Notes on the nomenclature and taxonomy of the Carex flava group in Europe

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ABSTRACT

The European taxa of the *Carex flava* group have been revised, using new information on demography, ecology, karyology, hybridization and morphology. The proposed classification includes two species and ten taxa at lower rank. Several taxa described as distinct entities in the literature are considered to be synonyms. *C. viridula* Michx (N. America) and *C. serotina* Mérat belong to the same species and the first name has priority. Other proposed nomenclatural changes are: subspecific status for *C. lepidocarpa* Tausch as **C. viridula** subsp. **brachyrrhyncha** (Čelak.) B. Schmid **comb. nov.**, for *C. demissa* Hornem. as **C. viridula** subsp. **oedocarpa** (N. J. Andersson) B. Schmid **comb. nov.**, and for *C. nevadensis* Boiss. & Reuter as **C. viridula** subsp. **nevadensis** (Boiss. & Reuter) B. Schmid **stat. et comb. nov.**, for *C. bergrothii* Palmgren as **C. viridula** var. **bergrothii** (Palmgren) B. Schmid **stat. et comb. nov.**, and for *C. oederi* Ehrhart **pulchella* Lönnr. as **C. viridula** subsp. *cedercreutzii* Fagerström as **C. viridula** subsp. *cedercreutzii* (Fagerström) B. Schmid **comb.** nov., and for *C. lepidocarpa* Tausch aver. **iepidocarpa** (Tausch) B. Schmid **comb.** nov., for *C. bergrothii* Palmgren as **C. viridula** var. **bergrothii** (Palmgren) B. Schmid **stat. et comb. nov.**, and for *C. oederi* Ehrhart **pulchella* Lönnr. as **C. viridula** var. **bergrothii** (Palmgren) B. Schmid **stat. et comb. nov.**; and new combinations for *C. tumidicarpa* N. J. Andersson subsp. *cedercreutzii* Fagerström as **C. viridula** subsp. **cedercreutzii** (Fagerström) B. Schmid **comb.** nov., and for *C. lepidocarpa* Tausch aver. **lepidocarpa** (Tausch) B. Schmid **comb.** nov.

INTRODUCTION

Carex is one of the largest and most ecologically diverse genera of flowering plants. The majority of its species are taxonomically well defined entities, but there are some critical groups. Hybridization in the genus is largely confined to these critical groups and they are probably the only ones with high evolutionary activity today.

The subject of the present study is the critical group *C. flava* L. sensu lato in Europe. It is characterised by small overall size, short rhizomes, fertile tillers bearing a single male spike at the end of the stem and normally two to four female spikes just beneath, and more or less inflated utricles with distinct and bifid beaks. The plants occur in open, wet habitats. In contrast to taller sedges, which form large, stable, high-density populations, they form small populations which fluctuate considerably in density. Random genetic drift, together with high selection pressures in extreme environments, are probably responsible for the immense number of variants, most of which have never been named.

The nomenclatural and taxonomic problems in the *C. flava* group are complex and have caused considerable confusion among botanists. Many specialists have written accounts of the group (e.g. Kükenthal 1909; Wiinstedt 1936, 1945, 1947; Senay 1950–1951; Davies 1953, 1955; Palmgren 1959; Patzke & Podlech 1960; Fagerström 1967; Crétin & Bidault 1974; Chater 1980). Chater's concept in *Flora Europaea* summarizes our present knowledge of the group accumulated over the last four decades. Most of this information has been obtained from herbarium material, with very little information derived from a study of the biology of the taxa. Hence important questions, like "What is the heritability of the characters used in the diagnoses of new *C. flava* group taxa?", and "Are natural populations of these taxa exchanging genes through hybridization and introgression?", are not answered.

The following revision of the *C. flava* group takes into account the results of empirical work on the demography, ecology, karyology, hybridization and morphology of Swiss representatives, which have been reported in previous papers (Schmid 1980, 1982). With this experimental taxonomic basis,

B. SCHMID

Swiss herbarium material, part of which had already been determined by earlier caricologists such as Kükenthal, Samuelsson, Thellung, Palmgren, Patzke and Podlech, was re-examined in order to obtain a calibration of the herbarium-based classifications in terms of a biological classification (i.e. one using a biological species concept). The application of this procedure led to the conclusion that several taxa described in the *C. flava* group have no systematic value and should no longer be recognized. The proposed classification groups the material in two species, which are further divided into ten taxa at lower rank.

MATERIALS AND METHODS

Besides the original material, thoroughly investigated for a biosystematic study of the *C. flava* group in Switzerland (Schmid 1980), collections of the group from the following herbaria were examined: **BAS, BERN, COI, FI, G, LAU, LISU, MA, NEU, TRT, Z, ZT**. The herbaria **BM, C, G, H, LE, P, PRC, S, UPS**, and **Z** provided type material. All methods used for the present study, including lists of characters and numerical analyses, are described in Schmid (1980).

RESULTS

KEY

Note: It is sometimes impossible to identify a specimen by its morphological characters only as the variation within taxa can exceed the boundaries between them. Where more than one taxon is present at a single locality (or was present in the past) hybridization and introgression are common.

