

SPECIAL INVITED PAPER

**AGRICULTURAL ORIGINS FROM THE GROUND UP:
ARCHAEOLOGICAL APPROACHES TO PLANT DOMESTICATION¹**

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The timing, geographical locations, causes, and consequences of crop domestication have long been major concerns of archaeologists, and agricultural origins and dispersals are currently more relevant than ever to scientists seeking solutions to elusive problems involving food insecurity and global health disparities. Perennial research issues that archaeologists continue to tackle include (1) thinking outside centers of origin that were based on limited and insufficient past knowledge; (2) distinguishing between single and multiple domestications of specific crops; (3) measuring the pace of domestication; and (4) decoupling domestication from agricultural economies. Paleoethnobotanists have expanded their toolkits to include analysis of ancient and modern DNA and have added increasingly sophisticated techniques in the field and the laboratory to derive precise chronological sequences to assess morphological changes in ancient and often fragmentary archaeobotanical remains and to correctly interpret taphonomy and context. Multiple lines of archaeological evidence are ideally brought together, and whenever possible, these are integrated with information from complementary sources. We discuss current perspectives and anthropological approaches to research that have as their goals the fuller and broader understanding of ancient farming societies, the plants that were domesticated, the landscapes that were created, and the culinary legacies that were passed on.

Key words: Amaranthaceae; archaeology of food; centers of agriculture; *Chenopodium* spp., crop domestication; Cucurbitaceae; *Lagenaria siceraria*; origins of farming; paleoethnobotany.

The domestication of plants and animals has fascinated anthropologists and researchers from many other fields for more than a century. From the beginning, archaeologists have been key members of interdisciplinary teams of scholars who contribute answers to long-standing questions and generate new avenues of inquiry as our perspectives shift and new analytical tools are applied. Newly reported fieldwork, novel techniques, and an expanded corpus of radiocarbon dates are changing interpretations of where and when crops came under human management. Although many domesticated plants are used for purposes other than food, the focus of research into agricultural beginnings is dominated by subsistence-related concerns. The recently growing popularity of food studies across the disciplines of biological sciences, social sciences, humanities, and medicine helps highlight the role of archaeologists and the potential of archaeobotanists to help understand when, where, how, and

why crops came to dominate human economies in so many parts of the world. Past and present consequences of shifts from foraging to farming are shared concerns, encompassing impacts on human health, demographic growth or decline, differential access to resources, increasingly complex social orders, and environmental repercussions on local, regional, and global scales.

Anthropologists use the terms “agriculture” and “domestication” in a number of different and sometimes inconsistent ways. According to Price and Bar-Yosef (2011, p. S165), the term “agriculture” should be restricted to situations where “Farming and/or herding predominate the activities of a particular community and determine the main diet, although hunting and gathering may continue.” Reconstructing proportions of plant and animal components in the diet of ancient people and societies is usually impossible, however, and the transition from foraging to farming is a continuum (Harris, 1989), making it difficult at times not to speak more broadly of agriculture and its origins. In this paper we treat domestication as a process that originally preceded the formation of agricultural economies, and we consistently make a distinction between the terms “cultivation” and “domestication.” We follow in the tradition of David Harris (1989, pp. 21–22) and adopt the usage of Fuller and Hildebrand (2013, p. 508), who defined cultivation as “a human action that enhances the survival, reproduction, or growth of certain plants. It may include preparing soil, planting seeds, seedlings, tubers, or other plants,” or performing other tasks to manage and improve their productivity. Domestication, on the other hand, “describes genetic and morphological changes on the part of a plant population in response to selective pressures imposed by cultivation” (p. 509).

We begin this paper by addressing issues that have concerned archaeologists for many decades and have left embedded theoretical and methodological legacies across the biological and

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social sciences, all of which have been subjected to considerable revision. These include (1) over-reliance on the concept of centers of origin, with a recent shift to multicentric models; (2) the closely related problem of discerning whether domestication of specific crops occurred once in a single location or if the process unrolled independently more than once in geographically separate areas; (3) the pace of domestication, whether rapid or protracted; and (4) the distinction between domestication of a given crop—or suite of crops—and the transition to agriculture in the sense of fully food-producing economies. The bottle gourd [*Lagenaria siceraria* (Molina) Stand.; Cucurbitaceae] is discussed as an example of a very early domesticated plant that crosses geographical, disciplinary, and theoretical spheres.

Next, we address methodological and contextual concerns such as the tricky business of securely dating archaeological plant remains, recognition of anatomical and morphological indicators of domestication, understanding depositional and post-depositional processes, and critically scrutinizing multiple lines of available evidence. We emphasize the importance of integrating all sources of data and the contributions made by interdisciplinary research teams. A full, forensic-level team effort is always necessary to avoid missteps that inevitably plagued past practitioners with less sophisticated chronometric, morphometric, and taphonomic toolkits.

We then turn to a discussion of anthropological perspectives on the causes of plant domestication, attempting to reconcile the ongoing debate among archaeologists who advocate and apply a human behavioral-ecology, theoretical approach and those who have criticized that strategy. We next discuss domestication-related research that focuses on food and cuisine. The broad purpose of this review is to present some of the most important questions for anthropological archaeologists studying domestication and the methods used to investigate them, for the use of botanists and plant geneticists working on related issues. We highlight aspects of research on plant domestication that fall under the purview of scientists trained as archaeologists including those such as ourselves who specialize in paleoethnobotany or archaeobotany, terms used as synonyms throughout this paper.

Two recent issues of the journal *Current Anthropology*—one published in 2009 (vol. 50, Issue 5) and the second in 2011 (vol. 52, supplement 4)—have featured papers by experts that cover geographical regions and methodological and theoretical overviews of agricultural origins. Even more recently, a special feature titled “The Modern View of Domestication,” published in the 29 April 2014 issue of the *Proceedings of the National Academy of Sciences, USA*, included six articles by authors representing the fields of genetics, archaeobotany, zooarchaeology, and geoarchaeology, beginning with an overview paper by Larson et al. (2014). The journal *Vegetation History and Archaeobotany* devoted a special issue to agricultural origins in the Near East in 2012 (vol. 21, issue 2). Recent books (Bellwood, 2005; Zeder et al., 2006; Colledge and Conolly, 2007; Denham et al., 2007; Gepts et al., 2012; Zohary et al., 2012) represent singly authored, coauthored, or edited volumes published in English within the past 10 years that focus on plant and animal domestication and include or are predominated by chapters written by archaeologists, including archaeobotanists. Many more journal articles have come out during the past few years and others are currently in press, making the task of keeping abreast of breaking developments increasingly challenging.

The relevance of this subject is broader now than ever, as engaged participants have come to include traditional farmers,

urban gardeners, chefs, food industry workers, policymakers on all levels, and scientists of many more disciplines than before. The broader implications of plant domestication touch nearly everyone who cares about food.

RETHINKING FUNDAMENTAL ISSUES

Archaeologists studying the origins of agriculture are confronted with perennial theoretical issues steeped in a legacy of paradigms such as “centers of agricultural origin” and the rapidity of the Neolithic Revolution. While often providing a framework for hypothesis testing and research on domestication, a strict adherence to these paradigms can inhibit our ability to conceptualize domestication. Here we discuss how ongoing research is addressing and challenging these perennial issues.

A centric or noncentric approach?—The concept of “centers of origin” of cultivated plants was developed by N. I. Vavilov in 1926, although an English translation complete with map was not published until 1951 (Vavilov, 1951). David Harris (1990, p. 15) aptly summarized the influence of Vavilov’s thinking on later scholars of plant domestication as follows: “Vavilov’s concept of centers of origin of cultivated plants has had such a profound effect on students of the beginnings of agriculture that it remains very difficult for anyone who takes a world view of agricultural origins to escape the mental template of the Vavilovian pattern of centers.” Vavilov understood the limitations of archaeological evidence available in the early 20th century, and his central concerns were phylogeographic distributions and relative amounts of genetic diversity across broad regions inside of which individual plants or core packages of crops were domesticated (Harlan, 1971; Harris, 1990). Nonetheless, the “template” he laid did and still can hinder willingness to consider new regions, especially those not correlated with major ancient civilizations.

With an increasingly complex map of regions where early agriculture occurred—sometimes independently and other times as a result of diffusion of seeds, vegetative propagules, livestock, skills, or colonizing peoples—previously recognized centers now often seem either too broadly or too rigidly bounded. Vavilov’s Mediterranean center no longer holds status as a cradle of either plant or animal domestication, and at least three regions—eastern North America, sub-Saharan Africa, and highland New Guinea—have been added to the list of areas where native crops were in fact domesticated (Fritz, 1990; Denham, 2007; Smith, 2011; Fuller and Hildebrand, 2013). Any proposed new hearth, however, has a difficult struggle for legitimacy given the legacy and strong hold of traditional centric thinking. Maps in recently published overviews reflect general agreement that agriculture was independently adopted in at least 10 regions around the world (Smith, 2006; Price and Bar-Yosef, 2011; Larson et al., 2014). At the high end of the range, Fuller and Hildebrand (2013) suggested that plant cultivation was initiated in as many as 24 separate areas of the world, although not all are primary, pristine centers where hunter-gatherers independently domesticated native plants before other crops were known or before domesticated animals became part of the economy.

