allows us to isolate identification criteria that emerge amongst the variations in form; allowing, for example, the distinctive features of different FTW types to be outlined in Paper 2. This means findings may be applied to studies which are not specifically employing GMM methods, i.e. more typical ‘by-eye’ identifications. Visual references can be

generated based on a wide range of morphological data, as opposed to the selection by archaeobotanists of individual specimens which they feel exemplify particular cultivars.

5.2 Archaeological Findings

The relatively high level of accuracy by which outlines of charred grains could be used to assign specimens to the (sub-)species level allowed for a number of archaeological insights to be made across the three case studies. In Paper 1, the distinction between wild and domesticated emmer and Timopheev's wheat was used to describe a gradual and co-evolutionary process of domestication at Neolithic Çatalhöyük, in which a grain which resembled modern wild ssp. *araraticum*, became more similar to domesticated ssp. *timopheevii* over time, a picture that was supported by a parallel study of chaff dehiscence. In contrast, the morphology of emmer wheat remained relatively unchanged throughout the sequence, with grain size and chaff analysis also supporting interpretation of the crop as fully domesticated from the earliest phase. These findings presented a picture of wheat cultivation at Çatalhöyük in which experimentation with new cultivars on a group or household basis occurred alongside the use of established crops.

In Paper 2, the ability to distinguish between hexaploid bread/club wheat and tetraploid durum and rivet wheats allowed for the identification of different FTW forms at Neolithic Çatalhöyük and Kouphovouno. Results indicated cultivation of a free-threshing form most closely resembling hexaploid bread/club wheat at 7th millennium BC Çatalhöyük and tetraploid durum wheat at 6th millennium BC Kouphovouno. These findings are of relevance to the proposed origins and trajectories of hexaploid and tetraploid FTWs between western Asia and Europe (Maier 1996; Kirleis and Fisher 2014) and indicate the potential for GMM to shed light on assemblages of unknown ploidy level from the earliest phases of FTW cultivation.

In Paper 3, the potential of the model to distinguish rivet wheat grains from other FTW forms, allowed for analysis of grains from multiple sites to support theories of rivet being introduced into Late Anglo-Saxon agricultural systems, during a time of rapid acceleration and

innovation in arable production. At one site, Houghton (Cambridgeshire), it was possible to draw parallels between two distinct grain forms with a bimodal distribution in $\delta^{15}N$ values and correspondence analysis of sample compositional data, suggesting two potentially distinct wheat taxa associated with autumn and spring sowing (Hamerow *et al.* in prep.).

As background to this research, much data were collected relating to our current state of knowledge of different archaeological wheats. In Paper 1, this included a summary of documented finds of the once widespread prehistoric 'new glume wheat', the identification of which as *Triticum timopheevii s.l.* was strengthened by GMM analysis of the grains. In Paper 2, a survey of the archaeobotanical evidence for the origins and trajectories of FTWs was made, highlighting areas in which further research may be needed, such as taxonomic ambiguity in the earliest material and the need for a better understanding of the role of club wheat, both archaeologically and in recent history. Paper 3 also highlighted ambiguity regarding the role of club wheat and collated data relating to archaeological and later historical evidence of tetraploid FTW cultivation in Britain.

It is hoped that, by summarising this evidence and resolving the degree to which different wheat cultivars can be distinguished on a taxonomic basis, this research will support further exploration of variation beyond these taxonomic categorisations and allow us to better understand the role of biodiversity in past agricultural strategies. Papers 2 and 3 highlight sensitivity of the method to intra-species variation, alongside evidence of morphological variation corresponding with both bread and club wheat forms among the archaeological wheats classified as hexaploid. In other cases, it was possible to attribute morphological variation not only to genetic diversity, but also to the diversity of ways in which humans interact with wheats, including gradual co-evolutionary domestication (Paper 1), dehusking of grains (Paper 1) and the malting of grains for the purposes of brewing (Paper 3).

Analysis further indicated apparent morphological variation corresponding to improvement status and geographic origin. Papers 2 and 3 demonstrated that archaeological grains were more similar in form to so-called 'traditional' or 'unimproved' varieties which were listed by their respective gene banks as being sourced from proximate geographic regions. Further

work could clarify these geographic associations further, but results tentatively suggest long-term preservation of regional morphotypes and indicate the importance of considering origin and improvement status when selecting modern reference material for comparison with archaeological remains.

Related questions concerning the influence of environmental conditions on grain shape were explored in experiments summarised in Appendix 1. Here, findings indicated a clear relationship between the number of grains produced per ear/spikelet and different manuring and irrigation regimes. Corresponding variations in grain shape and size were less distinct than those previously observed between different taxa or varieties, with shape differences relating more clearly to the number of grains produced per spikelet than to a particular growing regime. These findings are in line with research indicating that annual grain crops demonstrate greater plasticity in seed production than in the size of the seeds they produce (Sadras 2007), as well as observations previously made in a GMM study of barley landraces (Wallace *et al*. 2018, see Section 0.7). As noted, it is possible that analysis of grains which exhibit less variability in terms of grains produced per spikelet (such as einkorn or emmer) could provide further insight.

5.3 Archaeological Findings: Contemporary Relevance

The archaeological findings have the potential to provide insights of contemporary relevance in the context of a noted loss of genetic diversity in modern wheat crops (Gegas *et al*. 2010; Venske *et al*. 2019) and the associated sustainability concerns previously discussed (Camacho Villa *et al.* 2005; Mijatović *et al.* 2013; Pilling *et al.* 2020). In Paper 1, we see households at Çatalhöyük experimenting with a new crop (Timopheev's wheat) that offered a wider set of affordances which may have included resistance to certain diseases. This approach falls within a wider pattern of a broad-spectrum plant strategy that would have helped to offset the risk of individual resource failure (Bogaard *et al*. 2017). This strategy is strongly contrasted by the degree to which we are currently reliant on centralised production of a narrow range of cultivars, and particularly bread wheat; a situation which has recently

been thrown into sharp focus by the threat to global wheat supplies caused by Russian aggression in Ukraine (FAO 2022).

Paper 2 presented evidence of a similar level of flexibility in cultivation strategies, with evidence of shifts in practice when certain approaches became unsustainable. In earlier phases at Çatalhöyük, and especially Kouphovouno, we see evidence of high-input management of FTWs which likely related to both the cultural value and ecological requirements of those crops. The apparent predominance of tetraploid forms in the Mediterranean region from the earliest phases of cultivation, would appear to reflect the crop's current preference for warmer and drier conditions. It is likely, given the origins and ancestry of tetraploid FTW, that this was a pre-existing trait of the crop, although it would have continued to adapt to its cultivation conditions over time. The spread of the crop northwards through France and into southern Scandinavia suggests that it did possess potential for adaptation to more northerly climes, although it is possible that this did not prove sustainable in the long-term. At both Kouphovouno and Çatalhöyük, a shift in later phases towards increased cultivation of hulled cereals, as paralleled at other Neolithic sites, suggests a process by which the degree of preference for the crop was reassessed in the light of changing resource availability or other conditions which meant that intensive cultivation of FTWs was less sustainable, or at least less appealing, to those communities. Recognising when our own farming methods are becoming unsustainable and a willingness to adapt from our current preferences are also likely to be essential for our future food security.

Finally, Paper 3 offers relevant insight in highlighting evidence of strategic cultivation of a wider range of cereal crops according to soil type and environmental conditions in the later Anglo-Saxon period (McKerracher 2018), a trend which the introduction of rivet appears to follow. Later historical developments saw increasingly narrow requirements in terms of yield and suitability to mechanised harvesting, which, in conjunction with a decline in the thatching industry, led to an almost complete loss of the tradition of rivet wheat cultivation (Letts 1999). It is likely that this decline led to 'genetic bottlenecking' and relative loss of adaptive potential

in the few rivet cultivars which survived into the earlier 20th century (Robinson 2018). We therefore see a trajectory from regionally diverse cultivation strategies towards increasingly homogenised systems, a process which has clearly accelerated in recent times.

5.4 Research Implications

The refinement of taxonomic classifications, or 'calling each thing by its right name', is a necessary baseline for exploring biodiversity in past agricultural systems, as only once we assess the degree to which shape is diagnostic of taxa can we begin to look also at variation within individual cultivars. The results presented in this thesis indicate that there are predictable morphological differences at the ploidy and (sub-)species levels and that the same model is also sensitive to varietal-level morphological differences. There is therefore considerable potential for GMM to explore variation both within and between wheat cultivars.

The case studies have provided examples of ways in which this potential can be used to give insight into past agricultural practices, with findings that have implications for addressing contemporary sustainability concerns. In addition to these findings, certain areas are highlighted in which the method could provide further insight. Potential for further research includes the elucidation of the early development and trajectories of free-threshing forms, the effects of processes such as malting on grain morphology and further exploration of variation within hexaploid FTWs and of wheats grown under different environmental conditions.

Furthermore, while the overall number of grains analysed for this study was not insubstantial, those analysed represent only a snapshot of the diversity within the genus and, as previously emphasised, there is significant scope for expansion of modern reference datasets, particularly with an emphasis on traditional, regional varieties. Specific cultivars are also highlighted which would particularly benefit from further exploration. These include *Triticum turgidum* ssp. *carthlicum* ('Persian' or Dika wheat), which is unusual in possessing morphological features of both hexaploid and tetraploid wheats (see Paper 2), two-grained

einkorn, the taxonomic status of which remains uncertain (Paper 1) and club wheat, *Triticum aestivum* ssp. *compactum*, the historic role of which remains unclear (Papers 2 and 3).

As acknowledged, the field of GMM is one that is moving very rapidly, particularly towards three-dimensional image capture and use of machine-learning, methods which are now beginning to be applied to archaeobotanical remains (Evin *et al*. 2022). The potentially greater sensitivity of 3D approaches to small-scale morphological variations may allow for the refinement of varietal distinctions and for the diagnosis of more subtle differences associated with environmental growing conditions (Appendix 1). Such approaches would need to consider a range of factors, including not only diversity between and within (sub-)species, but also the natural variation observed within individual ears of wheat themselves. Analysing grains in two-dimensions presents certain advantages in terms of summarising key differences between grain types in ways that can be easily visualised and described, while using resources available to most archaeobotanical laboratories. While the larger amount of data generated by 3D-image capture is likely to be highly powerful in terms of analysis, the relative 'noise' of these data will also need to be summarised in a way that it can be applied more widely by other researchers in the field.

