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CYTOGENETICS OF SOME OF THE INDIAN UMBELLIFERS

by

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I. Introduction

The family Umbelliferae is one of the largest families of Angiosperms including innumerable species distributed under different genera occurring in India, both as wild and cultivated forms. Representatives in the hills undoubtedly outnumber those of the plains.

Most of the members of the family are important from the economic point of view. Commonly the family is referred as the "Spices group", for fruits of several plants are raised for spices and condiments. The modified root of *Daucus carota* is valued as the chief source of carotin and hence forms a nutritive vegetable. Among others *Ferula* yields the "asafoetida" of commerce. Parsnip, parsley and celery are used as vegetables. Last but not the least is the medicinal importance of some of the species, specially *Carum* and *Hydrocotyle*, the former in Allopathy while the latter mostly in Homoeopathy.

It is strange that though the members of the family are easily accessible and possess comparatively low number of chromosomes, the data regarding cytogenetical work is rather meagre. (Lindenbein 1932, Maude 1939, Meldris 1930, Ogawa 1929, Tamamschian 1933, Wanscher 1932, Garde & Malheiros-Garde, 1949). It is significant that Winge (1917) also states "no chromosome number has up to the present been given with certainty for the great family Umbelliferae". Some of the members are completely untouched, while discrepancies

are noted even in the data of the worked out members as presented by different authors.

OGAWA (1929) was the first to delve into the cytological studies of a limited number of Umbellifers. His investigations were carried out with the P.M.Cs. and hence present no evidence regarding the morphology of somatic chromosomes. WANSCHER (1931, 1932) made a more detailed investigation and worked out both the somatic and meiotic phases of the plants concerned. WANSCHER's report, taken in conjunction with the figures presented by him do not reveal the chromosome morphology with perfect clarity. It needs mention that both OGAWA and WANSCHER differ regarding the basic number of the family, the former believing in two basic numbers, while the latter in one. WHITAKER (1949) working on the cytology and systematic relationships of the carrot, also refers to the erroneous report regarding the numbers of *Daucus maximus* in WANSCHER's work. As the family represents easily available genera of much economic importance and also in view of the low number of chromosomes in most of the species, whereupon a thorough karyotype could be made, it was thought desirable to make a critical investigation of the Indian members of the family. The scanty literature of such an important family and the discrepancies in the previous observations, further made it advisable to evaluate and rectify the previous records, thus ascertaining its cytogenetics with absolute certainty.

Ten different species distributed under nine different genera have been worked out here, all being representatives of the plains. It has however been planned to carry out a comprehensive study of the hill genera too, later.

II. MATERIALS & METHODS

The materials for the present investigation were obtained from the following species.

1) *Hydrocotyle asiatica* Linn.
2) *Ammi majus* Linn.
3) *Oenanthe benghalensis* Benth.
4) *Coriandrum sativum* Linn.
5) *Peucedanum sowa* Kurz.
6) *Foeniculum vulgare* Gaertn.
7) *Daucus carota* Linn.

8) a. *Carum copticum* Benth.
   b. *Carum roxburghianum* Benth.
9) *Cuminum cyminum* Linn.

Of the above mentioned species *Hydrocotyle asiatica* L. grows as a way-side weed. *Ammi majus* L. is an ornamental plant while *Oenanthe benghalensis* Benth. grows wild, profusely along the muddy banks of jheels and ponds. The rest of the above mentioned species excepting *Daucus carota* L. which is used as a vegetable, are used as spices and condiments. All these species excepting *Hydrocotyle*, are winter flowering annuals save carrot, which is a biennial.

Methods:

For the study of the somatic chromosomes, seeds of *Coriandrum sativum*, *Peucedanum sowa*, *Foeniculum vulgare*, *Daucus carota*, *Carum copticum*, *Carum roxburghianum* and *Cuminum cyminum*, were obtained from the local markets, and grown in the University Botanical gardens, Calcutta, while seeds of *Ammi majus* were procured from the garden of the Royal Agri-Horticultural Society of India.

Root tips of *Hydrocotyle* and *Oenanthe* were collected by uprooting plants.

Fully imbibed matured seeds of *Peucedanum sowa* and *Carum copticum* were germinated on moist blotting paper in petri dishes.

But in case of seeds of the other materials, germination could not be initiated in the laboratory even by cold treatment or by simultaneous hot and cold shocks. In order to have a mass germination of all the seeds they were treated in the following way. A mixture of half saw-dust and half clay was first made and soaked in water. Each lot of seeds was placed then in separate small pots containing this mixture. They were kept in the open air, away from direct sunlight. Germination could be initiated in this way within seven days. Healthy root tips were collected from the germinating seeds. For satisfactory preparations, trials in various fixatives had to be given showing once again why the morphology of the somatic complement could not be made out previously.

In all the species investigated the peak period of mitotic division was between 11 & 12 A.M. during the winter months.

Best results were obtained in *Hydrocotyle asiatica* by fixing in 8 oxyquinoline added fixative. (SHARMA & GHOSH 1950).

The solutions were kept separate, and mixed just before use. The method however required a treatment of the materials in the fixative for one and half hours to two and half hours as the case might be at 15°C before its subsequent fixation at room temperature overnight.

Oenanthe benghalensis and *Peucedanum sowa* gave good results in P: F 1 : 2;

Coriandrum sativum and *Daucus carota* in C : F 1 : 2 fixative with two hours cold treatment at 15°C, subsequent to fixation at room temperature;

Foeniculum vulgare and *Carum copticum* in C : F 1 : 2;

Carum roxburghianum and *Cuminum cyminum* in 1% platinic chloride and 10% formalin in 1 : 2 proportion with cold treatment at 15°C for two hours.

Regarding the meiotic chromosomes the peak period of division was found to occur between 11 A.M. & 1 P.M. in bright sunlight excepting *Hydrocotyle* where it was between 8 & 10 A.M.

For the fixation of flower buds, Belling's Navashin A and B in equal proportions and Karpechenko's A : B: 4 : 5 with a pre-treatment in Carnoy's fluid were found to be most advantageous. Karpechenko's fluid proved most effective, specially in those cases where chromosomes presented stickiness.

Feulgen light green preparations (BHADURI 1938) were chiefly employed for counting the maximum number of nucleoli in the somatic telophase, and the atttachment of nucleolar chromosomes with the nucleolus was examined in somatic prophase. The scheduled scheme was followed including a post Feulgen treatment, in a mixture of

5 c.c. of N. HCl
5 c.c. of 10% K metabisulphide
90 c.c. of Dist. water

otherwise the cytoplasm due to its dirty appearance presented much hindrance in observation.

