

**Zeitschrift:** Berichte des Geobotanischen Institutes der Eidg. Techn. Hochschule, Stiftung Rübel

**Herausgeber:** Geobotanisches Institut der Eidg. Techn. Hochschule, Stiftung Rübel

**Band:** 40 (1969)

**Artikel:** *Antennaria carpatica* (Wahlenb.) Bluff et Fingerh. s.l. in Europe : a cycto-taxomonical study

**Autor:** Urbaska-Worytkiewicz, Krystyna

**DOI:** <https://doi.org/10.5169/seals-377667>

### **Nutzungsbedingungen**

Die ETH-Bibliothek ist die Anbieterin der digitalisierten Zeitschriften auf E-Periodica. Sie besitzt keine Urheberrechte an den Zeitschriften und ist nicht verantwortlich für deren Inhalte. Die Rechte liegen in der Regel bei den Herausgebern beziehungsweise den externen Rechteinhabern. Das Veröffentlichen von Bildern in Print- und Online-Publikationen sowie auf Social Media-Kanälen oder Webseiten ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. [Mehr erfahren](#)

### **Conditions d'utilisation**

L'ETH Library est le fournisseur des revues numérisées. Elle ne détient aucun droit d'auteur sur les revues et n'est pas responsable de leur contenu. En règle générale, les droits sont détenus par les éditeurs ou les détenteurs de droits externes. La reproduction d'images dans des publications imprimées ou en ligne ainsi que sur des canaux de médias sociaux ou des sites web n'est autorisée qu'avec l'accord préalable des détenteurs des droits. [En savoir plus](#)

### **Terms of use**

The ETH Library is the provider of the digitised journals. It does not own any copyrights to the journals and is not responsible for their content. The rights usually lie with the publishers or the external rights holders. Publishing images in print and online publications, as well as on social media channels or websites, is only permitted with the prior consent of the rights holders. [Find out more](#)

**Download PDF:** 24.03.2026

**ETH-Bibliothek Zürich, E-Periodica, <https://www.e-periodica.ch>**

# **Antennaria carpatica (Wahlenb.) Bluff et Fingerh. s.l. in Europe—a cyto-taxonomical study**

by KRYSZYNA URBAŃSKA-WORYTKIEWICZ

## Contents

1. Introduction .....	80
2. Cytology:	
2.1 Material and methods .....	84
2.2 Chromosome numbers .....	86
2.3 Analysis of the karyotype .....	88
3. Morphology:	
3.1 Material and methods .....	109
3.2 <i>Antennaria villifera</i> .....	110
3.3 <i>Antennaria carpatica</i> s.str. ....	118
3.4 Diagnostic characters in the <i>Antennaria carpatica</i> complex .....	121
4. Geographical distribution:	
4.1 <i>Antennaria villifera</i> .....	123
4.2 <i>Antennaria carpatica</i> s.str. ....	129
5. Ecology:	
5.1 <i>Antennaria villifera</i> .....	136
5.2 <i>Antennaria carpatica</i> s.str. ....	139
6. Discussion .....	141
7. Nomenclature:	
7.1 <i>Antennaria villifera</i> Boriss. ....	147
7.2 <i>Antennaria carpatica</i> (Wahlenb.) Bluff et Fingerh. s.str. ....	147
8. Description of the section <i>Carpaticae</i> and key for the determination of species belonging to the <i>Antennaria carpatica</i> complex	154
9. Description of species:	
9.1 <i>Antennaria carpatica</i> (Wahlenb.) Bluff et Fingerh. s.str. ....	155
9.2 <i>Antennaria villifera</i> Boriss. ....	155
9.3 <i>Antennaria lanata</i> (Hook.) Greene .....	156
9.4 <i>Antennaria pulcherrima</i> (Hook.) Greene .....	157
Summary .....	158
Acknowledgements .....	159
References .....	160

## 1. Introduction

*Antennaria* Gaertn. is an interesting but difficult and controversial group. About 200 taxa were described hitherto, mostly from North America. Numerous species are recorded exclusively from their type localities; however, not only endemism but also remarkably disjunctive ranges are known within the genus.

A high degree of karyological differentiation occurs in *Antennaria*. Besides the tetraploid species ( $2n=28$ ), also various higher polyploids have been found. Their chromosome numbers are:  $2n=40-42$ , c. 52, 56, 63, 70, 75-80, 84. It is interesting to note that the tetraploid species of *Antennaria* are sexual whereas higher polyploids show as a rule an apomictic mode of reproduction (JUEL 1900, STEBBINS 1932, BERGMAN 1935, NYGREN 1950, URBAŃSKA-WORYTKIEWICZ unpubl.). The only known exception is the *Antennaria carpatica* complex where not only tetraploids but also hexa- and octoploids show no tendency to a parthenogenetic seed development (URBAŃSKA-WORYTKIEWICZ 1961, 1962, 1962a, 1967, 1967a, 1967b, 1969, unpubl.).

In view of the apomixis frequently occurring within the genus *Antennaria*, its taxonomy varies greatly according to the divergent opinions concerning the taxonomical status of the apomicts. On the whole, the following sections were distinguished: *Carpaticae*, *Plantaginifoliae*, *Alpinae*, *Dioicae*, *Dimorphae* and *Racemosae* (FERNALD 1924, RYDBERG 1932, PORSILD 1950, 1965). European species of *Antennaria* were usually referred to the *Carpaticae*, *Alpinae* and *Dioicae*, respectively. Chromosome numbers and mode of reproduction occurring within these three sections are given in Table 1.

The section *Carpaticae* comprises a non-stoloniferous group of species with erect and elongate basal leaves which are oblanceolate or lanceolate. The *Antennaria carpatica* complex, which seems to be the only representative of the section, consists of the following species: *A. carpatica* (Wahlb.) Bluff et Fingerh. s.str., *A. villifera* Boriss., *A. lanata* (Hook.) Greene and *A. pulcherrima* (Hook.) Greene. This nomenclature, accepted by the present author for the species belonging to the *Antennaria carpatica* complex, is used in our whole work; the nomenclature problems are discussed in p. 152-153. *Antennaria lanata* and *A. pulcherrima* were reported exclusively from North America; *A. villifera* is an Eurasian species, whereas the range of *A. carpatica* s.str. is confined to Europe (Fig. 1).

The *Antennaria carpatica* complex represents in European flora an arctic-alpine element with a disjunctive area of distribution; its one centre is in North Fennoscandia and Russia (*A. villifera*) whereas the other corresponds to the mountains of Central and Western Europe (*A. carpatica* s.str.).



Fig. 1. Distribution of the *Antennaria carpatica* (Wahlenb.) Bluff et Fingerh. complex in Europe. Russian stations of *A. villifera* are not marked here.

A monographic investigation in *A. carpatica* has not been carried out hitherto. The data concerning its taxonomical status are rather incomplete and confused. The original concept of WAHLENBERG (1814, 1826) has been gradually extended to the whole area of distribution of the complex and subsequently decreased to some its regions. In addition, several authors have described a number of new taxa giving them various ranks. In view of this, it seemed advisable to revise the nomenclature, taxonomy as well as the geographical distribution and ecology of the complex.

*Antennaria carpatica* presents an interesting object for a biosystematic study. Karyological differentiation occurring within this group points to the fact that the polyploidization has played an important part in the evolution of the complex. The analysis of karyotype has not been performed hitherto in the genus. *A. carpatica* representatives proved to be very convenient for these studies in spite of their high chromosome numbers. Preliminary observations have already revealed differences occurring between the resp. cytotypes; therefore, it seemed interesting to carry out a more detailed investigation on material from various parts of the range.

The present work, dealing with the European representatives of the *A. carpatica* complex, is based on the studies carried out during twelve years

Table 1

The chromosome numbers and mode of reproduction within the sections Carpaticae, Alpinae and Dioicae of *Antennaria* Gaertn.

Species	2n	Ploidy	Reproduction
<b>Carpaticae:</b>			
<i>A. villifera</i> Boriss.	28	4x	sex
	28	4x	?
	42	6x	sex
<i>A. carpatica</i> (Wahlenb.)Bluff et Fingerh. s. str.	42	6x	?
	56	8x	sex
<i>A. pulcherrima</i> (Hook.)Greene	63	9x	?
-----			
<b>Alpinae:</b>			
<i>A. alpina</i> (L.)Gaertn.	70	10x	apo
	84	12x	apo
<i>A. canescens</i> (Lge)Malte	45-56	?	apo
	56	8x	?
<i>A. Ekmaniana</i> A. E. Porsild	84	12x	?
<i>A. Porsildii</i> Ekm.	63	9x	apo
	63	9x	apo
	70	10x	apo
-----			
<b>Dioicae:</b>			
<i>A. dioica</i> (L.)Gaertn.	28	4x	sex
	28	4x	sex
	28	4x	sex
<i>A. Nordhagiana</i> Rune et Rønning	28	4x	?
	28	4x	?
<i>A. Hansii</i> Kerner( <i>A. groenlandica</i> Porsild)	56	8x	apo
<i>A. affinis</i> Fern.	56	8x	apo
<i>A. intermedia</i> ( <i>A. alpina</i> var. <i>intermedia</i> Rosenv.)	84	12x	apo

Origin of material	Authors
Scandinavia	Urbańska-Worytkiewicz 1967, 1967a,b
Tschukotchka Peninsula	Zhukova 1968
Scandinavia	Bergman 1935, 1951, Urbańska-Worytkiewicz 1967, 1967a, b
Tschukotchka Peninsula	Zhukova 1968
Tatra Mts, Alps, Pyrenees	Urbańska 1959, Urbańska-Worytkiewicz 1961, 1962, 1962a, 1965, 1967, 1968, 1968a
Canada	Löve and Solbrig 1964
<hr style="border-top: 1px dashed black;"/>	
Scandinavia	Urbańska-Worytkiewicz 1967, Urbańska-Worytkiewicz unpubl.
Scandinavia	Bergman 1935, Nygren 1950, Löve a. Löve 1956, Urbańska-Worytkiewicz 1967, Urbańska-Worytkiewicz unpubl.
Scandinavia	Juel 1900
Greenland	Jørgensen, Sørensen and Westergaard 1958
Greenland	Jørgensen, Sørensen and Westergaard 1958
Greenland	Bøcher and Larsen 1950
Scandinavia	Nygren 1950
Scandinavia	Urbańska-Worytkiewicz 1967, Urbańska-Worytkiewicz unpubl.
<hr style="border-top: 1px dashed black;"/>	
Scandinavia	Juel 1900, Bergman 1935, Urbańska-Worytkiewicz 1967, Urbańska-Worytkiewicz unpubl.
?	Sokolovskaja and Strelkova 1948
S. Poland incl. Tatra Mts	Urbańska 1959, Urbańska-Worytkiewicz unpubl.
Bulgaria: Rila Mt.	Kozuharov a. Kuzmonov 1970
Alps	Urbańska-Worytkiewicz 1968, Urbańska-Worytkiewicz unpubl.
Sierra Nevada	Küpfer 1968
Scandinavia	Nygren (from Rune and Rønning 1956)
Greenland	Jørgensen, Sørensen and Westergaard 1958
Greenland	Jørgensen, Sørensen and Westergaard 1958
Greenland	Bergman 1935

(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: Javreoiv'vit, NE slope	c.1000m	28
14/68N	Troms, Kåfjord: Guolas'javre, between Gåd'dečårro and Sinaivarri	c.800m	28
-----			
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'dečårro	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

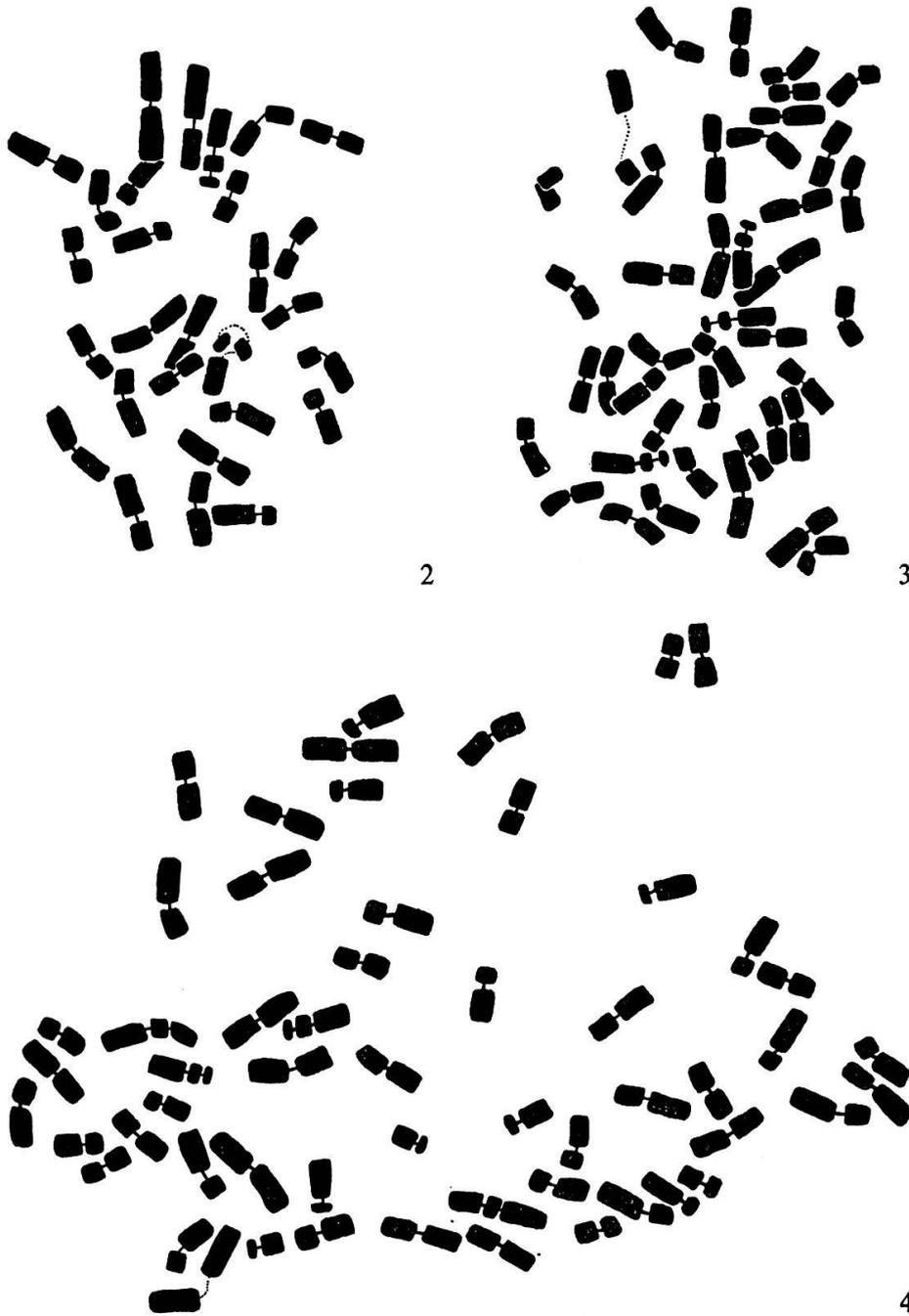
No of fixation	Place of origin	Altitude a. s. l.	2n
I. the Tatra Mts:			
1/69T	the cirque Kocioł Mięszowiecki	c.1850m	56
2/69T	NW slope of Żabie - over the Valley of Morskie Oko	c.1750m	56
3/69T	near the pass Przełęczka pod Żabią Czuba	c.1800m	56
4/69T	Pośrednia Turnia, NE ridge	c.1900m	56
5/69T	Gąsienicowa 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*,  $2n=42$ . 3. *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 4

A. villifera; variability of chromosome length in tetraploid type: results of measurements of the particular types of chromosomes in 63 plates (length in  $\mu$ )

Pair	Longer arm										Shorter arm										Satellite		
	1.00	1.25	1.50	1.75	2.00	2.25	2.50	2.75	3.00	3.25	0.75	1.00	1.25	1.50	1.75	2.00	2.25	2.50	2.75	0.50	0.75	1.00	
I	-	-	-	-	-	1	4	113	8	1	-	-	-	-	-	9	115	1	-	-	-	-	
II	-	-	-	-	1	123	1	1	-	-	-	-	-	-	2	120	3	1	-	-	-	-	
III	-	-	-	-	10	108	7	1	-	-	-	-	-	1	119	6	-	-	-	-	-	-	
IV	-	-	-	-	2	120	4	-	-	-	-	-	2	123	1	-	-	-	-	-	-	-	
V	-	-	-	-	9	113	4	-	-	-	6	117	3	-	-	-	-	-	-	-	-	-	
VI	-	-	4	1	119	2	-	-	-	-	-	-	7	118	1	-	-	-	-	-	-	-	
VII	-	-	2	2	120	2	-	-	-	-	-	6	118	2	-	-	-	-	-	-	-	-	
VIII	-	1	1	2	121	1	-	-	-	-	1	119	5	1	-	-	-	-	-	6	118	2	
IX	-	-	4	7	114	1	-	-	-	-	2	120	3	1	-	-	-	-	-	-	-	-	
X	-	1	2	9	106	8	-	-	-	-	-	124	2	-	-	-	-	-	-	-	-	-	
XI	3	9	112	2	-	-	-	-	-	-	-	3	117	6	-	-	-	-	-	-	-	-	
XII	2	4	119	1	-	-	-	-	-	-	-	19	101	7	-	-	-	-	-	-	-	-	
XIII	-	117	7	2	-	-	-	-	-	-	3	5	117	1	-	-	-	-	-	-	-	-	
XIV	2	118	5	1	-	-	-	-	-	-	1	9	116	-	-	-	-	-	-	-	-	-	

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

Table 8

Variability of the chromosome length in deviating karyotype of hexaploid *Antennaria villifera* from Gaetkuot'aiivit, 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.

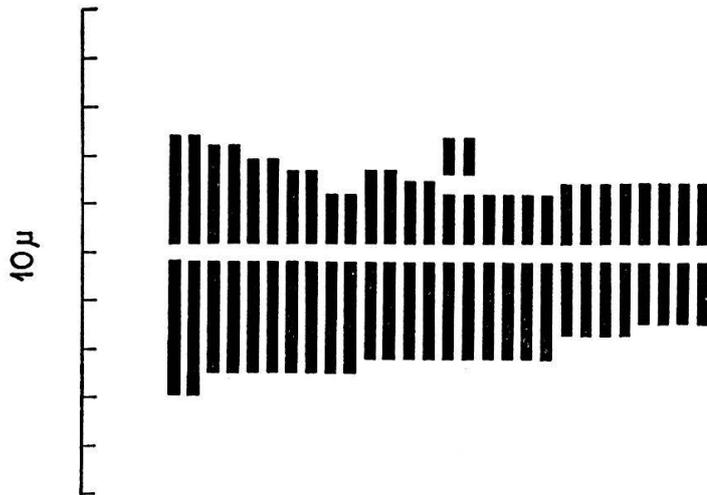


Fig. 5. Chromosome complement of tetraploid *Antennaria villifera*.

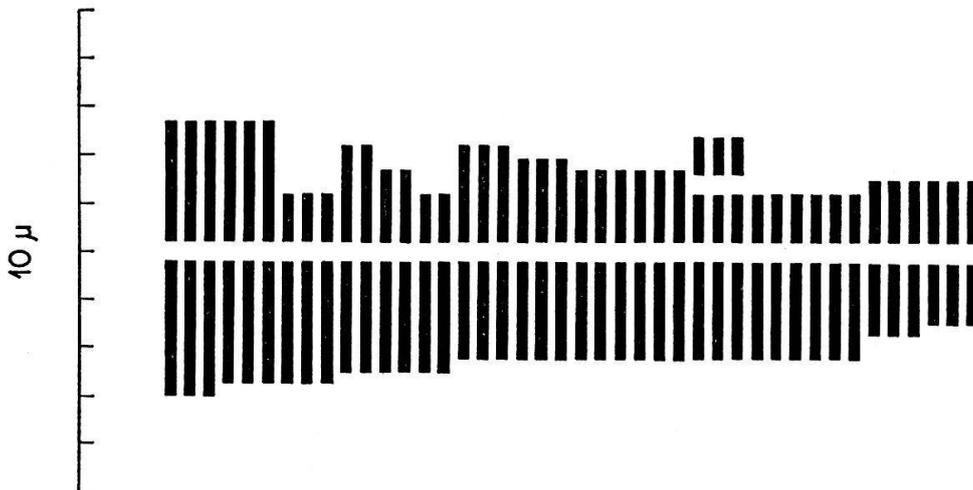


Fig. 6. Chromosome complement of hexaploid *Antennaria villifera*.

*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 (1.68–1.71  $\mu$ ) chromosomes with a subterminal centromere. The index (S.A./L.A.) comported 0.34–0.35. 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 (0.50–0.76  $\mu$ ). 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 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 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



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	-	3.75	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 % 0.41
Nordland, Sörfold: Boaimac, riksgränsa 7. VII. 1954 W. Apold, G. Brodal, O. Skifte	TROM	short	5	232	1 % 0.43
Troms, Balsfjord: Hattevarre 17. VIII. 1934 P. Benum	TROM	short	6	330	4 % 1.39
Troms, Storfjord: Skibotndalen, Rippovarre 15. VIII. 1936 P. Benum	TROM	short	6	267	7 % 2.62
Troms, Skjervøy: Vaddas, Lohtana 28. VII. 1937 Y. Mejland	O	short	6	348	15 % 4.37
Troms, Målselv: Alappen 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:					
Yakutsch: Buckar 25. VIII. 1898 H. Nilssen	S	short	5	227	31 % 13.66
Jenisey, Dudinka VIII. 1876 J. R. Sahlberg	LE	short	6	272	46 % 16.91

\*

all other studied specimens had no seeds.

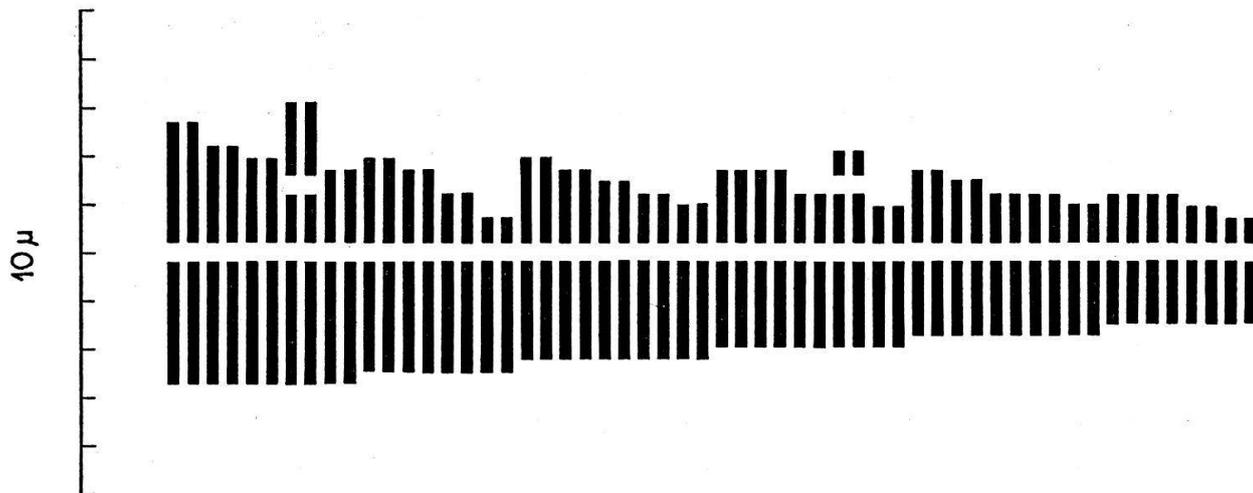


Fig. 7. Chromosome complement of *Antennaria carpatica* s.str. from the Tatra Mountains.

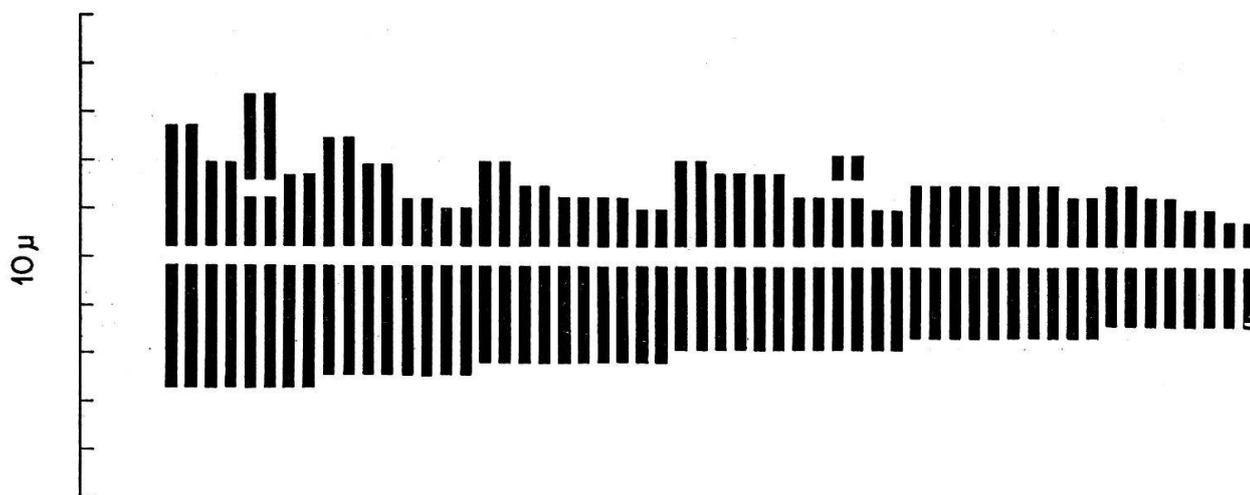


Fig. 8. Chromosome complement of *Antennaria carpatica* s.str. from the Alps.

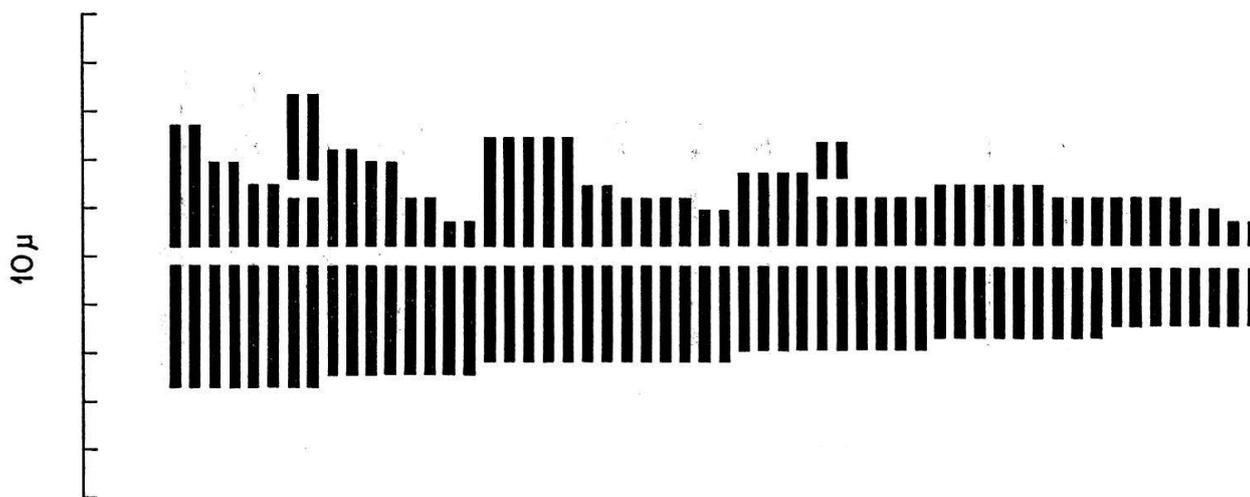


Fig. 9. Chromosome complement of *Antennaria carpatica* s.str. from the Pyrenees.

