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BIOLOGICAL CHANGES IN HUMAN POPULATIONS WITH AGRICULTURE

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ABSTRACT

Agriculture has long been regarded as an improvement in the human condition: Once *Homo sapiens* made the transition from foraging to farming in the Neolithic, health and nutrition improved, longevity increased, and work load declined. Recent study of archaeological human remains worldwide by biological anthropologists has shown this characterization of the shift from hunting and gathering to agriculture to be incorrect. Contrary to earlier models, the adoption of agriculture involved an overall decline in oral and general health. This decline is indicated by elevated prevalence of various skeletal and dental pathological conditions and alterations in skeletal and dental growth patterns in prehistoric farmers compared with foragers. In addition, changes in food composition and preparation technology contributed to craniofacial and dental alterations, and activity levels and mobility decline resulted in a general decrease in skeletal robusticity. These findings indicate that the shift from food collection to food production occasioned significant and widespread biological changes in human populations during the last 10,000 years.

INTRODUCTION

For much of Western history, the popular and scholarly perception of agriculture has been that once it was acquired, *Homo sapiens* had it made—life improved dramatically from a state of incessant work to abundant leisure, from

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deprivation to plenty, and from sickness to health and increased longevity. Moreover, the burden of constantly moving about the landscape in search of food was replaced by the security of settlement in permanent towns and cities from which the many advantages of civilization could be enjoyed (e.g. 24). Beginning in the late 1960s, a body of data began to emerge suggesting that this characterization of the shift from foraging to farming is inaccurate, and many hunter-gatherers may not have had it all that bad, especially with regard to work load or health (142, 241). Some researchers began to speculate that the adoption of an agricultural lifeway may not have been a positive development, at least with regard to its health costs (52).

Until recently, the literature lacked data that could be used to document and interpret biological changes in human populations with the transition from food collection to food production. Over the past decade or so, biological anthropologists (e.g. 55) have marshalled a wealth of data pertaining to human biological change in relation to the shift from foraging to farming. This record indicates that commonly held assumptions about the benefits of the agricultural transition for humankind are in need of reassessment (8, 53, 54).

This review relies on diachronic and other comparative studies of human skeletal remains recovered from archaeological sites in order to summarize and interpret biological changes with the shift from foraging to farming. Like other types of archaeological data sets, there are biases—such as cultural practices, differential preservation, excavation strategies, and selective curation—that potentially confound attempts to accurately reconstruct and interpret the past (211, 233, 256, 263). When these biases are evaluated carefully, however, human remains provide a valuable retrospective picture of health and behavior in the past that is not available from any other source of information (136).

For this review, I define agriculture broadly to include any type of plant cultivation practiced for dietary purposes (73). Independent centers of domestication occurred on all inhabitable continents (except Australia) within the last 10,000 years (93), first in the Old World and followed in the New World several thousand years later (74). Major crops included barley and wheat in the Near East; millet, sorghum, yams, and dates in Africa; millet and rice in northern China; rice, sugarcane, taro, and yams in Southeast Asia; maize, beans, and squash in Central America; and potatoes, sweet potatoes, and manioc in South America. Use of domesticated plants spread to adjacent regions (e.g. maize into the American Southwest and eastern North America and wheat and barley into Europe) at varying rates and involving localized circumstances (50, 58, 79, 93, 212).

Consideration of these centers and associated regions of domestication reveals a number of common themes that have implications for human biology, especially those linked to changes in health and behavior. This review is organized around the following themes: (*a*) composition and nutritional quality of food, (*b*) food processing technology and mastication, (*c*) population growth, (*d*) population distribution and health, and (*e*) work load and activity patterns. These themes are not mutually exclusive; health status, for example, was highly influenced by a number of factors, including nutrition, population distribution, and behavior. In addition, although biological changes have been identified with agricultural shifts worldwide, there are some notable exceptions, even within the same region. From 250 B.C. to A.D. 200 in the Eastern Woodlands of North America, use of cultivated seed-bearing plants (e.g. chenopod, sunflower, and cucurbit) coincided with social and economic transformations (222). Later, between A.D. 800 and 1100, the emphasis shifted to a single plant, maize (221). The earlier economic transition to seed plants appears to have had some influence on human biology, such as bone structural morphology and dental health (31, 200; see also 75). However, based on studies of numerous skeletal samples, maize agriculture had a far more profound impact on human populations than the earlier dietary regime, at least with respect to health status, demographic history, and activity (see below).

Some domesticated plants (e.g. maize, millet) consumed by past groups leave detectable chemical and isotopic signatures in human remains. The documentation of changes in these signatures has greatly increased the precision of the timing of the shift to agriculture in various human populations. The primary focus of this discussion is on health consequences and anatomical changes and not on the chronology of subsistence change. Therefore, bone chemistry and dietary reconstruction are not addressed here (see 125, 208, 214).

FOOD COMPOSITION AND NUTRITIONAL QUALITY

Dental Health

One of the most striking changes to occur with the adoption of agriculture is a decline in dental health, resulting largely from an increasing emphasis on carbohydrates in the diet. These changes are best illustrated in prevalence of dental caries and antemortem tooth loss.

DENTAL CARIES Dental caries is a disease process involving focal demineralization of dental hard tissues by organic acids produced by bacterial fermentation of dietary carbohydrates, especially sugars (176). Numerous workers have detailed increases in carious lesions (cavities) in agriculturalists compared to hunter-gatherers in North America, South America, Europe, Asia, and Africa (reviews in 55, 141, 165, 187, 242). From a sample of populations drawn globally, Turner (242) determined average frequencies of teeth affected (incisors + canines + premolars + molars): foragers, 1.7%; mixed (agriculture + foraging), 4.8%; and agricultural, 8.6%. Frequencies within each of these categories are highly variable, however. Few studies comparing caries prevalence for different types of cultigens (e.g. maize vs wheat) have been made. Based on caries prevalence data, Lubell and associates (144) observed that European Neolithic domesticates were either less cariogenic or had less dietary importance than maize in North America.

