Flora and phytogeography of the Czech Republic

Flóra a fytogeografie České republiky

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A review of the flora and phytogeography of the Czech Republic is given. The diversity of plants in this country reflects its geographic position in the centre of Europe, local natural conditions and the effect of intense human activity on the landscape. The Czech flora includes 148 families, 916 genera, 3557 species (plus 194 additional subspecies) and 609 hybrid vascular plants. Families richest in species are *Asteraceae* (662 species), *Rosaceae* (316), *Poaceae* (275), *Fabaceae* (170), *Brassicaceae* (148), *Cyperaceae* (127), *Lamiaceae* (112), *Caryophyllaceae* (108) and *Apiaceae* (100). Most of these species are native and 36.0% are alien. The spectrum of life-forms is dominated by hemicryptophytes (45.7%), followed by therophytes (22.3%), phanerophytes (14.4%), geophytes (9.3%), chamaephytes (5.1%) and hydrophytes (3.2%), while the percentage of epiphytes is negligible (only two species). Several species that occur in the Czech Republic are relicts from glacial and early postglacial periods. Examples of arctic, boreal, alpine, steppe and other sorts of relicts are listed. Because of the relatively small size of this country and the considerable climatic and vegetational changes caused by glaciations, which repeatedly eliminated the local flora, endemism is relatively low in the Czech Republic. All endemics are of Quaternary age (neoendemics). A revised list of endemic species and subspecies includes 74 taxa endemic to the Czech Republic and adjacent border regions, which is 2% of the total vascular plant diversity. Of these, 48 taxa are strictly Czech endemics (defined by the borders of the country), the distributions of the other 26 taxa extend slightly beyond the borders of this country (mostly by less than 1 km) in the summit areas of the Krkonoše/Karkonosze Mts and/or in the Králický Sněžník/Śnieżnik Kłódzki Mts. *Hieracium* and *Sorbus* are the genera with the greatest number of endemics (25 and 11 species and subspecies, respectively). Patterns in the distribution and occurrence of endemics in different types of habitat are discussed. The greatest concentration of endemics is in the Krkonoše Mts, where they occur mostly in subalpine habitats, such as natural grasslands above the timberline, summit rocks and rocky slopes, and various sites in glacial cirques including avalanche tracks. Other endemics of subalpine habitats occur in the Králický Sněžník Mts and Hrubý Jeseník Mts. Endemics at low altitudes mostly occur on rocky outcrops and in associated open thermophilous forests and grasslands, less frequently on open sandy areas, in fens and various types of forest. Maps of the distribution of endemics in the Czech Republic are presented. The majority of Czech endemics are rare and/or strongly endangered and included on the Red List of the Czech flora, and seven are extinct or missing. Changes in understanding of Czech endemics are reviewed and evolution of endemics discussed. The Czech Republic is situated at the intersection of several important European migration routes. The Czech flora is composed of almost all the floristic elements that occur in central Europe of which the Central-European geoelement is dominant. Other well represented geoelements include the Central-European-(sub-)alpine, Arctic-alpine, Boreal, Sub-boreal, Sub-Atlantic, Sub-Mediterranean, Pontic, Sub-pontic and South-Siberian. Examples of all geoelements are listed. The limits of the distributions of a number of widespread species are in the Czech Republic. These species are distinguished as boundary or outlying elements. Examples of species that in the Czech Republic are at the limits of their distributions, which range in different directions, are listed. Groups of species with similar ecogeographic features within the Czech Republic are distinguished as regional types of distribution (phytochorotypes). 15 basic phytochorotypes are listed, defined and illustrated using maps. Phytogeographical division of the Czech

Republic is described. Three principal phytogeographical regions are recognized within the country, which are based on the dominant flora and vegetation that reflects specific regional topography and climatic conditions. These regions are further subdivided into phytogeographical provinces, districts and subdistricts. All of these phytogeographical units (phytochoria) are listed and their position illustrated on a map.

K e y w o r d s: flora, phytogeography, Czech Republic, vascular plants, diversity, relicts, glaciation, migrations, refugium, endemics, evolution, speciation, floristic elements, geoelements, phytogeographical division

Introduction

The present-day flora of the Czech Republic reflects its geographic position, climate, vegetation history (particularly its late-glacial and postglacial development), diverse geology and topography, a rich mosaic of habitats and the effect of intense human activity on the landscape. The geographic position in the centre of the European continent means that its flora includes plants from the cold north and warm south as well as the oceanic west and continental east. The great changes in climate that occurred during the Pleistocene, with many cold (glacial) and warm (interglacial) periods, had major effects on the flora (Ložek 1973, 1988). The distributions of species repeatedly contracted and expanded, as well as shifted up and down mountains. During the glacial maxima the present-day Czech Republic was situated in the periglacial zone between the northern-European continental ice sheet and Alpine glaciers (Lang 1994).

The floristic composition of different regions is also substantially determined by their geology and topography. The Czech Republic is situated between two European mountain systems, the Alps and Carpathians. The geological bedrock is made up of two basic geological formations. The bedrock under the whole of Bohemia and the western and northwestern part of Moravia forms a part of the Bohemian Massif of Proterozoic and Palaeozoic rocks, whereas that under south-eastern and eastern Moravia is part of the young fold mountains of the West Carpathians, which are mostly covered by Tertiary flysch sediments (Chlupáč 2002).

Nowadays the Czech Republic is situated in the temperate zone of Europe with a seasonal climate that is not very hot in summer or cold in winter. The warmest month is July and it is also the month of the highest rainfall (Vesecký 1961). The countryside includes lowland plains, highlands and high mountains (Fig. 1). The altitude ranges from 115 m (the valley of the Labe river on the German border) to 1602 m (top of Mt Sněžka), with an average altitude of 430 m. The country is covered by a heterogeneous mosaic of cultural landscape with arable fields, deciduous, mixed and coniferous forests, meadows and human settlements. The dominant type of natural vegetation is forest. Natural treeless vegetation includes alpine and subalpine grasslands, steep rocky slopes, steppe, peat bogs and natural water bodies.

This paper provides a basic overview of the Czech flora, diversity of species and other taxa, glacial and postglacial relicts, endemic species and subspecies, most important geoelements and regional phytochorotypes and the concept of phytogeographical division. A parallel review of the vegetation of the Czech Republic is given in this issue by Chytrý (2012), and the diversity of Czech bryophytes and lichens is described by Kučera et al. (2012) and Liška (2012), respectively.

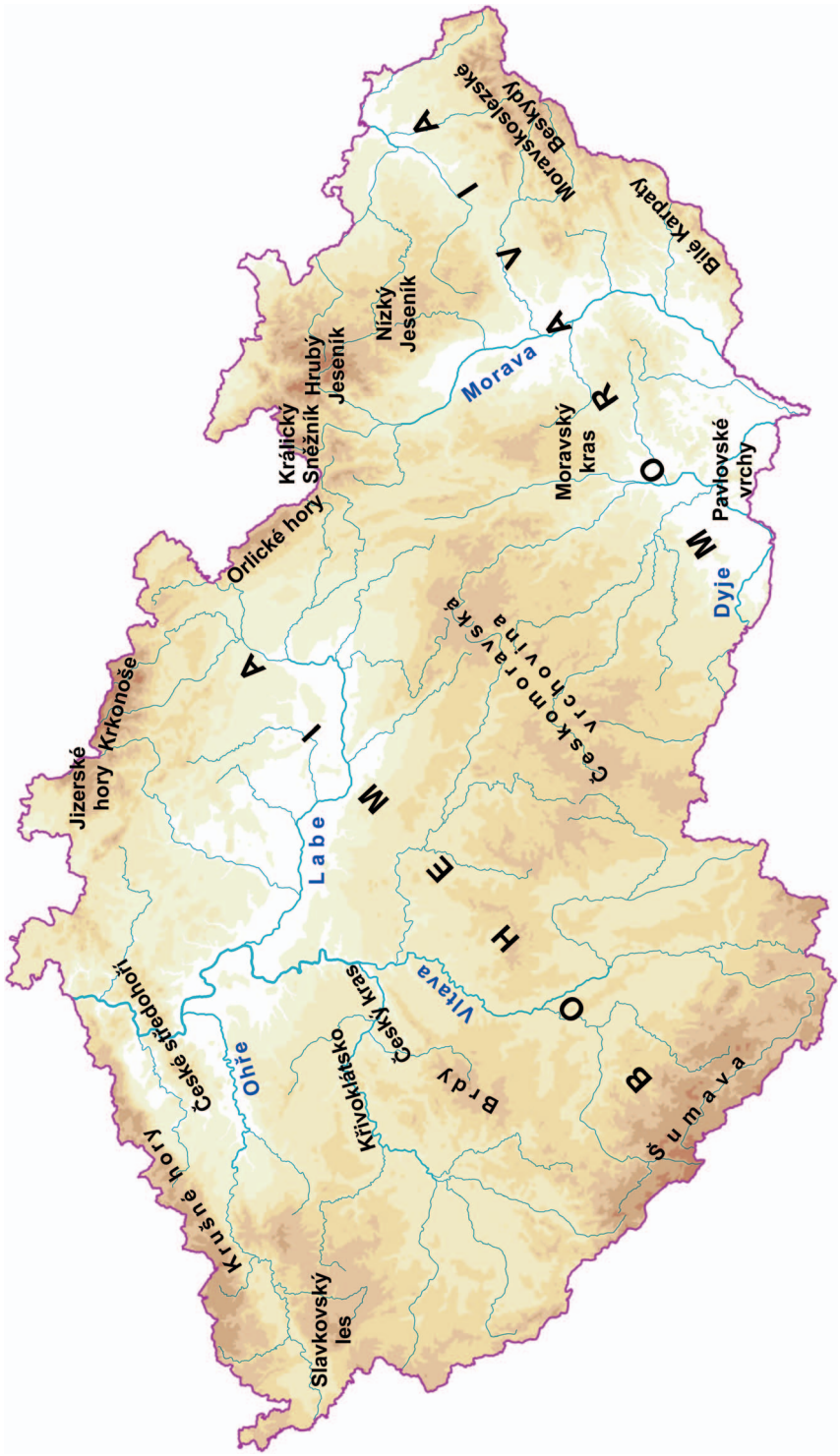


Fig. 1. – Topographic map of the Czech Republic.

Nomenclature mostly follows Danihelka et al. (2012). For taxa that are not listed in that paper, it follows Flora Europaea (Tutin et al. 1964–1980) or the literature cited.

Current treatments of the Czech flora and distribution atlases

Floristic research relevant to the area of the present-day Czech Republic dates back to the second half of the 18th century (Skalický et al. 1988, Pyšek et al. 2002, Kirschner et al. 2007, Krahulec 2012). The first attempt to produce a flora for this area was that of Schmidt (1793–1794), which, however, was not completed due to the premature death of the author. Several other botanists at that time wrote floras but the manuscripts remained, for various reasons, unpublished or incomplete. The notable flora by Pohl (1809, 1814) is an example of an incomplete treatment. The first complete Czech flora, which included almost 1500 species, was published by the Presl brothers (Presl & Presl 1819). Since then, a great number of floras covering various regions have appeared. The most notable milestones of the late 19th century were Prodromus of the Bohemian flora by Čelakovský (1867–1881) and two floras covering Moravia and adjacent Silesia by Oborny (1883–1886) and Formánek (1887–1897). The most influential floras of the 20th century for this area were written by Polívka (1900–1904), Polívka et al. (1928) and botanists led by Dostál (Dostál et al. 1948–1950, Dostál 1954, 1958). For details of the history of the floristic and phytogeographical exploration of the Czech Republic see Skalický et al. (1988) and Krahulec (2012).

The last complete treatment of the Czech flora appeared in Flora of Czechoslovakia written by Dostál (1989). This was largely based on the author's own experience. He reviewed a considerable amount of literature and summarized the published records for the former Czechoslovakia and bordering regions. Although this Flora substantially updated knowledge of the Czech and Slovak floras and was unrivalled at the time, some records were adopted uncritically and deemed erroneous in later monographic revisions based on the examination of herbarium material. The last outline of the Czech flora was presented in the field guide Klíč ke květeně České republiky (Key to the flora of the Czech Republic; Kubát et al. 2002) that followed the format of the well-established central-European field guides, namely the German Rothmaler's Exkursionsflora (Schubert & Vent 1994, Jäger & Werner 2002) and a similar guide for Austria (Adler et al. 1994). There is an up-to-date list of vascular plants of the Czech Republic, which incorporates well-founded recent changes in the systematics, in Danihelka et al. (2012).

A detailed taxonomic inventory of the diversity of plants in the Czech Republic is currently being undertaken within the project Květena České republiky (Flora of the Czech Republic). This is the first Czech multiauthored flora in which there is a monograph of each genus or family, based on up-to-date biosystematic knowledge and expert taxonomic re-evaluation of primary and literature data. The data on plant morphology and variation are based on field observations, cultivation experiments and extensive studies of herbarium material. The treatment of each species in the Flora includes nomenclature, list of exsiccate collections, morphological description, chromosome numbers, details of intraspecific variation, ecology and phytosociology, and a detailed description of its distribution in the Czech Republic and its total range. Because this involves the precise collecting and processing of primary data, it will inevitably take a few decades to complete this

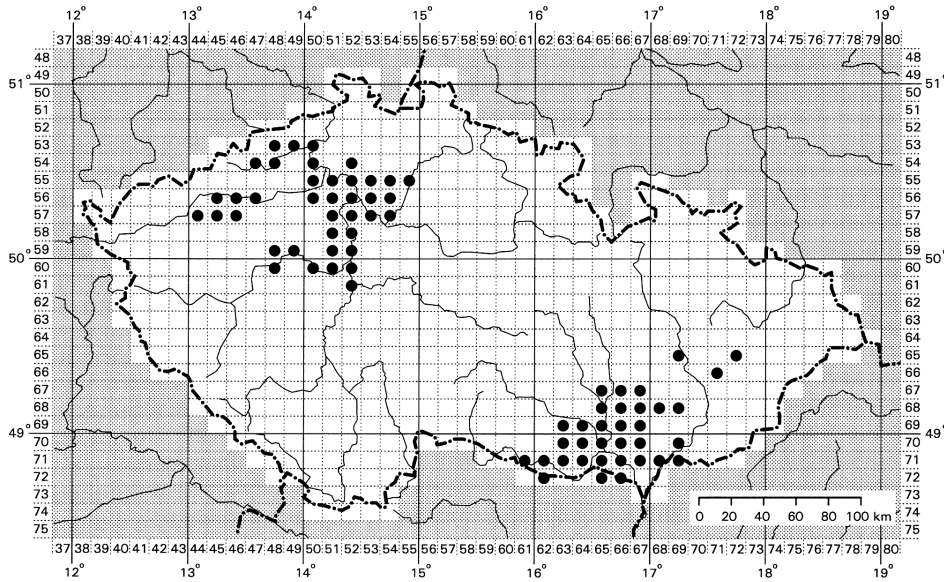
flora. The first volume of this compendium appeared in 1988 and eight of the ten planned volumes have been published (Hejný et al. 1988, 1990, 1992, Slavík et al. 1995, 1997, 2000, 2004, Štěpánková et al. 2010). The volumes published so far are those on lycopods, horsetails, ferns, conifers, dicots and part of the monocots. Preparation of the last two volumes, which include the rest of the monocots and supplements and updates to the previous volumes, is in progress.

A complete atlas of the distribution of vascular plants in the Czech Republic is not yet available. Four volumes of a grid-based atlas with a grid template of 10 × 6 arc minutes were published under the serial title Phytocartographical syntheses of the Czech Republic (Slavík 1986, 1990, 1998, Štěpánková 2012). These include maps of the distributions of lycopods, horsetails, ferns, conifers and most dicots (see Fig. 2 for a sample map). Altogether, 1225 distribution maps of taxa of 113 families have been published. 240 distribution maps of selected plants appeared in the introductory chapters of the respective volumes of the Flora of the Czech Republic (Slavík 1988, 1995, 1997, 2000, 2004b). Maps for 400 rare and endangered plants of the former Czechoslovakia were published in the Red Data Book of the Czech and Slovak Republics (Čeřovský et al. 1999). Many additional maps were published separately in studies that focus on taxonomy and distribution of selected taxa (e.g., Kaplan 2000–2003, 2010, Kubát & Kaplan 2000, Mandák & Procházka 2000, Trávníček 2000, 2001, 2010a, Weber 2000, Danihelka 2001a, b, Vašut 2003, Hroudová et al. 2004, Rybka 2004, Vašut & Trávníček 2004, Zieliński & Trávníček 2004, Brabec 2005, Ekrt et al. 2007, Trávníček & Zázvorka 2005, Trávníček et al. 2005, 2008, Vašut et al. 2005, Žíla & Weber 2005, Ducháček et al. 2006, 2007, Krahulec et al. 2006, Lepší & Lepší 2006, 2009, Duchoslav et al. 2007a, b, Ekrt 2008, Bureš et al. 2008, Trávníček & Štěpánek 2008, Danihelka et al. 2009, Duchoslav & Krahulec 2009, Lepší et al. 2009b, Ekrt et al. 2010, Zázvorka 2010, Chlumský & Štech 2011, Trávníček & Žíla 2011). These publications often resulted from revisions carried out during the preparation of the Flora of the Czech Republic. Contributions of Czech botanists (particularly of J. Holub, B. Slavík and J. Štěpánková) to Atlas Florae Europaeae (Jalas & Suominen 1972–1994, Jalas et al. 1996, 1999, Kurtto et al. 2004, 2007, 2010) also provide important records of the distributions of Czech vascular plants in the broader continental context.

Despite the long history of research on the Czech flora and the large body of taxonomic knowledge and data on distribution that has been collected, there is still no complete atlas of the distributions of Czech vascular plants based on data evaluated by taxonomic experts.

Basic overview of the flora of the Czech Republic

The flora of the Czech Republic includes 148 families of vascular plants (classification concept: Stevens 2001 onwards, Angiosperm Phylogeny Group 2009), with 916 genera, 3557 species (with 194 additional subspecies) and 609 hybrids (Danihelka et al. 2012). Genera with 30 or more species include *Taraxacum* (221 species), *Rubus* (127), *Carex* (87), *Hieracium* (59), *Pilosella* (59), *Veronica* (35) and *Trifolium* (34). Families richest in species are the *Asteraceae* (662 species), *Rosaceae* (316), *Poaceae* (275), *Fabaceae* (170), *Brassicaceae* (148), *Cyperaceae* (127), *Lamiaceae* (112), *Caryophyllaceae* (108) and *Apiaceae* (100).



1154 ***Orthantha lutea*** **(L.) WETTST – zahořanka žlutá**

Status: native Threat degree: C3 Frequency: **10,75**
Area: CSEEurSWAs

Fig. 2. – Distribution of *Odontites luteus* in the Czech Republic. A sample map authored by Slavík & Štěpánková from Phytocartographical syntheses of the Czech Republic (Štěpánková 2012).

Most of the taxa are native (2256 species and 145 additional subspecies), 36.0% (1350 taxa that can be assigned to 1301 species and 49 additional subspecies) are alien and the latter consist mainly of neophytes (76.0%), while archaeophytes are less frequent (24.0%) (Danihelka et al. 2012, Pyšek et al. 2012). Within the Raunkiær system of life forms, most frequently represented among Czech plants are hemicryptophytes (45.7%), followed by therophytes (22.3%), phanerophytes (14.4%), geophytes (9.3%), chamaephytes (5.1%) and hydrophytes (3.2%), while the percentage of epiphytes is negligible (only two species).

Human activities affect vegetation and result in considerable changes in the structure of the flora. Hundred-and-fifty-six species or subspecies (4.2% of the Czech flora) are extinct or vanished (e.g. *Betula humilis*, *Epilobium lanceolatum*, *Geranium bohemicum*, *Gymnadenia odoratissima*, *Herminium monorchis*, *Iris spuria*, *Linnaea borealis*, *Oenanthe fistulosa*, *Orchis coriophora*, *Pedicularis sceptrum-carolinum*, *Peucedanum arenarium*, *Plantago altissima*, *Potamogeton compressus*, *Selaginella helvetica*, *Sparganium angustifolium* and *Woodsia alpina*) while many others are endangered. An updated Red List of the Czech flora (Grulich 2012) includes 1564 taxa, which is 41.7% of the Czech vascular plants. In contrast, the Czech flora is enriched by new invaders. The alien flora is discussed in detail by Pyšek et al. (2012).

Besides common and widespread central-European species, the Czech flora includes also remarkable phytogeographical components such as diverse geoelements, boundary and outlying elements, glacial and postglacial relicts and local endemics. These are discussed in detail below.

Relicts

Because of the fluctuations in climate that occurred in glacial and interglacial phases and the associated severe changes in the central European landscape during the Pleistocene, no Tertiary relicts are thought to have survived in the Czech Republic and all relicts that persisted here are of Quaternary age or, probably more precisely, Late Quaternary. During the last glacial period, the landscape was predominantly treeless in central Europe, dominated by steppe tundra (West 2000, Stewart & Lister 2001, Granoszewski 2003, Müller et al. 2003, Ložek 2011), but local patches of boreal woodland or even more extensive forests existed especially in continental areas, and wet meadows were found at favourable sites (Willis & van Andel 2004, Jankovská & Pokorný 2008, Kuneš et al. 2008, Magyari et al. 2010, Pokorný 2011). Many arctic, alpine, boreal and steppe species were more widespread in central Europe during the last glacial period and in the Early Holocene (e.g., Szafer 1912, Tralau 1963, Lang 1994, Ložek 2007, 2009b, Birks & Willis 2008, Ehrich et al. 2008). Some of them later disappeared when there was a marked change in climate and forests became more widely distributed (Ložek 1988, 2011, Birks & Willis 2008, Chytrý et al. 2010). Others had markedly restricted ranges but survived in small and fragmented populations in suitable habitats (refugia), which resulted in the disjunct distributions (e.g. Rull 2008, 2010, Stewart et al. 2010). These relicts now occur mostly in few small areas in the Czech Republic, in some cases even at a single or a few localities. Depending on the species requirements, these refugia are rocky outcrops (mainly in deep valleys), screes, erosion-prone steep slopes with landslides, serpentine outcrops (particularly those covered with open pine forests), fens, mires, peat bogs, avalanche tracks in glacial cirques or natural subalpine to alpine grasslands above the timberline.

In contrast, human activities during the Middle and Late Holocene, particularly those that are now considered as "traditional management of the landscape", contributed to the local spread of several rare (and presumably relict) species of alpine and thermophilous grasslands, fens and other treeless communities. For example, subalpine to upper montane anthropogenic meadows in the Krkonoše Mts are rich in relict subalpine and alpine species such as *Viola lutea* and *Campanula bohemica*, but these meadows are below the natural timberline.

