She number, size and shape of the chromosomes are often used to trace the phylogenetic and taxonomic relationships of various taxa. Presently the study reveals that *Campanula medium*, *Lobelia tricorna*, *L. cardinalis*, *L. tenerior*, and *Scrophularia koenigii* are diploids, having larger chromosomes than the tetraploids *L. nicotianaefolia*, *L. oxyclem* and *Lobelia longiflora*. The chromosomes of the hexaploid *L. inflata* are smaller than the chromosomes of the tetraploid species. This is also the case with the diploid *L. medium* and the hexaploid *L. latifolia*. (A comparative analysis of karyotypes of the taxa investigated is given in Table 15).

Stebbins (1971) cites several examples from different taxa to show that the lower the chromosome number the greater the degree of karyotype asymmetry. This karyotype asymmetry in its turn correlated with advanced characters. This holds good for Campanales too (Table 15). The three genera viz., *Campanula*, *Wahlenbergia* and *Sphenoclea* are herbs with regular corollas possessing almost very similar karyomorphology. However, *Lobelia tricana* and *L. cardinalis*, both herbaceous annuals, have syngnathic flowers (with 2n=14).
Table 15: Comparative analysis of karyotypes

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Some tic of centromere type</th>
<th>No. of chromosome number</th>
<th>No. of set. chromosome</th>
<th>Relative length</th>
<th>Absolute length</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>M</td>
<td>nma</td>
<td>nma</td>
<td>net</td>
</tr>
<tr>
<td>1. Spergula medium L.</td>
<td>2n=34</td>
<td>12</td>
<td>20</td>
<td>2</td>
<td>-</td>
</tr>
<tr>
<td>2. C. latifolia L. 2n=102</td>
<td>28</td>
<td>74</td>
<td>-</td>
<td>-</td>
<td>2 nm</td>
</tr>
<tr>
<td>3. Weihenstephania maritima (Thunb.) A. DC. (1)</td>
<td>2n=54</td>
<td>30</td>
<td>22</td>
<td>2</td>
<td>-</td>
</tr>
<tr>
<td>4. W. meridiana (Thunb.) A. DC. (2)</td>
<td>2n=72</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>5. Sphenoclea zeylenica Gaertn.</td>
<td>2n=42</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>6. L. cardinale L.</td>
<td>2n=14</td>
<td>4</td>
<td>8</td>
<td>2</td>
<td>-</td>
</tr>
<tr>
<td>7. L. subtilis Roxb.</td>
<td>2n=18</td>
<td>6</td>
<td>12</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>8. L. tenuior R. Br.</td>
<td>2n=42</td>
<td>12</td>
<td>30</td>
<td>-</td>
<td>2 nm</td>
</tr>
<tr>
<td>9. L. inflata L.</td>
<td>2n=42</td>
<td>12</td>
<td>30</td>
<td>-</td>
<td>2 nm</td>
</tr>
<tr>
<td>10. L. nico-tniariafolia Hayne.</td>
<td>2n=28 1) 6 20</td>
<td>2</td>
<td>-</td>
<td>-</td>
<td>9.49</td>
</tr>
<tr>
<td>11. L. angustifolia L.</td>
<td>2n=42</td>
<td>12</td>
<td>16</td>
<td>-</td>
<td>2 nm</td>
</tr>
<tr>
<td>12. L. cardinale Presl.</td>
<td>2n=42</td>
<td>12</td>
<td>16</td>
<td>-</td>
<td>2 nm</td>
</tr>
<tr>
<td>13. Senecio kosmizii Vahl.</td>
<td>2n=16</td>
<td>2</td>
<td>10</td>
<td>4</td>
<td>-</td>
</tr>
</tbody>
</table>

Absolute length:

|       | 25.56 | 74.06 | 35.70 | 16.48 | 22.07 | 13.36 | 30.54 | 21.33 | 30.42 | 21.45 | 29.36 | 25.58 |
and exhibit the maximum karyotype asymmetry among the taxa investigated. *Sosevolia kosnicjii* (2n=16), a shrubby form with symmorphic flowers also has asymmetrical karyotype. When classified with reference to karyologic symmetry according to Stebbins (1971) method, *L. tricorne* and *Sosevolia kosnicjii* fall in group I A (along with all the other taxa) and *L. cardinalis* in 2 A (Table 16).

Thus, *Campanula, Kohlbergiae* and *Sphenoclea* with symmetrical karyotype can be considered to be less advanced than *Lobelia* and *Sosevolia*, which have a heterogeneous karyotype.

### Basic Chromosome Number

Tischler (1927 and 1931) suggests 8 as the primary basic number of the family Campanulaceae. He does so because, in five out of the eight genera of the family, 8 and 16 numbers are to be found, with secondary derivative 17 in *Campanula*, and 7 and 9 in *Lobelia*. Wanscher (1934) says that the base number 7 is the fundamental number of the multiple series 7-14-21-28....
Table 16: Classification of karyotype according to their asymmetry in thirteen taxa of order Campanales (Dill) based on Stebbins (1971)

