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Carex flava agg. (section *Ceratocystis*, Cyperaceae) in Poland: taxonomy, morphological variation, and soil conditions

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Abstract: Sedges of *Carex flava* agg., typical of moist or wet habitats, are difficult to classify because of a lack of clear-cut morphological differences between them and the existence of numerous hybrids. This monograph presents results of research conducted in 2007-2012 in various parts of Poland. The plant material consisted of 1852 living specimens of *Carex flava* agg., collected from 80 localities, and dried specimens from 26 herbaria and from 7 private collections. The analysis involved 45 morphological characters (34 quantitative and 11 qualitative) and 9 soil parameters. Univariate, bivariate, and multivariate statistical methods were used to process the data. The results confirm the taxonomic classification dividing the *C. flava* group into 4 species: *C. flava* s.s., *C. lepidocarpa*, *C. demissa*, and *C. viridula*. This classification is based on (*i*) a high observed level of morphological separation of these taxa, resulting mostly from differences in generative characters, i.e. length of the utricle and its beak, and percentage ratio of beak length to total utricle length; (*ii*) integrity of the taxa at the sites where they coexist, although some intermediate forms resulting from hybridization are also present; (*iii*) habitat preferences of the taxa, especially the preference of *C. lepidocarpa* for calcareous sites and of *C. demissa* for slightly acidic soils. Thus in Poland the analysed taxa are morphologically well-defined and show clear ecological preferences. Continuous variation of morphological characters was observed among specimens of *C. viridula*, so it is not justifiable to distinguish its subspecies (sometimes classified even as separate species), described previously in literature. Consequently, the 2 subgroups of *C. viridula* were treated as local variants (i.e. varieties: var. *viridula* and var. *pulchella*), considering their different habitat requirements. Additionally, 5 hybrids were distinguished within *C. flava* agg.: *C.* ×*alsatica* [= *C. demissa* × *C. flava*], *C.* ×*ruedtii* [= *C. flava* × *C. lepidocarpa*], *C.* ×*schatzii* [= *C. lepidocarpa* × *C. viridula*], *C.* ×*subviridula* [= *C. flava* × *C. viridula*], and *C. demissa* × *C. viridula*; as well as 2 hybrids with *C. hostiana* as one of the parents: *C.* ×*fulva* [= *C. demissa* × *C. hostiana*] and *C.* ×*leutzii* [= *C. hostiana* × *C. lepidocarpa*].

Key words: *Carex flava* agg., section *Ceratocystis*, Cyperaceae, taxonomic classification, morphology, variation, soil conditions, hybrids, key to identification

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1. Introduction

Carex L. is one of the most species-rich genera of vascular plants, as it includes about 2000 species distributed worldwide, usually in temperate to polar regions, including tropical alpine zones (Goetghebeur 1998; Egorova 1999; Frodin 2004; Govaerts *et al*. 2010). Species diversity of this genus is the highest in the temperate zone of the Northern Hemisphere, especially in western Asia and North America; the number of species of this genus is much lower in warmer regions, such as southern Asia and eastern Africa (Govaerts *et al*. 2010; Gehrke 2011). In Europe the genus is represented by about 200 species (Chater 1980; Koopman 2011).

On the basis of inflorescence structure, Kükenthal (1909) divided the genus *Carex* into 4 subgenera: *Carex* L., *Psyllophora* (Degl.) Peterm. (= *Primocarex* Kük.), *Vignea* (P. Beauv. ex Lestib) Peterm., and *Vigneastra* (Tuck.) Kük (= *Indocarex* (Baill.) Kük.). His classification is still valid, but recent molecular studies indicate that the subgenus *Carex* is probably paraphyletic, and may in fact include species of the subgenus *Vigneastra* (e.g. Yen & Olmstead 2000; Roalson *et al*. 2001; Hendrichs *et al*. 2004; Waterway *et al*. 2009).

Subgenus *Carex*, represented globally by about 1400 species of 60 sections (Egorova 1999), includes taxa that differ morphologically, especially in the sexual expression of spikes (Reznicek 1990; Molina *et al*. 2012). In Europe, 121 species of 24 sections have been recorded (Chater 1980). Within the subgenus *Carex*, the section *Ceratocystis* Dumort. is one of the most systematically difficult groups, because of a lack of clear discontinuities in their morphology, polymorphism, and the existence of many hybrids (Jiménez-Mejías *et al*. 2012a). Generally, the main morphological characteristics of the section *Ceratocystis* are: ovoid-ellipsoid utricles, not speckled, with a long bifid beak, obovate achenes, globose to oblong female spikes, and usually a solitary subcylindrical, sessile or pedunculate male spike (Chater 1980; Egorova 1999; Crins 2002).

The section *Ceratocystis* includes taxa of *Carex flava* agg., also referred to as the *Carex flava* group or complex. The group is known for its complicated pattern of morphological variation and contrasting differences in taxonomic classification (e.g. Skårman 1940; Wiinstend 1947; Palmgren 1959; Patzke & Podlech 1960; Schmid 1983; Pykälä & Toivonen 1994; Egorova 1999). Among European sedges, *C. flava agg.* is one of the most difficult complexes, with several ambiguously defined taxa. Considering the observed morphological variation, a lack of clear hiatus between taxa and frequent hybridization, delimitation of the segregates poses some difficulties. Only *C. flava* L. is a morphologically well-defined species, usually easily identifiable, whereas the taxonomic position of *C. lepidocarpa* Tausch, *C. demissa* Hornem., and *C. viridula* Michx. is still disputable (species, subspecies or varieties) (e.g. Schmid 1983; Pykälä & Toivonen 1994; Egorova 1999; Hedrén 2002).

The *C. flava* group has been studied in many European countries. Beside "traditional" taxonomic descriptions (Palmgren 1946, 1959; Davies 1953a, 1953b, 1953c; Schmid 1983; Crins & Ball 1989b; Pykälä & Toivonen 1994), available information concerns its cytology (Davies 1955; Schmid 1982; Halkka *et al*. 1992), ecology (Davies 1956; Schmid 1984a, 1984b, 1986b), morphology (Havlícková 1982; Schmid 1986a; Crins & Ball 1989a; Salo *et al*. 1994; Hedrén 1998; Blackstock & Ashton 2001; Meijden & Holverda 2006; Blackstock 2007), phenology (Vonk 1979), as well as phylogenetic (Crins & Ball 1988), allozymatic (Hedrén & Prentice 1996; Hedrén 1996, 2002; Blackstock 2007), and molecular studies (Jiménez-Mejías *et al*. 2012a).

However, despite so many studies, no consensus has been reached so far on the classification and description of taxa within this complex. Various classifications divide European sedges of the *C. flava* group into units of various size (Chater 1980; Egorova 1999; Hedrén 2004). The most radical approach, associated with the biological species concept (Mayr 1957), presented by Sell (1996), recognizes only a single species, *C. flava*

s.l. At the other extreme, usually related to the ecological species concept (van Valen 1976), 8 species are distinguished [*C. flava*, C. *lepidocarpa*, *C. jemtlandica* Palmgr., *C. demissa*, *C. viridula*, *C. pulchella* (Lönnr.) Lindm. (= *C. scandinavica* E. W. Davies), *C. bergrothii* Palmgr. and *C. nevadensis* Boiss & Reuter] (e.g. Davies 1953a, c; Palmgren 1959; Chater 1980; Egorova 1999). A recently described new species, *Carex derelicta* Štepánková, found at only one site in the Karkonosze Mts. in the Czech Republic, is probably of hybrid origin (Štepánková 2008). It was earlier described as *C. oederi* Retz. subsp. *pseudoscandinavica* (Holub *et al*. 1979; Havlícková 1982) or *C. viridula* Michx. subsp. *pseudoscandinavica* (Holub 1999; Grulich & Řepka 2002). The taxon is morphologically similar to *C. viridula* var. *pulchella* (Štepánková 2008), and in my opinion requires further research, with the use of molecular methods. The taxonomic status is also unclear in the case of *C. castroviejoi* Luceño & Jim.-Mejías, which was first described from Greece (Jiménez-Mejías & Luceño 2009), and recently found in Albania (Jiménez-Mejías *et al*. 2012b). According to Jiménez-Mejías & Luceño (2009), the taxon has deflexed utricles with bent and smooth beaks, and a widely fusiform male spike, at least 3 mm wide.

Classifications in some European floras (e.g. Rich 1998; Jermy *et al*. 2007) and in the *World Checklist of Cyperaceae* (Govaerts & Simpson 2007) are based on the taxonomic concept of Schmid (1983), who delimited taxa of the *C. flava* complex on the basis of fertility level of hybrids. Schmid (1983) reduced the number of species within the *C. flava* group to 2, namely *C. flava* s.s. and *C. viridula* s.l., including *C. lepidocarpa*, *C. demissa*, *C. oederi* Retz., and *C. nevadensis*; he classified them, as *C. viridula* subsp. *brachyrrhyncha* (Tausch) B. Schmid, *C. viridula* subsp. *oedocarpa* (Andersson) B. Schmid, *C. viridula* Michx. subsp. *viridula* (var. *viridula*, var. *bergrothii*, and var. *pulchella*), and *C. viridula* subsp. *nevadensis* (Boiss. & Reuter) B. Schmid, respectively. Besides, he showed that *C. oederi* is conspecific with *C. viridula* (Schmid 1983). On the basis of Swiss sedge populations, he observed morphological variation in specimens of *C. flava* s.s. along the topographic gradient and reported 2 topoclines: *C. flava* var. *flava* and var. *alpina* Kneuck. (Schmid 1983). Similar approaches to taxonomic classification of the *C. flava* group are presented by Crins & Ball (1989b) and Bruederle & Jensen (1991).

The classification proposed by Schmid (1983) has not been accepted by many scientists. In Scandinavia, where the pattern of variation of taxa of the *C. flava* complex seems to be most complicated, *C. lepidocarpa*, *C. demissa*, and *C. viridula* are still regarded as separate species (Palmgren 1959; Hedrén 1990, 1994, 1996, 1998, 2002, 2004; Pykälä & Toivonen 1994; Hedrén & Prentice 1996). This taxonomic approach is popular also among researchers in the Iberian Peninsula (Luceño & Castroviejo 1993; Luceño & Jiménez-Mejías 2007; Jiménez-Mejías *et al*. 2012a) and in Russia (Egorova 1999). Morphological and genetic analyses conducted in the British Isles also confirm that these taxa should be classified as species (Blackstock 2007).

With regard to taxa of the *C. flava* group, various intraspecific categories are used. Within *C. lepidocarpa*, 3 subspecies are distinguished: *C. lepidocarpa* Tausch subsp. *lepidocarpa*, subsp. *jemtlandica* Palmgr., and subsp. *scotica* E. W. Davies (Koopman 2011). *C. lepidocarpa* subsp. *jemtlandica* is found in Scandinavia, Russia, and Estonia (Hedrén 1990, 1996, 2002; Pykälä & Toivonen 1994) and in the British Isles (Blackstock 2007), while *C. lepidocarpa* subsp. *scotica* is reported from Scotland, Wales, and northern England (Davies 1953b). Within *C. demissa*, 3 subspecies are distinguished: *C. demissa* Hornem. subsp. *demissa, C. demissa* Hornem. subsp. *cedercreutzii* (Fagerström) Jac. Koopman, recorded on the Azores and Madeira (Fagerström 1967; Koopman 2011), and subsp. *iranica* Kukkonen, growing in Iran and Afghanistan (Kukkonen 1984).

The most variable morphologically is *C. viridula*, forming small, isolated populations regarded as varieties [*C. viridula* Michx. var. *viridula*, *C. viridula* var. *pulchella* (Lönnr.) B. Schmid, and *C. viridula* var. *bergrothii* (Palmgr.) B. Schmid] (Pykälä & Toivonen 1994) or subspecies [*C. viridula* Michx. subsp. *viridula*, *C. viridula* Michx. subsp. *bergrothii* (Palmgr.) Tzvelev, and *C. viridula* Michx. subsp. *pulchella* (Lönnr.) Malyschev] (Blackstock 2007). In addition, the nomenclature of those taxa in Europe is still subject to some confusion, e.g. Hedrén (2002) is of the opinion that the name *C. oederi* s.l. rather than *C. viridula* should be used, whereas Egorova (1999) uses the names *C. viridula* and *C. serotina*, to denote separate species.

In Spain in the Sierra Nevada Mts, *C. nevadensis* is found, but its taxonomic position is still discussed (Jiménez-Mejías *et al*. 2012a). Schmid (1983) treated it as a subspecies within *C. viridula* s.l., while Crins & Ball (1989b) classified it as a variety, *C. viridula* var. *nevadensis* (Boiss. & Reuter) Crins. By contrast, Luceño (1999) regarded it as a subspecies of *C. lepidocarpa* and named it *C. lepidocarpa* subsp. *nevadensis* (Boiss. & Reuter) Luceño.

In North America, *C. demissa*, *C. lepidocarpa*, and *C. viridula* are fused into a single species, as suggested by Schmid (1983). Additionally, 3 species included in the *C. flava* group are endemic to that region: *C. lutea* LeBlond, *C. cryptolepis* Mack., and *C. viridistellata* Derieg, Weil, Reznicek & Bruederle (Crins & Ball 1989a, 1989b; LeBlond *et al*. 1994; Crins 2002; Derieg *et al*. 2008, 2013).

The pattern of variation observed in *C. flava* agg. is complicated by the appearance of hybrids in mixed

populations. They are morphologically intermediate between the parental forms or are more similar to one of them (Wallace *et al*. 1975; Kiffe 1998; Więcław & Wilhelm 2014). They are usually completely sterile although some partly fertile hybrids and introgression have been reported (Schmid 1982).

Taxa of the *C. flava* complex are usually found on moist or wet sites: meadows, marshes, fens (especially in groundwater seepage areas), other types of mires, shores of lakes, seas, ponds, ditches, roadsides, rarely forests (Davies 1956; Schmid 1984a, 1984b).

In Poland the *C. flava* group was not studied in detail before. Research conducted in Poland covered sedges of various subgenera and sections, e.g. of the sections *Heleoglochin* Dumort. (= *Paniculatae* (Carey) Christ.) (Szczepanik-Janyszek 2003), *Phacocystis* Dumort. (= *Acutae* (Carey) Christ.) (Klimko 1981), *Phaestoglochin* Dumort. (= *Muehlenbergianae* Tuckerm. ex Kük.) (Szczepanik-Janyszek 2001; Janyszek & Jagodziński 2009), *Vulpinae* (Carey) Christ. (Szczepanik-Janyszek & Woźnica 2001), or concerned the taxonomy, distribution, and ecology of selected species, e.g. *C. atherodes* Spreng. (e.g. Krawiecowa & Kuczyńska 1959; Ćwikliński 1986; Więcław & Ciaciura 2005), *C. arenaria* L. and *C. ligerica* J. Gay (Urbaniak 1992, 1998; Urbaniak *et al*. 2000), *C. buxbaumii* Wahlenb. (Sotek 2006), *C. cespitosa* L. (Brzosko 1999, 2001), *C. curvata* Knaf (Szeląg 2002), *C. extensa* Gooden. (Bosiacka & Więcław 2012), *C. hartmanii* Cajander (Sotek 2008), *C. loliacea* L. and *C. disperma* Dewey (Pawlikowski 2010), *C. pallens* (Fristedt) Harmaja (Szeląg 2001), *C. pediformis* (Towpasz 1969), *C. posnaniensis* (Ceynowa 1969), *C. pseudobrizoides* (Żukowski & Lembicz 2000), *C. repens* Bellardi (Lembicz *et al*. 2010), or *C. secalina* Wahlenb. (Żukowski *et al*. 2005; Lembicz *et al*. 2006).

According to Mirek *et al*. (2002), in Poland 97 species of the genus *Carex* are found, including 5 species of the *C. flava* complex. In the Polish flora published in 1919 (Raciborski 1919), only 3 species of this group were listed: *C. flava*, *C. lepidocarpa*, and *C. oederi*. The fourth species, *C. demissa* was first recorded in Poland in 1965 (Jasiewicz 1965), whereas *C. viridula* var. *pulchella* (= *C. scandinavica*), in 1968 (Zając 1968),

In this study of taxa of the *C. flava* group, the following hypotheses were formulated: (*i*) application of the phenetic species concept and numerical analysis make it possible to identify borders of morphological variation between taxa of the *C. flava* complex from Polish populations; (*ii*) the taxonomic approach that fuses *C. lepidocarpa*, *C. viridula*, and *C. demissa* into one species disagrees with the clear morphological and habitat variation of these taxa in Poland; (*iii*) in Poland there are at least 4 well-defined taxa of the *C. flava* group; (*iv*) in the populations where 2-3 of the studied taxa grow sympatrically, hybrids with various levels of fertility appear; (*v*) plants included in *C. flava* agg. prefer moist habitats and are usually found on more or less alkaline soils.

To verify these hypotheses, the following research tasks were performed: (1) determination of the number and rank of taxa found in Poland, (2) determination of the level of their morphological variation and identification of most useful diagnostic features, (3) construction of a key to identification, and (4) measurement of soil parameters.

2. Material and methods

2.1. Field research and collection of specimens

Field research was conducted in 2007-2012 in the following macroregions of Poland (Kondracki 2002): Koszalin Coast District (Pobrzeże Koszalińskie), Gdańsk Coast Disctrict (Pobrzeże Gdańskie), Szczecin Coast District (Pobrzeże Szczecińskie), West Pomeranian Lakeland (Pojezierze Zachodniopomorskie), South Pomeranian Lakeland (Pojezierze Południowopomorskie), Chełmno-Dobrzyń Lakeland (Pojezierze Chełmińsko-Dobrzyńskie), Masurian Lakeland (Pojezierze Mazurskie), Lithuanian Lakeland (Pojezierze Litewskie), Milicz-Głogów Depression (Obniżenie Milicko-Głogowskie), Przedbórz Upland (Wyżyna Przedborska), Woźniki-Wieluń Upland (Wyżyna Woźnicko-Wieluńska), Nida Basin (Niecka Nidziańska), Western and Eastern Sudetes, and Eastern Beskid Mts (Appendix 1). From 80 localities, 1852 fruiting specimens were collected in total. At 14 of the 80 sites, local populations were mixed, composed of 2 well-defined taxa of the *C. flava* group, whereas at 4 localities, 3 taxa coexisted (Appendix 1). The investigated sites were at least 200 m apart and differed in soil conditions. Sedges were collected from various types of habitats, representing a complete ecological spectrum of these taxa, i.e. from typical, poor, and calcareous fens, moist meadows, marshes, partly overgrown ponds, ditches, roadsides, salt-marshes, peaty and sandy edges of lakes, depressions between dunes, thickets, and alder forests. From individual sites, 2-82 specimens were collected, depending on the local abundance of sedges and their morphological variation, suggesting coexistence of several species and hybrids on the same site. To minimize the probability of collecting species of the same clone, the sampled plants were about 3-6 m apart. For comparison, sedges of the *C. flava* group were collected also during field research in 2013 in Switzerland and the Netherlands. All the specimens have been deposited in the herbarium of Szczecin University (SZUB).

In this study, also dried specimens from Polish herbaria were taken into account (BIL, BNPH, BSG, BYDG, DRAPN, KRA, KRAM, KRAB, KTC, KTU,

Table 1. Morphological characters used for description of taxa of the *Carex flava* group (those used in statistical analyses are marked with asterisks)

No.	Character	Abbr.
1.	Culm height (cm)*	CH
2.	Culm width above uppermost cauline leaf (mm)	CW
3.	Cauline leaf width (cm)*	CLW
4.	Cauline leaf length (cm)*	CLL
5.	Cauline leaf sheath length (cm)	CLSL
6.	Basal leaf width (cm)	BLW
7.	Basal leaf length (cm)	BLL
8.	Ratio of culm height to leaf length* (1 – leaves up to half as long as culm, 2 – leaves about ¾ as long as culm, 3 – leaves as long as culm, 4 – leaves longer than culm)	C/L
9.	Ligule length (mm)	LL
10.	Inflorescence length (cm)*	IL
11.	Male spike length (cm)*	MSL
12.	Male spike width (cm)*	MSW
13.	Male spike peduncle length (cm)*	MPL
14.	Number of female spikes*	NFS
15.	Distance between 2 uppermost female spikes (cm)*	DUFS
16.	Distance between 2 lowest female spikes (cm)*	DLFS
17.	Lowest female spike length (cm)*	LFSL
18.	Lowest female spike width (cm)*	LFSW
19.	Lowest female spike peduncle length (cm)*	LPL
20.	Lowest female spike bract length (cm)*	LBL
21.	Lowest female spike bract width (cm)*	LBW
22.	Lowest female spike bract sheath length (cm)*	LBSL
23.	Ratio of lowest female spike bract length to inflorescence length* (1 – bract shorter than inflorescence, 2 – bract as long as inflorescence, 3 – bract up to twice as long as inflorescence, 4 – bract more than twice as long as inflorescence)	B/I
24.	Uppermost female spike length (cm)*	UFSL
25.	Uppermost female spike width (cm)*	UFSW
26.	Second female spike bract length (cm)*	SBL
27.	Second female spike bract width (cm)*	SBW
28.	Second female spike bract sheath length (cm)	SBSL
29.	Utricle length (mm)*	UL
30.	Utricle width (mm)	UW
31.	Utricle colour	UC
32.	Utricle beak length (mm)*	UBL
33.	Beak shape (1 – straight, 2 – curved)	BSH
34.	Beak surface (1 – numerous bristles, 2 – sparse bristles, 3 – smooth)	BSU
35.	Ratio of beak length to utricle length (%)*	B/U
36.	Presence of fruits in utricles (1 – absent, 2 – present)	PF
37.	Ratio of fruit size to utricle size (1 – fruit filling ⅓ to ½ of utricle body, 2 – fruit filling ½ of utricle body, 3 – fruit filling ½ to ⅔ of utricle body, 4 – fruit filling ⅔ to ¾ of utricle body, 5 – fruit completely filling utricle body)	F/U
38.	Female glume length (mm)*	FGL
39.	Female glume width (mm)*	FGW
40.	Female glume colour	FGC
41.	Female glume shape	FGS
42.	Male glume length (mm)*	MGL
43.	Male glume width (mm)*	MGW
44.	Male glume colour	MGC
45.	Male glume shape	MGS

LBLM, LOD, OLTC, OPOL, POZ, PUMA, TRN, SLTC, SPNH, SZCZ, SZUB, UGDA, WA, WRSL, WSRP, ZAMU; abbreviations of the names of herbaria follow Mirek *et al*. 1997), and from collections of Dr hab. B. Babczyńska-Sendek, Dr hab. K. Oklejewicz, Dr A. Błońska, P. Kalinowski, MSc, J. Koopman, MSc, P. Kobierski, MSc, and R. Ryś, MSc. The analysed material included also *C. flava* agg. from herbaria in Berlin

Table 2. Variation of morphological characters of taxa of the *Carex flava* group

Character	*C. flava* s.s.					*C. lepidocarpa*					*C. demissa*					*C. viridula* var. *viridula*				
	x	min	max	SD	*V*	*x*	min	max	SD	*V*	*x*	min	max	SD	*V*	*x*	min	max	SD	*V*
CH	40.0	12.5	67.3	12.56	31	52.4	20.3	84.2	10.84	21	25.3	6.1	56.5	9.33	37	17.7	2.9	44.9	9.30	52
CLW	00.3	00.2	0.5	0.07	20	0.3	0.2	0.4	0.04	17	0.3	0.2	0.4	0.04	16	0.2	0.1	0.3	0.03	14
CLL	17.6	07.9	29.1	3.98	23	11.9	5.5	22.4	3.35	28	8.6	2.9	17.8	3.07	36	10.4	3.1	23.1	3.85	37
C/L	03.0	1..	4.0	0.88	36	1.0	1.0	3.0	0.53	38	2.0	1.0	4.0	0.60	39	3.0	1.0	4.0	0.97	34
IL	4.2	1.5	20.1	2.74	66	6.5	2.6	23.4	3.47	53	8.8	1.6	33.4	6.35	72	3.9	1.1	16.1	2.47	62
MSL	1.5	0.8	2.3	0.29	20	1.8	1.0	3.1	0.39	21	1.4	0.8	2.2	0.30	21	1.1	0.4	2.0	0.41	37
MSW	0.2	0.1	0.2	0.02	15	0.2	0.1	0.2	0.02	12	0.2	0.1	0.2	0.02	13	0.2	0.1	0.2	0.03	17
MPL	0.2	0.0	1.4	0.27	125	1.7	0.2	6.0	1.14	66	0.5	0.0	2.1	0.34	69	0.2	0.0	2.1	0.36	164
NFS	3.0	2.0	5.0	0,61	22	2.0	1.0	4.0	0,65	33	3.0	2.0	5.0	0,61	19	4.0	2.0	7.0	0.98	28
DUFS	0.8	0.0	3.5	0.78	101	2.3	0.2	13.9	1.97	84	0.7	0.1	6.9	0.51	78	0.4	0.0	7.0	0.54	134
DLFS	2.0	0.1	16.2	2.86	143	5.3	1.0	19.9	5.02	94	6.3	0.4	27.3	5.88	93	1.8	0.0	11.6	2.08	117
LFSL	1.3	1.0	2.2	0.19	14	1.3	0.8	2.2	0.24	18	1.1	0.7	1.6	0.19	18	0.9	0.6	1.4	0.17	19
LFSW	0.9	0.7	1.1	0.08	8	0.8	0.7	1.0	0.07	9	0.7	0.4	0.9	0.08	11	0.6	0.4	0.8	0.07	11
LPL	0.5	0.0	3.2	0.53	111	0.4	0.0	3.3	0.67	155	0.4	0.0	2.1	0.35	95	0.2	0.0	3.2	0.40	192
LBL	12.0	3.2	26.5	3.66	31	6.3	0.6	17.7	2.96	47	8.3	2.4	18.8	3.01	36	8.0	2.8	21.7	3.33	42
LBW	0.3	0.2	0.5	0.06	23	0.2	0.0	0.3	0.05	35	0.2	0.2	0.4	0.04	15	0.2	0.1	0.3	0.03	14
LBSL	0.5	0.1	4.4	0.57	112	0.6	0.1	4.2	0.62	104	0.9	0.1	4.4	0.68	72	0.6	0.0	9.2	0.73	124
B/I	4.0	3.0	4.0	0.34	9	2.0	1.0	3.0	0.84	41	2.0	1.0	4.0	1.07	49	3.0	1.0	4.0	0.66	19
UFSL	1.2	0.9	1.7	0.13	12	1.2	0.8	1.9	0.21	18	0.9	0.6	1.3	0.14	15	0.7	0.4	1.3	0.14	20
UFSW	0.9	0.8	1.1	0.07	8	0.8	0.7	1.0	0.07	9	0.7	0.5	0.9	0.07	10	0.6	0.4	0.8	0.07	12
SBL	5.3	1.3	10.9	1.91	36	2.1	0.4	7.5	1.54	75	4.3	0.8	11.9	1.74	41	2.9	0.0	9.8	1.45	50
SBW	0.1	0.1	0.3	0.04	24	0.1	0.0	0.1	0.03	59	0.2	0.0	0.3	0.04	26	0.1	0.0	0.2	0.04	43
UL	4.8	3.9	6.2	0.44	9	4.0	3.5	4.8	0.30	7	3.6	2.9	4.3	0.35	10	2.9	2.1	4.1	0.34	12
UBL	2.2	1.8	2.8	0.21	10	1.5	1.1	1.8	0.14	10	1.3	0.9	1.8	0.17	12	0.9	0.6	1.3	0.14	15
B/U	46.0	41.0	50.0	2.07	5	36.0	30.0	45.0	2.74	8	41.0	35.0	45.0	2.44	6	31.0	23.0	36.0	2.63	8
FGL	3.0	2.3	4.2	0.39	13	2.5	2.1	3.3	0.22	9	2.6	2.0	3.5	0.33	13	2.1	1.5	3.0	0.28	13
FGW	1.5	1.2	1.8	0.12	8	1.5	1.2	1.8	0.11	8	1.5	1.1	2.0	0.13	9	1.3	1.0	1.7	0.15	11
MGL	3.6	2.9	4.4	0.30	8	3.5	2.9	4.2	0.21	6	3.9	3.1	5.2	0.42	11	3.2	2.4	4.2	0.32	10
MGW	1.5	1.1	1.9	0.14	9	1.6	1.3	2.1	0.12	8	1.6	1.2	2.0	0.13	8	1.4	1.2	2.1	0.13	9

Explanations: *x* – arithmetic mean, min and max – minimum and maximum values, SD – standard deviation, *V* – coefficient of variation for individual taxa, V_0 – coefficient of variation for all taxa analysed jointly. Characters abbreviated as in Table 1

(B) and Leiden (L). In total, identification of over 3500 herbarium specimens was verified and 1500 herbarium specimens were measured.