Relicts as discussed above are formerly widespread taxa but currently only occur in refugia that provide a suitable combination of long-term stable ecological conditions. However, our understanding of the exact history and distribution of the populations that survived during the Holocene is fragmentary due to the lack of palaeoecological data. Continuous occurrence of species throughout the Holocene can only be directly confirmed for species with easily determinable and well-preserved fossils. The precise evaluation and unequivocal proof of relict status is difficult and there is no good evidence for the supposed relict status of many species. The relict status of a species is usually inferred from knowledge of its current ecological requirements, dynamics of its recent habitats, its present distribution and general knowledge of the Holocene vegetation development in the region under study. There are many studies that record relict species in the Czech Republic. Assumed arctic and/or alpine glacial relicts include *Rubus chamaemorus* (Holub 1995, Slavík 1995, Ložek 2009b), *Pedicularis sudetica* (Hendrych & Hendrychová 1988), *Conioselinum tataricum* (Holub 1997a), *Pinus mugo* (Skalický 1988b), *Luzula spicata* (Kirschner 1989) and *Gentiana pannonica* (Holub et al. 1970). Another group, represented

by *Helictotrichon desertorum* (Holub 1962, 1999b), some species of *Stipa* (Martinovský 1965, 1975), *Allium strictum* (Martinovský 1969, Holub et al. 1970, Krahulec et al. 2006, Krahulec & Duchoslav 2010), *Orobanche coerulescens* (Zázvorka 1984) and *Bassia prostrata* (Tomšovic 1989) are considered to be glacial relicts of continental steppes. Other species, such as *Linum flavum* (Hendrych 1984), *Achillea pannonica* (Danihelka 2001a), *Ligularia sibirica* (Hendrych 2003, Slavík 2004a, Šmídová et al. 2011), *Viola ambigua* (Danihelka & Čeřovský 1999) and *Knautia arvensis* subsp. *pseudolongifolia* and subsp. *serpentinicola* (Štěpánek 1989, Kaplan 1998) are thought to be postglacial relicts, from the Preboreal and/or Boreal periods. Below selected species that are considered to be relicts are listed and as far as possible sorted according to their age and origin. Although this is based on a lot of indirect weak evidence, overall the inferences are strong (see also Pokorný et al. 2010).

There are a few well documented exceptions in the Czech flora. Pollen records indicate that *Betula nana* was widespread during the last glacial and Early Holocene (e.g. Pokorný 2002, Svobodová et al. 2002, Jankovská 2007, Kuneš et al. 2008) but it is now confined to several sites at old peat bogs in high mountains. Based on palaeobotanical finds (fossil fruits), Pokorný et al. (2010) record that meta-populations of *Cladium mariscus* survived in fens along the Labe river throughout the entire Holocene but now its distribution in Bohemia is more restricted than the fossil sites, which confirmed the previously assumed status of *Cladium mariscus* as a relict from at least the Early Holocene (Sádlo 2000). Additional data came from analyses of the genetic structure of populations. Hensen et al. (2010) record low genetic diversity within and high genetic differentiation between populations of *Stipa capillata*, which is thought to be a postglacial relict that experienced strong bottlenecks in central Europe, enhanced by isolation and selfing. A strong genetic differentiation between populations of *Saxifraga paniculata* is attributed to genetic drift in isolated populations and interpreted by Reisch et al. (2003) as evidence that this species is a glacial relict in central Europe.

Plant macrofossils and pollen records indicate that many arctic species were widespread in tundra at mid-altitudes in central Europe during the last glacial period (Birks & Willis 2008). The rapid climatic amelioration that occurred at the Pleistocene/Holocene boundary (and the Holocene thermal maximum) and the associated expansion of forest eliminated much of the arctic flora, remnants of which occur in northern Europe and/or at the highest altitudes. Some of the arctic species, however, survived in alpine grasslands or similar treeless sites above the timberline or habitats ecologically similar to tundra, such as peat bogs and mires. These glacial arctic relicts include *Andromeda polifolia*, *Betula nana*, *Carex bigelowii*, *C. capillaris*, *C. limosa*, *C. rupestris*, *C. vaginata*, *Eriophorum vaginatum*, *Juncus trifidus*, *Pedicularis sudetica* (Fig. 3), *Rhodiola rosea*, *Rubus chamaemorus* (Fig. 4), *Salix herbacea*, *S. lapponum*, *Saxifraga oppositifolia* and *Swertia perennis*.

Whereas the distributions of arctic species moved from northern Europe southwards and back with the waxing and waning of continental glaciers, those of species that originated in central-European high mountains (particularly in the Alps and Carpathians) experienced altitudinal shifts. After the retreat of glaciers, these alpines recolonized their original mountain ranges but some of them persisted also in Czech mountains. These Central-European mountain relicts include *Adenostyles alliariae*, *Gentiana asclepiacea*, *Homogyne alpina*, *Hypochaeris uniflora*, *Pinus mugo* and *Primula minima*. Species with centres of distribution in the Alps and Carpathians and now occurring in the Czech

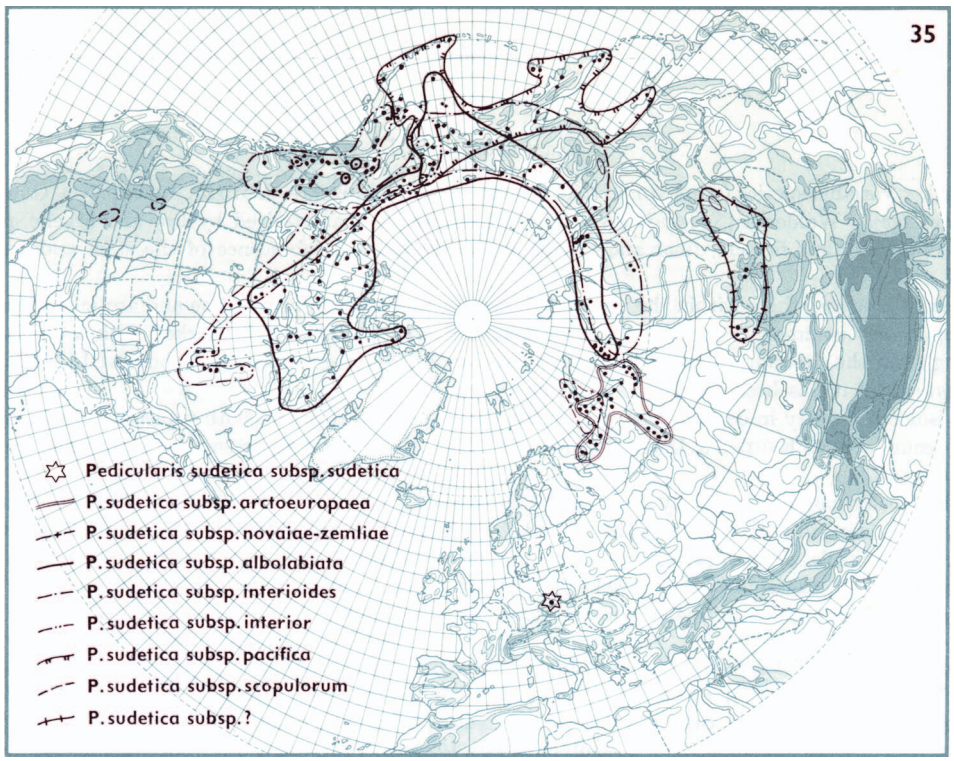


Fig. 3. – An isolated relict occurrence of *Pedicularis sudetica* subsp. *sudetica* in the Krkonoše Mts, along the Czech/Polish border, indicated by an asterisk with a dot in the middle. It represents a markedly remote and isolated part of the distribution of the *P. sudetica* complex, which has the highest diversity in the arctic and northern boreal areas. Reproduced from Hultén (1971), reproduced with permission.

Republic in predominantly lowland relict sites are represented by *Calamagrostis varia* and *Tofieldia calyculata*.

Another group includes continental plants that presumably colonized central Europe via cold periglacial steppes (particularly the loess steppe, see Ložek 2009b) along the Sarmatian migration route north of the Carpathians (Martinovský 1969, 1971, 1984). During the Last Glacial Maximum, cold and arid steppe was the dominant type of vegetation across northern Eurasia south of approximately 57°N and occupied a much larger area in Europe (Tarasov et al. 2000). This type of vegetation, sometimes called "steppe-tundra", included elements of modern steppic grassland and northern tundra. It probably does not have exact current analogues (Stewart & Lister 2001) but recent studies show that it was very similar in character to the cold continental landscapes of South Siberian mountains (Pelánková et al. 2008, Řičánková et al. 2010). These cold steppes were widespread south and east of the Fennoscandian ice-sheet (Birks & Willis 2008) including in the Czech lowlands as indicated by fossil pollen (e.g. Kuneš et al. 2008). The species of continental steppe that are thought to have colonized central Europe via the Sarmatian migration route in the Late Pleistocene are now often designated thermophilous species but they are

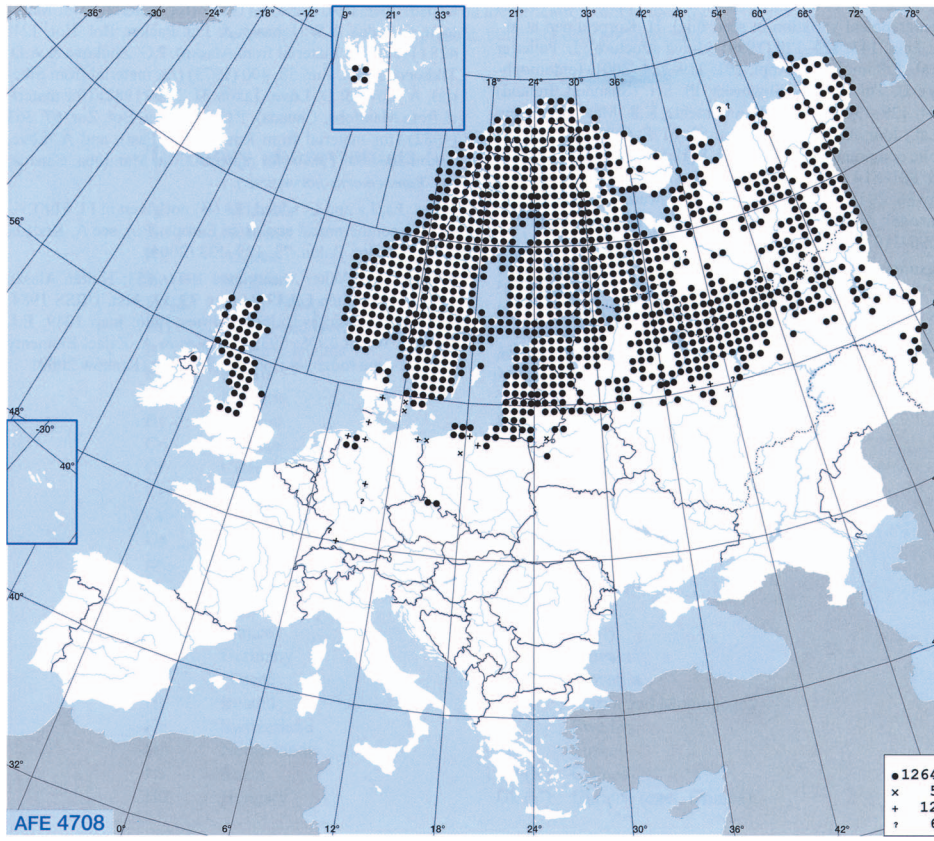


Fig. 4. – Distribution of *Rubus chamaemorus* in Europe. This Sub-arctic element is widespread in northern Europe. However, this species is found also in an isolated area in central Europe, namely in peat bogs in the Krkonoše Mts, where it occurs as a glacial relict. Reproduced from Kurtto et al. (2010), reproduced with permission.

actually dry-adapted and eurythermic (cold-tolerant). Spreading westwards north of the Carpathians they reached Bohemia and later survived in the warmest highlands in its north-central part; less frequently they occur also in southern Moravia. These glacial relicts associated with the Sarmatian migration route are represented by *Astragalus arenarius*, *A. danicus*, *Allium strictum*, *Helictotrichon desertorum*, *Jurinea cyanoides*, *Stipa tirsa* and species of *Stipa dasyphylla* agg.

Other species of continental steppe apparently spread along the Pannonian migration route south of the Carpathians and reached southern Moravia but not Bohemia. *Agropyron pectinatum*, *Bassia prostrata*, *Crambe tataria*, *Jurinea mollis*, *Prunus tenella* and *Taraxacum serotinum* are examples, and *Crepis pannonica*, *Onosma arenaria*, *Phelipanche caesia*, *Phlomis tuberosa*, *Scorzonera austriaca*, *Stipa borysthenica* and *Trinia ucrainica* apparently also belong to this group. The Pannonian endemic *Artemisia pancicii* is at the northwestern limit of its distribution in southern Moravia.

In addition to low temperatures, the climate in lowlands of northern Eurasia was, in general, extremely dry during the last glacial period (Hubberten et al. 2004). Saline meadows and salt marshes were therefore more frequent at suitable sites in central Europe than they are today. This vegetation largely disappeared later but saline soils locally remained treeless, which enabled heliophilous halophytes to survive there throughout the Holocene (Magyari et al. 2010). Glacial relicts associated with this kind of vegetation include *Glaux maritima*, *Plantago maritima*, *Salicornia prostrata*, *Suaeda prostrata* and *Taraxacum bessarabicum*.

Increasing climate warming at the end of the last glaciation and at the Pleistocene/Holocene boundary triggered major shifts in the ranges of species. Steppe persisted from the full glacial to the Early Holocene but cold steppe was gradually replaced by grass-rich steppe and forest-steppe, which were extensive in eastern and central Europe (Magyari et al. 2010). Thermophilous species that during the Pleistocene retreated to more temperate refugia returned and recolonized central Europe. Many light-demanding species underwent a rapid expansion, supported by open habitats where there was little competition. The thermophilous immigrants became mixed with eurythermic species, which were already present on cold steppes during the last glaciation.

Thermophilous plants migrated along several dispersal routes (e.g. Slavík 1995, Taberlet et al. 1998, Hewitt 1999, Petit et al. 2002, Sádlo 2007, Parisod 2008, Ložek 2009a, b, 2011, Magyari et al. 2010). The main migration routes for the re-colonization of the present-day Czech Republic passed through southern Moravia. The sub-Mediterranean element spread from the south along the Illyrian-Noric migration route that passes along the eastern edge of the Alps. Some species of the Pontic element may have migrated from the east and south-east along the Pannonian migration route that passes along the valley of the River Danube south of the Carpathians. The West-Sub-Mediterranean element migrated along the Rhône-Rhine pathway (following the main river valleys of the Rhône and Rhine) and Upper Danube Corridor north of the Alps into the western part of central Europe and reached Bohemia from the south-west. In addition, the South-Siberian-Pontic element continued to spread also along the Sarmatian migration route north of the Carpathians. Regardless of their origin, some of these thermophilous or eurythermic species that arrived and extended their ranges in the Preboreal and Boreal periods now occur in refugia and are considered to be postglacial relicts. These perhaps include *Astragalus exscapus*, *Linum flavum*, *Pedicularis exaltata* and *Viola ambigua*.

Fens (calciphilous and eutrophic mires) were widely distributed in the open landscape of the Early Holocene (Sádlo 2000) but were later mostly eliminated as a consequence of forest expansion. Sádlo (2000) suggests that species of open fens may have occurred in central Europe throughout the entire Holocene in shifting gaps in alder carrs. Cyclic alternations of open fens and alder carrs on lowland floodplains (Pokorný et al. 2000, Pokorný 2011) provided small refugia surrounded by woodlands that might have provided conditions for uninterrupted survival of open fens in the wooded phases of the Holocene. Similar hypotheses were proposed to account for the survival of relict plant populations in a dynamic mosaic of open habitats on a mountain floodplain (Sádlo & Bufková 2002) and for the long survival of fen species at the meta-population level in a river basin (Pokorný et al. 2010). Analysis of sediments in old calcareous fens in the West Carpathians revealed long-term persistence of rare vascular plants in old fens that match well the concept of glacial relicts (Hájek et al. 2011) but more convincing evidence is available for the relict occurrence of terrestrial snails, whose shells are abundant in fen sediments (Ložek 1964,

Hájek et al. 2011). The best example of a relict species from the postglacial calciphilous and eutrophic mires is *Cladium mariscus*, and *Betula humilis*, *Calamagrostis stricta*, *Carex buxbaumii*, *Eriophorum gracile*, *Ligularia sibirica*, *Schoenus ferrugineus* and *S. nigricans* possibly also belong to this group.

Increasing humidity in the early postglacial enabled also the expansion of boreal taiga. Species that are now typical of boreal coniferous forests were more widespread previously in central Europe. Examples of assumed postglacial relicts of boreal taiga include *Actaea europaea*, *Linnaea borealis*, *Rhododendron tomentosum*, *Rubus saxatilis*, *Stellaria longifolia* and *Trientalis europaea*.

Steppe grasslands, boreal taiga and other habitats characteristic of the Preboreal and Boreal periods were later increasingly replaced by deciduous forests. No relicts from more recent periods are distinguished.

Endemics

Definition of concepts

The distribution of endemics is usually defined in terms of conspicuous topographic features, such as a mountain range or an island, or other natural elements, such as a specific habitat of relict character. In central Europe, many endemics occur in alpine and subalpine grasslands on the summits of mountain ranges. However, Czech national borders often coincide with peaks and ridges in the summit areas. Consequently, the majority of narrow-range endemics occurring in these border areas are members of floras of two countries. Two of three mountains ranges in the High Sudetes in the north of the Czech Republic are situated on the border with Poland. Many of the species endemic to the Krkonoše/Karkonosze Mts (Riesengebirge in German, Giant Mts in English) or the Králický Sněžník/Śnieżnik Kłódzki Mts (Glatzer Schneeberg in German) occur both in the Czech Republic and Poland, although they only occur in an area of a few square kilometres. Paradoxically, none of these rare endemics would be formally designated as endemic if only endemism within political borders was considered. This would be highly unpractical as these taxa would be ignored in all lists of endemics, which are supposed to deserve the highest attention and conservation priorities. For these reasons, in addition to strictly Czech endemics (defined by the political borders), species and subspecies with distributions that only slightly exceed the borders of the country (generally by less than 1 km) and for which the majority of localities are in the Czech Republic, are also listed as endemics in this paper. If convenient, these latter taxa may be formally designated as Czech subendemics.

In terms of the extent of their distributions and the size of the Czech Republic, most of the endemics discussed here may be classified as stenoendemics (endemics confined to a small geographic area). Some of them are even confined to a single locality such as a glacial cirque or a rocky summit.

Changes in understanding of Czech endemics

There have been several attempts to compile a list of plants endemic to the Czech Republic. The first treatment of endemic species (as currently defined) that aimed to be complete and critically analysed was provided by Hadač (1977), who listed 118 Czech endemics

and subendemics (including apomictic taxa). He compiled records previously scattered in the literature and, in contrast, many previous putative endemics excluded on the basis of a re-evaluation of their taxonomy and distribution.

A revised list by Holub et al. (1979) appeared soon afterwards. It listed 43 endemic taxa completely or almost completely confined to the Czech Republic. Of the latter, only species with a slight transgression beyond the state borders were admitted (similar approach to that adopted in this paper). In addition to these Czech endemics, the authors list an additional 16 endemics with distributions that distinctly extend from the Czech Republic into bordering countries (subendemics) and 32 mainly central-European endemics that mainly occur outside the Czech Republic but with some localities in this country. These endemics, of which the Pannonian endemic *Artemisia pancicii* occurring in southern Moravia, eastern Austria and north-eastern Serbia (Danihelka 1995, Danihelka & Marhold 2003) is a good example, are not included in this paper.

Czech (and Slovak) endemics were discussed also by Hendrych (1981a) who provided the shortest list. He intentionally omitted all species known to be apomictic and listed only six supposedly Czech endemics (*Campanula bohemica*, *C. gelida*, *Cerastium alsinifolium*, *Dianthus carthusianorum* subsp. *sudeticus*, *Melampyrum bohemicum* and *Poa riphaea*). Eleven endemics are mentioned in the overview of the phytogeographical characteristics of the Czech Republic by Slavík (1988). Recently, Gerža (2009) published a list of 29 sexually reproducing endemics and 40 apomictic Czech endemics. Krahulec (2006) reviewed the endemics in the Krkonoše Mts (including the Polish part) and mentions several endemics that occur in other regions of the Czech Republic.

The considerable differences between these lists reflect not only the different approaches of the authors but also the changes in the state-of-the-art of taxonomy and plant distribution that have occurred over the last three decades. Some of the species that were previously considered to be Czech (or Czechoslovak) endemics were later recorded in neighbouring countries. For example, *Epipactis albensis* was described from floodplain forests along the middle course of the Labe river in central Bohemia (Nováková & Rydlo 1978) but later recorded in several other countries in central Europe (Delforge 2006, Batoušek 2010). *Tephroseris longifolia* subsp. *moravica* was described from a small area in the Bílé Karpaty Mts (Holub 1979) but later recorded also in the north-western part of the Slovenské stredohorie Mts in Slovakia (Kochjarová 1997, 1998, Holub 1999f, Kochjarová & Hrouda 2004). Similarly, *Taraxacum bohemicum* was described from a limited area in eastern Bohemia (Kirschner & Štěpánek 1986) and considered as a Czech endemic (Kirschner & Štěpánek 1994) but later found at one site in westernmost Slovakia (Kirschner & Štěpánek 1998) and therefore is a subendemic. *Potentilla lindackeri* was long known only from rocky slopes in river valleys and similar habitats in central Bohemia (e.g. Hadač 1977, Dostál 1989) but later also found in Saxony, Germany (Soják 1995, 2009a, Gerstberger 2003, Gregor & Müller 2005). Both *Aconitum plicatum* and *Gentianella praecox* subsp. *bohemica*, although having their centres of distribution in the mountains of the Bohemian Massif in the Czech Republic, occur also in adjacent areas in Austria, Germany and Poland (Skalický 1988a, Procházka & Skalický 1999, Kirschner & Kirschnerová 2000) and are better classified as subendemics rather than Czech endemics. *Knautia arvensis* subsp. *serpentinicola*, a relict restricted to serpentine outcrops, is endemic to the Bohemian Massif with most localities in the Czech Republic but also occurs at one site in Germany (Kaplan 1998). The endemic status of *Symphytum*

bohemicum depends on the taxonomic delimitation of this species. It was described from central Bohemia and Hadač (1977) and Kubát (2000) recognize it in the narrow sense as a Czech (Bohemian) endemic microspecies. However, very similar plants, often considered conspecific with the Bohemian taxon, occur in other areas of central and southern Europe, concentrated in about 8–9 isolated regions, ranging from Germany in the west and southern Poland in the north to western Ukraine and Romania in the east and to northern Italy and Serbia in the south (Holub 1999e, Kubát 2000). It is difficult to define the exact range of this species because white-flowered individuals of *S. officinale* are (particularly in western Europe) often misidentified as *S. bohemicum*, and consequently *S. bohemicum* as a taxon is inappropriately considered conspecific with *S. officinale*. However, true *S. bohemicum* has creamy to yellowish flowers with yellow-green corola tips, and also differs from *S. officinale* in having a different type of indumentum, features of leaf and stem morphology and size of fruit (Kubát 2000). A thorough taxonomic revision based on material from the entire range of this complex is needed. The endemic status of *Hieracium schmidtii* subsp. *candicans* is also unclear. It was described from central Bohemia and during a recent taxonomic revision (Chrtek 2004) shown to occur in rocky localities mainly in the České středohoří highlands, the valley of the River Vltava and the Křivoklátsko highlands. However, this taxon is also recorded from Germany, Austria and Hungary but these records require expert taxonomic confirmation (Chrtek 2004). Similarly, *Hieracium decipiens* was described from the Krkonoše Mts but some populations in the Carpathians may belong to this species (Chrtek 2004). Recently *Aconitum plicatum* subsp. *sudeticum* was described as an endemic of the Králický Sněžník Mts and the Hrubý Jeseník Mts (Mitka 2003). It is apparently of hybrid origin, resulting of introgression of *A. firmum* subsp. *moravicum* into *A. plicatum*. Its evolutionary history and taxonomic validity should be tested using molecular methods.