Another implication of this research is its demonstration of the value of creating a photographic record for material which is to undergo destructive analysis, such as radiocarbon dating or isotopic analysis. The successful utilisation of photographs taken by the FeedSax team to record grains prior to isotopic analysis (Paper 3) practically demonstrates this value, while the hosting of these photographs in an online archive in partnership with the Sustainable Digital Scholarship group (https://portal.sds.ox.ac.uk/feedsax) creates further potential for these images to be used in future studies. Given the relative ease with which accurate images can now be captured, 2D photography and 3D scanning of grain images may prove increasingly valuable as a means of archiving material for the long-term. Morphometric-grade image capture may also prove valuable in contexts where practical or political conditions inhibit the movement of physical

samples between territories; the seeds themselves may not always be able to cross borders, but their digital images can.

5.5 Final summary

Analysis of modern reference material demonstrated that Elliptic Fourier Analysis of charred grains is a useful tool for refining taxonomic classifications of archaeobotanical wheat remains, with the same model also demonstrated to be sensitive to varietal-level differences. The highest levels of correct reclassification according to taxa were obtained when the dorsal and lateral views of grains were used in combination, with the polar view found to be of limited diagnostic value in charred grains. Beyond model-based reclassification, using GMM tools to visualise multiple grain forms simultaneously also allows for identification criteria of different cultivars to be outlined, which may then be applied to non-GMM-based studies.

Methodological insights obtained from the study of modern material were subsequently applied to answer specific research questions across three different archaeological case studies. In Paper 1, analysis demonstrated a close morphological resemblance between archaeological grains from Neolithic Çatalhöyük and modern Timopheev's wheat, further indicating a gradual domestication process which was paralleled in a study of chaff dehiscence. These findings were contextualised as part of a broader pattern of diverse and experimental plant-based strategies at the settlement. In Paper 2, analysis of distinct FTW forms at Neolithic Çatalhöyük (Central Anatolia) and Kouphovouno (southern Greece), confirmed cultivation of a hexaploid FTW at the former, while revealing cultivation of a tetraploid wheat closely resembling durum wheat at the latter. Implications of these findings are interpreted in relation to the currently ambiguous early development of FTWs in western Asia, and theories relating to differing trajectories of hexaploid and tetraploid forms into Europe. In Paper 3, analysis of grains from a range of early medieval contexts supported the theory of a Late Anglo-Saxon introduction of rivet wheat, understood within the context of substantial changes in agricultural practice beginning in the 'long eighth century'. Findings across all three papers demonstrate shifting and flexible patterns of diversification and

specialisation in the cultivation of different wheat cultivars in response to both environmental and social conditions, contrasting modern trends of increasingly centralised and homogenised agro-ecological systems focussed on a very narrow range of intensively cultivated wheat types.

More broadly, morphological variation among archaeological grains classified as hexaploid was noted, corresponding with both modern bread and club wheats, and interpreted as potentially relating to diversity in cultivated forms. The potential for the cumulative expansion of modern reference datasets to elucidate this variation was noted, as informed by findings that indicate the importance of improvement status and geographic origin when comparing modern and archaeological material. Predictable morphological changes were also noted to relate to the processing of wheat crops, in relation to both dehusking (Paper 1) and malting of grains (Paper 3). The degree to which morphological diversity could be attributed to growing conditions was addressed in experiments comparing a single accession grown under different environmental conditions. These results suggested that yield is significantly influenced by manuring and irrigation regime, but that the corresponding size and shape differences are less distinct than those between different (sub-)species or varieties.

Overall, this research has demonstrated that a relatively simple approach, applying Elliptic Fourier analysis to 2D images of charred grains, has significant potential to enhance our understanding of wheat cultivation in the past, including the types of wheat grown, how these developed and varied and some of the specific ways in which humans processed these crops. This potential has been demonstrated in relation to specific archaeological research questions across the three case studies presented herein, but there is clear scope for further application of GMM to explore the diverse ways in which humans and one of our most important and widely-adapted crops have coevolved and interacted. Such research has the potential to provide an important contextual backdrop to the limited biodiversity and relative inflexibility of practice found in modern wheat agriculture, and the associated sustainability concerns that we face today.

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6.0 Appendix 2: Published version of Paper 1

“Geometric Morphometrics Sheds New Light on the Identification and Domestication Status of ‘New Glume Wheat’ at Neolithic Çatalhöyük”

Tina Roushannafas, Amy Bogaard, Michael Charles

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Geometric morphometrics sheds new light on the identification and domestication status of 'new glume wheat' at Neolithic Çatalhöyük

Tina Roushannafas*, Amy Bogaard, Michael Charles

School of Archaeology, University of Oxford, Oxford, OX1 3TG, United Kingdom

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Neolithic Anatolia

ABSTRACT

'New glume wheat' (NGW) is an archaeobotanical type increasingly recognised at Neolithic–Bronze Age sites across Europe and Western Asia. NGW has been recognised via aDNA and morphological analyses of chaff remains as a member of the *Triticum timopheevii* wheat group, recent cultivation of which is known only from western Georgia. This study combines geometric morphometric (GMM) analysis of NGW grains with updated results from a parallel study of chaff dehiscence, to assess the taxonomic classification and domestication status of NGW from the Neolithic East Mound at Çatalhöyük (central Anatolia).

Results confirm close comparability of NGW with modern wheats from the group *T. timopheevii*, in a form which has remained remarkably similar over thousands of years. Furthermore, the analysis suggests that NGW was undergoing selection for domestication traits in terms of shattering behaviour and grain form during the 1150-year East Mound sequence. These findings are interpreted in the context of substantial archaeobotanical evidence for a broad-spectrum plant strategy at Çatalhöyük which mitigated the risk of resource failure and supported experimentation in cropping. Possible cultural and practical incentives are considered for investment in the crop, made despite the availability of a fully-domesticated glume wheat (emmer) with similar growing and processing requirements. Alongside this, the study demonstrates the sensitivity of GMM to differences between and within wheat species, with methodological findings that can inform future studies.

1. Introduction

1.1. 'New glume wheat'

'New glume wheat' (NGW) was characterised by Jones et al. (2000) from a distinct group of archaeobotanical spikelet bases recovered from Neolithic and Bronze Age sites in northern Greece. Based on the chaff morphology and grain:chaff ratios of deposits it was concluded that these were remains of a tetraploid wheat. Of the modern specimens compared, Timopheev's wheat (*Triticum timopheevii* Zhuk.) most closely resembled the morphology of this newly-identified archaeobotanical group.

The *T. timopheevii* wheat group contains two tetraploid species: wild *T. araraticum* (syn. *T. timopheevii* Zhuk. ssp. *armeniacum* (Jakubz.) van Slageren) and domesticated *T. timopheevii* Zhuk. ssp. *timopheevii*. Cultivated Timopheev's wheat was first identified by Russian botanist P.M. Zhukovsky in Georgia in 1922 (Zhukovsky 1928) and is considered a narrowly endemic species, with cultivation documented in only a few villages of western Georgia (Badaeva et al. 2022). Grown as a 'maslin' crop known locally as 'Zanduri', *T. timopheevii* was mixed in varying proportions with einkorn wheat (Dekaprevelich and Menabde 1932). Wild *T. araraticum* was first collected by M.G. Tumanyan and A.G. Araratyan in 1925–28 in Armenia and has a broader distribution, with specimens recorded across Transcaucasia and in parts of Iran, Iraq, Syria and Turkey (Badaeva et al. 2022).

Despite recent cultivation of Timopheev's wheat not being known outside western Georgia, NGW has been recorded as a crop at a range of sites across Europe and Western Asia (Fig. 1; Table 1), dating from the Neolithic–Bronze Age and possibly into the Iron Age (Kenéz et al. 2014). In some cases, remains initially identified as 'atypical' emmer wheat were subsequently reassessed in the light of the newly characterised NGW class, such as the chaff recovered at Cafer Höyük, Turkey (Jones et al. 2000). Chiefly these identifications have been based on chaff remains, and while some morphological criteria of NGW grains have been published (Kohler-Schneider 2003), distinguishing the grains, particularly from those of emmer, has been noted as difficult (Valamoti 2017).

Abbreviations: NGW, New glume wheat; GMM, Geometric Morphometrics.

* Corresponding author.
E-mail address: tina.roushannafas@arch.ox.ac.uk (T. Roushannafas).

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The relationship between the narrowly endemic modern Timopheev's wheat and the widespread archaeological NGW is uncertain. It is possible that the small population in Georgia is a relic of a formerly much wider cultivated crop. aDNA analysis of Neolithic NGW grains from Çatalhöyük and Miechowice 4, Poland (Czajkowska et al. 2020) has identified the presence of the G genome, indicating that NGW is a member of the Timopheevii section of wheats, distinct from other polyploid wheats which carry the B genome (Fig. 2). The Timopheevii section contains tetraploid wild and domesticated Timopheev's wheat and the hexaploid wheat *T. zhukovskyi* Menabde & Ericzjan (Badaeva et al., 2022). The presence of the G genome does not, therefore, in itself provide a precise identification.

The aDNA findings also do not preclude the possibility of a separate domestication event having led to a wheat form related, but not ancestor to, modern Timopheev's wheat. Indeed, wheats sharing a genomic constitution may differ significantly in form and function; for example, spelt and bread wheat are both 'BBAADD' hexaploid wheats, but have quite different processing requirements and culinary qualities. Furthermore, recent DNA analysis (Badaeva et al., 2022) has highlighted two distinct lineages of wild *Triticum araraticum*, with the authors positing potential hybridisation between Timopheev's wheats and wild emmer. These insights lend weight to the possibility of multiple evolutionary pathways within the *T. timopheevii* group.

1.2. NGW at Çatalhöyük

A substantial body of Neolithic NGW remains have been recovered from Çatalhöyük, the archaeobotanical dataset of which is currently the largest available for an early farming community in western Asia (Bogaard et al. 2021b). The remains analysed in this study were recovered from the Neolithic East Mound dating 7100–5950 cal. BC. Within Turkey, the Çatalhöyük NGW remains are predated by NGW finds from the mid-9th millennium BC at Aşıklı Höyük (Ergun et al. 2018) and by two spikelet forks of the late 9th–early 8th millennium BC at Boncuklu Höyük (Baird et al. 2018). Spikelet bases at Cafer Höyük dating from the late 9th millennium BC and described as 'machaoid' emmer also appear to match the morphological characteristics of NGW, not yet characterised at the time of their identification (de Moulins 1993; Jones et al. 2000).

