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# Phytogeography of the sandstone areas in the Bohemian Cretaceous Basin (Czech Republic/Germany/Poland)

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## Introduction

Most sandstone regions in the Bohemian Cretaceous Basin have a landscape structure with core zones formed by an acidic pseudokarst (covering tens of square kilometres and a high percentage of the total area of the particular sandstone region), surrounded by forests, plateaus and locally occurring wetlands and calcareous sandstone outcrops. Other ecosystems (e.g., settlements, fields, alluvia, volcanic hills) are present mostly as patches or linear corridors. In contrast to most cultural landscapes, the species and community diversity in sandstone regions is significantly lower in the prevailing ecosystem types (on pseudokarst) than in locally occurring habitats. Therefore, a higher biodiversity in sandstone regions (formed of prevailing quartzose sandstones) is not related to landscape matrix but to patches (calcareous sandstones, volcanic hills, wetlands, etc.) and corridors (water streams). This is primarily due to the nutrient-poor substratum of quartzose sandstones. For this reason, the vegetation of sandstone regions, formed mainly by quartzose sandstones (e.g., Elbe Sandstones), varies significantly from regions with a higher proportion of other substrata (e.g., Polomené hory Hills) or those with large areas of open cultural landscape (e.g., Bohemian Paradise).

Despite sharing many similar features of flora and vegetation, the biodiversity of a particular sandstone region, in the Bohemian Cretaceous Basin, varies significantly due to different combinations of basic factors. The substratum (quartzose/calcareous sandstones), relief, altitude, microclimate and oceanity/continentality seem to be crucial elements that determine the final features of the natural vegetation in a particular sandstone landscape (Sádlo, Härtel and Marková, this volume). However, in cultural parts of these landscapes the importance of these primary factors can be substantially overlaid by human influence. Floristic differences among sandstone regions, based on different representations of phytogeographic species groups, are presented in Table 1.

In the following overview, the natural conditions of the individual sandstone regions of the Bohemian Cretaceous Basin are characterized with a particular focus on the flora and vegetation. For this survey, regions are geographically defined using the phytogeographic division of the Czech Republic (Skalický 1988). Where the sandstone regions extend into Poland and Germany these areas have also been included. The location of these sandstone regions can be seen in Figure 1.

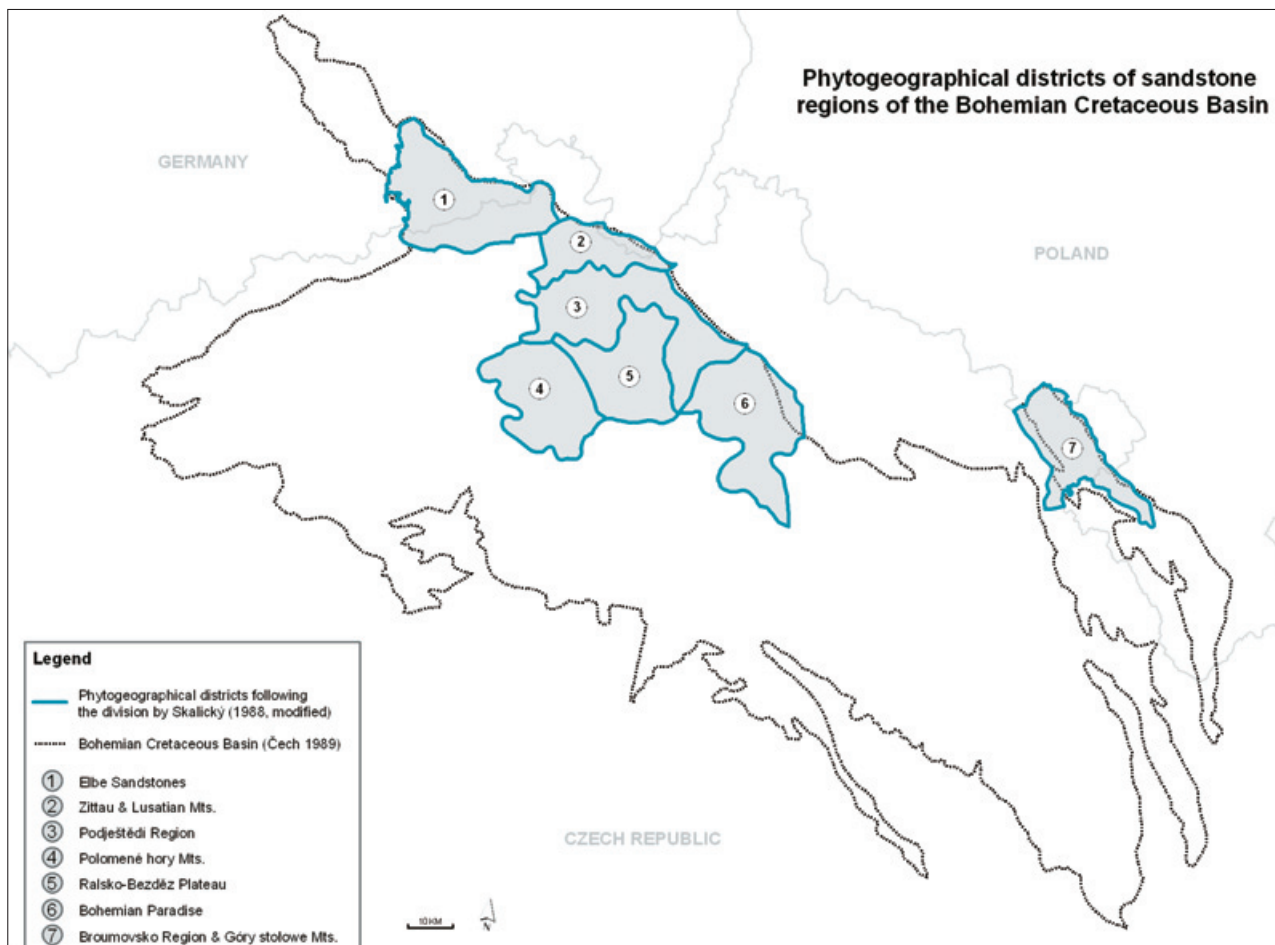
In the description of flora and vegetation, the volcanic patches were intentionally omitted because they are an independent source of biodiversity that barely interacts with the surrounding landscape. The phytogeographic characteristics used (sub-oceanic, sub-montane species, etc.) should be understood in the Central European context, rather than absolutely. Plant communities are summarized in the appendix.

