The Domestication and Dispersal of Large-Fruiting *Prunus* spp.

Subjects: Archaeology

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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.

plum peach apricot domestication horticulture

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 multiyear perspective and planning required for managing fruit trees before the first harvest [1][2][3][4], although there is some 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 scholars 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.

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 ^{[9][10]}. Over the past decade, much has been clarified regarding the domestication and dispersal of the apple (*Malus* domestica (Suckow) Borkh.) ^{[11][12][13]} ^[14], 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 ^{[15][16]}. Even the evolutionary history of members of the *Prunus* clade remains unsettled, with many contradictory systematics schemata ^[17].

There are many obstacles to studying the domestication and ancient dispersal of large-fruiting 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. ^[16]: **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 R. Spengler 2020, Jena, Germany; fruit collected by R. Spengler 2020, Jena, Germany, not to scale). Stones from the Modern Fruit Plant Reference Collection, Paleoethnobotany Laboratories, Max Planck Institute of Geoanthropology, Jena.

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 numerous subspecies and varieties based on both modern and ancient plum remains from Central Europe ^{[18][19]} [^{20][21][22]}. 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 *insititia* 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.

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 ^{[18][23]} and Bulgaria (Gudzhova, Mogila) ^[24]. However, other scholars have suggested that they may have originated in Western or Central Asia ^[25] ^[26], 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][27]}. 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 ^{[28][29]}.

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 ^[30].

2. The Domestication and Dispersal of Large-Fruiting *Prunus* spp.

There is considerable unevenness in the number of published records for each species and across regions and time periods. 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, it 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. 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 the 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, it 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.) ^[31], and one report of directly dated desiccated unspecified *Prunus* remains from Areni-1 in Armenia (4230–3800 B.C.E.) ^{[32][33]}.



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

2.1. 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 (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.) [27]. 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) ^[34], 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., [35] and used to claim that the peach was introduced to Japan as early as the 5th millennium B.C.E. [27]. Ikiriki produced 19 peach stones [36] (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 ^[36] (p. 47). These issues suggest that caution is required in accepting lkiriki as an example of a pre-Bronze Age introduction of *P. persica* to Japan.



Figure 3. Spatio-temporal distribution of *Prunus persica* remains from Eurasia and Northern Africa compiled within the database 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.

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.) ^[37]. 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.) ^[38]. 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.) ^{[39][40]}, Lleida in Spain (200–1 B.C.E.) ^[41], and throughout Italy, including Pompeii (200 B.C.E.–79 C.E.) ^{[42][43]} and northern Italy (100 B.C.E.–400 C.E.) ^[44].

2.2. 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.) ^{[27][45][46]}, Jiahu in Henan (7000–5500 B.C.E.) ^[47], 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 ^[48]. 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 ^[49]. 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 ^[49] (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 ^[37], 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. ^{[50][51][52]}, where peaches were also reported. Apricots have been found at Saqqara in Egypt (330 B.C.E.–350 C.E.) ^[47].



Figure 4. Spatio-temporal distribution of *Prunus armeniaca* remains from Eurasia and Northern Africa compiled within the database 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.

2.3. Sloe and Plums

2.3.1. 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 (**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.) ^{[53][54]}, Sammardenchia, Lugo di Romagna, Piancada and Pavia di Udine in Italy (6th/5th millennium B.C.E.) ^{[55][56][57]}, and La Draga in Spain (5400–4500 B.C.E.) ^[58]. Chronologically, there are no notable differences in the presence of sloe remains across time in Europe.



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

3.3.2. Cherry Plum

Cherry plum records are the least abundant across all regions (**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.) ^[59]. 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) ^[60]; Aachen-Burtscheid (50–150 C.E.) ^[61] and Ellingen in Germany (115–211 C.E.) ^[62], and Berenike in Egypt (1–400 C.E.; this is also the only record from Northeast Africa) ^[63]. 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.) ^[64], and at the site of Bazar-Dara in Tajikistan (800–1100 C.E.) ^[65], 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.



Figure 6. Spatio-temporal distribution of *Prunus cerasifera* remains from Eurasia and Northern Africa compiled within the database 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.

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.) ^[63], and another from Southwest Asia, where, at present, scholars find the earliest report for this species at the site of Khirokitia in Cyprus (6400–6100 B.C.E.) ^{[66][67][68]}. 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., respectively) ^[69], at the already mentioned site of Sacarovca in Moldova (5650–5500 B.C.E.) ^[59], and at the site of La Marmotta in Italy (5879–5074 B.C.E.) ^[56], 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**).



Figure 7. Spatio-temporal distribution of *insititia* type remains from Eurasia and Northern Africa compiled within the databasegrouped 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.

2.3.4. 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, 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.) ^[59] and Poduri in Romania (4700–4400 B.C.E.) ^{[70][71]}; and subsequently from Scarceta di Manciano in Italy (1443–1116 B.C.E.) ^[72]. There is only one report of *domestica* plum in West Asia, from Büklükale in Turkey (c. 1800–1650 B.C.E.) ^[73], and in Northern Africa, there are two reports of *P. domestica* from Antinopolis (c. 330 B.C.E.–300 C.E.) ^[74] and Berenike (1–400 C.E.) ^[63].



Figure 8. Spatio-temporal distribution of *domestica* type remains from Eurasia and Northern Africa compiled within the database 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: Karaspan-tobe.

3. Summary

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.

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 suggest that: (1) large-fruiting 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 agreed-upon 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.

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