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Meiotic behavior during microsporogenesis, responsible for male sterility in some species of *Salvia* sect. *Aethiopis* in Iran

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Abstract. The genus *Salvia* L. (Lamiaceae: tribe Mentheae) contains about 1000 species. Section *Aethiopis* in this genus has a distribution in the Mediterranean and central Asia and contains about 34 species in Iran. This study aimed to investigate the chromosome number and meiotic behavior in five species of *Salvia* sect. *Aethiopis*. To this end, pollen mother cells were used, and the squash method was employed. The results showed that *S. persepolitana* and *S. spinosa* had a chromosome number of 2n=2x=20, while *S. sclarea*, *S. hypoleuca*, and *S. limbata* had a chromosome number of 2n=2x=22. The study of meiotic behavior revealed the presence of abnormalities such as chromosome stickiness, cytomixis, non-synchronous segregation, chromosome bridges, laggard chromosomes, formation of micronuclei in tetrad cells, formation of tripolar cells, and pentapolar with different frequencies in the studied species. The meiotic index was reported as the highest in *S. persepolitana* and the lowest in *S. hypoleuca*. Pollen fertility was also affected by meiotic abnormalities, showing a decreasing trend from *S. persepolitana* to *S. spinose*. Meiotic abnormalities may have played a role in the evolution of aneuploidy and polyploidy in the *Salvia* genus.

Keywords: meiotic behavior, meiotic index, pollen mother cells, pollen fertility, *Salvia* sect. *Aethiopis*.

INTRODUCTION

The genus *Salvia* L. from the Lamiaceae, with about 900-1000 species, is spread throughout the old and new world, in subtropical and temperate regions. Western Asia and Mediterranean areas are considered the main distribution center of this genus (Sheidai et al. 2010; Celep et al. 2020). This genus is considered a suitable model for biological diversity and adaptive radiation studies (Standley and Williams, 1973; Wu and Li 1982). Salvia genus has about 55 species in Iran and they are distributed in tropical to arctic areas (Hedge 1982a).

Bahattacharya (1978) suggests that the *Salvia* species are recent and advanced members of a complex group, due to their highly irregular cytological behavior, advanced karyotype, and cytological numerical instability. Due to the small size of chromosomes in *Salvia*, chromosomal studies in this

genus are limited. Most of the studies carried out in *Salvia*, investigated the mitotic chromosomes and karyotype, and there is little information about the behavior of the chromosomes of this genus during meiosis and its chromosomal abnormalities. The behavior of meiotic chromosomes in different plant genera has been studied by scientists. Chromosome stickiness aberration is one of the common abnormalities in pollen mother cells. The visual appearance of stickiness varies from mild when only a few chromosomes are involved, to severe when it involves all the genome, especially during the formation of pachytene nuclei, and may even lead to chromatin destruction (Pagliarini 1990). Lagging chromosomes may be the result of delayed completion of karyokinesis (Pagliarini 1990). If lagging chromosomes do not reach the poles in time, they may cause the formation of micronuclei, micro-pollen, and pollen grains with unequal chromosome numbers. Such gametes may lead to aneuploidy (Utsunomiya et al. 2002; Defani-Scoarize et al. 1995). Chromosomes that form micronuclei during meiosis are separated by reaching the microspore wall and forming a bud called microspores. The separated microspores form small and non-viable pollen grains (Baptists-Giacomoelli et al. 2000). Meiotic aberrations lead to abnormal microsporogenesis like dyads, triads, tetrads with or without micronuclei (Tantray et al. 2021). Abnormalities such as triad and pentad may be due to cytomixis (Soodan and Wafai 1987). There are various other abnormalities in different stages of meiosis, which have been discussed further in *Salvia* species. In the chromosomal study of 19 species of the *Salvia* genus, Epling et al. (1962) examined the meiosis of natural hybrids only between *Salvia apiana* and *S. mellifera*. Systematic and evolutionary aspects of the genus in the light of the cytogenetic data were carried out in 13 species of *Salvia* from Argentina by Alberto et al. (2003). Sheidai et al. (2010), studied the behavior of the chromosomes in the meiosis of ten species of *Salvia*. Ranjbar et al. (2015), studied chromosome numbers and meiotic behavior in 12 species of *Salvia* from Iran. Alijanpoor and Safaeishakib (2023), studied cytomixis and other meiosis abnormalities in three species of *Salvia* (*S. nemorosa*, *S. staminea*, *S. verticellata*). The studies reported the number of chromosomes of different species of this genus as 12, 14, 16, 18, 20, 22, 24, 26, 28, 30, 32, 36, 38, 42, 44, 46, 52, 54, 56, 60, 64 (Epling et al. 1962; Vij and Kashyap 1976; Haque 1981; Sheidai et al., 2010; Eroglu et al. 2021; Martin et al. 2022). The chromosome base numbers observed in *S.* sect. *Aethiopis* include x = 8, 9, 10, and 11. The majority of species displayed a chromosome count of 2n = 22, with a lower percentage exhibiting 2n = 20. The base numbers x = 8 (in *S. moorcroftiana*) and x = 9 (in *S. verbascifolia*) were less frequent. Polyploidy has been reported in *S. ceratophylla* and *S. desoleana*, with a chromosome count of 2n = 4x = 44. (Afzal-Rafii 1980; Diana Corrias 1983; Ranjbar et al. 2015).

