

DISTRIBUTION AND HABITATS OF *CARDAMINOPSIS PETRAEA* IN HUNGARY

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The arctic-alpine, glacial relict *Cardaminopsis petraea* (L.) Hiitonen (Northern Rockcress) is a very rare plant species in Hungary. The distribution of the species in the country is reviewed on the basis of herbarium and literature data. The currently known stands are characterised by coenological relevés and documentation of the cryptogam taxa in three major populations (Tapolca-Diszel: Csobánc, Gyenesdiás: Kőmell, Balatongyörök: Bise-kő). In Hungary *Cardaminopsis petraea* survived on both dolomite and basalt bedrocks, mainly occurring on north facing stone walls and steep slopes.

Key words: *Arabidopsis lyrata* subsp. *petraea*, *Cardaminopsis petraea*, distribution, habitat, relict species

INTRODUCTION

Although *Cardaminopsis petraea* (L.) Hiitonen (Northern Rockcress) is a very rare plant species in Hungary it lacks the needed attention of nature conservation. The Hungarian Red Data Book mentions *Cardaminopsis petraea* as a potentially endangered taxon (RAKONCZAY 1989), but despite its rarity it is not protected by law. The conservational significance of this species is acknowledged in Europe; *Cardaminopsis petraea* is protected in several countries, it is listed in several Red Data Books and is recorded among the endangered taxa (CURTIS and MCGOUGH 1988, KORNECK *et al.* 1996, NIKLFELD 1999, HOLUB and PROCHAZKA 2000, ZAHLHEIMER 2001, CHEFFINGS and FARRELL 2005). *Cardaminopsis petraea* is a biogeographically important and well-searched species. Currently just a few confirmed occurrences are known in Hungary. The present study sums up Hungarian literature and herbarium data and describes the studied habitats by coenological relevés.

Based on TUTIN *et al.* (2002) the valid name of the taxon is *Cardaminopsis petraea* (L.) Hiitonen. Important synonyms or older names are: *Arabis petraea* L., *Arabis hispida* Mygind, *Arabis Crantziana* Ehrh., *Arabidopsis petraea* (L.) Lam., *Cardamine petraea* L., *Cardaminopsis hispida* (L.) Hayek. It is worth noting that O'KANE and AL-SHEHBAZ (1997) offered a new definition of the *Arabidopsis* genus based on molecular evidence, and mentioned the *Cardaminopsis* taxa under this genus. O'Kane and Al-Shehbaz treated *Cardaminopsis petraea* under the name of *Arabidopsis lyrata* (L.) O'Kane et Al-Shehbaz subsp. *petraea* (L.) O'Kane et Al-Shehbaz, which differs only on subspecies level from the subspecies of *Arabidopsis lyrata* native to Siberia, NE Asia and North America (subsp. *kamchatatica* (Fischer ex DC.) O'Kane et Al-Shehbaz; subsp. *lyrata* (L.) O'Kane et Al-Shehbaz). Molecular systematic studies by KOCH *et al.* (1999) confirmed these treatments.

Range maps of MEUSEL *et al.* (1965), HULTÉN and FRIES (1986), JALAS and SUOMINEN (1996) clearly show the disjunct distribution of the European taxon *Cardaminopsis petraea*. It occurs in North Europe (Iceland, Great Britain, Norway, Sweden, Faroe Islands) and in certain mountainous areas of Central Europe (Germany, Bohemia, Austria, Hungary). Its most southerly occurrence is known from the Italian Alps (JALAS and SUOMINEN 1996). It is considered extinct in Poland (JASIEWITZ 1985), although ČERNÝ *et al.* (2006) doubted its occurrence in Poland. Populations of *Cardaminopsis petraea* occur from the sandy and rocky seashores (only in North Europe) up to as high as the alpine areas (1,500 m). Most of the Central European stands, however, grow in rocky habitats of the submountainous and mountainous regions of the middle mountains (MEUSEL 1939, MILBRANDT 1976, ERICSON and MASCHER 1978, ČERNÝ *et al.* 2006).

Cardaminopsis petraea is generally considered to be a glacial relict, occupying an arcto-alpine position in Central Europe shown by its disjunct distribution (BORBÁS 1900, MEUSEL 1939, MÁTHÉ 1940, THORN 1960, MILBRANDT 1976, SCHUHWERK 1990, MĚSÍČEK *et al.* 1992). HEMP (1996) mentioned *Cardaminopsis petraea* as a progressive glacial element, and assumed the possibility of recent expansion. The relict character, the characteristics of distribution and habitats where competitors are largely absent make *Cardaminopsis petraea* (*Arabidopsis lyrata* subsp. *petraea*) an ideal subject for studying interconnections between abiotic stresses and the

species' distribution. The biogeographical factors shown by the latest studies evidently confirmed the relict character of the species. Molecular genetic evidences have proven that the species might have survived the last glaciation in steppe-tundra habitats of the periglacial areas and also in montane refugia in Central Europe. On the basis of analysing the genetic structure of the remnant populations of *Cardaminopsis petraea* in Pleistocene periglacial areas of Central Europe, CLAUSS and MITCHELL-OLDS (2006) concluded that there are low but significant differences between the isolated populations because of limited gene-flow. These Central European populations are characterised by widespread polymorphism and higher genetic diversity than the North European populations developing separately. The higher genetic diversity observed in Central Europe may be explained by the periglacial development. The genetic variation is high between the populations developed in different geographic areas (VAN TREUREN *et al.* 1997, SCHIERUP 1998, SAVOLAINEN *et al.* 2000, CLAUSS *et al.* 2002, ANSELL *et al.* 2007). There are significant differences between certain morphological features, *i.e.* the trichomes (KÄRKKÄINEN *et al.* 2004), the blooming season and floral display (RIHIMÄKI and SAVOLAINEN 2004, SANDRIG *et al.* 2007), the isoenzyme places (JONSELL *et al.* 1995), the micro-satellite (VAN TREUREN *et al.* 1997, GAUDEUL *et al.* 2007), the sequence alternation (SAVOLAINEN *et al.* 2000, WRIGHT *et al.* 2003), and nuclear and chloroplast-DNA diversity (ANSELL *et al.* 2007). On the basis of the nuclear and chloroplast-DNA diversity analysis of the European populations ANSELL *et al.* (2007) assumed the existence of two refuge areas during the glaciation (on an unknown location between the Scandinavian and the Alpine ice-fields, and on one Central European location), and see evidences of post-glacial recolonisation that has taken place in two waves. DAVEY *et al.* (2006) justified the cold tolerance of *Cardaminopsis petraea* through experiments as well. The differences among the geographically isolated populations were measured based on ecological and physiological data, but concerning the cold tolerance, eco-typical differences were not found within the species. The sexual reproduction of the species is characterised by outside pollen mediation of insects, its productive system being incompatible with itself. Dispersion by rhizomes was also revealed, but the contribution of such clone ramets to the population structure is geographically different (CLAUSS and MITCHEL-OLDS 2006).

On the basis of karyological analyses of *Cardaminopsis petraea* populations the species is diploid ($2n = 16$) (HEDBERG and HEDBERG 1961, POLATSCHKEK 1966, BURDET 1967), however, tetraploid populations were also documented ($2n = 4x = 32$) (POLATSCHKEK 1966, DART *et al.* 2004). DART *et al.* (2004) mention the hybrid (allopolyploid) origin or the gene alternation following the poliploidisation, authors also demonstrate the dynamic feature of the polyploid genome. The allopolyploid origin of the Austrian tetraploid populations in the Alps (the closest populations to the species' occurrences in Hungary) can be explained by the hybridisation with *Arabis arenosa* (= *Cardaminopsis arenosa*) (MATSCHINGER and KOCH 2003, DART *et al.* 2004). Mygind in LINNÉ (1774, 1784), later HAYEK (1908) on the basis of occurrences in eastern Austria probably consider this species ("fol. *hispida*...", "álsó szárlevelei lehetnek fogazottak..." [its lower stem-leaves may be dentate], etc.) as one broadly interpreted species (called *Arabis hispida* Myg. and/or *Cardaminopsis hispida* (Myg.) Hay.). So far, individuals of the Hungarian stands have not been analysed genetically, but morphologically they can be identified with these descriptions.

Regarding the habitat preferences of *Cardaminopsis petraea* it is generally discussed that it occurs on habitats characterised by low competition, sometimes with moderate disturbances (ERICSON and MASCHER 1978, HEMP 1996, ČERNÝ *et al.* 2006), and it also grows as a pioneer-like primary phanerogam in coastal areas. It was reported from various bedrocks (limestone, dolomite, basalt, anorthosite, dolerite, granite, serpentine, gabbro, sandstone, sand) (MEUSEL 1939, HOHENESTER 1960, HEGI 1960, SPENCE 1970, ERICSON and MASCHER 1978). The Central European populations, however, are found on calcareous or basaltic bedrocks and outcrops (MEUSEL 1939, HOHENESTER 1960, HEGI 1960, SPENCE 1970, MILBRANDT 1976, BORHIDI 1995, ELLENBERG 1996). Its Hungarian stands grow on dolomite in the Keszthely Mts, and on basalt on Csobánc Hill in the Balaton Uplands (FEKETE 1964). ZÓLYOMI (1942) lists *Cardaminopsis petraea* among the species of the Middle Danube flora boundary (confined to the southwestern part of Ősmátra, Transdanubian Mts).