The composition of food and the manner of its preparation have been linked to higher caries prevalence (192). Many agricultural societies prepare plant foods by boiling them, usually into a soft, gruel-like consistency. Consumption of these foods promotes the growth of bacterial colonies in fissures and grooves of premolars and molars and other areas of tooth crowns that are not cleansed mechanically by the action of saliva or mastication.

Some researchers have noted apparent negative correlations between caries prevalence and degree of occlusal wear in human populations with cariogenic diets (150, 165, 192). However, Meiklejohn and coworkers (155, 159) indicate that although a high-wear environment may be a cariostatic factor, dental caries and wear are independent variables and a relationship between them should not be generalized. For instance, various populations with rapid wear-rates also exhibit significant prevalence of dental caries resulting from consumption of highly cariogenic foods (94, 159).

Dental caries clearly increases with agriculture, but appreciable frequencies of carious lesions are not unique to human groups relying on starchy domesticated plants. For example, carious lesions are common in hunter-gatherer dentitions from the lower Pecos region of the Chihuahuan Desert of Texas, which is likely the result of reliance on high-carbohydrate plants with a sticky texture (e.g. succulent fibers, pecans, prickly-pear fruits) (94, 228). High caries prevalence in preagricultural Mesolithic series from Sicily and Portugal compared to other contemporaneous European dental samples (e.g. 156) points to the consumption of cariogenic nonagricultural foods (e.g. honey) or sweet, sticky fruits (e.g. dates or figs) (19, 70, 144, 155). Comparison of Mesolithic and Neolithic dentitions from Portugal indicates that the latter group did not have higher caries rates than their foraging-fishing predecessors (144, 155). Lukacs (146) has reported a high prevalence of caries in the Langhnaj Mesolithic sample from India, which he suggests may reflect inclusion of agricultural foods obtained through trade or exchange with nearby agriculturalists. Frequency of carious lesions declined from high to low levels on Santa Rosa Island, California, when groups shifted from reliance on nondomesticated plants (e.g. roots and tubers) to a marine-based diet (254). Levels of natural fluoride in ground water also appear to be associated with variation in dental decay; when diets are cariogenic, high fluoride prevents caries and low fluoride promotes it (148, 174, 219).

Furthermore, the increase in dental caries with agriculture was greater in women than in men in most regions (133, 141, 147, 255), which indicates widespread gender-based differences in preparation and consumption of food. Some evidence indicates that a combined high-carbohydrate and low-protein diet in females may have predisposed their teeth to more decay than males (132).

TOOTH LOSS Antemortem tooth loss is caused by a variety of factors. For example, periodontitis (periodontal disease) causes degeneration of the alveolar bone and other tissues anchoring the teeth in the jaws. As the resorption process progresses, the bony support is reduced, resulting in exfoliation of teeth (51, 96, 98). As with dental caries, consumption of soft carbohydrate foods promotes periodontal disease. Many studies documenting caries increase with the transition to farming or agricultural intensification also report elevated levels of tooth loss, suggesting a strong relationship between caries and tooth loss (e.g. 9, 11, 56, 91, 123, 147, 227; but see 48, 106, 157). Rapid or high wear-rates, pulpal exposure, and excessive buildup of plaque also contribute to antemortem tooth loss (51, 94).

Growth and Development

The shift from foraging to farming appears to have resulted in a decline in nutritional quality for many human groups. In this regard, agricultural populations consumed a narrower range of foods than did hunter-gatherers; this narrowing of the diet involved reduced availability of animal protein coupled with dependence on a limited number of domesticated plants. Archaeological documentation of prehistoric farming diets and observation of living peasant agrarian populations indicate that agricultural diets tend to be dominated by one or a few plants, such as rice in Asia, wheat in temperate Asia and Europe, millet or sorghum in Africa, and maize in the New World.

The nutritional value of some of these plants is marginal or poor. Maize, for example, is deficient in the essential amino acids lysine, isoleucine, and tryptophan (67). Niacin (vitamin B_3) in maize is chemically bound, which reduces the bioavailability of this nutrient to the consumer. Moreover, iron absorption in maize-based diets is exceedingly low (10). In many regions of the Old World, milled grains such as millet and wheat contain very little iron. In some settings (e.g. the Nile Valley), weaned children ate cereal grains containing virtually no iron (45). Rice is deficient in protein, even in the unmilled form. Moreover, the low availability of protein in rice inhibits vitamin A activity, even if the vitamin is provided through other food sources (261).

Many societies have developed means of improving the nutritional content of these so-called superfoods, such as alkali-processing of maize (120, 230). Nevertheless, the effects of over-reliance on these plants are profound, which is indicated by the anthropometric histories of individual populations, including secular changes in growth and adult body size (66).

GROWTH RATES Growth rates in children provide a highly reliable indicator of nutritional status (88). Studies of living populations experiencing nutritional deficiencies show that children are short for their age in comparison to populations with adequate diets (18, 66, 112). These findings underscore the great sensitivity of childhood growth to environmental factors, which affect all body tissues, including the skeleton (18).