Debates about centers of domestication continue so spiritedly in part because it is impossible to separate this question from other current issues and debates, including (1) single vs. multiple domestication trajectories; (2) the rapidity as opposed to relatively slow pace of domestication, and implications for

the degree of human intentionality involved; (3) chronological positioning of archaeological finds; and (4) diffusion as opposed to the independent increase in social complexity. The idea of a center of domestication is linked to the concept of founder crops or crop packages—groups of plants and animals that were simultaneously domesticated within the same agroecosystem (see Asouti and Fuller, 2012). Some scholars continue to interpret the evidence to favor “a specific core area ... where most, if not all founder Near Eastern crops were likely domesticated” (Abbo et al., 2010, p. 317; see also Lev-Yadun et al., 2000). The centric perspective, as expressed by Abbo and colleagues (2010, p. 325), also takes issue with a conception of domestication as an initially unintentional and prolonged co-evolutionary relationship, positing that from the beginning humans consciously selected seeds for desired characteristics. The separate issues of intentionality, pace, and geographic centeredness are linked in this case.

Other researchers working within Southwest Asia, arguably the most studied of the traditional centers, are now seeing independent subregional developments. Fuller et al. (2011, p. 641), who advocated a “multi-focal” or “noncentric” approach, describe the Near East as a “regional mosaic” in which a “diverse range of crop varieties and early livestock” were integrated over a time span of at least 1500 yr, rather than having encompassed a restricted core geographical area where the package of cereals and legumes widely referred to as founder crops were domesticated within a few generations. Nesbitt (2004), Willcox (2005), and Jones et al. (2013) also supported this position. Whether proposed “centers” beyond Southwest Asia were cradles for domestication of distinct packages of founder crops is also open to question. Fuller et al. (2011, pp. 641–642) raised similar examples of multifocal processes in Africa and Amazonia and pointed to crops such as Asian rice (*Oryza sativa* L.), which was initially the sole cultivated plant for people otherwise relying on wild resources.

China, one of Vavilov’s eight centers, has been subdivided into at least two and as many as five areas where transitions occurred that were distinct-looking but not necessarily isolated from each other (Cohen, 2011; Zhao, 2011). Broomcorn millet (*Panicum miliaceum* L.) and foxtail millet [*Setaria italica* (L.) P. Beauv.] were domesticated in northern China either along the banks of the Yellow River or in the hilly flanks of the loess plateau between southern Mongolia and the Huai River (Liu et al., 2009). Asian rice (*Oryza sativa* subsp. *japonica* S. Kato), on the other hand, was domesticated in wetland regions from the lower or middle Yangtze to the Huai River. During a period that is currently poorly understood, domestication of a different suite of crops, including tropical root crops, resulted in a southeast China “center” (Zhao, 2011), a pattern recognized earlier by Li (1970) and Harlan (1971).

In the Americas, it is difficult to accommodate the concept of a suite of crops having been domesticated at about the same time in any well-bounded region during the early transitions to farming. Vavilov had the insight decades ago to subdivide his South American center three ways, into northern and southern Andean regions plus an Amazonian region. Harlan (1971) envisioned a Mesoamerican center and a South American noncenter, which he defined as a broad, diffuse region where crops were domesticated, but not necessarily simultaneously or in precisely the same places. Even in Mesoamerica, it is now clear that at least one major crop and member of the historic triad of staples—the common bean (*Phaseolus vulgaris* L.)—was domesticated far later than would be necessary for it to be

considered a “founder” species. Today, it appears that the transport and dissemination of useful plants across diverse ecological zones in South America played such an important role in early crop domestication that it is counterproductive to draw boundaries around identifiable centers (Clement et al., 2010). The spatially diffuse nature of crop origins across South America is emphasized by Piperno (2011, p. S455), who advised against designating a core area of agriculture, pointing out that “origins of major and now minor crops are spread from the northern parts to the southern parts of the continent, west and east of the Andes.”

In South America, as elsewhere, genetic research on extant ancestral plant populations, combined with insights garnered by archaeobotanists, has proved critical in unraveling the geographic and temporal intricacies of domestication. Geneticists have determined that the wild ancestor of domesticated peanuts (*Arachis hypogaea* L.) is found in northwestern Argentina (Seijo et al., 2007), and that the wild ancestors of cotton (*Gossypium barbadense* L.) grow in southwestern Ecuador and northwestern Peru (Westengen et al., 2005). Very early in the process of domestication, these plants were traded and brought across ecological and terrestrial barriers such as the Andean cordillera. Peanuts and cotton have been recovered from archaeological contexts on the North Coast of Peru directly dated to 8000 BP and 5500 BP, respectively (Dillehay et al., 2007). Because subsets of the parent populations of these species were transferred to different geographic regions and grown under new ecological conditions, selection pressures resulted in further domestication. In contrast to the Near Eastern example, in this region, isolation of cultivated plants from wild populations via transhumance, migration, or trade may have increased the rate of domestication.

Sub-Saharan Africa was one of Harlan’s (1971) original noncenters. Fuller and Hildebrand (2013) later recognized five independent areas of crop domestication in Africa, listing a total of 30 species of millets, other grains, legumes, tubers, fruits, and additional domesticated plants with uses such as stimulants. After decades of persistent research by numerous individuals, eastern North America is finally included on maps of “major centers” such as the map published in Price and Baryosef (2011, fig. 1). This recognition rewards work documenting domestication of native crops including sunflower [*Helianthus annuus* var. *macrocarpus* (DC.) Cockerell], a quinoa-like grain (*Chenopodium berlandieri* subsp. *jonesianum* Smith and Funk), eastern pepo squash/gourd [*Cucurbita pepo* subsp. *ovifera* (L.) D. S. Decker], and others, collectively called the Eastern Agricultural Complex, all before maize (*Zea mays* L. subsp. *mays*) and other Mesoamerican taxa were introduced to this region. This suite of crops came together as an integrated multicropping system within the confines of the Midwest Riverine area, but it was not fully developed until thousands of years after the earliest species—*Cucurbita pepo* subsp. *ovifera*—was cultivated and had undergone recognizable signs of morphological domestication (Smith, 2011). Therefore, eastern North America seems similar to the Near East as described by Fuller et al. (2011): a “regional mosaic” within which processes of domestication were broadly parallel, but not simultaneous for all crops or spatially concentrated into one core area of the broader region.

Although Vavilov cannot be blamed for early 20th century gaps in evidence, a paradigmatic adherence to the classic concept of centers of domestication, sometimes coupled with the belief that these centers should coincide with regions where

genetic biodiversity of wild ancestral taxa is greatest, has in some cases impeded appreciation of developments outside those parts of the world where early archaeological research was best developed. This was the case for eastern North America, sub-Saharan Africa, and highland New Guinea, as mentioned earlier. It is not a coincidence that none of these regions figure prominently in discussions of the rise of early civilizations; therefore, they fell for decades within the geographical expanses where all farming was thought to have spread as a result of either migration or down-the-line diffusion of crops and knowledge.

While the concept of geographic centers of plant domestication is entrenched in our academic legacy and is arguably more useful in some regions of the world than others, proliferation of information about local trajectories of plant domestication has caused many to break away from rigid centric interpretations and to appreciate new archaeological and molecular data favoring more complex, multifaceted approaches. It is important to resolve this issue anew for each region where domestication occurred, since the spatial element has implications for other questions of anthropological interest, especially whether a given crop was domesticated and then disseminated by a specific group, or domesticated many times in locally distinct ways.

Single vs. multiple domestication trajectories—Genetic research has revealed a wide range of crops that were apparently domesticated multiple times. In the case of the Near East, this debate has been enlivened by possible inconsistencies between archaeological and molecular evidence. As discussed already, archaeobotanical data indicate that domestication may have taken place at multiple sites across the Levant, southern Turkey, Syria, Iraq, and Iran and involved several founder populations (Tanno and Willcox, 2006; Fuller et al., 2011; Riehl et al., 2013). In some cases, genetic research supports similar results (e.g., Morrell and Clegg, 2007; Jones et al., 2013). In other cases where independent domestication of crops was thought to have occurred, emerging evidence points instead to diffusion of propagules and skills for cultivating them (e.g., barley in Tibet, see: Dai et al., 2012; d'Alpoim Guedes et al., 2014).

Recently reported archaeobotanical evidence from the site of Chogha Golan in the Zagros Mountains of Iran is viewed as supporting a localized process of domestication from the end of the Younger Dryas (ca. 11 000 BP) to roughly 9800 BP. Using macrobotanical data recovered from that site, Riehl et al. (2013) document temporal continuity beginning with the cultivation of wild cereals, specifically wild barley [*Hordeum vulgare* subsp. *spontaneum* (K. Koch) Asch. & Graebn.] and wild wheat relatives (*Triticum boeoticum* Boiss., *T. dicoccoides* Aarons, and unidentified triticoid types), as well as wild forms of lentils (*Lens* spp.) and grass peas (*Lathyrus* spp.). By the end of this time frame, nonshattering spikelets of barley and wheat increased significantly in abundance, signaling morphological domestication. Because the transition from wild to domesticated forms of these crops is already documented farther west (Weiss and Zohary, 2011), the sequence either indicates that a gradual transition toward domestication took place in both regions or that domesticated seeds were spread and exchanged among communities already practicing predomestication cultivation (planting of seeds without observable phenotypic change). Riehl et al. (2013) see the site as significant in its lack of fit with a “core area”, rapid-domestication model. Willcox (2013, p. 39) comments that similar domestication sequences

exist at five distinct locations in Southwest Asia, also in line with multicentric thinking.

