Vegetative reproduction and clonal diversity in pleurocarpous mosses (Bryopsida) of xeric habitats

A combined molecular and morpho-anatomical study in the three mosses *Abietinella abietina* (Hedw.) Fleisch. (Thuidiaceae), *Homalothecium lutescens* (Hedw.) Robins. (Brachytheciaceae) and *Homalothecium sericeum* (Hedw.) Schimp. (Brachytheciaceae)

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Kathrin Lieske
(geb. in Herzberg/Elster)

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Prof. a.D. Dr. W. Frey

Prof. Dr. T. Romeis

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List of Abbreviations

♀	female
♂	male
&	and
±	more or less
#	number
acc.	according
AFLP	amplified fragment length polymorphism
BP	before present
ca.	approximately, about (circa)
cf.	confer, compare
col.	collected by
det.	determined by
e.g.	exempli gratia, for example
et al.	et alii, and others
etc.	et cetera, and other things
excl.	excluding
Feb	February
fo.	Forma
i.a.	inter alia, among other things
i.e.	id est, that is
incl.	including
Mar	march
m a.s.l.	meters above sea level
min	minute
Myr	million years
NJ	neighbour-joining
no.	number
PCR	polymerase chain reaction
pers. comm.	personal communication
resp.	respectively
s	second
SEM	scanning electron microscopy
s.l.	sensu lato, in a wide sense
spp.	species
s.str.	sensu stricto, in a narrow sense
var.	variety
vs.	versus

UPGMA	unweighted pair group method with arithmetic mean
yr	years

sample areas

region B	region Brandenburg
region SA	region Saxony-Anhalt
D	Dollenchen; Brandenburg
FN	Freyburg (Neuenburg); Saxony-Anhalt
L	Lindena; Brandenburg
Hb	Holzberg; Thuringia
Mb	Mönchsberg; Thuringia

1 Introduction

The genetic structure within and among plant populations is associated with the reproductive characteristics of a species, such as the comparative success of generative vs. vegetative reproduction, fertilising ability, partitioning of sexes, and dispersal distances (LOVELESS & HAMRICK 1984, HOCK et al. 2008). Sex expression rates and, in unisexual bryophyte species, the spatial segregation of sexes and female/male ratios influence the success of fertilisation (LONGTON 1976, LONGTON & SCHUSTER 1983, BISANG et al. 2004, LONGTON 2006). Thus, it is certainly not surprising that sporophytes are rare in dioicous species (GEMMELL 1950).

The process known as 'consequent vegetative multiplication' describes in particular the clonal growing bryophytes from patches after initial establishment of spores or vegetative reproduction s.l. and with vegetative reproduction s.l. (LONGTON & SCHUSTER 1983, FREY & LÖSCH 2004). For the majority of mosses, the vegetative reproduction s.l. is essential for development, maintenance and expansion of populations (LONGTON & SCHUSTER 1983). Extensive vegetative reproduction in bryophytes has been thought to lead to a reduced level of genetic variation. But considerable genetic variations exist in bryophyte species, presumably due to optional generative reproduction or somatic mutation (MISHLER 1988). Also, WIDÉN et al. (1994) reported that despite low levels of generative reproduction, clonal plants in general are as variable as other plants. Several studies found genetic variability in clonal mosses, for example in *Hylocomium splendens* (CRONBERG et al. 1997, CRONBERG 2002) and *Sphagnum angermanicum* (GUNNARSSON et al. 2005). However, in *Polytrichum juniperinum* (DERDA & WYATT 2003) or in *Rhytidium rugosum* (PFEIFFER et al. 2006) e.g., only a low genetic diversity within populations was detected. Moreover, especially taxa with predominantly vegetative reproduction often have a more restricted potential for long range dispersal than species which frequently produce small spores (LONGTON & SCHUSTER 1983, KIMMERER 1994).

The present reproductive biological characteristics are important, but the past history must not be neglected when looking at the structure of populations. In fact in formerly

glaciated regions the greatest effect on species distribution and genetic diversity can be attributed to the ice ages during Quaternary. Most of the extant native species, which can be found across Europe today, survived and then expanded from refugia in the south (Iberian Peninsula, Italy and the Balkans) and some even near the Caucasus and Caspian Sea (HEWITT 1999, 2004a). The general assumption is that the genetic diversity decreases to the north of Europe. This could be the result of rapid postglacial expansion northward and complex topography in the southern refugia (TABERLET et al.1998, HEWITT 1999).

The genetic structure and diversity in bryophyte populations and the small-scale relationships in correlation with the reproductive characteristics have already been examined in several molecular studies, by means of allozyme (e.g. CRONBERG et al. 2006) and AFLP [amplified fragment length polymorphism, VOS et al. (1995)] (e.g. VANDERPOORTEN & TIGNON 2000, PFEIFFER et al. 2006) as well as SSR (simple sequence repeat) and ISSR (inter-simple sequence repeat) (e.g. CASSIE et al. 2008, HOCK et al. 2008).

In this study, both molecular (AFLP) and morpho-anatomical approaches are performed to detect the relationship and relevance of vegetative reproduction in the three pleurocarpous mosses *Abietinella abietina* (Hedw.) Fleisch. (Thuidiaceae), *Homalothecium lutescens* (Hedw.) Robins. and *Homalothecium sericeum* (Hedw.) Schimp. (Brachytheciaceae). The main focus is set on the modes of vegetative reproduction, relevance of vegetative vs. generative reproduction, genetic diversity and pattern in patches and populations as well as habitat colonisation and maintenance. Furthermore genetic diversity and pattern at broad spatial scales are being analysed.

The xerophytic *A. abietina* and *H. lutescens* form large wefts and grow in sunny calcareous habitats such as limestone rubble or dry grassland. The meso-xerophytic *H. sericeum* forms small to large mats, mostly on calcareous rocks or tree trunks. All three dioicous species are quite common in their main distribution area and produce sporophytes relatively rarely (e.g. HOFMANN 1998, NEBEL et al. 2001, NEBEL & SCHOEPE 2001, DÜLL & DÜLL-WUNDER 2008). Since the production of sporophytes is scarce, it can be assumed that dispersal, colonisation and maintenance predominantly depend on vegetative reproduction structures. But specialised

propagules are till now unknown in all three species. In the case of *A. abietina*, DÜLL & DÜLL-WUNDER (2008) assume that whole plants or fragments are dispersed. But to date, a thorough study on vegetative reproduction and colonisation characteristics of these species has not been conducted.

All three analysed species have a circumpolar distribution with the main area in Europe, Asia and in the case of *A. abietina* also throughout North America. There are only a few molecular studies on the genetic diversity of bryophytes species of a broad geographical range, e.g. CRONBERG 2000, DERDA & WYATT 2003, HEDDERSON & NOVELL 2006. HEDDERSON & NOVELL (2006) analysed phylogeographic aspects and postglacial re-colonisation in *H. sericeum* based on the sequence variation in the nrDNA ITS1 (internal transcribed spacer 1). This study examines genetic diversity and distribution patterns in different geographical regions considering the aspect of postglacial colonisation history and reproductive ecological traits.

This study aims (1) to characterise the process of habitat colonisation and maintenance in *A. abietina*, *H. lutescens* and *H. sericeum* with morpho-anatomical and molecular methods, (2) to clarify the role of generative reproduction in comparison to vegetative reproduction s.l. and (3) to identify the mechanisms of vegetative reproduction s.l. through determination of types of vegetative diaspores and their dispersal. Further foci are (4) detecting whether patches develop from one initial diaspore or whether plants of patches belong to different genets and hence patches and populations are uniclonal or multiclonal, (5) assessing the genetic diversity and genetic patterns on four spatial scales (population, region, the distribution area in Germany and world-wide), (6) detecting whether the prevailing reproduction mode effects the genetic pattern on larger spatial scale and (7) revealing the colonisation history of Pleistocene glaciated regions.

2 Study species

2.1 *Abietinella abietina* (Hedw.) Fleisch., Musci Buitenzorg 4: 1497. 1923

2.1.1 Taxonomy

The moss genus *Abietinella* Müll. Hal. (Nuovo Giorn. Bot. Ital. n. ser. **3**: 115. 1896) belongs to the family Thuidiaceae. The basionym of the studied species *A. abietina* is *Hypnum abietinum* (Hedw.). SCHIMPER & GÜMBEL (1852) cite the moss as *Thuidium abietinum.* Due to the simple pinnate stems, the species was considered as a subgenus *Abietinella* Müll. Hal. by BROTHERUS (1909) and Fleischer (1923) also separated *Abietinella* from *Thuidium* as discrete genus. From then on, both *Thuidium abietinum* (e.g. POSPÍŠIL 1967, 1968, LAWTON 1971, DÜLL-HERMANNS 1981, 1985, NEBEL & SCHOEPE 2001) and *Abietinella abietina* (e.g. WATANABE 1972, HEDENÄS 1997, CROSBY et al. 2000, FRAHM & FREY 2004, SMITH 2004 and FREY & STECH 2009) were used in literature. In this study the species will be assigned to *Abietinella.*
Two varieties of *Abietinella abietina* are described, var*. abietina* and var*. histricosa*. The two taxa are linked by the intermediate var. *abietina* fo. *intermedium* Loeske (for a detailed description compare DÜLL-HERMANNS 1981).
Some authors (e.g. Pilous 1945, 1967, WATANABE 1972, CROSBY et al. 2000) regard var. *histricosa* as separate species *Abietinella histricosa* (Mitt.) Broth. whereas other authors doubt this high taxonomic category (e.g. KINDBERG 1896, NICHOLSON 1902, BEST 1905, LOESKE 1907, DIXON 1924, ALLORGE 1930, POSPÍŠIL 1967, DÜLL-HERMANNS 1981).

2.1.2 Morphology

Dioicous. Plants sturdy, stiff, frequent in extensive loose wefts. Young parts of stems green to yellow-green, older parts brownish-green to brown. Stems 12 (–14) cm long, ±arcuate, simply pinnate, rare branches of second- or higher order. Branches 5–12

mm long, terete, sometimes flagelliform. Paraphyllia abundant on stems, various occurrences on branch and leaf base; lanceolate, filiform, simple or branched, ends truncate, cells papillose, walls ±transverse. Stem leaves 1–2.5 mm long, 0.5–1 mm wide, patent, often curved, longitudinally plicate, broadly ovate with broad base, tapering to long acuminate apex; lamina cells irregularly shaped, roundish rhombic to oval, unipapillose, incrassate, 1–2 times as long as wide; basal leaf cells longer, incrassate, orange-brown coloured, often with porose walls; margin plane or recurved, entire-emarginate, partial papillose and occasional denticulate on apex; costa sturdy, extending ca. ¾ way up leaf. Branch leaves smaller, concave, broadly ovate to lanceolate, obtuse to acuminate, serrate above and serrulate to the base; lamina cells incrassate, unipapillose, rounded to elliptical, shorter toward the margin, 8–10 µm wide in mid-leaf; costa extending ca. ⅔ way up leaf. Inner perichaetial leaves linear-lanceolate; margin subulate; toothed apex, not ciliate. Seta reddish, 1.5–3 cm long. Capsule suberect, cylindrical and curved; urn ca. 2 mm long, operculum conical to short rostrated, 0.6 mm long; calyptra cucullate, early deciduously. Spores (9–) 12–16 (–18) µm, finely papillose, maturity in spring (compare, e.g. LAWTON 1971, NEBEL & SCHOEPE 2001, SMITH 2004).

Sporophytes very rare (e.g. HERZOG 1926, CRUM & ANDERSON 1981, DÜLL 1997, NEBEL & SCHOEPE 2001). In Baden-Württemberg it has only been seen in herbarium material (at 1900). Further, the last notice of sporophytes in Westphalia was in 1972 (SCHMIDT 2004). The absence of sporophytes was also remarked in literature for Denmark (HOLMEN 1959), Hungary (BOROS 1968), China (WU et al. 2002), Japan (WATANABE 1972) and Axel Heiberg Island (N.W.T. Canada) (KUC 1973). In North America, the presence of sporophytes is described in Colorado, Montana and Alaska (BEST 1901); sterile elsewhere (GROUT 1931). Specialised propagules are unknown (HERZOG 1926).

Chromosome number: n=10 (WIGH 1972a, FRITSCH 1991)

2.1.2.1 *Abietinella abietina* var. *abietina*

Plants lax yellowish green to brownish. Stems and branches ±terete with appressed leaves when dry. Stem leaves 1.0–1.4 (–3.2) mm long, ovate, acuminate, tapering to an acuminate apex. Branch leaves 0.6–1.0 (–1.8) mm long, broadly ovate, acute;

margin entire; mid-leafs cells 1.0–1.5 (–2.0) times as long as wide, 8–16 µm long. Capsules very rare (compare, e.g. DÜLL-HERMANNS 1981, 1985, HILL et al. 1994, NEBEL & SCHOEPE 2001, SMITH 2004) and unknown in China (WU et al. 2002).
Chromosome number: n=10 (FRITSCH 1991)

2.1.2.2 *Abietinella abietina* var. *histricosa* (Mitt.) Sakurai, Musci Jap. Exsic. 1954

Plants yellowish-brownish, frequently sturdier, closer and richer branched at stem. Shoot and branch apex frequently secund. Stem leaves 1.5–2.0 (–3.7) mm long, ovate-lanceolate, longly acuminate. Branch leaves patent when dry so that branches not terete. Leaves longer than in var. *abietinum* mostly 0.9–1.3 (–2.4) mm, 1.5–3.0 times as long as wide, ovate to lanceolate, shortly to longly tapering to acute to acuminate apex; margin entire to denticulate; mid-leafs cells 12–20 µm long. Capsules rare (compare, e.g. DÜLL-HERMANNS 1981, 1985, NEBEL & SCHOEPE 2001, SMITH 2004), unknown in Britain and Ireland (HILL et al. 1994, SMITH 2004) as well as China (WU et al. 2002).
Chromosome number: n=10 (FRITSCH 1991)

2.1.3 Ecology

The xerophytic moss grows sun-exposed, on chalkstone, limestone and basic substrates, open to half-open dry grassland, dry shrubs and open, somewhat humous chalk cliffs, secondary in quarries (MEINUNGER & SCHRÖDER 2007).
The species tolerates considerable dry periods and large temperature (≤65°C) and humidity fluctuations. The occurrence in Svalbard, Island, Alaska, Greenland and the Arctic region as well as in Mediterranean regions is possible because the species is thermally adapted to both low and high temperatures (STODIEK 1937, DÜLL-HERMANNS 1981, NEBEL & SCHOEPE 2001).

2.1.3.1 *Abietinella abietina* var. *abietina*

The variety occurs on dry, calcareous substrates with pH-values 5.6–7.9, sand slopes, basic montane rock ledges and slopes, chalk and limestone grassland in sunny S-, SW- and SE-exposition. *Abietinella abietina* var. *abietina* grows in habitats

with intense evaporation and heat and is more adapted to higher temperature and humidity fluctuations than the var. *histricosa* (DÜLL-HERMANNS 1981, 1985, SMITH 2004).

2.1.3.2 *Abietinella abietina* var. *histricosa*

Abietinella abietina var. *histricosa* grows on lime- or chalkstone substrates with pH-values 7.2–8.15, more often in half shade, W-, SW- and N-exposition on more or less gentle slopes. The variety prefers rather oceanic climate and avoids intense heat and has a higher water demand. The preferred occurrence on chalkstone (which is consistent with the main distribution area in SE-England) is related to the ability of chalkstone to temporarily accumulate water. That is probably the reason why the variety in Germany occurs rather in upper elevations with chalk substrate and high air humidity than in xeric regions with calcareous soil, which is permeable to water. But occurrence in dry grasslands like *A. abietina* var. *abietina* indicates the occasional adaptation of this variety to dehydration (DÜLL-HERMANNS 1981, 1985).

2.1.4 Sociology

Abietinella abietina is a differential species within the cryptogam community Rhytidio-Entodontetum orthocarpi STODIEK 1937 (SCHMIDT 2004 as Abietinelletum abietinae, DREHWALD & PREISING 1991 as Entodontetum orthocarpi).
The following species are associated with *A. abietina*: *Entodon concinnus, Rhytidium rugosum, Hylocomium splendens, Homalothecium lutescens, Thuidium delicatulum, Hypnum lacunosum, Tortella tortuosa* and occasionally with *Racomitrium canescens*, *Thuidium philiberti*, *Rhytidiadelphus triquetrus*, *Pleurochaete squarrosa*, *Campylium chrysophyllum* and *Ctenidium molluscum* (DÜLL-HERMANNS 1981, MEINUNGER & SCHRÖDER 2007).
In phanerogam communities *A. abietina* characterises the moss layer of the Xero- and Mesobrometum. In East Thuringia the taxa occurs in numerous plant communities: Teucrio-Seslerietum VOLK 1937, Teucrio-Stipetum MAHN 1965, Teucrio-Melicetum ciliatae VOLK 1937, Coronillo-Laserpitietum RAMEAU 1971 em. GILS 1978, Origano-Dictamnetum WENDELBERGER 1954 em. GILS and KOVAĆS

1977, *Sedum acre*-Pioneer communities and communities of rock vegetation, Viburno-Cornetum RAUSCHERT 1969 as well as dry forms of Onobrychido-Brometum (SCHERR 1925) TH. MÜLLER 1966 (MARSTALLER 1980).

2.1.5 Threat

Abietinella abietina is not endangered in its main distribution area in Germany. The species benefit from former extensive grassland management. After agricultural use and by following scrub encroachment, the occurrence decreased in the entire German distribution area in many cases. Outside of the limestone regions *A. abietina* is rare or missing today and classified as vulnerable (MEINUNGER & SCHRÖDER 2007).

2.1.6 Distribution

The distribution is circumpolar Boreo-arctic Montane (SMITH 2004).
In Germany *A. abietina* occurs in the North German plains as well as in the continental influenced arid region in the east, especially at the Lower Oder. In Central and Southern Germany the species is common to abundant and mainly distributed in limestone, seldom in silicate regions (Fig. 1). It is found in all elevations from lowland to the Alpine altitudes (<3000 m) (MEINUNGER & SCHRÖDER 2007). In East Thuringia the occurrence of *A. abietina* is associated with southern exposed slopes and slope sides. Such conditions are available on the Wellenkalk escarpment of the Middle Saaletal, the Saale Ilmplatte, Lower Unstrutplatten and Bryozoenledge of the Orlasenke (MARSTALLER 1980).
Abietinella abietina var. *abietina* is distributed across Europe. The distribution area extends in the north to Svalbard, in the south to the Mediterranean region, in the east to the Transcaucasus, in the west to France (in the very western provinces rare) (NYHOLM 1960). Out of Europe in Southwest, North-, Central-, and East Asia; in North America in Greenland and across the continent to the south to Colorado and Virginia (BEST 1901, DARLINGTON 1964); South Africa (MAGILL & SCHELPE 1979, VAN ROOY 2003). World-wide var. *abietina* occurs to an elevation of 3050 m (Gilgit, Himalaya) (DÜLL-HERMANNS 1981) or 3760 m (India, Sikkim, North District, 2 km south of Thanggu, D.G. Long, 17.07.1996, E), resp. (Fig. 2).

There is evidence which suggests that the prevalent occurrence of the var. *histricosa* in upper elevations in Germany, Italy, Poland, Switzerland, Spain, Czech Republic and Slovakia can be regarded as refuges. Outside of Europe the variety occurs in Asian Russia, Japan and China. The taxon is only known in Germany for the region of Lake Constanze and in upper elevations of the alpine region (≤2300m) (DÜLL-HERRMANNS 1985). The main distribution area of the variety is located on the chalk downs in South and Southeast England, with a few outliers on the Welsh limestone. In Ireland the variety is much more common than var. *abietina* (PORLEY & HODGETTS 2005).

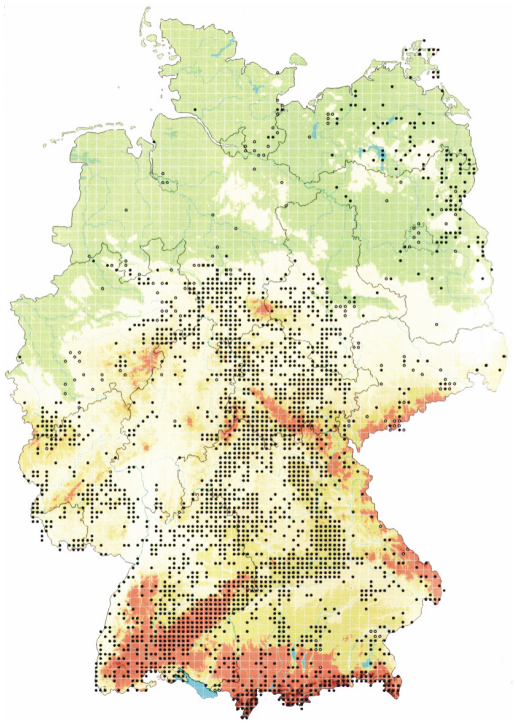


Fig. 1: Distribution of *Abietinella abietina* in Germany (acc. to Meinunger & Schröder 2007, dot matrix map based on quadrants of the topographical maps 1:25.000).

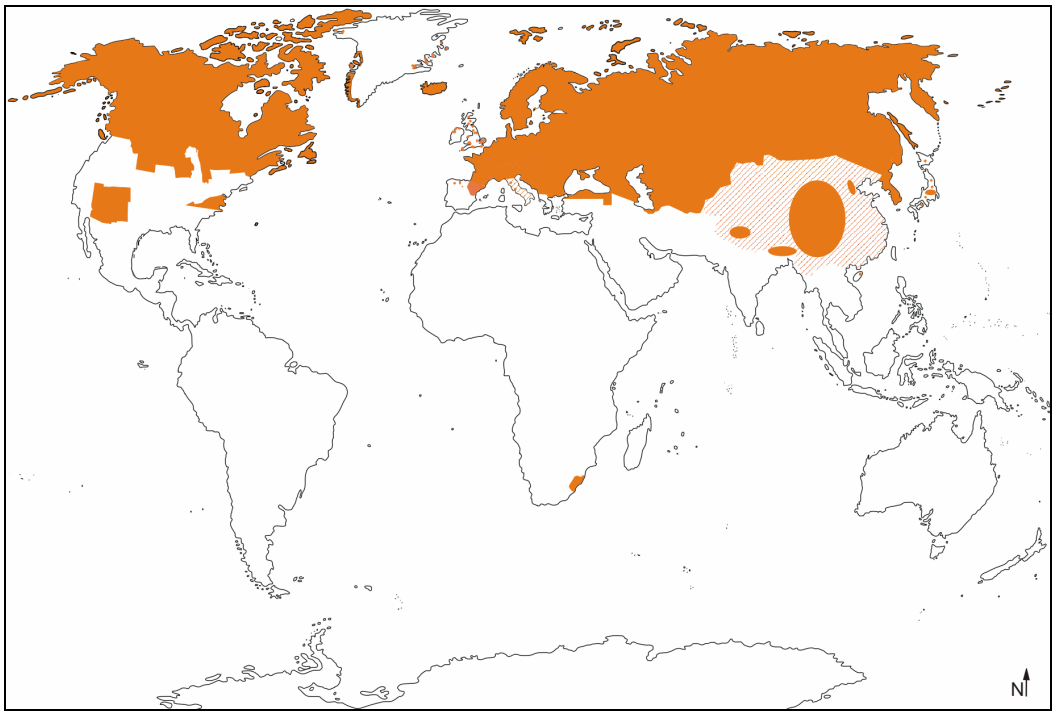


Fig. 2: World-wide distribution map of *Abietinella abietina* (compiled with literature, compare the following list of references). Uncertain data are display with hatching.

References for the world-wide distribution map:

(! var. *abietina*; # var. *histricosa*; * maps in literature; ? uncertain; 0 missing)

Africa: South Africa: KwaZulu-Natal Province (MAGILL & SCHELPE 1979, VAN ROOY 2003).

Europe: Finland, Norway, Sweden (BROTHERUS 1923, *NYHOLM 1960), Denmark (*HOLMEN 1959), Iceland (DÜLL-HERRMANS 1985), Greenland (*MOGENSEN & LEWINSKY 1982) Svalbard (KUC 1963), !European Russia, !Belorussia, !Ukraine, !#Baltic Republics (IGNATOV & AFONINA 1992, IGNATOV & IGNATOVA 2004), !#Caucasus (IGNATOV & AFONINA 1992), !# British Isles (*HILL et al. 1994), Netherlands (*VAN TOOREN & SPARRIUS 2007), Germany, France (DÜLL-HERRMANS 1981), Poland (KUC 1964), former Czechoslovakia [!#Czech Republic (KUČERA & VÁŇA 2003)], Hungary (BOROS 1968), Northeast Greece (DÜLL 1995), !#Spain (*CASAS et al. 1992, *CASAS et al. 2001), Italy (REIMERS 1956), former Yugoslavia [Croatia (SABOVLJEVIĆ 2006)].

Arctic: !European Arctic, !West Siberian Arctic, !East Siberian Arctic, !Beringian arctic (IGNATOV & AFONINA 1992).

Asia: **Central Asia**: !Kazakhstan, !Tadjikistan, !Kirgizstan, !Turkmanistan, !Uzbekistan (IGNATOV & AFONINA 1992) **North Asia**: [Siberia (!Western Siberia, !Eastern Siberia, !#Southern Siberia), !Russian Far East (Sakhalin, WATANABE 1991)] (IGNATOV & AFONINA 1992), !Mongolia (BAI & ZHAO 1996) **East Asia**: !# China (! widely distributed in Northern and Southwestern China, rare in Central China (GANGULEE 1978, VOHRA 1983, REDFEARN & WU 1986, *WU et al. 2002), !# Japan (*WATANABE 1972, WATANABE 1991), Korea (VOHRA 1983, WATANABE 1991) **Southwest Asia:** !# Turkey (*HENDERSON & PRENTICE 1969, *ABAY & ÇETIN 2003, KÜRSCHNER & ERDAĞ 2005), Iran (FREY & KÜRSCHNER 1991,

AKHANI & KÜRSCHNER 2004) **South Asia:** India (Jammu & Kashmir, Himachal Pradesh, Darjeeling) (*GANGULEE 1978), Nepal, Buthan (VOHRA 1983).

North America: U.S.A.: Alaska (WORLEY & IWATSUKI 1970, STEERE 1978), Montana (GROUT 1931), Utah (FLOWERS 1973), Wyoming, South Dakota, Minnesota, New York, New England (LAWTON 1971), Iowa (e.g. CRUM & ANDERSON 1981, CRUM 2004), Indiana (CRUM 2004), Michigan (*DARLINGTON 1964, CRUM 2004), Virginia, Colorado (e.g. *DARLINGTON 1964, CRUM & ANDERSON 1981), Arizona (e.g. HARING 1961, CRUM & ANDERSON 1981), Massachusetts (*HILFERTY 1960) **Canada:** British Columbia, Alberta, Saskatchewan, Manitoba, Ontario, Quebec, Labrador, Newfoundland, New Brunswick, Nova Scotia, Yukon Territory (STEERE & SCOTTER 1978), Northwest Territories [Bathurst Island (*BRASSARD & STEERE 1968), Axel Heiberg Island (*KUC 1973)] (*HOLMEN & SCOTTER 1971), Arctic Archipelago [Baffin Island (*BRASSARD et al. 1979), Banks Island, Bathurst Island, Devon Island, Ellesmere Island (BRASSARD 1971), Prince Patrick Island, Southampton Island, Victoria Island (*KUC 1969)].

2.2 *Homalothecium* SCHIMP. in Bruch et al., Bryol. Eur. 5: 91. 1851

2.2.1 Taxonomy

The genus *Homalothecium* Schimp. is a member of the Brachytheciaceae and comprises eight species acc. to HOFMANN (1998) resp. twelve species acc. to IGNATOV & HUTTUNEN (2002) and eleven acc. to HUTTUNEN et al. (2008). The genus is closely related to the genera *Brachythecium* Schimp. and *Palamocladium* C. Müll. (HOFMANN 1998). Based on ITS, *atpB-rbcL*, and *rpl16* sequence data the genus *Homalothecium* s.l. is not monophyletic. The core *Homalothecium* clade (=*Homalothecium* s.str.) encloses two main lineages in the 'crown *Homalothecium* clade' as well as one 'basal *Homalothecium* clade'. The basal clade includes *H. nuttallii* and *H. aureum*. Only American species are included in one of the two main lineages and the second one includes only Eurasiatic species. The studied species *H. sericeum* and *H. lutescens* are closely related (IGNATOV & HUTTUNEN 2002) and belong to the lineage of Eurasic species (HUTTUNEN et al. 2008).
Occasionally, the identification of the species of the genus *Homalothecium* is difficult due to the variability of many characters in all species. Sometimes specimens of *H. lutescens* and *H. sericeum* have characters of both species and are difficult to separate from each other. Further, HOFMANN (1998) assumed that the variation *H. lutescens* var. *fallax* (H. Philib.) Düll Bryol. Beitr. **5**: 192. 1985 is a hybrid between *H. sericeum* and *H. lutescens* or a mutant. *Homalothecium lutescens var. fallax* differs only from *H. lutescens* by an erect, straight capsule like that of *H. sericeum* or *H. philippeanum*.

2.2.2 *Homalothecium lutescens* (Hedw.) Robins., Bryologist 65: 98. 1962

2.2.2.1 Morphology

Dioicous. Plants medium-sized to robust, yellowish green (on shadowy locations green) to golden brown, in lax patches, sometimes extensive. Male plants dwarf or of similar size to female plants. Stems 5–10 (–15) cm long, procumbent to ascending with sparse rhizoids (only at base attached to substrate), irregularly branched,

branchlets frequent. Branches long, not crowded, directed forwards, straight when dry, seldom ascending. Axillary hairs 40–100 µm long. Leaves on stems and branches similar, erect when dry, erect patent when moist, strongly longitudinally plicate, triangular to lanceolate or ovate-triangular; apex acuminate, ±long filiform, often twisted; margin plane or narrowly recurved below, denticulate throughout, particularly at base and apex. Stem leaves (1.8–) 2.3–3.2 mm long and (0.4–) 0.6–0.9 mm wide. Branch leaves (1.2–) 2.0–3.2 mm long and 0.4–0.9 mm wide, 2–4 decurrent cells at base; costa thin, extending (40–) 60–90% way up leaf, ending sometimes on abaxial side in a spine; mid-leaf cells 48–80 x 5–7 µm (ca. 10 times as long as wide), thin-walled, and linear-vermicular eporose; alar cells incrassate, ±quadrate, frequently porose, forming decurrent auricles, outline of cells not clearly visible; basal cells rectangular to shortly linear, incrassate, porose. Perichaetial leaves straight to ±slightly falcate, inner ones tapering to a long and fine acumen some abruptly narrowed into acumen, slightly plicate, costa weak or lacking, to 2.1 mm long. Seta orange to reddish-brown, papillose, 1.0–3.2 cm long. Capsule erect or inclined, ±cylindrical to asymmetrical, straight or slightly curved, 1.9–3.0 mm long and 0.7–1.0 mm wide; operculum narrowly conical to rostrate, ca. 1.0 mm long; calyptra naked, cucullate. Spores 12–18 (–20) µm, finely papillose to almost smooth. Sporophytes rare, maturing in winter (compare, e.g. HOFMANN 1998, NEBEL et al. 2001, SMITH 2004). Sterile in Israel and adjacent regions (HEYN & HERRNSTADT 2004). The chromosome number is highly variable n=8, n=10, n=10+m, n=11, n=12, n=14, n=24 (WIGH 1972b, FRITSCH 1991). This is probably the cause of the differences in size (HOFMANN 1998).

2.2.2.2 Ecology

Homalothecium lutescens is a xerophyte and grows in exposed and mostly dry, calcareous habitats; chalk and limestone grasslands, cliff tops and sand-dunes, in deciduous and coniferous forests, rarely epiphytic and directly on rocks (mainly calcareous) or walls (HOFMANN 1998, NEBEL et al. 2001, SMITH 2004).

2.2.2.3 Sociology

Homalothecium lutescens is a differential species of the cryptogam community Rhytidio-Entodontetum orthocarpi STODIEK 1937. The following species are associated with *Homalothecium lutescens*: *Abietinella abietina*, *Hypnum lacunosum*, *Rhytidium rugosum, Entodon concinnus, Brachythecium glareosum*, *Campylium chrysophyllum* and *Fissidens taxifolius* on shadowy locations with *Anomodon viticulosus*.
Furthermore, the species frequently grows in dry regions with low precipitation on southern exposed slopes in Thuringia and here within numerous xerotherm phanerogam communities (cf. sociology of *A. abietina*) (MARSTALLER 1980, NEBEL et al. 2001, SCHMIDT 2004, MEINUNGER & SCHRÖDER 2007).

2.2.2.4 Threat

Homalothecium lutescens is common and often occurs in large populations in its main distribution area in Germany. The species is not endangered in the northeast nearby the Oder as well as in calcareous regions of South and Central Germany, but out of this area the species is vulnerable (MEINUNGER & SCHRÖDER 2007).

2.2.2.5 Distribution

Homalothecium lutescens is distributed European southern-temperate (SMITH 2004). The occurrence of *H. lutescens* in North America is mentioned in literature (e.g. NYHOLM 1965, DIERßEN 2001, NEBEL et al. 2001), but is presumably an error due to confusion with *H. fulgescens*.
In Germany *H. lutescens* occurs from lowland to submontane range on calcareous substrates. In upper elevation the species becomes sparse, but reaches the timber line on sunny southern slopes (in Bavaria to 1100m, in North Tirol to 1200 m and in Switzerland to 2160 m) (HOFMANN 1998, MEINUNGER & SCHRÖDER 2007, DÜLL & DÜLL-WUNDER 2008). *Homalothecium lutescens* is absent or rare in regions without limestone (cf. Fig. 3), especially in poor fen, sand regions of North Germany as well as on secondary habitats in southerly silicate regions which are opulent of conifer forests (MEINUNGER & SCHRÖDER 2007). In East Thuringia, *H. lutescens* has the same

distribution as *A. abietina* (cf. MARSTALLER 1980). World-wide the species is distributed throughout Europe, from Mediterranean northward to Iceland and to South Scandinavia; Macaronesian region and North Africa; Caucasus, Southwest Asia (e.g. NEBEL et al. 2001, HEYN & HERRNSTADT 2004; cf. Fig. 4).

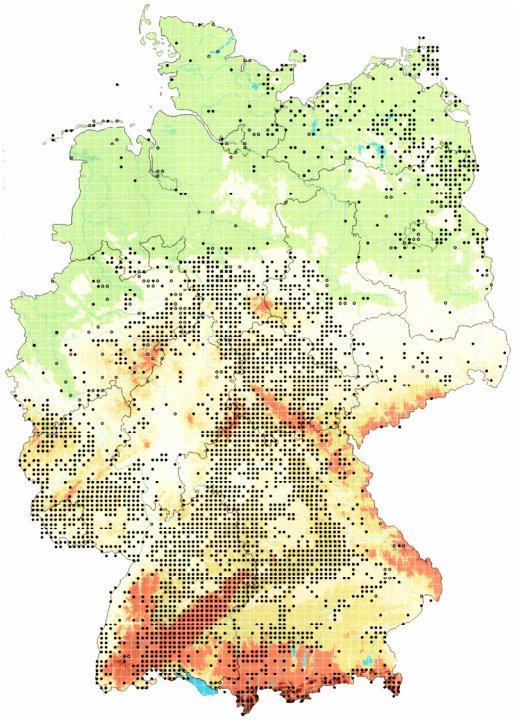


Fig. 3: Distribution of *Homalothecium lutescens* in Germany (acc. to Meinunger & Schröder 2007, dot matrix map based on quadrants of the topographical maps 1:25.000).

Fig. 4: World-wide distribution map of *Homalothecium lutescens* (compiled with literature, compare the following list of references). Uncertain data are display with hatching.

References for the world-wide distribution map:

(* maps in literature; ? uncertain; 0 missing)

Africa: North Africa (HEYN & HERRNSTADT 2004).

Europe: Iceland, Faeroes (SMITH 2004), Finland, Norway, Sweden (BROTHERUS 1923, *NYHOLM 1965), Denmark (*NYHOLM 1965), European Russia (?Northwest, ?northern part of Ural Mountains, 0East and Northeast European Russia, 0southern part of Ural), Belorussia, Ukraine, Baltic republics (IGNATOV & AFONINA 1992, IGNATOV & IGNATOVA 2004), Caucasus (IGNATOV & AFONINA 1992), Estonia (INGERPUU et al. 1994), British Isles (*HILL et al. 1994), Netherlands (*VAN TOOREN & SPARRIUS 2007), Belgium, Luxembourg, France, Germany, Poland (*WACŁAWSKA 1957, KUC 1964), former Czechoslovakia [Czech Republic (KUČERA & VÁŇA 2003)], Lichtenstein, Switzerland, Austria, Hungary (BOROS 1968), Italy [Sardinia, Sicily (REIMERS 1956)], former Yugoslavia (Croatia (SABOVLJEVIĆ 2006), Macedonia), Albania, Greece (DÜLL 1995), Romania, Bulgaria, Spain and Portugal [Macaronesia: Azores, Madeira, Canary Islands (VOHRA 1983), Balearic Islands: Majorca (*CASAS et al. 2001)] (HOFMANN 1998).

Asia: **Central Asia**: Kazakhstan, Tadjikistan, Kirgizstan, Turkmanistan, Uzbekistan (IGNATOV & AFONINA 1992); **East Asia**: China (REDFEARN & WU 1986); **Southwest Asia**: Turkey (*HENDERSON & PRENTICE 1969; FREY & KÜRSCHNER 1991, *ABAY & ÇETIN 2003, KÜRSCHNER & ERDAĞ 2005), Israel (FREY & KÜRSCHNER 1991, *HEYN & HERRNSTADT 2004), Syria (BROWN 1937, FREY & KÜRSCHNER 1991, HEYN & HERRNSTADT 2004), Lebanon (FREY & KÜRSCHNER 1991, HEYN & HERRNSTADT 2004) Iran (VOHRA 1983, FREY & KÜRSCHNER 1991, AKHANI & KÜRSCHNER 2004, HEYN & HERRNSTADT 2004), ?Iraq

(AGNEW & VONDRÁČEK 1975, FREY & KÜRSCHNER 1991, HEYN & HERRNSTADT 2004); **South Asia**: India (Kashmir) (VOHRA 1983).

2.2.3 *Homalothecium sericeum* (Hedw.) Schimp. In Bruch et al., Bryol. Eur. 5: 93, fig. 456. 1851

2.2.3.1 Morphology

Dioicous. Plants very variable in size, from small to moderately robust, glossy green to yellow green coloured, dense rough mats or patches, sometimes extensive. Stems 5–10 cm long, creeping, attached to substrate by rhizoids for most of their length, closely pinnately branched. Branches crowded, ±erect, usually curved when dry (except in very humid habitats), sometimes flagelliform or stoloniferous. Axillary hairs 24–42 µm long. Leaves crowded, strongly longitudinally plicate, appressed when dry, erect-patent when moist. Stem leaves (0.6–) 1.3–2.3 mm long, (0.2–) 0.5–0.9 mm wide, very narrowly triangular, often from a broadly ovate base abruptly attenuate to a narrow apex; margin plane or narrowly recurved below, denticulate at base, entire or faintly denticulate above; costa thin, extending (50–) 60–85% way up leaf, sometimes ending in a spine; basal cells oval, usually not pitted; alar cells ±quadrate, forming small decurrent auricles, incrassate, all other cells linear-vermicular, not pitted; mid-leaf cells (30–) 50–100 (–110) µm long, 3.4–7.1 µm wide (10–16 times as long as wide), thin walled, eporose. Branch leaves (–0.5) 0.8–2.5 mm long, 0.2–0.7 mm wide, with 4–6 decurrent cells at base, triangular to lanceolate-triangular; margin irregularly recurved, basal conspicuously denticulate often with recurved teeth, only slightly denticulate towards apex. Perichaetial leaves straight to slightly falcate, inner ones with very fine costa and abruptly narrowed to a long acumen, to 1.6 mm long, not or marginal plicate. Seta reddish-brown, (0.5–) 1.0–2.0 cm long, rough, straight. Capsule erect, cylindrical, straight or rarely slightly curved below mouth, 2.2–3.2 mm long and 0.7–1.0 mm wide; operculum shortly rostrate to narrowly conical, 0.8–1.0 mm long; calyptra naked, cucullate. Spores 8–22 (–24) µm, finely papillose. Sporophytes occasional, maturing in winter (compare, e.g. HOFMANN 1998, NEBEL et al. 2001, SMITH 2004). According to BOROS (1968) the species develops frequent sporophytes on bark but is sterile at lowland in Hungary. In Lebanon best fruiting of

H. sericeum occurs at the higher elevations (ARZENI 1965). In Iraq the species is sterile (AGNEW & VONDRÁČEK 1975). Specialised propagules are lacking (IRELAND 1975).
Chromosome number is highly variable n=8, n=9, n=10, n=10+m, n=10+3, n=11, n=11+m, n=11+2m, n=13 (WIGH 1972a, 1972b, FRITSCH 1991).

2.2.3.2 Ecology

The meso-xerophyte *H. sericeum* occurs on dry sunny to slightly sheltered horizontal to vertical, slightly acidic to calcareous substrates. The moss grows as epiphyte on tree trunks (preferably on lower and middle trunk areas), branches (*Populus*, *Fraxinus*, *Ulmus*, *Quercus*, *Salix*, *Olea*, *Acer*) on rocks as well as secondary on roofs and walls. The habitats are mostly shadier than in *H. lutescens* (HOFMANN 1998, NEBEL et al. 2001, SMITH 2004, MEINUNGER & SCHRÖDER 2007).

2.2.3.3 Sociology

Homalothecium sericeum is a differential species of the Tortulo-Homalothecietea sericei HERTEL 1974 and occurs also in Orthotrichetalia HADAC 1944 and occasionally in Grimmion tergestinae ŠMARDA 1947.
The following species are associated with *Homalothecium sericeum*: *Leucodon sciuroides*, *Tortula muralis, Orthotrichum anomalum, Tortella tortuosa, Ditrichum flexicaule, Hypnum cupressiforme*, *Anomodon viticulosus*, *Porella platyphylla*, *Neckera complanata, N. crispa, Campylium chrysophyllum* as well as *Brachythecium populeum* (DIERßEN 2001, NEBEL et al. 2001, MEINUNGER & SCHRÖDER 2007).
The species grows in several phanerogam communities e.g. Fagetalia PAWLOWSKI 1928 (DIERßEN 2001), Asplenietea rupestris BRAUN-BLANQUET 1934 (BRANDES 1987) or Sedo-Scleranthetea (BRAUN-BLANQUET 1955) em. TH. MÜLLER 1961. Especially the Sedo-Scleranthetea communities of ledges of rocks and wandering dunes are classified as natural or near natural habitats. Otherwise, these communities colonise also man-made habitats such as wall tops or roadsides. Loose *Sedum acre*-populations of limestone and oolite wall tops belong to the order Sedo-Scleranthetalia. These communities are mostly species poor. Besides the very

frequent *H. sericeum*, following bryophytes are also frequent in Sedo-Scleranthetalia: *Bryum caespiticeum*, *Bryum capillare*, *Brachythecium velutinum* and *Homalothecium lutescens* (BRANDES 1987, KORNECK 1993).

2.2.3.4 Threat

In Germany *H. sericeum* is frequent in its main distribution area and not endangered for the entire area. But lowland populations on walls of churches and cemeteries are worthy of protection. Mats provide habitat for numerous microorganism and, as a moss typically situated on walls, *H. sericeum* is important for filtration of fine particles in cities (MEINUNGER & SCHRÖDER 2007, DÜLL & DÜLL-WUNDER 2008).

2.2.3.5 Distribution

Homalothecium sericeum is distributed Eurosiberian southern-temperate (SMITH 2004). Some authors (e.g. GANGULEE 1978, HILL et al. 1994, DIERßEN 2001) mentioned *H. sericeum* in Central Africa, but is presumably an error based on confusion with *Palamocladium leskeoides,* which was former named as *Pleuropus sericeus* (HOFMANN 1998).

In Germany, *H. sericeum* occurs from lowland to the timberline of the Alps (above 800 m rarely, in Bavaria to 1820 m). The main distribution area in Germany is located in limestone regions and in rich deciduous forests. The species is rare, missing or secondary (on walls of churches and cemeteries) in sand, silicate as well as coniferous forest rich regions (Fig. 5). In Lower Lusatia *H. sericeum* is common and occurs almost exclusively at churches and cemeteries and rarely elsewhere (Totalreservat in Lutzketal on *Ulmus*). Since *H. sericeum* occurs mainly on older masonry, the occurrence of the species is apparently determined by the age of man-made habitat (OTTE 2002, MEINUNGER & SCHRÖDER 2007, DÜLL & DÜLL-WUNDER 2008).

In the European territory *H. sericeum* is common in the south and central part and rare or absent towards the north and the mountains (NYHOLM 1965). The distribution area extends northward to Iceland and Northern Fennoscandia; southward to Macaronesia, North Africa; Caucasus, Turkey, Cyprus. Furthermore the species

occurs in East and Central Asia and in Newfoundland. (HILL et al. 1994, NEBEL et al. 2001, cf. Fig. 6). The species is found from sea level to 2680 m a.s.l. (HOFMANN 1998).

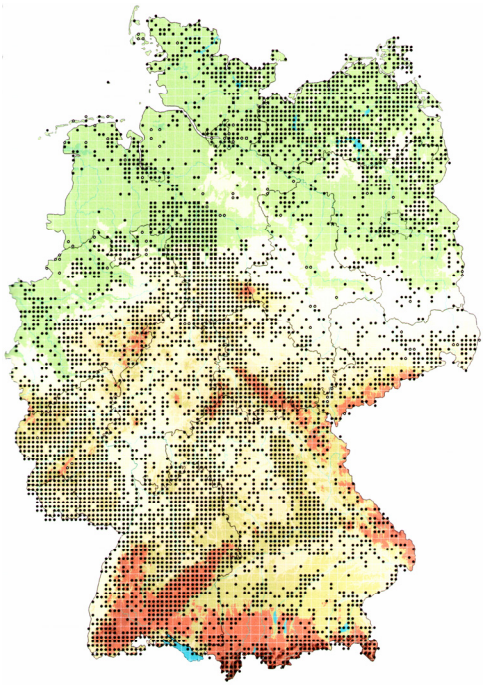


Fig. 5: Distribution of *Homalothecium sericeum* in Germany (acc. to Meinunger & Schröder 2007, dot matrix map based on quadrants of the topographical maps 1:25.000).

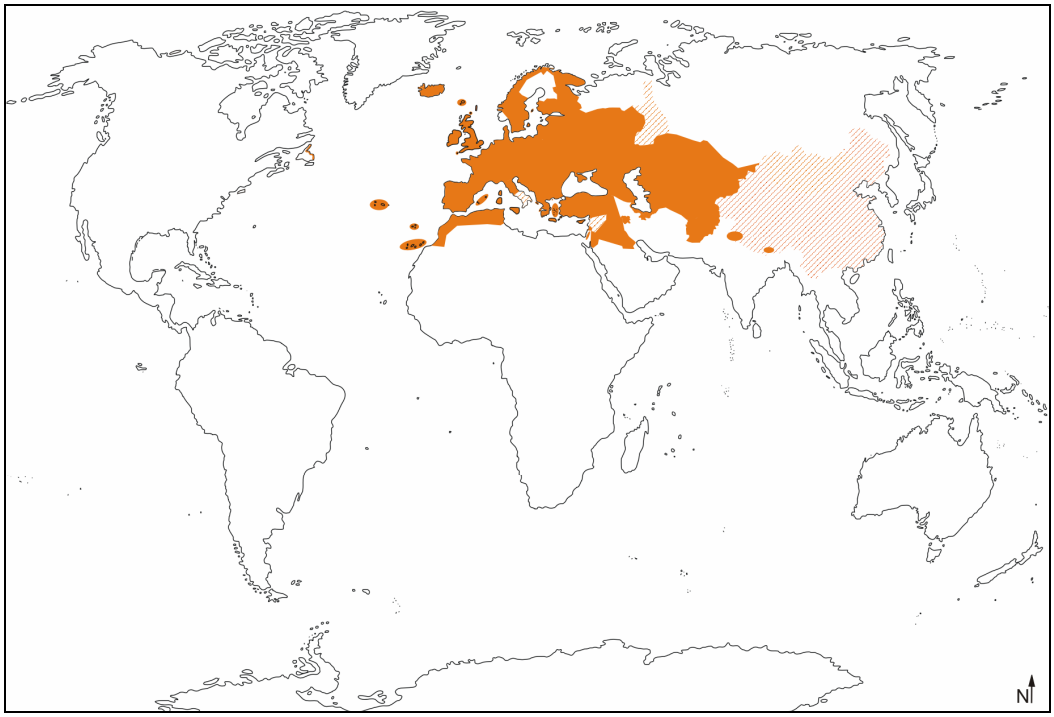


Fig. 6: World-wide distribution map of *Homalothecium sericeum* (compiled with literature, compare the following list of references). Uncertain data are display with hatching.

References for the world-wide distribution map:

(* maps in literature; ? uncertain; 0 missing)

Africa: North Africa: Algeria (*GANGULEE 1978), Tunesia, Morocco (NYHOLM 1965).

Europe: Iceland (Jones 1946, HILL et al. 1994), Faeroe (SMITH 2004), Estonia (INGERPUU et al. 1994), Finland, Norway, Sweden (BROTHERUS 1923, *NYHOLM 1965), Denmark (*NYHOLM 1965); European Russia (?south and northern part of Ural Mountains, 0Northeast European Russia), Belorussia, Ukraine, Baltic republics (IGNATOV & AFONINA 1992, IGNATOV & IGNATOVA 2004); Caucasus (IGNATOV & AFONINA 1992), British Isles (*HILL et al. 1994), Netherlands (*VAN TOOREN & SPARRIUS 2007), Poland (KUC 1964), France [Corsica (SOTIAUX et al. 2007)], Czechoslovakia [Czech Republic (KUČERA & VÁŇA 2003), Slovakia], Hungary (BOROS 1968), Belgium, Luxembourg, Germany, former Switzerland, Liechtenstein, Austria, Italy [Sardinia, Sicily (REIMERS 1956)], former Yugoslavia [Croatia (SABOVLJEVIĆ 2006), Macedonia], Albania, widespread in Greece (DÜLL 1995), Romania, Bulgaria, Portugal, Spain (*CASAS et al. 2001) [Macaronesia: Azores, Madeira, Canary Islands (GANGULEE 1978, VOHRA 1983), Balearic Islands: Majorca, Minorca, Eivissa, Formentera (*CASAS et al. 2001)]; (HOFMANN 1998).

Asia: **Central Asia**: Kazakhstan, Tadjikistan, Kirgizstan, Turkmanistan, Uzbekistan (IGNATOV & AFONINA 1992), **East Asia**: China (REDFEARN & WU 1986), **Southwest Asia**: Turkey (Cyprus) (*HENDERSON & PRENTICE 1969, EL-OQLAH et al. 1988, FREY & KÜRSCHNER 1991, *ABAY & ÇETIN 2003, KÜRSCHNER & ERDAĞ 2005), Israel (EL-OQLAH et al. 1988, FREY & KÜRSCHNER 1991, *HEYN & HERRNSTADT 2004), ?Syria, Iran (EL-OQLAH et al. 1988, FREY & KÜRSCHNER 1991, AKHANI &

KÜRSCHNER 2004), Iraq (AGNEW & VONDRÁČEK 1975, EL-OQLAH et al. 1988, FREY & KÜRSCHNER 1991), Lebanon (ARZENI 1965, EL-OQLAH et al. 1988, FREY & KÜRSCHNER 1991), Jordan (EL-OQLAH et al. 1988, FREY & KÜRSCHNER 1991), Afghanistan (FREY 1972, EL-OQLAH et al. 1988, FREY & KÜRSCHNER 1991), **South Asia**: India (Kashmir), Nepal (GANGULEE 1978, VOHRA 1983).

North America: Canada: Newfoundland, as a series of disjunctive populations in coastal habitats; only sterile female plants (IRELAND 1975, *BRASSARD & WEBER 1977, CRUM & ANDERSON 1981, BRASSARD 1984, IRELAND et al. 1987).

3 Study areas

3.1 Jena

3.1.1 Location and description of the study area of Holzberg and Mönchsberg near Jena (Thuringia)

The investigation area of *A. abietina* and *H. lutescens* is located in Thuringia in the Central Saale Valley. One of the studied areas, the Holzberg, is situated between the Jena district Winzerla and Nennsdorf southwest of the city centre of Jena and northwest of the Mönchsberg plots, the second area of investigation. The Mönchsberg is located south-southwest of the city centre of Jena, north of Leutra, south of the Jena district Winzerla and west of Göschwitz.
The Holzberg and the Mönchsberg are ca. 2.3 km apart from each other. The plots of the Holzberg are located 50°53'23.5"N–50°53'24.8"N and 11°33'15.7"E–11°33'17.0"E, 296–297 m a.s.l. and are following denoted as Hb. The plots of Mönchsberg are in the following referred to as Mb and are located 50°52'51.1"N–50°52'51.2"N and 11°34'56.6"E–11°34'57.3"E, 286 m a.s.l.

3.1.2 Geographical classification of natural landscapes, geology and soils

The Saale Valley has been indenting in Muschelkalk (shell bearing limestone) and Buntsandstein (bunter) regions at the edge of the Thuringian basin. The mountains of the landscape of Jena are remains of the uniform Ilm-Saale Muschelkalk plate in which the Saale and their tributaries have been indenting. The characteristic of the landscape is based on contrast of steep, mostly bare slopes which decline to the Saale or their tributaries and the forested and ploughed plateaus which are traversed by deep cutting valleys. The plain, lower parts of the valley slopes of the Middle Saale valley at Jena are composed of upper Buntsandstein and are overtopped by the escarpment of the lower Muschelkalk. The Muschelkalk lifts out plain eastward so that between Jena and Bürgel escarpments of less elevation reveal only sparse

Muschelkalk above Buntsandstein. Westwards the lower Muschelkalk immerses below the middle and upper Muschelkalk so that the western tributaries of the Saale expose the steep Muschelkalk slopes down to the bed of the valley and are overtopped on adjacent heights by the slight cuesta of the Trochiten chalk.
Frequently at the steep slopes of lower Muschelkalk Wellenkalk exists in forms of layers. On especially steep slopes, they can build cliffs. At low incline, loose rubble and weathering have a more compensative effect so that layers emerge only as narrow bands. The layers are opulent structured by gaps and crevices and offer bryophyte and lichen communities various habitats. Mountains south of Göschwitz and east of the Saale only consist of Buntsandstein. The once overlying Muschelkalk has been completely ablated. West of the Saale at Leutra, Dürrengleina and Rodias, the lower Muschelkalk has remained but is located above a high socket of Buntsandstein. In the Muschelkalk area predominantly Rendzina soil occurs. The steepest slopes are covered with limestone immature soil. The areas at the slopes are characterised by Mullrendzina (STODIEK 1937, MARSTALLER 1970a, HEYER 1990, WAGENBRETH & STEINER 1990).

3.1.3 Climate

Jena belongs to the warmest regions in Central Europe with high temperatures in summer and moderate frosts in winter. The landscape of Jena is situated in a transition area between the oceanic characterised climate of the southward adjacent foreland of the Thuringian Forest with high precipitation and relatively even temperatures and the continental characterised climate of the arid region of Central Germany with low precipitation, high temperature amplitude and higher mean temperature. The mean annual amount of precipitation in Jena is 560–580 mm and the mean annual temperature is +8.6°C (July +17.7°C, January -0.1°C). Figure 7 shows the temperature and precipitation data from Jena and adjacencies for 2006, the year when the field work was carried out. Within the vegetation period (between May and end of August) the precipitation amounts to 255 mm (in 2006, 275 mm; meteorological station, University of Applied Sciences Jena), but the precipitation deficit caused by the lee effect of the Saale valley has to be taken into account.

In addition, specific local climatic distinctions exist at the steep slopes of Muschelkalk in the south and southwest, where soil temperatures exceed 20°C in winter and more than 40°C in summer. Because of these conditions the occurrence of numerous thermophilous species with a main area of distribution in Southern Europe, such as the majority of native Orchidaceae, is possible (MARSTALLER 1970a, KNAPP & REICHHOFF 1975, HEYER 1990).

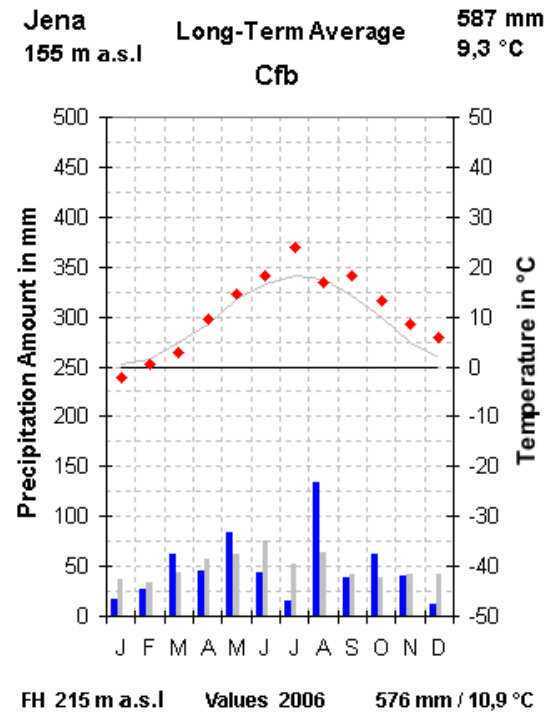


Fig. 7: Climate graph of Jena in 2006 compared with the long-term mean of precipitation (mm) and temperature (°C) (received from the weather station of the University of Applied Sciences Jena).

3.1.4 Natural and potential vegetation

During the Weichsel glacial period (ca. 100.000–10.000 years ago) large areas of Thuringia were covered with ice which expanded from north to south. Only few adapted species could survive on a narrow ice-free corridor. After the retreat of the glaciers these species expanded and developed a vegetation of tundra with dwarf-shrubs (*Betula nana*, *Empetrum* spp.) being the dominant element. With increased warming these arctic-alpine species were pushed back to few relic areas (raised bog of lower mountain ranges) and a development of forests with different aspects began.

Today's flora of the Unstrut area is characterised by the four currents of migration of plant species (late-glacial period, Nordic and high mountain species; pre-boreal period, continental species of eastern steppe; Atlanticum, thermophilous species from Mediterranean highlands; subatlantic period, Atlantic species of Western Europe). Most significant in this regard was the migration current of the Atlanticum during the *Quercus* mixed forest period. Hence, numerous Mediterranean/montane–Central European species can be found in the study area (MARSTALLER 1970b, KNAPP & REICHHOFF 1975, HEYER 1990).

The analyses were carried out on slopes exposed to the south. Large parts of these slopes are covered with *Sesleria albicans* and sparsely colonised with trees and shrubs such as *Rosa* spp., *Juniperus communis* and *Cotoneaster integerrimus.* Along with herbs, *Sesleria albicans* forms a more or less dense Seslerietum depending on the conditions and the location of the slopes (STODIEK 1937). *Abietinella abietina* and *H. lutescens* grow in the immediate vicinity of such shrubs, inside *Sesleria albicans* tussocks as well as in open locations on southern slopes.

3.1.5 Human influence on vegetation

Although recent structures and arrangements of individual plant communities reflect the influence of natural factors (climate and soil), todays vegetation is predominantly characterised by human influence.

In some valleys of the adjacent regions of Jena, the Röt locations are said to be ploughed since the Stone Age. Wine and woad (*Isatis tinctoria*) characterised the agriculture of Thuringia in the Middle Ages. On thermal favoured slopes, which stood out because of their characteristic plant species and communities, and in the Muschelkalk regions vineyards were mainly found. Since the creation of the first vineyards, Jena had emerged as an important wine-growing town. Besides viniculture, animal breeding, the production of wool and pasture management played a prominent role in Thuringia in 15th/16th century. Forestry was a further important factor in the modification of the landscape by humans. In 12th–15th century, large parts of the dominant beech forests on the Muschelkalk plateaus were cleared and cultivated. The remaining forests were degraded by excessive removal of wood in low and middle forest management as well as leaf litter extraction and forest pasture.

Hence, the south exposed slopes became waste land. In the bloom of viniculture in the closing years of the Middle Ages, the native vegetation was destroyed to a very large degree due to agricultural use of the entire land. At the same time as native vegetation was destructed, substitute vegetation developed. As a result, weed communities developed on fields and vineyards, *Arrhenatherum eliatus* meadows at the valley floor by hay crop and mesoxerotherm grassland and scrub at waysides and grazed habitats. Caused by deterioration of the climate and turmoil of the Thirty Years' War, the viniculture around Jena nearly came to a standstill. The structure of substitute vegetation altered due to changes in use. Former vineyards were repurposed as sheep pasture and the mesoxerotherm grassland spread out. In the first half of the 19th century afforestation began with non-native *Pinus nigra* on Muschelkalk habitats in the middle Saale valley (MEISEL 1924, HERZOG 1940, KNAPP 1973, HEYER 1990). Today's high forest stand in these habitats is a result of this afforestation in the previous century.

Hence, present substitute vegetation in Leutra have developed under the age-long influence of humans *Sesleria-Pinus* forests on Wellenkalk, Trochitenkalk, fields on middle Muschelkalk, native regenerated beech forests (Carci-Fagetum) at north exposed Wellenkalk slopes and Virburno-Cornetum at relatively late abandoned vineyards (KNAPP 1973).

3.2 Freyburg

3.2.1 Location and description of the study area in Freyburg (Neuenburg)

Freyburg is located in South Saxony-Anhalt and in the lower Unstrut valley, which is situated at the underflow of the Unstrut. The analysed wall is located on the left hand side in front of the entry of the Neuenburg. The construction of the Neuenburg at a spur above Freyburg started in 1062 (Kugler & Schmidt 1988).
The studied part of the wall is situated 51°12'32.6"N–51°12'32.8"N and 11°46'42.4"E–11°46'43.3"E, 208 m a.s.l. and in the following named as FN.

3.2.2 Geographical classification of natural landscapes, geology and soils

The landscape around Freyburg is characterised by layers of Trias. Prevalent are lower Muschelkalk and upper Buntsandstein (Röt) (SCHWAB 1988).
As a result of interaction of Unstrut and Ilm, with several changes of the courses of the rivers, the narrow Freyburger Unstrut valley with its small floodplain between Weischütz and Nißmitz developed. Freyburg is located at the outlet of a dry valley (preglacial valley of the Unstrut, BAUER 1962) and is imbedded between the 25–35° inclined and ca. 100 m high to the Neuenburg at the western border of the Freyburg Muschelkalkplateau ascending slopes and the plane east slopes of the Schweigenberge. The left-sided southern exposed slopes, at which the Neuenburg is located, are used for viniculture; the right-sided ones are forested. On the right side of the valley loess and loess transported soil can be found and on the left valley slope protruded banks of robust Terebratula- and foam limestone disrupt the shallow soils of the limestone- lime rubble Rendzina type (KUGLER & SCHMIDT 1988). The steep slope of the Muschelkalk accompanies the Unstrut valley from Karsdorf to Freyburg (WAGENBRETH & STEINER 1990). On the way from Freyburg to the Neuenburg, visible “schlottenartige” increments of desiccation cracks and chasms of limestones indicate the low karst formation of the Muschelkalk (KUGLER & SCHMIDT 1988).

3.2.3 Climate

The lower Unstrut valley is characterised by a dry and warm climate and belongs to one of the driest regions of Germany. The low annual precipitation amounts to ca. 500 mm and the mean annual temperatures is 9°C, with high mean summer temperatures (July 18°C). The climate is subcontinental and, similar to the eastern European climate, characterised by low precipitation amounts and a midsummer precipitations maximum. In comparison to eastern European steppes, the lower Unstrut valley is defined by mild winters, which are typical for the subatlantic-submediterranean regions. In contrast to the open plateaus, the valleys of Saale, Unstrut and Ilm are sheltered from the wind and protected from extremes of temperature. Therefore, viniculture is still being practised today on the terraced, south and west exposed light lime slopes at Unstrut and Saale valley (BAUER 1962, MAHN 1965, KUGLER & SCHMIDT 1988).

3.2.4 Natural and potential vegetation

Regarding to its vegetation, the region of the lower Unstrut has an exceptional position, caused by the local compound of continental and submediterranean distributed species. Within the xerotherm grassland, the eastern species benefit from the subcontinental climate, whereas the numerous calciphile southern species are promoted by predominant Muschelkalk-substrate and high temperatures. Moreover, the Unstrut valley is an important refuge for taxa of Mediterranean region and steppes. Hence, the region shows a relatively high diversity of species and consists of several xero- and mesoxerotherm grassland-communities. Adjacent to submediterranean distributed Brometalia erecti, the continental distributed Festucetalia valesiacae can be found. Within the respective community, submediterranean and continental elements are mixed very often

At the lower Unstrut region the forest takes up to 25% of the entire territory. Mixed deciduous forests are dominant, native *Quercus petraea-Fagus* mixed forest at upper elevations and *Quercus petraea-Tilia* forest at lower elevation. The eastern and northern parts on the other hand, at limy lower Buntsandstein and especially at the region of loess, are nearly woodless.

Rock vegetation (comprises spring annual plants and cryptogam rich vegetation on rocky shallow ground) is common at the lower Unstrut valley, but cover only small areas. They occur at plateau margin of Querfurt plate in abandon limestone quarries, gypsum undercut slopes of streams and rock platforms of middle Buntsandstein and Zechstein gypsum. Four different rock vegetation communities can be distinguished: Teucrio botryos-Melicetum ciliatae (KAISER 1926) VOLK 1937, *Festuca pallens*-Festucion pallentis-community, Poo badensis-Allietum montani GAUCKLER 1957, *Cerastium semidecandrum*-Alysso-Sedion-community. Nearly all this communities are located on southern to western exposed sites (BAUER 1962, BECKER 1999).

3.2.5 Human influence on vegetation

Neolithic settlement discoveries at Balgstädt, Freyburg, Weischütz and Nißmitz hint at an early colonisation of the Freyburg Unstrut valley. The settlements were mostly located at terraces or plateaus.

The landscape was clearly influenced by centuries-old quarrying for limestones. Foam limestone was mined in large quarries at Freyburg. Today, the whole lower Muschelkalk is used as a mineral resource in cement mills near Karsdorf.

Moreover, wine has been successfully cultivated at the escarpments of lower Muschelkalk at Freyburg for a long time. The favourable meso- and local climatic conditions and the south exposed valley slopes at lower Unstrut valley were already used for viniculture in the early medieval times. In contrast to historical vineyards at the steep Muschelkalk slopes, the recent plantations were arranged at less inclined slopes where the intensive cultivation does not allow a development of characteristic vineyard-weed vegetation. Remains of weed vegetation of vineyards between Freyburg and Dorndorf convey interesting evidence for the impact of humans on the vegetation. Today, most areas of cultivation are located at the south and west exposed slopes of the Unstrut valley or at the Muschelkalk cuesta, resp. Some regions of the Schweigenberge in Freyburg have been overgrown with grass and scrub or fruit trees have been planted (KUGLER & SCHMIDT 1988, WAGENBRETH & STEINER 1990).

3.3 Lower Lusatia

3.3.1 Location and description of the study areas in Lindena and Dollenchen

In Southern Brandenburg cemetery walls were studied in Lindena and in Dollenchen. The villages are situated in the western part of Lower Lusatia in the administrative district Elbe-Elster. Churches, cathedrals and their immediate surroundings are relevant important refugia for bryophytes in areas where the adjacent landscape is intensively farmed or built, or where there is little or no natural rock exposure (PORLEY & HODGETTS 2005). Since the surface of the Lower Lusatia is predominantly covered by Quaternary deposits, lime on walls is particularly important as habitats for calciphile species like *H. sericeum*.

Dollenchen is located 14 km east of Finsterwalde. The rectangular Granit church was built in the 13th century. The analysed cemetery wall in Dollenchen, in the following referred to as D, is located 51°36'28.3"N and 13°51'38.8"E and 124 m altitude.

Lindena is situated 13 km southwest of Finsterwalde and 22 km west of Dollenchen. The church of Lindena was built in the 13th century. For the lower parts of the church Raseneisenstein was used as a building material and bakestone for the upper parts. The cemetery wall was made of Raseneisenstein and cobblestone. The investigated area in Lindena is in the following referred to as L. The plots are located ca. 51°35'27.2"N to 51°35'27.9"N and 13°32'11.4"E to 13°32'13.9"E in 91 m a.s.l.

3.3.2 Geographical classification of natural landscapes, geology and soils

The area of investigation in the Lower Lusatia of *H. sericeum* is located in the Kirchhainer-Finsterwalder basin within the Lusatia basin and heath. It is a section of the old moraine landscape (Saale cold stage deposition) of the North German lowland. The Kirchhain-Finsterwalder basin, the greatest southern edge basin, is placed in the south camber of the Lusatia basin and has subsided in comparison to the borderlands with an altitude between 90 and 120 m. Larger plateau remainders arise in the middle of the basin between Finsterwalde and Kirchhain like islands. The plateaus consist of gravel and sand. The basin is mostly a gently undulating sand-loam-ground (late Saale glacial ground moraine plate) with plain basin and sandy

valley areas as well as boggy lowlands. The valley and basin sands are more or less humified on surface and tend to the development of raw humus (KLIX 1957a, 1957b, SCHOLZ 1962).

