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Chorological pattern in the *Aconito-Piceetum* in middle and northern taiga of European Russia

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Abstract. In accordance with the combined dominant-floristic approach to vegetation classification, three subassociations with five variants are recognized within the *Aconito-Piceetum*, the aconite spruce forest of European Russia. The presence of nemoral herbs is typical of the "western" subass. *aegopodietosum podagrariae*. In the variant of *Atragene sibirica* in the Severnaya Dvina River basin these herb species grow together with the Euro-Siberian tall herbs. The Karelian variant of *Convallaria majalis*, without the latter compound, is generally close to the analogous communities in Scandinavia. Nemoral plants are lacking in the "central-eastern" subass. *typicum*. Tall herb diversity is highest in the variant of *Cacalia hastata* in the floodplains of the rivers Mezen and Pechora. In the variant *inops* growing on watershed, the dominance is shared between *Aconitum septentrionale* and *Calamagrostis langsdorffii*. *C. langsdorffii* also dominates the herb layer in the cis-Uralian "north-easternmost" subass. *calamagrostietosum*, which is rich in several hypoarctic and poor in boreal-nemoral species.

1 Introduction

The aconite spruce forest (*Aconito-Piceetum*) occurs in the bottoms and the lower thirds of slopes of stream valleys, in above-floodplain and high-floodplain terraces, dells of mountain slopes within the coniferous forest belt, and karst ravines. A species-rich ground cover with two sub-layers is typical of this association. The upper sub-layer is dominated by *Aconitum septentrionale,* often with the presence of other tall hygro-mesophytic herbs, whereas *Oxalis acetosella* and *Equisetum pratense* usually prevail in the lower sub-layer mainly composed of forest mesophytes (VASILEVISH 2004). The unit is widespread in the taiga zone of Eurasia, from Fennoscandia to the western vicinities of the Lake Baikal in Siberia.

The *Aconito-Piceetum* has already been described by methods of both the dominant (SAMBUK 1932: *Piceetum inundatum*, *Piceetum filicosum*; KOLESNIKOV 1985: *Piceetum mixto-herbosum*; etc.), the dominant-floristic (VASILEVISH 2004), and the Braun-Blanquet (ZAUGHOLNOVA & MOROZOVA 2004) approaches, with the resulting units fairly coinciding with each other.

The association is either treated as chorologically uniform within European Russia (VASILEVISH 2004), or is provisionally subdivided into a western (with no name published) and an eastern variant (var. of *Abies sibirica*; ZAUGHOLNOVA & MOROZOVA 2004). However, the detailed regional pattern, caused by a complex set of factors, including the zonal gradient, the bedrock and landscape differences, and the Holocene vegetation history, has not been thoroughly studied up to now. An attempt to consider it is presented in this paper.

2 Study area and methods

A set of 137 relevés was collected in 1995-2007 in different localities (loc.) within the middle and northern taiga of European Russia, from Karelia to the Northern Urals foothills (Fig. 1). Additionally, six relevés from the Kivach Reserve (Karelia) made by J. Paal in 1976, and totally 11 relevés from published sources (ANDREEV 1935, KORCHAGIN 1956, KATENIN 1972, KOLESNIKOV 1985; see Fig. 1) are included.

