

## Pollen morphological analysis of papaya (*Carica papaya* L.)

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**Abstract:** *There is little information on pollen morphological analysis of papaya cultivars with different flesh color and origins. We observed pollen morphological characters of 17 papaya cultivars through scanning electron microscopy. The results showed that papaya pollen grains were monads, tricolporate, and small and medium-sized. The pollen grains were oblate-spheroidal to spheroidal. Foveolate, reticulate, and fossulate exine ornamentation were observed. Colpi width had maximum coefficient of variation of 25%; Shannon diversity index of all qualitative characters reached over 0.8. Using cluster analysis, 17 papaya cultivars were divided into three groups; there was no relationship between flesh colors and origins. The study findings suggest that pollen morphological analysis is valuable to provide references for breeding and genetic improvement of papaya.*

**Keywords:** *Cluster analysis, genetic diversity, papaya, pollen, scanning electron microscope*


### INTRODUCTION

Papaya (*Carica papaya* L.) is an important fruit widely distributed in tropical and subtropical areas (Kumari and Mishra 2019). It can be used in the food industry and medical and cosmetic products owing to its nutrients and phytochemicals (Srivastava et al. 2016, Jurandi et al. 2018). The growing demand for papaya in the international market evokes an increased concern regarding its genetic resource, breeding and s and improvement (Luz et al. 2018).

Genetic resources are the foundation materials for crop breeding and genetic improvement. Researchers investigating the genetic resources of papaya have highly focused on phenotypic and agronomic traits (Pan et al. 2011, Wu et al. 2011, Xiong et al. 2015, Xiong et al. 2019). Most phenotypical and agronomic traits are highly influenced by the environment (Damasceno Junior et al. 2018). Studies on molecular markers of papaya genetic resources have also been reported, such as RAPD (Huang et al. 2007), AFLP (van Droogenbroeck et al. 2002), SCAR (Liao et al. 2017), SRAP and ScoT (Cai et al. 2014), ISSR (Palei et al. 2019), SSR (Fang et al. 2016). Ming et al. (2012) reported the draft genome of transgenic papaya; this had a profound impact on papaya improvement. These molecular markers and genomic analysis improved our understanding of papaya genetic resources. However, their high costs constitute a drawback (Singh et al. 2020). Moreover, accurate operation of the above techniques and deep understanding of the complicated theory are warranted.

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Microscopical techniques using a scanning electron microscope (SEM) have become popular to assess micromorphology of plants (Ayaz et al. 2020, Lynn et al. 2020, Silva-Fourney et al. 2020, Gul et al. 2021, Ullah et al. 2021). Erdtman (1952) first described the pollen grains of papaya. Fisher (1980) observed pollen of several unnamed papaya cultivars of Latin American origin. Santos et al. (2008) described the pollen grain development of papaya cv. 'Solo'. Phuangrat et al. (2013) observed pollen of the Thai papaya cultivar 'Khak Nual'. Zini et al. (2018) studied pollen morphological characters of two papaya germplasms from Argentina. However, in all of these studies, there was little information on the pollen morphology of papaya cultivars with different flesh colors and origins.

Pollen can transmit genetic information of male gametes to a new generation (Payamnoor et al. 2019). Pollen size, shape, type, grain number, aperture structure and position, and exine ornamentation are highly diverse (Halbritter et al. 2018). Pollen morphological analysis using an SEM is cost-effective, is not or rarely affected by the environment, and yields high-resolution images that are visible and easy to understand. The objectives of this study were to examine pollen morphological characters of 17 papaya cultivars of different flesh colors and origins through SEM, investigate pollen diversity, and analyze genetic relations of 17 cultivars.