Most references agree on the basic ecological requirements of *Cardaminopsis petraea*. BORHIDI (1995) mentions it as a drought-resistant species that thrives on places of low nutrition content. A number of references deal with its light requirements, and consider it a photophilous species yet

preferring semi-shaded areas (THORN 1958, BORHIDI 1995, HEMP 1996, ČERNÝ *et al.* 2006). HEMP (1996) demonstrated the photophilous character of the *Cardaminopsietum petraeae* chasm-grassland – through the comparison of *Cystopteridetum*, *Asplenietum* and *Cardaminopsietum*. According to ELLENBERG (1996) – in the alpine region – *Cardaminopsis petraea* is the species of sunny limestone rocks and stone walls (*Potentillion caulescentis*), and can be found on south-facing chasms and rock ledges. Its relict populations exist in several middle mountainous areas in Central Europe (HOHENESTER 1960, POLATSCHEK 1966, MILBRANDT 1976, ČERNÝ *et al.* 2006), mainly in north-facing locations (ČERNÝ *et al.* 2006). This is also true for the Hungarian stands; in the submountainous region relict populations of montane, photophilous species (e.g. *Primula auricula*, *Saxifraga paniculata*) as well as *C. petraea* share similar habitat preferences and find their optimal environment in humid (mainly partly shaded) microclimatic recesses.

Shown by a number of references, there is obvious disagreement in its coenological preferences. For example (with reference of the association), JÁVORKA and SOÓ (1951) and CHYTRÝ and TICHÝ (2003) – *Seslerio-Festucion*; SOÓ (1968) and BORHIDI (1995) – *Bromo-Festucion pallentis*; BRANDES (1992) – *Asplenietea* Class; POTT (1995) – *Potentilletalia caulescentis ordo* within *Asplenietea*. ELLENBERG (1996) treats it as a character species of the *Potentillion caulescentis*-serial. [It should be noted here that "*Cardaminopsis petraea*" on the 90th diagram of POTT (1995) is in fact *Hornungia petraea* (L.) Rchb.].

Cardaminopsis petraea is the denominating species of several plant associations [e.g. "*Cardaminopsietum petraeae* Thorn 1958" (THORN 1958, POTT 1995), "*Arenaria norvegica-Cardaminopsis petraea-soc.*" (SPENCE 1970)]. SCHUHWERK (1990) designated the lectotype of "*Cardaminopsietum petraeae* Thorn 58", however he deleted the relevés relating to the earlier described *Asplenio trichomano-rutae-murariae* and *Asplenio-Cystopteridetum* from the association definition summarised in the name of *Cardaminopsietum petraeae* by Thorn. According to SCHUHWERK (1990) *Cardaminopsis petraea* (and other relict species from the Fränkischen Jura rock vegetation) belongs to the relict alternations of the above-mentioned associations, as well as to the "*Sesleria albicans* Gesellschaft". Other authors also pointed out occurrences of several other, mainly rocky plant associations: "*Bromo-Seslerietum*" (GAUCKLER 1938), "*Sesleria* grasslands" (MEUSEL 1939),

"*Helychriso-Festucetum sulcatae dolomiticum*" (HOHENESTER 1960), dolomite grassland dominated by *Festuca glauca* (ZÓLYOMI 1950), "*Alyso-Sedetum*", "*Asplenio-Cystopteridetum*" in extreme situation, and "*Bupthalmo-Pinetum*" (HEMP 1996), *Festuco ovinae-Saxifragetum decipientis*, *Diantho moravici-Seslerietum albicantis*, *Medicagini prostratae-Festucetum pallentis* (ČERNÝ *et al.* 2006), etc.

ZÓLYOMI (1950) mentioned *Cardaminopsis petraea* among the character species of dolomite rocky grasslands dominated by *Festuca glauca* of the Transdanubian Mts in Hungary (with the invariance value I) and made a comment that "csak a Keszthelyi-hegységen" ["only in the Keszthely Mts"]. His statement (with the names used for the associations, "*Festucetum glaucae hungaricum*", "*Seseli leucospermi-Festucetum pallentis*", etc.) was adopted by synthesising works (*e.g.* JÁVORKA and SOÓ 1951, SOÓ 1968, SIMON 2000).

MATERIAL AND METHODS

The Hungarian herbarium data were collected by reviewing the collection of the Hungarian Natural History Museum (BP) [the sheet inventory number is given after the abbreviation. Additional specimens were studied in the herbaria of the Eötvös Lóránd University (BPU), University of Debrecen (DE), Savaria Museum, Szombathely (SAV)].

Cardaminopsis petraea was examined in all habitats documented in the literature and in herbaria. Coenological relevés in three significant stands were taken in order to document the habitat. The vegetation was sampled with the BRAUN-BLANQUET (1964) quadrat method (using 2 m × 2 m quadrates). Altogether 35 coenological relevés representing the habitats are presented in this article (Tables 1–2). The cryptogam data were collected relating to stone walls or parts of the stone walls not to relevés. The typical cryptogam taxa from the sampling sites were collected and identified, however, their dominating relations and density per relevé were not analysed because these parameters are difficult to estimate in the field.

Nomenclature of the plant names follows SIMON (2000), that of the moss taxa ERZBERGER and PAPP (2004), the lichen taxa SIMON (1991) and VERSEGHY (1994), and the plant association names BORHIDI (2003).

Table 1. Coenological relevés of the habitat of *Cardaminopsis petraea* I. (Basic data of the relevés, 1–10. Csobánc Hill, northern stone wall; 11–20. Csobánc, northern side of the ruined castle wall; Settlement: 1–10. Tapolca-Diszel, 11–20. Gyulakeszi; Bedrock: 1–10 basalt rock, 11–20 basalt stone wall; Exposition: 1–20 N; Slope: 1. 60°, 2. 70°, 3–8. 60°, 9. 80°, 10. 60°, 11–20. 90°; Height above sea level: 1–7. ca 340 m, 8–10. 330 m, 11–20. 375 m)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Cardaminopsis petraea</i>	+	+	+	1	1	+	+	1	+	1	2	2	1	+	+	1	2	1	1	
<i>Allium montanum</i>	–	–	1	–	1	1	–	–	1	–	–	–	–	–	–	–	–	–	–	
<i>Alyssum alyssoides</i>	+	–	–	–	+	–	–	+	–	–	–	–	–	–	–	–	–	–	–	
<i>Anthericum ramosum</i>	–	–	–	1	1	–	1	–	1	–	–	–	–	–	–	–	–	–	–	
<i>Arenaria serpyllifolia</i>	–	–	+	–	+	–	–	–	–	+	–	–	–	–	–	–	+	–	–	
<i>Asplenium ruta-muraria</i>	–	–	–	–	–	–	–	–	–	1	2	1	1	1	1	1	1	2	1	
<i>Asplenium septentrionale</i>	–	+	–	+	+	–	–	+	–	–	–	–	–	–	–	–	–	–	–	
<i>Aurinia saxatilis</i>	+	1	1	–	3	–	1	2	1	1	1	1	2	2	–	2	2	2	1	
<i>Campanula rotundifolia</i>	+	–	+	–	+	1	1	–	+	+	–	+	–	2	–	–	–	+	+	
<i>Cerastium pumilum</i> subsp. glutinosum	+	+	+	–	–	+	–	–	+	–	–	–	–	–	–	–	–	–	–	
<i>Cerasus mahaleb</i>	–	–	–	–	–	–	+	+	1	–	–	–	–	+	–	–	–	–	–	
<i>Ceterach officinarum</i> agg.	–	–	–	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	
<i>Chamaecytisus ratisbonensis</i>	+	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	
<i>Dianthus pontederae</i>	+	+	+	–	+	–	–	+	–	–	–	–	–	–	–	–	–	–	–	
<i>Festuca pallens</i>	2	3	3	+	–	1	2	–	–	2	1	2	1	1	2	2	1	2	–	
<i>Galium austriacum</i>	+	1	+	–	–	+	+	1	–	–	–	1	1	1	–	1	–	1	–	
<i>Hieracium cymosum</i>	1	+	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
<i>Jovibarba hirta</i>	1	1	–	+	–	+	1	+	–	–	–	–	–	–	–	–	–	1	–	
<i>Koeleria cristata</i> agg.	1	–	–	2	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
<i>Linaria genistifolia</i>	–	–	+	–	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–	
<i>Phleum phleoides</i>	–	+	–	–	–	+	+	–	1	–	–	–	–	–	–	–	–	–	–	
<i>Poa bulbosa</i>	–	–	–	–	+	–	–	+	–	–	–	–	–	–	–	–	–	–	–	
<i>Sedum album</i>	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	2	1	2	–	
<i>Sedum maximum</i>	–	+	–	–	–	+	1	–	–	1	–	–	–	–	–	–	–	–	–	
<i>Sedum sexangulare</i>	1	1	–	1	–	+	–	–	–	–	1	–	–	–	–	–	–	–	–	
<i>Seseli osseum</i>	–	1	1	–	1	–	1	2	–	1	–	–	–	–	–	–	–	–	–	
<i>Thymus praecox</i>	2	1	1	1	1	–	–	1	1	–	–	–	–	–	–	–	–	–	–	
<i>Trifolium alpestre</i>	1	1	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–	

Other taxa: 1: *Festuca valesiaca* agg. 1, *Knautia arvensis* +; 2: *Festuca valesiaca* agg. 1, *Fraxinus ornus* 1, *Euphorbia cyparissias* +, *Polypodium vulgare* agg. +, *Viola arvensis* +, *Salvia pratensis* +; 3: *Potentilla argentea* agg. +; 4: *Polypodium vulgare* agg. +, *Luzula campestris* agg. +, *Stachys recta* +; 5: *Viola arvensis* +; 6: *Lychnis viscaria* +; 7: *Melica ciliata* +, *Saxifraga paniculata* 1, *Erysimum diffusum* +, *Lychnis viscaria* +; 8: *Erysimum diffusum* +, *Fraxinus ornus* 1; 9: *Anthemis tinctoria* +, *Tanacetum corymbosum* +, *Potentilla arenaria* +; 10: *Melica ciliata* 1, *Centaurea stoebe* agg. +, *Potentilla argentea* agg. +, *Pulsatilla pratensis* subsp. *nigricans* +; 11: *Euphorbia cyparissias* +; 14: *Chelidonium majus* +; 15: *Chelidonium majus* +; 19: *Falcaria vulgaris* +.

