

Indehiscent Anther: A New Type of Male Sterility in F1 Hybrids of *Camellia yuhsienensis* × *Camellia oleifera*

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Abstract

Camellia oleifera (Theaceae) is valued for its high seed oil content and economic significance. The use of male sterility is important in plant hybrid breeding. Currently, in-depth research on male sterility in *C. oleifera* remains limited. Previous studies have primarily focused on breeding characteristics and taxonomy. In this study, we examined normal anther development using paraffin sectioning and identified five distinct types of abnormal anther dehiscence in *C. oleifera* using scanning electron microscopy (SEM) and light microscopy (LM). We analyzed the morphology of both normal pollen and pseudopollen cells in these abnormal anthers. Notably, among the F1 hybrids of *Camellia yuhsienensis* × *C. oleifera*, accession ‘YS-15’ exhibited limited anther dehiscence, whereas accession ‘YS-21’ showed complete indehiscence, significantly impeding pollen release. Quantitative analysis revealed a gradual decline in the number of both normal pollen grains and pseudopollen cells across the five abnormal anther types. The normal pollen count in these anthers was significantly lower than in wild-type counterparts. Specifically, the number of pseudopollen cells gradually decreased among the five F1 hybrid accessions (‘YS-5’, ‘YS-8’, ‘YS-13’, ‘YS-15’, and ‘YS-21’), with no pseudopollen cells detected in the latter two accessions. This study identifies a novel male-sterile germplasm in *C. oleifera*, providing valuable genetic resources for hybrid breeding and advancing research on male sterility.

Keywords: *Camellia oleifera*; anther dehiscence; paraffin sectioning; pseudopollen cells; male sterility



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1. Introduction

Hybridization enables the combination of favorable traits from parental plants, potentially generating novel characteristics and heterosis (hybrid vigor) [1]. The selection of superior hybrids facilitates the development of high-yielding and stress-resistant cultivars, thereby helping to alleviate imbalances in agricultural production [2]. Recent studies have further demonstrated that heterosis can enhance plant adaptation to abiotic stresses such as drought, with hybrid genotypes exhibiting genotype-specific physiological responses and transcriptomic changes related to stress tolerance [3]. In this context, male-sterile plants are valuable breeding materials because their stamens fail to develop normally or produce viable pollen, while the pistils develop normally and retain reproductive capacity [4,5].

The utilization of male-sterile materials prevents self-pollination, thereby avoiding varietal degradation and yield reduction. Moreover, it eliminates the need for manual emasculation, greatly improving breeding efficiency [6,7]. Therefore, the exploration and utilization of male sterility are of great significance not only for large-scale hybrid seed production but also for germplasm innovation and elite cultivar breeding, ultimately contributing to sustainable agricultural development [8].

Camellia oleifera is an important woody oilseed species, alongside olive and oil palm, and is recognized as one of the world's three major woody oil crops [9]. Its oil is highly valued because of its high content of unsaturated fatty acids, particularly oleic acid (>80%) and linoleic acid (~8%), as well as bioactive compounds such as squalene, phytosterols, and vitamin E [10,11]. Recognized by the FAO as a healthy edible oil, *C. oleifera* oil possesses considerable economic and nutritional value. Hybrid breeding plays a key role in *C. oleifera* improvement and remains one of the primary approaches for developing new cultivars. In recent years, interspecific hybridization has been increasingly applied to broaden the genetic background of *C. oleifera* and introduce desirable traits, such as improved adaptability and productivity. However, the shortage of stable male-sterile germplasm resources remains a major limitation for the efficient utilization of heterosis and hybrid seed production [12]. Most previously reported male-sterile materials in *C. oleifera* are associated with abnormalities during microspore development, tapetal degeneration, or pollen abortion, ultimately leading to reduced pollen viability or complete loss of pollen function [12–14]. By contrast, male sterility associated with abnormal anther dehiscence has rarely been reported in this species. Because anther dehiscence represents the final step of pollen release, sterility arising from this process may involve distinct developmental and genetic regulatory mechanisms compared with previously reported male-sterile sources. Therefore, the identification of novel sterility types related to anther dehiscence could broaden the spectrum of available male-sterile germplasm and provide alternative resources for hybrid breeding and heterosis utilization [15].