## MATERIAL AND METHODS

We collected pollen from staminate floral flowers of 17 papaya cultivars (Table 1) cultivated in Fujian Province, China for SEM observation between 2019 and 2020 in blooming buds. Pollen was fixed in 5% glutaraldehyde for four hours, washed three times with 0.1 mol L<sup>-1</sup> PBS, fixed with 1% osmic acid for four hours, and eventually washed three times with distilled water. Different ethanol concentrations were used for dehydration (gradient elution using 50, 70, 80, 90 and 100% ethanol with each concentration for 10-15 minutes and 100% ethanol three times). Tert-butanol was used for dehydration two times. Pollen was dried using JEOL freeze dryer (JEOL Ltd., Tokyo), spread evenly on the sample stage, stuck with double-sided adhesive tape, and coated with gold in a sputter coater. Pollen grains were photographed at different magnifications, according to the working rules of SEM JSM-6380LV (JEOL Ltd., Tokyo) in the conditions of low vacuum (P = 60 Pa) under the following zooming specifications: 3000 times - during the measurements and 15000 times - while taking the pictures of the exine ornamentation features.

**Table 1.** Origin, flesh color and pollen morphological characters of 17 papaya cultivars

No.	Accession name	Origin	Flesh color	Polar axis length (P, $\mu\text{m}$ )	Equatorial axis length (E, $\mu\text{m}$ )	P/E	Pollen shape	Pollen size	Colpi length ( $\mu\text{m}$ )	Colpi width ( $\mu\text{m}$ )
1	Indigenous Guangxi papaya	Guangxi, China	Yellow	23.46±0.87	24.03±0.76	0.976	Oblate-spheroidal	Small	19.04	1.83
2	Golden	Brazil	Yellow	23.51±0.68	24.12±0.67	0.975	Oblate-spheroidal	Small	18.31	2.07
3	Hongxiu	Known-you Seed Co., Ltd	Red	25.73±0.46	26.07±0.54	0.987	Oblate-spheroidal	Medium	21.76	1.97
4	Jindu No.1	Zhuhai Nongfu Seed Co., Ltd, China	Red	22.77±0.62	24.49±0.71	0.907	Oblate-spheroidal	Small	18.56	2.21
5	Indigenous Jiexiang papaya	Jiexiang Country, Ruili City, Yunnan, China	Red	24.98±0.39	25.48±0.53	0.980	Oblate-spheroidal	Medium	21.04	2.36
6	American papaya	USA	Yellow	23.78±0.75	24.15±0.37	0.985	Oblate-spheroidal	Small	18.63	2.35
7	Indigenous Hansha papaya	Hansha Country, Ruili City, Yunnan, China	Red	22.93±0.79	23.72±0.51	0.967	Oblate-spheroidal	Small	19.37	2.62
8	One-foot papaya	Malaysia	Red	26.16±0.54	26.88±0.63	0.973	Oblate-spheroidal	Medium	20.42	2.41
9	Red lady	Known-you Seed Co., Ltd	Red	27.13±0.41	27.02±0.33	1.004	Spheroidal	Medium	22.5	2.86
10	Hongri No. 2	Guangdong, China	Red	23.51±0.66	24.07±0.54	0.977	Oblate-spheroidal	Small	20.71	1.07
11	Solo	Hawaii	Yellow	24.82±0.46	26.04±0.58	0.953	Oblate-spheroidal	Small	18.53	3.42
12	Sunrise	Hawaii	Red	25.07±0.81	26.73±0.42	0.937	Oblate-spheroidal	Medium	21.95	2.75
13	Indigenous Quanzhou papaya	Quanzhou City, Fujian, China	Yellow	23.52±0.65	25.17±0.77	0.934	Oblate-spheroidal	Small	19.3	3.42
14	Indigenous Meizhou papaya	Meizhou City, Guangdong, China	Yellow	23.27±0.49	24.56±0.62	0.947	Oblate-spheroidal	Small	19.17	1.8
15	Malaysia No.10	Malaysia	Red	24.19±0.73	24.54±0.22	0.986	Oblate-spheroidal	Small	22.3	1.79
16	Malaysia No. 7	Malaysia	Yellow	25.22±0.59	25.76±0.19	0.896	Oblate-spheroidal	Medium	20.9	2.4
17	Indigenous Myanmar papaya	Myanmar	Red	25.78±0.62	26.69±0.81	0.966	Oblate-spheroidal	Medium	19.54	3.01

