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# *Antennaria carpatica* (Wahlb.) Bl. et Fing. s.l. in North America. I. Chromosome numbers, geographical distribution and ecology

## *Antennaria carpatica* (Wahlb.) Bl. et Fing. s.l. in Nordamerika. I. Chromosomenzahlen, geographische Verbreitung und Oekologie

by

Krystyna M. URBANSKA

Contents

# 1. Introduction

The present paper is the first of a series dealing with the *Antennaria carpatica* group from North America. The studies form part of a long-term research carried out by the author. Aspects of variation and evolution in the European *Carpaticae* were mostly dealt with in the author's previous publications (e.g. URBANSKA 1959, 1961, 1962 a,b, 1967a,b, 1968 a,b) and subsequently summed up in a more comprehensive paper (URBANSKA 1970). The genus *Antennaria* Gaertn. being of North American origin, it was obvious that important clues to the evolution of the whole sect. *Carpaticae* were to be looked for in the American continent; however, data from this region were very fragmentary and it was imperative to get more information. To set a basis for further discussions on evolutionary trends within the group, chromosome numbers of the *Carpaticae* from North America were examined first; to the best of the author's knowledge, they were practically unknown to date. Our results are reported in the present paper together with some data on geographical distribution and ecology of the particular taxa. We should like to emphasize that the latter evaluations are yet incomplete and have to be considered as preliminary.

The taxonomy of the sect. *Carpaticae* is rather complex. As far as North America is concerned, four taxa viz. *Antennaria pulcherrima* (Hook.) Greene, *Antennaria anaphaloides* Rydb., *Antennaria lanata* (Hook.) Greene and *Antennaria eucosma* Fern. et Wieg. were originally recognized. Before a satisfactory taxonomical treatment of the whole group is devised, we propose to retain this nomenclature; it should be kept in mind, however, that a precise rank of particular taxa as well as the validity of some names are open to verification.

## Acknowledgements

The present paper, largely based on numerous field trips, was carried out at the Geobotanical Institute SFIT Zürich. The author collectively acknowledges loan of herbarium specimens from various institutions and thanks persons who helped sending live material and/or field information from

North America; they shall be separately addressed to in further publications. In the present paper, we should like to express very special thanks to Klaus and Gertrud Lackschevitz, University of Montana, Missoula, Joy D. Mastrogiuseppe, University of Washington, Pullman, as well as Lucy and Mark Uhlig, Seattle, who offered us the hospitality of their homes and helped in many other ways. Excellent field assistance of Dr. Regula Dickenmann and Dr. A. Fossati (Geobotanical Institute) was greatly appreciated. Prof. Dr. E. Landolt (Geobotanical Institute) helped with some field work in Colorado; his solitary one-day walk across the Dinosaur National Monument with the sole purpose of sampling for us a population of *Antennaria anaphaloides* shall be gratefully remembered. He also critically read our manuscript and translated the summary into German. We also thank Ms. A. Hegi who carefully prepared materials for our field trips and helped with some laboratory tests.

The study could not have been carried out without the generous travelling grant obtained in 1978 from Swiss Society of Natural Sciences as well as the financial support from Swiss Federal Institute of Technology, Zürich (in particular, grants 1973, 1980). Sincere thanks of the author are addressed to both these institutions.

## 2. Material and methods

Material for the present study was gathered during ten years (1973-1982). Prior to the field work, information on a general distribution and some ecological features of the *Antennaria carpatica* group in North America was compiled from various regional floras as well as herbarium specimen labels. Site conditions and population structure were studied in the wild. Materials for cytological investigations were taken in the field save for few live samples sent to the author from North America. Voucher specimens are at the time being kept in the author's personal herbarium and shall be transferred later to the Herbarium of SFIT Zürich (ZT).

On the whole, 869 individuals corresponding to 112 population samples were studied cytologically (Tables 1-5). Meristems were pretreated with 0.05% aqueous solution of colchicine for about 3 h. and subsequently fixed in acetic alcohol (1:3) with a small addition of ferric acetate and acetocarmine. For staining of preparations, lacto-propionic orcein was used with very satisfactory results.

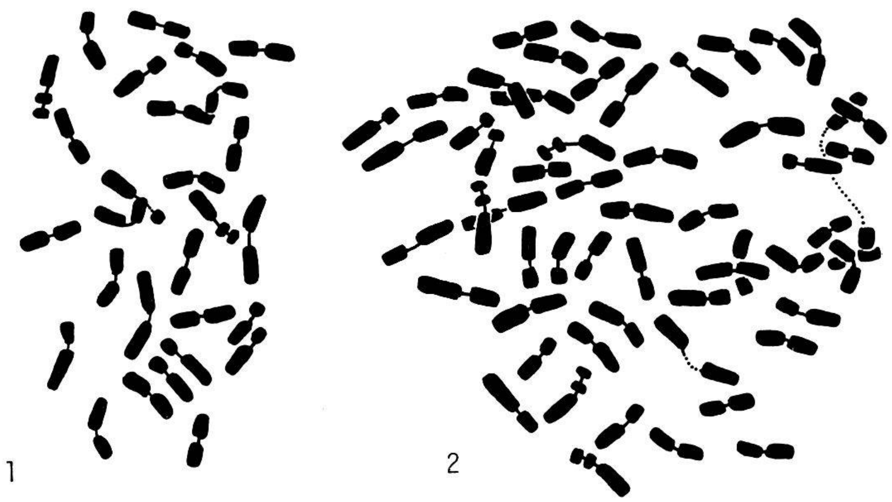
# 3. Results

## 3.1. *Chromosome numbers*

### 3.1.1. *Antennaria pulcherrima* 2n=28 (Figs 1-2)

*A. pulcherrima* studied in the course of the present investigations, originated mostly from Alaska, Yukon Territory, British Columbia and Alberta, only two populations being found much farther south i.e. in Wyoming and S Colorado, respectively (Fig. 3, Tables 1, 2). Altogether 317 individuals corresponding to 34 population samples were studied.

All the 288 plants examined from the northern part of the range of *A. pulcherrima* proved to be octoploid with the somatic chromosome number 2n=8x=56 (Figs 2, 3, 10, Table 1). On the other hand, 14 individuals from Wyoming and 5 plants from S Colorado were invariably tetraploid (2n=4x=28, Figs 1, 3, 10, Tables 1, 2).




Figs 1-2. *Antennaria pulcherrima*: somatic metaphases. Sample code is given in parentheses. 1. Wyoming (RM 13): 2n=28. 2. Alaska (AL 4): 2n=56. c. 1500x.

*A. pulcherrima: Somatische Metaphasen. (In Klammern steht die Abkürzung für die Fundorte). 1. Wyoming (RM 13): 2n=28. 2. Alaska (AL 4): 2n=56. ca. 1500x.*

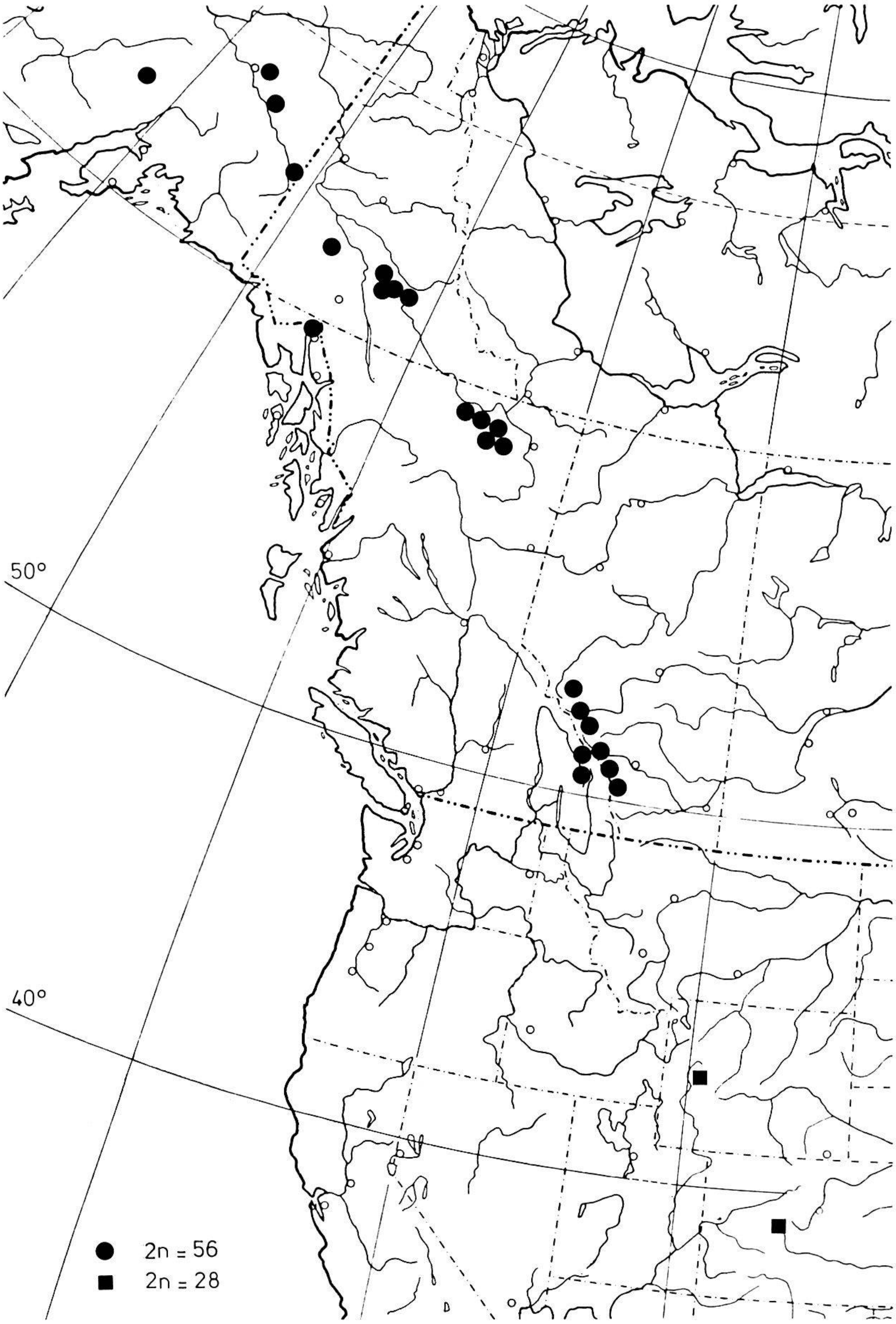



Fig. 3. *Antennaria pulcherrima*: geographical distribution of the studied material. Each dot may represent several sites.

