Study of the meiosis in some species of *Fumaria* (*Papaveraceae*) from Iran

Farzaneh Habibi Tirtash[1], Maryam Keshavarzi[1] & Masoud Sheidai[2]

[1] Biology Dept., Alzahra University, Vanak, Tehran, Iran, e-mail: neshat112000@yahoo.com (corresponding author)

[2] Faculty of Biological Sciences, Shahid Beheshti University, Evin, Tehran, Iran

Received: May 01, 2012 ▷ Accepted: October 25, 2012

Abstract. A meiotic study was carried out of four species of the genus *Fumaria* in Iran. New gametophyte counts for *F. parviflora*, *F. vaillantii*, *F. schleicheri* (n = 16), and *F. asepala* (n = 8) are reported. Partial desynapsis was observed in three species of *Fumaria*. A population of *F. parviflora* from Gonbad-e Qābus showed occurrence of B-chromosomes (0-1). The observed meiotic abnormalities included lagging chromosomes, stickiness, desynapsis, and cytomixis. Partial or complete diffuse stage was observed in some *Fumaria* species. Unreduced meiocytes and pollen grains were found out in all species due to cytomixis; anaphase failure and desynapsis proved also effective in speciation of *Fumaria*.

Key words: B chromosome, desynapsis, *Fumaria,* Iran, meiosis, stickiness, unreduced pollen

Introduction

Fumaria L. (*Papaveraceae*) is represented by eight species in Iran (Lidén 2000; Wendelbo 1974). In genus *Fumaria*, 46 out of 50 species are polyploid. Large-flowered species show a higher ploidy level, although the native species of Iran are small-flowered. Most species have manifested polyploidy and only four out of fifty are diploid (Lidén 1986). Diploids are not widely distributed in Iran (*F. asepala* Boiss.), in contrast to some of the polyploids which are distributed in various habitats of the country. As *F. parviflora* Lam. and *F. vaillantii* Lois. are recorded to be tetraploid (2n = 32), it seems that the high range of anatomical variation in these taxa may follow from their ploidy level. A hexaploid species like *F. indica* (Hausskn.) Pugsley (2n = 6x = 48) is restricted to small areas and holds a separate position in the anatomical studies (Keshavarzi & al. 2011a).

A palynological investigation by Keshavarzi & al. (2011b) has revealed unusual dimorphic pollen grains for some individuals of *F. parviflora* and *F. schleicheri* Soy.-Will. This could be due to sterility of the pollen grains. There are also pollen grains with six and 12 annuli in both *F. vaillantii* and *F. schleicheri* species. In the latter, 12 annuli are common, but in *F. vaillantii* hexa-annulate pollen grains are usually formed. It seems that there could be different ploidy levels and cytotypes of these species in Iran. Their observation has indicated considerable variation in the exine sculpture in the *Fumaria* species. The seven studied *Fumaria* species were effectively distinguished on the basis of shape, size, aperture number, and exine sculpture patterns.

Since Ruberg's (1960) publication on the chromosome numbers of *Fumarioideae*, the data have been further supplemented. Stern (1961) summarized the chromosome numbers known in *Dicentra* and data from some scattered reports on other taxa were added, the most important being those by Takeuchi (1971).

The *Fumarieae* tribe is a species group with chromosome counts of almost 90 % of its taxa (Lidén 1986).

Their author had studied the chromosome counts of most species of the genus *Fumaria*, most of them without any earlier counts. According to him (Lidén 1986), x = 8 was dominant in *Fumarioideae*, except for in *Cysticapnos vesicaria* (L.) Fedde with 2n = 28 and x = 7. There were some other records of the chromosome base number in this tribe, such as x = 6 for *Corydalis* DC and x = 7 for *Fumaria* (Negodi 1951), but they were not generally supported. The chromosomes in *Fumarioideae* are smaller than 1 µm and with a regular karyotype. Satellite chromosomes had been occasionally observed (Lidén, 1986).

