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三种淫羊藿属植物的减数分裂研究

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摘　要：采用去壁低渗法对3种淫羊藿属(*Epimedium*)植物川鄂淫羊藿(*E. fargesii* Franch)、黔岭淫羊藿(*E. leptorrhizum* Stearn)和柔毛淫羊藿(*E. pubescens* Maxim)的花粉母细胞进行了减数分裂观察。结果显示，3种植物的染色体数目均为$2n = 12$，减数分裂过程中染色体的构型和行为特征也非常相似，减数分裂过程基本正常。但也发现一些染色体的异常行为，如二价体的提前分离、染色体桥、姐妹染色单体提前分离、染色体断片和二次分裂不同步等异常现象。这些减数分裂过程中的染色体变异可能在一定度上推动了淫羊藿属植物的系统发育和物种形成。

关键词：淫羊藿；减数分裂；染色体异常

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Analysis of meiotic behavior in three species of *Epimedium*（Berberidaceae）

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Abstract：Detailed meiotic studies were performed on pollen mother cells of three *Epimedium* species（Berberidaceae），i. e.，*E. fargesii* Franch，*E. leptorrhizum* Stearn，and *E. pubescens* Maxim，using wall degradation and hypotonic treatment. Results showed that the chromosome number for each of the three species was $2n = 12$. Chromosome configurations and behaviors were very similar and most meiotic processes were normal. However，several abnormal meiotic behaviors were detected，including early separation of bivalents，chromosome bridges，early disjunction of sister chromatids，chromosome fragments，and asynchronous division. These chromosomal aberrations during meiosis may have induced the phylogenic evolution and speciation of *Epimedium* plants to a certain extent.

Key words：*Epimedium*；Meiosis；Chromosomal abnormality

Epimedium fargesii Franch，*E. leptorrhizum* Stearn，and *E. pubescens* Maxim are perennial herbs belonging to the genus *Epimedium*（Berberidaceae）. This genus currently contains 62 species，which are disjunctly and unevenly distributed across the Mediterranean region and

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western and eastern Asia[1, 2]. China is the distribution and diversity center of *Epimedium*, containing 52 species of the genus[2]. The dried leaves of *Epimedium* plants consist of various flavonoid components and are therefore well-known as a traditional Chinese medicine (Herba Epimedii)[3]. *Epimedium* plants are also horticulturally valuable and have gained wide attention due to their attractive foliage and flowers[4].

Cytological data can be used to study the evolution and diversity of plants[5, 6]. Previous studies have investigated the number of chromosomes and karyotypes of many *Epimedium* species[7-10]. To date, all examined species have been identified as diploid ($2n = 12$), except for *E. yingjiangense* ($2n = 24$). Furthermore, the karyotypes of most species are the relatively primitive 2A type, although several have been identified as the 1A or 3A type, suggesting that *Epimedium* is a very conservative taxon regarding karyotype evolution.

Meiosis is a complex process involving a large number of genes, which can provide abundant information about the viability of plant species[11, 12]. During meiosis, chromosome behaviors, such as synapsis, exchange, and separation, are related to inheritance and variation in organisms and can be utilized to clarify genetics, reproductive biology, and ecology[13]. Abnormal meiosis usually produces inactive gametes and pollen with low viability, which can impact plant reproduction[14]. Furness[15] explored the microsporogenesis of *Epimedium* and identified successive type cytokinesis. Sheng *et al.*[16] examined meiosis in pollen mother cells (PMCs) in F_1 hybrids of three Chinese *Epimedium* species, and found high pollen fertility (>76.10%) and little abnormal chromosomal behavior. Jiang *et al.*[17] investigated the meiotic behavior and pollen fertility of five *Epimedium* species (*E. chlorandrum* Stearn, *E. acuminatum* Stearn, *E. davidii* Franch, *E. ecalcaratum* G. Y. Zhong, and *E. pubescens* Maxim) from Sichuan, China, and found that all demonstrated normal meiotic processes and high pollen fertility (>76.67%). In contrast, Lone *et al.*[18] studied meiosis in *E. elatum* C. Morren & Decne from India, and found prominent abnormalities, such as chromosome stickiness and chromatin bridges.

