
Impact of cytomixis on meiosis, pollen viability and pollen size in wild populations of Himalayan poppy (*Meconopsis aculeata* Royle)

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We report the occurrence of cytomixis in wild populations of Himalayan poppy (*Meconopsis aculeata* Royle), which is considered to be an important and threatened medicinal plant growing in the high hills of the Himalayas. The impact of cytomixis on meiotic behaviour, reduced pollen viability and heterogeneous-sized pollen grains was also studied. Cytological studies in the seven wild populations from the high hills of Himachal Pradesh revealed that all the 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 caused various meiotic abnormalities. Chromatin transfer also resulted in the formation of coenocytes, aneuploid, polyploid 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 the meiotic course considerably and results in reduced pollen viability.

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1. Introduction

Cytomixis, the phenomenon of inter-pollen mother cell (PMC) transfer of chromatin material through cytotoxic channels, was first recorded by Kornicke (1901) in *Crocus sativus*. Since then, the phenomenon has been reported mainly during microsporogenesis in a wide range of flowering plants (Heslop-Harrison 1966; Singhal and Gill 1985; Bedi 1990; Bione *et al* 2000; Datta *et al* 2005; Ghaffari 2006; Lattoo *et al* 2006; Singhal *et al* 2007). However, cytomixis is also known to occur in somatic cells such as root meristematic cells (Jacob 1941; Sarvella 1958), leaf epidermal and subepidermal layers (Tarkowska 1960), tapetal cells (Cooper 1952), ovary cells (Koul 1990) and shoot apex (Guzicka and Wozny 2005).

Many workers consider cytomixis to be of considerable evolutionary significance (Falistocco *et al* 1995; Morikawa and Leggett 1996; Ghanima and Talaat 2003). Cytotoxic channels and chromatin transfer, which have a profound effect on the meiotic process and its end-products, is more

prevalent in genetically, physiologically and biochemically imbalanced plants such as triploids, haploids, hybrids, apomicts and aneuploids (de Nettancourt and Grant 1964; Haroun 1995; Nirmala and Rao 1996). There are also reports of cytomixis being more prevalent among polyploids (Semyarkhina and Kuptsou 1974; Singhal *et al* 2007) than their diploid counterparts.

The Himalayan poppy or Blue poppy (*Meconopsis aculeata* Royle) grows as a deciduous, perennial, prickly monocarpic herb with tapering rootstocks, deeply lobed radical leaves, and sky-blue to purplish blue flowers with numerous yellow-coloured stamens. The species, which is distributed between 3,300 and 4,600 m in the Western Himalayas from Kashmir to Kumaon (Hooker 1872), prefers light woodlands, moist soils, rock crevices and grows among boulders in the alpine zone. It is widely used as a medicine for rheumatic pains. The plant is also used as an analgesic, febrifuge, narcotic and to treat the bones especially around the ribs by Tibetans (Tsarong and Tsewang 1994). As per the information collected by the authors, its

Keywords. Aneuploid; chromosome stickiness; coenocyte; heterogeneous pollen grains; interbivalent connection; pyknotic chromatin

flowers are frequently used to cure asthmatic problems by the local people in Chamba and the Lahaul-Spiti region of Himachal Pradesh. Cytologically, *M. aculeata* is known to have intraspecific diploid, $2n=28$ (Sugiura 1937) and tetraploid, $2n=56$ (Ratter 1968; Jee *et al* 1989) cytotypes. However, so far, there is only one report from India of a tetraploid cytotype from the Kashmir Himalayas (Jee *et al* 1989). The species, which is endemic to East Asia, has been included in the International Union for Conservation of Nature (IUCN) list of threatened species in the high hills of Jammu and Kashmir, Himachal Pradesh and Uttar Pradesh (Kala 2000; Dhar *et al* 2002). Keeping in view the cytological variability, and endemic and threatened status of this medicinally important plant, we attempted to explore it cytologically from the Chamba (Manimahesh) and Kullu (Rohtang Pass) districts of Himachal Pradesh. The present study also discusses the impact of cytomixis on meiotic behaviour and reduced pollen viability as a consequence, and heterogeneous-sized pollen grains in the species.

