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Pollen morphology of selected apricot (*Prunus*) taxa

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ABSTRACT
The purposes of this study were to provide palynological information about apricots and to reveal the relationships among six ecological groups of apricots by describing the morphological characteristics of their pollen. The pollen grains of 175 accessions belonging to three species (*Prunus armeniaca* L., *Prunus sibirica* L., and *Prunus mume* Sieb. et Zucc.) of *Prunus* were examined using light microscopy and scanning electron microscopy. The pollen grains were isopolar monads, radially symmetric, medium to large in size, prolate or subprolate, and 3-colporate. Most pollen grains exhibited striate exine ornamentation, and a few exhibited striato-reticulate or cerebroid exine ornamentation. Cluster analysis divided the six ecological groups into two groups: one including the Central Asian, North China, and Dzhungar-Ili ecological group accessions and another including the Northeast Asian, European, and East China ecological group accessions. Principal component analysis revealed that equatorial diameter, colpus length, colpus width, and ridge width were the most important metrical pollen traits, and can be used as powerful diagnostic characters in apricot identification. We speculated that the cultivated apricots in Xinjiang were domesticated from wild apricots from the Ili Valley. This study describes the morphological characteristics of apricot pollen grains and provides some morphological information for future studies on the phylogenetic relationships of apricots.

KEYWORDS
Apricot; ecological group; pollen morphology; light microscopy; scanning electron microscopy

1. Introduction

Apricot belongs to the section *Armeniaca* (Lam.) Koch in the subgenus *Prunophora* Focke and the genus *Prunus* (Rosaceae) and has abundant germplasm resources (Rehder 1940). China and Central Asia are thought to be the primary centers of origin and domestication for apricot (Kostina 1931; Vavilov 1951; Zhebentyayeva et al. 2003; Maghuly et al. 2005). Following different taxonomic systems, apricots have been divided into 3–12 species (Bortiri et al. 2001; Folta and Gardiner 2009). However, six species are recognized by most scholars (Kryukova 1989; Faust et al. 1998; Bortiri et al. 2001): *Prunus armeniaca* L., *Prunus sibirica* L., *Prunus mandshurica* (Maxim.) Skv., *Prunus holosericea* (Batal.) Kost., *Prunus mume* Sieb. & Zucc., and *Prunus brigantina* Vill. Almost all cultivated apricots belong to *P. armeniaca* (Zhebentyayeva et al. 2003). Chinese scholars (Zhang and Zhang 2003) have classified apricots into six ecological groups based on their geographical distribution – namely, the Central Asian (CAG), North China (NCG), European (EG), Dzhungar-Ili (DZG), Northeast Asian (NAG), and East China (ECG) ecological groups.

The Kashgar, Hotan, and Kuqa oasis areas around the Tarim Basin in the southern part of the Xinjiang Uygur Autonomous Region, China, are the main apricot-producing areas in China and contain most apricot cultivars. The wild apricot forest in Ili, Xinjiang, China, is a relic of broad-leaved forest preserved from the Cenozoic and has played a decisive role in the domestication and cultivation of apricots worldwide (Zhebentyayeva et al. 2003). This forest is an important part of the deciduous broad-leaved forest located below mountain coniferous forests and above mountain grasslands in Xinjiang (Zhang and Zhang 2003). However, no observations or analyses of the morphological characteristics of wild apricot pollen in Xinjiang have been reported.

Because pollen grains have unique biological characteristics, contain a large amount of genetic information, and exhibit strong genetic conservation, they can be used for species identification (Schori and Furness 2014; Song et al. 2017; Dos Santos Almeida et al. 2019). Palynological characters mainly include pollen shape, size, aperture features, exine thickness, and exine ornamentation (Xue et al. 2017) and play important roles in phylogenetic studies of fruit trees (Evrenosoğlu and Misirli 2009). Light Microscopy (LM) and Scanning Electron Microscopy (SEM) are the main methods used to study pollen morphology (Luo et al. 1992).