About 44 % of the *Fumarieae* taxa are polyploids. Although polyploidy is more frequent in perennial than in annual species, this does not seem to be the case of this subfamily (Lidén 1986). Hill (1992) studied seven species of *Fumariaceae* from Virginia. Besides their chromosome numbers, he supplied an identification key and description of the taxa. Sidhu & al. (2011) investigated the chromosome number, pairing behaviour, ploidy level, and meiotic abnormalities in the *F. officinalis* species from Chandigarh and nearby areas. No record of the gametophyte chromosome number of the studied *Fumaria* species has been ever made. In Iran, there are few records of the chromosome number in *Papaveraceae* (Ghaffari, 2008). Ghaffari has found n = 7 in *Papaver fugax* Poir and *Roemeria refracta* DC.

This seems to result from cleistogamy, small flower buds and chromosome size. In this project, a cytogenetic study of four *Fumaria* species – *F. vaillantii, F. parviflora, F. schleicheri,* and *F. asepala* – has been conducted.

Material and methods

Four species of *Fumaria* were studied cytogenetically under this project: 1. *F. asepala,* 2n = 2x = 16; 2. *F. parviflora*, 2n = 4x = 32; 3. *F. vaillantii*, 2n = 4x = 32; 4. *F. schleicheri*, 2n = 4x = 32. All above-mentioned taxa are tetraploid, except *F. asepala* which is diploid (Table 1).

Young flower buds were collected from plants belonging to four wild species of the genus *Fumaria*, growing in different habitats of Iran (Fig. 1). The samples were fixed in a solution of glacial acetic acid: ethanol (1:3) for 24 hrs. Then they were washed out and preserved in 70 % ethanol at 4 °C until the squashing process (Sheidai & al. 1996). Cytological preparations were made by a squashing technique and 2 % aceto-orcein as stain. A thousand Pollen Mother Cells (PMCs) were analyzed for chromosome segregation during anaphase and telophase of the meiosis. Pollen fertility was checked by staining of minimum 1000 pollen grains from each taxon with a solution of 2 % acetocarmine: 50 % glycerin (1:1) for 1 hr. The well-stained and perfect pollen grains were regarded here as fertile, while the unstained or empty ones were considered as infertile.

Table 1. Gametophyte chromosome count and locality of the studied species under this project.

Species	Gametophyte chromosome count	Locality	Environmental conditions
F. vaillantii	n=16	Tehran, Dehvanak	at the foot of a hill
F. vaillantii	n=16	Tehran, Jamshidieh	alpine area
F. vaillantii var. *schrammii*	n=16	Tehran, Polemodiriat	near a draining channel
F. parviflora	n=16	Tehran, Darabad	alpine area
F. parviflora	n=16	Tehran, Jamshidieh	alpine area
F. parviflora	n=16	Tehran, Lavizan	at the foot of a hill
F. parviflora	n=16	Golestan, Gonbad-e Qābus	in a plain
F. schleicheri	n=16	Tehran, Jamshidieh	alpine area
F. asepala	n=8	Tehran, Chitgar	at the foot of a hill

Fig. 1. Locations of collection of some *Fumaria* species in this study. ⬟ for *F. schleicheri*, ✻ for *F. asepala*, ■ for *F. parviflora*, ● for *F. vaillantii*.

Results

In this study, during metaphase of the meiosis in PMCs, mainly univalents were formed. No bivalents were observed. Meiotic features comprise meiotic behaviour during anaphase, chromosomal abnormalities at different meiosis steps, pollen fertility, unreduced pollen formation, and pollen size (Fig. 2a & b). Data on the meiotic course, cytomixis, pollen fertility and pollen size in each population are shown in Table 2 and 3.

