



# **The Domestication and Dispersal of Large-Fruiting Prunus spp.: A Metadata Analysis of Archaeobotanical Material**

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**Abstract:** The *Prunus* genus contains many of the most economically significant arboreal crops, cultivated globally, today. Despite the economic significance of these domesticated species, the pre-cultivation ranges, processes of domestication, and routes of prehistoric dispersal for all of the economically significant species remain unresolved. Among the European plums, even the taxonomic classification has been heavily debated over the past several decades. In this manuscript, we compile archaeobotanical evidence for the most prominent large-fruiting members of *Prunus*, including peach, apricot, almonds, sloes, and the main plum types. By mapping out the chronology and geographic distributions of these species, we are able to discuss aspects of their domestication and dispersal more clearly, as well as identify gaps in the data and unanswered questions. We suggest that a clearer understanding of these processes will say a lot about ancient peoples, as the cultivation of delayed return crops is an indicator of a strong concept of land tenure and the specialization of these cultivation strategies seems to be tied to urbanism and reliable markets. Likewise, the evolution of domestication traits in long-generation perennials, especially within Rosaceae, represents awareness of grafting and cloning practices.

**Keywords:** *Prunus*; plum; peach; apricot; domestication; horticulture; hybridization; arboriculture; archaeobotany

## 1. Introduction

Scholars argue that the domestication of perennial crops, such as fruit trees, took place several millennia after the domestication of annual herbaceous plants (i.e., cereals and legumes), due to the increased complexity and multi-year perspective and planning required for managing fruit trees before the first harvest [1–4], although there is some



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**Copyright:** © 2023 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). evidence that a few fruits could have been managed alongside cereals during a long period of pre-cultivation management [5]. Some scholars have suggested that fruit tree management was closely linked with the rise of urbanism, the establishment of reliable exchange networks and markets, and the development of new forms of land ownership [1]. This is partially due to the fact that most fruit species propagate better clonally through grafting or budding than when grown from the seed. Vegetative propagation offers the advantage of better selection control of preferential qualities and shortens the pre-maturity stage (the period prior to the first fruit production) over growing from seeds, which takes a minimum of three to five years [6,7]. The main measurable changes derived from human management include an increase in size and sugar content, reduction in acidity of the fruit, and a loss of spines on the branches [3]. Archaeobotanically, the most useful trait hypothesized to accompany the domestication of long-generation perennials is the elongation of the fruit seed [8]. This may be a vestige of their endozoochoric legacy, whereas a fruit seed that increases evenly in size will evolve to be too large for the disperser to swallow, while elongation still allows the seed to be consumed. Evidence for the consumption of Prunus fruits is attested by at least the Neolithic (c. 8/7th millennium B.C.E.) at the two ends of the Eurasian continent, with a marked increase in remains starting around the terminal 4th or early 3rd millennium B.C.E. [1]. While we assume that the early *Prunus* pits represent foraging from the wild, the transition from foraging—to managing wild population—to low-investment cultivation, likely of hedgerows or trees scattered around occupation sites—to full orchards and irrigated populations, remains poorly understood. Likewise, despite the long, archaeologically documented history of human consumption, and their substantial economic importance from antiquity to today, many questions about their evolutionary trajectories and especially how the domesticated forms came to be so widespread across Eurasia and North Africa remain unanswered.

In this paper, we review the current archaeobotanical evidence on large-stone *Prunus* fruits from archaeological sites in Eurasia and North Africa. Through a metadata chronological analysis of *Prunus* types presence, we trace the routes and timing of the dispersal from antiquity to pre-industrial times (c. 1890 C.E.) of the following: *Prunus persica* [L.] Batsch (peach); *Prunus armeniaca* L. (apricot); *P. spinosa* L. (syn. *P. domestica* var. *spinosa* [L.] Kuntze; sloe); *P. domestica* L. (syn. *P. domestica* subsp. *oeconomica* (Borkh.) C.K. Schneid; plum, sometimes referred to as European plum, referred to as *domestica* type in this publication); *P. insititia* L. (syn. *P. domestica* subsp. *insititia* [L.] C.K. Schneid; bullace, referred to as *insititia* type in this publication), and *P. cerasifera* Ehrh. (cherry plum). We excluded *P. mume* (Siebold) Siebold & Zucc. and *P. salicina* Lindl. (Japanese apricots and plums, respectively) from our study due to their late dispersal out of East Asia, which was within the last two to three centuries [2,9] (p. 141), as they are, therefore, outside of the chronological focus of this research. We follow accepted nomenclature as listed in the "Plants of the World Online", facilitated by Royal Botanic Gardens, Kew [10].

## 1.1. Taxonomy of Plums

#### Debates and Identification Issues

The *Prunus* clade is situated within the Rosaceae family, one of the most widely cultivated families of angiosperms. Members of the family are prone to significant diversity under hybridization, leading to cultivated hybrid complexes, with individuals or genets often genetically locked into place through clonal reproduction. The subfamily Prunoideae is characterized by species that produce drupes known as "stone fruits" where the seed is encased in a hard, lignified endocarp referred to as the "stone", and the fleshy portion is a sugary mesocarp. Both the Prunoideae and Maloideae subfamilies include avian-dispersed and megafruiting forms, with megafruits evolving at least twice following very different pathways towards pomes and drupes [11,12]. Over the past decade, much has been clarified regarding the domestication and dispersal of the apple (*Malus* domestica (Suckow) Borkh.) [13–16], but economically important members of Prunoideae remain enigmatic. Many of the most consumed arboreal fruits of the world today are in *Prunus*, aclade

consisting of more than 400 species, with wild and cultivated varieties distributed across the temperate regions of all continents [17,18]. Even the evolutionary history of members of the *Prunus* clade remains unsettled, with many contradictory systematics schemata [19].

There are many obstacles to studying the domestication and ancient dispersal of largefruiting members of *Prunus*, including morphological similarities between the seeds/fruits of different clades and issues in taxonomic classification. Given the likelihood of hybridization across the family and the impressive ranges of phenotypic diversity in the clade, the phylogeny of large-fruiting members of Rosaceae has been challenging to parse out. As a result, many conflicting taxonomic systems exist (for a good summary, see Shi et al. [18]: Figure 1).