*A. pulcherrima: Herkunft des Untersuchungsmaterials (Jeder Punkt kann mehrere Fundorte umfassen).*

Chromosome numbers in *Antennaria pulcherrima* from Central and Northwest Pacific Range have not been studied hitherto. A previous report by LöVE and LöVE (in LöVE and SOLBRIG 1964) presenting a hexaploid chromosome number 2n=63 in *A. pulcherrima* from Yoho Valley, British Columbia, was based on an erroneous determination of the material (Dr. A. LöVE, personal communication). Another report by LöVE and LöVE (in LöVE 1982) dealing with a single dodecaploid (2n=84) individual of *A. pulcherrima* from Manitoba remains to be verified.

### 3.1.2. *Antennaria anaphaloides* 2n=28 (Fig. 4)

Chromosome number of *A. anaphaloides* was studied in 19 samples from British Columbia, Idaho, Montana (the type locality), Wyoming and Colorado (Fig. 5, Tables 1, 3). The 126 examined plants were invariably tetraploid (2n=4x=28, Fig. 4). The present results confirm a previous report by the author based on materials from three sites in Colorado (URBANSKA 1974). No other data on chromosome number in *A. anaphaloides* were published to date.

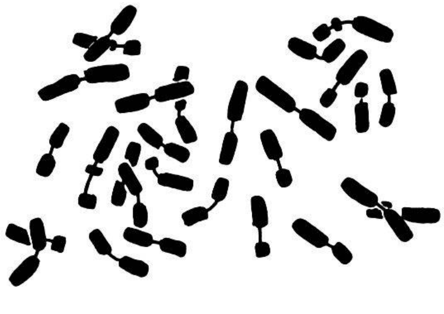


Fig. 4. *Antennaria anaphaloides*: somatic metaphase. Sample code is given in parentheses. Wyoming (RM 29): 2n=28. c. 1500x.

*A. anaphaloides: somatische Metaphase. (In Klammern steht die Abkürzung für den Fundort). Wyoming (RM 29): 2n=28. ca. 1500x.*

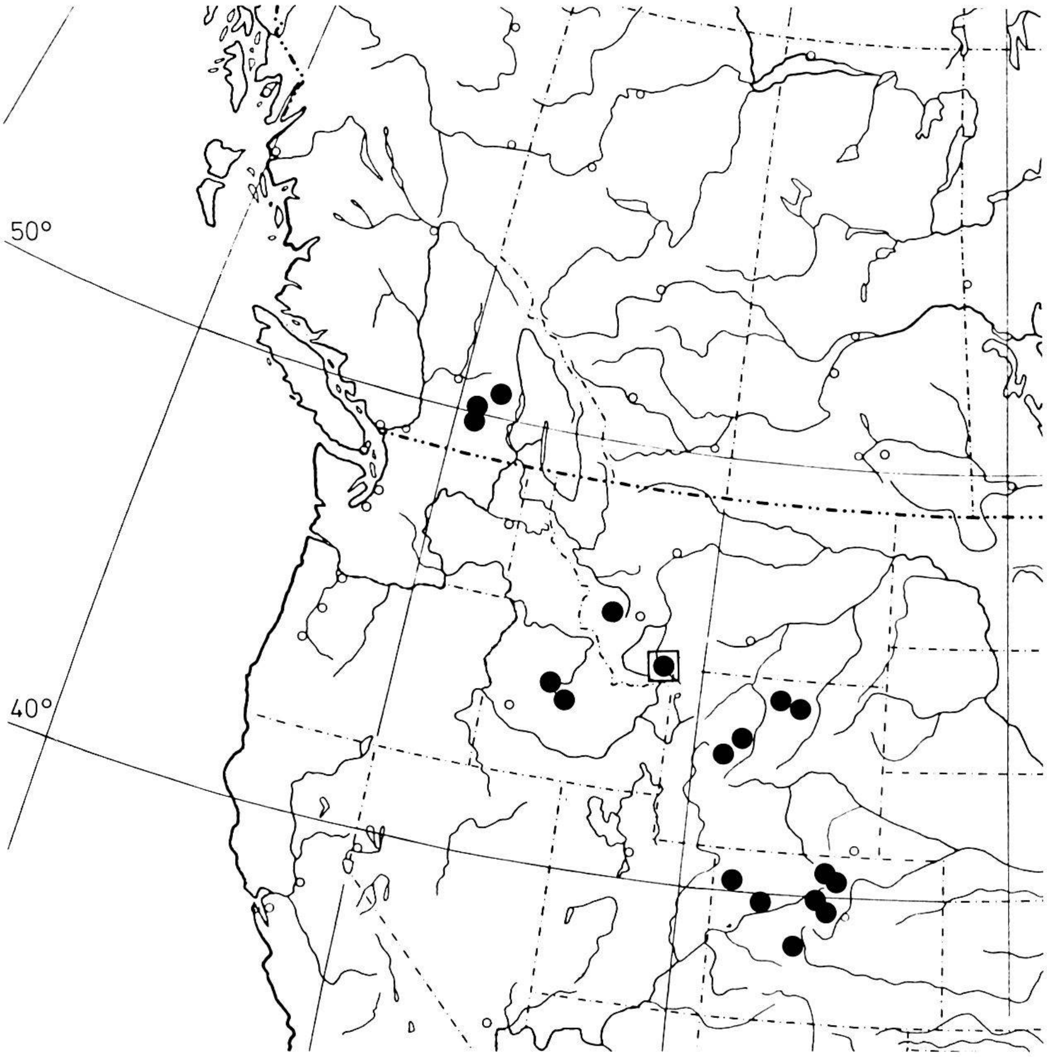



Fig. 5. *A. anaphaloides*: distribution of the studied material. Framed dot refers to the type locality. Each dot may represent several sites.

*A. anaphaloides: Herkunft des Untersuchungsmaterials. Der eingerahmte Punkt bezeichnet den Typus-Ort. (Jeder Punkt kann mehrere Fundorte umfassen).*

### 3.1.3. *Antennaria lanata* 2n=28 (Fig. 6)

*A. lanata* was studied from 54 sites distributed in various parts of the total range of the taxon (Fig. 6, Tables 1, 4). The ample material examined consisted of 385 individuals that were uniformly tetraploid (2n=4x=28, Fig. 7, Table 1).

The chromosome number of *A. lanata* is given here for the first time.

Fig. 6. *Antennaria lanata*: somatic metaphase. Sample code is given in parentheses. Wyoming (RM 19): 2n=28. c. 1500x.

*A. lanata: somatische Metaphase. (In Klammern steht die Abkürzung für den Fundort). Wyoming (RM 19): 2n=28. ca. 1500x.*

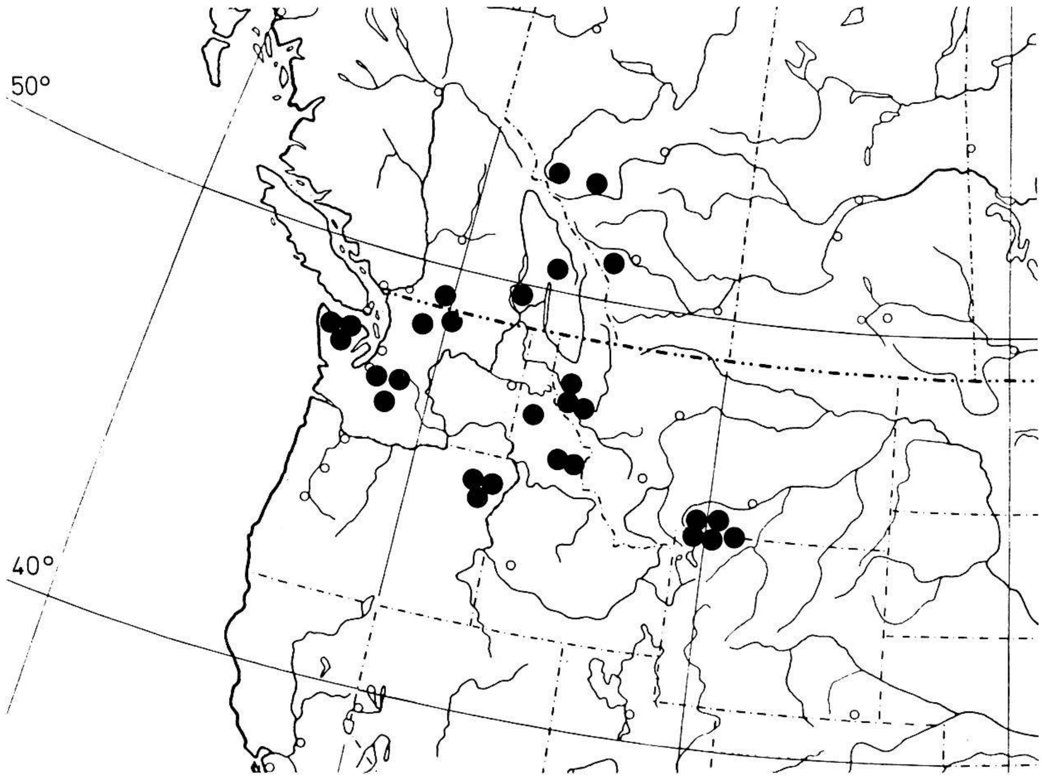



Fig. 7. *A. lanata*: geographical distribution of the studied material. Each dot may represent several sites.

