A Brief History of the Origin of Domesticated Date Palms

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Abstract

The study of crop origins is of great interest both in the fields of evolutionary biology and applied crop research. The understanding of plant domestication involves multiple disciplines, including phylogeography, population genetics, anthropology and archaeology. In the past decade, they have prompted new discoveries on the evolutionary history of crops, including the date palm. The date palm (*Phoenix dactylifera* L.) is the iconic fruit crop of hot and arid regions of North Africa and West Asia. It is the keystone species of oasis agrosystems and produces sugar-rich and nutritious fruits, the dates. There are many different date cultivars each with distinctive fruit traits as well as many wild *Phoenix* species forming a complex of related species. Alas, a complete understanding of date palm origins remains to be elucidated. The history of domestication and diversification of the date palm is a puzzling question. The consequences of these processes, both genetic and morphological, are only beginning to be revealed. The genetic architecture of the domestication traits is unknown. In this chapter, we place recent advances in the fields of population genomics and archaeobotany in the context of historical views of date palm domestication. We present new models for the possible origins of this emblematic species and detail the many areas in date palm domestication research that are uncertain and would benefit from further work.

3.1 Introduction

As a prelude to modern civilisations, the advent of agriculture was a major advance in human history. The transition from hunter-gatherer societies to sedentary farming communities fostered innovations in plant cultivation and animal husbandry. From this Neolithic Revolution (Childe 1936) emerged domesticated crops, primarily cereals and pulses. While the earliest evidence of domestication (see Appendix 1 for definition) of these crops date back to around 10,000 BCE, perennial fruit crops, including major Mediterranean crops such as grapes, olives and dates, were domesticated later on, from the end of the Neolithic period through the Bronze Age (6000–3000 BCE; Janick 2005; Zohary and

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Spiegel-Roy 1975). Although perennials might be the future of our food production system (Crews et al. 2018), they have been less studied than annuals, and the understanding of their evolutionary history is lagging (Gaut et al. 2015; Miller and Gross 2011). The Food & Agricultural Organization (2013) is now pressing for more studies in perennials. Recently, owing to affordable, high-throughput sequencing technologies and much more advanced statistical approaches, long-lived crops began receiving research attention.

Studies of domestication are at the forefront of multiple disciplines. They not only provide insights into our past history but also keys to the adaptation of our farming system to the challenges associated with global change. An understanding of where, when and how plants were brought into cultivation are central to reconstructing the events that led to the development of modern civilisations and the expansion of human societies. Besides, evolutionary biologists recognise that crop domestication provides a framework to understand the mechanisms of evolution through the study of domestication traits and the genes that control them, the evolution of reproductive barriers and the demographic and hybridisation events that have promoted the expansion of crops (Ross-Ibarra et al. 2007; Zeder 2017). In fact, Darwin (1859) developed his theory of evolution by natural selection to a large extent through observations of the effects of artificial selection in domesticated plants and animals. Finally, efforts focusing on modelling the demographic histories of crops and identifying the genes controlling key traits are of interest to biotechnologists and breeders interested in crop improvement (Sattar et al. 2017; Turner-Hissong et al. 2020).

The date palm (*Phoenix dactylifera* L.) is the major perennial fruit crop in hot and arid regions of Afro-Eurasia, and among the oldest cultivated fruit crops (Zohary and Spiegel-Roy 1975). It belongs to the Arecaceae (Palmae) family and, along with 12 or 13 other interfertile species, constitutes the genus *Phoenix* (Barrow 1998; Gros-Balthazard et al. 2021). This iconic species holds enormous economic, symbolic and social importance throughout its traditional range of cultivation from Morocco in the west, across the Arabian Peninsula and to northwestern India in the east (Barrow 1998; Krueger 2021). Its sweet date fruits served as a staple of subsistence farming and source of economic prosperity dating back to the earliest civilisations of West Asia (Fuller and Stevens 2019; Tengberg 2012).

Domesticated date palms probably originated in West Asia during the fourth millennium BCE, and later expanded throughout North Africa at the latest by the Roman period (Munier 1973; Nixon 1951; Tengberg 2012). Many of the earliest archaeobotanical remains are concentrated in the Gulf Region and the Tigris and Euphrates River valleys. Early civilisations in this region documented a rich history of phoeniciculture in ancient texts and left an iconographic history that dates back to the end of the fourth millennium BCE (Tengberg 2012).

Fresh insight into the domestication history of date palms has come from phylogenetics and population genomics where recent work has answered a number of fundamental questions (Gros-Balthazard et al. 2018). For instance, a recent study, combining genomics and archaeometry, suggests that relictual populations (i.e. that were more widely distributed in the past) of the wild progenitor of date palms persists today in the Arabian Peninsula (Gros-Balthazard et al. 2017). Another one supports a role for introgressive hybridisation in the diversification of the crop (Flowers et al. 2019). Other recent developments include a population genetic study of ancient, germinated seeds, which provides evidence of extensive East-West exchanges of date palms at the height of the Roman Empire (Sallon et al. 2020).

Despite these advances, many questions remain concerning the timing of events in the domestication history of date palms and how natural or artificial selection contributed to the domestication syndrome and trait evolution. Beyond the history of phoeniciculture, studies of date palm origins provide insights into the foundation of oasis agrosystems and how humans colonised and adapted to the hot and arid regions of North Africa and West Asia.

In this chapter, we review the current understanding of the origin of the domesticated date palm from patterns in the population genetic and archaeobotanical data and highlight the present knowledge gaps. We highlight the current knowledge of date palm wild relatives, review the status of wild progenitor, outline competing models of date palm origins, emphasise the human activities responsible for date palm domestication and discuss recent studies on the genetic basis and evolution of fruit traits.

3.2 *Phoenix* Wild Relatives and the Wild Ancestor of Domesticated Date Palms

Phoenix dactylifera is typically considered to be a domesticated species while its wild relatives, including other species subject to human exploitation such as *Phoenix sylvestris* L. and *Phoenix canariensis* Chabaud, are generally not. What is the basis for this distinction and is it appropriate?

3.2.1 Is Date Palm a Domesticated Crop?

Domestication is the process by which a wild plant is changed through artificial selection to better fit our needs (Doebley et al. 2006). The term domestication—from the Latin *domesticus*, meaning *belonging to the house*—is sometimes confused with cultivation. The cultivation of a plant corresponds to its maintenance by humans, but a plant can be cultivated without being domesticated, and cultivation does not necessarily lead to domestication. Gepts (2004) considers that the cultivation stage is a prerequisite for domestication. However, by eliminating undesirable phenotypes directly in wild populations, domestication without cultivation can occur (in situ domestication; Pickersgill 2007).

