12 Evaluating Potential Proximate and Ultimate Causes of Phenotypic Change in the Human Skeleton over the Agricultural Transition

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Gordon Childe coined the term "Neolithic Revolution" to characterize the fundamental changes in the human ecological niche driven by the domestication of plants and animals (Childe 1936). From Childe's viewpoint, this revolution resulted in technological innovations and trends toward sedentism that brought improvements in health, food quality, and a lessening of labor demands (Childe 1936). It is now understood that the adoption of agriculture was in fact a complex and gradual process that occurred independently among humans and in different species of insects (i.e., ants, termites, beetles) at different times and in many geographic areas of the world (Bar-Yosef 1998; Schultz et al. 2005; Stock and Pinhasi 2011; Armelagos and Cohen 2013; Biedermann and Vega 2020). Regarding humans, despite shifts in understanding since Childe's work, it can still be argued that agriculture resulted in pivotal changes in the relationship between human behavior and the natural environment, albeit with varied impacts in different populations.

There are ongoing discussions regarding the areas in which early agriculture originated independently and those in which it was secondarily adopted due to the diffusion of people or ideas (e.g., Bellwood 2005). Current consensus, however, points to at least the following eight regions of agricultural innovation: the Levant (10,000 BP), India (5,000–4,000 BP), the Yangtze and Yellow River basins in south China (8,000 BP), the New Guinea Highlands (7,000 BP), west sub-Saharan Africa (4,000–2,000 BP), Central Mexico (10,000–4,000 BP), western South America (8,000–5,000 BP), and eastern North America (5,000–4,000 BP) (Diamond and Bellwood 2003; Bellwood 2005; Price and Bar-Yosef 2011; chapter 10, this volume).

Over the past several decades, researchers have questioned the initial assumptions of the Childean school of thought, which suggested that the transition to agriculture was of unadulterated benefit to humanity. This has led to much discussion of the effects of different subsistence practices on human skeletal morphology in workshops and projects leading to influential books (Cohen and Armelagos 1984; Steckel and Rose 2002; Ungar 2006; Pinhasi and Stock 2011). More recently, dietary influences on skeletal morphology have been well documented in comparative analyses of recent populations from all around the world (e.g., von Cramon-Taubadel 2011; Noback and Harvati 2015; Katz, Grote, and Weaver 2017) and/or specific subcontinents (e.g., Pinhasi and Pluciennik 2004; Paschetta et al. 2010; Perez et al. 2011; Cheronet, Finarelli, and Pinhasi 2016). However, since

morphological variation between human populations results from several evolutionary and ecological processes, it becomes difficult to disentangle the impact of different subsistence practices on the skeleton. Additionally, the effect that diverse diets have on the skeleton differs when comparing populations at distinct geographical scales. For instance, on a worldwide scale, genetic drift is expected to have the strongest effect (von Cramon-Taubadel 2014; Katz, Grote, and Weaver 2017), while on smaller subcontinental or regional scales other factors such as diet or climate play a stronger role (Paschetta et al. 2010; Perez et al. 2011; Evteev et al. 2014).

In order to address the complexity of causative factors where possible, the association between subsistence and skeletal variation should be evaluated in diachronic sequences in areas where agriculture either originated locally or was acquired early via knowledge transfer. More specifically, geographic areas where agriculture was introduced as the result of migrations from other areas should be excluded from analysis in order to avoid biological variation due to the influx of a migrant population. Skeletal studies on the morphological changes resulting from the adoption of agriculture are available from only about half of the regions and time periods of agricultural innovation listed above. These include the Levant (Smith, Bar-Yosef, and Sillen 1984; Eshed, Gopher, and Hershkovitz 2006; Pinhasi, Eshed, and Shaw 2008; Pinhasi, Eshed, and von Cramon-Taubadel 2015; May et al. 2018; Pokhojaev et al. 2019), eastern North America (Illinois and Ohio; Buikstra 1984; Cassidy 1984; Cook 1984; Goodman et al. 1984; Perzigian, Tench, and Braun 1984; Paschetta et al. 2010), and the central South American Andes (~Peruvian Andes; Gehlert 1979; Allison 1984; Benfer 1984, 1990) (figure 12.1). In other areas such as India, the New Guinea Highlands, west sub-Saharan Africa, China (but see Li, Zhang, and Zhu 2012), and Central Mexico (but see Marquez-Morfin and Storey 2007), the skeletal changes over the time in question have not been explored so far, at least in the English- or Spanish-language literature. This could be due to a lack of available skeletal samples covering the whole diachronic sequence or to biases in the distribution of bioarchaeological investigation.

There are, however, other relevant skeletal studies in areas neighboring those regions of agricultural innovation, owing to systematic archaeological excavations and good bone preservation. Despite known population turnover in at least some of these regions (e.g., Japan, see Hudson, Nakagome, and Whitman 2020), we include them here to increase our ability to detect global trends, always relying more heavily on those populations where there is a good argument for biological continuity. Some examples of these neighboring regions include Nubia (Greene, Ewing, and Armelagos 1967; Carlson and Van Gerven 1977; Hinton and Carlson 1979; Martin et al. 1984; Calcagno 1986; Galland et al. 2016), Japan (Kaifu 1997; Kanazawa and Kasai 1998; Fukase and Suwa 2008; Fujita and Ogura 2009; Temple 2011; Hoover and Williams 2015), South Africa (Ginter 2011), the Maghreb (Sardi, Ramirez-Rozzi, and Pucciarelli 2004), Iran and Iraq (Rathbun 1984), western and southern North America (Larsen 1981, 1984; Dickel, Schulz, and McHenry 1984; Rose et al. 1984), South Asia (Kennedy 1984), and southeastern Europe (y'Edynak and Fleisch 1983; Pinhasi and Meiklejohn 2011; Cheronet, Finarelli, and Pinhasi 2016; Macintosh, Pinhasi, and Stock 2016) (figure 12.1).

By synthesizing results from studies documenting morphological changes across the agricultural transition from a global sample of research, we hope to better understand the impact that dietary change had on the skeleton and the evolutionary mechanisms underlying it, as detailed below. Despite the substantial body of research, the causes of agriculture-
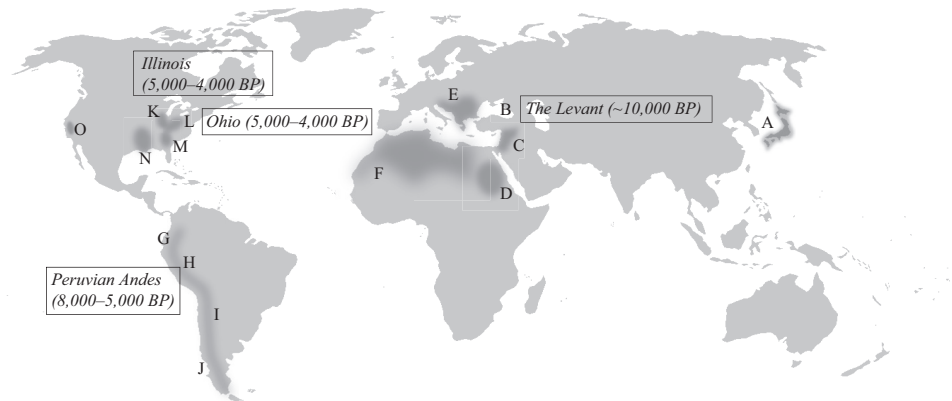
Figure 12.1
Map showing approximate regions referred to in text. (A) Japan, (B) the Levant, (C) Anatolia, (D) Nubia, (E) the Balkan Peninsula, (F) the Maghreb, (G) the Ecuadorean Andes, (H) the Peruvian Andes, (I) the Chilean Andes, (J) the southern Argentinian Andes, (K) Illinois, (L) the Ohio River Valley, (M) Georgia, (N) the Mississippi River Valley, (O) Central California. The centers of agricultural innovation that are mentioned in this chapter are labeled together with the approximate origin dates. Global map: Public domain.

related morphological changes remain unclear and are much debated. One way to organize the currently disparate interpretations of cause and effect is by applying Mayr's definition of proximate and ultimate causes (Mayr 1961). We understand the limitations of their application; notably, this framework does not allow us to invoke developmental mechanisms to explain evolutionary novelties (Baedke 2020); nor does it recognize that biological systems have a reciprocal relationship with their environments (Laland et al. 2013). However, in this chapter, we depart from an evo-devo perspective (Hall 2012) and consider developmental plasticity as an ultimate cause, because morphological changes occurring through developmental plasticity can have long-term evolutionary effects, just as selection does (Paaby and Testa 2018; Brown 2020). The proximate causes of the morphological changes associated with the adoption of agriculture may be a decrease in masticatory loading, the impact of dental pathology, or nutritional deficiency. The ultimate causes proposed for these morphological changes are developmental plasticity and/or generational responses to directional selection. It should be noted, however, that these definitions are working concepts that we apply as a means of grouping and understanding the different types of explanations current in the literature. In this chapter, we present a synthesis summarizing the morphological changes that have been linked to the transition to agriculture and discuss the main evolutionary explanations given for those changes.