**Figure 1.** Photos of modern examples of *Prunus* stones by species. 1. Peach (collected by K. Boxleitner, 2021, Surungur, Kyrgyzstan); 2. Apricot (collected by K. Boxleitner, 2021, Obishir-5, Kyrgyzstan); 3. Sloe (seeds and fruit collected by R. Spengler, 2020, Jena, Germany, fruit not to scale); 4. Cherry plum (collected by B. Zach, 1993, Botanical Garden Hohenheim, Germany; fruit collected by R. Spengler 2022, Issyk-kul, Kyrghistan, not to scale); 5. *insititia*-type plum, stone and fruit (stone collected by B. Zach, 1985, Tübingen, Germany; fruit collected by R. Spengler 2020, Jena, Germany, not to scale); 6. *domestica*-type plum, stone and fruit (stone collected by B. Zach, 1992, Tübingen, Germany; fruit collected by B. Zach, 1992, Jena, Germany; fruit collected by R. Spengler 2020, Jena, Germany; fruit collected by B. Zach, 1992, Tübingen, Germany; fruit collected by B. Zach, 1992, Tübingen, Germany; fruit collected by R. Spengler 2020, Jena, Germany, not to scale).

In our present synthesis, we focus on the evidence for domestication and dispersal of large fruiting members of *Prunus* sect. *Armeniaca*, sect. *Persicae*, and sect. *Prunus*, as defined by Shi et al. [18]. Often scholars have split the economically significant *Prunus* species into separate genera, notably by separating *Persica* from *Prunus*. However, phylogenetics has favored a single encompassing *Prunus* genus for peaches, apricots, sloes, plums, and other so-called *Prunus* fruits (i.e., cherries) [20,21]. Below the subgeneric level, species and subspecies classifications are still debated. For example, the currently accepted names for a species division of sloes, *domestica*, and *institia* type plums are *P. spinosa* L., *P. institia* L., and *P. domestica* L., respectively [22], but other scholars advocate for a subspecies differentiation into *Prunus domestica* var. *spinosa* (L.) Kuntze (sloes), *Prunus domestica* ssp. *institia* (L.) C. K. Schneid, and *P. domestica* ssp. *oeconomica* (Borkh.) C. K. Schneid. The latter clade is sometimes referred to as *P. domestica* ssp. *domestica* [23]. More recently, scholars are proposing a system more in line with the biological species concept, clumping any of the former species in the hybrid complex into *P. domestica* as subspecies or varieties, which

calls into question accepted divisions within the Prunus genus. In a 2019 study, a team of geneticists analyzed 405 specimens labeled Prunus domestica from germplasm facilities. Based on their data, they divided the large-fruiting European plums into four clades, which they labeled greengages, mirabelles, European plums, and d'Agen or prune plums [24]. Further complicating discussions of domestication, this group pulled out the sloe (P. spinosa) and the cherry plum (*P. cerasifera*) as the only truly wild relatives that are extant, suggesting a third, extinct member of the hybrid complex, and removed P. insititia from their classification. Instead of leaving *P. insititia* within the genus, the geneticists identified a polyploidy complex for P. cerasifera as the hybrid of P. cerasifera and P. spinosa, which traditionally has been labeled P. insititia. This study also demonstrated that many of the independent varieties in germplasm facilities were clones of each other or a single generation removed. Ultimately, this team concluded that the low genetic diversity across the group suggests that they are highly inbred and/or derived from a small number of original founders. Although the study focused on accessions from gene banks, likely missing any extant wild ancestors and wild accessions in herbaria and/or the archaeological record, illustrating how recent genetic studies have complicated more than they have clarified, leaving a need to try to integrate their results with other lines of data (especially archaeological and historical) and broader academic discourses.

When trying to integrate multiple lines of evidence, however, the lack of resolution within the nomenclature causes complications. When common names are used, especially in English, it is often unclear which species is being discussed; for example, with the term "damson" used indiscriminately to refer to both domestica and insititia type plums. This issue is less prominent within the archaeobotanical literature due to the use of Latin names; although, it is still a widespread practice across the popular literature (gardeners, garden centers, and plant aficionada). Issues still persist with regard to whether plums, especially domestica and insititia types, are to be considered two different species or two subspecies of *P. domestica*, as indicated above. In the academic literature, both views are used interchangeably among scholars, but with a more widespread use of the subspecies division. This is due to earlier classification systems put forward by European botanists and archaeobotanists, who classified plums into numerous subspecies and varieties based on both modern and ancient plum remains from Central Europe [25–29]. The most comprehensive modern Prunus classification was proposed by Koerber-Grohne [23] that combined archaeobotanical and modern material in line with current scientific nomenclature. Koerber-Grohne [23] favored a subspecies classification of domestica and institutia plums into P. domestica ssp. oeconomica and *P. domestica* ssp. *insititia*, listing numerous further varieties of each in what is still the most detailed work on ancient plum classification published to date.

In this paper, we adopt Koeber-Grohne's classifications of separate *domestica* and *insititia* types, and consider *domestica* plums those fruits that are oblong in shape, with blue/blueish skin color, sunken in-seam (lateral furrow) visible on the fruit, and pointy stone (at both ends) easily removable from the fruit flesh (sometimes called freestone fruits); *insititia* plum fruits, instead, are often more round in shape, can be either blue, green, yellow, or red colored, the fruit does not present a prominent seam, and the stone is not easily removed from the flesh (sometimes called clingstone fruits or cling fruits); the stone itself is roundish without a clear protruding base (Figure 1) [23]. It is worth noting that official floras of different countries do not offer such standardized characteristics for these fruits, and the accepted division is not universally agreed upon [30] (p. 10). For example, the *Flora of Turkey and the East Aegean Islands* does not have an entry for an *insititia* type plum even as a variety, and it lists the *domestica* type as a hybrid: *P*. × *domestica* [30] (p. 10). Additionally, we should clarify that these species or subspecies exist in a hybrid complex, and may contain more intermittent forms in some regions of Eurasia than in others.

We also assume that, whether archaeobotanists used the species or subspecies division for their identification in the academic literature, they refer to the same type of plum, and for the purposes of our database and analysis below, we have grouped *P. domestica* and *P. domestica* ssp. *oeconomica* (and other synonyms) with the *domestica* type plum, and *P. insititia* and *P. domestica* ssp. *insititia* with the *insititia* type plum. Given the persistent issues with common English names, and the unresolved species vs. subspecies division for these two plum types, we have decided to refer to these fruits as *domestica*-type and *insititia*-type plums throughout our article.

