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Morphological diversity of the Russian olive (*Elaeagnus angustifolia*) from Oxus civilization 4000 BP, Central Asia

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ABSTRACT

The region of Transoxiana underwent an early agricultural-demographic transition, leading to the emergence of the earliest proto-urban centers in Central Asia. However, the development of horticulture activity aspects of this cultural shift remain poorly understood, particularly regarding the role and place of long-generation nativity fruit trees, such as Russian olive (*Elaeagnus angustifolia*), in the horticulture system. In this research, we conduct a systematic modern carbonization experiment on Russian olive seeds, present directly AMS ^{14}C dated result, and use geometric morphometric methods to analyze the carbonized Russian olive seeds from the early community of Sapalli Tepa in southern Uzbekistan. The results show that the deformation during carbonization had minimal impact on the morphology of the seeds. The Russian olive seeds found at Sapalli Tepa include two types: *Elaeagnus angustifolia* and *Elaeagnus angustifolia* var. *orientalis*, both showing no signs of domestication. This suggests that the Russian olive in Bronze Age Southern Central Asia was not subjected to intensive selection by local people, and its sources may have included both cultivation and wild collection.

1. Introduction

The Greater Khorasan Civilization (Rante, 2015) is one of the least studied centers of ancient intensive agricultural development and urbanization in Eurasia. Current archaeological research suggests that the "Central Asian Interaction Sphere" (Possehl, 2002), with southern Central Asia as its core, played a significant role in the early processes of globalization, particularly in the emergence and development of long-distance trade networks(Dong et al., 2017; Jones et al., 2011; Spengler et al., 2021). A complex agricultural system gradually developed in the river valleys and oases of southern Central Asia between 7000 and 5000 BP (Vahdati et al., 2019; Winckelmann, 2000; Zadneprovsky, 1995). Around 5500–5000 BP, urban centers in the oases of southern Karakum and the Kopet Dag region began to expand in both size and population. The development of irrigation systems further promoted urbanization and the establishment of an elite class, marking the emergence of a unique culture within these urban agglomerations. This culture is known as the Oxus civilization or the Bactria–Margiana Archaeological Complex (BMAC) (Askarov, 1981; Dani and Masson, 1992; Hiebert, 1994).

Current archaeological research in this area has emphasized the development of exchange networks and globalization processes in the mid-Holocene (Frachetti et al., 2012; Lyonnet and Dubova, 2020; Mir-Makhamad et al., 2023; Spengler et al., 2021). The population peaked around 4000 BP, when the intensity of agricultural activities and handicraft production greatly increased (Chen et al., 2024; Kaniuth,

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2007). As early urban civilizations developed, irrigation systems were improved (Miller, 1999, 2003). Higher human density and regional demographic growth likely increased the demand for crop diversity, which appears to have promoted the emergence and development of arboriculture (Childe, 1936, 1950; Fuller and Stevens, 2019). The earliest evidence of the cultivation of grapes (*Vitis vinifera*) and fruit trees such as apples (*Malus pumila*), plums (*Prunus salicina*), and pistachios (*Pistacia vera*) in Central Asia comes from this period and region (Chen et al., 2022; Mir-Makhamad et al., 2022; Spengler, 2019)

Elaeagnus angustifolia, also called Russian olive, is a shrub or small thorny tree belonging to the Elaeagnaceae family, originating in the arid Central Asia region (Asadiar et al., 2013; Gu et al., 2024; Sun and Lin, 2010). Due to its strong tolerance to drought and saline-alkali soil, it is widely distributed in arid and semi-arid areas and has important ecological and economic uses (Little, 1961; Mao et al., 2022; Uzun et al., 2015). Current research has shown that since the Holocene, plants in *Elaeagnus* genus, represented by *Elaeagnus angustifolia,* have been widely found in early human activity records in the Iranian Plateau, BMAC, Xinjiang, and Tibet Plateau as an important source of fruit and fuel (Decaix et al., 2016; Liu et al., 2022; Shen et al., 2017; Spengler et al., 2018). Modern ethnobotanical studies also shown that *Elaeagnus angustifolia* is widely used for food, wine-making (Batsatsashvili et al., 2020; Bussmann, 2017) and traditional medicine activities (Sher et al., 2016; Sokolov, 1988) in the arid Central Asia, making it one of the

