

# Cytology

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(1958–1970). It comprises investigations on the karyology, morphology, geographical distribution and ecology of *Antennaria carpatica* s.str., *A. villifera* and, partially, *A. lanata*. The results of our cyto-embryological studies were previously published (URBAŃSKA 1959, URBAŃSKA-WORYTKIEWICZ 1961, 1962, 1962a, 1965, 1967, 1967a, 1967b, 1968, 1969); observations on the embryology of *Antennaria carpatica* s.str. from the Alps and the Pyrenees remained unpublished.

## 2. Cytology

### 2.1 Material and methods

Material for the present study consisted of plants collected in North Scandinavia, the Tatra Mountains, the Alps and the Pyrenees. The voucher specimens were deposited at the Institute of Special Botany, Swiss Federal Institute of Technology, Zurich; some of them were also forwarded to the Botanical Department of the Tromsø Museum, Tromsø, Norway.

Scandinavian plants and the material from the Tatra Mountains were fixed in their natural habitats. Fixation of the material from the Alps and the Pyrenees was mostly performed in the experimental garden of the Botanical Institute, University of Neuchâtel, where the plants were transferred from their alpine localities. The root tips were left for 3–4 hours in a 0.05% aqueous solution of colchicine. Subsequently, they were fixed in acetic alcohol (1 : 3) with a small addition of ferric acetate and acetocarmine. The squashes were stained with lacto-propionic orcein.

For the analysis of karyotype, *Antennaria carpatica* s.str. from 6 localities in the Tatra Mountains, 10 localities in the Alps and a single locality in the Pyrenees was selected (Table 3). It should be noted that plants with tomentose and non-tomentose upper surface of the rosette leaves were studied separately; however, no evident differences in the chromosome morphology were found. Likewise no differences of karyotype occurred between staminate and pistillate plants.

As far as *Antennaria villifera* is concerned, 15 clones were studied; 6 of them represented the tetraploid cytotype whereas 9 were hexaploid (Table 2).

For the studies on the chromosome morphology, 8–12 well-spaced metaphase plates of each plant were observed. In addition, we have measured chromosomes in incomplete plates; however, the results are not included into the material presented in the resp. tables. As a criterion for the same degree of contraction of the chromosomes the length of the SAT-chromosomes

Table 2

List of habitats of *Antennaria villifera* selected for the karyotype analysis

No. of fixation	Place of origin	Altitude a. s. l.	2n
4/68N	Troms, Nordreisa: Gaetkuot'aivit, N slope	c.800m	28
6/68N	Troms, Nordreisa: Gaetkuot'aivit, N slope	c.900m	28
7/68N	Troms, Nordreisa: Gaetkuot'aivit, NW slope	c.1000m	28
10/68N	Troms, Nordreisa: Gaetkuot'aivit, W slope	c.1000m	28
12/68N	Troms, Nordreisa: Javreoav'vit, NE slope	c.1000m	28
14/68N	Troms, Kåfjord: Guolas'javre, between Gåd'dečáro and Sinaivarri	c.800m	28
<hr/>			
1/68N	Troms, Nordreisa: Vuoddujåkka	c.700m	42
2/68N	Troms, Nordreisa: between Vuoddujåkka and Gaetkuot'aivit	c.750m	42
8/68N	Troms, Nordreisa: Gaetkuot'aivit, N slope	c.850m	42
11/68N	Troms, Nordreisa: Gaetkuot'aivit, the top ridge	1020m	42
13/68N	Troms, Kåfjord: Guolas'javre, Gåd'dečáro	c.800m	42
15/68N	Troms, Kåfjord: Sinaivarri, S slope	c.850m	42
16/68N	Troms, Storfjord: Paras, E slope	c.800m	42
18/68N	Troms, Storfjord: Paras, NE slope	c.950m	42
19/68N	Troms, Storfjord: Paras, SE ridge	c.950m	42

was used. In *Antennaria carpatICA* s.str. where two types of the SAT-chromosomes occur, the length of smaller SAT-chromosomes was checked. Measurements were performed on camera lucida drawings at the magnification  $4000\times$ . The accepted accuracy was  $0.25\ \mu$ .

The length of the two arms was measured separately for each chromosome. Subsequently, modal and average values for the length of each type of chromosomes were calculated. It should be emphasized that the length of the satellite region was included into the measurements as the differences in morphology of the SAT-chromosomes are well pronounced in the two species. The results of the metaphase analysis were compared with the prophase in order to check the structural differences occurring between the resp. types of chromosomes.

Table 3

List of habitats of *Antennaria carpatica* s. str. selected for the karyotype analysis

No of fixation	Place of origin	Altitude a. s. l.	2n
I. the Tatra Mts:			
1/69T	the cirque Kocioł Mięguszowiecki	c.1850m	56
2/69T	NW slope of Żabie - over the Valley of Morskie Oko	c.1750m	56
3/69T	near the pass Przełęczka pod Żabią Czuba	c.1800m	56
4/69T	Pośrednia Turnia, NE ridge	c.1900m	56
5/69T	Gąsienicowa Turnia, S steep rocky slope	c.2000m	56
6/69T	Pass Zmarzła	c.2100m	56
II. the Alps:			
67-927	the Bernese Alps: Oberaarsee	c.2350m	56
67-937	the Bernese Alps: Oberaarsee	c.2200m	56
67-940	the Fribourg Alps: Kaiseregg	2100m	56
67-876	the Pennine Alps: Simplon, Kaltwasser	c.2320m	56
4/69A	the Pennine Alps: l'Etherolla over Veyssonaz	c.2400m	56
67-938	the Pennine Alps: Mt. Rouge	c.2450m	56
67-935	the Pennine Alps: Riffelberg	c.2600m	56
6/69A	the Rhaetian Alps: Nufenenpass	c.2400m	56
26/67AM	the Maritime Alps: Cime de Mercantour, over the valley of Boréon	c.2775m	56
67-936	the Bergamo Alps: Val di Scalve, Passo di Vivione	c.2200m	56
III. the Pyrenees:			
68-1197	Vallée des Planès	c.2400m	56

## 2.2 Chromosome numbers

The *Antennaria carpatica* complex shows a karyological differentiation within the range of its distribution. First reports concerning the chromosome number of this group were given by BERGMAN (1935) who found a hexaploid, 40-42chromosomic cytotype in North Sweden. The present author's investigations carried out in Scandinavia led to reveal not only the hexaploid but also a tetraploid, 28chromosomic type (URBAŃSKA-WORYTKIEWICZ 1967,



1967a, 1967b). These results were recently confirmed by ENGELSKJØN and KNABEN (in press); they are also in accordance with the author's further cytological studies dealing with the Scandinavian material collected in 1968 (Figs. 2, 3, 27, 30).