## 1.2. Hypothesized Origins of Plum, Peaches, and Apricots

# 1.2.1. Plums and Sloes

The sloe is a native European species with clear morphological and genetic parameters and a native range spanning much of Europe. The cherry or myrobalan plum, *domestica* plum, and possibly *insititia* plum have all been at times suggested to also originate in Europe, with notable early archaeological remains of alleged wild *insititia* plum and cherry plum (cf. *cerasifera* plum) reported from sites in Germany [23,25] and Bulgaria (Gudzhova, Mogila) [31]. However, other scholars have suggested that they may have originated in Western or Central Asia [32,33], leaving each species' center of origin largely unresolved. The lack of understanding has been further exacerbated by a dearth of archaeobotanical investigations in Central Asia until rather recently.

#### 1.2.2. Apricots

It was accepted that the apricot originated in the Caucasus Mountains, likely tied to Pliny the Elder's claim that the tree originated there combined with a strong cultural affinity for the fruit in that part of the world today. However, a series of studies over the past few years has found early remains of apricots along with peaches in eastern China [1,34]. The lack of identification of any early apricot remains in the Caucasus has challenged thisorigin hypothesis, but left open a debate over whether the apricot could have secondarily originated in a different part of Central Asia. Ecologists have claimed that the wild apricot has a range that spans from Eastern China all the way to the Tian Shan Mountains in Central Asia [35,36]. Indeed, the most recent genetic studies of modern population distributions suggest two likely centers of origin, one in China (most likely northern or eastern China), and one in western Central Asia (presumably in the Fergana Valley), from where the fruit may have spread to the Mediterranean region through either southern Europe or northern Africa [2,37-40]. It is hypothesized that these two centers derive from populations that became isolated during glaciation periods [40]. Archaeologically, apricot remains in China predate those from Central Asia, but this may reflect the scarcity of archaeobotanical work undertaken in Central Asia as well as the difficulty in identifying fragmented Prunus stones to species level.

### 1.2.3. Peaches

The wild progenitor of the domesticated peach is unknown and most scholars believe it to be extinct. The scientific name for peach derives from the Greek persikon malon, and subsequently Latin *malum persicum*, meaning Persian apple, attesting to the early belief that peaches originated in Persia (or more generally somewhere to the east, as many customs and beliefs originating to the east of the Classical world were simply ascribed to Persia). This hypothesis was postulated by ancient Greek and Roman writers (see below) and adopted by European botanists before the 19th century [41]. Today, peaches are generally believed to have originated in Persia [42]; however, at present, the earliest securely identified and dated peach remains come from the site of Kuahuqiao, in the lower Yangzi Basin, dated to 8000–7500 B.C.E. [34]. Fossilized peach stones have also been found close to Kunming, in Yunnan, southwest China, dating to c. 2.6 million years ago [43]. These Pliocene peach stones closely resemble modern peach stones in size and shape, suggesting that initial selection of this fruit was most likely driven by large frugivorous mammals possibly including primates. Later evolution of domestication traits acted to increase fruit size and variety differentiation [1]. Phylogenetic reconstruction and analyses of the peach genome seems to support a Chinese origin, indicating a separation event of P. persica from wild species in China around three to four thousand years ago [44].

## 2. Materials and Methods

For the metadata of large-seeded *Prunus*, we consulted the available archaeological literature with reports of plant remains from sites across Eurasia and North Africa dating from the c. 10/9th millennia B.C.E. to c. 1890 C.E. When possible, we consulted original reports; however, we have also included all reasonable secondary references to Prunus remains, including data from regional reviews and previously published relevant databases [1,34,45]. When access to the primary sources was not available, this has been clearly indicated in the Table S1 ("Dataset of published *Prunus* finds and their chronologies from Eurasia and North Africa"). We have adopted a fully inclusive approach and collected all data regardless of the recovery methodology employed during excavation (e.g., hand-picked or flotation) and preservation conditions of the plant remains (e.g., charred, waterlogged, ormineralized), provided the remains were carpological and notwood charcoal. Many scholars identify Rosaceae wood charcoal only to subfamily, so we have eliminated all wood-based identification, due to a lack of agreement regarding possible specific traits. We took note of the original recording of the remains as provided in the publications (e.g., Latin binomial and common names) and we have indicated the availability of photographs of Prunus remains in the original literature (indicated by Y/N in Table S1). We limited our judgement about the accuracy of the identification and avoided any attempt at re-identifying the reported remains, unless otherwise stated in the text. Unclear finds have not been plotted in the figures below (Figures 2-8), but these have been included in Table S1 and indicated by a question mark.

We collected information on *Prunus* remains from a total of 432 individual sites, including unpublished data from two sites in Central Asia (Bukhara and Afrasiab; Table 1; Table S1). The compiled sites were divided into the following macro-regions (countries listed in alphabetical order):

- East Asia: China, Japan, Korea.
- Central Asia: China (Xinjiang Province), Kazakhstan, Kyrgyzstan, Tajikistan, Turkmenistan, Uzbekistan.
- Western Asia: Arabia, Armenia, Cyprus, Iran, Israel, Jordan, Syria, Turkey.
- South Asia: India, Nepal, Pakistan.
- Europe: Austria, Belgium, Bulgaria, Czechia, France, Germany, Greece, Hungary, Italy, Moldova, Netherlands, Poland, Portugal, Romania, Serbia, Spain, Switzerland, United Kingdom.
- North and Northeast Africa: Egypt, Morocco, Tunisia.

Species	East Asia	Central Asia	Western Asia	South Asia	Europe	N and NE Africa	Total
P. persica	125	16	6	7	82	12	248
P. armeniaca	65	13	2	12	3	3	98
P. spinosa	-	-	2	-	105	-	107
P. cerasifera	-	2	1	-	12	1	16
<i>insititia</i> plum	-	-	2	-	45	1	48
domestica-plum	-	1	1	2	50	3	57
Prunus sp.	19	13	17	2	39	-	90

**Table 1.** Summary of finds of large-fruiting *Prunus* remains per each macro-region.

To explore patterns in the presence/absence of the retrieved remains across time and space, and thus individuate early centers of foraging or cultivation of the fruits and potential routes or waves of dispersal for each species, we plotted the sites chronologically. Each site was plotted considering the mean occupation date, which was calculated from the established occupation range of the site. The dating of the sites considered for this study is not homogenous, with some sites dated through direct radiocarbon dating on *Prunus*  remains (indicated in the Table S1 as "C14 dir"), some sites dated through radiocarbon dating on other plant remains (seeds), charcoal, or bones (indicated in Table S1 as "C14 indir"), some dated by dendrochronological analysis of associated wood ("dendro"), and finally some dated through association to the archaeological material culture typology sequences (indicated in Table S1 as "assoc").