Other taxa are excluded from the list of endemics presented here following expert taxonomic re-evaluations of the given groups. For example, *Melampyrum bohemicum* was long considered a Czechoslovak endemic species (e.g., Hadač 1966, 1977, Hendrych 1981a), which evolved from *M. subalpinum* that is now confined to eastern Austria. However, in the revised delimitation by Štech (2000, 2006) the Czech populations and those in western Slovakia are considered to be conspecific with Austrian populations traditionally called *M. angustissimum*. *Crepis mollis* subsp. *velenovskyi* was described from a deciduous forest at Sadská in the Labe river basin in central Bohemia (Domin 1904) and was still listed as a Czech endemic by Hadač (1977). The type specimen is indeed morphologically peculiar and very distinct from all other plants of *C. mollis* agg. However, it is an aberrant phenotype as other collections from the type locality fall within the variation of *C. mollis* subsp. *succisifolia*. That is why the plant described as subsp. *velenovskyi* is not ascribed a rank (Kaplan & Kirschner 2004). Previously indicated endemic Bohemian subspecies of *Iris aphylla* are no longer accepted taxonomically (Hrouda & Grulich 2010). The level of morphological differentiation of *Dianthus lumnitzerii* subsp. *palaviensis* in the Pavlovské vrchy hills is rather low and does not warrant subspecific rank (Kovanda 1990). *Sorbus hardeggensis* from the Dyje/Thaya river valley was described as a hybridogenous species (Kovanda 1996b, 1999) but recent studies indicate that it is not a stabilized apomictic species but a recurrently formed population of primary and backcrossing hybrids (Šefl 2007).

In contrast, several new endemics were recently discovered during detailed taxonomic revisions of critical groups. Multidisciplinary revisions of Bohemian *Sorbus* (Lepší et al.

2008, 2009b, Velebil 2012, Vít et al. 2012) yielded five additional endemic species. A few of the regional species of *Rubus* discovered and described during the past two decades (Holub 1991, 1992, Weber 2000) are known only from the Czech Republic. Taxonomic and biosystematic revisions of subalpine *Hieracium* (Chrtek 1995, 1997, Chrtek & Marhold 1998) refined our understanding of the diversity and distribution within this group rich in endemics. An endemic sedge from the Krkonoše Mts that was recorded in the literature under the provisional names *Carex oederi* subsp. *pseudoscandinavica* (Holub et al. 1979) or *C. viridula* subsp. *pseudoscandinavica* (Holub 1999a) has only recently been thoroughly evaluated and validly described as *C. derelicta* (Štěpánková 2008). Other recent additions to the list of Czech endemics include, among others, *Carlina biebersteinii* subsp. *sudetica* (Kovanda 2002), *Dactylorhiza bohemica* (Businský 1989), *Minuartia corcontica* (Dvořáková 1999b), *M. smejkalii* (Dvořáková 1988) and *Scilla bifolia* subsp. *rara* (Trávníček et al. 2010).

An extraordinary case of endemism is *Oenothera moravica*, which evolved recently as a result of hybridization between two alien species, *Oe. fallax* and *Oe. victorinii* (Jehlík & Rostański 1995). Its origin is similar to that of two *Tragopogon* allopolyploids, *T. mirus* and *T. miscellus*, which evolved from three diploids (*T. dubius*, *T. pratensis* and *T. porrifolius*) introduced from Europe to North America (Ownbey 1950). *Oenothera moravica* was detected soon after it appeared and at that time reported as occurring only in two close-by localities in south-western Moravia (Jehlík & Rostański 1995). These authors did not think it was of recurrent polytopic origin because the parental species meet only exceptionally in the field but expected that this newly evolved species would spread. Indeed, additional three localities of *Oe. moravica* were recorded during a floristic inventory in the area of its occurrence in 2011 (M. Chytrý, J. Danihelka & V. Grulich, unpubl.).

Revised list of endemics

In assessing plant taxa for inclusion on the revised list of endemics of the Czech Republic presented in this paper, some subjective decisions had to be made, particularly about their taxonomic rank and delimitation. The taxonomic status mostly follows recent expert revisions of the Flora of the Czech Republic (Hejný et al. 1988, 1990, 1992, Slavík et al. 1995, 1997, 2000, 2004, Štěpánková et al. 2010) and the distribution records therein were particularly important in assessing endemic status. Only taxa at the rank of species and subspecies are considered. Endemic varieties and forms, such as *Salix lapponum* var. *daphneola* that occur at the Pančická louka peat bog in the Krkonoše Mts (Chmelař & Koblížek 1990) or *Dianthus lumnitzerii* f. *palaviensis* (Kovanda 1990, Weiss et al. 2002) in the Pavlovské vrchy hills, are not discussed here.

A number of taxa do not appear in the current list because they have been re-evaluated taxonomically and reduced to synonyms of more widespread species. Doubtful taxa of highly limited occurrence and not adopted and substantiated in recent revisions were generally excluded. They are often only minutely distinct from their widespread relatives. Examples include *Coronilla moravica*, which was based on a single herbarium specimen collected near Pašovice in the Bílé Karpaty Mts (Chrtková & Stavělová 1986) and has not been found in the field again. Several recently described species are taxonomically uncertain and may be reclassified in future revisions. In the absence of modern monographs, these are provisionally included here among recognized endemic taxa.

Among apomictic microspecies of *Hieracium* and *Taxacum* only those groups that were recently revised by experts in the Czech Republic are considered. These include the majority of subalpine groups of *Hieracium* (Chrtek 1995, 1997, 2004, Chrtek & Marhold 1998), *Taraxacum* sect. *Palustria* (Kirschner & Štěpánek 1998, Kirschner 2010) and *Taraxacum* sect. *Alpestria* (Štěpánek 2010, Štěpánek et al. 2011). In contrast, the subalpine *Hieracium prenanthoides* group, occurring above the timberline in the Krkonoše, Králický Sněžník and Hrubý Jeseník Mts, is likely to include local endemics (Chrtek 2004, Krahulec 2006) but this still waits detailed investigation. No modern taxonomic revision is available for the *Ranunculus auricomus* complex in the Czech Republic, which may also contain endemic microspecies.

Of the facultatively apomictic *Rubus* only regional species reported exclusively from the Czech Republic in the recent Atlas Florae Europaeae (Kurtto et al. 2010) were adopted, whereas individual plants (single bushes) and local biotypes (i.e., forms occupying an area smaller than 20 km in diameter) were not considered in accordance with the present-day batological approach (Weber 1977, 1995, 1996, Holub 1991, 1997b).

In this paper 74 species and subspecies are considered to be endemic to the Czech Republic and closely bordering regions (Table 1), which is 2% of the total vascular plant diversity. Of these, 48 species and subspecies (1.3% of the total diversity) are strictly Czech endemics, that is they occur only within the borders of the country, the distributions of the other 26 extend slightly beyond the borders of the country (mostly by less than 1 km) in the summit areas of the Krkonoše/Karkonosze Mts and/or in the Králický Sněžník/Śnieżnik Kłódzki Mts. There is no genus endemic to the Czech Republic. For habitats and distribution of the endemics, references to selected literature on taxonomy and biology and additional notes, see Table 1.

The Czech Republic and closely adjacent areas are not particularly rich in endemic species. The proportion of endemic plants reflects size (78 867 km^2) and geographic position of the country in Europe, absence of massive mountain ranges with extensive alpine belts and the Quaternary history of the central-European landscape. The glaciations during the Pleistocene with considerable climatic and vegetational changes repeatedly eliminated many species of previously established flora. The climatic conditions have stabilized since the end of the Pleistocene but there was not sufficient time in the Holocene for the evolution of a highly diversified flora with many local endemics. All Czech endemics are therefore of Quaternary age (neoendemics) and often not well differentiated morphologically, and there are no endemics of Tertiary age (palaeoendemics).

Table 1. – A revised list of species and subspecies endemic to the Czech Republic, with descriptions of their habitats, distributions and references to the literature. Subalpine taxa occurring on the summits of the Sudetes Mts whose distributions only slightly extend beyond the borders of the country (generally less than 1 km) but with the great majority of their localities in the Czech Republic are included. Endemics that occur only within the borders of the country are indicated as CZ in the column Notes. Only a selection of the most relevant literature on the taxonomy and biology is given.

Taxon	Habitat; distribution	Relevant literature	Notes
Alchemilla obtusa subsp. *trapezialis*	springs in meadows, alder carrs and wet meadows; about 75 localities at low altitudes in the West Sudetes, particularly in the foothills of the Jizerské hory Mts and Krkonoše Mts, 330–850 m a.s.l.	Plocek 1986, 1995	CZ
Campanula bohemica	species-rich subalpine and montane meadows and grasslands; Krkonoše Mts, ca 800–1500 m a.s.l., majority of localities above 1200 m	Kovanda 1975, 1977, 2000, Hadač 1977, Hendrych 1981a, b	apparently occasionally hybridizes with *C. rotundifolia*
Campanula gelida	summit rock and adjacent subalpine grasslands; Mt. Petrovy kameny in the Hrubý Jeseník Mts, ca 1440 m a.s.l.	Kovanda 1968, 1977, 2000, Hendrych 1981a, b, Bureš 1996, Procházka & Bureš 1999	CZ
Campanula rotundifolia subsp. *sudetica*	rocks and scree on treeless summits and in glacial cirques; about 12 localities in the Krkonoše Mts and Hrubý Jeseník Mts, ca 1070–1450 m	Kovanda 1977, 2000	CZ
Carex derelicta	subalpine spring and moist places on rocky flats; Velká Kotelná jáma glacial cirque in the Krkonoše Mts, ca 1320 m a.s.l.	Havlíčková 1983 (as *C. *pseudoscandinavica*), Holub 1999a (as *C. *pseudoscandinavica*), Štěpánková 2008	CZ
Carlina biebersteinii subsp. *sudetica*	grasslands on rocky slopes in glacial cirques; Velká kotlina and Malá kotlina glacial cirques in the Hrubý Jeseník Mts, ca 1250–1320 m a.s.l.	Bureš 1996 (as *C. longifolia*), Kovanda 2002, 2004	CZ; extinct in the Velká kotlina glacial cirque, recently observed only in the Malá kotlina glacial cirque
Cerastium alsinifolium	springs and ditches along tracks in forests on serpentines, less frequently in grasslands and on rocky outcrops; ca 13 localities in the serpentine area around the villages of Prameny, Sítiny and Mnichov, Slavkovský les Mts, ca 750–880 m a.s.l.	Novák 1960, Hendrych 1981a, b, Smejkal 1990, Klaudisová & Čeřovský 1999, Kolář & Vít 2008, Suda & Kaplan 2012	CZ; hybridizes with *C. arvense*, hybrids dominate on sunny and drier places, whereas "pure" plants of *C. alsinifolium* are more frequent in shaded and moist habitats in forests
Cortusa matthioli subsp. *moravica*	shaded and moist mossy places on limestone rocks and scree at the bottom of the Macocha abyss in the karst area of Moravský kras, distr. Blansko, ca 400 m a.s.l.	Podpěra 1921, 1923, Kovanda 1992a, Jatiová & Čeřovský 1999, Gerža 2009	CZ; seeds are not produced, the population persists by vegetative propagation; taxonomically uncertain, requires re-evaluation
Dactylorhiza bohemica	wet meadows and fens; between Jestřebí and Staré Splavy, distr. Česká Lípa, 259 m a.s.l.	Businský 1989, Průša 2005, Sczepanski & Kreutz 2007, Nordström & Hedrén 2009, Kubát 2010	CZ; rare hybrids with *D. maculata* and *D. majalis* recorded
Dactylorhiza carpatica	calcareous fen; Březová, distr. Uherské Hradiště, in the Bílé Karpaty Mts, 520 m a.s.l.	Batoušek & Kreutz 1999, Průša 2005, Kubát 2010	CZ; hybridizating with other *Dactylorhiza* species has apparently occurred; taxonomically uncertain, requires re-evaluation

Taxon	Habitat; distribution	Relevant literature	Notes
Dianthus arenarius subsp. *bohemicus*	open sandy grasslands and open pine forests; at Kleneč a Vražkov near Roudnice nad Labem, distr. Litoměřice, ca 200–220 m a.s.l.	Novák 1915, 1927, Toman 1970, Kovanda 1990, Kuncová & Bělohoubek 1996, Čeřovský & Abtová 1999, Kalůsková et al. 2010, Šlechtová & Bělohoubek 2010	CZ; extinct at Vražkov, occasional occurrence of hybrids with *D. carthusianorum* recorded at Kleneč
Dianthus carthusianorum subsp. *sudeticus*	subalpine grasslands and rocks on avalanche track; Velká kotlina glacial cirque in the Hrubý Jeseník Mts, 1160–1340 m a.s.l.	Kovanda 1980, 1990, Hendrych 1981a, Procházka et al. 1999a	CZ
Dianthus moravicus	rocks and rocky cliffs; six to eight localities in canyons of the Želetavka, Rokytná, Jihlava and Dyje rivers in south-western Moravia, 240–460 m a.s.l.	Kovanda 1982, 1984b, 1990, Čeřovský & Grulich 1999	CZ
Euphrasia corcontica	subalpine grasslands and rocks; slopes of Mt. Sněžka, Krkonoše Mts, ca 1100–1500 m a.s.l.	Smejkal 1963, Hadač 1977, Dvořáková M. 1999a, Smejkal & Dvořáková 2000, Krahulec 2006	CZ; extinct species; taxonomically uncertain
Galium sudeticum s.l.	open grasslands on rocks and screes in glacial cirques or on serpentine rocks; subalpine habitats in the Krkonoše Mts and the Hrubý Jeseník Mts, ca 1200–1300 m a.s.l., and serpentines in the Slavkovský les Mts, 740–800 m a.s.l.	Krahulcová & Štěpánková 1998, Štursa et al. 1999, Štěpánková & Kaplan 2000, Suda & Kaplan 2012	extinct in the Hrubý Jeseník Mts; may be taxonomically heterogeneous (populations from serpentines differ from subalpine populations) and requires molecular investigation
Hieracium albinum	subalpine grasslands and open dwarf scrub on mountain summits and in glacial cirques; Krkonoše Mts, ca 1050–1300 m a.s.l.	Procházka & Chrtek 1999, Chrtek 2004	
Hieracium apiculatum	subalpine grasslands and open dwarf scrub on mountain summits and in glacial cirques; Krkonoše Mts, 920–1450 m a.s.l.	Chrtek 2004	
Hieracium asperulum	subalpine grasslands and open dwarf scrub on mountain summits; western part of the Krkonoše Mts, 1300–1430 m a.s.l.	Chrtek 2004	
Hieracium chamaedenium	valley of the Dyje river near Konice, distr. Znojmo, ca 220 m a.s.l.	Chrtek 2004	CZ; known only from the type locality, now missing (probably extinct)
Hieracium chlorocephalum	subalpine grasslands and open dwarf scrub on mountain summits and in glacial cirques; Krkonoše Mts and Hrubý Jeseník Mts, 1100–1350 m a.s.l.	Chrtek 2004	
Hieracium chrysostyloides	subalpine grasslands and open dwarf scrub on mountain summits; Hrubý Jeseník Mts and Králický Sněžník Mts, ca 1400–1450 m a.s.l.	Chrtek 1995, 2004	

Taxon	Habitat; distribution	Relevant literature	Notes
Hieracium corconticum	subalpine grasslands and open dwarf scrub; Krkonoše Mts, 1000–1400 m a.s.l.	Chrtek 2004	
Hieracium fritzei	subalpine grasslands and open dwarf scrub on mountain summits; Krkonoše Mts, mainly the western part, 1170–1450 m a.s.l.	Chrtek & Marhold 1998, Chrtek 2004	
Hieracium glandulosodentatum	subalpine grasslands and open dwarf scrub on mountain summits; Krkonoše Mts, 1000–1550 m a.s.l.	Chrtek 2004	
Hieracium melanocephalum	subalpine grasslands and open dwarf scrub on mountain summits; Krkonoše Mts, ca 1000–1580 m a.s.l.	Chrtek 1997, 2004	
Hieracium nigrescens	subalpine grasslands and open dwarf scrub; Krkonoše Mts, 800–1550 m a.s.l.	Chrtek 2004	
Hieracium nigrostylum	subalpine grasslands and open dwarf scrub; Krkonoše Mts, 1180–1560 m a.s.l.	Chrtek & Marhold 1998, Chrtek 2004	
Hieracium nivimontis	subalpine grasslands and open dwarf scrub on mountain summits; Králický Sněžník Mts, 1380–1423 m a.s.l.	Chrtek 1995, 2004	
Hieracium pedunculare	subalpine grasslands and open dwarf scrub; Krkonoše Mts, 800–1500 m a.s.l.	Chrtek 2004	
Hieracium pseudalbinum	subalpine grasslands and open dwarf scrub; Krkonoše Mts, 995–1310 m a.s.l.	Chrtek 2004	
Hieracium purkynei	subalpine grasslands; two localities in the western part of the Krkonoše Mts, ca 1350 m a.s.l.	Procházka & Chrtek 1999, Chrtek 2004	CZ; extinct
Hieracium riphaeum	subalpine grasslands and open dwarf scrub; Krkonoše Mts, 900–1500 m a.s.l.	Chrtek 2004	
Hieracium rohlenae	subalpine grasslands and open dwarf scrub; Krkonoše Mts, 920–1570 m a.s.l.	Chrtek & Marhold 1998, Chrtek 2004	
Hieracium saxifragum subsp. *celakovskianum*	subalpine grasslands and open dwarf scrub on mountain summits and in glacial cirques; Krkonoše Mts, ca 1100–1420 m a.s.l.	Chrtek 2004	
Hieracium schmidtii subsp. *winkleri*	rocks and rocky cliffs; České středohoří highlands, middle Vltava river valley south of Prague, and Manětín and Plasy, distr. Plzeň-sever, 250–590 m a.s.l.	Chrtek 2004	CZ

Taxon	Habitat; distribution	Relevant literature	Notes
Hieracium schmidtii subsp. *diversifolium*	rocks and rocky cliffs; Kozí vrch and Mariánský vrch hills at Ústí nad Labem, ca 150–350 m a.s.l.	Chrtek 2004	CZ
Hieracium schneiderianum	subalpine grasslands and open dwarf scrub on mountain summits; Krkonoše Mts (mainly the eastern part), ca 1100–1580 m a.s.l.	Chrtek & Marhold 1998, Chrtek 2004	
Hieracium schustleri	subalpine grasslands and open dwarf scrub on mountain summits; Krkonoše Mts and Mt. Králický Sněžník, 1000–1520 m a.s.l.	Chrtek 1995, 1997, 2004	
Hieracium tubulosum	subalpine grasslands and open dwarf scrub; Krkonoše Mts, 980–1580 m a.s.l.	Chrtek 1997, 2004	
Hieracium uechtritzianum	subalpine grasslands and open dwarf scrub; Krkonoše Mts (mainly in the eastern part) and Králický Sněžník Mts, 920–1520 m a.s.l.	Chrtek & Marhold 1998, Chrtek 2004	
Knautia arvensis subsp. *pseudolongifolia*	open subalpine grasslands on outcrops of carbonate rocks in a cliff above the timberline; Kotelné jámy glacial cirque in the Krkonoše Mts, 1320–1400 m a.s.l.	Štěpánek 1989, 1997, Štěpánek & Procházka 1999	CZ
Minuartia corcontica	rocky slopes and rocks in glacial cirques; five localities in the Obří důl glacial cirque in the Krkonoše Mts, ca 1100–1250 m a.s.l.	Dvořáková 1990 (as *M. gerardii*), 1999b, 2003	CZ; recent occurrence confirmed only in ravines Čertova zahrádka and Čertova rokle on eastern slopes of Mt. Studniční hora
Minuartia smejkalii	rocks and grasslands in open pine forests on serpentines; at least four localities (near Mladá Vožice, Hrnčíře, Bernartice and Borek) in three areas on serpentine outcrops in south-eastern Bohemia, 380–480 m a.s.l.	Dvořáková 1988, 1990, Procházka & Klaudisová 1999, Kolář & Vít 2008	CZ; survives at two localities (Hrnčíře and Bernartice), extinct at the others
Oenothera moravica	roadsides; several localities in south-western Moravia, mostly in distr. Třebíč, ca 220–630 m a.s.l.	Jehlík & Rostański 1995, Jehlík 1997	CZ
Pedicularis sudetica subsp. *sudetica*	mossy springs in subalpine grasslands; Krkonoše Mts, (800–)1150–1450 m a.s.l.	Hultén 1961, Hendrych & Hendrychová 1988, Molau & Murray 1996, Procházka et al. 1999b, Hrouda 2000, Štursová & Kociánová 2005	known from a number of localities in the past but recently observed only at a few of them
Pilosella callimorphoides	perhaps open grasslands and meadows; at the abandoned village Pastviny, near Kadaň, distr. Chomutov, ca 550 m a.s.l., and near Česká Lípa, ca 350 m a.s.l.	Chrtek 2004	CZ; missing (probably extinct)

Taxon	Habitat; distribution	Relevant literature	Notes
Pilosella pseudocalodon	Bohosudov, distr. Teplice, 250 m a.s.l.	Chrtek 2004	CZ; known only from the type locality, now missing (probably extinct)
Pilosella tephrophyton	dry grasslands; Kraví hora hill at Znojmo, 300 m a.s.l.	Chrtek 2004	CZ; known only from the type collection, now extinct
Pinguicula vulgaris subsp. *bohemica*	mossy fens; about 10 localities in the middle Labe river basin and a few localities around Jestřebí, distr. Česká Lípa, 180–260 m a.s.l.	Krajina 1927, Domin 1944, Hadač 1977, Bělohlávková 1989, 2000, Krahulcová & Jarolímová 1991, Studnička & Hejný 1992, Procházka & Studnička 1999, Casper & Stimper 2009, Válová 2010, Suda & Kaplan 2012	CZ; now surviving only between Jestřebí and Staré Splavy, extinct in all other localities; hybrids with *P. vulgaris* subsp. *vulgaris* detected in two localities; claimed karyological differentiation between the subspecies was not confirmed in flow cytometric screening of all extant individuals of subsp. *bohemica*; relationships to similar forms occurring elsewhere require further study
Plantago atrata subsp. *sudetica*	subalpine grasslands and rocks; Velká kotlina glacial cirque in the Hrubý Jeseník Mts, ca 1250–1400 m a.s.l.	Holub et al. 1971, Hadač 1977, Bureš 1996, Holub 1999c, Chrtek 2000	CZ
Poa riphaea	summit rocks and rocky slopes in glacial cirque; Mt. Petrovy kameny, Tabulové skály rock and Velká Kotlina glacial cirque in the Hrubý Jeseník Mts, ca 1440 m a.s.l.	Jirásek & Chrtek 1963, Chrtek & Jirásek 1966, Hadač 1977, Hendrych 1981a, b, Bureš 1996, Holub 1999d, Hoták et al. 2012	CZ; now surviving only on the summit rock on Mt. Petrovy kameny, extinct in the other two localities
Potentilla psammophila	sandy places in open pine forests; Doksy and Bezděz, distr. Česká Lípa, ca 270–450 m a.s.l.	Soják 2009a, b	CZ; missing; closely related to *P. lindackeri* s. str., requires further study
Primula elatior subsp. *corcontica*	subalpine grasslands, montane meadows and glacial cirques; several localities in the Krkonoše Mts, ca (800–)1220–1350 m a.s.l.	Domin 1930, Kovanda 1992b, 1997	recent occurrence confirmed only in the Malá Kotelná jáma and the Velká Kotelná jáma cirques; requires further taxonomic study
Rubus bohemiicola	forest fringes, forest clearings and open forest; central, southern and eastern Bohemia, 300–685 m a.s.l.	Holub 1991, 1995, Krahulcová & Holub 1998, Trávníček & Zázvorka 2005	CZ
Rubus brdensis	coniferous forests and forest fringes; south-western Bohemia, particularly Brdy Mts and their foothills; ca 300–600 m a.s.l.	Holub 1991, 1995, Krahulcová & Holub 1998	CZ
Rubus centrobohemicus	mixed and coniferous forests, forest clearings and forest fringes; central Bohemia, ca 300–600 m a.s.l.	Holub 1991, 1995	CZ

