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Autor: Urbaska-Worytkiewicz, Krystyna

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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. ЗнУКОВА, 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 involucral 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 involucral 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 anthocyane 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.

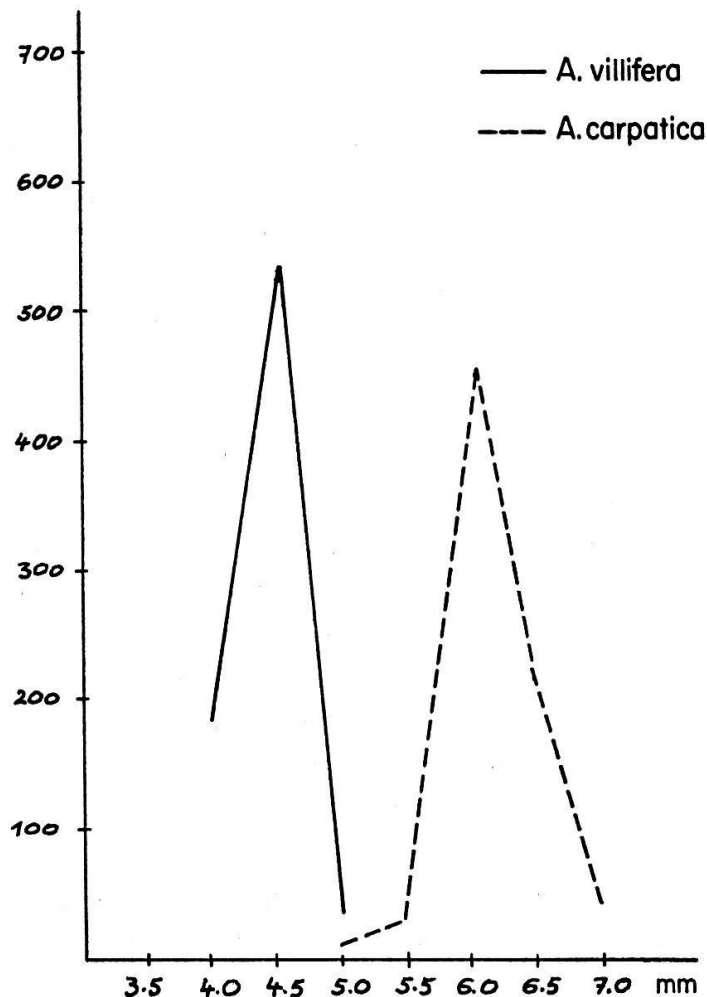


Fig. 11. Length of the innermost phyllaries in male heads of *Antennaria villifera* and *A. carpatica* s.str.

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.