3.3.3 Climate

The Lusatia basin and heath is situated in the East German continental climate with mean monthly temperatures between 17.5 and 18.5°C in July and between -1 and -0.5°C in January. The annual mean temperature is between 8 and 8.5°C. The eastern part of this area belongs to the warmest regions of East Germany in summer and shows high annual fluctuations of the temperature. The Lower Lusatia has an irregular distribution of precipitation. The lowest precipitation occurs in the northern part (e.g. Fürstenberg 496 mm) and increases southward and exceeds 600 mm in the Kirchhainer-Finsterwalder Basin (KLIX & KRAUSCH 1958, SCHOLZ 1962). Figure 8 shows the temperature and precipitation data from the weather station of Doberlug-Kirchhain for 2006, the year the study was carried out in the nearby Lindena and Dollenchen.

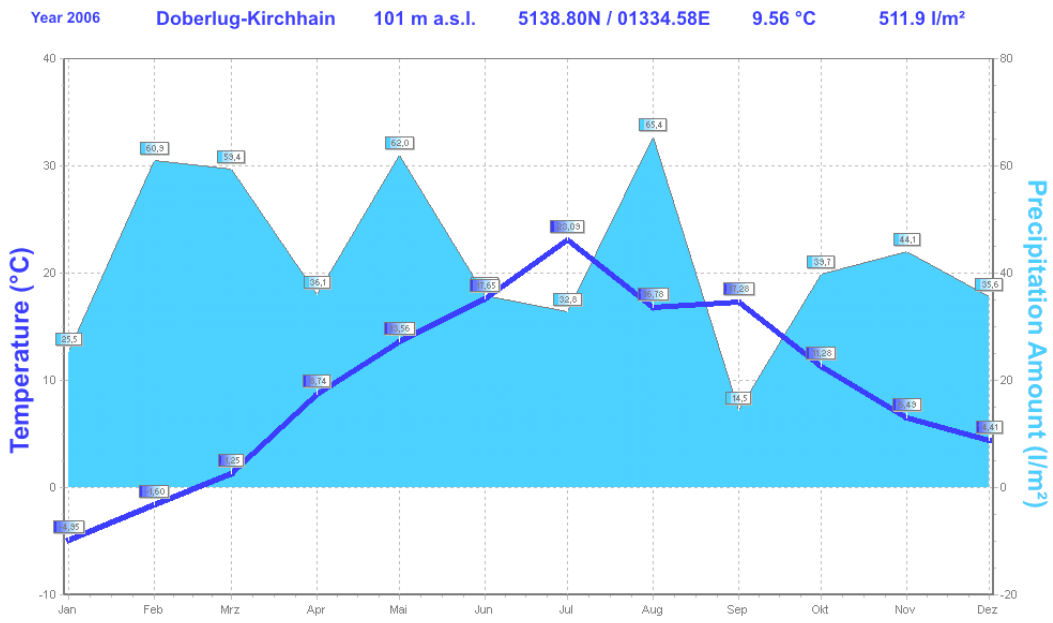


Fig. 8: Climate graph of Doberlug-Kirchhain in the year 2006 with precipitation amount (l/m²) marked light blue and temperature (°C) marked dark blue (received from the private weather station of Doberlug-Kirchhain).

3.3.4 Natural and potential vegetation

Without any human influence, the Lower Lusatia would be covered nearly completely with forest. As common for Brandenburg, subcontinental as well as suboceanic species can be found in the Lower Lusatia. In general, demanding plant communities of richer habitats are rarer and exist only on a small-scale. In the Kirchhainer-Finsterwalder basin the plant communities were composed of *Quercus robur-Betula* forests, *Pinus* mixed forests and *Abies* outpost forests. In the transient area between plateaus and lowland occurred *Quercus robur-Carpinus betulus* and in poorer habitats damp *Quercus robur-Betula* forests. At arid plateaus *Pinus-Quercus robur* forest were prevalent (MEUSEL et al. 1965, SCHOLZ 1962, KRAUSCH 1979). Probably *Homalothecium sericeum* occurs naturally only as epiphyte in the Lower Lusatia.

3.3.5 Human influence on vegetation

Especially during the Middle Age, a large part of the forest in the Lower Lusatia was supplanted by agricultural areas. Primarily the more suitable locations for agriculture with *Quercus* rich forests were cleared. Recently, a severe endangerment comes from the drainage of the lowland and the decrease of groundwater level, which also causes oligotrophy. Those forest areas were substituted by *Pinus* afforestations. Deciduous forests exist at terrace landscape of the Kleine Elster near Doberlug-Kirchhain. Furthermore, brown coal mining was the dominating influence for the landscape and vegetation in the Lower Lusatia. Subsequent to brown coal mining, vegetation complexes, which differ from native vegetation developed often after plantation and dissemination. Besides forest vegetation, dry grassland vegetation occurs in the Lower Lusatia. *Corynephorus canescens* communities are not endangered. Communities' rich of *Armeria* spp.*, Festuca ovina* and *Agrostis* spp. on the other hand are more endangered (KRAUSCH 1978, 1979). Nowadays, afforestation of more stable, multifunctional and regional typical forest ecosystems, which are structured near-natural and are irregularly planted, take place.

The distribution of *H. sericeum* in the Lower Lusatia is clearly influenced by man, since the species occurs almost exclusively on church and cemetery walls. On the usually species poor church and cemetery walls a few common Verrucarietea

species grow on mortar and are in some cases joined by *Homalothecium sericeum* and *Xanthoria calcicola* and sometimes *Xanthoria parietina* OTTE (2002).

3.4 Ecology of man-made habitats - walls

In contrast to *A. abietina*, *H. sericeum* and *H. lutescens* can grow on walls (e.g. DUCHOSLAV 2002). Several plant species (e.g. *Melica ciliata, Sedum album*, *Tortula muralis*, *Campylopus subulatus*) and communities occur natively only on rock faces or rock crevices in low or high mountain ranges. Since they have adapted to extreme local characteristics, such as drought, heat, cold and lack of nutrients, these species evade competition with higher and faster growing species (ELLENBERG 1996). Some species of rocks are able to colonise secondary anthropogenic habitats (walls, roofs, well shaft) (SPERBER 2003).

Walls are only a temporary habitat due to repeated cleaning. Hence, many species which are typical of rocks and rock crevices are absent on walls (DUCHOSLAV 2002). However, walls offer similar environmental conditions as rock faces or crevices in low or high mountain ranges. Especially south exposed walls undergo high daily and annual fluctuations in temperature. Walls rapidly become warmed by solar radiation but without an efficient retain of heat because at night walls quickly lose heat by radiation and therefore low temperatures are reached. In summer, the daily fluctuation can exceed 50°C. The temperature fluctuation decreases with the increasing size of the crevices (DARLINGTON 1981, KREMER & BELLMANN 2000). A crucial factor for the occurrence of vegetation on walls is water. Moisture of walls depends on the climate, the exposure of the surface, the nature of the substrate and the vegetation cover. Crustose lichens and drought-resistant acrocarpous mosses appear on walls that occasionally become very dry but which are not exposed to long periods of desiccation. Foliose lichens, pleurocarpous mosses (e.g. *H. sericeum*, *H. lutescens*) and vascular plants grow on walls which never dry for long periods, or do so only for very short periods at most. The number of plants and the variety of species increase as the moisture increases. Similar to native crevices, crevices in walls are low in nutrients (DARLINGTON 1981).

The vegetation of walls in villages or cities is of different origin, e.g. low mountain ranges of local rock or dry, stony locations with shallow layers of soil, cemeteries, gardens, forests or plants with light diaspores (spores or small vegetative diaspores s.l. in mosses) which can easily be carried by the wind and which grow on dry

locations. Moreover, the dispersal of diaspores by birds (e.g. seedlings of *Taxus baccata* or of the genus *Helianthus* or gametophyte fragments of mosses, attached to the plumage after foraging or lost during the transport of nesting material) and ants (for example *Chelidonium majus*, *Glechoma hederacea*, *Lamium album*) are relevant for the diversity of species on walls (BRANDES 1987, SPERBER 2003). The age of walls also plays an important role in plant colonisation since the gradual decomposition improves the conditions for a colonisation and further during time increases the input of diaspores (BRANDES 1992). In general, the species composition is determined by the stone type, the aspect, the inclination and the degree of shade (PORLEY & HODGETTS 2005).

A wall offers a complex of habitats: wall base, vertical wall surface (middle level, upper level), wall top and crevices. The vegetation differs in the wall zones depending on moisture and exposition. For example species of *Sedum* colonise the top of the wall and small species of *Asplenium* grow in gaps between the stones (DARLINGTON 1981, BRANDES 1987, SPERBER 2003). On mortar, a limestone flora occurs between crystalline or sandy stones (ELLENBERG 1996) even in districts where the soils themselves are non-calcareous (DARLINGTON 1981). The cover of plants is mostly sparse (BRANDES 1987).

The zones of the wall differ in their environmental conditions which induced the specific vegetation. The base of walls are characterised by changes of the microclimate, due to south or north exposition, the accumulation of chalk (falling mortar) and nutrients (faeces and urine) as well as the protection from mechanical damages. Nitrophils, such as *Polygonum aviculare* and members of the Urticaceae, often grow there. Furthermore, the base is considered to be the wettest zone. It offers favourable habitats for a range of mosses and also for some liverworts. The vegetation of the vertical wall surface is best developed on old walls of monuments and buildings in historical town centres, disintegrating castle fortification etc. The upper level of the vertical wall surface is more humid than the middle. This is caused by overshadowing of ledges between the wall top and the upper level or plants, which grow on top and retain moisture. The wall top, complying horizontal ledges of rock, is the principal zone receiving fruits and seeds dropped by passing birds. Species like *Berberis vulgaris* or *Cotoneaster* spp. sometimes become established

here. Plant growth begins to develop in crevices or pores of rough surfaces where water and finely dived solids are accumulated. This development of vegetation mostly depends on the level of disintegration of mortar or stones of the wall (DARLINGTON 1981, BRANDES 1987, DUCHOSLAV 2002). *Homalothecium sericeum* primarily occurs on wall tops and the upper vertical wall surface.

During the vegetational succession, lichens frequently function as pioneers on walls followed by a bryophyte flora, broadly similar with acrocarpous mosses (*Barbula revoluta*, *B. recurvirostra*, *Tortula muralis* (on top), *Bryum argenteum* (on base) which often precedes the pleurocarpous mosses. On horizontal surfaces, the cushions of the acrocarpous mosses offer germination beds for higher plants. Mostly, an increasing number of pleurocarpous mosses (*Homalothecium sericeum*, *Amblystegium serpens*) develops, which provides a foundation for the establishment of longer-lived angiosperm species (DARLINGTON 1981).

4 Materials and methods

4.1 Field work and sampling

All three species were analysed on four spatial scales: the scale of population, region, nation (Figs. 14+16+18) and the world-wide scale or the entire distribution area, resp. (Figs. 15+17+19). The habitat colonisation and maintenance and the spatial and genetic structures were studied in detail on several plots for each species (scale of population) and for comparison additional regional samples were collected. For the study of genetic variability specimens from the distribution area in Germany and from their entire distribution area were sampled in the field or alternatively obtained from herbaria (Appendix 1). Voucher samples are deposited in STU. In the following the conventions for the sample labelling will be elucidated (Table 1).

Table 1: Explanation of the sample labelling

Example	Abbreviation	Explanation
1	Hbl_247	Single plants which do not belong to a patch are only labelled with the plot name and number (optional) and on the second level with the collecting number.
2	HbIII_1_410	Samples from a patch start also with the name of the plot and number. On the second level follows the number of the patch and at the end the collecting number.
3	Hb_surr_481	Surrounding samples are likewise labelled with the plot name, the abbreviation “surr” for surrounding and finally the collecting number.
4	r3_Osmaritz G1_Mönchberg	In this case “r3” and “G1” represents the third regional resp. the first German sample followed by the name of the location.
5	A22_Mongolia	Global specimens start with an abbreviation of the species name (A - *A. abietina*, H.l. - *H. lutescens*, H.s. - *H. sericeum*) followed by the name of the location.

4.1.1 Sampling method

Plots were mapped by using a home made 1 x 1 m large wooden frame, with a 10 x 10 cm subdivision through strings. The length of the walls on the other hand was subdivided into one meter sections. The

height and length of the walls as well as the width of the top were recorded. Areas of the walls, which were covered with patches of *H. sericeum,* were measured with measuring tapes in detail and mapped.

In all cases the position, size and degree of coverage of the patches as well as the location of loose fragments of the analysed mosses were assigned to a 1:10 map on millimetre paper. Additionally, further noticeable elements were recorded (e.g. big stones, deadwood, trees and bushes with projection of their crowns).

The samples of the mosses were randomly selected in equal distances across the plots and walls. Criterion for the selection of collected plants was that they should have at least one relatively long and green stem for DNA extraction. From larger patches several shoots at regular intervals were sampled for a better evaluation of the genotype composition of the patches. From smaller patches on the other hand only one shoot was collected and some loose fragments outside the patches. Further samples were collected in the surroundings of the plots and walls. All samples were air-dried and stored in paper bags.

For all plots and walls the vegetation relevés were conducted acc. to the method of Braun-Blanquet (1964). The recording data are visible in Appendices 2+3. Also the coordinates, altitude (GPS Garmin *Geko 101*), exposition and inclination (determined with RECTA DP-6 compass), geological characteristics of the plots and characteristics of the stones of the walls were documented.

During the mapping of the plots and walls as well as on later inspections of the studied areas (for purposes of recording the vegetation) special attention was paid to the occurrences of sporophytes and vegetative diaspores. All in all, the studied populations were monitored over a period of three years.

4.1.1.1 Holzberg (Hb) and Mönchberg (Mb) near Jena

The sampling of *A. abietina* and *H. lutescens* at the Holzberg (Nennsdorf) took place in April 2006 (Fig. 9, Appendices 4+6). After an inspection of the area at the southern slope of the Holzberg, three suitable plots were determined on which both species occur. The first plot HbI had a dimension of 3 x 5 m² and HbII and HbIII were each one m². Plot HbII was located three meters westward and HbIII 12 m northward of HbI.

At the Mönchsberg (Jena, Göschwitz) in October 2006 a plane area was selected and two plots for *A. abietina* and one for *H. lutescens* were analysed (Fig. 10, Appendices 5+7). The first plot MbI was 3 x 3 m² and both species were mapped. The second plot MbII (1 x 2 m²) was located westward of MbI and only *A. abietina* grows there. The closest point between both plots was 7.30 m.

Fig. 9: Study area Holzberg (Hb).
Fig. 10: Study area Mönchsberg (Mb).
[(10.1) plot MbI, (10.2) plot MbII].

4.1.1.2 Neuenburg in Freyburg (FN), Lindena (L) and Dollenchen (D)

For *H. sericeum* only man-made habitats were analysed since there is a lack of extensive populations in native locations in the studied areas. Three populations were selected for the study, further referred to as FN, L and D.

In November 2005 a wall near the Neuenburg in Freyburg (FN) was studied. The wall is 66.55 m long and 1.0 m–1.46 m high. For the analyses the first 30 m of the northeastern part of the wall were selected and only the dense covered 0.4 m wide top of the wall was mapped (Fig. 11, Appendix 8).

The walls of the cemetery in Lindena (L) and Dollenchen (D) were analysed in August 2006. In Lindena several parts (LI, LII, LIII, LIV and LV) of the inner side of the wall were mapped. The wall is ca. 1.50 m high and all covered areas of the wall were examined. Besides the wall, two plots were additionally included in the study. One is a 1 x 4.9 m² large plot (LV) in front of the eastern wall and the other a 3.5 m² large plot (LVI) in front of the western wall (Fig. 12, Appendix 9).

In Dollenchen (D) *H. sericeum* only grows plenty at the inner side of the cemetery wall of the southeastern side. At this part of the wall mainly the vertical surface was mapped. The mapped area was 4.35 m in length and 1.0 m in height (Fig. 13, Appendix 10).

Fig. 11: Study area Freyburg/Neuenburg (FN).

Fig. 12: Study area Lindena (L) [(12.1) plot LIII+LIV, (12.2) plot LV].

Fig. 13: Study area Dollenchen (D).

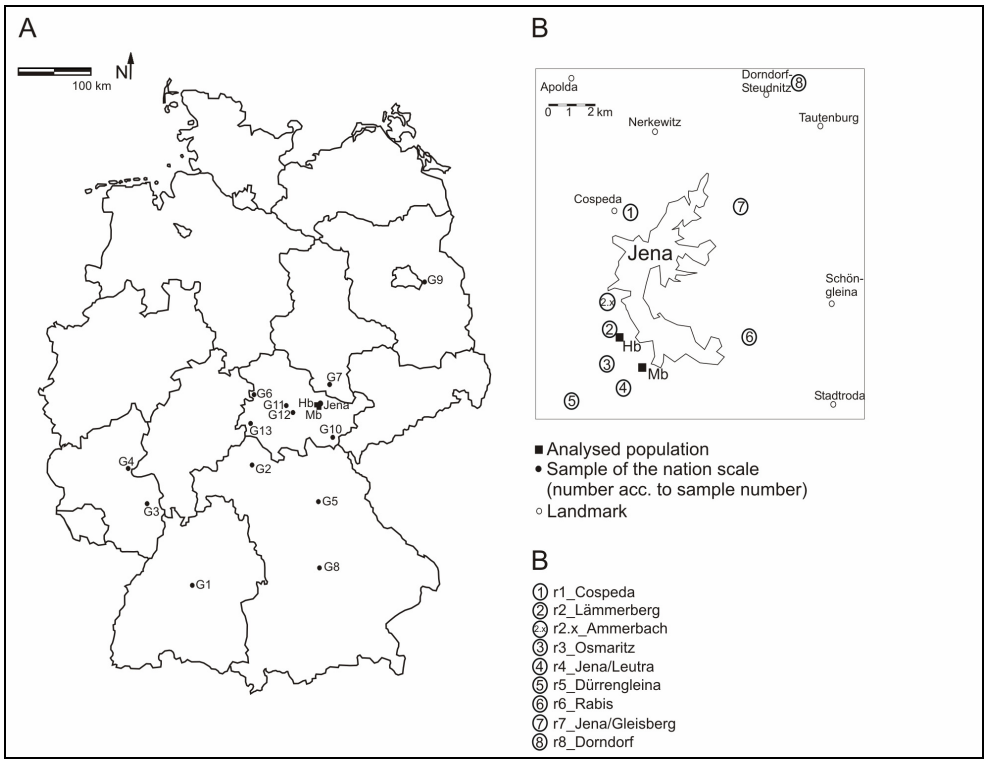


Fig. 14: Sampling localities of *Abietinella abietina* in Germany.
A gives an overview of the plot localities Hb, Mb and localities of the other German samples. **B** shows the sampling localities of regional samples in East Thuringia.

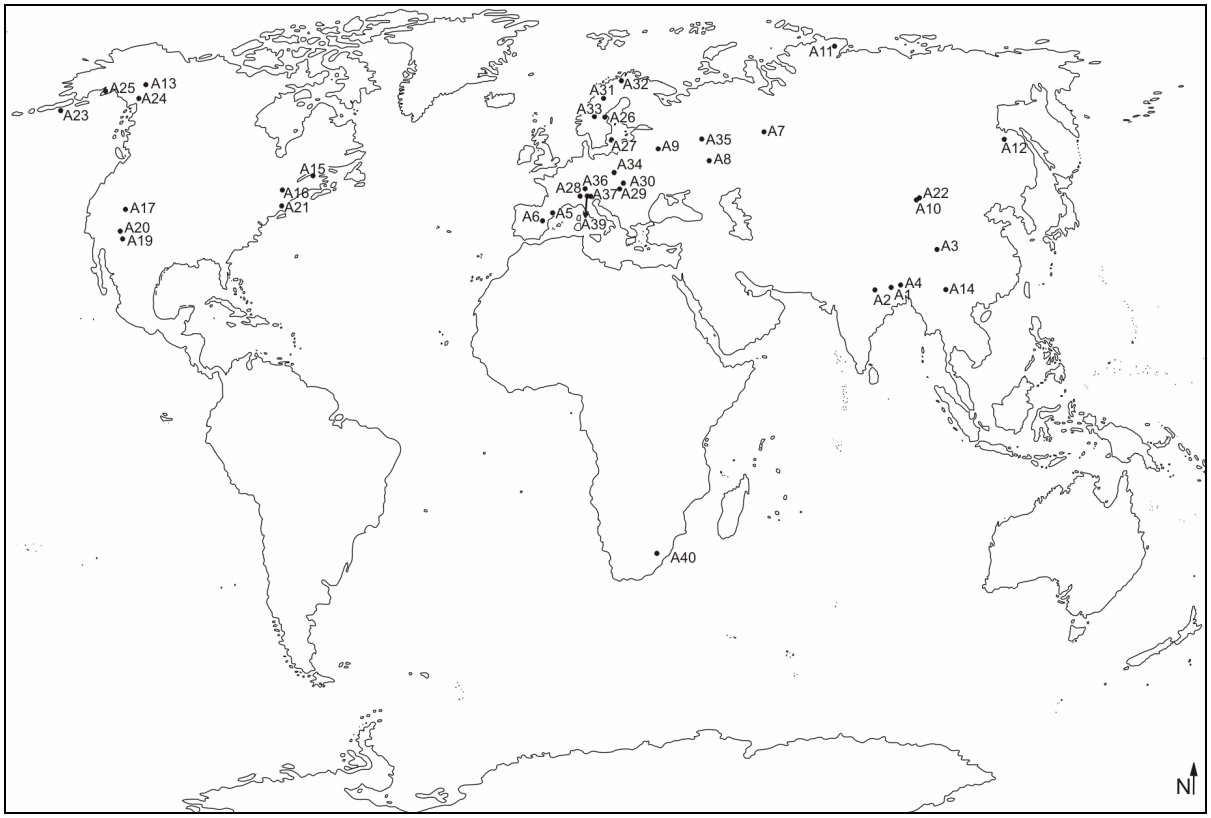


Fig. 15: World-wide analysed samples of *Abietinella abietina*.

Fig. 16: Sampling localities of *Homalothecium lutescens* in Germany.
A gives an overview of the plot localities Hb, Mb and localities of the other German samples. **B** shows the sampling localities of regional samples in East Thuringia.

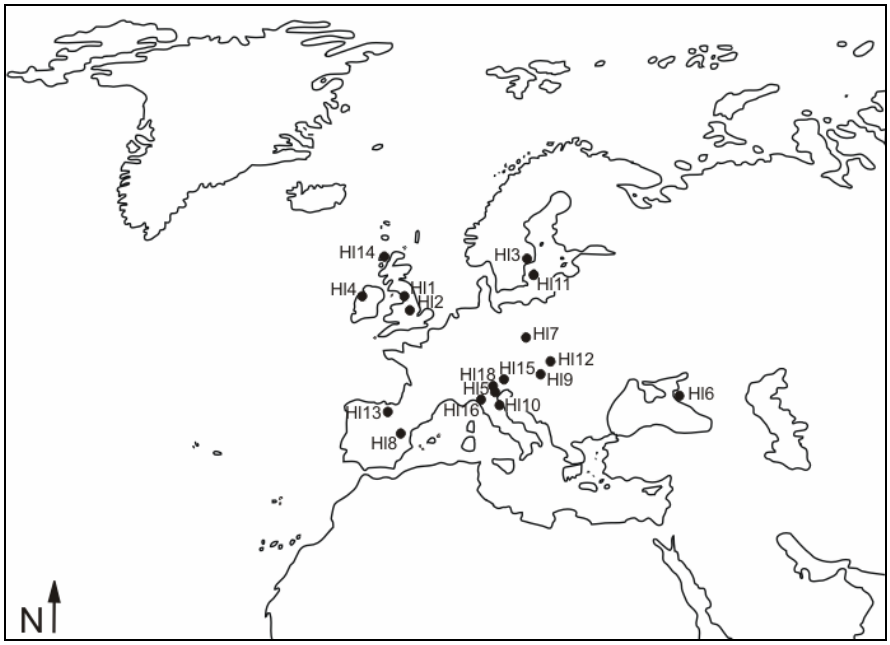


Fig. 17: World-wide analysed samples of *Homalothecium lutescens*.

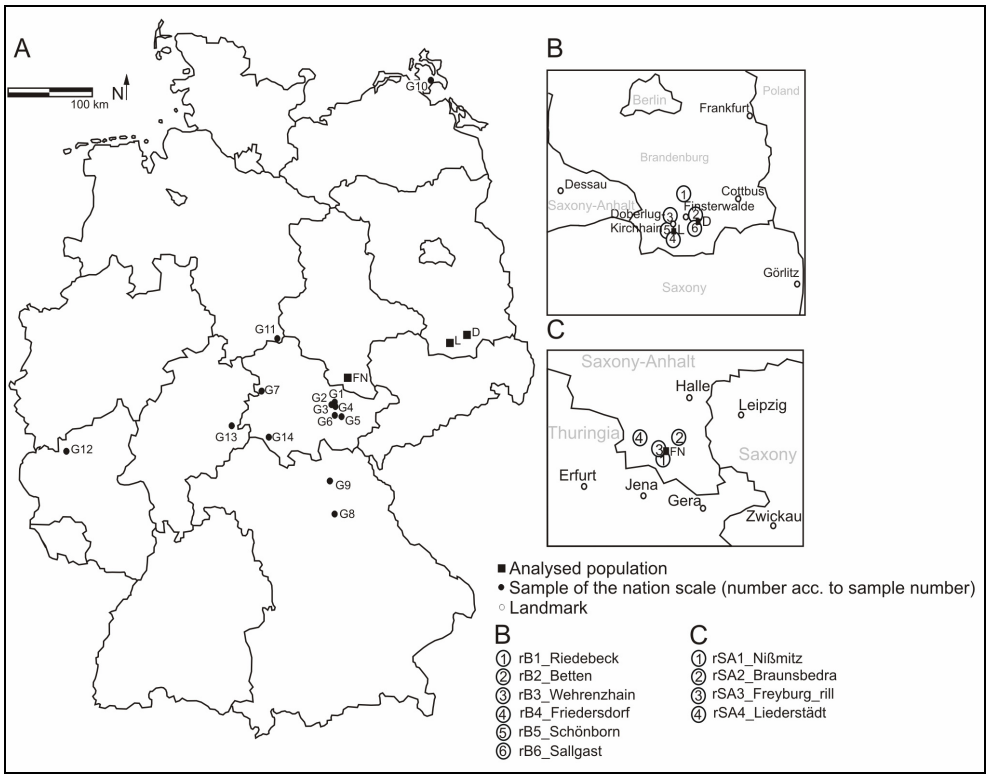


Fig. 18: Sampling localities of *Homalothecium sericeum* in Germany.
A gives an overview of the plot localities FN, L, D and localities of the other German samples. **B** shows the sampling localities of regional samples in Brandenburg and **C** illustrates the sampling localities of regional samples in Saxony-Anhalt.

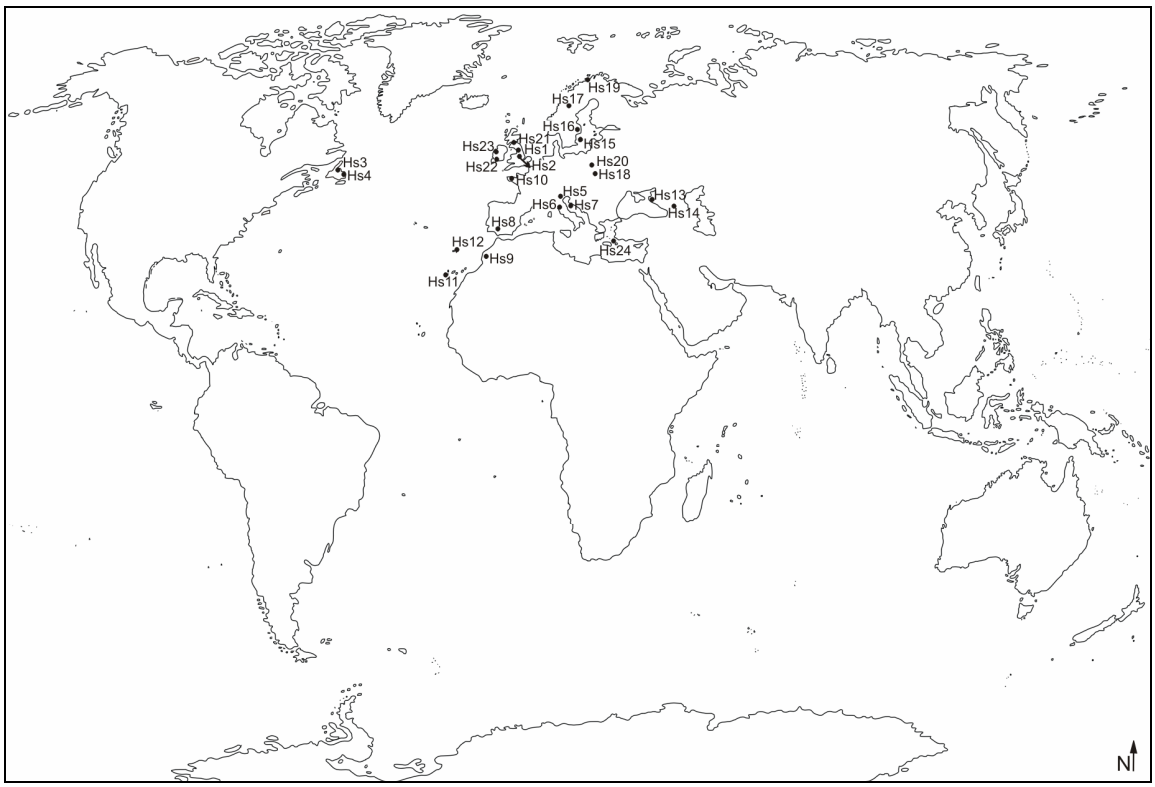


Fig. 19: World-wide analysed samples of *Homalothecium sericeum*.

4.1.1.3 Acquisition of reference samples for the determination of genetic diversity

The reference specimens were collected from three scales. The sampling of the regional specimens took place during the inspection of the regions which had typical environmental conditions for those species. According to MARSTALLER (1980) especially regions of the Muschelkalk slopes with southern exposition are advantageous for *A. abietina* and *H. lutescens*.

For sampling in the field in Thuringia the distribution maps of MEINUNGER (1992) and for Brandenburg the data reported by OTTE (2002) regarding the occurrence of *H. sericeum* were useful. The collected samples were air-dried and stored in paper bags. Furthermore, the geographical data of the areas were noted. Besides the self collected samples, the majority of the samples from the German distribution area, as well as the world-wide samples were obtained from herbaria (Appendix 1).

Additionally, two samples of *H. aureum* were analysed with the world-wide sample set of *H. sericeum*. One sample of each *H. aureum*, *H. philippeanum* and *H. fulgescens* was analysed with the world-wide sample set of *H. lutescens*.

4.2 Morphological analysis

The morphological analyses were carried out along with the cleaning of the plant material (cf. chapter 4.3.1) using a stereomicroscope (Wild M3C with cold-light source Leica KL 750, used magnification from 25x to 40x). The morphological study focused on the detection and description of the mechanisms of vegetative reproduction s.l. (cf. Table 2) and the characteristics of generative reproduction in each of the analysed species.

Plant fragments of both, field-collected as well as herbarium material, were analysed with a stereomicroscope.

Abscission zones (for example between shoot and branch, within shoot, detached shoot and branch apices) and conspicuously structures were examined in detail with scanning electron microscopes (Leo 430). The preparation of wet plant material was done with forceps, a razor blade (for prepare cuts) and a stereomicroscope.

The prepared part of plants were, after drying on absorbent paper, pasted with forceps on double faced adhesive tape on a aluminium table (Ø 13 mm).

Further the loaded tables were sputtered two times for 200 seconds at 40 mA with gold in a sputter (SCD 050, Balzers). Between both sputtering steps, the sputter was opened and the tables were rotated by an angel of 180° to distribute the gold particles equal. The observations with the scanning electron microscope (SEM) were saved as digital images.

4.3 Molecular analyses - AFLP-fingerprinting

4.3.1 Assortment and preparation of samples

Except for the samples of *A. abietina* from South Africa and *H. sericeum* from North America, only samples were used for the molecular analyses, which were not older than ten years (cf. Appendix 1).
The first apical section with ca. 10–14 green branches of one collected plant per sample was soaked and shacked in a little screw top jar, filled with deionised water, to separate contaminates as e.g. soil, parts of fungi, pollen or algae. With sterile forceps the branches were thereafter transferred into a Petri dish filled with deionised water. The branches were cleaned from all visible contaminations with two sterile forceps and use of a stereomicroscope (Wild M3C with cold-light source Leica KL 750, used magnification from 25x to 40x). In this process the water was changed several times. Extreme mouldy or dirty parts were abolished. The cleaned plant material was wrapped in absorbent paper and stored in Silica Gel Orange (Roth).

4.3.2 Isolation of DNA

In this study the total genomic DNA was isolated by using the NucleoSpin® Plant extraction kit (Macherey-Nagel-Inc., Easton, PA, USA). Unless otherwise noted, the procedure was conducted as described in the protocol of the kit (Appendix 15).
To homogenise a sample, a 2 ml Eppendorf-Tube was filled with the prepared silica gel-dried plant material with sterile forceps. Additionally two sterile steel balls were put into the tube. The filled tubes were shaken for 3 min at 30 Hz, using a mixer mill MM200 (Retsch), so that the plant material was triturated to a homogenous powder.
For cell lysis 400 µl of C0 [warmed to 45°C in a water bath (GFL 1003)] was added to the same tube (in case of damaged tubes, a new tube was used). The closed tube was inverted repeatedly by hand to form a suspension, and then incubated at 60°C for 30 min in a water bath.
The filtration/clarification of lysate was done by centrifugation of the sample for 5 min at 11000 r/min (Eppendorf Centrifuge 5415C).
Three hundred µl (2 x 150 µl) of the clear lysate were transferred into a 1.5 ml Eppendorf-tube. The next three steps (DNA binding to silica membrane, washing and drying of silica membrane) were in accordance with the protocol.
The DNA was eluted with 75 µl or, with sparse insert of raw material, 50 µl CE-buffer to increase the DNA concentration.
RNA was digested (not embodied in the protocol) by incubation for 30 min at 37°C (Biometra TB1 Thermoblock) after addition of 2 µl Ribonuclease I”A” (USB; 0.5 µg/µl) per 100 µl DNA.

4.3.3 AFLP

The DNA templates were used for the following AFLP-analyses, which were conducted acc. to the protocol of PFEIFFER et al. (2005). The fingerprinting was carried out using a S2 sequencing gel apparatus (GIBCO BRL by Life Technologies Whatman Biometra).

In deviation from the protocol the restriction cocktail contained 2.5 µl 10x OnePhorAll buffer (Amersham Biosciences), two restriction enzymes [0.25 µl *Eco*RI (1U/0.1 µl), 0.15 µl *Tru*1I (= *Mse*I; 1U/0.1 µl) (MBI Fermentas)], 19.6 µl deionised H_2O and 2.5 µl of diluted DNA aliquots (30–100 ng/µl). After incubation for 3 h at 37°C (Biometra TB1 Thermoblock) the 5 µl ligation mix [0.5 µl double-stranded *Eco*RI-adapter (5 pmol/µl), 0.5 µl double-stranded *Tru*1I-adapter (50 pmol/µl; Roth), 0.25 µl T4 DNA Ligase (~2 U; EPICENTRE), 0.25 µl ATP (25mM: EPICENTRE), 0.5 µl 10x T4 ligase buffer (EPICENTRE), 5 µl deionised H_2O] was added to the digestion sample.

After the overnight incubation at room temperature, two PCR steps were performed in a Biometra Tpersonal thermocycler.

Primers were used from Roth, all other PCR reagents from PeqLAB.

The cocktail for the preselective amplification contains 0.375 µl each of *Eco*RI+A (5´-GAC TGC GTA CCA ATT C**A**-3´) and *Mse*I+C (5´-GAT GAG TCC TGA GTA A**C**-3´) (50 ng/µL), 1.25 µl 10x PCR-buffer (Y), 0.25 µl dNTP-mix (2.5 pmol/µl each of dATP, dGTP, dCTP, dTTP; Roth), 0.125 µl *Taq* polymerase (5 U/µl), 6.125 µl deionised H_2O and 2.5 µl 5x Enhancer Solution P. To this mix 1.5 µL DNA template from the digestion/ligation solution were added, the samples were overlaid with 10 µl Chill-Out 14 Liquid Wax (MJ Research). After a preselective PCR (cf. parameters in Pfeiffer et al. 2005) the samples were diluted 1:9 with deionised H_2O.

For the selective amplification nine primer combinations (each primer with two additional bases compared with *Eco*RI+A and *Mse*I+C, one of them biotinylated at the 5´end) were tested with five samples of each species, to detect primer combinations with high levels of intraspecific polymorphism. Two primer combinations were selected for each studied species. For all species combination of 5'-biotinylated *Eco*RI+AAC [5'-GAC TGC GTA CCA ATT C**AAC**-3'] / unlabeled *Mse*I+CTT [5'-GAT GAG TCC TGA GTA A**CTT**-3'] were used for the AFLP-analyses. The second primer combination was in *A. abietina* unlabeled *Eco*RI+ATA [5'-GAC TGC GTA CCA ATT C**ATA**-3'] / 5'-biotinylated *Mse*I+CTA [5'-GAT GAG TCC TGA GTA A**CTA**-3'], in *H. lutescens* 5'-biotinylated *Eco*RI+AAC [5'-GAC TGC GTA CCA ATT C**AAC**-3'] / unlabeled *Mse*I+CGA [5'-GAT GAG TCC TGA GTA A**CGA**-3'] and in *H. sericeum* unlabeled *Eco*RI+ACC [5'-GAC TGC GTA CCA ATT C**ACC**-3'] / 5'-biotinylated *Mse*I+CTA [5'-GAT GAG TCC TGA GTA A**CTA**-3'].

The mix for the selective PCR contained 0.2 µl primer *Eco*RI-A**NN** (50ng/µl), 0.6 µl primer *Mse*I-C**NN** (50ng/µl), 0.4 µl dNTP mix, 2 µl 10x PCR-buffer (Y), 0.2 µl *Taq* polymerase (5 U/µl), 4 µl 5x Enhancer Solution P and 7.6 µl deionised H_2O. Further 5 µl of the diluted preselection PCR products were added to the cocktail and covered by 15 µl wax (cf. PCR parameters in Pfeiffer et al. 2005). After removing the liquid wax, 7 µl stop/loading buffer (EPICENTRE) was added to the selective PCR samples. Polyacrylamide gel electrophoresis was used to separate the DNA fragments of the selective

amplification. Polyacrylamide gels of 0.4 mm thickness were produced, which allowed the simultaneous run of 50 or 100 samples, resp.
Unlike the protocol of PFEIFFER et al. (2005), 6 µl of each PCR sample was loaded onto the gel for 50 samples and 3 µl onto the gel for 100 samples. Altogether, for each species and primer combination of the German sample set, two gels for the simultaneous run of 50 samples and one for the simultaneous run of 100 samples were generated. In the case of the world-wide sample sets, one gel was made for each species and primer combination for the simultaneous run of 50 samples.
One of the gels for the simultaneous run of 50 samples of the German sample sets was loaded with the samples of the population Hb and the second with the samples of population Mb, each for *A. abietina* and *H. lutescens*. For *H. sericeum*, the PCR samples of the region of Saxony-Anhalt and Brandenburg, resp., were separately loaded on one of the gels for the simultaneous run of 50 samples. The further German wide samples were arranged randomly and some samples were double loaded on both gels per primer combination to improve the simultaneous analysis of the two gels and a better determination of the position of the DNA fragments. In addition, one sample of each study species was analysed two times using different branches of the same shoot. For the German sample set, to facilitate the joint of two nylon membranes which covered 50 samples each (porablot NY amp, MACHEREY-NAGEL), a further gel of each primer combination, which covered 100 German samples, was generated.

4.3.4 Data scoring

The received AFLP fragments, which were blotted onto nylon membranes, were scored by eye. Presence (1) and absence (0) of bands were transferred into a binary matrix including monomorphic and polymorphic bands irrespective of their intensity. Monomorphic bands are present in all samples, whereas polymorphic bands are absent in at least one sample. Bands which could not be scored unambiguously were recorded as ambiguous and missing data (?), resp. The columns of the received binary matrices contained the samples and the rows the bands.

4.3.5 Data analyses

After import of the binary matrices into FAMD 1.108 beta (SCHLÜTER 2006), the matrices served as a base for calculating pairwise genetic distances (GD). The pairwise genetic distances were computed as complementary values of the calculated Jaccard´s similarity coefficients (SC_J) and Simple matching similarity coefficients (SC_{SM}):

$$GD = 1 - SC$$

$$SC_{J;ij} = \frac{n_{11}}{n - n_{00}} = \frac{n_{11}}{n_{11} + n_{01} + n_{10}}$$ (JACCARD 1908)

$$SC_{SM;ij} = \frac{n_{11} + n_{00}}{n} = \frac{n_{11} + n_{00}}{n_{11} + n_{01} + n_{10} + n_{00}}$$ (SNEATH & SOKAL 1973)

With n as the total number of scored bands, n_{00} as the number of absent, n_{11} the number of present bands, n_{01} as the number of absent bands in reference sample one (i) and n_{10} as the number of absent bands in reference sample two (j) (SNEATH & SOKAL 1973).

The Jaccard coefficient is unaffected by homoplastic absent bands (when the absence of the same band is due to different mutations), since the coefficient takes only those bands into account that are present in at least one of the two samples. The Simple matching coefficient on the other hand includes all scored bands (also double band absence) (BONIN et al. 2007).

FAMD 1.108 beta uses multiple estimates of similarity measures, based on random assignments of band presence-absence to the missing data. An interval of possible similarity values was calculated by using the number of pairwise comparisons that cannot be evaluated due to missing data. For example of Jaccard´s coefficient, the minimum and maximum values of Jaccard´s coefficient are defined, so that $SC_{J,\min} \le SC_J \le SC_{J,\max}$:

$$SC_{J\min;ij} = \frac{n_{11}}{n_{11} + n_{01} + n_{10} + n_{1?} + n_{?1} + n_{0?} + n_{?0}}$$

$$SC_{J,\max;ij} = \frac{n_{11} + n_{1?} + n_{?1} + n_{??}}{n_{11} + n_{01} + n_{10} + n_{1?} + n_{?1} + n_{??}}$$

$SC_{J,\min}$ and $SC_{J,\max}$ are differently affected by particular comparisons, e.g. 1-? comparisons affect $SC_{J,\max}$ if ?=1, and $S_{J,\min}$ if ?=0. Missing data predominantly scored as 0 would decrease $SC_{J,\max}$ and increase $SC_{J,\min}$. An estimate of the uncertainty introduced by missing data is computed by randomly drawing values of Jaccard´s coefficient that lie within the interval $[SC_{J,\min}; SC_{J,\max}]$ γ times. This enables estimation of the mean and variance of Jaccard´s coefficient (SCHLÜTER & HARRIS 2006, S. 570).

The received output values are the percentage of missing data points in each locus and in each individual (SCHLÜTER 2006).

Hence a similarity matrix was computed based on average similarities. Therefore the minimum and maximum similarity coefficients $S_{ij,\ min}$ and $S_{ij,\ max}$ were determined. The resulting average similarity

coefficient is defined as the arithmetic average of values drawn randomly (uniformly) from the interval $[S_{ij, min}; S_{ij, max}]$ (SCHLÜTER & HARRIS 2006, S. 570).

Based on calculated average distance matrices, dendrograms were constructed using the UPGMA (unweighted pair group method using arithmetic averages) and NJ (neighbour- joining) methods of FAMD. The Jaccard matrix, as well as the Simple matching matrix, was used to determine the bootstrap values (10,000 replicates and 1000 maxtrees, majority rule consensus threshold 50%).

For genotyping, a molecular threshold value for genet identity was identified from a histogram with pooled distance values (Douhovnikoff & Dodd 2003, Meirmans & Van Tienderen 2004).

The genetic structure was examined by an analysis of molecular variance (AMOVA) from distance matrices of Simple matching coefficients. This method is used to classify the genotypic variance within and among populations of each population (EXCOFFIER et al. 1992). The AMOVA analyses were also conducted by using FAMD software.

4.4 Reproduction biology

In the following subchapter an overview of the reproduction biology and colonisation in mosses is given. Knowledge of the reproduction characteristics is needed for the analyses of the clonal diversity and structure of bryophyte populations as well as for the understanding of processes of habitat colonisation and maintenance. In addition to the identification of the reproduction modes (cf. Table 2) and their relevance in life cycle, an understanding of dispersal ability is important.

4.4.1 Generative reproduction

Generative (sexual) reproduction leads to a recombination of the parental genomes (inter- and intrachromosomal recombination) and generates a wide range of new genotypes. Asexual spores, which are produced through selfing, form an exception (cf. Table 2). The genetic diversity is important for the adaptation to environmental change. Further, production of spores plays an important role in colony maintenance and expansion, in establishing new populations as well as in gene flow between populations (MILES & LONGTON 1990). The frequency of sporophyte production is different in monoicous and dioicous taxa. Since monoicous species has both male and female organs on the same gametophyte, such taxa generally reproduce sexually more frequently (e.g. Longton & Schuster 1983, During 2007). Rarity of sporophytes in many dioicous bryophytes is often associated with spatial segregation of sexes and skewed sex ratios (e.g. LONGTON 1976, LONGTON & SCHUSTER 1983, LONGTON 2006). Further, fertilisation of female eggs is only possible if plants bearing antheridia are in close contact to them, because spermatozoid dispersal distances only range up to <10 cm (except taxa that produce splash cups) (e.g. LONGTON 1976, 1997, WYATT 1982, LONGTON & SCHUSTER 1983, ≤34 cm BISANG et al. 2004).

4.4.2 Vegetative reproduction s.l.

Vegetative (asexual) reproduction s.l. comprises of vegetative reproduction s.str. and clonal reproduction (URBANSKA 1992, FREY & HENSEN 1995, FREY & LÖSCH 2004).
The vegetative reproduction s.str. takes place with fully specialised and/or ±specialised propagules (Table 2). The propagules are detached from the mother plant and do not resemble the mature plants at first (FREY & HENSEN 1995, FREY & LÖSCH 2004). Correns (1899) described the development and diversity of specialised propagules and regeneration from ±specialised caducous organs in mosses by comparing many species. The terminology for vegetative reproduction devices is inconsistent in literature (cf. LAAKA-LINDBERG et al. 2003). Vegetative reproduction s.str. is distinguished from fragmentation by development of differentiated abscission layers in the former, hence vegetative reproduction s.str. occurs along predetermined lines of weakness (SCHAUMANN 2005).

Clonal reproduction describes the separation and fragmentation of a genetic individual (= genet), by the destruction of the connecting structures (spacer) between modules, into ramets. Ramets, which are morphological and physiological independent units (dividuals) and genetically identical with the mother plant, result from forced (mechanical damage) or self-cloning (e.g. URBANSKA 1992, FREY & HENSEN 1995, FREY & LÖSCH 2004).

4.4.3 Dispersal

In the majority of mosses, meiospores are well adapted for dispersal by wind. Further dispersal agents are animals and water. A distinction is drawn between short range and long range dispersal (≥300 km, SCHUSTER 1983). Thereby, spores less than 20 µm (≤25 µm, VAN ZANTEN 1978) in diameter are most suitable for long range dispersal by wind. Larger spores are rather dispersed within a few metres of the parent plant (DURING 1979). During (2007) expected that successful germination and establishment is positively related to spore size. By contrast, the foundation of new populations would require successful dispersal, which might be favoured by the production of larger numbers of small spores.

In addition, the dispersal range depends on habitat structure (e.g. tree crowns or shrubberies are obstructive) and humidity (FRAHM 2001). Vegetative diaspores s.l. are dispersed over shorter distances, but dispersal in medium or longer distances is also possible. Moreover, especially animals play an important role in dispersal of vegetative bryophyte diaspores (e.g. FISCHER et al. 1996, HEINKEN 2000, HEINKEN et al. 2001). Besides the dispersal in space, a dispersal through time is also possible by regeneration from diaspores of diaspore banks (e.g. DURING & TER HORST 1983).

4.4.4 Colonisation

The following ecological differences between vegetative diaspores s.l. and spores were reported by NEWTON & MISHLER (1994): vegetative diaspores disperse mostly locally, germinate relatively better than spores in already colonised substrates and can be produced under more stressful conditions; spores require fertilisation, disperse farther and germinate best in previously uncolonised habitats. Further, the establishment of meiospores in field was only seldom observed (e.g. MILES & LONGTON 1990, CRONBERG et al. 2006, LONGTON 2006) compared with the establishment from fragments of gametophytes (e.g. HEINKEN & ZIPPEL 2004, KIMMERER 1994, 2005). The rare observation of spore establishment could be explained by difficulties in detection (MILES & LONGTON 1990). In general, liberation of generative as well as vegetative diaspores s.l. is crucial for the establishment of new populations as well as the maintenance of existing populations (LAAKA-LINDBERG et al. 2000). However, vegetative diaspores maintain colonies more effectively, whereas spores are more important for establishing new colonies (e.g. MILES & LONGTON 1990, NEWTON & MISHLER 1994).

Table 2: Reproduction modes in bryophytes (after Frey & Kürschner pers. comm., based on LONGTON & SCHUSTER 1983, PFEIFFER 2003 and SCHAUMANN 2005)

- **Generative reproduction through sexually produced spores (meiospores)**
- Special case: reproduction with asexual spores; spores produced sexually after selfing, asexual clone selfing or spore clone selfing between genetic identical individuals (NEWTON & MISHLER 1994)
- **Vegetative reproduction s.l.**
  - **1) Vegetative reproduction s.str. (with ±specialised propagules)**
    - a) Regeneration from ±specialised caducous organs (stems, branches, leaves etc.)
      - Leaves and leaf apices
        - Caducous leaves (complete, normal leaves)
        - Brood leaves (differentiated from normal leaves)
        - Caducous leaf apices (leaves with abscission layer in upper part)
        - Leaf fragments (leaves break along predetermined lines into random fragments)
      - ±Specialised branches and stems (caducous defined stem and thallus parts)
        - Caducous shoot apices (often little modified)
        - Caducous branchlets (condensed and deciduous branches in leaf axils)
        - Caducous flagelliform shoots (attenuate branches with vestigial leaves, in leaf axils)
        - Bulbils (highly condensed, with leaf primordia)
        - Cladia (small branches developing on leaves)
        - Caducous perianths
    - b) Production of specialised propagules
      - Protonemal brood cells
      - Brood bodies, gemmae
        - Protonemal gemmae (gemmiferous protonema)
        - Gemmae s.str. (produced on various parts of the gametophyte, e.g., laminar, coastal, axillary, cauline, gametangial or endogenous gemmae)
        - Rhizoidal tubers and rhizoidal gemmae
  - **2) Clonal reproduction**
    - a) Production of numerous buds on the protonema of single spore. Several gametophytes are produced and separated by the decay of the protonema.
    - b) Decay of older gametophyte parts leading to disjunction of the younger parts
    - c) Development of new aerial shoots from stoloniferous or rhizome-like subterranean shoots
    - d) Initiation of aerial gametophytic shoots on parts of the rhizoid system (rhizoid wicks)
    - e) Production of basitonic innovation plants in cauline position
    - f) Innovation from shoot or branch buds. Primordia, which are regularly produces in many mosses but normally remain dormant (FREY 1974).
    - g) Unspecialised fragmentation of gametophytes

5 Results

5.1 Structure of the study area

5.1.1 Holzberg and Mönchsberg near Jena

Abietinella abietina and *H. lutescens* were studied in two populations from East Thuringia, Holzberg (with the three plots HbI, HbII and HbIII, for both species) and Mönchsberg (MbI was analysed for both species and MbII only for *A. abietina*) near Jena. The results of the vegetation relevés of the plots Hb and Mb are shown in Appendix 2. Maps which display the structure of the study areas can be found in Appendices 4+6 (Hb) and 5+7 (Mb), resp.

All three plots of the Holzberg are more or less open and characterised by rather low vegetation coverage (≥60%) on rubble and very little soil. One metre above the plot HbI several *Juniperus communis* shrubs grow (not mapped) and a further scrub grows on the plot (D3). Near this scrub (D3) the ground was densely covered with mosses (mainly *A. abietina*, *H. lutescens*, but also *Rhytidium rugosum*). Several small *Prunus spinosa* shrubs grow on the plots HbI and HbII. *Abietinella abietina* occurs more common on the plot HbII than on HbIII. In the case of *H. lutescens* the density of coverage is vice versa.

The best developed soil layer, with a thickness of ca. 2 cm and a high diversity of plant species (Appendix 3), was found on MbI. This plot also shows a high coverage of vascular plants (≤100%) whereas particularly one *Clematis vitalba* plant stood out because of their dimension (at least 9 m²). In contrast, MbII is dominated by mosses which achieve a high coverage (≤80%) on rubble and very little soil. Eastwards the plot MbII is bordered by several shrubs. Both plots are separated by a ca. 6 m wide rubble band with little vegetation.

The habitat of Hb is more ancient and natural than the habitat of Mb. In former times the habitat of the population Mb is characterised by exploitation of limestone and was on the other hand used as a training area for the police of the former GDR.

On all analysed plots *A. abietina* and *H. lutescens* grow in numerous patches of variable dimensions and coverage. The spatial distribution of the patches in the analysed plots is shown in Appendices 4+6 (Hb) and 5+7 (Mb), resp. The dimensions of the patches vary from few centimetres to many decimetres. The largest patches of *A. abietina* were found in HbI (patch HbI_58) and MbII (patch MbII_1) with a diameter of ca. 1 m. In contrast to patch MbII_1, a large area of sparse coverage of *A. abietina* was observed for patch HbI_58. For *H. lutescens* the largest patch (patch HbI_22, with the same location as HbI_58) was detected at HBI with a diameter of >1 m. The highest number of single plants and loose plant fragments of both species were found in HbI, in the area with the most patches (*A. abietina*: C2–C3, D2–D3, E2–E3; *H. lutescens*: C1–C3, B2–B3). Apart from these findings, loose plant fragments occurred scattered.

5.1.2 Freyburg (Neuenburg), Lindena and Dollenchen

Maps which show the structure of the study areas of *H. sericeum* (FN, L, D) as well as their vegetation relevés can be found in Appendices 2+8–10, resp.

In Freyburg (Neuenburg) most soil accumulates on wall sections with carves and on stones with chipped off pieces, whereas even and bare limestones are not covered with soil. In Lindena and Dollenchen soil accumulation is missing at the analysed sections of the cobblestone walls. Generally, vascular plants mainly grow in carves at the vertical side of the wall. However, in FN the top of the wall is colonised too. Of all three studied locations, the wall in FN shows the highest coverage and diversity of plant species. An accumulation of seedlings from *Tilia cordata* grows on the top of the wall in the region of the mature tree. The tree is located in front of the wall. In the area between 23.5–24.2 m faeces of rodents were observed. In contrast, the examined walls in Brandenburg are species-poor and, with the exception of *H. sericeum*, sparsely colonised.

The analysed part of the limestone wall in FN is partially completely covered with the moss *H. sericeum* (at 6–11.3 m and 25.7–30 m). In the crown projection area of *Tilia cordata* the coverage of vegetation decreases almost to 0% at the top of the wall. The dimensions of the patches vary from few centimetres to several metres. Among all studied areas the largest patches were observed in FN. Here, the largest mapped

patch (FN_11) reaches ca. eight meters in length. On the plots LII–IV in Lindena only one larger patch exists. Patch LV_4 was the largest patch found, with a diameter of >4 m. As illustrated in Appendix 9, *H. sericeum* shows a widespread sparse coverage in patch LV_4. In Dollenchen the largest patch reaches a diameter of 1 m (patch D_8).

Loose single plants and plant fragments of *H. sericeum* were rarely observed outside the patches, with the exception of plot LIV and LV in Lindena. During the mapping of the sample area and the collecting activity, it was conspicuous that plant fragments were easily detached from patches and attached to clothes.

5.2 Morpho-anatomical analyses

5.2.1 Generative reproduction

5.2.1.1 *Abietinella abietina*

The overall number of samples with sex organs was 12.3%, with identified 10.7% female and 1.6% male plants, pooled over 122 sampling data (see Table 3). No gametangia were detected in the population of Hb. In the population of Mb only samples with archegonia were found. Among all analysed samples, antheridia were only detected in two foreign samples (A27_Sweden and A35_Russia).
The morpho-anatomical analyses of all samples of *A. abietina* (84 German and 38 foreign samples) and the observations of the study areas revealed no hints on present or past generative reproduction in the form of sporophytes or remnants of those.

5.2.1.2 *Homalothecium lutescens*

29.2 % of the 113 samples of *H. lutescens* were sexual (fertile) plants, with identified 27.4% female and 1.8% male plants (Table 3). In the studied population Hb one antheridia- and five archegonia-bearing plants were found out of 51 samples. In the population Mb, eight out of 22 analysed samples in total were archegonia-bearing plants. In all samples, only two male plants were found, one in the population Hb (Hb_surr_480) and the other in the sample r7_Jena/Gleisberg. Sporophytes were detected only in two samples from Spain (Hl8_Spain and Hl13_Spain).

5.2.1.3 *Homalothecium sericeum*

In all 110 studied samples of *H. sericeum* 57.3 % sexual plants were found (Table 3). Most sexual individuals were in the population of FN, with 20 archegonia-bearing plants out of 30 studied samples. Antheridia-bearing plants were found in Brandenburg (r2_Betten), Thuringia (G4_Zimmritz, G7_Schnellmannhausen), Mecklenburg-Western Pomerania (G10_Rügen) and the British Isles (Hs1_England,

Hs21_Scotland, and Hs23_Ireland). Sporophyte-bearing plants were only detected in the paper sample bag of G10_Rügen, Hs10_France and Hs21_Scotland.

Table 3: Percentage of detected sexual and asexual samples and samples with sporophytes on the population, regional, Germany-wide and world-wide scale in *Abietinella abietina*, *Homalothecium lutescens* and *Homalothecium sericeum*

	% of sexual samples (♀/♂)	% of asexual samples	% of detected samples with sporophytes
Abietinella abietina			
Hb	0	100	0
Mb	9.1 (9.1/0)	90.9	0
regional	7.0 (7.0/0)	93.0	0
total (Germany-wide)	9.5 (9.5/0)	90.5	0
total (world-wide)	12.3 (10.7/1.6)	87.7	0
Homalothecium lutescens			
Hb	11.8 (9.8/2.0)	88.2	0
Mb	36.4 (36.4/0)	63.6	0
regional	19.3 (16.9/2.4)	80.7	0
total (Germany-wide)	22.9 (20.8/2.1)	77.1	0
total (world-wide)	29.2 (27.4/1.8)	70.8	1.8
Homalothecium sericeum			
FN	66.7 (66.7/0)	33.3	0
L	52.6 (52.6/0)	47.4	0
D	66.7 (66.7/0)	33.3	0
regional SA	61.8 (61.8/0)	38.2	0
regional B	55.9 (52.9/2.9)	44.1	0
total (Germany-wide)	59.5 (54.7/4.8)	40.5	1.2
total (world-wide)	57.3 (50.9/6.4)	42.7	2.7

5.2.2 Vegetative reproduction s.l.

5.2.2.1 *Abietinella abietina*

The morpho-anatomical analyses of the vegetative reproduction s.l. yielded that in almost all specimens several shoot parts were absent and could mostly not be found in the paper sample bag (cf. Table 4). Occasionally a lack of shoot apices (main shoots and/or apices from branches with indeterminate growth) was observed.
The number of missing gametophyte parts differed between green and decaying sections. On the green sections of the shoots, as well as on branches with indeterminate growth, up to ten branch apices (mean 1.8±2.5), and up to eleven fragments of branches (mean 1.8±2.6), out of a mean of 29.3±37.9 branches in total, were detached. On the decaying parts up to 24 branch apices (mean 3.5±5.6) and up to 17 (mean 3.7±4.8) fragments of branches, out of a mean of 21±27.1 branches in total were missing.
Occasionally, branches with abruptly thinning apical branch sections were found (flagelliform branches, 6–20 mm, mean 10.7±6.1 mm). On the decaying parts of the plants, thinning branches with rhizoids at apices were frequently observed.
During the morphological examinations (a) decay of older gametophyte parts, (b) brood branches/branchlets sensu Correns (1899), (c) caducous shoot apices sensu CORRENS (1899), (d) unspecialised fragmentation of gametophytes and (e) caducous leaves (with basal rhizoids) sensu CORRENS (1899) were identified.

(a) Decay of older gametophyte parts
One of the dominate modes of clonal reproduction in *A. abietina* is the decay of older gametophyte sectors, so that younger sectors lose contact with the mother plant and (older) shoot parts were subsequent disintegrated.
This process results in vegetative multiplication (Longton & Schuster 1983). *Abietinella abietina* has pinnately arranged determinate branches and develops, in some distance of the parent shoot tip, branches with indeterminate growth which develop pinnately arranged determinate branches on their part. Frequently, plants with an accumulation of branches with indeterminate growth in the green apical part

of the plant were observed. Almost all analysed samples showed dead basal shoot sections (0–8.7 cm, mean 2±2.4 cm), followed by decaying (0–4 cm, mean 1.4±1 cm) and young green parts (0–2.8 cm, mean 1.2±0.7 cm). The decaying parts could include one or more successive indeterminate branches. The dead parts were very fragile, dark in colour and partly leafless. The also dark in colour and partly leafless branches in the dead section of the shoots were totally or at least partly detached. Sometimes, at the black and older basal shoot parts, young green buds or branches were observed. In some cases, decaying was detected in young and green shoot sectors. These localised areas showed sometimes rhizoids and were brown in colour (Fig. 20). Repeated decaying results in loose wefts with highly fragile, intertwining shoot systems. The disintegration of shoot parts leads to separation of ramets.
Due to the small dimensions of the leaves, branches and shoot apices (see Table 4), only larger fragments, such as shoot fragments with several branches, could be detected during the fieldwork (cf. Appendices 4-5). The abscission zones of larger plant fragments were mostly black and encapsulated, which could be interpreted as result of a decaying event.

(b) Brood branches/branchlets sensu CORRENS (1899)
Brood branches with reddish to brownish and mostly annular arranged rhizoids at the base of branches with indeterminate growth were occasionally observed (Figs. 21+22). Usually, only reddish to brownish colour at the base of branches with indeterminate growth could be detected. The analyses with a scanning electron microscope (SEM) could not identify a (pre)determined fracture line for the abscission zones of brood branches (Fig. 21).

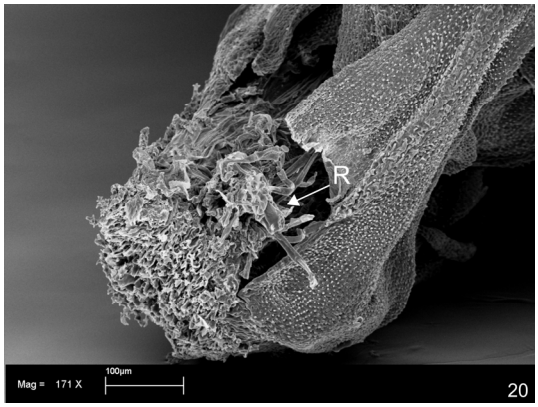
(c) Caducous shoot apices (with basal rhizoids) sensu CORRENS (1899)
Loose shoot apices were rarely found in the dry plant material. Branch apices were frequently detected. The bases of the shoot apices were mostly green, which can be interpreted as a result of fragmentation [see below (d)]. Sometimes bases with reddish to brownish colour were observed. Only once a caducous shoot apex with rhizoids at the base was detected separately in the dry plant material (Fig. 23). Those rhizoids had developed in the central part of the abscission zone.

(d) Unspecialised fragmentation of gametophytes

Fragmentation of the gametophyte is a main mode of clonal reproduction in *A. abietina.* In the paper bags with the dried samples, detached leaves, branches (Fig. 24), branch fragments, shoot and branch apices (Fig. 25) and shoot fragments were frequently detected. Otherwise branches, branch fragments, in some cases upper shoot parts or shoot apices in the green young and decaying part of the analysed samples were absent. The abscission zones were of fresh green colour, uneven and rhizoids were missing. Sometimes the fragmentation of the material was probably caused by handling and drying. During cleaning of specimens it was frequently observed, that plant structures disconnect easily.

(e) Caducous leaves (with rhizoids) sensu CORRENS (1899)

Frequently, detached leaves of green colour were found in the dry plant material. The detachment was mostly caused by fragmentation. Loose caducous leaves with rhizoids at base were very rarely detected (Fig. 26).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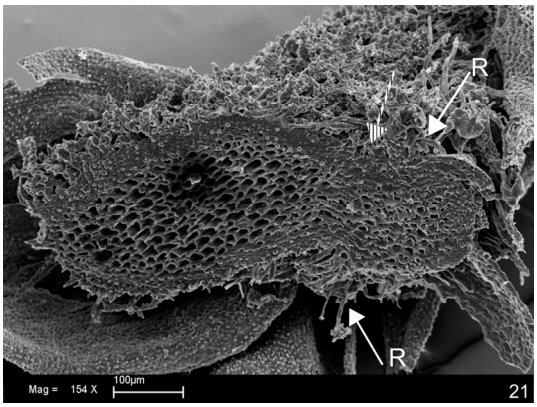
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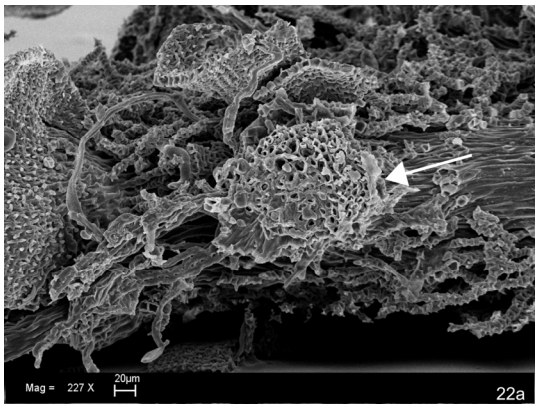
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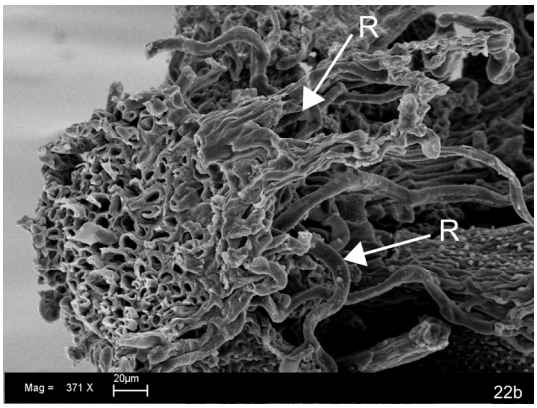
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R
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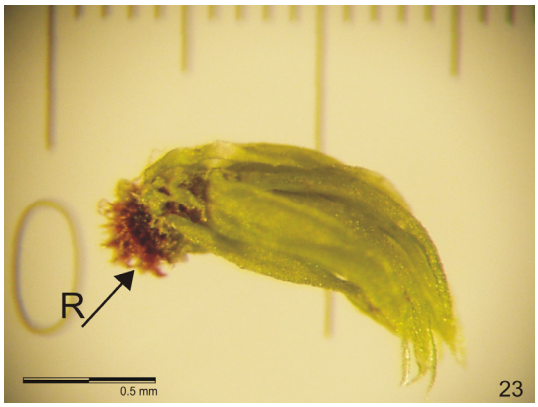
R
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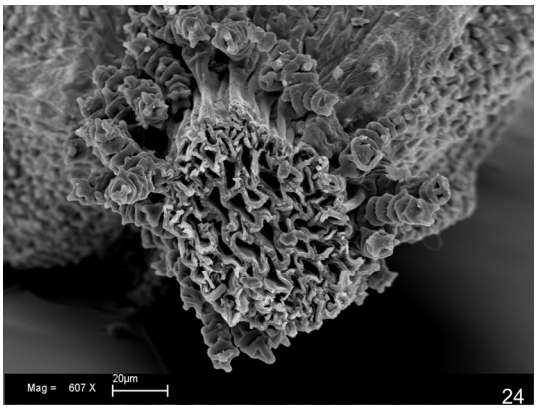
23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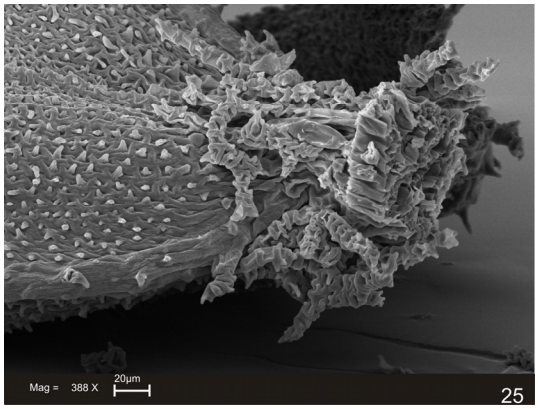
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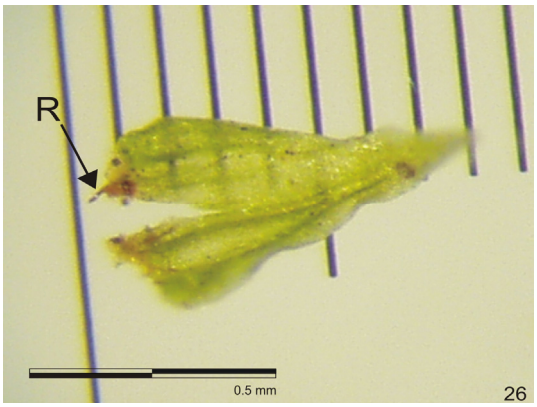

R
0.5 mm
26

Fig. 20: Basal part of detached main shoot with rhizoids, after decaying in a confined zone within green section of main shoot of *Abietinella abietina*, (R) (SEM-photo).

