Alchemilla parcipila Juz. and *A. stellaris* Juz. as polemochores in Finland – the first records outside Russia – and the correct identity of *A. polemochora* S.E.Fröhner

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Two species of the genus Alchemilla are reported from the province of Kainuu in eastern central Finland as new to the country. A. parcipila was collected in 2017 in the municipality of Kuhmo at the sites of two wartime Russian military camps. Review of older herbarium material (H, OULU) revealed several previous collections of the species from these two localities between 1957 and 2016. The species is native to western Siberia and the easternmost parts of European Russia in the Ural Mountains. From this original area, it was probably already introduced into parts of central and northwestern Russia in ancient times by Russian traders and settlers. A. stellaris was also collected in 2017 at the site of a Russian wartime camp in the municipality of Suomussalmi. This is the only known locality of the species in Finland. A. stellaris is endemic to the subboreal and southern boreal zone of European Russia, from Tver in the west to Perm and Ekaterinburg in the east. Outside its native range, the species is known as a neophyte in northwestern Russia from Chibiny, Kola Peninsula and Petrozavodsk, Republic of Karelia. Both species were found for the first time outside of Russia. Another Russian polemochore, A. polemochora, was described in 1981 from two localities in Finland, which have so far remained the only known finds of the species. A. polemochora is here synonymized with A. sergii, described from the province of Moscow, central Russia, in 1972.

Introduction

The eastern part of the Finnish province of Kainuu saw heavy fighting during the Finnish-Russian Winter War in 1939–40. Russian troops advanced westwards along the few existing road lines from the Finnish-Russian border and entrenched at many sites of Finnish farms, which offered open fields and meadows in the otherwise forested area. Parts of the municipalities of Kuhmo and Suomussalmi were occupied by Russian troops, in some areas from the start of the war on November 30, 1939 until the end of it on March 13, 1940. In several places, however, Russian military units were encircled and destroyed by Finnish troops during the war.

The Russian troops were partly horse-powered. Horses were used by service troops as draught animals to transport ammunition and other equipment as well as provisions, and cavalry units were also included. Forage - mainly dry hay and straw - for the animals was supplied from the area of origin of the troops and freighted along with them. Seed and other propagules of exotic plant species were imported with the hay, giving rise to new occurrences of neophytes (e.g. Huuskonen 1944, Fagerström 1957). Many of the neophytes were only casual, but some have managed to survive until modern times (Piirainen & Piirainen 2000). Several species of the genus Alchemilla L. belong to the survivors, which can still be found in old battlefields and military campsites today (e.g. Piirainen & Piirainen 2017). The longlasting presence of some Alchemilla species as far north as 69°40'N in some Russian World War II military camps in northern Norway provide evidence for the persistence of the plants (Piirainen & Alm 2001, Piirainen 2006).

Heikkinen (1969) noted that the rich polemochorous *Alchemilla* flora in the province of Kainuu was mainly of Russian origin, but partly also brought in by German troops in 1941–44. He regarded nine species of *Alchemilla* as Russian polemochores: *A. auriculata* Juz., *A. cymatophylla* Juz., *A. glabra* Neygenf., *A. glabricaulis* H.Lindb., *A. heptagona* Juz., *A. hirsuticaulis* H.Lindb., *A. leiophylla* Juz., *A. plicata* Buser and *A. propinqua* H.Lindb. ex Alexandrov & Nekr. In addition, several other species, which had been present in the province before the war, were also brought in by Russian troops. In 1994, J. Nurmi found still another polemochore from Suomussalmi, *A. gibberulosa* H.Lindb. (H-Arch.).

Piirainen & Piirainen (2000) visited several Russian military campsites in Kuhmo in 1997 and regarded at least seven species of *Alchemilla* as Russian polemochores in the localities examined: *A. baltica* Sam. ex Juz., *A. glabricaulis, A. heptagona, A. hirsuticaulis, A. leiophylla, A. sarmatica* Juz. and *A. semilunaris* Alechin. In 2000, they visited Suomussalmi (data in the floristic database Kastikka of the Finnish Museum of National History). The polemochorous *Alchemilla* species were more or less the same as in Kuhmo, and two species could be added: *A. plicata* and *A. propinqua*. During a short visit in 2017, *A. cymatophylla* was added to the list.

