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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 Pyrenaici*, 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 ZHUKOVA (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 Verkhoyansk 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-

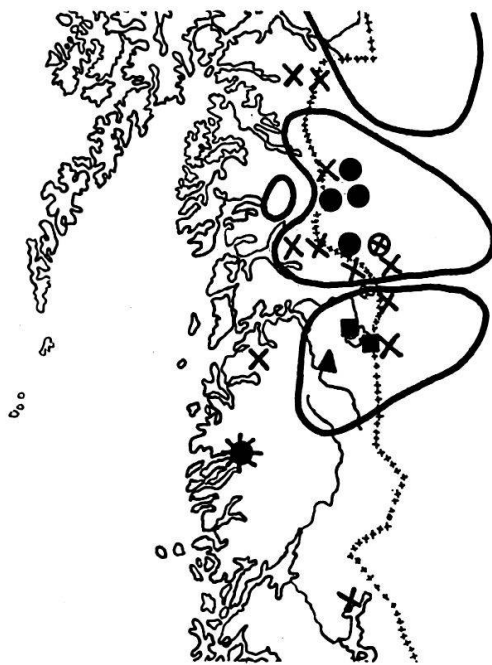


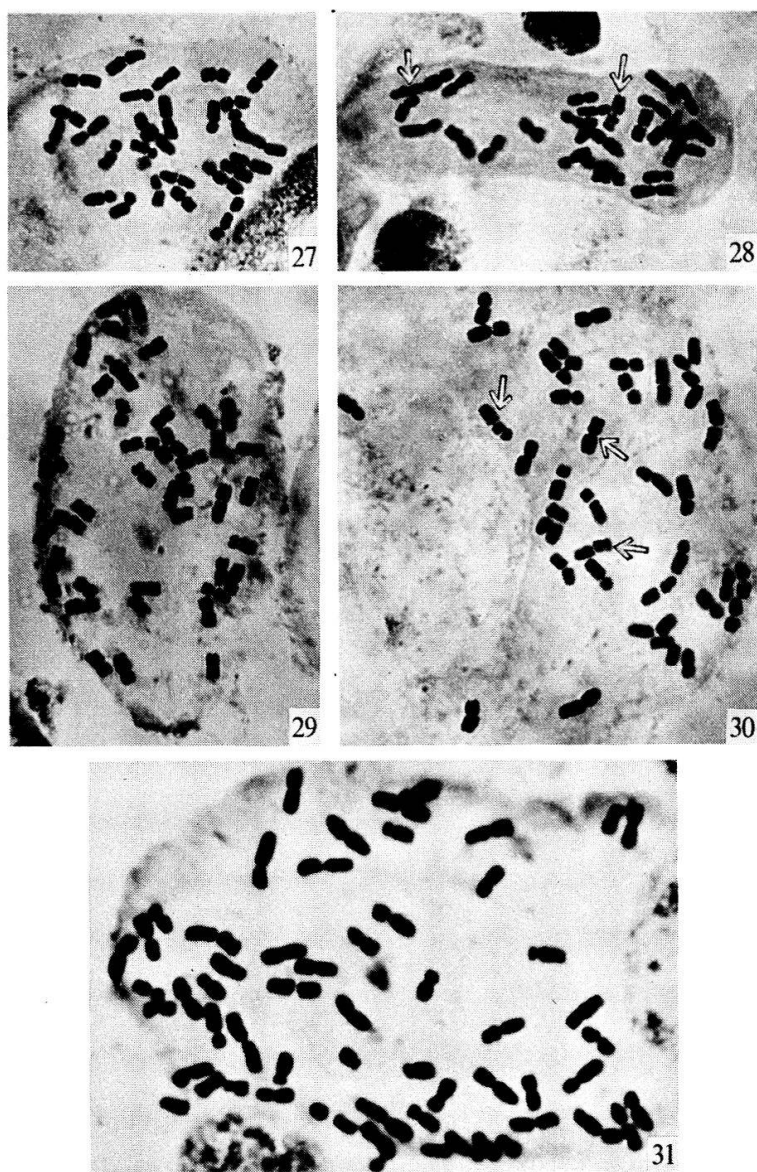
Fig. 26. Botanical indications of refugia in Nordland, Norway. Localities of *Arenaria humifusa* (dots); *Papaver radiculatum* ssp. *subglobosa* (asterisk); *Carex scirpoidea* (triangle); *Saxifraga aizoon* ssp. *laestadii* (squares); *Draba crassifolia* (crosses); *Potentilla hyparctica* (circle with 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).

