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Karyotype analysis in *Chaerophyllum cicutaria* Vill. with special emphasis on satellited chromosomes

WŁODZIMIERZ CHOJNACKI, JERZY BOHDANOWICZ

Department of Plant Cytology and Embryology, University of Gdańsk,
Czołgistów 46, 81-378 Gdynia, Poland

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Abstract

Karyological studies were carried out on plants of *Chaerophyllum cicutaria* (*Umbelliferae*), which came from both lowland and montane natural populations. The chromosome number in all the examined plants was $2n = 22$ and their karyotypes, though similar in general, showed some minute but distinct differences. There was a single pair of SAT chromosomes in the chromosome complement. They had compound satellites divided into two or three segments. Seven morphological types of SAT chromosomes differing in number and size of satellite segments were distinguished. With respect to SAT chromosome morphology, the species showed both intra- and interpopulational karyological variation.

Key words: *Chaerophyllum cicutaria*, *karyotype*, *polymorphic SAT chromosomes*

INTRODUCTION

The *Umbelliferae* family, to which *Chaerophyllum cicutaria* belongs, contains about 2.5 thousand species, many of which are economically important as vegetables, spices and medicinal plants. Although chromosome data are available for about 850 species, comprising some 30% of the family, most refer to chromosome numbers only (Moore 1971). Unlike other large angiosperm families, the bulk of the umbellifers studied so far are diploid and most of them have the same basic chromosome number $x = 11$. Small or at most medium-sized chromosomes did not encourage previous investigators to undertake more detailed karyological studies. Thus, with some exceptions (Sharma and Ghosh 1954, Hiroe 1955, Mitsukuri and Kurahori 1959, Sharma and Bhattacharyya 1959, Hatano et al. 1974a, b, 1975, 1977, Hore 1974, 1975a, b, 1976, 1977, Dvořák 1976, Gorovoy et al. 1979, Geldikhanov and Zakharjeva

1984), investigations on chromosome morphology and karyotype structure in the *Umbelliferae* family still remain to be made.

Chaerophyllum cicutaria is a species within which karyological differentiation could be expected. It shows considerable morphological variability, particularly as regards leaf and stem hair covering and leaf blade shape. Moreover, beyond its main distribution area in the mountains of central Europe, it also has some remote, isolated lowland localities. Previous karyological observations on the species were confined to chromosome counts (Wanscher 1931, Rohner 1954, Böcher and Larsen 1955, Żukowski and Słowińska 1979); in all cases the chromosome number was reported to be $2n = 22$. Therefore any possible karyological variation might be expected to be rather a matter of chromosome morphology, which is has not been studied yet.

MATERIAL AND METHODS

The plants for this study were obtained as transplants from both lowland and montane natural populations. Five specimens representing lowland populations came from localities distributed within the Kashubian Lake District (northern Poland), near Babi Dół (L-1), Kolbudy (L-2), Kartuzy (L-3), Strysza Buda (L-4) and Wejherowo (L-5), while the others were collected from southern Polish localities in such mountain ranges as the Sudeten Mts. (M-1a and M-1b), Beskid Śląski Mts. (M-2a and M-2b), Tatra Mts. (M-3), Pieniny Mts. (M-4) and Bieszczady Mts. (M-5).

Karyological studies were carried out on meristematic cells of actively growing root-tips of potted plants. Excised root-tips were pretreated in 0.1% colchicine solution for 2 h at room temperature and fixed in a 3:1 ethanol/glacial acetic acid mixture overnight. They were then stained with aceto-orcein (1% orcein solution in 45% acetic acid) and squashed in 45% acetic acid. Cells with well-spread chromosome complements were photographed and chromosomes were measured on microphotographs at a magnification of 5000×.