The genus *Epimedium* currently contains 62 species, which exhibit abundant inter- and intraspecies variations[1, 2]. So far, more than three-quarters of *Epimedium* species have not been reported on meiotic chromosome behaviors. *E. pubescens*, which is mainly distributed in Chongqing, Sichuan, and southern Shaanxi, shows abundant variation in morphology[19, 20]. Although Jiang *et al.*[17] reported on the meiosis of *E. pubescens* from Sichuan, research on meiosis in species from Shaanxi remains limited. In the present study, we investigated meiosis in PMCs of *E. pubescens*, *E. fargesii*, and *E. leptorrhizum* from Shaanxi. Our findings should enrich the cytological database and provide a reference for further studies on the phylogeny of this genus.

1 Materials and Methods

In the present study, plant materials of three medicinal *Epimedium* species, i. e., *E. fargesii*, *E. leptorrhizum*, *E. pubescens*, were collected for meiotic observations. Within *Epimedium*, the three species can be distinguished based on elongated rhizomes (*E. leptorrhizum*), relatively long stamens (*E. fargesii*)[1,2], and wide distribution and abundant morphological variations (*E. pubescens*)[19,20]. The collected plants were transplanted in the *Epimedium* germplasm nursery in Wuhan Botanical Garden, Chinese Academy of Sciences, for further meiotic study. Details on collection information are listed in Table 1.

For meiotic studies, the PMCs of immature floral buds were collected from late March to early

Table 1 Sample numbers, vouchers, localities, and chromosome number of three *Epimedium* species

Species	No. of plants observed	Voucher	Locality	Chromosome number (2*n*)
Epimedium fargesii Franch	3	*Zhang Y.J.**034*** (HIB)	Chengkou, Chongqing	12
Epimedium leptorrhizum Stearn	3	*Zhang Y.J.**030*** (HIB)	Shizhu, Chongqing	12
Epimedium pubescens Maxim	5	*Zhang Y.J.**098*** (HIB)	Taibai, Shaanxi	12