The pollen morphology of *Malus* Mill (apple), *Pyrus* L. (pear), and *Prunus* L. (plum, peach) was analyzed to explore their classification, origin, and genetic relationships (Currie et al. 1997; Evrenosoğlu and Misirli 2009; Mert 2009). Liu et al. (2010) used SEM to analyze pollen morphology and concluded that kernel-producing apricots originated from natural hybrids of *P. armeniaca* and *P. sibirica* and that some

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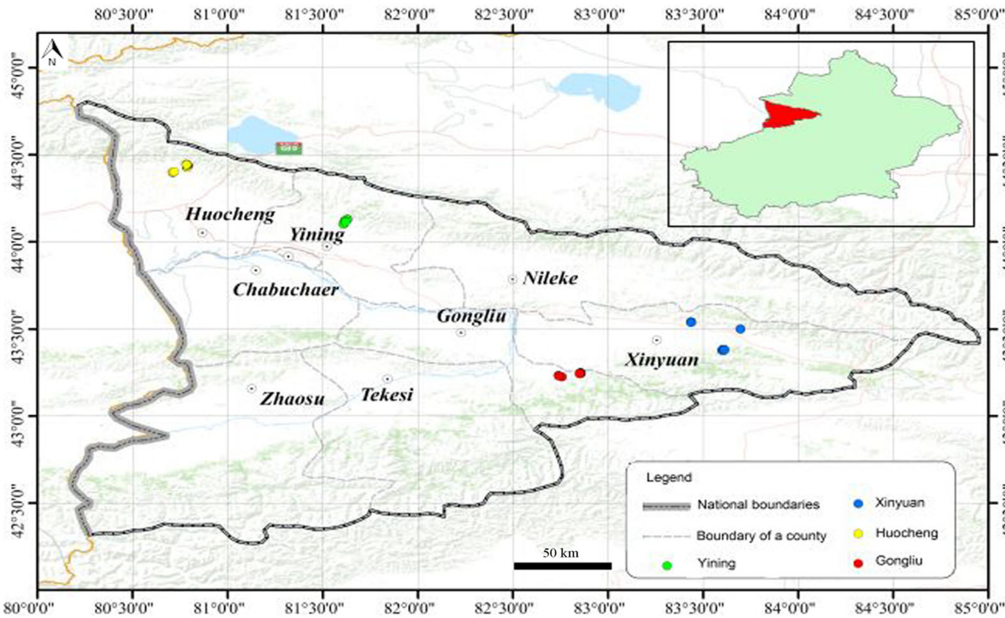

Figure 1. Distribution of wild apricots (*Prunus armeniaca*) collected in the Ili Valley. Source: bzdt.ch.mnr.gov.cn

kernel-producing apricots originated directly from a type of sweet *P. armeniaca*. Chwil (2015) argued that the results of studies on pollen grain exine ornamentation could be used for the classification of *Prunus*. Evrenosoǧlu et al. (2009) found that different parts of the exine of *P. armeniaca* cv. 'Tokaloğlu' and *P. armeniaca* cv. 'Tyrinthe' pollen grains display large or small verrucose shapes. Geraci et al. (2012) showed that the pollen grains of *P. armeniaca* cv. 'Rancinu' and *P. armeniaca* cv. 'Pirmintìu' are isopolar monads, of medium size, prolate, and 3-colporate. Although some studies of the pollen morphology of apricot cultivars have been performed, systematic studies of the pollen morphology of apricots in different ecological groups are lacking.

In this study, LM and SEM were used to study the pollen morphology of different ecological groups of apricots. We aimed to fill this research gap, improve the knowledge of pollen morphological characteristics, and clarify the relationships among different ecological groups.

2. Materials and methods

Closed but mature flower buds were chosen, collected pollen was put in a centrifuge tube after naturally drying in the shade, and samples were stored with silica gel desiccant. The age of the sample trees was over 20 years. According to our previous research, the materials used in this study were all diploid (Li et al. 2020). The pollen material was obtained from the Luntai National Fruit Germplasm Resources Garden of the Xinjiang Academy of Agricultural Sciences (where the annual average temperature and rainfall were 10.6 °C and 52 mm, respectively), the Yingjisha County Apricot National Forest Germplasm Bank (where the annual average temperature and rainfall were 13.43 °C and 17.38 mm, respectively), and the Xiongyue National Germplasm Resources Garden of the Liaoning Institute of Pomology (where the annual average temperature and rainfall were 9.6 °C and 700 mm, respectively). Wild apricots (*P. armeniaca*) were collected from Xinyuan, Gongliu, Yining, and Huocheng counties in Xinjiang (Figure 1). All the voucher specimens were deposited in the herbarium of Xinjiang Agricultural University.

The examined material is listed in Table S1 (Supplementary online data). The ecological groups studied were CAG, NCG, EG, DZG, NAG and ECG.

For LM, the pollinic material was treated following Erdtman's (1952) method of acetolysis. The slides were observed under a Nikon ECLIPSE 80i (Japan). ImageJ software was used to measure polar diameter (P), equatorial diameter (E), colpus length, colpus width, exine thickness, sexine thickness, and nexine thickness (Elysiane et al. 2018). The polar:equatorial ratio (P/E) was calculated.

