

## Nucleolar Organizing Region in the *Apiaceae (Umbelliferae)*<sup>1</sup>

By

I. A. Hamal, A. Langer, and A. K. Koul

(Received July 30, 1985; in definite form September 17, 1985)

**Key Words:** Angiosperms, *Apiaceae*. — Karyology, NOR, nucleolus, nucleolar bivalents, NOR evolution.

**Abstract:** Data available for the nucleolus organizing region in the family *Apiaceae* are reviewed. An attempt has been made to establish the exact number of this region in various subfamilies and tribes through studies on the karyotype and nucleolus. Most of the taxa have a single nucleolar chromosome per haploid complement. The location of the nucleolar organizing region (NOR) on the chromosome varies. Members of *Hydrocytoloideae* differ drastically from those of subfam. *Saniculoideae* and *Apioideae*, with respect to the location of NOR. Despite wide geographical distribution, varied ecological preferences and differences in morphology, anatomy and cytology, Umbellifers have attained stability in the number and location of NORs. Characters of NOR offer scope for utilization in understanding phylogenetic relationships at higher levels of taxonomic hierarchy.

*Apiaceae* is one of the largest dicotyledonous families, comprising over 2,700 species (RENDLE 1971). After differentiating from their pro-Araleaceous ancestors, sometime during the tertiary period (MATHIAS 1965), Umbellifers have dispersed to regions covering varied ecoclimatic conditions. Many species have become cosmopolitan in distribution.

Adaptation to diverse habitats has called for divergence in morphology, anatomy, pollen architecture, chromosome make up and the breeding system. As a consequence of this the present day species vary in habit from tiny herbs (members of subfam. *Hydrocytoloideae*) to large shrubs (*Prangos*, *Heracleum*, *Angelica*) and small trees (*Ferula*). Significant changes have also taken place in anatomy and pollen grain structure (CERCEAU-LARRIVAL 1971). Umbellifers display a wide range of variability in their breeding system as well; the species are hermaphrodite, andro-

<sup>1</sup> Studies on the Nucleolus and Nucleolar Chromosomes in Angiosperms XII.

monoecious, gynodioecious or dioecious. Even in respect of chromosome complement they exhibit a good deal of heterogeneity (HAMAL 1981); the haploid chromosome counts range from  $n = 4-84$ .

In view of this all round variability, it was considered an excellent group for evaluating the nature of nucleolar chromosomes. On account of their prominent physical landmarks, these chromosomes have assumed great importance in unravelling problems of ancestry and phylogeny (MAGGINI 1972, 1975, MAGGINI & al. 1976, LANGER 1980, LANGER & KOUL 1981, 1983, SHARMA 1984, SHARMA & al. 1986). An attempt has been made to explore the nature of variability existing within the family with respect to number, size and structure of these specialized chromosomes and to employ the data that are generated for evaluating phylogenetic relationships. The results and inferences drawn from this exploration constitute the contents of this communication.

So far, only 1,290 of the 2,700 species of *Umbelliferae* have been assessed for their chromosome number. Data on karyology are even more scanty. The number of species with known chromosome complements is just around 170. Even out of these, more than half are based on microtome sectioning (MELDERIS 1930, WANSCHER 1933, GARDE & MALHEIROS GARDE 1949, 1954, CAUWET 1967a, 1967b, 1968, 1971, ENGSTRAND 1970, QUEIROS 1972) and cannot therefore be depended upon for making comparisons. This dismal situation prompted MOORE (1971) to state that "almost at every hierarchical level in the *Umbelliferae*, we are still at the level of  $\alpha$ -cytotaxonomy". Even after more than a decade of this realization, the family has received no better deal in the hands of cytologists and cytotaxonomists, with the result that in his presidential address to the botanical section of the 68th session of the Indian Science Congress, DNYANSAGAR (1981) stated, "I hope this account of cytogenetics of the *Umbelliferae* will inspire many young workers to undertake work on those plants of the family which have not yet been tackled or the plants where the work is still inadequate". In persuance of these observations, we initiated work on such species of the family which abound in the western Himalayas. Our experience with Umbellifer chromosomes suggests that the paucity of cytological literature is partly due to the small flower size which makes their handling difficult and partly to the difficulty of germinating the seeds in vitro. Satisfactory chromosome scattering and staining is also difficult.

In the *Apiaceae*, the usefulness of data concerning Sat. chromosomes is at present, rather limited. This is primarily because only a handful of species have been studied from this angle. Even in such species which have been karyotyped, a great deal of confusion exists with respect to the number of NORs (Table 1).

Table 1. Details of data available on nucleolar chromosomes and nucleoli in the *Apiaceae*

Taxa	Chromo-some number (2 n)	Ploidy level	Number of Sat. chromosomes	Maximum number of interphase nucleoli	Reference
<b>HYDROCOTYLOIDEAE</b>					
<i>HYDROCOTYLEAE</i>					
<i>Centella asiatica</i> (L.) Urb.	18 18	2 × 2 ×	2 2	2	present work SHARMA & GHOSH 1954 SHARMA &
				—	BHATTACHARYA 1959
				—	MITSUKURI & KURAORI 1959
				—	SHARMA & BHATTACHARYA 1959
				—	WANSCHER 1933
				—	WANSCHER 1933
				—	WANSCHER 1933
<i>Hydrocotyle javanica</i> THUNB.					
	72	6 ×	4	—	SHARMA & BHATTACHARYA 1959
				—	present work QUEIROS 1972
<i>H. sibthoroides</i> LAM.					
	24	2 ×	2	2	—
	96	8 ×	—	—	—
<i>H. vulgaris</i> L.					
				—	WANSCHER 1933
				—	WANSCHER 1933
<i>MULINEAE</i>					
<i>Bowlesia tenera</i> SPRENG.	16	2 ×	—	—	—
<i>Druza oppositifolia</i> DC.	16	2 ×	—	—	—
<i>SANICULOIDEAE</i>					
<i>SANICULEAE</i>					
<i>Eryngium agavifolium</i> GRISEB.	16	2 ×	2	—	WANSCHER 1933
<i>E. billardieri</i> DEL.	16	2 ×	2	2	present work
<i>E. bourtgatii</i> GOUAN	16	2 ×	—	—	CAUWET 1968
<i>E. bromelijfolium</i> DELARB.	48	6 ×	—	—	WANSCHER 1933
<i>E. campestre</i> L.	14	2 ×	2	—	REESE 1969
<i>E. campestre</i> L.	28	4 ×	4	4	REESE 1969