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**Figure 1.** Main sandstone regions of the Bohemian Cretaceous Basin following the phytogeographical divisions of the Czech Republic (following Skalický 1988, modified)

As in the previous paper (Sádlo, Härtel and Marková, this volume), it has not been possible to include definitive localities, collectors and literature citations. Nor has it been possible to distinguish between historic and recent records. More information about flora and phytogeography of sandstone areas in the Bohemian Cretaceous Basin can be found, e.g. in Förster (1968), Härtel (2005), Härtel and Marková (2005), Kubát et al. (eds.) (1999), Kučera and Špryňar (1996), Militzer (1960), Müller (2003), Petříček (1987), Riebe et al. (1999), Slavík (1977), Sýkora (1975), Sýkora and Hadač (1984), Świerkosz (this volume), Vogel et al. (1993), Zittová-Kurková (1984).

### Elbe Sandstones

This region is defined by one main continuous sandstone cluster. Denuded pre-Cretaceous rock outcrops occur

locally along the Elbe River. The core part of Elbe Sandstones, formed by pseudokarst and covering approximately one-third of the region, is a forested and almost completely uninhabited sandstone landscape, protected as the Saxon and Bohemian Switzerland National Parks (Figure 2). In addition to the rock cities, another unique component of the landscape is the massive Elbe River canyon with its high rock walls. In the past, acidophilous beech forests (*Luzulo-Fagetum*) were dominant in the Elbe Sandstones. Today, these forests have been largely replaced by planted Norway spruce forests. Acidophilous pine forests (*Dicrano-Pinetum*) are abundant on cliff edges. Pine-oak forests (*Vaccinio vitis-idaeae-Quercetum*) occur fragmentarily on plateaus and waterlogged spruce forests (*Mastigobryo-Piceetum*) in deep and narrow gorges. When compared with other sandstone areas, this region is characterized by dominant quartzose sandstones and other sediments are



**Figure 2.** The core of the Elbe Sandstones with large rocky and forest areas which is protected as the Saxon-Bohemian Switzerland National Park (Photo by Zdeněk Patzelt)

rare. Among sandstone regions in the Bohemian Cretaceous Basin, Elbe Sandstones have the widest altitudinal range (110–726 m a.s.l.) (Table 2). The ecological effect of this large elevation difference is, however, modified by a strong climatic inversion in the deep valleys and gorges where (sub)montane vascular plants such as *Dentaria enneaphyllos*, *Festuca altissima* (Elbe River canyon), *Viola biflora*, *Circaea alpina*, *Streptopus amplexifolius*, *Lycopodium annotinum* and bryophytes *Dicranum majus*, *Geocalyx graveolens*, *Lophozia grandiretis*, *Harpanthus scutatus*, *Tetradontium*



**Figure 3.** *Hypericum pulchrum* is a species with a sub-Atlantic distribution. Within the Bohemian Cretaceous Basin this species occurs in the Elbe Sandstones only (Photo by Petr Bauer)

*brownianum*, *Hygrobrella laxifolia*, and *Anastrophyllum michauxii* (deep gorges in the pseudokarst) grow. The three latter species are recently known only from Elbe Sandstones in the Czech Republic. The region's climate, which for the Czech Republic is considerably oceanic, significantly influences the species composition. Examples of (sub)-Atlantic species are the ferns *Trichomanes speciosum* (gametophytes), *Blechnum spicant*, *Hymenophyllum tunbrigense* (†), the angiosperms *Galium saxatile*, *Juncus acutiflorus*, *Hypericum humifusum*, *H. pulchrum* (Figure 3), *Luronium natans* and *Epilobium hypericifolium* (†) and the bryophytes *Fissidens rufulus* and *Plagiothecium undulatum*. Boreal to boreo-continental elements can also be found, for instance *Eriophorum vaginatum*, *Oxycoccus palustris*, *Ledum palustre* and *Empetrum nigrum*, the occurrence of the latter two species is mainly on cliff edges above the gorges with climatic inversions and is characteristic for this region.

The low species richness and the floristic uniformity of the large pseudokarst areas are striking. These can be attributed to the extent of the nutrient-poor quartzose sandstones and the effect of the Norway spruce plantations. The region's diversity is increased in the areas adjacent to České středohoří Mountains, on volcanic hills and in the Elbe River canyon with its mesoclimatic effect, where the above-mentioned montane species combine with the thermophilous species (*Picris hieracioides*, *Trifolium alpestre*, *Acer campestre*, *Stachys recta*, *Petrorhagia prolifera*, *Dactylis polygama*, *Thalictrum minus*), often, however,

limited to the pre-Cretaceous bedrock and/or the synanthropic biotopes.

### Lusatian/Zittau Mountains and the Podještědí Region

This area is relatively heterogeneous. The Lusatian/Zittau Mountains and the Podještědí Region share a landscape with only sparse forms of the sandstone pseudokarst and have been incorporated into one region. It includes the territory at the margins of the Bohemian Cretaceous Basin separating the Elbe Sandstones from the Ralsko-Bezděz Plateau. Quartzose sandstones predominate in this region. However, the typical sandstone landscape is strongly fragmented into minor and isolated units, and the majority of the area is formed of a diverse, hilly landscape, additionally divided by numerous volcanic elevations. Altitudinal range is between 300 m to 795 m a.s.l. in Lusatian/Zittau Mountains and from 242–600 m in the Podještědí Region; the higher elevations are formed mostly of volcanic hills. Sandstone rock cities are found on the Saxon side of the Zittau Mountains (Oybin, Jonsdorfer Felsenstadt). On the Czech side, mainly isolated canyons (Peklo near Česká Lípa) or rocky slopes of hills (near Kozly, between Cvikov and Zákupy) are present. The region's climate fluctuates from oceanic in the northwest to a continental influence in the southeast.

Acidophilous beech forests (*Luzulo-Fagetum*), which were usually converted to Norway spruce monocultures on sandstones, are typical vegetation for the region. At lower altitudes, species-poor types of oak-hornbeam forests (*Melampyro-Carpinetum abietetosum*) occur. Acidophilous pine forests (*Dicrano-Pinetum*) are locally present, waterlogged spruce forests (*Mastigobryo-Piceetum*) are present only in the canyons with climatic inversions. Richer forest communities (herb-rich beech forests and ravine forests) are concentrated on the Tertiary volcanic hills, not on the sandstones.

