Carex ×*moravica* (*C. caryophyllea* × *C. fritschii*), a new nothospecies identified by morphological and anatomical characters

RADOMÍR ŘEPKA¹, TADEÁŠ ŠTĚRBA¹ & JAN ROLEČEK^{2, 3}

¹Department of Forest Botany, Dendrology and Geobiocenology, Faculty of Forestry and Wood Technology, Mendel University, Zemědělská 3, CZ-613 00 Brno, Czech Republic, e-mail: repka@mendelu.cz

²Department of Botany and Zoology, Masaryk University, Kotlářská 2, CZ-611 37 Brno

³Department of Vegetation Ecology, Institute of Botany, Academy of Sciences of the Czech Republic, Lidická 25/27, CZ-602 00 Brno; e-mail: honza.rolecek@centrum.cz

ŘEPKA R., ŠTĚRBA T. & ROLEČEK J. 2013: *Carex* ×moravica (*C. caryophyllea* × *C. fritschii*), a new nothospecies identified by morphological and anatomical characters. *Acta Musei Moraviae, Scientiae biologicae* (Brno) **98(1)**: 105–116. – Hybrids in the genus *Carex* occur quite frequently. However, only one hybrid with *C. fritschii* as a parental species has been reported to date. In 2010, plants with an appearance transitional between *C. caryophyllea* and *C. fritschii* were found at two sites in southern Moravia, Czech Republic. The results of morphological and anatomical analysis show that the plants are in many respects similar to *C. caryophyllea* in morphology, but some plants possess a combination of characters indicating an intermediate position between *C. caryophyllea* and *C. fritschii*. The fertility of the hybrid plants varies widely, between fully sterile and completely fertile. The anatomical characters of the leaf cross-section correspond largely to *C. caryophyllea*, but the teeth on the adaxial side of the leaf demonstrate the hybrid's position closer to *C. fritschii*. Based on the results of analysis, the plants discovered are considered the new nothospecies *Carex* ×moravica between members of two different sections of the subgenus *Carex* (*Mitratae* and *Acrocystis*).

Keywords. Cyperaceae, anatomy, hybridization, morphology, taxonomy, Czech Republic, southern Moravia

Introduction

Rich in species and of wide geographical distribution, the genus *Carex* is a rather exceptional genus of angiosperms (YEN & OLMSTEAD 2000). Such a large number of taxa, their morphological similarity, the great variability of some taxa, and relatively frequent hybridisation between species combine to render the entire genus taxonomically difficult (STACE 1986; KUKKONEN & TOIVONEN 1988). Hybrids in the genus *Carex* occur quite frequently (STACE 1986), although the number of such cases is often overestimated. Their actual frequency varies widely among the different subgenera and sections. In some sections they are found more frequently (e.g. *Phacocystis, Ceratocystis, Paludosae, Glareosae*, and *Vesicariae*) (CAYOUETTE & CATLING 1992), in others they have been found in only a few cases. Some species, or rather species of some sections, simply do not hybridise with others. Data from the literature mention complete sterility for hybrids of the subgenera may be sterile, partly fertile or fully fertile. Sterility in some *Carex* plants is not necessarily an indication of hybridisation. Identification of hybrids, whether sterile or fertile, demands considerable application in distinguishing their parental species and

knowledge of their variability, which may moreover be complicated by introgression by the parental species (CAYOUETTE & CATLING 1992).

From the early 19th century to the second half of the 20th century, *Carex* hybrids were distinguished according to merely morphological characters more or less intermediate between the parental species. The characters of the hybrid were most often compared with those of the parental species (e.g. LEPAGE 1956, 1976, CAYOUETTE & MORRISET 1985). The variability of hybrids is reported to be extensive (TOIVONEN 1980), but some show a lower or equal variability when compared with their parents (REZNICEK & CATLING 1986). Further, differences in variability between populations of one hybrid at individual sites are considerable (LEPAGE 1956). Hybrids which have been subject to introgression by their parents are hard to identify in the field. CAYOUETTE & CATLING (1992) consider the hypothesis that the number of hybrids is increasing, not only because of the process of recognition, but also through human activity in the wild, i.e. disturbance of biotopes, washing away differences in the ecology of habitats through nutrient increase.