2. Materials and methods

Materials for the meiotic studies were collected during the months of June and July in 2006 and 2007 from seven wild populations (table 1). Voucher specimens were deposited in the Herbarium, Department of Botany, Punjabi University, Patiala (PUN). Floral buds of suitable sizes were fixed in Carnoy fixative for 24 h and preserved in 70% alcohol at 4°C. For meiotic studies, the anthers were squashed in 1% acetocarmine. A number of slides were carefully examined for cytological analysis in each population, and chromosome counts were made and abnormalities recorded. Pollen fertility was estimated using a glyceracetocarmine (1:1) mixture. Well-filled pollen grains with stained nuclei were regarded as apparently fertile while shrivelled and unstained pollen were counted as sterile. Photomicrographs of chromosome counts were made from the meiotic preparations using the Leica Qwin Digital Imaging System.

3. Results

All the wild populations showed chromosome stickiness and only a few PMCs depicted 28_{II} at metaphase-I (MI) (figure 1) and 28:28 chromosome segregation at anaphase-I (AI) (figure 2). These Himalayan populations exist uniformly at the tetraploid level on $x=14$. The individuals of only one population from Bhairon Ghati showed a regular meiotic course and high pollen fertility, whereas others showed inter-PMC transfer of chromatin material resulting in various meiotic abnormalities and pollen malformation. The data on meiotic course, cytomixis, and pollen fertility and pollen size in each population are provided in table 2.

