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A Comparative Study of the Inflorescence in the Genus *Carex* (Cyperaceae)

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Abstract—The inflorescences of 110 species of *Carex* were studied in the context of the latest phylogenetic framework of the tribe Cariceae, including broad taxonomic coverage by sections. Their structure is analyzed to infer their taxonomic value and to place these structures within a phylogenetic framework based on recent work in the genus. The inflorescence-unit is a paracladium. It consists of a branch composed of a prophyll, peduncle, bract, and pseudospike with one or more spikelets. The particular features and general trends of the inflorescences are analyzed, summarized, and interpreted according to hypotheses of the evolution of the genus. Such evolutionary patterns as ramification, homogenization, reduction, and sexual specialization combine in different ways during the evolution of the *Carex* inflorescence. Taking into account the inflorescence structure, we discuss the inclusion of the unispicate species of *Carex* in the Caricoid Clade and the differences among Caricoid, *Vignea,* and Core *Carex* clades.

Keywords—Caricoid Clade, evolutionary process, inflorescence typology, paracladium, prophyll, pseudospike.

Carex L. (Cyperaceae) is one of the most species-rich genera in the Northern Hemisphere with more than 2,000 species (Frodin 2004). In the latest worldwide monograph of *Carex*, Kükenthal (1909) recognized four subgenera based on the structure of the inflorescences: *Carex*, *Psyllophora* (Degl.) Peterm. (= *Primocarex* Kük.), *Vignea* (P. Beauv. ex Lestib. f.) Peterm., and *Vigneastra* (Tuck.) Kük. [= *Indocarex* (Baill.) Kük.]. This classification and the limits of *Carex* with respect to other genera of the tribe Cariceae (*Cymophyllus* Mack., *Kobresia* Willd., *Uncinia* Pers., and *Schoenoxiphium* Nees) have been shown to be problematic (Kukkonen and Toivonen 1988; Reznicek 1990; Starr and Ford 2009). Recent molecular research (Starr et al. 1999; Yen and Olmstead 2000a, b; Roalson et al. 2001; Starr et al. 2004; Ford et al. 2006; Waterway and Starr 2007; Starr et al. 2008; Starr and Ford 2009; Waterway et al. 2009; Gehrke et al. 2010) has pointed to the existence of four major clades in most analyses of molecular works: the Core *Carex*, *Schoenoxiphium*, Core Unispicate, and *Vignea* clades. A fifth clade, the *Siderostictae* Clade, is also known from recent work (Waterway et al. 2009). Core *Carex* Clade groups most species of subgenera *Carex* and *Vigneastra*, which some authors had already joined in the single subgenus *Carex* (Ohwi 1936; Koyama 1962). The *Schoenoxiphium* Clade includes species of the genus *Schoenoxiphium* together with some species of *Psyllophora*. The Core Unispicate Clade groups unispicate androgynous *Carex* species together with species of other genera of Cariceae (*Uncinia*, *Kobresia*, and *Cymophyllus*). The *Vignea* Clade comprises all taxa of subgenus *Vignea*; *Vignea* is the only traditional subgenus that is monophyletic. Finally, the *Siderostictae* Clade is presumed to include the twelve species of the East Asian section *Siderostictae* Franch. ex Ohwi (subgenus *Carex*), though only five of these, including those with the lowest number of chromosomes in the genus (Tanaka 1939), have been studied to date using molecular data (Waterway et al. 2009).

Traditionally, the taxonomy of *Carex* was based on perigynium characteristics, the pattern of branching of the inflorescence (unispicate vs. multispicate), the distribution of the sexes in spikes (bisexual vs. unisexual), and the presence of a peduncle (sessile spike vs. pedunculate spike) (Kükenthal 1909; Chater 1980; Egorova 1999; Ball and Reznicek 2002). There are several studies about spikelets, flowers and inflorescence structure in Cariceae (Snell 1936; Mora Osejo 1966; Smith 1966; Kukkonen 1967; Haines and Lye 1972; Smith and Faulkner 1976; Meert and Goetghebeur 1979; Timonen 1985, 1989; Kukkonen 1990), but only a few works are focused on the inflorescence structure of *Carex* (Kukkonen 1984; Reznicek 1990; Timonen 1993, 1998), which is remarkable given the complexity and reduction of the inflorescence. Indeed, the inflorescence typology has been still less studied (Kukkonen 1984; Vegetti 2002, 2003). The typological method, which we follow in this study, is a comparative approach that analyzes the branching system and the position of each element of the inflorescence within the structural plan of the whole plant, allowing the comparison of homologous elements of the inflorescences (Weberling 1985).

Flowers in *Carex* are unisexual and lack a perianth. The male flowers consist of three stamens subtended by a glume and are directly inserted on the axis. The female flowers are enclosed in a sac-like organ, called the utricle or perigynium. *Carex*, *Uncinia*, and *Cymphyllus* are distinguished morphologically by the presence of a closed perigynium, in contrast to the other two Cariceae genera (*Kobresia* and *Schoenoxiphium*), whose perigynia are totally or partially open. It is accepted that the perigynium is a prophyll, which indicates the presence of a lateral axis (Kunth 1835; Kükenthal 1909; Snell 1936; Smith and Faulkner 1976; Kukkonen 1994). This lateral axis, often called the rachilla, has been the subject of controversy. It was considered an ancestral character in former hypotheses of *Carex* evolution (Kükenthal 1909; Mackenzie 1931–1935). Rachillae of different lengths are found occasionally in specimens of many species of *Carex* (Duval-Jouve 1864; Snell 1936; Le Cohu 1968; Svenson 1972; Smith and Faulkner 1976), thus their presence is not a primitive feature. Nevertheless, the morphology and anatomy of rachilla has phylogenetic importance in Cariceae (Reznicek 1990).

In *Carex,* the rachilla is usually short, inhibited at an early stage, and only in *Carex microglochin* Wahlenb. protrudes at the apex of the perigynium. In contrast, *Uncinia* always presents a hooked rachilla growing out of the perigynia. Generally, *Kobresia* and *Schoenoxiphium* (Gordon-Gray 1995) also bear a developed rachilla, which is fertile, yielding terminal male flowers making up bisexual spikelets.

The inflorescences of Cariceae, including *Carex*, are polytelic and indeterminate or open (Kukkonen 1984, 1994; Vegetti 2002). They are described in relation to their units, called inflorescence-units, which are the basis to compare different models of inflorescence. An important matter of inflorescence structure in Cariceae is the definition of the inflorescence-unit. In this work we use the paracladium (lateral branch) as the inflorescence-unit. We choose this option against others, such as the spike (Kukkonen 1984), the compound spike, called inflorescence unit in a more particular sense in Reznicek (1990), or the spikelet (Vegetti 2002), because Levyns (1945) and Timonen (1993, 1998) explained the need of having in mind the overall organization, all the elements including the prophylls, to analyze and compare these inflorescences.

In this study, we investigate whether inflorescence evolution follows any phylogenetic trend, which can give us clues to understand the circumscription of *Carex* in the tribe Cariceae. Therefore, the main goals of this study are to: interpret the inflorescence organization of *Carex*, applying the typological method to understand the often ambiguous *Carex* inflorescence; study the inflorescence structure of *Carex* in every clade to infer the phylogenetic value of the characters of the inflorescences; and, finally, interpret the main evolutionary processes in *Carex* on the basis of the inflorescences in light of recent phylogenetic work in the genus.

Materials and Methods

Terminology—Several works have established a basic terminology in Cyperaceae (Kukkonen 1984, 1994; Vegetti 2002, 2003; Vrijdaghs et al. 2009), and mainly Browning and Gordon-Gray (1999) who put into practice the works of Troll (1964) and Weberling (1985, 1989). The terminology of inflorescence structures that we use here follows mainly Browning and Gordon-Gray (1999), and Egorova (1999) to name the compound inflorescences. Figure 1 shows the main parts of the inflorescence and their terminology.

In the typological analysis of the inflorescence in *Carex,* we distinguish one or more floral groups called florescences. The lateral ones, called coflorescences, are located in the paracladia (P) or lateral branches. Each paracladium consists of a bract, a prophyll, a peduncle (called epipodium), and a florescence. In some cases in *Carex*, elements such as prophylls and peduncles can be absent. The florescence located in the apical end of the main axis is the main florescence (HF), the terminal one (Fig. 1 left and center). The main axis is not a paracladium: it has no bract, prophyll, nor peduncle. Development of the inflorescence is acropetal, and consequently the paracladia become smaller towards the distal end (Kukkonen 1984). Thus, to identify each paracladium, the numeration of axes increases from the bottom to the apex. According to Timonen (1985, 1989, 1993, 1998) the position of each paracladium is shown by a numerical code: the Roman numerals give the lateral order and the Arabic numerals give their sequence on the main axis or on the branches, counting from the base to the apex (Fig. 1, center and right). The lateral axes of the female flowers are not included in the paracladia numeration.

In *Carex,* the florescence has been variously referred to as the spike or the spikelet in different texts. Definitions and differences between the terms spike and spikelet have been discussed several times, and consequently the distinctions between the two are blurred (Kukkonen 1984; Timonen 1998). In this work, we follow Kukkonen (1994) and understand the term "spike" as a group of sessile, unisexual flowers that are compactly attached to the distal end of an axis, and the term "spikelet" as a small spike, referred only to the ultimate branch of the inflorescence. In the current study we will use the term pseudospike instead of "spike," as these structures are not true spikes, but rather compound structures (Reznicek 1990; Timonen 1998). Other authors used the terms "inflorescence unit" (Reznicek 1990), "spike" (Timonen 1993; Kukkonen 1994; Egorova 1999), or "spike-like" (Timonen 1998).

Pseudospikes in *Carex* may be male (staminate), female (pistillate), or bisexual collections of small units or spikelets. While all authors agree that a female spikelet is a single female flower wrapped in the perigynium and its glume (Smith 1966; Smith and Faulkner 1976; Haines and Lye 1972; Timonen 1998; Egorova 1999), they are not in agreement regarding the male spikelet concept. Smith (1966), Smith and Faulkner (1976) and Timonen (1998) suggested the male and the female flowers are equivalent, using the term male spikelet for the male flower with its glume. On the contrary, Haines and Lye (1972), who made a review of this concept, accepted the idea that the male spikelet in *Carex* is a group of male flowers with their glumes, and recent ontogenetic research (Vrijdaghs et al. 2010) supported this view. In the current study we follow this interpretation; therefore, while a female pseudospike consists of several female spikelets, a male pseudospike consists of one male spikelet, which itself consists of multiple male flowers.

Besides the perigynium, there are three kinds of prophylls in *Carex* located on the adaxial side of a lateral branch: the swollen (or inflorescence) prophyll, the cladoprophyll and the glumaceous prophyll. The swollen prophyll (Reznicek 1990) is at the base of paracladia in the Core *Carex* Clade. It is similar to an empty peryginium, so here it is referred to as the perigynium-like prophyll (Snell 1936). The cladoprophyll is a tubular sheath near the base of peduncles of pseudospikes. The glumaceous prophyll appears at the basal position on the bud; it is membranous, shorter and wholly devoid of color (Kukkonen 1994; Browning and Gordon-Gray 1999).

Material Studied—Material from the following herbaria was studied: BIO, BCN, C, CGE, CHR, COI, FCO, GDA-GDAC, H, JACA, JBAG, K, LEB, LISU, LY, MA, P, SANT, SEV, UPNA, VIT, W, and WU (Appendix 1). We studied more than 750 specimens of 110 species of *Carex* belonging to the four clades (Appendix 1; Table 1). We sampled species from most sections in Core *Carex* and *Vignea* clades present in Europe. We took special care in sampling taxa from most sections belonging to the Core Unispicate Clade. We also studied all Eurasian representatives of the section *Phaestoglochin* Dumort., and the complete section *Heleoglochin* Dumort., both of which belong to the *Vignea* Clade. Species were grouped by sections following Chater (1980) and Egorova (1999) for Eurasian species, Ball and Reznicek (2002) for North American ones, and Kükenthal (1909) for the rest. It is necessary to consider that the monophyly of most sections is not established, and molecular data does not seem to be available for some sections (e.g. *Hallerianae* (Asch. & Graebn.) Rouy, and *Scabrellae* Kük.)

Dissections—Inflorescences were mainly studied on fresh specimens fixed with FAA (70% ethanol, 98% acetic acid, 40% formaldehyde, 85:5:10) or on herbarium specimens after softening them in warm water and then fixing in FAA. Herbarium dissections were made only on taxa with abundant available material and for which we had permission of the herbaria. Vouchers and herbaria are cited in Appendix 1.

Measurements—Length and width of inflorescences and length of internodes, peduncles, basal bracts, and sheaths of the basal bracts were averaged over the studied specimens of each taxon/section. Mean and standard deviation values, as well as minimum and maximum values are indicated in the tables. Because of lack of material for some taxa, we took complementary data from the literature for inflorescence length and basal sheath length in sections *Indicae* Tuck. and *Polystachyae* Tuck. (Kükenthal 1909), and number of paracladia in section *Macrocephalae* Kük. (Mastrogiuseppe 2002). All observations were made using a Zeiss 9901 stereo microscope. Drawings of details were made with a Nikon SMZ800 dissecting microscope with a P-IDT drawing tube. Drawings of the inflorescence structure were made with AUTOCAD 2007.

Results

Core Carex Clade—Major results are presented in Fig. 2; Tables 2, 3. Inflorescences in this clade have a variable number (0–12) of first order paracladia. Each paracladium is formed by a prophyll, peduncle, and pseudospike subtended by a bract, sometimes a leaf sheath enclosed around the main axis, except in dioecious unispicate species. Prophylls are always present and of two forms: cladoprophylls in the proximal paracladia, closed around the axis; and perigynium-like prophylls in the distal paracladia.

