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

Authors: Ana Molina, Carmen Acedo, and Félix Llamas

Source: Systematic Botany, 37(2) : 365-381

Published By: The American Society of Plant Taxonomists

URL: https://doi.org/10.1600/036364412X635430
A Comparative Study of the Inflorescence in the Genus Carex (Cyperaceae)

Ana Molina, Carmen Acedo, and Félix Llamas

Department of Biodiversity and Environment Management, University of León E-24071, León, Spain.

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 paracodium. 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 Carex, Vignea, and Core Carex clades.

Keywords—Caricoid Clade, evolutionary process, inflorescence typology, paracodium, 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, Kükelenthal (1909) recognized four subgenera based on the structure of the inflorescences: Carex, Psyllophora (Degl.) Peterrm. (= 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). Recent molecular research (Starr et al. 1999; Yen and Olmstead 2000a, b; Roalson et al. 2003; Koike et al. 2003; 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). Carex Clade groups most species of subgenus 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 androgy nous 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) (Kükelenthal 1909; Chater 1980; Egorova 1999; Ball and Reznicek 2002). There are several studies about spikelets, flowers and inflorescence structure in Careiceae (Snell 1936; Mora Osejo 1966; Smith 1966; Kukkonen 1967; Haines and Lye 1972; Smith and Faulkner 1976; Meert and Goetghelbreur 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 Cymophyllus are distinguished morphologically by the presence of a closed perigynium, in contrast to the other two Careiceae 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; Kükelenthal 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 (Kükelenthal 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 polytetic 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
in 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. To do this, we followed 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.

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 (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 enumeration 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; Kukkonen 1984). 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).

Pseudospires 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 1986; Smith and Faulkner 1976; Haines and Lye 1972; Timonen 1996; Egorova 1999), they are not in agreement regarding the male spikelet concept. Smith (1986) 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.

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 perigynium, 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 pseudospires. 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, LBSU, LX, MA, P, SANT, SEV, UPNA, GIT, 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 Plastositchens Dumort., and the complete section Heliochlochum 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 Sabulveller 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 Macrocephala 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 unispecific 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 androgyneous bisexual pseudospires (e.g. Polystachyae, Indicae, and Sabulvrellae). In other sections pseudospires tend to be unisexual, with the proximal one female and the distal one male. Some, such as sections Placostychis Dumort. and Spirostachyae (Drejer) L. Bailey, have one to two male pseudospikes, and sections Aulocystis Dumort., Carex, Paludosae G. Don., and Vescariae (Heuff.) J. Carey have three to four male pseudospikes. The sections Chlorostachyae Tuck. ex Meinsch. and Digitatiae (Fr.) H. Christ. have only unisexual pseudospires. 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, Mexico, Breedlove 52083, CAS). In the center is shown an inflorescence which has PI₁, PI₂ and PI₃; this means there are three paracladia of first order. On the right, it shows PI₂ which is branching (PI₂₁, PI₂₂, ..., PI₂₅), that means there are five paracladia of second order in PI₂. The main florescence is shown by HF in the main axis and by PI₂HF in the paracladium PI₂. Horizontal bars = 1 mm and vertical bars = 5 mm. Drawing by Susan Reznicek. (Reproduced and modified with permission of A. A. Reznicek)
sections have a single male pseudospike that is the main florescence. The European taxa of section Acrocytis Dumort studied here also have unisexual pseudospikes, but some North American taxa have bisexual pseudospikes (Crins and Retting 2002). On the other hand, sections Aulocystis, Carex, Ceratocystis Dumort., Depauperatae Meisch., Mitratæ Kük., Paludosæ, Panicæ G. Don., Phacocystis, Sylviatæ Rouy (Fig. 2a), and Spirostachyæ have one or more androgyneous pseudospikes in the distal paradiadila. A few specimens have the main florescence androgyneous in sections Paniæae, Sylviatæ, and Vesciaeæ.