Male sterility may result from abnormalities in pollen development or pollen release. Among these processes, anther dehiscence is essential for successful pollen dispersal and fertilization. Previous studies in *Arabidopsis*, rice, and tomato have demonstrated that anther dehiscence is regulated by coordinated developmental events, including endothecium secondary wall thickening, lignification, septum degeneration, and hormone-mediated signaling pathways [16–19]. Defects in these processes often lead to anther indehiscence and functional male sterility despite the presence of apparently normal pollen [17–19]. In addition to anther dehiscence, pseudopollen cells or other pollen-like structures may influence pollen presentation and dispersal in flowering plants. Alterations in these pseudopollen cells may interfere with normal pollen release and are therefore potentially associated with functional male sterility. However, pseudopollen-like structural abnormalities have rarely been described in *C. oleifera*, and whether they are associated with abnormal anther dehiscence and pollen retention remains unknown. However, anther indehiscence-associated male sterility has rarely been reported in *C. oleifera*, and its developmental characteristics and breeding value remain unclear.

In this study, we identified a novel male-sterile phenotype in an F1 hybrid population derived from a distant cross between *C. yuhsienensis* 'YS-2' and *C. oleifera* 'Huashuo'. Phenotypic observations and microscopic analyses revealed that this sterility type is mainly characterized by abnormal anther development, which prevents normal anther dehiscence. Since functional fertility assessments, such as pollen germination and controlled pollination experiments, were not conducted in this study, we interpreted the male-sterile phenotype with caution. Therefore, the objectives of this study were to characterize the floral and anther phenotypes of this novel sterile germplasm, investigate the relationship between

abnormal anther dehiscence, pseudopollen-like structural alterations, and pollen retention, and evaluate its potential significance as a new breeding resource. The discovery of this phenotype is of considerable significance because it enriches the male-sterile germplasm resources of *C. oleifera*, provides new genetic materials for germplasm innovation, and offers a valuable sterile line for hybrid breeding. The effective utilization of this sterility resource may enhance the exploitation of heterosis and improve hybrid breeding efficiency. Furthermore, breeding programs based on this sterility phenotype may accelerate the development of *C. oleifera* cultivars with broad adaptability, high oil yield, and enhanced stress tolerance, thereby promoting the high-quality development of the tea oil industry.

2. Materials and Methods

2.1. Plant Materials

F1 hybrid offspring were obtained from a tea oil tree breeding base in Changsha City, Hunan Province, China (28°13'48" N, 112°55'53" E), where *C. yuhsienensis* was used as the maternal parent and *C. oleifera* 'Huashuo' as the paternal parent. A total of 407 F1 hybrid individuals were generated. During the flowering period, 200 flowering F1 individuals were examined for floral morphology and anther characteristics, among which 18 individuals (9.0%) consistently exhibited abnormal anther dehiscence associated with male sterility.

Based on repeated field observations, five representative F1 hybrid lines ('YS-5', 'YS-8', 'YS-13', 'YS-15', and 'YS-21') exhibiting stable indehiscent anther phenotypes were selected for detailed morphological and anatomical analyses. Floral organs and abnormal anthers from these five hybrid lines were collected for subsequent morphological, anatomical, and microscopic analyses.

2.2. Anther and Pollen Dissection

To investigate the anatomical structure of normal stamens, five hybrid *C. oleifera* lines ('YS-5', 'YS-8', 'YS-13', 'YS-15', and 'YS-21') grown at the experimental plantation were selected. One representative plant was selected from each hybrid line. From each plant, three pre-anthesis flower buds were collected from each of the east, south, west, north, and central canopy positions, resulting in 15 flower buds per line and a total of 75 flower buds across the five hybrid lines. All sampled flower buds were collected at the pre-anthesis stage, when the petals remained closed and the anthers had reached their final size but had not yet dehisced. Five stamens were randomly selected from each flower bud, yielding a total of 375 stamens for anatomical observation.

