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Taxonomy, Ecology, and Distribution of Six Remarkable Plant Taxa (*Spermatophyta*, *Bryophyta*, and *Lichenes*) of the Estonian Dry Grassland Flora

By

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With 1 Figure

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Summary

DENGLER J. & BOCH S. 2007. Taxonomy, ecology, and distribution of six remarkable plant taxa (*Spermatophyta*, *Bryophyta*, and *Lichenes*) of the Estonian dry grassland flora. – *Phyton* (Horn, Austria) 47 (1–2): 47–71, with 1 figure. – English with German summary.

We present new and remarkable flowering plant, moss, and lichen taxa to the flora of Estonia, which we recorded in dry grasslands on the island of Saaremaa. New to Estonia are *Bryum radiculosum* BRID. (*Bryophyta* – *Bryaceae*), *Caloplaca lithophila* H. MAGN. (*Lichenes* – *Teloschistaceae*), and *Festuca oelandica* (HACKEL) K. RICHTER (*Spermatophyta* – *Poaceae*). *Agonimia globulifera* BRAND & DIEDERICH in SÉRUSIAUX & al. (*Lichenes* – *Verrucariaceae*) was previously mentioned in a note by S. B. but without detailed ecological information. For *Allium schoenoprasum* subsp. *schoenoprasum* var. *alvarense* Hyl. (*Spermatophyta* – *Alliaceae*) and *Crepis tectorum* subsp. *pumila* (LILJEBLAD) STERNER (*Spermatophyta* – *Asteraceae*), diverging opi-

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nions existed in the literature as to whether they occur in Estonia or not and how they should be discriminated from the respective typical infraspecific taxon. We give detailed morphological descriptions of the collected specimens and characterise the stands of the newly found taxa ecologically and sociologically. Most of the new records originate from the *Crepido pumilae*-*Allietum alvarensis* (Sedo-Scleranthenea), an open alvar community of shallow, skeletal soils, whose stands are subject to inundation in winter and severe drought in summer. From a phytogeographical point of view, the occurrences of the three flowering plant taxa on Saaremaa are most remarkable, as they have been previously thought to be endemics of Öland and Gotland. They presumably have arisen following the glaciation under the harsh environmental conditions of the open alvar communities from their widespread and ecologically plastic ancestors.

Zusammenfassung

DENGLER J. & BOCH S. 2007. Taxonomie, Ökologie und Verbreitung von sechs bemerkenswerten Pflanzensippen (*Spermatophyta*, *Bryophyta* und *Lichenes*) der estnischen Trockenrasenflora. – *Phyton* (Horn, Austria) 47 (1–2): 47–71, mit 1 Abbildung. – Englisch mit deutscher Zusammenfassung.

Wir berichten über für Estland neue und andere bemerkenswerte Blütenpflanzen-, Moos- und Flechtentaxa, die wir in Trockenrasen der Insel Saaremaa nachgewiesen haben. Erstmals für Estland sind *Bryum radiculosum* BRID. (*Bryophyta* – *Bryaceae*), *Caloplaca lithophila* H. MAGN. (*Lichenes* – *Teloschistaceae*) und *Festuca oelandica* (HACKEL) K. RICHTER (*Spermatophyta* – *Poaceae*). *Agonimia globulifera* BRAND & DIEDERICH in SÉRUSIAUX & al. (*Lichenes* – *Verrucariaceae*) wurde zuvor schon in einer kurzen Notiz von S. B. veröffentlicht, jedoch ohne detaillierte ökologische Informationen. Bei *Allium schoenoprasum* subsp. *schoenoprasum* var. *alvarensis* HYL. (*Spermatophyta* – *Alliaceae*) und *Crepis tectorum* subsp. *pumila* (LILJEBLAD) STERNER (*Spermatophyta* – *Asteraceae*) existierten in der Literatur konträre Ansichten darüber, ob sie in Estland vorkommen und wie sie sich von dem jeweils typischen infraspezifischen Taxon unterscheiden. Wir beschreiben die von uns gesammelten Exemplare der sechs genannten Sippen eingehend morphologisch und charakterisieren ihre Standorte ökologisch und soziologisch. Die meisten der Aufsammlungen stammen aus dem *Crepido pumilae*-*Allietum alvarensis* (Sedo-Scleranthenea), einer offenen Alvargesellschaft flachgründiger, skelettreicher Böden, deren Standorte im Winter überflutet sind und im Sommer extrem stark austrocknen. Aus phytogeografischer Sicht sind die Vorkommen der drei Blütenpflanzen auf Saaremaa besonders bemerkenswert, da sie bislang als Endemiten von Öland und Gotland galten. Sie haben sich mutmaßlich postglazial unter den extremen Umweltbedingungen der Alvargesellschaften aus ihren weit verbreiteten und ökologisch plastischen Elterntaxa herausgebildet.

1. Introduction

The dry grasslands over superficial limestone bedrocks on the Swedish islands of Öland and Gotland, so-called alvars, have been intensively studied by botanists for centuries and are well known for their extraordinary small-scale species richness and their unusual species combinations and site conditions (cf. PETTERSON 1965, KRAHULEC & al. 1986, STERNER &

LUNDQVIST 1986, SJÖGREN 1988, LÖBEL & al. 2006). They also host some of the few endemic plant taxa that exist in the Nordic countries (BENGTSSON & al. 1988, JONSELL & KARLSSON 2004). Although the existence of similar alvar grasslands in Estonia has long been known (e.g., VILBERG 1927), they have been studied in more detail only in recent decades (e.g., ZOBEL & KONT 1992, PÄRTEL & al. 1999). However, these recent studies generally did not treat bryophytes, lichens, and critical vascular plant taxa, and they were focussed mainly on the more closed grassland communities of the slightly deeper soils (*Helictotrichon pratense* community in Table 1).

Table 1. Syntaxonomic overview of the dry grassland communities on the island of Saaremaa. A detailed description of the phytosociological classification is given in BOCH & DENGLER 2006, DENGLER & LÖBEL 2006, and DENGLER & al. 2006.

Class: Koelerio-Corynephoretea KLIKA in KLIKA & NOVÁK 1941
 Subclass: Koelerio-Corynephorenea (KLIKA in KLIKA & NOVÁK 1941) DENGLER in DENGLER & al. 2003
 Order: Corynephoretalia canescentis KLIKA 1934
 All.: Corynephorion canescentis KLIKA 1931
 Assoc.: Caricetum arenariae CHRISTIANSEN 1927
 Order: Trifolio arvensis-Festucetalia ovinae MORAVEC 1967
 All.: Armerion elongatae PÖTSCH 1962
 Assoc.: Sileno otitae-Festucetum brevipilae LIBBERT 1933 corr. KRATZERT & DENGLER 1999 nom. invers. propos.
 Order: Sedo acris-Festucetalia Tx. 1951 nom. invers. propos.
 All.: Koelerion glaucae VOLK 1931
 Assoc.: Helichryso arenarii-Jasionetum litoralis LIBBERT 1940
 Assoc.: Festucetum polesicae REGEL 1928
 Subclass: Sedo-Scleranthenea (Br.-Bl. 1955) DENGLER in DENGLER & al. 2003
 Order: Alyso alyssoidis-Sedetalia MORAVEC 1967
 All.: Tortello tortuosae-Sedion albi HALLBERG ex DENGLER & LÖBEL 2006
 Suball.: Tortello tortuosae-Sedenion albi (HALLBERG ex DENGLER & LÖBEL 2006) DENGLER & LÖBEL 2006
 Assoc.: Cladonio symphycaepae-Sedetum albi Tx. 1951 nom. invers. propos.
 Suball.: Tortello rigentis-Helianthemion oelandici DENGLER & LÖBEL 2006
 Assoc.: Crepido pumilae-Allietum alvarensis KRAHULEC & al. ex DENGLER & LÖBEL 2006
 Assoc.: Helianthemo oelandici-Galietum oelandici KRAHULEC & al. ex DENGLER & LÖBEL 2006
 Class: Festuco-Brometea Br.-Bl. & Tx. ex KLIKA & HADAČ 1944
 Order: Brachypodietalia pinnati KORNECK 1974
 Assoc.: *Helictotrichon pratense* community