The two above described cytotypes of *Antennaria villifera* do not only occur in European part of its arctic range; recently, ЗНУКОВА (1968) found tetra- and hexaploid plants in the Chukotchka Peninsula. In accordance



Figs. 2-4. Root-tip metaphases. 2. Tetraploid *Antennaria villifera*,  $2n=28$ . 3. Hexaploid *A. villifera*,  $2n=42$ . 4. *A. carpatica* s.str.,  $2n=56$ . C.  $2200\times$ .

with the present author's observations, she noted a notable morphological similarity occurring between the two types.

The results of the Russian author are particularly interesting in view of the fact that the Chukotchka Peninsula represents the easternmost limit of the range of *Antennaria villifera*. The occurrence of these same cytotypes in two opposite parts of the range seems to have an evolutionary value.

*Antennaria carpatica* s. str. shows a higher level of polyploidy. In the Tatra Mountains, the Alps and the Pyrenees the same octoploid chromosome number  $2n=56$  was found (URBAŃSKA 1959, URBAŃSKA-WORYTKIEWICZ 1961, 1962, 1962a, 1965, 1967, 1968, 1968a; Figs. 4, 31).

When compared to other arctic-alpine groups in the European flora, the *Antennaria carpatica* complex represents a less frequent pattern of polyploid differentiation: higher polyploids occur in Central and Western Europe whereas lower polyploids were found exclusively in the North.

Cytological data concerning the American representatives of the complex are still inadequate. The only chromosome number reported for *Antennaria pulcherrima* from Canada is  $2n=63$  (LÖVE and SOLBRIG 1964). In view of the fact that *A. pulcherrima* has rather a regular pollen and is supposed to be a sexual species (PORSILD 1965) it would be interesting to know its chromosome numbers from the whole area of distribution.

*Antennaria lanata* has not been studied cytologically hitherto. According to the measurements of the pollen diameter performed by the present author on some plants from British Columbia and Alberta, it seems to be a tetraploid type (Fig. 13). Further investigations in this respect are required.

### 2.3 Analysis of the karyotype

*Antennaria villifera*  $2n=28, 42$

Tetraploid cytotype. The length of chromosomes within the set of 28 chromosomal *Antennaria villifera* ranges from  $2.50 \mu$  to  $5.00 \mu$ . 14 chromosome pairs are presented in Fig. 5. The comparison of morphology and size of chromosomes led to distinguish 4 groups among these 14 pairs. Their short description is given below:

- (a) the smallest ( $2.47-2.49 \mu$ ) chromosomes with median centromere (Pairs XIII and XIV);
- (b) chromosomes with submedian centromere (Pairs III, IV, V, VI, VII, IX, X, XI and XII);
- (c) the biggest ( $4.26-4.98 \mu$ ) chromosomes with submedian centromere (Pairs I and II);

(d) SAT-chromosomes with submedian centromere (Pair VIII). The diameter of the satellite usually equals that of the chromosome arms; it corresponds also to the length of the shorter arm (Tables 4, 5).

Thus, the tetraploid set of *Antennaria villifera* consists of metacentric chromosomes. A special attention should be paid to a remarkable similarity occurring between some pairs of chromosomes. These types are: IX and X, XI and XII as well as XIII and XIV (Tables 4, 5). The length differences observed in most of the other pairs did not exceed  $0.27\ \mu$ , except Pair I where an average length difference amounted to  $0.72\ \mu$ . The most characteristic pair of the set was that of the SAT-chromosomes; it should be noted that the length of their arms corresponds to that of Pairs IX and X (Tables 4, 5).

The results of the present investigations are in favour of GUSTAFSSON's hypothesis concerning the somatic chromosome number  $2n=28$  as a tetraploid within the genus *Antennaria* (GUSTAFSSON 1947). The pronounced similarity occurring between some pairs of chromosomes in *Antennaria villifera* might be explained by doubling of a 14chromosomic type. On the other hand, the differentiation observed within the tetraploid set permits to assume that it represents an ancient cytotype in which the phylogenetic processes of length alteration could have proceeded at various speeds in the respective chromosomes; accordingly, some of them might have remained unaltered, whilst in the others, structural changes might have taken place. In view of this, tetraploid *Antennaria villifera* should be classified as a paleopolyploid type, according to the nomenclature proposed recently by FAVARGER (1961).

Hexaploid cytotype. The range of length variability of the chromosomes in hexaploid *Antennaria villifera* corresponds to that of the tetraploid type; it comports  $2.50\ \mu$  to  $5.25\ \mu$ . As in the tetraploids, metacentric chromosomes occur in the hexaploid set; among them three SAT-chromosomes could be observed (Figs. 3, 6, 30, Tables 6, 7).

The frequency of chromosomes belonging to the definite types deserves a special mention. Out of the 15 types distinguished according to their morphology, 12 comprised three chromosomes whereas three others consisted of chromosome pairs. This karyotype was established as a result of measurements performed on 74 metaphase plates belonging to plants from 8 localities in North Norway (Tables 6, 7). In addition, a deviating karyotype was found in the material from Gaetkuot'aivit, Troms (clone No. 2/68). In this particular set, type I consisted of a chromosome pair whereas type VI was represented by a single chromosome (Table 8). A comparison of the two karyotypes found in hexaploid *A. villifera* is given in Table 9.

Further interesting details were found in the course of a comparative morphological study on chromosomes occurring in tetra- and hexaploid sets.



Table 5

The chromosome length within the tetraploid set of *Antennaria villifera*; a comparison between the modal values and the average values (length in  $\mu$ )

Pair	Mo				M			
	Longer arm	Shorter arm	Satellite	Total length	Longer arm	Shorter arm	Satellite	Total length
I	2.75	2.25	-	5.00	2.77	2.21	-	4.98
II	2.25	2.00	-	4.25	2.25	2.01	-	4.26
III	2.25	1.75	-	4.00	2.24	1.75	-	3.99
IV	2.25	1.50	-	3.75	2.25	1.49	-	3.74
V	2.25	1.00	-	3.25	2.24	0.99	-	3.23
VI	2.00	1.50	-	3.50	1.98	1.48	-	3.46
VII	2.00	1.25	-	3.25	1.99	1.24	-	3.23
VIII	2.00	1.00	0.75	3.75	1.98	1.01	0.74	3.73
IX	2.00	1.00	-	3.00	1.97	1.00	-	2.97
X	2.00	1.00	-	3.00	1.98	1.00	-	2.98
XI	1.50	1.25	-	2.75	1.47	1.25	-	2.72
XII	1.50	1.25	-	2.75	1.48	1.23	-	2.71
XIII	1.25	1.25	-	2.50	1.26	1.23	-	2.49
XIV	1.25	1.25	-	2.50	1.25	1.22	-	2.47

Table 6

A. villifera; Variability of the chromosome length in hexaploid type: results of measurements of the particular chromosomes in 74 metaphase plates (length in  $\mu$ )