Table 2. Coenological relevés of the habitat of *Cardaminopsis petraea* II. (Basic data of the relevés, 21–30. Gyenesdiás: Varsás-hegy, Kőmell; Settlement: 21–30. Gyenesdiás; Bedrock: dolomite; Exposition: 21–24 W, NW, 25 N, 26 E, NE, 27–30 NE; Slope: 21–23. 90°, 24. 80°, 25. 60°, 26. 80°, 27–28. 90°, 29–30. 70°; Height above sea level: 21–30. ca 170–180 m); 31–35. Balatongyörök: Bise-kő; Bedrock: dolomite; Exposition: NW; Slope: 31–35. 90°; Height above sea level: 260–280 m

	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
<i>Cardaminopsis petraea</i>	1	1	1	1	1	1	1	+	1	2	1	2	1	1	1
<i>Acinos arvensis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—
<i>Allium montanum</i>	—	—	+	1	—	1	+	1	1	1	1	1	—	+	+
<i>Anthericum ramosum</i>	—	—	—	—	—	—	+	1	1	+	—	—	—	—	—
<i>Anthyllis polyphylla</i>	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—
<i>Arabis hirsuta</i>	—	—	—	—	—	+	+	—	—	—	—	—	—	—	—
<i>Arenaria serpyllifolia</i>	—	—	—	—	—	—	—	—	—	+	—	+	—	—	—
<i>Asplenium ruta-muraria</i>	—	—	—	—	—	+	+	—	—	1	+	+	1	1	—
<i>Asplenium trichomanes</i>	—	+	—	—	1	1	+	+	—	—	1	—	+	—	—
<i>Biscutella laevigata</i>	—	—	—	—	—	+	—	—	1	—	—	1	1	—	—
<i>Bromus pannonicus</i> var. <i>reptans</i>	—	—	—	—	—	2	1	2	—	—	—	—	—	—	—
<i>Campanula rapunculoides</i>	—	—	—	—	—	+	—	—	—	—	—	—	—	—	—
<i>Campanula rotundifolia</i>	+	—	—	—	—	+	—	+	—	+	1	1	+	—	—
<i>Carex humilis</i>	—	—	—	—	—	—	1	—	1	—	—	—	—	—	—
<i>Cerastium pumilum</i> subsp. <i>glutinosum</i>	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—
<i>Dianthus plumarius</i> agg.	—	—	—	—	+	—	—	—	—	—	1	—	—	—	—
<i>Euphorbia cyparissias</i>	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—
<i>Festuca pallens</i>	1	1	1	1	1	1	2	2	2	1	1	1	1	1	—
<i>Fraxinus ornus</i>	—	—	1	—	—	1	—	1	1	—	—	—	—	—	—
<i>Geranium lucidum</i>	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—
<i>Hieracium bifidum</i>	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—
<i>Hieracium glaucinum</i>	+	—	—	—	—	+	—	—	—	—	—	—	—	—	—
<i>Hippocratea emerus</i>	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
<i>Leontodon incanus</i>	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—
<i>Mercurialis ovata</i>	—	—	—	—	—	—	+	—	+	—	—	—	—	—	—
<i>Minuartia setacea</i>	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—
<i>Phyteuma orbiculare</i>	—	—	—	—	—	—	+	—	1	—	—	—	—	—	—
<i>Polygonatum odoratum</i>	—	—	—	—	—	+	1	—	+	—	—	—	—	—	—
<i>Polypodium vulgare</i> agg.	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
<i>Potentilla arenaria</i>	—	—	—	1	—	—	—	+	—	+	—	—	—	—	—
<i>Sedum album</i>	—	—	—	—	—	—	—	—	+	—	1	1	1	2	+
<i>Seseli leucospermum</i>	—	—	—	—	—	—	—	1	1	—	—	—	1	—	—
<i>Thalictrum pseudominus</i>	—	—	+	—	—	—	—	+	—	—	—	—	—	—	—
<i>Viola collina</i>	—	—	—	—	—	—	1	—	+	—	—	—	—	—	—

RESULTS AND DISCUSSION

Distribution in Hungary

Dot map of the distribution data of *Cardaminopsis petraea* in Hungary (Fig. 1) was made on the basis of herbarium and literature data. Current populations of the species were typically found at locations that coincide with the majority of herbarium data. Three major stands are known: one on Csobánc Hill (one of the basalt monadnocks in the Balaton Uplands), one on the "Kőmell" above Gyenesdiás (a dolomite rock of the Keszthely Mts) and one on the "Bise-kő" near Balatongyörök (another huge dolomite rock of the Keszthely Mts).

In handbooks, taxonomic handbooks (JÁVORKA 1925, JÁVORKA and SOÓ 1951, SOÓ 1968, etc.) and other synthetic works (FEKETE 1964) the most often referred Hungarian data come from the Csobánc Hill and the Keszthely Mts. SIMON (2000) only mentions it from the Keszthely Mts. In spite of systematic searches on many formerly confirmed habitats in Hungary the species was not found. Occurrence data not verified by herbarium vouchers are handled with reservation.



Fig. 1. Data of *Cardaminopsis petraea* from Hungary (full circle = data confirmed by collected specimen in herbarium; empty circle = literary data). Localities and CEU codes: Gyenesdiás, Vonyarcvashegy (several localities) 9269.2; "Büdöskúti-völgy" 9169.4; "Sipos-torok, Szobakő, Márványköfejtő" 9170.3; Balatongyörök: Bise-kő 9270.1; Csobánc 9171.1; Ódörögd:Viszló-erdő 9070.3; Nadap 8777.2; "Nagy-Szénás" 8479.1; "Almás" (Dunaalmás) 8275.4 or 8276.3; Pécs "Schneeburg", "Havihegy" 9975.1.

Keszthely Mts

Herb.: "Keszthely" leg. Hutter, s.d. (in Herbarium of Sadler József) [BP 73864]; "Keszthely" leg. Szenczy I. 1846 [SAV]; "Keszthely, in rupibus dolomiticis." leg. Borbás V., 04.05.1894 [BP 73857]; "Balatongyörök: in ruderatis dolomiticis retro Vonyarc ad Balatonem." leg. Jávorka S., 19.04.1927 [BP 73861, 73858]; "Comit. Zala, ad ripas lacus Balaton. In ruderatis dolomiticis declivium prope pag. Vonyarc-Vashegy." leg. Jávorka S., 19.04.1927 [BP 73863, 221956]; "Cott. Zala, in lapidosis dolomiticis vallis ultra pag. Vonyarcvashegy." leg. Jávorka S., 19.04.1927 [DE]; "Comit. Zala, ad ripas lacus Balaton. In ruderatis dolomiticis declivium prope pag. Vonyarc-Vashegy." 19.04.1927 [DE]; "Vonyarc ad Keszthely: in ruderatis et saxosis dolomiticis sub rara." leg. Jávorka S., 25.06.1927 [BP 73862]; "Cott. Zala, in graminosis saxosis declivium supra pag. Gyenesdiás." leg. Soó R., 04.1928 [BPU]; "Locus natalis: cott. Zala, in saxosis gramin. declivium supra pag. Gyenesdiás." leg. Soó R., 05.1928 [BP 403347]; "Comit. Zala: supra pagum Vonyarc." leg. Lengyel G., 20.04.1930 [BP 352541, 352539]; "Comit. Zala. In saxosis umbrosis supra pagum Vonyarc." leg. Degen Á., 20.04.1930 [BP 301122, 301123]; "Vonyarc-Vashegy, in montibus" leg. Zsák Z., 20.04.1930 [BP 428602]; "Locus natalis: comit. Zala, Mt. Keszthelyi-hegység, in saxosis umbrosis montibus prope pagum Vonyarcvashegy." leg. Újvárosi M., 19.04.1946 [BP 478330]; "Comit. Zala. In rupibus dolomit. sept. dumetos. "Kümell" prope Gyenesdiás. 200 m" leg. Boros Á., 14.05.1950 [BP 428564, 428565, 428603]; "Hungaria occ., com. Veszprém. In rupibus calcareis montis Kümell prope pag. Gyenesdiás." leg. Vajda L., 14.05.1950 [BP 403486]; "Keszthelyi hegység: Vonyarc-Vashegy északi árnyas dolomitos lejtőjén." leg. Jávorka S., 15.04.1951 [BP 73869, 73870]; "Keszthelyi hgs. Gyenesdiás mellett, a Büdöskuti völgy vége felé északi dolomitejtőn Brometum erecti ass." leg. Baksay L., 15.04.1951 [BP 209285]; "Keszthelyi hegység, sziklákön. 250 m" leg. Vajda Ernő, 15.04.1952 [BP 425439]; "Gyenesdiás. Erdős, sziklás hegyoldalon." leg. Siroki Z., 01.08.1955 [DE]; "Comitat. Veszprém. In rupibus dolomit. decl. mt. Kümellhegy supra pag. Gyenesdiás" leg. Károlyi Á., 11.05.1952 [BP 403465]; "Comitat. Zala. In rupibus dolomiticis montis Kümellhegy dit. pr. pag. Gyenesdiás" leg. Károlyi Á., 11.05.1952 [BP 403465]; "Comitat. Veszprém. Mtes. Keszthelyi hg. In lapidosis pr. pag. Gyenesdiás. 200 m" leg. Károlyi Á., 09.06.1962 [BP 298081]; "Gyenesdiás: Kőmell (Varsás-hegy). In rupibus dolomiticis, EOV 515653 161518" leg. Bauer N. [BP 689427]; "Vonyarcvashegy: Vas-hegy. Rarissima, in *Pinetum nigrae* cultum, in declivibus septentrionalibus EOV 518215 159839." leg. Bauer N., 07.04.2007 [BP 690253]; "Balatongyörök: Bise-kő. In rupibus dolomiticis, in declivibus occidentalibus EOV 520435 161418" leg. Bauer N. and Kenyeres Z., 11.04.2008 [BP 693198].