Additionally, herbarium specimens of *C. hostiana* were verified, as it also belongs to the section *Ceratocystis* and often forms hybrids with taxa of the *C. flava* complex (Kiffe 2001; Więcław & Koopman 2013). *C. hostiana*, as the only species of this section, has well-developed, short rhizomes and narrowly cylindrical, remote, female spikes usually on peduncles, and dark brown glumes (Chater 1980; Crins & Ball 1987). The collected information was used to construct a key to identification of sedges of the section *Ceratocystis* (Appendix 2).

2.2. Morphometric analysis

The operational taxonomic unit (OTU) in this study was a fresh or herbarium specimen described on the basis of 45 morphological characters (34 quantitative and 11 qualitative) (Table 1). All the analysed characters were used in species descriptions and for constructing a key to their identification. In statistical analyses, the morphological database was limited to 29 characters (marked with asterisks in Table 1), because of (*i*) difficulties with measurement of some characters in herbarium specimens and relating them to measurements of fresh specimens; (*ii*) low taxonomic value of some characters, e.g. glume colour and shape were similar in most of the compared taxa; (*iii*) specificity of some features to *C. flava*, which is the best-defined species of the analysed aggregate, e.g. ligule length; (*iv*) lack of some data, e.g. dimensions of basal leaves in herbarium specimens.

Culm height, leaf length, bract length, and inflorescence length were measured with a ruler to the nearest 0.1 cm. All the other vegetative characters were measured with Vernier callipers to the nearest 0.05 mm. Dimensions of utricles, glumes, and spikes, as well as peduncle length and ligule length were measured

C. viridula var. *pulchella*					V_0
x	min	max	SD	*V*	%
5.9	2.8	11.3	3.05	52	56
0.2	0.1	0.2	0.02	13	22
4.3	2.6	5.9	1.18	28	42
3.0	3.0	4.0	0.50	15	48
1.7	0.7	2.8	0.62	37	80
0.9	0.5	1.4	0.36	42	32
0.2	0.1	0.2	0.03	21	16
0.1	0.0	0.3	0.11	103	145
2.0	2.0	3.0	0.50	21	32
0.4	0.2	0.9	0.23	60	135
0.4	0.3	0.4	0.03	8	121
0.7	0.6	0.8	0.08	12	24
0.5	0.5	0.5	0.03	5	20
0.0	0.0	0.3	0.09	188	142
3.0	1.8	4.5	1.00	33	44
0.2	0.1	0.2	0.02	15	25
0.2	0.1	0.3	0.05	29	104
3.0	3.0	4.0	0.33	11	39
0.6	0.5	0.8	0.08	12	27
0.5	0.4	0.6	0.05	10	21
1.0	0.1	1.9	0.48	47	55
0.1	0.0	0.1	0.03	36	49
2.2	1.8	2.6	0.18	8	21
0.7	0.6	0.8	0.06	8	33
30.0	27.0	32.0	1.94	7	15
1.9	1.4	2.2	0.28	15	17
1.3	1.0	1.4	0.13	10	11
3.0	2.8	3.3	0.19	6	13
1.5	1.3	1.6	0.12	8	10

under a stereo microscope (ZEISS Discovery V12) to the nearest 0.01 mm. From the central part of a female spike of each specimen, 5 utricles and 5 glumes were isolated for measurements. Similarly, from the central part of the male spike of each specimen, 5 male glumes were isolated for measurements. For further analyses, mean values of the characters (utricles and glumes) were used. Utricles and glumes from the central part of the spike are regarded as the least variable ones, and are most often used in biometric studies (Blackstock & Ashton 2010). The percentage ratio of beak length to utricle length (B/U) was calculated from the formula:

$$\frac{\text{utricle beak length (UBL)}}{\text{total utricle length (UL)}} \times 100\%$$

Measurements under a stereo microscope were conducted at the Department of Invertebrate Zoology and Limnology, University of Szczecin.

2.3. Estimation of fertility level

During field research, some of the investigated populations were found to be mixed, composed of various taxa of the *C. flava* complex, including hybrids with lower fertility. Hence, fertility of live specimens was assessed on the basis of the percentage contribution of utricles with well-developed fruits. For this purpose, Hedrén's (2002) fertility scale was simplified as follows: 1-0% of well-developed fruits; 2-10% or less, but more than 0%; 3-50% or less, but more than 10%; 4 – less than 100%, but more than 50%; 5-100% of well-developed fruits. Sterile or less fertile specimens (scores 1-3) usually were morphologically intermediate between completely fertile specimens (score 5).

2.4. Analysis of soil samples

Soil samples were collected at each site from the depth of 0-15 cm, then dried at room temperature, and next sieved to remove the fraction >2 mm. In the material prepared in this way, the following soil parameters were evaluated: organic matter content (loss on ignition), pH (in 1 M KCl), assimilable nutrients (P, K, Mg, and Ca – using the American Society of Agronomy method), carbonates (using Scheibler's method), and total C and N content (using CHNS chemical analyser, Costech Analytical Technologies Inc.).

All the soil analyses were performed at the Department of Environmental Reclamation and Chemistry, West Pomeranian Technological University, Szczecin.

2.5. Statistical analysis

OTUs were classified using Ward's minimum variance method, based on Euclidean distances. The distinguished OTUs were assigned a taxonomic status. First, well-defined taxa were distinguished, according to the taxonomic concept presented by Pykäla & Toivonen (1994) and Hedrén (2003). Next, taxonomic status was given to completely sterile or partly fertile hybrids. For delimitation of the hybrids, field data were also used, i.e. coexistence (on the same site) of hybrids and putative parental species.

The hypothesis about morphological separation of the investigated sedge specimens was tested with the use of discriminant function analysis (DFA). The analysis required *a priori* assignment of each OTU to a selected taxon. The grouping of OTUs was possible thanks to the preceding classification procedure. DFA enabled comparison of percentage similarity of observed classifications (i.e. *a priori* defined) with classifications resulting from DFA, in the form of a classification matrix. In DFA, well-defined taxa should be assigned to distinct groups, whereas hybrids should be located in the DFA space defined by putative parents. DFA was performed in 3 steps. In the first step, the complete database was used. In the second step, *C. flava* s.s. and its hybrids were excluded from analyses. In the third step, *C. flava*,

C. lepidocarpa, and their hybrids were excluded. In the successive steps of DFA, the excluded species (with hybrids) was the one that was best distinguished by discriminant functions of other members of the *C. flava* group. As a result, the most similar species remained in the last step: *C. demissa* and C. *viridula*. This procedure allowed a relatively precise determination of morphological characters that distinguished between the analysed taxa.

To estimate the total morphological variation of sedge specimens and to determine relations between them, principal component analysis (PCA) was performed on the basis of a correlation matrix. Hybrids, also in this analysis, should fill the phenetic space between putative parental taxa. PCA was performed in 3 steps, using the same procedure as in DFA. Additionally, PCA was performed separately for *C. lepidocarpa* and *C. demissa*, since these taxa were poorly separated by PCA.

In statistical analyses, all living specimens collected during field research were used except *C.* ×*subviridula* (18 specimens) and *C. viridula* var. *pulchella* (9 specimens), which were found only in herbaria. Because of the large database (1852 living specimens), the scatterplots of DFA and PCA results, as well as the phenogram (phenetic tree) present data from a smaller data set, reduced to 561 specimens, including 409 specimens of well-defined taxa: 100 of *C. flava* s.s., 100 of *C. lepidocarpa*, 100 of *C. demissa*, 100 of *C. viridula* var. *viridula*, 9 of *C. viridula* var. *pulchella*, and 152 of hybrids.

Relationships between occurrence of taxa and soil parameters were tested using redundancy analysis (RDA, on the basis of the whole data set collected during field research), and presented as a scatterplot. Statistical significance of soil parameters and canonical axes was assessed by Monte Carlo permutation test (ter Braak & Šmilauer 2002).

For each morphological character, basic statistics were calculated, i.e. arithmetic mean, range (minimum and maximum values), standard deviation, and coefficient of variation. Relations between morphological characters were assessed on the basis of Spearman's correlation coefficient. For soil parameters, arithmetic mean and minimum and maximum values were calculated. Significance of differences in mean values of morphological characters of the analysed taxa of sedges

Table 3. Matrix of significance of Spearman's rank correlation coefficients for taxa of the *Carex flava* group: (A) *C. flava* s.s.; (B) *C. lepidocarpa*; (C) *C. demissa*; (D) *C. viridula* var. *viridula*

Explanations: 1, 4, 8… – character numbers as in Table 2. Absolute values ≥ 0.80 are marked in bold. Coefficients of correlation were not calculated for *C. viridula* var. *pulchella* because of the small number of specimens

(A)

Character	1	3	4	8	10	11	12	13	14	15	16	17	18	19	20	21	22	23
42	0.11	0.05	0.02	-0.10	0.25	0.25	-0.16	0.07	0.11	0.22	-0.03	0.12	-0.16	0.39	0.24	-0.01	0.31	-0.34
41	-0.12	0.30	0.12	0.09	-0.01	0.09	0.32	-0.41	0.17	-0.37	0.22	0.34	0.44	-0.09	0.07	0.30	0.01	0.13
38	0.11	0.48	0.02	-0.14	0.40	0.35	0.22	-0.17	0.31	-0.14	0.36	0.40	0.32	0.09	0.29	0.42	0.27	-0.03
37	-0.24	0.47	0.13	0.09	0.12	0.14	0.40	-0.25	0.22	-0.42	0.33	0.35	0.56	-0.19	0.13	0.40	0.09	0.08
34	0.25	-0.29	0.08	-0.16	0.06	0.10	-0.21	0.22	-0.10	0.28	0.00	0.08	0.03	0.11	0.03	-0.20	0.01	0.08
32	-0.03	0.10	0.13	0.27	-0.15	-0.03	0.27	-0.24	0.00	-0.30	0.08	0.21	0.58	-0.28	-0.10	0.14	-0.21	0.21
29	-0.16	0.23	0.10	0.34	-0.19	-0.06	0.39	-0.36	0.00	-0.40	0.05	0.19	0.62	-0.32	-0.12	0.23	-0.22	0.17
27	-0.09	0.17	-0.02	-0.08	0.37	0.27	0.11	-0.07	0.17	-0.03	0.21	0.10	0.01	0.19	0.26	0.32	0.29	-0.05
26	0.37	-0.01	0.26	-0.34	0.35	0.36	-0.13	0.09	0.14	0.25	0.07	0.23	-0.07	0.26	0.50	0.05	0.35	-0.04
25	-0.06	0.16	0.10	0.21	-0.17	0.06	0.28	-0.10	-0.19	-0.25	-0.10	0.26	0.63	-0.24	-0.08	0.12	-0.18	0.17
24	0.19	0.13	0.14	0.03	0.25	0.46	0.21	0.24	-0.12	0.12	-0.10	0.37	0.29	0.11	0.24	0.25	0.10	-0.01
23	-0.15	-0.20	-0.09	0.09	-0.36	-0.24	0.06	-0.09	-0.25	-0.19	-0.13	-0.19	0.16	-0.35	-0.23	-0.13	-0.31	
22	0.04	0.37	0.11	-0.38	**0.80**	0.36	0.09	0.01	0.55	0.11	0.58	0.31	-0.12	0.64	0.59	0.45		
21	-0.01	0.67	0.23	-0.07	0.55	0.44	0.47	-0.17	0.53	-0.28	0.54	0.51	0.28	0.27	0.47			
20	0.25	0.46	0.59	-0.29	0.72	0.52	0.23	0.02	0.58	0.00	0.52	0.45	0.07	0.54				
19	0.11	0.15	0.00	-0.33	0.70	0.37	0.00	0.10	0.40	0.26	0.35	0.28	-0.15					
18	-0.01	0.31	0.23	0.10	-0.03	0.17	0.27	-0.22	0.02	-0.30	0.05	0.39						
17	0.28	0.53	0.44	-0.10	0.48	0.65	0.41	0.00	0.36	0.04	0.29							
16	-0.04	0.49	0.25	-0.26	0.62	0.14	0.19	-0.38	**0.87**	-0.50								
15	0.26	-0.31	-0.11	-0.11	0.14	0.16	-0.17	0.54	-0.37									
14	0.10	0.48	0.38	-0.30	0.60	0.20	0.13	-0.41										
13	0.16	-0.13	-0.10	-0.05	0.09	0.24	-0.06											
12	-0.19	0.37	0.31	0.22	0.14	0.20												
11	0.35	0.49	0.33	-0.12	0.60													
10	0.22	0.46	0.23	-0.31														
8	-0.44	-0.12	0.02															
4	0.34	0.38																
3	0.06																	

and in mean values of soil parameters at their sites was estimated by one-way analysis of variance (ANOVA). To determine more precisely the character of differences detected by ANOVA, the *post hoc* Tukey HSD test for unequal *N* was used (Spjotvoll/Stoline test).

All the data used in multivariate statistical analyses were standardized, so that for each variable the arithmetic mean was 0 and standard deviation was 1. Calculations were made with the use of statistical software: Statistica 8.0 (StatSoft, 2007) and Canoco 4.5 (ter Braak & Šmilauer 2002).

3. Results

3.1. Variation in morphological characters; pair-wise correlations

Biometric analyses indicate that the *C. flava* group is characterized by exceptional morphological variation (Table 2). For the whole analysed dataset (excluding hybrids), high coefficients of variation ($V_0 \geq 50\%$) were recorded for inflorescence length (IL), male spike peduncle length (MPL), distance between 2 uppermost female spikes (DUFS), distance between 2 lowest female spikes (DLFS), lowest female spike peduncle length (LPL), lowest female spike bract sheath length (LBSL), second female spike bract length (SBL), and culm height (CH). The least variable characters ($V_0 \leq 25\%$) include utricle length (UL), ratio of beak length to utricle length (B/U), dimensions of female and male glumes (FGL, FGW, MGL, and MGW), dimensions of female spikes (LFSL, LFSW, UFSW), male spike width (MSW), lowest female spike bract width (LBW), and uppermost cauline leaf width (CLW) (Table 2). Variability of individual characters was similar in all groups of analysed taxa (Table 2). For 2 characters only – uppermost female spike length (UFSL) and utricle beak length (UBL) – disparity was observed between *V* calculated for the whole dataset (27% and 33%, respectively) and for individual taxa (12-20% and 8-15%, respectively).

The less variable characters ($V_0 \leq 25\%$) seem to be most suitable for distinguishing between taxa of the *C. flava* complex. Most useful for delimitation are characters of utricles (UL, UBL, B/U), female spikes (LFSL, LFSW, UFSL, and UFSW), and bracts (LBW). Characters concerning dimensions of glumes (FGL, FGW, MGL, and MGW), male spike width (MSW), and uppermost cauline leaf width (CLW) are not highly variable but have similar ranges of values in all the compared taxa, so they are not useful for identification of species within *C. flava* agg. (Table 2).

Spearman's correlation coefficients (Tables 3A-D) show relatively high (≥ 0.80) positive correlations (*i*) between inflorescence length (IL) and distance between 2 lowest female spikes (DLFS) (Table 3C-D), lowest female spike peduncle length (LBL) (Table 3B), and lowest female spike bract sheath length (LBSL) (Table 3A); (*ii*) between number of female spikes (NFS) and distance between 2 lowest female spikes (DLFS) (Table 3A); (*iii*) between second female spike bract length (SBL) and width (SBW) (Table 3B and D); (*iv*) between cauline leaf length (CLL) and lowest female spike bract length (LBL) (Table 3C); (*v*) between uppermost female spike length (UFSL) and width (UFSW) (Table 3B); and (*vi*) between utricle length (UL) and beak length (UBL) (Table 3A, C-D). High negative correlations were recorded between number of female spikes (NFS) and distance between 2 uppermost female spikes (DUFS) (Table 3D) and ratio of lowest female spike bract length to inflorescence length (B/I) (Table 3C).

3.2. Morphological distinctness of taxa of *Carex flava* agg.

Results of Ward's hierarchical clustering show division of specimens of *C. flava* agg. into clusters A, B, C, and D, corresponding to well-defined species:

24	25	26	27	29	32	34	37	38	41
0.18	-0.16	0.24	0.10	-0.33	-0.41	-0.05	-0.21	0.16	-0.16
0.04	0.35	-0.09	0.08	0.51	0.48	-0.06	0.59	0.34	
0.26	0.21	0.07	0.21	0.28	0.23	-0.04	0.54		
0.22	0.49	-0.09	0.21	0.63	0.55	-0.14			
0.04	-0.04	0.21	-0.05	-0.21	0.20				
0.25	0.64	-0.10	0.12	**0.88**					
0.22	0.67	-0.19	0.15						
0.32	0.06	0.55							
0.31	-0.09								
0.40									

(B)

Character	1	3	4	8	10	11	12	13	14	15	16	17	18	19	20	21	22	23
42	-0.20	0.48	0.16	-0.10	0.38	0.21	0.32	0.02	0.32	0.32	0.23	0.43	0.29	0.45	0.41	0.42	0.38	0.16
41	-0.18	0.29	0.00	-0.07	0.34	0.28	0.38	0.07	0.20	0.13	0.21	0.40	0.31	0.41	0.38	0.36	0.34	0.17
38	-0.01	0.22	-0.01	0.01	0.09	0.11	0.18	0.12	-0.02	0.04	-0.02	0.23	0.21	0.11	0.06	0.08	0.02	-0.05
37	0.10	-0.06	-0.05	0.05	0.11	0.19	0.21	0.17	-0.08	0.01	-0.08	0.25	0.04	0.05	0.06	0.00	0.09	-0.08
34	0.06	0.02	-0.12	0.11	-0.09	0.03	0.00	0.02	-0.01	-0.04	-0.01	0.11	0.00	0.11	-0.06	-0.02	-0.06	0.03
32	0.24	0.15	0.13	0.17	0.13	0.24	0.21	0.23	-0.07	0.02	-0.05	0.42	0.49	0.15	0.12	0.02	0.00	0.03
29	0.24	0.19	0.28	0.16	0.26	0.28	0.28	0.29	-0.08	0.08	-0.04	0.48	0.68	0.13	0.22	0.07	0.10	0.02
27	-0.13	0.34	0.13	-0.20	0.50	0.03	0.18	-0.16	0.60	0.45	0.43	0.06	-0.11	0.49	0.65	0.67	0.53	0.43
26	-0.19	0.41	0.15	-0.19	0.55	0.08	0.22	-0.11	0.62	0.47	0.46	0.14	-0.03	0.55	0.70	0.72	0.54	0.46
25	-0.01	0.51	0.33	-0.03	0.42	0.27	0.26	-0.11	0.59	0.62	0.18	0.42	0.44	0.44	0.59	0.49	0.40	0.37
24	0.02	0.45	0.28	-0.09	0.44	0.39	0.33	0.07	0.47	0.70	-0.02	0.47	0.26	0.48	0.58	0.45	0.40	0.34
23	-0.15	0.28	0.29	-0.08	0.07	-0.04	-0.02	-0.15	0.34	0.21	0.19	0.08	0.16	0.24	0.52	0.48	0.25	
22	-0.18	0.35	0.01	-0.11	0.66	0.10	0.26	-0.03	0.50	0.55	0.32	0.21	-0.01	0.63	0.68	0.68		
21	-0.30	0.52	0.08	-0.17	0.58	0.07	0.18	-0.14	0.63	0.48	0.47	0.22	0.05	0.65	0.75			
20	-0.02	0.54	0.46	-0.15	**0.82**	0.32	0.31	0.12	0.56	0.63	0.38	0.43	0.27	0.70				
19	-0.17	0.59	0.11	-0.14	0.69	0.27	0.33	0.08	0.47	0.53	0.34	0.47	0.16					
18	0.25	0.40	0.44	0.08	0.25	0.43	0.37	0.31	-0.10	0.08	-0.05	0.62						
17	0.19	0.58	0.39	0.00	0.50	0.76	0.63	0.44	0.04	0.24	0.00							
16	-0.16	0.17	0.05	0.05	0.37	-0.13	-0.01	-0.48	0.74	-0.10								
15	0.03	0.41	0.29	-0.12	0.57	0.23	0.26	0.03	0.43									
14	-0.15	0.32	0.14	-0.05	0.43	-0.07	0.04	-0.60										
13	0.23	0.16	0.21	-0.05	0.30	0.55	0.30											
12	0.06	0.45	0.20	-0.01	0.43	0.61												
11	0.24	0.47	0.33	-0.03	0.49													
10	0.10	0.52	0.37	-0.09														
8	0.11	-0.11	0.07															
4	0.48	0.35																
3	0.04																	

(C)

Character	1	3	4	8	10	11	12	13	14	15	16	17	18	19	20	21	22	23
42	0.27	0.21	0.10	-0.30	0.08	0.07	0.08	0.04	0.02	0.04	0.07	0.11	0.21	0.04	0.10	0.24	0.09	-0.05
41	0.30	0.20	0.32	-0.06	0.00	0.17	0.26	0.00	0.14	0.04	-0.02	0.30	0.49	0.28	0.22	0.28	-0.07	0.13
38	0.29	0.21	0.29	-0.13	0.16	0.25	0.27	0.17	0.03	0.16	0.14	0.24	0.20	0.03	0.27	0.27	0.15	-0.02
37	0.42	0.24	0.41	-0.14	0.08	0.38	0.28	0.12	0.10	0.15	0.01	0.44	0.63	0.17	0.27	0.33	0.05	0.06
34	0.20	0.16	-0.07	-0.34	-0.06	-0.06	-0.10	-0.09	0.00	-0.05	-0.02	0.05	0.05	-0.18	-0.07	0.13	-0.01	0.03
32	0.49	0.23	0.30	-0.32	0.12	0.30	0.12	0.09	0.14	0.15	0.08	0.39	0.59	0.11	0.22	0.34	0.11	-0.02
29	0.47	0.20	0.40	-0.17	0.17	0.39	0.21	0.16	0.18	0.21	0.09	0.46	0.69	0.26	0.31	0.34	0.15	-0.02
27	0.26	0.26	0.21	-0.12	0.32	0.22	0.18	0.43	-0.16	0.13	0.34	0.21	0.15	0.14	0.29	0.36	0.23	-0.18
26	0.40	0.24	0.49	0.08	0.36	0.28	0.23	0.42	-0.10	0.23	0.36	0.26	0.25	0.08	0.62	0.34	0.28	-0.09
25	0.36	0.22	0.36	-0.07	0.22	0.46	0.28	0.28	0.05	0.31	0.11	0.45	0.63	0.22	0.31	0.35	0.15	-0.07
24	0.37	0.21	0.36	-0.06	0.29	0.55	0.25	0.57	-0.16	0.43	0.16	0.56	0.44	0.24	0.35	0.29	0.19	-0.11
23	-0.02	0.01	0.23	0.23	**-0.81**	-0.24	0.02	-0.26	-0.20	-0.15	-0.76	0.06	0.06	-0.38	-0.06	-0.15	-0.54	
22	0.30	0.14	0.16	-0.13	0.70	0.28	0.04	0.19	0.30	0.19	0.67	0.14	0.18	0.28	0.44	0.24		
21	0.42	0.62	0.39	-0.08	0.40	0.37	0.16	0.02	0.41	0.09	0.37	0.36	0.30	0.22	0.49			
20	0.67	0.33	**0.84**	0.12	0.52	0.41	0.30	0.13	0.44	0.30	0.50	0.47	0.42	0.30				
19	0.14	0.03	0.20	0.00	0.50	0.23	0.16	0.13	0.32	0.19	0.45	0.26	0.15					
18	0.54	0.27	0.52	-0.07	0.14	0.44	0.34	0.16	0.10	0.25	0.04	0.60						
17	0.62	0.39	0.57	-0.08	0.16	0.61	0.25	0.26	0.14	0.36	0.04							
16	0.30	0.16	0.15	-0.15	**0.93**	0.22	0.08	0.12	0.52	0.11								
15	0.35	0.05	0.31	0.01	0.30	0.61	0.15	0.52	-0.17									
14	0.30	0.32	0.31	0.00	0.43	0.08	0.10	-0.44										
13	0.11	-0.07	0.11	-0.05	0.29	0.53	0.21											
12	0.28	0.04	0.39	-0.06	0.17	0.26												
11	0.43	0.32	0.42	-0.04	0.42													
10	0.35	0.17	0.20	-0.13														
8	-0.32	0.00	0.17															
4	0.69	0.37																
3	0.36																	

24	25	26	27	29	32	34	37	38	41
0.35	0.39	0.34	0.28	0.22	0.17	0.05	0.04	0.29	0.45
0.30	0.32	0.30	0.24	0.34	0.29	0.10	0.22	0.12	
0.12	0.12	0.01	-0.04	0.25	0.19	0.04	0.18		
0.14	0.06	0.09	0.09	0.36	0.46	0.25			
0.07	-0.02	0.00	0.01	-0.03	0.66				
0.23	0.24	0.03	0.00	0.68					
0.23	0.34	0.04	-0.02						
0.44	0.44	**0.96**							
0.49	0.50								
0.82									

C. demissa, *C. viridula*, *C. lepidocarpa*, and *C. flava* s.s., respectively (Fig. 1). Cluster B (*C. viridula*) includes specimens representing both varieties: the typical var. *viridula* and the smaller-sized var. *pulchella*. Hybrid

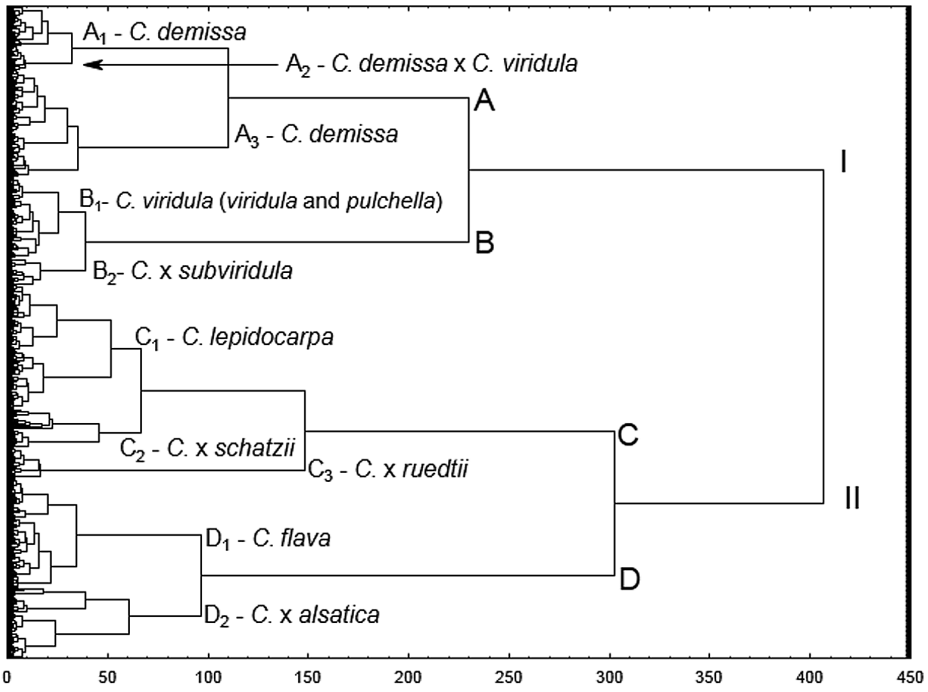

Fig. 1. Ward's hierarchical clustering of taxa of the *Carex flava* group, based on Euclidean distances
Explanations: I – taxa with straight utricle beaks, II – taxa with curved utricle beaks, A – cluster with *C. demissa*, B – cluster with *C. viridula* (var. *viridula* and var. *pulchella*), C – cluster with *C. lepidocarpa*, D – cluster with *C. flava*

24	25	26	27	29	32	34	37	38	41
0.03	0.16	0.13	0.20	0.28	0.33	0.20	0.30	0.45	0.31
0.17	0.49	0.12	0.16	0.66	0.55	0.06	0.74	0.22	
0.19	0.19	0.32	0.33	0.17	0.18	0.12	0.34		
0.30	0.64	0.15	0.17	0.77	0.67	0.09			
-0.07	0.02	-0.04	0.06	0.11	0.56				
0.30	0.59	0.13	0.17	**0.87**					
0.39	0.71	0.17	0.17						
0.42	0.27	0.76							
0.46	0.27								
0.60									

specimens are located in the cluster of one of the putative parents, morphologically closer, or fill the phenetic space between 2 putative parental forms. Cluster analysis indicates also that the analysed species of the *C. flava* complex are divided into those with a straight beak (cluster I), i.e. *C. demissa* and *C. viridula*, and whose with a curved beak (cluster II), i.e. *C. lepidocarpa* and *C. flava* s.s. (Fig. 1).