1.	Utricles usually longer than 4 mm, distinctly curved, gradually narrowed into 2–3 mm long beak with up to 10 bristles on each side; female spikes more than 7 mm in diameter; leaves of fertile tillers usually more than 3 mm wide, rarely more than 0.2 mm thick; free part of ligule conspicuous (up to 1 mm long); silica bodies usually 2 per silica cell	2
1.	Utricles usually shorter than 5 mm, straight or curved, more or less abruptly narrowed into 0.5–2 mm long beak with usually less than 5 bristles on each side; female spikes up to 8.5 mm in diameter; leaves of fertile tillers 2–4.5 mm wide, up to 0.3 mm thick; free part of ligule inconspicuous (less than 0.5 mm long); silica	-
2	bodies for 2 per sinca cen	2
2.	Mature stems up to 50 cm or more long, more than 1 mm thick; longest leaves of	
2	Tertile tillers usually more than 10 cm long	'a
2.	Mature stems farely more than 30 cm long, c. 1 mm thick; longest leaves of fertile	
2	tillers not more than 10 cm long Alb. C. <i>flava</i> var. <i>alpin</i>	la
3.	Utricles $2-4$ mm long, straight or slightly curved; beak of utricle $0.5-1.5$ mm long;	
	remaie spikes rarely more than / mm in diameter; leaves of fertile thiers up to 4.5	4
2	In the vide and 0.5 mm tinck, since boundes 1 of 2 per since cent	4
5.	ornicles 5.5–5 mm folig, distinctly curved, beak of utilities roraly more than 3 mm wide	
	spikes 7–6.5 min in diameter, leaves of fertile there ratery more than 5 min wide	0
4	Litricles resolv more than 3 mm long; beak of utricle 0.5.1 mm long; male spike	9
4.	contributes ratery more than 5 mm tong, beak of unite of 5-1 mm tong, male spike	
	sometimes with remain howers, stems straight, c. 1 min tinck, usually solid, leaves	5
4	Utrialeg usually langer then 2 mm back of utriale g 1.5 mm lange male spike youghly	5
4.	locking female flowers, store often surved and more than 1 mm thick hollow or	
	solid loaves flat silies bodies 1 or 2 per silies cell	7
5	Solid, leaves flat, since bodies 1 of 2 per since cent	/
5.	Rut mining utilete, leaves of fertile tillets c. 1–2 mining wide	Ia
5	Nut not filling utricle: leaves of fertile tillers c. 2.3 mm wide	6
5.	Famale spikes 2.5. growded: stems usually not longer than 20 cm	0
0.	B1a C viridula subsp. viridula var viridul	la
	Dia. C. Viriaula Subst. Viriaula val. Viriau	u

310

- 6. Female spikes 1–3, not crowded; stems usually longer than 20 cm
- B1b. C. viridula subsp. viridula var. bergrothii 7. Male spike usually more than 10 mm long; leaves of fertile tillers more than 3 mm
- 8
- Male spike c. 10 mm long; leaves of fertile tillers not more than 3 mm wide 7.
- 8.
- Lower bracts resembling leaves of fertile tillers B4. C. viridula subsp. cedercreutzii 8. 9.
 - Leaves of fertile tillers usually 10 cm or more long, c. 2 mm wide

B5a. C. viridula subsp. brachyrrhyncha var. lepidocarpa

9. Leaves of fertile tillers usually less than 10 cm long, c. 3 mm wide B5b. C. viridula subsp. brachyrrhyncha var. scotica

DIAGNOSTIC DESCRIPTIONS

4

A1a. C. flava L. var. flava. Stems hollow, erect, 20-50 cm long; leaves of fertile tillers long, flat, 3-5 mm wide, 0.15-0.2 mm thick, usually with 2 silica bodies per silica cell; free part of ligule 0.3-1 mm long; male spike c. 10-20 mm long; female spikes 10-15 mm long, 8-12 mm wide; utricles 4-5-6 mm long, distinctly curved, with beak 2-3 mm long and with up to 10 bristles on each side. 2n=(58) 60 (62). Acid to calcareous soils with constantly high moisture content. Europe except extreme south, W. and C. Asia, N. Africa, N. America.

A1b. var. *alpina* Kneucker. Smaller in all parts; stems 10–30 cm long; female spikes 8-5–13 mm long, 7.5-9.5 mm wide; utricles 4-5 mm long. 2n=60 (62). Replaces var. *flava* at high altitudes (over 1000 m) in C. Europe.

B1a. C. viridula Michx subsp. viridula var. viridula. Stems solid, erect, 5–20 cm long; leaves of fertile tillers canaliculate, 2-3 mm wide, 0.15-0.3 mm thick, usually with 1 silica body per silica cell; free part of ligule 0.05-0.2 mm long; male spike c. 10 mm long or less; female spikes 6-10 mm long, 5-6.5 mm wide; utricles 2.5–3.5 mm long, straight, with beak c. 1 mm long with 0–4 bristles on each side. 2n = (68) 70 (72). Acid, calcareous or brackish, wet soils with seasonally changing water regime, on bare ground or in very open vegetation. Europe except the south, W. and E. Asia, ?N. Africa, N. America.