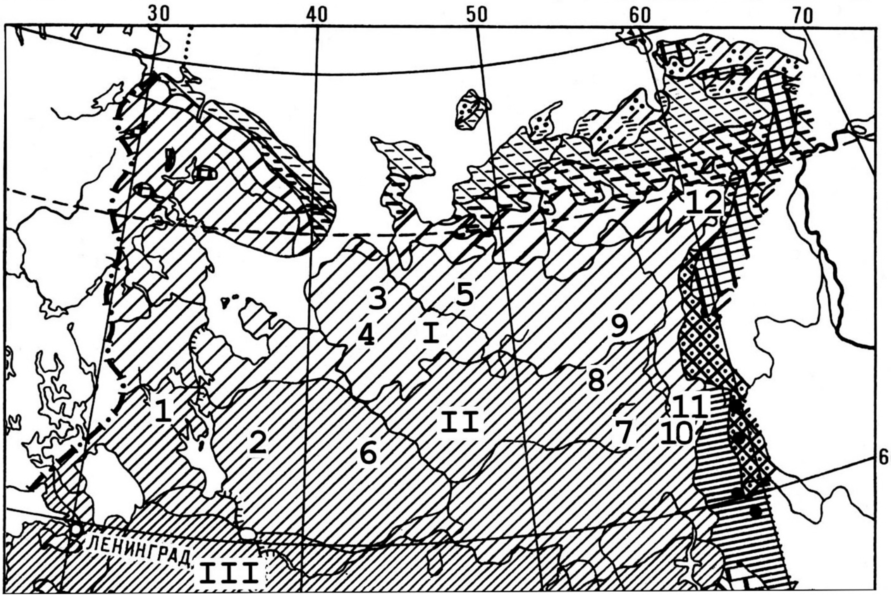

Fig. 1: Position of the studied localities: 1 – Karelia Rep., Kivach Reserve (62° N, 34° E). 2–6 – Arkhangelsk Region: 2: Kenozero National Park (61° 30' N, 38° E), 3: upper reaches of Kuloi R (65°N, 43° 30' E), 4: Pinega Reserve (64° 30' N, 43° E), 5*: Mezenskaya Pizhma R. basin (65° N, 49° E), 6: Ustya R. basin (61° 30' N, 44° E). 7-12 – Komi Rep.: 7*: upper reaches of Vychegda R. (61° N, 55° E); 8*: S Timan Ridge (63° N, 54° E); 9: watershed of rivers Izhma and Pechora (63° 30' N, 55° E), 10 & 11: upper reaches of Pechora R. with 10: plain area (61° N, 57° E) and 11: N Urals foothills (62° N, 58°30' E), 12*: forest-tundra field station "Sivaya Maska" (66° 30' N, 62° 30' E).
Sources from literature: 5: KORCHAGIN (1956); 7*: KOLESNIKOV (1985); 8*: ANDREEV (1935), 12*: KATENIN (1972).
Subzones of taiga: I – northern, II – middle, III – southern (ISACHENKO & LAVRENKO 1980). abbrev. R. = River, Rep. = Republic

The total data set was processed following the combined dominant-floristic approach to vegetation classification (VASILEVISH 1995). This means that the associations and subassociations outlined according to dominance are adjusted by composition of the differential groups of ecologically similar plant species (determinants; the variants can be distinguished only according to the latter). The uniformity of species distribution within each determinant group (both within the syntaxon, in the rest of the set, and in the total set) is finally checked by means of the Cochran distribution-free test (VASILEVISH 1995). The results of this method proved to be principally reproducible on the basis of different independent relevé sets; neither type selection and author citation, nor "transitional" relevé exclusion is needed (at cost that a unique relevé can be hardly related to a syntaxon because it can often be reliably included into more syntaxa than one).

The diagnostic (determinant) groups of the combined dominant-floristic approach are roughly, sometimes even exactly, close to the differential and characteristic species groups of the Braun-Blanquet approach. But the difference is that the species of the determinant groups have statistically proven similar distributions in the total data set (VASILEVISH 1995).

The dominant-floristic approach uses the association as a basic unit as in the Braun-Blanquet approach with subdivision in subassociations and variants. Associations are combined into groups and then into formations according to criteria of dominance, following the traditional dominant approach to vegetation classification (e. g. ALEKSANDROVA 1969). As the algorithm of separation of the units in the dominant-floristic approach is different from that in the Braun-Blanquet approach, the ranks of the syntaxa established in both systems are not automatically equivalent. An association of the dominant-floristic approach may correspond to (or be geographically replaced by) a subassociation and even variant of the Braun-Blanquet approach, and vice versa, although the accordance of ranks is also often the case. Any conclusion upon ranks presumes a preliminary treatment of the compared syntaxa within a single relevé table.

The taxonomic nomenclature of vascular plants follows CHEREPANOV (1995), of bryophytes IGNATOV & AFONINA (1992) and KONSTANTINOVA et al. (1992), of lichens VITIKAINEN et al. (1997).

3 Results

According to the classification results given in Tab. 1, the following three subassociations of the aconite spruce forest can be distinguished.

3.1 *Aconito-Piceetum aegopodietosum podagrariae*

The subass. *aegopodietosum* occurs in the western and south-western parts of the area, mainly in the middle taiga (loc. 1, 2, 6), with relict enclaves in the northern taiga (loc. 4;

see Fig. 1). The presence of nemoral and boreal-nemoral plants (Tab. 1, group J: *Aegopodium podagraria*, *Daphne mezereum, Lonicera xylosteum,* etc.), probably inherited from the Atlantic period of the Holocene (NEISHTADT 1957), is typical. The subassociation can be subdivided into two variants.

3.1.1 Var. of *Convallaria majalis*

This variant occurs in southern Karelia as well as in the south-westernmost Arkhangelsk Region (loc. 1, 2), and can probably also be met in Finland (see below). It grows mainly on silicate deposits of the Würm age. *Calamagrostis arundinacea* is constant and co-dominant together with *Aegopodium podagraria* and *Convallaria majalis*; *Galium triflorum* is constant as well (Tab. 1 groups C, I, J). The Euro-Siberian boreal tall herbs are generally absent, with the exception of the aconite itself. The unit is very rare in Karelia as it is bound to fertile mesic soils of valleys which were preferably involved into the agricultural (usually slash-and-burn) use up to the beginning of the XX century (LINKOLA 1916). However, few stands persisted on steepest slopes. In the SW Arkhangelsk Region, the community is more common, as the sorrel spruce forest sites were the first to be cut down and ploughed there.