Morphological Changes Associated with the Transition to Agriculture

The skeletal effects of the agricultural transition have been described mainly in the teeth, mandible, skull, and long bones (Cohen and Armelagos 1984; Larsen 1995, 2006; Pinhasi and Stock 2011; Macintosh, Pinhasi, and Stock 2016). This representation could be due either to a bias in research designs toward the study of those skeletal structures or to their being more affected due to their function and its relationship with diet and subsistence practices. The main morphological changes described as resulting from a shift to cultivated

foods can be summarized as a decrease in overall skeletal size, concomitant with allometric and shape changes that can be interpreted as a trend toward gracilization (i.e., less robust morphology) (Carlson and Van Gerven 1977; Larsen 2006). Additionally, across the studied populations, there are often morphological changes associated with the deterioration of health status, either as a consequence of a more sedentary life and/or of a less diverse diet (Diamond 1987; Ulijaszek 1991; Larsen 1995, 2006). In the following section we compile the evidence for morphological changes in the mandible, cranium, dentition, and long bones from studies with a wide geographic range.

The Mandible

Due to its primarily masticatory function, the mandible has been described as the bone most influenced by changes in subsistence (Lieberman 2011; von Cramon-Taubadel 2011). The global pattern of mandibular variation in recent humans reflects a dichotomous distinction between hunter-gatherer (HG) and agriculturalist/pastoralist subsistence economies (von Cramon-Taubadel 2011; Katz, Grote, and Weaver 2017). Both globally and regionally, the change in mandibular morphology from an HG economy to one based on animal and/or plant domesticates can be summarized as a trend of decreasing mandibular size and robusticity (Kaifu 1997; Fukase and Suwa 2008; Holmes and Ruff 2011; von Cramon-Taubadel 2011; Galland et al. 2016; Katz, Grote, and Weaver 2017; Pokhojaev et al. 2019) (figure 12.2).
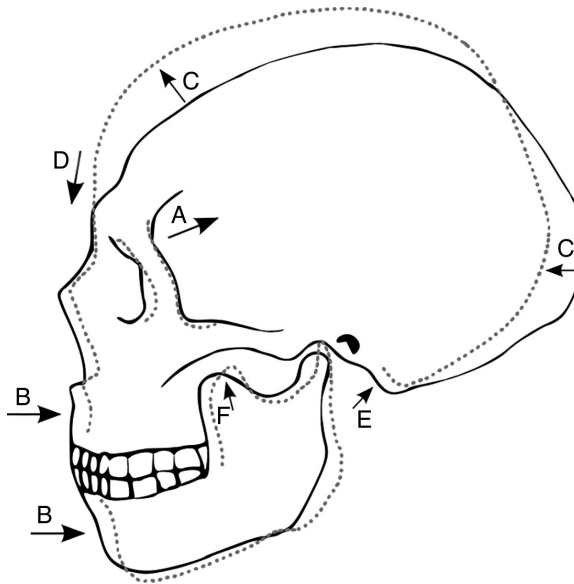
Figure 12.2
Summary of morphological changes in the skull and mandible observed in hunter-gatherers (black solid line) when compared with agriculturalists (dashed grey line). The main morphological changes are (A) a reduction in the size of the muscles of mastication and a relatively more posterior site of origin; (B) a reduced anteroposterior growth of the maxillomandibular complex; (C) a reduction in the relative length and increase in the relative height of the cranial vault, which becomes more globular; (D) a reduction in the size of the face, which becomes more inferoposteriorly located; (E) an overall reduction, expressed in some parts such as the mastoid; and (F) an increase in mandibular ramus height. Reduction in teeth size is not shown here. Adapted from Carlson and Van Gerven (1977).

Given that the Levant is one of the earliest centers of agricultural innovation, it is perhaps not surprising that much research on the skeletal effects of this dietary shift have focused there (Diamond and Bellwood 2003; Price and Bar-Yosef 2011). In the Levant, a reduction in mandibular size and robusticity, coinciding with the arrival of a domesticated diet, can be seen by comparing the HGs of the Natufian period to the later agriculturalist Neolithic populations. Natufian mandibles are short and heavy, and over time there is an increase in maximum length, corpus length, and ramus height, but a decrease in ramus width (Smith, Bar-Yosef, and Sillen 1984; Pokhojaev et al. 2019) (figure 12.2). The wider ramus in Natufian mandibles is accompanied by a shorter, wider coronoid process and wide mandibular notch, which gives way over time to a taller, narrower coronoid and a narrow mandibular notch in the Neolithic (May et al. 2018; Pokhojaev et al. 2019) (figure 12.2). Anterior symphyseal height reduces significantly in southern Levantine populations over time (Pinhasi, Eshed, and Shaw 2008; May et al. 2018), while the projection of the mental eminence increases (Pokhojaev et al. 2019). Natufian mandibles show a more lingual (horizontal) inclination of the posterior part of the body of the mandible, whereas later farming populations have a more buccal (vertical) orientation in this region (May et al. 2018).

In Nubian populations from northeastern Africa, Mesolithic individuals present larger mandibles with wider and more robust corpuses, shorter, wider, and more upright rami and coronoid processes, and longer mandibular condyles than later Neolithic agriculturalists (Galland et al. 2016) (figure 12.2). This reduction in mandible size over the course of a shift in subsistence corresponds to the smaller dimensions of the temporomandibular joint (TMJ) in the Nubian Neolithic (Greene, Ewing, and Armelagos 1967; Hinton and Carlson 1979). In general, during the transition to agricultural subsistence in Nubia, there is a reduction of the sexual dimorphism in TMJ size and more posteriorly positioned masticatory muscles (Hinton and Carlson 1979).

Several studies have compared different aspects of the mandibular morphology of prehistoric Japanese foragers (Jomon) with the agriculturalist Yayoi who succeeded them (Kaifu 1997; Kanazawa and Kasai 1998; Fukase and Suwa 2008). The latter are smaller and lighter with thinner cortical bone (Kaifu 1997; Fukase and Suwa 2008).

The Cranium

On a worldwide scale, diet-related morphological differences between recent populations of farmers and HGs are seen most strongly in temporalis muscle size and shape variation (Sardi, Ramirez-Rozzi, and Pucciarelli 2004; Noback and Harvati 2015; Cheronet, Finarelli, and Pinhasi 2016) (figure 12.2). Compared with crania from farmers whose diets are largely based on crops, crania from populations relying heavily on hunting and/or fishing show larger and more anteriorly placed masticatory muscles accompanied by widened alveolar processes, larger nuchal planes, larger mastoid processes, and wider faces (Noback and Harvati 2015). In general terms, the main craniofacial change in populations across the adoption of agriculture is an increase in cranial breadth, or a brachycephalization of the cranial vault (e.g., Sardi, Ramirez-Rozzi, and Pucciarelli 2004; Cheronet, Finarelli, and Pinhasi 2016).

On a regional level, in the Levant, the crania of Neolithic farmers are shorter than those of preceding Natufian HGs, and their zygomatic breadths are narrower, resulting in narrower faces and more globular (i.e., spherical) neurocrania (Smith, Bar-Yosef, and Sillen

1984). As the Levant is a widely accepted center of agricultural innovation, it is likely that there is biological continuity between HG and agriculturalist groups. Therefore, since there is no archaeological evidence for population replacement or migrations associated with agriculture (Smith, Bar-Yosef, and Sillen 1984; Bar-Yosef 1998; Cheronet, Finarelli, and Pinhasi 2016), diachronic comparisons in this region strengthen the evidence that these changes are diet-related.

Sardi and collaborators (2004) compared individuals from northwest Africa belonging to the Upper Paleolithic (Iberomaurisian Complex; Afalou and Taforalt archaeological sites in Morocco and Algeria) with Neolithic ones (Guanches from the Canary Islands, Phoenicians and Arabs from Tunis, and modern Berbers from Algeria), and found that overall cranial size is larger in the first group. More specifically, the most divergent variables between HG and agricultural groups in prehistoric northwest Africa are the rates of change in the sizes of the neural and facial parts of the cranium. In the Upper Paleolithic, the facial region is relatively larger than it is in the Neolithic, while in the Neolithic the neural region is relatively larger than it is in the Upper Paleolithic (Sardi, Ramirez-Rozzi, and Pucciarelli 2004) (figure 12.2). In Nubia, from the Mesolithic to Neolithic there is a decrease in the size and robusticity of the whole craniofacial complex (Carlson and Van Gerven 1977; Martin et al. 1984; Galland et al. 2016), and later agricultural populations show an increase in cranial height with a concomitant decrease in cranial length, effectively increasing cranial globularity (Carlson and Van Gerven 1977; Martin et al. 1984; Galland et al. 2016) (figure 12.2). Overall, there is a reorganization of the craniofacial complex such that the vault becomes more anterosuperiorly located, while the mid- and lower face becomes more inferoposteriorly located (Carlson and Van Gerven 1977; Martin et al. 1984) (figure 12.2). Neolithic Nubian faces are smaller, lower, and more retracted, compared with their Mesolithic forerunners. They present less deep, narrower zygomatics, less pronounced alveolar prognathism, less projecting glabella regions, and shorter mastoid processes (Galland et al. 2016). These changes result in the Neolithic crania being overall more gracile (i.e., less robust) and more globular, as with the Levantine agriculturalists when compared with preceding foragers (figure 12.2).