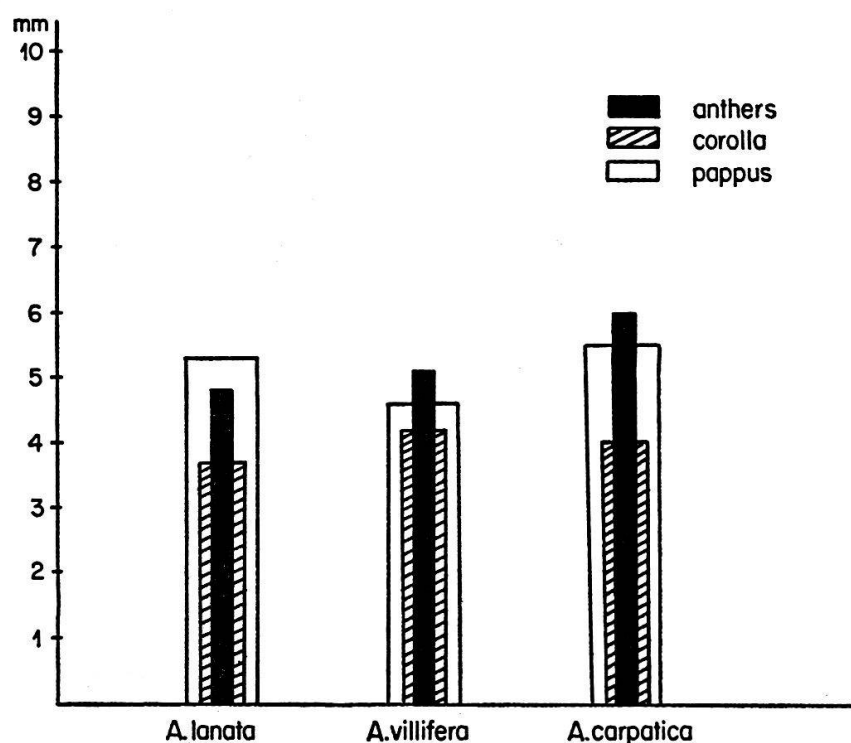


Fig. 12. Average length of the flower organs in staminate florets of *Antennaria carpatica* s.str., *A. villifera* and *A. lanata*.

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).

