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Cyto-geographical differentiation in *Antennaria carpatica* s.l.

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Abstract

K. M. Urbanska 1983. Cyto-geographical differentiation in *Antennaria carpatica* s.l. Bot. Helv. 93: 123-131. Cyto-geographical differentiation in the *Antennaria carpatica* group followed apparently distinct trends in North America and Eurasia. In North America, octoploids occur much farther north than the corresponding tetraploid taxa. On the whole, the boreal/subarctic area of octoploids is much larger than the montane/subalpine-alpine area of tetraploids. Two chromosomal races of *A. pulcherrima* have a distinctly polarized S-N distribution. In Europe, orophile octoploids occur much farther south than subarctic tetraploids and hexaploids; the total area of octoploids is minute compared to that of tetraploid/hexaploid races that both occur scattered over the considerable area ranging from Lapland to Chukotka Peninsula.

Evolutionary importance of cyto-geographical data is discussed and tetraploid taxa of *A. carpatica* s.l. are assigned to paleopolyploids following the classification proposed by Favarger (1961).

Introduction

The *Carpaticae*-section within the genus *Antennaria* Gaertn. forms a rather small but taxonomically complex group, further and more extensive biosystematic studies being necessary before a satisfactory treatment can be devised. On the other hand, the *Carpaticae* seem to be fairly uniform as far as their reproduction is concerned, for no asexual seed production has been observed. In this respect, the group differs from most other sections of the genus where high polyploidy levels usually are accompanied by the agamospermy (see e.g. Stebbins 1932, Gustafsson 1946-1947, Urbanska 1974).

Antennaria carpatica s.l. represents a very interesting object for a study in ecological genetics and speciation, various evolutionary patterns having been observed. Particularly instructive in this respect are some aspects of cyto-geographical differentiation. They are discussed in the present paper, largely based on a long-term research carried out by the author.

Travail dédié au professeur Claude Favarger, à l'occasion de son 70^e anniversaire

Geographical distribution

Antennaria carpatica s.l. has a general distribution of a boreal/subarctic - alpine type. It occurs both in North America as well as Eurasia (Figs 1-2). In North America, four taxa viz. *A. pulcherrima*, *A. anaphalooides*, *A. lanata* and *A. eucosma* were distinguished. In Europe, *A. carpatica* s.str. and *A. villofera* occur, respectively, in either of the two distinct distribution areas. The latter taxon is also the only representative of the *A. carpatica* group in Asia.

