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Too Warm and Too Dry—Decline and Threat of the Subarctic-Subalpine Liverwort *Hygrobiella laxifolia* in a Low Mountain Range in Central Europe under the Conditions of Climate Change

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Abstract: Using the liverwort *Hygrobiella laxiflora* as an example, this study aims to investigate the impact of climate change on montane species and their ecosystems. The study area is the Elbe Sandstone Mountains in Germany and the Czech Republic, where *Hygrobiella laxifolia* has an isolated occurrence in deeply carved gorges characterized by a specific microclimate (cellar climate). The focus is on determining the rate at which populations are affected. After little change in the population over a long period, a sudden sharp decline has been observed in recent years. The decline correlates with the mass proliferation of the European spruce bark beetle (*Ips typographus*) observed since 2017, which has led to a strong thinning of the forests in the area. In many areas of occurrence, the forests now have a much sparser tree layer or none at all. Competition from other, more competitive species also plays an important role as a cause of decline, as these have spread more widely on the sites due to the now higher light levels. The severe bark beetle infestation and the large-scale forest fire of 2022 both represent events that led to the almost complete deforestation of large parts of the study area, which was previously unknown on this scale. Since both the bark beetle infestation and the forest fire are strongly intensified by climate change, we assume that climate change is the main reason for the decline of *Hygrobiella laxifolia* in the area. The populations of *Hygrobiella laxifolia* of the Elbe Sandstone Mountains show some morphological peculiarities. As two new species have recently been described within *Hygrobiella*, we have integrated a sample from the area into a molecular phylogeny of *Hygrobiella* based on the plastid sequences of *trn*L-*trn*F intergenic spacer and *matK* to clarify the relationships. The sample from Elbe Sandstone Mountains fits well into the clade of *Hygrobiella laxifolia.*

Keywords: Hygrobiellaceae; bryophytes; distribution; global warming; Elbe Sandstones; Bohemian Switzerland; Saxon Switzerland; DNA taxonomy; morphology; ecology

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1. Introduction

Bryophytes respond rapidly and sensitively to global warming [1,2], which has been documented by the spread of thermophilic species [3,4]. Thus, a decline in montane bryophyte species is expected due to global warming, although there have been limited studies on such species to date.

The current study was carried out in the Elbe Sandstone Mountains, a sandstone massif located on the German–Czech border, on both sides of the Elbe river, southeast of Dresden and north of Děčín. This region, known as Saxon Switzerland on the German side and Bohemian Switzerland on the Czech side, is particularly affected by global warming.

In 2017, a mass proliferation of the European spruce bark beetle (*Ips typographus*) began, favoured by warm and dry weather. Initially, the infestation affected the eastern areas of the region and caused death to spruce stands that are typical forest plantations in this region. Since then, the infested area has become widely enlarged, resulting in the death of a large proportion of the spruce in the Elbe Sandstone Mountains. In the summer of 2022, the region experienced the largest forest fire recorded, affecting a total of 1146 hectares of forest (1031 ha in the Czech Republic and 115 ha in Saxony) [5].

The warming of the climate is reported by measurements [6] with the air temperatures recorded at the Sněžník and Děčín stations indicating an increasing trend. Compared to the period of 1961–1990, the annual mean temperature has risen by 1 to 1.2 °C in the period 1991–2021. Additionally, the average temperature from April to September has risen by 1.1 to 1.5 °C compared to the previous period. Furthermore, a trend towards decreasing precipitation has been observed at both stations in recent years. There has been an uninterrupted drought since May 2018, which also follows the drought from December 2014 to June 2017. Lastly, the drought in August 2022 on Sněžník was the most intense in the last 60 years [6].

The Elbe Sandstone Mountains are deeply dissected by the Elbe River and its tributaries and harbour a great variety of rugged rock formations. Steep rock faces, towers, and needles alternate with deeply incised valleys and flat, horizontal terrains. The proximity of sunny rock faces and cool, damp ravines on a very small scale results in strong, relief-related differences in local temperatures.

The Elbe Sandstone Mountains' cool and damp ravines are home to a unique flora. These gorges provide favourable living conditions for many montane elements due to the altitudinal temperature reversal despite their low elevation ("cellar climate") [7–9]. The proportion of boreo-montane species adapted to cold and moist environments is significantly higher here. Among the phanerogams, the glacial relicts *Viola biflora* and *Streptopus amplexifolius* are the best-known examples. Additionally, numerous bryophyte species with a distributional focus in mountainous habitats occur in these gorges, for instance, *Anastrophyllum michauxii*, which is subarctic-subalpine, *Cephalozia leucantha*, which is western boreal-montane, *Dicranodontium asperulum*, which is northern suboceanic-subalpine floristic element, and especially *Hygrobiella laxifolia*, which is subarctic-subalpine element.

In this study, we analysed the recent changes in the distribution and population size of the liverwort *Hygrobiella laxifolia* in the Elbe Sandstone Mountains. The occurrences of *Hygrobiella laxifolia* were recorded in Saxon Switzerland from 2014 to 2016 and in Bohemian Switzerland from 2017 to 2018. The main objective of this survey was to determine the species' distribution, population size, and habitat requirements. Moreover, we wanted to determine the current state of the populations after the very recent changes in habitats (i.e., decreasing shade due to forest decline by bark beetle infestation or fire) likely resulting in changes of the microclimate. Our selective re-mapping in 2023 showed a significant decline of population sizes at many sites or even the extinction of occurrences.

In addition, two new species have recently been described within the genus *Hygrobiella* [10], which was previously considered monotypic. To determine the identity of the *Hygrobiella* samples from the Elbe Sandstone Mountains, which exhibit some morphological peculiarities, we performed a molecular phylogenetic analysis based on two plastid markers.

2. Materials and Methods

The nomenclature of bryophytes is based on Hodgetts et al. [11] and that of ferns and seed plants on Müller et al. [12].

Vegetation surveys were carried out according to the Braun-Blanquet method but using the extended cover value scale according to Reichelt and Wilmanns [13]. The indicator values were taken from Ellenberg and Leuschner [14]; the N-values of the bryophytes were based on Simmel et al. [15]. The mean quantitative indicator values were calculated using the following equation:

$$mZ_{quant} = \sum(Z \times D\%)/\sum D\%.$$

where: mZ_{quant} = mean quantitative indicator value; Z = species-specific indicator value; D% is mean cover value (r = 0.01, + = 0.1, 1 = 2.5, 2 m = 5, 2 a = 10, 2 b = 20, 3 = 37.5, 4 = 62.5, 5 = 87.5).

At each record site, during the initial survey carried out in 2014–2018 and the follow-up survey carried out in 2023, all microhabitats suitable for colonization by the species were searched. These microhabitats were generally boulders in the creek bed and we recorded the presence of the species at the record site and the number of boulders colonized by the species. On each boulder, the area colonized by the species was measured with a ruler and a total sum of the area colonized by the species was determined for each record site. GPS coordinates, photos, and hand-drawn sketches of the colonized microhabitats of the record sites were taken during the initial survey in order to ensure that the occurrences could be reliably located. To determine changes in the habitat, a photo comparison was carried out at selected sites, in which photos were taken at approximately the same time of year and using the same perspective and the same section. Thus, photos from the year 2023 were compared with those from the period 2015–2018.

Material of *Hygrobiella laxifolia* from the Elbe Sandstone Mountains was compared with isotype material of *H. laxifolia* var. *notarisiana* deposited in B (B 30 0005352).

A Nikon compound microscope (Nikon Eclipse Ni-E; Nikon, Tokyo, Japan) was used to examine specimens by means of standard anatomical and morphological methods applied to bryophytes. Microscopic images were captured with a digital camera (Nikon DS-Ri2) attached to the microscope.

To elucidate species identity of the *Hygrobiella* material from the Elbe Sandstone Mountains we sequenced two plastid markers (*trn*L-F intergenic spacer, *matK*) of one specimen (voucher and GenBank accession, see Appendix A). These sequences were included in a phylogeny of *Hygrobiella* consisting of sequences of *H. laxifolia*, *H. intermedia*, and *H. squamosa* published by Bakalin and Vilnet [10] and deposited in GenBank (see Appendix A). *Cephaloziella konstantinovae* and *C. polystratosa* (taken from GenBank) were used as outgroups.

DNA was isolated from silica-gel dried plant material according to Dumolin et al. [16]. Primers for amplification of plastid markers were taken from Taberlet et al. [17] for the *trn*L-*trn*F intergenic spacer and Johnson and Soltis [18] for *matK*. Polymerase Chain reactions were performed in a volume of 20 µL consisting of 50 ng of template DNA, 1×S-Reaction Buffer (Peqlab, Erlangen, Germany), 3.125 mM $MgCl_2$, 0.25 mM dNTPs, 10 mM forward and reverse primer each, 0.5 U *Taq* DNA polymerase (Peqlab). The PCRs were performed in an Eppendorf Mastercycler EP S (Eppendorf, Hamburg, Germany) programmed for 180 s at 94 °C followed by 35 cycles of 30 s at 94 °C, 30 s at 55 °C (*trn*L-*trn*F intergenic spacer) or 49.6 °C (*matK*), and 45 s at 72 °C, and a final extension for 5 min at 72 °C. DNA sequencing according to the Sanger method [19] was performed on an ABI3730 (Life Technology, Darmstadt, Germany) automated sequencing machine at the laboratory at Senckenberg Biodiversity and Climate Research Centre (SBik-F).

