Making *Carex* monophyletic (Cyperaceae, tribe Cariceae): a new broader circumscription

GLOBAL CAREX GROUP

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*Carex* (Cyperaceae), with an estimated 2000 species, nearly cosmopolitan distribution and broad range of habitats, is one of the largest angiosperm genera and the largest in the temperate zone. In this article, we provide argument and evidence for a broader circumscription of *Carex* to add all species currently classified in *Cymophyllus* (monotypic), *Kobresia* (c. 60 species), *Schoenoxiphium* (c. 15 species) and *Uncinia* (c. 70 species) to those currently classified as *Carex*. *Carex* and these genera comprise tribe Cariceae (subfamily Cyperoideae, Cyperaceae) and form a well-supported monophyletic group in all molecular phylogenetic studies to date. *Carex* as defined here in the broad sense currently comprises at least four clades. Three are strongly supported (*Siderostictae*, core *Vignea* and core *Carex*), whereas the caricoid clade, which includes all the segregate genera, receives only weak to moderate support. The caricoid clade is most commonly split into two clades, one including a monophyletic *Schoenoxiphium* and two small clades of species of *Carex* s.s., and the other comprising *Kobresia*, *Uncinia* and mostly unisepulate species of *Carex* s.s. Morphological variation is high in all but the *Vignea* clade, making it extremely difficult to define consistent synapomorphies for most clades. However, *Carex* s.l. as newly circumscribed here is clearly differentiated from the sister groups in tribe Scirpeae by the transition from bisexual flowers with a bristle perianth in the sister group to unisexual flowers without a perianth in *Carex*. The naked female flowers of *Carex* s.l. are at least partially enclosed in a flask-shaped prophyll, termed a perigynium. *Carex* s.s. is not only by far the largest genus in the group, but also the earliest published name. As a result, only 72 new combinations and 58 replacement names are required to treat all of tribe Cariceae as a single genus *Carex*. We present the required transfers here, with synonymy, and we argue that this broader monophyletic circumscription of *Carex* reflects the close evolutionary relationships in the group and serves the goal of nomenclatural stability better than other possible treatments. © 2015 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2015, ••–••. 

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INTRODUCTION

From the initial naming of 29 species of Carex L. in Species Plantarum (Linnaeus, 1753), the genus has grown to >1830 accepted species (Govaerts et al., 2013). Carex is placed in tribe Cariceae, with Kobresia Willd., Uncinia Pers., Schoenoxiphium Nees and Cymophyllus Mack.; together they comprise c. 2150 species (Goetghebeur, 1998). Bruhl included a sixth genus, the monotypic Vescicarex Steyerm., in the tribe (Bruhl, 1995). In the most comprehensive global monograph of tribe Cariceae, Kükenthal (1909) recognized four genera [Carex, Kobresia (as ‘Cobresia’), Schoenoxiphium and Uncinia] and classified 793 broadly defined species into 69 sections of Carex distributed across four subgenera that differed in inflorescence structure, branching, gender distribution and number of spikes (Kükenthal, 1909). Although Kükenthal’s classification was criticized, particularly for its treatment of unisepicate species as a distinct subgenus (Kreczetovicz, 1936; Ohwi, 1936; Nelmes, 1952; Kern, 1958; Hamlin, 1959; Koyama, 1961), modifications of Kükenthal’s classification continue to be used to organize large regional floristic manuals (Chater, 1980; Haines & Lye, 1983; Egorova, 1999; Dai & Liang, 2000; Ball, Rezníček & Murray, 2002; Lučeno, Escudero & Jiménez-Mejías, 2008; Dai et al., 2010; Hoshino, Masaki & Nishimoto, 2011). With nomenclatural corrections, the four subgenera used explicitly or indirectly to order the sections of Carex s.s. in most modern floristic treatments are subgenus Psyllophora (Degl.) Pet. (= subgenus Prinocarex Kük.), subgenus Vignea (P.Beaup. ex T.Lestib.) Pet. (= subgenus Vigneastra (Tuck.) Kük. (= subgenus Indocarex (Baill.) Kük.) and subgenus Carex (= subgenus Eucarex Pet.). We use these subgeneric names to refer to groups in the traditional classification.

Ninety years after Kükenthal’s monograph, the first molecular phylogenetic analyses of tribe Cariceae were published (Starr, Bauer & Ford, 1999; Yen & Olmstead, 2000; Raalson, Columbus & Friar, 2001). These early studies were based on few genes and limited sampling, but already they suggested that, although Cariceae was monophyletic, Carex and Kobresia were polyphyletic or paraphyletic. Uncinia and Schoenoxiphium were each apparently monophyletic, but nested in Carex, as was the monotypic genus Cymophyllus. The only traditional subgenus of Carex that was largely monophyletic in any of these early studies was subgenus Vignea. Larger studies of phylogenetic relationships in Cyperoideae, incorporating additional gene regions, also strongly supported a monophyletic tribe Cariceae. This tribe has been suggested by most studies to be sister to tribe Scirpeae or nested in it (Muasya et al., 1998, 2009; Simpson et al., 2007; Escudero & Hipp, 2013; Hincliff & Raalson, 2013; Jung & Choi, 2013; Léveillé-Bourret et al., 2014), as predicted by evidence from associations with parasitic smut fungi in the genus Anthracoidea (Kukkonen & Timonem, 1979), rather than sister to previously suggested tribes having unisexual flowers, such as Sclericeae (Haines & Lye, 1972; Smith & Faulkner, 1976) or Rhynchosporaeeae (Koyama, 1961).

A broader and more representative sampling of tribe Cariceae using DNA from both nuclear and plastid genomes (Waterway & Starr, 2007) revealed three major clades that roughly corresponded to: (1) subgenus Vignea, hence named the Vignea clade; (2) subgenus Carex and Vigneastra, named the Carex clade; and (3) subgenus Psyllophora plus Cymophyllus, Kobresia, Schoenoxiphium and Uncinia, named the caricoid clade (Fig. 1). The first two were strongly supported in parsimony and Bayesian analyses, whereas the caricoid clade received only moderate support. In the caricoid clade, two clades were strongly supported in the Bayesian analysis: one with Schoenoxiphium and a few Carex spp. (the Schoenoxiphium clade) and one with Kobresia, Uncinia, Cymophyllus and several members of Carex subgenus Psyllophora (the core unisepicate clade). Starr, Harris & Simpson (2003, 2004, 2008) further explored the caricoid clade, noting a major difference between dioecious unispicate and androgynous species, and providing additional support for the monophyly of Uncinia. Dioecious unispicate Carex spp. showed affinities to multisepicate species in either the Vignea clade or the Carex clade, and the androgynous species formed part of the caricoid clade with androgynous species of Cymophyllus, Kobresia, Schoenoxiphium and Carex, in phylogenetic trees based on internal transcribed spacer (ITS) and external transcribed spacer (ETS) data (Starr et al., 2004). Further detailed study of Schoenoxiphium and the caricoid clade supported the monophyly of the African genus Schoenoxiphium and demonstrated sister group relationships of two other small clades of Carex spp. to Schoenoxiphium (Gehrke et al., 2010). The rest of the caricoid clade (core unisepicate clade) was moderately supported in that analysis.
but there was no support for a closer relationship to the Schoenoxiphium clade than to the Vignea or core Carex clades (Gehrke et al., 2010).

The discovery that section Siderostictae Franch. ex Ohwi, traditionally classified in subgenus Carex, formed a clade sister to all other species in tribe Cariceae confirmed that Carex in the traditional sense is a paraphyletic group with all other genera of tribe Cariceae nested in it (Waterway, Hoshino & Masaki, 2009). This Siderostictae clade was recently expanded to include species from two sections previously classified in Carex subgenus Vigneastra (sections Hemiscaposae C.B.Clarke and Surculosae Raymond) based on the analysis of ITS and trnL-trnF sequences (Yano et al., 2014). Although these new additions are broad-leaved species, like most species in section Siderostictae, they have inflorescences with more complex branching, thus expanding the range of variation found in this clade that is sister to the rest of tribe Cariceae. Taken together, these results from molecular systematic studies show clearly that Carex as traditionally defined is not monophyletic, nor are any of the traditional subgenera except Vignea (Fig. 1). Furthermore, continued recognition of those genera that appear to be monophyletic in tribe Cariceae (Uncinia and Schoenoxiphium) would leave Carex paraphyletic and Kobresia polyphyletic.

Figure 1. Generalized phylogenetic tree of Cyperaceae tribe Cariceae based on molecular phylogenetic studies to date. Full lines show relationships that are supported by all or most studies. Dotted branches show relationships that are frequently seen but more inconsistent among studies. Branches with consistently high bootstrap support are indicated with a filled ellipse. The number of subclades shown within the caricoid clade is arbitrary; resolution and support in this clade are inconsistent among studies and so a large polytomy is shown with many individual small clades grouping two or three taxa. Larger triangles in this polytomy indicate clades that comprise more than three taxa and show fairly consistent support across studies. It should be noted that the newly reported Hypolytroides clade (Starr et al., 2015) is sister to the Siderostictae clade shown here and that the Siderostictae + Hypolytroides clade has the same sister relationship to the rest of tribe Cariceae as shown here for the Siderostictae clade.
It is apparent that Carex and tribe Cariceae are overdue for a new classification that better reflects evolutionary relationships. The reclassification of tribe Cariceae was discussed at length at an international gathering of Cyperaceae specialists in 2011 at a BioSynC meeting in Chicago and again with an even larger group of Cyperaceae specialists at the Monocots V meeting in New York in 2013. The consensus at both meetings was to broaden the circumscription of Carex to include all species in tribe Cariceae, thus forming a monophyletic genus Carex with >2000 species. This approach was chosen as that most likely to provide nomenclatural stability. There was some question in 2011 whether increased sampling in China and South-East Asia would reveal new clades that should be segregated from Carex or help to define clear groupings in the caricoid clade. However, even with much more extensive sampling from China, South-East Asia and Africa since 2011 (Luceño et al., 2013; Waterway et al., 2013; Zhang et al., 2013; Yano et al., 2014; Starr, Jansen & Ford, 2015), including more complete studies of Kobresia and Schoenoxiphium, the conclusion that a single monophyletic Carex would be the best classification was strengthened rather than weakened. This article is the first in a series of planned contributions from the Global Carex Group to completely reclassify this expanded Carex at the sectional level. Our goals in this paper are to provide a brief background on the morphology of tribe Cariceae and its classification history, to summarize the molecular and morphological evidence for treating tribe Cariceae as the single genus Carex and to make the required nomenclatural changes.

Although a broader circumscription of Carex is in the interest of long-term nomenclatural stability, 130 nomenclatural changes are needed at this time to change the circumscription. Species of Cymophyllus and Vescicarex already have valid names as Carex spp., as do several species of Kobresia, Schoenoxiphium and Uncinia. Many other needed changes are simply new combinations, because several specific epithets currently used in Kobresia (23), Schoenoxiphium (six) and Uncinia (27) have never been used in Carex. For cases in which the specific epithets are already occupied, 58 are here given replacement names in Carex and 16 others adopt the specific, varietal or forma epithet from a previously published synonym. The changes are detailed in the taxonomic section below, including synonymy and notes on geographical distribution and any nomenclatural issues.

MATERIAL AND METHODS

We reviewed the major literature on the classification in Cyperaceae tribe Cariceae, including papers proposing evolutionary theories related to classification. We also reviewed recent work on inflorescence morphology and all molecular phylogenetic studies to date to provide a synthetic view of current evidence for phylogenetic relationships in the group. An initial list of names, with geographical distributions, for currently recognized species of Cymophyllus, Kobresia, Schoenoxiphium and Uncinia was constructed from the World Checklist of Cyperaceae (Govaerts et al., 2013) and then modified by those in our group most familiar with each genus (S.R.Z. and O.Y. for Kobresia, K.A.F., J.R.S. and K.L.W. for Uncinia and M.L. and S.M.-B. for Schoenoxiphium) to create the final taxonomic listing with new combinations and new names. The names fall into three categories: (1) species that already have a valid name in Carex; (2) species with specific epithets that are available in Carex; and (3) species with specific epithets that are not available in Carex. New combinations are made where appropriate and new names are created where a specific epithet was not available.

DISCUSSION

Morphological variation in tribe Cariceae

The inflorescence structure is complex and variable in tribe Cariceae and has long been seen as a rich source of taxonomic characters. An understanding of the terminology used to describe inflorescence structure is critical in evaluating theories of relationship that underpin the various classifications proposed for the group. Features of the inflorescence have been important in constructing classifications and identification keys, especially because vegetative features are quite similar across the group, with the exception of the unusual leaves of Cymophyllus, which lack a midrib (Reznicek, 1990), and some broad-leaved, pseudopetiolate Carex spp. from South-East Asia (Raymond, 1959). The interpretation of the flowers, spikelets and overall inflorescence architecture of Cyperaceae and tribe Cariceae goes back to the early 19th century (e.g. Kunth, 1835; Caruel, 1867) and has been a popular topic since then (e.g. Snell, 1936; Blaser, 1944; Levyns, 1945; Holtum, 1948; Kukkonen, 1967, 1984, 1990; Kern, 1974; Eiten, 1976; Smith & Faulkner, 1976; Goetghheur, 1986; Reznicek, 1990; Bruhl, 1991; Timonen, 1998; Richards, Bruhl & Wilson, 2006; Prychid & Bruhl, 2013). Detailed new typological interpretations of inflorescence structure in tribe Cariceae (Vegetti, 2002, 2003; Guarise & Vegetti, 2008; Molina, Acedo & Llamas, 2012; Reutemann et al., 2012) and ontogenetic studies of floral development in Cariceae using scanning electron microscopy published during the last decade (Vrijdaghs et al., 2009, 2010; Gehrke et al., 2012) demonstrate the similarities in basic architecture of
the inflorescence. The terminology used to describe inflorescences in Careceae has been applied inconsistently (Reznicek, 1990; Kukkonen, 1994; Vegetti, 2002; Molina et al., 2012; Reutemann et al., 2012) and efforts to apply typological principles to inflorescence description strictly, whilst demonstrating the similarity in inflorescence architecture across Careceae, have also resulted in a proliferation of terminology unfamiliar to non-specialists. Reconciling this terminology is an ongoing issue for cyperologists and requires additional study and discussion. Here, we provide only enough background to make our arguments for a broader circumscription of Carex clear.