From the earliest levels, a diverse range of cereal and pulse crops as well as wild food-plants are present at Çatalhöyük (Bogaard et al. 2017, 2021b). In early phases NGW is present but as a minor component only, with emmer (*Triticum turgidum* L. ssp. *dicoccum* (Schrank) Thell.) the dominant wheat crop. The earliest concentrated deposits of NGW were identified in neighbouring buildings of the mid-sequence phase 'North G', and it is not until the Late phase that we see concentrations in the South Area and the emergence of NGW as the most prevalent wheat crop (Bogaard et al. 2021b).

Emmer and NGW are both glume (or hulled) wheats. The ears of glume wheats are formed with a semi-brittle rachis, which when threshed break up into spikelets. These spikelets require further dehusking by pounding to release the grain from the tough glumes (Hillman 1984). In contrast, the rachis of 'free-threshing' wheats is thickened throughout, non-brittle and spikelets remain attached to the intact rachis. The glumes are thinner and the grains are easily released during threshing. Sample compositions indicate that, despite both being glume wheats with the same processing requirements, NGW and emmer were stored, and likely grown, separately, rather than as a mixed crop (Bogaard et al. 2017). Isotopic evidence (Vaiglova 2016; Stroud et al. 2021) and weed functional ecological analysis (Green et al. 2018) suggest that NGW was grown under similarly variable conditions to emmer. Therefore, rather than being environmentally-determined, adoption of NGW is interpreted as an example of household-level experimentation with an existing minor crop potentially relating to group-identity, culture and/or culinary preference (Bogaard et al. 2017, 2021b).

1.3. Archaeobotanical wheat grains and geometric morphometrics

In this study, modern and archaeological glume wheat grains are analysed and compared using geometric morphometrics (GMM). Archaeobotanical wheats grains can be challenging to identify with precision based on traditional morphological criteria (Jones 1998). Grains are usually preserved through charring but are distorted as a result, surviving in identifiable form only when charred within a narrow temperature range under low oxygen conditions (Charles et al. 2015). Charring aside, there is difficulty simply in establishing reliable characteristics by which to distinguish between taxa (Hillman et al. 1996). GMM offers new ways to approach these challenges of characterisation, with the potential to enhance descriptions of form variation

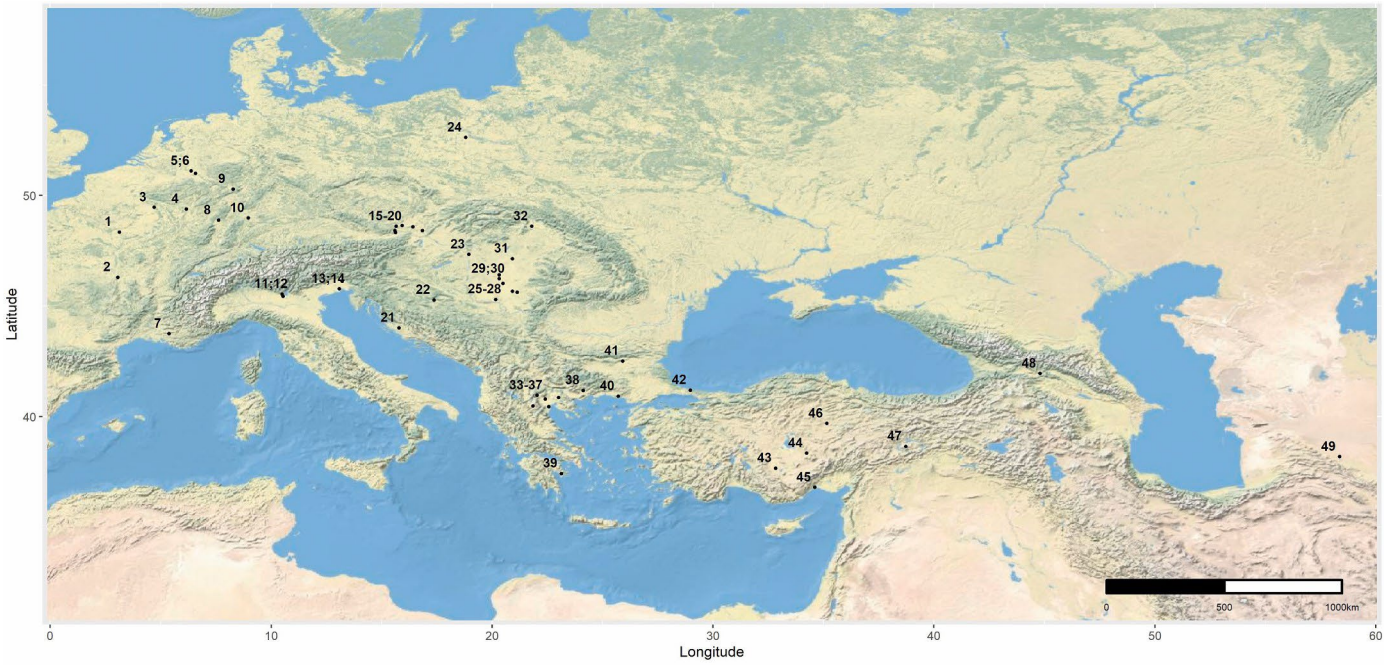

Fig. 1. Distribution map of NGW finds (see Table 1 for key).

and improve consistency of classifications.

Morphometrics is the application of statistical analyses to size and shape variables, enabling analysis of form in a comparable way to numeric data. In traditional morphometrics, multivariate statistics are applied to a predetermined set of variables, usually consisting of individually measured distances on an organism (Rohlf and Marcus 1993). The development of modern GMM and a suite of new techniques in the 1980s now allows us to analyse shapes as a whole (Adams et al. 2004). The accessibility of these methods has been vastly improved through the development and publication of functions in R (Claude 2008), the open software environment for statistical computing and graphics.

Within archaeobotany, GMM has been successfully applied to the study of grape seeds (Terral et al. 2010; Pagnoux et al. 2015), date palm stones (Terral et al. 2012) and olive stones (Terral et al. 2004; Newton et al. 2006, 2014). Previous studies of archaeobotanical cereals include that by Ros et al. (2014), in which GMM was used to identify two- and six-row barley from Roman contexts in southern France. Bonhomme et al. (2017) established the potential of GMM to distinguish between einkorn, emmer and barley grains before and after charring, further suggesting the potential for intra-species distinction. Wallace et al. (2018) expanded on these findings, using GMM to distinguish 'bere' barley grains from other British and Scandinavian landraces. Building on these studies, the potential of GMM in relation to morphologically-similar classes of glume wheats of different domestication statuses is explored here for the first time. Methodological uncertainties are also addressed in seeking to quantify which photographic views best allow us to distinguish between wheat types.

2. Methodology

The GMM analysis comprised four stages and is followed by a summary and update of results from a parallel chaff dehiscence study (Charles et al. 2021).

1. Testing the potential for GMM to distinguish between grains of modern glume wheat species.
2. Comparing archaeobotanical glume wheat grains from Çatalhöyük with modern reference material.
3. Analysing chronological changes in the morphology of the Çatalhöyük glume wheat grains

Table 1
Site names and references for NGW distribution map Fig. 1.

Fig. 1 key	Site Name	Country	References
1	Upper Seine Valley (multiple sites)	France	Toulemonde et al. (2015)
2	Petit Beaulieu	France	Toulemonde et al. (2015)
3	Vouziers	France	Toulemonde et al. (2015)
4	Hettange-Grande	France	Toulemonde et al. (2015)
5	Wanlo	Germany	Knörzer (1980); cited Jones et al. (2000)
6	Bedburg	Germany	Knörzer (1974); cited Jones et al. (2000)
7	Pié Fouquet	France	Toulemonde et al. (2015)
8	Gingsheim	France	Toulemonde et al. (2015)
9	Bad Camberg-Würges	Germany	Kreuz et al. (2005)
10	Vaihingen	Germany	Bogaard (2011)
11	Lucone	Italy	Perego (2015)
12	Lavagnone	Italy	Perego (2015)
13	Piancada	Italy	Rottoli and Castiglioni (2009)
14	Sammardenchia/Pavia di Udine	Italy	Rottoli and Castiglioni (2009)
15	Kamegg	Austria	Link (2004); cited Kenéz et al. (2014)
16 (/17)	Krems/Hundssteig	Austria	Kohler-Schneider and Caneppele (2009)
18	Sandberg	Austria	Caneppele et al. (2010)
19	Michelstetten	Austria	Kohler-Schneider and Heiss (2010)
20	Stillfried	Austria	Kohler-Schneider (2003)
21	Velištak	Croatia	Reed and Podrug (2016)
22	Slavča	Croatia	Reed (2017)
23	Százhalombatta-Földvár	Hungary	Stika and Heiss, 2012/3
24	Kujawy District	Poland	Bieniek (2007); Bieniek (2002)
25	Feudvar	Serbia	Borojevic (1991) cited Kohler-Schneider (2003); Reed (2016)
26	Dudeştii Vechi	Romania	Fischer and Rösch (2004)
27	Uivar	Romania	Fischer and Rösch (2004)
28	Parţa	Romania	Fischer and Rösch (2004)
29	Hódmezővásárhely	Hungary	Kenéz et al. (2014)
30	Klara Falva	Hungary	Kohler-Schneider (2003)
31	Ecsegfalva	Hungary	Bogaard et al. (2007)
32	Brehov-Pod	Slovakia	Hajnalova (2007)
33	Apsalos	Greece	Valamoti (2017)
34	Giannitsa	Greece	Valamoti and Kotsakis (2007)
35	Kleitos-Kremasti	Greece	Valamoti (2017)
36	Makriyialos	Greece	Jones et al. (2000)
37	Assiros Toumba	Greece	Jones et al. (2000)
38	Arkadikos	Greece	Jones et al. (2000)
39	Franchthi Cave	Greece	Hansen (1991) cited Jones et al. (2000)
40	Makri	Greece	Jones et al. (2000)
41	Karanovo	Bulgaria	Kreuz et al. (2005)
42	Yenikapı	Turkey	Ulaş and Fiorentino (2021)
43	Boncuklu/Çatalhöyük	Turkey	Baird et al. (2018); Bogaard et al. (2013), 2017
44	Aşıklı Höyük	Turkey	Ergun et al. (2018)
45	Mersin-Yumuktepe	Turkey	Ulaş and Fiorentino (2021)
46	Çadır Höyük	Turkey	von Baeyer et al. (2021)
47	Cafer Höyük	Turkey	de Moulins (1993) cited Jones et al. (2000)
48	Atskouri	Georgia	Kenéz et al. (2014)
49	Jeitun	Turkmenistan	Charles and Bogaard (2010)