A multiple alignment of the combined data set was performed with ClustalW [20] implemented in MEGA X v. 10.0.5 [21]. Maximum Likelihood phylogenies were computed in MEGA X. Based on a model test, the Tamura 3-parameter model [22] with gamma distributed rate variation among sites was chosen as the substitution model, and 1000 bootstrap replicates were computed. In addition, a Bayesian phylogeny was calculated with MrBayes v.3.2 [23] with two simultaneous runs over 10,000,000 generations, sampling every 100th generation, with a burn-in of 250,000 trees based on the above-mentioned substitution model.

3. Results

3.1. Distribution

The liverwort *Hygrobiella laxifolia* is evaluated as an (sub)arctic-(sub)alpine species with a distribution in the northern zones of all continents of the Holarctic [24,25]. The core area of the species is in Northern Europe, including Scandinavia (Norway, Sweden, Finland) and adjacent northwestern Russia (Murmansk Province, Karelia) [10]. The species is also present in Iceland and the Faroe Islands [26]. In central Europe, it is known to inhabit the Alps in Austria, Switzerland, France, Italy, and the Elbe Sandstone Mountains in Germany and Czech Republic. In Western and Southwestern Europe, it can be found in the Pyrenees and in mountainous and coastal areas of Great Britain, Ireland, Azores, and Madeira [26]. In Asia, it is distributed locally in boreal Pacific Asia, Japan, and China [10]. *Hygrobiella laxifolia* has a range in North America from British Columbia to Oregon and the Rocky Mountains, and in the east from Quebec, Newfoundland, Labrador, Nova Scotia to Greenland [10].

According to Schuster [27], the species belongs to a group of liverworts that formerly had a circum-Laurasian range, which was dissected and reduced by late Tertiary and Pleistocene events.

In Germany, the species is only known with certainty from Saxon Switzerland in Saxony. One record from the Black Forest is dubious and not accepted [24,28].

Hygrobiella laxifolia was initially discovered in Saxony in 1920 by E. Riehmer at the ravine Amselgrund and has since been reported at other sites in the region [29,30]. In 2004, the species was known from six recent localities in Saxon Switzerland [31]. A new occurrence in the Bielatal at the Silberquelle south of Königstein was discovered in 2015 [32]. According to Müller [32], there were no recent new confirmations at the historical sites Polenztal, Zscherrgrund, and Tiefer Grund near Hohnstein. During the subsequent intensive investigations during this study, the species could be detected again at the sites Polenztal and Tiefer Grund, so it seems to have become extinct only at the site Zscherrgrund.

In the Czech Republic, the species is only found in Bohemian Switzerland. The species was initially recorded in 2003 at three localities: two in the Suchá Kamenice valley and one in the creek valley from Mezní louka to Divoká soutěska near Vysoký most [33]. Upon re-examination of the occurrences in 2005, it was discovered that the population size at the already known localities was greater than previously described in [33]. Several populations of the species have been found, with some covering an area larger than 200 cm^2 and a total area exceeding several dozen dm^2 [34]. In 2008, a fourth Czech locality was discovered in the ravine Kachní potok, located 2.1 km north of the village of Kamenická Stráň and about 2 km west of the locality near Vysoký most [35]. Additionally, a new occurrence was discovered near Mezní můstek in 2018.

The current distribution of *H. laxifolia* in the Elbe Sandstone Mountains is shown in Figure 1.

The altitude of the sites in the region varies from 130 to 290 m. The lowest occurrence was found in the Höllgrund near Rathen (130 m), the highest (290 m) in Suchá Kamenice. Thus, the occurrences in the Elbe Sandstone Mountains are the lowest in Central Europe, since the species is largely restricted to the subalpine and alpine levels in Central Europe (1400–2500 m above sea level), with altitudes of 860 to 2500 m reported for Austria [36] and 280 m to 2330 m for Switzerland, whereby most Swiss occurrences are found between 1400–1800 m [37].

In western and northern Europe—in cooler or more Atlantic climate—*H. laxifolia* colonises lower altitudes; Paton [38], for example, gives a range of occurrence from near sea level to 1070 m for the British Isles.

In sum, the occurrences in the Elbe Sandstone Mountains are geographically strongly isolated with the closest sites in about 400 km distance in the Austrian Alps.

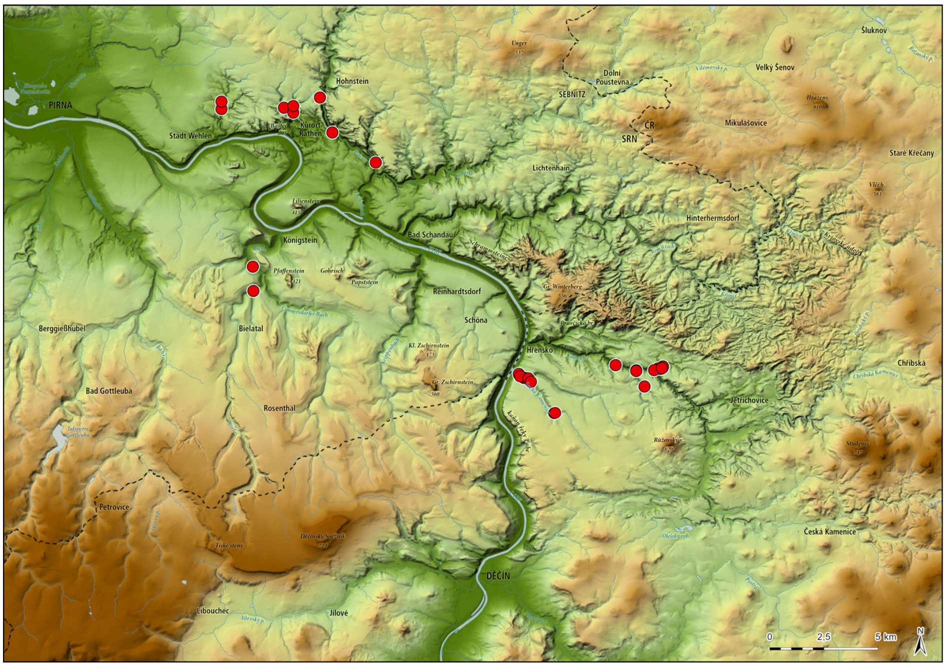

Figure 1. Map of the distribution of *Hygrobiella laxifolia* in the Elbe Sandstone Mountains. Basemap consists of data of topographic database of Bohemian Switzerland National Park Administration and digital terrain model data of Czech Survey Office, DMR4G, and Landesamt für Geobasisinformation Sachsen [GeoSN], DGM.

3.2. Taxonomy

For a long time, *Hygrobiella* Spruce was placed in its own subfamily Hygrobielloideae (Jörg.) R.M.Schust. ex Grolle within the family Cephaloziaceae Mig. until the genus was recently given its own monotypic family Hygrobiellaceae Konstant. et Vilnet [39–41]. Until recently, *Hygrobiella laxifolia* (Hook.) Spruce was thus the only member of the genus, until Bakalin and Vilnet [10] described two new species, i.e., *H. intermedia* Bakalin & Vilnet and *H. squamosa* Bakalin & Vilnet from Eastern Asia based on integrative taxonomical study relying on morphological and molecular data.

The specimens collected in the Elbe Sandstone Mountains show some peculiarities compared to the specimens from Scandinavia and the Alps. *Hygrobiella laxifolia* grows in this region almost exclusively in a filiform habit (Figures 2 and 3). The plants consist of very delicate, flagelliform shoots and branches. The leaves on the stems and branches are very distantly arranged and reduced in size, partly scale-like and undivided (Figure 3C). Among these filiform plants, somewhat more vigorous plants with clearly developed bilobed leaves becoming larger towards the shoot apex were rarely observed (e.g., in the region Kachní potok; herbarium specimens from Amselgrund, Dürrer Grund). These plants (Figure 3B) resemble the clearly leafy specimens from Scandinavian or Alpine populations, but they are smaller overall. Schade [29] assigned the plants of the Elbe Sandstone Mountains to var. *notarisiana* (C.Massal.) Schade because of these peculiarities in comparison to the more vigorous plants in Scandinavia and the Alps. His identification was confirmed at the time by C. Massalongo, the author of this variety, based on herbarium material sent to him [29]. The taxon was initially established by Massalongo as *Cephalozia notarisiana* C.Massal. based on material described by De Notaris in 1868 as *Jungermannia divaricata* var. *rivularis* De Not.:

Hygrobiella laxifolia var. *notarisiana* (C.Massal.) Schade, *Sitzungsberichte und Abhandlungen der Naturwissenschaftlichen Gesellschaft Isis* in Dresden 1922–23: 40. 1924.