3.1.2 Var. of *Atragene sibirica*

This variant is known from the middle taiga of the Kenozero Lake area (loc. 2) and through the basins of the Severnaya Dvina River (R.) left-hand tributaries (loc. 6), with a northern-taiga enclave in the middle reaches of the Pinega R. (loc. 4; see Fig. 1). Nemoral species (Tab. 1, group M: *Asarum europaeum, Pulmonaria obscura, Viola mirabilis,* etc.) are typical together with Euro-Siberian boreal tall (Tab. 1, groups N, O, P: *Crepis sibirica, Delphinium elatum, Thalictrum minus, Valeriana wolgensis,* etc.) and climbing (Tab. 1, group O: *Atragene sibirica*) herbs which belong to the so called betular florogenetic element, originated in the Siberian subalpine meadows and birch and larch forests in the upper Tertiary (KLEOPOV 1990). The richness in nemoral species (mainly bird- or ant-dispersed) can be explained due to migration of plants from the Volga R. basin into the Severnaya Dvina R. area during the Atlanticum and the Subboreal (NEISHTADT 1957). Because many representatives of the betular element are mainly ballistic- and (in the second turn) water-dispersed, they have not yet reached Fennoscandia, although they are very plastic in their ecology. The time passed in the Post-glacial was seemingly insufficient for their immigration, as there are no big rivers running westwards through the boreal-forest zone of the whole European Russia. This also means that *Aconitum septentrionale* is probably an earlier migrant, maybe of the Riss-Würm interglacial age, which survived in some peri-glacial refugia southwards.

Tab. 1: Floristic differentiation in *Aconito-Piceetum* and related syntaxa within middle and northern taiga of Northern Europe

Layer	Plant names	Syntaxa								Species groups
		Melico-Piceetum			*Aconito-Piceetum*					
		aconitetosum			*aegopodiet.*		*typicum*		*cala.*	
		1	2	3	4	5	6	7	8	
	Number of relevés	5	9	15	6	71	54	13	4	
c	*Stellaria longifolia*	V^2	I^1	-	-	I^1	I^1	-	-	A
c	*Viola biflora*	IV^4	-	-	-	I^1	I^1	II^2	-	
c	*Circaea alpina*	II^3	III^3	-	I^1	I^1	I^1	-	-	B
d	*Rhizomnium punctatum*	I^4	III^2	-	-	I^1	I^1	I^1	-	
d	*Dicranum majus*	I^2	III^3	IV^2	-	I^1	-	I^1	-	
d	*Plagiomnium affine*	I^2	IV^2	-	I^2	I^1	-	-	-	
d	*Atrichum undulatum*	II^2	III^2	I^1	-	-	I^1	-	-	
c	*Carex digitata*	II^3	I^2	IV^3	IV^2	IV^2	I^1	-	-	C
c	*Fragaria vesca*	V^3	V^3	V^3	V^2	IV^2	II^1	-	-	
c	*Calamagrostis arundinacea*	II^3	II^2	I^2	V^3	II^2	-	-	-	
c	*Paris quadrifolia*	I^1	III^2	II^2	III^1	IV^1	III^1	I^1	-	D
c	*Deschampsia cespitosa*	V^3	IV^2	V^3	I^1	III^1	I^1	I^1	-	
c	*Phegopteris connectilis*	III^3	V^4	V^4	II^2	I^1	II^2	-	-	
b	*Alnus incana*	III^5	I^1	II^4	III^2	II^2	II^1	-	-	
b	*Rubus idaeus* s. l.	V^3	IV^4	III^3	III^2	IV^2	III^2	-	-	
b	*Padus avium*	III^2	-	-	III^2	III^1	III^2	-	-	
b	*Sorbus aucuparia* s. l.	V^2	IV^3	IV^2	V^2	V^2	V^2	II^2	-	E
c	*Oxalis acetosella*	V^4	V^3	V^3	V^3	V^4	V^4	IV^3	-	
c	*Maianthemum bifolium*	III^2	IV^2	V^3	V^3	V^2	V^2	IV^2	-	
c	*Gymnocarpium dryopteris*	IV^4	V^3	V^3	V^3	IV^3	V^3	IV^2	-	
c	*Luzula pilosa*	II^3	V^2	V^3	II^1	IV^1	II^1	V^1	-	
d	*Rhytidiadelphus triquetrus*	V^5	V^3	V^4	V^3	V^4	V^4	II^1	-	
d	*Rhodobryum roseum*	II^2	V^2	IV^3	III^1	II^1	II^1	I^1	-	
d	*Plagiochila asplenioides* s. l.	II^2	V^3	IV^4	I^1	II^2	I^1	II^1	-	
c	*Viola riviniana*	-	V^2	V^3	II^1	I^1	-	-	-	F
d	*Hylocomium umbratum*	-	V^4	III^3	-	-	-	I^1	-	
c	*Anemone nemorosa*	-	V^3	V^3	-	-	-	-	-	
c	*Mycelis muralis*	-	IV^2	I^2	-	-	-	-	-	
c	*Valeriana sambucifolia*	-	II^3	I^1	-	-	-	-	-	
c	*Athyrium filix-femina*	-	II^4	II^3	II^2	II^2	II^2	-	-	G
c	*Dryopteris assimilis + expansa*	-	IV^3	III^2	-	II^2	II^1	-	-	
c	*Melica nutans*	-	III^2	III^3	V^2	V^2	III^2	IV^2	-	H
c	*Melampyrum sylvaticum* s. l.	-	I^1	IV^3	IV^1	III^1	I^1	IV^1	-	
d	*Rhytidiadelphus subpinnatus*	-	V^3	V^4	-	I^1	I^2	IV^2	-	
b	*Rosa majalis*	-	-	-	II^2	I^1	I^1	-	-	I
c	*Convallaria majalis*	-	-	-	V^2	I^1	-	-	-	
c	*Galium triflorum*	-	-	-	III^1	I^1	-	-	-	
c	*Lathyrus vernus*	-	I^4	-	IV^2	V^2	II^2	I^2	-	J
b	*Daphne mezereum*	-	-	-	IV^2	IV^1	II^1	-	-	
c	*Aegopodium podagraria*	-	-	-	III^2	III^3	I^1	-	-	
c	*Vicia sylvatica*	-	-	-	II^1	II^1	II^2	-	-	
b	*Lonicera xylosteum*	-	-	-	II^1	III^2	-	-	-	

