Ecology and distribution of Frullania bolanderi in Europe

Author: Lye, Kåre Arnstein

Source: Lindbergia, 37(2) : 6-21

Published By: Dutch Bryological and Lichenological Society and Nordic Bryological Society

URL: https://doi.org/10.25227/linbg.01047

Lindbergia 37: 6–21, 2014
ISSN 0105-0761
Accepted 18 February 2014

Ecology and distribution of *Frullania bolanderi* in Europe

Kåre Arnstein Lye

K. A. Lye (kare.lye@nmbu.no), Dept. of Ecology and Natural Resource Management, Norwegian Univ. of Life Sciences, PO Box 5003, Sørhellinga, Høgskolevegen 12, NO-1432 Ås, Norway.

Frullania bolanderi is in Europe known from Norway, Sweden and Russia only. The ecology of *F. bolanderi* in 16 Norwegian localities is described in some detail, while its ecology in Sweden and Russia is given from literature. *Frullania bolanderi* has a wide ecological amplitude growing on many different trees, often in shady ravines near streams and rivers, but sometimes in only slightly undulating forest, more rarely in an open landscape with scattered trees only. At the beginning of the year 2000 *Frullania bolanderi* was known from one locality in Sweden, three localities in Norway and about five localities in European Russia. However, during the years 2000–2013 numerous new localities were discovered and this hepatic is now known from about 150 localities in Norway [but only about 60 if merely localities more than 1 km apart are considered], three in Sweden and about 25 in European Russia. In the past *F. bolanderi* was considered as strongly endangered (EN) or critically endangered (CR) in Norway and Sweden, but the many new records have resulted in it being downgraded to a lower conservation category in Norway, i.e. vulnerable (VU) according to the newest Norwegian redlist. The plant is also a member of the European redlist, but should perhaps be removed from this list.

Frullania bolanderi Austin (Fig. 1) forms thin olive brown to reddish black closely appressed patches 1–5 cm in diameter on trunks of many different trees with smooth bark. Shoots are 1–2 cm long and 0.6–1 mm wide, irregularly 1–2 pinnate with numerous upright or curving flagelliform branches 2–10 mm long (Fig. 1, 2). Stems 0.1–0.15 mm in diam. The leaves are two-lobed (in addition to a narrow inconspicuous triangular reduced lobe named stylus) with one lobe folded over the other [conduplicate-bilobed], deeply divided into almost free lobes, the dorsal lobe imbricate, incubous, ovate to obovate, 0.3–0.7 mm long, somewhat deflexed, crossing the stem, without specialised enlarged cells (ocells), the ventral lobule helmet-shaped (galeate), 0.2–0.4 mm across (1/3 – 1/2 the size of the dorsal lobe); leaf cells rounded-hexagonal, thick-walled with fairly large trigones, 15–20 × 20–25 µm, smooth, the marginal cells often slightly smaller. Oil bodies 5–9 per cell, hyaline, globose to ovoid (Fig. 3). Underleaves two-lobed, 0.1–0.3 mm long, the lobes 1/3 – 1/2 the length of the leaf; margin plane (Fig. 4). Flagelliform upper part of shoots 1–4 mm long with about 0.1 mm thick branched or unbranched stems and 0.1 mm long stiff spreading underleaves (Fig. 2, 5) and modified caducous dorsal lobes of leaves (also named large discoid gemmae) 0.2–0.3 mm long and wide functioning as vegetative propagules, which often start germination from marginal leaf-cells while still attached to the shoot (Fig. 3). Dioecious. Sporophytes are rare and not known from Europe. For a more detailed description see Damsholt (2009).

The genus *Frullania* is a member of the family Frullaniaceae (Damsholt 2009) and the order Porellales; the genus is according to morphology as well as molecular analysis most closely related to the genus *Jubula*, a more tropical genus reaching as far north as Great Britain. The genus *Frullania* is sometimes included in the family Jubulaceae (Schuster 1992, Hentschel et al. 2009).

The classification of the different species of *Frullania* into subgenera and sections has been in a state of confusion, see "Similar species".

History of discovery

Frullania bolanderi was described from Tomales Bay in California (Austin 1870), and in Europe it was first collected 2 June 1879 near Oslo by F. Kiær. However, this first European collection was originally identified as *F. dilatata* (L.) Dumort. Jørgensen (1934) identified this collection as the American species *F. oakesiana* Austin, but noted that it sometimes produces decumbent upright flagelliform shoots with small 2-lobed leaves as described by Austin for *F. bolanderi*. In 1930 Verdoorn identified the

Figure 1. *Frullania bolanderi* from Sauherad in Telemark, Norway (locality 36: Lye 38419). Photo: K. A. Lye November 2013.

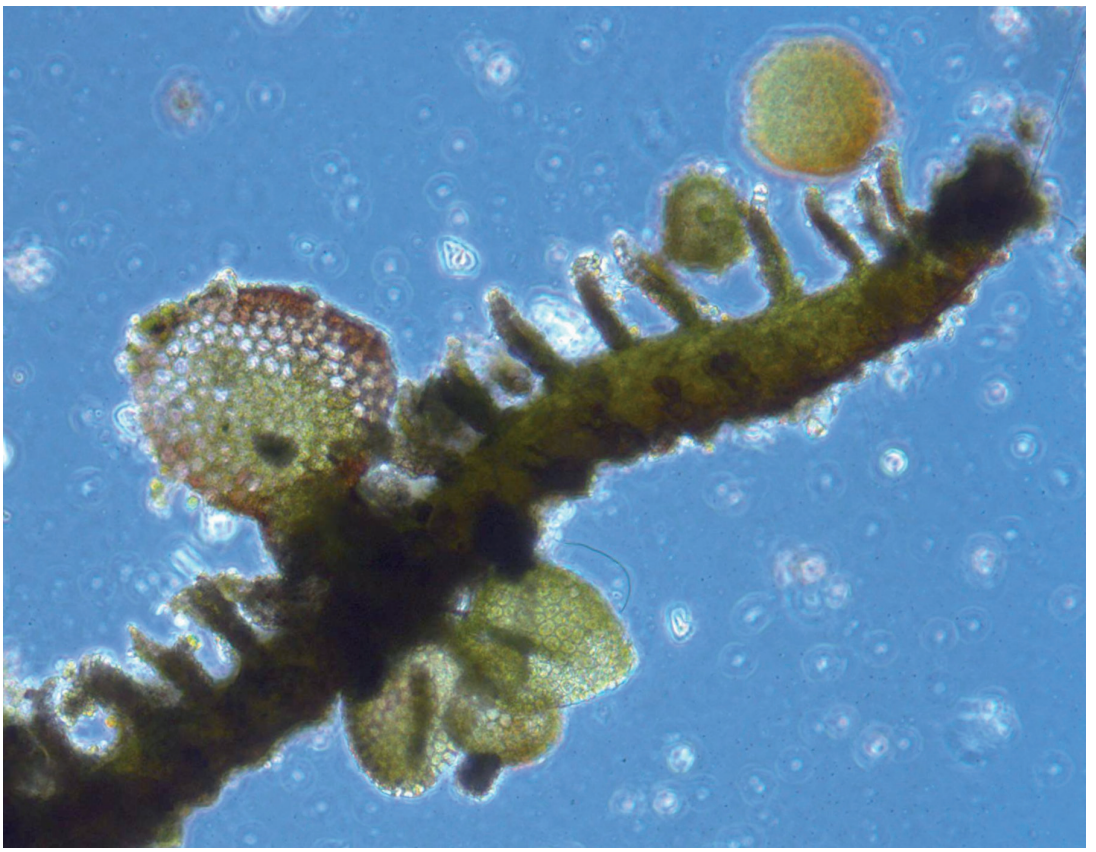

Figure 2. A 1.5 mm long part of a flagelliform branch of *F. bolanderi* with stiff spreading underleaves and thin caducous dorsal lobes of modified leaves (large discoid gemmae). Note that one of the leaves has started germinating prior to detachment. The largest modified leaf is about 0.3 mm across. Microphoto from Lye 36471 from Nesodden, Akershus (locality 15), Norway (January 2013).

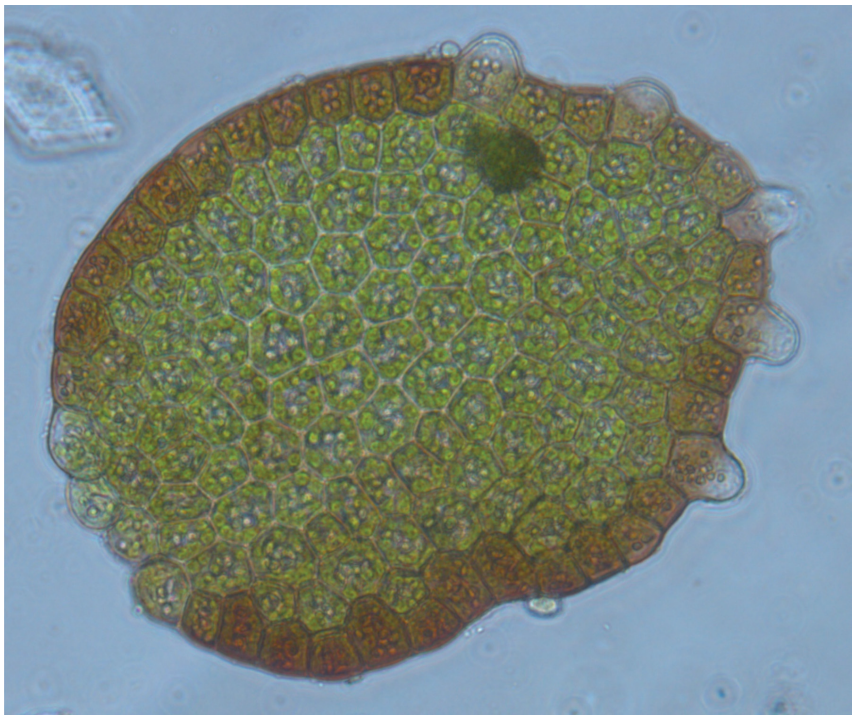

Figure 3. Young detached dorsal lobes of modified leaves (large discoid gemmae) of *F. bolanderi*, which has started to germinate, probably producing rhizoids on the right end and stem and leaves on the left end. The cells are 15–25 µm across. Note that most cells have 5–9 hyaline oil bodies. This modified leaf is about 0.3 mm long. Microphoto from Lye 36471 from Nesodden, Akershus (locality 15), Norway (January 2013).