Karyotype analyses were done on the basis of 55 metaphase plates and the morphology of SAT chromosomes was examined on 59 plates. Karyotypes were determined separately for each plant specimen on at least three plates (except for the M-1b plant, where a single plate was examined). Short arm length (s) and long arm length (l) were measured for each chromosome and total chromosome length ($t = l + s$) and arm ratio ($r = l \cdot s^{-1}$) were calculated. The chromosome length was expressed in relative values (diploid chromosome complement = 200%). On the basis of the above data the chromosomes were matched into pairs and the

Table 1

Mean values of relative chromosome length (t) and arm ratio (r) for eleven chromosome pairs of the *Chaerophyllum cicutaria* chromosome complement

Pair number		Plants from lowland populations					Plants from montane populations							Chromosome type
		L-1	L-2	L-3	L-4	L-5	M-1a	M-1b	M-2a	M-2b	M-3	M-4	M-5	
1	t	11.97±0.11	11.72±0.07	11.30±0.16	11.17±0.08	11.30±0.54	11.34±0.11	11.3 ±0.1	11.37±0.07	11.82±0.18	11.27±0.09	11.40±0.04	11.45±0.09	
	r	1.17±0.03	1.14±0.02	1.29±0.05	1.18±0.02	1.37±0.04	1.10±0.02	1.06±0.02	1.15±0.03	1.13±0.02	1.19±0.03	1.16±0.05	1.21±0.05	
2	t	10.33±0.16	10.42±0.05	10.60±0.07	10.56±0.04	10.75±0.21	10.72±0.05	10.5 ±0.0	10.55±0.12	10.52±0.09	10.63±0.05	10.67±0.07	10.97±0.10	
	r	1.07±0.02	1.15±0.01	1.08±0.03	1.13±0.02	1.19±0.05	1.22±0.02	1.50±0.00	1.13±0.03	1.22±0.04	1.10±0.02	1.10±0.02	1.15±0.03	
3	t	9.90±0.06	10.11±0.05	10.16±0.05	10.04±0.05	10.17±0.14	10.36±0.11	10.3 ±0.0	10.35±0.06	10.05±0.16	10.04±0.06	10.30±0.04	10.35±0.05	
	r	1.04±0.01	1.06±0.01	1.05±0.01	1.07±0.01	1.09±0.01	1.10±0.03	1.18±0.05	1.26±0.02	1.13±0.03	1.06±0.01	1.19±0.01	1.24±0.03	
4	t	9.73±0.04	9.88±0.04	10.11±0.05	9.95±0.05	9.60±0.06	10.02±0.08	10.0 ±0.1	10.00±0.11	9.92±0.10	9.86±0.05	9.67±0.02	9.97±0.05	
	r	1.14±0.02	1.28±0.02	1.30±0.04	1.26±0.03	1.07±0.01	1.27±0.04	1.02±0.02	1.10±0.03	1.41±0.05	1.24±0.03	1.12±0.03	1.05±0.01	
