Plant Domestication: Wild Date Palms Illuminate a Crop's Sticky Origins

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In a new study, previously unknown populations of wild date palm have been identified in remote areas of Oman. Genomic analyses indicate date palm domestication occurred in the eastern portion of the Arabian Peninsula and reveal substantial subsequent gene flow with African palm populations.

The transformation of wild plants into bountiful, reliable crops profoundly altered the trajectory of modern humans. Millennia before written history and the invention of cities, the development of early agriculture permitted human populations to abandon nomadic lifestyles and establish permanent settlements. Understanding how, where, and why past peoples domesticated plant species can shed light on the histories of civilizations and potentially improve modern crop varieties. For instance, wild relatives often harbor natural sources of resistance to emerging pathogens. Following a series of pioneering expeditions in the early twentieth century, Nikolai Vavilov [1] formulated a hypothesis for discrete prehistoric centers of domestication, where wild progenitors evolved into crops over hundreds to thousands of years of human-mediated selection. Many crops that emerged from these centers were spread through trade and are now cultivated worldwide, serving as dietary staples for millions to billions of people.

Despite decades of research, the identities of the wild progenitors from which several important crops were domesticated remain uncertain or unknown, potentially because wild descendants of those ancestors no longer persist. Thanks to exciting new findings reported by Gros-Balthazard and colleagues [2], published in this issue of *Current Biology*, the date palm (*Phoenix dactylifera*) is no longer among this group of orphan domesticates. The authors confirm wild date palm populations still flourish in remote areas of Oman, and in leveraging their discovery to unravel the complex history of this foundational crop species, their genetic analyses hint that further secrets of date palm's past remain to be discovered.

The date palm is arguably the most important domesticated plant in the hot, arid climates of North Africa and the Middle East. Besides being highly productive — in one year, a single tree may produce more than 100 kg of its eponymous, sugar- and nutrient-rich fruit [3] — the date palm is also the keystone species of the oasis agricultural system [4]. The trunks, which farmers scale to hand-pollinate flowers and to harvest fruit, can reach over 20 m in height. The fans of fronds of these lofty trees provide crucial shade for less hardy fruit trees, like fig and pomegranate, as well as annual cereals and pulses sown on the ground. Without the date palm, this agrosystem would not exist, and the inhospitable deserts could support far fewer inhabitants. The life-giving nature of the tree is venerated in many rituals and customs, including the Muslim tradition to consume dates at sunset during Ramadan.

For over a century, scholars contended that freely-growing date palms that dot the gullies and rocky outcrops of the Sahara Desert and the Arabian Peninsula are feral remnants or escapees descended from cultivars, rather than of truly wild origin [5,6]. Distinguishing individuals with uniquely wild heritage can be particularly difficult for clonally propagated, perennial fruit trees like date palm because sexual reproduction often yields offspring with wild-like traits, such as small and unpalatable fruits [7]. Therefore, to test whether uncultivated date palms previously found in the mountainous southeastern Arabian Peninsula do indeed represent relict populations of the wild progenitor (Figure 1A) [8,9], the authors first conducted a comparative analysis of seed morphology. Altered seed shape and size are important signals of domestication in many crops because human selection for larger fruits often indirectly impacts seed morphology [7]. Notably, through comparative analysis of hundreds of seeds from the putatively wild Omani trees to a database of thousands of seeds of domesticated varieties and a sister species, *Phoenix sylvestris*, the researchers determined that the Omani palms bore rounded seeds more similar to those of the wild sister species than to the oblong seeds of domesticated varieties (Figure 1B). Archaeological seeds recovered from excavations in Kuwait and dated as ~7000 years old also possessed the ancestral rounded seed shape of the putative wild date palms and *P. sylvestris*. Thus, these deposits likely represent collections from wild trees or an incipient cultivated lineage from a time in prehistory when date palm cultivation was still emerging [4].

