A re-assessment of the putative *Carex flava* agg. (Cyperaceae) hybrids at Malham Tarn (v.c. 64): A morphometric analysis

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ABSTRACT

Carex flava L., a rare species in the British Isles, is currently only recognised from one extant population. The presence of three putative *C. flava* × *C. viridula* Michx. subsp. *brachyrrhyncha* (Čelak.) B. Schmid hybrid (= *C.* × *alsatica* Zahn.) populations suggests that it may have formerly been more widespread. Alternative taxonomic treatments have been considered populations, including the possibility that they could be *C. flava* subsp. *jemtlandica* (Palmgr.) P. D. Sell, a Fennoscandian taxon not previously recorded in this country. Uni- and multivariate statistical analyses were used to elucidate the taxonomic affinity of the largest of these populations. A new combination *C. flava* subsp. *jemtlandica* to ***C. viridula*** Michx. subsp. ***brachyrrhyncha*** (Čelak.) B. Schmid var. ***jemtlandica*** (Palmgr.) Blackstock & P. A. Ashton, is made to bring the nomenclature of this taxon in line with the current nomenclature of this group. The presence of a second extant population of *C. flava* in the British Isles is also reported.

KEYWORDS: *Carex viridula* subsp. *brachyrrhyncha* var. *jemtlandica,* Principal Components analysis (PCA), ANOVA, Discriminant Analysis (DA).

INTRODUCTION

In the British Isles *Carex flava* L. (Large Yellow Sedge) is currently only recognised from one extant population and one historic record. In addition, populations generally considered to consist of *C. flava* × *C. viridula* Michx subsp. *brachyrrhyncha* (Čelak.) B. Schmid hybrids (= *C.* × *alsatica* Zahn) have been recorded from three sites; the Tarn Moss, Malham (v.c. 64) (Shaw 1946), Greywell Moors, Hants (v.c. 11) (Brewis *et al.* 1996) and by the River Corrib near Menlough, north-east of Galway City (v.c. H17) (Perring 1970). *C. flava* is considered to have formerly been extant at these localities but is now believed to be extinct, probably through hybridisation with *C. viridula.* subsp. *brachyrrhyncha* (Jermy *et al.* 1982). *C. flava* is categorised in *The British Red Data Book: 1. Vascular Plants* (Taylor 1999) as vulnerable in Britain, but not threatened in Europe. Populations are also found in Western and Eastern North America at latitudes similar to those in Europe.

Although early Floras covering the various regions of the British Isles are littered with accounts for *C. flava s. l.* (e.g. Goodenough 1792; Green 1933), the first authenticated specimen for *C. flava s. s.* was collected by J. Dickinson in 1836, somewhere in the Ennerdale area of Cumbria (v.c. 70). This population is now only known from one voucher specimen (**LIV**), although doubts as to the authenticity of the site locality have been raised (Halliday 1997). Evidence of a population previously unaccounted for in the British Floras comes from a herbarium specimen collected by T. W. Edmondson from Hebden, W. Yorks (v.c. 64) in 1906. This population is also only known from one voucher specimen (**GH**) which has been examined by W. J. Crins and has been determined by him to be *C. flava s. s.* (Crins 1985).

The only currently recognised extant population of *C. flava s. s.* is at Roudsea Wood, Haverthwaite, Cumbria (v.c. 69) being discovered by D. Lumb in 1913 (*B.E.C. Rpt vol* III pt VI p. 504). The Roudsea Wood population is well known and the number of plants there appears to be relatively stable at around 1500–2000 presumed genets (Blackstock, unpublished data).

In 1946 G. A. Shaw reported *C. flava* from the Tarn Moss, Malham (v.c. 64). This population was also referred to as *C. flava s. s.* by Davies (1953). However, doubts as to the true identity of this population were raised by Jermy & Tutin (1968). They state that "the only typical material" of

C. flava in Britain "is from N. Lancs" i.e. Roudsea Wood. Jermy *et al.* (1982) state categorically that "plants intermediate to *C. flava* and *C. lepidocarpa* Tausch. (= *C. viridula* subsp. *brachyrrhyncha*) ...occur at Malham Tarn, Lough Corrib and N. Hants, where *C. flava* presumably once occurred but is now extinct". Stace (1997) reiterates this view by formally referring to these populations as *C.* × *alsatica.*

A different approach to the putative *C.* × *alsatica* populations found at Malham Tarn, Lough Corrib and Greywell Moors has been taken by Sell & Murrell (1996) who classify them as *C. flava* subsp. *jemtlandica* (Palmgrn.) P. D. Sell (= *C. jemtlandica* Palmgrn.). This taxon is generally regarded as a Fennoscandian endemic (Hedrén & Prentice 1996; Pykälä & Toivonen 1994) and has not previously been recognised in the British Isles.

Clearly the Malham Tarn, Lough Corrib and Greywell Moors populations of yellow sedges have been subject to a degree of taxonomic confusion. Davies (1953) considers them to be *C. flava s. s.*; Jermy *et al.* (1982) consider them to be *C.* × *alsatica*, a *C. flava* × *C. viridula* subsp. *brachyrrhyncha* hybrid; while Sell & Murrell (1996) treat them as a subspecies of *C. flava* comparable with their classification of other *C. flava* subspecies.

