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MEIOTIC STUDIES IN SOME MEMBERS OF CARYOPHYLLACEAE JUSS. FROM THE WESTERN HIMALAYAS

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The paper reports meiotic studies on 50 populations comprising 12 species belonging to 5 genera of Caryophyllaceae from the Western Himalayas. The chromosome numbers in *Arenaria kashmirica* (n=20), *Silene conoidea* (n=20), *S. edgeworthii* (n=12 and n=24), *S. moorcroftiana* (n=24), *S. nepalensis* (n=12), *Stellaria media* (n=13), *S. monosperma* (n=13) and *S. semivestita* (n=13) are reported for the first time. The chromosome numbers in *Lychnis coronaria* (n=12) and *Silene vulgaris* (n=24) are given for the first time from India, along with *Gypsophilla ceratioides* (n=15) from the Western Himalayas. The course of meiosis varies from normal to abnormal in different populations of *Silene conoidea*, *S. edgeworthii, S. vulgaris, Stellaria media, S. monosperma* and *S. semivestita*. The course of meiosis was abnormal in all studied populations of *Lychnis coronaria*. Abnormal microsporogenesis (cytomixis, chromosomal stickiness, unoriented bivalents, formation of laggards and bridges) led to reduced pollen fertility and differences in pollen grain size.

Key words: Caryophyllaceae, chromosome numbers, meiosis, Western Himalayas.

INTRODUCTION

The family Caryophyllaceae Juss. comprises about 86 genera and 2,100 species worldwide (Trigas et al., 2007) including 25 genera and 112 species on the Indian subcontinent (Kumar and Subramaniam, 1986) which are distributed mainly in temperate and alpine regions (Sharma and Balakrishnan, 1993). The family is commonly known as the pink family. It is characterized by stems often swollen at the nodes, leaves almost always opposite and rarely whorled, flowers usually unisexual, receptacle often prolonged in an anthophore, stamens mostly obdiplostemonous, ovary unilocular with free central placentation, and fruit a capsule. Reports of chromosome counts began with seven species of this family from North America, Europe and Central Asia (Blackburn, 1928). At present there are chromosomal reports available for 66 genera all over the world including some important contributions by cytologists from outside India (Hartman, 1974; Aryavand and Favarger, 1980; Shildneck and Jones, 1986). From India chromosomal reports are available only for 18 genera covering 62 species (Fedorov, 1974; Kumar and Subramaniam, 1986). From the area of the Western Himalayas explored for cytological diversity at present, there are no chromosomal reports available for Caryopyllaceae. From different parts of the world have come cytogenetic observations on the presence of B chromosomes (Ghaffari and Bidmeshkipwor, 2002), chromosome number variability (Sheidai et al., 2008), the formation of unreduced pollen grains (Sheidai et al., 2009), abnormalities of the meiotic course (Sheidai et al., 2008, 2009; Fadaei et al., 2010), intraspecific chromosomal size variation and the phenomenon of reciprocal translocations (Sheidai et al., 2008) and intraspecific morphological variations (Sugawara and Horri, 1999; Sugawara et al., 2000) in different species of the family. Data are sparse for the Western Himalayas in general and for the covered areas in particular. Our present meiotic studies on these Caryophyllaceae taxa are intended to help fill the gaps, addressing genetic diversity at intra- and interspecific levels in less-studied angiosperm families.

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MATERIALS AND METHODS

For meiotic study, flower buds were collected from different localities of selected areas of the Western Himalayas (Tab. 1). Smears of flower buds were made after fixing with Carnoy's fixative using standard acetocarmine technique. Pollen fertility was estimated by mounting mature pollen grains in glycero-acetocarmine (1:1). Well-filled pollen grains with stained nuclei were deemed fertile, and shrivelled and unstained pollen grains were counted as sterile. Photomicrographs of pollen mother cells and pollen grains were made from freshly prepared slides using a Nikon 80i Eeclipse Digital Imaging System. Voucher specimens are deposited in the Herbarium of the Department of Botany, Punjabi University, Patiala, India (PUN).

RESULTS

Detailed population-level meiotic studies were made on 12 species belonging to 5 genera of the family Caryophyllaceae from different localities at 900–4000 m a.s.l. in Kangra and Sirmaur districts (Himachal Pradesh) and at 2000–3500 m a.s.l. in Kashmir. Table 1 gives data on altitude, accession number, present and previous chromosome numbers, ploidy level and the nature of the meiotic course for the populations.

CHROMOSOME NUMBERS

Arenaria kashmirica Edgew.

Both of the populations collected from Kashmir show n=20 (Fig. 1a). The present Indian chromosome count of n=20 based on x=10 is the first tetraploid report for the species. Earlier it was known to have 2n=26 (Khatoon and Ali, 1993).

A. serphyllifolia L.

Three populations from Kashmir and two populations from Himachal Pradesh show the same meiotic chromosome number, n=10 (Fig. 1b). The species is known to exhibit 2n=20 (Natrajan, 1988; Khatoon and Ali, 1993), 2n=30 (Kliphuis and Weiflering 1979), 2n=40 (Letz et al., 1999; Lovkvist and Hultgard, 1999) and 2n=44 (Blackburn and Morton, 1957); thus the present report of n=10 is in conformity with earlier diploid reports from inside and outside India.