Discriminant function analysis (DFA) also clearly separated the analysed species (Fig. 2). The high phenetic coherence of taxa is confirmed by a high percentage of similarity between observed classifications (defined *a priori*) and classifications resulting from DFA, forming a matrix of classifications (Table 4). For well-defined taxa, the similarity ranged from 88.9% for *C. viridula* var. *pulchella* to 98.0% for *C. flava* and *C. demissa*.

The first 3 discriminant functions explain 93% of the variation (Fig. 2). Discriminant axes are most strongly affected by utricle length, beak length, and their ratio (UL, UBL, and B/U). Mutual relations between taxa are well illustrated by their distribution along the first 3 discriminant axes. The first discriminant function

(D)

Character	1	3	4	8	10	11	12	13	14	15	16	17	18	19	20	21	22	23
42	0.18	0.05	0.17	-0.05	0.28	0.35	0.10	0.16	-0.16	0.21	0.15	0.26	0.16	0.03	0.26	0.00	0.18	-0.14
41	0.18	0.19	0.09	-0.08	0.41	0.46	0.13	0.29	-0.14	0.28	0.23	0.36	0.31	0.07	0.32	0.24	0.25	-0.18
38	0.15	0.03	0.17	-0.08	0.28	0.36	-0.06	0.25	-0.18	0.23	0.13	0.16	0.19	0.02	0.28	0.04	0.18	0.00
37	0.26	0.22	0.21	-0.08	0.31	0.42	0.10	0.39	-0.29	0.38	0.13	0.34	0.49	-0.02	0.29	0.21	0.28	-0.12
34	0.06	-0.02	0.08	0.04	0.11	0.14	0.10	0.12	0.03	0.05	0.07	0.23	0.10	0.03	0.14	0.09	0.06	0.04
32	0.30	0.20	0.23	-0.12	0.25	0.34	0.10	0.28	-0.13	0.27	0.09	0.42	0.57	-0.02	0.27	0.29	0.19	-0.09
29	0.36	0.30	0.24	-0.19	0.26	0.33	0.06	0.29	-0.18	0.32	0.09	0.41	0.68	-0.04	0.26	0.33	0.24	-0.15
27	0.17	0.00	0.08	-0.08	0.37	0.38	0.15	0.09	-0.07	0.22	0.35	0.20	0.11	0.14	0.39	0.17	0.31	-0.01
26	0.31	0.06	0.18	-0.16	0.41	0.47	0.10	0.20	-0.15	0.27	0.34	0.24	0.18	0.08	0.48	0.10	0.35	0.01
25	0.33	0.41	0.25	-0.12	0.25	0.49	0.13	0.46	-0.38	0.52	-0.01	0.52	0.74	-0.08	0.25	0.36	0.20	-0.09
24	0.32	0.24	0.28	-0.04	0.33	0.61	0.15	0.55	-0.51	0.64	0.05	0.54	0.50	-0.06	0.35	0.23	0.22	-0.08
23	0.24	0.00	0.41	0.00	-0.28	-0.12	-0.13	-0.11	0.18	-0.23	-0.14	0.06	-0.01	-0.05	0.27	-0.08	0.03	
22	0.18	0.11	0.16	-0.14	0.39	0.18	0.11	0.12	0.07	0.10	0.39	0.22	0.13	0.27	0.50	0.31		
21	0.09	0.55	0.14	0.01	0.39	0.13	0.16	0.08	0.19	0.08	0.35	0.36	0.27	0.25	0.32			
20	0.55	0.18	0.68	-0.10	0.67	0.48	0.07	0.18	0.14	0.19	0.58	0.45	0.24	0.30				
19	0.07	0.13	0.08	-0.05	0.34	-0.02	-0.03	-0.13	0.25	-0.06	0.39	0.07	-0.13					
18	0.45	0.33	0.37	-0.16	0.14	0.43	0.11	0.32	-0.24	0.35	-0.08	0.57						
17	0.47	0.34	0.53	-0.05	0.32	0.51	0.26	0.30	-0.02	0.23	0.12							
16	0.14	0.14	0.13	-0.10	**0.81**	0.21	0.08	-0.07	0.36	0.01								
15	0.20	0.09	0.09	-0.06	0.34	0.62	-0.03	0.61	**-0.80**									
14	-0.04	0.07	0.09	0.05	0.07	-0.45	0.17	-0.56										
13	0.22	0.12	0.15	-0.10	0.25	0.56	-0.08											
12	-0.01	0.10	-0.04	0.06	0.09	0.04												
11	0.45	0.11	0.34	-0.15	0.54													
10	0.27	0.20	0.24	-0.09														
8	-0.53	0.01	-0.02															
4	0.72	0.21																
3	0.14																	

clearly distinguishes *C. flava*, whose canonical means are positive, from the other taxa, whose canonical means are negative. The second function highlights the phenetic distinctness of *C. lepidocarpa* (Fig. 2A). Along the second axis, coordinates for *C. lepidocarpa* are positive, whereas for the other taxa they are negative. The third discriminant function separates *C. demissa*, but the third axis explains only 13% of the total variation (Fig. 2B). DFA performed after exclusion of *C. flava* s.s., shows a clear morphological distinctness of the group of speci-

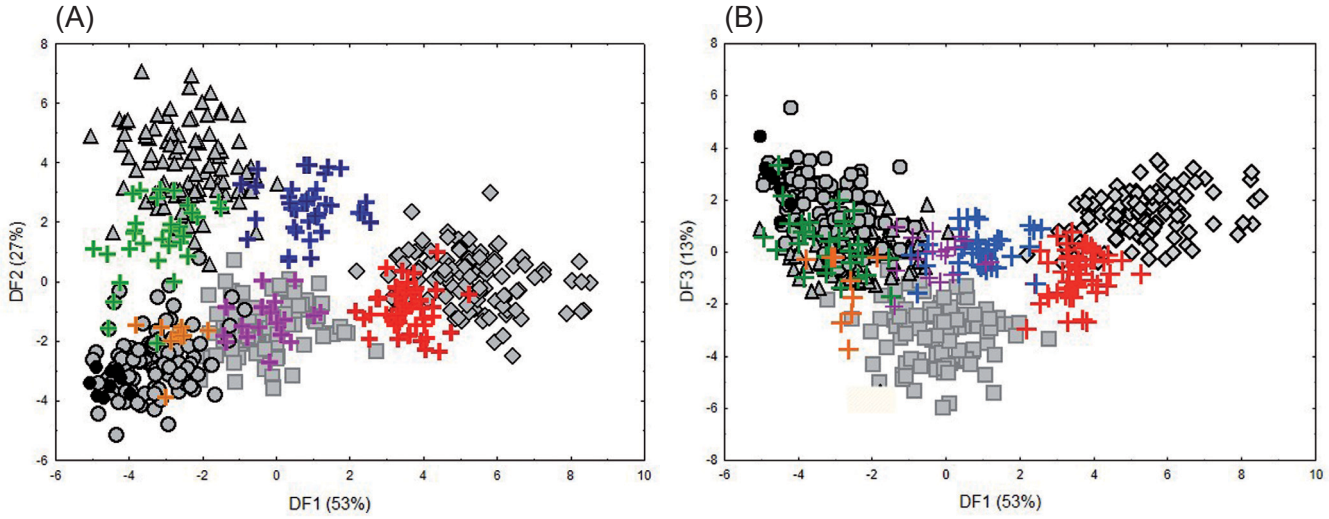

Fig. 2. Results of discriminant analysis (DFA) for the whole dataset of the *Carex flava* group: (A) along axes DF1 and DF2; (B) along axes DF1 and DF3

Explanations: ◇ – *C. flava*, ○ – *C. viridula* var. *viridula*, ● – *C. viridula* var. *pulchella*, □ – *C. demissa*, △ – *C. lepidocarpa*, + – *C.* ×*alsatica*, + – *C.* ×*ruedtii*, + – *C.* ×*schatzii*, + – *C.* ×*subviridula*, + – *C. demissa* × *C. viridula*. Loadings for the first axis (only absolute values > 0.50 are given, characters abbreviated as in Table 2): UL = 0.68, UBL = 1.47. Loadings for the second axis: UBL = -1.19, U/B = 0.60, UL = 1.29. Loadings for the third axis: UBL = 2.11, MGL = -0.66, B/U = -1.46, UL = -1.46

24	25	26	27	29	32	34	37	38	41
0.22	0.15	0.27	0.18	0.29	0.24	0.04	0.38	0.40	0.55
0.41	0.41	0.38	0.28	0.45	0.42	0.15	0.55	0.39	
0.29	0.28	0.21	0.15	0.30	0.21	-0.05	0.55		
0.48	0.54	0.27	0.15	0.60	0.55	0.19			
0.12	0.14	0.17	0.15	0.15	0.64				
0.43	0.61	0.25	0.18	**0.83**					
0.47	0.70	0.19	0.12						
0.21	0.20	**0.85**							
0.29	0.23								
0.72									

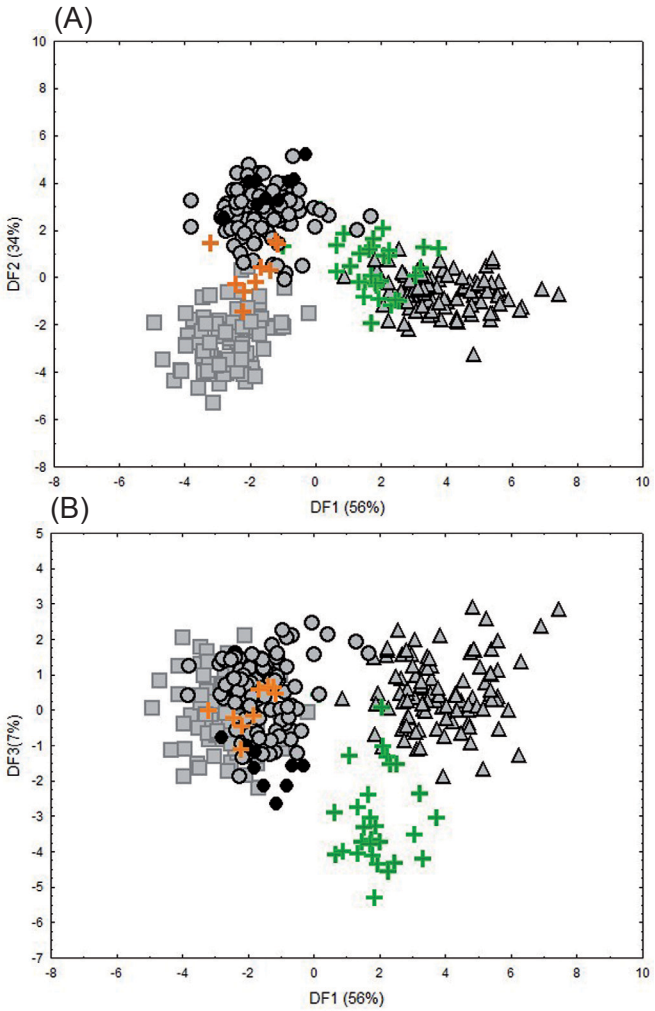

Fig. 3. Results of discriminant analysis (DFA) for a reduced dataset (after exclusion of *Carex flava* and its hybrids): (A) along axes DF1 and DF2; (B) along axes DF1 and DF3
Explanations: ○ – *C. viridula* var. *viridula*, ● – *C. viridula* var. *pulchella*, □ – *C. demissa*, △ – *C. lepidocarpa*, + – *C.* ×*schatzii*, + – *C. demissa* × *C. viridula*. Loadings for the first axis (only absolute values > 0.50 are given, characters abbreviated as in Table 2): UL = 1.04, UBL = -0.99, CH = 0.74, SBW = -0.65. Loadings for the second axis: B/U = -0.76. Loadings for the third axis: LBL = -0.97, UL = 0.90, UBL = -0.67, SBL = 0.58, LBW = 0.57, NFS = 0.56, CH = 0.54

mens of *C. lepidocarpa*, especially along the first axis, explaining 56% of the variation (Fig. 3). The first axis is most strongly affected by utricle characters (UL and UBL), culm height (CH), and second female spike bract width (SBW). The second axis separates *C. demissa*

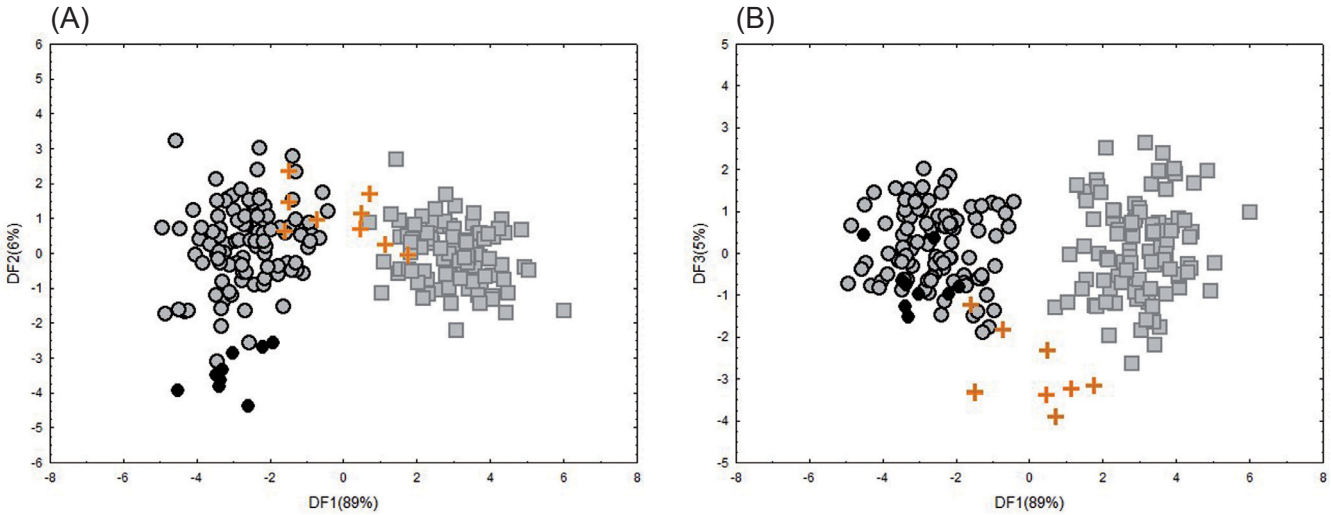

Fig. 4. Results of discriminant analysis (DFA) for a reduced dataset (after exclusion of *Carex flava*, *C. lepidocarpa*, and their hybrids): (A) along axes DF1 and DF2; (B) along axes DF1 and DF3
Explanations: ○ – *C. viridula* var. *viridula*, ● – *C. viridula* var. *pulchella*, □ – *C. demissa*, + – *C. demissa* × *C. viridula*. Loadings for the first axis (only absolute values > 0.50 are given, characters abbreviated as in Table 2): B/I = -0.60, UBL = 0.58. Loadings for the second axis: UBL = -3.49, UL = 3.25, B/U = 1.99, NFS = 0.76, SBL = 0.72. Loadings for the third axis: UL = -0.97, UBL = 0.92, LFSW = 0.62, UFSW = 0.53

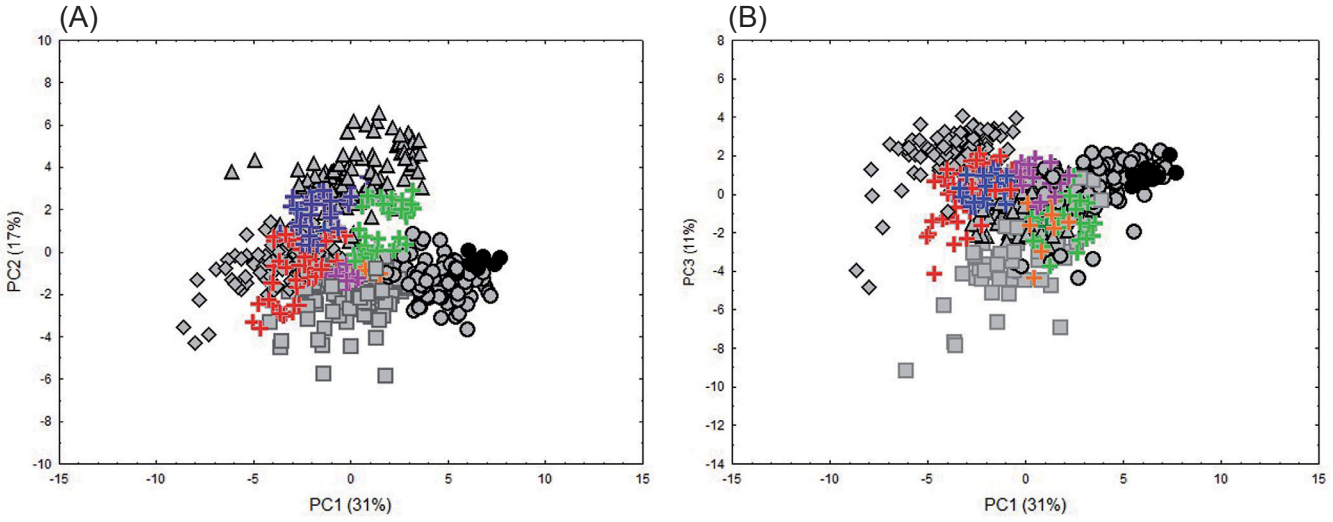

Fig. 5. Results of principal component analysis (PCA) for the whole dataset: (A) along axes PC1 and PC2; (B) along axes PC1 and PC3
Explanations: ◇ – *C. flava*, ○ – *C. viridula* var. *viridula*, ● – *C. viridula* var. *pulchella*, □ – *C. demissa*, △ – *C. lepidocarpa*, + – *C.* ×*alsatica*, + – *C.* ×*ruedtii*, + – *C.* ×*schatzii*, + – *C.* ×*subviridula*, + – *C. demissa* × *C. viridula*. Loadings for the first axis (only absolute values > 0.50 are given, characters abbreviated as in Table 2): CH = -0.53, CLW = -0.75, CLL = -0.66, MSL = -0.59, LFSL = -0.80, LFSW = -0.85, LBL = -0.64, LBW = -0.57, UFSL = -0.70, UFSW = -0.69, SBL = -0.55, UL = -0.87, UBL = -0.87, B/U = -0.74, FGL = -0.82, FGW = -0.56, MGL = -0.56). Loadings for the second axis: CH = 0.56, MPL = 0.70, NFS = -0.82, DLFS = -0.55, LBW = -0.66, SBL = -0.58, SBW = -0.68). Loadings for the third axis: C/L = 0.50, IL = -0.83, DLFS = -0.64, LBSL = -0.67, B/I = 0.79

from *C. viridula*, mostly on the basis of the ratio of beak length to utricle length (B/U) (Fig. 3A). The next discriminant analysis, performed after exclusion of *C. flava* and *C. lepidocarpa*, confirms the morphological separateness of *C. demissa* (Fig. 4). The most significant first axis explains 89% of the variance. It is primarily associated with utricle beak length (UBL) and the ratio of lowest female spike bract length to inflorescence length (B/I). *C. demissa* has longer beaks than *C. viridula*, as their mean values are 1.3 mm and 0.9 mm, respectively. The lowest female spike bracts in specimens of *C. demissa* are usually as long as the inflorescence, whereas in specimens of *C. viridula* they are usually much longer; however, bract length in specimens of *C. demissa* is highly variable (V_3 = 49%) (Table 2).

The analysed taxa are poorly segregated by principal component analysis (PCA), with the first, second, and third component explaining 31%, 17%, and 11% of the variance (Fig. 5). Along the first axis, specimens of *C. flava* s.s. and *C. viridula* form 2 clearly separate

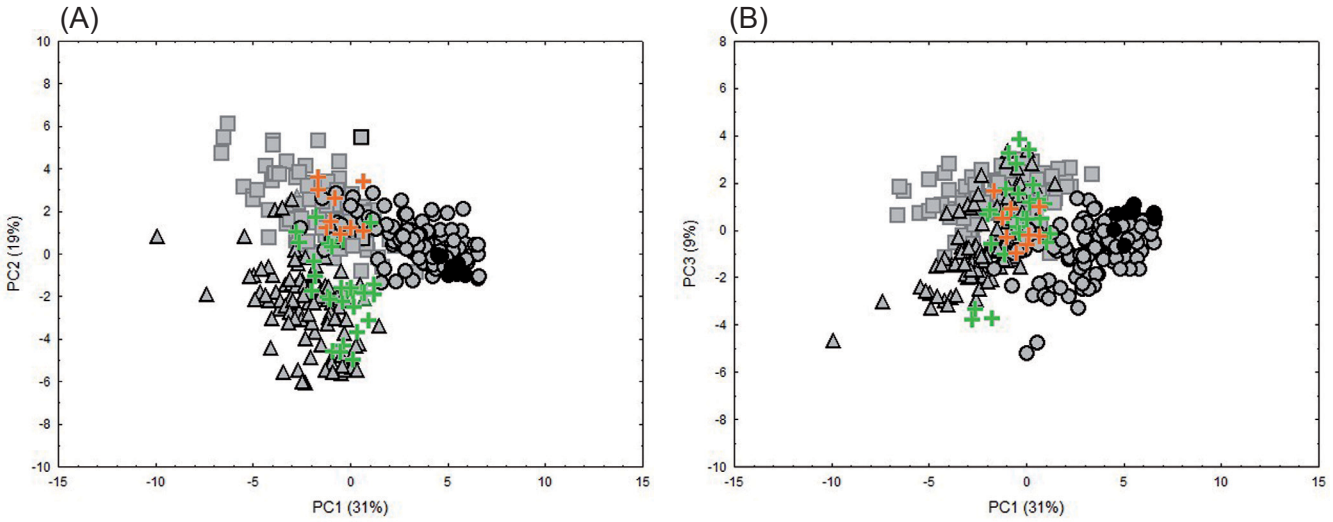

Fig. 6. Results of principal component analysis (PCA) for a reduced dataset (after exclusion of *Carex flava* and its hybrids): (A) along axes PC1 and PC2; (B) along axes PC1 and PC3
Explanations: ○ – *C. viridula* var. *viridula*, ● – *C. viridula* var. *pulchella*, □ – *C. demissa*, △ – *C. lepidocarpa*, + – *C.* ×*schatzii*, + – *C. demissa* × *C. viridula*. Loadings for the first axis (only absolute values > 0.50 are given, characters abbreviated as in Table 2): CH = -0.68, CLW = -0.60, C/L = 0.61, IL = -0.56, MSL = -0.77, MPL = -0.54, LFSL = -0.79, LFSW = -0.81, UL = -0.86, UBL = -0.85, B/U = -0.56, FGL = -0.78, FGW = -0.62, MGL = -0.63. Loadings for the second axis: IL = 0.50, MPL = -0.55, NFS = 0.78, DLFS = 0.67, LBL = 0.62, LBW = 0.86, LBSL = 0.51, SBL = 0.78, SBW = 0.82. Loadings for the third axis: CLL = -0.73, B/U = 0.56