Gynoeandrous pseudospikes located in the distal paradiadila or main florescence were found in sections Aulocystis, Bicólores (Tuck. ex L. H. Bailey) Rouy, Pseudocypereae Tuck. ex Kük., and Racemosæ G. Don (Fig. 2b). Some specimens of Carex paraflores (sect. Racemosæ) have only female flowers in the main florescence. We found an interesting abnormality in Carex pseudocyperus L. (sect. Pseudocypereæ). Some specimens have female pseudospikes where male flowers replace the female ones in narrow strips along the length of the pseudospikes. In Carex halleriæ Asso (sect. Halleriæae), male, female, and bisexual plants may be found in the same population. Bisexual plants in this species have female or androgyneous pseudospikes in the paradiadila, with the main florescence male.

Usually, the internodes and peduncles are long relative to the pseudospike. In sections Carex, Depauperatae, Pseudocypereæ, Spirostachyæ, and Sylviatæ, for example, the proximal inter-

---

**Table 1.** Classification of the taxa studied. Species are arranged alphabetically within clades and sectional orders. Sections are grouped according to the four clades of Carex. Section placement follows Ball and Reznicek (2002) for North American species, Chater (1980) and Egorova (1999) for Eurasian ones, and Küchel (1999) for the rest. The nomenclature in sect. Phleoglochin (Viguéa Clade) follows Molina et al. (2008, 2008b).

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 Junceiformes Boeck, Acicularis (Kük.) G. A. Wheeler, and Cargotheca V. I. Krecz. ex T. V. Egorova, along with the embedded genus Schoenoxiphium (Levyns 1945; Haines and Lye 1972; Kukkonen 1978; Starr et al. 2008). Some specimens of _Carex phyllostachys_ C. A. Mey. (sect. Cargotheca) 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 = Paracodium, 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.