In South America, farmers present a reduction in the size of the masticatory component of the cranium when compared with HG groups (Gonzalez-José et al. 2005). Most studies in this region have been conducted using variables identified following the craniofunctional method (Pucciarelli 2008; Sardi 2017), linking cranial components to specific functions such as mastication and allowing functional interpretations of the observed anatomical changes. In the southern Andes (central-west Argentina), in addition to the reduction in the masticatory component, the transition to agriculture is accompanied by a reduction in the posteroneuronal part of the cranium (Sardi, Novellino, and Pucciarelli 2006) (figure 12.2). This pattern of masticatory and posteroneuronal reduction is found throughout the South American continent, where there is a clinal pattern of size and allometric cranial shape variation from southeast to northwest. Dietary variation is a plausible explanation for the majority of this pattern, which is characterized by smaller sizes in the northwest and increasing robusticity toward the southeast of the continent. The most influential variables in this size variation are cranial width, height of the masticatory functional component, facial width, and neurocranial length (Perez et al. 2011; Menéndez et al. 2014). Generally, in South America there is sexual dimorphism in the extent of masticatory reduc-

tion across the shift to agriculture, with greater size reduction in females than in males (Sardi and Béguelin 2011).

In North America, particularly in individuals from the Ohio Valley, there are significant differences between HGs and farmers in the size of the temporal fossa and masticatory complex (including the TMJ), as well as allometric differences in the alveolar region (Paschetta et al. 2010) (figure 12.2). Similar trends of reduction in the size of the face and jaw are seen in populations from the American state of Georgia across 4,000 years of dietary changes (Larsen 1981, 1984). Despite localized skeletal changes, which fit with the wider global picture of responses to dietary change, HGs from the Ohio Valley actually present overall smaller cranial dimensions than farmers from the same region, combined with less robusticity or smaller facial size relative to total size (Paschetta et al. 2010), showing regional variation in the patterns of craniofacial response to changing diets. The evidence from the Ohio Valley is of particular importance, as it is one of those rare regions where biological continuity can be inferred with reasonable certainty, thus avoiding confounding factors such as population history that might also affect shape (Smith 1989; Paschetta et al. 2010).

The Dentition

There is a pattern of dental reduction in many populations after the adoption of agriculture as their main subsistence practice. This has been found in such disparate geographic regions as the Levant (Pinhasi, Eshed, and Shaw 2008), Nubia (Martin et al. 1984; Calcagno 1986; Calcagno and Gibson 1988), the eastern Mediterranean and Balkans (y'Edynak and Fleisch 1983; y'Edynak 1989), the American state of Georgia (Larsen 1981), Peru (Benfer 1990), and South Asia (Kennedy 1984). In addition to trends of decreasing dental size, there are changes in dental wear and the frequencies of dental and oral pathologies associated with dietary shifts.

In the Levant, Neolithic teeth are smaller than those of earlier groups, but dental size reduction appears to be restricted to buccolingual dimensions (Pinhasi, Eshed, and Shaw 2008). In Georgia (US), after the transition to agriculture there is a reduction in dental size that affects females to a greater extent than males, perhaps due to women being more responsible for agriculture-related activity and thus having a diet with a greater domesticated component (Larsen 1981). In Nubia, there is a strong decrease in dental length, breadth, and occlusal area in both males and females, starting in the Mesolithic and continuing across agricultural periods. This trend is followed by an ongoing, albeit diminished, trend of reduction for only the molar teeth between later agriculturalist groups (Calcagno 1986). Finally, dental asymmetry in buccolingual and mesiodistal diameters decreases, although the differences are not statistically significant, over the transition to agriculture in Peru, as seen from the diachronic sequence at Paloma (Gehlert 1979; Benfer 1984).

Alongside trends of dental reduction associated with dietary change, there are concomitant changes in dental wear. In some geographic areas, such as Japan (Fujita and Ogura 2009) and Peru (Benfer 1984), there is a reduction in the magnitude of dental wear associated with a transition to agriculture, due to the consumption of less abrasive foods. Yet in others, such as Ecuador (Buikstra 1984), dental wear increases from HG to agriculturalist populations, which could be explained by increased grit incorporated into food as a result of grinding grains (Hartnady and Rose 1991). Patterns of dental wear also tend to change

over a dietary shift from HG to domesticated foods, from flat to angled and cupped; this pattern is seen in the Levant, Nubia, and Japan (Smith, Bar-Yosef, and Sillen 1984; Kasai and Kawamura 2001; Pinhasi, Eshed, and Shaw 2008). That these changes are consistently associated with change in subsistence in such widely separated geographic regions suggests an effect of diet on dental wear patterns.

There is an extensive literature describing changes in dental health as a result of adopting agricultural subsistence strategies. In general, foragers are described as presenting higher degrees of dental wear, but less pathology such as caries, tooth rotation, crowding, alveolar lipping, and abscesses than agriculturalists, and fewer problems with bone remodeling and maintenance. Examples of this trend come from Nubia (Greene, Ewing, and Armelagos 1967; Martin et al. 1984; Martin and Armelagos 1984), Japan (Fujita and Ogura 2009), the Levant (Smith, Bar-Yosef, and Sillen 1984), Greece (Papathanasiou 2011), Peru (Allison 1984; Benfer 1990), Ecuador (Buikstra 1984), Chile (Allison 1984), South Asia (Kennedy 1984), Central California (Dickel, Schulz, and McHenry 1984), Dickson Mounds, Illinois (Goodman et al. 1984), and the Ohio valley (Perzigian, Tench, and Braun 1984). In one example, in the former Yugoslavia, y'Edynak and Fleisch (1983) found that Mesolithic individuals had more chipped and cracked teeth than Neolithic individuals, whereas the Neolithic group had a higher prevalence of hypoplasia and higher grades of alveolar resorption. However, this widespread trend is not universal. In Japan, Jomon and Yayoi individuals did not have significantly different carious tooth frequencies (Temple and Larsen 2007). This has been interpreted as a result of the Jomon reliance on cariogenic plants such as acorns, which have similar cariogenic properties to the wet rice that the Yayoi consumed (Temple and Larsen 2007).

The Postcranial Skeleton

Regarding variation in postcranial skeletal morphology related to the transition to agriculture, researchers have described changes in cortical thickness, body size, stature, degree of sexual dimorphism, and the frequency of degenerative joint diseases. Reduction in size is perhaps the most consistent change associated with a shift in subsistence and is seen in many disparate populations. This relates particularly to shorter stature in farmers, but also in some cases to reduced limb length and body mass. Compared with these fairly consistent shifts in size, changes in cortical thickness, which reflect bone strength, and sexual dimorphism show a more complex pattern that differs among the regions considered here.

There are numerous examples of stature reduction associated with shifts in subsistence practices in South America (Chile, Argentina, Ecuador) (Allison 1984; Buikstra 1984; Sardi and Béguelin 2011), the Levant (Smith, Bar-Yosef, and Sillen 1984), South Asia (Kennedy 1984), Nubia (Martin et al. 1984), the Ohio River Valley, Georgia (US), the lower Mississippi Valley, central California, and Dickson Mounds, Illinois, in North America (Dickel, Schulz, and McHenry 1984; Goodman et al. 1984; Larsen 1984; Perzigian, Tench, and Braun 1984; Rose et al. 1984). Despite being widespread, the trend of stature reduction does not seem to be universal, however. At the site of Paloma in Peru, where the earlier levels are HG and the later ones are agriculturalist, stature actually increases over time (Benfer 1984). This may be a sampling artifact, however, rather than an actual increase in height in farming populations, as the more recent chronological periods when agriculture was fully established are not well represented (Benfer 1984).

Stature also slightly increases in females from the lower Illinois Valley over the transition to agriculture (Cook 1984), and, in a comparative study, Auerbach (2011) argues that overall, stature is higher among southwestern agriculturalists (Arkansas, Louisiana) than southeastern foragers. These last results should be considered with caution, since the southwestern agriculturalists have not been shown to be direct descendants of the comparative sample of southeastern foragers, meaning that factors other than subsistence might explain such morphological differences, as mentioned above.

Decrease in body mass is recorded among Neolithic agriculturalists, when compared with previous HG populations from Nubia (Stock et al. 2011), with similar trends in the lower Mississippi (Rose et al. 1984), and Georgia (US) (Larsen 1984). As with changes in stature, however, this trend is not globally consistent; in the southern part of North America there are increases in southwestern agriculturalists' body masses when compared with southeastern foragers, with the former also presenting wider body breadths (Auerbach 2011).