b	*Ribes spicatum s. l. + acidum*	I^2	-	-	I^1	IV^2	III^2	III^1	-	K
c	*Dryopteris carthusiana*	-	I^3	-	IV^2	IV^1	II^2	-	-	
b	*Lonicera pallasii s. l.*	-	-	-	II^1	III^2	V^2	V^2	-	
c	*Angelica sylvestris*	-	-	-	V^2	III^1	III^1	V^2	-	
d	*Plagiomnium ellipticum*	-	-	-	I^1	II^2	II^2	IV^2	-	
c	*Equisetum pratense*	I^2	-	I^1	III^2	V^4	V^3	II^2	2^1	L
c	*Cirsium heterophyllum* s. l.	I^2	-	I^2	V^2	III^2	II^2	V^3	4^2	
c	*Milium effusum*	-	I^2	I^2	II^2	III^2	III^2	III^2	4^2	
c	*Calamagrostis purpurea* s. l. (incl. *C. langsdorffii*)	-	I^2	I^2	II^2	II^1	III^2	V^3	4^3	
c	*Trollius europaeus*	-	-	I^3	III^2	IV^2	III^2	V^2	4^2	
b	*Rosa acicularis*	-	-	-	III^2	IV^2	V^2	V^2	3^2	
c	*Viola epipsila*	-	-	-	III^2	III^2	I^2	IV^2	4^2	
c	*Actaea spicata*	-	I^3	-	-	II^1	I^1	-	-	M
c	*Viola mirabilis*	-	-	-	I^1	III^2	I^1	-	-	
c	*Cirsium oleraceum*	-	-	-	-	III^2	I^1	-	-	
c	*Pulmonaria obscura*	-	-	-	-	III^2	-	-	-	
c	*Ajuga reptans*	-	-	-	-	II^1	-	-	-	
c	*Crepis sibirica*	-	-	-	-	II^2	II^2	-	-	N
c	*Calamagrostis obtusata*	-	-	-	-	II^2	II^2	-	-	
c	*Stellaria bungeana*	-	-	-	-	I^2	III^2	-	-	
c	*Atragene sibirica*	-	-	-	-	IV^1	V^2	III^2	-	O
c	*Thalictrum minus* s. l.	-	-	-	-	II^2	IV^2	V^2	-	
c	*Valeriana wolgensis*	-	-	-	-	I^1	III^2	V^2	-	
c	*Stellaria holostea*	-	-	-	-	II^2	I^1	I^1	-	
b	*Spiraea media*	-	-	-	-	I^1	I^1	II^1	-	
c	*Ranunculus borealis*	-	-	-	-	II^1	III^1	V^2	4^2	P
c	*Veratrum lobelianum*	-	-	-	-	I^1	III^2	IV^2	4^2	
c	*Delphinium elatum*	-	-	-	-	I^1	III^1	-	3^2	
c	*Diplazium sibiricum*	-	-	-	I^3	I^2	II^3	-	-	Q
a,b	*Abies sibirica*	-	-	-	-	I^1	III^2	-	-	
c	*Cacalia hastata*	-	-	-	-	I^1	III^2	-	-	
c	*Pleurospermum uralense*	-	-	-	-	I^1	II^1	-	-	
a	*Pinus sibirica*	-	-	-	-	-	I^2	-	-	
c	*Senecio nemorensis*	-	-	-	-	I^1	III^2	II^1	-	R
c	*Conioselinum tataricum*	-	-	-	-	I^1	II^1	II^1	-	
c	*Ligularia sibirica*	-	-	-	-	I^1	-	II^2	-	
d	*Rhizomnium pseudopunctatum*	I^2	I^1	I^1	I^1	I^1	I^1	IV^2	1^2	S
c	*Galium palustre*	-	II^2	II^2	I^1	I^1	I^1	IV^1	-	
b	*Salix myrsinifolia* s. l.	-	-	I^2	-	I^1	I^1	III^2	-	
c	*Carex cespitosa*	-	-	-	-	I^1	I^1	IV^2	-	
c	*Caltha palustris*	-	-	-	-	I^1	-	III^1	-	
c	*Veronica longifolia*	-	-	-	-	-	I^1	IV^1	-	
c	*Comarum palustre*	-	-	-	-	-	I^1	III^1	-	
c	*Rubus arcticus*	-	-	-	I^1	I^1	II^1	V^2	4^2	T
d	*Sphagnum warnstorfii*	-	-	-	I^2	I^2	I^1	II^3	4^4	
c	*Rubus chamaemorus*	-	-	-	-	-	I^1	II^1	4^2	
c	*Parnassia palustris*	-	-	-	-	-	-	II^1	3^2	
c	*Moehringia lateriflora*	-	-	-	-	I^1	I^1	III^1	2^1	
b	*Salix jenisseensis*	-	-	-	-	I^1	-	-	4^2	U
b	*S. phylicifolia*	-	-	-	-	-	-	I^1	4^2	
c	*Trisetum sibiricum*	-	-	-	-	-	-	-	4^2	
b	*Salix glauca*	-	-	-	-	-	-	-	3^2	
b	*S. lanata*	-	-	-	-	-	-	-	3^2	
b	*Betula nana*	-	-	-	-	-	-	-	3^2	
c	*Petasites frigidus*	-	-	-	-	-	-	-	3^2	