<table>
<thead>
<tr>
<th>Ratio largest/smallest</th>
<th>Proportion of chromosomes with arm ratio (2:1)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0-0</td>
</tr>
<tr>
<td>1A</td>
<td></td>
</tr>
<tr>
<td>2A</td>
<td></td>
</tr>
<tr>
<td>3A</td>
<td></td>
</tr>
<tr>
<td>4A</td>
<td></td>
</tr>
</tbody>
</table>

| 2:1                    | Campanula medium | L. cardinalsia | - | - |
|                        | L. latifolia     |                |    |   |
|                        | Wahlenbergia     |                |    |   |
|                        | maxillata 1&2    |                |    |   |
|                        | Lobelia tricora  |                |    |   |
|                        | L. inflata       |                |    |   |
|                        | L. tenior        |                |    |   |
|                        | L. nicotianefolia|                |    |   |
|                        | L. excelsa       |                |    |   |
|                        | Isometum longiflorum |          |    |   |
|                        | Scaevola koeingii|                |    |   |

| 2:1-4:1                 | 1B | 2B | 3B | 4B |
|                        | -  |    |    |    |

| > 2:1-4:1               | 1C | 2C | 3C | 4C |
|                        | -  |    |    |    |

| 4:1                     | 1D | 2D | 3D | 4D |
|                        | -  |    |    |    |
Campanula

Gontawiriopoulus (1964) observes that it is a little difficult for the taxonomists to form an opinion as regards the genus Campanula, because of the diversity of species, which is sometimes due to plasticity in morphology and the variations occurring in chromosome numbers on account of either polyploidy or polyploidy (Bocher 1960, 1964). Reports on the different species of Campanula present a confusing picture. According to Fernandes (1962), Merxmüller and Demboldt (1962), Pfitz (1963), Böcher (1965), Podlech and Demboldt (1963), Canturközopoulou (1964, 1966, 1970, 1972, 1976) and Godela (1964, 1966), the basic chromosome numbers are \( x = 6, 7, 9, 10, 11, 12, 13, 14, 15, 16 \) and 17, the more frequent basic number being \( x = 17 \). Of the chromosome numbers reported for 238 species of Campanula (Federov, 1974), as many as 119 species have \( 2n = 34 \); seventeen species have \( 2n = 68 \); and ten species have \( 2n = 102 \) chromosomes.

Opinion varies as regards the basic chromosome numbers of the genus Campanula. According to some, it is \( x = 8 \) and 17 (Sugiura, 1942); others say that it is \( x = 8 \) (Böcher, 1960, Godela, 1966); and \( x = 6 \) (Fernandes, 1962). Sugiura (1942) opines that the two basic chromosome numbers 8 and 17 have arisen independently of each other and that taxa with \( x = 10, 13 \)
or 15 are derived from those with \( n = 17 \). Bocher (1960) feels that meiotic irregularities are responsible for polysemy. The trisomics \( 2n = 17 \) get stabilised by polyploidy and give rise to the tetraploids \( 2n = 34 \). Thus \( n = 17 \) can be considered a secondary basic number (Bocher 1960, Gadella 1966) which gives rise to a polyploid series with \( 2n = 34, 51, 68 \) and 102. Fernandes (1962) explains the polysemic origin of the different basic numbers, as also the amphihaploidy between plants with \( n = 8 \) and \( n = 9 \), giving rise to the species with \( n = 17 \). These form allotetraploids with \( 2n = 34 \).

Gadella (1966), however, says, in view of certain morphological resemblances among taxa with \( 2n = 30, 32 \) and 34, that \( n = 7 \) is derived from \( n = 8 \) by reduction and that \( 2n = 32 \) is obtained by the reduction of the number \( 2n = 34 \). According to Contramidiropoulos (1964), the genus has evolved in two ways — i.e., polyploidy and the variation of the basic chromosome number.

**Wahlenbergia**

The chromosome numbers of the five species of *Wahlenbergia*, as investigated by Galline (1950), are \( 2n = 18, 2n = 36, 2n = 54 \) and \( 2n = 72 \). This clearly indicates that the basic number of the genus is \( n = 9 \). *W. marginede* (Thunb.) DC
shows $2n=72$. In this species intraspecific cytological variations occur with $2n=54$, $2n=60$.90 (Borgmann, 1964), and $2n=72$ (Gadella, 1966). The two cytotypes of *S. marginata* investigated presently having $2n=54$ and 72 chromosomes further confirm that $x=9$ is the basic number of the genus.

**Sphenoclea**

Lewis et al. (1962) report the chromosome number as $n=12$, but Larsen (1966) says that it is $n=20$. Bhattacharyya (1972) reports $n=21$, and suggests that the basic number is $x=7$. The present investigation also shows $2n=21$, thus supporting the view that the basic number is 7.

**Lobelia**

For the genus *Lobelia*, $n=7,9,14$ and 21 have been recorded (Arnsen 1912, Sugiura 1936, 1937, 1940; Sokolovskaja 1962, Bowden 1958, 1959a & b, 1960a & b, Biers 1961, Borgmann 1964, Bhattacharyya 1972). Arnsen (1912) reports $x=5$ in *L. dortmanna* and *L. nicotianaefolia*. Sugiura (1940) finds both $n=7$ and 8 in *L. inflata*, and suggests $x=8$ is the basic number and $x=7$ is derived from this. However, other reports reveal $n=7$ as the most prevalent chromosome number in *Lobelia*. The basic number appears to be $x=7$, $n=9$ being derived from $x=7$. The present investigation is in accordance with this.
Isotoma

James (1963) reports $n=7$ as the basic number for the genus *Isotoma*. Subramanyam (1931) and Beuernberg and Hair (1959) too report the same number. The species investigated here with $n=14$ conforms to the basic number $n=7$.