Taxon	Habitat; distribution	Relevant literature	Notes
Rubus josholubii	forest fringes and clearings; central and north-eastern Bohemia, rarely also in western Bohemia, ca 210–600 m a.s.l.	Weber 2000	CZ
Rubus vratnensis	forest fringes, forest clearings and scrub; north-western Bohemia, ca 200–500 m a.s.l.	Holub 1992, 1995	CZ
Saxifraga rosacea subsp. *steinmannii*	rocks and screes in deep rocky valleys; several localities in two small areas: the valley of the Labe river south of Ústí nad Labem and that of the Jizera river at Semily, ca 150–350 m a.s.l.	Braun-Blanquet 1922, Hrouda & Šourková 1992, Nepraš 2006, Nepraš et al. 2008	CZ
Scilla bifolia subsp. *rara*	moist deciduous forest; Purkrábka forest between Suchohrdly and Těšetice, distr. Znojmo, 310 m a.s.l.	Trávníček 2010a, b, Trávníček et al. 2010	CZ; morphologically best differentiated subspecies of *S. bifolia*
Sorbus albensis	thermophilous woodlands and scrubland on slopes and rocks; 12 localities west to north of Litoměřice in the České středohoří highlands, 180–540 m a.s.l.	Lepší et al. 2009b	CZ
Sorbus alnifrons	open hornbeam forests; two hills by Templštejn castle in the canyon of the Jihlava river near Moravský Krumlov, distr. Znojmo, ca 330–350 m a.s.l.	Kovanda 1996b, 1999, 2002	CZ
Sorbus barrandienica	thermophilous open woodlands on limestone at the tops of hills; about 10 localities in the Český kras karst east of Beroun, 340–450 m a.s.l.	Vít et al. 2012	CZ
Sorbus bohemica	thermophilous woodlands and scrub, mostly on the tops of volcanic hills; about 30 localities in the České středohoří highlands, 280–620 m a.s.l.	Kovanda 1961, 1992c, 1999, 2002, Challice & Kovanda 1978, Jankun & Kovanda 1987, Procházka 1999a, Boublík et al. 2002, Lepší et al. 2008, 2009b	CZ
Sorbus eximia	open thermophilous and mesic oak forests on limestone; four localities in the Český kras karst south of Beroun, 350–460 m a.s.l.	Kovanda 1984a, 1992c, 1999, 2002, Challice & Kovanda 1986, Jankun & Kovanda 1988, Lepší et al. 2008, Vít et al. 2012	CZ
Sorbus gemella	open thermophilous oak woodlands and pine forests often on rocky cliffs; about 7 localities (over 20 individual microlocalities) in the area of Džbán, between the villages of Třeskonice, Břínkov and Pochvalov, distr. Louny, 350–480 m a.s.l.	Kovanda 1996a, 1999, 2002, Lepší et al. 2008, 2009a	CZ

Taxon	Habitat; distribution	Relevant literature	Notes
Sorbus milensis	thermophilous woodlands and xeric scrub on basaltic rocks and screes; Milá hill near Louny in the České středohoří highlands, 385–490 m a.s.l.	Lepší et al. 2008	CZ
Sorbus omissa	open oak woodlands on rocky slopes; two sections of the lower Vltava river valley between Dolany and Roztoky north of Prague, ca 200–290 m a.s.l.	Velebil 2012	CZ
Sorbus portae-bohemicae	open oak forests on slopes and rocky outcrops; Porta bohemica gorge and foot of Mt. Lovoš north of Lovosice, distr. Litoměřice, 210–290 m a.s.l.	Boublík et al. 2009, Lepší et al. 2009b	CZ
Sorbus quernea	oak-hornbeam woodlands and scrub; Jabloňka and Bílá skála hills in the valley of the Vltava river in Prague, 230–250 m a.s.l.	Kovanda 1996a, 1999	CZ; requires taxonomic re-evaluation
Sorbus rhodanthera	open oak and hornbeam woodlands on basaltic cliffs and scree; Chlumská hora hill near Manětín, distr. Plzeň-sever, 570–650 m a.s.l.	Kovanda 1996a, 1999, 2002, Lepší et al. 2008	CZ
Sorbus sudetica	avalanche tracks, open dwarf scrub and subalpine grasslands; glacial cirques Kotelné jámy, Labské jámy and Obří důl in the Krkonoše Mts, ca 1050–1350 m a.s.l.	Kárpáti 1960, Kovanda 1965, 1992c, 1999, Hadač 1977, Challice & Kovanda 1978, Hendrych 1981a, b, Jankun & Kovanda 1986, Procházka 1999b, Nelson-Jones et al. 2002, Krahulec 2006	CZ
Taraxacum alpestre	slightly disturbed sites in subalpine grasslands and on rocks; summit area of the Krkonoše Mts, ca 1400–1600 m a.s.l.	Procházka & Štěpánek 1999, Štěpánek 2010, Štěpánek et al. 2011	
Taraxacum indigenum	calcareous fens and fen meadows; recently found at three localities in southern and eastern Bohemia, 180–420 m a.s.l.	Kirschner & Štěpánek 1998, Kirschner 2010	CZ; distribution indicates relict occurrence, presumably more widespread in Bohemia in the past before it was distinguished

Distribution and habitats of endemics

The endemic taxa are very unevenly distributed in the country (Fig. 5). The highest numbers of endemics are confined to the High Sudetes, which are the only mountain ranges in the Czech Republic that extend above the timberline. Among the individual mountain ranges of the High Sudetes (Krkonoše Mts, Králický Sněžník Mts, and Hrubý Jeseník Mts), the number and size of glacial cirques and the extent of alpine and subalpine summit habitats is highest in the Krkonoše Mts, which host 31 endemics (Table 1). Of these, 26 taxa are confined to the Krkonoše Mts, with 6 occur only on the Czech side of the border (*Carex derelicta* – Fig. 6, *Euphrasia corcontica* – Fig. 6, *Hieracium purkynei*, *Knautia arvensis* subsp. *pseudolongifolia* – Fig. 7, *Minuartia corcontica* – Fig. 8, *Sorbus sudetica* – Fig. 9) and 20 also on the Polish side of the border (*Campanula bohemica* – Fig. 6, *Pedicularis sudetica* subsp. *sudetica* – Fig. 8, *Primula elatior* subsp. *corcontica* – Fig. 10, *Taraxacum alpestre* – Fig. 9, and 16 *Hieracium* species and subspecies – Fig. 7). Finally, two taxa also occur in the Hrubý Jeseník Mts (*Campanula rotundifolia* subsp. *sudetica* – Fig. 8, *Hieracium chlorocephalum*), two others in the Králický Sněžník Mts (*Hieracium schustleri*, *H. uechtritzianum*) and one in the the Hrubý Jeseník Mts and Slavkovský les Mts (*Galium sudeticum* s.l. – Fig. 11). Three *Hieracium* endemics, namely *H. chlorocephalum*, *H. pedunculare* and *H. tubulosum*, were each once recorded also in the closely adjacent Jizerské hory Mts (Bräutigam 2001, Chrtek 2004). However, these occurrences were associated with temporary introductions during the time of extensive land-use at high altitudes and all vanished immediately after the traditional management of the landscape ceased (Krahulec 2006). All Krkonoše endemics, including those that only occur on the Polish side of the border, are discussed in detail by Krahulec (2006).

Nine Czech endemics occur in the Hrubý Jeseník Mts, mainly in the two glacial cirques there, and on adjacent mountain summits. Five of them are restricted to these mountains (*Campanula gelida* – Fig. 7, *Carlina biebersteinii* subsp. *sudetica* – Fig. 6, *Dianthus carthusianorum* subsp. *sudeticus* – Fig. 11, *Plantago atrata* subsp. *sudetica* – Fig. 10, *Poa riphaea* – Fig. 9), two occur also in the Krkonoše Mts (*Campanula rotundifolia* subsp. *sudetica* – Fig. 8, *Hieracium chlorocephalum*), one also occurs in the Králický Sněžník Mts (*Hieracium chrysostyloides*) and the last one is the above-mentioned *Galium sudeticum* s.l.

There is a small area of subalpine habitat and a poorly developed cirque in the Králický Sněžník Mts. There is only one avalanche track, with infrequent avalanches and no removal of weathered material (Krahulec 1990). Four Czech endemics occur there but only one of them (*Hieracium nivimontis*) is exclusively endemic to these mountains, others also occur either in the Krkonoše Mts or the Hrubý Jeseník Mts.

In these mountains the endemics occur in a wide range of alpine and subalpine habitats, such as natural grasslands above the timberline, summit rocks and rocky slopes, and various sites in glacial cirques including avalanche tracks; less frequently they occur in moist places such as springs. Most of the endemics are restricted to these natural habitats but *Campanula bohemica*, *Primula elatior* subsp. *corcontica* and locally also some *Hieracium* species (such as *H. nigrescens*, *H. rohlenae* and *H. schustleri*) also occur in man-made subalpine or even montane meadows in the Krkonoše Mts. *Campanula bohemica* is the most frequent among the Sudetes endemics, while the majority of the others are rare and some of them (e.g. *Campanula gelida*, *Carex derelicta*, *Knautia arvensis*

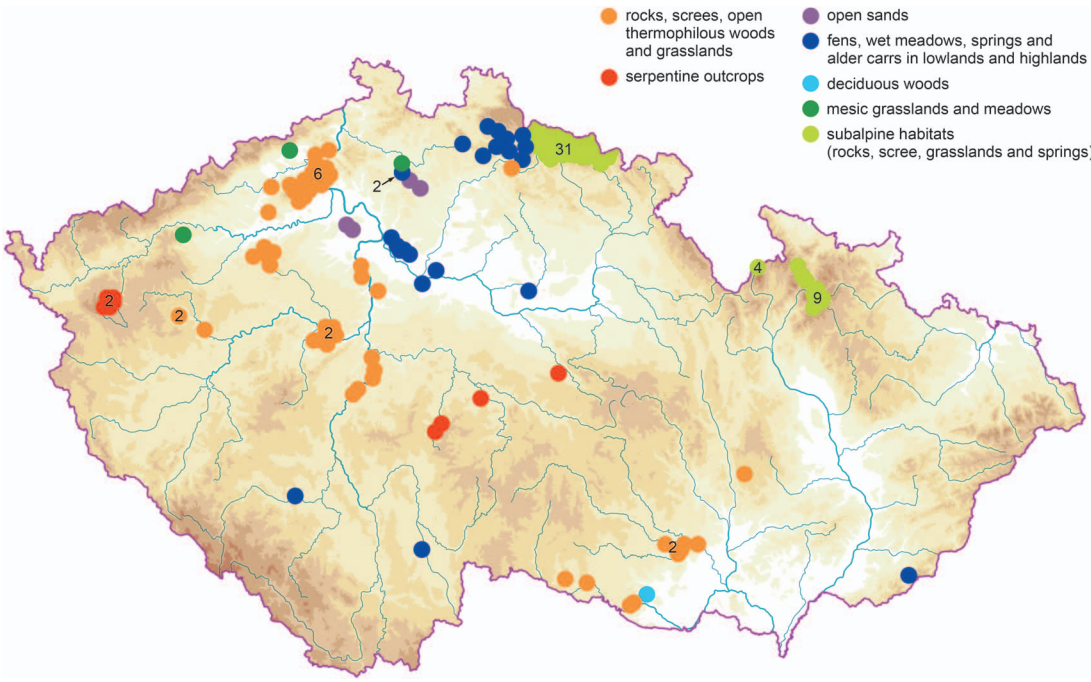


Fig. 5. – Distribution of the main habitats in which Czech endemics occur. Habitats of endemic species of *Rubus* and of *Oenothera moravica* are not mapped. Numbers indicate numbers of endemic taxa (if more than one) occurring in the indicated habitat and in a particular region or locality.

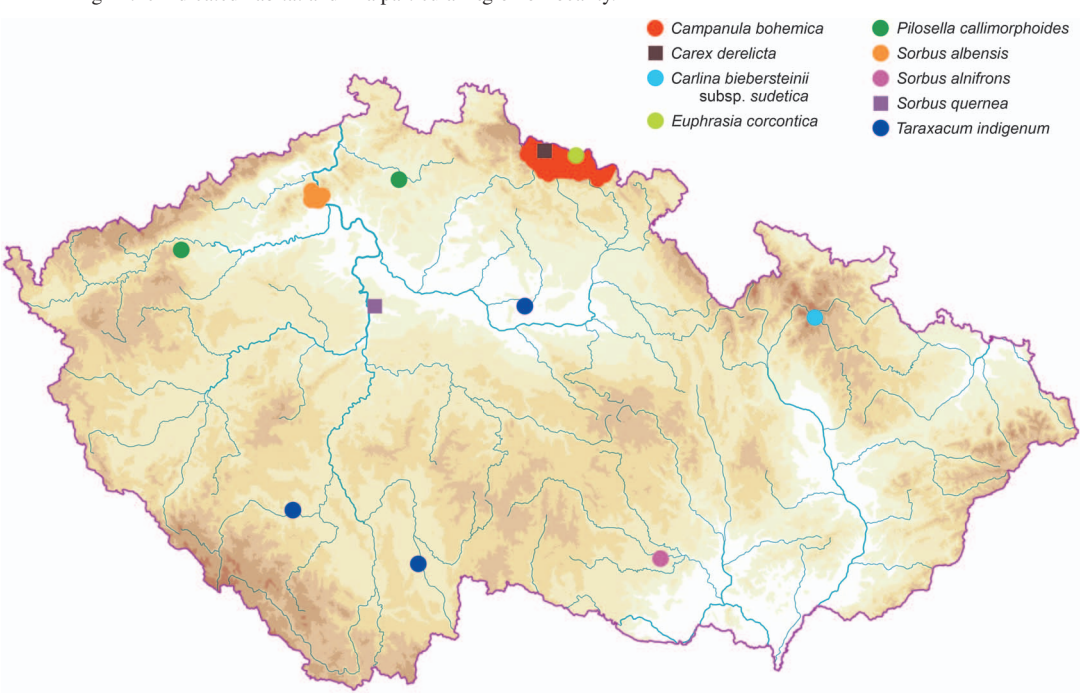


Fig. 6. – Distribution of selected endemic taxa in the Czech Republic.

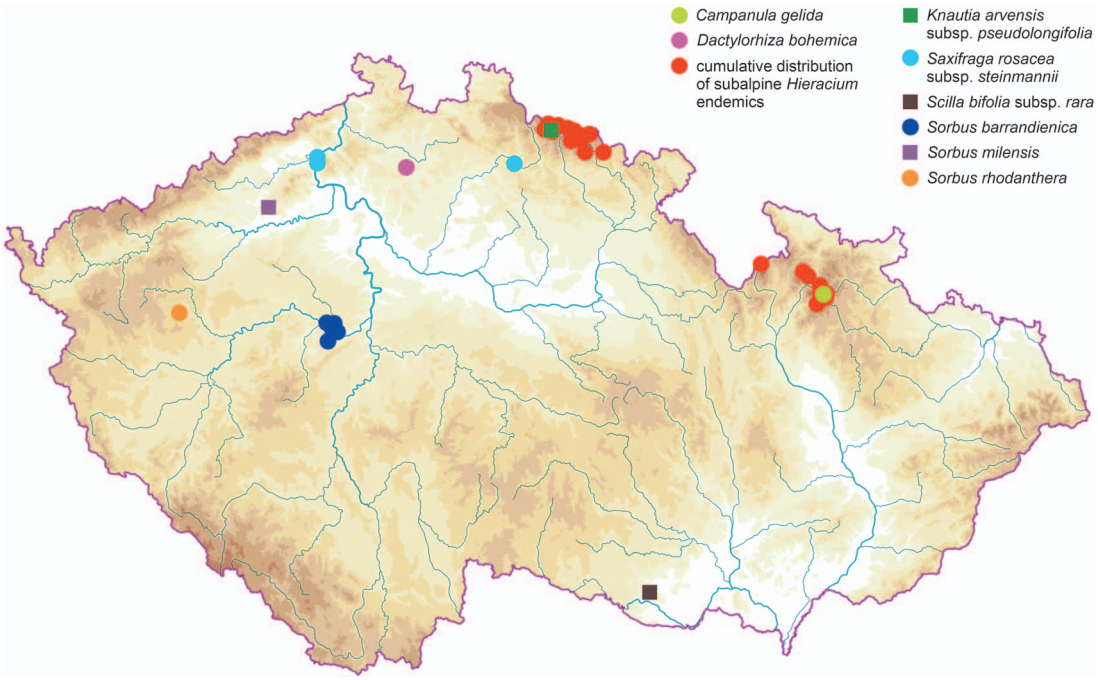


Fig. 7. – Distribution of selected endemic taxa in the Czech Republic.

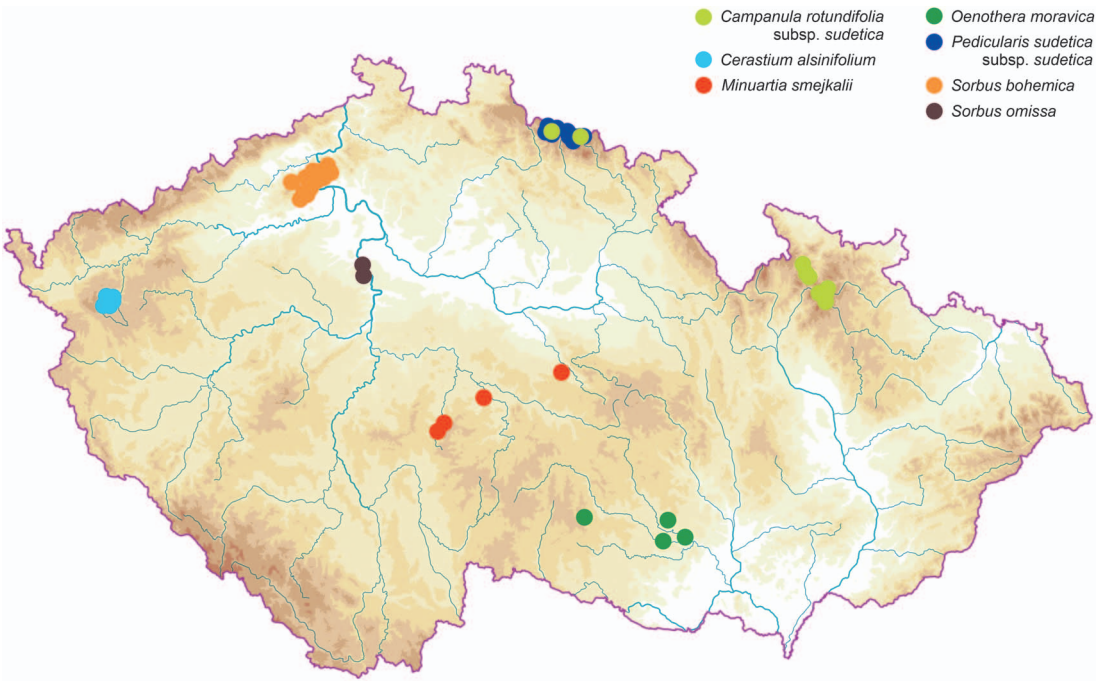


Fig. 8. – Distribution of selected endemic taxa in the Czech Republic.

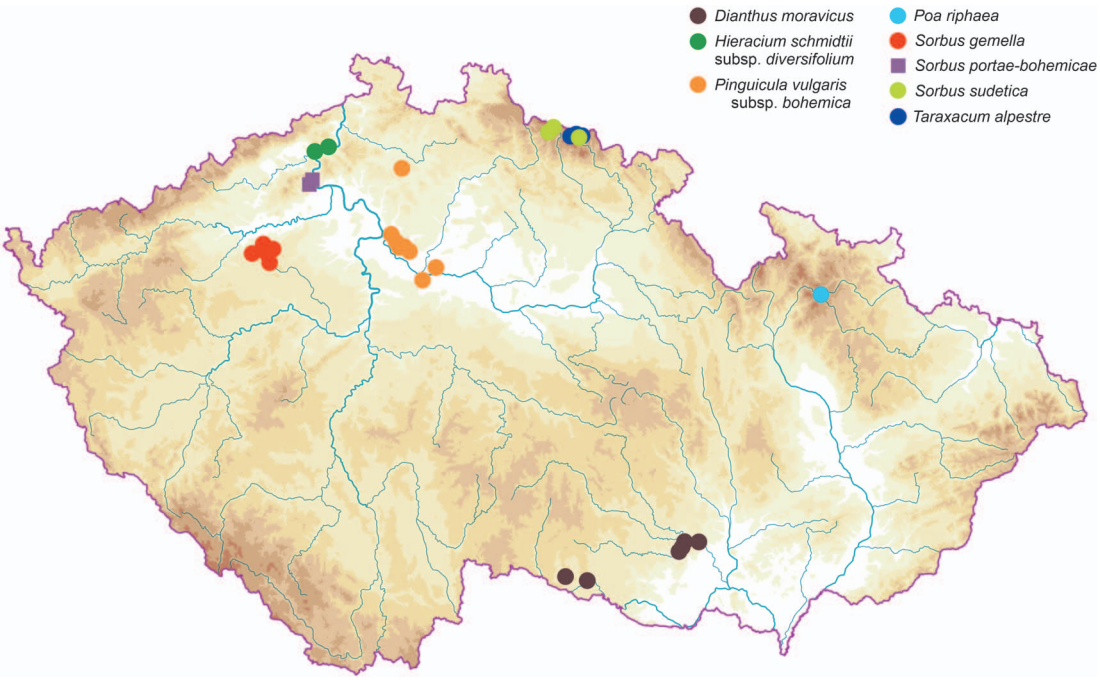


Fig. 9. – Distribution of selected endemic taxa in the Czech Republic.