5	t	9.75±0.05	9.65±0.04	9.71±0.06	9.61±0.06	9.52±0.28	9.72±0.06	9.5 ±0.2	9.87±0.06	9.55±0.07	9.54±0.05	9.72±0.06	10.01±0.05	*m*
	r	1.32±0.03	1.06±0.01	1.21±0.04	1.10±0.01	1.37±0.13	1.06±0.02	1.20±0.01	1.38±0.05	1.29±0.02	1.05±0.01	1.36±0.05	1.36±0.04	
6	t	9.50±0.04	9.56±0.05	9.45±0.08	9.49±0.07	9.42±0.19	9.48±0.05	9.3 ±0.0	9.30±0.06	9.33±0.12	9.58±0.05	9.37±0.02	9.52±0.04	
	r	1.09±0.02	1.22±0.02	1.08±0.02	1.26±0.02	1.00±0.00	1.19±0.03	1.00±0.00	1.22±0.03	1.04±0.01	1.17±0.02	1.25±0.05	1.25±0.03	
7	t	9.33±0.04	9.09±0.05	9.14±0.06	8.97±0.05	8.80±0.25	9.07±0.09	9.1 ±0.3	8.90±0.18	8.63±0.15	9.06±0.05	9.00±0.04	8.75±0.10	
	r	1.19±0.03	1.12±0.02	1.23±0.02	1.09±0.01	1.08±0.04	1.13±0.02	1.05±0.00	1.06±0.03	1.09±0.02	1.12±0.02	1.10±0.03	1.08±0.02	
8	t				9.10±0.10					8.88±0.10				
	r				1.61±0.03					1.61±0.16				
	t	8.67±0.17	8.61±0.08	8.64±0.11		8.57±0.11	8.65±0.14	9.6 ±0.3	9.02±0.15		8.61±0.11	9.15±0.18	8.76±0.15	*sm*
	r	2.36±0.09	2.09±0.04	2.08±0.06		1.74±0.04	1.99±0.09	1.99±0.39	1.83±0.04		1.88±0.03	1.82±0.11	1.95±0.03	
9	t	7.88±0.14	7.84±0.10	7.42±0.09	7.91±0.09	7.72±0.29	7.60±0.10	7.3 ±0.1	7.40±0.04	8.27±0.12	7.86±0.06	7.90±0.13	7.71±0.06	
	r	3.67±0.12	3.44±0.07	3.10±0.13	3.20±0.11	3.04±0.14	3.37±0.07	3.93±0.07	4.35±0.05	3.70±0.25	3.68±0.07	3.86±0.24	3.39±0.14	*st*
10	t	6.83±0.08	7.08±0.07	7.10±0.06	7.24±0.09	7.40±0.17	6.94±0.04	7.3 ±0.1	7.22±0.10	7.22±0.21	7.36±0.06	7.12±0.20	7.22±0.08	
	r	4.94±0.08	5.81±0.20	4.76±0.24	4.45±0.13	4.90±0.31	4.76±0.11	5.90±0.10	6.20±0.37	5.40—0.41	5.71±0.27	4.71±0.41	4.58±0.21	
11	t	6.12±0.08	5.95±0.09	6.26±0.13	5.89±0.12	6.32±0.25	6.01±0.09	5.8 ±0.1	6.07±0.14	5.83±0.09	6.14±0.06	5.60±0.16	5.39±0.11	SAT *st*
	r	3.74±0.20	3.58±0.10	3.87±0.24	3.60±0.14	4.19±0.37	3.51±0.09	5.58±0.08	3.81±0.34	4.30±0.30	3.28±0.09	4.70±0.15	4.01±0.24	
Number of examined plates		3	12	4	6	3	6	1	3	3	7	3	4	
Mean length of chromosome complement (μm)		104.4	100.0	94.9	93.2	121.2	115.4	94.8	104.6	122.2	118.7	121.2	101.6	