Several sections are characterized by the androgynous bisexual pseudospikes (e.g. *Polystachyae*, *Indicae*, and *Scabrellae*). In other sections pseudospikes tend to be unisexual, with the proximal one female and the distal one male. Some, such as sections *Phacocystis* Dumort. and *Spirostachyae* (Drejer) L. H. Bailey, have one to two male pseudospikes, and sections *Aulocystis* Dumort., *Carex*, *Paludosae* G. Don., and *Vesicariae* (Heuff.) J. Carey can have three to four male pseudospikes. The sections *Chlorostachyae* Tuck. ex Meinsh. and *Digitatae* (Fr.) H. Christ. have only unisexual pseudospikes. These

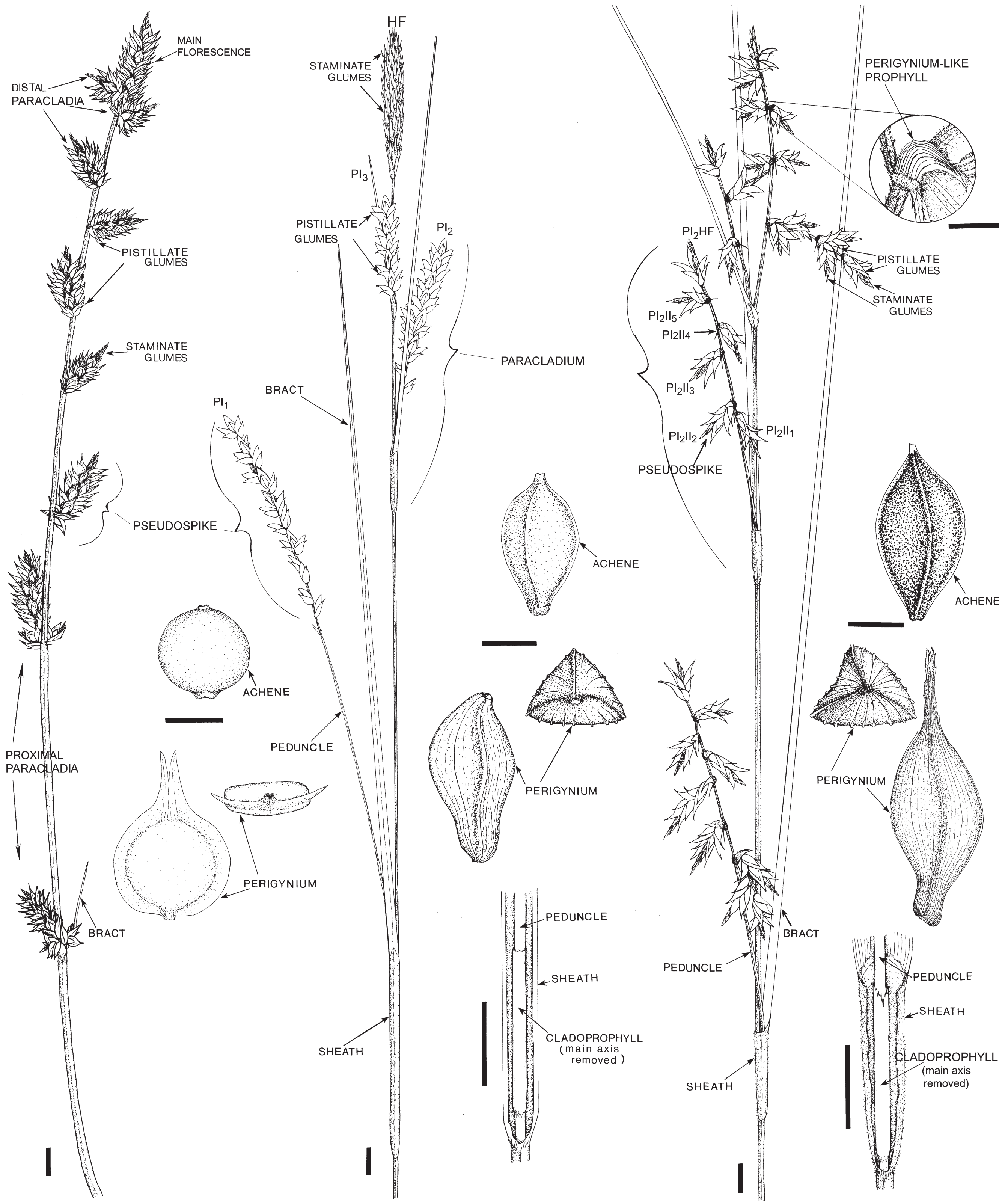

Fig. 1. Inflorescence terminology in the genus *Carex*. Left: *Vignea* Clade, *C. sparganioides* (drawn from Bucks Co., Pennsylvania, *Hermann 4299*, MICH). Center: Core *Carex* Clade (former subgenus *Carex*) *C. tetanica* (drawn from Norfolk Co., Ontario, *Reznicek 5531*, MICH). Right: Core *Carex* Clade (former subgenus *Vigneastra*), *C. standleyana* (drawn from Chiapas, México, *Breedlove 52083*, CAS). In the center is shown an inflorescence which has PI_1, PI_2 and PI_3; this means there are three paracladia of first order. On the right, it shows PI_2 which is branching. (PI_2II_1, PI_2II_2, ... PI_2II_5), that means there are five paracladia of second order in PI_2. The main florescence is shown by HF in the main axis and by PI_2HF in the paracladium PI_2. Horizontal bars = 1 mm and vertical bars = 5 mm. Drawing by Susan Reznicek. (Reproduced and modified with permission of A. A. Reznicek)

TABLE 1. Classification of the taxa studied. Species are arranged alphabetically within clades and sectional groups. Sections are grouped according to the four clades of Cariceae. Sectional placement follows Ball and Reznicek (2002) for North American species, Chater (1980) and Egorova (1999) for Eurasian ones, and Kükenthal (1909) for the rest. The nomenclature in sect. *Phaestoglochin* (*Vignea* Clade) follows Molina et al. (2008a, 2008b).

Core *Carex* Clade—Sect. *Acrocystis* Dumort.: *Carex montana* L., *C. pilulifera* L., *C. tomentosa* L.; **Sect. *Aulocystis* Dumort.:** *Carex ferruginea* Scop. subsp. *caudata* (Kük.) Pereda & Laínz, *C. frigida* All., *C. sempervirens* Vill.; **Sect. *Bicolores* (Tuck. ex L. H. Baley) Rouy:** *Carex bicolor* All.; **Sect. *Carex*:** *Carex hirta* L.; **Sect. *Ceratocystis* Dumort.:** *Carex demissa* Hornem, *C. flava* L., *C. lepidocarpa* Tausch.; **Sect. *Chlorostachyae* Tuck. ex Meinsh:** *Carex capillaris* L.; **Sect. *Depauperatae* Meinsh:** *Carex brevicollis* DC., *C. depauperata* Curtis ex Stokes; **Sect. *Digitatae* (Fr.) H. Christ:** *Carex ornithopoda* Willd.; **Sect. *Grallatoriae* Kük.:** *Carex grallatoria* Maxim.; **Sect. *Hallerianae* (Asch. & Graebn.) Rouy:** *Carex halleriana* Asso; **Sect. *Indicae* Tuck.:** *Carex cruciata* Wahlenb., *C. filicina* Nees; **Sect. *Mitratae* Kük.:** *Carex caryophyllea* Latourr., *C. depressa* Link subsp. *depressa*; **Sect. *Paludosae* G. Don:** *Carex acutiformis* Ehrh.; **Sect. *Paniceae* G. Don:** *Carex asturica* Boiss., *C. panicea* L.; **Sect. *Phacocystis* Dumort.:** *Carex elata* All. subsp. *reuteriana* (Boiss.) Luceño & Aedo, *C. nigra* (L.) Reichard, *C. trinervis* Degl.; **Sect. *Pictae* Kük.:** *Carex picta* Steud.; **Sect. *Polystachyae* Tuck.:** *Carex baccans* Nees; **Sect. *Pseudocypereae* Tuck. ex Kük.:** *Carex pseudocyperus* L.; **Sect. *Racemosae* G. Don:** *Carex atrata* L., *C. parviflora* Host; **Sect. *Scabrellae* Kük.:** *Carex rhizomatosa* Steud.; **Sect. *Scirpinae* (Tuck.) Kük.:** *Carex scirpoidea* Michx.; **Sect. *Spirostachyae* (Drejer) L. H. Bailey:** *Carex binervis* Sm., *C. extensa* Gooden., *C. puntacta* Gaudin; **Sect. *Sylvaticae* Rouy:** *Carex sylvatica* Huds. subsp. *sylvatica*; **Sect. *Vesicariae* (Heuff.) J. Carey:** *Carex rostrata* Stokes, *C. vesicaria* L.

***Schoenoxiphium* Clade—Sect. *Aciculares* (Kük.) G. A. Wheeler:** *Carex acicularis* Boott; **Sect. *Caryotheca* V. Krecz. ex T. V. Egorova:** *Carex phyllostachys* C. A. Mey.; **Sect. *Junceiformes* Boeck.:** *Carex setifolia* Kunze

***Vignea* Clade—Sect. *Ammoglochin* Dumort.:** *Carex arenaria* L.; **Sect. *Divisae* H. Christ ex Kük.:** *Carex divisa* Huds.; **Sect. *Foetidae* (Tuck. ex L. H. Bailey) Kük.:** *Carex foetida* All.; **Sect. *Gibbae* Kük.:** *Carex gibba* Wahlenb.; **Sect. *Glareosae* G. Don:** *Carex canescens* L.; **Sect. *Heleoglochin* Dumort.:** *Carex appressa* R. Br., *C. appropinquata* Schumach., *C. cusickii* Mack., *C. decomposita* Muhl., *C. diandra* Schrank, *C. incomitata* K. R.Thiele, *C. paniculata* L. subsp. *calderae* (A. Hansen) Lewej. & Lobin, *C. paniculata* L. subsp. *hansenii* Lewej. & Lobin, *C. paniculata* subsp. *lusitanica* (Schkuhr ex Willd.) Maire, *C. paniculata* L. subsp. *paniculata, C. prairea* Dewey, *C. secta* Boott, *C. sectoides* (Kük.) Edgar, *C. tenuiculmis* (Petrie) Heenan & de Lange, *C. tereticaulis* F. Muell., *C. virgata* Sol. ex Boott; **Sect. *Macrocephalae* Kük.:** *Carex macrocephala* Willd.; **Sect. *Ovales* Kunth:** *Carex leporina* L.; **Sect. *Phaestoglochin* Dumort.:** *Carex cyprica* Molina Gonz., Acedo & Llamas, *C. coriogyne* Nelmes, *C. divulsa* Stokes, *C. egorovae* Molina Gonz., Acedo & Llamas, *C. enokii* Molina Gonz., Acedo & Llamas, *C. leersii* F. W. Schultz, *C. magacis* Molina Gonz., Acedo & Llamas, *C. muricata* subsp. *ashokae* Molina Gonz., Acedo & Llamas, *C. muricata* L. subsp. *cesanensis* Molina Gonz., Acedo & Llamas, *C. muricata* L. subsp. *muricata, C. nordica* Molina Gonz., Acedo & Llamas, *C. omeyica* Molina Gonz., Acedo & Llamas, *C. otomana* Molina Gonz., Acedo & Llamas, *C. pairae* F. W. Schultz, *C. rosea* Schkuhr, *C. spicata* Huds. subsp. *andresii* Molina Gonz., Acedo & Llamas, *C. spicata* Huds. subsp. *spicata*; **Sect. *Phleoideae* (Meinsh.) T. V. Egorova:** *Carex foliosa* D. Don; **Sect. *Physoglochin* Dumort:** *Carex davalliana* Sm., *C. dioica* L.; **Sect. *Remotae* (Asch.) C. B. Clarke:** *Carex remota* L.; **Sect. *Stellulatae* Kunth:** *Carex echinata* Murray; **Sect. *Vulpinae* (Heuff.) H. Christ:** *Carex polyphylla* Kar. & Kir., *C. otrubae* Podp.

Core Unispicate Clade—Sect. *Capituligerae* Kük.: *Carex capitata* L.; **Sect. *Circinatae* Meinsh**.: *Carex circinata* C. A. Mey.; **Sect. *Curvulae* Tuck. ex Kük.:** *Carex curvula* All.; **Sect. *Dornera* Heuff.:** *Carex nigricans* C. A. Mey., *C. pyrenaica* Wahlenb.; **Sect. *Firmiculmes* (Kük.) Mack.:** *Carex geyeri* Boott; **Sect. *Inflatae* Kük.:** *Carex breweri* Boott; **Sect. *Leptocephalae* L. H. Bailey:** *Carex leptalea* Wahlenb.; **Sect. *Leucoglochin* Dumort.:** *Carex microglochin* Wahlenb., *C. parva* Nees , *C. pauciflora* Ligth.; **Sect. *Longespicatae* Kük.:** *Carex monostachya* A. Rich.; **Sect. *Nardinae* (Tuck.) Mack.:** *Carex nardina* Fr.; **Sect. *Obtusatae* (Tuck.) Mack.:** *Carex obtusata* Liljebl.; **Sect. *Phyllostachyae* Tuck. ex Kük.:** *Carex backii* Boott, *C. saximontana* Mack.; **Sect. *Psyllophora* (Degl.) Koch:** *Carex macrostyla* Lapeyr., *C. peregrina* Link, *C. pulicaris* L.; **Sect. *Rupestres* (Tuck.) Meinsch.:** *Carex rupestris* All.

sections have a single male pseudospike that is the main florescence. The European taxa of section *Acrocystis* Dumort studied here also have unisexual pseudospikes, but some North American taxa have bisexual pseudospikes (Crins and Rettig 2002). On the other hand, sections *Aulocystis*, *Carex*, *Ceratocystis* Dumort., *Depauperatae* Meinsh., *Mitratae* Kük., *Paludosae*, *Paniceae* G. Don., *Phacocystis*, *Sylvaticae* Rouy (Fig. 2a), and *Spirostachyae* have one or more androgynous pseudospikes in the distal paracladia. A few specimens have the main florescence androgynous in sections *Paniceae*, *Sylvaticae*, and *Vesicariae*.

Gynecandrous pseudospikes located in the distal paracladia or main florescence were found in sections *Aulocystis*, *Bicolores* (Tuck. ex L. H. Baley) Rouy, *Pseudocypereae* Tuck. ex Kük., and *Racemosae* G. Don (Fig. 2b). Some specimens of *Carex parviflora* (sect. *Racemosae*) have only female flowers in the main florescence. We found an interesting abnormality in *Carex pseudocyperus* L. (sect. *Pseudocypereae*). Some specimens have female pseudospikes where male flowers replace the female ones in narrow strips along the length of the pseudospike. In *Carex halleriana* Asso (sect. *Hallerianae*), male, female, and bisexual plants may be found in the same population. Bisexual plants in this species have female or androgynous pseudospikes in the paracladia, with the main florescence male.

Usually, the internodes and peduncles are long relative to the pseudospike. In sections *Carex, Depauperatae*, *Polystachyae*, *Spirostachyae*, and *Sylvaticae*, for example, the proximal internodes are often longer than 100 mm, while internodes and peduncles of the distal paracladia are shorter or absent. These sections with long internodes and peduncles frequently have longer pseudospikes. Some species belonging to sections *Bicolores*, *Hallerianae*, *Ceratocystis*, and *Mitratae* have remote pseudospikes with long peduncles. Meanwhile, sections *Acrocystis*, *Ceratocystis*, and *Mitratae* display the other extreme in internode variation, with sessile or subsessile female pseudospikes grouped near the male one.

There is a considerable variation in internode length, branching order, and length of the paracladia, resulting in several types of inflorescence: paniculiform, racemiform, subcorymbiform, and spiciform. The sections *Polystachyae*, *Indicae*, and *Scabrellae* have paniculiform inflorescences and third order paracladia. Sections *Aulocystis*, *Carex*, *Phacocystis*, *Paludosae*, *Spirostachyae*, *Vesicariae*, etc. are racemiform, with only first order paracladia. *Carex rhizomatosa* Steud. (sect. *Scabrellae*) has a racemiform inflorescence with two paracladia arising at the same node, each with its own prophyll. *Carex ornithopoda* Willd. (sect. *Digitatae* (Fr.) H. Christ) has a subcorymbiform inflorescence, the long-pedunculate paracladia located together in the upper half part of the stem. The dioecious sections *Scirpinae* (Tuck.) Kük., *Pictae* Kük., and *Grallatoriae* Kük. have apparently unbranched, spiciform inflorescences.