Scevola

According to the reports of Kausik (1939), Skottsberg (1955), Peacock (1963), Forssman (1964), and Brizicky (1966), the basic number of this genus is $n=8$. The present investigation confirms this finding.

Thus, the different taxa investigated in the present study show the basic chromosome number to be $n=17$ in the genus *Campanula*, $n=19$ in *Nahlenbergia*, and *Lobelia tenuior*, $n=7$ in the other species of *Lobelia*, *Isotoma* and *Sphenoclea*, and $n=3$ in *Scevola*.

The two species of *Campanula*, *C. medium* and *C. latifolia* belong to the section *Medium* and sub-section *quincluoculareae* and *trilocularae* respectively. The former with the basic number $n=17$, constitutes a homogonic group; and the latter, with $n=16$ and 17, is a less homogeneous group as far as karyotype is concerned (Contandriopoulus 1966). In the
subsection triloeulareo, some species of *Campanula* differ in their basic chromosome numbers, although they strongly resemble one another in morphological characters. Thus they constitute a very exceptional dysploidy series (Contandriopoulos 1976). Ehrendorfer *et al.* (1969) have elaborated upon the formation of different basic numbers owing to dysploid and polyploid changes. Ehrendorfer (1976) further suggests that dysploidy represents an early phylogenetic division, constituting a primary phase of variation in the chromosome number. Genic and structural differentiation of the chromosomes, followed by hybridization and polyploidy is the secondary phase. Both phases seem to be operative in *Campanula*. Gupta (1978) also holds, on the basis of his cytological investigations of Gramineae, Compositae, and Leguminosae, that both dysploidy and polyploidy play important roles in the evolution of plants.

Raven (1975) suggests that \( x=7 \) characterizes all the chief groups of angiosperms, and basic numbers like \( x=9 \) occur in some primitive woody forms. Favarger (1981) states that the most frequent basic numbers of angiosperms are \( x=6, 7, \) and 6. He states further that these, in the present-day taxa, are replaced by secondary basic numbers arising out of amphidiploidy. If so, the basic chromosome number \( x=7 \) of *Lobelia*, *Inostome* and *Sphenoclea*, and \( x=8 \) of *Sesuvium* should be regarded as primary, and the basic chromosome number \( x=9 \) of *Wahlenbergia*, *Lobelia tenuior*,
x=17 of *Campanula* as derived. The latter two can be considered as derived, but the genus *Lobelia* with x=7 and *Scaevola* with \(x=8\) seem to be more advanced than either *Wahlenbergia* or *Campanula* in the light of their morphology and karyotypes.

Stebbins (1966) feels that the woody plants gave rise to the herbaceous ones, which evolved with intense polyploidization but without any change in the primary basic number. Multiples of the basic numbers are seen in the different species of *Campanula*, *Wahlenbergia* and *Lobelia* investigated.

*Campanula* \(x=17\)

- \(2n=34\) - *C.* medium
- \(2n=102\) - *C.* latifolia

*Wahlenbergia* \(x=9\)

- \(2n=54\) - *W.* marginita (1)
- \(2n=72\) - *W.* marginita (2)

*Lobelia* \(x=7\)

- \(2n=14\) - *L.* trigona and *L.* cardinalis
- \(2n=28\) - *L.* nicotianaeformis and *L.* exoelsa
- \(2n=42\) - *L.* inflata

All species of the genus *Lobelia* investigated in the present study, except for the species *L.* tenuior have shown \(x=7\). This is in agreement with the earlier reports. The
basic number of this appears to be \( n = 7 \), and \( n = 9 \) derived from \( n = 7 \).

Apart from karyotype asymmetry, polyploidy is also associated with diminution of chromosomes (Stebbins 1950, Sharma 1959, Sharma 1974, Dey 1977). The data given in Table 15 clearly support this. The diploid plants have larger chromosomes as compared with tetra- or hexaploids. The size of the chromosome is inversely proportional to the ploidy level.

Variations in Chromosome Numbers

Somatic cells with different chromosome numbers in the same shoot tip were observed in two horticultural plants, *Campanula latifolia* and *Lobelia cardinalis*. Pankhauser (1945) explains such random occurrence of variations in chromosome number as "chromosome mosaic". It has been reported in many plants, mostly in vegetatively propagated plants like *Eucharis grandiflora* and *Hippeastrum rutilum* (Sato 1942), *Hymenocallis gelathium* (Snood 1955), *Lilium* (Kato 1955), *Caledium bicolor*, *Zephyranthes mezochloea*, *Hymenocallis* sp., and *Hymenocallis* sp. (Sharma 1956), *Orpinus* and *Neananthus* (Sharma & Sharma 1956), *Helix* (Hagwood & Hough 1953), *Achillea* (Ehrendorfer 1959), *wheat* (Swaminathan &
The variation in chromosome number is more common in the hexaploid Campanula latifolia than in the diploid Lobelia cardinalis. Other polyploids in which this phenomenon has been reported are: Rubus 6x, 7x and 8x (Britton & Hull 1957), tetraploid Amaryllis (Khoshoo & Frakolah Narain 1967), the tetraploid hybrid Pennisetum typhoides (Pantulu & Narasimha Rao 1977) and polyploid hybrid roses (Sahare & Shetry 1963). Other hybrids which exhibit chromosomal numeric mosaicism are: Oenothera hybrids (Kenzel & Brown 1952, Sarveela 1959) and Solanum nigrum complex (Fuku moto 1962, Venkateswarulu & Krishna Rao 1969). Of the twelve metaphase plates examined during the present study in the shoot tip tissue of Campanula latifolia, there were ten cells with $2n=102$ and two cells with $2n=85$, a relatively low frequency of abnormal numbers as compared with the normal ones. A similar situation has been observed in Calendula bicolor by Sharma (1956), in Lobelia terminalis (Bhattacharyya 1972) and in Coleus variegatus (Gokhale 1981, Chennaveeriah 1983). It may be noted that the number $2n=85$ is a multiple of the basic chromosome number of
C. latifolia. Such somatic cells with different chromosome numbers in multiples of the basic chromosome number has been reported by Sharma (1956) in Zephyranthes mengchloa. In Lobelia cardinalis too, the normal cells had $2n=14$ and cells showing variation $2n=7$.