Fig. 21: Cross section through potential abscission zone (marked by striped arrow), main shoot (left) and brood branch/branchlet (right) of *Abietinella abietina*. Basal branch part shows rhizoid growth (R) (SEM-photo).

Fig. 22: Brood branch/branchlet of *Abietinella abietina*. (a) Main shoot after detachment of brood branch (marked by arrow) (SEM-photo). (b) Basal part (abscission zone) of brood branch with rhizoids (R) (SEM-photo).

Fig. 23: Caducous shoot apex of *Abietinella abietina* with well-developed rhizoid growth (R) (photo).

Fig. 24: Basal part of detached branch of *Abietinella abietina* after fragmentation (SEM-photo).

Fig. 25: Base of shoot apex of *Abietinella abietina* after fragmentation (SEM-photo)

Fig. 26: Caducous leaf of Abietinella abietina with beginning rhizoid growth (R) (photo).

5.2.2.2 *Homalothecium lutescens*

The morpho-anatomical analyses of the vegetative reproduction s.l. yielded that in most of the studied samples several structures were absent (branches, apices as well as branches from shoots, shoot parts; cf. Table 4). Often the missing parts could not be found in the dried sample material. A lack of shoot apices (main shoots and/or apices from branches with indeterminate growth) was often observed as well.

Like *A. abietina*, the number of missing gametophyte parts differed between the green and the decaying sections. In the green section of the shoots, as well as on branches with indeterminate growth, up to 23 (mean 2.7±5) apices of branches and up to nine (mean 1.1±1.9) branch fragments, out of a mean of 17.1±15.4 branches in total, were missing. The decaying section showed up to 20 (mean 6±5.3) apices of branches and up to ten (mean 2.3±2.5) branch fragments, out of a mean of 16.8±11.1 branches in total, were detached.

The following vegetative reproduction modes s.l. were identified in *H. lutescens*: (a) decay of older gametophyte parts, (b) brood branches/branchlets sensu CORRENS (1899), (c) caducous shoot apices (with basal rhizoids) sensu CORRENS (1899) and (d) unspecialised fragmentation of gametophytes.

(a) Decay of older gametophyte parts

Decay of older shoot sections is a very important mode of clonal reproduction in *H. lutescens*. The gametophytes showed frequently a young and green section (0–3.5 cm, mean 0.8±1.1 cm in length) followed by a decaying section (0–4.7 cm, mean

1±1.2 cm in length) and an old and dead section at the base (0–5.2 cm, mean 1.7±1.3 cm in length). The latter section frequently included more than one successive branch with indeterminate growth. The dead sections of the shoots were brownish to black, fragile and partly leafless.

The shoot consists of multiple segments, since the parent shoot develops two apices. One of the two apices develops to a branch with indeterminate growth, which becomes the main shoot. This type of branching is repeated several times and can be considered as clonal growth. Further branches with indeterminate growth and determinate branches were frequently found lateral at all plant sections. Because of the fragility of the dead section, nearly all branches in the decayed parts were total or at least partly detached. Limited areas of decay were also found at otherwise young and green sections (Fig. 27). Disintegration of shoots caused by decay or fragmentation [see below (d)] lead to development of ramets.

(b) Brood branches/branchlets sensu CORRENS (1899)

At the bases of some branches (Fig. 28) and often at laterally branches with indeterminate growth (Fig. 29), a brownish to black colour with annular arranged rhizoids were observed. Analysis with a scanning electron microscope (SEM) revealed (pre)determinated fracture lines at the abscission zones of brood branches at the cortex (Fig. 30).

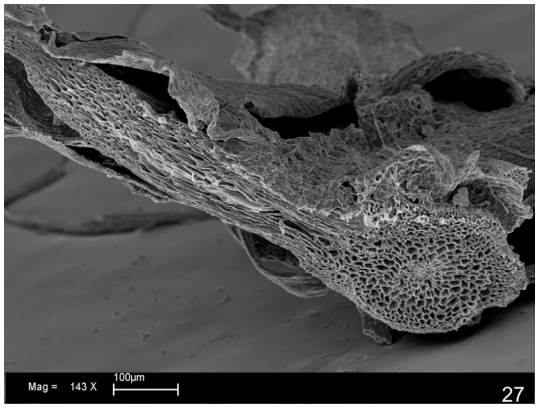
(c) Caducous shoot apices (with basal rhizoids) sensu CORRENS (1899)

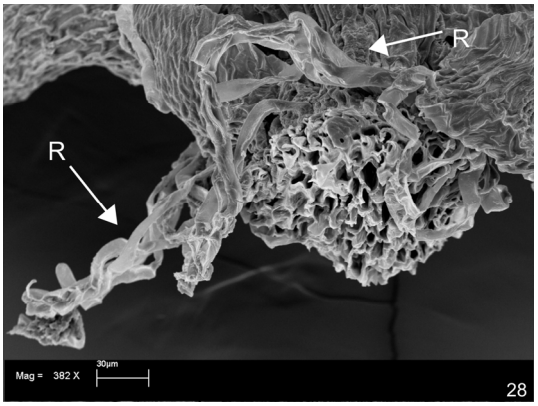
Very seldom and only in dry plant material separately caducous shoot apices could be detected. The base of the apices was black and rhizoids developed at the central part of the abscission zone (Fig. 31). Frequently, detached shoot and branch apices with a brownish to black coloured base, but without rhizoids, were found.

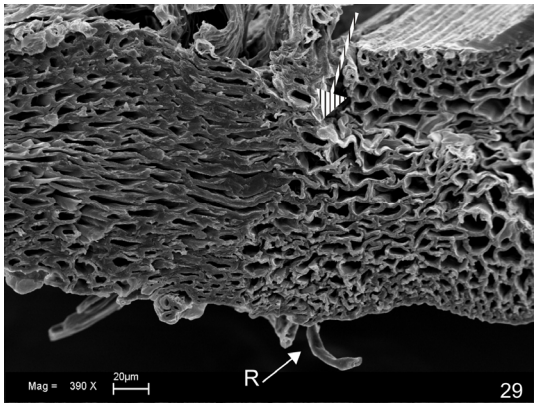
(d) Unspecialised fragmentation of gametophytes

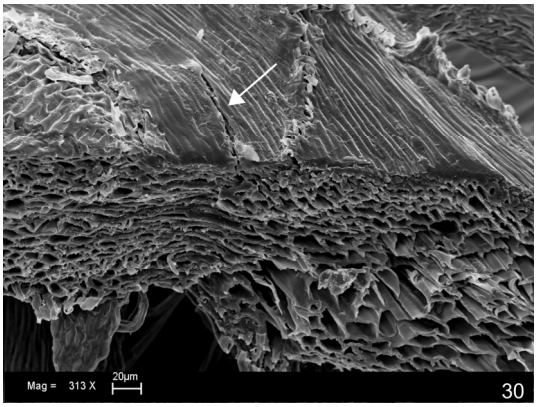
Despite the robust structure of plants, fragmentation is a common mode of clonal reproduction in *H. lutescens*. Most of the absent branch fragments, shoot apices (Fig. 32) and branch apices were detached by fragmentation. Fragmentation within shoots was also found. The abscission zones were of green colour, uneven and without

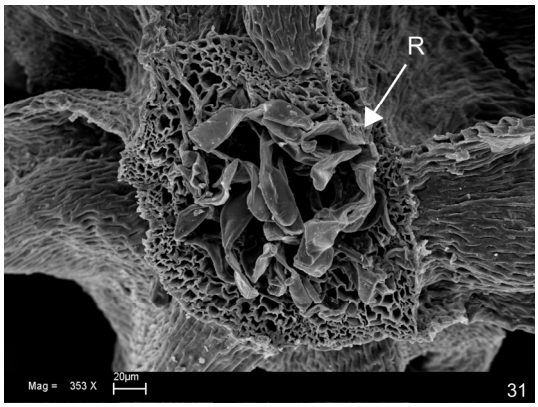
rhizoids. Some detected results of fragmentation might have been caused by handling and drying of the material. Fragmentation during the cleaning of samples was rare.











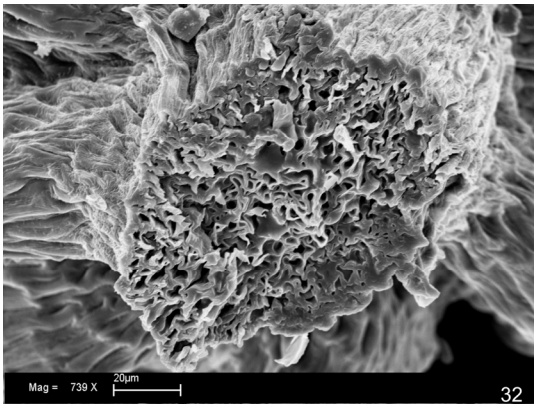


Fig. 27: Cross section through a confined decay zone within green section of the main shoot (right) of *Homalothecium lutescens*, longitudinal section through basal part of branch (left) (SEM-photo).

Fig. 28: Base of a brood branch/branchlet of *Homalothecium lutescens* with rhizoid growth (R) (SEM-photo).

Fig. 29: Cross section through a potential abscission zone (marked by striped arrow) between main shoot (right) and brood branch/branchlet (left) of *Homalothecium lutescens*. Rhizoid growth at the base of the branch (R) (SEM-photo).

Fig. 30: Brood branch/branchlet of *Homalothecium lutescens*. Incipient abscission (marked by arrow) between branch (left) and main shoot (right) (SEM-photo).

Fig. 31: Basal part of caducous shoot apex of *Homalothecium lutescens* with beginning rhizoid growth (R) (SEM-photo).

Fig. 32: Basal part of shoot apex of *Homalothecium lutescens* after fragmentation (SEM-photo).

5.2.2.3 *Homalothecium sericeum*

The morpho-anatomical analyses of the vegetative reproduction s.l. revealed that in most of the analysed samples of *H. sericeum*, structures such as branch apices, shoot apices or branch fragments were absent (cf. Table 4). About a quarter of the analysed samples had no shoot apices.

On the green sections of the shoots and branches with indeterminate growth, up to 28 (mean 4±6.3) branch apices and up to 23 (mean 2±4) branch fragments, out of a mean of 33.5±26.9 branches in total, were missing. In the decaying sections, up to 47 (mean 4.9±8.1) branch apices and up to eleven (mean 1.6±2.7) branch fragments, out of a mean of 14.7±19.7 branches in total, were detached. Arising from shoots, in some samples long, colourless, branchless and more or less leafless stoloniferous branches were found (Fig. 33).

Three modes of vegetative reproduction s.l. were observed in *H. sericeum*: (a) decay of older gametophyte parts, (b) brood branches/branchlets sensu CORRENS (1899) and (c) unspecialised fragmentation of gametophytes.

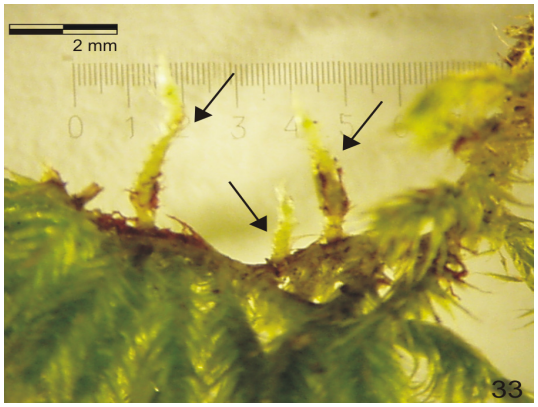
(a) Decay of older gametophyte parts

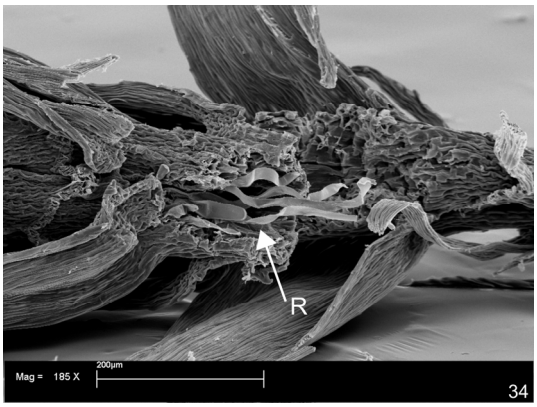
The plants frequently consist of a green section (0–4.2 cm, mean 1.5±1.3 cm in length), a decaying section (0–2.2 cm, mean 0.6±0.6 cm in length) and a dead section (0–2.5 cm, mean 0.6±0.7 cm in length). The latter is characterised by black colour, fragility and damage of nearly all branches. This decay of shoots is a very frequent mode of clonal reproduction in *H. sericeum*. Besides the decay of old shoot

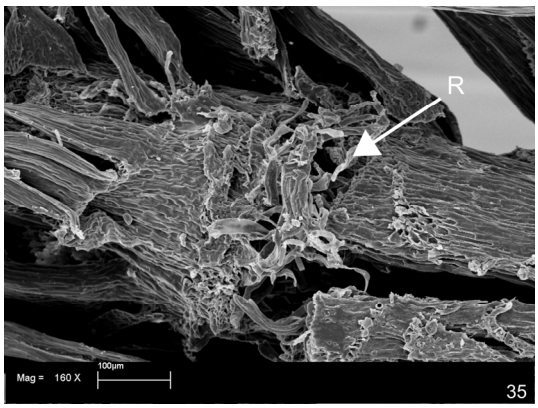
parts, but less frequent, localised zones of decay were observed on green sections of the shoots. By conducting an analysis of a decaying zone at an apical part with a scanning electron microscope (SEM), rhizoids could be found (Figs. 34-35). These rhizoids developed at the base and central part of the abscission zone of the apical, green branch part. The complementary part of the branch showed no rhizoids.
Decay of older shoot sections or local within green sections, resp., leads to separation of ramets by disintegration from the shoot system.

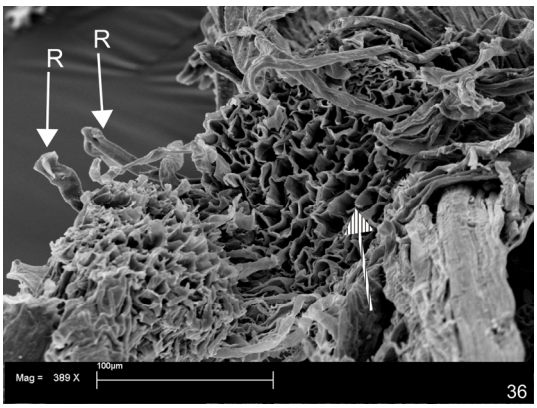
(b) Brood branches/branchlets sensu CORRENS (1899)
The detected brood branches/branchlets sensu CORRENS (1899) showed a basal brown to black colour and developed annular rhizoids (Fig. 36).
Analysis with the scanning electron microscope (SEM) showed that the detachment occurred through cells, without there being a (pre)determined fracture line.

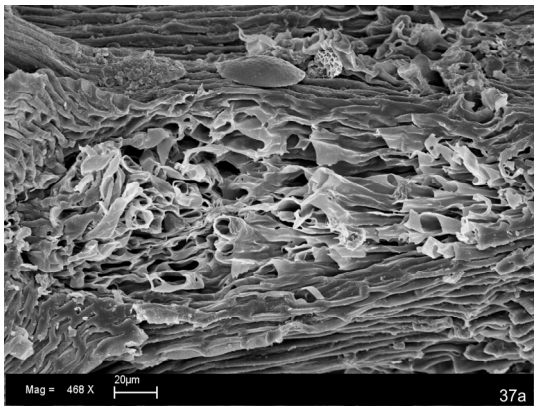
(c) Unspecialised fragmentation of gametophytes
In *H. sericeum* fragmentation is an important mode of clonal reproduction. Fragmentation within branches, shoots, from shoot and branch apices or between branches and shoots (Fig. 37) were very often found. The abscission zone caused by fragmentation was green, uneven and without rhizoids.











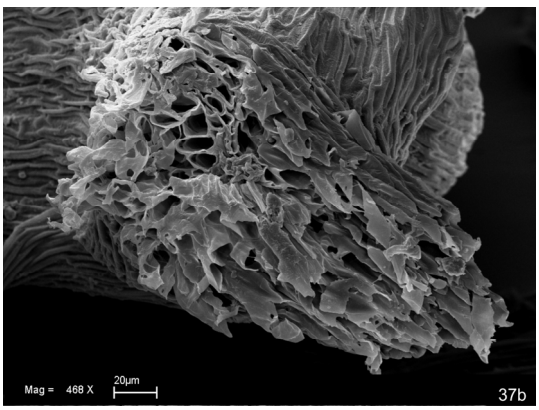


Fig. 33: Stoloniferous branches (marked by arrows) of *Homalothecium sericeum* (photo).

Fig. 34: Decay within green section of apical main shoot part in *Homalothecium sericeum*. Rhizoid growth at base of detaching apical part (R) (SEM-photo).

Fig. 35: Confined decay zone with rhizoid growth (R), within green section of main shoot of *Homalothecium sericeum* (SEM-photo).

Fig. 36: Brood branch/branchlet of *Homalothecium sericeum*, showing abscission zone at main shoot (right, marked by striped arrow) and base of branch with rhizoids (left, R) (SEM-photo).

Fig. 37: Fragmentation between branch and main shoot in *Homalothecium sericeum*. (a) Main shoot after detachment of branch (SEM-photo). (b) Basal part (abscission zone) of branch after fragmentation (SEM-photo).

Table 4: Length (mm) of loose morphological structures (branches, branch fragments, shoot and branch apices, shoot fragments and leaves) in *Abietinella abietina*, *Homalothecium lutescens* and *Homalothecium sericeum*

	length (mm)	average length ±standard deviation (mm)
Abietinella abietina		
branches	1.5–5.5	2.9±1.2
branch fragments	0.7–2.5	1.2±0.5
shoot apices	0.7–1.5	1.1±0.3
branch apices	0.5–0.8	0.7±0.1
shoot fragments	4.0–14.6	8.3±4.2
loose leaves	0.4–0.9	0.6±0.2
Homalothecium lutescens		
branches	6.5–24	12.5±5.9
branch fragments	2.2–8	4.7±1.9
shoot apices	2.2–4.5	3.3±1
branch apices	1.8–2.5	2.1±0.3
shoot fragments	8.1–22	13.6±6.1
Homalothecium sericeum		
branches	4.2–9.5	5.6±2
branch fragments	2.2–3.5	2.7±0.6
shoot apices	1.8–2.5	2.1±0.3
branch apices	0.9–1.5	1.1±0.2
shoot fragments	7.0–16	11.5±3.7
loose leaves	1.4–2.7	1.9±0.4

5.3 Molecular analyses

5.3.1 *Abietinella abietina*

The AFLP analyses were performed with two sets of samples (German- and world-wide sample set), and each with the two primer combinations *Eco*RI+AAC (5'biotinylated) / *Mse*I+CTT and *Eco*RI+ATA / *Mse*I+CTA (5'biotinylated). The total number of 122 samples is subdivided into 84 German samples and 45 world-wide samples including seven samples from the German also in the latter dataset.
The 84 German samples include the specimens of Hb (38), Mb (22), the region (11) and Germany-wide (13). Besides the mentioned seven German samples, the 45 world-wide samples include furthermore ten samples from North American, ten from Asian, one from South Africa and 17 from Europe (Appendix 1).

5.3.1.1 German sample set

Based on AFLP data, for all 84 German samples a total of 207 analysable bands (Data matrix dimensions: 17595 entries, Missing data: 0.06%) with 178 polymorphic bands (85.99%) were scored. Thereby 106 bands of *Eco*RI+AAC / *Mse*I+CTT with 93 polymorphic (87.74%) and 13 monomorphic bands were received. For *Eco*RI+ATA / *Mse*I+CTA the number of bands was 101, with 85 polymorphic (84.16%) and 16 monomorphic bands.
The 38 samples of the population of the Holzberg (excluding one sample of HbI_102_369; which was from the same plant but from different branches) showed 52 polymorphic bands (33.99%) out of a total of 153 bands and the 22 samples of the population of the Mönchsberg showed 45 polymorphic bands (29.22%) out of a total of 154 bands. For all regional samples (38 of Hb, 22 of Mb, eleven of region) 80 polymorphic bands (48.48%) out of a total of 165 bands were received (Table 5).
Samples with identical AFLP fingerprints were recorded in both populations and originated not only from the same patch (e.g. samples MbII_1_870, MbII_1_876, MbII_1_881) but also from different patches (e.g. samples HbI_93_289, HbI_73_249, HbI_58_226) or even from different populations (e.g. samples HbIII_2_409, Hb_surr_446, r1_Cospeda). In addition, the double samples of different branches of

the same shoot (HbI_102_369) showed an identical AFLP banding pattern (cf. Fig. 39, Appendices 12 I+16).

Histograms of the pooled distance values of Jaccard and Simple matching distance coefficients show a trimodal distribution with a pronounced gap in-between the second and third peak and an obvious minimum in-between the first and second peak (Fig. 38, Appendix 11A). The thresholds for clonal identity were fixed at GD_J=0.09420 and GD_{SM}=0.06280. This corresponds with the first minimum. By using these thresholds, 22 AFLP genotypes were received for the 84 analysed German samples, whereas for the regional samples ten and for each population five genotypes were yielded (Table 5).

Four clones could be detected using the threshold. Clone_1 comprised 43 analysed samples with 27 samples of the population Hb (HbI: 15 samples, HbII: two samples, HbIII: two samples, Hb_surr: eight samples), twelve samples of the population Mb (MbI: eight samples, Mb_surr: four samples) and four regional samples (r1_Cospeda, r2.1_Ammerbach, r3_Osmaritz, r6_Rabis). The pairwise genetic distances varied from 0 (e.g. between HbI_58_230, HbI_78_260, HbI_58_270, HbI_58_276 or between Mb_surr_863, Mb_surr_865) to GD_J=0.09420/GD_{SM}=0.06280 (e.g. between HbI_73_249 and MbI_27_796 or HbI_247 and r2.1_Ammerbach). Clone_2 consisted of ten samples, eight of Hb (HbI: seven samples, HbIII: one sample), one of Mb (Mb_surr_854) and r2.2_Ammerbach. The pairwise genetic distances varied from 0.00781 to 0.08955 for GD_J, but reached in one case a value of 0.09774, which is slightly above the threshold (HbI_25_199, HbII_383). The highest GD_{SM} was found with a value of 0.06280, also between the samples HbI_25_199 and HbII_383. The lowest pairwise genetic distance was yielded between HbI_12_168 and Mb_surr_854 with GD_J=0.00781/GD_{SM}=0.00483. For clone_3, which incorporated seven samples of Mb (MbI: four samples, MbII: three samples) and one sample of Hb (Hb_surr_465), pairwise genetic distances were received reaching from 0 (e.g. MbI_1_748 and MbI_33_798) to GD_J=0.07299/GD_{SM}=0.04831 (between the samples of MbII and MbI_1_748, MbI_33_798). Clone_4 has the largest detected spatial dimension in this sample set (42 km between G7_Freyburg and r7_Jena/Gleisberg) with the sample G7_Freyburg, three regional samples (r4_Jena/Leutra, r7_Jena/Gleisberg and r8_Dorndorf) and one surrounding sample of the population

Mb. Clone members showed a pairwise genetic distance from GD_J=0.03676/GD_{SM}=0.02415 (between r4_Jena/Leutra and r8_Dorndorf) to GD_J=0.08696/ GD_{SM}=0.05797 (between Mb_surr_862 and r8_Dorndorf).

The highest regional pairwise genetic distance was detected between r5_Dürrengleina and HbI_166 with GD_J=0.32857/GD_{SM}=0.22964. The maximum genetic distance between all studied German specimens was observed between the samples HbI_26_202 and G8_Altmühltal with a GD_J value of 0.65730 and between r4_Jena/Leutra and G8_Altmühltal with a GD_{SM} value of 0.57488, resp.

The molecular variance (AMOVA for all 84 samples) was significantly lower within (11.5%) than among (88.5%) the analysed populations of *A. abietina* (Table 6). Based on the pairwise genetic distance matrix of the Jaccard coefficient a UPGMA and NJ tree were calculated (Fig. 39, Appendix 12 I). Three distinct main clades (A, B, C) could be detected with a maximum BS of 100% (bootstrap support = BS; based on Jaccard´s/Simple matching coefficients). Clade_A comprises all samples of the populations Hb and Mb, further all regional samples (with the exception of r5_Dürrengleina) and the German samples G3_Alzey-Worms, G4_Weyer (Osteifel), G6_Volteroda, G7_Freyburg, G9_Rüdersdorf and G12_Martinroda. Clade_B includes samples from South Germany, two samples from Bavaria (G2_Burglauer, G5_Wiesenthau) as well as G1_Mönchberg from Baden-Württemberg. The samples G8_Altmühltal from South Germany and G10_Saalburg, G11_Kallenberg, G13_Bad Salzungen from Central Germany form clade_C. The pairwise genetic distances varied among all clusters from GD_J=0.44586/GD_{SM}=0.33816 (between A and C) to GD_J=0.65730/GD_{SM}=0.57488 (between B and C). Within the clusters, the pairwise genetic distances are lower and reached from 0 (minimum in clade_A) to GD_J=0.41123/GD_{SM}=0.29035 (minimum in clade_C) (Table 7).

Table 5: General characteristics of obtained AFLP profiles (primer combination *Eco*RI+AAC / *Mse*I+CTT and *Eco*RI+ATA / *Mse*I+CTA) for analysed German sample set of *Abietinella abietina* (#cf. 5.3.1.1)

	Germany-wide	population Hb	population Mb	region (incl. Hb and Mb)
number of samples				
total[a]	84	38	22	71
plot(s) total[a] (excl. surr_xx)		29	15	
plot I[a]		24	12	
plot II		3	3	
plot III		2		
polymorphy (absolute numbers of polymorphic bands)/%				
total[a]	178 (of 207)/ 85.99%	52 (of 153)/ 33.99%	45 (of 154)/ 29.22%	80 (of 165)/ 48.48%
plot(s) total[a] (excl. surr_xx)		43 (of 147)/ 29.25%	36 (of 148)/24.32%	
plot I[a]		43 (of 147)/ 29.25%	36 (of 148)/24.32%	
plot II		23 (of 142)/ 16.20%	0 (of 130)/0%	
plot III		1 (of 132)/0.75%		
detected distances (Jaccard/Simple matching)				
total[a]	0–0.65730/ 0–0.57488	0–0.23048/ 0–0.15719	0–0.19863/ 0–0.14010	0–0.32857/ 0–0.22964
plot(s) total[a] (excl. surr_xx)		0–0.23048/ 0–0.15719	0–0.19863/ 0–0.14010	
plot I[a]		0–0.23048/ 0–0.15719	0–0.19863/ 0–0.14010	
plot II		0.03030–0.15714/ 0.01932–0.10628	0/0	
plot III		0.00758/0.00483		
detected distances in genets (Jaccard/Simple matching)*				
clone_**1**	0–0.09420/ 0–0.06280			
clone_**2**[a]	0.00781–0.09774#/ 0.00483–0.06280			
clone_**3**	0–0.07299/ 0–0.04831			
clone_**4**	0.03676–0.08696/ 0.02415–0.05797			
genets*				
total number of genets	22	5	5	10
samples per clone				
clone_**1**		27	12	4
clone_**2**[a]		8	1	1
clone_**3**		1	7	
clone_**4**	1		1	3

*Determined thresholds for genet identity: GD_J=0.09420/GD_{SM}=0.06280
[a]Excluding one sample of HbI_102_369

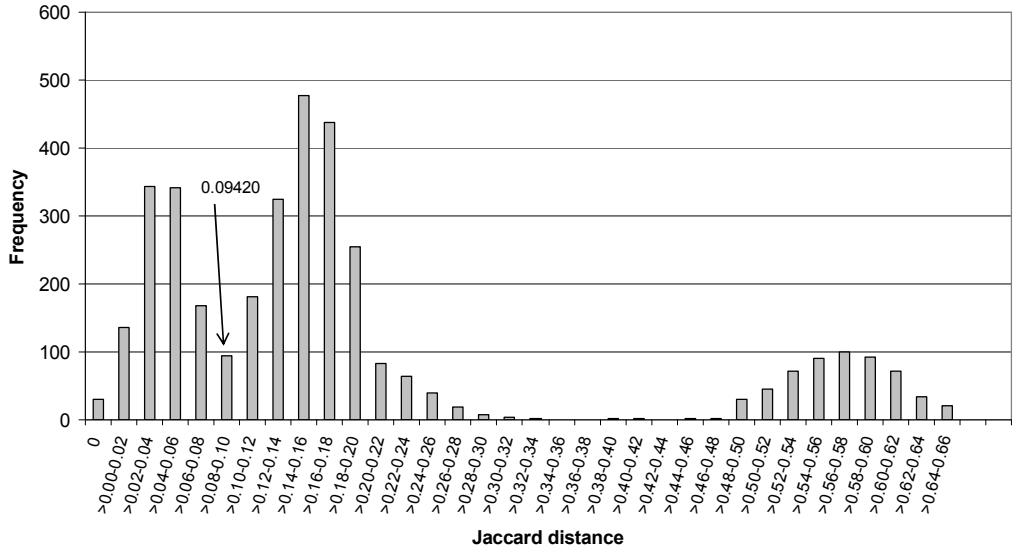


Fig. 38: Frequency histogram of pooled Jaccard distances of German samples of *Abietinella abietina*; the threshold for clonal identity is marked by an arrow.

Table 6: Results of analysis of molecular variance (AMOVA) within and among populations of *Abietinella abietina*, *Homalothecium lutescens* and *Homalothecium sericeum* in %

	AMOVA acc. to EXCOFFIER et al. (1992)
Abietinella abietina	
Va (among populations)	88.5%
Vb (within populations)	11.5%
Homalothecium lutescens	
Va (among populations)	78.9%
Vb (within populations)	21.1%
Homalothecium sericeum	
Va (among populations)	64.7%
Vb (within populations)	35.3%

Table 7: Minimum, maximum and mean of pairwise genetic distances (Jaccard/Simple matching) within and between clade_A, B and C of the German sample set of *Abietinella abietina*

	clade_A	clade_B	clade_C
clade_A	0–0.31469/ 0–0.21993 (mean=0.11572/0.07863)	-	-
clade_B	0.44586–0.60345/ 0.33816–0.51208 (mean=0.53980/0.44217)	0.1958–0.25361/ 0.12057–0.16429 (mean=0.21749/0.13843)	-
clade_C	0.51163–0.65730/ 0.42250–0.57488 (mean=0.58794/0.49790)	0.52121–0.60883/ 0.40101–0.49999 (mean=0.55891/0.43878)	0.17058–0.41123/ 0.10394–0.29035 (mean=0.33569/0.23117)

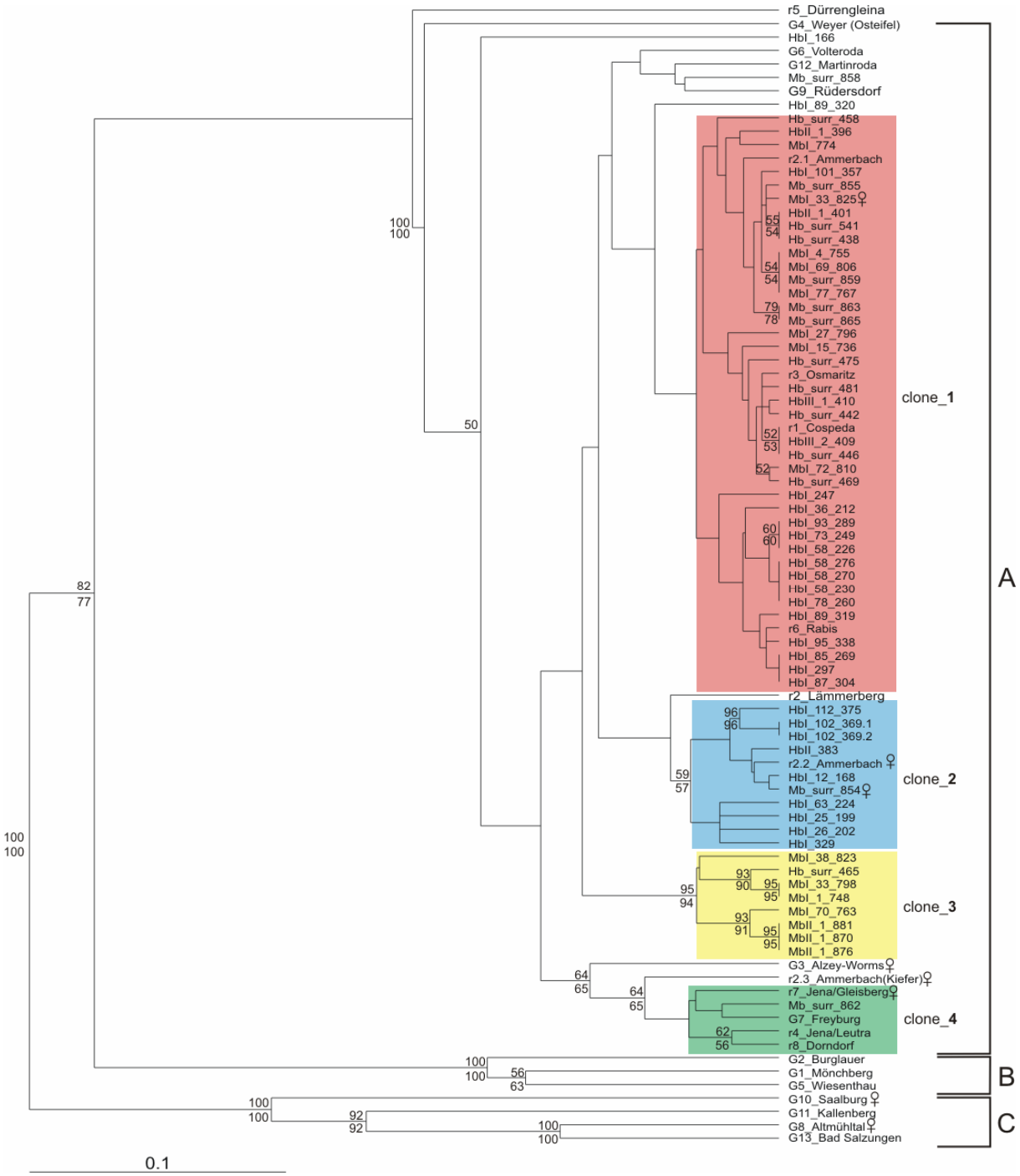


Fig. 39: UPGMA dendrogram based on Jaccard distances (calculated with FAMD 1.108 beta) of the German sample set of *Abietinella abietina* (♀ female plant).
Numerals above/below branches indicate bootstrap values >50% from calculation of a majority-rule consensus tree with 10,000 replicates (above branches BS values from calculations with the Jaccard coefficient, below branches BS values from calculations with the Simple matching coefficient). The data set contained 0.06% missing data. Genets [delimited using a clonal identity threshold (GD_J=0.09420/GD_{SM}=0.06280)] are highlighted with different colours; main clades are indicated by letters (see text for details).

5.3.1.2 World-wide sample set

For the AFLP analyses of the 45 world-wide samples of *A. abietina* a total of 196 analysable bands were obtained with 185 polymorphic (94.4%) and ten monomorphic bands (Data matrix dimension: 8820 entries, Missing Data: 0.20%). The primer combination *Eco*RI+AAC / *Mse*I+CTT provided 94 bands, whereas 88 were polymorphic (93.6%). 102 bands, of which 97 were polymorphic (95.1%), were obtained with the primer combination *Eco*RI+ATA / *Mse*I+CTA.

The polymorphy level for the European and Asian samples was identical with 90.48% (Table 9). The North American samples showed a lower polymorphy level with 81.72%. Among all analysed world-wide samples, the lowest polymorphy level with 31.88% was found within the samples from Scandinavia. The polymorphy level was therefore equally low as in the analysed populations Hb and Mb (Table 5).

Pairwise genetic distances within the world-wide analysed samples varied from a minimum of GD_J=0.07115/GD_{SM}=0.04333 [between A19_USA (New Mexico), A20_USA (New Mexico)] to a maximum of GD_J=0.70370/$GD_{SM=}$0.58163 (between A5_Spain and A12_Asian Russia). Analysis with the threshold for clonal identity, which was gained by the analyses of the German sample set, yielded that the samples A19_USA (New Mexico) and A20_USA (New Mexico) are part of the same genet with a pairwise genetic distance of GD_J=0.071150/GD_{SM}=0.04333. The samples A31_Sweden (Åsele) and A33_Sweden (Jämtland) also belong to one genet, with a pairwise genetic distance of GD_J=0.08485/GD_{SM}=0.05364. With ca. 170 km these samples showed the largest detected spatial distance within the samples of one genet in this study.

The obtained topologies for UPGMA and NJ trees differ only slightly (Fig. 40, Appendix 12 II). The UPGMA tree shows two main clades (A, B), which are supported by good to very high BS values (Fig. 40). The genetic separation of the two clades also becomes apparent on examination of the pairwise genetic distances. These were lower within the clades A and B than among the clades (for further details see Table 8, Appendix 17).

In the UPGMA dendrogram the samples of the main clade_A cluster with BS values of 70%/87% and are subdivided into two clades, whereas one of this clade contains three German (G1_Mönchberg, G2_Burglauer, G5_Wiesenthau), the South African

(A40_South Africa) and one North American sample [A23_USA (Alaska)]. The second clade of clade_A is subdivided into two further clades. One of this only contains samples from South Asia [A1_India (Sikkim), A2_Central Nepal, A4_Buthan] and China [A14_China (Sichuan)] and is supported by a maximum BS of 100%. Two further Asian samples [A3_China (Quinghai Prov.) and A10_Mongolia] cluster together and form a sister clade to the other samples of the second subclade, also supported by a maximum BS of 100%. This second subclade consists of two Asian [A11_Russia (Taymyr), A22_Mongolia], five North American and eight European samples. The three North American samples, A19_USA (New Mexico), A20_USA (New Mexico) and A17_USA (Colorado), cluster with maximum BS (100%). These samples are closely arranged to two samples from Canada [A24_Canada (Yukon), A15_Canada (Québec)] and are incorporated in the clade with mainly European samples. The remaining four North American samples [A13_USA (Alaska), A16_USA (NY), A21_USA (Connecticut) and A25_USA (Alaska)] belong to clade_B.

The samples of clade_B cluster with a BS of 99%/99%. Within clade_B only one sample originates from Asia (A12_Asia Russia). This sample is the easternmost Asian sample and clusters with two samples from USA (Alaska). Within the second clade all analysed Scandinavian samples are closely arranged. This Scandinavian samples are closely related to the samples A36_Austria, A39_Italy (Trafoi) and A28_Switzerland. The sister clade of this sample group consists of one sample from Hungary and one from Poland. Furthermore, this second clade of clade_B contains two samples from the east coast of North America, all European Russian samples and A7_Siberia.

Table 8: Minimum, maximum and mean of pairwise genetic distances (Jaccard/Simple matching) within and between clade_A and B of the world-wide sample set of *Abietinella abietina*

	clade_A	clade_B
clade_A	0.07115–0.61486/ 0.04333–0.46429 (mean=0.44487/0.32027)	-
clade_B	0.46405–0.70370/ 0.36224–0.58163 (mean=0.56855/0.45978)	0.08485–0.52264/ 0.05364–0.41294 (mean= 0.32132/0.23112)

Table 9: General characteristics of obtained AFLP profiles (primer combination *Eco*RI+AAC / *Mse*I+CTT and *Eco*RI+ATA / *Mse*I+CTA) for analysed world-wide sample set of *Abietinella abietina* (with examination of different geographical regions)

world-wide	North America	Asia	Europe (total)	South Europe	Scandinavia
number of samples					
45	10	10	24	4	5
polymorphy (absolute numbers of polymorphic bands)/%					
185 (of 196)/ 94.39%	152 (of 186)/ 81.72%	173 (of 192)/ 90.48%	171 (of 189)/ 90.48%	123 (of 170)/ 72.35%	44 (of 138)/ 31.88%
detected distances (Jaccard/Simple matching)					
0.07115–0.70370/ 0.04333–0.58163*	0.07115–0.62346/ 0.04333–0.51531	0.11207–0.64474/ 0.06633–0.51020	0.08485–0.61111/ 0.05364–0.50510*	0.16529–0.58228/ 0.10204–0.46939	0.08485–0.24593/ 0.05364–0.16586

*Excluding of pairwise genetic distances among German samples

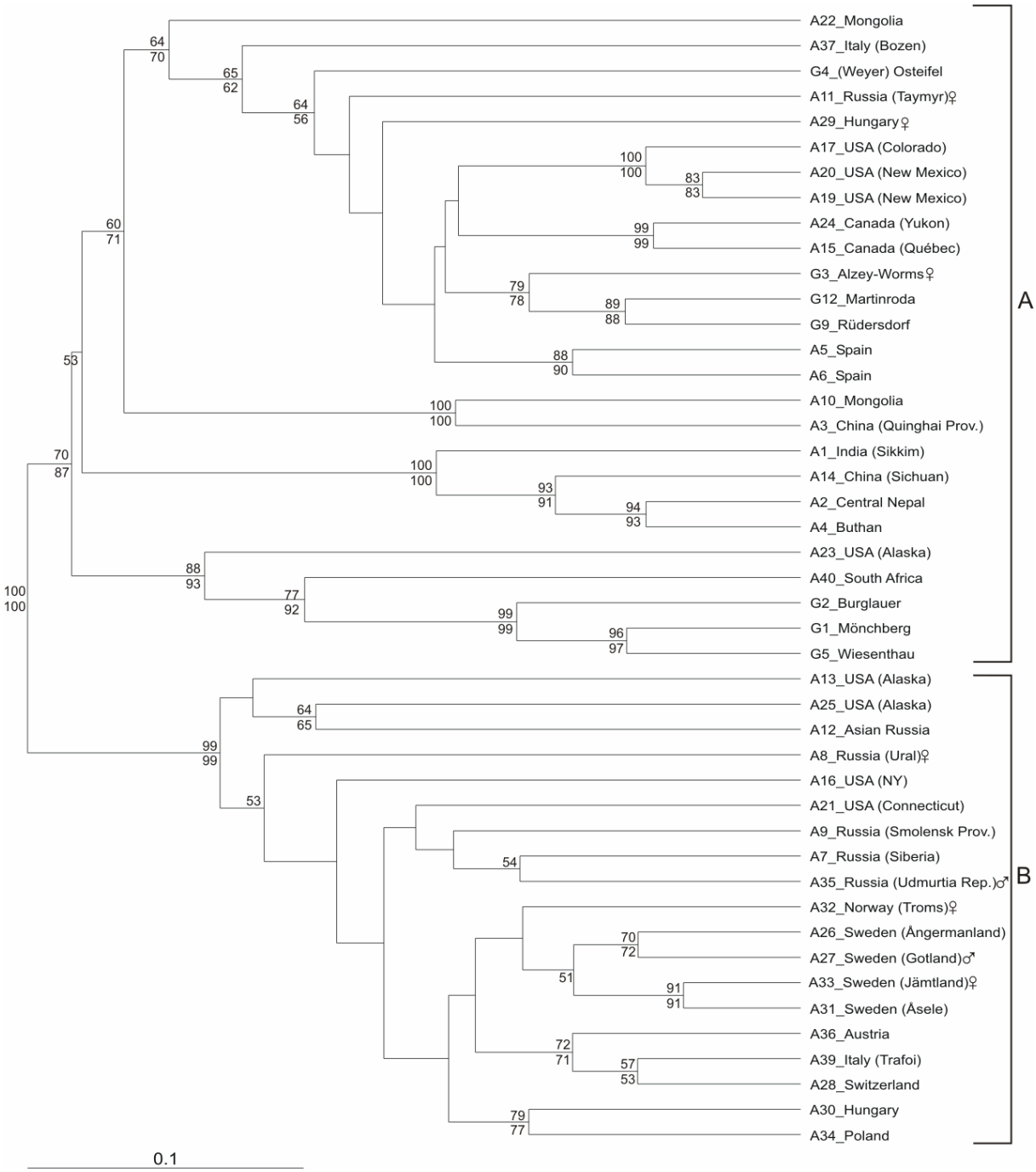


Fig. 40: UPGMA dendrogram based on Jaccard distances (calculated with FAMD 1.108 beta) of the world-wide sample set of *Abietinella abietina* (♀ female plant, ♂ male plant).
Numerals above/below branches indicate bootstrap values >50% from calculation of a majority-rule consensus tree with 10,000 replicates (above branches BS values from calculations with the Jaccard coefficient, below branches BS values from calculations with the Simple matching coefficient). The data set contained 0.20% missing data. Main clades are indicated by letters (see text for details).

5.3.2 *Homalothecium lutescens*

Homalothecium lutescens was molecular analysed with two sets of samples and for each with two primer combinations *Eco*RI+AAC (5'biotinylated) / *Mse*I+CTT and *Eco*RI+AAC (5'biotinylated) / *Mse*I+CGA. The first set consisted of 96 German samples which split up into 51 samples of the population Hb, 22 samples of the population Mb, ten regional samples and 13 Germany-wide samples.
The second set comprised 35 samples of the world-wide scale (including 18 German samples) and in addition a sample of each species of *H. aureum*, *H. fulgescens and H. philippeanum* (Appendix 1).

5.3.2.1 German sample set

For all 96 German samples a total of 219 analysable bands (Data matrix dimension: 9048 entries, Missing Data: 0.27%) with 121 polymorphic bands (55.25%) were recorded (Table 10). With the primer combination *Eco*RI+AAC / *Mse*I+CTT 74 polymorphic bands (54.81%) out of 135 bands in total were yielded. In the case of *Eco*RI+EAAC / *Mse*I+CGA the number of polymorphic bands was 47 (55.92%) out of 84 bands in total. The analysed populations Hb and Mb differ only slightly in polymorphy level. For the 51 samples of Hb 56 polymorphic bands (28.87%) out of 194 bands in total and for the 22 samples of Mb 47 polymorphic bands (24.87%) out of 189 bands in total were detected.
All samples of the region (51 of Hb, 22 of Mb and ten regional samples) showed 75 (38.07%) polymorphic bands of 197 bands in total.
Samples with identical AFLP fingerprintings originated from the same patch (e.g. Mb_1_833 and Mb_1_839 or Mb_20_791 and Mb_20_792) or from different patches (e.g. HbI_22_307, HbI_65_295 and HbI_86_349) of the same population. The double samples of different branches of the same shoot (r8_Rabis) were genetically identical (Fig. 42, Appendices 13 I+18).
The histograms of pooled values of the Jaccard and Simple matching distance coefficients show a trimodal distribution with a minimum in-between the first and second peak (Fig. 41, Appendix 11B). The minimum yielded the threshold for clonal identity, which was GD_J=0.04070 and GD_{SM}=0.03196. Using the threshold for clonal

identity for the 96 studied samples from Germany 47 AFLP genotypes were received. On the regional level 33 genotypes were detected, for the plots of Hb 14 and for the plots of Mb ten genotypes (Table 10).

For the studied region nine clones could be identified. The population Hb comprised four clones, whereas one also consisted of samples of the population Mb (clone_Hb/Mb). Clone_Hb1 included two samples from plot I and III with a pairwise genetic distance of GD_J=0.03977/GD_{SM}=0.02710. The two samples of clone_Hb2 showed a pairwise genetic distance of GD_J=0.03955/GD_{SM}=0.03196 and were sampled on plot I (HbI_8_194) and on the surrounding area (Hb_surr_480). Clone_Hb3 consisted of two samples of the plot II with a pairwise genetic distance of GD_J=0.00575/GD_{SM}=0.00457. Clone_Hb/Mb contained 34 samples (29 samples of HbI, one of HbIII, two of HB_surr and one sample of Mb and Mb_surr, resp.). The pairwise genetic distances varied from 0 (e.g. between HbI_392 and HbI_77_334) to GD_J=0.04023/GD_{SM}=0.03196 (between Hb_surr_431 and Mb_surr_866).

For the samples of the population Mb five clones could be identified. Two samples (Mb_20_790, Mb_surr_856) could be allocated to clone_Mb1 with a pairwise genetic distance of GD_J=0.03390/GD_{SM}=0.02740. Clone_Mb2 consisted of four samples (three of patch Mb_1 and one of patch Mb_2) and the pairwise genetic distances varied from 0 to GD_J=0.02326/GD_{SM}=0.01826 between samples Mb_1_839 and Mb_2_847. Clone_Mb3 comprised of four samples. Two of those samples originated from the same patch (Mb_20_791 and Mb_20_792) and showed an identical AFLP-fingerprinting profile. The highest genetic distance within this clone was found for Mb_12_760 and Mb_14_780 with GD_J=0.04070/GD_{SM}=0.03196. Clone_Mb4 included five samples of the population Mb (three samples of the plot and two surrounding samples). The pairwise genetic distances varied from GD_J=0.01149/GD_{SM}=0.00913 (between Mb_733 and Mb_21_789) to GD_J=0.03977/ GD_{SM}=0.03196 (between Mb_733 and Mb_17_793). In one case the value of the pairwise genetic distance reached GD_J=0.05026/GD_{SM}=0.04110 (Mb_733 and Mb_surr_757), which is slightly above the threshold.

Clone_r consisted of two samples (r5_Mädertal and r7_Jena/Gleisberg) and showed, with a distance of ca. 8 km between both samples, the largest spatial extension. The pairwise genetic distance was GD_J=0.04070/GD_{SM}=0.03196.

The highest regional pairwise genetic distance was detected between Hbl_263 and r2_Ammerbach with GD_J=0.15301/GD_{SM}=0.12785. For all analysed German samples the highest pairwise genetic distance was found between G5_Ebermannstadt and G13_Rambach with GD_J=0.33166/GD_{SM}=0.30137 (Appendix 18).

The analysis of molecular variance (AMOVA) revealed that the variance among populations was much higher (78.9%) than within populations (21.1%) (Table 6).

The UPGMA tree (Fig. 42) shows that all samples of the region of the analysed populations Hb and Mb cluster in one clade and are supported by medium BS values (66%/66%). Furthermore, this clade includes G3_Saalburg and G9_Rüdersdorf. All other studied German samples are distinguished from this clade in both tree types. The samples G5_Ebermannstadt and G7_Wiesenthau cluster together with maximum BS values (100%). Additionally, both samples from Rhineland-Palatinate (G11_Kyllburg, G12_Nohen) cluster together with medium BS values in both tree types. Also, but without BS values in the UPGMA dendrogram, the samples G1_Kallenberg and G8_Malchin are closely arranged. The other samples form a somewhat different arrangement in both tree types (cf. Appendix 13 I).

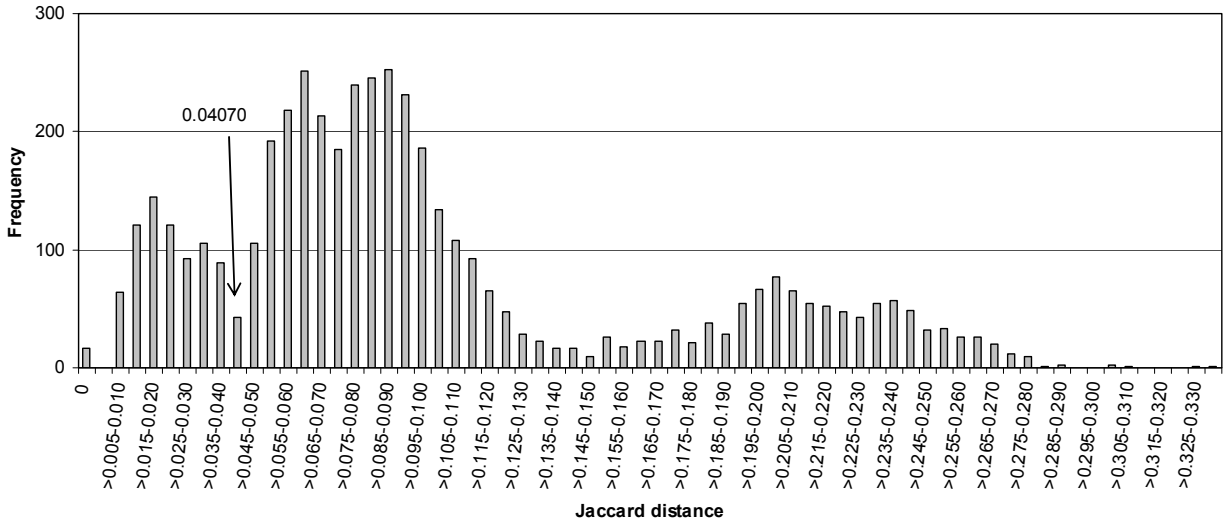


Fig. 41: Frequency histogram of pooled Jaccard distances of the German samples of *Homalothecium lutescens*; the threshold for clonal identity is marked by an arrow.

Table 10: General characteristics of obtained AFLP profiles (primer combination *Eco*RI+AAC / *Mse*I+CTT and *Eco*RI+AAC / *Mse*I+CGA) for analysed German sample set of *Homalothecium lutescens* (#cf. chapter 5.3.2.1)

	Germany-wide	population Hb	population Mb	region (incl. Hb and Mb)
number of samples				
total[a]	96	51	22	83
plot(s) total (excl. surr_xx)		41	15	
plot I		35		
plot II		2		
plot III		4		
polymorphy (absolute numbers of polymorphic bands)/%				
total[a]	121 (of 219)/ 55.25%	56 (of 194)/ 28.87%	47 (of 189)/ 24.87%	75 (of 197)/ 38.07%
plot(s) total (excl. surr_xx)		41 (of 192)/21.35%	38 (of 106)/35.85%	
plot I		38 (of 191)/19.90%		
plot II		1 (of 174)/0.54%		
plot III		14 (of 179)/7.82%		
detected distances (Jaccard/Simple matching)				
total[a]	0–0.33166/ 0–0.30137	0–0.14286/ 0–0.11872	0–0.12568/ 0–0.10502	0–0.15301/ 0–0.12785
plot(s) total (excl. surr_xx)		0–0.11602/ 0–0.09589	0–0.11667/ 0–0.09589	
plot I		0–0.11602/ 0–0.09589		
plot II		0.00575/0.00457		
plot III		0.02857–0.06704/ 0.04110–0.05479		
detected distances in clones* (Jaccard/Simple matching)				
clone_**Hb1**		0.03977/0.02710		
clone_**Hb2**		0.03955/0.03196		
clone_**Hb3**		0.00575/0.00457		
clone_**Mb1**			0.03390/0.02740	
clone_**Mb2**			0–0.02326/0–0.01826	
clone_**Mb3**			0–0.04070/0–0.03196	
clone_**Mb4**			0.01149–0.03977 (#0.05026)/0.00913–0.03196(#0.04110)	
clone_**Hb/Mb**		0–0.04023/ 0–0.03196		
clone_**r1**				0.04070/0.03196
genets*				
total no. of genets[a]	47	14	10	33
samples per clone				
clone_**Hb1**		2		
clone_**Hb2**		2		
clone_**Hb3**		2		
clone_**Mb1**			2	
clone_**Mb2**			4	
clone_**Mb3**			4	
clone_**Mb4**			5	
clone_**Hb/Mb**		32	2	
clone_**r**				2

*Determined thresholds for genet identity: GD_J=0.04070/GD_{SM}=0.03196
[a]Excluding one sample of r8_Rabis

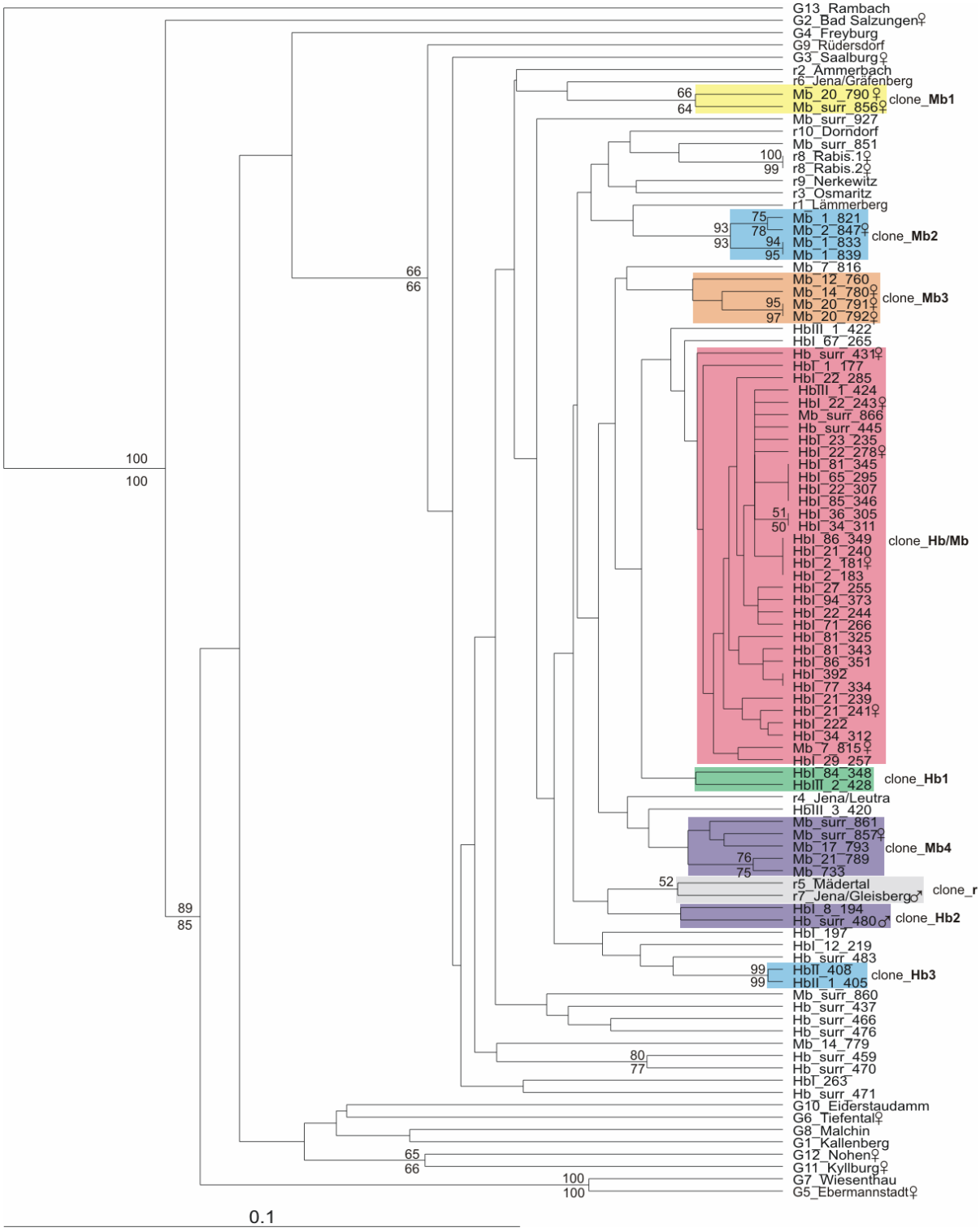


Fig. 42: UPGMA dendrogram based on Jaccard distances (calculated with FAMD 1.108 beta) of the German sample set of *Homalothecium lutescens* (♀ female plant, ♂ male plant).
Numerals above/below branches indicate bootstrap values >50% from calculation of a majority-rule consensus tree with 10,000 replicates (above branches BS values from calculations with the Jaccard coefficient, below branches BS values from calculations with the Simple matching coefficient). The data set contained 0.11% missing data. Genets [delimited using a clonal identity threshold (GD_J=0.04070/ GD_{SM}=0.03196)] are highlighted with different colours.

5.3.2.2 World-wide sample set

World-wide 35 samples of *H. lutescens* were molecular analysed and all in all 228 AFLP fragments with 158 polymorphic bands (69.30%) were received (data matrix dimension: 8208, Missing Data: 0.29%). With the primer combination *Eco*RI+AAC / *Mse*I+CTT 90 polymorphic bands (68.70%) out of a total of 131 bands and with *Eco*RI+EAAC / *Mse*I+CGA 68 polymorphic bands (70.10%) out of a total of 97 bands were detected. For the Mediterranean and the samples from the British Isles a similar polymorphy level was received (Table 11). The lowest polymorphy level was scored in the Scandinavian samples with 14.29%. The lowest pairwise genetic distance was found between Hl3_Sweden and Hl11_Sweden GD_J=0.14368/GD_{SM}=0.10965 (Table 11, Appendix 19). Between G5_Ebermannstadt and Hl18_Italy the highest pairwise genetic distance was detected with GD_J=0.44844/GD_{SM}=0.38370.

For the world-wide sample set a UPGMA and a NJ tree (Fig. 43, Appendix 13 II) were calculated likewise, based on the distance matrix of the Jaccard coefficient. In both trees the additional samples of *H. fulgescens, H. aureum* and *H. philippeanum* are well separated from the samples of *H. lutescens.* Including the three additional species a total of 232 bands were received with 209 polymorphic bands (90.09%). In the UPGMA tree the samples of *H. lutescens* are subdivided into two main clades (Table 12, Fig. 43). Clade_A is supported by good BS values and contains two samples from Italy and one sample from Austria, England and Germany, resp. Clade_B receives very good BS values and contains most of the analysed samples of the world-wide data set. The samples G2_Bad Salzungen, G3_Saalburg, G9_Rüdersdorf and the samples of the region of Jena are closely related to the Swedish samples, Hl6_Caucasus, Hl8_Spain and Hl9_Hungary.

The major difference among the tree types is that the samples G4_Freyburg, G11_Kyllburg, G12_Nohen, Hl4_Ireland and Hl14_Scotland as well as both Hungarian samples in the NJ tree are closer arranged with the sample group of clade_A, whereas in the UPGMA tree the clade_A is a sister clade of clade_B. In both tree types G1_Kallenberg, G5_Ebermannstadt, G6_Tiefental, G7_Wiesenthau, G8_Malchin and G10_Eiderstaudamm are closely related to Hl2_England, Hl7_Poland, Hl13_Spain and Hl16_Italy.

The comparison of pairwise genetic distances between clade_A and clade_B yielded the lowest distance values for clade_B (Table 12). Higher pairwise genetic distance values were obtained for samples of clade_A than for clade_B. But these values were still lower than the pairwise genetic distance values calculated from a pairwise comparison among the clades.

Table 11: General characteristics of obtained AFLP profiles (primer combination *Eco*RI+AAC / *Mse*I+CTT and *Eco*RI+AAC / *Mse*I+CGA) for analysed world-wide sample set of *Homalothecium lutescens* (with examination of different geographical regions)

world-wide[a]	British Isles	South Europe	Scandinavia
number of samples			
35	4	6	2
polymorphy (absolute numbers of polymorphic bands)/%			
158 (of 228)/69.30%	96 (of 201)/47.76%	140 (of 222)/63.06%	25 (of 175)/14.29%
detected distances (Jaccard/Simple matching)			
0.14368–0.44844/ 0.10965–0.38370*	0.17442–0.38575/ 0.13158–0.32009	0.18539–0.42696/ 0.14474–0.37281	0.14368/0.10965

*Excluding of pairwise genetic distances among German samples
[a]Excluding of one sample of r8_Rabis

Table 12: Minimum, maximum and mean of pairwise genetic distances (Jaccard/Simple matching) within and between clade_A and B of the world-wide sample set of *Homalothecium lutescens*

	clade_A	clade_B
clade_A	0.17919–0.38058/ 0.13596–0.31369 (mean=0.29943/0.22483)	-
clade_B	0.24731–0.44844/ 0.20175–0.38370 (mean=0.36386/0.30691)	0–0.31032/ 0–0.25968 (mean=0.20611/0.16170)

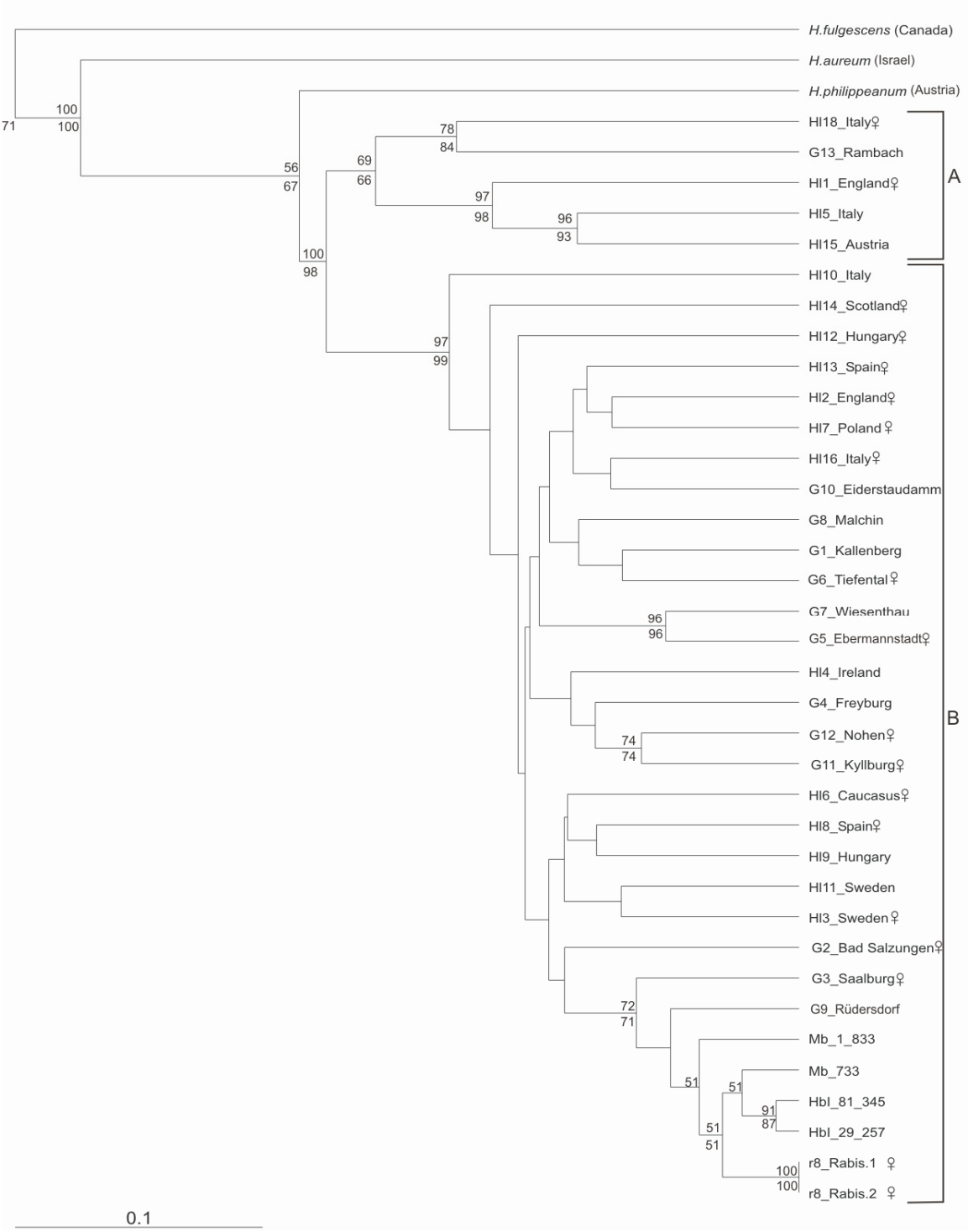


Fig. 43: UPGMA dendrogram based on Jaccard distances (calculated with FAMD 1.108 beta) of the world-wide sample set of *Homalothecium lutescens* (♀ female plant).
Numerals above/below branches indicate bootstrap values >50% from calculation of a majority-rule consensus tree with 10,000 replicates (above branches BS values from calculations with the Jaccard coefficient, below branches BS values from calculations with the Simple matching coefficient). The data set contained 0.27% missing data. In addition, the samples of *Homalothecium aureum*, *Homalothecium fulgescens* and *Homalothecium philippeanum* were analysed. Main clades are indicated by letters (see text for details).

5.3.3 *Homalothecium sericeum*

The AFLP analyses were performed with two sets of samples each with the two primer combinations *Eco*RI+AAC (5'biotinylated) / *Mse*I+CTT and *Eco*RI+ACC (5'biotinylated) / *Mse*I+CTA. The first data set consisted of 84 German samples. Besides, 16 Germany-wide samples (incl. 3 samples of G5_Kahla), 30 samples of the population FN and four regional samples from Saxony-Anhalt were studied. Furthermore 19 samples of the population L, nine of the population D and six regional samples from South Brandenburg were analysed. The second data set comprised 37 samples from the world-wide scale, including nine samples from Germany and two samples of *H. aureum* (Appendix 1).