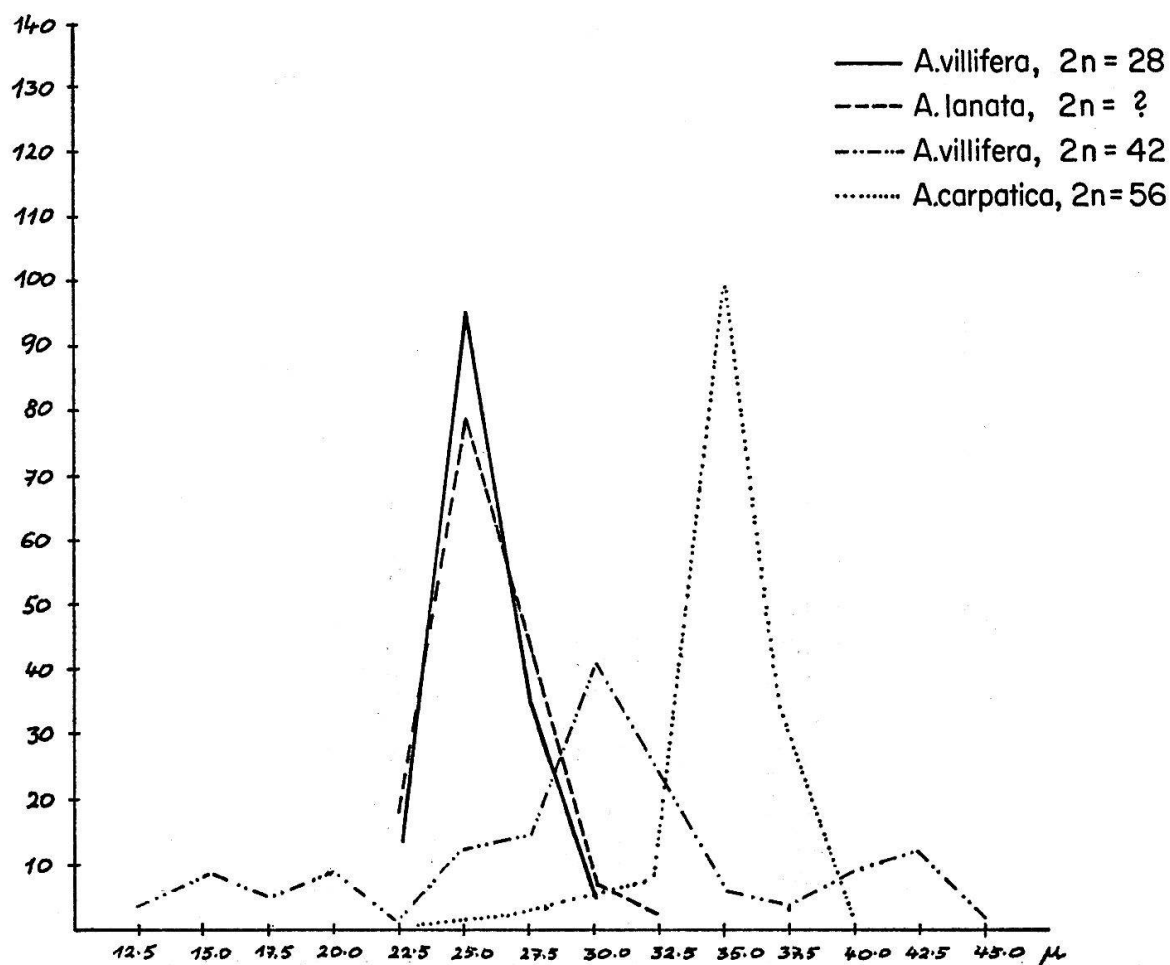
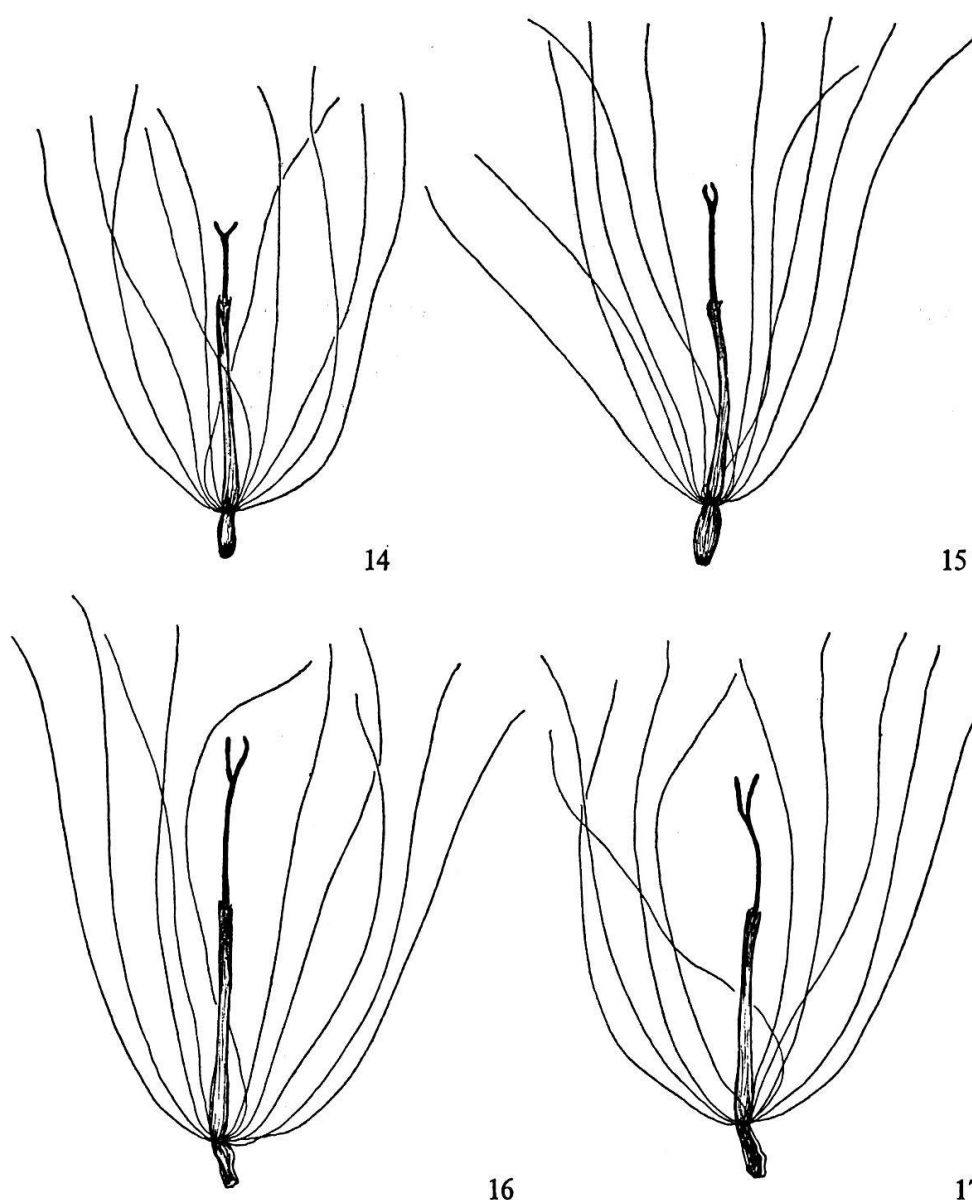