Taxa	Chromo-some-number (2n)	Ploidy level	Number of Sat. chromosomes	Maximum number of interphase nucleoli	Reference
<i>Eryngium coeruleum</i> BIEB.	16	2x	2	2	present work
<i>E. corniculatum</i> LAM.	16	2x	4	-	QUEIROZ 1972
<i>E. dilatatum</i> LAM.	16	2x	2	-	QUEIROZ 1972
<i>E. elatostachys</i> LAM.	16	2x	1	-	WANSCHER 1933
<i>E. glauciale</i> BOISS.	16	2x	-	-	CAUWET 1967b
<i>E. maritimum</i> L.	16	2x	-	-	QUEIROZ 1972
<i>E. pandanifolium</i> CHAM. & SCHLECHT.	48	6x	2	-	QUEIROZ 1972
<i>E. paniculatum</i> CAV.	48	6x	-	-	WANSCHER 1933
<i>E. sericeum</i> CHAM. & SCHLECHT.	16	2x	-	-	WANSCHER 1933
<i>E. tenuifolium</i> LAM.	16	2x	-	-	QUEIROZ 1972
<i>E. yuccifolium</i> MICHHAUX	96	12x	-	-	WANSCHER 1933
<i>Hacquetia epipactis</i> DC.	16	2x	-	-	WANSCHER 1933
<i>Sanicula elata</i> HAMIL.	16	2x	2	2	present work
<i>LAGOOCETAE</i>					
<i>Petagnia saniculifolia</i> Guss.	42	6x	-	-	WANSCHER 1933
<i>APIOIDEAE</i>					
<i>SCANDICEAE</i>					
<i>Anthicus caecalis</i> BIER.	14	2x	-	-	QUEIROZ 1972
<i>A. tenerrimus</i> BOISS. & SPRUNN.	14	2x	-	-	WANSCHER 1933
<i>A. silvestris</i> (L.) HOFFM.	16	2x	-	-	MELDERIS 1930
<i>CHAEROPHYLLACEAE</i>					
<i>Caucalis bifrons</i> (POMEL) MAIRE	22	2x	-	-	CAUWET 1968
<i>Chaerophyllum acuminatum</i> LINDL.	22	2x	2	2	present work
<i>C. cicutaria</i> (VILL.) BRIQ.	22	2x	-	-	CAUWET 1968
<i>C. temulentum</i> L.	14	2x	-	-	QUEIROZ 1972
<i>C. temulum</i> L.	14	2x	-	-	CAUWET 1968
<i>C. villosii</i> KOCH	22	2x	2	2	CAUWET 1968



Table 1 (continued)

Taxa	Chromo-some number (2n)	Ploidy level	Number of Sat. chromosomes	Maximum number of interphase nucleoli	Reference
<i>SMYRNIEAE</i>					
<i>Conium maculatum</i> L.	22	2x	2	2	present work
<i>Scaligeria cretica</i> (MILLER) BOISS.	20	2x	—	—	ENGSTRAND 1970
<i>S. halophila</i> (RECH. f.)	20	2x	—	—	ENGSTRAND 1970
<i>Smyrnium rotundifolium</i> MILLER	22	2x	—	—	ENGSTRAND 1970
<i>APIEAE</i>					
<i>Aciphilla squarrosa</i> FORST.	22	2x	—	—	WANSCHER 1933
<i>Anemone majus</i> L.	22	2x	2	2	present work
<i>A. visnaga</i> (L.) LAM.	20	2x	2	2	QUEIROS 1972
<i>Apium graveolens</i> L.	20	2x	2	2	present work
<i>A. leptophyllum</i> (PERS.) F. MUELL.	22	2x	2	2	QUEIROS 1972
<i>A. nodiflorum</i> REICHENB. f.	22	2x	4	—	QUEIROS 1972
<i>Berula erecta</i> (HUDS.) COV.	18	2x	2	2	present work
<i>Bupleurum affine</i> SADL.	16	2x	—	—	CHAUWET 1967a
<i>B. album</i> MAIRE	32	4x	—	—	CAUWET 1971
<i>B. atlanticum</i> MURBECK	32	4x	—	—	CAUWET 1971
<i>B. croceum</i> FENZL.	16	2x	—	—	CAUWET 1967a
<i>B. divaricatum</i> LAM.	16	2x	—	—	CAUWET 1967a
<i>B. fruticosum</i> L.	14	2x	—	—	WANSCHER 1933
<i>B. gerardii</i> ALL.	16	2x	—	—	GARDE &
<i>B. gibraltaricum</i> L.M.	16	2x	2	—	MALHERBOS-GARDE 1954
<i>B. irregularare</i> BOISS. & KOTSCHY	14	2x	2	—	QUEIROS 1972
	16	2x	2x	—	CAUWET 1967a

<i>B. junceum</i> L.	16	2 ×	—	—	CAUWET 1967a
<i>B. karelii</i> V. IS.	16	2 ×	—	—	CAUWET 1967a
<i>B. lancifolium</i> HORNB.	16	2 ×	2	—	QUEIROS 1972
<i>B. longifolium</i> L.	16	2 ×	—	—	CAUWET 1967a
<i>B. montanum</i> COSSON.	32	4 ×	—	—	CAUWET 1971
<i>B. mucronatum</i> WIGHT & WALK-ARNOTT	16	2 ×	—	—	CAUWET 1971
<i>B. mundii</i> CHAM. & SCHLECHTD.	16	2 ×	—	—	CAUWET 1971
<i>B. olympicum</i> BOISS.	16	2 ×	—	—	CAUWET 1967a
<i>B. parnassicum</i> HALACSY	16	2 ×	—	—	CAUWET 1967a
<i>B. petiolata</i> SMITH	16	2 ×	—	—	CAUWET 1967a
<i>B. pratatum</i> HOFFMGG. & LINK	14	2 ×	—	—	WANSCHER 1933
<i>B. ranunculoides</i> L.	28	4 ×	—	—	CAUWET 1967a
<i>B. rigidum</i> L.	16	2 ×	—	—	CAUWET 1967a
<i>B. rigidum</i> subsp. <i>paniculatum</i> (BROR.) H. WOLFF	14	2 ×	2	—	QUEIROS 1972
<i>B. rotundifolium</i> L.	16	2 ×	—	—	CAUWET 1967a
<i>B. sibthorpiatum</i> SMITH.	16	2 ×	—	—	CAUWET 1967a
<i>B. subuniflorum</i> BOISS. & HELDR.	16	2 ×	—	—	CAUWET 1971
<i>B. sulphurum</i> BOISS. & BAL.	16	2 ×	—	—	CAUWET 1971
<i>B. tenue</i> BUCH. HAM. ex DON.	16	2 ×	2	2	present work
<i>B. tenuissimum</i> L.	16	2 ×	—	—	CAUWET 1967a
<i>B. tianschanicum</i> FREYN.	14	2 ×	—	—	QUEIROS 1972
<i>Carum carvi</i> L.	20	2 ×	2	2	WANSCHER 1933
	22	2 ×	8	—	CAUWET 1967a
	22	2 ×	—	—	present work
	22	2 ×	—	—	HORE 1975a
<i>C. multiflorum</i> (SIBTH. & SM.) BOISS.	20	2 ×	—	—	ENGSTRAND 1970
<i>C. roxburghianum</i> BENTH.	20	2 ×	10	—	HORE 1975a
	18	2 ×	8	—	SHARMA & GHOSH 1954
	22	2 ×	—	—	MELDERIS 1930
<i>Cicuta virosa</i> L.	22	2 ×	—	—	QUEIROS 1972
<i>Conopodium capillifolium</i> BOISS.	22	2 ×	2	—	WANSCHER 1933
<i>Cortia hookeri</i> CLARKE	22	2 ×	—	—	mitsukuri & KURAHORI 1959
<i>Cryptotaenia japonica</i> HAASK.	18	2 ×	—	—	