The first record is found in József Sadler's herbarium concerning Keszthely with the comment "*Hutter Keszthely*". The specimen definitely comes from Hutter, who was one of the botany teachers in the first half of the 18th century at Georgikon and the Academic Grammar School in Keszthely. He may have collected the plant approximately the same time as his colleague, Imre Szency, whose sample was collected in 1846 and is now

preserved at the Savaria Museum. (Probably these were the first collected specimens of *Cardaminopsis petraea* in Hungary). The plant was also found by Vince Borbás who was researching the flora of the region around Lake Balaton; in his monograph BORBÁS (1900) mentions it among the alpine species of "Balaton-mellék" (the surroundings of Lake Balaton) under the name of *Arabis hispida* Mygind, with a more precise site indication: "Gyenes völgyében, sziklás helyen" ["In the valley of Gyenes, on a rocky place"]. Borbás also mentioned that he saw the plant – a rarity in Hungary – only from Nadap, in Tauscher's herbarium. In the environs of Balatongyörök and Vonyarcvashegy (Vas Mount) *Cardaminopsis petraea* was found for the first time by Sándor Jávorka. Ádám Boros and László Vajda made a more precise circumscription of the Gyenesdiás habitat: Kümell (= Kőmell) with a note "Büdöskuti-völgy vége felé" ["towards the end of Büdöskuti Valley"]. This specimen was collected by Leona Baksay. Subsequent collections confirmed this data. SZABÓ (1987) cites the previous data from the Keszthely Mts (after BORBÁS 1900 and SOÓ 1968), and adds three new localities: "Sipos-torok, Szobakő, Márványköfejtő". After the checking of the known data we found (N. Bauer and Z. Kenyeres) a new occurrence on a plumb wall of a huge dolomite rock, called "Bise-kő", near Balatongyörök.

Present knowledge of the occurrences in this region comprises of almost a hundred specimens on Kőmell's dolomite rock at Gyenesdiás, and almost 80 stems on the rock of Bise-kő, a few dozens of specimens in a planted *Pinus nigra* stand on the north slope of Vas Hill at Vonyarcvashegy, a few specimens in the Büdöskuti Valley, on the northeastern dolomite rocky slope of Öreg-Szék-tető facing Köves-árok.

Balaton Uplands

Herb.: "Csobánczvár" leg. Redl G., 04.05.1907 [BP 73856]; "In rupibus basalticis montis Csobánc prope pag. Gyulakeszi ad Balaton." leg. Jávorka S., 02.06.1925 [BP 73859]; "Comit. Zala. In rupibus basalt. sept.-occ. montis Csobánc prope Gyulakeszi. 300 m." leg. Boros Á., 01.05.1954 [BP 428567, 428568, 428569]; "Balatonvidék, Csobánc." leg. Vajda L., 01.05.1954 [BP 199374]; "Comit. Zala. In rupibus basalt. sept. montis Csobánc prope Diszel 300–370 m." leg. Boros Á., 01.05.1959 [BP 448619, 448620]; "Veszprém megye, Balaton-felvidék. Tapolca-Diszel: Csobánc, rara, in rupibus basalticis, in declivibus septentrionalibus." leg. Bauer N., 16.04.2005 [BP 687563]; "Veszprém megye, Balaton-felvidék. Gyulakeszi: Csobánc, in rupibus basalticis, in declivibus septentrionalibus." leg. Bauer N.,

02.06.2005 [BP 665335]; "Gyulakeszi: Csobánc. "Csobáncvár" EOV 532328 170833" leg. Bauer N., 27.04.2007 [BP 690837].

Cardaminopsis petraea grows at only one site in the Balaton Uplands, on one of the basalt monadnocks in the Basin of Tapolca, namely the Csobánc Hill. Its exploration is connected to Gusztáv Redl (1853–1917) – a teacher and plant collector from Tapolca; the habitat site indication of "Csobáncvár" refers to the fact that Redl collected the plant on the stone walls of the ruined castle on the hill-top. Jávorka was the first who collected *Cardaminopsis petraea* from the basalt rocks of Csobánc Hill; later its occurrence was confirmed by additional collections and literature sources (FEKETE 1964, KOVÁCS and TAKÁCS 1995, MESTERHÁZY *et al.* 2003) as well.

Currently the plant is found on the northerly steep, and sometimes the vertical rocky slopes of the hill (almost 50 and 100 specimens, respectively), and almost 50 specimens on one of the north-facing stone wall of the ruined castle.



Fig. 2. *Cardaminopsis petraea*. **A:** Gyenesdiás, Kőmell, 06.23.2007, photo: Bauer N.; **B:** Balatongyörök, Bise-kő, 04.11.2008, photo: Bauer N.

Bakony Mts

Herb.: "Tapolca, comit. Zala: in calcareis vallis infra Ódörögdi major in silva Viszlói erdő." leg. Jávorka S., 26.08.1927 [BP 73860].

Since the collection of Jávorka at the only known occurrence of *Cardaminopsis petraea* in the southern Bakony this site could not be verified, and the precise location is still to be searched for.

Velence Mts

Herb.: "Hungaria, Comitatus Alba. E vineis montis Csúcsos prope Nadap." leg. Tauscher Gy., 05.1869 [BP 73865]; "Hungaria scutalis, Comitatus Alba. E lapidosis montanis prope pagum Nadap." leg. Tauscher Gy., 05.1869 [BP 73866].

We are aware of only one proven occurrence in the Velence Mts – on "Csúcsos Hill" at Nadap. An interesting data from Gyula Tauscher (1831–1882) – a manor doctor of Ercsi and a noted plant collector – is mentioned in the work of BORBÁS (1900). JÁVORKA (1925) cites the Velence Mts occurrence with the comment "*a Meleg-hegyen Fehér megyében*" ["*on the Meleg Hill in Fehér county*"], but omits the same location in his later work (JÁVORKA 1937); SOÓ (1968) notes *Cardaminopsis petraea* as having a questionable occurrence in the Velence Mts ("Velencei-hg. ?").

Gerecse Mts

HILLEBRANDT (1858) reported on the observation of *Arabis petraea* Sam. while taking excursions with Count Zichy in Komárom county: "*auf dem Göbitiö (Steinberg), einem bei Almas sich erhebenden kleinen Tropstreiberg fanden wir...*". This occurrence could not be verified since then, however, it has been quoted in a number of synthetic works: NEILREICH (1866) "*auf dem Steinberg bei Almás im Com. Komorn.*"; JÁVORKA (1925) "*Almásnál Komárom megyében*"; SOÓ (1968) "*Komárom: Almás?*". Anyway, the occurrence appeared on the chorological map of JALAS and SUOMINEN (1996). According to BARINA (2006) this occurrence is questionable.

Buda Mts

SOÓ (1968) and SOÓ and KÁRPÁTI (1968) mentioned *Cardaminopsis petraea* from Mt "Nagy-Szénás" in the Buda Mts, a data of doubtful origin that requires verification.

Mecsek Mts

"*Arabis Crantziana* Ehr." was mentioned from the environs of Pécs with the note "bei Fünfkirchen" in the review of NEILREICH (1866). The author refers to the enumeration of K. NENDTVICH (1836). The species was not listed in the work of T. NENDTVICH (1846) about the rare plants of the environs of Pécs. KERNER (1863) called the attention to several erroneous data of K. NENDTVICH, but "*Arabis Crantziana*" was not mentioned by him. SIMONKAI (1876) was searching for it unsuccessfully on its presumed location near Pécs, on "Schneeberg", and also commented that it became extinct according to NENDTVICH V. The Mecsek occurrence has been cited in subsequent synthetic works as the species being extinct or its presence doubtful: HAZSLINSZKY (1872): "lelhelyei bizonytalanok s nyugoton keresendők" ["its occurrences are questionable and should be searched for in the west"]; HORVÁT (1942): "egykor... Pécs... Havihegy" ["erstwhile... Pécs... Havihegy"]; JÁVORKA (1925): "a Mecseken?" ["on the Mecsek?"]; SOÓ (1968): "Mecsek † ?" ["Mecsek † ?"]. Recent works do not reference the species from the environs of Pécs and the plant is cited on the maps of JALAS and SUOMINEN (1996) as extinct from this location. The hill called Havihegy in the town of Pécs is a residential area today.

Habitat preferences in Hungary

Careful survey of occurrence data of *Cardaminopsis petraea* in Hungary revealed the existence of three major (Csobánc, Kőmell, Bise-kő) and two minor populations (Vas Hill, Büdöskúti Valley).

