# 1

## Introduction

## Changing Paradigms in Our Understanding of the Transition to Agriculture: Human Bioarchaeology, Behaviour and Adaptation

### Jay T. Stock<sup>1</sup> and Ron Pinhasi<sup>2</sup>

 <sup>1</sup> Leverhulme Centre for Human Evolutionary Studies, Department of Biological Anthropology, University of Cambridge, Cambridge, UK
<sup>2</sup> Department of Archaeology, University College Cork, Cork, Ireland

The evolution and history of our species is often considered as a series of major transitions and processes of evolution, which collectively 'make' us human (Klein, 2009). In this context, it is easy to view modern human origins and dispersals as the end of a long process of cultural and biological evolution, and the point of demarcation between the end of biological evolution and the period when socio-cultural evolution and diversity becomes the hallmark of our species (Dyson, 1997). The 'Neolithic Revolution', a term coined by Gordon Childe, is the central component in this perspective, referring to the transition from hunting and gathering to agricultural subsistence in the Holocene. It has been seen as perhaps the single most significant social, cultural and biological transition since the origin of our species, marking the development of human control over the reproduction and evolution of plants and animals (Childe, 1936). A natural conclusion of this perspective suggests that the Neolithic marks the period where humans shifted from being subject to changes in the natural environment, to become the agents of environmental change in which the natural world is modified to suit human needs.

The transition to agriculture is often viewed as the beginning of a series of significant changes in human social organization, on the basis of the rise of food production and the storage of food surpluses. These are interpreted as leading to property ownership, social hierarchy, task specialization and runaway technological evolution, which is fuelled by a surplus of food (Diamond, 1997). In this context, agriculture can also be viewed as a form of niche

Human Bioarchaeology of the Transition to Agriculture Edited by Ron Pinhasi and Jay T. Stock © 2011 John Wiley & Sons, Ltd.

colonization, which allows populations to enter a new adaptive niche within the same environment as hunter-gatherers. When this is combined with food surpluses, it results in reduced interbirth intervals; increased birth stacking associated with alloparenting, and increased fertility (Wells and Stock, 2007). It has long been speculated whether demographic shifts amongst hunter-gatherer societies stimulated this cultural change, because greater numbers could not be sustained on the basis of hunter-gatherer subsistence (Boserup, 1965; Cohen, 1977), and it has recently been argued that consensus falls on this 'push' model (Cohen, 2009). Regardless of whether demography was a causal factor in development of agriculture in different regions, it is apparent that major demographic change was a primary consequence of the transition to agriculture (Bocquet-Appel and Bar-Yosef, 2008). Whether population size was an important catalyst for, or a consequence of, the transition to agriculture, the positive feedback between demography and culture certainly underpinned subsequent urbanization and state formation. Agriculture remains the primary means of production underpinning the global population and economy today.

### **1.1 THE ORIGINS OF AGRICULTURE**

The earliest evidence for the transition to agriculture occurs in the Levant, a region of the Eastern Mediterranean, including Syria, Lebanon, Israel, Palestine and Jordan. The late Epipalaeolithic 'Natufian' (about 14 500-11 600 calBP) period in this region is seen as reflecting a cultural precursor of the subsequent pre-pottery Neolithic, due to the extensive exploitation of wild grains and the use of groundstone, stone architecture and a variety of organized site structures, art and evidence for symbolic behaviour (Bar-Yosef, 1998; Belfer-Cohen and Bar-Yosef, 2000; Byrd, 2005; Goring-Morris, Hovers and Belfer-Cohen, 2009). These cultural characteristics are often interpreted as the earliest archaeological signature of the transition towards agriculture, with the final impetus for the Neolithic being the dramatic environmental cooling associated with the Younger Dryas climatic event (Bar-Yosef and Belfer-Cohen, 2002). The earliest evidence for plant cultivation comes from the site of Abu Hureyra at about 13 000 BP, and appears to be associated with a decline in wild plants associated with the Younger Dryas (Hillman et al., 2001). The subsequent Pre-pottery Neolithic A period shows the first evidence for larger permanent human settlements with architecture, and demonstrates the first evidence for intensive use of grains, as evidenced by the 11 kya granaries at 'Dhra in Jordan (Kuijt and Finlayson, 2009). These PPNA villages represent the earliest expression of the Neolithic, but they also reflect an extension of trends in social complexity, longer-term site use, and extensive use of wild grains which occurred earlier in the Natufian (Byrd, 2005). While these late Pleistocene and early Holocene cultures in the Near East and Anatolia reflect the earliest transition to farming, it is now well established that agriculture originated independently in different regions of the world at different times throughout the first half of the Holocene (Smith, 1998; Diamond, 2002; Bellwood, 2005). Other regions of primary plant domestication include southern China, Ethiopia, New Guinea, and three different regions of the New World: Southeast North America, Meso-America and western South America (Bellwood, 2005), and there were also a number of independent centres of animal domestication (Diamond, 2002).