Samples were vacuum infiltrated for 3–4 h to remove trapped air, after which the ovaries were excised and the remaining tissues were fixed in Carnoy's solution (ethanol:glacial acetic acid = 3:1, *v/v*) at 0–4 °C. Fixed samples were dehydrated through a graded ethanol series (85%, 95%, and 100%; 30 min at each concentration), cleared sequentially in xylene:ethanol (1:1, *v/v*) and pure xylene, infiltrated with a xylene:paraffin mixture (1:1, *v/v*), and embedded in paraffin after three to four changes of fresh paraffin at 60 °C (at least 4 h per change). Longitudinal sections (10 µm thick) were prepared using a rotary microtome (Leica RM2235, Leica Biosystems, Wetzlar, Germany). After deparaffinization and rehydration, the sections were stained with periodic acid–Schiff (PAS) reagent following standard histological procedures, dehydrated, mounted with neutral resin, and observed under an inverted microscope. Images were captured under both bright-field and ultraviolet illumination (330–380 nm), and three representative fields of view were recorded for each section.

To compare the natural morphology of normal pollen and pseudopollen cells, pollen suspensions were prepared by placing ten randomly selected dehiscent anthers

into a 1.5-mL centrifuge tube containing 1 mL of distilled water, followed by thorough vortexing to obtain a homogeneous suspension. Three biological replicates (pollen suspensions) were prepared for each hybrid line, resulting in a total of 15 pollen suspensions for microscopic observation.

2.3. Measurements of Pollen and Pseudopollen Cells

Pollen grains in the pollen suspensions were photographed, and the polar axis length, equatorial axis length, and surface area of both normal pollen grains and pseudopollen cells were measured from the lateral view using the image analysis software ImageJ v1.54 (National Institutes of Health, Bethesda, MD, USA) [20]. For each hybrid line, 30 normal pollen grains and 30 pseudopollen cells were randomly selected and measured from pollen suspensions prepared from three flowers collected from the single plant. Normal pollen was identified by its yellow color, powdery texture, and triangular morphology, whereas pseudopollen cells were distinguished by their white, semi-transparent, powdery appearance under microscopic observation.

2.4. Anthers and Pollen Morphology Analyses by LM

The *C. oleifera* anthers were examined under a stereomicroscope (Olympus SZX10, Olympus Corporation, Tokyo, Japan) equipped with a DP73 digital camera (Olympus Corporation, Tokyo, Japan) to observe their overall morphology, anther dehiscence, pollen release, and coloration, and representative photographs were taken for documentation. Each anther was observed repeatedly to ensure consistency of the observations. All images were captured at magnifications of 4×, 10×, and 20×.

2.5. Numbers of Pollen Grains and Pseudopollen Cells in Different Anther Types

The number of normal pollen grains and pseudopollen cells in each *C. oleifera* flower was determined using the cellulase digestion method. For each hybrid line, six flowers were randomly collected from a single plant. Fifteen intact anthers were sampled from each flower and used as one biological replicate. The anthers were placed into 1.5 mL centrifuge tubes and dried at 25 °C to allow complete pollen dispersion. Subsequently, 1 mL of 1% cellulase solution was added, and the mixture was thoroughly shaken and incubated for 24 h. A 2 µL aliquot of the suspension was then loaded onto a hemocytometer and counted under a microscope, with six repeated measurements performed for each sample. Statistical analyses were conducted using SPSS version 26.0.