The strongest stand of *Cardaminopsis petraea* in Hungary remained on one of the basalt volcanic monadnocks in the Balaton Uplands, namely on the Csobánc Hill. The majority of this population exists on the Upper Pannonian (Mio-Pliocene) basalt rocky outcrops of the northern slope

(BUDAI and SCHAREK 2005), mainly on the vertical rocky wall, in chasm vegetation (Table 1: 1–10). This vegetation on the basis of its species combination is considered an association variant of *Alyssum saxatile-Festucetum pallentis* Klika ex Cerovsky 1949 corr. Gutermann et Mucina 1993 (see MUCINA and KOLBEK 1993). The occurrence of this association in the Csobánc Hill and its description on the basis of species frequency was given by CSIKY (2003), and Csiky in BORHIDI (2003), without *Cardaminopsis petraea*. *Cardaminopsis petraea* also grows on the rocks of the debris slope forest (*Mercuriali-Tiliatum* Zólyomi et Jakucs in Zólyomi 1958) under the rocks, and some of its stems were also observed in the rocky grassland of the west-facing slope. The occurrence of the plant on secondary surfaces, i.e. built stone walls, is rather rare in Central Europe (BRANDES 1992). For this reason, it is especially interesting that it occurs with high density as other rocky grassland species on the Csobánc Hill on the northern side of one of the ruined castle walls (Table 1: 11–20). Of the dominant species of the *Alyssum saxatile-Festucetum pallentis* association on Csobánc Hill, *Allium senescens* subsp. *montanum*, *Aurinia saxatile*, *Festuca pallens*, *Jovibarba hirta*, *Seseli osseum*, *Asplenium septentrionale*, *Campanula rotundifolia* are typical in the habitats of *Cardaminopsis petraea*. Further notable elements of the rocky vegetation are *Saxifraga paniculata*, *Ceterach officinarum*, *Galium austriacum*, and *Asplenium ruta-muraria* is also frequent on the castle wall. *Cardaminopsis petraea* is found in the greatest density on the castle wall. Observations of relatively great density of this species have been reported from secondary habitats; Hemp's hypothesis (HEMP 1996) about the recent expansion of *Cardaminopsis petraea* is based on this phenomenon.

The composition of the lichen species found in the studied quadrates (Csobánc, relevés 1–20) represents a typical, acidic rocky lichen community with dominance of *Acarospora fuscata*, *Aspicilia cinerea*, *Candelariella vitellina*, *Lecanora rupicola*, *Pertusaria lactea*, *P. leucosora*, *Rhizocarpon geographicum*, *Rh. lavatum* and *Scoliciosporum umbrinum* (Table 3). *Micarea botryoides* (in relevés 1–10) is new for Hungary. At this place there is the 2nd, confirmed Hungarian occurrence for *Toninia aromatica* (in relevés 11–20 situated in the castle wall). Its first published occurrence from Lipótmező (SÁNTHA 1910, SZATALA 1942) is dubious in lack of the specimen. Another specimen from the Bükk Mts (collected by F. Fóriss) was revised later as *Scoliciosporum umbrinum*, thus the other (only former) confirmed

locality is in the Buda Mts (Bia: Dobogó-hegy) where it was found by Gy. Timkó in 1917.

The bryophyte assemblage of the studied quadrates consists of common species as *Hypnum cypresiforme*, *Dicranum scoparium*, *Brachythecium rutabulum* and *Homalothecium sericeum*. In the quadrates of Csobánc 11–20, (on the ruins of the castle wall) some common species characteristic in anthropogenic habitats (*Funaria hygrometrica*, *Tortula muralis*) do also occur. Two hepaticas collected in quadrates Csobánc 1–10 (*Barbilophozia barbata*, *Frullania tamarisci*) are indicator species of rocky places in good natural condition.

In the Keszthely Mts, from where the largest number of proven occurrence data is known, we found the strongest stand of *Cardaminopsis petraea* on the side of Mt Varsás above Gyenesdiás, mainly on the north-facing wall of the great almost vertical rock. The bedrock of the locally named Kőmell is upper Triassic dolomite (Rezi Dolomite Formation) (BUDAI and SCHAREK 2005). *Cardaminopsis petraea* only occurs here on the rock wall and a few individuals in the *Pinus nigra* stand planted under the rock. On the wall *Cardaminopsis petraea* is accompanied by species typical in the north-facing shaded dolomite rocky grasslands (*Festuco pallenti-Brometum pannonicum* Zólyomi 1958) of the Transdanubian Mts (*Festuca pallens*, *Bromus pannonicus* var. *reptans*, *Seseli leucospermum*, *Allium montanum*, *Phyteuma orbiculare*, *Thalictrum pseudominus*, *Viola collina*, *Leontodon incanus*, etc.) (Table 2). The total cover of vegetation is rather low here because of the geomorphological conditions. Based on the coenological relevés the plant association developed on dolomite substrate of the Transdanubian Mts is significantly rich in relict species. This particular association can be regarded as a distinct "chasm grassland-character variant" or "rocky wall variant" of the above association (in which *Cardaminopsis petraea* and all of the recorded species are frequent, typical elements of the association). Regarding this we share the opinion of Zólyomi in FEKETE et al. (1961). Zólyomi also identified the habitat of *Primula auricula* occurring in rocky walls as a variant of closed dolomite rocky grasslands fragmentally developed on cliffs. On the dolomite area of the Keszthely Mts *Aurinia saxatilis* only survived on one spot (Keszthely-Cserszegtomaj: Csókakő) on barren rocky walls with similar vegetation.

The list of lichens from the studied quadrates ("Kömell" relevés 21–30) is mostly composed of species which frequently colonise shaded calcareous rocks, like *Bacidina egenula*, *Catillaria lenticularis*, *Gyalecta jenensis*, *Lecidella stigmatica*, *Placynthium hungaricum* and *Protoblastenia rupestris*, while other species, such as *Aspicilia calcarea*, *Lecanora albescens*, *Lobothallia radiosa* and *Placocarpus schaeereri* (Table 4) usually prefer exposed rocks. *Dirina stenhammari* is a rare species with only 3 former localities from Hungary (VERSEGHY 1994). Not previously known from the Keszthely Mts, *Solenopsora candicans* had two former occurrences from Hungary (Buda Mts: Nagy-Szénás; Keszthely Mts: "Rezi csere"), but these have never been published. As the 3rd location of the species, it is 10 km far from the other locality in the Keszthely Mts ("Rezi csere").

Most of the bryophytes found in the studied quadrates are characteristic species of shaded rocks. Some of them prefer exposed rocky places as *Orthotrichum cupulatum* and *Radula complanata*. In the quadrates KÖMELL 28–30 some species living on soil in closed grassland or at forest margins were also detected (e.g. *Rhytidadelphus triquetrus*, *Scleropodium purum*, *Thuidium recognitum*). *Gymnostomum calcareum* collected in the quadrates KÖMELL 21–25 is an indicator species of shaded calcareous rocky places in good natural condition.

Situation of the stand in Bise-kő is equal to the stand of KÖMELL. In Bise-kő the common co-occurring species of *Cardaminopsis petraea* are *Asplenium ruta-muraria*, *Sedum album*, *Campanula rotundifolia*, *Allium montanum*, and *Festuca pallens*. In this habitat the relicts typical on dolomite in the Transdanubian Mts, as *Seseli leucospermum*, *Biscutella laevigata*, and *Dianthus plumarius*, are also present. The vegetation is a rocky wall variant of a dolomite rocky grassland community.

Concerning the habitat preferences of *Cardaminopsis petraea* in Hungary, the analyses based on relevés taken in Bohemia show similar results: there, it also grows on base-rich volcanic bedrocks and also on dolomite. CHYTRY (2007) stated that *Cardaminopsis petraea* occurs in *Festuco pallentis-Aurinetum saxatilis* association typical in the North Bohemian volcanic hills, and in *Saxifrago paniculatae-Seslerietum caeruleae* Klika 1941 association typical on limestone and on base-rich siliceous bedrocks.

Table 3. Occurrence of the bryophyte and lichen species in the studied quadrates of Csobánc Hill

Species	Csobánc 1–10	Csobánc 11–20
BRYOPHYTES		
<i>Barbilophozia barbata</i> (Schreb.) Loeske	+	
<i>Brachythecium rutabulum</i> (Hedw.) Schimp.		+
<i>Dicranum scoparium</i> Hedw.	+	
<i>Frullania tamarisci</i> (L.) Dumort.	+	
<i>Funaria hygrometrica</i> Hedw.		+
<i>Homalothecium sericeum</i> (Hedw.) Schimp.		+
<i>Hypnum cupressiforme</i> Hedw.	+	
<i>Tortula muralis</i> L. ex Hedw.		+
LICHENS		
<i>Acarospora fuscata</i> (Nyl.) Arnold	+	
<i>Aspicilia cinerea</i> (L.) Körb.	+	
<i>Caloplaca citrina</i> (Hoffm.) Th. Fr.		+
<i>Caloplaca holocarpa</i> (Hoffm.) A. E. Wade		+
<i>Caloplaca saxicola</i> (Hoffm.) Nordin		+
<i>Candelariella vitellina</i> (Hoffm.) Müll. Arg.	+	+
<i>Cladonia pyxidata</i> (L.) Hoffm.	+	
<i>Cladonia rangiformis</i> Hoffm.	+	
<i>Diplotomma alboatrum</i> (Hoffm.) Flot.		+
<i>Hypogymnia physodes</i> (L.) Nyl.	+	
<i>Lecanora albescens</i> (Hoffm.) Branth et Rostr.		+
<i>Lecanora dispersa</i> (Pers.) Röhl.		+
<i>Lecanora rupicola</i> (L.) Zahlbr.	+	
<i>Lecidella stigmatea</i> (Ach.) Hertel et Leuckert		+
<i>Melanelia glabratula</i> (Lamy) Essl.	+	
<i>Micarea botryoides</i> (Nyl.) Coppins	+	
<i>Parmelia sulcata</i> Taylor	+	
<i>Pertusaria lactea</i> (L.) Arnold	+	
<i>Pertusaria leucosora</i> Nyl.	+	
<i>Phaeophyscia orbicularis</i> (Neck.) Moberg		+
<i>Physcia dimidiata</i> (Arnold) Nyl.		+
<i>Porpidia tuberculosa</i> (Sm.) Hertel et Knoph	+	
<i>Rhizocarpon geographicum</i> (L.) DC.	+	
<i>Rhizocarpon lavatum</i> (Fr.) Hazsl.	+	+
<i>Scoliosporum umbrinum</i> (Ach.) Arnold	+	+
<i>Tephromela atra</i> (Huds.) Hafellner	+	+
<i>Toninia aromatica</i> (Turner ex Sm.) A. Massal.		+
<i>Trapelia</i> sp.	+	
<i>Verrucaria muralis</i> Ach.		+
<i>Xanthoparmelia stenophylla</i> (Ach.) Ahti et D. Hawksw.	+	