What explains the development of agriculture in different parts of the world remains an open question; however, it has been argued that there were a number of constraints on the domestication of plants and animals prior to the Holocene, including climate and social

organization (Richerson, Boyd and Bettinger, 2001; Bettinger, Richerson and Boyd, 2009). Regardless of these issues, it is clear that the global dominance of agricultural subsistence occurred through a combination of regional innovation with locally domesticable plant and animal species, demographic expansion and cultural diffusion (Bellwood, 2005; Pinhasi, Fort and Ammerman, 2005). The result of this transition is that agriculture is the dominant mode of subsistence today, which supports the large global human population and the socio-economic and technological systems of our species in the modern world.

#### **1.2 THE CONSEQUENCES OF AGRICULTURE**

A considerable emphasis of research has been placed on understanding the impact of the adoption of agricultural subsistence on health. This is based on the premise that a shift from diverse diets based on hunting and gathering towards dependence on one or a few highly productive domesticated plants, with a diet based predominantly on complex carbohydrates, can lead to a number of negative health outcomes, including nutritional deficiencies and dental caries. In addition, increasing sedentism associated with permanent or semi-permanent villages, and living in close proximity to domestic animals, leads to poor sanitation and an increased prevalence of zoonotic disease. Palaeopathologial studies have provided a considerable body of evidence that the origins of agriculture often had a negative impact on human health (Cohen and Armelagos, 1984; Cohen, 1989). The palaeopathological paradigm has dominated most research on the impact of agriculture in recent decades; however, it presents a paradox: if agriculture clearly underpins the dramatic demographic expansion and success of our species in the Holocene, how do we explain patterns of pathology? Is there a trade-off between reproductive capacity and health? In this context, we need to ask how the impact of agriculture varies through time and space, and under what cultural conditions it varies.

Recent research is beginning to investigate these questions. A study of linear enamel hypoplasia (LEH), bands of poor quality dental enamel that form during periods of childhood illness or malnutrition, has demonstrated a dramatic increase in the frequency of LEH between the late Palaeolithic and Neolithic of Egypt (Starling and Stock, 2007). While this would be expected based upon models of nutrition and hygiene with the transition to agriculture, the study also showed a gradual recovery in the frequency of LEH with the formation of the Egyptian state, showing that the negative health consequences of agriculture were short-term, and mediated by cultural factors over several millennia. Recent studies investigating health and subsistence transitions across a range of populations have demonstrated a greater diversity of evidence than previously known (Cohen and Crane-Kramer, 2007). These studies demonstrate that there is no simple relationship between subsistence change and health and, while there is still evidence for a decline in health indicators amongst many populations, the emerging picture is more regionally specific and diverse than previously thought.

While research has predominantly focused on the impact of agriculture on human health (Cohen, 1989) and demography (Bocquet-Appel and Bar-Yosef, 2008), there has also been study of the impact of agriculture on other aspects of human biology. A portion of this work, primarily on human remains from North America, has focused on elucidating behavioural correlates of subsistence transitions (Larsen, 1995). This area of research was amongst the earliest to begin to show evidence for regional diversity of human biological change with the transition to agriculture (Bridges, 1989; Ruff, 1999, 2008). Another area of enquiry has investigated the idea of 'human domestication', that human populations underwent similar

morphological (Leach, 2003) and behavioural changes (Wilson, 1991) as other species, following the transition to agriculture and the process of animal domestication. These approaches suggest a continuing feedback between cultural and human biological change (Durham, 1991). A frequently cited example of biological change associated with the origins of agriculture is dental and mandibular size reduction; however, it remains unknown whether this represents genetic evolution, a relaxation of directional selective pressures, or biological plasticity in response to changes in biomechanics associated with food preparation and dietary homogenization (Pinhasi, Shaw and Eshed, 2008).

# **1.3** AN ONGOING 'REVOLUTION' IN OUR UNDERSTANDING OF THE NEOLITHIC

The above discussion provides a brief, general and conservative picture of the origins of agriculture. A recent review of the issue of agricultural origins from a variety of perspectives, published as a special issue of *Current Anthropology*, generally supports these interpretations; namely that agriculture was a consequence of increasing population pressure, competition for resources and globally favourable climatic conditions, and it resulted in a general deterioration of health amongst agricultural populations (Cohen, 2009). However, a common theme in the commentary accompanying this issue is that these interpretations represent a broad-scale overview but do not explain regional and temporal variation that is apparent in the archaeological record (Denham, 2009; Belfer-Cohen and Goring-Morris, 2009; Zeder and Smith, 2009). On a surface level we could dismiss these disparities as inevitable conflict between the resolution of data found in specific archaeological contexts and the sort of generalizations that are necessary for understanding global trends. However, it begs the question, to what extent are broad-scale and global trends relevant to regional expressions of Holocene subsistence transitions? To what extent is regional variation important in understanding the 'big picture' of the causes and consequences of agriculture? If regional and temporal variation is so significant, can we even make such generalizations?

