Introduction: The Domestication of Plants and Animals: Ten Unanswered Questions

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Some 15,000 to 10,000 years ago, humans started seeding and harvesting plants and maintaining animals in order to augment the food they obtained from wild-growing plants and hunting. These seemingly simple activities set in motion a long-term process that has led to the dominance of agriculture as we know it today. With the exception of a few remaining hunter–gatherer groups, agriculture has now become the most important source of food for most people. Agriculture is also a major source of feed for animals and of fiber.

This transition from hunting–gathering to agriculture was without a doubt one of the most significant eras in the evolution of humans. It allowed food production on a more intensive and efficient scale than ever before, eventually leading to population increases, labor specialization (and especially a nonagricultural sector), the formation of villages, cities, and states, and the rise of more hierarchical societies and states (MacNeish 1991, Barker 2006).

The late Professor J. R. Harlan (1917–1998) understood that the complexity of the biological, societal, and environmental changes involved in the transition to agriculture, as well as their antiquity of up to 10,000 years, necessitated a multidisciplinary approach if one is to understand the factors and processes that have led to the "neolithic revolution." Anthropologists, archaeologists, climatologists, ethnobiologists, geneticists, geographers, linguists, physiologists, and other practitioners all contribute to the field of crop evolution studies.

J. R. Harlan also expressed concerns that the very development and spread of improved crop varieties were leading to losses in crop biodiversity, well before concerns about biodiversity became common knowledge. He made clear how the knowledge of evolutionary processes in crops facilitated the conservation of biodiversity and its use in the development of improved crop varieties.

The vision of Professor Harlan was the inspiration for the first Harlan Symposium, which took place in 1997 in Aleppo, Syria, at the International Center for Agricultural Research in the Dry Areas (ICARDA). That symposium was remarkable because it brought together plant scientists and archaeologists

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(Damania *et al*. 1998). By the way, 1997 is also the year in which the best-selling book *Guns, Germs, and Steel* by J. Diamond, a contributor to this volume, was published.

Since the first Harlan Symposium more than 10 years ago, the communications between archaeologists and both plant and animal biologists have continued, as reflected, for example, in the contributions of Zeder *et al*. (2006a,b). Compared with the first Harlan Symposium, substantial progress has been made in our understanding of crop domestication and evolution, justifying the organization of a second Harlan Symposium. As in other areas of science, such progress has provided answers to existing questions but has also raised new questions.

Among the questions are the following:

1. Why did agriculture originate where it did?

With notable exceptions such as the eastern part of North America (Smith 1995) and Central Asia (e.g., Harris *et al*. 2002), most domestication centers are located in subtropical or tropical regions within 30° latitude of the equator. Diamond (1997) pointed out the rich distribution of wild relatives of crops and farm animals in southwest Asia (the "Fertile Crescent") and attributed the headstart western European societies had obtained to this distribution. Gepts (2008) has shown that centers of domestication are located disproportionately frequently in biodiversity hotspots (as defined by Myers *et al*. 2000).

Conversely, one can ask the question why other regions with similar geographic and eco-climatic characteristics did not become centers of domestication. For example, although the California Floristic Province supported a rich diversity of Native American cultures, these cultures were only known to manipulate vegetation without actually turning to full-fledged agriculture.

2. What are some of the local ecological or palaeo-ecological conditions, including climate change and human population growth, that would have favored or impeded the transition from hunting–gathering to agriculture?

In addition to the richness in potential crop or farm animal ancestors, other environmental factors could impinge on the agricultural transition. Peake and Fleure (1927) and Harlan (1992, 1995) emphasized the role of biomes with an extended dry season in the domestication of many crops. Storage of harvests could provide a supplement of much-needed food during periods of scarcity, especially towards the end of the dry season and the start of the subsequent rainy season.

However, these general trends do not necessarily speak to the importance of local environmental conditions and their variability in space and time. Flannery (1973) sought to define a role for marginal areas with suboptimal resources (in contrast with nuclear areas) in the origin of agriculture (see also Wright 1992). Suboptimality could result from local population increases as well as a reduction in resources induced by environmental changes (or both).