There are several definitions of the term *domesticated plant*. Harlan (1992) defines a fully domesticated plant as one that cannot survive without human intervention. Similarly, Purugganan and Fuller (2011) consider a plant to be domesticated when it depends on humans for reproduction and survival. This definition applies well to domesticated cereals and legumes that have characteristics that do not allow them to survive off the field (loss of seed dispersal in particular). However, many perennial crops have evolved traits that distinguish them from their wild ancestors (the domestication syndrome; Appendix 1), and yet can survive and reproduce without human intervention (Miller and Gross 2011). Therefore, this definition is overly restrictive in the context of perennial crops as most would not be considered domesticated. In anthropology, it is human's perception of wild and cultivated plants that legitimizes the use or not of the term *domesticated plant*.

Here, we adopt the definition of domesticated plants proposed by Meyer et al. (2012): *'domesticated' refers more generally to plants that are morphologically and genetically distinct from their wild ancestors as a result of artificial selection, or are no longer known to occur outside of cultivation.* By this definition, date palms are considered domesticated, though some local communities consider them to be wild in their gardens (e.g. Tuaregs of the Tassili n'Ajjer, Algeria; Battesti 2004).

3.2.2 The Wild Progenitor of Domesticated Date Palms

The wild progenitor, or ancestor, of domesticated date palms, has remained unknown until recently. Prior to the application of genetic data, it was unknown whether domesticated date palms traced to a wild population of *Phoenix dactylifera,* an extant wild relative such as *P. sylvestris* or hybridisation between two or more *Phoenix* species (Pintaud et al. 2010; Zaid and Arias-Jiménez 1999). Independent studies have now excluded the possibility that the early domesticated population of *P. dactylifera* was the product of hybridisation between two wild *Phoenix* species and have established the identity of the progenitor. Specifically, a genetic study of *Phoenix* wild relatives determined that these species are all divergent from *P. dactylifera* and concluded that none of the known wild relatives is the direct ancestor of the domesticated species

(Pintaud et al. 2010). Nevertheless, at least one wild relative species, namely *Phoenix theophrasti* Greuter, has later contributed to the diversification of the date palm during/after its diffusion (Flowers et al. 2019).

3.2.2.1 Wild Versus Feral Date Palms

While searching for the wild ancestor of domesticated date palms, wild *Phoenix dactylifera*, a new issue arose: the difficulty to distinguish genuinely wild, ancestral populations, from feral populations. In date palms, like in many perennial fruit crops, untended stands become established either when a grove is abandoned, or when individuals *escape* cultivation via germination from seed. These palms, referred to as *feral* (Appendix 1 for definition), are not genuinely wild and may be mischaracterised as relictual populations of the ancestor of domesticated date palms due to shared phenotypic traits between the wild and the feral forms (Tengberg 2003).

Untended groups of date palms can be found throughout North Africa and Western Asia, and whether they are feral or wild is unknown in most cases (Gros-Balthazard et al. 2018). Whether wild or escaped domesticates, these populations may be critical to understanding key aspects of the origin and spread of date palms, as shown by the study of feral populations scattered in the desert near Siwa oasis, Egypt (Gros-Balthazard et al. 2020). Unfortunately, most studies have focused on the cultivated germplasm and these populations of uncultivated populations remain poorly understood.

Distinguishing truly wild from feral populations is a hard task in perennial crops (e.g. in olives; Besnard et al. 2018) and date palms are no exception. The domestication syndrome is expected to be limited (see Sect. 3.5). Differentiating wild from domesticated palms is thus arduous, such that distinguishing wild from feral individuals may be impossible. A study based on the quantitative analysis of seed shape in *Phoenix* pointed out that domesticated date palms display rather elongated seeds with pointed apices, while wild relatives have smaller and rounder seeds (Fig. 3.1) (Gros-Balthazard et al. 2016). Feral date palms included in the analysis also displayed elongated seeds so that the authors proposed that wild date palms could be distinguished from feral ones based on seed shape. Seed size, on the other side, is expected to be greatly impacted by the environment. Nonetheless, we note that a total reversion to a wild phenotype may be expected after many generations, due to the canalisation process (Waddington 1960), complicating the efforts for distinguishing feral from truly wild *P. dactylifera*. Further research is needed to understand the feralisation process and the evolution of *Phoenix* fruit and seed shape under human selection versus natural environments.

In the above seed morphometric study, uncultivated populations from Oman have attracted the attention of the authors as their seeds presented what is expected as a *wild*

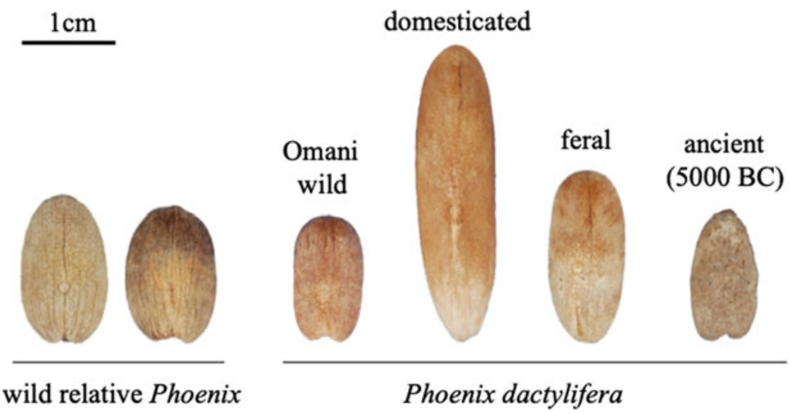

Fig. 3.1 Variation in seed size and shape in *Phoenix* (Figure constructed by M. Gros-Balthazard)

phenotype, that is, small and rounded seeds (Gros-Balthazard et al. 2017). A molecular study supported this hypothesis, presenting evidence that some of the uncultivated stands of *Phoenix dactylifera* growing in isolated areas of the Hajar Mountains of Oman are genuinely wild rather than feral palms. This provided the strongest support yet that a relictual population of the wild progenitor of domesticated date palms persists to the present-day and provides new opportunities to study the ancestor of the crop. Some of the uncultivated populations are nonetheless more likely feral or admixed, and identifying them requires evaluating the genetic and morphometrics of each specimen in the context of both wild and domesticated species.

3.2.2.2 The Native Range of the Progenitor of Domesticated Date Palms

The native range of the wild progenitor of date palms is unknown. Yet, the description of the native range of a crop's wild progenitor is a major issue when studying crop origins because domestication centres typically fall within or at the edge of this distribution range.

Today, wild *Phoenix dactylifera* have solely been described from the Hajar Mountains of Oman although many uncultivated populations could also represent wild populations and warrant verification through genetic and morphologic analyses (Gros-Balthazard et al. 2018, 2017).

Ancient evidence for wild *Phoenix dactylifera* can be found as archaeobotanical remains that date back to prehistoric times, before the domestication and the diffusion of domesticated date palms. Nevertheless, these finds cannot formally be identified to the species level given a lack of diagnostic criteria to distinguish *Phoenix* species (Gros-Balthazard et al. 2021). This ambiguity in species identification complicates the establishment of the native range of *P. dactylifera*.