For root tips and flower buds, paraffin sections were cut 16/μ and 16–18/μ thick respectively. A premordanting in 1% chromic acid became absolutely necessary in case of root tips before crystal violet staining. Regarding the meiotic chromosomes, post chromic treatment was found to be essential.

The figures were drawn at a table magnification of approximately

3,600 times using a Leitz compensating eyepiece No. 18 and a 1.3 apochromatic objective with a condenser 1.4 N.A.

III Observations

1. *Coriandrum sativum* ($2n = 22$)

The somatic chromosome number of this species has been found to be $2n = 22$ (Fig. 1) thus corroborating the previous report of Wanscher (1932).

Seven morphologically distinguishable types of chromosomes could be identified in the chromosome complement (Vide Idiogram).

1) The longest pair (6.1 μ each) of chromosomes with nearly median primary constrictions and each having a secondary constriction in the shorter arm (AA).

2) Two pairs of long chromosomes with sub-terminal primary constrictions (BB, B_1B_1). The members of one pair are shorter (4.4 μ — B_1B_1) than the other (5.0 μ — BB).

3) A pair of long (4.4 μ each) chromosomes with submedian primary constrictions and each having a secondary constriction in the shorter arm (CC).

4) Two pairs of long (4.2 μ each) chromosomes with submedian primary constrictions (DD, D_1D_1). It may be noted that a particular metaphase contained a distinct chromatic body situated in the vicinity of D_1 (Fig. 1) the true nature of which could not be determined.

5) A pair of long (4.2 μ each) chromosomes with median primary constrictions and a secondary constriction on one of the arms (EE). It is to be noted that one of the members of the pair possesses primary constriction much pronounced than the other.

6) Two pairs of medium sized (3.1 μ) chromosomes with subterminal primary constrictions (FF, F_1F_1).

7) Two pairs of short chromosomes (2.8 μ each) with subterminal primary constrictions (GG, G_1G_1).

In prophase, cases were observed where six nucleolar chromosomes were found to remain attached to the nucleolus (Fig. 10) thus coinciding with the six satellited chromosomes (AA, CC, EE) of the complement.

[1]) The terms longest, long, medium and short used for designating the lenghts of chromosomes in the complement of individual genera bear no relation to that of the other genera dealt with below.

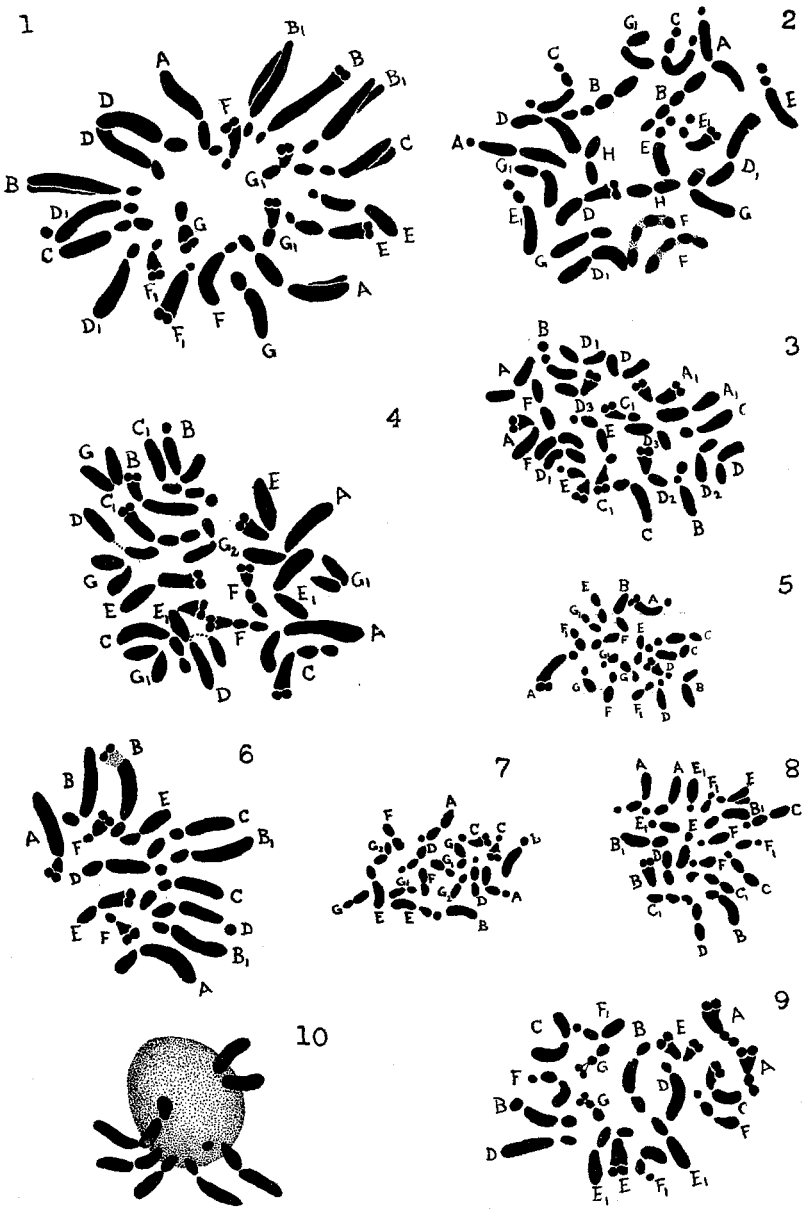
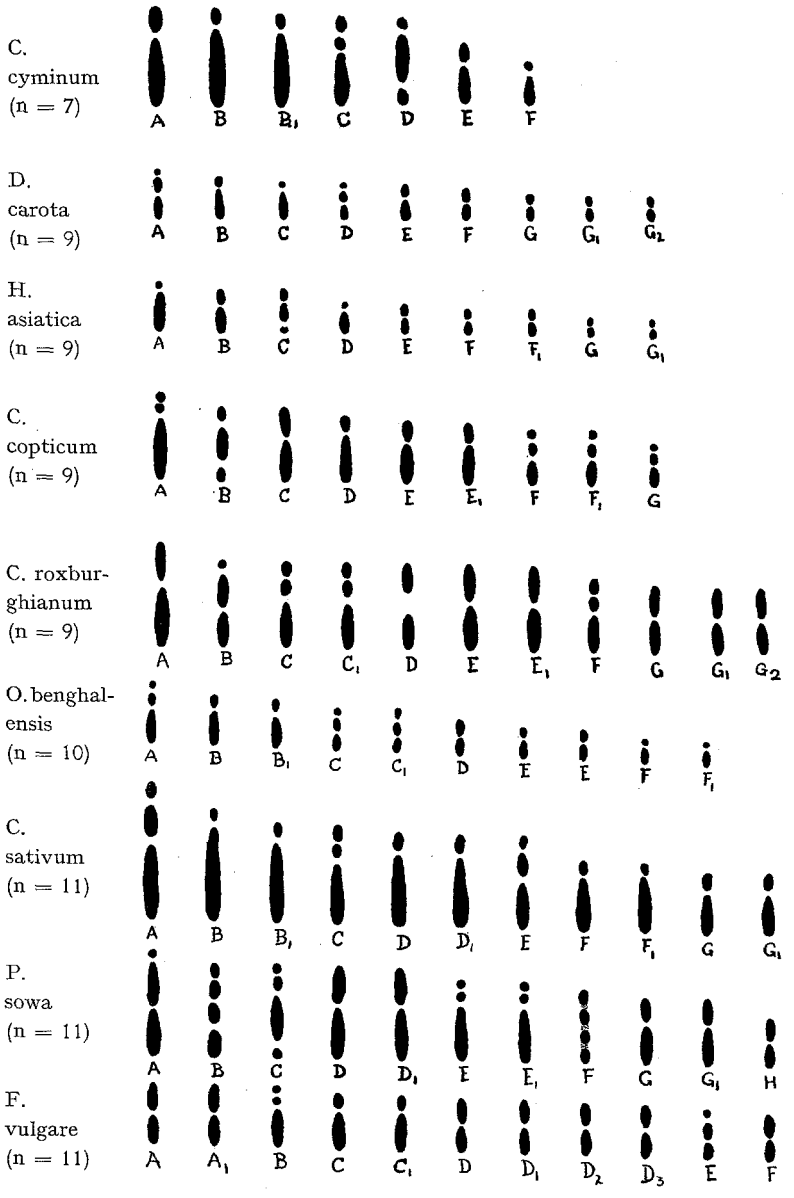