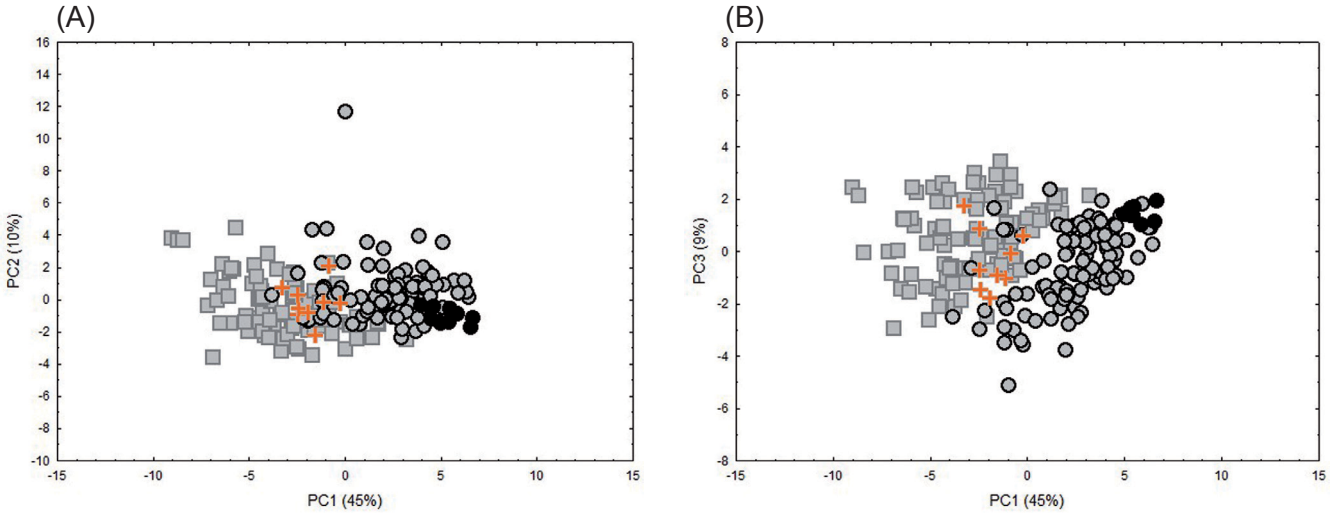

Fig. 7. Results of principal component analysis (PCA) for a reduced dataset (after exclusion of *Carex flava*, *C. lepidocarpa,* and their hybrids): (A) along axes PC1 and PC2; (B) along axes PC1 and PC3
Explanations: ○ – *C. viridula* var. *viridula*, ● – *C. viridula* var. *pulchella*, □ – *C. demissa*, + – *C. demissa* × *C. viridula*. Loadings for the first axis (only absolute values > 0.50 are given, characters abbreviated as in Table 2): CH = -0.72, CLW = -0.71, C/L = 0.59, IL = -0.67, MSL = -0.77, MPL = -0.65, DLFS = -0.60, LFSL = -0.75, LFSW = -0.83, LBL = -0.56, LBW = -0.76, B/I = 0.54, UFSL = -0.84, UFSW = -0.86, SBL = -0.67, SBW = -0.75, UL = -0.87, UBL = -0.87, B/U = -0.70, FGL = -0.83, FGW = -0.67, MGL = -0.77, MGW = -0.64. Loadings for the second axis: IL = 0.50, NFS = 0.78, DLFS = 0.53, LPL = 0.60, LBSL = 0.66. Loadings for the third axis: CLL = -0.85, LBL = -0.53, B/I = -0.67

groups. The first component is most strongly related to characters concerning utricle and beak size (UL, UBL, and B/U) as well as dimensions of female spikes (LFSL, LFSW, UFSL, and UFSW) (Fig. 5). *C. flava* s.s. has the longest utricles and beaks, and the largest female spikes among members of the *C. flava* complex (in contrast to *C. viridula*) (Table 2). The second component distinguishes *C. lepidocarpa* from *C. demissa* and is associated with vegetative characters, especially dimensions of bracts (LBL, LBW, SBL, and SBW), culm height (CH), male spike peduncle length (MPL), and number and arrangement of female spikes (NFS, DLFS) (Fig. 5A). *C. lepidocarpa* has relatively short and narrow bracts, long peduncles of male spikes, and usually 2 distant female spikes (Table 2). Along the third component, the most conspicuous division is visible between specimens of *C. flava* and *C. lepidocarpa*, resulting mostly from differences in inflorescence length (IL) and ratio of lowest female spike bract length to inflorescence length (B/I) (Fig. 5B;

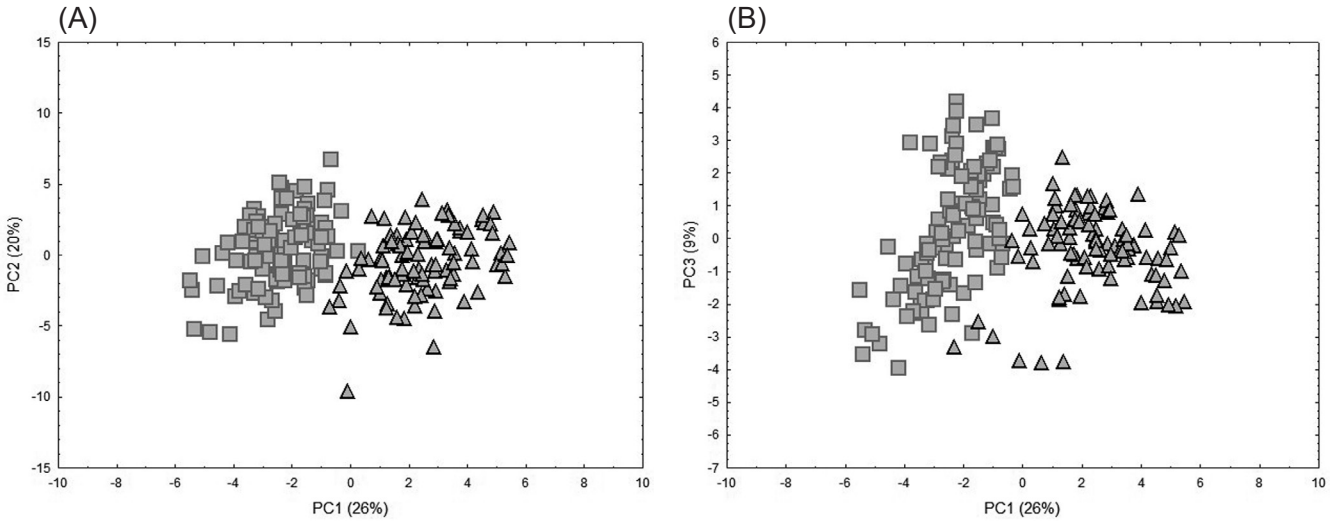

Fig. 8. Results of principal component analysis (PCA) for a reduced dataset (after exclusion of *Carex flava*, *C. viridula*, and their hybrids): (A) along axes PC1 and PC2; (B) along axes PC1 and PC3
Explanations: □ – *C. demissa*, △ – *C. lepidocarpa*. Loadings for the first axis (only absolute values > 0.50 are given, characters abbreviated as in Table 2): CH = 0.72, IL = -0.51, MPL = 0.64, NFS = -0.85, DLFS = -0.69, LFSW = 0.59, LBL = -0.53, LBW = -0.86, LBSL = -0.56, SBL = -0.79, SBW = -0.89, B/U = -0.64. Loadings for the second axis: CLL = -0.63, MSL = -0.63, LFSL = -0.70, LFSW = -0.61, LFPL = -0.58, LBL = -0.66, UL = -0.63, FGL = -0.51. Loadings for the third axis: IL = -0.65, DLFS = -0.51, LBSL = -0.53, B/I = 0.76

Table 4. Results of discriminant analysis of taxa of the *Carex flava* group, presented as a matrix of classifications

	Number and percentage of specimens classified into groups distinguished by DFA									
Taxon	D	L	V	F	P	Sch	A	R	DxV	Sub
D	98	0	0	0	0	0	0	0	2	0
	98.0%	0	0	0	0	0	0	0	2.0%	0
L	0	97	0	0	0	1	0	2	0	0
	0	97.0%	0	0	0	1.0%	0	2.0%	0	0
V	1	0	94	0	4	0	0	0	1	0
	1.0%	0	94.0%	0	4.0%	0	0	0	1.0%	0
F	0	0	0	98	0	0	2	0	0	0
	0	0	0	98.0%	0	0	2.0%	0	0	0
P	0	0	1	0	8	0	0	0	0	0
	0	0	11.1%	0	88.9%	0	0	0	0	0
Sch	0	2	2	0	0	27	0	0	0	0
	0	7.6%	7.6%	0	0	84.8%	0	0	0	0
A	0	0	0	1	0	0	51	0	0	0
	0	0	0	1.9%	0	0	98.1%	0	0	0
R	0	1	0	1	0	0	0	38	0	0
	0	2.5%	0	2.5%	0	0	0	95.0%	0	0
DxV	1	0	1	0	0	0	0	0	7	0
	11.1%	0	11.1%	0	0	0	0	0	77.8%	0
Sub	1	0	1	1	0	0	0	0	0	15
	5.5%	0	5.5%	5.5%	0	0	0	0	0	83.3%

Explanations: A – *C.* ×*alsatica*, D – *C. demissa*, D×V – *C. demissa* × *C. viridula*, F – *C. flava* s.s., L – *C. lepidocarpa*, P – *C. viridula* var. *pulchella*, R – *C.* ×*ruedtii*, Sch – *C.* ×*schatzii*, Sub – *C.* ×*subviridul*a, V – *C. viridula* var. *viridula*

Table 2). Distribution of specimens of *C. viridula* in the phenetic space is consistent with the results of Ward's hierarchical clustering, as specimens of *C. viridula* var. *viridula* and var. *pulchella* form one cluster (Figs. 1 and 5).

PCA conducted on a reduced data set (after exclusion of *C. flava* s.s. and its hybrids) shows morphological distinctness of specimens of *C. viridula* along the first axis, which is mostly affected by utricle length (UL) and beak length (UBL) (Fig. 6). The second component distinguishes *C. lepidocarpa* from *C. demissa* mostly on the basis of bract dimensions (LBL, LBW, SBL, and SBW), number of female spikes (NFS), and distance between 2 lowest female spikes (DLFS) (Fig. 6A). Along the third component, taxa are not segregated and form one cluster (Fig. 6B). Successive steps of PCA revealed that (*i*) *C. demissa* differs significantly from *C. viridula* in dimensions of utricles (UL, UBL, and B/U), glumes (FGL, FGW, MGL, and MGW), size and distribution of female spikes (LFSL, LFSW, UFSL, UFSW, IL, DLFS), length of male spikes and their peduncles (MSL and MPL), size of bracts and leaves (LBL, LBW, SBL, SBW, CLW, C/L), and culm height (CH) (Fig. 7; Table 2), (*ii*) *C. demissa* differs significantly from *C. lepidocarpa* in dimensions of bracts (LBL, LBW, SBL, and SBW), ratio of beak length to utricle length (B/U), number and arrangement of female spikes (NFS, DLFS, IL), male spike length (MSL), and culm height (CH) (Fig. 8; Table 2).

Results of ANOVA indicate that the analysed species vary significantly in all the analysed characters ($p \leq 0.001$) (Table 5). *F* values are the highest for utricle and beak characters (UBL, B/U, UL), dimensions of female spikes (LFSL, LFSW, UFSL, and UFSW), culm height (CH), bract width (SBW and LBW), glume length (FGL and MGL), male spike peduncle length (MPL), and ratio of lowest female spike bract length to inflorescence length (B/I) (Table 5). The *post hoc* Spjotvoll/Stoline test detected no significant differences between varieties of *C. viridula* (var. *viridula* and var. *pulchella*), except for cauline leaf length (CLL), number of female spikes (NFS), lowest female spike bract length (LBL), and utricle length (UL). The other taxa differ significantly ($p \leq 0.001$) in culm height (CH), width of female spikes (UFSW and LFSW), utricle length (UL), and ratio of beak length to utricle length (B/U) (Table 5). The longest utricles and widest female spikes are found in specimens of *C. flava*, the shortest beaks are in *C. viridula*, the highest ratio of beak length to utricle length is in *C. demissa*, whereas the longest culms, narrowest bracts and longest male spike peduncles are in *C. lepidocarpa* (Fig. 9; Table 2).

In delimitation of taxa from the *C. flava* group, a significant role is played primarily by the length of

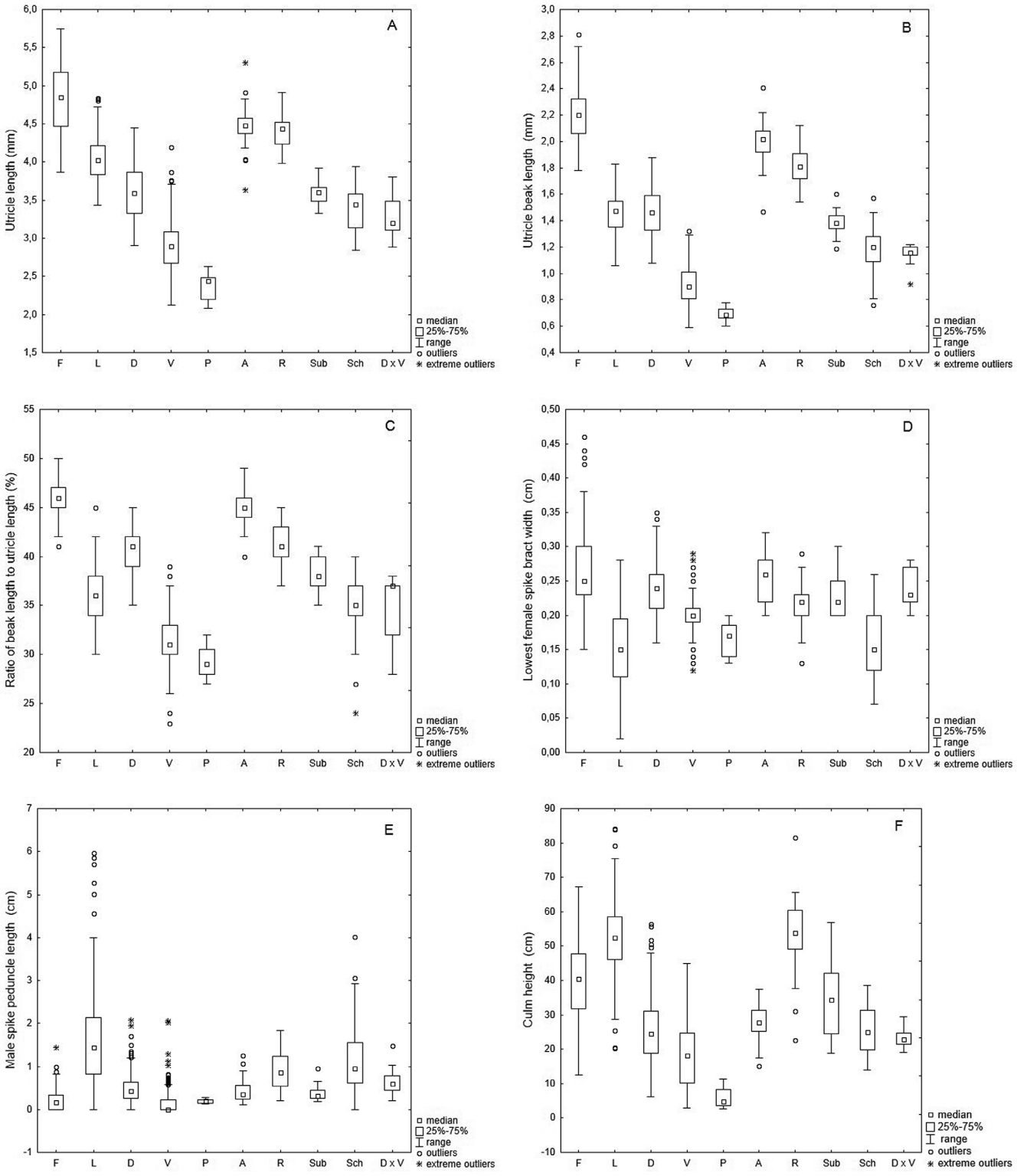

Fig. 9. Comparison of dimensions of selected morphological characters of taxa and hybrids of the *Carex flava* group.
Explanations: A – *C.* ×*alsatica*, D – *C. demissa*, D×V – *C. demissa* × *C. viridula*, F – *C. flava* s.s., L – *C. lepidocarpa*, P – *C. viridula* var. *pulchella*, R – *C.* ×*ruedtii*, Sch – *C.* ×*schatzii*, Sub – *C.* ×*subviridula*, V – *C. viridula*

utricle and its beak. The mean length of utricle and beak declines in the following order: *C. flava*, *C. lepidocarpa*, *C. demissa*, *C. viridula* var. *viridula*, and *C. viridula* var. *pulchella* (Fig. 9A-B; Appendix 3). The ratio of beak length to total utricle length (B/U) is also characteristic of the analysed taxa and its value declines from *C. flava* to *C. viridula* in a similar order, except *C. demissa*, B/U = 40%, and *C. lepidocarpa*, B/U = 36%, whose sequence is reverse) (Fig. 9C).

In summary, statistical analyses show clear (especially in DFA) morphological differences between species of the *C. flava* complex. Only *C. viridula* includes

Table 5. Results of one-way analysis of variance (ANOVA) and the *post hoc* Tukey HSD test for unequal *N* (Spjotvoll/Stoline test), showing significance of differences in morphological characters of taxa of the *Carex flava* group

	ANOVA		*Post hoc* Spjotvoll/Stoline test									
			F-L	F-D	F-V	F-P	L-D	L-V	L-P	D-V	D-P	V-P
Character	*F*	*p*	*p*	*p*	*p*	*p*	*p*	*p*	*p*	*p*	*p*	*p*
CH	373.69	***	***	***	***	***	***	***	***	***	***	ns
CLW	158.09	***	***	***	***	***	**	***	*	***	***	ns
CLL	120.15	***	***	***	***	***	***	ns	***	***	ns	**
C/L	138.96	***	***	***	*	ns	ns	***	***	***	***	ns
IL	51.61	***	***	***	ns	ns	***	***	ns	***	**	ns
MSL	111.78	***	***	ns	***	**	***	***	***	***	*	ns
MSW	40.69	***	***	*	**	ns	***	***	ns	ns	ns	ns
MPL	226.37	***	***	**	ns	ns	***	***	***	***	ns	ns
NFS	123.97	***	***	***	***	ns	***	***	ns	***	ns	**
DUFS	111.12	***	***	ns	*	ns	***	***	***	**	ns	ns
DLFS	38.76	***	*	***	ns	ns	ns	ns	ns	***	ns	ns
LFSL	201.69	***	ns	***	***	***	***	***	***	***	***	ns
LFSW	656.35	***	***	***	***	***	***	***	***	***	***	ns
LPL	10.24	***	ns	ns	***	ns	ns	***	ns	**	ns	ns
LBL	49.47	***	***	***	***	***	***	***	ns	ns	*	*
LBW	164.60	***	***	***	***	***	***	***	ns	***	**	ns
LBSL	11.94	***	ns	***	ns	ns	***	ns	ns	***	ns	ns
B/I	170.37	***	***	***	**	ns	ns	***	ns	***	ns	ns
UFSL	328.18	***	ns	***	***	***	***	***	***	***	**	ns
UFSW	639.74	***	***	***	***	***	***	***	***	***	***	ns
SBL	86.86	***	***	***	***	***	***	**	ns	***	***	ns
SBW	230.48	***	***	ns	***	***	***	***	ns	***	***	ns
UL	757.29	***	***	***	***	***	***	***	***	***	***	*
UBL	1458.16	***	***	***	***	***	ns	***	***	***	***	ns
B/U	866.57	***	***	***	***	***	***	***	***	***	***	ns
FGL	219.14	***	***	***	***	***	ns	***	***	***	***	ns
FGW	72.47	***	ns	ns	***	*	ns	***	ns	***	ns	ns
MGL	179.24	***	ns	***	***	**	***	***	*	***	***	ns
MGW	82.36	***	***	***	ns	ns	ns	***	ns	***	ns	ns

Explanations: D – *C. demissa*, F – *C. flava* s.s., L – *C. lepidocarpa*, P – *C. viridula* var. *pulchella*, V – *C. viridula* var. *viridula*, *F* – value of *F* test, ns – non-significant, *p* – significance level, * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$. Characters abbreviated as in Table 1

2 varieties; one of them, var. *pulchella*, was earlier regarded as a separate species or subspecies within *C. viridula* agg. (see Chater 1980; Schmid 1983; Pykälä & Toivonen 1994; Egorova 1999; Hedrén 2003; Koopman 2011).

3.3. Hybrids within the *Carex flava* agg.

Hybrids formed spontaneously within the *C. flava* group are completely sterile or may be partly fertile and backcross with either of the parental species. The performed classification of OTUs assigned hybrids to separate subgroups (A_2, B_2, C_2, C_3, and D_2) within clusters corresponding to pure species (A, B, C, D) (Fig. 1). Hybrids are morphologically intermediate between the parental taxa or they resemble more closely either of them. Thus cluster analysis indicated which putative parent is more similar to the hybrids in respect of the analysed characters (Fig. 1).

Relations between hybrids and parental taxa are reflected in their distribution in the phenetic space, which is consistent with results of the classification presented in the phenogram (Fig. 1). Distribution of OTUs along the first 3 PCA and DFA axes shows the morphologically intermediate position of hybrids in relation to parents or indicates the parent to which the hybrids are most similar, but PCA separated them less clearly than DFA did (Figs. 2-3). In DFA, phenetic distinctness of hybrids is well-defined, as 77.8-98.1% of OTUs were classified properly (Table 4).

Specimens of *C.* ×*alsatica* are located close to specimens of *C. flava*, which indicates their high phenetic similarity (Fig. 2). Specimens of *C.* ×*ruedtii* fill the space between *C. flava* and *C. lepidocarpa*, but some hybrids are closer to *C. lepidocarpa*. Specimens of *C.* ×*schatzii* are morphologically intermediate between *C. lepidocarpa* and *C. viridula*, or more similar to one

Table 6. Results of one-way analysis of variance (ANOVA) and the *post hoc* Tukey HSD test for unequal *N* (Spjotvoll/Stoline test), showing significance of differences in morphological characters of hybrids of the *Carex flava* group

Character	ANOVA		*Post hoc* Spjotvoll/Stoline test									
			A-R	A-Sch	A-DxV	A-Sub	R-Sch	R-DxV	R-Sub	Sch-DxV	Sch-Sub	DxV-Sub
	F	*p*	*p*	*p*	*p*	*p*	*p*	*p*	*p*	*p*	*p*	*p*
CH	79.24	***	***	ns	ns	ns	***	***	***	ns	**	*
CLW	13.22	***	ns	***	*	**	**	ns	ns	ns	ns	ns
CLL	18.72	***	ns	***	ns	ns	***	*	ns	ns	***	ns
C/L	6.95	***	ns	**	ns	ns	***	ns	ns	ns	**	ns
IL	2.38	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
MSL	6.76	***	ns	**	ns	ns	**	ns	ns	ns	ns	ns
MSW	9.29	***	ns	***	ns	ns	*	ns	ns	ns	***	ns
MPL	17.33	***	***	***	ns	ns	ns	ns	**	ns	***	ns
NFS	13.51	***	**	***	ns	ns	ns	ns	**	**	***	ns
DUFS	10.09	***	ns	***	ns	ns	**	ns	ns	ns	***	ns
DLFS	6.40	***	**	**	ns	ns	ns	*	ns	**	ns	ns
LFSL	16.97	***	ns	***	ns	*	***	**	***	ns	ns	ns
LFSW	105.15	***	ns	***	***	***	***	***	***	**	ns	**
LPL	2.11	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
LBL	10.04	***	**	***	ns	ns	ns	ns	ns	ns	**	ns
LBW	36.18	***	***	***	ns	ns	***	ns	ns	***	***	ns
LBSL	7.86	***	***	ns	ns	ns	***	*	ns	ns	ns	ns
B/I	21.01	***	ns	***	ns	ns	***	ns	ns	ns	***	**
UFSL	15.00	***	ns	***	ns	*	***	ns	**	ns	ns	ns
UFSW	22.51	***	ns	***	ns	ns	***	**	**	ns	ns	ns
SBL	33.32	***	***	***	ns	ns	ns	*	***	***	***	ns
SBW	67.29	***	***	***	ns	ns	***	***	***	***	***	ns
UL	156.26	***	ns	***	***	***	***	***	***	ns	ns	ns
UBL	215.99	***	***	***	***	***	***	***	***	ns	***	**
B/U	107.19	***	***	***	***	***	***	***	*	ns	***	**
FGL	41.33	***	***	***	***	***	***	ns	ns	ns	ns	ns
FGW	8.82	***	*	ns	ns	***	ns	ns	ns	ns	*	*
MGL	20.55	***	ns	***	ns	ns	***	ns	ns	ns	ns	ns
MGW	5.53	***	**	**	ns	ns	ns	ns	ns	ns	ns	ns

Explanations: A – *C.* ×*alsatica*, D×V – *C. demissa* × *C. viridula*, R – *C.* ×*ruedtii*, Sch – *C.* ×*schatzii*, Sub – *C.* ×*subviridula*, *F* – value of *F* test, ns – non-significant, *p* – significance level, * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$. Characters abbreviated as in Table 1

parent, usually to *C. lepidocarpa*. Specimens of *C.* ×*subviridula* in the DFA space along the first 2 axes cover the area between *C. viridula* and *C. flava*, and overlap with a group of specimens of *C. demissa* (Fig. 2). In that case, the classification of OTUs is inconsistent with their distribution in the DFA space. In cluster analysis, specimens of *C.* ×*subviridula* are located in cluster B, dominated by specimens of *C. viridula*. This situation probably results from morphological similarity of *C. viridula*, *C. demissa*, and this hybrid, especially in utricle dimensions, but all specimens of *C.* ×*subviridula* are completely sterile. For the hybrid *C. demissa* × *C. viridula*, also a slight inconsistency was observed between this classification and distribution of OTUs. In the phenogram, hybrids form one cluster with *C. demissa*, whereas in one of the scatterplots they are grouped with *C. viridula*, and in the other one, with *C. demissa* (Fig. 2). However, the phenetic distinctness of hybrids is quite clear in DFA, as the percentage of properly classified specimens reached 77.8% for *C. demissa* × *C. viridula* and 83.3% for *C.* ×*subviridula*. Several specimens of hybrids were classified by DFA to clusters of putative parents, e.g.: one specimen of *C. demissa* × *C. viridula* was grouped with *C. demissa*, while another, with *C. viridula* (Table 4).