To obtain SEM micrographs, dried pollen grains were distributed over a metal support previously covered with double-sided carbon adhesive tape and plated in gold (EvrenosoǧLu and Misirli 2009; Geraci et al. 2012). Electron micrographs were taken with a LEO-1430 VP (Germany). ImageJ software was used to measure ridge width, the distance between ridges (TDBR), punctum diameter (PD), and punctum number. Porosity was calculated by combining the measured area and punctum number. The terminology follows that in the studies of Erdtman (1952), Punt et al. (2007), and Hesse et al. (2009). The characters of 30 pollen grains randomly selected from a minimum of three slides were measured. The arithmetic mean ($-x$) and Standard Deviation (SD) of the standard materials were calculated.

The features described were the following: pollen shape, size, view, and exine ornamentation (Erdtman 1952).

Hierarchical cluster analysis (HCA) of the pollen metrical variables was performed using SPSS version 19.0 (SPSS, Inc., Chicago, IL, USA) (Figures 2 and 3). Principal component analysis (PCA) of the pollen metrical variables was performed using the FactoMineR and factoextra packages in R, and the first and second principal components were represented in a two-dimensional graph (Figure 4).

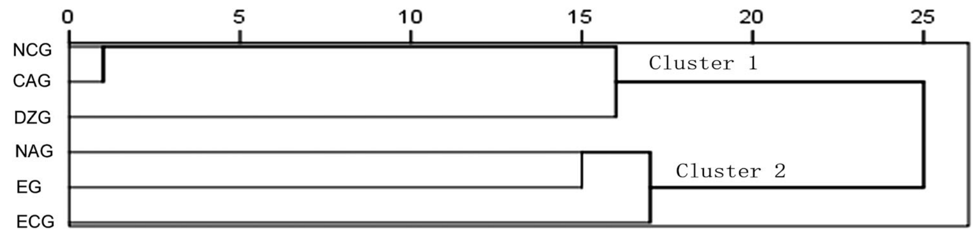

Figure 2. Cluster analysis performed with the pollen metrical variables from six ecological groups of apricot. NCG, North China ecological group; CAG, Central Asian ecological group; DZG, Dzhungar-Ili ecological group; NAG, Northeast Asian ecological group; EG, European ecological group; ECG, East China ecological group.

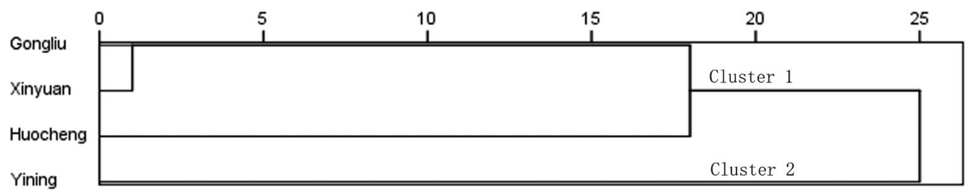

Figure 3. Cluster analysis performed with the pollen metrical variables from 4 groups of wild apricots (*Prunus armeniaca*).