Fig. 1-10. Somatic divisions in different members of *Umbelliferae*. Figs. 1-9. Metaphase plates of (1) *Coriandrum sativum*, (2) *Peucedanum sowa*, (3) *Foeniculum vulgare*, (4) *Carum roxburghianum*, (5) *Hydrocotyle asiatica*, (6) *Cuminum cyminum*, (7) *Daucus carota*, (8) *Oenanthe benghalensis*, (9) *Carum copticum*. Fig. 10. Somatic prophase of *Coriandrum sativum* showing six chromosomes attached to the nucleolus.



Idiogram table of different species of Umbelliferae.

* Idiogram drawn from a 21 chromosomed plate

Lettering of the chromosome types of each species bear no relation of that of the other.

During meiosis, pairing and chiasma formation was found to be normal. (Fig 11). Metaphase showed eleven clear bivalents (Fig. 13). Considerable meiotic irregularities were also observed. These included early separation (Fig. 17), late separation (Fig. 15), formation of inversion bridge with acentric fragment (Fig. 14), lagging (Fig. 16, 19) and non-disjunction (Fig. 12).

The percentage of irregularities as has been calculated from a large number of P.M.Cs. is 13.8. In the second meiotic division though the presence of eleven chromosomes was noted most frequently, sporadic cases with ten chromosomes in two nuclei were also observed (Fig. 18). This proves the existence of P.M.Cs with 20 chromosomes which possibly might have resulted due to premeiotic irregularities.

2. *Peucedanum sowa* (2n = 22)

The diploid chromosome number of this species was found to be $2n = 22$ (Fig. 2) as reported by SCHULTZ GOEBEL (1930). There are eight different types of chromosomes distinguishable from each other by their size and relative position of primary and secondary constrictions (Vide Idiogram). The following are the eight types:

1) A pair of very long chromosomes (4.7 μ each) with nearly median primary constrictions and each having a subterminal secondary constriction in one arm (AA).

2) A pair of long (4.2 μ each) chromosomes with supernumerary constrictions. There are altogether three constrictions per chromosome in which the primary one could not be distinguished (BB) from the two secondaries.

3) A pair of long chromosomes (4.2 μ each) with submedian primary constrictions and each provided with a secondary constriction on both arms (CC).

4) Two pairs of long (4.2 μ each) chromosomes with nearly submedian primary constrictions (DD, D_1D_1).

5) Two pairs of medium sized (3.6 μ each) chromosomes with submedian primary constrictions and each with a secondary constriction in the shorter arm (EE, E_1E_1).

6) A pair of medium sized (3.3 μ each) chromosomes which show faintly stained areas probably due to nucleic acid starvation (FF).

7) Two pairs of medium sized (3.1 μ each) chromosomes with submedian primary constrictions (GG, G_1G_1).

Fig. 11–49. Meiotic divisions in different species of Umbelliferae (Figs. 11–49). *Coriandrum sativum* (11–19), *Peucedanum sowa* (20–22), *Foeniculum vulgare* (23–26), *Oenanthe benghalensis* (27–29), *Daucus carota* (30–33), *Carum copticum* (34-36), *Carum roxburghianum* (37-39), *Hydrocotyle asiatica* (40-43), *Cuminum cyminum* (44-46), *Ammi majus* (47-49).

8) A pair of comparatively short (2.2 μ each) chromosomes with nearly median primary constrictions (HH).

In diakinesis, eleven bivalents have been observed (Fig. 20). Groupings of bivalents observed in the polar view of some metaphase plates, though gave the impression of secondary association between bivalents (Fig. 21), could not be given serious consideration because of the fact that such association was of rare occurrence and also that other members of Umbelliferae examined did not show such associations. Non-disjunction (Fig. 22) and early separation of bivalents have been noticed in some cases, accountable possibly to an upset in the time balance. During second meiotic division eleven chromosomes have been observed in both the spindles.

3. *Foeniculum vulgare* ($2n = 22$)

The somatic chromosome number of this species is $2n = 22$ (Fig. 3) which corroborates the previous observation of OGAWA (1929). The chromosomes are of six different types (Vide Idiogram) as follows:

1) Two pairs of comparatively long chromosomes (2.8 μ each) with nearly median primary constrictions (AA, A_1A_1).

2) A pair of same sized (2.8 μ each) chromosomes with submedian primary constrictions and each having a secondary constriction in the shorter arm (BB).

3) Two pairs of medium sized (2.5 μ each) chromosomes with submedian primary constrictions (CC, C_1C_1).