In the present study, the variable chromosome numbers in 5 species of *S.* sect. *Aethiopis* from different regions of Qazvin province, Iran were recorded. The processes of male meiosis and various abnormalities in microsporogenesis were investigated in detail for all studied species. Furthermore, the relationships of the irregular meiotic divisions with the meiotic Index, and male sterility are discussed.

MATERIAL AND METHODS

Plant material

During 2021 to 2022, plant materials were collected in various localities around Qazvin province, with fresh flower buds being the primary focus. Table 1 provides details of the locations where the 5 *Salvia* species (including *S. persepolitana* Boiss., *S. spinosa* L., *S.*

Table 1. Taxa studied of *Salvia* sect. *Aethiopis* species in Iran, Qazvin province.

Species	section	Locality	Collector	2n	x
S. persepolitana	*Aethiopis*	Iran, Qazvin: Abegarm to Avaj, 35°36'N, 49°12'E	Hajmoradi	20	10
S. spinosa	*Aethiopis*	Iran, Qazvin province, Tarom-e-Sofla 36°34'N, 49°31'E	Hajmoradi	20	10
S. sclarea	*Aethiopis*	Iran, Qazvin province, near Moallem Kalayeh 36°26'N, 50°28'E	Hajmoradi	22	11
S. hypoleuca	*Aethiopis*	Iran, Qazvin province, Chizeh village 36°34'N, 49°01'E	Hajmoradi	22	11
S. limbata	*Aethiopis*	Iran, Qazvin province, Alamut-e-Sharghi 36°24'N, 50°14'E	Hajmoradi	22	11

sclarea L., *S. hypoleuca* Benth. and *S. limbata*) used in this study were collected. Herbarium specimens were identified using the Oriental Flora (Boissier 1879), Flora Iranica (Hedge 1982a), and Turkish Flora (Hedge 1982b).

Cytological study

To conduct the cytogenetic study, a total of 15 flower buds were collected from a minimum of five plants at an appropriate stage of development. These buds were then fixed in a solution consisting of 96% ethanol, chloroform, and propionic acid (in a ratio of 6:3:2) for 24 hours at room temperature. After fixation, the buds were stored in 70% alcohol at 4°C until they were ready to be used. For studying pollen mother cells (PMCs), the anthers from the buds were squashed and stained with a 2% acetocarmine solution. To make the slides permanent, Venetian turpentine was applied. Chromosome photographs were taken using an Olympus BX-41 photomicroscope at an initial magnification of 1000. Chromosome counts were determined by examining well-spread metaphases in intact cells through direct observation and also by analyzing the photomicrographs.

Meiotic Index (MI)

The meiotic index (MI) was calculated by dividing the number of normal tetrads by the total number of observed tetrads and multiplying by 100 (Tedesco et al. 2002).

Pollen fertility

To estimate pollen fertility, the ability of pollen to stain was assessed. Pollen grains were obtained from the flowers of studied herbarium specimens and then stained with a mixture of acetocarmin and glycerin (1:1). After being stored at room temperature for 24-48 hours, 1000 pollen grains per flower were sampled to determine stainability. Documentation and examination of the slides were performed using an Olympus BX-51 photomicroscope. Pollen grains were considered fertile if they were well-stained and infertile if they were empty or unstained. The percentage of pollen fertility was calculated by dividing the total number of fertile pollen grains by the total number of pollen grains and multiplying the result by 100.