In tribe Careceae, the flowers are normally unisexual and lack a perianth. Their structure is simple: each staminate flower comprises three stamens (rarely fewer) and each pistillate flower comprises one uniovulate ovary arising from an annular primordium, with a single style and two or three stigmas (Vrijadhgs et al., 2009; Reynders et al., 2012). Complications arise in the ways in which these simple unisexual flowers are arranged into inflorescences.

The spikelet has traditionally been considered as the basic unit of the inflorescence in Cyperaceae (Snell, 1936; Holttum, 1948; Kukkonen, 1967). In most species of Cyperaceae subfamily Cyperoideae, perfect or unisexual flowers are arranged spirally or distichously on a spikelet axis, the rachilla, each flower being subtended by a scale-like floral bract, usually called a glume or a scale (Fig. 2A, B). Spikelets in many tribes of Cyperoideae, including those in Careceae, are considered polytelic (indeterminate). A prophyll, which usually encircles the base of the rachilla, is the first adaxial bract produced on each spikelet. This small prophyll, often called a cladoprophyll to emphasize its position on an axis, is in addition to the larger, often foliose bract that arises from the main inflorescence axis and subdents a spikelet or group of spikelets.

Spikelets in Careceae differ from those of more typical species of Cyperoideae in two important ways. First, the prophyll arising from the rachilla is modified into an enclosing sac-like or flask-shaped structure variously called a perigynium, utricle or utriculiform prophyll (Fig. 2C–G). A similar enclosing prophyll is found around the proximal flower on spikelets in Dulichium Pers. (tribe Dulicheae), but the flowers distal to this one on a Dulichium spikelet are each subtended only by a glume. In Careceae, each female flower is enclosed by a perigynium that is most often closed except for an apical orifice from which the style and stigmas emerge. However, the perigynium is only partially sealed in some Kobresia spp. (Fig. 2E) and the orifice may be quite wide on some perigynia in Schoenoxiphium (Fig. 2G). Kükenthal used the term utricle instead of perigynium, and many authors of floristic treatments have followed his example (e.g. Kern & Noteboom, 1979; Chater, 1980; Egorova, 1999; Luceno et al., 2008; Dai et al., 2010). However, in a broader botanical context, the term utricle may be misleading, because it refers to a type of fruit and thus to ovary tissue (Davis & Cullen, 1989; Harris & Harris, 1994; Spjut, 1994), not to a type of bract. Perigynium has also been used to refer to non-homologous structures, such as the stem tissue surrounding the ‘perianth’ in some foliose liverworts (e.g. Hentschel et al., 2006), and in Cyperaceae, to the cupule, interpreted as the perianth, surrounding the ovary in some Scleria spp. (Barros, 1960), but it has been most widely and consistently used, especially in North America, for the prophyllar bract surrounding the ovary in species of Careceae (e.g. Tuckerman, 1843; Bailey, 1886; Holm, 1903; Ivanova, 1939; Bruhl, 1995; Ball & Reznicek, 2002; Vrijadhgs et al., 2010; Hoshino et al., 2011). Here, we use the term perigynium, but recognize that both terms are widely used in floristic treatments and should be considered as synonyms when applied to Careceae.

Second, the rachilla is reduced compared with that of other Cyperaceae, often bearing only a single female flower that is at least partially enclosed by the perigynium. The rachilla is vestigial in Cymophyllus and absent or reduced to a tiny structure in most species of Carex s.s. (Reznicek, 1990; Vrijadhgs et al., 2010; Fig. 2C), but elongated to varying extents in Kobresia, Schoenoxiphium, Uncinia and a few species of Carex s.s. (Fig. 2D–G). In Schoenoxiphium, staminate flowers, subtended by glumes, may be produced distally on the rachilla, and these protrude from the perigynium with the stigmas (Fig. 2F, G). Distal staminate flowers or vestigial remnants of them or their glumes can also be found in many Kobresia spp. (Fig. 2E) and even rarely in Carex s.s. (Jin, Ding & Zheng, 2005). The rachilla in Uncinia extends beyond the perigynium as a hook-shaped tip that aids in dispersal (Fig. 2D), but only rarely bears staminate flowers (Hamlin, 1959). Thus, most spikelets in Careceae are much reduced compared with those in other Cyperaceae, appearing from the outside as perigynia with styles, stigmas and sometimes a rachilla bearing staminate flowers protruding from the apical opening.

Much of the confusion surrounding the use of the terms spikelet and spike in Careceae arises because these reduced spikelets of Careceae, subtended by glumes, are themselves spirally arranged on lateral branches into spike-like inflorescences that resemble the spikelets of other genera of Cyperaceae (compare Fig. 2B with 2H, I, K, L). Reznicek (1990) chose to abandon the term spikelet altogether, because it is sometimes used as described above and other times used incorrectly (notably by Kükenthal, 1909) to refer
Figure 2. See caption on next page.
to a lateral inflorescence unit that is a spike of spikelets which may also bear male flowers directly on the same axis. Rather than abandoning the term, we refer to perigynia and their enclosed flower-bearing axes as reduced spikelets in tribe Cariceae, thus maintaining a link to the equivalent structure in other groups of Cyperaceae (Timonen, 1998).

Most authors subsequent to Kükenthal (1909) referred to the set of flowers borne at the tip of the main culm as the terminal spike or spikelet, and to the aggregations of flowers on first-order lateral branches as lateral spikes. In Carex, Cymophyllus and Uncinia, these so-called spikes are really spikes of reduced spikelets or of mixed male flowers and reduced spikelets, except for the terminal one, which often bears only male flowers (Fig. 2H, I). Spikes may be unisexual, androgy nous (perigynia proximal and staminate flowers distal on the spike axis), gynoecandrous (staminate flowers proximal and perigynia distal), mesogynous (staminate flowers both proximal and distal to perigynia), mesandrous (perigynia both proximal and distal to staminate flowers) or with alternating staminate flowers and perigynia on the spike axis (Eiten, 1976). Early choices in identification keys for Carex s.s. often distinguish between unisepacite and multisepacite inflorescences.

Although terms such as spike, unisepacite and multispacite are widely used and relatively easy to understand for the large majority of Carex s.s., Cymophyllus and Uncinia spp., they are not technically correct and can be misleading when trying to interpret homology in inflorescence structure. What is generally called a spike in Cariceae is actually a spike of spikelets or stachyodium (Reutemann et al., 2012). This may be further ramified in Schoenoxiphium if additional perigynia are produced on the primary rachilla axis emerging from a perigynium (Levyns, 1945; Gehrke et al., 2010) (Fig. 2G). Molina et al. (2012) used the term pseudospike rather than spike to indicate that these aggregations of flowers are not true spikes because they often include flowers that are at different branching orders in the inflorescence. That is, the axis...
of the so-called spike may bear male flowers directly, but each female flower is borne in a perigynium on a rachilla that is actually a higher order branch (Fig. 2H–L). We acknowledge this problem here, but continue to use the term spike because it is widely used in nearly all floristic treatments, and to avoid awkward terminology, such as uni-pseudospicate and multi-pseudospicate, in reference to whole inflorescences. Flowering culms without lateral branching can be called spiciform, those with first-order lateral branching are often referred to as racemose or, more properly, as racemiform, whereas those with higher order branching are often called paniculate or, more properly, paniculiform (Molina et al., 2012).

Recent detailed studies of inflorescences in Cyperaceae, including those in Cariceae, follow typological methods and terminology that were originally developed for dicots by Troll (1964) and Weberling (1989) to describe sedge inflorescences in ways that make it easier to assess homology. Many of these terms are familiar only to specialists, and so only essential ones will be used here. Following recent interpretations (Guarise & Vegetti, 2008; Molina et al., 2012; Reutemann et al., 2012), each flowering culm in a sedge plant is a synflorescence that ends in a terminal aggregation of usually staminate flowers that represents the main florescence (Fig. 2H, I, K). Below this main florescence (a terminal spike in the older terminology), a flowering culm may have an enrichment zone (= paracladial zone) where it produces one or more lateral branches, each of which may also end in a terminal set of (usually staminate) flowers, termed a co-florescence (Fig. 2I, terminus of distal paracladium; Fig. 2J, K, terminus of proximal paracladium).

Each lateral branch, including the subtending bract on the main axis and prophyll on the new axis, is called a paracladium (Guarise & Vegetti, 2008; Molina et al., 2012). Unless they remain dormant, nodes in inflorescences of Cariceae have three options: to produce lateral branches (axes) of the next higher order; to produce rachillae (also axes) that each bear at least one pistillate flower and its surrounding perigynium; or to produce staminate flowers directly on that branch. This recurring pattern may be ramified into second-, third- or even higher order branching in some species. The three node types have been called inflorescence nodes, female flower nodes and male flower nodes, respectively (Smith & Faulkner, 1976). The first two of these node types are intrinsically similar in that the node is producing an axis (lateral branch or rachilla) that will produce at least one flower, either on that axis or after branching again.

Molina et al. (2012) applied this typological system to 110 Carex spp. from all four traditional subgenera. They treated the lateral branch or paracladium as the basic unit of the inflorescence, similar to Timonen's (1998) emphasis on the axis as the basic unit, viewing the inflorescence as a hierarchy of axes with recurring developmental patterns (Timonen, 1998). Summarizing the results of Molina et al. (2012) provides a convenient opportunity to demonstrate how the terminology is applied, although we use spike where they used pseudospike. It is important to note that, although Molina et al. (2012) indicated that each reduced spikelet, consisting of perigynium, rachilla or its vestiges, and unisexual flower(s), and subtended by a glume, can be thought of as the extreme reduction of a paracladium, they did not consider the reduced spikelets as paracladia in their analyses.

Instead, they interpreted the single androgynous spikes in subgenus Psyllophora as the main florescence on a flowering culm that lacks paracladia and has no bract subtending the spiciform inflorescence (Fig. 2H, K). The main florescence in species of subgenus Carex was interpreted as the terminal spike, which is entirely staminate in many species, but gynecandrous, androgynous or entirely pistillate in others. One to several first-order paracladia, comprising subtending bract, tubular cladoprophyll and a pistillate or androgynous spike, are found below the main florescence, resulting in a racemiform inflorescence (Fig. 2I), except in dioecious species, which are unispicate and lack paracladia. Spikes are usually on relatively long peduncles, may be entirely pistillate, androgynous, entirely staminate or, much less commonly, gynecandrous, and have a tendency for staminate flowers to be found only in distal paracladia. The few species examined from subgenus Vigneastra were interpreted to have a paniculiform or racemiform inflorescence with the main florescence androgynous and with androgynous spikes on the paracladia, which exhibit up to third-order branching from the main axis. Of note in subgenus Vigneastra is that each spike has a perigynium-like prophyll at its base, in contrast with the tubular cladoprophyll found at the base of the first-order paracladium. The axis of the first-order paracladium is also usually pedunculate, and more than one axis is sometimes produced at each node of the main axis, particularly from the lower nodes. In subgenus Vignea, Molina et al. (2012) interpreted the main florescence as the terminal spike, which can be androgynous, gynecandrous or entirely staminate or pistillate, as can the spikes in the paracladia. The inflorescence can be spiciform to paniculiform with first-, second- or even third-order paracladia branching below the main florescence. Spikes in subgenus Vignea are generally compact and sessile, subtended by relatively small, non-sheathing bracts and few species have cladoprophylls.

The inflorescence structure in Cariceae is thus based on a recurring architectural pattern in which...
each new lateral axis is subtended by a bract and enclosed in a prophyll at its base (Levyns, 1945; Timonen, 1998). The other recurring pattern is the production of pistillate flowers proximally and staminate flowers distally on each flowering axis (Fig. 2H–L), presumably under genetic or environmental control, mediated through growth regulators (Gehrke et al., 2010; Vrijdaghs et al., 2010). Ontogenetic studies in Carex s.s. suggest that each node of a flowering axis is flexible and can develop into either a male flower or a new flowering axis bearing a single female flower enclosed in a perigynium (Vrijdaghs et al., 2010). Ontogenetic study revealed no evidence that staminate flowers in Cariceae are highly reduced spikelets, as assumed by Timonen (1998). Bracts subtending the lateral and higher order spikes tend to decrease in size from the base to apex of the culm and vary from foliaceous to small scale-like structures. Processes such as truncation or axis abortion, homogenization, initiation or suppression of paracladia, elongation or reduction of internodes, increases or decreases in degree of branching, reduction or suppression of bracts or prophylls and others operate in different ways and combinations to give the variety of inflorescence forms seen in the tribe (Guarise & Vegetti, 2008; Reutemann et al., 2012). These recurrent patterns are least obvious in subgenus Vignea, in which the position effects on the production of female vs. male flowers appear to be minimal and additional processes must be invoked to derive the various patterns (for examples, see Timonen, 1998).