The authors then went on to demonstrate that although the putative wild Omani date palms show greater morphological affinity to *P. sylvestris*, these new populations do bear closer genetic affinity to cultivated varieties. For annual crops, it is commonly observed that sequence diversity is greater among individuals of the wild relatives than among cultivated varieties due to genetic bottlenecks that occur during domestication. However, perennial fruit trees rarely show such a clear genetic signal of domestication due to how their long maturation times and frequent vegetative propagation interact with selection by humans [10]. Because date palms grown from a seed take at least four years to yield fruit, most farmers propagate desirable trees by cutting and planting basal suckers. This form of genetic cloning means that favored cultivars may be separated from wild progenitors by only a few reproductive generations, even though hundreds or thousands of years have passed. Nonetheless, both with a limited number of genetic markers typed on many individuals and through high quality genome re-sequencing of a smaller group, the authors observed higher levels of genetic diversity in their wild collections than Middle Eastern domesticated varieties. Moreover, phylogenetic analyses revealed Middle Eastern varieties share a recent common ancestor nested within the diversity of the Omani trees, again consistent with these uncultivated individuals representing a relict population of wild date palms that gave rise to domesticated lineages.

Although these genetic patterns point to a date palm domestication center in the Middle East, the authors, like several others [11–13], also find that African date palm varieties are highly genetically diverse, puzzlingly contrary to the straightforward narrative suggested by the archaeological record. Chalcolithic (Copper Age) people near the Persian Gulf consumed dates by 5000 BCE, and cuneiform tablets and artwork indicate that a full-fledged agricultural system with domesticated date palms was established by 2500 BCE in Mesopotamia [7]. The African chronology is less well established, but there is little evidence to suggest that date palms were cultivated in North Africa before 1500 BCE [7]. If the scenario where date palms were simply domesticated in the eastern Arabian Peninsula and then later transported to Africa were true, one would expect African date palms to harbor less genetic diversity than Middle Eastern date palms, not more.

Gros-Balthazard *et al.* resolve the dissonance between the archaeological and genetic patterns by applying a relaxed phylogenetic analysis that permits evaluation of more complex evolutionary histories, including ones that allow for hybridization with closely related, but unsampled, populations. Based on this analysis, the authors propose that the diversity of African cultivated date palms is the result of

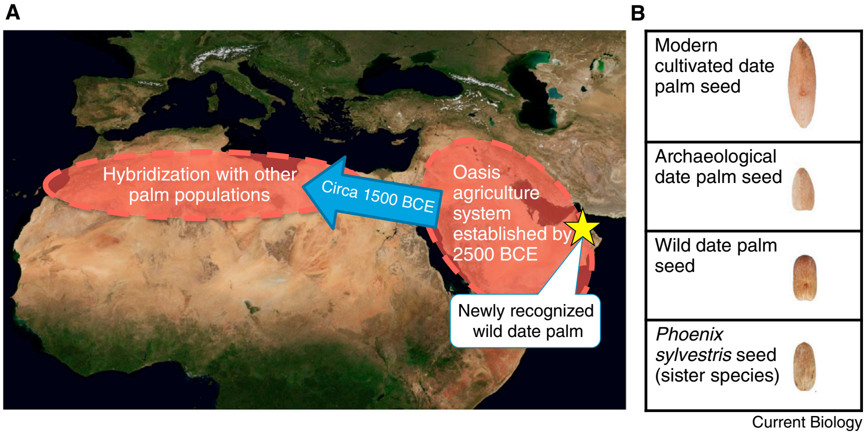

Figure 1. Geographic context of date palm domestication and variability in seed shape.
(A) Gros-Balthazard *et al.* argue wild date palms in Oman likely represent relict populations of the progenitor of the domesticated tree. Subsequent gene flow with unidentified populations in Africa replaced one third of the genome and may have led to local adaption. Image of Earth, NASA Blue Marble Project. (B) Seeds of the wild date palms are more similar in shape to seeds of the sister species and archaeological specimens dating to 5000 BCE than they are to modern cultivars. Seed images kindly provided by Muriel Gros-Balthazard.

interbreeding between domesticated date palms brought from the Middle East with an as-yet-unrecognized population of wild African palms (Figure 1A). As much as one-third of the genome of African cultivars may derive from local wild populations, and some of this introduced variation may have facilitated local adaptation to North Africa [11]. This explanation reinforces the increasingly recognized theme that hybridization with genetically distinct, local populations is a major influence on regional gene pools. Such contributions occurred not only as crops spread from domestication centers, as documented in maize adaptation to the Mexican highlands [14] and for the origins of rice [15], but also as modern humans themselves spread across the globe and interbred with other hominins, including the Neanderthals and Denisovans [16].