Table 1 (continued)

Taxa	Chromo-some number (2n)	Ploidy level	Number of Sat. chromosomes	Maximum number of interphase nucleoli	Reference
<i>Cuminum cyminum</i> L.	14 14	2x 2x	2 4	2 —	present work SHARMA & GHOSH 1954 BAJAJ & KOUL 1973
<i>Endressia pyrenaica</i> GAY. <i>Foeniculum capillaceum</i> Gilib. <i>F. vulgare</i> MILL.	22 22 22	2x 2x 2x	— 10 2	— — 2	SHARMA & BHATTACHARYA 1959 CAUWET 1968 HORE 1976
					present work SHARMA & GHOSH 1954 SINHA & SINHA 1978
					SHARMA & BHATTACHARYA 1959 HORE 1976
<i>Helosciadium inundatum</i> REICHENB. <i>Ligusticum acutifolium</i> Sieb. & Zuct.	22 22 22 22	2x 2x 2x 2x	— 6-10 — 2	— — — —	MITSUKURI & KURAHORI 1959 QUEIROS 1972 WANSCHER 1933
<i>L. elatum</i> CLARKE	22	2x	4	—	MITSUKURI & KURAHORI 1959 present work
<i>L. pyrenaicum</i> GOUAN. <i>L. thomsonii</i> CLARKE	22 22 22	2x 2x 2x	2 4 —	2 — —	SINHA & SINHA 1978 CAUWET 1968 present work
<i>Meum athamanticum</i> JACQ. <i>M. nevadense</i> BOISS.	22 22	2x 2x	— —	— —	CAUWET 1967b ENGSTRAND 1970
<i>Microsciadium minutum</i> (D'URV.) BRIG.	12	2x	—	—	MITSUKURI & KURAHORI 1959
<i>Nothosmyrrum japonicum</i> Miq.	20	2x	—	—	SHARMA & GHOSH 1954
<i>Oenanthe benghalensis</i> BENTH.	20	2x	6	—	SHARMA & BHATTACHARYA 1959
<i>O. crocata</i> L.	20	2x	4	—	QUEIROS 1972
<i>O. fistula</i> L.	22	2x	2	—	QUEIROS 1972
<i>O. globulosa</i> L.	22	2x	3	—	QUEIROS 1972
<i>O. javanica</i> (BLUME) DC.	20	2x	2	2	present work

<i>O. lachenalii</i> Gmel.	22	2 ×	QUEIROS 1972
<i>O. pinninelloides</i> L.	22	2 ×	QUEIROS 1972
<i>O. thomsonii</i> CLARKE	20	2 ×	SHARMA & BHATTACHARYA 1959
<i>Petroselinum sativum</i> HOFFM.	22	2 ×	MITSUKURI & KURAHORI 1959
<i>P. sativum</i> L.	22	2 ×	SHARMA & BHATTACHARYA 1959
<i>P. segetum</i> (L.) KOCH	18	2 ×	GARDE & MALHERES GARDE 1959
<i>Pimpinella diversifolia</i> DC.	18	2 ×	present work
<i>P. major</i> (L.) Huds.	18	2 ×	SHARMA & BHATTACHARYA 1959
<i>P. monoica</i> DALZ.	20	2 ×	HUNKLER & FAVERGER 1967
<i>P. peregrina</i> L.	22	2 ×	SINHA & SINHA 1978
<i>P. saxifraga</i> L.	20	2 ×	CAUWET 1968
<i>P. stewartii</i> (DUNN.) E. NASIR	18	2 ×	HUNKLER & FAVERGER 1967
<i>P. villosa</i> SCHOUB.	20	2 ×	HUNKLER & FAVERGER 1967
<i>Ridolfia segetum</i> (L.) MORIS	22	2 ×	present work
<i>Seseli indicum</i> WIGHT & ARN.	42	6 ×	QUEIROS 1972
<i>S. tortuosum</i> L.	22	2 ×	QUEIROS 1972
<i>Sium latifolium</i> CLARKE	12	2 ×	SHARMA & BHATTACHARYA 1959
<i>Trachyspermum ammi</i> (L.) SPRAGUE	18	2 ×	CAUWET 1967b
	18	2 ×	present work
	18	2 ×	SHARMA & GHOSH 1954
	18	2 ×	HORE 1975b
<i>Trinia hispida</i> Hoff.	18	2 ×	SINHA & SINHA 1978
<i>T. vulgaris</i> DC.	18	2 ×	WANSCHER 1933
<i>Vicaria conifolia</i> DC.	22	2 ×	WANSCHER 1933
<i>Xatardia scabra</i> MEISSN.	22	2 ×	present work
	22	2 ×	CAUWET 1968
<i>PEucedaneae</i>			
<i>Anethum graveolens</i> L.	22	2 ×	present work
<i>Angelica archangelica</i> L.	22	2 ×	present work
<i>A. razulii</i> GOUAN.	22	2 ×	CAUWET 1968
<i>A. sylvestris</i> L.	22	2 ×	QUEIROS 1972
<i>A. utilis</i> MAK. ex YABE	22	2 ×	MITSUKURI & KURAHORI 1959
<i>Elaeocarpus lagascae</i> Boiss.	22	2 ×	CAUWET 1967b
<i>Fernia chiliana</i> RECH. f.	22	2 ×	ENGSTRAND 1970
<i>F. communis</i> L.	22	2 ×	QUEIROS 1972
	22	2 ×	CAUWET 1968
			HORE 1975

Table 1 (continued)