5.3.3.1 German sample set

Based on all 84 analysed German samples and both primer combinations 161 bands with 119 polymorphic bands (73.91%) were found (Data matrix dimension: 13685, Missing Data: 0.44%). The primer combination *Eco*RI+ACC / *Mse*I+CTA 50 polymorphic bands (78.13%) of altogether 64 bands were yielded. For *Eco*RI+AAC / *Mse*I+CTT the number of bands was 97, with 69 polymorphic bands (71.13%).
For the samples of the population FN 67 polymorphic bands (45%) out of 148 bands in total were received; including the regional samples 77 polymorphic bands (51.68%) of altogether 149 bands were yielded (Table 13). The analysed populations from South Brandenburg showed a lower polymorphy level with 39.46% in the case of the population L and 21.48% for the samples of the population D. Otherwise, all samples of the region B have a slightly higher polymorphy level with 85 polymorphic bands (57.79%) out of 154 bands in total, compared with the polymorphy level of all samples of the region of Saxony-Anhalt.
Samples with identical AFLP fingerprints were detected in all three populations (FN, L, D), whereas the compared identical sample pairs originated from different patches (e.g. D_8_696 and D_2_699 or LV_4_637 and LV_10_629) (Fig. 45, Appendices 14 I +20). Samples of the same plant but from different branches (FN_11_47, FN_11_47.2) showed a difference in one band and a pairwise genetic distance of GD_J=0.00781/GD_{SM}=0.00613.

Histograms of pooled distance values of Jaccard and Simple matching distance coefficients show a bimodal distribution with a pronounced valley in-between (Fig. 44, Appendix 11C). This valley is in conformity with the threshold for clonal identity.

Based on 84 analysed German samples of *H. sericeum* and by use of a threshold for clonal identity with GD_J=0.08621/GD_{SM}=0.06748 a total of 44 AFLP genotypes were received (Table 13). For the region of Saxony-Anhalt 14 genets of all 34 analysed samples were identified. In the case of the population FN ten genets for the 30 analysed samples could be determined. The 34 analysed samples from Brandenburg yielded a total of 16 genets with seven genets for the 19 analysed samples of the population L, three genets for the nine analysed samples of the population D and six genets of the further regional samples.

For the population FN, three clones could be detected. Clone_FN1 consisted of 14 samples and was collected between 2.4 m and 13.7 m on top of the studied wall and in one case (FN_19_76) from the upper vertical surface of the wall at 21 m, resp. (Appendix 8). Four samples of this clone originated from patch 11 (FN_11_34, FN_11_47, FN_11_55 and FN_11_61) and three samples from patch 8 (FN_8_15, FN_8_16 and FN_8_22). The remaining samples of clone_FN1 were from different patches or in the case of FN_33 and FN_65 a fragment from outside the patches. The pairwise genetic distances varied from 0 (between FN_33 and FN_11_61) to GD_J=0.07692/GD_{SM}=0.06135 (between FN_11_47.2 and FN_65). Clone_FN2 with five detected dividuals included, besides two samples of the western studied wall section (FN_18_69, FN_23_80), three surrounding samples. Two surrounding samples (FN_surr_98, FN_surr_99) were located at the southwest part of the wall and showed a spatial distance to FN_23_80 of 25.70 m and 35.70 m, resp. The surrounding sample FN_surr_108 had a spatial distance to the wall (FN_1_1) of ca. 100 m. The pairwise genetic distances varied from GD_J=0.00813/GD_{SM}=0.00613 (between FN_18_69 and FN_23_80) to GD_J=0.07692/GD_{SM}=0.06135 (between FN_surr_98 and FN_surr_108). Clone_FN3 consisted of four samples (FN_1_1, FN_5_9, FN_4_10 and FN_6_11) and was located at 0 m–1.98 m of the analysed wall section (Appendix 8). In clone_FN3 the pairwise genetic distances varied from GD_J=0.00909/GD_{SM}=0.00613 (FN_1_1, FN_5_9) to GD_J=0.08621/GD_{SM}=0.06135 (FN_4_10 and FN_6_11). The pairwise genetic distance between the samples

FN_4_10 and FN_surr_110 with GD_J=0.30976/GD_{SM}=0.26406 was not only the highest in the population FN but also in the region Saxony-Anhalt.

For the analysed population L two clones could be detected. Clone_L1 included twelve samples with a pairwise genetic distance from 0 between three samples (e.g. between LV_4_637 and LV_10_629) to GD_J=0.08462/GD_{SM}=0.06748 (between LII_1_618 and LIV_13_622). Nine dividuals originated from plot LV and grew from the top to the base of the wall and the ground in front of the wall. All other samples of clone_L1 were collected from different wall sections (see Appendix 9; one sample each of LI, LII, LIV). Clone_L2 comprised only the two samples LIII_1_621 and LVI_23_670 (GD_J=0.08000/GD_{SM}=0.06135) which had a spatial distance of ca. 45 m. The highest pairwise genetic distance was found in the population L with GD_J=0.23571/GD_{SM}=0.20245 between the samples LIV_1_622 and L_surr_684 or LIII_1_621 and LV_77_639, resp.

For the population D one clone with seven samples was identified. Five samples of the analysed plot and two surrounding samples were included in clone_D. The pairwise genetic distance varied from 0 to GD_J=0.04098/GD_{SM}=0.03067 (between D_6_701 and D_16_705). On the analysed section of the wall, only one more genet was found (D_8_693). A further genet was detected in the surrounding at the base of the northward church wall (D_surr_689) (Appendix 10). The highest pairwise genetic distance with GD_J=0.17557/GD_{SM}=0.14110 was found between D_16_705 and D_surr_689. The maximum genetic distance between all studied samples from Brandenburg was observed between the samples rB5_Schönborn and rB6_Sallgast with a pairwise genetic distance of GD_J=0.32143/GD_{SM}=0.27607.

A further clone (clone_G5) with three samples was found in Kahla (G5_Kahla910, G5_Kahla912 and G5_Kahla913). Among all analysed German samples the highest pairwise genetic distance with GD_J=0.38512 was detected between G6_Röttelmisch and G10_Rügen or with GD_{SM}=0.34356 between G5_Kahla912 and G12_Vulkaneifel as well as between G5_Kahla913 and G12_Vulkaneifel.

The AMOVA calculation of all 84 German samples revealed a significant lower molecular variance within the populations (35.3%) than among the populations (64.7%) (Table 6).

The Jaccard UPGMA tree (Fig. 45) shows for all populations (FN, L, D and G5_Kahla) that within each population the samples are closely arranged. The clade of the population FN is separated into two subclades, but without BS support. One subclade includes the samples of clone_FN1 and is supported by very high BS values (97%/98%). Besides others, the second subclade consists of clone_FN2 and clone_FN3. The clade of clone_FN3 receives good BS values (up to 72%). Close to the population FN further regional samples (rSA1_Nißmitz, rSA2_Braunsbedra and rSA3_Freyburg_rill) are placed.

The sister clade of the population FN comprises the samples of the population L, several regional samples from Brandenburg (rB1_Riedebeck, rB2_Betten, rB3_Wehrenzhain, rB4_Friedersdorf), one sample from Saxony-Anhalt (rSA4_Liederstädt) and two samples from Thuringia (G4_Zimmritz, G7_Schnellmannhausen). The clade of clone_L1 is supported by very good BS values (94%/95%) and the clade of clone_L2 receives good BS values (70%/66%). All samples of the population D form a clade (BS 62%/64%) and the samples of clone_D are supported by very high BS values (96%/98%). Furthermore, population D is closely related to the samples of G5_Kahla, the regional sample rB6_Sallgast and three further samples from Thuringia (G2_Nennsdorf, G3_Göttern, G15_Meiningen). All other German samples are positioned outside the clade of the populations FN, L, D (Fig. 45). The NJ tree (Appendix 14 I) shows a somewhat other placement. The samples of Lindena (with the exception of clone_L2, LVI_22_674, LVI_44_680 and L_surr_684) are closely related to the samples from Dollenchen and Kahla.

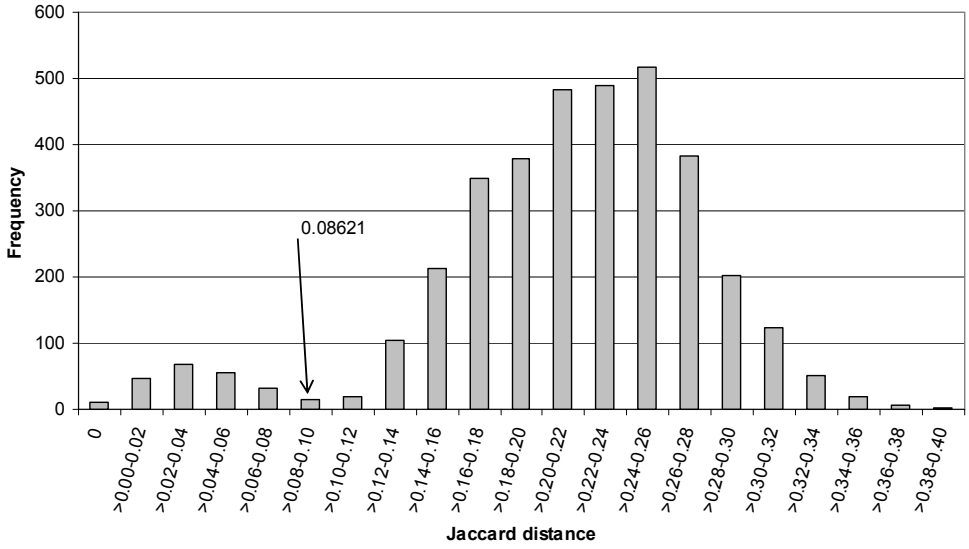


Fig. 44: Frequency histogram of pooled Jaccard distances of German samples of *Homalothecium sericeum*; the threshold for clonal identity is marked by an arrow.

Table 13: General characteristics of obtained AFLP profiles (primer combination *Eco*RI+AAC / *Mse*I+CTT and EcoRI+ACC / MseI+CTA) for analysed German sample set of *Homalothecium sericeum*

	Germany-wide	population FN	region SA (incl. FN)	population L	population D	region B (incl. L+D)
number of samples						
total[a]	84	30	34	19	9	34
plot(s) total[a] (excl. surr_xx)		25		17	6	
plot I				1		
plot II				1		
plot III				1		
plot IV				1		
plot V				10		
plot VI				3		
polymorphy (absolute numbers of polymorphic bands)/%						
total[a]	119 (of 161)/ 73.91%	67 (of 148)/ 45.27%	77 (of 149)/ 51.68%	58 (of 147)/ 39.46%	29 (of 135)/ 21.48%	85 (of 154)/ 57.79%
plot(s) total[a] (excl. surr_xx)		58 (of 148)/ 39.19%		55(of 144)/ 38.19%	17 (of 129)/ 13.18%	
plot V				24 (of 136)/ 17.65%		
plot VI				25 (of 132)/ 18.94%		
detected distances (Jaccard/Simple matching)						
total	0–0.38512/ 0–0.34356	0–0.30976/ 0–0.26406	0–0.30976/ 0–0.26406	0–0.23571/ 0–0.20245	0–0.17557/ 0–0.14110	0–0.32143/ 0–0.27607
plot(s) total[a] (excl. surr_xx)		0–0.27387/ 0–0.23002		0–0.23571/ 0–0.20245	0–0.11111/ 0–0.08589	
plot V				0–0.16788/ 0–0.14110		
plot VI				0.11024–0.19970/ 0.08589–0.16148		
detected distances* in clones (Jaccard/Simple matching)						
clone_**FN1**		0–0.07692/ 0–0.06135				
clone_**FN2**		0.00813–0.07692/ 0.00613–0.06135				
clone_**FN3**		0.00909–0.08621/ 0.00613–0.06135				
clone_**L1**				0–0.08462/ 0–0.06748		
clone_**L2**				0.08000/0.06135		
clone_**D**					0–0.04098/ 0–0.03067	
clone_**G5**	0.02459–0.05691/ 0.01840–0.04294					
genets*						
total No. of genets	44	10	14	7	3	16
samples per clone						
clone_**FN1**[a]		14				
clone_**FN2**		5				
clone_**FN3**		4				
clone_**L1**				12		
clone_**L2**				2		
clone_**D**					7	
clone_**G5**	3					

*Determined thresholds for genet identity: GD_J=0.08621/GD_{SM}=0.06748
[a]Excluding one sample of FN_11_47

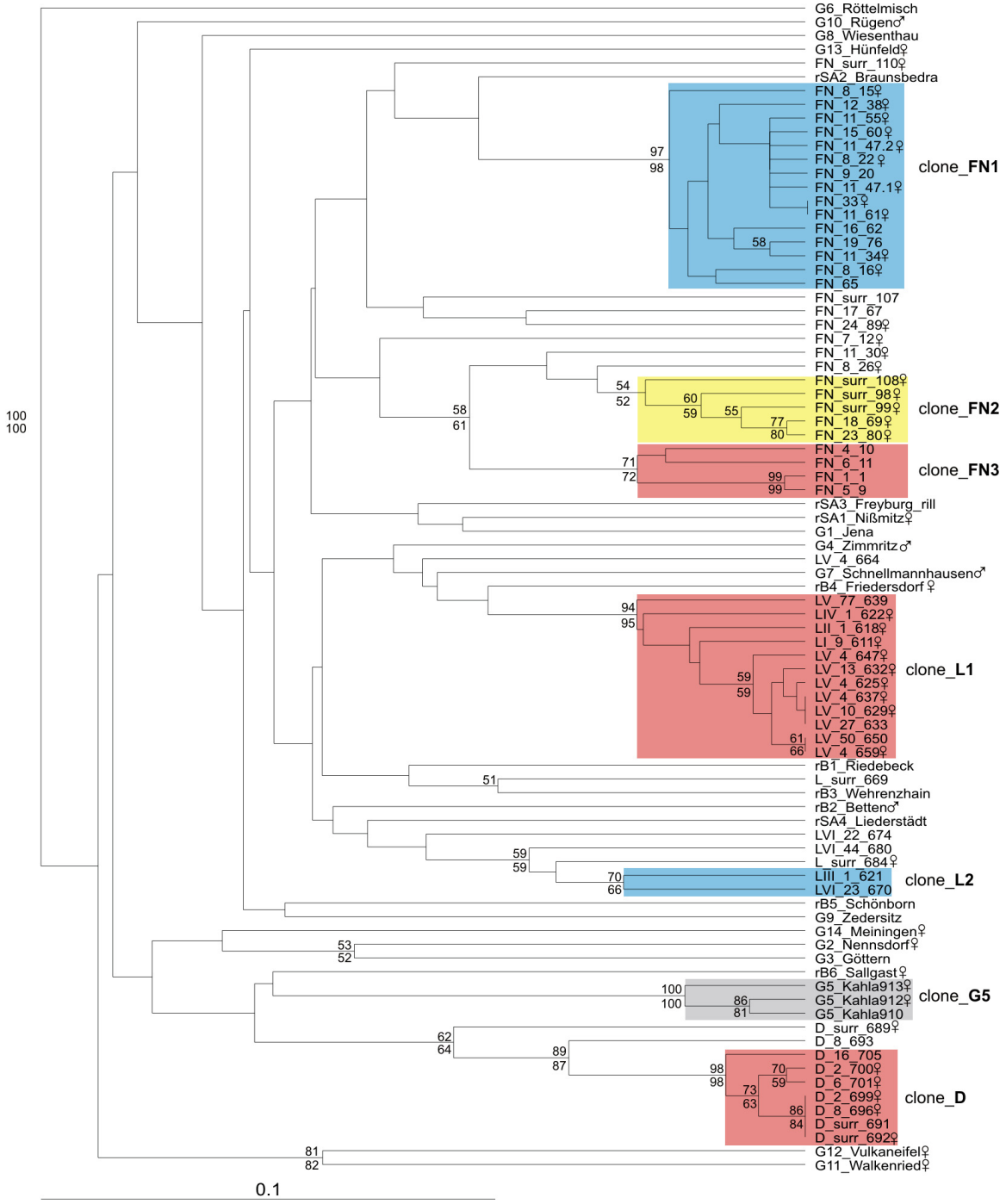


Fig. 45: UPGMA dendrogram based on Jaccard distances (calculated with FAMD 1.108 beta) of the German sample set of *Homalothecium sericeum* (♀ female plant, ♂ male plant).
Numerals above/below branches indicate bootstrap values >50% from calculation of a majority-rule consensus tree with 1000 replicates (above branches BS values from calculations with the Jaccard coefficient, below branches BS values from calculations with the Simple matching coefficient). The data set contained 0.43% missing data. Genets [delimited using a clonal identity threshold (GD_J=0.08621/GD_{SM}=0.06748)] are highlighted with different colours.

5.3.3.2 World-wide sample set

Thirty-five samples of the entire distribution area of *H. sericeum* were studied for the AFLP analysis. For both used primer combinations a total number of 175 analysable bands with 124 polymorphic bands (70.86%) were received (Data matrix dimension: 6125 entries, Missing Data: 0.85%). The primer combination *Eco*RI+ACC / *Mse*I+CTA yielded 75 bands with 56 polymorphic bands (74.67%) and 100 bands with 68 polymorphic bands (68%) were obtained with *Eco*RI+AAC / *Mse*I+CTT.

The detected polymorphy level of the samples from the British Isles and Scandinavia was similar with ca. 42% (Table 14). Among all examined geographical regions the samples from South Europe and North Africa showed the highest polymorphy level with 100 polymorphic bands (58.88%) out of 167 bands in total. For both analysed samples from Newfoundland only 10 polymorphic bands (7.41%) out of 135 bands were scored. The lowest pairwise genetic distance with GD_J=0.12687/GD_{SM}=0.09714 was detected between LVI_23_670 and Hs22_Ireland. The highest pairwise genetic distance was found between Hs11_El Hierro and Hs3_Newfoundland with GD_J=0.44349 and a GD_{SM}=0.36685.

The UPGMA and NJ tree show a differing arrangement of the sample set (Fig. 46, Appendix 14 II). But, in both trees the samples of *H. aureum* are well separated from the samples of *H. sericeum*. The clade of the *H. sericeum* samples receives maximum BS values (100%) in the UPGMA tree. Additionally, the tree position of the Macaronesian samples (Hs11_El Hierro, Hs12_Madeira) is monophyletic, which is supported by very good BS values.

Furthermore, the samples Hs5_Italy, Hs6_Italy, Hs7_Croatia and Hs15_Sweden are closely related in both calculated trees. The arrangement of Hs16_Sweden somewhat differs between the tree types but is always closely placed to the latter samples. The analysed female and male samples of Hs21_Scotland and Hs1_England cluster together and receive very good BS values. The samples of Hs21_Scotland are closely arranged to Hs18_Hungary and the samples of Hs1_England are closely related to Hs14_Poland and Hs25_Caucasus.

In the NJ tree the German samples cluster together with the exception of G8_Wiesenthau and G10_Rügen. In the UPGMA tree the German samples are closely arranged with the exception of the sample G10_Rügen and the samples from

population D. Most of the analysed German samples are closely related to Hs2_England, Hs22_Ireland, Hs21_Scotland and Hs18_Hungary. The samples from the disjunctive population from Newfoundland cluster together with good BS values and are located within the European samples but occupy different positions in both tree types (Fig. 46, Appendix 14 II).

Table 14: General characteristics of obtained AFLP profiles (primer combination *Eco*RI+AAC / *Mse*I+CTT and *Eco*RI+ACC / *Mse*I+CTA) for analysed world-wide sample set of *Homalothecium sericeum* (with examination of different geographical regions)

world-wide	Newfoundland	European (total)	British Isles[a]	South Europe + North Africa	Scandinavia
number of samples					
35	2	26	7	8	4
polymorphy (absolute numbers of polymorphic bands)/%					
124 (of 175)/ 70.86%	10(of 135)/ 7.41%	123 (of 175)/ 70.29%	67 (of 158)/ 42.41%	100 (of 167)/ 58.88%	67 (of 159)/ 42.14%
detected distances (Jaccard/Simple matching)					
0.12687–0.44349/ 0.09714–0.36685*	0.19670/ 0.14607	0.12687–0.44349/ 0.09714–0.36685*	0.08567–0.26207/ 0.06743–0.21714	0.14599–0.39583/ 0.11429–0.32571	0.19424–0.32639/ 0.15429–0.26857

*Excluding of pairwise genetic distances among German samples

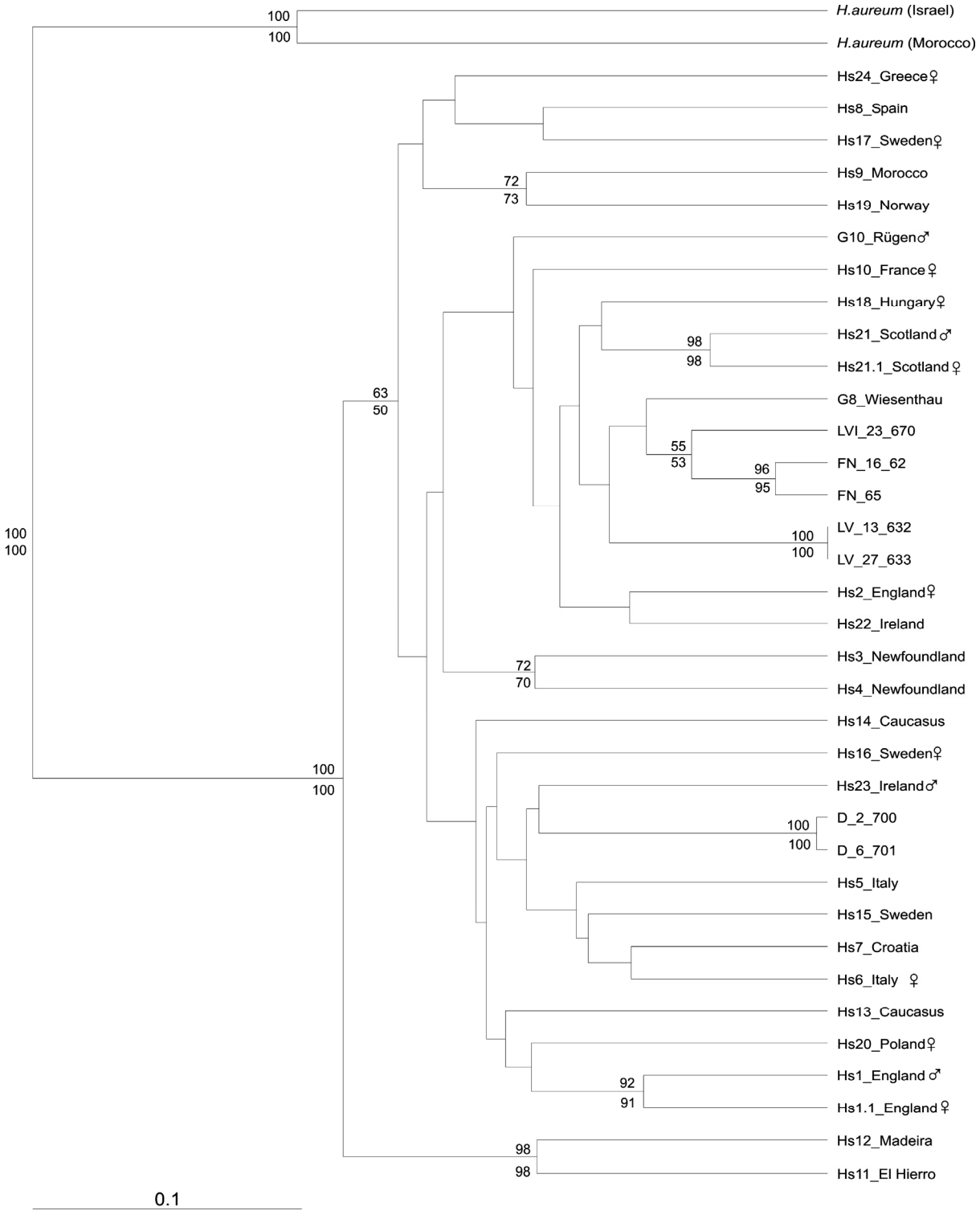


Fig. 46: UPGMA dendrogram based on Jaccard distances (calculated with FAMD 1.108 beta) of the world-wide sample set of *Homalothecium sericeum* (♀ female plant, ♂ male plant).
Numerals above/below branches indicate bootstrap values >50% from calculation of a majority-rule consensus tree with 10,000 replicates (above branches BS values from calculations with the Jaccard coefficient, below branches BS values from calculations with the Simple matching coefficient). The data set contained 0.85% missing data. In addition, the samples of *Homalothecium aureum* were analysed.

6 Discussion

6.1 Morpho-anatomical analyses

6.1.1 Generative reproduction

Within populations of dioicous mosses a lack of one sex or different frequencies of male and female plants can often be observed (LONGTON & SCHUSTER 1983).
In this study, for each analysed species a higher frequency of female plants and hence a skewed sex ratio was detected. The reasons for skewed sex ratios are manifold: e.g. clonal traits, differences in germination capacity and variation in ecological specialisation between female and male plants (BISANG & HEDENÄS 2005). Generally, the sex expression depends on chemical, demographic and environmental parameters and their interaction (STARK et al. 2001).
For the three analysed species, the lowest number of fertile specimens was observed in *A. abietina* and thereby only two plants with antheridia could be found (out of a total of 122 samples). Additionally, the fertile male specimens were from the world-wide data set. BISANG et al. (2004) reported for *A. abietina* a population sex ratio of 7.4♀:1♂ with 39% samples with no sex expression (N=802) and a very low sporophyte production. In this study, on the population as well as all other spatial scales, no sporophytes and a much higher number of sterile specimens were found for *A. abietina* (87.7% based on the total number of samples). In the population Hb, no fertile specimens were identified. This might be due to the season, when the sampling was carried out. The strongly skewed sex ratio and the smallest number of fertile specimens found in *A. abietina*, agrees with the molecular finding that among all analysed species within the German sample set, *A. abietina* has the lowest number of genets.
In contrast, the highest number of fertile female as well as male specimens was identified in *H. sericeum* (cf. Table 3). However, in the studied populations of *H. sericeum* (FN, L and D) no male plants could be detected. On the population scale in *H. lutescens* only one male plant was found in the population Hb. In general, it can

be assumed that the main reason for the low number of detected male plants is the strongly skewed sex ratio in the species.

Sporophytes were only observed in herbarium material of *H. lutescens* and *H. sericeum*. Despite the different frequency of male samples in both species (1.8% in *H. lutescens* and 6.4% in *H. sericeum*, based on the total number of samples per species) and the generally higher number of fertile specimens in *H. sericeum,* sporophytes were similarly frequently detected (1.8% in *H. lutescens* and 2.7% in *H. sericeum*, based on the total number of samples per species). Generally many bryophytes, especially dioicous species, produce sporophytes either rarely, only regionally, or not at all (LONGTON 1997). Although, the fertilisation incidence is dependent on the presence of gametangia (both antheridia and archegonia), the abundance of the rarer sex does not directly affect fertilisation success (BISANG & HEDENÄS 2005). The effect of male plant availability on reproductive success varies among bryophyte species (BISANG & HEDENÄS 2008). Besides the availability of male mates, the fertilisation success and subsequent the development of sporophytes is dependent on the distance of the spermatozoid source. Another possible influence on the fertilisation success is the habitat inclination. In this regard, BISANG et al. (2004) could prove a dependence of reproductive success to substrate inclination of plots in male transplanting experiments in *A. abietina*. Below the male transplants they found a significant higher number of sporophytes and larger distances between the sporophytes and the antheridia, than above. Further explanation for the lack or rarity of capsule production in dioicous mosses could also be e.g. aborted sporophytes [36% in *A. abietina*, unpublished data in BISANG & HEDENÄS 2008)] or the plant architecture. *Abietinella abietina* has loosely spreading branches with relatively few contact points, so that spermatozoid transport via capillary water, which is especially important in dry environments, is more difficult than in plants with robust and densely intertwined branches (BISANG & HEDENÄS 2008). In contrast, the other two analysed species of *Homalothecium* are more robust and especially *H. sericeum* has densely intertwined branches with many contacts.

In the present study, the absence of sporophytes in the studied populations could be mainly explained by the absence of male plants in all three species (with the exception of one male plant of *H. lutescens* of Hb). The lack of archegonia in the

case of *A. abietina* in the population Hb or an unfavourable season for sporophyte development during the field examinations might be further reasons for the absence.

6.1.2 Vegetative reproduction s.str.

In literature, there is no indication of vegetative reproduction s.str. in all three analysed species. Likewise, no specialised propagules could be identified in the present study. But in all three species ±unspecialised caducous organs (stems, branches, leaves etc.) were observed. In *A. abietina*, brood branches, caducous leaves as well as caducous shoot apices could be rarely found. In *H. lutescens*, brood branches and caducous shoot apices and in *H. sericeum* only brood branches were detected.

Vegetative diaspores s.str. as well as unspecialised fragments, which are formed after clonal reproduction, can develop further by already developed rhizoids or initials of those, resp., growing points of shoots as well as dormant buds (CORRENS 1899). Among the three analysed species, rhizoids on all plant parts (predominantly on upper side of the shoot) were most frequently in *H. sericeum*. In *A. abietina*, rhizoids were relatively frequently observed on the basal decaying plant parts and on the branch tips of long thin branches. The function of these rhizoids could be interpreted inter alia as an attachment to the substrate. Furthermore, rhizoids on vegetative diaspores enhance the possibility for successful establishment.

6.1.2.1 Brood branches, caducous shoot apices and caducous leaves

In all three species, caducous branches (brood branches) were identified. Mostly, the highest number of caducous branches could be found on the upper decaying part of the plants. Determinate as well as indeterminate brood branches were detected, the latter more frequent. Perhaps, the ability to establish is increased by the advanced stage of development of the indeterminate brood branches.

In general, the brood branches have rhizoids as well as darker colour at the base. In all species branches could be detected frequently, which had a dark coloured base on the one hand, but showed no rhizoids. Presumably, these are brood branches in an early stage with yet undeveloped rhizoids. If rhizoids were present on the base of

the branch, most of the times there was also rhizoid development on the corresponding part of the shoot (Figs. 22a+36). No details on the characteristics of the corresponding part of the caducous shoot apices can be given here, because caducous shoot apices were only found loose in the dry plant material. Due to the extreme rarity of the caducous shoot apices in *A. abietina* and *H. lutescens*, only a minor role of these organs can be assumed for the vegetative reproduction in these species.

In few cases, caducous leaves, which were found loosely in the dry sample material, were detected in *A. abietina*. Also, in *H. sericeum* leaves with rhizoids at apical plant parts were observed, whereas these plant regions generally showed a pronounced rhizoid development. Hence, a specialisation of these leaves is difficult to prove. All in all, caducous leaves are probably also insignificant for the vegetative reproduction in both species. Furthermore, the rarity of detected caducous shoot apices and caducous leaves is an explanation for the missing reference in literature.

6.1.2.2 Clonal reproduction

Clonal reproduction, fragmentation as well as decay of older gametophyte parts, is very frequent in all three species. Whilst decay of older gametophyte parts leads to self cloning, fragmentation occurs after forced cloning caused by e.g. animal activities [such as animal trampling, foraging by e.g. birds (DAVISON 1976), roe deer (HEINKEN et al. 2001) or rodents] or movements of substrates. Figs. 47–49 exemplifies the decaying process of older basal gametophyte parts, resp. the parts between side branches and the main shoot in *A. abietina, H. lutescens* and *H. sericeum*. Thus, the genetic individuals (genets; clones) are separated into genetically identical, morphologically different and physiologically independent units (ramets) (Figs. 47–49 number 1–3). Vegetative multiplication is a result of the decay of older basal gametophyte parts or branch bases, resp., so that younger green sectors are detached. This can be found abundantly in mosses (LONGTON & SCHUSTER 1983, PFEIFFER et al. 2006). The ramets develop to mature plants (Figs. 47–49 number 4–7) and form further ramets by repeated decay of older gametophyte parts or branch bases, resp. With this mechanism, larger patches can develop and establish.

Vegetative diaspores, which are formed after clonal reproduction, are more frequently in all three species than vegetative diaspores s.str. Hence, clonal reproduction is much more important for formation and expansion of patches and the colonisation of new habitats than vegetative reproduction s.str. The most fragile taxa among the analysed species is *A. abietina*, probably because of the relatively thin shoots and tenuous branches. In general, bryophytes of dry habitats are more brittle than taxa growing in wetter habitats. Hence, dry conditions promote fragmentation. In all three species and on all plant sections fragmentation could be detected. Especially at decaying and dead sections of the plants was observed that parts are absent because of fragmentation. In contrast to fragmentation, decaying occurs much more at the base of the shoot and at the base of the branches, resp. Seldom, decaying was found in restricted areas of the green sections of stems or branches in all analysed species. In these cases, decaying is perhaps induced by microorganisms.

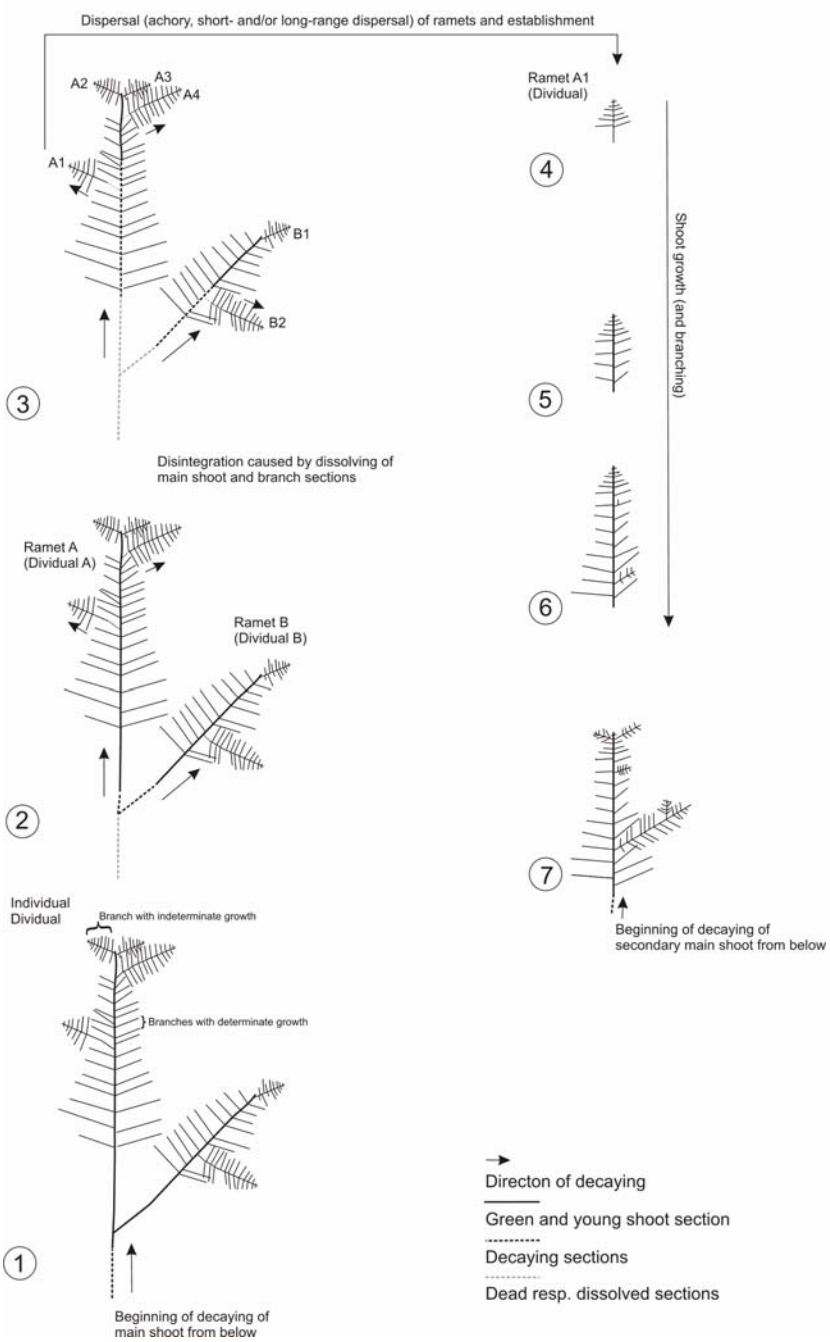


Fig. 47: Clonal reproduction and habitat colonisation in *Abietinella abietina*.

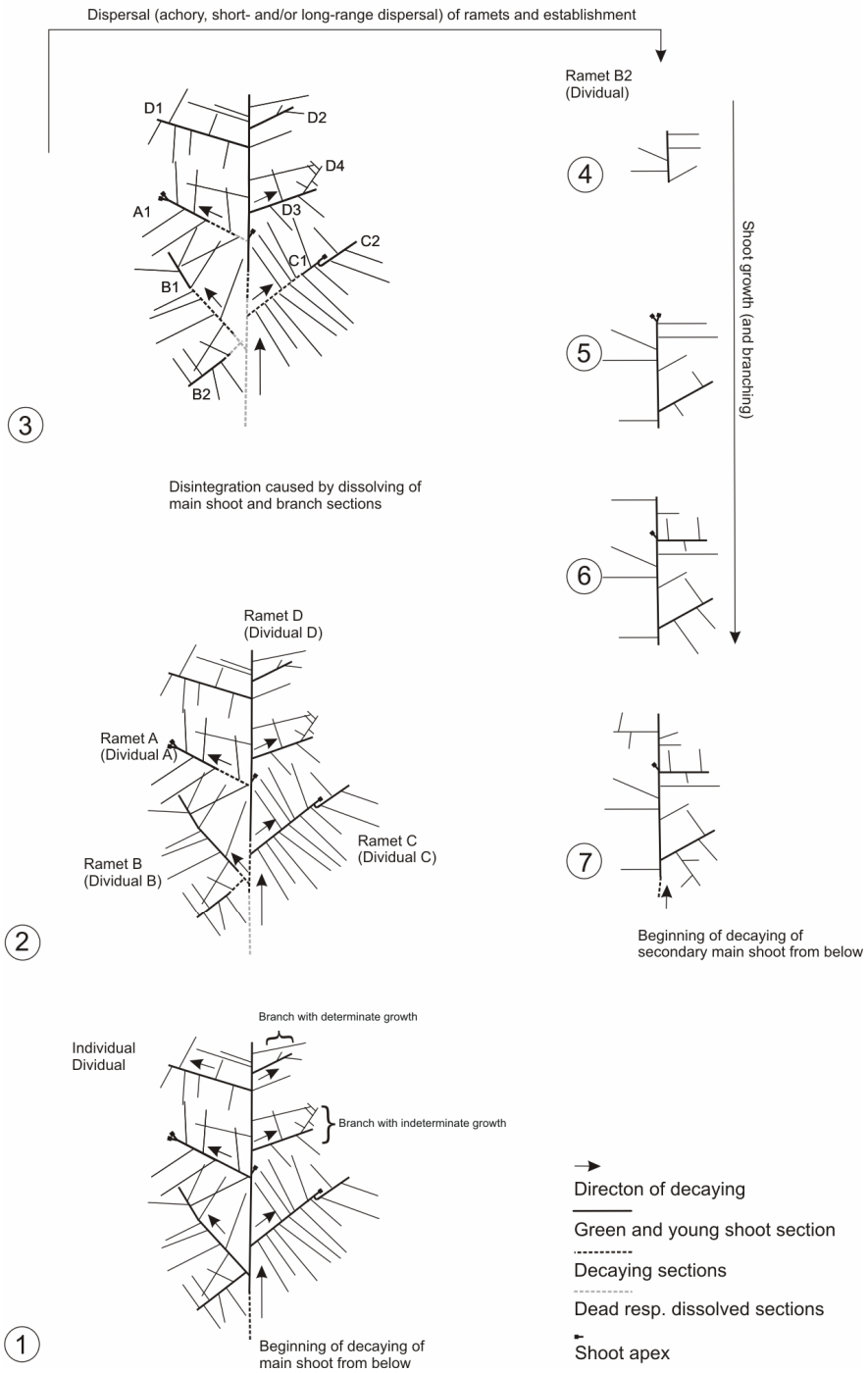


Fig. 48: Clonal reproduction and habitat colonisation in *Homalothecium lutescens*.

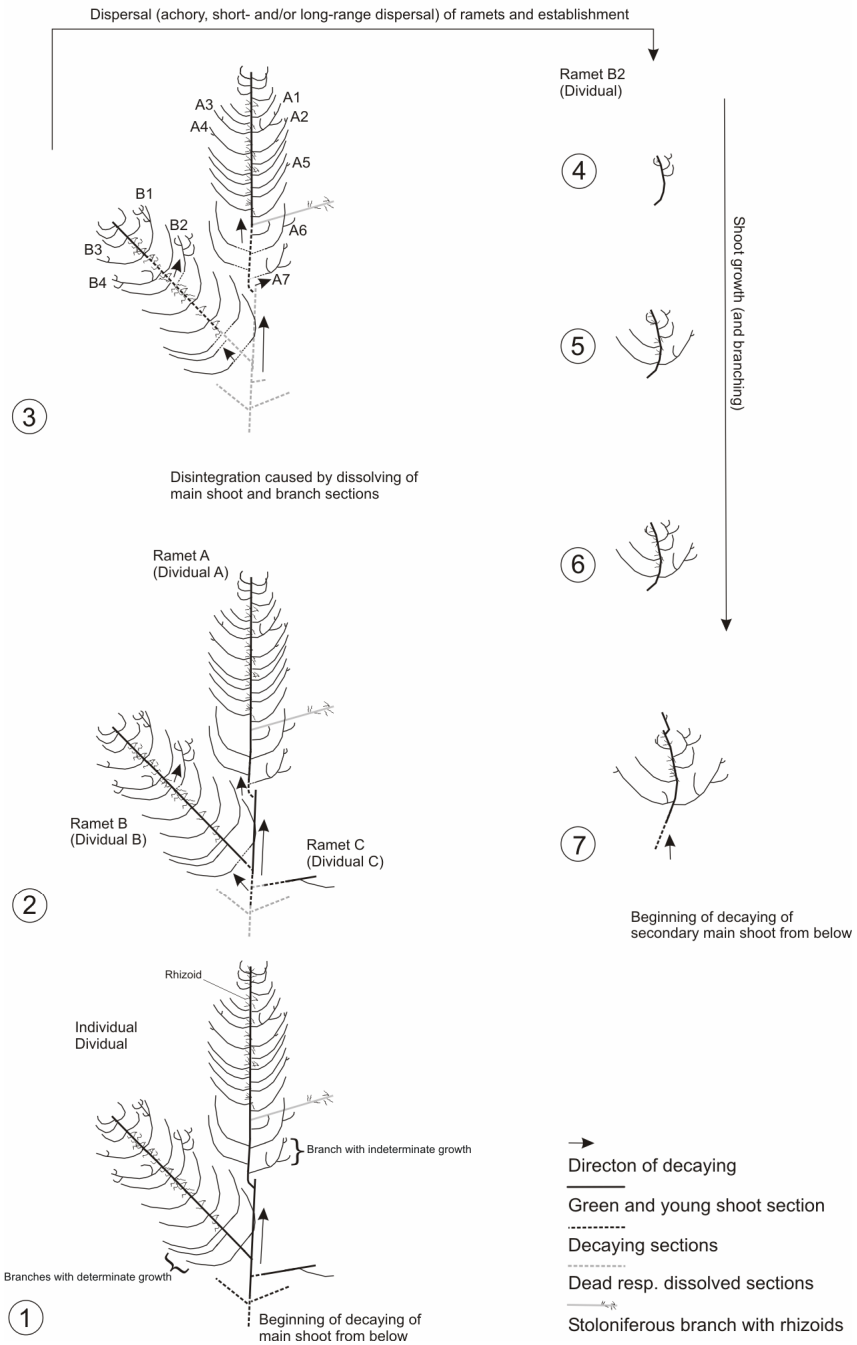


Fig. 49: Clonal reproduction and habitat colonisation in *Homalothecium sericeum*.

For all three species branches with indeterminate growth could be observed (illustrated in Figs. 47–49). Further, different branching pattern were detected for the species studied here. In *A. abietina* branches with indeterminate growth develop mainly close to the parent shoot tip as well as mostly sparsely in longer distance to the tip. In *Homalothecium lutescens* and *H. sericeum* shoots, which consists of successive indeterminate branches were frequently found. Furthermore, laterally of

the shoot growing, indeterminate branches are loosely arranged. All in all, the development of branches with indeterminate growth is mainly responsible for the development of colonies (patches) to their mature growth form, for their maintenance by the replacement of older, dead or dormant shoots as well as for colony expansion, even if slowly. In *H. sericeum* long, bright and nearly leafless branches could be found (Figs. 33+49). Since no hints for the development of new modules could be found on these branches, clonal growth, with resulting expansion of the plant, can be excluded. However, in this case the function of this structure is more likely limited to the attachment of the plant to the substrate.

6.1.3 Dispersal of diaspores

Many bryophyte species may reproduce and disperse via specialised vegetative propagules, i.e. gemmae (CORRENS 1899). Further, for many bryophytes unspecialised fragments are an important or even the only mode of reproduction. Also for the species studied here, mainly those unspecialised gametophyte fragments were found as diaspores. Unspecialised fragments are of different size (CORRENS 1899). Because of their generally larger size, unspecialised fragments will be transported over shorter distances and in smaller number than spores or gemmae. Otherwise, it is advantageous that they may have a higher probability of rapid and successful establishment (KIMMERER 2005). In vitro experiments (CORRENS 1899, MILLER & AMBROSE 1976) as well as observations in the field (HEINKEN & ZIPPEL 2004) showed that even small unspecialised shoot fragments of numerous bryophyte species (e.g. *Hypnum cupressiforme*, *Ceratodon purpureus*, *Pleurozium schreberi*) can easily regenerate and form mature plants. Thus, viable gametophyte fragments are likely to be able to function as vegetative diaspores, if they fall in suitable habitats.

The dispersal distances of such fragments are usually measured in centimetres rather than in meters (KIMMERER 1991, 1994, KIMMERER & YOUNG 1995). Probably, most of the vegetative diaspores in the analysed species fall passively to the base of the parental shoot. Afterwards, it is possible that diaspores carried further away by agents such as animals, water or wind.

6.1.3.1 Zoochory

Dispersal of bryophyte diaspores by animals is thought to be of much less importance than it is for phanerogames (VAN ZANTEN & PÓCS 1981). According to HEINKEN et al. (2001), a high significance of epizoochory in the dispersal of bryophytes to remote habitats is presumed especially for widespread species with rare generative reproduction and no specialised vegetative diaspores. Also *A. abietina*, *H. lutescens* and *H. sericeum* show rather rare generative reproduction and they develop numerous unspecialised gametophyte fragments. In contrast to the diaspores of phanerogames, mosses can be dispersed by animals throughout the year (DAVISON 1976, HEINKEN 2000) and have a high survival rate during autumn, when weather promotes extensive growth (DAVISON 1976).

Generally, to disperse gametophytes they have to fragment at first, for example, by the touch of animals. Fragmentation is easier under dry conditions and in slender mosses with brittle stems (cf. CORRENS 1899, VAN ZANTEN & PÓCS 1981). In addition, various morphological characteristics such as small size, numerous branches and erect or squarrose, acute leaves can also be an advantage for an attachment (HEINKEN 2000, HEINKEN et al. 2001). Species which grow as wefts or short turfs were commonly found on large mammals by HEINKEN (2000) and HEINKEN et al. (2001). *Abietinella abietina* and *H. lutescens* grow in wefts (sensu MÄGDEFRAU 1982) with ±plagiotropic, loosely growing main and lateral shoots, as well as with a covering which is easy to lift from the substrate. In contrast, *H. sericeum* grows in mats (sensu MÄGDEFRAU 1982), whereas the plagiotropic plants are closely attached to the substrate by rhizoids. However, it could be observed during the fieldwork that especially *H. sericeum* has a pronounced ability to attach epizoochorously. Even several days later, fragments of *H. sericeum* were found on the working clothes. Probably, fragment attachment is enhanced by ±acute leaves as well as by the easy fragmentation of the mostly curved branches on dry conditions. Furthermore, VAN ZANTEN & PÓCS (1981) reported that *Thuidium furfurosum*, which is morphological similar to *A. abietina*, attached to clothes of humans during dry weather in New Zealand.

Birds for example can be an important factor of dispersal of mosses in different ways. Since many birds procure a large part of their food by foraging on the ground and

thereby scraping or tossing leaves or other litter aside, they scatter portions of mosses during the feeding (DAVISON 1976). In the study areas, it is conceivable that birds regularly search for food. For example, numerous individuals of *Prunus spinosa* grow in the area of Hb and several scrub species can be found in the area of Mb (*Rosa canina*, *Corylus avellana, Viburnum lantana, Frangula alnus, Cornus sanguinea* and *Cotoneaster integerrimus*). The fruits of these shrubs are eaten and dispersed by birds. Besides plants, also soil invertebrates are sources of bird food. The gametophytes of mosses could be fragmented during the foraging and it is possible that fragments or portions of mosses are dispersed in short distance. Further, BREIL & MOYLE (1976) reported that bryophytes, frequent epigeic and pleurocarpous species, are often used as nesting material by several bird species. A supporting factor in the dispersal of these species may be gametophyte fragments, which were lost during the transport. During the study period, which was out of the breeding season, no collecting activities of birds could be observed in the study area. In Lindena and Dollenchen parts of a few centimetres in diameter in the middle of some patches were missing on the walls. One explanation could be that birds plucked out pieces of patches for nest-building and foraging. In most cases dispersal by birds occurs on a small scale. Further, long range dispersal of small fragments or bryophyte spores, which are attached to the plumage of the birds, is difficult to assess and presumably seldom (DAVISON 1976).

Especially for the plots at Hb it is possible that sheep (*Ovis ammon aries*) played an important role in the dispersal of vegetative diaspores of *A. abietina* and *H. lutescens* during the Middle Ages to the beginning of 20th century. According to FISCHER et al. (1996), almost all plant species in grasslands can be transported by sheep if they come in contact with the wool. The number of dispersed fragments is dependent on the cover of bryophytes in the analysed habitat as well as the adaptation of species to epizoochory. In the present study, the analysed species are abundant in all studied plots (cf. Appendices 2+3), which increases the probability of epizoochorous dispersal.

Further, in the case of Hb, dispersal by roe deer (*Capreolus capreolus*) may also play a role. A high frequency of roe deer can be assumed at this slope because of an adjacent forest and a trail between HbI and HbIII. That fragile shoot fragments are

often transported on fur and hooves of roe deer, was detected by HEINKEN et al. (2001). HEINKEN (2000) found also epizoochory of bryophyte diaspores in dog fur. This kind of dispersal is especially conceivable for the plots of Mb, since several walkers with dogs could be observed during the fieldwork. The detected size of dog-dispersed bryophyte fragments (HEINKEN 2000) varied between 1.5 and 41 mm (mean length of 10.5 mm) and in the case of roe deer dispersal between 0.5 and 35 mm (mean length of 3.6 mm) (HEINKEN et al. 2001). In the present study, the detected fragment length (cf. Table 4) corresponds with the length of dispersed fragments found by HEINKEN (2000), HEINKEN et al. (2001) and HEINKEN et al. (2007). In addition, at the location Mb dispersal could be affected recently by extensive human activity, because the area was used for police training in the former GDR and limestone quarrying.

Dispersal of fragile shoot fragments by rodents was reported by KIMMERER & YOUNG (1996). Rodents as dispersal agents are generally imaginable for all plots, but especially for the wall top in Freyburg, since a large area with rodent droppings was found at the top of the wall (Appendix 8). Besides vertebrates, bryophytes can also be transported by invertebrates, such as slugs (KIMMERER & YOUNG 1995) or ants (LAAKA-LINDBERG et al. 2003, HEINKEN et al. 2007). Endozoochory is probably rather rare in bryophytes. PARSONS et al. (2007) detected bryophyte fragments (ranging from fragments of whole shoots to separated leaves) in the droppings of flying foxes (*Pteropus conspicillatus*). Since there is a lack of such studies in Central Europe, it is difficult to assess the role of endozoochory for bryophytes in the local vegetation.

6.1.3.2 Anemochory

The ability of diaspores to get into higher air streams is essential for anemochory. As MARSHALL & CONVEY (1997) detected, spores are more abundant in the air than plant fragments. Further, because of their larger size, vegetative bryophyte diaspores disperse by wind over shorter distances than spores (e.g. LONGTON & SCHUSTER 1983, KIMMERER 1991). On the contrary, the probability of dispersal over longer distances increases with decreasing size of the diaspores (SCHUSTER 1983). SABOVLJEVIĆ & FRAHM (2008) reported dispersal of vegetative diaspores over distances of several 100 km by wind for sterile *Campylopus oerstedianus*. Since in

A. abietina clones with large spatial dimensions have been found [the largest spatial dimension with ca. 170 km was yielded for the genet of A31_Sweden (Åsele) and A33_Sweden (Jämtland)], dispersal of vegetative diaspores by wind over larger distances could be assumed as well. In the case of a thunderstorm or hurricane, vegetative diaspores could attain longer distances. In this way also larger vegetative diaspores, such as complete plants or agglomeration of several plants, could be dispersed.

Especially, in dry and open habitats, such as the plots at Hb and Mb as well as the analysed walls, wind is probably an important dispersal agent for at least short range dispersal of vegetative diaspores. This is in conformity with Düll-Hermann's assumption that besides dispersal by grazing animals also anemochory is important in the dispersal of dry structures of species with rarely produced sporophytes in grasslands (DÜLL-HERMANNS 1985). Among the plots in Thuringia, on MbI the densest cover of vascular plants was observed. Hence, wind dispersal is probably not so important than in the southern exposed, more open slope of the plots from Hb. For both species at Hb it could be assumed that dispersal by wind probably took place from HbIII downward to HbI, since samples of the same clone appeared in both plots (clone_1 in *A. abietina* and clone_Hb/Mb in *H. lutescens*, resp.). For *H. sericeum* it is conceivable that dispersal by wind is also important on walls, at least over short distances. BRANDES (1987) also assumed that, besides animals, wind is an important dispersal agent for plants on walls. But also barochory seems to be an important dispersal agent for the downward dispersal of diaspores from the upper wall surface to the ground. For example patch LV_4 in Lindena probably developed after the establishment of one or more dispersed vegetative diaspores from the upper patches of the wall.

MUÑOZ et al. (2004) could demonstrate that recent bryophyte distributions are mainly influenced by wind connectivity and less by geographic proximity. They found that anemochory of spores, as well as vegetative diaspores, along the main wind drift is the driving force for the recorded distribution pattern in the study area (Sub-Antarctic Islands). Regarding the long-distance transport, the effects of the harsh climatic conditions, prevailing in high altitude air (such as strong UV radiation, desiccation and freezing), on the viability of spores of bryophytes from the Southern Hemisphere

were examined by VAN ZANTEN (1978) and VAN ZANTEN & GRADSTEIN (1988). They reported for many moss species long range dispersal as a real possibility, provided that the species produce spores. Among the analysed species, long range dispersal of spores by wind is currently most conceivable in *H. sericeum* and *H. lutescens*, given the detection of generative reproduction, even if seldom (Table 3). However, since the genus is divided into a Eurasian and a North American lineage, HUTTUNEN et al. (2008) assumed that there is an intercontinental barrier to gene flow in the genus *Homalothecium*.

6.1.3.3 Hydrochory

Bryophyte diaspores can also be dispersed by water (VAN ZANTEN & PÓCS 1981, DALEN & SÖDERSTRÖM 1999). In case of the analysed species, which occur in dry habitat, dispersal by water can only take place via rainwater runoff. The dispersal of vegetative diaspores by water over shorter ranges seems especially possible for the populations Hb of *A. abietina* and *H. lutescens*, which are located on a slope with an inclination of ~30°. On the plane plots at Mb dispersal by water is, on the contrary, probably insignificant.

In the case of *H. sericeum*, rainwater, which flows down between the stones of the wall, could play an important role in the dispersal of diaspores. This assumption is supported by the finding that *H. sericeum* occurs predominantly in joints on the vertical surface of the wall of FN, the potential track of rain flows. An occurrence of *H. sericeum* in joints was also found on the other analysed walls. However, the dominant occurrence of this species in joints of the cobblestone walls might also be caused by the calcareous mortar. In any case it seems that rainwater can transport diaspores between the stones and subsequent lead to a colonisation of the joints. Generally, to be dispersed by hydrochory, the size of vegetative diaspores has to be rather small (e.g. apices, branches) in all three species. Branched plant fragments are probably too heavy to be transported via rainwater runoff.

6.2 Molecular analyses

6.2.1 Discussion of the method

The molecular analyses were conducted using the AFLP-method (amplified fragment length polymorphism). This method generates banding patterns of each DNA, irrespective of the origin and complexity. The quality and number of the detected AFLP fragments depends on which primer combination was used (VOS et al. 1995). In addition, primer combinations with a too low resolution can cause underestimated genetic distances. Hence, those primer combinations are not sensitive enough for differentiation between closely related genotypes. On the contrary, a too high resolution of the primer combination can cause that identical genotypes are separated or that genetic distances between closely related genotypes are overrated. Generally, AFLPs are deemed to be a very accurate, fast, highly reliable and reproducible fingerprinting technique (compare, e.g. JONES et al. 1997, MUELLER & WOLFENBARGER 1999). Additionally, it should be noted that incomplete restriction of the DNA due to either poor DNA quality or insufficient restriction enzymes may result in partial fragments. Hence, incomplete restriction might be interpreted as false polymorphisms, i.e. when one sample is partially restricted and the other is not.
This method makes it not only possible to detect genetic diversity within species [e.g. *Populus nigra* (ARENS et al. 1998), *Populus nigra* subsp. *betulifolia* (WINFIELD et al. 1998)] but also within populations [*Taraxacum officinale* (VAN DER HULST et al. 2000), *Avicennia germinans* (CERÓN-SOUZA et al. 2005)]. Due to the high resolution ability of the AFLPs it is possible to identify genetically identical dividuals (ramets) of a genet (clone) (MUELLER & WOLFENBARGER 1999). Clone identifications were realised with this method by e.g. DOUHOVNIKOFF & DODD (2003) in *Salix exigua*, ZIEGENHAGEN et al. (2003) in *Galium odoratum* as well as in studies, similar to this one, especially focussing on habitat colonisation and the role of vegetative reproduction s.l. in *Rhytidium rugosum* (PFEIFFER et al. 2006), *Asarum europaeum* subsp. *europaeum* (PFEIFFER 2007), *Maianthemum bifolium* (LIESKE & PFEIFFER 2007) and *Tussilago farfara* (PFEIFFER et al. 2008).

In general, dividuals of a genet should have an identical banding pattern. But in bryophytes the possibility of somatic mutation, which leads to genetic variation, has often been reported (LONGTON 1994, BURYOVÁ & HRADÍLEK 2006). Any mutation which occurs in the single apical cell of a branch or young individual can subsequently be transferred throughout a new plant (NEWTON & MISHLER 1994). Hence, in this way, vegetative diaspores s.l. and resulting ramets could be genetically different to their mother plant. Since clonal species can have very long life spans (SCHUSTER 1983, KLEKOWSKI 1997) it is possible that somatic mutations occur more than once in a genet. It seems that somatic mutation is the most likely cause for genetic variability within clumps of *Bryum argenteum* and *Hennediella heimii* (SELKIRK et al. 1998) as well as populations of *Sarconeurum glaciale* (SKOTNICKI et al. 1999). The revealed genetic variability within genets in the present study might be caused by somatic mutations as well (cf. Figs. 39+42+45 and Appendices 12 I–14 I). Further, NEWTON & MISHLER (1994) even assumed that somatic mutation in asexual lineages can provide levels of genetic variation equivalent to those of pure sexual lineages.

For a positive proof of clone identification it is important to receive a high resolution and enough AFLP fragments. If the number of fragments is too small, individuals with low genetic differences could be incorrectly assigned to one and the same genet (MUELLER & WOLFENBARGER 1999). Although at least 200 AFLP bands should be analysed in general for surveys of genetic diversity, population structure or genetic relatedness (CAVERS et al. 2005, SINGH et al. 2006, BONIN et al. 2007), it is sometimes difficult to achieve that number in practice. In the case of *H. sericeum* the number of received AFLP bands falls below 200 in the present study (Germany-wide 161 bands, world-wide 175 bands). This deficit of bands might be a reason for the different placement of some samples in the UPGMA and NJ dendrograms of *H. sericeum*. In *A. abietina* as well as in *H. lutescens* the number of received bands was about 200.

The method can only be applied to a certain extent to analyse the relationship of samples from larger geographic scales, since AFLP is prone to homoplasy. Homoplasy occurs by co-migration of nonhomologous fragments at the same position in an AFLP profile or by independent losses of a fragment. Hence, homoplasy leads to an underestimation of genetic diversity among samples and

restricts the resolution in studies (MEUDT & CLARKE 2007). By using the Jaccard coefficient, the homoplasy effect was reduced in the present study. The coefficient takes only those bands into account that are present in at least one of the two samples, hence the coefficient is unaffected by homoplastic absent bands.
The accuracy of estimates of the genetic diversity in populations depends on the number of analysed samples per population. Thus, KRAUSS (2000) reported that for about 30 individuals per population the most accurate results can be yielded in AFLP data. In the present study this number was analysed for at least one population of each species.
Misinterpretations could arise during the data scoring, because the bands can differ strongly in their intensity. Small variations in the DNA concentration of samples, which were loaded onto the gel, might have an influence on intensity. However, this variation may lead to false conclusions regarding the presence and absence of fragments, as also mentioned by VANDERPOORTEN & TIGNON (2000). PCR artefacts are a further source of errors. To minimise misinterpretations, uncertain fragments were recorded as missing data (marked by an "?") or omitted if the fragment was uncertain for several samples. Misinterpretations concerning the determination of clones could be minimised by the definition of a threshold for clone identity. This will be described in the next chapter.

6.2.2 Data evaluation

Although all ramets of one genet are principally genetically identical, somatic mutations can occur during lifetime and hence lead to small genetic differences (e.g. NEWTON & MISHLER 1994). On the other hand, despite the fact that the AFLP technique is considered as a very accurate, highly reliable and reproducible method (e.g. JONES et al. 1997, MUELLER & WOLFENBARGER 1999), error rates range from 2% to 5% (AJMONE-MARSAN et al. 2002, BONIN et al. 2004, BONIN et al. 2007) and genotyping errors are possible. Further pitfalls such as sample contamination, PCR artefacts, human errors (e.g. scoring errors) or low quality of DNA may cause small differences between samples of the same clonal lineages, which are then erroneously assigned to different clonal lineages (DOUHOVNIKOFF & DODD 2003,

BONIN et al. 2004). According to BONIN et al. (2007) in AFLP genotyping mainly two types of errors prevail: allele homoplasy and scoring errors.

In the present study methodical errors were reduced by duplicate molecular analyses on two levels. Firstly, the same material of one sample was analysed twice for each moss species (samples were only scored but not included in the calculations) and secondly, two samples of different branches of the same shoot were examined for each species.

In *A. abietina* as well as in *H. lutescens* the analysed double samples of different branches of the same shoot revealed a reproducibility of 100%, whereas the double sample of *H. sericeum* showed one difference in one fragment. This difference might be caused by somatic mutation or one of the above mentioned pitfalls except scoring errors, because the difference was verified repeatedly. In spite of the overall high reproducibility of the double samples (duplicate samples of the same branches as well as of different branches of the same shoot), the criteria for clone identification can not be 100% identical fingerprints of clone members for the following reasons. Firstly, minor differences between samples of one clone may occur due to the above mentioned technical pitfalls. Secondly, especially in species with mainly vegetative and low generative reproduction, it has to be assumed that occurring somatic mutations can sum up over the partly considerable life-span of clones.

Based on the reasons discussed above, a threshold for determining clonal identity was used to avoid excluding ramets from their clone due to a similarity range that is set too high. The determination of the threshold was done by using histograms based on pooled distance values.

In clonal taxa, the first peak in histograms of pooled genetic distances (Figs. 38+41+44, Appendix 11) represents the distances between ramets of one genet. The second peak typically summarises genetic distances of closely related genets (DOUHOVNIKOFF & DODD 2003). The valley in-between the first both peaks can be interpreted as an indication for the threshold (MEIRMANS & VAN TIENDEREN 2004). In previous examinations of phanerogams, thresholds for clonal identity and genotype assignment were determined e.g. by ARENS (1998) with SC_{SM}=0.98, DOUHOVNIKOFF & DODD (2003) with SC_J=0.988, LIESKE & PFEIFFER (2007) with SC_{SM}=0.9627 and PFEIFFER et al. (2008) with SC_{SM}=0.9484 in AFLP profiles. In this study the threshold

for clonal identity in *A. abietina* was determined with $SC_{J/SM}$=0.90580/0.93720, in *H. lutescens* with $SC_{J/SM}$=0.95930/0.96804 and in *H. sericeum* with $SC_{J/SM}$=0.91379/0.93252. One explanation for the different level of genetic similarity between the phanerogams and the studied bryophytes could be that, despite diligent cleaning, the plant material was contaminated by fungi or other microoranisms in the field. Since the method has the potential to amplify any present DNA, it may have consequences for the resulting AFLP profile. Furthermore, the analysed mosses were in closer contact with soil as well as with soil microorganisms. Thereby, the contamination potential was higher than in the phanerogams. A further explanation might be the dominant vegetative reproduction and the rare events of generative reproduction in bryophytes. It is conceivable that with continuous vegetative reproduction and repeated somatic mutation, ramets emerge, which differ in several fragments. Differences in somatic mutation rates could be related to the lower level of genetic similarity of the thresholds in *A. abietina* and *H. sericeum* compared to *H. lutescens.* The impact and frequency of somatic mutations in clonal species has to be the subject of further studies.

In *A. abietina* and *H. lutescens* the histograms of pooled genetic distances showed a second minimum, which corresponds fairly well with the received maximum distances from the regional samples (Tables 5+10). Further, the genetic distances between regional samples and closely related genets from the German scale were included in the second peak. In *A. abietina* these German wide samples are grouped in clade_A, clade_B or clade_C, resp. (Fig. 39, Appendix 12 I). In *H. lutescens* these German wide samples (G4_Freyburg, G3_Saalburg and G9_Rüdersdorf) are closely related to the samples of the region of Jena (Fig. 42, Appendix 13 I). The third peak included genetic distances between samples which were spatially distant from each other. In the case of *A. abietina*, a pronounced gap in-between the second and third peak is visible. The third peak summarised the genetic distances between samples of the clades A, B and C (see Table 7).

6.2.3 Genetic structure within and among populations

6.2.3.1 *Abietinella abietina*

In the study region in East Thuringia only ten genets of *A. abietina* were detected. An unambiguous indication of frequent vegetative reproduction s.l. in *A. abietina* is that the analysed populations Hb and Mb showed a relatively uniform genetic pattern with few genets. Both analysed populations are multiclonal, while two genets dominated each population (Fig. 39, Appendix 12 I). Most members were detected in clone_1 (43 samples) which was mostly found in Hb as well as in Mb and the surrounding of the plots. Dividuals of this genet were also detected in r6_Rabis, r1_Cospeda, r2.1_Ammerbach and r3_Osmaritz. The latter two sites are situated nearby the plots of Hb. The AFLP fingerprinting yielded that the sample r1_Cospeda is 100% genetically identical with HbIII_1_410 and Hb_surr_442. Remarkable is the relatively large spatial distance of ~5.8 km between these populations. This shows, on the one hand, the ability to disperse vegetative diaspores over longer distances as well as on the other hand the importance of vegetative diaspores for habitat colonisation. Clone_2 is the second prevalent genet in Hb (HbI+HbII) and was furthermore only detected in Ammerbach (r2.2_Ammerbach) and as surrounding sample of Mb. For the second prevalent genet in Mb (clone_3) only one sample outside of Mb was found in the surrounding of Hb. Clone_4 includes, with the exception of Mb_surr_862 and r7_Jena/Leura, only samples which were located northeastward of the study area. This genet attain a dimension of at least ~42 km. Due to the found dimension, distribution and frequency of the detected clones, it can be assumed that they are very ancient and have existed in this region for a long time.

In general, the analyses revealed that the populations Hb and Mb are dominated by only few and at the same time genetically similar clones. But the yielded results for the samples HbI_166 and Mb_surr_862 show that colonisation of more distantly related genets is also possible. Since HbI_166 was found as a fragment on plot HbI, the colonisation of this genet probably took place just recently and therefore, the genet has not yet established. Further HbI_166 showed the highest detected genetic distances among all regional samples (GD_J=0.28503/GD_{SM}=0.20532 with r4_Jena/Leutra and GD_J=0.32857/ GD_{SM}=0.22964 with r5_Dürrengleina). This might

be another indication, that the genet just recently colonised the region of Jena. For HbI as well as MbII dominant large patches were observed, whereas the development of these patches might have been possible in different ways. Enlargement might occur through repeated clonal growth and subsequent clonal reproduction of single patches or by fusion of different patches. The affiliated patches of such fusion could thereby originate from the same genet (e.g. patch MbII_1, HbI_58) or from different genets. The latter could explain the patch structure of MbI_33, which include at least the two genets (Appendix 5). Another explanation for the development of multiclonal patches is that diaspores of a different genet were inserted in an existing patch and established there.

