Current and Future Applications of Genetic, Archaeological, and Ethnobotanical Data to Uncovering Avocado Domestication

Kevin W. Wann[1*] and Heather B. Thakar[1]

[1]Department of Anthropology, Texas A&M University, College Station, Texas.

[*]kwann@tamu.edu

Abstract The domestication of fruit trees is a topic of increasing significance in anthropological research. The avocado is a perennial fruit domesticated in Central America with a complex history of management and dispersal since the arrival of humans in the New World. Archaeological data illustrates the avocado's domestication from wild to cultivar forms throughout the Holocene, while genetic and ethnobotanical evidence provide insights into ancient avocado cultivation patterns. It is only through the combined application of all three lines of evidence that we may fully understand the dynamic origins of this essential fruit.

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Introduction

The domestication of plants continues to be a subject of anthropological interest, as agriculture facilitated the development of civilizations and the maintenance of modern society. Scholars often rely on the archaeological and genomic records of annual grains (e.g., maize [*Zea mays*], rice [*Oryza sativa*], and wheat [*Triticum aestivum*]) to understand the reciprocal process of plant domestication (Allaby et al. 2022; Fuller et al. 2023), but these herbaceous field crops only make up a fraction of the total cultivated taxa in most ancient communities. Perennial fruits (e.g., apples [*Malus domestica*], grapes [*Vitis vinifera*], and citruses [*Citrus* spp.]) are another crucial component within ancient subsistence regimes, and in the Americas their domestication process may have begun before those of herbaceous plants (Kennett et al. 2023). Domestication traits in grain crops usually confer an increase in the number of seeds per fruit and the retainment of seeds prior to harvesting. Perennial trees require more intense and specific management practices to enable the production of valuable fruits, and many domestication-related traits differ from that of annuals, such as an increase in fruit flesh size and an alteration of reproduction to better suit human schedules (Miller and Gross 2011). As such, our knowledge of the origins of tree crops is lacking (Gaut et al. 2015).

Among the perennial fruits domesticated in the Americas, the avocado (*Persea americana*) is unequivocally the most essential to sustaining ancient and modern diets. Genomic studies focused on improving breeding efforts consistently segregate avocado cultivars into three ecotypes: Mexican (var. *drymifolia*), Guatemalan (var. *guatemalensis*), and Lowland (var. *americana*), and their genetic differentiation suggests they each follow independent domestication pathways (Chanderbali et al. 2013). Recent archaeological, genetic, and ethnobotanical research has greatly contributed to our understanding of the complex origins of domesticated avocados.

Avocado Domestication Documented in the Archaeological Record

New radiocarbon dates of 11.1 ka and 10.5 ka taken from avocado pits from the El Gigante Rockshelter, Honduras, and Huaca Prieta, Peru, respectively, show that Central and South American foragers exploited wild avocados as early as the Paleoindian Period (13-10 ka; Dillehay et al. 2017; Kennett et al. 2023). The initiation of the avocado's domestication process is signaled by a gradual increase in pit size (a proxy for fruit flesh content) throughout the Archaic (10-4 ka) and Formative and Classic (4-1 ka) periods. At Coxcatlán Cave, Puebla, Smith (1966) found that pit size increases slightly from the Ajuereado to the Abejas phases (10-5 ka) followed by a sharp increase during Santa María, Palo Blanco, and Venta Salada phases (3-0.5 ka), potentially reflecting the adoption of foreign cultivars. Unfortunately, early sample sizes are small, and the site's stratigraphic integrity has been called into question (Smith 2005). Fuller (2018) examined Coxcatlán pits solely within Formative and Classic contexts and still recorded a gradual increase. The only other reported morphometric analysis on avocado pit size is in a preliminary assessment of the El Gigante macrobotanical assemblage, in which Scheffler (2008) measured a gradual increase across El Gigante's entire occupation without any punctuated increase during the Formative period.

Recent excavations in Central and South America have unearthed a greater quantity of avocado remains, highlighting the domesticated species' relative importance in Late Holocene diets and enabling future morphometric studies. At Cuautémoc, Chiapas, Rosenswig et al. (2015) took 43 flotation samples spanning the site's Early (3.9-3 ka) and Middle Formative (3-2.4 ka) occupation. While Early Formative contexts contained a high abundance of avocado pit fragments (n = 73), they were virtually absent after 3 ka, suggesting that the intensification of maize farming replaced existing arboricultural practices. Despite the dominance of field crops in Late Holocene diets, avocados were still commonly cultivated as a secondary, but popular, food source. Dine et al. (2019) surveyed 22 Mayan *rejolladas*—sinkholes where households grew secondary crops to supplement maize agriculture—at the Late to Terminal Classic (1.4-1 ka) site of Xuenkal, Yucatán. *Persea americana* was present in six *rejolladas*, ranking among the most ubiquitous plant taxa recovered. Similarly, in South America, Masur et al. (2018) recorded a moderate abundance of avocado fragments at the Virú Valley, Peru. However, maize, beans, and squash still dominated this assemblage, suggesting that *P. americana* was likely a secondary food source and cultivated on the periphery of agricultural fields. Taken together, the available archaeological data illustrate that ancient communities began consuming wild avocados during the Paleoindian Period, then gradually selected for local higher quality fruits throughout the Archaic Period. Following the adoption of staple herbaceous agriculture in the Formative and Classic Periods, domesticated avocados were dispersed across cultural landscapes, still contributing as a substantial portion of ancient diets.