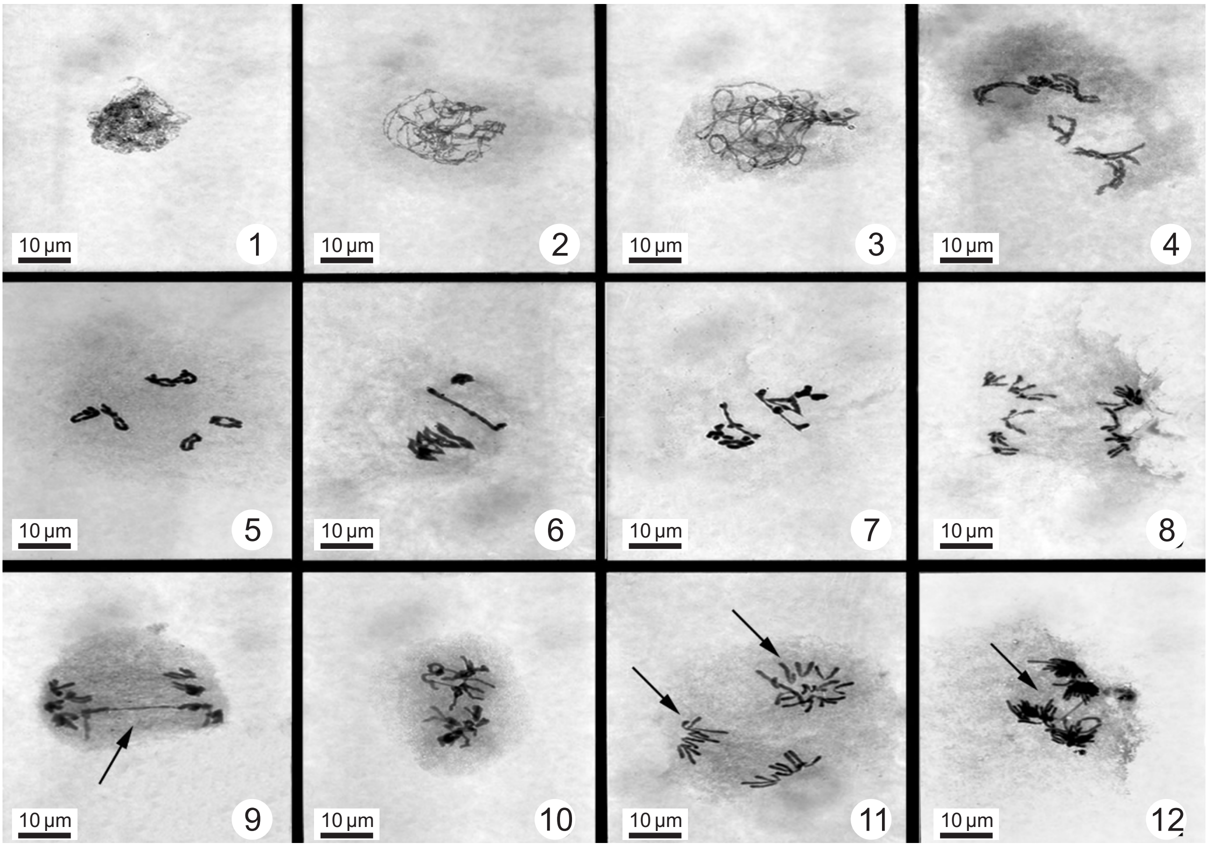
April 2019. After the sepals were removed, the anthers were then fixed in acetic acid: anhydrous alcohol (1 ∶ 3) for 30 min at room temperature. Chromosome preparations were performed using wall degradation and hypotonic treatment[21]. Chromosomes were observed and photographed using an Olympus BX51.

2 Results

The meiotic behaviors of PMCs of 11 individuals belonging to *E. fargesii*, *E. leptorrhizum*, and *E. pubescens* were observed. Results showed that chromosome behavior was similar and essentially normal. Detailed analysis of the chromosomal characteristics of each stage of meiosis was performed, as follows.