Table 4. Occurrence of the bryophyte and lichen species in the studied quadrates of Keszthely Mts

	Kőmell 21–25	Kőmell 26–27	Kőmell 28–30
BRYOPHYTES			
<i>Anomodon viticulosus</i> (Hedw.) Hook. et Taylor	+		
<i>Ctenidium molluscum</i> (Hedw.) Mitt.		+	+
<i>Encalypta streptocarpa</i> Hedw.		+	+
<i>Eurhynchium striatum</i> (Spruce) Schimp.		+	
<i>Fissidens dubius</i> P. Beauv.			+
<i>Gymnostomum calcareum</i> Nees et Hornsch.	+		
<i>Homalia besseri</i> Lobarz.		+	
<i>Homalothecium sericeum</i> (Hedw.) Schimp.	+		+
<i>Hypnum cupressiforme</i> Hedw.	+		
<i>Neckera complanata</i> (Hedw.) Huebener		+	
<i>Orthotrichum cupulatum</i> Brid.		+	
<i>Plagiochila porelloides</i> (Nees) Lindenb.			+
<i>Radula complanata</i> (L.) Dumort.	+		
<i>Rhytidiaadelphus triquetrus</i> (Hedw.) Warnst.			+
<i>Scleropodium purum</i> (Hedw.) Limpr.			+
<i>Thuidium recognitum</i> (Hedw.) Lindb.			+
<i>Tortella tortuosa</i> (Hedw.) Limpr.	+		+
LICHENS			
<i>Aspicilia calcarea</i> (L.) Körb.			+
<i>Bacidina egenula</i> (Nyl.) Vézda	+		
<i>Bilimbia sabuletorum</i> (Schreb.) Arnold	+		+
<i>Caloplaca cirrochroa</i> (Ach.) Th. Fr.	+		
<i>Caloplaca flavescens</i> (Huds.) J. R. Laundon	+		+
<i>Caloplaca saxicola</i> (Hoffm.) Nordin	+		
<i>Catillaria lenticularis</i> (Ach.) Th. Fr.	+	+	+
<i>Collema</i> sp.	+		
<i>Dirina stenhammari</i> (Arnold) Poelt et Föllmann	+		
<i>Gyalecta jenensis</i> (Batsch) Zahlbr.	+		
<i>Lecania erysibe</i> (Ach.) Mudd			+
<i>Lecanora albescens</i> (Hoffm.) Branth et Rostr.	+		
<i>Lecanora dispersa</i> (Pers.) Röhl.	+		
<i>Lecidella stigmatica</i> (Ach.) Hertel et Leuckert	+		
<i>Lepraria</i> sp.		+	+
<i>Lobothallia radiosa</i> (Hoffm.) Hafellner			+
<i>Physconia grisea</i> (Lam.) Poelt	+		
<i>Placocarpus schaeferi</i> (Fr.) Breuss		+	+
<i>Placynthium hungaricum</i> Gyeln.			+
<i>Protoblastenia rupestris</i> (Scop.) J. Steiner		+	+
<i>Solenopsora candidans</i> (Dicks.) J. Steiner			+
<i>Thelidium decipiens</i> (Hepp) Kremp.			+

CONCLUSIONS

Habitat analyses of the three major populations of *Cardaminopsis petraea* in Hungary provided results similar to those of other works (HEMP 1996, ČERNÝ *et al.* 2006). Based on the occurrence data and habitat features in Hungary and in Central Europe the plant generally grows on rocky habitats. Its appearance cannot be strictly connected to any particular plant association or higher vegetation unit (*cf.* ELLENBERG 1996, HEMP 1996, ČERNÝ *et al.* 2006). The occurrence of the plant is determined by micro-climatic and geomorphological features providing its basic ecological requirements and vegetation historic characters.

Hungary's mountainous regions were periglacial areas during glaciation in the Pleistocene with cold steppe and mosaic steppe and tundra vegetation (ZÓLYOMI 1952, FRENZEL *et al.* 1992), which certainly provided more favourable conditions for *Cardaminopsis petraea* and other alpine and boreal flora elements. Today *Cardaminopsis petraea* occurrences in the Balaton Uplands and in the Keszthely Mts can be characterised by intensive sub-Mediterranean features, in which the relict populations of any boreal and alpine species could only survive in the cool microclimatic micro-habitats, as minor remnants of formerly more extended areas. Under the current climatic conditions, *Cardaminopsis petraea* can only thrive on cooler north-facing rocky slopes and rock walls in Hungary's mountainous areas. The small populations that survived in the Transdanubian Mts – based on a higher diversity of other Central European populations (CLAUSS and MITCHELL-OLDS 2006, ANSELL *et al.* 2007) – represent a valuable gene pool. Because of their varied climatic and geomorphological characters, the Transdanubian Mts have been able to continuously provide suitable conditions for *Cardaminopsis petraea* since the end of the Pleistocene up to now. These areas – especially the dolomite areas (see ZÓLYOMI 1942) – are important refugia also shown by the presence of other de-alpine and/or boreal relict species with similar requirements (*Primula auricula*, *Moehringia muscosa*, *Allium victorialis*, *Festuca amethystina*, etc., see ZÓLYOMI 1942, 1958, SOÓ 1964). SIMON (1972) (in his paper about the rocky vegetation of the Zemplén Mts) called the attention to the fact that the rocky grasslands of the Hungarian volcanic middle mountains play an important role in preserving relict species. Simon's assumption gets plenty of support also by

previously published floras of low and small island-like basalt monadnocks (see BORBÁS 1900, SOÓ 1930, JÁVORKA and SOÓ 1951, FEKETE 1964). The geomorphological (differently exposed, often vertical stone walls; alternation of debris slopes and crumbling, block disintegrating stone types) and microclimate features (strongly depending on the geomorphology) of the volcanic monadnocks made the remaining of *Cardaminopsis petraea*, *Saxifraga paniculata*, *Aurinia saxatilis* and other glacial and postglacial rocky relicts on the Transdanubian basalt hills [e.g. *Dianthus plumarius* subsp. *lumnitzeri* (Szent György Hill, leg. Zsák Z., 1920, publ. BAKSAY 1972), *Hieracium wiesbaurianum* (Badacsony, Borbás 1900, Szent György Hill, Bauer ined.)] possible.

Because of their phytogeographical importance, the populations of *Cardaminopsis petraea* restricted to limited areas in Hungary would deserve greater attention of the nature conservation authorities. We are working on a proposal that will hopefully result in the declaration of the plants' remaining habitats strictly protected.

* * *

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REFERENCES

- ANSELL, S., GRUNDMANN, M., SCHNEIDER, H., RUSSELL, S. J. and VOGEL, J. C. (2007): *Arabidopsis lyrata* ssp. *petraea*: non-model patterns of glacial history in a model plant *Arabidopsis lyrata* ssp. *petraea*. – Botany and Plant Biology 2007 Congress, Session P, Biogeography Posters, P62001.
- BAKSAY, L. (1972): Biosystematik der *Dianthus plumarius* L. (sensu lato) in Ungarn. – *Symp. Biol. Hung.* **12**: 149–161.
- BARINA, Z. (2006): *A Gerecse hegység flórája*. (Flora of Gerecse Mountains). – MTM, DINPI Budapest, 612 pp.
- BORBÁS, V. (1900): *A Balaton tavának és partmellékének növényföldrajza és edényes növényzete*. [The vascular flora and phytogeography of Lake Balaton and its surroundings]. – A Balaton tudományos tanulmányozásának eredményei 1, Budapest, 432 pp.