Taxa	Chromo-some number (2n)	Ploidy level	Number of Sat. chromosomes	Maximum number of interphase nucleoli	Reference
<i>F. jaeschkeana</i> VATKE, ex DC.	22	2 x	2	2	present work
<i>Heracleum candidans</i> WALL ex DC.	22	2 x	2	2	present work
<i>H. granatense</i> BOISS.	22	2 x	-	-	CAUWET 1968
<i>H. nepalense</i> D. DON.	44	4 x	8	-	HORE 1975
<i>H. pyrenaicum</i> LAM.	22	2 x	-	-	CAUWET 1968
<i>Pastinaca sativa</i> L.	22	2 x	12	-	HORE 1975
<i>Peucedanum lancifolium</i> LANGE.	22	2 x	-	-	MELDERIS 1930
<i>P. ostruthium</i> (L.) KOCH.	22	2 x	2	-	SHARMA & BHATTACHARYA 1959
<i>P. sova</i> KURZ.	22	2 x	14	-	QUEIROZ 1972
<i>LASERPITIEAE</i>	22	2 x	10	-	CAUWET 1968
<i>Laserpitium sibiricum</i> L.	22	2 x	-	-	SHARMA & GHOSH 1954
<i>Thapsia decipiens</i> HOFFM.	22	2 x	1	-	QUEIROZ 1972
<i>T. villosa</i> L.	44	4 x	-	-	CAUWET 1968
<i>Selinum tenuifolium</i>	22	2 x	8	-	SHARMA & BHATTACHARYA 1959
<i>HORE 1975</i>					
<i>CAUWET 1968</i>					
<i>WANSCHER 1933</i>					
<i>QUEIROZ 1972</i>					
<i>CAUWET 1968</i>					
<i>SHARMA &amp; BHATTACHARYA 1959</i>					

### Material and Methods

The authors undertook karyology of 35 taxa, representing eight tribes and all the three subfamilies (*Hydrocotyloideae*, *Saniculoideae* and *Apioideae*), recognized in the *Apiaceae* by DRUDE (1898). The sample includes plants of diverse habits (ranging from herbs to large shrubs), habitats (300 to 6,000 m) and chromosome numbers ( $2n = 12, 14, 16, 18, 20, 22$ , and 26). For origin of the material see Table 2. Voucher specimens are preserved in the herbarium Jammu University. Root tips were treated in saturated solution of paradichlorobenzene or 0.008 M hydroxyquinoline for 3–4 hours and fixed in acetic-alcohol (1 : 3) for 24 hours. Before squashing in 1% aceto-orcein, root tips were hydrolysed in 9 : 1 mixture of aceto-orcein and 1 N HCl. For studies on nucleolus, root tips were fixed in a mixture comprising 12 parts 95% ethyl alcohol, 6 parts formaldehyde and 1 part glacial acetic acid for 24 hours. Fixed root tips were hydrolysed in 1 N HCl at 60°C for 2 hours before squashing in 1% aceto-carmine.

The number of NORs determined from karyology has been authenticated by data collected on the number of nucleoli organized in interphase nuclei (Table 1) and the number of nucleolar bivalents.

### Results and Discussion

Perusal of the table brings out two important points. First, that diversity in morphological, ecological, anatomical and cytological features notwithstanding, all taxa, barring *Coriandrum sativum*, have a single NOR per haploid complement (Figs. 1, 2). Second, that a strict numerical correlation exists between NORs and nucleoli. In the light of these findings, all those past reports which describe more than one nucleolar chromosome per monoploid complement, in these taxa, have been disregarded for present discussion.

As already mentioned, except for *Coriandrum sativum*, which has secondary constrictions on two chromosome pairs, all other species have only one pair of nucleolar organizing chromosomes. Of the two marker pairs in Coriander, one has the secondary constriction in the middle of long arm, while in the other, it is located towards the free end of the short arm. Interphase nuclei (in the root tip cells) of even this species organize only two nucleoli (Fig. 3b) indicating that only two of the four secondary constrictions bear active NORs, which parallels the situation obtaining in the other species of the family. Moreover, during pmc meiosis, only one bivalent remains terminally associated with the nucleolus (Fig. 4d) confirming that only the secondary constriction located in the short arm is functional in terms of nucleolar organization. In all other taxa as well, the terminal end of a single bivalent remains attached to the nucleolus (Fig. 4), which is in keeping with the number of secondary constrictions present in their somatic complements.

Although complete uniformity exists with respect to the number of NORs per complement, prominent differences exist in the morphology of