During our study of the plant diversity, ecology, and classification of the dry grasslands on the Estonian island of Saaremaa (BOCH 2005, BOCH &

DENGLER 2006), we found six new or remarkable flowering plant, moss, and lichen taxa for the dry grassland flora of Estonia. New to Estonia are *Bryum radiculosum*, *Caloplaca lithophila*, and *Festuca oelandica*. *Agonimia globulifera* had also been new at the time of our study but has been already briefly mentioned in SUJWA & al. 2005. Although *Allium schoenoprasum* subsp. *schoenoprasum* var. *alvarense* and *Crepis tectorum* subsp. *pumila* had been previously recorded from Estonia (*Allium*: EICHWALD & al. 1984; *Crepis*: LEHT 1999), Swedish authors still claim these two plants as endemic to Öland or Öland and Gotland (MOSSBERG & STENBERG 2003, JONSELL & KARLSSON 2004).

The aim of this article is to characterise our records morphologically, ecologically, and sociologically, and to contribute to the reconciliation of the contrasting taxonomic positions in the literature. In particular, we focus on the differences between the treated taxa and their close relatives. In a final section, we discuss the relevance of our findings for the understanding of biogeographic patterns and evolutionary processes of the taxa concerned as well as for priority setting in nature conservation.

2. Research Area

In Estonia, we studied the different dry grassland communities on the Baltic island of Saaremaa (2,673 km²; 57° 50' – 58° 40' N, 21° 45' – 23° 20' E). The bedrock of this island is formed by Silurian limestone (RAUKAS & TEEDUMÄE 1997), that is sometimes close to the surface but is more often covered by Weichselian moraines or Holocene marine sediments (POSKA & SAARSE 2002). The mean annual temperature on Saaremaa is about 6.0 °C (Anonymous 1970), and the annual precipitation varies regionally between 540 mm and 675 mm (RAUDSEPP & JAAGUS 2002).

Dry grassland areas are distributed all over the island. They occur on deep sandy soils poor in humus such as dunes (Koelerio-Corynepherea) and on shallow soils over limestone bedrock (alvar sites). Within the alvar dry grasslands, two different types of plant communities can be distinguished, (i) communities of very thin silt or clay soils rich in humus over limestone bedrock, often poorly drained and affected by frost movements due to repeated freezing and thawing (Sedo-Scleranthenea) and (ii) communities on somewhat deeper soils with intermediate site conditions (Festuco-Brometea) (BOCH & DENGLER 2006, DENGLER & al. 2006). Outside the alvars, similar communities also occur on (fossil) shore ridges and anthropogenic substrata such as stone embankments, concrete slabs, and gravel. We apply the syntaxonomic classification of BOCH & DENGLER 2006 (see Table 1), and use these syntaxon names in the text without specific epithets and author citations. The site conditions in the dry grasslands on Saaremaa and their floristic composition are quite similar to those of the

Table 2. Average environmental conditions and structural parameters of the dry grassland plots in which we found the new and remarkable taxa, as well as their close relatives on the island of Saaremaa. The soil data refer to the uppermost 10 cm. Arithmetic means (\pm standard deviation) are given unless otherwise indicated. Within the ordinal scales, 0 means absent, whereas 1 stands for very low values and 5 or 6 for the highest values (cf. BOCH 2005).

	Number of relevés	Mean species number on 4 m ²	Cover of vascular plants [%]	Cover of bryophytes [%]	Cover of lichens [%]	Cover of stones and rocks [%]	Microrelief [cm]	Humus content [%]	pH value (H ₂ O)	Cation exchange capacity [mval/100 g]	CaCO ₃ content [ordinal; 0-5] (median)	Proportion of soil skeleton [ordinal; 1-6] (median)	Soil depth [ordinal; 1-5] (median)
<i>Allium schoenoprasum</i> var. <i>alvarensis</i>	11	50.5 \pm 10.3	57 \pm 14	61 \pm 30	6 \pm 10	15 \pm 20	11 \pm 9	11 \pm 4	7.5 \pm 0.2	39 \pm 17	4	3	2
<i>Allium schoenoprasum</i> var. <i>schoenoprasum</i>	1	31.0	70	30	0	0	1	7	7.4	51	4	1	2
<i>Crepis tectorum</i> subsp. <i>pumila</i>	9	49.0 \pm 9.7	62 \pm 11	60 \pm 21	18 \pm 31	7 \pm 5	10 \pm 8	12 \pm 4	7.5 \pm 0.2	39 \pm 21	3	3	2
<i>Crepis tectorum</i> subsp. <i>tectorum</i>	9	31.0 \pm 13.0	40 \pm 18	45 \pm 29	16 \pm 17	24 \pm 39	6 \pm 4	5 \pm 4	7.3 \pm 0.3	61 \pm 31	4	2	2
<i>Festuca oelandica</i>	1	32.0	50	25	95	5	5	11	7.5	59	3	2	1
<i>Festuca nigrescens</i>	2	26.0 \pm 6.0	64 \pm 34	69 \pm 29	21 \pm 19	8 \pm 8	3 \pm 1	21 \pm 15	7.3 \pm 0.1	54 \pm 18	3	2.5	3
<i>Festuca rubra</i> subsp. <i>arenaria</i>	4	22.3 \pm 9.9	38 \pm 20	20 \pm 12	23 \pm 22	0 \pm 0	2 \pm 0	2 \pm 3	7.1 \pm 0.7	18 \pm 19	3	1	5
<i>Festuca rubra</i> subsp. <i>rubra</i>	80	39.8 \pm 10.8	78 \pm 23	62 \pm 26	5 \pm 12	5 \pm 15	5 \pm 5	10 \pm 6	7.2 \pm 1.0	41 \pm 23	3	1	3
<i>Bryum radiculosum</i>	3	52.7 \pm 8.5	47 \pm 13	56 \pm 32	5 \pm 3	13 \pm 4	7 \pm 4	11 \pm 1	7.6 \pm 0.1	47 \pm 13	4	4	1
<i>Agonimia globulifera</i>	21	55.6 \pm 7.5	58 \pm 14	45 \pm 20	20 \pm 15	11 \pm 10	8 \pm 4	13 \pm 4	7.5 \pm 0.3	37 \pm 17	3	3	2
<i>Caloplaca lithophila</i>	2	36.0 \pm 17.0	77 \pm 24	50 \pm 7	1 \pm 1	1 \pm 0	3 \pm 2	12 \pm 9	7.5 \pm 0.3	55 \pm 11	3.5	3.5	1.5
<i>Caloplaca holocarpa</i>	9	39.1 \pm 11.4	42 \pm 17	41 \pm 25	15 \pm 18	35 \pm 29	7 \pm 5	10 \pm 9	7.7 \pm 0.2	68 \pm 20	4	4	2

islands of Öland and Gotland (for detailed information, see BOCH 2005, BOCH & DENGLER 2006, DENGLER & al. 2006).

3. Material and Methods

During summer 2004, we sampled 231 phytosociological relevés on dry grassland communities on Saaremaa. Plots were 4 m² in size throughout and were selected based on the presence of visually homogenous vegetation. The plots were representatively distributed over the dry grasslands of the island, with the aim of including the full range of site conditions and floristic composition. We recorded all vascular plants, bryophytes, lichens, and macroscopic 'algae', including those of 'substrate strata', i.e. epiphytic, lignicolous and saxicolous taxa (cf. DENGLER 2003: 136). Plot coordinates were determined with a Global Positioning System (GPS). For each relevé, several environmental and structural parameters were recorded and/or measured in the laboratory (cf. Table 2; for detailed methods see BOCH 2005, BOCH & DENGLER 2006). Individual plot data are available in BOCH 2005 and in part also in DENGLER & al. 2006.