- BORHIDI, A. (1995): Social behaviour types, their naturalness and relative ecological indicator values of the higher plants of the Hungarian Flora. – *Acta Bot. Hung.* **39**: 97–182.
- BORHIDI, A. (2003): *Magyarország növénytársulásai*. [Plant associations of Hungary]. – Akadémiai Kiadó, Budapest, 610 pp.
- BRANDES, D. (1992): Asplenietea-Gesellschaften an sekundären Standorten in Mitteleuropa. – *Ber. d. Reinh.-Tüxen Ges.* **4**: 73–94.
- BRAUN-BLANQUET, J. (1964): *Pflanzensoziologie*. 3. Aufl. – Wien, 865 pp.
- BUDAI, T. and SCHAREK, P. (2005): *Magyarország földtani térképe L-33-47 Keszthely*. [Geological map of Hungary L-33-47 Keszthely]. – Fedett Földtani Térkép, 1:100,000, Magyar Állami Földtani Intézet, Budapest.
- BURDET, H. M. (1967): Contribution à l'étude caryologique des genres *Cardaminopsis*, *Turritis* et *Arabis* en Europe. – *Candollea* **22**(1): 107–156.
- ČERNÝ, T., PETŘÍK, P., BOUBLÍK, K. and KOLBEK, J. (2006): Habitat requirements of *Cardaminopsis petraea* – rare relict species of the Czech Republic. – *Biologia*, Bratislava **61**(1): 51–61.
- CHEFFINGS, C. and FARRELL, L. (eds) (2005): *The vascular plant red data list for Great Britain*. – Joint Nature Conservation Committee, Peterborough, Species Status **7**: 1–116.
- CHYTRÝ, M. (ed.) (2007): *Vegetace České Republiky I. Travinná a keříčková vegetace*. (Vegetation of the Czech Republic. 1. Grassland and Heathland Vegetation). – Academia, Praha, 497 p.
- CHYTRÝ, M. and TICHÝ, L. (2003): *Diagnostic, constant and dominant species of vegetation classes and alliances of the Czech Republic: a statistical revision*. – Masaryk University, Brno, 231 pp.
- CLAUSS, M. J. and MITCHELL-OLDS, T. (2006): Population genetic structure of *Arabidopsis lyrata* in Europe. – *Molec. Ecol.* **15**(10): 2753–2766.
- CLAUSS, M. J., COBBAN, H. and MITCHELL-OLDS, T. (2002): Cross-species microsatellite markers for elucidating population genetic structure in *Arabidopsis* and *Arabis* (Brassicaceae). – *Molec. Ecol.* **11**: 591–601.
- CSIKY, J. (2003): A Nógrád-gömöri bazaltvidék flórája és vegetációja. (The flora and vegetation of the Nôgrád-Gömör basalt region). – *Tilia* **11**: 167–339.
- CURTIS, T. G. F. and MCGOUGH, H. N. (1988): *The Irish Red Data Book I. Vascular Plants*. – Wildlife Service Ireland, Dublin, 80 pp.
- DART, S., KRON, P. and MABLE, B. K. (2004): Characterizing polyploidy in *Arabidopsis lyrata* using chromosome counts and flow cytometry. – *Canad. J. Bot.* **82**(2): 185–197.
- DAVEY, M. P., BONNAGE, S., NEWMAN, R., WOODWARD, F. I. and QUICK, W. P. (2006): *Intra- and interspecific differences of gas-exchange in cold-shocked Arabidopsis thaliana and Arabidopsis lyrata petraea*. – Genome to systems Conference, Manchester, UK, 22–24 March 2006 <http://abstracts.co.allenpress.com/pweb/esa2006/document/?ID=61291> (poster)
- ELLENBERG, H. (1996): *Vegetation Mitteleuropas mit den Alpen*. 5. Aufl. – Eugen Ulmer, Stuttgart, 1095 pp.
- ERICSON, L. and MASCHER, J. W. (1978): *Cardaminopsis petraea*, strandrav, i Angermanland. [Cardaminopsis petraea in Angermanland, E Central Sweden]. – *Svensk Bot. Tidskr.* **71**: 415–418.

- ERZBERGER, P. and PAPP, B. (2004): Annotated checklist of Hungarian bryophytes. – *Studia bot. hung.* **35**: 91–149.
- FEKETE, G. (1964): *A Bakony növénytakarója*. (Die Pflanzendecke des Bakony-Gebirges). – A Bakony természettudományi kutatásának eredményei I. Veszprém, 53 pp.
- FEKETE, G., MAJER, A., TALLÓS, P., VIDA, G. and ZÓLYOMI, B. (1961): Angaben und Bemerkungen zur Flora und zur Pflanzengeographie des Bakonygebirges. – *Annls hist.-nat. Mus. natn. hung.* **53**: 241–253.
- FRENZEL, B., PÉCSI, M. and VELICHKO, A. A. (eds) (1992): *Atlas of paleoclimates and paleo-environments of the Northern Hemisphere. Late Pleistocene–Holocene*. – Budapest, Stuttgart, 153 pp.
- GAUCKLER, K. (1938): Steppenheide und steppenheidewald der Fränkischen Alb in pflanzensoziologischer, ökologischer und geographischer Betrachtung. – *Ber. Bay. Bot. Ges.* **23**: 5–134.
- GAUDEUL, M., STENØIEN, H. K. and ÅGREN, J. (2007): Landscape structure, clonal propagation, and genetic diversity in Scandinavian populations of *Arabidopsis lyrata* (Brassicaceae). – *Amer. J. Bot.* **94**(7): 1146–1155.
- HAYEK, A. (1908): *Cardaminopsis*. – In: Flora von Steiermark. Berlin, pp. 477–481.
- HAZSLINSZKY, F. (1872): *Magyarhon edényes növényeinek fiúvészeti kézikönyve*. – Atheneum, Pest, 504 pp.
- HEDBERG, I. and HEDBERG, O. (1961): Chromosome counts in British vascular plants. – *Bot. Notiser* **114**(4): 397–399.
- HEGI, G. (1960): *Illustrierte Flora von Mittel-Europa*. Band IV. – J. F. Lehmanns Verlag, München, 491 pp.
- HEMP, A. (1996): Ökologie Verbreitung und Gesellschaftanschluss ausgewählter Eiszeits-relikte (*Cardaminopsis petraea*, *Draba aizoides*, *Saxifraga decipiens*, *Arabis alpina* und *Asplenium viride*) in Pegnitzalb. – *Ber. Bay. Bot. Ges.* **66–67**: 233–267.
- HILLEBRANDT, F. (1858): Beitrag zur Flora von Ungarn. – *Österr. Bot. Zeitschr.* **8**(9): 297–300.
- HOHENESTER, A. (1960): Grasheiden und Föhrenwälder auf Diluvial- und Dolomitsanden im Nördlichen Bayern. – *Ber. Bayer. Bot. Gesellsch.* **33**: 30–85.
- HOLUB, J. and PROCHAZKA, F. (2000): Red list of vascular plants of the Czech Republic. – *Preslia* **72**: 187–230.
- HORVÁT, A. (1942): *A Mecsekhegység és déli síkjának növényzete* 1–2. [The flora and vegetation of the Mecsek Mts and its southern foreground]. – Ciszterci Rend kiadása, Pécs, 103 + 159 pp.
- HULTÉN, E. and FRIES, M. (1986): *Atlas of North European vascular plants: north of the Tropic of Cancer I–III*. – Koeltz Scientific Books, Königstein.
- JALAS, J. and SUOMINEN, J. (eds) (1996): *Atlas Flora Europaea distribution of vascular plants in Europe 10. Cruciferae (Sisymbrium to Aubrieta)*. – Helsinki, 224 pp.
- JASIEWITZ, A. (ed.) (1985): *Flora Polski. Rośliny Naczyniowe*. Vol. IV. Ed. 2. – Państwowe Wydawnictwo Naukowe, Warszawa, Kraków, 306 pp.
- JÁVORKA, S. (1925): *Magyar Flóra. (Flora Hungarica)*. I–II. – Studium, Budapest, 1307 pp.
- JÁVORKA, S. (1937): *A magyar flóra kis határozója*. 2. kiadás. [Key to the vascular flora of Hungary. Ed. 2]. – Studium, Budapest, 346 pp.

- JÁVORKA, S. and SOÓ, R. (1951): *A magyar növényvilág kézikönyve I-II*. [Handbook of the Hunagrian Flora]. – Akadémiai Kiadó, Budapest, 1120 pp.
- JONSELL, B., KUSTÁS, K. and NORDAL, I. (1995): Genetic variation in *Arabis petraea*, a disjunct species in northern Europe. – *Ecography* **18**: 321–332.
- KÄRKKÄINEN, K., LØE, G. and ÅGREN, J. (2004): Population structure in *Arabidopsis lyrata*: evidence for divergent selection on trichome production. – *Evolution* **58**: 2831–2836.
- KERNER, A. (1863): Nachtrag zu C. M. Nendtvich's *Enumeratio plantarum territorii Quinque-Ecclesiensis*. – *Verh. zool.-bot. Ges. in Wien* **13**: 561–574.
- KOCH, M., BISHOP, J. and MITCHELL-OLDS, T. (1999): Molecular systematics of *Arabidopsis* and *Arabis*. – *Plant Biology* **1**: 529–537.
- KORNECK, D., SCHNITTNER, M. and VOLLMER, I. (1996): Rote Liste der Farn- und Blütenpflanzen (Pteridophyta et Spermatophyta) Deutschlands. – *Schr.-R. f. Vegetationskde.* **28**: 21–187.
- KOVÁCS, J. A. and TAKÁCS, B. (1995): A Balatonvidék bazaltvulkáni növényzetének sajátosságairól. [About the characteristics of the basalt volcanic vegetation in the Balaton-area]. – *Kanitzia* **3**: 51–96.
- LINNÉ, C. (1774): *Systema vegetabilium*. Ed. 13. – Göttingen, Gotha, 501 pp.
- LINNÉ, C. (1784): *Systema vegetabilium*. Ed. 14. – Göttingen, 600 pp.
- MÁTHÉ, I. (1940): Magyarország növényzetének flórakelemei. (Florenelemente (Arealytypen) der Pflanzenwelt des historischen Ungarn). – *Acta Geobot. Hung.* **3**: 116–147.
- MATSCHINGER, M. and KOCH, M. (2003): Molecular systematics, phytobiogeography and evolution of the genus *Cardaminopsis* Hayek (Brassicaceae), the closest relatives of the model plant *Arabidopsis thaliana* (L.) Heynh. – *Palm. Hort. Francofurt.* **7**: 196.
- MĚSÍČEK, J., SLAVÍK, B. and TOMŠOVIC, P. (1992): *Cardaminopsis (C. A. Meyer) Hayek* – řeřišničník. – In: HEJNÝ, S. and SLAVÍK, B. (eds): *Kévétena České Republiky*. 3. Academia, Praha, pp. 116–122.
- MESTERHÁZY, A., BAUER, N. and KULCSÁR, L. (2003): A kisalföldi bazalt tanúhegyek edényes flórája. [Vascular flora of the basalt hills in Kisalföld]. – *Tilia* **9**: 7–165.
- MEUSEL, H. (1939): Die Vegetationsverhältnisse der Gipsberge im Kyffhäuser und im südlichen Harzvorland. Ein Beitrag zum Steppenheidefrage. – *Hercynia* **2(4)**: 1–372.
- MEUSEL, H., JÄGER, E. and WEINERT, E. (1965): *Vergleichende Chorologie der zentraleuropäischen Flora. Band I. Karten*. – Jena, 258 pp.
- MILBRANDT, J. (1976): Nordische Einstrahlungen in der Flora und Vegetation von Nordbayern Dargestellt an ausgewählten Beispielen. – *Hoppea, Denkschr. Regensb. Bot. Ges.* **35**: 131–210.
- MUCINA, L. and KOLBEK, J. (1993): *Festuco-Brometea*. – In: MUCINA, L., GRABHERR, G. and ELLMAUER, T. (eds): *Die Pflanzengesellschaften Österreichs I. Anthropogene Vegetation*. Gustav Fischer Verlag, Jena, Stuttgart, New York, pp. 420–492.
- NEILREICH, A. (1866): *Aufzählung der in Ungarn und Slavonien bisher beobachteten Gefäßpflanzen nebst einer pflanzengeografischen Uebersicht*. – Wien, 390 pp.
- NENDTVICH, K. (1836): *Dissertatio inauguralis historicoo-naturalis exhibens enumerationem plantarum in territorio Quinque-Ecclesiensi sponte crescentium praemiso tractatu generali de natura geognostica montium deque situ climate et vegetatione ejusdem regionis*. – Buda, 38 pp.