Inflorescence architecture in Cariceae thus differs in fundamental ways from that of other Cyperaceae: female flowers are only produced when branching occurs in the inflorescence, and the first prophyll on the new branch encloses the female flower. Another fundamental difference between Cariceae and other Cyperaceae is the nature of the transition from a non-flowering to a flowering branch. In most Cyperaceae, the transition occurs at the final branching event, i.e. the one giving rise to the rachilla, which produces flowers. All nodes above this one produce either flowers subtended by scale-like bracts, variously called glumes or scales, or sterile bracts. This means that the ultimate level of inflorescence branch in most Cyperaceae is the spikelet axis (rachilla). Cariceae is quite different, because the transition to flowering in the lateral branches depends on whether the flower is male or female. Female flowers are produced only when branching occurs. This occurs on the spikelet rachilla, i.e. on the rachilla that is homologous to that in other Cyperaceae, but it can also occur on both higher and lower order branches. In Schoenoxiphium, the rachilla can branch after producing the first perigynium and produce one or more additional perigynia, each enclosing a pistillate flower or both a pistillate flower and male flowers on the new rachilla, before it produces the male flowers distally on the initial rachilla (Levyns, 1945; Gehrke et al., 2012; Fig. 2G). Thus, the first flower-producing rachilla is not always the ultimate branch in an inflorescence in Cariceae as it is in most Cyperaceae. Instead, the rachilla will branch each time it produces another pistillate flower. Ramification of the rachilla can be superposed on the primary inflorescence branching pattern to produce a complex inflorescence that is difficult to describe using traditional terms (Fig. 2G). Also, in Schoenoxiphium, a perigynium can be produced on a lower order axis than the spikelet, e.g. at the base of a first- or second-order paracladium. Whether or not this perigynium contains a pistillate flower appears to be determined by its position in the inflorescence, the likelihood being greater in proximal than in distal positions (Levyns, 1945). The lateral axis surrounded by this perigynium may give rise to a second-order paracladium which then produces bisexual spikelets or unisexual reduced spikelets similar to those in Carex s.s., or it may give rise directly to bisexual spikelets or reduced unisexual spikelets (Levyns, 1945) (Fig. 2J). Male flowers are generally produced when the inflorescence axis (of whatever order) stops branching. Thus, male flowers can be found on the distal tips of the main florescence, the paracladia, the spikes and the bisexual spikelets (of Kobresia and Schoenoxiphium only) (Fig. 2E–L), unless the axis is truncated. Both male and female flowers are thus produced at different levels of the inflorescence branching hierarchy, the females directly connected to branching events and the males most often produced at the tips of axes that no longer branch. We return to these fundamental differences in inflorescence structure in our argument for merging all species of Cariceae into Carex.

OVERVIEW OF PREVIOUS CLASSIFICATIONS

Classifications of Carex and its closely allied genera in Cariceae are numerous and conflicting, most being based on particular ideas of natural or evolutionary relationships. Robertson (1979) discussed this classification history from pre-Linnaean times until the mid-20th century, and Kern (1958) and Zhang (2001) reviewed the early classification history of Schoenoxiphium and Kobresia, respectively. Reznicek (1990) and Egorova (1999) provided good summaries of post-Linnaean classifications until the end of the 20th century, and Starr et al. (2004) summarized classification issues related to the segregate genera. Inflorescence morphology has played a key role in most classifications from Linnaeus’ first division of Carex s.s. into five groups, defined by the number of spikes and the arrangement of staminate and pistillate
flowers in the inflorescence. Early attempts to segregate smaller genera from Carex (Rafinesque-Schmaltz, 1840; Heuffel, 1844) were poorly justified and not widely accepted. However, much effort was expended during the 19th and early 20th centuries to organize species in this large genus into natural groups as subgenera, sections and series (e.g. Tuckerman, 1843; Drejer, 1844; Bailey, 1886; Holm, 1903; Kükenthal, 1909; reviewed by Robertson, 1979). We provide here an overview of previous 20th century classifications and associated theories of relationships, using the evolutionary terminology of the authors to give the flavour of the pre-cladistic thinking on which most of these classifications were based.

Subgeneric classification of Carex s.s.
Although Kükenthal’s (1909) division of Carex s.s. into four subgenera based on inflorescence structure is that most often followed, with some modifications, into four subgenera based on inflorescence structure in these groups. The relationship of allied genera to Carex s.s. and to each other
Kobresia, Uncinia and Schoenoxiphium, named in the early 19th century, have always been considered to be closely related to Carex s.s. and evolutionary scenarios forming the basis for classifications have included them. Kükenthal’s (1909) classification was based on the idea that Schoenoxiphium and Kobresia are the base of a reduction series in which the spikelet rachilla is gradually reduced from an elongated structure bearing distal male flowers (Schoenoxiphium, some Kobresia) to a sterile rachilla (some Kobresia and Schoenoxiphium, Uncinia and a few unispicate Carex) and then to a vestigial rachilla (Carex) in an enclosing prophyll (perigynium), the margins of which change from open in many Kobresia to sealed, except for a small terminal opening with only the style, stigmas and rachilla (if present) protruding from that orifice (e.g. Uncinia, Carex, Cymophyllus). Perigynia of Schoenoxiphium vary from having a rather broad opening to being almost completely sealed as in most of the other genera.

Many species in the allied genera are unispicate and androgy nous, leading to an early theory that unispicate Carex spp. are primitive and multispcicate Carex spp. are derived from them (Drejer, 1844). In line with this idea, Kükenthal (1909) named subgenus Primocarex Kük., circumscribing it to include all unispicate Carex, including C. fraseriana Ker Gawl., which was subsequently segregated as the monotypic genus Cymophyllus by Mackenzie (1913) based on its unique leaf morphology. Strong opposition to the idea that unispicate Carex spp. were primitive came from those who thought that at least some unispicate inflorescences were derived from multispcicate ones by reduction. They proposed systems that placed unispicate Carex spp. variously in subgenus Carex or subgenus Vignea rather than recognizing a distinct subgenus Psyllophora (Kreczetovicz, 1936; Ohwi, 1936; Nelmes, 1952; Koyama, 1962; Smith & Faulkner, 1976). Nelmes (1952) discussed the polyphyly of subgenus Psyllophora, speculating that nearly half of the species were ‘true Carices’ that could be accommodated in other subgenera of Carex s.s., whereas at least half of those remaining were probably derived from Carex s.s. and the remainder from Uncinia, Kobresia or Schoenoxiphium. Another view of subgenus Psyllophora was based on associations with smut fungi (Anthracoidea) and strongly influenced by the presence (or not) of the rachilla and by Heilborn’s chromosome data (Heilborn, 1924; Savile & Calder, 1953). Savile & Calder (1953)
considered subgenus *Psyllophora* to include rachilla-bearing unisepicate species only, referring to this group as ‘true *Primocarex*’, and moved the remaining unisepicate species lacking a rachilla either to subgenus *Vignea* or to their new subgenus *Kuekenthalia*. They considered this more narrowly circumscribed subgenus *Psyllophora* to be derived from *Kobresia* and ancestral to subgenera *Carex, Vignea* and *Kuekenthalia*. Kukkonen supported the basic ideas of Savile & Calder (1953), but proposed a new phylogenetic hypothesis in which subgenus *Vignea* was derived from *Kobresia* through subgenus *Psyllophora*, and subgenus *Carex* was independently derived from *Kobresia* through *Carex* section *Acrocystis* Dumort. in subgenus *Carex* (Kukkonen, 1963).

Hamlin (1959) proposed a putative caricoid ancestor with a large branching inflorescence having clado-prophylls and bearing spikelets that each had a basal female flower and a persistent rachilla bearing male flowers, the whole spikelet partially enclosed by a prophyll (perigynium). He postulated that this ancestor gave rise to two evolutionary lines, one retaining the rachilla, but reducing the inflorescence branching, and the other losing the rachilla, but retaining the compound inflorescence. The line retaining the rachilla then split to give rise to *Schoenoxiphium, Kobresia, Uncinia* and some species in *Carex* subgenus *Psyllophora*. The line retaining the highly branched inflorescence, but losing the rachilla, gave rise to *Carex* subgenus *Vigneastra* from which subgenera *Vignea* and *Carex* were derived along separate lines. He hypothesized that *Carex* subgenus *Psyllophora* was polyphyletic, comprising species with unisepicate inflorescences that arose in parallel by reduction from each of the six lineages in his evolutionary scenario. Hamlin’s solution to the classification problem that this scheme created was the division of *Carex* subgenus *Psyllophora* into several genera to accommodate those with different ancestry, rather than uniting the tribe into a single genus (Hamlin, 1959).

As noted by Kern (1958), discriminating among the genera in Cariceae was not difficult in the early 19th century when only a few species of each genus were described, but, as more species were discovered, the lines between them became blurred. The broader ciliate rachillae of *Schoenoxiphium* have been considered as a distinctive character contrasting with the less conspicuous, usually terete, rachillae of *Kobresia* (Clarke, 1883; Kükenthal, 1909), but intermediates (Kükenthal, 1940) and exceptions were discovered as many more *Kobresia* spp. were described from Asia. Nelmes (1952) pointed out that the same reduction series in inflorescence morphology that Kükenthal postulated for the evolutionary pathway from *Schoenoxiphium* to *Kobresia* to *Uncinia* to *Carex* s.s. could also be observed within *Schoenoxiphium* and within *Kobresia*, an observation further amplified by others (Koyama, 1961; Haines & Lye, 1972, 1983; Smith & Faulkner, 1976). Both genera vary in the extent of closure of their perigynia and in the extent of lateral branching in the inflorescence, resulting in overlap of traits between them. Ivanova (1939) transferred *Kobresia* spp. with paniculiform inflorescences to *Schoenoxiphium* and most of the currently recognized species of *Schoenoxiphium* into *Archaeocarex* Börner, but this genus has never been accepted. Many previous authors have argued that *Kobresia* and *Schoenoxiphium* could not be reliably distinguished on the basis of morphology (Nelmes, 1952; Kern, 1958; Smith & Faulkner, 1976). Koyama (1961) merged the two genera and made the necessary nomenclatural transfers from *Schoenoxiphium* to *Kobresia*. However, most 20th century authors maintained the traditional segregation of the two genera, in part because of their different geographical ranges and ecological preferences (Ivanova, 1939; Kukkonen, 1978, 1983; Haines & Lye, 1983; Rajbhandari & Ohba, 1991; Noltie, 1993; Zhang, 2001). Segregate genera *Elyna* Schrad. and *Hemicarex* Benth., defined on the basis of their spiciform inflorescences and bisexual and unisexual spikelets, respectively, and *Blysmocarex* N.A.Ivanova, characterized by distigmatic female flowers, are no longer recognized, but retained as subgenera of *Kobresia* in most classifications of that genus (Zhang, 2001). The similarity of *Uncinia* to *Carex* s.s. has also been noted (reviewed by Starr et al., 2008), but only Koyama (1961) proposed the merging of *Uncinia* into *Carex* s.s., although without making the necessary nomenclatural transfers. Koyama (1961) recognized only two genera, *Kobresia* and *Carex* s.s., in Cariceae, the latter with only two subgenera, *Carex* and *Vignea*. Although several authors have commented on the difficulty of clearly defining genera in Cariceae, only Mora Osejo (1966) proposed the inclusion of *Carex* s.s., *Kobresia, Schoenoxiphium* and *Uncinia* in one genus, recognizing each of them at the subgeneric level in genus *Carex* s.l., but without making valid nomenclatural transfers.

**Lack of support from molecular phylogenetics for previous classifications**

Previously proposed evolutionary scenarios for Cariceae and classifications based on them are not supported by molecular studies (Yen & Olmstead, 2000; Roalson et al., 2001; Starr et al., 2004, 2008; Waterway & Starr, 2007; Starr & Ford, 2009; Waterway et al., 2009; Gehrke et al., 2010; Jung & Choi, 2013) (Fig. 1). *Schoenoxiphium* and *Kobresia* are nested in a clade of species of *Carex* s.s., rather than being sister to *Carex* s.s. as proposed earlier (Kükenthal, 1909). The *Schoenoxiphium* lineage is...
distinct from that of *Kobresia* and includes two small clades of mostly unispicate *Carex* s.s. (Gehrke et al., 2010). *Kobresia* has been poorly sampled in all published papers to date, but it appears to be polyphyletic in the caricoid clade, a conclusion supported by more extensive sampling in recent work by Zhang et al. (2013). These *Kobresia* lineages are more closely related to various unispicate *Carex* s.s. than to *Schoenoxiphium*. *Uncinia* is firmly nested in the caricoid clade and is clearly not the progenitor of other groups as suggested by Nelmes (1952). The monotypic genus *Cymophyllus*, endemic to the south-eastern USA, is also nested in the caricoid clade and, despite its unusual leaves, does not warrant the generic status accorded it in recent North American floras (Mackenzie, 1931–1935; Reznicek, 2002). Similarly, the monotypic genus *Vesicarix* has been shown to be related to species of *Carex* section *Abditispiace* (core *Carex* clade) and treated as *Carex collumanthus* (Steyerm.) L.E.Mora (Mora Osejo, 1982; Wheeler, 1989), a conclusion supported by molecular data (Starr et al., 2004; Waterway & Starr, 2007). *Carex* section *Siderostictae* is not closely related to other broad-leaved species of *Carex* subgenus *Carex*, but forms a distinct lineage (Waterway et al., 2009). Recent work on *Carex* subgenus *Vigneastr* indicates that it is polyphyletic; species from sections *Hemiscaposae* and *Surculosae* belong to the same lineage as the early-diverging *Siderostictae* clade (Yano et al., 2014) and two recently sampled species of section *Hypolytroides* Nelmes (subgenus *Vigneastr*) are sister to this expanded *Siderostictae* clade (Starr et al., 2015). The early-diverging position of the broad-leaved species in the *Siderostictae* clade had earlier been suggested by Raymond (1959) for sections *Hemiscaposae* and *Surculosae* and by Egorova (1999), who considered section *Siderostictae*, with sections *Decorae* and *Curvulae*, as the least evolutionarily advanced groups in subgenus *Carex*. The most recent studies that include subgenus *Vigneastr* show that representatives from other sections of subgenus *Vigneastr* form one (Gehrke & Linder, 2009) or more (Waterway et al., 2009; Starr et al., 2015) early-diverging lineages in the core *Carex* clade. None of these groups of subgenus *Vigneastr* appears to be closely related to *Schoenoxiphium*, as Haines & Lye (1972, 1983) had suggested.