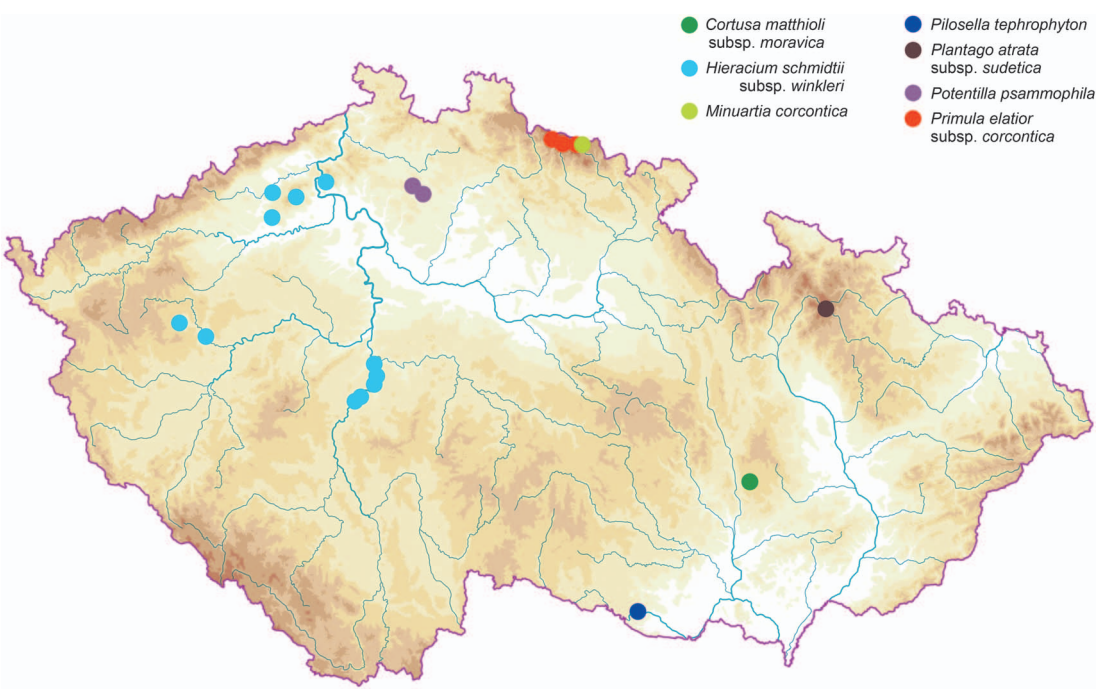


Fig. 10. – Distribution of selected endemic taxa in the Czech Republic.

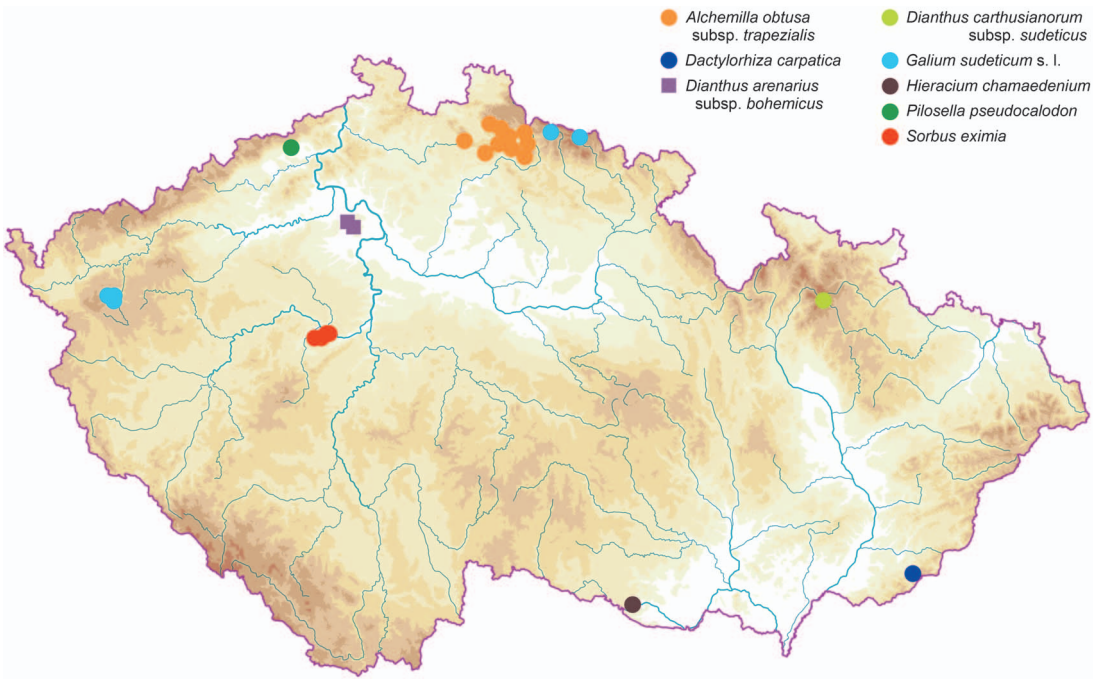


Fig. 11. – Distribution of selected endemic taxa in the Czech Republic.

subsp. *pseudolongifolia*, *Poa riphaea*) only found at a single locality. Two species (*Euphrasia corcontica*, *Hieracium purkynei*) are extinct.

Other endemic taxa are confined to specific habitats at low altitudes (Fig. 5). Seventeen endemics occur on rocks, screes or in associated open thermophilous forests and grasslands. *Dianthus moravicus* (Fig. 9) and *Saxifraga rosacea* subsp. *steinmannii* (Fig. 7) occur in open thermophilous vegetation on rocks in deep river valleys whereas *Cortusa matthioli* subsp. *moravica* (Fig. 10) occurs only on limestone rocks and scree at the bottom of the Macocha abyss in the karst area of Moravský kras. The eleven endemic *Sorbus* species are most frequent in thermophilous open woodlands on rocky outcrops and tops of limestone or basaltic hills (Figs 6–9, 11). Three *Hieracium* endemics of low altitudes (*H. chamaedenium* – Fig. 11, *H. schmidtii* subsp. *winkleri* – Fig. 10, *H. schmidtii* subsp. *diversifolium* – Fig. 9) occur in similar rocky habitats whereas *Pilosella tephrophyton* (Fig. 10) was recorded in dry grasslands. *Dianthus arenarius* subsp. *bohemicus* (Fig. 11) and *Potentilla psammophila* (Fig. 10) are the only Czech endemics occurring in sandy habitats.

The serpentine outcrops in the Bohemian Massif with their specific physical features, chemical properties (particularly the high Mg:Ca ratio, high proportion of heavy metals such as Ni, Cr and Co, and low amount of P) and specific type of vegetation (often relict open pine forests that probably persisted throughout the Holocene) provide unique habitats for three Czech endemics, *Cerastium alsinifolium* (Fig. 8), *Minuartia smejkalii* (Fig. 8) and *Galium sudeticum* s.l. (Fig. 11), and for several other subendemic taxa, such as

Armeria elongata subsp. *serpentini*, *Dianthus carthusianorum* subsp. *capillifrons*, *Knautia arvensis* subsp. *serpentinicola* and *Potentilla crantzii* subsp. *serpentini*.

Species-rich calcareous fens and wet meadows are the habitats of *Dactylorhiza bohemica*, *D. carpatica*, *Pinguicula vulgaris* subsp. *bohemica* and *Taraxacum indigenum*. These habitats are potentially suitable for agriculture and that is why they have been drained and converted to arable land at many sites. There are now only a small number of species-rich fens. The two endemic *Dactylorhiza* species are each known only from one locality (Figs 7 and 11). *Pinguicula vulgaris* subsp. *bohemica* occurred at about 10 localities in the past (Fig. 9), but only one is now extant. The distribution of *Taraxacum indigenum* (Fig. 6) indicates that it also was more widespread in the past but only three populations have been found since the species was recently distinguished taxonomically. A somewhat wider range of moist habitats is occupied by *Alchemilla obtusa* subsp. *trapezialis*, which occurs not only in wet meadows but also around springs and in alder carrs (Fig. 11).

The only endemic confined to moist deciduous forests is *Scilla bifolia* subsp. *rara*, which is known from a single locality (Fig. 7). In contrast, secondary, mostly coniferous forests and associated habitats such as forest fringes and clearings are the habitats of endemic species of *Rubus*. The recently evolved *Oenothera moravica*, which is still confined to a relatively limited area, occurs only in antropogenic habitats (Fig. 8).

A majority of the Czech endemics are rare and/or strongly endangered plants and included on the Red List of the Czech flora (Grulich 2012). Seven endemic species are extinct (*Euphrasia corcontica*, *Hieracium purkynei*, *Pilosella tephrophyton*) or missing and probably extinct (*Hieracium chamaedenium*, *Pilosella callimorphoides*, *P. pseudocalodon*, *Potentilla psammophila*).

Evolution of endemics

The origin of the majority of Czech endemics is associated with glaciation. In response to climatic changes, arctic species migrated from northern Europe southwards while central-European montane and alpine species descended to lower altitudes. After the retreat of the glaciers and climatic amelioration at the Pleistocene/Holocene boundary, most of these species returned to their original areas but relict populations of some species survived in suitable refugia. These peripheral populations were isolated from the main species range and mostly consisted of relatively few of individuals, which facilitated rapid evolution by means of genetic drift. Mutations and natural selection in response to different selection pressures also played their roles. Because the effect of genetic drift is greater and faster in small populations, the isolated relict populations could potentially accumulate enough genetic differences for allopatric speciation even within the relatively short period of time since the end of the last glacial period (approximately 11,600 cal. years BP). These evolutionary processes led in some groups to substantial genetic and phenetic divergence and the respective plants are recognized as distinct endemic taxa.

Ancestors of several endemics found suitable refugia on serpentine outcrops, which are scattered in highland areas of the Bohemian Massif. These serpentines often host open pine forests, which enabled heliophilous species to persist throughout the Holocene. *Cerastium alsinifolium* is an endemic that occurs only in the serpentine area near Mnichov in the Slavkovský les Mts in western Bohemia. It apparently evolved from a relict

population of an alpine species from the *C. alpinum* group that migrated to Bohemia from the Alps during glaciations (Novák 1960). After the expansion of forest in the Early Holocene it largely disappeared surviving only in open pine forests in serpentine areas where a small relict population evolved into a new species. In a similar way, *Minuartia smejkalii* appears to have evolved from populations of *M. gerardii* that descended from the Alps during the glacial period and survived in open pine forest on serpentine outcrops in the Českomoravská vrchovina highlands (Dvořáková 1988). Serpentines in the Slavkovský les Mts are one of the areas where of *Galium sudeticum* s.l. occurs whereas other localities are above the timberline in the Krkonoše and Hrubý Jeseník Mts. This taxon may be polyphyletic, having evolved from two different lineages within *G. pumilum* agg., which currently corespond to subalpine vs. serpentine populations. Their origin and exact taxonomic identity require further study.

Some endemics evolved from relicts of the arctic and alpine flora that survived the postglacial expansion of forest in grasslands or similar treeless habitats above the timberline. *Campanula bohemica* and *C. gelida* (Fig. 12) apparently evolved from *C. scheuchzeri* (Hadač 1977, Kovanda 1977, Hendrych 1981a). This species nowadays occurs in the Alps and a few other high mountains in southern Europe but in colder periods in the past, perhaps during the last glacial period, spread to lowlands in central Europe and remained isolated in the Sudetes Mts in the following postglacial period. Remnants of the isolated populations evolved into the two separate neoendemic species, *C. bohemica* in the Krkonoše Mts and *C. gelida* in the Hrubý Jeseník Mts. Similar processes of genetic and phenetic differentiation occurred in *Plantago atrata*, which diverged during the Holocene into several allopatric subspecies isolated in the high mountains in the southern half of Europe. The small population in the Hrubý Jeseník Mts is recognized as *P. atrata* subsp. *sudetica*. Another stenoendemic species in the Hrubý Jeseník Mts, *Poa riphaea*, apparently evolved from *P. glauca* s.l. (Jirásek & Chrtek 1963, Hadač 1977) that spread from the Arctic to central Europe during a glacial period and currently there are relic populations on some central-European mountains. The small relict population that survived on the Hrubý Jeseník Mts rapidly evolved into a new endemic species. *Minuartia corcontica* is a local endemic of rocky slopes in glacial cirques in the Krkonoše Mts that apparently originated in relict populations of *M. gerardii* (Dvořáková 1999b).

The *Pedicularis sudetica* complex consists of 7–9 taxa with arctic-alpine distributions (Hultén 1961, Molau & Murray 1996). It has the highest diversity in the arctic and northern boreal zones where there are at least six taxa whereas two taxa occur in southern mountain ranges. The population in the Krkonoše Mts is a relict of the arctic flora that occurred in central Europe during the last glacial period. Now it is a remote isolated population far from the continuous range of the *P. sudetica* complex (Fig. 3), with nearest localities on the Kola Peninsula ca 2300 km away, where *P. sudetica* subsp. *arctoeuropaea* occurs. Hultén (1961) classified the plants from the Krkonoše Mts as endemic *P. sudetica* subsp. *sudetica* (Fig. 13). In their recent revision, Molau & Murray (1996) pointed out that this population has been isolated from all the arctic taxa of this complex for a very long time and argued that it is well morphologically differentiated from the others and should be treated as a separate species, *P. sudetica* s. str.

In contrast, relatives of other endemics now restricted to refugia above the timberline have the centre of their present-day distributions in warmer low-altitude areas. Relict, mostly diploid populations of *Knautia arvensis* occur in several refugial localities on the

Fig. 12. – *Campanula gelida* on the summit rock on Mt. Petrovy kameny in the Hrubý Jeseník Mts (17th July 2003, photo Jan Suda).

Fig. 13. – *Pedicularis sudetica* subsp. *sudetica* near the Luční bouda chalet in the Krkonoše Mts (14th June 2007, photo Martin Hanzl).

Fig. 14. – *Carlina biebersteinii* subsp. *sudetica* in the Malá kotlina glacial cirque in the Hrubý Jeseník Mts (8th August 2000, photo Leo Bureš).

Fig. 15. – *Saxifraga rosacea* subsp. *steinmannii* on rocks in the valley of the Labe river at Ústí nad Labem (16th May 2011, photo Karel Nepraš).

Bohemian Massif, within an area otherwise occupied by the widespread tetraploids classified as *K. arvensis* subsp. *arvensis* (Štěpánek 1982, 1989, 1997, Kaplan 1998, Kolář et al. 2009). These relict populations are confined to two different types of habitat and are morphologically differentiated: populations occurring in open pine forest on serpentine outcrops in Bohemia and closely adjacent Bavaria are distinguished as *K. arvensis* subsp. *serpentinicola* (Štěpánek 1997, Kaplan 1998), whereas diploids restricted to subalpine habitats in the Kotelné jámy cirque in the Krkonoše Mts are treated as *K. arvensis* subsp. *pseudolongifolia* (Štěpánek 1989, 1997). The origin of these relict populations is thought to be remnants of an ancestral diploid of *K. arvensis* that was widespread in central Europe in the early postglacial period in non-forest vegetation, namely during the Preboreal and Boreal periods, before the expansion of forest (Štěpánek 1989, Kaplan 1998). Under these specific conditions, the isolated relict populations gradually diverged into new entities. The widespread tetraploids now occurring in man-made habitats in central Europe evolved from diploids displaced by the spreading forest to the southern part of central Europe. They later colonized most of the northern half of Europe when this area was deforested by humans (Kaplan 1998). A similar evolutionary history of continuous differentiation of small populations isolated in subalpine refugia may be hypothesized for *Campanula rotundifolia* subsp. *sudetica*, *Carlina biebersteinii* subsp. *sudetica* (Fig. 14), *Dianthus carthusianorum* subsp. *sudeticus* and *Primula elatior* subsp. *corcontica*, of which their closest relatives occur at low altitudes, often mainly in warm areas.

Endemics of another group have evolved from relicts surviving in specific habitats at low altitudes. *Cortusa matthioli* subsp. *moravica* has evolved from a small isolated population. Both *Dianthus moravicus* and *Saxifraga rosacea* subsp. *steinmannii* (Fig. 15) also originated on isolated rocky outcrops. *Dianthus arenarius* subsp. *bohemicus* (Fig. 16) is confined to open sandy habitats in the northern part of central Bohemia. The ancestral form of *D. arenarius* was apparently widespread in the northern part of central Europe and north and east of the Carpathians (Sarmatian element) during the Preboreal period (Novák 1927). Later isolation associated with the spread of forest led to differentiation into 4–5 currently recognized subspecies. Among them, subsp. *bohemicus* is isolated in the most south-western outpost of the species range (Fig. 18). In contrast to these predominantly dry habitats, *Pinguicula vulgaris* subsp. *bohemica* occurs in species-rich mossy fens.

Evolution of some endemic species was affected by hybridization events. These often occurred when two previously allopatric species temporarily came into contact during major shifts in the ranges of species triggered by climatic changes. In some groups, hybridization was followed by a change in the mode of reproduction to agamospermy.

In addition to mostly diploid sexually reproducing species, the genus *Sorbus* includes also apomictic polyploids that evolved from hybridization of diploids (Kárpáti 1960). Apomictic *S. sudetica* (Fig. 17) resulted from a past hybridization of *S. chamaemespilus* and *S. aria* s.l. (Kárpáti 1960, Challice & Kovanda 1978, Jankun & Kovanda 1986, Kovanda 1992c, Nelson-Jones et al. 2002). It probably originated during a temporary co-occurrence of the parental species in the Krkonoše Mts in the Early Holocene, perhaps during the Boreal period. The later climatic and vegetation changes caused the disappearance of parental species from Krkonoše but *S. sudetica* occurs in suitable habitats in two glacial cirques.

Other apomictic *Sorbus* endemics occur in relict rocky habitats in warmer areas. Chemotaxonomic investigations indicate that *S. bohemica* originated from hybridization

between *S. danubialis* and *S. torminalis* (Challice & Kovanda 1978) whereas *S. eximia* arose from backcrossing of a *S. aria* s.l. × *S. torminalis* F1 hybrid with *S. aria* s.l. (Challice & Kovanda 1986). Judging from its morphology, the recently described triploid *S. milensis* originated from a cross between sexual *S. aria* s.l. and *S. torminalis* (Lepší et al. 2008), while *S. albensis*, *S. portae-bohemicae* and *S. omissa* originated from crosses between *S. danubialis* and *S. torminalis* (Lepší et al. 2008, Velebil 2012) and *S. barrandienica* is assumed to have originated from a cross between *S. danubialis* or *S. aria* s.l. and *S. torminalis* (Vít et al. 2012).

Ancient hybridization associated with subsequent agamospermy has been the key speciation mechanisms also in *Taraxacum*, *Hieracium*, *Rubus* and *Alchemilla*. However, the parental species and when the currently recognized taxa originated are generally unknown because the variation and evolutionary histories within these genera are too complicated. Considering the fact that related sexual diploids of many of these apomictic taxa either occur in distant areas, such as the East Carpathians or southern Europe (*Hieracium*, *Taraxacum*), or may be extinct (*Alchemilla*), they may be very old lineages. Considering the pattern of distribution of the Krkonoše endemics in these groups and of their relatives, Krahulec (2006) assumes they are of pre-Holocene origin and occurred over a wide area at low altitudes during the glacial periods. At the end of the last (Weichselian/Würm) glaciation, some of them followed the retreat of the continental glaciers into northern Europe while others colonized high mountain ranges in the southern half of Europe.

The recently described *Potentilla psammophila* belongs to *Potentilla* subsect. *Collinae*, which includes apomictic species that originated from hybridization between *P. argentea* and *P. verna* or *P. incana*. The newly distinguished *P. psammophila* is a close relative of *P. lindackeri* s. str. and seven other microspecies that originated from *P. argentea* × *P. verna* (Soják 2009b).

In contrast to the relative stability of apomicts, small isolated populations of sexual plants are subject to genetic drift, which promotes speciation. It is hypothesized that the origin and evolution of *Carex derelicta* was dependent on a geographically isolated population of the NW European *C. scandinavica* (or a close relative of it) persisting in a refugium in the Krkonoše Mts as a glacial relict and subsequently being introgressed by another taxon of the subsect. *Serotinae*, perhaps *C. demissa* (Štěpánková 2008).

Another endemic in the Krkonoše Mts, *Euphrasia corcontica*, is thought to have originated from the hybridization of *E. micrantha* and *E. minima* (Smejkal 1963, Smejkal & Dvořáková 2000). The latter species currently does not occur in the Czech Republic but an isolated relict population still survives on the Polish side of Krkonoše/Karkonosze. The centre of its distribution is in the Alps and it may have colonized the lowlands from there during one of the glacial periods, like many other alpine species, and hybridized with local *E. micrantha* during the last glacial period or in the early Holocene. The hybridogenous population persisted in suitable subalpine refugia in Krkonoše throughout most of the Holocene and was repeatedly recorded by botanists during the 19th century. Unfortunately, this taxon is now extinct, which is why it is not possible to carry out a biosystematic investigation of its origin.

Most tetraploid European *Dactylorhiza*, including the widespread *D. majalis* and *D. traunsteineri*, are considered to be allotetraploids. These have evolved by repeated hybridization between diploid species *D. incarnata* s.l. and *D. fuchsii* s.l. (Hedrén 1996,

Fig. 16. – *Dianthus arenarius* subsp. *bohemicus* in open sandy grassland at Kleneč (1st July 2010, photo Jana Kalůsková).

Fig. 17. – *Sorbus sudetica* in the Obří důl glacial cirque in the Krkonoše Mts (20th June 2005, photo Petr Vít).

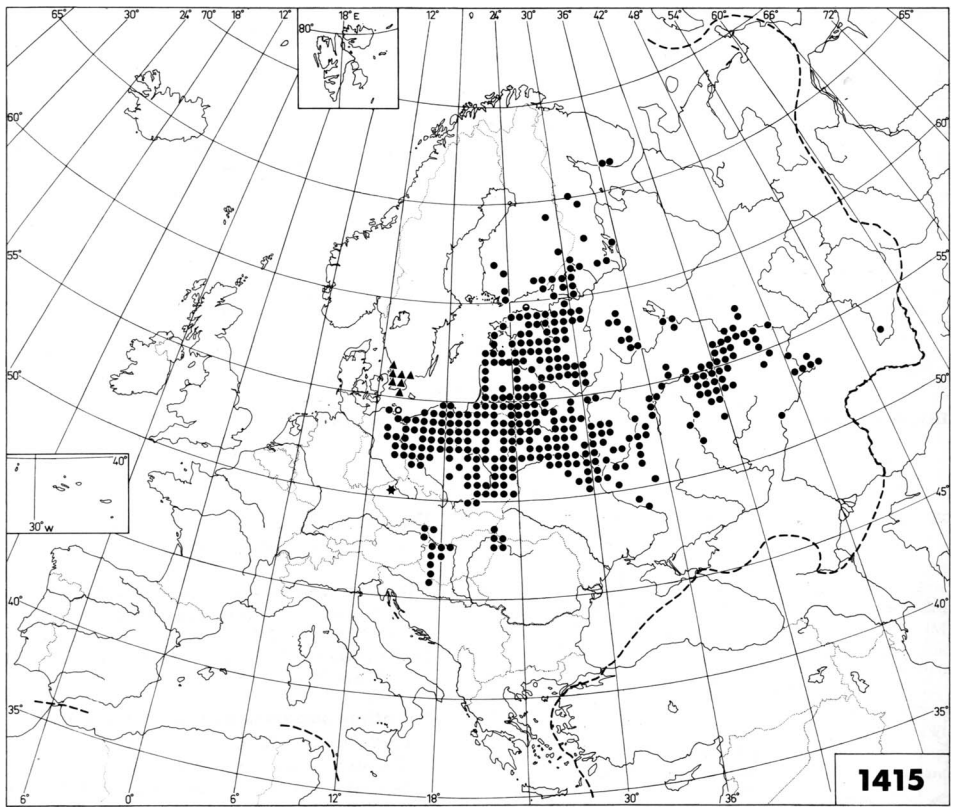


Fig. 18. – Total distribution of *Dianthus arenarius* s.l. The only locality of the local endemic subsp. *bohemicus* in central Bohemia, indicated by an asterisk, is the most south-western outpost of this species range. Reproduced from Jalas & Suominen (1986), reproduced with permission.