B1b. var. bergrothii (Palmgren) B. Schmid. Larger in general than var. viridula and with less compact inflorescences; stems 20-30 cm long; female spikes 7-12 mm long, 6-7.5 mm wide; utricles c. 3.5 mm long. 2n=?. Ecology unknown. N. E. Europe.

Blc. var. pulchella (Lönnr.) B. Schmid. Smaller in many parts than var. viridula; female spikes 5-8 mm long, 4-5 mm wide; utricles 2-2.5 mm long, beak c. 0.5 mm long. 2n=70. Ecology like var. viridula. N. Europe, N. America.

B2. C. viridula subsp. oedocarpa (N. J. Andersson) B. Schmid. Stems solid or hollow, curved, 5-30 cm long; leaves of fertile tillers flat, 3-4.5 mm wide, 0.15-0.3 mm thick, with 1-2 silica bodies per silica cell; free part of ligule 0.05-0.3 mm long; male spike c. 10-20 mm long; female spikes 7-12 mm long, 5.5–7.5 mm wide; utricles 3–4 mm long, straight, with beak c. 1.5 mm long with 0–4 bristles on each side. 2n=(68) 70. Acid, damp soils, sometimes in woods. Europe except the east, eastern N. America.

B3. C. viridula subsp. nevadensis (Boiss. & Reuter) B. Schmid. Similar to subsp. oedocarpa but smaller in all its parts; leaves of fertile tillers 2-3 mm wide; male spike c. 10 mm long. 2n=?68. Replaces subsp. *oedocarpa* in mountainous regions in S. Europe?

B4. C. viridula subsp. cedercreutzii (Fagerström) B. Schmid. Similar in overall size to subsp. *oedocarpa*; leaves of fertile tillers c. 2 mm wide; male spike c. 10 mm long. 2n=?. Ecology unknown. Azores, Madeira.

B5a. C. viridula subsp. brachyrrhyncha (Čelak.) B. Schmid var. lepidocarpa (Tausch) B. Schmid.

Stems hollow, erect, 15–50 cm long; leaves of fertile tillers flat, 2–3.5 mm wide, 0.15-0.2 mm thick, usually with 1 silica body per silica cell; free part of ligule 0–0.3 mm long; male spike c. 10–20 mm long; female spikes 8–12 mm long, 7–8.5 mm wide; utricles 3.5–4.5 mm wide, slightly curved, with beak 1.5–2 mm long with 1–5 bristles on each side. 2n=68. Calcareous, wet soils, in open vegetation. Europe except the east and south, ?N. Africa, eastern N. America.

B5b. var. *scotica* (E. W. Davies) B. Schmid. Leaves of fertile tillers shorter but wider ($2 \cdot 5-4$ mm wide); plants robust. 2n=68. Replaces var. *brachyrrhyncha* in mountainous regions of Britain.

EVIDENCE FOR THE EXISTENCE OF TWO SPECIES WITHIN THE C. FLAVA GROUP

The taxa of the *C. flava* group are normally listed in an order of decreasing size of the floral parts of the plants, e.g. *C. flava* var. *flava*>*C. flava* var. *alpina*>*C. viridula* subsp. *brachyrrhyncha* (=*C. lepidocarpa*)>*C. viridula* subsp. *oedocarpa* (=*C. demissa*)>*C. viridula* subsp. *viridula* var. *viridula* (=*C. serotina*)>*C. viridula* subsp. *viridula* subsp. *viri*

In a study of the karyology and hybridization of Swiss representatives of the *C. flava* group, the two groups *C. flava* var. *flava*/var. *alpina* and *C. viridula* subsp. *viridula*/subsp. *oedocarpa*/subsp. *brachyrrhyncha* were recognized (Schmid 1982). The first group includes taxa with n=29, 30, or 31, the second taxa with n=34, 35, or 36. Natural and artificial F_1 hybrids between the two groups set no seeds and produced only 0–c. 3% fertile pollen grains. Directional backcrossing (with either of the parent species acting as the female) over many generations leads to forms identical in morphology and fertility to the pure parent species, and the species remain distinct, although considerable gene flow may take place between them.

Artificial F_1 hybrids within the first group showed no reduced fertility. Within the second group seed set was reduced to *c*. 10–25% and pollen fertility to *c*. 30%. These fertility levels would allow an intermixing of taxa where originally different taxa of the same group grow together. Intermediate states of *C. viridula* subsp. *viridula* and subsp. *brachyrrhyncha* occur in western Ireland, of *C. viridula* subsp. *viridula* and subsp. *oedocarpa* in saltmarshes in the Outer Hebrides and Orkneys, and of *C. viridula* subsp. *brachyrrhyncha* and subsp. *oedocarpa* in Teesdale. They all may be partly of hybrid origin and partly have arisen independently. In most places, however, the *C. flava* group is represented by a single taxon only, the different ecology and general sparseness of the plants preventing them from hybridizing and intermixing.

The results summarized above indicate that a biological species concept for the *C. flava* group has to include all the taxa in one of the two species *C. flava* or *C. viridula*. In particular, *C. viridula* subsp. *brachyrrhyncha* belongs to *C. viridula* and is different from *C. flava*.