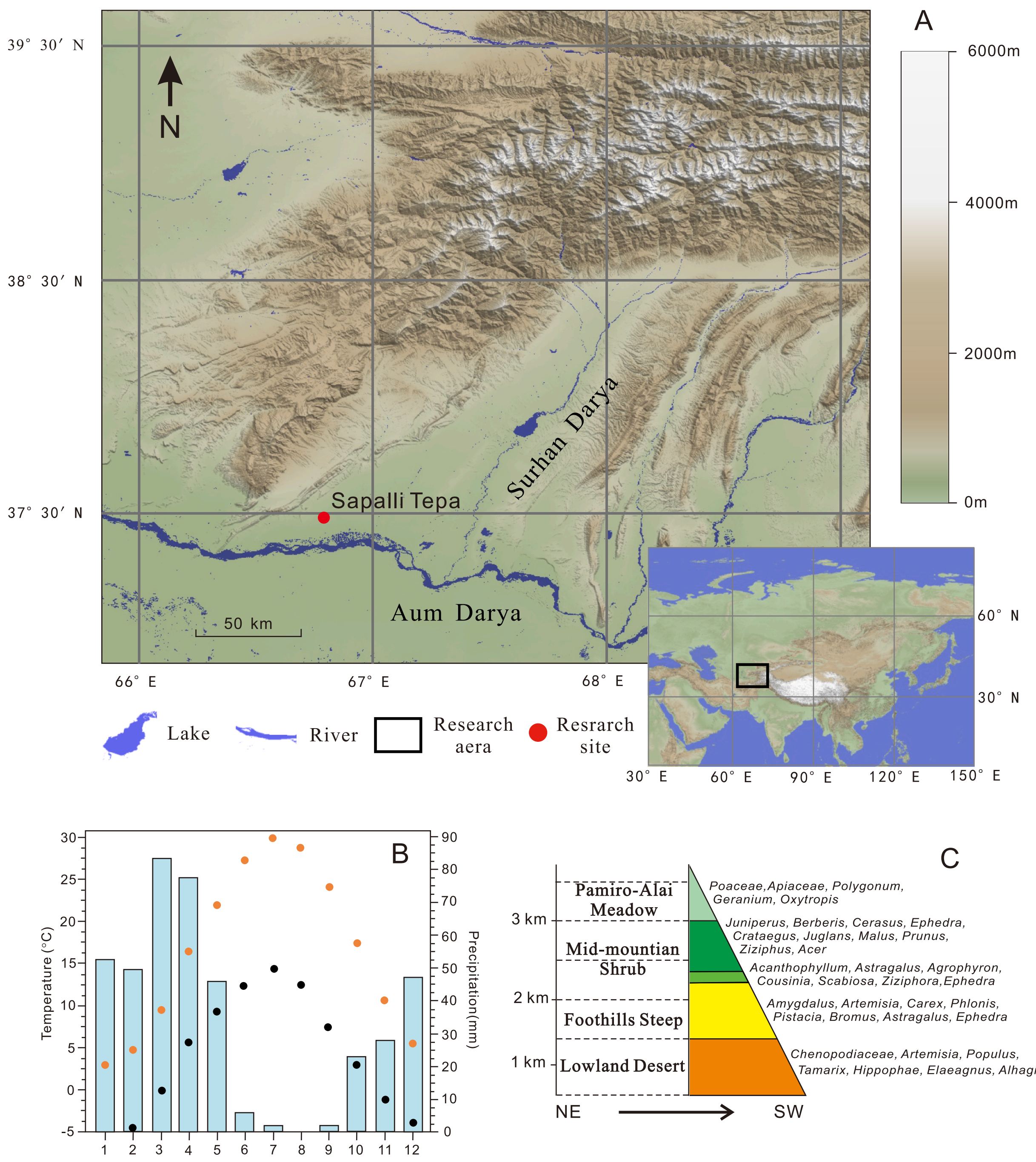

Fig. 1. Research area location, geomorphologic, climate record, archaeology site and vegetation distribution.
(A) Research area, geomorphologic and archaeology site distribution. (B) Monthly distribution of average temperature and annual average precipitation; (C) Vertical vegetation distribution in the typical Pamir-Altai mountain range (from Uzbekistan to Tajikistan).

region's important economic crops.

At present, archaeobotany research in the Greater Khorasan region mainly focuses on the reconstruction of agricultural systems and their role in early globalization (Billings et al., 2022; Moore et al., 1994; Spengler, 2015). However, the development of horticultural systems, preferences for different crops and fruits among various populations, and the diversification history of crop varieties under human management have not received widespread attention. In the past two decades, quantitative analysis combining traditional linear measurements and geometric morphometric methods (GMM) has been widely applied in the study of modern carbonization processes, auxiliary identification, and seed morphological diversity of cereals, legumes, and fruit seeds found in archaeological sites, proving effective in assessing ancient population variation (Bouby et al., 2018; Ros et al., 2014; Tarongi et al., 2023). Recently, linear measurements and geometric morphometric analysis have been widely used for representative fruits such as grapes (Chen et al., 2022; Pagnoux et al., 2015), cherries (*Prunus avium*) (Burger et al., 2011), jujube (*Ziziphus jujuba*) (Li et al., 2024), date palm (*Phoenix dactylifera*) (Terral et al., 2012) and olives (*Olea europaea*) (Newton et al., 2014).

In this study, we performed a systematic geometric morphological analysis on seeds of *Elaeagnus angustifolia* from the Bronze Age urban settlement of Sapalli Tepa in southern Uzbekistan. Well-preserved seeds were selected for this research to avoid deformation due to burial and carbonization. The goal of this study was to better understand development history of early horticultural activities in Central Asia, specifically to explore the native fruit trees utilization practice, local fruit trees domestication degree and whether people tended to select specific traits during early urban development in the Bronze age Central Asian oasis civilization.

2. Materials and methods

2.1. Site description and the surrounding environment

Archaeological samples were collected from the Sapalli Tepa in the Surkhandarya region of southeastern Uzbekistan (Fig. 1). The earliest archaeological activity in the area dates back to 1925. Archaeologists from the Soviet Union conducted extensive archaeological investigation in this area during the 1960s and 1970s, discovering numerous settlements from multiple periods (Askarov, 1973, 1981; Dani and Masson, 1992). The fertile river valley in this area was an important part of the Inner Asia Mountain Corridor, which was also an intensive agricultural center (Holdich, 2019; Lerner, 2015). The local climate is continental, with rainfall mainly occurring in spring. The average temperature in January is 3 °C, and in July it reaches 30 °C. The mean annual precipitation in the plain area ranges from 130 to 360 mm. Vegetation is mainly composed of low shrubs and open grasslands (Egamberdieva and Öztürk, 2018; Holdich, 2019)

Sapalli Tepa is the most representative site of the earliest agricultural civilization in the Bactria region. The Sapalli culture, named after this site, represents the Bronze Age settled agricultural culture in the Uzbekistan and southern Tajikistan, which can be divided into 4 stages: Sapalli, Djarkutan, Kuzalinski, and Molalli (Askarov, 1973, 1981). The main structure of the site is a square-shaped farm or fortress (Fig. 2), with a side length of 82 m, surrounded by a mud brick wall and rectangular corridor-shaped rooms, which were probably false entrances. In the center of the site is a square, surrounded by residential areas built in three periods. A total of 138 graves were discovered, many of which were situated under the floors of residential areas or streets, surrounded by rooms and corridors. These graves included many items such as ceramics, metal objects, jewelry, and ritual objects like seal-emblems.