The dataset from Japan was particularly detailed, thanks to the online open-access  $C^{14}$  database of the National Museum of Japanese History (https://www.rekihaku.ac.jp/up-cgi/login.pl?p=param/esrd/db\_param, accessed on 10 May 2022). We extracted direct radiocarbon dates on *P. persica* stones in addition to dates from a recent study by Fujio and colleagues [46]. This provided a total of 137 dates on *P. persica* endocarps from 69 sites. In cases where several dates derived from the same site and same cultural chronology, we combined them in our Table S1. A list of all original information and individual direct radiocarbon dates and relative entries, including indication of radiocarbon laboratory number and uncalibrated date, is provided in Table S2 ("Directly radiocarbon-dated *Prunus* remains from archaeological and early historic context in Japan published in the Radiocarbon Database of the National Museum of Japanese History"). We found no cases of *P. armeniaca* with direct dates in the National Museum of Japanese History's online database, but an archaeobotanical macrofossil database also housed by the National Museum of Japanese History (https://www.rekihaku.ac.jp/up-cgi/login.pl?p=param/issi/db\_param, accessed on 10 May 2022) lists 37 sites with reported *P. armeniaca* macrofossils from Japan.

## 3. Results

There is considerable unevenness in the number of published records for each species and across regions and time periods (Table 1). Peach remains are the most reported species, followed by sloe, and then *Prunus* sp. *Prunus* sp. remains from East Asia may represent Japanese plums and apricots (P. mume and P. salicina), while Prunus sp. remains from Southwest Asia may represent almond (*P. amygdalus* Batsch) since these are native to these regions. The great number of archaeobotanical remains simply classified as *Prunus* sp. (Figure 2) attests to the difficulty of identifying archaeobotanical remains to species level. When the preservation status of the remains was available in the reports, we found that published Prunus remains were mostly charred or waterlogged (79 and 49 occurrences respectively, with multiple occurrences of unspecified "uncharred" remains), but stones were also preserved by desiccation and mineralization (Table S1). In terms of recovery contexts, *Prunus* remains were found in a variety of contexts, including burials, dwellings, cesspits, hearths/ovens, or storage deposits, as well as general rubbish pits, wells, and cultural deposits. In most regions, outside Japan where fruit stones are often used to anchor ceramic chronologies, Prunus remains are usually not directly dated, with most sites in our database dated through either cultural association or radiocarbon dating on various associated archaeological material (bones, wood charcoal, or cereal grains). Beyond the already mentioned directly dated peach stones from Japan, we found only one other report of a directly dated peach stone from the tomb of Marquis Haihun in Nanchang, Jiangxi, China (95 B.C.E.–26 C.E.) [47], and one report of directly dated desiccated unspecified Prunus remains from Areni-1 in Armenia (4230–3800 B.C.E.) [48,49].



**Figure 2.** Spatio-temporal distribution of *Prunus* sp. remains from Eurasia compiled within the database (see Table S1) shown (**a**) on a topographic map and (**b**) in an age-longitude plot.

# 3.1. Peach

Archaeobotanically, peach is the most reported large-stone Prunus species, with 248 accounts of peaches from across all regions and time periods, but mostly found in East Asia, followed by Europe (Table 1; Figure 3). Chronologically, peach stones first appear in the archaeological record of China from at least the 8th millennium B.C.E. At present the earliest sites with reported peach remains are Kuahuqiao in Zhejiang (8000-7500 B.C.E.) and Bashidang in Hunan (8500-7600 B.C.E.) [34]. There are no reported peach remains outside of modern mainland China from the 8th to the 5th/4th millennia B.C.E., until peach stones were reported at P'aju Taenŭngri in Korea (3900-3400 B.C.E., dated by cultural association) [50], and at Ikiriki in Nagasaki, Japan (5000–3500 B.C.E.). Peach finds from the Ikiriki site have been frequently discussed in the English literature, e.g., [51] and used to claim that the peach was introduced to Japan as early as the 5th millennium B.C.E. [34]. Ikiriki produced 19 peach stones [52] (p. 47); of these, three are from Layer III, which is dated broadly between the Yayoi to medieval periods. Layer IV, which lacked cultural artefacts, produced two stones. Another three stones came from Layer V, dated to the Late-Final Jōmon. Finally, there were ten examples from the Early Jōmon strata: six from Layer VII (associated with Sobata pottery) and four from Layer VIII (associated with Todoroki B pottery). As described in the site report, the stratigraphy at Ikiriki was, in places, disturbed by what the excavators termed 'sand pipes', traces of ancient animal burrowing. Of the ten Early Jomon peach stones, nine come from deposits classified as type 'a' where the stratigraphic relationship with the 'sand pipes' is unclear. Only one example is type 'b', claimed to be from undisturbed deposits [52] (p. 47). These issues suggest that caution is required in accepting Ikiriki as an example of a pre-Bronze Age introduction of *P. persica* to Japan.



Longitude

**Figure 3.** Spatio-temporal distribution of *Prunus persica* remains from Eurasia and Northern Africa compiled within the database (see Table S1) shown (**a**) on a topographic map and (**b**) in an age-longitude plot. Sites mentioned in text listed in chronological order: 205: Kuahuqiao; 52: Bashidang; 165: Ikiriki; 323: P'aju Taenŭngri; 72: Burzahom; 153: Heraion; 90: Chehrabad; 114: el-Hibeh; 226: Lleida; 336: Pompeii; 209: Koy-Krilgan-kala; 359: Sampula. Site numbers refer to site ID as labelled in Table S1.

The earliest report of peaches outside East Asia comes from Burzahom, in Kashmir, where it has been reported throughout the occupation of the site (2400–1400 B.C.E. and 1000 B.C.E.–200 C.E.) [53]. While a photo of one of the fragments has been published, it is not diagnostic from the image and there are no direct dates. In Southwest Asia, peach and plum stones have been found in association with ancient contexts in a collapsed salt mine in Chehrabad, Iran (550–330 B.C.E.) [54]. Peach stones have been reported from archaeological sites in Europe only from the Roman period/1st millennium B.C.E., for example at Heraion in Greece (700–600 B.C.E.) [55,56], Lleida in Spain (200–1 B.C.E.) [57], and throughout Italy, including Pompeii (200 B.C.E.–79 C.E.) [58,59] and northern Italy (100 B.C.E.–400 C.E.) [60]. Similarly, peach has been reported from Africa at el-Hibeh in Egypt at the end of the 1st millennium B.C.E. (c. 100 B.C.E.) [61]. At present, peach finds from Central Asia date to much later than either those from East or southwest Asia, and have been reported from Koy-Krilgan-kala in Uzbekistan, dating to between 200 B.C.E. and 300 C.E. [61], and Sampula, in Xinjiang, China, dating to between 55 B.C.E. and 300 C.E.) [62–64].