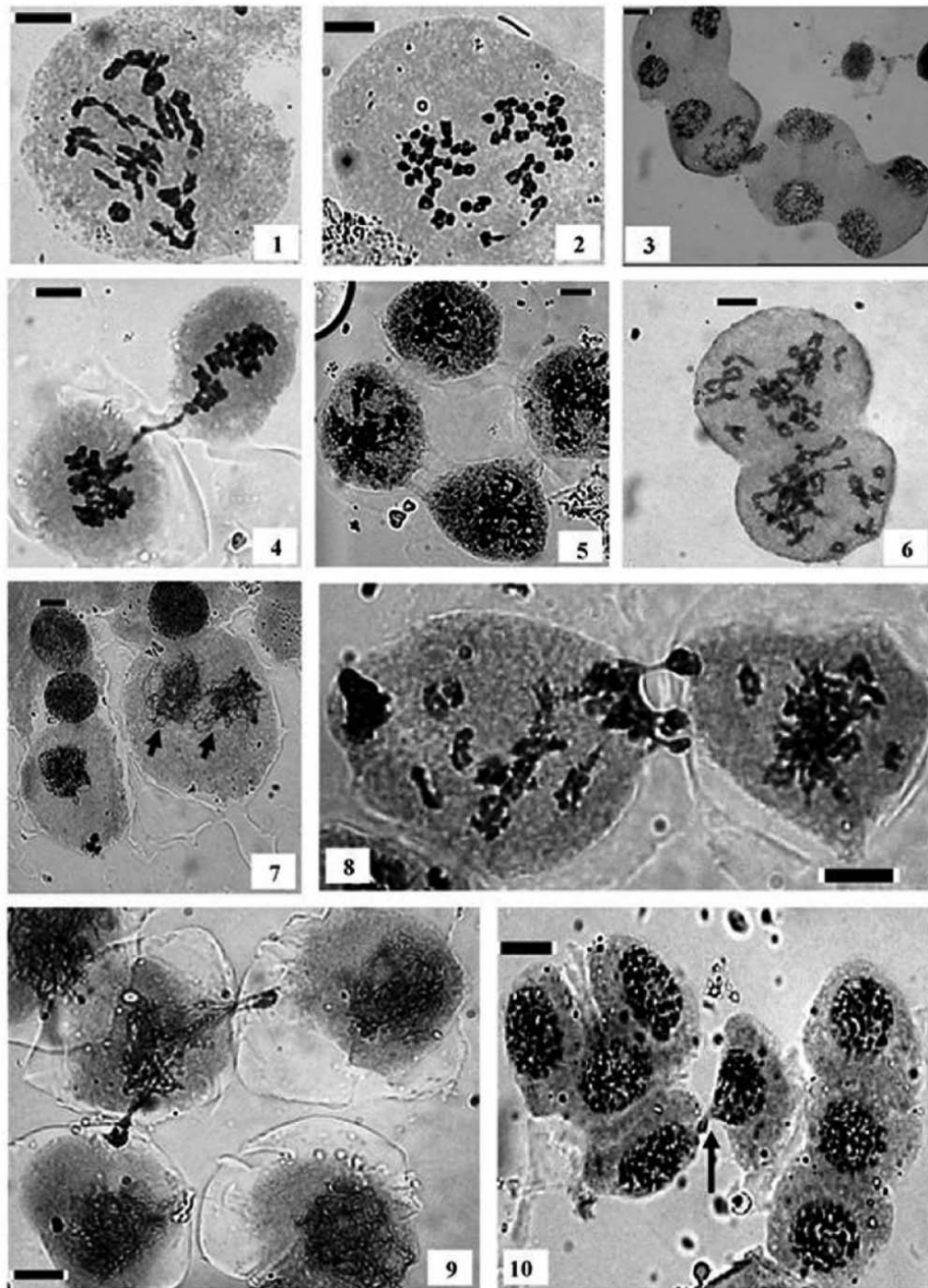
3.1 Cytomixis in pollen mother cells

Cytomixis involving transfer of chromatin material among proximate PMCs was observed in individuals of five populations. The chromatin transfer occurred through broad (figure 3) and narrow (figure 4) channels, but the broad channels were found at a relatively higher frequency. Cytomictic channels were represented by single and multiple threads that appeared like stretched strands involving two or more PMCs (figure 5). In rare cases, PMCs were directly fused to facilitate the transfer of chromatin (figure 6). Coenocytes with two synchronized nuclei were observed in early prophase in a few cases (figure 7). Chromatin transfer occurred either through single or multiple chromatin strands (figure 8). These chromatin strands had a much broader head and an end that tapered towards the recipient PMC (figure 8). The frequency of chromatin transfer was more efficient during MI, although it was present during the other stages, ranging from early prophase (figure 9) to the tetrad stage (figure 10). Interestingly, cytoplasmic connections were also observed between pollen grains (figure 11). In the majority of the cases, only 2–3 PMCs were involved in cytomixis but up to 4 PMCs were also involved in chromatin transfer

Table 1. Locality, altitude, accession number, ploidy level and meiotic chromosome number of wild plants of *M. aculeata*

Locality with altitude (m)		Accession numbers (PUN)*	Meiotic chromosome number (n)	Ploidy level
A. Chamba				
Manimahesh				
1. Bhairon Ghati	3,513	49362	28	4x
2. Dhancho	3,035	49363	28	4x
3. Dunali	2,684	49359, 49360	28	4x
4. Gauri Kund	3,927	49361	28	4x
5. Shiv Gharat	3,156	49357, 49358	28	4x
6. Sundarsi	3,371	49364	28	4x
B. Kullu				
7. Rohtang Pass	3,979	49365	28	4x

*Herbarium code of Botany Department Punjabi University, Patiala as per "Index Herbariorum" by Holmgren and Keuken (1974).



Figures 1–10. (1) A pollen mother cell (PMC) with 28_{II} at MI. (2) A PMC with 28:28 chromosome distribution at anaphase-I (AI). (3) Chromatin transfer through broad cytoplasmic channels. (4) Chromatin transfer through narrow cytoplasmic strands. (5) Group of PMCs connected through narrow and stretched cytoplasmic channels. (6) Direct fusion of two PMCs. (7) Coenocyte with two synchronized nuclei at early prophase-I (arrows). (8) Chromatin transfer through multiple chromatin strands. (9) Simultaneous transfer of chromatin from one PMC to other two PMCs. (10) Chromatin transfer between microspores of two tetrads (arrow).

(figure 12). The transfer of chromatin was either partial, involving a small part, or complete, involving the entire chromosome complement. Consequent to partial transfer of chromatin (figure 13), the resulting PMCs showed aneuploid chromosome numbers with 16 and 17 bivalents (figures 14 and 15). In some cases, due to total transfer of material, empty PMCs were also seen (figure 16). Simultaneous transfer of chromatin from one PMC to two other proximate PMCs was also observed (figure 9). Due to chromatin migration, PMCs showed extra chromatin masses lying away from the main chromosome complement (figure 17). In a few instances, broken chromatin strands and their remnants could also be seen attached to the PMCs.