Here, we introduce two new polemochorous species of *Alchemilla* found in Kuhmo and Suomussalmi in 2017: *A. parcipila* Juz. and *A. stel*- *laris* Juz. (The record of *A. stellaris* was previously dealt with in Finnish by Piirainen & Piirainen 2018). We also discuss the correct identity of *A. polemochora* S.E.Fröhner, a Russian polemochore known only from two localities in Finland.

Alchemilla parcipila

Alchemilla parcipila (Fig. 1), usually a medium to large-sized species, (20-)35-60 cm tall. Stems slightly hairy with patent hairs in lowermost internode(s), otherwise glabrous. Outer petioles glabrous, inner ones often very sparsely hairy with patent or deflexed hairs. Petioles of young and small summer leaves with still unfolded blades (if present) hairy with erectopatent hairs. Leaf blades almost flat, dark green, 5-9 cm, reniform (the outermost) to orbicular with only a narrow sinus. Leaf lobes 7-9, arcuate to broadly triangulate, with short incisions between them (usually 0.5-1.0 standard tooth length, rarely to 2.0 only for the outermost leaves). 11-15(-17) subovate, bluntish or acutish teeth in each lobe, with S-shaped lateral side. Blades rather sparsely hairy above, at least on folds and on marginal teeth, but more often over entire surface; hairy below only in apical third of main veins, otherwise glabrous. Pedicels and hypanthia glabrous.

Alchemilla parcipila is morphologically very similar to A. glabricaulis. The main difference is in the indumentum: the stems and petioles of A. glabricaulis are totally glabrous, as are also the petioles of the young, small summer leaves with still folded blades. The blades of the inner summer leaves are often more roundish in A. parcipila than in A. glabricaulis, but this character is only suggestive. Walters & Pawlowski (1968), in a note under A. glabricaulis, stated "Some material determined by Juzepczuk as this species has entirely glabrous petioles, however, and cannot be distinguished from 84 [= A. glabricaulis]". Vydrina (1988) included A. parcipila in A. glabricaulis, accepting the latter species as having either glabrous stems and petioles or very slightly hairy lower stem internodes and petioles of the inner leaves. Tikhomirov (2001) accepted the status of A. parcipila as a separate species. He included it in ser. Heteropodae, emphasizing that the indu-



Figure 1. Alchemilla parcipila collected from the site of the former Loso farm in Kuhmo (Kainuu, eastern central Finland) by M. Piirainen 7108 & P. Piirainen 4.VII.2017 (H-836573).

mentum of the species may vary within and between individuals, but that *A. glabricaulis* always has completely glabrous stems and petioles. In our opinion, *A. glabricaulis* differs in having (1) evenly hairy leaf blades above vs. often glabrescent in *A. parcipila*, (2) angle of leaf blade sector of the uppermost leaves from 45° (45°–50°) vs. less than 45° (35°–40°) and (3) rounded lateral side of teeth at the uppermost leaves vs. Sshaped.

Juzepczuk (1951) described Alchemilla parcipila, based on specimens collected from the western slope of the middle Ural Mountains. It grows in subalpine meadows or at the alpine tree line, usually with tall grasses and herbs, in normally or sufficiently moist habitats. Kurtto et al. (2007), who treat it as a separate species, stated that it has a very limited distribution on the European side of the Urals. However, all the material collected to the east of the Urals, based on which Vydrina (1988) noted A. glabricaulis for Siberia, have the features of A. parcipila. In addition to the middle and northern Urals, northwestern Siberia and the Altai Mountains, this species was collected in several synanthropic locations from central and northwestern Russia (Vologda prov., Gryazovets, K. Molodkina, 06.VI.2017, MW; Rep. Karelia, Petrozavodsk, 19.VI.2010, A. Kravchenko, PTZ; Ivanovo prov., Plyos, M. Golubeva, 02.VI.1998, MW). It was probably already introduced there in ancient times by Russian traders and settlers. A. parcipila is also accepted at the species level in the Euro+Med Plantbase (Kurtto 2009). The record presented here is the first outside of Russia.