Although peach finds remain relatively isolated in all regions except East Asia until the early 1st millennium B.C.E., a marked increase of peach finds is attested starting in the late 1st millennium B.C.E. and especially from the 1st millennium C.E. onwards.

#### 3.2. Apricot

According to present evidence, the earliest apricot finds, dating to the 6th millennium B.C.E., come from modern mainland China, where apricot stones have been reported from the sites of Kuahuqiao in Zhejiang (8000–7500 B.C.E.) [34,65,66], Jiahu in Henan (7000–5500 B.C.E.) [45], Fuxin 12D56 (also known as Jiajiagou West, 5900–5700 B.C.E.), and Fuxin 12D16 (also known as Tachiyingzi, 5500–5300 B.C.E.) in Liaoning Province [67]. Within East Asia, some records of apricots are available from Japan. Most of these are assigned on stratigraphic grounds to the Kofun period (250–700 C.E.) or later. Two of the finds are assigned to the Yayoi period and one to the Neolithic Jōmon. The Jōmon apricot is reported from the Tetori-shimizu site [68]. According to the site report, a single apricot stone was found in grid NH72, a former stream deposit, which produced pottery from the Jōmon, Yayoi, and Kofun periods [68] (p. 108, 370). Discounting this 'Jōmon' find as likely contamination, current evidence suggests *P. armeniaca* was introduced to Japan during the Kofun period, or in the third century C.E. at the earliest.

Comparable with the peach, the apricot remains were confined to East Asia for several millennia before dispersing to the other regions (Figure 4). Only from the 3rd/2nd millennium B.C.E. have apricot remains been reported from southern Asia, at Burzahom (2400–1000 B.C.E.) and Semthan (1500–200 B.C.E.) in Kashmir [53], where peaches have also been found. The apricot seems to be a late comer to Central Asia, Africa, and Europe, reaching Central Asia only during the late 1st millennium B.C.E., as evidenced from remains from Sampula, in Xinjiang, China (55 B.C.E.–300 C.E. [62–64], where peaches were also reported. Apricots have been found at Saqqara in Egypt (330 B.C.E.–350 C.E.) [45], and Bosra in Syria (100 B.C.E.–300 C.E.) [45]. In Europe, there is one tentative apricot identification from Aquileia in Italy (1–400 C.E.) [60] in the first millennium C.E. The rest of the records do not appear until the 2nd millennium C.E., and even then, there are only two sites with reported apricot remains: early Renaissance Ferrara in Italy (1250–1500 C.E.) [69,70] and late Medieval Paris (Cour Carrée of Louvre) in France (1300–1600 C.E.) [71]. In both later instances, apricot stones were reported from cesspits/latrines; no photos of these apricot remains were available and the stones have not been directly dated.

## 3.3. Sloe and Plums

## 3.3.1. Sloe

Sloe is considered a native species to Europe, and it is not surprising that most of the records for this species come from this region, with only one report from West Asia and no other finds from any of the other regions included in this study (Table 1; Figure 5). Sloe remains are reported from at least the 7th/6th millennium B.C.E. from broader southern Europe, including at Nea Nikomedeia in Greece (6400–6100 B.C.E.) [72,73], Sammar-denchia, Lugo di Romagna, Piancada and Pavia di Udine in Italy (6th/5th millennium B.C.E.) [74–76], and La Draga in Spain (5400–4500 B.C.E.) [77]. Chronologically, there are no notable differences in the presence of sloe remains across time in Europe.

There is one possible sloe report from Southwest Asia comes from Arslantepe in Turkey, 3350–3000 B.C.E. [78]; however, this reported as *P.* cf. *spinosa* and, therefore, should be considered with caution.



**Figure 4.** Spatio-temporal distribution of *Prunus armeniaca* remains from Eurasia and Northern Africa compiled within the database (see Table S1) shown (**a**) on a topographic map and (**b**) in an age-longitude plot. Sites mentioned in text and listed chronologically: 205: Kuahuqiao; 172: Jiahu; 413: Tetori-shimizu; 128: Fuxin 12D56; 127: Fuxin 12D16; 72: Burzahom; 376: Semthan; 368: Saqqara; 64: Bosra; 359: Sampula; 27: Aquileia; 120: Ferrara; 103: Cour Carrée of Louvre. Site numbers refer to site ID as labelled in Table S1.



**Figure 5.** Spatio-temporal distribution of *Prunus spinosa* remains from Eurasia and Northern Africa compiled within the database (see Table S1) shown (**a**) on a topographic map and (**b**) in an age-longitude plot. Sites mentioned in text and listed chronologically: 290: Nea Nikomedeia; 356: Sam-mardecchia; 229: Lugo di Romagna; 334: Piancada; 217: La Draga; 327: Pavia di Udine; 35: Arslantepe. Site numbers refer to site ID as labelled in Table S1.

## 3.3.2. Cherry Plum

Cherry plum records are the least abundant across all regions (Table 1; Figure 6). Chronologically, there is only one possible record of cherry plum dating to an early age; this comes from Sacarovca in Moldova (5650–5500 B.C.E.) [79]. All other reports date to much later, at the earliest to the very end of the 1st millennium B.C.E. onward. Cherry plum has been reported from Aşvan Kale (Hell) in Turkey (100–1 B.C.E., so far this is also the only reported cherry plum record from Southwest Asia) [80]; Aachen-Burtscheid (50–150 C.E.) [81] and Ellingen in Germany (115–211 C.E.) [82], and Berenike in Egypt (1–400 C.E.; this is also the only record from Northeast Africa) [83]. In Central Asia, cherry plum has been reported even later than that reported in the other regions, from the medieval sites of Balalyk Tepe in Uzbekistan (500–700 C.E.) [84], and at the site of Bazar-Dara in Tajikistan (800–1100 C.E.) [85], where over 10,000 cherry plum pits have been reported. Bazar-Dara is located at nearly 4000 m asl; since plums cannot grow at such a high altitude, the fruits might have been transported to the site preserved, either dried or fermented.



Longitude

**Figure 6.** Spatio-temporal distribution of *Prunus cerasifera* remains from Eurasia and Northern Africa compiled within the database (see Table S1) shown (**a**) on a topographic map and (**b**) in an age-longitude plot. Indication of sites mentioned in text and listed chronologically: 353: Sacarovca; 66: Brescia; 38: Aşvan Kale; 1: Aachen-Burtscheid; 116: Ellingen; 58: Berenike; 45: Balalyk Tepe; 53: Bazar-Dara. Site numbers refer to site ID as labelled in Table S1.