Before the end of the 19th century, papers appeared in which hybrids were also identified anatomically. The first of them was MARGGRAFF (1896), later followed by RAUNKIAER *in* OSTENFELD (1901) and SØRENSEN (1933) for the hybrid *C. limosa* × C. *subspathacea*. The anatomical method is largely used to study foliar anatomy and micromorphological characters on the surface of the leaves (papillae, stomata). Anatomical features in leaf cross-sections provide a range of valuable characters that can be used in the study of sedges at the species level. According to some authors (JALAS & HIRVELÄ 1964; CATLING 1996), anatomical characters are to a certain extent intermediate in *Carex* hybrids, whereby some morphological characters of one of the parents may prevail in the hybrid (TOIVONEN 1980). Anatomical studies, first based on the distribution of stomata on *C. aquatilis* leaves (STANDLEY 1986), later using characters of section *Phacocystis* and their hybrids (STANDLEY 1987).

Sedges of section *Acrocystis* Dum. (syn. *Montanae* Fries), distributed throughout Eurasia and North America, hybridize rarely among each other, and also with species of other sections. Data on their existence are scanty in the literature (WAISBECKER 1905, KÜKENTHAL 1909, Soó 1973, SCHULTZE-MOTEL 1977, KÜKENTHAL 1929, ŘEPKA 1992, EGOROVA 1999). In the list of hybrids for Czechoslovakia, DOSTÁL (1989: 1311) mentions combinations of Czechoslovak species not documented to date, three of which are from this section: *C. ×montanorum* Ciff. et Giac. (*C. ericetorum × C. montana*), *C. ×lackowitziana* R. Paul (*C. ericetorum × C. pilulifera*) and *C. ×vimariensis* Hausskn. ex Berthold (*C. montana × C. umbrosa*). KOOPMAN (2011) mentions seven hybrids from Europe with at least one parental species from section *Acrocystis*. *C. fritschii* Waisb. is a parental species only in the case of *C. ×villacensis* Kük. (*C. fritschii × C. pilulifera*).

The possibility of hybridisation of *C. fritschii* with other species of the section is limited by its disjunctive peri-alpine distribution, determined by specific habitat demands and the history of its distribution (MEUSEL *et al.* 1965). DANIHELKA *et al.* (2012) published material from a manuscript for "Flora of the Czech Republic" (GRULICH & ŘEPKA, in press), in which only two hybrids of section *Acrocystis* are mentioned:

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 $C. \times ginsiensis$ Waisb. (*C. montana* \times *C. pilulifera*) and *C. \times villacensis*, both confirmed in the Czech Republic, coincidentally in Moravia. Another hybrid, *C. \times sanionis* K. Richt. (*C. caryophyllea* \times *C. ericetorum*), was mentioned from the surroundings of Lhánice (JIČÍNSKÝ 1950 ZMT, DVOŘÁK 1970) but after revision it was identified as *C. caryophyllea* Latourr. (GRULICH & ŘEPKA in press).

During 2010 we found plants at two Moravian sites, which at first examination lacked distinct characters for any basic species, but had some characters according to which we tentatively considered them to be hybrids between the species *C. caryophyllea* and *C. fritschii*, a combination that has not been reported to date. Plants of the assumed parental species grew next to, or close to, the supposed hybrid. By means of an analysis of morphological and anatomical characters, the results of which are presented in this paper, we demonstrate the hybrid origin of the plants discovered and describe the new nothospecies, *Carex* ×*moravica*.