Hybrids vary significantly in nearly all the analysed morphological characters (ANOVA, $p \leq 0.001$) (Table 6). The greatest variation was observed in utricle characters (UBL, UL, and B/U), lowest female spike width (LFSW), culm height (CH), and second female spike bract width (SBW), whose *F* values exceeded 50 (Table 6). The *post hoc* Spjotvoll/Stoline test revealed the largest number of significant differences between *C.* ×*alsatica* [*C. flava* × *C. lepidocarpa*] and *C.* ×*schatzii* [*C. lepidocarpa* × *C. viridula*], while the smallest number of differences was between *C.* ×*schatzii* and *C.*

Table 7. Variation of morphological characters of hybrids of the *Carex flava* group

	C. ×*alsatica*					*C.* ×*ruedtii*					*C.* ×*schatzii*					*C. demissa* × *C. viridula*				
Character	*x*	min	max	SD	*V*	*x*	min	max	SD	*V*	*x*	min	max	SD	*V*	*x*	min	max	SD	*V*
CH	28.0	15.2	37.5	5.29	19	53.2	22.7	81.6	9.89	19	25.7	13.9	38.5	6.87	27	23.7	19.1	29.4	3.30	14
CLW	0.3	0.2	0.4	0.03	12	0.3	0.2	0.4	0.04	14	0.2	0.2	0.3	0.04	15	0.2	0.2	0.3	0.01	6
CLL	13.1	6.3	19.7	3.79	29	14.8	8.7	23.1	3.29	22	7.8	3.7	20.1	4.43	57	9.6	7.7	12.4	1.57	16
C/L	2	1	3	0.54	29	2	1	3	0.47	24	1	1	4	0.72	52	2	1	2	0.53	34
IL	6.1	2.5	21.6	3.93	65	4.9	2.9	9.7	1.35	28	5.6	2.6	12.2	2.64	47	8.0	4.6	16.4	4.11	51
MSL	1.7	1.0	2.2	0.28	16	1.7	0.5	2.6	0.36	21	1.4	1.0	1.9	0.24	17	1.7	1.3	2.0	0.20	12
MSW	0.2	0.1	0.2	0.02	11	0.2	0.1	0.2	0.02	11	0.2	0.1	0.2	0.03	15	0.2	0.1	0.2	0.01	9
MPL	0.4	0.0	1.3	0.26	63	0.9	0.0	1.8	0.47	52	1.3	0.0	4.0	0.94	75	0.7	0.2	1.5	0.38	56
NFS	3	2	4	0.58	20	2	1	3	0.54	23	2	1	4	0.68	33	3	2	4	0.50	17
DUFS	0.7	0.2	1.7	0.32	45	1.1	0.0	2.2	0.45	40	2.2	0.3	7.0	1.80	80	0.8	0.4	1.2	0.24	32
DLFS	4.1	1.1	17.2	3.84	94	2.4	1.1	4.5	0.99	42	4.5	2.6	7.1	1.80	40	4.7	0.0	13.2	4.23	90
LFSL	1.3	0.9	1.6	0.16	13	1.3	1.1	1.5	0.10	8	1.1	0.9	1.4	0.13	12	1.1	1.0	1.3	0.09	8
LFSW	0.9	0.7	1.0	0.05	6	0.9	0.8	1.0	0.05	6	0.7	0.6	0.8	0.06	8	0.6	0.5	0.7	0.06	10
LPL	0.3	0.0	0.9	0.28	95	0.2	0.0	1.3	0.28	128	0.5	0.0	3.2	0.68	149	0.1	0.0	0.6	0.19	148
LBL	11.0	3.4	19.9	4.30	39	7.8	3.9	15.9	2.63	34	6.4	1.8	21.7	4.36	68	9.4	7.9	11.1	1.07	11
LBW	0.3	0.2	0.3	0.03	13	0.2	0.1	0.3	0.03	15	0.2	0.1	0.3	0.05	32	0.2	0.2	0.3	0.03	12
LBSL	0.9	0.2	2.8	0.71	80	0.3	0.1	0.8	0.17	54	1.1	0.1	3.0	0.79	72	1.2	0.5	2.0	0.52	44
B/I	3	1	4	0.63	20	3	2	4	0.27	9	2	1	4	0.87	43	2	1	3	0.88	36
UFSL	1.1	0.7	1.4	0.15	14	1.2	1.0	1.5	0.11	9	0.9	0.8	1.3	0.13	13	0.9	0.7	1.0	0.10	11
UFSW	0.8	0.6	1.0	0.06	7	0.9	0.7	0.9	0.05	5	0.7	0.6	0.8	0.06	9	0.6	0.6	0.7	0.03	5
SBL	5.2	2.2	9.6	1.73	33	2.9	0.5	5.9	1.51	51	1.7	0.6	5.4	1.54	89	5.1	4.2	4.8	0.65	13
SBW	0.2	0.1	0.2	0.03	17	0.1	0.0	0.2	0.04	48	0.1	0.0	0.1	0.03	49	0.2	0.1	0.2	0.02	16
UL	4.5	3.6	5.3	0.24	5	4.4	4.0	4.9	0.23	5	3.4	2.8	3.9	0.29	8	3.3	2.9	3.8	0.30	9
UBL	2.0	1.5	2.4	0.14	7	1.8	1.5	2.1	0.14	8	1.2	0.8	1.6	0.19	16	1.1	0.9	1.2	0.09	8
B/U	45	40	49	1.57	3	41	37	45.0	2.01	5	35	24	40	3.49	10	35	28	38	3.61	10
FGL	2.9	2.4	3.5	0.20	7	2.6	1.7	3.1	0.19	7	2.4	2.0	2.9	0.23	10	2.5	2.3	2.8	0.12	5
FGW	1.6	1.3	1.8	0.12	8	1.5	1.2	1.7	0.09	6	1.5	1.2	1.8	0.14	10	1.6	1.3	1.8	0.13	8
MGL	3.7	3.1	4.1	0.21	6	3.6	3.4	4.5	0.20	5	3.3	2.8	3.9	0.27	8	3.5	3.3	3.6	0.11	3
MGW	1.6	1.3	1.9	0.16	10	1.7	1.3	2.3	0.18	11	1.7	1.4	2.0	0.16	10	1.6	1.5	1.7	0.09	5

Explanations: *x* – arithmetic mean, min and max – minimum and maximum values, SD – standard deviation, *V* – coefficient of variation for individual hybrid. Characters abbreviated as in Table 1

demissa × *C. viridula*, and between *C.* ×*subviridula* [*C. flava* × *C. viridula*] and *C. demissa* × *C. viridula* (Table 6).

In the delimitation of hybrids from the *C. flava* group, as in the case of pure species, a significant role is played by the length of utricle and its beak (Appendix 2). These characters are morphologically the least variable and can be used effectively to distinguish among hybrids and between hybrids and their putative parents (Tables 2

Table 8. Values of soil parameters at sites of taxa of the *Carex flava* group

Soil parameters	Taxon							
	C. flava s.s.		*C. lepidocarpa*		*C. demissa*		*C. viridula*	
	x	min-max	*x*	min-max	*x*	min-max	*x*	min-max
C (%)	14.4	1.7-39.7	25.4	11.6-40.7	8.7	1.7-37.5	10.4	0.03-40.7
N (%)	1.1	0.1-3.01	1.6	0.21-3.0	0.6	0.1-2.9	0.6	0.01-2.8
Org. mat. (%)	25.1	2.9-68.5	36.8	0.0-64.2	15.1	2.9-64.6	14.8	0.0-64.2
pH	5.9	3.8-7.6	7.0	5.5-7.9	4.8	3.8-7.1	6.2	4.2-8.1
P ($mg \cdot kg^{-1}$)	18.9	5.3-58.9	14.8	0.0-45.8	18.6	6.5-32.7	15.8	4.4-52.3
K ($mg \cdot kg^{-1}$)	93.3	21.4-250.1	68.7	16.9-318.9	123.0	7.9-250.1	57.7	16.2-244.6
Mg ($mg \cdot kg^{-1}$)	597.4	37.6-4207.9	1119.9	95.6-3366.6	573.9	35.7-4005.2	928.8	29.7-4005.2
Ca ($mg \cdot kg^{-1}$)	8752.6	105.6-62834.9	34826.6	93.7-110048.9	4389.4	6.3-21066.6	21360.8	45.0-136017.0
$CaCO_3$ (%)	5.2	0.0-58.8	30.1	0.0-85.0	1.1	0.0-16.4	14.6	0.0-93.9

Explanations: C – carbon, N – nitrogen, Org. mat. – organic matter content, pH – soil pH, P – exchangeable phosphorus, K – exchangeable potassium, Mg – exchangeable magnesium, Ca – exchangeable calcium, $CaCO_3$ – carbonates, *x* – arithmetic mean, min and max – minimum and maximum values

C. ×*subviridula*				
x	min	max	SD	*V*
34.7	18.9	56.9	11.96	34
0.2	0.2	0.3	0.04	15
14.3	7.5	21.6	4.04	28
2	2	3	0.24	11
5.1	2.2	13.5	3.04	60
1.5	0.9	2.0	0.27	18
0.2	0.1	0.2	0.02	10
0.3	0.0	1.0	0.26	100
3	2	5	0.76	24
0.6	0.2	1.2	0.25	42
2.7	0.8	9.5	2.82	103
1.1	0.8	1.4	0.14	13
0.7	0.6	0.9	0.05	8
0.3	0.0	1.3	0.36	107
11.0	4.9	16.8	3.03	27
0.2	0.2	0.3	0.03	13
0.8	0.2	4.2	0.92	120
3	2	4	0.62	18
0.9	0.7	1.1	0.13	15
0.7	0.6	0.8	0.07	10
5.7	2.4	11.7	2.55	44
0.2	0.1	0.3	0.04	26
3.6	3.3	3.9	0.14	4
1.4	1.2	1.6	0.10	7
39	35	41	1.98	5
2.5	2.3	2.7	0.12	5
1.4	1.2	1.5	0.10	7
3.6	3.2	3.9	0.24	7
1.6	1.4	1.9	0.10	6

and 7). The measurements and analyses indicate that dimensions of utricle and its beak in hybrids are intermediate between parental taxa. The mean length of utricle and beak declines in the following order: *C.* ×*alsatica*, *C.* ×*ruedtii*, *C.* ×*subviridula*, *C.* ×*schatzii*, and *C. demissa* × *C. viridula* (Fig. 9A-B; Table 7), whereas the ratio of beak length to total utricle length declines from *C.* ×*alsatica* to *C.* ×*schatzii* in a slightly different order: *C.* ×*alsatica*, *C.* ×*ruedtii*, *C.* ×*subviridula*, *C. demissa* × *C. viridula*, and *C.* ×*schatzii* (Fig. 9C; Table 7). Besides, utricles of hybrids are usually pale yellow or pale green soon after their formation and are flattened, usually empty.

3.4. Relationships between taxa and soil parameters

ANOVA revealed significant variation between habitats of taxa of the *C. flava* group in pH ($p \leq 0.001$), $CaCO_3$, C, and organic matter content ($p \leq 0.01$), and Ca, N, and K ($p \leq 0.05$) (Tables 8-9). Most significant differences in soil parameters were found between sites of *C. lepidocarpa* and *C. demissa* (Table 9). In soil samples collected from sites of *C. lepidocarpa*, the pH values as well as concentrations of $CaCO_3$, Ca, C, N, and organic matter were higher than in samples from sites of *C. demissa* (Table 8). No significant differences in soil parameters were detected between sites of *C. flava* and *C. demissa,* and between those of *C. flava* and *C. viridula*. During field research, populations were often mixed, composed of *C. demissa* and *C. flava*, less often of *C. flava* and *C. viridula.* By contrast, specimens of *C. lepidocarpa* and *C. demissa* did not occur together, except for one site (no. 23 in Appendix 1), where *C. demissa* was accompanied by several specimens of *C. lepidocarpa*. The broadest ranges of values of soil parameters were recorded for *C. viridula* (Table 8). It coexists with *C. lepidocarpa* or *C. demissa*, and less often with *C. flava* (Appendix 1).

The ordination diagram shows the location of taxa in the ordination space, the distribution of samples from 80 sites, and vectors of soil parameters (Fig. 10).

Table 9. Results of one-way analysis of variance (ANOVA) and the *post hoc* Tukey HSD test for unequal *N* (Spjotvoll/Stoline test), showing significance of differences in soil conditions at sites of taxa of the *Carex flava* group

Soil parameters	ANOVA		*Post hoc* Spjotvoll/Stoline test											
	all taxa		F-L		F-D		F-V		L-D		L -V		D-V	
	F	*p*	*p*		*p*		*p*		*p*		*p*		*p*	
C (%)	5.760	**	0.085	ns	0.553	ns	0.603	ns	0.003	**	0.007	**	0.989	ns
N (%)	3.873	*	0.414	ns	0.584	ns	0.441	ns	0.038	*	0.043	*	0.999	ns
Org. mat. (%)	4.088	**	0.468	ns	0.541	ns	0.326	ns	0.040	*	0.037	*	0.999	ns
pH	7.422	***	0.031	*	0.347	ns	0.449	ns	0.000	***	0.341	ns	0.026	*
P ($mg \cdot kg^{-1}$)	0.766	ns	0.761	ns	0.999	ns	0.767	ns	0.801	ns	0.994	ns	0.896	ns
K ($mg \cdot kg^{-1}$)	3.242	*	0.794	ns	0.634	ns	0.294	ns	0.184	ns	0.977	ns	0.049	*
Mg ($mg \cdot kg^{-1}$)	1.176	ns	0.594	ns	0.999	ns	0.718	ns	0.561	ns	0.968	ns	0.789	ns
Ca ($mg \cdot kg^{-1}$)	4.758	*	0.063	ns	0.969	ns	0.371	ns	0,021	*	0.564	ns	0.298	ns
$CaCO_3$ (%)	5.486	**	0.020	*	0.953	ns	0.447	ns	0.002	**	0.261	ns	0.049	*

Explanations: D – *C. demissa*, F – *C. flava* s.s., L – *C. lepidocarpa*, P – *C. viridula* var. *pulchella*, V – *C. viridula* var. *viridula*, *F* – value of *F* test, ns – non-significant, *p* – significance level, * p 0.05, ** $p \leq 0.01$, *** $p \leq 0.001$, C – carbon, N – nitrogen, Org. mat. – organic matter content, pH – soil pH, P – exchangeable phosphorus, K – exchangeable potassium, Mg – exchangeable magnesium, Ca – exchangeable calcium, $CaCO_3$ – carbonates

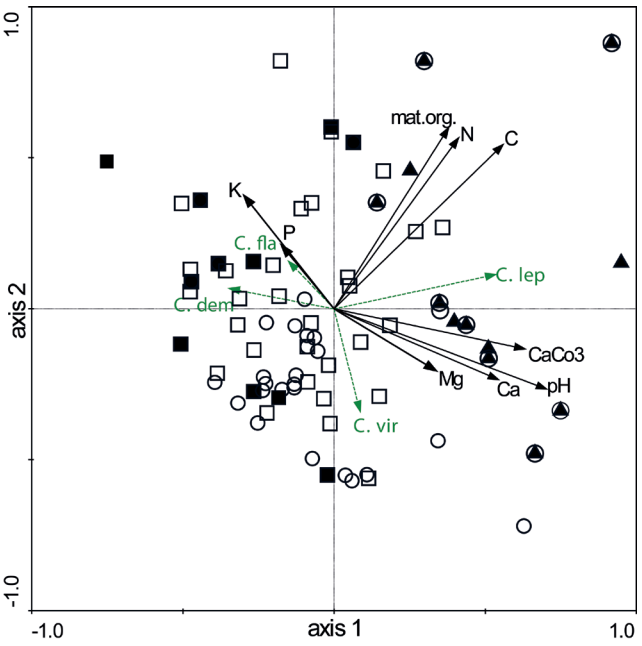

Fig. 10. Ordination diagram (redundancy analysis, RDA) showing correlations between taxa of the *Carex flava* group and soil parameters

Explanations: *C. dem* – *Carex demissa*, *C. lep.* – *Carex lepidocarpa*, *C. vir.* – *Carex viridula*, □ – samples from sites of *C. flava*, ○ – samples from sites of *C. viridula* var. *viridula*, ■ – samples from sites of *C. demissa*, ▲ – samples from sites of *C. lepidocarpa*. Loadings for the first axis: pH = 0.43, $CaCO_3$ = 0.38, C = 0.34, Ca = 0.33, N = 0.25, mat.org. (organic matter) = 0.23, Mg = 0.20, K = -0.18, P = -0.11. Loadings for the second axis: mat. org. (organic matter) = 0.20, N = 0.19, C = 0.18, K = 0.13, pH = -0.09, Ca = -0.08, P = 0.07, Mg = -0.07, $CaCo_3$ = 0.04

Table 10. Results of Monte Carlo permutation test (* $p \leq 0.05$) for taxa of the *Carex flava* group

Soil parameters	Lambda A	*p*	*F*
pH*	0.07	0.004	6.76
C* (%)	0.04	0.010	3.99
N (%)	0.02	0.056	2.64
K (mg•kg-1)	0.01	0.236	1.39
P (mg•kg-1)	0.01	0.388	0.93
Org. mat. (%)	0.02	0.216	1.55
Mg (mg•kg-1)	0.00	0.790	0.56
$CaCO_3$ (%)	0.01	0.706	0.56
Ca (mg•kg-1)	0.00	0.446	0.91

Explanations: C – carbon, N – nitrogen, Org. mat. – organic matter content, pH – soil pH, P – exchangeable phosphorus, K – exchangeable potassium, Mg – exchangeable magnesium, Ca – exchangeable calcium, $CaCO_3$ – carbonates

Along the first ordination axis, correlations between soil parameters and sample location were the highest for pH (Fig. 10). The first axis was less strongly connected with $CaCO_3$, C, and Ca (r = 0. 3840, r = 0.3399, and r = 0.3307, respectively). Along the second ordination axis, only relatively low correlations were recorded, for organic matter content, N, and C (r = 0.2013, r = 0.1899, and r = 0.1826, respectively) (Fig. 10). The test of significance of ordination axes shows a significant relationship between the analysed samples and gradients of canonical axes of RDA (first axis: F = 11.817, p = 0.002; all axes: F = 2.155, p = 0.006). The distribution of samples from sites of *C. lepidocarpa* along the first axis indicates their directly proportional relationship with pH and concentrations of $CaCO_3$, Ca, and C in the soil (in contrast to samples from populations of *C. flava* and especially of *C. demissa*). The distribution of taxa in the diagrams corresponds to observations during field research: mixed populations were usually composed of *C. flava* with *C. demissa*, or *C. lepidocarpa* with *C. viridula*, less often of *C. flava* with *C. lepidocarpa*, or *C. flava* with *C. viridula*, and only rarely of *C. lepidocarpa* with *C. demissa* (Appendix 1; Fig. 10).

The Monte Carlo permutation test ($p \leq 0.05$) shows that pH and organic carbon content are significant in the relationships between taxa and soil parameters. The other soil parameters are statistically not significant in this model but pH affects also some other parameters, e.g. Ca and $CaCO_3$, which are significantly correlated with each other and with soil pH. Values of pH and organic carbon content significantly explain 11% of the total variation in distribution of taxa from the analysed data set: 7% and 4%, respectively (Table 10).

3.5. Key to identification of taxa within the section *Ceratocystis*

The crucial morphological characters concern the utricle and its beak: utricle length, beak length, ratio of beak length to total utricle length, beak curvature, and presence of bristles. Sedges should be fully developed, as only mature utricles, from central parts of spikes, should be used for identification (especially when estimating the ratio of fruit size to utricle size). In the case of a species aggregate, like *C. flava* agg., many morphological characters should be used for identification of individual taxa. Whenever possible, several specimens from the same population should be compared, measured, and mean values of metric characters should be used (Tables 2 and 7).

The key takes into account all taxa of the section *Ceratocystis* (*C. flava* agg., *C. hostiana*, and hybrids) recorded in Poland.

1a All utricles with mature fruits (on fully mature plants) **2**

1b Utricles empty or only 10% to 20(30)% utricles with fully developed fruits.....**7**

2a Loosely tufted plants, with well-developed short rhizomes; female spikes distant, narrowly ovoid to terete,

lowest spike on peduncle of 10-50 mm in length; lowest female spike bract shorter than inflorescence, with sheath of 10-40 mm in length; glumes dark brown, with broad hyaline margin; utricle beak with white membrane at apex.....***Carex hostiana***
2b Tufted plants; female spikes close together, ovoid to spherical, lowest spike more or less distant from others, usually on peduncle of up to 35 mm in length; lowest female spike bract longer, even or slightly shorter than inflorescence; bracts with short sheaths, uppermost bracts usually sheathless; glumes light brown to rusty brown, with usually narrow hyaline margin; utricle beak without white membrane at apex....**3 (*Carex flava* agg.)**

3a Utricles with curved beaks.....**4**
3b Utricles with straight beaks.....**5**

4a Utricles 4-6(6.5) mm long, gradually narrowed into bifid beak, its outer surface usually scabrous (> 5 bristles on each tooth); beak ≥ 1.8 mm long (accounting for ½ of total utricle length); male spike sessile or rarely on peduncle of up to 10(15) mm in length; lowest female spike bract 2-5 times as long as inflorescence, usually 2-4(5) mm wide; cauline leaves usually as long as culm, rarely longer or slightly shorter; ligule well-defined, usually > 3 mm long.....***Carex flava* s.s.**
4b Utricles 3.5-4.5(5) mm long, abruptly narrowed into beak, smooth or with several bristles (< 5 on each tooth) beak ≤ 1.8 mm long (accounting for ⅓ of total utricle length); male spike on peduncle of 2-60 mm in length; lowest female spike bract usually as long as or shorter than inflorescence, rarely up to 1.5 times as long as inflorescence, 1-2(3) mm wide; leaves usually up to ½ as long as culm, rarely as long as or slightly longer than culm; ligule < 2.5 mm.....
Carex lepidocarpa (=*C. lepidocarpa* subsp. *lepidocarpa*)

5a Utricles 3-4(4.5) mm long; beak 0.9-1.8 mm long (accounting for 35-45% of total utricle length); female spikes 2-4(5), uppermost ones close together, lowest spike distant and often located below half the length of culm; male spike usually on peduncle of up to 21 mm in length; culm often slightly bent; leaves usually shorter than culm, rarely as long as or longer than culm.....
.....***Carex demissa***
5b Utricles ≤ 4 mm long; beak ≤ 1.5 mm long (accounting for 23-36% of total utricle length); female spikes 2-6(7), typically clustered below male spike, rarely distant; male spike sessile or rarely on peduncle of variable length; culm erect; leaves usually longer or as long as culm.....**6 (*Carex viridula*)**

6a Utricles 2-4 mm long; beak 0.6-1.3 mm long; female spikes (2)3-6(7), 4-8 mm wide; usually fruit filling < ¾ of utricle body.....***Carex viridula* var. *viridula***

6b Utricles 1.8-2.6 mm long; beak < 1 mm long; female spikes usually 2-3, 4-6 mm wide; fruit completely filling utricle body.....***Carex viridula* var. *pulchella***

7a Utricle beak with white membrane at apex; glumes with wide white membranous margin .....
.....**8 (*C. hostiana* × *C. flava* agg.)**
7b Utricle beak without white membrane at apex; glumes with narrow white membranous margin.....
.....**9 (hybrids within *C. flava* agg.)**

8a Female spikes 8-20 mm long and 5-7.5 mm wide, usually distant from one another; distance between first and second female spike 10-110 mm; male spikes on peduncles of up to 40 mm in length; utricle 3-4 mm long; beak 1-1.6 mm long (accounting for 35-44% of total utricle length).....
.....***Carex* ×*fulva*** [*C. demissa* × *C. hostiana*]
8b Female spikes 7-16 mm long and 6-9 mm wide, usually close together but sometimes distant, distance between first and second female spike 2-40 mm; male spikes on peduncles of up to 20 mm in length; utricle 3.5-4.5 mm long; beak 1.2-1.5 mm long (accounting for 30-38% of total utricle length).....
.....***Carex* ×*leutzii*** [*C. hostiana* × *C. lepidocarpa*]

9a Utricles usually 4-5 mm long; beak ≥ 1.5 mm.....**10**
9b Utricles ≤ 4 mm long; beak ≤ 1.6 mm.....**11**

10a Beak accounting for nearly ½ of total utricle length (40-49%); lowest female spike bract usually 3 mm wide; bract of second female spike usually about 2 mm wide
.....***Carex* ×*alsatica*** [*C. demissa* × *C. flava*]
10b Beak accounting for about ⅓ of total utricle length (37-45%); lowest female spike bract usually about 2 mm wide; bract of second female spike usually about 1 mm wide.....***Carex* ×*ruedtii*** [*C. flava* × *C. lepidocarpa*]

11a Female spikes 1-3(4); male spike usually on peduncle of up to 40 mm in length; lowest female spike bract usually 1-2(3) mm wide; bract of second female spike usually up to 1 mm wide; uppermost cauline leaves usually much shorter than culm, rarely as long or longer than culm.....***Carex* ×*schatzii*** [*C. lepidocarpa* × *C. viridula*]
11b Female spikes 2-4(5), male spike sessile or rarely on peduncle of up to 15 mm in length; lowest female spike bract usually 2-3 mm wide; bract of second female spike usually 2 mm wide.....**12**

12a Beak 1.2-1.6 mm long; female spikes 6-9 mm wide; male spike usually sessile or on peduncle of up to 10 mm long.....***Carex* ×*subviridula*** [*C. flava* × *C. viridula*]
12b Beak ≤ 1.2 mm long; female spikes 5-7 mm wide; male spike on peduncle of up to 15 mm long.....
.....***Carex demissa* × *Carex viridula***

3.6. Description of taxa and hybrids

Carex flava **L.** 1753, Sp. Pl.: 975. Type: LINN Savage Cat. No. 1100.40 (Lectotype: LINN).
Synonyms: – *C. flava* L. var. *densa* Gaud. 1830, Fl. Helv. 6: 97; – *C. flava* L. var. *rectirostra* Gaud. 1830, Fl. Helv. 6: 97; – *C. flava* L. var. *patula* Klett et Richter 1830, Fl. Leibzig: 758; – *C. flava* L. var. *rectirostris* Poterm. 1844, Flora 27: 338; – *C. flava* L. var. *deficiens* Poterm. 1844, Flora 27: 339; – *C. flava* L. var. *pygmaea* Anderss. 1849, Pl. Scand.: 25; – *C. flavofulva* Beurling 1853, Bot. Not.: 37; – *C. flava* L. var. *macrorrhyncha* Čelak. 1867, Prodr. Fl. Böhmen. 1: 71; – *C. flava* L. var. *alpina* Kneucker 1899, Allg. Bot. Z. Syst. 5: 8; – *C. flava* L. f. *umbrosa* Kneucker 1899, Allg. Bot. Z. Syst. 5: 8; – *C. flava* L. f. *uetliaca* (Suter) Aschers. et Graebner 1903, Syn. Mitteleur. Fl. 2(2): 200; – *C. flava* L. var. *brevirostris* Aschers. et Graebner 1903, Syn. Mitteleur. Fl. 2(2): 201; – *C. flava* subsp. *euflava* Aschers. et Graebner 1903, Syn. Mitteleur. Fl. 2(2): 199; – *C. flava* L. var. *gaspensis* Fernald 1906, Rhodora 8: 200; *C. lepidocarpa* Tausch var. *laxior* Kük. 1909 in Engler Pflanzenreich 38(20): 673; *C. oederi* Retz. f. *graminea* Kük. 1909 in Engler Pflanzenreich 38(20): 674; – *C. flavella* V. Kreč. in Majevski Fl. Centr. Rus.s, 6: 184, 1933; id. in Komarov Fl. USRR, 3: 388, 617, 1935; *C. laxior* (Kük.) Mackenze 1935, Fl. North. Amer., 18,5: 306; – *C. flava* L. var. *laxior* (Kük.) Gleason 1952, Phytologia 4: 22; – *C. nevadensis* Boiss. et Reuter subsp. *flavella* (V. Kreč.) Patzke et Podlech 1959 in Janchen Cat. Fl. Austr., 1(4): 774.