#### 3.3.3. Insititia Plum

*Insititia* plum (*P. insititia*, syn. *P. domestica* ssp. *insititia*) finds mostly occur within Europe, with only one example from Northeast Africa at the already mentioned site of Berenike in Egypt (1–400 C.E.) [83], and another from Southwest Asia, where, at present, we find the earliest report for this species at the site of Khirokitia in Cyprus (6400–6100 B.C.E.) [86–88]. Other early finds, dating to the 6th millennium B.C.E., are attested first from southern and eastern Europe, for example from Dzhulyunitsa and Samovodene in Bulgaria (6100–5700 B.C.E.; 5700–5400 B.C.E.) [79], and at the site of La Marmotta in Italy (5879–5074 B.C.E.) [75], but reports are generally quite scarce until

the beginning of the 1st millennium C.E. A marked increase of *insititia* plum finds can be attested only from the end of 1st millennium C.E. onward, especially from Central and Northern Europe (Figure 7). Some *Prunus* sp. fragments recovered by the authors from Bronze Age sites in Turkmenistan (Adji Kui 1 and Togolok 1) [90,91] resemble published drawings of *insititia* stones from Samovodene [89]; however, ethnobotanical remains of *Prunus* species collected in Central Asia, including *insititia* and *cerasifera* plums, look dissimilar to the archaeological specimens and the unclear taxonomic division hinders precise identification of such types of remains.



Longhado

**Figure 7.** Spatio-temporal distribution of *insititia* type remains from Eurasia and Northern Africa compiled within the database (see Table S1) grouped into 1000-year increments shown (**a**) on a topographic map and (**b**) in an age-longitude plot. Sites mentioned in text: 189: Khirokitia; 109: Dzhulyunitsa; 353: Sacarovca; 357: Samovodene; 218: La Marmotta; 58: Berenike. Site numbers refer to site ID as labelled in Table S1.

## 3.3.4. Domestica Plum

The earliest records of *domestica* plum (*P. domestica*, syn. *P. domestica* ssp. *oeconomica*, syn. *P. domestica* spp. *domestica*) date relatively later than all other species considered for this study, with the earliest available records coming from 6/5th millennium B.C.E. Europe (Figure 8). As with the earlier *insititia* and cherry plums, *domestica* plum has been reported from Sacarovca in Moldova (5650–5500 B.C.E.) [79] and Poduri in Romania (4700–4400 B.C.E.) [92,93]; and subsequently from Scarceta di Manciano in Italy (1443–1116 B.C.E.) [94]. There is only one report of *domestica* plum in West Asia, from Büklükale in Turkey (c. 1800–1650 B.C.E.) [95], and in Northern Africa, we have two reports of *P. domestica* from Antinopolis (c. 330 B.C.E.–300 C.E.) [96] and Berenike (1–400 C.E.) [83]. Stones of *domestica* have also been reported from the site of Burzahom in Kashmir (1000–600 B.C.E.) [53], the only site with this species in South Asia to date. The majority of *domestica* plum records, however, date to the 1st millennium C.E. onward, and they are mainly clustered in Europe. The only reported *domestica* plum remains from Central Asia come from Karaspan-tobe, in Kazakhstan (300–500 C.E.) [97]; however, this is



quoted in the original publication as a single "heavily destroyed carbonized stone" [97] (p. 88) and the report provides no photos, so it should be considered with caution.

**Figure 8.** Spatio-temporal distribution of *domestica* type remains from Eurasia and Northern Africa compiled within the database (see Table S1) shown (**a**) on a topographic map and (**b**) in an age-longitude plot. Sites mentioned in text and listed chronologically: 353: Sacarovca; 335: Poduri; 369: Scarceta di Manciano; 73: Burzahom; 69: Büklükale; 18: Antipolis; 58: Berenike; 184: Karaspantobe. Site numbers refer to site ID as labelled in Table S1.

#### 4. Discussion

## 4.1. Tracing Early Centers and Dispersal of Peaches

The current archaeobotanical record supports a Chinese center of origin for the peach, as already postulated by others and in line with genetic evidence [34,44,45]. Its dispersal outside of modern China only occurred after a few millennia of foraging from the wild and likely cultivation within mainland China and spread first within East Asia; only during the second half of the 1st millennium B.C.E. is there archaeobotanical evidence attesting to its spread to other regions. These data seem to fit the current understanding of the Trans-Eurasian Exchange, as other East Asian domesticated plants and animals appear to have rapidly dispersed to the far ends of two continents at the same time, notably rice and chicken [98–100].

Within East Asia, given that archaeological evidence clearly shows that Jōmon Japan was in frequent contact with the East Asian mainland, especially in the later phases of that period [101,102], it cannot be excluded that fruit was occasionally traded from the continent and possibly dispersed to Japan at an early date, but in the absence of direct radiocarbon dates, it seems prudent to be skeptical of finds of *P. persica* in Japan dated to the pre-Yayoi (1000 B.C.E.) periods. It is more likely that, as with Europe and Central Asia, during the second half of the 1st millennium B.C.E., arboriculture developed as part of a specialized agropastoral economy linked with trade and urbanization [1]. Following this assumption, the introduction of peaches and apricots into Japan followed other cultural changes. Early historical records from Japan mentioned below show that fruit trees formed an important

element in aristocratic and religious estates. The Makimuku site near Nara was a center of political power in the third-century C.E. [103–105]. Makimuku has produced 2765 peach stones, reported by Kidder [105] (p. 13) and Ikita [106], noting 2795 stones from a single large pit at the site. Such discoveries are consistent with the conclusion that Taoist ideas about 'immortal peaches' may have played a role in the increasing cultivation of this fruit in the last centuries of the Yayoi period. Nevertheless, ritual and political uses of the peach should not be seen as opposing interpretations, a point emphasized in Blan's [107] study of early medieval France.

The absence of early records of peach from Central Asia when compared to early records from South Asia, Western Asia, and even Europe may indicate that the peach dispersed westward following a southern but still temperate-zone route, possibly along the Himalayan foothills, similar to that of rice [100], a trajectory corroborated by the Persian origin of words for peach in the ancient languages of Central Asia (discussed below) [108]. At the beginning of the Roman Era, peach was a luxury item but became one of the most ubiquitous fruits throughout Italy during this period [60,109]. After the Roman Era, there is a sharp increase of records across all regions, including Europe. While an influence of better preservation conditions and more extensive archaeological research in those stratigraphic layers cannot be excluded, this might also indicate a growing popularity of the fruit following Roman times, and, as in Japan, was likely driven by increasing urbanization, stable markets, and intensive and extensive agricultural practices. The sharp difference between peach reports and other *Prunus* species considered for this study might be due to the relative ease of identifying this fruit in comparison to plums and apricots, given the distinctive corrugated features of peach stones.