3.2 Meiotic abnormalities

The transfer of chromatin material during microsporogenesis caused various meiotic abnormalities such as interbivalent connections, chromosome stickiness, laggards, bridges, late disjunction, pyknotic chromatin and unorganized chromatin threads.

3.2a Interbivalent connections: Interbivalent connections were observed in all the populations studied and were more frequent where cytomixis was present. These interbivalent connections were usually present at the terminal ends of bivalents. The number of bivalents involved in such connections ranged from 4 to 22. As a consequence of the formation of these bivalents, various types of associations were seen in the form of chains and rings (figure 18).

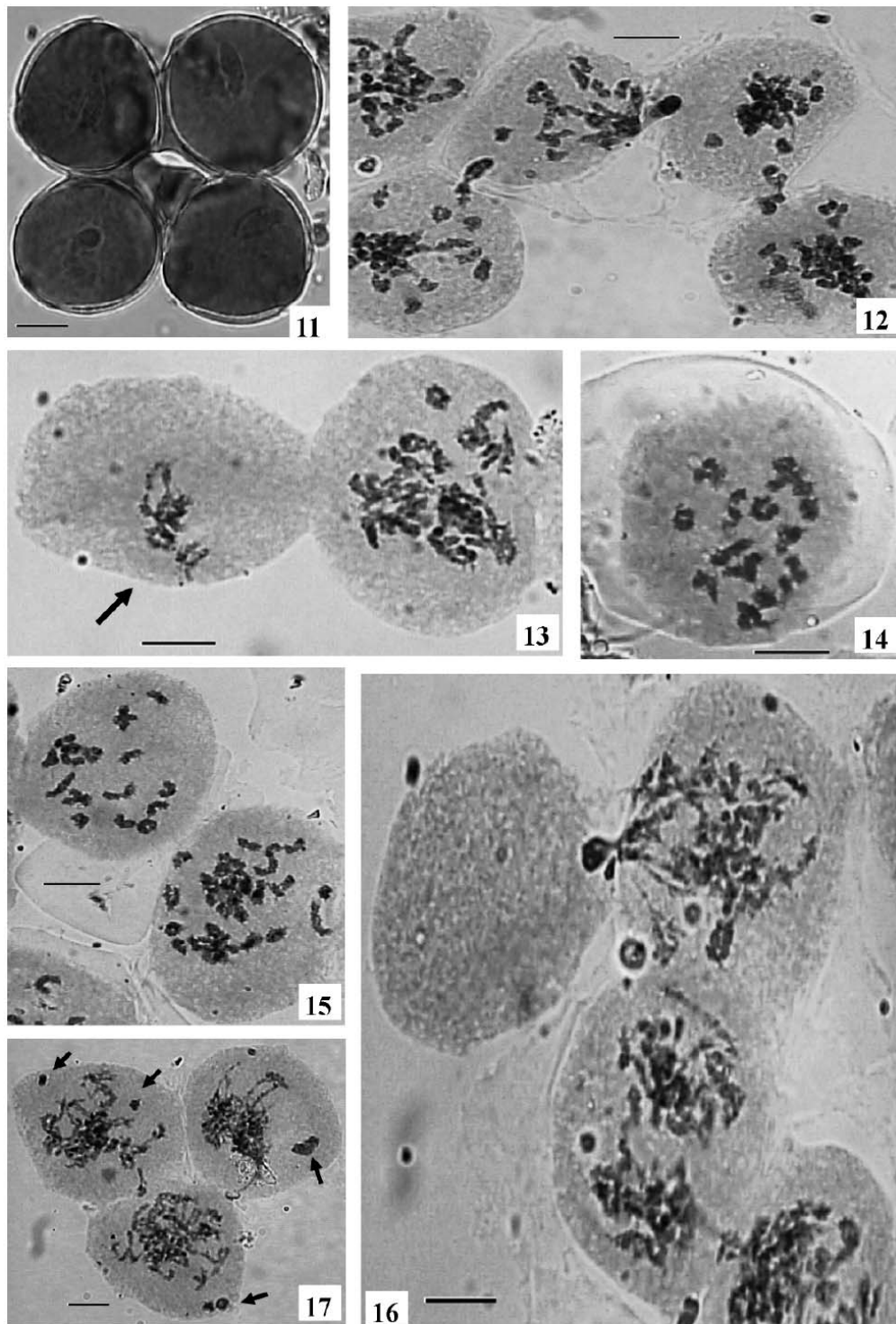
3.2b Chromosome stickiness: Chromosome stickiness was the other common meiotic anomaly encountered in all the seven populations. The percentage of PMCs exhibiting chromosome stickiness was rather low (18.12%) in individuals of the Bhairon Ghati population, as they did not depict any chromatin transfer. In comparison, all the other populations with cytomixis depicted a considerably higher percentage of PMCs with chromosome stickiness (29.46–91.23%). The phenomenon of chromosome stickiness was recorded from early prophase-I and persisted till the second meiotic division. However, it was more frequent in MI (figure 19). Due to this, the chromosomes lost their individuality completely. Chromosome stickiness either involved a few bivalents or the whole complement in MI.