Both >50 kyr (thousand years) old pollen and ca. 46 kyr old phytoliths attributed to the date palm were found in the Shanidar cave in Iraq (Henry et al. 2011; Solecki and Leroi-Gourhan 1961). Also, in Iraq, date palm phytoliths were retrieved from sediments dated to ca. 10,000 BCE (Altaweel et al. 2019). Excavations in the Levantine regions yielded a ~19 kyr old burnt stem and ~49–69 kyr old phytoliths (Henry et al. 2004; Liphschitz and Nadel 1997) that were attributed to *Phoenix dactylifera*, based on it being the only *Phoenix* growing in the region today. Palm phytoliths have also been found in Jebel Faya, United Arab Emirates, in sediments dated to 125 kyr, although it is unclear whether they belong to date palm or *Nannorrhops ritchiana* (Griff.) Aitch. (Bretzke et al. 2013). In southwestern Saudi Arabia, palm phytoliths were discovered in ~80 kyr deposits; these may be attributable to the date palm but the rarity in the assemblage may suggest long-distance transport by wind (Groucutt et al. 2015). In Africa, pre-Neolithic remains of *Phoenix* are almost nonexistent. The sole evidence is from the Egyptian oasis of Kharga, where carbonised seeds and a fossilised leaf of *Phoenix* were recovered from Pleistocene deposits (Caton-Thompson and Gardner 1932; Gardner 1935); nevertheless, only the sediment has been dated while the age of the *Phoenix* remains is unknown and they could represent more recent contaminating remains.

Based on these considerations, it seems likely that wild *Phoenix dactylifera* is native to Western Asia, although the precise distribution is unknown and a larger historical distribution, covering all or parts of North Africa cannot be ruled out (see Rivera et al. 2020 for attempts to model historical distributions). Paleoclimate models that predict a Green Sahara as recently as 5000 years ago suggest that the climate was wetter and supported diverse plant communities (Tierney et al. 2017). Given that date palms are vulnerable to high humidity and excess rainfall (Barrow 1998), a wet climate during this period likely has implications for the potential distribution of the species in North Africa in the past. Such open questions about the ancient distribution of wild *P. dactylifera* currently hamper understanding of date palm domestication and would benefit from additional palynological surveys and paleovegetation and species distribution modelling.

3.2.3 *Phoenix* Wild Relatives: Opportunities for Discovery in Evolutionary and Crop Improvement Research

Crop wild relatives consist of those phylogenetically related taxa that share a recent common ancestor with the domesticated species. Species in the *Phoenix* genus have weak barriers to gene flow and frequently hybridise in anthropogenic contexts (Gros-Balthazard 2013). These species are of tremendous interest both in evolutionary studies of domestication (see below) and in applied contexts. Indeed, many crop wild relatives are more tolerant of biotic and abiotic stresses and thus represent a reservoir of diversity for breeding and crop improvement (Burgarella et al. 2019; Migicovsky and Myles 2017; Zhang et al. 2017).

In date palms, vanishingly little is known about stress tolerances and other traits of interest in the 13 wild relatives of *Phoenix dactylifera* and most of what is known is based on observations of habitat occupancy such as the preference of *P. theophrasti* for coastal areas and ability to survive saltwater exposure (Barrow 1998). In the past decade, many molecular studies have integrated other *Phoenix* species while studying date palms (i.e. Cherif et al. 2016; Flowers et al. 2019) and a few have directly focused on the genetic diversity of these date palm wild relatives (i.e. Saro et al. 2018; Vardareli et al. 2019). In this chapter, we restrict our discussion to ways in which studies of *Phoenix* wild relatives have informed the domestication of date palm, but there is a great need for both molecular studies and experimental assessment of trait diversity in these species for advances both in applied and evolutionary studies (Hazzouri et al. 2020).

3.3 Origins and Diffusion of the Date Palm

The origins of domesticated date palms have been controversial since the beginning of the nineteenth century (Tengberg 2003). Scholars have advanced different theories about the wild progenitor species and debated the location of centre(s) of origin, the number of domestication events, and how hybridisation may have contributed to the origin and diversification of the crop. Here we briefly summarise some of the most prominent ideas and discuss in more detail hypotheses that are supported by existing data.

3.3.1 Origin Hypotheses

3.3.1.1 Evidence of Early Exploitation

Prior to cultivation and domestication, wild date palms had been exploited for millennia. For example, they were part of the Neanderthal diet 50,000 years ago, as evidenced by phytoliths found in dental calculus from teeth recovered in Shanidar cave, Iraq (Henry et al. 2011). The earliest evidence of date palm exploitation by modern humans has been found on two sites on the Gulf coast: Dalma Island, United Arab Emirates (Beech and Shepherd 2001) and Sabiyah, Kuwait (Parker 2010) and date back to approximately 5000 BCE (Fig. 3.2).

This early evidence of exploitation in the Gulf Region has informed current views on the geographic origins of cultivation, but there remain