An additional factor would be short-term climatic events such as the Younger Dryas (11,000 years ago), whose colder and drier conditions may have impelled local, more numerous hunter–gatherers in Southwest Asia and elsewhere to experiment with agriculture (Fuller 2006).

3. Are there specific characteristics in plants and animals that predispose them to domestication?

There are some 400,000 plant species (http://www.bgci.org/ourwork/1521, consulted 10 July 2010), but fewer than 500 have been at least partly domesticated (although a larger number is actually used by humans). Are these 500 domesticated species the result of experimentation by early farmers based on some favorable characteristics that stimulated their cultivation?

For example, could only plants that were relatively devoid of toxic compounds have been domesticated? The existence of an extended repertoire of detoxification methods for plant foods (even from wild plants; Johns and Kubo 1988) and numerous toxic crop plants (e.g., cassava, various legumes) suggests that this is not the case.

However, other biological factors may be in play. In many crop species genes for domestication are partly linked. This linkage may have assisted in maintaining the domestication syndrome during the first phase of domestication, marked by cross-pollination (Le Thierry D'Ennequin *et al*. 1999, Gepts 2004).

Or, alternatively, were these species domesticated as a historical contingency, i.e., were they in the "right" place at the "right" time? In the second hypothesis, factors other than ones intrinsic to the domesticate, such as human cultural advancement or the environment, could have played a role. Several of our major staple crops are annual and self-pollinating species. This situation may result from domestication in regions with a marked dry season in which such species may be abundant. In line with this potential historic contingency, some have argued that perennial plants could also be domesticated and become major staples (Glover *et al*. 2010).

Overall, this question remains one of the more tantalizing ones in the field of crop evolution studies. Further experiments are needed to resolve it, especially as the outcome may have important implications for the domestication of new crops.

4. What is the pattern of domestication for crops and animals?

The number and location of domestications of a crop are essential elements to understand not only the origins of agriculture in a particular region of the world, but also the overall distribution of genetic diversity in that crop. For example, a crop may have a single or multiple domestications. The latter may lead to divergent domestication gene pools (e.g., common bean: Gepts *et al*. 1986, Koenig and Gepts 1989, Kwak and Gepts 2009; rice: Sweeney and McCouch 2007). Traditionally, the origin of domestication of a crop has been determined based on the geographic distribution of the wild ancestor, complemented when possible with archaeological remains, which have become much more abundant since the introduction of the flotation technique (Smith 1995). More recently, the availability of molecular markers (Gepts 1993, Gross and Olsen 2010) has provided an additional tool to identify a more specific area of domestication within the general distribution area of the wild ancestor (e.g., common bean: Gepts 1988, Kwak *et al*. 2009; lima bean (Andean): Gutiérrez Salgado *et al*. 1995; maize: Matsuoka *et al*. 2002; potato: Spooner *et al*. 2005).

There are two caveats, however, in the search for the wild ancestor. First, the analyses are based on the current distribution of the wild ancestor, which may or may not be the same as during the initial phase of domestication. Second, the similarities identified by molecular markers may be due not only to ancestor–descendant relationships, but also to gene flow from the domesticated to the wild gene pool. This type of gene flow is more frequent than generally assumed (Ellstrand *et al*. 1999). Because agriculture represents a production system in which several crops (and farm animals) are assembled, joint information about the origin of the crop and animal components is necessary to fully understand the development of agriculture.

5. What is the timeline of the origins of agriculture? How quickly did agriculture become a major alternative to hunting–gathering?

Domestications in different centers of origin took place roughly some 10,000 years ago. The transition from hunting and gathering to agriculture was clearly not an event, but rather a more-or-less long process. Because the overall inheritance of the domestication syndrome is relatively simple (Gepts 2004), geneticists have proposed that the domestication process could have take place relatively quickly, i.e., in a time span of several decades to a few centuries (e.g., Hillman and Davies 1999). In contrast, archaeologists and particularly archaeobotanists have proposed a much more gradual transition involving millennia (e.g., Tanno and Willcox 2006). Important factors to address this question would be the actual selection pressure exerted by farmers and the inheritance of the traits involved. This transition included an important phase, predomestication cultivation, a necessary condition for domestication. Determining the actual pace of domestication is an important element in our understanding of the development of agriculture.