mean values of *t* and *r* were determined for each pair (Table 1). For centromere position the nomenclature of Levan et al. (1964) was used.

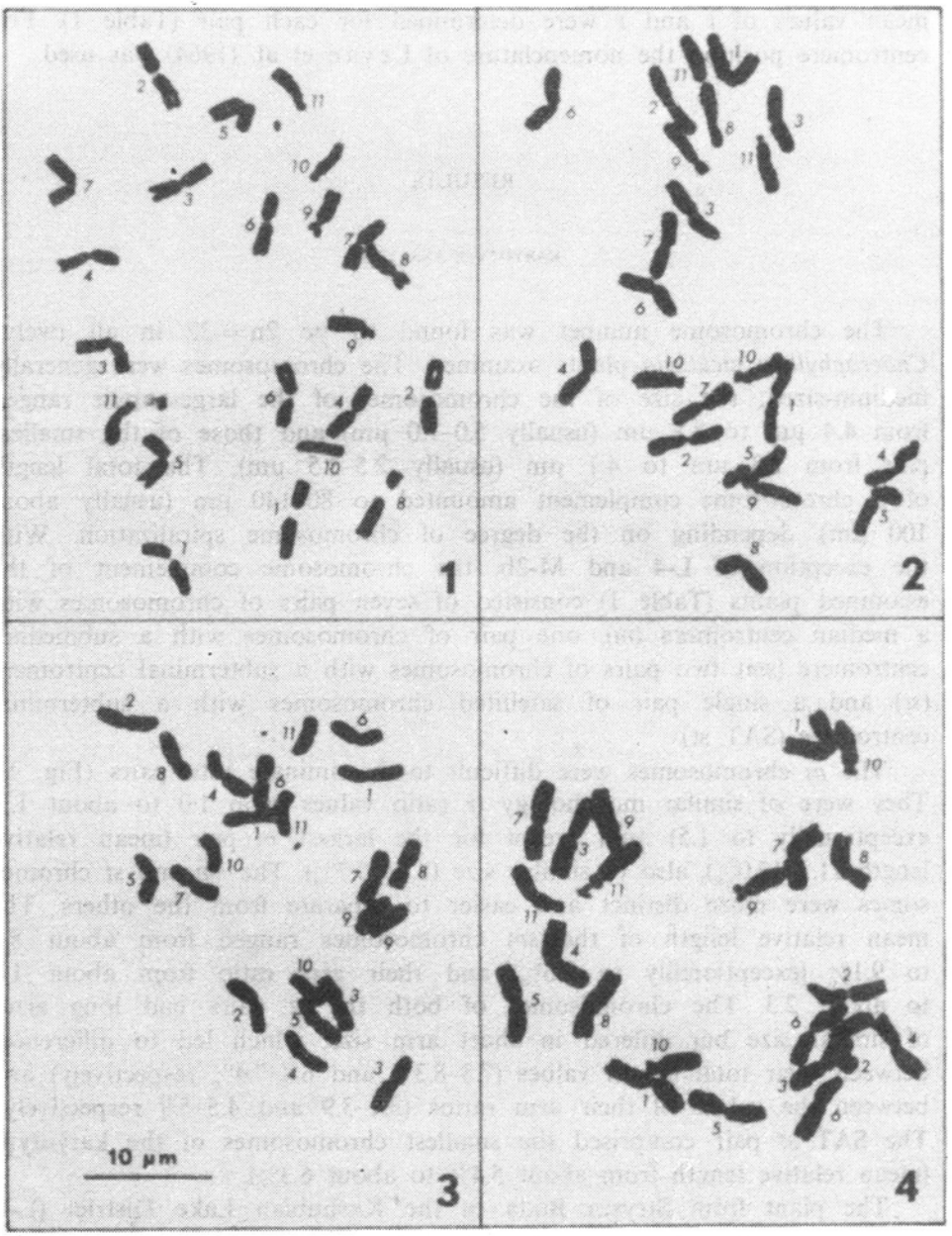
RESULTS

KARYOTYPE ANALYSIS

The chromosome number was found to be $2n = 22$ in all twelve *Chaerophyllum cicutaria* plants examined. The chromosomes were generally medium-sized; the size of the chromosomes of the largest pair ranged from 4.4 μm to 8.8 μm (usually 5.0–7.0 μm) and those of the smallest pair from 2.3 μm to 4.1 μm (usually 2.5–3.5 μm). The total length of a chromosome complement amounted to 80–140 μm (usually about 100 μm), depending on the degree of chromosome spiralization. With the exception of L-4 and M-2b, the chromosome complement of the examined plants (Table 1) consisted of seven pairs of chromosomes with a median centromere (*m*), one pair of chromosomes with a submedian centromere (*sm*), two pairs of chromosomes with a subterminal centromere (*st*) and a single pair of satellited chromosomes with a subterminal centromere (SAT st).

The *m* chromosomes were difficult to discriminate into pairs (Fig. 1). They were of similar morphology (*r* ratio values from 1.0 to about 1.3, exceptionally to 1.5) and, except for the largest *m* pair (mean relative length 11.2–12.0%), also of similar size (8.6–10.7%). The *sm* and *st* chromosomes were more distinct and easier to separate from the others. The mean relative length of the *sm* chromosomes ranged from about 8.6 to 9.1% (exceptionally to 9.6%) and their arm ratio from about 1.8 to about 2.3. The chromosomes of both the *st* pairs had long arms of similar size but differed in short arm size, which led to differences between their total length values (7.3–8.3% and 6.8–7.4% respectively) and between the values of their arm ratios (3.1–3.9 and 4.5–5.9 respectively). The SAT *st* pair comprised the smallest chromosomes of the karyotype (mean relative length from about 5.4% to about 6.3%).