Multivariate statistical analyses have been successfully used to clarify taxonomic problems in *Carex* complexes e.g. sects. *Vesicariae* (O. F. Lang) Christ. (Shepherd 1975), *Phyllostachys* (J. Carey) L. H. Bailey (Naczi *et al.* 1998) and *Ceratocystis* Dumort. (Crins 1985). Studies within sect. *Ceratocystis* have utilised multivariate statistical methods such as Detrended Correspondence Analysis (DCA) (Schmid 1980), Principal Components Analysis (PCA) (Crins 1985) and Discriminant Analysis (DA) (Crins 1985) based upon herbarium specimens. The use of two of these methods (PCA and DA) on living specimens of *C. flava, C. viridula* subsp. *brachyrrhyncha*, the putative *C.* × *alsatica* from Malham Tarn and *C. jemtlandica* has been adopted here to elucidate the taxonomic boundaries between these taxa. This study includes plants from North America, the British Isles and continental Europe and seeks to place the British and Irish taxa into a wider context, while clarifying the taxonomic status of the problematic Malham Tarn yellow sedges.

MATERIALS AND METHODS

Specimens were collected in the field, either as ramets or seed, from clumps situated at least 3 m apart from each other. Members of the *C. flava* agg. have a caespitose growth habit, so each sample was presumed to represent an individual genet. The individual specimens were cultivated under similar conditions at Edge Hill for 1–2 years until the plants had reached maturity. Specimens of *C. flava* from Canada provided a valuable comparison, as these populations are approximately 700 km away from the nearest *C. viridula* subsp. *brachyrrhyncha* population. Voucher specimens are currently held at Edge Hill College of Higher Education and it is intended that they will be deposited at **LIV** upon completion of the associated work. Details of the specimen localities are given in Table 1. Four a priori groups (Table 1) were identified for analysis: 1. *C. flava,* (40 specimens, eleven populations); 2. The putative *C.* × *alsatica* from Malham Tarn (MT) (ten specimens, one population); 3. *C. viridula* subsp. *brachyrrhyncha* (40 specimens, 13 populations) and 4. *C. jemtlandica* (ten specimens, four populations). All of the *C. jemtlandica* sites were included in a study of *C. lepidocarpa s. l.* (Hedrén & Prentice 1996). The specimens collected from Dalbyn, near Ore, Dalarna, Sweden are from the same site as specimens collected and photographed by Palmgren for his monograph of the *C. flava* agg. (Palmgren 1959). As no single classification recognises all of these groups, they will be referred to as listed above until their status is re-assessed later in this paper. The putative *C.* × *alsatica* from Greywell Moors is only known from a single plant and this has not been seen in recent years. Therefore this population has not been included in our analyses. In addition, it has not been possible to obtain samples of the putative *C.* × *alsatica* from Ireland.

Multivariate analyses provide a preliminary re-assessment of the a priori classification and of the phenetic relationships between the taxa. Eleven characters (Table 2) were included in the morphometric analysis. All morphometric data were derived from living plants that were producing a fertile culm with perigynia containing well-developed nutlets. This eliminated the possibility that F1-hybrids could be included in the data set and ensured that only complete data

TABLE 1. LOCALITIES OF THE POPULATIONS OF YELLOW SEDGES INCLUDED IN THE PCA. TAXON REFERS TO THE A PRIORI CLASSIFICATION OF THE GROUPS

Species Location	Country	Location	Number of individuals sampled	Taxon
Nr. Campbellville, Halton Co., Ontario	Canada	43°31'N 79°59'W	2	*C. flava*
Nr. Orangeville, Peel Co. Ontario	Canada	43°53'N 80°06'W	1	*C. flava*
8 km NW Tranås, Smaland	Sweden	58°06'N 14°58'E	2	*C. flava*
Tännäs, Härjedalen	Sweden	62°40'N 12°41'E	2	*C. flava*
Sjugelmyren, Sörboda, Dalarna	Sweden	61°07'N 15°13'E	1	*C. flava*
Lake Essen, Nr. Rättvik, Dalarna	Sweden	60°57'N 15°13'E	4	*C. flava*
Västanå, Boda, Dalarna	Sweden	60°59'N 15°12'E	7	*C. flava*
Romedenne	Belgium	50°10'N 04°42'E	5	*C. flava*
Roudsea Wood, Cumbria	England	54°14'N 03°08'W	6	*C. flava*
Nittedal Hakadal	Norway	60°05'N 10°50'E	9	*C. flava*
Kärnten	Austria	47°N 13°E	1	*C. flava*
Malham Tarn Fen, Mid-west Yorkshire	England	54°06'N 02°11'W	10	MT
Stromyren, Boda, Dalarna	Sweden	61°01'N 15°13'E	2	*C. jemtlandica*
Vadeermyran, Hammerdal, Jämtland	Sweden	62°52'N 15°16'E	3	*C. jemtlandica*
Ljusnedal, Härjedalen	Sweden	62°48'N 12°36'E	2	*C. jemtlandica*
Dalbyn,Ore, Dalarna	Sweden	61°08'N 15°10'E	3	*C. jemtlandica*
Benestads Bakan, Tomelilla, Skåne	Sweden	55°57'N 13°53'E	4	*C. viridula* subsp. *brachyrrhyncha*
Lyngsjon Lake, Skåne	Sweden	55°48'N 13°53'E	4	*C. viridula* subsp. *brachyrrhyncha*
Hiiumaa Island	Estonia	59°10'N 22°30'E	2	*C. viridula* subsp. *brachyrrhyncha*
Locheres	France	47°41'N 04°55'E	1	*C. viridula* subsp. *brachyrrhyncha*
Crummack Farm, Inglebrough, N. Yorkshire	England	54°08'N 02°21'W	1	*C. viridula* subsp. *brachyrrhyncha*
Crummack Dale, Inglebrough, N. Yorkshire	England	54°08'N 02°21'W	4	*C. viridula* subsp. *brachyrrhyncha*
Malham Tarn outflow, Mid-west Yorkshire	England	54°06'N 02°11'W	6	*C. viridula* subsp. *brachyrrhyncha*
Woodbastwick, E. Norfolk	England	52°41N 01°27'E	3	*C. viridula* subsp. *brachyrrhyncha*
Greywell Moor, Hants.	England	51°15'N 00°58'W	1	*C. viridula* subsp. *brachyrrhyncha*
Hawes Water, Lancashire	England	54°11'N 02°48'W	6	*C. viridula* subsp. *brachyrrhyncha*
Fearnan, Loch Tay, Perth & Kinross	Scotland	56°47'N 03°48'W	1	*C. viridula* subsp. *brachyrrhyncha*
Glen Fender, Perth & Kinross	Scotland	56°34'N 04°05'W	5	*C. viridula* subsp. *brachyrrhyncha*
Prission, S-Tirol	Austria	47°N 12°E	2	*C. viridula* subsp. *brachyrrhyncha*