In recent years, simultaneous developments in our understanding of long-term trends in the archaeology of human populations, human genetic diversity, and animal and plant evolution, have begun to dramatically change our views of the transition to agriculture. The Late Pleistocene and Holocene archaeological record from the Levant presents amongst the most clear archaeological evidence for long-term cultural change associated with the transition to agriculture; however, recent research has demonstrated that the cultural and biological change associated with this transition is more complex than previously thought. In particular, there is evidence that the cultural characteristics of the Neolithic develop over a considerable span of time (Twiss, 2007) from precursors found in the Natufian (Belfer-Cohen and Bar-Yosef, 2000). However, recent excavations suggest that many of the characteristic features of the Natufian period developed gradually over a long period of time in the Late Pleistocene (Maher, 2007; Nadel and Hershkovitz, 1991; Belfer-Cohen and Goring-Morris, 2009). Collectively, the emerging evidence from the Levant suggests that the origins of agriculture did not occur as a rapid Neolithic revolution per se, but as a complex and long-term process of social change in the relationship between human behaviour and the natural environment. This suggests that investigation of subtle cultural, behavioural and dietary change amongst hunter-gatherers, pastoralists and early agricultural populations should be considered on a fine scale, with increased temporal and spatial resolution.

This 'revolution' in our understanding of the Neolithic is not restricted to issues of cultural change in the Levant, as there is clear evidence for social complexity and long-term behavioural change in other regions (Denham, 2009; Zeder and Smith, 2009). A major factor underpinning the longer temporal span of the process of domestication may be the evolution of plants. Recent archaeobotanical research has moved away from simple identification of plant remains at archaeological sites, to examine the evolution of the plants themselves (Fuller and Allaby, 2009). This research demonstrates that the process of plant domestication occurs over a longer temporal span, and occurs across plant taxa and in different centres of domestication (Fuller and Allaby, 2009; Fuller, Allaby and Stevens, 2010). This not only has implications for the timing of cultural change associated with the agricultural transition, but also the expression of culture and habitual behaviour associated with subsistence activity. The evolution of domestic plants from wild progenitors involves a narrowing of the period of ripening of seeds from several months to several weeks, presenting what has been called a 'labour bottleneck' (Fuller, Allaby and Stevens, 2010). Furthermore, wild grasses generally disperse seeds by the presence of an 'abscission scar', which is often lost in the process of domestication. As a result, domestic plants often require human activity, in the form of threshing and winnowing, to separate and disperse seeds. This has been called a 'labour trap' of domestication (Fuller, Allaby and Stevens, 2010) associated with the transition to agricultural food sources. While this does not necessarily mean that agricultural subsistence is more labour intensive than other subsistence strategies in all circumstances, it suggests that the transition to agriculture is behaviourally complex and likely fuelled technological innovation throughout much of the Holocene.

A further area where there has been major change in our understanding of the transition to agriculture has been in human genetics. Until very recently, many assumed that human evolution is at a standstill in the modern world, due largely to human control over the natural environment (Dyson, 1997). This perspective was based largely on the assumption the technological developments following the origins of agriculture led to rapid technological evolution and increasingly successful 'niche construction', where humans successfully modify the natural environment, and thus remove pressures of natural selection. This assumption was never justified by the niche construction model, and it is increasingly clear that modification of the environment not only buffers environmental stress but actually exerts new selective pressures on the genome (Laland and Brown, 2006; Stock, 2008). Selective pressure on the genome resulting from stresses associated with the transition to agriculture has been detected through evidence for selection in a number of genes, related to malarial resistance (Tishkoff et al., 2001), lactase persistence (Burger et al., 2007; Tishkoff et al., 2007) and amylase gene copy variation (Perry et al., 2007). The latter two cases appear to be the results of direct selection of particular genes in response to dietary stress associated with domestication of animals and plants. These cases relate to the use of milk as a fallback food amongst Neolithic populations, and the shift towards higher components of dietary starch, which may have driven selection for higher AMY1 copy numbers to aid starch hydrolysis, respectively. Recent research has dramatically extended our understanding of recent human evolution, on the basis of new methods for the detection of signatures of natural selection within the genome (Sabeti et al., 2007). Further genetic analysis has identified greater genetic heterogeneity amongst modern humans than would be otherwise expected, leading to the speculation that the pace of human evolution has speeded up in recent prehistory (Hawks et al., 2007). It will take a considerable amount of research to sort out what specifically this genetic diversity means in terms of evolution, drift and demographic factors; but it does seem clear that recent cultural changes are a major force driving evolution within our species (Laland, Odling-Smee and Myles, 2010).