Gypsophilla ceratioides D. Don.

Five populations, including two from Kashmir and three from Himachal Pradesh, exhibit n=15 (Fig. 1c). This is the first cytological work on the species from the Western Himalayas. The present report of n=15 is in conformity with previous reports of 2n=30 from Eastern Himalayas and from outside India (Chatterjee, 1975), and not in accord with reports of aneuploid numbers of 2n=34–36 from outside India (Favarger, 1962).

Lychnis coronaria Lamak.

All four populations of the species show the same chromosome number, n=12, at different stages of meiosis (Fig. 1d). The present chromosome count of n=12 from the Western Himalayas is the first report of a diploid cytotype from India, as from outside India it is already known to have 2n=24 (Hill, 1989; Petrova and Stoyanova, 1998).

Silene conoidea L.

Of the seven populations studied, two populations from Kashmir and three from Himachal Pradesh show n=10 (Fig. 1e); the populations from Triund and Dharamshala (H.P.) show n=20 (Fig. 1f). The species is already known to have diploid cytotypes 2n=20 (Khoshoo, 1960; Aryavand and Favarger, 1980) and 2n=24 (Blackburn, 1928), both from India and from outside India. Thus the tetraploid cytotype (n=20) based on x=10 given here is the first such report.

S. edgeworthii Bocquet.

Of the seven populations studied, only one population from Pehalgam (Kashmir) shows n=12 (Fig. 1g) and exists as a diploid cytotype. All the other populations show tetraploid cytotypes with n=24 (Fig. 1h). Both these counts make the first chromosomal reports for the species.

S. moorcroftiana Wall.

The single population from Kashmir showing n=24 (Fig. 1i) is found to be tetraploid, and is the first chromosome count reported for the species.

S. nepalensis Majumdar

Both of the populations collected from Kashmir show n=12 and occur as diploids (Fig. 1j). This is the first chromosome count reported for the species.

S. vulgaris (Moench) Garcke.

Of the five populations studied, three from Kashmir and one from Himachal Pradesh show n=12 (Fig. 1k), and the only population from Bhagyanimata (H.P.) shows n=24 (Fig. 1l). The tetraploid cytotype is

TABLE 1. Location, altitude, accession number (in parenthesis), present chromosome number, figure number and ploidy level in different taxa of Caryophylaceae from the Western Himalayas