sets were included for subsequent analysis. Measurements were taken using Rabone vernier calipers graduated to 0·1 mm, with the exception of a coarse measurement (character VEGLEAF) which was measured to the nearest mm using a standard 30 cm line ruler. Previous morphometric studies, either within the *C. flava* agg. or *Carex* sub-genus *Carex,* have utilised a greater number of morphological characters (e.g. Shepherd 1975; Schmid 1980; Crins 1985; Hedrén 1998; Naczi *et al.* 1998). However, many of the characters included in the above studies are associated with the position of the pistillate spikelets. Such spikelets are not necessarily equivalent within the *C. flava* agg. Therefore, they and their associated characters have not been included in this study.

Characters BEAKL, PERLE and BRISTLE are all associated with the perigynia. Crins (1985) and Rothrock *et al.* (1997) noted that there was greater variability in perigynia from the lower parts of the pistillate spikelets. Therefore perigynia from the mid-section of the pistillate spikelets were used for the measurements of all perigynia characters. All characters were then used in PCA to summarise variation patterns within all of the taxa studied. Data were standardised for PCA so that

TABLE 2. MORPHOLOGICAL CHARACTERS, WITH THEIR ABBREVIATIONS, MEASURED FROM LIVING PLANT SPECIMENS OF THE *CAREX FLAVA* AGG. ALL CHARACTERS WERE INCLUDED IN THE PCA AND ANOVA

Character	Abbreviation
Vegetative leaf length/width ratio	VEGLEAF
Vegetative leaf width at base (mm)	VEGBAS
Ligule length (mm)	LIGL
Male spikelet length (mm)	MSPIKE
Male spikelet peduncle length (mm)	MPEDL
Beak length	BEAKL
Perigynum length (mm)	PERLE
Male glume length/width ratio	MGLUM
Female glume length/width ratio	FGLUM
No. bristles on one side of the perigynum	BRISTLE
Nutlet length excluding beak (mm)	NUTL

each variable would have a mean of 0 and a standard deviation of 1. PCA was carried out using the Multivariate Statistical Package version 3.0 from Kovach Computing Services (Kovach 1998). Data were further analysed using a stepwise DA (S.P.S.S. 1998).

Univariate statistical analyses (mean, range and standard deviation) were performed on all characters using Microsoft Excel 97. Differences in the mean values for single characters between all the taxa were tested using one way analysis of variance (ANOVA) with the data first being tested for variance equivalence using the F-test.

RESULTS

Scatter plots of the principal components PC I vs PC II (Fig. 1) and for PC I vs PC III (Fig. 2) for all the taxa and individuals depict two clusters. These can be identified as a *C. flava*/MT cluster and *C. viridula* subsp. *brachyrrhyncha*/*C. jemtlandica* cluster. No sub-clusters were evident within the *C. flava*/MT cluster. All individuals from the MT cluster with the *C. flava* individuals and are not intermediate between *C. flava* and *C. viridula* subsp. *brachyrrhyncha*. From Figs 1 and 2, two sub-clusters within the *C. viridula* subsp. *brachyrrhyncha*/*C. jemtlandica* cluster associated with *C. viridula* subsp. *brachyrrhyncha* and *C. jemtlandica* may be identified. However, the separation is not complete.

The first two principal components account for 46·6% of the variance within the data set, with PC I accounting for 32·5% and PC II accounting for 14·1%. PC III accounts for a further 11·5% of the variance within the data set. The variables with the highest component loadings (Table 3) on PC I are, in descending order, variables PERL, BEAKL, BRISTLE, MPEDL and LIGL. The first three variables are all associated with the perigynium. The highest component loading on PC II and PC III are for characters MSPIKE, VEGBAS, LIGL and NUTL, FGLUM respectively.

Morphometric data from the 100 specimens of the *C. flava* agg. were further analysed using a stepwise DA. The initial DA was constructed using the four a priori groupings listed above. The program selected eight differentiating variables in the following descending order: MPEDL, BRISTLE, NUTL, BEAKL, MGLUM, VEGLEAF, LIGL and FGLUM. DA succeeded in correctly classifying 94% of the group cases (Fig. 3). The first canonical discriminant function (CDF I) accounted for 76·1% of the variance, with 17·4% and 6·5% of the variance being accounted for on CDF II and CDF III (not shown) respectively. The greatest contribution to variate one is given, in descending order, by MPEDL, BEAKL, BRISTLE and FGLUM. Along variate two NUTL, VEGLEAF and LIGL give the greatest contribution.

