GENERAL DISCUSSION
It is believed that the family Brassicaceae has had its origin in the Mediterranean region with its taxa subsequently migrating to different parts of the world. Mediterranean region is not only rich in brassicaceous flora but it is here that maximum diversity is encountered in this family.

In the Indian subcontinent, the climate of Himalayan and sub-Himalayan regions is suitable for various taxa of this family. As a result of this, maximum number of species of this family are found in this part of our country. Table No. 38 (page 114) gives a general idea about the distribution pattern with particular reference to the genera included in the present study.
Table No. 38: Distribution and number of species of 11 genera of Brassicaceae included in the present study.
(Source: Hooker, 1872; Darlington and Wylie, 1955; Jafri, 1973; Naqshi, 1977; Present work)

<table>
<thead>
<tr>
<th>Genus</th>
<th>Total no. of species</th>
<th>Distribution in</th>
<th>India</th>
<th>Kashmir</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>in India</td>
<td>in Kashmir</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chorispora</td>
<td>10/3/3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Matthiola</td>
<td>60/3/2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tetracme</td>
<td>7/1/1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cheiranthus</td>
<td>12/5/1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Erysimum</td>
<td>100/9/5</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**TRIBE MATTHIOLEAE**

- **Chorispora**: 10/3/3
  - Distribution:
    - Caucasia, Western Asia, Himalaya, North China
  - Present in India:
    - Punjab, Kashmir
  - Present in Kashmir:
    - Meenamarg, Srinagar, Sheashnag, Kishenganga, Zanskar, Chenab valley, Sonamarg

- **Matthiola**: 60/3/2
  - Distribution:
    - Mediterranean region, Arabian
    - North India (M. incana & M. tristis are cultivated)
  - Present in India:
    - Srinagar, Ladakh
  - Present in Kashmir:
    - Ladakh

- **Tetracme**: 7/1/1
  - Distribution:
    - Central and Western Asia
  - Present in India:
    - Ladakh
  - Present in Kashmir:
    - Ladakh

**TRIBE HESPERIDEAE**

- **Cheiranthus**: 12/5/1
  - Distribution:
    - Temperate Europe, N. Africa, W. Asia, Arctic America, Canary Islands
  - Present in India:
    - Spiti, Zanskar
    - Single species (C. cheiri cultivated)
  - Present in Kashmir:
    - Baramulla, Pahalgam, Sarbal, Sonamarg, Srinagar, Harwan, Gulmarg, Lidderwat,
Table No. 38 (continued)

<table>
<thead>
<tr>
<th>Genus</th>
<th>Total no. of species in Kashmir</th>
<th>World</th>
<th>Distribution in India</th>
<th>Kashmir</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Goldbachia</em></td>
<td>2/1/1</td>
<td>Asia Minor, West to South Russia, Himalayas</td>
<td>Kashmir, Ladakh</td>
<td>Srinagar, Kharbu</td>
</tr>
<tr>
<td><em>Hesperia</em></td>
<td>30/1/1</td>
<td>Asia Minor, Greece, Central Europe, Japan, Western and Central Asia</td>
<td>Kashmir</td>
<td>Srinagar, Pahalgam</td>
</tr>
</tbody>
</table>

**TRIBE SISYMBRIEAE**

<table>
<thead>
<tr>
<th>Genus</th>
<th>Total no. of species in Kashmir</th>
<th>World</th>
<th>Distribution in India</th>
<th>Kashmir</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Alliaria</em></td>
<td>2/1/1</td>
<td>Europe, N. Africa, Caucasus, Himalaya</td>
<td>Kumaon to Kashmir</td>
<td>Srinagar</td>
</tr>
<tr>
<td><em>Arabidopsis</em></td>
<td>15/6/6</td>
<td>Temperate Asia, N. Africa, N. Europe, S. U. Asia</td>
<td>Entire Himalayas</td>
<td>Kashmir, Ladakh, Gurez</td>
</tr>
<tr>
<td><em>Descuriania</em></td>
<td>40/1/1</td>
<td>North America, U.S.A., Mexico, Japan, Arctic Urals</td>
<td>Temperate Himalayas, from Kumaon to Kashmir</td>
<td>Srinagar, Himis</td>
</tr>
<tr>
<td><em>Sisymbrium</em></td>
<td>70/18/4</td>
<td>Europe, West Asia, N. Africa, Mediterranean</td>
<td>Temperate Himalaya, Sikkim to Kashmir</td>
<td>Wide spread in Kashmir valley, Pahalgam, Ladakh</td>
</tr>
</tbody>
</table>