All plant specimens were collected and determined by S. B. unless otherwise stated (specimens deposited in herbaria are indicated in Table 3). In the descriptions,

Table 3. Synoptic table of the new and remarkable taxa as well as their close relatives in the different dry grassland communities on Saaremaa. The numbers in the columns indicate the percentage presence degree of the taxa in the associations. The abbreviations used in the column 'Herbarium' are the initials of the authors of this paper, and/or the Herbarium of the University Tartu (TU).

Association	Caricetum arenariae	Sileno-Festucetum	Helichryso-Jasionetum	Festucetum polesicae	Cladonio-Sedetum	Crepido-Allietum	Helianthemo-Galietum	<i>Helictotrichon</i> community	Herbarium
Number of relevés	6	24	12	43	22	37	14	73	
<i>Allium schoenoprasum</i> var. <i>alvarense</i>	27	7	.	S. B.
<i>Allium schoenoprasum</i> var. <i>schoenoprasum</i>	.	4	
<i>Crepis tectorum</i> subsp. <i>pumila</i>	24	.	.	S. B.
<i>Crepis tectorum</i> subsp. <i>tectorum</i>	.	4	.	5	14	3	7	1	S. B.
<i>Festuca oelandica</i>	3	.	.	S. B.; J. D.
<i>Festuca nigrescens</i>	.	4	.	.	5	.	.	.	
<i>Festuca rubra</i> subsp. <i>arenaria</i>	.	4	25	
<i>Festuca rubra</i> subsp. <i>rubra</i>	.	38	.	2	27	32	21	67	
<i>Bryum radiculosum</i>	8	.	.	S. B., TU
<i>Agonimia globulifera</i>	43	14	4	S. B., TU
<i>Caloplaca holocarpa</i>	.	4	8	.	14	5	14	.	S. B.
<i>Caloplaca lithophila</i>	5	3	.	.	S. B.

either morphometric values are given as ranges (with rare extremes in brackets) or as means with minimum and maximum values in brackets. Unless otherwise stated, the nomenclature of vascular plants follows TUTIN & al. 1968/1993, that of mosses HILL & al. 2006, that of liverworts GROLLE & LONG 2000, and that of lichens SANTESSON & al. 2004.

4. *Allium schoenoprasum* subsp. *schoenoprasum* var. *alvarense* (Spermatophyta – Alliaceae)

4.1. Taxonomy, Morphology, and Determination

According to STEARN 1980, *Allium schoenoprasum* L. is a variable and plastic species, which tends to develop locally differentiated populations. However, since characters exhibit considerable overlap, he refrains from accepting any of the numerous described infraspecific taxa in his treatment in 'Flora Europaea'. For similar reasons, FRIESEN 1996 and WISSKIRCHEN & HAEUPLER 1998 accept only two tetraploid subspecies from Spain in addition to the widespread diploid subsp. *schoenoprasum*, and no varieties. By contrast, Nordic authors generally accept several varieties within subsp. *schoenoprasum* [var. *schoenoprasum*, var. *sibiricum* (L.) GARCKE, var. *alvarense* HYL., and var. *jurmoense* O. A. EKLUND] (STERNER & LUNDQVIST 1986, MOSSBERG & STENBERG 2003, JONSELL & KARLSSON 2004). FRIESEN 1996 mentions low-growing types ('Type B') morphologically similar to var. *alvarense* from different mountain and limestone regions of Eurasia (e.g., var. *pumilum* BUNGE from the Altai mountains). According to genetic (RAPD) analyses by FRIESEN & BLATTNER 2000, type B plants from different localities are polyphyletic, however, they included only one such sample from a Nordic alvar site (Öland). This was phylogenetically closest to a sample of their type A (corresponding to var. *schoenoprasum*) from Finland. Due to the low number of samples from the Nordic region, their results do not provide arguments for or against the recognition of var. *alvarense*.

Var. *alvarense* is basically distinguished from the typical variety by its bluish-white cuticula (EICHWALD & al. 1984, MOSSBERG & STENBERG 2003) and shorter stems (STERNER & LUNDQVIST 1986, MOSSBERG & STENBERG 2003). EICHWALD & al. 1984 give 7–15 cm as compared to 10–30 for var. *schoenoprasum* (MOSSBERG & STENBERG 2003). Additional discriminating characters only mentioned by individual sources are the leaves being shorter than the inflorescence-supporting stem (EICHWALD & al. 1984) and remaining erect all the year (MOSSBERG & STENBERG 2003). The *Allium schoenoprasum* populations on alvar sites of Saaremaa looked very similar to those of the alvars of Öland (J. D.). The analysed plants ($n = 16$) had a height of (6–) 9.2 (–12) cm. The leaves had a bluish-white cuticula and were (4–) 7.5 (–13) cm long and thus mostly shorter than the inflorescence-supporting stem. The bulbs were growing individually or sometimes in pairs

and were (0.5–) 1.0 (–1.9) cm in size. The umbels had (1–) 9 (–20) flowers with (1.5–) 2.3 (–3.0) mm long pedicels, purple perigons with tepals (4.0–) 6.3 (–9.0) mm in size, and (2.5–) 3.3 (–4.0) mm long filaments. The involucre bracts were (5.0–) 6.9 (–9.0) mm long. The seeds were about 2.5 mm × 1.0 mm in size. Thus, we can conclude that the populations of *A. schoenoprasum* from alvar sites on Saaremaa fit well in the picture of *A. schoenoprasum* var. *alvarense* as described from Öland. They also were morphologically clearly separated from a population we collected on a non-alvar dry grassland (Sileno-Festucetum), which can be referred to as var. *schoenoprasum*. If var. *alvarense* is accepted as a valid taxon, it seems reasonable to include also the alvar populations of Estonia. However, according to our present knowledge, the two types are discriminated by only few characters, and these are of a kind that phenotypic plasticity cannot be ruled out.

4.2. Distribution, Ecology, and Sociology

Whereas *Allium schoenoprasum* var. *alvarense* was first thought to be an Öland endemic (e.g. BENGTTSSON & al. 1988), JONSELL & KARLSSON 2004 also state its occurrence on Gotland. However, the taxon was reported from Saaremaa and northern Estonia over twenty years ago by EICHWALD & al. 1984.

On Saaremaa, we found plants on several periodically inundated alvar sites with distinct microtopography and shallow silt and clay soils, rich in base cations, humus, carbonate, and skeletal content (Table 2). According to the supra-regional classification of DENGLER & al. 2006, *A. schoenoprasum* subsp. *schoenoprasum* var. *alvarense* is a character taxon of the suballiance Tortello-Helianthemion (cf. Table 1). On Saaremaa, where the second association in which it gains high constancies on Öland, the Fulgensio bracteatae-Poetum alpinae (ALBERTSON 1950) DENGLER & LÖBEL 2006, is missing, it can be assessed as a territorial character species of the Crepido-Allietum, but it also rarely occurred in the Helianthemo-Galietum (BOCH & DENGLER 2006, see Table 3). Among the vascular plants, the most frequent companions ($\geq 80\%$) were *Agrostis stolonifera*, *Artemisia rupestris*, *Festuca ovina*, *Galium verum* subsp. *verum*, *Sedum album*, and *Veronica spicata* subsp. *spicata*, and the cryptogam layer was usually dominated by *Ditrichum flexicaule*. By contrast, our only record with var. *schoenoprasum* originates from a Sileno-Festucetum stand with less soil skeletal content and a denser herb layer (Table 2 and 3).