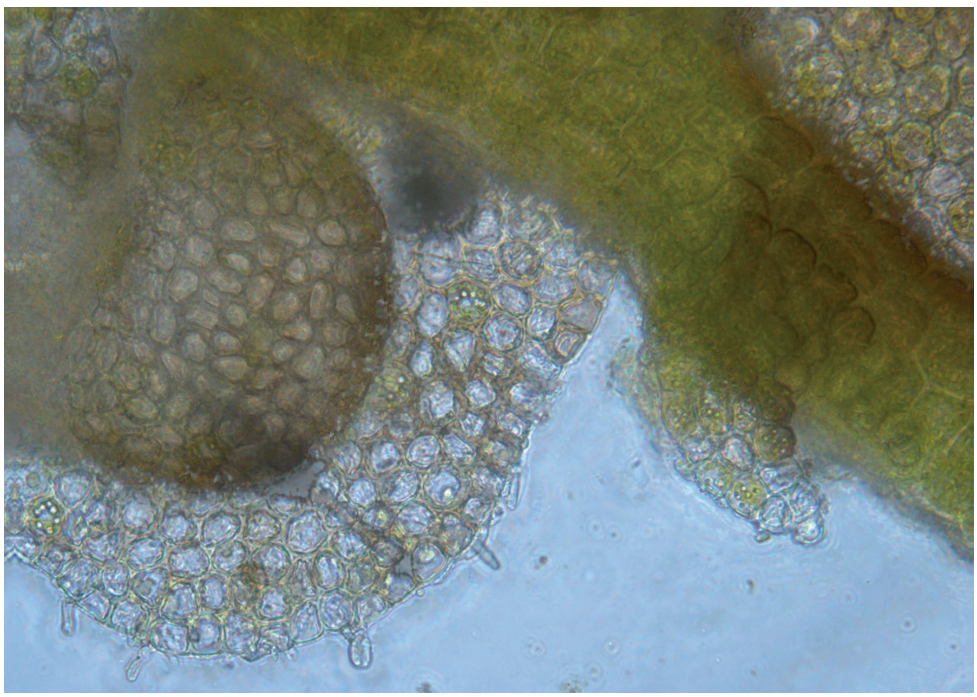

Figure 4. *Frullania bolanderi*. The two major lobes of the leaf with the helmet-shaped ventral lobule in front. An underleaf is seen to the right. Note the cylindrical to clavate 15–20 µm long outgrowth along the margin of the dorsal lobe. These are probably slime cells. Microphoto from Lye 36471 from Nesodden, Akershus (locality 15), Norway (January 2013).

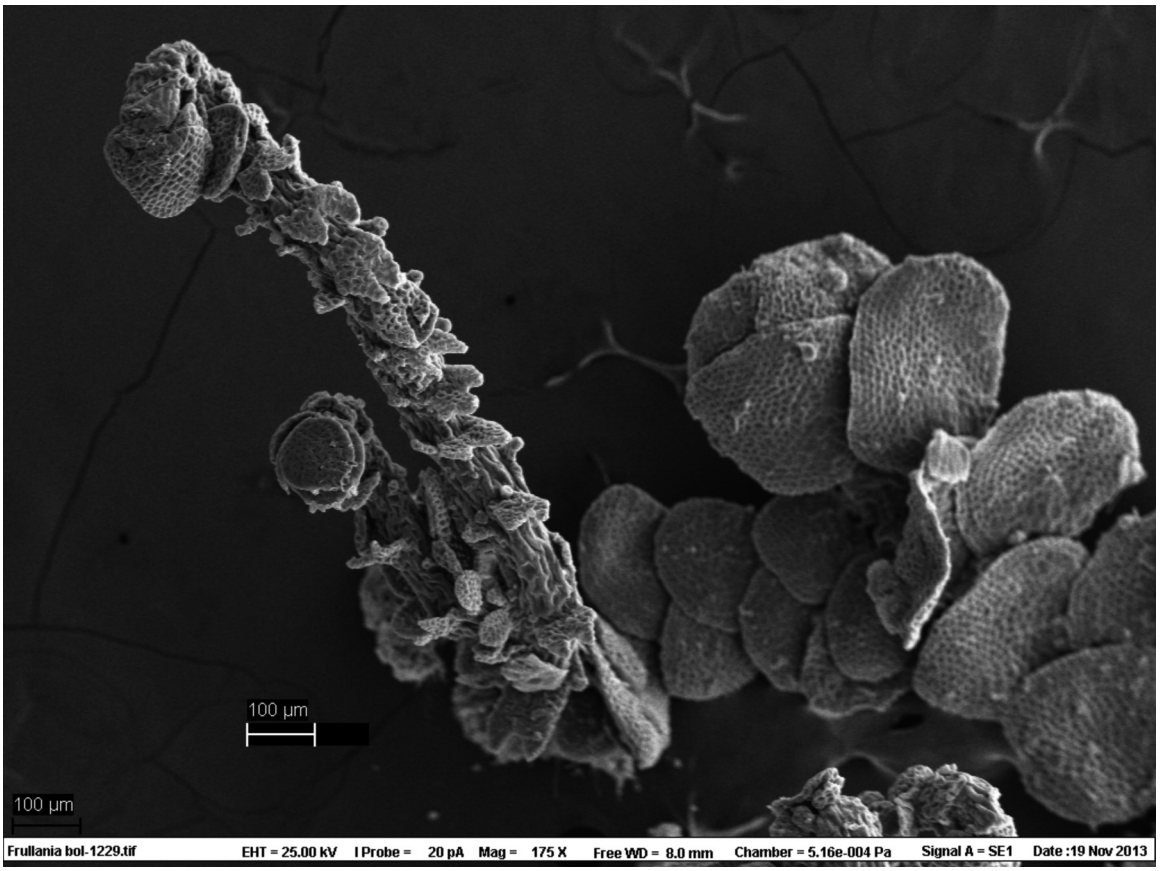

Figure 5. Two flagelliform erect branches of *F. bolanderi* with caducous dorsal lobes of modified leaves attached to a flat leafy shoot. SEM photo from Lye 38399 (locality 35: Sauar, Notodden, Telemark).

Norwegian collection as *F. bolanderi* (Grolle 1970). However, Grolle (1970) thought that this collection might have been wrongly labelled since *F. bolanderi* had not been found in Norway between 1879 and 1970. In Sweden *F. bolanderi* was first found in 1979 [Värmland, Djupdalen] by Nils Hakelier growing on the trunk of *Alnus incana* (Hedenäs 2000).

Ecology

In Värmland in Sweden *F. bolanderi* was described as growing on a single tree of *Alnus incana* and only on that side of the tree facing the stream; other bryophytes on the same tree were *Frullania oakesiana*, *Ulota coarctata* (P. Beauv.) Hammar and *U. crispa* (Hedw.) Brid. (Hallingbäck 1998). However, Hassel and Söderström (2008) studied *F. bolanderi* on three trees of *Alnus incana* (L.) Moench in Kampdalen, Värmland in 2002. Here they found this hepatic to be most commonly associated with *Frullania oakesiana.* In a new Swedish locality in Uppland discovered by N. Norell and H. Weibull *F. bolanderi* was growing on 60 trunks of *Corylus avellana* L., nine trunks of *Fraxinus excelsior* L., one trunk of *Salix caprea* L., one trunk of *Sorbus aucuparia* L. and on the twigs of two small *Picea abies* (L.) H. Karst., all growing close to a seasonal pool in dense forest (Norell and Weibull 2011). In Norrland *F. bolanderi* was found growing on two trunks of *Populus tremula* L. together with *Pylaisia polyantha* (Hedw.) Br.Eur. and *Pseudoleskeella nervosa* (Brid.) Nyh. (Dahlberg 2012).

In Norway *F. bolanderi* is known from the bark of several thousand trees in about 150 different microlocalities and from a number of host trees; the most common host trees are *Alnus incana, Corylus avellana, Fraxinus excelsior, Ulmus glabra* Huds., *Prunus padus* L., *Sorbus aucuparia* and *Acer platanoides* L. (Fig. 6, 7), more rarely this hepatic has been recorded on the trunks of *Populus tremula, Tilia cordata* Mill., *Quercus robur* L., *Fagus sylvatica* L., *Betula pubescens* Ehrh. and even on the conifer *Picea abies* (for details see the listed localities in Appendix 1). *Frullania bolanderi* is a pioneer hepatic and is almost always growing on trunks with a fairly smooth bark, sometimes overgrowing the crustaceous lichen *Graphis scripta* (L.) Ach. (Fig. 8); when the bark becomes more uneven or cracked this hepatic is gradually being outstripped by *Radula*

Figure 6. Mixed forest with *Picea abies, Alnus incana* and *Acer platanoides* beside Lake Pollen, Ås, Akershus, Norway (locality number 16). *Frullania bolanderi* is abundant on the trunks of *Acer platanoides*. Photo: K. A. Lye 10. April 2013.