NOMENCLATURE AND TAXONOMIC NOTES

A1. C. flava L., Sp. Pl. 975 (1753). Type: Europe, Savage Cat. no. 1100.40 (?holotype: LINN) Synonyms: C. flava β pygmaea Hartman, Handbok i Skandinaviens Flora, 35 (1820). Type: Sweden, Gävle, Skogmur, mid June 1845, ?Hartman in herb. Hartman (neotype: UPS)

C. flavella V. Kreczetovicz in Komarov, *Fl. USSR*, **3**: 617 (1935). Type: USSR, Melenkov and Vladimir provinces, Zakolp'e, 15 June 1914, *Nazarov* (holotype or lectotype material not seen; isotype: **LE**)

Probable synonyms:

C. jemtlandica (Palmgren) Palmgren, quoad lectotypus, *Mem. Soc. Fauna Fl. Fenn.*, **13**: 126 (1938) *C. lepidocarpa* Tausch subsp. *jemtlandica* Palmgren in Lindman, *Svensk Fanerogamflora*, 2nd ed., 153 (1926). Type: Sweden, Jämtland, Östersund, Frösön, 13 August 1910, *Palmgren 53* (lectotype: **H**)

A1a. C. flava var. flava

In unfavourable conditions (on dry soil or with trampling) C. flava var. flava is often dwarfed. These

313

dwarfs can easily be produced experimentally by limiting the water supply and are phenocopies of *C*. *flava* var. *alpina*. The lack of the typically deformed utricle in the descriptions and type specimens of var. *pygmaea* and *C*. *flavella* still allows a distinction to be made between the dwarf states of var. *flava* and the true var. *alpina*. The description and type material of *C*. *jemtlandica* refers to a plant intermediate between *C*. *flava* and *C*. *viridula* subsp. *brachyrryncha* and morphologically similar to *C*. *viridula* subsp. *brachyrryncha* backcrossed with *C*. *flava* \times *C*. *viridula* subsp. *brachyrryncha*. The Swiss material (in **ZT**) determined by Palmgren as *C*. *jemtlandica* belongs to *C*. *flava*, and that determined by him as intermediate between *C*. *jemtlandica* and *C*. *viridula* subsp. *brachyrryncha* he also put *C*. *flava* backcrosses with *C*. *flava* \times *C*. *viridula* subsp. *brachyrryncha* into *C*. *viridula* subsp. *brachyrryncha*. Without karyological, ecological, and experimental evidence it is questionable whether *C*. *jemtlandica* is a taxon different from *C*. *flava* var. *flava*.

A1b. C. flava var. alpina Kneucker, Allg. Bot. Zeitschr., 5: 8 (1899). Type: Switzerland, canton Uri, Hospenthal, 46° 31′ N, 26° 14′ E, alt. c. 1550 m, 2 August 1897, Kneucker 123 (lectotype: Z; isolectotypes distributed in Kneucker, Carices Exs. 5, e.g. **BERN**, G, LAU, ZT; paratype: *ibid.*, canton Bern, Haslital, 46° 38′ N, 25° 57′ E, alt. c. 1350 m, 11 August 1897, Kneucker 123, distributed in *loc. cit.* e.g. **BERN**, G, LAU, Z, ZT) Synonyms:

Č. flavella sensu Podlech & Patzke, *Ber. Bayer. Bot. Ges.*, **33**: 106 (1960) (non V. Kreczetovicz) *C. nevadensis* subsp. *flavella* (sensu Podlech & Patzke, non V. Kreczetovicz) Patzke & Podlech in Janchen, *Cat. Fl. Austr.*, **1** (4): 774 (1960)

C. flava var. alpina represents one extreme of a topocline correlated with altitude, the other extreme being typified by var. flava (Schmid 1980). It is an alpine ecotype whose distinct phenotype is maintained in cultivation in lowland regions. From the specimens distributed by Kneucker a lectotype had to be chosen (in \mathbb{Z}).

It is clearly the taxon to which Patzke & Podlech refer in their works as *C. flavella*, but has little in common with *C. nevadensis* – the name used in *Flora Europaea* (see page 319).

B. C. viridula Michx, Fl. Bor.-Amer., 2: 170 (1803). Type: Canada, between Montréal and Les Trois Rivières, Michaux in herb. Michaux (holotype:P)

Synonyms:

C. serotina Mérat, *Nouv. Fl. Env. Paris*, 2nd ed., **2**: 54 (1821). Type: France, district Seine, Aulnay near Bondy, 21 August 1814, *Mérat* (holotype: **P**)

C. oederi sensu Palmgren, Fl. Fenn., 2: 81 (1959), et sensu Fagerström, Acta Soc. Fauna Fl. Fenn., 79(3): 4 (1967), et auct. mult., non Retz., Fl. Scand. Prodr. 179 (1779), subsp. oederi

C. oederi subsp. fennica Palmgren, Comment. Biol., 20(3): 8 (1958), var. fennica. Type: Finland, Karelia australis, Vehkalahti, Pyhältö, 5 July 1951, Fagerström (holotype: H, not seen)

C. oederi subsp. *fennica* var. *serpentini* Palmgren, *Comment. Biol.*, **20**(3): 10 (1958). Type: Norway, Sör-Tröndelag, Brekken, 23 August 1957, *Kotilainen* (holotype: **H**, not seen).