Basionym: *Cephalozia notarisiana* C.Massal., *Le Epatiche dell'Erbario Crittogamico Italiano Revisione Critica* 19. 1903. Type-Protologue: Italy. Note: Monterosso sotto Cavandone in Val Intrasca al Lago Maggiore, autumn 1868, leg. De Not.

Figure 2. *Hygrobiella laxifolia* at the site Nasser Grund near Rathen in Elbe Sandstone Mountains. Patches with flagelliform shoots and branches, growing together with *Dichodontium pellucidum* and *Rhizomnium punctatum*. Photo F. Müller, 30 August 2023.

Jungermannia divaricata var. *rivularis* De Not., *Erbario Crittogamico Italiano*, Series 2, 3: no. 113. 1868. with Latin description on label.

An isotype of *Cephalozia notarisiana* could be examined in B (Herb. H. Reimers 1799. *Hygrobiella laxifolia* (Hook.) Spr. [Alpi insubrici:] "In rupi irrigati ad un ruscella del Monte rosso, sotto Cavandone, in Val Intrasca, Lago Maggiore. Autumn 1868 *De Notaris. Erbar. Critt. Ital.* 115 (as Jungerm. divaricata rivularis c. diagn.)" (B 30 0005352)). The type locality is situated in northern Italy on the western shore of Lake Maggiore, at a comparably low altitude of about only 350–500 m. The type material is in good correspondence with the plants collected in the Elbe Sandstone Mountains. The isotype material consists of filamentous, sparsely, or very loosely leafed stems and very small leaves (Figure 4). Occasionally, perianths could be found in the material; these were elongate-fusiform (Figure 4E). Chavoutir et al. [42] reported similar-looking specimens from the French Alps with only mainly flagelliform colonies. Müller [43] did not distinguish var. *notarisiana* and placed it as a synonym of *H. laxifolia* because he regarded its morphological peculiarities as ecologically induced modifications.

Material from pacific East Asia was previously regarded as depauperate forms of the widely distributed *H. laxifolia* but was then described as two new species *H. intermedia* and *H. squamosa* [10]. In particular, morphological characteristics such as the degree of underleaf development, correlation of inner and outer stem cell size, and thickness of perianth cell walls, which were formerly regarded as environmentally induced, but in fact have taxonomical value and strongly correspond to molecular data, were used for differentiation. Both species have a certain morphological similarity with the forms of *H. laxifolia* occurring in the Elbe Sandstone Mountains. In comparison to *H. laxifolia*, they are characterised by a smaller plant size and distant and small-leaved shoots and branches. However, a separation based purely on morphological characteristics proved to be difficult. We therefore decided to include a sample from the Elbe Sandstone Mountains in a molecular phylogeny.

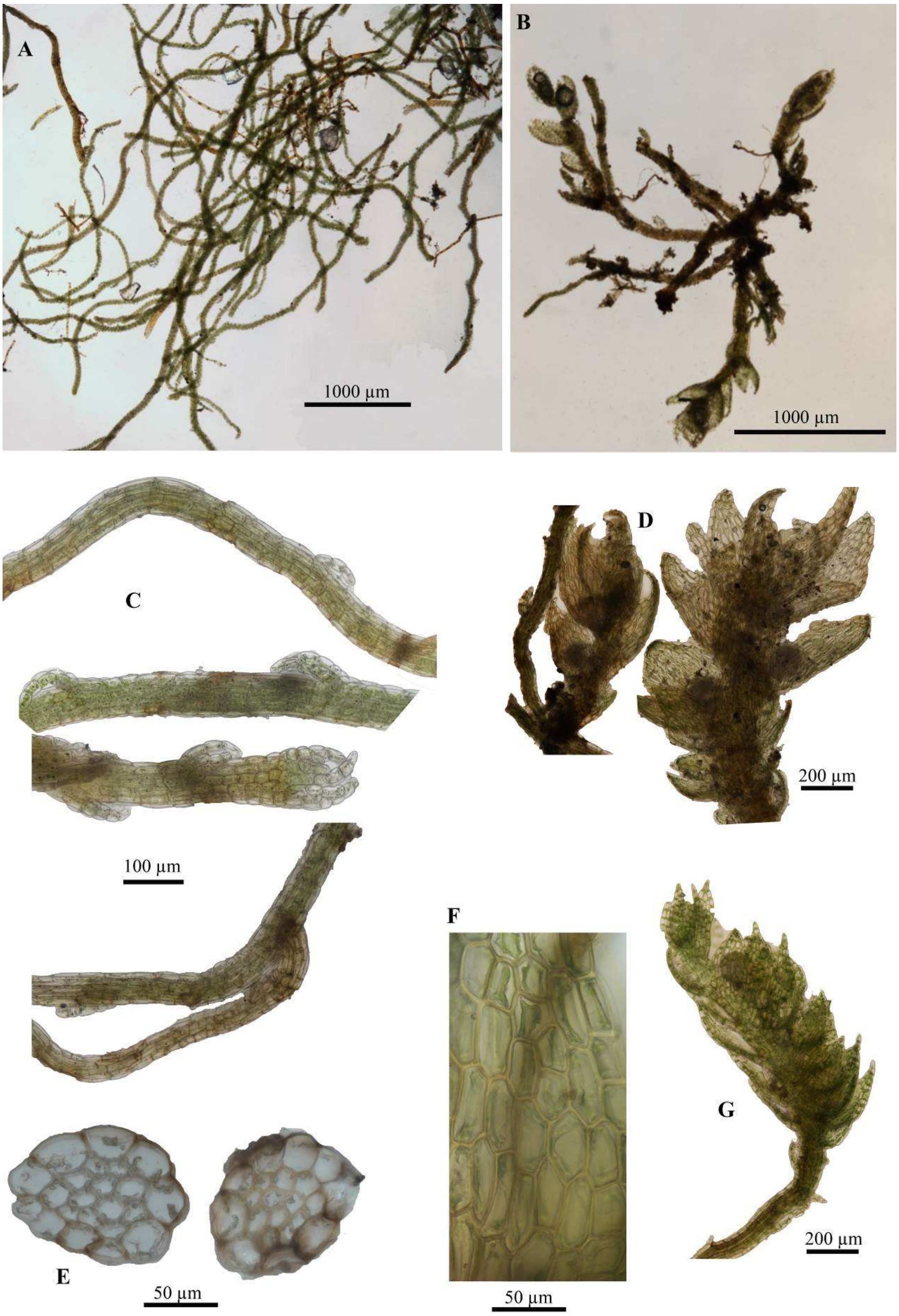

Figure 3. *Hygrobiella laxifolia*. Details of the plants from Elbe Sandstone Mountains. (**A**)—stems with reduced leaves; (**B**)—stems with well-developed leaves; (**C**)—details of stems; (**D**)—details of stems with leaves and underleaves; (**E**)—stem cross sections; (**F**)—leaf cells; (**G**)—male plant with antheridia. **A**,**C** from Rathen (Rathen DR047345); **B**,**D**,**F** from Koutský potok 26.04.2003 (DR); **E** from Riehmer 06.1928 (DR 1105), **G** from Bielatal (DR).