Type	Longer arm										Shorter arm							Satellite			
	0.75	1.00	1.25	1.50	1.75	2.00	2.25	2.50	2.75	3.00	0.75	1.00	1.25	1.50	1.75	2.00	2.25	2.50	0.50	0.75	1.00
I	-	-	-	-	-	-	1	16	200	5	-	-	-	-	-	2	13	207	-	-	-
II	-	-	-	-	-	-	-	221	1	-	-	-	-	-	1	12	18	191	-	-	-
III	-	-	-	-	1	2	10	206	3	-	18	198	3	3	-	-	-	-	-	-	-
IV	-	-	-	-	5	6	136	1	-	-	-	-	-	-	19	129	-	-	-	-	-
V	-	-	-	-	2	5	141	-	-	-	-	-	7	139	2	-	-	-	-	-	-
VI	-	-	-	-	1	19	124	4	-	-	9	132	5	2	-	-	-	-	-	-	-
VII	-	-	-	-	14	200	5	3	-	-	-	-	-	2	16	197	7	-	-	-	-
VIII	-	-	-	-	-	217	1	4	-	-	-	-	-	13	206	3	-	-	-	-	-
IX	-	-	-	1	14	196	5	6	-	-	1	5	8	203	4	1	-	-	-	-	-
X	-	-	1	6	9	202	4	-	-	-	-	3	16	186	15	2	-	-	-	-	-
XI	-	-	-	9	16	191	6	-	-	-	1	213	5	3	-	-	-	-	1	218	3
XII	-	-	-	7	8	182	20	5	-	-	16	202	4	-	-	-	-	-	-	-	-
XIII	-	-	-	6	30	179	5	2	-	-	8	194	13	5	2	-	-	-	-	-	-
XIV	-	6	18	176	19	3	-	-	-	-	1	18	192	9	2	-	-	-	-	-	-
XV	2	7	196	11	6	-	-	-	-	-	3	17	201	1	-	-	-	-	-	-	-

Table 7

The chromosome length in the typical hexaploid set of *Antennaria villifera*: a comparison between the modal values and the average values (length in  $\mu$ )

Type	Mo				M			
	Longer arm	Shorter arm	Satellite	Total length	Longer arm	Shorter arm	Satellite	Total length
I	2.75	2.50	-	5.25	2.71	2.48	-	5.19
II	2.50	2.50	-	5.00	2.50	2.44	-	4.94
III	2.50	1.00	-	3.50	2.25	0.98	-	3.23
IV	2.25	2.00	-	4.25	2.18	1.96	-	4.14
V	2.25	1.50	-	3.75	2.23	1.49	-	3.72
VI	2.25	1.00	-	3.25	2.22	0.99	-	3.21
VII	2.00	2.00	-	4.00	1.99	1.98	-	3.97
VIII	2.00	1.75	-	3.75	2.01	1.73	-	3.74
IX	2.00	1.50	-	3.50	2.01	1.48	-	3.49
X	2.00	1.50	-	3.50	1.95	1.49	-	3.44
XI	2.00	1.00	0.75	3.75	1.96	1.01	0.75	3.72
XII	2.00	1.00	-	3.00	2.01	0.98	-	2.99
XIII	2.00	1.00	-	3.00	1.96	1.01	-	2.97
XIV	1.50	1.25	-	2.75	1.49	1.24	-	2.73
XV	1.25	1.25	-	2.50	1.21	1.22	-	2.43

Table 8

Variability of the chromosome length in deviating karyotype of hexaploid *Antennaria villifera* from Gaetkuot'aivit, Troms: results of measurements in 12 metaphase plates (length in  $\mu$ )

Type	Longer arm									Shorter arm									Satellite	
	1.00	1.25	1.50	1.75	2.00	2.25	2.50	2.75	3.00	0.75	1.00	1.25	1.50	1.75	2.00	2.25	2.50	0.50	0.75	1.00
I	-	-	-	-	-	1	2	20	1	-	-	-	-	-	1	2	21	-	-	-
II	-	-	-	-	-	-	31	5	-	-	-	-	-	-	1	2	33	-	-	-
III	-	-	-	-	-	2	34	-	-	3	28	4	1	-	-	-	-	-	-	-
IV	-	-	-	-	5	27	4	-	-	-	-	-	1	1	31	3	-	-	-	-
V	-	-	1	1	2	30	2	-	-	-	-	3	28	4	1	-	-	-	-	-
VI	-	-	-	-	1	8	3	-	-	1	9	1	1	-	-	-	-	-	-	-
VII	-	-	-	-	36	-	-	-	-	-	-	-	-	2	34	-	-	-	-	-
VIII	-	-	-	-	35	1	-	-	-	-	-	-	1	32	2	1	-	-	-	-
IX	-	-	-	2	31	3	-	-	-	-	-	3	30	3	-	-	-	-	-	-
X	-	-	-	8	26	1	1	-	-	-	2	3	26	4	1	-	-	-	-	-
XI	-	-	-	2	33	1	-	-	-	2	29	4	1	-	-	-	-	1	34	1
XII	-	-	1	1	29	4	1	-	-	3	29	2	2	-	-	-	-	-	-	-
XIII	-	-	1	2	32	-	1	-	-	-	31	3	2	-	-	-	-	-	-	-
XIV	-	4	32	-	-	-	-	-	-	-	3	30	2	1	-	-	-	-	-	-
XV	4	31	1	-	-	-	-	-	-	-	2	33	1	-	-	-	-	-	-	-



Table 9

Hexaploid *A. villifera*: frequency of particular chromosome types in a typical set as well as in a deviating one (modal values of the chromosome length in  $\mu$ )

Longer arm	Shorter arm	Satellite	Total length	Number of chromosomes	
				Typical set	Deviating set
2.75	2.50	-	5.25	3	2
2.50	2.50	-	5.00	3	3
2.50	1.00	-	3.50	3	3
2.25	2.00	-	4.25	2	3
2.25	1.50	-	3.75	2	3
2.25	1.00	-	3.25	2	1
2.00	2.00	-	4.00	3	3
2.00	1.75	-	3.75	3	3
2.00	1.50	-	3.50	3	3
2.00	1.50	-	3.50	3	3
2.00	1.00	0.75	3.75	3	3
2.00	1.00	-	3.00	3	3
2.00	1.00	-	3.00	3	3
1.50	1.25	-	2.75	3	3
1.25	1.25	-	2.50	3	3

Some notably similar types were found in both forms; their modal and average values as well as the resp. frequency are presented in Table 10. Pairs: II, III, VI, VIII, IX, X, XI and XIV of the tetraploid set had exactly corresponding types in the hexaploid form. It should be emphasized that the SAT-chromosomes, the most characteristic pair of the tetraploid set and the three SAT-chromosomes found in the hexaploids showed identical modal values and their average values differed only in 0.21  $\mu$ .