Taxa	Locality, altitude (m), accession numbers	Present chromosome number (Fig. no.)	Ploidy level
Arenaria kashmirica Edgew. (=*Minuartia kashmirica* (Edgew.) Mattf.)	Thajwas, Ganderbal Dist. (Kashmir); 3,000 (54387)	20 (Fig. 1a)	4x
	Gulmarg, Baramulla Dist. (Kashmir); 2,600 (54388)	20	4x
A. serphyllifolia L.	Yusmarg, Budgam Dist. (Kashmir); 2,600 (54389)	10 (Fig. 1b)	2x
	Pehalgam, Anantnag Dist. (Kashmir); 2,200 (54390)	10	2x
	Chumnai, Anantnag Dist. (Kashmir); 3,500 (54391)	10	2x
	BaraBhangal, Kangra Dist. (H.P*.); 4,000 (54459)	10	2x
	Haripurdhar, Sirmaur Dist. (H.P); 2,600 (54460)	10	2x
Gypsophilla ceratioides D.Don.	Thajwas, Ganderbal Dist. (Kashmir); 3,000 (54385)	15 (Fig. 1c)	2x
	Gulmarg, Baramulla Dist. (Kashmir); 2,600 (54386)	15	2x
	Triund, Kangra Dist. (H.P.); 3,000 (54381)	15	2x
	Tisri, Sirmaur Dist. (H.P.); 3,000 (54383)	15	2x
	Haripurdhar, Sirmaur Dist. (H.P.); 2,600 (54384)	15	2x
Lychnis coronaria Lamak. (=*Agrostmma coronaria* L.)	Mahadev, Srinagar Dist. (Kashmir); 3,000 (54395)	12 (Fig. Id)	2x
	Gulmarg, Baramulla Dist. (Kashmir); 2,600 (54396)	12	2x
	BaraBangal, Kangra Dist. (H.P.); 4,000 (54401)	12	2x
	ChurDhar, Sirmaur Dist. (H.P.), 3,600 (54402)	12	2x
Silene conoidea L.	Tral, Pulwama Dist. (Kashmir); 2,000 (54457)	10 (Fig. 1e)	2x
	Aharbal, Kulgam Dist. (Kashmir); 2,500 (54458)	10	2x
	Bhanala, Kangra Dist. (H.P.); 900 (54450)	10	2x
	Triund, Kangra Dist. (H.P.); 3,000 (54451)	20 (Fig. 1f)	4x
	Dharmshala, Kangra Dist. (H.P.);1,600 (54452)	20	4x
	Haripurdhar, Sirmaur Dist. (H.P.); 2,800 (54453)	10	2x
	Gunduri, Sirmaur Dist. (H.P.); 2,600 (54454)	10	2x
S.edgeworthii Bocquet (= *Lychnis fimbriata indica* var. Edgew. & Hook. f.)	Pehalgam, Anantnag Dist. (Kashmir); 2,300 (54446)	12 (Fig. 1g)	2x
	Gulmarg, Baramulla Dist. (Kashmir); 2,800 (54447)	24 (Fig. 1h)	4x
	Chumnai, Anantnag Dist. (Kashmir); 3,500 (54448)	24	4x
	Dharmshala, Kangra Dist. (H.P.); 1,600 (54438)	24	4x
	Baghasunag, Kangra Dist. (H.P.);1,500 (54439)	24	4x
	HaripurDhar, Sirmaur Dist. (H.P.); 2,800 (54442)	24	4x
	Gunduri, Sirmaur Dist. (H.P.); 2,600 (54443)	24	4x
S. *moorcroftiana* Wall.	Aharbal, Kulgam Dist. (Kashmir); 2450 (52491)	24 (Fig. 1i)	4x
S. nepalensis Majumdar (=*Lychnis multicaulis* Wall. ex Benth.)	Tral, Pulwama Dist. (Kashmir); 2,000 (54455)	12 (Fig. 1j)	2x
	Aharbal, Kulgam Dist. (Kashmir); 2,300 (54456)	12	2x
S. vulgaris (Moench) Garcke. (= *Silene inflata* Sm.)	Sonmarg, Ganderbal Dist. Kashmir); 2,800 (54430)	12 (Fig. 1 k)	2x
	Gulmarg, Baramulla Dist. (Kashmir); 2,600 (54431)	12	2x
	Aharbal, Kulgam Dist. (Kashmir); 2400 (54432)	12	2x
	Bhagyanimata, Sirmaur Dist. (H.P.); 2,800 (54434)	24 (Fig. 1 l)	4x
	Dharmshala, Kangra Dist. (H.P.);1,600 (54426)	12	2x
Stellaria media L. (= *Alsine media* L	Aharbal, Kulgam Dist. (Kashmir);2,300 (54421)	13 (Fig. 1 m)	2x
	Gulmarg, Baramulla Dist. (Kashmir);2,700 (54422)	13	2x
	Triund, Kangra Dist. (H.P.); 3,000 (54417)	13	2x
	Rajgundha, Sirmaur Dist. (H.P); 3,000 (54418)	13	2x
	Tisri, Sirmaur Dist.(H.P); 3,000 (54419)	13	2x
S. monosperma Buch.-Ham. (= *Stellaria crispata* Wall. ex Edgew.)	Pehalgam, Anantnag Dist. (Kashmir); 2,300 (54408)	13 (Fig. 1 n)	2x
	Yusmarg, Budgam Dist. (Kashmir); 2,400 (54409)	13	2x
	Triund, Kangra Dist. (H.P.); 3,000 (54405)	13	2x
	Chota Bhangal, Kangra Dist. (H.P.); 2,800 (54407)	13	2x
	Haripurdhar, Sirmaur Dist. (H.P.); 2,600 (54412)	13	2x
	Bhangyanimata, Sirmaur Dist. (H.P.); 2,800 (54413)	13	2x
S. semivestita Edgew.	Sonmarg, Ganderbal Dist. (Kashmir); 2,800 (54424)	13 (Fig. 1 0)	2x
	Triund, Kangra Dist. (H.P.); 3, 000 (54423)	13	2x
	Tisri , Sirmaur Dist. (H.P.); 3,000 (54425)	13	2x

*H.P. – Himachal Pradesh

reported for the first time from India. The species is already known to have 2n=24 from India and from outside India; (Baltisberger, 1995; Gupta et al., 2009); 2n=48 is known only from outside India (Degraeve, 1980; Horovitz and Dolverger, 1983).

Stellaria media L.

All five populations collected from various localities in Kashmir and Himachal Pradesh show n=13 (Fig. 1m). In the population from Rajgundha, 3 of the 13 bivalents are smaller, 2 are intermediate and 8 are normal-sized in PMCs at diakinesis/ metaphase-I. The present chromosome number n=13 based on x=13 adds a new diploid cytotype for the species, as it was previously reported to have 2n=18 (Krasnikov and Schaulo, 1990), 2n=40 (Bir and Sidhu, 1980), 2n=40 (Morton, 1993; Nishikawa, 1985), 2n=42 (Lara Ruiz, 1993) and 2n=44 (Sidhu and Bir, 1983; Slavik et al., 1993).

S. monosperma Buch.-Ham.

Two populations from Kashmir and four from Himachal Pradesh show a single chromosome number n=13 as diploid cytotype. The present chromosome count gives a new diploid cytotype for the species. The single previous report for the species is 2n=52, from India (Charterjee, 1975).