RESULT

Meiotic abnormalities

In studied species of *Salvia* sect. *Aethiopis*, chromosome numbers and meiotic behavior were determined and their cytological features are summarized in Table 2. Figure 1 provides illustrations of the chromosomes and their abnormalities. The species studied were diploid and had 2n = 20 and 22 chromosome numbers. PMCs at diakinesis without any abnormality showed the normal chromosome pairing as 10 bivalents in *S. persepolitana* and *S. spinosa* (2n = 20) and 11 bivalents in *S. sclarea, S. hypoleuca, and S. limbata* (2n = 22).

A total of 589 cells in diakinesis and metaphase I, 1029 cells in anaphase I and telophase I, 451 cells in metaphase II, and 1619 cells in anaphase II and telophase II were analyzed in the studied species of *Salvia*. The meiotic irregularities observed in the studied populations included: chromosome stickiness, cytomixis, non-synchronous segregation, chromosome bridges, laggard chromosomes, formation of micronuclei in tetrad cells, formation of tripolar cells, and pentapolar which have been discussed below (Figure 1).

Chromosome stickiness is one of the chromosomal abnormalities that is seen more frequently than other abnormalities in all studied species during diakinesis/metaphase I and metaphase II. *S. hypoleuca* showed the highest percentage of this abnormality at 21.3±0.12, while *S. sclarea* showed the lowest at 10.7±0.07 during diakinesis/metaphase I. In metaphase II, the highest percentage of stickiness was observed in *S. spinosa* and the lowest in *S. limbata* (4.8±0.03 and 1.3±0.02, respectively). The physical appearance of stickiness varies from mild, when only a few chromosomes are involved, to severe, when it may involve the entire genome, and may even lead to the destruction of chromatin. The transfer of chromosomes or chromatin content from one cell to one or more other cells is called cytomixis, which occurs through cytoplasmic bridges. This abnormality was observed in three out of the five studied species, with *S. sclarea* showing the highest frequency and *S. hypoleuca* showing the lowest. In *S. sclarea*, the transfer of chromosomes through this phenomenon was observed partially or completely, involving the entire genome. Cytomixis abnormalities had a higher frequency in meiosis I than in meiosis II (Figure 1C). The phenomenon of cytomixis was not reported in any stage of meiosis in *S. persepolitana* and *S. limbata.*

Chromatin bridges with various thicknesses are another anomaly observed in most of the studied species during anaphase I and II stages (Figure 1D), while *S. sclarea* did not show this abnormality in any of the

Table 2. The number of pollen mother cells (PMCs) analyzed and the percentage of PMCs meiotic behavior in *Salvia* sect. *Aethiopis*.

Meiotic characters/taxa	*S. persepolitana*	*S. spinosa*	*S. sclarea*	*S. hypoleuca*	*S. limbata*
Total cell number	704	751	746	758	729
D/MI	110	123	103	136	117
% D/MI	15.6	17.2	13.8	17.9	16
% Sticky chromosome	14.2±0.03	18.4±0.14	10.7±0.07	21.3±0.12	15.8±0.03
% Cytomixis	-	3.4±0.04	4.7±0.12	-	-
AI/TI	184	209	214	195	227
% AI/TI	26.1	29.2	28.6	25.7	31.1
% non-synchronous segregation	-	-	1.2±0.02	2.3±0.07	-
% Bridge	1.3±0.03	0.8±0.01	-	2.3±0.05	1.6±0.01
% Laggard	0.8±0.02	-	-	0.7±0.01	1.2±0.04
% Cytomixis	-	-	1.7±0.04	0.9±0.01	-
MII	95	87	108	79	82
% MII	13.4	11.5	14.4	10.4	11.2
% Sticky chromosome	4.3±0.08	4.8±0.03	2.1±0.02	1.5±0.07	1.3±0.02
% Cytomixis	-	-	1.2±0.08	-	-
AII/TII	315	332	321	348	303
% AII/TII	44.7	44.2	43	45.9	41.5
% Laggard	-	-	1.3±0.05	0.8±0.01	-
% Bridge	-	1.2±0.02	-	1.7±0.03	-
% Cytomixis	-	2.4±0.08	1.3±0.06	-	-
%non-synchronous segregation	0.6±0.01	-	-	-	
% micronucleus	1.3±0.08	-	0.8±0.01	1.5±0.06	0.5±0.01
% Tripolar	-	1.2±0.1	-	0.9±0.02	2.7±0.09
% Pentapolar	2.8±0.08	2.3±0.01	1.5±0.12	-	4.3±0.23