a	*Picea abies* s. l.	V^5	V^5	V^5	V^5	V^5	V^5	V^5	4^4
a	*Betula pubescens*	IV^2	-	-	I^3	IV^3	IV^3	V^3	4^5
a	*B. pendula*	-	-	I^2	III^2	I^2	I^2	-	-
a	*Larix sibirica*	-	-	-	I^1	I^2	I^2	I^1	-
b	*Juniperus communis* s. l.	III^2	-	-	-	II^1	I^1	V^2	4^2
c	*Aconitum septentrionale*	V^4	V^4	V^3	V^4	V^4	V^4	V^2	4^2
c	*Trientalis europaea*	IV^3	IV^2	V^3	V^2	V^2	IV^2	V^2	4^2
c	*Geranium sylvaticum* s. l.	I^3	III^3	V^3	V^2	V^2	V^2	V^3	4^2
c	*Vaccinium vitis-idaea*	III^2	II^2	IV^3	V^2	V^2	III^2	V^3	4^2
c	*Solidago virgaurea* s. l.	III^2	V^3	III^2	V^2	I^1	III^2	V^2	3^2
c	*Rubus saxatilis*	I^2	IV^3	IV^3	V^3	V^3	V^2	II^1	2^1
c	*Linnaea borealis*	III^3	III^3	V^3	III^1	III^2	IV^2	IV^2	3^2
c	*Vaccinium myrtillus*	II^2	IV^2	IV^3	V^3	IV^2	II^2	II^1	4^3
c	*Orthilia secunda*	I^3	II^2	IV^3	III^1	IV^2	III^2	V^1	3^2
c	*Avenella flexuosa*	II^4	III^3	IV^3	III^1	I^1	I^1	I^1	2^2
c	*Moneses uniflora*	III^2	II^2	III^2	I^1	I^1	I^1	II^1	3^1
c	*Galium boreale*	I^1	-	I^2	I^1	I^1	IV^2	V^2	1^1
c	*Filipendula ulmaria* s. l.	-	IV^4	IV^3	II^2	IV^2	III^2	V^2	2^2
c	*Equisetum sylvaticum*	-	I^1	II^2	IV^2	III^2	IV^2	V^3	4^2
c	*Geum rivale*	-	II^3	III^2	I^1	IV^2	I^1	II^2	4^2
c	*Crepis paludosa*	-	III^2	IV^3	II^2	III^2	I^1	II^1	-
c	*Vicia sepium*	-	III^2	-	II^1	IV^1	III^1	IV^1	-
c	*Pyrola rotundifolia* s. l.	-	-	III^2	III^2	IV^2	II^2	I^1	-
c	*P. minor*	-	-	III^2	-	II^1	I^1	IV^1	4^2
d	*Hylocomium splendens*	V^5	V^3	V^4	IV^3	IV^2	IV^4	IV^3	4^5
d	*Pleurozium schreberi*	I^2	II^2	IV^3	V^2	III^2	III^2	IV^3	4^2
d	*Dicranum scoparium*	I^3	I^2	IV^3	III^1	III^2	I^1	I^1	-
d	*Brachythecium oedipodium*	I^2	II^1	-	IV^2	II^2	I^2	II^1	-
d	*Climacium dendroides*	III^3	I^1	I^3	-	III^2	II^2	IV^2	-
d	*Brachythecium salebrosum*	III^3	III^2	II^3	-	I^1	I^1	I^1	-
d	*Polytrichum commune*	III^3	-	-	I^1	I^1	I^1	IV^1	3^2
d	*Ptilium crista-castrensis*	-	IV^3	IV^3	-	I^1	I^2	II^2	2^1
d	*Plagiomnium medium*	I^4	-	I^3	I^2	I^2	I^1	-	-

Notes: Layer: **a**: tree, **b**: shrub, **c**: dwarf-shrub & herb, **d**: bryophyte & lichen.