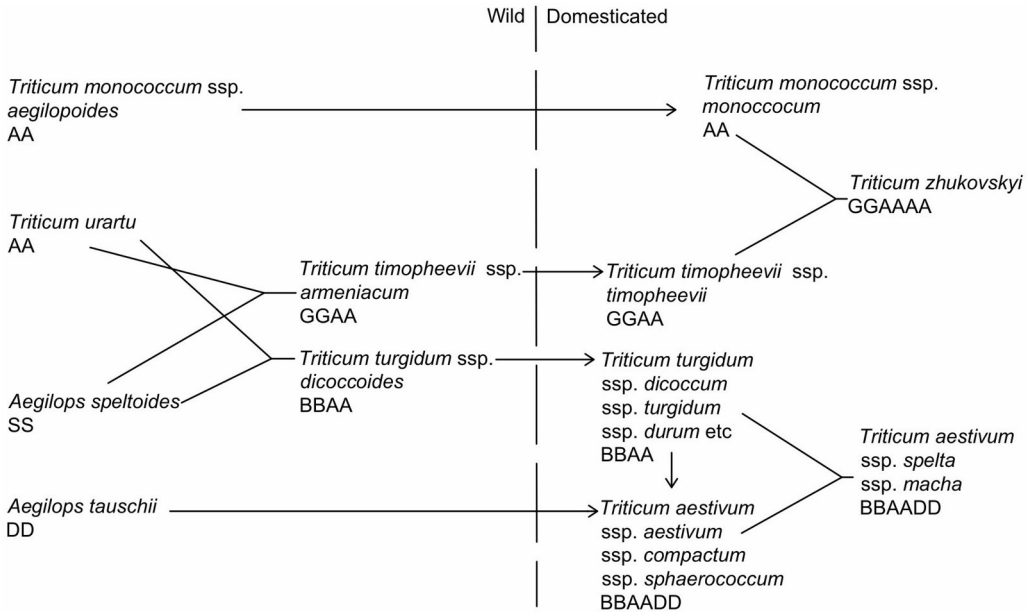

Fig. 2. Simplified genetic diagram showing relationships between wheat species after Li and Gill (2006).

4. Assessing the morphology of Çatalhöyük glume wheat grains as relating to processing stage

2.1. Approach

Because the form of a cereal grain is broadly 'continuous', the GMM methodology comprised a type of outline analysis, as opposed to a landmark-configuration approach dependent upon strongly-defined homologous points between individuals (Bonhomme et al. 2014). Here a set of points are still used to describe the shapes and 'landmarks' to align them, but the analysis assumes a closed outline in which the form is roughly circular or displays strong bilateral symmetry.

The outline analysis uses 'Fourier Series', which approach shapes as periodic functions, decomposing outlines into a series of harmonic sums of trigonometric functions weighted with harmonic coefficients (Bonhomme et al. 2014). The specific technique utilised is Elliptic Fourier Analysis (Giardina and Kuhl 1977; Kuhl and Giardina 1982) which has the advantage of not requiring equally spaced points and allowing for virtually any outline to be fitted (Bonhomme et al. 2014). It is applied using the package 'Momocs' (1.2.9) in R (3.6.2), as developed by Vincent Bonhomme, based on functions published by Claude (2008).

To establish a basis of comparison for the archaeological wheat grains, the outlines of multiple accessions of modern wheat grains were captured. Modern grains were photographed before and after charring, with charring conditions designed to replicate well-preserved archaeological material. Photographs were digitised and aligned before extraction into Momocs. The same procedure (minus charring) was applied to the archaeobotanical grains.

2.2. Sampling and photography

Modern reference material was acquired primarily through gene banks with multiple ears used to assess variation within and between accessions. To account for in-ear variation, accessions for which whole ears could be obtained were prioritised, as were those from geographically proximate locations to Çatalhöyük. Grains were sampled from the base, middle and top of the ear with row number and spikelet position recorded. Where whole ears could not be obtained – e.g. as with wild forms which typically shatter before harvest – ear position was reconstructed by counting vascular bundles to procure an equivalent sample (after Whingwiri et al. 1981).

The final comparative dataset of modern material consisted of 438 grains (Table 2), with the primary dataset comprised of wild and domesticated emmer and Timopheev's wheat. Part-way through analysis it was observed that archaeological 'two-grained einkorn' (*Triticum monococcum* ssp. *monococcum* L.) was similar in appearance to modern *T. araraticum*. Therefore, reference specimens of two-grained einkorn were added to the dataset. As direct comparability of the (potentially environmentally-influenced) modern two-grained einkorn and the archaeologically-observed form remains uncertain (Kreuz and Boenke 2002), this category was represented by modern accessions (Table 2) supplemented by five well-preserved, securely-identified grains from Neolithic Vaihingen, Germany (Bogaard 2011), numbering 38 grains in total. This category was added primarily to prevent misidentification between NGW and two-grain einkorn. However, as relatively limited quantities of material were available, a more systematic analysis of this wheat type would be desirable in the future.

Archaeological grains were selected based on preservation, with those exhibiting clear distortion or damage excluded. Observed signs of distortion resulting from high charring temperatures included protrusions resulting from endosperm exudation, severe blistering of pericarp and large cavities within the grain (Charles et al. 2015). Abraded grains for which there was little or no survival of the outer pericarp were also excluded.

Grains were photographed in dorsal, lateral and polar view (Fig. 3) using a Nikon SMZ25 stereo microscope with an apochromatic optical system and Pixelink M12BC-CYL microscopy camera.

2.3. Charring

Modern grains were charred to replicate well-preserved archaeological material after Charles et al. (2015). Grains were individually wrapped in foil and buried in beakers of sand to reduce oxygen availability. The beakers were then placed in a preheated oven at 230 °C for 6 h. Temperature was monitored using thermacouples and a datalogger to ensure a consistent temperature was maintained throughout.

Table 2

List of modern accessions used as comparative material for GMM analysis. 'In gl.' = in glume. * = used for Stage 1 analysis. In addition, five securely identified 2-grain einkorn grains from Vaihingen were included to a total comparative dataset of 443 grains.

Subspecies	Common name	Source	Accession	Origin	No. grains
monococcum	Einkorn (2-grain form)	Berzsenyi College	FOT145142	Romania	26
monococcum	Einkorn (2-grain form)	Mark Nesbitt (Kew)	RMN7537	Unknown	7
araraticum	Wild timopheev's	Gatersleben	TRI11509	Iran	27*(+27 in gl.)
araraticum	Wild timopheev's	John Innes	1150001	Azerbaijan	27*
araraticum	Wild timopheev's	John Innes	1150003	Unknown	27*
timopheevii	Domestic. timopheev's	John Innes	T1160001	Georgia	27*
timopheevii	Domestic. timopheev's	Gatersleben	TRI677	Soviet Union	27* (+27 in gl.)
timopheevii	Domestic. timopheev's	CGN Wageningen	CGN10497	Soviet Union	27*
dicoccoides	Wild emmer	Gatersleben	TRI11501	Turkey	27*
dicoccoides	Wild emmer	Gatersleben	TRI11502	Turkey	27*
dicoccoides	Wild emmer	Gatersleben	TRI16629	Israel	27*
dicoccum	Domestic. emmer	John Innes	1070018	Georgia	27*
dicoccum	Domestic. emmer	Gatersleben	TRI17251	Switzerland	27* (+27 in gl.)
dicoccum	Domestic. emmer	USDA	PI434999	Bosnia & Herzegovina	27*



Fig. 3. Dorsal, lateral and polar views of a grain of domesticated Timopheev's wheat, traced and with alignment points added.

2.4. Digitisation

Grain outlines were traced and aligned using AutoCAD, a design and drafting program. Embryos were excluded as these neither consistently remain attached, nor are likely to be equally developed across specimens (Fig. 3). After Bonhomme et al. (2017), polar views were flipped to face the same direction to account for the strong bilateral asymmetry often exhibited.

Coordinates of outlines were then extracted and saved as. txt files, which take up little file space, can be easily shared and avoid loss of resolution. The number of coordinate points per outline varied between 35 and 80. Comparison with outlines using a wider range (25–155 points) affected reclassification rates by <1%, suggesting the method is not sensitive to the precise number of points used. Repeatability was tested after Evin et al., (2020, 3–4), whereby five grains of the same species were each

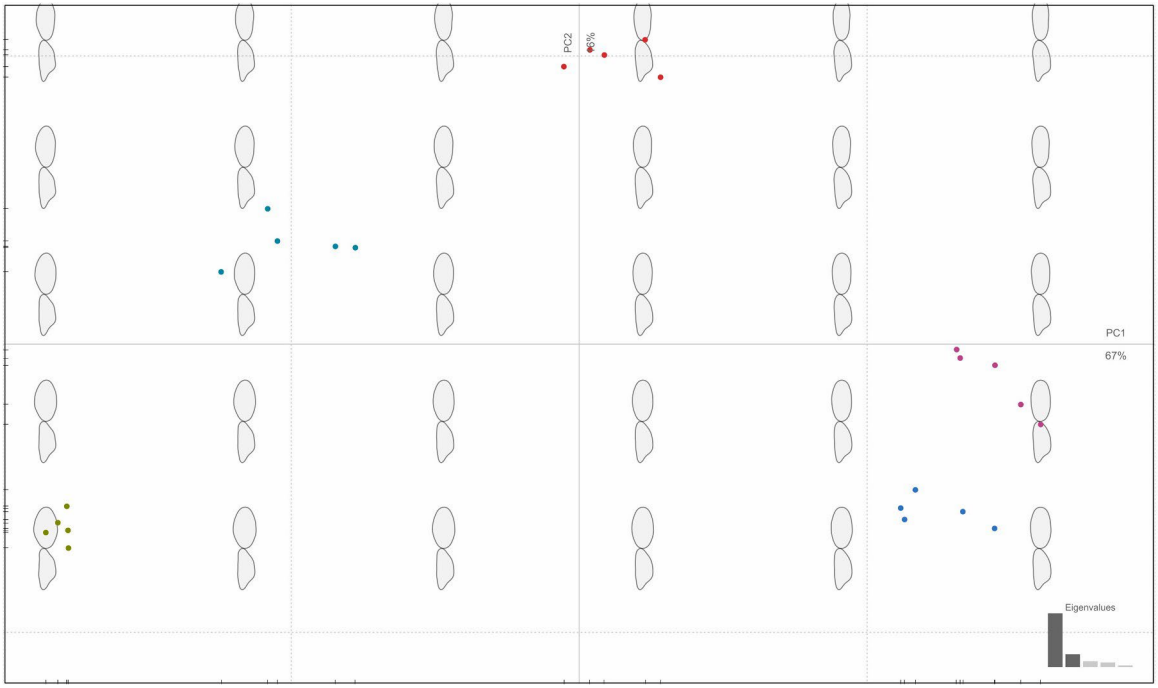

Fig. 4. PCA results of combined dorsal and lateral views when five grains from the same accession were each photographed and digitised five times (each colour = one specimen).

photographed and digitised five times in five separate sessions. When a principal components analysis (PCA) was performed on combined dorsal and lateral outlines (see Section 3, Stage 1, below) it produced clustering by specimen, although some variation was noted (Fig. 4). Measurement error was calculated after Claude (2008, 65), using Procrustes ANOVA of PCA scores, as 12.51% for the dorsal view and 9.55% for the lateral view. In both views, ANOVA produced significant scores ($p = 0.001$) when specimen was used as an independent variable, and non-significant scores (0.999–1.000) when session was used. This suggests the five sessions did not produce significantly different sets of grain shapes and that variation between session was less significant than variation between specimens.