Generally, the proximal paracladia have leaflike sheathing bracts, but the distal bracts are setaceous. Sections *Acrocystis*, *Racemosae*, *Mitratae*, *Paludosae*, *and Pseudocypereae* have short

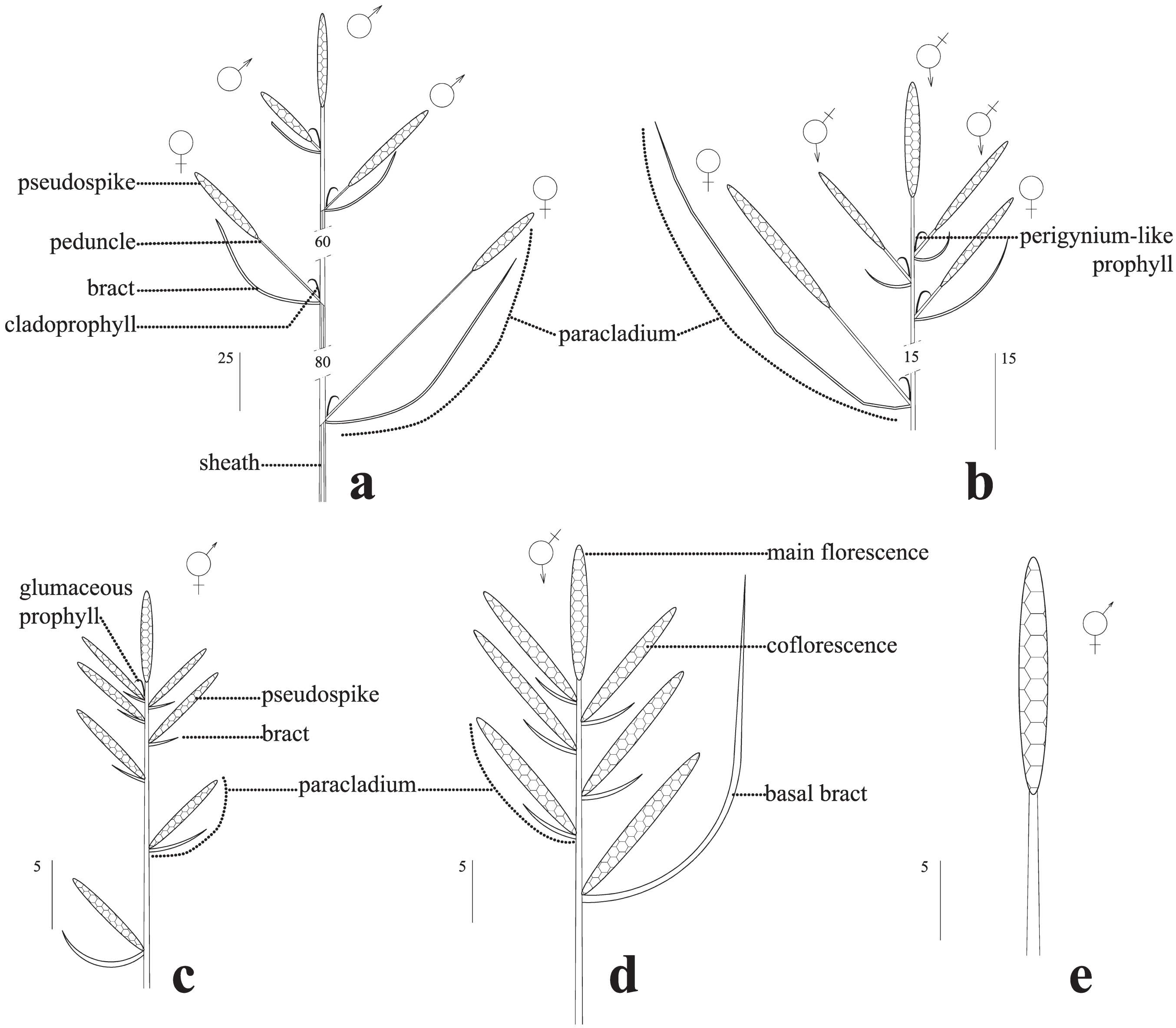

Fig. 2. Typological analysis of *Carex* inflorescences. a. *Carex sylvatica* subsp. *sylvatica* (LEB78160), Core *Carex* Clade. b. *Carex atrata* (LEB 80849), Core *Carex* Clade. c. *Carex muricata* subsp. muricata (MA 169375), *Vignea* Clade. d. *Carex leporina* (LEB 79017), *Vignea* Clade. e. *Carex pyrenaica* (LEB 67621), Core Unispicate Clade. Scale bar in mm.

or absent bract sheaths. Female flowers in the Core *Carex* Clade have three stigmas (rarely two; i.e. sections *Bicolores* and *Phacocystis*) and usually lack a rachilla. Some anomalies can appear: we found a specimen of *Carex parviflora* (LEB 16903) with four stigmas in some flowers. The number of female and male flowers varies greatly in the clade, but in general, there are more female flowers than male.

Schoenoxiphium Clade—Major results are presented in Table 4. Species of *Carex* in this clade belong to sections *Junciformes* Boeck, *Acicularis* (Kük.) G. A. Wheeler, and *Caryotheca* V. I. Krecz. ex T. V. Egorova, along with the embeded genus *Schoenoxiphium* (Starr et al. 2004; Waterway and Starr 2007; Starr et al. 2008; Starr and Ford 2009; Waterway et al. 2009; Gehrke et al. 2010). All *Carex* studied have apparently unbranched inflorescences, and the solitary pseudospike is always androgynous. The female spikelets have a flat rachilla with ciliate or scabrous margins, similar to the majority of the species of the genus *Schoenoxiphium* (Levyns 1945; Haines and Lye 1972; Kukkonen 1978; Starr et al. 2008). Some specimens of *Carex phyllostachys* C. A. Mey. (sect. *Caryotheca*) are not unispicate; they have at least a paracladium with a fertile prophyll at the base, and *Carex setifolia* Kuntze (sect. *Junceiformes*) has two sterile basal bract-like glumes (6–11 mm length).

Vignea Clade—Major results are presented in Fig. 2; Tables 5, 6. Inflorescences in this clade are compact, with 0–20 first order paracladia that are sometimes branched. Each paracladium is formed by a peduncle and pseudospike protected by a non-sheathing bract, except in dioecious unispicate species. Some taxa have prophylls, e.g. *Carex arenaria* L. has perigynium-like prophylls, and *C. echinata* Murray occasionally has cladoprophylls. In general, the bracts are setaceous in proximal paracladia, and glumaceous in the distal ones. The internodes decrease upwards and are often lacking in the distal part of the inflorescence. Peduncles are short or absent in proximal paracladia and lacking in distal

Table 2. Characteristics of the inflorescences of the Core *Carex* Clade. All measurement in mm. P = Paracladium, L = Length, HF = Main florescence Ps = Pseudospike. Inflorescence type: P = Paniculiform, R = Racemiform, S = Spiciform, sC = Subcorymbiform. Pseudospike type: A = Androgynous, G = Gynecandrous, U = Unisexual, Um = Male unisexual Uf = Female unisexual. If more than one species has been studied within a section, just the name of the first is given.

Section	*Acrocystis*	*Aulocystis*	*Bicolores*	*Carex*	*Ceratocystis*	*Chlorostachyae*	*Depauperatae*	*Digitatae*	*Grallatoriae*	*Hallerianae*	*Indicae*	*Mitratae*
Studied species	*C. montana*	*C. frigida*	*C. bicolor*	*C. hirta*	*C. demissa*	*C. capillaris*	*C. brevicollis*	*C. ornithopoda*	*C. grallatoria*	*C. halleriana*	*C. cruciata*	*C. caryophyllea*
Inflorescence	S	R	sC	R	S	R	R	sC	S	R	P	S, R
Length	12–36 (18.5 ± 5.1)	50–290 (121.0 ± 57.7)	30–75 (45.6 ± 15.8)	165–406 (316.5 ± 92.7)	26–170 (63.9 ± 32.8)	26–72 (38.4 ± 15.7)	160–411 (280.2 ± 83.7)	13–22 (15.2 ± 4.2)	7–20 (13.0 ± 4.1)	90–150 (112.5 ± 27.0)	200–500 (388.0 ± 100.2)	15–240 (66.4 ± 67.5)
Width	8–12 (10.0 ± 1.3)	15–30 (26.0 ± 3.7)	12–15 (13.5 ± 1.5)	15–20 (18.4 ± 3.8)	8–20 (13.7 ± 3.3)	7–17 (10.3 ± 4.1)	15–30 (24.0 ± 5.8)	8–10 (9.0 ± 0.8)	1.7–4 (2.7 ± 0.8)	7–10 (8.1 ± 1.1)	38–100 (69.0 ± 31.0)	9–20 (12.8 ± 3.3)
Máx. P order	1	1	1	1 (2)	1	1	1	1	-	1	3	1
No. PI	1–4 (2.0 ± 1.0)	1–5 (2.4 ± 1.6)	2–3 (2.5 ± 0.5)	3–5 (7) (4.5 ± 0.5)	1–4 (2.5 ± 1.0)	2–3 (2.5 ± 0.5)	2–4 (3.2 ± 0.8)	3	-	1–3 (2.0 ± 0.8)	5–6	1–3 (2.0 ± 0.7)
No. P II / PI	0	0	0	0 (3)	0	0	0	0	-	0	5–8	0
First internode L	2.7–12 (5.0 ± 2.7)	45–190 (74.0 ± 44.6)	20–65 (38.3 ± 17.5)	73–200 (125.3 ± 49.3)	9–212 (59.3 ± 71.4)	30–50 (40.0 ± 8.2)	80–195 (146.7 ± 40.7)	3–6 (4.8 ± 1.1)	-	75–90 (83.3 ± 6.2)	60–97 (77.2 ± 15.2)	1–150 (50.9 ± 50.1)
Last internode L	1–4 (1.7 ± 1.3)	1–70 (17.3 ± 21.8)	1–4.5 (1.5 ± 1.3)	5–10 (7.5 ± 2.1)	2–18 (9.7 ± 5.9)	0–5 (1.7 ± 2.4)	25–60 (40.2 ± 13.8)	1–2 (1.7 ± 0.2)	-	5–10 (7.7 ± 2.1)	3–5 (4 ± 0.8)	0–21 (7.0 ± 6.5)
First peduncle L	0	5–72 (28.9 ± 19.2)	3–35 (15.8 ± 14.5)	0–11 (2.8 ± 4.8)	3–35 (11.9 ± 11.0)	10–10.5 (10.2 ± 0.2)	20–70 (48.3 ± 23.5)	1.5–3 (2.2 ± 0.6)	-	7–25 (14.3 ± 6.8)	25–45 (34.2 ± 8.2)	3–50 (14.7 ± 16.1)
Last peduncle L	0	0–30 (5.3 ± 9.0)	0.5–1 (0.75 ± 0.25)	0	0–2 (0.3 ± 0.7)	7–9 (8.0 ± 0.8)	3–10 (7.0 ± 3.1)	0	-	0	2–10 (7.0 ± 3.6)	0–5 (2.1 ± 1.9)
Basal sheath L	0	8–30 (15.8 ± 7.2)	3–10 (6.2 ± 2.6)	12–48 (28.0 ± 11.9)	1–29 (7.7 ± 8.6)	7–9 (8.2 ± 0.8)	23–40 (30.0 ± 6.0)	0.5–2 (1.2 ± 0.6)	-	9–15 (11.3 ± 2.6)	30–62.5 (46.3 ± 16.3)	0–4 (1.9 ± 1.3)
Basal bract L	8–22 (12.7 ± 4.5)	50–110 (67.8 ± 20.9)	28–43 (37.5 ± 5.7)	115–362 (268.3 ± z92.6)	40–215 (106.9 ± 54.4)	14–24 (18.3 ± 4.2)	30–190 (124.2 ± 52.5)	3–6 (4.4 ± 1.2)	-	30–40 (35.0 ± 4.1)	160–250 (205.0 ± 45.0)	5–165 (52.5 ± 66.7)
Ps of the P	Uf, A	U, A	Uf	U, A	Uf, A	Uf	Uf, A	Uf	U, A	U, A	A	Uf, A
Ps of the HF	Um	Um, G	G	Um	Um	Um	Um	Um	Uf, Um	U	A	Um
No. male Ps	1	0–4	0	3–4	1	1	1	1	0–1	0–1	0	1
No. stigmas	3	3	2	3	3	3	3	3	3	3	3	3
Remote Ps	-	-	-	-	yes	-	-	-	-	yes	-	yes

Table 3. Characteristics of the inflorescences of the Core *Carex* Clade (cont). All measurement in mm. P = Paracladium, L = Length, HF = Main florescence Ps = Pseudospike. Inflorescence type: P = Paniculiform, R = Racemiform, S = Spiciform, sC = Subcorymbiform. Pseudospike type: A = Androgynous, G = Gynecandrous, U = Unisexual, Um = Male unisexual Uf = Female unisexual. If more than one species has been studied within a section, just the name of the first is given.

Section	*Paludosae*	*Paniceae*	*Phacocystis*	*Pictae*	*Polystachyae*	*Pseudocyperus*	*Racemosae*	*Scabrellae*	*Scirpinae*	*Spirostachyae*	*Sylvaticae*	*Vesicariae*
Studied species	*C. acutiformis*	*C. asturica*	*C. nirga*	*C. picta*	*C. baccans*	*C. pseudocyperus*	*C. atrata*	*C. rhizomatosa*	*C. scirpoidea*	*C. binervis*	*C. sylvatica*	*C. rostrata*
Inflorescence	R	R	R	S	P	R	R	R	S	R	R	R
Length	130–220 (181.8 ± 38.3)	50–140 (79.0 ± 22.7)	37–160 (89.9 ± 39.1)	20–56 (36.6 ± 10.5)	300–410 (353.3 ± 45.0)	80–120 (103.8 ± 15.6)	9–88 (33.1 ± 26.2)	170–470 (264.0 ± 112.9)	8–30 (17.1 ± 6.8)	30–300 (187.8 ± 126.5)	160–540 (330.0 ± 136.0)	170–300 (217.5 ± 51.2)
Width	38–55 (44.3 ± 7.6)	10–20 (14.3 ± 3.8)	10–20 (14.6 ± 4.1)	4–7 (5.8 ± 1.1)	70–150 (121.7 ± 36.6)	65–80 (71.7 ± 6.2)	8–30 (18.0 ± 7.9)	20–25 (21.7 ± 2.4)	3–5 (4.2 ± 0.7)	12–25 (18.0 ± 3.8)	25–45 (32.5 ± 7.5)	25–35 (30.0 ± 5.0)
Max. P order	1	1	1	1	3	1	1 (2)	3	(1)	1 (2)	1	1
No. PI	4–5 (4.8 ± 0.8)	2–3 (2.3 ± 0.5)	3–4 (3.8 ± 0.4)	0–1	6–12 (8.7 ± 2.5)	4–5 (4.5 ± 0.5)	3–5 (3.8 ± 0.8)	5–7 (5.7 ± 0.9)	0–1	3–5 (4.2 ± 0.7)	4–6 (4.8 ± 0.7)	5–7 (6.0 ± 1.0)
No. P II / PI	0	0	0	0	5–8	0	0 (2)	4–5	0	0	0	0
First internode L	42–83 (60.8 ± 14.5)	32–70 (51.9 ± 13.1)	21–44 (28.0 ± 7.2)	12–14 (13.0 ± 1.0)	70–140 (113.3 ± 30.9)	25–55 (40.0 ± 12.7)	4–28 (13.6 ± 10.6)	64–130 (91.3 ± 28.1)	19–22 (20.5 ± 1.5)	103–230 (61.0 ± 45.4)	50–225 (125.3 ± 64.2)	36–80 (57.3 ± 18.0)
Last internode L	8–21 (17.0 ± 5.2)	7–24 (15.6 ± 6.2)	2–25 (11.6 ± 9.5)	-	2–5 (3.7 ± 1.2)	7–9 (7.8 ± 0.8)	0.5–3 (1.6 ± 0.9)	1–4 (2.2 ± 1.3)	-	3–16 (9.5 ± 6.5)	2–10 (6.3 ± 3.3)	1–15 (7.0 ± 5.9)
First peduncle L	3–18 (10.9 ± 7.1)	5–35 (15.5 ± 9.9)	1–18 (6.9 ± 5.3)	8	15–20 (17.5 ± 2.5)	13–40 (24.0 ± 11.6)	2–25 (10.3 ± 9.2)	25–85 (57.3 ± 24.7)	-	0–55 (23.4 ± 22.2)	42–125 (88.0 ± 30.2)	8–25 (14.3 ± 7.6)
Last peduncle L	0	4–6 (5.0 ± 0.7)	0	-	0–5 (2.3 ± 2.1)	5–17 (9.5 ± 5.7)	0–4 (1.8 ± 1.8)	0	-	0–8 (2.3 ± 3.3)	3–4	0
Basal sheath L	0	10–22 (15.4 ± 4.2)	0–5 (2.0 ± 1.6)	0	60–83 (72.7 ± 9.5)	0	0–1	25–32 (29.0 ± 2.9)	-	5–58 (33.7 ± 15.7)	15–60 (40.0 ± 16.2)	0–10 (5.0 ± 4.1)
Basal bract L	160–290 (221.4 ± 43.8)	16–60 (36.6 ± 14.8)	40–160 (87.6 ± 35.4)	12	400–600 (483.3 ± 85.0)	340–640 (486.0 ± 122.6)	10–77 (36.3 ± 23.6)	52–82 (68.0 ± 12.3)	23–36 (29.5 ± 6.5)	110–270 (161.2 ± 58.7)	92–200 (138.0 ± 44.4)	165–360 (251.7 ± 81.1)
Ps of the P	U, A	Uf, A	U, A	U, A	A	Uf, A	Uf, G	A	U	U, A	U, A	U
Ps of the HF	Um	Um, A	Um	Uf, Um	A	Um, G	U, G	A	Uf, Um	Um	Um, A	Um, (A)
No. male Ps	2–4	0–1	1–2	0–1	0	0–1	0–1	0	0–1	1–2	0–1 (7)	2–3
No. stigmas	3	3	2	3	3	3	3	3	3	3	3	3
Remote Ps	-	-	-	-	-	-	-	-	-	-	-	-

Table 4. Characteristics of the inflorescences of the *Schoenoxiphium* Clade. All measurement in mm. P = Paracladium, L = Length, HF = Main florescence Ps = pseudospike. Inflorescence shape: O = oblong, Oo = Oblong-ovate. Pseudospike type: A = Androgynous.