Fig. 13. Graph of pollen diameter.

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 LYNGE (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. $5\times$.

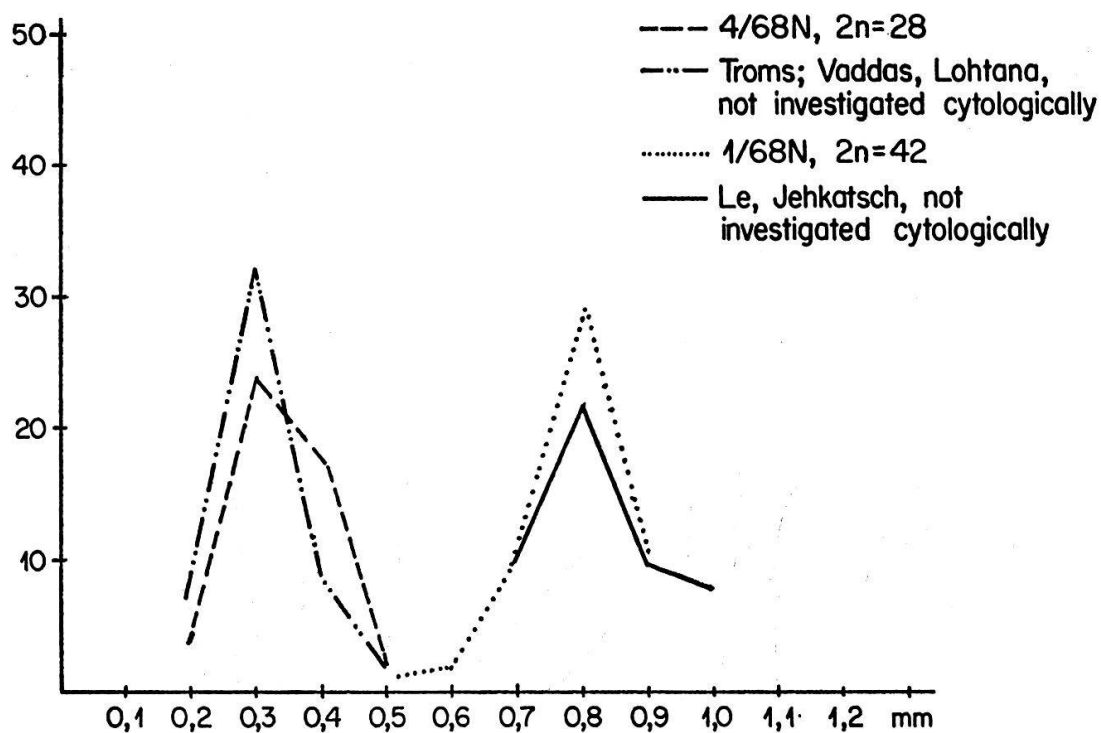


Fig. 18. Length of the stigma lobes in *Antennaria villifera*: a comparison between the materials studied cytologically and plants with unknown chromosome numbers.