*A. lanata: Herkunft des Untersuchungsmaterials (Jeder Punkt kann mehrere Fundorte umfassen).*

3.1.4. *Antennaria eucosma* 2n=56 (Fig. 8)

*A. eucosma* was studied from five localities in Newfoundland, including the type locality at Table Mtn. (Fig. 9). The material examined comprised 41 individuals; all of them were octoploid (2n=8x=56, Fig. 8, Table 1).

*A. eucosma* has not been cytologically studied hitherto.

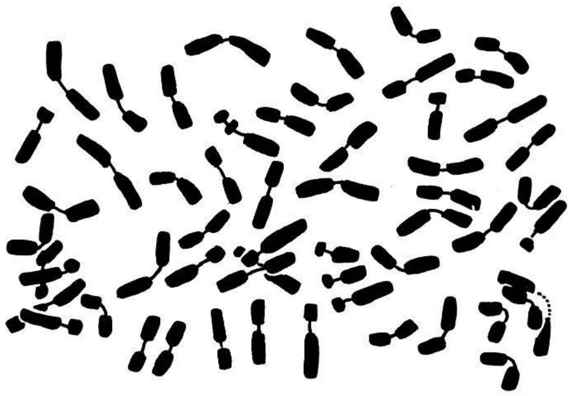


Fig. 8. *Antennaria eucosma*: somatic metaphase. Sample code is given in parentheses. Newfoundland (NF 5, the type locality): 2n=56. c. 1500x.

*A. eucosma: somatische Metaphase. (In Klammern steht die Abkürzung für den Fundort). Neufundland (NF 5, Typus-Ort): 2n=56. ca. 1500x.*

The present study reveals an interesting pattern of karyological differentiation within the *Antennaria carpatica* group in North America (Table 1, Fig. 10). The two levels of polyploidy recognized within the group correspond, on the one hand, to an interspecific differentiation; on the other hand, intraspecific differentiation in *A. pulcherrima* seems to stay in some relation to the geographical distribution of the taxon, the South-North gradient being rather distinct (Table 1, Figs 2, 10).

Table 1. Chromosome numbers observed within *Antennaria carpatica* s.l. in North America

*Chromosomenzahlen von A. carpatica s.l., die in Nordamerika beobachtet wurden*

| Taxon | 2n | Polyploidy level | Origin of the studied material |
|---|---|---|---|
| *A. pulcherrima* | 56 | 8x | Alaska, Yukon Territory, British Columbia, Alberta |
| | 28 | 4x | Wyoming, Colorado |
| *A. anaphaloides* | 28 | 4x | British Columbia, Washington, Idaho, Montana, Colorado |
| *A. lanata* | 28 | 4x | Olympic Mts, N Cascades, Blue Mts, Rocky Mts (British Columbia, Alberta, Idaho, Montana/Wyoming) |
| *A. eucosma* | 56 | 8x | Newfoundland |

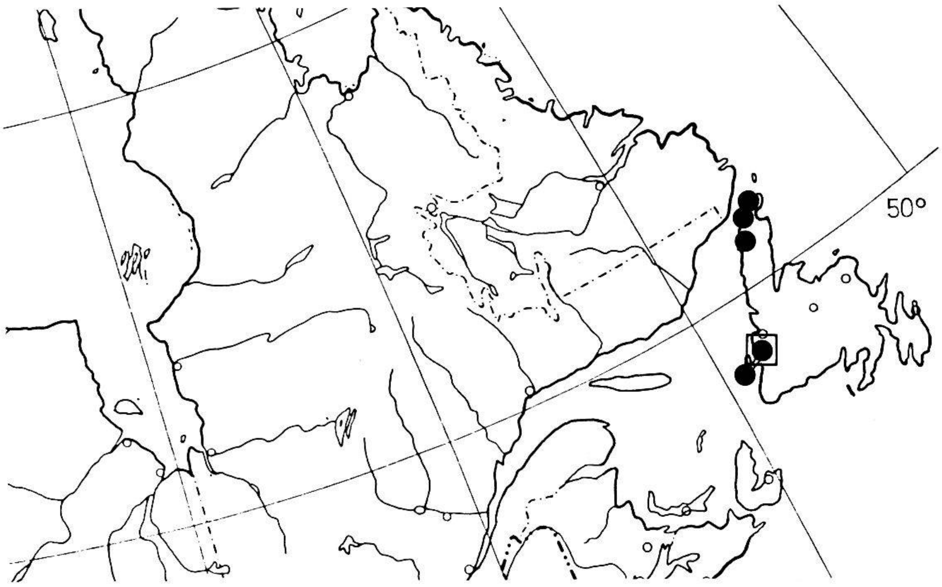
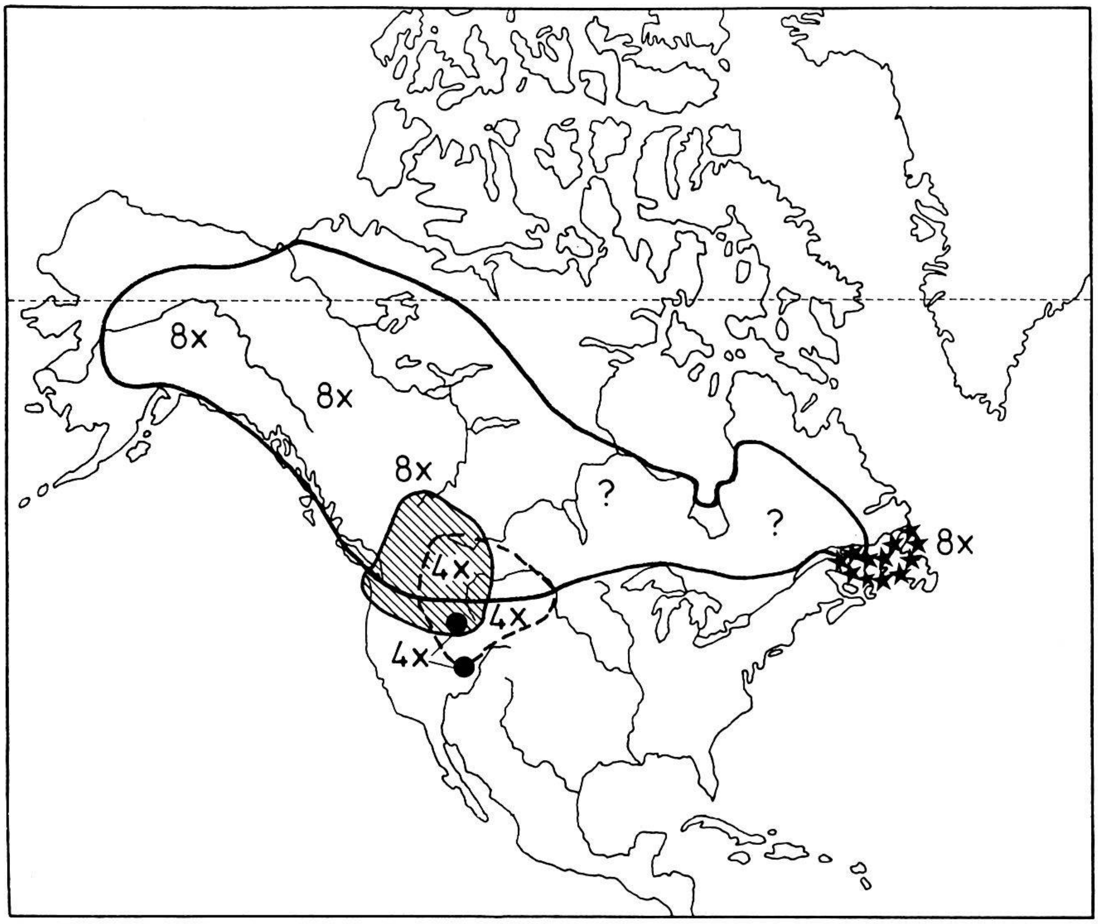



Fig. 9. *A. eucosma*: distribution of the studied material in Newfoundland. Framed dot refers to the type locality.

*A. eucosma: Herkunft des Untersuchungsmaterials in Neufundland. Der eingerahmte Punkt bezeichnet den Typus-Ort.*

### 3.2. *Geographical distribution*

A global distribution area of the *Antennaria carpatica* group in North America is very large and comprises a considerable part of Canada as well as some parts of the United States in Central and Pacific Northwest Range (Fig. 10). It should be noted, however, that particular taxa of the group greatly differ from one another both as to the actual area size as well as patterns of occurrence within a given area.




| | | | |
|---|---|---|---|
| ——— | *Antennaria pulcherrima* | ★★★ | *Antennaria eucosma* |
| - - - - | *Antennaria anaphaloides* | ● | *tetraploid A. pulcherrima* |
| ▧ | *Antennaria lanata* | | |

Fig. 10. General patterns of geographical distribution of *A. carpatica* group in North America.