**Table 2.** Variation of quantitative characters of pollen

Quantitative characters	Range	Mean	Standard deviation	Coefficient of variation (%)
Polar axis length (P, $\mu\text{m}$ )	22.77-27.13	24.46	1.23	5.0
Equatorial axis length (E, $\mu\text{m}$ )	23.72-27.02	25.27	1.11	4.4
Ratio of polar axis length to equatorial axis length (P/E)	0.896-1.00	0.96	0.03	2.9
Colpi length ( $\mu\text{m}$ )	18.31-22.50	20.12	1.38	6.9
Colpi width ( $\mu\text{m}$ )	1.07-3.42	2.37	0.59	25.0

**Table 3.** Frequency and Shannon diversity index of qualitative characters of pollen

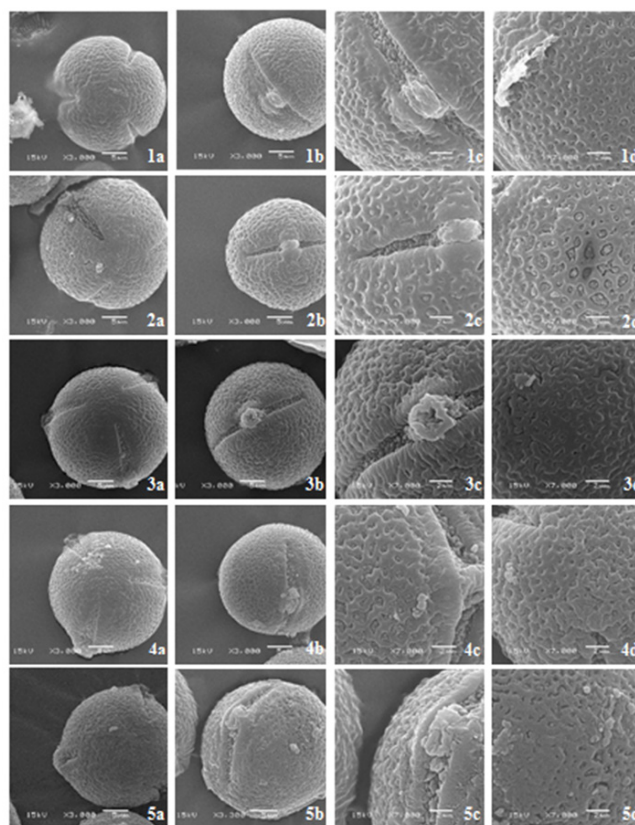
Qualitative characters	Shannon diversity index	Coding frequency (%)		
		1	2	3
Aperture membrane	1.018	Finely granulate 0.235	Granulate 0.235	Coarsely granulate 0.530
Exine ornamentation	0.874	Foveolate 0.647	Reticulate 0.118	Fossulate 0.235
Ridge width on tectum	1.037	Narrow 0.176	Medium 0.412	Wide 0.412
Ridge depth on tectum	0.804	Shallow 0.706	Medium 0.118	Deep 0.176
Foveola size	0.894	Small 0.648	Medium 0.176	Large 0.176
Foveola density	1.037	Few 0.412	Medium 0.412	Abundant 0.176

Pollen descriptions and terminology followed the criteria of Punt et al. (2007) and Hesse et al. (2009). Polar axis length, equatorial axis length, P/E ratio, colpi length, and colpi width were determined in 20 randomly selected pollen grains. Variation of quantitative characters was shown in Table 2 and frequency and Shannon diversity index of qualitative characters was shown in Table 3. Cluster analysis was performed using SPSS 20.0 for genetic relations based on unweighted pair-group method with arithmetic means (UPGMA), wherein averages are weighted by the number of taxa in each cluster at each step, and each distance contributes equally to the final result.