Table 2. Cytomixis, meiotic course, pollen fertility and pollen size in the wild populations of *M. aculeata*

Populations	Cytomixis			Meiotic course			Pollen		
	Percentage of PMCs involved	No. of PMCs involved	Meiotic stage/s	PMCs with laggards at AI/TI, AII/TII (%)	PMCs with bridges at AI/TI, AII/TII (%)	PMCs with chromosome stickiness (%)	Fertility	Size (μm) %	Relative frequency of small-, medium- and large-sized pollen grains*
A. Chamba, Manimahesh									
1. Bhairon Ghati	00.00	00.00	----	00.00	00.00	18.12	98.10	32.76×30.94	100
2. Dhancho	03.16	2-4	Metaphase-I	0.167	00.96	82.76	77.60	31.49×30.18	100
3. Dunali	13.71	2	Metaphase-I	00.00	00.00	66.31	96.47	39.23×38.16 27.98×26.56 20.29×20.13	01.71 92.00 06.29
4. Gauri Kund	10.40	2	Metaphase-I	00.00	01.96	75.45	61.45	39.28×38.91 33.21×32.90 20.31×20.01	63.83 12.06 24.11
5. Shiv Gharat	27.11	2-3	Metaphase-I	00.00	00.00	91.23	85.00	31.61×29.12	100
6. Sundarsi	11.22	2-5	Early prophase, metaphase-I, telophase I and II, tetrad stage	02.19	01.34	35.12	90.18	51.38×43.05 36.11×30.55 26.38×23.61	84.16 02.59 13.25
B. Kullu									
7. Rohtang Pass	00.09	2-3	Metaphase-I	03.14	02.59	29.46	99.78	32.27×30.78	100

*Observed number of (small, medium or large) pollen grains/total number of fertile pollen grains.

PMC, pollen mother cell; AI/II, anaphase-I/II; TI/II, telophase-I/II.



Figures 11–17. (11) Pollen grains showing cytoplasmic channels. (12) A group of four pollen mother cells (PMCs) involved in chromatin transfer. (13) A PMC showing partial transfer of chromatin (arrow). (14). A PMC with 17_{II}. (15). A (PMC) with 16_{II}. (16) An empty PMC showing complete transfer of chromatin to a proximate PMC. (17) Three PMCs showing extra chromatin masses (arrows).

In severe cases, chromosome stickiness resulted in thick chromatin bridges at telophase-II (TII) (figure 20). In some PMCs, chromatin bridges formed a ring connecting all the four poles in TII (figure 20).

3.2c Laggards, chromatin bridges and late disjunction of bivalents: Lagging of chromatin material in the form of 1–2 laggards (figure 21) and chromatin bridges (figure 22) in AI/TI and AII/TII, and late disjunction of some bivalents were also observed in some PMCs (figure 23). However, in one population from Shiv Gharat, chromatin migration did not cause any meiotic abnormality during anaphase/telophase.