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 preceding 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.

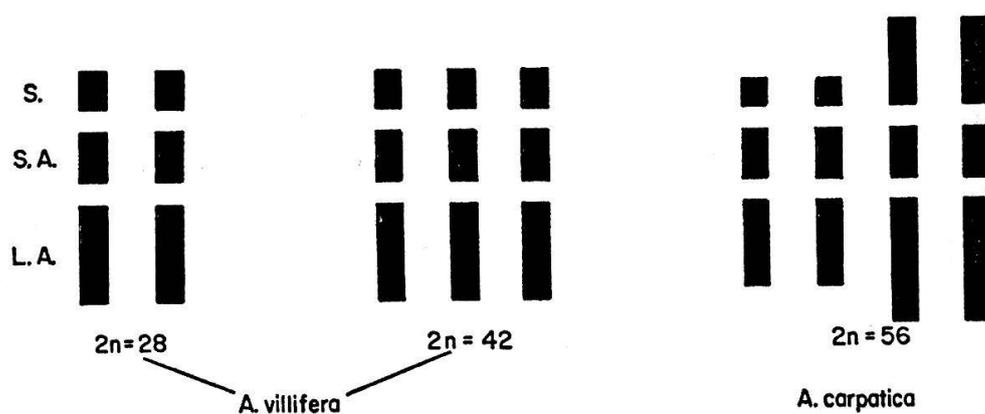


Fig. 10. Diagrammatic representation of SAT-chromosomes occurring in *Antennaria villifera* as well as in *A. carpatica* s. str.

### 3. Morphology

#### 3.1 *Material and methods*

The specimens of *Antennaria villifera* studied cytologically originated from 48 localities in North Scandinavia. In addition to the Scandinavian material, *A. villifera* from the Chukotchka Peninsula, investigated cytologically by P. ЗИУКОВА, Leningrad, was examined.

As far as *Antennaria carpatica* s.str. is concerned, plants with known chromosome numbers were collected in 24 localities in the Tatra Mountains and in 61 habitats of the Alpine range. Material from the Pyrenees consisted of two populations: one originated from Port d'Envalira, the other from Val des Planès.

Herbarium materials with unknown chromosome numbers were got on loan from the following institutions:

The Botanical Museum, University of Lund (L)  
The Botanical Department, Museum of the Natural History, Stockholm (S)  
The Botanical Museum, University of Uppsala (UPS)  
The Botanical Museum, University of Bergen (BG)  
The Botanical Department, Tromsø Museum, Tromsø (TROM)  
The Botanical Museum, University of Helsinki (HEL)  
The Botanical Department, University of Turku (TUR)  
The Botanical Institute, the Jagellonian University, Krakow  
Botanisches Institut der Universität Innsbruck (IB)  
Tiroler Landesmuseum Ferdinandeum, Innsbruck (IBF)  
Naturhistorisches Museum, Wien (W)  
Botanisches Institut der Universität Wien (WU)  
Botanische Staatssammlung, München (M)  
Geobotanisches Institut der ETH Zürich (RUEB)  
Institut für spezielle Botanik der ETH Zürich (ZT)  
Botanisches Institut der Universität Zürich (Z)  
Institut de Botanique, Université de Neuchâtel (NEU)  
Conservatoire et Jardin botanique, Genève (G)  
Musée botanique cantonal, Lausanne (LAU)  
Institut de Botanique, Université de Grenoble (GR)  
Institut de Botanique, Faculté des Sciences, Toulouse (TL)  
Istituto botanico dell'Università, Torino (TO)

It should be added that not only European representatives of *Antennaria carpatica* were examined; for comparison, we studied also *A. villifera* from Siberia as well as *A. lanata* and *A. pulcherrima*, mostly from Canada.

The following qualitative characters were scored: shape of the rosette leaves, morphology of stem leaves, arrangement of heads, colour of involucre phyllaries and their morphology, colour and morphology of flower organs in staminate and pistillate florets. For each male specimen a "pollen test" was

made: 150 pollen grains were measured and the ranges of their variability were established. Observations on the seed development were also carried out.

As far as the quantitative characters are concerned, the length and width of the rosette leaves and the length of the involucrel phyllaries, were measured. The flower organs were measured in 50 florets from each specimen; it should be noted that only plants with fully developed inflorescences were selected for these investigations.

Some plants of *Antennaria carpatica* s. str. were transferred to the experimental garden; thus, observations on the variability performed on plants "in situ" could be accomplished by the resp. notes taken during two consecutive seasons. These observations concerned chiefly the morphology of the rosette leaves; according to some authors (CHRTEK and POUZAR 1960, 1962) this character was supposed to have a decisive diagnostic value for *Antennaria carpatica*.

### 3.2 *Antennaria villifera*

The variability observed within *A. villifera* manifested itself chiefly in size differences. The length of the stem ranged from 2.8 cm to 19.0 cm. The smallest plants were collected in snow-bed localities situated in the upper part of a middle-alpine belt whereas more vigorous specimens occurred at lower altitudes, in well protected places. It seems probable that the observed differences are of a phenotypic character.

The rosette leaves of *Antennaria villifera* are mostly lanceolate, acute and 3nerved. The mean value of their width comported 4.2 mm whereas the minimal and maximal values were 2.0 mm and 8.2 mm, respectively. The length of the rosette leaves ranged from 29.0 mm to 71.1 mm. Both sides of the leaves were greyish-pubescent. The leaves and stem were most frequently suffused with anthocyanine and their colour was grey-violet. The most intensively coloured parts of the leaves were their edges, nerves and petioles.

Stem leaves are few, sessile and narrower than those of the rosettes. On the lower part of the stem, leaves are acute, on the upper part they have scarious, usually blackish appendages. At the base of the appendages a slight trace of violet is often visible. The appendages are mostly narrow and twisted.

Heads are compressed, very short pedunculate and tomentose. In some plants, however, more open inflorescences were observed as a result of the occurrence of longer peduncles in the lateral heads. The number of heads was variable; the most frequent were plants with 4–6 heads, in some specimens, however, 8–9 heads could be observed. The external phyllaries of female heads are obovate, green and tomentose at the base; in the middle a trace of

violet frequently occurs. The upper part is scarious and blackish. The internal phyllaries are narrow and acuminate. Their colour is similar to that of the external phyllaries; they are often cream-tipped at later developmental stages.

The external phyllaries of male heads are usually broader than those of the female inflorescences. They are spatulate; the internal phyllaries are acuminate and longer; their modal value comports 4.5 mm (Fig. 11). The distribution of colour is similar to that of the female heads. It should be noted that differences in the colour and length of the phyllaries permit to distinguish *A. villifera* from *A. carpatica* s.str. as well as from *A. lanata* with which it was sometimes identified.

The corolla of the staminate florets of *A. villifera* is greenish at the base. Its upper part is purple and even blackish at early developmental stages.

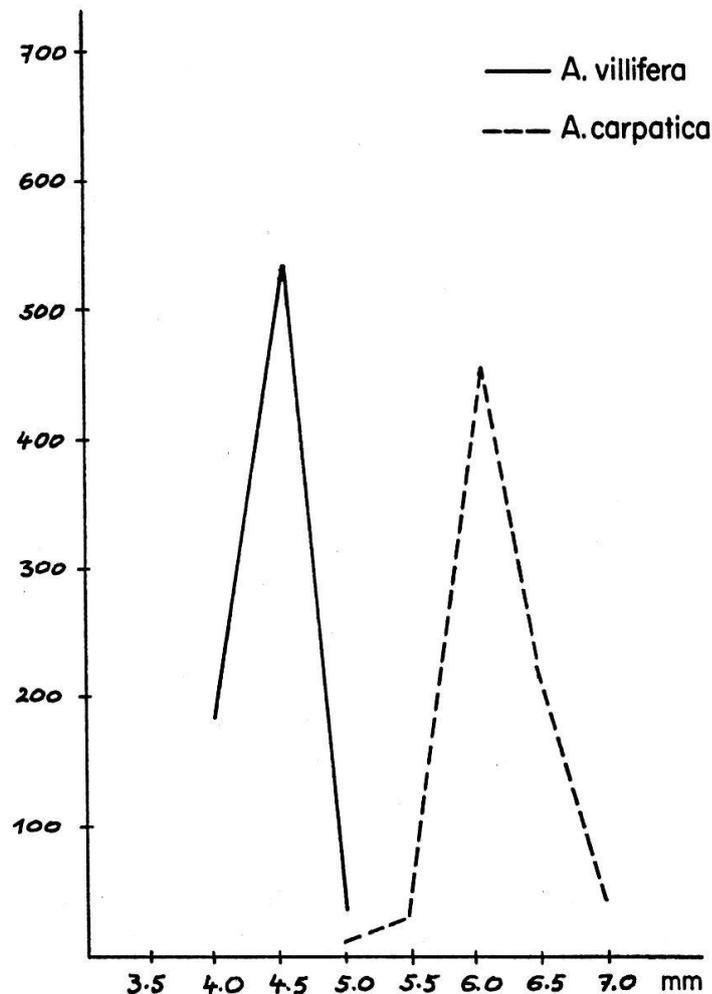


Fig. 11. Length of the innermost phyllaries in male heads of *Antennaria villifera* and *A. carpatica* s.str.

Few-celled, glandular hairs occur there in various number. The tips of the corolla are often papillose. The anthers are bright yellow and glabrous (Fig. 33).

The colour of the corolla and the anthers in the staminate florets proved to be an important diagnostic character of *A. villifera*. It seems to be a constant feature and could be recognized, with only a few exceptions, even in old herbarium specimens.

The pappus is white, only occasionally are single bristles pinkish. The length of the pappus is more or less equal to that of the staminate florets. The resp. average values of length of the corolla, anthers and pappus are presented in Fig. 12. The bristles are mostly serrate, clavate at the uppermost part. Sometimes cylindrical bristles, not flattened at the top, were also observed in the studied material.

Two different types of pollen occurred in *A. villifera*. The results of the present investigations are in accordance with the author's previous reports (URBAŃSKA-WORYTKIEWICZ 1967a, 1967b). It should be added that our predictions as to some relationship occurring between the type of pollen and the chromosome number were confirmed in the course of the present study. In 1968 we visited some localities of *A. villifera* from which we have previously studied the herbarium specimens. The chromosome numbers found in this material proved to be in accordance with the type of pollen: plants with a rather normal pollen had a tetraploid chromosome number ( $2n=28$ ) whereas plants with a highly irregular pollen were found to have a hexaploid number ( $2n=42$ ). The pollen diagrams of the two types are presented in Fig. 13. Thus, it seems possible that the "pollen test" may help to distinguish tetraploids from hexaploids. The two cytotypes are notably similar to each other.

The pistillate florets are greenish or straw-coloured on the lower part; the upper part of the corolla is purplish. Multicellular hairs occur on its topmost part. Their length and colour are variable; however, they were observed in all of the studied specimens. The present results differ in this respect from the recent data of ZHUKOVA (1968) who reported the occurrence of hairs only in hexaploid *Antennaria villifera* from the Chukotchka Peninsula.

The pistil was exerted about 2.5 mm. The style and stigma are usually purplish-brown. Only in a few plants collected in snow-bed localities were the flower organs pale-green.

Special attention should be paid to the length of the stigma lobes observed in the studied material. According to the original diagnosis of *Antennaria villifera* given by BORISSOVA (1959) the stigma was slightly cleft. On the other hand, two well-marked types of pistillate florets were found in the course of the present study: one of them had short stigma lobes (modal value 0.3 mm),

whereas in the other the stigma lobes were rather long (modal value 0.8 mm). The two types are presented in Figs. 14, 15, 16, 17, 37. It should be noted that in the tetraploid plants "the short stigma type" was invariably found; the hexaploids represented "the long stigma type". The ranges of variability established for definite cytotypes corresponded with the resp. ranges established for the herbarium material with unknown chromosome numbers (Fig. 18). It may be inferred that "the short stigma type" corresponds to tetraploids whereas "the long stigma type" is typical of hexaploids.

The length of the pappus ranged from 4.6 mm to 10.9 mm. It should be noted, however, that the ratio: style/pappus was rather constant in studied material. In most of the specimens studied at the post-floral stages the pappus was longer than the pistillate florets; an average difference comported 2.5 mm (Fig. 19). In some specimens, however, the pappus was either equal in length or even shorter than the florets.

Seed development. *Antennaria villifera* from Fennoscandia is almost completely sterile. The first author to report this phenomenon was BERGMAN (1951) who studied the embryology of hexaploid plants from North Sweden. He observed highly irregular developmental processes in the ovules; at later stages he examined hundreds of embryo-sacks and found only one containing an embryo surrounded by endosperm.

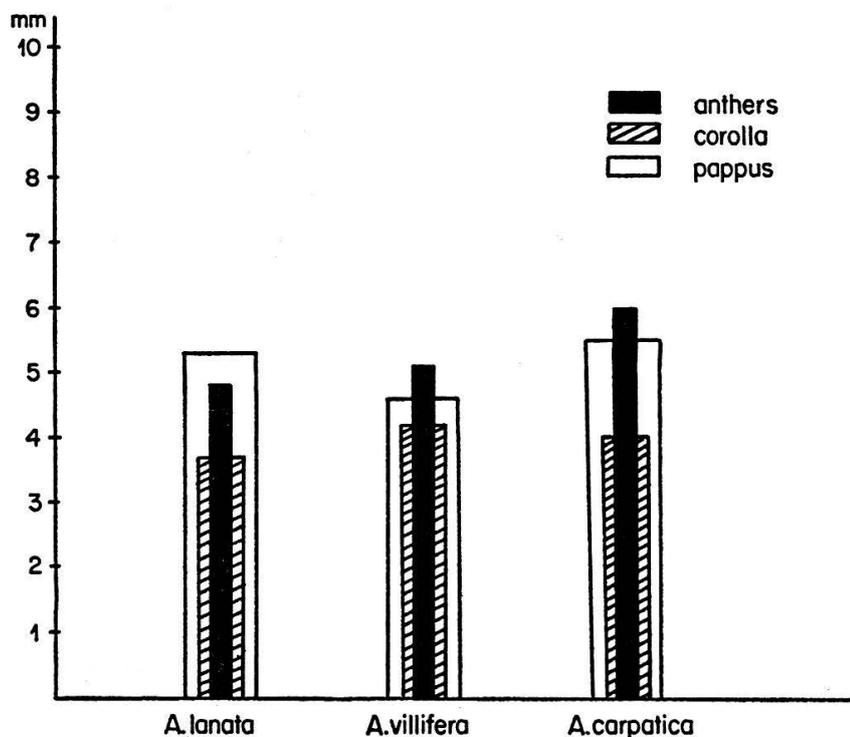


Fig. 12. Average length of the flower organs in staminate florets of *Antennaria carpatica* s.str., *A. villifera* and *A. lanata*.

The present author's embryological investigations in Scandinavian plants revealed some differences occurring between the two cytotypes. In hexaploid plants, highly abnormal micro- and macrosporogenesis was found, in accordance with BERGMAN's data. Viable gametes only occurred in a small percentage. 42chromosomic plants apparently represent a case of gametic sterility; it can not be excluded, however, that in exceptional cases some of the gametes may be functional.

On the contrary, meioses in the anthers and ovules of the tetraploid plants mostly resulted in normal gametes. We have assumed that seed-failure in the tetraploid type might be principally due to some ecological factors (URBAŃSKA-WORYTKIEWICZ 1967a, 1967b).

In the course of the present investigations we found in the whole of the material studied only 9 herbarium sheets in which a limited number of achenes could be observed (Table 18). They were glabrous, purple-tinged and c. 0.8 mm long (Fig. 38).

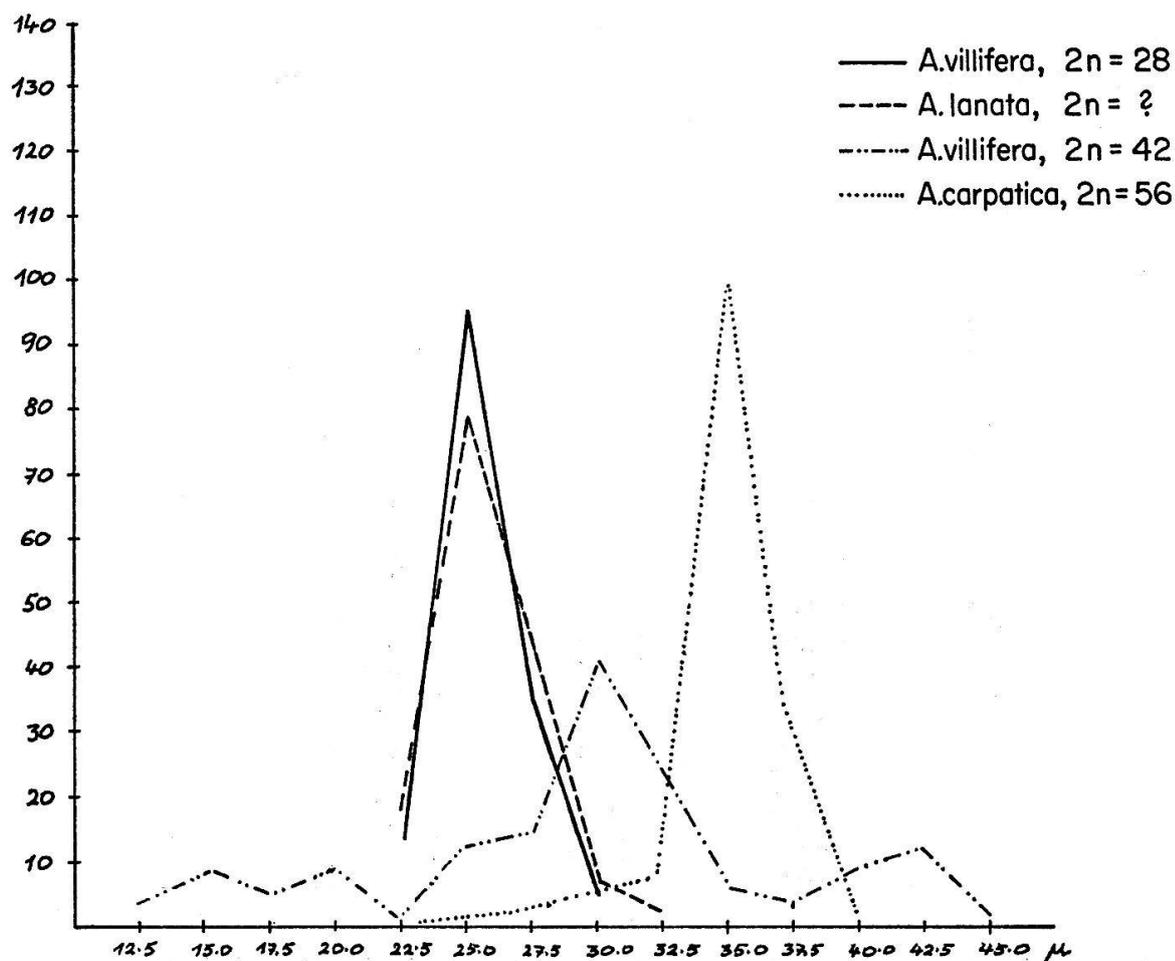
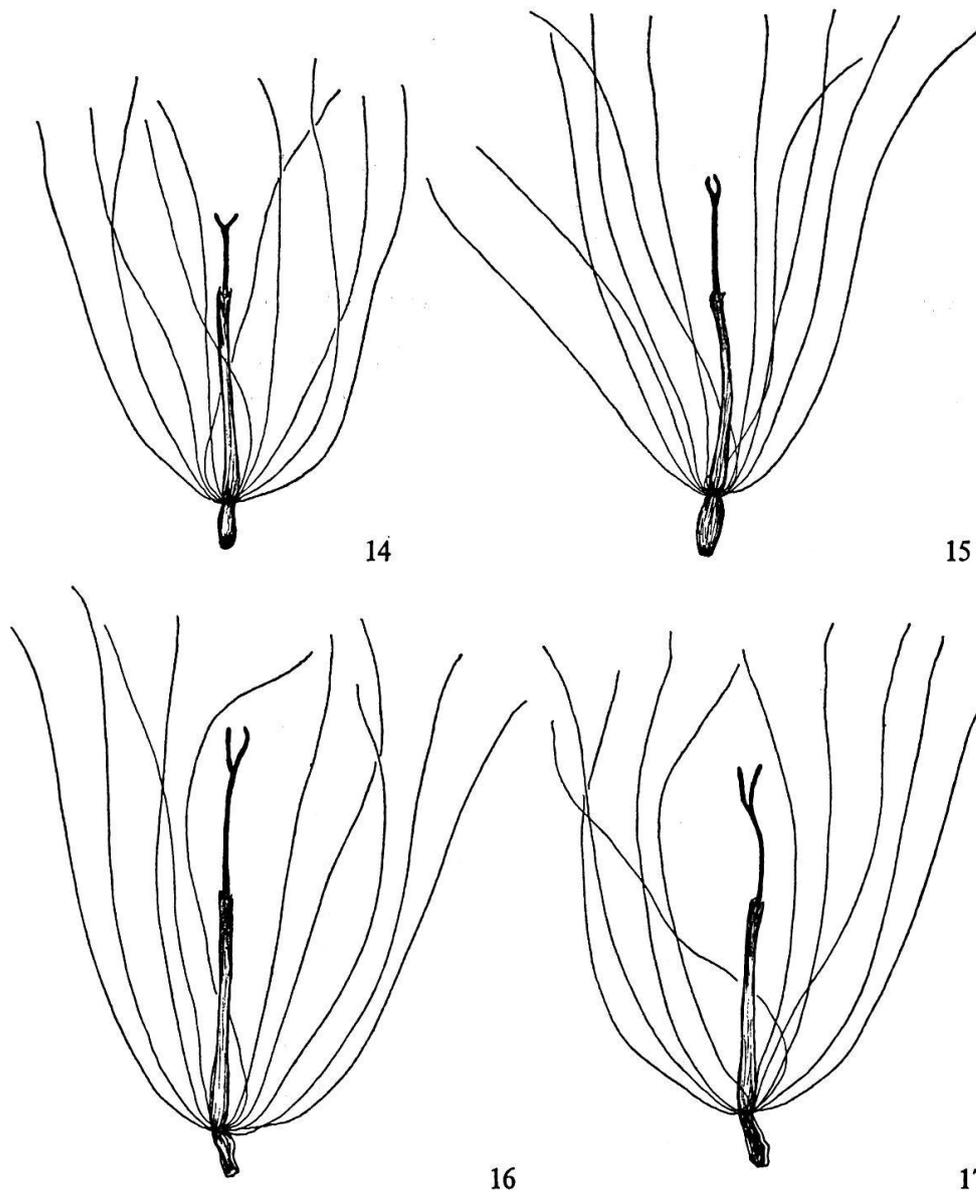


Fig. 13. Graph of pollen diameter.

Particularly interesting is the frequency of achenes occurring in *Antennaria villifera* in various parts of its range. In Scandinavia, seed development is exceedingly rare; the author has never observed them in the field and no more than 4.5% were found in the herbarium material (Fig. 20). On the other hand, plants from Kolguyev had about 11% of achenes; the material from Siberia (Yenisey, Yakutsk) represented some higher values viz. 13.6% and 16.9%, respectively. It should be added that LYNGBE (1923) observed fruiting plants in Novaya Semlya. Unfortunately, the Russian material studied by



Figs. 14–17. *Antennaria villifera*: pistillate florets at the post-floral stage; 14. 4/68N,  $2n=28$ . 15. Herbarium specimen from Kolguyev, not investigated cytologically. 16. 17/68N,  $2n=42$ . 17. Herbarium specimen from Torne Lappmark, Sweden, not investigated cytologically. C.  $5\times$ .

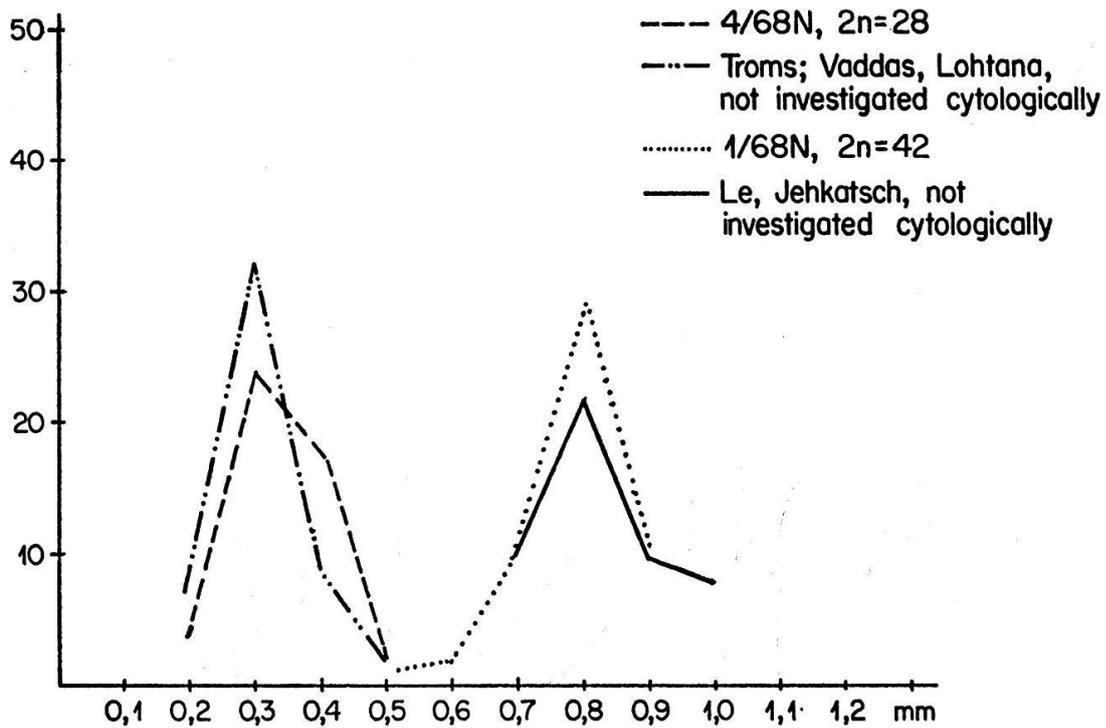


Fig. 18. Length of the stigma lobes in *Antennaria villifera*: a comparison between the materials studied cytologically and plants with unknown chromosome numbers.

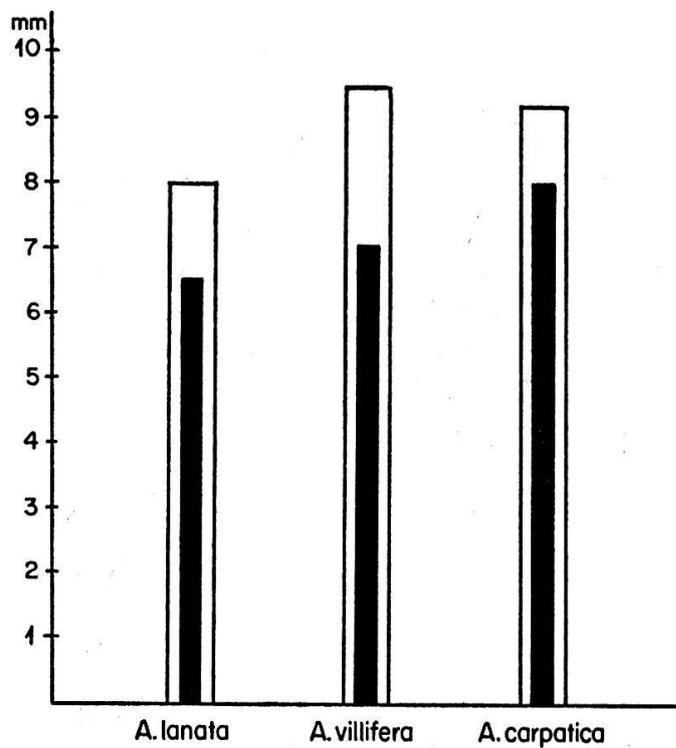


Fig. 19. Average length of style and pappus in pistillate florets of *Antennaria carpatica* s.str., *A. villifera* and *A. lanata*.

the present author chiefly consisted of plants at younger developmental stages; a more detailed study on the seed development of *A. villifera* from the eastern part of its range would be very interesting.