Sections	*Aciculares*	*Caryotheca*	*Junceiformes*
Studied species	*C. acicularis*	*C. phyllostachys*	*C. setifolia*
Inflorescence shape	Oo	O	Oo
Length	5–8 (6.6 ± 1.2)	12–24 (16.6 ± 4.2)	5–7 (5.5 ± 1.3)
Width	3.5–4.6 (4.2 ± 0.4)	7–8 (7.5 ± 0.5)	3–6 (4.2 ± 1.2)
Max P order	-	1	-
No. P I	-	0–1	-
First internode L	-	0–6.5 (3.7 ± 2.7)	-
First peduncle L	-	-	-
Basal bract L	-	90–150 (109.0 ± 25.4)	6–11 (11.0 ± 2.0)
Ps type	A	A	A
No. stigmas	3	3	3
Rachilla	flat, scabrid	flat, ciliate	flat, ciliate

paracladia. The female flower has two (rarely three) stigmas. Pseudospikes are generally bisexual, androgynous, gynecandrous or mesogynous, or rarely unisexual.

The androgynous sections *Heleoglochin* Dumort., *Phleoideae* (Meinsh.) T. V. Egorova, and *Vulpinae* (Heuff.) H. Christ. have highly branched inflorescences, having up to 15–18 first order paracladia. Most of the studied specimens have second and third order paracladia. Two species belonging to section *Heleoglochin* have a different inflorescence structure than the remaining taxa of the group. *Carex diandra* Schrank. has the first five paracladia of first order (PI_1-I_5) with 1–5 branches of second order (PII) while the rest (PI_6 -I_{11}) are not branched. *Carex secta* Boott is the only species of this section with long peduncles, about 10 mm. In the inflorescences of these three sections there are more female flowers than male. Male flowers increase progressively upwards, while female flower number is stable or decreases upwards.

Other androgynous sections, such as *Foetidae* (Tuck. ex L. H. Bailey) Kük., *Divisae* H. Christ ex Kük., and *Phaestoglochin* Dumort (Fig. 2c), have few (6–13) paracladia that are little if at all branched (branching varies among taxa, especially within the morphologically heterogeneous *Phaestoglochin*). Section *Divisae* does not present any second order paracladia. The Eurasian taxa belonging to section *Phaestoglochin* are characterized by simpler inflorescences, occasionally with 1–2(–4) second order branches in the proximal paracladia (PII). Most of the studied specimens of Eurasian *Phaestoglochin* (18 of 27) have one to four perigynium-like or glumaceous prophylls in young branches (Fig. 3). In general, the number of female flowers is similar to or scarcely greater than the number of male flowers in each paracladium. *Carex foetida* All. (sect. *Foetidae*) has a variable number of male and female flowers in each pseudospike and sometimes has unisexual pseudospikes, with the androgynous or female pseudospikes proximal to the male ones. Some specimens have most of their flowers female, whereas others have almost the opposite.

Carex arenaria (sect. *Ammoglochin* Dumort.) has branched inflorescences, with 8–12 first order paracladia, all of them have a perigynium-like prophyll. The arrangement of male and female flowers changes along the axis of the inflorescence. The proximal pseudospikes have female flowers in the middle; all the specimens dissected are mesogynous, having two to three male flowers in the lowest part of the pseudospike. Occasionally, the basal paracladia PI_1-I_3 have branches PII_1 with male pseudospikes. The number of male flowers increases distally and from PI_5-PI_6 to the apex the pseudospike is only male. The main florescence is also male.

The gynecandrous sections *Gibbae* Kük., *Glareosae* G. Don., *Ovales* Kunth (Fig. 2d), *Remotae* (Asch.) C. B. Clarke, and *Stellulatae* Kunth only have first order paracladia. All the

Table 5. Characteristics of the inflorescences of the *Vignea* Clade. All measurement in mm. P = Paracladium, L = Length, HF = Main florescence Ps = Pseudospike. Inflorescence type: P = Paniculiform, S = Spiciform. Pseudospike type: A = Androgynous, G = Gynecandrous, M = Mesogynous, U = Unisexual, Um = Male unisexual Uf = Female unisexual. If more than one species has been studied within a section, just the name of the first is given.

Section	*Ammoglochin*	*Divisae*	*Foetidae*	*Gibbae*	*Glareosae*	*Heleoglochin*	*Macrocephalae*
Studied species	*C. arenaria*	*C. divisa*	*C. foetida*	*C. gibba*	*C. canescens*	*C. appressa*	*C. macrocephala*
Inflorescence	S	S	S	S	S	S, P	S
Length	38–57 (45.0 ± 8.1)	7–34 (15.18 ± 7.7)	11–20 (15.7 ± 2.9)	30–60 (43.4 ± 9.7)	16–31 (23.3 ± 4.9)	20–200 (92.8 ± 51.9)	35–52 (46.4 ± 6.2)
Width	13–20 (17.0 ± 2.5)	4–14 (8.5 ± 2.9)	10–15 (12.1 ± 2.0)	4–6 (5.0 ± 0.8)	7–8 (7.5 ± 0.5)	7–35 (15.7 ± 7.7)	25–35 (29.0 ± 3.4)
Max. P order	2	1	2	1	1	3	2
No. P I	8–12 (10 ± 1.2)	4–6 (5 ± 0.9)	9–12 (10.5 ± 1.1)	4–6 (5.0 ± 0.7)	3–5 (4.0 ± 0.8)	5–18 (11.3 ± 3.9)	14–20
No. P II/ PI	2	-	7	-	-	9	4–5
No. P III/PII	-	-	-	-	-	8	-
First internode L.	5–50 (16.0 ± 16.0)	1.5–3 (1.8 ± 0.6)	1–2 (1.5 ± 0.4)	13–15 (13.8 ± 0.8)	5–12 (8.7 ± 2.6)	3–67 (18.8 ± 15.7)	3–4 (3.5 ± 0.4)
Last internode L.	0.5–1.5 (1.0 ± 0.4)	0.25–1 (0.5 ± 0.2)	0.25–0.5 (0.4 ± 0.1)	2–4 (3.0 ± 0.8)	0.5–1.5 (1.0 ± 0.4)	0.25–1 (0.6 ± 0.3)	0.25–0.5 (0.4 ± 0.1)
First peduncle L	-	-	-	-	-	0–9 (2.1 ± 3.2)	-
Basal bract L	16–40 (30.6 ± 13.3)	4–130 (35.4 ± 34.5)	7–20 (12.4 ± 4.8)	125–150 (126.3 ± 17.8)	3–7 (4.3 ± 1.5)	5–40 (13.9 ± 8.3)	36–42 (38.7 ± 1.9)
Prophyll	yes	-	-	yes	-	-	-
Ps of the P	M, Um	A	A, Uf (Um)	G	G	A	A, Uf
Ps of the HF	Um	A	A, Uf	G	G	A	A, Uf
No. male Ps	6–12	-	-	-	-	-	-
No. stigmas	2	2	2	3	2	2	3

Table 6. Characteristics of the inflorescences of the *Vignea* Clade (cont.). All measurement in mm. P = Paracladium, L = Length, HF = Main florescence Ps = Pseudospike. Inflorescence type: P = Paniculiform, S = Spiciform. Pseudospike type: A = Androgynous, G = Gynecandrous, M =Mesogynous, U = Unisexual, Um = Male unisexual Uf = Female unisexual. If more than one species has been studied within a section, just the name of the first is given.

Section	*Ovales*	*Phaestoglochin*	*Phleoidae*	*Physoglochin*	*Remotae*	*Stellulatae*	*Vulpinae*
Studied species	*C. leporina*	*C. cyprica*	*C. foliosa*	*C. davalliana*	*C. remota*	*C. echinata*	*C. otrubae*
Inflorescence	S	S	S	S	S	S	S, P
Length	18–27 (23.3 ± 3.6)	17–109 (39.1 ± 19.3)	50–62 (56.7 ± 5.0)	10–15 (12.3 ± 1.7)	85–150 (112.0 ± 24.5)	18–22 (20.0 ± 1.4)	26–71 (41.0 ± 15.0)
Width	10–17 (14.0 ± 2.3)	5–14 (10.1 ± 1.8)	8–10 (8.7 ± 0.9)	3–5 (4.0 ± 0.7)	8–10 (9.2 ± 0.8)	9–10 (9.7 ± 0.5)	10–18 (13.0 ± 2.5)
Max. P order	1	2	2	-	1	1	3
No. P I	5–6 (5.5 ± 0.5)	3–10 (14) (7.7 ± 2.6)	12–15 (13.7 ± 1.2)	-	5–6 (5.7 ± 0.5)	3–5 (3.8 ± 0.7)	13–15 (14.2 ± 0.8)
No. P II/ PI	-	4	4	-	-	-	7
No. P III/PII	-	-	-	-	-	-	3
First internode L.	2–3.5 (2.6 ± 0.6)	2.5–63 (11.2 ± 10.4)	15–18 (16.5 ± 1.5)	-	27–55 (42.5 ± 10.1)	4–6 (5.1 ± 0.5)	4–20 (10.2 ± 5.8)
Last internode L.	0.25–1 (0.6 ± 0.3)	0.25–0.5 (0.4 ± 0.1)	0.25–0.5 (0.4 ± 0.1)	-	0.25–0.5 (0.4 ± 0.1)	0.25–1 (0.6 ± 0.3)	0.25–0.5 (0.4 ± 0.1)
First peduncle L	-	0–3 (0.6 ± 1.1)	1	-	-	-	-
Basal bract L	12–60 (28.2 ± 14.7)	4–75 (12.9 ± 14.7)	7–10 (8.5 ± 1.5)	-	155–280 (241.2 ± 68.1)	3–7.5 (5.2 ± 1.8)	11–54 (30.0 ± 14.4)
Prophyll	-	sometimes	-	-	yes	sometimes	-
Ps of the P	G	A	A	U	G	G	A
Ps of the HF	G, Uf	A	A	U	G, Um	G	A
No. male Ps	-	-	-	0–1	0–1	-	-
No. stigmas	2	2	2	2	2	2	2

studied European taxa have only four to six paracladia, less than the androgynous sections, although many North American taxa belonging to section *Ovales* have more than six paracladia (Mastrogiuseppe et al. 2002). *Carex gibba* Wahlenb**.** and *C. remota* L. have small glumaceous and transparent prophylls, less than one mm. *Carex echinata* occasionally has cladoprophylls (Fig. 4). However, in sections *Ovales* and *Glareosae* the cladoprophylls were never seen. There is a higher number of female than male flowers in all of these sections. Sometimes, *Carex leporina* L. has only female flowers in the main florescence, and some species of section *Stellulatae* are commonly unisexual or unispicate.

Section *Physoglochin* Dumort. is dioecious. All specimens studied of *Carex davalliana* Sm. and *C. dioica* L. have spiciform, unisexual inflorescences. *Carex macrocephala* Willd. (sect. *Macrocephalae*) has been also reported as dioecious (Kükenthal 1909). It has branched inflorescences, with 14–20 paracladia, and is one of the few species in *Vignea* Clade with three stigmas. Studied specimens only showed female unisexual and androgynous shoots, a condition known as paradioecy (Standley 1985).

Core Unispicate Clade—Major results are presented in Fig. 2; Table 7. The species of *Carex* in this clade have fertile

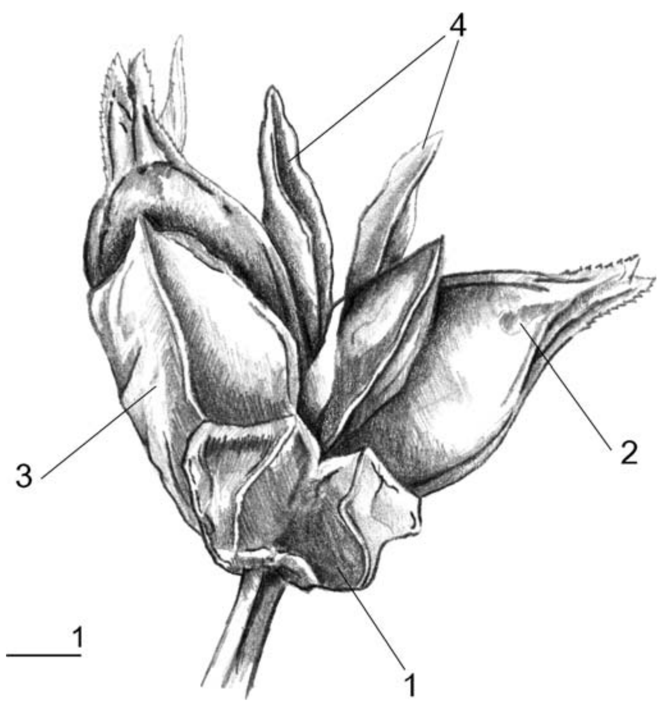

Fig. 3. Perigynium-like prophyll in PI_8 of *Carex pairae* F. W. Schultz (LEB 79018). 1. Perigynium-like prophyll. 2. Perigynium. 3. Female glume. 4. Male glumes. Scale bar in mm.

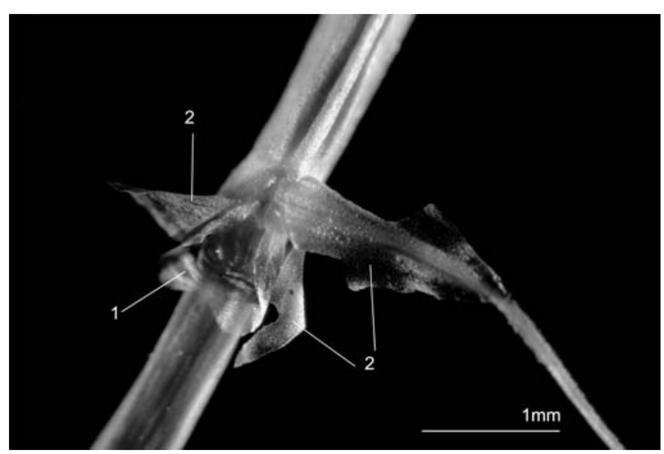

Fig. 4. Cladoprophyll in PI_1 of *Carex echinata* Murray (LEB 78169). The pseudospike has been removed and the bract is broken to show the cladoprophyll. 1. Cladoprophyll. 2. Bract. Scale bar in mm.