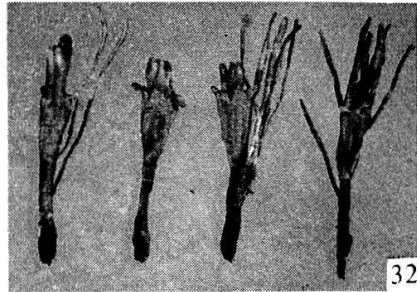
As far as the origin and development of *Antennaria carpatica* s.str. is concerned, the present investigations support ENGLER's opinion as to a Siberian origin of this species (ENGLER 1905). *Antennaria carpatica* s.str. is undoubtedly related to *A. villifera*. Some details of the chromosome morphology suggest that it could have being 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



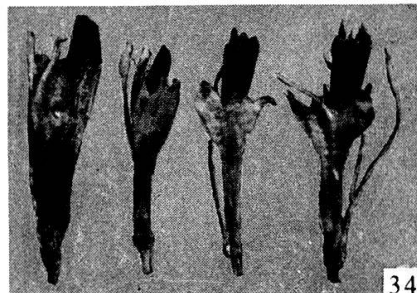
Figs. 27-31. Microphotos of root-tip metaphases. 27-28. Tetraploid *Antennaria villifera*, $2n=28$. 29-30. Hexaploid *A. villifera*, $2n=42$. 31. *A. carpatica* s.str., $2n=56$. C. $1000\times$.



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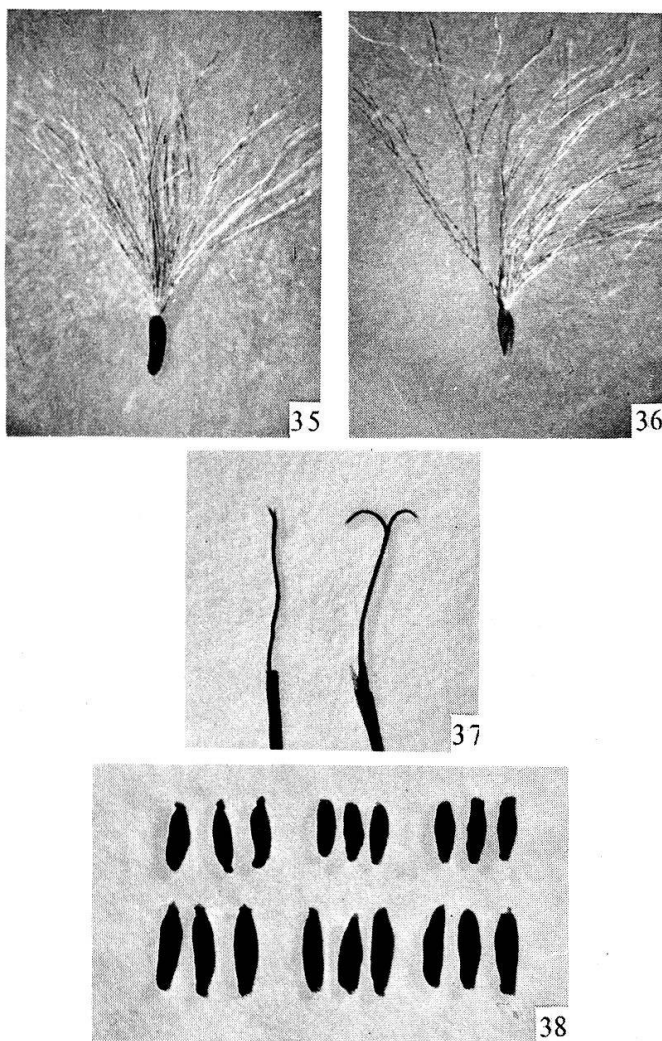