Figure 7. *Frullania bolanderi* almost fully covering the circumference of a young *Acer platanoides* tree near Lake Pollen, Ås, Akershus, Norway (locality number 16). Photo: K. A. Lye 10. April 2013.

complanata (L.) Dum. (Fig. 9) and *Orthotrichum speciosum* Hedw., and later by pleurocarpous mosses like *Hypnum cupressiforme* Hedw., *Platygyrium repens* (Brid.) Br. Eur. and *Pylaisia polyantha* or foliaceous lichens. Hofton (2012, Fig. 1.10 p.15) has a photo showing *Frullania bolanderi* being overgrown by the rare lichens *Heterodermia speciosa* (Wulfen) Trevis and *Cetrelia olivetorum* (Nyl.) Culb. et Culb. on a trunk of *Alnus incana* (Noreåsen, Buskerud). Hassel and Söderström (2008) write that *F. bolanderi* and *F. oakesiana* are both pioneer species, have a similar ecology, often grow together and avoid habitats with crustaceous lichens. While the two species sometimes grow together close to streams or rivers in Sweden and at lower altitudes in the Oslofjord region, *F. bolanderi* often grows high above the bottom of ravines or riverbeds in upland regions with a higher rainfall or in localities where the sun is shaded by high mountains. Recently *F. bolanderi* was even found on an oak trunk in a gently east-sloping spruce forest southeast of Oslo, and in Bærum in Akershus on trees in a more open flat landscape. In Ås municipality (Akershus) *F. bolanderi* grows abundantly on more than 30 trees of *Alnus incana* and *Acer platanoides* (Fig. 6) ranging in size from a trunk diameter of 2–30 cm; on the smallest trees this hepatic covers the complete circumference (Fig. 7).

In southeastern Norway I have investigated the associate species of *F. bolanderi* in 16 different localities and on five different tree species (Table 1). It is most often associated with the bryophytes *Orthotrichum speciosum* (63 %), *Ulota crispa* (56 %), *Radula complanata* (50 %) and the lichen *Graphis scripta* (63 %). While crustaceous lichens are often frequent on young smooth trunks where *F. bolanderi* is able to establish itself, foliaceous lichens are almost absent in such sites; only minute fronds of *Melanelia fuliginosa* (Duby) Essl. and *Parmelia sulcata* Taylor were seen. However, in more continental parts of the country *F. bolanderi* may be associated with other foliaceous lichens like *Hypogymnia physodes* (L.) Nyl., *Heterodermia speciosa* and *Cetrelia olivetorum* (Hofton 2012).

In the southern Ural Mountains *F. bolanderi* grows on the trunks of *Betula verrucosa, Tilia cordata* and *Populus tremula* in a fairly continental region with an annual precipitation of 400–600 mm. On *Betula* it grows in an

Figure 8. The crustaceous lichen *Graphis scripta* overgrown by *Frullania bolanderi*. From the bark of an *Acer platanoides* tree near Lake Pollen, Ås, Akershus, Norway (locality number 16). In upper half of picture are shown a number of scattered detached dorsal lobes of modified leaves from flagelliform shoots of *F. bolanderi*; in middle and upper part two young plants recently developed from such detached propagules. Photo: K. A. Lye 10. April 2013.

Orthotrichetum speciosi association (*Tortulion laevipilae* alliance in the Braun–Blanque classification system) with *Orthotrichum speciosum*, *Pylaisia polyantha* and the lichen *Hypogymnia physodes* as the most abundant species (Baisheva 1995). On *Tilia* it grows in a *Platygyrietum repentis* association (*Dicrano–Hypnion* alliance) with *Platygyrium repens*, *Pylaisia polyantha, Orthotrichum speciosum* and *Pseudoleskeella nervosa* as the most abundant species (Baisheva 1995). On *Populus tremula F. bolanderi* grows in a *Leskeetum polycarpae* association *with Leskea polycarpa* Hedw.*, Pylaisia polyantha, Amblystegium serpens* (Hedw.) Br.Eur.*, Brachythecium salebrosum* (Web. & Mohr) Br.Eur. and *Callicladium haldanianum* (Grev.) Crum (Baisheva et al. 1994). In Caucasus Otte (2006) reports *F. bolanderi* in apple tree orchards together with *F. dilatata*, *F. parvistipula* Steph., *Orthotrichum* species and lichens. From Caucasus Konstantinova and Savchenko (2013) record *F. bolanderi* from the bark of *Fagus*, *Carpinus*, *Sorbus* and *Acer* in beech–oak, beech–hornbeam, beech–maple and fir–beech forests, and also once collected on rock.

In North America *F. bolanderi* usually grows on the trunks of deciduous trees and shrubs like *Acer, Alnus,*

Figure 9. *Frullania bolanderi* overgrown by *Radula complanata*. From the bark of an *Acer platanoides* tree near Lake Pollen, Ås, Akershus, Norway (locality number 16). Photo: K. A. Lye 10. April 2013.

Amelanchier, Betula, Fagus, Fraxinus, Ostrya, Quercus, Sorbus, Tilia and *Ulmus*, more rarely on conifers like *Abies* and *Picea* (Schuster 1992, Miller and Miller 1998). It grows both in relatively dry sites in open forest and in deep humid forests, and is very rarely found on rocks.

Climatic demands

In Scandinavia *F. bolanderi* is restricted to regions with a mean annual precipitation between 700 and 1500 mm; consequently it avoids both the driest valleys in the interior and the wet oceanic regions of western Norway (Table 2). It further grows in localities where the mean July temperature varies between 11 and 17.5°C, and the mean temperature of the coldest month varies between –3 and –8°C (Table 2). The difference between January and July temperatures is between 18 and 22°C. This means that this hepatic is absent from coastal sites in Norway with relatively high winter temperatures as well as the coldest inland localities. In Sweden (Brattfors in Table 2) the climate is rather similar to that in Norway, while in Russia the climate in some localities is more extreme with a warmer summer.

Distribution

Figure 10 shows the distribution of *Frullania bolanderi*. In Europe, before the 2nd millennium, *F. bolanderi* was considered to be extremely rare and known from a single Swedish locality (Damsholt and Hallingbäck 1987, Hallingbäck 1998, Hedenäs 2000), three Norwegian localities (Hassel 2000, Söderström et al. 2002, Damsholt 2003, 2009) and a handful of Russian localities, i.e. from

Table 1. *Frullania bolanderi synedria* from Norway. Frequency is given in Roman numbers (I = 10–20 %, II = 21–40 %, III = 41–60 %, IV = 61–80 %, V = 81–100 %). Cover is given in percent (Arabic numbers). Locality 1 is from Øverland, Bærum (Akershus), 2–3 from Pollevatn, Ås (Akershus), 4 from Hval, Asker (Akershus), 5 from Fleskum, Bærum (Akershus), 6 from Sauar, Notodden (Telemark), 7 from Hjartsjå, Hjartdal (Telemark), 8 from Bøelva, Bø (Telemark), 9 from Hallangen, Frogn (Akershus), 10 from Tveitan, Nome (Telemark), 11 from Flåtin-Nesland, Sauherad (Telemark), 12 from Berger, Nesodden (Akershus), 13 from Tronstad, Lier (Buskerud), 14 from Askerelva, Asker (Akershus), 15 from Brennsrud, Asker (Akershus), 16 from Bjørnstad, Røyken (Buskerud). Abbreviations: Ai = *Alnus incana,* Ap = *Acer platanoides,* Fe = *Fraxinus excelsior*, Pp = *Prunus padus* and Sa = *Sorbus aucuparia*.

Locality number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Locality no. in locality list	7	16	17	4	11	35	32	31	13	34	36	15	25	3	5	30
Samples analyzed	10	5	5	5	5	5	5	5	5	5	5	5	5	5	5	2
Height above the base	80–250	80–200	70–200	40–150	100–180	160–350	150–200	170–300	160–200	150–170	100–170	120–170	160–220	40–170	80–170	90
Tree species	Ai	Fe	Fe/Ai	Fe	Ap	Ai/Fe	Sa	Ai/Pp	Ai	Ap/Fe	Ai	Ap	Fe	Ap	Ap	Ai
Trunk diameter in cm	40	20–25	2–30	20	25	15–20	25–30	10–35	10–15	15–20	30	5–35	35	25–30	15–25	90
Frullania bolanderi	V.18	V.20	V,20	V.37	V.32	V.68	V.27	V.34	V.31	V.15	V.25	V.31	V.30	V.27	V.15	V.45
Frullania dilatata									II.30							
Metzgeria furcata	V.18	IV.3	IV.2									III.3				
Radula complanata	I.1	V.12	IV.7					II.10		I.2		II.2	III.6		III.1	
Homalothecium sericeum	IV.8		III.1													
Hypnum cupressiforme	I.2	IV.5	I.5					I.3	I.10							
Leucodon sciuroides										II.11		II.7				
Orthotrichum speciosum	II.2	II.1	III.1	V.11	V.3					V.4	I.2	IV.5	V.1			V.1
Platygyrium repens				I.10	V.3											
Pylaisia polyantha						V.2							III.15	III.4	II.2	
Sanionia uncinata											III.2	III.3	III.5			V.6
Ulota crispa	II.2		IV.2			II.3	I.2	III.2			V.6	I.2		II.2	I.2	
Arthonia radiata	II.3	III.2	I.1						II.8	I.3	I.1					
Graphis scripta	V.14	V.10	III.1			IV.5			V.30		II.15	II.5	V.35	IV.7	III.60	
Lecanora sp.	I.8	II.8	II.2			V.20				II.3						
Melanelia fuliginosa	I.6		II.13													
Parmelia sulcata							III.32								I.1	
Phlyctis argena		III.5	I.3							V.13			IV.10	II.4		

Table 2. Mean temperature (in °C) and precipitation (in mm) for Scandinavian and Russian climatic stations near or between localities for *Frullania bolanderi* [Norwegian stations calculated for the period 1981–2010; the Swedish station from the last hundred year period].