Alchemilla stellaris

Alchemilla stellaris (Fig. 2), usually a small or medium-sized species, app. 20–40 cm tall. Stems hairy with patent hairs in lower parts, upper part glabrous. Petioles hairy with patent hairs, but often glabrescent in uppermost parts; such petioles often also very sparsely and only unilaterally hairy. Leaf blades flat, dark green, 2–6 cm \times 2–7 cm, reniform to orbicular reniform in outer leaves, orbicular in inner ones; sinus of inner leaves narrow or basal lobes touch each other. Leaf lobes 7–9, rather long, giving leaves a star-shaped appearance; lobes of outer leaves roundish semielliptic, those of inner leaves ovate to rather sharply triangular, incision between them short (less than 1.5 standard tooth lengths) in outer leaves, in inner leaves almost missing. 11–17(–19) obliquely triangular, sharp teeth in each lobe. Blades of outer leaves usually glabrous or glabrescent above, hairy below only along main veins. Middle leaves sparsely hairy on both sides. Inner leaves hairy only on folds and teeth above, glabrous below except for apical part of main veins. Monochasia rather lax, flowers small, pedicels and hypanthia glabrous, sepals with solitary or few hairs.

Juzepczuk (1933) described Alchemilla stellaris, based on specimens collected from the provinces of Tver and Moscow. The species is endemic to the subboreal and southern boreal zone of European Russia, approximately from Tver in the west to Perm and Ekaterinburg in the east (Kurtto et al. 2007, Chkalov 2012). It occurs sporadically, usually only solitary or a few specimens, avoiding very dense polydominant Alchemilla meadows, mostly in the forest edges, low-grass meadows and abandoned fields. It rarely forms a monodominant community with very high cover, which is probably caused by occasionally low interspecific competition. The species is sometimes regarded as near threatened (NT), at least in the provinces of Kirov (Baranova et al. 2014) and Nizhny Novgorod (Bakka & Kayumov 2014). Outside its native range, the species is known as a neophyte in northwestern Russia from Chibiny (Ramenskaya & Andreeva 1982), Kola Peninsula, and Petrozavodsk, Republic of Karelia (Kravchenko et al. 2016). The record presented here is the first outside of Russia.

Localities

Alchemilla parcipila is known from two localities in Kuhmo. (Specimens deposited at H and OULU have been checked so far.) All the herbarium specimens were previously filed under *A*. *glabricaulis*. They were sorted out of *A. glabricaulis* by M. Piirainen in 2018 and identified as *A. parcipila* after e-mail consultation with A. Chkalov.



Figure 2. *Alchemilla stellaris* collected from Harjula (= Likoharju) farm, Suomussalmi (Kainuu, eastern central Finland) by M. Piirainen 7107 & P. Piirainen 3.VII.2017 (H-836571).

(1) Kuhmo, Saunajärvi, Riihivaara, Saarivaara, 63°54'30"N, 30°13'27"E (WGS84), alt. 250 m above sea level (a.s.l.).

Herbarium specimens: L. Heikkinen s.n., 10.VII.1957, H-010175; A. Parnela s.n., 19.VII.1993, OULU-152575; M. Piirainen 3593 & P. Piirainen, 24.VII.1997, H-730354 (collected as *A. semilunaris*, det. as *A. glabricaulis* by S. Ericsson 1999); H. Kämäräinen 2001-297, 15.VII.2001, H-749365; H. Kämäräinen 2001-312, 15.VII.2001, H-749363; T. Hietanen 5516, 20.VII.2016, H-836465 (collected as *Alchemilla* sp., det. as *A. glabricaulis* by M. Piirainen 2017); M. Piirainen 7111b, 4.VII.2017, H-833077, dupl. in NNSU.