2.5. Analysis

Once imported into Momocs, outlines were scaled by centroid size to focus the analysis on shape differences. After Bonhomme et al. (2017), Elliptical Fourier Transforms were calculated for the outlines of each grain view individually, before being combined. Eight harmonics were retained for each view, gathering at least 99% of the total harmonic power. In Elliptic Fourier Analysis four coefficients per harmonic are obtained and multivariate analyses can then be performed on these Fourier coefficients (Bonhomme et al. 2014, 8).

Both principal components analysis (PCA) and linear discriminant analysis (LDA) were performed on the transforms, with the former allowing for visual exploration of the data including spotting alignment errors. LDA with leave-one-out cross-validation was used to test the extent to which grains which could be correctly reclassified by species, scoring each known species ('actual') against its designation using the model ('classified'). When archaeobotanical material was introduced as an unknown category, the LDA classified it according to the known type it most closely resembled. When plotted, the LDA uses known class data (e.g. species) to visualise the maximum possible separation based on morphology. When archaeobotanical material is introduced, the plot indicates where the material most closely aligns on the modern spectrum.

3. Results

The following results were generated using data available under supplementary material folders 'GrainCoordinates' (.txt grain outlines), 'GrainDataFrames' (associated.csv files) and 'Classification Files' (summaries of classifications), together with the accompanying R script (https://github.com/TinaRoushan/New-Glume-Wheat-Geometric-Morphometrics).

3.1. Stage 1: modern baseline study

Grains of wild and domesticated Timopheev's wheat (hereafter '*T. araraticum*' and '*T. timopheevii*') and domesticated emmer wheat ('*T. dicoccum*') were compared, to establish whether GMM could accurately reclassify them as the correct species and which photographic views were most useful in doing so. A total of 81 grains were used per species from nine accessions in total (Table 2).

Pre-charring, reclassification by species was almost perfect at 99.2% (Table 3). These rates decreased slightly after charring, with dorsal and lateral views in combination correctly reclassifying at 96.3% (Table 4), a slightly higher score than when all three views were used. Regardless of charring status, the polar proved the least useful single view, while the lateral view produced the highest scores when used alone (Tables 3 and 4). The polar view is seemingly not only the least diagnostic pre- charring, but also distorts more than other views during charring. It was therefore concluded that there was strong justification to exclude this view from further analyses.

Table 3
Results of LDA showing percentage of modern grains correctly classified by species before and after charring when different photographic views used. Highest scores before and after charring are in bold.

View	Uncharred reclassification rate (%)	Charred reclassification rate (%)
Dorsal	90.9	83.1
Lateral	97.5	94.2
Polar	72.4	60.5
Dorsal and lateral	**99.2**	**96.3**
Dorsal and polar	95.5	88.5
Lateral and polar	98.8	94.2
Dorsal, lateral and polar	**99.2**	95.1

Table 4
Results of LDA showing percentage of modern grains correctly classified by species after charring when dorsal and lateral views used in combination.

	Classified as		
Actual	*T. araraticum*	*T. dicoccum*	*T. timopheevii*
T. araraticum	78	0	3
T. dicoccum	0	79	2
T. timopheevii	1	3	77
Class correctness	96.3%	97.5%	95.1%
Leave-one-out cross validation	96.3% (234/243)		

Subsequently, the modern dataset was expanded using dorsal and lateral views of an equivalent sample of wild emmer grains (*Triticum turgidum* ssp. *dicoccoides* (Körn. ex Asch. & Graebn.) Thell.; Table 2). With this addition, separation between species after charring remained robust (Fig. 5), with reclassification rates reducing only slightly to 95.4%.

This stage of analysis was able to confirm the ability of the GMM model to distinguish between charred grains of wild/domesticated emmer and Timopheev's wheat to a high level of accuracy. The highest reclassification rates were achieved when the dorsal and lateral views were used in combination.

3.2. Stage 2: comparison with archaeobotanical material from Çatalhöyük

Dorsal and lateral views of well-preserved emmer and NGW grains from a range of East Mound contexts were subsequently compared with the modern wheat grains.

Initially, 86 archaeological grains confidently identified from 'pure deposits' of either emmer or NGW (Appendix A) were added to the LDA as separate named categories, alongside the known modern types analysed above and the smaller sample of two-grain einkorn. It was observed that the grains plotted as two distinct groups: archaeological emmer overlapping with modern emmer and NGW plotting between wild and domesticated Timopheev's wheat (Fig. 6). These results support the morphological affinity between NGW and Timopheev's wheat as previously observed in chaff remains (Jones et al. 2000).

To expand the dataset, archaeological grains from less certain 'mixed' deposits (i.e. containing more than one type of wheat identification) were then added as an unknown category for reclassification. Based on the LDA, they were assigned as either emmer, NGW or excluded (e.g. if classified as 'two-grained einkorn'; see supplementary data for further details). The aim of this approach was to not allow the original archaeobotanical identification of a grain to pre-determine the assigned category, but rather to rely on the GMM model. As a result, numerous grains of uncertain classification (e.g. labelled 'emmer/NGW') could be identified, while a few grains were reassigned to different species

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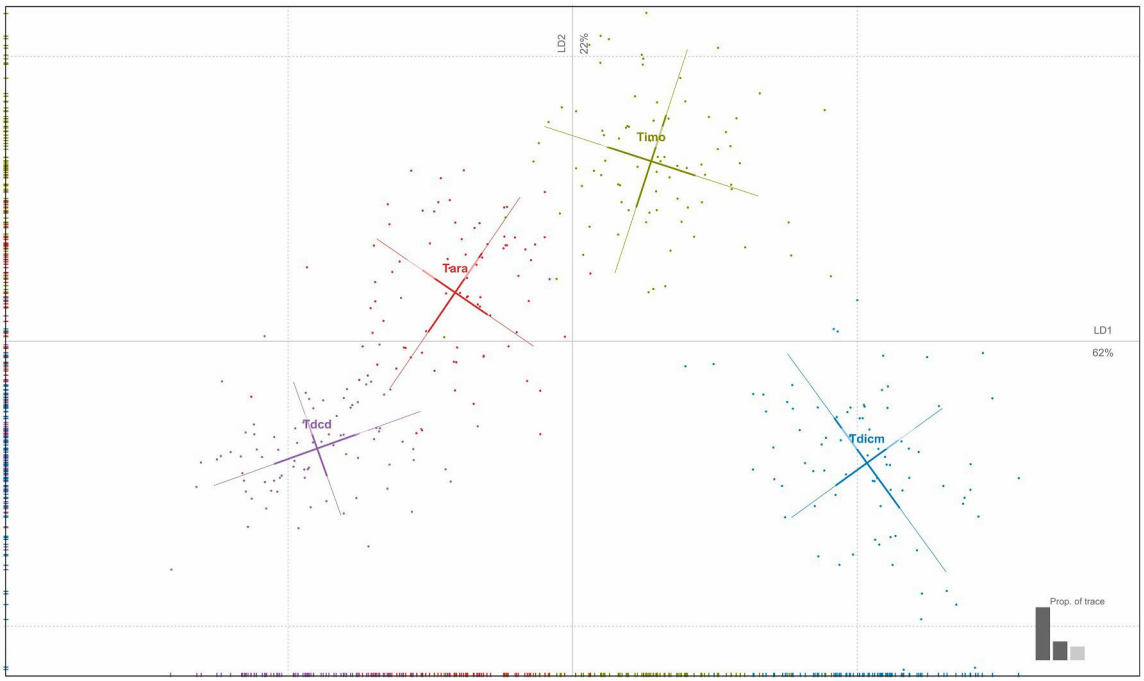

Fig. 5. LDA results showing separation of modern glume wheat species based on grain shape ('Tdcd' = *T. dicoccoides*, 'Tara' = *T. araraticum*, 'Timo' = *T. timopheevii*, 'Tdicm' = *T. dicoccum*).

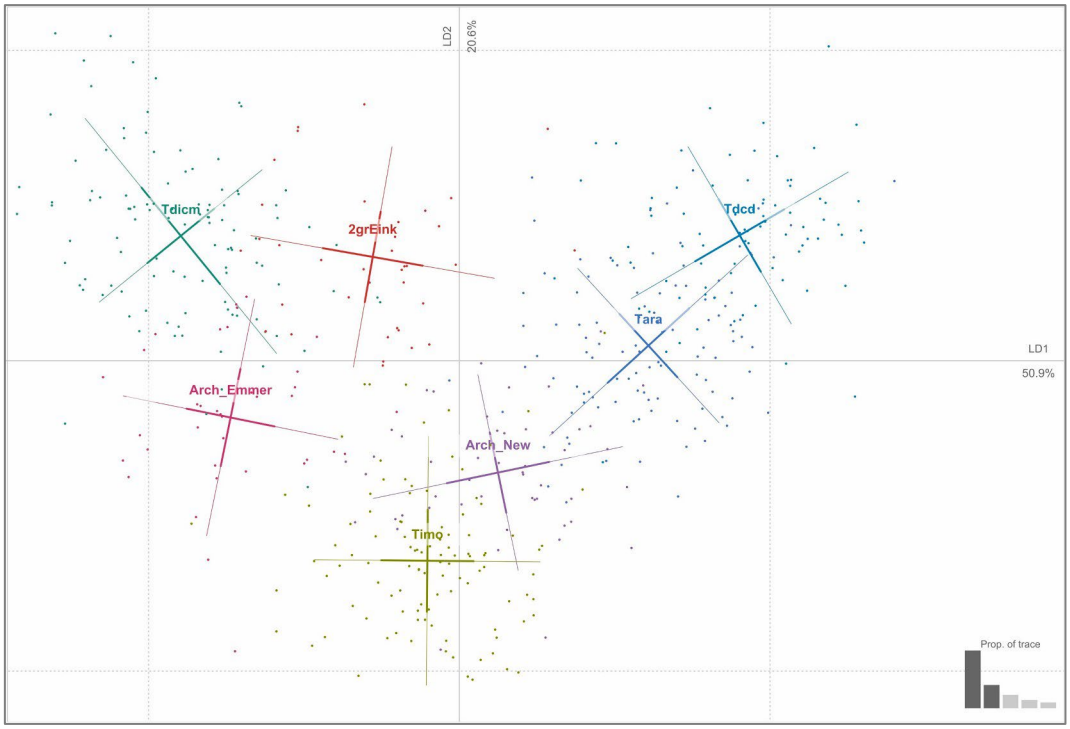

Fig. 6. LDA showing relationship of archaeological emmer ('Arch_Emmer') and NGW ('Arch_New') grains from 'pure' deposits to comparative dataset of glume wheats. NGW grains are positioned between wild ('Tara') and domesticated ('Timo') Timopheev's wheat. ('Tdicm' = *T. dicoccum*, '2grEink' = two-grained einkorn, 'Tdcd' = *T. dicoccoides*).