	Brattfors		Oslo		Nesbyen		Værnes		Moskva	
January	–5.8	44	–2.9	55	–7.2	32	–1.7	75	–6.5	52
February	–5.3	30	–2.6	41	–7.5	21	–1.4	65	–6.7	41
March	–1.9	33	0.7	50	–3.9	22	1.0	54	–1.0	35
April	3.2	40	5.4	48	0.7	24	4.9	44	6.7	37
May	9.1	45	11.2	54	5.2	43	9.3	56	13.2	49
June	13.1	61	14.9	70	8.8	58	12.3	69	17.0	80
July	15.4	76	17.2	85	11.6	77	14.8	88	19.2	85
August	14.0	84	16.0	98	11.4	73	14.2	91	17.0	82
September	9.7	64	11.4	82	6.9	53	10.6	96	11.3	68
October	4.6	64	6.3	90	2.0	54	6.1	83	5.6	71
November	–0.7	62	1.5	80	–3.1	40	1.5	70	–1.2	55
December	–4.4	51	–2.4	52	–7.0	28	–1.3	82	–5.2	522
Sum		654		805		524		873		707

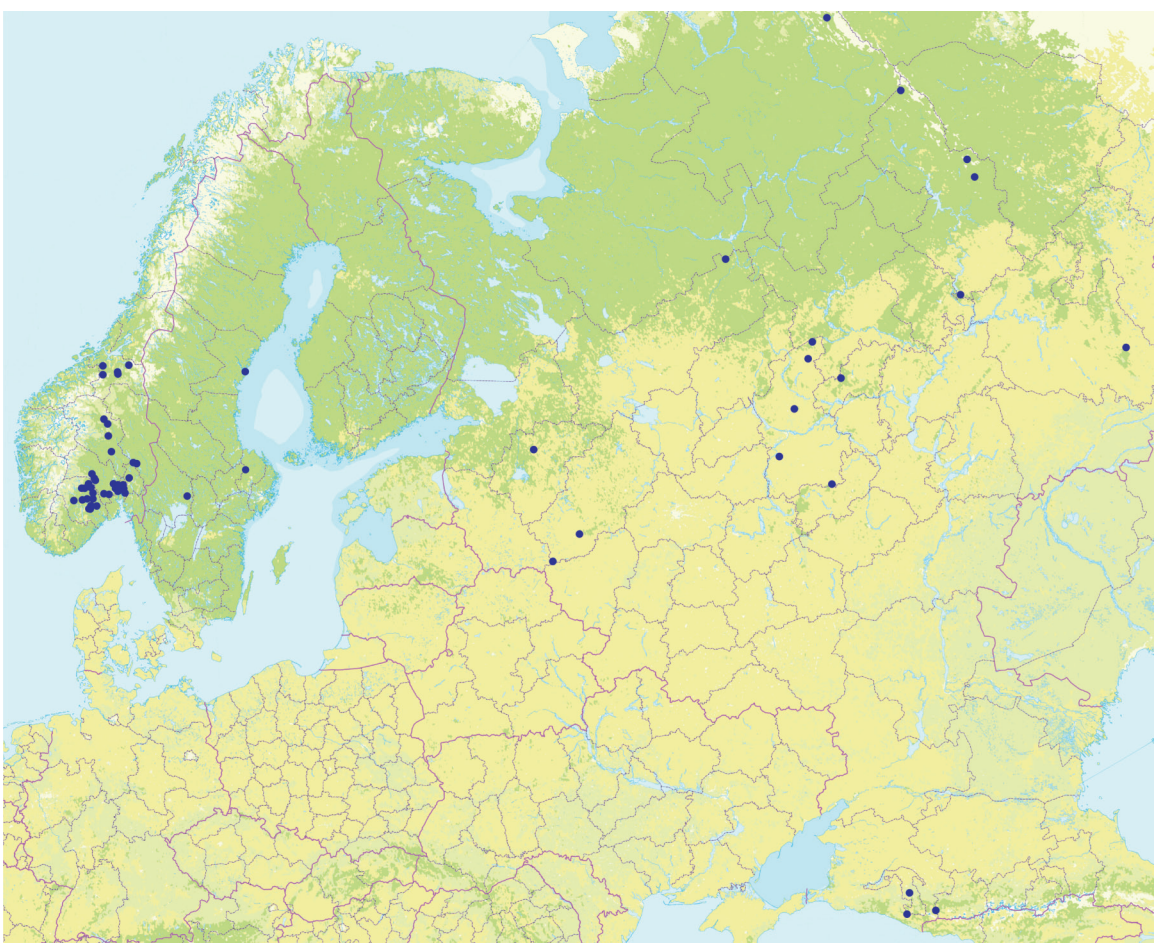

Figure 10. Distribution of *Frullania bolanderi* in Europe.

the Vologda region and near the eastern border of Europe along or near the Ural mountains (Ladyzhenskaja and Zinovjeva 1964, Akhminova and Zhukova 1971, Schljakov 1982, Baisheva et al. 1994, Baisheva 1995).

Since the year 2000 *F. bolanderi* has been found in many new localities in all three countries. In Sweden it was actually collected from two closely situated ravines (within 2 km) near Brattfors in 1979 and 1981. More recently it was found in a third locality in Uppland (Hallingbäck 2010, Norell and Weibull 2011) and a fourth locality in Norrland (Dahlberg 2012). In Norway *F. bolanderi* was collected in Bærum in 1879, in Oslo in 1985 (Kell Damsholt and Arne Pedersen) and then in numerous localities from 2000 onwards (Hassel 2000, Blindheim and Røsok 2005, Olsen and Reiso 2005, Blindheim and Friis 2006, Hassel and Söderström 2008, Blindheim et al. 2009, Reiso and Olsen 2009a, b, Røsok 2009, Olberg et al. 2009, Hofton 2011, Hofton and Reiso 2012, Thylén 2012).

In European Russia *F. bolanderi* is now known from more than twenty localities from south of St. Petersburg (Potemkin and Kotkova 2006, Konstantinova and Bakalin 2009, Konstantinova and Savchenko 2012) to near the Asian border in Caucasus (Otte 2006, Konstantinova and Savchenko 2013) and the southern Ural mountains (Baisheva et al. 1994, Baisheva 1995).

The main distribution area for *F. bolanderi* is boreal North America. Here it is widespread but uncommon from its type locality in California to near the eastern coasts both in Canada and the USA. (Frye and Clark 1937–47, Schuster 1992, Miller and Miller 1998). *Frullania bolanderi* also occurs in Asia from Japan (Hattori 1981), Sakhalin Islands (Bakalin et al. 2006), Kamchatka (Bakalin 2009) and Yakutia (Sofronova 2013) to the Altai and Ural mountains (Ladyzhenskaja and Zinovjeva 1964, Schljakov 1982, Konstantinova et al. 2010).

Dispersal

In Europe *F. bolanderi* is dispersed by vegetative propagules only, since sporophytes have never been observed. The vegetative propagules are detached dorsal lobes of modified leaves produced on specialised vegetative branches (Fig. 2, 3). In Fig. 8 both detached propagules and young plants recently developed from such propagules are seen on a tree trunk covered by the lichen *G. scripta*. It is obvious that such dispersal is efficient on a local scale. However, since we do not know if these propagules can survive drying out for longer periods, we do not know if they are efficient for long-distance dispersal.

Conservation and threats

All known European *F. bolanderi* populations are situated in Norway, Sweden and Russia, and 95% of the Scandinavian and about 70% of the known European plants live in southern Norway. Thus Norway has a special responsibility for providing good habitats for this hepatic in all future. However, most probably *F. bolanderi* is increasing in abundance in Norway as well as elsewhere in Europe.

In Sweden *F. bolanderi* was classified as critically endangered (CR) in the early redlist (Hallingbäck 1998), but as strongly endangered (EN) in the recent redlist (Hallingbäck 2010). In Norway it was considered endangered (1E) in the first redlist (Frisvoll and Blom 1993) and critically endangered (CR) in the second (Frisvoll and Blom 1997). In the most recent redlists (Kålås et al. 2006, 2010) it is downgraded to vulnerable (VU). The many new collections may indicate that it could be downgraded further to Near Threatened (NT) or even taken out of the redlist altogether. However, since Norway has the majority of localities for *F. bolanderi* in Europe, it must be recognized as a "Priority species" that should be given special attention from the environmental protection agency.

Similar species and molecular information

In Europe *F. bolanderi* is most similar to *F. oakesiana* Austin, but that species is easily separated by frequently having perianths and always lacking erect terminal branches with caducous dorsal lobes of leaves (large discoid gemmae). *Frullania dilatata* (L.) Dumort. is also similar, but differs from *F. bolanderi* in the same characters as *F. oakesiana*. *Frullania jackii* Gottsche, which grows on siliceous rocks, is most closely related to *F. dilatata* and differs from all in its large reniform underleaves (Damsholt 2009). *Frullania fragilifolia* (Taylor) Gottsche et al. and *F. tamarisci* (L.) Dumort. differ from the other species in their narrow ventral lobes twice as long as wide. In eastern Asia Hattori (1981) considers *F. koponenii* Hatt. to be the species most closely related to *F. bolanderi.* Schuster (1992 pp. 188–189) compares *F. bolanderi* with some American species including *F. inflata* Gottsche, which by molecular phylogeny (Hentschel et al. 2009) was found to be the most closely related species. *F. inflata* has recently been recorded from Dagestan in Russian Europe (Konstantinova and Savchenko 2012) and is also known from more central parts of Europe, viz. Albania, Austria, Czechia, Hungary and Switzerland (Frahm 2013).