Abbreviations: D/MI = diakinesis/metaphase I; AI/TI = anaphase I/telophase I; MII = metaphase II; AII/TII = anaphase II/telophase II. All values are expressed as mean ± SE (standard error).

mother pollen cells. Chromosomes without orientation in the equatorial plane of the cell, also known as lagging or laggard chromosomes, are another abnormality that was observed in the anaphase I/telophase I stage in three species including *S. persepolitana*, *S. hypoleuca*, and *S. limbata* (Figure 1E). In the anaphase II/telophase II stages, only *S. sclarea* (Figure 1F) and *S. hypoleuca* showed this abnormality. Non-synchronous segregation of chromosomes is one of the meiotic abnormalities that may occur early or late. This abnormality was observed in all species. *S. sclarea* and *S. hypoleuca* exhibited this anomaly in meiosis I (with frequencies of 1.2±0.02 and 2.3±0.07, respectively), while *S. persepolitana* showed it only in meiosis II with a frequency of 0.6±0.01. Micronucleus is another meiotic abnormality that was observed in the tetrad stage in all studied species except *S. spinosa*. *S. hypoleuca* showed the highest frequency at 1.5±0.06 (Figure 1G), while *S. limbata* showed the lowest at 0.5±0.01. In the final stages of meiosis, tetrads with three (Figure 1H) and five poles (Figure 1I) are another abnormality that was observed in different frequencies in the studied species. No tripolar tetrads were observed in *S. persepolitana* and *S. sclarea*, and no pentapolar tetrads were observed in *S. hypoleuca*.

Meiotic index

The meiotic index, which is obtained by dividing the number of normal tetrads by the total number of observed tetrads and multiplying by 100, was reported to have the highest value in *S. persepolitana* and the lowest value *S. hypoleuca* among the studied species (Figure 2). The order of the meiotic index in the studied species was

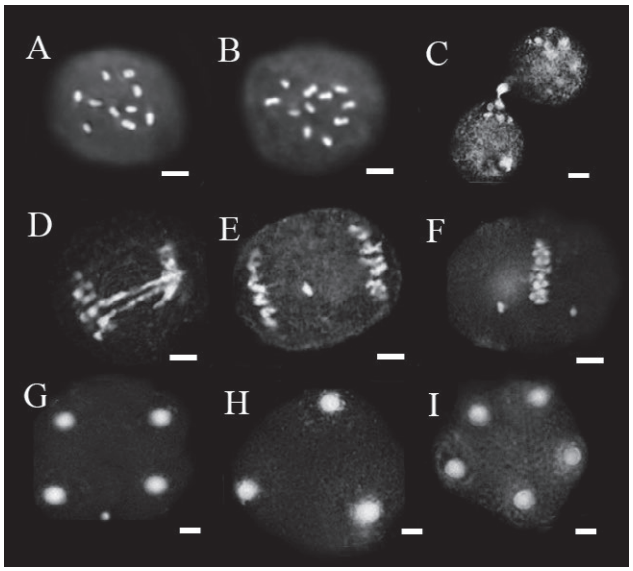

Figure 1. Representative meiotic cells in studied species of *S.* sect. *Aethiopis* (A-I). A: Diakinesis in *S. Spinosa* (showing 10 bivalents). B: Diakinesis in *S. sclarea* (showing 11 bivalents). C: Cytomixis in *S. hypoleuca*. D: Bridge in *S. limbata*. E: Laggards in *S. persepolitana*. F: Precocious separation in *S. sclarea*. G: Micronucleus in *S. hypoleuca*. H: Tripolar in *S. limbata*. I: Pentapolar in *S. spinose*. Scale bar: 3 µm.