S. semivestita Edgew.

Two populations collected from Himachal Pradesh and one from Kashmir have the same chromosome number, n=13 (Fig. 1n). This is the first report of this number for the species.

MEIOTIC ABNORMALITIES

We recorded meiotic abnormalities in some populations of *Lychnis coronaria*, *Silene conoidea*, *S.edgeworthii*, *S. vulgaris*, *Stellaria media*, *S. monosperma* and *S. semivestita*. In those populations, abnormalities in the form of cytomixis, chromatin stickiness, unoriented bivalents, bridges, laggards or multipolarity were observed at different stages of meiosis (Tab. 2, Fig. 2a–j). Chromatin transfer from early prophase to pollen formation was evident in most of those populations, with the highest percentage recorded in populations of *S. vulgaris* (Tab. 2). Cytomixis in these populations led to the formation of pollen mother cells (PMCs) with different chromosome numbers, and even empty PMCs in some cases (Fig. 2c). All these meiotically abnormal populations quite frequently showed the presence of chromosomal laggards and bridges at anaphase and telophase. Multipolar PMCs at telophase II were also seen in some populations of these species. Chromatin stickiness involving partial or often complete clumping of bivalents was seen from prophase I to metaphase I in most of these populations. The frequency of unoriented bivalents at metaphase I was highest in populations of *Stellaria media* (Tab. 2). These meiotic abnormalities led to abnormal microsporogenesis and the formation of pollen grains differing in size – unreduced large and smaller fertile pollen grains (Tab. 3, Fig. 2k–s). The frequency of large pollen grains ranged from 7% to 9% in the different populations, and consequently pollen grain fertility was reduced (65–80%). Other populations showed very high pollen grain fertility (97–99%).

DISCUSSION

The family Caryophyllaceae comprises subfamilies Alsinoideae with x=6, 9, 10, 11, 12, 13, 14 and 19 and Silenoideae with x=12–18. Our cytological studies are based on 50 populations comprising 12 species from five genera of the family Caryophyllaceae. The chromosome numbers are based on x=10, 12, 13 or 15. The chromosome number data on 70 species make it clear that the genus *Arenaria* L. is dibasic, exhibiting x=10, 11 (Darlington and Wylie, 1955). Our study of *Arenaria kashmirica* and *A. serphyllifolia* shows that the Western Himalayan populations represent 71.42% diploid and 28.57% tetraploid cytotypes based strictly on x=10. About 26 species of *Gypsophilla* L. are cytologically known, showing the dibasic nature of the genus with x=15 and 17, but our studied populations of *G. ceratioides* from the Western Himalayas show cytotypes with x=15. Cytologically compiled data for 16 species of *Lychnis* L. reveal that it is a monobasic genus based on x=12, and our work on *Lychnis coronaria* confirms it as a diploid species. *Silene* L. with about 230 cytologically known species is mostly diploid with 2n=2x=20, but some polyploids have also been reported with 2n=48, 72 (Bari, 1973). Our 22 studied populations covering 5 species of the genus represent 54.54% diploids [with x=10 (22.72%) and x=12 (31.8%)] and 45.45% tetraploids [with x=10 (9.09%) and x=12 (36.36%)]. The genus *Stellaria* L. with 101 cytologically known species is observed to be polybasic based on x=10–13 (Darlington and Wylie, 1955), but our 14 populations representing 3 *Stellaria* species show only diploid status (n=13, 2n=2x=26). Of the 50 populations we examined, 76% were found to be diploids and only 24% tetraploids.

Cytomixis leads to the production of aneuploid plants (Sheidai et al., 2003; Sheidai and Fadael, 2005) or results in the production of unreduced gametes in several grasses (Falistocco et al., 1995;

TABLE 2. Data on cytomixis, meiotic course and pollen size in different species of Caryophyllaceae from the Western Himalayas