## RESULTS AND DISCUSSION

Studies on pollen morphological characters of cultivars through SEM have proved to be indispensable in the characterization and evaluation of genetic resources (Ayaz et al. 2020, Gul et al. 2021, Horčinová Sedláčková et al. 2021, Ullah et al. 2021).

In the present study, we examined in detail pollen characters of 17 papaya cultivars to highlight the importance of pollen in analyzing diversity of pollen and genetic relationship among cultivars. Papaya was eurypalynous. Papaya pollen grains were monads, isopolar, and radially symmetric (Figures 1 1a-5a, 2 1a-5a, 3 1a-5a, 4 1a-5a). All pollen grains of 17 papaya cultivars were small to medium-sized with diameter ranging from 15 to 40  $\mu\text{m}$  (Figures 1 1b-5b, 2 1b-5b, 3



**Figure 1.** Pollen morphological characters of five papaya cultivars (1. Indigenous Guangxi papaya, 2. Golden, 3. Hongxiu, 4. Jindu No.1, 5. Indigenous Jiexiang papaya). a. Polar view (3000 $\times$ ), b. equatorial view (3000 $\times$ ), c. colporate (7000 $\times$ ), d. exine ornamentation (7000 $\times$ ).

1b-5b, 4 1b-5b). Polar view was circular (Figures 1 1a-5a, 2 1a-5a, 3 1a-5a, 4 1a-5a) and equatorial view was subcircular (Figures 1 1b-5b, 2 1b-5b, 3 1b-5b, 4 1b-5b). Pollen shapes were oblate-spheroidal to spheroidal (Table 1). Papaya pollen grains were zonoaperturate with three colpi (Figures 1 1a-5a, 2 1a-5a, 3 1a-5a, 4 1a-5a). Fisher (1980), Phuangrat et al. (2013) and Zini et al. (2018) also showed that pollen grains were tricolporate, isopolar, radiosymmetric, small- and medium-sized, and spheroidal.

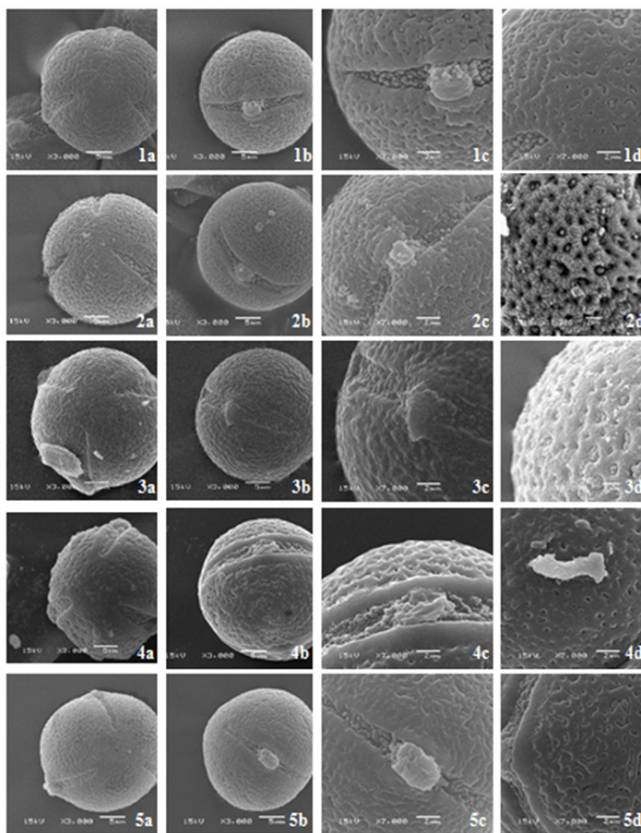
The colpi were situated equatorially and evenly, and had coarsely membrane (Figures 1 1b-5b, 2 1b-5b, 3 1b-5b, 4 1b-5b). Endoaperture was in the center of the colpi (Figures 1 1b-5b, 2 1b-5b, 3 1b-5b, 4 1b-5b). Colpus membrane was uneven with coarsely irregular granules and colpi margin was uneven with granules (Figures 1 1c-5c, 2 1c-5c, 3 1c-5c, 4 1c-5c).