Species with a (sub)-Atlantic distribution are represented by *Hydrocotyle vulgaris*, *Arum maculatum*, *Ornithopus perpusillus*, *Chrysosplenium oppositifolium*, *Hypericum humifusum*, *Spergula morisonii*, *Teesdalia nudicaulis*, *Teucrium scorodonia*, *Juncus acutiflorus*, *Trichomanes speciosum* (gametophytes), *Blechnum spicant*, and in the past also by oceanic fern *Osmunda regalis*. Among the thermophilous species, mainly the less-demanding species of secondary open lands, occur such as *Campanula persicifolia*, *Agrimonia eupatoria*, *Rhamnus cathartica*, *Peucedanum oreoselinum*, etc. (Sub)-montane species including *Blechnum spicant*, *Lycopodium annotinum*, *Huperzia selago*, *Trientalis europaea*, *Circaea alpina*,

*Lonicera nigra*, and *Petasites albus* occur in deep valleys or at higher elevations on mainly volcanic hills.

Small wetlands, peat bogs and heaths (Brazilka, Noldenteich, Jedlovské rybníky Ponds) host *Drosera rotundifolia*, *Pedicularis sylvatica*, *Oxycoccus palustris* and the bryophytes *Sphagnum fallax*, *S. fimbriatum*, *S. palustre*, *Warnstorfia fluitans*, *W. exannulata*, *Caliergon cordifolium* etc. The rare occurrence of *Ledum palustre* in this region is restricted to the peat bogs and is not found on the cliffs. In the vicinity of Chřibská, *Carex davalliana*, *C. pulicaris*, *Epipactis palustris*, *Triglochin palustris*, *Dactylorhiza fuchsii*, *Eriophorum latifolium* etc. grow on marls.

The Českolipská kotlina Basin shares many species with the adjacent Ralsko-Bezděz Plateau.

### Polomené hory Hills

This region is formed by one extensive pseudokarst area based in the floodplains of two streams. The valley system is wedged into the surrounding flat landscape; the forested plateaus are strongly divided by gorges. Of the studied regions, this one has the highest occurrence of xerothermic vegetation due to the influence of its low altitude (165–614 m a.s.l.), the warm and dry climate (in the southern region precipitation amounts to 550 mm at 8.5 °C) and rich substrata (marlstones, calcareous sandstones, and loess) shared with the neighbouring regions (Polabí, Pojizeří). Simultaneously, the Polomené hory Hills, because of the climatic inversions, are also a “cold tongue“ that goes deep into the interior of the Bohemian Basin. Therefore, many species (e.g., with oceanic distribution) occur here at the border of their area of distribution.

Acidophilous beech forests (*Luzulo-Fagetum*) and pine-oak forests (*Vaccinio-Quercetum*) are a typical combination for the pseudokarst on quartzose sandstones. Of the thermophilous elements, the most abundant include mainly dry grasslands (*Bromion*); plant communities of the alliances *Prunion spinosae* and *Geranion sanguinei* are present as well. Among thermophilous species are *Linum flavum*, *Campanula bononiensis*, *Cirsium eriophorum*, *Sorbus aria*, *Thesium linophyllum*, *Melica transsilvanica*, *Cirsium acaule*, *Anthericum ramosum*, *Bupleurum falcatum*, *Aster linoxyris*, *Inula hirta*, *Iris aphylla*, *Pulsatilla pratensis*, *Scorzonera hispanica*, *Stipa capillata*, *Stipa pennata*, *Dictamnus albus*, *Vicia pisiformis*, *Anemone sylvestris*, *Prunus fruticosa* and *Cirsium acaule*. On the nutrient-rich substrata, forest communities of the alliances *Carpinion* and *Fagion* are present including the occurrence of *Sorbus torminalis*, *Hierochloë australis*, *Melica uniflora* and *Daphne mezereum*. Various (sub)-oceanic elements, such as *Chrysosplenium*

*oppositifolium*, *Teesdalia nudicaulis*, *Corynephorus canescens*, *Vulpia myuros*, *Armeria vulgaris*, *Spergula morisonii*, *Trichomanes speciosum* (gametophytes) and the bryophytes *Leucobryum juniperoideum*, *Mnium hornum*, *Pseudotaxiphyllum elegans* also occur in this region. In deep and narrow valleys characteristic species related to local bog spruce forests can be found, such as *Trientalis europaea*, *Calamagrostis villosa*, *Huperzia selago* and the bryophytes *Bazzania trilobata*, *Plagiothecium undulatum*, *Polytrichastrum alpinum* and *Plagiomnium medium*. Furthermore, in the gorges with climatic inversion, the liverworts *Anastrophyllum minutum*, *Tritomaria exsectiformis* and the rare liverwort *Bazzania tricrenata* can be found; among the mosses *Campylopus fragilis* and *Dicranodontium asperulum*.

Wetlands connected to the floodplains of streams are of a peat to fen nature at the upper stream, whereas the lower streams have the usual vegetation of the loamy floodplains of a cultural landscape. For instance, *Berula erecta*, *Carex paniculata*, *Eleocharis quinqueflora* and *Equisetum telmateia* grow here. Small sites of calciphilous pine forests occur locally, harbouring, for example, *Daphne cneorum* and *Carex ornithopoda*.

## Ralsko-Bezděz Plateau

The sandstone bedrock of this plateau creates one large continuous area. The altitude ranges from 240 to 696 m a.s.l., however, higher altitudes are reached almost exclusively by volcanic hills. This region differs from the other sandstone regions because of the predominance of flat or slightly undulating elevations while rock cities are low and limited in area. Large cliffs are missing from most of the area. The flat nature of the landscape is enriched by extensive valleys with wetlands (calcareous and mesotrophic fens, alder carrs, and reed beds). Calcareous sandstones are abundant and concentrated in the area between Hradčany and Hamr, where they form cliffs, and between Bělá pod Bezdězem and Mohelnice nad Jizerou, where they form mainly calcareous slopes without cliffs. A large part of the region has poor soils (partially due to decalcification).