2.6. Anthers and Pollen Morphology Analyses by SEM

For scanning electron microscopy (SEM) analysis, mature anthers were collected and carefully positioned at the center of a microscope slide using tweezers and a dissecting needle. The samples were gently washed with distilled water for 30 min to remove surface impurities and then air-dried at room temperature. The pollen grains were transferred onto double-sided conductive adhesive tape mounted on a specimen stub. The samples were sputter-coated with gold for 3–5 min and subsequently examined using a JSM-660LV scanning electron microscope (JEOL Ltd., Tokyo, Japan). For each hybrid line, 20 anther samples were observed and recorded. Representative fields were examined at magnifications of 50×, 100×, and 2000×, and 10 representative pollen grains from each hybrid line were selected for morphometric measurements.

2.7. Data Analysis

The main morphological characteristics of pollen and pseudopollen-like structures were analyzed using one-way analysis of variance (ANOVA). When significant differences were detected, Tukey's honestly significant difference (HSD) test was performed for multi-

ple comparisons among the five lines. Prior to ANOVA, data normality and homogeneity of variance were assessed using the Shapiro–Wilk test and Levene’s test, respectively. All statistical analyses were performed using SPSS version 26.0, and differences were considered statistically significant at $p < 0.05$.

3. Results

3.1. Normal Anther Structure

The anther of *C. oleifera* consists of pollen sacs containing numerous normal pollen grains and connective tissue. Histological staining revealed abundant starch accumulation within the anther, while the anther wall cells exhibited a high degree of lignification. Notably, clusters of vacuolated pseudopollen cells were observed between the two pollen sacs, characterized by distinct boundaries and compact arrangement. The outermost layer of pseudopollen cells was closely connected to the pollen sacs. Normal pollen grains were bright yellow and distributed on both sides of the connective tissue, whereas pseudopollen cells were white and translucent and were located within the connective tissue (Figure 1a,b).

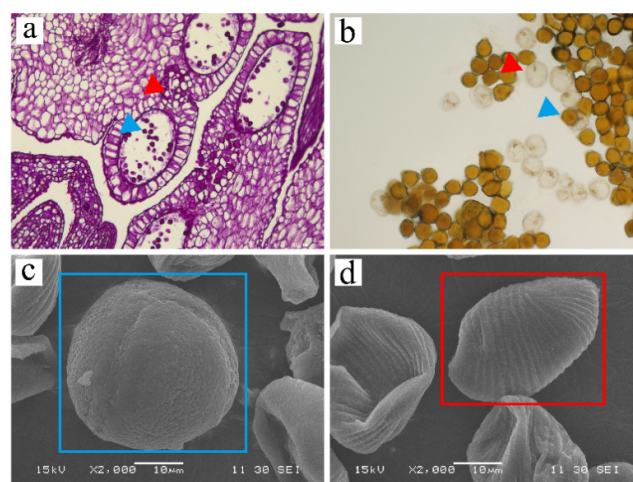


Figure 1. Paraffin sections and pollen morphological characteristics. (a) Paraffin sections: the blue arrow is the location of pseudopollen, and the red arrow is the location of pollen; (b) Pollen suspension staining: the blue arrow refers to pollen, and the red arrow refers to pseudopollen; (c,d) The morphology of normal pollen grains and pseudopollen cells under SEM, respectively.

Normal pollen grains and pseudopollen cells differed markedly in morphology and exine ornamentation (Table 1). Normal pollen grains were nearly spherical with a reticulate exine pattern, whereas pseudopollen cells were flattened and irregular in shape, with the exine surface exhibiting a nearly striate ornamentation (Figure 1c,d).

Table 1. Morphological characteristics of normal pollen grains and pseudopollen cells of *C. oleifera*.

Type	Polar Axis (μm)		Equatorial Diameter (μm)		Size (μm^2)	
	A $\pm$ S	CV	A $\pm$ S	CV	A $\pm$ S	CV
Pollen	38.75 $\pm$ 3.28 *	0.08	24.56 $\pm$ 1.37	0.06	735.44 $\pm$ 54.32	0.07
Pseudopollen cells	33.67 $\pm$ 5.57	0.17	28.12 $\pm$ 3.35 *	0.12	773.01 $\pm$ 192.13	0.26

Data are presented as mean $\pm$ SD. CV, coefficient of variation. * indicates a significant difference between pollen grains and pseudopollen cells for the corresponding trait (independent-sample *t*-test, $p < 0.05$).