The previous discussion has presented evidence that we are in the midst of a major change in our interpretation of the origin of agriculture. This includes several fundamental shifts in perspective:

- 1. that socio-cultural and dietary change likely occurred over a considerable range of time, involving change within socially complex hunter-gatherers, pastoralists and agriculturalists;
- 2. that the process of the transition to agricultural subsistence was regionally specific, and we cannot expect to find universal trends and characteristics of this transition;
- 3. that evolution of plants during the process of domestication posed both constraints upon the process of cultural change, and its own influence on behavioural adaptation through the 'labour trap' associated with winnowing and threshing; and
- 4. that cultural change associated with the transition to agriculture exerted its new selective pressures on human populations, driving continuing human evolution within the Holocene.

# **1.4 HUMAN BIOARCHAEOLOGY OF THE TRANSITION TO AGRICULTURE**

Human remains comprise the primary evidence for human biology with the transition to agriculture. In this volume, we provide a synthesis of the bioarchaeological evidence for changes in mobility, behaviour, diet, growth, population dynamics and evolution associated with the transition to agriculture. We assemble the work of a number of researchers who have been independently tackling questions relating to human biology associated with major dietary transitions of the Late Pleistocene and early Holocene. Given recent and major shifts in our understanding of the complexity of the transition to agriculture in different parts of the world, it would be impossible for a volume of this sort to be exhaustive, or to provide a comprehensive review of all evidence. Instead we aim to provide a synthesis of current approaches to understanding the biological correlates and consequences of major subsistence transitions in the Late Pleistocene and Holocene, in the hope that these studies will stimulate further research.

The contributions presented here are innovative in several ways: they emphasize the complexity of social and cultural change, and often employ multidisciplinary approaches to understanding the context and consequences of the agricultural transition. Major themes in the book include:

- the direct evidence for dietary change through the use of stable isotope analyses; variation in growth associated with dietary and cultural change;
- skeletal biomechanics and evidence for variation in habitual behaviour; craniofacial morphology, population history and adaptation; and
- evidence for genetic adaptation relating to Holocene cultural change.

In addition, several chapters build upon the dismantling of the traditional hunter-gatherer/ agriculturalist dichotomy, by investigating subtle variation in human biology amongst huntergatherers, pastoralists, and early cultivators and agriculturalists. Other studies take a very broad geographical or temporal approach to understanding change. Collectively the contributions emphasize the benefits of adopting multidisciplinary approaches to investigating change through time and space.

Given the multidisciplinary nature of many of the papers presented here, it is challenging to find ways to categorize approaches in order to organize the volume. In this context we have arranged the book into four sections that define general themes of the paper, but these are not mutually exclusive categories of the research and there is considerable overlap from one section to another. Section A focuses on evidence for subsistence transitions using stable isotopes and broad bioarchaeological perspectives. Section B focuses more closely on variation in growth, and variation in body size in relation to the transition to agriculture. Section C discusses biomechanical evidence for behaviour, through time and space across subsistence transitions. The final section combines a variety of approaches, which are interrelated: genetics and evolution; cranial morphology and adaptation; and demographic trends with the transition to agriculture.

The chapter by Schulting (Chapter 2) begins the volume with a broad and comprehensive overview of isotopic evidence for the Mesolithic to Neolithic transition throughout Europe. It provides compelling evidence for a shift from regional isotopic and dietary heterogeneity in the Mesolithic period, towards isotopic signatures that are relatively homogenous throughout Europe. This homogeneity is particularly striking in coastal regions where changes in isotopic signatures are most marked. The following chapter (Chapter 3) by Lillie and Budd investigates dietary change from hunting and gathering through the Neolithic in the Dniepr Rapids region of the Ukraine, using stable isotope data and radiocarbon dates. The study provides evidence of an increase in fish consumption in the later Mesolithic and into the Neolithic period, possibly stimulated by shifting environmental conditions in this area. Grupe and Peters (Chapter 4) assess stable carbon and nitrogen isotope indicators of the contribution of C<sub>4</sub>-plants to the diet of fully domesticated animals and their human consumers during the Neolithic transition in Anatolia. Using oxygen isotopes as a proxy for climate, they demonstrate that early Neolithic farmers were able to take advantage of C<sub>4</sub>-plants, which are more suitable for animal fodder than human consumption, to reduce food competition between domestic stock and the owners of the animals. Their work provides evidence of complex plant resource management in Neolithic human subsistence strategies. Human skeletal remains are used by Papathanasiou in Chapter 5, to investigate dietary health implications of the transition to agriculture in Greece. In this region, palaeodietary analyses provide evidence for a swift and complete shift from foraging to farming. Palaeopathological stress indicators indicate that Early Neolithic Greek populations had relatively low prevalence of stress and that their stature was close to the upper limits of the range found within the Late and Final Neolithic periods. The following chapter by Ginter (Chapter 6) shifts focus to the mid-Holocene Eastern Cape of Southern Africa. Her bioarchaeological analysis identifies a decrease in body size during a period of intensification of foraging between 3500 and 2000 BP, followed by a recovery of body size associated with the adoption of pastoralism by some groups. These changes are accompanied by general cranial homogeneity, which likely reflects population continuity, suggesting that cultural change, and in particular the intensification of foraging, was driving phenotypic variation amongst foragers prior to herding. These results are interpreted in the context of evidence for a gradual and incomplete adoption of herding as a delayed return subsistence technique amongst hunter gatherers over a considerable span of the late Holocene.