Taxa/ Accessions	Cytomixis: PMCs at Meiosis-I/ Meiosis-II (%)	Cytomixis: Number of PMCs	Meiotic course showing PMCs with: Chromosomal stickiness at M-I (%)	Unoriented bivalents at M-I (%)	Bridges at Meiosis -I/ Meiosis-II (%)	Laggards at Meiosis-I/ Meiosis-II (%)	Multipolarity at T-II (%)	Average size (µm) of fertile pollen grains
Lychinis coronaria								
54395	13.33 (14/105)/ 5.71 (6/105)	2–5	7.69 (5/65)	11.29(7/62)	9.18(9/98)/ 8.16 (8/98)	18. 36 (18/98)/ 11.22 (11/98)	5.00 (2/40)	25.58 × 25.40 – 21.45 × 21.20
54396	8.18 (9/110)/ 5.45 (6/110)	2–3	10.00 (7/70)	–	11.76 (12/102)/ 8.82 (9/102)	10.47 (11/105)/ 10.47 (11/105)	1.88 (1/53)	
54401	–/ –	–	–	7.14 (5/70)	8.18 (9/110)/ 6.36 (7/110)	15.45 (17/110)/ 6.36 (7/110)	–	
54402	–/ –	–	9.09 (6/66)	8. 45 (8/95)	13.18 (12/91)/ 5.49 (5/ 91)	12.90 (12/93)/ 6.45 (6/93)	–	
Silene conoidea								
54458	–/ –	–	–	–	8.91 (9/101)/ 11.88 (12/101)	20.79 (21/101)/ 8.91 (9/101)	–	19.96 × 19.47– 16.45 × 16.20
54451	17.85 (20/112)/ 7.14 (8/112)	2–6	–	8.53 (7/82)	9.78 (9/92)/ 8.69 (8/92)	10.16 (12/118)/ 8.47 (10/118)	6.55 (4/61)	
54452	–/ –	–	10.00 (7/70)	7.14 (5/70)	10.71 (12/112)/ 5.35 (6/112)	8.42 (8/95)/ 7.36 (7/95)	1.92 (1/52)	
S. edgeworthii								
54446	–/ –	–	8.82 (6/68)	8.06 (5/62)	9.23 (6/65)/ 7.69 (5/65)	10.66 (8/75)/ 9.33 (7/75)	1.44 (1/69)	20.18 × 20.05– 17.24 × 17.10
54448	4.08 (4/98)/ 7.14 (7/98)	2–3	–	–	9.67 (6/62)/ 8.06 (5/62)	11.29 (7/62)/ 12.90 (8/62)	3.63 (2/55)	
54438	–/ –	–	–	5.55 (4/72)	10.00 (5/50)/ 8.00 (4/50)	11.11(6/54)/ 9.25 (5/54)	1.63 (1/61)	
54443	–/ –	–	5. 55(4/72)	–	10.00 (5/50)/ 8.00 (4/50)	–/ –	7.40 (4/54)	
S. vulgaris								
54430	33.33 (45/135)/ 13.33 (18/135)	2–5	4.40 (3/68)	3.07 (2/65)	–/ –	6.84 (5/73)/ 5.47 (4/73)	3.77 (2/53)	18.83 × 18.24– 16.45 × 16.05
54431	21.25 (27/127)/ 16. 53 (21/127)	2–4	–	–	5.45 (6/110)/ 3.63 (4/110)	13.09 (11/84)/ 8.33 (7/84)	1.69 (1/59)	
54434	– /–	–	–	8.00(6/75)	11.42 (8/70)/ 5.71 (4/70)	13.97 (13/93)/ 9.67 (9/93)	–	
54426	–/ –	–	5.55 (4/72)	–	–/ –	14. 28 (10/70)/ 12.85 (9/70)	–	
Stellaria media								
54422	15. 65 (18/115)/ 17.39 (20/115)	2–5	8.53 (7/82)	8.00 (6/75)	11.76 (12/102)/ 7.84 (8/102)	13.09 (11/84)/ 14. 28 (12/84)	2.98 (2/67)	20.94 × 20.05– 18.45 × 18.25
54417	22. 83 (25/120)/ 13.33 (16/120)	2–4	–	8.97 (7/78)	6.12 (6/ 98)/ 4.08 (4/98)	14.28 (14/98)/ 10.20 (10/98)	1.47 (1/68)	
S. monosperma								
54408	10.37 (14/135)/ 7.40 (10/135)	2–3	7.69 (6/78)	5.55 (4/72)	–/ –	13. 86 (14/101)/ 15.84 (16/ 101)	1.53 (1/65)	20.45 × 19.25– 18.75 × 17.93
54405	14.54 (16/110)/ 20.00 (22/110)	2–6	9.21 (7/76)	5.95 (5/84)	9.82 (11/112)/ 7.14 (8/112)	18. 75 (21/112)/ 10.71 (12/112)	1/75 (1/57)	
S. semivestita								
54423	16.19 (17/115)/ 15.23 (16/115)	2–5	–	7.14 (5/70)	11.88 (12/101)/ 6.93 (7/101)	13.40 (13/ 97)/ 8.24 (8/ 97)	–	21.91 × 21.93– 19.75 ×19. 32

Figures in parenthesis denote observed number of abnormal PMCs in the numerator and total number of observed PMCs in denominator.

TABLE 3. Data on abnormal microsporogenesis (given in %) in different species of Caryophyllaceae from different areas of the Western Himalayas