Thus, out of the 14 pairs representing the karyotype of tetraploid *Antennaria villifera*, only two were missing in the hexaploid set; on the other hand, three types found in the hexaploids had no exactly corresponding pairs in the tetraploid form.

The results of the present investigations confirm the author's previous observations on microporogenesis in *Antennaria villifera* from North Scan-

Table 10

*Antennaria villifera*: frequency of particular chromosome types in tetra- and hexaploid set (length in  $\mu$ )

Type	Tetraploid set			Hexaploid set		
	Mo	M	Number of chromosomes	Mo	M	Number of chromosomes
I	5.00	4.98	2	5.25	5.19	3
II	4.25	4.26	2	4.25	4.14	2
III	4.00	3.99	2	4.00	3.97	3
IV	3.75	3.74	2	3.75	3.72	2
V	3.25	3.23	2	3.25	3.21	2
VI	3.50	3.46	2	3.50	3.49	3
VII	3.25	3.23	2	3.50	3.44	3
VIII	3.75	3.73	2	3.75	3.72	3
IX	3.00	2.97	2	3.00	2.97	3
X	3.00	2.98	2	3.00	2.99	3
XI	2.75	2.72	2	2.75	2.73	3
XII	2.75	2.71	2	-	-	-
XIII	2.50	2.49	2	-	-	-
XIV	2.50	2.47	2	2.50	2.43	3
	-	-	-	3.75	3.74	3
	-	-	-	3.50	3.23	3
	-	-	-	5.00	4.94	3

dinavia (URBAŃSKA-WORYTKIEWICZ 1967a). The occurrence of trivalens as well as variable and incomplete chromosome pairing found in the hexaploids could be explained by the fact that the resp. types mostly comprised three chromosomes. This particular frequency, in connection with a notable similarity of the chromosome types occurring within the tetra- and hexaploid sets permits to infer a close mutual relationship between the two cytotypes. This is in favour of our hypothesis concerning a putative origin of a hexaploid *Antennaria villifera*: it seems probable that it could have derived from a tetraploid form with a part of an unreduced gamete.

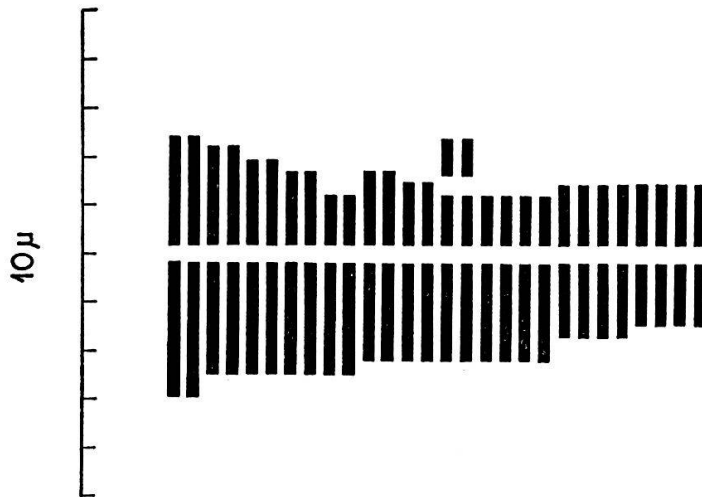


Fig. 5. Chromosome complement of tetraploid *Antennaria villifera*.

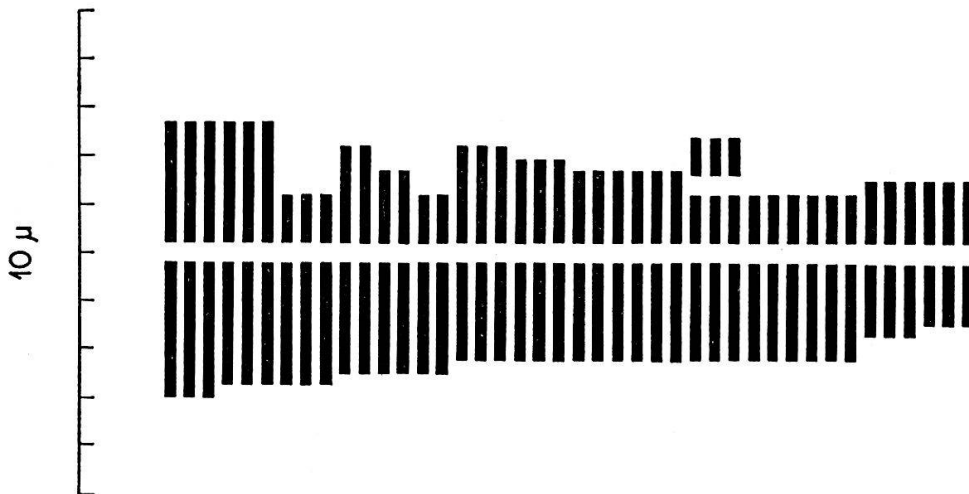


Fig. 6. Chromosome complement of hexaploid *Antennaria villifera*.

*Antennaria carpatica* s.str.  $2n=56$

As it was noted above, *A. carpatica* s.str. represents the same level of polyploidy within its whole range of distribution: in all plants studied from the Tatra Mountains, the Alps as well as from the Pyrenees, an octoploid chromosome number  $2n=56$  was invariably found.

The length of the chromosomes within the octoploid set ranged from  $1.69 \mu$  to  $5.02 \mu$ . The chromosomes were mostly metacentric; however, four pairs of acrocentric chromosomes also occurred in studied material. In this respect *Antennaria carpatica* s.str. differs from *A. villifera* whose sets consist exclusively of chromosomes with median or submedian centromeres.

It should be noted that the identification of some of the homologous chromosomes presented serious difficulties in view of the fact that some morphological types were sometimes represented by more than one pair. These identical pairs found in the material from the Tatra Mountains were: Pairs XV and XVI, XXII and XXIII, XXV and XXVI (Tables 11, 12, Fig. 7). In the plants from the Alps, the frequency of identical types was somewhat different: one type was represented by four pairs (XX–XXIII); in addition, Pairs XV and XVI as well as XI and XII were almost impossible to distinguish from each other (Tables 13, 14, Fig. 8). The highest frequency of exactly corresponding types was observed in a single population studied from the Pyrenees: as many as 11 pairs were grouped into similar types (Pairs XII–XIII, XV–XVI, XVIII–XIX, XX–XXII, XXIV–XXV). Moreover, type XXIII comprised five chromosomes instead of two pairs. Unfortunately, lack of a comparative material from the Pyrenees renders impossible any definite conclusion concerning this deviation (Tables 15, 16, Fig. 9).