**ARGUMENT FOR ONE GENUS**

Published molecular phylogenetic hypotheses for *Cariceae* are quite consistent, despite differences in DNA regions used, taxon density and analytical methods (see Fig. 1 for a summary diagram of relationships). All recent analyses agree that the expanded *Siderostictae* clade or the *Siderostictae* + *Hypolytroides* clade, recently termed the ‘minor *Carex* alliance’ by Starr et al. (2015), is monophyletic and sister to the rest of the tribe, which is also strongly supported as monophyletic (Waterway et al., 2009, Jung & Choi, 2013; Yano et al., 2014), that the *Vigneastr* clade is monophyletic (Ford et al., 2006, 2012; Waterway & Starr, 2007; Starr & Ford, 2009; Waterway et al., 2009; Jung & Choi, 2013), and that the large core *Carex* clade is monophyletic only with the inclusion of at least part of subgenus *Vigneastr* with nearly all species of subgenus *Carex* (Waterway & Starr, 2007; Gehrke & Linder, 2009; Starr & Ford, 2009; Waterway et al., 2009; Starr et al., 2015). Some analyses show a monophyletic caricoid clade, but support for this clade is weak (Starr et al., 2004, 2008; Gehrke & Linder, 2009) to moderate (Waterway & Starr, 2007; Starr & Ford, 2009; Waterway et al., 2009). Except for the position of the *Siderostictae* clade as sister to the rest of Cariceae, the molecular data have not yet resolved the relationship among the major clades (for a summary, see Starr & Ford, 2009). No analysis has contradicted the monophyly of the tribe as a whole.

Given the strong and consistent molecular evidence for monophyly of *Cariceae* and the frequent nesting of the allied genera in one of the major clades of *Carex* s.s., it is clear that a new classification is needed to reflect the evolutionary relationships in this group more accurately. With the goal of monophyletic genera, only three reasonable possibilities exist in the Linnean system: (1) recognizing each of the four or five major clades in the molecular phylogenetic trees as a distinct genus; (2) recognizing the three strongly supported clades as distinct genera and naming each of the dozen or more lineages in the caricoid clade as a distinct genus; or (3) broadly circumscribing *Carex* s.l. to include all species in tribe *Cariceae*. We discuss these options in turn below.

**Option 1: Major clades as separate genera**

As described above, support for three of the clades (*Siderostictae*, core *Carex* and *Vigneastr*) is strong in all recent studies, but there is considerable morphological variation in the first two of these clades, making it difficult to find consistent morphological traits by which to diagnose them. Species in the *Siderostictae* clade, as expanded by Yano et al. (2014) to include *Carex* sections *Hemiscaposae* and *Surculosae*, have similar growth forms and share several other features. Vegetative and reproductive culms arise separately on short rhizomes and most species have broad leaves near the base of vegetative culms and bladeless sheaths at the base of lateral reproductive culms. Each female flower is enclosed by a perigynium from which the trifid style emerges, and both male flowers and perigynia are subtended by scale-like glumes. All species in this clade have low chromosome numbers
(n = 6 or 12), and some species exhibit euploidy, in contrast with the aneuploid series that characterizes Carex (Escudero et al., 2012; Chung, Yang & Lee, 2013; Yano et al., 2014). However, inflorescence structure varies considerably in the expanded Siderostictae clade. Section Siderostictae is characterized by terminal staminate or androgynous spikes and lateral androgynous spikes; that is, the main florescence terminates in a spike of male flowers, in some cases with proximal perigynia, and co-forescences arising from the culm nodes are usually androgynous with proximal perigynia and distal male flowers (Chung et al., 2013). Each paracladium comprises a subtending sheathing bract varying from spathe-like to foliaceous, a cladoprophyll and an androgynous spike. Nodes are sometimes binate, bearing two pedunculate spikes rather than the usual single spike. Lateral spikes have a few spirally arranged perigynia near the base and a spiral of male flowers produced distally, sometimes with an elongated internode between the two types of flower. The terminal spike is simply the tip of the main culm axis that bears spirally arranged male flowers, often with a single perigynium at the base. In contrast, species of sections Hemiscaposeae and Surculosae have paniculiform inflorescences with higher order branching. Each node of the reproductive culm in section Hemiscaposeae bears one or two compound inflorescences having second- or third-order branching, subtended by spathe-like bracts with short blades. Lateral axes form bisexual androgynous spikes, each subtended by a cladoprophyll that resembles a perigynium, but does not bear a female flower. Species in section Surculosae also have androgynous lateral branches arranged in compound inflorescences, single or binate from nodes, subtended by smaller, more scale-like bracts. Raymond (1959) reported that some of the cladoprophylls in C. surculosa Raymond (= C. tsiangii F.T.Wang & Tang) bear fertile female flowers, reminiscent of Schoenoxiphium. Despite this high level of variation, the Siderostictae clade is strongly supported as monophyletic with molecular data and has a restricted geographical distribution, being found only in eastern and south-eastern Asia in temperate to subtropical forests.

This variation in inflorescence structure, together with variation in leaf morphology from narrow cauline leaves (e.g. C. tumidula Ohwi, C. grandiligulata Kük.) to basal clusters of broad leaves (one to several centimetres wide), makes it difficult to consistently define the Siderostictae clade. In addition, the features of the Siderostictae clade are not limited to that clade. Binate inflorescences are also found in the core Carex clade and in Schoenoxiphium, and compound inflorescences composed of androgynous lateral axes can also be found in all three other major clades. Broad leaves are also found in shade-tolerant species of the core Carex clade. In short, characters that might be considered synapomorphies for the Siderostictae clade all exhibit extensive homoplasy in the larger Cariceae clade.

A similar problem exists for the core Carex clade because of the variability introduced by the inclusion of species from subgenus Vigneasra in phylogenetic trees based on molecular data (Gehrke & Linder, 2009; Waterway et al., 2009). Core Carex is by far the largest clade of Cariceae (c. 1400 species) and includes most species currently classified in Carex subgenus Carex and probably at least half of those in Carex subgenus Vigneasra, although relatively few have yet been included in DNA-based phylogenetic studies. Inflorescence structure in subgenus Carex is similar in the majority of species. Most have terminal staminate spikes (the main florescence) and mostly pedunculate pistillate lateral spikes, each of which is subtended by a more or less leafy bract and enclosed at the base of the lateral axis with a tubular cladoprophyll (the first-order paracladia; Fig. 2). Variations on this theme occur in a few lineages that are characterized by having additional distal staminate spikes or androgynous lateral spikes, especially towards the apex of the inflorescence. In a few cases, the terminal spikes are gynandroceous rather than staminate [e.g. some species in sections Racemosae G.Don, Porocystis Dumort., Hymenochlaenae (Drejer) L.H.Bailey], and a few species are unispicate and dioecious [e.g. sections Pictae Kük. and Scirpinae (Tuck.) Kük.]. Members of subgenus Vigneasra are characterized by pedunculate, bisexual spikes that are often much branched and have cladoprophylls that are relatively large and resemble perigynia in shape. Sequenced species of Carex subgenus Vigneasra appear to be part of at least two lineages in the core Carex clade (Starr et al., 1999, 2004, 2008, 2015; Waterway & Starr, 2007; Gehrke & Linder, 2009; Waterway et al., 2009). As a result, the core Carex clade has an even larger range of variation in inflorescence structure than the Siderostictae clade, varying from dioecious unispicate species to species with unisexual or androgynous lateral spikes, sometimes binate at proximal nodes, with one or more distal staminate spikes, to species with higher order branching culminating in androgynous lateral axes and distal staminate spikes on the main axis. Most species in this clade have three stigmas as in the Siderostictae clade, but there are three sections with distastic flowers [Phacocystis s.l., Bicolores (Tuck. ex L.H.Bailey) Rouy, Abdictispicae] and occasional reductions to two stigmas in other sections (e.g. C. saxatilis L. in section Vesicariae). Cladoprophylls vary from tubular to perigynium-like, a few even bearing a pistillate flower (Nelmes, 1951), as in some
Schoenoxiphium spp. In short, although most species follow a fairly simple inflorescence plan with first-order lateral branching only, the variability in inflorescence structure and the fact that similar variants are found in other clades suggest homoplasy in any characters used to define the core Carex clade.

The Vignea clade is easier to define, most species having bisexual terminal spikes, sessile, bisexual lateral spikes that generally lack cladophylls and female flowers with only two stigmas. Most sections have androgynous spikes, but a few of the larger lineages (e.g. sections Ovales Kunth, Glareosae D.Don, Stellulatae Kunth) have gynoecandrous spikes (Ford et al., 2006; Hipp et al., 2006), and some species have mesogynous or mesandrous spikes or alternate staminate and pistillate flowers in the spikes. Exceptions to this pattern are relatively few. For example, a few species are unisinate, some are dioecious (e.g. section Physoglochin) and a few lineages with condensed inflorescences have higher order branching (Ford et al., 2006, 2012; Hipp et al., 2006, 2013; Waterway & Starr, 2007; Jung & Choi, 2013). Three stigmas are found in only a few early-diverging species in the group, including C. gibba Wahlenb., which is sister to the rest of the Vignea clade in molecular analyses (Ford et al., 2006; Waterway et al., 2009; Jung & Choi, 2013). Although support reported for the monophyly of subgenus Vignea is strong, the topology of the tree in the Vignea clade is quite variable, depending on the genes used, taxon sampling and analytical methods.

Given the inclusion of all four segregate genera of Cariceae, the caricoid clade is almost impossible to define with consistent morphological synapomorphies, a situation that has been discussed at length by Starr and co-workers (Starr et al., 2004; Starr & Ford, 2009). Inflorescence architecture and vegetative structure vary widely in the group, perigynia can be open or closed, and stigma number varies from two to three. Furthermore, the level of support for the caricoid clade is never strong and depends on taxon density, DNA regions and analytical methods used (Starr & Ford, 2009; Gehrke et al., 2010). We are thus hesitant to consider this clade as the basis for recognizing a fourth genus in parallel with the other three clades. Conferring generic status on this clade would mean including in it species from all four of Küen-Thal’s subgenera of Carex and species from all four other genera of Cariceae; this would require at least as many name changes as uniting the whole tribe into the genus Carex s.l. With so much variation in form, it would not be a practical solution to the problem of paraphyly in Carex s.s., especially because we are not sure that additional gene and taxon sampling will continue to support the recognition of the caricoid clade. Another related possibility might be to recognize each of the two clades that make up the caricoid clade, especially because they do not together form a monophyletic group in some analyses (Gehrke et al., 2010; Jung & Choi, 2013). This would not solve all problems, however, because the core unispicate clade also has fairly weak support and is highly variable, whereas the Schoenoxiphium clade includes several species of Carex s.s. that do not strongly resemble Schoenoxiphium (see below for more detail). We thus reject the first option of recognizing each of the major clades as a distinct genus because that would create more problems than it solves.

Option 2: Many genera

The second option is to recognize each strongly supported clade (Siderostictae, core Carex and Vignea) as a genus, and to divide the caricoid clade into smaller monophyletic groups that could be recognized as genera. There is some appeal in this alternative approach, because a few groups in the caricoid clade appear to be both monophyletic and distinctive. Uncinia and Schoenoxiphium have been sampled quite extensively, although with relatively few genes, and are monophyletic in the best sampled molecular studies (Starr et al., 2003, 2004, 2008; Gehrke et al., 2010; Luceño et al., 2013). An elongate rachilla with a hooked tip is shared by all Uncinia spp., although the hook in the controversial U. kingii Boott [= C. kingii (Boott) Reznicek] has a different derivation (Starr et al., 2004). However, U. kingii is sister to a clade including all other sampled Uncinia spp., meaning that the entire group is also monophyletic, although its relationships to other species in the caricoid clade are not clear (Starr et al., 2008). Uncinia spp. also share a perigynium that is closed, except at the orifice where the style and rachilla emerge, and all have three stigmas. Except for the hooked tip of the rachilla, these features are not unique to Uncinia, but together they make the genus easy to recognize and describe. Uncinia also has a coherent and limited Gondwanan distribution, most species occurring in New Zealand, Australia and southern South America, ranging north to Hawaii and the Philippines in the Eastern Hemisphere and to the Caribbean region in the Western Hemisphere. The main problem with recognizing it as a distinct genus is that it is nested in the caricoid clade with several species of unispicate Carex s.s. and Kobresia.