This study demonstrates the power of cutting-edge interdisciplinary collaborations between geneticists, botanists, and archaeologists to unearth domestication histories of non-model species. From an archaeological perspective, several promising avenues lie ahead for the date palm, including ancient DNA research. DNA recovered from archaeological seeds could further refine the domestication history of date palm, potentially enabling researchers to characterize genes under selection and track changes in population structure across millennia [17]. Although hot climates tend to degrade nucleic acids in archaeological specimens, date palm seeds appear to have an unprecedented ability to protect genetic material, as demonstrated by the successful germination of a 2000-year-old archaeological specimen [18]. By highlighting an as-yet-undiscovered source of diversity in cultivated date palm, the study's findings should also encourage future exploration to identify relict populations in Africa. Such populations may harbor novel genetic diversity that could be sourced to acquire additional agronomically useful traits. In the face of climate change and desertification [19], the arid-adapted date palm may provide a unique agricultural solution for future generations [20], and thus further investigation into the complexities of its domestication history may be particularly helpful in management and diversification of its gene pool.

REFERENCES

1. Vavilov, N.I. (1992). Origin and Geography of Cultivated Plants (English translation) (New York: Cambridge University Press).

2. Gros-Balthazard, M., Newton, C., Ivorra, S., Paradis, L., Vigouroux, Y., Carter, R., Tengberg, M., Battesti, V., Santoni, S., Falquet, L., *et al.* (2017). The discovery of wild date palms in Oman reveals a complex domestication history involving centers in the Middle East and Africa. Curr. Biol. *27*, 2211–2218.

3. Chao, C.T., and Krueger, R.R. (2007). The date palm (*Phoenix dactylifera* L.): Overview of biology, uses, and cultivation. HortScience *42*, 1077–1082.

4. Tengberg, M. (2012). Beginnings and early history of date palm garden cultivation in the Middle East. J. Arid. Environ. *86*, 139–147.

5. Fischer, T. (1881). Die Dattelpalme: ihre geographische Verbreitung und culturhistorische Bedeutung (Gotha: Justus Perthes).

6. Zohary, D., and Spiegel-Roy, P. (1975). Beginnings of fruit growing in the old world. Science *187*, 319.

7. Zohary, D., Hopf, M., and Weiss, E. (2012). Domestication of plants in the Old World: the origin and spread of domesticated plants in Southwest Asia, Europe, and the Mediterranean Basin (Oxford: Oxford University Press).

8. Gros-Balthazard, M., Newton, C., Ivorra, S., Pierre, M.-H., Pintaud, J.-C., and Terral, J.-F. (2016). The domestication syndrome in *Phoenix dactylifera* seeds: toward the identification of wild date palm populations. PLoS One *11*, e0152394.

9. Terral, J.-F., Newton, C., Ivorra, S., Gros-Balthazard, M., Tito de Morais, C., Picq, S., Tengberg, M., and Pintaud, J.-C. (2012). Insights into the historical biogeography of the date palm (*Phoenix dactylifera* L.) using geometric morphometry of modern and ancient seeds. J. Biogeog. *39*, 929–941.

10. Miller, A.J., and Gross, B.L. (2011). From forest to field: perennial fruit crop domestication. Am. J. Bot. *98*, 1389–1414.

11. Hazzouri, K.M., Flowers, J.M., Visser, H.J., Khierallah, H.S.M., Rosas, U., Pham, G.M., Meyer, R.S., Johansen, C.K., Fresquez, Z.A., Masmoudi, K., *et al*. (2015). Whole genome re-sequencing of date palms yields insights into diversification of a fruit tree crop. Nat. Commun. *6*, 8824.