4.3. Records

Northwest of Kuressaare, close to the main road 78, northeast of Mullutu: 58° 17' 16.3" N / 22° 24' 13.5" E, 5 m a.s.l., Crepido-Allietum; and 58° 17' 15.8" N / 22° 24' 25.9" E, 5 m a.s.l., Helianthemo-Galietum; both 08.VII.2004. – Southwest of Kur-

essaare, south of the main road 77: 58° 14' 8.0" N / 22° 26' 2.3" E, 2.5 m a.s.l., *Crepido-Allietum*, 17.VII.2004. – Northwest of Kuressaare, close to Randvere: 58° 17' 13.6" N / 22° 23' 50.8" E, 6 m a.s.l., *Crepido-Allietum*, 26.VII.2004. – About 9 km to the north-east of Kuressaare, alvar to the north of Ipla: 58° 18' 36.9" N / 22° 38' 24.2" E; 58° 18' 5.9" N / 22° 38' 31.4" E; and 58° 18' 0.8" N / 22° 38' 22.4" E; all 20 m a.s.l., *Crepido-Allietum*, 14.VIII.2004.

5. *Crepis tectorum* subsp. *pumila* (*Spermatophyta* – *Asteraceae*)

5.1. Taxonomy, Morphology, and Determination

In 'Flora Europaea', three subspecies are distinguished within *Crepis tectorum*: besides the widespread tall-growing and multi-flowered subsp. *tectorum*, SELL 1976 distinguishes two low-growing subspecies with few capitula, subsp. *nigrescens* (POHLE) P. D. SELL from sea and river shores in the Arctic region and subsp. *pumila* (LILJEBLAD) STERNER from shallow soils over limestone rocks on the Swedish islands of Öland and Gotland. The plants from alvar are not mere modifications but mostly based on genetic differences, as has been shown in various cultivation experiments (e.g. ANDERSSON 1989a, 1989b, 1993). The three named subspecies are also accepted by MOSSBERG & STENBERG 2003, who, however, include the plants from alvar sites on Gotland as var. *glabrescens* NEUM. into subsp. *tectorum* (similarly in KARLSSON & JONSELL 2004). The assumption that the alvar populations of Gotland would be phylogenetically closer to the weedy populations of subsp. *tectorum* than to subsp. *pumila* from Öland first appeared in the paper of ANDERSSON 1990. He analysed numerous herbarium specimens of *C. tectorum* from 'weed' and 'outcrop' populations throughout Fennoscandia and Estonia morphometrically. In his cluster analysis, the outcrop populations of Öland and southern Finland were separated from all other Nordic populations, including the outcrop populations of Gotland and Estonia. However, his conclusion may be erroneous for several reasons: (i) the outcomes of cluster analyses are influenced by many arbitrary choices and thus one single such analysis is not sufficient to establish phylogenetic relationships; (ii) ANDERSSON 1990 did not use characters of individual plants or populations for his cluster analysis but mean values for 18 geographic regions, each separated in weedy and outcrop plants; (iii) his assignment of specimens to the weedy or the outcrop groups, respectively, was based in 70% of all cases simply on plant height since no ecological information was given on the herbarium sheets. Having a second look on ANDERSSON's 1990 data, they much better support a closer relationship between the alvar populations of Öland and Gotland. On the one hand, these jointly occupy a well-separated area in his ordination diagram where practically no weedy populations and only outcrop populations from a few other regions (Swedish mainland around Stockholm and

southernmost part of Finland, including many islands) can be found. On the other hand, his overview of mean values for the analysed ten characters for his 36 groups (18 regions differentiated into weedy and outcrop; ANDERSSON 1990: table 2) reveals that the alvar plants of Öland and Gotland together fall completely out of the range of all other groups for half of the characters. Thus, they are much lower-growing, have fewer nodes, show higher ratios both of the number of capitula and of terminal branches to height, and produce smaller achenes. Furthermore, the author himself found the alvar populations of Gotland to be closer to those of Öland than to weedy populations in a number of previous and subsequent studies where he applied different methods (ANDERSSON 1989a, 1989b, 1993).

On Saaremaa, we found two conspicuously different 'forms' of *Crepis tectorum* (Table 4), referred to as subsp. *tectorum* and subsp. *pumila*. The latter completely conformed with the descriptions of subsp. *pumila* in the literature (SELL 1976, MOSSBERG & STENBERG 2003) and also to the morphometric values of ANDERSSON 1990 for outcrop populations on Öland (Table 4). In particular, these plants were mostly smaller than 7 cm in height and had fewer than seven capitula per plant, which are considered the best discriminative characters against subsp. *tectorum*. Apart from the morphometric differences (Table 4), the collected individuals of subsp. *pumila* were hairy but not tomentose with glandular hairs being frequent at least under the capitula but partly also on most other organs, whereas the individuals of subsp. *tectorum* were densely tomentose throughout but had fewer glandular hairs restricted to the capitula. The specimens of subsp. *pumila* from Saaremaa had no auricles at either cauline or basal leaves and they also were lacking basal side branches.

Table 4. Comparison between the morphometric characters of *Crepis tectorum* subsp. *tectorum* (two plants of two different populations) and subsp. *pumila* (ten plants of four different populations) on Saaremaa. Both arithmetic means and ranges are given.

	Height of plant [cm]	Height of main stem [cm]	Number of capitula	Number of branches at main stem	Number of nodes on the main stem	Length of cauline leaves [mm]	Length of basal leaves [mm]	Capitula Ø [mm]	Length of ligulate florets [mm]	Length of outer involucre bracts [mm]	Length of inner involucre bracts [mm]	Length of pappus [mm]
subsp. <i>tectorum</i>	12.5 10-14	10.3 8.5-12.0	16.0 11-21	12.5 11-14	17.0 15-19	20 15-30	50 30-70	15.0 12-20	9 8-11	3 2-4	8 6-10	6 4-7
subsp. <i>pumila</i>	6.3 3-11	5.7 2.5-9.5	2.1 1-4	0.7 0-2	2.6 2-4	8.8 3-18	10 4-20	7.5 4-13	8 6-9	2 1-3	5.4 4-7	4 4-5

In conclusion, the plants named 'subsp. *pumila*' (Table 4) according to all available determination keys belong to subsp. *pumila*. They are not referable to any of the four species into which *C. tectorum* is split in the recent flora of the European part of the former Soviet Union (CZEREPANOV 2003), though they are most similar to *C. astrachanica* STEV. ex CZER. from the Astrakhan region (included in *C. tectorum* subsp. *tectorum* in 'Flora Europaea'). The alvar plants from Saaremaa are completely different from those samples that ANDERSSON 1990 referred to as Estonian outcrop plants, especially in their being smaller (5.7 cm vs. 10.9 cm) and having fewer nodes (2.6 vs. 7.9). Most probably ANDERSSON's 1990 samples at least partly consisted of low-growing individuals of subsp. *tectorum* from dry, nutrient-poor sites as those in Table 4, which he probably would have assigned as outcrop forms since they do not exceed 20 cm in height. As we indicated above, we also regard the populations of alvar sites on Gotland as belonging to subsp. *pumila*. Whether their small but seemingly consistent morphological differences compared with the Ölandic populations (ANDERSSON 1990, MOSSBERG & STENBERG 2003) as well as the fact that they are largely self-fertile in contrast to these (ANDERSSON 1989c) justify the retention of a separate variety within this subspecies should be subject to future studies. Within the likewise circumscribed subspecies, the populations from Saaremaa are morphologically closer to those from Gotland than those from Öland, as they have largely undivided leaves and show no basal branching.