A second DA was then carried out on the same data set with the exception that the *C. flava* and MT populations were condensed into one group. The discrimination efficiency improved to classify 99% of the group cases correctly. However, condensing the groups gave a similar pattern and spatial arrangement to that seen in Fig. 3. The first canonical discriminant function (CDF I)

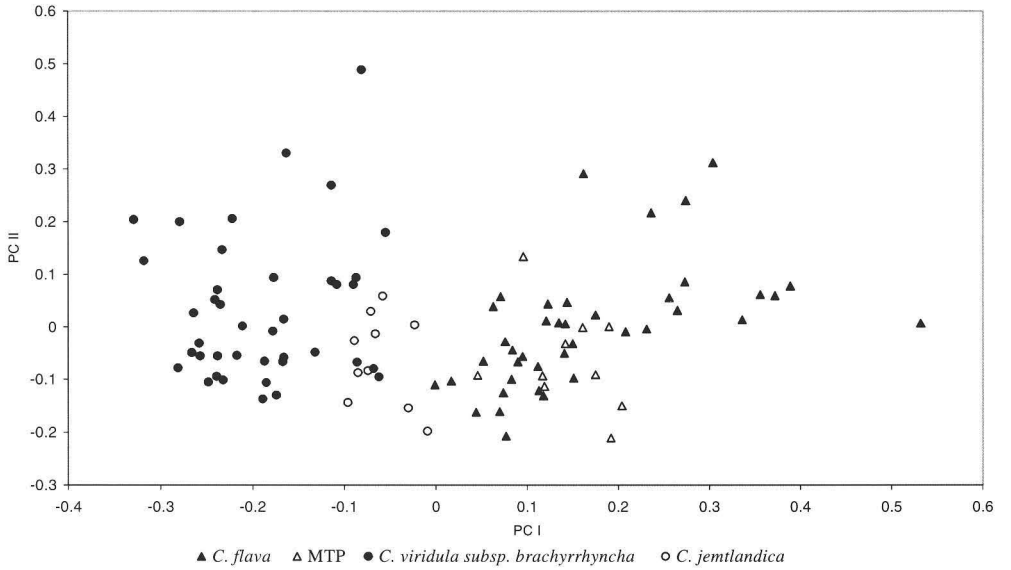

FIGURE 1. Scatter plot of PC I vs PC II from PCA of the measurements of *C. flava*, MTP, *C. viridula* subsp. *brachyrrhyncha* and *C. jemtlandica*.

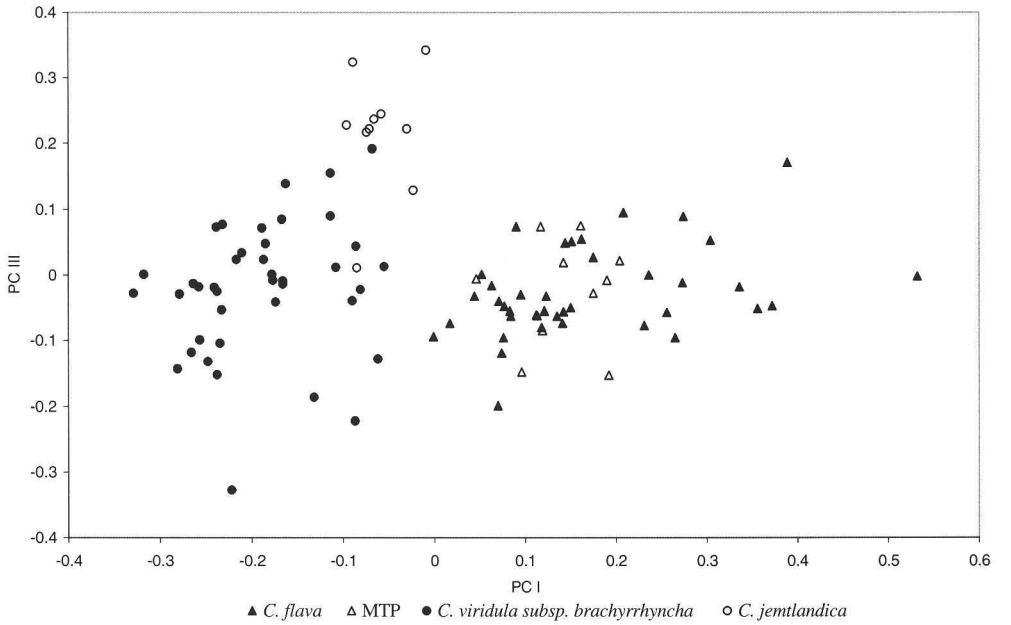

FIGURE 2. Scatter plot of PC I vs PC III from PCA of the measurements of *C. flava*, MTP, *C. viridula* subsp. *brachyrrhyncha* and *C. jemtlandica*.

TABLE 3. LOADINGS FOR THE FIRST THREE PRINCIPAL COMPONENTS FROM PCA OF SPECIMENS OF *C. FLAVA*, THE MT POPULATION, *C. VIRIDULA* SUBSP. *BRACHYRRHYNCHA* AND *C. JEMTLANDICA*.

Character	PC I	PC II	PC III
VEGLEAF	0·160	0·294	0·230
VEGBAS	0·277	0·452	-0·084
LIGL	0·328	0·422	-0·126
MSPIKE	-0·197	0·550	0·131
MPEDL	-0·399	0·234	-0·071
BEAKL	0·415	-0·134	-0·016
PERLE	0·446	0·034	0·041
MGLUM	0·209	-0·203	0·288
FGLUM	0·075	-0·258	-0·633
BRISTLE	0·407	0·023	-0·118
NUTL	0·077	-0·217	0·634

Abbreviations follow Table 2.

accounted for 83·5% of the variance, with 16·5% of the variance being accounted for on CDF II. The greatest contribution to variate one is given, in descending order, by MPEDL, BRISTLE , BEAKL and FGLUM. Along variate two NUTL, VEGLEAF and LIGL give the greatest contribution.