2.2. Sample collection and experimental methods

2.2.1. Archaeological samples

The archaeological plant remains from the site were mainly obtained using the flotation method. The samples from Sapalli Tepa were collected from the storage area on the northwest side of the site. A total of 51 samples were collected, each weighing over 20 L. All samples were separated from the sediments by flotation using a 0.3 mm mesh screen. The plant remains were further sorted and identified using a Leica M250 C microscope at the Key Laboratory of Vertebrate Evolution and Human Origin of the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences. Due to the large size of the *Elaeagnus angustifolia* seeds, images were captured using a Nikon DF camera with a Nikon AF Micro Nikkor 70–180 mm 1:4.5–5.6 D lens. A total of 50 archaeological *Elaeagnus angustifolia* seeds with complete appearances and minimal deformation were selected for subsequent measurement and analysis.

2.2.2. Modern samples

Current research shows that there are three wild *Elaeagnus* species in the Uzbekistan region (Institute of Botany et al., 2010), include *Elaeagnus angustifolia, Elaeagnus angustifolia* var. *orientalis*, and *Elaeagnus oxycarpa*. Wild *Elaeagnus* seeds from Central Asia used in this study were provided by the Germplasm Bank of Wild Species (GBOWS). All seeds were collection in Aksu, Xinjiang, China (for details, see EMS 1). Cultivated *Elaeagnus angustifolia* seeds were purchased from Wuwei, Gansu province, China. The seeds used for GMM analysis in the study

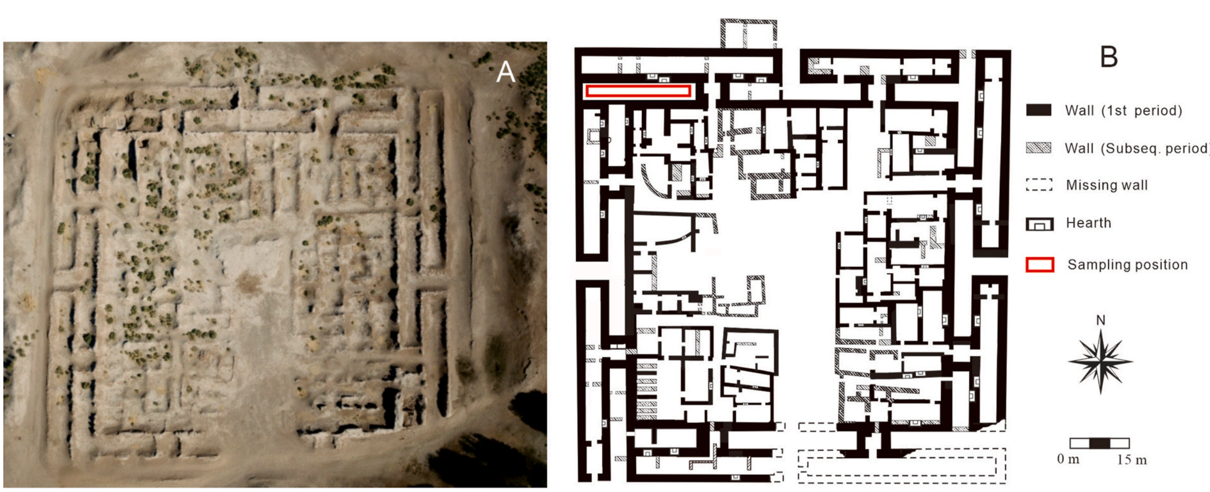

Fig. 2. Aerial images, plans and sample collection locations of the Sapalli Tepa. (A) Aerial image of the site (B) Plan of the site.

included 60 cultivated *Elaeagnus angustifolia*, 60 wild *Elaeagnus angustifolia*, 30 *Elaeagnus angustifolia* var. *orientalis* and *Elaeagnus oxycarpa*. Seeds were photographed under the same conditions before and after carbonization to measure the effects on morphology.

2.2.3. Modern carbonization process

The seeds were dried in a drying oven at 60 °C for 24 h. Each sample consisted of 30 seeds, which were photographed and measured before and after carbonization. All samples were carbonized in a laboratory muffle furnace. The three variables set in the preliminary experiments were oxygen content, temperature, and heating time (Table 1).

For oxygen content, two conditions were set. Open conditions: The seeds were simply arranged on an open plate in the oven, a few centimeters apart from each other. Seal conditions: The seeds were covered in several layers of aluminum foil.

Regarding the temperature and duration of heating time, the combination of temperature and heating time was required to completely carbonize the seeds while maintaining their intact morphology. We set the temperature at 150 °C, 300 °C, and 450 °C, and the duration of heating was set to 1 h, 2 h, and 3 h. Preliminary results show that under 150 °C, whether open or sealed, the seeds turned dark brown after 3 h of heating but were not completely carbonized. Under 300 °C, the seeds in the open condition started to ash after 2 h of heating and were completely destroyed after 3 h. Under sealed conditions, a small number of cracks appeared on the surface after 3 h of heating, but the seeds were completely carbonized while remaining intact and relatively hard in texture. Under 450 °C, the seeds in an open environment were completely ashed after 1 h of heating, and the seeds in a sealed environment for 2 h became partially ashed, which could not be measured.