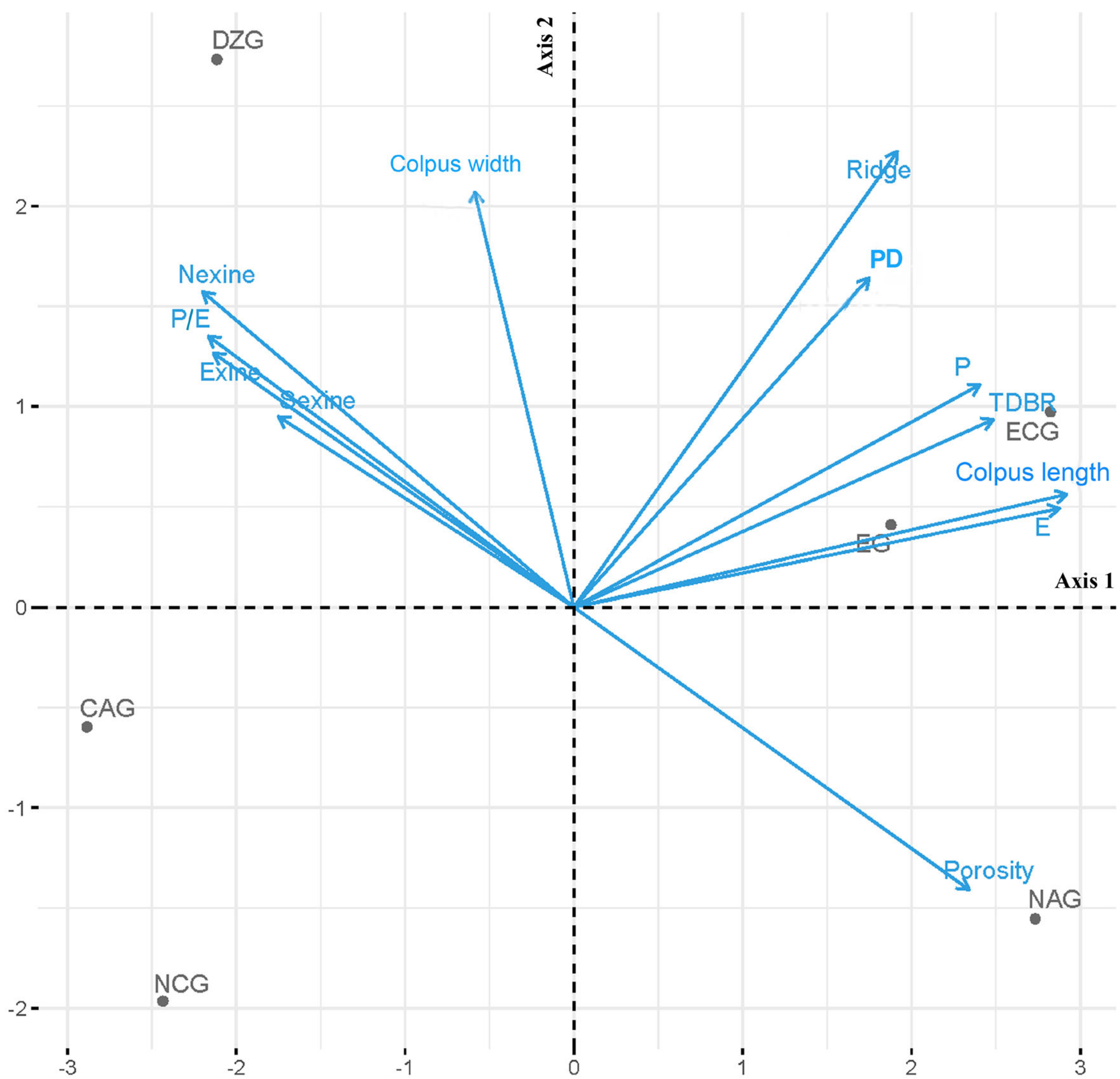

Figure 4. Principal component analysis (PCA) performed with the pollen metrical variables from six ecological groups of apricot. NCG, North China ecological group; CAG, Central Asian ecological group; DZG, Dzhungar-Ili ecological group; NAG, Northeast Asian ecological group; EG, European ecological group; ECG, East China ecological group; P, pollen diameter; E, equatorial diameter; DP, punctum diameter; TDBR, the distance between ridges.

3. Results

3.1. Pollen morphological description

We analyzed the pollen grains of 175 accessions of apricots (Table S2). Representative pollen grains are shown in Plates 1 and 2. The pollen grains of all accessions were isopolar monads, radially symmetric, medium to large in size, and prolate or subprolate (Plates 1 and 2). The pollen grains appeared circular (Plate 1, figures 1, 3, 5, 7, 9; Plate 2, figures 1, 4, 7, 10, 13, 19; Table S2) or triangular (Plate 1, figures 11, 13, 15; Plate 2, figure 16; Table S2) in polar view. Puncta of varying size and density were scattered between the exine striae (Plate 2, figures 3, 6, 9, 12, 15, 18, 21; Table S2).

The pollen grains mainly exhibited striate exine ornamentation (Plate 2, figures 3, 6, 9, 18; Table S2), and a few exhibited striato-reticulate exine ornamentation (Plate 2, figure 12; Table S2) or cerebroid exine ornamentation (Plate 2, figure 21; Table S2). There were seven types of exine ornamentation. In type I, the exine exhibited striate ornamentation, with striae parallel to the polar diameter and flat ridges. There were a few small puncta between the striae (Plate 2, figure 3). In type II, the exine of the pollen grains exhibited striate ornamentation, with striae parallel to the polar diameter and flat ridges. There were many large puncta between the striae (Plate 2, figure 6). In type III, the exine of the pollen grains exhibited striate ornamentation, with striae parallel to the polar diameter. The ridges were slender and prominent, with puncta between the striae (Plate 2, figure 9). In type IV, the exine of the pollen grains exhibited striato-reticulate ornamentation, consisting of protruding muri and lumina. A few small puncta were found between the muri (Plate 2, figure 12). In type V, the exine of the pollen grains exhibited striato-reticulate ornamentation. There were many puncta of different sizes between the muri (Plate 2, figure 15). In type VI, the exine of the pollen exhibited striate ornamentation, with no puncta between striae (Plate 2, figure 18). In type VII, the exine of the pollen grains exhibited cerebroid ornamentation. The ridges were curved and varied in width. TDBR was very insignificant (Plate 2, figure 21).