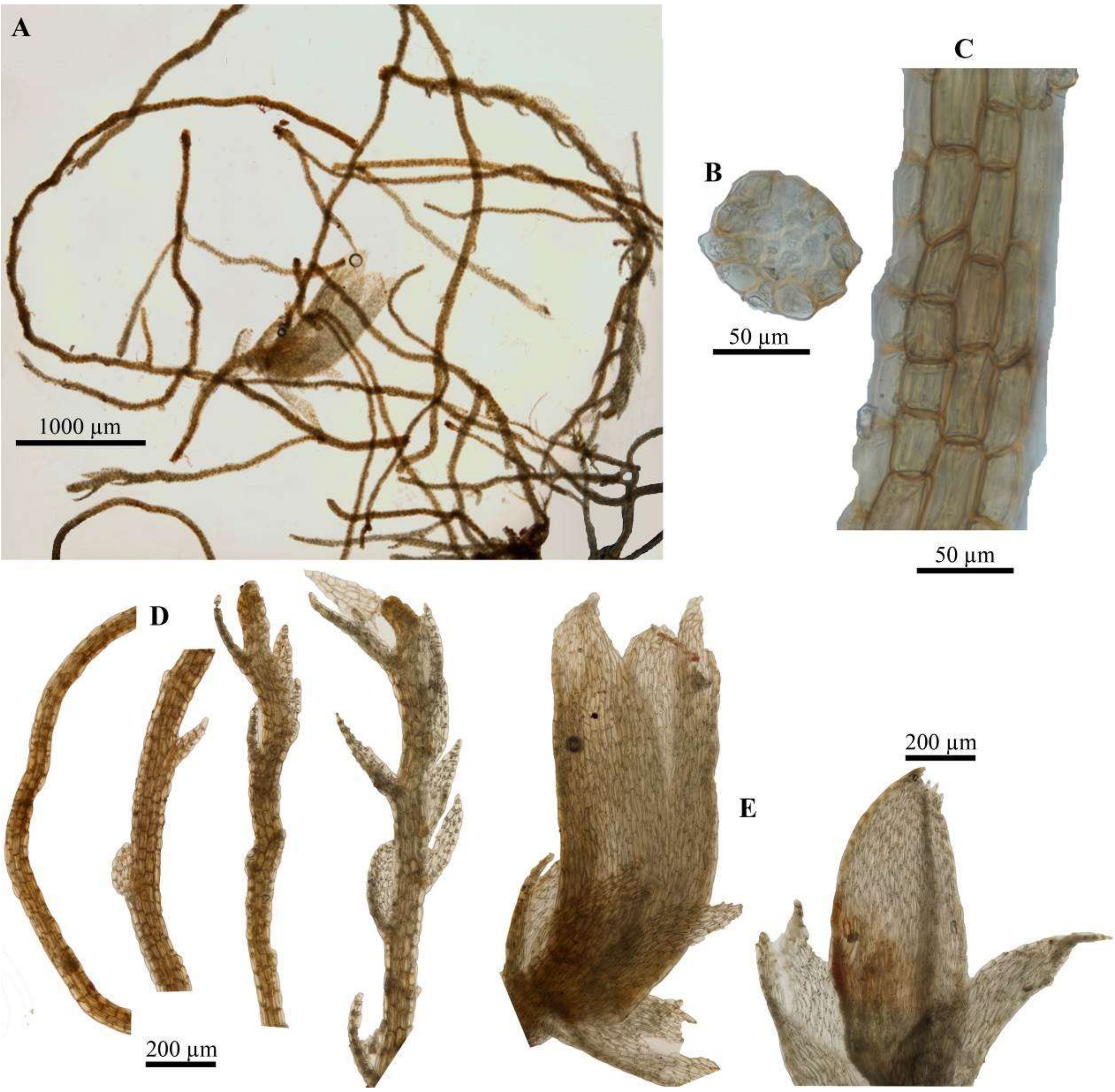

Figure 4. *Hygrobiella laxifolia* var. *notarisiana* (C.Massal.) Schade from isotype material in B ("In rupi irrigati ad un ruscella del Monte rosso, sotto Cavandone, in Val Intrasca, Lago Maggiore. Autumno 1868 *De Notaris. Erbar. Critt. Ital.* 115 (als Jungerm. divaricata rivularis c. diagn.)", B 30 0005352). (**A**)—sterile stems and one stem with perianth; (**B**)—stem cross section; (**C**)—outer side of a nearly leafless stem; (**D**)—different stems, left stems nearly leafless, right stems with leaves; (**E**)—perianths.

The main morphological feature for the separation of *H. intermedia* from *H. laxifolia* is similar cell size in the stem cross-section with outer cells 12–18 µm in diameter and inner cells with 8–18 µm in diameter, and both inner and outer cell walls are slightly thickened [10]. In stem cross-section of *H. laxifolia*, outer cells are larger, 17–30 µm in diameter compared to inner cells which are 7–12(–15) µm in diameter. In addition, only outer cell walls are slightly thickened. Stem cross-sections of the material from the Elbe Sandstone Mountains correspond to the characteristics given for *H. laxifolia* (Figure 3E).

Hygrobiella squamosa differs morphologically from *H. laxifolia* by small, scale-like leaves and strongly reduced underleaves on sterile shoots, versus normally isophyllous stems in *H. laxifolia* [10]. The description of the leaves and underleaves is in good agreement with the plants occurring in the Elbe Sandstone Mountains. However, species differ also in perianth shape that is shortly fusiform to clavate in *H. squamosa*, versus elongate-fusiform in *H. laxifolia*. During the current investigations, perianths were never observed in the populations of the Elbe Sandstone Mountains. The only reference to the observation of perianths in the region can be found in Schade [29], who observed plants with perianths repeatedly in the valley Uttewalder Grund. Unfortunately, Schade's collections were destroyed by fire in 1945. In the examined herbarium material of *H. laxifolia* from Elbe Sandstone Mountains in DR and B, perianths were absent. Male plants were found by Schade [29] in the Bielatal above Königsbrunn and later [30] in the valley Tiefer Grund near Brand. At the same site as also mentioned by Schade (Bielatal), few ♂plants were found in the course of the current investigations (Figure 3G).

Since the affiliation of the material from Elbe Sandstone Mountains to *H. squamosa* cannot be completely ruled out on the basis of morphology—and in particular due to lacking perianth features—we also integrated *H. squamosa* into the molecular phylogeny. The sample from Elbe Sandstone Mountains was clearly part of the well-supported clade of *H. laxifolia* (Figure 5).

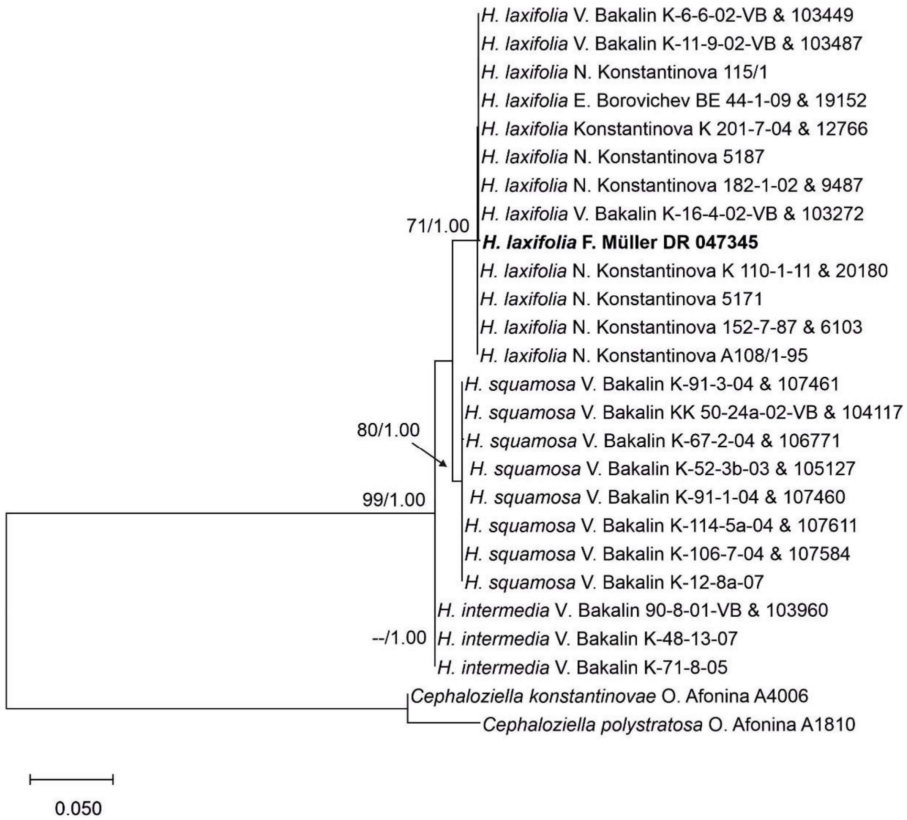

Figure 5. Maximum Likelihood phylogeny based on the plastid sequences of *trn*L-*trn*F intergenic spacer and *matK* of *Hygrobiella*. The sequence of the sample *H. laxiflora* F. Müller DR 047345 from the Elbe Sandstone Mountains, Germany, was newly obtained (presented in bold); the remaining sequences were taken from GenBank (see also [10]). Bootstrap values (1000 replicates) and posterior probabilities of a Bayesian phylogeny resulting in nearly the same topology are given above branches.

3.3. Habitat Requirements

The species grows in the Elbe Sandstone Mountains on moist, periodically or episodically flooded sandstone boulders in creek valleys of sandstone gorges. In one case, *H. laxifolia* was found on a periodically flooded vertical sandstone rock face (Figure 10). Many sites were only flooded during high water.

The ravines with occurrences of the species are usually deeply carved into the terrain. They have a narrow floodplain with a width of 15–40(–70) m and steep and rugged, nearly vertical slopes dominated by rock faces. The difference in altitude between the valley floor and the mountain plateau varies from 35 to 220 m. In localities with a narrow valley floodplain, the difference in altitude can be less, e.g., in the Wehlener Grund; in those with a wider floodplain it can be greater (e.g., Bielatal), and it is also greater in those with a notch valley character (V-cross-section), e.g., Nasser Grund, Dürrer Grund, Bielatal.

Marstaller [44] published the first relevés with *H. laxifolia* from Saxon Switzerland. *Hygrobiella laxifolia* was included in 21 of his relevés and were recorded from the sites Wehlener Grund, Uttewalder Grund, Amselgrund, Höllgrund, and Nasser Grund. He assigned four relevés to Scapanietum undulatae dichodontietosum pellucidae, *Racomitrium aciculare*-variant and 17 relevés to Brachythecietum plumosi (six to the typical subassociation, *Dichodontium pellucidum* variant, 11 to the subassociation racomitrietosum acicularis, *Dichodontium pellucidum* variant). There is no occurrence of the species in the aquatic moss communities *Brachythecio rivularis-Hygrohypnetum luridi* (too alkaline and too nutrient-rich, partly due to wastewater discharges) and Oxyrrhynchium rusciformis (too mineral-rich, too fast-flowing, permanently water-bearing), which have higher nutrient requirements.