Culms 12-70 cm high, 0.7-1.8 mm wide (width measured above uppermost cauline leaf). Leaves yellow-green, usually as long as culm, rarely longer or slightly shorter; uppermost cauline leaf 8-30 cm long and 2-5 mm wide, with well-developed sheath of 10-120 mm in length and ligule usually > 3 mm long; basal leaves 6-35 cm long and 3-6 mm wide. Inflorescence 1.5-6(20) cm long. Male spike single, terminal, 8-22 mm long, 1-2 mm wide, usually sessile or on peduncle of 10(15) mm in length; male glumes usually obtuse, obovate 2.9-4.4 mm long, 1.1-1.9 mm wide, usually brown or rusty brown, with pale midrib region and narrow hyaline margin. Female spikes 1-3(5), usually 2 uppermost close together, remaining spikes distant from them, ellipsoid or spherical, 9-22 mm long, 7-11 mm wide, all sessile or lowest spike on peduncle of 5 (up to 32) mm long. Lowest female spike bract 2-5 times as long as inflorescence, 3.2-26.5 cm long, 2-4(5) mm wide, bract sheath 1-44 mm long; bract of second female spike 1.3-10.9 mm long, 1-2(3) mm wide, usually sheathless. Utricles 4-6(6.5) mm long, 1.0-1.9 mm wide, gradually tapering into curved, bifid beak, its outer surface usually scabrous (> 5 bristles on each tooth); beak 1.8-2.8 mm long, usually accounting for ½ of total utricle length. Fruit only partly filling utricle body (⅓ to ½). Female glumes variable, from obtuse to acute, or rarely acuminate, 2.3-4.2 mm long, 1.2-2.1 mm wide, light to dark brown, with green midrib region and narrow hyaline margin.

Carex lepidocarpa **Tausch** 1834, Flora (Regensburg) 17: 179. Type: Czechoslovakia, Praha, (no collector), no. 1636 (lectotype: PRC, isolectotype: PRC, selected by Crins 1985).
Synonyms: – *C. flava* var. *elatior* Schltdl. 1823, Fl. Berol. 1: 477; – *C. oederi* Retz. var. *elatior* Gaudin 1830, Fl. Helv. 6: 96; – *C. flava* L. var. *polystachya* Gaudin 1830, Fl. Helv. 6: 97; – *C. flava* L. var. *lepidocarpa* (Tausch) Godr. 1844, Fl. Lorraine, 3: 118; – *C. flava* L. var. *brachyrrhyncha* Čelak. 1867, Prodr. Fl. Böhmen. 1: 71; – *C. lepidocarpa* Tausch var. *pseudolepidocarpa* Kneucker 1899, Allg. Bot. Z. Syst. 5: 9; – *C. lepidocarpa* Tausch f. *rectirostris* Kneucker 1899, Allg. Bot. Z. Syst. 5: 9; – *C. lepidocarpa* Tausch f. *laeviculmis* Kneucker 1899, Allg. Bot. Z. Syst. 5: 10; – *C. lepidocarpa* Tausch f. *major* Kneucker 1899, Allg. Bot. Z. Syst. 5: 10; – *C. lepidocarpa* Tausch f. *intermedia* (Coss. et Germ.) Aschers. et Graebner 1903, Syn. Mitteleur. Fl. 2(2): 200; – *C. lepidocarpa* Tausch var. *nelmesiana* Raymond 1952, Bull. Soc. Bot. Fr. 99: 194; – *C. viridula* Michaux subsp. *brachyrrhyncha* (Čelak.) B. Schmid var. *lepidocarpa* (Tausch) B. Schmid 1983, Watsonia 14: 317; *C. viridula* Michaux subsp. *brachyrrhyncha* (Čelak.) B. Schmid var. *elatior* (Schltdl.) Crins 1989, Can. J. Bot. 67: 1058.

Culms 20-85 cm high, 0.7-1.3 mm wide (above uppermost cauline leaf). Leaves yellow-green, usually much shorter than culm; uppermost cauline leaf 5.5-22.5 cm long and 2-4 mm wide, its sheath 9.5-100 mm long, and ligule usually < 2.5 mm long; basal leaves 6.5-30.5 mm long, 2.5-6 mm wide. Inflorescence 2.5-10(23) cm long. Male spike single, terminal, 10-31 mm long, 1-2 mm wide, on peduncle of 2-60 mm in length; male glumes 2.9-4.2 mm long, 1.3-2.1 mm wide, light to dark brown, with pale midrib region and narrow to broad hyaline margin. Female spikes 1-3(4), usually distant, ellipsoid, 8-22 mm long, 7-10 mm wide, all sessile or lowest spike rarely on peduncle of 4 (up to 33) mm long. Lowest female spike bract usually as long or shorter than inflorescence, rarely up to 1.5 as long as inflorescence, 0.6-17.7 cm long, 1-2(3) mm wide, bract sheath 1-42 mm long; bract of second female spike 0.4-7.5 mm long, usually < 1 mm wide, sheathless. Utricles 3.5-4.5(5) mm long, 1.1-2.0 mm wide, abruptly contracted into usually curved, bifid beak, its outer surface smooth or scabrous (< 5 bristles on each tooth); beak 1.1-1.8 mm long, usually accounting for

⅓ of total utricle length. Fruit filling about ½ of utricle body. Female glumes variable, from obtuse to acute, 2.1-3.3 mm long, 1.3-2.1 mm wide, light to dark brown, with green midrib region and hyaline margin.

***Carex demissa* Hornem.** 1808, Fl. Dan. 8(23): 4. Type: Denmark, in rupibus Telemarkiae, Vahl (Holotype: C). Synonyms: – *C. tumidicarpa* Andersson 1849, Bot. Not.: 16; – *C. oederi* Retz. subsp. *oedocarpa* Andersson 1849, Pl. Scand: 25; – *C. flava* L. f. *demissa* (Hornem.) Kük. 1909 in Engler Pflanzenreich, 38(20): 672; – *C. oederi* Retz. f. *oedocarpa* (Andersson) Kük. 1909 in Engler Pflanzenreich, 38(20): 674; – *C. viridula* Michaux subsp. *oedocarpa* (Andersson) B. Schmid 1983, Watsonia 14: 316; – *C. flava* L. subsp. *oedocarpa* (Andersson) P. D. Sell 1996 in Sell & Murrell, Fl. Great Britain Ireland 5: 110.

Culms 6-60 cm high, 0.6-1.4 mm wide (above uppermost cauline leaf), usually decumbent. Leaves usually shorter than culm, less often as long or longer than culm; uppermost cauline leaf 3-18 cm long, 2-4 mm wide, its sheath 10-60 mm long and ligule up to 2.5 mm long; basal leaves 4.5-30 cm long, 2.5-5.5 mm wide. Inflorescence 2-12(34) cm long. Male spike single, terminal, 8-22 mm long, 1-2 mm wide, usually on peduncle of up to 21 mm in length; male glumes 3.1-5.2 mm long, 1.2-2.0 mm wide, usually dark brown, with pale midrib region and narrow hyaline margin. Female spikes 2-4(5), usually 2-3 uppermost ones close together, lowest distant from them, often located below half the length of culm; ellipsoid, 6-16 mm long, 4-9 mm wide, sessile or lowest spike on peduncle of 4 (up to 21) mm in length. Lowest female spike bract usually as long or, less often, shorter or longer than inflorescence, 2.4-18.8 cm long, 2-3(4) mm wide, bract sheath 1-44 mm long; bract of second female spike 0.8-11.4 mm long, usually up to 1-2 mm wide, sheathless. Utricles 3-4(4.5) mm long, 1.1-1.9 mm wide, gradually tapering into straight or rarely slightly curved bifid beak, smooth or scabrous (with sparse bristles); beak 0.9-1.8 mm long (accounting for 35-45% of total utricle length). Fruit only partly filling utricle body (½ to ⅔). Female glumes 2.0-3.5 mm long, 1.1-2.0 mm wide, variable, from obtuse to acute, light to dark brown, with green midrib region and narrow hyaline margin.

***Carex viridula* Michx.** 1803, Fl. Bor.-Amer. 2: 170. Type: Canada, entre Montreal et Trois Rivieres, Michaux (Holotype: P).
Synonyms: – *C. oederi* Ehrhart 1791, Beitr. Naturk. 6: 83; – *C. serotina* Mérat 1821, Nouv. Fl. Env. Paris, ed. 2, 2: 54; – *C. subglobosa* Mielichhofer 1839, Flora (Regensburg) 22: 257; – *C. oederi* Retz. var. *brevirostris* Aschers. et Graebner 1903, Syn. Mitteleur. Fl. 2(2): 201; – *C. oederi* Retz. f. *alpestris* Aschers. et Graebner 1903, Syn. Mitteleur. Fl. 2(2): 201; – *C. oederi* Retz. f. *thalassica* Aschers. et Graebner 1903, Syn. Mitteleur. Fl. 2(2): 202; – *C. flava* var. *viridula* (Michx.) Aschers. et Graebner. 1903, Syn. Mitteleur. Fl. 2(2): 201; – *C. oederi* Retz. f. *tenuis* Zapałowicz 1906, Consp. Fl. Gallic. Crit. 1: 114; – *C. oederi* var. *pumila* (Cosson and Germain) Fernald 1906, Rhodora 8: 201; – *C. oederi* Retz. var. *viridula* (Michaux) Kük. 1909 in Engler Pflanzenreich, 38(20): 674; – *C. oederi* Retz. f. *argillacea* (Townson) Kük. 1909 in Engler Pflanzenreich, 38(20): 674; – *C. oederi* Retz. f. r*ecterostrata* (L. H. Bailey) Kük. 1909 in Engler Pflanzenreich, 38(20): 674; – *C. kotilainii* Palmgr. 1944, Memoranda Soc. Fauna Fl. Fenn. 19: 89; – *C. oederi* Retz. subsp. *fennica* Palmgr. 1958, Commentat. Biol. 20(3): 8; – *C. serotina* Mérat subsp. *fennica* (Palmgr.) Á. Löve & D. Löve 1961, Bot. Not. 114: 5; – *C. serotina* Mérat subsp. *philocrena* (V. I. Kreč.) Kukkonen 1984, Ann. Bot. Fenn. 21: 387; – *C. viridula* Michaux subsp. *serotina* (Mérat) Malyschev 1990 in Fl. Sibir., 3: 130; – *C. viridula* Michaux subsp. *viridula* var. *viridula*, B. Schmid 1983, Watsonia 14: 313; – *C. flava* L. subsp. *serotina* (Mérat) P. D. Sell in 1996 in Sell & Murrell, Fl. Great Britain Ireland 5: 110.

Culms 3-40(50) cm high, 0.5-1.1 mm wide (above uppermost cauline leaf), usually erect. Leaves usually shorter than culm; uppermost cauline leaf 3.1-23.1 cm long, 1-3 mm wide, its sheath 5.5-30 mm long and ligule usually < 1 mm long; basal leaves 3.5-35 cm long, 2-4 mm wide. Inflorescence 1.2-6(16.1) cm long. Male spike single, terminal, 4-20 mm long, 1-2 mm wide, usually sessile, rarely on peduncle of about 1-3 mm in length (exceptionally 20 mm); male glumes 2.4-4.2 mm long, 1.2-2.1 mm wide, variable, lanceolate to ovate, obtuse to acute, usually dark brown with pale midrib region and narrow hyaline margin. Female spikes (2)3-6(7), usually close together, sometimes lowest distant from them, may be located below half the length of culm, spherical or ellipsoid, 4-14 mm long, 4-8 mm wide, sessile or lowest spike on peduncle of 2 (up to 32) mm long. Lowest female spike bract usually longer than inflorescence, 2.8-21.7 cm long, 1-3 mm wide, bract sheath 0-50(92) mm long; bract of second female spike 9.8 mm long, up to 1-2 mm wide, sheathless. Utricles 2.1-4.1 mm long, 0.9-1.5 mm wide, gradually tapering into straight, smooth, bifid beak; beak 0.6-1.3 mm long (accounting for 23-36% of total utricle length). Fruit only partly filling utricle body (⅔ to ¾). Female glumes 1.5-3.0 mm long, 1.0-1.7 mm wide, light to dark brown, with green midrib region and narrow hyaline margin.

***Carex viridula* Michx. var. *pulchella* (Lönnr.) B. Schmid** 1983, Watsonia 14: 316

Type: Sweden, Gottland, Norrlanda, Lönnroth (Lectotype: UPS)
Synonyms: – *C. oederi* Retz. f. *pygmaea* Andersson 1849, Pl. Scand.: 25; – *C. oederi* Retz. subsp. *pulchella* Lönnr. 1854, Obs. Crit. Pl. Suec.: 24; – *C. pulchella* (Lönnr.) Lindman 1918, Svensk Fanerogamfl.: 143; – *C. serotina* Mérat subsp. *pulchella* (Lönnr.) Ooststr. 1949, in H.Heukels and W. H. Wachter, Bekn. Schoolfl. Nederl. ed. 7: 319; – *C. scandinavica* E. W. Davies 1953, Watsonia 3: 66; – *C. viridula* Michaux subsp. *viridula* var. *pulchella* (Lönnr.) B. Schmid 1983, Watsonia 14: 316; – *C. viridula* Michaux subsp. *pulchella* (Lönnr.) Malyschev 1990 in Fl. Sibir. 3: 130; – *C. flava* L. subsp. *pulchella* (Lönnr.) P. D. Sell in 1996 in Sell & Murrell, Fl. Great Britain Ireland 5: 110; – *C. oederi* Retz. var. *pulchella* (Lönnr.) Hedrén & Lassen 2003, Nord. J. Bot. 22: 262.

Culms 2.8-11.3 cm high, 0.6-0.9 mm wide (above uppermost cauline leaf), usually erect. Leaves usually as long as culm; uppermost cauline leaf 2.5-6 cm long, and 1-2 mm wide, with well-developed sheath of 1.5-2 mm in length, and poorly developed ligule, usually < 1 mm long; basal leaves 3.5-11.5 cm long, 1.5-3 mm wide. Inflorescence 0.7-3 cm long. Male spike single, terminal, 5-14 mm long, 1-2 mm wide, sessile or on peduncle of up to 3 mm in length; male glumes 2.8-3.3 mm long, 1.3-1.6 mm wide, dark brown with pale midrib region and narrow hyaline margin. Female spikes 2-3, usually close together, spherical or ellipsoid, 5-8 mm long, 4-6 mm wide, sessile or lowest spike on peduncle of up to 3 mm in length. Lowest female spike bract usually longer than inflorescence, 1.8-4.5 cm long, 1-2 mm wide, bract sheath 1-3 mm long; bract of second female spike 0.1-1.9 mm long, usually < 1 mm wide, sheathless. Utricles 1.8-2.6 mm long, 0.8-1.1 mm wide, gradually tapering into straight, smooth, bifid beak; beak 0.6-0.8 mm long (accounting for 27-32% of total utricle length). Fruit completely filling utricle body. Female glumes 1.4-2.2 mm long, 1.0-1.4 mm wide, usually dark brown with green midrib region and narrow hyaline margin.

***Carex* ×*fulva* Gooden.** 1794, Trans. Linn. Soc. London 2: 177
C. demissa Hornem. × C. *hostiana* DC.
Synonyms: – *C.* ×*flavescens* Host 1809, Icon Descr. Gram. Austriac. 4: 53; – *C. biformis* F. W. Schultz var. *sterilis* 1841, Flora 24: 55; – *C.* ×*appeliana* Zahn 1890, Oesterr. Bot. Z. 40: 364; *C.* ×*brueggeri* K. Richter 1890, Pl. Eur. 1: 170.

Culms 18.0-54.5 cm high, 0.8-1.1 mm wide (above uppermost cauline leaf). Leaves usually shorter than culm; uppermost cauline leaf 5.5-14.2 cm long and 2-3 mm wide, with sheath of 10-50 mm in length. Inflorescence 4.1-17.1 cm long. Male spike single, terminal, 12-24 mm long, 1-2 mm wide, sessile or on peduncle of up to 40 mm in length. Male glumes with broad hyaline margin. Female spikes 1-3, usually distant, distance between first and second female spike 10-110 mm (on average 40 mm); female spikes 8-20 mm long, 5-7.5 mm wide, sessile or lowest spike on peduncle of up to 30 mm in length. Lowest female spike bract usually shorter than inflorescence, 3.7-12.9 cm long, 2-3 mm wide, bract sheath 2.4-28 mm long. Utricles 3-4 mm long, 1.1-1.8 mm wide; beak 1-1.6 mm long (accounting for 35-44% of total utricle length) with white membrane at apex. Female glumes with variable hyaline margin.

***Carex* ×*leutzii* Kneuck.** 1891, in Seubert, Excurs. Fl. Baden, ed.5: 68
C. hostiana DC. × *C. lepidocarpa* Tausch
Synonyms: – *C.* ×*xanthocarpa* Degland var. *leutzii* (Kneucker) Rouy 1912, in Rouy & Foucaud, Fl. France 13: 475; – *C.* ×*pseudofulva* Fernald 1933. Rhodora 35: 231.

Culms 21.5-52.7 cm high, 0.8-1.3 mm wide (above uppermost cauline leaf). Leaves usually shorter or as long as culm; uppermost cauline leaf 4.9-10.9 cm long and 2-3 mm wide, with sheath of 10-48 mm long. Inflorescence 3.6-10.5 cm long. Male spike single, terminal, 12-24 mm long, 1-2 mm wide, sessile or on peduncle of up to 20 mm in length. Male glumes with broad hyaline margin. Female spikes 1-3, usually close together but sometimes distant, distance between first and second female spike 2-40 mm (on average 16 mm); female spikes 7-16 mm long, 6-9 mm wide, sessile or lowest spike on peduncle of up to 11 mm in length. Lowest female spike bract usually shorter than inflorescence, 3.5-7.5 cm long, 1-2.5(3) mm wide, bract sheath 2.1-24 mm long. Utricles 3.5-4.5 mm long, 1.1-1.8 mm wide; beak 1.2-1.5 mm long (accounting for 30-38% of total utricle length) with white membrane at apex. Female glumes with variable hyaline margin.

***Carex* ×*alsatica* Zahn** 1890, Oesterr. Bot. Z. 40: 363
C. demissa Hornem. × *C. flava* L.

Culms 15.2-37.5 cm high, 0.8-1.4 mm wide (above uppermost cauline leaf). Leaves usually slightly shorter or as long as culm; uppermost cauline leaf 6-20 cm long and 2-4 mm wide, with sheath of 10-60 mm in length; basal leaves 7.5-32.5 cm long, 3-5 mm wide. Inflorescence 2.5-21.6 cm long. Male spike single, terminal, 10-22 mm long, 1-2 mm wide, sessile or on peduncle of up to 13 mm long; male glumes 3.1-4.1 mm long, 1.3-1.9 mm wide, brown with pale midrib region and narrow hyaline margin. Female spikes 2-4, usually lowest

distant from others, ellipsoid or spherical, 7-16 mm long, 6-14 mm wide, sessile or lowest spike on peduncle of up to 9 mm long. Lowest female spike bract usually longer than inflorescence, 3.5-19.9 cm long, 2-3 mm wide, bract sheath 2-28 mm long; bract of second female spike 2.2-9.6 mm long, 1-2 mm wide, usually sheathless. Utricles 3.6-5.3 mm long, 1.1-1.8 mm wide, gradually tapering into slightly curved or straight, bifid beak, smooth or scabrous (with sparse bristles); beak 1.5-2.4 mm long (accounting for 40-49% of total utricle length). Female glumes 2.4-3.5 mm long, 1.3-1.8 mm wide, dark brown with green midrib region and narrow hyaline margin, obtuse or acute at apex, variable.

***Carex* ×*ruedtii* Kneuck.** 1891, in Seubert, Excurs. Fl. Baden, ed. 5: 67
C. flava L. × *C. lepidocarpa* Tausch
Synonyms: – *C. pieperiana* Junge 1904, Verh. Naturwiss. Vereins Hamburg 3(12): 18.

Culms 22.7-81.6 cm high, 0.8-1.2 mm wide (above uppermost cauline leaf). Leaves usually shorter or as long as culm; uppermost cauline leaf 8.7-23.1 cm long and 2-4 mm wide, with sheath of 15-75 mm long; basal leaves 14-35.5 cm long, 3-5 mm wide. Inflorescence 2.9-9.7 cm long. Male spike single, terminal, 5-26 mm long, 1-2 mm wide, sessile or on peduncle of up to 18 mm long; male glumes 3.4-4.4 mm long, 1.3-2.3 mm wide, brown with pale midrib region and hyaline margin. Female spikes 1-3, usually close together, ellipsoid, ellipsoid-spherical or ellipsoid-terete, 7-15 mm long, 7-10 mm wide, sessile or lowest spike on peduncle of up to 13 mm in length. Lowest female spike bract usually longer than inflorescence, 3.9-15.9 cm long, 1-3 mm wide, bract sheath 1-8 mm long; bract of second female spike 0.5-5.9 mm long, usually 1 mm wide or narrower, sheathless. Utricles 4.0-4.9 mm long, 1.1-1.9 mm wide, gradually tapering into curved, bifid beak, scabrous or sometimes smooth; beak 1.5-2.1 mm long (accounting for 37-45% of total utricle length). Female glumes 1.7-3.1 mm long, 1.2-1.7 mm wide, dark brown with green midrib region and narrow hyaline margin, obtuse or acute at apex, variable.

***Carex* ×*schatzii* Kneuck.** 1891, in Seubert, Excurs. Fl. Baden, ed. 5: 67
C. lepidocarpa Tausch × *C. viridula* Michaux

Culms 13.9-38.5 cm high, 0.6-1.2 mm wide (above uppermost cauline leaf). Leaves usually shorter than culm, less often as long or longer than culm; uppermost cauline leaf 3.7-20.1 cm long and 2-3 mm wide, with sheath of 10-65 mm long; basal leaves 6-29 cm long, 2.7-5 mm wide. Inflorescence 2.6-12.2 cm long. Male spike single, terminal, 10-19 mm long, 1-2 mm wide, sessile or on peduncle of up to 40 mm long; male glumes 2.8-3.9 mm long, 1.4-2.0 mm wide, light to dark brown, with pale midrib region and narrow hyaline margin. Female spikes 1-3(4), usually close together, ellipsoid or nearly spherical, 8-14 mm long, 6-8 mm wide, sessile or lowest spike on peduncle of up to 32 mm in length. Lowest female spike bract usually as long as inflorescence, 1.8-21.7 cm long, 1-2.5(3) mm wide, bract sheath 1-30 mm long; bract of second female spike 0.6-5.4 mm long, up to 1 mm wide, sheathless. Utricles 2.8-3.9 mm long, 0.8-1.3 mm wide, gradually tapering into straight, smooth, bifid beak; beak 0.8-1.6 mm long (accounting for 24-40% of total utricle length). Female glumes 2.0-2.9 mm long, 1.2-1.8 mm wide, dark brown with green midrib region and narrow hyaline margin, obtuse or acute at apex, variable.

***Carex* ×*subviridula* Fernald** 1933, Rhodora 35: 231
C. flava L. × *C. viridula* Michaux
Synonyms: – *C.* ×*mixta* Corbière 1894, Nouv. Fl. Normandie: 607.

Culms 18.9-56.9 cm high, 0.7-1.2 mm wide (above uppermost cauline leaf). Leaves usually shorter or as long as culm; uppermost cauline leaf 7.5-21.6 cm long and 2-3 mm wide, with sheath of 5-60 mm long; basal leaves 10-35 cm long, 3-4.5 mm wide. Inflorescence 2.2-13.5 cm long. Male spike single, terminal, 9-20 mm long, 1-2 mm wide, sessile or on peduncle of up to 10 mm long; male glumes 3.2-3.9 mm long, 1.5-1.9 mm wide, dark brown with pale midrib region and hyaline margin. Female spikes 2-5, usually close together or lowest distant from others, ellipsoid or nearly spherical, 7-14 mm long, 6-9 mm wide, sessile or rarely lowest spike on peduncle of up to 13 mm in length. Lowest female spike bract usually longer than inflorescence, 4.9-16.8 cm long, 2-3 mm wide, bract sheath 2-42 mm long; bract of second female spike 2.4-11.7 mm long, 1-3 mm wide, sheathless. Utricles 3.3-3.9 mm long, 1.0-1.5 mm wide, gradually tapering into straight, scabrous (with sparse bristles) or smooth, bifid beak; beak 1.2-1.6 mm long (accounting for 35-41% of total utricle length). Female glumes 2.3-2.7 mm long, 1.2-1.5 mm wide, light to dark brown with green midrib region and narrow hyaline margin, obtuse or acute at apex, variable.

***Carex demissa* Hornem. × *Carex viridula* Michx.**

Culms 19.1-29.4 cm high, 0.6-1.2 mm wide (above uppermost cauline leaf). Leaves usually shorter than culm; uppermost cauline leaf 7.7-12.4 cm long and 2-3 mm wide, with sheath of 5-30 mm long; basal leaves 6-18 cm long, 2.5-3 mm wide. Inflorescence 4.6-16.4 cm long. Male spike single, terminal, 13-20 mm long, 1-2 mm wide, on peduncle of 2-15 mm

long; male glumes 3.3-3.6 mm long, 1.5-1.7 mm wide, brown with pale midrib region and narrow hyaline margin. Female spikes 2-4, usually close together, or lowest distant from others, ellipsoid or nearly spherical, 7-13 mm long, 5-7 mm wide, sessile or lowest spike on peduncle of up to 6 mm long. Lowest female spike bract usually as long as inflorescence, 7.9-11.9 cm long, 2-3 mm wide, bract sheath 5-20 mm long; bract of second female spike 4.2-5.8 mm long, 1-2 mm wide, sheathless. Utricles 2.9-3.8 mm long, 0.8-1.3 mm wide, gradually tapering into straight, smooth or scabrous, bifid beak (with sparse bristles); beak 0.9-1.2 mm long (accounting for 28-38% of total utricle length). Female glumes 2.3-2.8 mm long, 1.3-1.8 mm wide, dark brown with green midrib region and narrow hyaline margin, obtuse or acute at apex, variable.

4. Discussion

4.1. Species concept and delimitation of taxa

This study is based on the phenetic species concept (Sokal & Crovello 1970; Sneath & Sokal 1973). It is generally consistent with the concepts used by taxonomists from northern Europe (Du Rietz 1930; Hedrén 2002), suggesting that species can be separated on the basis of at least 2 morphological characters or a set of characters that are genetically or evolutionarily independent. Species, as a morphological-systematic unit, has specific morphological characters that determine its systematic position. Morphological characters are usually products of a long history of natural selection and a phenotypic reflection of genotype (Kaźmierski 2004). In angiosperm taxonomy, morphological distinctness is still the dominant criterion of identification, verification, and description of individual species (Latowski 2004). This results primarily from the International Code of Nomenclature, including the principle of typification and the principle of priority. Morphological characters are often variable, but their variability can be objectively classified by the use of numerical taxonomy methods. These methods can be used to distinguish taxa on the basis of their morphological similarity (Sneath & Sokal 1973).