Saarivaara was occupied by Russian troops throughout the Winter War. Relatively large numbers of troops were housed there, including artillery (Siilasvuo 1944). The locality is well known for its rich polemochorous flora (Piirainen & Piirainen 2000). A special case is Alchemilla auric*ulata*, which is an eastern species from a limited area in the Ural Mountains (Kurtto et al. 2007). The species was first reported from Finland by Heikkinen (1969). He found it in 1958 at Kontiomäki railway station in Paltamo, Kainuu. The locality is far from the battle areas of the Winter War, so the species must have been brought there either from Kuhmo or Suomussalmi, possibly in connection with transport of Russian war material captured by the Finnish troops - including horses and hay. Stefan Ericsson (UME) determined in 1995 one specimen collected by L. Heikkinen from Kuhmo, Saarivaara in 1963 as A. auriculata. Heikkinen's determination had been A. obtusa Buser (A. samuelssonii Rothm. ex S.E.Fröhner in modern taxonomy; for further information and other records, see Piirainen & Piirainen 2017). Other Russian polemochorous Alchemilla species from Saarivaara include A. baltica, A. cymatophylla, A. glabra, A. glabricaulis, A. heptagona, A. hirsuticaulis, A. leiophylla, A. plicata, A. propingua, A. sarmatica and A. semilunaris.

There was a Finnish farm on the top of a low hill at Saarivaara before and after the war, but it was abandoned decades ago. There is still an area of app. 3.2 ha of more or less open field and meadow left. Although most of the fields have been more or less uncultivated for several decades they have been kept open by cutting the hay annually. Part of the meadow is dominated by *Deschampsia cespitosa* (L.) P. Beauv., while part has more diverse herb and grass vegetation. (2) Kuhmo, Saunajärvi, Losovaara, Loso, 63°54'57''N, 30°4'40''E, alt. app. 260 m a.s.l.

Herbarium specimens: M. Piirainen 3577 & P. Piirainen 24.VII.1997, H-835127 (collected as the *Alchemilla* Retropilosae group, determined as *A. glabricaulis* by M. Piirainen 2016): M. Piirainen 3582 & P. Piirainen, 24.VII.1997, H-730355; M. Piirainen 7108 & P. Piirainen 4.VII.2017, H-836573.

Loso farm was occupied by Russian troops on December 1, 1939. It was encircled and isolated by Finnish troops on January 29, 1940, but regardless of several attempts to take it back by the Finnish army, it remained under Russian control until the end of the war. The strength of the Russian troops at Loso was about one battalion (Siilasvuo 1944). Piirainen & Piirainen (2000) were the first to survey the flora in the locality in 1997 and found *Alchemilla acutiloba* Opiz, *A. baltica, A. glabricaulis, A. hirsuticaulis, A. monticola* Opiz, *A. semilunaris* and *A. subcrenata* Buser, together with several polemochores in other genera.

The former Loso farm was abandoned several decades ago. In 1997, the fields and meadows covered an area of app. 7.5 ha, but almost all of it was either afforested or naturally overgrown with young forest during a short visit by M. Piirainen and P. Piirainen in 2017. All previously seen *Alchemilla* species were found again, except for *A. hirsuticaulis*.

Alchemilla stellaris was found during fieldwork by M. Piirainen and P. Piirainen in Suomussalmi in 2017.

(1) Suomussalmi, Alavuokki, Harjula (= Likoharju) along the Raate road 64°49'32"N, 29°29'13"E, alt. app. 225 m a.s.l.

Herbarium specimens: M. Piirainen 7106 & P. Piirainen, 3.VII.2017, H-836570; M. Piirainen 7107 & P. Piirainen, 3.VII.2017, H-836571, dupl. in NNSU.