There were differences among the apricot accessions (Table S2). The polar diameter was 32.14–58.36 μm, with an average of 42.66 μm. The equatorial diameter was 20.12–39.47 μm, with an average of 27.22 μm. The P/E ratio was 1.24–1.99, with an average of 1.58. The colpus length was 26.52–52.81 μm, with an average of 37.38 μm. The colpus width was 3.40 μm–17.80 μm, with an average of 8.38 μm. The exine thickness was 1.04–3.28 μm, with an average of 1.74 μm. The sexine thickness was 0.56–1.77 μm, with an average of 0.99 μm. The nexine thickness was 0.44–1.51 μm, with an average of 0.75 μm. The ridge width was 0.13–0.44 μm, with an average of 0.28 μm. TDBR was 0.23–0.69 μm, with an average of 0.41 μm. The PD was 0–0.71 μm, with an average of 0.30 μm. The porosity was 0–2.42 grains μm^{-2}, with an average of 0.52 grains μm^{-2}.

3.2. Hierarchical cluster analysis

Based on the apricot pollen morphological data, hierarchical clustering was used to explore the genetic relationships among the six ecological groups (Figure 2). The HCA produced two clusters (Figure 2): cluster 1, comprising the NCG, CAG, and DZG; and cluster 2, comprising the NAG, EG, and ECG.

HCA was used to analyze four populations of wild apricots in Xinjiang and to explore the genetic relationships among them. The HCA produced two clusters (Figure 3): cluster 1, comprising the Gongliu County, Xinyuan County, and Huocheng County populations; and cluster 2, comprising the Yining County population.

3.3. Principal component analysis

The first and second axes from the PCA explained 73.49% of the variance (Table 1). The first principal component explained 52.38% of the variance, with equatorial diameter and colpus length being the most significant variables (Table 1). The second principal component explained 21.11% of the variance in the data, with colpus width and ridge width being the most significant variables (Table 1). Accessions from the ECG, NAG, and EG had positive values on the first axis, while accessions from the DZG, CAG, and NCG had negative values (Figure 4).

4. Discussion

The shape and size of pollen have significant value in botanical classification (Smitha et al. 2018). As palynological features are highly conserved in many plants, they are commonly used for taxonomic classification (Doğan and Baysal 2019).

DoĞan et al. (2019) described the pollen of *Limonium* species and separated the species into three informal groups according to their palynological features. Arzani et al. (2005) studied the pollen grains of 11 apricot cultivars (*P. armeniaca*) from Iran by SEM and found that the pollen grains were isopolar monads, radially symmetric, of medium size, prolate, and 3-colporate. The pollen grains appeared circular or triangular in polar view. Tong et al. (1995) showed that the pollen of *P. armeniaca* was mainly prolate, of medium size, and occasionally triangular in polar view. Chwil (2015) observed the pollen grains of the 'Early orange' and 'Harcot' cultivars by SEM and showed that the pollen grains were medium in size. Wang (1996) argued that treatments of pollen grains might have some effect on pollen size. For example, the polar diameter of pollen grains remains unchanged or changes very little when the grains are dried, while the equatorial diameter decreases due to a polarity effect on the surface of the pollen grains and aperture depression. In this paper, dry pollen was studied by LM. The pollen grain size was 42.66×27.22 μm, which was generally consistent with the above range. We consider the use of dry pollen to be feasible for palynological research. The pollen grains of 175 accessions in six ecological groups of apricots were examined by LM and SEM. Prior to this study, no systematic analysis of the pollen morphology of apricots had been reported. This is the first comprehensive study on the pollen morphology of the six ecological groups of apricot.

Yang (2000) found that the pollen grains of *P. armeniaca* were 3-colporate, while those of *P. sibirica* were mostly 3-colporate and occasionally 2-colporate. However, in this study, no 2-colporate pollen was observed in *Prunus* spp., indicating that this observation needs further verification.