Material and methods

Documentary (voucher) and also further study material was collected at two sites in Moravia:

- Phytogeographical region 16, Znojemsko-brněnská pahorkatina, Vedrovice, Krumlovský les Forest, gentle slopes with oak forest above gamekeeper's lodge, in game reserve, 1.5 km NE–NNE of the village centre, altitude 317 m (49.031888 N, 16.389772 E).
- (2) Phytogeographical region 18a, Dolnomoravský úval, Hodonín, Dúbrava Forest, gently undulating aeolian relief of lowland oak-pine forest on sand 1.4–1.65 km E–ENE of Zbrod gamekeeper's lodge, altitude 187 m (48.890556 N, 17.085833 E).

Morphological characters were measured on herbarium material using a $12 \times$ magnification Brinell lens. The data were evaluated in Microsoft Excel 2007. The characters of the parental species were measured on plants collected outside the hybrid swarm.

For comparison of the leaf cross-section, material from herbarium vouchers of the hybrid and the parental species (deposited in BRNL) was used. Preparation of the leaves followed the method employed by STANDLEY (1987). Segments 5 cm long were clipped from the central part of a leaf-blade of sterile shoots. The dried leaf parts were rehydrated in water at 100°C, in which they were immersed for 10 min. From samples acquired this way manual cross-sections were taken, which were then observed on a microscope slide under an Olympus BX 51 binocular microscope with an accessory Canon EOS 1100D camera. A microphotograph of each cross-section was taken for further study. All microphotographs were adjusted in the QuickPHOTO MICRO 3.0 program and are deposited in the authors' archive. Due to the limited amount of study material, quantitative anatomical characters (e.g. number of vascular bundles, length and width of epidermal cells) were not evaluated.

Abbreviations of herbarium collections follow Index Herbariorum (http://sweetgum. nybg.org/ih/).

Results and Discussion

Circumstances of the finds

The first site. The hybrid grows here in an opening in an oak forest of the *Sorbo* torminalis-Quercetum association on a gentle slope near an unused forest drive. In the middle of the opening grow two lax tussocks, conspicuous for their very long stems and leaves. The utricles are partly fertile, the inflorescences quite atypically interrupted, and their spikes resemble *C. fritschii* rather than *C. caryophyllea*. Some inflorescences are somewhat pauperised, with small sterile spikes or more often with conspicuous foliaceous bracts. A third tussock grows close to the drive, about 10 m from the other two. It is completely sterile and its spikes resemble *C. caryophyllea*. One parental species *C. caryophyllea* grows next to the first two tussocks of the hybrid, and the other one, *C. fritschii*, in a large tussock at least 5 m from the hybrid tussocks.

The second site contains two populations of the hybrid. One population includes only two hybrid tussocks that give the impression of intermediate forms between both assumed parental species. They have no creeping rhizome shoots like C. caryophyllea, the leaves are yellowish, and the utricles empty. The assumed parental species grow at distances of about 10 m (C. fritschii) and 15 m (C. caryophyllea) from the hybrid tussocks. Another, larger population was found at about 300 m from the former one. From the first population, extensive herbarium material was collected and later subjected to morphological analysis. The site lies on a gently sloping, relatively low dune in a mixed oak-pine forest on aeolian sand, where about 20 lax tussocks grow with characters closer to C. caryophyllea. Below the dune, a moist depression stretches out, at the margin of which grow plants with characters intermediate between the assumed parents, and not far from it one of them, C. fritschii as well. Plants of the other assumed parental species, C. caryophyllea, corresponding to this species in all their characters and fully fertile, grow at a distance of about 30 m from the tussocks that have characters of the hybrid. In this population, forms closer in characters to C. caryophyllea were found and the plants here are partly or completely fertile. Rarely a form occurs with characters intermediate between those of both assumed parents, and there is also an isolated tussock having characters closer to C. fritschii.

Morphological characters

A comparison of morphological characters of the newly described hybrid and its parental species is given in Table 1. It includes characters of the hybrid classified as two forms: *intermediate form* observed at both sites and form close to *C. fritschii* observed in Dúbrava Forest.