4) Four pairs of medium sized chromosomes with nearly median primary constrictions (DD, D_1D_1, D_2D_2, D_3D_3). All the chromosomes are almost equal in length with slight differences varying from 2.4 μ to 2.6 μ.

5) A pair of comparatively short sized (2.2. μ each) chromosomes with nearly median primary constrictions and each having a secondary constriction in the middle of the short arm (EE).

6) One pair of same sized (2.2 μ each) chromosomes with median primary constrictions (FF).

The first meiotic division of the P.M.Cs showed eleven clear bivalents at diakinesis (Fig. 23). The first meiotic metaphase presented eleven bivalents in the polar view. Normal disjunction of bivalents do occur but cases of non-disjunction were not rare. Lagging bivalents were also noticed and they were found to occur in the interpolar region or away from the spindle (Fig. 24). Inversion-bridge with the corre-

sponding acentric fragment was rarely seen (Fig. 25). Early and late separation of bivalents were also seen indicating that the time balance was not similar for all the chromosomes.

Second meiotic division is almost regular. Metaphase II showed eleven chromosomes (Fig. 26). Among the irregularities found during the second division, late separation was met with more frequently than the other types of irregularities. Random observation showed that out of one hundred mother cells only four presented laggards and non-separation.

4. *Oenanthe benghalensis* ($2n = 20$)

The diploid chromosome number of this species was found to be $2n = 20$ (Fig. 8). Six morphologically distinguishable types of chromosomes could be identified in its somatic chromosome complement (Vide Idiogram). They are as follows:

1) A pair of medium sized (2.8 μ each) chromosomes with nearly median primary constrictions and each having a subterminal secondary constriction in the shorter arm (AA).

2) Two pairs of comparatively short (2.2 μ each) chromosomes with submedian primary constrictions (BB, B_1B_1).

3) Two pairs of (1.9 μ each) chromosomes of the same size as B B_1 with nearly median primary constrictions and nearly submedian secondary constrictions (CC, C_1C_1).

4) A pair of short (1.7 μ each) chromosomes with nearly median primary constrictions (DD).

5) Two pairs of short (1.4 μ each) chromosomes with nearly submedian primary constrictions (EE, E_1E_1).

6) Two pairs of very short (1.1 μ each) chromosomes with subterminal primary constrictions (FF, F_1F_1).

The sections of root tips showed typical hydrophytic characters in the presence of aerenchymatous tissue particularly in the outer cortex. Divisional figures were therefore more frequent in the inner cortex.

Regular pairing and subsequent segregation occurred in the first meiotic division of the P.M.Cs. In diakinesis, ten bivalents were found with various stages of terminalization of chiasmata. A plate was found to contain one trivalent and an univalent and the other members formed bivalents (Fig. 27).

Cases of late separation were not of infrequent occurrence (Fig. 28).

During this stage, several extranuclear chromatic granules occur irregularly scattered in the cytoplasm (Fig. 28). The occurrence of these bodies is similar to that in *Carum roxburghianum* described later, where their nature has also been discussed. Division II is normal (Fig. 29).

5. *Daucus carota* ($2n = 18$)

The number of chromosomes in the somatic complement of this species is $2n = 18$ (Fig. 7) which was first reported by LINDENBEIN (1932). A critical study of the morphology of the chromosomes reveals seven different types distinguishable from one another by their lenghts and the positions of their primary and secondary constrictions (Vide Idiogram).

1) A pair of medium sized chromosomes (2.2. μ each) with nearly median primary constrictions and each having a secondary constriction in one arm (AA).

2) A pair of medium sized (1.9 μ each) chromosomes with almost subterminal primary constrictions (BB).

3) A pair of (1.7 μ each) chromosomes of comparatively smaller size than BB, with subterminal primary constrictions (CC).

4) A pair of (1.7 μ each) chromosomes of same size with median primary constrictions and each having a secondary constriction (DD).

5) A similar sized (1.6 μ each) chromosome pair with submedian primary constrictions (EE).

6) A pair of short (1.4 μ each) chromosomes with median primary constrictions (FF).

7) Three pairs of very short (1.1 μ each) chromosomes with median primary constrictions (GG, G_1G_1, G_2G_2).

During meiosis in the pollen mother cells, pairing and subsequent disjunction were found to be normal (Fig. 30). The first meiotic metaphase showed nine bivalents in polar view (Fig. 32). Anaphasic separation (Fig. 31, showing also non co-orientation of one bivalent) and the second division were normal (Fig. 33). Cases of meiotic irregularities were very rare, and any number other than nine were never found to occur.

6. *Carum copticum* ($2n = 18$)

The diploid chromosome number of this species is $2n = 18$ (Fig. 9).

An anlysis of the chromosomes showed that there are altogether seven morphologically distinguishable types of chromosomes (Vide Idiogram) as described below:

1) The longest pair of chromosomes (3.9 μ each) with submedian primary constrictions and each having a secondary constriction in the shorter arm (AA).

2) A pair of long (3.3 μ each) chromosomes with submedian primary constrictions and each having a secondary constriction on the longer arm (BB).

3) One pair of long (3.3 μ each) chromosomes with nearly submedian primary constrictions (CC).

4) One pair of long (3.1 μ each) chromosomes with almost subterminal primary constrictions (DD).

5) Two pairs of medium sized (2.8 μ each) chromosomes with submedian primary constrictions (EE, E_1E_1).

6) Two pairs of medium sized (2.5 μ long) chromosomes with nearly median primary constrictions and secondary constriction in one arm (FF, F_1F_1).

7) A pair of short (1.9 μ long) chromosomes with nearly median primary constrictions and a secondary constriction in one arm (GG).

The first meiotic division of the P.M.Cs is normal and distinct: nine bivalents were noted in diakinesis (Fig. 34). The first division metaphase presented nine bivalents (Fig. 35). In addition to normal anaphasic separation, a negligible small percentage of P.M.Cs showed irregularities in the form of non-disjunction, early separation and lagging of bivalents. Nine chromosomes were found in the metaphase plates of the second division (Fig. 36).

7. *Carum roxburghianum* ($2n = 18$)

The somatic chromosome number of this species is $2n = 18$ which has also been substantiated from a study of meiosis. One root was however, found to possess $2n = 20$, 21 and 22 chromosomes instead of the normal number $2n = 18$. Among these abnormal numbers, 20 was found to be most frequent. Cases have not been recorded where the normal and abnormal numbers occur together. Unfortunately none of the plates having the normal number i.e., $2n = 18$ displayed satisfactory appearance of the chromosomes from where a karyotype

analysis could be made. Karyotype study therefore had to be made from plates having abnormal numbers of chromosomes. Figure 4, represents such a plate with $2n = 21$ chromosomes. From this figure the 21 chromosomes could be classified into the seven morphological types (Vide Idiogram):

1) The longest pair (4.7 μ each) of chromosomes with nearly median primary constrictions (AA).