Barley is a good example of a crop for which the question of single or multiple domestications has been much debated. It was domesticated as early as 10 000 yr ago from a wild, brittle-rachised, two-rowed, hulled ancestor (Zohary et al., 2012, p. 53). Badr et al. (2000), Blattner and Mendez (2001), and Li et al. (2004) have argued for monophyly of barley, although several other studies have suggested a diphyletic or polyphyletic status (Molina-Cano et al., 2005; Azhaguvel and Komatsuda, 2007). Multiple regions of barley domestication have been proposed, including the western Mediterranean and Ethiopia (Molina-Cano et al., 2005), Morocco (Molina-Cano et al., 1999), Tibet (Xu, 1982; Ma et al., 1987; cf. Yang et al., 2008), and elsewhere. Morrell and Clegg (2007) proposed that separate domestication east of the Fertile Crescent might have occurred in southern Turkmenistan (Jeitun Culture) or the Indus Valley region of Pakistan (Mehrgarh). However, considering the closely interconnected nature of exchange and technological flow across this area that began 8000 yr ago and the fact that the earliest recovered barley remains from the Jeitun Culture are fully domesticated, it seems hard to justify a second totally independent pathway on archaeological grounds.

The Tibetan hypothesis for barley domestication is tantalizing given the deeply enrooted cultural significance of barley on the Plateau, which was believed to extend deep into antiquity. Continuing archaeological and genetic research in this region are both needed and ongoing. While several researchers have proposed that barley was independently domesticated in Tibet (Xu, 1982; Ma et al., 1987; cf. Yang et al., 2008), Dai et al. (2012) suggested that fully domesticated barley spread onto the Tibetan Plateau, with genes from wild local relatives introgressing after introduction, supporting earlier findings by Li et al. (2004). Recent paleoethnobotanical research by d'Alpoim Guedes and colleagues (2014) indicates that broomcorn and foxtail millets were the first crops in the region, with barley appearing later, possibly as late as the end of the fourth millennium BP, also putting the archaeological evidence at odds with a proposal for an independent domestication in the Himalayas.

The most recent model proposed for barley domestication, that of Jones et al. (2013), took the genetic-based conclusions of Morrell and Clegg (2007) a step further and posited three to four roughly contemporaneous, isolated domestication pathways, all spreading north along different trajectories from various parts of Southwest Asia. Jones et al. (2008) further supported the potential for multiple domestication processes for barley within Southwest Asia, suggesting that the photoperiod response allele, responsible for the success of the crop in northern latitudes, resulted from the domestication of wild barley from the mountains of Iran or the Levant (further discussed by Fuller et al., 2012).

It is clear that a combination of archaeological (including archaeobotanical) and genetic data (including, one hopes, more and more successful efforts to extract DNA from ancient plant remains) is necessary to determine which crops were domesticated independently more than once, and which were not. Gross and Zhao (2014) demonstrated how productive a cross-disciplinary, collaborative effort can be, in their overarching discussion of the long-debated evolutionary history of rice domestication in East and South Asia. These authors (Gross and Zhao, 2014, p. 6196) concluded that, currently, genetic and archaeological approaches together “suggest the independent origins of rice cultivation in China and India, followed by the

introgression of domestication traits from *japonica* into proto-*indica* cultivated plants to result in the establishment of the domesticated *indica* [*O. sativa* subsp. *indica* S. Kato] subspecies.” Later, in the section on “Dating archaeological beginnings,” we discuss how direct radiocarbon dating of broomcorn millet grains from eastern Europe led to a reassessment of both monophyly and regional antiquity of this crop, with evidence currently supporting a single domestication in East Asia, followed by much later spread into Europe (Motuzaitė-Matuzevičiūtė et al., 2013). Only by unraveling the complex elements of individual case studies will light be shed on the diverse trajectories of plant domestication.

The pace of crop domestication—The term “Neolithic Revolution”, coined by V. Gordon Childe (1934), invokes a mental image of a rapid and dramatic transformation that has permeated scholarly and popular thinking alike for many decades and continues to exert a strong effect—another lasting legacy—on the field. Closely connected to the issue of monophyletic or polyphyletic trajectories and geographic foci for certain crops (discussed already) and relevant to concerns about the role played by climate change in prehistory, the amount of time for domestication to occur is receiving closer attention. One outcome has been to shift the paradigm from revolutionary to protracted processes of domestication. A result of this paradigm shift is that fewer crops can now be counted as domesticated soon after the end of the Pleistocene. Evidence for this shift is illustrated in the very recent overview article by Larson et al. (2014, p. 6140, fig. 1), in which the authors provided a map “depicting likely centers where the domestication of at least one plant or animal took place.” Of the 11 regions bounded by a solid black line on this map, signifying “widely accepted centers of independent domestication”, only four—Mesoamerica, the northwestern coast of South America, Southwest Asia, and the millet zone of northern China—are designated as Early Holocene in time frame. The others, if classified as to timing at all, are Middle Holocene.

The question of timing is closely linked to that of human intentionality and the elucidation of early cultivation practices in general. Experiments have shown that grains can be domesticated in a few generations when consciously and systematically selected (ca. 20–30 yr for self-pollinating annuals) (Hillman and Davies, 1990; see also Honne and Heun, 2009), but we consider it unlikely that the first crops were developed by plant breeders with clear end products in mind. Recently, many scholars have presented evidence that domestication was slower and more gradual than previously envisioned in several regions. Fuller et al. (2011), for example, maintained that crucial morphological and therefore likely genetic changes in Southwest Asian crops were preceded by a 1000 to 2000 yr span of time during which nonfarming people sowed wild-type grains and pulses. This protracted period of cultivation and domestication is supported by archaeobotanical evidence for very low proportions of nonshattering rachis fragments of wheat and barley until the Pre-Pottery Neolithic B time frame, approximately 10–10500 yr ago (Fuller, 2007; Jones and Brown, 2007; Willcox et al., 2008; Fuller et al., 2011). Tanno and Willcox (2006) examined rachis morphology from across several millennia of the archaeological record in northern Syria and southeastern Turkey, concluding that the fixing of the nonbrittle trait took more than 1000 yr of cultivation. Two possible explanations for this protracted scenario are proposed: (1) early farmers harvested immature (green) grain to reduce seed loss, before natural

dehiscence mechanisms took effect; and (2) early cultivators collected grain from wild stands during poor harvest seasons, mixing their genetic stock.

Nonetheless, some scholars have argued that domestication of Southwest Asian crops such as legumes took place rapidly, with mutations possibly occurring in a few crop generations (Abbo et al., 2011; Heun et al., 2012). Honne and Heun (2009) favored a short-term model and emphasized the importance of the experimental data provided by Hillman and Davies (1990). Focusing on the founder legume crops, Abbo et al. (2011) argued that a protracted model would not work because of thick seed coats and high dormancy rates, as high as 90% for lentils. Therefore, without rapid selection for reduced dormancy and thinner seed coats, it is easy to project that cultivation of these crops would have been abandoned due to net seed loss. Unfortunately, it is currently difficult or even seemingly impossible to demonstrate the transition from wild to domesticated forms morphologically for legumes, tubers, and some fruit crops based on plant remains preserved in the archaeological record. Furthermore, Olsen and Gross (2008) emphasized that neither genetic bottlenecks nor human selective pressure can be discounted as potential forces for rapid speciation, considering genetic data alone.

In regions where morphological domestication is viewed as a protracted event, at least by some researchers, the dating of fully agricultural systems has shifted into the more recent past. For example, in East Asia, wild rice (*Oryza rufipogon* Griff.) was cultivated as far back as 8000 BP (Zhao, 2011). Although some researchers (e.g., Jiang and Liu, 2006) had suggested that this early evidence for rice cultivation signaled domestication, Fuller et al. (2007) subjected the available evidence to closer scrutiny and demonstrated that the shift to nonshattering spikelets of rice did not arise until after 7000 BP, well into Middle Holocene times as reflected in fig. 1 of Larson et al. (2014, p. 6140). Specifically, the vast majority of earlier spikelet bases recovered by flotation conformed to freely shattering wild populations rather than domesticated forms, signaling predomestication cultivation. Additionally, the people who harvested these freely shattering rice spikelets were still relying heavily on the other wild plants and animals that had sustained previous generations for millennia. This example illustrates why it is important to use the terms cultivation and domestication consistently and to be explicit about their relationship to the definition of agriculture.

The debate over a rapid as opposed to a protracted model for agricultural origins is ongoing and likely to continue for some time, exemplifying the need for close communication between geneticists and archaeologists, including those with archaeobotanical expertise. As stated by Olsen and Gross (2008, p. 13702), “for understanding the complete picture of crop domestication, we will always benefit by combining the insights gained from both genetic and archaeological data.” Plant and animal domestication had profound, long-term social, economic, and ecological impacts. Still, the continuities exposed by viewing a longer transition period and the biocultural and environmental changes taking place during these extended episodes—whether subtle or dramatic—are worthy of full consideration.