Devos et al. 2006, Pillon et al. 2007, Nordström & Hedrén 2009). Morphologically, geographically and/or ecologically separated allotetraploids of this complex are recognized as species or subspecies. Some even hybridize with each other or backcross with parental taxa. This hybridogenous complex includes two morphologically distinct local populations in the Czech Republic, which were described as *D. bohemica* (Businský 1989) and *D. *carpatica* (Batoušek & Kreutz 1999).

The diversity of *Pilosella* includes so called (1) basic species, (2) intermediate hybridogenous species, and (3) recent hybrids (e.g. Nägeli & Peter 1885, Zahn 1921–1923, Chrtek 2004, Rotreklová et al. 2005, Krahulec et al. 2008, 2011, Křišťálová et al. 2010). The latter two groups both include plants of hybrid origin, of which the intermediate hybridogenous species are stabilized and often occur in the absence of their parental species unlike the F1 hybrids or very early subsequent generations. Based on their morphology two Czech *Pilosella* endemics are of hybrid origin. *Pilosella callimorphoides* apparently originated from hybridization between *P. levieri* and *P. officinarum* (formula *P. levieri* < *P. officinarum*) whereas *P. pseudocalon* is the result of a cross between *P. calodon* and *P. setigera* (Chrtek 2004). Their taxonomic identity and evolutionary history cannot be investigated because both species are now extinct.

Floristic geoelements

Analysing the ranges of species provides a basis for distinguishing geographic (floristic) elements (geoelements), which are groups of species with similar distributions. The traditional concept of geoelements is based on heuristic approaches of classification using visual inspection of distribution maps and expert judgement. There is no analytical revision of European geoelements using numerical methods mainly because there is no complete synthesis of the distribution data at the continental level. Finnie et al. (2007) recently attempted to provisionally identify floristic elements in the European flora using a numerical analysis of the distributions of species mapped in 12 volumes of Atlas Florae Europaeae (Jalas & Suominen 1972–1994, Jalas et al. 1996, 1999), which represent approximately 20% of the European flora. Their clustering procedure classified the species into 18 floristic elements. This, however, cannot be considered to be a final revision of European elements because it is not based on a taxonomically representative sample. For these reasons, the floristic characteristics given here inevitably rely on the geoelements traditionally distinguished in central European literature.

The flora of the Czech Republic includes mainly lowland to mountain central-European plants. The Czech Republic is situated at the intersection of several important European migration routes. The Czech flora is composed of almost all the floristic elements occurring in central Europe. Based on similarities in the geographic distributions of species (see e.g. Hultén 1964, 1971, Meusel et al. 1965, 1978, Jalas & Suominen 1972–1994, Hultén & Fries 1986, Meusel & Jäger 1992, Jalas et al. 1996, 1999, Kurtto et al. 2004, 2007, 2010), a number of geoelements are distinguished in central European literature (e.g. Meusel et al. 1965, Walter & Straka 1970, Hendrych 1984, Walter 1986, Slavík 1988, 1995). Their number, delimitation and hierarchical subdivision vary between authors. For example, a species that is characterized as sub-arctic-alpine by an author can be viewed as boreal by another. In the absence of an analytical revision based on extensive sets of complete data, only the principal geoelements traditionally distinguished in central Europe and relevant to the Czech Republic are discussed here.

The Central-European geoelement (in a narrow sense) includes species with their centres of distribution entirely in or in a large part of central Europe, but sometimes extending north to central Scandinavia, south to mountains in southern Europe and east to the Ural Mts. Its species mostly occur in the zone of deciduous or mixed forests (with dominance of oak, hornbeam and beech forests) where the summers are mild with a relatively high precipitation and mild winters with a short period of frost. This is the geoelement most frequently represented in the Czech flora. Woody plants are represented by *Acer platanoides*, *A. pseudoplatanus*, *Alnus glutinosa*, *Carpinus betulus*, *Cornus sanguinea*, *Corylus avellana*, *Fagus sylvatica*, *Fraxinus excelsior*, *Hedera helix*, *Prunus avium*, *Quercus petraea* and *Tilia cordata*, herbaceous plants in this geolement include *Ajuga reptans*, *Aquilegia vulgaris*, *Alliaria petiolata*, *Allium ursinum*, *Arrhenatherum elatius*, *Arum maculatum*, *Astrantia major*, *Atropa bella-donna*, *Briza media*, *Campanula patula*, *Carex brizoides*, *C. sylvatica*, *C. umbrosa*, *Cirsium oleraceum*, *Colchicum autumnale*, *Corydalis cava*, *Cynosurus cristatus*, *Dentaria enneaphyllos*, *Euphrasia officinalis*, *Euphorbia cyparissias*, *Ficaria verna*, *Galeobdolon luteum*, *G. montanum*, *Galium sylvaticum*, *Genista germanica*, *G. tinctoria*, *Geranium robertianum*, *Glyceria fluitans*, *Helianthemum grandiflorum* subsp. *obscurum*, *Hepatica nobilis*, *Hordelymus europaeus*, *Hylotelephium*

maximum, *Hypericum montanum*, *Lathraea squamaria*, *Lunaria rediviva*, *Luzula luzuloides*, *Lysimachia nummularia*, *Mercurialis perennis*, *Petasites albus*, *Phyteuma spicatum*, *Pimpinella major*, *Polygonatum multiflorum*, *Pulmonaria officinalis*, *Ranunculus lanuginosus*, *Stachys sylvatica*, *Stellaria holostea*, *Thalictrum aquilegiifolium* and *Trifolium medium*.

The distributions of some species have shifted towards eastern Europe, often as far as the Ural Mts, and these are sometimes distinguished as the Sarmatian geoelement (or subelement). They are more tolerant of a continental climate, which is drier and with a greater oscillation in temperature between summer and winter. In the Czech Republic they have limited distributions, often being relicts from late glacial or early postglacial ages. *Astragalus arenarius* (Fig. 19), *Dianthus arenarius*, *Jurinea cyanoides* and *Thesium ebracteatum* may be cited as examples.

The Central-European-(sub-)alpine geoelement includes species of subalpine to alpine belts with centres of distribution in the mountains of central Europe. This geoelement includes *Alnus alnobetula*, *Biscutella laevigata*, *Calamagrostis villosa*, *Gentiana asclepiadea*, *G. punctata*, *Geum montanum*, *Hieracium villosum*, *Homogyne alpina*, *Hypochaeris uniflora*, *Lilium bulbiferum*, *Luzula sylvatica*, *Meum athamanticum*, *Pinus mugo*, *Potentilla aurea*, *Primula minima*, *Rosa pendulina*, *Scabiosa lucida* and *Sesleria caerulea*. The species that occur mainly or exclusively at high altitudes in the Alps and Carpathians, however, are sometimes placed in the Alpine-Carpathian geoelement.

The Carpathian geoelement is confined to the Carpathians or sometimes extend into adjacent regions. It includes alpine, subalpine and montane species, which in the Czech Republic occur mainly in the easternmost part particularly in the Moravskoslezské Beskydy Mts. Examples include *Aconitum firmum* subsp. *moravicum*, *Cardamine amara* subsp. *opicii*, *Centaurea oxylepis*, *Dentaria glandulosa* (Fig. 20), *Euphrasia slovaca*, *Salix silesiaca*, *Scilla kladnii* and *Thymus pulcherrimus*.

The Alpine geoelement occurs mainly in the Alps, and sometimes also in their foothills. Several species reach the Czech Republic, occurring either in the Šumava Mts or the whole of western Bohemia, but only exceptionally at isolated localities further east. *Erica carnea*, *Gentiana pannonica*, *Polygala chamaebuxus*, *Salix appendiculata*, *Soldanella montana*, *Thesium rostratum* and *Willemetia stipitata* subsp. *stipitata* may be given as examples.

The Arctic geoelement, with centres of distribution in northern tundra where there is permafrost, is absent in the Czech Republic but the Arctic-alpine geoelement, which occurs also in more southern mountains, is represented here by *Bartsia alpina*, *Carex atrata*, *C. rupestris*, *Diphasiastrum alpinum*, *Epilobium anagallidifolium*, *Gnaphalium norvegicum*, *Hieracium alpinum*, *Juncus trifidus*, *Luzula spicata*, *Pedicularis sudetica* (s.l.) (Fig. 3), *Pseudorchis albida*, *Rhodiola rosea*, *Salix herbacea* and *Saxifraga oppositifolia*. Similarly the Sub-arctic element extends further south than the Arctic geoelement and occurs in forest tundra, which in the Czech Republic is represented by the Sub-arctic-alpine geoelement with species such as *Betula nana*, *Carex capillaris*, *C. chordorrhiza*, *Eriophorum vaginatum*, *Phleum alpinum*, *Polystichum lonchitis*, *Rubus chamaemorus* (Fig. 4), *Salix myrtilloides*, *Selaginella selaginoides*, *Trichophorum alpinum* and *Viola biflora*.

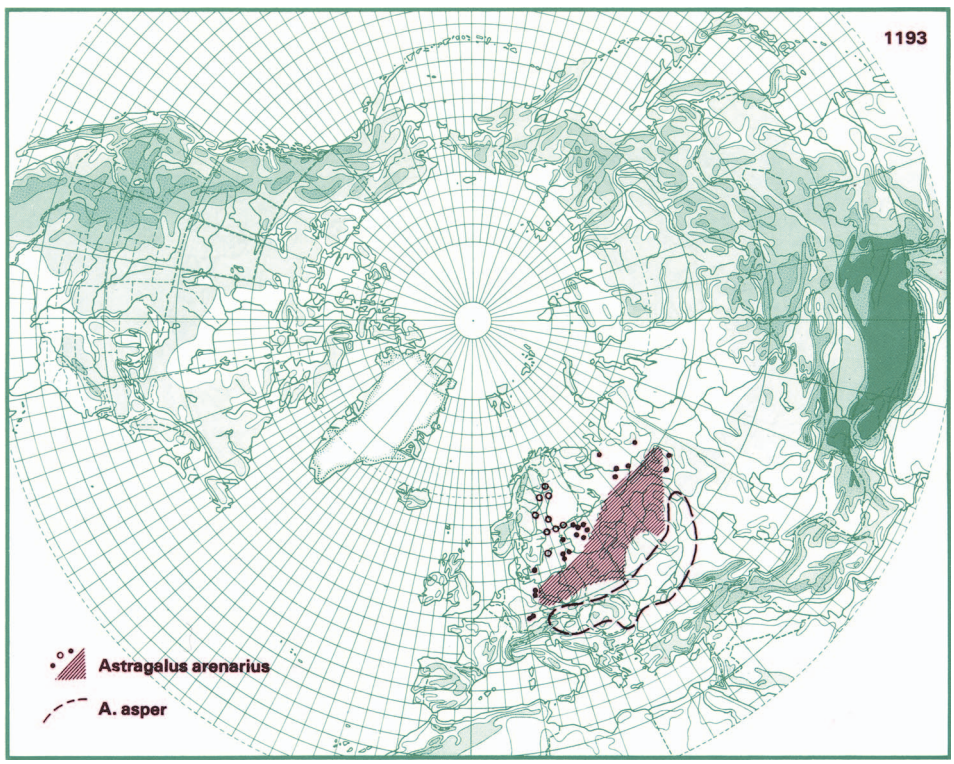


Fig. 19. – Distribution of *Astragalus arenarius*, a Sarmatian geoelement, and *Astragalus asper*, a Pontic-South-Siberian geoelement. Both species reach the western limit of their distributions in central Europe. Reproduced from Hultén & Fries (1986), reproduced with permission.

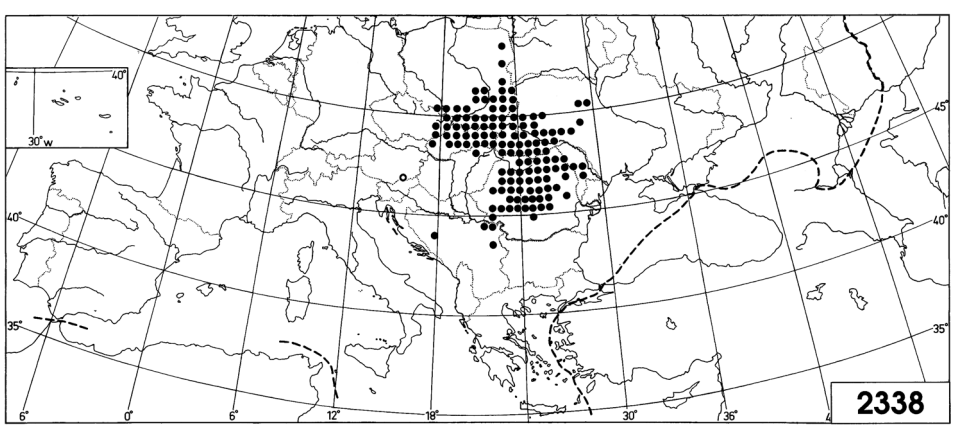


Fig. 20. – *Dentaria glandulosa* is an example of the Carpathian geoelement that entered the Czech Republic from the east and whose western border of distribution is in Moravia. Reproduced from Jalas & Suominen (1994), reproduced with permission.

The Boreal geoelement includes species adapted to long winters with centres of distribution in the boreal zone, which occur further south mostly in mountains, usually in coniferous forests (in more oceanic regions they sometimes occur in mixed or broad-leaved deciduous forests). Their occurrence at low altitudes is often associated with the occurrence of wet habitats such as marshes and peat bogs. These plants were more frequent in central Europe during the early postglacial period but many still occur in some types of vegetation. This geoelement is represented, for example, by *Calla palustris*, *Carex canescens*, *Cirsium heterophyllum*, *Coeloglossum viride*, *Corallorhiza trifida*, *Epilobium angustifolium*, *Eriophorum angustifolium*, *Geranium pratense*, *Lycopodium annotinum*, *Maianthemum bifolium*, *Melampyrum sylvaticum*, *Menyanthes trifoliata*, *Persicaria amphibia*, *Rhododendron tomentosum*, *Trientalis europaea*, *Vaccinium myrtillus* and *V. vitis-idaea*.

The Sub-boreal geoelement is similar to the Boreal geoelement but extends further south, particularly in the more oceanic regions. In these areas it is more frequent in mixed and deciduous forests and at low altitudes. This geoelement is one of the most common in the Czech flora. It includes, for example, the trees, *Alnus incana*, *Betula pubescens*, *Frangula alnus*, *Juniperus communis*, *Pinus sylvestris*, *Salix caprea*, *Sorbus aucuparia* and *Viburnum opulus*, and herbaceous plants, *Achillea ptarmica*, *Angelica sylvestris*, *Athyrium filix-femina*, *Bistorta officinalis*, *Cardamine pratensis*, *Carex acuta*, *Chrysosplenium alternifolium*, *Circaea alpina*, *Delphinium elatum*, *Deschampsia cespitosa*, *Dryopteris filix-mas*, *Filipendula ulmaria*, *Geum rivale*, *Glyceria maxima*, *Gnaphalium sylvaticum*, *Gymnadenia conopsea*, *Heracleum sphondylium*, *Hypericum perforatum*, *Lycopodium clavatum*, *Melampyrum pratense*, *Melica nutans*, *Milium effusum*, *Oxalis acetosella*, *Paris quadrifolia*, *Phalaris arundinacea*, *Poa nemoralis*, *Potamogeton natans*, *Potentilla erecta*, *Pyrola rotundifolia*, *Rumex acetosa*, *Sanguisorba officinalis*, *Scirpus sylvaticus*, *Symphytum officinale* and *Urtica dioica*.

The South-Siberian geoelement includes species distributed mainly in southern Siberia and adjacent regions. Many of them occur in Europe and may be called the European-South-Siberian geoelement. They tolerate extreme continental climate with a short growing season, warm but short summers and long winters with severe frosts. They occur in a broad range of habitats including steppes and forests. The examples occurring in the Czech Republic are *Adenophora liliifolia*, *Artemisia campestris*, *Brachypodium pinnatum*, *Fragaria viridis*, *Filipendula vulgaris*, *Inula salicina*, *Koeleria glauca*, *Lilium martagon*, *Phleum phleoides*, *Platanthera bifolia*, *Pimpinella saxifraga*, *Rhamnus cathartica*, *Silene nutans*, *Veratrum album* subsp. *lobelianum* and *Vicia sylvatica*.

The Pontic geoelement (sometimes called the Pontic-Pannonian geoelement) has centres of distribution in the steppes and forest-steppes of southern Ukraine and southern part of European Russia. Many of these species spread west or south-west through the Pannonian basin to central Europe, or even extends further west. This element comprises species that tolerate a continental climate with warm and dry summers and extremely cool winters. Within this geoelement, Slavík (1988) distinguishes the Pannonian subelement that differs from the Pontic-South-Siberian element that occurs along the northern coast of the Black Sea and in the south-Siberian steppes. Examples of the Pontic geoelement (in the broad sense) include *Adonis vernalis*, *Artemisia pontica*, *Clematis integrifolia*, *C. recta*, *Crepis pannonica*, *Echium maculatum*, *Galium glaucum*, *Inula germanica*, *I. hirta*, *Iris pumila*, *Linaria genistifolia*, *Linum flavum*, *Melica transsilvanica*, *Prunus*

fruticosa, *Ranunculus illyricus*, *Scabiosa ochroleuca*, *Scorzonera purpurea* and *Stipa pennata*. The Sub-pontic geoelement is similarly distributed and its species have similar ecological requirements as those of the Pontic geoelement but tend to occur more frequently in open forests than on steppes. They more frequently occur in central Europe and are more numerous there than species of the Pontic geoelement. Species occurring in the Czech Republic include *Anemone sylvestris*, *Astragalus glycyphyllos*, *Chamaecytisus ratisbonensis*, *Cota tinctoria*, *Euonymus verrucosus*, *Gentiana cruciata*, *Iris aphylla*, *Ononis arvensis*, *Potentilla recta*, *Prunus spinosa*, *Securigera varia*, *Seseli annuum*, *Stachys recta*, *Tanacetum corymbosum*, *Trifolium montanum*, *Verbascum lychnitis* and *Vincetoxicum hirundinaria*.

The Mediterranean geoelement occurs around the Mediterranean Sea or in parts of this region. Its species occur where the winters are short and mild with high precipitation and can tolerate hot and dry summers. They extend northwards to the southern edge of central Europe but do not reach the Czech Republic. The Sub-Mediterranean geoelement occurs further north and also occurs in central Europe. Those species that reach the Czech Republic mostly spread through the Balkan Peninsula and from the southern and eastern edges of the Alps and often occur in thermophilous oak forests. This geoelement is well represented in the Czech Republic, e.g. by *Bifora radians*, *Bromus erectus*, *Buglossoides purpurocaerulea*, *Carex michelii*, *Cornus mas*, *Coronilla vaginalis*, *Danthonia alpina*, *Euphorbia amygdaloides*, *Globularia bisnagarica*, *Heliotropium europaeum*, *Ligustrum vulgare*, *Linum tenuifolium*, *Loranthus europaeus*, *Medicago minima*, *Melica ciliata*, *Melittis melissophyllum*, *Muscari comosum*, *Ophrys apifera*, *Orchis purpurea*, *Orlaya grandiflora*, *Quercus pubescens*, *Potentilla micrantha*, *Prunella laciniata*, *Pseudoturritis turrita*, *Rosa gallica*, *Salvia verticillata*, *Sorbus torminalis*, *Staphylea pinnata*, *Teucrium chamaedrys*, *Thlaspi perfoliatum*, *Trinia glauca*, *Viburnum lantana* and *Viola alba*.

The Atlantic geoelement occurs mainly along the coast of the Atlantic Ocean and in adjacent regions from Portugal to Norway. Its species occur where the winters are mild and sometimes frostless and the summers are mild with high precipitation. This geoelement is in its strict sense represented in the Czech Republic only by *Erica tetralix* (questionably native) and *Narthecium ossifragum* (a single locality, now extinct); their Czech localities are at the border of their distribution. The Sub-Atlantic geoelement extends further on to the European mainland and is slightly more tolerant of frost and drought. It is more numerous in the Czech Republic than the Atlantic geoelement, and is represented e.g. by *Aira praecox*, *Hypericum humifusum*, *H. pulchrum*, *Calluna vulgaris*, *Carex pseudobrizoides*, *Chrysosplenium oppositifolium* (Fig. 21), *Cytisus scoparius*, *Euphrasia nemorosa* (s.l.), *Luronium natans*, *Lysimachia nemorum*, *Pedicularis sylvatica*, *Polygala serpyllifolia*, *Potamogeton polygonifolius*, *Rhynchospora fusca* and *Sagina subulata*.

The Sub-Atlantic-Sub-Mediterranean geoelement is in many respects transitional between the two respective geoelements. It extends into central Europe from the south and/or west. Its species usually occur in deciduous forests where the winters are mild and short and the summers not extremely dry and hot. Examples include *Asplenium scolopendrium*, *Genista pilosa*, *Hippocrepis comosa*, *Lathyrus nissolia*, *Osmunda regalis*, *Saxifraga granulata* and *Trifolium striatum*.

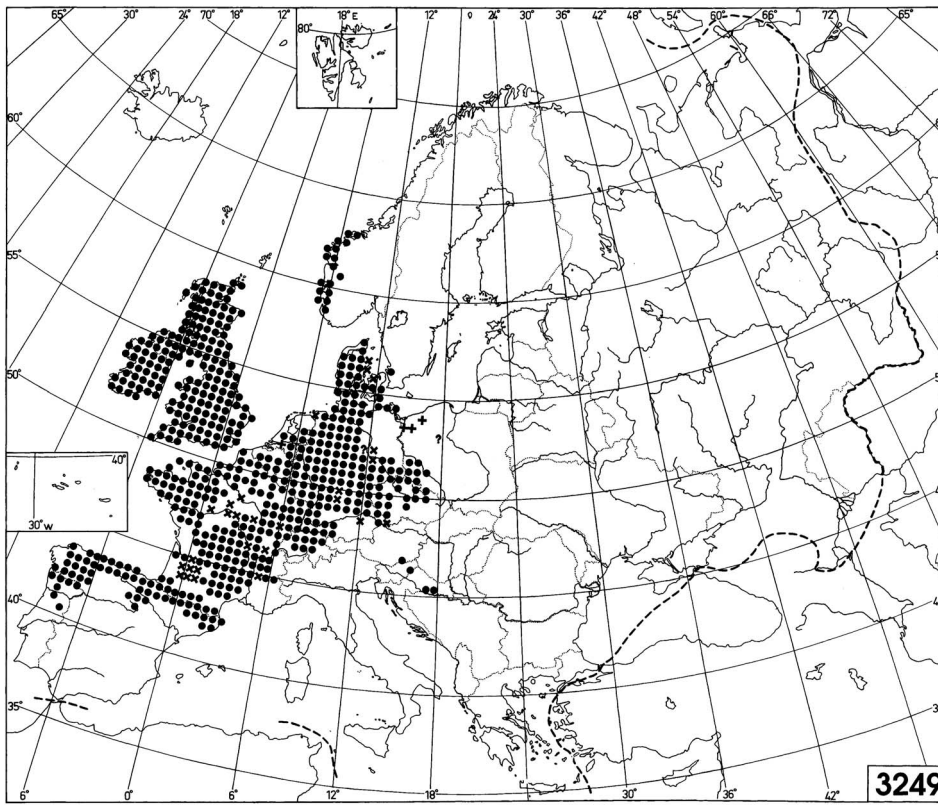


Fig. 21. – The Sub-Atlantic geoelement *Chrysosplenium oppositifolium* has the eastern limit of its continuous distribution in the Czech Republic. Reproduced from Jalas et al. (1999), reproduced with permisson.