Explanations given by several authors for the existence of this phenomenon are - hybridity per se (Love 1953), incompatible gene combinations (Smith 1955), spindle abnormalities in hybrids (Tantalu & Harasimow Reo 1977), diploid and tetraploid hybrids in Viola (Gold & Serness 1934), spindle deformities in the Festuca - Lolium hybrid (Darlington & Thomas 1937), faulty spindle formation (Ehrendorfer 1961), disturbances in cytokinesis (Sarvella 1958), meiotic irregularities (Ehrendorfer 1959) and a tendency to revert to diploid level in successive generations (Gottschalk 1959).

It might be stated in the light of the present investigation that Campanula latifolia and Lobelia cardinalis being ornamental plants, initial hybridisation may be the cause of the variation in chromosome numbers. There were no spindle abnormalities either in mitosis or in meiosis in C. latifolia. The meiotic divisions were very regular. A few mitotic irregularities, however, were noted in L. cardinalis.
This phenomenon has been observed mainly in vegetatively propagated plants, evidently providing a method of speciation in addition to sexual reproduction (Sharma & Sharma 1956). The two plants investigated show vegetative propagation too, and the variation in chromosome numbers may result in the formation of new species or varieties. Codiaeum variegatum is another vegetatively propagated horticultural plant which exhibits variation in chromosome numbers in somatic cells. When raised by seeds, the plant produces different phenotypes leading to the production of a number of varieties from a single plant (Chennavasiriah 1983).

Other Mitotic Irregularities

The present investigation showed up some other anomalies of Lobelia cardinalis in the dividing mitotic cells such as mitotic anaphase with stickiness (Fig. 85) and laggards (Fig. 86). Van and Grant (1967) had observed such anomalies in Viola faba, induced in somatic cells by use of pesticides. It is possible that Lobelia cardinalis being a garden plant, the use of pesticides had the same effect there too. Bose and Benerjee (1968) have reported such somatic anaphasic bridge in tomato plants treated by X-rays and colchicine.
Structural Variations

Earlier reports on meiosis are very few. Gairdner and Darlington (1931) and Darlington and Gairdner (1937), recognized translocation in *Campanula persicifolia* by the presence of rings or chains of chromosomes at meiosis. In addition, a large number of structural hybridity obtained by crossing plants of *C. persicifolia* from different geographic regions, 'floating' translocation heterozygotes in the cross fertilized population, and semisterile hybrids between individuals of the same species in *Campanula* were recorded by Darlington and Gairdner (1937); Darlington and LeCoomer (1950).

Normal meiosis was observed in most of the species of *Lobelia* (Bowden 1959a, b, 1960a, b) and in *Campanula rotundifolia* (Hibbec 1961). Presence of multivalents and bridges due to stickiness in *C. rotundifolia* (Böcher 1963) laggards in anaphase I and telophase II, and micronuclei in *C. arvensis* (Demboldt 1966) have been reported.

In the present study many meiotic abnormalities were noticed mostly in the members of the family Lobeliaceae, and to a certain extent in *Genus *Lobelia*. Various irregularities like multinucleolate diakinetic cells, presence of multivalents, secondary association and clumping,
stickiness, precociousness in metaphase I and II, multipolar spindles, micronuclei, microspores, polypory etc. were noted.

Multinucleolated diakinetic cells were seen in *Campanula medium* (Figs. 5 & 9), *Lobelia trigona* (Fig. 76), *L. cardinalis* (Fig. 89), and *L. excelsa* (Figs. 186-188). Except *L. excelsa*, a tetraploid, others are diploids. Pandita and Mehra (1981) observed that the number of nucleoli were high in desynaptic tetraploids of *Allium*. In the taxa investigated here, perhaps they represent the degenerating nucleolus of the diakinetic cell.

The formation of rod bivalents in *Lobelia cardinalis* (Fig. 88) in contrast to the formation of ring bivalents in the other species of *Lobelia*, is an indication that the species has more homologous chromosomes than homologous chromosomes, which may be the result of outcrossing and structural alterations in its chromosomes. This reduces the chiasma frequency which is often seen in many of the outcrossing species; this is further corroborated by the asymmetric karyotype of *L. cardinalis* falling under group 2A of Stebbins (1971) classification (Table 16).