3.2. Abnormal Anther Morphology

In comparison with normal anthers, the five abnormal anther types exhibited varying degrees of dehydration, with dark brown tissue observed at the sites of pollen sac dehis-

cence (Figure 2(a1–e1)). Among them, the anthers of ‘YS-5’ showed the mildest phenotype, displaying only a slight whitish coloration. Under suitable conditions, the anthers dehiscid normally and appeared relatively full, with only slight dehydration and shrinkage observed (Figure 2(a1)). In the anthers of ‘YS-8’, distinct brown tissue was present at the dehiscence sites, although this discoloration did not extend to other regions. Normal pollen release could still be observed, and no obvious dehydration occurred (Figure 2(b1)). In ‘YS-13’, the brown tissue became darker; however, the anthers were still able to dehiscid normally and release pollen (Figure 2(c1)). The anthers of ‘YS-15’ differed markedly from the previous types. The dehiscence sites became dark brown, and the entire anther exhibited severe dehydration and a dry appearance. Anther dehiscence was greatly reduced, with only two narrow openings visible at the apex and a small central gap through which pollen could be released. The anthers of ‘YS-21’ showed even more severe wilting than those of ‘YS-15’ and appeared unable to dehiscid normally (Figure 2(d1,e1)).

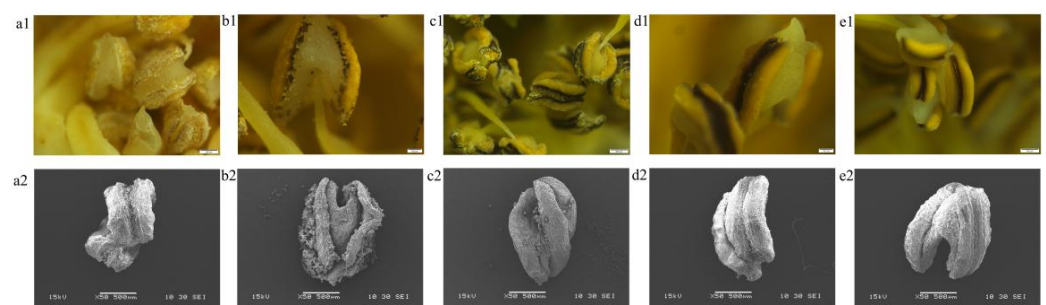


Figure 2. Different types of anther morphology. (a1–e1) Morphology of the natural state of the anther of ‘YS-5’, ‘YS-8’, ‘YS-13’, ‘YS-15’ and ‘YS-21’; (a2–e2) Morphology of the SEM state of the anther of ‘YS-5’, ‘YS-8’, ‘YS-13’, ‘YS-15’ and ‘YS-21’.

3.3. Anther Dehiscence of Different Anther Types

Scanning electron microscopy (SEM) analysis revealed differences in the size of the anther dehiscence openings among the five abnormal types. The anthers of ‘YS-5’ dehiscid normally and exhibited well-formed openings (Figure 3(a1)). Abundant pollen grains were observed at the dehiscence sites (Figure 3(a2)). In contrast, the dehiscence openings of ‘YS-8’ and ‘YS-13’ were markedly smaller than those of ‘YS-5’ (Figure 3(b1,c1)). Despite the presence of dark brown tissue around the openings in both ‘YS-8’ and ‘YS-13’, pollen release still appeared normal (Figure 3(b2,c2)).