Uncoupling domestication and agricultural economies: A lesson from bottle gourds—While domestication is most often discussed as an element of the transition to agriculture, the process first occurred independently of any such change. The

bottle gourd is one of the oldest domesticated plants in the world—possibly *the* oldest—and yet it was not included in fig. 1 of the overview by Price and Bar-Yosef (2011) who outlined 11 “major centers of domestication” and listed key crops. Native wild-growing populations are known only in Africa, but to our knowledge, there are no early archaeological reports of this plant from its home continent. It is not mentioned by Fuller and Hildebrand (2013) in their recent comprehensive treatment of African plant domestication. Fuller et al. (2010a, p. 261) placed the earliest bottle gourd finds from East Asia in Shiga Prefecture, Japan (Awazu site), where they are “associated with directly dated nuts of 8500–9000 B.C.E.,” but evidently not directly dated themselves. In the western hemisphere, direct dates on bottle gourd specimens from both eastern Florida (Little Salt Spring), and southern Mexico (Guilá Naquitz rockshelter) demonstrate that New World peoples possessed and valued domesticated bottle gourds 10000 yr ago, before there is evidence for cultivation of any other crop besides *Cucurbita pepo* gourds (Smith, 1997; Kistler et al., 2014).

Gourds would obviously have been useful as containers, rattles, and net floats, and despite being bitter, the seeds and young fruits are edible. It would not be surprising to find that early, fully modern humans used and spread *Lagenaria siceraria* across Africa and Eurasia well before 10000–12000 BP. Whether people played a role in helping bottle gourds reach the western coast of Africa, it appears that they floated from there across the Atlantic, where they were found by Early Holocene hunter-gatherers in the Americas who domesticated them multiple times in widely separated regions. Recent work on ancient DNA by Kistler et al. (2014) reverses the earlier conclusions of Erickson et al. (2005), who had suggested an Asian origin and circum-Pacific route of introduction for the early bottle gourds found in the western hemisphere. This case study underscores the necessity for considering alternative hypotheses during early stages of ancient DNA research, when sample sizes are very small. It also shows the need to keep models of domestication open to plants other than those that are famous for their status as “founder” crops that achieved worldwide economic and monetary significance.

Where gourds were rare, they could have been domesticated rapidly by planting and tending them beyond where parent *Lagenaria* populations were found. Selection on the parts of humans appears to have been intentional, most likely for larger fruits with sturdier rinds. Increased sedentism was not required, as gourds need little attention, and their successful maturation does not interfere with the scheduling of other foraging activities (Hanselka, 2010). As previously noted by Erickson et al. (2005) and Fuller et al. (2010a), neither gourds nor dogs sparked a Neolithic revolution, yet they were either the very earliest or among the earliest species to enter the fully domestic realm. Although this example might seem peripheral to the development of serious food-producing economies or social complexity, it highlights early, intimate plant–people relationships and the abilities of people to modify their environments to enhance availability of desirable resources.

REFINING METHODS AND INTEGRATING TECHNIQUES

We next discuss the use of botanical remains from archaeological sites to address questions about the timing, scale, and causes of domestication. Our goal is to highlight areas where

new methods are being developed or old ones improved. We also point out some biases and weaknesses of archaeobotanical data for the information of nonspecialists who draw upon them.

Dating agricultural beginnings—Journalists and science writers often give the impression that a central goal of researchers studying crop domestication is to push the dates for early agriculture deeper into the past by finding increasingly early evidence for agriculture in any given region of the world. Discoveries of older and older evidence might sometimes seem like a general trend, especially in areas where little fieldwork has been done or where archaeologists had not previously concentrated on collecting plant and animal remains. However, there have been several high-profile cases where the antiquity of particular crops or of food production itself in a region has been shortened rather than lengthened, usually as a result of submitting specimens such as single seeds or other tiny fragments of plant material for direct radiocarbon dating rather than relying on the age of associated material such as wood charcoal. Examples include (1) barley and einkorn wheat from the Wadi Kubaniya site in Egypt, initially believed to be 17000–18000 yr old, are actually no more than 5000 yr old (Wendorf et al., 1984); (2) common beans from the Tehuacán Valley and elsewhere in Mexico, which were thought for decades to be at least 6000–7000 yr old, are no older than 4000 yr (Kaplan and Lynch, 1999); and (3) much of the maize from Bat Cave in New Mexico, believed to have been deposited 4500 yr ago, is centuries or even millennia younger (Wills, 1990). Direct dating of very small amounts of organic material has been feasible since the late 20th century when accelerator mass spectrometry (AMS) ¹⁴C dating became routine. Thus, there is no longer any reason to speculate about the true ages of specimens that might have been subject to postdepositional movement in spite of lack of obvious disturbance or mixing of the strata in which they were buried. Especially when a great deal of effort will be made to extract ancient DNA from archaeological material, it is imperative to ensure that the suspected antiquity be verified, as was done by Erickson et al. (2005), Kistler and Shapiro (2011), and Kistler et al. (2014) during their pioneering studies of ancient *Lagenaria* and *Chenopodium* DNA.

Firm, precise dating is integral to debates surrounding the pace of domestication, whether a crop was domesticated once or multiple times, and whether domestication occurred in independent “centers” as opposed to colonization or diffusion through intergroup contact. Domestication is, of course, an evolutionary process rather than an event, and the earliest signs of human-mediated selection did not bring agricultural economies into being or cause major cultural changes. An example of a region where current thinking has truncated the antiquity of plant domestication is the western Fertile Crescent, where finds at Tell Abu Hureyra of a few morphologically domestic-looking grains of rye (*Secale cereale* L.), along with a suite of seeds from weedy plants indicative of tilled fields, led to the conclusion that Epipaleolithic villagers living in northern Syria 11500 yr ago were the earliest known farmers (Moore et al., 2000). Upon further reflection and examination of the complex evidence, it appears that reliable signs of domestication—in the form of a high proportions of spikelet bases from wild-type, shattering wheats—are not manifested anywhere in Southwest Asia until 10000–10500 BP (Weiss and Zohary, 2011), although predomestication cultivation of phenotypically wild grains at Abu Hureyra and elsewhere was almost certainly an early step toward this outcome.

A more recent example from the Old World involves the antiquity of broomcorn millet, a crop suggested to have either been domesticated independently in eastern Europe more than 7000 yr ago or to have spread from northern China (where domestication is well documented by 8000–9000 BP) across the vast expanse of the Eurasian steppe, where it is now documented archaeologically by 4500–4200 BP (Spengler et al., 2014). A close examination of the reported contexts of early millets in Europe, many of which were excavated before AMS dating was an option, failed to support either their antiquity or their morphological status as domesticates (Boivin et al., 2012; Motuzaite-Matuzeviciute et al., 2013). To resolve this question, Hunt et al. (2008, 2011) called for directly dating all archaeobotanical millets from Europe suspected of predating 7000 BP, along with reexamination of reported Early Neolithic ceramic items described as containing impressions of millet grains. The results so far fail to support claims of millet cultivation in Europe preceding the late fifth millennium BP, placing diffusion of domesticated broomcorn millet from east to west within a Bronze Age time frame congruent with other evidence for active exchange across Eurasia (Motuzaite-Matuzeviciute et al., 2013; Valamoti, 2013). For now, the issue seems to be resolved in favor of a single East Asian domestication, followed by westward diffusion of seed stock thousands of years later. Due to the many opportunities for small seeds to move vertically through the soil—a process that becomes especially problematic at multicomponent sites—it is imperative that archaeologists take advantage of improved radiocarbon techniques that allow the direct dating of single grains, as did the researchers already cited, to address such long-standing questions.

In the western hemisphere, we are currently engaged in heated discussions, especially about the antiquity of maize's domestication and spread beyond Mexico, that revolve around microscopic phytoliths, pollen, and starch grains that cannot be directly dated as individual specimens, even by AMS dating, in the same way as a single maize kernel or cob fragment (see discussions by Blake, 2006; Sluyter and Dominguez, 2006; Pohl et al., 2007; Shillito, 2013). There is no challenge to the validity of direct AMS dates on charred residues adhering to ceramic vessels or on dental calculus from which diagnostic microbotanical remains of cultigens have been found. That strategy differs from relying on dated organic material such as charcoal from the same stratigraphic level—however undisturbed the strata might seem—or dating concentrations of thousands of pollen grains or phytoliths derived from on-site or off-site sediments. When concentrated samples of microfossils are submitted for dating, they may or may not include the targeted taxon and might have been subjected to postdepositional disturbances.

The date of 9000 BP is widely cited for maize domestication, based on the molecular clock reckoning of Matsuoka et al. (2002), combined with microfossil evidence that was indirectly dated (an AMS date on charcoal found in the same 8- to 10-cm thick layer as stone tools with maize phytoliths and starch grains) from the Xihuatoxtla rockshelter in southwestern Mexico (Piperno et al., 2009; Ranere et al., 2009, pp. 5015–5016). Matsuoka et al. (2002), however, acknowledged a very large error of uncertainty for their 9100 BP “midpoint”—as early as 12000 or as late as 6400 BP—and at one point (p. 6083) stated that the true date of separation between maize and its wild ancestor, *Z. mays* subsp. *parviglumis* (Iltis & Doebley), is likely to be toward the more recent end of that range. The oldest directly dated maize macroremains are uncharred cobs from Guilá

Naquitz rockshelter in Oaxaca, which are less than 7000 yr old (Piperno and Flannery, 2001). Until directly dated remains are reported, we are not convinced that a date as early as 9000 BP can be supported for the existence of domesticated maize in Mesoamerica.