Syntaxa: 1–3: *Melico-Piceetum* subass. *aconitetosum* (Caj. 21) K.-Lund 62 (KIELLAND-LUND 1981: 178–180: Tab. 39, Cols. 11, 13, 17): **1**: dry calcicolous valley race; **2** & **3**: var. of *Crepis paludosa* in central area (2) and highland area (3). 4–8: *Aconito-Piceetum*: **4** & **5**: subass. *aegopodietosum* var. of *Convallaria majalis* (4) and var. of *Atragene sibirica* (5); **6** & **7**: subass. *typicum* var. of *Cacalia hastata* (6) and var. *inops* (7); **8**: subass. *calamagrostietosum langsdorffii*.

Companions with constancy II or less in all of the syntaxa, also species difficult for exact identification (*Hieracium* spp., several cryptogams), known from some locations but probably overlooked in the others, are mainly omitted. Standard 20% interval constancy classes are used; combined abundance-cover values are given as superscripts: 1: <1 % (r in the Braun-Blanquet scale, un.-rr. in the Drude scale), 2: 1-5 % (+, sol.), 3: 5-12 % (2a, sp.), 4: 13-25 % (2b, cop.^{1}), 5: 26-50 % (3, cop.^{2}), 6: 51-75 %(4, cop.^{3}), 7: >75 % (5, soc; e. g. PONYATOVSKAYA 1964).

Determinant groups: **A**, **I**, **L**: extracted statistically; **B**: hygromesophytes and hygrophytes (hereafter with ranges of different types, if not mentioned); **C**: Eurasian and European-S Siberian-montane W Asian boreal-nemoral light-forest mesophytes; **D**: Eurasian and European-S Siberian boreal-nemoral nitrogen-demanding species; also circumboreal fertility-demanding ferns; **E**: Eurasian and Eurosiberian dark-coniferous boreal forest mesophytes; **F**: mainly European nemoral and nemoral-montane mesophytes and hygromesophytes; **G**: boreal and boreal-nemoral tall ferns; **H**, **K**: boreal-nemoral forest mesophytes; **J**, **M**: boreal-nemoral and nemoral forest mesophytes (M – partly also hygromesophytes): J: European-SW Siberian-Altai, M: Central and E European, or European-montane W Asian (often incl. SW Siberia); **N**, **O**, **P**, **Q**, **R**: E European-Siberian (often also montane W Asian) boreal subalpine meadow-light forest plants of the betular florogenetic complex, mainly tall, also climbing or creeping herbs, O: also nemoral herbs (*Stellaria holostea*) which survived in the peri-glacial refugia of the Middle Urals; Q: also E European-Siberian boreal/hemiboreal conifer trees and dark-coniferous hemiboreal forest ferns; **S**: boreal and boreal-nemoral forest swamp hygrophytes; **T**, **U**: circumpolar or NE European-N Siberian northern-boreal or hypoarctic hygromesophytes, hygrophytes, and oxylophytes; also some mesophytic representatives of the betular complex (*Moehringia lateriflora*, *Trisetum sibiricum*). Species distribution characters mostly refer to vasculars (HULTÉN & FRIES 1986); the cryptogamic species ranges are usually broader due to their age and most often insufficiently studied.

Stands of this unit are developed either on carbonate moraines or on carbonate/ sulfate rock outcrops, also in karst ravines and in sites with mineral-rich water supply. All these habitats are favorable for both nemoral and tall-herb forest plants, as many of them depend on rich soils (especially rich in nitrogen) at least within the studied subzones. It is known that the carbonate soils of the forest zone are more warm and dry, with better aeration and the acidity close to neutral; all these conditions are favorable for nirtification (LARCHER 1976). In the southern taiga, the forests of var. of *Atragene* occur on silicate soils as well. These soils, probably more warm and better aerated due to their southward location, are expected to be neutral to moderately acidic. But this problem demands further (and detailed) studies for any reasonable conclusions.

Stands of this variant are very typical of the southern taiga of European Russia (VASILEVICH 2004) and the hemiboreal subzone of Western Siberia and the Altai (KLEOPOV 1990). Most probably, they served as maternal in the process of genesis of floras of the other syntaxa discussed, as they originated before the beginning of the glaciation age and to the southeast of the glaciation area (see KLEOPOV 1990).

3.2 *Aconito-Piceetum typicum*

The typical subassociation is found in the central and eastern parts of the area, in both middle and northern taiga. Nemoral and boreal-nemoral species are absent with the occasional exception of *Lathyrus vernus*. The tall-herb complex is well-presented; some of its species (*Conioselinum tataricum, Senecio nemorensis;* see Tab. 1, group R) serve as subassociation preferentials. Two variants can be distinguished.