Presence of B chromosome in *F. parviflora* from Gonbad-e Qābus accession and a diffuse stage in some populations of the studied species have been recorded for the first time in the world (Fig. 2a). Occurrence of a diffuse stage has been reported in several plant species (Sybenga 1992). That stage is complete when all chromosomes decondense, or partial when only some parts of the genome are in this condition. The present study has shown occurrence of partial and of complete diffuse stage in some populations of *F. parviflora, F. vaillantii* and *F. schleicheri.*

B chromosomes were circular and not paired with A chromosomes. Due to the low frequency of B chromosomes and high frequency of univalents (bivalents were not observed), it was impossible to evaluate statistically the effect of B chromosomes on chiasma frequency.

Results of the analysis of meiotic behaviour in three *F. vaillantii* populations (Table 2 and 3) have shown that both varieties (*F. vaillantii* var. *schrammii* and F. *vaillantii* var. *vaillantii*) are tetraploid and this is in concordance with Lidén's (1986) findings. This is the first record of meiotic behaviour for this species. In the present study, the chromosome behaviour in different meiotic stages and chromosome stickiness were studied for three accessions of this species. Pollen fertility was found to be almost 90 % for all of them. Four accessions of *F. parviflora* (Tables 2 & 3) were studied similarly. All studied populations were tetraploid, with 2n = 4x = 32, and the results coincided with those of Kliphuis & Barkoudah (1977), Soler (1981), Querios (1980), and Lidén (1986). Although these authors had studied the sporophytic content of *F. parviflora*, meiotic studies were not performed. Pollen fertility was found to be almost 90 % in this species.

One population was studied for each of the species *F. asepala* and *F. schleicheri* (Tables 2 and 3). *F. asepala* has shown 2n = 2x = 16 and this is its first record, while Lidén (1986) recorded the sporophytic content of this species.

Table 2. Meiotic abnormalities in the studied *Fumaria* species (in %).

Species	Locality	Polynucleus gamete	Cytomixis (prophase I)	Stickiness (metaphase I)	Lagging chromosomes (anaphase I)	Stickiness (anaphase I)	Desynapsis
F. vaillantii	Tehran, Dehvanak	+	8	6	–	4	–
F. vaillantii	Tehran, Jamshidieh	+	10	4	8	6	44
F. vaillantii var. *schrammii*	Tehran, Polemodiriat	–	4	4	–	20	–
F. parviflora	Tehran, Darabad	–	–	–	4	–	–
F. parviflora	Tehran, Jamshidieh	+	–	22	4	15	15
F. parviflora	Tehran, Lavizan	–	–	6	–	–	10
F. parviflora	Golestan, Gonbad-e Qābus	+	–	4	6	10	20
F. schleicheri	Tehran, Jamshidieh	+	4	22	10	4	10
F. asepala	Tehran, Chitgar	–	2	4	–	2	–

Table 3. Multipolar cells and pollen abnormalities in the studied *Fumaria* species (in %).

Species	Location	Pollen 2n	Tripolar	Pentapolar	Polipolar	Pollen fertility
F. vaillantii	Tehran Dehvanak	16.5	2	–	–	95
F. vaillantii	Tehran, Jamshidieh	45	26	8	6	84
F. vaillantii var. *schrammii*	Tehran Polemodiriat	11	8	6	–	94
F. parviflora	Tehran, Darabad	15	–	–	–	88
F. parviflora	Tehran, Jamshidieh	30	–	–	–	92
F. parviflora	Tehran, Lavizan	17	–	–	–	95
F. parviflora	Glestan, Gonbad-e Qābus	11	–	–	–	80
F. schleicheri	Tehran, Jamshidieh	27	6	10	–	90
F. asepala	Tehran, Chitgar	10	–	–	–	95