Table 7. Characteristics of the inflorescences of the Core Unispicate Clade. All measurement in mm. P = Paracladium, L = Length, Ps = Pseudospike. Inflorescence shape: O = oblong, Oe = Obong-elongated, Oo = Oblong-ovate, L = linear. Pseudospike type: A = Androgynous, Um = Male unisexual. If more than one species has been studied within a section, just the name of the first is given

Sections	Capituligerae	Circinatae	Curvulae	Dornera	Firmiculmes	Inflatae	Leptocephalae	Leucoglochin	Longespicate	Nardinae	Obtusatae	Phyllostachyae	Psyllophora	Rupestres
Studied species	C. capitata	C. circinata	C. curvula	C. nigricans	C. geyeri	C. breweri	C. leptalea	C. microglochin	C. monostachya	C. nardina	C. obtusata.	C. backii	C. macrostyla	C. rupestris
Inflorescence shape	Oo	L	O, Oo	O, Oo	O	O	L	O, Oo	L	Oo	Oe	O	L	O
Length	7–10 (7.9 ± 1.1)	20–25 (21.3 ± 2.0)	11–20 (15.6 ± 2.9)	10–21 (13.9 ± 3.3)	15–22 (17.8 ± 3.5)	15–20 (17.8 ± 2.0)	10–16 (11.9 ± 2.2)	5–15 (8.8 ± 3.1)	25–50 (33.5 ± 7.9)	5–10 (7.5 ± 1.6)	8–12 (10.4 ± 1.4)	15.5–44 (29.5 ± 10.1)	13–30 (19.6 ± 4.5)	15–20 (15.8 ± 2.6)
Width	5.5–8 (6.5 ± 0.8)	3–5 (3.7 ± 0.9)	5–13 (8.6 ± 2.3)	5–8 (6.5 ± 1.0)	5–7 (6.4 ± 0.8)	8–11 (9.2 ± 1.2)	3–4 (3.5 ± 0.4)	4–10 (7.1 ± 2.1)	5–8 (6.6 ± 1.2)	4.5–7 (5.2 ± 0.8)	3–6 (4.4 ± 1.0)	4–7 (5.4 ± 1.1)	3–7 (5.2 ± 1.3)	4–5 (4.5 ± 0.5)
Max P order	-	-	1	-	-	-	-	-	-	-	-	-	-	-
No. P I	-	-	2–8	-	-	-	-	-	-	-	-	-	-	-
First internode L	-	-	0.5–2.5 (1.8 ± 0.8)	-	-	-	-	-	-	-	-	-	-	-
First peduncle L	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Basal bract L	-	-	7–10 (7.6 ± 1.2)	-	-	-	-	-	-	-	-	-	-	-
Ps type	A	A	A, Um	A	A	A	A	A	A	A	A	A	A	A
No. stigmas	2	3 (2)	3	3 (2)	3	3	3	3	2	2	3	3	2	3
Rachilla	yes	-	yes	-	-	yes	-	yes, no	yes	yes	yes	-	usually not	-
Perigynium reflexed	-	-	-	yes	-	-	-	yes	-	-	-	-	yes	-

prophylls and sometimes rachillae, which when present are never flat, ciliate, or scabrous on the margin. Most of them have apparently unbranched inflorescences, and the solitary pseudospike is always androgynous, lacking bracts, peduncles, and prophylls. Embedded within this clade are the genera *Kobresia*, *Uncinia*, and *Cymophyllus* (Yen and Olmstead 2000a, b; Roalson et al. 2001; Starr et al. 2004; Waterway and Starr 2007; Starr et al. 2008; Starr and Ford 2009; Waterway et al. 2009; Gehrke et al. 2010), but species of those genera were not investigated for this study.

Carex curvula (sect. *Curvulae* Tuck. ex Kük.) differs from the remaining species of *Carex* in this clade in its dense, short-spiciform inflorescence and paracladia with a perigynium-like prophyll subtending an ovary at the base. Each female flower bears a rachilla, and its perigynium is trigonous, with three stigmas. *Carex curvula* only has two to eight first order paracladia and the pseudospikes are androgynous.

All the other sections in this clade have the same inflorescence structure and just differ in inflorescence shape, stigma number, presence/absence and type of rachilla, and whether the perigynia are deflexed or not at maturity. Sections *Nardinae* (Tuck.) Mack., *Capituligerae* Kük., *Longespicatae* Kük., *Obtusatae* (Tuck.) Mack., and *Rupestres* (Tuck.) Meinsh. have glumaceous perigynia, with smooth rachillae in all except section *Rupestres*. They share some vegetative characters, similar to unispicate *Kobresia* subgenus *Kobresia* (Zhang 2001). They are densely tufted plants, with short rhizomes and persistent basal leaf sheaths. Sections *Phyllostachyae* (*C. backii* Boott and *C. saximontana* Mack.) and *Firmiculmes* (*C. geyeri* Boott) have a similar appearance, resembling *Kobresia fragilis* C. B. Clarke in having a sheathing, basal leaf-like glume and an androgynous pseudospike with the male part linear and the female flowers slightly separated. The sections *Dornera* Heuff. (Fig. 2e), *Leucoglochin* Dumort., and *Psyllophora* (Degl.) Koch [which Kükenthal (1909) treated in section *Unciniaeformes* Kük.] resemble *Uncinia* section *Uncinia* in their oblong-ellipsoid, aplanate perigynia gradually narrowing into a beak, tapered below to a short stout pedicel, becoming deflexed at maturity. In some species (i.e. *Carex pulicaris* L.) the glumes are deciduous and can be seen only in young specimens.

Discussion

Four major clades have been found in most of the Cariceae molecular studies, but the relationship among them remain obscure (Waterway and Starr 2007; Starr and Ford 2009); the more recently identified *Siderostictae* clade (Waterway et al. 2009) is supported as sister to the rest of the genus. All the studies agree that *Carex* is not monophyletic and, although further taxonomic sampling is needed, in several studies *Schoenophixium* appears close to Core Unispicate Clade, as part of the Caricoid Clade (Roalson et al. 2001; Starr et al. 2004; Starr et al. 2008; Starr and Ford 2009; Waterway et al. 2009). Moreover, most of the topologies are in favor of a Caricoid Clade sister to a clade composed of core *Carex* plus *Vignea* (Starr and Ford 2009). In the Core *Carex* and *Vignea* clades the paracladium consists of a bract, a prophyll, a peduncle, and a pseudospike, where some elements such as prophylls and peduncles can be absent. The prophyll, marking the paracladium beginning, is usually sterile. In contrast, the Caricoid Clade presents a fertile prophyll (possessing an ovary) in the paracladium base (Gordon-Gray 1995). Most *Kobresia* and *Schoenoxiphium* species have a fertile rachilla as well, exserted from the apex of the prophyll and bearing several male flowers (Nelmes 1952; Haines and Lye 1972; Timonen 1985, 1989). Therefore, we point out that the Core *Carex* and *Vignea* clades show a slight difference in the paracladium type from the Caricoid Clade because of the sterile prophyll.

Kreczetowicz (1936), Levyns (1945), Smith (1966), Smith and Faulkner (1976), and Timonen (1998), studying the unispicate androgynous taxa of *Carex*, assumed that each female spikelet, the single female flower with its perigynium and glume, represents the last step in the reduction of a paracladium of the Caricoid branching species. We are in broad agreement that this female spikelet is the fertile prophyll, pointing out the existence of a paracladium, and the controversial rachilla present in some taxa (Svenson 1972; Reznicek 1990) is the remains of a lateral axis (Kreczetowicz 1936) or, in contrast, the beginning of a fertile growing one. In fact, we can see in the multispicate specimens of *Carex phyllostachys* the development of a pseudospike leaving a fertile perigynium at the base (Kreczetowicz 1936; Egorova 1999; Starr et al. 2008). So the seemingly unispicate inflorescence has several paracladia, each of them consisting of one fertile prophyll, and molecular analyses place these taxa in the Caricoid Clade (Yen and Olmstead 2000a; Waterway and Starr 2007; Starr et al. 2008; Waterway et al. 2009). Nelmes (1952) and Haines and Lye (1972) suggested this reduction had a different origin from *Unicinia*, *Kobresia,* or *Schoenoxiphium*, but these hypotheses are not supported by molecular analysis to date. To the contrary, *Uncinia* is a monophyletic group (Starr et al. 2008; Starr and Ford 2009), which might allow for a common origin of reduction in this genus and the unispicate carices of the Caricoid Clade but precludes an *Uncinia* origin for unispicate *Carex*.

The morphology of the rachilla appears to be the only character to distinguish the paracladia of the Core Unispicate Clade from the *Schoenoxiphium* Clade in the unispicate taxa. Our results in the Caricoid Clade are similar to those of Nelmes (1952). He postulated the phylogeny of most of the species in the traditional subgenus *Primocarex* based on morphological characters. As expected, the characters referred to the female spikelet, as presence and type of rachilla or perigynium morphology appear, but none of them is related to the inflorescence structure, because all are identical. Molecular analyses support section *Leucoglochin* as polyphyletic (Starr et al. 2008). *Carex parva*, *C. pauciflora,* and *C. microglochin* are scattered and more closely related to *Kobresia* than to *Uncinia* (Starr et al. 2008; Starr and Ford 2009). Such characters as deciduous glumes and deflexed perigynia may be plesiomorphic for the Caricoid Clade as a whole, a question that bears investigation using phylogenetic comparative methods.

Morphological studies may provide insight into placement of taxa not fully resolved by molecular analyses. One example is the placement of sect. *Psyllophora*. *Carex pulicaris* (sect. *Psyllophora*) falls in the *Schoenoxiphium* Clade in several molecular studies (Starr et al. 2004; Waterway and Starr 2007; Starr et al. 2008; Starr and Ford 2009; Waterway et al. 2009). The most recent phylogenetic study of *Schoenoxiphium* (Gehrke et al. 2010) places section *Psyllophora* in the *Carex distachya* Clade but does not show a significant support for the relationship between *C. distachya* and *Schoenoxiphium* clades. In the present study, we found that the morphology of the rachilla of the members of section *Psyllophora* is more similar to the species in the Core Unispicate Clade than those in the *Schoenoxiphium* Clade. A second example is *Carex curvula,* peculiar due to its fertile perigynium-like prophyll. Although this species has been variously classified in subgenus *Vignea* (Chater 1980) or subgenus *Carex* (Egorova 1999), it is different from other species in the genus *Carex.* Molecular data (Starr et al. 2004; Ford et al. 2006; Starr and Ford 2009) show that *C. curvula* is close to *Kobresia*, as Ivanova (1939) proposed.

Considering that the polarity of pseudospike evolution in *Carex* has yet to be demonstrated convincingly, the current study provides important information for future studies of character evolution in the genus. Starting from a basal androgynous lineage for the entire genus (the *Siderostictae* Clade), the *Vignea* Clade presents a complex situation with all possible variants in flower arrangement: dioecious or paradioecious plants, and androgynous, gynecandrous or mesogynous pseudospikes. The placement of *Carex gibba* as sister to the *Vignea* Clade (Ford et al. 2006; Starr and Ford 2009; Waterway et al. 2009) may suggest that gynecandry is the ancestral state for the clade. Without additional phylogenetic data, however, it is not clear whether the gynecandrous pseudospike is ancestral or derived. Gynecandrous pseudospikes appear in several scattered lineages, probably as an adaptation to severe conditions (Egorova 1999), which argues as strongly for gynecandry as a derived condition. The Core *Carex* Clade has similar diversity in the sexuality of the pseudospikes, although there are not mesogynous ones. The sections *Carex* and *Vesicariae*, which usually have only unisexual pseudospikes and several distal male pseudospikes, are placed in a derived position in this clade (Hendrichs et al. 2004b; Waterway and Starr 2007; Waterway et al. 2009).

Dioecy appears in both clades. Dioecy is advantageous in an environment with changing conditions (Bertin 2007), but is quite rare in *Carex,* occurring in only 0.68% of species (Guibert et al. 2009). The derived positions of the dioecious species *Carex scirpoidea* Michx. and *C. picta* in the Core *Carex* Clade (Roalson et al. 2001; Waterway and Starr 2007; Starr and Ford 2009; Waterway et al. 2009) supports the hypothesis that they are the result of a particular evolutionary regime, which may be rather rare; or that the evolutionary path to dioecy involves many steps. A similar case is the dioecious section *Physoglochin,* which it is in an advanced position in the *Vignea* Clade (Hendrichs et al. 2004a; Waterway and Starr 2007; Starr and Ford 2009). Timonen (1998) also considered dioecious species the most specialized. Guibert et al. (2009) suggested that hybridization between monoecious species with conflicting sexual morphology (gynecandrous and androgynous) could induce dioecy. The inflorescence of the dioecious species is similar to the androgynous unispicate *Carex* of the *Caricoid* Clade. This is a good example of convergence on an important reproductive / life history trait, whose origins may bear additional study (see, for example, Friedman and Barrett 2009).

The internode and peduncle lengths are valuable characters for separating clades and even sections. We suggest that the ancestral states are the presence of internodes and peduncles as in the *Siderostictae* Clade. The derived states, short or absent internodes and peduncles, are present in the *Vignea* Clade. There are reversals in some sections: long internodes, for example, are present in sections *Remotae* and *Gibbae*. The same occurs at the species level in *Carex secta* (sect. *Heleoglochin*) and *C. divulsa* (sect. *Phaestoglochin*), both of which have long peduncles and internodes. The primitive and most common characters in Core *Carex* Clade are long peduncles and internodes. They are seen in taxa belonging to the former subgenus *Vigneastra* (*Carex cruciata*, *C. baccans*, *C. polystachya*, *C filicina*, etc.), which fall in basal positions in the Core *Carex* Clade in all molecular research (Starr et al. 1999; Yen and Olmstead 2000b; Roalson et al. 2001; Hendrichs et al. 2004b; Starr et al. 2004; Waterway and Starr 2007; Starr et al. 2008; Starr and Ford 2009; Waterway et al. 2009). The Core *Carex* Clade shows more variation than the *Vignea* Clade (Tables 2–3, 5–6). We only studied the 5% of taxa of the whole genus so the figures are estimated, the internode length of the taxa studied in the Core *Carex* Clade ranges from one to 230 mm (63.5 ± 56.8) while in the *Vignea* Clade it varies between one and 67 mm (12.9 ± 13.8). In the same way, the peduncle length varies from 0–125 mm (21.2 ± 23.3) in the Core *Carex* Clade but 0–9 mm (0.9 ± 2.1) in the *Vignea* Clade. Core *Carex* Clade also shows more variation within the sections, e.g. sect. *Mitrae* and *Ceratocystis* with short and large internodes, while others (e.g. sect. *Carex*) have long internodes with short peduncles.

Other important features are the presence and type of prophyll. Traditionally, *Vignea* has been characterized by the lack of any kind of prophyll except the perigynium (Kükenthal 1909; Smith and Faulkner 1976; Kukkonen 1984; Yen and Olmstead 2000b). However, Alexeev (1978) pointed out that prophylls are present in some species, Song-Wang (1994) described them in *Carex gibba*, and Smith (1966) found prophyll traces in shoots of the subgenus *Vignea* species that he studied. We can corroborate that several specimens belonging to the *Carex muricata* group have perigynium-like or glumaceous prophylls in the branch buds (Fig. 3), and we also found glumaceous prophylls in *C. gibba*, a gynecandrous species that appears as the sister to all other *Vignea* in some molecular analyses (Ford et al. 2006; Starr and Ford 2009; Waterway et al. 2009). Our research confirms that prophylls appear in subg. *Vignea*, mainly in gynecandrous sections, and it may be that study of more taxa and more specimens in each taxon will reveal more examples of prophylls in the clade. Further research is needed to know if the presence of cladoprophylls is an ancestral character in the *Vignea* Clade, because the character reconstructions on a recent molecular phylogeny are ambiguous (Starr and Ford 2009). However, there is no doubt that the presence of the cladoprophylls is the ancestral state in the Core *Carex* Clade (Starr and Ford 2009); prophylls, cladoprophylls in the proximal paracladia and perigynium-like prophylls in the distal ones, are nearly always present in this clade. We only found a single specimen of *Carex bicolor* (sect. *Bicolores*) lacking a cladoprophyll in the second paracladium of the first order (PI_2). Reznicek (1990) hypothesized a different origin for the cladoprophylls, having a secondary origin from empty glumes in subgenus *Carex*. Dissecting the specimens, we found out that the cladoprophylls changed their appearance gradually while the sheath length decreased, turning into a perigynium-like prophyll, so it is difficult to establish a dividing line between cladoprophylls and perigynium-like prophylls. Hence, our results suggest that both kinds of prophylls could be considered the same structure with different morphology depending on their placement.