All researchers who rely on archaeological dates to build models and inform interpretations need to consider exactly what is being dated, both conceptually and physically. In some of the instances just cited, the date for “agriculture” will become later or earlier depending upon whether the researcher bases his or her definition on cultivation or domestication. Some landscapes are not conducive to the preservation of plant remains, and some ancient practices inherently leave little archaeological evidence. The dating of bulk samples of microfossils consisting of multiple taxa from a core or soil sample, a strategy developed to overcome a lack of macrobotanical remains, does not result in directly dated evidence in the same sense as dating a single, firmly identified specimen. Whenever one artifact is used to date another artifact (indirect dating), the possibility arises that two artifacts were not deposited at the same time. In the case of plant microfossils, which are tiny and can move through soil by multiple natural processes (Shillito, 2013), such indirect dating is a concern that must be overcome by documenting exceptionally secure, self-contained contexts.

Bayesian modeling has spurred a major methodological shift in the interpretation of radiocarbon dates, in some ways comparable to breakthroughs brought about by AMS dating and dendrochronological calibration (Bronk Ramsey, 1994; Bayliss, 2009, p. 125; Kennett et al., 2011, p. 245). This modeling technique uses a priori data, such as stratigraphy or associated materials of known age, to order radiocarbon dates, thereby narrowing the statistical error range of calibrated dates and identifying outliers. Meticulous methods for selecting and processing samples together with larger quantities of dates and the use of Bayesian modeling have enabled archaeologists to refine and narrow error ranges (Bayliss, 2009). Manning and colleagues (2011) used Bayesian modeling of AMS-dated pearl millet seeds [*Pennisetum glaucum* (L.) R. Br.], together with chaff-tempered potsherds dated by both the AMS C-14 and optically stimulated luminescence methods, to document the domestication of pearl millet in Mali at no later than 4000 BP. Notably, the best evidence for morphological domestication came from SEM-aided examination of casts of impressions of pearl millet spikelets in chaff-tempered pottery, although AMS dates on the organic content of the sherds themselves were suspiciously too early, likely due to incorporation of sediment-derived carbon. This is an excellent example of the need to combine as many methodological advances as possible and the importance of revising inferences as evidence emerges.

Morphological indicators—In this section, we concentrate on new ways of looking at morphological indicators that signal domestication. For decades, archaeobotanists have conducted systematic research attempting to document direct evidence for domestication based on discernible morphological changes in fruits, seeds, and other plant parts recovered from archaeological contexts. The seemingly obvious rule of thumb that sizes of grains or fruits increased under domestication, however, cannot always serve as proof that the process was underway. When using seed size as an indicator of domestication, it is necessary to control for puffing, shrinkage, or both (puffing for seed width and shrinkage for length, for example), which affect archaeological specimens preserved through charring. Most of the

assemblages used to track plant domestication are charred, but variables such as the temperature of the fire, the distance from the source of heat, and the moisture, fat, and starch content of the seeds or other plant parts when they were burned are usually impossible to reconstruct. Experimental studies have been instrumental in alerting archaeobotanists to the variables and pitfalls involved (Wright, 2010; Smith, 2014). Claims of domestication based on morphology should optimally rest on multiple variables, such as shape, size, fruit or seed coat thickness, surface texture, and dehiscence mechanism, depending on the organism in question. Experimental carbonization should always be included in any such studies.

For example, in grasses, researchers now look closely at attachment scars on rachis internodes of wheat chaff and similar features on spikelets of rice and other crops for firmer evidence that high enough proportions of nonshattering grains were represented to infer that nonwild populations were represented. As already discussed, Riehl et al. (2013) recently reported evidence for more than 2000 yr (ca. 12 000–10 000 BP) of harvesting of phenotypically wild-type emmer wheat at Chogha Golan in the Zagros foothills of Iran, followed by an increase in abundance of domesticated-type emmer spikelets after 9800 BP. Proportions of arable weed taxa increase at the same time, providing additional support for heightened farming activities at this time.

Advances in microscopy have greatly facilitated the ability to discern phenotypic changes resulting from selection, at times involving a change in seed coat surface texture, a measurable reduction of seed or fruit coat thickness, or a change in some other anatomical feature of archaeological specimens. In the case of the Eastern Agricultural Complex in North America, archaeologists relied on SEM to identify a cultigen chenopod (*Chenopodium berlandieri* subsp. *jonesianum*) whose domesticated forms have gone extinct (Smith, 1984; Fritz and Smith, 1988). The technique was subsequently applied by archaeobotanists working in the Andes to study domestication of quinoa (*C. quinoa* Willd).

Preoccupation with looking for an increase in seed size as a necessary indicator of domestication interfered with initial research into the Eastern Agricultural Complex because one of the most important crops, the native *C. berlandieri* subsp. *jonesianum*, experienced a different type of transformation. Rather than selection for increased diameter of this small-seeded pseudocereal, fruits underwent dramatic reduction in testa thickness (Fritz and Smith, 1988). The much thinner seed coats were sometimes still black, like wild chenopods, but the texture was smooth rather than alveolate as found on all but a very small percentage of their wild and weedy counterparts. In rarely preserved uncharred assemblages from dry rockshelters, cultigen specimens have outer seed coat layers (the outer epiderm) so reduced as to be translucent, or this outer layer seems to be absent altogether. The pale specimens were assumed to be incomplete due to damage resulting from age and possibly excavation trauma, rather than being domesticated, until Wilson (1981) demonstrated that they were still surrounded by their papery pericarps, the fruits had undergone no physical alteration, and were structurally identical to modern, pale-seeded Mexican *Chenopodium berlandieri* subsp. *nuttalliae* (Saff.) Wilson and Heiser. Both thin-and-black archaeological specimens and pale-and-uncharred ones are truncate-margined (rectangular) rather than lenticular in cross section and display larger, oval embryos that enclose a somewhat expanded perisperm area. The antiquity of morphologically domesticated chenopods in

eastern North America, verified by direct AMS dating of archaeological specimens, now extends back to 3800 BP (Smith and Yarnell, 2009). *Chenopodium berlandieri* subsp. *nuttalliae* in Mexico, by contrast, has no demonstrated pre-Columbian record.

In the Andes near Lake Titicaca, evidence indicates that *C. quinoa* was independently domesticated. Fruits from Bolivian sites with notable morphological changes corresponding to those just discussed for North American have been directly dated to approximately 3500 BP (Bruno, 2006). Three qualitative and three quantitative indices have been used to distinguish the presence of domesticated varieties and their weedy counterparts. Qualitative indicators include margin configuration, seed coat texture, and beak prominence, and quantitative measurements include seed coat thickness, seed diameter, and ratio of seed coat thickness to diameter (Bruno and Whitehead, 2003; Bruno, 2006; Langlie et al., 2011). While advances in microscopy and the study of chenopods expand our knowledge about the domestication of chenopods in the New World, advances in the study of plant DNA has engaged molecular geneticists. For example, Kistler and Shapiro (2011) confirmed, using DNA sequencing of archaeological specimens, that chenopods in eastern North America were indeed independently domesticated in the region and not introduced from Mexico.

In Mexico, domesticated chenopods are grown today for greens (quelites), grain (called chia but not to be confused with *Salvia hispanica* L.), and broccoli-like inflorescences called huauhtzontli, which are harvested in the budding stage, coated with batter, and fried in oil (Gordon, 2006). Seeds of these cultivated varieties exhibit morphological characters that correspond to the dark-seeded and pale-seeded morphotypes, now extinct, from eastern North America, and have been suspected of being the source populations for them. However, as McClung de Tapia and Rios-Fuentes (2006) noted, there is no pre-Colonial evidence for *Chenopodium* domestication in Mexico. This case highlights the utility of integrating multiple lines of evidence in the study of domestication. For *Chenopodium* research, the evidence has included seed morphology, ancient DNA, and historical research, which have all tended to reinforce one another.

Microfossil evidence—Plant microfossils (starch granules, pollen, and phytoliths) are also widely used to study plant domestication both alongside and in lieu of macrobotanical remains (e.g., Pearsall, 2000; Logan, 2006; Piperno, 2006). As with seeds and fruits, morphological analyses are strongest when they include several different indicators. The study of microfossils requires specialized comparative collections for the region in question, and each assemblage presents challenges and opportunities for identification. In many cases, microbotanical and macrobotanical data provide complementary data sets and can answer different questions. Phytoliths, for example, provide evidence of plant parts such as stems, leaves, and glumes, which are rarely preserved in the macrobotanical record. Starch granules are often used to document the presence of tuber crops that are poorly represented by seeds or fruits. Pollen can be used to reconstruct the local environment and is especially useful for signaling changes in climate or landscape management. Researchers studying each of these classes of microbotanical remains have provided valuable insight into past subsistence and landscape management, in many cases building on macrobotanical and genetic results as a complementary data set. Plant microfossils, however, are subject to different forces

of deposition and postdepositional alteration than macrobotanical remains and thus sometimes provide conflicting evidence (Shillito, 2013).