Analysis of juvenile long bones from prehistoric North America reveals evidence of growth retardation in agricultural and mixed-subsistence economies (210). In children less than six years of age in the lower Illinois Valley, matching of femur length to dental age reveals that growth is impeded in incipient agriculturalists as compared to earlier foragers (56). Interestingly, individuals who are short for their age tend to have a higher frequency of physiological stress indicators [e.g. cribra orbitalia (lesions in the eye orbits) and tooth enamel defects] than do individuals who are tall for their age, lending further support to nutritional deficiency as a factor contributing to growth retardation (56). Similarly, in the late prehistoric Dickson Mounds populations from west-central Illinois, growth of long bones (humerus, tibia, femur) from birth to adulthood declined appreciably (especially for two- to five-year-olds) during the period of intensive agriculture relative to earlier periods of less intensive agriculture (83). Circumferences of long bones express an equivalent pattern of retarded growth, although the greatest discrepancy between the later intensive agriculturalists and the earlier population at Dickson Mounds was between ages 10 and 15 (83).

Mortality bias in cemetery samples—especially that involving the inclusion of a relatively greater number of physiologically stressed children—might present a skewed picture of juvenile body size and growth retardation. One would expect to find a higher proportion of sick (and shorter) children in cemetery samples. Saunders & Hoppa (211), however, demonstrate that although mortality bias exists in archaeological juvenile remains, the effects are small and are far outweighed by errors introduced by other factors (e.g. aging methodology, sample size, and preservation status).

STATURE Substantial evidence drawn from the study of living populations reveals the strong relationship between growth retardation and attainment of adult body size, including terminal height (e.g. 72). That is, growth-retarded children should be short-statured adults. Abundant evidence shows that stature is linked with environmental factors. Comparison of successive periods (e.g. by decade) in living or historically documented populations indicates that during periods of increased dietary stress and food shortages, stature of children and adults reduces (68, 231, 232, 265); with improved nutrition, stature increases (66).

Several geographic settings show stature declines with agriculture adoption or intensification in prehistoric societies (7, 83, 123, 132, 135, 157, 178, 188). In contrast, other regions show increases or no change in stature (48, 56, 198, 246, 248). Thus, there is evidence for stature reduction with agriculture in selected settings, but this is not a universal pattern. The ambiguous picture of stature change in comparisons between prehistoric populations adopting agriculture may involve differences in access to critical dietary resources (e.g. protein) during years of growth that are especially sensitive to environment (e.g. the period of catch-up growth in adolescence). Thus, in some populations, nutritionally deprived children may have had better diets during adolescence, resulting in growth rebounds and, hence, full growth and normal attainment of stature as adults (e.g. 231).

CORTICAL BONE THICKNESS A strong relationship has been demonstrated between nutritional quality and bone mass or thickness in tubular bones (e.g. femur, metacarpals). Losses in cortical bone thickness in nutritionally stressed living populations have resulted from reduced growth as well as from increased endosteal (interior bone surface) resorption (76, 78, 99). In archaeological remains, temporal changes in or characteristics of cortical thickness have been related to nutritional status (56, 110, 111, 183). That is, relatively thin cortical bone frequently is interpreted as reflecting poor nutrition.

Nutrition is linked closely to skeletal maintenance. However, the mechanical environment is also an important consideration in interpreting cortical bone thickness and distribution. The external surface (subperiosteum) and internal surface (endosteum) of cortical bone continue to expand or become more outwardly distributed throughout adulthood (76). This expansion is influenced strongly by the level of mechanical or functional demand that occurs during one's lifetime. Cortical thickness frequently is calculated as percent cortical area (PCCA) or percent cortical thickness (PCCT), which are simple measures of the amount of cortical bone relative to the subperiosteal area or overall breadth of the bone (e.g. 76). Declines in these values in archaeological remains may represent decreases in nutritional status (e.g. 56). However, both the subperiosteum and endosteum may be expanded, resulting in considerably reduced PCCA or PCCT (201). In these circumstances, although there is less bone tissue relative to outer dimensions, the outward redistribution of bone provides greater mechanical strength (see below). Thus, in interpreting patterns of cortical thickness, both systemic (nutritional) and mechanical (structural) factors need to be evaluated carefully.

BONE HISTOLOGY Like any other living tissue, bone continually renews itself. The renewal process is unique in bone and involves resorption followed by deposition—specialized cells called osteoclasts remove bone, and osteoblasts replace it. The histologic structures, osteons or Haversian systems, associated with this process can be measured precisely, revealing important information on health status and nutritional quality in earlier societies (153, 235). Stout (234) has compared bone-remodeling rates of prehistoric hunter-gatherers and maize agriculturalists in North America (Gibson, Ray, and Ledders sites, Illinois) and South America (Paloma, Peru). This histomorphometric analysis documents greater remodeling rates in maize agriculturalists (Ledders) than in hunter-gatherers, which Stout suggests may reflect the effects of overproduction of parathyroid hormone resulting from the low calcium/high phosphorus ratios characteristic of high maize diets.

To compensate for bone losses in aging adults (especially after age 40), structural adaptations may occur involving more outward distribution or expansion of bone tissue (202, 205). Greater remodeling rates may supplement these changes (39). Thus, remodeling differences may reflect mechanical responses that are not necessarily tied to nutritional factors.

TOOTH SIZE Tooth size appears to be under greater genetic control than is bone size (124). The pattern of reduction in human tooth-size over the course of hominid evolution (22, 23, 41, 42, 69, 124, 145) suggests that this is largely evolutionary (genetic) change, although the mechanism remains elusive (124). This trend of tooth-size reduction has continued in the Holocene (but see 115, 216) and has been related alternatively to dietary change and the adoption of agriculture, use of pottery and cooking, increasing sedentism and population density, migration and gene flow, craniofacial or body-size variation, dental disease, or other factors (e.g. 22, 23, 41, 42, 63, 89, 132, 145, 151, 224).