All studied specimens which had developed achenes represented “the short stigma type” (Fig. 36). It might be assumed that they are tetraploid. This detail, being of a special interest, corresponds with our previous results concerning the embryology of *Antennaria villifera*. It seems possible that tetraploid gametes are mostly functional; however, seed setting only occasionally takes place and ecological factors constitute the most important cause of sterility in 28chromosomic plants.

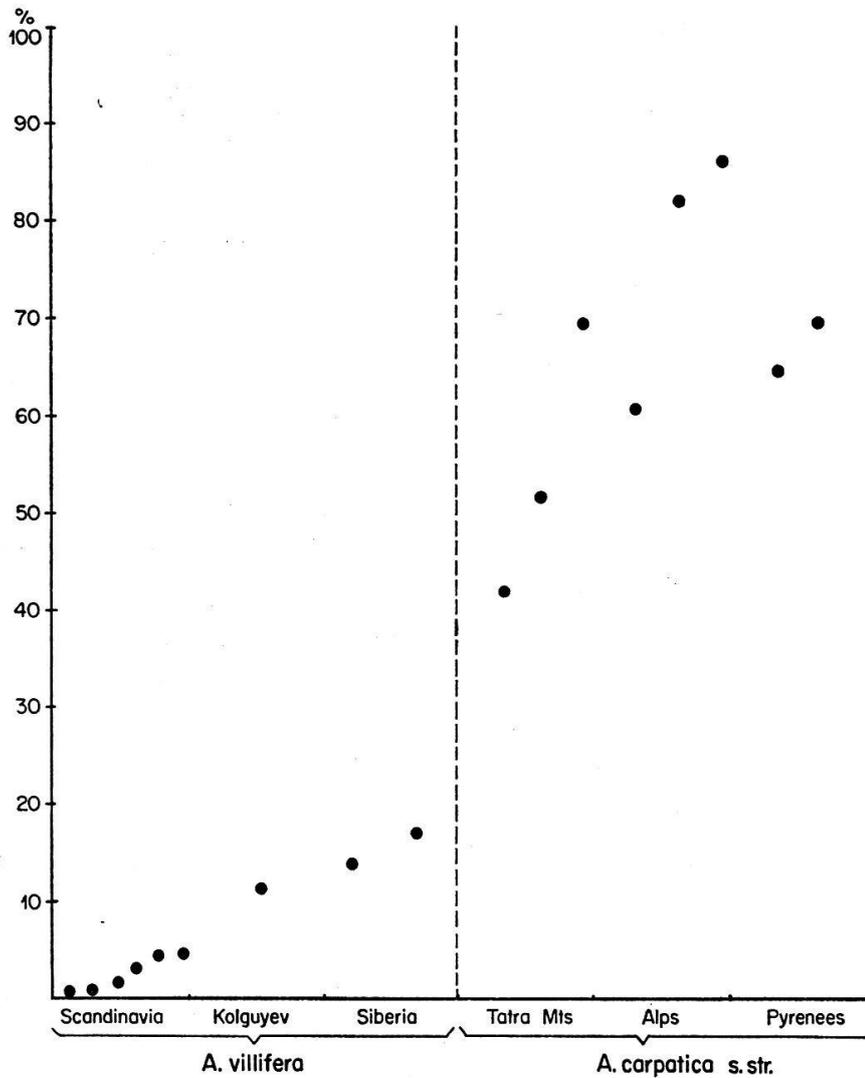


Fig. 20. Seed-setting in *Antennaria villifera* and *A. carpatica* s.str.

### 3.3 *Antennaria carpatica* s.str.

*A. carpatica* s.str. is a rather variable species. It seems possible, however, that the differences observed in the course of the present study are mostly the result of some modifications. This chiefly concerns the size of plants, morphology of the rosette leaves and tomentum occurring on their upper surface.

As far as the size of plants is concerned, it ranged from 3.5 cm to 24.2 cm in height. The smallest plants were collected on steep ridges where the humus layer was rather defective. On the other hand, well developed specimens were usually found in the optimal phases of the resp. associations; their vigour is apparently influenced by environmental conditions.

The shape of the rosette leaves varied from lanceolate to oblanceolate (Fig. 40). Most frequently they were acute; sometimes obtuse leaves were also observed. The maximal width of the leaves ranged from 3.8 mm to 11.1 mm. It should be noted that in some localities plants with broad leaves most frequently occurred within the population. However, oblanceolate leaves, 5.6 mm to 5.9 mm broad, seem to be the most representative for *Antennaria carpatica* s.str. from its whole range of distribution.

Observations performed on a great number of specimens in natural localities as well as on the herbarium material corresponded in this respect with the results obtained after two years of cultivation in the experimental field. The scale of variability in the cultivated plants was narrower than that found within the natural populations; on the other hand, the modal value was nearly the same (Fig. 21).

Two types of leaves may be distinguished in *Antennaria carpatica* s.str.: some of them are tomentose on both surfaces whereas in the other the upper surface is glabrous. It should be emphasized, however, that this character is considerably variable and transitional forms between the two types were frequently observed in the same population. Some differences were found in the frequency of the resp. types in various parts of the range of *A. carpatica* s.str. In the Tatra Mountains plants with glabrous leaves were much more frequent than the tomentose ones. Within the Alpine range both types seemed to be equally frequent; only in the Maritime Alps did the tomentose form chiefly occur. In the material studied from the Pyrenees plants with tomentose leaves represented the most frequent type.

The notable variability in the morphology of the rosette leaves renders its diagnostic value highly questionable. It should be noted that CHRTEK and POUZAR (1960) recently described *Antennaria helvetica* on the basis of this particular character; however, it seems probable that the newly described

taxon represents an example of general variability occurring within *Antennaria carpatica* s.str. and therefore should not be considered as a separate species.

The colour of the leaves and stem is usually greyish-green or green. Sometimes the petioles are slightly violet. The stem leaves are similar to those of *A. villifera*: they are sessile, lanceolate and acute. Scarios appendages occurring in upper stem leaves are of a brownish colour.

The arrangement of the heads in *Antennaria carpatica* s.str. is similar to that of *A. villifera*; however, their number is usually higher (8–9 heads). The heads are short pedunculate and tomentose.

The involucrel phyllaries are green at the base; about the middle they are dark brown and the upper part is brown or olive green becoming whitish at the age. As far as the morphology of phyllaries in the male heads is concerned, they are similar to those of *Antennaria villifera*, but usually longer (Fig. 11).

The lower parts of the staminate florets are greenish. The upper part of the corolla is cream-coloured; sometimes its tips are pinkish. Multicellular glandular hairs occur on the corolla. The anthers are glabrous and intensively purple (Fig. 34).

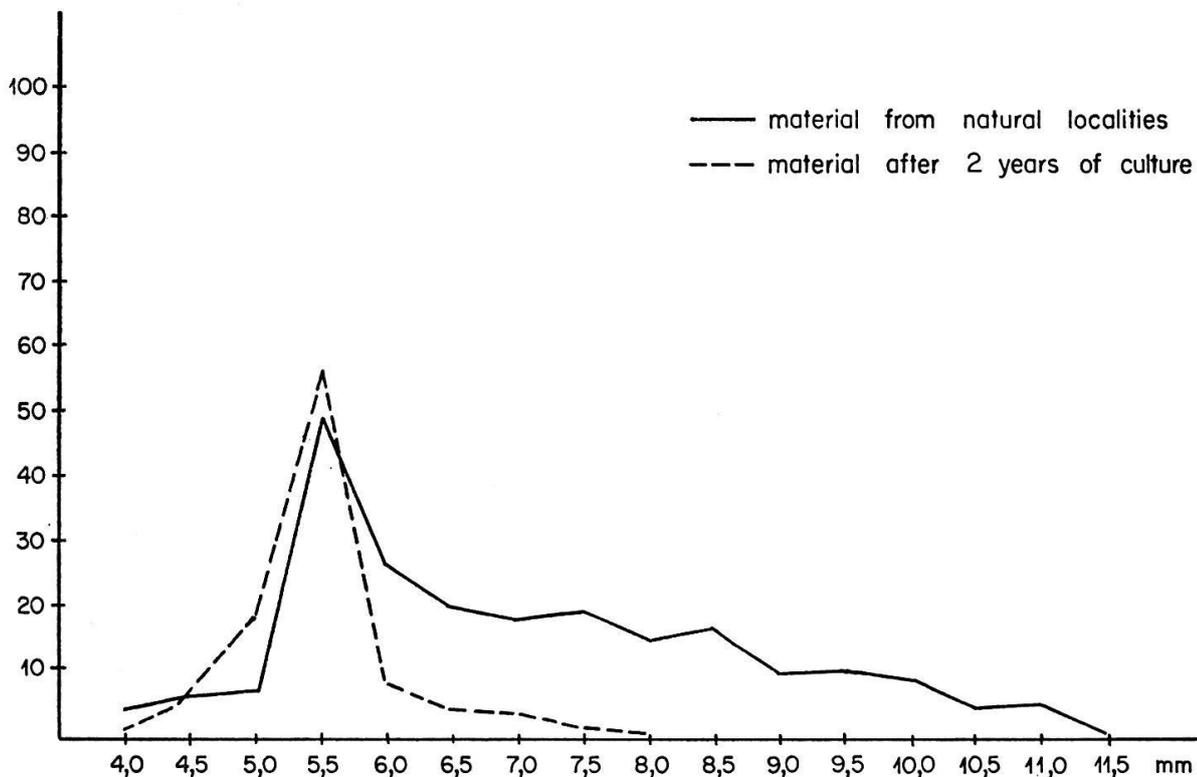


Fig. 21. Width of the rosette leaves of *Antennaria carpatica* s.str.: a comparison between the material sampled in natural localities and the plants kept for two years in the experimental field.

As it was the case in *Antennaria villifera*, differences in the colour of the resp. parts in the staminate florets are also a valuable diagnostic character for *A. carpatica* s. str.

The pappus in male heads is white; its length is more or less equal to that of the staminate florets at the time of anthesis (Fig. 12). The morphology of the pappus bristles is very similar to that of *A. villifera*; only occasionally serrate bristles with very broad, flattened tops were observed.

The pollen of *Antennaria carpatica* s. str. is rather regular. Its range of variability is quite typical (Fig. 13); the modal value comports 35  $\mu$ . Fairly viable, normal pollen is in accordance with the author's previous investigations on microsporogenesis in *A. carpatica* s. str. (URBAŃSKA-WORYTKIEWICZ 1962, URBAŃSKA-WORYTKIEWICZ unpubl.).

The female heads of *A. carpatica* usually consist of a higher number of florets than those of *A. villifera*. The involucrel phyllaries are green and tomentose at the base; in the middle part they are dark brown with well-marked limits of the darkest colour; their upper part is most frequently light-brown or whitish. The shape of the phyllaries resembles *Antennaria villifera*.

The lower parts of the pistillate florets are green. Middle and upper parts of the corolla are purplish with some hairs occurring most frequently in the topmost region. The style and stigma are purplish-brown and usually deeply cleft.

Some differences were found in the degree of the exertion of style. In the material from Eastern Carpathians as well as in many specimens from the Alps only slightly exerted style was observed. In some other plants, however, the length differences between corolla and style amounted to 4 mm. It seems doubtful that these differences are due to some developmental deviations as they were found in plants with apparently normal achenes. It should be added that the length of the stigma lobes in *Antennaria carpatica* s. str. seems to be variable and no well-separated types could be distinguished.

The pappus was white or yellowish; its length sometimes exceeded that of the pistillate florets. In most of the studied plants, however, these differences were not pronounced (c. 1.5 mm, Fig. 19).

The achenes in *Antennaria carpatica* s. str. are considerably well developed in the material from the whole range of distribution. They are glabrous, brown and c. 1.5 mm long (Fig. 38). The high percentage of developed achenes found in the studied material corresponds with the normal, sexual reproduction revealed in *A. carpatica* s. str. (URBAŃSKA-WORYTKIEWICZ 1961, 1962, 1962a, URBAŃSKA-WORYTKIEWICZ unpubl.). Thus, the two European species of the complex differ notably from each other in their seed setting. The

average percentage of developed achenes comports 70% to 75% in *A. carpatica* s.str.; by contrast, the highest frequency found in *A. villifera* did not exceed 17%.

The fully normal life cycle of *Antennaria carpatica* s.str. points to its apparently balanced genetical structure; this species seems to be well adapted to rather extreme ecological conditions occurring in the alpine belt of the mountains in Central and Western Europe.

### 3.4 Diagnostic characters in the *Antennaria carpatica* complex

Characters of a diagnostic value which were found within *A. carpatica* may be assigned to three categories:

1. Characters which permit the whole section *Carpaticae* to be distinguished from the others of the genus *Antennaria*;
2. Characters which are typical for the resp. species of the complex;
3. Details which appear to correspond with tetra- and hexaploid type of *Antennaria villifera*.

On the whole, the section *Carpaticae* may be characterized by the growth habit: procumbent stolons do not occur; rosette leaves are well developed, erect, oblanceolate or lanceolate, mostly 3nerved. The heads are grouped at the topmost part of stem.

The above mentioned characters were reported in all previous diagnoses (WAHLENBERG 1814, 1826, BLUFF and FINGERHUTH 1825, HOOKER 1840, GREENE 1897–1898, etc.). They are typical for the section; however, they do not seem to be of much use for a description of the particular species, as they show rather a wide scale of variability even within a single population. In this respect the *Carpaticae* differ from the other sections of the genus, i.e. the *Alpinae* in which the value of the growth habit seems to be significant for the individual species (MALTE 1934, PORSILD 1950, 1965).

Another important detail is the occurrence of both staminate and pistillate plants reported in all species belonging to the *Carpaticae*. It should be noted that many species of the *Alpinae* and the *Dioicae* are represented exclusively by pistillate plants; these sections are predominantly apomictic (KERNER 1876, JUEL 1900, BERGMAN 1935, JØRGENSEN, SØRENSEN and WESTERGAARD 1958). By contrast, no tendency to an apomictic seed development was found either in *Antennaria villifera* (BERGMAN 1951, URBAŃSKA-WORYTKIEWICZ 1967a, 1967b) or in *A. carpatica* s.str. (URBAŃSKA-WORYTKIEWICZ 1961, 1962, 1962a, URBAŃSKA-WORYTKIEWICZ unpubl.). It seems probable that both

*A. lanata* and *A. pulcherrima* are also sexual; it may be inferred from an equal frequency of staminate and pistillate plants as well as from the occurrence of highly viable and normal pollen (PORSILD 1965).

As far as the morphology of the stem leaves is concerned, it appears to be an useful character for the *Antennaria carpatica* complex. In *A. carpatica* s. str. scarious appendages occurring on the upper stem leaves are brown and narrow; in *A. villifera* they are blackish with a trace of violet at the base, twisted and also narrow. In *A. lanata* the stem leaves are broader than in the two former species; scarious appendages on the upper stem leaves are yellowish-brown, rather flat and broad. In *A. pulcherrima* the stem leaves are numerous and rather broad, but scarious appendages did not occur in most of the studied material.

Details of the morphology of the stem leaves in the *Carpaticae* species were reported previously by some authors (BORISSOVA 1959, CHRTEK and POUZAR 1962). The diagnostic value of this character was often emphasized by authors who studied some other species (FERNALD 1924, 1931, PORSILD 1950, 1965).

The colour of the phyllaries seems to present a further character which should be taken into consideration for a description of the resp. species. In fully developed plants the differences are rather well-marked. In *Antennaria carpatica* s. str. the phyllaries are green and tomentose at the base; about the middle part they are dark brown with conspicuous limits of the darkest colour; the upper parts are usually light brown, sometimes whitish in the male heads. In *A. villifera* the middle part of the phyllaries is most frequently blackish or black; the same colour frequently occurs in the upper part. In *A. lanata* the phyllaries are much more tomentose than in the former species. In the middle part a dark green or blackish colour occurs; the upper part is snowy-white. In *A. pulcherrima* light brown phyllaries most frequently show no dark spot in the middle part.

The length differences observed in the innermost phyllaries of the male heads help to distinguish *A. carpatica* s. str. from *A. villifera*; on the whole, however, they do not seem to present a good diagnostic character for all species of the complex.

A particularly useful feature, by which the resp. species may be distinguished, is the colour of the staminate florets. In *Antennaria villifera* the corolla is purple and the anthers are bright yellow. In *A. carpatica* s. str. they are cream-coloured with purple anthers. In *A. lanata* the florets are white with pale yellow anthers. In *A. pulcherrima* they are straw-coloured and the anthers are intensively yellow.

In view of the decisive diagnostic value of this character we have included it into the descriptions of species belonging to the *A. carpatica* complex. It

would be interesting to know similar details for other groups of the genus *Antennaria* as they are rather scarce in the literature.

The ratio of the length of the pistillate florets and the pappus presents different values for *A. carpatica* s.str., *A. villifera* and *A. lanata* (Fig. 19). The relative length of the flower organs also differs in the staminate florets (Fig. 12). It should be noted, however, that these quantitative characters may be not always recognizable in poorly collected herbarium specimens; therefore, they should be considered as additional criteria of classification.

Seed development shows notable differences between *A. carpatica* s.str. and *A. villifera*. In addition, the length of the achenes and their colour seem to be helpful in determining of the resp. species: in *A. carpatica* s.str. the achenes are brown and c. 1.5 mm long; those of *A. villifera* are purplish-brown and 0.8 mm long, but exceedingly rare; in *A. lanata* the achenes are c. 1 mm long and their colour is olive-brown whereas *A. pulcherrima* has brownish achenes about 2 mm long.

It should be noted that some of the details found in *Antennaria villifera* seem to correspond with the two cytotypes occurring within this species. In view of the fact that both the pollen types and the stigma types are rather well separated from each other, it seemed advisable to accomplish the description of *A. villifera* by these details.

Thus, it appears possible that the present concept of species within the *Antennaria carpatica* complex should be based upon a series of minute characters which nevertheless are fairly constant. This chiefly concerns the morphology of the florets. The morphology of the rosette leaves as well as the length of the involucrel phyllaries do not seem to have a decisive diagnostic value in view of their notable variability.

It should be added that similar results were obtained by the authors working on the *Antennaria* representatives from North America (FERNALD 1924, PORSILD 1950, 1965).

## 4. Geographical distribution

### 4.1 *Antennaria villifera*

In Scandinavia, *A. villifera* shows a slightly discontinuous unicentric distribution in the northern part of the mountain range (Fig. 22). It is confined to the inland mountains. Its local southern limit corresponds to the Arctic Circle (Saltdalen, Nordland) whereas the northernmost localities were reported

from East Finmark (Masöy, Snøfjord, c. 70°48', DAHL 1934; Mount Rastigaissa, NORDHAGEN 1939). The eastern limit in Fennoscandia is in Mount Jordbagaissa and Mount Gednagaissa, also in East Finmark.

The localities of *Antennaria villifera* in Arctic Russia are separated from those of Scandinavia by a gap of c. 700 km. It occurs in Kolguyev, Vaigatsch, Novaya Semlya and in the northernmost part of the Ural Mountains (LYNGE 1923, UHLWORN and PASCHER 1928, TOLMATSCHEV 1926, 1930, HULTÉN 1955, BORISSOVA 1959). It should be added that *Antennaria villifera* was also

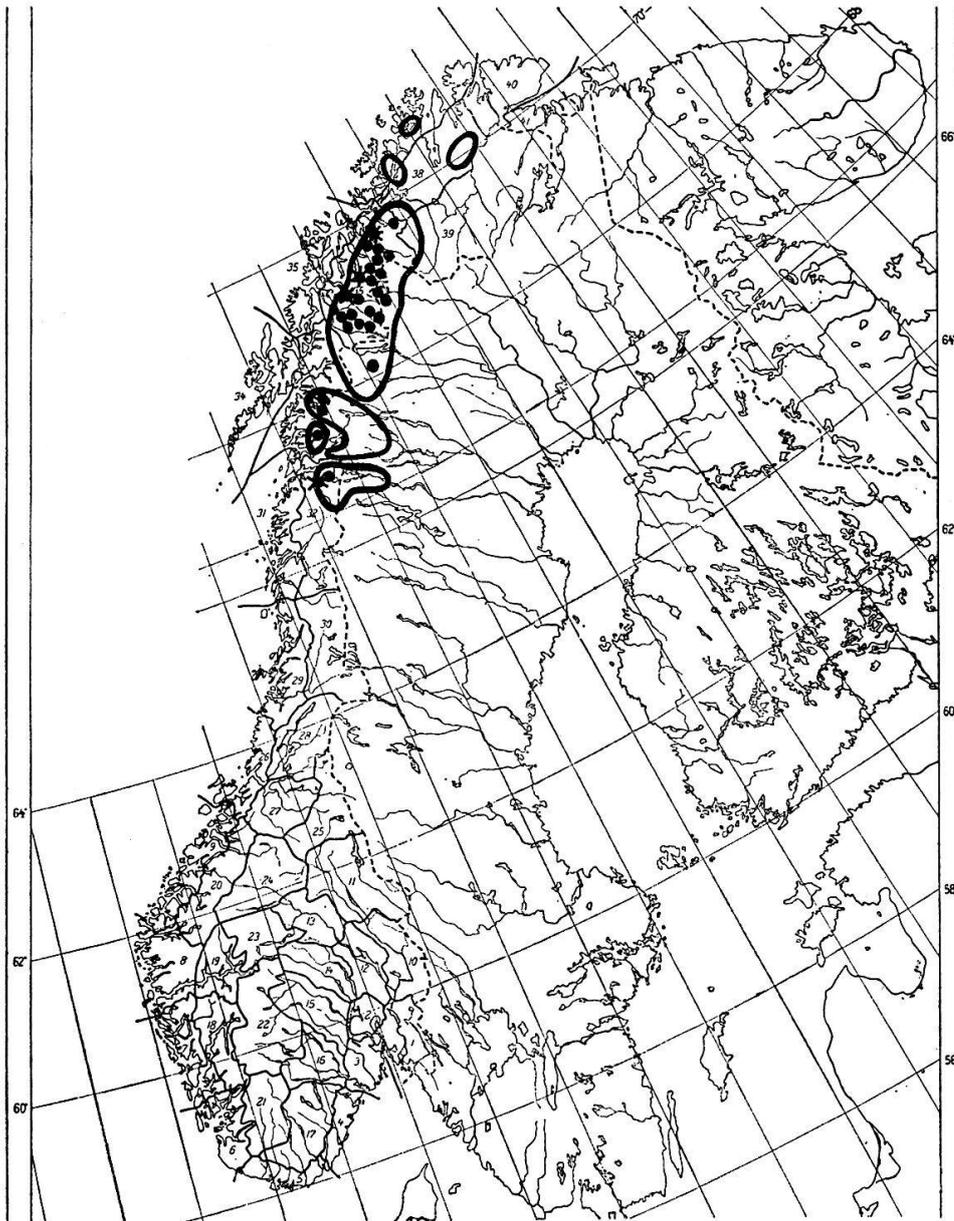


Fig. 22. Distribution of *Antennaria villifera* in Scandinavia. Unbroken lines represent local areas of distribution; dots mark some localities of plants studied cytologically; asterisks correspond to the places from where the herbarium materials with developed achenes were found.

reported from the Asiatic part of the USSR as occurring in Yamal, Taimyr, Yakutia. The easternmost limit of its range corresponds to the Chukotchka Peninsula where *A. villifera* occurs rarely in the region of Anadyr. Some localities of *A. villifera* were noted also in East Siberia, in the region of Irkutsch (the Sayan Mounts: basin of Kitoj river). The distribution of *A. villifera* in Eurasia is presented in Fig. 23.

#### Localities of *Antennaria villifera* Boriss.

##### Europe

##### I. Fennoscandia

##### A. Norway:

Nordland. Sörfold: Mount Guorkoi (Korken), c. 1060 m, T. Engelskjøn, O. Skifte et H. Saetra,  $2n=28$ , TE\*; Fauske, Blåmansisen, c. 1000 m, S. Sivertsen TROM; Blåmansisen V: Stormfjellet, S. Sivertsen TROM; 1.9.1967, S. Sivertsen TROM; Balvand "Sueten" O; Hamarøy, Cokkuljavrrre S, c. 800 m, S. Sivertsen TROM; Fauske, Dalen N vor Rautind, S. Sivertsen TROM; fjellet op Ny-Sulitjelma, A. Notø, O; Töfla, A. Notø O; Sörfolden, fjellet vor Fågebak, J.M. Norman O; Ankenes, Skjomen, Slettjord, 600 m, L. et S. Slettjord O; Tysfjord: Rombotindan, 1230 m, W. Apold et G. Brodal O; Bangevatn NW, S. Sivertsen O; Messingmalmvatna, W. Apold, G. Brodal et O. Skifte TROM; Naidi, 950 m, T. Engelskjøn et B. Rørslett TROM; Øvre Tverrelvdal, NNE 1127, 750 m, T. Engelskjøn et B. Rørslett TROM; Kjerringvatn-Giccečocca, 800 m, S. Sivertsen et O. Skifte TROM; Bangeaksla, 1090 m, W. Apold TROM; under Bjørntoppen, T. Engelskjøn et B. Rørslett TROM; Naidivatn, c. 800 m, T. Engelskjøn et B. Rørslett TROM; NE part of glacier Giccečokka, c. 800 m,  $2n=42$ ,  $2n=28$ , TE; Ballangen, Mereftasfjell, c. 950 m, Ø. Michelsen et S. Sivertsen TROM; Fauske: riksgrensenströkka NØ vor Sulitjelma, c. 1100 m, O. Skifte, S. Slettjord et R. Wara TROM; riksgrensa, like sør for Hedre Sorjusjavre, c. 1000 m, O. Skifte, S. Slettjord et R. Wara TROM; the same but 885 m, TROM; Nordsida av Øvre Sorjusjavre, 960–1050 m, W. Apold, G. Brodal et O. Skifte TROM; Sulitjelma trakten, R. Nordhagen BG; Akselfjellet, O. Nyhuus O; Saltdal: V-siden av Saulotjønnene, E. Smalsvik et S. Sivertsen TROM; N-Saulo, foten NW-siden, 800 m, E. Smalsvik et S. Sivertsen TROM; N-Saulo, 1000 m, E. Smalsvik et S. Sivertsen TROM; Sörfold: Boaimac, Riksgrensa, W. Apold, G. Brodal et O. Skifte TROM; Vest for riksgrensa, W. Apold, G. Brodal et O. Skifte TROM; line vest for Ciegkimcorro, 950 m, W. Apold, G. Brodal et O. Skifte TROM; Söransida av Flatkjolen, 795 m, W. Apold, G. Brodal et O. Skifte TROM.