In this study, the association of the species was recorded in a total of 54 relevés covering the entire site spectrum (Table S1). Twenty-one of these relevés were taken in Bohemian Switzerland, while on the German side, relevés were taken at the same sites already investigated by Marstaller [44] in 1985–1986 and at the new sites Polenztal, Tiefer Grund, and Bielatal.

Most of the relevés belonged to the association Scapienetum undulatae (45 relevés); in 12 of these relevés, *Brachythecium rivulare*, which is considered a characteristic species of the association *Brachythecio rivularis-Hygrohypnetum luridi*, was represented with high cover values (2a and higher). These relevés were still classified here as Scapanietum undulatae due to the equally high cover of *Scapania undulata*. The presence of *Brachythecium rivulare* indicated a higher nutrient richness of the sites and a development in the direction of *Brachythecio rivularis-Hygrohypnetum luridi*. Two relevés were classified as Brachythecietum plumosi, and four relevés from Bohemian Switzerland as Hygrohypnetum ochracei. *Scapania undulata* was missing in three relevés and characteristic species of the other associations of Racomitrion acicularis were also absent or only present with very low coverage. These relevés could only be assigned to the level of alliance, i.e., Racomitrion acicularis. It is striking that in these three relevés *Oxyrrhynchium hians*, which hardly appeared in the other relevés as an accompanying moss of *Hygrobiella laxifolia*, occurred with higher cover values. This occurrence can be interpreted as an indicator of prolonged drought and high nutrient supply.

The most common associates of *Hygrobiella laxifolia* were, in order of decreasing frequency, *Scapania undulata*, *Dichodontium pellucidum*, *Rhizomnium punctatum*, *Brachythecium rivulare*, *Sciuro-hypnum plumosum*, *Fissidens pusillus*, *Pellia epiphylla*, *Hygrohypnella ochracea*, and *Jungermannia pumila*.

To assess the environmental conditions of the habitat of *H. laxifolia*, the mean qualitative and quantitative Ellenberg indicator values were calculated on the basis of the current relevés (Table 1). The indicator values for *H. laxifolia* were given in the literature for Central Europe [14,15].

N (nutrients) = 5 (occurring at moderately nutrient-rich sites, and less frequently at poor and rich sites), L (light) = 7 (half-light plant, mostly occurring at full light, but also in the shade up to about 30% of diffuse radiation in an open area), T (temperature) = 3 (cool indicator, mainly in subalpine areas), K (continentality) = 6 (subcontinental), M (moisture) = 8 (between 7 [humidity indicator, mainly on moist, but not wet soils] and 9 [wetness indicator, mainly on often soaked, poorly aerated soils]), R = 2 (between 1 [indicator of strong acidity, never occurring in slightly acidic to alkaline conditions] and 3 [acidity indicator, occurring mainly in acidic conditions, exceptionally in neutral conditions]).

The N-values and T-values, which were here determined by analysing the vegetation surveys, ranged from 4.69 to 4.90 and 3.05 to 3.19, respectively, depending on the calculation method, and show good agreement with the indicator values from the literature. The newly calculated M-value was in the range 7.33 to 7.74 and indicates a tendency towards 7 instead of 8.

The K-value was shifted somewhat more towards oceanic climates (4.88–5.50 instead of 6). This calculation seems plausible due to the preference of the species for coastal areas, at least in Europe [25,38].

The R-value was in the range 4.58–5.42, when cover values of *H. laxifolia* were omitted. However, taking into account the mostly high cover values of *H. laxifolia* it resulted in 3.80, which is still remarkably higher than the R-value of 2 from the literature. In the region, *H. laxifolia* is a moderate acid indicator which is consistent with information that the species is "tolerating weakly basic substrates" [25] or occurs on mildly base-rich rocks [38].

The mean L-values calculated based on the relevés were in the range 4.41 to 6.04, and were therefore significantly below the previously given value of 7. The highest value was resulted from a calculation taking *H. laxifolia* into account (6.04) since *H. laxifolia* usually dominated the relevés.

Table 1. Mean qualitative and quantitative (taking cover into account) Ellenberg indicator values of the 54 relevés with *H. laxifolia* from the Elbe Sandstone Mountains. Both calculations were carried out either by including or excluding the cover values of *H. laxifolia*.

	Qualitative Indicator Values		**Quantitative Indicator Values**	
	incl. *H. laxifolia*	excl. *H. laxifolia*	incl. *H. laxifolia*	excl. *H. laxifolia*
N-value	4.77	4.69	4.90	4.76
L-value	5.13	4.41	6.04	4.42
T-value	3.16	3.19	3.05	3.12
K-value	5.07	4.88	5.50	5.09
M-value	7.42	7.33	7.74	7.52
R-value	4.58	5.11	3.80	5.42

3.4. Changes in Occurrence and Population Size

Populations of *H. laxifolia* were already lost in the region in historical times. In Saxon Switzerland, the historically documented occurrences at the site Wehlener Grund (from here numerous herbarium specimens from 1944 in B, e.g., Wehlener Grund, large block in the dry creek bed below the mouth of the Teufelsgrund, 27 May 1944, H. Reimers (B 30 0005334)) and at the site Zscherrgrund [29] are extinct. In the lower part of the Wehlener Grund, the creek bed was completely re-modelled (Figure 12E). It originally consisted of natural boulders, but was levelled and paved, most recently as part of measures to repair flood damage after 2002, but even in previous years it had a less natural character. In the Zscherrgrund, the path running through the valley was converted into a tarmac road and the creek bed was enclosed by walls.

The long-term population development of the Bohemian occurrences can hardly be evaluated as the species was only recently discovered there in 2003.

The comparison of vegetation surveys with *H. laxifolia* carried out in the same areas of occurrence (Wehlener Grund, Uttewalder Grund, Amselgrund, Höllgrund, and Nasser Grund) in Saxon Switzerland between the years 1985–1986 (21 relevés) [44] and 2014–2016 (22 relevés) already indicated major changes during these 30 years, although the massive spruce mortality due to bark beetle infestation had not yet occurred in this period (Table 2). The species *Sciuro-hypnum plumosum*, *Mnium hornum*, *Pellia epiphylla*, *Conocephalum conicum*, *Racomitrium aciculare*, and *Marsupella emarginata* had clearly decreased in frequency, while the species *Thamnobryum alopecurum*, *Brachythecium rivulare*, *Fissidens pusillus*, *Chiloscyphus polyanthos*, and *Jungermannia pumila* had become much more common. The species with declining frequency included those typical of rather acidic, nutrient-poor sites, some of which (*Racomitrium aciculare* and *Marsupella emarginata*) have a montane distribution. In contrast, the significantly higher frequency of *Brachythecium rivulare*, typical of nutrient-rich sites, and *Thamnobryum alopecurum*, characteristic of slightly acidic to slightly basic conditions, is particularly striking. This clearly indicates a change in the aquatic bryophyte community towards *Brachythecio rivularis-Hygrohypnetum luridi* with higher nutrient requirements.

Table 2. Comparison of the frequencies of bryophyte species in relevés with *H. laxifolia* in Saxon Switzerland (Wehlener Grund, Uttewalder Grund, Amselgrund, Höllgrund, and Nasser Grund) between the years 1985–1986 (21 relevés) [44] and 2014–2016 (22 relevés).

	1985–1986 Frequency in %	**2016–2018 Frequency in %**
Hygrobiella laxifolia	100	100
Dichodontium pellucidum	100	90.9
Scapania undulata	95.2	90.9
Rhizomnium punctatum	61.9	72.7
Cephalozia bicuspidata	4.8	9.1
Atrichum undulatum	9.5	4.5
Species with significant decline		
Sciuro-hypnum plumosum	71.4	31.8
Mnium hornum	23.8	4.5
Pellia epiphylla	38.1	18.2
Conocephalum conicum	28.6	9.1
Racomitrium aciculare	66.7	22.7
Marsupella emarginata	38.1	4.5
Species with significant increase		
Thamnobryum alopecurum	9.5	27.3
Brachythecium rivulare	28.6	63.6
Fissidens pusillus	4.8	40.9
Chiloscyphus polyanthos	4.8	36.4
Jungermannia pumila	9.5	18.2
Newly added species		
Scapania nemorea		9.1
Oxyrrhynchium hians		18.2
Solenostoma hyalinum		4.5
Chrysosplenium oppositifolium		4.5
Chrysosplenium alternifolium		4.5
Plagiomnium affine		9.1
Disappeared species		
Marchantia polymorpha	4.8	
Jungermannia sphaerocarpa	14.3	
Heterocladium heteropterum	14.3	
Plagiothecium succulentum	9.5	
Kindbergia praelonga	9.5	

To determine the current population development, the sites already investigated in the years 2014–2018 were visited again in 2023. A total of 17 sites were compared (Table 3, Figure 6). The site Kachní potok could not be visited as the area was inaccessible due to numerous fallen trees. *Hygrobiella laxifolia* could no longer be detected at five sites, a very strong decline by more than 80% was observed at four sites, a strong decrease by 40–80% at three sites, a slight decrease of less than 40% at one site, and the populations remained constant at only four sites. However, three of the four occurrences of constant populations were small with the species only occurring on one boulder with an area of a few dm^2. The extinct and declining populations were often large-sized populations that are now significantly reduced in size.