<table>
<thead>
<tr>
<th>Section</th>
<th>Acrocystis</th>
<th>Aulocystis</th>
<th>Bicolores</th>
<th>Carex</th>
<th>Ceratoctysis</th>
<th>Chlorostachyae</th>
<th>Depauperatae</th>
<th>Digitatae</th>
<th>Grallatoriae</th>
<th>Hallerianae</th>
<th>Indicae</th>
<th>Mitrateae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Studied species</td>
<td>C. montana</td>
<td>C. frigida</td>
<td>C. bicolor</td>
<td>C. hirta</td>
<td>C. demissa</td>
<td>C. capillaris</td>
<td>C. brevicollis</td>
<td>C. ornithopoda</td>
<td>C. grallatoria</td>
<td>C. halleriana</td>
<td>C. cruciata</td>
<td>C. carophylla</td>
</tr>
<tr>
<td>Inflorescence</td>
<td>S</td>
<td>R</td>
<td>R</td>
<td>S</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>sC</td>
<td>R</td>
<td>S</td>
<td>P</td>
<td>S</td>
</tr>
<tr>
<td>Inflorescence type</td>
<td>P</td>
<td>R</td>
<td>sC</td>
<td>R</td>
<td>S</td>
<td>P</td>
<td>R</td>
<td>S</td>
<td>P</td>
<td>R</td>
<td>S</td>
<td>R</td>
</tr>
<tr>
<td>Max. P order</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Ps of the P</td>
<td>1–4</td>
<td>1–5</td>
<td>3–5</td>
<td>3–5</td>
<td>3–5</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>No. PI</td>
<td>(2.0 ± 1.0)</td>
<td>(2.4 ± 1.6)</td>
<td>(2.5 ± 0.5)</td>
<td>(2.5 ± 0.5)</td>
<td>(2.5 ± 0.5)</td>
<td>(3.2 ± 0.8)</td>
<td>-</td>
<td>(2.0 ± 0.8)</td>
<td>-</td>
<td>(2.0 ± 0.7)</td>
<td>-</td>
<td>0</td>
</tr>
<tr>
<td>No. PI / PI</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>5–8</td>
<td>0</td>
</tr>
<tr>
<td>First internode</td>
<td>2.7–12 (74.0 ± 44.6)</td>
<td>20–65 (38.3 ± 17.5)</td>
<td>72–200 (125.3 ± 49.3)</td>
<td>20–72 (59.3 ± 71.4)</td>
<td>30–50 (40.0 ± 82.0)</td>
<td>25–60 (146.7 ± 40.7)</td>
<td>1–2</td>
<td>2–3 (83.0 ± 6.2)</td>
<td>7–10</td>
<td>60–97</td>
<td>1–150</td>
<td>0</td>
</tr>
<tr>
<td>Last internode</td>
<td>1–4 (17.3 ± 21.8)</td>
<td>1–4.5 (7.5 ± 2.1)</td>
<td>1–5 (9.7 ± 5.9)</td>
<td>2–18 (1.7 ± 2.4)</td>
<td>5–10 (40.2 ± 13.8)</td>
<td>10–70 (4.8 ± 1.1)</td>
<td>1–3</td>
<td>2–3</td>
<td>5–8</td>
<td>3–5</td>
<td>0–150</td>
<td>0–21</td>
</tr>
<tr>
<td>First peduncle</td>
<td>0</td>
<td>5–72 (28.9 ± 19.2)</td>
<td>3–35 (15.8 ± 14.5)</td>
<td>0–11 (2.8 ± 4.8)</td>
<td>3–35 (11.9 ± 11.1)</td>
<td>10–20 (48.3 ± 23.5)</td>
<td>2–4</td>
<td>3–10 (14.3 ± 6.8)</td>
<td>7–25</td>
<td>25–45</td>
<td>3–50</td>
<td>0–21</td>
</tr>
<tr>
<td>Last peduncle</td>
<td>0</td>
<td>0–30 (5.3 ± 9.0)</td>
<td>0–11 (0.3 ± 0.7)</td>
<td>0–2 (8.0 ± 0.8)</td>
<td>0–2 (7.0 ± 3.1)</td>
<td>0–10 (2.2 ± 0.6)</td>
<td>0</td>
<td>2–10 (7.0 ± 3.6)</td>
<td>0–4</td>
<td>30–62.5</td>
<td>5–165</td>
<td>0–21</td>
</tr>
<tr>
<td>Basal sheath</td>
<td>0</td>
<td>8–30</td>
<td>12–48</td>
<td>14–20</td>
<td>7–9</td>
<td>1–29</td>
<td>0–2</td>
<td>3–10</td>
<td>9–15</td>
<td>30–62.5</td>
<td>5–165</td>
<td>0–21</td>
</tr>
<tr>
<td>Basal bract</td>
<td>0</td>
<td>50–110 (127.2 ± 4.5)</td>
<td>28–43</td>
<td>115–362 (67.8 ± 20.9)</td>
<td>40–215 (37.5 ± 5.7)</td>
<td>14–24</td>
<td>20–190</td>
<td>30–190</td>
<td>30–40</td>
<td>160–250</td>
<td>5–165</td>
<td>2–3</td>
</tr>
<tr>
<td>Ps of the HF</td>
<td>Um</td>
<td>Um, G</td>
<td>G</td>
<td>Um, A</td>
<td>U, A</td>
<td>U, A</td>
<td>U, A</td>
<td>U, A</td>
<td>U, A</td>
<td>U, A</td>
<td>A</td>
<td>Um</td>
</tr>
<tr>
<td>No. male Ps</td>
<td>1</td>
<td>0–4</td>
<td>0</td>
<td>3–4</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0–1</td>
<td>0–1</td>
<td>0</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>No. stigmas</td>
<td>3</td>
<td>3</td>
<td>2</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Remote Ps</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>yes</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>yes</td>
<td>-</td>
<td>yes</td>
<td>-</td>
</tr>
</tbody>
</table>
Table 3. Characteristics of the inflorescences of the Core Carex Clade (cont). All measurement in mm. P = Paracodium, 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.