Taxa / Accessions	Microsporogenesis							
	Monads		Diads		Triads		Tetrads	
	WMN	WM	WMN	WM	WMN	WM	WMN	WM
Lychnis coronaria								
54395	3.12 (2/64)	–	1.56 (1/64)	3.12 (2/64)	3.12 (2/64)	6.25 (4/64)	67.18 (43/64)	15.62 (10/64)
54396	1.26 (1/79)	3.79(3/79)	5.06 (4/79)	3.79 (3/79)	5.06 (4/79)	5.06 (4/79)	59.96 (45/79)	18.98 (15/79)
54401	2.63 (2/76)	6.57(5/76)	6.57 (5/76)	–	–	2.63 (2/76)	68.42 (52/76)	13.15 (10/76)
54402	–	–	3.03 (2/66)	6.06 (4/66)	–	1.51 (1/66)	72.72 (48/66)	16.66 (11/66)
Silene conoidea								
54458	–	–	8.33(9/108)	3.70(4/108)	7.40(8/108)	–	66.66(72/108)	13.88(15/108)
54451	2.79 (4/143)	1.39(2/143)	6.99(10/143)	4.89(7/143)	7.69(11/143)	2.79(4/143)	59.44(85/143)	13.98(20/143)
54452	6.66 (8/120)	4.16(5/120)	9.16(11/120)	5.83(7/120)	12.50(15/120)	0.83(1/120)	43.33(52/120)	17.50(21/120)
S. edgeworthii								
54446	2.56 (2/78)	–	3.84(3/78)	2.56(2/78)	3.84(3/78)	5.12(4/78)	61.53(48/78)	20.51(16/78)
54448	1.14 (1/87)	2.29(2/87)	2.29(2/87)	4.59(4/87)	–	4.59(4/87)	64.36(56/87)	20.68(18/87)
54438	–	–	1.14(1/89)	2.24(2/89)	4.49(4/89)	3.37(3/89)	74.15(66/89)	14.06(13/89)
54443	1.20 (1/83)	–	2.40(2/83)	–	2.40(2/83)	2.40(2/83	71.08(59/83)	20.49(17/83)
S. vulgaris								
54430	6.36 (7/110)	1.81 (2/110)	5.45 (6/110)	–	3.63 (4/110)	2.72 (3/110)	61.81 (68/110)	18.18 (20/110)
54431	4.76 (6/126)	2.38 (3/126)	6.34 (8/126)	3.17 (4/126)	5.55 (7/126)	3.17 (4/126)	57.14 (72/126)	17.46 (22/126)
54434	4.31 (6/139)	0.71 (1/139)	1.43 (2/139)	5.03 (7/139)	11.51 (16/139)	6.47 (9/139)	52.51 (73/139)	17.98 (25/139)
54426	–	2.53 (2/79)	5.06 (4/139)	–	5.06 (4/79)	–	68.35 (54/79)	18.98 (15/79)
Stellaria media								
54422	3.33 (3/90)	–	4.44 (4/90)	–	1.11 (1/90)	2.22 (2/90)	74.44 (67/90)	14.44 (13/90)
54417	1.16 (1/86)	1.16 (1/86)	2.32 (2/86)	1.16 (1/86)	–	–	82.55 (71/86)	11.62 (10/86)
S. monosperma								
54408	2.89 (2/69)	–	1.44 (1/69)	–	2.89 (2/69)	1.44 (1/69)	69.56 (48/69)	21.73 (15/69)
54405	3.03 (2/66)	6.06 (4/66)	1.51 (1/66)	–	3.03 (2/66)	1.51 (1/66)	68.18 (45/66)	16.66 (11/66)
S. semivestita								
54423	–	2.85 (2/70)	–	2.85 (2/70)	2.85 (2/70)	1.42 (1/70)	68.57 (48/70)	21.42 (15/70)

WMN – without micronuclei; WM – with micronuclei.
Figures in parenthesis denote observed number of abnormal PMCs in the numerator and total number of observed PMCs in denominator.