Troms. Kirkestind, SW slope, 1100 m, T. Engelskjøn,  $2n=28$  O; the same but 1150 m, T. Engelskjøn et S. Thoresen TROM; Balvand, Salten, H. Guldberg LD; Njunis, N slope of summit 1094, K. Urbańska-Worytkiewicz et T. Engelskjøn,  $2n=42$ , UW; Njunis, NW valley, rocks near the river, 760 m,  $2n=42$ , K. Urbańska-Worytkiewicz et T. Engelskjøn UW; Gaicačacca, 820 m,  $2n=42$ , K. Urbańska-Worytkiewicz et T. Engelskjøn UW; Njunis, NW valley, E side of river, 850 m,  $2n=42$ , K. Urbańska-Worytkiewicz et T. Engelskjøn UW; N slope of 1094, 880 m,  $2n=42$ , K. Urbańska-

\* TE = herbarium of T. Engelskjøn

\* UW = herbarium of the present author

Worytkiewicz et T. Engelskjøn UW; the same but 920 m,  $2n=42$ , UW; Njunis, NW valley, dry hill near the river, 950 m,  $2n=42$ , K. Urbańska-Worytkiewicz et T. Engelskjøn UW; small grassy slope near the river junction, 950 m,  $2n=42$ , K. Urbańska-Worytkiewicz et T. Engelskjøn UW; NE slope of 1094, 1000 m,  $2n=42$ , K. Urbańska-Worytkiewicz et T. Engelskjøn UW; the same but more to the right,  $2n=28$ , UW; NE slope of 1050, upper part, c. 1000 m,  $2n=42$ , K. Urbańska-Worytkiewicz et T. Engelskjøn UW; bajit Riidagier'do, NE slope, c. 1000 m,  $2n=28$ , K. Urbańska-Worytkiewicz et T. Engelskjøn UW; the same, upper parts, 1120 m,  $2n=42$ , K. Urbańska-Worytkiewicz et T. Engelskjøn UW; Riidagier'do, N slope, 900 m,  $2n=28$ , K. Urbańska-Worytkiewicz et T. Engelskjøn UW; Baegasangai'ssa, NW slope, c. 1020 m,  $2n=42$ , K. Urbańska-Worytkiewicz et T. Engelskjøn UW; the same but 950 m, T. Engelskjøn et S. Thoresen TROM; Riidagier'do, NE slope 1000 m, T. Engelskjøn et S. Thoresen TROM; Baegasangai'ssa, NW slope, between the tops 1178 and 1141,  $2n=42$ , c. 1100 m, K. Urbańska-Worytkiewicz et T. Engelskjøn UW; little Jer'ta, SW slope, 890 m,  $2n=42$ , K. Urbańska-Worytkiewicz et T. Engelskjøn UW; the same but 910 m,  $2n=42$ , UW; the same but 930 m, isolated,  $2n=42$  UW; Rostafjellet, W slope of Rostakulen, c. 1050 m,  $2n=42$ , K. Urbańska-Worytkiewicz et T. Engelskjøn UW; J.M. Norman BG; the same but 1100 m,  $2n=42$ , UW; Rostadalen: Dolpevarre, c. 900 m, P. Benum TROM; Storfjord: Paras, SE ridge, 950 m,  $2n=28$ , K. Urbańska-Worytkiewicz et T. Engelskjøn UW; H. Smith UPS; Paras, E slope, c. 800 m,  $2n=42$ , K. Urbańska-Worytkiewicz UW; N slope, 950 m,  $2n=42$ , K. Urbańska-Worytkiewicz UW; E slope, c. 700 m,  $2n=42$ , K. Urbańska-Worytkiewicz UW; Nordreisa: Vuoddujåkka, 650–700 m,  $2n=42$ , K. Urbańska-Worytkiewicz et M. Elvestadt UW; between Vuoddujåkka and Gaetkuot'aivit, NE slope, 700 m,  $2n=42$ , K. Urbańska-Worytkiewicz et M. Elvestadt UW; Gaetkuot'aivit, NE slope, 750 m,  $2n=42$ , K. Urbańska-Worytkiewicz et M. Elvestadt UW; E. Fridtz O; N slope, 800 m,  $2n=28$ , K. Urbańska-Worytkiewicz et M. Elvestadt UW; the same but in a snow-bed locality,  $2n=28$ , K. Urbańska-Worytkiewicz et M. Elvestadt UW; the same but 900 m,  $2n=42$ , UW; the same but 950 m,  $2n=42$  UW; Gaetkuot'aivit, the top part, 1020 m,  $2n=42$ , K. Urbańska-Worytkiewicz et M. Elvestadt UW; Javreoavve, c. 900 m,  $2n=28$ , K. Urbańska-Worytkiewicz et M. Elvestadt UW; R. Ruotsalo HEL; Y. Mejland O; Bihka Hihtama, Y. Mejland O; Gatmasvagge, Y. Mejland BG; Rokkilnjune, 800 m, R. E. Fridtz O; Roggeoavve, Y. Mejland O; Jahkavarres, Y. Mejland O; Geinačokka, Y. Mejland O, BG; Geidioavve, Y. Mejland O; Gabmasvagge, Y. Mejland O; Gieidinjудue, Y. Mejland O; Sakkevoarre, Y. Mejland O; Ballusoavve, Y. Mejland O; Fatavarre, Y. Mejland O; Kåfjord: Guolasjav're, between Gåddečårro and Sinaivarri, c. 800 m,  $2n=42$ , K. Urbańska-Worytkiewicz UW; Gåd'dečårro, c. 850 m,  $2n=28$ , K. Urbańska-Worytkiewicz UW; Sinaivarri, S slope, c. 800 m,  $2n=42$ , K. Urbańska-Worytkiewicz UW; Guolasjav're, A. Notø O; P. Benum TROM; E. Jorgensen O; H. Resvoll-Holmsen O; O. Skifte TROM; Kvaenangen, Nabar S,  $2n=28$ , S. Sivertsen TROM; Cuonja čobba, Y. Mejland TROM; mellom toppen av Stisavarre og molnelva, O. Rønning TROM; Goalsevarre, B. Benum TROM; Storfjord: Govdajaurre, J. Holmboe BG; Trolldelvdalen, J. Holmboe BG; Mikkafjellet, J. Holmboe BG, O; Sikka, R. Nordhagen BG; Malla, J. Holmboe UPS; Kåbdåvanka, R. F. Fristedt UPS; Stortind, C. M. Norrman UPS; Agjakreppo, mellom Mandalen og Skibotn, A. Notø O; Benum TROM; Moskogaissa, E. Haglund O; Storfjell (Bjørnen) S, 900–1100 m, S. et T. Engelskjøn O; Madagaissa, 1200 m, T. Engelskjøn et S. Thoresen TROM; Favresvarre, Skibotndalen, J. Holmboe O; Y. Mejland BG; S. Mårtensson UPS; Lyngen: Malla's skraning mot Goodavagge, J. Holmboe O, TROM; Likkavarre, J. M. Norman HEL; Faurevarre, P. Benum TROM; Rippovarre, P. Benum TROM; Dirnoavve, P. Benum TROM; Sallojaure, P. Benum TROM; Gaskavagge, T. Engelskjøn et S. Thoresen TROM; Hysingjordfjell, S-topp av Båtfjell, 630 m, T. Engelskjøn et S. Thoresen O, TROM; Balsfjord: Hattevarre, P. Benum O, TROM; Dopparčacca, S. Mårtensson O, UPS;

Aismålstind, J. Devold O; Lifjellet, O. Nyhuus O; Målselv: Alappen, O. Nyhuus O, TROM; A. Landmark LD; E. Haglund O; Kirkestind, 1080 m, T. Engelskjøn et S. Thoresen TROM; C.M. Norrman LD; Middagsfjellet, O. Rønning TROM; C.M. Norrman UPS; Kobbrygen: Lifjeld, P. Benum TROM; Rubben, P. Benum TROM; Iselvdal: Sorhallet, 1150 m, P. Benum TROM; Røjelvdal: Balgesoavve, O. Rønning et O. Skifte TROM; Skjervoy: Jøvanden, O. Rune et O. Rønning TROM; Vaddas, Lohtana, Y. Mejland O; Tverdfjellet, Rostadalen, P. Benum O; Aslakčacca, J. Holmboe O; Galbber (öst for Dividalen), J. Holmboe O; Dreggfjellet, 1150 m, T. Engelskjøn O; Th. C. E. Fries UPS; Skaret NØ Skinskardtind, Ø. Michelsen et S. Sivertsen TROM; Røyvassberget, Ø. Michelsen et S. Sivertsen TROM; Sordalen: Rissovarre, A. Notø TROM.

Finmark. Måsoy: Ryggefjord, O. Dahl O; under Jordbagaissa nor Rastigaissa, O. Dahl O; Polmak, under Gednogaissa, O. Dahl O; Grasfjellet, O. Rune et O. Rønning TROM; Tana, S-skraningen av Uccagaissa, 540 m, L. Ryvanden TROM; Rastigaissa, R. Nordhagen BG.

## B. Sweden:

Pite Lappmark. Mount Baatskavat, O. Dahl et R. Nordhagen O; Mavosjaure R. Nordhagen BG; between Mavosjaure and Norwegian border, O. Dahl UPS; Ikesjaureområdet, Neitatjåkko, Th. et A. Arwidsson S; Pieskejaureområdet: Nuorta Saulo, Th. Arwidsson S; Mavas-området: Årjil Saulo, c. 1200 m, O. Rune S.

Lule Lappmark. Alatjåkko, 780–1210 m, S. Selander S; Kappa, S. Selander et N. Dahlbeck S; Jållo vis Sårjäsjaure, S. Selander et N. Dahlbeck S; Vaisaluokka, c. 1200 m, O. Rune S; Vaisa, Kalpik, 925 m, G. Björkman LD; H. W. Rosendahl S; E. Nyman S; S. Selander et N. Dahlbeck S; Vaisa, Rätjat, c. 970 m, G. Björkman UPS; Vaisa, Rautoåive, W part, G. Björkman UPS; Puolaure, C. G. Alm et H. Reuter-skiöld LD; UPS; BG; HEL; G. Björkman UPS; A. Nannfeldt S; Njunnats E. A. G. Kleen LD; Kaitumtjåkko, N. Svensson LD; Ruodmas, J. Andersson LD; Virihaure, Stalotjåkko NE, T. Svedberg UPS; J. Andersson UPS; Kierkevare, C. L. Laestadius UPS; E. C. J. Ledersträhle LD; Ahrling et Brandelius UPS; A. Mander HEL; E. Astrid LD; Kautoaive S, c. 1100 m, G. Björkman UPS; Naddit, S. Selander UPS; T. Vestergren LD; Tjågnöisi, Th. A. Tengwall UPS; LD; Gällivarre: Kallaktjåkko, G. Björkman UPS; Särekfjellen, T. Vestergren UPS; Muratjåkko, G. Björkman UPS; Poljats, G. Björkman UPS; Alkavarre, Th. A. Tengwall UPS; LD; HEL; Rissavarre, Th. A. Tengwall UPS; Shavvavagge, Th. A. Tengwall UPS; Raulåire N, G. Björkman UPS; Sitasjaure, Skeltas, B. Bohlin LD; Skeron S, Selander et N. Dahlbeck UPS; Jeknafo Mountain, S. Selander et N. Dahlbeck UPS; Niåtsosvage, Th. A. Tengwall HEL.

Torne Lappmark. Jukkasjärvi: Mount Nissontjärro, 1000–1200 m, C. G. Alm et H. Smith HEL; UPS; E. Nyholm LD; Moskana, Peldsavagge, C. G. Alm et Th. A. Tengwall HEL; UPS; J. Lid O; G. Samuelsson S; Peldsa, NE slope of Low Peak, 900 m,  $2n=42$ , K. Urbańska-Worytkiewicz et T. Engelskjøn UW; Peldsa, middle part of the slope between Low Peak and High Peak, 1000 m,  $2n=42$ , K. Urbańska-Worytkiewicz et T. Engelskjøn UW; Peldsa, NE slope of Low Peak, upper part, 1100 m,  $2n=28$ , K. Urbańska-Worytkiewicz et T. Engelskjøn UW; Peldsa, c. 1300 m, H. Smith UPS; c. 1100 m, H. Smith UPS; c. 950 m, H. Smith UPS; Påltsamavanka, H. Smith UPS; Moskana SE, c. 900 m, H. Smith UPS; Nirjijaure, H. Smith UPS; mallam Knobletjåkko och Kuolkotjåkko, H. Smith UPS; Tjuonaktjåkko, E sida, H. Smith UPS; Pesisvare, N. Sylvén UPS; G. Samuelsson LD; Abisko: Låktatjåkko, c. 775 m, L. Fagerström HEL; Abisko, c. 1000 m,  $2n=42$ , UW; Låktatjåkko, c. 850 m, L. Fagerström HEL; C. G. Alm et H. Smith UPS; T. et E. Nyholm LD; Lulletjärro, H. Smith O; UPS; Nuolja, R. Nordhagen O; C. G. Alm UPS; Th. Fries UPS; O. Holmberg LD; Moskofjellet, C. P. Laestadius UPS; Nissontjåkko, E-sida, H. Smith UPS; C. G. Alm UPS; G. Björkman S; Btovare, c. 900 m, H. Smith UPS; Tsassinjarkatjåkko, T. A.

Tengwall UPS; Njuonjevarre, c. 900 m, C.G. Alm UPS; Vassitjåkko, c. 700 m, C.G. Alm UPS; T. Håkansson LD; the same but 850 m, C.G. Alm UPS; Gardetjåkko, H. Smith UPS; Nissonrättejokk, c. 900 m, C.G. Alm UPS; Vaddetjåkko, c. 1000 m C.G. Alm UPS; Pallamtjåkko mot Nissonvagge, C.G. Alm UPS; Håikamavagge, c. 1000 m, A. Nygren UPS; Kartetjåkko, c. 1400 m, H. Smith UPS; Tjålmojtjåkko mot Kamavagge, H. Smith UPS; Sjängeli: Ruopsok, H. Smith UPS; G. Björkman S; Knobletjåkko, H. Smith UPS; Nisson-rappejokk, H. Smith UPS; Anavares NW, E. Asplund UPS; Latujatjärro, 1000 m, A. Nygren UPS; Tjuonjavagge, c. 1100 m, A. Nygren UPS; LD; Pesisvare, 800–950 m, C.G. Alm et H. Smith UPS; Atjaktjåkko SE, 1200 m, H. Smith UPS; Låktavagge, E. Nyholm LD; Airavarre, S. Ellerström LD; Rankejaure, H. Weimarck LD; Nissontjåkko, c. 1300 m, R. Holmberg LD; N. Sylvén LD; Ortovarre, R. Holmberg LD; Kopparåsen, c. 800 m, R. Holmberg LD; O. Lönquist LD; Suorijokk, F. Lonnquist LD; Nissonjokk, F. Ahlberg LD; Lulletjärro, c. 800 m, G. Samuelsson et A. Zander S; Håikamatjärro, 1000–1100 m, G. Samuelsson S.

### C. Finland:

Le, Riduitstrohka, P. Niamali TUR; Le, Fehkatsoch, H. Sättin TUR; Le, Jehkatn, NW-rin, P. Kallio TUR; Le, Enontekiö, Jahkatsu-tunturi, O.K. Silkkilä TUR; H. Sälzin TUR; Le, Sunjavarri, A. Vuorisato TUR; Le, Guonjavarra N, P. Kallio TUR; Le, Enontekiö, NW-osa, T. Laine TUR; Cuontekiö, suurimman Pihtsuavankan, T. Laine TUR; Le, Pikku-Luokkmiobba, T. Laine HEL; NW Le, near Sarijokka, c. 850 m, J.I. Livo et H. Roivainen HEL; Le, W-Ridnitschokka, 950–1000 m, H. Roivainen HEL; Le, Goosjarvaara, M.v.Schantz HEL; Le, mellan Guonjavarri och Tuoljikukpukt, G. Marklund HEL; Le, S-Tuoljikukpukt, 850 m, H. Roivainen HEL; Le, Haltia, K.J. Lounamaa HEL; Le, Guonjavarri "satula", K.J. Lounamaa HEL; Le, N-Koutuskaisi, 900 m, H. Roivainen et U. Saxen HEL; Le, W-Tuoljikukpukt, 1000 m, H. Roivainen HEL; NW-Le, W-Ridnistrokka, L. et H. Roivainen HEL; Le, W-Veaijehoavi, 800 m, L. et H. Roivainen HEL; NW-Le, N-Koutuskaisi, c. 850 m, H. Roivainen HEL.

### II. Kolguyev

Insula Kolguyev, R. Pohle HEL; Kossaya River, A. Tolmatshev LE; Velikaya River, A. Tolmatshev LE; Pestchanka River, S. Kertzelli LE; Dorozhkina River, I. Bogdanovskaya-Gienef LE; Paarchicha River, Z. Smirnova LE.

### III. Novaya Semlya

Northern Island. Tschirikina River, Matochkin Shar Strait, A. Tolmatshev LE.  
Southern Island. Shumilina River, Matochkin Shar Strait, A. Tolmatshev LE; Matotschkin Shar, O. Ekstam S; M. Weber UPS; Malyje Karmakuly, L. Savicz LE; Karmakola, T. Alm S; O. Ekstam UPS; sinus Karmakulski, O. Ekstam UPS; Peninsula Belushiy, A. Zubkov LE; V. Aleksandrova LE; Inlet Propashkaya Guba, S. Skribova LE; Grebovaya, nordsidum, Lynge HEL; Besemenaya, Lynge UPS; Mezdusharskiy Island, V. Aleksandrova LE; Habarovo, Yugorskiy Shar Strait, A. Tolmatshev LE; P. Polilov LE; Pay-Hoy range, O-yu River, V. Andreev et Z. Savkina LE; mouth Malaya Ussa River, A. Tolmatshev et O. Rebristdya LE; Fontes Kara River, O. Rebristdya LE; ad Ussam, Arep Mikit, R. Pohle LE.

### IV. Vaigatsch

Varnek-Harbour, A. Tolmatshev LE; S. Kertzelli LE; O. Ekstam LE; P. Polilov LE; cape North-Eastern, P. Polilov LE; Fretum Jugor, F.R. Kjelman et A.N. Lundström UPS; Ljamtochinabukten, Aagward UPS.

## V. The Ural Mountains

Polar Ural Mountains. Region of Longot-Yugan River, K. Igoshina LE; Longot-Yugan Mountain, K. Igoshina LE; sources of Eletz River, K. Igoshina LE; Mount Harbey, K. Igoshina LE; Great Hadata Lake, K. Igoshina LE; mouth of Parova River, K. Igoshina LE; Schtchutchya River, K. Igoshina LE; Nerussovey Lake, K. Igoshina LE; Kara River, V. Sukatshev LE; Pyderata River, V. Sukatshev LE; sources of Huuta River, V. Sukatshev LE; sources of Haramatlau River, B. Gorodkov LE; sources of Voykar River, B. Gorodkov LE.

North Ural Mountains. Kozhim River, V. Sotchava LE; sources of Naroda River, V. Sotchava LE.

## Asia

Arctic Siberia. Peninsula Tazovsky, Eselava River, Zh. Belorussova LE; Peninsula Yamal, inter cape Jam-sale and Nahodka-Harbour, LE; Yamal, cape Mare-sale, LE; Yamal, Nahodka-Harbour, A. Bushewitch LE; Yamal, Yurubey River, B. Zhitkov LE; Yamal, Yasovey River, B. Zhitkov LE; Yamal, Novy Port, D. Tchubynin LE; Tazovskaya Bay, cape Krugly, R. Pohle et A. Rozdestvensky LE; mouth of Taz River, R. Pohle et A. Rozdestvensky LE; Hantakya River, N. Kuznetsov et V. Reverdatto LE; sources of Kindun River, F. Sambuk LE; Heta River, F. Sambuk LE; Volotchanka (Taimyr), F. Sambuk LE; Goltchicha, N. Kuznetsov et V. Reverdatto LE; Tchokoto River (Phokina River), N. Kuznetsov et V. Reverdatto LE; Balagan-chan, N. Kuznetsov et V. Reverdatto LE; Dudinka, Yenisei, J. R. Sahlberg HEL; mouth of Dudypta River (Taimyr, basin of Pyagsina River), A. Vinogradova LE; Yenisei, Tolstoinos, H. W. Arnell LE; HEL; Yenisei, c. Kap Gostiuj, A. N. Lundström UPS; ad fluv. Gyda, F. Schmidt LE; mouth of Hatanga River, O. Pigulvskaya LE; E; Taimyr, Yamutarida, A. Tolmatshev LE; LD; S; Taimyr, Yamu-Nery River, A. Tolmatshev LE; Yenisei, Sopotchnaya Karga, A. Tolmatshev LE; Verkhnya Taimyra River, G. Malysheva LE; Pyassino Lake, T. Polozova LE; mouths of Tareya River (region of Pyassina River), Kozlitina LE; Putorana Mountains, sources of Dyamkan River, O. Mironenko LE; Yakutsk, Tiksi harbour, V. Petrovsky LE; mouth of Lena River, Ephimova LE; Urung-Haya (Anabar River), G. Aleksandrova LE; sources of Haraulah River, V. Sheludyakova LE; Balaganach (Lena River), N. H. Nilsson LE; Cape Elidyen, M. Brusnev LE; between Olenek and Lena, near Golimer stream, Czekanovski LE; between Olenek and Lena, sources of Kolung-bas stream, Czekanovski LE; middle part of Tomba stream, A. Czekanovski et F. Muller LE; between Maigda stream and Alakit stream, A. Czekanovski et F. Muller LE; Buckar, H. Nilsson S.

Chukotchka. Kanchalan River (basin of Anadyr River), N. Menshikov LE; Egvekinot (Olovannya-Harbour), T. Derviz-Sokolova LE; Ugatkin River (Anadyr Range), T. Derviz-Sokolova LE; Kuekvun River (Chukotsch Range),  $2n=42$ , P. Zhukova et V. Petrovsky LE; Erguveem River (Chukotschky Peninsula), V. Petrovsky LE; Komarinaya River (Anadyr Range),  $2n=28$ , E. Katienin et V. Petrovsky LE.

East Siberia. Irkutsk: Sayan Mountains, sources of Sagan-Hor River (basin of Kitoy River), M. Nazarov LE.

### 4.2. *Antennaria carpatica* s. str.

*A. carpatica* s. str. occurs as an oreophytic species in the Carpathians, the Alps as well as in the Pyrenees. Its easternmost limit corresponds to the Eastern Carpathians from where it is recorded as appearing in a few localities

(BRANDZA 1879–1883, BORZA 1947). The maximal frequency of *A. carpatica* s.str. within the Carpathian range is noted in the Tatra Mountains with a local limit in Western Tatra (SZAFER, PAWŁOWSKI and KULCZYŃSKI 1952, DOŠTAL 1950). It also occurs in the Low Tatra (Ďumbier, Kralova hola).

In the Alps *Antennaria carpatica* s.str. shows a tolerably continuous distribution from the Karawankian Alps to the Maritime Alps (Fig. 25 p. 139). The most frequent records are from the central part of the range.

As far as the distribution of *A. carpatica* s.str. in the Pyrenees is concerned, it appears to be more frequent in the eastern part of this mountain group.

Localities of *Antennaria carpatica* (Wahlenb.) Bluff et Fingerh. s.str.

#### The Pyrenees

Piz Blanc, P. Bordère TL; W; IB; Castanèse, J.E. Zetterstedt LD; HEL; UPS; Val d'Eyne, 2300 m, H. Coste TL; Héas, crêtes calcaires d'Aguila, 2400 m, H. Coste TL; Piz de Valibierne, südlich des Maladetta, Aragon, G. Müller RUEB; Hourquette d'Aure, E. Timbal-Lagrave et E. Marcais WU; hauteurs de la Mijane, dans Carança près Lhonès (P.O.), A. Guirèr TL; Val des Planès, 2n=56, Ph. Küpfer UW; Port d'Envalira, Andorra, c. 2400 m, 2n=56, Ph. Küpfer UW; Port d'Vo, J. Lange UPS; parties élevées du plateau de Camforeils, P. Baudière UW; La Coume Mijane, Candref. Z.



Fig. 23. Distribution of *Antennaria villifera* Boriss. and *A. carpatica* (Wahlenb.) Bluff et Fingerh. s.str. in Europe and Asia.

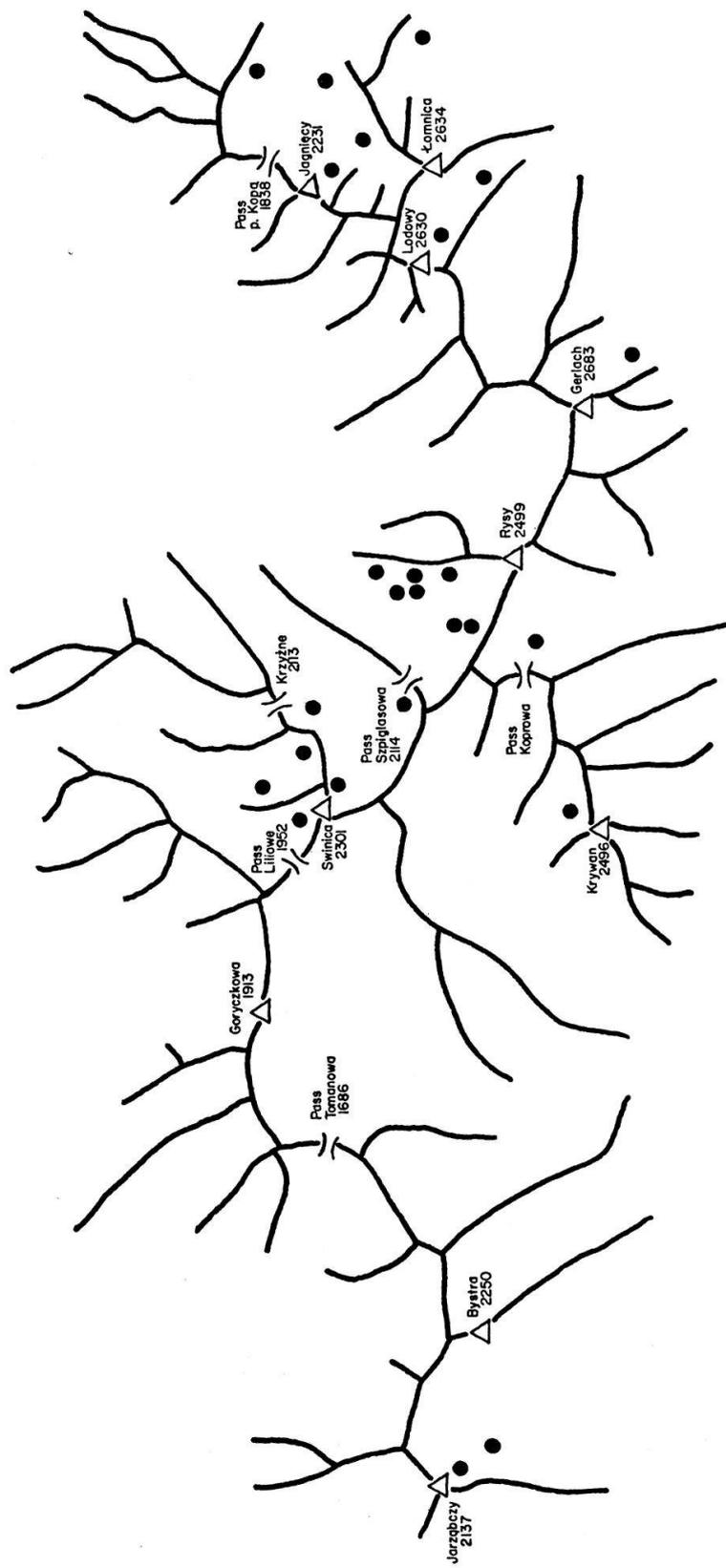


Fig. 24. Localities of *Antennaria carpatica* s.str. studied cytologically from the Tatra Mountains (after URBAŃSKA 1959, completed).