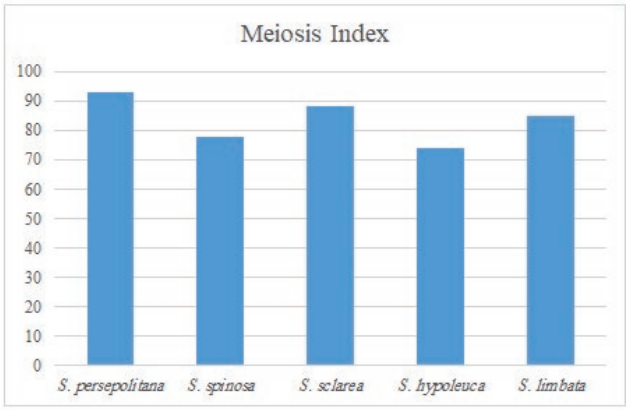

Figure 2. Comparison of Meiosis Index in studied species of *S.* sect. *Aethiopis.*

as follows: *S. persepolitana* > *S. sclarea* > *S. limbata* > *S. spinosa* > *S. hypoleuca*

Pollen fertility

Regarding pollen fertility, in the study of pollen grains in the *Salvia* genus, it was found that the fertility of pollen grains in all of them is above 80%. *S. persepolitana* showed the highest fertility (95%) and *S. spinosa*

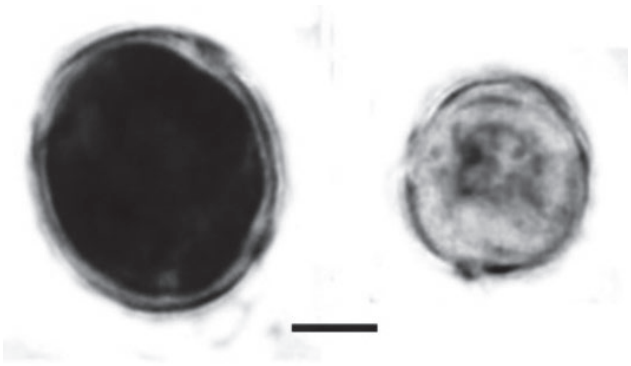

Figure 3. The fertile pollen is on the left side and the sterile pollen is on the right side. Scale bar: 5 µm.

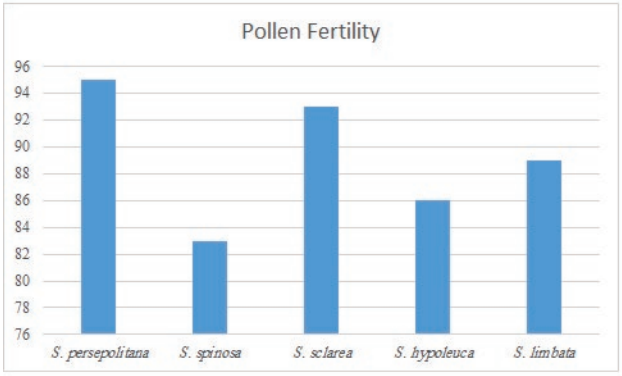

Figure 4. Comparison of pollen fertility in studied species of *S.* sect. *Aethiopis.*

showed the lowest fertility (83%) (Figures 3 and 4). The order of pollen fertility in different species is as follows: *S. persepolitana* > *S. sclarea* > *S. limbata* > *S. hypoleuca* > *S. spinosa*.

DISCUSSION

This study was conducted to investigate meiotic behavior, pollen fertility, and chromosomal abnormalities in five species of the genus *Salvia*. By studying the mother cells of pollen at the diakinesis stage, 10 and 11 bivalents were observed in the species under investigation. *S. persepolitana* and *S. spinosa* showed 2n = 20, which confirmed previous studies (Aryavand 1977; Kliphuis and Barkoudah 1977; Patudin et al. 1975; Afzal-Rafii 1981; Al-Turki et al. 2000; Sheidai et al. 2010; Ranjbar et al. 2015). *S. sclarea, S. hypoleuca, and S. limbata*, with 2n=22, also confirmed previous studies (Aryavand 1977; Afzal-Rafii 1980; 1981; Diaz et al. 1984; Rosúa and

Blanca 1988; Sheidai et al. 2010; Martin et al. 2011; Ranjbar et al. 2015). *Salvia* species have been reported to have varying chromosome numbers falling within different aneuploid series, inclung x = 6, 7, 8, 9, 10, 11, 13, 16 (Sheidai et al. 2010; Ranjbar 2015; Martin et al. 2022). Bahattacharya (1978) suggests that base numbers 7 and 8 are the primitive numbers from which secondary base numbers were established. These numbers then diversified in various directions, with base number 11 being common in many species. Martin et al. (2015) identified the chromosomal base number of 11 as a probable ancestral base number in the genus *Salvia*.