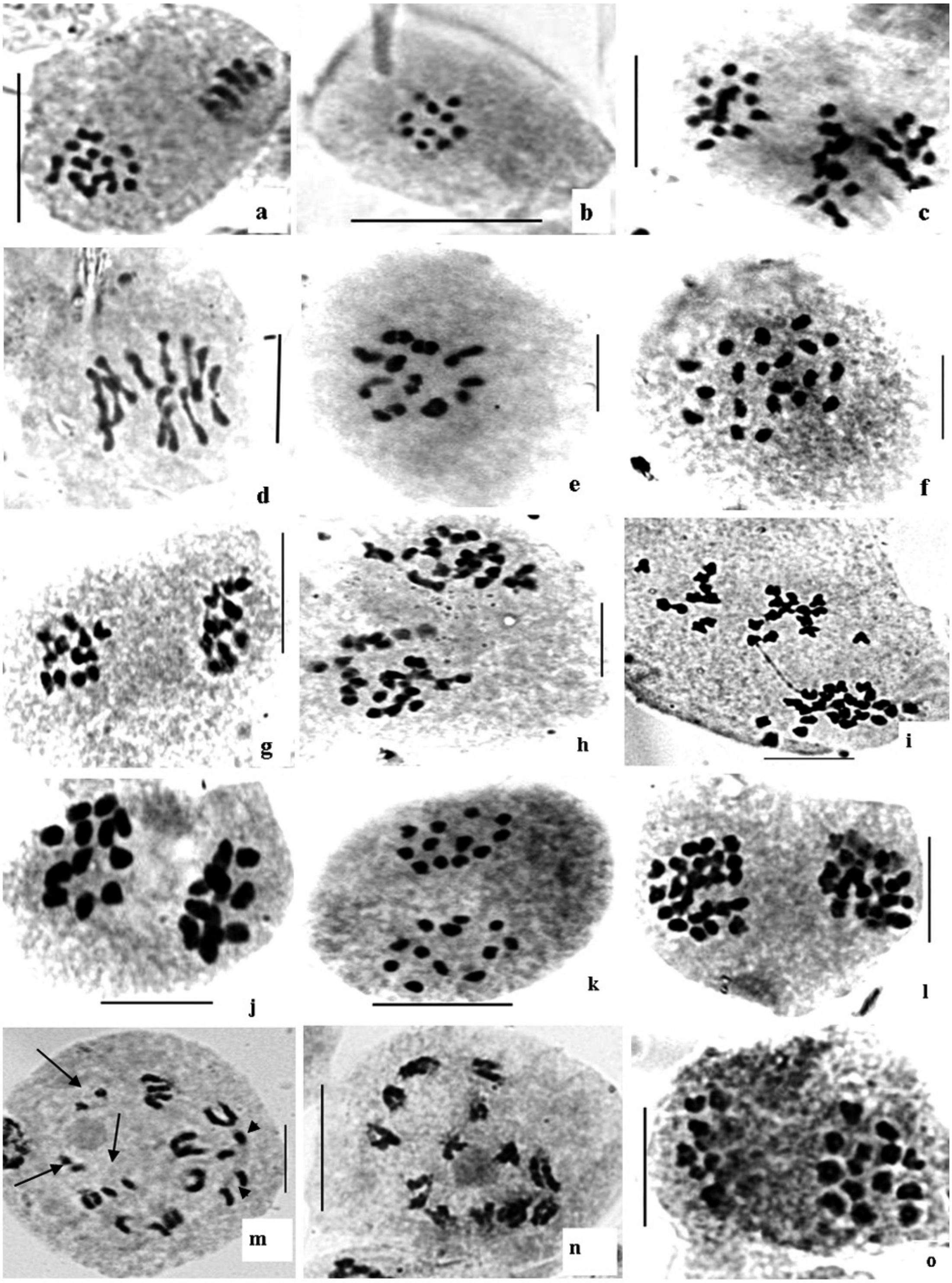

Fig. 1. (**a**) *Arenaria kashmirica* (n=20), PMC at anaphase I, (**b**) *Arenaria serphyllifolia* (n=10), PMC at metaphase I, (**c**) *Gypsophilla ceratioides* (n=15), PMC at anaphase I, (**d**) *Lychnis coronaria* (n=12), PMC at metaphase I, (**e**) *Silene conoidea* (n=10), PMC at metaphase I, (**f**) *Silene conoidea* (n=20), PMC at metaphase I, (**g**) *Silene edgeworthii* (n=12), PMC at anaphase I, (**h**) *Silene edgeworthii* (n=24), PMC at anaphase I, (**i**) *Silene moorcroftiana* (n=24), PMC at anaphase I, (**j**) *Silene nepalensis* (n=12), PMC at anaphase I, (**k**) *Silene vulgaris* (n=12), PMC at diakinesis, (**l**) *Silene vulgaris* (n=24), PMC at anaphase I, (**m**) *Stellaria media* (n=13), PMC at diakinesis (arrows indicate relatively smaller bivalents; arrowheads indicate intermediate-size bivalents), (**n**) *Stellaria semivestita* (n=13), PMC at diakinesis, (**o**) *Stellaria monosperma* (n=13), PMC at diakinesis. Bar = 10 μm.