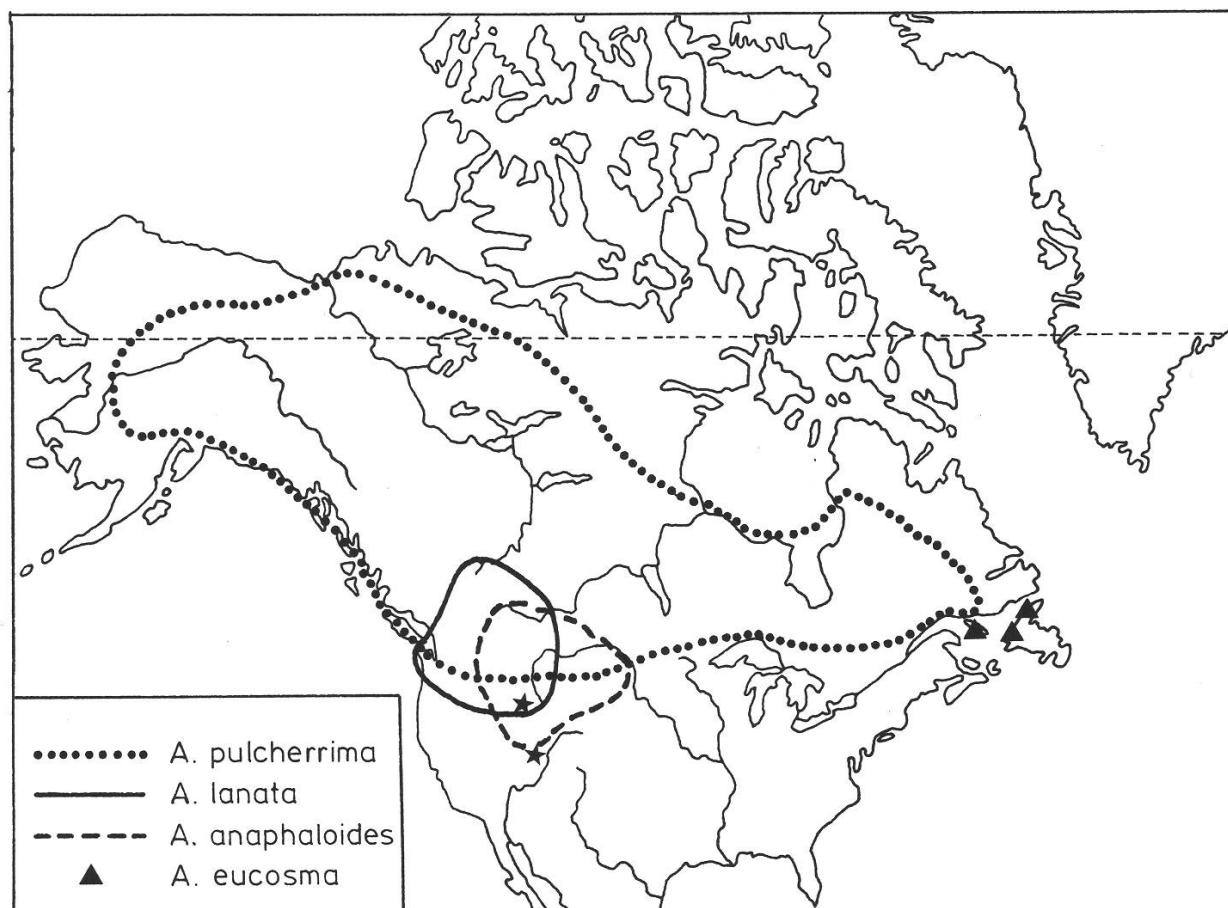


Fig. 1. Approximate distribution of the *Antennaria carpatica* group in North America. Two isolated stations of tetraploid *A. pulcherrima* ($2n = 28$) are marked by asterisks.

A. pulcherrima has the largest distribution area of all North American taxa of the group. It ranges from Central Alaska north to the Arctic Coast in the region of the Mackenzie River Delta, east through NW Territories and surroundings of Hudson Bay in N Manitoba/N Ontario to N Quebec and northern coast of Gulf of St. Lawrence, south through Yukon Territory and British Columbia/Alberta to N Washington, Idaho and Montana. Precise limits of occurrence of *A. pulcherrima* remain open to verification; of a particular interest are small, rare and very isolated stations that apparently are situated far south from the main area (Urbanska 1983).

A. anaphalooides ranges from British Columbia and Alberta south to Wyoming, Colorado and west to NE Nevada. Eastern and northern limits of its distribution area should be further investigated.

A. lanata occurs within a rather well-defined area ranging from Olympic Mts and North Cascades to Central Rocky Mts. It reaches from British Columbia and Alberta south to Washington and NE Oregon and east to Montana. Southern limits of occurrence of *A. lanata* correspond to the Beartooth Plateau near the stateline Montana/Wyoming.

A. eucosma seems to be confined to Newfoundland as well as Anticosti Island in the Gulf of St. Lawrence.

In Europe, *A. carpatica* s.str. occurs in the Carpathians, the Alps and the Pyrenees, its tricentric pattern of distribution being very distinct. The second European representative of the group viz. *A. villifera* has a unicentric distribution in subarctic Scandinavia; it also occurs in Kolguyev, Vaigatsch, Novaja Zemlya and in the northernmost part of the Ural Mts. *A. villifera* is as well the sole representative of the Carpaticae in Asia, where it occurs scattered over North Siberia from Yamal and Taimyr east to Chukotcha Peninsula; southernmost stations of *A. villifera* in Asia are known to date from the Sayan Mts. in East Siberia.

