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

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

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

II. Low Tatra

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

III. Eastern Carpathians

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

5. Ecology

5.1. *Antennaria villifera*

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

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

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

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

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

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

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

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

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

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

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

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

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

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

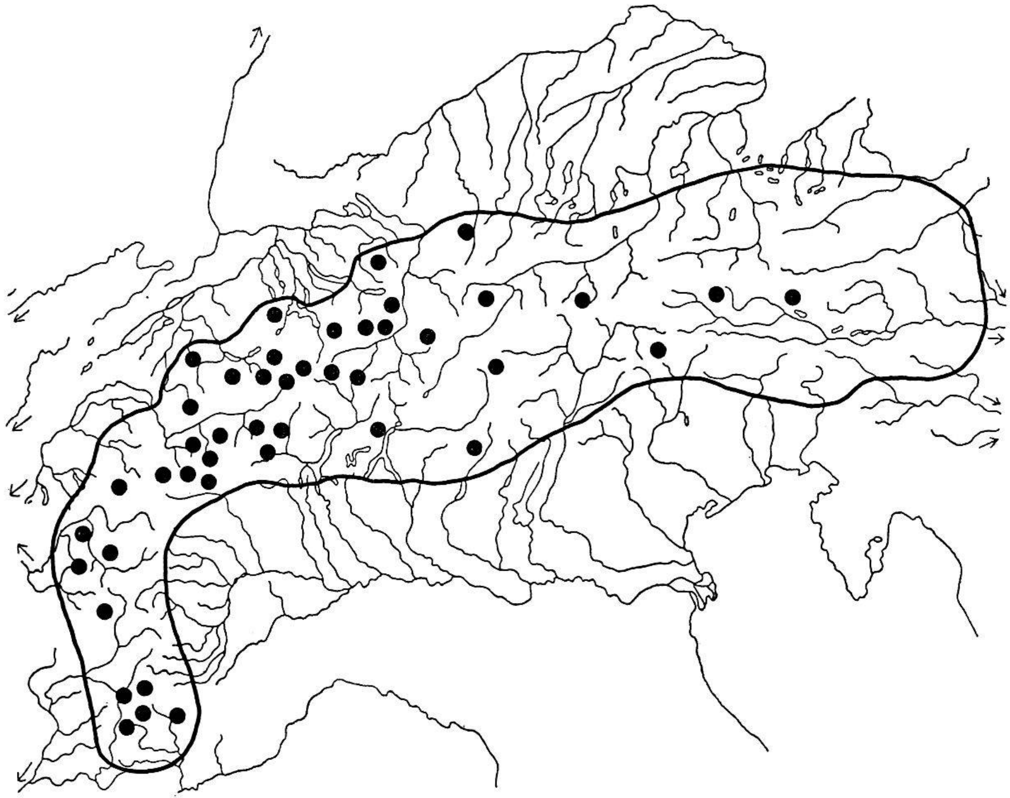

Fig. 25. Distribution of *Antennaria carpatica* s. str. in the Alps. Unbroken line: limits of the range. Dots mark some localities studied cytologically (partly after Urbańska-Worytkiewicz 1968).

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

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

5.2 *Antennaria carpatica* s. str.

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

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

As far as the edaphic factors are concerned, it should be noted that *Antennaria carpatica* s. str. occurs on both granitic as well as on calciferous substrata. However, the resp. pH values are not always influenced immediately by the type of rock as it seems to be the case in Fennoscandia. For example, *Antennaria carpatica* s. str. occurs as a very characteristic component in the *Versicolori-Agrostetum* in the granitic part of the Tatra Mountains; the soil is there strongly irrigated by water containing mineral salts, especially $CaCO_3$ washed out from the rocks. Accordingly, its reaction is circumneutral or weakly alcalic. On the other hand, the *Elynetum (alpinum)* distributed on calciferous rocks in the Alps, sometimes shows a well developed layer of the humus decalcified in its upper part; in consequence the pH values are more or less acidic (Braun-Blanquet and Jenny 1926).

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

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

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