The molecular study (Hentschel et al. 2009) found rather poor correlation between morphology and molecular phylogeny concerning the Nordic species of *Frullania*. In this study *F. bolanderi* [in subgen. *Microfrullania*] was found to be closer to *F. fragilifolia* and *F. tamarisci*. in subgenus *Thyopsiella* than to *F. dilatata* and *F. jackii* in subgen. *Frullania*. Unfortunately neither *F. oakesiana* nor *F. koponenii* was included in this study. Damsholt (2009) places *F. bolanderi* together with *F. dilatata* in subgen. *Trachycolea* and sect. *Dilatata*, which is in great conflict with the ideas of Hentschel et al. (2009). Schuster (1992) is

utterly confusing in his treatment; on page 15 he writes that the type of the genus *Frullania* is "*F. major* Raddi [= *F. dilatata* (L.) Dumort.]", but on page 43 he writes that the type of subgenus *Frullania* Raddi is "*F. tamarisci* (L.) Dumort. [= *F. major* Raddi]". Bonner in Index hepaticarum in 1953 selected *F. dilatata* as type of the genus, while Frye and Clark (1937–47) selected *F. tamarisci* as the type (Grolle 1976). However, Evans (1918) avoided any ambiguity by stating "Type species: *F. dilatata* (L.) Dum." under *Frullania* Raddi (Grolle 2004). The earliest selection is the valid one.

BioFokus

It is thanks to the efforts of members of staff at the foundation BioFokus (previously Siste Sjanse) that our knowledge of the distribution of *F. bolanderi* in Norway is so dramatically increased since 2007. Øystein Røsok discovered this hepatic as new to Sør-Trøndelag in June 2007 (Gaarder et al. 2009), Jon T. Klepsland found the plant as new to Oppland in September 2007 (Gaarder et al. 2009) and new to Hedmark in June 2008, and Sigve Reiso found it as new to Telemark in November 2007 (Reiso et al. 2008). In Buskerud it was first collected by Tom H. Hofton in October 2008, but had been noted by Jon. T. Klepsland in July 2008.

Acknowledgements – I would like to thank Torbjørn Høitomt who first introduced me to the ecology of *Frullania bolanderi* in 2012. I am also grateful to Kell Damsholt who provided some useful comments to an earlier version of this paper. The SEM photography was made possible through Elin Ørmen at the Dept of Plant and Environmental Sciences, Microscopy Division, Norwegian Univ. of Life Sciences.

References

Akhminova, M. P. and Zhukova, A. L. 1971. To the liverwort flora of the Vologda Region (in Russian). – News Lower Plants Syst. 8: 345–354.

Andrejeva, E. N. and Shestakova, A. A. 2009. New liverwort records from Nizhni Novgorod Region (in Russian). – Arctoa 18: 255–257.

Austin, C. F. 1870. Characters of some new Hepaticae (mostly North American), together with notes on a few imperfectly described species. – Proc. Acad. Nat. Sci. Philadelphia 21 (1869): 218–234.

Baisheva, E. Z. 1995. Bryophyte vegetation of Bashkiria (South Urals). II. Epiphytic and epixylic communities of north eastern Bashkiria. – Arctoa 4: 55–63.

Baisheva, E. Z., Solometch, A. I. and Ignatova, E. A. 1994. Bryophyte vegetation of Bashkiria, South Urals. I. Epiphytic and epixylic communities. – Arctoa 3: 139–152.

Bakalin, V. A. 2009. Flora and phytogeography of liverworts of Kamtchatka and adjacent islands (in Russian). – KMK, Moscow, Russia.

Bakalin, V. A., Cherdantseva, Y. Y. A., Gorobets, K. U. et al. 2006. Contributions to the knowledge on liverworts of Sakhalin Islands (West Pacific). – Arctoa 14: 143–154.

Blindheim, T. and Røsok, Ø. 2005. Naturverdier i Mærradalen, Oslo kommune. – Siste Sjanse Notat 2005–2: 1–41.

Blindheim, T. and Friis, H. 2006. Naturverdier langs Lysakerelva i Oslo og Bærum kommuner. – Siste Sjanse rapport 2006–9: 1–62.

Blindheim, T. (ed.), Gaarder, G., Hofton, T. H. et al. 2009. Naturfaglege registreringer av bekkekløfter i Buskerud, Telemark, Aust-Agder og Møre og Romsdal. – BioFokus rapport 2009–28: 1– 90.

Dahlberg, J. 2012. Pälsfrullania *Frullania bolanderi* – ny art för Norrland. – Myrinia 22: 56–61.

Damsholt, K. 2003. Notes on Nordic hepatics 6–17. – Lindbergia 28: 120–128.

Damsholt, K. 2009. Illustrated Flora of Nordic Liverworts and Hornworts, 2nd edn. – Nordic Bryological Society, Lund.

Damsholt, K. and Hallingbäck, T. 1987. The Nordic Bryological Society's excursion 1986. – Lindbergia 12: 174–176.

Dulin, M. V., Philippov, D. A. and Karmazina, E. V. 2009. Current state of knowledge of the liverwort and hornwort flora of the Vologda Region, Russia. – Folia Cryptog. Estonica, Fasc. 45: 13–22.

Evans, A. W. 1918. Hepaticae. – In: Britton, N. L. (ed.), Flora of Bermuda. C. Scribner's sons, New York.

Frahm, J.-P. 2013. Guide to Bryological hot spots in Europe 6. Ticino in Switzerland. – Arch. Bryol. 194: 1–9.

Frisvoll, A. A. and Blom, H. H. 1993. Trua moser i Norge med Svalbard; raud liste. – NINA Utredning 42: 1–55.

Frisvoll, A. A. and Blom, H. H. 1997. Trua mosar i Noreg med Svalbard. – Førebels faktaark. Norges Teknisk-Naturvitenskapelige Univ. og Vitenskapsmuseet, Trondheim, Bot. Notat 1997–3: 1–170.

Frye, T. C. and Clark, L. 1937–47. Hepaticae of North America. – Univ. Wash. Publ. Biol. 6: 1–1018.

Gaarder, G., Hofton, T. H. and Blindheim, T. 2009. Naturfaglige registreringer av bekkekløfter i Hedmark, Oppland og Sør-Trøndelag i 2007. – BioFokus rapport 2008–31: 1–82.

Grolle, R. 1970. Zur Kenntnis der Frullanien in Europa und Makaronesien. – Wiss. Z. Math.-Nat. Reihe 19: 307–319.

Grolle, R. 1976. Verzeichnis der Lebermoose Europas und benachbarter Gebiete. – Feddes Rep. 87: 171–279.

Grolle, R. 2004. Some overlooked earlier lectotypifications of generic names of hepatics (Marchantiopsida). – J. Bryol. 26: 61–62.

Hallingbäck, T. 1998. *Frullania bolanderi* pälsfrullania. – In: Hallingbäck, T. (ed.), Rödlistade mossor i Sverige. ArtDatabanken, SLU, Uppsala, pp. 139–140.

Hallingbäck, T. 2010. *Frullania bolanderi* pälsfrullania. – Revised edition of T. Hallingbäck (ed.), Rödlistade mossor i Sverige. ArtDatabanken, SLU, Uppsala. <www.artfakta.se/artfaktablad/Frullania_Bolanderi_662.pdf>.

Hassel, K. 2000. *Frullania bolanderi* Aust. er funnet på en ny lokalitet i Norge. – Myrinia 10: 3.

Hassel, K. and Söderström, L. 2008. *Frullania bolanderi* og *Frullania oakesiana* – substrat og forekomst i Värmland og Oslo. – Myrinia 18: 16–22.

Hattori, S. 1981. Notes on the Asiatic species of the genus *Frullania*, Hepaticae, XIII. – J. Hattori Bot. Lab. 49: 147–168.

Hedenäs, L. 2000. Tidligare okända svenska fynd av *Frullania bolanderi* pälsfrullania och *F. oakesiana* värmlandsfrullania. – Myrinia 10: 3.

Hentschel, J., von Konrat, M. J., Pócs, T. et al. 2009. Molecular insights into the phylogeny and subgeneric classification of *Frullania* Raddi (Frullaniaceae, Porellaceae). – Mol. Phylogenet. Evol. 52: 142–156.

Hofton, T. H. 2011. Naturtypekartlegging i Bø kommune (Telemark) 2010. – BioFokus rapport 2011–19: 1–77.

Hofton, T. H. 2012. Elfenbenslav (*Heteroderma speciosa*) i Norge. Faggrunnlag for handlingsplan. – BioFokus rapport 2012–5: 1–65.

Hofton, T. H. and Reiso, S. 2012. Neselva, Senningselva og Vesleelva i Kongsberg og Øvre Eiker – naturverdier og konsekvenser ifbm. planer om vannoverføring til Hakavik kraftverk. – BioFokus rapport 2012–3: 1–43.

Jørgensen, E. 1934. Norges Levermoser. – Bergen Museums Skrifter Nr. 16: 1–343, kartblad I–XXV.

Konstantinova, N. A. 2004. Hepatics of the Kerzhenskiy State Reserve (Nizhniy Novgorod province, European Russia); in Russian. – Arctoa 13: 89–99.