3.2.1 Var. of *Cacalia hastata*

This variant is known from the basins of the rivers Kuloi (loc. 3), Mezenskaya Pizhma (loc. 5; KORCHAGIN 1956), Pechora (loc. 10, 11; see also SAMBUK 1932), and the right-hand tributaries of the Severnaya Dvina R., including the Pinega R. (loc. 4) and the upper reaches of the Vychegda R. (loc. 7; KOLESNIKOV 1985; see Fig. 1). It occurs mainly in the floodplain and on the above-floodplain terraces of big rivers with well-developed valleys. In the calcareous N Urals foothills it is also known from sites along minor streams, at the bases of rock outcrops, and in karst ravines. The variant has the highest diversity of tall herbs (*Atragene sibirica, Cacalia hastata, Delphinium elatum, Pleurospermum uralense, Thalictrum minus, Veratrum lobelianum,* etc.; see Tab. 1, groups N, O, P, Q, R) and the highest constancy of Siberian montane fir forest plants like *Diplazium sibiricum* (Tab. 1, group Q) historically associated with the betular complex (KLEOPOV 1990). *Abies sibirica* occurs in the southern and south-eastern, and *Pinus sibirica* additionally in the eastern part of the variant area (Tab. 1, group Q).

The variant of *Cacalia* is roughly similar to the variant of *Abies sibirica* described by ZAUGHOLNOVA & MOROZOVA (2004) but differs in the determinant species set. The latter authors mention only *Abies sibirica, Diplazium sibiricum*, and *Vicia sepium* (which is common in the floodplain forests of the area but proved to be a companion, not a determinant) but omit the most of the tall-herb species (ZAUGHOLNOVA & MOROZOVA 2004: 320–321) which shape the ecological and florogenetical "face" of the syntaxon.

Along the Pechora R. the variant of *Cacalia* reaches the subarctic open woodland subzone (SAMBUK 1932).

3.2.2 Var. *inops*

This variant is peculiar of the southern part of the Timan Ridge (loc. 8; ANDREEV 1935) and the plain watershed of the rivers Izhma and Pechora where it is restricted to brook valleys. There is a huge set of hygrophytes differential for this unit, like *Carex cespitosa, Comarum palustre, Galium palustre,* and the most common *Rhizomnium pseudopunctatum* (Tab. 1, group S). Still we prefer to name this syntaxon "*inops*" as several tall-herb species (Tab. 1, groups N, Q: *Crepis sibirica, Cacalia hastata, Pleurospermum uralense*) are lacking while the abundance and constancy of *Calamagrostis langsdorffii* and *Vaccinium vitis-idaea* is increased.

Both variants, var. *Cacalia hastata* and var. *inops* occur at the same latitudes, often in adjacent landscapes, and are known from both silicate and carbonate bedrock. The possible reason for their floristic differentiation may be a relative difference in the spring melt water level in the minor and major river floodplains. In major river floodplains, gravity-dispersed plants like *Pleurospermum uralense* are successful in their secondary dispersal by water, which can hardly be effective along minor streams because of lower spring flooding scales. As a result, wind- and bird-dispersed plants are favored along minor streams. However, in var. *inops* also the tall ferns (*Athyrium filix-femina, Dryopteris expansa* s. l.; Tab. 1, group G) and the plants of the *Alnus incana-Padus avium* group (Tab. 1, group D), present in all syntaxa mentioned above, are lacking. The cause of this fact is yet unclear; probably, it is just a decrease in human influence.

3.3 *Aconito-Piceetum calamagrostietosum langsdorffii*

This subassociation described from the "Sivaya Maska" forest-tundra field station area (field data of KATENIN 1972), is the north-easternmost type (loc. 12; see Fig. 1). *Aconitum septentrionale* is yet constant but with lower abundance. The dominant role is "passed on" to *Calamagrostis langsdorffii* (the tendency is already perceptible in var. *inops*) and *Geranium sylvaticum* s. l. The unit is impoverished in many dark-coniferous forest mesophytes (Tab. 1, group E: e.g. *Oxalis acetosella, Maianthemum bifolium*), which played an important role in both subass. *aegopodietosum* and subass. *typicum*. At the same time, hypoarctic plants like *Betula nana, Salix glauca* etc. (Tab. 1, groups T, U) become determinant, some of them (*Rubus arcticus, R. chamaemorus*; Tab. 1, group T) already occurring in var. *inops*. The distinction of this subassociation is most surely climatically determined. Nevertheless, we hesitate to include it into a corresponding community, the *Geranio-Piceetum*, specific of the Kola-Karelian North and the timberline in the Urals (VASILEVICH 2004), because the *Geranio-Piceetum* seems to lack the betular element species totally, with the exception of *Geranium sylvaticum* and

Trollius europaeus, inherited from the Alleröd (RAMENSKAYA 1983), as well as *Milium effusum,* an Atlantic migrant in Fennoscandia. In contrast, many representatives of the betular complex (Tab. 1 groups P, T, U and the companions: *Aconitum septentrionale, Delphinium elatum, Veratrum lobelianum*, *Moehringia lateriflora* and *Trisetum sibiricum*) are constant in the subass. *calamagrostietosum*. Therefore this syntaxon is adjoined to the *Aconito-Piceetum*, as the presence of the betular complex species imply the common trends of vegetation history, namely the involvement in the same "waves" of plant migration and/or the probable common ancestral community types.