The intermediate form from Krumlovský les Forest is characterised by features of both parental species. The plants are relatively tall (stems nearly as tall as in *C. fritschii*) and possess at their base tufted shoots both old and fresh in slightly curved rhizomes with

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Character/species	C. caryophyllea	C. caryophyllea	C. × <i>moravica</i> intermediate form	C. × <i>moravica</i> intermediate form	C. × <i>moravica</i> form close to <i>C. fritschii</i>	C. fritschii
Site	Dúbrava Forest	Krumlovský les Forest	Krumlovský les Forest	Dúbrava Forest	Dúbrava Forest	Dúbrava Forest
Root diameter (mm)	0.4-0.6	0.3–0.4	0.3-0.5	0.35-0.6	0.5-1.0	0.6–1.8
Rhizome	Shortly to longer creeping by diageotropic shoots	Shortly to longer creeping by diageotropic shoots	pseudo-tussocks to lax tussocks with shorter and longer shoots	pseudo-tussocks to tussocky with shorter lax tussocks with and longer shoots shorter and longer covered with light shoots fibres	tussocky with short shoots covered with light fibres	forming lax tussocks; short shoots covered with light fibres creating circles and horseshoes
Diageotropic rhizome shoots	thin, ascending, brown with slightly split scales, 30-110 mm long	thin, ascending, brown thin, ascending, with slightly split brown, 15-50-6 scales, 30-50 mm long mm long	thin, ascending, brown, 15–50–80 mm long	ascending, thin, 35–50 mm long, with fraying light fibres	very short, up to 10 mm long	very short to short, ascending, 10-25 mm long
Stem length (cm)	20–37	18-28	27-49	34-38	19–22	46–54
Stem diameter (mm)	0.5-0.8	0.55-0.6	0.55-0.6	0.7-0.8	0.5-0.6	0.7-0.8
Leaf length (cm)	15–36	17–24	21-35	30-50	46-51	31-52
Leaf width (mm)	2.1–3.3	1.5–1.8	1.6-2.7	2.2–2.6	2.2–2.7	2.1–3.0
Inflorescence length (mm)	22-52	2229	7–(19–32)	35-45	17–19	28-45
Length of female spike (mm)	6–15	7–10	5-10	10-15	5-6	6.5-10
Female scale: length/width (mm)	1.69-2.17	1.85–2.31	1.77–1.87	2.00	2.62	1.50-1.88
Perigynium: length/width (mm)	1.67–2.00	2.21–2.31	1.71–2.22	1.79	2.13	1.09-1.88

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Tab. 1. Comparison of selected morphological characters of C. ×moravica and their parental species.

very short diageotropic** shoots up to 5 cm long, covered with light-coloured, decomposing fibres (strongly resembling rhizomes of *C. fritschii*), covered in light-coloured, fibrous scales. Its roots are relatively thin, in diameter corresponding with *C. caryophyllea*. New apogeotropic* shoots originate in a similar way to those of *C. fritschii*, i.e. they create an erect tubular structure 5 cm tall with short blades. The leaves are very long and possess a continuous or interrupted row of teeth on their margin, corresponding with *C. fritschii*. They die back to their bases at the end of the vegetation season. The inflorescence is very similar to that of *C. caryophyllea*, but longer and more robust. Spikes, glumes and utricles are fully identical to *C. caryophyllea*. The plants form nutlets in at least some utricles. The utricles have a particular shape, rather long, inflated, and hairy only in the upper half, resembling those of *C. fritschii*.