Results for the univariate analyses of the mean, standard deviation and range for each character are given in Table 4. A one-way ANOVA of each individual character showed no significant differences in the mean values between the taxa included in the *C. flava* and MT cluster. Significant differences were identified between the taxa in the *C. flava*/ MT cluster and the taxa included in the *C. viridula* subsp. *brachyrrhyncha*/*C. jemtlandica* cluster. However no single character could be identified that clearly delimited the taxa as all characters had some degree of overlap in their range. This is consistent with previous studies on the *C. flava* agg. (e.g. Schmid 1980; Havlícková 1982; Crins 1985; Pykälä & Toivonen 1994). The perigynium characters BEAKL, PERLE and BRISTLE were found to be significantly different ($p<0·05$) between the *C. flava*/ MT cluster and the *C. viridula* subsp. *brachyrrhyncha*/*C. jemtlandica* cluster.

Although the sample size of *C. jemtlandica* from Sweden is very small, PCA gives a clear disjunction along PC I between these and the MT plants. DA gives a similar disjunction along CDF I. This is further supported by results of the ANOVA, which reveals statistically significant differences in the mean values for characters MSPIKE, BEAKL, BRISTLE, PERLE and NUTL ($p<0·05$) between the two groups. Within the *C. viridula* subsp. *brachyrrhyncha*/*C. jemtlandica* cluster the mean length of characters MPEDL and NUTL gave the clearest differentiation ($p<0·001$) between *C. viridula* subsp. *brachyrrhyncha* and *C. jemtlandica* with characters PERLE and BEAKL also being significantly different ($p<0·01$).

DISCUSSION

Morphometric analysis does not support the classification of *C. jemtlandica* as a subordinate taxon of *C. flava*. From PCA there is marked separation along PC I between *C. jemtlandica* and *C. flava* and between *C. jemtlandica* and the MT plants. However, *C. jemtlandica* is not clearly differentiated from *C. viridula* subsp. *brachyrrhyncha* although it does form a sub-cluster within this group. Differentiation between *C. jemtlandica* and *C. flava* and between *C. jemtlandica* and the MT plants is maintained in the results of the DA with marked separation along CDF I. Unlike the results from PCA *C. jemtlandica* forms a distinct cluster when CDF I is plotted against CDF II. However, this cluster is not clearly separated from the *C. flava*/MT or *C. viridula* subsp. *brachyrrhyncha* clusters along either CDF I or CDF II individually. These results support the close phenetic relationship that exists within the *C. flava* agg. *C. viridula* subsp. *brachyrrhyncha* and *C. jemtlandica* have been recognised as two distinct species under the names *C. lepidocarpa* (= *C. viridula* subsp. *brachyrrhyncha*) and *C. jemtlandica* respectively (Palmgren 1938;

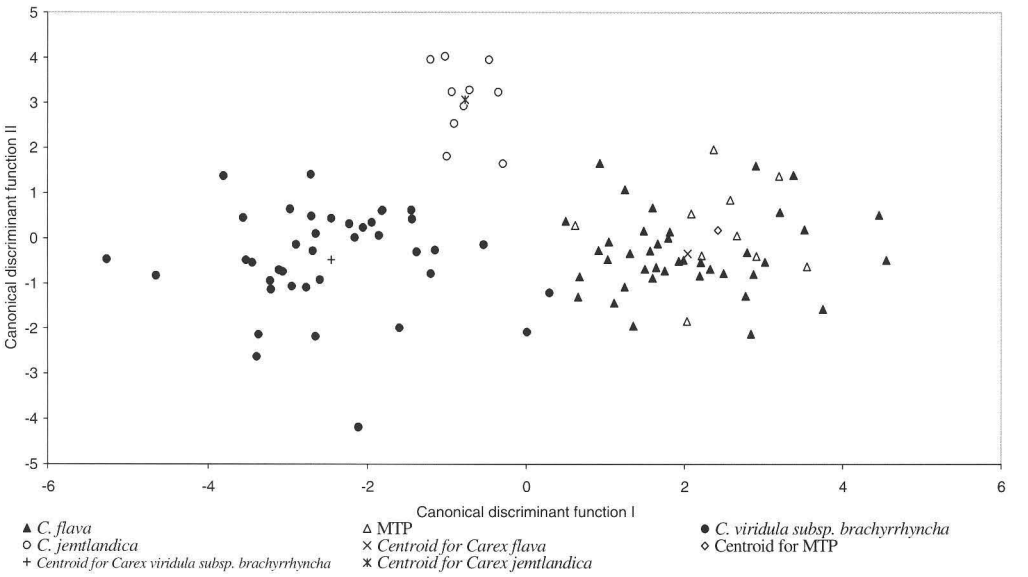

FIGURE 3. Scatter plot of CDF I vs CDF II for the measurements of *C. flava*, MTP, *C. viridula* subsp. *brachyrrhyncha* and *C. jemtlandica*.

Halkka *et al.* 1992); however, they are generally united by Scandinavian botanists under the name *C. lepidocarpa* and accorded subordinate rank as *C. lepidocarpa* subsp. *lepidocarpa* and *C. lepidocarpa* subsp. *jemtlandica* (Palmgr.) Palmgr. (Palmgren 1926, 1959; Pykälä & Toivonen 1994; Hedrén & Prentice 1996). *C. lepidocarpa* subsp. *jemtlandica* is described by Hedrén (1996) as endemic to Fennoscandia, largely replacing *C. lepidocarpa* subsp. *lepidocarpa* north of the *limes norrlandicus*. This northern distribution is reflected in the original name (*nomen nudum*) given to this taxon in 1910 by Palmgren as *C. lepidocarpa* Tausch * *septentrionalis* Palmgr. forma *jemtlandica*. Extensive studies on morphology (Hedrén 1994, 1996) and genetic differentiation using allozymes (Hedrén & Prentice 1996) support the recognition of this taxon as a subordinate of *C. lepidocarpa* (=*C. viridula* subsp. *brachyrrhyncha*).