The presence of small teeth in physiologically stressed individuals in living populations suggests that environment (e.g. nutritional or maternal health status) also influences tooth size (77, 239). Therefore, like body size, tooth size should provide a measure of deviation from genetic growth potential. However, unlike body size, teeth are not subject to catch-up growth or rebound during the adolescent growth spurt. Prehistoric maize agriculturalists on the southeastern US Atlantic coast have smaller teeth than did their foraging predecessors (134). Because deciduous tooth crowns are formed largely in utero, smaller teeth in the agricultural population may reflect a reduction in maternal health status and placental environment as a result of consumption of nutritionally poor food (maize). Reduction in permanent-tooth size has also been observed in this setting (132) and elsewhere (e.g. 63, 105, 160) with the shift to agriculture. Given the narrow temporal window of tooth-size reduction in recent past populations (less than several hundred years), and especially when viewed in the context of reduced health and dietary quality, these changes may reflect, at least in part, decline in nutritional status. This does not mean, however, that tooth-size reduction can be explained fully by nonevolutionary factors. Calcagno (41), for example, has documented a relatively greater reduction in posterior-tooth size than anterior-tooth size in Nubian populations. He has tied this change to a selective advantage for smaller posterior teeth in caries-prone agriculturalists.

The years of growth and development of the dentition (4 months in utero to age 12) involve a period of elevated stress for human populations (220). Therefore, individuals experiencing relatively greater stress during this period should have smaller tooth crowns. Comparison of crown dimensions of preadult and adult age-at-death cohorts shows that preadults had smaller permanent teeth than did adults (90, 220). These studies document the failure of teeth to reach their genetic size potential in nutritionally stressful settings. Moreover, they imply that individuals with small teeth had a reduced lifespan, a finding that is consistent with other hard-tissue investigations (e.g. 49, 56, 81). It is unlikely, however, that small teeth led to reduced longevity. Rather, size reduction is symptomatic of environmental factors (e.g. undernutrition) that contributed to smaller teeth and perhaps to premature death.

DENTAL ENAMEL DEFECTS Various kinds of dental enamel defects are represented abundantly in past populations (82, 86, 87). The most frequently observed defects are hypoplasias, which are deficiencies of enamel expressed as circumferential lines, grooves, or pits resulting from the death or reduced function of enamel-producing cells (ameloblasts) and failure to form enamel matrix (86). A suite of causes of enamel defects have been identified, including various infectious diseases and nutritional deficiencies (86, 87). Studies of living populations demonstrate a strong link with nutritional status (84).

Comparisons between foragers and farmers generally reveal the latter to have more hypoplasias, which is interpreted to represent an increase in physiological perturbation (48, 56, 83, 123, 188, 195, 198, 247, 248; but see 106, 266). One investigation has documented a decrease in individuals affected by hypoplasias, but agriculturalists have wider hypoplasias, suggesting that there was a reduction in number of stress events, which were either longer or more severe following the adoption of maize (113, 138; see also 17). Other studies of agricultural populations, both prehistoric and contemporary, reveal elevated frequencies of hypoplasias in nutritionally compromised individuals with low socioeconomic status (85, 259). Goodman and coworkers (83) reported that stress in agricultural children peaked earlier than in hunter-gatherer children from the same archaeological locality in the American Midwest. Thus, physiological stress is higher and socially and demographically patterned in this agricultural population.

Stress-related histological defects of tooth enamel (e.g. Wilson bands and other microdefects) accord well with hypoplasia prevalence in comparisons between hunter-gatherer and agricultural populations (86; but see 61, 199). Rose and colleagues have found a fourfold increase in enamel microdefects in intensive agriculturalists in comparison to incipient agriculturalists in Illinois; they link this increase to a decline in nutrition and an increase in susceptibility to infection (85, 128, 197, 199). Although many studies of physiological stress in prehistoric agriculturalists identify nutrition as a primary cause, most acknowledge the important synergy between poor diet and infection: Undernourished individuals are more prone to infection, and infection detrimentally affects nutritional status (218).

FOOD PROCESSING AND MASTICATION

Dental Attrition and Trauma

Mastication involves preparation of food with the incisors and canines followed by reduction of food with the premolars and molars. As a result, the teeth wear as they come into contact with food and with each other. The wear rates are highly influenced by the consistency and texture of food, which is determined either by the characteristics of the food itself (e.g. presence of phytoliths or cellulose in plants) or by the manner of its preparation. Plants are processed in a number of different ways (230), some of which may involve the introduction of abrasive elements that promote tooth wear (e.g. use of grinding stones for making flour from cereal grains). Wear on tooth surfaces is documented both visually (macrowear) and microscopically (microwear).

MACROWEAR Wear on the chewing surfaces of teeth varies widely between human populations, owing to localized behavioral characteristics, cultural practices, age, sex, and diet (173, 185, 253). Because many Western populations consume soft, highly processed foods that include little extraneous material, tooth wear proceeds exceedingly slowly from birth through adulthood. In many nonindustrial societies, however, grit inclusions and minimal processing of food contribute to rapid wear rates (94).