Boundary and outlying elements

A number of widespread species are on the borders of their distributions in the Czech Republic (Slavík 1988). Boundary elements are at the limit of their more or less continuous distributions here, whereas outlying elements occur at a few isolated sites in the Czech Republic, which are well separated from the rest of their distribution. The limits of their distributions are often not the absolute limit in a particular geographic direction but rather the regional edge of the distribution.

Most frequently represented are thermophilous species of the Sub-Mediterranean and Pontic-South-Siberian geoelements that occur in the Pannonian Basin and have their northern or north-western (in a few cases north-eastern) boundaries in the warm and dry area of southern Moravia or even in Bohemia. These include *Allium flavum*, *Astragalus asper* (Fig. 19), *A. austriacus*, *Buglossoides purpurocaerulea*, *Cirsium brachycephalum*, *Clematis integrifolia*, *Cotoneaster melanocarpus*, *Crambe tataria* (Fig. 22), *Crypsis alopecuroides*, *C. schoenoides*, *Danthonia alpina*, *Draba nemorosa*, *Euphorbia epithymoides*, *Globularia bisnagarica*, *Helianthemum canum*, *Himantoglossum adriaticum*, *Iris*

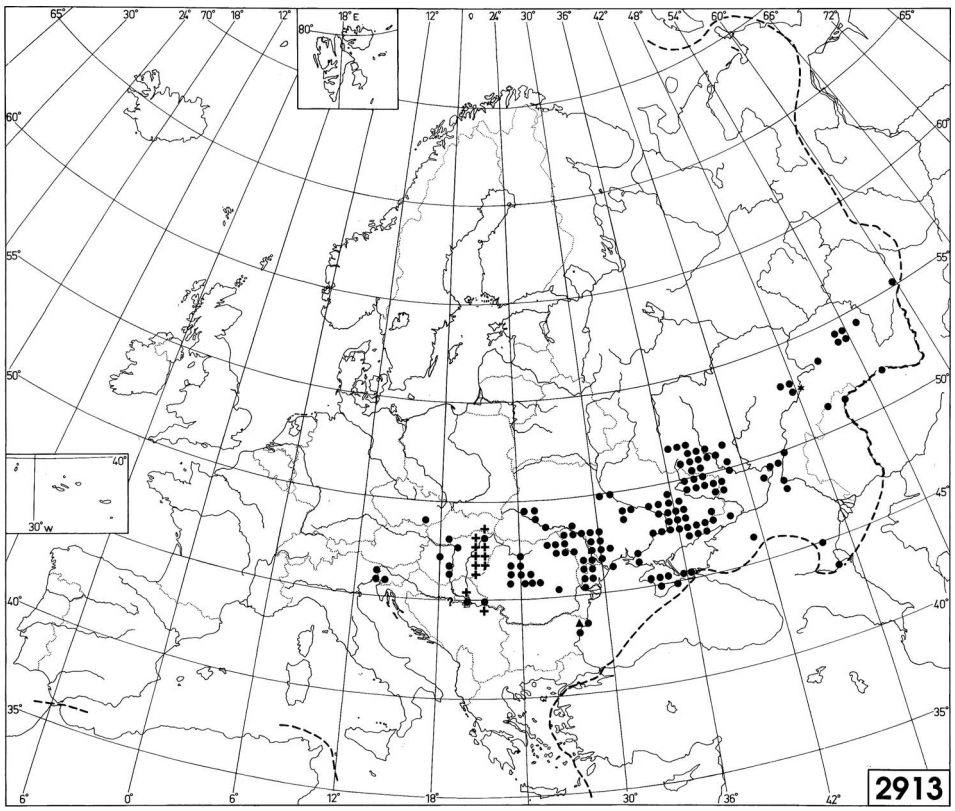


Fig. 22. – The European part of the extensive distribution of *Crambe tataria*. The localities in southern Moravia are at the north-western border of its distribution. Reproduced from Jalas et al. (1996), reproduced with permisson.

arenaria, *I. pumila*, *Linum flavum*, *L. hirsutum*, *Medicago monspeliaca* (Fig. 23), *Minuartia glaucina*, *Notholaena marantae* (Fig. 24), *Onosma arenaria*, *Orlaya grandiflora*, *Potentilla micrantha*, *P. patula*, *Prunella laciniata*, *Prunus tenella*, *Quercus cerris* (Fig. 25), *Q. pubescens*, *Salvia aethiopis*, *Seseli pallasii*, *Sorbus aria*, *Thesium arvense*, *T. dollineri*, *Trinia glauca* and *Veratrum nigrum*. Other thermophilous species (mainly of the West-Sub-Mediterranean geoelement) came from the south-west and either reached their limits in Bohemia (such as *Anthericum liliago* and *Dianthus gratianopolitanus*) or in Moravia (*Arenaria grandiflora* – Fig. 26, *Sedum reflexum*, *Teucrium botrys*). Several species spreading from the Alps also reach their northern or north-eastern limits in this country, mostly in the mountains or highlands in southern and/or western Bohemia, seldom in south-western Moravia. Examples include *Alnus alnobetula*, *Cyclamen purpurascens*, *Gentiana pannonica*, *Ranunculus aconitifolius* (Fig. 27), *Salix appendiculata*, *Soldanella montana*, *Thesium rostratum*, *Veratrum album* subsp. *album* and *Willemetia stipitata*.

The eastern or north-eastern limits of the ranges of some Atlantic-Sub-Mediterranean species such as *Fourraea pauciflora*, *Lathyrus linifolius*, *Juncus subnodulosus* and *Polygala chamaebuxus* are in western Bohemia and in a few cases in south-western

Fig. 23. – Distribution of *Medicago monspeliaca*, the northernmost locality of which is in the České středohoří highlands. Reproduced from Meusel et al. (1978), reproduced with permisson.

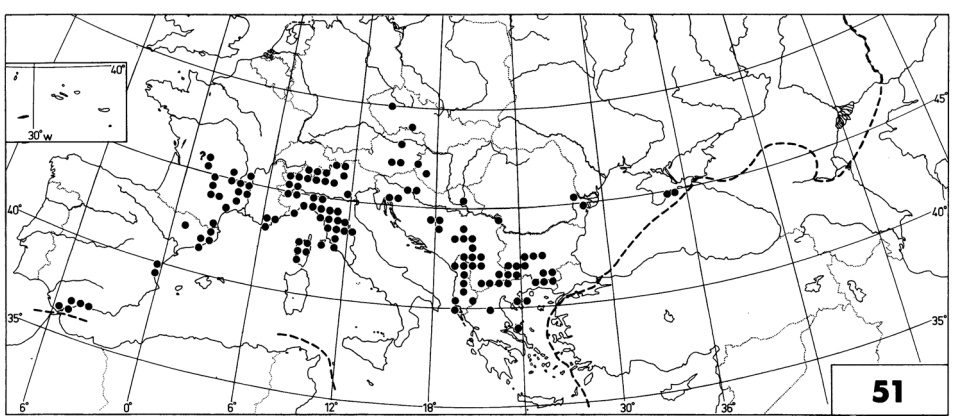


Fig. 24. – *Notholaena marantae* is an example of the Mediterranean geoelement that reaches the absolute northern boundary of its distribution in the Czech Republic. Adopted from Jalas & Suominen (1972) and supplemented with the northernmost locality recently recorded in the Český kras karst. Reproduced with permisson.

Fig. 26. – The European distribution of *Arenaria grandiflora*. The north-easternmost locality of this species is in the Pavlovské vrchy hills in southern Moravia. Reproduced from Jalas & Suominen (1983), reproduced with permisson. ▶

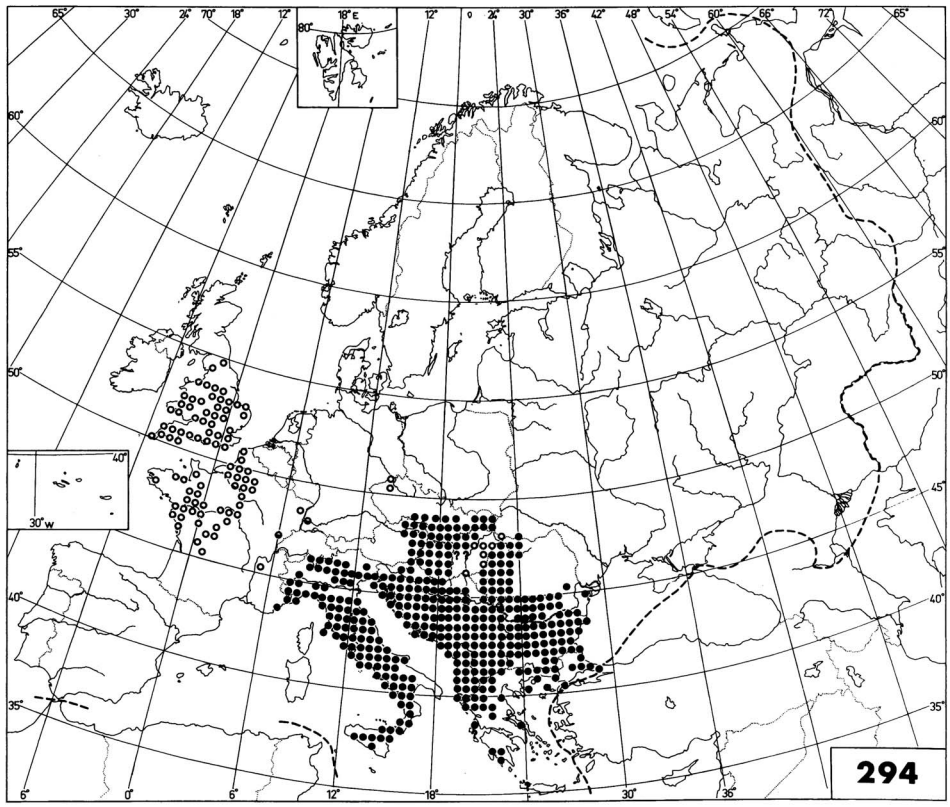
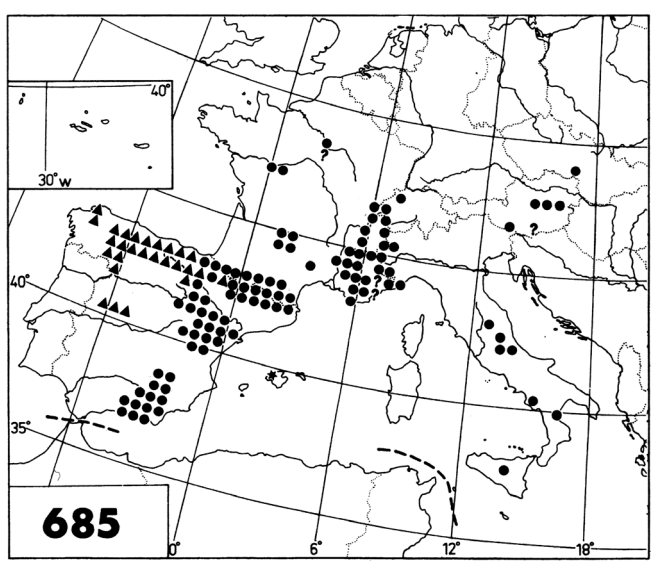


Fig. 25. – The European distribution of the Mediterranean geoelement *Quercus cerris*. The northern limit of its native distribution runs through southern Moravia. Reproduced from Jalas & Suominen (1976), reproduced with permisson.



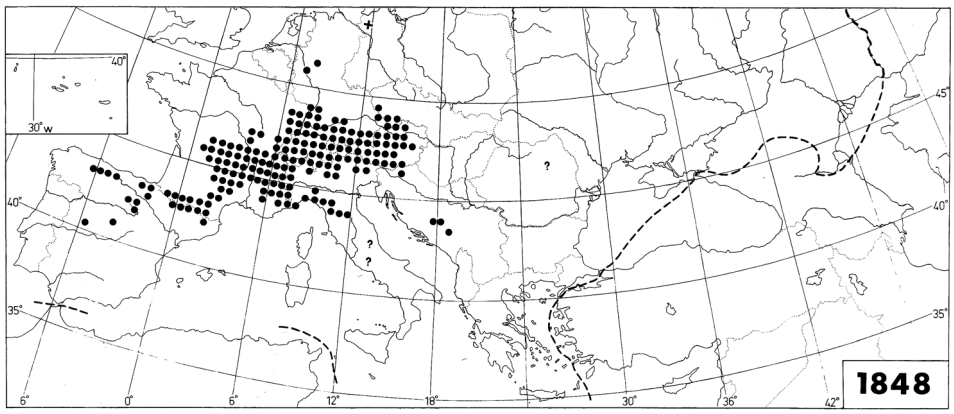


Fig. 27. – The core of the distribution of *Ranunculus aconitifolius* is in the Alps and its north-eastern limit in the Šumava Mts in south-western Bohemia. Reproduced from Jalas & Suominen (1989), reproduced with permisson.

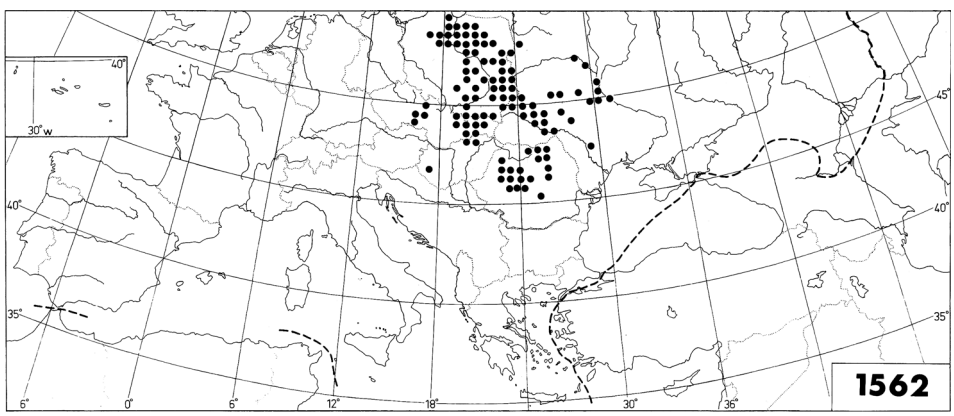


Fig. 28. – Distribution of *Actaea europaea*, the westernmost localities of which are in the Czech Republic. Reproduced from Jalas & Suominen (1989), reproduced with permisson.

Moravia. There are a relatively large number of Sub-Atlantic species that spread from the north-west, which are at the south-eastern (or eastern) limit of their continuous distributions in the Czech Republic. It includes *Arnoseris minima*, *Chrysosplenium oppositifolium* (Fig. 21), *Corrigiola littoralis*, *Hydrocotyle vulgaris*, *Hylotelephium telephium*, *Illecebrum verticillatum*, *Juncus bulbosus*, *Lotus pedunculatus*, *Lysimachia nemorum*, *Myriophyllum alterniflorum*, *Pedicularis sylvatica*, *Polygala serpyllifolia*, *Potentilla anglica*, *P. sterilis*, *Radiola linoides*, *Spergula morisonii*, *Stachys arvensis* and *Teesdalia nudicaulis*.

In contrast, some sub-arctic and boreal species reach the regional or absolute southern limit of their distributions in Czech mountains, or rarely in lowland relict sites; examples include *Betula nana*, *Calamagrostis phragmitoides*, *Carex vaginata*, *Pedicularis sceptrum-carolinum*, *P. sudetica* (s.l.) (Fig. 3), *Rhododendron tomentosum*, *Rubus chamaemorus* (Fig. 4), *Salix myrtilloides* and *Trichophorum cespitosum*. Another species,

Calamagrostis stricta, occurs mainly in lowland mires. The Sarmatian element with its south-western boundary in the Czech Republic is represented by *Astragalus arenarius* (Fig. 19), *Dianthus arenarius* (Fig. 18), *Jurinea cyanoides*, *Pulsatilla patens* and *Thesium ebracteatum*.

Finally, the distributions of several species extend from the West Carpathians or their foothills and reach their western limits in Moravia or north-eastern Bohemia. These (mostly Carpathian) taxa include *Aconitum firmum* subsp. *moravicum*, *Actaea europaea* (Fig. 28), *Cardamine amara* subsp. *opicii*, *Dentaria glandulosa* (Fig. 20), *Euphrasia slovaca*, *Hacquetia epipactis*, *Pedicularis exaltata*, *Salix silesiaca*, *Scilla kladnii* and *Thymus pulcherrimus*. Several of the species that have extensive ranges also have the western boundary of their distributions in the Czech Republic. Most of them are continental plants that occupy large areas that extend to southern Siberia. Examples include *Conioselinum tataricum*, *Crepis pannonica*, *C. sibirica* (Fig. 29), *Echium maculatum*, *Erigeron podolicus*, *Gypsophila paniculata*, *Helictotrichon desertorum*, *Pilosella echioides*, *P. onegensis*, *Stipa glabrata*, *Trinia ucrainica* and *Verbascum speciosum*. For many of them the Czech Republic is also at the northern limit of their distribution in central Europe.

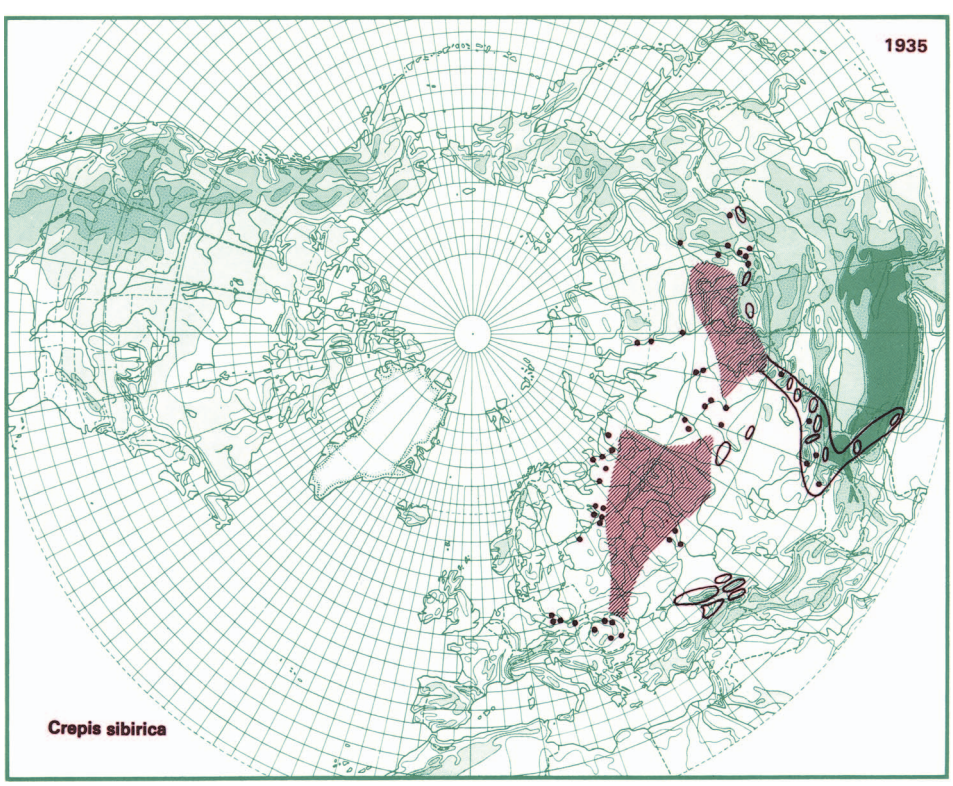


Fig. 29. – *Crepis sibirica* has a wide distribution in eastern Europe and western and central Asia. Its westernmost locality is in the Velká kotlina glacial cirque in the Hrubý Jeseník Mts. Reproduced from Hultén & Fries (1986), reproduced with permisson.

Phytochorotypes of the Czech flora

Based on similar principles to those used to distinguish geoelements at higher levels (such as the European continent), species can be classified according to their distribution within a country. Based on a comparison of several hundred distribution maps of vascular plants in the Czech Republic, Slavík (1984) identified 15 basic regional types of distribution of groups of species with common ecological requirements and geographical distributions, for which he proposed the term phytochorotypes. Species are assigned to phytochorotypes based on the similarity of their distributions within the Czech Republic, which reflect not

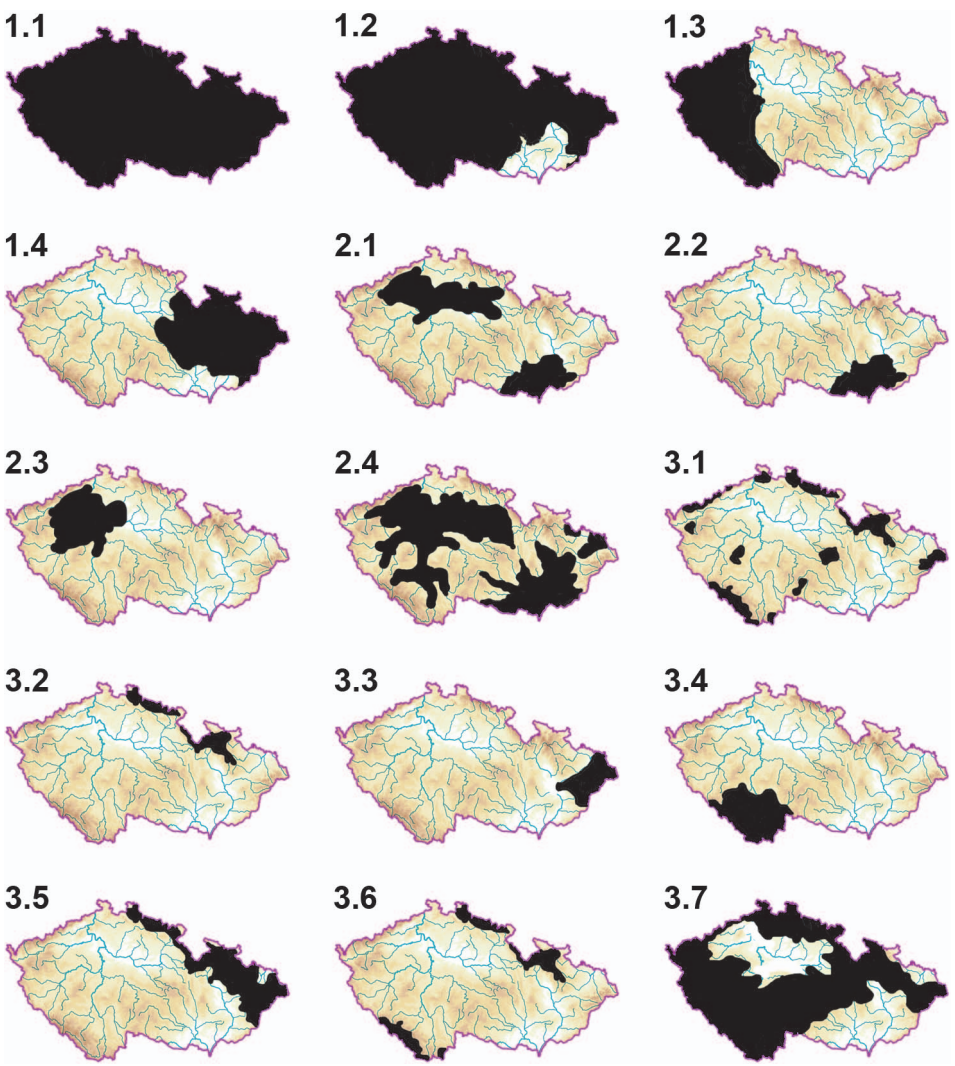


Fig. 30. – Schematic maps of the distributions of basic phytochorotypes of the Czech Republic. Redrawn from Slavík (1984) and slightly modified.

only local climate, geology and geomorphology but also migration history. Total ranges of species are not considered at this scale, which is why species of different major geoelements can belong to the same phytochorotype. Only native species and archeophytes with relatively stable distributions were used for the comparisons.