Phuangrat et al. (2013) observed reticulate exine ornamentation at 2500 ×. In our studies, foveolate, reticulate, and fossulate exine ornamentation were observed at 7000 ×. ‘Indigenous Hansha papaya’ showed reticulate exine ornamentation (Figure 2 2d); ‘Jindu No.1’ (Figure 1 4d), ‘Indigenous Jiexiang papaya’ (Figure 1 5d), ‘Hongri No.2’ (Figure 2 5d) and ‘Solo’ (Figure 3 1d) showed fossulate exine ornamentation, and other cultivars showed foveolate exine ornamentation. Phuangrat et al. (2013) observed reticulate exine ornamentation. It could be explained that an accurate description of pollen exine ornamentation depends on the magnification (Halbritter et al. 2018).

Our study also provided other pollen characters of papaya shown in Tables 2 and 3, including polar and equatorial axis length, ratio of polar to equatorial axis length, colpi length and width, aperture membrane, ridge width and depth on tectum, and foveola size and density. Pollen characters were first introduced to conduct the genetic diversity analysis of papaya cultivars. Colpi width had maximum coefficient of variation, reaching 25.0%, whereas other quantitative characters had less than 10% of coefficient of variation. Ma et al. (2015) believed that one character with more than 100% of coefficient of variation had a strong level of variation, one character with coefficient of variation between 10% and 100% had a medium-level variation, and one character with less than 10% of coefficient of variation had a weak-level variation. Significantly, colpi width had maximum coefficient of variation, reaching 25.0% in our study, representing a medium-level variation, and could be an important indicator in further pollen morphological analysis of papaya.

Over 50% of the cultivars were coarsely granulate, 82.4% cultivars had medium and wide exine ridge, 70.6% of the cultivars had shallow exine ridge, 64.8% cultivars had small foveola on exine, and 82.4% of the cultivars had few or medium foveola. Shannon diversity index ranged from 1.037 (Ridge width on tectum and foveola density) to 0.804 (Ridge depth on tectum), and all qualitative characters reached over 0.8, showing high genetic diversity that could be helpful in the evaluation and characterization of papaya cultivars.

Our study is one of the first reports on cluster analysis based on pollen characters of papaya. Cluster analysis revealed three groups (G1-G3) (Figure 5). G3 was the largest group, comprising ‘Indigenous Guangxi papaya’, ‘Golden’, ‘Jindu No.1’, ‘American papaya’, ‘Hongri No. 2’, ‘Indigenous Meizhou papaya’ and ‘Malaysia No.10’. ‘Hongri No. 2’ was closely related to ‘Malaysia No.10’; ‘Jindu No.1’ was closely related to ‘Indigenous Meizhou papaya’; ‘Golden’ was closely related



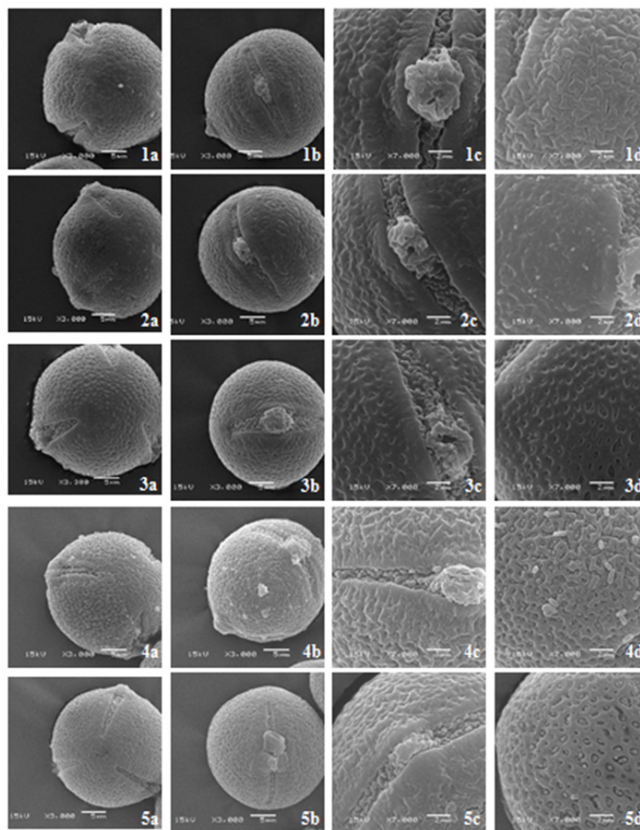
**Figure 2.** Pollen morphological characters of five papaya cultivars (1. American papaya, 2. Indigenous Hansha papaya, 3. One-foot papaya, 4. Red lady, 5. Hongri No. 2). a. Polar view (3000×), b. equatorial view (3000×), c. colporate (7000×), d. exine ornamentation (7000×).