The final dataset contained 443 grains of comparative material (Table 2) and 231 Çatalhöyük grains identified as emmer or NGW, combining both grains from 'pure deposits' and those identified in comparison with these using GMM analysis, from a total of 60 contexts (Appendix A). This dataset was then used to conduct analyses by phase and relating to processing stage.

3.3. Stage 3: analysis by phase

Archaeological grains were subsequently coded by chronological phases as defined in Hodder (2021, 11): Early (7100–6700 cal. BC), Middle (6700–6500 cal. BC) and Late(-Final) (6500–5950 cal. BC). This time, the LDA showed that NGW grains from the Early phase plotted more closely to *wild* Timopheev's

wheat and over time plot increasingly closely to *domesticated* Timopheev's wheat, with the most significant shift apparent between Early and Middle phases (Fig. 7). When archaeological emmer grains were coded by phase no such pattern was apparent.

NGW grains were then entered as 'unknowns' into an LDA using wild and domesticated Timopheev's wheat as classifiers. In the Early phase 57.1% of NGW grains classified as wild, decreasing to 20.4% by the Late phase (Table 5). A chi-squared test on the classifications produced p- values of <0.05 when comparing Early with Middle and Late phases, but produced a value of 0.3654 when Middle and Late phases were compared. This gives confidence in a significant shift between Early and Middle phases towards the domesticated form, if not between Middle and Late phases.

Comparing stacked outlines of NGW grains across phases revealed only subtle changes (Fig. 8). In the lateral view, dorsal curvature becomes slightly more pronounced, with the widest point of the grain shifting towards its apex. In the dorsal view, the widest point of the grain shifts slightly in the same direction, particularly in the Middle phase. Potentially these changes are concentrated towards the top of the grain because it is less tightly constrained by the glumes. These outlines provide useful identification criteria for NGW grains in line with those reported by Kohler-Schneider (2003), including a 'rather rounded apex' and dorsal edge running more parallel to the ventral than emmer when viewed laterally (Fig. 9).

Grain size was also measured, taking length and width in the dorsal view and depth in the lateral (after Charles et al. 2021). Between the Early and the Middle phase all three average NGW measurements increased, decreasing very slightly in the Late phase. For the emmer grains the largest measurements are from the *Early* phase with no clear differentiation between Middle and Late phases (Table 6).

In summary, analysis of both shape and size suggest a shift in NGW grains between Early and Middle phases towards larger grains which more consistently resemble domesticated Timopheev's wheat in shape. This development in form persists into the Late phase, although a small size decrease is noted (<0.07 mm in any dimension). In contrast, emmer grains at no stage resemble wild emmer and are well-developed in size from the earliest phase.

Table 5
Results of LDA classification when NGW grains entered as unknowns against modern *T. araraticum* and *T. timopheevii* grains and p-values of chi-squared test performed on frequency tables.

Phase	Grains classified as *T. araraticum*	Percent classified as *T. araraticum*
Early	16/28	57.1%
Middle	16/53	30.2%
Late	10/49	20.4%
P-value (all phases)	0.0037	
P-value (early vs mid only)	0.0339	
P-value (mid vs late only)	0.3654	
P-value (early vs mid + late)	0.0032	

3.4. Stage 4: analysis by processing stage

This stage sought to establish whether the archaeological grains were charred within their glumes (i.e. prior to dehusking) or as individual grains. Therefore, the data was recoded to reflect the subset of modern grains charred within their glumes (Table 2) and extracted before photographing.

In the LDA results, both NGW grains and emmer grains consistently plotted more closely to modern 'in glume' grains than those charred individually (Fig. 10), indicating that the archaeobotanical grains more closely resemble grains charred in their glumes. Results suggest a morphological distinction between grains charred, prior to, and after, dehusking, with glume-enclosed grains appearing slightly laterally compressed and 'hunched' in appearance (Fig. 11). Based on the analysis we can propose that the majority of grain at Çatalhöyük came to be charred whilst stored in its glume

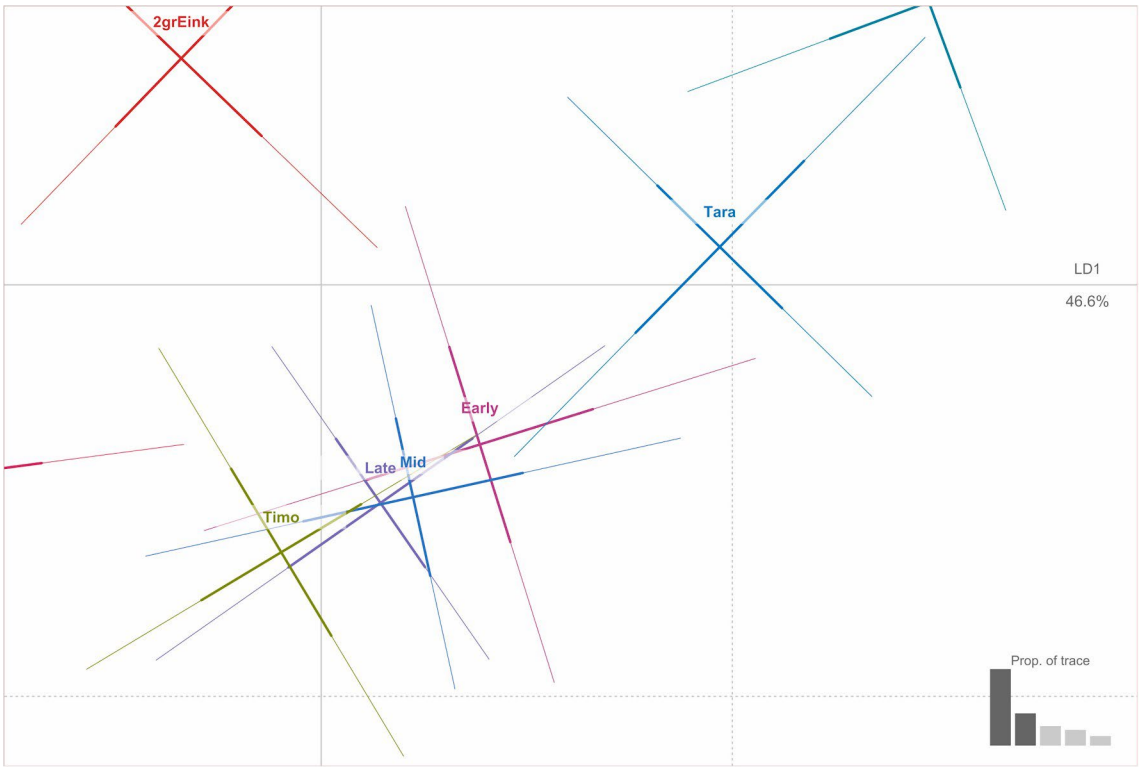

Fig. 7. LDA results when plotted with full dataset and NGW grains recoded as 'Early', 'Mid' and 'Late' phase (Timo = *T. timopheevii*, Tara = *T. araraticum*).

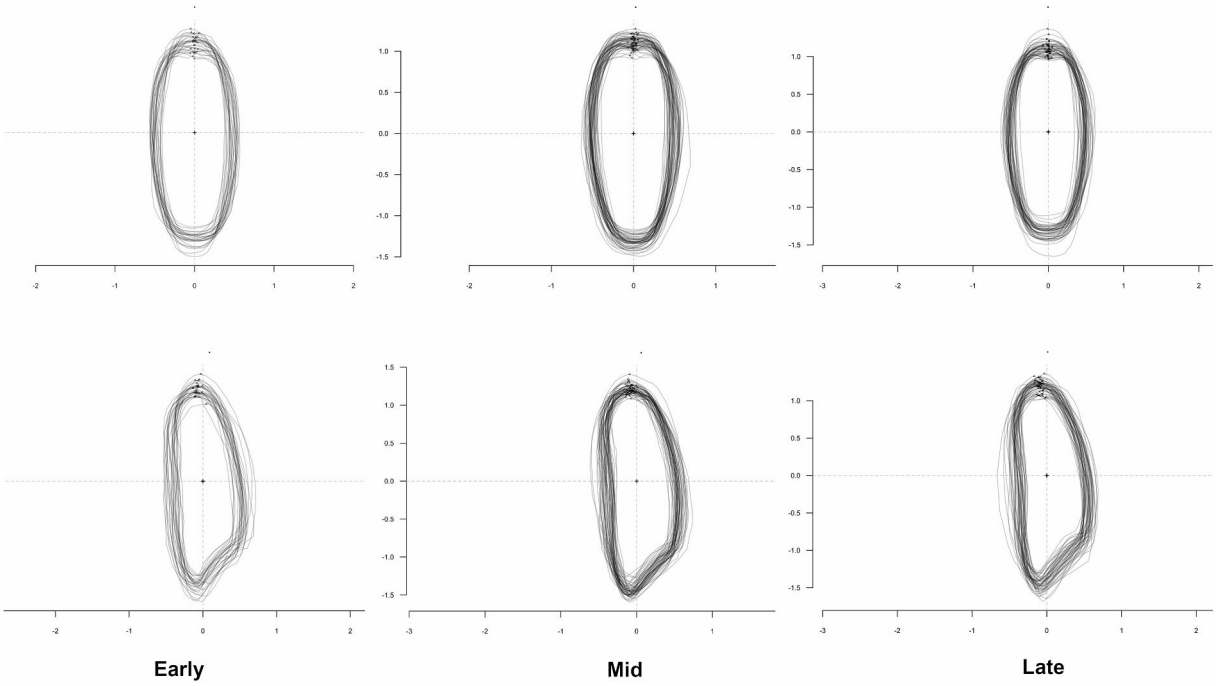

Fig. 8. Stacked outlines of Çatalhöyük NGW grains from Early, Mid and Late phase contexts.