The spatial structures of the plots showed that dividuals of one genet are often spatially close (e.g. HbII_1_396 and HbII_2_401 or HbI_12_168, HbI_25_199 and HbI_26_202 or MbI_69_806 and MbI_77_767). Hence, the associated patches of these dividuals could have developed after short range dispersal of vegetative diaspores s.l. of an existing patch or could be the remains of a previous larger patch.

The number of singular shoots and shoot fragments on these plots (Appendices 4–5) suggests that short range dispersal of vegetative diaspores s.l. in *A. abietina* is frequent.

In particular, in the analysed populations of *A. abietina* the number of genets compared to the number of collected ramets is relatively low. It should be noted that the number of genets could possibly be higher, because the threshold for clonal identity was set relatively high compared with the value of *H. lutescens* as well as the values found in literature (cf. chapter 6.2.2). Nevertheless, the number of samples with identical fingerprints as well as the spatial distance between these samples, indicate the high importance of vegetative reproduction in the life cycle of this species (Fig. 39, Appendix 12 I). That generative reproduction plays an inferior role in the life cycle of *A. abietina* was demonstrated by the results of the morphological analysis (Table 3) and is in accordance with the findings of e.g. DÜLL-HERMANNS (1985) and HERZOG (1926).

6.2.3.2 *Homalothecium lutescens*

In contrast to *A. abietina*, which was analysed in the same area, the identified genets in *H. lutescens* are less widespread, mostly restricted to one population and higher in number (Fig. 42, Appendix 13 I). In clone_r the largest dimension of a clone (~8 km) was detected.

Both analysed populations are multiclonal with ten genets in Mb and 14 in Hb, resp. Considering the ratio of number of genets to the total number of samples, the found number of genets is relatively low in the population Hb in comparison to the population Mb (Table 10). Also the plot structure reflected the low number of genets in the population Hb, because only one genet (clone_Hb/Mb) was mainly identified in HbI. Thirty two samples of the clone_Hb/Mb were observed in the population Hb, whereas in population Mb only two dividuals of this clone were detected. The largest patch of HbI (patch HbI_22) and most of the examined patches across plot HbI belong to clone_Hb/Mb. In contrast to Hb, the population Mb is dominated not only by one genet, but at least by three genets. The respective samples of the clones were located closely to each other. One explanation for the difference in the number of genets in both populations could be the difference in age of the habitats. The habitat of Hb is more ancient and natural, whereas the habitat of Mb is still young in its present structure. Over time, a small number of genets could establish in the population Hb, whereas several genets might have coexisted in the younger habitat of Mb, but until now, no specific clone has prevailed there.

In contrast to HbI and HbII, in HbIII four different genets within only one m² were identified. The differences between these three plots of Hb could be the result of different habitat structures, because HbIII is more open than the other two plots. In open habitats, for example, insertion of diaspores is easier e.g. by means of dispersal by wind. Additionally, due to lower competition in the more open habitat, a higher number of genets could establish.

Besides the conditions and the development of the habitat, there are further factors which affect the number of genets in populations of clonal species. On the one hand, clonal growth and the resulting competition between genets could cause the displacement of genets and genetic impoverishment. Hence, only few genets would survive and dominate in such populations. On the other hand, due to clonal growth it

is possible that female and male genets come into contact with each other and reproduce sexually. The competition between the new genets could allow the establishment of genetically different genets and this would increase the genetic diversity of populations. It is the interaction of all these factors that influence the clonal diversity in populations.

The development of patches on the plots is possible in different ways. Smaller patches of the clone_Hb/Mb on HbI could have developed after the dispersal of vegetative diaspores s.l. of the patch HbI_22 and hence could be outposts of the large patch HbI_22. In this way, the genet could have expanded spatially. Indicators for short range dispersal were the numerous singular plants or fragments around patch HbI_22. Otherwise, the smaller patches could be remains of a former larger and area-wide patch of the clone_Hb/Mb. That patches can decrease in size, can be seen, for example, on the patches HbI_21 or HbIII_1, which partly showed a loose cover. Non-covered areas were also detected within patches (Appendix 6). These areas could be a result of a decrease in coverage or the fusion of different patches.

Molecular analyses showed that most examined patches are uniclonal. It is conceivable that these patches developed from a single diaspore through consequent vegetative multiplication. In the case of HbIII_1, Mb_7, Mb_14 and Mb_20 was found that the patches are composed of more then one genet. Causes for the development of multiclonal patches can be manifold. One reason might be a fusion of two or more patches of different genets. The dispersal of genetic different diaspores within an existing patch might be a further reason.

As already shown in the results of morphological analysis, generative reproduction in *H. lutescens* seems to be more frequent than in *A. abietina*. On the one hand, female and male plants were detected at all in *H. lutescens* in the region of Jena, which thus allows a generative reproduction. On the other hand, molecular analysis showed a higher genetic diversity in *H. lutescens* with 33 genets in contrast to only ten genets in *A. abietina* in the region of Jena. In spite of the low number of detected male plants in *H. lutescens*, it seems that generative reproduction takes place once in a while. The dendrogram (Fig. 42) illustrates that all regional samples (incl. population Hb and Mb) form a cluster. The close relation of the samples indicates that the local

populations mostly developed through vegetative reproduction s.l. and generative reproduction occurred between more or less genetically closely related genets.

6.2.3.3 *Homalothecium sericeum*

A similar proportion of genets to the number of samples was found in *H. sericeum* as in *H. lutescens* (Tables 10+13). The highest number of clone members with a 100% identical AFLP profile was detected in the population D (four of nine analysed samples). In contrast, only two samples with an identical AFLP profile were found for the 30 analysed samples in the population FN (Fig. 45, Appendix 14 I). One explanation for the relatively high number of samples with identical fingerprinting in the population D is that it is relatively young and consequently the modification of genotypes by somatic mutation is probably lower than in older populations. The low colonisation level of *H. sericeum* is an indication that the population D is still young. Furthermore, the wall is generally sparsely covered with vegetation (Appendix 3). The relatively low number of genets found in Dollenchen could be a further indication of a young, still growing population, since the number of genotypes depends on colonisation events of new genets, as well as the presence of generative reproduction. Both could increase genet diversity during time. Due to cleaning and elimination of plants, even on walls young populations can be found.

In Lindena two clones were identified. Clone_L1 was mainly detected on the wall surface of the plot LV as well as on the large patch LV_4 in front of the wall. This patch evolved probably from ramets of clone_L1, which have fallen off the wall. The colonisation and maintenance in *H. sericeum* on the ground could have been supported by cutting grass, which caused disintegration of ramets and subsequent dispersal. Furthermore, clone_L1 was also detected at LI, LII and LIV. Clone_L2, with only two members, was found at LIII and LVI (Appendix 9).

Genetically distantly related samples in the population (e.g. LIII_1_621 and LV_77_639 with GD_J=0.23571/GD_{SM}=0.20245) suggest a repeated colonisation and establishment of different genets in this population. Thus, the molecular analyses revealed that the sample L_surr_669 is closely related to rB1_Riedebeck and rB3_Wehrenzhain as is the samples G7_Schnellmannhausen and G4_Zimmritz.

The population FN is probably the oldest among all analysed populations in *H. sericeum*. On the one hand, the wall is several centuries old [probably from the time, the Neuenburg was build (11th century)], but it is likely to have been cleaned several times by men. Moreover, the top of the wall is partially completely covered with dense patches of *H. sericeum*, which again indicates that the colonisation did not take place recently. The molecular analyses indicate that the wall of FN was colonised by different genets with larger genetic distances (see Table 13). Hence, it can be assumed that in this case a multiple colonisation and establishment of different genets has taken place.

The largest detected patch in FN, as well as in general, is FN_11 with a dimension of ~7.7 m. This patch developed out of at least two genets, whereas a fusion of different patches could have been possible (Appendix 8). One point, at which patches might have joined to patch FN_11, could be at ca. 8 m. To the west of this point of the patch, only dividuals of clone_FN1 were found. An enlargement of this part of the patch has happened through vegetative multiplication. A further point of fusion could have been at 5.8 m. Only eastward of this point (4.6–5.8 m), in patch FN_11 a different genet than clone_FN1 was identified. The genetic and morphologic structure of patch FN_11 supports the assumption that after the colonisation of genetic different, as well as genetic similar, diaspores at first at least three patches have developed through consequent vegetative multiplication. At the time when the study was conducted, the patches apparently united to one large patch. It seems that short range dispersal of vegetative diaspores and their successful establishment occurs frequently in *H. sericeum*, which is demonstrated by the colonisation patterns of the genets on the analysed walls. For example, members of clone_FN1 were found at the neighbouring patches of patch FN_11 (e.g. FN_8, FN_9 and FN_15) and patches of clone_FN3 were only detected within the first two metres of the analysed wall section. Compared to the other two studied species, the spatial dimension of detected clones are quite low. The largest identified dimension of a clone in *H. sericeum* is ~80 m and was found within the clone_FN2 (between FN_18_69 and FN_surr_108). Due to the relatively high threshold for clonal identity, it is possible that, similar to *A. abietina*, the number of genets might be higher and the spatial

dimension of clones might be lower. However, the results yielded that the clones of *H. sericeum* have the lowest spatial dimension among the three studied species.

A lower dispersal ability of the vegetative diaspores s.l. could explain the spatial restriction of clones, but, compared with *H. lutescens*, in *H. sericeum* smaller vegetative diaspores s.l. were found (see Table 4). Hence, the dispersal range must be at least similar as in *H. lutescens*. Furthermore, since many vegetative diaspores s.l. were detected during fieldwork and the morphological studies, dispersal of vegetative diaspores s.l. is generally possible. Another explanation for the detected spatial restriction of clones could be that colonisation of new uncolonised habitat occurs by spores rather than by vegetative diaspores s.l (Newton & Mishler 1994). Since walls are cleaned once in a while, they offer frequent suitable conditions for germination of spores. The fact that generative reproduction is more important in the life cycle of *H. sericeum* than in *A. abietina* has already been assumed because the findings of the morphological examinations of the generative reproduction. Spores are generally higher in number, smaller [in *H. sericeum* 8–22 (–24) µm; in *H. lutescens* 12–18 (–20) µm (HOFMANN 1998, NEBEL et al. 2001) and in *A. abietina* (9–) 12–16 (–18) µm (NEBEL & SCHOEPE 2001, SMITH 2004)] and more exposed than the vegetative diaspores. All these characteristics of spores increase the chance of dispersal by wind. Hence, it is easier for spores to reach new habitats than for vegetative diaspores. The relatively high genetic distance values found in population FN and L indicate that habitats on their part are probably more often colonised by new genets of *H. sericeum* than by the other two species. Further, the spatial expansion of a genet of *H. sericeum* in a habitat is thereby probably limited by the competition for resources. However, the occurrence of dividuals of a clone at different locations within the populations shows that the dispersal of vegetative diaspores s.l. is important for the growth and establishment of populations. In all three studied populations, only one genet (clone) was found to be dominant, besides these dominant clones, several genets coexist, at least in the population FN and L. The occurrence of different genets, with low genetic distances among themselves, can be seen as an indicator of the generative reproduction between different genets of a population. Generative reproduction requires thereby a colonisation of at least two different genets of the opposite sex. But it should be noted that only female

plants were found in these populations (see Table 3). However, a colonisation of similar genets could also explain the presence of genetically closely related genets.

6.2.4 Regional and Germany-wide genetic distribution pattern

6.2.4.1 *Abietinella abietina*

For the most part, the regional samples around Jena (incl. population Hb+Mb) were genetically closely related to each other. Most of the samples could be assigned to a clone. This shows that for the colonisation and maintenance of a habitat vegetative reproduction plays an important role. Moreover, the low genet diversity and the genetically close relationship between the found genets show the restricted gene flow between genetically and spatially distant populations. Reasons for the restricted gene flow may be the rarity or absence of spores. When comparing all regional samples, only two samples could be found with higher genetically distances to the remaining regional samples (r5_Dürrengleina, Hbl_166; cf. Appendix 16). In this way it was detected that gene flow in *A. abietina* is present between remote populations, even if it occurs very seldom. Long range dispersal and gene flow between remote populations can also be assumed for the genetically close and spatially distant samples of G3_Alzey-Worms, G6_Volteroda and G9_Rüdersdorf as well as G12_Martinroda (Figs. 14+39).

Considering the rarity or absence, resp., of generative reproduction, it is conceivable that genetic distances between populations have increased over a long period of time due to somatic mutations, after colonisation and establishment of diaspores. On the other hand it is possible that genetic distances, which arise through somatic mutation, have decreased due to the homoplasy effect. Furthermore, genetically close genotypes might have developed through generative reproduction between similar genotypes in times when generative reproduction was common in this species.

The detected main clades A, B and C within the Germany-wide analysed samples show high genetic distances to each other (Table 7). Due to the high genetic distances and at the same time rarity/absence of generative reproduction, it can be assumed that the genotypes of the three detected mains clades have probably been

genetically isolated from each other for a long period of time. Further, genetic recombination between the different sample groups seems theoretically possible; because all samples groups have a relatively wide geographical range with partly closely spatial relationships to other groups (Thuringian samples of clade_C as well as of clade_A, cf. Figs. 14+39). The large genetic distances between clades A, B and C might be a result of the fact that the genotypes of these sample groups originated from different Pleistocene refuges. Furthermore, it can be assumed that after re-colonisation of the formerly glaciated regions, no or only rare generative recombination took place between these groups and therefore the genetic differences have remained.

6.2.4.2 *Homalothecium lutescens*

Similar to *A. abietina* all regional samples of *H. lutescens* (incl. population Hb+Mb) were genetically closely related. In *H. lutescens* the regional samples are more separated from the other Germany-wide analysed samples (Fig. 42). The molecular data suggest that in the examined region around Jena, the vegetative reproduction is more important for habitat colonisation and maintenance than the generative reproduction. But the detected genetic distances, even if low, as well as the number of genets, imply that generative reproduction also occurs. In addition, it can be assumed that the dispersal of genetically and spatially distant genets is very seldom, since the found overall genetic distances between the regional samples are relatively low.

With the exception of G13_Rambach from Hesse, no distinct groups could be found in Germany in *H. lutescens* which are equally genetically separated from each other than *A. abietina*. The analysis of the world-wide sample set yielded a placement of G13_Rambach within the sample group A. The origin of the sample group A is predominantly the Alps and surrounding areas (cf. Figs. 17+43 and Appendix 13 II). Hence, one explanation for the genetic separation from the other Germany-wide samples could be that G13_Rambach and the other German samples originated from different refugial source populations. The colonisation of the region Rambach could have taken place postglacial or in recent times after the dispersal of vegetative or generative diaspores from the Alps or the refugial source population, resp. That

H. lutescens has mainly not evolved genetically separated sample groups in the German distribution area could be explained by the higher frequency of generative reproduction, whereas a recombination and genetic mixture of different genotypes is possible. Absence or rarity of genetically distinct groups could also be explained by the survival of the species in only a few refugia or a postglacial re-colonisation from only a few refugia, resp. In general, in *H. lutescens* a somewhat closer relationship between spatial and genetic distances in the Germany-wide sample set could be detected than in *A. abietina*. The samples close to the study area around Jena, i.e. G3_Saalburg and G4_Freyburg, are also closely related in the dendrogram (Fig. 42). An explanation might be the possibility of gene flow between those populations. On the other hand, spatially distant samples showed also higher genetic distances to the region of Jena. But these samples are genetically close to the samples in their vicinity. Hence, the samples from Rhineland-Palatinate (G11_Kyllburg and G12_Nohen) as well as from Bavaria (G5_Ebermannstadt and G7_Wiesentau) cluster together (Fig. 42, Appendix 13 I).

Referring to the dispersal of diaspores to disjunctive, ecologically suitable areas, such as Rüdersdorf, it can be assumed that the starting point of this dispersal has been rather the main distribution area of these species than the sparsely colonised regions as for example North Germany. This theory is supported by the results of the molecular analyses. It showed for both, *A. abietina* and *H. lutescens*, that the samples from Rüdersdorf are genetically close to the main distribution area of the species in East Thuringia.

In both trees, the North German samples G8_Malchin and G10_Eiderstaudamm are closely arranged with the Central German samples (Fig. 42, Appendix 13 I). In accordance with the molecular findings, it can be said that the genotypes in North Germany of *H. lutescens* probably originated from the more southern regions.

6.2.4.3 *Homalothecium sericeum*

In general, the molecular analyses revealed that the regional samples of *H. sericeum* are more genetically distinct among each other, than in case of the regional samples of the other two species. This was demonstrated for the region of Brandenburg as well as Saxony-Anhalt. The number of detected genets and the maximum genetic

distances in both analysed regions (Table 13) showed that *H. sericeum* has a similar genetic variability in the main distribution area (South Saxony-Anhalt) and in the region with mainly man-made habitats (Brandenburg). The similar genetic variability could be explained by the relatively frequent occurrence of generative reproduction in general and the increased dispersal ability of spores, by e.g. anemochory, in contrast to vegetative diaspores. The UPGMA dendrogram shows that the populations FN, L and D are well separated from each other and that the samples within the respective populations are closely arranged. Between the two analysed regions, Saxony-Anhalt and Brandenburg, it is conspicuous that the regional samples from Saxony-Anhalt for their part are somewhat closer in their genetic structure. In contrast, the samples of population L from Brandenburg are genetically closer related to the samples of the population FN (L/FN with a mean of GD_J=0.18783/GD_{SM}=0.15736) than with the samples of the population D (L/D with a mean of GD_J=0.23955/GD_{SM}0.20442) (Fig. 45, Appendix 14 I). The genotype diversity and the partly low genetic relation between the samples from Brandenburg showed the dispersal ability and possibility of gene flow between remote populations of this species. Perhaps, sparsely colonised regions are more often colonised by genets which originate from the main distribution area than by genets from regions with an infrequent occurrence of the species. This might be explained by the more frequent occurrence, and in consequence increased production and dispersal of diaspores of the species in main distribution areas, than in sparsely colonised regions. It should be noted that transport of limestone building material might be a factor in the dispersal of *H. sericeum,* but also in other taxa. Hence, the transport of limestone building material to South Brandenburg, with attached diaspores of *H. sericeum*, could explain the genetic relation of samples from South Brandenburg to samples from limestone regions. Furthermore, different origins of the building material could also explain the detected genetic diversity among the analysed populations from South Brandenburg. For instance, it was found that most of the samples of the population L are genetically close to the samples from G4_Zimmritz (East Thuringia) and G7_Schnellmannhausen (West Thuringia). Further, population D is genetically close to the samples of the population from Kahla (East Thuringia). That gene flow in some cases also occurred among the populations from South Brandenburg is

demonstrated by the genetically closely related samples rB1_Riedebeck, rB3_Wehrenzhain and L_surr_669.

In general, comparing the samples from Germany, no significant relation between genetic and spatial closeness was detected. For example G12_Vulkaneifel and G11_Walkenried are genetically related and spatially distant. It is noticeable that in the UPGMA tree these two samples are arranged outside of the most analysed German samples. Further, the sample G6_Röttelmisch is clearly genetically different to the rest of the East Thuringian and German samples (Fig. 45).

At least two hypotheses could explain this result. On the one hand, it is also for this species conceivable that a colonisation of the analysed German distribution area has taken place from different Pleistocene refuge localities. This would explain the genetic distinction of G6_Röttelmisch, G11_Walkenried and G12_Vulkaneifel compared to the other German samples. But, on the other hand, the colonisation of spatially and genetically distinct genets could have taken place more recently, considering the high dispersal ability of the spores. In this case, it is more likely, that new and genetically distinct genotypes colonise other regions. Regarding the dimension of the spores, dispersal and colonisation of spatially and genetically distinct genets is also conceivable in the other two species. The placement of the Germany-wide analysed samples in the UPGMA and NJ dendrogram is mostly inconsistent, which might be correlated with methodical issues (cf. chapter 6.2.1; e.g. insufficient number of bands or homoplasy effect).

6.2.5 Genetic diversity and pattern of distribution in the world-wide sample set

In general, the Northern Hemisphere biogeography is inseparably linked with the Pleistocene glaciations (e.g. HEDDERSON & NOWELL 2006). About 2.4 million years BP ago, the flora of Eurasia and North America was influenced by substantial periods of continental ice sheet expansion, which have been interrupted by warmer periods (DYKE & PREST 1987, DYKE et al. 2002). Hence, the present genetic diversity may be affected by a combination of re-colonisation, starting from south of the Pleistocene margins of glaciations, and the survival northward of the Pleistocene ice sheets (SCHUSTER 1983, HEWITT 2004b). Some studies (e.g. STEHLIK 2002, STEHLIK et al. 2002) found evidence for glacial survival of alpine plants on ice-free mountain tops

(nunataks). In the present study, such a glacial survival in the alpine region was only in *A. abietina* theoretically possible. The other two species do not grow at this altitude. Two main areas in Laurasia, Eastern Asia and the Appalachians, were not significantly affected by the glaciations and were moist enough to serve as a refugia. In contrast to Central and Northern Europe, where a massive extension probably took place, a higher number of species preserved in the Appalachians and even more in Eastern Asia (SCHUSTER 1983). Most of the organisms, which are currently distributed across Europe, survived at the height of glaciations 18 000 BP in refugia in the south (Iberian Peninsula, Italy, and the Balkans, and some possible near the Caucasus and Caspian Sea). According to previous studies (e.g. TABERLET et al. 1998, HEWITT 1999, CRONBERG 2000, HEWITT 2004b, EHRICH et al. 2007), the unglaciated South European regions have more genetic diversity than those of the north. A reason for this could be the rapid northward expansion of the taxa and the varied topography of the southern refugia.
Again, it should be pointed out that genetic distances between geographically distant samples can be affected by homoplasy. Hence, the received relations between the analysed samples could be partially biased and should be treated with some caution.

6.2.5.1 *Abietinella abietina*

The molecular results of the present study yielded the lowest genetic diversity in Scandinavia among all European regions (maximum GD_J=0.24593/GD_{SM}=0.16586) (cf. Table 9). In spite of the occurrence of generative reproduction in Scandinavia (at least in SE Sweden, cf. Bisang et al. 2004), the analysed samples are genetically very similar. Furthermore, by means of the threshold for clonal identity, it was detected that A31_Sweden and A33_Sweden probably represent one clone. The low genetic diversity in Scandinavia indicates that the re-colonisation after the Pleistocene glaciations based on immigration of *A. abietina* from few refugia. It is conceivable that pioneer genets could have expanded rapidly by prevalent vegetative reproduction s.l. and subsequent dispersal of vegetative diaspores. Before more genets could colonise the new areas of suitable habitat, probably the pioneer genets already dominated the new populations. As already shown in the population study of *A. abietina*, these results again demonstrate that vegetative reproduction is important

for habitat colonisation and maintenance, at least nowadays. In the dendrograms, the samples from Scandinavia are closely arranged to samples from the region of the Alps as well as Hungary and Poland (Fig. 40, Appendix 12 II). It can be assumed that post-glacial colonisation of Scandinavia as well as the Alps took place starting from the Tundra, which was situated between the main ice sheet and southern mountain blocks at the end of the last ice age. But also re-colonisation from southern refugia cannot be excluded.

The placement of the German samples within the world-wide samples suggests a re-colonisation of the German area from different refuge areas. The close relation between G3_Alzey-Worms, G9_Rüdersdorf, G12_Martinroda and the Spanish samples indicates that re-colonisation started from refugia in the Iberian Peninsula. For the rest of the analysed German samples, a clear determination of the refuge origin is not possible. This would require a larger number of samples from potential refuge regions.

The genetically close relation of A40_South Africa and A23_USA (Alaska) to Central European samples (G1_Mönchberg, G2_Burglauer and G5_Wiesenthau) could be explained by diaspores, which have been introduced by man (e.g. brought sheep or agrarian raw material) or by long range dispersal. In the case of the disjunctive South African population (Fig. 2), bird migration could have played a role in the dispersal of *A. abietina*. The Intertropical Convergence Zone (ITCZ) temporally hindered a meridional transequatorial movement (FELICÍSIMO et al. 2008). Hence, spore dispersal across the equator is limited.

In general, the North American genetic pattern suggests on the one hand long range dispersal from European genotypes or vice versa and on the other hand the appearance of indigenous genotypes. Fossil records from the late Pleistocene of Wisconsin (ca. 11.000 yr BP) (CULBERSON 1955), Alaska (12.420 ±1.080 yr BP) and Yukon Territory (JANSSENS 1983) give evidence of indigenous populations in North America. In Miocene time the flora of northwestern North America, especially of Alaska, showed strong eastern Asiatic affinities (SHARP 1972, SCHUSTER 1983). Eastern Siberia and Alaska were connected by the Bering land bridge at various times during the Pleistocene. Many bryophytes survived the Pleistocene glaciations in unglaciated refuges in coastal British Columbia and possibly coastal Alaska. In

many cases those species remained near their area of survival (SCHOFIELD 1984). The survival of *A. abietina* in coastal refuges or in the ice-free land mass of Beringia could explain, on the one hand, the close relationship of A12_Asian Russia to A13_USA (Alaska) and A25_USA (Alaska) with genetic distances of GD_J=0.35115–0.38806/GD_{SM}=0.23469–0.26531, and, on the other hand, the separation of those genotypes from the other samples of clade_B (Fig. 40). The genotypes of these samples could also be introduced by long range dispersal from western North America to Northeastern Asia or vice versa.

Noticeable are the large genetic distances among A12_Asian Russia and the other East Asian and South Asian samples with GD_J=0.58000–0.64474/GD_{SM}=0.44388–0.50510. Within the East Asian and South Asian samples, lower genetic distances were detected with GD_J=0.11207–0.54730/GD_{SM}=0.06633–0.41327. Probably, *A. abietina* could survive in this area during the Pleistocene, because significant glaciations were missing in East Asia. Long range dispersal and colonisation of European genotypes in Asia, or vice versa, seems unlikely because of the relatively good genetic separation of European and Asian genotypes. The low genetic distance between A2_Central Nepal and A4_Buthan (GD_J=0.11207/GD_{SM}=0.06633) suggests that vegetative reproduction is also prevalent and important for the habitat colonisation and maintenance in this part of the world.

Further, it was found, that the eastern North American samples A21_USA (Connecticut) and A16_USA (NY) are related to several Russian samples. Their genotypes could be remnants of the former undivided Laurasian continent. The survival of these genotypes during the glaciations in eastern North America could have been possible in the Appalachians. The molecular analyses revealed that the European Russian samples are genetically related. Here, the genotypes could have survived in the tundra, which extended eastward across Russia to the Ural (HEWITT 1999). That these genotypes were not detected in Central Europe could be explained by the extinction of the species during the Pleistocene and the re-colonisation of Central Europe with South European genotypes.

The samples from the southwestern part of North America are closely related in the trees to two samples from Canada. Further, several German samples and the Spanish samples are genetically closely related to these samples (Fig. 40, Appendix

12 II). The low level of genetic divergence among the European and North American samples suggests that Europe could be the origin of these North American populations. The fact that Spanish colonisation activities were related to the introduction of plants into southern and western parts of North America has, for instance, been established for weeds (NEUFFER & HURKA 1999). *Abietinella abietina* e.g. could have been introduced by sheep, which came along with Spanish settlers. A further possibility of the introduction of mosses into North America could have been the arrival of ships from Spain. PEREZ et al. (2009) detected that mosses were used as caulking material for ships in Spain in the 15th century. Introduction into northern and eastern parts of North America was mainly related to the colonisation activities of the French, the British and other nations (NEUFFER & HURKA 1999). In the present study, the assumption of a recent introduction of the species in the southwestern part of North America is supported by the low genetic diversity and low genetic distances between A17_USA (Colorado), A19_USA (New Mexico) and A20_USA (New Mexico) with clonal relationship among A19_USA (New Mexico) and A20_USA (New Mexico) on the one hand and the disjunctive occurrence of *A. abietina* in New Mexico and Colorado to the rest of North America on the other hand. Based on the large spatial distance and low genetic distances (GD_J=0.10656/GD_{SM}=0.06633) of A15_Canada (Quebec) and A24_Canada (Yukon) and the close genetic relationship to European samples, introduction from Europe could also be assumed in this case. In conclusion, the analyses of the world-wide sample set show that vegetative reproduction and dispersal of vegetative diaspores s.l. is generally important for colonisation and maintenance of habitats in *A. abietina*, since low genetic distances and variability was found for several regions of the world. Furthermore, low genetic differentiation between distant samples indicates a relatively recent long range dispersal and colonisation events.

Noticeable is the genetic subdivision of the world-wide sample set in the UPGMA dendrogram (Fig. 40). No morphological differences have been detected among both groups. Hence, it is excluded that this dichotomy is based on genetic differences between var. *histricosa* and var. *abietinum*. However, the var. *histricosa* was only detected in A3_China (Quinghai Prov.) and A10_Mongolia. The genetic subdivision could be explained by cryptic speciation with a genetic differentiation but without any

morphological differences. The phenomenon of cryptic speciation in bryophytes was documented e.g. by SHAW (2001), FELDBERG et al. (2004) and HEDENÄS & ELDENÄS (2007). But in the present study a cryptic speciation is not very plausible, because the samples of both main clades occur in all three continents. Otherwise, SHAW (2001) reported that the pattern of cryptic species have often broadly overlapping ranges. He further assumed that morphologically indistinct cryptic species are either ancient, or that these taxa are able to disperse in the Northern Hemisphere in a highly effective way. The latter seems unlikely for *A. abietina*, because spores are seldom and specialised propagules are absent. Further, the genetic differentiation (cf. Table 8) of samples from close locations (e.g. A29_Hungary and A30_Hungary or A37_Italy and A39_Italy) suggests that in these regions genetic recombination is rare or absent in *A. abietina*, at least nowadays.

6.2.5.2 *Homalothecium*

In both species of *Homalothecium*, a similar range of genetic distances was detected (Tables 10-11+13-14). Noticeable is that, in comparison to *A. abietina*, both species of *Homalothecium* show much lower maximum values of genetic distances (cf. Tables 5+9). One explanation for this difference between the species of *Homalothecium* and *A. abietina* could be the chosen primer combination (cf. chapter 6.2.1). On the other hand, the lower genetic distance values in *H. lutescens* and in *H. sericeum* could be caused by the younger age of these species. This would concur with the following: acc. to HUTTUNEN et al. (2008) the genus *Homalothecium* is divided into two main lineages, one American clade and one Eurasiatic clade. *Homalothecium sericeum* and *H. lutescens* are included in the Eurasiatic clade and probably evolved after the postglacial flooding of the Bering land bridge. *Abietinella abietina*, on the contrary, is widespread in North America as well as in Eurasia. An occurrence of this species in North America as well as in Eurasia is conceivable for the time when the land bridge between America and Eurasia still existed. Otherwise, transoceanic long range dispersal after sundering of the land bridge, could also explain the transoceanic distribution of *A. abietina*.

6.2.5.2.1 *Homalothecium lutescens*

Further species of *Homalothecium* (*H. aureum*, *H. philippeanum* and *H. fulgescens*) were molecular analysed in the world-wide sample set of *H. lutescens*, because of the ambiguity of morphological characteristics in the genus *Homalothecium* (cf. HOFMANN 1998). In this way, the correct determination of the samples of *H. lutescens* could be verified. The additional species of the genus *Homalothecium* are genetically well separated from the samples of *H. lutescens* in the UPGMA dendrogram (Fig. 43). The NJ dendrogram shows that the sample group of clade_A is, regarding the genetic relationship, closer to the other species of *Homalothecium* (Appendix 13 II). One explanation for the subdivision of the *H. lutescens* samples and the genetic relation of clade_A to the other species of *Homalothecium* could be that the samples of clade_A were hybrids. However, the determination of gametophytic morphological traits of the samples of clade_A (samples were without sporophytes) gave no hints for a hybridisation. But a hybridisation cannot be definitely excluded, because a differentiation and determination of hybrids is, in most cases, only possible by means of sporophyte characteristics (cf. HOFMANN 1998). Another explanation for the genetic separation of clade_A could also be the cryptic speciation. This assumption is supported by the predominantly restricted appearance of these genotypes in the region of the Alps. Genotypes of clade_A in Germany and England probably reached these regions after post-glacial re-colonisation or dispersed recently via long range dispersal. Considering the small dimension of spores of *H. lutescens*, long range dispersal is generally conceivable.

The samples of the study area in Thuringia, G2_Bad Salzungen, G3_Saalburg, as well as G9_Rüdersdorf, are closely related to the Swedish samples, Hl8_Spain and Hl6_Caucasus in the trees. Hence, the genotypes of these Central and North European populations probably survived in southern European regions and colonised these areas in a northerly direction, via Central Europe up to Scandinavia. The genetic relation of the Spanish and Caucasian samples is also explainable by postglacial colonisation events. A postglacial spreading in eastward or southwestward direction could be possible. But, since the species can be found mainly throughout Europe, it is more likely that spreading occurred in an eastward

direction. Fossils could give information of the Pleistocene occurrence of *H. lutescens* in the Caucasus. In general, because of the fragility and the chemical nature of the cell wall of mosses, fossil records are rare (STEERE 1942, CULBERSON 1955).

Further in the trees, Central European and British samples are mainly closely related to the two genetically distinct Mediterranean Italian populations (HI16_Italy, HI10_Italy) and HI13_Spain. In conclusion, postglacial re-colonisation or recent colonisation of Central Europe and the British Isles started from different regions of South Europe. Furthermore, some German samples (G4_Freyburg, G11_Kyllburg as well as G12_Nohen) are closely related to HI4_Ireland in the UPGMA dendrogram and further with HI14_Scotland in the NJ dendrogram. This indicates the survival of *H. lutescens* during the Pleistocene glaciations in the British Isles and/or adjacent mainland regions and subsequent post-glacial spreading in an eastward direction.

The polymorphy level and the highest genetic distance value among the South European samples are similar to those of all samples (cf. Table 11). This result confirms the assumption that the genetic diversity of species is higher in South Europe than in northern regions (e.g. TABERLET et al. 1998, HEWITT 1999, CRONBERG 2000, HEWITT 2004b, EHRICH et al. 2007). The diversity of genotypes in the South European region could be the result of the survival of genotypes during the Pleistocene glaciations in this area and/or of more frequent generative reproduction because of more favourable environmental conditions. The latter assumption is supported by the fact that sporophytes could only be detected in Spanish samples. CRONBERG (2000), for example, found different reproduction biology between North and South European populations in *Leucodon sciuroides*. To test this assumption for *H. lutescens*, the investigation of a larger number of samples from southern populations would be necessary.

Low genetic distances between spatially distant samples suggest recent long range dispersal and colonisation events. For example HI3_Sweden and HI6_Caucasus (with GD_J=0.14620/GD_{SM}=0.10965) or HI2_England and HI7_Poland (with GD_J=0.15116/GD_{SM}=0.11404) showed genetic distances, which are comparable to those of the samples of the region around Jena (maximum GD_J=0.15301/GD_{SM}=012785, cf. Table 10). But, especially genetic distances of

distant samples can be affected by homoplasy. With similar GD_J values, the above mentioned examples show lower GD_{SM} values between distant samples than the spatially closer regional samples. This difference is probably the result of homoplasy, since the Simple matching coefficient is more affected by homoplasy than the Jaccard coefficient. Hence, the underestimation of genetic diversity among samples is larger with the Simple matching coefficient than with the Jaccard coefficient.

6.2.5.2.2 *Homalothecium sericeum*

A correct determination of the *H. sericeum* samples is assured, since the samples of *H. aureum* are well separated in the dendrogram from the *H. sericeum* samples in the world-wide sample set (Fig. 46, Appendix 14 II). The monophyletic Macaronesian samples (Hs11_El Hierro, Hs12_Madeira) are a sister clade of the European samples. This result is in accordance with the findings of VANDERPOORTEN et al. (2007) for the phytogeographic affinities of the Macaronesian moss flora. HUTTUNEN et al. (2008) reported an age of 2.52 Myr for the ancestral node of the examined Macaronesian samples of *H. sericeum*. Hence, the Macaronesian endemism in *H. sericeum* is probably of fairly recent, neoendemic origin (VANDERPOORTEN et al. 2007, HUTTUNEN et al. 2008). In general, the flora of islands is, for the most part, isolated by oceanic barriers, which consequently causes a reduced gene flow between islands and continental areas. This could explain the separation of the analysed Macaronesian samples.

HEDDERSON & NOWELL (2006) detected a high genetic diversity in their study for the South European samples of *H. sericeum* (yielded by analyses of the variation in ITS1 sequences), a finding that could be confirmed in the present study. The placement of the northern samples in different clades (Fig. 46) and the values of genetic distances (Table 14) indicate a higher genetic diversity among the northern samples of *H. sericeum* than in contrast to *A. abietina*. Because of the small number of northern samples, a comparison with *H. lutescens* is not feasible. In *H. sericeum*, the higher genetic diversity of the northern distribution area could be explained by the more frequently produced spores. Generative reproduction and spore production increases the local genetic diversity and the likeliness of long range dispersal. Further, the close arrangement of the northern and southern samples in the dendrograms

(Hs19_Norway clusters with Hs9_Morocco; Hs17_Sweden is closely related to Hs8_Spain and Hs24_Greece; Hs15_Sweden is closely related to Hs5_Italy, Hs6_Italy and Hs7_Croatia) could be a result of postglacial re-colonisation of North Europe by genotypes, which survived in several genetically variable refugia in the south.

In the present study, some samples from the British Isles and adjacent mainland areas are closely related in the NJ dendrogram (Hs2_England, Hs22_Ireland, Hs10_France and G10_Rügen cf. Appendix 14 II). HEDDERSON & NOWELL (2006) assumed that *H. sericeum* survived the last glacial episodes in the British Isles and/or adjacent mainland regions, particularly Northwest France. This assumption can be confirmed, since most of the samples from the British Island analysed here showed no relation to samples from South Europe. In the case of Hs1_England, Hs1.1_England as well as Hs20_Poland, the genotype seems to have survived in refugia in the Caucasus during the Pleistocene glaciations. The German samples were mostly genetically related to samples from the British Isles and it can be assumed that the species expanded from glacial refugia in West Europe. Recent long range dispersal and colonisation events can be suggested because of the very low genetic distances between spatial distant samples (e.g. GD_J=0.12687/GD_{SM}=0.09714 between Hs22_Ireland and LVI_22_670; GD_J=0.14493/ GD_{SM}=0.11429 between Hs15_Sweden and FN_16_62).

The molecular analyses revealed that both samples from Newfoundland are genetically closely related to the European samples. A recent appearance of *H. sericeum* in North America must be taken into account for several reasons. The species occurs only in specific areas of Newfoundland (Fig. 6). The genetic distance between both analysed Newfoundland samples was of the same magnitude as found for the population FN and L. Moreover, the first mention in literature was by IRELAND in 1975, whereas *H. sericeum* was already found in Newfoundland in 1817 by de la Pylaie (date acc. to TUOMIKOSKI et al. 1973). The minor genetic differences suggest that probably only one or a few introductions have been taken place.

6.3 Habitat colonisation and maintenance

Using both morpho-anatomical and molecular analyses, the role of clonal growth and subsequent clonal reproduction for habitat colonisation and maintenance were described in previous studies of flowering plants (PFEIFFER 2005, 2007, LIESKE & PFEIFFER 2007, PFEIFFER et al. 2008) and of the bryophyte *Rhytidium rugosum* (Pfeiffer et al. 2006). LONGTON & SCHUSTER (1983) and FREY & LÖSCH (2004) e.g. reported that vegetative reproduction in bryophytes is undoubtedly of utmost importance for population development and maintenance as well as for population spread, in most if not in all mosses. More often, it is the dispersed vegetative diaspores which can establish more rapidly and successfully than the vast number of produced spores in bryophytes (LONGTON & MILES 1982, KIMMERER 1991, NEWTON & MISHLER 1994, KIMMERER 2005).

Following the initial colonisation and establishment of generative or vegetative diaspores s.l., in all analysed species patches were formed through continuous, indeterminate shoot growth, with subsequent clonal reproduction and establishment of ramets (Figs. 47–49). In general, the molecular analyses revealed that within-populations molecular variances are very low compared to variances among populations (Table 6). The low molecular variance within populations is due to the predominance of one or a few clones. Further, with the exception of clone_1 in *A. abietina*, the predominance of the found clones is restricted to one population. Hence, after the establishment of a genet, the habitat is rapidly occupied by ramets (dividuals), developed by vegetative reproduction s.l. The genetic structure in populations indicates that the mechanism of consequent vegetative multiplication is more important for the establishment and maintenance of populations than the generative reproduction. Comparing the molecular and morpho-anatomical results of the three species, it seems that the clonal diversity in populations can either increase or decrease, depending on the frequency of generative reproduction. Moreover, the present study revealed that the spatial expansion of clones decreases with the increase of generative reproduction in the analysed species. Thus, in *A. abietina* the lowest number of genets, the lowest number of fertile plants (Table 3) and the largest

clones were found (e.g. 42 km between G7_Freyburg and r7_Jena/Gleisberg, 170 km between samples from Scandinavia).

In the two species of *Homalothecium*, similar genet diversity was received within the populations, which is higher than in *A. abietina* (Tables 5+10+13). It should be noted that in the analysed populations of *H. sericeum* a higher number of fertile plants was found (fertile male plants were not identified) than in *H. lutescens.* Thus, it can be assumed that in populations with both sexes of *H. sericeum* the genetic diversity is probably higher. In this species, dividuals of clones were only identified on population scale. In contrast, in *H. lutescens* dividuals of clones were found on regional scale but in comparison to *A. abietina* with much lower expansion (8 km between r5_Mädertal and r7_Jena/Gleisberg). The low number of genets, the large dimension of genets and the low relevance of generative reproduction suggest that *A. abietina* is almost clonal, at least in the analysed region. PFEIFFER et al. (2006) found in *Rhytidium rugosum* a similar genetic pattern in a population with only one dominant genet and several closely related genets. The current distribution area of *A. abietina* was probably colonised in times when the species developed more capable dispersal agents, such as spores or specialised propagules (HERZOG 1926). Further, it is conceivable that, inter alia, sheep pasturing in the Middle Ages (KNAPP 1973) or other man activities promoted the dispersal of vegetative diaspores in the region of Jena. Given the dominance and dimension of clones and the extreme rarity or absence of spores, it can be assumed that recent colonisation of new sites occurs predominantly by vegetative diaspores. The dispersal distance of vegetative diaspores is in most cases low (e.g. LONGTON & SCHUSTER 1983, KIMMERER 1991). Hence, colonisation of predominantly nearby habitats can be expected. On the one hand, the partly large expansion of clones (e.g. clone_4) and on the other hand, the occasionally found genets with relatively high genetic differentiation, compared to the majority of population and regional samples (e.g. r5_Dürrengleina, HbI_166), indicate that diaspore dispersal over larger distances is possible in *A. abietina*, at least occasionally. However, the genetic structure in the analysed populations suggests that only a few well adapted genets survive and dominate the populations. The regional genetic pattern of *A. abietina* is conform with SCHUSTER's (1983) assumption that dioicous taxa with rare generative reproduction and rare spore dispersal exist as

large clones, whereas the clones tend to become very old. In addition, since closely related genets were found in the studied region, it can not be excluded that generative reproduction occurred in the past or present. The molecular results revealed a higher genetic diversity for the populations of the two *Homalothecium* species than for the populations of *A. abietina*. But, the dominance of a few genets in the populations indicates that the habitat establishment and maintenance proceed similar to *A. abietina*, mainly via vegetative reproduction s.l. and subsequent dispersal. Colonisation of the habitat occurred by locally dispersed vegetative diaspores s.l., which establish new patches through mechanisms of consequent vegetative multiplication at some distance from the source. Thus, in *H. lutescens* and *H. sericeum* dividuals of a clone were detected in different patches within populations and in surrounding samples. Furthermore, some dividuals were also found on the regional scale in *H. lutescens*. Otherwise, the higher genet diversity and the occurrence of genetically closely related genets in the populations indicate that generative reproduction is more important in the studied regions of *H. lutescens* and *H. sericeum* than in those of *A. abietina*. Colonisation and establishment of a dispersed diaspore from distant sources can be assumed for the population L of *H. sericeum.* This assumption is supported by the observed relation of some samples from Brandenburg to samples from the main distribution area in Thuringia.

In conclusion, several questions remain for future research: What is the rate of somatic mutation in clonal mosses? How strong is the actual influence of somatic mutation on genetic diversity in clonal taxa? Are populations of clonal bryophytes with more capable dispersal agents, such as specialised propagules, genetically more diverse? How does the occurrence of both sexes in populations change the genetic structure? Are there differences in the frequency of generative reproduction in other geographical regions? Does the genetic structure of populations vary in different geographical regions? In future studies, these questions could be answered by cultivation experiments and comparative population studies between ancient and recent populations as well as between different geographical regions. Furthermore, in comparative studies of clonal bryophytes with frequently produced specialised propagules the effect of more capable dispersal agents on the genetic structure of populations can be analysed.

All three studied species are ±endangered by habitat loss, fragmentation and air pollution, resp. *Abietinella abietina* and *H. lutescens* are frequent in Xero- and Mesobrometum. But these communities are endangered by e.g. imission, continuous nutrient input, afforestation, land-use change of extensively managed grasslands and chemical contamination of air and soil. *Homalothecium sericeum* is especially endangered on wall habitats through cleaning. Removal of *H. sericeum* from walls can influence the diversity of biotopes on walls, since this moss serves as a habitat for invertebrates and microorganisms, the base of the food chain. Further, *H. sericeum* can play an important role in cities to trap and absorb particulate matter. In general, the destruction of these habitats could cause the disappearance in some areas, as it has already happened in the North German Plains with *A. abietina*. A re-colonisation of suitable habitats can take a long time, depending on the distance and number of diaspore sources.

7 Summary

The examined pleurocarpous mosses *Abietinella abietina* (Thuidiaceae), *Homalothecium lutescens* and *Homalothecium sericeum* (Brachytheciaceae) grow in distinct patches, which develop predominantly through clonal growth and subsequent vegetative reproduction. The main focus of this study is a morpho-anatomical and molecular (AFLP) analysis of the vegetative reproduction mechanisms and genetic patterns within patches and populations of these three species, clarifying the role of vegetative and generative reproduction and the genetic structure in populations, thus becoming able to draw conclusions on the strategy for habitat colonisation and maintenance. The second emphasis lays on the analysis of genetic diversity and distribution patterns within the entire distribution area of the species.

All three taxa exhibit vegetative diaspores: ramets, resulting from disintegration of older shoot parts after fragmentation or decay, resp., and brood branches/branchlets. Furthermore, caducous shoot apices were identified in *A. abietina* and *H. lutescens* and caducous leaves were only discovered in *A. abietina*. The AFLP analysis includes two sets of samples, one taken from the distribution area in Germany and one world-wide. The sample set from the distribution area in Germany was analysed on three spatial scales (population, region and nation-wide). The population samples of *A. abietina* and *H. lutescens* originate from two sites in East Thuringia, those of *H. sericeum* from a population in South Saxony-Anhalt and two populations in Southern Brandenburg. In *A. abietina* the AFLP analysis yielded 4 clones out of 84 samples, comprising 5, 8, 10 and 43 samples. Clones occurred on population and regional scale. In *H. lutescens* 9 clones with 2 to 34 samples were identified out of 96 samples. Most clones were restricted to a single population, except for one clone which was found in two populations and a further one only found in regional samples. AFLP fingerprinting of 84 samples of *H. sericeum* revealed 7 clones, comprising 2 to 14 samples. In this species, clones were only detected on a population scale. In particular with *A. abietina* and *H. lutescens*, the occurrence of clone members beyond population scale indicates a dispersal of vegetative diaspores.

The world-wide sample set includes 45 samples of *A. abietina*, 35 of *H. lutescens* and 35 of *H. sericeum*. The genetic pattern of the North American samples of *A. abietina* revealed both indigenous genets as well as closely related genets to European samples. The Asian samples are mostly well separated from the North American and European samples. All three species show that the North European samples are genetically related to samples from the southern regions. The molecular analysis of the Scandinavian samples of *A. abietina* revealed a very low genetic variability, partly with clonal relation. In contrast, the comparatively high genetic diversity in Scandinavian samples of *H. sericeum* suggesting that spore dispersal occurs occasionally. Central European samples are genetically predominantly related to southern regions; but in *H. sericeum* a strong relation to West European samples was found. The samples from Southern Europe show a high genetic diversity. The molecular results for the disjunctive populations of *A. abietina* in South Africa and one of *H. sericeum* in Newfoundland revealed a recent colonisation. Particularly the partly low genetic distances between distinct samples in *A. abietina* indicate that the genetic pattern is influenced on large spatial scale by the prevalent vegetative reproduction. The latter plays a strong role for all three species when considering their habitat colonisation and maintenance. A comparison of all analysed taxa indicates an increase of genets and a decrease of spatial expansion with increasing generative reproduction.

8 Zusammenfassung

Die untersuchten pleurokarpen Laubmoose *Abietinella abietina* (Thuidiaceae), *Homalothecium lutescens* und *Homalothecium sericeum* (Brachytheciaceae) treten vorzugsweise in voneinander abgegrenzten Flecken („patches“) auf, die sich in erster Linie durch klonales Wachstum und anschließende vegetative Reproduktion entwickeln. Schwerpunkt dieser Arbeit sind die morphologisch-anatomischen und molekularen (AFLP) Analysen der vegetativen Reproduktionsmechanismen und der genetischen Muster innerhalb von Populationen und „patches“ der drei Arten. Ist die Rolle der generativen und vegetativen Reproduktion, sowie die genetische Struktur innerhalb von Populationen bekannt, können Rückschlüsse auf die Strategie der Habitatbesetzung gezogen werden. Ein weiterer Schwerpunkt ist die Untersuchung der genetischen Vielfalt und des genetischen Verbreitungsmusters innerhalb des gesamten Verbreitungsgebietes der untersuchten Arten.

Bei allen drei Arten treten folgende vegetative Diasporen auf: Ramets, die durch Abtrennung von älteren Stämmchenteilen nach Fragmentation bzw. Verrottung entstehen und Brutäste. Bei *A. abietina* und *H. lutescens* sind zudem Brutknospen, bei *A. abietina* Brutblättchen identifiziert worden. Die AFLP Analysen umfassen zwei Probensätze (einen mit Verbreitungsschwerpunkt in Deutschland und einen weltweiten). Der Probensatz des deutschen Verbreitungsgebietes wurde auf drei räumlichen Ebenen analysiert (Population, Region und deutschlandweit). Die Populationsproben von *A. abietina* und *H. lutescens* stammen von zwei Standorten in Ostthüringen, die Proben von *H. sericeum* aus einer Population im südlichen Sachsen-Anhalt und aus zwei Populationen in Südbrandenburg.

Die AFLP Analysen von 84 Proben ergaben bei *A. abietina* 4 Klone, mit jeweils 5, 8, 10 bzw. 43 Proben. Die Klone wurden auf der Populations- und regionalen Ebene identifiziert. Bei *H. lutescens* wurden aus 96 Proben 9 Klone mit 2 bis 34 Proben nachgewiesen. Die Klone waren auf Populationsebene begrenzt, mit der Ausnahme eines Klons, der in beiden Populationen vorkam und eines weiteren Klons, der nur in regionalen Proben gefunden wurde. Bei *H. sericeum* waren die Klone auf

Populationsebene begrenzt. Aus 84 untersuchten Proben wurden 7 Klone mit 2 bis 14 Proben identifiziert. Besonders bei *A. abietina* und *H. lutescens* ist das Vorkommen der Klone über die Populationsebene hinaus ein Indiz für die Ausbreitung vegetativer Diasporen.

Der weltweite Probensatz umfasst 45 Proben von *A. abietina* und jeweils 35 von *H. lutescens* und *H. sericeum*. Das genetische Muster der nordamerikanischen Proben von *A. abietina* weist sowohl auf ein Vorkommen von indigenen Genets, als auch auf Genets die nah mit europäischen Proben verwandt sind, hin. Die asiatischen Proben sind größtenteils gut von den nordamerikanischen und europäischen Proben getrennt. Bei allen drei Arten sind die nordeuropäischen Proben mit Proben von südlichen Regionen verwandt. Die molekulare Untersuchung ergab für die skandinavischen Proben von *A. abietina* eine sehr geringe genetische Vielfalt mit z.T. klonaler Beziehung. Dagegen findet sich in den skandinavischen Proben von *H. sericeum* eine vergleichsweise hohe genetische Vielfalt. Dies weist darauf hin, dass eine Ausbreitung von Sporen zumindest gelegentlich vorkommt. Die mitteleuropäischen Proben sind überwiegend mit Proben der südlichen Regionen verwandt, jedoch wurde für *H. sericeum* eine starke Beziehung zu westeuropäischen Proben festgestellt. Die südeuropäischen Proben zeigen generell eine hohe genetische Vielfalt. Die molekularen Ergebnisse der disjunkten Populationen, von *A. abietina* in Süd-Afrika und *H. sericeum* in Neufundland, deuten auf eine neuzeitliche Besiedlung hin. Besonders bei *A. abietina* zeigen die z.T. geringen genetischen Distanzen zwischen entfernten Proben, dass die vorherrschende vegetative Reproduktion auch auf höherer räumlicher Ebene einen Einfluss auf das genetische Muster hat. Für alle drei Arten konnte eine große Bedeutung der vegetativen Reproduktion für die Habitatbesetzung nachgewiesen werden. Beim Vergleich der untersuchten Taxa zeigt sich, dass mit zunehmender generativer Reproduktion die Vielfalt der Genets zu- und die räumliche Ausdehnung abnimmt.

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11 Appendix

Appendix 1: Sample data

Sample	Herbarium (Nr.)	Country	Date	Col.	Det.	Location	Habitat	Sex	Coordinates	Inclination/ Exposition	Altitude [m a.s.l.]
Abietinella abietina											
HbI (24 samples)	K. Lieske	Germany	04.04. - 08.04.06	K. Lieske	K. Lieske	Thuringia, Nennsdorf near by Jena, Holzberg, lower slope	limestone, xerothermic grassland		50°53'24"N 11°33'17"E	50°SSW	300-305
HbII (3 samples)	K. Lieske	Germany	08.04.06	K. Lieske	K. Lieske	Thuringia, Nennsdorf near by Jena, Holzberg, lower slope	limestone, xerothermic grassland		50°53'24"N 11°33'16"E	50°SSW	300-305
HbIII (2 samples)	K. Lieske	Germany	11.04.06	K. Lieske	K. Lieske	Thuringia, Nennsdorf near by Jena, Holzberg, middle slope	limestone, xerothermic grassland		50°53'25"N 11°33'17"E	50°SSW	310
Hb_surr_438	K. Lieske (#438)	Germany	11.04.06	K. Lieske (A.a.APO4)	K. Lieske	Thuringia, Nennsdorf near by Jena, Holzberg, lower slope, in 9 m distance eastward from HbI	limestone, xerothermic grassland		50°53'24"N 11°33'17"E	50°SSW	300-305
Hb_surr_442	K. Lieske (#442)	Germany	11.04.06	K. Lieske (A.a.APO6)	K. Lieske	Thuringia, Nennsdorf near by Jena, Holzberg, lower slope, in 20 m distance eastward from HbI	limestone, xerothermic grassland		50°53'24"N 11°33'18"E	50°SSW	300-305
Hb_surr_446	K. Lieske (#446)	Germany	11.04.06	K. Lieske (A.a. APO8)	K. Lieske	Thuringia, Nennsdorf near by Jena, Holzberg, lower slope, in 30 m distance eastward from HbI	limestone, xerothermic grassland		50°53'24"N 11°33'19"E	50°SSW	300-305
Hb_surr_458	K. Lieske (#458)	Germany	13.04.06	K. Lieske (A.a.APN8)	K. Lieske	Thuringia, Nennsdorf near by Jena, Holzberg, middle slope, in 20 m distance northward from HbI	limestone, xerothermic grassland		50°53'25"N 11°33'17"E	50°SSW	310
Hb_surr_465	K. Lieske (#465)	Germany	13.04.06	K. Lieske (A.a.APW4)	K. Lieske	Thuringia, Nennsdorf near by Jena, Holzberg, lower slope, in 10 m distance westward from HbII	limestone, xerothermic grassland		50°53'24"N 11°33'15"E	35°SSW	300-305
Hb_surr_469	K. Lieske (#469)	Germany	13.04.06	K. Lieske (A.a APW6)	K. Lieske	Thuringia, Nennsdorf near by Jena, Holzberg, lower slope, in 9 m distance westward from HbII	limestone, below scrub		50°53'24"N 11°33'15"E	35°SSW	300-305
Hb_surr_475	K. Lieske (#475)	Germany	13.04.06	K. Lieske (A.a.APS3)	K. Lieske	Thuringia, Nennsdorf near by Jena, Holzberg, lower slope, in 9.5 m distance southward from HbI	limestone, below scrub		50°53'23"N 11°33'17"E	38°SSW	300
Hb_surr_481	K. Lieske (#481)	Germany	13.04.06	K. Lieske (A.a.APS6)	K. Lieske	Thuringia, Nennsdorf near by Jena, Holzberg, in 20 m distance southward from HbI	limestone, below scrub		50°53'22"N 11°33'17"E	25°SSW	295
Hb_surr_541	K. Lieske (#541)	Germany	13.04.06	K. Lieske (A.a.APW7)	K. Lieske	Thuringia, Nennsdorf near by Jena, Holzberg, in 270 m distance westward from HbII	limestone, xerothermic grassland		50°53'27"N 11°33'04"E	20°S	270
MbI (12 samples)	K. Lieske	Germany	09.10 - 11.10.06	K. Lieske	K. Lieske	Thuringia, Jena Göschwitz, Mönchsberg	limestone, mesothermic grassland		50°52'51"N 11°34'57"E		286
MbII (3 samples)	K. Lieske	Germany	11.10.06	K. Lieske	K. Lieske	Thuringia, Jena Göschwitz, Mönchsberg	limestone, mesothermic grassland		50°52'51"N 11°34'57"E		286
Mb_surr_854	K. Lieske (#854)	Germany	11.10.06	K. Lieske (Mb A.a.A3)	K. Lieske	Thuringia, Jena Göschwitz, Mönchsberg, 3 m southward from MbI	limestone, mesothermic grassland	♀	50°52'51"N 11°34'57"E		286

Sample	Herbarium (Nr.)	Country	Date	Col.	Det.	Location	Habitat	Sex	Coordinates	Inclination/ Exposition	Altitude [m a.s.l.]
Mb_surr_855	K. Lieske (#855)	Germany	11.10.06	K. Lieske (Mb A.a.A4)	K. Lieske	Thuringia, Jena Göschwitz, Mönchsberg, 20 m eastward from MbI	limestone, mesothermic grassland		50°52'51"N 11°34'58"E		286
Mb_surr_858	K. Lieske (#858)	Germany	11.10.06	K. Lieske (Mb A.a.A5)	K. Lieske	Thuringia, Jena Göschwitz, Mönchsberg, 17 m southward from MbI	limestone, mesothermic grassland		50°52'50"N 11°34'57"E	10°SSE	281
Mb_surr_859	K. Lieske (#859)	Germany	11.10.06	K. Lieske (Mb A.a.A6)	K. Lieske	Thuringia, Jena Göschwitz, Mönchsberg, 10 m eastward from MbI	limestone, mesothermic grassland		50°52'51"N 11°34'58"E		286
Mb_surr_862	K. Lieske (#862)	Germany	11.10.06	K. Lieske (Mb A.a.A7)	K. Lieske	Thuringia, Jena Göschwitz, Mönchsberg, 20 m westward from MbI	limestone, mesothermic grassland		50°52'51"N 11°34'56"E		286
Mb_surr_863	K. Lieske (#863)	Germany	11.10.06	K. Lieske (Mb A.a.A8)	K. Lieske	Thuringia, Jena Göschwitz, Mönchsberg, 30 m northward from MbI	limestone, mesothermic grassland		50°52'52"N 11°34'57"E		286
Mb_surr_865	K. Lieske (#865)	Germany	11.10.06	K. Lieske (MbA.a.A10)	K. Lieske	Thuringia, Jena Göschwitz, Mönchsberg, 16 m northward from MbI	limestone, mesothermic grassland		50°52'52"N 11°34'57"E		286
r1_Cospeda	K. Lieske (#511)	Germany	12.04.06	K. Lieske (A.a.AP17)	K. Lieske	Thuringia, Cospeda, Windknollen	dry grassland		50°56'49"N 11°34'06"E	40°S	231
r2_Lämmerberg	K. Lieske (#543)	Germany	13.04.06	K. Lieske (A.a.AP29)	K. Lieske	Thuringia, Nennsdorf, Lämmerberg	limestone, mesoxerotherm grassland		50°53'47"N 11°33'05"E	11°SSW	233
r2.1_Ammer-bach	K. Lieske (#505)	Germany	13.04.06	K. Lieske (A.a. APNW1)	K. Lieske	Thuringia, between Ammerbach and Nennsdorf	mesoxerophytic grassland		50°53'47"N 11°33'04"E	10°NNW	232
r2.2_Ammer-bach	K. Lieske (#507)	Germany	13.04.06	K. Lieske	K. Lieske	Thuringia Ammerbach, wayside, Coppanzerstr.	mesoxerophytic grassland	♀	50°54'30"N 11°54'30"E	5°SS0	262
r2.3_Ammer-bach	K. Lieske (#531)	Germany	13.04.06	K. Lieske (A.a.AP25)	K. Lieske	Thuringia, Ammerbach	mesoxerophytic grassland, below *Pinus*	♀	50°54'23"N 11°33'07"E	5°SW	231
r3_Osmaritz	K. Lieske (#539)	Germany	05.04.06	K. Lieske (A.a.AP28)	K. Lieske	Thuringia, Osmaritz, Ziegenberg, hillock	limestone, meso-xerotherm grassland		50°52'40"N 11°32'24"E	50°NW	328
r4_Jena/Leutra	K. Lieske (#503)	Germany	06.04.06	K. Lieske (A.a. AP16)	K. Lieske	Thuringia, Jena, Leutra	dry grassland, nearby shrubbery		50°51'52"N 11°35'07"E	30°S	234
r5_Dürrengleina	K. Lieske (#498)	Germany	06.04.06	K. Lieske (A.a.AP14)	K. Lieske	Thüringia, road to Dürrengleina, left side, slope below forest	limestone		50°51'20"N 11°31'34"E	40°SSW	404
r6_Rabis	K. Lieske (#522)	Germany	12.04.06	K. Lieske (A.a.AP22)	K. Lieske	Thuringia, Rabis, southeastward of Jena	mesoxerophytic grassland		50°53'30"N 11°40'04"E	40°S	283
r7_Jena/ Gleisberg	K. Lieske (#160)	Germany	03.04.06	K. Lieske (A.a. AP11)	K. Lieske	Thuringia, Jena, Gleisberg	mesoxerophytic grassland		50°57'22"N 11°38'58"E	20°SSE	276
r8_Dorndorf	K. Lieske (#515)	Germany	12.04.06	K. Lieske (A.a.AP19)	K. Lieske	Thüringia, Dorndorf-Steudnitz, by traditional orchard below forest with *Corylus*, *Sorbus aucuparia*, *Lonicera* spp., *Cornus* spp.	limestone, mesoxerophytic grassland		50°00'02"N 11°40'51"E	40°NWW	190

Sample	Herbarium (Nr.)	Country	Date	Col.	Det.	Location	Habitat	Sex	Coordinates	Inclination/ Exposition	Altitude [m a.s.l.]
G1_Mönchberg	S. Fritz (#301)	Germany	08.04.06	S. Fritz	S. Fritz	Baden-Württemberg, Mönchberg, Schönbuch	limestone, xerothermicgrassland		48°35'14.5"N 08°55'19.1"E	W	509
G2_Burglauer	S. Fritz (#297)	Germany	08.04.06	S. Fritz	S. Fritz	Bavaria, Burglauer	limestone, field edge, hedge		50°16'38.8"N 10°11'34.5"E	SW	270
G3_Alzey-Worms	(Je) Herbar Hausknecht, Jena	Germany	28.08.99	C. Reuker, A. Beyer (451)		Rhineland-Palatinate, Alzey Worms, NSG "Kalksteinbrüche Rosengarten" at Schloßweg eastward Ober-Flörsheim (MTB 6315 Viertelquadrant 11 Raster 1)	chalk-pit, mesoxerophytic grassland	♀			240
G4_Weyer (Osteifel)	(Je) Herbar Hausknecht, Jena	Germany	21.02.99	R. Düll (5405/4b)	R. Düll	Rhineland, Easteifel, SSE Weyer, slope below Wurmberg	M.Devon			SW	450
G5_Wiesenthau	K. Lieske (#536)	Germany	09.04.06	K. Lieske (A.a.AP27)	K. Lieske	Bavaria, Wiesenthau, Walberla	limestone, meso-xerophytic grassland		49°43'17"N 11°08'58"E	30°S	427
G6_Volteroda	K. Lieske (#516)	Germany	12.04.06	K. Lieske (A.a.AP20)	K. Lieske	Thuringia, Volteroda	mesoxerophytic grassland		51°04'16"N 10°12'06"E	2°SSO	298
G7_Freyburg	K. Lieske (#924)	Germany	13.10.06	K. Lieske (A.a.S-A)	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), Edelacker, right roadside	turf		51°13'20"N 11°46'52"E	18°SSW	200
G8_Altmühltal	S. Fritz (#225)	Germany	06.10.05	S. Fritz	S. Fritz	Bavaria, Kinding, Altmühltal,	limestone, upper range of mesoxerophytic grassland, *Juniperus* spec., *Rosa* spec.	♀	49°00'12"N 11°22'23"E	15-30°SW	390
G9_Rüdersdorf	K. Lieske (#929)	Germany	05.11.06	K. Lieske (A.a.Br1)	K. Lieske	Brandenburg, Rüdersdorf, turf southward of the church in district Kalkberge	turf		52°28'17"N 13°47'06"E	0°	45
G10_Saalburg	K. Lieske (#487)	Germany	09.04.06	K. Lieske (A.a.AP12)	K. Lieske	Thuringia, between Saalburg and Gräfenwarth	below limestone boulder on way side	♀	50°31'41"N 11°44'56"E	20°S	450
G11_Kallenberg	K. Lieske (#525)	Germany	12.04.06	K. Lieske (A.a.AP20)	K. Lieske	Thuringia, Wandersleben, at the foot of Kallenberg	limestone, meso-xerophytic grassland, above with *Pinus*		50°53'04"N 10°50'26"E	0°SSO	289
G12_Martinroda	S. Fritz	Germany	19.10.05	S. Fritz	S. Fritz	Thuringia, Martinroda, Veronikaberg	margin of *Fagus* forest, limestone crevice		50°43'40.9"N 10°53'29.7"E	S	460
G13_Bad Salzungen	(Je) Herbar Hausknecht, Jena	Germany	15.11.02	H.J. Zündorf (20268)	L. Meinunger (2004)	Thuringia, Rhoen, Bad Salzungen, Geisaer Stadtwald eastward of Dermbach, NNE Zitters (5226/33)	epigeal in xerothermic grassland above of Dichemich				600
A1_India (Sikkim)	(E) Royal Botanic Garden, Edinburgh	India (Sikkim)	17.07.96	D.G. Long (26518)	D.G. Long	NORTH DISTRICT: 2km south of Thanggu	Degraded bouldery scrubby hillside; on boulder under Lonicera		27°52'28"N 88°32'31"E		3760
A2_Central Nepal	(E) Royal Botanic Garden, Edinburgh	Central Nepal	13.10.01	D.G. Long (30593)	D.G. Long	RASUWA DISTRICT: Langtang valley between Sindum and Kyanjin Gompa	Dry hillside with boulders and scrub; amongst dwarf Rhododendron		28°12'34"N 85°32'56"E		3520

Sample	Herbarium (Nr.)	Country	Date	Col.	Det.	Location	Habitat	Sex	Coordinates	Inclination/ Exposition	Altitude [m a.s.l.]
A3_China (Quinghai Prov.)	(E) Royal Botanic Garden, Edinburgh	China (Qinghai Province)	18.07.97	D.G. Long (27073)	D.G. Long	ZEKU COUNTY: Qukuhu Xiang, Lagong, Langzhang Valley	Steep valley with Picea, Populus, Betula woodland; on boulder under trees by river		35°20'03"N 101°55'41"E		2860
A4_Buthan	(E) Royal Botanic Garden, Edinburgh	Bhutan	15.09.99	D.G. Long (28680)	D.G. Long	BUMTHANG DISTRICT: above Shingkar near Ura	Cleared, grazed Picea forest; on grassy bank		27°30'N 90°57'E		3420
A5_Spain	(MUB) Universidad de Murcia (#8460)	Spain	17.07.98	Albertos, Cano, Garilleti y Lara	M.J. Cano	Lleida: Montant, vertiente sur la Sierra del Cadi	Suelo eu Carrescal				1220
A6_Spain	(MUB) Universidad de Murcia (#17192)	Spain	05.06.04	M.J. Cano (1591)	M.J. Cano	Cuenca: Tragacete (30TXK0365)	Base de Pinus		40°19'56"N 01°46'44"W		1500
A7_Russia (Siberia)		Russia (Siberia)	29.05.06	Dale Vitt	Dale Vitt	confluence of the Ob and Artusch Rivers in western Siberia - NW of the city of Khanty-Mansiysk (UTM 484936, 6771462)					
A8_Russia (Ural)	(MHA) Main Botanical Garden, Moscow	Russia (Bash-kortostan)	18.06.01	Zolotov (12-76)		Ural (south) Bashkortostan Ishimbai Distr.		♀			
A9_Russia (Smolensk Prov.)	(MHA) Main Botanical Garden, Moscow	Russia (Smolensk Prov.)	16.07.04	Ignatov	Ignatov				55°30'N 31°54'E		
A10_Mongolia	(MHA) Main Botanical Garden, Moscow	Mongolia	22.06.01	Ignatov (01-477)					43°30'N 104°04'E		2300
A11_Russia (Tamyr)	Moscow University	Russia (Siberia)	07.07.04	V. Fedosov		Taymyr, Taymyr Lake, Ledyanaya Bay		♀			
A12_Asian Russia	(Mo) Missouri Botanical Garden Herbarium (#5215860)	Russia (Khab-arovsk Territory)	10.08.97	B.C. Tan (# 97-252)	B.C. Tan	(7) Around lake shore and eastern cliff/slope of Medvezh´e Lake, Bureinskij State Nature Reserve, Dusse-Alin Range, Verkhnebureinskij District	on rock		52°05'N 135°01'E		