Cortical thickness is a determinant of long bone strength. Changes in cortical thickness, calculated as the percentage of cortical area in relation to the total area, are associated with nutritional and mechanical factors (Larsen 1995). Despite being developmentally plastic (e.g., Ruff, Walker, and Trinkaus 1994), cortical thickness does not appear to respond consistently to changes in lifestyle associated with the transition to agriculture across different geographic regions, although some general trends can be established. In general, farmers present a decrease in long bone shaft cross-sectional dimensions and an increase in circularity, suggesting reduced strength and activity (figure 12.3). There is a reduction in cortical thickness when comparing long bones from HGs with those of later agriculturalists in Nubia (Martin et al. 1984), and Dickson Mounds, Illinois (Goodman et al. 1984), but no significant changes in cortical thickness when comparing HGs with later agriculturalists in the Illinois Valley (Cook 1984). Long bone diameter and rigidity, additional

Hunter-gatherer   Agriculturalist
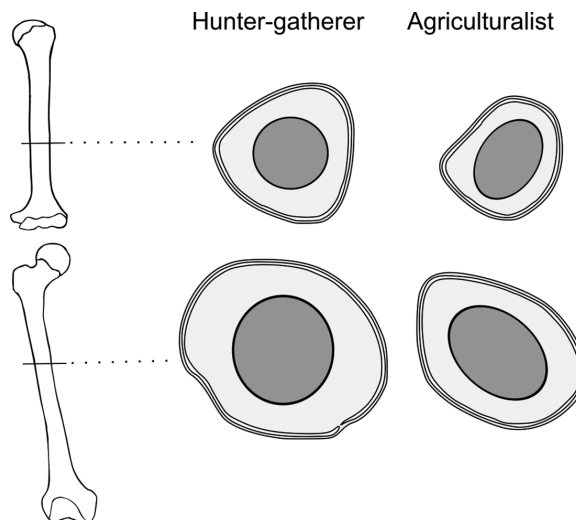
Figure 12.3
Long bone cross-sections showing the main changes in shape, size, and distribution of subperiosteal bone in the humerus and femur among hunter-gatherers and agriculturalists.

proxies for bone strength, are reduced in agriculturalists when compared with previous HGs in Illinois (Cook 1984), Paloma, Peru (Benfer 1984), the Danube Gorges in southeast Europe (Pinhasi et al. 2011), and the Nile Valley (Stock et al. 2011). However, again these are not ubiquitous trends: Larsen and Ruff (2011) and Rose and collaborators (1984) describe an increase in femoral diameter across the transition to agriculture in the lower Mississippi Valley, while Sardi and Béguelin (2011) describe an increase in femoral mid-shaft shape index (also denoting an increase in bone strength) among farmer females, compared with HG females, from the southern Andes.

In addition to the divergent diachronic changes in female height in North America and the change in female femoral strength in the southern Andes described above, there is other evidence of sexual dimorphism in skeletal responses to a change in diet. In Georgia (US) females show a greater diet-related decrease in skeletal size, robusticity, and stature than males (Larsen 1984). In fact, there is often an increase in sexual dimorphism accompanying a change in subsistence from HGs to agriculturalists. This is the case among central-west Argentinian farmers compared with earlier HGs (Sardi and Béguelin 2011), in agricultural populations from Ohio River Valley compared with previous HGs (Perzigian, Tench, and Braun 1984), in Georgia (Larsen 1984), in most archaeological sites from the Mississippi Valley (Rose et al. 1984), and overall in North America (Auerbach 2011). However, as with most of the postcranial trends associated with the transition to agriculture, these patterns are not the same in all populations. At the archaeological site of Caddoan in the Mississippi Valley, as well as at sites in Peru and the Nile Valley, sexual dimorphism decreases, rather than increases, in agricultural groups when compared with earlier HGs from the same regions (Benfer 1984; Rose et al. 1984; Stock et al. 2011). Finally, there are no changes in the degree of sexual dimorphism when comparing HGs with later agriculturalists from Dickson Mounds, Illinois (Goodman et al. 1984).

As with the dental evidence, frequencies of postcranial skeletal pathologies change after the transition to agriculture in many populations (Cook 1984; Goodman et al. 1984; Larsen 1984, 1995, 2006; Martin et al. 1984; Rose et al. 1984). In Georgia (US), there is an increase in the frequency of postcranial periosteal reactions, reflecting a decline in skeletal health, but a decrease in pathology related to mechanical stress (degenerative joint disease; Larsen 1981). A decrease in degenerative joint disease is also present among agriculturalists from Nubia (Martin et al. 1984) and the lower and central Mississippi Valley (Cook 1984; Rose et al. 1984). In general, both nonspecific markers of skeletal health and degenerative diseases associated with high levels of activity decline with the adoption of agriculture (Cook 1984; Larsen 1981; Martin et al. 1984; Rose et al. 1984). These results are congruent with previous findings that hunter-gatherers present a higher frequency of degenerative joint disease (osteoarthritis) than agriculturalists (Jurmain 1977; Larsen 1981). However, this trend may be population-dependent to an extent, since after studying a large sample of postcranial remains from individuals from across southern North America, Auerbach (2011) claims there is no general decline in health despite previous evidence to the contrary (Larsen 1995, 2006), and an increase in health is actually described among agriculturalists from Illinois in comparison with their HG ancestors (Goodman et al. 1984).

Discussion

Convergent and Divergent Trends Worldwide

The research we present above shows that the skeletal effects of the transition to agriculture are modest, directional, and most pronounced in craniofacial and mandibular features directly involved in mastication. There are some consistent trends seen in many geographically disparate regions (table 12.1). The mandible presents a size reduction and gracilization trend and a move toward a less upright ramus (von Cramon-Taubadel et al. 2011; Galland et al. 2016; Katz, Grote, and Weaver 2017). Over the course of the transition to agriculture, farmers tend to present more globular neurocranial vaults relative to lower faces, shorter and more inferiorly placed temporalis muscles, reduction in the maxillomandibular complex, smaller faces, modestly taller palates, shorter toothrows, and posterior displacement of the dentition due to the reduced length of the maxilla (Katz, Grote, and Weaver 2017). There is a generalized trend toward dental reduction in many regional studies conducted on teeth in North America, the Levant, North Africa, and South America, although the specific pattern of reduction is somewhat variable (y'Eynak and Fleisch 1983; Kennedy 1984; Larsen 1984; Martin et al. 1984; Calcagno 1986; Benfer 1990; Pinhasi, Eshed, and Shaw 2008). These changes are accompanied by an increase in dental caries (Larsen 1995, 2006), except in some areas such as East Asia, where agriculture was based on rice and caries frequency does not follow this trend (Temple and Larsen 2007).

Conversely, some anatomical structures appear to change as a result of the transition to agriculture but do not follow a widespread trend, instead varying with population or geographic region (table 12.1). These include most of the postcranial changes associated with shifts to domesticated diets, such as changes in stature, body mass, cortical thickness, and especially patterns of sexual dimorphism. In the following section we evaluate the potential proximal and ultimate causes for trends in morphological change across the transition to agriculture.

Table 12.1
Convergent and divergent phenotypic trends across geographic regions after the adoption of agriculture

	Near East	North Africa	North America	South America
Gracilization and mandibular size reduction	X	X	?	?
Trend toward less upright mandibular ramus	X	X	?	?
More globular neurocrania	X	X	X	X
Lower and smaller facial skeleton	X	X	X	X
Shorter temporalis muscle	X	X	X	X
Dental size reduction	X	X	X	X
Stature reduction	X	X	X	X
Body mass reduction	?	X	X	?
Postcranial bone cortical thickness reduction	?	X	X	X
Sexual dimorphism	?	Reduction	Variable	Increase

Notes: X = presence in region; ? = uncertainty due to insufficient data.

Proximate and Ultimate Causes of Morphological Change across the Agricultural Transition

As suggested at the beginning of this chapter, one way to organize the currently disparate interpretations of the morphological effects of agriculture is to apply Mayr's (1961) definition of proximate and ultimate causes. This approach allows us to distinguish between different levels of explanation that are not mutually exclusive but refer to different aspects of the phenomenon. In his influential essay, Mayr wrote that "proximate causes govern the responses of the individual (and his organs) to immediate factors of the environment, while ultimate causes are responsible for the evolution of the particular DNA code of information with which every individual of every species is endowed" (Mayr 1961, 1503). According to more recent perspectives, proximate causation can be equated with immediate factors (for example, physiology) and ultimate causation with evolutionary explanations (for example, selection) (Laland et al. 2011). Here we use Mayr's framework to discuss the following potential proximate causes for the morphological differences between HGs and farmers: (1) direct biomechanical changes due to alterations in the intensity of masticatory loading or physical activity and (2) systematic changes due to adjustments in dietary nutrition or activity levels resulting in alterations in hormonal circulation levels. We then examine possible ultimate causes (i.e., the evolutionary processes behind the morphological changes) and evaluate the potential roles of (3) phenotypic plasticity as a result of environmental influences on individuals during development and (4) directional selection, whereby morphological adaptation involves changes to DNA sequences over many generations. Since developmental plasticity, the ability of an individual to alter its phenotype in response to the environment (Fusco and Minelli 2010), has a relevant role in evolutionary change (Nijhout 1990; Gilbert 2001; Pigliucci 2001; West-Eberhard 2003), we will here consider it as an ultimate cause, despite the fact that this is a highly debatable point (see Brown 2020).

Proximate Causes of Morphological Changes over the Agricultural Transition

When evaluating explanations provided for proximate causes behind morphological changes across the transition to agriculture, most interpretations in the literature can be attributed to one of two alternative mechanisms: (1) direct biomechanical changes due to alterations in loading or (2) systematic changes due to adjustments in the diet or changes in physical activity.

Direct Biomechanical Causes

Biomechanical explanations for diet-related morphological changes in the skull are very widespread (Lieberman 2011). They usually invoke a decrease in masticatory stress due to changes in food preparation techniques (cooking, grinding, and so on), which were critical in producing softer food, and/or the reduction or complete replacement of meat and fiber resulting in a diet with a large proportion of softer, grain-based foods (food consistency). As these factors are usually entangled and could be causally related, they will be considered together.