Russian troops occupied Harjula from December 5, 1939 to January 7, 1940 (Siilasvuo 1940). In the last phase of the battle, a Russian frontier guard battalion of about 600 men, a cavalry squadron and smaller numbers of other troops were encircled in the area (Onttoni 1940). When Finnish troops took back Harjula, the booty included about 50 living horses. The owner of the farm (pers. comm. 2017) stated that several dozen horses killed in the battle were also buried at the field margin.

The owner of the farm was aware of several Russian polemochorous plant species (pers. comm. 1997). *Briza media* L. was growing by the Winter War monument along the Raate road, and more of it could be found in the meadows south of the farm buildings. *Centaurea phrygia* L. also appeared south of the buildings after the war; people first thought it was a type of thistle and were surprised because it had no spines. Other species regarded as Russian polemochores were *Galium album* Mill., *G. boreale* L., *Hypericum maculatum* Crantz and *Veronica chamaedrys* L.

During a visit in 2001 (M. Piirainen), five species of Alchemilla were found at Harjula: A. glabricaulis, A. monticola, A. plicata, A. propinqua and A. subcrenata. In addition, A. baltica, A. micans Buser, A. murbeckiana Buser and A. sarmatica were reported from the site by Heikkinen (1969). In 2017, A. cymatophylla and A. leiophylla could be added to the list. Alchemilla stellaris was found scattered in the meadows west of the buildings, standing out as unusually dark green patches with star-shaped leaves. Herbarium specimens were collected from two sites. The specimens were collected in the field as possible A. filicaulis Buser, but were determined as A. stellaris after closer examination in the herbarium, using the keys in Juzepczuk (1941) and Tikhomirov (2001). The determinations were confirmed from digital photographs and a duplicate specimen by A. Chkalov in 2018.

Harjula farm is still inhabited. Only part of the former fields are under active cultivation, but most are kept open by annual cutting. The open area in 2017 was app. 2.6 ha; many of the former fields and meadows have been afforested.

Identity of Alchemilla polemochora

Fröhner (1981) described Alchemilla polemochora from two Russian wartime campsites in Suomussalmi and Kuusamo (province of Kuusamo District), Finland. The species is certainly of Russian origin, although it has never been recorded outside of these two Finnish localities. It was last seen in Kuusamo in 1966. However, *A. polemochora* seems to be identical to another species described from central Russia 9 years earlier than Fröhner's species, i.e. *A. sergii* V.N.Tikhom. (Tikhomirov 1972). We base our opinion on comparison of the protologues and examination of the original material of *A. polemochora* at H and OULU (the latter from digital images).

Fröhner (1981) cited the collection of L. Heikkinen from Suomussalmi, Juntusranta July 3, 1964 as the [holo]type. There are three sheets of this collection at OULU. The specimen OULU-105272 is the holotype, since it is the only specimen seen and annotated by Fröhner. According to the protologue, the specimen should belong to H (cited as "HE" by Fröhner). The specimen was sent on loan to Fröhner via H in March 1968, and the loan records at H show that the specimen was still part of Heikkinen's private herbarium at the time. The specimen label has the printed heading "Museum Botanicum Universitatis, Helsinki", which clearly mislead Fröhner into believing it belonged to H (at the time, the herbarium sheets at H and OULU were not stamped and numbered). Later, probably at the time when Heikkinen donated his private herbarium to OULU, the heading was crossed out with a pen. Thus, Fröhner saw only one sheet of the gathering, which he thought would belong to herbarium H, because of the title printed on the specimen label. He also annotated only this sheet and not the other two, which confirms that he did not see the two isotypes (OULU-105846, OULU-105891). Heikkinen did not send the isotypes on loan to Fröhner, probably because he had (mis)determined them as A. haraldii Juz. and failed to realize that all three sheets belonged to the same unknown taxon. These two sheets were determined as A. polemochora by T. Ulvinen in 1983.