Table 3. Comparison of the population development between 2014–2018 and 2023 at 17 investigated sites of *H. laxifolia* in the Elbe Sandstone Mountains with indications of the causes of extinction and decline. Categories of the trend of the dimensions of the population size: +—extinction; <<<—very strong decline, decrease by more than 80%; <<—strong decline, decrease by 40–80%; <—slight decline, decrease of less than 40%; =—unchanged. Reasons for decline or extinction: 1 = forest fire, 2 = deforestation, 3 = spruce dieback due to bark beetle infestation, 4 = increasing light, 5 = spreading of other bryophytes and of algae; 6 = increase in the cover of the herb and shrub layer.

No.	Country	Site	Trend of the Dimensions of the Population Size	Reasons for Decline or Extinction
1	CZ	Lower part of Suchá Kamenice near bunker O1/4/E	<<<	3, 4, 5, 6
2	CZ	Janovský potok, near the confluence with Suchá Kamenice	<<	3, 4, 5, 6
3	CZ	Suchá Kamenice, c. 300 m above the Janovský potok confluence	<<	3, 4, 5, 6
4	CZ	Suchá Kamenice, approx. 50 m above a tributary from the direction of Arnoltice	+	3, 5
5	CZ	Kamenice, near Mezní můstek	=	
6	CZ	Koutský potok, lower part a little above the confluence with the Kamenice	<<<	2, 3, 4, 5, 6
7	CZ	Koutský potok, middle section below Divoká soutěska	<<<	1, 2, 3, 4, 5, 6
8	DE	Tiefer Grund, near Waitzdorf	+	2, 3, 4, 5, 6
9	DE	Valley of the Polenz, near Waltersdorfer Mühle	+	3, 5, 6
10	DE	Valley of the Polenz, under the rock massif Ameisenhörner	=	
11	DE	Amselgrund, below Amselfall	+	2, 3, 4, 5
12	DE	Höllgrund, near Rathen	+	2, 3, 4, 5, 6
13	DE	Nasser Grund, near Rathen	<<<	3, 4, 5, 6
14	DE	Valleys Uttewalder Grund and Wehlener Grund below the restaurant "Waldidylle"	<<	4, 5, 6
15	DE	Valley Uttewalder Grund above the restaurant "Waldidylle"	=	
16	DE	Valley of the Biela, near Rollborn, south of Königstein	<	3, 5, 6
17	DE	Valley of the Biela, near the spring Silberquelle, south of Königstein	=	

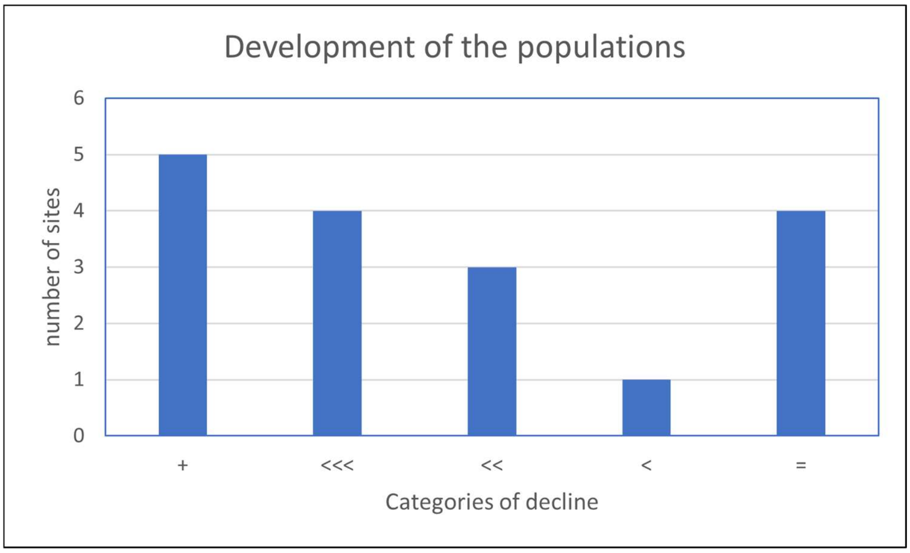

Figure 6. Comparison of the population development between 2014–2018 and 2023 at 17 investigated sites of *H. laxifolia* in the Elbe Sandstone Mountains. Categories of the development of the population size dimensions: +—extinction; <<<—very strong decline, decline by more than 80%; <<—strong decline, decline by 40–80%; <—slight decline, decline by less than 40%; =—unchanged.

This alarming decline of populations and the change in habitat conditions is illustrated with a few examples in more detail.

The upper part of the site Koutský potok was affected by the forest fire of 2022 and the entire area has been affected by the death of spruce due to bark beetle infestation. It therefore currently has no forest cover with a shade-casting tree layer. At the burnt places, only nutrient indicators were found on the boulders in the creek (*Ceratodon purpureus*, *Funaria hygrometrica*, *Leptobryum pyriforme*). At the unburnt sites, an increase in the cover of the herb layer and a spread of other, more competitive bryophytes, especially *Scapania undulata*, *Marsupella emarginata*, *Dichodontium pellucidum*, *Atrichum undulatum*, *Polytrichum commune*, was observed in the spots previously colonised by *H. laxifolia* (Figure 7). In the entire area of the site Koutský potok (middle and lower section), the species was found on 16 boulders with a total area of 0.83 m^2 in 2018, but only on two boulders with a coverage of 0.0004 m^2 in 2023 corresponding to a 99.95% decline in population size.

Figure 7. Comparison of the site Koutský potok between the years 2018 and 2023. (**A**)—27 September 2018, (**B**)—9 Novemeber2023. In 2018, *H. laxifolia* was present in a population of 0.5 m^2 in the areas with a patchy herb layer shown in the foreground. In 2023, the species was no longer present. In addition to an increase in cover of the herb layer, a spread of other, more competitive bryophytes, especially *Scapania undulata*, *Marsupella emarginata*, *Dichodontium pellucidum*, *Atrichum undulatum*, *Polytrichum commune*, was observed.

In the lower part of Suchá Kamenice, the amount of light close to the ground was significantly increased due to bark beetle-induced death of the spruce (Figures 8 and 9). The resulting increase in herbaceous plants and more competitive bryophytes, e.g., *Scapania undulata*, *Racomitrium aciculare*, *Marsupella emarginata*, *Dichodontium pellucidum*, *Brachythecium rivulare* caused the very strong decline of *H. laxifolia*.

In the years 2015 and 2016, *H. laxifolia* was found on a wet vertical sandstone rock face covering a total area of 1 × 3 m, of which approx. 1.5 m^2 the species formed a pure stand at the site Waltersdorfer Mühle (Figure 10). The species could not be found in 2023 and the former locations were instead occupied by dense stands of *Scapania undulata* (Figure 12F).

Due to increased light exposure because of dead spruces, a significant increase in vegetation cover was observed for ferns and *Rubus pedemontanus*.

Figure 8. Comparison of the site Suchá Kamenice between the years 2017 and 2023. (**A**)—7 December 2017, (**B**)—9 November 2023. *Hygrobiella laxifolia* was present in large populations on the vertical block in 2017 and became extinct in 2023. The reasons for extinction are the thinning of the tree layer due to bark beetle infestation and the spread of more competitive bryophytes, e.g., *Brachythecium rivulare*, *Dichodontium pellucidum*.

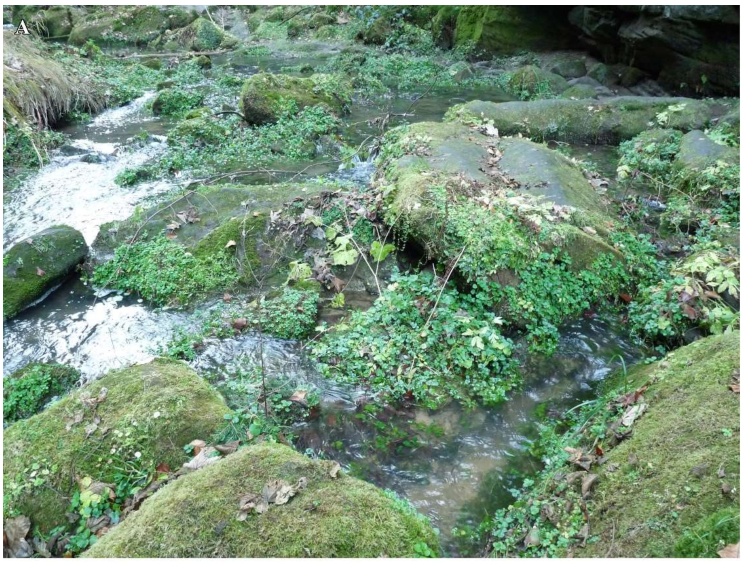

Figure 9. *Cont.*

Figure 9. Comparison of the site in Suchá Kamenice between the years 2017 and 2023. (**A**)—7 December 2017, (**B**)—9 November 2023. The section shown here harboured one of the largest stands of *H. laxifolia* in the Czech part of the Elbe Sandstone Mountains in 2017. Due to thinning of the tree layer caused by bark beetle infestation, light exposure significantly increased. As a result, the cover of the herb layer has increased and *H. laxifolia* has been displaced in the bryophyte layer by more competitive species, especially *Scapania undulata*. The area colonised by *H. laxifolia* in 2023 was only 11.2 dm^2. This is over 80% less than at the time of the survey in 2017.