2) A pair of long (3.9 μ each) chromosomes each with nearly median primary constriction and a secondary constriction at the distal end of the slightly longer arm (BB).

3) Two pairs of long (3.9 μ each) chromosomes with nearly median primary constrictions and each with a secondary constriction placed medianly in the comparatively shorter arm (CC, C_1C_1).

4) One pair of long (3.9 μ each) chromosomes with median constrictions (DD). The constriction is markedly pronounced. It has been suggested that such pronounced constriction region may represent both primary and secondary constrictions, where the chromatin matter in between the two constrictions is too small to be resolved under the microscope (cf. BHADURI and BOSE 1947).

5) A pair of long (3.9 μ each) chromosomes with nearly median primary constrictions (EE, E_1E_1).

6) A pair of medium sized (3.3 μ each) chromosomes with median primary constrictions and each having a secondary constriction median to the comparatively shorter arm (FF).

7) Two pairs and an odd member of short (3.1 μ each) chromosomes with nearly median primary constrictions (GG, G_1G_1, G_2G_2).

Nine bivalents were observed as a rule during the first meiotic division of the pollen mother cells (Fig. 37). The pairing and anaphasic separation of the nine bivalents were normal. The second division also was normal (Fig. 39).

A peculiar feature of the pollen mother cells following first anaphasic separation of their chromosomes is the occurrence of small extranuclear bodies in their cytoplasm (Fig. 38). They range from specks to minute droplets and were either freely scattered or associated in groups. It is yet to be seen with the aid of critical tests, namely, Feulgen and light green staining whether these bodies are chromatic or nucleolar in nature. The occurrence of such bodies which have been found to be

either chromatic or nucleolar has been interpreted by different authors (PAINTER 1943, SPARROW and HAMMOND 1947) in different ways. Most of the authors agree that these bodies probably are the extrusion products of the nucleus and irrespective of their chromatic or nucleolar nature, have some significance in connection with the nucleoprotein synthesis of the cytoplasm, thus playing an important role in cell metabolism.

8. *Hydrocotyle asiatica* ($2n = 18$)

This species has 18 chromosomes in the root tip cells as could be determined from a critical observation of a large number of well fixed plates (Fig. 5). The diploid chromosome complement of the species could be identified into seven different morphological types clearly distinguishable from one another by their size difference and relative position of primary and secondary constrictions. The seven types are as follows (Vide Idiogram):

1) The comparatively long pair (2.2 μ each) of chromosomes with subterminal primary constrictions (AA).

2) A pair of long (1.9 μ each) chromosomes with submedian primary constrictions (BB).

3) A pair of long (1.9 μ each) chromosomes with submedian primary constrictions and a satellite in the longer arm of each (CC).

4) A pair of medium sized (1.4 μ each) chromosomes with subterminal primary constrictions (DD).

5) A pair of medium sized (1.4 μ each) chromosomes with median primary constrictions (EE).

6) Two pairs of short (1.1 μ each) chromosomes with median primary constrictions (FF, F_1F_1).

7) Two pairs of very short (0.8 μ each) chromosomes with median primary constrictions (GG, G_1G_1).

In most cases meiosis in P.M.Cs was found to be normal. The normal number of bivalents was found to be nine in diakinesis (Fig. 42), but cases of ten bivalents (Fig. 43), eight bivalents (Fig. 41) and seven bivalents (Fig. 40) have also been recorded though in an insignificant percentage of mother cells.

It may be concluded from the above observations that some premeiotic irregularities must have been responsible for the production of

pollen mother cells with abnormal chromosome numbers. In the normal case, the somatic chromosomes ($2n = 18$) split longitudinally in the usual way and pass to the two poles in equal numbers. In those cases with ten and eight bivalents, it may be assumed that in the premeiotic mitosis, out of the eighteen split chromosomes sixteen go to each pole and of the remaining four chromatids all four go to one pole. Thus the resulting chromosomal constitution of the ensuing daughter cells entering meiosis may be explained as follows:

$18 + 2 = 20$ or 10 bivalents (Fig. 52)
$18 - 2 = 16$ or 8 bivalents (Fig. 53)

In the case of seven bivalents and the corresponding eleven bivalent ones (though not found), higher number of chromosomes must have been involved in non-separation during the premeiotic division. Cases of such premeiotic non-separation of sister chromatids of some of the chromosomes leading to the formation of pollen mother cells with variable chromosome numbers in the same anther have also been recorded by BHADURI and SHARMA (1946) in *Datura*.

If the above explanation be correct, then trivalent formation is expected on theoretical grounds. But no such case could however be detected.

Anaphasic separation and the second division were found to be normal.

9) *Cuminum cyminum* ($2n = 14$)

The somatic chromosome number of this species is $2n = 14$ (Fig. 6). From a critical analysis of the chromosomes it appears that there are six morphological types (Vide Idiogram) as follows:

1) A pair of long (4.4 μ each) chromosomes with submedian primary constrictions (AA).

2) Two pairs of long chromosomes with subterminal primary constrictions (BB, B_1B_1). The pair BB is slightly longer (4.4 μ each) while each of the B_1B_1 is 4.2 μ long.

3) A pair of long (4.2 μ each) chromosomes with submedian primary constrictions and each having a secondary constriction located on the shorter arm. The secondary constriction region appears to be extremely pronounced (CC).

4) A pair of long (3.9 μ each) chromosomes with submedian primary

constrictions and a secondary constriction on the longer arm (DD).

5) A pair of medium sized (2.9 μ long) chromosomes with nearly submedian primary constrictions (EE).

6) A pair of short (1.9 μ each) chromosomes with subterminal constrictions (FF).

The meiosis in the pollen mother cells was found to be normal. Seven bivalents were found in the first meiotic metaphase (Fig. 44). Cases of late separation of a few bivalents (Fig. 45) could also be noticed during anaphase. Seven chromosomes could be counted clearly in the second meiotic metaphase (Fig. 46).

10. *Ammi majus* ($n = 11$)

The somatic chromosomes of this species could not be examined, due to failure in germinating the seeds. The observation on meiosis however, confirms the previous record of SCHULZ-GOEBEL (1930) that the haploid number of this species is $n = 11$.