The plant from Strysza Buda in the Kashubian Lake District (L-4) and one of the plants from the Beskid Śląski Mts. (M-2b) differed from the others in that they lacked a typical *sm* pair. Instead of this, they had a pair that consisted of two morphologically different chromosomes (Figs. 2 and 3). Judging by their arm ratio values, one of the chromosomes belonged to the *m* group while the second belonged to the *sm* group. The mean arm ratio of the pair as a whole did not exceed 1.7, so it should be classified as an *m* pair. Therefore the above two plants



Figs. 1–4. Root-tip metaphase plates of *Chaerophyllum cicutaria*. X 1700. Fig. 1 — A plate from the L-3 plant. 1–7 — *m* pairs, 8 — an *sm* pair, 9–10 — *st* pairs, 11 — a SAT *st* pair. Fig. 2 — A plate from the M-2b plant. 8 — a heteromorphic *m* pair, the other pairs as in Fig. 1. Fig. 3 — A plate from the L-4 plant. Pairs as in Fig. 2. Fig. 4 — A plate from the M-1a plant. Pair 1 is heteromorphic, the others as in Fig. 1

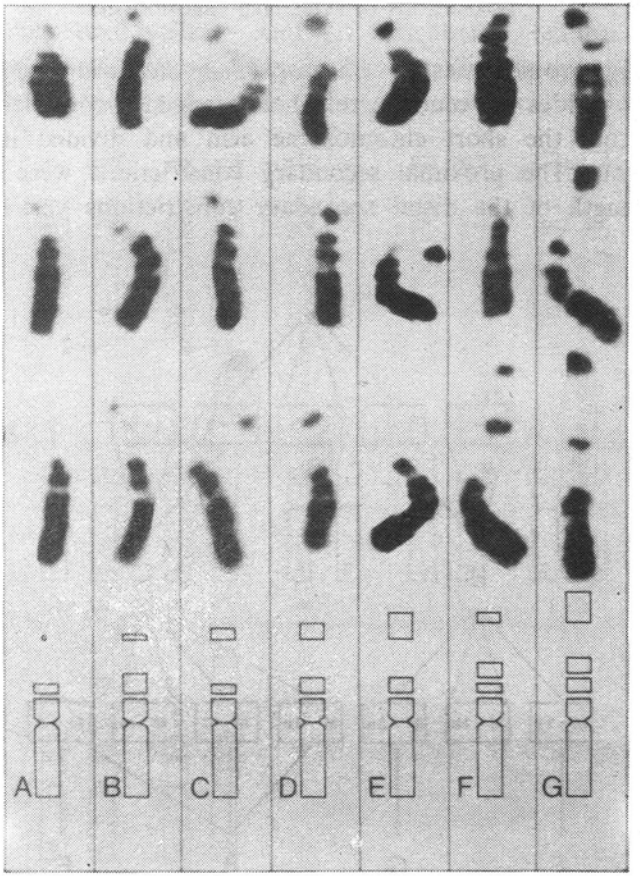


Fig. 5. Satellited chromosome types distinguished in *Chaerophyllum cicutaria*. Each column (A-G) contains a diagrammatic representation of the SAT chromosome type and three examples of this chromosome chosen from plates showing various degree of chromosome contraction. X 5000

had eight *m* pairs instead of seven (Table 1). Some similar differentiation between two chromosomes making up a pair existed in other plants too. In the M-1a plant, for instance, it was displayed by the chromosomes of the largest *m* pair (Fig. 4).

Although the karyotypes of the examined plants were very similar, they showed some minute but distinct differences. Apart from the above mentioned lack of the *sm* pair in two plants, further variation could be observed (Table 1). A morphologically variable first chromosome pair (*r* values from 1.06 in M-1b to 1.37 in L-5), the different morphology of the second pair in the M-1b plant and the relatively large chromosomes of the ninth pair in the M-2b plant are good examples of such variation.

MORPHOLOGY OF SATELLITED CHROMOSOMES

The SAT chromosomes of *Chaerophyllum cicutaria* had two or three constrictions besides the centromere. These secondary constrictions separated a satellite from the short chromosome arm and divided it into two or three segments. The proximal secondary constrictions were usually short, while the length of the distal secondary constrictions varied considerably