B1. C. viridula subsp. viridula

B1a. C. viridula subsp. viridula var. viridula

Comparison of European and North American material

The smallest plants of the *C. flava* group are generally called *C. viridula* in North America and *C. serotina* or *C. oederi* in Europe. Some workers (Senay 1950–1951, Kern & Reichgelt in Weevers 1954) suggested that the two taxa are identical, but until now nobody has formally united them.

About 50 individuals from each of a wide range in North America (*C. viridula* subsp. *viridula*) and the comparatively very small area of Switzerland (*C. serotina*) were compared by means of multivariate analyses (Dixon & Brown 1977, Schmid 1980) among themselves and in contrast to the other Swiss representatives (*C. flava* var. *flava* and var. *alpina*, *C. viridula* subsp. *brachyrrhyncha*, and *C. viridula* subsp. *oedocarpa*). Variance analyses and Chi-square tests revealed many significant differences in mean character values between *C. viridula* subsp. *viridula* and *C. serotina*.



FIGURE 1. Discriminant analysis for Swiss material of *C. flava* var. *flava* (\blacksquare) and var. *alpina* (\Box), *C. viridula* subsp. *brachyrrhyncha* (\triangle), *C. viridula* subsp. *oedocarpa* (\blacktriangle), *C. viridula* subsp. *viridula* (formerly *C. serotina*) (\blacklozenge), and North American material of *C. viridula* subsp. *viridula* (\bigcirc). Symbols represent individual plants; overlap by different symbols is indicated by *. Group means: f=*C. flava* var. *flava*, a=*C. flava* var. *alpina*, 1=*C. viridula* subsp. *viridula* from Switzerland, v=*C. viridula* subsp. *viridula* from North America.

B. SCHMID

Nevertheless, the differences were smaller than between any other two recognised taxa. In factor analysis, the three ellipsoids representing C. viridula subsp. oedocarpa, subsp. viridula, and C. serotina showed a great deal of overlap. The most striking evidence that C. viridula subsp. viridula and C. serotina can be incorporated in a single taxon came from cluster analysis: here all but four (three C. serotina and one C. viridula subsp. viridula) individuals of the 'two' taxa developed a very tight C. viridula subsp. viridula/C. serotina-cluster, which contained only a low proportion of the C. viridula subsp. oedocarpa plants and two C. flava var. alpina individuals. Several discriminant analyses with different classification functions and different taxa combinations were carried out, the result of one being shown in Figure 1. From all of them it became clear that while the four taxa C. flava, C. viridula subsp. brachyrrhyncha, C. viridula subsp. oedocarpa and C. viridula subsp. viridula/serotina are distinguishable, this is not true for the two pairs C. flava var. flava/var. alpina and C. viridula subsp. viridula/C. serotina. With the first pair this is due to the existence of morphologically intermediate individuals from the middle of a cline ranging from typical C. flava var. flava to typical C. flava var. alpina. For the second pair one has to explain not why they cannot be properly distinguished, but why there are any differences at all. The reason could be that the observed plants belong to different subsets from the whole set of plants named C. viridula subsp. viridula or C. serotina. The more probable interpretation of the differences between C. viridula subsp. viridula and C. serotina is that I actually compared the subset C. serotina (represented by Swiss material) with the whole set C. viridula subsp. viridula (represented by material from all over North America). The discriminant analysis was a partially successful attempt to distinguish elements of a set from elements of a subset of this set. It should also be mentioned that only 42% of the investigated material from North America possessed male spikes with female spikelets intermingled with the male ones, and that these 'abnormal' inflorescences were sometimes also found in Swiss material; therefore it can no longer serve as the main character for dividing C. viridula subsp. viridula into the two taxa C. viridula subsp. viridula and C. serotina.

Since the North American and European material seems to belong to the same species, the name *C. serotina* can no longer be used, as *C. viridula* is the earlier valid name. It cannot be retained even at a lower rank because the type of *C. viridula* is indistinguishable from plants of the '*C. serotina*' subset of *C. viridula*.

The name C. oederi

The name *C. oederi* must be discussed, because it would gain priority if its legitimacy could be proven. Most taxonomists of the *C. flava* group seem to agree that the type of *C. oederi* in Retzius' herbarium is *C. pilulifera*, yet this mistake remains a controversial subject. Retzius, in a later paper (Retzius 1793), wrote of "*Carex pilulifera*" L. as misunderstood by himself and referred to in *Florae Scandinaviae Prodromus* under the name *C. oederi*. But according to Palmgren (1959) there is also true *C. viridula* under the name *C. oederi* in Retzius' herbarium. The original description is likely to be based on plate 371 in *Flora Danica*. Thus, one might argue that the name *C. oederi* is still legitimate if plate 371 represents *C. viridula* (e.g. Rauschert 1982). But, as Palmgren (1959) already pointed out, the lack of beaks on the utricles shows that it does not; as a consequence the name *C. oederi* must not be used for any taxon of the *C. flava* group. The argument of Palmgren that Retzius perhaps lost the original type and replaced it mistakenly by a specimen of *C. pilulifera* is by no means convincing.