   The suggestion that reduced masticatory stress seen across the transition to agriculture led to the morphological changes in the skull has been well developed by Carlson and Van Gerven (1977) as a set of premises that compose the masticatory-functional hypothesis

(MFH). The MFH states that shifts from HG to agricultural diets resulted in decreasing functional demands on the masticatory complex, bringing about alterations in skull morphology, including a reduction in size of the masticatory muscles, reduction in the growth of the maxillomandibular complex, and compensatory changes in the shape of the cranial vault. As a consequence, individuals from agricultural populations tend to present allometric shape changes, such as a more posterior origin of masticatory muscles, a more inferiorly placed and retrognathic face, a more globular vault, and concomitant size reductions in teeth and alveolar region (Carlson and Van Gerven 1977). The first assumption behind the MFH is known as *Wolff's law*, which states that bone is deposited in presence of functional demand and resorbed in its absence in such a way that a decrease in musculoskeletal stress results in size reductions (Wolff 1892, 1986). Though the nuances of this relationship have been much questioned, the basic relationship between stress and bone deposition is supported (Ruff, Holt, and Trinkaus 2006). The second, implicit, assumption is that an HG diet results in greater stresses on the masticatory complex than an agricultural one (Carlson and Van Gerven 1977).

A reduction in the magnitude and change in direction of masticatory forces resulting from changes in subsistence and food-producing techniques has been claimed as the main mechanism behind morphological change in many disparate geographic regions. The MFH has been invoked to account for the decrease in cranial, mandibular, and TMJ size in populations from Nubia (Hinton and Carlson 1979; Galland et al. 2016), the former Yugoslavia (y'Edynak & Fleisch 1983), Japan (Kaifu 1997; Hoover and Williams 2015), the Maghreb (Sardi, Ramirez-Rozzi, and Pucciarelli 2004), and the Levant (Pinhasi , Eshed, and Shaw 2008; Pinhasi, Eshed and von Cramon-Taubadel 2015; May et al. 2018; Pokhojaev et al. 2019). Despite morphological integration between the mandible and maxillary regions, they can evolve independently (von Cramon-Taubadel 2011), and studies comparing responses to dietary change from HG to farming across the whole skull provide a complex scenario. Some describe diet-related morphological changes in the shape of the whole skull (Carlson and Van Gerven 1977; Larsen 1995; Gonzalez-José et al. 2005; Sardi, Ramirez-Rozzi, and Pucciarelli 2004; Perez et al. 2011), while others describe more localized changes, such as the more geographically widespread changes in the attachment of the temporalis muscle area (Paschetta et al. 2010; von Cramon-Taubadel 2011; Noback and Harvati 2015). The size reduction of the masticatory component and posteroneuronal region in crania from the southern Andes has been interpreted as a direct and localized change resulting from changing masticatory loading due to reduced dietary hardness in agriculturalists (Sardi, Novellino, and Pucciarelli 2006). An increase in the vertical height of the mandible, combined with a reduction in the mandibular condyle and coronoid process, as described from Levantine and Nubian sites, are all associated with the reduction in stresses resulting from anterior dental loading (Hinton and Carlson 1979), which is known to be reduced in agriculturalists compared with foragers (Hinton and Carlson 1979; y'Edynak and Fleisch, 1983; Galland et al. 2016; May et al. 2018). Similarly, the changes in orientation in the posterior part of the mandibular body from a more lingual inclination to a more buccal one in later Levantine populations may suggest a reduction in torsional forces on the mandible, resulting from a diet that was easier to chew (May et al. 2018).

Support for a causal relationship between the morphological changes described across the transition to agriculture and reduced masticatory stress comes from experimental

studies on nonhuman models. Studies comparing animals raised on foods varying in consistency (hardness or toughness) support the conclusions drawn from the bioarchaeological literature, as described above, by showing morphological differentiation in the same parts of the cranium and mandible (Bouvier and Hylander 1982; Corruchini and Beecher 1982, 1984; Hinton 1983, 1992; Yamada and Kimmel 1991; Tuominen, Kantomaa, and Pirttiniemi 1993; Ciochon, Nisbett, and Corruccini 1997; Liberman et al. 2004). Experimental studies on nonhuman primates fed tough foods also indicate that high strains are generated in the same regions as those seen to undergo change in the human cranium during the course of the agricultural transition (Hylander, Johnson, and Picq 1991; Ross and Hylander 1996; Ravosa et al. 2000), suggesting these regions would be where adaptation would be most likely, according to Wolff's law.

Dental size reduction in agriculturalists, compared with forager groups, has most often been interpreted as a secondary consequence of facial reduction driven by biomechanical shifts (Carlson and Van Gerven 1977; Smith, Bar-Yosef, and Sillen 1984; Lieberman 2011), yet there is no uniform association between facial and dental reduction. In the Levant, for example, teeth are reduced in buccolingual dimensions, but facial size reduction appears to be restricted to the mandible, with specific changes to the corpus height at the mandibular symphysis and a reduction in ramus breadth (Pinhasi, Eshed, and Shaw 2008). Since it is difficult to see how these specific mandibular changes would affect buccolingual dental dimensions, this may indicate that, at least in some populations, the reduction in masticatory stresses is acting directly on dental size.

Diachronic changes in dental wear patterns in the Levant, Nubia, and Japan have been interpreted as evidence of reduction in dietary toughness from an HG diet to an agricultural one consisting of cereal-based foods (Smith, Bar-Yosef, and Sillen 1984; Kasai and Kawamura 2001; Pinhasi, Eshed, and Shaw 2008). The cooking practices required to make such foods edible may further reduce toughness and dental wear (Eshed, Gopher, and Hershkovitz 2006; Fujita and Ogura 2009). Where the reverse is seen—namely, an increase in dental wear from earlier forager to more recent farmer populations—it is interpreted as a side-effect of non-cooking food processing techniques, such as grinding, which can introduce grit into food and lead to considerable wear (Watson 2008). The increase in dental pathologies seen in adopters of agriculture may be a side-effect of facial reduction resulting from biomechanical changes. Y'Edynak and Fleisch (1983) argue that softer food produces less stress on the mandible and that in turn the mandible does not achieve its maximum phenotypic development. The shortened mandible then produces crowded and rotated teeth resulting in possible maladjustments. Maladjustments such as crowded and rotated teeth produce uneven stresses on the periodontal membrane, resulting in inflammation of the gingival tissue, diseases of the periodontium, and eventually tooth loss and alveolar resorption, as seen at higher levels in many agriculturalist populations compared with foragers (y'Edynak and Fleisch 1983). Additionally, most agricultural diets are richer in carbohydrates than those of foragers, and these foodstuffs are more cariogenic, a situation worsened by maladjustments that lead to food sticking to teeth and contribute to the greater frequencies of caries in agriculturalist populations (Hillson 1986; Larsen 1997; Ogden 2008). In contrast, HGs tend to use their anterior dentition much more than agriculturalists, which involves greater loading on the temporalis and masseter muscles, and results in an increased incidence of dental chipping in HG groups (y'Edynak and Fleisch 1983).

The widely seen reduction in postcranial skeletal size and robusticity across the agricultural transition has been linked to biomechanical factors resulting from a less active lifestyle. The exact mechanism thought to underpin changes is rarely specified explicitly, however. A lifeway based on hunting and gathering appears to involve more functional demand on the body than one in which agriculture is the primary mode of subsistence (Larsen 1984; Ruff, Larsen, and Hayes 1984; Stock and Pfeiffer 2001; Macintosh, Pinhasi, and Stock 2016). This reduction in functional demand in farmers could be at least in part the result of a decrease in mobility (Larsen and Ruff 1991). Ruff, Larsen, and Hayes (1984) have shown that the cross-sectional geometric properties of limb bones reflect a reduction in biomechanical demands from HG to farmers in Georgia (US), following Wolff's law. They propose that HG activity is characterized by climbing and running, while farmers perform more walking, lifting, and carrying (Ruff, Larsen, and Hayes 1984). These results are supported by longitudinal and comparative studies in contemporary populations that show increases in bone size, cross-sectional geometric measures of bone strength, bone mineral density, and body mass when performing moderate to high exercise (Taaffe et al. 1997; Bradney et al. 1998; Daly et al. 2004; Guadalupe-Grau et al. 2009; Shaw and Stock 2009; Suominen 2012).

Theories about changes in levels of sexual dimorphism over the agricultural transition have often used biomechanical processes as their implicit underpinning. The increase in sexual dimorphism in postcranial strength accompanying a change in subsistence from HG to agriculture in many geographic regions has been interpreted as resulting from strong sexual division of labor in farmers, as opposed to both sexes being involved more evenly in foraging activities (Larsen 1984; Perzigian, Tench, and Braun 1984; Rose et al. 1984; Auerbach 2011; Sardi and Béguelin 2011). In contrast, a decrease in size sexual dimorphism over the transition to agriculture has been reported for some populations. In those cases, the decrease results from a relative increase in female size, which may be due either to an increasing physical demand in females (Cook 1984; Rose et al. 1984) or to lessening sexual division of labor (Benfer 1990). The lack of a global pattern in sexual dimorphism likely relates to the types of task being carried out by both sexes and how differentiated they are, factors that differ with local diet, culture, and ecology.