The fertility of the prophyll and rachilla are important characters for separating the main clades. Although the fertile prophylls, the proliferation (or reduction) of the rachillae and the formation of bisexual spikelets may occur in all Cariceae clades, some trends seem to be clear. Our study confirms that the *Vignea* and Core *Carex* clades generally have sterile prophylls at the paracladium base; in fact, most of the species of the *Vignea* Clade do not even have prophylls; as an exception, we found fertile prophylls in the paracladia of only *Carex hirta* and *C. arenaria.* Sometimes they have been reported as abnormalities in other taxa, even developing a fertile rachilla that bears male flowers (Snell 1936; Le Cohu 1968; Smith and Faulkner 1976; Song-Wang 1994; Timonen 1993), mainly in disturbed places (Svenson 1972). Alternatively, the paracladium of the species of *Carex* in the Caricoid Clade has been interpreted as consisting of only a fertile prophyll, and we also found fertile prophylls in all specimens of *Carex curvula*. As has been observed previously, the paracladium typical of the Caricoid Clade has a fertile prophyll. The fertile prophyll is occasionally absent in the proximal paracladia of first and second order in branched specimens (Levyns 1945; Timonen 1989; pers. obs.). On the other hand, section *Siderostictae* has also been reported as often having a well developed rachilla (Kükenthal 1909; Egorova 1999) which can be occasionally fertile with terminal male flowers (Waterway et al. 2009). More research is needed to know the environmental conditions that affect the expression of fertility, but most data suggest the fertility of the prophyll and the rachilla are probably the ancestral states in Cariceae and that the sterile conditions in the Core *Carex* and the *Vignea* clades are derived.

The type of basal bract and its length are distinctive characters of the inflorescence. Probably, the ancestral characters are long, leaflike basal bracts, as present in the *Siderostictae* Clade, which appears in the Core *Carex* Clade as well. In the *Vignea* Clade, bracts are setaceous, short and not sheathing (with some exceptions, such as *Carex remota*), suggesting that this character state is derived. The characters of bracts are constant and have taxonomic value at section level, though length can vary widely even within species. In the same way the lowest inflorescence bract sheath varies within in the Core *Carex* Clade and helps in the differentiation of sections. According to Egorova (1999), long sheaths are primitive. Although we do not have enough data to evaluate this proposal rigorously, we have observed the longest sheaths in a unisexual section (sect. *Carex*) and in an androgynous one (sect. *Polystachyae*) which are respectively in more derived and basal positions in the clade.

Inflorescences in *Carex* range from paniculiform to seemingly unbranched (spiciform). Molecular analyses (Starr and Ford 2009) suggest that the multispicate inflorescence (only first lateral order) was the ancestral condition in Cariceae and that reduction, homogenization, truncation, ramification, and reversion have all taken place in the evolution of the current structures (Vegetti 2002; Guarise and Vegetti 2008). Taxa belonging to the former subgenus *Vigneastra* (*Carex cruciata*, *C. baccans*) are now known to occupy basal positions in the Core *Carex* Clade (Starr et al. 1999; Roalson et al. 2001; Starr et al. 2004; Waterway and Starr 2007; Starr et al. 2008; Starr and Ford 2009). As multispicate or compound inflorescences are primitive in this clade (Starr and Ford 2009), the panicle of *Vigneastra* may be similar to the ancestral inflorescence type. In the clade, a process of homogenization takes place leading to the simplification and standardization of the branches (Rua 1996). Homogenization in successive steps without reversals would lead to a single first order paracladium at the top of the clade (e.g. sections *Vesicariae,* *Phacocystis*). But homogenization is not the only process at play in inflorescence evolution: compound inflorescences have evolved in some lineages (e.g. *Carex filicina*, sect. *Indicae*). Homogenization and proliferation also occurred in the *Vignea* Clade, where a multispicate inflorescence was ancestral (Starr and Ford 2009). The results are spiciform inflorescences as in *Carex leporina* (sect. *Ovales*) or *C. echinata* (sect. *Stellulatae*), or paniculiform inflorescences as in *C. paniculata* (sect. *Heleoglochin*) or *C. otrubae* (sect. *Vulpinae*).

It is worth noting that the racemiform inflorescence with two or more paracladia arising at the same node in *Carex rhizomatosa* are rare in the tribe Cariceae, and in the monocotyledons in general, but they have been reported in *C. echinochloe* Kunze, section *Indicae* and in *Schoenoxiphium* (Haines and Lye 1972), and, surprisingly, in section *Siderostictae* (Kükenthal 1909; Waterway et al. 2009). All species belonging to the former subgenus *Vigneastra* studied in molecular research fall in the Core *Carex* Clade to date (Starr et al. 1999; Yen and Olmstead 2000a, b; Roalson et al. 2001; Starr et al. 2004; Waterway and Starr 2007; Starr and Ford 2009; Waterway et al. 2009) and they do not have a direct connection with *Schoenoxiphium* as previous studies hypothesized (Haines and Lye 1972; Smith and Faulkner 1976), so this type of inflorescence is likely to be the result of convergent evolution.

Inflorescences of the *Vignea* Clade are identified by their short internodes and paracladia with setaceous basal bracts, short or absent peduncles, and female spikelets with distigmatic ovaries. The Core *Carex* Clade is characterized by long internodes, foliaceous basal bracts, long peduncles, and female spikelets with tristigmatic ovaries. Assuming the polarization of characters that we have hypothesized in the current study, the *Vignea* Clade comprises more derived characters than the Core *Carex* Clade. In the *Vignea* Clade, highly branched species with some unisexual pseudospikes like section *Ammoglochin* (= *Arenariae*) (Starr and Ford 2009; Hendrichs et al. 2004a) and species with complex paniculiform inflorescences like sections *Phaestoglochin* and *Vulpinae* (Ford et al. 2006) are placed in a derived position. Species with sexual specialization and long basal bracts such as those in sections *Vesicariae* and *Lupulinae* (Hendrichs et al. 2004b; Waterway and Starr 2007) fall in a derived position at the top of the Core *Carex* Clade. We interpret our study as suggesting that the main evolutionary processes in *Carex* are: increase in the branching number (*Vignea* Clade), increase in the branching degree (Core Carex and *Vignea* clades), sexual specialization of the pseudospikes (Core Carex and *Vignea* clades), paracladia homogenization (Core Carex and *Vignea* clades), and paracladium reduction (Core Unispicate Clade). However, there are several other processes in lateral clusters generating the great diversity of the genus, such as sexual reversion, changes in branching number, changes in internode length, and changes in peduncle length. Apparently, different evolutionary processes operate at diverse times and at different speeds in such a way that the same inflorescence type may be reached via different pathways (e.g. racemiform inflorescences, mentioned above).

In summary, in this study we have developed Levyns's (1945) and Timonen's (1993, 1998) ideas, treating the paracladium as the inflorescence-unit rather than the spikelet or pseudospike as is usually done, within a coherent phylogenetic framework. The three main lineages (Caricoid, *Vignea*, and Core *Carex* clades) show different trends in the evolution of the paracladium. We highlight the importance of the prophyll, because the presence of a fertile prohyll characterizes the species of *Carex* belonging to the Caricoid Clade. This type of paracladium helps to understand why the unispicate taxa of *Carex* are placed in phylogenetic trees nearer to branched taxa of *Kobresia* and *Schoenophyxium* than to the remainder of *Carex*. Moreover, our study also confirms the presence of prophylls in five sections of *Vignea*. Although the principal trends in inflorescence evolution in the *Vignea* and Core *Carex* clades have been established, much more effort is needed. We need to study other characters of the unispicata taxa, apart from the rachilla, to distinguish morphologically the Core Unispicata and *Schoenoxiphium* clades. Knowledge of the polarity of certain characters, like the length of the basal bract sheaths in the Core *Carex* Clade or the sexuality of the pseudospike, lets us better understand evolutionary processes in the genus. Not only would it be desirable to study more characters of the inflorescences but also more species and sections of *Carex*, mainly sect. *Siderostictae*, and also the remaining genera of tribe Cariceae, mainly *Kobresia* and *Schoenoxiphium*. For a definitive circumscription of the genus *Carex* we must wait to have more molecular data.

Contrary to Timonen (1998) our research interpreted the inflorescences of *Carex* according to the typological method (Weberling 1985). This method assumes that the florescences (main florescence and coflorescences) have homologous components, which are pseudospikes and spikelets (Weberling 1989). As the inflorescences in *Carex* are complicated (Timonen 1998), we expanded this idea of homology to the entire paracladium, supposing that the paracladia with their elements, prophylls, peduncles, bracts, pseudospikes with one or more spikelets, are equivalent. The concept of paracladium as inflorescence-unit is effective and it can easily be extended to other genera of Cariceae. As a result the typological analysis of the inflorescences is a useful tool in the systematics of the genus but it must be used with caution and compared with more data. In brief, a deep knowledge about what inflorescence structures are and how they evolve contributes to a better understanding of the phylogeny of Cariceae.

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Appendix 1. Material studied. Specimens are cited by section, species and country. Individual specimens are identified by herbarium acronym and accession number where available or by collector and collector number if not.

Core Carex Clade—**Sect.** ***Acrocystis*** **Dumort.** ***Carex montana*** **L.** SPAIN. Burgos: MA 017372. Huesca: FCO 07657. Navarra: LEB 62610, LEB 83705. Santander: JBAG 765. ***C. pilulifera*** **L.** FRANCE. Pyrenées: LEB 83951, LEB 83719, LEB 78521, LEB 83932, LEB 80871. SPAIN. La Coruña: SANT 49599. León: LEB 79001, LEB 81158. Oviedo: LEB 83706. ***C. tomentosa*** **L**. FRANCE. Alpes Haute Provence: LEB 81144. SPAIN. León: LEB 49867, LEB 82706. Soria: MA 321081, MA 342390. Valladolid: MA 530738.

Sect. ***Aulocystis*** **Dumort.** ***Carex ferruginea*** **subsp.** ***caudata*** **(Kük.) Pereda & Laínz**. SPAIN. Alava: MA 314873, VIT 7735, VIT 7734, VIT 7731. Oviedo: *M. Laínz, Herb Hispanicum Boreo-Occidentale s.n.* (K). Burgos: MA 622634, MA 163059, BIO 9308, BIO 5582. Cantabria: SANT 21262, FCO 14531, MA 505687, MA 524221, MA 462965, LEB 62472, MA 309437, MA 486563, BIO 1726, VIT 78746, VIT 78745, BIO 1727, BIO 2730, MA 342467, BIO 5449, BIO 5448, BIO 6053, BIO 1245, BIO 5369, BIO 1248, MA 163057, MA 462960, MA 23410, *R. K. Brummitt & A. O. Chater 116* (K), BIO 9528. Guipuzcoa: BIO 2676. León: MA 342468. Navarra: MA 590406, MA 479971, BIO 26598. Oviedo: JBAG 759, JBAG 755, JBAG 782, JBAG 785, JBAG 788, JBAG 789, LEB 92333, MA 386899, SANT 22542, FCO 09766, FCO 11476, FCO 14532, FCO 14530, FCO 14529, FCO 14528, FCO 14527, FCO 14526, JBAG 786, MA 152826, LEB 92332, JBAG 790. Vizcaya: VIT 7732, VIT 7733, BIO 2677, BIO2675. ***C. frigida*** **All**. FRANCE. Alpes Haute Provence: LEB 80878. Pyrenées: LEB 80877, LEB 83923, LEB 83939, LEB 80876, LEB 83937. Rhône-Alpes: LEB 80853, LEB 83739. ITALY. Piamonte: LEB 80879. SPAIN. Cantabria: MA 623411. Gerona: UPNA 3385. León: LEB 39805. SWITZERLAND. Valais: MA 519204. ***C. sempervirens*** **Vill.** FRANCE. Alpes Haute Provence: LEB 81145. Pyrenées: LEB 80862, LEB 83733, LEB 83938, LEB 83915, LEB 83934, LEB 83936, LEB 83922, LEB 83740. Rhône-Alpes: LEB 83747. ITALY. Piamonte: LEB 81154. SPAIN. Cantabria: JBAG 739. Huesca: BCN 45575. Navarra: UPNA 2967, LEB 83732. León: LEB 78553. Oviedo: LEB 92301. SWITZERLAND. Schwyz: BCN 45572.

Sect. ***Bicolores*** **(Tuck. ex L. H. Bailey) Rouy.** ***Carex bicolor*** **All.** FRANCE. Alpes Haute Provence: LEB 80897.

Sect. ***Carex***. ***Carex hirta*** **L.** DENMARK. Isle of Aero: MA 274435. FRANCE. Landes: LEB 83925, LEB 83926, LEB 83927. GERMANY. Bayern: MA 387284. FINLAND. Nylandia: MA 274436. MORROCO. Meknes: MA 243690. PORTUGAL. Portelo a Montezinho: MA 194292. SPAIN. Almería: MA 579195. Barcelona: MA 143609. Galicia: MA 18417. Guadalajara: LEB 77739. León: LEB 75507, LEB 79013, LEB 85000, LEB 79013. Lugo: MA 530591. Navarra: MA 555369. Palencia: LEB 37201, LEB 42542, LEB 42549. Salamanca: MA 236939, MA 236957. SWEDEN. Västmanland: MA 59890. SWITZERLAND. Wintterthur: MA 18398.

Sect. ***Ceratocystis*** **Dumort.** ***Carex demissa*** **Hornem.** FRANCE. Landes: LEB 83947. Limoges: LEB 83941. Midi-Pyrenees: LEB 78512, LEB 78525. SPAIN. Cantabria: FCO 14436. La Coruña: LEB 62630. León: LEB 39801, LEB 83955, LEB 81156. Lugo: LEB 83896, LEB 83895. Oviedo: LEB 83711. Zamora: LEB 82688. ***C. flava*** **L.** FRANCE. Alpes Haute Provence: LEB 81146. Rhône-Alpes: LEB 80852. ITALY. Piamonte: LEB 80881. SWEDEN. Upland: LY 741-Herb Rouy. ***C. lepidocarpa*** **Tausch.** FRANCE. Alpes Haute Provence: LEB 80875, LEB 81148. Pyrénées Atlantiques: LEB 80873, LEB 80874. SPAIN. Alava: FCO 23861. Cantabria: FCO 14427. León: LEB 81167, LEB 81160, LEB 78545, LEB 78542, LEB 83722, LEB 78513. Navarra: LEB 83736. Oviedo: LEB 92300. UNITED KINGDOM. Riremackie: CGE 8579.

Sect. ***Chlorostachyae*** **Tuck. ex Meinsh.** ***Carex capillaris*** **L.** FRANCE. Alpes Haute Provence: LEB 80895, LY 724 -Herb Rouy. SPAIN. Cantabria: MA 519109, FCO 14411. Huesca: UPNA 3397. León: MA 519109. Logroño: MA 338993.

Sect. ***Depauperatae*** **Meinsh.** ***Carex brevicollis*** **DC.** FRANCE. Ain: LY 719 -Herb Rouy. SPAIN. Burgos: MA 314908. Cantabria: LEB 62444. León: LEB 62446, MA 315749. Navarra: LEB 05230, UPNA 9217. Oviedo: LEB 82703, LEB 92296. ***C. depauperata*** **Curtis ex Stokes.** SPAIN. Cáceres: LEB 45086. Huesca: UPNA 3395. León: LEB 82673, LEB 82670, LEB 82672, LEB 83725, LEB 82695, LEB 83724, LEB 78176. Lugo: SANT 15666.

Sect. ***Digitatae*** **(Fr.) H. Christ.** ***Carex ornithopoda*** **Willd**. SPAIN. Alava: MA 017837. Cantabria: LEB 62616. León: LEB 30977, LEB 15084, FCO 19845. Navarra: LEB 83727, LEB 83730, LEB 83729. Oviedo: JBAG 772, MA 172118, FCO 07436, LEB 92303, MA 519095.