To examine the effect of carbonization on seed morphology, we selected parameters with deeper carbonization and relatively complete seed morphology for subsequent batch carbonization experiments. The carbonization parameters for subsequent modern samples were all carried out in a sealed environment and heated at 300 °C for 3 h.

2.2.4. Chronology

Seeds of annual herbaceous plants were selected from the carbonized seed remains for AMS^{14}C dating. All samples were sent to BETA laboratories in the United States for analysis. The pretreatment of the chronological samples was carried out using the acid-base-acid method. The specific process is as follows: first, the sample was crushed and dispersed in deionized water, then rinsed with heated HCl to remove the carbonates, and NaOH was then used to remove secondary organic acids from the sample. Finally, it was rinsed with acid, neutralized, and dried after the solution had been neutralized. The calendar-corrected age was obtained using OxCal v4.4 software with InCal20 as the reference database (Ramsey, 2009; Reimer et al., 2020)

Table 1
Combinations of conditions in the experiment and their effects to seed carbonization process.

Temp./°C	Condition	Duration/min		
		60	120	180
150	Open	Dark Brown, hard texture	Dark Brown, hard texture	Dark Brown, hard texture
150	Seal	Dark Brown, hard texture	Dark Brown, hard texture	Dark Brown, hard texture
300	Open	Black, Intact	Black, with white ash at tip	Complete ashing
300	Seal	Black, Intact	Black, Intact	Black, fragments relatively easily
450	Open	Complete ashing	Complete ashing	Complete ashing
450	Seal	Black, with white ash at tip	Complete ashing	Complete ashing

2.2.5. Geometric morphological analysis

This study used Generalized Procrustes analysis (GPA) to measure the morphological changes in space (Zelditch et al., 2012). Before the analysis, the seed image was converted to black and the centroid was placed in the center of the image. Two discrete homologous points at the apex and base of the seed were defined as landmarks, and landmarks were collected using tpsUtil and tpsDig. Starting from the apex, the cv2 package in Python was used to detect the edges and collect 22 coordinate points equidistantly placed between the apex and base as semi-landmarks (Fig. 3). The landmarks and semi-landmarks were then imported into MorphoJ for GPA and Principal Component Analysis (PCA). The highest levels of morphological variation (PC1 and PC2) were explained using transformation grids and wireframe plots. In addition, linear discriminant analysis (LDA) was also conducted to test the effectiveness of the PCA results for the classification of archaeological samples.

3. Result

3.1. Chronology result

Direct radiocarbon dating result is essential for verifying the age of archaeological remains. Some seeds without carbonization were found at Sapalli Tepa. In previous research around arid Central Asia, some archaeological sites have preserved dried plant remains without carbonization (Chen et al., 2012). Considering that uncarbonized plant remains are generally regarded as modern intrusive contamination in archaeobotanical research, in this study, we appropriately excluded some completely uncarbonized seed remains from Sapalli Tepa during the dating process to ensure the accuracy of the samples used in this research.

In the well-preserved samples from T1-T4 at Sapalli Tepa, some carbonized plant remains were selected for AMS^{14}C dating. The dating materials used included plant seeds and charcoal, and a total of 5 AMS^{14}C dating results were obtained. The results show that Sapalli Tepa dates to approximately 4086–3698 cal BP, corresponding to the Bronze Age. This result is consistent with the chronology established based on the excavation relics. The specific dating results are shown in Table 2.

3.2. Modern carbonization result of Elaeagnus seeds

Since most of the seed remains found in the site have been carbonized, determining the impact of the carbonization process on the morphology of *Elaeagnus* seeds is important for interpreting the results using seed morphology. Modern wild and cultivated *Elaeagnus angustifolia* seeds were used for carbonization experiments, and the changes in seed length and thickness before and after carbonization were measured and compared. Meanwhile, GMM analysis was also conducted to analyze the morphological changes before and after carbonization.

The linear measurement results of modern cultivated and wild *Elaeagnus angustifolia* seeds before and after carbonization showed that, during the carbonization process, the changes were mainly reflected in seed length and thickness. After complete carbonization, the volume of *Elaeagnus angustifolia* seeds was about 12 % smaller than that uncarbonized status (Table 3).

In this research, we employed Generalized Procrustes Analysis (GPA) as our geometric morphometric methods to quantify shape variation in different sample. This methodologically rigorous approach isolates shape variation by eliminating extraneous variables through translation (positional alignment), rotation (axial orientation standardization), and scaling (size normalization) (Gower, 1975; Rohlf and Slice, 1990; Zelditch et al., 2012). By superimposing homologous coordinate landmarks across specimens, GPA effectively dissociates size-related parameters from pure shape characteristics, thereby enabling rigorous quantification shape divergence independent of other factor.