The lower ranking taxa subsp. *fennica* var. *fennica* and var. *serpentini* of Palmgren, especially the latter, seem to be, according to their descriptions, merely states of *C. viridula* subsp. *viridula* var. *viridula*.

B1b. C. viridula subsp. viridula var. bergrothii (Palmgren) B. Schmid stat. et comb. nov. Basionym:

C. bergrothii Palmgren, *Comment. Biol.*, **20**(3): 4 (1958). Type: Finland, Kuusamo, Repuso, 18 July 1940, *M. & A. Palmgren* (holotype: **H**)

Probable synonym:

C. kotilaini Palmgren, *Comment. Biol.*, **20**(3): 6 (1958). Type: Finland, Kuusamo, Tulilampi, 16 July 1937, *M. & A. Palmgren* (holotype: **H**)

According to the type and original description, this taxon stands morphologically between the two

narrow-leaved subspecies *C. viridula* subsp. *brachyrrhyncha* and *C. viridula* subsp. *viridula*, but resembles more the latter. A. O. Chater showed me material from Ireland of *C. viridula* subsp. *viridula*, which sometimes matches *C. bergrothii* perfectly. Similar morphological tendencies, though to a lesser extent, can be found in Switzerland. All these plants are within the range of the taxon *C. viridula* subsp. *viridula*. Thus it seems appropriate to call the most extreme variants with the respective character differences *C. viridula* subsp. *viridula*

It is not clear from which material Palmgren described his *C. kotilaini*. From the description it may be concluded that it should be a *C. viridula* subsp. *viridula* var. *bergrothii* with utricles of the same size as in var. *viridula*. M. & A. Palmgren collected on 16th July, 1937, at Tulilampi, Kuusamo, Finland, the following material:

— Specimens of the holotype, perfect *C. viridula* subsp. *viridula* var. *bergrothii*. One inflorescence was photographed for plate 20 in Palmgren (1959).

— Plant photographed for plate 8 in Palmgren (1959), which most probably belongs to *C. viridula* subsp. *viridula* var. *viridula*.

It is uncertain whether this confusion is due to undetected hybridization and introgression at the type locality.

B1c. C. viridula subsp. viridula var. pulchella (Lönnr.) B. Schmid stat. et comb. nov. Basionym:

C. oederi Ehrhart **pulchella* Lönnr., *Obs. Pl. Suec.*, **24**(1854). Type: Sweden, Gotland, Gothem, 21 July 1853, *Lönnroth* (holotype: **UPS**)

Synonyms:

C. oederi subsp. pulchella Palmgren, Fl. Fenn., 2: 96 (1959)

C. scandinavica E. W. Davies, Watsonia, 3: 66 (1953). Nom. nov. pro C. oederi *pulchella Lönnr.

Lönnroth, in dealing with *C. oederi* Ehrhart **pulchella*, cites type material which most likely belongs to *C. viridula* subsp. *viridula* var. *viridula*, but gives a suitable description for the variety, which distinguishes it from var. *viridula*. Later, Davies and Palmgren provided more accurate descriptions for the same taxon. It is one extreme of the wide, multidimensional range of variation in *C. viridula* subsp. *viridula*, which probably arose as a product of random genetic drift rather than ecoclinal differentiation (Schmid 1980). It is easy to find almost every intermediate between *C. viridula* var. *viridula* and var. *pulchella*.

B2. C. viridula subsp. oedocarpa (N. J. Andersson) B. Schmid comb. nov.

Basionym:

C. oederi *oedocarpa N. J. Andersson, Cyper. Scand. 25 (1849) Synonyms:

Č. oederi subsp. *oedocarpa* (N. J. Andersson) Lange, *Haandb. Danske Fl.*, 4th ed., 144 (1886) *C. tumidicarpa* N. J. Andersson, *Bot. Notiser*, **1849**: 16 (1849). Type: Sweden, Uppland, Rånäs, 1848, *Andersson* (holotype: S)

C. demissa Vahl ex Hartman, Handbok i Scandinaviens Flora 35 (1820). Plate 1342, Flora Danica (lectotype)

C. demissa Hornem., Dansk Oecon. Plantelaere, 3rd ed., 1: 939 (1821)

C. viridula subsp. oedocarpa had for a long time been included in the synonymy of C. viridula subsp. viridula (=C. serotina). Andersson himself first described it as a species under the name C. tumidicarpa but then renamed it as "C. oederi *oedocarpa". According to A. O. Chater (in litt. 1982), "the epithets asterisked in Andersson (1849) (Cyper. Scand.) cannot be considered as subspecies except in the few cases where he says they are subspecies; he often calls them formae, and in other cases, such as *oedocarpa, he gives no indication of their rank. Similarly, the asterisked epithets in Lange, Haandb. Danske Fl., are described as 'Udmaerkede Varieteter' in eds 1–3, and it is only in ed. 4, where he describes them as 'Udmaerkede Varieteter eller Underarter', that they can be accepted as subspecies." It is a broad-leaved, dwarf plant which has the same chromosome number as C. viridula subsp. viridula but is ecologically quite different. The plant photographed by Wiinstedt (1947) and given by him as the type specimen of C. demissa has been lost. Material collected by Vahl in Norway still exists (in herb. Drejer, C) and is very similar to the photograph; it is

likely to belong to the same collection. These plants are small states of *C. flava* or backcrosses with *C. flava* \times *C. viridula* subsp. *oedocarpa*, rather than true *C. demissa* in the sense of Wiinstedt (1947), Senay (1950–1951), Davies (1953) and many later caricologists. The descriptions of Hartman and Hornemann fail to give a clear definition of the taxon. Both authors of *C. demissa*, however, refer to plate 1342 in *Flora Danica* which Chater and I found represents the pure *C. viridula* subsp. *oedocarpa* well enough, although it was probably drawn from one of Vahl's specimens. *C. demissa* is lectotypified here with this plate.