The most characteristic components of the octoploid set, occurring invariably in all of the studied metaphase plates, were three pairs of chromosomes. One of them was a pair of the smallest ( $1.68\text{--}1.71\ \mu$ ) chromosomes with a subterminal centromere. The index (S.A./L.A.) comported  $0.34\text{--}0.35$ . Two other pairs consisted of SAT-chromosomes. In view of their characteristic morphological differences a detailed description is given below.

SAT-chromosomes occurring within the octoploid set were divided into three well-defined regions: the long arm region (L.A.) extending from the distal end of the long arm to the centromere; the short arm region (S.A.) extending from the centromere to the secondary constriction; the short arm region "S" extending from the secondary constriction to the distal end of the satellite. The two types are presented in Fig. 10.

The first pair of SAT-chromosomes had a submedian centromere. The index values comported  $0.57$  in the material from the Tatra Mountains as well as from the Pyrenees; in the plants from the Alps the resp. value was slightly lower ( $0.54$ ). The length of the satellite was about a half of the short arm ( $0.50\text{--}0.76\ \mu$ ). The secondary constriction was mostly conspicuous; in some cases, however, the satellite was adpressed to the short arm.

The second pair of SAT-chromosomes showed a quite different morphology. The index values ranged from  $0.38$  to  $0.40$ . The length of the short arm was nearly the same as in the first type; by contrast, the long arm was much longer than that of the first pair. The resp. length differences between the two pairs amounted to  $0.84\ \mu$ .

The most remarkable characteristic was the length of the "S" region. Its average values were established as  $1.50\ \mu$  in the material from the Tatra

Table 11

Variability of the chromosome length of *Antennaria carpatica* s. str. from the Tatra Mts: results of measurements in 54 metaphase plates (length in  $\mu$ )

Pair	Longer arm										Shorter arm										Satellite									
	0.75	1.00	1.25	1.50	1.75	2.00	2.25	2.50	2.75	0.25	0.50	0.75	1.00	1.25	1.50	1.75	2.00	2.25	2.50	2.75	0.25	0.50	0.75	1.00	1.25	1.50	1.75	2.00		
I	-	-	-	-	-	1	2	102	3	-	-	-	-	-	-	-	3	2	102	2	-	-	-	-	-	-	-	-	-	
II	-	-	-	-	-	-	1	106	1	-	-	-	-	-	-	-	1	2	104	1	-	-	-	-	-	-	-	-	-	
III	-	-	-	-	-	1	5	97	5	-	-	-	-	-	-	-	2	104	1	-	-	-	-	-	-	-	-	-	-	
IV	-	-	-	-	-	-	3	103	2	-	5	100	2	1	-	-	2	1	-	-	-	-	-	-	-	-	-	-	-	
V	-	-	-	-	-	2	2	100	4	-	-	1	4	95	8	-	4	95	8	-	-	-	-	-	-	-	-	-	-	
VI	-	-	-	-	-	8	97	3	-	-	-	-	-	-	-	-	5	102	1	-	-	-	-	-	-	-	-	-	-	
VII	-	-	-	-	-	1	4	101	2	-	-	-	-	1	103	4	-	-	-	-	-	-	-	-	-	-	-	-	-	
VIII	-	-	-	-	-	-	6	96	5	1	-	5	101	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
IX	-	-	-	-	-	1	2	104	1	-	1	106	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
X	-	-	-	-	-	5	98	4	-	-	-	-	-	-	-	-	3	99	4	2	-	-	-	-	-	-	-	-	-	
XI	-	-	-	-	-	2	100	4	2	-	-	-	1	2	103	1	1	-	-	-	-	-	-	-	-	-	-	-	-	
XII	-	-	-	-	-	8	97	3	-	-	-	2	101	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
XIII	-	-	-	-	-	3	105	-	-	-	7	98	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
XIV	-	-	-	-	-	4	101	2	1	-	3	103	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
XV	-	-	-	-	-	4	98	2	-	-	-	1	2	102	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
XVI	-	-	-	-	-	3	103	2	-	-	-	-	2	99	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
XVII	-	-	-	-	-	4	97	5	-	-	-	4	100	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
XVIII	-	-	-	-	-	1	1	104	2	-	1	105	2	-	-	-	2	1	-	-	-	-	-	-	-	-	-	-	-	
XIX	-	-	-	-	-	2	4	101	1	-	-	107	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
XX	-	-	-	-	-	2	106	-	-	-	-	-	3	2	100	3	-	-	-	-	-	-	-	-	-	-	-	-	-	
XXI	-	-	-	-	-	5	94	5	2	-	-	-	4	101	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	
XXII	-	-	-	-	-	3	101	3	-	-	-	-	105	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
XXIII	-	-	-	-	-	5	99	2	-	-	-	2	102	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
XXIV	-	-	-	-	-	3	100	5	-	-	-	4	101	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
XXV	-	-	-	-	-	4	102	2	-	-	-	7	99	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
XXVI	1	2	97	7	1	-	-	-	-	-	-	4	103	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
XXVII	1	2	104	1	-	-	-	-	-	1	2	102	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
XXVIII	-	6	98	3	1	-	-	-	-	30	76	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	

Table 12

The chromosome length within the set of *A. carpatica* s. str. from the Tatra Mts: a comparison between the modal values and the average values (length in  $\mu$ )

Pair	Mo				M			
	Longer arm	Shorter arm	Satellite	Total length	Longer arm	Shorter arm	Satellite	Total length
I	2.50	2.50	-	5.00	2.49	2.50	-	4.99
II	2.50	2.00	-	4.50	2.50	1.98	-	4.48
III	2.50	1.75	-	4.25	2.49	1.75	-	4.24
IV	2.50	1.00	1.50	5.00	2.49	0.99	1.50	4.98
V	2.50	1.50	-	4.00	2.49	1.50	-	3.99
VI	2.25	1.75	-	4.00	2.23	1.74	-	3.97
VII	2.25	1.50	-	3.75	2.24	1.50	-	3.74
VIII	2.25	1.00	-	3.25	2.25	0.99	-	3.24
IX	2.25	0.50	-	2.75	2.24	0.50	-	2.74
X	2.00	1.75	-	3.75	1.99	1.76	-	3.75
XI	2.00	1.50	-	3.50	2.01	1.49	-	3.50
XII	2.00	1.25	-	3.25	1.98	1.25	-	3.23
XIII	2.00	1.00	-	3.00	1.99	0.99	-	2.98
XIV	2.00	0.75	-	2.75	2.00	0.74	-	2.74
XV	1.75	1.50	-	3.25	1.74	1.49	-	3.23
XVI	1.75	1.50	-	3.25	1.74	1.51	-	3.25
XVII	1.75	1.00	-	2.75	1.74	0.99	-	2.73
XVIII	1.75	1.00	0.50	3.25	1.74	1.00	0.50	3.24
XIX	1.75	0.75	-	2.50	1.73	0.75	-	2.48
XX	1.50	1.50	-	3.00	1.49	1.48	-	2.97
XXI	1.50	1.25	-	2.75	1.50	1.25	-	2.75
XXII	1.50	1.00	-	2.50	1.50	1.00	-	2.50
XXIII	1.50	1.00	-	2.50	1.48	1.00	-	2.48
XXIV	1.50	0.75	-	2.25	1.50	0.74	-	2.24
XXV	1.25	1.00	-	2.25	1.24	0.99	-	2.23
XXVI	1.25	1.00	-	2.25	1.26	0.99	-	2.25
XXVII	1.25	0.75	-	2.00	1.24	0.74	-	1.98
XXVIII	1.25	0.50	-	1.75	1.25	0.44	-	1.69