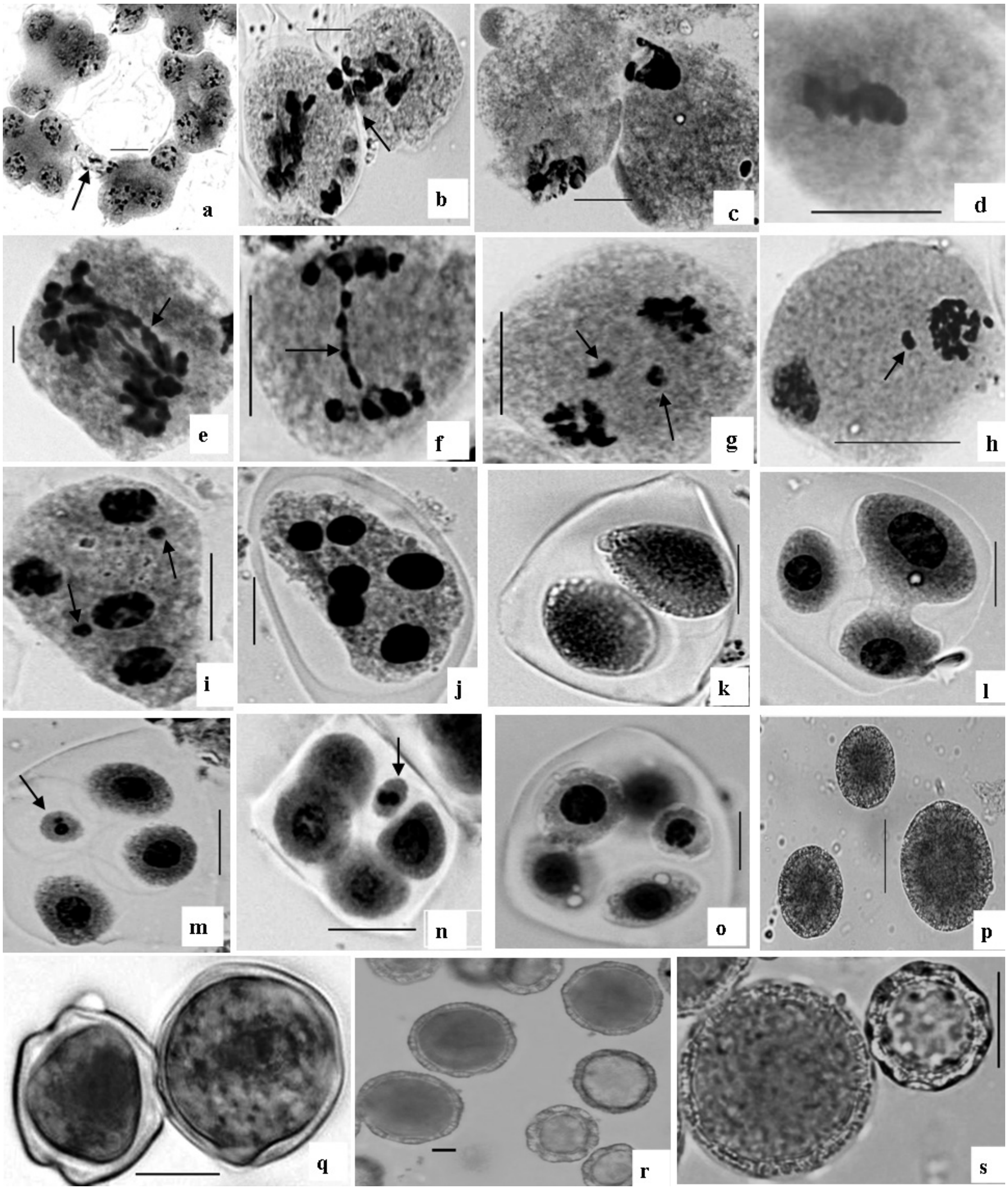

Fig. 2. (**a–c**) Transfer of chromatin (arrowed) in pollen mother cells (PMCs) at different stages of meiosis, (**d**) PMC showing chromatin stickiness at metaphase I, (**e**) PMC with bridges (arrowed) at anaphase I, (**f**) PMC showing bridge (arrowed) at telophase I, (**g**) PMC with laggards (arrowed) at late anaphase I, (**h**) PMC showing laggard (arrowed) at telophase I, (**i**) PMC with micronuclei (arrowed) at telophase II, (**j**) PMC with six poles at telophase II, (**k**) Diad, (**l**) Triad, (**m**) Triad with micronuclei (arrowed), (**n**) Tetrad with micronuclei (arrowed), (**o**) Polyad (pentad), (**p, q**) Fertile pollen grains differing in size in *Lychnis coronaria*, (**r**) Fertile and sterile pollen grains in *Stellaria monosperma*, (**s**) Large unreduced pollen grain in *Silene*. Bar = 10 μm.

Sheidai and Nouroozi, 2005; Ghaffari, 2006; Sheidai and Bagheri-Shabastari, 2007) and in *Arenaria* (Fadaei et al., 2010). The formation of unreduced gametes is of evolutionary significance in that it can lead to the production of plants with higher ploidy through polyploidization (Villeux, 1985). The cytomixis, chromosomal stickiness, unoriented bivalents, laggards and bridges we found among the studied species at population level indicate intraspecific or genetic diversity. Such genetic differences have been seen in different plant species (Baptista-Giacomelli et al., 2000; Sheidai et al., 2003). Cytomixis and chromatin stickiness are considered to be the result of genetic factors (Bellucci et al., 2003; Ghaffari, 2006; Fadaei et al., 2010) and environmental factors (Nirmala and Rao, 1996) as well as genomic-environmental interaction (Baptista-Giacomelli et al., 2000), and these factors no doubt are at work in the populations we investigated. Cytomixis or the occurrence of multipolar cells and meiotic irregularities in anaphase segregation of chromosomes are possible mechanisms for the formation of unreduced pollen grains and reduced fertility in meiotically abnormal populations, as has been reported in *Silene* (Sheidai et al., 2008) and *Arenaria gypsophiloides* (Fadaei et al., 2010). All these meiotic abnormalities may lead to anomalous microsporogenesis and in turn to variable-size pollen grains and the occurrence of aneuploidy (Villeux, 1985; Nirmala and Rao, 1996). Giant pollen grains, possibly unreduced 2n pollen grains, have been reported in several species (Vorsa and Bingham, 1979; Bertagnolle and Thomson, 1995; Sheidai et al., 2008; Fadaei et al., 2010). Pollen grain fertility in these meiotically abnormal populations/species is reduced with the formation of pollen grains varying in size. Such enormous intra- and interspecific variation demands extensive cytological studies at population level.

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