Fröhner's annotation on the holotype sheet is identical ("certissime species nova...") to the one he made on the specimen collected July 22, 1966 by T. Ahti & L. Hämet-Ahti 22138 from Kuusamo (H-083905, a paratype); this specimen was included in the same loan to Fröhner as the holotype. Fröhner cultivated the species in his garden from seed of this specimen. He used the name Alchemilla polemochora in his herbarium and garden since at least 1972, because on the labels of the three cultivated specimens (1973-74) at H (H-732894, H-732895, H-732896; paratypes) he wrote "det. S. Fröhner 1972". However, he waited too long in publishing the name, and Tikhomirov's name was published earlier. Thus, Fröhner and Tikhomirov knew the species at the same

time, and both also cultivated it before publishing, but they were not aware of each other's work.

In the protologues, one difference between the two species seems to be revealed: the flat leaf blades of *Alchemilla sergii* and the undulate of *A. polemochora*. Actually, this statement is false. The leaves of *A. sergii* are mostly plicate, often even the outermost; the innermost summer leaves are evidently undulate (but usually they are absent in herbarium material collected from natural habitats). The outermost and middle (spring) leaves of *A. polemochora* are often flat. Some species of this affinity normally vary in degree of leaf blade folding.

Morphologically, the species seem similar, although most specimens of A. polemochora were collected later (in late July) and have summer leaves. The structure of the leaves, especially the lobe form, depth of the incisions between the lobes, size of the apical teeth, inflorescence and monochasia are similar. The dense erectopatent pubescence of the pedicels is also common to both species; this characteristic is very unusual for species of this group. A few differences include: (1) the angle of the leaf blade sector of A. sergii is smaller (37°-45°), but there is an overlap between the species and (2) the more acute, slightly larger and more clearly outwards-directed teeth of A. sergii. But the last feature is very variable in closely related species, e.g. A. monticola. So there are no differences in taxonomically important stable features, and A. polemochora is merely a synonym of A. sergii.

Origin of the species and some historical notes

Several distinct distribution patterns can be recognized by examining the total distribution (Kurtto et al. 2007) of the polemochorous Russian species of *Alchemilla* found in Kainuu.

(1) The Eastern European species Alchemilla glabricaulis, A. heptagona, A. leiophylla, A. propinqua, A. semilunaris and A. stellaris are widespread throughout all European Russia from the Urals to the Baltic and partly even in central Europe. They are mostly found in the subboreal or southern boreal, rarely the nemoral zone. In addition, several species with the same type of distribution have recently been found in the Republic of Karelia, northwestern Russia: *A. mininzonii* Czkalov, *A. schistophylla* Juz., *A. substrigosa* Juz., *A. tichomirovii* Czkalov and *A. vorotnikovii* Czkalov (Kravchenko 2007, Kravchenko et al. 2016). *A. sergii* (*A. polemochora*) is a poorly known species, but is endemic to central Russia and more locally distributed than most species of this group. *A. gibberulosa* also belongs here.

(2) The second group is very peculiar, with the disjunctive Uralian-Altaic species *Alchemilla parcipila* and *A. auriculata*. In their native range, they are confined to the high-mountain belts.

(3) Alchemilla baltica, A. cymatophylla, A. hirsuticaulis and A. sarmatica belong to the Eastern European-Siberian group. Their ranges extend from eastern Siberia, sometimes from Mongolia to the Baltics or even central Europe. They are now rather common species and, at least in the middle boreal zone, they can grow in natural habitats, such as damp meadows, moist open woodlands, stream banks and wet pastures with Trollius europaeus L., Geum rivale L. and Geranium pratense L. A. baltica is also known from high-mountain belts of both the Urals and Altai. The primary frequency of these species was probably directly proportional to the area of such vegetation communities, i.e. quite low. Human activity has expanded the area of mesophilous grassy communities, which are the most favourable for most species of Alchemilla, and their occurrence has increased proportionally. Most species of Alchemilla are clearly apophytes, and anthropogenic pastures and their seminatural derivatives offer them a suitable ecological niche with restrained disturbances conducive to resettlement, low competition from trees and tall herbs, and promote invasion of both indigenous and adventive species of Alchemilla. In Finland, these four species are clearly eastern. A. baltica and A. hirsuticaulis are regarded as archaeophytes, the other two as neophytes; A. cymatophylla is confined to Russian campsites from World War II.