Table 13

Variability of the chromosome length of *Antennaria carpatica* s. str. from the Alps: results of measurements in 86 metaphase plates (length in  $\mu$ )

Pair	Longer arm										Shorter arm										Satellite									
	0.75	1.00	1.25	1.50	1.75	2.00	2.25	2.50	2.75	3.00	0.25	0.50	0.75	1.00	1.25	1.50	1.75	2.00	2.25	2.50	2.75	0.25	0.50	0.75	1.00	1.25	1.50	1.75	2.00	
I	-	-	-	-	-	2	5	164	1	-	-	-	-	-	-	-	-	-	1	8	162	1	-	-	-	-	-	-	-	-
II	-	-	-	-	-	3	8	155	5	1	-	-	-	-	2	7	160	3	-	-	-	-	-	-	-	-	-	-	-	-
III	-	-	-	-	-	1	4	162	5	-	-	3	2	163	4	-	-	-	-	-	-	-	-	-	-	-	3	6	161	2
IV	-	-	-	-	-	-	2	170	-	-	-	-	-	2	2	164	4	-	-	-	-	-	-	-	-	-	-	-	-	-
V	-	-	-	-	-	1	2	166	2	-	-	-	-	-	-	-	-	-	2	167	2	-	-	-	-	-	-	-	-	-
VI	-	-	-	-	-	4	4	156	7	1	-	-	-	-	1	6	160	4	1	-	-	-	-	-	-	-	-	-	-	-
VII	-	-	-	-	-	4	8	159	1	-	-	-	-	-	5	162	8	-	-	-	-	-	-	-	-	-	-	-	-	-
VIII	-	-	-	-	-	1	9	156	6	-	-	1	3	160	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
IX	-	-	-	-	-	2	163	5	2	-	-	-	-	-	-	1	4	161	6	-	-	-	-	-	-	-	-	-	-	-
X	-	-	-	-	-	9	158	4	1	-	-	-	-	7	161	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-
XI	-	-	-	-	-	1	167	4	-	-	-	-	1	164	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
XII	-	-	-	-	-	4	166	2	-	-	-	-	2	169	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
XIII	-	-	-	-	-	6	158	5	-	-	-	7	162	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
XIV	-	-	-	-	-	5	161	6	-	-	-	-	-	-	-	2	170	-	-	-	-	-	-	-	-	-	-	-	-	-
XV	-	-	-	-	-	2	163	4	1	-	-	-	-	1	3	167	1	-	-	-	-	-	-	-	-	-	-	-	-	-
XVI	-	-	-	-	-	9	156	7	-	-	-	-	-	1	3	164	4	-	-	-	-	-	-	-	-	-	-	-	-	-
XVII	-	-	-	-	-	1	8	160	2	1	-	-	1	3	162	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-
XVIII	-	-	-	-	-	4	165	3	-	-	-	6	21	143	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
XIX	-	-	-	-	-	1	7	156	8	-	-	5	163	3	1	-	-	-	-	-	-	-	-	-	-	-	-	1	167	4
XX	-	-	-	-	-	1	169	2	-	-	-	-	-	-	4	167	1	-	-	-	-	-	-	-	-	-	-	-	-	-
XXI	-	-	-	-	-	1	162	4	2	-	-	-	-	-	4	164	2	1	-	-	-	-	-	-	-	-	-	-	-	-
XXII	-	-	-	-	-	9	156	7	-	-	-	-	-	1	8	160	1	3	-	-	-	-	-	-	-	-	-	-	-	-
XXIII	-	-	-	-	-	1	2	166	3	-	-	-	-	-	2	7	162	-	-	-	-	-	-	-	-	-	-	-	-	-
XXIV	-	-	-	-	-	6	158	5	1	-	-	-	-	1	2	170	-	-	-	-	-	-	-	-	-	-	-	-	-	-
XXV	-	-	-	-	-	6	162	2	2	-	-	-	-	-	2	164	6	-	-	-	-	-	-	-	-	-	-	-	-	-
XXVI	-	-	-	-	-	1	167	4	-	-	-	2	1	8	154	6	1	-	-	-	-	-	-	-	-	-	-	-	-	-
XXVII	-	-	-	-	-	4	7	159	1	-	-	1	6	163	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
XXVIII	-	-	-	-	-	5	161	4	3	-	-	126	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 14

The chromosome length of *Antennaria carpatica* s. str. from the Alps: a comparison between the modal values and the average values (length in  $\mu$ )

Pair	Mo.				M			
	Longer arm	Shorter arm	Satellite	Total length	Longer arm	Shorter arm	Satellite	Total length
I	2.50	2.50	-	5.00	2.49	2.49	-	4.98
II	2.50	1.75	-	4.25	2.51	1.74	-	4.25
III	2.50	1.00	1.75	5.25	2.50	0.99	1.73	5.22
IV	2.50	1.50	-	4.00	2.48	1.48	-	3.96
V	2.25	2.25	-	4.50	2.24	2.24	-	4.48
VI	2.25	1.75	-	4.00	2.24	1.75	-	3.99
VII	2.25	1.00	-	3.25	2.23	0.99	-	3.22
VIII	2.25	0.75	-	3.00	2.24	0.75	-	2.99
IX	2.00	1.75	-	3.75	2.01	1.75	-	3.76
X	2.00	1.25	-	3.25	1.99	1.25	-	3.24
XI	2.00	1.00	-	3.00	2.00	1.01	-	3.01
XII	2.00	1.00	-	3.00	2.00	1.00	-	3.00
XIII	2.00	0.75	-	2.75	1.99	0.74	-	2.73
XIV	1.75	1.75	-	3.50	1.74	1.74	-	3.48
XV	1.75	1.50	-	3.25	1.75	1.49	-	3.24
XVI	1.75	1.50	-	3.25	1.75	1.50	-	3.25
XVII	1.75	1.00	-	2.75	1.74	1.00	-	2.74
XVIII	1.75	1.00	0.50	3.25	1.75	0.95	0.50	3.20
XIX	1.75	0.75	-	2.50	1.75	0.75	-	2.50
XX	1.50	1.25	-	2.75	1.50	1.24	-	2.74
XXI	1.50	1.25	-	2.75	1.50	1.25	-	2.75
XXII	1.50	1.25	-	2.75	1.50	1.23	-	2.73
XXIII	1.50	1.25	-	2.75	1.50	1.23	-	2.73
XXIV	1.50	1.00	-	2.50	1.50	1.00	-	2.50
XXV	1.25	1.25	-	2.50	1.25	1.25	-	2.50
XXVI	1.25	1.00	-	2.25	1.25	0.99	-	2.24
XXVII	1.25	0.75	-	2.00	1.23	0.74	-	1.97
XXVIII	1.25	0.50	-	1.75	1.26	0.43	-	1.69