5.2. Distribution, Ecology, and Sociology

Based on the re-assessment of the data of ANDERSSON 1990 and our own collections on Saaremaa, the distribution of subsp. *pumila* on Gotland (SELL 1976) could be confirmed in contrast to recent concepts of Swedish authors (ANDERSSON 1990, MOSSBERG & STENBERG 2003, KARLSSON & JONSELL 2004), and the record of this taxon from an alvar site in the north-western part of mainland Estonia by LEHT 1999 also seems credible. Whether some of ANDERSSON's 1990 'outcrop forms' from southern Finland or the Swedish mainland also belong to subsp. *pumila* will require further studies.

On Saaremaa, subsp. *pumila* occurs on several periodically inundated alvar sites with shallow soils rich in humus, carbonate, and skeletal content as well as a distinct microrelief (Table 2). The site conditions are thus similar to those on Öland (cf. DENGLER & al. 2006). On a larger scale, *Crepis tectorum* subsp. *pumila* can be considered as character taxon of the Tortello-Helianthemion, with the highest constancy values in the Crepido-Allietum (DENGLER & al. 2006). On Saaremaa, we found subsp. *pumila* exclusively in the latter association and thus regard it as territorial character species (BOCH & DENGLER 2006, see Table 3). Among the vascular plants,

the most frequent companions ($\geq 80\%$) are *Acinos arvensis*, *Agrostis stolonifera*, *Artemisia rupestris*, *Galium verum* subsp. *verum*, *Sagina nodosa*, *Sedum album*, and *Veronica spicata* subsp. *spicata*. The cryptogam layer of the recorded stands is co-dominated by *Ditrichum flexicaule* and *Fissidens dubius*, and also *Nostoc* sp., *Peltigera rufescens*, and *Riccia bifurca* reach 100% constancy. By contrast, subsp. *tectorum* occurred scattered in most dry grassland communities of Saaremaa (Table 3), where it often inhabited rather rocky sites (Table 2). Due to the varying sociological positions of its stands, the most frequent vascular companions of *Crepis tectorum* subsp. *tectorum* in dry grasslands only reach 67% (*Sedum acre* and *Thymus serpyllum* subsp. *serpyllum*).

5.3. Records

Southwest of Kuressaare, south of the main road 77: 58° 14' 8.0" N / 22° 26' 2.3" E, 2.5 m a.s.l., 17.VII.2004. – Tagamoisa ps, close to the main road 78: 58° 24' 27.3" N / 21° 59' 12.1" E, 4 m a.s.l., 25.VI.2004. – Alvar close to Katri pank, about 3 km to the south of Pilguse: 58° 14' 23.2" N / 21° 58' 3.1" E, 03.VII.2004; and 58° 14' 24.6" N / 21° 58' 5.0" E, 28.VII.2004; both 3 m a.s.l.

6. *Festuca oelandica* (Spermatophyta – Poaceae)

6.1. Taxonomy, Morphology, and Determination

Festuca oelandica (HACKEL) K. RICHTER belongs to the *F. rubra* aggregate, where it is either accepted at species level (AUQUIER 1971, MARKGRAF-DANNENBERG 1980, BENGTSSON & al. 1988) or included in *F. rubra* L. as subsp. *oelandica* (HACKEL) STERNER (LID & GJÆREVOLL 1987, MOSSBERG & STENBERG 2003, JONSELL & KARLSSON 2004) or var. *oelandica* HACKEL (STERNER & LUNDQVIST 1986).

Apart from the detailed diagnosis of *F. oelandica* by MARKGRAF-DANNENBERG 1980 and a figure of a leaf section by LEVITSKY & KUZMINA 1927, only rather coarse descriptions of this species can be found in the floristic literature (HYLANDER 1953, AUQUIER 1971, MOSSBERG & STENBERG 2003). For this reason, we compare the plants from Saaremaa both with the diagnosis of MARKGRAF-DANNENBERG 1980 and with characteristics of herbarium specimens of *F. oelandica* collected by J. D. on the Great Alvar of Öland (Table 5). Morphometrically, the specimens from Saaremaa completely match those from Öland and the description of MARKGRAF-DANNENBERG 1980. With their caespitose growth (i.e., few and short stolons), *F. oelandica* plants from both islands rather resemble *F. ovina* agg. than typical *F. rubra* agg. at the first glance. With the extravaginal insertion of non-flowering shoots and the leaf sheaths being closed to the mouth, however, they clearly belong to *F. rubra* agg. The specimens of *F. oelandica* are also distinguished from the other taxa of this group that occur on Saaremaa [*F. rubra* L. subsp. *rubra*, *F. rubra* subsp. *arenaria* (OSBECK)

Table 5. Morphometric characterisation (ranges, rare extremes in brackets) of collections of *Festuca oelandica* from Saaremaa and from Öland compared with the diagnosis given by Markgraf-Dannenberg 1980.

	Plants from Saaremaa	Plants from Öland	Description 'Flora Europaea'
Culm height [cm]	23-38	27-35	20-37 (-47)
Leaf length [cm]	2-14	8-16	
Leaf diameter [mm]	0.73-1.01	0.67-1.13	
Veins	5-7 (-8)	7	7 (-9)
Furrows	4 (-7)	4 (-5)	
Sclerenchyma-layers beneath the main vein	3-12	4-13	stout
Sclerenchyma in ribs	rare, with 1-2 cells	rare, with 1-2 cells	rare
Panicle length [cm]	2.8-7.0	2.5-5.7	4-6
Spikelet length [mm]	6.0-9.0	6.7-7.5	6.5-8.7
Flowers per spikelet	4-5	3-6	
Upper glume [mm]	3.0-4.0	3.7-4.1	2.8-4.9
Awn [mm]	0.0-0.7	0.0-1.0	0.0-1.3
Lemma	dark violet	light violet	glaucous or dark violet

S. ARESCHOUG, *F. nigrescens* LAM., cf. BOCH 2005] by their short stems, their short, curved, rigid, acute, and bluish-green leaves, their small panicles with short spikelets consisting of rather few flowers, and the absent to short awns of the lemmas. The most distinctive feature of *F. oelandica*, however, is the arrangement of the sclerenchyma-strands. In many leaves, they form a closed, evenly thickened ring, which reaches 10 or more cell-layers beneath the main nerve. In this respect, the plants from Saaremaa also completely resemble those from Öland (Fig. 1) and the drawing in LEVITSKY & KUZMINA 1927. The only other European taxon of the *F. rubra* aggregate with confluent sclerenchyma-strands is *F. juncifolia* CHAUB. in ST.-AMANS [*F. arenaria* subsp. *oraria* (DUMORT.) DENGLER], which occurs on Atlantic coastal dunes eastwards to the Netherlands and which differs in having very long stolons and densely villose upper leaf-surfaces (AUQUIER 1971, MARKGRAF-DANNENBERG 1980). It must, however, be mentioned that leaves with thinner and non-confluent sclerenchyma-strands can usually also be found on the same plants but to a lesser extent on both Öland and Saaremaa (Fig. 1). Even in such leaves, however, the groups of sclerenchyma are usually thicker and more extended than they are in the other representatives of the *F. rubra* aggregate in the region. Sometimes, there are also small 'islands' of sclerenchyma (one or two cells each) in the ribs of the upper leaf-surface.