Chromatin transfer causes other meiotic abnormalities such as pyknotic chromatin material (figure 24) and unorganized chromatin threads in the cytoplasm during early prophase-I (figure 25).

3.3 Reduced pollen viability and heterogeneous-sized pollen grains

Chromatin transfer and associated meiotic abnormalities in the species resulted in malformation of pollen (figure 26) (0.22–38.55%) and heterogeneous-sized pollen grains. On the basis of size, these pollen grains were categorized into small ($20.29\text{--}26.38\text{ }\mu\text{m} \times 20.01\text{--}23.61\text{ }\mu\text{m}$), medium ($27.98\text{--}33.21\text{ }\mu\text{m} \times 26.56\text{--}32.90\text{ }\mu\text{m}$) and large ($39.23\text{--}51.38\text{ }\mu\text{m} \times 38.16\text{--}43.05\text{ }\mu\text{m}$) (figures 27 and 28). The relative frequency with which different-sized pollen grains were seen varied among the different populations. In individuals where chromatin transfer in the PMCs was either absent or very low and meiotic abnormalities were almost negligible, all the pollen grains were fertile and of medium size.

4. Discussion

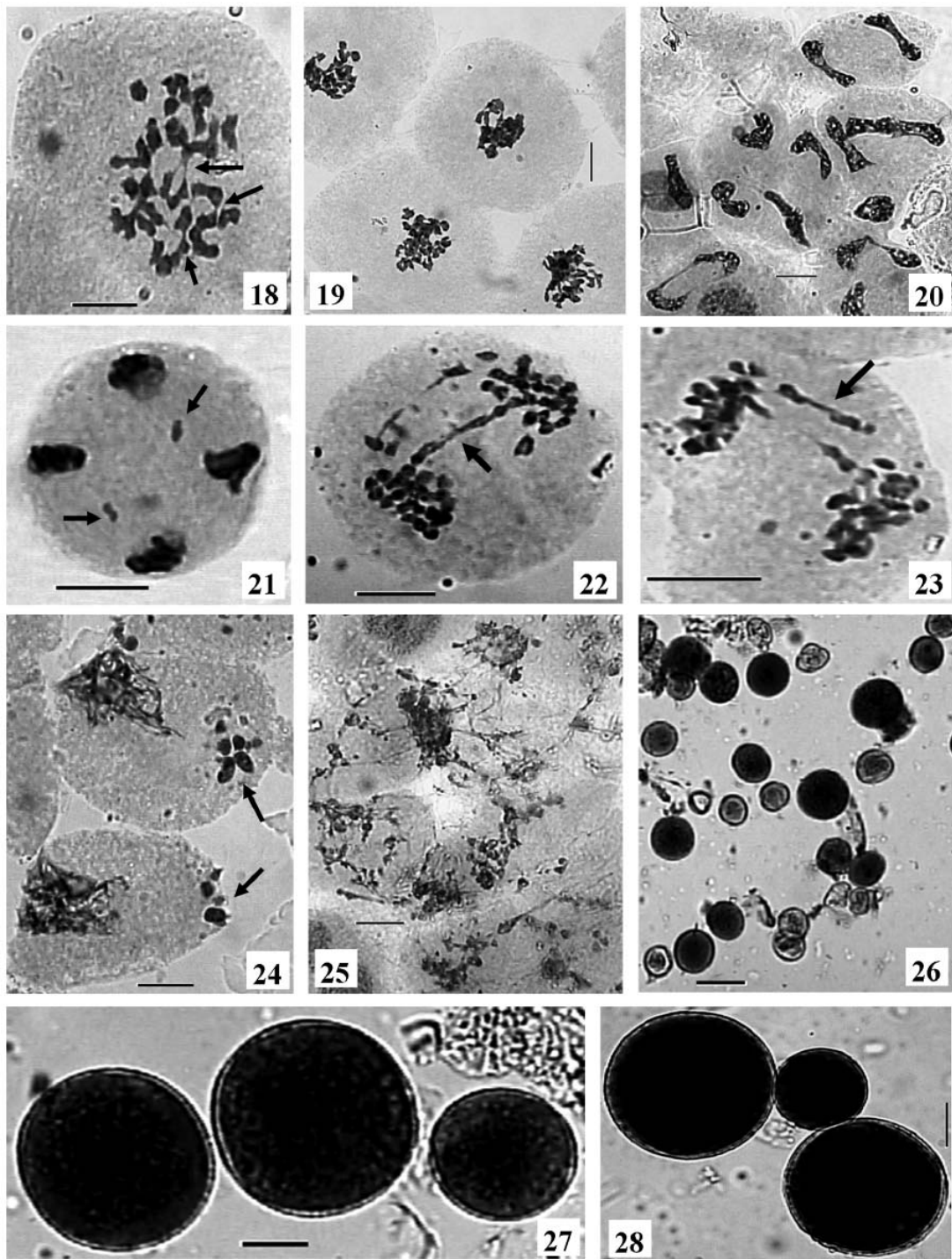
The present chromosome count of $2n=56$ in *M. aculeata* is in conformity with the earlier reports from the Kashmir Himalayas (Jee *et al* 1989) and elsewhere (Ratter 1968). However, a chromosome count of $2n=28$ reported by Sugiura (1937) from outside India indicates that the species exhibits the existence of intraspecific polyploidy. At present, opinions are varied regarding the basic number of chromosomes of the genus *Meconopsis* and the level of ploidy in the species. Ernst (1965) and Ratter (1968) suggested $x=7$ and 8 as the basic chromosome numbers and, accordingly, *M. aculeata* depicts the existence of $4x$ and $8x$ cytotypes. However, so far no chromosome record is available with either $2n=14$ or $2n=16$. Therefore, the possibility of $x=14$ as the most probable base number is more accurate as has also been documented by Ying *et al* (2006). Accordingly, *M. aculeata* has been depicted as diploid ($2n=28$) and tetraploid ($2n=56$)