Figure 10. Comparison of the site Waltersdorfer Mühle between the years 2015 and 2023. (**A**)—11 July 2015, photo by S. Buschmann, (**B**)—11 September 2023. In the years 2015 and 2016, *H. laxifolia* was found on a wet vertical sandstone rock covering a total area of 1 × 3 m, of which about 1.5 m^2 formed a pure stand. The species was absent in 2023. The former sites were instead occupied by dense stands of *Scapania undulata*. Increased light exposure due to the loss of spruce trees has led to a significant increase in cover of ferns and *Rubus pedemontanus*.

The site Wehlener Grund harboured one of the largest occurrences of *H. laxifolia* in the region in the years 2014–2016. The species was present here on numerous blocks in large dominant stands. During the survey in 2023, *H. laxifolia* was only found on 11 boulders and with a total area of 2.6 m^2. The cover of the herb layer has increased significantly, and vegetation shifted towards more competitive species (Figure 11). Despite these negative trends, the site Wehlener Grund still harbours the largest populations in the Elbe Sandstone Mountains. The site is characterized by a higher proportion of deciduous trees and is therefore less affected by bark beetle infestations. However, as the creek is lined by a footpath, trees had been felled several times in the past to secure the path, which has led to additional thinning.

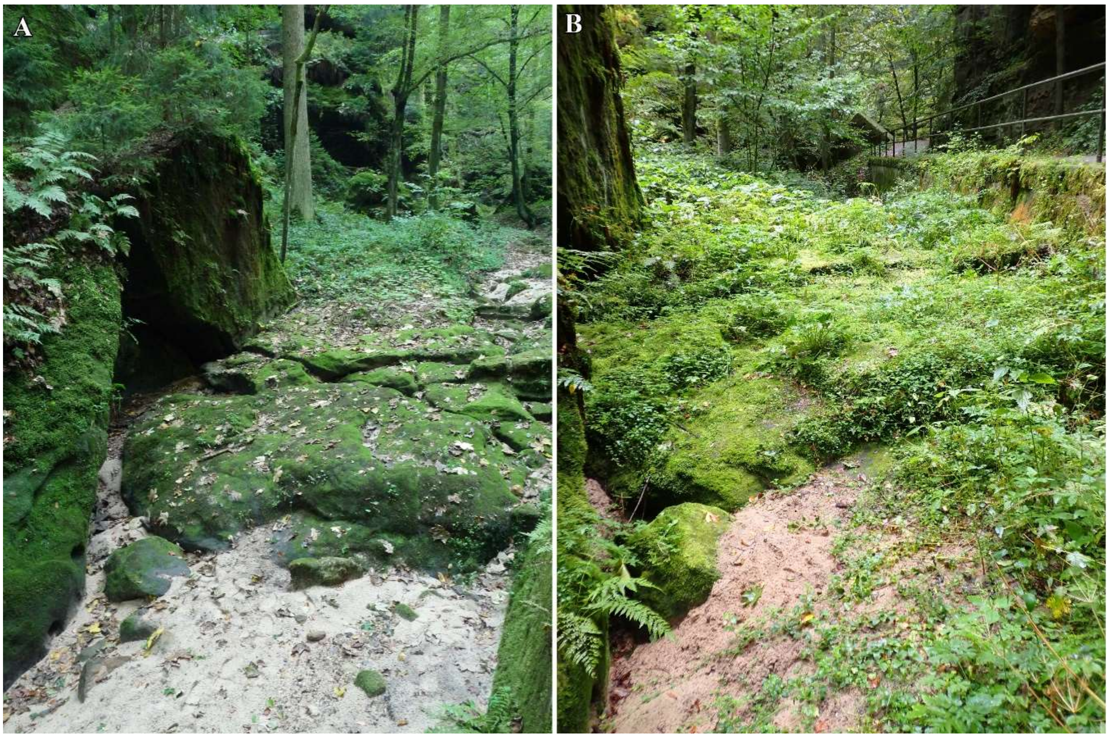

Figure 11. Comparison of the site Wehlener Grund. (**A**)—8 September 2016, (**B**)—14 September 2023. The site hosted one of the largest occurrences of *H. laxifolia* in the years 2014–2016. The species was present on numerous boulders in extensive dominant stands, some of which were over 1 m^2 in size. In 2023, *H. laxifolia* was found on only 11 boulders and with a total population size of 2.6 m^2. The cover of the herb layer has increased significantly, and there was a shift towards more competitive species in the bryophyte layer. Despite these negative trends, the site Wehlener Grund still harbours the largest populations in the Elbe Sandstone Mountains. The site is characterized by a higher proportion of deciduous trees and is therefore less affected by thinning.

The site Höllgrund (Figure 12B) was very severely affected by bark beetle infestation. Spruces died and have been completely cleared. The creek is now fully exposed to sun and very strongly overgrown with herbs. In 2016, *H. laxifolia* was found on a total of 19 boulders and covered a total area of 61.9 dm^2. In 2023, the species was absent.

The situation in the nearby site Nasser Grund area was similar, but less severe. The loss of the spruces reduced the cover of the tree layer but there is still a continuous stand of trees. In 2016, *H. laxifolia* was found on 24 boulders covering a total area of 4.86 m^2; in 2023 it was only observed on five boulders with a total area of 0.54 m^2, resulting in a decrease of 88.9%. The main reason for the decline is the competition with other bryophytes, particularly *Thamnobryum alopecurum*, *Brachythecium rivulare,* and *Dichodontium pellucidum*.

The reasons for the species' decline in the Elbe Sandstone Mountains are complex (Figure 12) but deforestation due to heavy bark beetle infestation has had a severe impact. *Picea abies*, which had dominated the tree layer in large parts of the forests, largely disappeared. In the German part of the study area, the dead trees were felled if close to hiking trails, so that creeks are now fully exposed to the sun. This applies, for example, to the site Höllgrund and parts of the site Amselgrund (Figure 12A,B). In the Czech part, the standing dead spruce were usually not removed and thus provide at least a little shade. Therefore, light-exposed areas experienced an increase in cover of the shrub and herb layer (e.g., strong spread of *Rubus* spp., *Urtica dioica*, and others) and of other, more competitive bryophytes (Figure 12D).

Figure 12. Reasons for the decline of *Hygrobiella laxifolia* in the Elbe Sandstone Mountains. (**A**)—deforestation, Amselgrund, 23 November 2023, (**B**)—deforestation, Höllgrund, 30 August 2023, (**C**)—forest fire, Koutský potok, 9 November 2023, (**D**)—death of Norwegian spruce and spread of *Rubus* spp., *Urtica dioica,* and other plants and bryophytes, Janovský potok, 9 November 2023, (**E**)—paving of the creek bed, Wehlgrund, 9 December 2016, (**F**)—competition and spread of other bryophyte species, in this case *Scapania undulata*, Waltersdorfer Mühle, 11 September 2023.

The site Koutský potok, already severely impacted by dying of spruces, was directly affected by the forest fire in 2022 (Figure 12C). In 2023, only nutrient indicators were found on the boulders in the creek at the burnt site.

Forest fires, deforestation, and the death of spruce due to bark beetle infestation led to a loss or a strong thinning of the tree layer and thus to an increase in the exposure of the areas close to the ground and a change in the microclimate typical of the ravines. The result is an increase in the degree of cover of the shrub and herb layer and a favouring and strong spread of certain species of the bryophyte layer (especially *Scapania undulata*, *Dichodontium pellucidum*, *Thamnobryum alopecurum*, *Brachythecium rivulare*), which displace *Hygrobiella laxifolia*.