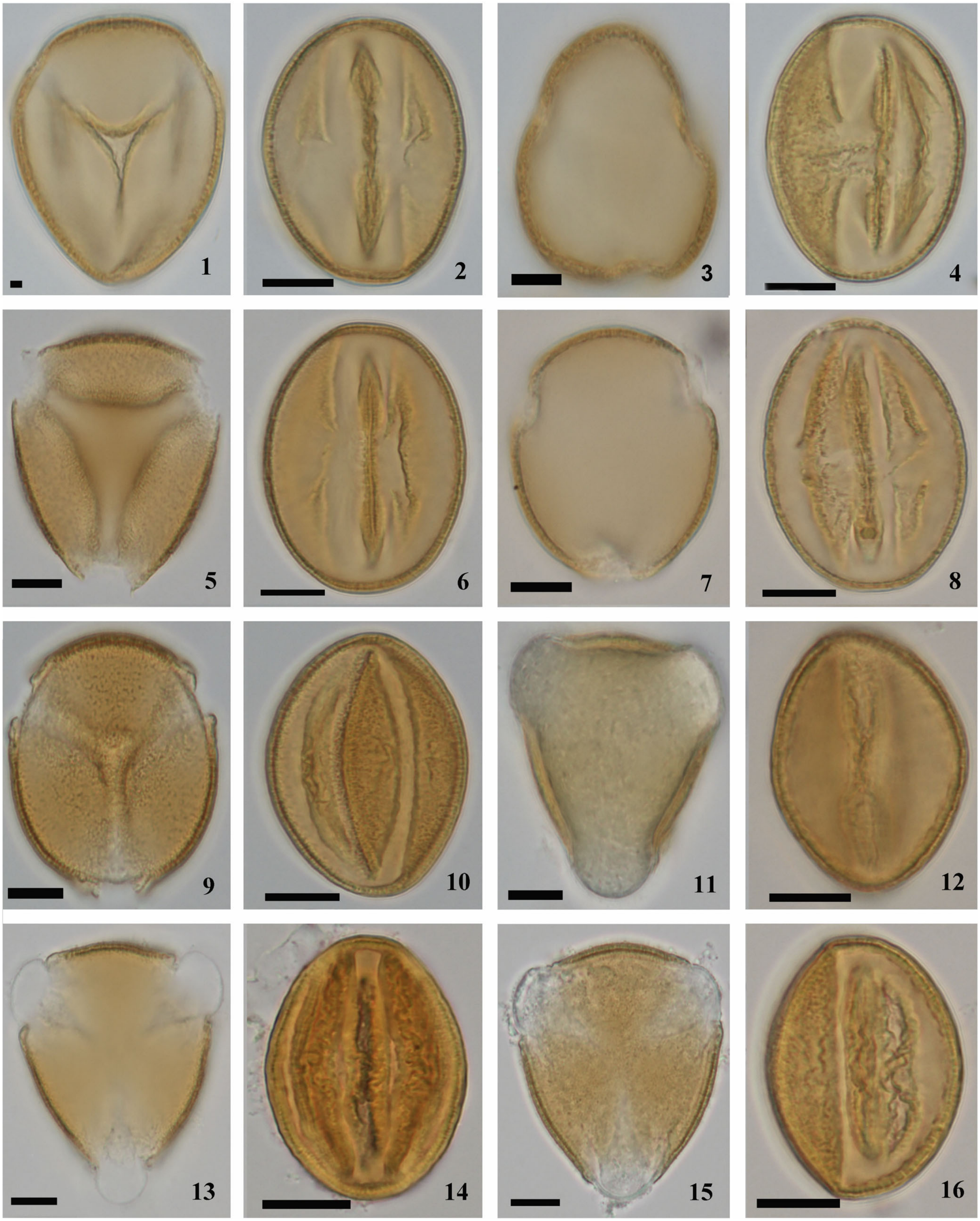

Plate 1. Light microscopy micrographs of apricot pollen grains. 1–2. *Prunus armeniaca*. 1. Polar view, EG02. 2. Equatorial view, EG02. 3–4. *P. armeniaca*. 3. Polar view, ECG02. 4. Equatorial view, ECG02. 5–6. *P. sibirica*. 5. Polar view, NAG04. 6. Equatorial view, NAG04. 7–8. *P. armeniaca*. 7. Polar view, DZGxyt75. 8. Equatorial view, DZGxyt75. 9–10. *P. armeniaca*. 9. Polar view, CAG73. 10. Equatorial view, CAG73. 11–12. *P. armeniaca*. 11. Polar view, DZGxyt97. 12. Equatorial view, DZGxyt97. 13–14. *P. armeniaca*. 13. Polar view, DZGxya79. 14. Equatorial view, DZGxya79. 15–16. *P. armeniaca*. 15. Polar view, DZGglb51. 16. Equatorial view, DZGglb51. Scale bars = 10 μm.