*Allgemeines Verbreitungsmuster der A. carpatica-Gruppe in Nordamerika.*

*Antennaria pulcherrima*. - Of all the North American *Carpaticae*, *A. pulcherrima* has by far the largest total area of distribution (Fig. 10). It can be characterized as a high-subarctic/temperate transcontinental type (for the terminology, see SCOGGAN 1978). *A. pulcherrima* ranges from Alaska north to the Arctic Coast in the region of the Mackenzie River Delta, east through Northwest Territories, central and N Saskatchevan, N Manitoba, N Ontario to N Quebec and northern coast of the Gulf of St. Lawrence; it was also reported from few stations in Anticosti Island. As far as the gradient North-South is concerned, *A. pulcherrima* ranges from Alaska through Yukon Territory, British Columbia and Alberta to N Washington, Idaho, Montana and Colorado. The distribution of *A. pulcherrima* being generally discontinuous, it is not quite clear at the time being whether the stations corresponding to the southernmost range of the taxon are still situated within the main area or, in fact, stay outside it.

A rather distinct difference in appearance of populations was noted between boreal/subarctic vs temperate areas. Northern populations of *A. pulcherrima* frequently were large, widespread and sometimes fairly concentrated within a given local area (e.g. Pelly Mts in Yukon, Muncho Lake in British Columbia or Banff National Park in Alberta). Southern populations, on the contrary, were apparently rare and small (e.g. the site RM 13 at Warm Spring Creek, Wind River Range, Wyoming). Further studies within the whole distribution area of *A. pulcherrima* are required for a better understanding of the intriguing pattern observed in the course of the present study.

*Antennaria anaphaloides* has a temperate western distribution (Fig. 10). Its general area is much smaller than that of *A. pulcherrima*; it ranges from SW British Columbia and Alberta south to Wyoming and Colorado and west to Nevada and Oregon. Populations of *A. anaphaloides* are usually small or medium-large at their best, particular individuals being most frequently scattered within a given site. The only more conspicuous stands of *A. anaphaloides* were observed by the author within the uppermost subalpine vegetation belt in Colorado, where *A. anaphaloides* occurs as the sole representative of the *Carpaticae* at higher altitude (e.g. the site RM 33 in vicinity of Cumberland Pass on the Continental Divide, about 3400 m a.s.l.).

*Antennaria lanata* also has a general distribution of a temperate western type (Fig. 10). The area of this subalpine/alpine taxon seems, on the whole, to be rather well-defined: it ranges from Olympic Mts through N Cascades to Rocky Mts. *A. lanata* reaches from British Columbia and Alberta south to Washington and NE Oregon; it is very well represented in Idaho and Montana. Southern limits of occurrence of *A. lanata* correspond to the Beartooth Plateau at the border of Montana and Wyoming. It is interesting to note that *A. lanata* occurs very abundantly within the Plateau and its surroundings but is not seen anymore farther south.

Compared to the total area of the *Carpaticae* in North America, the area of *A. lanata* is rather small; however, populations of this taxon occur rather frequently throughout the area and often are not only wide-spread but exceedingly dense, a great many individuals occurring within given sites and frequently dominating their general aspect (Fig. 15).

*Antennaria eucosma* has a distribution area approaching a low-subarctic eastern type (Fig. 10). The taxon seems to be confined to Newfoundland as well as few sites in Anticosti Island. Except for the large population occurring at Table Mtn. (the type locality) and a medium-large colony at Big Brook in northern Newfoundland, populations of *A. eucosma* are exceedingly small. The precise situation in Anticosti Island is not known, but the limited occurrence of *A. eucosma* seems in general to be reflected not only in its limited area of distribution and the actual number of populations, but also in the total number of individuals.

## 3.3. *Ecology*

Precise ecological requirements of North American *Carpaticae* are not yet fully assessed, but the data gathered so far suggest some trends in ecological differentiation of particular taxa.

### 3.3.1. *Antennaria pulcherrima*

*A. pulcherrima* mostly occurs within montane and subalpine vegetation belt, stations above timberline being infrequent and confined to high mountain areas sometimes influenced by the proximity of glaciers (e.g. Columbia Icefields). It is interesting to note that the taxon was reported from a broad altitude range in Mackenzie District of Northwest Territories (900-2100 m a.s.l., specimens collected by JOHNSON and MUNRO in 1962, presently at Vascular Plant Herbarium, Biosystematic Research Institute, Ottawa).

*A. pulcherrima* seems to have a distinct preference for well-watered, mostly fine-textured, alluvial soils often subject to intermittent flooding (Table 2). Its representative niche apparently corresponds to river flats or stream/river banks; the taxon frequently occurs in willow shrub thickets. A striking affinity in ecological requirements observed in stations of *A. pulcherrima* so far apart as Yukon Territory and Wyoming (Figs 11-12) and inhabited by populations representing two different levels of polyploidy viz. 8x and 4x is of particular interest. Further studies in sites of *A. pulcherrima* in Central and S Rocky Mts as well as eastern part of its range should be most interesting.

Some authors (e.g. PORSILD 1943) considered *A. pulcherrima* as restricted to calcareous soils. It seems, however, that soil moisture level has a commanding influence on patterns of occurrence of the taxon and the soil parent material might represent a collateral factor. Some aspects of reproductive strategy of *A. pulcherrima* are in favour of this assumption (URBANSKA, in preparation).

*A. pulcherrima* occasionally occurs in well-developed soils with rather dense vegetation cover. It seems possible that the taxon may well respond to a higher nutrient content of the soil, but is not sufficiently competitive to establish itself successfully in numerous sites of that type.

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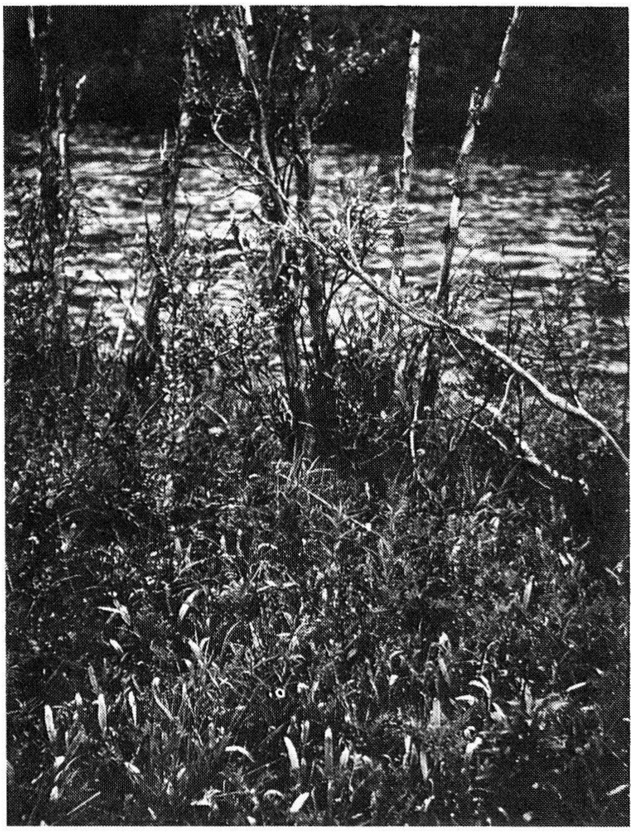
*Abb. 11-12. Typische Standorte von A. pulcherrima. 11. Yukon Territory: Alluvialflächen des Rose River (YU 3). 12. Wyoming, Fremont Co., Wind River Range: Sandbank der Warm Springs Creek (RM 13). A. pulcherrima wächst im Vordergrund und in den Weidenbüschen.*



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Figs 11-12. Representative sites of *A. pulcherrima*. 11. Yukon Territory: alluvial flats of Rose River (YU 3). 12. Wyoming, Fremont Co., Wind River Range: sandy bank of Warm Springs Creek (RM 13). *A. pulcherrima* in foreground as well as in willow shrub thickets. Author's photos, 14 Aug. 1980 and 14 Aug. 1978, respectively.