The 15 basic phytochorotypes are divided into three groups according to their prevailing relation to one of the three principal phytogeographical regions in the Czech Republic (see below). The phytochorotypes were named after pairs of species typical of a given phytochorotype. Only a brief account of their characteristics is given here. For a description of the phytogeographical division of the Czech Republic and definitions of phytogeographical regions (Thermophyticum, Mesophyticum and Oreophyticum) see below. Details, characteristic species and distribution maps of the species in each phytochorotype are given by Slavík (1984). This concept was applied by Slavík in his later studies (Slavík 1998, 2002), a slightly modified version supplemented with a group of edaphically specialized phytochorotypes is proposed in the introductory chapters to the Flora of the Czech Republic (Slavík 1988). Schematic illustrations of the 15 phytochorotypes based on Slavík's analysis and refined according to updated maps of distributions are given in Fig. 30.

1. Species common throughout the country or with their centres of distribution in Mesophyticum.
   - 1.1. Phytochorotype: *Achillea millefolium-Urtica dioica*
     Species distributed throughout or nearly throughout the Czech Republic.
   - 1.2. Phytochorotype: *Hypericum maculatum-Luzula pilosa*
     Species distributed throughout most of the Czech Republic but absent or rare in the Pannonian subregion in southern Moravia.
   - 1.3. Phytochorotype: *Chaerophyllum aureum-Polygala chamaebuxus*
     Species largely confined to the western half of Bohemia, regardless of the regional phytogeographical division.
   - 1.4. Phytochorotype: *Euphorbia amygdaloides-Galium rivale*
     Species largely confined to the eastern half of the Czech Republic, occurring exclusively in Moravia or reaching only the eastern part of Bohemia.
2. Species with their centres of distribution in Thermophyticum.
   - 2.1. Phytochorotype: *Buglossoides purpurocaerulea-Ranunculus illyricus*
     Species distributed in both Bohemian and Pannonian thermophyticum.
   - 2.2. Phytochorotype: *Euphorbia epithymoides-Hesperis tristis*
     Species of Pannonian thermophyticum, particularly of its warmest parts in southern Moravia. This region is often the area where these species reach the northern or north-western limit of their distributions.
   - 2.3. Phytochorotype: *Erysimum crepidifolium-Lactuca perennis*
     Species that occur in Bohemian thermophyticum, sometimes with local extensions south to the warmer parts of Mesophyticum (up to the Plzeň area and to the middle Vltava river valley).
   - 2.4. Phytochorotype: *Bothriochloa ischaemum-Scabiosa ochroleuca*
     Slightly thermophilous species with their centres of distribution in Thermophyticum and also occurring in warmer parts of Mesophyticum.

3. Species with their centres of distribution in Oreophyticum that occasionally occur in the cooler parts of Mesophyticum, particularly at sites with temperature inversions in valleys and ravines or peat bogs.
   3.1. Phytochorotype: *Rumex arifolius-Streptopus amplexifolius*
   Species that occur on all or most high mountains in the Czech Republic (Krkonoše, Jizerské hory, Orlické hory, Králický Sněžník, Hrubý Jeseník, Moravskoslezské Beskydy, Šumava, and Krušné hory) and sometimes also on mountains at lower altitudes (Slavkovský les, Brdy, Novohradské hory, Česko-moravská vrchovina, Teplicko-adršpašské skály, and Nízký Jeseník).
   3.2. Phytochorotype: *Anemonastrum narcissiflorum-Delphinium elatum*
   Species that occur only in the Sudetes Mts, particularly in the High Sudetes (Krkonoše, Králický Sněžník, Hrubý Jeseník) and sometimes also other mountains in the Sudetes range (Lužické hory, Jizerské hory, Teplicko-adršpašské skály, Orlické hory, Nízký Jeseník). Some of them only occur in the Krkonoše and Hrubý Jeseník Mts, which have a well-developed subalpine belt.
   3.3. Phytochorotype: *Dentaria glandulosa-Luzula luzulina*
   Carpathian species that have their centres of distribution in the Czech Republic in the Moravskoslezské Beskydy Mts and which sometimes occur in adjacent parts of Mesophyticum.
   3.4. Phytochorotype: *Salix appendiculata-Veratrum album* subsp. *album*
   Species that occur in Oreophyticum in southern Bohemia (particularly those that came from the Alps) and in adjacent parts of Mesophyticum (mainly aquatic plants).
   3.5. Phytochorotype: *Potentilla aurea-Veratrum album* subsp. *lobelianum*
   Species that occur in the Sudetes and Carpathian Mts, and occasionally in adjacent parts of Mesophyticum.
   3.6. Phytochorotype: *Epilobium anagallidifolium-Trichophorum cespitosum*
   Species that occur both in the Sudetes Mts and Oreophyticum in southern Bohemia where there is an Alpine influence.
   3.7. Phytochorotype: *Montia fontana-Polygonatum verticillatum*
   Species that are found throughout (almost) the Czech Republic in Oreophyticum and cooler parts of Mesophyticum.

Phytogeographical division

In phytogeography, a process complementary to the identification of floristic elements, areas are divided up into floristic regions in each of which the flora is broadly similar. In the phytogeographical division of Europe proposed by Meusel et al. (1965), the Czech Republic occurs in the temperate zone of the Holarctic floristic kingdom, and in its Middle European region. Within this region, most of the Czech Republic is situated in Middle European subregion (and its Central European province) while the mountains of eastern Moravia are in the Carpathian subregion (and its Northwest Carpathian province). The Pannonian province in the Pontic-South-Siberian subregion does not reach the Czech Republic under this concept. There is another concept proposed by Takhtajan (1986) under which there are 20 floristic provinces in Europe, Asia Minor and the Caucasus, and in which the whole of the Czech Republic is in the Central European province.

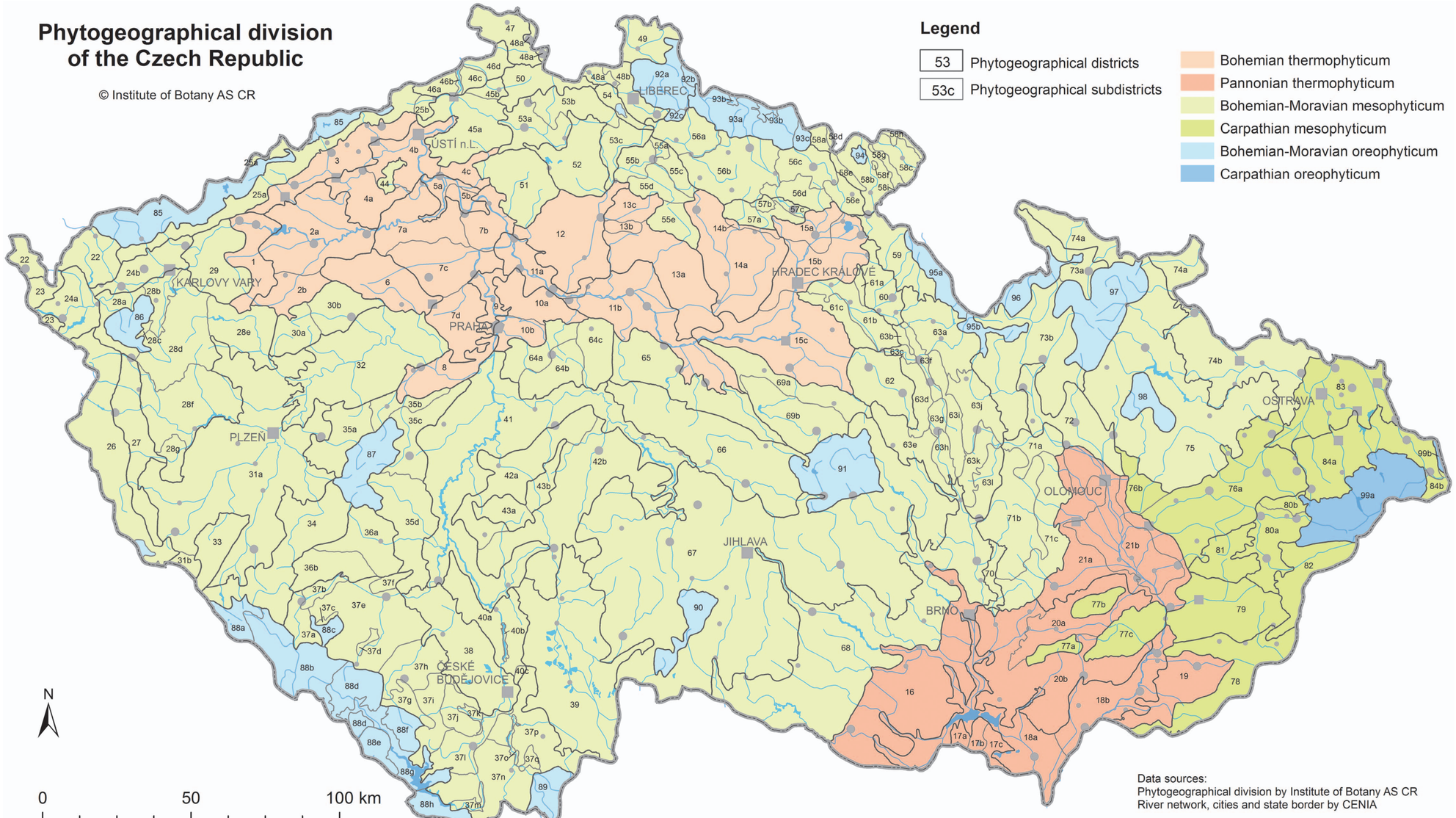


Fig. 31. – Phytogeographical division of the Czech Republic. Codes for the phytogeographical districts and subdistricts are listed in Electronic Appendix 3.

The system of Meusel et al. (1965) was modified and refined by Slavík (1988) who argued that the Pannonian lowland is an isolated area of forest-steppe, separated from the Pontic-South-Siberian subregion by the Carpathian mountain range and influenced by a Sub-Mediterranean geoelement. He distinguished this area as a separate Pannonian subregion and extended it (in contrast to Meusel's Pannonian province) in the north-west to southern Moravia.

Within the Czech Republic, the currently used concept of regional phytogeographical division was elaborated by phytogeographical experts of the Czech Botanical Society coordinated by V. Skalický (Skalický 1982, 1988c). This system replaced the previous phytogeographical divisions of Czechoslovakia by Dostál (1957, 1960), which more closely reflected the central-European context and occurrence of geoelements. The final version of his division (Dostál 1960) included three regions in the Czech Republic, namely Hercynicum, with central-European temperate forest vegetation; Pannonicum, with termophilous vegetation; and Carpaticum occidentale, with vegetation typical of the West Carpathians. The concept published by Skalický is the basic system used for recording the distribution of species and subspecies in the Flora of the Czech Republic (Hejný et al. 1988, 1990, 1992, Slavík et al. 1995, 1997, 2000, 2004, Štěpánková et al. 2010) as well as in many floristic and taxonomic studies. Species and plant communities diagnostic and characteristic of each region are listed by Skalický (1988c).

A four-level hierarchical system of phytogeographical units (phytochoria) is used in the phytogeographical division of the Czech Republic (see Electronic Appendices 1–3). Three principal phytogeographical regions are recognized, based on the dominant flora and vegetation that reflects specific regional geomorphological and climatic conditions: Thermophyticum, Mesophyticum and Oreophyticum (Fig. 31, and Electronic Appendix 1). Mesophyticum is the basic region with flora and vegetation typical for the central European temperate zone. In terms of the altitudinal zonation of vegetation (Skalický 1988c, Chytrý 2012), Mesophyticum occurs in the supracolline and submontane belts. The other two regions are partly extrazonal. Thermophyticum includes warm areas with a thermophilous flora and vegetation, often characteristic of the sub-meridional floristic zone. It includes the lowland and colline belts. In contrast, Oreophyticum is a cold region with mountain flora and vegetation corresponding to forests of the boreal zone, with smaller areas above the timberline similar to habitats in the artic zone; thermophilous species generally do not occur there except at some protected sites in cirques. It occurs in montane, supramontane, subalpine and alpine belts.

Each of the phytogeographical regions has a characteristic flora and vegetation, which have diagnostic value. Thermophyticum is characterized by the occurrence of basiphilous thermophilous oak forests of the *Quercion pubescenti-petraeae*, *Aceri tatarici-Quercion* and *Quercion petraeae* alliances and oak-hornbeam forests of the *Carpinion betuli* alliance, dry scrub of the *Prunion fruticosae* alliance and particularly dry grasslands of the *Festuco-Brometea* class; beech forests are nearly absent. There are the remains of softwood floodplain forests of the *Salicion albae* alliance and hardwood floodplain forests of the *Alnion incanae* suballiance in lowland basins. Other communities differentiating Thermophyticum from Mesophyticum include the alliances *Geranion sanguinei*, *Festucion valesiacae*, *Onopordion acanthii*, *Spergulo arvensis-Erodion cicutariae*, *Eragrostion cilianensi-minoris*, *Corynephorion canescentis* and *Hydrocharition*. This region largely overlaps the distribution of loess deposits. Peat bogs are absent, but remnants of calcareous fens are

present in some areas (*Junco subnodulosi-Schoenetum nigricantis*, *Cladietum marisci*) and locally there are remnants of saltmarshes and saline meadows (*Meliloto dentati-Bolboschoenion maritimi*, *Salicornion prostratae*, *Puccinellion limosae*, *Juncion gerardii*). Differential species of Thermophyticum include *Adonis vernalis*, *Astragalus exscapus*, *Buglossoides purpurocaerulea*, *Cytisus procumbens*, *Loranthus europaeus*, *Lotus maritimus*, *Quercus pubescens*, *Rumex hydrolapathum*, *Sesleria uliginosa*, *Sium latifolium*, *Viburnum lantana* and *Viola ambigua*.

The potential natural vegetation in Mesophyticum consists mainly of various types of mesic beech or hornbeam forests. Communities differentiating Mesophyticum from Oreophyticum include meadows and grasslands of alliances *Arrhenatherion elatioris*, *Molinion caeruleae* and *Bromion erecti*, mesic herbaceous forest fringes of the *Trifolium medii* alliance and some specific communities such as the vegetation on the exposed bottoms of fishponds of the *Eleocharition ovatae* alliance. Communities differentiating Mesophyticum from Thermophyticum include alliances *Luzulo-Fagion*, *Fagion sylvaticae* and *Trifolion medii*.

Oreophyticum is dominated by coniferous forests (mainly acidophilous spruce forests) or by mixed forests with a high abundance of conifers. The area of treeless communities is relatively small. Natural subalpine and alpine grasslands occur only at the highest altitudes and most of the present-day subalpine and montane meadows were made by humans. The following montane, subalpine and alpine communities are characteristic of this region: *Luzulo-Fagion sylvaticae*, *Piceion abietis*, *Alnetum incanae*, *Pinion mugo*, *Nardion strictae*, *Oxycocco microcarpi-Empetrion hermaphroditi*, *Adenostylion alliariae*, *Calamagrostion villosae*, *Calamagrostion arundinaceae*, *Dryopterido filicis-maris-Athyrion distentifolii*, *Rumicion alpini*, *Androsacion alpinae*, *Agrostion alpinae*, *Juncion trifidi*, *Littorellion uniflorae* and *Salicion silesiacae*. Differential species include montane and subboreal species, such as *Aconitum firmum*, *A. plicatum*, *Carex pauciflora*, *Hieracium alpinum* agg., *Juncus trifidus*, *Ligusticum mutellina*, *Listera cordata*, *Luzula sylvatica*, *Meum athamanticum*, *Pinus mugo*, *Swertia perennis*, *Trichophorum cespitosum* and *Viola biflora*, other species mainly occurring in the Czech Republic in Oreophyticum are for example *Doronicum austriacum*, *Gentiana asclepiadea*, *Homogyne alpina*, *Huperzia selago* and *Streptopus amplexifolius*.

Each of these three regions is subdivided into two provinces (Fig. 31). Thermophyticum occurs in two separate areas, one being Bohemian thermophyticum, which is an isolated area of thermophilous vegetation in the northern half of Bohemia, the other Pannonian thermophyticum, which is located in southern Moravia and connected to the forest-steppe area centered in the Pannonian Basin. Mesophyticum and Oreophyticum are each subdivided based on their assignment to major mountain systems and floristic differences reflecting the proportion of Hercynian vs. Carpathian flora and the gradient of oceanity vs. continentality (increasing from the west to the east). Accordingly, most of Mesophyticum that is associated with the Bohemian Massif is recognized as Bohemian-Moravian mesophyticum whereas the smaller part in eastern Moravia and that associated with the West Carpathians belongs to Carpathian mesophyticum. In parallel, Oreophyticum is divided into Bohemian-Moravian oreophyticum and Carpathian oreophyticum. Based on the specific and relatively uniform composition of the local flora and vegetation and particularly the contrast with that in neighbouring areas, these provinces are further subdivided into 99 phytogeographical districts (see Electronic Appendix 3 for a list and codes and Fig. 31 for

their position), of which 21 are in Thermophyticum, 63 in Mesophyticum and 15 in Oreophyticum. Some of the districts, which are more heterogeneous than others, are subdivided into subdistricts. Many of these phytochoria do not have sharp boundaries and are separated from the others by transitional zones. Exceptions are the boundaries that follow highly contrasting natural conditions, such as the geological boundary between calcium-rich rocks and acid sands.

See http://www.preslia.cz for Electronic Appendices 1–3.

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Souhrn

Článek přináší základní přehled flóry a fytogeografie České republiky. Na diverzitu rostlin v tomto území má největší vliv poloha ve středu evropského kontinentu, místní klima, vývoj vegetace během čtvrtohor, různorodost horninového podkladu, členitost reliéfu, diverzita stanovišť a vliv člověka. Květena cévnatých rostlin České republiky zahrnuje 148 čeledí, 916 rodů, 3557 druhů (s 194 dalšími, obvykle nenominátními poddruhy) a 609 dostatečně zdokumentovaných kříženců. Druhově nejbohatší čeledi jsou *Asteraceae* (662 druhů), *Rosaceae* (316), *Poaceae* (275), *Fabaceae* (170), *Brassicaceae* (148), *Cyperaceae* (127), *Lamiaceae* (112), *Caryophyllaceae* (108) a *Apiaceae* (100). Většina druhů je u nás původních, 36.0 % rostlin je zavlečených. Z hlediska životních forem jsou nejvíce zastoupeny hemikryptofyty (45,7 %), následované terofyty (22,3 %), fanerofyty (14,4 %), geofyty (9,3 %), chamaefyty (5,1 %) a hydrofyty (3,2 %); podíl epifytů je zanedbatelný (pouze dva druhy). Četné druhy naší květeny jsou relikty z dob ledových nebo z raného postglaciálu. V článku jsou uvedeny příklady arktických, boreálních, alpínských, stepních a dalších skupin reliktů. Míra endemismu je v České republice relativně nízká. Výrazné klimatické výkyvy související se střídáním dob ledových a meziledových v pleistocénu opakovaně drasticky ochuzovaly místní flóru. Veškeré české endemity jsou čtvrtohorního stáří (neoendemity), třetihorní endemity (paleoendemity) se u nás nevyskytují. Na základě taxonomické a chorologické revize naší květeny byl vytvořen seznam 74 endemických druhů a subspecií, což odpovídá 2 % celkové diverzity našich cévnatých rostlin. Z těchto endemitů je 48 vázáno výhradně na území České republiky, zbývajících 26 taxonů má těžiště rozšíření v České republice a jen nevýrazně (většinou méně než 1 km) zasahují v Krkonoších nebo na Králickém Sněžníku na území Polska. Na endemity nejbohatší rody jsou *Hieracium* s (nejméně) 25 druhy a poddruhy a *Sorbus* s 12 druhy. Základní charakter rozšíření a vazba na stanoviště jsou uvedeny pro všechny naše endemity, většina endemitů je i vymapována. Nejvíce endemitů se vyskytuje v Krkonoších, kde rostou převážně na subalpínských stanovištích, jako jsou trávníky nad horní hranicí lesa, vrcholové skály a sutě a nejrůznější typy stanovišť v ledovcových karech včetně lavinových drah. Kromě Krkonoš se endemity vysokohorských poloh vyskytují ještě na Králickém Sněžníku a v Hrubém Jeseníku. V nižších polohách se endemity nejčastěji vyskytují na skalách a v přilehlých řídkých teplomilných lesích a na trávnících, méně často na hadcových výchozech, písčinách, slatinách, v různých typech lesů, výjimečně i na jiných stanovištích. Většina našich endemitů jsou vzácné a silně až kriticky ohrožené rostliny zahrnuté do Červeného seznamu. Původ a evoluce českých endemitů jsou v článku stručně popsány. Díky umístění České republiky ve středu Evropy se na našem území v minulosti protínaly různé migrační proudy. Česká flóra proto obsahuje téměř všechny floristické elementy ovlivňující střední Evropu. Nejvíce zastoupený je středoevropský geoelement, výraznější zastoupení mají dále geoelementy středoevropsko-(sub)alpínský, arkticko-alpínský, boreální, subboreální, subatlantický, submediteránní,

pontický, subpontický a jihosibiřský. Pro každý geoelement je uvedena stručná charakteristika a výčet vybraných druhů. Četné druhy dosahují na území České republiky hranici svého víceméně souvislého rozšíření nebo se zde vyskytují okrajové arely. Článek přináší příklady těchto mezních a exklávních prvků. Na základě porovnání rozšíření druhů v České republice byly vytvořeny skupiny druhů s podobným rozšířením, tzv. fytochorotypy, které jsou stručně definovány a charakter jejich rozšíření je ilustrován na mapách. Popsáno je i v současnosti používané fytogeografické členění České republiky. Podrobněji jsou charakterizovány tři základní fytogeografické oblasti, které se dále hierarchicky dělí na fytogeografické obvody, okresy a podokresy. Poloha všech fytochorionů je zobrazena na mapě.

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