Taxonomy

Despite the fact that the plants of this family are easily identifiable by the tetradynamous conditions of stamens and cruciform corolla, the taxonomic treatment of this family has had a torturous history. The major reason for this is that the family is very large. The controversies regarding its phyletic position in angiosperms persist till date. While Bentham and Hooker (1862-67) and Hutchinson (1948) were of the view that this family has evolved from papaveraceous ancestors, Cronquist (1968) is of the opinion that Brassicaceae has evolved from capparidaceous ancestors. The morphology and anatomy of androecium and gynaecium, however, seem to support the latter view (Laurence, 1967).

Like the controversies about the phyletic position of this family, groupings of its innumerable genera and species into various tribes have also posed problems. Since the time of Linnaeus (1753), many workers have classified this family into different number of tribes following their own reasonings. History of nomenclature of this assemblage and groupings within this family as given by various taxonomists at different times has been summed up on page 117.

De Jussieu (1789) was the first taxonomist to coin
Linnaeus (1753)
Class: Tetradyndamia (on the basis of unique androecium characters)  - divided into 2 orders

De Jussieu (1789) coined the name Cruciferae

Lindley (1830) gave the name Brassicaceae to this family

C. Haraaninov (1847) proposed the name Raphanaceae for this family

Bentham & Hooker (1862 - 1867)
Characters: Mode of dehiscence of pods and relative position of the radicle and cotyledons  - divided the family into 5 series

Hayek (1911)
Characters: Form and distribution of nectaries  - divided into 9 tribes

Schulz (1936)
All the characters considered by his predecessors  - divided into 19 tribes

Janchen (1942)
Modified Hayek's (1911) classification  - divided into 15 tribes

History of nomenclature and classification of Brassicaceae

* c.f. Lawrence (1967)
the term "Cruciferae" on the basis of cruciform corolla of the taxa of this family. However, earlier to that Linnaeus (1753) grouped the taxa with a peculiar tetrudynamous condition of stamens under class "Tetrudynamia". Since, according to International Code of Botanical Nomenclature, the name of a family should end with the epithet 'aceae' which was not the case with 'Cruciferae' the taxonomists were made to choose from the names Brassicaceae (Lindley, 1830) and Raphanaceae (Haraninov, 1847 c.f. Lawrence, 1967) based on the type genera Brassica and Raphanus respectively. The term Brassicaceae, because it was proposed earlier than the other name, was retained and continues to be so.

Among all the classifications given for this family, by different workers, that of Schulz (1936) is the most accepted one. This is so because this classification takes into account many characters, while those given by other workers are based on one or two characters only. In a large and homogenous family such as Brassicaceae, one cannot depend on one or two characters only for delimiting different groups.

The 19 tribes as delimited by Schulz (1936) are:

Pringleae, Stanleyeae, Romanschulzieae, Streptantheae, Cromolobeae, Chamireae, Brassiceae, Heliophileae, Schizopetalaeae, Lepidieae, Enclidiaceae, Stenopetalaeae,
Alysseae, Lunariaee, Drabeae, Arabideae, Matthiolaeae, Hesperideae and Sisymbrieae.

Schulz (1936) while giving this classification for Brassicaceae opined that Pringleee forms the basic stock for all other tribes included in this family with Sisymbrieae as the most advanced one. Mukerjee (1975) while accepting the groupings of Schulz (1936) for taxonomic purposes, disagrees, on the basis of chromosome morphology, on the relationships between these tribes as proposed by the latter.

Out of the 19 tribes of this family only 9 are represented in the Kashmir valley and adjoining areas (Naqshi, 1977). These are: Brassiceae, Lapidieae, Euclidieae, Alysseae, Drabeae, Arabideae, Matthiolaeae, Hesperideae and Sisymbrieae.