Variability of the chromosome length of *Antennaria carpatica* s. str. from the Pyrenees (Vallée des Planès): results of measurements in 12 metaphase plates (length in  $\mu$ )

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Table 16

The chromosome length of *Antennaria carpatica* s. str. from the Pyrenees (Vallée des Planès): a comparison between the modal values and the average values (length in  $\mu$ )

Mo				M			
Longer arm	Shorter arm	Satellite	Total length	Longer arm	Shorter arm	Satellite	Total length
2.50	2.50	-	5.00	2.53	2.49	-	5.02
2.50	1.75	-	4.25	2.46	1.73	-	4.19
2.50	1.25	-	3.75	2.57	1.24	-	3.81
2.50	1.00	1.75	5.25	2.50	0.95	1.73	5.18
2.25	2.00	-	4.25	2.31	2.01	-	4.32
2.25	1.75	-	4.00	2.26	1.74	-	4.00
2.25	1.00	-	3.25	2.21	1.00	-	3.21
2.25	0.50	-	2.75	2.23	0.58	-	2.81
2.00	1.75	-	3.75	1.95	1.72	-	3.67
2.00	1.75	-	3.75	1.99	1.75	-	3.74
2.00	1.75	-	1.75	2.03	1.77	-	3.80
2.00	1.25	-	3.25	2.01	1.34	-	3.35
2.00	1.00	-	3.00	2.01	1.00	-	3.01
2.00	1.00	-	3.00	1.93	0.99	-	2.92
2.00	0.75	-	2.75	1.99	0.75	-	2.74
1.75	1.50	-	3.25	1.73	1.54	-	3.27
1.75	1.50	-	3.25	1.75	1.46	-	3.21
1.75	1.00	-	2.75	1.76	1.03	-	2.79
1.75	1.00	0.75	3.50	1.74	1.00	0.76	3.50
1.75	1.00	-	2.75	1.71	0.98	-	2.69
1.50	1.25	-	2.75	1.50	1.25	-	2.75
1.50	1.25	-	2.75	1.52	1.29	-	2.81
1.50	1.25	-	2.75	1.48	1.23	-	2.71
1.50	1.00	-	2.50	1.52	0.94	-	2.46
1.50	1.00	-	2.50	1.54	0.93	-	2.47
1.25	1.00	-	2.25	1.26	1.02	-	2.28
1.25	1.00	-	2.25	1.25	1.02	-	2.27
1.25	0.75	-	2.00	1.26	0.77	-	2.03
1.25	0.50	-	1.75	1.27	0.44	-	1.71

Table 17

*Antennaria carpatica* s. str.: a comparison of frequency of particular chromosome types in the material from the Tatra Mts, the Alps as well as from the Pyrenees (modal values of length in  $\mu$ )

Longer arm	Shorter arm	Satellite	Number of chromosomes		
			Tatra Mts	Alps	Pyrenees
2.50	2.50	-	2	2	2
2.50	2.00	-	2	-	-
2.50	1.75	-	2	2	2
2.50	1.50	-	2	2	-
2.50	1.25	-	-	-	2
2.50	1.00	1.75	-	2	2
2.50	1.00	1.50	2	-	-
2.25	2.25	-	-	2	-
2.25	2.00	-	-	-	2
2.25	1.75	-	2	2	2
2.25	1.50	-	2	-	-
2.25	1.00	-	2	2	2
2.25	0.75	-	-	2	-
2.25	0.50	-	2	-	2
2.00	1.75	-	2	2	5
2.00	1.50	-	2	-	-
2.00	1.25	-	2	2	2
2.00	1.00	-	2	4	4
2.00	0.75	-	2	2	2
1.75	1.75	-	-	2	-
1.75	1.50	-	4	4	4
1.75	1.00	0.75	-	-	2
1.75	1.00	0.50	2	2	-
1.75	1.00	-	2	2	4
1.75	0.75	-	2	2	-
1.50	1.50	-	2	-	-
1.50	1.25	-	2	8	6
1.50	1.00	-	4	2	3
1.50	0.75	-	2	-	-
1.25	1.25	-	-	2	-
1.25	1.00	-	4	2	4
1.25	0.75	-	2	2	2
1.25	0.50	-	2	2	2

Table 18

Seed development in *Antennaria villifera* Boriss.

Locality	Herbarium	Stigma	Number of heads	Total number of florets	Number of achenes
I. Scandinavia *					
Lule Lappmark: Gallivarre					
2. VIII. 1936					
G. Björkman	UPS	short	5	244	1
Nordland, Sörfold: Boaimac, riksgrensa					% 0.41
7. VII. 1954					
W. Apold, G. Brodal, O. Skifte	TROM	short	5	232	1
Troms, Balsfjord: Hattevarre					% 0.43
17. VIII. 1934					
P. Benum	TROM	short	6	330	4
Troms, Storfjord: Skibotndalen, Rippovarre					% 1.39
15. VIII. 1936					
P. Benum	TROM	short	6	267	7
Troms, Skjervøy: Vaddas, Lohtana					% 2.62
28. VII. 1937					
Y. Mejland	O	short	6	348	15
Troms, Målselv: Alappen					% 4.37
J. M. Norman	UPS	short	6	251	11
					% 4.38
-----					
II. Kolguyev:					
Insula Kolguyev (typus locality ?)					
1902					
R. Pohle	HEL	short	6	248	28
					% 11.29
-----					
III. Siberia:					
Yakutsk: Buckar					
25. VIII. 1898					
H. Nilssen	S	short	5	227	31
Jenisey, Dudinka					% 13.66
VIII. 1876					
J. R. Sahlberg	LE	short	6	272	46
					% 16.91

\*

all other studied specimens had no seeds.