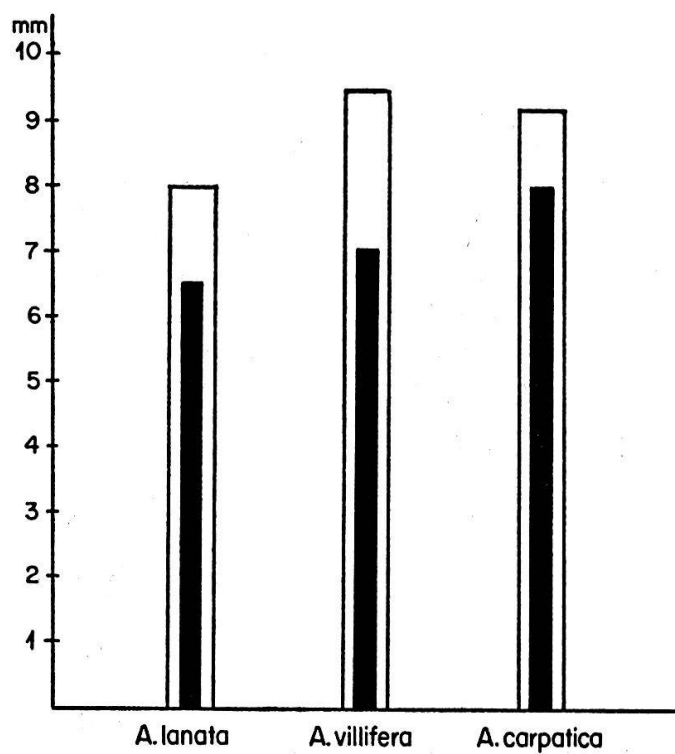


Fig. 19. Average length of style and pappus in pistillate florets of *Antennaria carpatica* s.str., *A. villifera* and *A. lanata*.

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.