Charred plant remains have limitations for directly addressing ancient cuisine because they are carbonized and often represent waste rather than food. Likewise, macrobotanical remains preserved in other ways, such as in dry rockshelters, are normally more informative about storage practices than cooking. Paleofeces have also provided some insights into ancient diets. For example, the desiccated human feces recovered from Salts and Mammoth Caves in Kentucky contained entire seeds of various members of the Eastern Agricultural Complex, providing direct evidence that they made up an important part of Early Woodland diets. In addition, overlaps between pollen and seeds in these paleofeces have been used to explore which foods were preserved throughout the year, and what types of plants were normally consumed together (Gremillion and Sobolik, 1996). Such examples of macro- and microbotanical remains being recovered from demonstrably gastronomical contexts, though, are rare.

Microfossils, on the other hand, can be recovered from human dental calculus, cooking residues on ceramic vessels, and on the surfaces of grinding stone tools. For species with diagnostic domesticated microfossils, such as maize, remains from these contexts can simultaneously inform us as to the spread of domesticates and their culinary context. For example, the earliest currently known maize remains east of the Great Plains come from maize phytoliths in food residues on a ceramic vessel from New York State (Hart et al., 2007). This residue is hundreds of years earlier than the earliest macroremains, kernel and cob fragments recovered from the Mississippi Valley (Riley et al., 1994). It is thought that maize entered eastern North America from the Southwest via the Great Plains, so the earliest remains should ultimately come from the Plains or Midwest. The fact that no earlier kernels or cobs have been found in this extremely well-investigated region raises the possibility that maize first entered eastern North America in the form of traded food, centuries before easterners began raising it as a crop. Furthermore, the identification of maize on cooking pots establishes a link between improving ceramic technology in the Northeast and changing plant use as agriculture was adopted in this region, a connection that has been hypothesized for other regions in eastern North America and elsewhere (Braun, 1987).

Taphonomy—All archaeologists, including paleoethnobotanists, face the continuing challenge of understanding taphonomic processes to determine how macro- or microbotanical remains became deposited in the soil, how they were preserved, whether their presence is the direct result of human action, and how mechanical disturbances or bioturbation have affected them after deposition. Broadly speaking, the science of taphonomy is the study of decay processes following the death of an organism until it is fossilized or exhumed. As Théry-Parisot et al. (2010) noted, archaeologists expand this definition to include both natural and cultural processes that led to the preservation of an artifact. Multiple lines of evidence should be considered when researchers examine the taphonomic processes of preserved macrobotanical remains.

Paleoethnobotanists most often study plant remains preserved as a result of charring (partial carbonization), a process that frequently leaves distinguishable morphological traits important for analytical purposes. We also study plant remains that are desiccated, waterlogged, or preserved by other exceptional

means. While rarer than carbonized remains, plants preserved by other means often provide researchers unique opportunities to understand past human–plant interactions. For example, at the Cerén site in El Salvador, an ancient Mayan village was preserved intact under a blanket of volcanic ash and magma. Due to these exceptional taphonomic conditions, paleoethnobotanists were able to identify the species of grass used in thatched roofs (Lentz et al., 1996), and entire manioc field systems were uncovered (Sheets et al., 2011).

When plant remains are recovered from an archaeological context, researchers must determine whether they were deposited and/or charred as a result of seed rain, food waste, activities such as burning dung as fuel, thatching material, bedding, floor sweepings, byproducts from processing, spills during food preparation, etc. In some cases, these processes are nearly indistinguishable in the archaeobotanical record; for example, wild herbaceous seeds in an assemblage from an agricultural village could be interpreted as agrestal weeds, whereas the same species at a preagricultural, forager encampment could represent broad-scale collecting. At a pastoralist site, similar wild or weedy seed types could be considered the remains of dung burning as fuel, an interpretation that considerably alters the reconstruction of human diet.

In places where both animals and plants were domesticated such as Asia, northern Africa, and the Andes of South America, one particular taphonomic consideration sheds lights on human–animal relationships, and human–environmental interactions. Miller (1996) and colleagues (Miller and Smart, 1984) asserted that many herbaceous seeds in macrobotanical assemblages from Southwest Asia are the result of humans burning dung that was laden with seeds that passed through the digestive systems of their herd animals. People around the world today and in the past have used dung as fuel, especially in environments where wood resources are sparse. Since Miller and Smart (1984) published their article on archaeological dung burning, a shift has taken place in paleoethnobotany, and researchers are looking at processes that could be specific to a site, time period within a site, or a single seed category within the assemblage. For example, using dung remains, Shahack-Gross and Finkelstein (2008) and Shahack Gross (2011) reconstructed the subsistence economy at Iron Age Atar Haroa, Israel, concluding that the inhabitants of this site were committed to full-season pastoralism and did not partake in seasonal dry-farming. Spengler et al. (2013) compared wild seeds from experimentally burned modern dung to archaeobotanical remains from Bronze Age sites in Central Asia to reconstruct human use patterns on the landscape, including herding practices. In the Andes of South America, the ways in which taphonomic processes of dung burning affect paleoethnobotanical assemblages has become a standard part of interpretation for researchers working in the region (Hastorf and Wright, 1998; Bruno, 2008; Langlie, 2011). Importantly, the identification of wild herbaceous seeds, even if they are in a pastoralist context, cannot be unequivocally designated as remains of dung, nor can such seeds recovered from hearth features automatically be assumed to be human food remains (Hastorf and Wright, 1998, p. 222).

Our interpretations are strengthened by research designs that include multiproxy data. Shahack-Gross and Finkelstein (2008) examined archaeological remains of dung by using mineralogical analyses of monohydrocalcite, gypsum, and high phosphate compounds, the presence of calcareous spherulites (calcium carbonates that form in the guts of animals and are excreted in

their feces), and by means of phytolith counts (greater than two million phytoliths per gram of sediment). Multiple lines of evidence were also put to use by Lancelotti and Madella (2012), who analyzed phytoliths, chemical signatures, and spherulites to suggest direct evidence of dung burning at sites in northern India. When multiple lines of evidence are incorporated, taphonomic processes can be identified. Archaeobotanists can then use these data to more confidently draw conclusions about ancient diets of people and their animals.

Interdisciplinary research efforts—Archaeology is a forensic science. Like all forensic data, archaeological remains are unique, finite, and dependent on context for much of their interpretive value. Archaeological data sets are also not distributed randomly. They are dependent on certain processes of deposition and preservation, making sites or classes of artifacts in some environments extremely rare or difficult to find. Not all human activities will create lasting sites or recognizable artifacts. These disciplinary parameters have encouraged archaeologists to work in multidisciplinary teams to maximize recovery of useful information from excavations. Although plant scientists may primarily be interested in combing archaeological publications for specific paleoethnobotanical data, they should be aware that this information is almost always part of a larger analysis. Other forms of archaeological evidence, including animal and human bones, tools, soils, and settlement structure, as well as variation in all of these factors through time, can inform an evolutionary perspective on domestication.

Zooarchaeology, the analysis of animal bones from archaeological sites, is a subdiscipline that often informs discussions of plant domestication. For one thing, many zooarchaeologists also study domestication and are at the forefront of defining domestication in anthropological terms (Marshall and Hildebrand, 2002; Zeder, 2006; Marshall and Weissbrod, 2011). But zooarchaeological analyses in and of themselves can also enhance our understanding of the specific processes leading to plant domestication. In the Levant, for example, Munro (2004) and Davis (2005) have used the relative abundance and age-at-death of certain prey animals to show that as humans were beginning to cultivate cereals, they were also increasingly exploiting smaller game and younger gazelle. Using optimal foraging theory to predict human hunting strategies, these authors have argued that the prey choices indicate resource pressure. Throughout this period of predomestication cultivation, “constant resource pressure ... undoubtedly encouraged pre-adaptation to cereal ‘management’” (Munro, 2004, p. 21).

A decade ago, archaeologists believed that the domestication of animals followed the domestication of cereals by 1000 yr or more, but it now seems that both processes were underway simultaneously and were intimately connected (Zeder, 2011). For example, Makarewicz and Tuross (2012) have used ratios of stable isotopes within 10000-yr-old goat and gazelle bones to show that provisioning of goats with fodder was one of the earliest methods of husbandry practiced in the Near East. Whether early herders were managing plants to harvest as fodder or controlling the grazing patterns of wild animals, they would have changed the plant communities and selective pressures brought to bear on plants within their range.

The linkage between plant and animal domestication is becoming a global trend. Early (ca. 9000 BP), morphologically domesticated cereals from Cyprus are associated with the introduction of nonnative animals to the island, including goat,

sheep, cattle, pigs, fallow deer, and foxes (Willcox, 2005, p. 535; Vigne et al., 2011). This evidence demonstrates that grains and animals were integrated parts of very early agroecologies. Recently, stable isotope research has indicated that millet was an important part of the Neolithic diet of the early domesticated pigs in northern China, further supporting the proposition that the domestications of cereals and animals were mutually reinforcing (Chen et al., 2014). Similarly, researchers have long speculated that the domestication of camelids and high-elevation pseudocereal and tuber crops in the Andes may have been linked processes, and the details of this relationship are beginning to be understood (Kuznar, 1993; Pearsall, 2008; Langlie, 2011).