Sample	Herbarium (Nr.)	Country	Date	Col.	Det.	Location	Habitat	Sex	Coordinates	Inclination/ Exposition	Altitude [m a.s.l.]
A13_USA (Alaska)	(Mo) Missouri Botanical Garden Herbarium (#5367386)	USA (Alaska)	20.07.01	W.B. Schofield, S.S. Talbot (11798)	W.B. Schofield	Tetlin National Wildlife Reserve	over shaded outcrop		63°09'43"N 142°05'28"W		548.64
A14_China (Sichuan)	(Mo) Missouri Botanical Garden Herbarium (#4464614)	China (Sichuan)	04.09.97	Jia Yu (J02911)	Si He, (1998)	Sichuan Luhuo Co., Mt. Laozei.	on soil				4200
A15_Canada (Québec)	(Mo) Missouri Botanical Garden Herbarium (#5282376)	Canada (Québec)	20.06.00	Herbier J. Faubert (5222)		Bic, Prov. Québec, East of village, south of road #132.	Calcareous cliff, under tree cover.Syn.: Thuidium abietum		48°21'N 068°47'W		
A16_USA (NY)	(Mo) Missouri Botanical Garden Herbarium (#5644840)	USA (New York)	24.10.03	P.M. Eckel		Jefferson Co., Town of Alexandria Bay, within a mile of the St. Lawrence River, north of Rte. 12.	Area of rounded granitic outcrops, apparently calcifilic species around; boulders with sparse vegetation (alvar) in crevice pockets, with *Polypodium virginianum*, *Thuidium abietum* abundant, *Sedum acre* in carpets; in creek feeding the Bay, borders of *Phalaris arundinacea*, *Polygonum canby*i, *Solidago caesia*, *Spirodela polyrhiza*				
A17_USA (Colorado)	(Mo) Missouri Botanical Garden Herbarium (#5223916)	USA (Colorado)	27.05.00	Weber & Wittmann		LARIMER CO.: Big Thompson Canyon, west of Loveland, Ford Park	on northeast-facing steep slopes and rock outcrops				~1890

Sample	Herbarium (Nr.)	Country	Date	Col.	Det.	Location	Habitat	Sex	Coordinates	Inclination/ Exposition	Altitude [m a.s.l.]
A19_USA (New Mexico)	(Mo) Missouri Botanical Garden Herbarium (#5261458)	USA (New Mexico)	11.08.01	William R. Buck (39783A)	10.10.01 C.E. Darigo	Santa Fe County, Santa Fe National Forest, Sangre de Cristo Mountains, Dalton Canyon, near end of Forest Service Road 123	moist forest along stream with Salix and Alnus		35°40'17"N 105°43'22"W		2317
A20_USA (New Mexico)	(Mo) Missouri Botanical Garden Herbarium (#5630201)	USA (New Mexico)	21.08.04	R.D. Worthington (32811)	Det. from dupl. at COLO by W. Weber	NM: Rio Arriba Co., Tusas Mountains, Vallecitos Ranch and adjacent Carson Natl. Forest, at Vallecitos River and Rock Creek	igneous substrate N slopes with spruce and fir; S slopes with ponderosa pine, valley a wet meadow with streams, ponds and river; rugged outcrops of igneous rock shaded bank near river		36°38.34'N 106°11.95'W		~2682
A21_USA (Connecticut)	(Mo) Missouri Botanical Garden Herbarium (#5637901)	USA (Connec-ticut)	21.09.03	Bruce Allen (26017)		Litchfield County, Town of Canaan.Limestone quarry west of Sand Road, 0.5 miles north of CT 126. <26017-26051>	on ground at rim of quarry		41°58'56"N 073°21'28"W		300
A22_Mongolia	(Mo) Missouri Botanical Garden Herbarium (#5270626)	Mongolia	23.06.01	B.C. Tan (2001-156)	X.L.Bai & B.C.Tan	Dzunsaikhan, Modotyn Am forested ridge, Gurvansaikhan NP, Omnogovi Province.	Betula-Salix forest with lots of Orthotrichum		43°29'N 104°05'E		2500-2300
A23_USA (Alaska)	(Mo) Missouri Botanical Garden Herbarium (#4432430)	USA (Alaska)	17.07.96	W.B. Schofield (106066)		Simeonof Island, Shumagin Is.: sand isthmus			54°55'N 159°15'W		
A24_Canada (Yukon)	(Mo) Missouri Botanical Garden Herbarium (#4464481)	Canada (Yukon Territory)	02.05.97	Carl E. Darigo and Francesca Risse (2913)		rest area SW side of Hwy 1,3 mi NW of Haines Junction	medium-size patch on soil beneath trees, aspen forest, edge of highway rest area				~305

Sample	Herbarium (Nr.)	Country	Date	Col.	Det.	Location	Habitat	Sex	Coordinates	Inclination/ Exposition	Altitude [m a.s.l.]
A25_USA (Alaska)	(Mo) Missouri Botanical Garden Herbarium (#5232086)	USA (Alaska)	31.07.97	W.B. Schofield (108801)		Anchorage: Rabbit Creek, near old Seward Highway	on Populus log		59°46'N 151°54'W		
A26_Sweden (Ångermanland)	(S) Swedish Museum of Natural History (B69213)	Sweden	09.08.01	Lars Hedenäs		Ångermanland, Högsjö, Högsjö old church	Church yard wall				
A27_Sweden (Gotland)	(S) Swedish Museum of Natural History (B31898)	Sweden	28.05.00	Lars Hedenäs		Gotland, Fårö, Broa	Alvar with Juniperus	♂			
A28_Switzer-land	(S) Swedish Museum of Natural History (B11885)	Switzer-land	21.06.99	Lars Hedenäs		Obwalden, Giswil, Arnischwand	Wall				1370
A29_Hungary	(S) Swedish Museum of Natural History (B104412)	Hungary	24.08.05	Lars Hedenäs		W of Kecskémet, Fülöpháza	sandy soil in forest	♀	46°52'N 19°26'E		
A30_Hungary	(S) Swedish Museum of Natural History (B104402)	Hungary	21.08.05	Lars Hedenäs		Zemplén Mts, Kéked	Soil in sloping, dry meadow		48°34'N 21°20'E		535
A31_Sweden (Åsele)	(S) Swedish Museum of Natural History (B95258)	Sweden	29.06.04	Lars Hedenäs		Åsele Lappmark, Dorotea, Mt. Kalvberget ca. 9 km WSW of Risbäck, around small lake and in the dolomite escarpment	Base of escarpement		64°44'N 15°21'E		580-640
A32_Norway (Troms)	(S) Swedish Museum of Natural History (B82982)	Norway	17.07.03	Lars Hedenäs		Troms, Lyngen, Vardu, around large waterfall of River Storelva	On cliff shelf in spray zone	♀	69°37'N 20°15'E		170

Sample	Herbarium (Nr.)	Country	Date	Col.	Det.	Location	Habitat	Sex	Coordinates	Inclination/ Exposition	Altitude [m a.s.l.]
A33_Sweden (Jämtland)	(S) Swedish Museum of Natural History (B104939)	Sweden	14.09.05	Lars Hedenäs		Jämtland, Kall, around abandoned small farm 700m ESE of Mt. Stavattsberget	Rock in forest	♀	63° 28'N 13°20'E		400
A34_Poland	(S) Swedish Museum of Natural History (B110364)	Poland	18.06.05	Adam Stebel (#118)		Silesian Lowland, Równina Opolska Plain, between Ziętek and Krupski Młyn (Krupski Młyn commune), ATMOS grid square:FD 00	Sandy soil on wayside slope near the road Ziętek - Krupski Młyn, forest section		50°35'33"N 18°38'15"E		
A35_Russia (Udmurtia Rep.)	(MHA) Main Botanical Garden, Moscow	Russia (Udmurtia Republik)	21.07.00	Munizina		Kamskoe		♂			
A36_Austria	(Je) Herbar Hausknecht, Jena	Austria	12.08.02	R. Düll (3b./12)		Lechtaler Alpen:im Mühlbachtal, 0,5-1km nordwestl. Namlos (8629/2)	Kalk (cf. Hauptdolomit)				1200-1160
A37_Italy (Bozen)	(Je) Herbar Hausknecht, Jena	Italy	22.04.96	Irene & Ruprecht Düll (2/22)		Südtirol/Pr. Bozen:TK9534/2 Breibachtal oberhalb (ca. 0,5km) Blumau (TK9534/2)	calcareous				330
A39_Italy (Trafoi)		Italy	05.09.06	W.Frey	W.Frey	Trafoi/Ortler	limestone				1550
A40_South Africa	Herbarium Pretoria (#87-34)	South Africa	Feb 87	J. van Rooy (3629)	J. van Rooy 1987	Natal Drakensberg. Sani Top. Along basalt cliffs below escarpment, east of Border Post.Alpine heath-grassland. 2929CB	among grass at base of basalt cliff				2800
Homalothecium lutescens											
HbI (35 samples)	K. Lieske	Germany	04.04. - 08.04.06	K. Lieske	K. Lieske	Thuringia, Nennsdorf near by Jena, Holzberg, lower slope	limestone, xerothermic grassland		50°53'24"N 11°33'17"E	50°SSW	300-305
HbII (2 samples)	K. Lieske	Germany	08.04.06	K. Lieske	K. Lieske	Thuringia, Nennsdorf near by Jena, Holzberg, lower slope	limestone, xerothermic grassland		50°53'24"N 11°33'16"E	50°SSW	300-305
HbIII (4 samples)	K. Lieske	Germany	11.04.06	K. Lieske	K. Lieske	Thuringia, Nennsdorf near by Jena, Holzberg, middle slope	limestone, xerothermic grassland		50°53'25"N 11°33'17"E	50°SSW	300-305
Hb_surr_431	K. Lieske (#431)	Germany	11.04.06	K. Lieske (H.I.APO1)	K. Lieske	Thuringia, Nennsdorf near by Jena, Holzberg, lower slope, in 0.5 m distance eastward from HbI	limestone, xerothermic grassland	♀	50°53'24"N 11°33'17"E	50°SSW	300-305
Hb_surr_437	K. Lieske (#437)	Germany	11.04.06	K. Lieske (H.I.APO4)	K. Lieske	Thuringia, Nennsdorf near by Jena, Holzberg, lower slope, in 9 m distance eastward from HbI	limestone, xerothermic grassland		50°53'24"N 11°33'18"E	50°SSW	300-305

Sample	Herbarium (Nr.)	Country	Date	Col.	Det.	Location	Habitat	Sex	Coordinates	Inclination/ Exposition	Altitude [m a.s.l.]
Hb_surr_445	K. Lieske (#445)	Germany	11.04.06	K. Lieske (H.l.APO8)	K. Lieske	Thuringia, Nennsdorf near by Jena, Holzberg, lower slope, in 30 m distance eastward from Hbl	limestone, xerothermic grassland		50°53'24"N 11°33'19"E	50°SSW	300-305
Hb_surr_459	K. Lieske (#459)	Germany	13.04.06	K. Lieske (H.l.APN8)	K. Lieske	Thuringia, Nennsdorf near by Jena, Holzberg, middle slope, in 20 m distance northward from Hbl	limestone, xerothermic grassland		50°53'25"N 11°33'17"E	50°SSW	310
Hb_surr_466	K. Lieske (#466)	Germany	13.04.06	K. Lieske (H.l.APW4)	K. Lieske	Thuringia, Nennsdorf near by Jena, Holzberg, lower slope, in 10 m distance westward from HblI	limestone, xerothermic grassland		50°53'24"N 11°33'15"E	35°SSW	300-305
Hb_surr_470	K. Lieske (#470)	Germany	13.04.06	K. Lieske (H.l.APW6)	K. Lieske	Thuringia, Nennsdorf near by Jena, Holzberg, lower slope, in 9 m distance westward from HblI	limestone, below scrub		50°53'24"N 11°33'15"E	35°SSW	300-305
Hb_surr_471	K. Lieske (#471)	Germany	13.04.06	K. Lieske (H.l.APN9)	K. Lieske	Thuringia, Nennsdorf near by Jena, Holzberg, upper slope, in 40 m distance northward from Hbl	limestone, *Pinus* forest		50°53'25"N 11°33'17"E	30°SSW	315
Hb_surr_476	K. Lieske (#476)	Germany	13.04.06	K. Lieske (H.l.APS2)	K. Lieske	Thuringia, Nennsdorf near by Jena, Holzberg, in 9.5 m distance southward from Hbl	limestone, below scrub		50°53'23"N 11°33'17"E	38°SSW	300
Hb_surr_480	K. Lieske (#480)	Germany	13.04.06	K. Lieske (H.l.APS5)	K. Lieske	Thuringia, Nennsdorf near by Jena, Holzberg, in 15 m distance southward from Hbl	limestone, xerothermic grassland	♂	50°53'23"N 11°33'17"E	25°S	300
Mb (15 samples)	K. Lieske	Germany	09.10. - 11.10. 06	K. Lieske	K. Lieske	Thuringia, Jena Göschwitz, Mönchsberg	limestone, mesothermic grassland		50°52'51"N 11°34'57"E		286
Mb_surr_851	K. Lieske (#851)	Germany	11.10.06	K. Lieske (MbH.l.A1)	K. Lieske	Thuringia, Jena Göschwitz, Mönchsberg, 5.9 m southward from Mb	limestone, mesothermic grassland		50°52'51"N 11°34'57"E		286
Mb_surr_856	K. Lieske (#856)	Germany	11.10.06	K. Lieske (MbH.l.A3)	K. Lieske	Thuringia, Jena Göschwitz, Mönchsberg, 25 m eastward from Mb	limestone, mesothermic grassland	♀	50°52'51"N 11°34'58"E		286
Mb_surr_857	K. Lieske (#857)	Germany	11.10.06	K. Lieske (MbH.l.A4)	K. Lieske	Thuringia, Jena Göschwitz, Mönchsberg, 17 m southward from Mb	limestone, mesothermic grassland	♀	50°52'50"N 11°34'57"E	10°SSE	281
Mb_surr_860	K. Lieske (#860)	Germany	11.10.06	K. Lieske (MbH.l.A5)	K. Lieske	Thuringia, Jena Göschwitz, Mönchsberg, 10 m eastward from Mb	limestone, mesothermic grassland		50°52'51"N 11°34'58"E		286
Mb_surr_861	K. Lieske (#861)	Germany	11.10.06	K. Lieske (MbH.l.A6)	K. Lieske	Thuringia, Jena Göschwitz, Mönchsberg, 19.3 m westward from Mb	limestone, mesothermic grassland		50°52'51"N 11°34'56"E		286
Mb_surr_866	K. Lieske (#866)	Germany	11.10.06	K. Lieske (MbH.l.A7)	K. Lieske	Thuringia, Jena Göschwitz, Mönchsberg, 16 m northward from Mb	limestone, mesothermic grassland		50°52'52"N 11°34'57"E		286

Sample	Herbarium (Nr.)	Country	Date	Col.	Det.	Location	Habitat	Sex	Coordinates	Inclination/ Exposition	Altitude [m a.s.l.]
Mb_surr_927	K. Lieske (#927)	Germany	11.10.06	K. Lieske (MbH.l.A9)	K. Lieske	Thuringia, Jena Göschwitz, Mönchsberg, 3 m southward from Mb	limestone, mesothermic grassland		50°52'51"N 11°34'57"E		285
r1_Lämmerberg	K. Lieske (#542)	Germany	13.04.06	K. Lieske (H.l.AP26)	K. Lieske	Thuringia, Nennsdorf, Lämmerberg	limestone, mesoxerotherm grassland		50°53'47"N 11°33'05"E	11°S	233
r2_Ammerbach	K. Lieske (#532)	Germany	13.04.06	K. Lieske (H.l.AP22)	K. Lieske	Thuringia, Ammerbach, near by Jena, wayside of trail from Ammerbach to Nennsdorf	below *Pinus nigra*		50°54'23"N 11°33'07"E	5°SW	231
r3_Osmaritz	K. Lieske (#540)	Germany	05.04.06	K. Lieske (H.l.AP25)	K. Lieske	Thuringia, Osmaritz, Ziegenberg, hillock	limestone, mesoxerotherm grassland		50°52'40"N 11°32'24"E	50°NW	328
r4_Jena/Leutra	K. Lieske (#504)	Germany	06.04.06	K. Lieske (H.l.AP13)	K. Lieske	Thuringia, Jena, Leutra, NO of forest	limestone, xerotherm grassland		50°52'03"N 11°34'13"E	30°NW	228
r5_Mädertal	K. Lieske (#530)	Germany	13.04.06	K. Lieske (H.l.AP 21.1)	K. Lieske	Thuringia, Jena, Mädertal,	limestone, mesoxerotherm grassland		50°55'12"N 11°33'28"E	40°S	283
r6_Jena/Gräfen-berg	K. Lieske (#492)	Germany	10.04.06	K. Lieske (H.l.AP10)	K. Lieske	Thuringia, Jena, Gräfenberg	limestone, mesoxerotherm grassland		50°53'22"N 11°37'17"E	20°S	281
r7_Jena/Gleis-berg	K. Lieske (#161)	Germany	03.04.06	K. Lieske (H.l.AP8)	K. Lieske	Thuringia; Jena Gleisberg	limestone, mesoxerotherm grassland	♂	50°57'09"N 11°39'31"E	10°SSW	278
r8_Rabis	K. Lieske (#523)	Germany	12.04.06	K. Lieske (H.l.AP19)	K. Lieske	Thuringia, Rabis, hillock	upper Bunter, mesoxerotherm grassland,shrubbery	♀	50°53'31"N 11°40'04"E	40°S	296
r9_Nerkewitz	K. Lieske (#521)	Germany	12.04.06	K. Lieske (H.l.AP18)	K. Lieske	Thuringia, slope between Nerkewitz and Neuengönna	limestone, mesoxerotherm grassland, *Sorbus aucuparia*		50°59'19"N 11°36'04"E	28°W	242
r10_Dorndorf	K. Lieske (#519)	Germany	12.04.06	K. Lieske (H.l.AP17)	K. Lieske	Thüringia, Dorndorf-Steudnitz, near by traditional orchard below forest with *Corylus avellana*, *Sorbus aucuparia*, *Lonicera* spec.*, Cornus sanguinea*	limestone, mesoxerophytic grassland		51°00'02"N 11°40'51"E	40°NWW	190
G1_Kallenberg	Kathrin Lieske (#526)	Germany	12.04.06	K. Lieske (H.l.AP20)	K. Lieske	Thuringia, Wandersleben, at the foot of Kallenberg	limestone, mesoxerophytic grassland, above with *Pinus*		50°53'04"N 10°50'26"E	0°SSO	289
G2_Bad Salzungen	(Je) Herbar Hausknecht, Jena	Germany	15.11.02	H.J. Zündorf (20269)	L. Meinunger (2004)	Thuringia, Rhoen, Bad Salzungen, Geisa forest park, eastward of Dermbach, above the Dichemich ca. 600m NNO Zitters (5226/33)	epigeal in xerotherm grassland	♀			

Sample	Herbarium (Nr.)	Country	Date	Col.	Det.	Location	Habitat	Sex	Coordinates	Inclination/ Exposition	Altitude [m a.s.l.]
G3_Saalburg	Kathrin Lieske (#488)	Germany	09.04.06	K. Lieske (H.l.AP9)	K. Lieske	Thuringia, between Saalburg and Gräfenwarth	below limestone boulder on way side	♀	50°31'41"N 11°44'56"E	20°S	450
G4_Freyburg	Kathrin Lieske (#925)	Germany	13.10.06	Kathrin Lieske (H.l.SA1)	Kathrin Lieske	Saxony-Anhalt, Freyburg (Unstrut), Edelacker, right roadside	turf		51°13'20"N 11°46'52"E	18°SSW	200
G5_Ebermann-stadt	(Je) Herbar Hausknecht, Jena	Germany	28.04.01	H.J. Zündorf (#18471)	L. Meinunger (2004)	Bavaria, Franconian Switzerland, Bayreuth, Ebermannstadt, area of Streitburg northward of Streitberg (6133/34)	epigeal in limestone-xerotherm grassland	♀			
G6_Tiefental	(Je) Herbar Hausknecht, Jena	Germany	07.05.96	Wiebke Schröder	Meinunger	Bavaria, Tiefental NO Eichstätt (MTB 7032/4)		♀			
G7_Wiesenthau	Kathrin Lieske (#537)	Germany	09.04.06	K. Lieske (H.l.AP24)	K. Lieske	Bavaria, Wiesenthau, Walberla	mesoxerophytic grassland		49°43'17"N 11°08'58"E	30°S	427
G8_Malchin	(Je) Herbar Hausknecht, Jena	Germany	21.04.00	H.J. Zündorf (#17553)	H.J. Zündorf	Mecklenburg-Western Pomerania, Mecklenburg Switzerland: Malchin, by Saalenberg ca. 2km ONO Remplin	epigeal in sandy oligotrophic grassland				
G9_Rüdersdorf	Kathrin Lieske (#930)	Germany	05.11.06	Kathrin Lieske (H.l. Br 1)	Kathrin Lieske	Brandenburg, Rüdersdorf, turf on wayside	turf		52°28'16"N 13°46'27"E	0°NW	44
G10_Eiderstau-damm	(Je) Herbar Hausknecht, Jena	Germany	18.10.98	Wiebke Schröder	Wiebke Schröder	Schleswig-Holstein, dike S of Eiderstaudamm (MTB 1719/3)					
G11_Kyllburg	(Je) Herbar Hausknecht, Jena	Germany	21.10.00	R. Düll (9.)	Wiebke Schröder	Rhineland-Palatinate: Hocheifel: 5905/4A: northern slope above edge of town Kyllburg at junction Gerolsteiner street	bunter sandstone	♀			ca. 300-310
G12_Nohen	(Je) Herbar Hausknecht, Jena	Germany	29.09.04	R. Düll (1.)		Rhineland-Palatinate: Kalkeifel: 5606/3c: surrounding of Nohner mill at the Nohner creek valley	M.Devon, shady boulder	♀			ca. 360-380
G13_Rambach	(Je) Herbar Hausknecht, Jena	Germany	02.07.01	R.M.		Hesse, Eschenberg near by Rambach, Eschwege					
HI1_England		England	04.06.06	T.L. Blockeel	T.L. Blockeel	Cumbria: Helsington Barrows, near Brigsteer (SD484897)	on limestone scree	♀			170
HI2_England		England	29.05.06	T.L. Blockeel	T.L. Blockeel	Derbyshire: by Odin Mine, near Castleton (SK 134835)	on bank below limestone wall	♀			270

Sample	Herbarium (Nr.)	Country	Date	Col.	Det.	Location	Habitat	Sex	Coordinates	Inclination/ Exposition	Altitude [m a.s.l.]
HI3_Sweden	(S) Swedish Museum of Natural History (B5541 5)	Sweden	22.04.01	Lars Hedenäs		Södermanland, Frustuna, Bergudden	Grassy road-side slope	♀			
HI4_Ireland	(Mo) Missouri Botanical Garden Herbarium (#5912763)	Ireland	22.05.03	Robert Merrill King, Robert M. Garvey (#B.38-2)	C. Darigo MO 2005	County Mayo. In town of Westport.	on ground		53°47'55"N 09°32'24"W		ca. 17
HI5_Italy	(S) Swedish Museum of Natural History (B75359)	Italy	08.10.02	Lars Hedenäs	Lars Hedenäs	Vénéto, Borso del Grappa, above Semenozo	rock				405
HI6_Caucasus	(MHA) Main Botanical Garden, Moscow	Russia	19.08.04	Golub (#413)		North Caucasus, Temryuk		♀			
HI7_Poland	(S) Swedish Museum of Natural History (B110388)	Poland	27.07.05	Adam Stebel		Slesian Upland, Chełm Mound, Strzelce Opolskie	Calcareous soil in abandoned limestone quarry in north-eastern part of town (ATMOS grid square: FC 18)	♀	50°31'21"N 18°19'58"E		
HI8_Spain	(MUB) Universidad de Murcia (#17935)	Spain	04.06.04	J. Guerra	J. Guerra	GUADALAJARA:Chequilla. Piedra del Cuervo. 30TWK9895	Hab. T aludes	♀			1300
HI9_Spain	(MUB) Universidad de Murcia (#18154)	Hungary	22.10.97	S.&T. Pócs and B.O. van Zanten (#97200/F)	B.O. van Zanten	Bács-Kiskun County, DUNA-TISZA KÖZE SOLTI SÍKSÁG. N of SÜKÖSD village, on small, NW facing, natrual loess cliff	natrual loess cliff		46°16.2'N 18°59.3'E		100
HI10_Italy	(Je) Herbar Hausknecht, Jena	Italy	04.09.01	Rolf Marstaller		Marche: Felsen von San Leo					
HI11_Sweden	(S) Swedish Museum of Natural History (B31898)	Sweden	28.05.00	Lars Hedenäs	Lars Hedenäs	Gotland, Fårö , Broa	Alvar with Juniperus				

Sample	Herbarium (Nr.)	Country	Date	Col.	Det.	Location	Habitat	Sex	Coordinates	Inclination/ Exposition	Altitude [m a.s.l.]
HI12_Hungary	(S) Swedish Museum of Natural History (B104365)	Hungary	22.08.05	Lars Hedenäs		Zemplén Mts,castle hill near Füzer village	rocks in steep, rocky grassland	♀	48°34'N 21°27'E		520-535.
HI13_Spain	(Mo) Missouri Botanical Garden Herbarium (#5368291)	Spain	20.11.05	M.J. Cano (2574)	M.J. Cano	España: Cantabria.Valderredible, Villaescusa de Ebro, El Tobazo	Hábitat. Roca caliza	♀	42°49'23"N 03°49'34"W		750
HI14_Scotland	(Mo) Missouri Botanical Garden Herbarium (#5364982)	Scotland	17.05.04	Robert Merrill King and Robert M. Garvey (No. B154)	C. Darigo MO 2005	Scotland: Highland. Isle of Skye, Dunvegan Castle and vicinity.	on wall	♀	57°26'52"N 06°35'10"W		29
HI15_Austria	Herbar Hausknecht, Jena (Je)	Austria	27.07.01	R. Düll (2c. (2/27))	R. Düll	Kärnten Groß-Glocknerregion: 8942/4 climb to "Leiteralpe" between Gössnitz-Brücke below G.Gall near by Heiligenblut-Wicke.	silicate partly calcareous)				1330-1350
HI16_Italy	(Je) Herbar Hausknecht, Jena	Italy	01.05.96	R. Düll (#4/1)		Pr. La Spezia after Carro, turnoff to Masso.	moist rock	♀			100
HI18_Italy	(Je) Herbar Hausknecht, Jena	Italy	22.04.96	R.Düll		Südtirol/Pr. Bozen: TK 9534/2 Breibachtal above (ca. 0,5km) Blumau	Calcareous	♀			330
Homalothecium sericeum											
FN_33	K. Lieske (#33)	Germany	27.10.05	K. Lieske	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), wall near by the Neuenburg (wall top)	on horizontal surface of limestone wall	♀	51°12'33"N 11°46'43"E	plane	208
FN_65	K. Lieske (#65)	Germany	27.10.05	K. Lieske	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), wall near by the Neuenburg (wall top)	on horizontal surface of limestone wall		51°12'33"N 11°46'42"E	plane	208
FN_1_1	K. Lieske (#1)	Germany	26.10.05	K. Lieske	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), wall near by the Neuenburg (wall top)	on horizontal surface of limestone wall		51°12'33"N 11°46'43"E	plane	208
FN_4_10	K. Lieske (#10)	Germany	26.10.05	K. Lieske	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), wall near by the Neuenburg (wall top)	on horizontal surface of limestone wall		51°12'33"N 11°46'43"E	plane	208

Sample	Herbarium (Nr.)	Country	Date	Col.	Det.	Location	Habitat	Sex	Coordinates	Inclination/ Exposition	Altitude [m a.s.l.]
FN_5_9	K. Lieske (#9)	Germany	26.10.05	K. Lieske	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), wall near by the Neuenburg (wall top)	on horizontal surface of limestone wall		51°12'33"N 11°46'43"E	plane	208
FN_6_11	K. Lieske (#11)	Germany	26.10.05	K. Lieske	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), wall near by the Neuenburg (wall top)	on horizontal surface of limestone wall		51°12'33"N 11°46'43"E	plane	208
FN_7_12	K. Lieske (#12)	Germany	26.10.05	K. Lieske	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), wall near by the Neuenburg (wall top)	on horizontal surface of limestone wall	♀	51°12'33"N 11°46'43"E	plane	208
FN_8_15	K. Lieske (#15)	Germany	26.10.05	K. Lieske	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), wall near by the Neuenburg (wall top)	on horizontal surface of limestone wall	♀	51°12'33"N 11°46'43"E	plane	208
FN_8_16	K. Lieske (#16)	Germany	26.10.05	K. Lieske	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), wall near by the Neuenburg (wall top)	on horizontal surface of limestone wall	♀	51°12'33"N 11°46'43"E	plane	208
FN_8_22	K. Lieske (#22)	Germany	26.10.05	K. Lieske	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), wall near by the Neuenburg (wall top)	on horizontal surface of limestone wall	♀	51°12'33"N 11°46'43"E	plane	208
FN_8_26	K. Lieske (#26)	Germany	26.10.05	K. Lieske	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), wall near by the Neuenburg (wall top)	on horizontal surface of limestone wall	♀	51°12'33"N 11°46'43"E	plane	208
FN_9_20	K. Lieske (#20)	Germany	26.10.05	K. Lieske	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), wall near by the Neuenburg (wall top)	on horizontal surface of limestone wall		51°12'33"N 11°46'43"E	plane	208
FN_11_30	K. Lieske (#30)	Germany	27.10.05	K. Lieske	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), wall near by the Neuenburg (wall top)	on horizontal surface of limestone wall	♀	51°12'33"N 11°46'43"E	plane	208
FN_11_34	K. Lieske (#34)	Germany	27.10.05	K. Lieske	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), wall near by the Neuenburg (wall top)	on horizontal surface of limestone wall	♀	51°12'33"N 11°46'43"E	plane	208
FN_11_47	K. Lieske (#47)	Germany	27.10.05	K. Lieske	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), wall near by the Neuenburg (wall top)	on horizontal surface of limestone wall	♀	51°12'33"N 11°46'42"E	plane	208
FN_11_55	K. Lieske (#55)	Germany	27.10.05	K. Lieske	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), wall near by the Neuenburg (wall top)	on horizontal surface of limestone wall	♀	51°12'33"N 11°46'42"E	plane	208
FN_11_61	K. Lieske (#61)	Germany	27.10.05	K. Lieske	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), wall near by the Neuenburg (wall top)	on horizontal surface of limestone wall	♀	51°12'33"N 11°46'42"E	plane	208
FN_12_38	K. Lieske (#38)	Germany	27.10.05	K. Lieske	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), wall near by the Neuenburg (wall top)	on horizontal surface of limestone wall	♀	51°12'33"N 11°46'43"E	plane	208

Sample	Herbarium (Nr.)	Country	Date	Col.	Det.	Location	Habitat	Sex	Coordinates	Inclination/ Exposition	Altitude [m a.s.l.]
FN_15_60	K. Lieske (#60)	Germany	27.10.05	K. Lieske	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), wall near by the Neuenburg (wall top)	on horizontal surface of limestone wall	♀	51°12'33"N 11°46'42"E	plane	208
FN_16_62	K. Lieske (#62)	Germany	27.10.05	K. Lieske	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), wall near by the Neuenburg (wall top)	on horizontal surface of limestone wall		51°12'33"N 11°46'42"E	plane	208
FN_17_67	K. Lieske (#67)	Germany	28.10.05	K. Lieske	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), wall near by the Neuenburg (wall top)	on horizontal surface of limestone wall		51°12'33"N 11°46'42"E	plane	208
FN_18_69	K. Lieske (#69)	Germany	28.10.05	K. Lieske	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), wall near by the Neuenburg (wall top)	on horizontal surface of limestone wall	♀	51°12'33"N 11°46'42"E	plane	208
FN_19_76	K. Lieske (#67)	Germany	28.10.05	K. Lieske	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), wall near by the Neuenburg (upper wall level)	on vertical surface of limestone wall		51°12'33"N 11°46'42"E	90°NW	208
FN_23_80	K. Lieske (#80)	Germany	28.10.05	K. Lieske	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), wall near by the Neuenburg (wall top)	on horizontal surface of limestone wall	♀	51°12'33"N 11°46'42"E	plane	208
FN_24_89	K. Lieske (#89)	Germany	28.10.05	K. Lieske	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), wall near by the Neuenburg (wall top)	on horizontal surface of limestone wall	♀	51°12'33"N 11°46'42"E	plane	208
FN_surr_98	K. Lieske (#98)	Germany	28.10.05	K. Lieske (FNAP3)	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), wall near by the Neuenburg, in 48 m distance SW from FN_1_1 (wall top)	on horizontal surface of limestone wall	♀	51°12'32"N 11°46'41"E	plane	208
FN_surr_99	K. Lieske (#99)	Germany	28.10.05	K. Lieske (FNAP4)	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), wall near by the Neuenburg, in 58 m distance SW from FN_1_1 (wall top)	on horizontal surface of limestone wall	♀	51°12'32"N 11°46'41"E	plane	208
FN_surr_107	K. Lieske (#107)	Germany	30.10.05	K. Lieske (FNAP11)	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), in front of the wall near by the Neuenburg, in ca. 8 m distance NNW from FN_1_1	ground on concrete of manhole		51°12'33"N 11°46'43"E	plane	208
FN_surr_108	K. Lieske (#108)	Germany	12.10.05	K. Lieske (FNAP12)	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), on stone right hand of entry of Neuenburg in ca 80 m distance SW from FN_1_1	limestone	♀	51°12'32"N 11°46'38"E	60°NNE	208
FN_surr_110	K. Lieske (#110)	Germany	30.10.05	K. Lieske (FNAP13)	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), deciduous forest below the Neuenburg, in ca. 290 m distance SSW from the wall of FN	limestone	♀	51°12'27"N 11°46'33"	5°SSW	172
D_2_699	K. Lieske (#699)	Germany	31.07.06	K. Lieske	K. Lieske	Brandenburg, Dollenchen, wall of churchyard (upper level)	on vertical surface of cobblestone wall	♀	51°36'29"N 13°51'39"E	90°NW	124

Sample	Herbarium (Nr.)	Country	Date	Col.	Det.	Location	Habitat	Sex	Coordinates	Inclination/ Exposition	Altitude [m a.s.l.]
D_2_700	K. Lieske (#700)	Germany	31.07.06	K. Lieske	K. Lieske	Brandenburg, Dollenchen, wall of churchyard (upper level)	on vertical surface of cobblestone wall	♀	51°36'29"N 13°51'39"E	90°NW	124
D_3_701	K. Lieske (#701)	Germany	31.07.06	K. Lieske	K. Lieske	Brandenburg, Dollenchen, wall of churchyard (upper level)	on vertical surface of cobblestone wall	♀	51°36'29"N 13°51'39"E	90°NW	124
D_15_693	K. Lieske (#693)	Germany	31.07.06	K. Lieske	K. Lieske	Brandenburg, Dollenchen, wall of churchyard (lower level)	on vertical surface of cobblestone wall		51°36'29"N 13°51'39"E	90°NW	124
D_8_696	K. Lieske (#696)	Germany	31.07.06	K. Lieske	K. Lieske	Brandenburg, Dollenchen, wall of churchyard (upper level)	on vertical surface of cobblestone wall	♀	51°36'29"N 13°51'39"E	90°NW	124
D_16_705	K. Lieske (#705)	Germany	31.07.06	K. Lieske	K. Lieske	Brandenburg, Dollenchen, wall of churchyard (middle level)	on vertical surface of cobblestone wall		51°36'29"N 13°51'39"E	90°NW	124
D_surr_689	K. Lieske (#689)	Germany	31.07.06	K. Lieske	K. Lieske	Brandenburg, Dollenchen, wall of church (lower level)	on vertical surface of cobblestone wall	♀	51°36'29"N 13°51'38"E	90°NW	124
D_surr_691	K. Lieske (#691)	Germany	31.07.06	K. Lieske	K. Lieske	Brandenburg, Dollenchen, wall of churchyard (lower level)	on vertical surface of cobblestone wall		51°36'29"N 13°51'38"E	90°NW	124
D_surr_692	K. Lieske (#692)	Germany	31.07.06	K. Lieske	K. Lieske	Brandenburg, Dollenchen, wall of churchyard (middle level)	on vertical surface of cobblestone wall	♀	51°36'29"N 13°51'37"E	90°NW	124
LI_9_611	K. Lieske (#611)	Germany	01.08.06	K. Lieske	K. Lieske	Brandenburg, Lindena cemetery wall (lower level)	on vertical surface of cobblestone wall	♀	51°35'27"N 13°32'13"E	90°NW	91
LII_1_618	K. Lieske (#618)	Germany	01.08.06	K. Lieske	K. Lieske	Brandenburg, Lindena cemetery, wall of a House (lower level)	on vertical surface of cobblestone wall	♀	51°35'27"N 13°32'13"E	90°NW	91
LIII_1_621	K. Lieske (#621)	Germany	01.08.06	K. Lieske	K. Lieske	Brandenburg, Lindena cemetery wall (upper level)	on vertical surface of cobblestone wall		51°35'27"N 13°32'14"E	90°NW	91
LIV_1_622	K. Lieske (#622)	Germany	01.08.06	K. Lieske	K. Lieske	Brandenburg, Lindena cemetery wall (upper level)	on vertical surface of cobblestone wall	♀	51°35'27"N 13°32'14"E	90°SW	91
LV_4_625	K. Lieske (#625)	Germany	01.08.06	K. Lieske	K. Lieske	Brandenburg, Lindena cemetery wall (lower level)	on vertical surface of cobblestone wall	♀	51°35'28"N 13°32'14"E	90°SW	91
LV_4_637	K. Lieske (#637)	Germany	02.08.06	K. Lieske	K. Lieske	Brandenburg, Lindena cemetery	ground	♀	51°35'28"N 13°32'14"E	plane	91
LV_4_647	K. Lieske (#647)	Germany	02.08.06	K. Lieske	K. Lieske	Brandenburg, Lindena cemetery	ground	♀	51°35'28"N 13°32'14"E	plane	91
LV_4_659	K. Lieske (#659)	Germany	02.08.06	K. Lieske	K. Lieske	Brandenburg, Lindena cemetery	ground	♀	51°35'28"N 13°32'14"E	plane	91
LV_4_664	K. Lieske (#664)	Germany	03.08.06	K. Lieske	K. Lieske	Brandenburg, Lindena cemetery	ground		51°35'28"N 13°32'14"E	plane	91
LV_10_629	K. Lieske (#629)	Germany	01.08.06	K. Lieske	K. Lieske	Brandenburg, Lindena cemetery wall (upper level)	on vertical surface of cobblestone wall	♀	51°35'28"N 13°32'14"E	90°SW	91
LV_13_632	K. Lieske (#632)	Germany	01.08.06	K. Lieske	K. Lieske	Brandenburg, Lindena cemetery wall (wall top)	on horizontall surface of cobblestone wall	♀	51°35'28"N 13°32'14"E	90°SW	91
LV_27_633	K. Lieske (#633)	Germany	01.08.06	K. Lieske	K. Lieske	Brandenburg, Lindena cemetery wall (middle level)	on vertical surface of cobblestone wall		51°35'28"N 13°32'14"E	90°SW	91
LV_50_650	K. Lieske (#650)	Germany	02.08.06	K. Lieske	K. Lieske	Brandenburg, Lindena cemetery	on soil, ground		51°35'28"N 13°32'14"E	plane	91

Sample	Herbarium (Nr.)	Country	Date	Col.	Det.	Location	Habitat	Sex	Coordinates	Inclination/ Exposition	Altitude [m a.s.l.]
LV_77_639	K. Lieske (#639)	Germany	02.08.06	K. Lieske	K. Lieske	Brandenburg, Lindena cemetery	on soil, ground		51°35'28"N 13°32'14"E	plane	91
LVI_22_674	K. Lieske (#674)	Germany	03.08.06	K. Lieske	K. Lieske	Brandenburg, Lindena cemetery	on soil, ground		51°35'28"N 13°32'11"E	plane	91
LVI_23_670	K. Lieske (#670)	Germany	03.08.06	K. Lieske	K. Lieske	Brandenburg, Lindena cemetery	on soil, ground		51°35'28"N 13°32'11"E	plane	91
LVI_44_680	K. Lieske (#680)	Germany	03.08.06	K. Lieske	K. Lieske	Brandenburg, Lindena cemetery	on soil, ground		51°35'28"N 13°32'11"E	plane	91
L_surr_669	K. Lieske (#669)	Germany	03.08.06	K. Lieske	K. Lieske	Brandenburg, Lindena cemetery wall (middle level)	on vertical surface of cobblestone wall		51°35'27"N 13°32'12"E	90°NW	91
L_surr_684	K. Lieske (#684)	Germany	03.08.06	K. Lieske	K. Lieske	Brandenburg, Lindena cemetery	on stone on ground	♀	51°35'28"N 13°32'11"E	plane	91
rB1_Riedebeck	K. Lieske (#496)	Germany	30.04.06	K. Lieske (H.s.AP8)	K. Lieske	Brandenburg, Riedebeck, wall of churchyard	on vertical surface of cobblestone wall		51°48'17"N 13°40'43"E	90°W	66
rB2_Betten	K. Lieske (#685)	Germany	04.08.06	K. Lieske (H.s.B2)	K. Lieske	Brandenburg, Betten, wall of churchyard	on vertical surface of cobblestone wall	♂	51°37'40"N 13°46'03"E	90°NNW	123
rB3_Werenz-hain	K. Lieske (#707)	Germany	24.09.06	K. Lieske (H.s.B3)	K. Lieske	Brandenburg, Werenzhain, wall of churchyard	on vertical surface of cobblestone wall		51°39'14"N 13°32'10"E	90°NO	99
rB4_Frieders-dorf	K. Lieske (#687)	Germany	04.08.06	K. Lieske (H.s.B4)	K. Lieske	Brandenburg, Friederdorf near by Rückersdorf, wall of churchyard	on vertical surface of cobblestone wall	♀	51°33'53"N 13°32'25"E	90°N	93
rB5_Schönborn	K. Lieske (#686)	Germany	04.08.06	K. Lieske (H.s.B5)	K. Lieske	Brandenburg, Schönborn near by Doberlug-Kirchhain, wall of churchyard	on vertical surface of cobblestone wall		51°35'41"N 13°30'17"E	90°N	95
rB6_Sallgast	K. Lieske (#688)	Germany	31.07.06	K. Lieske (H.s.B6)	K. Lieske	Brandenburg, Sallgast, castle courtyard	on vertical surface of cobblestone wall	♀	51°35'19"N 13°50'52"E	90°NW	141
rSA1_Nißmitz	K. Lieske (#918)	Germany	14.10.06	K. Lieske (H.s.SA1)	K. Lieske	Saxony-Anhalt, Nißmitz near by Freyburg (Unstrut), wall of churchyard	on vertical surface of limestone wall	♀	51°11'57"N 11°46'19"E	90°E	113
rSA2_Brauns-bedra	K. Lieske (#919)	Germany	14.10.06	K. Lieske (H.s.SA2)	K. Lieske	Saxony-Anhalt, Braunsbedra, wall of churchyard	below *Corylus avellana* on concrete of wall		51°16'59"N 11°53'04"E	90°E	113
rSA3_Freyburg_ rill	K. Lieske (#920)	Germany	14.10.06	K. Lieske (H.s.SA3)	K. Lieske	Saxony-Anhalt, Freyburg (Unstrut), wall "Am Graben"	on on vertical surface of limestone wall		51°12'40"N 11°46'10"E	90°SSW	106
rSA4_Lieder-städt	K. Lieske (#931)	Germany	14.05.07	K. Lieske (H.s.SA9)	K. Lieske	Saxony-Anhalt, Liederstädt, wall of churchyard	on vertical surface of limestone wall		51°18'31"N 11°34'58"E	90°N	125
G1_Jena	K. Lieske (#510)	Germany	12.04.06	K. Lieske (H.s.AP10)	K. Lieske	Thuringia, Jena, Cospedaer Grund, right hand wayside of the trail to the Sonneberg	on limestone block		50°56'14"N 11°33'29"E	85°NNW	191
G2_Nennsdorf	K. Lieske (#486)	Germany	07.04.06	K. Lieske (H.s.AP5)	K. Lieske	Thuringia, Nennsdorf, right hand wayside of the trail to the Holzberg	on limestone block	♀	50°53'31"N 11°32'51"E	80°NNW	225
G3_Göttern	K. Lieske (#491)	Germany	06.04.06	K. Lieske (H.s.AP6)	K. Lieske	Thuringia, Göttern, wall of churchyard	on vertical surface of limestone wall		50°53'46"N 11°27'48"E	90°N	279
G4_Zimmritz	K. Lieske (#495)	Germany	06.04.06	K. Lieske (H.s.AP7)	K. Lieske	Thuringia, Zimmritz	on concrete at roadside	♂	50°51'18"N 11°29'57"E	plane	415

Sample	Herbarium (Nr.)	Country	Date	Col.	Det.	Location	Habitat	Sex	Coordinates	Inclination/ Exposition	Altitude [m a.s.l.]
G5_Kahla910	K. Lieske (#910)	Germany	13.10.06	K. Lieske (Kahla II2)	K. Lieske	Thuringia, Kahla, Dohlensteinbruch	on bark of *Fraxinus excelsior*		50°48'23"N 11°35'48"E	90°SW	168
G5_Kahla912	K. Lieske (#912)	Germany	13.10.06	K. Lieske (Kahla II4)	K. Lieske	Thuringia, Kahla, Dohlensteinbruch	mesoxerophytic grassland	♀	50°48'23"N 11°35'48"E	18°SW	168
G5_Kahla913	K. Lieske (#913)	Germany	13.10.06	K. Lieske (Kahla II5)	K. Lieske	Thuringia, Kahla, Dohlensteinbruch	mesoxerophytic grassland	♀	50°48'23"N 11°35'48"E	18°SW	168
G6_Röttelmisch	K. Lieske (#115)	Germany	11.10.05	K. Lieske (H.s.AP1)	K. Lieske	Thuringia, Röttelmisch	on vertical surface of limestone wall		50°48'54"N 11°30'45"E	NE	253
G7_Schnell-mannhausen	K. Lieske (#524)	Germany	12.04.06	K. Lieske (H.s.AP11)	K. Lieske	Thuringia, Schnellmannhausen	on vertical surface of limestone wall	♂	51°06'15"N 10°13'06"E	SE	222
G8_Wiesenthau	K. Lieske (#533)	Germany	09.04.06	K. Lieske (H.s. AP12)	K. Lieske	Bavaria, Wiesenthau, Walberla	on limestone block		49°43'17"N 11°08'59"E	N	430
G9_Zedersitz	S.Fritz	Germany	30.09.06	S. Fritz	S.Fritz	Bavaria, Upper Franconia, Zedersitz, wayside	rock		49°59'20"N 11°17'36"E	E	447
G10_Rügen	(Je) Herbar Hausknecht, Jena	Germany	12.08.00	H.-J. Zündorf (18317)	C. Meinunger (2004)	Mecklenburg-Western Pomerania, Rügen: Putbus, palace garden at south margin of centre, Kastanienallee between Schwanenteich and orangery	on bark of A*esculus hippocastanum*	♂			
G11_Walken-ried	(Je) Herbar Hausknecht, Jena, ex. Herbarium Rolf Marstaller Jena	Germany	27.06.03	Rolf Marstaller	Rolf Marstaller	Lower Saxony, Itelklippen near by Walkenried, district Osterrode	dolomite	♀			
G12_Vulkaneifel	(Je) Herbar Hausknecht, Jena , ex. Herbarium R.Düll Bad Münstereifel	Germany	12.11.98	R.Düll (5607/2A)	R.Düll	Rhineland-Palatinate, Vulkaneifel: at "Kreuzweg" near by Kirchberg, above Adenau-hospital, basement	on volcanic rock (sek.!)	♀			
G13_Hünfeld	(Je) Herbar Hausknecht, Jena	Germany	14.11.03	H.-J. Zündorf (20968)	C. Meinunger (2004)	Hesse, Rhoen, Fulda, Hünfeld, on westward exposed boulder field at top of "Stallberg" ca. 3.5 km westward of Rasdorf (5225/33)	on with soil covered basalt boulder	♀			
G14_Meiningen	(Je) Herbar Hausknecht, Jena	Germany	13.11.03	H.-J. Zündorf (20902)	C. Meinunger (2004)	Thuringia, middle Werra Valley, beech forest at northern slope of Dolmar ca. 3 km NNW Kühndorf (5328/42)	on shady chalk rock	♀			
Hs1_England		England	03.06.06	T.L. Blockeel	T.L. Blockeel	Cumbria: Whitbarrow, 3 km west of Brigsteer, SD 448887	on shaded limestone wall	♂			95

Sample	Herbarium (Nr.)	Country	Date	Col.	Det.	Location	Habitat	Sex	Coordinates	Inclination/ Exposition	Altitude [m a.s.l.]
Hs1.1_England		England	03.06.06	T.L. Blockeel	T.L. Blockeel	Cumbria: Whitbarrow, 3 km west of Brigsteer, SD 448887	on shaded limestone wall	♀			95
Hs2_England		England	21.05.06	T.L. Blockeel	T.L. Blockeel	Derbyshire: Calver Low, near Stoney Middleton, SK235747	on lightly shaded limestone wall	♀			175
Hs3_Newfound-land	(UBC) University of British Columbia (ACC# B186760)	Canada	01.04.88	T.A.J. Hedderson (No. 5638)		Bryophytes of Newfoundland, Canada, Avalon Peninsula, Brigus South	Abundant over rocks in meadows				10
Hs4_Newfound-land	(UBC) University of British Columbia (ACC #B155091)	Canada	10.07.94	W.B. Schofield (No. 101045)		Bryophytes of Newfoundland, Canada, Avalon Penninsula: Blackhead, near Cape Spear	cliff crevices		47°32'N 52°39'W		
Hs5_Italy	(Je) Herbar Hausknecht, Jena	Italy	20.04.96	Irene u. Ruprecht Düll (20.04.96/1/20)		Sürtirol/Pr. Bozen Eisacktal: kleiner Säben above Klausen, TK 9335/3					530-600
Hs6_Italy	(Je) Herbar Hausknecht, Jena	Italy	01.05.03	Rolf Marstaller	Rolf Marstaller	Toscana (Siena) Abbadia S. Salvatore M. Amiata, southern slope		♀			1300
Hs7_Croatia		Croatia	06.09.06	S. Fritz	S. Fritz	southward of Cres	limestone wall		44°54'59"N 14°24'58"E		270
Hs8_Spain	(MUB) Universidad de Murcia (#1583)	Spain	03.08.03	J. Guerra		Cádiz: Sierra del Pinar, Grazalema	Spifiti? de Avies pinsapa				
Hs9_Morocco	(MUB) Universidad de Murcia (#21186)	Morocco	22.06.04	Draper, Medina (AA231)	I. Draper	Murruecoa. Ascensión al Tichka desde Imi-n-Tanoute, carrascal joven. Base de encina, altura hasta 5 cm, diámetro 25 cm, recubrimiento comunidad:60%, UTM: 39RNQ2536			31°3'42"N 8°43'52"W		1750
Hs10_France	(MUB) Universidad de Murcia (#1058)	France	09.11.03	M.J. Cano	M.J. Cano	Île-de-France: Fontainebleau	Tronco de árbol	♀	48°24'N 02°41'E		
Hs11_El Hierro		Spain	Mar. 06	I. Hildebrandt 35/06-13		El Hierro	on bark				

Sample	Herbarium (Nr.)	Country	Date	Col.	Det.	Location	Habitat	Sex	Coordinates	Inclination/ Exposition	Altitude [m a.s.l.]
Hs12_Madeira	(MUB) Universidad de Murcia (#1315)	Portugal	26.08.03	M.J. Cano	M.J. Cano	Madeira: Isla de Porto Santo, Pico Branco	Roca volcanica		33°05'44"N 16° 18'01"E		350
Hs13_Caucasus	(MHA) Main Botanical Garden, Moscow	Utrish	04.05.05	Ignatov & Ignatova (05-612a)		Caucasus, Utrish			44°42'N 37°28'E		
Hs14_Caucasus	(MHA) Main Botanical Garden, Moscow	Kabardino -Balkaria	30.07.04	Ignatov & al.		Caucasus, Kabardino-Balkaria			43°28'N 43°13'E		1000
Hs15_Sweden	(S) Swedish Museum of Natural History (B57827)	Sweden	14.06.95	Lars Hedenäs		Gotland, c. 1km SSE of Fårö church Prov.: Gotland Par.:Fårö	Epigeic in pine forest near the shore				
Hs16_Sweden	(S) Swedish Museum of Natural History (B32404)	Sweden	12.06.00	Lars Hedenäs		Södermanland, Hölö, W-faving escarpment 0.5 km S of Ulriksdal	Escarpment	♀			
Hs17_Sweden	(S) Swedish Museum of Natural History (B96087)	Sweden	29.06.04	Lars Hedenäs		Åsele Lappmark, Dorotea, Mt. Kalvberget ca. 9 km WSW of Risbäck, around small lake and in dolomite escarpment	base of escarpment	♀	64°44'N 15°21'E		580-640
Hs18_Hungary	(S) Swedish Museum of Natural History (B104364)	Hungary	22.08.05	Lars Hedenäs		Zemplén Mts, castle hill near Füzer village	Rocks in steep, rocky grassland	♀	48°34'N 21°27'E		520-535.
Hs19_Norway	(S) Swedish Museum of Natural History (B59862)	Norway	24.07.01	Lars Hedenäs	Lars Hedenäs	Finnmark, Söröysund, Seiland (Siev`jo), along the road between Skoltbukta and Hellegjengneset	rock		70°33'N 23°25'E		5-10
Hs20_Poland	(S) Swedish Museum of Natural History (B99099)	Poland	28.06.97	Adam Stebel		Kraków-Częstochowa Upland, Płaskowyż Olkuski Plateau, "Ostra Góra" nature reserve (Trzebinia commune), ATMOS grid square: Fd56;	Limestone in E part of the reserve	♀			

Sample	Herbarium (Nr.)	Country	Date	Col.	Det.	Location	Habitat	Sex	Coordinates	Inclination/ Exposition	Altitude [m a.s.l.]
Hs21_Scotland	(Mo) Missouri Botanical Garden Herbarium (#5364899)	Scotland	18.05.04	Robert Merrill King and Robert M. Garvey (No B169)	C. Darigo MO 2005	Highland. Along A82, S of Inverness, at Urquhart Castle.	on wall	♂	57°19'28"N 04°26'40"W		40
Hs21.1_Scot-land	(Mo) Missouri Botanical Garden Herbarium (#5364899)	Scotland	18.05.04	Robert Merrill King and Robert M. Garvey (No B169)	C. Darigo MO 2005	Highland. Along A82, S of Inverness, at Urquhart Castle.	on wall	♀	57°19'28"N 04°26'40"W		40
Hs22_Ireland	(Mo) Missouri Botanical Garden Herbarium (#5912768)	Ireland	18.05.03	Robert Merrill King and Robert M. Garvey (No. B38-8)	R. Magill C. Dargio Mo 2005	County Cork. At Blarney Castle.			51°56'04"N 08°33'52"W		30
Hs23_Ireland	(Mo) Missouri Botanical Garden Herbarium (#5912762)	Ireland	22.05.03	Robert Merrill King and Robert M. Garvey (No. B38-7)	R. Magill C. Dargio Mo 2005	County Mayo. In town of Westport.	on tree	♂	53°47'55"N 09°32'24"W		17
Hs24_Greece	(Je) Herbar Hausknecht, Jena	Greece		R. Düll (4.-leg)	R.Düll	S. Aegaeis, Karpathos, West Coast: Mesohori. Coasts (-W-) slope in and near by place. At 160 m downward (incl. 2/12.5).	limestone	♀			160
Homalothecium aureum (Israel) formerly determined as *H. lutescens*	The Hebrew University of Jerusalem	Israel	26.04.03	Dimentman	Herrnstadt	Golan Heights W of Mas´ada, N. slopes on rock					
Homalothecium aureum (Morocco) formerly determined as *H. sericeum*	(MUB) Universidad de Murcia (#10731)	Morocco	17.03.97	M.J. Cano, M.T. Gallego & R.M. Ros	J.A. Jiménez	Bab Taza, base del Jbel Bouhalla	Roca protegida bajo carrasca, encinar calcícola con quejigos africanos		35°05'45"N 5°09'10"W		1250
Homalothecium fulgescens		Canada	03.02.07	W.B. Schofield	W.B. Schofield	Dunhock near Vancouver	on *Acer macrophyllum*	♀			

Sample	Herbarium (Nr.)	Country	Date	Col.	Det.	Location	Habitat	Sex	Coordinates	Inclination/ Exposition	Altitude [m a.s.l.]
Homalothecium philippeanum formerly determined as *Homalothecium lutescens*	(Je) Herbar Hausknecht, Jena	Austria	06.07.04	R.Düll		Kärnten, below Plöckenpass, *Picea* forest region with rockslide (Devon. dolomit. limestone): at the start of the trail to the Valentinsalm (TK 9343/3)	on mostly shady bloc	♀			1050-60

Appendix 2: Vegetation relevés of Holzberg (Hb) and Mönchsberg (Mb) plots

	Teucrio-Seslerietum Volk 37	Mesobrometum Br.-Bl. ap. Scherr. 25	Mesobrometum Br.-Bl. ap. Scherr. 25
Plot	**Hb**	**MbI**	**MbII**
Locality	Holzberg/Nennsdorf	Mönchsberg/Nennsdorf	Mönchsberg/Jena
Country	Thuringia	Thuringia	Thuringia
Date	12.05.07/07.06.08	13.05.07/07.06.2008	13.05.2007/07.06.08
Latitude, Longitude	50°53'23.4''N 11°33'15.3''E	50°52'51.1''N 11°34'57.1''E	50°52'51.0''N 11°34'56.7''E
Altitude [m a.s.l.]	296	286	286
Altitudial zone	colline	colline	colline
Inclination/Exposition	30°S	0°	0°
Relief	lower slope	plane (mesa)	plane (mesa)
Geological stratum	Lower Muschelkalk (Upper Wellenkalk)	Lower Muschelkalk (Upper Wellenkalk)	Lower Muschelkalk (Upper Wellenkalk)
Soil type	Calcareous lithosols	Calcareous lithosols	Calcareous lithosols
Stones/open soil [%]	40	10	5
Tree cover [%]/hight [m]	5/2.0	0/0	15/≥6
Shrub cover [%]/hight [m]	15/0.3	15/0.2	15/2
Herb cover [%]/hight [m]	50/0.3	90/0.5	20/0.3
Moss cover [%]	15	30	80
Sample area [m²]	27	15	15
Trees			
Acer platanoides			1
Betula pendula			r (seedling)
Fraxinus excelsior	+ (seedling)		1
Pinus sylvestris		+ (seedling)	
Quercus robur			+ (seedling)
Shrubs			
Prunus spinosa	2a		
Rosa rubiginosa	1m		
Clematis vitalba		1	
Cornus sanguinea	+ (seedling)		1
Corylus avellana			1
Cotoneaster integerrimus			1
Frangula alnus			1
Juniperus communis	1		
Rosa canina			1
Viburnum lantana			1
Herbs			
Sesleria albicans	3	1	+
Arrhenatherum eliatius		2a	
Bromus erectus	2a	1	
Festuca rupicola		2a	
Hieracium pilosella		2a	1m
Teucrium montanum	2a	1m	1
Thymus praecox	1		2a
Anthemis tinctoria		1m	
Bupleurum falcatum	1	1m	1m
Cirsium vulgare		1m	
Hippocrepis comosa	1m		

Lotus corniculatus		1m	+
Ranunculus bulbosum		1m	
Pimpinella saxifraga		1m	
Sanguisorba minor	1	1m	1m
Teucrium chamaedrys	1m		1
Anthericum ramosum	1		
Asperula cyanchica	1		
Brachypodium pinnatum		1	
Campanula rapunculoides	1	+	+
Carex humilis	1		
Centaurea scabiosa	1		
Daucus carota		1	
Fragaria vesca			1
Inula conyzae	1	1	
Hieracium murorum		1	
Hieracium lachenalii		1	
Hieracium piloselloides		1	1
Medicago lupulina		1	
Origanum vulgare	1	1	
Picris hieracioides		1	
Polygala comosa			1
Sedum acre		1	
Tanacetum corymbosum	1		
Astragalus glycyphyllos	r	+	
Campanula rotundifolia		+	
Carlina vulgaris		+	
Echium vulgare		+	
Euphorbia cyparissias	+	r	
Epipactis atrorubens			+
Galeopsis angustifolia		+	
Hypericum perforatum		+	
Melilotus officinalis		+	
Ononis repens			+
Tanacetum corymbosum		+	
Verbascum lychnitis		+	
Aster amellus	r		
Campanula persicifolia	r		
Helianthemum nummularium	r		
Polygala amarella			r
Potentilla neumanniana	r		
Pulsatilla vulgaris	r		
Vincetoxicum hirundinaria	r	r	
Viola hirta	r		
Bryophytes			
Abietinella abietina	2a	2a	2b
Tortula ruralis		2a	2b
Homalothecium lutescens	2a	2a	
Tortella inclinata			2b
Tortella tortuosa		2a	1m
Ditrichum flexicaule		1	1m
Hypnum lacunosum		1m	
Campylium chrysophyllum	+		

Rhytidium rugosum	+	
Homalothecium sericeum		+

(r) 1 Individual, of smaller growth form; (+) 2-5 Individuals, cover ≤ 5% of smaller growth form; (1) 6-50 Individuals, cover ≤ 5%, incl. 1-5 individuals of larger growth form; (1m) >50 Individuals, cover ≤ 5%; (2a) Any number of individuals, cover >5-15%; (2b) Any number of individuals, cover > 15-25%; (3) Any number of individuals, cover > 25-50%; (4) Any number of individuals, cover > 50-75%; (5) Any number of individuals, cover > 75-100%

Appendix 3: Vegetation relevés of Freyburg/Neuenburg (FN), Lindena (L) and Dollenchen (D)

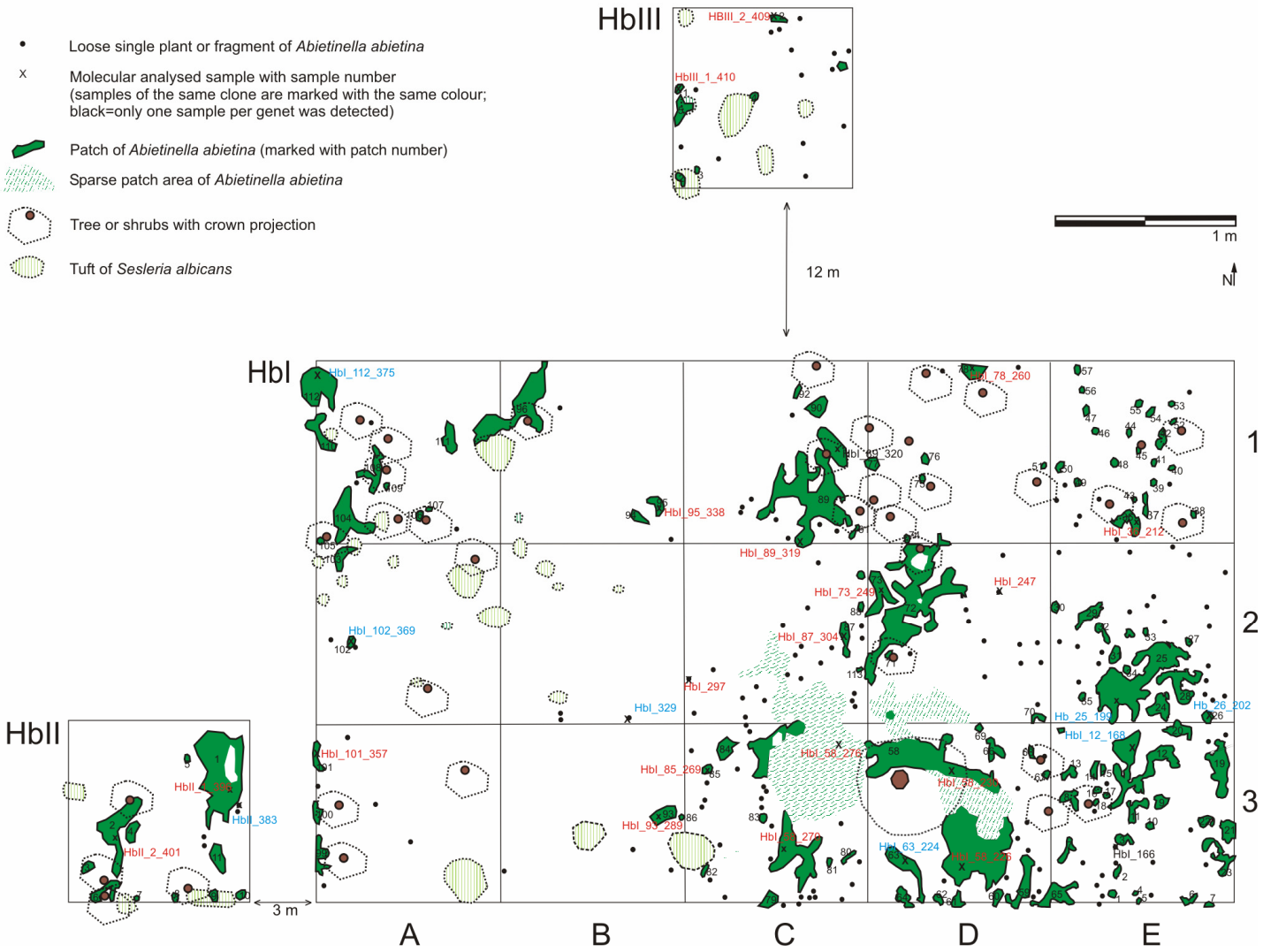
		Festuco-Cynosuretum Tx. in Bük. 42		Festuco-Cynosuretum Tx. in Bük. 42		Saxifrago tridactylitis-Poetum compressae (Kreh 45) Géhu u. Leriq 57
Plot	**LI** (wall)	**LV** (ground)	**LV** (wall)	**LVI** (ground)	**D** (wall)	**FN** (wall)
Locality	Lindena	Lindena	Lindena	Lindena	Dollenchen	Freyburg
Country	Brandenburg	Brandenburg	Brandenburg	Brandenburg	Brandenburg	Saxony-Anhalt
Date	03.05.08/ 31.05.08	03.05.08/ 31.05.08	03.05.08/ 31.05.08	03.05.08/ 31.05.08	31.05.2008	08.06.2008
Latitude, Longitude	51°35'28"N 13°32'13"E	51°35'28"N 13°32'13"E	51°35'28"N 13°32'13"E	51°35'28"N 13°32'11"E	51°36'28"N 13°51'39"E	51°12'33"N 11°46'42"E
Altitude [m a.s.l.]	91	91	91	91	124	208
Altitudial zone	lowland	lowland	lowland	lowland	lowland	colline
Inclination/exposition	90°NW	plane	plane/90°SW	plane	90°NW	plane
Stone type	Raseneisenstein, cobblestone		Raseneisenstein, cobblestone		cobblestone	limestone
open stones/soil [%]	90	5	90	20	80	40
Herb cover [%]/hight [cm]	5/15	95/30	5/15	75/20	5/10	40/40
Moss cover [%]	5	80	10	40	20	60
Sample area [m²]	**6**	10	10	10	15	9 (top of wall)
Trees						
Acer pseudoplatanus						r (seedling)
Quercus petraea						r (seedling)
Quercus spec.				r (seedling)		
Syringa vulgaris				1		
Tilia cordata						1
Shrubs						
Ilex aquifolium					+ (seedling)	
Herbs						
Achillea pannonica						2b
Centaurea stoebe ssp. stoebe						2b
Festuca trachyphylla		2b		1		