The form close to *C. fritschii*, found in Dúbrava Forest, is similar to *C. fritschii* in most of the characters of its vegetative organs. The upper side of the leaves possess clear papillae, which are exceptional on leaves of *C. caryophyllea* and absent in *C. fritschii* (Fig. 1F). The stems are, however, much shorter than the leaves (half the length of *C. fritschii* leaves at the time of utricle ripening), the inflorescence is shorter than in *C. fritschii*, glomerate, with 2–3 smaller, almost sessile female spikes. The colouring of the bracts of male and female flowers, together with other characters, tends to resemble *C. fritschii*, but the spikes are smaller, the utricles have a different, elongated shape and are soft, small and empty, and no nutlets are formed. However, in this locality, the form close to *C. caryophyllea* with the prevailing character of this species was represented at the highest number of tussocks.

Anatomical characters

The most pronounced differences in leaf cross-section between the taxa are summarised in Table 2.

General characterisation (and leaf margin). The structure of the leaf cross-section in the hybrid and both parental species is similar (see Fig. 1). The blade is keeled in cross-section and the keel is markedly rounded (Fig. 1A), but in *C. caryophyllea* leaves may have an unpronounced keel. Small differences are noticeable on the margin of the leaf. In *C. caryophyllea* the margin is usually rounded, lacking teeth or with hardly noticeable teeth, but in *C. fritschii* it is sharp and teeth are always present. In *C. ×moravica* the leaves are quite sharp at their margin and the presence of teeth is very variable. We studied the presence, shape, and distribution of teeth on herbarium vouchers and found that whereas the teeth in *C. caryophyllea* are clearly smaller when compared to *C. fritschii*, their shape and arrangement are very variable, and in some leaves the teeth may be completely absent. *C. fritschii* has teeth larger, narrower and more or less uniform compared to the former species. In the hybrid, these characters vary between those of the parental species. We observed leaves of various sizes and with differing tooth shapes, and occasionally we encountered leaves without teeth or with only papillae (Figs 1 D, F).

^{*}Apogeotropic and **diageotropic shoot: according to the direction of growth, *Carex* shoots may be divided into apogeotropic (upright, vertical) and diageotropic (horizontal). This characteristic was given by ALEXEEV (1966) and EGOROVA (1999).

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Tab. 2. Comparison of anatomical characters of leaf cross-section between C. ×*moravica* and its parents (0 – absent, 1 – present).

Character	Carex caryophyllea	<i>Carex</i> × <i>moravica</i> Krumlovský les	<i>Carex</i> × <i>moravica</i> Dúbrava	Carex fritschii
Sclerenchyma fibres (without connected vascular bundle) along leaf margin	1	1	1	0
Papilla on adaxial side of leaf	0 (-1)	0	1	0
Ratio vascular bundle length : leaf thickness 2 : 1.5	0	(0-) 1	(0–) 1	1
Teeth on adaxial side of leaf	0 (-1)	1	1	1
Teeth on leaf margin	0	(0–) 1	(0–) 1	1
Intercellular space in centre	0	0	0	1

Adaxial epidermis. In *C. caryophyllea*, the epidermal cells on the adaxial side of the leaves are round, with minor differences in size, and covered with a thick cuticulum. Teeth or papillae are rarely present. In *C. fritschii* adaxial epidermal cells are also round, but variable in size and covered with a thin cuticulum. Teeth or papillae are always present on the adaxial side of the leaves (Figs. 1 D, F). The adaxial epidermis of *C.* ×moravica is in most characters similar to *C. fritschii*; teeth are present in the plants from Krumlovský les Forest, but in plants from Dúbrava Forest the adaxial side of the leaves is densely covered with papillae. At the latter site, plants were also collected resembling *C. caryophyllea* in most morphological characters, but covered with papillae on the adaxial side (Fig. 1 D).

Vascular bundles. Colateral, two types. (1) Larger vascular bundles on the adaxial and abaxial sides are connected by sclerenchyma bundles and are mostly elliptical in shape. (2) Smaller vascular bundles are round in outline and a sclerenchyma is usually missing or is present only on one side of the vascular bundle (Figs. 1 B, F). In some cases, smaller vascular bundles may be absent (some leaves of *C. ×moravica* from Krumlovský les Forest, Figs 1 C, D). In all the taxa compared, the smaller vascular bundles are predominantly closer to the adaxial epidermis and positioned over the intercellular ones, but some leaves of *C. fritschii* may have smaller vascular bundles between intercellular ones. The ratio between the length of the longest vascular bundle and leaf thickness (in the middle of the leaf) is 2:1 in *C. caryophyllea*, 2:1.5 in *C. fritschii*, and 2:1-1.5 in *C. ×moravica* (see Table 2).