Human bones likewise tell the tale of how human health, diet, physical exertion, intergroup violence, and mobility changed with the domestication of plants. Methodologies used to track these changes are diverse, and even a brief summary is beyond the scope of this paper (see Pinhasi and Stock, 2011). One outcome of plant and animal domestication was the Agricultural Demographic Transition, an increase in fertility (and human population size) thought to be associated with a more consistent food supply and decreasing mobility (Bocquet-Appel, 2011). In some regions, the domestication of plants has also coincided with an increase in chronic stress caused by crowd diseases, repetitive manual labor, and homogenous diets, with outcomes such as smaller stature, greater incidence of arthritis, and poor oral health (Stock et al., 2011).

However, it is now recognized that these patterns of declining health with the advent of agriculture are not universal. They may occur during the process of domestication, or thousands of years after farming economies have been established (Papathanasiou, 2011), or may in fact be reversed. For example, Auerbach (2011) has shown that in eastern North America, stature and body mass both *increased* from the period of Archaic hunter-gatherers to that of Mississippian farmers. Although generally agricultural beginnings have been associated with increased upper body strength and stress in females who are usually responsible for processing crops, in eastern North America differences in stress on female farmers were dependent on the subtle evolution of the agricultural system: female upper body strength is greater in Middle Woodland forager-farmers than in their Mississippian agricultural descendants (Bridges et al., 2000). Such results indicate that human health outcomes are probably just as dependent on harvesting, processing, and food distribution norms within a society as they are on the relative reliance on domesticates.

We have highlighted human and animal bones as potential sources of information about plant domestication, but the same could be argued for other classes of archaeological data, such as household structure and storage features, agricultural and culinary tools, and soil morphology. If our goal is to understand how and why domestication occurred as an historical and evolutionary process, it is often necessary to go beyond archaeological remains.

ANTHROPOLOGICAL PERSPECTIVES ON THE CAUSES OF PLANT DOMESTICATION

Archaeologists still struggle to explain *why* transitions from foraging to food production happened when and where they did. Are there commonalities between domestication episodes worldwide? If so, can we borrow terms from biological evolution

and refer to these as instances of cultural parallelism or convergence (Fuller et al., 2014)? While all researchers agree that local, multicausal trajectories are coming into focus, they disagree about the desirability of attempting to simplify these narratives in the interest of comparative study (Zeder and Smith, 2009; Gremillion et al., 2014). For Zeder and Smith (2009, p. 687), the transition to agriculture, encompassing domestication, is best understood as a story with many characters and subplots, all of which are important to explaining the outcome: “Isolating and selectively emphasizing any of these very general, macro-level overarching factors ... does not explain very much about how the process unfolded on the ground...” This approach is explicitly data driven and inductive. Critics of this trend (Gremillion et al., 2014, p. 6172) worried that explanations based on narrative details are inflexible and overly reliant on the current available evidence. They insisted that hypothesis-driven research is best carried out by simplifying what we know to be a complex situation in the interest of model building. They argued that models can be used to isolate potentially important factors and study their effects. These authors raised concerns about what they see as a retreat from theory, particularly *evolutionary* theory, among anthropologists studying the origins of agriculture (Gremillion et al., 2014, p. 6173).

It may seem strange that a debate about research design (the relative merits of inductive vs. deductive reasoning) should spin off into a defense of evolutionary theory in archaeology. The association of these topics has roots too deep in the history of anthropological thought to recount here. But it is true, although perhaps surprising to those outside the discipline, that some archaeologists consider evolutionary explanations and frameworks to be ahistorical and mechanistic (as characterized by Gremillion et al., 2014, p. 6173), partly due to the pervasive conflation of biological and cultural evolution within the discipline. For example, in a now classic paper on the state of archaeological theory, Hegmon (2003, p. 225) writes that archaeologists have shifted away from evolutionary explanations because they recognize that “many cultural changes are neither unilinear nor unidirectional,” concepts associated not with biological evolutionary theory, but with a particular strain of antiquated cultural evolutionary theory. She (Hegmon, 2003, p. 226) goes on to point out exceptions to this trend in the work of Rindos (1984) and Smith (1992) discussing biological coevolution—human behavior acting as a selective pressure on plants that led to domestication—not cultural evolution. In a more recent case, Fuller et al. (2014, p. 6151) discussed how various domesticated plants may exhibit parallelism or convergence, then discussed how farming cultures may show the same, without making any explicit theoretical distinction between the two cases. For some archaeologists, the very idea that cultures may evolve conjures up the unilinear social Darwinian hierarchy obliquely referenced by Hegmon (2003, p. 225), with its savages and barbarians. But for most, objections are more specific and not directed at the use of evolutionary theory broadly conceived, but rather at the particulars of how it is employed.

The ways that concepts from biological evolution are applied to processes of cultural change vary between approaches and are much contested (Boone and Smith, 1998). For example, the debate in the previous paragraph (Smith, 2009; Zeder, 2012; Gremillion et al., 2014) actually revolves around a particular adaptationist framework referred to as human behavioral ecology. This theoretical perspective was adapted from evolutionary ecology by anthropologists seeking a way to quantitatively

test the hypotheses generated by the cultural ecology of the 1960s (Zeder, 2012). Human behavioral ecology also draws on microeconomic theory and posits that human agency on a societal scale can be understood as different individual strategies to maximize energy intake and minimize energy expenditure within certain environmental parameters (Kennett and Winterhalder, 2006; Gremillion and Piperno, 2009). Objections to this theoretical framework are not necessarily objections to either evolutionary theory or model building *in general*. Instead, dissenters express disagreement with assumptions of some human behavioral ecology models, especially that “as foragers encounter resources, a stringent assessment of their net energy value is the solitary criteria for ranking and selection” (Smith, 2009, p. 533; see also Zeder, 2012, p. 256).

Both camps within this debate are in fact working within anthropological evolutionary frameworks. Despite their methodological differences, researchers within all of such frameworks have been drifting in the same direction since the 1970s, by challenging environmental determinism and prime mover explanations for the transition to agriculture. Whether testing models of environmental and economic imperatives, or reacting against this approach, archaeologists have uncovered the ways that humans modify their environments or change their tools and strategies when they face ecological constraints and opportunities (Crumley, 1994; Gremillion and Sobolik, 1996; Terrell et al., 2003; Balée, 2006; Smith, 2007; Crawford, 2011; Zeder, 2012, among many others).

Drawing on the seminal works of Harlan et al. (1973), de Wet and Harlan (1975), and Rindos (1984), in recent decades many anthropologists have elucidated the reciprocal nature of the culture–environmental relationship and the process of domestication as coevolution (Laland and O’Brien, 2010). Domestication is one example of how human environmental engineering, or niche construction, can lead to permanent changes in the productive capacity of the landscape, thus allowing cultural developments that would otherwise have been impossible (Smith, 2007). The increasing resolution of the archaeological record in some centers of domestication has allowed archaeologists to examine factors such as land clearance, fertilization, harvesting methods, and crop processing and storage practices that effected selective pressures on plants and humans and modified energy flows within human-inhabited ecosystems (Fritz, 2000; Gremillion, 2004; Fuller et al., 2010b; Wollstonecroft, 2011).

Yet debates continue over how much control ancient people had over their environments, the importance of factors such as climate change and population pressure, and how exactly to model or conceptualize the wild card: human agency. Anthropological archaeologists face the challenge of framing theoretical discussions of domestication broadly enough to be integrated with biological evolution, yet without discounting the intelligence of people living thousands of years ago who were responsible and deserve credit for solving problems such as feeding all members of their kin groups and engaging in complicated social negotiations on local and regional scales. Active human participants were not intentionally trying to transition from foraging to farming, nor did they respond mechanically to environmental conditions. As discussed elsewhere in this essay, archaeobotanical evidence has lengthened the duration of the agricultural “revolution” to more than a millennium in key parts of the world. The current archaeological evidence for a long process of domestication may be used to support a variety of scenarios: (1) many of the earliest domestications were instances

of coevolution with relatively little intentional selection; (2) early farmers were targeting and trying to improve certain plants, but were unable or unwilling to exert strong selective pressure because they were also invested in many other tasks and were not constrained by lack of wild resources; or (3) social networks were not adequate to distribute or exchange knowledge and domesticated plants, which thus tended to remain local innovations for a long time. Some combination of these factors may best explain why it took so long for domesticated varieties of plants to become ubiquitous within different centers of domestication.

Since the transition to food production did eventually occur in the vast majority of human societies, anthropologists argue about whether early farmers (or herders) were “pushed” or “pulled” into agricultural economies. This question is less about the evolutionary process of domestication than it is about how cultures and (especially) economies change, the core concern of our discipline. Those who argue that humans were “pushed” into agriculture believe that increasing populations and/or decreasing resource availability forced people to intensify food production or expand diet breadth (Flannery, 1969; Cohen, 1977, 2009). Intensification and/or shifting resource use then led to domestication. Others argue that early farmers were “pulled” into agricultural economies. In these scenarios, there was no internal need for a greater or more reliable source of food. Instead, stable populations of hunters and gatherers domesticated wild plants in settings where predictable and diverse resources presented an opportunity to invest more in managing the local landscape (Zeder, 2012, p. 258). Risk avoidance models may posit either scarce or abundant resources, but see seasonal or yearly predictability as the goal of early cultivating and herding practices (Marshall and Hildebrand, 2002; Fuller et al., 2014, p. 6151).