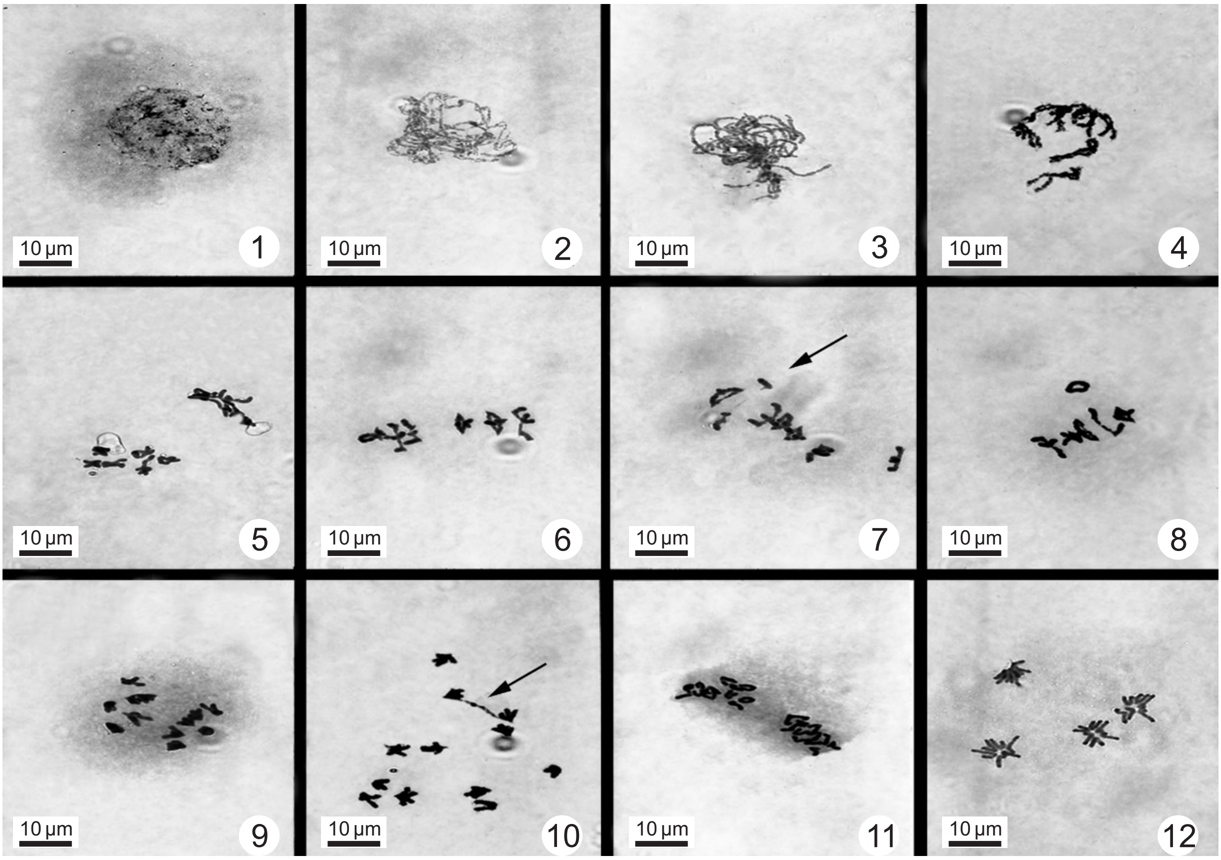
2.1 Prophase Ⅰ

During prophase Ⅰ chromatins condensed into chromonemata and gradually became thicker and shorter. At the leptotene stage, thin and thread-like chromonemata appeared in the nucleus; sometimes they gathered in the nucleus or scattered to one pole to form a bouquet structure. Due to chromosome condensation, many granular structures were visualized on the chromonemata and some homologous chromosomes started pairing at the late leptotene stage (Fig. 1: 1, Fig. 2: 1, Fig. 3: 1). At the zygotene stage, homologous



1 – 5: Prophase Ⅰ. PMC shows 12 bivalents at diakinesis; 6, 7: Metaphase Ⅰ; 8, 9: Anaphase Ⅰ. Arrow shows chromosome bridge; 10: Telophase Ⅰ; 11: Anaphase Ⅱ. PMC shows asynchronous division; 12: Arrow shows chromosome bridge.