## The Alps

### A. France

The Maritime Alps. Col du Restefond, S slope, c. 2400 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; Col de la Cayolle, c. 2500 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; Vallée du Boréon, Cime de Mercantour, c. 2400 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; Mont-Formose près du Col de Tende, E. Bourgeau W; Madonna delle Finestre, Moris IB; GR; Vallée du Boréon, sur le lac de Tres Colpas, 2300 m, E. Wilczek et D. Dutoit LAU; Punta di Peyrafica, à l'est du col del Sabbione, 2400 m, E. Wilczek LAU; Haute-Tinée, 2600 m, A.St. Yves LA; Col de Jallorgues, 2500 m, A.St. Yves LAU; Mont-Ubonnier, Carres, 2250 m, A.St. Yves LAU; Col de Crousette, 2500 m, A.St. Yves LAU; Millefuons, Tête-de-Velai, 2620 m, A.St. Yves LAU; Argenton, E. Reverchon et A. Derbez W.

The Cotian Alps. Mont-Vizo, Grenin G; Vallon le Vaeta, A. Maillard G; Vallon d'Escreins, 2400 m,  $2n=56$ , R. Ruffier-Lanche UW; en dessous du lac de Clausis, sur Ceillac (Queyras), 2400 m,  $2n=56$ , C. Favarger UW; Ceilhac, Hautes-Alpes, en Gueyras, G. Didier W; Col de l'Iseran, 2750 m,  $2n=56$ , E. Landolt UW.

The Dauphine Alps. Lautaret, Grenin G; Schukters ZT; Jäggi ZT; TO; Lautaret, vallon de Roche-Noire, 2300 m, Guétal et al. GR; Z; 2100 m, E. Wilczek et G. Maillefer LAU; Faure LAU; Isère, La Salette, col au-dessus sanctuaire, Bec M; La Piolite, 2500 m, Geras G; Trois-Evêches, sur la route après col du Lautaret, c. 2500 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW.

The Graian Alps. Mont-Cenis, M. Bonjeau G; ZT; Mont-Cenis à Patta Creusa, Huguenin G; Bonjeau M.

The Savoyan Alps. Vallon de Zfluhalp, 2530–2550 m, L. Marret G; Cornette de Bise, R. v. Sargneuse G; Dent-d'Oche, F. Besson LAU; Alpe d'Annecy, Tournette, 2000 m, G. Beauverd G; Mont-Meri, 2300–2400 m, Timothée RUEB; ex herb. Payoti LAU; Massif des Aravis, G. Beauverd G; Combe de Cardavant à la Grande-Forclaz, Aravis, 2400 m, G. Beauverd G; Combe de la Balmaz sous la Rouelle, 2500 m, G. Beauverd G; Mont-Clusaz, Haute-Savoie, Duparre G; Brizon, Savoyen, Timothée LD; PRC; Col de Balafac près de Bonneville, A. Huguenin G; Mont-Vergy, E. Bourgeau Z; Timothée Z; LD; Col de Balafrasse, Pittard G; Glacier de Zaufleron, E. Wilczek LAU; Col de Balme, M. E. Moricand G; Mont-Vergy, 2400 m, E. Blachers LAU.

### B. Switzerland

The Pennine Alps. Col du Grand-Saint-Bernard, c. 2500 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; Saint-Bernard: Chemin de Cheveaux, c. 2700 m, E. Landolt ZT; Saint-Bernard: Mont-Telliers, c. 2600 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; Col de Fenêtre, Beauverd G; Pâturages col de Fenêtre, 2700 m, H. Romieux RUEB; Alpes d'Alesse, Bas-Valais, J. Muret LAU; Bella Lui, près Cry d'Er, c. 2400 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; Val d'Anniviers, F. Duflon LAU; Val de Bagnes, R. Renard G; Chanrion, val de Bagnes, Ch. Girardet LAU; Chermontagne, val de Bagnes, 2500 m, E. Wilczek LAU; H. E. Landolt Z; Mauvoisin, val de Bagnes, R. Renard G; entre Mauvoisin et La Liaz, P. Rambert LAU; Col d'Emaney, 2400 m,  $2n=56$ , C. Favarger UW; Glacier de Corbassière, Goudet G; L'Etherolla sur Veysonnaz, c. 2400 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; Crête de Thyon, F. O. Walberg Z; entre l'Etherolla et Mont-Carré, 2400 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; entre Mont-Carré et Mont-Rouge, c. 2400 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; Mont-Rouge, c. 2450 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; Mont-Loère, c. 2600 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; près cabane des Diablerets, c. 2400 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; Riffel, 2500 m, J. Coaz ZT; L. Favrat ZT; I. Peter ZT; Riffelberg sur Zermatt, 2585 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; Riffelalp, Zermatt, M. Lenzinger Z; Val de Zermatt, 2400 m, ex herb. A. Romieux RUEB;

Hörnli, F. Duflon LAU; Riffel, J. Muret LAU; R. Masson LAU; E. Sieche RUEB; J. Vetter LAU; H. Goudet G; entre Rotenboden et Gornergrat, c. 2850 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; Gornergrat, 2700 m, Schibler Z; F.O. Walberg Z; Lac Noir sur Zermatt, c. 2800 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; L. Favrat ZT; E. Wilczek LAU; J.C. Ducommun LAU; Hörnli beim Schwarzsee, A.T. Hottinger LAU; entre Staffelalp et Lac Noir, 2300 m, A. Maillefeler LAU; Plattjen sur Saas-Fee, c. 2350 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; Maillefeler LAU; Schwarzenbergalp, Saaser Tal, c. 2400 m, K. Egli ZT; Gallenalp ob Fee im Saaser Tal, L. Favrat ZT; C.E. Fries Z; E. Rambert LAU; Egginhorn, Saas-Fee, P. Rambert LAU; Distelalp, val de Saas, 2300 m, F. Bourgeois LAU; Gletscheralp ob Fee im Saaser Tal, L. Favrat ZT; S. Fries Z; H. Goudet G; Glacier au Ignes Arolla, H. Goudet G; Arolla, Ch. Müller Z; Simplon, L. Favrat ZT; Col du Simplon: moraine frontale du glacier de Kaltwasser, 2320 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; 2500 m, H.E. Landolt Z; Mäderhorn, NW slope, c. 2700 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; Mäderhorn, lower peak, c. 2850 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; Bistinenpass, W slope, c. 2100 m,  $2n=56$ , E. Landolt UW; Rothorn, au-dessus d'Alpjer, 2250 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW.

The Bernese Alps. Kleine Scheidegg: Lauberhorn, versant sud, c. 2400 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; W. Koch ZT; Kleine Scheidegg: Eigergletscher, F.v. Favel Z; Grande-Scheidegg, S. Jeanjaquet ZT; Mürren, Bietenlucke, 2700 m, E. Rübél RUEB; Faulhorn, c. 2300 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; Bachalp, Faulhorn, Ducommun LAU; Schwabhorn, J. Murst LAU; Niesen, 2362 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; Kandersteg, A.R. Paul M; Hochgant, 2200 m, W. Lüdi RUEB; Gantrisch,  $2n=56$ , C. Favarger UW; Grimsel: au-dessus de l'Oberaarsee, c. 2350 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW.

The Fribourg Alps. Kaiseregg, NW slope, 2090 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; Petit-Moléson, E. Wilczek LAU; Saanenland, Rotthal, val de Gelten, 2100 m, P. Dutoit LAU; Javernaz W; Fauret LAU; Muret LAU; ZT; Z; 2000 m, E. Rambert LAU; J. Vetter LAU; Z; A. Bally LAU; L. Favrat ZT; Dent-de-Morcles, J. Muret LAU; H. Jaccard LAU; 2400 m, E. Wilczek LAU; versant sud de la Dent-de-Morcles, J. Muret ZT; Anzeindaz, 2000 m, Jacob LAU; Duflon LAU; Vetter LAU; Vallée d'Avançon d'Anzeindaz, l'Ecuellaz, 2260 m, P. Villaret LAU; Fillasses sur Anzeindaz, gazons près du lac, 2135 m, P. Villaret LAU; Sen Dzen, 1960 m, P. Villaret LAU; Tour d'Anzeindaz, 2100 m, P. Villaret LAU; Col de Poreyttaz, 2050 m, P. Villaret LAU; Paneycrossaz, 2150 m, P. Villaret LAU; Alessa, alpes de Fully, J. Muret ZT; La Croix, E. Secretan LAU; Vanil-Noir, Jaccard LAU; E. Bardet LAU; Dent-de-Brenlière, 2100 m, W. Lüdi RUEB; 2300 m, E. Burdet LAU; Creux-de-Combe, 2000 m, Ch. Gétaz LAU.

Col du Saint-Gothard, au pied du Monte Prosa, c. 2300 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; Monte Prosa, R. Seeger Z; Kleines Furkahorn, c. 2700 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; Furka, F. Vogel ZT; Realp, Kleines Furkahorn, 2600 m, C. Correns M; Val Bedretto, C. Correns M; Val Piora, 2150 m, G. Müller RUEB; G. Huguenin Z; Monte Camoghè, 2100 m, J. Bornmüller PRC; Como di Gesone, Camoghègebiet, M. Jäggli Z; Camoghè, 2225 m, M. Jäggli Z; Val Onsernone, Pizzo Medano, I. Bär Z; Gazzirola, Val Colla, J. Coaz ZT; M. Jäggli Z; the top ridge of Gazzirola, c. 2200 m,  $2n=56$ , K. Urbańska-Worytkiewicz et H. Heller UW; Pizzo Cramalene, I. Bär Z; Punta di Robbia, 2400 m, I. Bär Z; Laita dura ob Airolo, 2400 m, J. Coaz ZT; Val Torta im Bedretto-Tal, L. Favrat ZT; Nufenenpass, W slope, c. 2400 m,  $2n=56$ , K. Urbańska-Worytkiewicz, M. Hauser et F. Grossman UW; Poschiavo, Lassalbo, A. Pozzi ZT; Bernhardin, C. Brügger ZT; Sankt Bernhardin, M. Belanger G; Piz Vizan, 2200 m, C. Correns M; Piz Coromba, 2400 m, Furro RUEB; Pizzo Ucello, C. Brügger ZT; Pizzo Lumbredo, C. Brügger ZT; Col du San Bernardino, c. 2150 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW.

Pilate, versant SE, c. 1920 m, 2n=56, K. Urbańska-Worytkiewicz UW; c. 2080 m, 2n=56, K. Urbańska-Worytkiewicz UW; Pilatus, 1900 m, Berker PRC; Jäggli ZT; Bauernfeld Z; Klimserhorn am Pilatus, N. Reber ZT; Ch. Brügger ZT; Pilatus-Kulm, S-Seite, 1800 m, H. Jenny ZT; C. Schröter ZT; Titlis: Laubersgrat, c. 2400 m, 2n=56/K. Urbańska-Worytkiewicz UW; Säntis, Lagger PRC; Säntis: Lisengrat près Rotsteinpass, versant sud, c. 2200 m, 2n=56, K. Urbańska-Worytkiewicz et E. Landolt UW; Säntis: Lisengrat vers Chalbersäntis, exposition est, c. 2300 m, 2n=56, K. Urbańska-Worytkiewicz et E. Landolt UW; à la Scheye, Alpes de Glaris, 2200 m, LAU; Säntisgebiet: Kraialpfirst, 2000–2100 m, A. Koller Z; Käserruck ob Unterwasser, 2050–2200 m, W. Koch ZT; Käserruck, Churfirsten, 1800–1900 m, M. Vogt Z; Churfirsten: Schlachtboden, E. Müller Z; Lehmgipfel, 2200 m, M. Vogt Z; SW vor Mels: Schwarzkopf auf Alp Tamons, 1959 m, H. Seitler ZT; Pizol, c. 2230 m, 2n=56, E. Landolt UW.

The Rhaetian Alps. Bandfluh, Cresta, Avers, H. Zimmerli Z; Val Avers, Lindtan, G. Bachman ZT; C. Sulger-Buel Z; Cresta, Val d'Avers, C. Nachenius ZT; M. Rikli ZT; C. Schröter ZT; Juf (Avers): entre Mozzaspitz et Foppaspitz, c. 2450 m, 2n=56, K. Urbańska-Worytkiewicz UW; Wiessberg, Cresta Avers, Aubert LAU; Val Zawretta, S Piz Muot, W. Koch ZT; Cresta Avers, Cucal-Nair-Berg P 2637, W. Koch ZT; Piz Beverin, Ch. Brügger ZT; Albula, M. Bovelin ZT; L. Favrat ZT; J. Muret LAU; B. Branger RUEB; I. Bär Z; Dschimels, versant NW, c. 2450 m, 2n=56, K. Urbańska-Worytkiewicz UW; Piz Uertsch, 2500 m, ex herb. Romieux RUEB; Palfries Gauschla, 1800 m, H. Hangart Z; ZT; Parpaner Rothorn über Churwalden, C. Brügger ZT; Parpaner Rothorn, c. 2850 m, 2n=56, K. Urbańska-Worytkiewicz UW; Flimsenberg, W. Vogel ZT; Flimsenstein, c. 2700 m, 2n=56, K. Zarzycki UW; Flimsenstein, I. Bär Z; Cassons près Flims, c. 2400 m, 2n=56, K. Zarzycki UW; Alp Grüm, Mandra, c. 2360 m, 2n=56, K. Zarzycki UW; c. 2150 m, K. Zarzycki UW; P. Moesola, exposition SW, c. 2360 m, 2n=56, K. Urbańska-Worytkiewicz UW; Val Medel: Piz Miez, c. 2400 m, 2n=56, K. Urbańska-Worytkiewicz UW; Arosler Weisshorn, 2450 m, H. Beger Z; Schiesshorn, SE-Hang, 2400 m, H. Beger Z; Montalin ob Chur, 2200 m, A. Volkart Z; Arosa-Hörnli, D. Rohrer Z; Carmenapass, I. Bär Z; Strela, Davos, 2550 m, Schibler Z; c. 2450 m, 2n=56, A. Gigon UW; Calanda, Prättigau, 2400 m, C. Schröter ZT; Calanda, L. Favrat ZT; Casanapass, G. Hegi Z; Casanna auf Rase, ex herb. Rübel RUEB; Berggipfel ob Fideris, Hochwang, Prättigau, W. Schibler G; Piz Padella, 2300 m, B. Branger Z; c. 2450 m, W. Koch ZT; Hahnensee bei St. Moritz am Aufstieg zur Furocla Surlej, c. 2300 m, W. Koch ZT; Fuorela Surlej, J. Coaz ZT; M. Caviezel ZT; Henle M; Rübel RUEB; Claviziel, fl. Bernina, ex herb. C. Correns M; Bernina, ex herb. Lerescher LAU; près de l'hospice de Bernina, T. Brown WU; Bernina, Lago Bianco, 2230 m, W. Koch ZT; Col de la Bernina, c. 2300 m, 2n=56, K. Urbańska-Worytkiewicz UW; Forcla di Cristallina, 2585 m, J. Coaz ZT; Diavolezza, E. Hayren HEL; bei Sils, B. Brauger RUEB; Oberseite des Lunghinpasses bei Maloja, c. 2400 m, W. Koch ZT; F.v. Tavel ZT; Ch. Brügger ZT; SE Piz Lagalb, 2450 m, W. Koch ZT; Piz Nair, E. Oberholzer ZT; B. Kramper Z; B. Branger Z; ex herb. Paiot LAU; Val Grano, Sasso della Guardia, C. Waiser RUEB; Munt da Cherus, Samnaun, C. Sulger-Buel Z.

### C. Austria

Massif de la Silvretta: Lobspitze, c. 2500 m, 2n=56, K. Urbańska-Worytkiewicz UW; Ulmerhütte ob St. Kristof am Arlberg, 2230 m, E. Preismann W; auf dem Furgler bei See im Paznauntal, 2600–2800 m, Handel-Mazetti WU; Venetberg bei Landeck, H. Zerny W; Vernagthütte bei Rofen im Ötztal, J. Vetter W; Obergurgl, c. 2100 m, 2n=56, A. Pisek UW; Saile bei Innsbruck IBF; Gamskogel im Senderstal bei Innsbruck, 2600 m, Handel-Mazetti WU; Steinach a. Br. Duterjoch, IBF; Schnurzjoch im Gschnitztal, Kerner WU; Muttenjoch, Schofferer PRC; ob Flix, 2500 m, Arnold M; Prat des Hohen Kammes M; Blaufeld bei Kitzbühel W; A. Sauter M; Trautsteiner W; St. Peter

Heuberger, am Mittagsspitze, 2260 m, H. Beger RUEB; Rofanspitze am Sonnenwendjoch, J. Wognar HEL; bei Kitzbühl, IB; Dolliner W; IBF; Traunsteiner G, IBF, M; K. Domin PRC; Grossglockner, W; Grossglockner: Franz-Josephs-Höhe, c. 2500 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; Pasterze, Sarntheim PRC; UPS; M; Hoppe M; Z; Glocknerhaus, Sterneck PRC; Bergelkogel IBF; Bergeralpe bei Prägraten im Virgener Tal, J. Vetter W; Brennerbad, 2000 m, ex herb. C. Correns M; Monte Zirago am Brenner, 2300 m, Huter W; am Kühkar in der Fuchs im Pinzgau, J. Vetter W; Graukogel bei Badgastein, J. Fryberg LD; Lonza sur Mallnitz, c. 1900 m,  $2n=56$ , F. Widder UW; Felsen der Feldwand am Mallnitzer, T.E. Berroyer W; Pusterthal, in den Alpen im Kalsertal, J. Pischler LD; Lirschbaumer Alpen, au-dessus de Lienz, Lerescher LAU; zwischen Kirschbaumer Alpe und Zoche bei Lienz, W; Witting W; Rosengarten bei Oberdrauburg, 1900–2200 m, L. Keller W; Zochenpass, Wolfert W; Ortascha, Sieber PRC; Steinwändleralpe (Schladmingtal), O. Simony W; Steinkarzikken bei Schladming, WU; oberhalb des Schwarzsees, zwischen Tweng und Zederhaus, 1900–2200 m, Handel-Mazetti WU; unter dem Schwarzsee-Murursprung, 1900 m, F. Vierhapper WU; Pleisnitzkogel, F. Virhapper WU; Laareck, Lungau, 1900 m, F. Vierhapper WU; Hochachwung, F.G. Strobl W; Königseegebiete, Schneibstein, Matten am Gipfel, 2200 m, H. Paul M; bei Rappenseehütte, M; Eisenhut propre Turrach, c. 2000 m, B.F. Murrau Z; Graue Wand, R. Seeger Z.

#### D. Italy

Piemont, de Gressonay au d'Olen, E. Wilczek et P. Jaccard LAU; Vallée de Cogne, 2400–2500 m, E. Burdet LAU; ob Alpe Pila (Granson), c. 2150 m, E. Landolt et H. Hess ZT; Vallée de Cogne, c. 2000 m, TO; Val d'Aosta: Monte Jortin, 2700 m, D. Ferrari TO.

Bergamo Alps. Val di Scalve, 2400 m, E. Wilczek LAU; Val di Scalve, passo di Vivione, 2200 m,  $2n=56$ , E. Landolt UW; oberes Val Brembana, passo di Portula, c. 2300 m, E. Landolt ZT.

Trento Alps. Cornetto di Bondone bei Trento, Luibold IBF; Valsulzano ex alpe Cunelle p. sopra Tornecium, F. Ambrosi LAU; Judicaries, Loss IBF; Monte Tombeau, F.v. Wettstein M.

Dolomites. Val d'Ansiel, piano di Lavaredo, c. 2500 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; Sciliar, Barnard LAU; Terra rosa ex herb. Tiepffer M; Viezena, 2100 m, K. Kugler LAU; Platkofel, IBF; Tchutchenthaler, IB; WU; 2100 m, M; Bernard LAU; Val Travnolo, Lusia, C. Correns M; Monte Castellazzo, Arnold M; Gröden, am Hochjoch, Geislerspitze, 2500 m, J. Bornmüller IBF; M. d. Sardinia WU; Schwarzhorn bei Bozen, P. Morandel PRC.

Julian Alps. Wischberg prope Predil, 2000 m, Huter LD; Bärenlahner am Wischbergem, Huter PRC; an der Prevala-Alp bei Plezzo, W; Pletzing-Alp bei Plezzo, W.

#### E. Germany

Allgäu Alps. Himmeleck, 2020 m,  $2n=56$ , H. Merxmüller UW; Himmeleck, H. Paul M; 2000 m, Troll M; Nebelhorn, G. Hegi M; Kreuzeck und Rauheck, M. Linserskopf, F. Dobel M.

Berchtesgaden, Schönanger am Kleinen Teufelshorn, 2050 m, H. Paul M.

### The Carpathians

#### I. Tatra Mountains

Western Tatra. Račkové Stavy, c. 1900 m, G. Wahlenberg S; rocks over the lake Raczkowy Stawek, c. 1800 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; S slope of Jarząbczy Wierch, c. 2000 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; Ostry Roháč, c. 1900 m, PRC.

High Tatra. Path to Przełęczka pod Żabią Czubą, c. 1600 m,  $2n=56$ , K. Urbańska-Worytkiewicz UW; NW slope of Żabie—over the Valley of the lake Morskie Oko,

c. 1750 m, 2n=56, K. Urbańska-Worytkiewicz UW; near Przełęczka pod Żabią Czubą, c. 1800 m, 2n=56, K. Urbańska-Worytkiewicz UW; Żabia Lalka, c. 1900 m, Z. Radwańska-Paryska KR; slopes below Żabi Szczyt Niżni, c. 1800 m, 2n=56, K. Urbańska-Worytkiewicz UW; Owczy Żleb—path to Pass Owcza, c. 1800 m, 2n=56, K. Urbańska-Worytkiewicz UW; Niżnie Rysy, c. 1800 m, 2n=56, K. Urbańska-Worytkiewicz UW; path to Pass pod Chłopkiem—the cirque Kocioł Mięgoszowiecki, c. 1850 m, 2n=56, K. Urbańska-Worytkiewicz UW; rocks below the Pass pod Chłopkiem, c. 2200 m, 2n=56, K. Urbańska-Worytkiewicz UW; rocks below the Pass Szpiglasowa near the path from the Valley of Five Polish Lakes, c. 2000 m, 2n=56, K. Urbańska-Worytkiewicz UW; NE slope of Krywań, c. 1850 m, 2n=56, K. Urbańska-Worytkiewicz UW; Pośrednia Turnia, c. 1800 m, 2n=56, K. Urbańska-Worytkiewicz UW; S steep rocky slope of Gąsienicowa Turnia, c. 1900 m, 2n=56, K. Urbańska-Worytkiewicz UW; rocks below Pass Karb, NW slope, c. 1800 m, 2n=56, K. Urbańska-Worytkiewicz UW; Pass Zmarzła, c. 2100 m, 2n=56, K. Urbańska-Worytkiewicz UW; eastern cliffs of Zadni Granat, c. 2000 m, 2n=56, K. Urbańska-Worytkiewicz UW; SE slope below Pass Koprova, c. 2000 m, 2n=56, K. Urbańska-Worytkiewicz UW; Koprova Pass, HEL; Szatan, 2100 m, J. Hustich HEL; E slope of Gerlach, c. 1950 m, 2n=56, K. Urbańska-Worytkiewicz UW; Valley of Five Spish Lakes—at the bottom of Żółta Ściana, c. 1850 m, 2n=56, K. Urbańska-Worytkiewicz UW; path from Pass Czerwona Ławka to the Valley of Five Spish Lakes, c. 2200 m, 2n=56, K. Urbańska-Worytkiewicz UW; S slope of Huncovski Szczyt, c. 1850 m, 2n=56, K. Urbańska-Worytkiewicz UW; Valley Kiezmarska—the neighbourhood of the lake Zielony Staw Kiezmarski, c. 1700 m, 2n=56, K. Urbańska-Worytkiewicz UW; in herboris graniticis supra lacum “Késmarki-Zöld-to” ad cataractas infra vallem Kis Papyrus-völgy, c. 1600 m, F. Filarszky et G. Timko ZT; HEL; UW; Z; N steep rocky slope of Mały Kiezmarski Szczyt, c. 1950 m, 2n=56, K. Urbańska-Worytkiewicz et J. Worytkiewicz UW.

Belan Tatra. Sub cacumine montis Hlupy, c. 1900 m, solo calcareo, J. Chrtek et Z. Krisa LD; Jatki Bielskie, c. 1900 m, K. Urbańska-Worytkiewicz UW.

## II. Low Tatra

Ďumbir, c. 1900 m, PRC; Kralova Hola, c. 1850 m, PRC.

## III. Eastern Carpathians

Maramures Mountains in alp Bliznica, c. 1700 m, A. Margitai HEL.

# 5. Ecology

## 5.1. *Antennaria villifera*

The vegetation zones in which *A. villifera* occurs in Fennoscandia are classified as low-alpine and middle-alpine belts (DU RIETZ 1930). The altitudinal limits are as follows: 300 m a. s. l. (Snøfjord, Finmark) and 1440 m a. s. l. (Mesatjåkko, Torne Lappmark HEDBERG 1947; Mount Jeknaffo, Lule Lappmark, SELANDER 1950). The most frequent reports are from 800–1200 m in Nordland, 700–1200 m in Troms and 700–1000 m in Finmark. In Sweden and Finland they comport 400–1300 m and 700–1100 m, respectively. We did not get, unfortunately, more detailed data concerning the Russian material.

In the above mentioned parts of the alpine belt the vegetation period lasts

about two months and the precipitations occur there mostly in winter (FRIES 1913). The most significant factors for the stands with *Antennaria villifera* seem to be protection from the wind and duration of the snow cover; both these elements strongly influence a distribution and appearance of the populations. *Antennaria villifera* in Fennoscandia does not occur in wind-exposed localities; it requires a snow cover which in some cases may persist for a very long time. Apparently this species does not tolerate the extreme temperatures of winter.

As to the edaphic conditions, *A. villifera* shows in Fennoscandia a well-marked preference for basic, circumneutral soils rich in Ca<sup>+</sup>. Several authors considered it as a "kalkstedt" (calciphilous) species, decidedly confined to this type of soil (TENGWALL 1925, FRIES 1925, ARWIDSSON 1943, GJAEREVOLL 1950). The present author's investigations fully correspond with the previous data: we have almost always found *Antennaria villifera* on limestones, mica-schists and other basic rocks belonging to the Caledonian Mountain range. In addition, we have observed it sometimes on solifluxion lobes; this seems to confirm HEDBERG's opinion that a counteracted process of leaching may result in a suitable substrate for calcicoles (HEDBERG *et al.* 1952).

There are no indications that a local occurrence or a general distribution of *Antennaria villifera* are determined by more specific soil components such as the amount of potassium, phosphorus, or some micro-nutrients.

A further important edaphic factor is the water content in the soil. As it was emphasized by numerous Scandinavian authors, the degree of soil moisture plays often a decisive role in the competition between the resp. plant associations (FRIES 1913, TENGWALL 1925, NORDHAGEN 1928, 1936, 1943, LIPPMAA 1929, KALLIOLA 1939, SÖYRINKI 1938/39, DU RIETZ 1942, GJAEREVOLL 1949, 1950). *Antennaria villifera* which apparently represents in Fennoscandia a slightly hygrophilous species has its ecological optimum in the associations requiring rather a wet soil.

Biotic factors do not seem have an important influence on the type of vegetation in the region where *A. villifera* occurs. The grazing of reindeer may sometimes result in a disturbed vegetation (Javreoaiv've, Troms, the author's observations from 1968); however, such phenomena are rather local.

The plant associations in which *Antennaria villifera* occurs in Fennoscandia may be in a general way, classified as belonging to four alliances: *Ranunculo-Poion alpinae* Gjaerevoll 1950, *Potentillo-Polygonion vivipari* Nordhagen 1936, *Kobresio-Dryadion* Nordhagen 1936, 1943 and *Luzulion arcticae* Gjaerevoll 1950 (*Luzulion nivalis* Nordhagen 1939).