The second section of the book builds upon the theme of body size introduced by Ginter in Section A, but focuses more exclusively on variation in growth and body size associated with

subsistence transitions in different regions. The chapter by Mieklejohn and Babb (Chapter 7) provides a systematic comparison of long bone lengths, and hence stature, throughout the late Pleistocene and Early Holocene of Europe. This paper demonstrates a clear decrease in long bone length between the Early and Late Upper Palaeolithic, but there is a general stasis in stature from the Late Upper Palaeolithic through the Neolithic. These results overturn the general impression that the most significant shifts in body size occurred between the European Mesolithic and Neolithic. Chapter 8, by Pinhasi and colleagues, investigates variability in growth trajectories of limb bones amongst Neolithic populations of the Danube Gorges and Greece, using variation in attainment of bone lengths relative to dental age. Bone lengths per age of subadults in these samples are compared to standards from the Denver growth study, and more recent skeletal growth variation within Europe. The results of these comparisons show variation throughout the skeleton in growth for age, between the Danube Gorges Mesolithic, Neolithic and Greek Neolithic, but also highlight general trends such as increased variation in distal limb segments. The general theme of body size variation and growth is continued by Auerbach (Chapter 9), with a specific focus on broad patterns of body size variation in North America throughout the Holocene. The analysis tests a number of hypotheses, but identifies a general trend towards different morphological patterns associated with the transition to agriculture in the Southeastern relative to Southwestern populations. Overall, the results suggest that the transition to agriculture in these regions did not lead to a general decline in health, measured by stature and body mass, as might be predicted by previous palaeopathological evidence. The theme of bone growth and size variation in prehistoric Japan is explored by Temple (Chapter 10), who provides evidence for shorter leg lengths amongst preagricultural Jomon foragers when compare to Yayoi farmers. This is linked to greater femoral growth rates in the latter population, which may indicate a reduction in chronic infectious disease and nutritional stress following the transition to wet rice economies. This provides further support that the biological impact of agriculture is regionally specific and dependent upon local conditions.

The third section includes four chapters focusing largely but not exclusively on biomechanical properties of bone and indicators of habitual activity in the context of subsistence transitions. The first of these (Chapter 11) by Lieverse and colleagues is linked closely to themes first discussed in Section A, by using stable isotope evidence from carbon, nitrogen and strontium isotopes, to investigate diet and mobility amongst mid-Holocene hunter-gatherers in the Lake Baikal region of Siberia. A multivariate approach is then applied to the interpretion of diet, mobility and behaviour, by combining the isotopic results with those obtained from the analyses of musculo-skeletal stress markers and long-bone cross-sectional geometry as indicators of skeletal biomechanics. The results are suggestive of a trend towards more frequent deep water fishing and use of watercraft to extend foraging ranges from the earlier to later mid-Holocene. While there were no domestic plants or animals in this region throughout this period, this study demonstrates the viability of multidisciplinary approaches for detecting subtle patterns of dietary and behavioural change amongst hunter-gatherers, prior to full-blown agriculture. This approach may be useful for detecting the behavioural precursors of agriculture amongst socially complex hunter-gatherers in other regions.

The following chapter by Larsen and Ruff (Chapter 12) also employs multiple approaches to the issue of understanding changes in habitual activity associated with the transition to agriculture. Here, osteoarthritis and cross-sectional geometric properties of long bones are used to investigate behavioural change in three regions of eastern North America: the Pickwick Basin, Georgia Bight and lower Illinois River Valley. The results demonstrate that osteoarthritic

and cross-sectional geometric analyses do not always produce the same results. Despite this trend, they suggest that the transition from foraging to farming and subsequent farming intensification involved significant behavioural change that is regionally specific. An intriguing result is that preagricultural people from the Illinois River Valley show a shift in behaviour prior to the adoption of maize agriculture. Evidence that the adoption of agriculture was regionally specific is also presented by Marchi and colleagues (Chapter 13), who demonstrate that lower limb robusticity is very high in the Ligurian Neolithic of Italy, and similar to highly mobile European Late Upper Palaeolithic and Mesolithic populations. This, they argue, reflects a high level of terrestrial mobility in the Neolithic associated with pastoralism, but also considerable terrain relief in the region, demonstrating that morphological trends may be driven by regional variation in both habitual activity and topography. Section C concludes with a paper by Stock and colleagues (Chapter 14), which investigates trends in body size and biomechanics from the Late Palaeolithic through Neolithic and Dynastic periods of the Nile Valley, spanning over 10 000 years. The paper demonstrates a reduction and subsequent increase in body size through this period. Comparisons of biomechanical properties of long bones demonstrate a general reduction in humeral and femoral rigidity, but one that differs in timing between sexes. Male gracilization occurs between the Late Palaeolithic and Neolithic, but amongst females it occurs between the Neolithic and late Predynastic period.