<table>
<thead>
<tr>
<th>Section</th>
<th>Paludosae</th>
<th>Paniceae</th>
<th>Phacocystis</th>
<th>Pictae</th>
<th>Polystachyae</th>
<th>Pseudocyperus</th>
<th>Racemosae</th>
<th>Scabrellae</th>
<th>Scirpinae</th>
<th>Spirostachyae</th>
<th>Sylvaticae</th>
<th>Vesicariae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Studied species</td>
<td>C. acutiformis</td>
<td>C. asturica</td>
<td>C. globularis</td>
<td>C. picta</td>
<td>C. baccans</td>
<td>C. pseudocyperus</td>
<td>C. atrata</td>
<td>C. rhizomatosus</td>
<td>C. scirpoides</td>
<td>C. binervis</td>
<td>C. sylvatica</td>
<td>C. rostrata</td>
</tr>
<tr>
<td>Inflorescence</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>S</td>
<td>R</td>
<td>P</td>
<td>R</td>
<td>R</td>
<td>S</td>
<td>R</td>
<td>R</td>
<td>R</td>
</tr>
<tr>
<td>Max. P order</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>1(2)</td>
<td>3</td>
<td>1(2)</td>
<td>1(2)</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>No. PI</td>
<td>4–5</td>
<td>2–3</td>
<td>3–4</td>
<td>0–1</td>
<td>6–12</td>
<td>4–5</td>
<td>3–5</td>
<td>5–7</td>
<td>0–1</td>
<td>3–5</td>
<td>4–6</td>
<td>5–7</td>
</tr>
<tr>
<td>Length</td>
<td>8–21</td>
<td>7–24</td>
<td>2–25</td>
<td>-</td>
<td>2–5</td>
<td>7–9</td>
<td>0–3</td>
<td>1–4</td>
<td>-</td>
<td>3–16</td>
<td>2–10</td>
<td>1–15</td>
</tr>
<tr>
<td>Last peduncle L</td>
<td>10.9</td>
<td>7.1</td>
<td>6.9</td>
<td>5.3</td>
<td>17.5–25</td>
<td>24.0–11.6</td>
<td>10.3–2.2</td>
<td>57.3–24.7</td>
<td>-</td>
<td>23.4–22.2</td>
<td>88.0–30.2</td>
<td>14.3–7.6</td>
</tr>
<tr>
<td>Basal sheath L</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0–5</td>
<td>5–17</td>
<td>0–8</td>
<td>0</td>
<td>-</td>
<td>3–16</td>
<td>15–60</td>
<td>0–10</td>
</tr>
<tr>
<td>Ps of the P</td>
<td>U, A</td>
<td>U, A</td>
<td>U, A</td>
<td>A</td>
<td>A</td>
<td>U</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>U</td>
<td>U</td>
</tr>
<tr>
<td>Ps of the HF</td>
<td>Um, A</td>
<td>Um, A</td>
<td>Um, A</td>
<td>U, A</td>
<td>U, A</td>
<td>Uf, G</td>
<td>A</td>
<td>U</td>
<td>A</td>
<td>U</td>
<td>U</td>
<td>U</td>
</tr>
<tr>
<td>No. male Ps</td>
<td>2–4</td>
<td>0–1</td>
<td>1–2</td>
<td>0–1</td>
<td>0–1</td>
<td>0</td>
<td>0–1</td>
<td>0–1</td>
<td>1–2</td>
<td>0–1(7)</td>
<td>2–3</td>
<td>-</td>
</tr>
<tr>
<td>No. stigmas</td>
<td>3</td>
<td>3</td>
<td>2</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Remote Ps</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
paradisia. The female flower has two (rarely three) stigmas. Pseudospikes are generally bisexual, androgynous, gyne-
candrous or mesogynous, or rarely unisexual.

The androgynous sections Heleoglochin Dumort., Phleoidae
(Meinsh.) T. V. Egorova, and Vulpinae (Heuff.) H. Christ have
highly branched inflorescences, having up to 15–18 first
order paradisia. Most of the studied specimens have second
and third order paradisia. 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 paradisia of first order (PI 1–I5) with 1–5 branches of
second order (PII) while the rest (PI 6–I11) 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) paradisia 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 paradisia.
The Eurasian taxa belonging to section Phaestoglochin are char-
terized by simpler inflorescences, occasionally with 1–2(–4)
second order branches in the proximal paradisia (PII). Most
of the studied specimens of Eurasian Phaestoglochin (18 of 27)
have one to four perigynium-like or glumeaceous 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 paradisia. Carex foetida All. (sect.
Foetidae) has a variable number of male and female flowers
in each pseudospike and sometimes has unisexual pseudo-
spikes, with the androgynous or female pseudospikes prox-
imal 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 paradisia, all of them
have a perigynium-like prophyll. The arrangement of male
and female flowers changes along the axis of the inflores-
cence. 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 paradisia PI 1–I3 have
branches PII with male pseudospikes. The number of male
flowers increases distally and from PI 3–PI 6 to the apex the
pseudospike is only male. The main florescence is also male.