On the basis of work on demography, ecology, karyology, hybridisation and morphology of Swiss material Schmid (1983) reduced the status of *C. lepidocarpa* to that of a subspecies of *C. viridula* Michx. He further considered that the name of *brachyrrhyncha* Čelakovsky to have priority over that of *lepidocarpa*. Former subspecies of *C. lepidocarpa* were thus recognised as subordinate taxa of *C. viridula* subsp. *brachyrrhyncha* and given varietal status. The exception to this was *C. jemtlandica,* which Schmid did not recognise at any level (cf. Schmid 1983). Based on biometric analysis of herbarium specimens Crins (1985) similarly concluded that *C. jemtlandica* did not merit recognition at any taxonomic level. However, the studies by Schmid (1983) and Crins (1985) included specimens of *C. jemtlandica* collected from a greater geographical range, extending as far south as Switzerland, than the range of the taxon recognised by Hedrén (1996). Crins further renamed *C. viridula* subsp. *brachyrrhyncha* var. *lepidocarpa* as *C. viridula* subsp. *brachyrrhyncha* var. *elatior* (Schltdl.) Crins.

Studies of allozyme variation by Bruederle & Jensen (1991) within the *C. flava* agg. concluded that *C. flava* was enzymatically distinct from *C. viridula*, but that within *C. viridula* agg. clear differentiation was not possible. However, they noted that *C. viridula* subsp. *brachyrrhyncha* formed a relatively distinct group within the aggregate. They concluded that their data were insufficient to justify a reclassification of this taxon and so they retained the classification of Schmid. They also reported that *C. jemtlandica* was not separable from *C. flava* using allozymes. This is in contrast to Hedrén & Prentice (1996) who found in their larger study of *C. jemtlandica* that it was enzymatically distinct. Pykälä & Toivonen (1994) suggest that Bruederle & Jensen may have included specimens of *C. flava* in their study rather than *C. jemtlandica*.

TABLE 4. MEAN, RANGE AND ± 1 SD FOR MORPHOLOGICAL CHARACTERS MEASURED FOR SPECIMENS OF *C. FLAVA*, THE MT POPULATION, *C. VIRIDULA* SUBSP. *BRACHYRRHYNCHA* AND *C. JEMTLANDICA*.

Character	*C. flava* (n=40)	MT (n=10)	*C. viridula* subsp. *brachyrrhyncha* (n=40)	*C. jemtlandica* (n=10)
VEGLEAF	53·41 (±18·48)	39·28 (±5·97)	40·95 (±19·17)	55·82 (±27·70)
	21·41–105·05	31·77–52·79	11·22–107·76	21·27–109·83
VEGBAS	5·46 (±1·48)	5·10 (±1·24)	4·23 (±1·28)	3·69 (±0·47)
	3·02–11·78	3·50–7·29	2·30–8·79	2·89–4·54
LIGL	3·68 (±1·57)	2·57 (±1·07)	2·04 (±1·58)	1·21 (±0·37)
	1·15–8·25	1·50–5·21	0·81–9·42	0·70–1·80
MSPIKE	11·48 (±4·25)	9·72 (±1·80)	15·17 (±5·18)	15·64 (±5·01)
	3·81–22·01	6·79–13·12	5·32–24·89	9·63–25·51
MPEDL	1·61 (±1·85)	1·03 (±1·21)	13·86 (±7·50)	6·41 (±3·06)
	0·00–6·58	0·00–2·42	0·00–36·34	3·81–11·24
BEAKL	2·18 (±·038)	2·32 (±0·27)	1·45 (±0·31)	1·82 (±0·17)
	1·17–3·00	1·94–2·82	0·73–2·38	1·61–2·01
PERLE	5·08 (±0·73)	5·14 (±0·46)	3·80 (±0·27)	4·49 (±0·57)
	4·02–6·63	4·51–5·74	3·12–4·48	3·72–5·28
MGLUM	3·19 (±0·44)	3·11 (±0·39)	2·73 (±0·38)	3·01 (±0·51)
	2·27–4·23	2·11–4·01	2·06–3·45	2·35–3·65
FGLUM	2·09 (±0·29)	2·00 (±0·31)	1·92 (±0·36)	1·69 (±0·21)
	1·53–3·10	1·72–2·61	1·14–2·65	1·38–1·99
BRISTLE	7·33 (±2·03)	8·40 (±1·71)	3·50 (±1·92)	4·10 (±0·74)
	3–11	5–11	0–8	3–5
NUTL	1·60 (±0·13)	1·73 (±0·11)	1·56 (±0·19)	1·96 (±0·17)
	1·37–1·91	1·61–1·91	0·92–1·38	1·68–2·21

Abbreviations follow Table 2.

Although the present study shows that morphological differences between *C. viridula* subsp. *brachyrrhyncha* and *C. jemtlandica* are not fully developed there is a degree of separation indicated by the PCA and DA analyses. The same chromosome number of 2n=68 and limited morphological distinction supports the recognition of these taxa at a very close taxonomic level. However, caricologists working in Fennoscandia, where both *C. viridula* subsp. *brachyrrhyncha* and *C. jemtlandica* occur, consistently classify them as distinct taxa (e.g. Palmgren 1959; Pykälä & Toivonen 1994; Hedrén 1996). We support the recognition of *C. jemtlandica* at a subordinate level to that of *C. viridula* subsp. *brachyrrhyncha*. In order to bring the current nomenclature for *C. jemtlandica* into line with that used by Crins (1985) it is proposed that this taxon be renamed ***C. viridula*** Michx subsp. ***brachyrrhyncha*** (Čelak.) B. Schmid var. ***jemtlandica*** (Palmgr.) Blackstock & P. A. Ashton ***comb. et stat. nov***.