Tooth wear is strongly influenced by age: Older individuals have been exposed to factors resulting in attrition for a longer period of time than have younger individuals. Because of the difficulty of age determination in archaeological human remains, wear rates are quantified imprecisely (97, 217). However, valuable information can be generated by comparison of age groups within populations (e.g. five-year intervals). Comparisons between earlier hunter-gatherers and agriculturalists or populations undergoing agricultural intensification reveal general declines in degree or severity of tooth wear in a wide range of settings (1, 2, 9, 12, 14, 48, 105, 107, 109, 114, 123, 144, 177, 184, 185, 187, 191, 192, 200, 216, 225, 251). This trend reflects the reduction in consistency, hardness, or abrasiveness of foods consumed by agriculturalists. For many regions, the introduction of ceramic vessels and accompanying food-preparation practices involving extended cooking engendered reduction in food consistency (23, 172). Some settings involving agriculture had an increase in use of grinding stones, thus resulting in relatively more rapid occlusal wear than in preagricultural peoples (e.g. 171, 226).

Types or patterns of wear have also changed in the shift to agriculture. Smith (223) has found a dichotomy of occlusal wear patterns in molars: Hunter-gatherers have evenly distributed flat wear, and agriculturalists have highly angled wear. The change in wear pattern in comparisons between earlier foragers and later farmers was interpreted to reflect a reduction in "toughness" of agricultural diets. Other researchers have confirmed this finding but with some notable exceptions (e.g. 144, 213, 215).

In specific regions additional distinctive wear patterns have been documented, including the presence of cupped wear on occlusal surfaces of molars (144, 184, 223) and incisors (100) of agriculturalists but not hunter-gatherers. Hinton (102) has identified greater interproximal wear (wear on nonocclusal surfaces of adjacent teeth) in prehistoric hunter-gatherers from Tennessee, which he relates to increased magnitude and frequency of masticatory forces in hunter-gatherers (also 187).

MICROWEAR Recent application of microscopic techniques, especially scanning electron microscopy (SEM), to the study of tooth wear has facilitated understanding of dietary change and adoption of agriculture in past populations (171, 238). Comparisons between hunter-gatherers and agriculturalists reveal a decrease in frequency of microwear features (e.g. pits and scratches) on occlusal surfaces (38, 107, 191, 200, 238). Like the macrowear evidence, this finding indicates consumption of softer foods, which results in fewer microscopic features, such as pits, in agriculturalists than in hunter-gatherers.

In contrast, comparison of Mesolithic, Neolithic, and Chalcolithic microwear in dental series from South Asia and Mesolithic and Neolithic dental series from northern Syria shows an increase in frequency of microwear features, especially large pits (171, 184–186). This pattern appears to reflect the use of coarse grinding stones by Neolithic and later agriculturalists in preparing cereal grains, and the shift from consumption of small-grained seeds to large-grained cereals. The pattern also reflects the shift from roasting meat directly on coals or air-drying to cooking with ceramic vessels. Analysis of later agriculturalists (post–5300 B.C.) from Syria reveals a reversal of this trend. That is, there is a sharp decrease in frequency of microwear features, which appears to be related to the introduction of ceramics and cooking of cereals into soft mushes (172).

DENTAL CHIPPING Some populations consuming abrasive diets display fractures, cracking, and other evidence of damage to tooth crowns. A number of foraging groups consume tough foods containing various abrasives and, as a result, have a relatively high frequency of damaged teeth (19, 244). Milner & Larsen (169) have reviewed reports on dental trauma, but few studies have indicated differences between hunter-gatherers and agriculturalists. Patterson (187), however, observed a marked decline in dental trauma in comparisons between prehistoric foragers and farmers from Ontario. He interpreted this trend as reflecting a reduction in the use of teeth for food processing in the agriculturalists. Comparisons between foraging and farming dentitions in East Asia suggest a decline in dental trauma (243).

Craniofacial Adaptation

CRANIOFACIAL GRACILIZATION A trend in recent human evolution toward a decrease in face size has long been recognized by anthropologists and others. In pre-twentieth-century British populations, for example, Keith (32:198) observed "maxillary shrinkage" and facial reduction in recent populations compared to those of earlier periods. He attributed these changes to consumption of "cooked food and soft cereals replacing tough meats and imperfectly ground corns." Recent studies have reported a consistent pattern of reduction in craniofacial robusticity and/or vault shape in populations that underwent the transition from foraging to farming, both in the Old World (41, 46, 47, 62, 64, 114, 227, 237, 264) and in the New World (2, 20, 101, 132, 136, 177). To varying degrees, changes are similar to those documented in Nile Valley crania by Carlson and colleagues (44, 46, 47, 103, 104, 249, 250), who argue that craniofacial alterations (i.e. shorter and rounder cranial vaults, smaller and more posteriorly placed faces, general reduction in size and robusticity of faces and jaws) resulted from "progressive alterations in maxillomandibular growth in response to developmental variation in the size and position of the muscles of mastication" with a shift to the consumption of soft, agricultural foods (47:574).

MALOCCLUSION Other orofacial changes accompanying shifts from hard-textured to soft-textured foods include tooth crowding and malocclusion. Although relatively little research has been devoted to explaining underlying causes of malocclusion, a great deal of information exists on occlusal variation in humans, past and present (see 57). In general, nonindustrial groups masticating and ingesting hard foods possess "edge-to-edge" bite, whereby the upper teeth come into greater occlusal contact with lower teeth. In contrast, industrial or other groups consuming soft foods have high frequencies of occlusal abnormalities and crowding (e.g. overjet, overbite, crossbite, tooth impaction, tooth rotation) (57). Mechanisms for occlusal abnormalities are controversial, but experimental studies involving controlled feeding of soft- and hard-textured foods to laboratory animals indicate the primacy of food consistency in interpreting prevalence of malocclusion: Consumption of predominantly soft foods promotes the development of occlusal abnormalities (57).