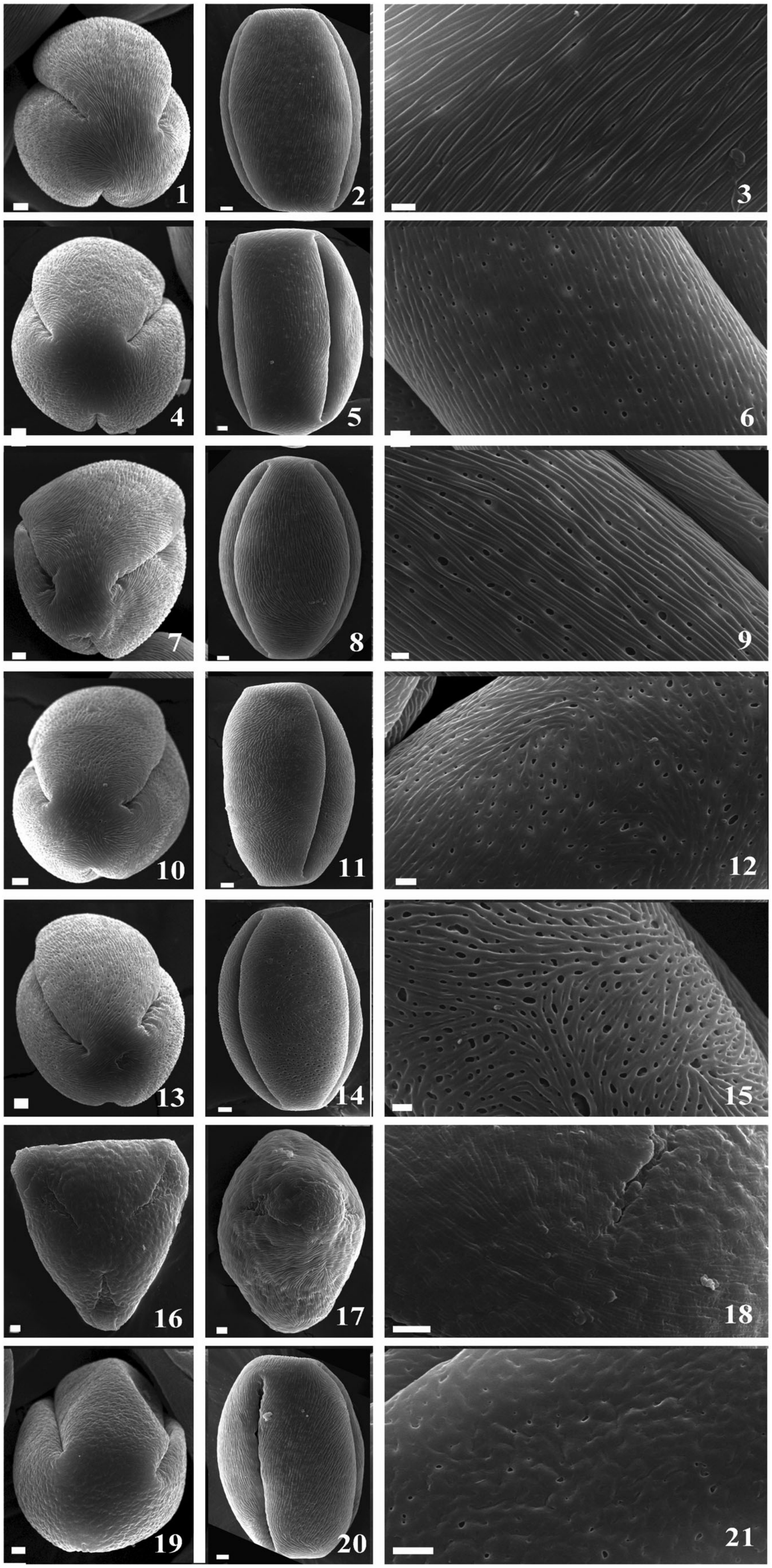

Plate 2. Scanning electron microscopy micrographs of apricot pollen grains. 1–3. *Prunus armeniaca*. 1. Polar view, DZGhcmd14. 2. Equatorial view, DZGhcmd14. 3. Exine ornamentation, DZGhcmd14. 4–6. *P. armeniaca*. 4. Polar view, DZGhcm34. 5. Equatorial view, DZGhcm34. 6. Exine ornamentation, DZGhcm34. 7–9. *P. armeniaca*. 7. Polar view, DZGhcm29. 8. Equatorial view, DZGhcm29. 9. Exine ornamentation, DZGhcm29. 10-12. *P. armeniaca*. 10. Polar view, CAG81. 11. Equatorial view, CAG81. 12. Exine ornamentation, CAG81. 13–15. *P. armeniaca*. 13. Polar view, DZGhcm27. 14. Equatorial view, DZGhcm27. 15. Exine ornamentation, DZGhcm27. 16–18. *P. armeniaca*. 16. Polar view, DZGxya78. 17. Equatorial view, DZGxya78. 18. Exine ornamentation, DZGxya78. 19–21. *P. armeniaca*. 19. Polar view, DZGhcmd12. 20. Equatorial view, DZGhcmd12. 21. Exine ornamentation, DZGhcmd12. Scale bars: 1, 2, 4, 5, 7, 8, 10, 11, 13, 14, 16, 21 = 2 μm; 3, 6, 9, 12, 15 = 1 μm.