The gynecandrous sections Gibbæae Kük., Glaresæae G. Don.,
Ovales Kunth (Fig. 2d), Remotæ (Asch.) C. B. Clarke, and
Stellulatae Kunth only have first order paradisia. All the

<table>
<thead>
<tr>
<th>Page 372</th>
<th>SYSTEMATIC BOTANY</th>
</tr>
</thead>
</table>

### Table 4. Characteristics of the inflorescences of the Schoenoxiphium Clade. All measurement in mm. P = Paradadium, L = Length, HF = Main florescence Ps = pseudospike. Inflorescence 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.

<table>
<thead>
<tr>
<th>Sections</th>
<th>Aciculares</th>
<th>Carpopoda</th>
<th>Junciformes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Studied species</td>
<td>C. acicularis</td>
<td>C. phyllostachya</td>
<td>C. setifolia</td>
</tr>
<tr>
<td>Inflorescence shape</td>
<td>Oo</td>
<td>Oo</td>
<td>Oo</td>
</tr>
<tr>
<td>Length</td>
<td>5–8</td>
<td>12–24</td>
<td>5–7</td>
</tr>
<tr>
<td>Width</td>
<td>(6.6 ± 1.2)</td>
<td>(16.6 ± 4.2)</td>
<td>(5.5 ± 1.3)</td>
</tr>
<tr>
<td>Max P order</td>
<td>3.5–4.6</td>
<td>7–8</td>
<td>3–6</td>
</tr>
<tr>
<td>No. P I</td>
<td>(4.2 ± 0.4)</td>
<td>(7.5 ± 0.5)</td>
<td>(4.2 ± 1.2)</td>
</tr>
<tr>
<td>First internode L</td>
<td>-</td>
<td>0–1</td>
<td>-</td>
</tr>
<tr>
<td>No. P II</td>
<td>0–6–5</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>First peduncle L</td>
<td>-</td>
<td>(3.7 ± 2.7)</td>
<td>-</td>
</tr>
<tr>
<td>Basal bract L</td>
<td>-</td>
<td>(90–150)</td>
<td>(109.0 ± 25.4)</td>
</tr>
<tr>
<td>Ps type</td>
<td>-</td>
<td>(11.0 ± 2.0)</td>
<td>(11.0 ± 2.0)</td>
</tr>
<tr>
<td>No. stigmas</td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Rachilla</td>
<td>flat, scabrid</td>
<td>flat, ciliate</td>
<td>flat, ciliate</td>
</tr>
</tbody>
</table>

| Studied species | A. arenaria | A. divisa | A. foetida | A. gibba | A. canescens | A. appressa |
| Inflorescence | S | S | S | S | S | P |
| Length | (38–57) | 7–34 | 11–20 | 30–60 | 16–31 | 20–200 |
| Width | (450 ± 8.1) | (15.18 ± 7.7) | (15.7 ± 2.9) | (43.4 ± 9.7) | (23.3 ± 4.9) | (92.8 ± 51.9) |
| Max. P order | (17.0 ± 2.5) | (8.5 ± 2.9) | (12.1 ± 2.0) | (5.0 ± 0.8) | (7.5 ± 0.5) | (15.7 ± 7.7) |
| Basal bract L | 6–11 | (109.0 ± 25.4) | (11.0 ± 2.0) | (11.0 ± 2.0) | (11.0 ± 2.0) | (11.0 ± 2.0) |
| Ps type | A | A | A | A | A | A |
| No. stigmas | 3 | 3 | 3 | 3 | 3 | 3 |
| Rachilla | flat, scabrid | flat, ciliate | flat, ciliate | flat, ciliate | flat, ciliate | flat, ciliate |

### Table 5. Characteristics of the inflorescences of the Vignea Clade. All measurement in mm. P = Paradadium, 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.