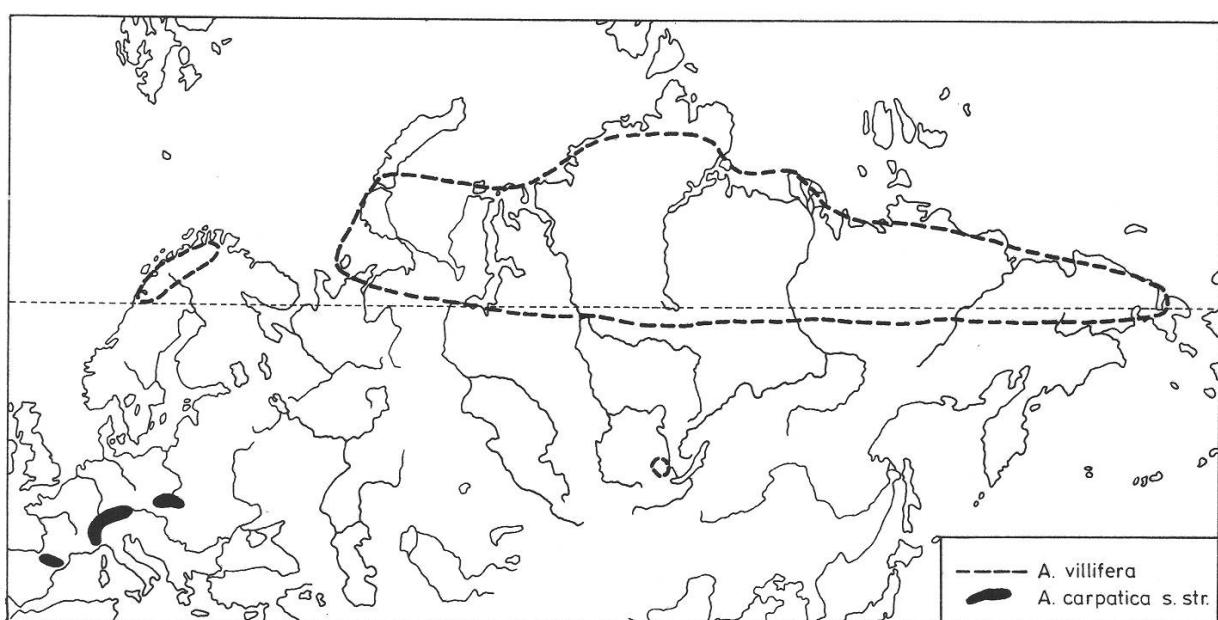


Fig. 2. Approximate distribution of the *Antennaria carpatica* group in Europe and Asia.

Although the available data are still incomplete, they permit to characterize in a general way patterns of geographical distribution occurring within the *A. carpatica* group. Some American taxa of the Carpaticae are largely allopatric; this is particularly the case of *A. pulcherrima* in northern and north-eastern parts of its distribution area and also that of *A. anaphalooides* in southern part of its range. *A. eucosma* seems to occupy a small, separate and discontinuous area, more or less adjacent to the range of *A. pulcherrima* in its easternmost part. *A. lanata*, *A. anaphalooides* and *A. pulcherrima* are partially sympatric, especially in the region of central Rocky Mts. *A. carpatica* s.str. and *A. villifera* are distinctly allopatric.