Fig. 1 Chromosomes of *Epimedium fargesii* in meiosis



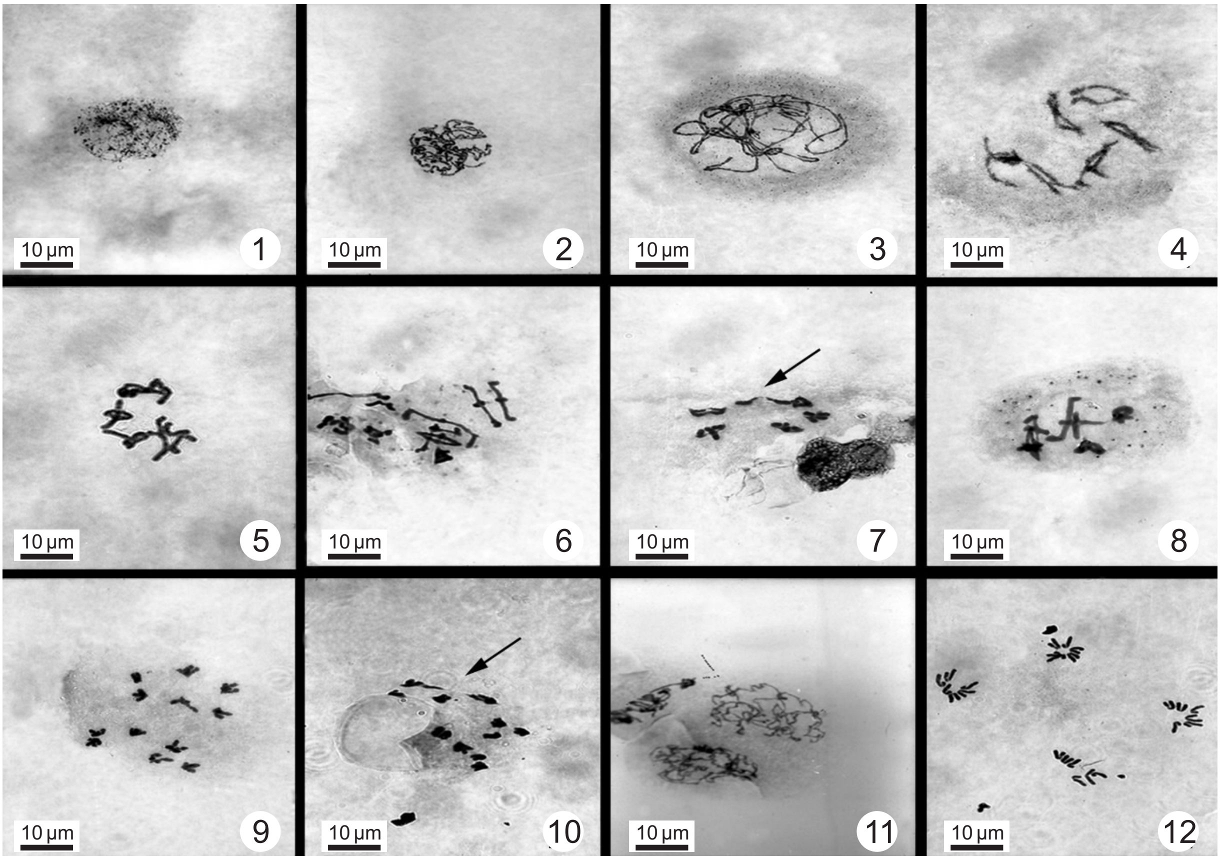
1 – 5：Prophase Ⅰ；6 – 8：Metaphase Ⅰ. Arrows show early segregation of bivalents；9，10：Anaphase Ⅰ. Arrow shows chromosome bridge；11：Metaphase Ⅱ；12：Anaphase Ⅱ.

Fig. 2　Chromosomes of *Epimedium pubescens* in meiosis

chromosomes began to pair. Homologous chromosomal pairing proceeded at several sites along the whole length simultaneously and the paired regions of homologous chromosomes were significantly thicker than the unpaired regions (Fig. 1：2, Fig. 2：2, Fig. 3：2). At the pachytene stage, the chromosomes were still in intimate contact with the nuclear envelope and the chromonemata were tangled with each other on the sides of the nucleus in a bouquet formation. The chromosomes became shorter and thicker but were still relatively long and tightly associated. Under an optical microscope, 12 closely linked bivalents could be observed and counted, but one or two bivalents contained regions without synapsis (Fig. 1：3, Fig. 2：3, Fig. 3：3). During the diplotene stage, six bivalents were detected, and chromosomes became shorter and thicker. Homologous chromosomes separated, although some were still connected at several sites. Because the number of chiasmata varied from one to many, the bivalents were presented in many different shapes, e. g., X, 8, and chain (Fig. 1：4, Fig. 2：4, Fig. 3：4). During the diakinesis stage, chromosomes continued to shorten and condense, and the chiasmata moved to the end of the chromosome arms, which led to the various bivalent shapes (Fig. 1：5, Fig. 2：5, Fig. 3：5).

2. 2　Metaphase Ⅰ

At metaphase Ⅰ (Fig. 1：6 – 7, Fig. 2：6 – 8, Fig. 3：6 – 8), the bivalents clustered at the equatorial plate of the cell. Because the number and location of chiasmata were different, chromosome configuration could be divided into circular or rod shapes. Early separation of bivalents was observed in *E. leptorrhizum* and *E. pubescens* (3.13% and 4.90%, respectively) (Table 2).