In examining the meiotic behavior and comparing the studied species, various types of chromosomal stickiness, cytomixis, lagging, and so on, with different frequencies, were observed. Among the studied species, *S. spinosa* showed the highest and *S. persepolitana* showed the lowest meiotic abnormalities in their PMCs.

Chromosomal stickiness

Chromosomal stickiness, which was observed in all the studied species with varying frequencies, was first observed in maize as chromatin clusters at the stage of pachytene (Beadle 1932). Sheidai et al. (2010) also reported the occurrence of this abnormality, either partially or completely, in all the studied species of the genus *Salvia* from the early stages of prophase to the final stages of meiosis. Ranjbar et al. (2015) reported chromosomal stickiness and chromosome bridges resulting from stickiness in some species of *Salvia*, including *S. hypoleuca* and *S. perseppolitana*. In this study, *S. hypoleuca* showed the highest percentage of chromosomal stickiness. Species with different evolutionary trajectories may have distinct mechanisms for chromosome segregation, potentially leading to variations in stickiness (Santos et al., 2017). Also, this abnormality is influenced by environmental and genetic factors (Pagliarini 2000).

Cytomixis

Chromosome displacement between PMCs, called cytomixis, was observed in different directions and at different stages of meiosis I and II in all the studied species, except for *S. perseppolitana*. The occurrence of cytomixis can be a cause of abnormal pollen grain formation. Ranjbar et al. (2015) reported this abnormality in *S. aethiopis* and *S. indica*. Kaur and Singhal (2019) reported this abnormality in *S. nubicola*. Alijanpoor and Safaeishakib (2022) mentioned the occurrence of cytomixis in *S. nemorosa*, *S. verticellata*, and *S. staminea*. The occurrence of cytomiixis can vary depending on the developmental stage of the plant. Factors such as cell differentiation, hormonal regulation, and tissue-specific gene expression may influence the propensity for cytomiixis in different plant species (Bhattacharya et al. 2016). Moreover, different species may encounter varying environmental factors, which can contribute to the diversity of cytomiixis abnormalities (Dutta and Chaudhuri, 2019).

Lagging chromosomes

Among the studied species, the highest frequency of lagging chromosome abnormality was observed in *S. hypoleuca*. Similar abnormalities have also been reported in other species of the genus *Salvia* (Sheidai et al. 2010; Ranjbar et al. 2015). In the study by Ranjbar et al. (2015), *S. hypoleuca* showed the highest frequency of lagging chromosomes. This abnormality was also reported in *S. nubicola* in another study (Kaur and Singhal 2019). The diversity of lagging chromosome abnormalities in studied species can be influenced by various factors. Differences in chromosomal organization among plant species and environmental factors may contribute to the diversity of lagging chromosome abnormalities (Kleckner 2006; Babu et al. 2016).

Bridges

Bridges, another abnormality, were observed in all the studied species except for *S. sclarea*, with different numbers and thicknesses. The overall incidence of this abnormality in meiosis I was almost twice that of meiosis II. In another study, while bridge abnormality was reported in *S. hypoleuca* in meiosis I, it was not observed in *S. perseppolitana* (Ranjbar et al. 2015). Kaur and Singhal (2019) also reported this abnormality in *S. nubicola*, and Alijanpoor and Safaeishakib (2022) reported it in several species of the genus *Salvia* such as *S. staminea*. Genetic and environmental factors are considered influential factors in these abnormalities and cause different frequencies in plant species. (Nirmala and Rao 1996).

Non-synchronous segregation

In the studied PMCs, both precocious and late separation were observed. This abnormality was not observed in *S. spinose* and S. *limbata* species. *S. hypoleuca* also showed this abnormality in the study by Ranjbar et al. (2015), while it was not observed in *S. persep-*

politana. Another study reported this abnormality in *S. nubicola* (Kaur and Singhal 2019). precocious separation of bivalents does not affect the normal separation of chromosomes, while late separation of chromosomes can lead to the formation of lagging chromosomes, chromatin bridges, and a decrease in pollen fertility (Kumar et al. 2010). Differences in chromosomal organization among plant species may contribute to the diversity of non-synchronous segregation abnormalities (Kleckner, 2006). Moreover, different plant species may encounter varying environmental factors, which can contribute to the diversity of non-synchronous segregation abnormalities (Babu et al., 2016).