Chromosome numbers

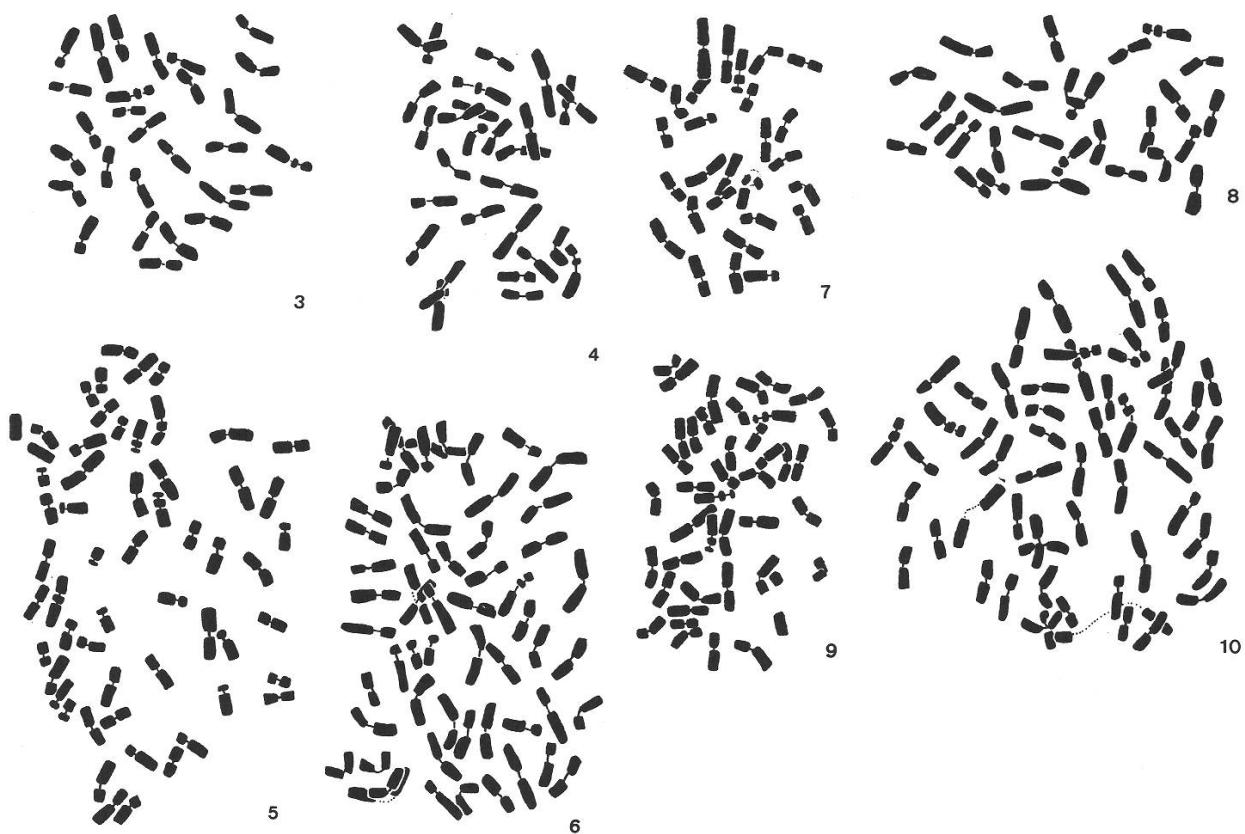
The *A. carpatica* group is cytologically differentiated, three levels of polyploidy viz. $4\times$, $6\times$ and $8\times$ having been recognized to date (Table).

Table: Chromosome numbers occurring within the *Antennaria carpatica* group (after Urbanska 1983, completed)