(4) Alchemilla acutiloba, A. monticola and A. subcrenata are Euro-Siberian, highly synanthropic and are distributed more widely than the previous group, occurring in both the Alps and the Mediterranean. It is almost impossible to reveal the exact origin and the distribution paths of representatives in this group, especially because they are regarded as archaeophytes in Finland and are very common in most of the country, including Kainuu. *A. glabra* also formally belongs to this group, but it is a hypoarctic-alpine species. In Finland, it is native in the south, but a very rare neophyte in Kainuu.

(5) The range of the central and Northern European *Alchemilla plicata* reaches the central regions of European Russia. It is impossible to judge the origin of the species in Kainuu, where it is regarded as a neophyte, because it is a relatively common archaeophyte in southern Finland and quite common both in the Baltics and to the east in Russian territory.

The extensive anthropogenic distribution of several species of *Alchemilla* and the presence of some Uralian and Siberian species in the eastern parts of central Russia can be understood in a wider historical perspective (reviewed here after Oborin 1990). The middle Urals (the present territory of the Perm region) has a long history of various relationships with the northwestern and central areas of European Russia. The region was associated with medieval Europe, Turkey and Persia via tax collectors and tradesmen. The medieval state of Novgorod began trading with indigenous tribes since at least the 11th century. It tried to colonize this territory in the 11th to 15th

Figure 3. Total European distribution of 10 Russian polemochorous species of the genus Alchemilla found in Kainuu: A. auriculata, A. cymatophylla, A. gibberulosa, A. glabricaulis, A. heptagona, A. leiophylla, A. parcipila, A. semilunaris, A. sergii (syn. A. polemochora) and A. stellaris. The symbols show the number of species in the grid squares used in Atlas Florae Europaeae. Data compiled from Kurtto et al. (2007).

centuries, including military measures, taxing these tribes regularly and collecting tolls. Since the 12th century, the same actions were undertaken by the state of Vladimir-Suzdal: the fortresses of Glyaden (1173) and Velikiy Ustyug (1212) were founded here to protect their interests. These crusades mainly used the so-called «North Way» from the river basins of the Volkhov, Onega and Volga via the valleys of the Sukhona and Vychegda rivers to the Pechora and Kama basins.

After the Mongol invasion of the 13th century, a great part of the population escaped from the Kama basin to the west. The state of Moscow inherited Vladimir-Suzdal and continued colonization, founding fortresses and towns, resettling people from the northern regions of Russia, spreading Christianity and sometimes resorting to military sanctions. By the late 15th century, this territory was included as a part of the state of Russia extending into Siberia already in the 15th century through the «North Way» across the Ural Mountains. The route served for a long time as the key transport artery. In the 17th century, a mass resettlement of peasant families to the Kama basin occurred along this route, mostly from the Vologda and Arkhangelsk regions, forming a substantial part of the population. Thanks to this, family ties also maintained the connections between these highly remote regions.

The species of Alchemilla have a remarkable ability to spread over long distances with human aid. Their seeds are effectively dispersed over long distances in the dry hay used as fodder for horses and cattle, or as cushions in sledges and carts. There is good reason to conclude that much of the current distribution of several Alchemilla species is of (archaeophytic) anthropogenic origin. The origin of the hay used as fodder by the Russian troops in Kuhmo and Suomussalmi is probably somewhere in central Russia, perhaps in the area between Moscow - Vologda – Mari El (Fig. 3). Central Russia belongs to the diversity centres of the genus in Europe, with at least 31 species endemic to the area (Kurtto et al. 2007, Chkalov & Vorotnikov 2009), some of which have recently been found outside Finland in the Russian Republic of Karelia (Kravchenko 2007, Kravchenko et al. 2016). After closer examination of Russian campsites, might some species perhaps still be found even today in Finland, 80 years after the Winter War?

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