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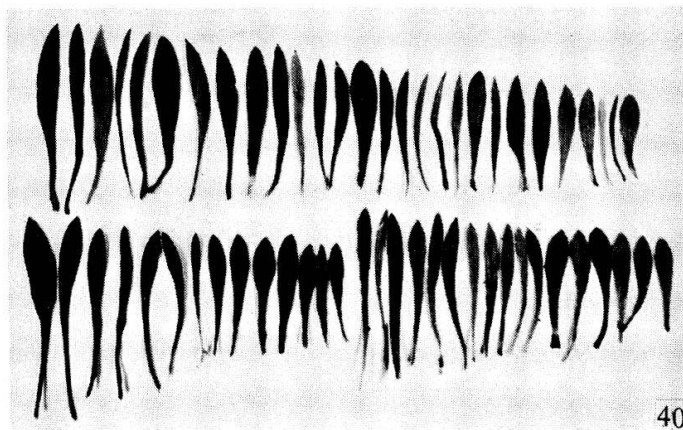
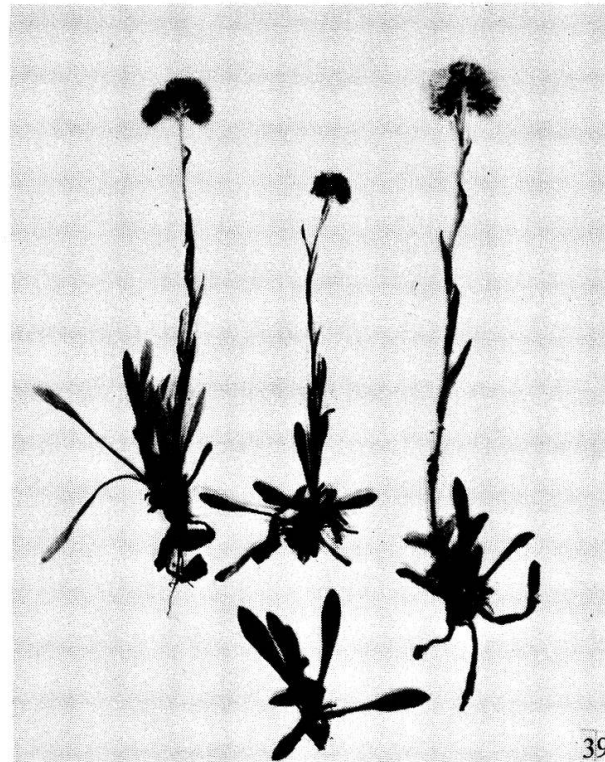


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Figs. 32–34. Staminate florets; 32. *Antennaria lanata*; 33. *A. villifera*; 34. *A. carpatica* s.str. C. 4.5 ×.



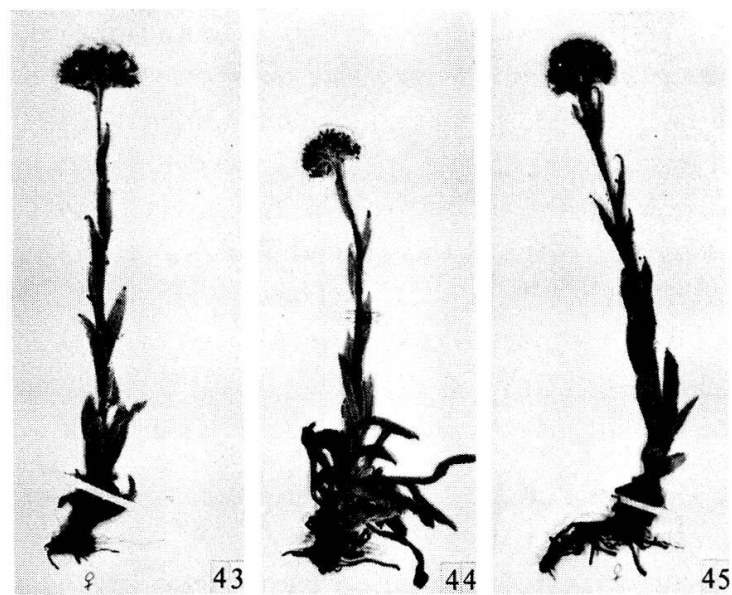
Figs. 35–38. Post-floral stage; 35. Pistillate floret of *Antennaria carpatica* s.str.; 36. Floret of *A. villifera*, c. $4.5\times$; 37. Two types of stigma found within *A. villifera*; 38. Ripe achenes: upper row, left and right: *Antennaria villifera* from Scandinavia and Kolguyev; upper row, middle: *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* β *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