Systematic Explanations

Some scholars argue that many size reductions in populations transitioning to an agricultural diet may be related to a lack of protein and other nutrients, at the expense of an increase in the consumption of carbohydrates, experienced during development. Environmental influences during growth and development have been shown to have profound consequences on the subsequent phenotypic expression of biological traits during adulthood (Bogin 1999; Frisancho 2009). This mechanism has been suggested for interpreting morphometric patterns in crania and postcrania particularly among South American populations (Sardi, Novellino, and Pucciarelli 2006; Perez et al. 2011; Menéndez et al. 2014), but also for North American ones (Larsen 1981, 1984, 1995; Martin et al. 1984; Perzigian, Tench, and Braun 1984). In South America, smaller and more gracile crania from the northwest of the continent have been interpreted as a result of diets based mostly on processed carbohydrates, which, being less nutritious than varied forager diets, would have induced systematic changes leading to a general decrease in cranial and body size, together

with allometric changes in shape (Menéndez 2015). Both South American and North American populations traditionally shared a reliance on maize, a cereal low in two essential amino acids: lysine and tryptophan. Amino acids are essential for cell multiplication in the growth and differentiation of structural tissues, such as muscle and bone (Stini 1971). While humans synthesize some amino acids, others must be ingested. If any of them is lacking in the diet, however, this will preclude the utilization of the rest (Stini 1971). The cessation of amino acid supply reduces the maintenance and growth processes of skeletal muscle, producing a slow and delayed growth that results in the size reduction of the skeleton (Stini 1975).

In an experiment conducted on squirrel monkeys, Cónsole and collaborators (2001) found that a low-protein diet induced a decrease in growth hormone (GH) and prolactin cell populations, resulting in changes of craniofacial morphology, especially in the masticatory module. Low protein intake impairs both the production and action of insulin-like growth factor-I, which is essential for longitudinal bone growth and bone formation, as it stimulates proliferation and differentiation of chondrocytes in the epiphyseal plate (Bonjour et al. 2001). Cranial and mandibular size changes associated with the adoption of a diet overly reliant on carbohydrates and with reduced protein are further supported by experimental studies on rats and squirrel monkeys (Pucciarelli 1980, 1981; Dressino and Pucciarelli 1999; Miller and German 1999). Decrease in skull size associated with dietary shifts also could be interpreted as the result of changes in hormonal pathways due to the under-availability of nonprotein nutrients required for growth (Nijhout 2003). Ginter (2011) proposed a reduced-growth model for South African populations after the adoption of agriculture. She suggests that decrease in skeletal size resulted from stunted development, mitigating nutritional insufficiency, and that this explains the later rebound in stature after improvements in agricultural practices (Ginter 2011). Direct evidence of malnutrition in the archaeological populations where size reduction has been recorded comes from palaeopathology analyses; studies have linked the presence of pathologies such as *cribra orbitalia* in prehistoric populations with nutritional deficiencies in proteins, calcium, and iron (Angel 1984; Rathbun 1984; Smith, Bar-Yosef, and Sillen 1984; Ulijaszek 1991). These theories are supported by comparative studies in human populations undergoing protein malnutrition, in which individuals have reduced body size and stature (Frisancho, Garn, and Ascoli 1970; Stini 1972; Bogin and MacVean 1981).

Changes in hormonal pathways as a result of reduced physical activity have also been proposed for interpreting changes in the skull (both mandible and cranium) and postcranial skeleton across the agricultural transition (Smith, Bar-Yosef, and Sillen 1984; Sardi, Ramirez-Rozzi, and Pucciarelli 2004). Regarding the systematic effects of reduced activity on bone growth, some studies have found a direct association between growth hormone circulation and intensity of physical activity, in which GH circulation increases following moderate to intense exercise, promoting the incremental growth of skeletal and muscle mass (Vogl et al. 1993; Kalu, Banu, and Wang 2000; Weltman et al. 2001). Variation in GH circulation during development is linked to variation in the length of the limbs (Ohlsson et al. 1998), while in adults it is associated with variation in muscle strength and bone mineral density (Johansson et al. 1994). A more sedentary lifestyle and changes in activity type might have reduced GH circulation in farmers, which contributes to lower skeletal mass and accounts for many of the size and strength differences in the postcranial

skeleton observed when they are compared with HGs (Pfeiffer and Sealy 2006). Sardi, Ramirez-Rozzi, and Pucciarelli (2004) suggest that the relative reduction in the face and midneural component in Neolithic northwest Africans, as a result of overall skull reduction, could be explained by the differences in subsistence and mobility in comparison with Upper Paleolithic HGs. Smith, Bar-Yosef, and Sillen (1984) suggested that a combination of reduced game hunting and the more complex tool kit, including for example projectile points, which characterized most agriculturalists, could have led to smaller, more gracile bodies. This hypothesis originally was proposed for a Neolithic to Upper Paleolithic comparison in Europe (Frayer 1980), and it has been argued that there is insufficient evidence to support it in the Levantine context (Smith, Bar-Yosef, and Sillen 1984), thus it cannot be invoked as a general mechanism across populations.

Ultimate Causes of Morphological Changes over the Agricultural Transition

The long-term patterns of morphological variation, such as those seen across the agricultural transition, could be interpreted as a result of developmental plasticity in each generation and/or directional selection. Distinguishing between plasticity and selection is not an easy task due to the complexity of their interactions within and between populations (Gilbert and Epel 2009). Some expectations can be drawn, however, to infer the prevalence of one over the other in different circumstances. In this section we explore how the contribution of these processes are interpreted in the literature with regard to morphological changes in populations that shifted from HG to agricultural subsistence.

Developmental Plasticity
Developmental plasticity is a long-term process by which an individual adjusts to environmental conditions during growth and development (West-Eberhard 2003). Plasticity-induced variants have been interpreted as being adaptive or as accelerating the pace of genetic adaptation by providing a source of raw variability upon which natural selection can act to shape subsequent genetic adaptation (Baldwin 1896; Schmalhausen 1949; Waddington 1953; West-Eberhard 2003). Although the long-term effects of plasticity have not yet been fully considered as an alternative ultimate explanation for explaining morphological change, work by Waddington (1953), as recently explained by Fabris (2018, 2019), emphasized the role that developmental plasticity has in evolution.

Through developmental plasticity, human populations can evolve relatively rapidly when confronted with environmental change (Perez et al. 2011). The phenotype may adjust to recent changes or prevailing conditions by reorganizing life history strategies and altering the balance of energy allocation among the areas of growth, maintenance, defense, and reproduction (Wells and Stock 2020; chapter 13, this volume). Most of the morphological changes interpreted as resulting from the transition to agriculture are inferred to be the outcomes of developmental plasticity exclusively. This is especially the case for research on craniofacial data (Larsen 1984; Gonzalez-José et al. 2005; Holmes and Ruff 2011; Perez et al. 2011; Katz, Grote, and Weaver 2017), but also applies to dental and postcranial differences between groups (Kaifu 1997; Macintosh, Pinhasi, and Stock 2016).

These plastic interpretations of morphological change resulting from the adoption of agriculture are supported by a wealth of evidence. Holmes and Ruff (2011) compared ontogenetic changes in mandibular morphology in two human populations with contrasting

diets: late prehistoric Inuit HG from Alaska, who are characterized by a very demanding masticatory regime, and proto-historic Arikara farmers from South Dakota. Although they found large differences in mandibular morphology between the Inuit and Arikara adults, those differences were very subtle between the youngest juveniles of both series. These authors suggest that mandibular shape differences between these populations developed gradually during growth due to increasing exposure to dietary loading, suggesting plasticity as the main evolutionary process behind them (*sensu* Lieberman 2011). This argument is reinforced by *in silico* biomechanical modeling analyses of Paleolithic, Mesolithic, and recent human mandibles that show that differences in mandibular size and shape between populations are consistent with plasticity acting on variation in mandibular loading during ontogeny (Stansfield, Evteev, and O'Higgins 2018). Regarding the craniofacial complex, Gonzalez-José and collaborators (2005) compared phenotypic distances for different cranial modules between populations from South America with different subsistence practices. They stated that, since the level of phenotypic differentiation between subsistence groups is lower than the level of intrapopulation variation, the morphological changes observed are not genetically fixed and concluded that plasticity is the most plausible explanation. The mandible also provides evidence for plasticity. Kaifu (1997) argued that the speed of the rapid changes observed in mandibular size reduction accompanying dietary change in Japan shows that developmental plasticity is a better explanation for this trend than selection. The effects of plastic responses to diet in the skull are demonstrated by bioarchaeological studies on dental health, showing greater malocclusion and dental crowding among farmers (Larsen 2006; Lieberman 2011; von Cramon-Taubadel 2011; Katz, Grote, and Weaver 2017). These conditions result from an inadequate coordination between facial and dental growth, since bone responds directly to biomechanical forces, while teeth do not (von Cramon-Taubadel 2017). As a consequence, in a population that has recently changed to a softer diet, the degree of tooth size reduction is considerably less than the degree of reduction of the supporting jaw and facial skeleton, which produces less room for the dentition. Tooth crown reduction is also much greater among permanent teeth than deciduous ones (Hillson and Trinkaus 2002). The difference is due to the fact that the former grow while the individual is already chewing with the deciduous teeth, allowing changes due to epigenetic mechanisms (i.e., non-DNA-based, developmentally induced regulatory forms of phenotypic modulation; Jablonka and Lamb 2010). According to Lieberman (2011), given the lack of membrane separating the developing teeth from the alveolus, expectations from the MFH (Carlson and Van Gerven 1977) and Wolff's law (Wolff 1892, 1986), which were described above, can be also extended to the permanent teeth. Thus, the chewing of highly processed food may have contributed to the size decline observed in permanent teeth during human evolution.