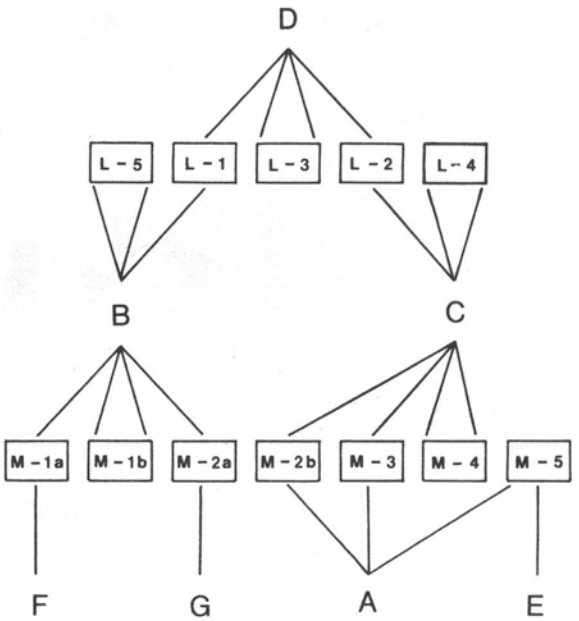


Fig. 6. Occurrence of the SAT chromosome types (A–G) in *Chaerophyllum cicutaria* plants from lowland (L–1 to L–5) and montane (M-1a to M-5) localities

(Fig. 5). The size and number of satellite segments were constant within a particular plant; on the other hand, distinct differences were observed between the examined plants in this respect.

Seven types of satellited chromosomes were distinguished (Fig. 5). Five of the types (A, B, C, D and E) had double satellites. They differed one from another chiefly in the size of the distal satellite segment, which was smallest in the A type and largest in the E type. The proximal satellite segment was also variable (Fig. 5). Apart from two satellite segments, small chromomeres were sometimes visible along proximal secondary constrictions in SAT chromosomes of the B, C and D types. They were single or double and then arranged in tandem, and could be discerned only in not fully spiralized chromosomes, whose proximal secondary constrictions were comparatively long.

The remaining two types (F and G) had their satellites divided into three segments. They differed from each other in the size of the distal satellite segment, which was larger than the short chromosome arm in

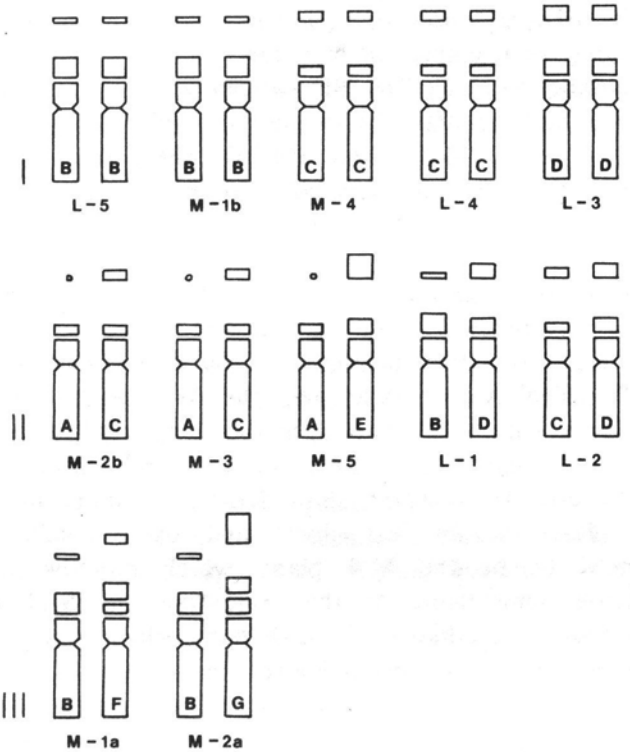


Fig. 7. Comparison of the *Chaerophyllum cicutaria* plants with respect to their satellited chromosomes. I — plants structurally homozygous for the SAT chromosome pair, II — plants with SAT chromosomes having satellite segments of different size, III — plants whose SAT chromosomes differ in size and number of satellite segments; L-1 to M-5 — plant symbols; A-G — SAT chromosome types

the G type and much smaller in the F type. The other satellite segments were of similar size in both types (Fig. 5).

The SAT chromosome types occurred with varying frequency in the *Chaerophyllum cicutaria* plants examined (Fig. 6). The A, B, C and D types were more frequent than the others. They were found in three to five individuals; the A type only in plants coming from the mountains, the D type only in those from lowland localities and the B and C types in representatives of both the montane and lowland populations. Each of the remaining three types (E, F and G) was found only once, all in plants collected from montane localities (Fig. 6).