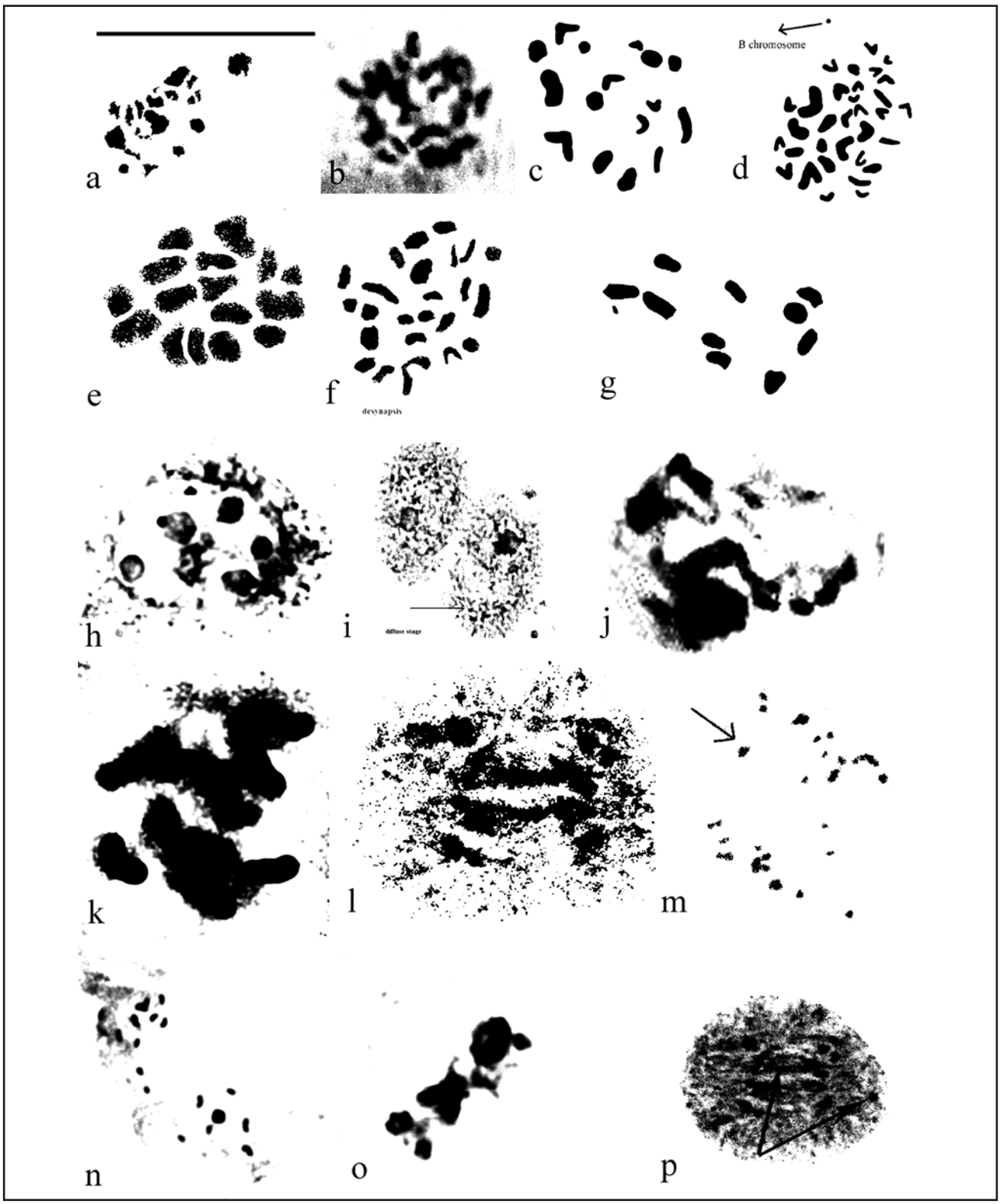

Fig. 2a. Representative meiotic cells in the studied *Fumaria* species: **a** and **b** – meiocytes showing normal n = 16 and a desynaptic cell showing univalents in *F. schleicheri,* respectively; **c** and **d** – meiocytes showing normal n = 16 and a desynaptic cell in metaphase I showing univalents and B-chromosomes (arrow) in *F. parviflora*; **e** and **f** – meiocytes showing normal n = 16 and a desynaptic cell showing univalents in *F. vaillantii*; **g** – meiocytes showing normal n = 8 in *F. asepala*; **h** – polynuclear gamete in *F. schleicheri*; **i** – diffuse stage in *F. vaillantii*; **jm** – chromosome stickiness occurring in most populations from early prophase to late telophase II, leading to the formation of lagging chromosomes (arrow); **n** – chromosome migration between adjacent meiocytes in *F. asepala*; **o** and **p** – chromosome stickiness in metaphase I, chromosome stickiness and trail chromosome in anaphase I (arrow) in *F. parviflora*. Scale bar = 20μm.