Results of this study show morphological distinctness of taxa included in *C. flava* agg., very much like results presented by Scandinavian researchers (Palmgren 1959; Hedrén 1990, 1996, 1998, 2002, 2004; Pykälä & Toivonen 1994; Hedrén & Prentice 1996). The most important for delimitation of these taxa were the least variable reproductive characters, i.e. length of utricle and its beak, and ratio of beak length to total utricle length. Among other characters, the most important were: bract length and width, length (or absence) of peduncles of male spikes, and number and arrangement of female spikes. In literature there are, however, reports on variation in spike distribution and arrangement of male and female flowers within *C. flava* s.s., depending on environmental conditions, especially on temperature and photoperiod (Heide 2004). Thus some researchers, when considering taxa of the *C. flava* complex, do not take into account measurements of inflorescence characters, especially estimation of distance between female spikes (Blackstock & Ashton 2010). In this study, these characters were included in statistical analyses in spite of their relatively high variability. The measurements are useful if spike distribution is considered in the whole complex, e.g. in specimens of *C. demissa*, the lowest spike is usually basal, while in specimens of *C. viridula*, female spikes are close together. During field research, in some sedge populations of the *C. flava* group, some anomalies in floret distribution within spikes were observed. Within male spikes, especially in their uppermost or central parts, female florets were found, whereas within female spikes, most frequently at the apex, some male flowers were present. Occurrence of abnormally developed spikes in sedges is also known from literature and is more often observed in hybrids than in the pure species (see Vonk 1979; Heide 2004). Specimens with such anomalies in spikes were excluded from statistical analyses.

The analysed taxa differed primarily in mean values of characters, whereas ranges of their values usually overlapped between all the distinguished taxa. In spite of the anomalies and observed relatively high variability of many characters, it was possible to identify taxa of the *C. flava* complex to the species level.

Thus results of this study confirm the taxonomic concept that distinguishes *C. flava*, and especially *C. lepidocarpa*, *C. demissa*, and *C. viridula* as separate species. This concept is based on (*i*) a high observed level of morphological separation of these taxa; (*ii*) integrity of these taxa at the sites where they coexist (despite the presence of intermediate forms resulting from hybridization); and (*iii*) habitat preferences of individual taxa, especially of *C. lepidocarpa* in contrast to *C. demissa*. Thus in Poland the analysed taxa are morphologically well-defined and show clear ecological preferences.

Among members of the *C. flava* complex, *C. viridula* is characterized by the highest phenotypic plasticity (Więcław 2011; Więcław & Podlasiński 2013). In this study, according to definitions of form, variety, and subspecies by Du Rietz (1930), the 2 subgroups of *C. viridula* were treated as local variants of species, i.e. varieties (local or ecological race, ecotype). Varieties can be distinguished because some local populations of the same species differ in several morphological characters, usually presence of qualitative characters (e.g. ratio of fruit size to utricle size), which deviate from the typical variety and may form ecotypes (Turesson 1922). As emphasized by Hedrén (2002), individual

varieties may differ in habitat preferences, so there is still a need to distinguish them. It can be hypothesized that extreme forms of *C. viridula* have developed locally in response to different selection pressure (Schmid 1984b).

In northern Europe, on the basis of utricle size, *C. viridula* is divided into 3 varieties, without any clear hiatus. Within populations of *C. viridula* continuous variation is observed, and specimens reaching extreme values are usually classified as different varieties (Schmid 1983). The smallest variety, *C. viridula* var. *pulchella*, has small and narrow utricles, completely filled by fruits. In Poland it was found in salt marshes along the Baltic coast (Zając 1968), but currently it seems to be absent there. *C. viridula* var. *bergrothii*, endemic to northern Europe, has the largest utricles, whereas the most common *C. viridula* var. *viridula* has medium-sized utricles (Hedrén 1998; Pykälä & Toivonen 1994).

Local populations with values of morphological characters intermediate between these 3 varieties are quite common in Scandinavia and Poland, so delimitation of varieties on the basis of morphological characters is not clear and unambiguous (Zając 1968; Pykälä & Toivonen 1994). In Poland, ranges of values of utricle characters of var. *viridula* and var. *pulchella* overlap. According to Zając (1968), utricle and beak are 1.9-2.8 mm and 0.2-0.6 mm long, respectively, for the typical variety, and 1.1-3.0 mm and 0.2-0.8 mm for var. *pulchella*. For comparison, Palmgren (1959) reported utricle length of (2.1)2.5-3.5 mm for var. *viridula* and (1.8)2-2.5(2.9) for var. *pulchella*, while according to Davies (1953a, c) in var. *viridula* utricles are (1.7)2.0-2.5(3) mm long and beaks are 0.25-0.5 mm long, whereas in var. *pulchella* their length is much lower: utricle (1.0)1.5-2.5 mm long and beak up to 0.25 mm long. A major character for distinguishing between these varieties is the ratio of fruit size to utricle size, i.e. the degree of filling the utricle body by the fruit (e.g. Havlícková 1982; Pykälä & Toivonen 1994; Egorova 1999). Usually in the typical variety the fruit fills ⅔ to ¾ of the utricle body, while in var. *pulchella* the fruit completely fills the utricle body. The ratio can be calculated only for fully developed plants. Within a local population, individuals at various stages of development are found, so it is difficult to determine unambiguously (for the whole population) the true ratio of fruit size to utricle size, i.e. the degree of filling the utricle body by the fruit. This character is also less valuable for analysis of dried material; herbarium specimens often include plants with immature utricles, and their imbibition also does not give satisfactory effects. For varieties of *C. viridula*, information about habitat seems crucial, since specimens of var. *pulchella* are usually found in salt marshes along sea coasts (e.g. Chater 1980; Hedrén 2002).

C. viridula var. *pulchella* and *C. viridula* var. *bergrothii* were treated by some taxonomists as species, namely *C. pulchella* (= *C. scandinavica*) and *C. bergrothii*, respectively (Davies 1953a, 1953c; Egorova 1999) or as subspecies: *C. viridula* subsp. *pulchella* and *C. viridula* subsp. *bergrothii*, respectively (see Palmgren 1959; Chater 1980). The present detailed morphological study of Polish individuals indicates a lack of hiatus between individuals of *C. viridula* (var. *viridula* and var. *pulchella*), so it is not justifiable to treat them as separate species. Populations of *C. viridula* (var. *viridula* and var. *pulchella*) form a mosaic within their range of distribution, so it is impossible to distinguish geographic variants (geographic races) (Hedrén 2002). However, they occupy various adaptation zones, so varieties of *C. viridula* can be regarded as so-called ecological species (van Valen 1976), although they are not a strictly monophyletic unit (Hedrén 2004).

Classification of the *C. flava* group is still subject to discussions, usually concentrating on 2 major approaches: synthetic and analytic, i.e. 1-2 biological species versus 4 morphological species (Jiménez-Mejías *et al*. 2012a). The synthetic approach, which fuses *C. lepidocarpa*, *C. demissa*, and *C. oederi* into one species, named *C. viridula* s.l., presented by Schmid (1983), is still controversial and does not reflect fully the complex pattern of variation within this group (Hedrén 1990, 2002, 2004; Pykälä & Toivonen 1994). Schmid (1983) suggested that in the *C. flava* complex the relative biological species concept should be used, basing on hybrid viability, and distinguished 2 species on this basis: *C. flava* s.s. and *C. viridula* s.l. In fact, *C. flava* s.s. crosses with all plants of the *C. flava* group but the hybrids are characterized by very low fertility, i.e. 0-3% of fertile pollen and variable seed set (Schmid 1982). According to Schmid (1983), such a low level of viability observed in the hybrids justifies distinguishing of *C. flava* as a separate species. By contrast, F_1 plants resulting from hybridization between the other members of the complex are characterized by partly reduced fertility: about 30% of pollen grains are fertile and 10-25% of seeds are well developed (Schmid 1982). According to the biological species concept used by Schmid (1983), the observed lowered fertility of these hybrids did not provide sufficient evidence to distinguish *C. lepidocarpa*, *C. demissa*, and *C. viridula* as separate species, although these taxa could be distinguished in the field (Schmid 1986a). An even more radical taxonomic approach to *C. flava* agg., consistent with the strict biological concept, was proposed by Sell (1996). Because of the lowered fertility of forms intermediate between *C. flava* s.s. and other members of this group, he distinguished only one species, namely *C. flava* s.l., and classified all the others as subspecies.

The material collected for this study included also specimens that were morphologically intermediate between pure species and varied widely in percentage of well-developed fruits (from completely sterile plants to some having well-developed fruits in > 50% of utricles). These plants could represent both F_1 hybrids and backcross hybrids. Some partly fertile specimens were morphologically intermediate between *C. flava* s.s. and other taxa, which suggests that introgression between them is possible. Thus, if the biological species concept was used, it would be justified to fuse all the analysed taxa into one species, as suggested by Sell (1996). However, application of the biological species concept in plants, where hybridization in common, would lead to classifying of morphologically divergent entities as one species, which could be composed of independent evolutionary lines (Hedrén 2002). Such an approach could lead to a remarkable decrease in number of plant species and fusion of well-defined and unproblematic taxa (Grant 1981; Stace 1989).

All the species distinguished in this study cross with one another but most plants from mixed populations, where at least 2 species of the *C. flava* group occur sympatrically, can be identified to species level, which can be regarded as an empirical test for delimitation of pure species (Grant 1981; Hedrén 2002). Mixed populations were often found in Sweden, Norway, Finland, Estonia, and Switzerland, where also most plants could be identified to species level (Schmid 1981; Hedrén 2002). In the British Isles, coexistence of 2 or more species at the same site is observed less frequently (Davies 1956; Wallace *et al*. 1975; Sell 1996), very much like in North America (Crins & Ball 1989a, 1989b), where hybridization between taxa of the *C. flava* group has been relatively poorly studied.

Taxonomic research on the genus *Carex*, especially of critical groups, such as the *C. flava* group, should be conducted in relation to biology and ecology of populations in the field. Only such field research can be supplemented with analysis of herbarium material. According to conventional Linnaean taxonomy, the subject of taxonomic research should be a real species, which in the field is an identifiable entity with specific ecological preferences, characterized by distinct biology and a specific range of distribution (Bachmann 1995; Mitka 2004).

Conventional taxonomy is not limited to research on exomorphic characters. On the contrary, it is aimed to construct classification systems based on a comprehensive data set, including also endomorphic characters (Mitka 2004). Simultaneous allozymatic and morphological research conducted in the *C. flava* group shows that taxa of this group are in fact better separated than it appeared on the basis of morphological analysis alone (Hedrén 2002; Blackstock 2007). Thus allozymatic research confirms even more clearly the validity of the analytic approach to the *C. flava* complex, which indicates that 4 morphological species exist.

In many cases, molecular research is obviously necessary, e.g. in cryptic species, which are morphologically identical but isolated reproductively; thus they are real species in the light of the biological species concept (Odrzykoski 2004). Besides, molecular studies provide important additional information necessary for more precise interpretation of the taxonomic status of complex plant groups (López & Morrone 2012).

Results of preliminary molecular research (Jiménez-Mejías *et al*. 2012a) on taxa of the section *Ceratocystis*, including taxa of the *C. flava* group, are consistent with results of their morphological analysis, confirming the validity of distinguishing *C. lepidocarpa*, *C. demissa*, and *C. viridula* as separate species. The resultant *rps16-5'trnK* phylogenesis corresponds to the general division of species of the *C. flava* complex into those with a curved beak (*C. flava* s.s., *C. lepidocarpa*) and those with a straight beak (*C. demissa*, *C. viridula*) (e.g. Chater 1980; Egorova 1999; Crins 2002), which are grouped as separate clades (Jiménez-Mejías *et al*. 2012a).

Taxa of the *C. flava* complex are relatively poorly distinguished on the basis of chromosome number. Different chromosome numbers are reported for both *C. flava* s.s. and *C. lepidocarpa*: 5 and 7 cytotypes, respectively (Rotreklová *et al*. 2011). For *C. flava* s.s., according to literature, the usual chromosome number is $2n = 60$, less often $2n = 56$, 58, 64, and 70 (Davies 1955; Schmid 1982; Stoeva & Štěpankova 1990; Halkka *et al*. 1992; Luceño 1994; Roalson 2008; Hipp *et al*. 2009; Rotreklová *et al*. 2011). For *C. lepidocarpa*, usually $2n = 68$, less often $2n = 58$, 62, 66, 69, 70, and 72 (Davies 1955; Schmid 1982; Stoeva & Štěpankova 1990; Luceño 1994; Rotreklová *et al*. 2011). The chromosome number indicates a close relationship between *C. demissa* and *C. viridula*, as in both taxa it is $2n = 68$ and 70, so it is impossible to conclude about their separation on the basis of cytological data (Davies 1955; Schmid 1982; Stoeva & Štěpankova 1990; Halkka *et al*. 1992; Luceño 1994; Roalson 2008; Rotreklová *et al*. 2011). Chromosome numbers in varieties of *C. viridula* are also similar: for var. *bergrothii* and var. *pulchella* $2n = 70$, while for var. *viridula* $2n = 68$, 70, 72 (Halkka *et al*. 1992).

In relation to the *C. flava* group, various taxonomic concepts have been used, but there is a general consensus about relationships between them, as similar patterns of variation are observed in various parts of Europe (e.g. Schmid 1982; 1986a; Pykälä & Toivonen 1994; Hedrén 2002). *C. flava* s.s was always regarded morphologically as most distinct, which is also confirmed by my research on Polish specimens of sedges. The greatest similarity is noticeable between varieties of *C. viridula*,

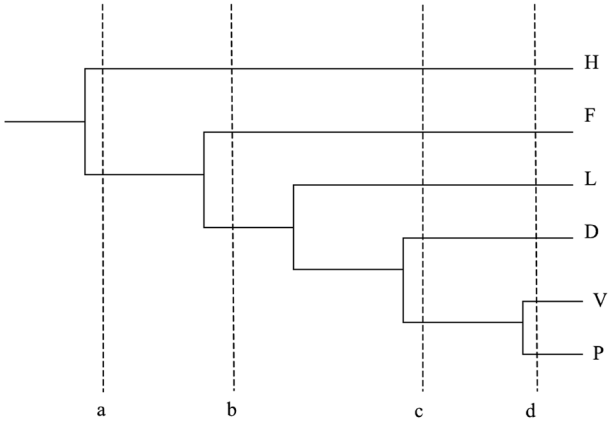

Fig. 11. Summary of classifications and phylogenetic links within the section *Ceratocystis* (including the *Carex flava* group and *C. hostiana*) according to Hedrén (2004), modified to match the situation observed in Poland

Explanations: a – biological species concept, only 2 species, hybrids between them completely sterile (Sell 1996), b – relative biological species concept, based on the level of hybrid viability, 3 species (Schmid 1982, 1983; Crins & Ball 1988), c – morphological species concept, 5 species (Pykälä & Toivonen 1994; Hedrén 2003; Blackstock 2007), d – ecological species concept, 6 species (Davies 1953a; Palmgren 1959; Egorova 1999), D – *C. demissa*, F – *C. flava* s.s., H – *C. hostiana*, L – *C. lepidocarpa*, P – *C. viridula* var. *pulchella*, V – *C. viridula* var. *viridula*

especially var. *viridula* and var. *pulchella* (e.g. Hedrén 2002). Because of the lack of clear discontinuities between varieties and the great variability of *C. viridula*, many authors have opposed to distinguishing these taxa and maintenance of infraspecific ranks (Crins & Ball 1989b; Jermy *et al*. 2007). Some researchers emphasize the absence of clear separation between *C. viridula* and *C. demissa* (Bruederle & Jensen 1992), but most authors regard them as separate taxa (e.g. Schmid 1981, 1983; Pykälä & Toivonen 1994; Egorova 1999; Koopman 2011). Phylogenetic links within the *C. flava* complex were discussed by Schmid (1982), Crins & Ball (1988), and Hedrén (2002) (Fig. 11).

4.2. Natural hybridization

Hybridization is more or less frequent among vascular plants. Spontaneous hybrids recurring and surviving in natural conditions are the driving force of plant speciation (e.g. Barton & Hewitt 1989; Rieseberg 1995, 1997; Arnold 1997; Barton 2001; Wissemann 2005). Members of the *C. flava* group often coexist at the same site and in the direct contact zone usually hybrids are present, composed of F_1 plants and their offspring resulting from backcrosses to parental taxa (Schmid 1982, 1986). Schmid (1982) suggests that critical groups of sedges, e.g. those of the section *Ceratocystis* (including *C. flava* group) are currently in the dynamic phase of evolution. In relation to a taxon endemic to Scandinavia, *C. viridula* var. *bergrothii*, a hypothesis of hybrid origin has been considered (Hedrén 1990, 1998). The hypothesis that this taxon results from hybridization and introgression (between *C. viridula* s.l. and *C. lepidocarpa* s.l.) is confirmed by a situation observed by Hedrén (1990) at several natural sites in Scandinavia, where putative parental taxa (*C. lepidocarpa* subsp. *jemtlandica*, endemic to Scandinavia, and *C. viridula* var. *viridula*) coexisted with *C. viridula* var. *bergrothii* and sterile specimens of *C. lepidocarpa* × *C. viridula*; but the last 2 taxa were morphologically very similar and intermediate between pure *C. lepidocarpa* subsp. *jemtlandica* and *C. viridula* var. *viridula* (Hedrén 1990).

In Poland some populations are also mixed, composed of 2 or rarely 3 species of the *C. flava* complex as well as numerous morphologically intermediate specimens. The most frequently coexisting species were *C. flava* and *C. demissa*, accompanied by completely sterile specimens of *C.* ×*alsatica*. The hybrid was morphologically similar (but not identical) to *C. flava* or intermediate between both parental species. Similarity to *C. flava* was determined primarily by vegetative characters, and, to a lesser extent, dimensions of utricle and beak (in most specimens of hybrid of intermediate size, but tending to reach the dimensions of utricles and beaks of *C. flava*) and size of female spikes. Blackstock & Jermy (2001) reported that specimens of *C.* ×*alsatica* found in Britain were also sterile and similar both to immature *C. flava* and to large atypical *C. demissa*, having elongated inflorescences with female spikes clustered around the male spike, like in *C. flava*. In one locality in northern Poland, specimens of *C.* ×*alsatica* occasionally had a similar arrangement of female spikes as that observed in *C. demissa* (lower spike located below half the length of the culm). Sterility of *C. flava* × *C. demissa* was confirmed by research conducted by Schmid (1982) in Switzerland (pollen fertility in artificial hybrids did not exceed 1%). However, Davies (1955) found that pollen fertility in natural hybrids *C. flava* × *C. demissa* from the British Isles reached 22%.

Similar differences in pollen fertility were noticed also in hybrid specimens of *C. flava* × *C. lepidocarpa*. According to Schmid (1982), specimens of *C.* ×*ruedtii* from Switzerland were characterized by low pollen fertility, of up to 2% (in artificial hybrids up to 3%), whereas according to Davies (1955), pollen fertility in specimens from British Isles reached 29%. In Poland, completely sterile specimens of *C.* ×*ruedtii* were recorded as well as plants having usually several to about a dozen per cent of utricles with well-developed fruits. The specimens of hybrid were morphologically similar to *C. lepidocarpa* or their morphological characters were intermediate between both parental taxa, e.g. length of utricle and beak, or length and width of the lowest female spike bract. At all the localities where hybrids appeared, most of the plants were classified as pure *C. lepidocarpa*, whereas specimens of *C. flava*

s.s. were infrequent and found only at the edges of habitats. Blackstock & Ashton (2010), who studied a population of *C. flava* × *C. lepidocarpa* in Britain, also observed a high morphological similarity of *C.* ×*ruedtii* and *C. lepidocarpa*, but the hybrids coexisted with a population of pure *C. lepidocarpa*, whereas *C. flava* was absent. It seems that the hybrid, despite a low level of pollen fertility, will form backcrosses with *C. lepidocarpa*, which is more common in the studied Polish localities (than the infrequent *C. flava*), or like in Britain, with one parental taxon present at the same site (Blackstock & Ashton 2010).

Specimens of *C.* ×*schatzii* are usually intermediate between both parental taxa or more similar to *C. lepidocarpa*. In utricles of some specimens, fruits were normally developed (sometimes even more than 50% of utricles with well-developed fruits), so they may be F_n hybrids or backcrosses, which would attest to the possibility of introgression towards *C. lepidocarpa*. Schmid (1982) reported that in artificial hybrids *C. lepidocarpa* × *C. viridula*, seed set varied from 6% to 12%, while pollen fertility, from 25% to 37%. Schmid (1982) did not study the fertility of natural hybrids but supposed that they may be less fertile than hybrids produced in laboratory conditions. Davies (1955) assessed the fertility of natural hybrids *C. lepidocarpa* × *C. viridula* from 2 British localities, where it reached 20% and 25%, respectively. Interestingly, the parental species differ very much in flowering season. *C. lepidocarpa* flowers the earliest among all members of the analysed group, whereas *C. viridula* flowers the latest (Vonk 1979). However, their flowering period may overlap and sometimes late-flowering populations of *C. lepidocarpa* may start flowering at the same time or even later than the earliest-flowering populations of *C. viridula* (Vonk 1979). Besides, flowering season depends on environmental factors, including temperature and photoperiod, as shown in controlled conditions by Heide (1997). Consequently, spontaneous crossing of these species is possible, so the resultant partly fertile hybrids will probably most often cross back with specimens of *C. lepidocarpa*, which are then at the height of the flowering season, rather than with specimens of *C. viridula*, which only start to flower.

Specimens of *C. demissa* × *C. viridula* are partly fertile and morphologically very similar to *C. demissa*. In artificial hybrids, seed set ranged from 18% to 25% (Schmid 1982), whereas pollen fertility in natural hybrids reached 29% (Davies 1955). *C. demissa* starts flowering as the third species of the *C. flava* group, whereas – as mentioned earlier – *C. viridula*, is the latest flowering species (Vonk 1979). Thus introgression will probably be directed towards *C. demissa.*

During phenetic analysis, a group of OTUs, represented by sterile herbarium specimens, filled the space between *C. flava* and *C. viridula*. These specimens were classified as *C.* ×*subviridula*. In herbarium material originating from the same sites, both the above-mentioned hybrid were found as well as potential parental taxa, i.e. *C. flava* and *C. viridula*. This hybrid had characters common to both putative parents or some specimens were more similar to the tall *C. viridula*. Pollen fertility of natural hybrids *C. flava* × *C. viridula* in Swiss sedge populations varied from 2% to 7% (Schmid 1982).

C. demissa and *C. lepidocarpa* coexisted only at one site in West Pomerania and did not form hybrid. Herbarium material did not include hybrid between these taxa either. It seems that in Poland these are environmentally the most isolated taxa among members of the *C. flava* complex.

Within the section *Ceratocystis*, some hybrids between *C. hostiana* and members of the *C. flava* group have been found (Kiffe 2001; Koopman 2010; Więcław & Koopman 2013). The hybrids were completely sterile (see Davies 1955; Schmid 1982), more or less similar to *C. hostiana* or morphologically intermediate between parental forms. All hybrids had a characteristic white membrane at the beak apex and female glumes with wide transparent margins, like in *C. hostiana* (Crins & Ball 1987; Egorova 1999; Blackstock & Jermy 2001). In herbarium material some specimens were completely sterile and filled the phenetic space between *C. hostiana* and members of the *C. flava* group. One group of OTUs was intermediate between *C. hostiana* and *C. lepidocarpa*, while another group of OTUs was intermediate between *C. hostiana* and *C. demissa*, so the specimens were classified as hybrids: *C.* ×*leutzii* and *C.* ×*fulva*, respectively (Więcław & Koopman 2013). Contrasting views can be found in literature on nomenclature of the hybrids and their putative parents of the *C. flava* group. Wallace *et al*. (1975) report that *C.* ×*fulva* is a cross between *C. hostiana* and *C. lepidocarpa*, whereas Koopman (2010, 2011) states that the parents are *C. hostiana* and *C. demissa*. The reason for the confusion about nomenclature of hybrids between *C. hostiana* and *C. flava* agg. was the material collected by Goodenough, who on this basis described *C. fulva* as a species in spite of sterility of the analysed specimens (Crins & Ball 1987; Cayouette & Catling 1992). Actually, the material included very probably both hybrids: *C. hostiana* × *C. demissa* and *C. hostiana* × *C. lepidocarpa* (Koopman, pers. comm.). Besides, specimens of *C. demissa* × *C. hostiana* are very similar to *C. hostiana* × *C. lepidocarpa*, and according to Wallace *et al*. (1975) they can be distinguished only on the basis of spike size (spikes are narrower and slightly shorter than in hybrid of *C. demissa*). A study conducted by Więcław & Koopman (2013) shows that specimens of *C.* ×*fulva* have shorter utricles, male spikes on longer peduncles,

and narrower female spikes, usually more distant from one another than in specimens of *C.* ×*leutzii*. Another significant difference is also the ratio of beak length to total utricle length, which is higher for *C.* ×*fulva* than for *C.* ×*leutzii*. Finally, *C.* ×*fulva* grows in more or less compact tufts, like *C. demissa*, whereas *C.* ×*leutzii* grows in very loose tufts, more like *C. hostiana*.

Natural hybrids within the section *Ceratocystis* can be identified on the basis of their complete sterility or partial fertility, presence of intermediate characters and characters of either of the parental species. Important characters for delimitation of hybrids include dimensions of utricle and beak, and ratio of beak length to utricle length. Most of the analysed morphological characters in hybrids have values intermediate between the parental species, so it is difficult to indicate characters specific to hybrids except their reduced fertility, reflected in the presence of empty utricles. However, a general trend can be observed: utricle length and beak length in hybrids are usually closer to that recorded in the parent with longer utricles and beaks. Thus specimens of *C.* ×*ruedtii*, and especially of *C.* ×*alsatica*, have relatively long utricles and beaks, which in many specimens of *C.* ×*alsatica* reach even the same dimensions as in pure *C. flava*. Similarly, values of these characters in *C. demissa* × *C. viridula* corresponds to dimensions recorded in pure *C. demissa* (Więcław & Wilhelm 2014).

The length of utricle and beak in hybrids between *C. hostiana* and the members of *C. flava* agg. is strongly related to values of these characters in parental taxa of the *C. flava* complex. Utricle length declines in the following order: *C.* ×*xanthocarpa* (*C. flava* as a parent), *C.* ×*leutzii* (*C. lepidocarpa* as a parent), and *C.* ×*fulva* (*C. demissa* as a parent). Ratio of beak length to utricle length is high for *C.* ×*fulva* (like for *C. demissa*) and low for *C.* ×*leutzii* (like for *C. lepidocarpa*) (Więcław & Koopman 2013).

Useful for delimitation of hybrids of the *C. flava* complex are also field data, i.e. coexistence of putative parental species and hybrids. It is much more difficult to identify hybrids if one (or even both) parental species no longer exist at the same site and if putative hybrids are fertile to a large extent and have well-developed fruits. In such a situation, determination of hybrid origin of sedges of the *C. flava* group requires molecular analyses. Schmid (1982) described them as stabilized cryptic backcrosses, as they can be distinguished only on the basis of genetic research.