In the PCA results from GMM analysis (Fig. 4), PC1 and PC2

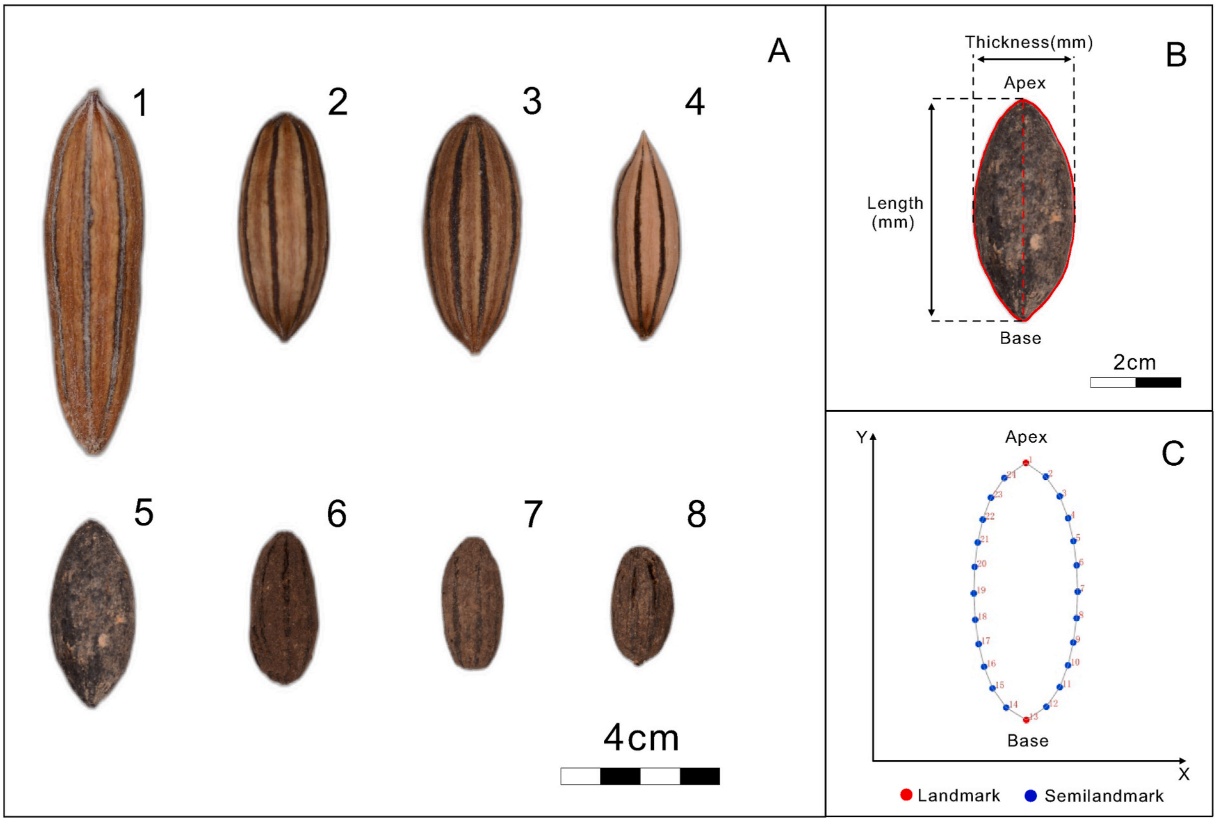

Fig. 3. Modern and archaelolgical sample of *Elaeagnus* seeds, Measurement parameters and Landmark setting.
(A) Modern and archaeological *Elaeagnus* seeds used, 1 *Elaeagnus angustifolia* (modern cultivation), 2 *Elaeagnus angustifolia* (modern wild), 3 *Elaeagnus angustifolia* var. *orientalis*; 4 *Elaeagnus oxycarpa*; 5–8 *Elaeagnus angustifolia* (archaeological sample); B. Measurement parameters of *Elaeagnus* seeds; C. Landmarks and semi-landmarks setting.

Table 2
AMS^{14}C dating results of Sapalli Tepa.

Lab NO.	Sample NO.	Marital	Age/BP	σ	Calibrate age/ cal. BP
Beta-459967	SPL-4	*Panicum miliaceum*	3520 ± 30	2	3880–3698
Beta-637137	SPA 3-2	*Vitis vinifera*	3500 ± 30	2	3869–3650
Beta-459965	SPL-3	*Panicum miliaceum*	3520 ± 30	2	3880–3698
Beta-400298	SPL-2	Charcoal	3660 ± 30	2	4086–3897
Beta-459964	SPL-1	*Triticum aestivum*	3540 ± 30	2	3908–3700

accounted for 87.96 % of the total variance, with PC1 accounting for 82.27 %, primarily reflecting the differences in the width of the middle section of the seed. Modern wild and cultivated *Elaeagnus angustifolia* clearly separated into two independent groups. The intervals of different types of *Elaeagnus angustifolia* before and after carbonization of the same seed type generally overlapped, indicating that the shape characteristics did not change significantly before or after carbonization. Because GPA excludes scale differences between different samples during analysis, in the GPA process comparing the morphological differences between *Elaeagnus angustifolia* seed types, while ensuring that the seeds remained relatively intact, the carbonization conditions between different seeds did not significantly impact the GMM analysis results.

3.3. Morphology of Elaeagnus seeds in Sapalli Tepa

The PCA results based on GPA between modern and archaeological *Elaeagnus* seeds from Sapalli Tepa (Fig. 5) show that there are certain similarities between the *Elaeagnus* seeds found in Bronze Age Central Asia and modern wild *Elaeagnus* seeds, but there are still significant morphological differences among individuals. The first two principal components (PCs) of the PCA explained 83.056 % of the total variance (Fig. 5). Among them, the changes in PC1 (76.154 % of variance) reflect the sharpness of the apex and base, as well as the thickness variation among different *Elaeagnus* seeds, which is the most noticeable morphological difference across all samples. The morphological changes represented by PC2 (6.902 % of variance) point to the difference in apex width among different seeds. These two characteristics constitute the

Table 3
Changes in length and thickness of modern wild and cultivated *Elaeagnus angustifolia* seeds before and after carbonization.