Table 2. Collection sites of *Antennaria pulcherrima*

*Fundorte von A. pulcherrima*

| Sample code | Site description | Date |
|---|---|---|
| AL 1 | Alaska, Northway Road: willow shrub thicket at the roadside. Also in the neighbouring burnt spruce forest. Mossy alluvial soil. | 30 Jul. 1980 |
| AL 2 | Alaska, Mt. MacKinley National Park: Wonder Lake, moist lake shore at N end of the lake. about 630 m a.s.l. | 1 Aug. 1980 |
| AL 3 | Alaska, Tenana River at Big Delta: among *Equisetum arvense* along the road and in the neighbouring alder thicket. Moist silty soil. | 2 Aug. 1980 |
| AL 4 | Alaska: in a muskeg, about 16 km E of Fairbanks. | 4 Aug. 1980 |
| NT 1 | Alaska, North Tongass National Forest: wet alluvial soil at the Haines airport. | 28 Jul. 1980 |
| YU 1 | Yukon Territory: Pelly Mts.: W bank of Nisutlin River, on wet alluvial soil in a willow shrub thicket. 916 m a.s.l. | 12 Aug. 1980 |
| YU 2 | Yukon Territory, Pelly Mts.: Canol Road Mile 90, in moist gravel at the roadside and also among willow shrubs. About 1330 m a.s.l. | 13 Aug. 1980 |
| YU 3 | Yukon Territory, Pelly Mts.: Canol Road Mile 94, alluvial flats of Rose River, among willow shrubs. About 1330 m a.s.l. | 14 Aug. 1980 |
| YU 4 | Yukon Territory, Boulder Creek: disturbed rocky stream bed. Locally in shallow pockets of fine-textured alluvial soil. About 1350 m a.s.l. | 15 Aug. 1980 |
| YU 5 | Yukon Territory, about 2 km of Boulder Creek: alluvial flats of Lapie River. | 15 Aug. 1980 |
| YU 6 | Yukon Territory, about 8 km of Boulder Creek: in very wet gravel off the road. | 15 Aug. 1980 |
| SWY | Yukon Territory: Mile 1148 Alaska Highway, about 1.6 km W of Edith Creek. In a willow shrub thicket, on mossy soil. | 29 Jul. 1980 |
| BC 1 | British Columbia, Muncho Lake Provincial Park: Mile 1148 of Alaska Highway, in willow shrubs. | 17 Aug. 1980 |
| BC 2 | British Columbia, Muncho Lake Provincial Park: E shore of the lake, in willow shrub dominated vegetation on moist gravelly soil. | 17 Aug. 1980 |
| BC 3 | British Columbia, Muncho Lake Provincial Park: E slope with scattered willow shrubs. Rather dry soil with patches of loose gravel. | 17 Aug. 1980 |

Table 2. (continued - *Forts.)*

| Sample code | Site description | Date |
|---|---|---|
| BC 4 | British Columbia, Alaska Highway Mile 401.5: flat surface with scattered willow shrubs and a spruce forest in background. Moist gravelly soil. | 18 Aug. 1980 |
| BC 5 | British Columbia, road to Summit Pass within the Stone Mtn. Provincial Park: between hummocks and willow shrubs, on moist soil. About 1350 m a.s.l. | 18 Aug. 1980 |
| BC 6 | British Columbia: road descending from Summit Pass to Tetsa River. Among willow shrubs on a moist gravel. | 18 Aug. 1980 |
| BC 7 | British Columbia, Yoho National Park: Takkawa Falls: silty flats with willow shrubs, partly also between spruce trees. About 1570 m a.s.l. | 24 Aug. 1980 |
| BC 8 | British Columbia, Yoho National Park: established bar along Kicking Horse River. Locally dense willow thicket, moist gravelly/silty soil. About 1230 m a.s.l. | 24 Aug. 1980 |
| ALB 1 | Alberta, Jasper National Park: moist sandy meadow just on the left bank of Athabasca River, about 5 km W of Jasper. Some willow shrubs. | 21 Aug. 1980 |
| ALB 2 | Alberta, Jasper National Park: left bank of Alabasca River, between willow shrubs and spruces. Moist alluvial soil. | 21 Aug. 1980 |
| ALB 3 | Alberta, road to Pocahontas: moist meadow on fine alluvial soil. Disturbed vegetation. | 21 Aug. 1980 |
| ALB 5 | Alberta, about 8 km N of the Jasper National Park entrance. Moist, exceptionally well-developed, fine textured forest soil. Dense vegetation off the road. | 23 Aug. 1980 |
| ALB 6 | Alberta, Jasper National Park: Flats of Athabasca River about 10 km W of Athabasca Falls. Among willow shrubs and saplings on silty soil. | 23 Aug. 1980 |
| ALB 7 | Alberta, Jasper National Park: on a stream bank about 12 km E of junction between Rd 93 and 93a in the park. Moist openings in willow shrub thicket. | 23 Aug. 1980 |
| ALB 7a | Alberta, Jasper National Park: about 10 km E of site ALB 7: in openings of spruce forest, moist alluvial soil. | 23 Aug. 1980 |
| ALB 8 | Alberta, Columbia Icefields: moist rocky slope at the roadside. About 2330 m a.s.l. | 23 Aug. 1980 |
| ALB 9 | Alberta, Banff National Park: silty river bank at the valley bottom. | 23 Aug. 1980 |

Table 2. (continued - *Forts.)*

| Sample code | Site description | Date |
|---|---|---|
| ALB 10 | Alberta, Banff National Park: river flats and the neighbouring willow shrub thicket. Moist sandy/ silty soil. | 24 Aug. 1980 |
| RM 13 | Wyoming, Fremont Co. Wind River Range: moist sandy bank of Warm Springs Creek. About 2800 m a.s.l. | 14 Aug. 1978 |
| RM 34 | Colorado, Gunnison Co.: by East River, between Cothic and Crested Butte. Moist stream bank, partly among willow shrubs. | 25 Aug. 1978 |

### 3.3.2. *Antennaria anaphaloides*

*Antennaria anaphaloides* occurs, in general, within a very wide altitude bracket ranging from plains and foothills zones to about timberline. However the occurrence of the taxon in particular vegetation belts seems to be partly related to the actual latitude of given areas. In SW British Columbia and Alberta, *A. anaphaloides* mostly occurs in grassland and open dry woods, whereas farther south it is frequently observable at higher elevations. For instance in Colorado, *A. anaphaloides* was reported from about timberline (e.g. near Cumberland Pass, 3400 m a.s.l.). Nothwistanding the altitude differences, *A. anaphaloides* shows a preference for open and sunny sites with loose, permeable soils. Sites of the taxon are frequently characterized by the occurrence of sagebrush (Fig. 13), the scattered individuals of *A. anaphaloides* being often observed in shelter of the shrub. Interestingly enough, the most densely populated stands of *A. anaphaloides* were observed by the author at highest altitudes reached by the taxon in S Colorado (Fig. 14). *A. anaphaloides* is apparently well-adapted to a prolonged period of dryness, as indicated by its reproductive strategy (URBANSKA, in preparation).

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*Abb. 13-14. Typische Standorte von A. anaphaloides. 13. Idaho, Custer Co., Lost River Range, Double Spring Pass: Trockener offener Hang mit vereinzelten Artemisia-Büschen (RM 11). 14. Colorado, Gunnison Co.: sonniger, steiniger, südexponierter Hang in der Nähe des Cumberland Passes (RM 33)*

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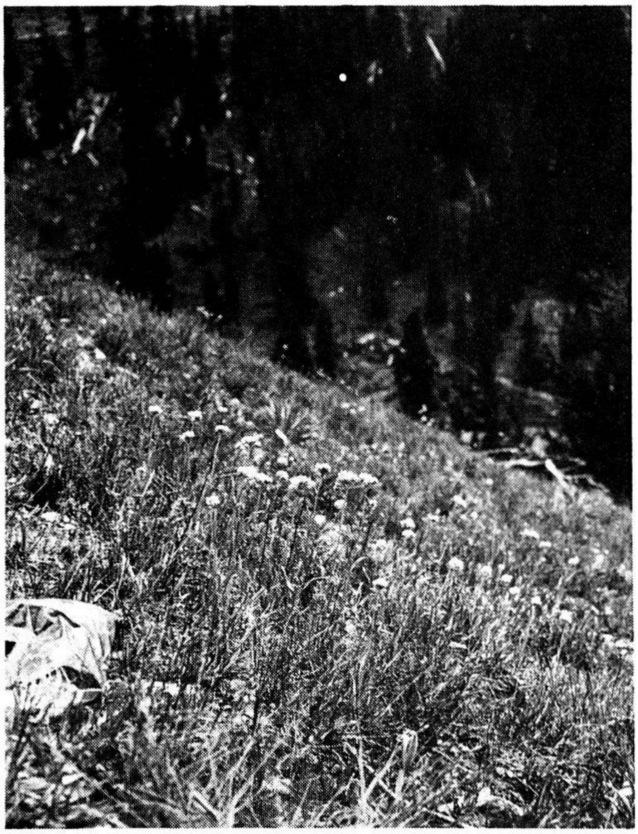

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Figs 13-14. Representative sites of *A. anaphaloides*. 13. Idaho, Custer Co. Lost River Range, Double Spring Pass: dry open hillside with scattered sagebrush (RM 11). 14. Colorado, Gunnison Co.: sunny SW-facing steep slope near Cumberland Pass (RM 33). About 3400 m a.s.l. Author's photos, 12 Aug. and 28 Aug. 1978, respectively.