<table>
<thead>
<tr>
<th>Section</th>
<th>Ammoglochin</th>
<th>Divisae</th>
<th>Foetidae</th>
<th>Gibbæae</th>
<th>Glaresæae</th>
<th>Heleoglochin</th>
<th>Macrolepides</th>
</tr>
</thead>
<tbody>
<tr>
<td>Studied species</td>
<td>C. arenaria</td>
<td>C. divisa</td>
<td>C. foetida</td>
<td>C. gibba</td>
<td>C. canescens</td>
<td>C. appressa</td>
<td>C. macrocephala</td>
</tr>
<tr>
<td>Inflorescence</td>
<td>S</td>
<td>S</td>
<td>S</td>
<td>S</td>
<td>S</td>
<td>P</td>
<td>S</td>
</tr>
<tr>
<td>Length</td>
<td>(38–57)</td>
<td>7–34</td>
<td>11–20</td>
<td>30–60</td>
<td>16–31</td>
<td>20–200</td>
<td>35–52</td>
</tr>
<tr>
<td>Width</td>
<td>(15.18 ± 7.7)</td>
<td>(15.7 ± 2.9)</td>
<td>(43.4 ± 9.7)</td>
<td>(23.3 ± 4.9)</td>
<td>(92.8 ± 51.9)</td>
<td>(46.4 ± 6.2)</td>
<td>(29.0 ± 3.4)</td>
</tr>
<tr>
<td>Max. P order</td>
<td>(17.0 ± 2.5)</td>
<td>(8.5 ± 2.9)</td>
<td>(12.1 ± 2.0)</td>
<td>(5.0 ± 0.8)</td>
<td>(7.5 ± 0.5)</td>
<td>(15.7 ± 7.7)</td>
<td>(29.0 ± 3.4)</td>
</tr>
<tr>
<td>First internode L</td>
<td>(10 ± 1.2)</td>
<td>(5 ± 0.9)</td>
<td>(10.5 ± 1.1)</td>
<td>(5.0 ± 0.7)</td>
<td>(4.0 ± 0.8)</td>
<td>(11.3 ± 3.9)</td>
<td>(25.0 ± 3.9)</td>
</tr>
<tr>
<td>Last internode L</td>
<td>2–3</td>
<td>6–7</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>First peduncle L</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Basal bract L</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Ps of the P</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Ps of the HF</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>No. male Ps</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>No. stigmas</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Prophyll</td>
<td>yes</td>
<td>yes</td>
<td>yes</td>
<td>yes</td>
<td>yes</td>
<td>yes</td>
<td>yes</td>
</tr>
<tr>
<td>Length</td>
<td>(30.6 ± 13.3)</td>
<td>(35.4 ± 34.5)</td>
<td>(12.4 ± 4.8)</td>
<td>(126.3 ± 17.8)</td>
<td>(43.3 ± 1.5)</td>
<td>(139 ± 8.3)</td>
<td>(38.7 ± 1.9)</td>
</tr>
</tbody>
</table>
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 (Küchenthal 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 PI₈ of Carex pairae F. W. Schultz (LEB 79018). 1. Perigynium-like prophyll. 2. Perigynium. 3. Female glume. 4. Male glumes. Scale bar in mm.](https://bioone.org/journals/Systematic-Botany/2013/18/2/10.3366/systbot.2012.0963/s2 Campo%200963%203.jpg)

![Fig. 4. Cladoprophyll in PI₁ 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.](https://bioone.org/journals/Systematic-Botany/2013/18/2/10.3366/systbot.2012.0963/s2 Campo%200963%204.jpg)
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; Gehrk et al. 2010), but species of those genera were not investigated for this study.