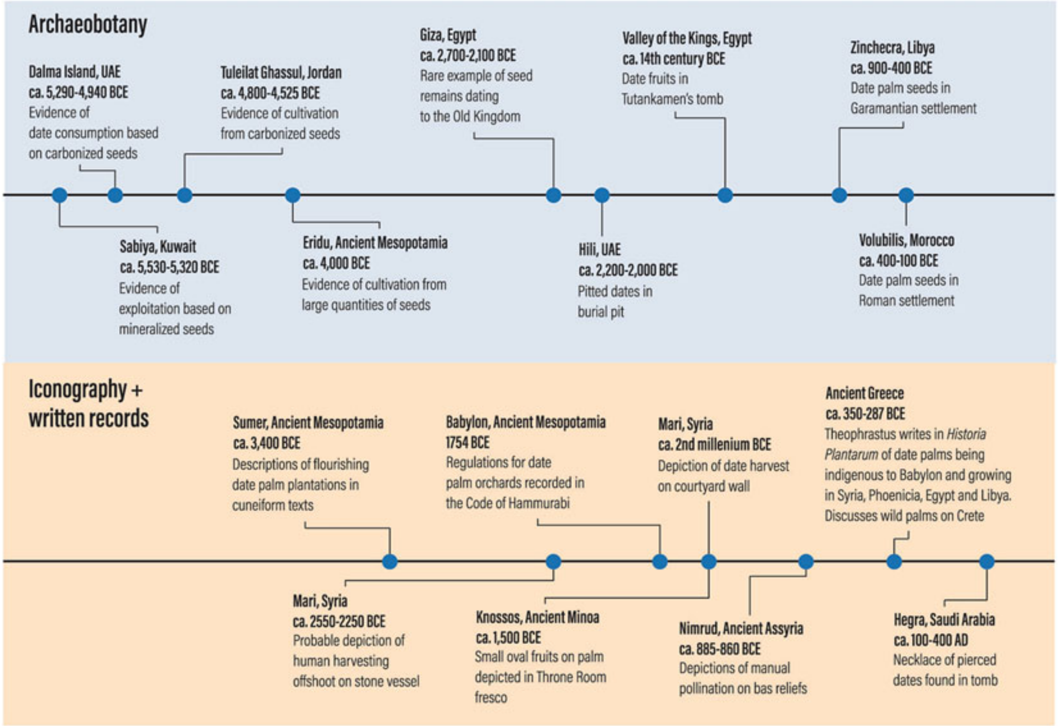

Fig. 3.2 A timeline of important events in the domestication history of date palms. Dates correspond to those reported in the references Sarton (1934), Zohary and Spiegel-Roy (1975), Murray (1990), Aruz (2003), Méry and Tengberg (2009), Tengberg (2012), Terral et al. (2012), Zohary et al. (2012), Malleson (2016), Galanakis et al. (2017), Fuller and Pelling (2018), Malleson and Miracle (2018), Flowers et al. (2019). (Figure constructed by J. Flowers)

significant outstanding questions about the origins of the domesticated date palm.

3.3.1.2 Geographic Origins

The diversity of hypotheses that have been advanced concerning the geographic origin of domesticated date palms reflect the poor understanding of both the identity and historical range of the ancestral species as detailed above. In fact, origin hypotheses have been proposed for most regions where date palms are cultivated in the Old World. Researchers have proposed geographic origin scenarios ranging from Northwest Africa in the West, to Ethiopia in the South, to the Western India in the East and many locales in between (Barrow 1998; Goor 1967; Munier 1981; Tengberg 2003). Most recent scholars, however, have considered the Gulf region to be the most likely origin, in keeping with available evidence on the prehistoric distribution of *Phoenix dactylifera*, ancient written records, archaeological remains and archaeobotanical finds (Fuller and Stevens 2019; Tengberg 2012, 2003; Zohary and Spiegel-Roy 1975).

3.3.1.3 Number of Domestication Events

Whether date palms were independently domesticated one or more times is a source of ongoing debate, as it is in the studies of many crop species, for example, in olives (Besnard et al. 2018). These controversies emerge in population genomics from challenges associated with reconstructing complex historical events from patterns of genetic ancestry and population structure and associating these patterns with human-mediated selection and other domestication-related activities. This problem is exacerbated in relatively poorly studied crops, including date palms.

Population genetic studies of regional populations of domesticated crops often find distinct ancestries that are commonly interpreted as evidence of multiple domestication events. Choi et al. (2017) argued, however, that evidence of distinct genetic ancestries may not reflect independent *de novo* domestication but may instead represent single domestication with multiple origins. Multiple origins in this context refer to the number of independent ancestral gene pools from which a crop is derived irrespective of whether the ancestral populations were independently domesticated.

Identifying multiple origins is relatively straightforward with population genomic data, but it is considerably more difficult to determine if different sources of genetic variation were subject to independent selection regimes that are a hallmark of multiple domestication. In the case of rice, unidirectional gene flow of functional alleles at key loci that control domestication-related traits provide evidence of a single origin of domestication traits. This supports a single domestication despite multiple origins apparent in the distinct genetic ancestries of subspecies of domesticated rice (Choi et al. 2017). Thus, genomic data frequently support multiple origins, but evidence of multiple domestications remains tenuous in most study systems.

Domesticated date palms are geographically structured into eastern and western populations (Arabnezhad et al. 2012; Hazzouri et al. 2015; Mathew et al. 2015; Zehdi-Azouzi et al. 2015), with additional minor divisions within each of these regions (Gros-Balthazard et al. 2020; Mohamoud et al. 2019; Zango et al. 2017; Zehdi-Azouzi et al. 2015). Population genetic studies have in some cases interpreted this geographic structure as evidence of multiple domestications ranging from two to four events. For example, Zehdi-Azouzi et al. (2015) and Mathew et al. (2015) proposed that the geographic structure detected between North African and West Asian date palms supports two domestications. However, the geographic structure observed in date palms may also be explained by a multiple origin, single domestication model. For example, it is possible that domestication-related traits were selected in the East and alleles controlling these traits were later introduced to a proto-domesticated or wild population in North Africa. This scenario could account for population structure without multiple *de novo* domestications.

Determining the number of domestication events will continue to be challenging in date palms. There is a need to continue to evaluate evidence that date palms are the product of multiple domestications or if factors such as hybridisation could be the source of the distinct genomic ancestries in geographic populations of date palm (see below) without the need to invoke multiple domestications. There is also a need to consider that domestication of date palms may not be attributable to origins from well-defined cultivation centres but is a geographically diffuse process as has been suggested for other perennial fruit crops (Miller and Gross 2011).

3.3.2 Introgressive Hybridisation

The North African population of date palms is of particular interest in the context of introgressive hybridisation. This population is genetically distinct from West Asia (Arabnezhad et al. 2012), consists of multiple sub-populations (Gros-Balthazard et al. 2020; Zango et al. 2017; Zehdi-Azouzi et al. 2015), has at least 20% higher genetic diversity than populations in the Arabian Peninsula and elsewhere in West Asia (Gros-Balthazard et al. 2017; Hazzouri et al. 2015) and has distinct and deeply divergent chloro- (i.e. Pintaud et al. 2013) and mito-types (Flowers et al. 2019; Mohamoud et al. 2019) that are found at high frequency and largely restricted to North Africa. Hazzouri et al. (2015) speculated that these patterns may be at least partially explained by introgressive hybridisation with a wild relative.

Evidence supporting introgression from wild *Phoenix* in North Africa has begun to accumulate

(Gros-Balthazard et al. 2017, 2020; Flowers et al. 2019). Direct evidence of introgression was first reported by Flowers et al. (2019) using whole-genome resequencing of date palms and its closest wild relatives. In this study, explicit tests of admixture (e.g. ABBA-BABA and f_3 tests) supported introgression between the North African population and a closely related congeneric *Phoenix theophrasti*, or a *P. theophrasti*-like population (i.e. a possibly extinct species or population that is closely related to *P. theophrasti* and may have been the direct source of introgressed alleles). Introgression was further supported by the segregation of *theophrasti*-like alleles in North Africa, population modelling that included admixture between North African date palms and *P. theophrasti*, haplotype sharing in introgressed genomic regions and patterns of linkage disequilibrium that is consistent with a recent history of admixture with a distant population. In addition, genome-wide estimates of population divergence supported reduced divergence in the North Africa-*theophrasti* comparison versus West Asia-*theophrasti*.

Evidence of introgressive hybridisation with a *Phoenix theophrasti*-like population has also been implicated in a microsatellite-based study of date palms in the Siwa Oasis, Egypt. Gros-Balthazard et al. (2020) surveyed more than a hundred cultivated and feral date palms and found that both shared alleles with *P. theophrasti* to a greater extent than samples from West Asia. Interestingly, the degree of allele sharing was higher in the samples from Siwa oasis, Egypt, than in the other samples from North Africa, and especially high in the feral accessions. Whether this intriguing pattern reflects patterns of selection favouring *wild* alleles in feral populations or reflects differences in demographic history and the history of hybridisation is an area of ongoing research.