Table 3. Collection sites of *Antennaria anaphaloides*

*Fundorte von A. anaphaloides*

| Sample code | Site description | Date |
|---|---|---|
| RM 11 | Idaho, Custer Co., Lost River Range, Double Spring Pass: dry open hillside with scattered sagebrush. | 12 Aug. 1978 |
| RM 12 | Idaho, Custer Co., Lost River Range, descent from Double Spring Pass towards Chilly: hillside with scattered sagebrush, very dry sandy soil. | 12 Aug. 1978 |
| LA 3 | Montana, Granite Co., Anaconda-Pintlar Range: on grassy ridge, 2190 m a.s.l. | 8 Aug. 1980 |
| RM 14 | Montana, Gallatin Co.:Spanish Basin, dry hilltop with scattered few poplar and spruce trees. Very abundant sagebrush. Loose, gravelly/sandy soil. | 19 Aug. 1978 |
| RM 28 | Wyoming, Big Horn Co. road to Granite Pass: sagebrush hill near Granite Creek. Dry, sandy soil. About 2550 m a.s.l. | 19 Aug. 1978 |
| RM 29 | Wyoming, Big Horn Co. Burgess Junction: flat pasture on dry, gravelly soil. About 2410 m a.s.l. | 19 Aug. 1978 |
| RM 30 | Wyoming, Fremont Co. Owl Range: Birdseye Mtn. Just about the summit. 2220 m a.s.l. | 20 Aug. 1978 |
| RM 31 | Wyoming, Fremont Co. Wind River Range, road to Moccasin Lake. Mountain meadow with scattered sagebrush on dry gravelly soil. About 2970 m a.s.l. | 21 Aug. 1978 |
| RM 32 | Colorado, Garfield Co. White River Plateau: dry meadow near Deep Creek lookout. About 2700 m a.s.l. | 24 Aug. 1978 |
| CO 4 | Colorado, Moffat Co. Dinosaur National Monument: Roundtop Mtn., near fire lookout on N slope. Rocky sandstone and limestone, very steep slope. 2800 m a.s.l. | 12 Aug. 1973 |
| CO 1 | Colorado, Gilpin Co. Rolling Pass, W slope. Alpine vegetation on dry, rocky soil. About 3400 m a.s.l. | 5 Aug. 1973 |
| CO 2 | Colorado, Gilpin Co. in the valley near Tolland: dry hill. About 2700 m a.s.l. | 5 Aug. 1973 |
| CO 3 | Colorado, Larimer Co., about 11 km E of Aspen Lodge. Dry grassland on sandy soil. About 2400 m a.s.l. | 5 Aug. 1973 |
| RM 33 | Colorado, Gunnison Co.: open steep slope at timberline near Cumberland Pass. Dry gravelly soil. About 3400 m a.s.l. | 28 Aug. 1978 |

Table 3. (continued - *Forts.*)

| Sample Code | Site description | Date |
|---|---|---|
| BC 10 | British Columbia, Douglas Lake Road: in open dry pine woods. About 750 m a.s.l. | 26 Aug. 1980 |
| BC 11 | British Columbia, Crow Range, about 19 km N of Aspen Grove: open dry aspen-conifer forest. About 690 m a.s.l. | 26 Aug. 1980 |
| BC 12 | British Columbia, Aspen Grove, on the road to Princeton: open aspen wood on dry soil. | 26 Aug. 1980 |
| BC 13 | British Columbia, about 8 km S of Aspen Grove: open, dry aspen-conifer forest. | 26 Aug. 1980 |
| BC 14 | British Columbia, about 5 km farther south from BC 13: grassy vegetation at the edge of aspen-conifer forest. | 26 Aug. 1980 |

*A. anaphaloides* was sometimes observed in coniferous forests within the subalpine vegetation belt. Those stations are of a particular interest in view of a possible contact of *A. anaphaloides* with *A. lanata*. During the whole field work, the present author has seen only once the two taxa in the same site and it was just an open coniferous forest in N Washington (Table 4, sample code NC 6).

According to some herbarium data, *A. anaphaloides* is also supposed to occur occasionally in moist, shady sites that seem to be representative of *A. pulcherrima*. Such places should be given a particular attention in further investigations.

As far as the type of substratum is concerned, precise requirements of *A. anaphaloides* were not yet fully assessed. No marked preferences were revealed so far, but the problem should be investigated in detail.

### 3.3.3. *Antennaria lanata*

*A. lanata* occurs in subalpine and alpine vegetation belt. Corresponding to differences in climatic conditions occurring between various parts of Olympic Mts., N Cascades and Rocky Mts., the whole altitude bracket of *A. lanata* is large ranging approximately from 1440 m a.s.l. (e.g. sites at

Mt. Adams, Washington) to about 3000 m a.s.l. (summit of Clay Butte, Beartooth Range, Montana/Wyoming).

*A. lanata* usually avoids the most extreme, wind-exposed places. It was frequently observed in rocky ledges as well as some protected scree slopes, but populations of the taxon are there usually small and fairly localized. The representative sites of *A. lanata* correspond to open coniferous forests about the timberline as well as mountain meadows (Fig. 15) and early snowbanks. The taxon apparently has its ecological optimum in gravelly or sandy loam soils that are snow-covered in winter and moderately- to rather well-drained in summer. Our field observations suggest that a protection from temperature fluctuations as well as a sufficient amount of soil moisture are particularly important to *A. lanata* early in season, during initial and pre-reproductive life phases. The subsequent flowering and seed-setting do not seem to be greatly affected by a rather low moisture regime.

Fig. 15. A representative site of *A. lanata*. Washington, Clallam Co., Olympic Mts. National Park, Hurricane Drive (MO 3). Large meadow merging with an early snowbank. Very abundant *A. lanata* in foreground. Author's photo, 28 Jul. 1978.

*Typischer Standort von A. lanata. Washington, Clallam Co., Olympic Mts. National Park, Hurricane Drive (MO 3). Wiese mit relativ früh ausaperndem Schneetälchen. A. lanata sehr häufig im Vordergrund.*

Table 4. Collection sites of *Antennaria lanata*

*Fundorte von A. lanata*

| Sample code | Site description | Date |
|---|---|---|
| OG 1 | Alberta, Jasper National Park: Wilcox Pass area, moist meadow at N end of Nigel Lake. 2250 m a.s.l. | 8 Jun. 1974 |
| ALB 4 | Alberta, Jasper National Park: Signal Mtn., NE slope, timberline meadow. About 2100 m a.s.l. | 22 Aug. 1980 |
| OG 2 | Alberta: Kananaskis Valley, Marmot Creek: small meadow within the timberline forest. 2250 m a.s.l. | 13 Aug. 1974 |
| BC 9 | British Columbia, Mt. Revelstoke: large meadow about timberline. *A. lanata* very abundant. About 1900 m a.s.l. | 25 Aug. 1980 |
| BC 15 | British Columbia, Apex Mts.: open slope at timberline. About 2000 m a.s.l. | 26 Aug. 1980 |
| NC 3 | Washington, Okanogan Co.: Slate Peak, on a small open ridge about 60 m from the summit. About 2000 m a.s.l. | 30 Jul. 1978 |
| NC 4 | Washington, Okanogan Co.: descent from Slate Peak towards Harts Pass. Large moist depression on SW-facing slope. About 1900 m a.s.l. | 30 Jul. 1978 |
| NC 5 | Washington, Okanogan Co.: Harts Pass, in open coniferous forest. About 1860 m a.s.l. | 30 Jul. 1978 |
| NC 6 | Washington, Okanogan Co.: Tiffany Mtn., Freezout Ridge: in open coniferous forest. About 1950 m a.s.l.* | 30 Jul. 1978 |
| NC 7 | Washington, Okanogan Co., Freezout Ridge: large openings in coniferous forest. Very abundant. About 2000 m a.s.l. | 30 Jul. 1978 |
| NC 1 | Washington, Skagit Co.: Sahale Arm above Cascade Pass: half-open alpine vegetation on a dry ridge. | 29 Jul. 1978 |
| NC 2 | Washington, Skagit Co.: Cascade Pass: small, *Carex nigricans*-dominated depression. | 29 Jul. 1978 |
| NC 10 | Washington, Pierce Co. Mt. Rainier National Park: Glacier Vista SW-facing ridge, in an early snow-bank. About 1800 m a.s.l. | 1 Aug. 1978 |
| NC 11 | Washington, Pierce Co., Mt. Rainier National Park: Paradise Park. About 1650 m a.s.l. | 1 Aug. 1978 |
| NC 12 | Washington, Pierce Co., Mt. Rainier National Park: Clover Lake, moist lake side. About 1500 m a.s.l. | 1 Aug. 1978 |

* the only site where *A. lanata* and *A. anaphaloides* were observed close to each other

Table 4 (continued - *Forts.*)

| Sample code | Site description | Date |
|---|---|---|
| N 13 | Washington, Pierce Co., Mt. Rainier National Park: Sunrise Ridge, under coniferous trees at the top of the ridge. | 1 Aug. 1978 |
| NC 14 | Washington, Pierce Co., Mt. Rainier National Park: Berkeley Park, open alpine slope. About 1950 m a.s.l. | 1 Aug. 1978 |
| MA 2 | Washington, Yakima Co.: Hellroaring Meadow, E slope of Mt. Adams. Subalpine meadow, about 1800 m a.s.l. | 15 Sept.1976 |
| NC 15 | Washington, Yakima Co.: Mt. Aix, krummholz zone, NW-facing steep slope. About 1900 m a.s.l. | 2 Aug. 1978 |
| MO 1 | Washington, Clallam Co., Olympic Mts. National Park: Elk Mtn., early snowbed. 2030 m a.s.l. | 28 Jul. 1978 |
| MO 2 | Washington, Clallam Co., Olympic Mts. National Park: descent from Elk Mtn. towards Obstruction Point: WSW-facing slope. | 28 Jul. 1978 |
| MO 3 | Washington, Clallam Co., Olympic Mts. National Park: subalpine meadow merging with early snow-bank. Very abundant. | 28 Jul. 1978 |
| MO 4 | Washington, Clallam Co., Olympic Mts. National Park: Hurricane Drive, early snowbank. | 28 Jul. 1978 |
| BM | Oregon, Wallowa Co., Blue Mts., Eagle Cap Wilderness: Mirror Lake, among rocky ledges near the lake. About 2250 m a.s.l. | 5 Aug. 1978 |
| BM 2 | Oregon, Wallowa Co., Blue Mts., Eagle Cap Wilderness: in open coniferous forest. About 1900 m a.s.l. | 5 Aug. 1978 |
| BM 3 | Oregon, Wallowa Co., Blue Mts., Eagle Cap Wilderness: subalpine meadow along the path from Two Pan Campground to Eagle Cap Basin. About 1700 m a.s.l. | 5 Aug. 1978 |
| RM 1 | Idaho, Benewah Co., Freezeout Mtn.: small SE-exposed ridge at timberline. About 1800 m a.s.l. | 4 Aug. 1978 |
| RM 2 | Idaho, Benewah Co., Long Hike Peak: large meadow below timberline on SE-facing slope. Very abundant. About 1900 m a.s.l. | 4 Aug. 1978 |
| RM 3 | Idaho, Idaho Co., Wildhorse Lake: open coniferous forest about the lake. 2400 m a.s.l. | 7 Aug. 1978 |
| RM 4 | Idaho, Idaho Co., Orogrande summit. Among rocks on rather dry soil. About 2300 m a.s.l. | 7 Aug. 1978 |
| RM 8 | Idaho, Lemhi Co., Salmon Mtn., N slope: open coniferous forest. About 1800 m a.s.l. | 11 Aug. 1978 |