Another specific feature of the region is the high occurrence of relicts in the flora and vegetation. Areas of several tens of square kilometres are of a pronounced relictual nature, including the predominant vegetation units of the region, which are the taiga-like forests of the association *Dicrano-Pinetum* which are bound to the arenaceous Podzols and are characterised by the dynamic alternation of pines and spruce. Their relict nature is indicated by a great abundance of *Trientalis europaea* and locally by *Pulsatilla vernalis*, *Daphne cneorum*, *Chimaphila umbellata*, *Moneses uniflora*,



**Figure 4.** *Gypsophila fastigiata* is a continental species growing on calcareous sandstones on the Ralsko-Bezděz Plateau (Photo by Handrij Härtel)

*Carex ericetorum*, *Diphasiastrum complanatum*, *Arctostaphylos uva-ursi* and *Equisetum variegatum*. The second significant relict biotope is the pine forest on calcareous sandstones (*Peucedano-Pinetum*) and the related rock vegetation. The relict nature is ascribed to species such as *Sesleria caerulea*, *Biscutella laevigata*, *Minuartia caespitosa*, *M. setacea*, *Aster amellus*, *Scabiosa canescens*, *Festuca pallens*, *Astragalus arenarius*, *Anemone sylvestris*, *Scabiosa columbaria*, *Gentiana cruciata*, *Carex pediformis* subsp. *macroura*, *Pulsatilla pratensis*, *P. patens*, *Gypsophila fastigiata* (Figure 4), *Calamagrostis varia*. The third type of relict biotope are the peat bogs (with *Ledum palustre*, *Andromeda polifolia*, *Oxycoccus palustris*, *Vaccinium uliginosum* and the bryophytes *Sphagnum papillosum*, *S. teres*, *Polytrichum strictum*), alder carrs (with *Ligularia sibirica*, *Calla palustris*, *Cicuta virosa* and *Dryopteris cristata*) and fens (with *Liparis loeselii*, *Tofieldia calyculata* and the bryophytes *Hamatocaulis vernicosus*, *Scorpidium scorpioides*, *Calliergon giganteum*, *Tomenthypnum nitens*, *Brachythecium mildeanum*, *Hypnum pratense*, *Plagiomnium ellipticum*, *Fissidens adianthoides*, and with endemic taxa *Pinguicula vulgaris* subsp. *bohemica* and *Dactylorhiza bohemica*).

(Sub)-oceanic species are frequent in this region. They are associated mainly with wetlands (such as *Hydrocotyle vulgaris*, *Lotus uliginosus*, *Chrysosplenium oppositifolium*, *Juncus acutiflorus*, *Rhynchospora alba*, *Littorella uniflora*, *Lycopodiella inundata*), with sands (such as *Hypericum humifusum*, *Spergula morisonii*, *Teesdalia nudicaulis*, *Arnoseris minima*, *Armeria vulgaris*, *Aira praecox*, *Corynephorus canescens*, *Ornithopus perpusillus*), and seldom with sandstone rocks (gametophytes of the fern

*Trichomanes speciosum*). In forest communities, there occur many common sub-oceanic mosses, such as *Campylopus flexuosus*, *Leucobryum glaucum*, *Mnium hornum*, *Pseudotaxiphyllum elegans* and *Rhizomnium punctatum*. The sub-oceanic-montane liverworts *Mylia taylorii*, *Odontoschisma denudatum* and the moss *Schistostega pennata* are related to rock biotopes.

Boreo-montane elements include *Circaea alpina*, *Lastrea limbosperma*, *Huperzia selago* and *Lycopodium annotinum*, and the bryophytes *Dicranella cerviculata*, *Sphagnum quinquefarium*, *Anastrophyllum minutum*. The sub-Mediterranean elements include *Cirsium acaule*, *Bothriochloa ischaemum* and *Prunella grandiflora*.

The relict nature of the region is also reflected by the scarcity of the usual types of vegetation of historically younger origin. The rare occurrence of oak-hornbeam forests and beech forests with typical species such as *Carpinus betulus*, *Fraxinus excelsior*, *Acer* sp. div., *Stellaria holostea* and *Galium odoratum* is also striking. These are found mainly close to settlements, indicating their secondary, anthropogenic origin in this region.

## The Bohemian Paradise

This region with an elevation range of 289–744 m a.s.l. is characterized by a fragmentation of the sandstone landscape into several isolated clusters. The sandstone rocks form very striking elevations that sharply contrast with lower parts of the cultural landscape found on softer and nutrient-richer sediments. There are cuestas and large tablelands with pseudokarst (for example the Prachovské skály Cliffs, Klokočské skály Cliffs, Hrubá skála Rock City, etc.) with acidophilous vegetation (Figure 5) (especially *Luzulo-Fagetum*, *Dicrano-Pinetum* and *Betulo carpaticeae-Pinetum*).

In some places there are developed valleys with flat bottoms where peat bogs, fens, fen meadows and ponds are found. These host species such as *Eriophorum gracile*, *Drosera rotundifolia*, *Epipactis palustris*, *Liparis loeselii*, *Iris sibirica*, *Carex davalliana*, *C. lasiocarpa*, *C. pulicaris*, *Parnassia palustris* and the moss *Hamatocaulis vernicosus*, but the typical raised bog species such as *Oxycoccus palustris* are missing. Springs with the abundant occurrence of *Equisetum telmateia* are indicative of areas where the sandstone meets the lower-lying marlstone layers.

Of the forest communities in the surrounding landscape, oak-hornbeam forests (*Melampyro-Carpinetum*) can often be found as well as thermophilous species such as *Cirsium acaule*, *Lathyrus niger*, *Achillea collina* and *Artemisia campestris*. At the margin of the region there is the deep valley of the Jizera River close to Malá Skála (with sandstones

and in other places with predominant marlstones) and a wetland basin near Sedmihorky with a fossil lake.

Among the sub-Atlantic species, the following occur in the Bohemian Paradise: *Hydrocotyle vulgaris*, *Juncus bulbosus*, *Corynephorus canescens*, *Hypericum humifusum*, *Isolepis setacea*, *Spergula morisonii*, *Teesdalia nudicaulis*, *Arnoseris minima*, *Euphrasia micrantha*, *Trichomanes speciosum* (gametophytes), *Lycopodiella inundata* and the bryophyte *Plagiothecium undulatum*, among common sub-oceanic bryophytes are *Leucobryum glaucum*, *L. juniperoideum*, *Mnium hornum*, *Pseudotaxiphyllum elegans* and *Rhizomnium punctatum*. The (sub)-continental species, found mainly on the marlstones and on the volcanic rocks, include *Stipa pennata*, *Allium senescens* subsp. *montanum* and *Carex pediformis* subsp. *rhizodes*.