cytotypes, with all the Indian populations at the tetraploid level.

Out of the seven Himalayan populations scored presently, one population from Bhairon Ghati did not show any chromatin transfer and depicted normal meiotic behaviour with some chromosome stickiness and nearly cent per cent pollen fertility. The populations studied from Rohtang Pass and Dhancho showed a relatively low frequency of chromatin transfer (00.09–03.16%) and, consequently, less meiotic abnormalities. In the remaining populations, cytomixis affected the meiotic course considerably, resulting in pollen malformation and pollen grains of heterogeneous sizes. The frequency of chromatin transfer in such individuals was much higher during the first meiotic division than the second, which is in agreement with earlier findings (De and Sharma 1983; Consolaro and Pagliarini 1995; de Souza and Pagliarini 1997; Pierozzi and Benatti 1998). However, chromatin transfer extended up to the tetrad stage in some PMCs. Cytomixis, through the formation of single or multiple chromatin strands as seen in this study, has also been observed in *Medicago sativa* by Bellucci *et al* (2003). The simultaneous transfer of chromatin from a single PMC to two different PMCs observed in this study has also been recorded in *Vicia faba* by Bhat *et al* (2006). Transfer of chromatin, either partial or complete, determines the fate of the PMCs involved in cytomixis – whether these result in aneuploids or polyploids or anucleated forms. The formation of such PMCs as a consequence of cytomixis has also been noticed earlier by other workers (Gottschalk 1970; Ashraf and Gohil 1994; Dagne 1994; Poggio *et al* 1997; de Souza and Pagliarini 1997). The extra chromatin masses present in the PMCs do not pair with the main chromatin and remain in the cell as a separate mass. The fate of such additional masses of chromatin is not known, but they probably form micronuclei or micropollen as suggested by Bhat *et al* (2006).

The inter-PMC transfer of chromatin material results in various meiotic abnormalities, such as unorganized chromatin, interbivalent connections, chromosome stickiness, laggards and chromatin bridges. The role of cytomixis in inducing such meiotic irregularities has been reported in other plants as well (Mary 1979; Chauhan 1981; Mary and Suvarnalatha 1981; Singhal and Gill 1985). Interbivalent connections have been observed mainly during the diplotene and diakinesis stages in *Crotalaria* (Akpabio 1990) and *Capsicum* (Falusi 2006). These workers were of the opinion that with the advancement of meiosis there is a reduction in the frequency of interbivalent connections. However, in *M. aculeata*, these connections continue up to MI.