Micronuclei

Micronuclei were a common abnormality in the studied species except for *S. spinose*. This abnormality was reported with a frequency of 50% in *S. limbata* in another study (Alijanpoor and Safaeishakib 2022). Laggards can contribute to the formation of micronuclei and may also result in aneuploid gametes, thereby playing a role in chromosomal evolution. Plant species with higher levels of genomic instability may exhibit a greater diversity of micronucleus abnormalities. Factors such as repetitive DNA content, transposable elements, and chromosomal rearrangements can contribute to genomic instability (Nagaki et al., 2012). Also, various environmental factors, such as radiation, chemical pollutants, and exposure to heavy metals, can induce micronucleus formation in plant cells (Jha et al. 2020).

Triad and pentad

In the studied species, the highest frequency of trisomy and pentasomy was reported in *S. limbata* and *S. persepolitana*, respectively. Such cells may lead to the formation of tetrad and abnormal and non-viable pollen grains. Bahattacharya (1978) reported triploid cells in two varieties of *S. splendens*. Sheidai et al. (2010) reported tripolar and multipolar cell formation due to anaphase I and II failure in *Salvia* species. Variations in genes involved in meiotic processes, such as synaptonemal complex formation, chromosome pairing, and cytokinesis, may lead to alterations in the formation of tetrads, resulting in triad or pentad abnormalities (Prieto et al. 2018). Different plant species may encounter varying environmental factors such as temperature, light intensity, nutrient availability, or exposure to stressors which can contribute to the diversity of triad and pentad abnormalities (Babu et al. 2016).

Overall, the frequency of meiosis abnormalities in studied species of *Salvia* sect. *Aethiopis* can vary due to factors such as genetic variation, environmental conditions, and evolutionary history. Genetic differences and chromosomal arrangements affect meiotic processes. The evolutionary history of a genus can also impact meiotic stability, with some species evolving mechanisms to reduce errors (Pawlowski and Cande 2005; Madlung 2013). Pagliarini (2000) suggested that anomalies affecting fertility can arise from mutations in genes controlling meiosis, with some abnormalities leading to complete male sterility in certain species. Variation in the activity of key meiotic genes (Caryl et al. 2003), recombination, chromosome synapsis, cell cycle control, chromosome distribution, and polyploidy (Mercier et al. 2015) can account for the varying levels of meiosis abnormalities observed among different species within a plant genus. The discrepancies in meiotic progression and recombination patterns between species can likely be attributed to variations in genome size and organization resulting from differences in repetitive DNA content and ploidy level (Lambing and Heckmann 2018). Natural variations in polymorphisms at the recombination site and specific DNA sequence motifs contribute to the variability in meiotic recombination frequency within and between species (Lawrence et al. 2017).

It's important to note that the specific research on meiosis abnormalities in plants may be limited. Further studies are needed to investigate the underlying mechanisms and factors contributing to the diversity of triad and pentad abnormalities in different plant species.

There is an inverse relationship between the meiotic index and chromosomal abnormalities during meiosis. Species that show the highest chromosomal abnormalities in their meiotic behavior have the lowest meiotic index and vice versa. In this study, *S. persepolitana* showed the highest meiotic index, and the total observed chromosomal abnormalities in this species were lower than in other studied species. *S. hypoleuca* had the lowest meiotic index with the highest frequency of meiotic abnormalities. According to Alberto et al. (2003), the degree of pollen grain stainability in the studied species of *Salvia* ranged from 75.7 to 97.6%. Sheidai et al. (2010), pointed out high pollen fertility (>0.90%) in their studied *Salvia* species.

CONCLUSIONS

Detailed cytological studies in species of *Salvia* sect. *Aethiopis* including *S. persepolitana*, *S. spinosa*, *S. sclarea*, *S. hypoleuca* and *S. limbata* showed diploid pro-

phase with two basic chromosomes (10 and 11). However, the examined species exhibited various chromosomal abnormalities, such as chromosomal stickiness, failures in normal separation during anaphase, cytomixis, and other anomalies, resulting in a decrease in pollen fertility. It is important to note that meiotic abnormalities do not always have detrimental effects and can contribute to the generation of genetic diversity. However, further research is necessary to gain a comprehensive understanding of these intricate interactions. Considering the numerous reports of varied chromosome numbers and ploidy levels in different species of the *Salvia* genus, such meiotic abnormalities may be a cause of the evolution of aneuploidy and polyploidy in this genus.

LIST OF ABBREVIATIONS

PMC: Pollen Mother Cell
MI: Meiotic Index

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