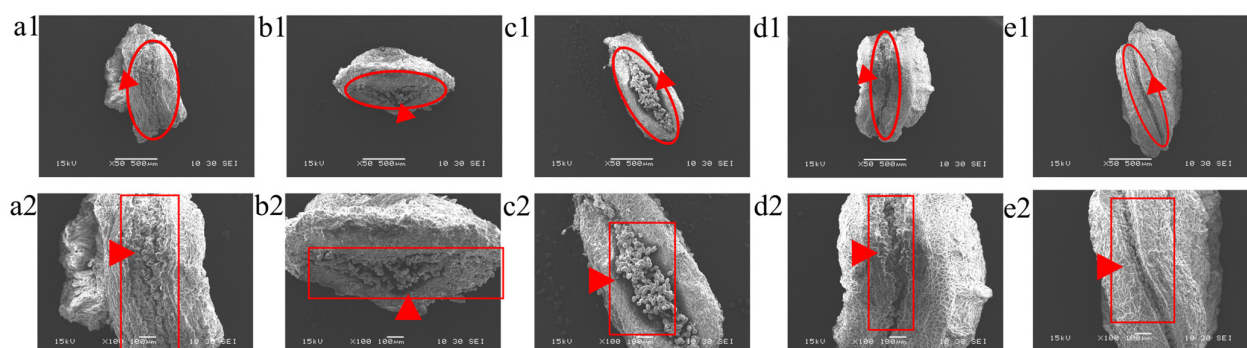


Figure 3. SEM observations of anther dehiscence in five F1 hybrid lines. (a1–e1) Dehiscence openings of ‘YS-5’, ‘YS-8’, ‘YS-13’, ‘YS-15’, and ‘YS-21’ (red circles/arrows indicate the opening regions); (a2–e2) pollen release or pollen retention at the corresponding dehiscence regions, with the retained pollen accumulation in ‘YS-21’ highlighted.

Compared with the first three abnormal types, the anthers of ‘YS-15’ contained only a small amount of pollen at the dehiscence sites (Figure 3(d1)). The anthers of ‘YS-21’ exhibited extremely limited dehiscence (Figure 3(e1)), and a large accumulation of pollen grains remained within the pollen sacs (Figure 3(e2)), indicating substantial pollen retention within the anthers.

3.4. Variation in Pollen Quantity

Quantitative analysis of normal pollen grains and pseudopollen cells revealed clear differences among the five abnormal anther types (Figure 4). The anthers of ‘YS-5’ and ‘YS-8’ contained the highest numbers of normal pollen grains. In contrast, the anthers of ‘YS-13’ and ‘YS-21’ exhibited similarly low pollen counts, each containing fewer than 200 pollen grains, whereas ‘YS-15’ showed an intermediate level of approximately 390 pollen grains. The number of pseudopollen cells exhibited a progressive decline from ‘YS-5’ to ‘YS-21’. Notably, pseudopollen cells were completely absent in both ‘YS-15’ and ‘YS-21’.

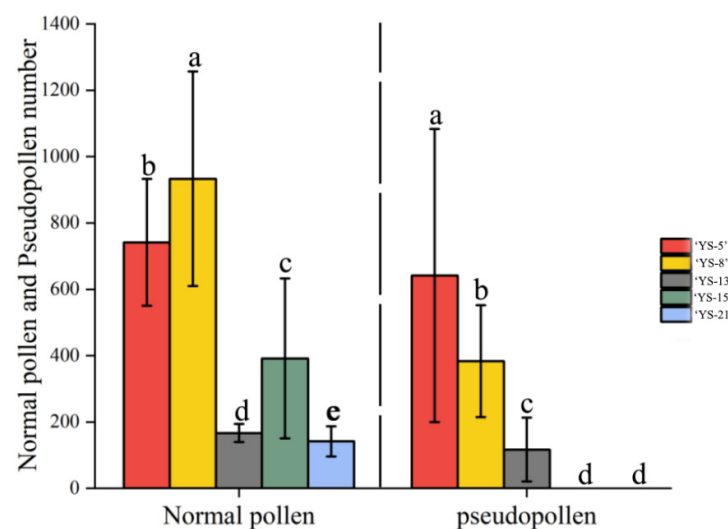


Figure 4. Numbers of normal pollen grains and pseudopollen-like structures in anthers from five F1 hybrid lines. Different letters indicate significant differences at $p < 0.05$.