Taxon	2n	Poly-ploidy level	Origin of material	Author(s)
<i>A. pulcherrima</i>	28	4x	Wyoming, Colorado	Urbanska 1983
	56	8x	Alaska, Yukon T., British Columbia, Alberta	Urbanska 1983
<i>A. anaphaloides</i>	28	4x	British Columbia	Urbanska 1983
	28	4x	Washington, Idaho, Montana, Colorado	Urbanska 1974, 1983
<i>A. lanata</i>	28	4x	Olympic Mts	Urbanska 1983
	28	4x	N Cascades, Blue Mts	Urbanska 1983
	28	4x	Rocky Mts (British Columbia, Alberta)	Urbanska 1983
	28	4x	Rocky Mts (Idaho, Montana/Wyoming)	Urbanska 1983
<i>A. eucosma</i>	56	8x	Newfoundland	Urbanska 1983
<i>A. villifera</i>	28	4x	N Scandinavia	Urbanska 1967, 1970, Engelskjøn and Knaben 1971
	28	4x	Chukotchka	Zhukova 1968, Zhukova and Tikhonova 1971, 1973, Zhukova, Petrovsky and Plieva 1973
<i>A. carpatica</i>	40–42	6x	N Scandinavia	Bergman 1935, 1951
	42	6x	N Scandinavia	Urbanska 1967, 1970, Engelskjøn and Knaben 1971
	42	6x	Chukotchka	Zhukova 1968
	42	6x	Yakutia	Yurtsev and Zhukova 1982
<i>s. str.</i>	56	8x	Carpathians (Tatra)	Urbanska 1959, 1961, 1962, 1970
	56	8x	Alps	Urbanska 1968a, b, 1970, unpubl.
	56	8x	Pyrenees	Urbanska 1970

Out of the six taxa forming the group, *A. lanata* and *A. anaphaloides* are represented solely by tetraploid populations ($2n = 28$, Figs 3–4). *A. carpatica* s. str. and *A. eucosma* are uniformly octoploid ($2n = 56$, Figs 5–6). On the other hand, both *A. villifera* as well as *A. pulcherrima* consist of two chromosomal races each. Interestingly enough, either taxon represents a different pattern of polyploidization: *A. villifera* comprises a tetraploid and a hexaploid race ($2n = 28$, $2n = 42$, Figs 7,9), whereas *A. pulcherrima* was found so far octoploid ($2n = 56$, Fig. 10) except for two isolated tetraploid stations ($2n = 28$, Fig. 8).

Cyto-geographical differentiation occurring in *A. villifera* and *A. pulcherrima* apparently followed distinct pathways. In *A. pulcherrima*, octoploids consistently occur farther north, whereas rare tetraploids were found to date exclusively outside the octoploid range. Contrary to this pattern, two chromosomal races occurring in *A. villifera* do not have separate areas of distribution, tetraploids and hexaploids apparently being both scattered over the whole range of the taxon i.e. from Lapland to Chukotchka Peninsula.



Figs 3-6. Somatic chromosome numbers of *Antennaria carpatica* s.l. 3. *A. lanata*, $2n=28$. 4. *A. anaphaloides*, $2n=28$. 5. *A. carpatica* s.str., $2n=56$. 6. *A. eucosma*, $2n=56$. C. $2200\times$. Partly from Urbanska 1970, 1983.

Figs 7-10. Somatic chromosome numbers of *Antennaria carpatica* s.l. 7. Tetraploid *A. villifera*, $2n=28$. 8. Tetraploid *A. pulcherrima*, $2n=28$. 9. Hexaploid *A. villifera*, $2n=42$. 10. Octoploid *A. pulcherrima*, $2n=56$. C. $2200\times$. Partly from Urbanska 1970, 1983.

Discussion

Cyto-geographical data are very important for a better assessment of mechanisms involved in the process of speciation. Amongst the scientists who not only developed the pioneer ideas of Hagerup (1928, 1932), Manton (1932, 1934, 1937) and Tischler (1934) but also presented important concepts of their own, Favarger holds an outstanding rank. In the following discussion, a special attention shall be payed to some brilliant contributions of this author (Favarger 1961, 1964, 1967).

The representatives of *A. carpatica* s.l. apparently are closely related and can be considered as corresponding taxa (Löve 1954, Favarger 1967). The lowest level of polyploidy within the *Carpaticae* and also within the whole genus is represented by the chromosome number $2n=28$, considered as tetraploid in *Antennaria* Gaertn. (see e.g. Stebbins 1932, Urbanska 1959, 1967, 1968, 1970).