Konstantinova, N. A. and Bezgodov, A. G. 2006. Hepatics of Vishera State Nature Reserve (Perm' province, northern Ural) (in Russian). – Arctoa 14: 163–176.

Konstantinova, N. A. and Bakalin, V. A. 2009. Checklist of liverworts (Marchantiophyta) of Russia. – Arctoa 18: 1–64.

Konstantinova, N. A. and Savchenko, A. N. 2012. Hepatics in regional Red Data Books of European part of Russia. – <http://eccb_bryo8.nhmus.hu/eccb_files/presentation/ECCBB_Konstantinova.pdf>

Konstantinova, N. A. and Savchenko, A. N. 2013. Russian Caucasus distribution of fourteen hepatics rare and threatened in Europe. – Pol. Bot. J. 58: 573–584.

Konstantinova, N. A., Akatova, T. V. and Savchenko, A. N. 2009. Hepatics of the Caucasian State Nature Reserve (western Caucasus, Russia). – Arctoa 18: 121–134.

Konstantinova, N. A., Bezgodov, A. G. and Savchenko, A. N. 2010. Liverworts of "Basegi" State Reserve (The Middle Urals, Permsky Territory). – Novosti Sist. Nizsch. Rast. 44: 322–336.

Kålås, J. A., Viken, Å. and Bakken, T. (eds) 2006. Norsk rødliste 2006. – Artsdatabanken, Trondheim.

Kålås, J. A., Viken, Å., Henriksen, S. et al. (eds) 2010. Norsk rødliste for arter 2010. – Artsdatabanken, Trondheim.

Ladyzhenskaja, K. I. and Zinovjeva, L. A. 1964. *Frullania bolanderi* Aust. – In: Flora Hepaticarum URSS minus cognita. – Novit. Syst. Pl. Non Vasc. [Nov. Sist. Nizsh. Rast.] 1: 269–275.

Mezaka, A., Potemkin, A. D., Urbanavichene, I. N. et al. 2013. New liverwort records from Mordovia Republic. 1. – Arctoa 22: 247.

Miller, N. G. and Miller, A. D. 1998. Occurrence of the Leafy Liverwort, *Frullania bolanderi*, in old-growth forests of northeastern North America. – J. Torrey Bot. Club 125: 109–116.

Norell, B. and Weibull, H. 2011. Några sällsynta kryptogamer vid Nedre Dalälven och i Uppland 2007–2009. – Länsstyrelsen i Uppsala län. Länsstyrelsens meddelandeserie 2011, 3: 1–81.

Olberg, S., Gammelmo, Ø., Hofton, T. H. et al. 2009. Kartlegging av naturtyper i Selbu kommune. – BioFokus rapport 2008–30: 1–43.

Olsen, K. M. and Reiso, S. 2005. Biologisk mangfold i Askerelva, Asker kommune. – Siste Sjanse Notat 2005–3: 1–22, vedlegg 1–6.

Otte, V. 2004. Die Pflanzengeographische Ozeanitätsgliederung der Holarktis und die Ozeanitätsbindung der Pflanzenareale. – Feddes Rep. 79: 157–335.

Otte, V. 2006. Erster Nachweis von *Frullania bolanderi* (Marchantiophyta: Jubulaceae) im Kaukasus. – Herzogia 19: 353–354.

Potemkin, A. D. and Kotkova, V. M. 2006. To the liverwort flora of the Leningrad Province. New and little known taxa for the Province (in Russian). – Novosti Sist. Nizsh. Rast. 40: 330–333.

Potemkin, A. D. and Kotkova, V. M. 2013. New liverwort records from Kirov Province. 1 (in Russian). – Arctoa 22: 245–246.

Potemkin, A. D. and Notov, A. A. 2011. New bryophyte records from Tver Province. 3 (in Russian). – Arctoa 20: 249–251.

Reiso, S., Klepsland, J. T. and Svalastog, D. 2008. Naturfaglige registreringer i forbindelse med vern av skog på Statskog SFs eiendommer. Del 5: Årsrapport for registreringer i Troms, Nordland, Nord-Trøndelag og Telemark. – Biofokus rapport 2008–2: 1–187.

Reiso, S. and Olsen, K. M. 2009a. Naturtypekartlegging i Kviteseid kommune 2009. – Biofokus rapport 2010–17: 1–43.

Reiso, S. and Olsen, K. M. 2009b. Naturtypekartlegging i Tokke kommune 2009. – Biofokus rapport 2010–21: 1–44.

Røsok, Ø. 2009. Biologiske registreringer og konsekvensvurderinger i forbindelse med reguleringsplaner ved Bergerskogen på Nesodden. – BioFokus rapport 2009–21: 1–28.

Schljakov, R. N. 1982. Hepaticae of the northern USSR, Vol. 5 (in Russian). – NAUKA, Leningrad.

Schuster, R. M. 1992. The Hepaticae and Anthocerotae of North America. V. – Columbia UP, New York.

Sofronova, E. V. 2013. Liverworts of the Algama river basin (Tokinsky Stanovik range, south-eastern Yakutia). – Arctoa 22: 139–144.

Söderström, L., Hassel, K. and Weibull, H. (eds) 2002. Preliminary distribution maps of bryophytes in northwestern Europe, vol. 1 Hepaticae and Anthocerotae. – Nordic Bryological Society and Mossornas Vänner, Trondheim.

Thylén, A. 2012. Kartlegging og vurdering av naturmiljø i Stubberud skogpark og Østernbekken. – BioFokus rapport 2011–29: 1–29.

Appendix 1

List of localities

A) Localities in Norway (selected localities only; usually only one record per parish except when collections are from far apart. Localities used for the ecosociological studies in Table 1 are given in bold numbers):

Oslo

1. Ullern parish, Mærradalen, lower part behind the radio station, NM922,460, 7 July 1985, on old *Ulmus glabra*, 60 m, Kell Damsholt and Arne Pedersen 85-178 (C,TRH-B164361), s.n. (O-B10425/01, TRH-B164361).
2. Ullern parish, Lysakerelva, foot bridge north of Jar station, NM911,447, on *Fraxinus excelsior*, 20 m, 6 May 2000, Kristian Hassel s.n. (TRH-B7498 and 7499). Hassel (2000).

Akershus

3. Asker municipality: above Askerelva [west of Asker church], NM783,335, 10°23'43.9"E and 59°49'55.0"N, 5 December 2013, on trunk of *Acer platanoides* in mixed forest, 120 m, Kåre A. Lye 38424 (O). First recorded from this parish by Øystein Røsok in 2004.
4. Asker municipality: Hval, 50 m west of road 165, NM831,349, 10°28'56.4"E and 59°50'37.5"N, on trunk of *Fraxinus* in small woodland on rocky outcrop, 12 m, 8 November 2013, Kåre A. Lye 38394 (O).
5. Asker municipality: Brennsrud, 100 m west of Hogstadvatn, NM783,335, 10°23'43.9"E and 59°49'55.0"N, on trunk of *Acer platanoides* in woodland by stream, 160 m, 5 December 2013, Kåre A. Lye 38427 (O).
6. Bærum municipality, Bryn parish, Isidalen, Bjørum Sag, NM797,454, on 100 year old *Ulmus glabra* at 2–2.5 m above the base, 110 m, 19 August 1989, Arne Pedersen (O-B12104/01 and B10436/01) and on *Fraxinus excelsior*, at 1–1.5 m above the base (O-B12109/01) and on *Acer platanoides* at 1 m above the base (O-B12105/01).
7. Bærum municipality, Høvik parish, Øverlandselva, below Bekkeveien 16, NM867,816, 10°33'05.0"E and 59°54'11.8"N, on trunk of *Alnus incana*, 10 m, 8 April 2013, Kåre A. Lye 36614 (O). First recorded from this parish by Terje Blindheim in 2005.
8. Bærum municipality, Jar parish, Lysakerelva [directly opposite Rolighet], NM9130,4525, 10°38'01.6"[10,6336000002921]E and 59°56'03.5"[59,934299999848]N, on *Fagus sylvatica*, 80 m, 11 October 2005, Kristian Hassel and Terje Blindheim s.n. (TRH-B690089/1).
9. Bærum municipality, Østerås parish, Østernbekken [east of Nordby], NM8960,4690, 10°36'15.1"[10,6041999999434]E and 59°56'58.3"[59,9494000002742]N, on *Corylus avellana* and *Acer platanoides*, 80 m, 6 June 2007, Øystein Røsok and Terje Blindheim s.n. (TRH-B673337/1).
10. Bærum municipality, Tanum parish, Sandvikselva east of Emma Hjorts hjem, NM8395,4055, 10°29'59.5"[10,5004000002518]E and 59°53'39.0"[59,8938999995589]N, on *Alnus incana* in peninsula with deciduous trees, 30 m, 10 October 2007, Øystein Røsok s.n. (TRH-B673372/1).
11. Bærum k.: Haslum parish, Fleskum, 50 m east of farm house, NM858,428, 10°32'11.6"E and 59°54'51.2"N, on trunk of *Acer platanoides* in woodland, 95 m, 8 November 2013, Kåre A. Lye 38390 (O).
12. Eidsvoll municipality, lower part of Budalen [on border to Hedmark], PN229,091, 10°27'05"[11,2372999191284]E and 60°53'34"[60,4991989135742]N, 145 m, 7 September 2010, Tom H. Hofton and R. Solvang s.n. (TRH-B691352/1).
13. Frogn municipality, south of Nordre Hallangen midway to Hallangspollen, NM924,206, 10°38'45.3"E and 59°42'45.8"N, on trunk of 10 cm thick *Alnus incana* 1 m N of stream, 50 m, 14 November 2013, Kåre A. Lye 38409 (O). First collected from this parish by T. Høitomt in 2013.
14. Nannestad municipality, south of Krokfoss, PM155676, 11°04'41"[11,0804004669189]E and 60°07'51"[60,1301002502441]N, 130 m, 8. October 2012, Torbjørn Høitomt M845Høi (BIOFOKUS).
15. Nesodden municipality, Berger, 100 m north of Ekely eldresenter, NM942,341, 10°40'46.0"E and 59°50'00.8"N, on trunk of 5 cm thick *Acer platanoides* by the stream in mixed forest, 90 m, 1 December 2013, Kåre A. Lye 38420 (O). First collected from this parish by Ø. Røsok in 2009.
16. Ås municipality, Nordby, northeast side of Lake Pollen, NM988,240, 10°45'28.4"E and 59°44'28.8"N, on trunk of 20 cm thick *Populus tremula* in *Alnus–Picea abies* mixed forest, 8 m, 19 March 2013, Kåre A. Lye 36553 (O). First collected from this parish by T. Høitomt in 2013.