4. Discussion

Male sterility in plants may result from abnormal stamen development, defective pollen formation, impaired pollen release, or reduced pollen function while female organs remain fertile [17,18]. Functional male sterility is often associated with the production of morphologically normal pollen that cannot be released effectively because anther dehiscence is impaired [17–19]. Because the present study did not evaluate pollen viability, in vitro germination, fertilization capacity, female fertility, or heritability, the phenotype is interpreted here as an anther-indehiscence phenotype consistent with putative functional male sterility rather than confirmed male sterility.

In *Camellia*, previously described male-sterile phenotypes include petaloid and abortive types [21–23]. The material examined in the present study did not exhibit petaloid conversion of anthers into petal-like organs. Instead, the predominant phenotype was impaired anther dehiscence accompanied by pollen retention. These observations suggest that the phenotype observed in the F1 hybrids of *C. yuhsienensis* × *C. oleifera* differs from the previously reported petaloid and abortive male-sterility systems.

Microscopic observations revealed dark brown tissue around the anther dehiscence region and a gradient of impaired anther opening among the five F1 hybrid lines. The most severe line, ‘YS-21’, retained a large amount of pollen within the anther, whereas

pollen was more readily observed at the dehiscence sites of 'YS-5' and 'YS-8'. These observations indicate increasing pollen retention associated with progressively restricted anther dehiscence [15]. The visible dry or shriveled appearance of the anthers is described here as a dehydration-like symptom because water content, endothecium thickness, and secondary wall thickening were not measured. Whether the five phenotypic categories represent distinct abnormal types or successive stages of the same developmental process requires further anatomical and developmental investigation.

Previous observations suggested that anther opening in *C. oleifera* may be associated with pseudopollen cell formation at specific positions near the pollen sacs [24]. In the present material, reduced or absent pseudopollen-like structures coincided with smaller dehiscence openings and increased pollen retention. However, the present observations demonstrate only a correlation and do not establish a causal relationship between pseudopollen cell formation and anther dehiscence. Future studies should quantify dehiscence aperture size, water content, endothecium development, secondary wall thickening, and the timing of separation of pseudopollen cells, and combine these analyses with molecular studies of genes regulating anther dehiscence.

From a breeding perspective, if future studies demonstrate stable inheritance of this phenotype together with normal female fertility, limited pollen release, and satisfactory seed set following controlled pollination, the anther-indehiscence phenotype may represent a useful breeding resource by reducing the need for manual emasculation and facilitating hybrid seed production [8]. At present, however, its practical application remains speculative because these functional characteristics have not yet been experimentally verified.

Overall, this study identifies a previously undescribed anther-indehiscence phenotype in F1 hybrids of *C. yuhsienensis* × *C. oleifera*. The phenotype is characterized by restricted anther opening, increased pollen retention, and a reduction in pseudopollen-like structures, which together are consistent with putative functional male sterility. Further studies incorporating pollen viability tests, in vitro germination assays, fertilization assessment, female fertility evaluation, seed-set analysis, heritability analysis, together with anatomical, physiological, genetic, and controlled pollination experiments, will be required to determine the underlying mechanism and evaluate its breeding potential.

5. Conclusions

This study identified a previously undescribed anther-indehiscence phenotype in F1 hybrids of *C. yuhsienensis* × *C. oleifera*. The phenotype was characterized by restricted anther dehiscence, increased pollen retention, and a reduction in pseudopollen-like structures compared with normal anthers. These observations distinguish this phenotype from the previously reported petaloid and abortive male-sterility types in *Camellia* and suggest that it is consistent with putative functional male sterility. However, because pollen viability, fertilization capacity, female fertility, heritability, and seed set were not evaluated, the mechanism and reproductive significance of this phenotype remain to be confirmed. Future studies integrating anatomical, physiological, genetic, and controlled pollination analyses will be essential to clarify its biological basis and assess its potential application in *Camellia* breeding.

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