Polyplloidization within the *A. carpatica* group offers some interesting aspects. As far as the hexaploid *A. villifera* ($2n=42$) is concerned, indications of an autoploid origin are rather numerous. The formation of trivalents in meiosis suggests a rather high degree of homology between particular chromosomes (Urbanska 1967a); comparative

studies in chromosome morphology of tetraploid and hexaploid *A. villifera* revealed that most chromosome types occurring in pairs within the tetraploid complement were grouped by three in the hexaploid set (Urbanska 1970). It seems therefore plausible that the hexaploid *A. villifera* could have arisen from the tetraploid race with a part of an unreduced gamete.

The octoploid race of *A. pulcherrima* ($2n = 56$) might as well result from an autoploidization, but in this case a full doubling of the tetraploid chromosome set seems to have been involved. Our preliminary observations on chromosome morphology (Urbanska unpubl.) reveal that some chromosomes occurring in pairs within the tetraploid complement of *A. pulcherrima* are represented by four homologues in the octoploid set; particularly instructive in this respect seem to be the chromosomes with secondary constrictions. Further studies in this subject are, however, required.

A comparison between the distribution areas of tetraploid taxa with those of higher polyploids brings about an evolutionary component to the geography of the *A. carpatica* group. The data on the *Carpaticae* fully support the opinion of Favarger (1961) concerning the importance of chromosome numbers for historical geobotany.

In North America, octoploid populations reach much farther north than the tetraploid ones and their total area is also much larger. This tendency is not only observable in the distribution of the two chromosomal races of *A. pulcherrima*, but also represents a more general pattern when various taxa of the group are being considered. The rather pronounced S-N gradient occurring in North America corresponds to the concept of a pseudo-vicariance of austral-septentrional type (Favarger 1964). This pattern of distribution of corresponding taxa and/or chromosomal races was reported in several Alpine or Pyrenean plant groups (e.g. Favarger 1962, 1964, Küpfer 1974). Its phylogenetical implications not only help to assess a relative age of given groups, but also suggest possible migration paths. Another type of the pseudo-vicariance consists, according to Favarger (1964) in occurrence of diploids or lower polyploids at higher altitudes, whereas the corresponding higher polyploids inhabit lowlands. A comparable trend was sometimes recognized in the distribution of the *Carpaticae* in North America: for instance, in Jasper National Park (Alberta, Canada) where distribution areas of *A. lanata* ($2n = 28$) and *A. pulcherrima* ($2n = 56$) partially overlap, the tetraploid taxon was observed within the uppermost subalpine belt and about timberline (Ogilvie, personal communication, Urbanska 1983) whereas the octoploids were invariably found in river banks and/or stabilized river bars (Urbanska 1983).

Interestingly enough, an inverse situation is observable in Europe. The octoploid *A. carpatica* s.str. is a high-mountain taxon (Urbanska 1959, 1968, 1970) occurring much farther south than the subarctic, tetraploid and hexaploid *A. villifera* (Bergman 1935, 1951, Urbanska 1967, 1970, Engelskjøn and Knaben 1971). The North - South gradient corresponds to Favarger's concept of a pseudo-vicariance of septentrional - austral type (Favarger 1964) and is rather infrequently observed in plants representing a boreal/arctic - alpine element in orophile floras of Europe.

The total area of octoploid populations in Europe is minute compared to that of tetraploids and hexaploids spreading from Lapland east to Chukotchka Peninsula (Zhukova 1968, Zhukova and Tikhonova 1971, 1973, Zhukova, Petrovsky and Plieva 1973, Yurtsev and Zhukova 1982). It should be stressed that both chromosomal races of *A. villifera* are apparently scattered over North Siberia and Lapland; in this respect, the Eurasian taxon differs from *A. pulcherrima* where the distribution of the two chromosomal races is distinctly polarized (Urbanska 1983).