B3. C. viridula subsp. nevadensis (Boiss. & Reuter) B. Schmid stat. et comb. nov. Basionym:

C. nevadensis Boiss. & Reuter, *Pugillus* 118 (1852). Type: Spain, Sierra Nevada, July 1849, *Reuter* (lectotype: G)

Most of the plants originating from southern parts of Europe, especially from the Pyrenees, Corsica, Sardinia, Sicily and Morocco, are morphologically within the limits of *C. viridula* subsp. *oedocarpa*, but sometimes they approach *C. flava* var. *alpina*. The rich type collections of Boissier and Reuter from the Sierra Nevada in Spain show, in fact, a range of morphological variation from plants similar to *C. viridula* subsp. *oedocarpa* to '*C. viridula* subsp. *oedocarpa*-like *C. flava* var. *alpina*'. The lectotype chosen by Burdet, Charpin and Jaquemoud in 1979 and the original description cannot refer to a taxon which could be included in the species *C. flava*, but probably belongs to *C. viridula*. It is suggested that the taxon should be treated as a subspecies of *C. viridula* until more is known about its biology.

B4. C. viridula subsp. cedercreutzii (Fagerström) B. Schmid comb. nov.

Basionym:

C. tumidicarpa subsp. *cedercreutzii* Fagerström, *Acta Soc. Fauna Fl. Fenn.*, **79**(3): 3 (1967). Type: Azores, Terceira, Achada, 4 June 1938, *Cedercreutz* (holotype: H, not seen)

The *C. flava* group is represented on the Azores by very distinctive plants. Fagerström gives an excellent description of the taxon and from this and plant material it is clear that it is closest to *C. viridula* subsp. *oedocarpa*. It seems, however, justified to keep it at the rank of a subspecies because of its geographical and morphological distinctness.

B5. C. viridula subsp. brachyrrhyncha (Čelak.) B. Schmid comb. nov. Basionym:

C. flava subsp. brachyrrhyncha Čelak., Prodr. Fl. Böm., 1: 71 (1867)

Synonyms:

C. lepidocarpa Tausch, Flora (Regensb.), 17: 179 (1834). Type: Czechoslovakia, Praha, (no collector) no. 1636 (?neotype: PRC)

C. lepidocarpa var. *turgida* Palmgren & Florström, *Comment. Biol.*, **20**(3): 15 (1958). Type: Finland, Alandia, Jomala, 5 August 1908, *Palmgren 14* (lectotype: **H**) Probable synonyms:

C. jemtlandica var. *gotlandiae* Palmgren, *Comment. Biol.*, **20**(3): 12 (1958). Type: Sweden, Gotland, Othem, 14 June 1910, *Palmgren* (holotype or lectotype material not seen; isotype: **H**).

C. jemtlandica var. *kainuensis* Palmgren, *Comment. Biol.*, **20**(3): 13 (1958). Type: Finland, Ostrobottnia kajanensis, Suomussalmi, Ruthinaansalmi, Rytisuo, 10 July 1937, *Kyyhkynen* (holotype: **H**)

C. jemtlandica var. jemtlandica pro parte (see below)

B5a. C. viridula subsp. brachyrrhyncha var. lepidocarpa (Tausch) B. Schmid, comb. nov. Basionym:

C. lepidocarpa Tausch, Flora (Regensb.), 17: 179 (1834)

Synonym:

Č. lepidocarpa var. *lepidocarpa* (Tausch) Petermann, *Anal. Pflanzenschl. Leipzig* 509 (1846), pro autonym.

C. flava subsp. lepidocarpa (Tausch) Nyman, Consp. 771 (1882)

C. flava subsp. lepidocarpa (Tausch) Lange, Haandb. Danske Fl., 4th ed., 144 (1886)

B. SCHMID

This taxon has hitherto nearly always been treated as a separate species, with the traditional name *C. lepidocarpa*, by specialists of the *C. flava* group. Celakovsky first gave it subspecific rank and created the new name *C. flava* subsp. *brachyrrhyncha*. As he cited *C. lepidocarpa* as synonym it seems best to consider it based on, and thus typified by, *C. lepidocarpa*. Tausch's description is very short and the name *C. lepidocarpa* was often used in too loose a sense. It has not been possible to locate a type specimen and it is not clear if one even exists. Palmgren, Patzke, Podlech, and many others have identified Swiss herbarium material of *C. flava* var. *flava* backcrosses with 'loose' inflorescences as *C. viridula* subsp. *brachyrrhyncha*. *C. viridula* subsp. *brachyrrhyncha* is best separated from *C. flava* by its narrow leaves (fresh material!). Its close genetic relationship with *C. viridula* subsp. *viridula* is not apparent from its morphology, but is so from its chromosome numbers (n=29–31 in *C. flava*, n=34 in *C. viridula* subsp. *brachyrrhyncha*, n=34-36 in *C. viridula* subsp. *viridula*).