*Carex curvula* (sect. *Curvulaceae* 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 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., *Longespicateae* Kük., *Obtusatae* (Tuck.) Mack., and *Rupestres* (Tuck.) Meinh. 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 *Unciniaformes* 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 *Schoenoxiphium* 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 paracadum 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 paracadum of the Caricoid branching species. We are in broad agreement that this female spikelet is the fertile prophyll, pointing out the existence of a paracadum, 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 multispecific 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 Uncinia, 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 paracadia 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 curtula, 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. curtula 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 paradoecious plants, and androgynous, gynecandrous or mesogynous pseudospikes. The placement of Carex gibba as sister to the Vignea Clade (Ford et al. 2006; 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 Vesicaria, 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 Physoglacin, 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 monoeocious species with conflicting sexual morphology (gynecandrous and androecious) could induce dioecy. The inflorescence of the dioecious species is similar to the androecious 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 (P2). 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 panicleiform to seemingly unbranched (spiciform). Molecular analyses (Starr and Ford 2009) suggest that the multispeciate 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 multispeciate 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 (Rúa 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,
Phacocysts). 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. Heloglochin) or C. otrubae (sect. Vulcanica).

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. echinochlor Kunze, section Indicae and in Schoenoxiphium (Haines and Lye 1972), and, surprisingly, in section Siderostictae (Kukenthal 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 distigmate 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 Vulpinia (Ford et al. 2006) are placed in a derived position. Species with sexual specialization and long basal bracts such as those in sections Vescariae 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), paracladium 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 phyllogenetic 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 prophyll characterizes the species of Carex belonging to the Caricoid Clade. This type of paracladium helps to understand why the unisepicata taxae of Carex are placed in phylogenetic trees nearer to branched taxae of Kobresia and Schoenophyixum 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 unisepicata taxa, apart from the rachilla, to distinguish morphologically the Core Unispicate and Schoenophyixum 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 Schoenophyixum. 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.

Acknowledgments. We are grateful to A. A. Reznicek who generously gave permission to reproduce Figure 1 in this paper, and to the curators and staff from 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 who allowed us to study specimens under their care. We also thank Jorge Magaz for helping us with the drawings and Bernardo Miranda for taking the photo in Figure 4, Amelia Llamas and Judith Martinez for correcting the English version, and the anonymous reviewers for their valuable comments. A. C. Veggetti helped with the methodology; A. L. Hipp provided helpful advice on the earlier drafts, and his suggestions and comments have greatly strengthened the manuscript. The Junta de Castilla y León granted a High Studies License to the first author during the course 2005-06, and the grant LE025A05, and the research team TaCoVe from the University of León (Spain) partially supported our work.

Literature Cited
C. tomentosa
Valladolid: MA 530738.

Weberling, F. 1985. Aspectos modernos de la morfología del aspecto
Cytology and Morphology of the Cyperaceae. Botanical Review
71: 35–46.

Vijayag, A. M. Muasya, P. Goethgebeur, P. Caris, A. Nagels, and E.
Smet. 2009. A floral ontogenetic approach to questions of homology
within the Cyperaceae (Cyperaceae). Botanical Review 75: 30–51.

2010. Spikelet structure and development in Cyperoideae (Cyperaceae):
a monopodial general model based on ontogenetic evidence. Annals
Botanici Fennici 40: 35–46.

Carex (Cyperaceae) based on nested analyses of four molecular data

richness, and ecological specialization in Carex Tribe Carexaceae.

Weberling, F. 1985. Aspectos modernos de la morfología de las

Weberling, F. 2000b. Morphology of flowers and inflorescences. Cambridge:
Cambridge University Press.

Yen, A. C. and R. G. Olmstead. 2000a. Phylogenetic analysis of
Carex (Cyperaceae): generic and subgeneric relationship based on chloro-
plast DNA. Pp. 602–609 in Monocots: Systematics & evolution vol. 2,

tribes Carexaceae based on two chloroplast DNA regions: ndhF and trnL

Zhang, S. R. 2001. A preliminary revision of the supraespecific classifica-

APPENDIX 1. Material studied. Specimens used for infraspecific, spe-
cies and country. Individual specimens are identified by herbarium acro-
nym and accession number where available or by collector and collector
number if not.