The final section of the book includes contributions on current and ancient genetic signatures of the transition to agriculture, palaeodemography, and both skeletal and craniofacial change. Burger and Thomas provide the first of two genetic studies (Chapter 15), by investigating the relationship between modern genetic signatures and the history of Neolithic expansion in Europe. Their paper presents evidence that lactase persistence, as reflected by the -13 910-T allele, arose in Transdanubia with the LBK Culture (about 5700 BC), spreading to central Europe ca. 5500 BC. This ability to metabolize lactose into adulthood began to rise in frequency and by the Middle Neolithic after the emergence of specialized dairying cultures, lactase persistence spread throughout Northern Europe. The paper provides key evidence for gene-culture coevolution associated with subsistence change and demographic expansions in the Neolithic of Europe. An analysis of ancient DNA variation in the Neolithic of Sweden is provided by Linderholm (Chapter 16). Of primary interest in this region is the emergence of different Neolithic cultural traditions. The first agriculturalists were the Funnel Beaker culture, but their cultural expression lies in contrast to the marine resource based Pitted Ware Culture, which developed shortly after the initial Neolithic. This study provides evidence that these groups were genetically distinct, with the Funnel Beaker culture having its origin in continental Europe. In contrast, the people associated with the Pitted Ware culture seem to arrive from the east and then disappear without leaving a subsequent genetic signature.

Eshed and Galili (Chapter 17) present a paleodemographic study of Pre-Pottery Neolithic (PPN) B and C populations of the southern-central Levant, by constructing mortality curves for large samples of subadult and adult remains, and specific sites including Atlit-Yam, Kfar HaHoresh and Ain Ghazal. The results demonstrated a pattern of greater life expectancy at birth at the site of Atlit-Yam, while Kfar HaHoresh had higher mortality at younger ages (20–29), and Ain Ghazal had the highest rates of child mortality. These results demonstrate variation in mortality profiles for different sites within the same region. In Chapter 18, Sardi and Béguelin investigate variation in facial, humeral and femoral morphology between hunter-gatherers and farmers of the Diamante River in Argentina. The prehistoric people of this region adopted plant and animal domestication around 3000–2000 calBC, after which agricultural dependence intensified. The results illustrate a systemic reduction in size of the face and limb bones

amongst farmers, but while facial variation affected both males and females, limb bone reduction primarily affected females.

The final chapter in Section D by Pinhasi and Mieklejohn (Chapter 19) investigates diachronic changes in the tooth size amongst Central European populations from the Upper Palaeolithic through Mesolithic to Neolithic, spanning the period from about 35 000 to 4500 calBC. The results indicate a significant reduction trend in Central Europe from the Late Pleistocene to the Middle Holocene (Upper Palaeolithic/Mesolithic/Early Neolithic). These differ from the pattern and pace of dental reduction identified in previous studies, and indicate that the magnitude and nature of the reduction trend in Europe differs from the change reported for early agricultural populations in the southern Levant. These results highlight that while the transition to farming resulted in significant changes in dental dimensions, the magnitude and nature of the changes need to be addressed on a case-to-case basis before it is possible to draw conclusions about universal evolutionary trends.

### 1.5 CURRENT AND FUTURE RESEARCH IN HUMAN BIOARCHAEOLOGY OF THE TRANSITION TO AGRICULTURE

As discussed earlier in this chapter, we are in the midst of a 'revolution' in our understanding of the transition to agriculture. This paradigm shift is coming from a number of perspectives, emphasizing:

- the long-term socio-cultural change associated with subsistence transitions;
- regional specificity of the process of the origin and adoption of agriculture;
- the relationship between plant and animal evolution with domestication, and their impact on our own species; and
- that cultural evolution stimulated biological evolution within the Holocene.

The chapters presented in this volume demonstrate that human bioarchaeology plays a central role in this paradigm shift. They demonstrate that the complexity of long-term cultural and dietary change associated with these subsistence transitions are manifest in variation of the human biological response to the agricultural transition. We cannot conclusively interpret the causes and consequences of the agricultural transition throughout the world in a single volume. However, the contributions assembled here provide new evidence that the subtleties and regional variation in dietary change, growth and morphological change, biomechanics and behaviour, and continuing human evolution were complex and region-specific. They also highlight the advantages of high resolution multidisciplinary approaches to the study of human biological and cultural variation associated with cultural and dietary transitions.