Five out of the twelve examined plants appeared to be homozygous for SAT chromosome morphology (Fig. 7). The BB and CC patterns

were observed twice, once in a lowland population and once in a montane one, and the DD pattern was found once in a lowland population. The next five plants had SAT chromosomes differing from each other in satellite segment size (Fig. 7). Among them, the AC pattern was found twice and the BD, CD and AE patterns once. The SAT chromosomes in the remaining two plants differed not only in satellite segment size but also in number (Fig. 7). The BF pattern was observed in one of two plants from the Sudeten Mts. (M-1a) and the BG pattern in one of two plants from the Beskid Śląski Mts. (M-2a). These two populations were the ones that displayed the greatest morphological diversity of their individuals.

No direct correlations were observed between morphological features and the presence of particular SAT chromosome types in the investigated plants. Most of the plants had their stems and leaves more or less densely covered with hairs, thus they belonged to the *Chaerophyllum cicutaria* var. *hirsutum* (Lam.) Thel. variety, and only the M-3 plant from Tatra Mts., which was almost entirely devoid of hairs, represented the *Chaerophyllum cicutaria* var. *glabratum* (Lam.) Briq. variety. SAT chromosomes in the glabrous M-3 individual, however, showed the AC pattern like those in the hairy M-2b plant. As for leaf shape and overall habitus, the most different seemed to be the M-4 plant, which moreover, was covered with very dense, long hairs. At the same time, its SAT chromosomes were both of the C type, like in the L-4 plant, which was morphologically similar to other plants from lowland localities.

DISCUSSION

The *Chaerophyllum cicutaria* plants examined appear to have the same chromosome number and very similar karyotypes. Nevertheless, some karyological differentiation exists among them. This resembles the relationships observed in other representatives of the *Umbelliferae* family, such as *Angelica acutiloba* (Hatano et al. 1974a), *Daucus carota* (Hore 1974) or the species of the *Carum* and *Foeniculum* genera (Hore 1975b, 1976). It has therefore been claimed, that small structural changes of chromosomes play a great role in the evolution of umbellifers at the level of population and species (Hore 1974, 1975a, 1976), while euploid and aneuploid changes of chromosomes number seem to be far less important here.

The mitotic chromosomes of *Chaerophyllum cicutaria* are rather small and, apart from those of the largest *m* pair and those of the *sm* and *st* pairs, they also show similar size and centromere position. Such a situation makes mistakes more probable. If a single chromosome is damaged or

deformed while preparing the squash, it may lead to the wrong classification not only of this particular one, but also of several other chromosomes. In order to avoid such errors, the karyotypes, with a single exception, were determined on the basis of at least three metaphase plates. Still, there was no certainty whether the structural heterozygosity found in some plants and karyological differences observed between them were real. As the only chromosomes that could always be indentified beyond doubt were those of the SAT *st* pair, they were subjected to a more detailed examination.

SAT chromosomes have often been used as markers in karyological and cytogenetic studies (Keep 1962, Strid 1969, Maggini 1972, Fujishima and Kurita 1973, Bougourd and Parker 1976, Yampol 1977, Malakhova 1979, Sharma et al. 1984). Generally, the location of secondary constrictions as well as the number and size of satellites are characterized by great constancy, so they are treated as features specific to a high degree for a given species. On the other hand, these chromosome segments may also manifest a variability (Strid 1969, Bougourd and Parker 1976, Yampol 1977, Malakhova 1979). This variability is due to two different factors. Firstly, it may result from structural rearrangements. When various cytotypes revealing differences of this kind occur in a population, they are inherited as simple Mendelian characters (Bougourd and Parker 1976, Yampol 1977).

The second factor influencing the morphology of SAT chromosomes is the differential length of the secondary constriction, depending on the degree of its spiralization. This, in turn, depends on its activity as a nucleolar organizer (NOR). The activity of some NORs may change according to the presence and location of other NORs (Rieger et al. 1979, Cermeño et al. 1984). When a NOR is not active, the secondary constriction may vanish completely and the SAT chromosome then becomes impossible to identify (Yampol 1977, Sato et al. 1980a). In *Chaerophyllum cicutaria*, only the distal secondary constrictions are elongated during early metaphase, while the proximal ones are always short. This may mean that only the former, or that mainly the former, function as NORs.