Chromosomal aberrations like presence of multivalents, a common occurrence in many polyploid plants, was seen in the diploid *Lobelia trigona* where 4 bivalents forming a
ring (Fig. 74) and a close association of 4 (Fig. 75) and 3 chromosomes (Fig. 76) were noted. This perhaps is the cause of stickiness exhibited by a few cells in anaphase I (Figs. 79 & 80). Such multivalents were observed in a diploid Solanum melongena (Choudhuri, 1975). Darlington (1929) reporting the presence of multivalents in a diploid Rhaga, explained that it may indicate the presence of translocation heterozygotes. The presence of ring formations in L. trigona is perhaps also due to translocations.

In Lobelia inflata, a hexaploid, 3-4 bivalents formed a ring (Fig. 104) or a chain (Fig. 105), an indication of its polyploid nature. Such chain bivalents at metaphase I were seen in Triticum aestivum by Kempenna and Riley (1964) who explain that these abnormalities suggest translocations. Due to multivalency there is a slight disorientation in further divisions which results in laggards (Fig. 109), formation of microspores (Fig. 110) and polysporo (Fig. 111). This evidently affects the viability for though 92% of the pollen was fertile, only 51% was viable (Table 17). Thus here too, multivalent formation is correlated with sterility, as reported by Vida (1970) in Asplenium.

Secondary association:

The grouping of bivalents at meiotic metaphase which is spoken of as secondary association is interpreted to
reveal ancestral homology. This has been observed in *Campanula medium* (Figs. 5 & 7), *Lobelia nicotiannefolia* (Fig. 128) and *Rosavala kypistii* (Fig. 252). Clumping, which is also an indication of secondary association was clearly evident in *L. nicotiannefolia*. The number of the chromosomes involved was variable and inconsistent resulting in a few and in extreme cases one mass of chromosomes (Figs. 129-132, 134-137) or a ring (Fig. 164). Attraction between genetically and structurally similar chromosomes was thought to be the cause of the secondary association (Darlington & Moffett 1930, Lawrence 1931). Heilborn (1936) believed secondary association to be an artefact. According to Stebbins (1950), secondary association can be considered as suggesting the polyploid nature of the species. Kemp and Riley (1964) by their observation in *Arctium senitum*, a hexaploid explain that it may result when homologous and homeologous chromosomes are attracted together at meiotic prophase.

Secondary association is said to be an inherent characteristic of allopolyploid plants (Lawrence 1929) and is reported in tetraploid Dahlia (Singh & Roy, 1973), in members of tribe Cichorieae (Remann & Mehra, 1974), *Neuithena leavio* (Mehra & Sharan, 1975) and in X-ray and Colchicine treated tomato plants (Dose & Banerjee, 1963).
The secondary association of chromosomes in the diploid *Q. medium* and *Scevola kornicola* may be due to structurally similar chromosomes in a hybrid and due to polyploidy in *L. nictianasfolia*. Chromosome bridges (Figs. 162, 163), telophase bridge (Fig. 166), varying number of chromosome groups and formation of micronuclei (Figs. 167-169) perhaps can be attributed to the clumping and stickiness of the chromosomes.

**Spindle abnormalities:** Spindle abnormalities like irregular multipolar, miniature, truncated and split spindles occur in cells, especially in those with polyploid and aneuploid number of chromosomes under abnormal conditions (Lettre and Lettre, 1959). Their occurrences in normal cells under the influence of certain substances were reported by Barthelmesse (1957). Spindle abnormalities are known to occur in many plants – in *Ribes* (Vaarama 1949), in *Saccharum* (Parthasarathy, 1951, Alexander 1969) etc.

In *Campanula medium*, tripolar configuration, perhaps due to the failure of spindle mechanism results in three irregularly distributed groups of chromosomes (Fig. 18). This may lead to the formation of triads, which were quite frequent in the plant. The spindle abnormalities result in irregular distribution of chromosomes in anaphase (Fig. 8),
laggards in telophase I (Figs. 8 and 11), enaphase II and
telophase II (Figs. 13-17) resulting in the formation of
micronuclei (Figs. 12, 16 & 17). Such tripolar spindles
were observed in Rubus hybrids (Vaarama 1953), Artemisia
maritima (Kaul 1965) and Aceratum comyoides (Kaul, 1974).
Distinct tripolar nuclei were observed in telophase I in
aesculea kosmici (Fig. 266), Lobaria nicotianae folia
(Figs. 170-172) and L. exsulca (Fig. 205).

Multipolar spindles are reported in Seccharum
spontaneum (Mehra & Sooda, 1974), in root tips of Allium cope
when treated with algal extracts, especially of Chlorophyceae
(Chamea & Gupta, 1959), in Clarkia exilis (Veen, 1962),
Triticale (Yamagata et al., 1977). Incomplete
splitting of the spindle was observed in Bromus hybrid (Walters, 1958). Both multipolar and split spindles were
seen in L. nicotianae folia (Figs. 170-172 and 176) which
perhaps are responsible for the formation of 5 spores in a
tetrad (Fig. 175), spores of unequal size (Fig. 181),
polygyropy (Figs. 182, 183), 1-4 disintegrating nuclei
(Figs. 178-180), laggards (Fig. 147) and micronuclei (Figs.
167-169). Polygyropy like pentads and hexads due to multiple
spindles are also reported in Durum wheat (Bozaini & Martini, 1971).
Stickiness, bridges, non-disjunction and multipolar spindle, evidently hinder the separation and free movement of the chromosomes in the spindle fibres, leading to irregularities with regard to chromosome separation and distribution, formation of micronuclei etc. in Campanula medium, Lobelia nicotianae folia and Senecio konigii.