Sect. ***Grallatoriae*** **Kük.** ***Carex grallatoria*** **Maxim**. JAPAN. Kai, pref. Yamanashi: *Miyoshi Furuse 20789* (K). Musashi: *Miyoshi Furuse 19269* (K). *Miyoshi Furuse 19270* (K). Ohsumi: *Miyoshi Furuse 39726* (K).

Sect. ***Hallerianae*** **(Asch. & Graebn.) Rouy.** ***Carex halleriana*** **Asso**. SPAIN. León: LEB 46291, LEB 07777, LEB 79006, LEB 16955, LEB 35544. Palencia: LEB 37204.

Sect. ***Indicae*** **Tuck.** ***Carex cruciata*** **Wahlenb.** NORTH VIETNAM. Annam: *M. Poilane 30247* (K). Tonkin, Mont-Bavi: *B. Balansa 2816* (K). Thailand. N12 Phitsanulok: K 000494109. NE17. Loei: P. *Chantaranothai, J. Parnell, D. Simpson & K. Sridit 90/175* (K). ***C. filicina*** **Nees.** THAILAND. N2. Chieng Mai: *Phengklai C. et al. 6701* (K), K 000494086. N5, Nan Pua: *D. Simpson & J. Parnell 1723* (K).

Sect. ***Mitratae*** **Kük.** ***Carex caryophyllea*** **Latourr.** FRANCE. Midi Pyrenées: LEB 83715. Pyrénées Atlantiques: LEB 80893. SPAIN. Cantabria: JBAG 777. Huesca: LEB 62821, UPNA 3387. León: LEB 78516, LEB 78179, LEB 78156, LEB 78555, LEB 81159, LEB 83720, LEB 82705, LEB 83712, LEB 83889, LEB 83888, LEB 81182, LEB 81179. Navarra: LEB 83743, LEB 83735. Zamora: LEB 83701. UNITED KINGDOM. 58, Chester: CGE 1807. ***C. depressa*** **Link subsp.** ***depressa*****.** SPAIN. León: LEB 82704, LEB 83890.

Sect. ***Paludosae*** **G. Don.** ***Carex acutiformis*** **Ehrh**. FRANCE. Hautes Alpes: LEB 80898. SPAIN. Burgos: MA 18468. León: LEB 73684, LEB 28410. Soria: MA 387770.

Sect. ***Paniceae*** **G. Don.** ***Carex asturica*** **Boiss.** SPAIN. León: LEB 78158, LEB 78168. Logroño: MA 547445. Oviedo: LEB 92307, JBAG 780. Soria: MA 342701. ***C. panicea*** **L.** FRANCE. Alpes Haute Provence: LEB 81150. Rhône-Alpes: LEB 80851. ITALY. Piamonte: LEB 80867. SPAIN. La Coruña: SANT 43940. Lugo: LEB 83897. León: LEB 78517, LEB 78541, LEB 81164, LEB 82674.

Sect. ***Phacocystis*** **Dumort.** ***Carex elata*** **All. subsp.** ***reuteriana*** **(Boiss.) Luceño & Aedo.** SPAIN. León: LEB 78175, LEB 78161, LEB 81174, LEB 78540. Madrid: FCO 10656. Oviedo: FCO 11460. ***C. nigra*** **(L.) Reichard.** FRANCE. Alpes Haute Provence: LEB 80870. SPAIN. León: LEB 78551, LEB 83899, LEB 83903, LEB 83904, LEB 83905, LEB 83959, LEB 78167, LEB 78546, LEB 92172, LEB 92308, LEB 92309. ***C. trinervis*** **Degl.** PORTUGAL. Beira Litoral: LEB 83698, LEB 83702, LEB 83704, LEB 83700, LEB 83699, LEB 83703.

Sect. ***Pictae*** **Kük.** ***Carex picta*** **Steud.** U. S. A. Alabama: *"from Peter", in herb. Boott* (K). Indiana: *R. M. Kriebel & T. J. Owens 635* (K). Tennesse: *H. K. Svenson 9051* (K).

Sect. ***Polystachyae*** **Tuck.** ***Carex baccans*** **Nees**. THAILAND. Chiang Mai: C 8010. Northern Thailand: C 596. Doi Chingdao: C 6228, C 797, *Put 325* (K), *T. Sorensen s.n* (K), *A. F. G. Kerr 16792* (K).

Sect. *Pseudocypereae* Tuck. ex Kük. *Carex pseudocyperus* L. FRANCE. Pyrenées Atlantiques: FCO 21960. PORTUGAL. Beira Litoral: FCO 19622. SPAIN. Burgos: UPNA 3651, FCO 27269, LEB 80715. León: LEB 26751, LEB 18626, MA 314883, LEB 86776, LEB 9148, LEB 18629, LEB 78999. Lugo: SANT 51388.

Sect. *Racemosae* G. Don. *Carex atrata* L. AUSTRIA. Niederösterreich: SANT 53802. FRANCE. Rhône-Alpes: LEB 80849. SPAIN. Cantabria: JBAG 748. León: LEB 61787. Palencia: LEB 19667, LEB 82718. ***C. parviflora* Host.** FRANCE. Alpes Haute Provence: LEB 80864, LEB 80863, LEB 80865. Rhône-Alpes: LEB 80850. SPAIN. Cantabria: FCO 14538, FCO 14535, MA 342523. Huesca: UPNA 3384. León: LEB 66515, LEB 67629, LEB 8769, LEB 39452, LEB 16903, LEB 30979. Oviedo: LEB 92299, FCO 14540. Palencia: MA 560374, LEB 48209, LEB 62437, LEB 34736.

Sect. *Scabrellae* Kük. *Carex rhizomatosa* Steud. INDIA. Munipur: *G. Watt 6033* (K). Ranchi, Paloman: *H. H. Haines 4355* (K). Thoyung: *C. B. Clarke 37554 A* (K). PHILIPPINES: Bontoc, Luzon: *M. Vanoverbergh 325* (C).

Sect. *Scirpinae* (Tuck.) Kük. *Carex scirpoidea* Michx. RUSSIA: Magadan: *T. Derviz-Sokolova 5617* (K). Siberia: *V. Soceara s.n.* (K). U. S. A. Alaska: *C. Wright s.n. Coll*. (K).

Sect. *Spirostachyae* (Drejer) L. H. Bailey. *Carex binervis* Sm. FRANCE. Midi-Pyrénées: LEB 78526. SPAIN. La Coruña: SANT 56448. León: LEB 81168, LEB 81165, LEB 83886, LEB 72171, LEB 83921. Lugo: LEB 83893, LEB 83898, SANT 56449. Oviedo: LEB 83713, LEB 83714. Zamora: LEB 82690. ***C. extensa* Gooden.** SPAIN. La Coruña: SANT 49607, LEB 78536, SANT 49593, LEB 78371, SANT 49822. Pontevedra: SANT 46445. ***C. puntacta* Gaudin.** FRANCE. Landes: LEB 83928, LEB 83928. SPAIN. La Coruña: SANT 56427, LEB 78534. Gerona: LEB 51877. Oviedo: FCO 11424.

Sect. *Sylvaticae* Rouy. *Carex sylvatica* Huds. subsp. *sylvatica*. FRANCE. Midi-Pyrénées: LEB 83707. Rhône-Alpes: LEB 83737. SPAIN. Cantabria: LEB 14176. Guipúzcoa: LEB 40262. León: LEB 78160. Navarra: LEB 83726.

Sect. *Vesicariae* (Heuff.) J. Carey. *Carex rostrata* Stokes. FRANCE. Alpes Haute Provence: LEB 81149. ITALY. Piamonte: LEB 81153. SPAIN. Cantabria: JBAG 763. León: LEB 83721, LEB 81161, LEB 92168, LEB 83958, LEB 92169, LEB 78550, LEB 78544. Zamora: LEB 82689. ***C. vesicaria* L.** SPAIN. Avila: LEB 40178. Burgos: UPNA 10179, LEB 83591. León: LEB 83957, LEB 71340, LEB 62831, LEB 78520. Ourense: LEB 83258. Oviedo: LEB 54895, FCO 07486. Vizcaya: SANT 44538, UPNA 3767, LEB 36993.

***Schoenoxiphium Clade*—Sect. *Aciculares* (Kük.) G. A. Wheeler. *Carex acicularis* Boott.** NEW ZEALAND: *R. & E. F. Melville 5997* (K). *Colenso s.n* (K), *B. G. Hamlin 538* (K).

Sect. *Caryotheca* V. I. Krecz. ex T. V. Egorova. *Carex phyllostachys* C. A. Mey. GEORGIA. Transcaucasia: *B. Schischkin 129* (K). IRAN. *L. Merton 3324* (K). TURKEY: Hatay, *Davis & Hedge D 27073* (K).

Sect. *Junceiformes* Boeck. *Carex setifolia* Kuntze. CHILE: Claud. *Gay s.n.* (K). Colehaqua: *Prof. G. Montero 733* (K). Valparaiso: *P. C. Hutchison 102* (K).

***Vignea Clade*—Sect. *Ammoglochin* Dumort. *Carex arenaria* L.** FRANCE. Landes: LEB 83944, LEB 83940. SPAIN. Cantabria: SANT 25043. La Coruña: LEB 79012, FCO 18360. Oviedo: FCO 29315. Segovia: MA 374474.

Sect. *Divisae* H. Christ ex Kük. *Carex divisa* Huds. FRANCE. Landes: LEB 83948. PORTUGAL. Alto Alentejo: BCN 44733. SPAIN. Almeria: GDA-GDAC 43168. Baleares, Mallorca: BCN 44764. Barcelona: BCN 44759. Burgos: BCN 44757. Córdoba: GDA-GDAC 39684. Granada: GDA-GDAC 45772. Huesca: BCN 44746. León: LEB 78155, LEB 78184, LEB 78165, LEB 81183. Murcia: BCN 44742. Oviedo: FCO 26732. Palencia: FCO 26264. Sevilla: SEV 161468. Teruel: JACA 125698. Toledo: FCO 26106. Valladolid: LEB 51500. Zamora: LEB 21634.

Sect. *Foetidae* (Tuck. ex L. H. Bailey) Kük. *Carex foetida* All. FRANCE. Alpes Haute Provence: LEB 80882, LEB 80884, LEB 80883.

Sect. *Gibbae* Kük. *Carex gibba* Wahlenb. CHINA. Anhui: *S. Song-Wang 94003* (K). Guangxi: *L. Zhen-Yu et al. 892145* (K). JAPAN. *Ch. Hashimoto 1272* (K). Sagami: *Miyoshi Furuse s.n.* (K), *Miyoshi Furuse 19208* (K). Yokohama: *Maximowicz* (*Iter secundum s.n*) (K).

Sect. *Glareosae* G. Don. *Carex canescens* L. SPAIN. Burgos: FCO 19715. León: LEB 39165, LEB 41667, LEB 78157. Logroño: MA 547440. Oviedo: MA 623337, LEB 83710, MA 542691. Palencia: MA 560395, MA 557205. Zamora: MA 585482.

Sect. *Heleoglochin* Dumort. *Carex appressa* R. Br. AUSTRALIA. New South Wales: *M. J. Taylor 94* (K), *S. T. Blake 7545* (K), *A. N. Rodd 6113* (K), *K. L. Wilson 9544* & *A. Muasya* (K). South Australia: MA 509049. Tasmania: *A. M. Buchanan*, *K. Gulliver, K. S. T. Blake 18412* (K). Victoria: *K. L. Wilson 9509* & *A. Muasya* (K), *S. T. Blake 7395* (K), *S. T. Blake 7235* (K). NEW GUINEA. *Walker ANU 558* (K). NEW ZEALAND. Campbell Island: *D. R. Given 9248* (K). ***C. appropinquata* Schumach.** AUSTRIA. Niederösterreich: MA 721430. DENMARK. Hirfih: *Schumacher s.n* (C). Lyngby Moor: *Schumacher*, *C. J. Lange* (C). FINLAND. Varsinais-Suomi: MA 478301. FRANCE. Haut-Rhin: MA 387790. GERMANY. Baden: *A. Kneucker 71* (K). IRELAND. Westmeath: MA 462752. SWEDEN. Närke: MA 175274. ***C. cusickii* Mack**. CANADA. British Columbia: *J. A. Calder & R. L. Taylor 35288* (K), *J. W. Eastham 8916* (K). Vancouver Islands: *J. Macoun 94* (K). U. S. A. California: *P. Ruetzoff 554* (K), *H. L. Mason 11923* (K), *Sander, C. CA330-18* (K). Idaho: *J. H. Sandberg, D. T. MacDougal & A. A. Heller s.n* (K). Oregon: *M. E. Peck 09247* (K). ***C. decomposita* Muhl.** U. S. A. Licely Island: *Dr. C. Peck s.n*, Herb. Careyanum (K). Missouri: *J. A. Steyermark 83541* (K). New York: *H. P. Sartwell s.n* (K). Ohio: *W. S. Sullivant s.n*, Herb. Careyanum (K), *Dewey s.n* (K), *Dr. Torrey s.n* (K). Virginia: *M. L. Fernald & B. Long 12951* (K). ***C. diandra* Schrank**. AUSTRIA. Austria inferior: *Strasser 3930*, (K). CANADA. Ottawa: *A. J. Breitung s.n* (K). FRANCE. Jura: BCN 44777. GERMANY. Rhenanae: H. *Andres 775* (K). FINLAND. Koillismaa: JACA 266883. JAPAN. Hokkaido: *Miyoshi Furuse 9027* (K). NEW ZEALAND. Lake Tekafo: *H. Talbord 858* (K). PAKISTAN. Kashmire: *T. Thomson s.n*, Herb Hoekerianum 1867 (K). SPAIN. Asturias: JBAG 730. León: LEB 78554, LEB 92173. Lérida: MA 442221. SWEDEN. Närke: *C. G. Alm 549* (K). UNITED KINGDOM. *Goodenough s.n* (K), *Dr Wood 1936*, Herb Churchillanum (K). ***C. incomitata* K. R.Thiele.** AUSTRALIA. New South Wales: *L. A. S. Johnson* & *B. P. Constable s.n* (K). Tasmania: *W. R. Barker 1127* (K), *F. H. Long 290* (K). Victoria: *A. Strid 22060* (K). ***C. paniculata* L. subsp. *calderae* (A. Hansen) Lewej. & Lobin**. SPAIN. Canary Islands, Tenerife: *E. Bourgeau 1176* (K), C 6196, C 2155, K 000363420, K 000363438, MA 531369. ***C. paniculata L. subsp. hansenii* Lewej. & Lobin**. CABO VERDE. San Antao: *W. Lobin 2134* (COI). ***C. paniculata* subsp. *lusitanica* (Schkuhr ex Willd.) Maire.** PORTUGAL. Barcelos: LEB 54583. SPAIN. Cáceres: LEB 28489. León: LEB 78183, LEB 32671. Palencia: LEB 39460. Pontevedra: LEB 38329. Toledo: LEB 56287. ***C. paniculata* L. subsp. *paniculata*.** SPAIN. Almeria: LEB 74484. SWITZERLAND. Valais: *L. V. Lester-Garland*, *F.L.S. 141* (K). ***C. prairea* Dewey**. CANADA. Ottawa: *Mckague*, *A. J. Breitung s.n* (K). U. S. A. Kentucky: *C. W. Short, M. D. s.n* (K). Michigan: *Herb. Careyanum s.n* (K). New York: *Alpany s.n* (K). Penn Yan: *H. P. Sartwell s.n.* (K). Oriskany: Herb Geo. *Vasey, N. Y.* s.n (K). Dexter: *F. J. Hermann 9440* (K). Ohio: Columbus, *W. S. Sulliwant s.n* (K). Vermouth: *Hanville s.n, Herb. Careyanum* (K). ***C. secta* Boott.** NEW ZEALAND. *Colenso 1075* (K). Alexandra: *W. Arthur Sledge 407* (K). Canterbury: *W. R. Philipson 10.115* (K), *R. & E. F. Melville 5589* (K), *R. & E. F. Melville 5772* (K). Kaikoura: *R. Mason 9175* (K). Lake Rotoiti: *R. & E.F. Melville 6091* (K). North Auckland: *R. Melville 5366* & *L. B. Moore* (K). Wellington: *B. G. Hamlin 403* (K), *B. G. Hamlin 599* (K), *B. G. Hamlin 578* (K). ***C. sectoides* (Kük.) Edgar**. NEW ZEALAND. Chathan Island: CHR 464793, CHR 436622. ***C. tenuiculmis* (Petrie) Heenan & De Lange**. NEW ZEALAND. Graigieborn: *A. Wall s.n* (K). ***C. tereticaulis* F. Muell**. AUSTRALIA. Blandorok: *F. Mueler s.n* (K). New South Wales: *K. L. Wilson 9503* & *A. Muasya* (K), *J. H. Camfield s.n* (K). South Australia: *Clarendon S. A. s.n* (K), *M. K. Jones* 26 & *B. Morphett* (K). Tasmania: *P. Stuar s.n* (K), *W. M. Curtis s.n* (K), *D. I. Morris s.n* (K). Victoria: *Herb. Dr. A. Morrison s.n.* (K), *Raleigh A. Black 1152* (K). West Australia: *Herb. Hookerianum 1867* (K). ***C. virgata* Sol. ex Boott**. NEW ZEALAND. M. Hombron: *Herb. Mus. Paris, s.n* (K), *Colenso s.n Herb. Hookerianum 1867* (K). Auckland: *com. J. J. Cheeseman s.n, Herb. Hookerianum 1867* (K). North Island: *H. Walter 5445* (K). Canterbury: *R. & E. F. Melville 5772* (K). Greymonth: *A. Puller 423* (K). Islands Waihalui: *Dr. Sinclair s.n Herb. Hookerianum 1867* (K). Little Barrier Island: *R. Melville 6581* & *W. M. Hamilton* (K). North Island: *P. J. Edwards 57* (K).