In meiosis, pairing and chiasma formation were found to be normal. Eleven bivalents occur at diakinesis (Fig. 47).

Occurrence of laggards either bivalent or univalent (Fig. 49) were rarely observed during the first anaphase. In later stages the laggards were found to be adjacent to the mother cell wall (Fig. 49).

In the second metaphase eleven chromosomes were distinctly observed (Fig. 48). The arrangement of univalents was generally normal, but cases of metaphase plates showing configuration as expected according to the floating magnet theory (cf. NANDI 1936) were also occasionally observed.

IV. DISCUSSION

1. *Nature of the species as revealed by the cytological data.*

The family Umbelliferae has been grouped into three subfamilies by DRUDE and HARMS in ENGLER and PRANTL's Die natürlichen Pflanzenfamilien, III. 8, the subdivisions being *Hydrocotyloideae, Saniculoideae* and *Apioideae*. Among the genera investigated, *Hydrocotyle asiatica* falls under *Hydrocotyle* group of *Hydrocotyloideae*. No species of *Saniculoideae* has been worked out. The rest of the genera examined come under *Apioideae* and falls in different groups. Thus, *Coriandrum sati-*

vum and *Cuminum cyminum* belong to the *Coriandrum* group, *Ammi majus*, *Carum copticum* and *Carum roxburghianum* come under the *Carum* group, *Oenanthe benghalensis* and *Foeniculum vulgare* fall under the *Seseli* group, *Peucedanum sowa* belongs to the *Ferula* group and *Daucus carota* under the *Daucus* group.

The chromosome numbers of the Umbelliferae of which only 10% are known varies considerably from 6–48 (WANSCHER 1932). Seventy-one species constituting a great majority of the species of which the chromosome numbers are known, possess $n = 11$ chromosomes.

It is further evident from WANSCHER's report that the class with eight chromosomes in the haploid set comes next in order of numerical importance in that, twenty two species have this number. WANSCHER, relying on his observations on the secondary association of bivalents in some species, suggested that four had been the primitive haploid number for the members of Umbelliferae. He further suggested that the haploid number eight, might have arisen by duplication from the basic set of four. It appears that during the course of evolution and natural selection the original ancestral species with four as the basic number disappeared, leaving progenies with $n = 8$. An early crossing between four and eight before the former became extinct followed by doubling, might have given rise either to forms with twelve or to forms with eleven. The number eleven has been assumed to have arisen from twelve through either loss of one, or fusion of two chromosomes.

OGAWA (1929) on the basis of his observations on twelve species of Umbelliferae, concluded that the number eleven might be taken as one of the basic numbers of the family. As species with eight chromosomes in the haploid set have also been recorded, he suggested that there are at least two different series of plants in the Umbelliferae in respect to the number of chromosomes.

The possibility of those species investigated here being either autopolyploid, allopolyploid, or amphidiploid forms, is perhaps excluded by the absence of any multivalent formation during meiosis or secondary association of bivalents. In view of these facts coupled with the evidence obtained from karyotype studies, it may be inferred that the members of the Umbelliferae particularly those investigated here are diploids.

Such a suggestion however, is in contradiction to that of WANSCHER (1932) who regarded eight as the basic number on the basis of secondary association between bivalents in *Hydrocotyle novae-zealandiae* where the bivalents associate in eight groups. WANSCHER moreover added, that this was the case in the other genera too. The homozygosity sofar as the structural changes of chromosomes, of the species investigated here, are concerned, is indicated by their normal pairing behaviour. The presence of inversion-bridges in some of the species viz., *Coriandrum sativum* and *Foeniculum vulgare* indicates that structural changes of chromosomes do occur in the life histories of these plants. In the absence of any evidence of the occurrence of numerical multiplication of chromosomes and hybridization during the course of evolution within the family, the only other alternative to explain the mechanism of speciation, is the suggestion of the incidence of structural rearrangements of chromosome segments. The presence of supernumerary constrictions in *Peucedanum sowa* may also be adduced in support of the above contention.

If one is to assume that structural changes of chromosomes is partly responsible for evolution within the family, the logical inference will be that most of our present day species, in view of their regular normal meiotic behaviour, are homozygous for such changes.

Excepting *Oenanthe benghalensis* and *Hydrocotyle asiatica* all the species investigated belong to the "spices" group, which are extensively cultivated. The acquirement of such homozygous condition may therefore be looked upon as to have been brought about by continued cultivation and judicious selection through untold generations.

It is significant that seed setting is profuse in those types (*Coriandrum sativum* and *Foeniculum vulgare*) where most of the irregularities in meiosis occur. Moreover as no plants with irregular numbers could be found in natural population, it is possible that gametes with irregular numbers do not survive; otherwise there would have been the presence of trisomics and tetrasomics and other aneuploids in nature. These facts lead one to conclude that only plants having regular chromosome number and homozygous constitution possessing some sort of selective value, survive competition.

2. *Chromosome-nucleolus relationship*

From a considerable amount of data gathered from the works on

chromosome-nucleolus relationship in widely different groups of plants, it (GATES, 1942, BHADURI, 1938, 40, 41, 42) has been postulated that the maximum number of nucleoli in a species is constant and corresponds exactly to the number of secondary constrictions present in the chromosome complement. Further, it has been emphasized (BHADURI, 42) that the size difference between the nucleoli is also a constant feature. The homomorphosity of the nucleoli indicates homozygosity, as against heteromorphosity for heterozygosity, so far as the nucleoli and the nucleolar chromosomes of a species are concerned. The secondary constriction regions are chemically distinct and are set apart for the production of nucleolar substance. These hypotheses have subsequently been confirmed by several of the later workers (BHADURI and BOSE, 1947, BHADURI and KAR, 1948, BHADURI and SHARMA, 1946, SHARMA, 1947, CHAKRAVORTY, 1948). In the present investigation too, by the application of Feulgen light green technique (BHADURI 1938) it has been shown that satellited chromosomes correspond with those attached to the nucleolus, in *Coriandrum sativum*, where such studies could be carried out. In this species it has been found that the maximum number of satellited chromosomes corresponds with the maximum number of nucleoli in the telophase nuclei of the root tip cells and also with the number of chromosomes attached to the nucleolus in the prophase stage.

The question might arise as to why there should be more than two nucleoli in the members of Umbelliferae which have been supposed earlier to be true diploids.