How much of the North African genomic ancestry traces to *Phoenix theophrasti* or the *theophrasti*-like population? Estimates of *P. theophrasti* ancestry in North African date palms was estimated at 5–18% (Flowers et al. 2019). The upper bound of this estimate is remarkably consistent with an estimate of ancestry from an unsampled *ghost* population (18%) in North African date palms (Gros-Balthazard et al. 2017). The signature of introgression is strongest in cultivars from the Maghreb that have 15–18% of their genomic ancestry that traces to *P. theophrasti*, while cultivars from Egypt and Sudan showed a smaller (5%) ancestry fraction. It is unknown whether this is because western date palms experienced higher or more recent gene flow from a *theophrasti*-like population or whether the *theophrasti*-like ancestry of eastern African varieties has been diluted by introgression from Asian cultivars.

Phoenix theophrasti has a present-day distribution limited to Crete and the Aegean Sea region (Boydak 2019; Vardareli et al. 2019), but once may have had a broader geographic range in the Eastern Mediterranean (Fuller and Stevens 2019; Kislev et al. 2004). The fact that the current range of *P. theophrasti* does not overlap with the range of date palm remains a source of uncertainty concerning the geography of introgressive hybridisation between these species (Flowers et al. 2019).

Questions related to the geographic context of hybridisation, the age of the introgression event (s), whether hybridisation was human-mediated, or the product of natural events are the subject of continuing work. These questions are currently being addressed through expanded surveys of genomic variation, studies of ancient DNA, and population genetic modelling. Other areas of active investigation include studies of other *Phoenix* wild relatives to determine the extent to which hybridisation with additional species may have contributed to the diversity of date palms (Pintaud et al. 2010).

3.3.3 Models of Domesticated Date Palm Origins

We have outlined patterns in the population genetic, archaeobotanical and other sources of data that are consistent with some models for the origins of domesticated date palms and inconsistent with others. Here we expand on geographic models of date palm domestication and highlight sources of evidence that are either consistent or inconsistent with each model. We outline the simplest models that could account for current data.

3.3.3.1 Expansion Model

Prior to the availability of genetic data, the preferred model for date palm origins proposed a domestication centre in West Asia followed by range expansion (Tengberg 2003). Under this model, the current range of cultivation in the Old World—from North Africa to Northwestern India—resulted from westward dispersal from a domestication centre in the east via trade routes traversing the Sahara (Munier 1973) or sea-faring routes across the Mediterranean (Nixon 1951) and any population of wild *Phoenix* that may have inhabited North Africa was replaced without admixture.

Key elements of this model are supported by archaeobotanical and archaeological remains. For example, various sources support a thriving date palm culture in ancient Mesopotamia and the Upper Gulf Region by the early Bronze Age (late fourth/early third millennia BCE) (Tengberg 2012) (Fig. 3.2). By contrast, there is limited evidence of ancient date palm cultivation or wild *Phoenix* remains in North Africa. The earliest evidence of cultivation dates to the New Kingdom, mid-second millennium BCE, in the Nile River Valley (Popenoe 1924; Tengberg and Newton 2016), and from the beginning of the first millennium BCE in Fezzan in modern-day Libya (Pelling 2005) (Fig. 3.2). Prior to that, there are only sparse remains in Egypt (reviewed in Gros-Balthazard et al. 2020; e.g. Giza, 2700–2100 BCE; Malleson 2016; Malleson and Miracle 2018) and no reliable remains recorded further west (Flowers et al. 2019). The earliest remains in the Maghreb date to much later, first appearing at the Roman settlement of Volubilis (Morocco) in the Classical Period (ca. 400–100 BCE; Flowers et al. 2019; Fuller and Pelling 2018) (Fig. 3.2). The expansion model is the simplest way to account for the absence of wild *Phoenix* remains in North Africa and the disparity in ages of remains in North Africa and the Upper Gulf/Eastern fringe of the Fertile Crescent (Tengberg 2012).

This expansion model is attractive in its simplicity, but population genetic studies indicate a more complex history. Arguably, the two most difficult patterns to reconcile with a simple expansion is the higher nucleotide diversity in the western population and evidence of introgression in North Africa. The difference in diversity is inconsistent with a population genetic bottleneck that presumably would have accompanied the founding of a new population on the African continent (Hazzouri et al. 2015), while introgression is inconsistent with a simple expansion. Despite this, there is evidence of a westward expansion from genetic data that support gene flow from West Asia to North Africa. For example, asymmetrical gene flow into North Africa has been proposed to account for the low to moderate frequency of the *eastern* cpDNA and Y-chromosome haplotypes in North Africa, but the near absence of the *western* cpDNA and Y-chromosome haplotypes in the Arabian Peninsula and elsewhere in West Asia (Cherif et al. 2013; Hazzouri et al. 2015; Mathew et al. 2015; Zehdi-Azouzi et al. 2015). Second, Gros-Balthazard et al. (2017) and Flowers et al. (2019) estimated that ~82% of North African ancestry can be traced to West Asian date palm. While there are alternative explanations for these patterns, the simplest explanation is the gene flow of eastern alleles into North Africa at a time of geographic expansion of the crop.

3.3.3.2 *Leaky* Expansion Model

The *leaky* expansion model includes the westward movement of West Asian date palm into North Africa as proposed by the expansion model but also proposes admixture with a *Phoenix* wild relative such as *P. theophrasti* or a *theophrasti*-like population. Although two independent reports support hybridisation between date palm and *P. theophrasti* (Flowers et al. 2019; Gros-Balthazard et al. 2020), details of the nature of hybridisation are unclear and it is presently difficult to distinguish among various competing scenarios (Fig. 3.3). The disjunct