1 – 5: Prophase Ⅰ; 6 – 8: Metaphase Ⅰ. Arrows show early segregation of bivalents; 9, 10: Anaphase Ⅰ. Arrow shows chromosome bridge; 11: Telophase Ⅰ; 12: Anaphase Ⅱ.

Fig. 3 Chromosomes of *Epimedium leptorrhizum* in meiosis

Table 2 Percentage of abnormalities observed in different meiotic stages

Meiotic stage	Abnormality	*Epimedium fargesii*	*Epimedium leptorrhizum*	*Epimedium pubescens*
Metaphase Ⅰ	Early segregation of bivalents	0/60 0.00	3/96 [a] (3.13%)	5/102 (4.90%)
Anaphase Ⅰ	Chromosome bridges	6/106 (5.66%)	4/83 (4.82%)	4/67 (5.97%)
	Early disjunction of sister chromatids	0/66 0.00	2/52 (3. 85%)	0/60 0.00
	Chromosome fragments	0/70 0.00	2/64 (3.13%)	0/65 0.00
Anaphase Ⅱ	Chromosome bridges	2/39 (5.13%)	0/45 0.00	0/49 0.00
	Asynchronous division	1/39 (2.56%)	0/40 0.00	0/37 0.00

Note: a, number of abnormal PMCs/total number of PMCs analyzed.

2.3 Anaphase Ⅰ and Telophase Ⅰ

During anaphase Ⅰ, the homologous pairings separated and were pulled to the two poles (Fig. 1: 8 – 9, Fig. 2: 9 – 10, Fig. 3: 9 – 10), with the chromosome number at each pole identified as $n = 6$. Chromosome bridges were observed in all three species (5.66%, 4.82%, and 5.97%, respectively) (Table 2), and early disjunction of sister chromatids and chromosome fragments were observed in *E. leptorrhizum* (3.85% and 3.13%, respectively) (Table 2). During telophase Ⅰ, chromosome de-condensation and chromatin agglutination were observed at both poles of cells (Fig. 1: 10, Fig. 3: 11).

2.4 Anaphase Ⅱ

During anaphase Ⅱ, when the centromere of each chromosome split, the chromatids moved to the two poles. Chromosome bridges, as well as asynchronous division, were observed in *E. fargesii*. While the chromatids at one pole had completed second meiotic division, this process had not yet begun at the other pole (Fig. 1: 11). The percentage of chromosome bridges and asynchronous division was 5.13% and 2.56%, respectively (Table 2).

3 Discussion

Here, we investigated the meiotic processes in PMCs from *E. fargesii*, *E. leptorrhizum*, and *E. pubescens*. Although Jiang *et al.*[17] previously reported on meiosis in PMCs of *E. pubescens* from Sichuan, we explored the meiotic differences in PMCs of *E. pubescens* between the two regions based on their obvious morphological variations. Based on the meiotic results, the chromosome number of all three species was $2n = 12$, consistent with previous cytological studies[9, 10]. Furthermore, the whole meiotic process in the PMCs of the three species was essentially normal and the chromosome configurations and behaviors were similar, consistent with previous meiotic studies on *Epimedium*[16, 17]. From the early leptotene to pachytene stages, the chromonemata tangled with each other at one pole of the nucleus to form a bouquet structure. Because the number and location of chiasmata differed, the bivalents presented various shapes (e.g., X, 8, and chain) at the diplotene and diakinesis stages. At metaphase Ⅰ, the chromosome configurations usually showed circular- or rod-shaped bivalents.

At present, the chromosome number and karyotype of more than 50 *Epimedium* species have been reported[7-10]. Except for *E. yingjiangense*, which is a tetraploid species ($2n = 24$), all examined *Epimedium* species are diploid ($2n = 12$). Furthermore, the karyotype symmetry of most species is the relatively primitive 2A type, except for a few with 1A or 3A. These high identities of the chromosome number and karyotype symmetry in *Epimedium* probably led to the similarities of the chromosome configurations and behaviors of *Epimedium* during meiosis.