Since the plants that we collected on Saaremaa resemble *F. oelandica* in every respect, while they are highly distinct from any other re-

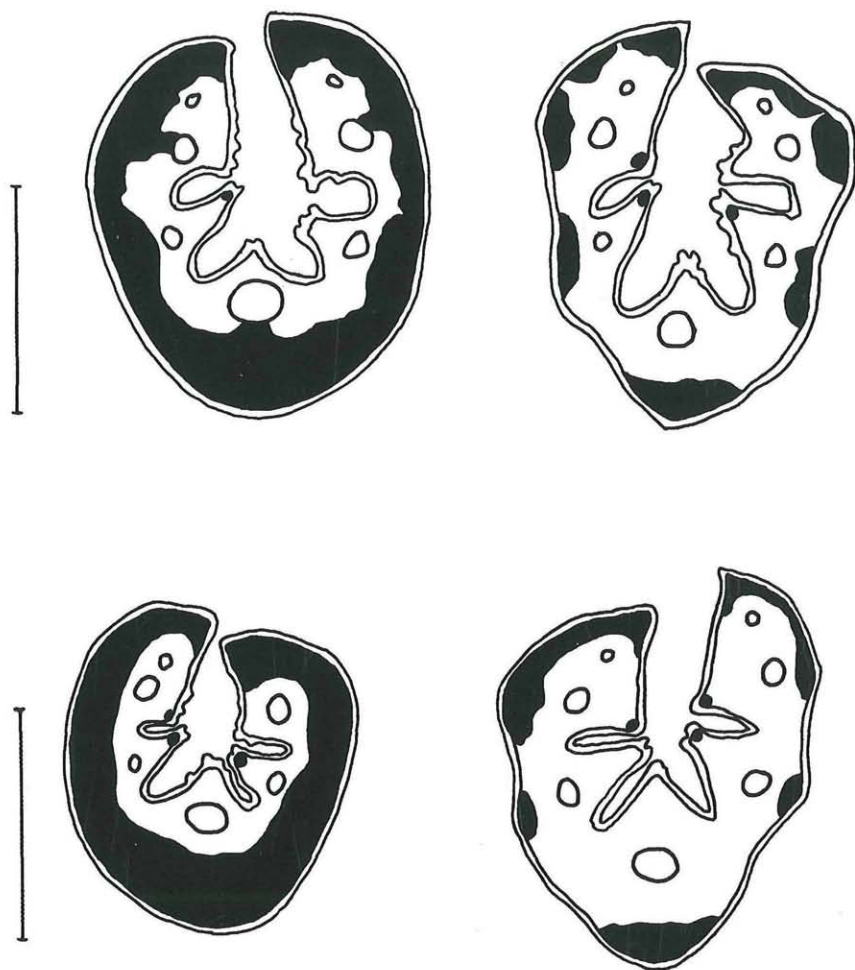


Fig. 1. Semi-schematic drawings of mid-leaf sections of non-flowering shoots of *Festuca oelandica* specimens from Öland (above) and Saaremaa (below). In both cases, two sections are shown that represent the range from leaves with a maximum to those with a minimum of sclerenchyma to be found on one shoot (bars = 500 μm).

representative of *F. rubra* agg., we conclude that they belong to the same taxon. It is highly probable that these morphological characteristics are not pure modifications due to the harsh environment of the inhabited alvar sites since similar morphological traits have never been reported from *F. rubra* s.str. (cf. KERGUÉLEN & PLONKA 1989, CONERT 1998, DENGLER 1998), and because on the alvar sites of Saaremaa and Öland *F. rubra* subsp. *rubra* also occurs frequently (Table 3) and without intermediates. Finally, as *F. oelandica* differs by more characters from *F. rubra* subsp. *rubra* than any

other European taxon of the aggregate, we consider the specific rank to be justified.

6.2. Distribution, Ecology, and Sociology

Festuca oelandica has long been considered endemic to Öland (AUQUIER 1971, LID & GJÆREVOLL 1987), while more recently also Gotland has been added to its presumed range (MARKGRAF-DANNENBERG 1980, MOSSBERG & STENBERG 2003, JONSELL & KARLSSON 2004). Plants similar to *F. oelandica* have, however, never before been mentioned in the relevant floras of Estonia (TZVELEV 1984, FEDOROV 1999).

On Saaremaa, we have now found a large population of *Festuca oelandica* in one alvar site in the southwestern part. There, it was found growing on periodically inundated, shallow soils, rich in skeletal content, which corresponds to the situation on Öland (STERNER & LUNDQVIST 1986, MOSSBERG & STENBERG 2003, own observations). The newly found site on Saaremaa has also a very shallow, base-rich soil and an open sward (Table 2). The species might be present at other localities as well. According to DENGLER & LÖBEL 2006, *F. oelandica* is a character species of the suballiance Tortello-Helianthemion (cf. Table 1). On Öland, it is most frequent in the Crepido-Allietum (DENGLER & LÖBEL 2006), to which the only documented stand in Estonia also belongs. In the only relevé so far with *F. oelandica* from Saaremaa, *Artemisia rupestris* and *Agrostis stolonifera* dominate the herbaceous layer and *Crepis tectorum* subsp. *pumila* is also present.

6.3. Record

Alvar close to Katri pank, about 3 km south of Pilguse: 58° 14' 23.2" N/ 21° 58' 3.1" E, 3 m a.s.l., periodically inundated alvar site, Crepido-Allietum, 03.VII.2004, leg./det. J. D.

7. *Bryum radiculosum* (Bryophyta – Bryaceae)

7.1. Taxonomy, Morphology, and Determination

Bryum radiculosum BRID. belongs to the *B. atrovirens* aggregate [FREY & al. 1995; = *Bryum* subsect. *Apalodictyon* (MÜLL. HAL.) PODP]. It is distinguished from the other nine European microspecies of this complex by its pronounced, long-excurrent, yellow to reddish nerve (NYHOLM 1993), and from the most similar species, *B. subapiculatum* HAMPE (*B. microerythrocarpum* MÜLL. HAL. & KINDB. ex MACOUN) mainly by the smaller rhizoidal gemmae [120–180 (–220) µm vs. 190–260 (–330) µm], the quadratic to shortly rectangular basal cells (vs. rectangular), the dense rhizoidal tomentum, and the growth in compact (vs. loose) tufts (NYHOLM 1993, FREY & al. 1995, AHRENS 2001, SMITH 2004). The collected plants were 3–12 mm tall and growing in compact tufts. They had numerous spherical, red to brown

rhizoidal gemmae about 180 µm diameter. The leaves were lanceolate and acuminate with a strong red-yellow nerve. The cells in the middle of the leaves were incrassate and 10–12 µm × 45 µm. The spores were 10–12 µm diameter. This matches entirely with the morphological characters given in the cited floras.

7.2. Distribution, Ecology, and Sociology

Bryum radiculosum is globally distributed from the austrosubtropical to the temperate zone and is considered as moderately to considerably thermophytic (DIERSSEN 2001). In Europe, it has a Submediterranean-Subatlantic range but is rather rare at its northern distributional limits (NYHOLM 1993, SMITH 2004, DENGLER & al. 2005). According to these authors, the known distribution of the species reaches north to W. Sutherland in northern Scotland (ca. 58° 30' N) and northeast to the Danish island of Sealand (ca. 56° N / 12° E). From Estonia, so far only three species of the aggregate have been recorded, each very rarely (*B. klinggraeffii*, *B. rubens*, *B. subapiculatum*; cf. INGERPUU & al. 2005). Our new records from Saaremaa mark the northeasternmost outpost of this thermophilic species, some 700 km from the nearest known locality in Denmark and on the same latitude as the site in Scotland but under a far more continental climate. Astonishingly, no occurrences are known from Öland and Gotland, though Sweden is bryologically well studied and the alvar sites on these islands should match the requirements of the species. On Saaremaa, we only collected plants west and northeast of Kuressaare but we assume that this inconspicuous species also grows at other places on the island.

Generally, *Bryum radiculosum* inhabits dry, open habitats rich in lime, such as dry grasslands, rocks and mortar of walls (AHRENS 2001, DIERSSEN 2001, SMITH 2004). On Saaremaa, we found it on basic, periodically inundated alvar sites of the Crepido-Allietum, which are, however, extremely dry in summer (cf. Table 2). The herb layer of plots is dominated by *Sedum album*, and *Allium schoenoprasum* subsp. *schoenoprasum* var. *alvarense* also occurs in all available relevés. The cryptogam layer is well developed, including an average of 20 bryophyte species on 4 m² with *Ditrichum flexicaule*, *Homalothecium lutescens*, *Fissidens dubius*, *Hypnum cupressiforme* var. *lacunosum*, *Thuidium assimile* and/or *Tortella fragilis* being the dominants.