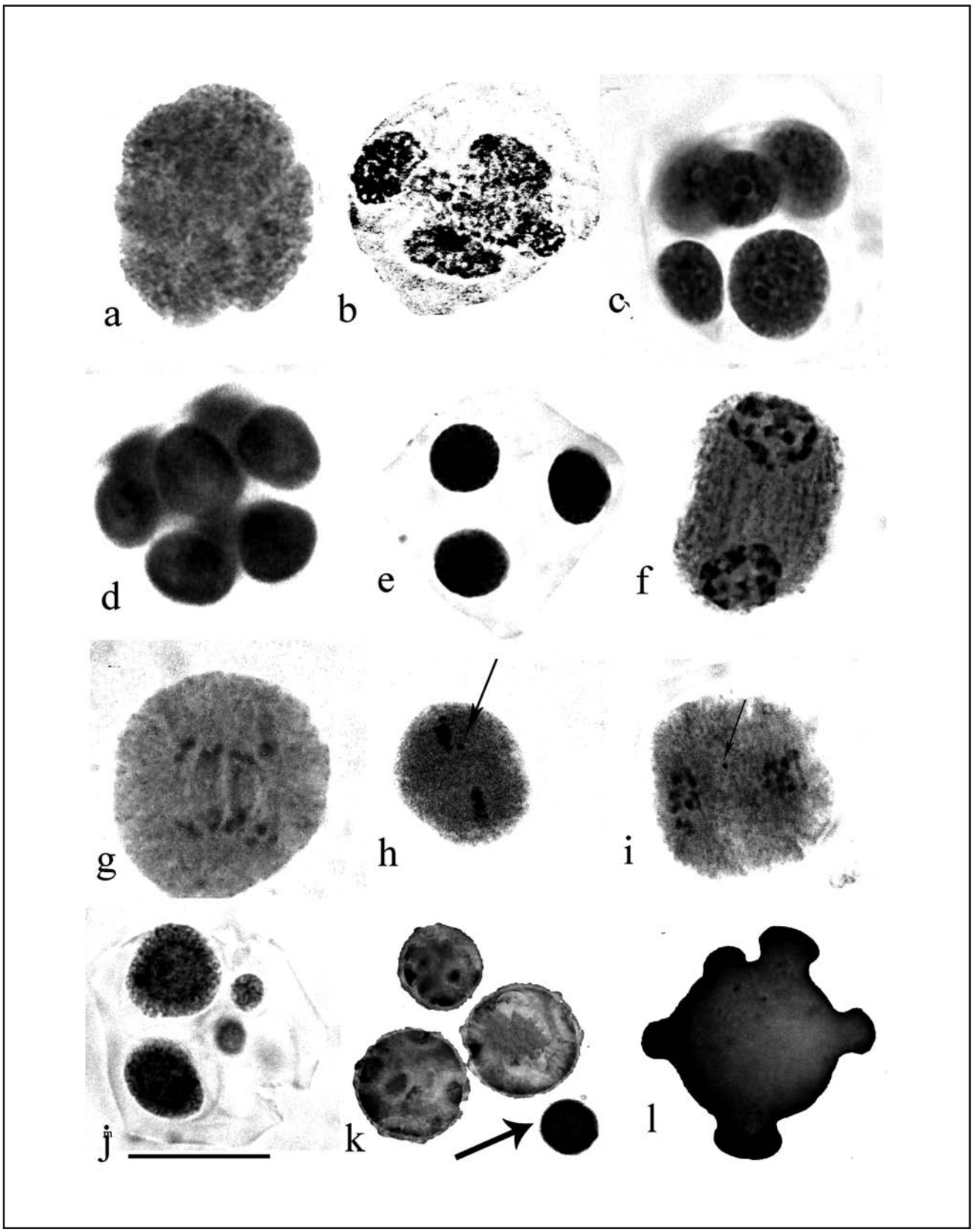

Fig. 2b. Representative meiotic cells in the studied *Fumaria* species: **a**, **b** and **c** – pentapolar cells in *F. vaillantii* and *F. vaillantii* var. *schrammii*; **d** and **e** – multipolar and tripolar cells in *F. schleicheri* and *F. vaillantii*; **f** and **g** – normal cells in telophase I and anaphase I; **h** and **i** – forward chromosome in anaphase II and lagging chromosome forming dyad in *F. parviflora*; **j** and **k** – abnormal and normal tertad, unreduced and unfertilized (arrow) pollen grains (bigger pollen) in *F. vaiilantii*; **l** – deformate pollen in *F. vaillantii*.

Anaphase and metaphase stickiness may be responsible for the diploid pollen formation.

Our results on *F. schleicheri,* with 4x = 2n = 32, confirmed the sporophytic content of this species recorded by Gvinianidze & Avazneli (1982) and Lidén (1986).

Cytomixis: chromatin or chromosome migration to various ordinations in all studied species was observed in different percentage (except in *F. parviflora*). Occasionally, one or more chromosome migrated to the neighboring meiocyte, resulting in aneuploid formation or cells and pollen with extra chromosomes. Syncyte formation and total chromosome migration can also be found in meiocytes by doubling the normal chromosome number. Such unreduced meiocytes cause the formation of unreduced pollen grains (2n). This phenomenon was observed in the studied *Fumaria* species, for example, in the Jamshidiyeh population of *F. vaillantii*. The occurrence of large pollen grains (possibly 2n) was observed, besides the smaller (normal) ones in all populations of *Fumaria.* These abnormal pollen grains may result from cytomixis and desynapsis. The presence of large pollen grains (possibly 2n) between normal pollen grains was observed in all studied populations (Fig. 2b and Table 3). The average diameter of reduced pollen grains is 19–20 µm and in unreduced pollen grains it is from 30 µm to 40 µm.