Table 4 (continued - *Forts.*)

| Sample code | Site description | Date |
|---|---|---|
| RM 9 | Idaho, Lemhi Co.: Ajax Mtn., openings in coniferous forest. About 2000 m a.s.l. | 11 Aug. 1978 |
| RM 10 | Idaho, Lemhi Co., Ajax Mtn.: below site RM 9, in open coniferous forest. About 1700 m a.s.l. | 11 Aug. 1978 |
| LA 1 | Montana, Ravalli Co., Johnson Peak, Anaconda-Pintlar Range. | 18 Sept.1974 |
| MA 1 | Montana, Rivalli Co., St. Mary Peak: in cirque above McCalla Lake. About 2500 m a.s.l. | 5 Oct. 1975 |
| RM 5 | Montana, Rivalli Co., Trapper Peak: saddle just below the summit. Wind-exposed alpine tundra in rocky soil. About 2950 m a.s.l. | 9 Aug. 1978 |
| RM 6 | Montana, Rivalli Co., Trapper Peak: moraine soil above timberline. About 2500 m a.s.l. | 9 Aug. 1978 |
| RM 7 | Montana, Rivalli Co., Trapper Peak: open coniferous forest. About 1700 m a.s.l. | 9 Aug. 1978 |
| RM 15 | Montana, Park Co., Daisy Park below Scotch Bonnet Mtn.: open alpine slope. About 2900 m a.s.l. | 17 Aug. 1978 |
| RM 16 | Montana, Park Co., Daisy Park: moist depression in open alpine slope. About 2880 m a.s.l. | 17 Aug. 1978 |
| RM 17 | Montana, Park Co.: subalpine meadow on path to Daisy Pass. About 2500 m a.s.l. | 17 Aug. 1978 |
| RM 18 | Montana, Park Co.: in open coniferous forest along the path to Goose Lake. About 2500 m a.s.l. | 17 Aug. 1978 |
| RM 27 | Montana, Carbon Co., Beartooth Plateau: immediately adjacent to the state-line Montana/ Wyoming, in a fellfield. About 3100 m a.s.l. | 18 Aug. 1978 |
| RM 19 | Wyoming, Park Co., Clay Butte: wind-exposed, dry summit of the butte. 3000 m a.s.l. | 18 Aug. 1978 |
| RM 20 | Wyoming, Park Co., Beartooth Lake: ledges and grassy terraces just above the lake. About 2760 m a.s.l. | 18 Aug. 1978 |
| RM 21 | Wyoming, Park Co., Beartooth Lake: edge of mixed coniferous forest. About 2750 m a.s.l. | 18 Aug. 1978 |
| RM 22 | Wyoming, Park Co. About 2 km of Beartooth Lake: among dwarf coniferous trees. About 2700 m a.s.l. | 18 Aug. 1978 |
| RM 23 | Wyoming, Park Co., Beartooth Plateau, Island Lake: moist meadow and peat hummocks. About 2940 m a.s.l. | 18 Aug. 1978 |
| RM 24 | Wyoming, Park Co., Beartooth Plateau: *Deschampsia caespitosa*-meadow. *A. lanata* very abundant. About 3000 m a.s.l. | 18 Aug. 1978 |

Table 4 (continued - *Forts.*)

| Sample code | Site description | |
|---|---|---|
| RM 25 | Wyoming, Park Co., Beartooth Plateau: road from Long Lake to Beartooth Pass: *Deschampsia caespitosa*-meadow. About 3000 m a.s.l. | 18 Aug. 1978 |
| EF 1 | Wyoming, Park Co., Beartooth Plateau: beneath *Pinus albicaulis* at the top of a ridge near Long Lake. 3040 m a.s.l. | 29 Jun. 1974 |
| EF 2a | Wyoming, Park Co., Beartooth Plateau: near Long Lake, in a S-facing slope with open coniferous forest. About 3030 m a.s.l. | 29 Jun. 1974 |
| EF 2b | Wyoming, Park Co., Beartooth Plateau: moist meadow near Long Lake. About 3013 m a.s.l. | 29 Jun. 1974 |
| RM 26 | Wyoming, Park Co., Beartooth Pass: early snowbank. About 3250 m a.s.l. | 18 Aug. 1978 |

Parent material of soils inhabited by *Antennaria lanata* correspond to both siliceous as well as carboniferous substrata. However, the best performance of *A. lanata* was actually observed in rather developed, frequently podsolic soils where a direct influence of substratum is modified by occurrence of organic litter as well as leaching processes. It seems therefore that principal factors determining the occurrence of *A. lanata* in given sites might be physical soil properties, snow cover depth and time of snowmelt and not the very chemical composition of the underlying rock.

### 3.3.4. *Antennaria eucosma*

*A. eucosma* seems to be rather specialized ecologically. Its representative site corresponds to a limestone barren, only a single population being recorded upon serpentine (Dr. E. ROULEAU, personal communication). *A. eucosma* shows a preference for rather dry and wind-exposed sites. Some of its stations are situated close to the sea (Fig. 16) and may therefore be subject to an occasional salt spray.

Fig. 16. A representative site of *A. eucosma*: Pistolet Bay, Cook Harbour (NF 1), about 51°39'N; 55°53'W. Limestone barren on the shore. Author's photo, 24 Jul. 1982.

*Typischer Standort von A. eucosma: Pistolet Bay, Cook Harbour (NF 1), ungefähr 51°39'N; 55°53'W. Kalkbank an der Küste.*

Table 5. Collection sites of *Antennaria eucosma* in Newfoundland.

*Fundorte von A. eucosma in Neufundland.*

| Sample code | Site description | Date |
|---|---|---|
| NF 1 | Pistolet Bay, Cook Point: gravelly and peaty limestone barrens in a close proximity to the sea. | 24 Jul. 1982 |
| NF 2 | Cape Norman, Boat Harbour: turfy limestone barren. | 24 Jul. 1982 |
| NF 3 | Big Brook: limestone barrens on high shore, just above a narrow pebble beach. Very dry site. | 24 Jul. 1982 |
| NF 4 | Cape St. George: limestone barrens and open slopes near the edge of the cliff. Dry, wind-exposed site. | 25 Jul. 1982 |
| NF 5 | Port au Port, Table Mtn.: dry limestone upper slopes and tableland. 200-300 m a.s.l. | 26 Jul. 1982 |

## 4. Discussion

Differentiation patterns revealed in the course of the present study suggest diversified speciation mechanisms that have operated within the *Antennaria carpatica* group in North America.

*A. lanata* and *A. anaphaloides* are partly allopatric; their distribution areas overlap within a rather limited region where tetraploid *A. pulcherrima* was also found. The occurrence of three tetraploid *Carpaticae* within the same area suggests a primary speciation centre. It is conceivable that each of the 28chromosomic taxa gradually developed adaptations to a different set of environmental conditions, the ecological differentiation eventually resulting in a rather pronounced spatial isolation. On the other hand, it is not excluded that hybridization on homoploid level might also have played a rôle in the differentiation of the group e.g. in the formation of *A. pulcherrima*.

Chromosome numbers as well as trends in geographical distribution and ecology obviously are useful for better assessment of speciation within the *Carpaticae*. It seems that also data on population appearance have an important informative value as far as the biological success of particular taxa and their further evolulutionary potential is concerned. Of the three tetraploid taxa within the group, *A. lanata* forms the largest and most densely populated stands. The excellent performance of the taxon was previously observed in Olympic Mts by BLISS (1969) and later in North Cascades by DOUGLAS and BLISS (1977) who distinguished a separate *A. lanata*-community type in high mountain vegetation of the latter region. The abundance of *A. lanata* in alpine meadows of the Beartooth Plateau was noted previously by JOHNSON and BILLINGS (1962). The taxon is apparently well-adapted to its representative biotopes throughout the whole area of its distribution.

*Antennaria anaphaloides* usually forms smaller and less conspicuous populations than *A. lanata*, except for stands observed at timberline in S Rocky Mts. Genetic make-up of the taxon apparently included adaptations both to a prolonged period of aridity as well as specific elements of a high mountain environment. It should be noted, however, that the timberline populations of *A. anaphaloides* occur in regions where *A. lanata* is not observable anymore; in high mountain sites within the Beartooth Plateau and northwards from the Plateau, competition from *A. lanata* is apparently too strong to allow the occurrence of *A. anaphaloides* at high elevations.