The *Ranunculo-Poion alpinae* alliance represents a group of snow-bed vegetation. It requires constant irrigation and high degree of soil moisture.

Most of the habitats on Mount Njunis, Troms, studied by the present author together with T. ENGELSKJØN in 1965 belong to this alliance. *Antennaria villifera* frequently occurs there, in rather small tetra- and hexaploid clones.

The *Potentillo-Polygonion vivipari* alliance requires likewise a long-lasting snow cover; on the other hand, irrigation is not very extensive in the summer time. *Antennaria villifera* is a constant component of some facies.

The classification of the *Kobresio-Dryadion* is much more complicated as this alliance seems to be rather variable and has a wide ecological amplitude. It should be emphasized that *Antennaria villifera* in Fennoscandia is definitely confined to associations not exposed to wind and requiring a snow cover during the winter. In the present work we followed the nomenclature given by HEDBERG *et al.* (1952) which seems to be rather representative for some stands with *Antennaria villifera*. According to the Swedish authors, it frequently occurs in the *Tetragono-Dryadetum*. This association is free of snow rather early in summer. It has a well developed field layer chiefly consisting of *Hylocomium splendens*, *Rhytidium rugosum*, *Ptilidium ciliare*, *Dicranum* ssp. as well as *Cetraria nivalis*, *C. islandica* and *C. cucullata*. The irrigation is not very strong, yet rather constant.

The present investigations are mostly in agreement with HEDBERG's characteristics. We have found, however, some stands in Pältsa, Torne Lappmark, where the soil was highly irrigated by an adjacent snow field; it seems, therefore, that the degree of soil moisture may be rather variable in the *Tetragono-Dryadetum*.

The second, more hygrophilous association of the *Kobresio-Dryadion* in which *Antennaria villifera* frequently appears, is the *Tomenthypno-Dryadetum*. The field layer is built of abundant mosses (*Tomenthypnum nitens*, *Aulacomnium palustre*, *A. turgidum*, *Hylocomium splendens*, *Sphagnum warnstorffianum*, *Orthothecium chryseum*, *Ditrichium flexicaule*, *Mnium* ssp.) which form a continuous carpet. This association, being free of snow rather early in summer, is considerably irrigated.

In the upper part of the middle-alpine belt where the continuous vegetation ceases, *Antennaria villifera* occurs in the *Luzulion arcticae*, which is characterized by very late thawing of snow. In consequence, the soil shows a very high degree of moisture. In addition, it is influenced by solifluxion. According to HEDBERG (1947, 1952) this association is related to the *Tomenthypno-Dryadetum* but with an open field layer. It seems to be confined to irrigated, N-exposed slopes with a moist local microclimate. Some species occurring in this association belong to the most exclusive arctic element of North Scandinavia (*Luzula arctica*, *Poa arctica* ssp. *caespitosa*, *Sagina caespitosa*, *Stellaria crassipes*, *Papaver radicans*).



Fig. 25. Distribution of *Antennaria carpatica* s.str. in the Alps. Unbroken line: limits of the range. Dots mark some localities studied cytologically (partly after URBAŃSKA-WORYTKIEWICZ 1968).

Thus, on the whole, *Antennaria villifera* represents in Scandinavia a basiphilous, slightly hygrophilous species, occurring within the Arctic Circle in a lower-alpine and a middle-alpine belt, requiring a snow cover in winter and not being exposed to wind. Its ecological amplitude is rather narrow and it seems to be generally confined to the niches where the competition from more aggressive species is negligible.

Data concerning autoecology of *Antennaria villifera* from the Russian part of its range are very incomplete. It should be noted that BORISSOVA (1959) reported it from some dry localities in tundra; however, no more detailed characteristics of the ecological conditions were given. It would be very interesting to compare environmental factors occurring in the eastern part of the range of *A. villifera* with those of Scandinavia.

### 5.2 *Antennaria carpatica* s.str.

In accordance with a rather wide range of the geographical distribution, *Antennaria carpatica* s.str. seems to be well adapted to the variable microclimatic conditions occurring in the Carpathians, the Alps as well as in the

Pyrenees. It should be emphasized that in most part of the range it shows a notable resistance to wind action. Contrasting in this respect with Scandinavian populations of *Antennaria villifera*, *A. carpatica* s.str. occurs on steep rocky slopes and along ridges strongly exposed to wind. The snow there is very often blown away. *A. carpatica* s.str. does not apparently tolerate an excessively long duration of the snow cover and is able to survive even a completely snowless winter. The present author's observations performed in the Tatra Mountains and the Alps are in agreement with the previous data (BRAUN-BLANQUET 1913, 1926, 1948, 1969, SZAFER, PAWŁOWSKI and KULCZYŃSKI 1927, PAWŁOWSKI 1926, 1935, PAWŁOWSKI and STECKI 1925, PAWŁOWSKI *et al.* 1927, 1928).

As far as the edaphic factors are concerned, it should be noted that *Antennaria carpatica* s.str. occurs on both granitic as well as on calciferous substrata. However, the resp. pH values are not always influenced immediately by the type of rock as it seems to be the case in Fennoscandia. For example, *Antennaria carpatica* s.str. occurs as a very characteristic component in the *Versicolori-Agrostetum* in the granitic part of the Tatra Mountains; the soil is there strongly irrigated by water containing mineral salts, especially CaCO<sub>3</sub> washed out from the rocks. Accordingly, its reaction is circumneutral or weakly alcalic. On the other hand, the *Elynetum (alpinum)* distributed on calciferous rocks in the Alps, sometimes shows a well developed layer of the humus decalcified in its upper part; in consequence the pH values are more or less acidic (BRAUN-BLANQUET and JENNY 1926).

As a result of strong exposure to wind, the soil of stands with *Antennaria carpatica* s.str. is often dried out. In the localities where the humus layer is better developed, some degree of moisture may be maintained for a longer time. On the whole, however, *A. carpatica* s.str. does not require such an extensive irrigation as that reported for *A. villifera* in Fennoscandia.

*Antennaria carpatica* s.str. mainly and typically occurs in the plant associations belonging to the *Seslerietalia varia* Br. Bl. 1926. In the Tatra Mountains it occurs in the *Versicolori-Agrostetum alpinae* chiefly distributed on wind-exposed ridges; according to PAWŁOWSKI (1928) *A. carpatica* represents a characteristic species of this association occurring in its initial, optimal and terminal phases. The present author's observations confirm this opinion. In addition, a sporadic occurrence of *A. carpatica* was also noted in the basiphilous *Caricetum firmae*.

In the Alps *Antennaria carpatica* s.str. occurs also in the *Firmetum*; however, it seems to be a rather occasional constituent of this association. On the other hand, it represents a characteristic component of the wind-resistant *Elynetum (alpinum)* Br. Bl. 1913. In the Pyrenees it occurs, also as a charac-

teristic species, within the *Elyno-Oxytropidetum Foucaudii*, a wind-exposed association with extreme temperatures, considered by BRAUN-BLANQUET (1948, 1969) as homologous with the *Elynetum*.

The second group of plant associations, in which *Antennaria carpatica* s. str. occurs, is the order *Caricetalia curvulae* Br. Bl. 1926. In the Tatra Mountains it occurs in the climax association of the alpine belt, the *Trifido-Distichetum* Szafer, Pawłowski, Kulczyński 1927; it was also recorded from the *Distichetum subnivale* Pawł. 1926. In the Alps it appears in the *Caricetum curvulae* (Kerner) Brockm. Jerosch 1907, being rather frequent in the subass. *Curvuletum elynetosum*; in addition, it was noted in the subass. *Curvuletum cetrarietosum* (BRAUN-BLANQUET 1969). As far as the Pyrenees are concerned, *Antennaria carpatica* s. str. was reported from two associations belonging to the *Caricetalia curvulae*; one of them was the microthermic *Curvuleto-Leontidetum Pyrenaiici*, where *A. carpatica* occurs in the facies with *Elyna myosuroides*; the other was classified as the *Pumilo-Festucetum supinae* (BRAUN-BLANQUET 1969). On the whole, *Antennaria carpatica* s. str. seems to occur in circumneutral variants of the *Caricetalia curvulae*.

As it was emphasized above, *A. carpatica* s. str. has its ecological optimum in wind-exposed localities with rather dry or damp soil, which are often free of snow in winter. These extreme environmental conditions do not apparently affect the vigour of the species which shows a normal sexual reproduction resulting in highly viable seeds. On the contrary, *Antennaria villifera* in Fennoscandia mostly occurs in wet localities, rather protected from wind, where the snow cover may persist for a long time. Thus, some of the ecological requirements seem to be quite different in the two species. Moreover, *Antennaria carpatica* s. str. manifests a notable phytosociological affinity which permitted it to be distinguished as a characteristic component of some units, whereas *Antennaria villifera* in Fennoscandia always occurred as an indifferent, subordinate constituent of the resp. associations.

## 6. Discussion

The results of the present investigations contribute to the elucidation of two problems concerning the *Antennaria carpatica* complex: the mutual relationship occurring between some of its representatives as well as their putative origin and age.

Observations on the morphology of plants from the arctic-boreal part of the range confirmed the results of BORISSOVA (1959) who described the representatives of the *Antennaria carpatica* complex from Russia as a new

species, *A. villifera* Boriss. Fennoscandian material studied in the course of the present work apparently belongs to the same species. The morphological similarity of the resp. plants corresponds with the cytological data: tetra- and hexaploid chromosome numbers  $2n=28$  and  $2n=42$ , previously reported from Scandinavia (BERGMAN 1935, 1951, URBAŃSKA-WORYTKIEWICZ 1967, 1967a, 1967b), were recently found in the Chukotchka Peninsula (ZHUKOVA 1968). Thus, *Antennaria villifera* represents these same levels of polyploidy in the two opposite limits of its range.

Karyotype analysis performed on tetra- and hexaploid plants of *Antennaria villifera* revealed their close relationship. Most of the chromosome types occurring in the 28chromosomic set could be recognized in the 42chromosomic one; the resp. chromosome pairs of the tetraploid form were mostly represented by three chromosomes in the hexaploids. These results suggest that hexaploid cytotype has arisen from a tetraploid form with a part of an unreduced gamete (URBAŃSKA-WORYTKIEWICZ 1967a, 1967b).

The two types differed morphologically in the length of the stigma lobes in the pistillate florets; they showed also differences in the type of pollen. On the whole, however, tetra- and hexaploids are notably similar to each other. Likewise, they do not show any essential difference in their ecology. In view of this we did not give them a separate rank.

A comparative morphological study of *A. villifera* and *A. carpatica* s.str. revealed differences which permitted to distinguish these species from each other. This concerns especially the staminate and pistillate florets whose morphology seems to have a decisive diagnostic value for the *Antennaria carpatica* complex. Another useful character is the morphology of the stem leaves. It should be noted that similar results were previously obtained in other groups of the genus *Antennaria* (FERNALD 1924, 1931, 1933, M. PORSILD 1931, POLUNIN 1940, A. PORSILD 1943, 1950, 1965). On the other hand, the growth habit, which constitutes an important diagnostic character for the species of the sections *Alpinae* and *Dioicae* (MALTE 1934), does not seem to have an essential value for the *Antennaria carpatica* representatives.

Observations on the morphology of the rosette leaves of *Antennaria carpatica* s.str. revealed a particular variability in this character. Accordingly, its diagnostic value is rather limited. In view of the above results, the taxonomical status of *Antennaria helvetica* described by CHRTEK and POUZAR (1960, 1962) as an endemic species of the Alpine flora, seems to be highly questionable. The newly described taxon probably represents an example of general variability within *A. carpatica* s.str. and therefore should not be regarded as a separate species.

The morphological differences occurring between *Antennaria villifera* and

*A. carpatica* s.str. do not only correspond with their separate ranges of distribution; the two species also differ from one another in respect to their ecology. Still more remarkable is the phytosociological affinity of *Antennaria carpatica* s.str. which apparently represents a well established species; by contrast, *A. villifera* does not seem to support strong competition and occurs in the resp. associations as their subordinate, indifferent constituent.

Karyological investigations afford further evidence in favour of a separate taxonomical rank of *Antennaria carpatica* s.str. and *A. villifera*. The latter species shows a lower degree of polyploidy than *A. carpatica*; it is represented by tetra- and hexaploids ( $2n=28, 42$ ), whereas *A. carpatica* s.str. is octoploid within its whole range of distribution ( $2n=56$ ). Moreover, *A. carpatica* s.str. has apparently a more specialized karyotype, consisting not only of meta-centric chromosomes but also of acrocentric ones.

CHRTEK and POUZAR (1960, 1962) are of the opinion that the *Antennaria carpatica* complex is represented in Central and Western Europe by three species. According to them, *A. carpatica* s.str. is endemic for the Carpathians. As far as the plants from the Alps are concerned, the Czechoslovakian authors distinguished two taxa: *A. helvetica*, endemic for Switzerland, and *A. lanata*, which they identified with *A. villifera*. The results of the present investigations do not permit us to agree with the suggestions of CHRTEK and POUZAR; by contrast, differences occurring between *A. villifera* and *A. lanata* are in favour of their separate classification.

Details in the morphology, karyology, geographical distribution and ecology of the *Antennaria carpatica* complex in Europe suggest that it is represented in the North by *Antennaria villifera* Boriss., whereas in Central and Western Europe *A. carpatica* (Wahlenb.) Bluff et Fingerh. s.str. is the only species to occur.

As far as the estimation of the putative origin and age of *A. villifera* and *A. carpatica* s.str. are concerned, the following criteria seem to be helpful:

- details of cytology and karyotype differentiation
- the geographical distribution and ecology
- the seed-setting

The cytological data show a well-marked North-South trend occurring within the *Antennaria carpatica* complex in Eurasia. In view of this, the opinion of KULCZYŃSKI (1924) concerning the Alpine origin of the complex does not seem to be reliable. Results of the karyotype analysis of *Antennaria villifera* point to its ancient age. Cytological processes resulting in the formation of the tetraploid type were undoubtedly long-lasting; they involved not only a doubling of a 14chromosomic type but also some structural changes of chromosomes. The karyological differentiation occurring within *Antennaria*

*villifera* is also in favour of the opinion that this species should be regarded as a paleopolyploid type.

A comparison of the cytological data concerning *A. villifera* with its geographical distribution is particularly interesting. These same chromosome numbers,  $2n=28$  and  $2n=42$ , were found in the regions as far apart as Scandinavia and the Chukotchka Peninsula. It should be added that the notable morphological similarity of the two cytotypes was observed not only by the present author but also by ЗНУКОВА (1968) in the plants from the easternmost Asia. These coincidences do not seem to be merely casual but point to a common origin of the hexaploid type.

A disjunctive local range of *Antennaria villifera* in Scandinavia where it occurs as a northern unicentric species, and a pronounced separation of the Scandinavian localities from those in Russia seem to be due to historical factors. This is probably also the case in Russia where the localities of *A. villifera* are grouped mostly between the region of the Kara Bay and the mouth of Lena; their frequency seems to diminish eastwards and southwards (BORISSOVA 1959).

The genetic relationship between Eurasian and American groups of the *Antennaria carpatica* complex is clear. However, none of the *A. carpatica* representatives is Amphi-Beringian; this permits to infer that the two groups were separated a long time ago, at least before the Riss glaciation reached its maximum. At that time an exchange of biota between Asia and America was prevented by the Cordilleran and the Continental Ice Sheets as well as by numerous local glaciers occurring in Eastern Siberia (HULTÉN 1950, 1968).

Two possible centers of origin of *Antennaria carpatica* may be taken into consideration: North American Cordillera as well as Arctic Siberia. The genus *Antennaria* is predominantly North-American and at least some of its species are supposed to be of a pre-Pleistocene origin (PORSILD 1965). On the other hand, data concerning paleoclimatology and paleobotany show that some parts of NW Siberia remained unglaciated during the whole Pleistocene and tundra was a dominating type of vegetation there (GERASIMOV and MARKOV 1939, FRENZEL and TROLL 1952, FRENZEL 1959, 1960, 1968, STRAKA 1970). Accordingly, this region offered better opportunities for the development of *Antennaria carpatica* than the strongly glaciated region of the Cordillera (FLINT 1947). It may be assumed that the tetraploid *Antennaria villifera* has arisen from a diploid ancestor-type of American origin through a doubling of its chromosome set. Details of the chromosome morphology observed in the course of the present investigations are in favour of this opinion. Later on, a tetraploid type gave rise to a hexaploid form with a part of an unreduced gamete and both cytotypes spread over North Eurasia. It might be inferred

that they already represented the species of a stabilized morphology. The development of *Antennaria villifera* and its karyological differentiation probably took place before the last glaciation; an apparently rare occurrence of this species in the easternmost part of the range could be explained by a strong local glaciation of the Verkhojansk and Chersky Mountains as well as that of the Anadyr Range.

As far as the occurrence of *A. villifera* in Scandinavia is concerned, it might be supposed that it came from Siberia during early post-glacial time. This was probably also the case in Vaigatsch, Novaya Semlya and Kolguyev. According to numerous authors, the flora of these regions is mostly of a post-glacial origin (KUDRIASOV 1925, TOLMATSHEV 1930, ALEKSANDROVA 1956, SCHAEFER and FRENZEL 1959, FRENZEL 1960). However, the peculiar distribution of *A. villifera* in Fennoscandia rather points to a possibility of its survival of the last glaciation there. It should be also noted that the ecological limits of *A. villifera* in Scandinavia are rather narrow. Remarkably defective seed-setting presents a further argument in favour of the assumption that this species survived glaciation in Scandinavia and might have lost its ability to spread over very long distances.

The theory of glacial survivors in Scandinavia is still discussed and contradictory opinions are expressed in this matter. However, numerous bio-



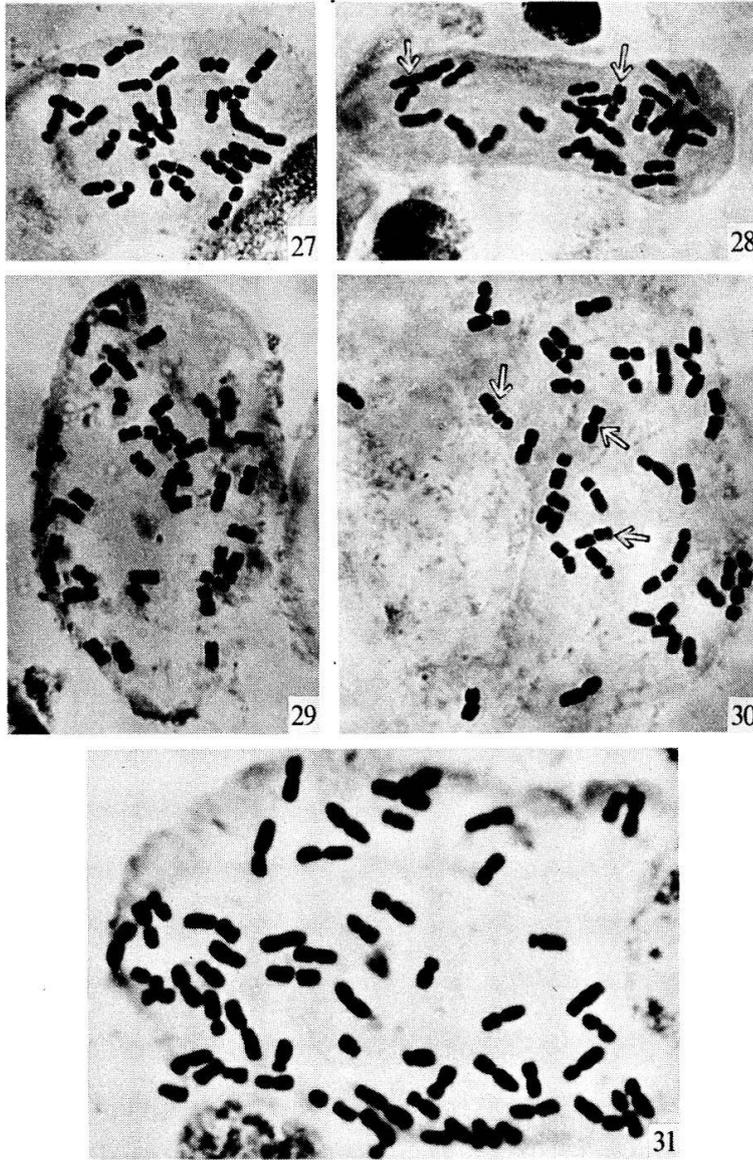
Fig. 26. Botanical indications of refugia in Nordland, Norway. Localities of *Arenaria humifusa* (dots); *Papaver radicum* ssp. *subglobosa* (asterisk); *Carex scirpoidea* (triangle); *Saxifraga aizoon* ssp. *laestadii* (squares); *Draba crassifolia* (crosses); *Potentilla hyparctica* (circle with cross). Unbroken lines: local areas of distribution of *Antennaria villifera*. Partly after GJAEREVOLL (in LÖVE and LÖVE 1963).

geographers have agreed that it seems to be the only suitable explanation for the distribution patterns of some biota in Scandinavia (NORDHAGEN 1935, NANNFELDT 1958, LINDROTH 1958, GJAEREVOLL 1959, 1963, DAHL 1961). According to GJAEREVOLL (1963) there are important botanical indications of refugia in the mountain region of Nordland (Norway). The peculiar distribution of some taxa is rather difficult to explain by their postglacial migration; it seems more likely to have been a result of their survival in situ. GRÖNLIE (1927) pointed out that some geological data indicated the occurrence of ice-free areas exactly in the region where important and rare plant species are concentrated. It is interesting to note that some local disjunctive areas of distribution of *Antennaria villifera* in Nordland partially overlap places considered as putative refugia (Fig. 26).

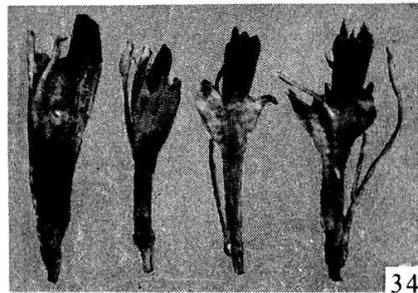
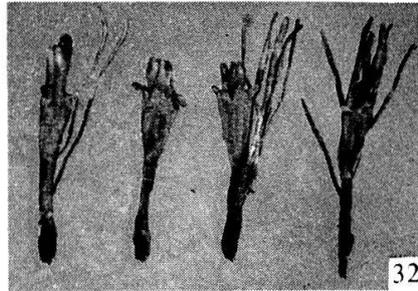
As far as the origin and development of *Antennaria carpatica* s.str. is concerned, the present investigations support ENGLER's opinion as to a Siberian origin of this species (ENGLER 1905). *Antennaria carpatica* s.str. is undoubtedly related to *A. villifera*. Some details of the chromosome morphology suggest that it could have been derived from *A. villifera* as an autopolyploid type; the morphological similarity of the two species is in favour of this assumption. However, it can also be supposed that *A. carpatica* s.str. might have arisen through hybridization between *A. villifera* and some other species which have become extinct. According to STEBBINS (1932) allopolyploidy has played an important part in the evolution of the genus *Antennaria*.

The karyotype of *A. carpatica* s.str. is rather specialized. It seems probable that not only polyploidization but also various alterations of the chromosomes contributed to its formation. It is a well-known fact that the structural changes of the chromosomes play an important part in the speciation processes within some genera. Recent investigations of SKALIŃSKA (1966, 1968) point to this way of differentiation of the genus *Crocus*. KNABEN (1959) who studied the *Papaver radicum* complex showed that the evolution within this group corresponded to chromosome alterations and the resp. karyological differences were phenotypically distinct.

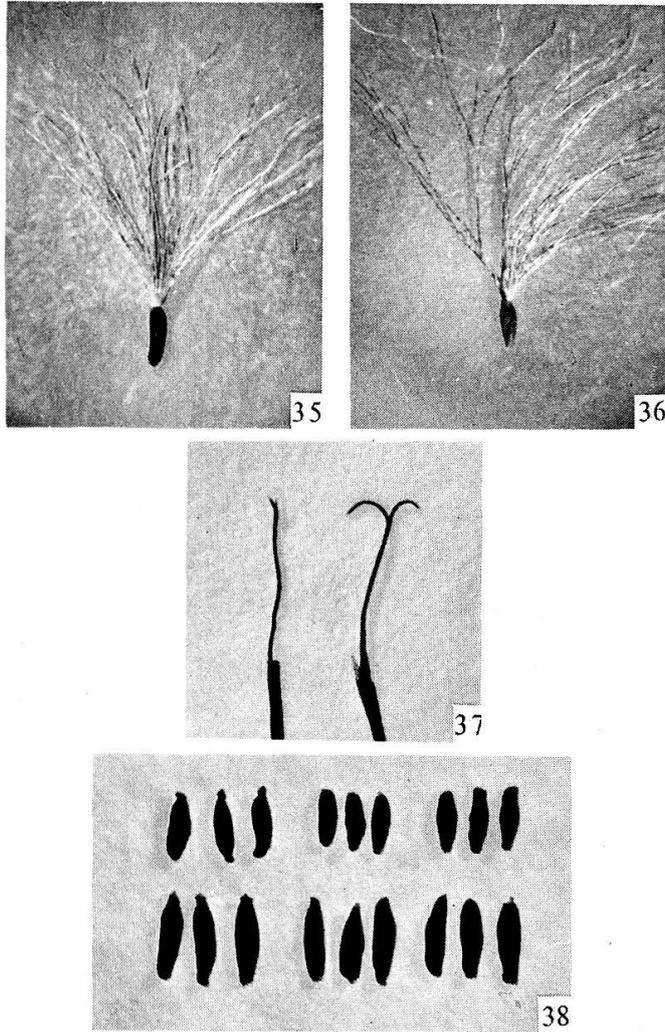
The formation of an octoploid cytotype which was the first step in the development of *Antennaria carpatica* s.str. might be considered as an indication of varying environmental conditions. It seems possible that these processes took place soon after the formation of the tetraploid *Antennaria villifera*, at the time when tundra vegetation of Europe and Asia was still rather a continuous zone; Siberian biota could then have possibly reach the Carpathians, the Alps and the Pyrenees. The newly developed octoploid species established itself in these mountains and maintained its ability to a



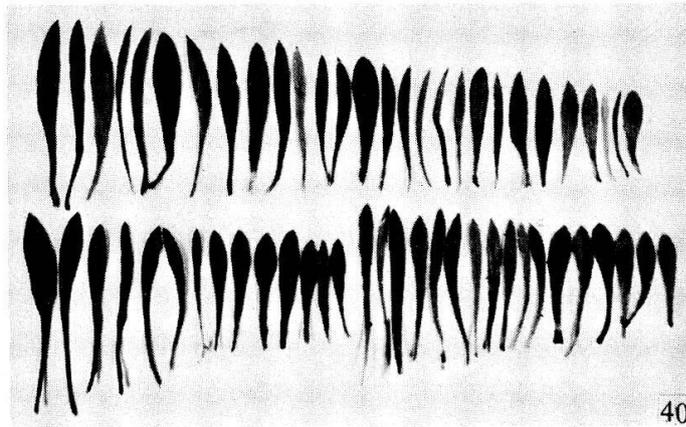
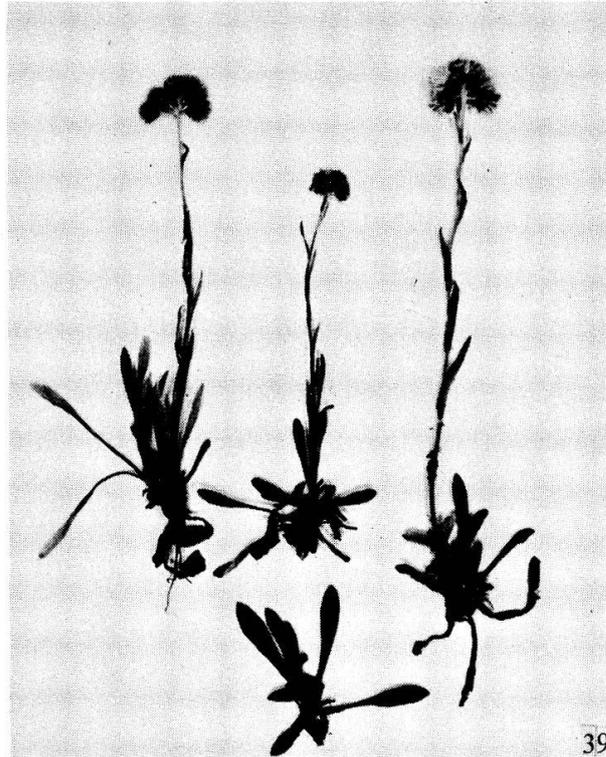
Figs. 27-31. Microphotos of root-tip metaphases. 27-28. Tetraploid *Antennaria villifera*,  $2n=28$ . 29-30. Hexaploid *A. villifera*,  $2n=42$ . 31. *A. carpatica* s.str.,  $2n=56$ . C.  $1000\times$ .