Another interesting aspect of the present investigation was the formation of coenocytes in early prophase-I as a consequence of cytomixis. Coenocytism during microsporogenesis has been reported earlier in the



Figures 18–27. (18) A pollen mother cell (PMC) showing ring and chain configuration (arrows) due to interbivalent connections. (19) Chromosome stickiness at metaphase-I (MI). (20) Chromosome stickiness in telophase-II (TII). (21) Laggards in telophase-II (TII) (arrows). (22) Chromatin bridges in anaphase-I (AI) (arrow). (23) Late disjunction of bivalents in anaphase-I (AI) (arrow). (24) Two PMCs showing pyknotic chromatin (arrows). (25) Unorganized chromatin threads scattered in the cytoplasm at early prophase-I. (26) Fertile (dark) and sterile (transparent) pollen grains. (27 and 28) Fertile heterogenous-sized pollen grains. Bar = 10 μ m (figures 1–25, 27 and 28) and 30 μ m (figure 26).

intergeneric hybrids of *Triticeae* (Kagawa 1929; Kihara and Lilienfeld 1934; Villax and Mota 1953; Nakajima 1954a, b), *Psathyrostachys huashanica* x *Secale montanum* (Wang 1988), *Roegneria ciliaris* x *Psathyrostachys huashanica* (Yen *et al* 1993) and *Brachiaria decumbens* (Mendes-Bonato *et al* 2001). Such coenocytes may be formed either by the passage of a nucleus from one PMC into another (Price 1956) or through the fusion of PMCs as suggested by Mehra and Kalia (1973). The coenocytes formed due to cytomixis lead to the formation of abnormal-sized pollen grains as suggested earlier by Mendes-Bonato *et al* (2001).

Although transfer of chromatin material has been reported in numerous species, there are conflicting opinions and explanations regarding the causes and significance of cytomixis. Possible causes suggested earlier include the effect of fixation (Heslop-Harrison 1966; Haroun 1995), pathological changes (Bobak and Herich 1978; Morisset 1978), physiological control (Bell 1964; Bahl and Tyagi 1988), chemicals and herbicides (Bobak and Herich 1978; Ajay and Sarbhoy 1987; Haroun 1995), pollution (Haroun *et al* 2004), temperature (Narain 1976), stress factors and genetic control (Ghanima and Talaat 2003). Pressure differences (Tarkowska 1965; Morisset 1978) and clumped chromatin bridges during premeiotic anaphase (Mendes and Rijo 1951) are the other explanations put forth by some authors. In the present case, cytomixis seems to be a natural phenomenon under direct genetic control as mentioned by other workers (Omara 1976; De and Sharma 1983; Singhal and Gill 1985; Haroun 1995; Bellucci *et al* 2003; Ghanima and Talaat 2003; Haroun *et al* 2004; Lattoo *et al* 2006; Singhal *et al* 2007).

The present study reveals that cytomixis is directly responsible for abnormal meiotic behaviour, pollen grains of different sizes and pollen sterility in *M. aculeata*. Similar findings regarding the effects of cytomixis on meiotic course have been reported in *Coix* (Sapre and Deshpande 1987), *Alopecurus arundinaceus* (Koul 1990), *Polygonum tomentosum* (Haroun 1995), *Hordeum vulgare* (Haroun 1996), *Brassica napus* var. *oleifera* and *B. campestris* var. *oleifera* (Alice and Maria 1997), and *Vicia faba* (Haroun *et al* 2004). Sharma and Gaur (1987), while studying the palynology of *M. aculeata*, reported that pollen grains are uniformly spheroidal to subprolate with a size of $35.5 \times 30 \mu\text{m}$. However, the presence of heterogeneous-sized pollen grains in the populations examined in this study seems to be the product of aneuploid or polyploid PMCs following cytomixis. Cytoplasmic connections among pollen grains were also observed in some individuals in this study. Such connections among pollen grains had already been noticed in the intergeneric hybrids of *Roegneria tsukushiensis* x *Psathyrostachys huashanica* and *Triticum aestivum* x *Psathyrostachys huashanica* (Sun *et al* 1993, 1994).

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