DE MOL (1928) basing his observations mainly on *Hyacinthus* propounded that a haploid genome must have one nucleolus, diploids two, tetraploids four and so on. Thus increase in number of nucleoli is brought about through polyploidy. Later BHADURI (1942) after careful observations on widely different plant species brought forth evidences suggesting that, in addition to numerical and secondary polyploidy, increase in number of nucleoli may also be effected through translocation involving nucleolar and non-nucleolar chromosomes, as well as fragmentation of nucleolar chromosomes across the secondary constriction region. (BHADURI and BOSE 1947, CHAKRAVORTI 1948).

It is not unlikely that in case of Umbellifers too, such non-homologous interchanges might have been responsible for the increase in the number of nucleoli and also the production of chromosome having

supernumerary constrictions in its body. As has already been pointed out earlier, from the pairing behaviour of the species it may be inferred that in all probability, the present day members, due to continued cultivation, represent types homozygous for such structural changes.

3. *Origin of aneuploid number in the somatic cells*

Among all the species so far investigated, occurrence of abnormal number of chromosomes in the somatic complement, has been detected only in *Carum roxburghianum*. As has been pointed out in the text, that in addition to normal 18 chromosomes in the somatic complement, root tips have been found where aneuploid numbers such as $2n = 20$, 21, 22 chromosomes are found. Such change in the chromosome number has previously been reported in other plants by SATO 1936, RAGHAVAN and VENKATASUBBAN 1939, BHADURI and SHARMA 1946, and AVANZI 1949. As the duplication involves only one or two chromosomes, such alterations could easily have been brought about by non-separation of chromosomes during mitosis. But in the present case it is significant however, that no such irregular number could be observed in a root tip, where eighteen chromosomes are found in other cells. In other words, root tips having normal chromosome number never show irregular numbers in any of the cells. Root tips having such abnormal complement generally however contain, in majority of the cells 20 chromosomes. In these cases it seems likely that 20 chromosomes are the regular diploid number of such root tips and the rare occurrence of 21, 22 comes about through non-separation.

As no trisomics and tetrasomics have yet been found in nature it is likely that such abnormal roots originate through non-disjunction during the branching of the main root, and as such may be found in the same individual, along with its normal roots. Obviously, such phenomenon do not occur in the shoot apex. On the basis of such assumption, complement with twenty chromosomes should be regarded as the normal number for those abnormal root tips originating through non-disjunction in the branch initial of the roots; and rare occurrence of nuclei with 21 or 22 chromosomes in such root tips are to be assumed to have come about through the same phenomenon.

However the origin of such roots with chromosomes more than the normal one ($2n = 18$) does not appear at the present state of our knowledge, to have any significance in the evolution of chromosome numbers.

4. *Origin of the different genera and their general interrelationships*

From an anlysis of the species investigated here, it is apparent that there are different haploid numbers viz., 7, 9, 10 and 11 as represented by the different genera of the family. The question is whether these have evolved along a single evolutionary line or along diverse lines independent of each other. It needs no repetition that WANSCHER on the basis of his observations in a large number of plants suggested eight to be the basic haploid complement for the family as a whole. OGAWA, who only came across eight and eleven chromosomed haploid complement claimed that the two numbers are completely independent of each other. In view of the meiotic data presented here, showing no secondary association and a critical karyotype study, taken in conjunction with the total amount of chromatin per chromosome complement (cf. Table I), there seems little reason te believe in the existence of a single basic complement.

TABLE I

Species	Somatic Chrom. No.	Range of Chrom. length	Total length of chromatin per haploid complement
1. *Cuminum cyminum*	14	1.9 μ—4.4 μ	25.8 μ
2. *Daucus carota*	18	1.1 μ—2.2 μ	13.8 μ
3. *Hydrocotyle asiatica*	18	0.8 μ—2.2 μ	12.6 μ
4. *Carum copticum*	18	1.9 μ—3.9 μ	25.1 μ
5. *C. roxburghianum* [1])	18	3.1 μ—4.7 μ	33.7 μ
6. *Oenanthe benghalensis*	20	1.1 μ—2.8 μ	17.7 μ
7. *Coriandrum sativum*	22	2.8 μ—6.1 μ	44.3 μ
8. *Peucedanum sowa*	22	2.2 μ—4.7 μ	40.4 μ
9. *Foeniculum vulgare*	22	2.2 μ—2.8 μ	27.8 μ

In addition to meiotic data from the karyotypes of the different genera so far studied (Vide Idiogram table) and the total chromatin length per chromosome complement (Table I), it appears that there is no common basic number for this family, but mostly the haploid constitution of each represents the basic number of the individual genus.

[1]) Figures given from a 21-chromosomed plate (cf. Fig. 44).

It may be suggested that there are at least six basic lines of evolution within the family as indicated by the different genera investigated. These are — 1) *Cuminum* line with seven as the haploid number; 2) *Daucus-Hydrocotyle* line with nine as the haploid number including also *Oenanthe* where $n = 10$ is supposed to have originated from $n = 9$ by duplication of one chromosome followed by structural changes; 3) *Carum* line with $n = 9$; 4) *Foeniculum* line with $n = 11$; 5) *Coriandrum* line with n = 11 and finally 6) *Peucedanum* line with $n = 11$ chromosomes.

The *Cuminum* line having seven chromosomes in the haploid complement, possesses a total chromatin length of 25.8 μ and the individual members are quite long varying in length from 1.9 μ to 4.4 μ. In addition to these features, from the general appearance and morphology of the chromosomes, the genus may be regarded as representing quite a distinct line of evolution. HOOKER has placed *Cuminum* in the *Coriandrum* group under the subfamily *Apioideae*. *Daucus* and *Hydrocotyle* may be regarded as members of the same evolutionary series, as in both of them, nine chromosomes are present in the haploid complement. A marked similarity between the two is also exhibited by their karyotypes and also the total chromatin length. The morphology of some of the chromosomes in the two genera are also similar in their detailed structure. In addition, the presence of very short chromosomes, two in *Hydrocotyle* and three in *Daucus* in their haploid complements, carries the similarities further. The size difference of the chromosomes varies in case of *Hydrocotyle* between 0.8 μ and 2.2 μ, the total length being 12.6 μ and in case of *Daucus* between 1.1 μ and 2.2 μ, the total length being 13.8 μ.

The genus *Oenanthe* though possesses ten chromosomes in the haploid set, still in view of its gross morphology and the total length of chromatin per complement which comes to 17.7 μ, seems to be related to *Daucus-Hydrocotyle* line. In that case, the number $n = 10$ should be regarded as a derived number from $n = 9$. The presence of the very short chromosomes in duplicate in this species strengthens this view.