A large body of data exists on occlusal abnormalities in living human populations, including nonindustrial societies (57). Early contact period Eskimo and Aleut populations pursuing traditional dietary practices had a low prevalence of malocclusion; when food consumption practices shifted to softer westernized diets, dental crowding and occlusal variations increased (175, 262). Diachronic changes in archaeological settings have been reported only minimally. However, evidence from the eastern Mediterranean (3), South and East Asia (92, 123, 149, 237), and the American Southeast (177) indicates that the shift to agriculture or more intensified agriculture was accompanied by an increase in dental crowding and malocclusion.

POPULATION GROWTH

One of the most significant changes in human evolution is the dramatic increase in population size during the Holocene, especially in areas adopting agriculture (8, 53, 95). Various causes have been proposed to explain this growth, but evidence suggests that increase in fertility and birthrate plays a central role. However, this is a point of contention among anthropologists and demographers (53). A fertility-based argument for population increase is consistent with the generally greater fertility seen in agriculturalists as opposed to nonagriculturalists in ethnographic settings (15, 16), albeit with a high degree of heterogeneity (43).

Paradoxically, skeletal series of agriculturalists show lower mean age-at-death than do hunter-gatherers, which generally has been interpreted to reflect an increase in mortality and declining life expectancy with the shift to agriculture (83, 123, 126, 135, 258). Reevaluation of demographic profiles in skeletal series suggests, however, that mean age-at-death is related to fertility and birthrate, and not mortality (209; see also 36, 116, 140, 158, 168, 172). These studies suggest that human populations experiencing growth will have a greater number of younger individuals, resulting in a larger proportion of juvenile skeletons relative to adult skeletons. Thus, population growth appears to influence the distribution of age-at-death in cemetery assemblages.

In the lower Illinois River region, birthrate (which is inversely proportional to the ratio of number of deaths over age 30 to number of deaths over age 5) shows an increase prior to, and especially during, the adoption and intensification of maize agriculture in late prehistory (36). Mortality shows no change over the same period. Although various factors are likely involved, the shift to a high-starch diet coupled with improved ceramic technology and cooking techniques would have facilitated earlier weaning and decreased birth interval because of the availability of soft, easily digestible foods (36; cf 172).

Other evidence suggests that the shift to agriculture was accompanied by a general increase in birthrate. In the comparison of hunter-gatherer and agricultural skeletal samples from throughout North America, Buikstra & Konigsberg (35) found that foragers have mortality curves that rise rapidly with increasing age; agriculturalists have much flatter mortality curves. This pattern indicates a younger sample (and thus greater fertility) among agriculturalists than hunter-gatherers.

Although usually difficult to identify, factors contributing to mortality can be recognized in osteological samples. As discussed above, various indicators of morbidity are well represented in skeletal series (e.g. infectious disease). Moreover, traumatic death resulting from warfare and conflict have been documented in prehistoric osteological samples worldwide, with some of the best evidence coming from North America (e.g. 130, 167, 260). This evidence indicates that a number of late prehistoric agricultural societies were involved in conflict situations resulting in an increased risk of early death. Reports on skeletal trauma arising from malevolent activities suggest that there was an increase in frequency of deaths arising from conflict and warfare among late prehistoric agriculturalists compared with earlier groups (167). The causes of conflict and warfare in these late prehistoric settings are difficult to determine, but competition for increasingly limited resources (e.g. arable or otherwise productive lands) may have been a factor (167).

SETTLEMENT AND POPULATION DISTRIBUTION

Infectious Disease

Reduced population mobility and increased aggregation provide conditions that promote the spread and maintenance of infectious and parasitic diseases and the increase in pathogen load in humans. That is, closer, more crowded living conditions facilitate greater physical contact between members of a settlement, and permanent occupation can result in decreased sanitation and hygiene. Diachronic comparisons of prevalence of nonspecific infections (or generalized skeletal inflammations called periosteal reactions or periostitis) and some specific infectious diseases (e.g. tuberculosis, treponematosis) indicate that more densely settled agricultural societies were more prone to infection than were earlier groups (7, 37, 48, 56, 83, 128, 132, 135, 137, 157, 188, 198, 200, 246, 248; but see 106, 180). These changes did not result directly from shift in diet, but rather from increased sedentism and aggregation of population and general deterioration of living conditions. This conclusion is corroborated by the presence of similar patterns of increased infection rates in nonagricultural groups that became less mobile. For example, in the Santa Barbara Channel Islands of coastal southern California, increasing population density and declining mobility were accompanied by an elevated prevalence of periostitis (129, 131). Sedentism, however, does not explain fully the general pattern of very high infection rates observed in some prehistoric agriculturalists (55, 65, 166, 167). In this regard, the synergy between infection and other stressors—e.g. poor nutrition, warfare, anemia, social disruption—is key to understanding patterns of remarkably poor health in some late prehistoric agricultural groups.

Anemia

Many archaeological skeletal series have appreciable frequencies of sieve-like cranial lesions in the eye orbits (called cribra orbitalia) and flat vault bones (called porotic hyperostosis). These lesions typically are accompanied by expanded blood-forming marrow, indicating that the condition represents a response to various types of anemia and increased production of red blood cells (236; cf 182). In archaeological remains, cribra orbitalia and porotic hyperostosis have been attributed mostly to iron deficiency anemia caused by consumption of iron-poor foods, parasitism, infantile diarrhea, and other chronic stressors that influence iron metabolism (80, 83, 236).