Using only two characters namely fruit variation and base numbers, Naqshi (1977) while studying the taxonomy of brassicaceous flora of this region outlined the relationship between these 9 tribes (page 120).

He (Naqshi, 1977) is of the opinion that Brassiceae due to great diversity in fruit characters and variation in base numbers apparently represents the basic stock with Sisymbrieae as the most advanced one.
Phyletic position of 7 tribes of Brassicaceae as given by Naqshi (1977)

\[ x = \text{Base numbers as given by Naqshi (1977)} \]

\[ *x = \text{Actual base numbers present} \]

\[ \text{MCL} = \text{Range of mean chromat length in the taxa studied} \]

Siyembrisae
\[ x = 7, 8 \]
\[ *x = 3, 5 - 11, 20 \]
\[ \text{MCL} = 1.08 - 1.8 \text{ um} \]

Hesperideae
\[ x = 7 \]
\[ *x = 6 - 10, 12, 13 \]
\[ \text{MCL} = 1.2 - 5.73 \text{ um} \]

Matthioleae
\[ x = 7 \]
\[ *x = 6, 7, 8 \]
\[ \text{MCL} = 2.08 - 3.8 \text{ um} \]

Oroideae
\[ x = 7, 8 \]
\[ *x = 5 - 9 \]
\[ \text{MCL} = 1.4 - 2.08 \text{ um} \]

Euclidieae
\[ x = 7 \]
\[ *x = 7, 12 \]

Lepidieae
\[ x = 7, 8 \]
\[ *x = 4 - 12 \]
\[ \text{MCL} = 1.9 - 5.5 \text{ um} \]

Brassicaceae
\[ x = 8, 9, 10 (11, 12, 13) \]
\[ *x = 6 - 12 (15, 17, 18, 19) \]
\[ \text{MCL} = 0.4 - 3.3 \text{ um} \]

Arabideae
\[ x = 7, 8 \]
\[ *x = 6 - 8, 11, 15 \]
\[ \text{MCL} = 0.9 - 1.7 \text{ um} \]

Alyssaceae
\[ x = 8 \]
\[ *x = 6 - 8 \]
\[ \text{MCL} = 1.24 - 2.9 \text{ um} \]

\[ \text{Phyletic position of 7 tribes of Brassicaceae as given by Naqshi (1977)} \]

\[ x = \text{Base numbers as given by Naqshi (1977)} \]

\[ *x = \text{Actual base numbers present} \]

\[ \text{MCL} = \text{Range of mean chromat length in the taxa studied} \]
However, his (Naqshi, 1977) contention suffers on two accounts:

(i) Although many more base numbers are known in these 9 tribes, Naqshi (1977) has taken recourse to only a few. A great deal of variation in base numbers is found not only in Brassicae but also in Hesperideae and Sisymbrieae.

(ii) The mean chromatin length of the taxa of these tribes also does not seem to favour the view expressed by Naqshi (1977). As is evident from page 120 mean chromatin length shows an increase from Brassicae to Lepidiae, then decrease in Drabeae, followed by a significant increase in Matthioloae and Hesperidea and then again a sudden and abrupt decrease in Sisymbrieae. It is rather inconceivable that chromosome size must have undergone these bumpy and sudden changes.

In view of all this it seems that no definite relationship between these tribes can be drawn on the basis of cytological data. All these changes (shift in base numbers and increase or decrease in the chromosomal size) seem to have occurred in different tribes independently, without having any bearing on or relationships with other tribes. A somewhat similar opinion has also been expressed
Fig. 94: Percentage frequency of various ploidy levels met in family Brassicaceae

Fig. 95: Percentage frequency of various base numbers met in family Brassicaceae
earlier by Mukarjee (1975).

CHROMOSOME NUMBERS

Diploid chromosome numbers in this family range from 6 (Arabidopsis thaliana) to 256 (Dentaria lacinata). Out of 3000 species grouped under this family, chromosome numbers of only 850 (28%) are on record. Fig. 94 sums up the frequency of various ploidy levels met in this family.