*A. lanata* and *A. anaphaloides* differ from one another in their adaptive features but both are apparently well-established in their respective ecological niches. Tetraploid *A. pulcherrima*, on the contrary, seems to be declining. Its populations being not only very rare and isolated but also small, the tetraploid race might be considered as genetically depleted (STEBBINS 1942). On the other hand, the octoploid *A. pulcherrima* is, to all appearances, very vigorous and frequently forms large, locally dense populations. This pattern of behaviour is particularly interesting when the harsh environment of the octoploids is taken into consideration. According to SOLBRIG (1980), population density tends to be low in environments with high physical stress in view of carrying capacity limits; consequently, competition is there less important. On the other hand, the physical stress is usually low in environments where density and competition are high. In former sites, heterozygosity is favoured through heterosis, whereas the latter ones promote outbreeding. Populations of the tall-growing octoploid *A. pulcherrima* apparently are able to withstand successfully both the physical stress and the competition for limited resources; it might be due to an advantageous combination of the obligate outbreeding and heterosis.

Karyological differentiation observed in *A. pulcherrima* represents a rather distict South-North gradient. Comparable phenomena, reported also from other regions (e.g. the Alps, the Pyrenees, FAVARGER 1962, 1964, KüPFER 1974) suggest possible differentiation pathways within given polyploid groups. In case of *A. pulcherrima*, octoploids might have been formed in the North and their further spread followed the retreat of the Wisconsin glaciers, colonizing the regions where tetraploid populations have long disappeared.

In spite of differences in geographical distribution, chromosome number as well as population appearance, tetraploids and octoploids of *A. pul-*

*cherrima* have striking ecological affinities. This aspect might be related to a possible autopolyploid origin of the 56chromosomic race, as autopolyploids are known to be ecologically similar to their diploid ancestors (e.g. *Achlys triphylla*, FUKUDA 1967). Preliminary observations on chromosome morphology in *A. pulcherrima* (URBANSKA unpubl.) suggest as well an autopolyploid character of the octoploid race.

Autopolyploidy was previously found within the *Carpaticae*. The Eurosiberian taxon of the group, *A. villifera*, is differentiated into two chromosomic races viz. tetraploids and hexaploids. Both 28- and 42chromosomic plants are scattered over Lapland (BERGMAN 1935, 1951, URBANSKA 1967a, b, ENGELSKJØN and KNABEN 1971) as well as Siberia, reaching eastwards to Chukotchka Peninsula (ZHUKOVA 1968, ZHUKOVA and TIKHONOVA 1971, 1973, ZHUKOVA, PETROVSKY and PLIEVA 1973, YURTSEV and ZHUKOVA 1982). Hexaploids occur generally more frequently than tetraploids but otherwise do not occupy a separate ecological niche. Data on population appearance from Siberia are not known; on the other hand, the author's field observations in North Scandinavia revealed some differences between tetraploids and hexaploids. Tetraploids formed exceedingly small populations often consisting of only male or only female clones, whereas hexaploid populations were relatively larger and frequently comprised both genders (URBANSKA 1967b,1970, URBANSKA unpubl.). Chromosome morphology of *A. villifera* as well as meiotic behaviour of hexaploids bring evidence of autopolyploid origin of the 42chromosomic race (URBANSKA 1967b,1970). It might be that this particular form of speciation occurred also in North America in *A. pulcherrima*.

*Antennaria eucosma* deserves a brief remark. The taxon represents the same level of polyploidy as do the northern populations of *A. pulcherrima*. It is not excluded that *A. eucosma* might have arisen as a result of quantum speciation from a peripheral population of *A. pulcherrima*; the two taxa undoubtedly are closely related. As suggested by numerous authors, peripheral i.e. geographically marginal populations are also marginal in ecological sense (e.g. ANTONOVICS 1976, LEWIS 1973, VASEK 1968). *A. eucosma* is ecologically rather specialized and seems to be adapted to extreme ecological conditions. It appears that very small populations of *A. eucosma* remaining isolated from the main distribution area of *A. pul-*

*cherrima* might well have developed under influence of genetic drift and/ or unusually strong selective pressures. The importance of quantum speciation in plant evolution is generally recognized (e.g. LEWIS 1962, GRANT and GRANT 1960, GRANT 1981, SOLBRIG 1960). Still unknown data on chromosome numbers and behaviour of *A. pulcherrima* from eastern part of its distribution area are very important for getting a more complete picture of evolution within the group.

The few aspects presented above show that much information on the North American *Carpaticae* is still required. Further investigations in the group, both in the field as well as laboratory, offer numerous exciting possibilities. The study is in progress.

## Summary

Chromosome number, geographical distribution, ecology and population appearance were studied in the North American taxa of *Antennaria carpatica* s.l.

*A. lanata* and *A. anaphaloides* proved to be uniformly tetraploid (2n=28), whereas differentiation was revealed in *A. pulcherrima:* large northern population of this taxon were octoploid, but rare, small southern colonies represented the tetraploid level.

*A. pulcherrima* has the largest total distribution area of all the North American *Carpaticae*; it can be characterized as high-subarctic/temperate transcontinental type. *A. anaphaloides* and *A. lanata* have a temperate western distribution and inhabit rather small areas, whereas *A. eucosma* approaches a low-subarctic eastern distribution type and its area is exceedingly restricted. The North American *Carpaticae* are largely allopatric, overlapping of some area being observed in a rather limited region.

It seems that physical soil properties (esp. soil moisture), snow cover depth and time of snowmelt represent principal factors determining the occurrence of most *Carpaticae*, the chemical composition of the substratum apparently playing a direct rôle only in *A. eucosma*. *A. pulcherrima* has a preference for well-watered, fine textured alluvial soils often subject to an intermittent flooding. Its representative niche corresponds to river bank with willow shrubs; tetraploid and octoploid populations have striking ecological affinities. *A. anaphaloides* is well-adapted to a prolonged period of aridity and mostly occurs in loose, permeable and dry soils frequently characterized by the occurrence of sagebrush. *A. anaphaloides* occurs as well about timberline, but only in Colorado where *A. lanata* is not observable anymore. *A. lanata* is a subalpine/alpine taxon; it occurs mostly in gravelly or sandy loam soils, snow-covered in winter and moderately- to well-drained in summer. Representative sites of *A.*

*lanata* are open coniferous forests, mountain meadows and early snowbanks. *A. eucosma* is mostly confined to dry limestone barrens, wind-exposed and sometimes subject to an occasional salt spray from the sea.

Data on population appearance, helpful for assessment of evolutionary potential of particular taxa as well as various facets of primary speciation within the *A. carpatica* group are briefly discussed.

## Zusammenfassung

Von den nordamerikanischen Arten der *Antennaria carpatica*-Gruppe wurden die Chromosomenzahlen, die geographische Verbreitung, die Oekologie und das Populationsverhalten untersucht.

*A. lanata* und *A. anaphaloides* erwiesen sich als einheitlich tetraploid (2n=28), *A. eucosma* als oktoploid (2n=56). *A. pulcherrima* dagegen zeigte eine karyologische Differenzierung: Grosse Populationen dieser Art aus dem Norden waren oktoploid und seltene kleine Populationen aus dem Süden tetraploid.

*A. pulcherrima* ist von allen nordamerikanischen Arten der Gruppe am weitesten verbreitet. Sie hat eine transkontinentale Verbreitung in der hochsubarktischen Zone und in den Gebirgen südlich davon (high-subarctic temperate transcontinental type). *A. lanata* und *A. anaphaloides* haben eine westliche Verbreitung innerhalb der Gebirge der gemässigten Zone und besiedeln relativ kleine Areale; *A. eucosma* hat dem gegenüber eine östliche Verbreitung (Neufundland), ihr Areal ist extrem beschränkt. Die nordamerikanischen Arten von *A. carpatica* s.l. sind vorwiegend allopatrisch und ihre Areale überlappen sich nur begrenzt.

Es scheint, dass physikalische Bodeneigenschaften (besonders Bodenfeuchte) und Schneebedeckung (Dicke der Schneedecke, Ausaperungszeit) entscheidende Faktoren für das Aufkommen der meisten Arten sind. Die chemische Zusammensetzung des Muttergesteins spielt dagegen wahrscheinlich nur bei *A. eucosma* eine direkte Rolle. *A. pulcherrima* bevorzugt gut durchfeuchtete, feinkörnige alluviale Böden, die oft zeitweise überflutet werden; sie ist vorwiegend an mit *Salix* bewachsenen Uferbänken anzutreffen. Tetraploide und oktoploide Populationen verhalten sich ökologisch überraschend ähnlich. *A. anaphaloides* erträgt längere Trockenperioden und wächst hauptsächlich in lockeren, gut durchlässigen, trockenen Böden, zusammen mit *Artemisia*-Büschen. *A. anaphaloides* kann auch oberhalb der Waldgrenze angetroffen werden, aber nur in Colorado, wo *A. lanata* nicht mehr auftritt. *A. lanata* hat eine subalpine/alpine Verbreitung und gedeiht vor allem auf kiesigen oder sandigen Lehmböden, die im Winter schneebedeckt und im Sommer mässig bis sehr trocken sind. *A. lanata* kommt am häufigsten in offenen Nadelwäldern, auf Gebirgswiesen und in relativ früh ausapernden Schneetälchen vor. *A. eucosma* ist mehrheitlich auf trockene, windexponierte und gelegentlich von Meerwasser bespritze Kalkflächen beschränkt.

Angaben über das Populationsverhalten, die über das Evolutionspotential der *Antennaria carpatica*-Arten Auskunft geben können, sowie verschiedene Aspekte der primären Artbildung innerhalb der Gruppe werden kurz diskutiert.

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