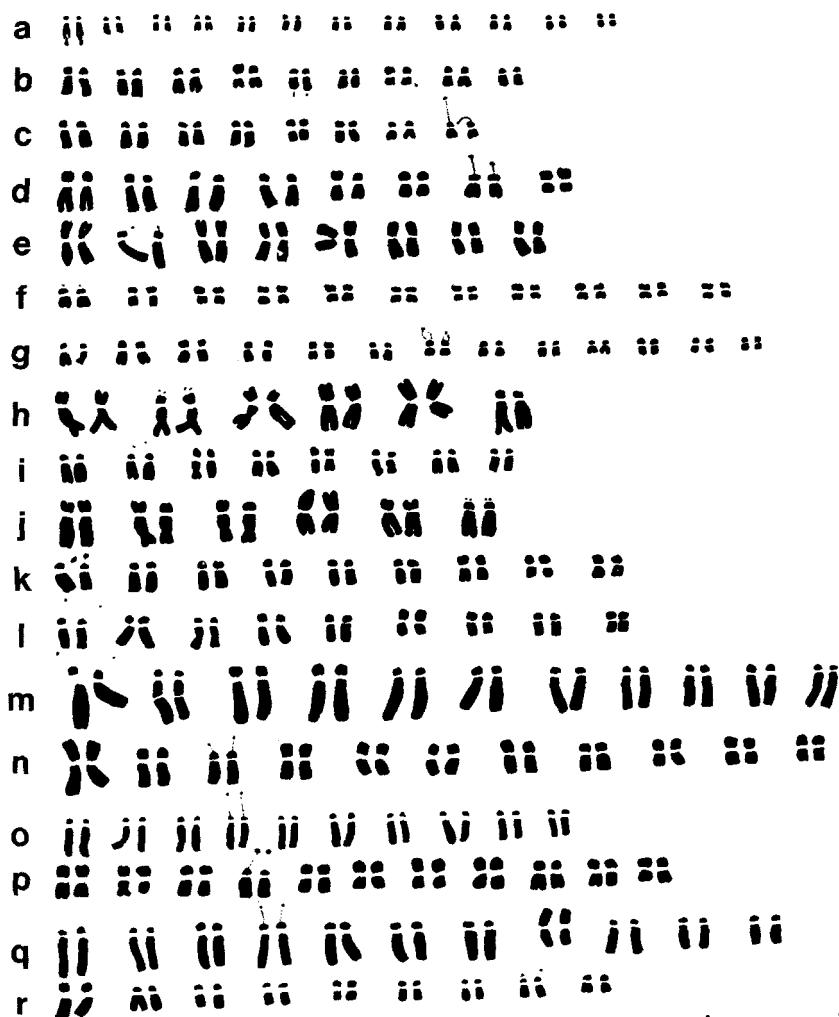


Fig. 1. Karyoidiograms of Umbellifers: a *Hydrocotyle sibthorpoidea*; b *Centella asiatica*; c *Eryngium billardieri*; d *E. coeruleum*; e *Sanicula elata*; f *Chaerophyllum acuminatum*; g *Scandix pecten-veneris*; h *Torilis arvensis*; i *T. japonica*; j *T. leptophylla*; k *Daucus carota* subsp. *carota*; l *D. carota* subsp. *sativus*; m *Coriandrum sativum*; n *Conium maculatum*; o *Ammi majus*; p *A. visnaga*; q *Apium graveolens*; r *Berula erecta*. Bar 10 µm

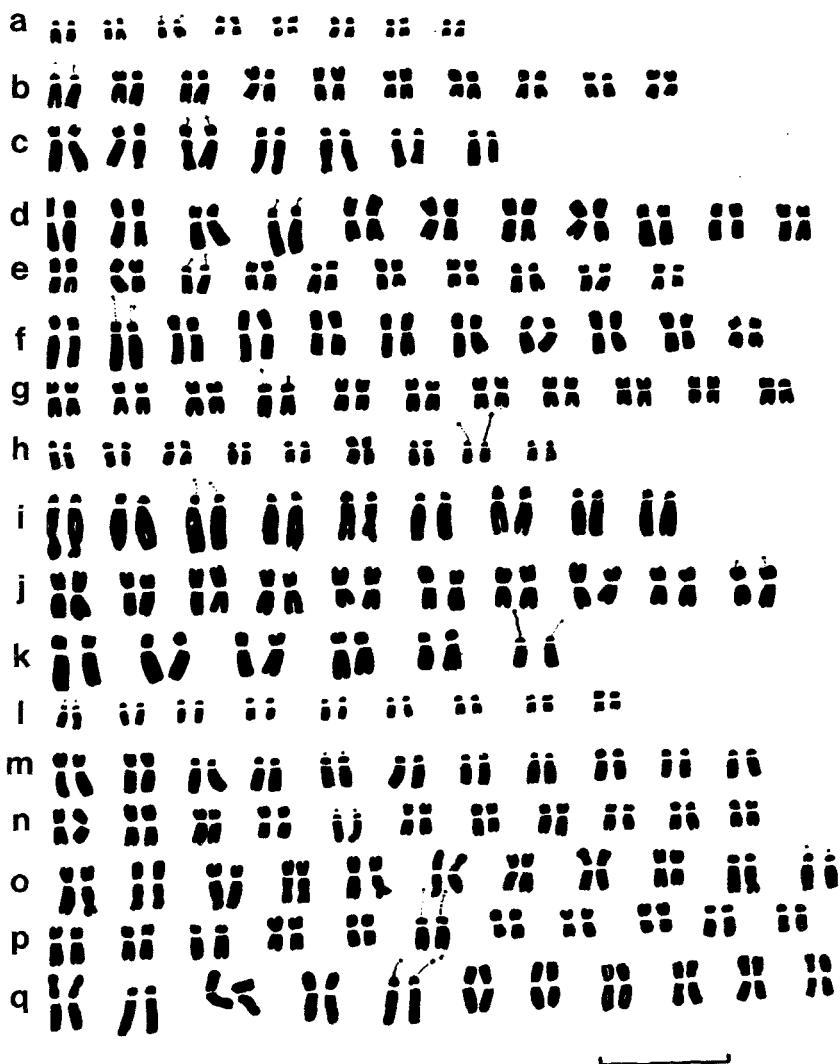


Fig. 2. Karyoidiograms of Umbellifers: *a* *Bupleurum tenue*; *b* *Carum carvi*; *c* *Cuminum cyminum*; *d* *Foeniculum vulgare* subsp. *vulgare*; *e* *F. vulgare* subsp. *piperitum*; *f* *Ligusticum elatum*; *g* *L. thomsonii*; *h* *Oenanthe javanica*; *i* *Pimpinella diversifolia*; *j* *P. stewartii*; *k* *Sium latijugum*; *l* *Trachyspermum ammi*; *m* *Vicatia conifolia*; *n* *Anethum graveolens*; *o* *Angelica archangelica*; *p* *Ferula jaeschkeana*; *q* *Heracleum candicans*. Bar: 10 µm

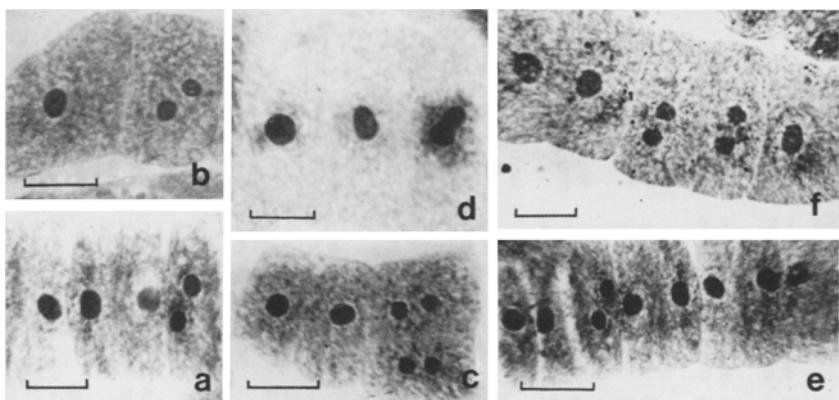


Fig. 3. Interphase nuclei from root meristem of Apiaceae: *a* *Scandix pecten-veneris*; *b* *Coriandrum sativum*; *c* *Sium latijugum*; *d* *Ammi majus*; *e* *Torilis arvensis*; *f* *Daucus carota*. Nuclei of all species are either mono- or binucleolate. Bar: 10 µm