- NENDTVICH, T. (1846): Pécs és környékének viránya. [The flora of Pécs and its surroundings]. – A MOT hatodik naggyűlésének történeti vázlata és munkálatai, Pécs, pp. 288–291.
- NIKLFELD, H. (1999): *Rote Listen gefährdeter Pflanzen Österreichs*. 2. Auflage. – Grüne Reihe des Bundesministeriums für Gesundheit und Umweltschutz, Band 5, Wien.
- O'KANE, S. L. and AL-SHEHBAZ, I. A. (1997): A synopsis of *Arabidopsis* (Brassicaceae). – *Novon* **7**(3): 323–327.
- POLATSCHEK, A. (1966): Cytotaxonomische Beiträge zur Flora der Ostalpenländer I. – *Österr. Bot. Zeitschr.* **113**: 1–46.
- POTT, R. (1995): *Die Pflanzengesellschaften Deutschlands*. 2. Auflage – Verlag Eugen Ulmer, Stuttgart. 622 pp.
- RAKONCZAY, Z. (1989): *Vörös Könyv. A Magyarországon kipusztult és veszélyeztetett növény- és állatfajok*. [Red Data Book of Hungary]. – Akadémiai Kiadó, Budapest, 360 pp.
- RIHIMÄKI, M. and SAVOLAINEN, O. (2004): Environmental and genetic effects on flowering differences between northern and southern populations of *Arabidopsis lyrata* (Brassicaceae). – *Amer. J. Bot.* **91**: 1036–1045.
- SANDRIG, S., RIHIMÄKI, M., SAVOLAINEN, O. and ÅGREN, J. (2007): Selection on flowering time and floral display in an alpine and a lowland population of *Arabidopsis lyrata*. – *J. Evol. Biol.* **20**: 558–567.
- SÁNTHA, L. (1910): Adatok a budai hegység zuzmóflórájának ismeretéhez. (Beiträge zur Flechtenflora der Budapester Gebirges). – *Bot. Közlem.* **9**(1): 3–35.
- SAVOLAINEN, O., LANGLEY, C. H., LAZZARO, B. P. and FRÉVILLE, H. (2000): Contrasting patterns of nucleotide polymorphism at the alcohol dehydrogenase locus in the out-crossing *Arabidopsis lyrata* and the selfing *Arabidopsis thaliana*. – *Molec. Biol. Evol.* **17**(4): 645–655.
- SCHIERUP, M. H. (1998): The effect of enzyme heterozygosity on growth in a strictly out-crossing species, the self-incompatible *Arabis petraea* (Brassicaceae). – *Hereditas* **128**: 21–31.
- SCHUHWERK, F. (1990): Relikte und Endemiten in Pflanzengesellschaften Bayerns – eine vorläufige Übersicht. – *Ber. Bayer. Bot. Ges.* **61**: 303–323.
- SIMON, T. (1972): Die Pflanzengesellschaften der Felsenvegetation im Zempléner Gebirge. – *Ann. Univ. Sci. Budapest. Rol. Eötvös, Sect. Biol.* **14**: 133–158.
- SIMON, T. (ed. 1991): *Baktérium-, alga-, gomba-, zuzmó- és mohahatározó*. [Taxonomic handbook of the bacterium, alga, fungus, lichen and moss taxa]. – Tankönyvkiadó, Budapest, 793 pp.
- SIMON, T. (2000): *A magyarországi edényes flóra határozója*. [Key to the vascular flora of Hungary]. – Tankönyvkiadó, Budapest, 976 pp.
- SIMONKAI, L. (1876): Adatok Magyarhon edényes növényeihez. [Contributions to the vascular flora of Hungary]. – *Math. Term. tud. Közlem.* **11**(6): 157–211.
- SOÓ, R. (1930): Adatok a Balatonvidék flórájának és vegetációjának ismeretéhez II. [Data to the knowledge of the flora and vegetation of Balaton region]. – *Magy. Biol. Kut. Munk.* **3**: 167–185.

- SOÓ, R. (1964): *Magyarország növényzetének története. Magyarország florisztikai és cönológiai növényföldrajza*. – In: SOÓ, R.: A magyar flóra és vegetáció rendszertani-növényföldrajzi kézikönyve I. Akadémiai Kiadó, Budapest, pp. 87–129.
- SOÓ, R. (1968): *A magyar flóra és vegetáció rendszertani-növényföldrajzi kézikönyve III. (Synopsis systematico-geobotanica florae vegetationisque Hungariae III)*. – Akadémiai Kiadó, Budapest, 655 pp.
- SOÓ, R. and KÁRPÁTI, Z. (1968): *Növényhatározó II. Harasztok – virágos növények*. [Key to the flora of Hungary II. Pteridophytes – flowering plants]. – Tankönyvkiadó, Budapest, 846 pp.
- SPENCE, D. H. N. (1970): Scottish serpentine vegetation. – *Oikos* **21**: 22–31.
- SZABÓ, I. (1987): A Keszhelyi-hegység növényvilágának kutatása. [Investigations on the flora and vegetation of Keszhely Mountains]. – *Folia Mus. Hist.-Nat. Bakonyiensis* **6**: 77–98.
- SZATALA, Ö. (1942): Lichenes Hungariae III. – *Folia Cryptog.* **2**(5): 267–460.
- THORN, K. (1958): Die dealpinen Felsenheiden der Frankenalb. – *Sitzungber. phys. med. Soz. Erlangen* **78**: 128–199.
- THORN, K. (1960): Bemerkungen zu einer Übersichtskarte vermutlicher Glazialreliktpflanzen Deutschlands. – *Mitteil. flor.-soz. Arbeitsgemeinsch.* **8**: 81–85.
- TUTIN, T. G., BURGES, N. A., CHATER, A. O., EDMONDSON, J. R., HEYWOOD, V. H., MOORE, D. M., VALENTINE, D. H., WALTERS, S. M. and WEBB, D. A. (2002): *Flora Europea. Vol. 1. Psilotaceae to Platanaceae*. 2nd ed. – Cambridge University Press, Cambridge, 581 pp.
- VAN TREUREN, R., KUITTINEN, H., KARKKAINEN, K., BAENA-GONZALEZ, E. and SAVOLAINEN, O. (1997): Evolution of microsatellites in *Arabis petraea* and *Arabis lyrata*, outcrossing relatives of *Arabidopsis thaliana*. – *Molec. Biol. Evol.* **14**: 220–229.
- VERSEGHY, K. (1994): *Magyarország zuzmóflórájának kézikönyve*. (The lichen flora of Hungary). – Magyar Természettudományi Múzeum, Budapest, 415 pp.
- WRIGHT, S., LAUGA, B. and CHARLESWORTH, D. (2003) Subdivision and haplotype structure in natural populations of *Arabidopsis lyrata*. – *Molec. Ecol.* **12**: 1247–1263.
- ZAHLHEIMER, W. A. (2001): Die Farn- und Blütenpflanzen Niederbayerns, ihre Gefährdung und Schutzbedürftigkeit. – *Hoppea, Denkschr. Regensb. Bot. Ges.* **62**: 5–347.
- ZÓLYOMI, B. (1942): A középdunai flóraválasztó és a dolomitjelenség. (Die Mitteldonau-Florenscheide und das Dolomitphänomen). – *Bot. Közlem.* **39**: 209–231.
- ZÓLYOMI, B. (1950): Фитоценозы и лесоомелиорации обнажений гор Буды. – *Acta Biol.* **1**(1–4): 7–67.
- ZÓLYOMI, B. (1952): Magyarország növénytakarójának fejlődéstörténete az utolsó jégkor-szaktól. [Phylogeny of the Hungarian flora and vegetation since the last glaciation]. – *MTA Biol. Oszt. Közlem.* **1**(4): 491–530.
- ZÓLYOMI, B. (1958): *Budapest és környéke természetes növénytakarója*. [Flora and vegetation of Budapest and its environs]. – In: PÉCSI, M. (ed.): Budapest természeti képe. Akadémiai Kiadó, Budapest, pp. 509–642.

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