Figs. 32–34. Staminate florets; 32. *Antennaria lanata*; 33. *A. villifera*; 34. *A. carpatica* s. str. C. 4.5 ×.



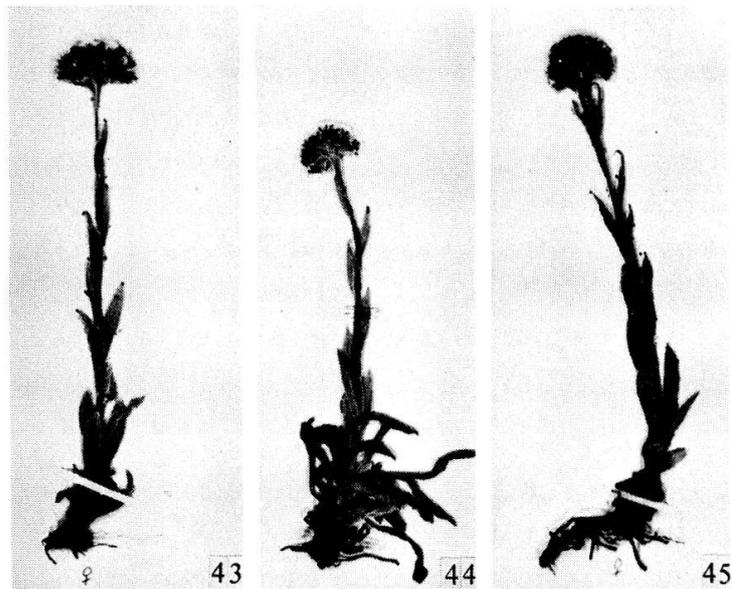
Figs. 35–38. Post-floral stage; 35. Pistillate floret of *Antennaria carpatica* s.str.; 36. Floret of *A. villifera*, c.  $4.5\times$ ; 37. Two types of stigma found within *A. villifera*; 38. Ripe achenes: upper row, left and right: *Antennaria villifera* from Scandinavia and Kolguyev; upper row, middle: *A. lanata* from Canada; lower row, left to right: *Antennaria carpatica* s.str. from the Tatra Mountains, the Alps as well as from the Pyrenees. C.  $6\times$ .



Figs. 39-40. *Antennaria carpatica* (Wahlenb.) Bluff et Fingerh. s.str.; 39. Staminate and pistillate plants; 40. The rosette leaves; upper row: material from the Alps; lower row: left—plants from the Tatra Mountains, right—plants from the Pyrenees. C.  $\frac{1}{3}$  natural size.

Figs. 41-42. *Antennaria villifera* Boriss. from Scandinavia; 41. Staminate plants; 42. Pistillate plants. C.  $\frac{1}{3}$  natural size.

Figs. 43-45. *Antennaria lanata* (Hook.) Greene from British Columbia, Canada. C.  $\frac{1}{3}$  natural size.



normal seed-setting. The latest phases of karyotype differentiation probably took place independently in the resp. mountain groups; however, they did not influence the morphology of *Antennaria carpatica* s. str. which at that time probably represented a well developed taxon.

In the present work we have tried to give an interpretation of evolutionary trends of the *Antennaria carpatica* complex in Europe. Various processes of speciation of this group have taken place under different environmental conditions, which have been either changed by a sequence of historical factors or met by the resp. types in their migratory tracks. Now it would be very interesting to perform a parallel study on the American group of the complex in order to establish affinities and differences occurring within the whole circumpolar range of *Antennaria carpatica*.

## 7. Nomenclature

### 7.1 *Antennaria villifera* Boriss.

Plants from the North were for a long time assigned to *Gnaphalium carpaticum* Wahlenb. and subsequently to *Antennaria carpatica*. In some Russian floras the name *Gnaphalium alpinum* Willd. non Linné was also used.

HERDER (1867) classified plants from Arctic Russia as *Gnaphalium carpaticum*  $\beta$  *lanatum*. Later on, TRAUTVETTER described *Antennaria carpatica* var. *Laestadiana* from the Chukotchka Peninsula (TRAUTVETTER 1879). It is interesting to note that HULTÉN in his recent flora of Alaska accepted this latter name (HULTÉN 1968).

BORISSOVA (1959) was the first author who definitively distinguished plants occurring in Arctic Russia from *A. carpatica* and described them under the name *Antennaria villifera* Boriss. The diagnosis of the Russian author does not seem to be quite complete and we have added some details which may be useful for a description of this species; however, the nomenclature given by BORISSOVA refers to the plants from Scandinavia as well as from Russia.

It should be added that CHRTEK and POUZAR (1962) identified *Antennaria villifera* Boriss. with *A. lanata* (Hook.) Greene; by contrast, the present investigations point to a separate taxonomical rank of these two species.

### 7.2 *Antennaria carpatica* (Wahlenb.) Bluff et Fingerh. s. str.

The first diagnosis of *Antennaria carpatica* was given by WAHLENBERG (1814) who described plants from the Tatra Mountains under the name *Gnaphalium carpaticum*. Later on, WAHLENBERG extended his conception of

the species including plants from Scandinavia (1826). He denoted two taxa: taxon  $\alpha$  (folia supra glabra) corresponded to plants from the Carpathians whereas Scandinavian material was assigned to taxon  $\beta$  with leaves tomentose on both surfaces.

In 1825 BLUFF and FINGERHUTH validly transferred *Gnaphalium carpaticum* to the genus *Antennaria*. However, in numerous floras an abbreviation of R. BROWN's name is used, in spite of the fact that this author did not cite the species in combination with the generic name *Antennaria* (BROWN 1818).

Alpine plants were for rather a long time assigned to *Gnaphalium alpinum* Willd. The diagnosis given by WILLDENOW (1804) comprised the characters of both *Antennaria carpatica* and *A. alpina*.

The first author to distinguish in some way *Antennaria carpatica* in the Alpine flora was GAUDIN (1829) who described it as *Gnaphalium alpinum* L.  $\beta$  *elatius*. GAUDIN was also the only author who mentioned in his diagnosis the colour of the staminate florets ("pellucido-albidi"), an important diagnostic feature for *Antennaria carpatica* s.str. DUCOMMUN followed the classification of GAUDIN and reported in his flora *Antennaria carpatica* var. *elatior* Gaud. (DUCOMMUN 1881). It should be noted that a different name was used by HERDER (1867) who assigned *Antennaria carpatica* to *Gnaphalium carpaticum*  $\alpha$  *humile*; he distinguished it from *Gnaphalium carpaticum*  $\beta$  *lanatum* occurring in the North.

DALLA TORRE (1912) described the Alpine plants as *Antennaria carpatica* var. *lanata* Hook.; this nomenclature was proposed by HOOKER (1840) for the plants found in North America.

Recently, CHRTEK and POUZAR (1960, 1962) suggested the following classification of plants from Central and Western Europe: the name *Antennaria carpatica* (Wahlenb.) Bluff et Fingerh. was to be used exclusively for plants occurring in the Carpathians. The Alpine plants were assigned to two species: *Antennaria helvetica* Chrtek et Pouz., a species endemic for the Alps and *A. lanata* (Hook.) Greene which was considered by the Czechoslovakian authors as identical with *A. villifera* Boriss.

The results of the present studies are in a sharp contrast to the opinion of CHRTEK and POUZAR. The only species occurring in the Carpathians, the Alps and the Pyrenees seems to be *Antennaria carpatica* (Wahlenb.) Bluff et Fingerh. s.str.; *Antennaria helvetica* apparently represents an example of general variability occurring within *A. carpatica* s.str., it should not therefore be regarded as a separate taxon. *Antennaria villifera* occurring in arctic-boreal Europe and Asia differs in many respects from the American *A. lanata*; in view of this, separate taxonomical ranks for the two species should be maintained.

8. Description of the section *Carpaticae* and key  
for the determination of species belonging to the  
*Antennaria carpatica* complex

*Section Carpaticae:*

Plants non-stoloniferous; rosette leaves erect and elongate, oblanceolate to lanceolate, acute, 3nerved.

1. Plants 3–18 cm tall; stem leaves 4–9, upper ones with scarious appendages.
2. Stem leaves linear to lanceolate; heads mostly glomerulate (peduncles not longer than 5 mm); pappus in male heads of  $\pm$  equal length with the staminate florets.
3. Stem leaves with brownish appendages; involucral phyllaries brown, sometimes whitish when aged; staminate florets cream-coloured, anthers purple; achenes common, glabrous, c. 1.5 mm long; pappus in female heads white or yellowish, c. 1.2 mm longer than the pistillate florets. Carpathians, Alps, Pyrenees.

*Antennaria carpatica* (Wahlenb.) Bluff et Fingerh. s. str.

- 3.\* Stem leaves with blackish appendages which are narrow and twisted; involucral phyllaries usually blackish; staminate florets purple, anthers bright yellow; achenes exceedingly rare, purpletinged, c. 1 mm long; pappus in female heads c. 2.5 mm longer than the pistillate florets. Arctic-boreal-Europe and Asia.

*Antennaria villifera* Boriss.

- 2.\* Stem leaves mostly oblanceolate; heads often pedunculate (peduncles up to 10 mm long); pappus in male heads c. 1.5 mm longer than the staminate florets. North America.

*Antennaria lanata* (Hook.) Greene

- 1.\* Plants 30–50 cm tall; stem leaves numerous, without scarious appendages. North America.

*Antennaria pulcherrima* (Hook.) Greene

## 9. Description of species

### 9.1 *Antennaria carpatica* (Wahlenb.) Bluff et Fingerh. s. str.

Comp. Fl. Germ. I, 2: 348, 1825 (Fig. 39)

*Gnaphalium carpaticum*  $\alpha$  Wahlenberg Fl. Carp. Princ. 258, 1814; *Gnaphalium alpinum* Willd. non L., Sp. Pl. v. 3, 1883; *Gnaphalium alpinum* L.  $\beta$  *elalius* Gaud. Fl. Helv. 5; 249, 1829; *Gnaphalium carpaticum*  $\alpha$  *humile* Herder Bull. Soc. Nat. Moscou 40, P. 1, 412, 1867; *Antennaria carpatica* var. *elatior* Gaud. Ducomm. Tasch. Schw. Fl. 394, 1881; *Antennaria carpatica* var. *lanata* (Hook.) Dalla Torre et Sarnthein, Farn. Blütenpfl. Tir. 6: 502–504, 1912; *Antennaria helvetica* Chrtek et Pouz. Nov. Bot. Delect. Sem. Hort. Bot. Univ. Car. Prag. 1960: 20–22, p. p.; *Antennaria lanata* (Hook.) Greene sensu Chrtek et Pouz. non auct.; *Antennaria villifera* Boriss. sensu Chrtek et Pouz. non auct.

Plant 3.5–24.2 cm tall; rosette leaves oblanceolate to lanceolate, 32–86 mm long and 3.8–11.1 mm broad, acute, tomentose on both surfaces or glabrous at the upper one. The stem leaves few, sessile, acute, upper ones with scarious, brownish appendages.

Heads numerous (6)7–9(11), usually compressed. Involucral phyllaries green and tomentose at the base, brown with well-marked limits of the darkest part about the middle; upper part light brown or whitish. Phyllaries of female heads usually narrower than those of male inflorescences.

Staminate florets cream-coloured; anthers purple, glabrous. Pappus white; its length is more or less equal to that of the florets. Bristles of the pappus serrate, clavate at the uppermost part.

Pistillate florets purplish with multicellular hairs at the top part of the corolla; style exserted, purplish-brown, stigma usually cleft. Pappus white or yellowish, c. 1.2 mm longer than the style.

Pollen grains regular, c. 35  $\mu$  in diameter; seeds normally developed, glabrous, brown, c. 1.5 mm long. VI–VIII.

Geographical distribution: the Carpathians (Eastern Carpathians, the Tatra Mountains, the Low Tatra), the Alps, the Pyrenees. Occurs in the alpine belt (c. 1500–3180 m a.s.l.), in wind-exposed localities; steep rocky slopes and ridges; mostly on circumneutral soil.

Chromosome number:  $2n=56$ , plants octoploid.

### 9.2 *Antennaria villifera* Boriss.

Notul. Syst. Herb. Inst. Bot. Acad. Sc. USSR 20: 292, 1959 (Figs. 41–42)

*Gnaphalium carpaticum*  $\beta$  Wahlenberg Fl. Suec. 2: 515, 1826; *Gnaphalium alpinum* Willd. non L. Trautv. Acta Hort. Bot. Petrop. 8, 1: 23–268; *Antennaria alpina* Ledeb. Fl. Ross. 1: 2–612, 1845–1846; *Gnaphalium carpaticum*  $\beta$  *lanatum* Hook. Herder Bull. Soc. Nat. Moscou 40, 2: 412, 1867; *Antennaria carpatica* var. *Laestadiana* Trautv. Acta Hort. Bot. Petrop. 6, 1: 24, 1879 p. p.; *Antennaria carpatica* R. Br. auct. fl. ross. eur. et sib.: Krylov Fl. Zap. Sib. 11, 2695; *Antennaria lanata* (Hook.) Greene sensu Chrtek et Pouz. non auct.

Plant 2.8–19.0 cm tall; rosette leaves mostly lanceolate, acute, greyish-tomentose on both surfaces. The stem leaves sessile, upper ones with scarious blackish appendages which are narrow and twisted.

Heads numerous (3) 4–6 (9), tomentose at the base. Involucral phyllaries with a trace of violet occurring frequently about the middle; upper part of phyllaries scarious, blackish, sometimes cream-tipped at the age.

Staminate florets purple, tips of the corolla often papillose. Anthers bright yellow. Pappus white, bristles serrate, clavate at the top.

Pistillate florets purplish at the upper part with the multicellular hairs at the top of the corolla. Style exerted c. 2.5 mm, usually purplish-brown. Stigma either deeply cleft (hexaploid plants) or with short lobes (the tetraploids). Pappus whitish, usually 2.5 mm longer than the pistillate florets.

Two types of the pollen: rather normal grains, about 25  $\mu$  in diameter correspond to tetraploids; the other type, very irregular (modal value of diameter c. 30  $\mu$ ) is typical of hexaploids.

Achenes exceedingly rare, purple-tinged, glabrous, c. 0.8 mm long. VII–VIII.

Geographical distribution: North Scandinavia, the northernmost part of the Ural Mountains, Kolguyev, Vaigatsch, Novaya Semlya. Reported also from Siberia (Yamal, Taimyr, Yakutia). Rare in the Chukotchka Peninsula and in the region of Irkutsch. Occurs in lower-alpine and middle-alpine belts in Fennoscandia (400–1440 m a. s. l.), in wind-protected places as well as in snow-bed localities. Dry habitats in the Russian tundra (BORISSOVA 1959).

Chromosome number:  $2n=28, 42$ , plants tetra- and hexaploid.

### 9.3 *Antennaria lanata* (Hook.) Greene

Pittonia 3: 288, 1898 (Figs. 43–45)

*Antennaria carpatica* var.  $\beta$  *lanata* Hook. Fl. Boreal.-Amer. 1: 329, 1840; *Antennaria pulcherrima* (Hook.) Greene sensu Malte Rhodora 36: 105–106, 1934, non auct.; *Antennaria villifera* Boriss. sensu Chrtek et Pouz. 1962, non auct.

Plant 9.8–20.1 cm tall; rosette leaves 28–92 mm long, oblanceolate, acute, tomentose on both surfaces. The stem leaves mostly oblanceolate, upper ones have usually broad, light-brown appendages.

Heads in number (6)7–9(12), pedunculate (peduncles to 10 mm long); involucrel phyllaries tomentose at the base, greenish black in the middle part, upper part white.

Staminate florets whitish, anthers usually pale yellow. Pappus white, c. 1.5 mm longer than the florets. Bristles serrate, often flattened at the top.

Pistillate florets straw-coloured; style exserted, stigma deeply cleft. Pappus white, c. 1.5 mm longer than the florets.

Pollen very regular, c. 25  $\mu$  of diameter; achenes olive-brown, glabrous, c. 1 mm long.

Geographical distribution: the Rocky Mountains (Alberta and British Columbia to Colorado). Occurs in open slopes and in alpine meadows, on rather dry soil (GREENE 1898).

Chromosome number: not investigated.

#### 9.4 *Antennaria pulcherrima* (Hook.) Greene

Pittonia 3: 176, 1897

*Antennaria carpatica* var.  $\gamma$  *pulcherrima* Hook. F. Boreal.-Amer. 1: 329, 1840; *A. carpatica* Macoun Cat. Can. Pl. Pt. 2, 236, 1884, non Bluff et Fingerh.; *A. lanata* (Hook.) Greene sensu Malte 1934, non auct.; *Antennaria* sp. Ostensfeld, Gjoa Exp. Kristiania Vid. Selsk. Skr. 1910, 67; *Antennaria eucosma* Fern. et Wieg. Rhodora 13: 23, 1911, p. p.; *Antennaria anaphaloides* Rydb. Mem. N.Y. Bot. Garden 1, 1900; incl. *Antennaria pulcherrima* var. *angustisquamata* Porsild Can. Field Nat. 64: 11, 1950.

Plant 30–50 cm tall; rosette leaves oblanceolate, elongate, acute, 8–12 cm long, tomentose on both surfaces. The stem leaves numerous, oblanceolate to linear, without scarious appendages.

Heads in number (5)7–16(20), pedunculate, not compressed; involucrel phyllaries woolly tomentose at the base, greenish in the middle, light brown at the upper part.

Staminate florets straw-coloured, anthers intensively yellow. Pappus c. 1.5 mm longer than the florets. Bristles of the pappus whitish, serrate, slightly thickened upward.

Pistillate florets cream-coloured with purplish tips, style exserted, cleft, brownish; pappus white, usually c. 3 mm longer than the pistillate florets.

Pollen grains regular, c. 40  $\mu$  in diameter. Achenes brown, glabrous, c. 1.3 mm long. VI–VIII.

Geographical distribution: Central Alaska, Yukon, Mackenzie, south to Colorado and Washington, east to the Hudson Bay with isolated stations in Quebec and Newfoundland. Occurs in open woods, in moist grassy areas and river flats.

Chromosome number:  $2n=62$ , plants nonaploid.

### Summary

The present investigations deal with the karyology, morphology, geographical distribution and ecology of the *Antennaria carpatica* complex in Europe.

Two species of the complex occur in Europe: *Antennaria villifera* Boriss. and *A. carpatica* (Wahlenb.) Bluff et Fingerh. s.str. They differ from each other in respect to their cytology. *A. villifera* is represented by two closely related cytotypes ( $2n=28, 42$ ); its chromosome sets consist of metacentric chromosomes. *Antennaria carpatica* s.str. shows higher level of polyploidy ( $2n=56$ ) and its karyotype is more specialized.

A comparative morphological study of *A. villifera* and *A. carpatica* s.str. revealed further differences occurring between the two species. The morphology of the florets and the stem leaves proved to be useful criteria for classification. On the other hand, a notable variability of the rosette leaves found in *A. carpatica* s.str. renders the diagnostic value of this character highly questionable. In view of this, *Antennaria helvetica* recently described by CHRTEK and POUZAR (1960, 1962) should not be considered as a separate species; it probably represents an example of general variability occurring within *A. carpatica* s.str.

*Antennaria villifera* and *A. carpatica* s.str. have separate ranges of geographical distribution: *A. villifera* occurs in arctic-boreal Europe and Asia, whereas *A. carpatica* s.str. appears as an oreophytic species in Central and Western Europe. The two species also differ in some of their ecological requirements. *A. villifera* usually grows in wind-protected, moist localities; by contrast, *A. carpatica* s.str. occurs on wind-exposed, steep rocky slopes and ridges.

*A. villifera* and the American taxon *A. lanata* (Hook.) Greene apparently represent two different species. Their separate taxonomical rank should be maintained in spite of the opinion of CHRTEK and POUZAR (1962).

The putative origin and age of the European representatives of the complex are discussed in the light of the obtained results.

## Zusammenfassung

Die vorliegenden Untersuchungen behandeln die Karyologie, Morphologie, geographische Verbreitung und Ökologie der *Antennaria carpatica*-Artengruppe in Europa.

In Europa kommen von dieser Gruppe zwei Arten vor: *Antennaria villifera* Boriss. sowie *A. carpatica* (Wahlenb.) Bluff et Fingerh. s. str. Sie unterscheiden sich in der Zytologie. *A. villifera* ist durch zwei nahe verwandte Zytotypen ( $2n=28, 42$ ) vertreten; ihre Chromosomensätze bestehen aus metazentrischen Chromosomen. *A. carpatica* s. str. ist höher polyploid ( $2n=56$ ) und ihr Karyotyp ist spezialisierter (vier Paare akrozentrischer Chromosomen).

Vergleichende morphologische Untersuchungen von *Antennaria villifera* und *A. carpatica* s. str. zeigten, dass weitere Unterschiede zwischen den beiden Arten bestehen. Die Morphologie der Einzelblüten sowie diejenige der Stengelblätter erwiesen sich als gute Merkmale für die Bestimmung. Dagegen lässt eine bei *Antennaria carpatica* s. str. festgestellte bemerkenswerte Variabilität in Form und Behaarung der Rosettenblätter den diagnostischen Wert dieser Merkmale als sehr fragwürdig erscheinen. Dies bedeutet, dass die kürzlich von CHRTEK und POUZAR (1960, 1962) nur auf Grund unterschiedlicher Merkmale von Rosettenblättern beschriebene *Antennaria helvetica* nicht als eigene Art betrachtet werden sollte; sie stellt offensichtlich ein Beispiel der allgemeinen Variabilität dar, die innerhalb *A. carpatica* s. str. vorkommt.

*A. villifera* und *A. carpatica* s. str. besitzen verschiedene Verbreitungsgebiete: *A. villifera* kommt im arktisch-borealen Europa und Asien vor, wogegen *A. carpatica* s. str. eine Gebirgspflanze Zentral- und Westeuropas ist. Die zwei Arten besitzen auch verschiedene Ansprüche bezüglich einiger Standortsfaktoren. *Antennaria villifera* gedeiht meistens an windgeschützten und feuchten Orten; *A. carpatica* s. str. hingegen kommt an dem Wind ausgesetzten, steilen und felsigen Hängen und Gräten vor.

*A. villifera* und das amerikanische Taxon *A. lanata* (Hook.) Greene stellen offensichtlich zwei verschiedene Arten dar und sollten trotz der gegenteiligen Ansicht von CHRTEK und POUZAR (1962) beibehalten werden.

Die vermutliche Entstehung und das Alter der europäischen Vertreter der Artengruppe werden anhand der erhaltenen Ergebnisse diskutiert.

## Acknowledgements

The work was carried out at the Institute of Plant Anatomy and Cytology, the Jagellonian University, Cracow (Poland) and then was continued at the Institute of Geobotany, Swiss Federal Institute of Technology, Zürich. I am glad to have opportunity to express my gratitude to Professor Dr. M. SKALINSKA, the Jagellonian University, for

her valuable advice and constant interest in my investigations. My sincere thanks are also due to Professor Dr. E. LANDOLT, Head of the Institute of Geobotany, for stimulating discussions, suggestions and criticism during the preparation of the manuscript.

I am greatly obliged to Professor Dr. C. FAVARGER, University of Neuchâtel, who very kindly permitted to keep the plants in the experimental garden of the Botanical Institute and sent us some fixed materials.

The cooperation of Cand. real. Ola SKIFTE, the Botanical Department, the Tromsø Museum as well as of Cand. real. T. ENGELSKJØN, University of Oslo, is greatly appreciated. I thank also to Dr. P. ZHUKOVA, the Botanical Institute, Academy of Sciences USSR, Leningrad, for precious information concerning *Antennaria villifera*.

Thanks are also due to the Keepers of the Herbaria for loan of specimens.

## References

- ALEKSANDROVA, V.D., 1956: Die Vegetation der Südinsel von Novaya Semlya zwischen 70°56' und 72°12' Br. Rastitelnost krajnego Severa i jejo osvojenie 2, 187–306.  
– 1960: Some regularities in the distribution of the vegetation in the Arctic tundra. Arctic 13, 147–163.
- ALM, C.G. och Th.C.E. FRIES, 1925: Floristiska anteckningar från Karesuando och Enontekis socknar. Sv. Bot. Tidskr. 19, 251–262.
- ALMQUIST, E., 1929: Upplands vegetation och flora. Acta Phytogeogr. Suec., Stockholm.
- ANDREIEV, V.N., 1934: Die Tundren-Untersonen des nordeuropäischen Teiles der UdSSR. Bot. Jahrb. 66, 119–127.
- ARWIDSSON, TH., 1926a: Floristiska notiser från Pite Lappmark huvudsakligen nordvästligaste delen. Bot. Not. 1926.  
– 1943: Studien über die Gefäßpflanzen in den Hochgebirgen der Pite Lappmark. Acta Phytogeogr. Suec. 17.
- ÅBERG, B., 1952: Kärleväxternas höjmgränser i Lule Lappmark och i Graubünden, en jämförelse. Sv. Bot. Tidskr. 46, 286–312.
- BERGMAN, B., 1935: Zur Kenntnis der Skandinavischen *Antennaria*-Arten. Sv. Bot. Tidskr. 26, 99–106.  
– 1951: On the formation of reduced and unreduced gametophytes of *Antennaria carpatica*. Hereditas 37, 501–518.
- BJÖRKMANN, G., 1939: Kärleväxtfloran inom Stora Sjöfjällets nationalpark jämte angränsande delar av Norra Lule Lappmark. Kgl. Sv. Vet.-Akad. Avhdl. i Naturskydd. 2. Stockholm.
- BLUFF, M.J., and C.A. FINGERHUTH, 1825. Compendium Florae Germanicae 2. Norimbergae.
- BLYTT, A., og M. BLYTT, 1881–1886: Norges Flora. Christiania.
- BLYTT, A., 1876. Essay on the Immigration of the Norwegian Flora during Alternating Dry and Rainy Periods. Christiania.
- BORISSOVA, A.G., 1959: Rod *Antennaria* Gaertn. in Flora USSR 25. Moskva-Leningrad.  
– 1960: De genere *Antennaria* Gaertn. notulae systematicae. Bot. Mat. Gerb. Bot. Inst. Akad. Nauk SSSR 20, 289–295.
- BORZA, A., 1947: Conspectus Florae Romaniae regionumque affinum. I–II. Cluj.  
– 1963: Pflanzengesellschaften der Rumänischen Karpaten. Biologia 18, 856–863.  
– und N. BOSCAIU, 1965: Intruducere in studiul covorului vegetal. Edit. Acad. Rep. Popul. Române.
- BOSE, S., 1956: Aberrations in the nucleolar chromosomes of inbred rye. Hereditas 42, 263–292.
- BØCHER, T.W., 1951: Distribution of plants in the circumpolar area in relation to ecological and historical factors. Journ. Ecol. 39, 376–395.