Although the whole meiotic process in the PMCs of *E. fargesii*, *E. leptorrhizum*, and *E. pubescens* was basically normal, several anomalous behaviors were also observed. At metaphase Ⅰ, early separation of bivalents was observed in *E. leptorrhizum* and *E. pubescens*. The nonsynchronous segregation of bivalents has been observed in many meiotic studies. These abnormalities may have resulted from the expeditious rate of chiasma terminalization and least genetic homology, which may have resulted in the unequal distribution of genetic material and variations in chromosome number[22,23].

Chromosome bridges were observed at anaphase Ⅰ/Ⅱ in *E. fargesii*, *E. leptorrhizum*, and *E. pubescens*, as detected in other *Epimedium* taxa[16-18]. Chromosome bridges are a common phenomenon of meiosis in plants, such as *Withania somnifera*, *Solanum tuberosum*, and *Saccharum officinarum*[24-26]. Chromosome bridges may be attributed to chromosome stickiness, with synapsed bivalents during metaphase leading to the formation of bridges at anaphase[27, 28].

Early disjunction of sister chromatids and chromosome fragments were observed during anaphase Ⅰ in *E. leptorrhizum*. Early disjunction of sister chromatids has been reported in other plants, such as *Brassica oleracea* var. *capitata* and *Petunia hybrida* Vilm, and is considered to be closely related to the early formation of univalents at prophase Ⅰ, leading to the unequal segregation of chromosomes and aneuploid male gametes[29, 30]. Chromosome fragments have also been reported in other species, and are likely caused by paracentric inversion or chromosome breakage at anaphase Ⅰ, resulting in partial gamete sterility or various aneuploid gametes[31]. Based on meiotic analysis, the chromosome fragments in *E. leptorrhizum* may have been caused by chromosome breakage during anaphase Ⅰ.

Asynchronous division was also observed at anaphase Ⅱ in *E. fargesii*, with the chromatids at one pole having completed second meiotic division, but not yet started this process at the other pole. Asynchronous division has also been reported in *Vicia*, *Miscanthus*, and *Medicago*, which was attributed to mutations affecting the spindle checkpoint, leading to the formation of triads and tetrads with uneven-sized microspores[24, 32-34].

Epimedium pubescens Maxim is widely distributed in China, but predominantly in Chongqing, Sichuan, and southern Shaanxi with considerable variation[2]. In the Sichuan populations, the leaflet abaxial surface contains long straight hairs and the inner sepals are narrowly lanceolate; in contrast, in the Shaanxi populations, the leaflet abaxial surface contains long appressed hairs and the inner sepals are lanceolate[1, 2, 20]. While chromosome bridges occurred in both populations at anaphase I, lagging chromosomes were reported in the Sichuan population, whereas early segregation of bivalents was found in the Shaanxi population. The differences in abnormal meiotic behavior in *E. pubescens* from the two regions may be related to their different genetic backgrounds and long-term adaptation to different environments[19, 20].

In conclusion, we examined the meiotic processes in PMCs of *E. fargesii*, *E. leptorrhizum*, and *E. pubescens*. Although meiosis was essentially normal, several meiotic anomalies were detected in the three species, with total meiotic abnormalities of 13.35%, 14.93%, and 10.87%, respectively. These abnormalities included early segregation of bivalents, early disjunction of sister chromatids, chromosome fragments, and asynchronous division. *Epimedium* species are cross-compatible and self-incompatible. Thus, the speciation of some Chinese *Epimedium* species may have originated from hybridization, which gives rise to the disordered and complex relationships among species[1, 35]. Therefore, the observed meiotic abnormalities may be related to the breeding system of this genus. These chromosomal abnormalities may have induced the evolution of *Epimedium*, which warrants further study.

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