The importance of the role of developmental plasticity in explaining morphological variation between populations with different subsistence practices is further supported by numerous experimental studies on nonhuman samples. This research shows rapid changes in the size and shape of the maxilla, orbital plane, and mandibular ramus and corpus depending on whether animals were fed hard/high masticatory stress food or soft/low masticatory stress food. In addition to the characteristic bony morphology of animals fed on soft diets, they also exhibit dental malocclusions as adults, as seen in humans with arguably less biomechanically demanding diets (Larsen 2006; Lieberman 2011; von Cramon-Taubadel 2011; Katz,

Grote, and Weaver 2017). These results have been repeated in a variety of phylogenetically and morphologically diverse taxa (e.g., Corruccini and Beecher 1982, 1984; Yamada and Kimmel 1991; Ross and Hylander 1996; Ciochon, Nisbett, and Corruccini 1997; Lieberman et al. 2004; Scott et al. 2014).

Finally, an additional source of support for developmental plasticity responding to dietary specializations and biological differences across populations comes from studies on the gut microbiome (Schnorr et al. 2014; Schnorr 2018). Schnorr and collaborators (2014) studied gut microbiome richness in Hazda HGs in comparison with neighboring farmers and urban groups and found that the Hadza display unique features that enhance their ability to digest and extract valuable nutrition from fibrous wild plant foods. Since the gut microbiome is acquired by each individual during ontogeny, its phylogenetic diversity and taxonomic variation will be shaped by the subsistence economy and the lifetime exposure to a certain natural environment (Schnorr 2018). Therefore, both biological differences between HGs and farmers, and the existence of convergent traits between groups with similar diets could be interpreted as a result of their specific lifestyle and ecological niche, particularly in terms of diet.

Directional Selection

In addition, or as an alternative, to developmental plasticity, directional selection has been proposed as an evolutionary process, or ultimate cause, that might explain some of the morphological changes associated with the transition from an HG to an agricultural diet. Selection has been invoked particularly to account for the trend in dental reduction (Greene, Ewing, and Armelagos 1967; O'Connor, Franciscus, and Holton 2005), but there are also some claims for its influence on the postcranial skeleton (e.g., Ginter 2011).

Specific mandibular traits have been interpreted as resulting from selection, independently of the dentition. These include the thick basal cortical bone of the mandible in Japanese HGs (Kanazawa and Kasai 1998) and the large mandibular condyle size in Nubian foragers (Hinton and Carlson 1979). Pinhasi, Eshed, and Shaw (2008) pointed out that since only very specific mandibular traits, such as mandibular ramus breadth and anterior height, are reduced in combination with dental buccolingual dimensions, simple systematic explanations cannot be invoked, and selective pressures acting locally might be the most plausible explanation. Similarly, May and collaborators (2018) claimed that the complex changes in chin height and mandibular angle associated with the adoption of an agricultural diet cannot be explained solely through developmental plasticity and reduced stresses on the masticatory system. Instead, decreases in the size and robusticity of the mandible are argued to be subject to selective pressures, while the width and robusticity of the facial skeleton might be due to masticatory-induced phenotypic plasticity (Galland et al. 2016).

The idea that selection is the main process behind dietary adaptation in the skull is supported by studies showing that some morphological differences consistent with variation in dietary functional demands are manifested very early in development and therefore likely indicate a genetic component (Fukase and Suwa 2008; Gonzalez, Perez, and Bernal 2010; Katz, Grote, and Weaver 2017). Fukase and Suwa (2008) found greater bone mass and significantly thicker cortical bone in mandibles from HGs (Jomon) than recent Japanese people, which they relate to differences in diets. More importantly, even the youngest

Jomon mandibles in this ontogenetic sample exhibited most of the adult characteristics that differ from recent Japanese mandibles. Considering that the more robust morphology of the Jomon is found even in presumably pre-weaning infants, Fukase and Suwa (2008) suggest that there is at least a genetic component to the overall robusticity of the mandible, although they acknowledge the likely existence of complementary plastic remodeling in response to lifetime diet. Similarly, Gonzalez, Perez, and Bernal (2010) analyzed the ontogenetic development of craniofacial robusticity in human populations from South America by performing morphometric comparisons of populations with different degrees of robusticity. They found that the robust cranial traits of Fueguians, which are consistent with the functional requirements of a HG diet, are already established early in life and that differences in the extension of allometric trajectories contributed to the variation in robust traits that is observed in adults.

Teeth do not remodel as bone does, though epigenetic mechanisms may alter developing teeth to some extent (Lieberman 2011); thus they are far less developmentally plastic to environmental stimuli than the rest of the skeleton. This means that consistent association between dental morphology and diet may provide the strongest evidence of directional selection. Tooth reduction in agriculturalists compared with preceding HGs has been interpreted as a result of directional selection in South Asia (Kennedy 1984), Nubia (Martin et al. 1984; Calcagno and Gibson 1988), and Anatolia (Pinhasi, Eshed, and von Cramon-Taubadel 2015). Pinhasi and Meiklejohn (2011) suggest that the most parsimonious mechanism behind dental reduction is directional selection, since drift alone could not explain a significant diachronic reduction process. Y'Edynak and Fleisch (1983) argue that in the absence of the need for large, robust jaws suited to tough forager diets, by the Neolithic selection had led to populations with reduced posterior teeth and as a result, still smaller, developmentally less costly jaws. In a related hypothesis with a slightly different focus, Greene, Ewing, and Armelagos (1967) postulated that selection for less-complex and more caries-resistant teeth resulted in a smaller and morphologically less complex dentition in farmers from Sudan. Carlson and Van Gerven (1977), however, claimed that although Green's hypothesis had merit, it was not the only causal process involved. They explained the diachronic alteration and gracilization of the craniofacial complex in prehistoric Nubians as the result of two independent processes. Since agricultural foodstuffs resulted in an increased prevalence of caries and related pathologies, selective pressures may have acted to reduce overall size and morphological complexity of the dentition. Simultaneously, reduction in the functional demands on the masticatory complex would have also led to alterations in the growth of the maxillomandibular complex in such a way that the face became smaller, less robust, and oriented more inferoposteriorly (Carlson and Van Gerven 1977; see above). This dual-mechanism theory likely reflects the real-world complexity of integrated skeletal changes resulting from the interplay of multiple, interrelated factors.

In terms of postcranial shifts in morphology, Smith, Bar-Yosef, and Sillen (1984) suggested that reduced selective pressures resulting from a combination of reduced hunting and more sophisticated Neolithic technology could have led to smaller size and reduced sexual dimorphism. As noted above, however, in many populations we see increased, rather than decreased, sexual dimorphism after the transition to agriculture (Larsen 1984; Perzigian, Tench, and Braun 1984; Rose et al. 1984; Auerbach 2011; Sardi and Béguelin

2011), which reduces the strength of this argument in that respect at least. Ginter (2011) offers a more nuanced and complex model for the interaction between nutritional insufficiency and body size. She suggests that developmental plasticity in the first instance, but also longer-term directional selection, could have combined to produce the decrease in skeletal size in South African populations seen after the adoption of agriculture. Selection would have resulted from the energetic advantages of being small-bodied in a resource-poor environment (Ginter 2011)—another important reminder that evolutionary mechanisms in nature rarely act independently. Wells and Stock (2020) provide a life-history framework within which these mechanisms may interact. They propose that, as a result of the shift to farming, size reduction is a product of changes in energy allocation toward immune defense and reproduction at the expense of growth and maintenance. In complementary fashion, Gawne and McKenna (chapter 13, this volume) consider such size changes as morphogenetic trade-offs resulting from high-level developmental processes that govern the production of form during ontogeny. These suggestions bring together insights into the subtle and complex ways in which multiple mechanisms lead to morphological change at the individual and population levels.

A final source of support for the assertion that dietary specializations show discernable patterns of genetic divergence between HGs and farmers, and thus likely directional selection, comes from genetic studies on diet-related pathways (Perry et al. 2007; Tishkoff et al. 2007; Fumagalli et al. 2015; Heath et al. 2016; Raj et al. 2019). A pioneering study by Perry and collaborators (2007) provided an example of selection in populations with high-starch (agricultural) diets. They found a strong positive correlation between the copy number of the salivary amylase gene (AMY1) and salivary amylase protein level, which is present at higher levels in individuals from populations with high-starch diets and improves the digestion of starchy foods. Some adaptive responses to different subsistence practices such as lactase persistence in Eurasians and Africans (Tishkoff et al. 2007) and low iron levels in Europeans (Heath et al. 2016), which both emerged with agriculture, are widespread, while others, such as adaptations to fatty marine HG diets in Greenland Inuit (Fumagalli et al. 2015), are more specialized. With direct relevance to crop-based agricultural diets, Raj and collaborators (2019) studied genetic variation in 29 Asian populations to evaluate if the range of domesticated foods available in different regions has created regionally distinct nutrient intake profiles and deficiencies. They found a correlation between genetic variation in diet-related pathways and dietary differences among Asian populations. They conclude that diet-related selection on genes for salivary glands and cellular processes in the pancreas drove the genetic adaptations of Asian populations. This research demonstrates some of the adaptation via directional selection that has taken place in recent humans to aid adaptation to an agricultural diet. Since such physiological dietary adaptations can be shown to be encoded in the genome, this suggests evidence for selection leading to skeletal adaptations will also be found there.