Schoenoxiphium also forms a well-supported monophyletic group in the most recent analysis, in which 85% of the named species were sampled (Gehrke et al., 2010), but Schoenoxiphium is more difficult to distinguish from other genera of Cariceae, especially Kobresia. The genus was originally defined by the flattened ciliate rachilla that often bears male flowers distally and emerges from the orifice of a closed
perigynium. These features are in contrast with the shorter, terete rachillae of many *Kobresia* spp., in which the male flowers are fewer in number or suppressed completely and the perigynium is often open on one side nearly to the base (Fig. 2E). Inflorescence nodes in *Schoenoxiphium* tend to be more evenly spread along the flowering culm than in *Kobresia*, and inflorescence bracts tend to be leaf-like and often sheathing in some *Schoenoxiphium* spp., but much reduced in *Kobresia* (Reznicek, 1990). Most *Schoenoxiphium* spp. also have more highly branched inflorescences than those of most *Kobresia* spp. Morphological variability in *Schoenoxiphium* appears to be almost as great within some species as across the genus (Levyns, 1945; Haines & Lye, 1983). Some individuals of *S. lehmannii* (Nees) Steud. are almost Carex-like, having perigynia closed except at the orifice and arranged in lateral androgy nous spikes, as well as a terminal staminate spike, each spike except the terminal subtended by a foliaceous bract (Haines & Lye, 1983). Even the rachilla in these individuals is sterile and short. Other individuals of the same species have a fully developed rachilla that emerges from the perigynium and bears a set of male flowers distally (Haines & Lye, 1983). Branching can be complex in *Schoenoxiphium* involving third- or higher order branching from the main axes and spikes of spikelets bearing perigynia from within female or bisexual spikelets on the ultimate flowering axes (Gehrke et al., 2012). Pistillate flowers borne in the axil of a branch on which spikelets are borne have an enclosing, but more open, cladoprophyll that resembles the unsealed perigynia of *Kobresia* (Fig. 2G).

The molecular evidence suggests that two small clades of species of *Carex* s.s. with reduced inflorescence, named the *C. andina* and *C. distachya* clades, and together including representatives from three of Kükenthal’s subgenera, are more closely related to *Schoenoxiphium* than are any *Kobresia* spp. (Gehrke et al., 2010; Fig. 1). *Schoenoxiphium* plus the *C. andina* and *C. distachya* clades form a monophyletic group, but differ strongly in morphology and distribution. *Schoenoxiphium* is endemic to eastern and southern Africa, the *C. andina* clade is endemic to southern South America and Australasia, and species from Europe, the Mediterranean Region, Macaronesia and central Africa form the *C. distachya* clade. Most species in the *C. andina* clade and some in the *C. distachya* clade have at least some unisepitate individuals, whereas most *Schoenoxiphium* spp. have at least some individuals with higher order branching in the inflorescence. If the option of breaking up the caricoid clade into smaller genera, each with more consistent morphological features, were to be followed, three genera could be recognized from the *Schoenoxiphium* clade, one for *Schoenoxiphium* itself and one for each of the sister clades.

The rest of the caricoid clade would be more difficult to segregate into monophyletic genera (Fig. 1). A major problem is the genus *Kobresia*, which is polyphyletic in all molecular analyses so far (Yen & Olmstead, 2000; Starr et al., 2004; Gehrke & Linder, 2009; Gehrke et al., 2010; Jung & Choi, 2013). Some lineages include both *Kobresia* spp. and unisepitate *Carex* spp. However, only a small proportion of *Kobresia* spp. have been included in molecular studies until now. In a much more comprehensive study of *Kobresia*, Zhang et al. (2013) found five distinct lineages variously nested in the caricoid clade, but without good correspondence to the previous subgeneric categories of *Kobresia*. If we continue the logic of naming monophyletic groups in the caricoid clade as distinct genera, we would have to recognize at least these five lineages that include *Kobresia* spp. and at least seven lineages of unisepitate *Carex*. Many of these small groups already have names at the generic level as these highly reduced unisepitate species were seen as unusual by many 19th century botanists. One problem with doing this is that, despite considerable study of this clade, few genes have been used, and the tree topology in the caricoid clade is not consistent across studies using different genes (Starr et al., 2004; Waterway & Starr, 2007; Gehrke & Linder, 2009; Gehrke et al., 2010). Taking the approach of recognizing numerous genera in the caricoid clade would not serve the goal of long-term nomenclatural stability and, given the superficial similarity of many unisepitate species in this group, would cause considerable confusion.

**Option 3: One genus**

At this point, it should be clear that there are problems with recognizing each of the major clades as distinct genera and even more difficulties with recognizing three of the major clades and at least a dozen lineages in the caricoid clade as distinct genera. Neither of these first two options is optimal to meet the goals of nomenclatural stability, generic monophyly and ease of use. Instead, we propose here to take the third choice listed above, and merge all genera currently treated as tribe *Cariceae* (*Cymophyllus, Kobresia, Schoenoxiphium, Uncinia*) into the genus *Carex*. Analysis of molecular data has consistently shown this group of genera to be strongly supported as monophyletic in comprehensive studies of Cyperaceae (Muasya et al., 1998, 2009; Simpson et al., 2007; Jung & Choi, 2010), and in more detailed analyses of the tribe in relation to outgroups suggested by family-level analyses (Starr et al., 2004; Waterway & Starr, 2007; Gehrke & Linder, 2009; Starr & Ford, 2009; Waterway et al., 2009; Gehrke et al., 2010; Fig. 1).
et al., 2010; Jung & Choi, 2013; Léveillé-Bourret et al., 2014). In contrast with the difficulty in finding consistent morphological synapomorphies for the major clades, as detailed above, it is much easier to list clear synapomorphies for Carex s.l. in the broadened circumscription proposed here. The combination of unisexual flowers and perigynia surrounding the female flowers is unique in Cyperaceae. As described earlier, what appear to be pistillate flowers in Cariceae are actually reduced spikelets in which the proximal female flower is surrounded by the enclosing prophyll (perigynium) and the spikelet axis is either vestigial or elongated, with or without distal staminate flowers. Processes at play in this change from a multi-flowered spikelet with a spiral of bisexual flowers having a bristle perianth, as in the closely related tribe Scirpeae, involve suppression of perianth, modification of sex expression resulting in unisexual flowers and expansion and at least partial fusion of the prophyll into a perigynium. It is easy to envisage selection against maintenance of the rachilla and its distal male flowers within an enclosure like the perigynium, especially because it is possible for any axis in the synflorescence to produce the needed staminate flowers directly from the same type of primordia that produce the reduced female spikelets (Vrijdaghs et al., 2010).

Classifications have been based largely on features of inflorescences and perigynia, in part because they are more obvious than floral differences within the perigynia, and in part because vegetative features in Carex s.l. have more variation within segregate genera than among them. Other than the unusually thick leaves of C. fraseriana, which lack a midrib, and the broad, pseudo-petiolate leaves of some South-East Asian species, no distinctive vegetative features set any group apart from the others. As we have described above, inflorescence structure also varies substantially in clades and even within species. Furthermore, mutant individuals in the core Carex clade sometimes exhibit inflorescence and floral forms of the allied genera. Occasional teratological specimens with rachillae bearing male flowers in species that normally have only a tiny vestigial rachilla have been found naturally and can be induced experimentally by application of growth regulators or by damaging the root tips (Smith & Faulkner, 1976). Section Hangzhouenses C.Z.Zheng, X.F.Jin & B.Y.Ding was described in Carex subgenus Vigneastro to accommodate an unusual specimen of Carex from eastern China that had perigynia with protruding, elongated rachillae bearing staminate flowers (Jin et al., 2005). Comparison of DNA sequences with species growing on the same cliff, however, revealed that these specimens were more likely to be aberrant specimens of Carex simulans C.B.Clarke of section Rhomboidales Kük., subgenus Carex (X. F. Jin and M. J. Waterway, unpubl. data) than a new species in a new section of subgenus Vigneastro. These results suggest that, although suppression may appear to be genetically fixed in particular clades, it can be reversed under certain conditions. Various teratological specimens have been illustrated showing similar Schoenoxiphium-like spikelets in specimens of Carex crinita Lam., C. albicans Willd. ex Spreng. var. emmonsii (Dewey ex Torr.) Rettig, C. pallescens L., C. sprengelii Steud. and C. sitchensis Bong. (Penzig, 1894; Holm, 1896; Clarke, 1909; Svenson, 1972). Perigynia enclosing stamens rather than a pistil in C. acuta L. and pistils subtended by glumes rather than enclosed in perigynia have also been noted (Holm, 1896; Smith & Faulkner, 1976; Timonen, 1998). Suppression of lateral branching resulting in unisporate individuals of normally multi-spicate Carex spp. (e.g. C. flaca Schreb.) has also been found sporadically in natural Carex populations and can be easily induced by the application of 2,3,5-triiodobenzoic acid (TIBA) (Smith & Faulkner, 1976). Reports of these aberrant individuals or populations frequently mention trampling or other disturbance, suggesting that damage to meristems or environmental factors may be involved (Svenson, 1972; Smith & Faulkner, 1976).

Bisexual flowers are another aberration that has been reported infrequently in Kobresia and Schoenoxiphium (Timonen, 1998), most recently as sporadic occurrences in populations of S. lehmannii and S. burkei C.B.Clarke (Gehrke et al., 2012). Detailed observations on several individuals revealed a full transition series from proximal female spikelets to bisexual spikelets having distal male flowers on the rachilla to bisexual flowers directly on the lateral axis and to distal male flowers at the apex of the lateral axis. These bisexual flowers were produced directly on the lateral axis in the transition zone between multi-flowered bisexual spikelets and distal male flowers. The bisexual flowers were similar to male flowers in being subtended by a scale-like glume, but they lacked a perigynium. In addition to the normal whorl of three stamens found in male flowers, these bisexual flowers had a biconvex dististigmatic ovary at the centre, in contrast with the tristigmatic ovary found in female flowers (Gehrke et al., 2012). These observations provide further support to the idea that the position on the axis is important in the control of sex expression and that primordia on the spikelet can be regulated, either internally or externally, to produce either spikelets or single flowers (Vrijdaghs et al., 2009, 2010). The extreme variability in inflorescence structure not only among Schoenoxiphium spp., but also within species and even within different parts of the same inflorescence, was already noted by Levyns (1945), whose invaluable observations on
fresh material of four species provide a clear picture of structural variability. She emphasized the strong influence of position in the inflorescence and vigour of the plant in determining branching patterns, sex expression and whether or not a perigynium contains a flower. Such variability in floral and inflorescence structure in response to environment, either internal or external, calls into question their value as taxonomic characters. An understanding of the intrinsic and extrinsic controls on inflorescence structure would be useful in evaluating similarities in inflorescence form across clades in Carex s.l.

With new insights from molecular biology regarding the control of floral and inflorescence structure in angiosperms, and especially in other commelinids such as Poaceae, it is becoming clear that even small changes in the regulation of gene expression can have significant effects on floral and inflorescence morphology (Doust & Kellogg, 2002; Bommert et al., 2005; Thompson & Hake, 2009). For example, a single amino acid substitution in the transcription factor OsMADS1 can cause paleas, lemmas and lodicules to become leafy and can decrease stamen number in rice plants with this mutation (Jeon et al., 2000; Bommert et al., 2005). The behaviour of meristems in the inflorescence is regulated by a variety of transcription factors (e.g. MADS-box genes) that control whether meristems produce branches or flowers, the nature of the associated bracts, the extent of internode elongation and the identity of different parts of the flowers and spikelets in grasses (Kellogg, 2000; Bommert et al., 2005; Thompson & Hake, 2009). A dynamic model of grass inflorescence development describes a series of developmental switches that determine whether meristems will branch or will terminate in flowers. These switches also regulate the number of meristems produced, the extent of internode or bract growth and the phyllo-taxy (Kellogg, 2000; Bommert et al., 2005). Given the conservation of regulatory function among dicots, there is good reason to expect that similar models might apply to both sedges and grasses, because they are both commelinid monocots with spikelets arranged in complex and variable inflorescences. It is clear from the earlier discussion that control of branching and the fate of meristems are critical not only to the architecture of the inflorescence of Carex s.l., but also to patterns of sex expression, pistillate flowers being produced only at branching events and staminate flowers most often positioned on axes where branching has stopped.

Genetic and regulatory controls of inflorescence structure are important, but environmental and hormonal signals also play a role (McSteen, 2009). Auxin, cytokinin and strigolactone are all involved in the fate of meristems within the inflorescence. Basipetal movement of auxin from the apical meristem inhibits bud meristems from growing (apical dominance) and acropetal movement of cytokinin and strigolactone promotes and inhibits bud growth, respectively. Shading is also known to inhibit branching, and soil nutrients can promote it. Genetic, regulatory, hormonal and environmental controls thus determine the final structure of an inflorescence (McSteen, 2009). It is important to remember that the induction of flowering is a dynamic process, mediated by growth regulators, which are influenced by intrinsic and extrinsic factors, including the carbohydrate status of the plant, temperature and day length. Position in relation to root and shoot meristems that produce growth regulators can be a strong influence on whether male or female flowers are produced in monoecious plants such as Carex s.l. We do not yet have a complete understanding of the way in which these various regulatory pathways interact, but it appears likely that simple changes in the regulation of floral and inflorescence structure can explain the variability we see in Carex s.l. Understanding how these regulatory systems work should help us evaluate which aspects of floral and inflorescence structure are stable within clades and which are not, making it easier to select appropriate characters to define subgroupings in Carex s.l.