Cytomixis

Cytomixis as defined by Gates (1911) is the transfusion of chromatin material from the nucleus of one pollen-mother cell into the adjacent pollen mother cell. This phenomenon was first observed by Digby (1909) in Saltonia odoratissima and ever since has been reported in a number of plants belonging to different families of angiosperms. It occurs in PMCs, meristematic and somatic tissues. Bocher (1937) reports of frequent occurrence of cytomixis in Campanula rotundifolia.

The phenomenon of cytomixis is explained as an artefact of preparation (Woodworth, 1931, Gelin, 1934). Finding cytomixis restricted to genetically unbalanced types like haploids, triploids hybrids etc., Loven (1941) explained it as occurring in plants showing irregular physiological or cytological behaviour. Linhart (1955) observing it limited to the early stages of the first
meiotic prophase in different species of *Salvia*, concluded that it is due to the action of the fixative. Rybom (1946) finding it in a tetraploid pot plant of *Primula malacoides* grown in a room, felt the cause to be the unfavourable climatic conditions. The "furious" cytomixis during prophase is considered as an abnormality caused by pathological changes of the physiological conditions of the cells (Vaerama 1941). Mechanical injury, as shown in root apex of *Allium* may also cause cytomixis (Bowes, 1973).

In the present investigation, cytomixis was observed in different members of Lobelioseae - *L. tenuior*, *L. nicotianaefolia* and *Isotoma longiflora*, and in the genus *Scaevola* of the Goodeniaceae. Only a few isolated cells showed cytomixis in *L. tenuior* in the diakinetic stage (Fig. 100) and of the clumped chromosomes in *L. nicotianaefolia* (1) (Fig. 133) in metaphase I. But it was quite pronounced in *Isotoma* and *Scaevola* (Figs. 238-243 & 254-259).

Cytomixis at and after pachytene was observed by Mendez and Rijjo (1951), Kamara (1950), Sadasiviah and Magoon (1969), Habib and Chattamurugan (1976), Lakshmi and Rao (1977); as late as second tetraphere (Prakash 1979) and in all stages of microsporogenesis (Gottschohl, 1970), who observed it in radiation induced mutants of *Pisum sativum*. 
He opines that the phenomenon cannot be interpreted as a pathological one, supporting the view of Sarvella (1958) and Baquar and Hussin (1969).

The earlier stages of meiotic prophase were considered to be specially favourable for the origin of cytomixis (Levan, 1941). Heslop-Harrison (1966) mentions about the initiation of cytomictic channels in the pro-leptotene period and formation of massive cytoplasmic connections between pollen mother cells in the anthers of several species of angiosperms. In *Scaevola*, such cytoplasmic connections between meiocytes was observed in very early stages of prophase and cytomixis was observed from early leptotene to telophase II (Figs. 254–259) and in *Isotoma* from diakiniese to metaphase II (Figs. 236–243). A group of more than twelve cells may be involved in *Scaevola* and a single cell may be connected through cytoplasmic bridges with 1–4 cells at a time (Figs. 257 & 259). Thus the chromosomes moving in different directions result in some cells becoming enucleate (Figs. 256 & 257) and some with unequal groupings of chromosomes. This is reflected in increase number of chromosomes in meiotic cells and irregularities like unequal separation (Figs. 262 & 263), tripolar configuration and polyspores (Figs. 265–268). In *Isotoma*, irregular grouping
of chromosomes (Fig. 227), nondisjunction and unequal separations are seen (Figs. 231 & 232), resulting in different chromosome numbers in the meiotic cells (Figs. 236 & 237). Such variable chromosomal numbers in RHG's are reported by Löve (1944), Sarvalla (1958), Nybom (1946) and Lakshmi & VeeraRagavaiH (1951). Unequal separation, laggards, non-disjunction, scattering of chromosomes, micronuclei in spores have been reported by Lakshmi and VeeraRagavaiah (1951), stickiness and abnormal shapes of pollen by Nybom (1946). In the present study, malformed pollen grains were noted both in Leptosa and Secyola. Hede (1957) feels cytomixis to be the cause of formation of dwarf pollen grains observed in \textit{Campanula rotundifolia}. Such irregularities may lead to sterility as reported by Upcott (1939), of the formation of a genetically male sterile plant in \textit{Lathyrus odoratus}.

In \textit{Trigonella} (Lakshmi and VeeraRagavaiah, 1951), find cytomixis both in fixed and unfixed material, proving that it is not an artefact due to fixation. In \textit{Boechera alpina}, it appears to be a constant aspect of meiosis (Schnick and Fehlisen, 1957). Hence, it can be considered as a normal, but infrequent cytological phenomenon. In the present investigation too, both the wild and cultivated plants of
Scaevola exhibit this phenomenon, disproving that it is an artefact or caused by the unfavourable climatic conditions. It seems reasonable to conclude that at least in Scaevola it is inherent, a natural phenomenon under genetic control.