In all studied populations pollen fertility exceeded 80 percent. There is a relationship between pollen fertility and meiotic abnormalities as metaphase I and anaphase I: stickiness, lagging chromosomes, cytomixis, and desynapsis. Thus these abnormalities could be responsible for decrease of fertility in the studied species of genus *Fumaria*.

Desynapsis, which is an efficient factor in 2n gametes formation, is recorded for the first time in the world in populations of *F. vaillantii, F. parviflora* and *F. schleicheri*. In the Jamshidiyeh population of *F. vaillantii,* frequency of desynapsis was 44 % (Table 2). The same abnormality but with different percentage has been observed in *F. parviflora* populations too (Table 2 and 3).

Discussion

In *Fumarieae,* the chromosomes are small (less than 1 µm) and the karyotype is rather regular. Satellites can be seen in some species. In *Corydaleae* (especially in the tuberous species), the chromosomes are about 2 µm (Lidén 1986). This corresponds to the findings of Rees & Hazarika (1969), who claim that inbreeding annuals usually have smaller chromosomes than outbreeding perennials. The tribes differ in degree of ploidy. In *Corydaleae,* 28 % of the species are polyploid, whereas in *Fumarieae* there are 94 % of polyploids (Lidén 1986). The common statement that perennials have a higher degree of ploidy than annuals seems to contradict the findings in *Fumarioideae,* as most *Fumarieae* are annual and most *Corydaleae* perennial. However, this rule applies only when allogamous plants are compared.