Studies have documented higher prevalence of either cribra orbitalia or porotic hyperostosis in sedentary farmers compared with mobile foragers (4, 5, 7, 45, 48, 56, 83, 123, 127, 180, 188, 195, 198). There are exceptions to this pattern, however, pointing to factors influencing iron bioavailability that do not involve subsistence directly. Foragers from North America's Pacific coast, for example, have a relatively high prevalence (59, 60, 131, 252) and, conversely, some agriculturalists show very low prevalence of cribra orbitalia and porotic hyperostosis (140, 193). These situations indicate that a range of nondietary factors are important in the etiology of iron deficiency anemia in past populations (45, 80, 161, 196).

WORK LOAD AND ACTIVITY

There has been an ongoing discussion in anthropology about the demands of labor and other physical behaviors in foraging vs farming lifestyles (52, 53). Study of skeletal series from hunter-gatherers and later agriculturalists has provided abundant information on the biological concomitants of activity, especially with respect to degenerative pathology in articular joints, other articular joint modifications arising from specific and generalized types of activity, and structural adaptations of long bones.

Osteoarthritis and Osteophytosis

Osteoarthritis is a disorder involving the mechanical degeneration of skeletal articulations, resulting in buildup of bone along joint margins (lipping), loss of bone on joint surfaces, or a combination of both. Degenerative changes involving the margins of vertebral disks results in lipping or osteophytosis (30). Because degenerative changes in joints result largely from physical demands occurring over the course of an individual's lifetime (108), their prevalence in past populations provides an important perspective on activity in both living and extinct societies. Observations on osteoarthritis and osteophytosis have been made by anthropologists and others since the nineteenth century, including those comparing foragers and farmers (30). Recent studies have documented decreases in prevalence, severity, or both in a number of settings, including the southeastern United States (28, 132, 134), South Asia (123), and Europe (157). Comparisons of skeletal samples from different regions have shown that although the results are highly variable, hunter-gatherers tend to have more osteoarthritis and osteophytosis than do agriculturalists (117–119, 181, 190). On the other hand, some settings show either no difference or greater frequency of these disorders in agriculturalists than in hunter-gatherers (30, 83, 152, 189). In summary, these studies indicate that although a number of populations underwent change in articular degenerative pathology and presumably also in the behaviors that caused it, no definitive pattern relating prevalence and subsistence mode emerges except with regard to specific geographic settings.

Other Activity-Related Articular Modifications

SPONDYLOLYSIS Spondylolysis is a bilateral (or rarely, unilateral) separation of vertebral neural arches in the area between the superior and inferior articular processes (called the pars interarticularis), mostly in lumbar vertebrae. No other primate shares this trait with humans, suggesting that bipedality and associated behaviors play an important role in its etiology (26, 163). In living populations, high frequencies of spondylolysis are found among individuals who participate in activities that entail heavy mechanical demands on the lower back, suggesting that it is a type of fracture (26, 163).

Eskimos have an unusually high spondylolysis prevalence, which is consistent with their physically demanding lifestyle in traditional settings (e.g. 162). Bridges (26) has documented a higher prevalence in foragers than in later farmers in prehistoric Tennessee. She notes that although an association of specific activities with spondylolysis is not possible, the defect may be related to specific activities or postures rather than to overall activity levels.

SPECIFIC TASKS AND SKELETAL MODIFICATIONS Distinctive patterns of degenerative joint disorders (especially osteoarthritis) have been identified in hunter-gatherers and agriculturalists. In prehistoric populations from the American Southwest, bilateral elbow osteoarthritis is commonplace in some populations, especially in women (164). This pattern reflects physical activities requiring the use of both arms, such as preparation of cereals into flour with grinding stones. In prehistoric agricultural populations in Syria and Ecuador, the ends of the first metatarsals show extensions of articular surfaces, indicating extreme bending of the toes backward, apparently in kneeling postures (170, 245). With regard to the Syrian evidence, tomb art depicts an individual with toes bent backwards while grinding cereals in a stone quern (170).

Other behaviors that may be unique to prehistoric foragers have been reconstructed from size and robusticity of muscle attachment areas in arm bones. Kennedy (122), for example, has found that terminal Pleistocene and Mesolithic hunter-gatherers in South Asia commonly exhibit well-developed supinator muscle attachment areas on the ulna (one of the two bones of the forearm). He suggests that spear throwing was the activity associated with this feature. The lower frequency of the hyperdeveloped supinator attachment site in later agriculturalists suggests that activities involving heavy demands on the lower arm declined appreciably with the adoption of agriculture.

Robusticity and Structural Adaptation

GENERAL ROBUSTICITY PATTERNS The size and structure of cortical bone is highly sensitive to mechanical stimuli (154). Accordingly, human populations experiencing demanding physical regimes have larger and more robust skeletal elements than do sedentary or less-active populations (201, 207). Comparisons between hunter-gatherer and farming populations from archaeological settings indicate a pattern of decrease in dimensions of long-bone shafts and muscle attachment sites, which presumably reflects a decline in physical demand and work load following sedentism (132, 135, 188, 227; but see 21, 25, 27).

Some investigators have compared long-bone cross-sections from hunter-gatherers and agriculturalists. In many cases, the shafts of bones (e.g. femur) of agriculturalists are more circular in cross section (13, 109, 132, 134, 188). Increasing circularity of long-bone shafts is apparently part of a worldwide trend since the late Pleistocene (34, 143, 203). In hunter-gatherers, femur midshafts (mid-thigh region) and femur proximal shafts (hip region) tend to be more compressed from side-to-side and from front-to-back, respectively, than in agriculturalists or sedentary groups (132, 206). This flattening of long bones in foragers has been interpreted to reflect suboptimal nutrition (6, 40, 109). However, analysis of structural properties indicates that mechanical factors and physical activity are more important in explaining this change (see below).