Sect. *Macrocephalae* Kük. *Carex macrocephala* Willd. CANADA. British Columbia: *J. A. Calder*, *J. A. Parmelee & R. L. Taylor 16317* (K). U. S. A. Oregon: *Nuttall s.n* (K), *L. F. Henderson s.n* (K). Washington: *J. M. Grant s.n* (K).

Sect. *Ovales* Kunth. *Carex leporina* L. ITALY. Piamonte: LEB 80869. FRANCE. Midi Pyrenées: LEB 83716. SPAIN. Cantabria: JBAG 743. León: JBAG 741. La Coruña: LEB 79017. TURKEY. Tauria: H 1309383.

Sect. *Phaestoglochin* Dumort. *Carex cyprica* Molina Gonz., Acedo & Llamas. CYPRUS. Distr. Paphos: MA 495407. Akamas: *L. F. H. Merton 3021* (K). Distr. Kyrenia: H 1302858. Mandria: *E. W. Kennedy 1438* (K). ***C. coryogine* Nelmes**. TURKEY. Lydia: B 100325385, K 000307996. ***C. divulsa* Stokes**. FRANCE. Garonne: LEB 78511. IRELAND: Limerick: *R. B. Drummond 736* (K). IRAN: Chalus: *P. Furse 2888* (K). MOROCCO: Xouen: MA 16808. PORTUGAL. Madeira: *C. Menezes 5* (P). SPAIN. Cáceres: LEB 24812. León: LEB 78171, LEB 78182, LEB 79002. TURKEY: Zonguldak: *Davis*, *Coode & Yaltarik 37793* (K). ***C. egorovae* Molina Gonz., Acedo & Llamas**. CYPRUS: Kythrea: *R. D. Meikle 2556* (K). GREECE. Thasos: *W. R. Price 1224* (K). IRAN. Trorth Gonbad: *T. F. Henr 3872* (K). IRAQ: Mam district: *O. Polunin 5110b* (K). MRO district Shaqlawa: W 01133. TURKEY. Bilecik B2: H 1492360. ***C. enokii* Molina Gonz., Acedo & Llamas**. LIBYA. Libia Cirenaica: *R. Pampanini & R. Pichi-Sermolli*

1156 (K). PALESTINA. Above Acie Fit: *F. S. Meyers & J. E. Dinsmore 91781* (K). TURKEY. Antalya: *Hennipman et al. 366*, *Iter leydense* (K). ***C. leersii* F. W. Schultz.** BELGIUM. Buissons: MA 016826. CROATIA. Ins. Korcula: *C. C. Townsed 76/36* (K). GERMANY. Baden: *A. Kneucker s.n* (K). HUNGARY. Villany: *Herb. Dr. A. de Degen, Koces s.n* (K). SPAIN. León: LEB 82662. Zaragoza: MA 016838. SWITZERLAND. Valais: *L. Favrat s.n* (K). UNITED KINGDOM. Norfolk: *C. E. Hubbard s.n* (K). ***C. magacis* Molina Gonz., Acedo & Llamas**. ANDORRA. S. Julià de Lòria: MA 714438. FRANCE. Hautes Pyrénées: LEB 82663. SPAIN. Navarra: LEB 82649. ***C. muricata* L. subsp. *ashokae* Molina Gonz., Acedo & Llamas**. INDIA. Kashmir: *C. B. Clarke 28644* (K). TAJIKISTAN. Kondara valley: H 1498323. ***C. muricata* L. subsp. *cesanensis* Molina Gonz., Acedo & Llamas.** AUSTRIA. Nordtirol: W 1976-02093. FRANCE. Iseré: LEB 82650. ITALY. Piamonte: LEB 80889. ***C. muricata* L. subsp. *muricata***. DENMARK. Hjorto: W 1961-14286. FRANCE. Alpes de Savoie: *E. Bourgeau s.n* (K). POLAND. Albertusoka Hill: *Beyer Schilling & Keesing 18* (K). RUSSIA. Pskow: *W. Andrejew s.n* (K). SPAIN. León: LEB 70509. ***C. nordica* Molina Gonz., Acedo & Llamas.** BELGIUM. Liège: LEB 48138. Namur: MA 236900. SWEDEN. Skane: *G. Samuelsson s.n* (K). ***C. omeyica* Molina Gonz., Acedo & Llamas.** SPAIN. Granada: MA 410621. ***C. otomana* Molina Gonz., Acedo & Llamas**. IRAN. E. Mazandaran: *H. Akhani 11898* (H 1695176). KAZAKHSTAN. Asia centralis, Alma–Ata: W 11223. UZBEKISTAN. distr. Andizham: *Litrovinov s.n* (K). ***C. pairae* F. W. Schultz**. FRANCE. L'Aude: MA 257383. GERMANY. Schleswig-Holstein: MA 388490. PORTUGAL. Castelo Bon: JACA 078273. Bragança: LEB 61347, Madeira: *C. Menezes 7* (P). SPAIN. La Coruña: LEB 79018. León: LEB 16737, LEB 81177, LEB 54544, LEB 78514, LEB 78181. TURKEY. Adana: *Davis 19608* (K). UNITED KINGDOM. Surry: MA 158554. ***C. rosea* Schkuhr**. U. S. A. New York: MA 175276. **C. *spicata* Huds. subsp. *andresii* Molina Gonz., Acedo & Llamas.** PORTUGAL. Serra do Soajo: WU 828. SPAIN. Córdoba: GDA-GDAC 42316. Guadalajara: MA 477226. Lugo: SANT 19928. León: LEB 78166, LEB 79022. Teruel: MA 475213. Toledo: JACA 025967. ***C. spicata* Huds. subsp. *spicata*.** BELGIUM. Pont-á-Celles: MA 627306. BULGARIA. Bei Tirnoivo: *Prof. Urumoff s.n* (WU). FINLAND. Aböensis: MA 274612. FRANCE. Hautes Pyrénées: LEB 82671. IRAN. East Azerbaijan: *M. Grant 16396* (W). IRELAND. Roscommon: *M. McCallum Wekter 7603* (K). POLAND. Breslau: *Callier s.n* (K). SWEDEN. Uppland: SANT 33621. UNITED KINGDOM. Wales: Radnor, *R. Lewis 1927* (K).

Sect. *Phleoideae* (Meinsh.) T. V. Egorova. *Carex foliosa* D. Don. CHINA. prope vicum Bahan (Pehalo): WU 2730. INDIA. Nagar: H 1654681. Jammu & Kashmir: H 1654287. NEPAL. *Wallich 3387* (K).

Sect. *Physoglochin* Dumort. *Carex davalliana* Sm. FRANCE. Alpes Haute Provence: LEB 80892. SPAIN. Alava: SANT 50555. A Coruña: LEB 38328. Guadalajara: LEB 47660. Navarra: UPNA 377. Teruel: LEB 53835. ***C. dioica* L.** FINLAND: Satakunta: *H. Lagström 1070a* (K). FRANCE. Jura: MA 016611. POLAND. Opole: *S. Ganeschin 4213b* (K). SWEDEN. Gostenbrung: *Tuckerman s.n* (K). Helsingland: *Gottfrid Lidman 9/33* (K). Lappland: *C. C. Townsend 83/198* (K).

Sect. *Remotae* (Asch.) C. B. Clarke. *Carex remota* L. FRANCE. Midi-Pyrenees: LEB 78524. SPAIN. La Coruña: SANT 49597. León: LEB 78174. Navarra: LEB 83744. Oviedo: FCO 25676. Soria: LEB 57068.

Sect. *Stellulatae* Kunth. *Carex echinata* Murray. FRANCE. Midi-Pyrenées: LEB 78523. ITALY. Piamonte: LEB 81155. MOROCCO: Tanger: SEV 160963. SPAIN. León: LEB 78169.

Sect. *Vulpinae* (Heuff.) H. Christ. *Carex polyphylla* Kar. & Kir. IRAQ. Penjwin: *Dr. Rawi 12248* (K). RUSSIA. Assu, circa montes Tarkagatai: *Karelin & Kirilow s.n* (K). ***C. otrubae* Podp.** FRANCE. Aude: LEB 82665. GREECE. Ioanninon: H 1557072. DENMARK. Sjaeland: LISU-G 14763. SPAIN. Huelva: LEB 47864. León: LEB 81178.

***Core Unispicate Clade*—Sect. *Capituligerae* Kük. *Carex capitata* L.** NORWAY. Salten: *R. E. Fridtz s.n* (K). SWEDEN. Jämtland: *E. Asplund 330* (K), Torne Lappmark: *Carl. G. Alm 1837* (K).

Sect. *Circinatae* Meinsh. *Carex circinata* C. A. Mey. U. S. A. Alaska: *W. J. Eyerdam 3222* (K), *W. J. Eyerdam 543* (K). CANADA. British Columbia: *A. Calder 21466* (K).

Sect. *Curvulae* Tuck. ex Kük. *Carex curvula* All. FRANCE. Alpes Haute Provence: LEB 80894. Rhône-Alpes: LEB 83753, LEB 83751, LEB 83750.

Sect. *Dornera* Heuff. *Carex nigricans* C. A. Mey. CANADA. Athabasca Plains: *Prof. Macoun 1731* (K). British Columbia: *T. R. G. Moir 318* (K). U. S. A. Alaska: *W. J. Eyerdam 1831* (K), Drummond: *W. B. s.n.* (K). ***C. pyrenaica* Wahlenb.** FRANCE. Pyrenées: UPNA 2311, LEB 83928. SPAIN. Cantabria: MA 623343. León: LEB 67621, LEB 67621. Lérida: LEB 5859, LEB 29956. Palencia: MA 169370, LEB 48208.

Sect. *Firmiculmes* (KüK.) Mack. *Carex geyeri* Boott. CANADA. Alberta: *J. Macoun 10749* (K). British Columbia: *J. Macoun 1775* (K). U. S. A. Rocky Mountain: *A. Nelson & E. Nelson 6105* (K).

Sect. *Inflatae* Kük. *Carex breweri* Boott. U. S. A. California: *Brewer 1392* (K), *J. T. Howell 21518* (K), *W. H. Brewer 2176* (K), *P. H. Raven 7473* (K).

Sect. *Leptocephalae* L. H. Bailey. *Carex leptalea* Wahlenb. CANADA. Ontario: *M. I. Moore 2900* (K), *J. A. Calder & W. J. Cody 936* (K). U. S. A. Alaska: *J. A. Calder 6188*, (K).

Sect. *Leucoglochin* Dumort. *Carex microglochin* Wahlenb. GERMANY. Bavaria Super.: *Herbarium Mart II, Progel s.n* (K). ITALY. Piamonte, Mont-Cenis: Herb Rouy-LY 763. Tirol: *Huter s.n., Herbarium Churchillanum* (K). Rochemelon, *J. Ball from J. Thaherne Moggridge s.n* (K). UNITED KINGDOM. Bernicia: *T. Birch Wolfe s.n* (K). ***C. parva* Nees.** INDIA. Pamir & Thian Shan: *H. Appleton s.n* (K). UZBEKISTAN. Asia media. Fergama: *D. Litrinow s.n* (K). ***C. pauciflora* Lightf.** AUSTRIA. Tirol: Stubaital, *D. Vaushaw 20* (K). Vogesi Mte Hoheneck, *Jhühlenbeck s.n* (K). GERMANY. Bohemia: *Ant. Schott (Buchers) 1*, (K).

Sect. *Longespicatae* Kük. *Carex monostachya* A. Rich. ETHIOPIA. Semien: *A. Pichi Sermolli 2665* (K).

Sect. *Nardinae* (Tuck.) Mack. *Carex nardina* Fr. GERMANY. Svalbard: *F. Schuhwerk 91/917* (K). NORWAY. Norland fylko: *A. Notó s.n* (K). SWEDEN. Torne Lappmark: *H. Smith s.n* (K). *E. Asplund s.n* (K).

Sect. *Obtusatae* (Tuck.) Mack. *Carex obtusata* Liljebl. SWEDEN. Öland: *A. J. Snell s.n* (K), *Wickström s.n* (K). Runsten: *J. M. Sjöstrand s.n* (K). Scania: *Harold Fries s.n* (K).

Sect. *Phyllostachyae* Tuck. ex Kük. *Carex backii* Boot. Coulton House: *H. Boot s.n* (K). CANADA. Ontario: *W. K. W. Baldwin & A. J. Breitung 3186* (K), *J. A. Calder*, *D. B. O. Savile*, *J. A. Parmelee & R. L. Taylor 23904* (K). Quebec: *M. Raymond & L. Cinq-Mars 31* (K). U. S. A. New York: *H. P. Sartwell, M.D. 9* (K), *H. Watertorn s.n* (K). ***C. saximontana* Mack**. CANADA. Manitoba: *M. O. Malte s.n* (K). U. S. A. *I. W. Clokey 3255* (K). Colorado: *I. W. Clokey 3691* (K).

Sect. *Psyllophora* (Degl.) Koch. *Carex macrostyla* Lapeyr. FRANCE. Midi-Pyrénées: LEB 83933, LEB 83935. Pyrénées Atlantiques: LEB 80872. SPAIN. Cantabria: JBAG 771, MA 342534. Huesca: LEB 32663. León: LEB 30978, LEB 71036, LEB 67615. Navarra: LEB 83731, LEB 83907. Oviedo: LEB 92302. ***C. peregrina* Link.** ETHIOPIA. Bale region: *M. Thulin, A. Hunde & M. Tudesse 3700* (K). KENYA. Mt Alberdare: *Exp. 1921-22 2650* (K). K2: *M. Thulin & A. Tidigs 112* (K). PORTUGAL. Azores: *H. C. Watson 175* (K). *T. C. Hunt s.n.* (K). Madeira: *G. Mandon 257* (K), *M. Lowe s. n.* (K). TANZANIA. Kilimanjaro: *JMG 94669* (K). Arusha Nat. Park: *D. Vesey-Fitzgerald 6769* (K). **C. pulicaris L.** SPAIN. La Coruña: SANT 56386. León: LEB 78549, LEB 83709.

Sect. *Rupestres* (Tuck.) Meinsh. *Carex rupestris* All. SPAIN. Asturias: MA 170290. Huesca: LEB 62813. León: LEB 78558. Navarra: MA 598416.