Considered apart, trends of cyto-geographical differentiation in *A. carpatica* s.l. from Eurasia and North America may seem contradictory and confusing. On the other hand, an interesting pattern emerges when the group is regarded as a whole.

Antennaria Gaertn. is supposed to be a North-American genus. The occurrence of several tetraploid taxa of the sect. *Carpaticae* within a rather limited part of North-American Cordilleras might serve as indication of their origin. Tetraploid taxa of the *A. carpatica* group have partly sympatric distribution in North America, but they are rather differentiated ecologically and show accordingly varied life strategies (Urbanska 1983, Urbanska, in preparation). It seems that an adaptive radiation played an important rôle in the primary speciation of the group.

No taxon of the *A. carpatica* group is Amphi-Beringian. The disjunction separating *A. villifera* from American tetraploids is exceedingly large: it corresponds to the joint area of Chukotchka Peninsula, Bering Strait, Alaska, Yukon Territory and a large part of British Columbia. On the other hand, the octoploid *A. pulcherrima* is apparently long-established in central Alaska as well as Yukon Territory and northern British Columbia. It seems obvious that tetraploid taxa of the *A. carpatica* group have separated a long time ago. *A. villifera* or its ancestral taxon possibly arrived to Siberia from North America following some ancient migration paths across the Bering Strait and a subsequent differentiation has taken an independent course in either of the two territories. Various steps of autoploidization might result in the formation of hexaploids in Siberia and octoploids in North America. As far as the octoploid *A. carpatica* s.str. from Europe is concerned, its rather specialized karyotype suggest that it might be of an allopolyploid origin, tetraploid *A. villifera* being one of its putative parent taxa (Urbanska 1970).

Cyto-geographical data permit to characterize tetraploid taxa of the *Carpaticae* as paleopolyploids according to the classification proposed by Favarger (1961). Putative diploid parents of tetraploids are totally unknown, not only within the sect. *Carpaticae* but also within the whole genus *Antennaria*. The occurrence of higher polyploids representing various taxonomic rank suggests as well that tetraploids indeed are very old. Data on chromosome morphology of 28chromosomal plants as well as meiotic behaviour of chromosomes (Urbanska 1967a, 1970, Urbanska unpubl.) further support this opinion. The pertinent classification of polyploids proposed by Favarger (1961) is exclusively based on cytological criteria yet inevitably comprises the geographical aspect. As far as tetraploids of the *A. carpatica* group are concerned, patterns of geographical distribution (e.g. large disjunction, mostly small areas) indicate rather clearly an old age of the 28chromosomal taxa.

A more comprehensive discussion on possible speciation trends and relative age of taxa within the *A. carpatica* group must be postponed until more data are evaluated, those concerning *A. pulcherrima* from its whole distribution range being particularly important. We can conclude however, that further investigations in *A. carpatica* s.l. incontestably offer exciting perspectives. The study is in progress.

Résumé

Différenciation cyto-géographique d'*Antennaria* grex *carpatica* a suivi apparemment des chemins différents en Amérique du Nord et en Eurasie. En Amérique du Nord, les octoploïdes se rencontrent beaucoup plus au nord que les taxons tétraploïdes correspon-

dants. L'aire totale boréale/subarctique des octoploïdes est beaucoup plus étendue que l'aire montane/subalpine-alpine des tétraploïdes. Deux races chromosomiques d'*A. pulcherrima* ont une distribution polarisée Sud-Nord. En Europe, les octoploïdes orophiles s'observent plus au sud que les tétraploïdes et les hexaploïdes subarctiques. Le territoire des octoploïdes est très restreint par rapport à celui des tétraploïdes/hexaploïdes qui sont les deux dispersés dans l'aire totale s'étendant de Laponie jusqu'à la péninsule de Chukotchka.

L'importance évolutive des données cyto-géographiques est discutée et les tétraploïdes d'*A. carpatica* s.l. sont classifiés parmi les paléopolyploïdes suivant la classification de Favarger (1961).

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