7.3. Records

Southwest of Kuressaare, south of the main road 77: 58° 14' 8.0" N / 22° 26' 2.3" E, 2.5 m a.s.l., 17.VII.2004, teste C. DOLNIK. – About 9 km northeast of Kuressaare, alvar north of Ipla: 58° 18' 5.9" N / 22° 38' 31.4" E, 20 m a.s.l., 14.VIII.2004, teste C. DOLNIK.

8. *Agonimia globulifera* (Lichenes – Verrucariaceae)

8.1. Taxonomy, morphology, and determination

Agonimia globulifera BRAND & DIEDERICH in SÉRUSIAUX & al. in the past has been confused with *A. gelatinosa* (ACH.) BRAND & DIEDERICH in SÉRUSIAUX & al., which is a montane-boreal species without sterile globules (SÉRUSIAUX & al. 1999). The common *A. tristicula* (NYL.) ZAHLBR., on the other hand, has a distinct squamulose thallus, no globules, and larger ascospores.

A. globulifera in the collected samples of biological soil crusts only became visible at high magnification by its numerous shiny, black, sterile globules (80–150 µm). We only found one single perithecium with large muri-form ascospores (35–60 cells visible in section; 45 µm × 20 µm). These morphological characters match with the description of SÉRUSIAUX & al. 1999.

8.2. Distribution, Ecology, and Sociology

Agonimia globulifera is also known from central Europe (Belgium, Luxembourg, the Netherlands, Germany, Switzerland, Slovakia) and Mediterranean Spain (CULBERSON & al. 2006). It also has been collected on an alvar site of Öland (SANTESSON & al. 2004). The records from Saaremaa (cf. APTROOT & al. 2005, SULJA & al. 2005, RANDLANE & al. 2006) thus represent the northeastern limits of the range of *A. globulifera*.

On Saaremaa, the inconspicuous species was growing on soil rich in humus, over bryophytes, on organic litter, or directly on limestone (cf. Table 2), which match to the ecological preferences given in SÉRUSIAUX & al. 1999 and SANTESSON & al. 2004. On Saaremaa, the taxon is common in all alvar sites and not as rare as mentioned by APTROOT & al. 2005. It can be assessed to be a territorial character species of the Crepido-Allietum (BOCH & DENGLER 2006), but it also occurs in the Helianthemo-Galietum and rarely in the *Helictotrichon pratense* community (Table 3). With an average of 55.6 species on 4 m², the plots with *Agonimia globulifera* exhibited an even higher small-scale species density than the Crepido-Allietum as the most species-rich dry grassland community on Saaremaa (49 species, cf. BOCH & DENGLER 2006). The herb layer was mostly dominated by *Agrostis stolonifera*, *Artemisia rupestris*, *Festuca ovina*, *Sedum album*, and/or *Thymus serpyllum*. The most frequent companion taxa (≥ 90%) of the cryptogam layer were *Cladonia pocillum*, *C. symphyrcarpia*, *Peltigera rufescens*, *Verrucaria muralis*, *V. nigrescens*, *Barbula convoluta*, *Ditrichum flexicaule*, *Fissidens dubius*, and *Nostoc* sp.

8.3. Records

Alvar about 2 km east of Atla: 58° 17' 54.5" N / 21° 56' 27.3" E, 1.5 m a.s.l., 09.VI.2004 and 58° 18' 3.3" N / 21° 56' 5.3" E, 10 m a.s.l., 16.VIII.2004; both from a

periodically inundated alvar site, Crepido-Allietum, teste: L. B. SPARRIUS. – Tagamoisa ps (northwest of the island), close to the main road 78, west of Tammese: 58° 25' 19.0" N / 21° 59' 35.0" E, 21.VI.2004, 15 m a.s.l. and 58° 25' 16.6" N / 21° 59' 40.1" E, 16 m a.s.l., 24.VII.2004; both from a periodically inundated alvar site, Crepido-Allietum, teste: L. B. SPARRIUS. – Southwest of Kuressaare, south of the main road 77: 58° 14' 8.0" N / 22° 26' 2.3" E, 2.5 m a.s.l., periodically inundated alvar site, Crepido-Allietum, 17.VII.2004, teste: L. B. SPARRIUS. – Northeast of Karida, close to the local road 120: 58° 18' 36.0" N / 22° 19' 44.3" E, 7 m a.s.l., periodically inundated alvar site, 18.VII.2004, teste: L. B. SPARRIUS. – About 0.5 km east of Väkra, 2.5 km south of Ralla: 58° 27' 19.5" N / 22° 50' 34.7" E, 3 m a.s.l., periodically inundated alvar site, *Helictotrichon pratense* community, 28.VII.2004, teste: L. B. SPARRIUS. – Katri pank, about 3 km south of Pilguse: 58° 14' 24.6" N / 21° 58' 5.0" E, 3 m a.s.l., periodically inundated alvar site, Crepido-Allietum, 28.VII.2004, teste: L. B. SPARRIUS.

9. *Caloplaca lithophila* (Lichenes – Teloschistaceae)

9.1. Taxonomy, Morphology, and Determination

There is no general agreement on the taxonomic value and rank of *Caloplaca lithophila* H. MAGN. In Estonia as in Fennoscandia, *C. lithophila* was not differentiated from *C. holocarpa* (HOFFM. ex ACH.) A. E. WADE in recent checklists (SANTESSON & al. 2004, RANDLANE & al. 2006). In other regions such as the Netherlands (VAN HERK & APTROOT 2004) and the British Isles (DOBSON 2005), the species received attention again during the last years. The former authors distinguish the species from *C. holocarpa* s.str. by its smaller and darker (more orange-red) apothecia. According to the latter author, *C. holocarpa* s.l. is probably an aggregate of several similar species. DOBSON mentions that 'specimens with apothecia about 0.2 mm diam and pale margins when young are recognised by many as *C. lithophila*'. As *C. holocarpa* s.str. and *C. lithophila* are always clearly distinct and even grow together without intermediate types occurring (own observation of S. B. from Germany), the specific rank of *C. lithophila* seems well justified.

The collected samples of *C. lithophila* from Saaremaa had a very thin, partly indistinct thallus. The numerous, densely crowded, red-orange apothecia had a slightly brighter margin and a diameter up to 0.2 mm. The ascospores were 11–13 µm × 57 µm with a 3–4 µm wide septum. These morphological characters match with the descriptions of VAN HERK & APTROOT 2004 and DOBSON 2005.

9.2. Distribution, Ecology, and Sociology

So far, the overall distribution of *Caloplaca lithophila* is not well known since it has only recently been resurrected in the literature. It seems to be widely distributed throughout North America, Europe and the Mediterranean region (own search in "Biological Abstracts"). In the Netherlands, *C. lithophila* is considerably more frequent than *C. holocarpa* s.str.

(VAN HERK & APTROOT 2004). On Saaremaa, we found *C. lithophila* at only two sites but we assume that it is common on concrete or limestone in the research area. According to our relevés, *C. holocarpa* s.str. is clearly the more frequent micro-species on Saaremaa.

Our two records originate from two different dry grassland communities of shallow skeletal soils (Tortello-Sedion), where *C. lithophila* grew on limestone together with other saxicolous species such as *Verrucaria muralis* and *V. nigrescens*.