In the genus *Fumaria,* a beautiful polyploidy series was found, with numbers ranging from 2x to 14x, except 12x. This is the maximum ploidy series in annual species (Lidén 1986). Higher levels of ploidy have been observed in the large-flowered species. Aneuploidy was rare and was only recorded twice. The other genera of this tribe were totally tetraploid (except *Pseudofumaria lutea* (L.) Borckh., 2n = 64) (Lidén 1986).

Fumaria officinalis has n = 7 chromosomes at metaphase. Meiosis is regular in this species (Sidhu & al. 2011). The findings of these authors coincide with those of Maude (1939) who mentioned x = 7 for this species, while presenting the chromosome numbers in British flowering plants. Grant (1982) recorded the chromosome numbers for various angiosperms and found that x = 7 was the basic chromosome number for genus *Fumaria.*

Singhal & Kumar (2008) reported the occurrence of cytomixis in wild populations of Himalayan poppy (*Meconopsis aculeate* Royle.). Cytological studies of seven wild populations from the high hills of Himachal Pradesh have revealed that all Himalayan populations exist uniformly at the tetraploid level (2n = 56) on x = 14. The phenomenon of chromatin transfer among the proximate pollen mother cells (PMCs) in six populations was causing various meiotic abnormalities. Chromatin transfer also resulted in the formation of coenocytes, aneuploids, polyploidy, and anucleated PMCs. Among individuals that showed chromatin transfer, chromosome stickiness and interbivalent connections were frequently observed in some PMCs. The phenomenon of cytomixis in the species seems to be directly under genetic control; it affects considerably the meiotic course and results in reduced pollen viability (Singhal & Kumar 2008).

Diploid species are not aggressive weedy species, in contrary to tetraploid ones. The tetraploid species of

Fumaria, such as *F. vaillantii* and *F. parviflora* are widely distributed in Iran, but *F. asepala* being a diploid has a very limited distribution in the country. By studying the gametophytic chromosome count in this study, the diploid position of *F. asepala* and the tetraploid position of the other three studied *Fumaria* species are emphasized (Kliphuis & Barkoudah 1977; Querios 1980; Soler 1981; Gvinianidze & Avazneli 1982; Lidén 1986).

The present study records the occurrence of cytomixis, desynapsis, B chromosome, and diffuse stage for the first time in wild populations of *F. parviflora, F. vaillantii, F. schleicheri*, and *F. asepala* in Iran.

Various reasons have been suggested for the occurrence of diffuse stage. For instance, high synthetic activity analogous to the lampbrush stage in amphibian oocyte; shedding of the lateral elements in the synaptonemal complex; post pachytene elimination or modification of histone proteins and meiotic arrest to withstand the adverse environmental conditions (Sheidai & Inamdar 1991). As *F. parviflora, F. vaillantii* and *F. schleicheri* populations grow wild under different environmental conditions, possibly adaptation to such adverse environmental conditions may be the reason for the occurrence of diffuse stage in the species.

B chromosomes (0-1) were observed in individuals of *F. parviflora.* A large number of B chromosomes results in decrease in plant growth and longevity. B chromosomes can significantly modify the chiasma frequency. The low frequency of B chromosome in the *F. parviflora* population of Gonbad-e Qābus may be an adaptive strategy against inappropriate environmental conditions. B chromosome in *F. parviflora* was recorded for the first time here.

Cytomixis is unimportant feature from evolutionary viewpoint, but it may result in the formation of aneuploid plants with special morphological characters and unreduced gametes. This phenomenon was observed earlier in different grasses (Falistocoo & al. 1995; Sheidai & al. 1999).