The hypothesis that the MT plants are of hybrid origin is not supported by this study. Jermy *et al.* (1982) preferred to recognise hybrids as being both morphologically intermediate between the parents and also being wholly sterile. However, they acknowledged that the MT plants are fertile. It is implied that this fertility may be due to the population being a stabilised introgressed hybrid between *C. flava* and *C. viridula* subsp. *brachyrrhyncha*, with the former species now being extinct at this site. In Switzerland natural and cultivated hybrid populations between *C. flava* and *C. viridula* subsp. *brachyrrhyncha* have been studied by Schmid (1983). F1-hybrids were found to be almost completely sterile with 0% seed set and pollen fertility of only 0–c.3% (Schmid 1983). When directional backcrosses do arise, forms identical to the parent species in both morphology and fertility may eventually result. In these populations it is *C. viridula* subsp. *brachyrrhyncha* that may be out-competed and eventually ousted by *C. flava*, the F1-hybrid or backcrosses with either parent (Schmid 1980). This does not fit with the model cited by Jermy *et al.* (1982) who suggested that *C. flava* was probably eliminated by introgression with *C. viridula* subsp. *brachyrrhyncha*, and the putative hybrids at Malham Tarn, Greywell Moors and Lough Corrib being a product of

TABLE 5. PERIGYNIUM LENGTHS (MM) FOR *C. FLAVA*

Author and Year	Area	Perigynium length (mm)
Robertson (1984)	North America	3·0–6·0
Hedrén, *in litt.*	Sweden	3·5+
Havlícková (1982)	Czechoslovakia	3·8–6·3
Crins (1985)	North America	4·0–6·3
Mackenzie (1935)	North America	4·5–6·0
Schmid (1985)	Europe	4·5–6·0
Palmgren (1958)	Scandinavia	4·5–6·7
Hultén (1968)	North America	5·0–6·0
Chater (1980)	Europe	5·0–7·0
Nelmes (1945)	UK	5·0–7·0
Sell & Murrell (1996)	UK	5·0–7·0
Davies (1953)	UK	5·25–7·0
Stace (1997)	UK	5·5–6·5
Jermy *et al.* (1982)	UK	6–6·5
Rose (1989)	UK	6–6·5

this process. The hypothesis that the MT plants are intermediate in morphology is also unsupported, as there is marked separation in the PCA along PC I between *C. viridula* subsp. *brachyrrhyncha* and the MT plants, but no separation between *C. flava* and the MT plants. A similar separation occurs along CDF I using DA. Based on the biometric data presented here the MT plants are aligned with *C. flava s. s.*

A chromosome count of a specimen from the MT population by Davies (1953) gave a haploid number of n=30. This is consistent with other chromosome counts for *C. flava s. s.* (Davies 1953; Halkka *et al.* 1992; Schmid 1982) but inconsistent for chromosome counts for *C. viridula* subsp. *brachyrrhyncha* (n=34) (Davies, 1953; Halkka *et al.* 1992; Schmid 1982) and *C.* × *alsatica* (n=irregular) (Schmid 1982).

Difficulties over the correct classification of the MT plants may be due, in part, to its apparently obvious morphological dissimilarity to the Roudsea Wood population of *C. flava*. It should be noted that although both populations are situated at approximately the same latitude, the Roudsea Wood population is situated in a semi-shaded wood near sea level whereas the MT population is situated on an exposed site at approximately 380 m. It would appear that these two populations are approaching the opposite extremes of morphological range within this species. When continental European and North American material is taken into consideration it becomes apparent that both populations fit within the phenotypic range of this species. Table 5 indicates that there may be an over reliance upon large utricle size to separate *C. flava* from its closely related allies within the British Isles.

In conclusion the population of yellow sedges discovered by G. A. Shaw in 1946 at the Tarn Moss, Malham should be recognised as a second extant population of *C. flava s. s.* in the British Isles. Furthermore, problematic populations whose identity is uncertain such as those already identified as *C. flava* hybrids at Greywell Moors, Hants and by the River Corrib near Menlough north-east of Galway City need to be reviewed as soon as material is available. In light of the evidence presented here it is possible that *C. flava* is not as rare as currently thought in the British Isles but has been overlooked or misidentified in the past.

TAXONOMIC TREATMENT

The following key should serve to discriminate between *C. flava*, *C. viridula* subsp. *brachyrrhyncha* var. *elatior* and *C. viridula* subsp. *brachyrrhyncha* var. *jemtlandica* . However, it should be noted that no single character can satisfactorily discriminate between the taxa and where two or more of the taxa are sympatric the taxonomic affinities may be further confused. Where possible several specimens from one population should be carefully compared and mean character values used. Only perigynia from the middle of a pistillate spikelet should be used.