		Mean			Reduction		
Species	Type	Length/mm	Thickness/mm	Aspect ratio	Length/%	Thickness/%	Aspect ratio/%
Elaeagnus angustifolia (pre-carbonization)	Cultivate	17.732	5.174	3.433	\	\	\
Elaeagnus angustifolia (pre-carbonization)	Wild	12.041	5.194	2.322	\	\	\
Elaeagnus angustifolia (post-carbonization)	Cultivate	15.819	4.5246	3.501	89.214	87.478	98.064
Elaeagnus angustifolia (post-carbonization)	Wild	10.716	4.5966	2.334	88.988	88.523	99.488

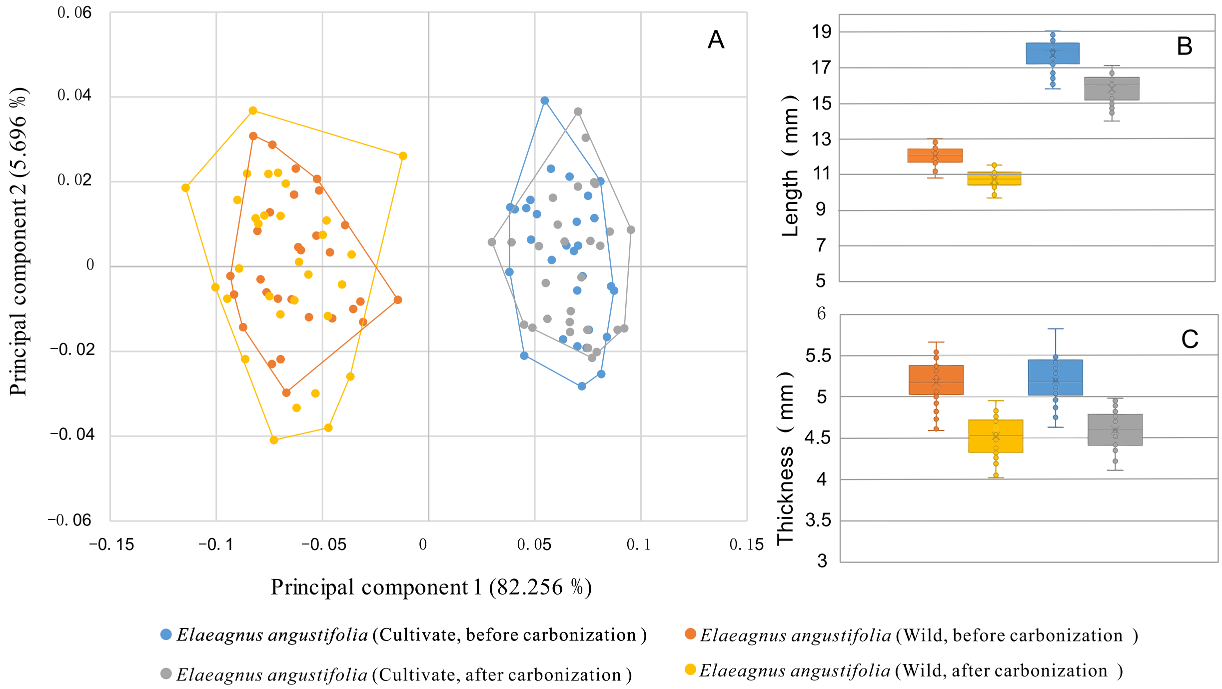

Fig. 4. PCA result on the morphological changes, lenth and thickness change from modern wild and cultivated *Elaeagnus angustifolia* seeds before and after carbonization.
(A) PCA result on the morphological changes; (B)Seed lenth change; (C) Seed thickness change.