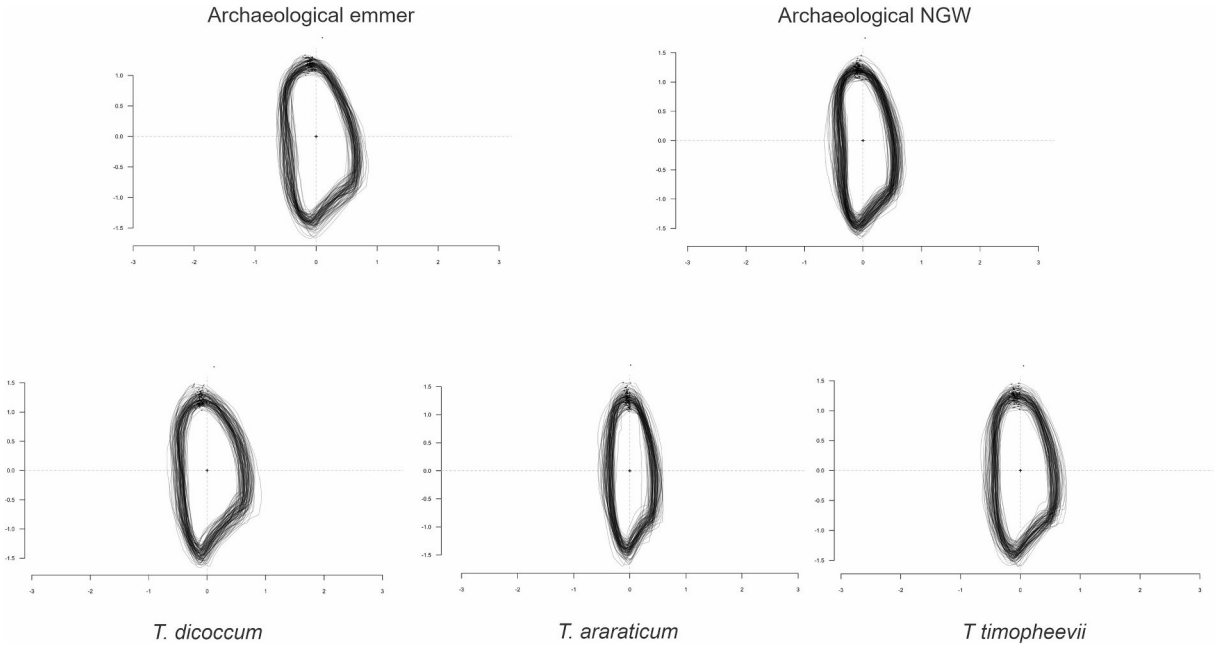

Fig. 9. Stacked outlines of Çatalhöyük emmer and NGW grains (all phases) alongside modern *T. dicoccum*, *T. araraticum* and *T. timopheevii* in lateral view.

Table 6

Average dimensions of Çatalhöyük NGW and emmer grains summarised by phase. Depth = widest point of grain in lateral view

	Average length (mm)	Average width (mm)	Average depth (mm)
Emmer			
Early	5.8834	2.9028	2.5585
Middle	5.4368	2.8435	2.4745
Late	5.7331	2.8368	2.4556
NGW			
Early	5.3095	2.1425	1.8984
Middle	5.6882	2.4428	2.0626
Late	5.6561	2.3823	2.0520

and prior to dehusking; this complements direct evidence of spikelet storage in the form of intact NGW spikelets recovered from Building 77 (Bogaard et al. 2013).

3.5. Assessing dehiscence from chaff morphology

A previous study of NGW chaff remains from Çatalhöyük supports the theory that the crop underwent domestication during the course of the settlement (Charles et al. 2021). This study is summarised here and updated with an increased sample of chaff remains from the Early phase.

The study analysed spikelet bases after Tanno and Willcox (2012), on the basis that domesticated wheats do not 'shatter' to distribute their seeds, i.e.

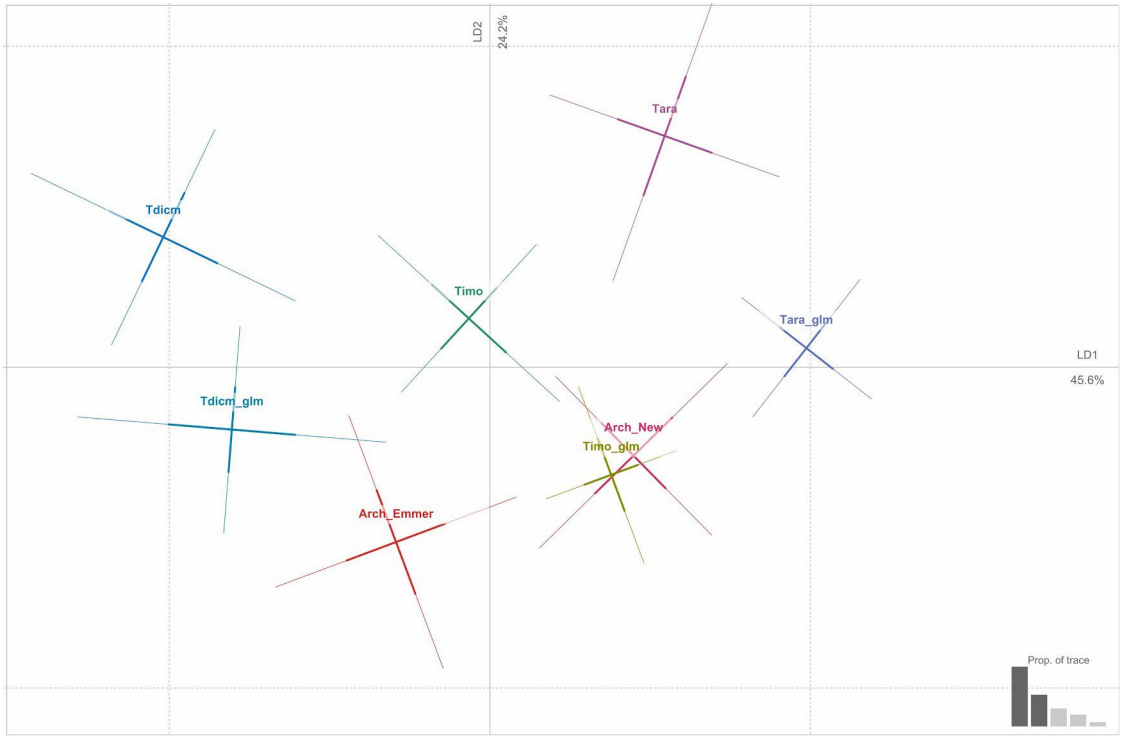

Fig. 10. LDA showing archaeological grains ('Arch_Emmer' and 'Arch_New') plotting more closely to modern grains which were charred in chaff ('_glm'). ('Tdicm' = *T. dicoccum*, 'Timo' = *T. timopheevii*, 'Tara' = *T. araraticum*).

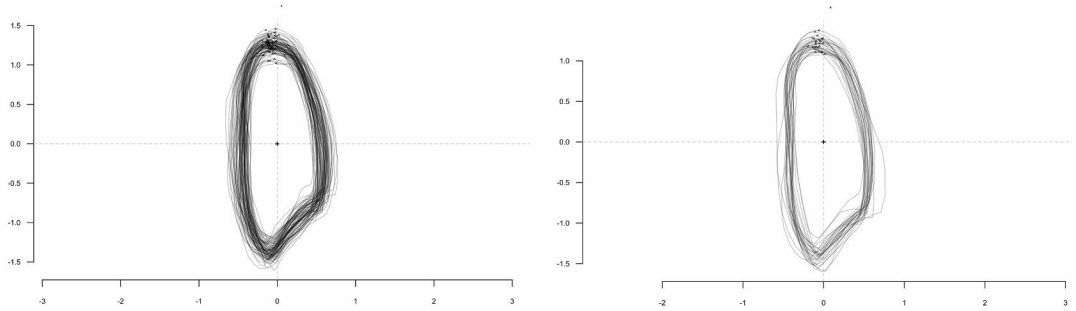

Fig. 11. Stacked outlines of *T. timopheevii* grains when charred as individual grains (left) and when charred within glume/chaff (right).

the ear does not disarticulate into individual spikelets upon maturity but needs to be threshed after harvesting. The attachment point of each spikelet (or 'abscission scar') will therefore show signs of tearing, with part of the adjoining rachis segment more likely to remain attached. Wild forms detach naturally when ripe and the abscission scars are more likely to be smooth (Fig. 12; see also Charles et al. 2021). However, sometimes part of the rachis internode can remain attached to wild forms, and in emmer wheat these can be distinguished by profile (Weide 2015).

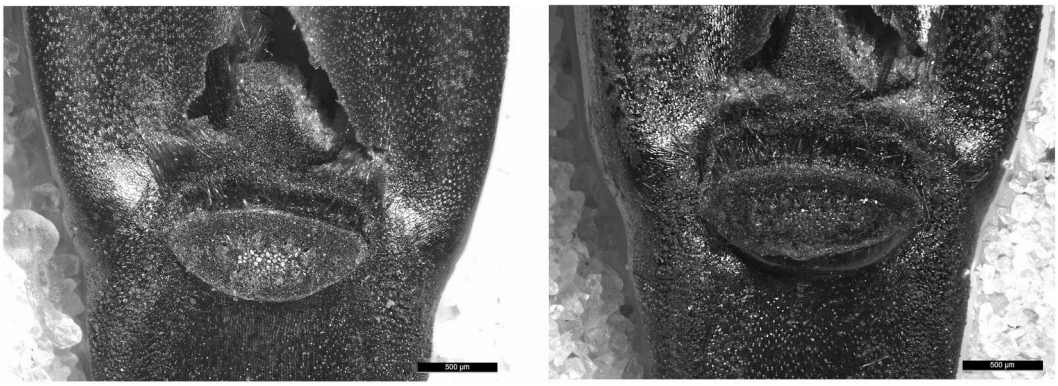

Fig. 12. Abscission scars of *T. araraticum*, showing the more common 'smooth' form (left) and the less common protruding form with tearing visible (right).