Early written accounts of peaches can be found in several Chinese texts dating to at least the first millennium B.C.E. These accounts include descriptions of the elegance of the peach tree and the edibility of its fruits in several *Shijing* poems (*Book of Odes*, 1027–476 B.C.E.) [110,111]. Additionally, descriptions of the blossoming of the peach tree are found in the *Li Ji* (*Classic of Rites*, 475–221 B.C.E.); reference to flowering times of peach (and apricot) trees are found in the *Xia Xiaozheng* (*the Lesser Canon of the Xia*), an early astronomical almanac listing star and constellation movements for each of the yearly seasons as well as describing the related agricultural and political activities to be undertaken throughout the year. The text describes events occurring during the Xia Dynasty (c. 2100–1600 B.C.E.), but it was more likely written in c. 100–200 C.E. [112–114].

In Japan, the *Engishiki*, a text completed in 927 C.E., but building on earlier records, describes an orchard attached to a hospice run by the Tōdaiji temple with 83 fruit trees in 771 C.E., and noted the imperial court orchard had 460 fruit trees, including 100 peach trees and 30 large jujubes [115] (p. 201), attesting to the later widespread importance of the fruit.

As noted above, Greco-Roman Classical writers placed the origins of the peach to the east, as indicated in the Persian nomenclature. The first written accounts of peaches in these Classical texts date to the first century C.E. in works by the Greek author Dioscorides (*De Materia Medica*, 50–70 C.E.) [116], and by Roman authors Virgil (*Eclogae* II: 53; 70–19 B.C.E.) [117], Columella (*De Re Rustica*, 4–70 C.E.) [118], and Pliny the Elder (*Naturalis Historia*, 23/24–79 C.E.) [119]. These include the mention of cultivation guidelines as well as medicinal properties of the fruits (for example, crushed peach leaves were thought to be a remedy for hemorrhaging). Beyond describing its possible medical properties, Pliny also famously complained that the peach is a delicate fruit, which does not keep fresh for long, stating that no other fruit "keeps worse: the longest time that it will last after being plucked is two days" [107] (p. 541). The Middle Persian word for peach, *šiftālūg*, is a creation resulting from the word for 'plum' modified by the word *šift* 'sweet, milky' [120] (p. 71) and is commonly found across Central Asia [108] (pp. 86–87). There is no separate word for peach that seems to originate from Central Asia.

### 4.2. Tracing Early Centers and Dispersal of Apricots

Although genetic studies suggest that the apricot might have two distinct centers of origin, at present, this is not supported by the archaeobotanical record, with archaeobotanical reports of apricot from China currently dating to a few millennia earlier than those from southern Central Asia. However, this might be due to the shorter history of archaeobotanical research in Central Asia and the more challenging preservation conditions in comparison to China. At present, apricots seem to follow a similar dispersal trajectory to that attested for peaches. Apricot remains are found only within modern mainland China for a few millennia before dispersing to broader East Asia and South Asia, from where, through a southern dispersal route, the fruit seems to have reached Western Asia, Northeast Africa, and Europe by the 1st millennium C.E.  $z\bar{u}li$ 

The linguistic evidence supports the dispersal trajectory seen in the archaeobotanical record. In Central Asia, there is a string of words for the apricot that points to its spread from East Asia. Well-established connections exist between languages of the Hindu Kush and Pamir (e.g., Yidgha *čiray* 'apricot', Prasun *čirē*, Pashto *čaraī*, Munji *čīrī* 'apricot', and Kashmiri *cēr*) all the way to the Caucasus (Armenian *ciran* and Georgian *čerami*), while west Tibetan *čuli*, Balti *suri*, and Sanglichi *čuwē*! [121] (pp. 8–16), [122] (p. 27), [123] (p. 540fn1), [124] (p. 59) have been considered intermediary forms to the cluster surrounding Burushaski *ju*, Shina *žūri*, Khowar *žū*!*i*, and Domaki *žužūi* [125] (p. 39), but a specific source language has not been identified. None of the forms can be reconstructed to ancient stages of their respective language families, although Burushaski, as a language isolate without known relatives and with a long presence in the region, may represent the earliest recoverable form. The linguistic trajectory thus points to the apricot traveling west through the Hindu Kush.

The historical record suggests that apricots were known by at least the 1st millennium B.C.E. In ancient Chinese texts, apricot is first referenced in the *Xia Xiaozheng* [112–114]. In Japan, the *Engishiki* lists apricot as a medicine with five provinces making annual tax payments of apricots to the court at the time [115] (p. 201).

In Greco-Roman written sources, Dioscorides uses *mailon/armeniacon* in his *De Materia Medica* [116]; Pliny refers to *pomum armeniacum/armeniaca arbor* in his *Naturalis Historia*, and so does Columella in *De Re Rustica* [118,119]. The Latin *malum armenicum* (Armenian apple), from which the later scientific nomenclature was derived, attests to the ancient belief that the fruit had a Caucasian origin, as well as its widespread presence in ancient Greece and Rome from at least the early 1st millennium C.E. The English word *apricot* is a later phenomenon travelling through several distinct speech communities surrounding the Mediterranean basin, ultimately from Byzantine Greek [126] (p. 10–13). Middle Persian *zardālūg* 'apricot' reused the plum word  $\bar{a}l\bar{u}g$  with the adjective *zard* (yellow) [120] (p. 98) and spread in the Persian cultural sphere of influence (e.g., Pashto and Balochi *zardālū*).

It is striking that there are so few reports of *P. armeniaca* in Europe as compared to *P. persica*, especially since, according to Greco-Roman written evidence, apricot was known and available at least in areas like Southern Europe and Northern Africa from the late 1st millennium B.C.E. This discrepancy is not solely due to the lack of sampling; in a study of 114 Roman sites in northern Italy, Bosi et al. [60] recorded a single site with possible apricot remains at Aquileia. In contrast, peach was recorded at 27 of the sites. It is possible that peach stones preserve better than apricot stones, although the Bosi et al. [60] study had a large dataset of charred and uncharred remains. It is also possible that the lack of identification, since there are no standardized identification criteria for apricots and they do not possess the distinctive deep furrows of peaches.