4. Discussion

During the re-mapping of occurrences in 2023, a significant decline in the populations of *H. laxifolia* in the Elbe Sandstone Mountains was observed (Table 3, Figure 6). This severe decline within less than 10 years (comparative period 2014–2018) is very surprising. The species' decline in the region correlates with the mass proliferation of the European spruce bark beetle (*Ips typographus*) observed since 2017 leading to a strong thinning of the forests. At numerous sites, the forests have a much sparser tree layer or none at all and *H. laxifolia* is outcompeted by more light-tolerant vascular plants and bryophytes. Since such bark beetle infestations as well as large-scale forest fires as in 2022, which led to a complete loss of the forest in large parts, have not been observed in the region in previous times, and since both events are favoured by climate change, we argue that climate change has a strong amplification effect and is thus the main cause of the decline of *H. laxifolia* in the Elbe Sandstone Mountains. *Hygrobiella laxifolia* is a glacial relict in the area with very specific site requirements. The current sites in the region represent the last and only possible colonisation areas, and the species is unable to switch to new sites. The deeply carved gorges of the Elbe Sandstone Mountains provided the co-called "cellar climate" enabling montane and subarctic-subalpine species to survive. This "cellar climate" is caused by the relief, but also by the shading provided by the forest cover. The thinning of the forest, as caused by the heavy bark beetle infestation, leads to more sunlight reaching the gorges and thus to a mitigation of this "cellar effect."

The Ellenberg L (light)-value of 7 in *H. laxifolia* for Central Europe [14] may apply rather to populations in the subalpine and alpine altitudinal zones, where the species grows under cooler climatic conditions in unshaded areas near and above the tree line. Marstaller [44] gave cover values of 70–95% of the tree layer with an average value of 87% for the relevés with *H. laxifolia* in the Elbe Sandstone Mountains in the years 1985–1986. The species can generally cope with a higher light intensity, but not in this area, as the low shade effect of the trees disturbs the cool microclimate in the ravines. If *H. laxifolia* was excluded from the L-value calculations and only accompanying bryophytes were taken into account—which are more common bryophytes in Central Europe, for which the indicator values are more reliable—significantly lower values (4.41–4.42) were obtained, i.e., between shade and semi-shade plants. As *H. laxifolia* usually dominated the vegetation records, i.e., had a high cover value, the quantitative calculation resulted in significantly higher mean L values (6.04) than if the species is excluded (4.42) and thus an even greater deviation from the real site conditions in the region. The L-value of *Hygrobiella laxifolia* for Central Europe should be changed based on our investigations from 7 to 5, the R-value from 2 to 5.

For predictions on bryophyte distribution in the future taking the influence of climate change into account, it is important to consider the dispersal limitations of the individual species [2,45]. Taking the dispersal ability into account, the forecast for the *H. laxifolia* occurrences in the Elbe Sandstone Mountains is very unfavourable. No perianths have been observed anywhere in the area in recent years and male plants with antheridia have only been observed once. The possibility of generative reproduction is therefore very limited. In other regions where the species has been observed with perianths, sporophytes have been rarely reported [25,38]. The dispersal via spores generally appears to be very limited and in the Elbe Sandstone Mountains it is thus restricted to vegetative propagation, i.e., dropping of flagellar branches. However, this does not allow long-distance dispersal, but at most dispersal through water within the same valley. Thus, genetic exchange with other areas is nearly impossible because the closest occurrences are in a distance over 400 km.

Zanatta et al. [2] predicted a loss of arctic-alpine bryophytes in low mountain ranges and most areas of the high mountains of Central Europe by 2050. For the occurrences of *H. laxifolia* in the Elbe Sandstone Mountains, the decline and loss appear to be even faster due to a combination of many unfavourable events (bark beetle infestation, forest fire). Within just a few years, a dramatic change unexpected in its extent was observed. However, a comparison of relevés from 1985–1986 and 2014–2018 indicated that the species' habitats in the area must have already changed unnoticed in the previous years.

In the Red List of Germany [46], *H. laxifolia* is categorised as R (extremely rare, long-term and short-term population trend constant, no risk factors). The species was still classified in this category in the older version of Saxony's Red List [47]. In the new Red List of Saxony published in 2023 [48], *H. laxifolia* has already been reclassified. It is now assigned to category 1 (CR = critically endangered) because of an actual deterioration and, as a risk factor, low competitive ability compared to other groups. Since *H. laxifolia* only occurs in the Elbe Sandstone Mountains in Germany, the Red List classification in Saxony is also relevant at federal level. When the Red List of Germany is revised, its status should be adjusted accordingly in critically endangered (CR).

In the Red List of the Czech Republic published in 2003 [49], the species was categorised as CR because of its small population size. In a new version of the Red List from 2012 [50], the species was, however, downgraded to vulnerable (VU). In a new revision, it should also be reclassified as CR.

Due to the species' severe endangerment and severe decline, a long-term monitoring of the remaining populations should be urgently established. This is especially important because the populations in the Elbe Sandstone Mountains are the only populations in Germany and the Czech Republic.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d16050258/s1, Table S1: Relevés of the sites with *Hygrobiella laxifolia* in the Elbe Sandstone Mountains.

Author Contributions: Conceptualization, F.M. and I.M.; methodology, F.M., I.M. and C.M.R.; field research, F.M. and I.M.; formal analysis, F.M., I.M. and C.M.R.; investigation, F.M., I.M. and C.M.R.; writing—original draft preparation, F.M., I.M. and C.M.R.; writing—review and editing, F.M., I.M. and C.M.R.; visualization, F.M., I.M. and C.M.R. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The data presented in the study are included in the article and supplementary material.

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Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A

Voucher information and GenBank accession numbers of the specimens used in the molecular study, ordered *trn*L-*trn*F intergenic spacer, *matK*. Newly obtained sequences are printed in bold.

Hygrobiella squamosa Bakalin & Vilnet: Russia, Kuril I., Iturup Isl. 2, V. Bakalin K-12-8a-07 (VLA) KF008585, –. Russia, Commander Islands, Medny Isl. 2, V. Bakalin K-67-2-04 and 106771 (KPABG), KF008578, KF008607. Russia, Kuril I., Paramushir I. 3, V. Bakalin K-106-7-04 and 107584 (KPABG) KF008580, KF008606. Russia, Kuril I., Paramushir I. 4, V. Bakalin K-114-5a-04 and 107611 (KPABG) KF008579, KF008608. Russia, Kuril I., Paramushir I. 1, V. Bakalin K-91-1-04 and 107460 (KPABG) KF008577, KF008604. Russia, Eastern Kamchatka, V. Bakalin K-52-3b-03 and 105127 (KPABG) KF008576, KF008603. Russia, Central Kamchatka, V. Bakalin KK 50-24a-02-VB and 104117 (KPABG) KF008575, KF008602. Russia, Kuril I., Paramushir I. 2, V. Bakalin K-91-3-04 and 107461 (KPABG) KF008574, KF008605.

Hygrobiella intermedia Bakalin & Vilnet: Russia, Kuril I., Shikotan, V. Bakalin K-48-13-07 (VLA) KF008582, –.. Russia, Kuril I., Iturup I. 2, V. Bakalin K-71-8-05 (VLA) KF008583, --. Russia, Central Kamchatka, V. Bakalin 90-8-01-VB and 103960 (KPABG) KF008581, KF008609.

Hygrobiella laxifolia (Hook.) Spruce: Russia, Murmansk Prov., Umbozero Lake 2, N. Konstantinova K 201-7-04 and 12766 (KPABG) KF008562, KF008587. Russia, Murmansk Prov., Khibiny Mts. 4, N. Konstantinova 182-1-02 and 9487 (KPABG) KF008563, KF008595. Russia, Murmansk Prov., Monche-tundra Mts., E. Borovichev BE 44-1-09 and 19152 (KPABG) KF008564, KF008588. Russia, Murmansk Prov., Khibiny Mts. 6, N. Konstantinova K 110-1-11 and 20180 (KPABG) KF008565, KF008596. Russia, Murmansk Prov., Khibiny Mts. 1, N. Konstantinova 5187 (KPABG) KF008566, --. A47o = Russia, Murmansk Prov., Rybachy Peninsula, N. Konstantinova 5171 (KPABG) KF008567, KF008599. Russia, Murmansk Prov., Sredny Peninsula, N. Konstantinova 115/1 (KPABG) KF008568, KF008591. Russia, Murmansk Prov., Lavna-tundra Mts., N. Konstantinova 152-7-87 and 6103 (KPABG) KF008569, KF008601. Russia, Commander Islands, Bering Isl. 3, V. Bakalin K-16-4-02-VB and 103272 (KPABG) KF008570, KF008592. Russia, Commander Islands, Bering Isl. 1, V. Bakalin K-6-6-02-VB and 103449 (KPABG) KF008571, KF008594. USA, N. Konstantinova A108/1-95 (KPABG) 008572, KF008600. Russia, Commander Islands, Bering Isl. 2, V. Bakalin K-11-9-02-VB and 103487 (KPABG) KF008573, KF008593. Germany, Elbe Sandstone Mountains, F. Müller DR 047345 **PP291467, PP291468**.

Cephaloziella konstantinovae Mamontov & Vilnet: Russia, Republic of Buryatia, O. Afonina A4006 (KPABG) KF471664, KF471670.

Cephaloziella polystratosa (R.M.Schust. & Damsh.) Konstant.: Russia, Republic of Buryatia, O. Afonina A1810 (KPABG) JX630046, KF471671.

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