*Streptopus amplexifolius*, *Thalictrum aquilegifolium*, *Circaea alpina*, *Trientalis europaea*, *Huperzia selago*, *Lycopodium annotinum* and *Blechnum spicant* belong to the demontane species associated with the inversion sites in the gorges. Characteristic bryophytes of the rock cities are the sub-oceanic-montane species *Mylia taylorii*, *Odontoschisma denudatum* and *Schistostega pennata*. The montane species *Rumex alpinus* and *Anthriscus nitida* are associated with the valley of the Jizera River coming to the Bohemian Paradise from mountainous areas. Boreo-montane species of bryophytes in the Bohemian Paradise are represented by mosses including *Sanionia uncinata*, *Rhytidiadelphus subpinnatus*, *Hygrohypnum ochraceum*, *Ptilium crista-castrensis* and the rare liverworts *Bazzania tricrenata*, *Tritomaria exsectiformis* and *Jungermannia leiantha*.

The occurrence of *Sesleria caerulea*, *Platanthera bifolia*, *Cephalanthera damasonium*, *Asplenium viride* and *Gymnocarpium robertianum* is connected mainly with the calcareous sandstones and marlstones.

## Broumovsko Region/Góry Stołowe Mountains

This sandstone region is comprised of several sandstone clusters surrounded by a lower agricultural landscape. For practical reasons, the phytogeographical districts of Adršpašsko-teplické skály Cliffs and the Middle Sudetes, including the Góry Stołowe Mountains on the Polish side, are united into one region – the Broumovsko/Góry Stołowe Mountains. Those parts of Middle Sudetes that lie outside the Bohemian Cretaceous Basin were not included.

This region forms the highest part of the Bohemian Cretaceous Basin with an altitudinal range of 355–919 m. The montane nature of the flora is most evident in the Adršpašsko-teplické skály Cliffs (due to the strong climatic

inversion) and in the upper parts of the Góry Stołowe Mountains (due to their higher altitude). In contrast to other sandstone regions of the Bohemian Cretaceous Basin, a higher proportion of spruce and a lower percentage of pine is significant.

The following European submontane, montane and sub-alpine species occur in this region: *Salix silesiaca*, *Rosa pendulina*, *Lonicera nigra*, *Homogyne alpina*, *Anthriscus nitida*, *Aconitum variegatum* (native localities only in the Czech part), *Melampyrum sylvaticum*, *Senecio hercynicus*, *Carduus*

*personata*, *Cicerbita alpina*, and only on the Polish side *Cardamine amara* subsp. *opizii*, *Rumex alpinus*, *Epilobium nutans* (†), *Ranunculus platanifolius* and *Pinus mugo*.

Among the species with a sub-Alpine-sub-Arctic distribution *Viola biflora* is worth mentioning (probably extinct on the Polish side), and of the species with a boreomontane distribution the following should be listed: *Huperzia selago*, *Lycopodium annotinum*, *Trientalis europaea*, *Veratrum album* subsp. *lobelianum*, *Athyrium distentifolium* (extinct on the Polish side), *Empetrum*



**Figure 5.** In the Bohemian Paradise, extensive rock cities are formed by quartzose sandstones and covered by acidophilous vegetation: Prachovské skály Rock City (Photo by Lukáš Bílek)

*nigrum*, *Streptopus amplexifolius*, *Vaccinium uliginosum* and *Ledum palustre*. Many montane bryophytes occur on the ADRŠPAŠSKO-TEPLICKÉ SKÁLY Cliffs, including the rare sub-Arctic-Alpine moss *Dicranum sendtneri*; the sub-Arctic-sub-Alpine mosses *Polytrichastrum alpinum*, *Anoetangium aestivum* and *Tetrodontium repandum*; the boreo-montane species *Dicranella subulata* and *Pohlia elongata*. Exclusive to the peat bogs (especially the Wielkie Torfowisko Batorowskie peat bog) are the following species: *Pinus rotundata* (= *P. x rhaetica* sensu auct. polon.), *Carex pauciflora*, *Andromeda polifolia*, *Drosera rotundifolia*, *Eriophorum vaginatum*, *Oxycoccus palustris*, and extinct species *Drosera anglica*, *D. intermedia*, *Eriophorum gracile*, *Carex chordorrhiza*, *C. limosa*, *Listera cordata*, *Trichophorum alpinum*, *Malaxis monophyllos*, *Scheuchzeria palustris*, *Salix myrtilloides* and *Lycopodiella inundata*.

Although the quartzose sandstones prevail in the region, locally there are marlstones and calcareous sandstones, especially on the Polish side with a calcareous and basiphilous flora, e.g. *Asplenium viride*, *Platanthera chlorantha*, *Gladiolus imbricatus*, *Carex davalliana*, *C. dioica*, *C. pulcaris*, *Epipactis palustris* (extinct on the Polish side), *Gymnadenia conopsea* subsp. *densiflora*, *Traunsteinera globosa*, *Phyteuma orbiculare* and *Saxifraga rosacea* subsp. *sponhemica* (the only locality in Poland).

The (sub)-Atlantic species are comparatively poorly represented in this region (they include *Juncus squarrosus*, *Galium saxatile*, *Blechnum spicant*, and *Equisetum telmateia*). The gametophytes of *Trichomanes speciosum* have not been recorded, as the local climate is probably too cold and dry. Thermophilous species are rare and inhabit mainly the lowest parts of region. They include *Lonicera xylosteum*, *Chamaecytisus supinus*, *Thlaspi perfoliatum*, *Trifolium ochroleucon* and *Allium vineale*.

The characteristic natural vegetation of the Broumovsko Region/Góry Stołowe Mountains are spruce-pine forests (*Betulo carpaticae-Pinetum*) (Figure 6). A very small area, only on the highest peaks, is occupied by montane spruce forests (*Calamagrostio villosae-Piceetum*, *Mastigobryo-Piceetum*, *Anastrepto-Piceetum*). Peat bogs (*Sphagnion medii*), acidophilous beech forests (*Luzulo-Fagion*), montane herb-rich forests (*Dentario enneaphylli-Fagetum*, *Festuco altissimae-Fagetum*), montane spruce-beech forests (*Calamagrostio villosae-Fagetum*) and ravine forests (*Tilio-Acerion*) are only locally dispersed as patches. The most interesting among the semi-natural communities are mountain meadows (*Polygono-Trisetion*) and species-rich pastures (*Nardion*).