- BRANDZA, D., 1879–1883: Prodrumul Florei Române. București.
- BRAUN, J., 1913: Die Vegetations-Verhältnisse der Schneestufe in den Rätisch-Lepon-tischen Alpen. Neue Denkschr. Schweiz. Nat. Ges. 48.
- BRAUN-BLANQUET, J., und H. JENNY, 1926: Vegetations-Entwicklung und Bodenbil-dung in der alpinen Stufe der Zentralalpen. Neue Denkschr. Schweiz. Nat. Ges. 53, 2.
- BRAUN-BLANQUET, J., 1948: La végétation alpine des Pyrénées orientales. An. Inst. Edaf. Ecol. y Fisiol. veg. 9. Comm. de la SIGMA 96.
- 1954: La végétation alpine et nivale des Alpes françaises. Comm. de la SIGMA 125.
- 1969: Die Pflanzengesellschaften der rätischen Alpen im Rahmen ihrer Gesamtver-breitung. I T. Chur.
- BRITTON, N., and A. BROWN, 1898: Illustrated flora of the Northern USA. III. N. York.
- BROCKMANN-JEROSCH, H., 1907: Die Pflanzengesellschaften der Schweizeralpen. I. Die Flora des Puschlavs und ihre Pflanzengesellschaften. Leipzig.
- BROWN, R., 1816: Observations on the natural Family of Plants called *Compositae*. Trans. Linn. Soc. London 12, 122–123.
- CHRTEK, J., and Z. POUZAR, 1960: *Antennaria helvetica* nov. spec., a new species of the Alpine flora. Nov. Bot. et Del. Sem. Hort. Bot. Univ. Carol. Prag. 20–22.
- 1961: Notes on the Scandinavian species of the genus *Antennaria* Gaertn. Nov. Bot. et Del. Sem. Hort. Bot. Univ. Carol. Prag. 11–15.
- 1962: A contribution to the taxonomy of some European species of the genus *Anten-naria* Gaertn. Acta Univ. Carol. Biol. Vol. 105–136.
- CLEMENTS, F. F., and E. CLEMENTS, 1914: Rocky Mountains flowers. N. York.
- COMAN, A., 1946: Enumeratio plantarum vascularum districtus Maramures in Romania. Bull. Jard. et Mus. Bot. Univ. Cluj.
- COOMBE, D. E., and E. WHITE, 1951: Notes on calcicolous communities and peat for-mation in Norwegian Lappland. Journ. Ecol. 39, 33–62.
- DAHL, E., 1946: On different types of unglaciated areas during the Ice Ages and their significance to phytogeography. N. Phytol. 45, 225–242.
- 1955: Biogeographic and geological indications of unglaciated areas in Scandinavia during the Glacial Ages. Bull. Geol. Soc. Amer. 66, 1499–1519.
- 1956: Rondane. Mountain vegetation in South Norway and its relation to the envi-ronment. Skr. Norske Vidensk.-Akad. I. Mat.-Naturv. Kl. 3. Oslo.
- 1959: Amfiatlantiske planter. Problems of Amphi-Atlantic plant distribution. Blyt-tia 16, 93–121.
- 1961: Refugienproblemet og de kvartoergeologiske metodene. Sv. Naturv. 14, 81–96.
- DAHL, OVE, 1934: Floraen i Finmark fylke. Nytt Mag. f. Naturv. 69, 1–430.
- DUCOMMUN, J. C., 1881. Taschenbuch für den schweizerischen Botaniker. Luzern.
- DU RIETZ, G. E., 1925a: Die regionale Gliederung der skandinavischen Vegetation. Sv. Växt. Soc. Sällsk. Hdl. 8, 1–160.
- 1942: De svenska fjällens växtarld. Norrland. Natur, befolkning och näringar. Ymer. Stockholm.
- 1942a: Rishedförband i Torneträskomradets lågfjällbälte. Sv. Bot. Tidskr. 36.
- EKMAN, E., 1927: Notes on some Greenland *Antennariae*. Sv. Bot. Tidskr. 21, 49–57.
- ENGELSKJØN, T., and G. KNABEN (in press): Chromosome numbers of Scandinavian arctic-alpine plants species. III. Acta Borealia. A. Scientia. Tromsø.
- ENGLER, A., 1879. Versuch einer Entwicklungsgeschichte der extratropischen Gebiete der Nördlichen Hemisphäre. Leipzig.
- 1905: Grundzüge der Entwicklung der Flora Europas seit der Tertiärzeit. Engler's Bot. Jahrb. 36, 5–27.
- FAVARGER, C., 1961: Sur l'emploi des nombres chromosomiques en géographie botanique. Ber. Geobot. Forsch. Inst. Rübel 32, 119–146.
- 1964b: Die Zytotaxonomische Erforschung der Alpenflora. Ber. Dtsch. Bot. Ges. 77, 73–83.

- 1967: Cytologie et distribution des plantes. *Biol. Rev.* 42, 163–206.
- FERNALD, M. L., 1898: The genus *Antennaria* in New England. *Proc. Bost. Soc. Nat. Hist.* 28, 237–249.
- 1914: Some *Antennarias* of NE America. *Rhodora* 16, 129–134.
- 1925: Persistence of plants in unglaciated areas of boreal America. *Mem. Amer. Acad. Arts and Sc.* 15, 241–342.
- 1929: Some relationships of the floras of the Northern Hemisphere. *Proc. Int. Congr. Plant Sc.* 2, 1487–1507.
- 1933: The genus *Antennaria* in the Newfoundland flora. *Rhodora* 35, 327–346.
- 1950. *Gray's Manual of Botany*. VIIIth Ed. N. York.
- FLINT, R. F., 1947: *Glacial Geology and the Pleistocene Epoch*. N. York.
- Flora Arctica USSR. I–V. Moskva-Leningrad 1966.
- FRENZEL, B., und C. TROLL, 1952: Die Vegetationszonen des nördlichen Eurasiens während der letzten Eiszeit. *Gegenw.* 2, 154–167.
- FRENZEL, B., 1959: Die Vegetations- und Landschaftzonen Nord-Eurasiens während der letzten Eiszeit und während der postglazialen Wärmezeit. I T. *Abh. Akad. Wiss. u. Lit. Mainz* 13, 941–1099.
- 1960: Die Vegetations- und Landschaftzonen Nord-Eurasiens während der letzten Eiszeit und während der postglazialen Wärmezeit. II T. *Abh. Akad. Wiss. u. Lit. Mainz*, 291–453.
- 1967: Der gegenwärtige Stand und die wichtigsten Aufgaben vegetationsgeschichtlicher Forschung in Nord-Eurasien. *Ber. Dtsch. Bot. Ges.* 80, 669–681.
- 1968: Grundzüge der pleistozänen Vegetationsgeschichte Nord-Eurasiens. Wiesbaden.
- FRIES, TH. C. E., och S. MÅRTENSSON, 1910: Floristiska anteckningar från de alpina och subalpina delarna av Karesuando och Jukkasjärvi socknar norr om Torne Träsk. *Sv. Bot. Tidskr.* 4, 55–75.
- FRIES, TH. C. E., 1913: *Botanische Untersuchungen im nördlichsten Schweden – ein Beitrag zur Kenntnis der alpinen und subalpinen Vegetation in Torne Lappmark*. Uppsala.
- 1917: Über die regionale Gliederung der alpinen Vegetation der Fennoskandischen Hochgebirge. *Vetensk. o. prakt. unders. i Lappl. Fl. o. Fauna* 4, 1–45.
- 1919: *Antennaria alpina* (L.) Gaertn. och dess skandinaviska elementararter. *Sv. Bot. Tidskr.* 13.
- 1925: Die Rolle des Gesteinsgrundes bei der Verbreitung der Gebirgspflanzen in Skandinavien. *Sv. Växtsociol. Sällsk. Handl.* 6, 1–18.
- GAUDIN, J., 1829: *Flora Helvetica*. V. Turici.
- GERASIMOV, I. P., und K. K. MARKOV, 1939: Die Eiszeit auf dem Territorium der UdSSR. *Trudy Inst. Geogr. Akad. Nauk SSSR* 33.
- GJAEREVOLL, O., 1949: Snöleivegetasjonen i Oviksfjellene. *Acta Phytogeogr. Suec.* 25.
- 1950: The snow-bed vegetation in the surroundings of lake Torneträsk, Swedish-Lappland. *Sv. Bot. Tidskr.* 44, 387–440.
- GREENE, E. L., 1897–1898: *Studies in Compositae*. *Pittonia* 3, 172–185; 264–298.
- 1898: Critical notes on *Antennaria*. *Pittonia* 3, 318–323.
- GRÖNLIE, O. T., 1927: The Folden Fiord. *Quaternary Geology*. *Tromsø Mus. Skr.* I (II), 1–73.
- On the traces of ice ages in Nordland, Troms and SW part of Finmark. *Norsk Geol. Tidskr.* 20, 1–70.
- GUINOCHET, M., 1938: *Etudes sur la végétation de l'étage alpin dans le bassin supérieur de la Tinée (Alpes maritimes)*. *Comm. de la SIGMA* 59.
- GUSTAFSSON, A., 1947: Apomixis in higher plants. I–III. *Lunds Univ. Arsskr.* 43.
- HADAC, E., 1942: Et bidrag til historien om Björnöyas flora. *Naturen* 1941, 5.
- 1948. The history of the flora of Spitzbergen and Bear Island and the age of some Arctic plant species. *Preslia* 32, 225–253.

- HAMBERG, A., 1907: Die Eigenschaften der Schneedecke in den Lappländischen Gebirgen. Naturwiss. Unters. der Sarekgeb. in Schw. Lappl. I, 3. Stockholm.
- HANSON, H. C., 1953: Vegetation types in NW Alaska and comparison with communities of other arctic regions. Ecology 34, 111–140.
- HEDBERG, O., 1947: Bidrag till Torne Lappmark flora. Bot. Not., 178–181.
- O. MÅRTENSSON and S. RUBERG, 1952: Botanical investigations in the Pältsa region of northernmost Sweden. Bot. Not. Suppl. III. Lund.
- HERDER, F., 1867: Reisen in den Süden von Ostsibirien in den Jahren 1885–1895. Bull. Soc. Imp. Nat. Moscou.
- HOLM, TH., 1920: *Antennaria alpina* and *A. carpatica*. Rhodora 22, 138–143.
- HOOKE, W. J., 1840: Flora Boreali-Americana. I. London.
- HULTÉN, E., 1928: On the American component in the flora of E Siberia. Sv. Bot. Tidskr. 22, 220–229.
- 1937: Outline of the history of Arctic and Boreal biota during the Quaternary period. Stockholm.
- 1949b: On the races in the Scandinavian flora. Sv. Bot. Tidskr. 43.
- 1950: Flora of Alaska and Yukon. X. Lund.
- 1950: Atlas över växternas utbredning i Norden. Stockholm.
- 1955: The isolation of the Scandinavian mountains flora. Acta Soc. pro Fauna et Flora Fenn. 72, 8, 1–22.
- 1958: The Amphi-Atlantic plants and their phytogeographical connections. Kgl. Sv. Vetensk. Akad. Handl. Ser. 4, 7 (1), 1–340.
- 1968: Flora of Alaska and neighboring territories. Stanford.
- IVERSEN, J., 1958: The bearing of glacial and interglacial epochs on the formation and extinction of plant taxa. Uppsala Univ. Arsskr.
- JALAS, J., 1949: Floristisches aus Lapponia enontekiensis, Lapponia tornensis und Troms fylke. Arch. Soc. Zool. Bot. Vanamo.
- JØRGENSEN, R., 1937: Die Höhegrenzen der Gefäßpflanzen in Troms fylke. Kgl. Norske Vid. Selsk. Skr. Trondheim.
- JØRGENSEN, C. A., TH. SØRENSEN and M. WESTERGAARD, 1958: The flowering plants of Greenland. A taxonomical and cytological survey. Biol. Skr. Danske Vidensk. Selsk. 9, 4, 1–172.
- JUEL, O., 1900: Vergleichende Untersuchungen über typische und parthenogenetische Fortpflanzung bei der Gattung *Antennaria*. Kgl. Sv. Vet. Akad. Handl. 33, 1–59.
- KALLIOLA, R., 1932: Über die alpine Vegetation im Kammikivi-Gebiet von Petsamo-Lappland. Ann. Zool. Bot. Soc. Fenn. Vanamo 2, 2, 1–121.
- 1939: Pflanzensoziologische Untersuchungen in der alpinen Stufe Finnisch-Lapplands. Ann. Zool. Bot. Soc. Fenn. Vanamo 13, 2, 1–328.
- KERNER, H., 1876: Parthenogenesis einer angiospermen Pflanze. Sitzungsber. K. Akad. Wiss. Pt 1, 469–476.
- KIHLMAN, O. A., 1890: Pflanzenbiologische Studien aus Russisch-Lappland. Acta Soc. Fl. et Fauna Fenn. 6, 3, 1–263.
- KNABEN, G., 1959a: On the evolution of the radicum-group of the *Scapiflora* Papavers as studied in 70 and 56-chromosome species. A. Opera Bot. 2, 3, 1–76.
- 1959b: On the evolution of the radicum-group of the *Scapiflora* Papavers as studied in 70 and 56-chromosome species. B. Opera Bot. 3, 3, 1–96.
- 1961: Cyto-ecological problems in Norwegian flora groups and significance of polyploidy. Hereditas 47, 451–479.
- KULCZYŃSKI, ST., 1924: Das boreale und arktisch-alpine Element in der mitteleuropäischen Flora. Bull. Intern. de l'Acad. pol. Sc. Cracovie.
- KÜPFER, PH., 1968: Nouvelles prospections cytologiques dans la flore orophile des Pyrénées et de la Sierra Nevada. Bull. Soc. Neuchât. Sc. Nat. 91, 87–104.

- LINDBERG, K., und B. RING, 1969: Beitrag zur Kenntnis der Flora des Njuonjevare-Gebiets (Torne Lappmark, Nordschweden). Bot. Not. 122, 284–294.
- LIPPMAA, TH., 1929: Pflanzenökologische Untersuchungen aus Norwegisch- und Finnisch-Lappland. Acta Inst. Hort. Bot. Univ. Tartuens. 2, 1–146.
- LÖVE, A., and D. LÖVE, 1942: Cytotaxonomical studies on boreal plants. I. Some observations on swedish and icelandic plants. Kgl. Fysiogr. Sällsk. Lund, 12, 6.
- and D. LÖVE, 1956: Cytotaxonomical conspectus of the Icelandic flora. Acta Hort. Gotoburg. 20, 69–291.
- and D. LÖVE, ed. 1963: North Atlantic biota and their history. Oxford.
- and T. O. SOLBRIG, 1964: IOBP chromosome numbers report. Taxon 13, 3, 109.
- LYNGE, O., 1923. Vascular plants from Novaya Zemlya. Kristiania.
- MALTE, M. O., 1934: *Antennaria* of Arctic America. Rhodora 36, 101–117.
- MANSFELD, R., 1940: Zur Nomenklatur der Farn- und Blütenpflanzen Deutschlands. IX. Fedd. Repert. 49, 41–51.
- MEJLAND, Y., 1938: Litt om planteveksten på Lohtana i Troms. Nytt Mag. f. Naturv. 78.
- 1939: Om floraen på Javreaivve, i Nordreisa. Nytt Mag. f. Naturv. 79.
- MOSKALENKO, N. G., 1970: A contribution to the knowledge of the flora of the environs of Noriljsk (NW extremity of the Central-Siberian plateau). Bot. Zhurn. 55, 2, 263–272.
- NANNFELDT, J. A., 1940: On the polymorphy of *Poa arctica* R. Br. with special reference to its Scandinavian forms. Symb. Bot. Uppsala. 4, Uppsala.
- NEJŠTADT, B., 1957b: Waldgeschichte und Paläogeographie der UdSSR in Holozän. Moskva.
- NORDHAGEN, R., 1928: Die Vegetation und Flora des Sylenegebietes. I, II. Skr. utg. av det Norske Vid.-Akad. i Oslo, Naturv. Kl.
- 1935: Om *Arenaria humifusa* Wg., og dens betydning for utforskningen av Skandinavias eldste florallement. Berg. Mus. Arb. Naturv. rekke 1. Bergen.
- 1936: Versuch einer neuen Einteilung der subalpinen-alpinen Vegetation Norwegens. Berg. Mus. Arb. 2, 1–88.
- 1939: Bidrag till fjellet Pältsas flora, et nytt fun av *Stellaria longipes*. Bot. Not. 691–700.
- 1955: *Kobresieto-Dryadion* in Northern Scandinavia. Sv. Bot. Tidskr. 49, 63–87.
- PAWŁOWSKI, B., und K. STECKI, 1925: Die Pflanzenassoziationen des Miętusia-Tales und des Hauptmassivs der Czerwone Wierchy. Bull. Acad. Pol. Sc. Ser. B. Cracovie. 79–121.
- PAWŁOWSKI, B., M. SOKOŁOWSKI und K. WALLISCH, 1927: Die Pflanzenassoziationen des Tatra-Gebirges. VII. Die Pflanzenassoziationen und die Flora des Morskie Oko-Tales. Bull. Acad. Pol. Sc. Ser. B. Cracovie. 205–272.
- PAWŁOWSKI, B., 1928: Die geographischen Elemente und die Herkunft der Flora der subnivalen Vegetationsstufe im Tatra-Gebirge. Bull. Acad. Pol. Sc. Ser. B. Cracovie. 161–202.
- 1935: Über die Klimaxassoziationen der alpinen Stufe der Tatra. Bull. Acad. Pol. Sc. Ser. B. Cracovie. 115–145.
- POHLE, R., 1903: Pflanzengeographische Studien über die Halbinsel Kanin und des angrenzenden Waldgebietes. I. Acta Hort. Petrop. 21, 1, 19–130.
- POLUNIN, N., 1940: Botany of the Canadian eastern Arctic. Nat. Mus. Can. Bull. 92, 1–408.
- 1959: Circumpolar arctic flora. Oxford.
- PORSILD, M., 1915: On the genus *Antennaria* in Greenland. Medd. o. Grøn. 51, 265–281.
- PORSILD, A. E., 1950: The vascular flora of the North America Arctic. Proc. VIIth Int. Bot. Congr. Stockholm. 613–614.
- 1965: The genus *Antennaria* in Eastern Arctic and Subarctic America. Bot. Tidsskr. 61, 22–25.
- ROTH, E., 1895: Die Flora der Tschuktschen-Halbinsel. Natur. Jahrg. 1895.

- ROULEAU, E., 1956: A check-list of the vascular plants of the province of Newfoundland including the French islands of St. Pierre and Miquelon. *Contr. de l'Inst. Bot. de l'Univ. de Montréal* 69, 41–105.
- RUNE, O., and O. I. RÖNNING, 1956: *Antennaria Nordhagiana* nova species. *Sv. Bot. Tidskr.* 50, 115–128.
- RYDBERG, P. A., 1922: Flora of the Rocky Mountains and adjacent plains. II ed. N. York.
- SAMUELSSON, G., 1917: Studien über die Vegetation bei Finse. *Nytt Mag. f. Naturv.* 55, 1–108.
- SCHAEFER, H., und B. FRENZEL, 1957: Beiträge zur Kenntnis der Flora des Ostteiles der Grossen Samojeden-Tundra. *Bot. Jahrb.* 78, 367–434.
- SCHRÖTER, C., 1923–1926: Das Pflanzenleben der Alpen. Zürich.
- SELANDER, S., 1950: Floristic phytogeography of SW Lule Lappmark. I, II. *Acta Phytogeogr. Suec.* 27, 28.
- SKALIŃSKA, M., 1966: Cyto-taxonomical studies in the genus *Crocus*. *Acta Biol. Crac. Ser. Bot.* 9, 137–152.
- 1968: Further cytological studies in the genus *Crocus* L. *C. albiflorus* Kit. *Acta Biol. Crac. Ser. Bot.* 11, 31–37.
- SMITH, H., 1920: Vegetationen och dess utvecklingshistoria i det centralsvenska Högfjällsområdet. *Norrl. Handbibl.* 9. Uppsala.
- SOKOLOVSKAJA, A. P., und N. STRELKOVA, 1941: Polyploide und karyologische Rassen in arktischen Bedingungen – Untersuchungen über die Flora der Insel Kolguyev. *Compte rendu de l'Acad. Sc. USSR.*
- 1960: Geographic distribution of the polyploid species in plants in the Eurasian Arctic. *Bot. Zhurn.* 45, 369–381.
- SÖYRINKI, N., 1938–1939: Studien über die generative und vegetative Vermehrung der Samenpflanzen in der alpinen Vegetation Petsamo-Lapplands. *Ann. Zool. Bot. Soc. Fenn. Vanamo* 11, 1–323.
- STANKOV, S. S., i W. T. TALIEW, 1949: Opređielitel' wyzsih rastenij europejskoj czasti SSSR. Moskva.
- STEBBINS, G. L., 1932: Cytology of *Antennaria* I, II. *Bot. Gaz.* 94, 134–149; 322–345.
- SUKAČEV, V. N., 1938: Die Geschichte der Vegetation der UdSSR während Pleistozäns. *Rastitelnost SSSR* 1, 183–234.
- SZAFER, W., B. PAWŁOWSKI und ST. KULCZYŃSKI, 1923: Die Pflanzenassoziationen des Tatra-Gebirges. I. Die Pflanzenassoziationen des Chochołowska-Tales. *Bull. Acad. Pol. Sc. Ser. B. Cracovie.* 1–78.
- SZAFER, W., ed. 1966: The vegetation of Poland. Oxford-Warsaw.
- TENGWALL, TH. A., 1916: Über die Bedeutung des Kalkes für die Verbreitung einiger schwedischer Hochgebirgspflanzen. *Sv. Bot. Tidskr.*
- 1920: Die Vegetation des Sarek-Gebietes. II. *Abt. Nat. Unters. der Sarekgeb. in Schw.-Lappl.* III, 4, 270–436; 3, 8.
- ТИХОМИРОВ, B. A., 1946: K filocenogenesu nekotorych rastitielnych formacii arkticeskoj Eurasii. *Bot. Zhurn.* 31, 27–41.
- 1951: On the role of the wind in the plants distribution in the Far North. *Priroda*, 23–25.
- TOLMATSCHEV, A. I., 1926: Contribution to the flora of Vaigatsch and of the Coast of the Yugor Strait. *Trav. du Mus. bot. de l'Acad. Sc. USSR* 19.
- 1930: Sur la provenance de la flore du Vaigatsch et de la Novaya Semlya. *Trav. du Mus. bot. de l'Acad. Sc. USSR* 22.
- 1932: Flora des Inneren von Ost-Taimyr. *Trudy Polarnoj Komisji* 8.
- 1939: O niekotorych zakonomiernostiach razpiedelienija rastitielnych sobščestv Arktiki. *Bot. Zhurn.* 5–6.
- 1952: K istorii rasvitia flor sovietskoj Arktiki. *Areal* 1.

- 1957: Die Probleme der Entwicklung und der Entwicklungsgeschichte der arktischen Flora. Delegiertenversammlung der Allunion-Bot. Ges. S. der Fl. u. Veg. Leningrad.
- 1958: Materialy do issledovania flory i rastiennosti SSSR. Leningrad-Moskva.
- 1960a: Der autochthone Grundstock der arktischen Flora und ihre Beziehungen zu den Hochgebirgsfloraen Nord- und Zentralasiens. Bot. Tidsskr. 55, 269-276.
- 1966: Die Evolution der Pflanzen in Arktisch-Eurasien während und nach der quaternären Vereisung. Bot. Tidsskr. 62, 27-36.
- TRAUTVETTER, E. R., 1883: Incrementa Florae phaenogamae Rossicae. 2. Petropolis.
- 1879: Flora terrae Tschuktschorum. Acta Hort. Petrop. 6, 1.
- TURILL, W. B., 1950: Modern trends in the classification of plants. Adv. Sc. 26, 1-16.
- UHLWORN, O., und W. PASCHER, 1928: Beiträge zur Flora und Pflanzengeographie von Novaya Semlya, Vaigatsch und Kolguyev. Beih. Bot. Zentralbl. 44, 283-361.
- URBAŃSKA, K., 1959: Cytology of *Antennaria carpatica* and *A. dioica*. Acta Biol. Crac. Ser. Bot. 2, 43-49.
- URBAŃSKA-WORYTKIEWICZ, K., 1961: Embryological investigations in *Antennaria* Gaertn. I. Development of the ovules in *A. carpatica* (Wahlb.) Bl. et Fing. Acta Biol. Crac. Ser. Bot. 4, 49-64.
- 1962: Embryological investigations in *Antennaria* Gaertn. II. Development of the pollen of *A. carpatica* (Wahlb.) Bl. et Fing. Acta Biol. Crac. Ser. Bot. 5, 97-102.
- 1962a: Embryological investigations in *Antennaria* Gaertn. III. Experimental hybrids between *A. carpatica* (Wahlb.) Bl. et Fing and *A. dioica* (L.) Gaertn. Acta Biol. Crac. Ser. Bot. 5, 103-116.
- 1965: Cytological studies in experimental hybrids between *Antennaria carpatica* (Wahlb.) Bl. et Fing and *A. dioica* (L.) Gaertn. Acta Biol. Crac. Ser. Bot. 8, 51-61.
- 1967: Cytological investigations in *Antennaria* Gaertn. from North Scandinavia. Acta Borealia. A. Scientia. Tromsø.
- 1967a: Embryological investigations in *Antennaria* Gaertn. IV. Microsporogenesis in *A. carpatica* (Wahlb.) Bl. et Fing. from North Scandinavia. Acta Biol. Crac. Ser. Bot. 10, 85-98.
- 1967b: Cyto-embryological investigations in *Antennaria carpatica* (Wahlb.) Bl. et Fing. from North Scandinavia. Genetica Pol. 8, 181-183.
- 1968: Recherches cytologiques sur les populations alpines d'*Antennaria* Gaertn. Bull. Soc. Bot. suisse 78, 191-201.
- 1968a: A new hybrid of the Alpine flora: *Antennaria carpatica/A. dioica*. Ber. Geobot. Inst. ETH, Stiftung Rübel, 38, 20-27.
- 1969: Embryological investigations in *Antennaria* Gaertn. V. Micro- and macrosporogenesis in natural hybrids between *A. carpatica* (Wahlenb.) Bluff et Fingerh. and *A. dioica* (L.) Gaertn. Acta Biol. Ser. Bot. 12, 21-33.
- VESTERGREN, T., 1902: Om den olikformiga snöbetäckningens inflytande på vegetationen i Sarjekfjällen. Bot. Not., 241-268.
- WAGENITZ, G., 1964-1968: Compositen, II. Teil, in Hegi: Illustrierte Flora von Mitteleuropa, Bd. VI/3, Lief. 1-4.
- WAHLENBERG, G.: 1814: Flora Carpatorum Principalium. Goettingae.
- 1826: Flora Suecica II. Uppsaliae.
- WALTER, H., und H. STRAKA, 1970: Arealkunde. Einführung in die Phytologie. III. Stuttgart.
- WILLDENOW, I., 1804: Species plantarum 3/3. Berolini.
- ZHUKOVA P. G 1968. Chromosome numbers in some plant species from the North-East of the USSR III. Bot. Zhurn. 53, 365-368.