17. Ås municipality, Nordby, northeast side of Lake Pollen, NM988,241, 10°45'28.4"E and 59°44'29.2"N, on trunk of 20 cm thick *Alnus incana* in *Alnus-Picea abies* mixed forest, 10 m, 19 March 2013, Kåre A. Lye 36558 (O). First collected from this parish by T. Høitomt in 2013.

Oppland

18. Gausdal municipality, Dørdalen [northeast of Flutua and Snertingdalen], NN5255,9745, 10°33'27.1"[9,98130000010133]E and 59°55'05.5"[61,3083999995142]N, on trunk of *Alnus incana,* (*Prunus padus* and *Sorbus aucuparia*) in *Alnus–Prunus* padus forest along rivulet, 80 m, 21 September 2007, Jon Klepsland s.n. (TRH-B672305/1).
19. Nord-Fron k.: Sødorp sogn, by the river Sula straight west of Illstad, NP415,298, 9°46'51"[9,78139972686768]E and 61°35'56"[61,6002006530762]N, on trunk of *Sorbus aucuparia*, 400 m, 1 August 2012, T. Høitomt and K. A. Lye in Høitomt 276123 and 276124 (TRH) and Lye 35610 (O).
20. Nordre Land k.: Baggerudsberga, NP415,298, 9°46'51"[9,97680000029504]E and 60°35'56"[60,8476999998093]N, 325 m, 10 July 2012, T. Høitomt M365 (TRH-B773809/1).
21. Ringebu municipality, Frya at Svenstad, NP533,307, 10°00'15"[10,0059995651245]E and 61°36'22"[61,6053009033203]N, 400 m, 31 July 2012, Tom Hellik Hofton THH 12266 (BIOFOKUS).

Hedmark

22. Nord-Odal municipality, south of Steppberget, PN342,077, 11°26'28"[11,4409999847412]E and 60°28'57"[60,4832992553711]N, 320 m, 5 June 2008, Jon T. Klepsland JK08-M002 (BIOFOKUS).

Buskerud

23. Kongsberg municipality, lower parts of Senningelva, NM4625,0415, 9°49'03.3" [9,81859970092773] E and 59°34'24.2" [59,5728988647461] N, 160 m, 6 October 2011, Tom H. Hofton THH 11560 (BIOFOKUS). Hofton and Reiso (2012).
24. Lier municipality, Sjåstad parish, south of Kulberg, [north side of R. Glittra], NM6998,3651, 10°14'57.3"[10,4237000001594]E and 59°51'35.2"[59,7352000009269]N, on large *Prunus padus* in ravine with *Ulmus glabra*, *Prunus padus* and *Alnus incana*, 55 m, 7 October 2008, Tom Hellik Hofton (TRH-B691531/1).
25. Lier municipality, Sylling parish, Skjeggeruddalen, NM699.392, 10°14'52.8"E and 59°53'00.9"N, on trunk of *Fraxinus excelsior*, 75 m, 13 December 2013, Kåre A. Lye 38532. (O).
26. Modum municipality, Kimmerudbekken, NM6765,5109, 10°12'46.7"[10,2125000003725]E and 59°59'29.1"[59,9914999995381]N, on *Ulmus glabra* in *Ulmus–Fraxinus* forest along stream, 85 m, 5 October 2008, Tom Hellik Hofton (TRH-B691533/1).
27. Nore og Uvdal municipality, Borgeål [near Skjønne church], NM0005,8035, 9°00'01.6"[9,00088977813721]E and 60°15'34.2"[60,2597007751465]N, 310 m, 26 July 2008, Jon T. Klepsland JK9\08-M066. (BIOFOKUS).
28. Nore og Uvdal municipality, south of Svensrud, NM004,724, 9°00'25"[9,00714015960693]E and 60°11'18"[60,1884994506836]N, 305 m, 29 April 2011, Tom Hellik Hofton THH 11063 (BIOFOKUS).
29. Rollag municipality, east of Tveiten northwest of Veggli, NM076,569, 9°18'15"[9,13696002960205]E and 60°02'54"[60,0491981506348]N, 290 m, 26 April 2011, Tom Hellik Hofton THH 11043 (BIOFOKUS).
30. Røyken municipality, between Bjørnstad and Villingstad, NM942,341, 10°40'46.0"E and 59°50'00.8"N, on *Alnus incana* in mixed forest, 90 m, 5 December 2013, Kåre A. Lye 38420 (O). First collected from this parish by Øystein Røsok in 2009.

Telemark

31. Bø municipality, Bøelva, east side 50 m south of foot bridge along road to Notodden, NL0415,8750, 9°04'23.0"E and 59°25'32.9"N, on trunk of large *Alnus incana* immediately below the path, 60 m, 12 November 2013, Kåre A. Lye 38406 (O). First collected from this parish by Jon T. Klepsland in 2010.
32. Hjartdal municipality, 250 m southeast of Søndre Hjartsjå, 20 m west of Svigsåi, MM875,076, 8°46'39.3"E and 59°36'23.5"N, on trunk of *Sorbus aucuparia*, 165 m, 12 November 2013, Kåre A. Lye 38402 (O). First collected from this parish by Sigve Reiso in 2007.

33. Kviteseid municipality, Morgedalsåi [west of Uppgardåsen], ML699,878, 8°28'01"[8,46929999999702]E and 59°25'45"[59,4276999998838]N, on *Fraxinus excelsior* (25 cm) and *Alnus incana* (10 cm) in *Fraxinus–Alnus* forest along stream, 80 m, 17 July 2008, Øystein Røsok s.n. (TRH-B691345/1).
34. Nome municipality, Tveitan, 100 m below the road, NL11,38, 9°09'44.7"E and 59°48'28.4"N, on the trunk of *Acer platanoides* tree along a ravine, 70 m, 28 November 2013, Kåre A. Lye 38411 (O). First observed from this parish by Sigve Reiso in 2009.
35. Notodden municipality, 200 m west of øvre Sauar, NM0325,0750, 9°03'24.6"E and 59°36'10.9"N, on the trunk of a large *Alnus incana* in clay ravine, 70 m, 12 November 2013, Kåre A. Lye 38397 (O) and [25.4"E and 20.3"N], 38399 (O). First collected in this parish by Sigve Reiso in 2010.
36. Sauherad municipality, Nes parish, between Flåtin and Nesland, NL134,827, 9°14'00.2"E and 59°23'02.1"N, on the trunk of a *Alnus incana* tree along stream, 20 m, 28 November 2013, Kåre A. Lye 38419 (O). First collected from this parish by Sigve Reiso in 2009.
37. Tinn municipality, Dal parish, north of Tvergrot, [in Vestfjorddalen], MM812,385, 8°40'15"[8,66380000021309]E and 59°53'02"[59,8838999997824]N, abundant on the trunk of *Sorbus aucuparia* in rich low herb forest, 300 m, 5 November 2007, Sigve Reiso (TRH-B672005/1).
38. Tinn municipality, Mæl parish, above Mæl (church) [in Vestfjorddalen], MM878,438, 8°41'03"[8,7823999999091]E and 59°53'24"[59,9320999998599]N, abundant on the trunk of 100–200 trees of *Alnus incana, Prunus padus, Ulmus glabra, Populus tremula, Betula, Picea abies, Sorbus aucuparia* and *Corylus avellana* in low herb mixed deciduous forest [previously grazed meadow], 330 m, 1 January 2008, Sigve Reiso (TRH-B672639/1).
39. Tinn municipality, Rjukan parish, south of Gamlenut [in Vestfjorddalen], MM777,386, 8°36'43"[8,602300000377]E and 59°52'57"[59,884299999103]N, on *Corylus avellana*, 600 m, 21 October 2008, Sigve Reiso (TRH-B673032/1).
40. Tinn municipality, Hovin parish, Skirva, [south of søre Tveit], MN010,351, 9°01'04"[9,0182999996096]E and 59°51'08"[59,8532999996096]N, on the trunk of *Alnus incana* along stream in ravine, 330 m, 22 October 2008, Sigve Reiso (TRH-B673033/1).
41. Tokke municipality, east of Tokkeåi [near road to Omdal], ML410,938, 7°57'38"[7,960300000038445]E and 59°28'42"[59,4785999991]N, on the trunk of 20–30 trees of *Fraxinus excelsior* near bottom of ravine, 230 m, 24 September 2008, Sigve Reiso (TRH-B673027/1).
42. Tokke municipality, Rolvshus [above Dalåi], ML342,899, ca 7°50'06"[7,84059999976307]E and 59°26'05"[59,4422999992967]N, on old *Corylus avellana* in rich mixed forest, 370 m, 20 August 2009, Sigve Reiso (TRH-B691605/1).