In the regional descriptions above, only the larger sandstone regions have been included. There are other,

smaller, isolated sandstone areas in the Bohemian Cretaceous Basin, such as the Zderazské Cuestas and Budislavské skály Cliffs near Proseč in eastern Bohemia and the sandstone cliffs in Prague and its vicinity. Among these smaller sandstone areas, the isolated sandstone hills of the Northwest Sudetes Foreland near Złotoryja in Poland are of phytogeographic importance. Besides localities of *Cephalanthera damasonium*, *Moneses uniflora*, *Orthilia secunda*, *Equisetum telmateia* and *Matteuccia struthiopteris* in this region, there are some old kaolin quarries and peat bogs with *Lycopodiella inundata*, *Drosera rotundifolia* and *Ledum palustre*. However, this sandstone region is particularly important as the northeastern border of the European distribution of *Trichomanes speciosum* (gametophytes) (Krukowski and Świerkosz 2004, Świerkosz and Krukowski 2005).

## Appendix: Overview of important communities

This appendix should not be considered a comprehensive overview of plant communities found in sandstone landscapes as such a list would contain a high number of communities that are not specific to sandstones (for example, units of ruderal vegetation and meadow communities). Therefore, only the following plant communities were included: (a) covering large areas, at least in some sandstone regions (b) covering small areas but with a high number of occurrences in the typical biotopes of sandstone areas (c) rarer but differential, i.e., strongly linked with sandstone substratum. The list includes explanatory notes that characterises the units listed in this paper and in the previous paper (Sádlo, Härtel and Marková, this volume).

### Woody vegetation

#### Vaccinio-Piceetea

***Betulo carpaticae-Pinetum* Mikyška 1970.** Birch-pine forests with spruce are linked with a complicated rock relief (boulder screes, erosion cliff edges) of the quartzose sandstones. *Betula carpatica* is an uneasily identifiable form of *B. pubescens* found on the rocky areas (see Sádlo, Härtel and Marková, this volume).

**Comm. *Ledum palustre-Pinus sylvestris*.** Rocky peat moss-pine forests with *Ledum palustre* on the rock cliffs in micro-climatically wet gorges of quartzose sandstones.

***Dicrano-Pinetum* Preisling et Knapp ex Oberd. 1957.** Species-poor moss and lichen pine forests with a rich spatial





**Figure 6.** Spruce-pine forest (*Betulo carpaticae-Pinetum*) is a characteristic vegetation of the uppermost part of the Góry Stołowe Mountains (Photo by Handrij Härtel)

structure which are linked to rocky relief with shallow soils on the sunny edges of gorges on quartzose sandstones.

***Peucedano-Pinetum* Matuszkiewicz 1962.** Dry pine forests with a combination of acidophilous and thermophilous (often continental) species are typical for slopes, gorges and fringes of plateaus on calcareous sandstones. In the presented concept, *Peucedano-Pinetum* represents one broad association, while Kolbek (2004) divided this vegetation into several independent associations.

***Anastrepto-Piceetum* Stöcker 1967.** These wet spruce forests have a strongly developed, species-rich moss layer. On sandstones, they are linked with the bottoms of gorges with a combination of climatic inversion and higher altitudes.

***Mastigobryo-Piceetum* Br.-Bl. et Sissingh in Br.-Bl. et al. 1959.** Waterlogged spruce forests with *Sphagnum* sp. div. occur on waterlogged soils in gorges with climatic inversion.

***Calamagrostio villosae-Piceetum* Hartmann in Hartmann et Jahn 1967.** Montane spruce forest occurs in extreme climatic conditions on the top of the highest peak of the Góry Stołowe Mountains (Szczeliniec Wielki Mount), at an elevation of 900 to 919 m.

***Vaccinio uliginosi-Pinetum sylvestris* Kleist 1929.** Pine mire forests with *Vaccinium* sp. div. occur on peaty land on the fringes of peat bog depressions.

***Eriophoro vaginati-Pinetum sylvestris* Hueck 1951 em. Neuhäusl 1984.** An oligotrophic birch-pine carr. These pine mire forests represent an extreme type of forest at the physiological limit of tree growth. The vegetation colonizing sites with accumulated peat is low and sparse, with raised bogs species in the undergrowth.

**Comm. *Betula pubescens-Molinia caerulea*.** An insufficiently known complex of communities of sparse birch forests on a peat bog or fen substratum.

***Quercetea robori-petraeae***

***Vaccinio vitis-idaeae-Quercetum* Oberdorfer 1957.** These pine-oak forests vary in the proportion of both woody species. They have a species-poor undergrowth with a prevalence of shrub vegetation. They occur on plateaus and slopes, on deeper but nutrient-poor soils.

***Querco-Fagetea***

***Luzulo-Fagetum* Meusel 1937.** Acidophilous beech forest with *Luzula luzuloides* is one of the most frequent vegetation types on sandstone, however, they are common also on other nutrient-poor substrata from colline level to montane level.

***Calamagrostio villosae-Fagetum* Mikyška 1972.** This acidophilous spruce-beech forest is typical for the montane zone of the Bohemian Cretaceous Basin.

***Vaccinio vitis-idaeae-Abietetum* Oberdorfer 1957.** These acidophilous forests with a combination of spruce, pine and fir provide a habitat analogous to *Luzulo-Fagetum*. Their occurrence probably depends on management and is linked with marginal parts of the sandstone areas, often in contact with the agricultural landscape.

**Comm. *Deschampsia cespitosa-Carpinus betulus*.** Anthropogenic hornbeam forests with acidophilous undergrowth occur in higher areas at the margin of the hornbeam's area of distribution.

***Alnetea glutinosae***

***Carici acutiformis-Alnetum* Scamoni 1935.** An alder carr, with the dominance of *Carex acutiformis* in its undergrowth, and often with the occurrence of fen species. It occurs on substrata rich in carbonates.

***Carici elongatae-Alnetum* Schwickerath 1933.** An alder carr with the occurrence of acidophilous species and frequent marsh plants. It is linked with nutrient-poor substrata.

***Salicetum pentandro-cinereae* Passarge 1961.** Willow carrs with the dominance of *Salix cinerea* that are frequently in contact with reed beds.