12. Mathew, L.S., Seidel, M.A., George, B., Matthew, S., Spannagl, M., Haberer, G., Torres, M.F., Al-Dous, E.K., Al-Azwani, E.K., Diboun, I., *et al*. (2015). A genome-wide survey of date palm cultivars supports two major subpopulations in *Phoenix dactylifera*. G3 *5*, 1429.

13. Zehdi-Azouzi, S., Cherif, E., Moussouni, S., Gros-Balthazard, M., Abbas Naqvi, S., Ludeña, B., Castillo, K., Chabrillange, N., Bouguedoura, N., Bennaceur, M., *et al*. (2015). Genetic structure of the date palm (*Phoenix dactylifera*) in the Old World reveals a strong differentiation between eastern and western populations. Ann. Bot. *116*, 101–112.

14. van Heerwaarden, J., Doebly, J., Briggs, W.H., Glaubitz, J.C., Goodman, M.M., Sanchez Gonzalez, J.J., and Ross-Ibarra, J. (2011). Genetic signals of origin, spread, and introgression in a large sample of maize landraces. Proc. Nat. Acad. Sci. USA *108*, 1088–1092.

15. Choi, J.Y., Platts, A.E., Fuller, D.Q., Hsing, Y.I., Wing, R.A., and Purugganan, R.A. (2017). The rice paradox: multiple origins but single domestication in Asian rice. Mol. Biol. Evol. *34*, 969–979.

16. Prufer, K., Racimon, F., Patterson, N., Jay, F., Sankaraman, F., Sawyer, S., Heinze, A., Renaud, G., Sudmant, P.H., de Filippo, C., *et al*. (2014). The complete genome sequence of a Neanderthal from the Altai Mountains. Nature *505*, 43–49.

17. Brown, T.A., Cappellini, E., Kistler, L., Lister, D.L., Oliveira, H.L., Wales, N., and Schlumbaum, A. (2015). Recent advances in ancient DNA research and their implications for archaeobotany. Veg. Hist. Archaeobot. *24*, 207–214.

18. Sallon, S., Solowey, E., Cohen, Y., Korchinsky, R., Egli, M., Woodhatch, I., Simchoni, O., and Kislev, M. (2008). Germination, genetics, and growth of an ancient date seed. Science *320*, 1464–1464.

19. Le Houérou, H.N. (1996). Climate change, drought and desertification. J. Arid. Environ. *34*, 133–185.

20. Shabani, F., Kumar, L., and Taylor, S. (2012). Climate change impacts on the future distribution of date palms: a modeling exercise using CLIMEX. PLoS One *7*, e48021.

Human Development: Faces in the Womb

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In the first day of life, infants respond specifically to the crude configuration of a human face. New research finds that this visual sensitivity is present even in the weeks before birth.

What sensory and cognitive equipment do newborn infants bring into their new world? It is one of the oldest and most enduring problems in the quest to understand the roots of human nature. Many researchers have assessed infants' abilities in the first days after birth, but it is hard to know just what effect even a few hours of visual input may have on the development of the brain. A study by Reid *et al.* [1], reported recently in *Current Biology*, breaks new ground by testing babies who can be assured to have no patterned visual experience, because they are still in the warm darkness of the womb.

It is well established that the fetus can show active sensory responses *in utero*, notably to auditory stimuli. In particular, the mother's speech sounds reach the womb and, as well as eliciting immediate responses, lead to long-term learning [2]. There is also some evidence of neural responses to light [3] both *in utero* and in prematurely born infants. But until now there has not been any evidence that the fetus can show visually stimulated behaviour.

Two aspects of visual behaviour are quite well established in the hours after birth: infants will turn their head and eyes to orient to a prominent stimulus [4]; and they will prefer to look at and follow a face-like pattern over a pattern which lacks key geometrical features of a face [5,6]. There has been extensive debate on exactly what these key features are, but a triangular, point-down configuration of high-contrast features (two eyes plus mouth) appears to be highly effective in driving newborns' attention. There can be a rather fruitless debate on whether this constitutes a face-specific bias, or reflects an intrinsic preference for some non-specific structural properties of the visual stimulus [7]. Either way, infants'