In one charismatic risk avoidance scenario, prestige-seeking individuals created a demand for surplus, particularly grains or fruits for fermented beverages and novel foods for feasting (Hayden, 2009). This perspective has been described as paleopolitical ecology because it focuses on surplus as a means to both reduce risk and promote the self-interest of the individuals who control it (Hayden, 2009). In this and related theories, social or economic dynamics are the prime mover, and both population pressure and the evolutionary process of domestication are merely outcomes. It is not necessary for one of these scenarios to explain all transitions to agriculture. Indeed, all of these situations may have occurred in the same region but at different points during the long transition from foraging to farming; hence, both constructing local historical narratives and modeling the impact of particular factors are valid approaches to explaining why the transitions occurred.

Elucidating changes in social structure that preceded, accompanied, or followed the domestication of plants is usually the ultimate goal of anthropological studies. Following domestication, increases in productivity encouraged sedentism and necessitated the creation of institutions to deal with land tenure and distribute (or hoard) surplus. Many realms of social change are thought to be in some way related to the beginnings of food production, including relations between farmers and hunters and gatherers as agricultural economies expanded, changes in ideology and iconography, architecture and settlement structure, paleopathology and morbidity, the distribution of wealth, and the gendered division of labor. Thus anthropological writing on domestication is situated within and must respond to the even more vast literature on the origins of social hierarchies, chiefdoms, and the state.

THE FRAMEWORK OF FOOD

Anthropological studies of agricultural origins tend to be subsistence-oriented in the general sense that they track changes through time in hunting, harvesting, and herding practices and associated cultural behaviors that become increasingly dependent upon production of domesticated food plants and animals. It may seem odd that, with exceptions including stable isotope studies that measure proportions of C_4 pathway crops consumed, there has been relatively little discussion of actual diet in terms of how crops were prepared, what sorts of dishes or drinks were served, how particular cuisines evolved through time, or how foodways varied regionally. Robert Braidwood (1953), inspired by a query from Jonathan Sauer, started a conversation about the possibility that widespread fermentation of grains to produce beer in the ancient Near East preceded the use of cereals as staple, nonalcoholic foods. Although this beer-before-bread (or more realistically, beer-before-gruel) scenario is an appealing way to approach plant domestication in introductory lecture courses, it is not taken seriously, at least not in print, by many archaeologists due to lack of evidence. Better detection methods might provide the evidence, however. Katz and Voigt (1986), for example, make a case for the nutritional as well as psychological advantages of low-alcohol fermented grain products, and recommend that Epipaleolithic or very early Neolithic human skeletons be examined for the effects of build-ups of urates (serum uric acids) that could indicate beer consumption. These researchers admitted in 1986 that “direct evidence that beer consumption led to domestication of barley and wheat is lacking” (Katz and Voigt, 1986, p. 33). Even more recently Hayden et al. (2013, p. 142) concluded that “there is still no smoking brew pot” to clinch the case for Epipaleolithic beer brewing in the Near East having fueled the demand for cereals and led to their domestication. However, enough evidence is presented for the existence of adequate fermentation technology and “sufficient degree of social complexity” (Hayden et al., 2013, p. 131) to keep alive for many years to come the appealing hypothesis that beer making played a key role in the domestication process.

Lyons and D’Andrea (2003) made a case for the cultivation and processing of indigenous tef [*Eragrostis tef* (Zuccagni) Trotter] in highland Ethiopia prior to the introduction of wheat, barley, or other Southwest Asian crops. Tef was recovered in Ethiopia at sites dating to the 21st century BP, as were Near Eastern domesticates, making it difficult to determine which came first: African grains or Southwest Asian cereals. Preservation factors would work against archaeological recovery and identification of the tiny-seeded tef, which is much more likely than wheat or barley to be burned to ash if exposed to direct heat, yet less likely to become charred (and thereby preserved) due to the methods used to cook it. The antiquity of ceramic griddles equals that of both types of grains: ca. 2500 BP (Lyons and D’Andrea, 2003), with griddles still used today to cook the spongy Ethiopian bread called *injera* that is made from tef. Tannur-style ovens used elsewhere for baking loaves of bread are absent in both ancient and recent, traditional Ethiopian culture. Combining insights gained from ethnoarchaeological observations and analogies, Lyons and D’Andrea (2003, p. 526) argued that “in highland Ethiopia, griddle-baking emerged with indigenous subsistence practices based on domesticated or wild tef, finger millet, and other starchy foods lacking gluten but was capable of adopting Near Eastern domesticates into a well-integrated socio-technical system of cereal production.”

Fuller and Rowlands (2011) contributed a broad and insightful, food-oriented perspective on regional preferences in East Asia for grains with sticky or waxy starch properties. They synthesized the archaeological evidence for grain grinding and baking (grindstones and tandir-style ovens) across West Asia, in contrast with the evidence for boiling as a preferred cooking method among societies in East Asia. This research not only examines selection for specific phenotypic traits during early stages of rice and millet domestication in China, but spans millennia of more recent developments including the eastward spread of barley from Southwest Asia and even the post-Columbian adoption of New World crops by Chinese farmers. In all cases, the traditional East Asian taste for sticky or waxy cereals was satisfied by breeding varieties that fit into the local cuisine. For example, when high-gluten forms of wheat were adopted in China approximately 4500 yr ago, wheat was not used to bake bread, but was rather transformed into noodles and dumplings, consistent with long-standing culinary methods of boiling and steaming. The same appropriation process took place with Job's tear grains (*Coix lacryma-jobi* L.) from South Asia, and sorghum [*Sorghum bicolor* (L.) Moench], an African domesticate. New World maize and amaranth (*Amaranthus hypochondriacus* L.) were made suitable for Japanese cuisine after European colonial introduction of these crops by quickly breeding “sticky” varieties. Asian “culinary worlds” (Fuller and Rowlands, 2011) seem to have developed in the deep past, echoing the cultural reality that we are all aware of: food is culturally ingrained. Hence, cuisines provide people with social identities, nationalism, spirituality, and a package of cognitive tools for coping with their environment. Without a doubt, culturally constructed food preferences played a role in the origins and spread of agriculture.

CONCLUSION

Since the era of Charles Darwin, researchers across scientific fields have turned to evolutionary models to better understand biological systems. Evolutionary processes underpin many of the issues discussed in this paper, including Vavilov's centers of origin, the number of domestication episodes per crop, and the relative pace of the Neolithic Revolution, used by archaeologists to understand the origins of agriculture. Thus, it is imperative that archaeobotanists participate in universal debates on evolutionary theory. Although older models are inevitably rooted in past assumptions and perspectives, researchers have at times dogmatically adhered to the specifics of these legacy models. However, archaeological evidence indicates that every case of transition from hunter-gatherers to agricultural economies was unique. Consequently, archaeologists have moved away from these early models to frame their research, in ways we detailed throughout this article. New models, data from across the biological sciences, and sometimes-discordant researchers have contributed to our understanding of the distinct nature of each case. Identifying the specific nature of when, where, and how domestication occurred will undoubtedly elucidate how agriculture transformed the trajectory of human societies.

Going forward, we believe that it is paramount for researchers from all scientific backgrounds to continue to challenge models on the origins of agriculture, particularly in light of new data and methodologies. The amassing archaeological data on the origins of agriculture has shed light on the specifics of how this evolutionary process occurred throughout the prehistoric

world. Methodological and technological advances will, without a doubt, continue to be important to identifying the particularities of the origins of agriculture. Determining the timing and pace of domestication both hinge on secure control over archaeological context and chronology, and a nuanced understanding of morphological indicators is critical for evaluating the domesticatory status of archaeobotanical remains.

A holistic understanding of domestication will involve investigating agricultural technologies and social norms governing the distribution of food. We look forward to the advancement of theories on foodways and the role of cuisine preferences throughout the transition to agriculture. A number of researchers have tried to understand how differential harvesting, processing, and storage technologies shaped agricultural systems and drove domestication (e.g., Gremillion, 2004; Fuller et al., 2010b). In regions where tubers, tree fruits, or other noncereals were the most important domesticates, the study of anthropogenic soils, field systems, and ground stone technology has sometimes formed the backbone of domestication studies (e.g., Denham, 2007). Where extensive modification of soils, hydrography, and plant and animal communities can be demonstrated, researchers speak of domesticated landscapes, rather than specific domesticated plants (Terrell et al., 2003; Erickson, 2008).

Archaeologists continue to take responsibility for excavating, analyzing, and interpreting primary evidence for domestication of plants. We ask and attempt to answer questions relevant to colleagues in our own and other academic fields, as well as to the billions of humans who depend upon crops for sustenance. Many of the issues we have discussed obviously overlap and intersect across multiple planes. Archaeologists have benefited enormously from breakthroughs in the biological and geological sciences, and numerous collaborative research efforts attest to successful academic synergism. We look forward to ongoing, multidisciplinary conversations on one of the most significant transitions in the history of our species.

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