***Rhamno-Prunetea***

***Junipero communis-Cotoneastretum integerrimae* Hofmann 1958.** Low rocky bushes of *Cotoneaster integerrimus* and *Sorbus aria* that occur rarely on calcareous sandstones.

***Calluno-Ulicetea***

***Cladonio-Callunetum* Krieger 1937.** A uniform vegetation of heather with lichens that occurs on the very dry rock edges of quartzose sandstones (Figure 7).

***Rhodococco-Vaccinietum myrtilli* Sýkora 1972.** A species-poor vegetation of blueberry with cowberry and the

participation of mosses and lichens is frequent on the edges of the sandstone cliffs with a moderately wet micro climate.

***Ledo-Vaccinietum vitis-idaeae* Sýkora et Hadač 1984.** A shrub vegetation with the occurrence of mire species which is linked with shady cliff edges with a wet micro climate.

***Convallario-Vaccinietum myrtilli* Sýkora 1972.** This vegetation with a combination of shrubs and some thermophilous herbs is typical for the tops of decalcified rocky edges of calcareous sandstones.

**Grassland and herbaceous vegetation of xeric and mesic habitats*****Polypodietea***

***Hypno-Polypodietum vulgare* Jurko et Peciar 1963.** A vegetation of *Polypodium vulgare* with a very low number of species of higher plants which often colonizes the shady rocky walls of quartzose sandstones.

***Cystopteridetum fragilis* Oberd. 1958 (*Asplenio viridis-Cystopteridetum* Oberd. (1936) 1949).** A community dominated by *Asplenium viride* and *Cystopteris fragilis*, typical for marlstones and calcareous sandstones in the Góry Stołowe Mountains.

**Comm. *Phegopteris connectilis-Gymnocarpium dryopteris*.** A community of these species is linked with the permanently wet crevices of shady rocks in gorges formed of quartzose sandstones.

**Comm. *Chrysosplenium oppositifolium-Conocephalum conicum*.** A vegetation dominated by the liverwort *Conocephalum conicum* and several species of vascular plants that are limited to rocky springs and dripping rocks. *C. conicum* indicates a moderate enrichment of the substratum with carbonates.

***Koelerio-Corynephoretea***

***Airetum praecocis* Krausch 1967.** Vegetation dominated by *Aira praecox* that occurs on ruderalized areas with a sandy substratum.

***Festuco glaucae-Sedetum acris* Firbas 1924.** A xerophilous community of an uncertain syntaxonomic position which is only known from several localities where it colonizes the sunny rocky edges of calcareous sandstones.

***Festuco-Brometea***

***Minuartio setaceae-Thymetum angustifolii* Preis in Klika 1939.** A low and sparse vegetation of xerophilous species that is limited to the vicinity of the village Hradčany in the Ralsko-Bezděz Plateau where it colonizes the rocky cliffs on calcareous sandstones.

**Figure 7.** *Cladonio-Callunetum* is a heather-lichen vegetation type on the very dry rock edges of quartzose sandstones (Photo by Handrij Härtel)



**Comm. *Sesleria caerulea-Carex digitata*.** Species-poor rocky grasslands of an uncertain syntaxonomic position which occur on the calcareous sandstones of the Ralsko-Bezděz Plateau.

***Scabioso ochroleucae-Brachypodietum pinnati* Klika 1953.** Grasslands on marl soils are typical for spongilitic marlstone substrata of an open landscape. Locally, they also occur in sandstone areas on marlstone interbeds and on calcareous sandstones.

#### ***Trifolio-Geranietea***

***Cynancho-Calamagrostietum arundinaceae* Sýkora 1972.** Tall-grass vegetation with species of thermophilous fringes is limited to the rocky edges of calcareous sandstones.

#### ***Galio-Urticetea***

**Comm. *Athyrium filix-femina - Chrysosplenium oppositifolium*.** A tall fern vegetation with frequent nitrophilous species that is linked with the wet bottoms and brook fringes in gorges with climatic inversion. The syntaxonomic position of the vegetation is not sufficiently clear.

#### ***Mulgedio-Aconitetea***

***Athyrietum alpestris* Hadač 1956 em. W. et A. Matuszkiewicz 1960.** A tall vegetation with the dominance of *Athyrium distentifolium* is frequent in the highest parts of the Sudetes Mountains. On sandstones, it is limited to the Broumovsko Region.

**Table 1.** Distribution of the various phytogeographic species groups in the individual sandstone regions of the Bohemian Cretaceous Basin  
 Legend: ◆ recent occurrence, † historic record, (◆), (†) the species occurs (occurred) in parts of the region that are formed by non-sandstone substrata (mostly on volcanic hills, etc.). In the table, only native occurrences have been taken into consideration