Nucleolar chromosomes, both satellited ones and those with terminally located NORs, have been found to be morphologically variable in a number of plant species. Their structures have been closely examined mostly in plants whose karyotypes comprise more than one nucleolar chromosome pair, for example, in representatives of such genera as *Allium* (Bougourd and Parker 1976, Yampol 1977, Sato et al. 1980a, b, Sato 1981), *Bellevalia* (Maggini 1972), *Aconitum* (Malakhova 1979) or *Plantago* (Sharma et al. 1984). As a result of these studies, several types of nucleolar chromosomes have been distinguished. Various characters, such

as chromosome size, arm ratio, secondary constriction length and position, presence and size of satellites (Hore 1974, 1975a, b, 1976, 1977, Bougourd and Parker 1976, Yampol 1977, Malakhova 1979, Sato et al. 1980b, Sato 1981) as well as C-banding patterns (Sato et al. 1980a) have been taken into consideration to distinguish the types. In satellited chromosomes of *Chaerophyllum cicutaria*, the length of chromosome arms and the location of satellites are in all cases alike and it is the satellite itself that is the only variable chromosome part. It is divided into two or three segments, whose sizes vary to such extent that seven SAT chromosome types can be distinguished.

Satellites divided into segments and secondary constrictions with chromomeres visible along their length are not uncommon features of nucleolar chromosomes (Dyer 1963, Bougourd and Parker 1976). In the *Umbelliferae* family, chromosomes with "tandem satellites" very similar to those observed in *Chaerophyllum cicutaria* have been found in two varieties of *Angelica acutiloba* (Hatano et al. 1974a), in *Heracleum candicans* (Hamal et al. 1983) and in *Ormopterum turcomanicum* (Geldikhanov and Zakharjeva 1984). Moreover, chromosomes with three constrictions (described as primary, secondary and supernumerary ones) have been reported in several other umbellifers (Sharma and Ghosh 1954, Hore 1974, 1975a, b, 1976, 1977).

The occurrence of polymorphic SAT chromosomes in *Chaerophyllum cicutaria* proves that karyological differentiation does exist within the species. The variation observed in the chromosomes of other pairs is therefore more likely to be real than artificial, even if there is scarcely any correlation between it and the variation in SAT chromosomes. For example, the L-5 and M-1b plants, whose SAT chromosomes are of the same type, show considerable differences in the morphology of the largest *m* pair and the *sm* pair.

Since the *Chaerophyllum cicutaria* plants examined represent various populations of the species, the karyological differentiation observed among them may to some extent attest to an interpopulational variation. On the other hand, as only single plants have been examined from most of the populations, some other karyotypes may occur within particular populations in addition to the ones described. This problem requires further studies, all the more so since an intrapopulational karyological variation has been shown to exist here as well. Apart from the M-1 and M-2 populations from which the two plants studied appeared to be karyologically different in both cases, karyological variation may also be expected in all those populations whose specimens are structural heterozygotes. Future studies should involve far more individuals from selected populations.

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Analiza kariotypu Chaerophyllum cicutaria Vill. ze szczególnym uwzględnieniem chromosomów satelitarnych

Streszczenie

Badano rośliny *Chaerophyllum cicutaria* (*Umbelliferae*) pochodzące z naturalnych stanowisk, zarówno górskich jak i niżowych. Wszystkie rośliny miały $2n = 22$ chromosomy, lecz ich kariotypy, mimo że bardzo do siebie podobne, wykazywały pewne drobne lecz wyraźne różnice. W skład diploidalnego zestawu chromosomów wchodziła pojedyncza para chromosomów z satelitami, które składały się z dwóch lub trzech odcinków odgraniczonych przewężeniami. Wyróżniono siedem typów chromosomów satelitarnych różniących się między sobą liczbą i wielkością odcinków satelity. Pod względem morfologii chromosomów satelitarnych badany gatunek wykazywał między- i wewnątrzpopulacyjną zmienność kariologiczną.