The subass. calamagrostietosum is expected to be met also in the other parts of the Usa R. basin.

In some of the studied localities, more than one of the *Aconito-Piceetum* sub-units were found. The subass. *aegopodietosum* var. of *Atragene* and subass. *typicum* var. of *Cacalia* occur in the Pinega R. middle reaches (loc. 4), the former in few ravines in combination with dryad-pine forests of *Carici albae-Pinetum* and other relict community types, the latter is widespread. Both variants of the subass. *aegopodietosum*, var. of *Convallaria* and var. of *Atragene*, are known from the SW Arkhangelsk Region (loc. 2) where they grow on silicate loamy sand and carbonate sandy loam, respectively.

The lower reaches of the Vychegda R. and most of the Mezen R. basin represent the "blank pages" in the *Aconito-Piceetum* distribution knowledge (Fig. 1). It is impossible to reliably map the ranges of var. of *Atragene* and var. of *Cacalia* in that part of the area without further field studies.

4 Discussion: Relations of the *Aconito-Piceetum* to analogous Scandinavian forests

The aconite-rich spruce forests of Finland and Scandinavia are described under the names *Aconitum*-Typ (e. g. CAJANDER 1921), *Melico-Piceetum aconitetosum* (Caj. 21) K.-Lund 62 (KIELLAND-LUND 1981, DIERβEN 1996) and *Picea abies-Geranium sylvaticum-Aconitum lycoctonum*-typ (PÅHLSSON 1994). Subalpine open aconite-spruce woodlands are also known from Norway as *Poo remotae-Aconitetum* K.-Lund 1962 (KIELLAND-LUND 1981).

The floristic composition of the *Melico-Piceetum aconitetosum* has much in common with that of the *Aconito-Piceetum*. They share light-forest mesophytes of the *Calamagrostis arundinacea-Carex digitata* group (Tab. 1, group C), boreal-nemoral nitrophilous species of the *Alnus incana-Padus avium* group (Tab. 1, group D), dark-coniferous forest mesophytes of the *Oxalis acetosella-Gymnocarpium dryopteris* group (Tab. 1, group E), tall ferns like *Athyrium filix-femina* (Tab. 1, group G), boreal-nemoral forest mesophytes of the *Melica nutans* group (Tab. 1, group H), and finally *Geum rivale* and *Crepis paludosa* among the companions.

The dry carbonate lowland race of *M.-P. aconitetosum* is rather similar to the "impoverished" form of var. of *Convallaria*, the westernmost (but silicate!) unit of the *Aconito-Piceetum.*

Nevertheless, we can treat the latter and *M.-P. aconitetosum* only as geographically replacing syntaxa but not as synonyms or subordinates, because, due to the more atlantic climate, the *M.-P. aconitetosum*, especially in its moist var. of *Crepis paludosa* contains more hygrophytes (*Rhizomnium punctatum*) and hygromesophytes (*Circaea alpina, Plagiomnium affine;* Tab. 1, group B). Moreover, the ground cover dominance is shared between *Aconitum septentrionale, Filipendula ulmaria* and tall ferns (*Dryopteris assimilis, Athyrium filix-femina*). Thus, the *M.-P. aconitetosum* is ecologically intermediate between the *Aconito-Piceetum* and the *Filipendulo-Piceetum* (VASILEVICH 2004), which is a more hygrophilous East-European forest association. The *M.-P. aconitetosum* replaces both the *Filipendulo-Piceetum* and *Aconito-Piceetum* in the atlantic sector of the Northern Europe (VASILEVICH 2004). The distinction of the *Aconito-Piceetum* as a separate unit is also supported by the presence of a number of species, not only tall herbs of the betular complex (see Tab. 1, groups N, O, P, Q, R) but nemoral and boreal-nemoral forest plants as well (see Tab. 1., groups I, J, K, L, M), which are typical of the *Aconito-Piceetum* (or some of its subassociations) but absent in the *M.-P. aconitetosum.*

Stands, which are ecologically intermediate between the *Aconito-* and the *Filipendulo-Piceetum* (*F.-P. aconitetosum*) and close to the *M.-P. aconitetosum,* with *Circaea alpina, Cirsium oleraceum, Chrysosplenium alternifolium,* and *Matteuccia struthiopteris* as constants and the moss cover composed of *Brachythecium oedipodium* s. l., *B. rivulare*, *Plagiomnium* spp., also *Plagiochila asplenioides* and *Conocephalum conicum*, have been described by the author from minor river alluvia in the S Arkhangelsk Region (loc. 2, 6; see Fig. 1). But they differ from *M.-P. aconitetosum* in the high constancy of tall herbs like *Crepis sibirica*, *Veratrum lobelianum, Valeriana wolgensis* and even *Cacalia hastata*.

The boundaries separating the range of *M.-P. aconitetosum* from *Aconito-Piceetum aegopodietosum* var. of *Convallaria majalis* in East Fennoscandia, are yet unclear. Both syntaxa could be expected (although rather seldom) in SE and Central Finland but up to now, no data exist to prove or contradict this idea.

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