to 'American papaya'; 'Indigenous Guangxi papaya', 'Golden' and 'American papaya' were in a subgroup. The second-largest group was G1, and it comprised 'Indigenous Jiexiang papaya', 'One-foot papaya', 'Red lady', 'Sunrise', 'Malaysia No. 7' and 'Indigenous Myanmar papaya'. 'Indigenous Jiexiang papaya' was closely related to 'Malaysia No. 7'; 'One-foot papaya' was closely related to 'Indigenous Myanmar papaya'; 'Red lady' was closely related to 'Sunrise', being accordant with RAPD analysis of Huang et al. (2007). SRAP and SCot analysis also showed that 'Red lady' and 'Sunrise' were clustered into a subgroup with 'Hawaii' (Cai et al. 2014). 'Red lady' is a hybrid from Known-you Seed Co., Ltd, Taiwan and 'Sunrise' is a Hawaii hybrid. Our results were accordant with previous results (Huang et al. 2007, Cai et al. 2014). The smallest group, G2, included 'Hongxiu', 'Indigenous Hansha papaya', 'Solo' and 'Indigenous Quanzhou papaya'. 'Hongxiu' was used as the basis in G2, and 'Indigenous Hansha papaya' was closely related to 'Indigenous Quanzhou papaya'.

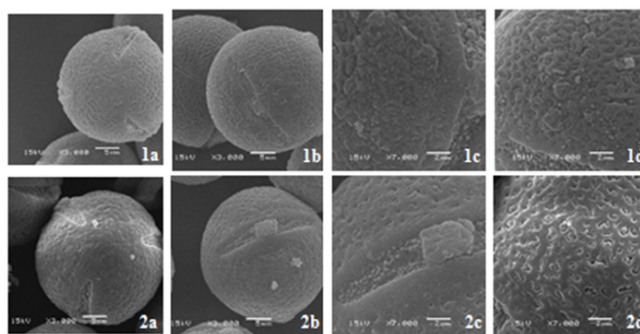
In our study, there were ten cultivars with red flesh and seven cultivars with yellow flesh. They could not be clustered distinctly. This is not accordant with the results of Aikpokpodion (2012), who reported that accessions with yellow flesh could be distinct from that with red flesh. There might be two reasons: papaya cultivars in our study were from several countries and not included accessions from Nigeria, while papaya accessions in the study of Aikpokpodion (2012) were from Nigeria. Notably, flesh color of papaya is caused by carotenoid accumulation, and does not follow the rule of dominant inheritance (Pecker et al. 1996).

Papaya cultivars from different origins were not clustered. There are two explanations. First, it showed the complexity of papaya's genetic background, and the genetic introgression of papaya clearly existed. Indigenous China cultivars could not be separated from foreign cultivars. It proved that indigenous China cultivars had close genetic relations and high frequency of germplasm exchange with foreign cultivars. It could be disadvantageous in breeding and genetic improvement of papaya. Therefore, it is essential to explore and introduce more foreign papaya genetic resources in China for obtaining improved cultivars. Second, our study included seventeen papaya cultivars that originated in China, Thailand, Hawaii, American, Malaysia and Myanmar. We need more papaya germplasms from other origins to further validate cluster groupings based on origins.