4.3. Ecological preferences

Carex viridula has the widest ecological niche among members of the *C. flava* complex, and is characterized also by the highest phenotypic plasticity (Schmid 1984a). It colonizes various types of sites, from organic to sandy, from acidic to alkaline, usually humid but sometimes growing on flooded or periodically dry sites (see Davies 1956; Schmid 1984b; Crins & Ball 1989b). Vonk (1979) showed that within the *C. flava* group, only specimens of *C. viridula* are able to flower as early as in the first growing season. Schmid (1984b, 1986b) observed a high survival rate at the germination stage and earlier maturity of specimens of *C. viridula* than of *C. flava*. Populations of *C. viridula* are thus characterized by a broad range of tolerance to diverse and variable environment, as well as fast development, potential for early and fast reproduction, relatively low and variable population size, and short life cycle (Schmid 1984a, 1984b; Vonk 1979).

Carex viridula usually grows in open habitats in our country, and poorly competes with other plant species (see Davies 1956). A broad range of pH values recorded at its sites suggests that soil pH does not limit its occurrence. In Poland, *C. viridula* grows on soils with pH ranging from 4.2 to 8.1, like in Bulgaria and former Czechoslovakia (pH 4.7-8.3; Stoeva & Štepánková 1990), in the British Isles (pH 5.4-8.5; Davies 1956), Switzerland (pH 6.3-8.2; Schmid 1984b), and North America (pH 5.2-7.6; Crins & Ball 1989a).

Carex lepidocarpa prefers calcareous sites, with pH 5.5-7.9 (mean 7.0). In Poland, *C. lepidocarpa*, usually grows on moist, calcareous meadows and fens, rarely in intermediate mires (poor fens). In Switzerland the taxon was recorded on soils with pH 6.8-8.2 (Schmid 1984a), compared to pH 5.8-8.2 in the British Isles, (Davies 1956) and pH 6.4-8.3 in Bulgaria and former Czechoslovakia (Stoeva & Štepánková 1990). Clymo (1962) showed that calciphily of this species is due to its sensitivity to aluminium. Aluminium ions dissolved in the soil with lowered pH cause injuries to roots of calciphiles (Clymo 1962), including *C. lepidocarpa*. Besides, this taxon is found on wet sites and is relatively sensitive to lower water level (Pykälä 1994).

Carex demissa usually grows on slightly acidic meadows, marshes, poor fens, along forest roads and paths. The species was found on soils with a wide range of pH values, from 3.8 to 7.1, but most often on slightly acidic sites (mean pH 4.8). Similarly, in Central Europe *C. demissa* is usually recorded at acidic sites (Patzke & Podlech 1960), e.g. at pH 5.1-6.4 in Switzerland (Schmid 1984a) or pH 5.4-6.3 in Bulgaria and former Czechoslovakia (Stoeva & Štepánková 1990). In the British Isles, it was sporadically found on soils with pH 7.5 (Davies 1953). In Finland it is even calciphilous, growing on soils rich in nutrients (Pykälä & Toivonen 1994). According to Pykälä & Toivonen (1994), the distribution of *C. demissa* in Finland reflects the known phenomenon that species are more demanding at the limits of their distribution ranges. In Poland, *C. demissa* grew on soil with pH > 7 at only one, the northernmost

site (near the town of Kołobrzeg), about 700 m from the Baltic coast. At the other sites, pH varied from 3.9 to 6.7. This species tolerates aluminium ions dissolved in the soil (Clymo 1962). It can survive at sites with lowered pH, i.e. where other species of the *C. flava* group, especially *C. lepidocarpa*, die because of aluminium sensitivity (Clymo 1962).

Carex flava s.s. is found on moist meadows, wetlands and marshes, roadsides, in ditches, and alder thickets and woods. In Poland it grows on soils with a wide range of pH, from 3.8 to 7.6, but prefers slightly alkaline sites (mean pH 5.9). In other European countries, soil pH at sites of *C. flava* was higher than in Poland, e.g. 6.8-8.2 in Switzerland (Schmid 1984a), or 5.2-8.3 in Bulgaria and former Czechoslovakia (Stoeva & Štepánková 1990). In the British Isles, *C. flava* is rare, and soil pH was measured at only 2 sites, where it amounted to 6.5 on average (Davies 1956). In North America, *C. flava* is found on moist or wet sites, usually with a high concentration of calcium cations and pH 5.8-8.5 (Crins & Ball 1989a, 1989b).

5. Final remarks and conclusions

Numerical analysis of morphological characters in 1852 living specimens of sedges of the *Carex flava* group collected from 80 localities and in 1500 herbarium specimens from 26 herbaria and 7 private collections made it possible to distinguish 4 species and 7 hybrids. The latter comprise 5 hybrids resulting from hybridization within the *C. flava* complex, and 2 hybrids resulting from hybridization between members of *C. flava* agg. and *C. hostiana*.

The results of this study confirm the taxonomic concept that 4 species can be distinguished within the *C. flava* group: *C. flava* s.s., *C. lepidocarpa*, *C. demissa*, and *C. viridula*. A high level of morphological separation of these taxa was observed in Poland, reflected mostly in generative characters: length of utricle and utricle beak, as well as percentage ratio of beak length to total utricle length. Other characters useful for delimitation of species include bract length and width, length (or absence) of peduncles of male spikes, and number and arrangement of female spikes. The synthetic approach (associated with the biological species concept, based on the lowered fertility of hybrids), which fuses *C. lepidocarpa*, *C. demissa*, and *C. oederi* into one species, named *C. viridula* s.l., does not reflect fully the complex pattern of variation within the *C. flava* group.

The highest phenotypic plasticity is observed in *C. viridula*. Continuous variation of morphological characters is noticeable among specimens of this species, so it is not justified to distinguish its subspecies (sometimes classified even as separate species) described earlier in literature. Specimens of *C. viridula* were grouped into local variants of species, i.e. varieties: var. *viridula* and var. *pulchella*. These taxa differ in habitat preferences: specimens of *C. viridula* var. *pulchella* are usually found in salt marshes along sea coasts, whereas *C. viridula* var. *viridula* is common in meadows, marshes, peatlands, edges of lakes, ponds, ditches, roadsides, and in depressions between dunes. The application of molecular methods may allow a more precise determination of intraspecific variability of *C. viridula* in its wide range of morphological variation.

Some local populations in Poland were mixed, composed of 2 or rarely 3 species of the *C. flava* complex, accompanied by numerous morphologically intermediate hybrids. Most frequently coexisting species were *C. flava* and *C. demissa*, accompanied by completely sterile speciemens of hybrid. Quite often, coexistence of *C. lepidocarpa* and *C. viridula* was observed, but they formed hybrids infrequently, because of differences in flowering season. In Poland, *C. lepidocarpa* and *C. demissa* seemed to be ecologically the most isolated taxa of the *C. flava* group, both during field research and examination of herbarium specimens in the laboratory, no hybrids between these species have been found.

Natural hybrids appearing within the *C. flava* group and the whole section *Ceratocystis* can be identified on the basis of their complete sterility or partial fertility, reflected in the high percentage of empty utricles (70-100% of utricles of hybrids do not contain fully developed fruits) and the presence of intermediate characters or characters of one and the other parental species. Important characters for delimitation of hybrids include dimensions of utricle and beak, and ratio of beak length to total utricle length. Utricle length and beak length in hybrids is usually closer to that recorded in the parent with higher mean values of these characters. For instance, *C. ×alsatica* has relatively long utricles and beaks, which in many specimens reach even the same dimensions as in pure *C. flava*.

In Poland the following hybrids were recorded: *C. ×alsatica* [*C. demissa* × *C. flava*], *C. ×ruedtii* [*C. flava* × *C. lepidocarpa*], *C. ×schatzii* [*C. lepidocarpa* × *C. viridula*], *C. ×subviridula* [*C. flava* × *C. viridula*], *C. demissa* × *C. viridula*, *C. ×fulva* [*C. demissa* × *C. hostiana*], and *C. ×leutzii* [*C. hostiana* × *C. lepidocarpa*]. Hybrids between *C. hostiana* and members of the *C. flava* group, as well as *C. ×alsatica* and *C. ×subviridula*, were completely sterile, whereas some specimens of *C. flava* × *C. lepidocarpa*, *C. lepidocarpa* × *C. viridula*, and *C. demissa* × *C. viridula* were partly fertile. Those plants could be F_n hybrids or backcrosses, which would indicate the possibility of introgression.

Sites of taxa of the *C. flava* group differ in pH and concentrations of $CaCO_3$ and Ca in the soil. Most significant differences in soil parameters were found between

sites of *C. lepidocarpa* (preferring calcareous habitats) and *C. demissa* (usually growing on slightly acidic soils). The widest range of pH values was recorded at the studied sites of *C. viridula*; it seems that soil pH does not limit its distribution.

Taxa of the *C. flava* complex grow on wet or moist sites and are generally (except for *C. viridula*) relatively sensitive to lower water level. These species prefer open habitats, especially *C. viridula*, which rather poorly competes with other plants growing at the same site.

In Poland, taxa of the *C. flava* complex are morphologically well-defined and show clear habitat preferences. Most plants from mixed populations, where at least 2 species of the *C. flava* group occur sympatrically, could be identified unambiguously despite the presence of intermediate forms resulting from hybridization. Other reasons for maintenance of their species rank are provided by ecological analyses, concerning primarily soil pH, water supply, and ecological specialization associated with competition.

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Appendix 1. Geographic location of collection sites of sedges of the *Carex flava* group

No.	Location of collection sites	No. of specimens	Taxon
	Koszalin Coast District (Pobrzeże Koszalińskie)		
1	Słowińskie Coast (Wybrzeże Słowińskie), Kluki, meadow S of village 54°40'02.0"N, 17°20′18.4"E	24	D
2	Słowińskie Coast, Retowo, pasture S of Lake Gardno 54°37′29.1"N, 17°06′37.3"E	21	D
3	Słowińskie Coast, Gardna Wielka, meadow near E edge of Lake Gardno 54°39′07.5"N, 17°10′17.7"E	22	D
4	Słowińskie Coast, Łeba, depression between dunes, N of Lake Łebsko 54°44′56.4"N, 17°25′16.9"E	30	V
5	Słowińskie Coast, Łeba, depression between dunes, N of Lake Łebsko 54°44′43.4″N, 17°24′30.9″E	15	V
6	Białogard Plain (Równina Białogardzka), Bagicz, roadside depression, N of road Sianożęty-Bagicz 54°11′55.1"N, 15°41′32.4"E	25	D
7	Białogard Plain, Sianożęty, damp depression on cliff, about 150 m W of village 54°12'20.70"N, 15°42'31.44"E	25	V
	Gdańsk Coast District (Pobrzeże Gdańskie)		
8	Kashubian Coast District (Pobrzeże Kaszubskie), Osłonino near Puck, low-sedge fen in nature reserve "Beka" 54°39'21.84"N, 18°27'38.70"E	38	L,V,Sch
9	Białogóra, sandy depression 54°49'25.56"N, 17°58'31.02"E	28	V
10	Sławoszynko, forest and roadside near nature reserve "Bielawa", E of village 54°48'00.12"N, 18°13'37.26"E	15	V
	Szczecin Coast District (Pobrzeże Szczecińskie)		
11	Trzebiatów Coast (Wybrzeże Trzebiatowskie), Łowno near Międzywodzie, salt-marsh 53°59'49.0"N, 14°41′09.6"E	2	V
12	Pyrzyce-Stargard Plain (Równina Pyrzycko-Stargardzka), Grędziec, meadow near emergent vegetation of E edge of Lake Miedwie 53°13'10.50"N, 14°55'05.88"E	20	V
13	Pyrzyce-Stargard Plain, Lubiatowo, N edge of Lake Torfowe 53°09'42.12"N, 15°01'59.01"E	28	L,V
14	Pyrzyce-Stargard Plain, Lubiatowo, ditch and chalk pit near pasture 53°10'13.56"N, 15°02'36.72"E	4	V
15	Pyrzyce-Stargard Plain, Będgoszcz, waterlogged meadow near N edge of Lake Będgoszcz 53°14'54.00"N, 14°48'22.62"E	32	L
16	Pyrzyce-Stargard Plain, Zaborsko, meadow, SE edge of Lake Zaborsko 53°10′28.7"N, 15°00′20.8"E	29	L,V,Sch
17	Police Plain (Równina Wkrzańska = Równina Policka), Stolec, meadow and depression near waterhole, E of village 53°33′05.0"N, 14°20′52.6"E	28	V
18	Police Plain, Zalesie, meadow, S of Forest District headquarters near Lake Świdwie 53°34'42.24"N, 14°21'25.08"E	20	F
19	Goleniów Plain (Równina Goleniowska), Modrzewie, fen 53°34'45.96"N, 14°42'53.52"E	36	F,L,R,V
20	Goleniów Plain, Krępsko, fen 53°35'31.08"N, 14°43'12.06"E	10	F
21	Goleniów Plain, Ogorzele, forest meadow, E of village 53°42′14.6"N, 15°01′17.9"E	30	F
22	Goleniów Plain, Budzeń near Stepnica, meadow 53°36'54.42"N, 14°40'51.72"E	14	F
	West Pomeranian Lakeland (Pojezierze Zachodniopomorskie)		
23	Choszczno Lakeland (Pojezierze Choszczeńskie), Kiełpino, forest meadow 53°13′22.6"N, 15°40′ 45.9"E	82	D,F,A,L
24	Choszczno Lakeland, Kiełpino, alder carr 53°13′22.8"N, 15°40′ 45.4"E	10	F

No.	Location of collection sites	No. of specimens	Taxon
25	Myślibórz Lakeland (Pojezierze Myśliborskie) Sitno, calcareous fen near Lake Tchórzyno 53°00′40.0"N, 14°51′08.9"E	74	L,V,Sch
26	Myślibórz Lakeland, calcareous meadow near Lake Chłop 52°59'23.52"N, 14°54'00.24"E	49	L,V,Sch
27	Ińsko Lakeland (Pojezierze Ińskie), Ińsko, N edge of Lake Długie 53°26′31.7”N, 15°35′37.3”E	22	V
28	Ińsko Lakeland, Studnica, E edge of Lake Kiełpino Duże 53°26′29″N, 15°37′10″E	25	V
29	Drawsko Lakeland (Pojezierze Drawskie), Kluczewo, meadow near W edge of Lake Prosino 53°38'44.52"N, 16°11'32.82"E	30	F
30	Drawsko Lakeland, Kluczewo, alder carr near W edge of Lake Prosino 53°38'49.86"N, 16°11'35.52"E	15	F
	South Pomeranian Lakeland (Pojezierze Południowopomorskie)		
31	Tuchola Forest (Bory Tucholskie), Lake Wdzydze, meadow, Sidły Island 54°59′12″N, 17°53′36″E	20	F,L
32	Tuchola Forest, Schodno, meadow near SW edge of Lake Bielawy 54°02′42"N, 17°49′50"E	21	L
33	Tuchola Forest, Schodno, poor fen near SW edge of Lake Bielawy 54°02′38″N, 17°49′17″E	4	L
34	Tuchola Forest, S of road Wdzydze Kiszewskie-Gołuń, ecological area “Kiszewskie Bagno” near N edge of Lake Gołuń, poor fen 54°00′28"N, 17°57′47"E	25	L,V
35	Tuchola Forest, Zazdrość, meadow, SE of village, near forester’s lodge 53°39'26.58"N, 18°14'07.08"E	18	F
36	Tuchola Forest, N of village Łążek, edge of Lake Piaseczno 53°39'38.94"N, 18°15'35.58"E	20	V
37	Tuchola Forest, Laski, meadows, E of village, near Grzybienica Mała river 53°40'04.92"N, 18°14'06.66"E	18	F
38	Tuchola Forest, Stara Rzeka, meadows, W of village, near Czyściewnica river 53°39'29.52"N, 18°16'35.28"E	20	F
39	Tuchola Forest, Osie, Stary Tartak (old sawmill), alder carr near edge of Lake Czerno 53°34'50.76"N, 18°20'25.05"E	9	F
40	Tuchola Forest, Wda river valley, meadow, forest edge 53°33'55.38"N, 18°19'25.56"E	23	F
41	Świecie Plateau (Wysoczyzna Świecka), Wałkowiska, fen near E edge of Lake Sierosławek 53°33'37.08"N, 18°19'50.10"E	49	F,L,R
	Chełmno-Dobrzyń Lakeland (Pojezierze Chełmińsko-Dobrzyńskie)		
42	Lubawa Hump (Garb Lubawski), Dąbrówno, meadow, SE of village 53°24'27.96"N, 20°04'07.44"E	25	F
	Masurian Lakeland (Pojezierze Mazurskie)		
43	Region of Great Masurian Lakes (Kraina Wielkich Jezior Mazurskich), Borki, nature reserve “Nietlickie Bagno”, meadow, E of village 53°52'11.46"N, 21°48'42.36"E	30	F
	Lithuanian Lakeland (Pojezierze Litewskie)		
44	East Suwałki Lakeland (Pojezierze Wschodniosuwalskie), Kramnik, wetland, N of village 54°18'38.76"N, 22°45'58.68"E	22	F
45	East Suwałki Lakeland, Potopy near Wiżajny, pasture, NE of village 54°20'45.42"N, 22°58'35.34"E	30	F
46	East Suwałki Lakeland, Berżniki, meadow in village, near Kunisjanka stream 54°04'37.26"N, 23°27'59.46"E	56	F,L,R
47	West Suwałki Lakeland (Pojezierze Zachodniosuwalskie), Szczebra, peatland in Rospuda river valley 53°54'59.88"N, 22°54'48.96"E	20	L

No.	Location of collection sites	No. of specimens	Taxon
	Milicz-Głogów Depression (Obniżenie Milicko-Głogowskie)		
48	Milicz Basin (Kotlina Milicka), Nowe Grodziska, meadow in village, 51°33'24.9″N, 17°21′24.6″E	6	F
	Przedbórz Upland (Wyżyna Przedborska)		
49	Przedbórz-Małogoszcz Range (Pasmo Przedborsko-Małogoskie), Kajetanów, ditch, E of village 50°59'58.4"N, 20°01′36.8"E	7	F
50	Przedbórz-Małogoszcz Range, Kajetanów, meadow, E of village 50°59'58.4"N, 20°01′36.8"E	26	F
51	Przedbórz-Małogoszcz Range, Kajetanów, meadow, E of village 50°59'48.1"N, 20°01′49.0"E	18	F
52	Przedbórz-Małogoszcz Range, Stanowiska, moist depression close to tall emergent vegetation 50°58'05.8"N, 19°56′30.8"E	9	V
	Woźniki-Wieluń Upland (Wyżyna Woźnicko-Wieluńska)		
53	Wieluń Upland (Wyżyna Wieluńska), Strugi near Kochlew, meadow, S of Florian's Spring (Źródło Floriana) 50°12'07.8"N, 18°47′02.3"E	11	F,V
54	Wieluń Upland, Bobrowniki, Żabi Staw (pond), edge of water body, W of village 51°06'17.5"N, 18°46′06.2"E	9	V
	Nida Basin (Niecka Nidziańska)		
55	Nida Valley (Dolina Nidy), Włochy, meadow, S of village 50°31'27.2"N, 20°33′55.8"E	16	F
56	Nida Valley, Włochy, depression with standing water on meadow, S of village 50°31'28.8"N, 20°34′30.0"E	8	V
57	Nida Valley, Włochy, anthropogenic depression among meadows, on sandy substrate, S of village 50°31'28.4"N, 20°34′32.4"E	20	V
	Western Sudetes (Sudety Zachodnie)		
58	Jelenia Góra Basin (Kotlina Jeleniogórska), Mysłakowice, roadside ditch, 50°50'25.3"N, 15°46'23.0"E	20	D
59	Rudawy Janowickie Mts, Karpniki, forest roadside (green tourist trail) 50°51'07.3″N, 15°33′38.8″E	27	F,D
60	Rudawy Janowickie Mts, Karpniki, forest roadside (yellow tourist trail) 50°51'15.1″N, 15°54′32.1″E	15	F,D
61	Rudawy Janowickie Mts, Karpniki, forest roadside (blue tourist trail) 50°50'45.5″N, 15°54′38.5″E	18	D
62	Rudawy Janowickie Mts, Rędziny, Przełęcz Rędzińska (mountain pass), meadow 50°49'59.3″N, 15°56′22.1″E	28	F
63	Karkonosze Mts, Karpacz, forest roadside (green tourist trail) 50°46'10.0"N, 15°43′36.8"E	27	D
64	Karkonosze Mts, Karpacz, forest roadside (green tourist trail) 50°46'07.2″N, 15°43′05.4″E	18	D
	Eastern Sudetes (Sudety Wschodnie)		
65	Massif of Śnieżnik (Masyw Śnieżnika), Międzygórze, pasture 50°13'14.7"N, 16°45′53.9"E	52	D,F,A
66	Massif of Śnieżnik, Międzygórze, forest roadside (yellow tourist trail) 50°13′33.8″N, 16°45′50.7″E	10	D,F
67	Massif of Śnieżnik, Jaworek, meadow 50°12'40.2″N, 16°44′29.6″E	20	F
68	Massif of Śnieżnik, Nowa Wieś, roadside 50°12'17.0"N, 16°45′30.0"E	10	F
69	Massif of Śnieżnik, along stream in village Bielice 50°16'25.9″N, 17°00′22.2″E	14	F

No.	Location of collection sites	No. of specimens	Taxon
70	Massif of Śnieżnik, Bielice, thicket with *Equisetum palustre* 50°15'59.2″N, 17°00′06.1″E	21	F
	Eastern Beskid Mts (Beskidy Wschodnie)		
71	Western Bieszczady Mts (Bieszczady Zachodnie) Wołosate, Przełęcz Beskid (mountain pass), roadside ditch 49°03'13.4"N, 22°42′21.8"E	70	D,F,V,A, D×V
72	Western Bieszczady Mts, Wołosate, meadow in Szczawinka river valley 49°03'16.5"N, 22°41′30.7"E	30	D
73	Western Bieszczady Mts, Wołosate, forest roadside in Szczawinka valley 49°03'15.2"N, 22°41′29.1"E	23	F,D,A
74	Western Bieszczady Mts, Wołosate, meadow, N of village 49°04'41.6"N, 22°39′42.4"E	15	F
75	Western Bieszczady Mts, Wołosate-Ustrzyki Górne, roadside ditch 49°04'02.2"N, 22°40′47.4"E	19	F
76	Western Bieszczady Mts, Przełęcz Bukowska (mountain pass), along a stream 49°03'13.92"N, 22°46'22.56"E	11	F
77	Western Bieszczady Mts, Przełęcz Bukowska, near tourist trail along a stream 49°03'24.78"N, 22°45'39.90"E	15	F
78	Western Bieszczady Mts, Brzegi Górne, roadside ditch 49°08'26.94"N, 22°34'07.14"E	16	F
79	Western Bieszczady Mts, Połonina Caryńska, depression with standing water 49°08'22.92"N, 22°35'51.66"E	20	F
80	Western Bieszczady Mts, Wetlina, steep river bank 49°09'35.2"N, 22°27′36.4"E	10	F

Explanations: A – *C.* ×*alsatica*, D – *C. demissa*, D×V – *C. demissa* × *C. viridula*, F – *C. flava* s.s., L – *C. lepidocarpa*, R – *C.* ×*ruedtii*, Sch – *C.* ×*schatzii*, V – *C. viridula*

Appendix 2. Sedges of the section *Ceratocystis*: (A) *C. hostiana*, Włochy, *leg.* H. Więcław 2010 (SZUB); (B) *C. flava,* Dąbrówno, *leg.* H. Więcław 2010 (SZUB); (C) *C. lepidocarpa,* Wałkowiska, *leg.* H. Więcław 2009 (SZUB); (D) *C. demissa*, Karpacz, *leg*. H. Więcław 2011 (SZUB); (E) *C. viridula* var. *viridula*, Grędziec, *leg*. H. Więcław 2009 (SZUB) (photograph by B. Kurnicki)


(B)
006682
Herbarium Stetinensis
SZUB
UNIWERSYTET SZCZECIŃSKI
HERBARIUM STETINENSIS
Carex flava L.
Pojezierze Chełmińsko-Dobrzyńskie
Garb dubowski, Dębowina
Torf. na SE od 4di
53°24'27.96"N 20°04'07.44"E
leg. H. Hięcław
det. H. Hięcław
08.07.2010


(C)
006684
Herbarium Stetinensis
SZUB
UNIWERSYTET SZCZEC
HERBARIUM STETINENSIS
Carex lepidocarpa Tausch.
Pojezierze Południowopomorskie, Wysoczyzna Świecka, Hałkowisko torfowisko mistie, E brzeg jez. Sienno
53°33'37.08" N 18°19'50.10"E
leg. H. Więcław
det. H. Więcław
14.07.2008


(D)
006683
Herbarium Stetinensis
SZUB
UNIWERSYTET SZCZECIŃSKI
HERBARIUM STETINENSIS
Carex demissa Hornem.
Sudety Zachodnie, Karkonosze
Karpacz
przydroże leśne (Hrabatki zielonego
szlaku 50°46'07.2"N 15°43'05.4"E
leg. H. Hięciaw
det. H. Hięciaw
03.08.2011


(E)
006685
Herbarium Stetinensis
SZUB
UNIWERSYTET SZCZECIŃSKI
HERBARIUM STETINENSIS
Carex viridula Michx
Pobrzeże Szczecińskie, Równina Pyrzycko-Stargardzka, Grzędziec
Łąki na E od jeziora Miedwie
52°13'10.50" N 14°55'05.88" E
leg. H. Więcław
det. H. Więcław
23.07.2008

Appendix 3. Utricles of *Carex* taxa and hybrids of the section *Ceratocystis* (from left to right): (A) *C. flava* (Dąbrówno, *leg.* H. Więcław 2010, SZUB), *C. lepidocarpa* (Wałkowiska, *leg.* H. Więcław 2009, SZUB), *C. demissa* (Karpacz, *leg.* H. Więcław 2011, SZUB), *C. viridula* var. *viridula* (Grędziec, *leg.* H. Więcław 2009, SZUB), *C. viridula* var. *pulchella* (Rewa, *leg.* J. Kornaś 1959, KRA); (B) *C.* ×*alsatica* (Kiełpino, *leg.* H. Więcław 2011, SZUB), *C.* ×*ruedtii* (Berżniki, *leg.* H. Więcław 2010, SZUB), *C.* ×*subviridula* (Kodrąb, *leg.* J. Hereźniak 1966, LOD), *C.* ×*schatzii* (Mironów, *leg.* B. Kurnicki 2010, SZUB), *C. demissa* × *C. viridula* (Wołosate, *leg.* H. Więcław 2010, SZUB); (C) *C. demissa* (Karpacz, *leg.* H. Więcław 2011, SZUB), *C.* ×*fulva* (Jonkowo, *leg.* L. Olesiński 1958, OLTC), *C. hostiana* (Włochy, *leg.* H. Więcław 2010, SZUB), *C.* ×*leutzii* (Psary, *leg.* J. Hereźniak 1978, LOD), *C. lepidocarpa* (Wałkowiska, *leg.* H. Więcław 2009, SZUB) (photograph by H. Więcław)