Although the similarity of form in genera of Cariceae has long been recognized (e.g. Clarke, 1883; Nelmes, 1951; Kern, 1958), they have been maintained as distinct genera for so long in part because of their allopatry. Schoenoxiphium is restricted to eastern and southern Africa, with a single species reaching the south-western parts of the Arabian Peninsula, whereas Uncinia grows around Antarctica, ranging from Australia, New Zealand, Chile and Argentina north to the Philippines, Hawaii and the Caribbean. Kobresia has its centre of distribution and greatest species richness in the Himalayas, with a few wide-ranging circumboreal species. Given the flexibility of inflorescence structure and the possibilities for differential suppression of parts that might become genetically fixed, it is reasonable to expect that the same basic constraints on the inflorescence might give parallel results in lineages that colonized different regions of the world. Although not identical by descent, the rachillae bearing male flowers apically in Schoenoxiphium and Kobresia have positional homology and could reasonably represent parallel evolution of similar structures (Vrijdaghs et al., 2010). Similarly, selection pressures in the harsh, windy and often nutrient-poor conditions in which many unisipicate species of Carex s.l. (including Kobresia) are found may have favoured reduced branching and smaller stature, again resulting in parallel development of the same traits in different lineages.
CONCLUSIONS

Much has been accomplished towards an understanding of Carex s.l. since the publication of Kükenthal’s (1909) monograph, from species discovery to detailed analysis of floral and inflorescence morphology to DNA-based phylogenetic trees. Species of Carex s.l. continue to be discovered at a surprising rate even in well-explored areas, such as Europe, North America, Japan, Australia and New Zealand, and at even higher rates in China, South-East Asia, Africa and South America. Detailed studies of floral and inflorescence morphology have been conducted for most major groups of Carex s.l., although more work is needed on the Vigneastra group and Kobresia. At least one gene has been sequenced for more than half of the species in the tribe, and nuclear and plastid DNA regions, coding and non-coding, have been sequenced for more than half of these in ongoing phylogenetic studies. Despite this progress, there has been understandable hesitancy for anyone to reclassify a large and widespread group such as Cariceae unilaterally, despite frequent comments on the difficulty of distinguishing the genera in it. As a global group of Cyperaceae and Cariceae specialists, we think it is time to overcome the inertia of the traditional classification and make the required nomenclatural changes to recognize all species in the tribe as the genus Carex s.l. Much remains to be accomplished on a global scale to continue exploration and species discovery, to understand the ways in which genetic and environmental factors influence inflorescence variability within and between species, and to take advantage of the constantly expanding set of molecular tools and analytical methods to formulate phylogenetic hypotheses for the monophyletic genus Carex s.l.

The new broader circumscription of Carex proposed here is just the first step in the reclassification of the genus. The Global Carex Group is working towards a complete global sampling of species of Carex s.l., sequencing multiple DNA regions per species, to aid in placing species into natural sectional groups in the genus. Molecular phylogenetic work already completed on Carex section Ovales (Hipp et al., 2006), section Spirostachyae (Drejer) L.H.Bailey (Escudero et al., 2007; Escudero & Luceño, 2009, 2011), section Phyllostachyae Tuck. ex Kük. (Starr et al., 1999) and section Ceratocystis Dumort. (Jiménez-Mejías, Martín-Bravo & Luceño, 2012; Derieg et al., 2013) illustrates the potential for clarifying the relationships at the sectional level with DNA analyses. Projects currently in progress by our group include: an expanded phylogenetic analysis and new monograph of Schoenoxiphium as a section of Carex, a new molecular phylogenetic analysis of Carex subgenus Vignea, and additional work on the rest of the carioeid clade to elucidate natural groups in Kobresia and unispicate species. We are also working on reclassifications of sections Glareosae, Phleoideae (Meinsh.) T.V. Egorova and Remotae (Asch.) C.B.Clarke in the Vignea clade and sections Aulocystis Dumort., Chlorostachyae Tuckerm. ex Meinsh., Hymenochaenae s.l., Porocystis, Phacocystis s.l., Racemosae, Mitratae Kük., Rhomboideas, Laxiflorae (Kunth) Mack., Paniceae G.Don, Bicoles, Careyanae Tuck. ex Kük., Griseae (L.H.Bailey) Kük., Granulares (O.Lang) Mack., Rostrales Meinh., Vesicariae, Paludosae, Carex, Lupulinae, Squarrosoae J.Carey, Sylvaticae Rouy, Rhynchocystis Dumort. and Indicae Tuck. in the core Carex clade based on global sampling and informed by molecular data.

TAXONOMIC TREATMENT

NEW NAME IN CAREX

Carex zikae E.H.Roalson & M.J.Waterway, nom. nov.


Distribution: North-western North America.

Etymology: The new name for this Pacific Northwest species recognizes the important contributions of Peter Zika (WTU, University of Washington, Seattle, WA, USA) to Carex systematics in western North America.

Note: Despite the long usage of Carex brevicaulis Mack. in North America, it is clear that this is a later homonym of Carex brevicaulis Thouars (Esquisse Fl. Tristan d’Acugna: 35. 1808), a species most recently treated in Uncinia. Carex brevicaulis Thouars has priority in Carex over C. brevicaulis Mack.

INCLUSION OF CYMOPHYLLUS MACK. EX BRITTON & A.BR. IN CAREX L.


Mapania Sylvatica Pursh, Fl. Amer. Sept. 1: 47. 1813, nom. illeg.


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Distribution: eastern USA (southern Appalachian Mts.).

Transfers from Kobresia Willd. to Carex L.

Carex alatauensis S.R.Zhang, nom. nov.


Distribution: Central Asia, north-western China.

Etymology: The type of the replaced synonym, Elyna humilis C.A.Mey. ex Trautv., was collected from the Alatau Mountains in Central Asia.

Carex bhutanensis S.R.Zhang, nom. nov.


Distribution: Eastern Himalaya (Nepal, Sikkim, Bhutan) to south-western China.

Etymology: The type of the replaced name, Kobresia prainii Kük., was collected in Bhutan.

Carex bistaminata (W.Z.Di & M.J.Zhong)
S.R.Zhang, comb. nov.


Distribution: From Karakorum to western China.

Carex bonatiana (Kük.) Ivanova, Bot. Zhurn. SSSR 24: 501. 1939


Distribution: Nepal, Sikkim, Bhutan, south-western China.

Note: The correct name for this species if the segregate genus is recognized is Kobresia fragilis.

Carex borealipolaris S.R.Zhang, nom. nov.

Kobresia arctica A.E.Porsild, Sargentia 4: 15. 1943, non Meinsh. (1901).


Distribution: Subarctic to north-western USA.

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Etymology: The species is circumboreal, and common in the North Polar area. The epithet refers to the distributional pattern of the species.

**Carex brandisii** (C.B.Clarke ex Jana & R.C.Srivast.) O.Yano, **comb. nov.**

**Distribution:** Western Himalaya (India).

**Carex breviprophylla** O.Yano, **nom. nov.**

**Distribution:** Nepal to Sikkim.

Etymology: This species is characterized by a prophyll that is shorter than the nutlet.

**Carex burangensis** (Y.C.Yang) S.R.Zhang, **comb. nov.**

**Distribution:** South-western China (western Tibet).

**Carex capillifolia** (Decne.) S.R.Zhang, **comb. nov.**

Kobresia brunnescens Boeckeler, Beitr. Cyper. 1: 40. 1888.
Kobresia elata Boeckeler, Beitr. Cyper. 2: 32. 1890.
Kobresia thomsonii Maxim. ex Ivanova, Bot. Zhurn. SSSR 24: 486. 1939, pro syn.

**Distribution:** From Caucasus to western China.

**Carex cercostachys** Franch., Bull. Soc. Philom. Paris, 8, 7: 27. 1895

**Distribution:** Bhutan, Sikkim, south-western China.

**Carex clavisipica** S.R.Zhang, **nom. nov.**

**Distribution:** Himalaya, south-western China.

Etymology: The inflorescence of the species is a clavate spike.

**Carex coninux** (F.T.Wang & Tang) S.R.Zhang, **comb. nov.**
Kobresia karakorumensis Dickoré, Stapfia 39: 77. 1995, syn. nov.

**Distribution:** Karakorum, western Himalaya, northern and western China (Gansu, Hebei, Nei Mongol, Qinghai, Shanxi, Sichuan, Tibet and Yunnan).

Note: The correct name for this species if the segregate genus is recognized is Kobresia pusilla.

**Carex curticeps** C.B.Clarke in J.D.Hooker, Fl. Brit. India 6: 749. 1894

**Distribution:** Central & eastern Himalaya to southern Tibet.

**Carex deasyi** (C.B.Clarke) O.Yano & S.R.Zhang, **comb. nov.**


Distribution: From Caucasus to western China.

Note: The correct name for this species if the segregate genus is recognized is Kobresia schoenoides.

Carex esbirajbhandarii (Rajbh. & H.Ohba) O.Yano, comb. nov.

Distribution: Nepal.

Carex esenbeckii Kunth, Enum. Pl. 2: 522. 1837


Carex filispica S.R.Zhang, nom. nov.


Distribution: Eastern Himalaya, south-western China.

Etymology: The first part of the name, fili-, thread-like, from filum, a thread, here refers to the narrowly linear spike of this species.

Carex fissiglumis (C.B.Clarke) S.R.Zhang & O.Yano, comb. nov.

Distribution: Central Himalaya (western Nepal) to south-western China.

Carex gammiei (C.B.Clarke) S.R.Zhang & O.Yano, comb. nov.


Distribution: Nepal, Bhutan, Sikkim, south-western China.

Carex handel-mazzettii (Ivanova) S.R.Zhang, comb. nov.


**Carex harrae** (Rajbh. & H.Ohba) O.Yano, *comb. nov.*


**Distribution**: South-western China (Sichuan, Tibet, Yunnan), Nepal.

**Carex hohxilensis** (R.F.Huang) S.R.Zhang, *comb. nov.*


**Distribution**: India, Nepal.

**Carex hughii** S.R.Zhang, *nom. nov.*


**Distribution**: Western China (Gansu, Qinghai, Tibet).

**Carex kanaii** (Rajbh. & H.Ohba) S.R.Zhang & O.Yano, *comb. nov.*


**Distribution**: Western China (Gansu, Qinghai, Shaanxi, Sichuan, Tibet, Yunnan).

**Etymology**: The epithet of the species is adopted to commemorate Rev. Fr. Hugh, the collector of the type of *Kobresia graminifolia* C.B.Clarke.

**Carex kantungensis** S.R.Zhang, *nom. nov.*


**Distribution**: China (Sichuan, Gansu).

**Etymology**: Kangding (Sichuan, China) is the locality in which the type of *Kobresia falcata* F.T.Wang & Tang ex P.C.Li was collected.

**Carex kobresioidea** (Kük.) S.R.Zhang, *comb. nov.*


**Distribution**: Northern Sumatra.
Etymology: Liangshan (Sichuan, China) is the locality in which the type of the replaced synonym was collected.

**Carex littledalei** (C.B.Clarke) S.R.Zhang, **comb. nov.**

Distribution: South-western China (Sichuan and Tibet).

**Carex macroprophylla** (Y.C.Yang) S.R.Zhang, **comb. nov.**


Kobresia pratensis Freyn, Oesterr. Bot. Z. 40: 266. 1890; non Carex pratensis Hosé (1797).

Distribution: Northern China, Mongolia, Siberia.

Note: The correct name for this species if the segregate genus is recognized is Kobresia filifolia.

**Carex mallae** (Rajbh. & H.Ohba) O.Yano, **comb. nov.**

Distribution: Nepal.

**Carex myosuroides** Vill., Prosp. Hist. Pl. Dauphine 17–18. 1779


Distribution: Europe, northern Asia, northern North America, Greenland.

**Carex neesii** S.R.Zhang, **nom. nov.**


Distribution: Western Himalaya to south-western China.

Etymology: The epithet of the species is adopted to commemorate Christian Gottfried Daniel Nees von Esenbeck (1776–1858) who published the first name for this species.

**Carex noltiei** S.R.Zhang, **nom. nov.**

Distribution: Bhutan, south-western China (southern Tibet).

Etymology: The epithet of the species is adopted to commemorate Henry John Noltie (Royal Botanic Garden, Edinburgh) who published the replaced synonym Kobresia woodii.

**Carex nudicarpa** (Y.C.Yang) S.R.Zhang, **comb. nov.**
Distribution: South-western China, Himalaya, eastern Karakorum.

Note: The correct name for this species if the segregate genus is recognized is *Kobresia macrantha*.

**Carex ovoidispica** O.Yano, **nom. nov.**  
*Replaced synonym:* *Kobresia nitens* C.B.Clarke, *J. Linn. Soc.*, Bot. 20: 379, pl. 30, f. 7. 1883; non *Carex nitens* Phil. (1873).

Distribution: Northern Pakistan to Nepal.

Etymology: The specific epithet refers to the conspicuous ovoid spikes.

**Carex paramjiti (Jana, Noltie, R.C.Srivast & A.Mukh.) O.Yano, **comb. nov.**  

Distribution: Sikkim.

**Carex parvula** O.Yano, **nom. nov.**  

Distribution: From Himalaya to northern and western China.

Etymology: The specific epithet refers to the dwarf habit.

**Carex peichuniana** S.R.Zhang, **nom. nov.**  

Distribution: South-western China (north-western Yunnan, south-eastern Tibet).

Etymology: The epithet of the species is adopted to commemorate Pei-Chun Li (Shenzen Fairy Lake Botanical Garden, Guangdong, China), who published the replaced synonym *Kobresia inflata*.

**Carex praunii** Kük., *Bull. Herb. Boissier*, sér. 2, 4: 51. 1903  

Distribution: Nepal to Assam.