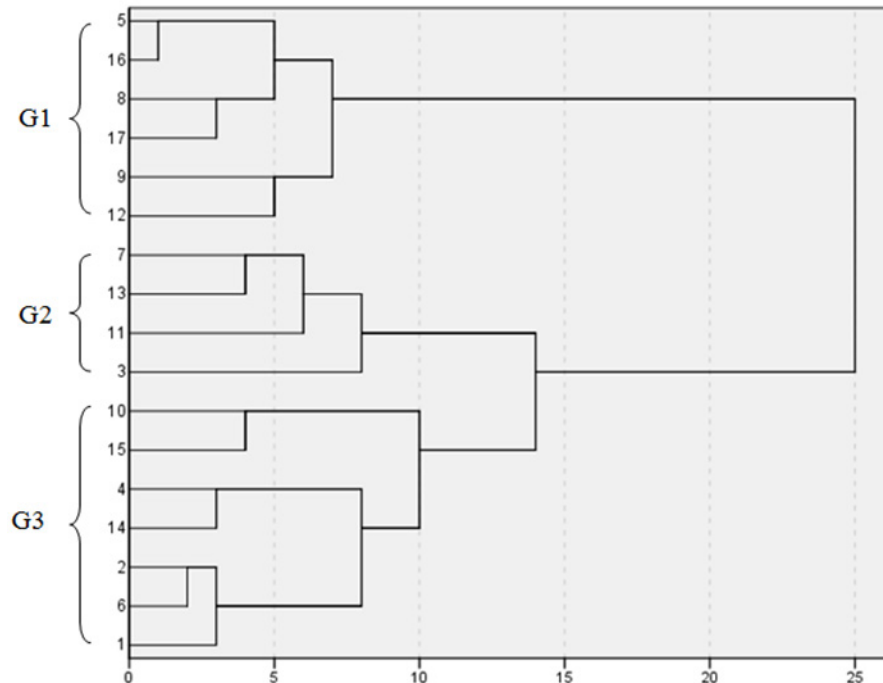
This study is one of the first to analyze pollen morphology of papaya with different flesh colors and from different origins under SEM. SEM study of papaya pollen plays an important role in the analysis of pollen diversity and genetic relationship among papaya cultivars. Cluster analysis can provide some helpful



**Figure 3.** Pollen morphological characters of five papaya cultivars (1. Solo, 2. Sunrise, 3. Indigenous Quanzhou papaya, 4. Indigenous Meizhou papaya, 5. Malaysia No.10). a. Polar view (3000×), b. equatorial view (3000×), c. colporate (7000×), d. exine ornamentation (7000×).



**Figure 4.** Pollen morphological characters of two papaya cultivars (1. Malaysia No. 7, 2. Indigenous Myanmar papaya). a. Polar view (3000×), b. equatorial view (3000×), c. colporate (7000×), d. exine ornamentation (7000×).



**Figure 5.** UPGMA dendrogram of pollen morphological characters of 17 papaya cultivars (1. Indigenous Guangxi papaya, 2. Golden, 3. Hongxiu, 4. Jindu No.1, 5. Indigenous Jiexiang papaya, 6. American papaya, 7. Indigenous Hansha papaya, 8. One-foot papaya, 9. Red lady, 10. Hongri No. 2, 11. Solo, 12. Sunrise, 13. Indigenous Quanzhou papaya, 14. Indigenous Meizhou papaya, 15. Malaysia No.10, 16. Malaysia No. 7, 17. Indigenous Myanmar papaya).

information on exploration and identification of papaya genetic resources and on genetic improvement. Moreover, pollen morphological analysis through SEM is relatively easy and cost-effective compared with molecular and genomic analysis.

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## Pollen morphological analysis of papaya (*Carica papaya* L.)

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