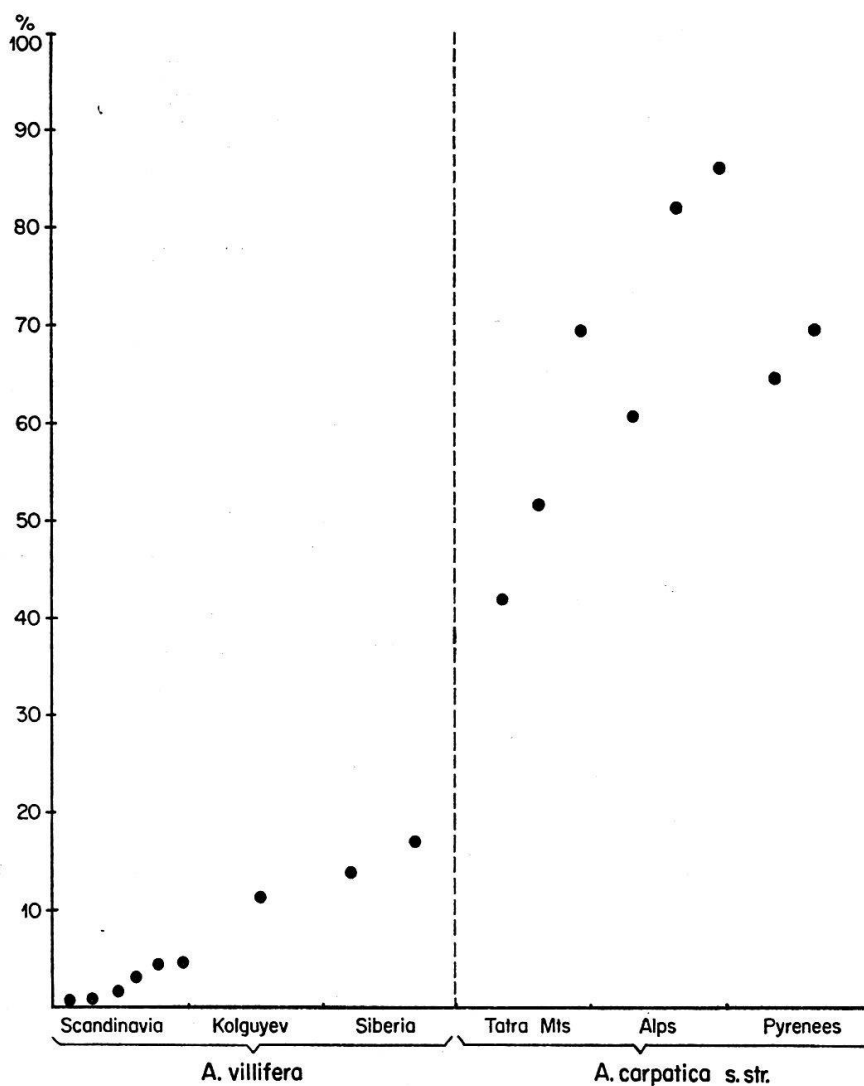


Fig. 20. Seed-setting in *Antennaria villifera* and *A. carpatica* s.str.

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. Scarious 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).

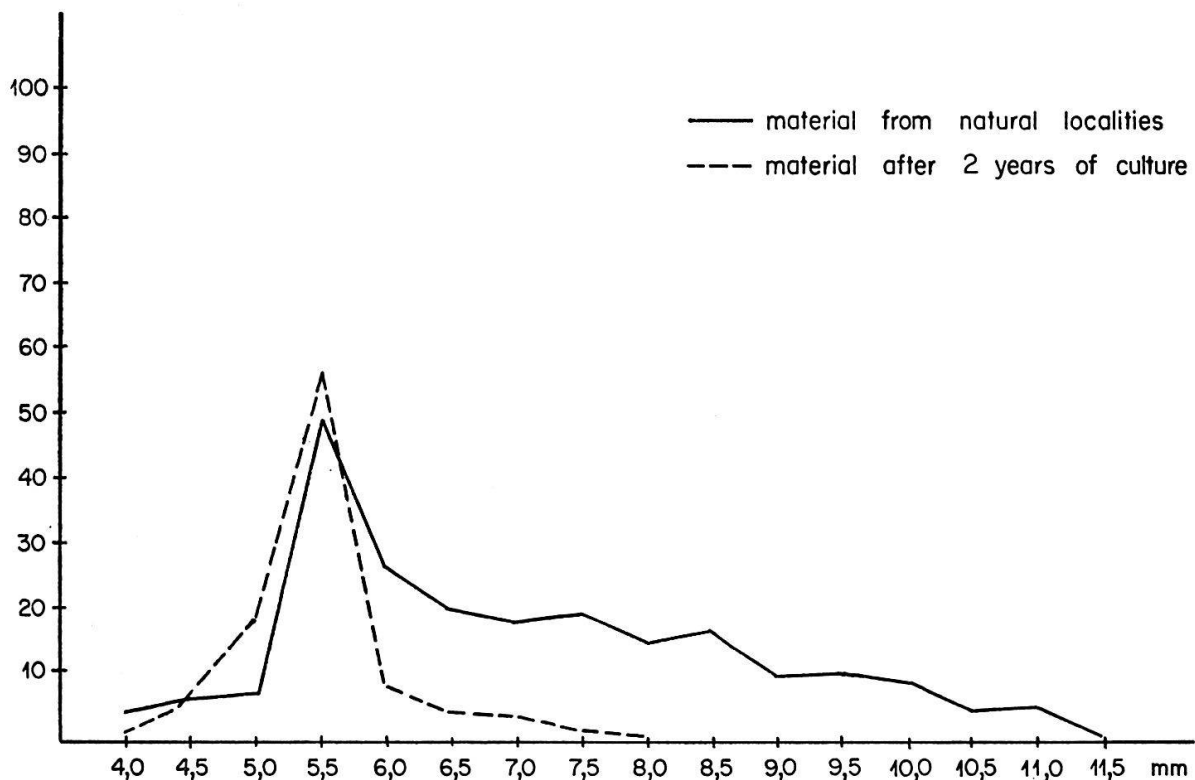


Fig. 21. Width of the rosette leaves of *Antennaria carpatica* s.str.: a comparison between the material sampled in natural localities and the plants kept for two years in the experimental field.

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 μ . 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 involucral 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