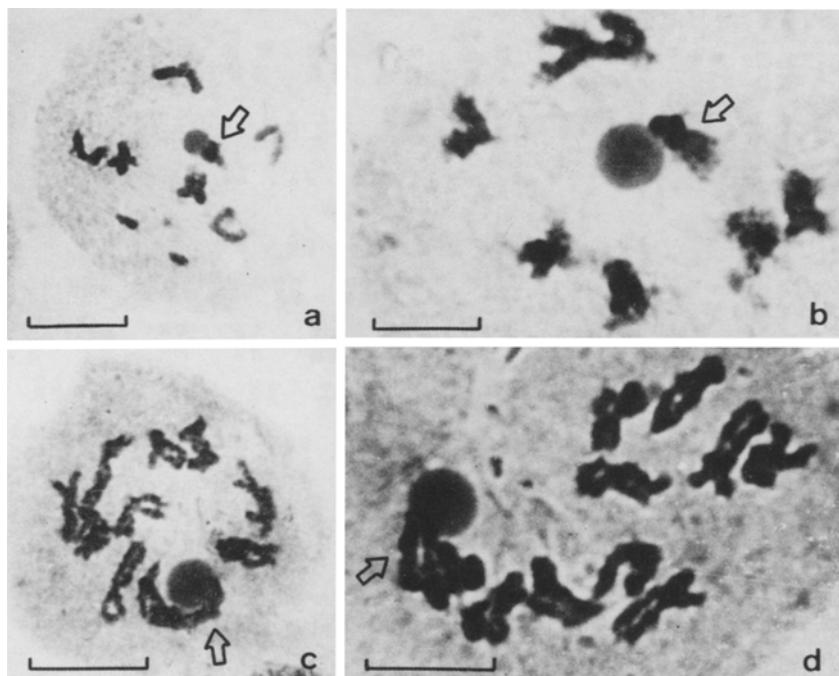


Fig. 4. Prophase pollen mother cells of Apiaceae: *a* *Eryngium coeruleum*; *b* *Sanicula elata*; *c* *Foeniculum vulgare* subsp. *vulgare*; *d* *Coriandrum sativum*. Note the presence of a single bivalent, terminally attached to the nucleolus, in all the species (arrows). Bar: 10 µm

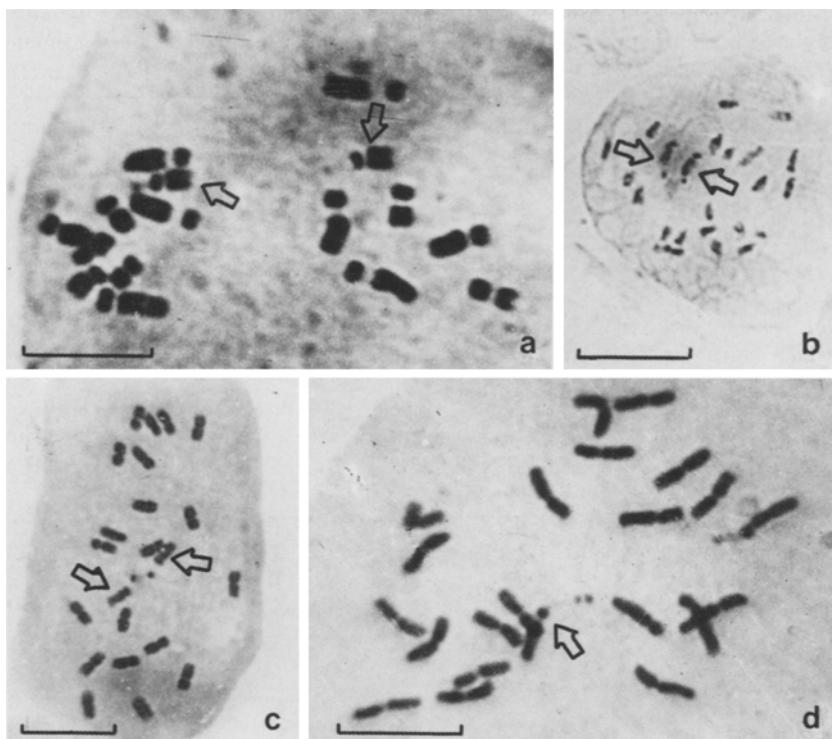


Fig. 5. Chromosome complements of *Apiaceae*: a *Eryngium coeruleum*; b *Hydrocotyle sibthorpoidea*; c *Ferula jaeschkeana*; d *Heracleum candicans*; showing A, B, C, and D nucleolar chromosome types respectively (arrows). Bar: 10 µm

these chromosomes (Fig. 5). Four morphotypes have been identified whose characteristics are:

Type A: Submetacentric (arm ratio 2.00 to 2.66), satellites attached to short arm (Fig. 5A).

Type B: Subtelocentric; satellites attached to long arm (Fig. 5b).

Type C: Subtelocentric; satellites attached to short arm (Fig. 5c).

Type D: Modified version of "type C", with a chromatin body intercalated between the short arm and the satellite (Fig. 5d).

Table 2 lists the relative representation of the four types of nucleolar chromosomes in the taxa studied hitherto.

The B-type nucleolar chromosome is restricted to members of the *Hydrocotyloideae*. Similarly, type D has been discovered only in *Heracleum candicans*. This chromosome seems to have originated by the

Table 2. Representation of different nucleolar chromosome types among Apiacean taxa presently studied. All places in J & K State, India; K = Kashmir Province, J = Jammu Province