Insights Gained from Emerging Genetic Research

Recent genetic studies focused on improving commercial breeding efforts continue to support the claim of a tripartite domestication of avocados, while offering new insights. Talavera et al. (2019) characterized a set of DNA markers that reliably identify the ecotype origin(s) of novel cultivars. They also demonstrate that the lack of sterility barriers between growth environments of each genotype allowed for ancient hybridization events, rendering it difficult to distinguish between hybrid and non-hybrid cultivars. Ruiz-Chután et al. (2023) show that local wild avocados of Guatemala possess greater genetic diversity than previously assumed. The authors attribute this enriched local variation to an ancient legacy of human protection of ancestral populations that preserved regional diversity within the wild Guatemalan population, while selecting for high-quality cultivars within forest gardens.

Lastly, Solares et al. (2023) identified a disproportionate number of genes under selection associated with fruit ripening and development in Guatemalan (var. *guatemalensis*) cultivars. Their analysis points to past human selection for larger fruits in the domestication and improvement of this ecotype, a process supported by archaeological data. These newer genomic studies provide evidence that ancient communities independently managed and cultivated regional avocado varieties, leading to the emergence of the three contemporaneous domesticate ecotypes. They also indicate that early horticultural groups selected for larger fruits and may have even experimented with tree hybridization to produce economically beneficial fruits prior to European Contact.

Traditional Avocado Usage Revealed through Ethnobotany

The vast majority of Central American ethnobotanical studies identify the avocado as an important food with high nutritional value. More recent studies have further documented avocado fruits as being a common ingredient in the daily consumption of tostadas and carnitas in Western and Southeastern Mexico, respectively (Figure 1; Salazar et al. 2016; Zizumbo-Villarreal et al. 2016). It is intriguing that avocados are now mainly included as a topping to maize-based dishes, rather than being consumed on their own, as they presumably had been for some six thousand years prior to the dispersal of maize agriculture (Kennett et al. 2023). The role of avocado fruits likely switched during the Mid to Late Holocene from a staple fruit to an ingredient secondary to surplus foods, supported by its relative abundance to maize in Late Holocene archaeobotanical assemblages. In this scenario, people may have selected for traits conferring easier fruit access and peeling, rather than flesh size.

Ethnobotanists also recently documented Indigenous tree management techniques that improve avocado tree quality. Basurto et al. (2023) note that traditional communities in the highlands of Central Mexico apply limewash to avocado trunks and prune unproductive branches. The former protects the tree from pests that bore through bark and kill branches, which worsens tree productivity (Peña et al. 2013), while the latter has been shown to improve fruit yield by 9% when performed early on in flower development (Roe and Morudu 2000). The adoption of intensive tree management strategies such as these may have played an important role in growing higher quality fruits throughout Prehistory, alongside any genetic changes associated with the species' domestication. While the archaeological record suggests humans were selectively planting the seeds of more beneficial fruit trees, it is just as likely that the experimentation of cultivation strategies contributed to the apparent increase in fruit flesh content over time, and communities dispersed these behaviors across cultural boundaries. With further ethnohistoric research, we may better understand the timing and cultural dissemination of avocado tree management techniques and their contribution to the avocado's domestication process.

Figure 1 Traditional culinary dishes that include avocados, as documented in recent ethnobotanical studies (Salazar et al. 2016; Zizumbo-Villarreal et al. 2016).

Future Directions

While emerging research has broadened our understanding of avocado domestication, the current body of research still lacks any integration of genomic and ethnobotanical data (e.g., Gros-Balthazard et al. 2020), leaving a multitude of unanswered questions: Why were avocados valued in the first place? To what extent were their fruits and associated horticultural knowledge disseminated across Central America? How did the crop change alongside the introductions of staple food production, intensive agriculture, and Spanish Conquest? Working alongside traditional avocado gardeners, regional cultivar genomes can be compared to those of wild and commercial trees for a greater understanding of cultivar origin and the genetic basis for domestication traits. Most importantly, scholars should examine the genomes of archaeological *P. americana* remains recovered from ancient contexts, which would provide clues for the traits under selection at different time periods and identify signals of seed transport across cultural boundaries (e.g., Kistler et al. 2020). Only through the collaborative efforts of archaeologists, geneticists, and ethnobotanists may we achieve a complete understanding of avocado domestication and the cultivation of perennial New World fruits.

Declarations

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