6. How did agricultural ecosystems develop?

Most of the focus of genetic studies involves individual crop or animal species. Yet, agriculture is not just the sum of its individual component crops or farm animals. Agriculture is a system consisting of agronomically and nutritionally complementary systems. For example, most centers of domestication include a combination of protein (legume) and starch (cereal or root) staple crops, which provides more balanced nutrition.

Compared with hunting and gathering, agriculture was a more effective way – on a per unit land base – of obtaining food. All other things being equal, one would then expect agricultural societies to take over the world, as indeed they did.

As agriculture expanded, its ecological footprint became larger as well. In turn, this situation has increased the need for a more sustainable type of agriculture that maintains its resource basis.

As agriculture developed, humans became increasingly reliant on it for their food procurement. In turn, agriculture could potentially start exerting selection pressures that affect human phenotypes, such as resistance to malaria, starch consumption, and lactose intolerance (Hancock *et al*. 2010, Holden and Mace 2010). Thus, the agricultural context provides further evidence of continued evolution of the human species (Templeton 2010). Further research is needed, however, to better understand the involvement of humans and the spread of agriculture.

7. How did agricultural ecosystems spread from the centers of origin?

Two, nonmutually exclusive, modes of dispersal have been proposed to account for the spread of agriculture (Ammerman and Cavalli-Sforza 1984, Pinhasi *et al*. 2005). Under the first mode, agriculture was dispersed culturally through adoption by nonmigrating populations of the technology (including the crops). The second mode posits population migration from the center of domestication as the major driver. Although the phenomenon is the best studied in Europe, where the second mode appears to have operated at least for part of the continent (Pinhasi *et al*. 2005), information is also available for the Pacific migrations from east Asia (e.g., McCoy and Graves 2010) but needs to be developed further for other centers of domestication.

8. How can biodiversity be maintained or enhanced in agroecosystems?

Biodiversity is the sum total of biological diversity occurring at various levels of organization, including the infraspecific level, species diversity, the variability of habitats, and the overall variation in the landscape. Replacing native biomes by agricultural vegetation is one of the major factors in the loss of overall biodiversity. When faced with increased demand for agricultural products (whether for food, feed, fiber, or fuel), several responses have been suggested to maintain agrobiodiversity, including creation of biosphere reserves, modifications in agricultural production systems to make them more benign (e.g., shade-grown coffee, hedgerows), and maximizing agricultural production to allow set-aside programs for marginal lands.

Furthermore, agroecosystems can be adapted in such a way that production is increased by applying ecological principles and maximizing the use of agrobiodiversity (Scherr and McNeely 2008, Brussaard *et al*. 2010, Jackson *et al*. 2010). Thus, information about the evolution of crop plants has an important applied component in the development of more sustainable cropping systems. This information will take on added significance in the light of global climate change.

9. How does California benefit from agricultural biodiversity?

The benefits of agrobiodiversity to California are innumerable. As mentioned before, California is not a center of agricultural origins. Yet this state boasts a very diverse plant and animal agricultural industry. It illustrates the benefits in the introduction of germplasm. Examples are the world-famous wine industry based on judicious choice of varietals adapted to the diverse ecological niches offered by the topography of the state (and the attendant yeast germplasm). Likewise, the dairy industry, based on both animal and forage germplasm, especially alfalfa, has become a major part of the agricultural sector. In addition to alfalfa, many other California crops rely on insect pollinators, whose activity is increasingly threatened.

10. What can crop evolution studies tell us about the potential for future domestications?

Finally, the information gathered in crop evolution studies can help us consider the following situations. How do we expand the repertoire of domesticated species? The current repertoire is limited compared with the total number of plant (and animal) species. It is clear, however, that as human needs increase, there are new opportunities for domestication. These include tree domestication in agroforestry and novel crops for biofuel production. It may also involve re-domestication of existing crops for novel purposes.

The presentations of the second edition of the Harlan Symposium, held September 14–18, 2008, on the campus of the University of California, Davis, that most directly addressed the above questions have been assembled into this volume. The members of the editorial committee would like to thank all the authors for their contributions and patience during the editorial process. We look forward to the next edition of the Harlan Symposia, which will no doubt bring further exciting advances in the field of the origins of agriculture and crop and animal domestications.

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