Sedum acre						2b
Echium vulgare						2a
Sedum album						2a
Trifolium repens		2a				
Arabis glabra		1m				
Ánthemis tinctória						1m
Bromus tectorum						1m
Euphorbia cyparissias						1m
Hedera helix			1m		1	+
Poa annua						1m
Allium scorodoprasum						1
Arenaria serphyllifolia						1
Arrhenatherum elatius						1
Bellis perennis		1				
Camelina microcarpa						1
Campanula rapunculoides		1			+	
Carex arenaria		1				
Cerastium holosteoides		1				
Hieracium pilosella		1				
Plantago lanceolata		1				
Ranunculus repens		1				
Rumex acetosella		1		+		
Taraxacum officinale		1				r
Trifolium campestre		1		+		
Achillea millefolium		+				
Anthriscus caucalis						+
Bromus sterilis				+		
Chelidonium majus			+			+
Dactylis glomerata		+				
Erigeron acris		+				
Galium aparine				+		
Geranium robertianum	+			+		
Lamium album	r		r			
Melica ciliata						+
Papaver rhoeas						+

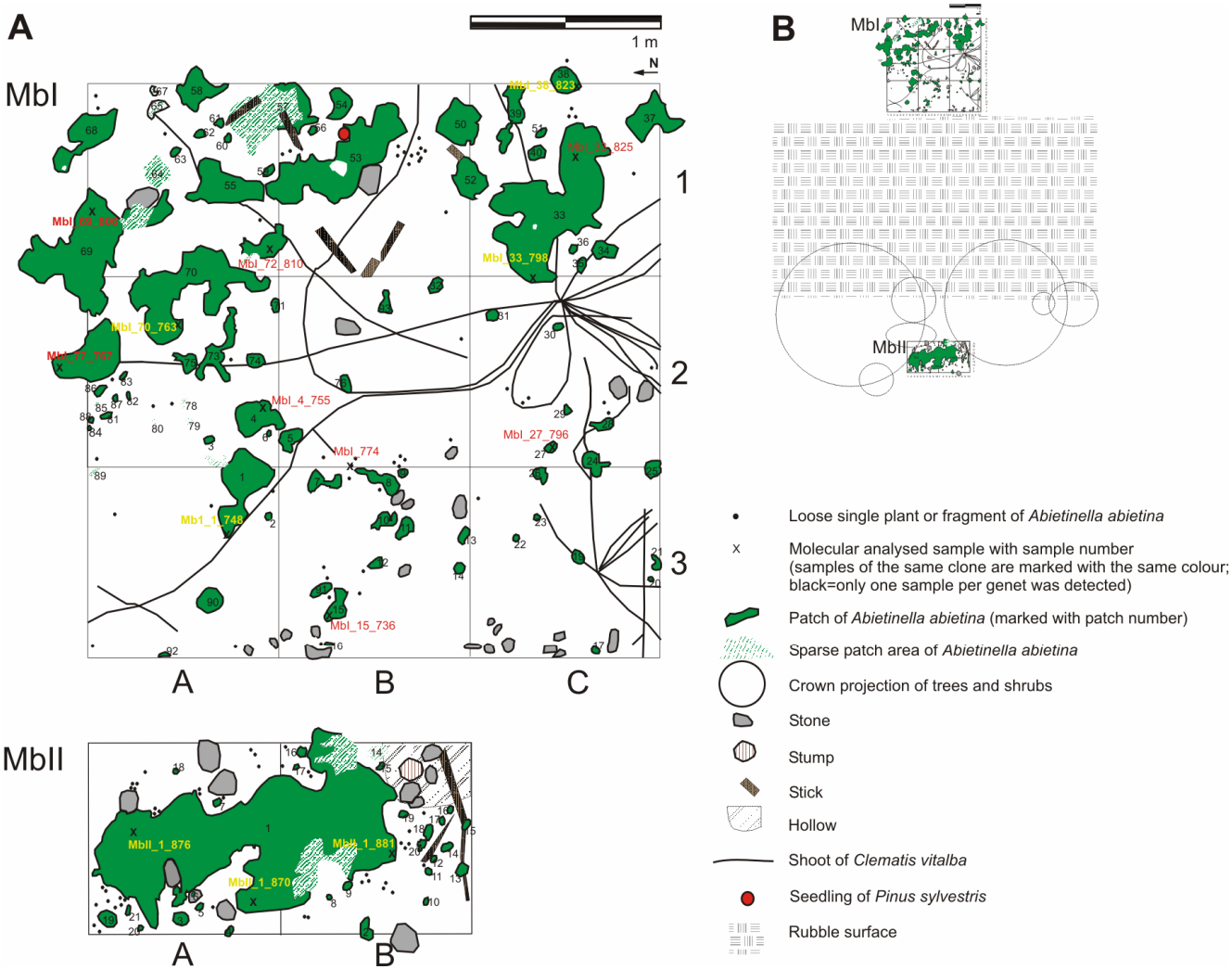
Potentilla reptans		+				
Scirpoides holoschoenus		+				
Veronica arvensis		+				
Veronica hederifolia			+		r	
Senecio vernalis						r
Pteridophytes						
Asplenium rúta-murária						+
Bryophytes						
Homalothecium sericeum	2a	2b	2a	2a	2b	5
Rhytidiadelphus squarrosus			2b			
Hypnum lacunosum	2a		2a	1		
Barbula unguiculata		1m				
Tortula muralis	1m		1	+		r
Tortula ruralis		1m				1
Pottia lanceolata						1
Amblystegium serpens		+				
Bryum inclinatum			+			
Plagiomnium rostratum			1m			
Pleurozium schreberi			+			
Campylium chrysophyllum						r

(r) 1 Individual, of smaller growth form; (+) 2-5 Individuals, cover ≤ 5% of smaller growth form; (1) 6-50 Individuals, cover ≤ 5%, incl. 1-5 individuals of larger growth form; (1m) >50 Individuals, cover ≤ 5%; (2a) Any number of individuals, cover >5-15%; (2b) Any number of individuals, cover > 15-25%; (3) Any number of individuals, cover > 25-50%; (4) Any number of individuals, cover > 50-75%; (5) Any number of individuals, cover > 75-100%

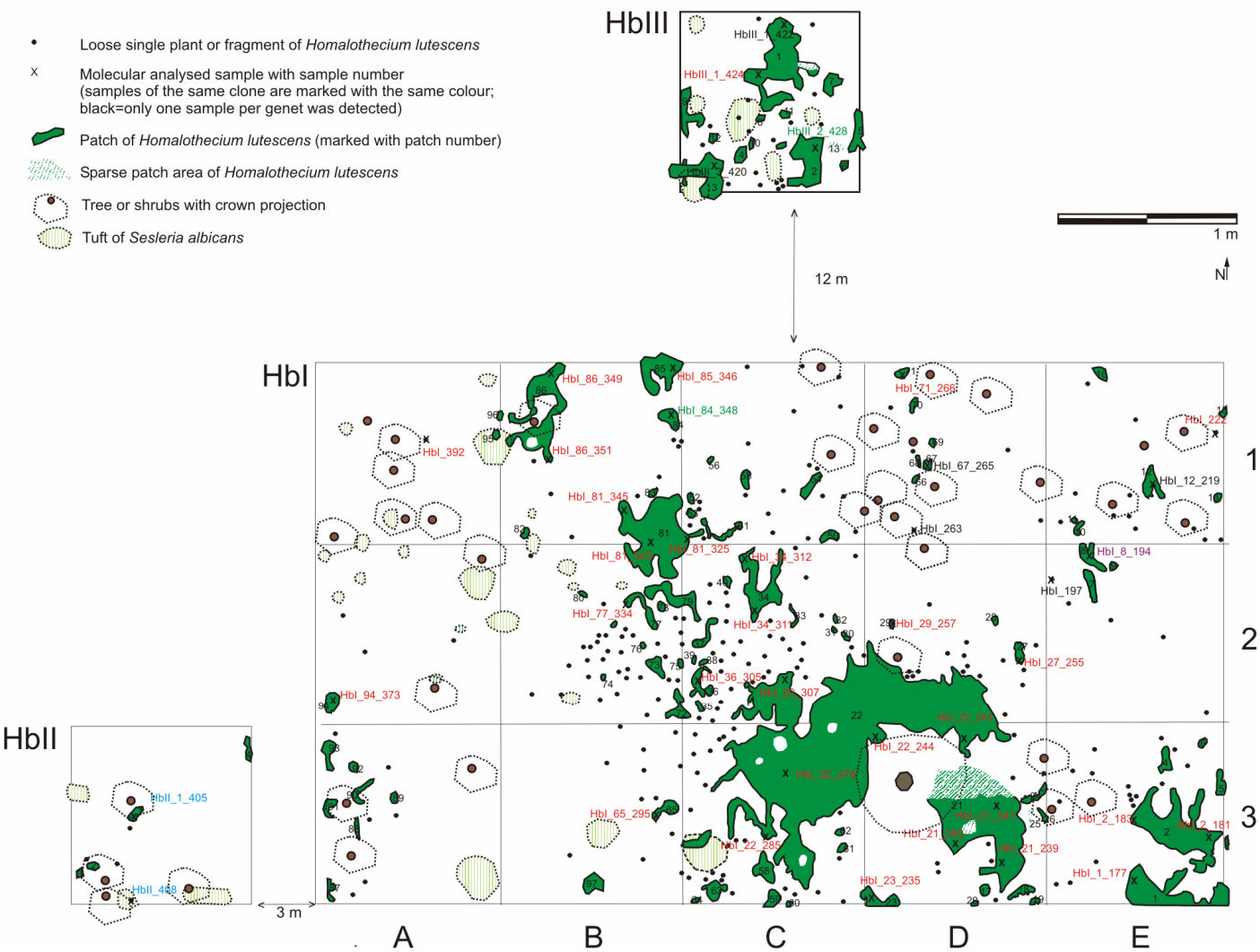
Appendix 4: Map of the Holzberg (Hb) plots of *Abietinella abietina*



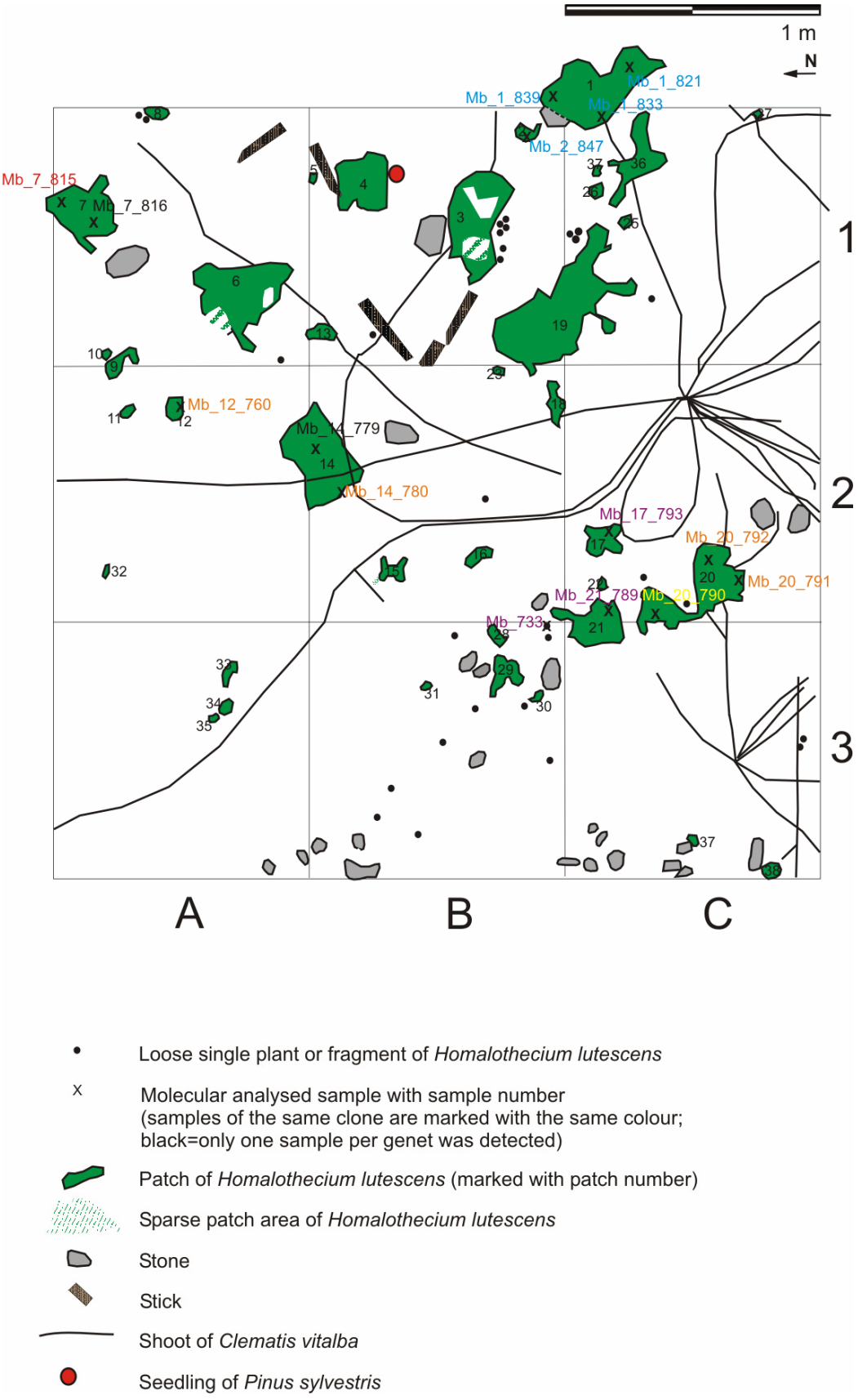
Appendix 5: Map of the Mönchsberg (Mb) plots of *Abietinella abietina* (A) and overview of the study area (B)



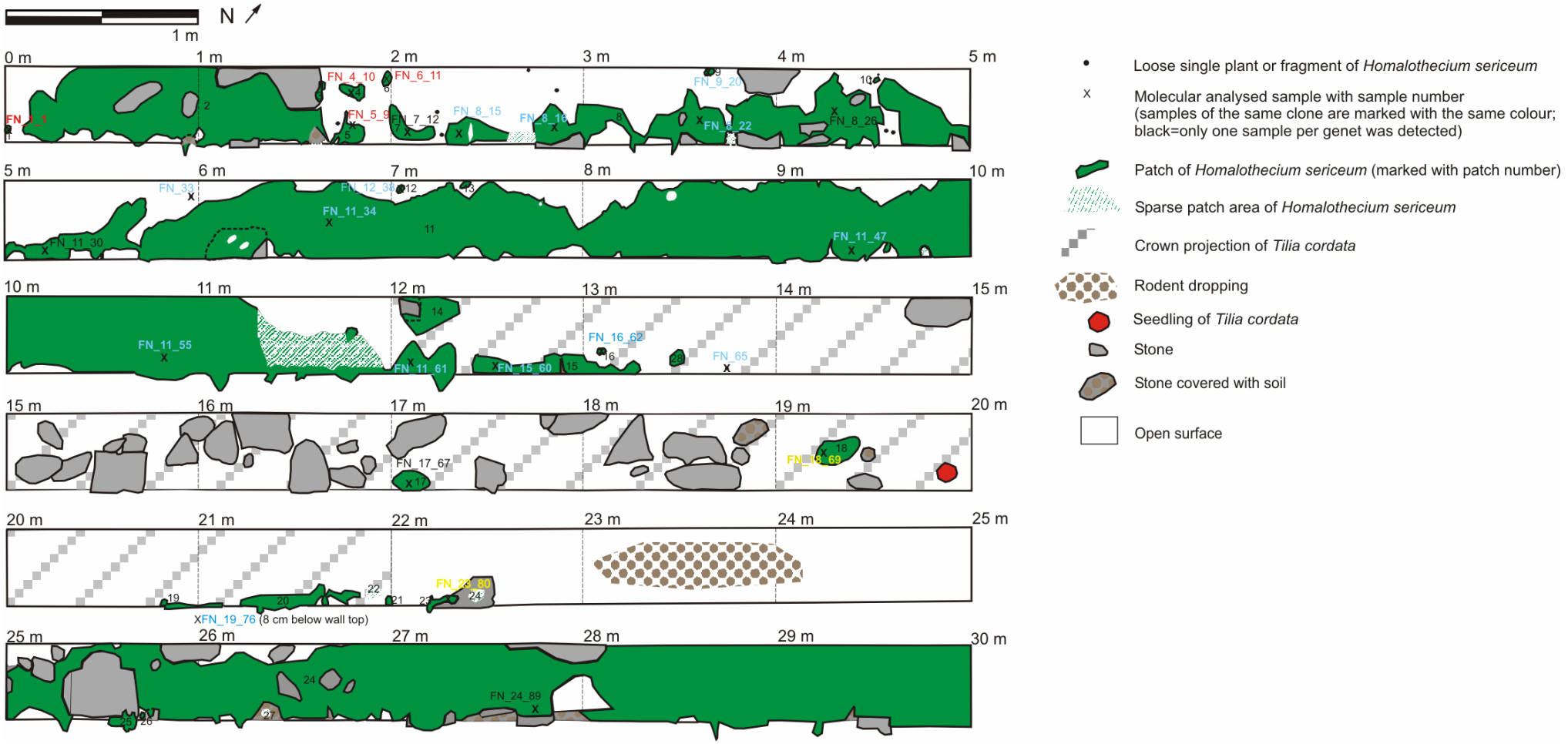
Appendix 6: Map of Holzberg (Hb) plots of *Homalothecium lutescens*



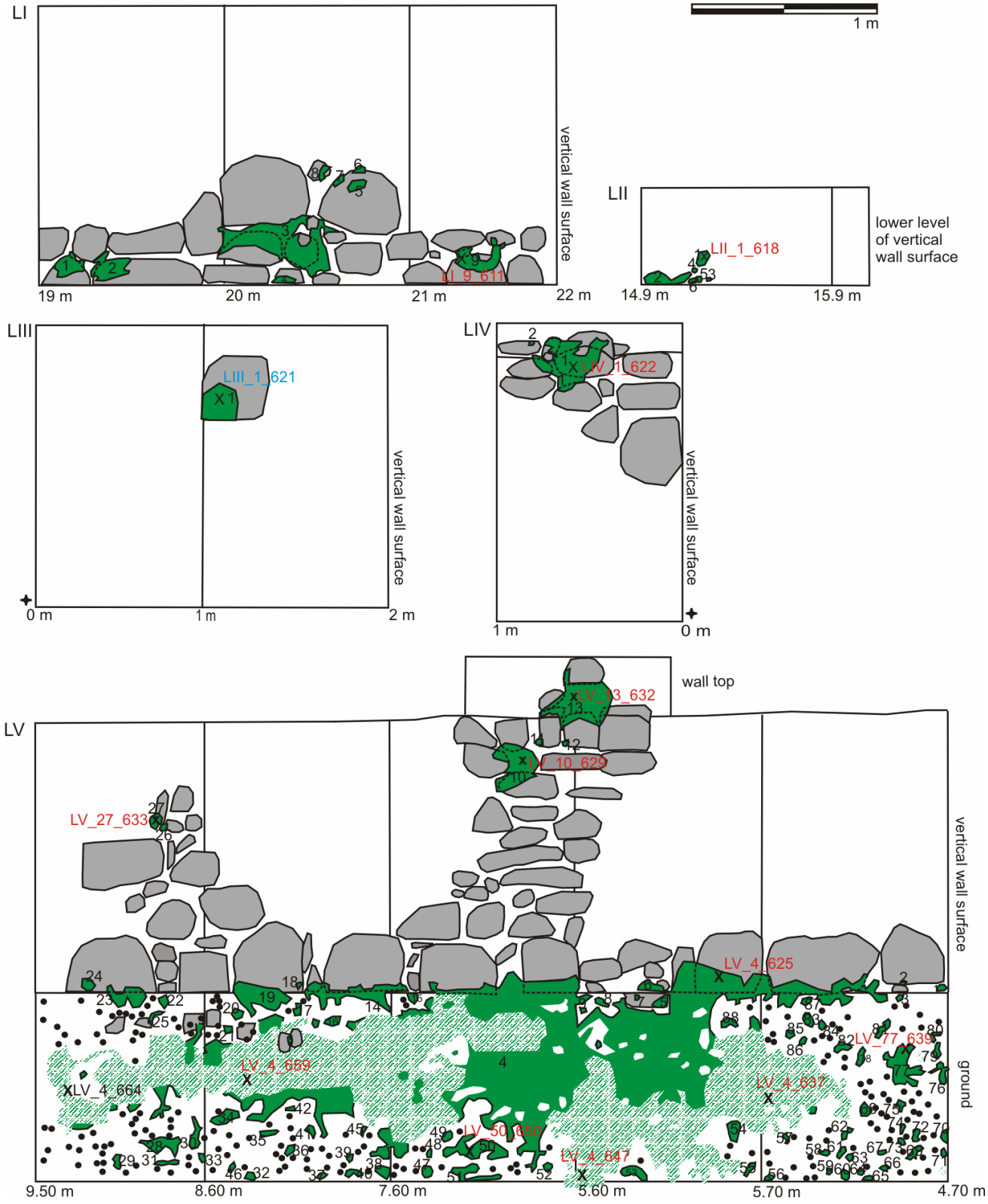
Appendix 7: Map of the Mönchsberg (Mb) plot of *Homalothecium lutescens*

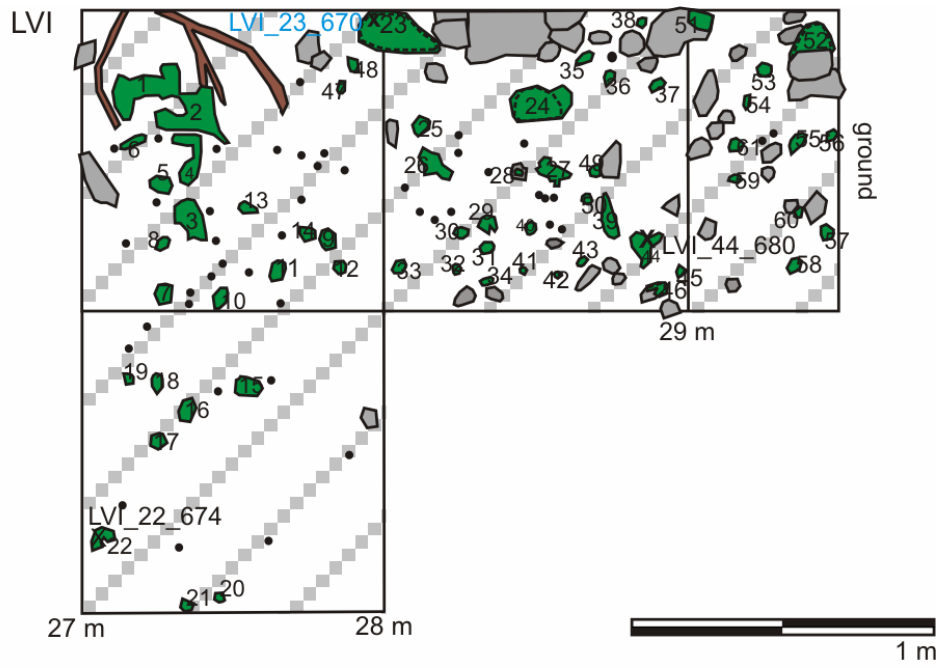


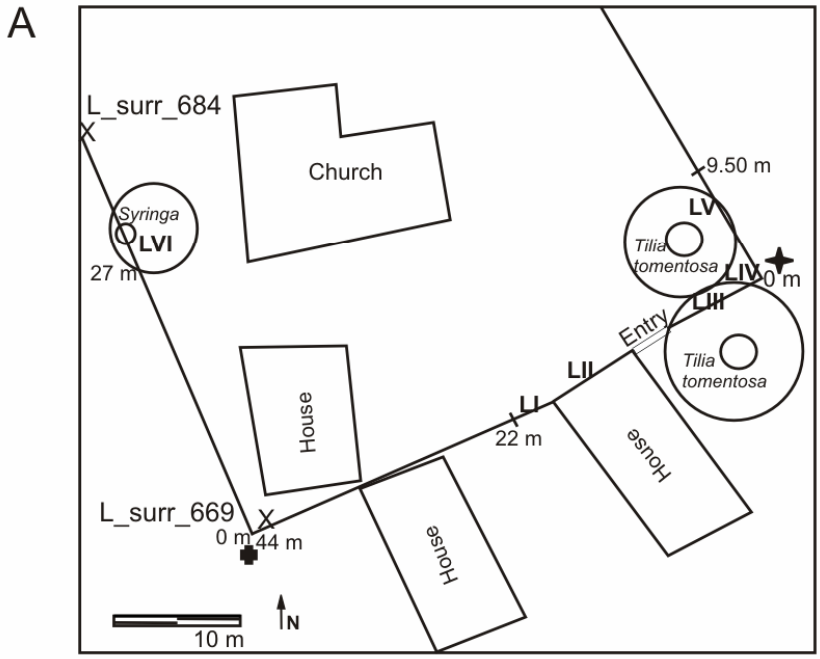
Appendix 8: Map of spatial distribution of patches of *Homalothecium sericeum* on wall top in Freyburg/Neuenburg (FN), serial order of wall sections is displayed consecutively



Appendix 9: Map of spatial distribution of patches of *Homalothecium sericeum* in Lindena (LI-LV) and overview of the study area (A), perspective is described on the left side of wall sections







• Loose single plant or fragment of *Homalothecium sericeum*

x Molecular analysed sample with sample number
(samples of the same clone are marked with the same colour;
black=only one sample per genet was detected)

Patch of *Homalothecium sericeum* (marked with patch number)

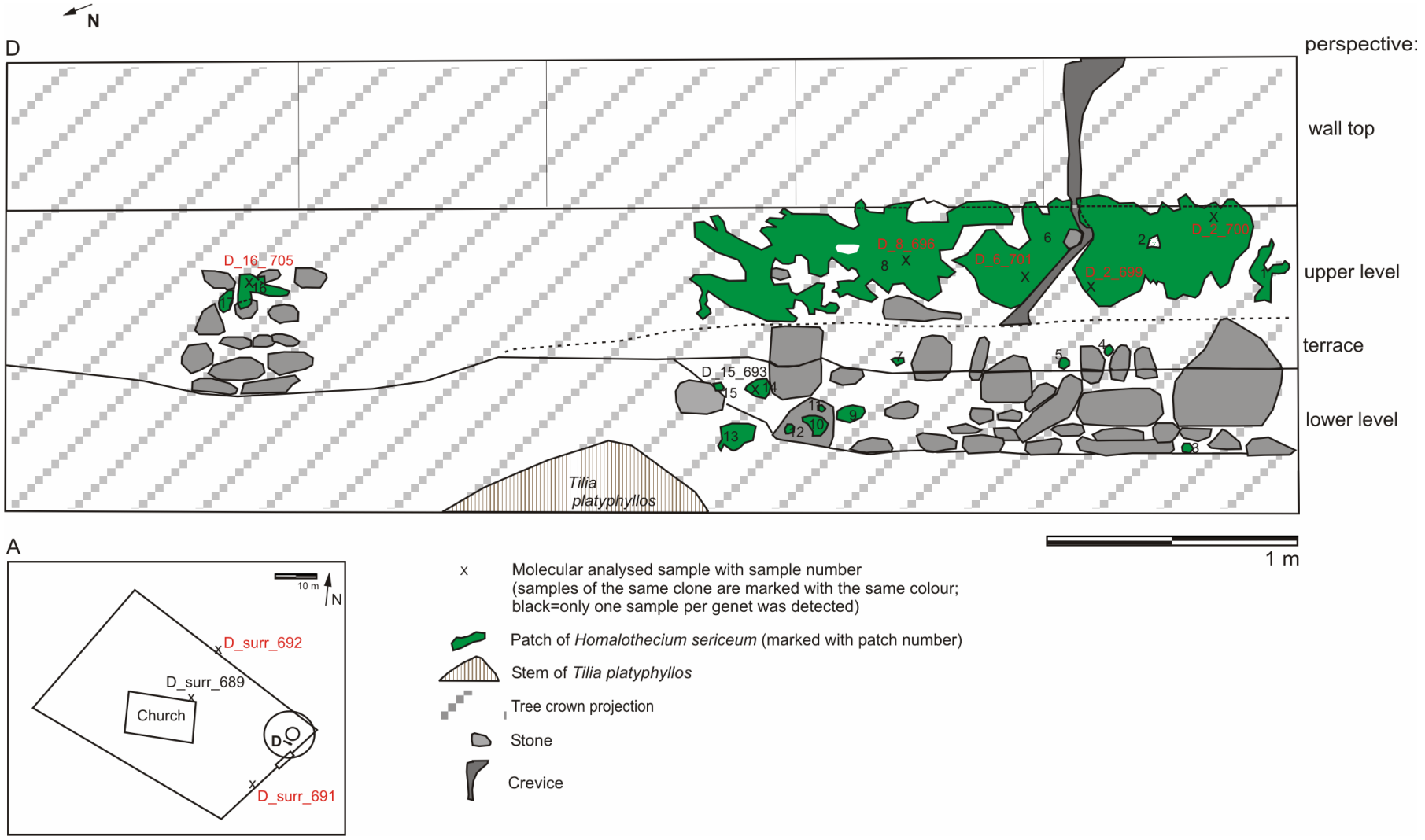
Sparse patch area of *Homalothecium sericeum*

Crown projection *Syringa vulgaris*

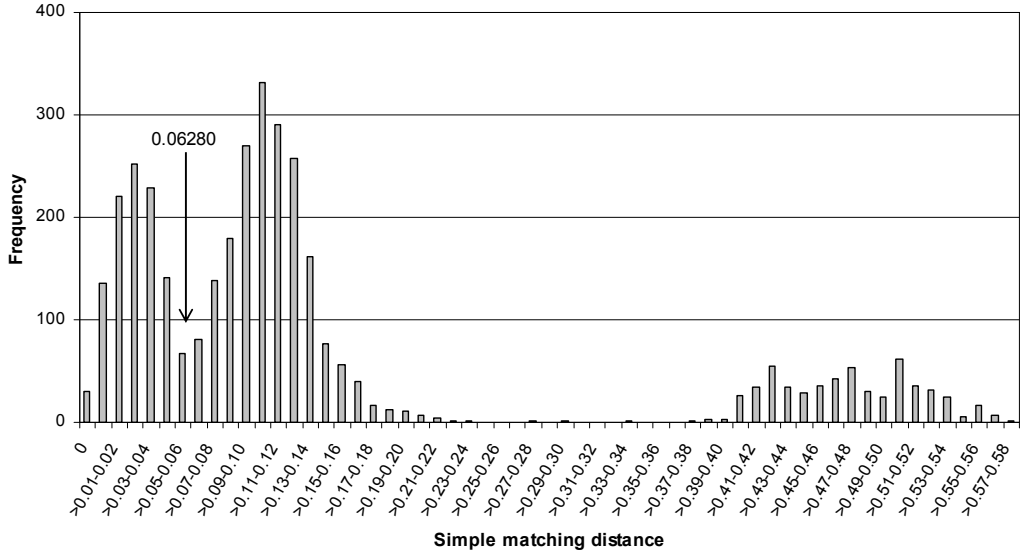
Stone

Root

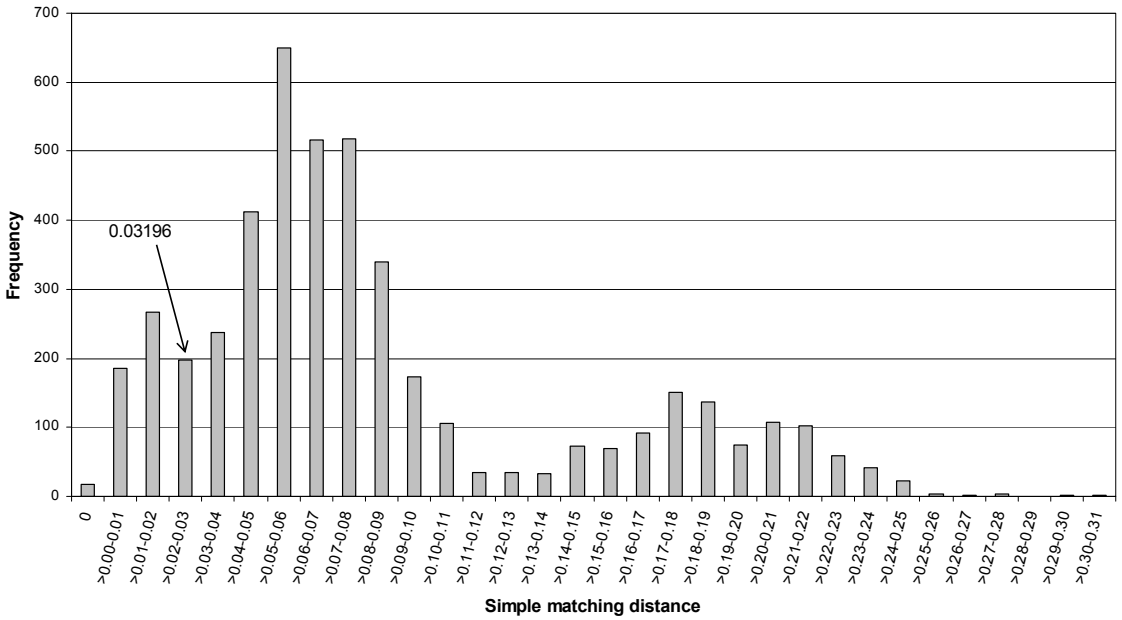
Appendix 10: Map of spatial distribution of patches of *Homalothecium sericeum* in Dollenchen (D) and overview of the study area (A)



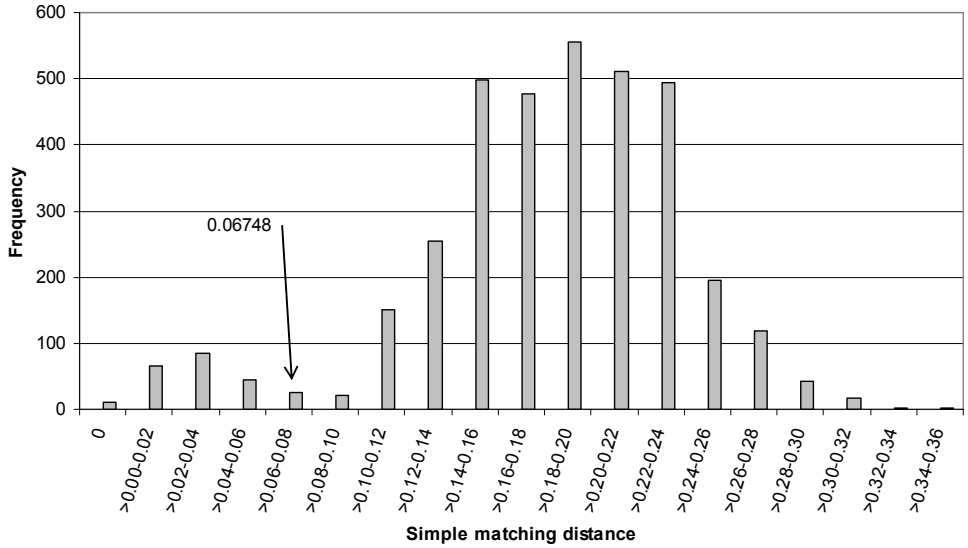
Appendix 11: Frequency histogram of pooled Simple matching distances of German samples of *Abietinella abietina* (A), *Homalothecium lutescens* (B) and *Homalothecium sericeum* (C)



A: Frequency histogram of pooled Simple matching distances of German samples of *Abietinella abietina*; the threshold for clonal identity is marked by an arrow.

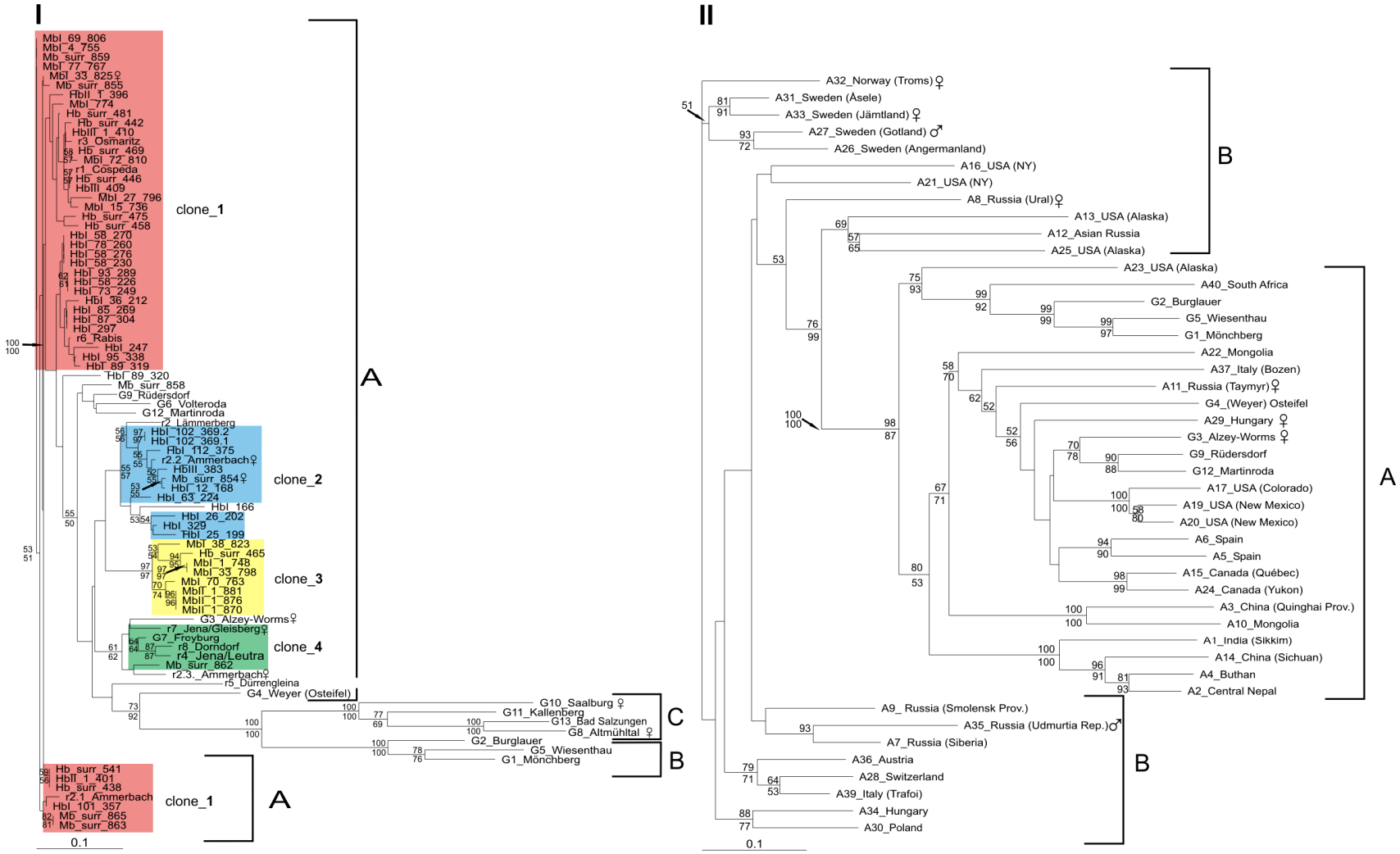


B: Frequency histogram of pooled Simple matching distances of German samples of *Homalothecium lutescens*; the threshold for clonal identity is marked by an arrow.

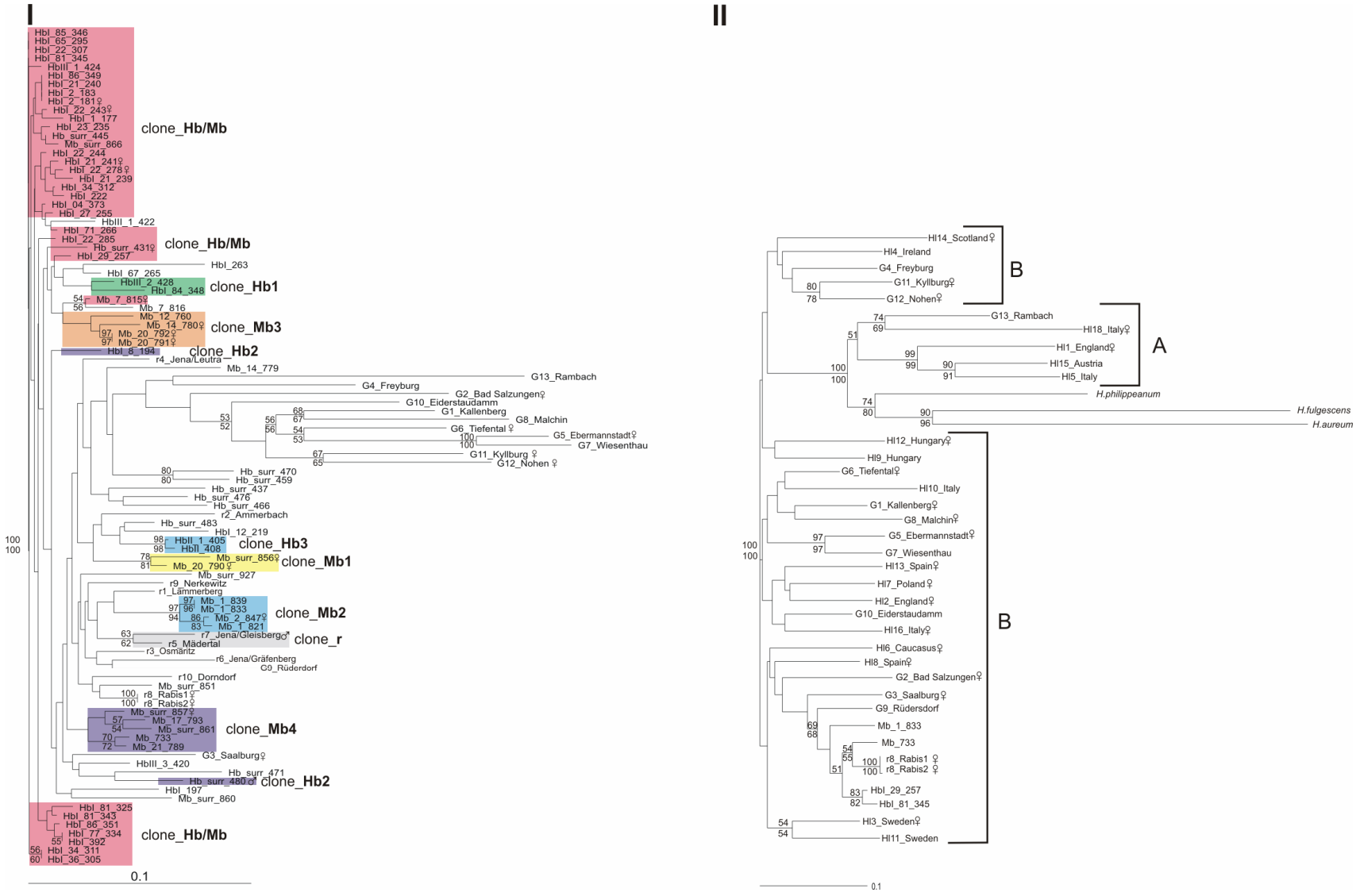


C: Frequency histogram of pooled Simple matching distances of German samples of *Homalothecium sericeum*; the threshold for clonal identity is marked by an arrow.

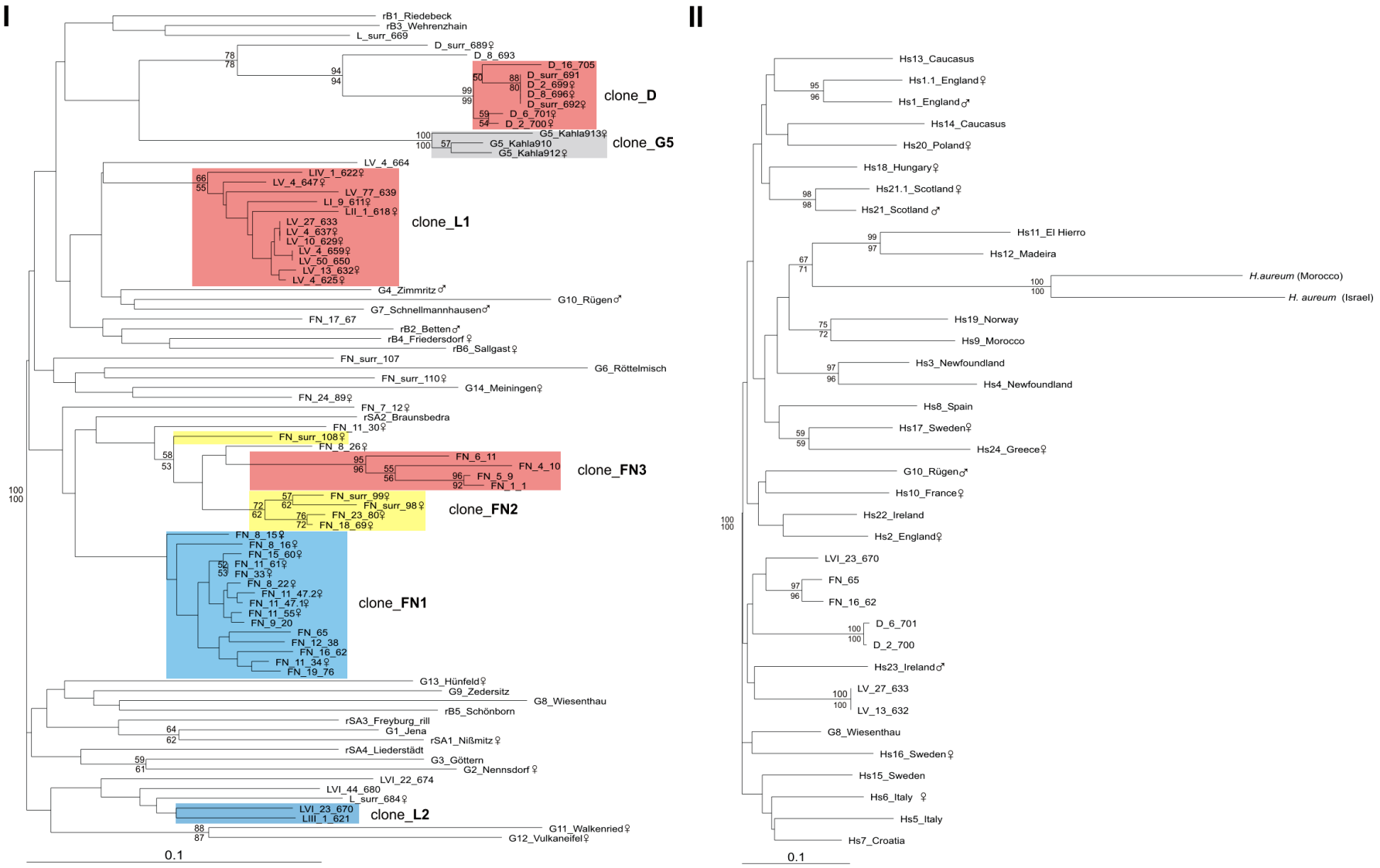
Appendix 12: Neighbour-joining dendrogram based on the Jaccard distances between all German samples (I) and all world-wide samples (II) of *Abietinella abietina*



Appendix 13: Neighbour-joining dendrogram based on the Jaccard distances between all German samples (I) and all world-wide samples (II) of *Homalothecium lutescens* (In addition, sample of *H. aureum*, *H. philippeanum* and *H. fulgescens* were analysed)



Appendix 14: Neighbour-joining dendrogram based on the Jaccard distances between all German samples (I) and all world-wide (II) samples of *Homalothecium sericeum* (In addition, samples of *Homalothecium aureum* were analysed)



Appendix 15

Protocols for DNA isolation from plant

Genomic DNA purification with NucleoSpin® Plant (lysis buffer C1 and C0)

1 Homogenize sample

Homogenize up to 100 mg wet weight or up to 20 mg dry weight (lyophilized) plant material (for homogenization methods see section 2.5).

homogenize samples

*Remember to preheat **buffer C0 for 10 min at 45°C** and mix well before use.*

2 Cell lysis

Transfer the resulting powder to a new tube and add **400 µl buffer C1** or **C0**. Vortex the mixture thoroughly.

+ 400 µl C1 or C0

*If the volume of lysis buffer is not large enough, the plant powder can be resuspended in additional **buffer C1** or **C0**. If the volume is changed, do not forget to increase the volumes of **buffer C4** and **ethanol** proportionally (see step 4).*

*Optional: If samples contain large amounts of RNA, we recommend the addition of **10 µl RNase A** solution to the **C1/C0 lysis mixture**.*

Incubate the suspension for **30 min at 60°C**.

60°C 30 min,

3 Filtration / Clarification of lysate

Centrifuge the mixture for **5 min at 11,000 x g**. Transfer 300 µl of the clear lysate to a new tube.

5 min 11,000 x g

*Alternatively, **NucleoSpin® Filter columns** can be used (not included, see ordering information). For this purpose, place a **NucleoSpin® Filter column** into a new tube and load the lysate onto the column. Centrifuge for **5 min at < 11,000 x g** and collect the clear flow-through.*

4 Adjust DNA binding conditions

Add **300 µl buffer C4** and **200 µl ethanol**. Mix by inverting the tube 2-4 times.

300 µl C4

200 µl ethanol

*C4 and **ethanol** may be premixed.*

NucleoSpin® Plant

5 Bind DNA

Place a NucleoSpin® Plant column into a 2 ml centrifuge tube and load sample.

load sample

Centrifuge for **1 min at 11,000 x g**. Discard flow-through. Repeat this step until all of the lysate has passed through the NucleoSpin® Plant column.

1 min 11,000 x g

6 Wash silica membrane

1st wash

Add **400 µl buffer CW** to the NucleoSpin® Plant column. Centrifuge for **1 min at 11,000 x g**. Discard flow-through.

+ 400 µl CW

+ 700 µl C5

2nd wash

Add **700 µl buffer C5** to the NucleoSpin® Plant column. Centrifuge for **1 min at 11,000 x g**. Discard flow-through.

1 min 11,000 x g

7 Wash / Dry silica membrane

3rd wash

Add another **200 µl buffer C5** to the NucleoSpin® Plant column. Centrifuge for **2 min at 11,000 x g** in order to remove **buffer C5** completely respectively to dry the silica membrane.

+ 200 µl C5

2 min 11,000 x g

8 Elute highly pure DNA

Place the NucleoSpin® Plant column into a new 1.5 ml centrifuge tube. Pipette **100 µl elution buffer CE (preheated to 70°C)** onto the membrane. Incubate at room temperature for **5 min**. Centrifuge for **1 min at 11,000 x g** to elute the DNA.

+ 100 µl CE (70°C)

RT 5 min

1 min 11,000 x g

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Appendix 16: Distance values between *Abietinella abietina* specimens of the German-wide sample set. Simple matching distances are given in the upper right, Jaccard distances in the lower left part of the matrix

			Population Hb									
			1	2	3	4	5	6	7	8	9	10
Population Hb	1	Hbl_166	0	0.13761	0.13780	0.07003	0.08936	0.07014	0.07006	0.12804	0.13798	0.14262
	2	Hbl_247	0.20064	0	0.02899	0.10628	0.09662	0.12560	0.11594	0.03865	0.03865	0.03382
	3	Hbl_297	0.20220	0.04412	0	0.10628	0.09662	0.12560	0.12560	0.00966	0.00966	0.00483
	4	Hbl_329	0.10972	0.15493	0.15603	0	0.03865	0.01932	0.01932	0.09662	0.10628	0.10145
	5	Hbl_12_168	0.13804	0.14184	0.14286	0.06061	0	0.04831	0.04831	0.10628	0.09662	0.09179
	6	Hbl_25_199	0.11045	0.18182	0.18310	0.03101	0.07576	0	0.03865	0.11594	0.12560	0.12077
	7	Hbl_26_202	0.11032	0.16901	0.18310	0.03101	0.07576	0.06154	0	0.11594	0.12560	0.12077
	8	Hbl_36_212	0.18944	0.05839	0.01504	0.14286	0.15603	0.17021	0.17021	0	0.01932	0.01449
	9	Hbl_58_226	0.20347	0.05882	0.01515	0.15714	0.14388	0.18440	0.18440	0.03008	0	0.00483
	10	Hbl_58_230	0.20946	0.05147	0.00758	0.15000	0.13669	0.17730	0.17730	0.02256	0.00763	0
	11	Hbl_58_270	0.20957	0.05147	0.00758	0.15000	0.13669	0.17730	0.17730	0.02256	0.00763	0.00000
	12	Hbl_58_276	0.20936	0.05147	0.00758	0.15000	0.13669	0.17730	0.17730	0.02256	0.00763	0.00000
	13	Hbl_63_224	0.12507	0.15603	0.14388	0.03101	0.06107	0.06154	0.06154	0.15714	0.13139	0.13768
	14	Hbl_73_249	0.20320	0.05882	0.01515	0.15714	0.14388	0.18440	0.18440	0.03008	0.00000	0.00763
	15	Hbl_78_260	0.20951	0.05147	0.00758	0.15000	0.13669	0.17730	0.17730	0.02256	0.00763	0.00000
	16	Hbl_85_269	0.20196	0.04412	0.00000	0.15603	0.14286	0.18310	0.18310	0.01504	0.01515	0.00758
	17	Hbl_87_304	0.20222	0.04412	0.00000	0.15603	0.14286	0.18310	0.18310	0.01504	0.01515	0.00758
	18	Hbl_89_319	0.20950	0.03704	0.02256	0.16312	0.15000	0.17730	0.17730	0.03731	0.03759	0.03008
	19	Hbl_89_320	0.23048	0.10145	0.05970	0.17143	0.15827	0.18571	0.19858	0.07407	0.06015	0.05263
	20	Hbl_93_289	0.20382	0.05882	0.01515	0.15714	0.14388	0.18440	0.18440	0.03008	0.00000	0.00763
	21	Hbl_95_338	0.20191	0.02963	0.01504	0.15603	0.14286	0.18310	0.17021	0.02985	0.03008	0.02256
	22	Hbl_101_357	0.18455	0.08029	0.03759	0.13768	0.16429	0.16547	0.16547	0.05224	0.02290	0.03030
	23	Hbl_102_369.1	0.15048	0.11429	0.11511	0.06015	0.03053	0.07519	0.08955	0.12857	0.11594	0.10870
	24	Hbl_102_ 369.2	0.15048	0.11429	0.11511	0.06015	0.03053	0.07519	0.08955	0.12857	0.11594	0.10870
	25	Hbl_112_375	0.13878	0.14286	0.13043	0.06107	0.03101	0.07634	0.07634	0.14388	0.13139	0.12409
	26	HbII_383	0.15924	0.14894	0.13669	0.06818	0.02326	0.09774	0.08333	0.15000	0.13768	0.13043
	27	HbII_1_396	0.18469	0.06618	0.03759	0.12409	0.15108	0.15217	0.15217	0.05224	0.05263	0.04511
	28	HbII_1_401	0.18353	0.06569	0.03731	0.12319	0.15000	0.15108	0.15108	0.05185	0.03759	0.03008
	29	HbIII_1_410	0.18918	0.04412	0.04444	0.14286	0.16901	0.17021	0.15714	0.05882	0.05926	0.05185
	30	HbIII_2_409	0.19689	0.05147	0.05185	0.15000	0.17606	0.16429	0.16429	0.06618	0.06667	0.05926
	31	Hb_surr_438	0.18377	0.06569	0.03731	0.12319	0.15000	0.15108	0.15108	0.05185	0.03759	0.03008
	32	Hb_surr_442	0.19503	0.03676	0.05147	0.14894	0.17483	0.17606	0.16312	0.06569	0.06618	0.05882
	33	Hb_surr_446	0.19662	0.05147	0.05185	0.15000	0.17606	0.16429	0.16429	0.06618	0.06667	0.05926
	34	Hb_surr_458	0.15090	0.07299	0.05926	0.11679	0.14388	0.14493	0.14493	0.07353	0.05970	0.06667
	35	Hb_surr_465	0.20756	0.15862	0.17241	0.17483	0.16197	0.18881	0.18881	0.18493	0.18621	0.17931
	36	Hb_surr_469	0.18189	0.05109	0.05147	0.13571	0.16197	0.16312	0.15000	0.06569	0.06618	0.05882
	37	Hb_surr_475	0.17614	0.05839	0.05882	0.12950	0.15603	0.15714	0.14388	0.07299	0.07353	0.06618
	38	Hb_surr_481	0.18329	0.05147	0.03731	0.13669	0.16312	0.16429	0.15108	0.05185	0.05224	0.04478
	39	Hb_surr_541	0.18329	0.06569	0.03731	0.12319	0.15000	0.15108	0.15108	0.05185	0.03759	0.03008
Population Mb	40	Mbl_774	0.19769	0.06618	0.03759	0.15108	0.17730	0.17857	0.16547	0.05224	0.05263	0.04511
	41	Mbl_1_748	0.20059	0.13889	0.16552	0.16783	0.15493	0.19444	0.18182	0.17808	0.17931	0.17241
	42	Mbl_4_755	0.19828	0.08029	0.03759	0.13768	0.16429	0.15217	0.16547	0.05224	0.03788	0.03030
	43	Mbl_15_736	0.19995	0.06277	0.06309	0.13990	0.16643	0.15452	0.15490	0.07730	0.07759	0.06948
	44	Mbl_27_796	0.18189	0.05109	0.07971	0.13571	0.16197	0.15000	0.15000	0.09353	0.09420	0.08696
	45	Mbl_33_798	0.20075	0.13889	0.16552	0.16783	0.15493	0.19444	0.18182	0.17808	0.17931	0.17241
	46	Mbl_33_825	0.19097	0.07299	0.03008	0.13043	0.15714	0.15827	0.15827	0.04478	0.03030	0.02273
	47	Mbl_38_823	0.21479	0.13986	0.15385	0.16901	0.15603	0.18310	0.19580	0.16667	0.15493	0.16084
	48	Mbl_69_806	0.19800	0.08029	0.03759	0.13768	0.16429	0.15217	0.16547	0.05224	0.03788	0.03030
	49	Mbl_70_763	0.20925	0.14685	0.14789	0.16312	0.13669	0.16429	0.19014	0.16084	0.14894	0.14184
	50	Mbl_72_810	0.17535	0.05797	0.05839	0.12857	0.15493	0.15603	0.14286	0.07246	0.07299	0.06569
	51	Mbl_77_767	0.19758	0.08029	0.03759	0.13768	0.16429	0.15217	0.16547	0.05224	0.03788	0.03030
	52	MbII_1_870	0.20330	0.15385	0.15493	0.14388	0.11679	0.14493	0.17143	0.16783	0.15603	0.14894
	53	MbII_1_876	0.20337	0.15385	0.15493	0.14388	0.11679	0.14493	0.17143	0.16783	0.15603	0.14894
	54	MbII_1_881	0.20368	0.15385	0.15493	0.14388	0.11679	0.14493	0.17143	0.16783	0.15603	0.14894
	55	Mb_surr_854	0.14556	0.14894	0.13669	0.06818	0.00781	0.08333	0.08333	0.15000	0.13768	0.13043
	56	Mb_surr_855	0.19641	0.07971	0.03731	0.13669	0.16312	0.16429	0.16429	0.05185	0.03759	0.03008
	57	Mb_surr_858	0.14365	0.10714	0.09420	0.09559	0.10949	0.11029	0.12409	0.10791	0.09489	0.08759
	58	Mb_surr_859	0.19761	0.08029	0.03759	0.13768	0.16429	0.15217	0.16547	0.05224	0.03788	0.03030
	59	Mb_surr_862	0.24647	0.14685	0.12143	0.17606	0.15000	0.19014	0.20280	0.13475	0.12230	0.11511
	60	Mb_surr_863	0.19814	0.09420	0.05224	0.15108	0.17730	0.16547	0.17857	0.06667	0.03788	0.04511
	61	Mb_surr_865	0.19769	0.09420	0.05224	0.15108	0.17730	0.16547	0.17857	0.06667	0.03788	0.04511
Regional samples	62	r1_Cospeda	0.19669	0.05147	0.05185	0.15000	0.17606	0.16429	0.16429	0.06618	0.06667	0.05926
	63	r2_Lämmerberg	0.17856	0.11511	0.14286	0.08955	0.07519	0.11852	0.09023	0.15603	0.14388	0.13669
	64	r2.1_Ammerbach	0.18475	0.09420	0.05224	0.13768	0.17730	0.16547	0.16547	0.05224	0.03788	0.04511
	65	r2.2_Ammerbach	0.13830	0.12857	0.12950	0.04580	0.01550	0.07576	0.06107	0.14286	0.13043	0.12319
	66	r2.3_Ammerbach	0.23056	0.14184	0.12950	0.17143	0.11765	0.18571	0.18571	0.14286	0.13043	0.12319
	67	r3_Osmaritz	0.19639	0.05147	0.05185	0.15000	0.17606	0.17730	0.16429	0.06618	0.06667	0.05926
	68	r4_Jena/Leutra	0.28503	0.13889	0.13986	0.19310	0.18056	0.21918	0.21918	0.15278	0.14085	0.13380
	69	r5_Dürrengleina	0.32857	0.23586	0.20052	0.25288	0.24188	0.26734	0.27944	0.21163	0.18881	0.19362
	70	r6_Rabis	0.19515	0.03676	0.00752	0.14894	0.13571	0.17606	0.17606	0.02239	0.02256	0.01504
	71	r7_Jena/Gleisberg	0.23622	0.12500	0.12587	0.15385	0.14085	0.18056	0.18056	0.13889	0.13986	0.13287
	72	r8_Dorndorf	0.26867	0.13287	0.14685	0.18750	0.16197	0.21379	0.20139	0.15972	0.14789	0.14085
National samples	73	G1_Mönchberg	0.55916	0.52704	0.53902	0.56264	0.56299	0.57567	0.57105	0.53814	0.53252	0.53563
	74	G2_Burglauer	0.53759	0.50292	0.49704	0.51190	0.52941	0.53254	0.52381	0.49704	0.50000	0.49405
	75	G3_Alzey-Worms	0.30105	0.17481	0.17572	0.22794	0.21574	0.24188	0.25343	0.18845	0.16413	0.17013
	76	G4_Weyer (Osteifel)	0.31469	0.23448	0.24828	0.27586	0.28767	0.28966	0.30137	0.26027	0.23776	0.24306
	77	G5_Wiesenthau	0.59296	0.57386	0.56897	0.59195	0.59195	0.60345	0.60345	0.56897	0.56395	0.56647
	78	G6_Volterode	0.21471	0.12676	0.14085	0.15603	0.16901	0.18310	0.15714	0.15385	0.14184	0.13475
	79	G7_Freyburg	0.26833	0.11972	0.10714	0.17483	0.16197	0.20139	0.20139	0.12057	0.10791	0.10072
	80	G8_Altmühltal	0.63261	0.62011	0.60795	0.65363	0.63842	0.64972	0.65730	0.60795	0.61143	0.61364
	81	G9_Rüdersdorf	0.17067	0.07971	0.08029	0.10949	0.09559	0.13768	0.12409	0.09420	0.08088	0.07353
	82	G10 _Saalburg	0.61200	0.57995	0.56692	0.59842	0.61421	0.61779	0.60190	0.56661	0.57034	0.57257
	83	G11_Kallenberg	0.52686	0.53143	0.53448	0.55747	0.54913	0.56069	0.54386	0.53448	0.54598	0.54023
	84	G12_Martinroda	0.14463	0.12143	0.12230	0.12409	0.11029	0.13869	0.12500	0.13571	0.10949	0.11594
	85	G13_Bad Salzungen	0.63075	0.59114	0.58636	0.64740	0.63229	0.64341	0.65095	0.58650	0.58976	0.59202

Appendix 17: Distance values between *Abietinella abietina* specimens of the world-wide sample set. Simple matching distances are given in the upper right, Jaccard distances in the lower left part of the matrix

			International samples									
			1	2	3	4	5	6	7	8	9	10
International samples	1	A1_India (Sikkim)	0	0.14796	0.38776	0.15306	0.40816	0.39796	0.46939	0.44388	0.46939	0.38776
	2	A2_Central Nepal	0.23387	0	0.34184	0.06633	0.39286	0.35204	0.50510	0.44898	0.47449	0.40306
	3	A3_China (Quinghai Pr	0.52414	0.47183	0	0.34694	0.40816	0.39796	0.45918	0.42347	0.45918	0.15306
	4	A4_Buthan	0.24390	0.11207	0.48227	0	0.39796	0.36735	0.51020	0.45408	0.47959	0.39796
	5	A5_Spain	0.54054	0.52027	0.54422	0.53061	0	0.10204	0.45918	0.45408	0.44898	0.37755
	6	A6_Spain	0.52000	0.46939	0.52349	0.48980	0.16529	0	0.43878	0.46429	0.43878	0.38776
	7	A7_Russia (Siberia)	0.57500	0.60000	0.56962	0.60976	0.56604	0.53750	0	0.19898	0.14286	0.48980
	8	A8_Russia (Ural)	0.56129	0.56051	0.54605	0.57051	0.57051	0.56875	0.28467	0	0.22959	0.45408
	9	A9_Russia (Smolensk	0.57862	0.57764	0.57325	0.58750	0.56051	0.54088	0.21053	0.32374	0	0.48980
	10	A10_Mongolia	0.52778	0.53741	0.25000	0.53793	0.51748	0.51701	0.60000	0.57792	0.60377	0
	11	A11_Russia (Taymyr)	0.54626	0.48856	0.46066	0.49831	0.35750	0.33829	0.53967	0.50619	0.52492	0.47445
	12	A12_Asian Russia	0.60000	0.58000	0.59459	0.60000	0.70370	0.66667	0.43662	0.41606	0.41727	0.64474
	13	A13_USA (Alaska)	0.56774	0.53896	0.57143	0.55844	0.59494	0.59259	0.42953	0.39860	0.44295	0.56579
	14	A14_China (Sichuan)	0.28906	0.18033	0.50345	0.17500	0.53020	0.50000	0.60000	0.61350	0.61212	0.54730
	15	A15_Canada (Quebéc)	0.56051	0.48344	0.48649	0.50331	0.28788	0.24242	0.51250	0.54375	0.51572	0.46897
	16	A16_USA (NY)	0.56209	0.57051	0.60256	0.58065	0.63354	0.62195	0.35461	0.43448	0.30882	0.62420
	17	A17_USA (Colorado)	0.53061	0.47917	0.51389	0.50000	0.28571	0.27907	0.58385	0.57962	0.57862	0.48571
	18	A19_USA (New Mexico	0.53788	0.47786	0.49652	0.49818	0.28972	0.26336	0.53144	0.56284	0.53471	0.46817
	19	A20_USA (New Mexico	0.54545	0.48667	0.50000	0.50667	0.26357	0.25758	0.55215	0.54717	0.54658	0.46154
	20	A21_USA (Connecticut	0.56493	0.61709	0.61410	0.64403	0.59687	0.57652	0.24088	0.31759	0.26982	0.61755
	21	A22_Mongolia	0.53741	0.51701	0.45652	0.47518	0.45324	0.44366	0.54487	0.59494	0.58491	0.52448
	22	A23_USA (Alaska)	0.52258	0.47368	0.55414	0.48344	0.48344	0.46405	0.49375	0.55215	0.47771	0.51974
	23	A24_Canada (Yukon)	0.55556	0.49664	0.51020	0.51678	0.27344	0.19841	0.53459	0.56604	0.54717	0.49306
	24	A25_USA (Alaska)	0.52980	0.52941	0.57143	0.55844	0.62963	0.62651	0.37500	0.42069	0.43243	0.58442
	25	A26_Sweden (Ångerma	0.54570	0.58165	0.56804	0.59190	0.58304	0.54935	0.27573	0.37241	0.29082	0.60867
	26	A27_Sweden (Gotland)	0.53896	0.57500	0.57962	0.59375	0.61111	0.57407	0.25735	0.34286	0.25926	0.61006
	27	A28_Switzerland	0.55414	0.56250	0.60248	0.57233	0.56329	0.54375	0.31690	0.31655	0.28261	0.59748
	28	A29_Hungary	0.51389	0.48266	0.49672	0.49300	0.29295	0.32449	0.57266	0.52139	0.57614	0.47868
	29	A30_Hungary	0.55901	0.57576	0.58896	0.57669	0.55000	0.55758	0.29371	0.38514	0.27143	0.60976
	30	A31_Sweden (Åsele)	0.56410	0.59006	0.60377	0.59119	0.58228	0.56250	0.21212	0.32609	0.22727	0.63354
	31	A32_Norway (Troms)	0.56688	0.57500	0.55195	0.57595	0.61111	0.58282	0.30714	0.34286	0.29710	0.60127
	32	A33_Sweden (Jämtland	0.55380	0.58839	0.58005	0.59833	0.58510	0.56579	0.23842	0.32376	0.23989	0.59696
	33	A34_Poland	0.54902	0.59375	0.62500	0.58599	0.53947	0.52903	0.27941	0.38732	0.28148	0.62025
	34	A35_Russia (Udmurtia	0.58842	0.57887	0.55710	0.58870	0.53083	0.50243	0.20334	0.40282	0.29228	0.59577
	35	A36_Austria	0.57862	0.58642	0.60870	0.58750	0.56962	0.54088	0.25000	0.32374	0.21212	0.61250
	36	A37_Italy (Bozen)	0.51748	0.49650	0.52113	0.51748	0.39394	0.42029	0.56410	0.56863	0.56774	0.47059
	37	A39_Italy (Trafoi)	0.56604	0.59146	0.62195	0.59259	0.56604	0.54658	0.28571	0.33333	0.23704	0.61728
	38	A40_South Africa	0.54861	0.54795	0.55245	0.55862	0.56849	0.54730	0.58333	0.55034	0.56863	0.56643
National samples	39	G1_Mönchberg	0.51748	0.49650	0.54167	0.51748	0.57718	0.54667	0.57325	0.51020	0.53947	0.53521
	40	G2_Burglauer	0.50000	0.46939	0.53333	0.50000	0.53947	0.48000	0.52830	0.49342	0.53165	0.51701
	41	G3_Alzey-Worms	0.53947	0.46939	0.51351	0.50000	0.29231	0.28571	0.54658	0.52258	0.54088	0.48611
	42	G4_Weyer (Osteifel)	0.57050	0.48533	0.45871	0.52533	0.34572	0.34857	0.55043	0.56007	0.53426	0.51237
	43	G5_Wiesenthau	0.50704	0.48592	0.55172	0.51748	0.59603	0.55629	0.58228	0.50000	0.54902	0.55556
	44	G9_Rüdersdorf	0.53333	0.50336	0.46479	0.50340	0.24000	0.22047	0.55000	0.51634	0.55346	0.43478
	45	G12_Martinroda	0.51370	0.48276	0.49650	0.48252	0.27778	0.24409	0.55063	0.52632	0.55414	0.48936