Sclerenchyma bundles. A pronounced character of the leaf cross-section distinguishing *C. caryophyllea* from *C. fritschii* is the presence of isolated sclerenchyma bundles not connected to vascular bundles on the leaf margin (Fig. 1 B). In *C. caryophyllea* these are

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always present, whereas they are always absent in *C. fritschii* (Fig. 1 H). In the hybrid, sclerenchyma bundles occur in plants from both sites and are larger than in *C. caryophyllea* (Fig 1 D, F). Adaxial sclerenchyma bundles connected to larger vascular bundles are usually longer in *C. caryophyllea* (ratio between length of vascular bundle and sclerenchyma length *c.* 3 : 2) and narrower than in *C. fritschii* and *C. ×moravica* (ratio 2 : 1) (see Fig. 1).

Intercellular cavities. These cavities are variable in shape and size. Nevertheless, certain differences can be observed between the taxa. In *C. caryophyllea* the cavities are positioned closer to the abaxial side of the leaf (Fig. 1 B), in *C. fritschii* they are situated more or less in the middle (Fig. 1 H). The position of the intercellular space strongly depends on the thickness of the chlorenchyma on the adaxial and abaxial sides of the leaf.

Study of the leaf cross-section of the compared taxa confirmed that C. ×moravica is more similar in anatomical characters to C. caryophyllea, although its morphological characters are often at an intermediate level (see Table 2).

Carex ×moravica Řepka et Roleček, nothosp. nov. (*Carex caryophyllea × C. fritschii*)

Diagnosis. Plant with long creeping or slightly tussocky rhizome. Diageotropic shoots of the rhizome ascending, variable, 10–80 mm long, at the base often with fibrously frayed, brown, but also light sheaths. Rhizome either similar to C. fritschii and then with shoots up to 30 mm long, with light brown, shiny, slightly fibrous sheaths at base, forming a loose, horseshoe-shaped tussock, or more similar to C. caryophyllea, having a branched rhizome with shoots (rhizome branches) up to 100 mm long, covered with brown scales fraying into coarse tips. Roots tough, 0.3–0.6 mm in diameter, in plants rather similar to C. fritschii up to 1.0 mm in diameter. Stems on average longer than in C. caryophyllea, 19-38(-49) cm long, erect or slightly laterally curved, 0.5-0.8 mm thick. Leaves of varying lengths, 21-51 cm long, mostly longer than in common C. caryophyllea, however not reaching the length of C. fritschii summer leaves, 1.6-2.7 mm thick. Some leaves may have small, clear papillae, which are usually absent from leaves of both parental species (sporadically present in C. caryophyllea). Inflorescence intermediate in length between the parents, some types being similar to C. fritschii, contracted and with sessile spikes, others having spikes like C. caryophyllea, however more remote and pauperised, inflorescence exceptionally markedly interrupted. Female spikes varying in length between the parental species, mostly oblong and more resembling those of C. caryophyllea in shape, glume colour and utricles, 5-15 mm long. Glumes of female spikes oblong or ovate, brown with green midrib, or broadly ovate and reddish; ratio between length and width highly variable, 2.5 : 1 to 1.8 : 1. Utricles in fertile plants fully developed, inside with ripe nutlet; in sterile plants greyish, laxly tomentose in upper part, not more than about 2.0 mm long, with undeveloped nutlet. Most ripening utricles resembling C. caryophyllea, obovate, covered with hairs in upper part, up to 2.5 mm long and 1.2–1.4 mm broad. Exceptionally plants with broadly ovate utricles were observed, which were covered with sparse yellowish hairs, coming close to C. fritschii utricles in