#### 4.3. Tracing Early Centers and Dispersal of Plums and Sloes

Many questions persist regarding the early centers of origin for plums, with *P. cerasifera*, *P. insititia*, and *P. domestica* plums at times suggested as originating in Europe, West Asia, or Central Asia. Additionally, genetic studies seem to suggest that *P. cerasifera* might have had an ancestral role to the development of *P. domestica*, through hybridization with *P. spinosa*,

but also a possible ancestral role to the development of *P. spinosa* itself [24]. At present, however, archaeobotanical records of *P. cerasifera* are not only very scarce in comparison to the other species, but also date to comparatively later, with securely identified reports only dating from the 1st millennium C.E. onward. This would seem to contradict its potential progenitor contribution to the development of other plum species. Among the four species considered in this study, *P. spinosa* has the largest and oldest archaeobotanical record, with reports older than any of the other species, and consistent presence throughout all time periods studied, possibly indicating not only its European origin, but also a consistent use and popularity of this fruit throughout the ages.

Archaeobotanical reports of *insititia* and *domestica* plums are also largely confined to Europe. There are no reports of *insititia* plums in Central Asia, and only two reports of *domestica* plums outside of Europe, one in South Asia and one in Central Asia. These data would seem to suggest that both species possibly originated in Europe and did not spread much outside of it. Their dates (which are later than *P. spinosa*) are in line with a later evolution of these species. However, due to the shorter history of archaeobotanical research in Central Asia, their possible origin in an area other than Europe and their spread cannot be totally excluded. The frequent reports of *Prunus* sp. from Central Asia also suggest that many of those finds could be any of the species considered, and future, more precise identifications might help in resolving these issues.

Within Europe, there is a marked increase in the variety of plum species reported following the Roman Empire, which may be due to better archaeological preservation conditions but also to a more widespread and intensive practice of arboriculture attested in medieval times.

The earliest attested term in Central Asia is the Middle Persian word for plum  $\bar{a}l\bar{u}g$  [120] (p. 79), which was culturally disseminated and associated with the oasis city of Bukhara, yielding Pashto  $\bar{a}l\bar{u}$  bukhārā 'plum' and Burushaski álubuxára 'plum'. It is likely, however, that the Persian word itself derives from an older Central Asia word, which is also the source of Common Turkic \*ärük 'type of stone fruit', that in the extant languages generally denotes plum, apricot, and peach, but seldom smaller fruits like cherries [130] (p. 259–60) [131] (p. 222). Neither of the forms have established etymologies, and since they belong to distinct language families, it is reasonable to surmise that it has been borrowed from an unknown language of Central Asia. This may be further corroborated by yet another group of early words for peach in the Indic (e.g., Nepali āru and Pashai arū') and Nuristani languages (e.g., Ashkun arú) of the Hindu Kush and Himalayas, as they only imperfectly match the assumed Iranic sources [132] (p. 37); [133] (p. 50).

Modern English sloe is a cognate with other Germanic forms (e.g., Danish *slåen*, Old High German *slåha*) and presumably held a consistent and concise function in the speech community since at least the middle of the first millennium B.C.E. [134] (p. 1050). That the Germanic word is closely related to the Slavic word for plum, *slíva* points to a Northern European innovation from an ancient word for the color blue (cf. Latin *lividus* 'of a bluish color, black-and-blue' and Welsh *lliw* 'color, splendor') [135] (p. 660).

#### 5. Conclusions

The rich archaeobotanical record available on finds of large-seeded *Prunus* fruits, (peaches, apricots, plums, and sloes) across Eurasia and North Africa attest to the continued popularity of this fruit since prehistory. The compilation of large datasets based on the available published records, and metadata studies like the one presented here show the potential of such studies to look for long-term patterns in the use of specific plant species, as well as current limitations.

Among the fruits considered for this study, peach is the best understood, originating in China, as supported both by genetic and archaeobotanical finds, and spreading to both ends of the Eurasian supercontinent and North Africa by the end of the 1st millennium B.C.E. Looking beyond the peach, the data that we present here suggest that: (1) largefruiting forms of plums existed in Europe prior to the domestication of what we referred to as insititia plum, what most researchers have called *P. domestica* ssp. insititia, a taxon challenged by recent genetics work; (2) insititia plums are absent outside of Europe, but several Prunus sp. remains from Central Asia, such as those from Togolok and Adju Kui, could be local insititia types or wild relatives; (3) cherry plums (P. cerasifera) are largely absent from the archaeobotanical record of Europe prior to the past three millennia; (4) apricot is largely absent from the archaeobotanical report in Europe, in contrast with written evidence attesting to its presence, at least in Southern Europe from the end of the 1st millennium B.C.E.; (5) the great number of reports simply classified as *Prunus* sp., or large Prunus stones, attest to the difficulty encountered by archaeobotanists when identifying remains to species level, possibly due to a lack of systematic studies and universally agreedupon identification criteria. Regardless of the species, there is a visible increase of Prunus stones from all regions starting during the last centuries of the 1st millennium B.C.E. We suggest that this reflects a more organized arboriculture, stepping beyond maintenance of wild or feral populations and low-investment cultivation. The transition to intentional cultivation of long-generation perennials may have been linked with increased urbanism, accompanied by more reliable land tenure and market economies.

In addition to these conclusions, we suggest that follow-up research should focus on the inclusion of aDNA to parse out the genetic relationship of archaeobotanical *insititia* and its place in the hybrid origin of the larger clade. We would like to see further genetic and archaeobotanical work for testing the hypothesis that *P. cerasifera* had a native range restricted to Central Asia, and whether its dispersal along the early Silk Road trade routes may have facilitated the hybridization that led to the *domestica*-type plum. The poor understanding of the evolutionary trajectories of plum species, notwithstanding the wealth of accumulated archaeobotanical records available, as highlighted in this study, with contradicting information from genetic and archaeobotanical records, calls for more work on standardized identification criteria and more direct radiocarbon dating to fully clarify the antiquity of each species' use and dispersal. Finally, future research should also investigate the reasons behind the lack of archaeological reports of *P. armeniaca* from European sites, given the evidence from written sources that this fruit was known, at least in Southern Europe, from the end of the 1st millennium B.C.E.

**Supplementary Materials:** The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/agronomy13041027/s1, Table S1: Dataset of published *Prunus* finds and their chronologies from Eurasia and North Africa, Table S2: Directly radiocarbon-dated *Prunus* remains from archaeological and early historic context in Japan published in the Radiocarbon Database of the National Museum of Japanese History.

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