#### REFERENCES

- Bar-Yosef, O. (1998) The Natufian culture in the Levant: Threshold to the origins of agriculture. *Evol. Anthropol.*, **6** (5), 159–177.
- Bar-Yosef, O. and Belfer-Cohen, A. (2002) Facing environmental crisis: societal and cultural changes at the transition from the Younger Dryas to the Holocene in the Levant, in *The Dawn*

of Farming in the Near East, Studies in Early Near Eastern Production, Subsistence and Environment 6 (eds R.T.J. Cappers and S. Bottema), ex oriente, par Margareta Tengberg, Berlin, pp. 55–66.

- Belfer-Cohen, A. and Bar-Yosef, O. (2000) Early sedentism in the near east: a bumpy ride to village life, in *Life in Neolithic Farming Communities: Social Organization, Identity, and Differentiation* (ed. I. Kuijt), Kluwer Academic/Plenum Publishers, New York.
- Belfer-Cohen, A. and Goring-Morris, N. (2009) For the first time. Curr. Anthropol., 50 (5), 669-672.

Bellwood, P. (2005) First Farmers: The Origins of Agricultural Societies, Blackwell Publishing, Oxford.

- Bettinger, R., Richerson, P. and Boyd, R. (2009) Constraints on the development of agriculture. *Curr. Anthropol.*, **50** (5), 627–631.
- Bocquet-Appel, J.P. and Bar-Yosef, O. (2008) Prehistoric demography in a time of globalization, in *The Neolithic Demographic Transition and its Consequences* (eds J.P. Bocquet-Appel and O. Bar-Yosef), Springer Science+Business Media.
- Boserup, E. (1965) The Conditions of Agricultural Growth, George Allen and Urwin, London.
- Bridges, P.S. (1989) Changes in activities with the shift to agriculture in the southeastern United States. *Curr. Anthropol.*, **30** (3), 385–394.
- Burger, J., Kirchner, M., Bramanti, B. et al. (2007) Absence of the lactase-persistence associated allele in early Neolithic Europeans. PNAS, 104, 3736–3741.
- Byrd, B. (2005) Reassessing the emergence of village life in the Near East. J. Archaeol. Res., 13, 231–290.
- Childe, V.G. (1936) Man Makes Himself, Watts and Co., London.
- Cohen, M.N. (1977) *The Food Crisis in Prehistory: Overpopulation and the Origins of Agriculture*, Yale University Press, New Haven.
- Cohen, M.N. (1989) Health and the Rise of Civilization, Yale University Press, London.
- Cohen, M.N. and Armelagos, G.J. (eds) (1984) *Paleopathology at the Origins of Agriculture*, Academic Press, Orlando, FL.
- Cohen, M.N. and Crane-Kramer, G.M.M. (2007) Ancient health: Skeletal indicators of agricultural and economic intensification, in *Bioarchaeologial Interpretations of the Human Past: Local, Regional, and Global Perspectives*, (Series editor C.S. Larsen), University Press of Florida, Gainesville.
- Cohen, M.N. (2009) Introduction: Rethinking the origins of agriculture. *Curr. Anthropol.*, **50** (5), 591–595.
- Denham, T. (2009) A practice-centered method for charting the emergence and transformation of agriculture. *Curr. Anthropol.*, **50** (5), 661–667.
- Diamond, J. (1997) *Guns, Germs, and Steel: The Fates of Human Societies*, W.W. Norton and Company, New York.
- Diamond, J. (2002) Evolution, consequences and future of plant and animal domestication. *Nature*, **418**, 597–603.
- Durham, W.H. (1991) *Coevolution: Genes, Culture, and Human Diversity*, Stanford University Press, London.
- Dyson, F. (1997) The era of Darwinian evolution is over. New Perspect. Q, 24, 58-59.
- Fuller, D.Q. and Allaby, R. (2009) Seed dispersal and crop domestication: shattering, germination and seasonality in evolution under cultivation, in *Fruit Development and Seed Dispersal, Annual Plant Reviews*, vol. **38** (ed. L. Ostergaard), Wiley-Blackwell, Oxford, pp. 238–295.
- Fuller, D.Q., Allaby, R.G. and Stevens, C. (2010) Domestication as innovation: the entanglement of techniques, technology and chance in the domestication of cereal crops. *World Archaeology*, 42 (1), 13–28.
- Goring-Morris, A.N., Hovers, E. and Belfer-Cohen, A. (2009) The dynamics of Pleistocene and Early Holocene settlement patterns and human adaptations in the Levant: an overview, in *Transitions in Prehistory: Essays in Honor of Ofer Bar-Yosef* (eds J. Shea and D. Lieberman), Oxbow Books, Oxford.