Analysis of modern Timopheev's wheat spikelets established that no distinction between wild and domesticated forms could be made based on *individual* scar profiles. However, there were clear differences in the proportions of scar types, with domesticated populations having a much higher proportion of 'rough' and 'protruding' (with partial rachis segment attached) scars while wild specimens had predominantly 'smooth' scars (Fig. 12). When NGW chaff from Çatalhöyük was examined it was observed that, where the rachis segment remained attached, it exhibited the same profile as in Timopheev's wheats: an abrupt or 'knee-shaped' transition to the upper rachis segment. Furthermore, a clear temporal trend from smoother to rougher scars was observed in the NGW remains, suggesting decreased shattering tendency over time (Fig. 13). Also observed was an increase in 'terminal' spikelets (i.e. from the top of the ear) between the Early and Late phase, significant because these generally detach first in shattering forms. Emmer spikelet bases from Çatalhöyük neither exhibited a comparable trend as regards proportions of 'rough' scars, nor were any spikelets identified which exhibited the 'wild-type' rachis attachment profile described in Weide (2015).

Overall the chaff evidence suggests selection for non-shattering forms in NGW over the course of the East Mound settlement sequence. In comparison, the morphology of emmer wheat as a non-shattering wheat was apparently established prior to the earliest settlement phase.

4. Discussion

4.1. Domestication processes

The GMM grain analysis and parallel chaff study support close comparability of NGW with modern Timopheev's wheats. Moreover, the findings demonstrate changes to grain size/shape and ear shattering behaviour during the East Mound sequence. These changes constitute a shift from remains more closely resembling wild Timopheev's wheat to those more closely resembling the domesticated crop. The developments emerged gradually over a period of 1150 years, prompting consideration of the degree to which these traits were consciously selected by cultivators.

A co-evolutionary approach to domestication considers human-plant interactions as relationships with both intended and unintended consequences (Jones et al. 2021). Niche construction forms part of a broader process of co-evolution in which all organisms actively and continuously participate (Bogaard et al. 2021a). Human interaction with the environment creates specific conditions in which certain functional ecological traits may gain competitive advantage: for example, by modifying growing conditions or acting as dispersal agents. In turn, humans become increasingly dependent on those plants which thrive in anthropogenic environments (Rindos et al. 1980; Rindos 1984).

As regards ear shattering behaviour, selection for decreased dehiscence continued into the Late phase as the crop was increasingly relied upon as a staple across the settlement. Changes in dehiscence are usually explained in terms of harvesting methods (Charles et al. 2021). Chert and obsidian sickle-type blades are attested from Early phase levels at Çatalhöyük (Carter 2011) and use-wear analysis of blades indicates repeated cutting of cereals, albeit in a limited number of cases (Lemorini and D'Errico 2021). Sickle harvesting, or any harvesting method that recovers the entire ear (as opposed to hand-gathering mature spikelets), gives 'non-shattering' plants a competitive advantage, with seeds from non-shattering plants more likely to be harvested and sown the following year, whilst also enhancing reliability and yield of the crop for humans. However, sickle-harvesting is not the sole mechanism for increasing indehiscence, and annual harvesting and sowing cycles may also exert a gradual influence (or 'weak selection') even when ears are not cut (Maeda et al. 2016) which may over time increasingly encourage the use of sickles.

The gradual pace of change in grain form, and the fact that seed-size by itself is not a predictor of yield (Jones et al. 2021), mean we cannot explain this process purely in terms of human desire to increase harvests. Research has demonstrated that larger seeds of wild crop progenitors are more successful in rich, disturbed anthropogenic environments, germinating more quickly and producing larger seedlings/plants with more robust root systems (Jones et al. 2021). Analysis of arable weed flora suggests that Çatalhöyük crops were grown in tilled and fertile soil (Green et al. 2018), i.e. conditions conducive to selection for larger seeds. As seed size increased, and the plants adapted to these types of conditions, they would become increasingly dependent on human amendment of the soil to thrive. It is therefore likely that both human intervention and environmental selection interacted to produce the developments in NGW at Çatalhöyük, and that the role of human intention was both 'complex and indirect' (Bogaard et al. 2021a, 10).

The observed changes do not represent an entire domestication sequence, as NGW remains from the earliest phase are not entirely 'wild'; rather, a greater proportion more closely resemble wild forms, and these early populations are perhaps best described as 'semi-shattering'. A possible alternate theory is that during periods of early adoption, seed stock of domesticated NGW was bolstered by wild stands (Willcox 2005). However, although wild Timopheev's wheat has been identified in Turkey, these observations are confined to the south-east of the country (Mitrofanova et al. 2016; Badaeva et al., 2022), outside Central Anatolia. While we cannot rule out *T. araraticum* having been present in the region during the Neolithic period, it seems more likely that a partially-domesticated form of the wheat was available from the earliest phases and continued to undergo adaptation during the course of the settlement.

4.2. Incentives for cultivation of NGW

The more widespread cultivation of NGW and its adoption in the South Area by the Late phase coincides with the development of desirable qualities

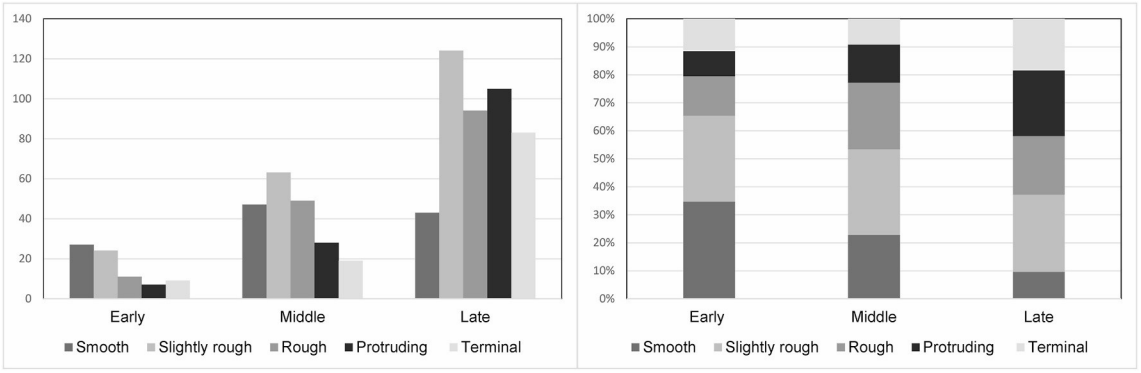

Fig. 13. Number and proportion of different categories of abscission scar types at Çatalhöyük by phase.

in the crop relating to seed size and shattering. We may, however, question what motivated initial investment in this crop in the North Area — particularly when emmer wheat, a crop with similar processing and environmental requirements was readily available in domesticated form.

The inhabitants of Çatalhöyük had a broad subsistence base of cultivated and gathered food-plants, and experimentation with different resources was potentially a way of buffering risk against individual resource failures (Bogaard et al. 2017). It is therefore possible that cultivating multiple wheat crops was considered 'less risky' in the face of potential climate fluctuation or disease. While we cannot be certain of the specific traits of NGW or how they were perceived, modern Timopheev's wheat possesses significant resistance to fungal diseases including leaf and stem rust (Leonova et al. 2002). Both Turkey and Georgia fall within the region vulnerable to highly damaging wheat rust diseases (Food and Agriculture Organization of the United Nations, 2014), so potentially this resistance was advantageous at Çatalhöyük and/or within the context of its cultivation in the recent past.

Other factors providing more personalised incentives might include the culinary qualities of specific plants and/or their ability to mark social differentiation between households. In Georgia, as part of the maslin 'Zanduri', fragile ears of Timopheev's wheat were harvested using a pair of wooden rods called 'shnakvi' (Mitrofanova et al., 2016). The grain was used to make 'Zanduri bread' which was associated with special occasions (Jorjadze et al. 2014) and for feeding fowl, while the straw was used for roofing (Mitrofanova et al. 2016). It is possible that while potentially adapted to multiple functions, NGW was also used in specific culinary preparations associated with particular households, other social groupings and/or occasions. Its cultivation may also have been associated with certain tools or practices which marked out its farmers as a distinct group.

5. Conclusion

GMM analysis of NGW grains from Çatalhöyük established a strong morphological similarity with modern Timopheev's wheat. These findings reinforce links previously made using chaff (Jones et al. 2000) and aDNA (Czajkowska et al. 2020) and we therefore propose that NGW be described in future as *Triticum timopheevii s.l.* (*sensu lato*) (after Badaeva et al. 2022), reserving *T. timopheevii s. str*. (*sensu stricto*) for the narrowly endemic modern form.

Results further demonstrate the potential of GMM to distinguish between charred grains of morphologically-similar wheat species and sub-species of differing domestication status; particularly when the dorsal and lateral views of the grain are used. The method even appears sufficiently sensitive to suggest whether grains were dehusked before storing. Applications of GMM to archaeobotanical studies of wheat therefore seem promising, including at sites where identification of *T. timopheevii s.l.* remains uncertain, or for further studies of the transition between wild and domesticated wheats. Research into refining identifications of free-threshing wheats forms and expanding modern comparative datasets is also currently underway.

At Çatalhöyük, comparison of NGW with modern Timopheev's wheats suggests that the crop underwent domestication processes during the Neolithic East Mound sequence. In the Early phase a higher proportion of NGW grains resemble wild Timopheev's wheat and become more similar to the domesticated form over time, accompanied by a size increase. Changes in grain form were most marked between the Early and Middle phases, coinciding with more widespread adoption of the crop in the North Area. Building on previous work (Charles et al. 2021) analysis of NGW chaff morphology also detected a reduction in shattering. This decrease in shattering continued into the Late Phase, by which time the NGW had apparently replaced emmer as the settlement's main wheat crop. In contrast to NGW, emmer wheat was found to be more fixed in form, being well-developed in both size and non-shattering properties from the earliest phase.

It is proposed that a partially-domesticated form of NGW was available from the earliest phases and continued to undergo adaptation over the course of the settlement. Sickle harvesting and cultivation in relatively fertile and disturbed soil facilitated a gradual co-evolutionary process whereby both human intervention and environmental conditions selected for mutually beneficent traits of reproduction and yield. The role of human intention in these changes is understood to be 'complex and indirect' (Bogaard et al. 2021a, 10) as opposed to a unidirectional process of selection. Possible incentives in the initial uptake of the crop may have included culinary qualities, cultural differentiation between households, its resistance to fungal disease and/or its multi-functional properties. More broadly, investment in the crop may be understood within the context of a broad-spectrum plant strategy (Bogaard et al. 2017), in which risk of individual resource failure was offset by diverse strategies at the household level.

Declaration of competing interest None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jas.2022.105599.

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