Core Carex Clade— Sect. Acrocystis Dumort. Carex montana L. SPAIN.
Sanander: JBG 765. C. piluliformis L. FRANCE. Pyrénées: LEB 83951, LEB
83719, LEB 78521, LEB 83932, LEB 88671. SPAIN. La Coruña: SANT 49599.
Navar: LEB 78001, LEB 81158. Oviedo: LEB 83703. Alpes Haute Provence:
LEB 83297. LEB 83704. Alpes Maritimes: LEB 83297. LEB 83704. Alpes

Core Carex Clade— Sect. Acrocystis Dumort. Carex montana L. SPAIN.
Sanander: JBG 765. C. piluliformis L. FRANCE. Pyrénées: LEB 83951, LEB
83719, LEB 78521, LEB 83932, LEB 88671. SPAIN. La Coruña: SANT 49599.
Navar: LEB 78001, LEB 81158. Oviedo: LEB 83703. Alpes Haute Provence:
LEB 83297. LEB 83704. Alpes Maritimes: LEB 83297. LEB 83704. Alpes

Core Carex Clade— Sect. Acrocystis Dumort. Carex montana L. SPAIN.
Sanander: JBG 765. C. piluliformis L. FRANCE. Pyrénées: LEB 83951, LEB
83719, LEB 78521, LEB 83932, LEB 88671. SPAIN. La Coruña: SANT 49599.
Navar: LEB 78001, LEB 81158. Oviedo: LEB 83703. Alpes Haute Provence:
LEB 83297. LEB 83704. Alpes Maritimes: LEB 83297. LEB 83704. Alpes

Core Carex Clade— Sect. Acrocystis Dumort. Carex montana L. SPAIN.
Sanander: JBG 765. C. piluliformis L. FRANCE. Pyrénées: LEB 83951, LEB
83719, LEB 78521, LEB 83932, LEB 88671. SPAIN. La Coruña: SANT 49599.
Navar: LEB 78001, LEB 81158. Oviedo: LEB 83703. Alpes Haute Provence:
LEB 83297. LEB 83704. Alpes Maritimes: LEB 83297. LEB 83704. Alpes

Core Carex Clade— Sect. Acrocystis Dumort. Carex montana L. SPAIN.
Sanander: JBG 765. C. piluliformis L. FRANCE. Pyrénées: LEB 83951, LEB
83719, LEB 78521, LEB 83932, LEB 88671. SPAIN. La Coruña: SANT 49599.
Navar: LEB 78001, LEB 81158. Oviedo: LEB 83703. Alpes Haute Provence:
LEB 83297. LEB 83704. Alpes Maritimes: LEB 83297. LEB 83704. Alpes

Core Carex Clade— Sect. Acrocystis Dumort. Carex montana L. SPAIN.
Sanander: JBG 765. C. piluliformis L. FRANCE. Pyrénées: LEB 83951, LEB
83719, LEB 78521, LEB 83932, LEB 88671. SPAIN. La Coruña: SANT 49599.
Navar: LEB 78001, LEB 81158. Oviedo: LEB 83703. Alpes Haute Provence:
LEB 83297. LEB 83704. Alpes Maritimes: LEB 83297. LEB 83704. Alpes

Core Carex Clade— Sect. Acrocystis Dumort. Carex montana L. SPAIN.
Sanander: JBG 765. C. piluliformis L. FRANCE. Pyrénées: LEB 83951, LEB
83719, LEB 78521, LEB 83932, LEB 88671. SPAIN. La Coruña: SANT 49599.
Navar: LEB 78001, LEB 81158. Oviedo: LEB 83703. Alpes Haute Provence:
LEB 83297. LEB 83704. Alpes Maritimes: LEB 83297. LEB 83704. Alpes
K. L. Wilson 9509

C. vesicaria


Hautes Pyrénées: LEB 82663. SPAIN. Navarra: LEB 82649. ANDORRA. S. Julió del Lluís: MA 714438. FRANCE. Acedo & Llamas C. E. Hubbard s.n

L. subsp. cesanensis C. C. Townsend 76/36 F. W. Schultz.


L. subsp. cesanensis C. C. Townsend 76/36 F. W. Schultz.


L. subsp. cesanensis C. C. Townsend 76/36 F. W. Schultz.


L. subsp. cesanensis C. C. Townsend 76/36 F. W. Schultz.