Sør-Trøndelag

43. Meldal municipality, Resdalen, east of Resdalssætra, south-facing slope above R. Resa, NQ3376,8143, in old tall herb boreal deciduous forest, 370 m, 18 June 2007, Jon T. Klepsland JK07-M076 (O-B17788/01).
44. Midtre Gauldal municipality, Budalen, Bua, 800 m south of Buabrua, northeast-facing steep slope, NQ7461,88251, 10°28'20"[10,471400000155]E and 62°57'51"[62,9647000003606]N, on *Alnus incana* in rich mixed spruce/deciduous forest, 220 m, 29 August 2007, Tom Hellik Hofton s.n. (TRH-B672251/1).
45. Midtre Gauldal municipality, Rogga [east of Rødstenen], NQ7393,8810, 10°27'40"[10,4605000000447]E and 63°00'56"[63,015000000596]N, on *Alnus incana*, 280 m, 12 September 2007, Kristian Hassel s.n. (TRH-B693478/1).
46. Orkdal municipality, Vormdal, Vorma, above Håggåndammen, NQ3673,0757, 9°43'47"[9,73010000027716] E and 63°11'43"[63,1954999994487]N, on *Ulmus glabra* in south-facing slope, 130 m, 15 June 2007, Øystein Røsok s.n. (TRH-B673340/1).
47. Selbu municipality, Raudberga Nature Reserve, PR136,037, 11°15'18"[11,2540999995545]E and 63°08'39"[63,1445000004023]N, on *Alnus incana* in *Alnus-Ulmus* forest, 210 m, 21 June 2007, Øystein Røsok s.n. (TRH-B673350/1).

B) Localities in Sweden:

Värmland

1. Filipstad municipality, Brattfors, Lungälvsravinerna, Djupadalen, ca 14°01'E and 59°39'N, on trunk of *Alnus incana* in bottom of deep ravine, ca 150 m, 21 July 1979, Nils Hakelier (S-B29134).
2. Filipstad municipality, Brattfors, Lungälvsravinerna, Kampdalen, ca 14°01'E and 59°39'N, on trunk of *Alnus incana* in bottom of wet ravine, ca 150 m, 12 July 1981, Nils Hakelier (S-B29135). Hassel and Söderström (2008).

Uppland

3. Uppland, Uppsala municipality, Hocksboglupen (south of Lake Tämnaren), RT90: 6665921;1586370, ca 17°21' 30"E and 60°07'50"N, ca 40 m, on nine trunks of *Fraxinus excelsior*, one trunk *of Salix caprea*, one trunk of *Sorbus aucuparia* and 60 stems of *Corylus avellana*, B. Norell and Henrik Weibull (Hallingbäck 2010, Norell and Weibull 2011).

Norrland

4. Ångermanland, Kramfors municipality, Nordingrå parish, Halsviksravinen, 18.431°E and 62.92377°N, in *Picea abies* forest facing SSE just east of swamp forest with seeping water, fairly abundant on two trees of *Populus tremula* with rough bark, 10 August 2012, Johan Dahlberg 6956724 (B195696 in S); Dahlberg (2012).

C) Localities in European Russia

1. Bashkiria province (South Urals): Kyga district, Al River, 15 km SW from Mezjevoi, 58°51'E and 55°11'N, on trunk of *Populus tremula*, 18 July 1992, Baisheva et al. (1994).
2. Bashkiria province (South Urals): Kyga district, 8 km from Allaguzovo S, 58°40'E and 55°32'N, on trunk of *Tilia cordata*, 13 June 1993, Elvira Z. Baisheva (1995).
3. Bashkiria province (South Urals): Salavat district, Lakly, 58°30'E and 55°11'N, on trunk of *Betula verrucosa*, 15 June 1993, Elvira Z. Baisheva (1995).
4. Tver province: Nelidovsky district, west of Staroselye, 32°55'50"E and 56°28'58"N, on bark of old aspen in forest with spruce, grey alder and understory of mountain ash, ca 250 m, 12 October 2011, A. A. Notov 813 (LE,TVBG); Potemkin and Notov (2011).
5. Tver province: Nelidovsky district, near Bolshoye Fedorovskoye, 32°57'46.0"E and 56°27'19.2"N, on bark of grey alder in floodplain in partially shaded habitat, together with *Frullania oakesiana*, ca 250 m, 7 September 2011, A. D. Potemkin and Kotkoval C-38 (LE); Potemkin and Notov (2011).
6. Nizhniy Novgorod province, Kerzhenskiy State Reserve, mouth of Pugai River, 44°54'E and 56°23'N, N. A. Konstantinova 207; Konstantinova (2004).
7. Nizhniy Novgorod province, Kerzhenskiy State Reserve, valley of Kerzhenets River near the cordon Chernooser'e, 44°51' E and 56°26' N, N. A. Konstantinova 179; Konstantinova (2004).
8. Nizhniy Novgorod province, Pochinkovsky district, vicinity of Sadovka, 44.39°E and 54.60°N, on Ulmus glabra in an oak grove, 10 May 1999, A. A. Shestakova; Andrejeva and Shestakova (2009).
9. Nizhniy Novgorod province, Tonsha district, vicinity of Sherstki, 47.40° E and 57.90° N, on aspen in floodplain with spruce-fir-lime, 22 August 2000, A. A. Shestakova; Andrejeva and Shestakova (2009).
10. Nizhniy Novgorod province, Tone Kinsky district, Tonkin Reserve, 46.45°E and 57.34°N, on aspen in spruce-fir-lime forst, 22 August 2000, A. A. Shestakova; Andrejeva and Shestakova (2009).
11. Nizhniy Novgorod province, Arzamas district, vicinity of St. Deserts, 43.58°E and 55.67°N, on linden in oak forest, 22 August 2000, A. A. Shestakova; Andrejeva and Shestakova (2009).
12. Vologda oblast and province, Tot'ma district, vicinity of Sovetskiy settlement, ca 43°34'20"E and 60°29'45"N, 1969, Akhinova and Zhukova (1971); Dulin et al. (2009).
13. Mordovia republic, Mordovia State Nature Reserve, close to Lake Inorki, in *Tilietum – Urticosum* broad-leaved flat forest with no living ground cover, 43°11'90"E and 54°73'21"N, on *Tilia cordata* stem bark at 1.3 m height,

together with *Pseudoleskeella nervosa, Myrinia pulvinata, Pylaisia polyantha* and *Orthothecium speciosum*, 12 September 2013, I. N. Urbanavichene and G. P. Urbanavichus s.n. (LE); Mezaka et al. (2013).

14. Kirov province, Nurgush reserve, Nurgush plot, 40 m from eastern shore of Lake Nurgush, 48°27' 53.1"E and 58°00'16.4"N, on *Tilia cordata* trees 30–35 cm diameter, 12 September 2013, A. D. Potemkin s.n. (LE); also seen on elms and oaks; see Potemkin and Kotkova (2013).
15. Perm province, Vishera State Nature Reserve, Northern Ural, 59°02'E and 61°06'N, 520 m, N. A. Konstantinova and A. G. Bezgodov 121a-1994; Konstantinova and Bezgodov (2006).
16. Caucasus: Krasnodarskij kraj.: Mostovskij rajon, near Mt. Bol'soj Tchac, Tchac stream, ca 40°27'E and 44°02'N, on various deciduous trees and *Picea abies* in mist forest, ca 1500–1700 m, 12 September 1998, V. Otte B-2840 (Otte 2004 and 2006).
17. Caucasus: Adygeja republic: Maikopskij rajon, Sachrai [Novoprochladnoje] village, 200 m SE of graveyard, east of stream, on apple trees, ca 650 m, ca 40°17'30"E and 44°08'N, ca 650 m, 3 July 2002, V. Otte GLM-B-21224 (Otte 2004 and 2006).
18. Caucasus: Caucasus Strict Nature Reserve, southern spurs of Khuko Mountain, near the trail to Cherkeskiy Pass, 39°50'07"E and 43°54'08"N, on bark of *Fagus orientalis* in beech forest with *Rhododendron ponticum*, 960 m, N. A. Konstantinova K375-1-08 (Konstantinova et al. 2009).
19. Caucasus: Caucasus Strict Nature Reserve, left bank of Urushten River, 40°40'53"E and 43°55'57"N, on bark of *Fagus orientalis* at a height of ca 1.5 m in beech forest, 810 m, N. A. Konstantinova K110-2-09 (Konstantinova et al. 2009).
20. Caucasus: Adygeya republic, right bank of Mishoko River (left tributary of Belaya River), 40°11'47"E and 44°16'39"N, on beech bark in beech-oak forest, 510 m, N. A. Konstantinova K416-2-10 (Konstantinova and Savchenko 2013).
21. Caucasus: Adygeya republic, left bank of Mishoko River, 40°11'50"E and 44°16'38"N, on beech bark, 550 m, N. A. Konstantinova K418-2a,b,c-10 (Konstantinova and Savchenko 2013).
22. Caucasus: Adygeya republic, Malaya Laba River Basin, right bank of Urushten River, 40°40'28"E and 43°55'53"N, on beech barkin fern-beech-hornbeam forest at a height of ca 2 m, 820 m, N. A. Konstantinova K418-2a,b,c-10 (Konstantinova and Savchenko 2013).
23. Caucasus: Adygeya republic, Snegovalka Ridge, 40°39'43"E and 43°54'01"N, on *Sorbus* bark in fir-beech forest, 1750 m, N. A. Konstantinova K162-3a-09; also on beech bark in beech grass-fern forest, K163-1a,2a-09; and on bark of maple in beech-maple forest, K164-09 (Konstantinova and Savchenko 2013).