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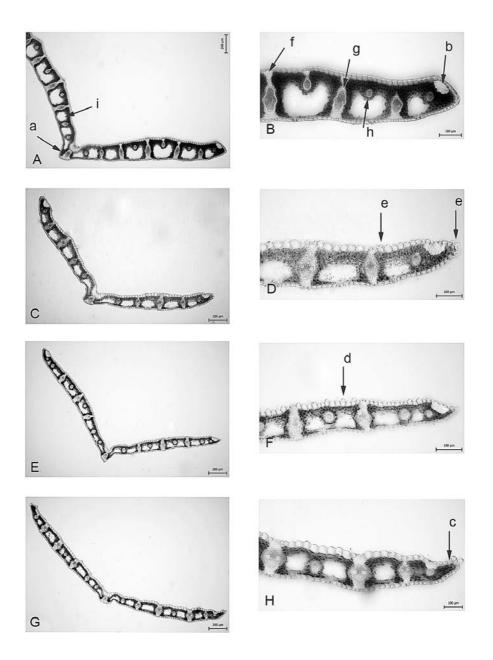


Fig. 1. Leaf cross-sections and details for C. ×moravica and its parental species (A, B – C. caryophyllea; C, D – C. ×moravica, Krumlovský les Forest; E, F – C. ×moravica, Dúbrava Forest; G, H – C. fritschii; arrows indicate different characters: a – keel of leaf, b – sclerenchyma bundle on the leaf margin, c – the leaf margin without sclerenchyma bundle, d – papillae, e – teeth, f – sclerenchyma, g – larger vascular bundle, h – smaller vascular bundle, i – intercellular space).

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shape and size. At the sites where plants of the hybrid grow, types (forms) close to *C*. *caryophyllea*, intermediate form and rare form close to *C*. *fritschii* were found.

Typus. Phytogeographical district 16. Znojemsko-brněnská pahorkatina, village of Vedrovice, Krumlovský Forest, gentle slopes with oak forest above gamekeeper's lodge, 1.5 km NE–NNE of the village centre, 317 m a.s.l. (49.031888 N; 16.389772 E), leg. R. Řepka & J. Roleček, 26 June 2010 (holotype), BRNM 752045, the isotypes and other documented herbarium material is deposited in BRNL.

Etymology. The name of the hybrid refers to the territory of Moravia (eastern part of the Czech Republic), where it was first discovered by the authors.

Conclusions

Plants discovered at two Moravian sites, suspected to have originated from hybridisation of the species C. caryophyllea and C. fritschii, were subjected to an analysis of morphological and anatomical characters. The results demonstrate that these plants are more often similar to C. caryophyllea in morphology, but some plants possess a combination of characters indicating an intermediate position between the two parents (short diageotropic rhizome shoots, type of fraying and colour of rhizome sheaths, length of leaves and inflorescences). These characters overlap with the variability of characters of the parental species. Plants in which characters of C. fritschii clearly prevail were not observed, although in some plants indications of characters of this parental species (glumes, spikes, arrangement of spikes in the inflorescence) were detected. The fertility of the hybrid plants varies strongly from fully sterile to completely fertile. Anatomical characters of the leaf cross-section more often correspond with C. caryophyllea (sclerenchyma fibres along the leaf margin, papillae on the adaxial side of the leaf; position of intercellular cavities). At both sites, teeth were observed on the leaf margin of hybrid plants, and the ratio between length of vascular bundle and leaf thickness indicates an intermediate position between the parents. The teeth on the adaxial side of the leaf, on the other hand, demonstrate the hybrid's position closer to C. fritschii.

Based on the results of the analyses, the plants discovered are described here as *Carex* \times *moravica*. It is a taxon of hybrid origin, resulting from crossing between members of two different sections of the subgenus *Carex* (*Acrocystis* and *Mitratae*).

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