**Carex pseudogammiei** S.R.Zhang, **nom. nov.**  

Distribution: South-western China (north-western Yunnan, western Sichuan).

Etymology: The species is morphologically similar to *Carex gammiei* (C.B.Clarke) S.R.Zhang.

**Carex pseudolaxa** (C.B.Clarke) O.Yano & S.R.Zhang, **comb. nov.**  

Distribution: Kashmir to central Himalaya.

Note: The correct name for this species if the segregate genus is recognized is *Kobresia laxa*.
Carex pseuduncinoides (Noltie) O.Yano & S.R.Zhang, **comb. nov.**
  Kobresia kansuensis Kük., Acta Horti Gothob. 5: 38. 1930; non Carex kansuensis Nelmes (1939).

_Distribution:_ Bhutan, India, Nepal, western China.

**Note:** The correct name for this species if the segregate genus is recognized is _Kobresia kansuensis._

Carex _rcsrivastavae_ (Jana) E.H.Roalson, **comb. nov.**

_Distribution:_ India (Uttaranchal).


_Distribution:_ Eastern Afghanistan to western Himalaya.

Carex _sargentiana_ (Hemsl.) S.R.Zhang, **comb. nov.**

_Distribution:_ Western China, Sikkim.

**Note:** The correct name for this species if the segregate genus is recognized is _Kobresia robusta._

Carex _setschwanensis_ (Hand.-Mazz.) S.R.Zhang, **comb. nov.**

_Distribution:_ Western China (southern Gansu, southern Qinghai, Sichuan, Tibet, Yunnan).

Carex _siamensis_ (Ohwi) S.R.Zhang, **comb. nov.**

_Distribution:_ Eastern Himalaya to northern Thailand.

**Note:** The correct name for this species if the segregate genus is recognized is _Kobresia curvirostris._

  Carex _mirabilis_ Host, Icon. Descr. Gram. Austriac. 4: 44, pl. 78. 1809.
  Carex _lobata_ Willd. ex Kunth, Enum. Pl. 2: 533. 1837, pro syn.

_Distribution:_ Europe to Caucasus, subarctic America to western USA.

*Distribution:* North-western China (southern Gansu, eastern Qinghai).

Carex tibetikobresia S.R.Zhang, *nom. nov.*

*Distribution:* Bhutan, western China.

*Etymology:* The epithet is based on the replaced synonym, *Kobresia tibetica*. The species is mainly distributed in the eastern Tibetan Plateau.

Carex tunicata (Hand.-Mazz.) S.R.Zhang, *comb. nov.*

*Distribution:* South-western China (north-western Yunnan).

Carex uncinoides Boott, *Ill. Gen. Carex* 1: 8, pl. 23. 1858

*Distribution:* Eastern Himalaya (Nepal to Bhutan), northern Myanmar, south-western China.

Carex vaginosa (C.B.Clarke) S.R.Zhang, *comb. nov.*

*Distribution:* Nepal, Sikkim, south-western China.

**Carex vibhae** (Jana, R.C.Srivast & Bhaumik) O.Yano, *comb. nov.*

*Distribution:* South-eastern Himalaya.


*Distribution:* Himalaya (Nepal, Sikkim, Bhutan) to western China.

Carex yadongensis (Y.C.Yang) S.R.Zhang, *comb. nov.*

*Distribution:* South-western China (south-western Tibet).


*Distribution:* South-western China (south-western Sichuan).

**Transfers from Schoenoxiphium Nees to Carex L.**

Carex basutorum (Turrill) Luceño & Martín-Bravo, *comb. nov.*

*Distribution:* South Africa (Free State), Lesotho.

Carex burkei (C.B.Clarke) Luceño & Martín-Bravo, *comb. nov.*

Distribution: South Africa (Cape Province, Natal), Lesotho.

**Carex capensis** Thunb., Prodr. Pl. Cap.: 14. 1794


*Schoenoxiphium ecklonii* var. unisexualae Kük. in Engler, Pflanzenr. 38(IV, 20): 33. 1909.

**Note:** The correct name for this species if the segregate genus is recognized is *Schoenoxiphium ecklonii*.

**Carex chermezonii** Luceño & Martín-Bravo, nom. nov.


**Distribution:** Northern Madagascar (Mt. Tsaratanana).

**Etymology:** The epithet honours Henri Chermezon (1885–1939), a French botanist and explorer, who first described this species in 1923.

**Carex distincta** (Kukkonen) Luceño & Martín-Bravo, comb. nov.


**Distribution:** South Africa (Free State?, Natal), Lesotho.

**Carex killickii** Nelmes, Kew Bull. 10: 89. 1955


**Distribution:** South Africa (Cape Province, Free State, Natal), Lesotho.

**Carex kukkoneniana** Luceño & Martín-Bravo, nom. nov.


**Distribution:** South Africa (Cape Province, Natal), Lesotho.

**Carex lancea** (Thunb.) Baill., Hist. Pl. 12: 341. 1894


**Carex ramosa** Eckl. ex Kunth, Enum. Pl. 2: 531. 1837, nom. illeg.

**Schoenoxiphium capense** Nees, Linnaea 7: 531. 1832.

**Schoenoxiphium meyerianum** Kunth, Enum. Pl. 2: 530. 1837.

**Schoenoxiphium sickmannianum** Kunth, Enum. Pl. 2: 530. 1837.

**Distribution:** South Africa (Cape Province).

**Carex ludwigii** (Hochst.) Luceño & Martín-Bravo, comb. nov.

**Basionym:** *Schoenoxiphium ludwigii* Hochst., Flora, 28: 764. 1845.


**Schoenoxiphium dregeanum** Kukkonen, Bot. Not. 131: 263. 1978; non *Carex dregeana* Kunth (1837).
Schoenoxiphium burkei sensu Govaerts et al., World Checklist of Cyperaceae (2007): 673, non C.B.Clarke.
Schoenoxiphium buchananii sensu Govaerts et al., World Checklist of Cyperaceae (2007): 673, non C.B.Clarke.

Distribution: South Africa (Cape Province, Natal, Northern provinces, Swazilandia), Lesotho.

Carex multispiculata Luceño & Martin-Bravo, nom. nov.

Distribution: South Africa (Natal, Northern provinces), Madagascar.

Etymology: From the Latin multus, many, and spicula, spikelet.

Carex perdensa (Kukkonen) Luceño & Martin-Bravo, comb. nov.

Distribution: South Africa (Cape Province, Natal).

Carex pseudorufa Luceño & Martin-Bravo, nom. nov.

Distribution: South Africa (Natal).

Etymology: From the Greek ψευδη´ς (pseudo, resembling but not equalling) and the Latin rufus, -a, -um (red), alluding to the resemblance of this species to Carex ludwigi, which was formerly known as Schoenoxiphium rufum.

Carex schimperiana Boeckeler, Linnaea 40: 373. 1876

Carex schweickerdtii (Merxm. & Podlech) Luceño & Martin-Bravo, comb. nov.

Distribution: South Africa (Natal).


Carex dregeana Kunth, Enum. Pl. 2: 511. 1837.
Carex dregeana var. major C.B. Clarke in Harvey & auct. suc. (eds.), Fl. Cap. 7: 304. 1898.
Carex esenbeckiana Boeckeler, Linnaea 40: 372. 1876.
Carex indica Schkuhr, Beschr. Riedgräs. 1: 37. 1801, nom. illeg.


Distribution: Ethiopia to South Africa.

Note: The correct name for this species if the segregate genus is recognized is Schoenoxiphium lehmannii.

Transfers from Uncinia Pers. to Carex L.

Carex aspericaulis (G.A.Wheeler) J.R.Starr, comb. nov.

Distribution: Juan Fernández Islands (Alejandro Selkirk).

Carex astricta K.A.Ford, nom. nov.

Distribution: New Zealand (North & South Islands, Stewart Island).

Etymology: From the Latin astrictus, drawn together tight, referring to the densely caespitose habit of this species.

Carex auceps (de Lange & Heenan) K.A.Ford, comb. nov.

Distribution: New Zealand (Chatham Islands).

Carex aucklandica (Hamlin) K.A.Ford, comb. nov.

Distribution: New Zealand (South Island, Stewart Island, Auckland Islands, Campbell Island).

Carex austrocompacta K.L.Wilson, nom. nov.

Distribution: South-eastern Australia.

Etymology: The first component of the name is from the Latin australis, southern, referring to the Southern Hemisphere occurrence of this species, added to the original epithet, which presumably refers to the small stature of this species, to provide a link between the new name and the original name.

Carex austroflaccida K.L.Wilson, nom. nov.
Uncinia tenella var. robustior Kük., Bot. Centralbl. 76: 211 (1898).

Distribution: South-eastern Australia.

Etymology: The first component of the name is from the Latin australis, southern, referring to the Southern Hemisphere occurrence of this species, added to the original epithet, which refers to the soft-textured leaves of this species, to provide a link between the new name and the original name.

Carex austrosulcata K.L.Wilson, nom. nov.

Distribution: South-eastern Australia.

Etymology: The first component of the name is from the Latin australis, southern, referring to the Southern Hemisphere occurrence of this species, added to the original epithet, which refers to the rather channelled leaves of this species, to provide a link between the new name and the original name.

Carex austrotenella K.L.Wilson, nom. nov.
Uncinia tenella Poir. in Lamarck, Encycl., Suppl. 3: 282. 1813, nom. illeg.; non Carex tenella Thuill. (1790).

Distribution: South-eastern Australia.

Etymology: The first component of the name is from the Latin australis, southern, referring to the Southern Hemisphere occurrence of this species, added to the original epithet, which presumably refers to the small stature of this species, to provide a link between the new name and the original name.

Carex banksiana K.A.Ford, nom. nov.
var. banksii (Boott) C.B.Clarke, J. Linn. Soc., Bot. 20: 392. 1883; non Carex banksii Boott (1846).


Distribution: New Zealand (North & South Islands).

Etymology: This name honours Sir Joseph Banks (1743–1820), as did the previous epithet.

Carex brevicaulis Thouars, Esquisse Fl. Tristan d’Acuigna: 35. 1808
Uncinia brevicaulis (Thouars) Kunth, Enum. Pl. 2: 528. 1837.


Uncinia rigida Boeckeler, Flora 65: 64. 1882.


Distribution: Hawaii (eastern Maui), Peru, southern Chile to subantarctic islands.

Carex cheesemanniana (Boeckeler) K.A.Ford, comb. nov.


Distribution: South-eastern Australia, New Zealand (South Island).

Note: The correct name for this species if the segregate genus is recognized is Uncinia nervosa.

Carex corynoidea K.A.Ford, nom. nov.


Distribution: New Zealand (North & South Islands).

Carex crispa K.A.Ford, nom. nov.


Distribution: New Zealand (North & South Islands, Stewart Island).

Carex corynoidea K.A.Ford, nom. nov.


Distribution: New Zealand (North & South Islands).


Distribution: Chile to southern Argentina.

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Note: Uncinia delacosta Steudel is a nomen nudum and therefore of no nomenclatural consequence. Kuntze can therefore be interpreted under the provisions of the Code (Art. 6.11 and Art. 58.1) as having published a replacement name in Carex for Uncinia macloviana Gaudich. There is no description or type mentioned by Kuntze associated with his new name, but he clearly indicated that he is publishing a replacement name for U. macloviana, which is a valid and legitimate name.

Carex dikei (Nelmes) K.L.Wilson, comb. nov.

Distribution: South Africa (Marion Island, Prince Edward Island).

Note: Nelmes published the epithet as ‘dykei’ in the mistaken belief that Dyke was the surname of the person concerned. Nelmes corrected the spelling to dikei when he found out that the correct spelling of the surname was Dike (Nelmes, 1949).

Carex dolichophylla J.R.Starr, nom. nov.

Uncinia bella Phil., Linnaea 30: 204. 1859; non Carex bella L.H.Bailey (1892).


Uncinia bracteosa Phil., Anales Univ. Chile 93: 503. 1896; non Carex bracteosa Schwein. (1824).

Distribution: Southern Chile.

Etymology: The epithet combines the Greek word for long (dolichos) with the Greek word for leaves (phylla) to highlight the long leaves that typically surpass the inflorescence of this rather large species.

Carex drucei (Hamlin) K.A.Ford, comb. nov.


Distribution: New Zealand (North & South Islands, Stewart Island).

Carex ecuadorensis (G.A.Wheeler & Goeth.) J.R.Starr, comb. nov.

Distribution: Northern and central Ecuador.

Carex edura K.A.Ford, nom. nov.


Distribution: Australia (Macquarie Island), New Zealand (North & South Islands, Campbell Island).

Etymology: From the Latin edurus, or tough, referring to the harsh environmental conditions this species withstands.

Note: We consider that Art. 53.3. of the Code, which states that confusingly similar names should be treated as homonyms, applies here, making the epithet clarkei unavailable in Carex because of the publication of the fossil species Carex clarkii E.W.Berry in 1905.

Carex egmontiana (Hamlin) K.A.Ford, comb. nov.


Distribution: New Zealand (North & South Islands, Stewart Island).

Carex erebus K.A.Ford, nom. nov.

Distribution: Australia (Macquarie Island), New Zealand (Stewart Island, Antipodes Island, Auckland Islands, Campbell Island).

Etymology: Named for the ship HMS Erebus on which Joseph Dalton Hooker sailed on the Voyage to the
Antarctic 1839–1843, during which this species was first collected from the Auckland Islands.

**Carex erinacea** Cav., Icon. 5: 40. 1799

_Agistron erinacea_ (Cav.) Raf., Good Book: 28. 1840.
_Uncinia longifolia_ Kunth, Enum. Pl. 2: 527. 1837.