Conclusion

In this chapter we have provided a geographically wide-ranging synthesis of the phenotypic changes in the human skeleton resulting from the transition to agriculture, as interpreted from morphological analyses, by accounting for the plausible proximate and

ultimate explanations within an evolutionary biology framework. We find that, while some of the morphological consequences of transferring from a mixed, wild diet to one based mostly on domesticated crops have been similar across the world (e.g., tooth reduction, gracilization of the skull), others are expressed differently and vary locally (e.g., degree of sexual dimorphism, tooth decay) (table 12.1).

Underlying the various morphological trends observed, there is evidence for several different mechanisms at work alone or in combination. Alternate proximate mechanisms could have produced morphological changes in populations undergoing separate dietary shifts and, due to the modular complexity of the skeleton, each of its parts could be influenced by different factors to varying extents. This being the case, given the current evidence available to us, it is not possible to determine without doubt the causes of any specific morphological change associated with the transition to agriculture. Though it is undeniably complicated, however, there are specific morphological trends in which the balance of evidence points toward a majority role for one proximate cause or another.

Perhaps the strongest argument for a subsistence-related biomechanically driven proximate cause is in changes to mandibular morphology. This claim can be supported using a number of sources of evidence: archaeological, functional, comparative, and computer modeling. The closest relationship between diet and global variation in human skeletal morphology is found in the mandible (von Cramon-Taubadel 2011), and when specifically considering changes over the course of the agricultural transition, some mandibular changes such as the lengthening and narrowing (anteroposteriorly and mediolaterally) of the ramus are repeatedly seen in disparate geographic regions such as the Levant (Smith, Bar-Yosef, and Sillen 1984; May et al. 2018; Pokhojaev et al. 2019), Nubia (Galland et al. 2016), and Japan (Kaifu 1997). At least one of these regions, the Levant, is likely a region of biological continuity over the transition (Bar-Yosef 1998). Biomechanical analysis shows that a short, wide ramus is advantageous for a high-strain diet, as it results in a more vertically oriented (providing greater efficiency) and larger temporalis muscle and reduces regionally high levels of strain (Korioth, Romilly, and Hannam 1992; Nicholson and Harvati 2006; Sella-Tunis et al. 2018). Thus, it seems reasonable to suggest optimization of the mandible to reduce masticatory forces resulting from a shift to agriculture was largely responsible for the changes in ramus shape seen in many populations undergoing this shift.

Systematic hormonal effects as a proximate cause are most plausible in the trend for smaller body size in farmers. Some size reduction in skeletal regions not functionally related to subsistence practices is likely the consequence of stunted growth due to insufficient protein and other nutrients. Reducing growth buffers the maintenance of essential bodily functions under conditions of malnutrition (Ginter 2011; Menéndez 2015). As described above, the results of malnutrition on size are well documented from a wide range of human biomedical and comparative experimental studies in other species. The differential effects of this particular physiological process and other factors leading to smaller size on specific populations will have varied depending on local environments and diets, but it may be possible to identify stunting, as it preferentially affects certain regions of the body (Pomeroy et al. 2012). Stunting may also be accompanied by other nonspecific indicators of stress, such as linear enamel hypoplasia (Temple 2008; Vercellotti et al. 2014), and, taken together, these pathologies enable a better understanding of the mechanisms resulting in smaller-sized agricultural populations.

The co-occurrence of the same proximate mechanisms in different individuals from the same population and the persistence of the subsequent morphological changes over many generations could be interpreted as a result of different ultimate mechanisms acting on the human skeleton. Although distinguishing between these mechanisms is again difficult, there are specific morphological trends in which the action of a particular ultimate cause is more likely.

There is a strong case for developmental plasticity as the ultimate mechanism in the gracilization of specific masticatory regions of the skull, such as those where the mastica-tory muscles attach, as a result of a decrease in the loading of the masticatory apparatus. This gracilization is seen in numerous populations from different geographic regions and is duplicated both in diachronic sequences across the transition to agriculture and in con-temporaneous groups with different subsistence strategies. Ontogenetic series showing that population-specific morphology is not established at birth are particularly convincing (Holmes and Ruff 2011). The relationship between bone deposition, remodeling, and masticatory strain has been shown by both comparative studies using primates (Hylander 1979), hyraxes (Lieberman et al. 2004), and rodents (Yamada and Kimmel 1991) and *in silico* simulations of human morphology (Korioth, Romilly, and Hannam 1992; Sella-Tunis et al. 2018); Wolff's law is a persuasive argument for the mechanism behind these functional changes (Wolff 1892, 1986; Ruff, Holt, and Trinkaus 2006).

The lack of remodeling in teeth, particularly those that develop *in utero*, makes them less subject to developmental plasticity than other parts of the skeleton (Hillson and Trinkaus 2002; Lieberman 2011). Dental changes are therefore the best evidence for the ultimate cause of directional selection resulting from dietary change over the transition to agriculture. At least some of the trends for dental reduction likely result from directional selection, possibly due to selective pressures for smaller, less complex teeth to avoid tooth decay (e.g., Pinhasi, Eshed, and Shaw 2008). The strength of the potential selective pres-sure is evident in the increasing levels of caries across a globally distributed sample of diachronic series (Allison 1984; Buikstra 1984; Dickel, Schulz, and McHenry 1984; Goodman et al. 1984; Kennedy 1984; Martin et al. 1984; Perzigian, Tench, and Braun 1984; Smith, Bar-Yosef, and Sillen 1984; Papathanasiou 2011), and additional factors such as decreasing jaw size (Larsen 2006; Lieberman 2011; von Cramon-Taubadel 2011; Katz, Grote, and Weaver 2017) may have intensified this pressure by leading to malocclusions, which further increase the risk of caries.

Ultimately the interplay between alternate proximal and ultimate causes is complex and no doubt varies between individuals and populations, yet when considered as a whole, the research on the consequences of adopting agriculture reveals repeated phenotypic trends and suggestive evidence of their causal mechanisms, as detailed in this chapter. Our com-parative approach, addressing the underlying mechanisms driving phenotypic changes in human populations that adopted agriculture, is relevant when establishing connections with the evolution of agriculture in other taxa. It particularly allows inferences to be drawn on the impact that such relatively recent dietary change has had on phenotype, the dif-ferential responses between populations of a species with a global spread, and the possible proximate and ultimate causes driving some of those changes.

We conclude with some suggestions for investigators working in this area and hopes for future research, drawn from our synthesis of the existing literature. An additional

source of complexity that could be somewhat mitigated in future work is morphological covariance. Patterns of integration and modularity within the human skeleton affect to what extent adaptation in one region leads to changes in others. These patterns are as yet incompletely understood, which complicates unpicking which morphological changes associated with the transition to agriculture are the direct consequences of dietary change and which are indirectly affected via covariance. By studying functional cranial modules separately, it might be possible to reduce the complexity of the question and untangle the different evolutionary processes influencing each of them (Gonzalez-José et al. 2005).

Throughout this synthesis we have used, where possible, archaeological evidence from populations with probable biological continuity over the transition to agriculture, such as those from the Levant (Bar-Yosef 1998; May et al. 2018) and Ohio (Smith 1989; Paschetta et al. 2010). In many regions of interest, however, such data are not available, and this impedes the understanding of the morphological changes associated with the transition to agriculture by introducing variation due to population history or adaptation to different local environments. Increasingly the combination of archaeological, bioarchaeological, and genetic approaches may clarify population history in regions of interest and enable the identification of further skeletal series with biological continuity over the transition to agriculture. One example of where this has begun is in the exploration of the population turnover accompanying the arrival of Neolithic culture in Britain and other parts of Western Europe (Brace et al. 2019).

To better assess alternative proximate causes associated with phenotypic change, we suggest future researchers comparatively evaluate levels of intrapopulation variation within collections of skeletal remains. To date there are few accounts of these data, yet they can be extremely informative. If plasticity leads to morphological change, we expect considerable variation within a population for each of the studied traits, as a result of the different genetic backgrounds of each individual. In this case, the most adaptive phenotype will be present only among some individuals. On the other hand, if directional selection for particular traits has been involved, then we expect the resultant intrapopulation variation to be more con-strained to the phenotypes that present the most adaptive traits, due to greater underlying genetic similarity achieved over generations of selection (Gonzalez-José et al. 2005). Where possible, the study of ontogenetic series is also extremely informative in building a case for the action of plasticity or selection in causing a particular morphological change (e.g., Fukase and Suwa 2008; Gonzalez, Perez, and Bernal 2010; Holmes and Ruff 2011).

Finally, interdisciplinary studies combining morphometric analysis with techniques such as nitrogen and carbon stable isotopic analysis, dental macro- and microwear analysis, cross-sectional geometry, biomechanics, and bone remodeling patterns from the same set of individuals (Hogue and Melsheimer 2008; Menéndez et al. 2014; May et al. 2018; Stansfield, Evteev, and O'Higgins 2018; Brachetta-Aporta et al. 2019), should be con-ducted to answer some of the remaining questions regarding the impact of this fundamental change in subsistence practices on the phenotype.

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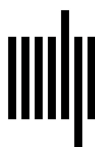**Edited by:** Ted R. Schultz, Richard Gawne, Peter N. Peregrine

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