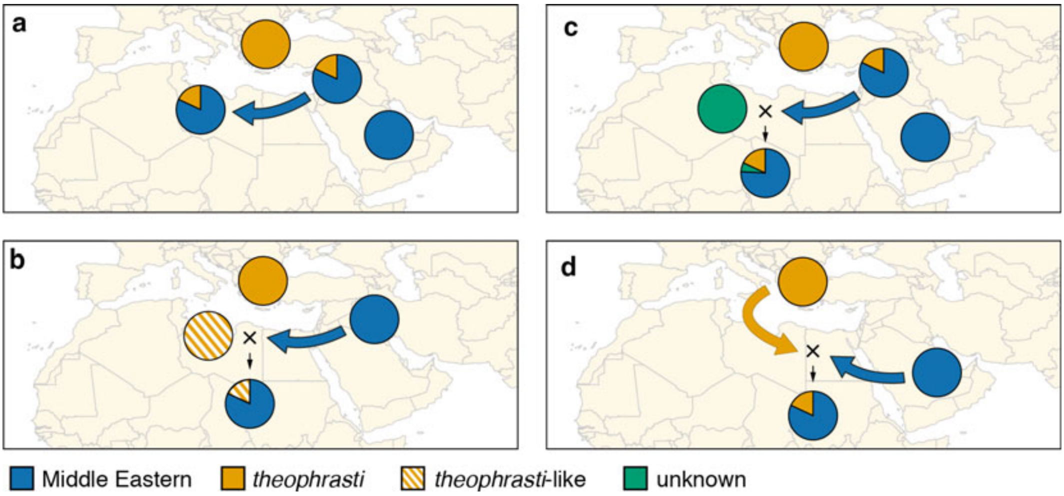

Fig. 3.3 Models of date palm population history. (**a**) A model where West Asian date palms and *Phoenix theophrasti* hybridised in an unknown location in the Eastern Mediterranean followed by expansion to Africa from the hybrid source. (**b**) A model where a resident African *P. theophrasti*-like population hybridised with West Asian date palm following range expansion. Introgressive hybridisation between *P. dactylifera* and resident populations of *P. theophrasti* in Greece and Turkey may not have occurred. (**c**) A model similar to (**a**) but including hybridisation with a third unknown source of variation. (**d**) A model that invokes both the expansion of West Asian date palms and transport of *P. theophrasti* to North Africa where hybridisation occurred. Pie charts illustrate the genomic ancestry of a population. Thick arrows represent migration. *X* indicates introgressive hybridisation. Thin arrows point to the product of introgressive hybridisation. (Figure constructed by J. Flowers)

present-day distributions of cultivated date palms and *P. theophrasti* add uncertainty to the geography of hybridisation in the past.

For example, one possibility is that introgression occurred prior to range expansion of the West Asian crop outside of Africa, where the two species ranges may have once come into contact (Fig. 3.3a; Flowers et al. 2019). *Phoenix dactylifera* X *P. theophrasti* hybrid populations from Epidaurus, Peloponnese (Flowers et al. 2019) and possibly Turkey (Boydak and Barrow 1995) represent extant examples of such admixed populations.

An alternative model incorporates the expansion of West Asian date palms to North Africa but proposes that the introgressive hybridisation occurred in situ with a resident *theophrasti* or *theophrasti*-like population (Fig. 3.3b). This model could explain *theophrasti* introgression signatures in North Africa. However, the North African populations is segregating high-frequency cpDNA and mtDNA haplotypes that are not shared with *Phoenix theophrasti* (hence the reference to “*theophrasti*-like”) and found at very low frequency elsewhere (<4%; Zehdi-Azouzi et al. 2015). This *North African* haplotype may allude to a more complex history such as an additional source of ancestry in this population (Fig. 3.3c). An alternative hypothesis is that this haplotype is not North African per se, but traces in origin to the Arabian Peninsula (where it is found at low frequency) and its current frequency on the African continent is the product of demographic events following range expansion. Additional population genetic modelling is required to distinguish among these possibilities.

Both models illustrated in Fig. 3.3b,c propose a resident wild population of date palm in North Africa of which there is little or no support in the archaeobotanical record. However, there is a twentieth-century description of *Phoenix atlantica* A. Chev. var. moroccana A. Chev. in Morocco (Chevalier 1952) and more recent unverified reports of possible wild date palms in isolated areas (Zehdi-Azouzi et al. 2016; Zohary et al. 2012). Whether these reports describe feral date palms or wild *Phoenix* is unknown, but it remains possible that the archaeobotanical record is incomplete and that such a *ghost* population could be a source of genetic ancestry in North African cultivars (Gros-Balthazard et al. 2020).

Finally, Cyrenaica (modern-day Libya) and Crete had close geopolitical ties and comprised a senatorial province during the Roman Empire (Chevrollier 2016). It is conceivable that ancient trade routes such as those connecting Crete to continental Africa may have facilitated the transport of *Phoenix theophrasti* to North Africa (e.g. for construction materials or other uses). This is one example of related hypotheses that posit both the expansion of date palm and transport of *P. theophrasti* to the African continent where hybridisation may have occurred (Fig. 3.3d).

3.3.3.3 Additional Complexity

There are features of the population genomic data that are not easily explained by the above models. For example, Flowers et al. (2019) broke the genome into segments and estimated the introgression fraction between *Phoenix theophrasti* and North African date palm in each genomic region. Segments of the genome with higher introgression fraction had correspondingly higher nucleotide diversity in North Africa consistent with introgression from *P. theophrasti* contributing to the elevated nucleotide diversity in this population (Gros-Balthazard et al. 2017; Hazzouri et al. 2015). Other regions in the genome did not show evidence of introgression between North Africa and *P. theophrasti*. The potentially revealing observation is that these non-introgressed genomic segments still showed higher nucleotide diversity on average in North Africa compared to West Asia, albeit not as pronounced as the difference observed in genomic regions introgressed by *P. theophrasti* alleles. This suggests that *P. theophrasti* introgression may not fully account for the higher diversity in North Africa.

What does this suggest about models of population history? The above observation is inconsistent with a simple *leaky* expansion model because there is no evidence of a population bottleneck even in non-introgressed genomic regions. To account for this pattern, it may be necessary to consider factors that increase North African diversity relative to West Asia in addition to introgression from *Phoenix theophrasti*. For example, additional sources of genetic ancestry in North Africa or bottlenecks, inbreeding or stronger diversity-reducing effects of natural or artificial selection in West Asia could account for this pattern (Flowers et al. 2019). These and other population genetic scenarios would benefit greatly from extensive population genetic modelling of the domestication history of date palms.

3.4 Process of Domestication and Origins of Cultivation Practices

The domesticated date palm finds its origins in the human practices that have shaped the genetic makeup of *Phoenix dactylifera* and favoured desirable phenotypes through time, leading to a distinction between wild and domesticated populations.

The initial cultivation of date palms by early farmers represents the earliest stage of domestication. The practices adopted by these pioneering farmers were primarily related to reproduction and propagation (detailed below), but also include practices such as leaf removal, pruning of fruit bunches and selection for desirable traits such as larger and better-tasting fruit. Here we detail what is known about these processes in the context of date palm domestication and discuss recent advances in studies of the evolution of date palm fruit traits (Sect. 3.5).

3.4.1 Vegetative Propagation

One of the most important events in the domestication of fruit-bearing crops was the capacity to vegetatively propagate the crop. In perennial plants, 75% of cultivated species are propagated clonally (by grafting, cutting, layering or planting offshoots), which confers several advantages over sexual reproduction (McKey et al. 2010; Miller and Gross 2011).

Date palms are dioecious, and phoeniciculture, the cultivation of date palm, includes a mix of clonal and sexual propagation (Johnson et al. 2013). Traditionally, female cultivars are propagated asexually from offshoots growing at the base of the palm, which is planted independently of the mother palm and themselves provide offshoots for further propagation.