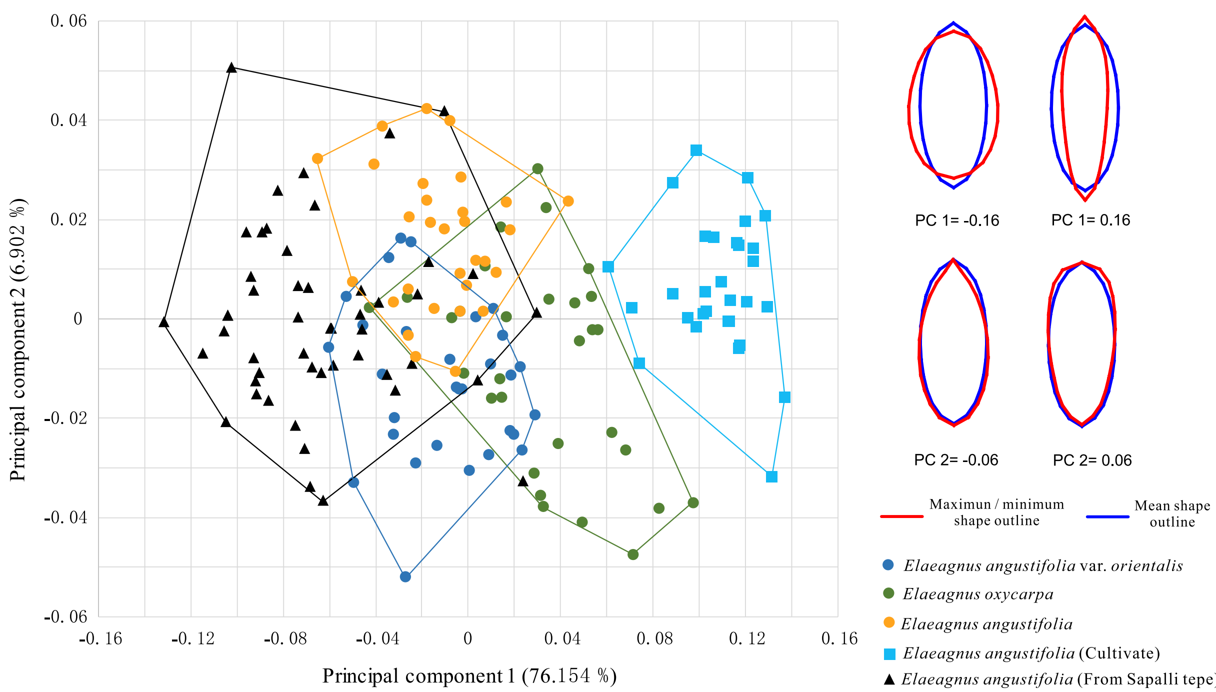

Fig. 5. PCA results of modern wild and cultivated *Elaeagnus* seeds the archaeological sample.

most typical morphological differences between different varieties of *Elaeagnus* seeds.

In order to further determine the attribution of the *Elaeagnus* seeds in the archaeological samples, the LDA results showed that the cross-check accuracy of the confusion matrix for the classification of different types of modern *Elaeagnus* seeds was 85.71 %. This indicates that different types of modern *Elaeagnus* seeds could be distinguished relatively accurately based on morphological data. The results of using this matrix to distinguish archaeological samples showed that 82 % of archaeological samples were effectively classified (correct >0.9), with 18 % yielding controversial classification results (correct <0.9) (Detailed classification statistics in EMS 2). Among the effectively classified results, *Elaeagnus angustifolia* var. *orientalis* accounted for the highest proportion, at 48 % of all archaeological samples, followed by *Elaeagnus angustifolia,* which accounted for 34 %, with no *Elaeagnus oxycarpa* or modern cultivated *Elaeagnus angustifolia* components appearing.

4. Discussion

4.1. Effects of carbonization on the Russian olive morphology

Archaeologists have long been aware of the impact of the carbonization process on the morphological changes in most seeds, and even questioned the possibility of using measurements of carbonized seeds to distinguish morphological changes between different seed individuals (McGovern et al., 2003; Wright, 2003). Therefore, conducting modern carbonization process experiments on different seeds is an important prerequisite for archaeobotanical morphological studies (Ucchesu et al., 2016; Yang et al., 2011). The results of the modern carbonization process on wild and cultivated Russian olive seeds showed that both the length and thickness were reduced by about 12 %. The shrinkage in length and thickness was relatively consistent, and the length-to-thickness ratio did not change significantly, which closely follows proportional scaling. This morphological consistency laid a good foundation for subsequent geometric morphological analysis.

Since GPA method was used in this study for geometric morphological analysis, this method can eliminate factors unrelated to the shape of the sample, reducing the impact of size differences between different individuals and focusing the results on morphological changes (Gower, 1975; Rohlf and Slice, 1990; Zelditch et al., 2012). The PCA results of GPA between wild and cultivated Russian olive seeds before and after carbonization showed that different types of Russian olive seeds before and after carbonization basically overlapped. Combined with the linear measurement data, the above results prove that the degree of carbonization in different samples does not affect the results of the geometric morphological analysis result in this study.

4.2. Russian olive diversity in Bronze Age central Asia

Elaeagnus is a widely distributed economic and ecological plant in the arid areas of Central Asia. Currently, only three species of *Elaeagnus* are found in Bactria, namely, *Elaeagnus angustifolia*, *Elaeagnus angustifolia* var. *orientalis* and *Elaeagnus oxycarpa*. Among them, *Elaeagnus angustifolia* var. *orientalis* is considered a subspecies of *Elaeagnus angustifolia*, although there is still some controversy regarding whether *Elaeagnus oxycarpa* is a subspecies of *Elaeagnus angustifolia* or not (Li, 2007; Powo, 2023). However, since the fruit of *Elaeagnus oxycarpa* is much smaller than *Elaeagnus angustifolia*, and its seed morphology, especially the apex, differs from *Elaeagnus angustifolia*, the taxonomic controversy is not the primary focus of this research. Therefore, we adopt the classification standards of the Flora of China (Li, 2007) in this study, regarding *Elaeagnus angustifolia* var. *orientalis* as a subspecies of *Elaeagnus angustifolia* and still regard *Elaeagnus oxycarpa* as an independent species.

The results of the geometric morphological analysis of different modern and archaeological *Elaeagnus* seeds show that 2 types of *Elaeagnus* seed were appeared in the Bronze Age Bactria region. Among them, the number of *Elaeagnus angustifolia* var. *orientalis* is the numerous, accounting for 48 % of all archaeological samples, followed by *Elaeagnus angustifolia*, which accounts 34 % of all archaeological samples. The identification results still remaining 18 % are controversial. The controversial samples also mainly between, *Elaeagnus angustifolia* and *Elaeagnus angustifolia* var. *orientalis*. Since this 2 kind of Russian olive are only subspecies-level relationships and have similar morphology, a large overlap between the 2 species can also be found in PCA results. Therefore, it is understandable that there are some controversies regarding the morphological classification results. Meanwhile, no clear individuals of modern cultivated *Elaeagnus angustifolia* were found in the archaeological samples, which is completely different from cultivated fruits such as grapes from this period.