Appendix 18: Distance values between *Homalothecium lutescens* specimens of the German-wide sample set. Simple matching distances are given in the upper right, Jaccard distances in the lower left part of the matrix

			Population Hb																															
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Population Hb	1	Hbl_197	0	0.05479	0.08219	0.05479	0.04566	0.04566	0.04566	0.05936	0.05936	0.05479	0.04566	0.04566	0.04566	0.05479	0.05479	0.05023	0.05023	0.05023	0.05023	0.05023	0.05479	0.05023	0.05479	0.05023	0.05023	0.05936	0.05479	0.05936	0.05023	0.05023	0.08278	0.05479
	2	Hbl_222	0.06742	0	0.07306	0.01826	0.02740	0.01826	0.01826	0.03196	0.06849	0.01826	0.01826	0.00913	0.01826	0.00913	0.01826	0.01370	0.01370	0.02283	0.01370	0.02283	0.00913	0.00457	0.00913	0.01370	0.03196	0.01370	0.01826	0.01370	0.01370	0.01370	0.05032	0.04566
	3	Hbl_263	0.10056	0.08889	0	0.08219	0.07306	0.06393	0.06393	0.09589	0.09589	0.07306	0.06393	0.07306	0.07306	0.07306	0.07306	0.06849	0.06849	0.06849	0.06849	0.06849	0.06393	0.07763	0.06393	0.06849	0.05023	0.06849	0.08219	0.06849	0.07763	0.06849	0.07317	0.08219
	4	Hbl_392	0.06742	0.02273	0.09945	0	0.02740	0.01826	0.01826	0.02283	0.06849	0.01826	0.01826	0.01826	0.01826	0.01826	0.01826	0.01370	0.01370	0.01370	0.01370	0.02283	0.01826	0.01370	0.01826	0.01370	0.03196	0.02283	0.00000	0.01370	0.00457	0.01370	0.05926	0.05479
	5	Hbl_1_177	0.05682	0.03409	0.08939	0.03409	0	0.00913	0.00913	0.03196	0.07763	0.02740	0.00913	0.01826	0.00913	0.01826	0.01826	0.02283	0.01370	0.01370	0.02283	0.02283	0.01826	0.02283	0.01826	0.01370	0.03196	0.02283	0.02740	0.03196	0.02283	0.01370	0.04535	0.05479
	6	Hbl_2_181	0.05714	0.02299	0.07910	0.02299	0.01163	0	0.00000	0.03196	0.07763	0.01826	0.00000	0.00913	0.00913	0.00913	0.00913	0.01370	0.00457	0.00457	0.01370	0.01370	0.00913	0.01370	0.00913	0.00457	0.02283	0.01370	0.01826	0.02283	0.01370	0.00457	0.04603	0.04566
	7	Hbl_2_183	0.05714	0.02299	0.07910	0.02299	0.01163	0.00000	0	0.03196	0.07763	0.01826	0.00000	0.00913	0.00913	0.00913	0.00913	0.01370	0.00457	0.00457	0.01370	0.01370	0.00913	0.01370	0.00913	0.00457	0.02283	0.01370	0.01826	0.02283	0.01370	0.00457	0.04550	0.04566
	8	Hbl_8_194	0.07263	0.03933	0.11475	0.02825	0.03955	0.03977	0.03977	0	0.08219	0.03196	0.03196	0.03196	0.02283	0.03196	0.03196	0.02740	0.02740	0.02740	0.02740	0.02740	0.03196	0.02740	0.03196	0.02740	0.04566	0.03653	0.02283	0.03653	0.02740	0.02740	0.05455	0.06849
	9	Hbl_12_219	0.07345	0.08333	0.11602	0.08333	0.09444	0.09497	0.09497	0.09890	0	0.07763	0.07763	0.07763	0.06849	0.07763	0.08676	0.07306	0.07306	0.08219	0.06393	0.07306	0.06849	0.07306	0.06849	0.07306	0.07306	0.07306	0.06849	0.05479	0.06393	0.07306	0.08646	0.04110
	10	Hbl_21_239	0.06742	0.02273	0.08889	0.02273	0.03409	0.02299	0.02299	0.03933	0.09392	0	0.01826	0.00913	0.01826	0.00913	0.00913	0.02283	0.02283	0.01370	0.01370	0.01370	0.02740	0.01370	0.02740	0.02283	0.02283	0.01370	0.01826	0.02283	0.02283	0.02283	0.05493	0.06393
	11	Hbl_21_240	0.05714	0.02299	0.07910	0.02299	0.01163	0.00000	0.00000	0.03977	0.09497	0.02299	0	0.00913	0.00913	0.00913	0.00913	0.01370	0.00457	0.00457	0.01370	0.01370	0.00913	0.01370	0.00913	0.00457	0.02283	0.01370	0.01826	0.02283	0.01370	0.00457	0.04604	0.04566
	12	Hbl_21_241	0.05682	0.01149	0.08939	0.02286	0.02299	0.01163	0.01163	0.03955	0.09444	0.01149	0.01163	0	0.01826	0.00913	0.00913	0.01370	0.01370	0.01370	0.01370	0.01370	0.01826	0.00457	0.01826	0.01370	0.02283	0.01370	0.01826	0.02283	0.01370	0.01370	0.05448	0.05479
	13	Hbl_22_243	0.05682	0.02286	0.08939	0.02286	0.01156	0.01163	0.01163	0.02841	0.08380	0.03409	0.01163	0.02299	0	0.00913	0.01826	0.01370	0.00457	0.01370	0.01370	0.02283	0.00913	0.01370	0.00913	0.00457	0.03196	0.01370	0.01826	0.02283	0.01370	0.00457	0.04138	0.04566
	14	Hbl_22_244	0.06780	0.01149	0.08939	0.02286	0.02299	0.01163	0.01163	0.03955	0.09444	0.02286	0.01163	0.01156	0.01156	0	0.00913	0.01370	0.00457	0.01370	0.01370	0.02283	0.00913	0.00457	0.00913	0.00457	0.03196	0.00457	0.01826	0.02283	0.01370	0.00457	0.05000	0.04566
	15	Hbl_22_278	0.06780	0.02286	0.08939	0.02286	0.02299	0.01163	0.01163	0.03955	0.10497	0.01149	0.01163	0.01156	0.02299	0.01156	0	0.02283	0.01370	0.00457	0.02283	0.02283	0.01826	0.01370	0.01826	0.01370	0.03196	0.01370	0.01826	0.03196	0.02283	0.01370	0.05449	0.05479
	16	Hbl_22_285	0.06215	0.01714	0.08380	0.01714	0.02857	0.01734	0.01734	0.03390	0.08889	0.02841	0.01734	0.01724	0.01724	0.01724	0.02857	0	0.00913	0.01826	0.00913	0.01826	0.01370	0.00913	0.01370	0.00913	0.01826	0.01826	0.01370	0.01826	0.00913	0.00913	0.05525	0.05023
	17	Hbl_22_307	0.06250	0.01724	0.08427	0.01724	0.01734	0.00585	0.00585	0.03409	0.08939	0.02857	0.00585	0.01734	0.00581	0.00581	0.01734	0.01156	0	0.00913	0.00913	0.01826	0.00457	0.00913	0.00457	0.00000	0.02740	0.00913	0.01370	0.01826	0.00913	0.00000	0.04564	0.04110
	18	Hbl_23_235	0.06250	0.02857	0.08427	0.01724	0.01734	0.00585	0.00585	0.03409	0.10000	0.01724	0.00585	0.01734	0.01734	0.01734	0.00581	0.02299	0.01163	0	0.01826	0.01826	0.01370	0.01826	0.01370	0.00913	0.02740	0.01826	0.01370	0.02740	0.01826	0.00913	0.05040	0.05023
	19	Hbl_27_255	0.06215	0.01714	0.08380	0.01714	0.02857	0.01734	0.01734	0.03390	0.07821	0.01714	0.01734	0.01724	0.01724	0.01724	0.02857	0.01149	0.01156	0.02299	0	0.00913	0.01370	0.00913	0.01370	0.00913	0.01826	0.00913	0.01370	0.00913	0.00913	0.00913	0.04562	0.05023
	20	Hbl_29_257	0.06215	0.02841	0.08380	0.02841	0.02857	0.01734	0.01734	0.03390	0.08889	0.01714	0.01734	0.01724	0.02857	0.02857	0.02857	0.02286	0.02299	0.02299	0.01149	0	0.02283	0.01826	0.02283	0.01826	0.01826	0.01826	0.02283	0.01826	0.01826	0.01826	0.04112	0.05936
	21	Hbl_34_311	0.06780	0.01149	0.07865	0.02286	0.02299	0.01163	0.01163	0.03955	0.08380	0.03409	0.01163	0.02299	0.01156	0.01156	0.02299	0.01724	0.00581	0.01734	0.01724	0.02857	0	0.01370	0.00000	0.00457	0.03196	0.01370	0.01826	0.01370	0.01370	0.00457	0.04094	0.03653
	22	Hbl_34_312	0.06215	0.00575	0.09444	0.01714	0.02857	0.01734	0.01734	0.03390	0.08889	0.01714	0.01734	0.00578	0.01724	0.00578	0.01724	0.01149	0.01156	0.02299	0.01149	0.02286	0.01724	0	0.01370	0.00913	0.02740	0.00913	0.01370	0.01826	0.00913	0.00913	0.05463	0.05023
	23	Hbl_36_305	0.06780	0.01149	0.07865	0.02286	0.02299	0.01163	0.01163	0.03955	0.08380	0.03409	0.01163	0.02299	0.01156	0.01156	0.02299	0.01724	0.00581	0.01734	0.01724	0.02857	0.00000	0.01724	0	0.00457	0.03196	0.01370	0.01826	0.01370	0.01370	0.00457	0.04119	0.03653
	24	Hbl_65_295	0.06250	0.01724	0.08427	0.01724	0.01734	0.00585	0.00585	0.03409	0.08939	0.02857	0.00585	0.01734	0.00581	0.00581	0.01734	0.01156	0.00000	0.01163	0.01156	0.02299	0.00581	0.01156	0.00581	0	0.02740	0.00913	0.01370	0.01826	0.00913	0.00000	0.04559	0.04110
	25	Hbl_67_265	0.06250	0.03977	0.06250	0.03977	0.04000	0.02890	0.02890	0.05618	0.08939	0.02857	0.02890	0.02874	0.04000	0.04000	0.04000	0.02299	0.03448	0.03448	0.02299	0.02299	0.04000	0.03429	0.04000	0.03448	0	0.02740	0.03196	0.02740	0.02740	0.02740	0.05930	0.06849
	26	Hbl_71_266	0.07303	0.01714	0.08380	0.02841	0.02857	0.01734	0.01734	0.04494	0.08889	0.01714	0.01734	0.01724	0.01724	0.00578	0.01724	0.02286	0.01156	0.02299	0.01149	0.02286	0.01724	0.01149	0.01724	0.01156	0.03429	0	0.02283	0.01826	0.00913	0.00913	0.04537	0.05023
	27	Hbl_77_334	0.06742	0.02273	0.09945	0.00000	0.03409	0.02299	0.02299	0.02825	0.08333	0.02273	0.02299	0.02286	0.02286	0.02286	0.02286	0.01714	0.01724	0.01724	0.01714	0.02841	0.02286	0.01714	0.02286	0.01724	0.03977	0.02841	0	0.01370	0.00457	0.01370	0.05932	0.05479
	28	Hbl_81_325	0.07263	0.01705	0.08333	0.01705	0.03955	0.02857	0.02857	0.04469	0.06704	0.02825	0.02857	0.02841	0.02841	0.02841	0.03955	0.02273	0.02286	0.03409	0.01143	0.02273	0.01714	0.02273	0.01714	0.02286	0.03409	0.02273	0.01705	0	0.00913	0.01826	0.04605	0.05023
	29	Hbl_81_343	0.06215	0.01714	0.09444	0.00575	0.02857	0.01734	0.01734	0.03390	0.07821	0.02841	0.01734	0.01724	0.01724	0.01724	0.02857	0.01149	0.01156	0.02299	0.01149	0.02286	0.01724	0.01149	0.01724	0.01156	0.03429	0.02286	0.00575	0.01143	0	0.00913	0.05481	0.05023
	30	Hbl_81_345	0.06250	0.01724	0.08427	0.01724	0.01734	0.00585	0.00585	0.03409	0.08939	0.02857	0.00585	0.01734	0.00581	0.00581	0.01734	0.01156	0.00000	0.01163	0.01156	0.02299	0.00581	0.01156	0.00581	0.00000	0.03448	0.01156	0.01724	0.02286	0.01156	0	0.04543	0.04110
	31	Hbl_84_348	0.09920	0.06130	0.08844	0.07225	0.05583	0.05687	0.05590	0.06624	0.10353	0.06621	0.05664	0.06719	0.05096	0.06151	0.06626	0.06670	0.05604	0.06128	0.05583	0.05018	0.05023	0.06634	0.05039	0.05600	0.07236	0.05567	0.07193	0.05498	0.06684	0.05637	0	0.07733
	32	Hbl_84_483	0.06780	0.05618	0.10000	0.06704	0.06742	0.05682	0.05682	0.08287	0.05114	0.07778	0.05682	0.06742	0.05650	0.05650	0.06742	0.06180	0.05114	0.06215	0.06180	0.07263	0.04545	0.06180	0.04545	0.05114	0.08380	0.06180	0.06704	0.06145	0.06180	0.05114	0.09357	0
	33	Hbl_85_346	0.06250	0.01724	0.08427	0.01724	0.01734	0.00585	0.00585	0.03409	0.08939	0.02857	0.00585	0.01734	0.00581	0.00581	0.01734	0.01156	0.00000	0.01163	0.01156	0.02299	0.00581	0.01156	0.00581	0.00000	0.03448	0.01156	0.01724	0.02286	0.01156	0.00000	0.05645	0.05114
	34	Hbl_86_349	0.05714	0.02299	0.07910	0.02299	0.01163	0.00000	0.00000	0.03977	0.09497	0.02299	0.00000	0.01163	0.01163	0.01163	0.01163	0.01734	0.00585	0.00585	0.01734	0.01734	0.01163	0.01734	0.01163	0.00585	0.02890	0.01734	0.02299	0.02857	0.01734	0.00585	0.05613	0.05682
	35	Hbl_86_351	0.07303	0.02841	0.09444	0.00575	0.02857	0.01734	0.01734	0.03390	0.08889	0.02841	0.01734	0.02857	0.01724	0.01724	0.01724	0.02286	0.01156	0.01156	0.02286	0.03409	0.01724	0.02286	0.01724	0.01156	0.04545	0.02286	0.00575	0.02273	0.01149	0.01156	0.06672	0.06180
	36	Hbl_94_373	0.06780	0.02286	0.07865	0.02286	0.02299	0.01163	0.01163	0.03955	0.08380	0.02286	0.01163	0.02299	0.01156	0.01156	0.02299	0.01724	0.00581	0.01734	0.00578	0.01724	0.01156	0.01724	0.01156	0.00581	0.02874	0.00578	0.02286	0.01714	0.01724	0.00581	0.05088	0.05650
	37	HbII_408	0.06742	0.06667	0.10989	0.06667	0.06704	0.06742	0.06742	0.07182	0.06180	0.07735	0.06742	0.07778	0.05618	0.06704	0.06704	0.07222	0.06180	0.06180	0.07222	0.08287	0.05618	0.07222	0.05618	0.06180	0.09392	0.07222	0.06667	0.07182	0.07222	0.06180	0.08223	0.04520
	38	HbII_1_405	0.06215	0.06145	0.10497	0.06145	0.06180	0.06215	0.06215	0.06667	0.05650	0.07222	0.06215	0.07263	0.05085	0.06180	0.06180	0.06704	0.05650	0.05650	0.06704	0.07778	0.05085	0.06704	0.05085	0.05650	0.08889	0.06704	0.06145	0.06667	0.06704	0.05650	0.08764	0.03977
	39	HbIII_1_422	0.07303	0.02841	0.09444	0.03955	0.05085	0.04000	0.04000	0.05587	0.09945	0.02841	0.04000	0.02857	0.03977	0.02857	0.03977	0.03409	0.03429	0.04545	0.02286	0.03409	0.03977	0.02286	0.03977	0.03429	0.04545	0.02286	0.03955	0.03390	0.03409	0.03429	0.06719	0.07263
	40	HbIII_1_424	0.05682	0.02286	0.08939	0.02286	0.02299	0.01163	0.01163	0.03955	0.09444	0.03409	0.01163	0.02299	0.01156	0.01156	0.02299	0.01724	0.00581	0.01734	0.01724	0.02857	0.01156	0.01724	0.01156	0.00581	0.04000	0.01724	0.02286	0.02841	0.01724	0.00581	0.06126	0.04545
	41	HbIII_2_428	0.08939	0.04520	0.06780	0.05618	0.04545	0.03448	0.03448	0.06145	0.10497	0.04520	0.03448	0.04545	0.04545	0.04545	0.04545	0.05085	0.04000	0.04000	0.03977	0.02857	0.03429	0.05085	0.03429	0.04000	0.05114	0.03977	0.05618	0.03955	0.05085	0.04000	0.03388	0.07821
	42	HbIII_3_420	0.09444	0.03955	0.09444	0.05056	0.06180	0.05114	0.05114	0.05587	0.09945	0.06145	0.05114	0.05085	0.05085	0.05085	0.06180	0.03409	0.04545	0.05650	0.04520	0.04520	0.03977	0.04520	0.03977	0.04545	0.05650	0.05618	0.05056	0.04494	0.04520	0.04545	0.07758	0.07263
	43	Hb_surr_431	0.06818	0.03429	0.08989	0.03429	0.03448	0.02326	0.02326	0.05085	0.10556	0.03429	0.02326	0.02312	0.03448	0.03448	0.03448	0.02874	0.02890	0.02890	0.02874	0.02874	0.03448	0.02874	0.03448	0.02890	0.04023	0.04000	0.03429	0.03977	0.02874	0.02890	0.05636	0.07865
	44	Hb_surr_437	0.11050	0.07778	0.12088	0.09890	0.07821	0.07865	0.07865	0.07222	0.13587	0.08840	0.07865	0.07821	0.07821	0.07821	0.07821	0.09392	0.08380	0.08380	0.09392	0.08333	0.07821	0.08333	0.07821	0.08380	0.10497	0.08333	0.09890	0.09341	0.09392	0.08380	0.07791	0.10989
	45	Hb_surr_445	0.06780	0.02286	0.08939	0.01149	0.02299	0.01163	0.01163	0.02841	0.09444	0.02286	0.01163	0.02299	0.01156	0.01156	0.01156	0.01724	0.00581	0.00581	0.01724	0.02857	0.01156	0.01724	0.01156	0.00581	0.04000	0.01724	0.01149	0.02841	0.01724	0.00581	0.06154	0.05650
	46	Hb_surr_459	0.12849	0.09551	0.12849	0.10615	0.09605	0.08571	0.08571	0.11111	0.12291	0.10615	0.08571	0.09605	0.09605	0.09605	0.09605	0.10112	0.09091	0.09091	0.10112	0.09040	0.08523	0.10112	0.08523	0.09091	0.11236	0.10112	0.10615	0.10056	0.10112	0.09091	0.08449	0.09605
	47	Hb_surr_466	0.10383	0.08197	0.11413	0.09239	0.09290	0.08287	0.08287	0.07650	0.11892	0.08197	0.08287	0.08242	0.09290	0.08242	0.07182	0.09783	0.08791	0.07735	0.09783	0.08743	0.08242	0.08743	0.08242	0.08791	0.10870	0.08743	0.09239	0.09730	0.09783	0.08791	0.10266	0.07182
	48	Hb_surr_470	0.13260	0.10000	0.13260	0.11050	0.10056	0.09040	0.09040	0.11538	0.13736	0.11050	0.09040	0.10056	0.10056	0.10056	0.10056	0.10556	0.09551	0.09551	0.10556	0.09497	0.08989	0.10556	0.08989	0.09551	0.11667	0.10556	0.11050	0.10497	0.10556	0.09551	0.09984	0.08989
	49	Hb_surr_471	0.08989	0.08889	0.10056	0.09945	0.11050	0.10056	0.10056	0.10440	0.10556	0.10989	0.10056	0.10000	0.10000	0.10000	0.11050	0.08380	0.09497	0.10556	0.09444	0.09444	0.08939	0.09444	0.08939	0.09497	0.09497	0.10497	0.09945	0.09392	0.09444	0.09497	0.11491	0.07865
	50	Hb_surr_476	0.08427	0.07263	0.10556	0.09392	0.07303	0.07345	0.07345	0.08840	0.08939	0.08333	0.07345	0.07303	0.07303	0.07303	0.07303	0.08889	0.07865	0.07865	0.08889	0.07821	0.07303	0.07821	0.07303	0.07865	0.10000	0.07821	0.09392	0.08840	0.08889	0.07865	0.07281	0.07303
	51	Hb_surr_480	0.11050	0.06704	0.12088	0.06704	0.07821	0.07865	0.07865	0.03955	0.10497	0.07778	0.07865	0.07821	0.06742	0.07821	0.07821	0.07263	0.07303	0.07303	0.07263	0.07263	0.06742	0.07263	0.06742	0.07303	0.09444	0.08333	0.06704	0.07222	0.07263	0.07303	0.09351	0.08889
Population Mb	52	Mb_733	0.08380	0.03955	0.08380	0.05056	0.05085	0.05114	0.05114	0.06667	0.07821	0.05056	0.05114	0.05085	0.05085	0.05085	0.06180	0.04520	0.04545	0.05650	0.03409	0.04520	0.03977	0.04520	0.03977	0.04545	0.04545	0.04520	0.05056	0.03390	0.04520	0.04545	0.06077	0.08333
	53	Mb_1_821	0.09551	0.09444	0.14754	0.10497	0.08427	0.09551	0.09551	0.09945	0.12155	0.11538	0.09551	0.10556	0.08427	0.09497	0.10556	0.10000	0.08989	0.10056	0.10000	0.10000	0.08427	0.10000	0.08427	0.08989	0.11111	0.10000	0.10497	0.09945	0.10000	0.08989	0.08871	0.10556
	54	Mb_1_833	0.10000	0.07778	0.14130	0.08840	0.07821	0.08939	0.08939	0.08287	0.11538	0.09890	0.08939	0.08889	0.07821	0.08889	0.09945	0.08333	0.08380	0.09444	0.08333	0.08333	0.07821	0.08333	0.07821	0.08380	0.09444	0.09392	0.08840	0.08287	0.08333	0.08380	0.08257	0.09945
	55	Mb_1_839	0.10000	0.07778	0.14130	0.08840	0.07821	0.08939	0.08939	0.08287	0.11538	0.09890	0.08939	0.08889	0.07821	0.08889	0.09945	0.08333	0.08380	0.09444	0.08333	0.08333	0.07821	0.08333	0.07821	0.08380	0.09444	0.09392	0.08840	0.08287	0.08333	0.08380	0.08259	0.09945
	56	Mb_2_847	0.09040	0.08939	0.14286	0.10000	0.07910	0.09040	0.09040	0.10497	0.11667	0.11050	0.09040	0.10056	0.07910	0.08989	0.10056	0.09497	0.08475	0.09551	0.09497	0.10556	0.07910	0.09497	0.07910	0.08475	0.10615	0.09497	0.10000	0.09444	0.09497	0.08475	0.09479	0.10056
	57	Mb_7_815	0.06818	0.03429	0.10056	0.03429	0.03448	0.02326	0.02326	0.03977	0.09497	0.03429	0.02326	0.02312	0.03448	0.03448	0.03448	0.02874	0.02890	0.02890	0.02874	0.01734	0.03448	0.02874	0.03448	0.02890	0.04023	0.04000	0.03429	0.03977	0.02874	0.02890	0.06718	0.06780
	58	Mb_7_816	0.06857	0.05682	0.12222	0.05682	0.05714	0.04624	0.04624	0.06215	0.10615	0.05682	0.04624	0.04598	0.05714	0.05714	0.05714	0.05143	0.05172	0.05172	0.05143	0.04023	0.05714	0.05143	0.05714	0.05172	0.06286	0.06250	0.05682	0.06215	0.05143	0.05172	0.08921	0.07910
	59	Mb_12_760	0.07910	0.04545	0.08989	0.05650	0.05682	0.04598	0.04598	0.07263	0.09497	0.05650	0.04598	0.04571	0.05682	0.05682	0.05682	0.04000	0.05143	0.05143	0.05114	0.05114	0.04571	0.05114	0.04571	0.05143	0.05143	0.06215	0.05650	0.05085	0.05114	0.05143	0.07846	0.07865
	60	Mb_14_779	0.10734	0.09551	0.11798	0.10615	0.08523	0.08571	0.08571	0.11111	0.13333	0.10615	0.08571	0.09605	0.09605	0.09605	0.09605	0.09040	0.09091	0.09091	0.10112	0.09040	0.08523	0.10112	0.08523	0.09091	0.08000	0.10112	0.10615	0.10056	0.10112	0.09091	0.10565	0.11732
	61	Mb_14_780	0.07429	0.05143	0.10674	0.06250	0.06286	0.05202	0.05202	0.06780	0.10112	0.06250	0.05202	0.05172	0.06286	0.06286	0.06286	0.05714	0.05747	0.05747	0.05714	0.04598	0.05172	0.05714	0.05172	0.05747	0.05747	0.06818	0.06250	0.05682	0.05714	0.05747	0.08408	0.08475
	62	Mb_17_793	0.10000	0.05618	0.10000	0.06704	0.05650	0.05682	0.05682	0.07222	0.11538	0.07778	0.05682	0.06742	0.05650	0.05650	0.06742	0.06180	0.05114	0.06215	0.06180	0.06180	0.04545	0.06180	0.04545	0.05114	0.07303	0.06180	0.06704	0.06145	0.06180	0.05114	0.07163	0.08889
	63	Mb_20_790	0.09444	0.06145	0.12568	0.07222	0.06180	0.06215	0.06215	0.08791	0.08889	0.08287	0.06215	0.07263	0.06180	0.06180	0.07263	0.06704	0.05650	0.06742	0.06704	0.07778	0.05085	0.06704	0.05085	0.05650	0.08889	0.06704	0.07222	0.06667	0.06704	0.05650	0.09787	0.05085
	64	Mb_20_791	0.07386	0.02874	0.10615	0.04000	0.05143	0.04046	0.04046	0.05650	0.08989	0.05114	0.04046	0.04023	0.04023	0.04023	0.05143	0.03448	0.03468	0.04598	0.03448	0.04571	0.02890	0.03448	0.02890	0.03468	0.05714	0.04571	0.04000	0.03429	0.03448	0.03468	0.07852	0.06250
	65	Mb_20_792	0.07386	0.02874	0.10615	0.04000	0.05143	0.04046	0.04046	0.05650	0.08989	0.05114	0.04046	0.04023	0.04023	0.04023	0.05143	0.03448	0.03468	0.04598	0.03448	0.04571	0.02890	0.03448	0.02890	0.03468	0.05714	0.04571	0.04000	0.03429	0.03448	0.03468	0.07826	0.06250
	66	Mb_21_789	0.08380	0.03955	0.09444	0.05056	0.05085	0.05114	0.05114	0.05587	0.08889	0.06145	0.05114	0.05085	0.05085	0.05085	0.06180	0.04520	0.04545	0.05650	0.04520	0.04520	0.03977	0.04520	0.03977	0.04545	0.05650	0.05618	0.05056	0.04494	0.04520	0.04545	0.06141	0.08333
	67	Mb_surr_851	0.08989	0.05650	0.11111	0.06742	0.05682	0.05714	0.05714	0.07263	0.08427	0.07821	0.05714	0.06780	0.04571	0.05682	0.06780	0.06215	0.05143	0.06250	0.06215	0.07303	0.04571	0.06215	0.04571	0.05143	0.07345	0.06215	0.06742	0.06180	0.06215	0.05143	0.07226	0.06780
	68	Mb_surr_856	0.10440	0.08242	0.14516	0.09290	0.09341	0.09392	0.09392	0.09783	0.09890	0.10326	0.09392	0.09341	0.09341	0.09341	0.10383	0.08791	0.08840	0.09890	0.08791	0.08791	0.08287	0.08791	0.08287	0.08840	0.10929	0.09836	0.09290	0.08743	0.08791	0.08840	0.11830	0.08287
	69	Mb_surr_857	0.08840	0.04469	0.09890	0.05556	0.04494	0.04520	0.04520	0.06077	0.11413	0.06630	0.04520	0.05587	0.04494	0.04494	0.05587	0.05028	0.03955	0.05056	0.05028	0.05028	0.03390	0.05028	0.03390	0.03955	0.07222	0.05028	0.05556	0.05000	0.05028	0.03955	0.06109	0.06667
	70	Mb_surr_860	0.08427	0.07263	0.12637	0.07263	0.06215	0.06250	0.06250	0.07778	0.12088	0.07263	0.06250	0.07303	0.06215	0.07303	0.06215	0.07821	0.06780	0.05682	0.07821	0.07821	0.06215	0.07821	0.06215	0.06780	0.08939	0.07821	0.07263	0.07778	0.07821	0.06780	0.08280	0.08380
	71	Mb_surr_861	0.09945	0.05587	0.10989	0.05587	0.06704	0.06742	0.06742	0.06111	0.10440	0.06667	0.06742	0.06704	0.06704	0.06704	0.06704	0.06145	0.06180	0.06180	0.06145	0.06145	0.05618	0.06145	0.05618	0.06180	0.07263	0.07222	0.05587	0.06111	0.06145	0.06180	0.08257	0.08840
	72	Mb_surr_866	0.07345	0.02857	0.09497	0.01724	0.02874	0.01744	0.01744	0.03409	0.10000	0.02857	0.01744	0.02874	0.01734	0.01734	0.01734	0.02299	0.01163	0.01163	0.02299	0.03429	0.01734	0.02299	0.01734	0.01163	0.04571	0.02299	0.01724	0.03409	0.02299	0.01163	0.06596	0.06215
	73	Mb_surr_927	0.09497	0.07263	0.13661	0.08333	0.07303	0.08427	0.08427	0.07778	0.10000	0.07263	0.08427	0.07303	0.07303	0.07303	0.08380	0.07821	0.07865	0.08939	0.06742	0.06742	0.08380	0.06742	0.08380	0.07865	0.07865	0.06742	0.08333	0.07778	0.07821	0.07865	0.09888	0.10497
Regional samples	74	r1_Lämmerberg	0.07303	0.05056	0.11538	0.06145	0.05085	0.06215	0.06215	0.06667	0.08889	0.07222	0.06215	0.06180	0.05085	0.06180	0.07263	0.05618	0.05650	0.06742	0.05618	0.06704	0.05085	0.05618	0.05085	0.05650	0.06742	0.06704	0.06145	0.05587	0.05618	0.05650	0.08815	0.07263
	75	r2_Ammerbach	0.12222	0.07865	0.15301	0.08939	0.08989	0.09040	0.09040	0.09444	0.08475	0.10000	0.09040	0.08989	0.07910	0.08989	0.10056	0.08427	0.08475	0.09551	0.08427	0.09497	0.07910	0.08427	0.07910	0.08475	0.10615	0.09497	0.08939	0.08380	0.08427	0.08475	0.09962	0.08989
	76	r3_Osmaritz	0.09444	0.06145	0.11538	0.06145	0.05085	0.05114	0.05114	0.07735	0.12022	0.07222	0.05114	0.06180	0.05085	0.06180	0.06180	0.04520	0.04545	0.05650	0.05618	0.06704	0.05085	0.05618	0.05085	0.04545	0.06742	0.05618	0.06145	0.06667	0.05618	0.04545	0.08820	0.07263
	77	r4_Jena/Leutra	0.08380	0.06145	0.10497	0.07222	0.05085	0.05114	0.05114	0.06667	0.09945	0.07222	0.05114	0.06180	0.05085	0.06180	0.06180	0.06704	0.05650	0.05650	0.06704	0.05618	0.05085	0.06704	0.05085	0.05650	0.06742	0.06704	0.07222	0.06667	0.06704	0.05650	0.06092	0.09392
	78	r5_Mädertal	0.06818	0.05650	0.11111	0.06742	0.06780	0.06818	0.06818	0.05085	0.08427	0.07821	0.06818	0.06780	0.05682	0.06780	0.07865	0.06215	0.06250	0.07345	0.06215	0.07303	0.05682	0.06215	0.05682	0.06250	0.07345	0.07303	0.06742	0.06180	0.06215	0.06250	0.09412	0.06780
	79	r6_Jena/Gräfenberg	0.11111	0.07821	0.14208	0.09945	0.08939	0.08989	0.08989	0.10440	0.10556	0.09945	0.08989	0.08939	0.08939	0.07865	0.08939	0.09444	0.08427	0.09497	0.09444	0.10497	0.07865	0.08380	0.07865	0.08427	0.10556	0.08380	0.09945	0.09392	0.09444	0.08427	0.12513	0.08939
	80	r7_Jena/Gleisberg	0.08523	0.07345	0.13812	0.08427	0.08475	0.08523	0.08523	0.06780	0.09040	0.09497	0.08523	0.08475	0.07386	0.08475	0.09551	0.07910	0.07955	0.09040	0.07910	0.08989	0.07386	0.07910	0.07386	0.07955	0.09040	0.08989	0.08427	0.07865	0.07910	0.07955	0.10495	0.09551
	81	r8_Rabis.1	0.08427	0.05085	0.10556	0.06180	0.05114	0.05143	0.05143	0.07778	0.10000	0.07263	0.05143	0.06215	0.05114	0.05114	0.06215	0.05650	0.04571	0.05682	0.05650	0.06742	0.04000	0.05650	0.04000	0.04571	0.06780	0.05650	0.06180	0.05618	0.05650	0.04571	0.07812	0.06215
	82	r8_Rabis.2	0.08427	0.05085	0.10556	0.06180	0.05114	0.05143	0.05143	0.07778	0.10000	0.07263	0.05143	0.06215	0.05114	0.05114	0.06215	0.05650	0.04571	0.05682	0.05650	0.06742	0.04000	0.05650	0.04000	0.04571	0.06780	0.05650	0.06180	0.05618	0.05650	0.04571	0.07796	0.06215
	83	r9_Nerkewitz	0.08475	0.07303	0.12707	0.07303	0.05143	0.06286	0.06286	0.07821	0.11111	0.08380	0.06286	0.07345	0.05143	0.06250	0.07345	0.06780	0.05714	0.06818	0.06780	0.07865	0.06250	0.06780	0.06250	0.05714	0.07910	0.06780	0.07303	0.07821	0.06780	0.05714	0.09953	0.08427
	84	r10_Dorndorf	0.08889	0.07735	0.12022	0.07735	0.05618	0.06742	0.06742	0.08242	0.09392	0.08791	0.06742	0.07778	0.05618	0.06704	0.07778	0.06145	0.06180	0.07263	0.07222	0.08287	0.06704	0.07222	0.06704	0.06180	0.07263	0.07222	0.07735	0.08242	0.07222	0.06180	0.07710	0.08840
National samples	85	G1_Kallenberg	0.19372	0.19171	0.17460	0.21026	0.19271	0.19372	0.19372	0.18653	0.19792	0.19171	0.19372	0.19271	0.19271	0.19271	0.19271	0.19689	0.19792	0.19792	0.19689	0.18750	0.19271	0.19689	0.19271	0.19792	0.18848	0.18750	0.21026	0.19588	0.20619	0.19792	0.16300	0.20207
	86	G2_Bad Salzungen	0.23428	0.19059	0.20228	0.20885	0.20128	0.20168	0.20125	0.20377	0.21547	0.19972	0.20131	0.20015	0.20018	0.19084	0.20025	0.19603	0.19637	0.20629	0.19523	0.20478	0.19133	0.19564	0.19051	0.19568	0.18563	0.18555	0.20904	0.19420	0.20445	0.19622	0.20472	0.20959
	87	G3_Saalburg	0.11111	0.08889	0.14208	0.06742	0.08939	0.07910	0.07910	0.08333	0.12637	0.08889	0.07910	0.08939	0.07865	0.07865	0.07865	0.08380	0.07345	0.07345	0.08380	0.08380	0.07865	0.08380	0.07865	0.07345	0.09497	0.08380	0.06742	0.08333	0.07303	0.07345	0.10438	0.11050
	88	G4_Freyburg	0.16129	0.15957	0.19048	0.16931	0.15054	0.15135	0.15135	0.16402	0.17553	0.16931	0.15135	0.16043	0.15054	0.16043	0.16043	0.16489	0.15591	0.15591	0.16489	0.15508	0.15054	0.16489	0.15054	0.15591	0.17553	0.16489	0.16931	0.16402	0.16489	0.15591	0.14008	0.15054
	89	G5_Ebermannstadt	0.25000	0.25641	0.21277	0.26531	0.25773	0.25000	0.25000	0.26904	0.23560	0.25641	0.25000	0.25773	0.25773	0.25773	0.25773	0.25258	0.25389	0.25389	0.25258	0.24352	0.24870	0.25258	0.24870	0.25389	0.24479	0.25258	0.26531	0.25128	0.26154	0.25389	0.22925	0.23037
	90	G6_Tiefental	0.20361	0.20189	0.19415	0.22021	0.21203	0.20362	0.20400	0.20569	0.21737	0.20150	0.20382	0.20257	0.21234	0.20247	0.20276	0.20689	0.20801	0.20785	0.20696	0.19729	0.20272	0.20699	0.20265	0.20809	0.19843	0.19743	0.22033	0.20569	0.21638	0.20791	0.18232	0.21193
	91	G7_Wiesenthau	0.25389	0.26020	0.25389	0.27778	0.27041	0.26289	0.26289	0.26396	0.24870	0.26904	0.26289	0.26154	0.27041	0.26154	0.26154	0.26531	0.26667	0.26667	0.27411	0.26531	0.26154	0.26531	0.26154	0.26667	0.26667	0.26531	0.27778	0.27273	0.27411	0.26667	0.25086	0.23438
	92	G8_Malchin	0.22123	0.23154	0.20270	0.25058	0.23273	0.23342	0.23507	0.23092	0.25155	0.22780	0.23233	0.22861	0.24002	0.23065	0.23218	0.23455	0.23488	0.23309	0.23560	0.22403	0.23489	0.23430	0.22914	0.23589	0.22674	0.22376	0.25015	0.23559	0.24519	0.23497	0.21245	0.23379
	93	G9_Rüdersdorf	0.15269	0.10036	0.15340	0.12109	0.11108	0.11167	0.11200	0.10494	0.15729	0.12115	0.11159	0.11050	0.11031	0.10020	0.11119	0.10560	0.10648	0.11679	0.11626	0.11637	0.10025	0.10601	0.10040	0.10640	0.11653	0.10536	0.12044	0.11528	0.11577	0.10612	0.13602	0.13212
	94	G10_Eiderstaudamm	0.20064	0.16916	0.19082	0.18875	0.18009	0.17109	0.17101	0.17380	0.21410	0.17919	0.17117	0.17022	0.18022	0.17026	0.17030	0.18439	0.17551	0.17591	0.18446	0.17454	0.17061	0.17491	0.17030	0.17561	0.18561	0.17451	0.18888	0.18367	0.18449	0.17574	0.16931	0.19926
	95	G11_Kyllburg	0.19355	0.21053	0.20321	0.21053	0.20213	0.20321	0.20321	0.19577	0.19786	0.21053	0.20321	0.20213	0.20213	0.21164	0.21164	0.20635	0.20745	0.20745	0.20635	0.19681	0.21164	0.20635	0.21164	0.20745	0.20745	0.21579	0.21053	0.21466	0.20635	0.20745	0.20999	0.20213
	96	G12_Nohen	0.20706	0.22358	0.21667	0.22363	0.21522	0.21644	0.21645	0.20900	0.23024	0.21404	0.21663	0.21572	0.21538	0.22464	0.22503	0.21973	0.22069	0.22078	0.21009	0.20057	0.22508	0.21967	0.22492	0.22088	0.21122	0.21946	0.22365	0.21830	0.21968	0.22061	0.20412	0.23425
	97	G13_Rambach	0.21277	0.23834	0.27692	0.22917	0.23958	0.24084	0.24084	0.23316	0.20745	0.24742	0.24084	0.23958	0.23037	0.23958	0.24870	0.22513	0.23560	0.24479	0.23438	0.23438	0.23958	0.23438	0.23958	0.23560	0.23560	0.24352	0.22917	0.23316	0.22513	0.23560	0.23738	0.22105

Appendix 19: Distance values between *Homalothecium lutescens* specimens of the world-wide sample set and further *Homalothecium* spp. samples. Simple matching distances are given in the upper right, Jaccard distances in the lower left part of the matrix

			International samples																	National samples																			Further *Homalothecium* species		
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
International samples	1	Hl1_England	0	0.26754	0.30702	0.27632	0.18421	0.30263	0.28509	0.33772	0.30263	0.34649	0.25877	0.30263	0.31140	0.32009	0.19737	0.29825	0.30470	0.32018	0.34685	0.30702	0.31140	0.33333	0.29825	0.31579	0.31089	0.35526	0.27846	0.30702	0.32895	0.25439	0.30263	0.31579	0.30263	0.31579	0.30263	0.30263	0.46983	0.48707	0.32759
	2	Hl2_England	0.33333	0	0.16228	0.13158	0.32018	0.17544	0.11404	0.14912	0.11404	0.19298	0.14912	0.15789	0.13158	0.20541	0.27193	0.17982	0.35289	0.13158	0.17600	0.18860	0.18421	0.16228	0.14474	0.14474	0.17053	0.16667	0.12925	0.17105	0.17544	0.32018	0.17544	0.18860	0.17544	0.19737	0.17544	0.17544	0.46552	0.48276	0.29741
	3	Hl3_Sweden	0.36458	0.20787	0	0.16228	0.35088	0.10965	0.16228	0.12719	0.15351	0.19737	0.10965	0.17105	0.16228	0.19653	0.31140	0.14035	0.32226	0.15351	0.17434	0.14912	0.14474	0.15789	0.13158	0.17544	0.19045	0.12719	0.15136	0.18421	0.17982	0.24561	0.11842	0.12281	0.11842	0.12281	0.12719	0.12719	0.49569	0.44397	0.31897
	4	Hl4_Ireland	0.33871	0.17442	0.20556	0	0.29386	0.18421	0.14912	0.14912	0.15789	0.21930	0.15789	0.17544	0.17544	0.18541	0.24561	0.17982	0.32671	0.15789	0.21901	0.14474	0.14035	0.18860	0.15351	0.17982	0.20478	0.15789	0.14248	0.15351	0.13158	0.29386	0.14035	0.15351	0.16667	0.15351	0.14912	0.14912	0.47414	0.48276	0.32328
	5	Hl5_Italy	0.24000	0.37824	0.39801	0.34896	0	0.32895	0.31140	0.33772	0.34649	0.33772	0.30263	0.35526	0.37281	0.36673	0.13596	0.34211	0.31369	0.31140	0.34209	0.30702	0.29386	0.35088	0.29825	0.32456	0.35885	0.30263	0.30946	0.33333	0.32018	0.30263	0.30263	0.30702	0.31140	0.28947	0.30263	0.30263	0.47845	0.48707	0.31897
	6	Hl6_Caucasus	0.37097	0.22989	0.14620	0.23729	0.38860	0	0.17544	0.13158	0.14912	0.17544	0.18421	0.15789	0.18421	0.22479	0.34211	0.13596	0.36201	0.16667	0.14995	0.15351	0.16667	0.13596	0.10965	0.17105	0.21989	0.16667	0.15561	0.18860	0.15789	0.27632	0.13158	0.12719	0.11404	0.11842	0.13158	0.13158	0.50000	0.46552	0.32328
	7	Hl7_Poland	0.34392	0.15116	0.20330	0.19101	0.36224	0.22472	0	0.17544	0.15789	0.20175	0.16667	0.13158	0.13158	0.21466	0.28947	0.15351	0.37061	0.14035	0.19610	0.18860	0.17544	0.17982	0.13596	0.16228	0.19569	0.17544	0.12065	0.19737	0.15789	0.31140	0.18421	0.19737	0.18421	0.17982	0.19298	0.19298	0.45690	0.50000	0.32328
	8	Hl8_Spain	0.40104	0.19653	0.16571	0.19429	0.39286	0.17647	0.22222	0	0.12281	0.21930	0.14035	0.15789	0.14912	0.20130	0.31579	0.17982	0.34440	0.14035	0.14060	0.14474	0.14035	0.16228	0.13596	0.14474	0.17264	0.11404	0.16451	0.17982	0.15789	0.27632	0.12281	0.11842	0.12281	0.13596	0.13158	0.13158	0.51724	0.43966	0.32328
	9	Hl9_Hungary	0.36702	0.15385	0.19663	0.20455	0.40102	0.19767	0.20225	0.16374	0	0.21930	0.15789	0.14035	0.16667	0.19399	0.31579	0.18860	0.34411	0.17544	0.15718	0.17105	0.17105	0.17105	0.11842	0.14474	0.18958	0.16667	0.14683	0.17105	0.17544	0.28509	0.16667	0.17982	0.16667	0.15351	0.16667	0.16667	0.49138	0.44828	0.30603
	10	Hl10_Italy	0.40102	0.24176	0.24064	0.26738	0.38500	0.22346	0.24599	0.26882	0.26882	0	0.21053	0.21053	0.21930	0.25968	0.33333	0.17982	0.37066	0.15789	0.20584	0.19737	0.19298	0.17982	0.13596	0.21491	0.18647	0.21053	0.19949	0.20614	0.19298	0.27632	0.20175	0.20614	0.20175	0.18860	0.20175	0.20175	0.48276	0.47414	0.34914
	11	Hl11_Sweden	0.32065	0.19540	0.14368	0.20339	0.35751	0.23729	0.21111	0.18391	0.20455	0.25806	0	0.20175	0.16667	0.19643	0.27193	0.17982	0.34418	0.18421	0.17522	0.17982	0.18421	0.17105	0.15351	0.17105	0.19721	0.13158	0.14690	0.18860	0.20175	0.24123	0.15789	0.16228	0.15789	0.16228	0.14912	0.14912	0.46552	0.43103	0.33190
	12	Hl12_Hungary	0.36316	0.20455	0.21429	0.22222	0.40500	0.20571	0.16949	0.20339	0.18286	0.25668	0.25137	0	0.21053	0.19311	0.30702	0.17982	0.37940	0.17544	0.19776	0.17982	0.17544	0.18860	0.12719	0.18860	0.18447	0.19298	0.14690	0.22368	0.16667	0.27632	0.18421	0.18860	0.17544	0.16228	0.18421	0.18421	0.47414	0.48276	0.32328
	13	Hl13_Spain	0.37173	0.17341	0.20442	0.22222	0.42079	0.23596	0.16949	0.19318	0.21348	0.26596	0.21229	0.25946	0	0.20681	0.33333	0.14474	0.36164	0.14912	0.16602	0.18860	0.21053	0.15351	0.15351	0.16228	0.14092	0.16667	0.12944	0.16667	0.20175	0.32895	0.17544	0.18860	0.18421	0.21491	0.19298	0.19298	0.49138	0.48276	0.33190
	14	Hl14_Scotland	0.38575	0.26399	0.24854	0.23518	0.42434	0.28616	0.26888	0.25611	0.24678	0.31032	0.25127	0.24329	0.25845	0	0.34710	0.22895	0.32821	0.20053	0.20124	0.20105	0.18036	0.21990	0.20130	0.22224	0.20241	0.20248	0.17382	0.16153	0.20155	0.31476	0.19764	0.21061	0.21613	0.21037	0.21093	0.21033	0.51040	0.45455	0.36503
	15	Hl15_Austria	0.25568	0.33155	0.36224	0.30108	0.17919	0.40206	0.34197	0.37306	0.37306	0.38191	0.32804	0.36082	0.38579	0.40265	0	0.34649	0.28292	0.28947	0.32960	0.31140	0.28947	0.35526	0.28509	0.32018	0.32097	0.29825	0.29600	0.32018	0.29825	0.25877	0.29825	0.30263	0.31579	0.31140	0.30702	0.30702	0.48276	0.48276	0.30603
	16	Hl16_Italy	0.35789	0.22905	0.17877	0.22652	0.39196	0.17919	0.19444	0.22778	0.23757	0.22283	0.22652	0.22527	0.18539	0.28191	0.39698	0	0.36638	0.17982	0.17164	0.14035	0.20614	0.17544	0.17544	0.21930	0.20773	0.16228	0.11610	0.21053	0.21491	0.27193	0.12719	0.13158	0.11842	0.14912	0.12719	0.12719	0.46983	0.49569	0.31897
	17	Hl18_Italy	0.37971	0.42171	0.38280	0.39192	0.38058	0.43192	0.42914	0.41077	0.41095	0.42696	0.40884	0.43926	0.42311	0.39576	0.35027	0.42618	0	0.34441	0.31815	0.27850	0.29174	0.38370	0.33978	0.33122	0.35327	0.30042	0.33821	0.32251	0.34403	0.21714	0.28289	0.29581	0.30920	0.31349	0.30896	0.30892	0.51077	0.45043	0.30826
National samples	18	G1_Kallenberg	0.38021	0.17341	0.19444	0.20225	0.36410	0.21591	0.17978	0.18286	0.22346	0.19890	0.23204	0.22099	0.19101	0.25548	0.34375	0.22527	0.40705	0	0.17572	0.16228	0.13158	0.16228	0.10965	0.17105	0.12760	0.12281	0.12952	0.13596	0.15789	0.26754	0.14912	0.15351	0.16667	0.15351	0.16667	0.16667	0.49138	0.47414	0.34914
	19	G2_Bad Salzungen	0.41130	0.22821	0.22322	0.27419	0.39865	0.19818	0.24768	0.18566	0.20780	0.25656	0.22589	0.24864	0.21308	0.26144	0.38742	0.21934	0.38813	0.22467	0	0.15798	0.18880	0.19796	0.14494	0.18417	0.19036	0.12353	0.14713	0.19725	0.19387	0.25434	0.13180	0.13571	0.13993	0.14489	0.13995	0.14072	0.48271	0.46188	0.31476
	20	G3_Saalburg	0.37037	0.24157	0.19101	0.18857	0.36269	0.20231	0.23626	0.18966	0.22034	0.24457	0.22905	0.22778	0.23757	0.25597	0.36788	0.18182	0.34520	0.20787	0.20640	0	0.14474	0.19298	0.14912	0.20175	0.20795	0.10965	0.13353	0.17544	0.15351	0.20175	0.04825	0.06140	0.08333	0.09649	0.09211	0.09211	0.45259	0.42672	0.32759
	21	G4_Freyburg	0.36979	0.23333	0.18333	0.18079	0.34536	0.21469	0.21858	0.18182	0.20225	0.23656	0.23077	0.21978	0.25806	0.23086	0.34197	0.25269	0.35385	0.16949	0.23844	0.18644	0	0.17105	0.12719	0.15351	0.20248	0.13158	0.17309	0.13596	0.11404	0.24123	0.12281	0.12719	0.14035	0.10965	0.14035	0.14035	0.48276	0.44828	0.34052
	22	G5_Ebermannstadt	0.39791	0.21264	0.20225	0.24022	0.40609	0.18235	0.22778	0.21143	0.22159	0.22652	0.22034	0.23889	0.19886	0.27843	0.41117	0.22346	0.44844	0.20904	0.25341	0.24581	0.21788	0	0.13158	0.07895	0.15760	0.19737	0.16006	0.14035	0.17105	0.28070	0.20614	0.21053	0.20614	0.20175	0.21491	0.21491	0.48707	0.46983	0.35345
	23	G6_Tiefental	0.35602	0.18750	0.16760	0.19553	0.34872	0.14620	0.17318	0.17614	0.15517	0.17222	0.19553	0.16384	0.19444	0.25133	0.33679	0.21858	0.39946	0.14286	0.18760	0.19101	0.16292	0.17143	0	0.14035	0.14873	0.14474	0.11627	0.16667	0.13596	0.23684	0.15351	0.15789	0.15351	0.13158	0.15351	0.15351	0.49569	0.44397	0.31897
	24	G7_Wiesenthau	0.37696	0.18966	0.21978	0.22778	0.37755	0.22159	0.20556	0.18857	0.18857	0.26203	0.21788	0.23626	0.20670	0.27379	0.37436	0.26882	0.39527	0.21667	0.23614	0.25275	0.19553	0.10778	0.17978	0	0.17736	0.17982	0.16007	0.14912	0.14474	0.26316	0.20614	0.21930	0.21491	0.21053	0.21491	0.21491	0.50431	0.47845	0.32759
	25	G8_Malchin	0.37112	0.21909	0.23559	0.25201	0.40883	0.27585	0.24262	0.21638	0.23799	0.23192	0.24563	0.23155	0.17740	0.25541	0.37511	0.25441	0.41982	0.16507	0.23824	0.25546	0.24973	0.20546	0.18878	0.22347	0	0.20997	0.15198	0.16386	0.17927	0.28191	0.22656	0.24174	0.24462	0.23269	0.22338	0.22559	0.50368	0.45587	0.38736
	26	G9_Rüdersdorf	0.41117	0.21348	0.16292	0.20112	0.35385	0.21469	0.21858	0.15029	0.21229	0.25532	0.17045	0.23913	0.20994	0.25481	0.35052	0.20442	0.36242	0.15909	0.16122	0.14451	0.16854	0.24725	0.18333	0.22527	0.25888	0	0.14699	0.18860	0.18421	0.23246	0.06140	0.06579	0.07018	0.08333	0.07895	0.07895	0.48276	0.43103	0.32328
	27	G10_Eiderstaudamm	0.34048	0.17146	0.19277	0.18523	0.36307	0.20403	0.15701	0.21187	0.19133	0.24590	0.19044	0.18935	0.16833	0.22199	0.35159	0.15242	0.40199	0.16853	0.19206	0.17529	0.21817	0.20711	0.15150	0.20513	0.19398	0.18796	0	0.13836	0.13812	0.25659	0.12925	0.14241	0.15565	0.16014	0.16434	0.16436	0.47200	0.46330	0.32991
	28	G11_Kyllburg	0.37433	0.22414	0.23333	0.20115	0.39175	0.24571	0.24862	0.23295	0.22286	0.25683	0.24157	0.27869	0.21023	0.21220	0.38021	0.26374	0.39278	0.17919	0.25424	0.22727	0.17816	0.18713	0.21348	0.19540	0.20943	0.23889	0.18246	0	0.09211	0.26316	0.17105	0.17544	0.19737	0.20175	0.21491	0.21491	0.51293	0.45259	0.37069
	29	G12_Nohen	0.39474	0.22857	0.22778	0.17442	0.37824	0.20930	0.20339	0.20690	0.22727	0.24176	0.25556	0.21469	0.25414	0.25921	0.35789	0.26776	0.41304	0.20455	0.24899	0.20115	0.15116	0.22286	0.17714	0.18966	0.23012	0.23333	0.18244	0.12727	0	0.25000	0.15789	0.16228	0.18421	0.16228	0.20175	0.20175	0.49138	0.41379	0.36638
	30	G13_Rambach	0.31351	0.37436	0.29319	0.34536	0.30688	0.33333	0.35859	0.32984	0.33854	0.32308	0.29255	0.32642	0.37688	0.37119	0.31217	0.32124	0.27634	0.31771	0.30868	0.25137	0.28947	0.33508	0.28421	0.31414	0.32969	0.28042	0.30772	0.31915	0.30481	0	0.21491	0.21930	0.22368	0.20175	0.21491	0.21491	0.46983	0.43534	0.27586
	31	Hbl_29_257	0.36316	0.22472	0.15341	0.18182	0.35567	0.17442	0.22951	0.16185	0.21348	0.24731	0.20225	0.23077	0.22099	0.24967	0.35233	0.16477	0.34711	0.19101	0.17419	0.06667	0.15909	0.25824	0.19444	0.25543	0.27611	0.08284	0.16842	0.22034	0.20455	0.26344	0	0.01316	0.03509	0.06579	0.05263	0.05263	0.46552	0.44828	0.30603
	32	Hbl_81_345	0.37895	0.24157	0.16000	0.19886	0.36269	0.17059	0.24590	0.15789	0.23034	0.25405	0.20904	0.23757	0.23757	0.26659	0.35938	0.17143	0.36296	0.19774	0.18034	0.08485	0.16571	0.26519	0.20112	0.27174	0.29422	0.08929	0.18558	0.22727	0.21143	0.27027	0.01863	0	0.03070	0.07018	0.05702	0.05702	0.46983	0.44397	0.30172
	33	Mb_733	0.36508	0.22599	0.15429	0.21348	0.36598	0.15385	0.23077	0.16279	0.21469	0.24865	0.20339	0.22222	0.23204	0.27014	0.37113	0.15517	0.37495	0.21229	0.18546	0.11310	0.18079	0.25967	0.19553	0.26630	0.29655	0.09467	0.20039	0.25140	0.23596	0.27419	0.04878	0.04321	0	0.05702	0.03509	0.03509	0.47414	0.45690	0.30603
	34	Mb_1_833	0.37306	0.24725	0.15730	0.19553	0.34021	0.15698	0.22283	0.17614	0.19663	0.23118	0.20556	0.20442	0.26203	0.26364	0.36224	0.18889	0.37437	0.19444	0.18706	0.12791	0.14205	0.25137	0.16760	0.25806	0.28145	0.10983	0.20282	0.25275	0.20787	0.24731	0.08824	0.09467	0.07738	0	0.05702	0.05702	0.45259	0.45259	0.31897
	35	r8_Rabis.1	0.36316	0.22472	0.16384	0.19209	0.35567	0.17442	0.23913	0.17241	0.21348	0.24731	0.19209	0.23077	0.24044	0.26366	0.36082	0.16477	0.37316	0.21111	0.18450	0.12353	0.17978	0.26776	0.19444	0.26486	0.27396	0.10526	0.20961	0.26923	0.25414	0.26344	0.07186	0.07831	0.04878	0.07692	0	0.00000	0.46552	0.47414	0.28879
	36	r8_Rabis.2	0.36316	0.22472	0.16384	0.19209	0.35567	0.17442	0.23913	0.17241	0.21348	0.24731	0.19209	0.23077	0.24044	0.26417	0.36082	0.16477	0.37297	0.21111	0.18479	0.12353	0.17978	0.26776	0.19444	0.26486	0.27455	0.10526	0.20969	0.26923	0.25414	0.26344	0.07186	0.07831	0.04878	0.07692	0.00000	0	0.46552	0.47414	0.28879
Further *Homalothecium* species	37	*H. aureum*	0.60556	0.59341	0.60526	0.59459	0.60000	0.62703	0.57297	0.63492	0.61290	0.59259	0.58696	0.59140	0.60638	0.63453	0.60541	0.58602	0.64769	0.60638	0.60914	0.57692	0.59574	0.61081	0.60526	0.61905	0.61741	0.59574	0.59190	0.63636	0.61622	0.58602	0.58378	0.59239	0.59459	0.56757	0.58378	0.58378	0	0.43103	0.40086
	38	*H. fulgescens*	0.62431	0.61202	0.56284	0.60541	0.61081	0.60000	0.61376	0.56983	0.57778	0.58824	0.55866	0.60215	0.60215	0.59056	0.60870	0.61170	0.59736	0.59459	0.59319	0.55618	0.56831	0.59890	0.56284	0.60000	0.57815	0.55249	0.58743	0.58659	0.54857	0.55801	0.57143	0.57222	0.58242	0.57065	0.59459	0.59459	0.66667	0	0.45259
	39	*H. philippeanum*	0.41304	0.37705	0.38947	0.39894	0.39572	0.40541	0.39474	0.40107	0.38378	0.41753	0.40741	0.39683	0.40526	0.44643	0.38378	0.39153	0.39709	0.42188	0.39498	0.40426	0.41146	0.43158	0.38947	0.40212	0.45888	0.39474	0.40484	0.45026	0.44503	0.34783	0.37968	0.37838	0.38172	0.38947	0.36216	0.36216	0.55357	0.60694	0

Appendix 20: Distance values between *Homalothecium sericeum* specimens of the German-wide sample set. Simple matching distances are given in the upper right, Jaccard distances in the lower left part of the matrix

			Population FN	
			1	2
Population FN	1	FN_33	0	0.04294
	2	FN_65	0.05426	0
	3	FN_1_1	0.23134	0.22901
	4	FN_4_10	0.23111	0.22299
	5	FN_5_9	0.22388	0.22137
	6	FN_6_11	0.20149	0.19847
	7	FN_7_12	0.15507	0.16628
	8	FN_8_15	0.03053	0.06870
	9	FN_8_16	0.04615	0.03937
	10	FN_8_22	0.00781	0.06202
	11	FN_8_26	0.14179	0.16541
	12	FN_9_20	0.02326	0.06202
	13	FN_11_30	0.16547	0.14815
	14	FN_11_34	0.02326	0.03150
	15	FN_11_47.1	0.01550	0.06923
	16	FN_11_47.2	0.02326	0.07692
	17	FN_11_55	0.01563	0.05469
	18	FN_11_61	0.00000	0.05426
	19	FN_12_38	0.04651	0.03968
	20	FN_15_60	0.00781	0.04688
	21	FN_16_62	0.03906	0.04762
	22	FN_17_67	0.12593	0.14925
	23	FN_18_69	0.16176	0.15789
	24	FN_19_76	0.03846	0.04688
	25	FN_23_80	0.16788	0.15038
	26	FN_24_89	0.14942	0.16611
	27	FN_surr_98	0.17518	0.15789
	28	FN_surr_99	0.16176	0.14394
	29	FN_surr_107	0.16788	0.17778
	30	FN_surr_108	0.14493	0.16788
	31	FN_surr_110	0.14700	0.16294
Regional sampels from Saxony-Anhalt	32	rSA1_Nißmitz	0.22059	0.20455
	33	rSA2_Braunsbedra	0.16912	0.13740
	34	rSA3_Freyburg_rill	0.19286	0.18978
	35	rSA4_Liederstädt	0.14179	0.19259
Population D	36	D_2_699	0.25352	0.25180
	37	D_2_700	0.24113	0.23913
	38	D_6_701	0.24648	0.24460
	39	D_8_693	0.20290	0.21324
	40	D_8_696	0.25352	0.25180
	41	D_16_705	0.25532	0.25362
	42	D_surr_689	0.18248	0.21898
	43	D_surr_691	0.25352	0.25180
	44	D_surr_692	0.25352	0.25180
Population L	45	LI_9_611	0.14354	0.17985
	46	LII_1_618	0.15441	0.19118
	47	LIII_1_621	0.17037	0.18045
	48	LIV_1_622	0.13235	0.16912
	49	LV_4_625	0.12902	0.16555
	50	LV_4_637	0.12500	0.16176
	51	LV_4_647	0.11111	0.14815
	52	LV_4_659	0.13235	0.16912
	53	LV_4_664	0.18116	0.21739
	54	LV_10_629	0.12500	0.16176
	55	LV_13_632	0.13545	0.17230
	56	LV_27_633	0.12500	0.16176
	57	LV_50_650	0.13235	0.16912
	58	LV_77_639	0.15827	0.19424
	59	LVI_22_674	0.20647	0.23134
	60	LVI_23_670	0.18248	0.19259
	61	LVI_44_680	0.19708	0.22059
	62	L_surr_669	0.17266	0.22143
	63	L_surr_684	0.19565	0.23188
Regional sampels from Brandenburg	64	rB1_Riedebeck	0.16547	0.20144
	65	rB2_Betten	0.18705	0.21014
	66	rB3_Werenzhain	0.17518	0.22464
	67	rB4_Friedersdorf	0.20000	0.23571
	68	rB5_Schönborn	0.21324	0.26277
	69	rB6_Sallgast	0.20290	0.21324
Natiuonal samples	70	G1_Jena	0.18382	0.19403
	71	G2_Nennsdorf	0.21014	0.22059
	72	G3_Göttern	0.21683	0.23309
	73	G4_Zimmritz	0.18486	0.20784
	74	G5_Kahla910	0.23404	0.21898
	75	G5_Kahla912	0.24113	0.22628
	76	G5_Kahla913	0.26761	0.25362
	77	G6_Röttelmisch	0.29166	0.29242
	78	G7_Schnellmannhausen	0.20567	0.24113
	79	G8_Wiesenthau	0.24088	0.26471
	80	G9_Zedersitz	0.22464	0.26087
	81	G10_Rügen	0.27273	0.30769
	82	G11_Walkenried	0.27505	0.28646
	83	G12_Vulkaneifel	0.21739	0.22794
	84	G13_Hünfeld	0.16541	0.20301
	85	G14_Meiningen	0.23172	0.25245

Appendix 21: Distance values between *Homalothecium sericeum* specimens of the the world-wide sample set and *Homalothecium aureum* samples. Simple matching distances are given in the upper right, Jaccard distances in the lower left part of the matrix

			International samples		
			1	2	3
International samples	1	Hs1_England	0	0.10857	0.17143
	2	Hs1.1_England	0.13669	0	0.20000
	3	Hs2_England	0.20979	0.23810	0
	4	Hs3_Newfoundland	0.32891	0.34628	0.34801
	5	Hs4_Newfoundland	0.28307	0.30815	0.27094
	6	Hs5_Italy	0.29174	0.32285	0.24068
	7	Hs6_Italy	0.26712	0.27027	0.17986
	8	Hs7_Croatia	0.22759	0.26667	0.17730
	9	Hs8_Spain	0.29054	0.27027	0.27891
	10	Hs9_Morocco	0.31973	0.33333	0.27273
	11	Hs10_France	0.26531	0.25676	0.22917
	12	Hs11_El Hierro	0.35862	0.33793	0.32394
	13	Hs12_Madeira	0.34932	0.34014	0.29078
	14	Hs13_Caucasus	0.22759	0.21918	0.23973
	15	Hs14_Caucasus	0.27465	0.28966	0.28671
	16	Hs15_Sweden	0.26351	0.24324	0.23973
	17	Hs16_Sweden	0.25175	0.26712	0.25175
	18	Hs17_Sweden	0.25170	0.26667	0.27517
	19	Hs18_Hungary	0.22819	0.23179	0.21622
	20	Hs19_Norway	0.27273	0.31081	0.29655
	21	Hs20_Poland	0.21168	0.22857	0.23741
	22	Hs21_Scotland	0.18750	0.20408	0.20000
	23	Hs21.1_Scotland	0.18963	0.21962	0.19624
	24	Hs22_Ireland	0.21277	0.25342	0.14706
	25	Hs23_Ireland	0.26207	0.24138	0.23776
	26	Hs24_Greece	0.30612	0.33113	0.37255
National samples	27	G8_Wiesenthau	0.23611	0.22759	0.22378
	28	G10_Rügen	0.30137	0.29252	0.21583
	29	FN_65	0.22378	0.22759	0.18571
	30	FN_16_62	0.21678	0.23288	0.20423
	31	LV_13_632	0.24138	0.24490	0.21678
	32	LV_27_633	0.24138	0.24490	0.21678
	33	LVI_23_670	0.21678	0.24490	0.17857
	34	D_2_700	0.27083	0.29730	0.23404
	35	D_6_701	0.26389	0.29054	0.23944
H. aureum samples	36	*H. aureum* (Israel)	0.58389	0.57333	0.59333
	37	*H. aureum* (Morocco)	0.58667	0.56667	0.52778

Der Lebenslauf ist in der Online-Version aus Gründen des Datenschutzes nicht enthalten.

Eidesstattliche Erklärung

Ich erkläre hiermit an Eides statt, dass ich die vorliegende Dissertation selbständig und ohne unerlaubte Hilfe angefertigt habe, andere als die angegebenen Quellen und Hilfsmittel nicht benutzt und die den benutzen Quellen wörtlich oder inhaltlich entnommenen Stellen als solche kenntlich gemacht habe.

Berlin, März 2010

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Kathrin Lieske