9.3. Records

North of Karida, close to the local road 120, old drill ground: 58° 19' 2.3" N / 22° 19' 37.3" E, 7.5 m a.s.l., saxicolous on calcareous rock, Cladonio-Sedetum, 19.VII.2004, teste: L. B. SPARRIUS. – Ninase ps, Ninase pank, about 0.5 km to Tagaranna: 58° 32' 47.6" N / 22° 12' 34.8" E, 4 m a.s.l., saxicolous on calcareous rock, Crepido-Allietum, 03.VIII.2004, teste: L. B. SPARRIUS.

10. General Discussion and Conclusions

In this article, we report the occurrence of six taxa (three flowering plants, one moss, two lichens) from the dry grassland flora of Saaremaa as new to Estonia or confirm previous records that have been questioned by other authors. Four of these (*Festuca oelandica*, *Bryum radiculosum*, *Agonimia globulifera*, *Caloplaca lithophila*) are accepted at species rank but belong to aggregates of closely related micro-species, two are regarded as infraspecific to species previously known from Estonia (*Allium schoenoprasum* subsp. *schoenoprasum* var. *alvarense*, *Crepis tectorum* subsp. *pumila*).

Several reasons may have led to these six taxa being ignored in Estonia. First, 'micro-species' and infraspecific taxa are not treated by many botanists since they are not easy to distinguish or not thought to be important. Second, two of the taxa (*Allium schoenoprasum* var. *alvarense*, *Caloplaca lithophila*) are not generally accepted as valid in modern floras. Third, at least the three cryptogams are very inconspicuous. Fourth, the community in which we found most of these species, the Crepido-Allietum, on the first view, seems not very attractive to botanists as it looks grey and sparsely vegetated, and lacks colourful blooming aspects. In the case of *Allium schoenoprasum* var. *alvarense* and *Crepis tectorum* subsp. *pumila*, for which earlier records from Estonia (EICHWALD & al. 1984, LEHT 1999) exist, it is unclear why recent Nordic floras (MOSSBERG & STENBERG 2003, KARLSSON & JONSELL 2004) nevertheless maintained their status as Swedish endemics.

From a biogeographic and evolutionary point of view, the three newly recorded or confirmed flowering plants are most remarkable. For *Festuca oelandica*, the specific status seems well justified as it significantly differs

in various characters from all other taxa of *Festuca rubra* agg., many of which are now generally accepted as species, and there is also evidence that these morphological differences are not merely due to phenotypic modification (see above). *Crepis tectorum* subsp. *pumila* is separated from its sibling taxon (presumably subsp. *tectorum*) by fewer but still several presumably independent characters, and these have been proved to be largely genetically fixed (e.g. ANDERSSON 1989a, 1989b, 1993). Thus, the traditional rank of a subspecies seems appropriate here (for the taxonomic concepts, see JONSELL 2004). Of the three, *Allium schoenoprasum* var. *alvarensense* is least separated from its sibling taxon (presumably var. *schoenoprasum*), however, it appears as a distinct type in the field. We do not know of cultivation experiments to prove the genetic basis of this phenotypic differentiation. Thus, for the time being, this taxon seems to be best accepted at the varietal rank. With our findings, all three taxa become joint endemics of the alvar sites of Öland, Gotland, and Estonia (mainly on Saaremaa, but presumably also on other islands and on the mainland), whereas they before had been considered as exclusive endemics of Öland or Öland and Gotland. Öland and Gotland are well known to host a considerable proportion of the Nordic endemics among the vascular plants, most of them inhabiting calcareous, open habitats (alvar sites) (JONSELL & KARLSSON 2004). Only two of these, *Artemisia maritima* subsp. *humifusa* and *Cotoneaster canescens*, have been previously generally accepted to occur on Saaremaa (TUTIN & al. 1976, JONSELL & KARLSSON 2004). Additionally, there is one sub-endemic moss species of alvar sites (*Tortella rigens*), which is known from Öland, Gotland, Estonia and a few alvar sites on the Swedish mainland (ALBERTSON 1946, NYHOLM 1986) but which was not found in our study on Saaremaa. The close floristic connections between the Baltic islands of Öland, Gotland and Saaremaa is not surprising, given their geological (EMBLETON 1984, ERIKSSON 1992) and climatic similarity, their relative proximity, and the fact that they all host extensive areas of similar dry grassland types (PÄRTEL & al. 1999, DENGLER & al. 2006).

These taxa must be of rather young evolutionary origin as all the present-day alvar regions were covered by the Scandinavian ice-shield during the Weichselian glaciation (EMBLETON 1984). Subsequently, the islands were submerged in the Baltic Ice Lake but the different sources do not agree whether their highest parts firstly emerged from the water already during this period (ca. 10,500 BP) or only later from the so-called Yoldia Sea (ca. 10,000 BP) (DIERSSEN 1996, BACKÉUS 1999, SJÖRS & al. 2004). At least since then the islands continuously existed and increased their size due to an ongoing isostatic land-uplift (presently ca. 3 mm per year, see ZOBEL & KONT 1992), however, they never were connected to the mainland in post-glacial times (SJÖRS & al. 2004). Thus, their total floras, including the ancestors of the endemics, must have migrated across the Baltic wa-

ters. Accordingly, the assumption of ANDERSSON 1990 that the Baltic alvar 'forms' of *Crepis tectorum* are derivatives rather than surviving ancestors of the widespread non-alvar 'forms' seems also highly plausible for *Allium schoenoprasum* var. *alvarense* and *Festuca oelandica*. All three belong to widespread complexes of ecologically plastic, polymorphic taxa, which seem to have developed morphologically distinct types that are adapted to the extraordinary ecological conditions of the open alvar sites within a relative short time of not more than several thousand years. Although in the present-day landscape the putative parental taxa are growing nearby outside (and partly also inside) the alvars, there must be either genetic isolation mechanisms or strong ecological forces that lead to the obvious maintenance of the distinct alvar 'types'. In the future, molecular methods should be used to test whether the corresponding alvar types from the three islands are of monophyletic origin and how their migration routes then were or whether they developed more than once in a convergent way.

By contrast, the three newly found cryptogams have larger distributional ranges. The moss *Bryum radiculosum* has a Submediterranean-Subatlantic range in Europe and occurs with its northeastern-most outlier on Saaremaa. In this respect, it shows a similar distributional range as it is known from some typical alvar species among the vascular plants (e.g., *Potentilla tabernaemontani*, *Scabiosa columbaria*). Finally, the two lichens probably have large distributional ranges but have not previously been recorded from Estonia because of taxonomic problems or due to their inconspicuousness. Further studies are needed to determine the distribution ranges of all six taxa much more comprehensively for all of Estonia than was possible in our article. For the three 'alvar endemics' among the flowering plants, it should additionally be studied whether or not they also occur along the southern coast of Finland, on the Åland islands, and in some limestone regions on the southern Swedish mainland.

Although we studied all dry grassland types on Saaremaa, the vast majority of all new records originate from only one of the distinguished eight associations, the Crepido-Allietum (see Table 3). This association comprises open alvar stands of shallow skeletal soils, which are exposed to a regular change of inundation in winter and extreme drought in summer plus cryoturbation, and is restricted to alvar regions in Västergötland, Öland, Gotland, and Estonia (DENGLER & LÖBEL 2006, DENGLER & al. 2006). It belongs to the suballiance Tortello-Helianthemion of dry, open alvar communities (see Table 3), which is endemic to the southern Baltic region. These communities are generally extremely species-rich at small scales (DENGLER & LÖBEL 2006). In Estonia, the Crepido-Allietum with an average of 49 species on 4 m² is by far the most species-rich dry grassland community (BOCH & DENGLER 2006) and potentially the richest of all plant communities. The extreme environmental conditions may be both the reason for the co-existence of so many different taxa on small areas and for

the development and maintenance of highly adapted but less competitive endemics. Thus, it seems urgent that national and international nature conservation efforts focus much more on the Estonian alvar communities in the future, including these open types, for reasons of their endemic plant taxa and plant communities as well as their unique ecology and landscape history.

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