Table 1. Cumulative variance and vector values of principal component analysis (PCA) using palynological characters of 6 ecological groups of apricots. The most significant values are marked in bold.

Name of variables	PC1	PC2
Cumulative variance (%)	52.38	21.11
Characters	Axis	
Pollen diameter (P)	0.7890	0.3630
Equatorial diameter (E)	**0.9430**	0.1610
P/E	−0.7100	0.4430
Colpus length	**0.9570**	0.1840
Colpus width	−0.1930	**0.6780**
Exine	−0.7010	0.4150
Sexine	−0.5740	0.3110
Nexine	−0.7210	0.5150
Ridge width	0.6280	**0.7450**
The distance between ridge (TDBR)	0.8140	0.3060
The punctum diameter (PD)	0.5730	0.5380
Porosity	0.7670	−0.4620

Porosity may be a valuable feature for taxonomic classification (Faegri et al. 1989). In this study, there were puncta of different sizes and densities between the striae. A change in punctum number may be caused by environmental factors, such as drought and poor soil (Bredenkamp and Wyk 1996). In this study, there were six accessions of *P. armeniaca* with no puncta between the striae. This variation may occur at both population and individual levels (Walker and Doyle 1975). Changes in punctum diameter may be caused by genetic factors, such as ploidy level, and environmental conditions, such as temperature, humidity, latitude, or altitude (Till-Bottraud et al. 1995; Zhao et al. 2016).

The exine ornamentation of pollen grains is complex, and there may be differences among individuals that can be used for plant classification and identification (Elysiane et al. 2018). The exine ornamentation of pollen grains plays an important role in the study of plant genetic evolution and systematic taxonomy (Zhang et al. 2017). Chwil (2015) studied the pollen morphology of 'Early orange' and 'Harcot' cultivars and found that their ridge widths were greater than those of other specimens, which is consistent with the results of this study. Liu et al. (2010) provided the first description of upturned, ridge-like, granular, and verrucous appendages as part of the exine ornamentation of *P. armeniaca*, based on the critical point drying method. However, no appendages were found on the exine in this study, which is consistent with the results of Chwil (2015).

Wagenitz (1976) and Blackmore et al. (2009) considered colpus length and spine length to provide valuable information for the classification of members of the Asteraceae. Gültepe et al. (2018) identified equatorial diameter and aperture diameter as the most valuable traits for the classification of *Tragopogon* species. We used PCA to show that polar diameter, colpus length, colpus width, and ridge width were important variables of the first and second principal components. Other palynological characters are also valuable for the classification of apricots. Therefore, the characters cannot be used independently for classification and identification.

Maghuly et al. (2005) performed simple sequence repeat analysis and reported that most EG accessions likely originated from the Iran-Caucasus subgroup accessions. Yuan et al. (2007) concluded, based on amplified fragment length polymorphisms, that members of the DZG and CAG of *P. armeniaca* were the most similar among the members of all groups. He et al. (2007) considered the genetic diversity of wild apricots (*P. armeniaca*) in the Ili Valley to be the highest, with particularly high genetic diversity in the Xinyuan population. According to HCA of pollen morphology, the CAG, NCG, and DZG (Ili Valley) accessions were clustered together. There is only one mountain between the southern Xinjiang and Ili areas in the northern Tianshan Mountains, and there are several corridors between the northern and southern Tianshan Mountains. Geographically, the cultivated apricots in the Xinjiang and southern Tianshan Mountains (CAG) most likely evolved as a result of the spread of wild apricots in the Ili Valley (DZG; Zhang and Zhang 2003).

5. Conclusion

The CAG and DZG accessions were closely related. We speculated that the CAG accessions were domesticated from the DZG (Ili Valley) accessions. This study described the morphological characteristics of apricot pollen grains and provided a morphological basis for future studies of the phylogenetic relationships of apricots. We also provided new insights into the origins of cultivated apricots in Xinjiang.

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Disclosure statement

No potential conflicts of interest were reported by the authors.

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