Taxon	Chromo-some number (2n)	No. of nucleolar chromo-somes	Nucleolar chromo-some type	Origin
<b>HYDROCOTYLOIDEAE</b>				
<i>Hydrocotyle</i>				
<i>sibthorpoides</i>	24	2	A	Srinagar, K. IAH 103.
<i>Centella asiatica</i>	18	2	A	Kathua, J. IAH 86.
<b>SANICULOIDEAE</b>				
<i>Eryngium billardieri</i>	16	2	B	Srinagar, K. IAH 94.
<i>E. coeruleum</i>	16	2	C	Harwan, K. IAH 104.
<i>Sanicula elata</i>	16	2	C	Patni Top, J. IAH 159.
<b>APIOIDEAE</b>				
<i>Chaerophyllum acuminatum</i>	22	2	B	Baba Reshi, K. IAH 162.
<i>Scandix pecten-veneris</i>	26	2	B	Poonch, J. IAH 170.
<i>Torilis arvensis</i>	12	2	B	Jammu. IAH 182.
<i>T. japonica</i>	16	2	C	Patni top, J. IAH 161.
<i>T. leptophylla</i>	12	2	C	Srinagar, K. IAH 137.
<i>Daucus carota</i> subsp. <i>carota</i>	18	2	C	Jammu. IAH 93.
<i>D. carota</i> subsp. <i>sativus</i>	18	2	C	Harwan, K. IAH 149.
<i>Coriandrum sativum</i>	22	2	C	Jammu. IAH 204.
<i>Conium maculatum</i>	22	2	C	Srinagar, K. IAH 106.
<i>Ammi majus</i>	22	2	C	Jammu. IAH 67.
<i>A. visnaga</i>	20	2	C	Jammu. IAH 68.
<i>Apium graveolens</i>	22	2	C	Srinagar, K. IAH 100.
<i>Berula erecta</i>	18	2	C	Srinagar, K. IAH 107.
<i>Bupleurum tenue</i>	16	2	C	Mansar, J. IAH 155.
<i>Carum carvi</i>	20	2	C	Gulmarg, K. IAH 127.
<i>Cuminum cyminum</i>	14	2	B	Jammu. IAH 72.
<i>Foeniculum vulgare</i>				
subsp. <i>vulgare</i>	22	2	C	Jammu IAH 70.
<i>F. vulgare</i> subsp. <i>piperitum</i>	22	2	C	Kishtwar, J. IAH 109.
<i>Ligusticum elatum</i>	22	2	C	Patni Top, J. IAH 158.
<i>L. thomsonii</i>	22	2	B	Pahalgam, K. IAH 144.
<i>Oenanthe javanica</i>	20	2	C	Jammu. IAH 71.
<i>Pimpinella diversifolia</i>	18	2	C	Patni Top, J. IAH 179
<i>P. stewartii</i>	18	2	C	Poonch, J. IAH 200.
<i>Sium latifolium</i>	12	2	C	Srinagar, K. IAH 99.
<i>Trachyspermum ammi</i>	18	2	C	Jammu IAH 92.
<i>Vicatia conifolia</i>	22	2	C	Gulmarg, K. IAH 125.
<i>Anethum graveolens</i>	22	2	C	Jamu. IAH 79.
<i>Angelica archangelica</i>	22	2	C	Gulmarg, K. IAH 131
<i>Ferula jaeschkeana</i>	22	2	C	Sonamarg, K. IAH 147.
<i>Heracleum candicans</i>	22	2	D	Harwan, K. IAH 102

translocation of the satellite and NOR from one chromosome to another already in possession of a nucleolar organizer. This structural modification does not alter its role in nucleolar organization which is evident from the fact that cells of the root meristem of *H. candicans* have either mono- or binucleolate nuclei (HAMAL & al. 1983).

The C-type nucleolar chromosome is most common. Out of the 35 taxa of *Apiaceae* tested for the purpose, 26 have this chromosome type. The A-type nucleolar chromosome has been recorded in one member of subf. *Saniculoideae* and five of *Apioideae*. Going by the arm ratio, the submetacentric A-type is more like type-C. To sum up, it can be concluded that in all taxa of the *Saniculoideae* and *Apioideae* the NORs are located within the secondary constriction located towards the terminal end of the short arm.

The uniformity of Umbellifers in respect of the number of NORs per genome does not undermine the role of these chromosomes as characters of taxonomic and phylogenetic importance. This is because the nucleolar chromosomes vary with respect to location of secondary constriction (see Table 2). Commenting on the nature of nucleolar chromosomes in relation to phylogeny, LANGER (1980) proposed that in the primitive taxa, the NOR occupies an interstitial position. When at the distal position, it is usually located within the long arm. In comparatively advanced members, the NOR is located towards the distal end of the short arm. Observations on members of the *Apiaceae* fall in line with this proposition. The subfam. *Hydrocotyloideae*, members of which have the NOR in the long arm, has been ranked as the most primitive of the three subfamilies, on grounds of plant morphology, anatomy, palynology (HAMAL 1981) and phytochemistry (HEYWOOD 1971).

Data on plants of diverse phylogenetic status suggest that, in the plant kingdom as a whole, evolution often has involved reduction in number of nucleolar chromosomes per genome (LANGER 1980, KOUL & LANGER 1984). Concurrently, the NOR seems usually to have shifted from the intercalary to terminal position. The presence of a single distal NOR per haploid complement, in members of *Apiaceae*, which is a highly advanced family among polypetalous dicots, is in keeping with this contention. It would be quite pertinent to quote the suggestion of MAGGINI (1975) and MAGGINI & al. (1976) on some aspects of NOR at the molecular level. While studying the ribosomal nucleotide sequences in plants of diverse phylogenetic status (including different Gymnosperm and Angiosperm families), these workers have concluded that plants differ with respect to the magnitude of conservativeness of these sequences, depending upon their evolutionary complexity. Accordingly, the old families of long standing have attained much stability in the ribosomal nucleotide

sequences while those that are more recent are still in an evolutionary flux. Going by the age of the family *Apiaceae* (which has differentiated in the temperate environment of the palaeotropics, during the Tertiary period), it seems that its members have attained stability of NOR not only at the morphological (present observations) but even at the molecular level.

The financial assistance from Council of Scientific and Industrial Research, New Delhi to two of us (I. A. & A. L.) has made this work possible.

### References

- BAIJAL, S. K., KOUL, B. K., 1973: Karyomorphological studies in *Coriandrum sativum* L. and *Cuminum cyminum* L. — *Cytologia* **38**, 211–217.
- CAUWET, A. M., 1967a: Contribution à l'étude caryosystématique du genre *Bupleurum* L. I. — *Bull. Soc. Bot. Fr.* **114**, 371–384.
- 1967b: Contribution à l'étude caryologique de quelques Ombellifères d'Espagne. — *Naturalia Monspeliensis*, Ser. Bot. **18**, 201–210.
- 1968: Contribution à l'étude caryologique des Ombellifères de la partie orientale des Pyrénées. — *Naturalia Monspeliensis*, Ser. Bot. **19**, 5–27.
- 1971: Contribution à l'étude caryosystématique du genre *Bupleurum* (TOURN) L. III. — *Bull. Soc. Bot. Fr.* **118**, 55–68.
- CERCEAU-LARRIVAL, M. TH., 1971: Morphologie pollinique et corrélations phylogénétiques chez les Ombellifères. — In HEYWOOD, V. H., (Ed.): *The Biology and Chemistry of the Umbelliferae*, 109–156. — London: Academic Press.
- DNYANSAGAR, V. R., 1981: Cytogenetics of *Umbelliferae*. — Presidential address delivered at the Botany Section of the 68th session of Indian Science Congress.
- DRUDE, C. G. O., 1898: *Umbelliferaeae*. — In ENGLER, A., PRANTL, K., (Eds.): *Die Natürlichen Pflanzenfamilien* **3**(8), 63–250. — Leipzig.
- ENGSTRAND, L., 1970: Studies in the Aegean Flora XVIII. Notes on Chromosome numbers in Aegean *Umbelliferae*. — *Bot. Not.* **123**, 384–393.
- GARDE, A., MALHEIROS-GARDE, N., 1949: Contribuição para o estudo cariológico da família *Umbelliferae* I. — *Agron Lusitana* **11**(2), 91–140.
- 1954: Contribuição para o estudo cariológico da família *Umbelliferae* III. — *Broteria*, Ser. Cienc. Nat. **23**, 5–35.
- GATES, R. R., 1942: Nucleoli and related nuclear structures. — *Bot. Rev. (Lancaster)* **8**, 337–409.
- HAMAL, I. A., 1981: Cytotaxonomy of the Umbellifers of Kashmir Himalayas. — Ph. D. thesis approved by University of Jammu, India.
- KOUL, A. K., LANGER, A., 1983: Studies on nucleolus and nucleolar chromosomes in Angiosperms IV. Aberrant nucleolar chromosomes in *Heracleum candicans* WALL. — *Chromosome Information Service* **34**, 6–7.
- HEITZ, E., 1931: Die Ursache gesetzmäßiger Zahl, Lage, Form und Größe pflanzlicher Nucleolen. — *Planta* **12**, 775.
- HEYWOOD, V. H., (Ed.), 1971: *The Biology and Chemistry of the Umbelliferae*. — London: Academic Press.
- HORE, A., 1974: Karyotype studies in *Daucus carota*. *Ind. Agric.* **18**(3), 271–278.
- 1975a: Karyomorphological studies of the genus *Carum* L. — *Ind. Agric.* **19**, 303–312.
- 1975b: Chromosome studies in some species of *Peucedaneae* (*Umbelliferae*). — *Proc. Second All India Congr. Cytol. & Genet.*, 91–97.