- Hawks, J., Wang, E.T., Cochran, G.M. *et al.* (2007) Recent acceleration of human adaptive evolution. *PNAS*, **104** (52), 20753–20758.
- Hillman, G., Hedges, R., Moore, A. *et al.* (2001) New evidence of Lateglacial cereal cultivation at Abu Hureyra on the Euphrates. *The Holocene*, **11** (4), 383–393.
- Klein, R.G. (2009) *The Human Career: Human Biological and Cultural Origins*, 3rd edn, University of Chicago Press, Chicago.
- Kuijt, I. and Finlayson, B. (2009) Evidence for food storage and predomestication granaries 11 000 years ago in the Jordan Valley. PNAS, 106 (27), 10966–10970.
- Laland, K.N. and Brown, G.R. (2006) Niche construction, human behaviour, and the adaptive-lag hypothesis. *Evol. Anthropol.*, **15**, 95–104.
- Laland, K.N., Odling-Smee, J. and Myles, S. (2010) How culture shaped the human genome: Bringing genetics and the human sciences together. *Nat. Rev. Genet.*, **11**, 137–148.
- Larsen, C.S. (1995) Biological changes in human populations with agriculture. *Ann. Rev. Anthropol.*, **24**, 185–213.
- Leach, H.M. (2003) Human domestication reconsidered. Curr. Anthropol., 44 (3), 349-368.
- Maher, L.A. (2007) Microliths and mortuary practices: New perspectives on the Epipalaeolithic in Northern and Eastern Jordan, in *Crossing Jordan: North American Contributions to the Archaeology of Jordan* (eds T.E. Levy, P.M.M. Daviau, R.W. Younker and M. Shaer), Equinox, London.
- Nadel, D. and Hershkovitz, I. (1991) New subsistence data and human remains from the earliest Levantine Epipalaeolithic. *Curr. Anthropol.*, **32**, 631–635.
- Perry, G.H., Dominy, N.J., Claw, K.G. *et al.* (2007) Diet and the evolution of human amylase gene copy number variation. *Nat. Genet.*, **39** (10), 1256–1260.
- Pinhasi, R., Fort, J. and Ammerman, A.J. (2005) Tracing the origin and spread of agriculture in Europe. *PLoS Biology*, **3** (12), e410.
- Pinhasi, R., Shaw, P. and Eshed, V. (2008) Changes in the masticatory apparatus following the transition to farming in the Levant. Am. J. Phys. Anthropol., 135, 136–148.
- Richerson, P.J., Boyd, R. and Bettinger, R.L. (2001) Was agriculture impossible during the Pleistocene but mandatory during the Holocene? A climate change hypothesis. *Am. Antiq.*, **66**, 387–411.
- Ruff, C.B. (1999) Skeletal structure and behavioral patterns of prehistoric Great Basin populations, in Understanding Prehistoric Lifeways in the Great Basin Wetlands: Bioarchaeological Reconstruction and Interpretation, (eds B.E. Hemphill and C.S. Larson), University of Utah Press, Salt Lake City, pp. 290–320.
- Ruff, C.B. (2008) Biomechanical analyses of archaeological human skeletal samples, in *Biological Anthropology of the Human Skeleton*, 2nd edn (eds M.A. Katzenburg and S.R. Saunders), John Wiley and Sons, New York, pp. 183–206.
- Sabeti, P.C., Varilly, P., Fry, B. *et al.*, The International HapMap Consortium (2007) Genomewide detection and characterization of positive selection in human populations. *Nature*, **449**, 913–918.
- Starling, A. and Stock, J.T. (2007) Dental indicators of heath and stress in early Egyptian and Nubian agriculturalists: Difficult transition and gradual recovery. Am. J. Phys. Anthropol., 134 (4), 520–528.
- Smith, B.D. (1998) The Emergence of Agriculture, Scientific American Library, New York.
- Stock, J.T. (2008) Are humans still evolving? in *The Future of our Species*, EMBO Reports, **9**, Science and Society, Special Issue, pp. S51–S54.
- Tishkoff, S.A., Varkonyi, R., Cahinhinan, N., *et al.* (2001) Haplotype diversity and linkage disequilibrium at human G6PD: Recent origin of alleles that confer malarial resistance. *Science*, **293**, 455–462.
- Tishkoff, S.A., Reed, F.A., Ranciaro, A. *et al.* (2007) Convergent adaptation of human lactase persistence in Africans and Europeans. *Nat. Genet.*, **39** (1), 31–40.
- Twiss, K. (2007) The Neolithic of the southern Levant. Evol. Anthropol., 16 (1), 24-35.

Wells, J.C.K. and Stock, J.T. (2007) The biology of the colonizing ape. *Yearbook of Physical Anthropology*, **50**, 191–222.

Wilson, P.J. (1991) The Domestication of the Human Species, Yale University Press, New Haven, p. 201.

Zeder, M.A. and Smith, B.D. (2009) A conversation on agricultural origins: Talking past each other in a crowded room. *Curr. Anthropol.*, **50** (5), 681–691.