Palmgren's *C. lepidocarpa* var. *turgida* is probably not worth recognizing. Two varieties and part of the typical *C. jemtlandica* from Palmgren could also well belong to *C. viridula* subsp. *brachyrrhyncha* var. *lepidocarpa*. Here again, more information about their karyology and ecology, and experimental data, are necessary to identify the taxa.

B5b. C. viridula subsp. brachyrrhyncha var. scotica (E. W. Davies) B. Schmid stat. et comb. nov. Basionym:

C. lepidocarpa subsp. *scotica* E. W. Davies, *Watsonia*, **3**: 71 (1953). Type: Scotland, Mid Perth, Creag-an-Lochain, alt. 1000 m, 4 September 1951, *Davies* (holotype: **BM**)

This taxon, described in Britain by Davies as one extreme of a topocline correlated with altitude and latitude which remains constant in cultivation, is analogous with *C. flava* var. *alpina* and should probably have a corresponding taxonomic rank.

DISCUSSION

The revision of the European taxa of the *C. flava* group presented here was made after six years of field and experimental work on the biology of the Swiss representatives *C. flava* var. *flava* and var. *alpina, C. viridula* subsp. *brachyrrhyncha, C. viridula* subsp. *oedocarpa,* and *C. viridula* subsp. *viridula*. The majority of the populations investigated from a demographical, ecological, biometrical, and karyological viewpoint during the course of this period are also represented by much herbarium material accumulated over many decades in Swiss collections. It was thus possible to see how caricologists like Kükenthal, Samuelsson, Thellung, Palmgren, Patzke and Podlech determined the same material and interpreted it according to their various concepts of the *C. flava* group. From all these comparisons the conclusion was reached that, in this highly critical group, a classification based only on the morphology of dried specimens cannot represent all the genetic relationships and similarities between the taxa involved. The reasons for this are:

1. It is often overlooked that members of the group, when growing together, usually show evidence of introgressive hybridization (Schmid 1982), which causes a wide range of variation within taxa. Some recombinants are easily misinterpreted as distinct entities.

2. A large part of the variability can be environmentally induced, such as, for example, dwarfing and deformations in dry conditions or when trampled, 'spongy' broad leaves when submerged, etc.

3. Some characters, such as the colour of different parts of the plant, stem height, and form of the utricle, change during the post-floral growth of tillers; others, e.g. width of the leaf, or straightness of the stem, change during the drying process in collected material. A single taxon can be described in different ways according to its age or whether fresh or dried material is analysed.

The classification given in this paper is thus of limited value where only morphological information is available. This applies especially to material from Scandinavia and south-western Europe. To leave the provisional classification open for later refinements, a conservative tactic, i.e. one which accepts only the most distinctive of the different taxa described so far in the literature, has been adopted in such cases. The justification for this lies in the assumption that there is a trend within the *C. flava* group to overestimate the number of taxa when considering only their morphology.

The differences between Chater's (1980) treatment of the *C. flava* group in *Flora Europaea* and the treatment given here are represented in Table 1.

TABLE 1. COMPARISON OF THE CLASSIFICATION OF THE C. FLAVA GROUP GIVEN IN FLORA EUROPAEA AND IN THIS PAPER.

CHATER (1980)	SCHMID
C. flava	C. flava var. flava
	C. flava var. alpina
C. jemtlandica	C. flava var. flava, or C.
	viridula subsp. brachyrrhyncha
	var. lepidocarpa
C. lepidocarpa	C. viridula subsp. brachyrrhyncha var.
	lepidocarpa and var. scotica
C. demissa subsp. demissa	C. viridula subsp. oedocarpa
[C. demissa] subsp. cedercreutzii	C. viridula subsp. cedercreutzii
C. nevadensis pro parte	C. viridula subsp. nevadensis
C. bergrothii	C. viridula subsp. viridula var.
	bergrothii
C. serotina subsp. serotina	C. viridula subsp. viridula var.
	viridula
C. serotina subsp. pulchella	C. viridula subsp. viridula var.
	pulchella

ACKNOWLEDGMENTS

I thank A. O. Chater for considerable help with nomenclatural problems and much discussion and comment which helped to improve the manuscript, and C. D. K. Cook for reading two earlier drafts of the manuscript. In discussion with A. O. Chater, R. W. David, and A. C. Jermy I reached the decision to reduce the number of species from four (*C. flava, C. lepidocarpa, C. demissa, C. viridula*) to two (*C. flava, C. viridula*). I also thank the keepers of the herbaria **BAS, BERN, BM, C, COI, FI, G, H, LAU, LE, LISU, MA, NEU, P, PRC, S, TRT, UPS, Z, ZT** for providing plant material and information about type specimens.

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(Accepted December 1982)