The variations in the chromosome number in PMC observed in Scaevola (Figs. 262-264) and also reported by others, may lead to the formation of aneuploid gametes. This of course, may play a significant role in bringing about evolutionary divergence and could be an important factor in creating spontaneous variation (Jakshmi & Veera Raghebiv, 1981). However, both Lectome and Scaevola, presently investigated show a high percentage of fertility and viability indicating that the genetically unbalanced pollen grains do not survive. This perhaps explains the presence of malformed pollen grains in these two taxa.

Of the five plants investigated of family Campanulaceae, only Centaurea showed irregularities like multinucleolate condition, secondary association, unequal separation in anaphase I resulting in one large and one small micronuclei, laggards in telophase I & II and anaphase II, resulting in the formation of many micronuclei, failure of spindle mechanism and groupings of chromosomes in threes, later perhaps resulting in trisomes. Being an ornamental plant
with large showy flowers, continuous crossings for new varieties, might have resulted in such irregularities due to the presence of incompatible chromosomes. The fertility test, however, revealed a high percentage of fertile pollen grains, nearly 99%, indicating the loss of micronuclei before tetrad formation, but a low percentage of viability, only 6% was noted (Table 17).

The other taxon, O. latifolia, a hexaploid, surprisingly for the large number of chromosomes involved, showed a very normal meiotic division, resulting in normal tetrads. Though 99% of the pollen grains were fertile, the viability was 21% higher than that of O. medium (Table 17). This and a comparison of the karyotypes of the two species of O. medium and O. latifolia (Table 15), the difference especially in their floral morphology, and the absence of multivalents in O. latifolia indicate that this species is an allopolyploid.

Both U. marginata (1) a hexaploid with 2 bivalents attached to the nucleolus and U. marginata (2) an octoploid, with 4-6 bivalents attached to the nucleolus, showed normal reductional division, except for the presence of one or two micronuclei in U. marginata (1), which was eventually lost. Even in the octoploid, it was regular except for early disjunction of some bivalents in anaphase I, precociousness
91

in metaphase I, and early and late disjunction of chromosomes in anaphase I. The fact that even the high level of ploidy has not affected the meiotic divisions, strongly favours the conclusion that these two wild growing plants are allopolyploids. Pollen fertility was nearly 99% in both (Table 17).

In Sphenoclea too, except for the laggards in anaphase I and II and late disjunction of some chromosome in anaphase I, which are of no consequence, meiotic divisions proceeded normally resulting in normal tetrads. The same has been reported by Shattacharyya (1972). This plant seems to be an allopolyploid.

All the above four plants show normal meiosis which indicates that they are stable species. They also have a high percentage of pollen fertility. It is difficult to comment upon the viability, since all the five taxa of the Campanulaceae showed a uniform poor or no response to germination in 4% sucrose solution (Table 17).

Most of the irregularities, however, were noted in the members of the families, Lobelioeae, (Lobelia and Sectoma) and in Genyole of Goodeniaceae. Various abnormalities include multivalents, secondary association, abnormal spindle
types, cytomixis, stickiness, chromosome bridges, non-
disjunction, precociousness, unequal separation of 
chromosomes at second division, micronuclei, microspores, 
and polypory. Non-congression of some chromosomes at 
the equatorial region, bivalents moved away from the group 
at metaphase I (Figs. 190-193), laggards in anaphase II 
(Fig. 196), irregularities in anaphase I & II, metaphase II 
(Figs. 197-204), formation of a thin chromatin bridge in 
metaphase II (Fig. 203) and telophase II with unequal sized 
nuclei were seen in Lobelia escelsa.

In spite of the above mentioned abnormalities the 
pollen fertility was in the range of 91-97% in Ipomoea, 
Scaevola and all the species of Lobelia except L.cardinalis 
which showed a low percentage of fertility (Table 17).
Only the diakinetic stages could be studied in L.cardinalis 
hence it is not possible to comment on the low fertility 
of pollen grains. The viability test revealed only 29% of 
the pollen grains as viable. This indicates that the 
irregularities in the reductive divisions, might have 
resulted in genetically unbalanced pollen grains. Similarly 
L.nicollianaefolia (1) shows only 63% fertile pollen grains 
and 56% viability (Table 17). The clumping of the chromo-
some may be responsible for this.
The high meiotic instability exhibited by the above genera does not seem to affect the reproduction of the plants to a large extent, since many of them show vegetative propagation, e.g. *Lobelia cardinalis* and *L. nicotianaefolia*. *Lobelia cardinalis* can be propagated by transplanting the stem with basal rosettes of leaves (Simonet 1947). In *Lobelia nicotianaefolia*, suckers arise from the base of the axis and roots. Even in *Senecio*, the vegetative propagation is seen in the low spreading branches. In addition, the pachycaulous *Lobelia* have large inflorescences with numerous flowers. Each five fertile anthers of a single flower produces a large quantity of pollen grains. Seed setting is especially good in *Lobelia nicotianaefolia* and *Isotoma longiflora*.

**Pollen grains**


Chromosome number, pollen type, size, fertility and viability in the different taxa investigated are listed in Table-17.
All the species of *Lobelia* investigated, *Iuctome longiflora* and *Scaevola koenigii* have 5-colporate pollen grains. This agrees with the reports of Avetisjan (1967), Chapman (1967) and Dunbar (1975b). *Sphenoclea azlanica* has tricolporate, small sized pollen grains. This has been reported by others (Erdtman 1952, Chapman 1967, Avetisjan 1967 and Dunbar 1975b).