- HORE, A., 1976: Cytogenetical studies of the genus *Foeniculum* (*Umbelliferae*). — Ind. Agric. **20**(3), 183–191.
- 1977a: Study of the structure and behaviour of chromosomes of different varieties of *Apium graveolans* (Celery). — Cytologia **42**, 21–28.
  - 1977b: Study of the structure and behaviour of chromosomes of different agricultural strains of *Coriandrum sativum* (Coriander). — Caryologia **30**(4), 445–449.
- HUNKLER, C., FAVARGER, C., 1967: Contribution à la cytotaxonomie du genre *Pimpinella* L. — Bull. Soc. Neuchat. Sci. Nat. **90**, 219–239.
- JACOB, K. T., 1940: Chromosome numbers and the relationship between satellites and nucleoli in *Cassia* and certain other *Leguminosae*. — Ann. Bot. (London) **4**, 201–223.
- KAMALA, T., 1976: Nucleolus organizing chromosomes in *Brassica* and their bearing on the phylogeny of the genus. — Cytologia **41**, 615–620.
- KOUL, A. K., LANGER, A., 1984: Nucleolar chromosomes. — In GOHIL, R. N., (Ed.): Recent Trends in Botanical Research. — Jodhpur, India: Scientific Publishers.
- LANGER, A., 1980: Studies on nucleolar organization in Angiosperms. — Ph. D. thesis approved by University of Jammu, India.
- KOUL, A. K., 1981: Is *Allium cepa* var. *viviparum* a hybrid between *A. cepa* and *A. fistulosum*? — In MANNA, G. K., SINHA, U., (Eds.): Perspectives in Genetics and Cytology **3**, 157–160. — New Delhi, India: Hindasia Publishers.
  - 1983: Studies on nucleolus and nucleolar chromosomes in Angiosperms. VII. Nature of nucleolar chromosome polymorphism in *Allium cepa* var. *viviparum* (METZG.) ALEF. — Cytologia **48**(2), 323–332.
- MAGGINI, F., 1972: The chromosome complement of *Bellevalia dubia* (Guss) R. & S., and the problem of *B. Webbiana* PARL. — Ann. Bot. (London) **31**, 115–123.
- 1975: Homologies of ribosomal RNA nucleotide sequences in monocots. — J. Molec. Evolution **4**, 317–332.
  - DE DOMINICIS, R. I., SALVI, G., 1976: Similarities among ribosomal RNAs of *Angiospermae* and *Gymnospermae*. — J. Molec. Evolution **8**, 329–335.
  - 1977: The ribosomal RNA gene number and the length of the nucleolar secondary constriction in *Bellevalia romana* and *B. dubia* (Liliaceae). A possible correlation. — Caryologia **30**, 97–103.
  - GARBARI, F., 1977: Amounts of ribosomal DNA in *Allium* (Liliaceae). — Pl. Syst. Evol. **128**, 201–208.
- MATHIAS, M. E., 1965: Distribution patterns of certain *Umbelliferae*. — Ann. Missouri Bot. Gard. **52**, 387–398.
- MELDERIS, A., 1930: Chromosome numbers in *Umbelliferae*. — Acta Hort. Bot. Univ. Latviensis **5**(1), 1–8.
- mitsukuri, Y., KURAHORI, Y., 1959: Cytogenetical studies in *Umbelliferae*. II. The chromosome numbers and karyotypes of some Japanese species. — Kromosomo **40**, 1354–1361.
- MOORE, D. M., 1971: Chromosome studies in *Umbelliferae*. — In HEYWOOD, V. H., (Ed.): The Biology and chemistry of the *Umbelliferae*, 233–255. — London: Academic Press.
- QUEIROS, M., 1972: Contribuição ao conhecimento citotaxonomico das spermatofyta de Portugal. VII. *Umbelliferae*. — Anuário Soc. Brot. **38**, 293–314.
- REESE, G., 1969: Cytotaxonomische Untersuchungen an di- und tetraploiden

- Sippen von *Eryngium campestre* L. und einem Artbastard mit  $2n = 15$ . — Österr. Bot. Z. **117**, 223–247.
- RENDLE, A. B., 1971: The Classification of Flowering Plants II. — Cambridge: Cambridge Univ. Press.
- SHARMA, A. K., GHOSH, C., 1954: Cytogenetics of some Indian Umbellifers. — Genetica **27**, 17–44.
- BHATTACHARYA, N. K., 1959: Further investigations on several genera of *Umbelliferae* and their interrelationships. — Genetica **30**, 1–68.
- SHARMA, P. K., 1984: Cytogenetic studies on some Himalayan species of genus *Plantago* L. — Ph. D. thesis approved by University of Jammu, India.
- LANGER, A., KOUL, A. K., 1986: Studies on nucleolus and nucleolar chromosomes in Angiosperms. XI. *Plantago* L. — Ann. Bot. (London) **57**, 145–154.
- SINHA, B. M. B., SINHA, A. K., 1978: The chromosomes of certain species of *Umbelliferae*. — The Botanique **8**, 117–122.
- WANSCHER, J. H., 1933: Studies on the chromosome numbers of the *Umbelliferae* III. — Bot. Tidsskr. **42**, 384–399.

Address of the authors: Department of Biosciences, University of Jammu, Jammu-180001, J & K, India.