As is clear from Fig. 94 there is almost an equal frequency of diploids (57.5%) and polyploids (42.5%) in this family. This indicates that polyploidy has played a vital role in evolution within this family.

In the 21 species studied during the present investigation the chromosome numbers range from $2n = 10$ (Arabidopsis thaliana) to 42 (Sisymbrium brassiciforme). These 21 species are composed of 61.9% diploid, 33.34% tetraploids and a single species (4.76%) turned out to be a hexaploid (inset Fig. 94). As such, even in the present collection, polyploidy is quite frequent.

Although, in the family Brassicaceae the ploidy level reaches as high as 32x (Dentaria lacinata), tetraploids constitute the bulk. This might be due to the failure of the taxa to efficiently bear drastic numerical changes.
One significant point which emerges from Fig. 94 is that as compared to evenploids, the frequency of oddploids is considerably low (4.35%). This low frequency of oddploids can be explained on the basis of:

(i) Brassicaceae comprises mostly herbaceous annual or biennial taxa which propagate by means of seeds only. The sterility of oddploids prevents them from producing seeds and as such they fail to perpetuate.

(ii) Oddploids are not able to stand the competition from evenploids or once oddploids are formed they get converted to evenploids by chromosome doubling.

**Base Numbers**

In all, 13 base numbers (3 - 13, 15 and 20) have been reported in various taxa belonging to family Brassicaceae. In addition, the genus *Brassica* has also three secondary base numbers of 17, 18 and 19. The lowest base number $x = 3$ is known in *Arabidopsis* and the highest $x = 20$ in Camelina (Darlington and Wylie, 1955; Fedorov, 1969).

The frequency of various base numbers met in this family have been presented in Fig. 95.
Although family Brassicaceae exhibits a lot of variation with regard to base numbers, cytotypes based on series 7 and 8 are predominant (67.94%) as compared to the rest. In the present investigation the base numbers ranged from 5 to 10 with 7 as the secondary base number for Erysimum altaicum. The species with \( x = 7 \) and 8 constitute the bulk (71.41%) as compared to the rest (inset Fig. 95) in the family Brassicaceae. This would suggest that either of these two numbers (particularly \( x = 8 \)) is the ancestral base number or there have been different lines of evolution and forms with \( x = 7 \) and 8 must have played a significant role in giving rise to new forms with increased or decreased base numbers. Fig. 95 (inset) reveals that, in Brassicaceae, number of cytotypes with base numbers below 7 and above 8 are considerably low, pointing towards the probability that base numbers below 7 and above 8 are derived ones. It is worth mentioning here that in Brassicaceae there are many diploic or polyploid species. Although this dysploidy has not impaired the specific status of those forms where it is met, all the cytogenetical studies made in this family indicate that changes in the base numbers have played a vital role in the evolution within this family.

**Problem of high base numbers in Brassicaceae**

It is generally considered that base numbers above
12 do not represent primary base numbers and are certainly derived ones (Stebbins, 1971). Despite this the strikingly high base numbers (15 and 20), although very rare in this family, have also been referred to as primary base numbers (Darlington and Wylie, 1955). $x = 15$ has been observed in three genera namely **Crambe**, **Carmamine** and **Leavenworthia** and $x = 20$ in **Camelina**. Out of these, **Crambe** is the only genus where all the species investigated so far are based on $x = 15$ (Fedorov, 1969). **Leavenworthia** is dibasic with $x = 11$ and 15 (Fedorov, 1969). Although species based on $x = 6, 7, 8, 9, 10$ and 12 are also known in **Camelina**, eight species of this genus have $2n = 40$ chromosomes (Fedorov, 1969). In the absence of any report of $2n = 20$ in any of the species of **Camelina**, it has naturally been presumed that 20 is the primary base number for these species.

The situation in **Cardamine** is quite interesting. Although $x = 15$ (apart from 6, 7, 8 and 10) has been reported in this genus, a close scrutiny of available literature reveals that there is no report of any species of this genus whose chromosome count can be safely presumed to be based on $x = 15$. There are reports of cytotypes of **C. palustris** and **C. pratensis** with $2n = 30$ and 60 apart from other chromosomal races. As $x = 10$ is already known in **Cardamine**, it is rather difficult to say
whether these cytotypes (30 and 60) are based on 10 or 15.