_Distribution_: Magellan Region of South America.

**Carex erythrovaginata** K.A.Ford, _nom. nov._
_Replaced synonym_: _Uncinia laxiflora_ Petrie, Trans. & Proc. New Zealand Institute 17: 271. 1885; non _Carex laxiflora_ Lam. (1792).

_Distribution_: New Zealand (North & South Islands, Stewart Island).

_Etymology_: The name refers to the reddish sheaths of the leaves of this species.

**Carex fernandesiana** (Nees ex Boeckeler) _J.R. Starr, comb. nov._
_Basionym_: _Uncinia fernandesiana_ Nees ex Boeckeler, Linnaea 41: 347. 1877.
_Uncinia angusta_ Nees, Linnaea 9: 305. 1834, nom. inval.
_Uncinia angustata_ Boeckeler, Linnaea 41: 347. 1877.

_Distribution_: Juan Fernández Islands.

_Note_: The correct name for this species if the segregate genus is recognized is _Uncinia douglasi_ii.

**Carex firmula** (Kük.) _J.R. Starr, comb. & stat. nov._

_Distribution_: Central America to Falkland Islands.

_Note_: The correct name for this species if the segregate genus is recognized is _Uncinia tenuis_.

**Carex goethebeurai** _J.R. Starr, nom. nov._

_Distribution_: South-eastern Ecuador.

_Etymology_: The epithet honours the prominent cyperologist Paul Goetghaer of Ghent University (GENT, Belgium) who described this species with Gerald A. Wheeler (MIN, USA).

**Carex hamata** Sw., Prodr. Veg. Ind. Occ.: 18. 1788
_Carex jamaicensis_ Poir. in Lamarck, Encycl., Suppl. 3: 246. 1813.
_Uncinia multifolia_ Boeckeler, Bot. Jahrb. Syst. 8: 207. 1887.

_Distribution_: Mexico to Tropical America.

**Carex hamlinii** K.A.Ford, _nom. nov._

_Distribution_: New Zealand (North & South Islands).

_Etymology_: The epithet of the species is adopted to recognize Bruce G. Hamlin (1929–1976) and his important contributions to the flora of New Zealand, where this species is found.
Carex healyi K.A.Ford, nom. nov.
Distribution: New Zealand (North & South Islands).
Etymology: The epithet of the species is adopted to recognize Arthur J. Healy (1917–2011) and his important contributions to the flora of New Zealand.

Carex horizontalis (Colenso) K.A.Ford, comb. nov.
Distribution: New Zealand (North & South Islands, Chatham Islands, Stewart Island).

Note: The correct name for this species if the segregate genus is recognized is Uncinia rupestris.

Carex imbecilla K.A.Ford, nom. nov.
Distribution: New Zealand (North & South Islands, Stewart Island).
Etymology: The name refers to the fragile habit of this species.

Carex koyamae (Gómez-Laur.) J.R.Starr, comb. nov.
Distribution: Mexico (Chiapas), Costa Rica.

Carex laegaardii J.R.Starr, nom. nov.
Distribution: North-eastern Colombia to Peru.
Etymology: The new name honours Simon Laegaard (AAU, Denmark) who collected the holotype for this and three other Carex spp. from northern South America that were formerly treated in Uncinia (Wheeler & Goetghhebeur, 1995, 1997).

Carex lechleriana (Steud.) J.R.Starr, comb. nov.
Distribution: Chile to southern Argentina.

Carex lectissima K.A.Ford, nom. nov.
Uncinia rupestris var. capillacea Kük. in Engler (ed.), Pflanzenr. 38 (IV, 20): 64. 1909.
Distribution: New Zealand (North & South Islands, Stewart Island).
Etymology: From the superlative of the Latin adjective lectus, selected for the delicate fine-leaved habit of this species.

Carex longifructus (Kük.) K.A.Ford, comb. nov.
Distribution: New Zealand (North & South Islands).

Carex macloviformis (G.A.Wheeler) J.R.Starr, comb. nov.
Distribution: Juan Fernández Islands (Alejandro Selkirk).

Carex macrotrichoides J.R.Starr, nom. nov.
Distribution: South-central Chile to Argentina (Rio Negro).
Etymology: When described by Wheeler (1997b), this species was only known from Chile, but it is now documented from at least two localities in Argentina (Starr, 2001; Wheeler, 2005). The new epithet com-
bines the Greek macros, long, with the Greek trichoides, hair-like, to highlight the extremely long rachillae of this species, which are probably the longest known in Carex (Wheeler, 1997b).

**Carex madida** J.R.Starr, nom. nov.

**Distribution**: North-central Ecuador.

**Etymology**: The new epithet comes from the Latin madidus for moist or wet, and it refers to the occurrence of this páramo species in humid habitats, such as those at the margins of lakes (Wheeler & Goetghebeur, 1995).

**Carex megalepis** K.A.Ford, nom. nov.


**Distribution**: New Zealand (North & South Islands, Stewart Island).

**Etymology**: This species has large glumes that are much longer than the perigynia; from the Greek mega-, big, and lepis, lepidos, a scale.

**Carex meridensis** (Steyerm.) J.R.Starr, comb. nov.

Uncinia macrolepis Decne. in Dumont d’Urville, Voy. Pôle Sud 2: 13. 1853; non Carex macrolepis DC. (1813).

**Distribution**: North-western Venezuela to subantarctic islands.

**Note**: The correct name for this species if the segregate genus is recognized is Uncinia macrolepis.

**Carex minor** (Kük.) K.A.Ford, comb. & stat. nov.


Uncinia rupestris var. planifolia Kük. in Engler (ed.), Pflanzenr. 38 (IV, 20): 64. 1909.

**Distribution**: New Zealand (North & South Islands, Stewart Island).

**Note**: The correct name for this species if the segregate genus is recognized is Uncinia angustifolia.

**Carex multifaria** (Nees ex Boott) J.R.Starr, comb. nov.


**Distribution**: South-central & southern Chile.

**Carex negeri** (Kük.) J.R.Starr, comb. nov.

Uncinia negeri var. araucana Gunckel, Revista Univ. (Santiago) 30: 58. 1945.

**Distribution**: Chile to south-western Argentina.

**Carex nemoralis** (K.L.Wilson) K.L.Wilson, comb. nov.

**Distribution**: South-eastern Australia.

**Carex obtusifolia** (Heenan) K.A.Ford, comb. nov.

**Distribution**: New Zealand (North & South Islands, Stewart Island).

**Carex papualpina** K.L.Wilson, nom. & stat. nov.

**Distribution**: New Guinea (Mt Wilhelm, Mt Giluwe).

**Etymology**: The first component of the epithet is taken from an earlier name for this broad region,
Papua, added to the original epithet, referring to the habitat of this taxon on the two highest mountains in Papua New Guinea.

**Carex parvispica** K.A.Ford, *nom. nov.*
*Replaced synonym:* Uncinia sinclairii Boot in J.D.Hooker, Handb. N. Zeal. Fl. 1: 309. 1864; non Carex sinclairii Boot ex Cheeseman (1906).

**Distribution:** Eastern New Zealand (South Island); also in south-eastern Australia (probably naturalized there).

**Etymology:** The name refers to the small spikes found in this species.

**Carex penalpina** K.A.Ford, *nom. nov.*

**Distribution:** New Zealand (North & South Islands, Stewart Island).

**Etymology:** The name refers to this species being often found in almost alpine tussock-grassland; from the Latin *paene* or *pene*, nearly, and *alpinus*, alpine.

**Carex perplexa** (Heenan & de Lange) K.A.Ford, *comb. nov.*

**Distribution:** New Zealand (North Island).

**Carex phleoides** Cav., *Icon.* 5: 40. 1799
Agistron phleoides (Cav.) Raf., Good Book: 28. 1840.


**Uncinia cumingii** Nees, Linnaea 9: 305. 1834, nom. inval.

**Uncinia longifolia** É.Desv. in C.Gay, Fl. Chil. 6: 226. 1854, nom. illeg.

**Uncinia trichocarpa** É.Desv. in C.Gay, Fl. Chil. 6: 227. 1854.


Uncinia longispica Boeckeler, Flora 41: 650. 1858.
Uncinia monteana Phil., Linnaea 30: 205. 1859.
Uncinia chlorostachya Phil., Linnaea 33: 275. 1865.
Uncinia leptostachya Phil., Linnaea 33: 274. 1865.
Uncinia lasiocarpa Steud. ex Boeckeler, Linnaea 41: 349. 1877.


Uncinia loliaecea Phil., Anales Univ. Chile 93: 503. 1896.


Uncinia phleoides var. krausei Kük., Bot. Centralbl. 76: 211. 1898.

**Distribution:** Central Mexico, north-western Venezuela to southern South America.

**Carex plurinervata** J.R.Starr, *nom. nov.*

**Distribution:** Juan Fernández Islands (Alejandro Selkirk).

**Etymology:** The epithet *costata*, ribbed, refers to the many prominent veins on the perigynium of this species known only from its type locality (Wheeler, 2007). The new epithet *plurinervata* combines the Latin prefix *pluri-*-, many, with *nervata*, nerved, to convey the same meaning.

**Carex potens** K.A.Ford, *nom. nov.*


**Distribution:** New Zealand (North & South Islands).

**Etymology:** The name refers to the strong and harsh habit of this species.
Carex punicea K.A.Ford, nom. nov.
Uncinia rubra var. fallax Kük. in Engler (ed.), Pflanzenr. 38 (IV, 20): 64. 1909.

Distribution: New Zealand (North & South Islands, Stewart Island).

Etymology: The name refers to the red colour of the whole plant.

Carex purpurata (Petrie) K.A.Ford, comb. nov.

Distribution: New Zealand (South Island).

Carex rapaensis (H.St.John) K.L.Wilson, comb. nov.

Distribution: Austral Islands (Rapa-Iti).

Carex × rubrovaginata (Hamlin) K.A.Ford, comb. nov.

Distribution: New Zealand (North Island).

Carex salticola J.R.Starr, nom. nov.

Distribution: South-central Chile to south-western Argentina.

Etymology: The epithet refers to the fact that the species grows in forests (saltus = forest; -cola = dweller).

Carex scabrida J.R.Starr, nom. nov.

Distribution: Southern Chile to south-western Argentina.

Etymology: The name refers to the delicate habit of this species.

Carex sclerophylla (Nelmes) K.L.Wilson, comb. nov.
Basionym: Uncinia sclerophylla Nelmes, Kew Bull. 4: 143 (1949).

Distribution: New Guinea highlands.

Carex silvestris (Hamlin) K.A.Ford, comb. nov.

Distribution: New Zealand (North Island).

Carex strictissima (Kük.) K.A.Ford, comb. nov.

Distribution: New Zealand (North & South Islands, Antipodes Islands).

Carex subsacculata (G.A.Wheeler & Goetgh.) J.R.Starr, comb. nov.

Distribution: Ecuador (Pichincha).

Carex subtilis K.A.Ford, nom. nov.

Distribution: Australia (Tasmania); New Zealand (South Island).

Etymology: The name refers to the delicate habit of this species.
Carex subtrigona (Nelmes) K.L.Wilson, \textit{comb. nov}.


\textit{Distribution:} Borneo (Mt Kinabalu), Philippines (Mt Apo), New Guinea highlands.

Carex subviridis K.A.Ford, \textit{nom. nov.}


\textit{Distribution:} New Zealand (North Island).

\textit{Etymology:} The name refers to the light green leaves of this species.

Carex triangula J.R.Starr, \textit{nom. nov.}

\textit{Distribution:} Magellan Region of South America.

\textit{Etymology:} The new epithet \textit{triangula} has the same meaning in Latin as \textit{triquetra} (three-cornered).

Carex turbaria J.R.Starr, \textit{nom. nov.}

\textit{Distribution:} Southern Chile to Tierra del Fuego.

\textit{Etymology:} The epithet is derived from the Latin \textit{turbarium} for peat-bog and refers to the occurrence of this species in persistently wet, base-poor sites, such as \textit{Sphagnum} bogs.

Carex umbricola K.L.Wilson, \textit{nom. nov.}

\textit{Distribution:} South-eastern Australia.

\textit{Etymology:} From the Latin \textit{umbra}, shade, and -\textit{cola}, the Latin for a dweller, referring to the shady habitat preferred by this species.

\textit{Carex uncinata} L.f., \textit{Suppl. Pl.}: 413. 1782
\textit{Carex} hamosa Thouars, Esquisse Fl. Tristan d’Acugna: 35. 1808, nom. illeg.
\textit{Uncinia} scaberrima Nees, Linnaea 9: 305. 1834, nom. inval.
\textit{Uncinia} lindleyana Kunth, Enum. Pl. 2: 526. 1837.

\textit{Distribution:} New Zealand (North & South Islands, Chatham Islands, Stewart Island, Auckland Islands), Pacific islands, New Caledonia, Hawaii.

Carex wheeleri J.R.Starr, \textit{nom. nov.}

\textit{Distribution:} South-central Chile (La Araucaria).

\textit{Etymology:} The name honours Gerald A. Wheeler (MIN, USA), who described this species and dozens of others in a continuing series of significant revisions of the genus \textit{Carex} (including \textit{Uncinia}) in South America.

Carex zotovii (Hamlin) K.A.Ford, \textit{comb. nov.}

\textit{Distribution:} New Zealand (North & South Islands, Stewart Island, Chatham Islands).

\textit{TRANSFER FROM VESICAREX STEYERM. TO CAREX L.}

Distribution: Western South America to north-western Venezuela.

Uncertae Sedis


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