CROSS-SECTIONAL GEOMETRY Because of their tubular shape, long bones (and other skeletal elements that are long relative to their width) can be modeled as hollow beams and subjected to mechanical analysis in the same way that building materials are analyzed by civil and mechanical engineers (203). In a beam (or long bone) undergoing bending or torsion (twisting), mechanical stress increases with distance from a central or neutral axis running through the shaft. Thus, the greatest mechanical stresses occurring in a lower limb bone (e.g. femur)—such as during running, walking, or lifting—are located in the outermost fibers of the bone. Therefore, a femur shaft with a more outward distribution of bone has relatively greater strength or ability to resist fracture during periods of elevated mechanical demand (179, 203).

In archaeological settings, it has long been suspected that adults having long bones with large external dimensions were physically active during life (21, 132). The analysis of cross-sectional geometric (structural) properties that measure bone strength has provided strong support for this model. On the prehistoric Georgia coast, for example, declines in external dimensions of long bones with agriculture was interpreted to reflect a decrease in mechanical demand associated with the shift from a lifeway based on hunting, gathering, and fishing to one depending at least in part on maize agriculture (132). Confirmation of this interpretation is provided by comparison of bones representing the leg (femur) and arm (humerus) whereby both sexes showed a reduction in cross-sectional properties associated with bending and torsion (139, 206). In contrast to these findings, comparisons between prehistoric foragers and agriculturalists in Alabama showed that the latter had greater bone strength (27, 29), thus indicating that the behavioral changes associated with the transition to agriculture were likely quite different in coastal (Georgia) and interior (Alabama) settings. Biomechanical analysis of human remains from other regions of North America confirm the variable nature of activity patterns in agricultural settings (33, 204).

Analysis of cross-sectional shape of long bones provides insight into the degree of mobility of past populations. Comparing human groups ranging from highly mobile hunter-gatherers to sedentary industrial populations, Ruff (201) has found that sedentary groups have a ratio approaching 1.0 in anterior-posterior bending stress (I_x) to medial-lateral bending stress (I_y) in the adult femur midshaft. Values near or at 1.0 reflect a circular shape of the bone cross-section, and represent decline in physical activities, such as running and long-distance walking. Comparisons of long-bone mechanical properties representing different subsistence technologies within specific regions indicate that agriculturalists tend to have values closer to 1.0 than do earlier hunter-gatherers (25, 33, 139). These findings suggest that, although behavioral adaptation varies between regions, human populations share a common theme involving a decline in mobility and long-distance travel in the transition from foraging to farming. Thus, the shape changes in external long-bone dimensions discussed above likely reflect an overall reduction in mobility in humans during the Holocene (203). Although the shape change occurs for human populations generally, it is especially pronounced for males. This result suggests that alterations in types of physical activity with subsistence change were greater in males than in females (201).

Comparisons of cross-sectional geometric properties and the ratio I_x/I_y for males and females show a decline in sexual dimorphism with the transition from hunting and gathering to agriculture or agriculture intensification (139, 201, 203, 204). Ethnographic documentation of mobility patterns in hunter-gatherers indicates that long-distance movement and acquisition of protein resources through hunting is nearly always done by males, whereas in agricultural and industrial societies, like females, males are involved in sedentary tasks (201, 203). Thus, the greater similarity of I_x/I_y values in males and females in agricultural populations in comparison to hunter-gatherer populations represents increasing sedentism in both sexes (203).

Structural comparison of diaphyses of left and right humeri in hunter-gatherer vs later agricultural populations within the same setting indicates a more equal distribution of mechanical demand on and use of left and right arms in later farmers. Fresia and coworkers (71) have identified a reduction in bilateral asymmetry in humeral strength in the American Southeast, a pattern that continues after European contact, when populations became more intensive maize agriculturalists. Similarly, Bridges (25, 27) documented a decrease in asymmetry of humerus strength in prehistoric Alabama, suggesting the shift to the use of both left and right arms in subsistence-related activities (e.g. pounding of maize with wooden mortars and pestles). These studies also show a decrease in sexual dimorphism in bilateral asymmetry, indicating the involvement of both women and men in similar kinds of activities in agricultural settings (27, 203, 240).

CONCLUSIONS

Within a remarkably short amount of time, agriculture became the dominant mode of subsistence, having profound effects on the landscape and populations occupying it. The shift from foraging to farming led to a reduction in health status and well-being, an increase in physiological stress, a decline in nutrition, an increase in birthrate and population growth, and an alteration of activity types and work loads. Taken as a whole, then, the popular and scholarly perception that quality of life improved with the acquisition of agriculture is incorrect.

Biological changes did not occur uniformly within populations adopting agriculture. Rather, segments of past societies were affected differentially. This pattern is especially clear in view of differences between adult females and males in dental health and activity patterns. Contrary to earlier assertions (e.g. 257), there has been a great deal of biological change in humans subsequent to the beginning of agriculture in the late Pleistocene and early Holocene. Finally, the shift to agriculture and associated biological changes in general show worldwide variability, suggesting that dietary changes and accompanying hard-tissue alterations may have been configured by highly localized circumstances.

When discussing the transition to food production, anthropology textbooks typically emphasize the social, cultural, and technological transformations that accompanied this adaptive shift. Generally not included is the biological record drawn from the study of human osteological remains. This record provides a compelling index for assessing the history of the human condition and the role that agriculture played in shaping it in recent human evolution. This review would suggest that biological changes are an essential component of lifeway transitions and should be incorporated into discussions of the consequences of the most important dietary and economic transformation in the history of humankind.

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