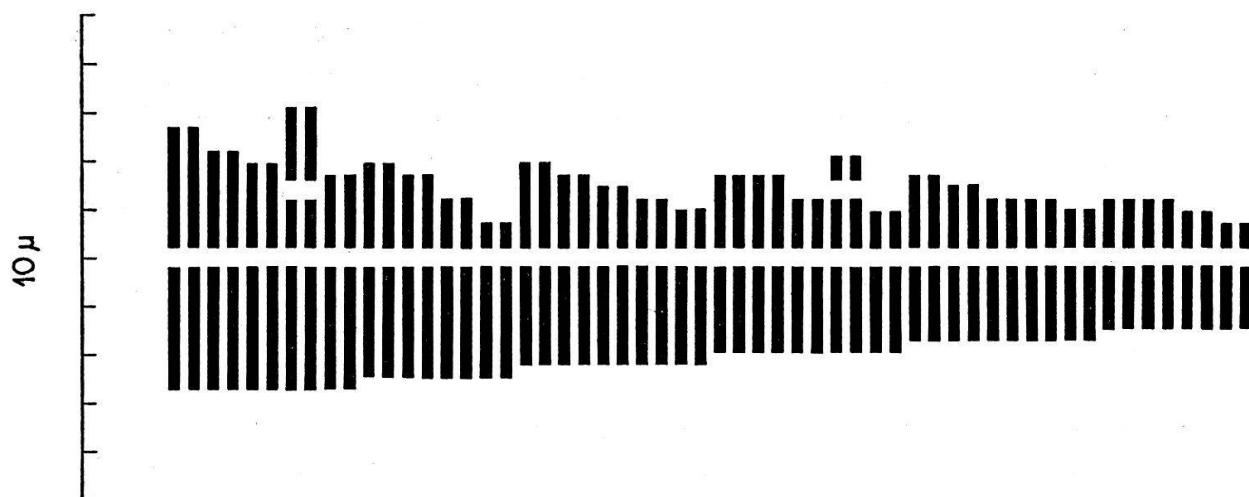


Fig. 7. Chromosome complement of *Antennaria carpatica* s.str. from the Tatra Mountains.



Fig. 8. Chromosome complement of *Antennaria carpatica* s.str. from the Alps.

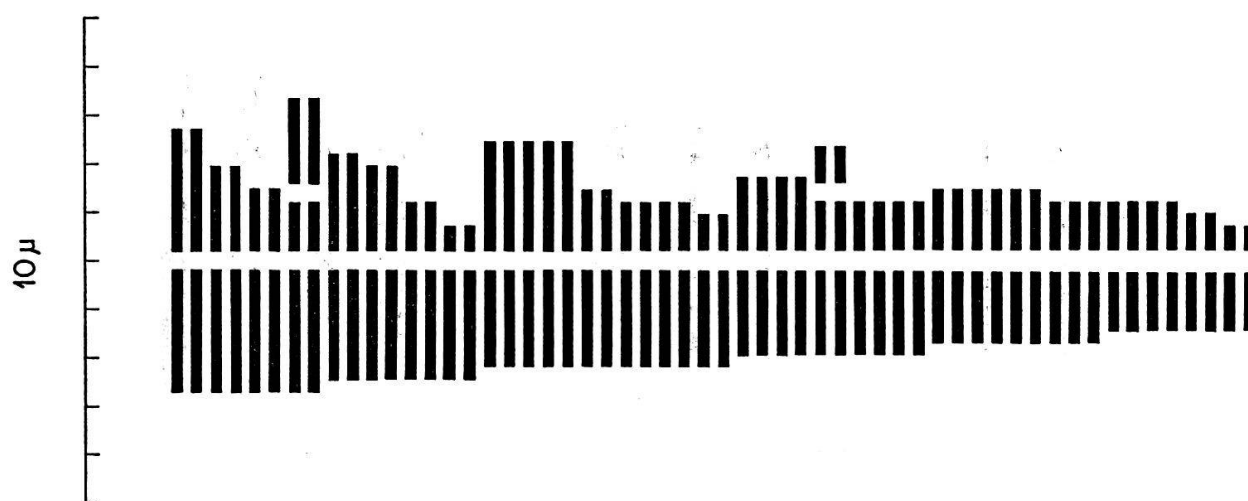


Fig. 9. Chromosome complement of *Antennaria carpatica* s.str. from the Pyrenees.

Mountains and  $1.73\ \mu$  in all other plants. Thus, the big "satellite" was about three times longer than the small one occurring in the first pair.

A comparative morphological study of the material from the Tatra Mountains, the Alps and the Pyrenees revealed a rather high degree of similarity occurring between the resp. karyotypes. Most of the chromosome types could be recognized in all of the studied plates; the three characteristic pairs described above occurred invariably in the octoploid set. It should be noted that the materials from various mountain groups differed from one another in some details: certain types of chromosomes occurred exclusively in one groupe whereas in the others they were missing (Tables 17, 18). The frequency of some morphological types was also variable. On the whole, however, the length differences occurring between the particular chromosomes in the studied material did not exceed  $0.25\ \mu$ .

The above results point to close relationship between the octoploid plants of *Antennaria carpatica* s.str. from various parts of its range. It seems probable that they might have a common origin. The octoploid type could have arisen as an allopolyploid or autopolyploid form; however, the polyploidization was an evolutionary step preceeding the structural changes of the chromosomes e.g. translocations or terminal deficiencies. On the other hand, certain differences occurring in the material from separated mountain groups permit to assume that further processes of karyotype differentiation could have taken place independently in the Tatra Mountains, the Alps and the Pyrenees.

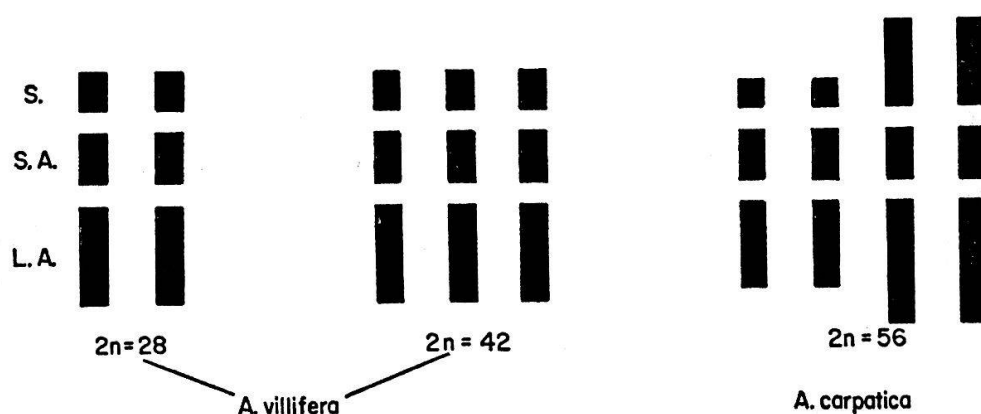


Fig. 10. Diagrammatic representation of SAT-chromosomes occurring in *Antennaria villifera* as well as in *A. carpatica* s.str.