In view of the above discussion it is quite apparent that 15 and 20 are quite a high numbers to be considered as primary base numbers and as such represent secondary base numbers only. It seems that either the diploid forms of these cytotypes have got extinct or have not been isolated so far. It is also quite possible that species with "high base numbers" might have originated as a result of crosses between forms with different and lower base numbers followed by chromosome doubling. Such an assumption is not far fetched is clear from the study of various species of Brassica in which secondary base numbers 17, 18 and 19 have evolved as a result of crosses between forms with \( x = 8, 9 \) and 10 (U, 1935; Yarnell, 1956).

As already discussed, 7 and 8 seem to be the ancestral base numbers in this family. From forms with these two numbers, the secondary ones have evolved following two lines (i) ascending or descending dysploidy and (ii) crosses between forms with different base numbers followed by chromosome doubling.

**SOMATIC CHROMOSOMES**

Members of the family Brassicaceae have chromosomes too small to permit detailed analysis. It is not possible in many taxa of this family to study the chromosome
morphology with respect to the position of the centromeres and other landmarks like secondary constrictions and satellites. Because of this reason most of the studies conducted in this family are limited to measuring the chromosome size and calculating the total and mean chromatin lengths. It is only in a few tribes like Lepidieae, Hesperideae and Matthioleae where some species have chromosomes large enough to permit detailed studies.

Of the three tribes included in the present investigation chromosomes of only some species of Matthiola, Tetracone (tribe Matthioleae), Cheiranthus, Erysimum, Hesperis (tribe Hesperideae) and Alliaria (tribe Sisymbrieae) were such that detailed studies could be conducted. In all other species, the chromosomes were too small. In the tribe Sisymbrieae nearly all the species studied had small chromosomes. On the basis of total and mean chromatin length members of this tribe are at the lower limit while Matthioleae is at the other extreme. In the entire family Brassicaceae, on the whole, the smallest chromosome measuring 0.4 μm is known in Crambe hispanica (Sikka and Sharma, 1979) and the largest measuring 9.6 μm has been recorded in Hesperis matronalis (present work). These two species also represent the cases of minimum (1.1 μm) and maximum (5.74 μm) mean chromatin lengths in Brassicaceae.
The small chromosome size in this family has induced cytologists to take up critical pachytene studies for a better understanding of karyotypes in its various taxa. However, this study too is mostly limited to some species of *Brassica* and *Raphanus* only (Kamala, 1976, 1978, 1980). It is so, because of the known limiting factor of high chromosome number in most of the taxa of this family. In such of the taxa where detailed chromosome study is possible the chromosomes are of median, submedian or subterminal types (Mulligan, 1967a, 1967b; Ranzi, 1969; Bhattacharyya, 1974; Dvořák and Dádeková, 1976; Tácíná, 1977, 1978).

In all those taxa of *Brassicaceae* where polyploid cytotypes are also found, the polyploids invariably have less of chromatin material as compared to the diploids. As such the numerical increase in chromosomes is accompanied by a decrease in chromatin length.

*Brassicaceae* is a natural group of taxa where many cytogenetical factors seem to be operating in the process of evolution. Increase in the ploidy level and variation in base numbers are significantly active in giving rise to new forms. Presence of multivalents, bridges and laggards in many species (Sikka, 1940; Khoshoo, 1964; Wills, 1966; Ene, 1971; Bhattacharyya, 1974; Dayal, 1979; Favarger, 1980)
indicate that structural alterations in chromosomes are also active for producing variation which may lead to speciation. Successful inter varietal, specific and generic crosses made or observed (Karpechenko, 1924; U, 1935; Sikka, 1940; Yarnell, 1956; Dass and Nybom, 1967; Ena, 1971; Tokumaeu and Kato, 1980) in this family have clearly established that hybridisation followed by chromosome doubling has also played a vital role in the evolution in this family.

To sum up, all the known cytogenetical factors like changes in base numbers, structural heterozygosity, hybridisation and polyploidy are responsible for evolution and speciation in the family Brassicaceae.