		Elbe Sandstones	Lusatian / Zittau Mts.	Polomené hory Mts.	Ralsko-Bezděz Plateau	Podještědí Region	Bohemian Paradise	Broumovsko region / Góry Stożowe Mts.
European montane species	<i>Rosa pendulina</i>	◆			◆	◆	◆	◆
	<i>Lonicera nigra</i>	◆	◆	◆		◆	◆	◆
	<i>Melampyrum sylvaticum</i>		◆				◆	◆
	<i>Cicerbita alpina</i>		◆					◆
	<i>Homogyne alpina</i>		◆					◆
	<i>Anthriscus nitida</i>						◆	◆
	<i>Rumex alpinus</i>						◆	◆
	<i>Pinus mugo</i>							◆
	<i>Ranunculus platanifolius</i>							◆
	<i>Salix silesiaca</i>							◆
	<i>Cardamine amara</i> subsp. <i>opizii</i>							◆
Boreo-montane, boreo-continental & subalpine-subarctic species	<i>Trientalis europaea</i>	◆	◆	◆	◆	◆	◆	◆
	<i>Huperzia selago</i>	◆	◆	◆	◆	†	◆	◆
	<i>Lycopodium annotinum</i>	◆	◆	◆	◆	†	◆	◆
	<i>Viola biflora</i>	◆	(†)					◆
	<i>Ledum palustre</i>	◆	◆		◆	◆		◆
	<i>Streptopus amplexifolius</i>	◆	(◆)				◆	◆
	<i>Rubus saxatilis</i>		(◆)	◆		◆		◆
	<i>Empetrum nigrum</i>	◆				†		◆
	<i>Andromeda polifolia</i>				◆			◆
	<i>Salix myrtilloides</i>							†
	<i>Scheuchzeria palustris</i>							†
	<i>Veratrum album</i> subsp. <i>lobelianum</i>							◆
	<i>Athyrium distentifolium</i>							◆
	<i>Carex pediformis</i> subsp. <i>macroura</i>				◆			
	<i>Ligularia sibirica</i>				◆			
Thermophilous continental & sub-Mediterranean species	<i>Anemone sylvestris</i>		◆	◆	◆	◆		
	<i>Scabiosa ochroleuca</i>	(◆)		◆	◆	◆	◆	◆
	<i>Berula erecta</i>	◆		◆	◆	◆	◆	
	<i>Verbascum phoeniceum</i>			◆	◆	◆		
	<i>Viola rupestris</i>			◆	◆	◆	◆	
	<i>Potentilla arenaria</i>			◆	◆			
	<i>Orphantha lutea</i>			◆				
	<i>Astragalus arenarius</i>				◆			
	<i>Equisetum variegatum</i>				◆			
	<i>Gypsophila fastigiata</i> subsp. <i>fastigiata</i>				◆			
	<i>Pulsatilla patens</i>				◆			
	<i>Oxytropis pilosa</i>				◆			
	<i>Chrysosplenium oppositifolium</i>	◆	◆	◆	◆	◆		
<i>Trichomanes speciosum</i>	◆	◆	◆	◆	◆	◆		
<i>Pedicularis sylvatica</i>	◆	◆		◆	◆	◆	◆	
<i>Galium saxatile</i>	◆	◆		◆		◆	◆	
<i>Teesdalia nudicaulis</i>	†	◆		◆	◆	◆		
<i>Hydrocotyle vulgaris</i>				◆	◆	◆		
<i>Hymenophyllum tunbridgense</i>	†							
<i>Hypericum pulchrum</i>	◆							
<i>Luronium natans</i>	◆							
<i>Rubus pyramidalis</i>	◆							
<i>Ornithopus perpusillus</i>					◆			
<i>Osmunda regalis</i>			(†)					

### *Epilobietea angustifolii*

***Epilobio-Digitalietum purpureae* Schwickerath (1935) 1944.** Clearings following acidophilous beech forests, in areas under oceanic influence, with the naturalized occurrence of *Digitalis purpurea*.

**Comm. *Pteridium aquilinum-Carex pilulifera*.** Extremely species-poor clearings with bracken following pine forests and pine-oak forests.

***Carici leporinae-Agrostietum tenuis* Hadač et Sýkora in Sýkora 1971, *Vaccinio myrtilli-Avenelletum flexuosae* (Schlüter 1966) Passarge 1984, *Avenello-Molinietum caeruleae* Passarge 1984.** A group of low and species-poor acidophilous grassland communities of forest roads, clearings and forest glades.

## Wetland vegetation

### *Potametea*

***Potametum alpini* Br.-Bl 1949, *Batrachio-Callitrichetum hamulatae* Oberdorfer 1957 em. Th. Müller 1977.** A group of communities of smaller and nutrient-poor watercourses with a smooth flow without any significant turbulence.

### *Phragmito-Magnocaricetea*

***Beruletum angustifoliae* Roll 1958.** This is a riparian to submerged vegetation, dominated by *Berula erecta* and *Veronica anagallis-aquatica*, which is typical for streams in the areas of sandstones and marlstones. The condition for occurrence of this vegetation it is a smooth, laminar flow of water and enrichment of substratum with carbonates. The bottom is usually muddy as well as sandy.

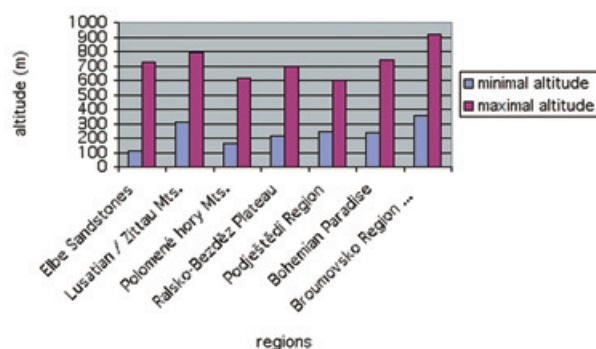
***Caricetum acutiformis* Egger 1935.** This vegetation of tall sedge beds with *Carex acutiformis* is typical for the valleys with a flat bottom and substrata moderately rich in bases. This vegetation is often formed on meadows that have not been managed for a long time.

***Caricetum paniculatae* Wangerin 1916.** A vegetation of tall sedge beds with *Carex paniculata* is typical for the valleys with a flat bottom on substrata moderately enriched with bases. This vegetation is often formed in the littoral zone of ponds.

**Comm. *Phragmites australis-Molinia caerulea*.** A tall-grass vegetation with a combination of reed and purple moor grass that represents, with regard to succession, a stable phase during the overgrowth of fens. It is developed on large areas, especially in the region of Doksy (Sádlo 1998).

### *Isoeto-Litorelletea*

***Sparganietum minimi* Schaaf 1925.** A community of small shallow pools in peat bogs.



**Table 2.** Altitudinal ranges of individual sandstone regions of the Bohemian Cretaceous Basin

### *Scheuchzerio-Caricetea fuscae*

***Valeriano dioicae-Caricetum davallianae* (Kuhn 1937) Moravec in Moravec et Rybníčková 1964.**

A sedge-moss community of calcareous fens.

***Drepanoclado revolventis-Caricetum lasiocarpae* (Koch 1926) Rybníček in Rybníček et al. 1984, *Scorpidio-Utricularietum* sensu Rybníček 1964, *Phragmito-Caricetum lasiocarpae* Rybníček in Rybníček et al. 1984, *Sphagno subsecundi-Rhynchosporietum albae* (Koch 1926) Rybníček in Rybníček et al. 1984.** A group of sedge-moss communities of mesotrophic peat bogs, bog meadows, transitional mires and peaty banks of water pools.

### *Oxycocco-Sphagneteta*

***Scirpo austriaci-Sphagnetum papilloso* Osvald 1925.** A community of mosses, shrubs and sedges belongs to the complex of oceanic peat bogs.

***Eriophoro vaginati-Sphagnetum recurvi* Hueck 1925.** An initial stage of raised bog vegetation of a sub-continental distribution that occurs in peaty depressions (the area of Doksy) as well as in the open parts of sandstone gorges (Broumovsko Region/Góry Stołowe Mountains, Elbe Sandstones).

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