KEY TO TAXA:

1 Utricles straight or curved, usually <5 mm long, abruptly contracting into a conspicuous beak usually <2 mm long with usually <5 bristles on each side of the beak margin. Leaves of the fertile tiller usually <4·5 mm wide, longer or shorter than the culm. Ligule usually <2·5 mm long acute to rounded. Solitary staminate spikelet ± sessile to conspicuously pedunculate, terminal 2

1 Utricles curved usually >3·8 mm long, gradually tapering into a long 1·5–3 mm beak with a conspicuously scabrous margin of usually 5–11 bristles on each side. Leaves of fertile tiller usually >3 mm wide, usually ± as long as the culm. Ligule usually >3 mm, acute. Solitary staminate spikelet ± sessile, terminal ..... 1. *C. flava*

2 Utricles usually 3·5–5 mm long; beak 1·5–2 mm long. Leaves of fertile tiller usually <3 mm wide 3

2 Utricles usually <4 mm long: beak usually <1·5 mm long. Leaves of fertile tiller 1·5–4·5 mm wide ..... 2. Other members of the *C. viridula* agg.

3 Utricles ± dense; beak usually deflexed. Staminate spikelet usually conspicuously pedunculate. Pistillate spikelets usually 2–3, ± separate, ovate to cylindrical. Leaves of fertile tiller usually shorter than half of the culm ..... 2aa. *C. viridula* subsp. *brachyrrhyncha* var. *elatior*

3 Utricles ± lax; beak usually straight. Staminate spikelet usually sub-sessile to shortly pedunculate. Pistillate spikelets usually 1–2 ± contiguous to approximate, globose to ovate. Leaves of fertile tiller usually longer than half of the culm ..... 2ab. *C. viridula* subsp. *brachyrrhyncha* var. *jemtlandica*

The following is a brief taxonomic treatment and includes only some of the most important synonyms. For a fuller taxonomic treatment see Schmid (1983) and Crins (1985).

1. *C. flava* L., Sp. Pl. 2: 975 (1753). Type: **LINN** Savage Cat. No. 1100.40 (Holotype: **LINN**).
Synonyms:
C. patula Host., *Icon. Descr. Gram. Austriac.* **1**: 48–49 (1801). Type: Austria (Holotype: **W**, destroyed).
C. flava subsp. *gaspensis* Fernald, *Rhodora* **8**: 200 (1906). Type: Canada, Quebec, gravelly banks of Bonaventure River, 8 August 1904, *J. F. Collins, M. L. Fernald & A. S. Pease s.n.* (Lectotype: **GH**, *n.v.* selected by Crins 1988).

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

2a. *C. viridula* subsp. *brachyrrhyncha* (Čelakovsky) B. Schmid, *Watsonia* **14**: 317 (1983).
Basionym:
C. flava subsp. *brachyrrhyncha* Čelakovsky, *Prodr. Fl. Böm.* **1**: 71 (1876).
Synonyms:
C. lepidocarpa Tausch, *Flora (Regensb.)* **17**: 179 (1834). Type: Czechoslovakia, Praha, (no collector), no. 1636 (lectotype: **PRC**, isolectotype: **PRC**, selected by Crins 1985).

2aa. *C. viridula* subsp. *brachyrrhyncha* var. *elatior* (Schlectendal) Crins, *Canad. J. Bot.* **67**(4): 1058 (1989).
Basionym:
C. flava var. *elatior* Schltdl., *Fl. Berol.* **1**: 477 (1823). Type: Germany, Berolinensi (Holotype: **B** *n.v.*).
Synonyms:
C. viridula subsp. *brachyrrhyncha* var. *lepidocarpa* (Tausch) B. Schmid *Watsonia* **14**: 317 (1983).
C. lepidocarpa Tausch, *Flora (Regensb.)* **17**: 179 (1834).
C. lepidocarpa var. *lepidocarpa* (Tausch) Petermann, *Anal. Pflanzenschl. Leipzig* 509 (1846), pro autonym.
C. flava subsp. *lepidocarpa* (Tausch) Godr. *Fl. Lorraine.* **1**: 118 (1843).
C. flava subsp. *lepidocarpa* (Tausch) Nyman, *Consp.* 771 (1882).
C. flava subsp. *lepidocarpa* (Tausch) Lange, *Haandb. Danske. Fl.,* 4th ed., 144 (1886).

2ab. *C. viridula* subsp. ***brachyrrhyncha*** var. ***jemtlandica*** (Palmgr.) Blackstock & P. A. Ashton ***comb. et stat. nov.***

Basionym:

C. lepidocarpa Tausch subsp. *jemtlandica* Palmgr. in Lindman. Sv. Fanerogamfl., ed. 2: 153 (1926). Type: Sweden, Jämtland, Ostersund, Frösön, 13 August 1910, *A. Palmgren*, Caric. Fulv. No. 53 (lectotype: **H**, selected by Crins 1985).

Synonyms:

C. lepidocarpa Tausch * *septentrionalis* Palmgr. forma *jemtlandica* Palmgr., Caric. Fulvellae Exs. No. 52-54 (1910) (*nom. nud.*).

C. jemtlandica (Palmgr.) Palmgr., *Mem. Soc. Fauna Flora Fenn.* **13**: 126 (1937).

C. jemtlandica (Palmgr.) Palmgr. var. *gotlandiae* Palmgr., *Comment. Biol.* **20**(3): 12 (1958). Type: Sweden, Gotland, par. Othem, 14 June 1910, *A. Palmgren* (Holotype: **H**, Isotype: **H**, photo!).

C. jemtlandica (Palmgr.) Palmgr. var. kainuensis Palmgr., *Comment. Biol.* **20**(3): 13 (1958). Type: Finland, Ostrobottnia kajanensis, Suomussalmi, Ruhtinaansalmi, Rytisuo, 10 July 1937, *O. Kyyhkynen* (Holotype: **H**, photo!).

C. flava L. subsp. *jemtlandica* (Palmgr.) P. D. Sell *Fl. of Great Britain and Ireland* **5**: 110 (1996).

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