*Campanula medium* has 5-4 porate pollen grains with epinuliferous exine which tallies with the findings of Avetisjan (1967). Dunbar (1975a) reports 3-porate pollen grains in this species. *C.latifolia* has 4-5 porate pollen grains with a smooth exine. Though a hexaploid, this has smaller sized pollen grains than that of the diploid *C.medium* (Table 17). Perhaps, a correlation between the size of the pollen grains and ploidy cannot be found here, as the two taxa, though belonging to the same section, are included under two separate subsections based on the number of carpels. Moreover, Gedella (1964) points out that *Campanula* species with 2n=34 are heterogeneous with respect to the size of the pollen grains. In some of the species belonging to the X=10, series, *C.abietina*, an octoploid, has pollen size more or less equal to that of the diploid *C.porruculata*. In *C.pollina*, the pollen grains of the
diploid species are larger than the tetraploid ones. However, correlation between degree of polyploidy and size of the pollen grains has been noted in x=8 series, only diploids and tetraploids of x=10, and in C. rotundifolia.

The two cytotypes of Wahlenbergia marginata, considered to be the same species, differ to a certain extent in their floral morphology. The pollen grains of these two taxa do show a correlation between the size of the pollen grains and ploidy level, but W. marginata (1) has 3-porate pollen grains and W. marginata (2) has distinct 4-porate pollen grains. Dunbar (1975a) reports 3-porate pollen grains in ten species of Wahlenbergia, 3(-5) porate in W. madagascariensis, and (3)-4(5) or 3-porate in W. uppendulina. It is interesting to note that W. marginata (2) and Campanula latifolia have tetraporate pollen grains (Table 17). Both show some similarities in floral morphology like campanulate corolla, 5 free anthers and inferior trilocular ovary. Dunbar (1975b, 1979) observed a closer relationship in the sexine pattern between some species of Wahlenbergia and that of Campanula like C. americana.
<table>
<thead>
<tr>
<th>Taxa</th>
<th>Diploid number</th>
<th>Type as observed under light microscope with or without coloration</th>
<th>Size of pollen grains (μm)</th>
<th>Percent of fertile pollen</th>
<th>Viability of pollen grains in 4% sucrose solution</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Campanula medium L.</td>
<td>2n=34</td>
<td>Trisporate or tetraporate oxine spinuliferous</td>
<td>39.6-56.1</td>
<td>95%</td>
<td>6-6%</td>
</tr>
<tr>
<td>2. C. latifolia L.</td>
<td>2n=102</td>
<td>Tetra or pentaporate</td>
<td>33-44.0</td>
<td>99%</td>
<td>21%</td>
</tr>
<tr>
<td>3. Wallenberga mericincta (Thunb.) A. DC. (1)</td>
<td>2n=54</td>
<td>Tricollporate</td>
<td>31.9-38.5</td>
<td>93%</td>
<td>No response</td>
</tr>
<tr>
<td>4. W. mericincta (Thunb.) A. DC. (2)</td>
<td>2n=72</td>
<td>Tetraporate</td>
<td>37.4-44.0</td>
<td>97.9%</td>
<td>No response</td>
</tr>
<tr>
<td>5. Sphenoclea zeylanica Gaertn.</td>
<td>2n=42</td>
<td>Tricollporate</td>
<td>14.3-17.6</td>
<td>96-97%</td>
<td>No response</td>
</tr>
<tr>
<td>6. Lobelia trigona Roxb.</td>
<td>2n=14</td>
<td>Tricollporate</td>
<td>20.9-33</td>
<td>97%</td>
<td>94%</td>
</tr>
<tr>
<td>7. L. cardinalis L.</td>
<td>2n=14</td>
<td>Tricollporate</td>
<td>20.9-35.2</td>
<td>31%</td>
<td>71%</td>
</tr>
<tr>
<td>8. L. tenue L.</td>
<td>2n=18</td>
<td>Tricollporate</td>
<td>34.1-50.6</td>
<td>20.94%</td>
<td>84%</td>
</tr>
<tr>
<td>9. L. inflata L.</td>
<td>2n=42</td>
<td>Tricollporate</td>
<td>22.0-38.5</td>
<td>92%</td>
<td>51%</td>
</tr>
<tr>
<td>10. L. mononotona eucalyptoides Hayne</td>
<td>2n=28</td>
<td>Tricollporate</td>
<td>22-33</td>
<td>63%</td>
<td>56%</td>
</tr>
<tr>
<td>11. L. excelens Lesch.</td>
<td>2n=28</td>
<td>Tricollporate</td>
<td>27.5-34.1</td>
<td>97.1%</td>
<td>20%</td>
</tr>
<tr>
<td>12. Isotoma longiflora Presl.</td>
<td>2n=28</td>
<td>Tricollporate</td>
<td>38.5-46.2</td>
<td>99%</td>
<td>94%</td>
</tr>
<tr>
<td>13. Sesovale koenigii Vahl.</td>
<td>2n=16</td>
<td>Tricollporate</td>
<td>37.4-61.6</td>
<td>94%</td>
<td>86%</td>
</tr>
</tbody>
</table>