The different genera, namely *Daucus*, *Hydrocotyle* and *Oenanthe* may then be regarded as to have evolved from a common basic stock with nine as the basic number, involving considerable structural changes in different directions during their specialization. However, in the delimitation of the different genera of Umbelliferae, taxonomists

have regarded *Daucus* and *Oenanthe* in the same subfamily *Apioideae*.

The third line includes *Carum copticum* and *C. roxburghianum* which are considered as members of a series having 9 chromosomes in the haploid set. Though the haploid number is the same as that of the previous line, still in view of the appearance of the chromosome complement and the total chromatin length, it appears, that the haploid set of nine of *Carum* represents a distinct series completely independent of the *Daucus* line. The apparent similarity in the basic number of the two lines may then be regarded as purely accidental. The total amount of chromatin has been recorded to be 25.1 μ and 33.7 μ in *C. copticum* and *C. roxburghianum* respectively, in contrast to the *Daucus* line where only 12.6 μ-13.8 μ has been found to be the range in total chromatin length. It is however surprising to note that there exists considerable difference between the chromatin length of the two species belonging to the same genus. It may be recalled that the total chromosomal length of *Carum roxburghianum* was calculated from a metaphase plate having twenty one chromosomes which had three chromosomes in excess of the normal ones with $2n = 18$ chromosomes. Even with due respect to this consideration, *C. roxburghianum* possesses a greater chromatin length. In order to explain this discrepancy it may be suggested, that considerable structural changes of chromosomes might have taken place during the differentiation of the various species of the genus, resulting in the variation in the chromosome length of the different species.

Foeniculum vulgare with eleven as the haploid number forms another evolutionary line. The size difference of the chromosomes ranges from 2.2 μ to 2.8 μ and the total chromosomal length of all the chromosomes comes to 27.8 μ. The haploid chromosome number of this species happens to be the same as those of *Coriandrum* and *Peucedanum*. However, considering the marked difference in gross morphology and total chromosomal lengths between *Foeniculum* and the other two genera, *Coriandrum* and *Peucedanum*, one is tempted to separate *Foeniculum* and put it under a distinct line, as already mentioned. Taxonomists have put *Foeniculum* and *Oenanthe* together under the group *Seseli* in the subfamily *Apioidea*. In spite of the similarity of the two groups in certain minor characters, there is great difference in the total chromatin length of the two groups, *Oenanthe* having 17.7 μ and *Foeniculum* 27.8 μ of chromosome lengths. In view of this it is advi-

sable to keep the two groups apart pending the accumulation of additional data.

The genera *Coriandrum* and *Peucedanum* though having the same chromosome number i.e., $n = 11$ seem to represent two more evolutionary lines. That the two genera *Coriandrum* and *Peucedanum* are completely independent in their evolution, distinct from the *Foeniculum* series, is apparent from the gross morphology of their chromosomes and also from their total chromatin lengths (cf. Table I). So far as the two genera, *Coriandrum* and *Peucedanum* are concerned their total chromatin lengths do not vary much, in being 44.3 μ and 40.4 μ respectively. The length of the individual chromosomes in the two genera varies from 2.8 μ to 6.1 μ and 2.2 μ to 4.7 μ respectively (Table I). Nevertheless, the two genera show such a marked degree of diversity with regard to gross morphology of their chromosomes, as to indicate independent lines of evolution. If one is to regard these two genera as members of the same phylogenetic series, then one has indeed to assume occurrence of revolutionary structural changes of chromosomes during the differentiation of these two genera.

It apparently seems fallaceous to visualize so many independent lines of evolution within a natural group like Umbelliferae, particularly those having the same number of chromosomes in the basic set. But as no definite evidence of the existence of a common basic stock has been obtained during the present investigation, it seems wise to suggest at the present state of our knowledge, the occurrence of such diverse evolutionary lines within the family. It is however presumed that a thorough and critical investigation into the cytogenetics of all the genera of Umbelliferae may yield such data as to enable one to establish a more phylogenetic interrelationship between the different genera.

V. Summary

1) Cytogenetical studies have been carried out in the following species of Umbelliferae.

i) *Hydrocotyle asiatica* L.
ii) *Ammi majus* L.
iii) *Oenanthe benghalensis* Benth.
iv) *Coriandrum sativum* L.

v) *Peucedanum sowa* Kurz.
vi) *Foeniculum vulgare* Gaertn.
vii) *Daucus carota* L.
viii) *Carum copticum* Benth.
ix) *Carum roxburghianum* Benth.
x) *Cuminum cyminum* L.

2) Pairing behaviour of the chromosomes of all the above species was found to be almost regular, with occasional cases of non-disjunction, early separation, lagging and inversion.

3) Somatic chromosomes were analysed from root tips fixed in chromic-formalin and platinic chloride-formalin mixtures with or without the addition of Oxyquinoline (OQ).

4) Idiogram studies have indicated that the different species are characterized by distinctive karyotypes particularly with reference to the nucleolar chromosomes. The number of chromosomes with secondary constrictions or satellites varies from species to species as will be evident from the following.

i) *Hydrocotyle asiatica* ($2n = 18$)	— 2	Secondary	constrictions
ii) *Daucus carota* ($2n = 18$)	— 4	,,	,,
iii) *Cuminum cyminum* ($2n = 14$)	— 4	,,	,,
iv) *Foeniculum vulgare* ($2n = 22$)	— 4	,,	,,
v) *Oenanthe benghalensis* ($2n = 20$)	— 6	,,	,,
vi) *Coriandrum sativum* ($2n = 22$)	— 6	,,	,,
vii) *Carum roxburghianum* ($2n = 21$)	— 8	,,	,,
viii) *Carum copticum* ($2n = 18$)	— 10	,,	,,
ix) *Peucedanum sowa* ($2n = 22$)	— 10	,,	,,

5) In *Carum roxburghianum*, the diploid chromosome number is variable as observed in root tip cells. In addition to the normal number of $2n = 18$, scattered cells have been found to contain aneuploid numbers like $2n = 20$, 21 and 22. The origin of these aberrant numbers has been explained as due to non-separation of one or more chromosomes.

6) Feulgen light green technique was employed where chromosome-nucleolus relationship was studied. In *Coriandrum sativum* the number of sat-chromosomes and the number of chromosomes attached to the nucleolus numerically correspond with the maximum number of nucleoli.

7) On cytogenetical considerations, it has been suggested that evolution within the family Umbelliferae took place along different lines. The establishment of these lines was initiated by structural changes of chromosomes along different directions. In view of normal pairing of the representative types of the different evolutionary lines, it appears that the zygotic constitution of each line is homozygous so far as any structural change of chromosomes that might have taken place ancestrally.

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