Vegetative propagation holds several advantages over sexual reproduction. First, it allows ascertaining that a female will grow while when planting seed, the ratio of male/female is 50/50. Second, the juvenile phase is reduced, and date palms will provide more rapidly the sought fruits. Lastly, and more importantly, vegetative propagation allows the selection of individuals with interesting phenotypic traits (especially the fruits of the desired quality) and their identical reproduction. Only in rare cases does sexual reproduction yield palms producing dates that are as high/better quality as that of the parents (4% according to Peyron 2000).

Clonal propagation of date palms is a very ancient practice. The oldest evidence of it is from a soft-stone vessel that probably shows a scene of date palm propagation by offshoot dating back to the second half of the third millennium BCE (Tengberg 2012) (Fig. 3.2).

While this practice remains common today, the tremendous expansion of the date palm crop over the past 40 years was facilitated by propagation through tissue culture primarily via somatic embryogenesis (Zaid and Arias-Jiménez 1999).

3.4.2 Manual Pollination

The second main farming practice associated with phoeniciculture is manual pollination (Roué et al. 2015). Pollination of the female inflorescence is necessary for fruit development and ripening, as already known by the Sumerians in Iraq, ca. 2300 BCE (Janick 2005). In the wild, it is taken care of by either insects or wind (Barrow 1998). But for the oasis system to be efficient, despite water and irrigable land shortage, oasis communities maintain 95–99% of female palms. Opting for such an artificial sex ratio requires hand pollination. A very low proportion of male palms in the gardens prevents the natural pollination of all female flowers, leading to a loss in fruit yield.

Manual pollination was probably already in use in southern Mesopotamia from the late 4th millennium BCE (Landsberger 1967; Tengberg 2003). Its first mention in texts goes back to the eighteenth-century BCE, in the famous code of Hammurabi, a Babylonian king, where it was associated with religious practices and later this practice was prominent in Assyrian iconography (Sarton 1934) (Fig. 3.2).

3.4.3 Other Cultivation Practices

The domestication of the date palm is associated with the origins of oasis agrosystems, of which it is the keystone species (Tengberg 2012). A major constraint in this environment is the scarcity of water resources and the high intra- and inter-annual variability in their availability. The development of oasis agrosystems has thus been accompanied by the development of irrigation systems, such as the ancient irrigation system *falaj* or *qanat*. These systems are hardly precisely dated, and where they originate is unknown. Nevertheless, they occur since at least the Iron Age in Southeast Arabia and could be as old as the Bronze Age (reviewed in Charbonnier 2013).

3.5 Consequences of Domestication in Date Palms

In date palm, the recent discovery of relictual populations of the wild progenitor should enable an updated description of the domestication syndrome. Nevertheless, prior to this discovery, Pintaud et al. (2013) listed potential selected traits for this species, and studies of domestication syndrome in other fruit crops may provide further insights into the date palm domestication syndrome.

Characters related to the fruit and fruit production are expected to be the main targets of human selection. Overall, an increase in productivity is likely as well as a reduced inter-annual variability in yield. Domesticated dates are bigger than those of wild relatives and wild date palms (Barrow 1998; Gros-Balthazard pers. obs.). Seeds have indirectly been affected by human selection on the fruits (Alcántara and Rey 2003; Bolmgren and Eriksson 2010; Fuller 2018). They are longer, their shape is more elongated (larger length/width ratio), and extremities are more pointed (Fig. 3.1; Fuller 2018; Gros-Balthazard et al. 2016; Terral et al. 2012). Fruit shape is expected to be more variable in domesticated date palms, although this has not been tested, but is visible in the seeds (Fig. 3.1; Gros-Balthazard et al. 2016). Fruit flesh (mesocarp) is presumably thicker (Pintaud et al. 2013). The fruit should become more palatable with an increase in sweetness, decreasing acids and increased variance in organoleptic characters related to selection on secondary metabolites. Other characters related to fruiting that could have been selected during the domestication process are a more dense and compact fruit bunch, a synchronic fruit maturation and delayed fruit abscission (Pintaud et al. 2013). The development of fruit without ovule fecundation (parthenocarpic fruit) has been described in other crops (e.g. fig, Zohary and Spiegel-Roy 1975 or banana, Kennedy 2008). In date palm, it would alleviate the burden of manual pollination. Yet, to our knowledge, there are no cultivars that have been selected for this trait, and in most, if any cases, fruits do not develop without pollination, and when they do, they don't reach maturity and are not palatable. According to Pintaud et al. (2013), the phenology may also have been affected by domestication with the selection of plants having early or late flowering and fruiting to increase fruit season duration.

Vegetative organs could also have been affected by domestication. Pintaud et al. (2013) proposed a reduction in basal and aerial ramification. Reduced defense of the reproductive organs through reduction of acanthophylls (spines at the base of the leaves) size that would have facilitated harvest is also a potential syndrome, as observed in the peach palm (*Bactris gasipaes* Kunth; Balick 1984).

3.5.1 The Evolution of Date Palm Fruit Traits

Fruit quality traits such as size, shape, colour, flavour and texture are primary targets of selection in fruit crops and a key component of the domestication syndrome in date palm (Appendix 1). Clues to the origin and evolution of date palm fruit traits come from studies of the diversity of date palm fruits (Zaid and Arias-Jiménez 1999), comparisons of fruits of domesticated *Phoenix dactylifera* and its wild relatives (Amorós et al. 2009, 2014), changes in seed size and shape apparent in the archaeobotanical record (Fig. 3.1) (Fuller 2018; Terral et al. 2012), and genetic studies of fruit traits (Hazzouri et al. 2015, 2019).

A visit to the souks of the Arabian Peninsula or North Africa and the diversity in colour, shape, size, texture and taste of date palm fruits are on full display. At the fresh (khalal or bisser) stage when select varieties are consumed, the fruits range from pale yellow (e.g. cv. Barhee) to deep red (e.g. cv. Hayany), with many intermediate colours including shades of pink and orange. Even after-ripening is complete, the colour remains an important distinguishing feature with exceptional varieties such as Ajwa assuming a dark black colour at the dry stage.

Many other varieties are recognisable based on their shape, size and flavour. Shapes include round (Braim), ovoid (Khalas), and elongate (Deglet Noor) and sizes range from small-fruited varieties (Lulu) to large-fruited varieties (Anbar, Medjool). Each variety is also characterised by distinctive texture and taste. Many North African varieties are dry, while those of the Arabian Peninsula and West Asia are more typically semidry or soft. These textures are correlated with sugar composition with dry varieties frequently retaining sucrose through ripening whereas semidry and soft varieties typically hydrolyse sucrose to glucose and fructose

(Dowson and Aten 1962). An exceptional example of a sucrose-type variety is Sukkary, which deposits sucrose in high concentrations in the fruit pulp and is valued in Arabia and beyond for its unusually sweet taste.