Since *Elaeagnus angustifolia* is a widely distributed plant in Central Asia, it is impossible to clear distingue whether the Russian olive seeds found at the site was collected from the wild or cultivated in an orchard. However, the morphological comparison results show that cultivated Russian olive seeds differ significantly from wild Russian olive seeds in terms of fruit and seed size. Compared to wild *Elaeagnus angustifolia,* cultivated *Elaeagnus angustifolia* seeds are at least 30 % larger in seed length. The Russian olive seeds obtained from Sapalli Tepa are generally smaller in size. Although some seeds have been carbonized and undergone some volume reduction, their morphology still closely resembles that of modern wild Russian olive, particularly in the relatively small length-to-thickness ratio. This may indicate that in the Bronze Age Bactria region, the Russian olive in the local early agricultural community was closer to the wild population and had not yet been systematically selected.

We also found that the Russian olive seeds from the archaeological site are significantly smaller than the carbonized modern wild Russian olive seeds. Archaeological samples are only 80 % of the size of the carbonized modern wild seeds. Botanical studies on modern *Elaeagnus angustifolia* show that the growth of *Elaeagnus angustifolia* trees is influenced by several factors, such as groundwater depth, atmospheric CO_2 concentration, and soil salinity. An increase in atmospheric CO_2 and high groundwater levels will significantly increase plant height and extend the growth period (Ainsworth and Long, 2005; Geng et al., 2021; Perry et al., 2013; Shi et al., 2008). Paleoclimate studies indicate that in the mid-Holocene, the global atmospheric CO_2 concentration was about 280×10^{-6}, which was significantly lower than the 345×10^{-6} of the modern reference value in 1985 (PMIP 1) (Joussaume and Taylor, 1995). Therefore, considering the diverse sources of *Elaeagnus angustifolia* and the limitations of early irrigation technology in Bronze Age Central Asia, the increase in global atmospheric CO_2 concentrations since the Industrial Revolution may be an important factor contributing to the size difference between modern wild Russian olive and archaeological samples.

4.3. Russian olive utilization in the Bronze Age southern Central Asia

In the Bronze Age, the early agricultural civilization of Central Asia represented by the Sapalli culture had already carried out a many early horticultural practices. The abundance of fruit remains, such as grapes and pistachios, indicates that horticultural activities played a significant role in the local agricultural system. Since the Russian olive is a native plant widely distributed across Central Asia, the specific source of Russian olive at the site cannot be conclusively determined with the current data. However, based on seed and fruit size, among the 3 wild *Elaeagnus* existing in Central Asia, the fruit of *Elaeagnus angustifolia* var. *orientalis* is the largest, followed by *Elaeagnus angustifolia*, and the smallest is *Elaeagnus oxycarpa*. In the Sapalli Tepa, relatively large fruits like *Elaeagnus angustifolia* var. *orientalis* and *Elaeagnus angustifolia.* are the most common, but no domesticated *Elaeagnus angustifolia* seeds have been found. This may be due to the fact that, unlike foreign cultivated crops that grow only in orchards, native fruits like the Russian olive may have been collected from the wild in addition to being artificially cultivated.

In early agriculture and other production processes, local people likely had some selection preferences for different types of crops and fruits. Current research shows that the early agricultural population of the Sapalli culture selectively cultivated larger individuals of grapes for sacrificial activities (Chen et al., 2022). At relatively smaller settlements like Sapalli Tepa, a large number of Russian olive seeds were found, even exceeding those of foreign fruits like grapes. However, the situation appears to be different at other contemporary sites. In larger urban settlement such as Djarkutan, while a large number of grapes were found, the number of Russian olive seeds was relatively small (Chen et al., 2024). Some studies suggest that during the early stages of globalization, foreign crops at these sites were often used as status symbols by high-ranking elites or for religious and sacrificial purposes (Spengler, 2019). Given the differences in social hierarchy between temples and ordinary settlements, Russian olive may have been more commonly consumed by civilians compared to fruits like grapes, which were introduced from other regions.

5. Conclusion

This study is the first systematic geometric morphological analysis of Russian olive seeds found in archaeological sites, providing a detailed examination of the morphological characteristics of *Elaeagnus* seeds from Bronze Age Central Asia. The results show that the Russian olive plants found at Sapalli Tepa include two types: *Elaeagnus angustifolia* and *Elaeagnus angustifolia* var. *orientalis*. Among them, the number of *Elaeagnus angustifolia* var. *orientalis* seeds is relatively large, and they show no signs of domestication. This may indicate that the Russian olive found in the agricultural civilizations of Bronze Age Southern Central Asia were not subject to intensive selection by local people, and their sources may have been diverse, including both cultivation and wild collection.

Meanwhile, the systematic study of the modern carbonization process of *Elaeagnus angustifolia* seeds confirmed that the shrinkage and deformation during carbonization had minimal impact on the morphology of the seeds, demonstrating the potential for geometric morphological analysis of fruit seeds found in archaeological sites. This provides important data for plant geometric morphological studies at archaeological sites. Our study also confirms that *Elaeagnus angustifolia* played a significant role in the horticultural systems of early agricultural civilizations in Bronze Age Southern Central Asia. The systematic study of its varieties is crucial for further understanding early horticultural activities, especially the use of local plant resources by ancient communities.

CRediT authorship contribution statement

Guanhan Chen: Writing – original draft, Visualization, Funding acquisition, Formal analysis. **Xinying Zhou:** Supervision, Investigation, Funding acquisition, Conceptualization. **Mutalibjon Khasanov:** Investigation. **Nasibillo Kambarov:** Investigation. **Hui Shen:** Supervision. **Jingyi Wang:** Visualization, Supervision. **Jian Ma:** Supervision, Funding acquisition. **Jianxin Wang:** Supervision. **Farhod Maksudov:** Supervision, Investigation. **Akhmadali Askarov:** Supervision. **Xiaoqiang Li:** Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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