The occurrence of tripolar, pentapolar or multipolar cells was observed almost in all studied populations in Iran for the first time so far. Formation of tripolar cells leads to the formation of two reduced and one unreduced pollen grains, while pentapolar cells observed in some populations may lead to the formation of abnormal tetrads and infertile pollen grains. The spindle apparatus is normally bipolar and acts as a single unit, playing a crucial role in the chromosome alignment during metaphase. Any distortion or breakage in the division spindle may result in random subgrouping of the chromosomes, which function independently (Nirmala & Rao 1996). In several instances, spindle abnormalities have led to the production of aneuploid gametes, for example, in polyploidy hybrids and derivatives of *Aegilops* × *Triticum* hybrids, amphiploid *Triticineae*, amphiploids of *Solanum* hybrids, etc. They are also considered a reason for the production of unreduced (2n) gametes in *Solanum* (Villeux 1985).

Desynapsis is regarded as precocious separation of bivalents in metaphase of meiosis I, leading to the formation of univalents to a varyious degree. Partial desynapsis was observed for the first time in three species of *Fumaria*: *F. parviflora*, *F. schleicheri* and *F. vaillantii* (Table 2 and Fig. 2a). In partial desynapsis, some bivalents are separated to form univalents, while in complete desynapsis all bivalents are separated to form univalents. Such desynaptic cells with double chromosome number may form unreduced pollen grains. Desynapsis occurs either due to the action of recessive *ds* genes in a homozygous situation, or to early chiasma terminalisation, which may lead to formation of meiocytes by doubling of the normal chromosome number. In several cases, such univalents may have difficulty during anaphase-I movement and may lag behind, therefore producing aneuploid gametes that reduce pollen fertility of plants. However, they may skip the first anaphase and form a restitution nucleus resulting in the formation of unreduced gametes, as reported in *Solanum* (Villeux 1985).

The present gametophyte count n = 16 in *F. parviflora, F. vaillantii* and *F. schleicheri,* and the gametophyte count of n = 8 in *F. asepala* are the first such record from the study area and are in conformity with the earlier reports of sporophytic counts (Kliphuis & Barkoudah 1977; Queiros 1980; Soler 1981; Gvinianidze & Avazneli 1982; Lidén 1986). In the *Fumaria* species, the tetraploid level is unimportant for chromosome doubling in the speciation of this genus (Lidén 1986). Our results indicate that such factors as formation of desynapsis, stickiness in different phases of meiosis I, cytomixis, and diploid gametes formation are also effective in the speciation of genus *Fumaria*.

Large pollen grains are a sign of 2n gametes production (Bretagnolle & Thompson 1995). This kind of pollen grains was present in many populations (almost exceeding 10 %) of the studied species. In this project, unreduced pollen grains were observed for the first time in genus *Fumaria*. This kind of gametes

results in a higher ploidy level by sexual polyploidization. Multipolar, tripolar, pentapolar cells, irregularities in chromosomes separation through anaphase, and desynapsis are main factors in unreduced gametes production in the studied taxa.

Contrary to Lidén's opinion (Lidén 1986), there are high morphological variabilities in the *Fumaria* species in Iran (Keshavarzi & al. 2011b). Owing to the presence of desynapsis in the meiosis, this seems to be the reason of such variability.

There were some degrees of chromosome stickiness which seemed to be caused by environmental and genetic factors (Nirmala & Rao 1996). Desynapsis in *F. parviflora* and cytomixis and stickiness in *F. vaillantii* and *F. schleicheri* seem to be responsible for the unreduced gametes formation.

Conclusion

Our results have shown that such factors as formation of desynapsis, stickiness in different phases of meiosis I, cytomixis, and diploid gametes formation are also effective in the speciation of genus *Fumaria*. Partial or complete diffuse stage was observed in some *Fumaria* species. Unreduced meiocytes and pollen grains were observed in all species due to cytomixis, anaphase failure and desynapsis.

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