The origin and selective mechanisms acting on fruit traits have great potential to inform understanding of date palm domestication. As a first step, characterisation of the genes and mutations that control these traits are fundamental to understanding the process of date palm domestication. Hazzouri et al. (2015) reported a statistical association between genotypes at the *VIRESCENS* locus in date palm and khalal stage fruit colour. *VIRESCENS* codes for an R2R3-MYB transcription factor that is expressed in the fruit and activates anthocyanin biosynthesis. A genome-wide association study (GWAS) subsequently confirmed that *VIRESCENS* is the primary locus that controls colour variation in date palm fruits (Hazzouri et al. 2019).

Candidate mutations for the causal polymorphisms for fruit colour have been identified at the *VIRESCENS* locus. Hazzouri et al. (2015, 2019) reported a polymorphic retrotransposon insertion (named *Ibn Majid* after the fifteenth-century Arab navigator) in the third exon that disrupts the open reading frame. This mutation acts as a dominant-negative that suppresses anthocyanin production. Hazzouri et al. (2019) reported a translation initiation codon mutation (ATG-> ATA) that acts as a recessive loss-of-function mutation. These two mutations in *VIRESCENS* support a model that accounts for much of the variation in fruit colour. Taken together, the relatively uniform yellow fruit colour in wild stands of the closest relatives of date palm (*Phoenix sylvestris*, *P. theophrasti*), the diversity in date palm fruit colour (Jaradat and Zaid 2004), and multiple independent mutations in date palm *VIRESCENS* and parallelism with oil palm (Hazzouri et al. 2015) suggest that fruit colour was selected during date palm domestication.

Sugar composition is a prominent trait that varies among date palm cultivars. Date palms deposit large concentrations of sugar during fruit development with as much as 80–85% in the form of sucrose at the fresh, or khalal, stage (Chao and Krueger 2007). At the onset of ripening, many varieties such as Khalas invert sucrose to reducing sugars to the extent that there is little, or no sucrose retained in the tamar (dry) stage. Other varieties such as Sukkari retain sucrose in high concentrations in the dry stage. Hazzouri et al. (2019) reported a quantitative trait locus (QTL) on linkage group 14 that controls variation in this trait in date palm fruits. They found that within the QTL is a cluster of cell wall invertases and an alkaline/neutral invertase and reported what appear to be multiple deletions in this region including the homozygous deletion of a cell wall invertase in many of the sucrose-type varieties. This suggests that sucrose-rich varieties may have evolved via the selection on loss-of-function alleles at the invertase locus. A similar finding was reported in a subsequent independent study (Malek et al. 2020).

Amorós et al. (2014) surveyed sugar composition and other compounds in developing fruits of date palms and their *Phoenix* wild relatives. *Phoenix dactylifera* were the only *Phoenix* species surveyed to deposit large amounts of sucrose in khalal stage fruit, whereas only trace amounts were reported for *P. loureiroi* Kunth, *P. canariensis*, *Phoenix roebelenii* O'Brien and *Phoenix reclinata* Jacq. This suggests that the process of sucrose deposition in date palms is unique to domesticated date palm and further suggests a two-phase model for the origin of the sweet sucrose-rich varieties. In the first stage, date palms were selected by early farmers to increase the deposition of sucrose in the early stages of fruit development perhaps to offset the acidic taste at the fresh stage. In the second stage, the sukkary-type varieties were selected to retain sucrose throughout the ripening process.

Future research on the fruit colour and sugar QTL regions will focus on the origins of the alleles and the selective forces (e.g. soft or hard sweeps) that may be operating at these loci.

3.6 Conclusions and Prospects

The last decade has seen tremendous progress in the study of date palm domestication and the origins of the crop. Yet, despite these gains, there remain many significant outstanding questions in many areas of research. There is a need for extensive population genetic modelling of population history to estimate the ages of key events such as the expansion of the crop and the timing of hybridisation and to distinguish various competing models of population history. Genetic studies of key traits, including those that control the domestication syndrome, and those that underlie traits that differ among varieties would greatly enrich understanding of domestication particularly if coupled with population genomic studies of the origins of alleles and the history and type of selection acting on these genes. Finally, while a handful of studies have begun to apply genetic and genomic methods to *Phoenix* wild relatives, studies of domestication would benefit from studies of traits such as offshoot production, fruit traits such as gene expression and metabolomic variation during fruit development in both date palms and their wild relatives. Such studies would provide important insight into the genes controlling the domestication syndrome and shed light on the origins and diversity of fruit traits that are valued by consumers and enthusiasts worldwide.

Appendix 1 and Terminology

Term	Definition
Artificial selection	The process where either desirable genotypes (under conscious selection) or higher fitness genotypes (under unconscious selection) increase in frequency owing to human activity in an anthropogenic context
Center of domestication	The geographic region where a crop was first domesticated. In perennial crops, domestication may be geographically diffuse and lacking distinct centres
Cultivar	Clonally propagated named types (i.e. Khalas or Deglet Noor) are formally referred to as "cultivars" in the literature (informally as "varieties"), although local categorisation practices at the origin of given palm names may be more complex (Battesti 2013, Battesti et al. 2018, Gros-Balthazard et al. 2020). *True-to-type cultivars* refer to palms that are indeed exclusively propagated through offshoots under a single name. On the other side, *ethnovarieties* are groups of multiple clonal lines of palms, displaying the *same form* and the *same* dates according to farmers. Other given names (*local categories*) may refer to groups of palms having a heterogeneous combination of genes and also heterogeneous morphologies, but are assigned a common name because of a shared characteristic (example: khalt, meaning palms growing from a seed in the Maghreb)
Cultivation	The activities leading to the production of food or other services from plants. The cultivation of date palm, phoeniciculture, involves only limited cultivation practices (see Sect. 3.4)
Domestication	The process by which a wild crop is modified genetically and phenotypically by human activities that impact its life cycle (reproduction, propagation, selection)
Domestication syndrome	The phenotypic traits in a domesticated species that distinguish it from a wild species. Individual genotypes may have a mix of wild traits and domesticated traits
Feral	Feral date palms are individuals originating from domesticated date palms but growing without human intervention during the life cycle. Feral populations may arise either when a cultivated population is abandoned, or when individuals *escape* from cultivation by

(continued)

Term	Definition
	scattering seeds outside the fields in a natural environment that is conducive to population settlement and expansion. Although they look wild, they are not considered as genuinely wild (see Wild)
Introgression	The transfer of genetic material from one population or species to another
Wild	An adjective referring to a population or species of plant that has not been domesticated. The term is often appropriately applied to the relatives or progenitor (i.e. ancestor) of a domesticated crop, but wrongly applied to uncultivated populations without consideration if the ancestry of the population traces to a relative (or ancestor) or the domesticated crop (see Feral)

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